MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 175

Comments on the Subgenera of Darters (Percidae) with Descriptions of Two New Species of *Etheostoma* (*Ulocentra*) from Southeastern United States

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ABSTRACT

Bailey, Reeve M. and David A. Etnier. 1988. Comments on the Subgenera of Darters (Percidae) with Descriptions of Two New Species of Etheostoma (Ulocentra) *from Southeastern United States. Misc. Publ. Mus. Zool. Univ. Michigan, 175:1–48, figs. 1–2, pl. 1.*—Darters are classified in three genera of which *Percina,* with nine subgenera and about 35 species, is the most primitive, *Ammocrypta,* with two subgenera and seven species, is highly adapted to a sand habitat, and *Etheostoma,* with over 100 species, is the most diverse. The history of classification of darters over the past half century is briefly reviewed, and the subgenera in current use for *Percina* and *Ammocrypta* are adopted. In order to assess phyletic trends, principal differential character states of darters are examined for polarity of primitive versus derived conditions. Genus *Etheostoma* is classified into five groups consisting of 18 subgenera. The most generalized are the *Allohistium* and *Litocara* groups, each with a single subgenus. The *Etheostoma* group consists of subgenera *Etheostoma s.s.* and *Ulocentra.* Reinterpretation of the relationship of *E. zonale* and *E. lynceum,* with their assignment to *Etheostoma s.s.,* dictates resurrection of subgenus *Ulocentra* for the snubnose darters to replace *Nanostoma* as proposed by Page (1981b). The *Boleosoma* group includes subgenera *Boleosoma, Vaillantia, Ioa,* and *Doration,* with 10 species. Many of the most advanced darters belong to the *Oligocephalus* group of 10 subgenera: *Nothonotus, Catonotus, Psychromaster, Oligocephalus, Ozarka, Fuscatelum, Belophlox, Villora, Hololepis,* and *Microperca,* with 61 described species. Several subgenera are equivalent to those recognized by Page (1981b), but two that were merged with *E. exile* as subgenus *Boleichthys* by Page, *Hololepis* and *Microperca,* are again recognized with the same limits as given for *Hololepis* by Collette (1962) and *Microperca* by Burr (1978), and *E. exile* is assigned to *Oligocephalus. E. okaloosae,* of somewhat questionable status, is also placed in *Oligocephalus.* Most of the subgenera, with the possible exception of *Oligocephalus,* are believed to be monophyletic but uncertainties remain as to the interrelationships.

Subgenus *Ulocentra* consists of two species groups, the *duryi* group in which the premaxilla is free from the upper lip and the vomer usually has one or a few teeth, and the *simoterum* group, with a narrow premaxillary frenum but with the vomer consistently devoid of teeth. Two new species of the *duryi* group are described. The firebelly darter, *E. pyrrhogaster,* has large scales, and a continuous broad red band in the anal fin and in both dorsal fins in adult males; it is restricted to the Obion and Forked Deer river systems in western Tennessee and southwestern Kentucky. The bandfin darter, *E. zonistium,* has six distinct, alternating pigmented and clear horizontal bands in the spinous dorsal fin in adult males, ovoid lateral blotches, and the underparts orange to yellow below the lateral stripe in adult males; it inhabits largely Coastal Plain areas in the Tennessee River drainage of western Tennessee and Kentucky, northwestern Alabama, and northeastern Mississippi but occurs also in headwaters of the upper Black Warrior system in Alabama and in Spring Creek of the upper Hatchie River system in Tennessee.

Key words: *Percidae,* Etheostoma, Ulocentra, *darters, Tennessee.*

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INTRODUCTION

Nearly forty years ago one of us (RMB) initiated a revision of the subgenus *Ulocentra* that has been pursued intermittently ever since. That study established the existence of many undescribed forms, some of which had been first recognized even earlier by Carl L. Hubbs. Existence of many of these unnamed species has been well known for years (e.g., Winn, 1958; Smith-Vaniz, 1968; Page and Whitt, 1973a, b; Jenkins, 1976; Page, 1981b; Kuehne and Barbour, 1983; Page, 1983). Four species of *Ulocentra* have been described recently by others (Bouchard, 1977; Page and Burr, 1982). The original primary purpose of this paper was to provide names and descriptions of two species; both occur in Kentucky and Tennessee and one lives also in Alabama and Mississippi. A third species from Kentucky and Tennessee is being described by us elsewhere. At the outset, however, we found ourselves in disagreement with Page (1981b) who removed *Etheostoma zonale* from subgenus *Etheostoma* and grouped it with the species of *Ulocentra* as subgenus *Nanostoma* because *E. zonale* is the type species of *Nanostoma* Jordan, 1877, a name senior to *Ulocentra* Jordan, 1878 (Collette and Knapp, 1966). We contend that similarities noted by Page result from convergence, errors in interpretation or coding of characters, and omission of important features, that *E. zonale* is related to the other species of *Etheostoma sensu stricto* as interpreted by Tsai and Raney (1974:3), and that *Ulocentra* is a monophyletic sister group of *Etheostoma s.s.*, worthy of subgeneric recognition. This led to reconsideration of some other classificatory changes suggested by Page (1974, 1981b), and followed by Page (1983). In 1983 two comprehensive volumes devoted to darters appeared, each illustrated in color, provided with descriptive accounts, keys, geographic distribution maps, and aimed at a general audience (Page, 1983; Kuehne and Barbour, 1983). There is notable agreement in these volumes in species treated, nomenclature, and depth, quality, and effectiveness of literature coverage. Both are valuable and welcome books. The Kuehne and Barbour work largely follows conventional views on darter classification; that by Page reflects his own research. There are some discrepancies in the two volumes in subgeneric assignments in *Etheostoma,* and as a second objective of this paper we present our views on relationships and subgeneric classification.

RECENT HISTORY OF DARTER CLASSIFICATION

The Percidae are a major component of the North American freshwater fish fauna, especially in smaller creeks and rivers. Robins *et al.* (1980) listed 129 percids from Canada and the United States. Others live in Mexico, and the number of recognized species continues to increase. In American Percidae three species in two genera are well known larger food and sport fishes of no concern here. The remaining approximately 140 described species of darters were formerly placed by some in a family Etheostomidae or Etheostomatidae, more recently in a tribe Etheostomatini of subfamily Etheostomatinae (Page, 1985) or tribe Etheostomatini of subfamily Percinae (Collette and Bănărescu, 1977).

Darters are small (few exceed 10 cm in standard length), mostly benthic fishes, and though usually inconspicuous many are brightly colored. Collette (1967) has presented a taxonomic history of the darters.

Darter classification has long been troubled. The final attempt at their organization by Jordan and his colleagues (Jordan, Evermann and Clark, 1930), although of value in assembling almost all names of proposed taxa, is, in retrospect, wholly inadequate. These authors listed 31 genera and 104 species of which 74 are currently recognized as valid species. Some appear under different names in two or three genera, for example *Etheostoma exile* as *Oligocephalus iowae, Nivicola borealis,* and *Boleichthys exilis.* Some presently recognized species were listed only as synonyms and name changes have been numerous. Recent authors have drastically reduced the number of genera, but former names are often employed for subgenera. Basic disagreement in classification is evident, however, in that of 31 genera, 13 were complex; that is, they contained species now assigned to from two to four subgenera. Modern subgenera of darters are not merely downgraded genera of an earlier era.

In a survey of vertebral numbers in American percids (Bailey and Gosline, 1955), the inadequacy of the then existing classification was apparent. During this period Bailey was actively investigating darter classification and, using his familiarity with the group, erected a provisional classification of genera and subgenera for presentation of the data. For most groups no justification was provided. The framework consisted of three genera, *Percina* with eight subgenera, *Ammocrypta* with two, and *Etheostoma* with 12.

A comparable survey of breeding tubercles in the Percidae was presented by Collette (1965) who, although not necessarily subscribing to it, adopted essentially the same arrangement of darters except for the addition of *Villora.* This subgenus of *Etheostoma* was believed to be "an offshoot of the *asprigene-swaini* nontuberculate group of the subgenus *Oligocephalus*" (Collette, 1965:602; Collette and Yerger, 1962). Collette's survey provided a wealth of new information to assist in establishing relationships among darters and permitted refinements in subgeneric classification. He found inconsistency in tubercle development among species of subgenus *Boleosoma,* calling for division into species groups without and with tubercles. This led to the recognition of additional subgenera (*Doration* and *Vaillantia*) for the tuberculate species (Cole, 1967:29). As Collette (1965) reported, tubercles appear rather erratically in the family; they are present in the Old World genera *Zingel* and *Romanichthys* and in the three genera of darters, but are absent in *Perca* and its relatives and in *Stizostedion.* In darters they are found in *Ammocrypta* and in some but not all subgenera of *Percina* and *Etheostoma.* In the subgenera *Etheostoma, Belophlox, Oligocephalus,* and perhaps *Vaillantia* some species have tubercles and some do not, and related groups of species may have distinctive patterns of tubercle distribution. Collette's study (1965:607) demonstrated that patterns of tubercle development in darters, though of no value at the generic level (if three inclusive genera are recognized), are useful in showing phylogenetic relationships for lower taxa. It is apparent that percids have a genetic capacity to develop tubercles in various areas to meet certain needs associated with reproduction. The plesiomorphic condition in percids is judged to be nontuberculate, but tubercles have developed independently and in diverse patterns, or been lost repeatedly secondarily, to produce the spotty distribution through the family.

A serious difficulty in use of tubercles to evaluate relationships concerns their ephemeral appearance at the height of the spring breeding season (Collette, 1965:568). Unless observational data are rigorous, negative evidence can be misleading. For example, in his survey Collette failed to find tuberculation in subgenera *Hypohomus* and *Cottogaster* of *Percina* or in *Percina* (*Ericosma*) *palmaris,* but subsequently all were discovered to develop tubercles (Denoncourt, 1976:58). Page (1981a) discovered tubercles in *Etheostoma* (*Austroperca*) *australe,* providing supportive evidence for his reassignment of that species in the tuberculate species group of *Oligocephalus.* Jenkins (1971) discovered that breeding but not postbreeding males and females of *Etheostoma* (*Ioa*) *vitreum* have tubercles on the pectoral and pelvic fins, a condition different from the presumably related *Boleosoma.* Discovery of tubercles in males only of *Etheostoma blennius* (Thompson, 1973; Burr, 1979) aided in determination of its relationship in the subgenus *Etheostoma.* A single male of *Etheostoma* (*Allohistium*) *cinereum* was found to have tubercles on the pelvic and anal fins (Shepard and Burr, 1984). Ryon's (1986) discovery of anal fin tubercles in *E. trisella* strengthens its inclusion in subgenus *Ozarka.* Mayden (1985) has recently found that non-keratinized fleshy ridges occasionally appear in subgenus *Catonotus,* but these are not nuptial tubercles.

Comparative studies of other characters expanded understanding of darter interrelationships and contributed to an improved classification. Richards (1966:824–825) provided useful notes on dentition following an examination of known species. Winn's (1958) observations on reproductive habits of 14 species of darters are instructive and have stimulated similar studies by others, but the breeding behavior of many species remains unknown. The lateralis system of darters was reviewed by Page (1977).

Thorough modern revisionary analyses of species or groups of species have also contributed much to improvements in darter systematics. Among these are Collette (1962), Collette and Yerger (1962), Richards (1966), Cole (1967), Tsai (1968a, b), Zorach (1972), Tsai and Raney (1974), Burr (1978, 1979), Braasch and Mayden (1985), and others cited by Kuehne and Barbour (1983) and Page (1983).

Electrophoretic approaches to evaluate relationships and to test classification of darters were initiated by Page and Whitt (1973a, b). They discovered that the lactate dehydrogenase (LDH) B_4 isozyme of 19 species of

Percina possessed an identical electrophoretic mobility that was not present in 45 of 46 species of *Etheostoma* (excepting only *E. cinereum*) or in two species of *Ammocrypta* examined. Reproductive characteristics and morphology suggest that *Percina* includes the primitive darters, and a distinctive B_4 isozyme mobility was interpreted as an expression of genetic conservatism absent in species of the more advanced genera, except for *E. cinereum* (Page and Whitt, 1973b:5). These authors believed that enzymatic and morphological evidence (modified midventral scales) for a monophyletic origin of all species of *Percina* is persuasive. They argued for an inclusive genus *Percina* with division into subgenera. The apparently unique LDH B_4 isozyme mobility of *cinereum* among the species of *Etheostoma* was viewed by them as retention of a primitive character otherwise lost in *Etheostoma* (and in *Ammocrypta*). Page and Whitt (1973a) also found support for the assumed monophyly of *Percina* and of *Etheostoma* from electrophoretic patterns and mobilities.

Heightened activity in darter systematics during the period 1950–1980 paved the way first for publication of reviews of the subgenera of *Percina* (Page, 1974) and the genera and subgenera of darters (Page, 1981b), followed by the appearance of the darter books by Page (1983) and Kuehne and Barbour (1983). Page's (1974) analysis of 28 species of *Percina,* an increase of eight from Bailey and Gosline's (1955) list, recognized one new subgenus (*Odontopholis*) separated from *Hypohomus,* elevated subspecies *crassa crassa* and *c. roanoka* to specific rank, and transferred them from subgenus *Ericosma* to subgenus *Alvordius.* These systematic innovations in *Percina* were unchanged in Page (1981b, 1983) and were adopted by Kuehne and Barbour (1983); we support them. The number of recognized species of *Percina s.s.* remains fluid since they are still under active study; *carbonaria* was treated as a subspecies by Kuehne and Barbour (1983), as a full species by Page (1983), and Thompson (1985) described still another new species (*jenkinsi*). Page (1981b) analyzed 34 species of *Percina* of which five were then unnamed. Four or more species of the genus still await description.

Two subgenera and five species of sand darters were recognized as genus *Ammocrypta* (Bailey and Gosline, 1955). A few authors (e.g., Moore, 1968) have given *Crystallaria* full generic status, as was done by Jordan, Evermann, and Clark (1930). Williams (1975) revised subgenus *Ammocrypta,* including descriptions of two new species, and treated *Crystallaria* as a subgenus. At least for the present the generic and subgeneric classification of *Percina* and *Ammocrypta* appears stable. Other generic or subgeneric arrangements might be adopted, and Page (1981b:16) has discussed and rejected some alternatives. We agree with his treatment of the genera and with the inclusiveness of *Etheostoma s.l.,* as do Page (1983) and Kuehne and Barbour (1983). Each of the subgenera has been diagnosed by Page (1981b, 1983). We are confident, as was Page (1981b), that each of the three genera of darters as now recognized is a monophyletic group.

Recent workers on *Etheostoma* are consistent in employing a single genus, relying on subgenera and species groups to indicate relationships. Page (1981b) analyzed 101 species using 52 characters, most of them continuously variable or multistate, and produced three phenograms and two cladograms using a variety of methods. No one of these agrees even closely with Page's or our interpretation of relationships in *Etheostoma.* Species of some subgenera tended to cluster, especially small groups such as *Doration* and *Litocara* and a few larger groups of similar species such as *Nothonotus* and *Catonotus.* Yet even here there is notable failure of some obviously related forms to sort out as natural units. *Oligocephalus, Boleosoma,* and *Ozarka* cluster out from three to nine times each in the several diagrams, the obvious sister species *E.* (*Nothonotus*) *camurum* and *chlorobranchium* are virtually indistinguishable but fail to cluster closely in any of his phenograms, and other notable deviations occur. Page's final arrangement is essentially traditional and intuitive rather than conforming to any of the diagrams. He utilized the analysis to point up possible misinterpretations in existing classification.

Bailey and Gosline (1955) listed 12 subgenera of *Etheostoma.* Collette and Yerger (1962) resurrected *Villora* as a subgenus to include *edwini* (formerly *Hololepis*) and *okaloosae* (previously unplaced). Collette (1965) and Cole (1967) reduced *Boleosoma* by removing *jessiae* and *stigmaeum* to *Doration,* and *chlorosomum* to *Vaillantia.* Page and Whitt (1973b) resurrected *Litocara* from *Oligocephalus* for placement of *nianguae* and *sagitta.* Williams and Robison (1980) described subgenus *Ozarka* to include *boschungi, trisella* (from provisional inclusion with *tuscumbia* in *Psychromaster*), *cragini, pallididorsum,* and *punctulatum* (formerly in *Oligocephalus*). Page (1981b), following Howell (1968), added *davisoni* (formerly in synonymy of *stigmaeum*) to *Vaillantia.*

Recognition of *Villora, Vaillantia, Doration, Ozarka,* and *Litocara* had thus increased *Etheostoma* subgenera from 12 to 17. The major reinterpretation by Page (1981b) resulted in several changes in subgeneric allocation, combination of subgenera, and use of new (*Fuscatelum*) or long unused (*Belophlox* Fowler) subgeneric names. This work, which recognized 17 subgenera, represents a readjustment in our understanding of relationships within *Etheostoma,* and we offer comments where we differ with Page's view or suspect that further refinements may be needed.

PRIMITIVE VERSUS DERIVED CHARACTERS

Several authors have expressed views on the polarity of characteristics commonly employed in darter classification, for example Hubbs and Cannon (1935:20–21), Collette (1962:123–124), Williams (1975:31), Burr (1978:46), Page (1977, 1981b), and Braasch and Mayden (1985:57–83). For most characters there is agreement among these workers and ourselves. For a few characters, however, there are differing views, and proper determination of the plesiomorphic state may be crucial to determination of evolutionary trends. Following is a discussion of polarity of characters useful in deciphering evolutionary trends in darters. Under each feature, we first list the condition we interpret to be generalized in darters as a group. Several of these characters are not present in non-darter percids and are thus synapomorphies for darters (especially 3, 7, 9, 12, 13, 24, 26), but become plesiomorphies when considering some advanced darters.

1. Body relatively slender and slightly compressed, as is typical of most species of *Percina.*

2. Size relatively large. Outgroup comparisons indicate that percids other than darters are, with few exceptions (e.g., *Percarina, Romanichthys*), of moderate size, over 200 mm to more than a meter in length. Darters, on the other hand, are all small; *Percina* (*Hadropterus*) *lenticula,* the largest, attains a standard length of 169 mm. *Hadropterus* is regarded as the most primitive subgenus of *Percina,* which in turn is the most generalized of the three darter genera (Page, 1974; Collette and Bănărescu, 1977). Diminution in size is a phyletic trend among darters. Five of nine subgenera of *Percina* have at least one species over 100 mm SL, and *P.* (*Cottogaster*) *copelandi* (61 mm) and *P.* (*Imostoma*) *antesella* are the smallest. In *Ammocrypta, A.* (*Crystallaria*) *asprella* attains 130 mm; the six species of subgenus *Ammocrypta* reach maximum lengths of 59 to 70 mm. Among the 18 subgenera of *Etheostoma* here admitted, only four species reach (*cinereum, sagitta*) or exceed (*nianguae,* 111; *blennioides,* 138) 100 mm SL. These species are included on the basis of this and other characters in the three least modified subgenera. Among the 15 other subgenera only five (nine species) equal or exceed 75 mm, and the large majority (56) of species attain maximum lengths of 50 to 74 mm. The dwarfs among darters are the 13 species (in seven subgenera) which fail to reach 50 mm SL. Small size has clearly evolved repeatedly in the group (Page and Burr, 1979).

3. Premaxillary frenum well developed. Larger percids have protractile premaxillae, presumably the ancestral condition in the family. But a frenum is present in most generalized lineages in *Percina,* in subgenus *Crystallaria* of *Ammocrypta,* and in the most primitive subgenera of *Etheostoma.* The few groups of darters with protractile premaxillae appear to have developed this capacity secondarily.

4. Snout moderate, neither notably produced as in several species of *Swainia* nor extremely blunt as in *Ulocentra.*

5. Vomer with teeth.

6. Palatine with teeth.

7. Preopercle entire. Most of the above workers (p. 5) have adopted the view of Hubbs and Cannon (1935:20) that the hypothetical ancestor of the darters had a serrate preopercle. Although most darters have an entire preopercle, non-darter percids have the preopercle serrate (Collette and Bănărescu, 1977:1431) and this is regarded as the plesiomorphic condition in the family. As an outgroup to *Ammocrypta* and *Etheostoma* we may examine the primitive darter genus *Percina.* In *Percina* only subgenus *Hadropterus* has serrae, which are present in at least some individuals of all four species. Serrae are usually few, often weakly developed, and are concen-

trated near the angle of the preopercle or extend part way up the ascending arm. In *P. nigrofasciata* most fish lack serrae and in subspecies *P. sciera apristis* there are usually 0 to 2 serrae (Hubbs, 1954:214). The preopercular serrae in *Hadropterus,* believed to be the most primitive subgenus, may well be retained from earlier percid ancestry. Alternatively they may have been lost and newly evolved in this small group of species.

Elsewhere among darters, including the other eight subgenera of *Percina,* we know of preopercular serrae only in a few highly evolved taxa. They are absent in *Ammocrypta* and apparently in all subgenera of *Etheostoma* except *Catonotus, Hololepis,* and *Microperca.* The posterior margin of the preopercle was reported to be usually or partially serrate in three species of the *pellucida* group of *Ammocrypta* by Williams (1975:18, 21, 25). In casual examination of specimens we note a rough or irregular preopercular margin that he may have considered serrate. This is much different from the regularly spaced projections (serrae) elsewhere in percids. Serrations occur in a few species only, scattered among three advanced subgenera. They vary in structure and are interpreted as *de novo* developments rather than retention of the plesiomorphic state. Braasch and Mayden (1985:82), we believe, correctly regarded the "crenulate preopercule edge" in the five species of the *Etheostoma* (*Catonotus*) *virgatum* species group as a derived condition. The seven to ten serrae are on the vertical arm of the preopercle. In *Etheostoma* (*Hololepis*) *serriferum* the vertical limb of the preopercle bears many fine serrae, closely spaced and visibly different from those in the *virgatum* group. We interpret them as of independent origin. In the sister-species *E.* (*H.*) *fusiforme,* Collette (1962:117, 187–188, Table 24) has found that the preopercle is partially but weakly serrate in some individuals of each of two subspecies, usually less than 10 percent in the northern *E. f. fusiforme* and most often more than 25 percent in the southern *E. f. barratti.* In their review of *Hololepis,* Hubbs and Cannon (1935) overlooked the occasionally serrate preopercle in this species. Other species of *Hololepis* have the preopercle entire. In the closely allied subgenus *Microperca,* Burr (1978:6) found the preopercle to be entire except in one population of *E. proeliare,* in which it was serrate. It is not known whether the occurrence of serrae in at least some individuals of three species in these two advanced subgenera results from a single origin, but that the condition is ancestral seems remote.

8. Branchiostegal membranes separate or narrowly connected.

9. Branchiostegal rays 6 (Burr, 1978:5). Larger percids have 7 rays, presumably the ancestral number in the family, but 7 appears only as a variant count among darters, most often in the generalized subgenus *Swainia* of *Percina.*

10. Branchiostegal membranes without scales. This condition characterizes all percid fishes except *Etheostoma* (*Psychromaster*) *tuscumbia* and almost all percoid fishes. The frequent presence of scales in specimens of *E. tuscumbia* is surely a derived condition.

11. Lateral line complete or extending a short distance onto caudal fin,

and straight or very gently curved. In some larger percids (e.g., *Perca, Gymnocephalus*), the line is arched to conform with the contour of the back. Among darters the only significant arching occurs in a few species (notably in subgenus *Hololepis*) with an incomplete lateral line, and appears to be a *de novo* feature.

12. Preoperculomandibular pores 10 (Page, 1977).

13. Infraorbital canal complete, with 8 pores (Hubbs and Cannon, 1935).

14. Supratemporal canal complete, with 3 pores.

15. Interorbital pores present (Collette, 1962).

16. Pectoral fin of moderate length, much shorter than head.

17. Pelvic fins well separated.

18. Electrophoretic mobility of lactate dehydrogenase (LDH) B_4 as in *Percina* (Page and Whitt, 1973b).

19. Anal fin with 2 spines and about 9 to 12 soft rays.

20. Vertebrae about 41–45 (Bailey and Gosline, 1955).

21. Flesh opaque.

22. Conical genital papilla (Hubbs and Cannon, 1935).

23. No nuptial tubercles (p. 3).

24. Eggs buried in gravel or sand (Page, 1985).

25. No parental care of nest or eggs (Page and Swofford, 1984).

26. No scales on top of head. Hubbs and Cannon (1935:21), believed that presence of parietal and interorbital scales was plesiomorphic among darters. However, scales are lacking on the parietal and interorbital areas of all species of *Percina* (except *macrolepida*) and *Ammocrypta* and also in all subgenera of *Etheostoma* except *Psychromaster* and *Hololepis*. *Percina* (*P.*) *macrolepida* has a few to several exposed, ctenoid scales in a parietal area that extends from the occiput one-third to three-fifths the distance forward to the coronal pore. The interorbit is scaleless. In *E.* (*Psychromaster*) *tuscumbia* the parietal area (posterior to the coronal pore) is heavily invested with exposed, ctenoid scales, but the interorbital area is naked. In *E.* (*Hololepis*) *serriferum* the parietal is completely covered with imbedded to exposed cycloid or ctenoid scales; the interorbital has scales that vary in number geographically but are consistently present (Collette, 1962:131–132). In the wide-ranging *E.* (*H.*) *fusiforme*, southern populations (*E. f. barratti*) consistently have the parietal well scaled, whereas in the north (*E. f. fusiforme*) many fish have the parietal scaleless or with a few scales. Similarly, the interorbital scales in this species show clinal variation from many (usually 10 to 20) in the south to few (0 to 5) in the north (Collette, 1962:165–166). The acquisition of scales on top of the head correlates with the synapomorphy in preopercular serrae in the same two species (item 7). The four remaining species of *Hololepis* lack scales on the parietal and interorbit. We interpret the presence of scales on the parietal of *P.* (*P.*) *macrolepida* and *E.* (*P.*) *tuscumbia* and on the parietal and interorbit of sister species (*serriferum* and *fusiforme*) of *Hololepis* as three independent, convergent apomorphies. These scales are correlated with scaled cheeks, opercles, nape, and breasts, and the species of *Etheostoma* are inhabitants of quiet, sluggish

waters and springs, usually well vegetated. The modifications are probably adaptive in this environment (see item 27 below).

In larger percids scales are usually absent from the top of the head, as, for example, in *Perca flavescens* and *P. fluviatilis,* in *Gymnocephalus cernuus* and *G. schraetser,* and in specimens examined of *Stizostedion lucioperca.* In *S. canadense* and often in *S. vitreum* ctenoid scales are present near the midline in the interorbital area; these are either continuous with or separated posteriorly from an incompletely scaled parietal area. In *Zingel streber* the top of the head differs in squamation dramatically from any other percid we have examined. A broad investiture of exposed ctenoid scales extends between the orbital rims forward to in advance of the anterior nostril and backward to the occiput; the parietal area is completely or partially covered. Whether or not scales on top of the head in these three species is plesiomorphic is uncertain, but we are confident that the ancestral state in darters, as found in all species of *Percina* except *macrolepida* of subgenus *Percina,* is lack of scales.

27. Scales present on cheek and opercle. Many darters in all three genera have these areas well scaled, but other species lack scales in one or both areas. The plesiomorphic state is inferred because the larger percids usually have scaled cheek and opercle, and because of the prevalence of the condition in darters, especially among subgenera judged primitive on other grounds. Nevertheless, in darters there is notable variation in squamation not only of the cheek and opercle but also of the nape, breast, prepectoral area, and belly, often among different populations of a species, for example *E. olmstedi* (Cole, 1967), *E. nigrum* (Lagler and Bailey, 1947), and *E. zonale* (Tsai and Raney, 1974). Despite a genetic basis for the morphologic differences (e.g., Lagler and Bailey, 1947), plasticity is evident and reversal of phenotype is probable. Darters living in a sand environment are especially likely to lack scales on one or more of these areas, whereas those in quiet vegetated waters are commonly well scaled. Cole (1967:41–43) has commented on the close parallel of habitat preferences with squamation; the nominal *E. olmstedi atromaculatum* and *E. nigrum eulepis* are large river or lacustrine morphotypes with well scaled nape, cheek, opercle, and breast, whereas *E. o. olmstedi* and *E. n. nigrum,* chiefly smaller stream or lake inhabitants, have reduced squamation or are naked in these areas. In the upper Cumberland River form (*E. n. susanae*) even the opercle is naked. In *E. zonale,* Tsai and Raney (1974:6–7) found variation in the scales on the breast and cheek from full investment to naked and on the belly from fully to partially scaled.

28. Scales generally distributed on body. This is the usual condition in larger percids and in most darters. The distribution of scales on the branchiostegal membranes and head are discussed in items 10, 26, and 27 above. In percid fishes there is much variation in the squamation of the breast and prepectoral area, the belly, and the nape. In the primitive *Percina* subgenus *Hadropterus* the breast, belly, and nape are fully scaled or nearly so, the interpreted plesiomorphic condition in darters. Elsewhere in

Percina scales are commonly present but may be lost in these areas. It is reasonable to suspect that once lost, scales could redevelop, especially in taxa that have invaded quiet water. In *Etheostoma* there is wide variation. For example, in *Nothonotus* the nape is naked in all species except *juliae,* a presumptive synapomorphy. *Etheostoma juliae* is unique in the subgenus also in the wide junction of the branchiostegal membranes (see item 8 above), which we interpret as an autapomorphy. It is possible that the scaled nape is a reversal in *juliae.* The lability in squamation of the breast and nape in species of subgenus *Boleosoma* (Cole, 1967 and included references) underlines the difficulty or impossibility of identifying a phenotype in a particular fish as plesiomorphic, apomorphic, or reversed.

There are two phyletic lines in darters that display notable specializations in squamation. One is *Ammocrypta,* which shows progressive reduction in body scales. The morphological sequence begins with the incompletely scaled cheek and opercle and naked breast and belly in *A. asprella,* and ranges through the series from *vivax* to *beani* and *bifascia* with reduction, then loss of scales on the nape, prepectoral area, cheek, opercle, and upper and lower sides. The last named species are largely scaleless, with a lateral-line row and one or a few scale rows above and below (Williams, 1975).

The second specialization is in *Percina,* in which the midventral line characteristically has an enlarged, specialized scale or scales between the pelvic fin bases, along the belly, and commonly on the breast (Page, 1976), a synapomorphy that diagnoses the genus. The modification is most evident in adult males, and specialized scales are reduced or occasionally lost secondarily in *Imostoma,* a subgenus in which the belly and breast, as in *Ammocrypta,* have reduced ventral scales associated with a sand habitat.

29. Body scales of moderate or small size, with 50 or more lateral line scales.

30. Absence of gaudy colors and sexual dichromatism. In generalized percids, orange to red bands are absent from the spinous dorsal fin and sexual dichromatism is not conspicuous. In darters, such bands are widespread. In *Percina* a red-orange band, sometimes weakly expressed, occurs in at least some species of all subgenera except *Odontopholis,* but sexual dichromatism occurs only in two subgenera (*Ericosma, Hypohomus*), and then only during the breeding season. In genus *Etheostoma,* gaudy colors are present in generalized subgenera (*Allohistium, Litocara, Etheostoma*), but conspicuous sexual dichromatism is associated with the breeding season. Sexual dichromatism that is persistent throughout the year occurs only in more advanced subgenera (*Ulocentra,* some species of *Nothonotus, Oligocephalus, Villora*). We conclude that loss of bright colors in *Etheostoma* represents a derived condition evolved independently in several lineages, and that sexual dichromatism associated with the breeding season is plesiomorphic to persistent sexual dimorphism.

31. Dorsal blotches (saddles) 8 or more and irregular. Since dark dorsal markings are surely cryptic and of high selective value, assessment of polarity is difficult. The number of possible patterns is limited. For instance,

the pattern of 4 or 5 blotches that angle down and forward has evolved repeatedly and independently in a variety of groups including cottids, triglids (*Prionotus*), catostomids (*Hypentelium*), and several times in percids: *Stizostedion canadense, Romanichthys* and *Zingel, Ammocrypta asprella,* subgenus *Imostoma* of *Percina,* and one to three times in subgenus *Etheostoma* (*sellare, variatum* group, *blennius*). In non-darter percids dorsal blotches are numerous and irregular in *Gymnocephalus, Percarina,* and *Stizostedion* other than *canadense,* 6 or 7 and quite consistent in *Perca,* and 4 or 5, consistent in position, in *Zingel, Romanichthys,* and *Stizostedion canadense* as noted above. In genus *Percina,* dorsal blotches are typically numerous and irregular (*Hadropterus, Swainia, Percina s.s., Hypohomus, Alvordius, Odontopholis, Ericosma, Cottogaster*); blotches are few and consistent only in four of five species of *Imostoma* (4 saddles) and in *P.* (*Alvordius*) *roanoka* (6 saddles). In genus *Etheostoma* saddles are few and regular only in subgenera *Etheostoma* (4 to 7), *Boleosoma* (6), *Doration* (6), and *E.* (*Ozarka*) *trisella* (3).

32. Principal caudal rays (branched plus 2) 17. This basic number in larger percids is preserved in generalized species of *Percina;* reduction reaches its maximum in subgenus *Microperca* with 11 to 13 (Burr, 1978).

33. Dorsal fin spines relatively numerous. Reduction in count is notable especially in *Catonotus* (6)7 to 10(11) and in *Microperca* (5)6 to 8(9).

SUBGENERA OF *ETHEOSTOMA*

In view of the numerous species and subgenera of *Etheostoma,* an attempt at a phyletic sequence of groups is in order. It is recognized, however, that the complexities of differentiation cannot be adequately shown in a linear fashion. Parts of earlier sequences can be utilized but initiation of the series with *Psychromaster,* one of the highly modified groups, as was done by Page (1981b) and followed by Kuehne and Barbour (1983), or with *Ioa,* another highly specialized subgenus, as by Collette and Bănărescu (1977:1455), is unacceptable. That position for *Psychromaster* was chosen, presumably, on the assumption that the extreme development of squamation (scales on parietal and on branchiostegal membranes) in the single species (*tuscumbia*) is ancestral whereas we interpret it as derived, as are many other characters in this species. *Ioa* was given first position based on its presumed retention of a plesiomorphic lateralis system (Page, 1977). Actually, we find *Ioa* to have the derived condition of modally nine rather than ten preoperculomandibular canal pores as reported by Page (1977, 1981b, 1983).

In the following pages we comment on varied subgeneric or specific assignments for certain nominal species of *Etheostoma.* These are summarized in Table 1.

The subgenera may be arranged in five groups: (1) the *Allohistium* group consisting of the single species *Etheostoma* (*A.*) *cinereum;* (2) the *Litocara* group with a single subgenus and two species; (3) the *Etheostoma* group, including *Etheostoma s.s.* and *Ulocentra;* (4) the *Boleosoma* group of subgenera *Boleosoma, Vaillantia, Ioa,* and, provisionally, *Doration;* and (5) the *Oligocephalus* complex of 10 subgenera arranged tentatively in sequence *Nothonotus, Catonotus, Psychromaster, Oligocephalus, Ozarka, Fuscatelum, Belophlox, Villora, Hololepis,* and *Microperca.*

ALLOHISTIUM GROUP

We initiate the sequence with subgenus *Allohistium* in part because, as discovered by Page and Whitt (1973b), *Etheostoma cinereum* is the only one among 46 species of *Etheostoma* to display electrophoretic mobility of the lactate dehydrogenase (LDH) B_4 isozyme identical (in EBT buffer) with that found in 19 species of *Percina* tested. This agreement with the most primitive darter genus is suggestive of a plesiomorphic position in *Etheostoma,* as indicated by Page (1977). Most other characters of *Allohistium* are also interpreted as plesiomorphic. Apomorphic features include the absence of palatine teeth, sexual dimorphism with bright colors (Shepard and Burr, 1984), the notable height of the second dorsal fin especially in adult males, and tubercles developed on the pelvic and anal fins of nuptial males (Shepard and Burr, 1984). The relationship of the single species remains uncertain but the predominance of primitive features dictates its placement near the base of the genus.

LITOCARA GROUP

The second group in *Etheostoma* is the subgenus *Litocara* with two species (*E. nianguae* and *E. sagitta*). *Litocara* was originally named as a subgenus of *Poecilichthys* by Bailey (1948), was included in subgenus *Oligocephalus* of *Etheostoma* by Bailey and Gosline (1955) and Kuehne and Bailey (1961), and was accorded subgeneric status in *Etheostoma* by Page and Whitt (1973a, b). The subgenus has been adequately characterized in the above cited works and in Page (1983). Apomorphic features of *Litocara* are lateral line usually incomplete, with 0–23 unpored scales (Kuehne and Bailey, 1961:3), and opercle naked. In *Litocara* nuptial tubercles are developed in breeding males on the belly or lower side, along the scales above the anal base, and on the lower side of the caudal peduncle (Bailey, 1948; Page, 1983) as in species of the *variatum* group of *Etheostoma s.s.* Nuptial colors of *Litocara* and the *variatum* group are also very similar in the two groups.

ETHEOSTOMA GROUP

Etheostoma s.s. and *Ulocentra* (*Nanostoma* of Page) make up a distinctive third group in *Etheostoma.* The lateralis system is mostly plesiomorphic, with the lateral line straight or gently arched anteriorly and complete, and the infraorbital and supratemporal canals complete; the preoperculomandibular pores may be 10 or reduced to 9. The pelvic fins are well separated. Synapomorphies uniting the two subgenera include the usually broad

TABLE 1
SUBGENERIC ASSIGNMENTS FOR SOME SPECIES OF DARTERS
(GENUS *Etheostoma*) AMONG RECENT AUTHORS

Species	Page (1981b, 1983)	Kuehne and Barbour (1983)	This Paper
zonale	*Nanostoma*	*Etheostoma*	*Etheostoma*
lynceum	(included with *zonale*)	(included with *zonale*)	*Etheostoma*
atripinne	*Nanostoma*	*Ulocentra*	(included with *simoterum*)
coosae, duryi, etnieri, simoterum	*Nanostoma*	*Ulocentra*	*Ulocentra*
baileyi, barrenense, rafinesquei	(not named)	*Ulocentra*	*Ulocentra*
*sanguifluum**	(not recognized)	(not recognized)	*Nothonotus*
parvipinne	*Fuscatelum*	*Oligocephalus*	*Fuscatelum*
australe	*Oligocephalus*	*Austroperca*	*Oligocephalus*
fricksium, mariae	*Belophlox*	*Oligocephalus*	*Belophlox*
okaloosae†	*Belophlox*	*Villora*	*Oligocephalus*
exile	*Boleichthys*	*Oligocephalus*	*Oligocephalus*
collis, fusiforme, gracile, saludae, serriferum, zoniferum	*Boleichthys*	*Hololepis*	*Hololepis*
fonticola, microperca, proeliare‡	*Boleichthys*	*Microperca*	*Microperca*

*Given species rank in *Nothonotus* by Page, 1985.
†Assigned to *Villora* by Collette and Yerger, 1962.
‡Assigned to *Microperca* by Burr, 1978.

(moderate in *sellare*) union of the gill membranes, blunt snout profile, and large and expansive pectoral fins which are longer than the short head (data in Page, 1981b). The only other darters with an equally large pectoral fin/head length ratio and broadly joined gill membranes are *E. longimanum* and *E. podostemone;* they are clearly referable to *Boleosoma.* We consider the long female urogenital tube as an additional synapomorphy for the two subgenera, with its absence in *E. sellare* a reversal. Alternatively, the enigmatic *E. sellare* may have diverged from this clade prior to development of the urogenital tube, in which case strict adherence to monophyly would dictate placement in a monotypic subgenus. Several features contradict such an hypothesis, however (see Fig. 1). We provisionally retain *sellare* in *Etheostoma s.s.*

In *Etheostoma s.s.* and *Ulocentra* there is considerable variation in dentition (Richards, 1966), tuberculation, and other characters. For example, vomerine and palatine teeth may be well developed, or variously reduced or wanting. The pattern of nuptial tubercles, if present, is as in *Litocara,* present on scales of belly or lower side of flank, near base of anal fin, and on lower side of caudal peduncle, but not on fins as in *Allohistium* and as is usual in *Oligocephalus* (Collette, 1965). This condition, either a convergence or a synapomorphy uniting subgenus *Litocara* with *Etheostoma s.s.* plus *Ulocentra,* is variably expressed in *Etheostoma s.s.* and is completely wanting in *Ulocentra.*

Etheostoma s.s. embraces a wider range of morphological variation than does *Ulocentra.* Hypothesized synapomorphies for subgenus *Etheostoma* include (1) dorsal saddles few (4–6, 7 in *blennioides* and *thalassinum*) and consistent in position, (2) anterior saddle remote from the occiput, and (3) head broad, its width 13.9–16.4% of SL except in *lynceum* and *zonale* (12.6–14.0% in *Ulocentra*) (data from Page, 1981b, as means of measurements of included species). In our hypothesized phylogeny, the similarity of body shape of *lynceum* and *zonale* with subgenus *Ulocentra* (Page, 1981b:18–19) is considered convergent, likely due to a morphological response to similar habitats. Including *lynceum* and *zonale* with *Ulocentra* (diagnosed by at least six synapomorphies, Fig. 1 and p. 22), would demand that all six of these characters be reversed in *lynceum* and *zonale,* and is unwarranted.

Etheostoma s.s. consists of three species groups (Richards, 1966; Tsai and Raney, 1974), plus *E. sellare.* The *variatum* group contains five species which retain vomerine and palatine teeth, a broad premaxillary frenum, and a moderately produced snout. Shared derived features include development of nuptial tubercles in females as well as males, 4 primary saddles across the back, and additional dark and pale bands under the red marginal band on the spinous dorsal fin. Wiley and Mayden (1985:627) included *E. blennius* in this group based on the presumed synapomorphies of the dorsal saddle pattern and the fifth (under anterior part of eye) infraorbital canal pore and its canal being directed dorsally. Dorsal direction of this pore and its canal occurs widely in genus *Percina* and in all species of the *thalassinum* group, and is not a synapomorphy for the *variatum* group as conceived by Wiley and Mayden. The *thalassinum* group of four species, including *E. blennius* (Burr, 1979), is morphologically intermediate between the *variatum* and *blennioides* groups, and its relationship is uncertain. As in the *variatum* group there is a broad premaxillary frenum, vomerine teeth are present, and there are 6 branchiostegal rays. In the *thalassinum* group, palatine teeth are reduced or absent, the snout is declivous, nuptial tubercles are typically present in males only, the female genital papilla is a very

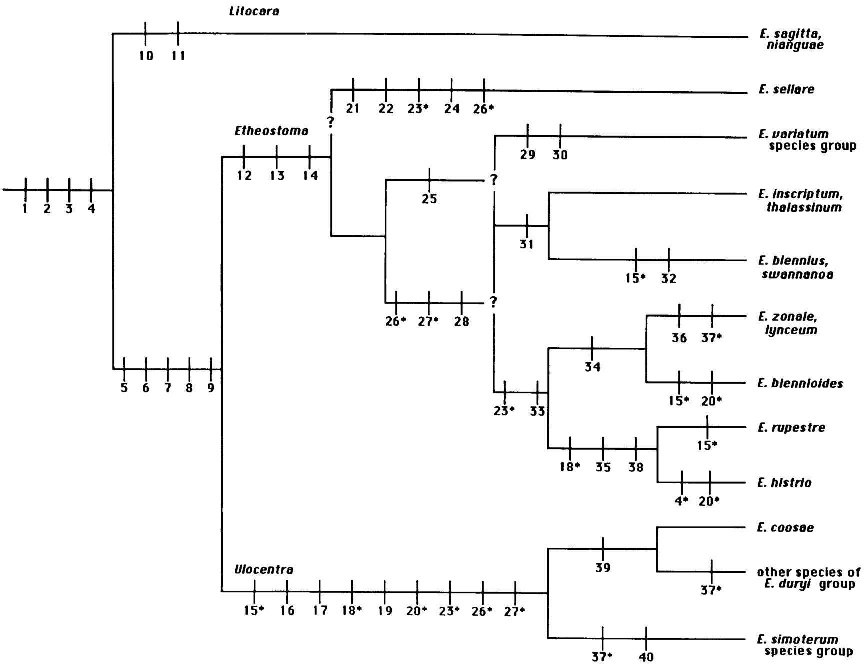

FIG. 1. Hypothesized relationships among species of subgenera *Etheostoma, Litocara,* and *Ulocentra.* Apomorphies 1–40 are discussed in the text or are self-explanatory. Presumed homoplasies are indicated with an asterisk. Autapomorphies for individual species are not included unless believed to be homoplasies. (1) nuptial tubercles on ventral body scales of males; (2) nuptial males with red lower sides; (3) nuptial males with red spots on soft dorsal and caudal fins; (4) nuptial males with red margin on spinous dorsal fin; (5) female genital papilla elongate; (6) gill membranes broadly connected; (7) snout blunt and/or declivous; (8) pectoral fin elongate; (9) anal-fin soft rays modally 9 or fewer (secondarily 10 in *euzonum*); (10) lateral line incomplete; (11) opercle naked; (12) dorsal saddles or blotches 4–7, consistent in position; (13) anterior dorsal blotch remote from occiput; (14) head extremely broad; (15) palatine teeth absent; (16) eggs laid singly; (17) sexes dichromatic throughout year; (18) preoperculomandibular canal pores 9; (19) red ocellus in spinous dorsal fin; (20) frenum reduced; (21) loss of elongate female genital papilla; (22) loss of sexual dichromatism; (23) nuptial tubercles absent or (*blennioides*) rarely developed; (24) nape and belly naked; (25) head profile changes abruptly above orbit, resulting in a bluntly to moderately pointed snout with mouth near ventral margin of head; (26) loss of red spots on soft dorsal and caudal fins; (27) anal-fin soft rays modally 8 or fewer; (28) palatine teeth reduced; (29) nuptial males with additional green and/or yellow bands below marginal red band of spinous dorsal fin; (30) nuptial tubercles developed on females; (31) female genital papilla a very long, slender tube; (32) nuptial males with horizontal rows of red spots on side; (33) nuptial males with marginal green band on spinous dorsal fin; (34) nuptial males with basal red band in spinous dorsal fin; (35) infraorbital canal pores 7; (36) head width reduced; (37) branchiostegal rays often reduced to 5; (38) anal-fin soft rays modally 7; (39) loss of frenum; (40) loss of vomerine teeth.

long slender tube, the spinous dorsal fin has a rusty marginal band and no additional banding, and there are 6 or 7 blotches on the back (4 saddles in *blennius*). In the third (*blennioides*) group of five species (*lynceum* is added following Etnier and Starnes, 1986), vomerine teeth are reduced (sometimes absent in *blennioides*), palatine teeth are absent (*blennioides, rupestre*) to occasionally present (*histrio, lynceum, zonale*), the snout is notably declivous, nuptial tubercles are usually absent (infrequently and weakly developed in males of *blennioides* only), the red band in the spinous dorsal fin, if present, is basal (submarginal in *histrio*), and there are usually 6 (often 7 in *blennioides*) blotches on the back, with the anterior blotch remote from the occiput. Nuptial males usually have a marginal green band on the spinous dorsal fin (submarginal band of orange-red with white edge in *histrio*). The premaxillary frenum may be well developed (*lynceum, rupestre, zonale*), narrow (*histrio*), or narrow or crossed by a groove (*blennioides*). The preoperculomandibular pores are reduced from 10 to 9 in *histrio* and *rupestre,* and infraorbital pores from 8 to 7 in *rupestre* and often in *histrio,* and branchiostegal rays often from 6 to 5 in *lynceum* and *zonale.* In addition to the above three groups there is the enigmatic *E. sellare,* of uncertain relationship but which seems clearly assignable to this subgenus, perhaps best as a fourth group. Vomerine and palatine teeth are present, the premaxillary frenum is well developed, the snout is rather blunt, nuptial tubercles have not been found, the nape, breast, and belly are naked, and the pectoral fin is long as in other species of the subgenus. There are 4 prominent dorsal saddles. Unlike all other members of the subgenus, sexual dichromatism is apparently undeveloped, the genital papilla of the female is a short pad rather than a long tube (Page, 1983:62), and the gill membranes are only moderately conjoined.

The "genus" *Ulocentra* as envisaged by Jordan and Evermann (1896:1047–1052) and Jordan, Evermann, and Clark (1930:286–287) included the then-known species of *Ulocentra* with an admixture of less closely related forms (*gilberti, histrio, blennius, phlox, stigmaea*). After removal of these extraneous species, currently assigned to four other subgenera in *Percina* and *Etheostoma,* most recent authors have circumscribed an apparently monophyletic group as the subgenus *Ulocentra* of *Etheostoma* (Bailey and Gosline, 1955; Winn, 1958; Richards, 1966; Page and Whitt, 1973a, b; Bouchard, 1977; Kuehne and Barbour, 1983).

In contrast to *Etheostoma s.s., Ulocentra* is an assemblage of darters that is geographically compact and similar both morphologically and, so far as known, in natural history characteristics, especially reproductive behavior. All live in streams, most often of small or moderate size, typically clear and with alternating pools and riffles. All occur in the area south of the Ohio River from the Kentucky River west, east of the Mississippi River, west of the Appalachian Mountains but avoiding higher elevations, and north of the Gulf of Mexico, including its tributaries from the Choctawhatchee west to the Mobile basin. All species, including several still undescribed, are small or of moderate size (maximum SL 47–68 mm), the males somewhat larger than females. They are more or less terete and relatively robust. As in *Etheostoma s.s.* the cephalic and lateral-line canals are complete, the pelvic fins are well separated, there are two stiff anal spines, the pectoral fins are large and expansive (about 24–30% of SL) though shorter than in most species of *Etheostoma s.s.*, the caudal fin is truncate or very shallowly notched, and the fins vary but little in spine and soft ray counts. The upper lip is protractile or attached to the snout with a slender bridge of tissue, never with a well-developed frenum as is characteristic of *Etheostoma s.s.* There are no nuptial tubercles.

Foreshortening of the head region is characteristic of *Ulocentra,* with the branchiostegal membranes broadly united (the union at midline much closer to pelvic fin base than to mandibular symphysis) and the snout very short and declivous (hence, snubnose darters). These features are least extreme in *coosae,* in which the branchiostegal membranes form a blunt angle of about 90° to 110° instead of a smoothly rounded curve and the snout is perceptibly longer than in other species (Bouchard, 1977, fig. 5).

Etheostoma coosae has been characterized as an aberrant species in *Ulocentra.* It is the only species in the subgenus that typically has 6 branchiostegal rays, but otherwise it is not unusual. It has 9 preoperculomandibular pores (Page, 1981b:57, and our observations), not 10 as stated by Page, 1981b:table 3). An obvious, distinctive synapomorphy in *Ulocentra* is the bright red or carmine ocellus on the first interradial membrane in the spinous dorsal fin of adult males (and sometimes females); contrary to the comment by Page (1983:80) it is present in *E. coosae,* often followed posteriad by a series of similar marks as illustrated by Page (1983, pl. 18), confirming our observations. Vomerine teeth, previously thought to be unique to *coosae* in *Ulocentra,* are now shown to be present in one of the species groups (see below).

We recognize two species groups in subgenus *Ulocentra.* The premaxillary frenum, well developed in most of *Etheostoma s.s.* (narrow in *histrio* and absent or almost so in *blennioides,* which has highly specialized mouthparts), is much reduced or absent in species of *Ulocentra.* In the *duryi* group (*duryi, coosae, etnieri, pyrrhogaster, zonistium,* and at least three unnamed species) the premaxilla is free from the snout and a needle can be passed under the free flap of snout tissue. (There is some variability in the frenum in *etnieri,* and in an unnamed species from the upper Mobile basin.) In the *simoterum* group (*s. simoterum, s. atripinne*—here regarded as a subspecies of *simoterum*—*baileyi, barrenense,* and *rafinesquei*) there is a strand of tissue connecting the upper lip and the snout, in effect a very narrow frenum. These forms typically have a shallow groove between the premaxilla and the snout, or a narrow frenum may be present, but the protraction of the upper lip is minimal. Correlated with this character is a difference in vomerine dentition. Members of the *duryi* group typically retain one or a few vomerine teeth, certainly the ancestral state (some individuals but no species lack teeth). The vomerine teeth (or tooth) are relatively long and strong, and perhaps function as a weapon on which to impale prey. There may be a functional interplay involving the dentition and the protractility of the upper jaw in this species group. We have not observed vomerine teeth in members of the *simoterum* group.

Species of the *simoterum* group are more northeastern in distribution, in the Tennessee, Cumberland, and Ohio river drainages; those of the *duryi* group are more southern and western, in Gulf of Mexico and Mississippi drainages, and the lower Tennessee and Cumberland basins. The usual presence of vomerine teeth and 6 branchiostegal rays in one species are indications that the *duryi* group is the more primitive. This suggests dispersal to the north from Gulf Coastal origins east of the lower Mississippi River. This scenario renders the total absence of *Ulocentra* from west of the Mississippi River and its limited distribution in the Ohio River drainage plausible. Their dispersal into the Tennessee, Cumberland, and Ohio river drainages was probably too recent to allow them easy (pre-glacial Teays River) access to the seemingly suitable *Ulocentra* habitats in the Ozark region and parts of the Mississippi River embayment.

Reduction of branchiostegal rays from the generalized 6 (character 9, p. 7) to 5 has occurred independently in *Etheostoma s.s.* (*zonale* and *lynceum*), in subgenus *Ulocentra* (most species), and in subgenus *Microperca* (*microperca,* see Burr, 1978:53). In *Ulocentra, E. coosae* typically has 6 rays and all other species (including undescribed forms) have 5, a derived condition. *Etheostoma zonale* and *E. lynceum,* formerly regarded as subspecies, were shown by Etnier and Starnes (1986) to merit full species rank. Each of these forms commonly has 5 branchiostegal rays on each side (Tsai and Raney, 1974, tables 4, 5, 6). Nevertheless, as pointed out by Tsai and Raney (1974:5) " ... two discontinuous populations, one from the Yazoo River to the Obion River [*lynceum*] and another from the Little Tennessee River to the upper Hiwassee River [*zonale*] still usually have six branchiostegals. The presence of this primitive characteristic in these separated populations suggests that *E. zonale* originally had six." We find that 6 is the modal count in populations of *lynceum* in the Yazoo and Hatchie river systems, and in those of *zonale* from the Hiwassee, Little Tennessee, Duck, Buffalo, and Elk rivers and Indian Creek, Tennessee. Reduction in branchiostegal ray count may have occurred independently in *zonale* and *lynceum,* or may reflect a shared genetic basis allowing variability of this character. In *Ulocentra, E. coosae* retains the plesiomorphic 6 branchiostegal rays, an undescribed species from the Etowah River system has variably 5 or 6, and all other species have 5. We consider lower branchiostegal ray counts to be independently evolved in *Ulocentra* and associated with reduced body size. In grouping the species of *Ulocentra* with *zonale* (and *lynceum*) as subgenus *Nanostoma,* Page (1981b:18–19) emphasized not only the branchiostegal rays but also three fin and body-proportion ratios which contrasted with those of other species of *Etheostoma s.s.* That these proportional changes have occurred independently rather than in a common ancestral line leading to *zonale, lynceum,* and all species of *Ulocentra* is evident based on consideration of other characters.

Character differences among *Etheostoma s.s., Ulocentra, E. zonale,* and *E. lynceum* are shown in Table 2. *Etheostoma zonale* and *E. lynceum* retain the generalized features of 10 preoperculomandibular pores (9 in all *Ulocentra* except usually 10 in *baileyi,* a presumed reversal to the primitive count), absence of a brilliant red spot midway on the first interradial membrane of the first dorsal fin (present in most *Ulocentra,* apparently secondarily lost in one or two undescribed species), a well developed premaxillary frenum (narrow or absent in *Ulocentra*), vomerine teeth (lost in *simoterum* species group), and palatine teeth occasionally present (not present in *Ulocentra*). *Etheostoma zonale* and *E. lynceum* have the derived reduction to 6 dorsal blotches, the most anterior of which is well separated from the occiput (8 or 9 in all species of *Ulocentra* with the anterior blotch in close proximity to the occiput). Nuptial tubercles have not been found in *E. zonale, E. lynceum,* or any species of *Ulocentra.*

Insofar as data are available, the species of *Ulocentra* and of the *Etheostoma blennioides* species group display notable differences in reproductive behavior and breeding sites that supplement and support distinctions between these two groups based on morphology. Winn (1958:202–205) investigated two species of *Ulocentra,* since described as *E. barrenense* (Barren River form) and *E. rafinesquei* (Green River form) in the field and in the laboratory. No differences in reproductive behavior were noted between them, and in fact cross mating occurred in aquaria. In the field in pools and raceways of small streams, males were observed to defend territories under rocks of 15 to 30 cm in diameter and in depths of 30 to 300 cm or in deep pools (50 to 90 cm deep) over silt-free bedrock with fairly swift current. The key reproductive stimulus was discovered in aquaria where at a water depth of 20 cm mating was unsuccessful, but when depth was increased to 37 cm breeding ensued. In spawning, the female followed by a territorial guardian male swam vertically up a rock wall to a height of as much as 30 cm, was mounted by the male while at an angle of 45° to over 90°, and deposited a single egg or several single eggs which adhered to a vertical or inclined surface. Extensive field and aquarium observations of breeding behavior by Stiles *et al.* (1987) of 13 species of *Ulocentra* likewise indicate that eggs are attached singly to boulder surfaces in pool areas. O'Neil (1981) and Page and Mayden (1981) provide essentially identical descriptions of reproductive behavior in aquarium observations of *E. coosae* and *E. simoterum* respectively.

Reproductive behavior for *Etheostoma zonale* has been summarized by Becker (1983) and for both *E. zonale* and *E. blennioides* by Pflieger (1975) and Trautman (1981). These authors commented on the striking similarities in habitat and breeding behavior of these two species. Winn (1958) investigated the breeding behavior of *blennioides.* The species, though differing notably in size, are similar in appearance and in reproductive behav-

TABLE 2

COMPARISON OF SUBGENERA *Etheostoma* AND *Ulocentra* (GENUS *Etheostoma*), WITH *E. lynceum* AND *E. zonale* OF THE *blennioides* SPECIES GROUP OF SUBGENUS *Etheostoma* SHOWN SEPARATELY

CHARACTER	*Etheostoma*	*lynceum*	*zonale*	*Ulocentra*
Dorsal saddles or blotches	4 to 7	6	6	(7)8 or 9(10)
Position of anterior saddle	Well behind occiput	Well behind occiput	Well behind occiput	In close proximity to occiput
Preoperculomandibular pores (modally)	10 (9 in *histrio* and *rupestre*)	10 (9 or 10 in southern populations)	10	9 (10 in *baileyi*)
Premaxillary frenum	Present, well developed except in *blennioides* and sometimes in *histrio*	Present, well developed	Present, well developed	Absent or very narrow
Vomerine teeth	Present (few or absent in *blennioides* group)	Present, usually several	Present, usually several (rarely absent)	Present (few), or absent
Palatine teeth	Present or absent	Occasionally present	Occasionally present	Absent
Breeding tubercles	Present or absent	Absent	Absent	Absent

TABLE 2 (continued)

Character	*Etheostoma*	*lynceum*	*zonale*	*Ulocentra*
Branchiostegal rays (usually)	6	5 (6 in some localities—see text)	5 (6 in some localities—see text)	5 (usually 6 in *coosae*)
Breeding behavior (as known)	Gravel nest site or in vegetation in current	Presumably as in *zonale*	In vegetation in current	Eggs deposited singly on usually flat, inclined boulder or log surfaces in pools
First dorsal fin (adult males)	Usually red margin or red to brown band at base	Red-brown band at base	Red-brown band at base	Usually brilliant carmine spot midway on first membrane (undeveloped in some gulf drainage forms); no red-brown band at base

ior (Table 2). Both species have a brick-red or red-brown band at the base of the spinous dorsal fin (not present in *Ulocentra*). They breed on rock or stone riffles of moderate or steep gradient and deposit eggs in vegetation, usually the green alga (*Cladophora*) or water moss (*Fontinalis*), that is attached to boulders. The eggs emerge in groups of 4 to 7 per vibration and adhere in clumps of 2 to 7 (Winn, 1958). Pflieger (1975) found that eggs of *blennioides* were laid about 40 at a time. The two species commonly share the same riffles but largely avoid competition because *blennioides* breeds earlier than *zonale,* and *zonale* uses shallower, more sluggish riffles and shorter, sparser clumps of algae and mosses (Trautman, 1981:659). Stiles *et al.* (1987) observed that in *zonale,* eggs are attached to vegetation in areas of considerable current, and that in both *zonale* and *lynceum* males utilize a vertical movement of the head to tap the female's dorsum during courtship. Stiles *et al.* had not noted this behavior in any species of *Ulocentra.*

Both *E. blennioides* and *E. zonale* are wide ranging whereas the species of *Ulocentra* are much restricted, usually to one or two adjacent river systems. It seems likely that the differences in habitat and breeding behavior contribute to distributional divergence. Both *blennioides* and *zonale* commonly occur in moderate or large streams if these provide the rock riffles with abundant aquatic vegetation, clarity, and steep gradient that is preferred. *Ulocentra* species, by contrast, most often occur in small streams with deep pools and alternating riffles with vertical or near vertical surfaces for oviposition. We speculate that the more lowland species of *Ulocentra,* such as *pyrrhogaster* and *zonistium,* in a habitat usually devoid of boulders, employ logs, snags, or other surfaces for oviposition. In aquaria, Carney and Burr (pers. comm.) have noted that both *pyrrhogaster* and *zonistium* have spawning behavior essentially as in other species of *Ulocentra.*

We interpret the notable similarities in morphology and in reproductive behavior of *blennioides* and *zonale* (and presumably of *lynceum*) as strong evidence for their more intimate relationship with one another than with the species of *Ulocentra.* Page's (1981b) grouping of *zonale* with the species of *Ulocentra* as subgenus *Nanostoma* is therefore rejected.

In summary, *Ulocentra* is viewed as the monophyletic sister group of subgenus *Etheostoma* (Fig. 1), and diagnosed by the following synapomorphies: (1) premaxillary frenum absent or very narrow; (2) preoperculomandibular pores characteristically 9 (secondarily 10 in *baileyi*); (3) a brilliant carmine ocellus near middle of first interradial membrane of dorsal fin in adult males (secondarily occluded or lost in one or more undescribed forms); (4) loss of palatine teeth, (5) oviposition (so far as known) involving deposition of single eggs on a usually vertical or inclined surface in rather deep water, and (6) sexual dichromatism persistent all year. All species of *Ulocentra* have other common characteristics, as discussed above, but these are shared or convergent with those of some species of *Etheostoma s.s.* That subgenus is distinguished from *Ulocentra* in the reduction of dorsal blotches to 4 to 7 (7 to 10, usually 8 or 9 in *Ulocentra*), the anterior blotch remote from the occiput (close to the occiput and well in advance of first dorsal spine in *Ulocentra*), and head extremely broad.

BOLEOSOMA GROUP

Boleosoma, Vaillantia, and *Ioa* seem to constitute an interrelated group of darters with which we associate *Doration* at least provisionally. With the sole exception of *E.* (*Doration*) *jessiae,* all members of this group have protractile premaxillae, an hypothesized synapomorphy. Elsewhere in darters* protractile premaxillae occur in subgenera *Cottogaster* and *Imostoma* of *Percina,* in subgenus *Ammocrypta,* and in subgenera *Ulocentra* and *Etheostoma* (*blennioides,* frenum narrow in *histrio*) of *Etheostoma. Etheostoma jessiae* and *E. stigmaeum* are very similar, and it seems probable that the presence of a frenum in *jessiae* is a secondary result of the elongate snout in that species. In all members of the group, the pelvic fins are rather widely spaced. There is considerable variation in other features: the lateral-line, supraorbital, infraorbital, and supratemporal canals may be complete or incomplete; vomerine and palatine teeth may be present or absent; the gill membrane connection varies; there may be one or two anal spines, either flexible or stiff; and the colors may be bright (*Doration, E.* (*B.*) *longimanum,* and *E.* (*B.*) *podostemone*) or somber.

As now circumscribed, *Boleosoma,* with five species, is distinctive in the group in lacking breeding tubercles and in having a bilobed genital papilla in adult females. As an additional synapomorphy, all species deposit eggs on the lower surface of rocks or other objects where they are tended by the male. Vomerine teeth are present but palatine teeth may be present (as in *olmstedi*) or absent (*nigrum*). The pectoral fins are notably long in *podostemone* and *longimanum,* more so than in any darters except some species of *Etheostoma s.s.* and *E. vitreum;* the former species also have broadly conjoined gill membranes. The two species of *Vaillantia* were discussed and contrasted by Page (1981b). They differ from one another in several characters including the reported absence of nuptial tubercles in *davisoni.* The monotypic subgenus *Ioa* (*vitreum*), with many apomorphic characters, is one of the most distinctive of darters. It parallels *Ammocrypta* in the translucent flesh and sand habitat. The vomer and palatines are toothless, the anus is surrounded by numerous fleshy papillae, the snout is relatively long, the pectorals are very long, the body is slender and the interorbital is narrow, the anal spines are variably one or two, and nuptial tubercles are present on the pectoral and pelvic fins of breeding fish of both sexes (Jenkins, 1971).

The species of *Doration* were included in *Boleosoma* by Bailey and Gosline (1955), but were set apart by Cole (1967) as a subgenus, a treatment adopted

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*Page (1981b:66) inadvertently recorded *E. chlorobranchium* as having frenum absent or extremely narrow.

by Page (1981b) and others. We accept this separation and note that *Doration* differs from other subgenera of the *Boleosoma* group in its bright colors, including a blue band over a red band in the first dorsal fin, the less widely spaced pelvic fins, and the premaxillary frenum in one species. It is possible that the relationships of *Doration* are with *Oligocephalus.* Page (1981b:56) reported that the palatine is toothless in *Doration.* We find variation; in both *jessiae* and *stigmaeum* one or a few teeth are often present.

OLIGOCEPHALUS GROUP

The remaining 10 subgenera include most of the darters regarded as highly advanced. Nevertheless, plesiomorphic characters are prominent. All have vomerine and palatine teeth, a well developed premaxillary frenum, and pectoral fin of short or moderate length (less than 28% of SL). Branchiostegal rays are modally 6–6 except in *E.* (*M.*) *microperca* (5–5), perhaps the most specialized of darters. Characters that indicate specialization are small to moderate size, attaining maximum standard lengths of from 35 to 94 mm; pelvic fins typically closely approximated; vertebrae from 31 to 40; marked sexual dichromatism, with bright colors in adult males of most species; many have specialized breeding behavior; and there are noteworthy apomorphies in most of the subgenera. The lateral-line, infraorbital, and supratemporal canals vary from complete to interrupted, the gill membranes range from separate to broadly united, and nuptial tubercles may be present or absent. In some the lateral line is arched upward anteriorly, a development that we believe has evolved in two or more phyletic lines. Distinctive among darters (except for *Percina macrolepida,* p. 8) is the occasional presence of scales on the top of the head and on the branchiostegal membranes. We interpret such scalation as apomorphic.

SUBGENUS *Nothonotus.*—As delineated by Page (1981b:35–36) *Nothonotus,* with 13 described species including *E. juliae* (earlier assigned to *Oligocephalus*), is an apparently monophyletic group. Synapomorphies include horizontal lines on the side of the body, a distinctive slab-sided body shape, and darkened anterior interradial membranes in the spinous dorsal fin. Most species are of moderate size but *E. tippecanoe* is one of the smallest of darters and the only *Nothonotus* which consistently has the lateral line incomplete. In *Nothonotus* the infraorbital and supratemporal canals are complete; the gill membranes are separate, narrowly or widely (*juliae*) united, and nuptial tubercles are lacking. Breeding habits vary; some species bury eggs in gravel, others deposit clumps of eggs under rocks.

SUBGENUS *Catonotus.*—*Catonotus* was diagnosed by Page (1981b) and has recently been reviewed by Braasch and Mayden (1985). The latter authors admitted 12 species in three species groups. They provided strong evidence for the monophyly of the group based on eight characters (p. 57), several of which are synapomorphies that mark *Catonotus* as one of the most advanced and distinctive of the subgenera of darters. Among these are the development of fleshy or, in some species, bony enlargements of the tips of dorsal spines or soft rays in breeding males, first dorsal fin low and with few spines, interruption or incompleteness of cephalic and lateral-line canals, specialized genital papillae in females, and egg deposition in a single layer (clustering) on the underside of slab rocks or wood fragments. Presence of a complete infraorbital canal in all or most individuals of two of the most generalized species of the group was interpreted as a reversal (p. 59) from the interrupted condition; we consider this a plesiomorphy retained from the usual primitive condition in darters.

The interrelationship of *Catonotus* with other darter subgenera has not been established. The absence of nuptial tubercles is a characteristic shared by *Catonotus* with all *Nothonotus,* some species of *Oligocephalus,* and single species of *Psychromaster, Belophlox,* and *Villora.* Egg clumping by some species of *Nothonotus* and clustering by all species of *Catonotus* may be an indicator of kinship, but Page (1985) interprets these as independently derived from burying egg layers (*Nothonotus*) and attaching behavior (*Catonotus*). Both groups are characterized by laterally compressed bodies and many species in each subgenus have a characteristic pattern of horizontal dark lines along the side. We place *Catonotus* adjacent to *Nothonotus* as an unverified suggestion of possible relationship.

Subgenus *Psychromaster.*—This distinctive taxon contains, since the transfer of *trisella* to *Ozarka* (Williams and Robison, 1980), only *E. tuscumbia.* It was diagnosed by Page (1981b:30). As discussed earlier, we interpret the heavy investiture of cephalic scales, on the parietal region and commonly on the branchiostegal membranes (unique in darters and a rarity in percoids, e.g., Priacanthidae), as specializations approached among darters only in *Percina macrolepida* and in two species of *Hololepis.* The presence of a single, well-developed anal spine and incomplete lateral-line and supratemporal canals are additional apomorphies. In lacking nuptial tubercles *Psychromaster* agrees with the two preceding subgenera. The relationships of this specialized subgenus are obscure.

Subgenus *Oligocephalus.*—As visualized by Bailey and Gosline (1955), this was the largest subgenus of *Etheostoma,* and by comparison with the current arrangement was polyphyletic. *Etheostoma juliae* is now placed in *Nothonotus.* Four small groups (*Litocara, Ozarka, Belophlox,* and *Fuscatelum*) totaling 10 species are presently recognized as separate subgenera. Except for *Litocara* (p. 12) these are probably close to or derived from *Oligocephalus. Austroperca* (*australe*) is now merged in *Oligocephalus* (Page, 1981a), and several new species have been described in recent years. The subgenus as emended has been diagnosed by Page (1981b), and the species have been described and illustrated (Page, 1983). To the 15 species accepted by Page we add *exile* (placed by him in *Boleichthys*—see p. 28) and, provisionally, *okaloosae* (included by Page in *Belophlox* and by Collette and Yerger, 1962 in *Villora,* see p. 27).

With 17 species, *Oligocephalus* remains the largest subgenus of darters. The species mostly have highly colored males with a blue, green, or dusky margin on the spinous dorsal fin and an orange or reddish submarginal band. Males usually exceed females in size. The lateral line is characteristically incomplete in all species, but an occasional individual has a full complement of pored scales. The supratemporal and infraorbital canals may be complete or interrupted, more often complete for each canal. The typical preoperculomandibular count is 10 in all species except *okaloosae* (9). Divested of some of its formerly more distinctive species, *Oligocephalus* may now be monophyletic. On the other hand, it remains more diverse than other darter subgenera and clear evidence of diagnostic synapomorphies has not been presented.

Subgenus *Ozarka.*—Williams and Robison (1980) removed four species from *Oligocephalus* (*punctulatum, boschungi, cragini* and *pallididorsum*) and one from *Psychromaster* (*trisella*) to comprise this subgenus, a notable behavioral feature of which is spawning on aquatic vegetation in shallow flooded seepage areas, commonly in or near springs. As in *Oligocephalus* mature males have a dark margin and an orange submarginal band in the first dorsal fin, and all species have nuptial tubercles on body scales and on anal and pelvic fins (reported in *trisella* by Ryon, 1986). Morphologically the group is diverse (Page, 1981b and 1983): there may be two anal spines or one (*trisella*), and the supratemporal canal and lateral line may be complete (*trisella*) or incomplete, scale size varies with *punctulatum* having notably small scales (58–80 in lateral series), and infraorbital pores may be 8 or reduced to 7. Breeding males of all species have a broad longitudinal red-orange flank and lack bright colors in the soft dorsal fin. Under subgenus *Fuscatelum* we emphasize the need for further study of *E. parvipinne* to clarify its relationship with *Ozarka.*

Subgenus *Fuscatelum.*—The monotypic *Fuscatelum* Page (1981b), based on *Etheostoma parvipinne,* calls attention to characters of this species that are not consistent with its assignment in *Oligocephalus,* but offers nothing toward an understanding of its true relationships. It lacks the bright colors of *Oligocephalus,* has gill membranes that are more broadly connected than in species of *Oligocephalus,* and has variably one or two anal spines instead of two (except that *E.* (*Oligocephalus*) *australe* has a single spine). Alternatively, *parvipinne* shares with the species of *Ozarka* a tuberculate anal fin in breeding males, with *E.* (*Ozarka*) *trisella* a reduction in anal spine number, and with *E.* (*Ozarka*) *pallididorsum* and *E. cragini* a distinctly depigmented nape. Although it lacks the bright colors of the species of *Ozarka,* its preferred habitat of small streams, late winter reproductive season, and concentration of adults in even smaller watercourses during late winter suggest that it is a somber species of *Ozarka* that shares with those species the synapomorphic "temporarily flooded field" breeding site. Elucidation of breeding behavior of *E. parvipinne* should be very helpful in clarifying relationships within the *Oligocephalus* complex of *Etheostoma.*

Subgenus *Belophlox.*—Page (1981a:37) resurrected *Belophlox* Fowler from synonymy and included three species (*mariae, fricksium,* and *okaloosae*) previously assigned to subgenera *Oligocephalus* and *Villora.* As discussed under

Villora, we doubt an intimate relationship of *okaloosae* and *E.* (*Villora*) *edwini.* In *okaloosae* the orange band in the first dorsal fin of mature males lies proximal to the dark margin, as in *Oligocephalus,* and the lateral line is typically incomplete (with 0–4, usually 1 to 3, unpored scales; Collette and Yerger, 1962), as in members of the *asprigene-swaini* group of *Oligocephalus.* The greatest similarity appears to be with *swaini,* hence our transfer of *okaloosae* to *Oligocephalus* (p. 25).

The two species of *Belophlox, E. mariae* and *E. fricksium,* occupy small ranges in the eastern Carolinas and Georgia (Page, 1983). Both have a broad orange marginal band in the spinous dorsal fin, a possible synapomorphy, and have the lateral line complete or with few unpored scales. The two species differ in pigmentation and several other respects. *Etheostoma mariae* lacks nuptial tubercles and has broadly united branchiostegal membranes (anal fin tubercles present in nuptial males of *fricksium* and branchiostegal membranes moderately conjoined); *mariae* has reduced numbers of pores in the complete preoperculomandibular and infraorbital series (9 and 7, versus 10 and 8 in *fricksium*). The subgenus is not well corroborated but the two included species are probably each others' closest relatives.

Subgenus *Villora.*—*Etheostoma edwini* was placed in subgenus *Hololepis* by Bailey and Gosline (1955), in *Villora* with *E. okaloosae* by Collette and Yerger (1962), and in a monotypic *Villora* by Page (1981b). We concur with Page (1981b:27) that close affinities between *edwini* and *okaloosae* are not apparent. We cannot confirm that *E. okaloosae* has a somewhat arched lateral line as reported by Collette and Yerger (1962); rather, it is straight or very gently curved as in most species of *Oligocephalus,* to which subgenus we provisionally assign *E. okaloosae* (see above, and p. 25). *E. edwini* differs from the species of *Hololepis* primarily in lacking nuptial tubercles and in having males considerably larger than females; its closest affinities may be with *Hololepis* as suggested by Bailey and Gosline (1955). *Etheostoma edwini* and *Hololepis* have a characteristic head physiognomy, and *E. edwini* uniquely shares with *Hololepis* and *Microperca* a distinctly though less strongly arched lateral-line canal (arching of the canal may have evolved independently two or more times in darters). In *edwini,* as in *Hololepis* and *Microperca,* the posterior nasal pore is closely approximated to the enlarged posterior nostril. Page's (1981b) lumping of *Hololepis* and *Microperca* into *Boleichthys* (together with *E. exile;* see discussion under *Hololepis*), while not acceptable to us, creates a sufficiently broad subgeneric concept to incorporate *edwini,* whose affinities are perhaps with those species. Alternatively, we note that phylogenetic considerations of *E. edwini* have belabored the question of relationship to *Hololepis* while virtually ignoring the possibility of affinities elsewhere within a broadly construed *Oligocephalus.* For the present we regard *Villora* as a monotypic subgenus that displays some distinctive features. It may have relationships with either *Hololepis* or *Oligocephalus.*

Subgenus *Hololepis.*—This subgenus and its six species were discussed in detail by Collette (1962). Comments concerning relationships within this group and between it and the potentially related subgenera *Microperca* and *Villora* appear under those subgenera. We restrict this discussion to Page's (1981b) treatment of *Etheostoma exile* as more closely related to *Hololepis* than (as it has been traditionally placed) to *Oligocephalus*. In evaluating characters potentially useful in resolving this problem, we find that *Etheostoma exile* resembles *Oligocephalus* and differs from *Hololepis* in lacking nuptial tubercles in mature males (lacking or present in *Oligocephalus*, present in all species of *Hololepis*), in lacking a strongly arched lateral line, in having the posterior nasal pore well separated from the posterior nostril (closely approximated in all species of *Hololepis*), in having red colors on the body and soft dorsal fin in addition to the spinous dorsal fin, and in having 10 preoperculomandibular pores (10 pores in all species of *Oligocephalus* except *okaloosae*, 10 in *E.* (*H.*) *gracile* and *zoniferum*, 9 in other species of *Hololepis*). In all of the above *exile* displays the plesiomorphic condition, showing no synapomorphies with *Hololepis*. The head and body shapes of *exile* are similar to the species of *Hololepis* but not notably different from some species of *Oligocephalus* (e.g., *asprigene, lepidum*). As in *Hololepis* there is no red on the anal fin in *exile*, but several species of *Oligocephalus* (e.g., *australe, collettei, grahami, hopkinsi, luteovinctum, spectabile*) also lack red in that fin. *Etheostoma exile* appears to differ from *Hololepis* more than does *E.* (*Villora*) *edwini*. In *Etheostoma exile* the lateral-line canal is at most weakly curved.

Page's (1983:23) transfer of *exile* from *Oligocephalus* to *Hololepis* (*auct.*) depended, in addition to the variable but always low arch of the lateral line in *exile* (see above), on two ratios: "percent of scales in lateral-line row pored" and "second dorsal fin length divided by distance from front of base of second dorsal fin to caudal base in males" (Page, 1983:25, fig. 11). Examined individually these ratios, as given by Page, have broad overlap between *Oligocephalus* and *Boleichthys* (*Hololepis* plus *Microperca*), but when plotted as a scattergram the three subgenera for the most part cluster separately, with *exile* falling among the species of *Hololepis*. However, transfer of *exile* to *Hololepis*, following Page's methodology, would necessitate shift also of *serriferum* from *Hololepis* to *Oligocephalus*, since on the plot it falls among the species of that subgenus and well apart from the other species of *Hololepis*.

In summary, the weight of character differences favors retention of *exile* in *Oligocephalus*. Students of darter phylogeny should continue to pursue additional lines of inquiry that might lead to more precise understanding of the phyletic position of *E. exile*.

SUBGENUS *Microperca*.—That the three species currently placed in subgenus *Microperca* comprise a natural group was recognized by Jordan and Evermann (1896:1103–1105). Subsequent to reduction of darter genera to three, *Microperca* has been consistently employed as a subgeneric name through Burr's (1978) monograph. Page's (1981b) action of uniting *Microperca* with *Hololepis* and *E. exile* as *Boleichthys* is novel, and worthy of careful consideration. Page (1981b:23) cited Burr (1978) as having "... discussed the closeness of the two subgenera [*Hololepis* and *Microperca*] and noted the intermediacy of *E.* [(*H.*)]*saludae* and *E.* [(*H.*)] *collis* between the two subgenera" and continued "It seems apparent that *E. saludae* and *E. collis* are more similar to species of *Microperca* than they are to some species of *Boleichthys* [*sensu* Page], and that *E. saludae, E. collis,* and *Microperca* share a common ancestor." Burr (1978:9) actually concluded "... the existing morphological data suggest that the relationships of *Hololepis* and *Microperca* can best be expressed as subgenera within *Etheostoma.*" The species of *Microperca* and *Hololepis* all share the derived features of nuptial tubercles on the pelvic and anal fins and an arched lateral-line canal (if the line is short the angle of the tubes indicates an arch). Synapomorphies for *Microperca* include mean dorsal spine counts of 6.4–7.8 (9.0–11.1 in *Hololepis*), modally 32–36 vertebrae (36–39 in *Hololepis*), a bilobed or otherwise distinctive (*microperca*) female urogenital papilla (unlike those of *Hololepis*), a drastically modified pelvic fin in nuptial males (flap of tissue anterior to pelvic spine and pelvic fin length greater than 25% of SL, versus no such flap and pelvic fin length less than 23% of SL in *Hololepis*), an interrupted infraorbital canal with modally 4 or fewer pores (mode 4–5 or more in *Hololepis*), 8 or fewer preoperculomandibular canal pores (9 or 10 in *Hololepis*), 10 or fewer pectoral-fin rays (11 to 13 in *Hololepis*), and a unique indentation of mature ova in *Microperca* not shared by *Hololepis* (Burr, 1978). This impressive array of synapomorphies strongly supports the monophyly of subgenus *Microperca.*

We fail to find evidence of relationship of *Microperca* with *collis* and *saludae* as visualized by Page. Of *Microperca* characters shared with some but not all species of *Hololepis,* bright colors (plesiomorphic) are retained only in spinous dorsal fins of males of *gracile* and *zoniferum.* The distinctly bilobed female urogenital papilla of *E. proeliare* and *fonticola* is most closely approximated by that of *serriferum* among *Hololepis* (Burr, 1978:7–8), maximum pelvic fin length in *Hololepis* occurs in *serriferum* (22.9% of SL; Page 1981b:63), and the reduced number of dorsal soft rays (mean 11.0 or less) occurs in *Hololepis* only in *fusiforme* and *zoniferum* (Collette, 1962). *Etheostoma* (*H.*) *collis* and *E.* (*H.*) *saludae,* the supposed "link" between *Hololepis* and *Microperca,* are notably absent in the above scrutiny. One or both of these two species of *Hololepis* have in common with *Microperca* a mean of 17 or fewer pored lateral-line scales (also true of *zoniferum*), a mean of 44 or fewer scales in lateral series, and reduced squamation of the breast and head (Collette, 1962; Burr, 1978). Similarities noted between *Microperca, saludae,* and *collis* are reductional ones perhaps associated with small size.

Collette's (1962) placement of *serriferum* as the most primitive *Hololepis* follows Hubbs and Cannon (1935). These workers considered a serrate preopercle to be the plesiomorphic condition in darters. Although this is possible, we contend (p. 6) that the reverse is true in genus *Etheostoma.* We also believe that bright color in dorsal fins of males is primitive within *Etheostoma* lineages, and that extensive head squamation is a derived character strongly correlated with quiet water habitats. We incorporate these views into reconsideration of Table 1 in Hubbs and Cannon (1935:21), and note that *E. gracile* replaces *E. serriferum* as being more representative of the ancestral *Hololepis.* We believe this to be the case. Parsimony is poorly served by *Boleichthys sensu* Page (1981b), since brightly colored male dorsal fins would have been lost (*collis* and *saludae*) and regained in *Microperca. Microperca* is a monophyletic group that we regard as the sister group of *Hololepis,* and we treat each of these well defined subgenera in the traditional sense employed by their recent monographers, Burr (1978, *Microperca*) and Collette (1965, *Hololepis*), although we know of no synapomorphies for the latter group.

SPECIES DESCRIPTIONS

Materials and Methods

With the exception of one lot of *Etheostoma zonistium* provided by the University of Alabama, all specimens utilized in the following descriptions were originally deposited in collections of the University of Michigan and the University of Tennessee. Counts and measurements were made as described in Hubbs and Lagler (1958) unless mentioned below. Parenthetical counts occurred with a frequency of 10% or less. Transverse scales were counted on the left side from the dorsal midline at the origin of the soft dorsal fin to the base of the anal fin. Gill rakers were counted on the right side, with both dorsal and ventral rudiments included in the counts. Measurements were made with a needle-point divider and distances, estimated to the nearest 0.1 mm, were read from a millimeter rule. Head length was measured to the tip of the opercular spine. Trans-pelvic width was measured between the outer bases of the pelvic spines.

With the exception of the University of Alabama Ichthyological Collection, standard symbolic codes to indicate location of study collections follow the recommendations of Leviton *et al.* (1985), as follows: AMNH = American Museum of Natural History. ANSP = Academy of Natural Sciences of Philadelphia. AUM = Auburn University Museum. CAS = California Academy of Sciences. CU = Cornell University. INHS = Illinois Natural History Survey. KU = University of Kansas. LACM = Los Angeles County Museum of Natural History. NLU = Northeast Louisiana University. OS = Oregon State University Museum of Natural History. OSM = Ohio State University Museum. OSUS = Oklahoma State University. ROM = Royal Ontario Museum. SIUC = Southern Illinois University (Carbondale). TU = Tulane University. UAIC = University of Alabama Ichthyological Collection. UF = University of Florida, Florida State Museum. UMMZ = University of Michigan Museum of Zoology. UOMZ = University of Oklahoma Stoval Museum of Zoology. USNM = National Museum of Natural History. UT = University of Tennessee.

Etheostoma ***pyrrhogaster,*** new species
Firebelly Darter
Plate 1

Etheostoma (*Ulocentra*) sp.—Bouchard, 1974 (taxonomic status and distribution); Jenkins, 1976 (undescribed species, distribution); Starnes and Etnier, 1980:B-127 (on Tennessee's list of rare wildlife).

Etheostoma sp.—Kuehne and Barbour, 1983:100 ("lowland snubnose darter"); Burr, 1980:78 (red snubnose darter, Kentucky distribution); Burr and Warren, 1986:329 (firebelly darter, Kentucky distribution).

Etheostoma pyrrhogaster.—Gill, 1982:14 (color plate, *nomen nudum*).

Red snubnose darter.—Page, 1983:15C, 15D (color illus.); Starnes and Etnier, 1986:355 (Obion and Forked Deer rivers).

HOLOTYPE.—Adult male, UMMZ 213924, 56.6 mm standard length (SL), Clear Creek, tributary to North Fork Obion River, at unnumbered county road crossing 2.7 air km S co. rd. 8172, 5.1 air km SW Puryear, Henry Co., Tenn., 30 Oct. 1971, J. E. Deck, W. C. Dickinson, J. Vaughn.

PARATOPOTYPES.—Collected with the holotype are UT 91.705(5), USNM 270857(4), and UMMZ 213925(4). Additional paratopotypes are INHS 68217(3) and UF 42062(3), 13 Mar. 1972; UAIC 7740.01(4) and TU 139772(4), 27 Apr. 1972; UT 91.2324(9), 3 Nov. 1972; UT 91.2757(8) and CAS 56327(3), 14 Dec. 1984.

OTHER PARATYPES.—**Obion River system, Tennessee:** UT 91.277(1), Thompsons Creek at Tenn. Hwy. 54, Weakley Co.; CU 70726(2), ANSP 153833(3), AMNH 55779(3), LACM 43797–1(3), NLU 56290(3), AUM 25552(3), UT 91.2231(3), KU 21182(6), SIUC 11396(6), UOMZ 43325(6), and ROM 46458(6), Terrapin Creek 150 m below Tenn. Hwy. 69, 0.5 km S of Kentucky border, Henry Co. **Obion River system, Kentucky:** UMMZ 202964(2), Terrapin Creek at Ky. Hwy. 97, Tenn. border, Graves Co. **Forked Deer River system, Tennessee:** UMMZ 168524(28), tributary to South Fork Forked Deer River at U.S. Hwy. 45, 3.5 km SE Pinson, Chester Co.; UMMZ 177684(8), South Fork Forked Deer River, 5.5 km NW Henderson, Chester Co.; UT 91.1250(1), Jones Creek at road 7.2 km NNW Henderson, Chester Co.; OSM 60339(3), Clarks Creek at road 8.3 km NNE Henderson, Chester Co.; OS 11034(7) and OSUS 11991(6), Sweetlips Creek and adjacent Jacks Creek, 7.4 km SE Henderson, Chester Co.; UT 91.1283(6), Jacks Creek at Tenn. Hwy. 22A, Chester Co.; UT 91.852(1), Harris Creek at road 11.2 km ENE Jackson, Madison Co.; UT 91.2707(12), Blair Lake on Spring Creek, 19.3 km NE Jackson, Madison Co.; UT 91.853(4), Brown Creek at co. rd. 8059, 8.7 km E Jackson, Madison Co.; UT 91.2708(4), Bear Creek at co. rd. 8059, 9.2 km E Jackson, Madison Co.; UT 91.2709(1), Middle Fork Creek at co. rd. 8061, 16.4 km SW Lexington, Henderson Co.; UT 91.1149(7), Cane Creek at Tenn. Hwy. 104, 17.5 km NW Lexington, Henderson Co.; UT 91.1151(4), Hogwallow Creek at road 20.0 km N Selmer, McNairy Co.

DIAGNOSIS.—A member of the subgenus *Ulocentra* as diagnosed by

Bouchard (1977). It is unique in having a continuous broad red band in the anal fin and in both dorsal fins in adult males. Differs from members of the *simoterum* species group (*Etheostoma baileyi, E. barrenense, E. rafinesquei, E. s. simoterum,* and *E. s. atripinne*) in having vomerine teeth and in consistently lacking a premaxillary frenum. Differs from *E. coosae* in having 5 rather than 6 branchiostegal rays. It agrees with remaining *Ulocentra,* members of the *duryi* species group (*E. duryi, E. etnieri, E. zonistium* described herein, and several additional undescribed species), all of which consistently or often (*etnieri* and one undescribed upper Mobile Basin species) lack a frenum and have 5 branchiostegal rays. Differs from all *Ulocentra* except some Cumberland River populations of *E. baileyi* in having only 7 infraorbital canal pores. Differs further from all *Ulocentra* except *E. rafinesquei* in its larger scales (Table 3), with lateral-line scales 36–46, usually 43 or fewer, versus usually 42 or more in other species.

DESCRIPTION.—*Etheostoma pyrrhogaster* is a moderate-sized member of the subgenus *Ulocentra,* with males reaching a maximum of 56.6 mm SL (70 mm TL). Females attain a maximum of about 45 mm SL. Males as small as 34 mm SL are apparently sexually mature and have well developed red bands in the dorsal fin. Females as small as 30 mm SL have well developed urogenital tubes and are presumably sexually mature.

Frequency distributions of scale and fin ray counts appear in Tables 3 and 4. Lateral line complete, with 36–46 scales. Transverse scales 10–13. Scales around caudal peduncle (14)15–17(18). Dorsal fin with (9)10–11(12) spines and 11–12(13) soft rays. Anal fin with 2 spines (single anal spine in 1 of 79 specimens counted) and 7–8(9) soft rays. Pectoral fin rays 13–14(15). Principal caudal fin rays 15–17, usually 16 or 17. Vertebrae 38 (4 specimens) or 39 (11 specimens), Terrapin Creek, Henry Co., Tenn. Branchiostegal rays 5–5 (5–6, 6–5, or 6–6 in 4 of 58 specimens counted). Branchiostegal membranes broadly connected. Cephalic sensory canals complete with 9(38) or 10(2) preoperculomandibular pores and 6(1), 7(27), or 8(12) infraorbital pores. Lateral canal with 5 pores, supratemporal canal complete with 3 pores, supraorbital canal with 4 pores, coronal pore single. Gill rakers 7(13), 8(14), 9(10), or 10(1), with length of longest gill rakers about 1–1.5 times their basal width. Belly, opercle, cheek, nape, and prepectoral area covered with exposed scales. Breast typically with anterior half naked and posterior half covered with embedded or weakly exposed scales.

Nuptial males (Plate 1) with bright red band in both dorsal fins. Red pigment in first interradial membrane of spinous dorsal fin occupies the middle four-fifths or more of the membrane; the absence of dark brown chromatophores within the red pigmented area of this membrane (present in more posterior membranes) plus its black ventral border produce an "ocellus" typical of many species within the subgenus. Red pigment in the second membrane occupies the distal half to two-thirds of the membrane. On more posterior membranes red pigment gradually becomes more extensive, covering virtually all of the last two or three membranes. Below this red band the fin is gray to gray green, often paler at the ventral margin

TABLE 3

FREQUENCY DISTRIBUTION OF SCALE COUNTS IN *Etheostoma pyrrhogaster* AND *E. zonistium**

	Lateral-line scales																		
	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	N	X̄
Etheostoma pyrrhogaster																			
Obion River system				4	4	17	18	23	**6**	4	2							78	42.2
Forked Deer River system	2	10	13	16	13	10	-	-	-	1	-							65	39.0
Etheostoma zonistium																			
Tennessee River drainage					5	5	14	35	39	48	**55**	34	21	19	8	3		286	45.4
Hatchie River system						4	5	4	8	24	7	3	5	1	1	-	1	63	45.0
Black Warrior River system									1	1	2	6	10	8	4	3		35	48.3

	Transverse scales						Scales around caudal peduncle							
	10	11	12	13	N	X̄	14	15	16	17	18	19	N	X̄
Etheostoma pyrrhogaster														
Obion River system	6	18	**10**	1	35	11.2	2	8	**14**	5			29	15.8
Forked Deer River system	1	13	11	2	27	11.5	1	4	3	16	2		26	16.5
Etheostoma zonistium														
Tennessee River drainage		**11**	50	60	121	12.4		1	16	**72**	12	12	113	17.2
Hatchie River system	4	31	5		40	11.0	1	14	14	9			38	15.8
Black Warrior River system		6	13	11	30	12.2			1	21	6	2	30	17.3

*Counts for holotypes indicated in boldface.

TABLE 4

FREQUENCY DISTRIBUTION OF FIN RAY COUNTS IN *Etheostoma pyrrhogaster* AND *E. zonistium**

	Dorsal spines						Dorsal soft rays					
	9	10	11	12	N	X̄	10	11	12	13	N	X̄
Etheostoma pyrrhogaster												
Obion River system	4	**24**	22	1	51	10.2		24	**24**	3	51	11.6
Forked Deer River system		9	18	1	28	10.7		14	13	1	28	11.5
Etheostoma zonistium												
Tennessee River drainage	10	**135**	43	1	189	10.2	25	**132**	31		188	11.0
Hatchie River system	1	55	7		63	10.1	9	23	1		33	10.8
Black Warrior River system	1	21	10		32	10.3	5	24	3		32	10.9

	Anal soft rays						Left pectoral rays					Principal caudal rays					
	6	7	8	9	N	X̄	13	14	15	N	X̄	15	16	17	18	N	X̄
Etheostoma pyrrhogaster																	
Obion River system		9	**38**	4	51	7.9	18	**33**		51	13.6	5	16	**30**		51	16.5
Forked Deer River system		15	12	1	28	7.5	5	21	2	28	13.9	5	13	5		23	16.0
Etheostoma zonistium																	
Tennessee River drainage	12	**132**	22		166	7.1	50	**188**	50	288	14.0	7	**29**	103	1	140	16.7
Hatchie River system	4	26	3		33	7.0	18	44	1	63	13.7	9	17	37		63	16.4
Black Warrior River system	1	18	13		32	7.4		23	9	32	14.3	2	10	16		28	16.5

*Counts for holotypes indicated in boldface.

of the red pigment and at the base of the fin, creating a vague dark stripe with paler bands above and below. Red band in second dorsal fin oblique, occupying middle third of anterior membranes and gradually widening to occupy basal half of posterior membranes. Area above and below this red band pale gray to gray green. Anal fin also with red band oblique, occupying middle half to two-thirds of fin anteriad and broadening slightly as it angles toward the body to occupy the basal three-fourths of the fin posteriad. Pale areas above and below red band in anal fin are gray to gray green. Red band in anal fin often absent or developed only on posterior part of fin in sub-nuptial males. Caudal fin with red base, color becoming more extensive in highest males where the entire fin may be red. Pectoral fin membranes mostly immaculate, but often stippled with dark pigment on distal part of ventral membranes; all pectoral fin rays uniformly stippled with dark chromatophores. Pelvic fin with dark gray rays and membranes, occasionally with greenish or bluish cast. Body with series of about 8 dark midlateral blotches which become increasingly confluent anteriad; anterior half of lateral-line canal pale, separating confluent dark blotches into dorsal and ventral parts. Lateral stripe centered on lateral line on caudal peduncle, with blotches extending 0.5–1.5 scale rows above and below lateral line; on anterior part of body dark pigment extends 0.5–1 scale row above lateral line and 1.5 scale rows below lateral line, 2–4 scale rows below in areas where blotches are deepest. Lower side orange from base of pectoral fin to caudal base. Upper side yellowish brown anteriad, becoming increasingly orange posteriad. Dorsal midline with 8 or 9 irregular, often confluent, dark saddles that extend down the side only about 2 scale rows. Head with lateral stripe more or less continuous across dorsal margin of opercle and cheek. Preorbital dark bar continuous around snout, but poorly defined on tip of snout. Suborbital dark bar with concave posterior and convex anterior borders, extending to ventral margin of cheek. Breast and lower side of head gray to gray green. In preservative much of this pattern remains, with the red band in the dorsal fin evident as concentrations of brown chromatophores.

Females are much less colorful. Spinous dorsal fin with red ocellus margined with black in first interradial membrane. More posterior membranes with submarginal band of red spots often incomplete and best developed posteriad. Second dorsal fin with alternating brown and pale areas on rays, and a band of small red spots often present and forming a submedian red band that extends from the posterior membranes anteriad but is typically absent from the anterior two to four membranes. Anal and pelvic fins immaculate or virtually so. Pectoral fin with brown pigment separated by pale areas on distal parts of middle rays, forming about 3 vague vertical brown bands. Caudal fin with membranes immaculate; alternating brown and pale areas on rays form about 5 irregular vertical brown bands. Body with dark midlateral stripe broader and more confluent than in males, extending from 1 scale row above to 2 scale rows below lateral line on caudal peduncle, broadening to cover 4 or 5 scale rows below and 1 scale row above lateral line anteriad. Anterior half of lateral line unpigmented. Ventral margin of lateral stripe irregular, often with isolated brown spots below band and at anal fin base. Lower and upper side pale brownish yellow. Dorsal saddles as described for males. Head with dark pigment as in males, but cheek and opercle typically with brown pigment extending ventrad to cover or nearly cover dorsal halves of these areas. Little of this color pattern is lost in preservative, with red pigment areas in dorsal fin visible as a dark-margined yellowish spot in the anterior interradial membrane and as blotches of brown chromatophores in more posterior membranes.

Sexual dimorphism (Table 5) is apparent in maximum body size and lengths of all fins, with males having the higher values in all cases.

VARIATION.—Counts of lateral-line scales differ considerably between specimens from the Obion and the Forked Deer river systems (Table 3), with Obion specimens averaging about three more scales. Slight differences in mean fin-ray counts between Obion and Forked Deer specimens are apparent (Table 4), with Obion specimens having fewer dorsal spines and more anal and principal caudal rays. Differences in other meristic characters and pigment patterns between specimens from the two river systems are not apparent.

HABITAT, DISTRIBUTION, AND STATUS.—*Etheostoma pyrrhogaster* is restricted to the Obion and Forked Deer river systems of western Tennessee and a small area of southwestern Kentucky (Fig. 2). Streams and rivers in these systems are typical of Coastal Plain habitats, which most often have substrates consisting of silt, sand, and fine gravel, and lacking rocks, boulders, and extensive areas of swift current. The firebelly darter is most common in swifter currents with fine gravel substrate, but it also occurs in pools adjacent to such habitats. Specimens have also been taken in the shelter and swifter current provided downstream from buried snags and beaver dams. Associated benthic fishes in the current-swept, fine-gravel habitats include *Phenacobius mirabilis, Noturus hildebrandi lautus, Etheostoma* (*Boleosoma*) sp. cf. *nigrum,* and *E. lynceum. Percina sciera* and *Etheostoma swaini* are frequent associates in flowing pools and in areas below snags and beaver dams. Extensive rechanneling has occurred in both river systems, and has certainly had an adverse impact on this geographically restricted darter. Although in no immediate danger of extinction, it is recognized as a species of special concern in Tennessee (Starnes and Etnier, 1980), and will probably be added to Kentucky's list of jeopardized fishes. Additional habitat degradation in these river systems could quickly deplete this darter to the point where it would warrant consideration for Threatened status by the U.S. Department of Interior Office of Endangered Species. Current status of the firebelly darter is being periodically monitored by Jim Deck and Andy Sliger, University of Tennessee at Martin.

BIOLOGY.—The biology of this Coastal Plain *Ulocentra* is unreported although we learn that it is under study. Related species of more upland

TABLE 5

MEASUREMENTS IN THOUSANDTHS OF STANDARD LENGTH FOR *Etheostoma pyrrhogaster** AND *E. zonistium†*

	E. pyrrhogaster				*E. zonistium*			
	Males		Females		Males		Females	
	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range
Standard length (mm)	47.4	41.2-56.6	42.3	39.4-44.4	47.4	36.4-56.0	42.8	37.0-55.0
Head length	244	229-254	242	248-269	246	237-263	241	229-254
Body depth at dorsal origin	228	218-246	215	189-225	215	192-231	215	200-233
Snout length	69	64-73	63	58-69	68	61-74	69	63-78
Orbit length	70	64-78	73	66-78	69	61-74	73	68-78
Spinous dorsal fin length	303	274-317	278	243-299	306	286-320	292	273-304
Longest dorsal spine	152	143-162	126	118-142	146	137-161	136	115-150
Soft dorsal fin length	296	279-320	276	264-288	276	255-300	258	249-277
Longest dorsal soft ray	166	157-179	157	149-165	156	145-168	146	131-159
Caudal peduncle length	281	269-306	286	275-301	296	277-315	295	278-305
Caudal peduncle depth	106	99-112	99	93-104	105	95-112	99	95-104
Anal fin length	278	262-288	258	245-279	245	231-253	236	224-249
First anal spine length	89	66-103	83	77-92	86	71-98	90	76-102
Longest anal soft ray	159	147-169	154	143-168	149	140-158	148	143-154
Caudal fin length	240	226-257	223	215-232	207	190-223	191	147-216
Pectoral fin length	276	262-296	265	252-277	240	231-261	236	213-251
Pelvic fin length	236	212-255	224	208-234	219	209-233	214	196-224
Trans-pelvic width	78	74-81	72	66-77	78	67-84	77	70-83
Maximum body width	146	123-155	146	136-156	135	114-157	140	130-149
Interorbital width	50	44-57	51	47-54	43	39-47	46	41-49

*Ten paratopotype males, ten paratopotype females.

†Males from UT 91.2592(3), UAIC 7741.01(2), TU 139773(1), INHS 68218(3), UF 42061(1); females from UT 91.2280(5), UAIC 7741.01(2), TU 139773(3).

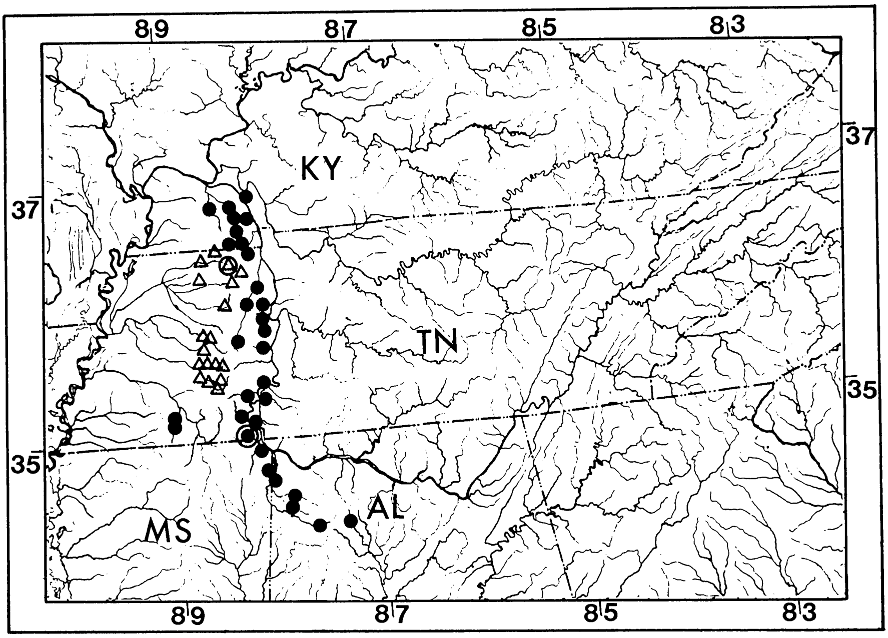

FIG. 2. Distribution of *Etheostoma pyrrhogaster* (open triangles) and *E. zonistium* (solid circles). Type localities are enclosed in open circles.

areas spawn in early spring, with females depositing eggs singly on the sides of large boulders or rock walls (Winn, 1958:202–203; O'Neil, 1981; Page and Mayden, 1981; Stiles *et al.*, 1987). It is likely that submerged logs and snags are utilized as spawning substrates in the absence of boulders. A large collection from Terrapin Creek, Henry County, Tennessee, 24 June, included no young-of-year; fish slightly older than one year (assuming an April or May spawning period) averaged about 35 mm SL and dominated the collection, and three specimens 40–43 mm SL may represent a second age group. An 18 September collection from the same locality contained young-of-year that averaged about 20 mm SL. Specimens larger than 50 mm SL are probably three or four years old.

ETYMOLOGY.—The name *pyrrhogaster,* a substantive, is from the Greek *pyrrho* = flame colored, red, or yellowish red, and *gaster* = belly or stomach, in reference to the bright reddish-orange undersurface, lower side, and anal fin, especially in nuptial males. We recommend the vernacular firebelly darter.

Etheostoma ***zonistium,*** new species
Bandfin Darter
Plate 1

Etheostoma (*Ulocentra*) sp.—Bouchard, 1974 (taxonomic status and distribution); Dycus and Howell, 1974:23–24, 27–28 (Black Warrior River system records, Alabama, attributed to stream capture from Tennessee River drainage); Clay, 1975:324–325 (Clarks River, Kentucky); Jenkins, 1976 (undescribed species, distribution).

Etheostoma sp.—Burr, 1980:78 (lowland snubnose darter, Kentucky distribution); Kuehne and Barbour, 1983:96–97, pl. 12 ("redbelly snubnose darter," characterized, range map); Burr and Warren, 1986:328 (bandfin darter, Kentucky distribution); Starnes and Etnier, 1986:346 (lowland snubnose darter, table of Tennessee and Cumberland river drainage fishes).

Etheostoma rufescens.—Gill, 1982:14 (color pl., *nomen nudum*).

Lowland snubnose darter.—Page, 1983: pl. 15A, 15B (color illus.).

HOLOTYPE.—Adult male, UMMZ 213926, 55.5 mm SL, Leath Creek, tributary to Chambers Creek, at unnumbered county road crossing 3.2 km NW Counce, Hardin Co., Tenn., 27 Oct. 1973, B. F. Clark, G. A. Schuster, E. M. Scott.

PARATOPOTYPES.—Collected with the holotype are UMMZ 213927(16).

OTHER PARATYPES.—**Tennessee River drainage, Kentucky:** UMMZ 213928(78), Jonathan Creek at mouth of Wolf Branch, U.S. Hwy. 68, Marshall Co.; UMMZ 168362(2), East Fork Clarks River, 2.4 km E Hardin, Ky. Hwy. 80, Marshall Co.; UMMZ 168342(1), Middle Fork Clarks River, 3.2 km S Murray, U.S Hwy. 641, Calloway Co.; UT 91.2592(18), Middle Fork Clarks River at Martin Chapel Road, 4.5 km SSW Murray, Calloway Co. **Tennessee River drainage, Tennessee:** UMMZ 132334(1), Sulphur Creek, Hardin Co.; UMMZ 168463(106), UMMZ 177665(78), and UT 91.5(20), Lick Creek at Tenn. Hwy. 142, Hardin Co.; USNM 270858(10), Miles Creek at Tenn. Hwy. 69, Hardin Co.; UT 91.835(36), Robinson Creek at Tenn. Hwy. 57, Hardin Co.; UT 91.1160(5), Owl Creek at Tenn. Hwy. 142, Hardin Co.; INHS 68218(6), North Fork of Beason Creek at co. rd. 8088, Hardin Co.; UF 42061(4), Gattis Creek at Tenn. Hwy. 22, Hardin Co.; UAIC 7741.01(8) and TU 139773(7), Walker Branch, tributary to Mud Creek at road 5.0 km SSW Savannah, Hardin Co.; CU 70727(4), Barbwood Branch, tributary to Hatley Creek, at Tenn. Hwy. 128, Hardin Co.; UT 91.2711(3), Clear Creek at co. rd. 8122, McNairy Co.; UT 91.1059(60), Stewman Creek at co. rd. 8197, Decatur Co.; UT 91.1171(3), Horney Head Creek at road 7.4 km N Parsons, Decatur Co.; UMMZ 168510(1), Turnbo Creek at Tenn. Hwy. 69, Decatur Co.; UT 91.722(4), Big Sandy River at I-40, Henderson Co.; UT 91.2322(8), Scarce Creek at co. rd. 8134, Henderson Co.; UT 91.1166(1), Allen Creek drainage canal at co. rd. 8024, Carroll Co.; UMMZ 113981(1), Cypress Creek, Camden, Benton Co.; UMMZ 168443(88), ANSP 153834(15), AMNH 55780(14), LACM 43798–1(14), and NLU 56291(14), Sycamore Creek 0.8 km E Holladay at Tenn. Hwy. 69, Benton Co.; AUM 25551(6), Burnside Creek at co. rd. 8043, Camden, Benton Co.; OSM 60340(11) and OS 11035(11), Wolf Creek at Tenn. Hwy. 69, Benton Co.; UT 91.2280(50) and UT 91.2386(4), Birdsong Creek at Tenn. Hwy. 69, Benton Co.; UT 91.2712(4), Turkey Creek at Tenn. Hwy. 69A, Benton Co.; CAS 56328(4), Rushing Creek drainage canal at Tenn. Hwy. 69A, 9.5 km N Camden, Benton Co.; OSUS 11992(5) and UOMZ 43326(5), Blood River at co. rd. 8160, Henry Co.; KU 21183(12) and SIUC 11397(11), West Sandy Creek at co. rd. 8024, Henry Co.; UT 91.1143(4), Barnes Fork drainage canal at co. rd. 8024, Henry Co. **Tennessee River drainage, Alabama:** UMMZ 132403(4), Bear Creek, Colbert Co. **Tennessee River drainage, Mississippi:** UMMZ 105664–5(11), and UMMZ 132388(1), Little Bear Creek, Tishomingo Co.; UMMZ 105663(6), Indian Creek, Tishomingo Co. **Mississippi River drainage, Hatchie River system, Hardeman Co., Tennessee:** UT 91.524(2), Spring Creek at co. rd. 8158; UT 91.525(23), UT 91.2713(1), UT 91.851(15), UT 91.1356(26), UT 91.2284(40), and UT 91.2385(32), West Fork Spring Creek at co. rd. 8252; UT 91.909(1), Marshall Creek at co. rd. 8252. **Mobile Bay drainage, Black Warrior River system, Alabama:** UT 91.2053(10), Hubbard Creek at Bankhead National Forest rd. 210, Lawrence Co., T8S, R9W, S32; UT 91.2198(15) and ROM 45706(8), stream at Ala. Hwy. 60 (= Winston co. rd. 23, = Bankhead National Forest rd. 210) 3.8 km SW Bankhead National Forest rd. 203, Winston Co.; UAIC 4113.03(58) and UMMZ 212379(59), Basin Creek at Camp Maxwell, Lawrence Co., T8S, R9W, S31.

DIAGNOSIS.—A member of the subgenus *Ulocentra* as diagnosed by Bouchard (1977). Differing from *Etheostoma baileyi, E. barrenense, E. rafinesquei, E. s. simoterum,* and *E. s. atripinne* in having vomerine teeth and in consistently lacking a premaxillary frenum. Differs from *E. etnieri* in consistently lacking a frenum (narrow frenum variably present or absent in *etnieri*), in having modally 10 rather than 11 dorsal spines, and in many aspects of pigmentation. Among remaining *Ulocentra* (*E. coosae, E. duryi, E. pyrrhogaster,* the "saffron darter" of the Tennessee and Cumberland river drainages, and several undescribed species from the lower Mississippi River and Gulf Coast drainages), all of which consistently (variable in one undescribed species from upper Mobile Basin) lack a frenum and often (*E. duryi,* "saffron darter") or consistently have vomerine teeth, it is most similar to *E. coosae.* The pigmentation of the spinous dorsal fin of adult males of these two species differs from all other *Ulocentra* in having six distinct, alternating pigmented and clear, horizontal bands. The bandfin darter differs markedly from *E. coosae* in having 5 rather than 6 branchiostegal rays, in having lateral blotches ovoid and confined to the lateral-line area (vertically produced to form lateral bars in *E. coosae*), and in having the lower side and venter orange to yellow below lateral stripe in adult male.

DESCRIPTION.—*Etheostoma zonistium* is a moderate-sized member of the subgenus *Ulocentra,* with both males and females reaching a maximum of 57 mm SL (71 mm TL). Sexual dimorphism is apparent in the development of the urogenital tube in females as small as 25 mm SL, but the distinctive banding of the spinous dorsal fin of males is not apparent at sizes below 30 mm SL.

Frequency distributions of scale and fin ray counts appear in Tables 3 and 4. Lateral line complete with 40–52 scales. Transverse scales 10–13. Scales around caudal peduncle (14)15–18(19). Dorsal fin with (9)10–11(12) spines and 10–12 soft rays. Anal fin with 2 spines (single anal spine in 1 of 231 specimens counted) and 6–8 soft rays. Pectoral fin with 13–15 rays. Principal caudal fin rays 15–17(18). Vertebrae 37(21), 38(91), or 39(15). Branchiostegal rays 5–5 (5–6 or 6–5 in 3 of 276 specimens counted). Branchiostegal membranes broadly connected. Cephalic sensory canals complete with 8(1), 9(52), or 10(1) preoperculomandibular pores and 7(4), 8(46), or 9(4) infraorbital pores. Lateral canal with 5 pores, supratemporal canal complete with 3 pores, supraorbital canal with 4 pores, coronal pore single. Gill rakers 7(14), 8(28), 9(21), or 10(1), with length of longest gill rakers 1–1.5 times their basal width. Belly, opercle, cheek, nape, and prepectoral area covered with exposed scales (in Mobile Basin populations the cheek and prepectoral scales are typically embedded). Breast typically with anterior half naked and posterior half with embedded to weakly exposed scales.

Nuptial males (Plate 1) with three conspicuous, narrow, dark, horizontal bands separated by two clear bands in spinous dorsal fin. All of these bands, and the basal clear band, are subequal in width. Outer dark band marginal and black to pale blue. Clear band below marginal dark band slightly wider. Dark band below distal clear band with dark brown to black pigment nearly or completely obscuring red pigment except in the first interradial membrane where a bright red ocellus contains few if any dark chromatophores. The red ocellus extends ventrad to contact the submedian dark band, virtually obliterating the clear median band in the first membrane. Submedian dark band below median clear band often narrowing posteriad. Pale basal band variously stippled or blotched with melanophores, typically with dark blotches at base of fin forming a weak seventh band. Soft dorsal fin with distal third black to pale blue. Below this is a clear band about half the width of the marginal band. An oblique median red band occupies the posterior two-thirds of the fin, angling to the posterior base; the anterior third of this band is dark gray. The anterior base of this fin is also dark gray, typically separated from the median band by a narrow clear band. Anal fin with broad blue-green margin (often with narrow white margin posteriad) and gray base. Red pigment in anal fin variable, forming anterior and/or posterior basal blotches or a basal band. Pectoral fin with clear membranes, rays uniformly stippled with melanophores. Pelvic fins gray. Caudal fin with orange of posterior lower side and brick red of band above lateral line extending onto basal third; remainder of fin with clear membranes and darkly pigmented rays, dark pigment on rays punctuated with about three irregular vertical rows of yellow spots. Body with 9 dark lateral blotches extending 1–2 scale rows above and below lateral line posteriad, and 1 scale row above and 1.5–2 scale rows below lateral line anteriad. Lateral line unpigmented from head posteriad to under end of soft dorsal fin. Above lateral-line canal is a dark brown (anteriad) to brick red (posteriad) horizontal stripe .5 scale row wide anteriad, gradually widening to 1.5 scale rows wide on caudal peduncle. Upper side above this stripe yellowish, occasionally with darker ventral extensions of dorsal saddles. Dorsal saddles 8, typically extending to either side of the midline about 2.5 scale rows anteriad and 1.5 scale rows posteriad, but occasionally even more confined to the dorsal midline. Lower side and venter orange, grading to yellow immediately below lateral stripe. Yellow area widest anteriad, obliterated by orange on caudal peduncle. Breast blue gray. Lateral stripe continues on head as a dark mark across upper margin of operculum and cheek, and as a preorbital dark bar that fades anterior to the nostrils. Suborbital bar usually prominent and vertical, but occasionally indistinct. Lips, gular area, branchiostegal membranes, and lower side of head with scattered melanophores. In preservative the dark bands in the spinous dorsal fin remain distinct and the ocellus in the first interradial membrane persists as a cream-colored spot. The narrow dark stripe above the lateral-line canal remains conspicuous and less darkly pigmented than the lateral dark markings below the lateral line. Areas of red pigment in the soft dorsal and anal fins are apparent as concentrations of brown chromatophores on the membranes of these fins.

Life colors of females are much more subdued. Spinous dorsal fin lacks a marginal dark band or this band weakly developed posteriad. Two median dark bands usually present, with distal band darker and often extending posteriad from a red to orange ocellus in first interradial membrane. Submedian dark band often wanting. Soft dorsal fin with alternating clusters of dark pigment along rays to weakly banded; red may appear in middle parts of posterior membranes. Anal and pelvic fins typically immaculate. Pectoral fins as in male but usually lacking pigment on lower one to three rays. Caudal fin with pigment on rays interrupted by clear areas to form about four irregular vertical dark bands. Lateral blotches 8, more distinct and extensive than in males, extending about 4 scales below (anteriad) to 2 scales below (posteriad) lateral line. Dark stripe above lateral line scarcely developed. Upper and lower side with yellow background color. Upper side with dark brown pigment variously extending between lower margins of saddles or from lower margins of saddles to lateral stripe. Head as in males, but gular area, branchiostegal membranes, and lips immaculate to very weakly pigmented. In preservative, red pigment in first interradial membrane of spinous dorsal fin often represented by an immaculate, cream-colored area, especially on larger females. Females have smaller median fins than males, but other measurements (Table 5) show little if any sexual dimorphism.

VARIATION.—Specimens from the Black Warrior River system have more lateral-line scales (Table 3), and more deeply embedded breast, prepectoral, and cheek scales, but otherwise conform to Hatchie and Tennessee river specimens in pigmentation, meristics, and other morphological characters.

HABITAT, DISTRIBUTION, AND STATUS.—The bandfin darter (Fig. 2) is a common species in a wide variety of small stream habitats. Western tributaries to the lower Tennessee River are mostly Coastal Plain streams with low gradients and fine gravel to sandy substrates. In parts of Benton and Decatur counties, Tennessee, the Western Highland Rim extends to the west side of the Tennessee River, and in these Highland Rim streams the bandfin darter is replaced by another *Ulocentra, E. duryi.* This remarkable fidelity to Coastal Plain habitats is evident in Hardin County, Tennessee, where the Coastal Plain extends east of the Tennessee River in a small area just north of Pickwick Dam. The streams draining this area, Mud and Hatley creeks, contain *E. zonistium,* several other Coastal Plain fishes (*Notropis chrysocephalus isolepis, Etheostoma parvipinne, E. proeliare*) and no other *Ulocentra.* Elsewhere, bandfin darters occur east of the lower Tennessee River in Pony Creek, tributary to Hardin Creek, Hardin Co., Tenn., and (Burr and Warren, 1986) in the Land Between the Lakes area of southwestern Kentucky. *Etheostoma zonistium* and two additional *Ulocentra* (*E. duryi* and *E. simoterum*) occur in the Bear Creek system of the Tennessee River drainage in Alabama and Mississippi. This system, while mostly Coastal Plain, has parts of its headwaters on Cumberland Plateau and Highland Rim strata. *Etheostoma duryi* and *E. simoterum* were found sympatric at several stations during a survey of this system by B. R. Wall, Jr. (pers. comm.), and they are broadly sympatric elsewhere in the Tennessee River drainage. *Etheostoma zonistium* did not co-occur with either of these species (Wall's Masters thesis mentions both *zonistium* and *duryi* as occurring at his station 13, but under species taken at that station he cites *duryi* and *simoterum*). *Etheostoma zonistium* was virtually restricted to Coastal Plain areas in the northwestern part of the Bear Creek system (Pennywinkle and Little Cripple Deer creeks, Tishomingo County, Mississippi) and in the upper Bear Creek proper where the latter enters the Coastal Plain in the extreme southern part of the system (near shared boundaries of Lawrence, Marion, and Winston counties, Alabama). The bandfin darter's Coastal Plain distribution may be related to competitive interactions with *E. duryi* and/or *E. simoterum,* since it occurs in upland habitats (Cumberland Plateau) in the upper Mobile Basin (Black Warrior River system) where it inhabits clear, cool streams with abundant areas of boulder and bedrock substrates. It is allopatric to an undescribed *Ulocentra* that occurs farther downstream in the Black Warrior system (Dycus and Howell, 1974), and it seems likely that it entered the upper Black Warrior system by headwater piracy from upper Bear Creek of the Tennessee drainage as they suggested. In the well surveyed Hatchie River system *E. zonistium* is known only from the Spring Creek watershed, where habitats are cool, spring-fed streams with silt and fine sand substrates in areas of swampland forest. Spring Creek is remote from the Tennessee drainage, and its *E. zonistium* population may be a relict associated with late Tertiary drainage adjustments ultimately uniting the westward flowing middle Tennessee River with the northward flowing lower river (Starnes and Etnier, 1986:331).

Biology.—Bandfin darters typically reach sexual maturity at one year of age, at lengths of about 25–35 mm SL. Based upon gonadal condition of females, peak reproductive activity apparently occurs in April and May as is typical for the subgenus *Ulocentra.* Three size groups occur in several large collections examined, suggesting a three-year life span. Rubble and boulders are not available for spawning substrates throughout most of the bandfin darter's range. In the absence of these substrates (used for spawning by species of *Ulocentra* whose life history has been studied), it is likely that eggs are deposited on surfaces of submerged logs and snags. Growths of rooted aquatic vegetation do not typify their habitat, making it unlikely that eggs are attached to plant stems.

Etymology.—The name *zonistium,* a substantive, from the Greek *zona* = band and *histium* = fin or sail, in reference to the distinctive and diagnostic banding in the spinous dorsal fin, was originally coined by Carl L. Hubbs who long ago was the first to recognize this distinctive species. The recommended vernacular name is bandfin darter.

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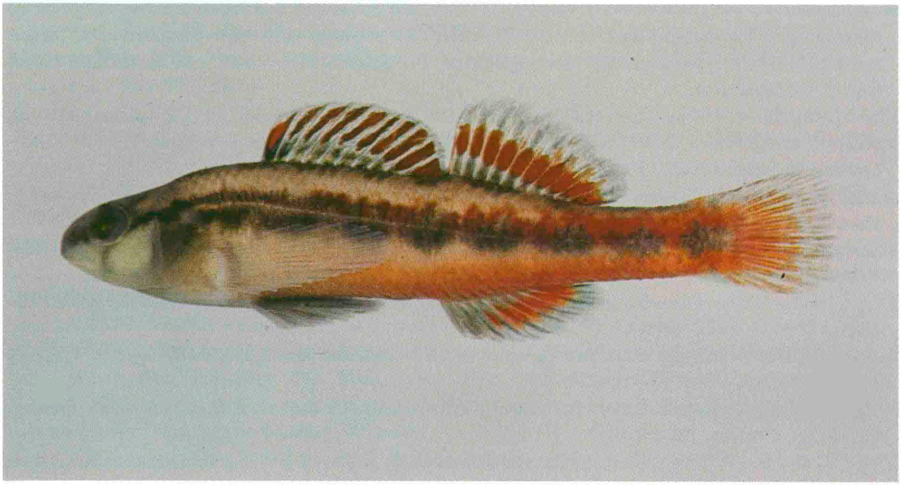
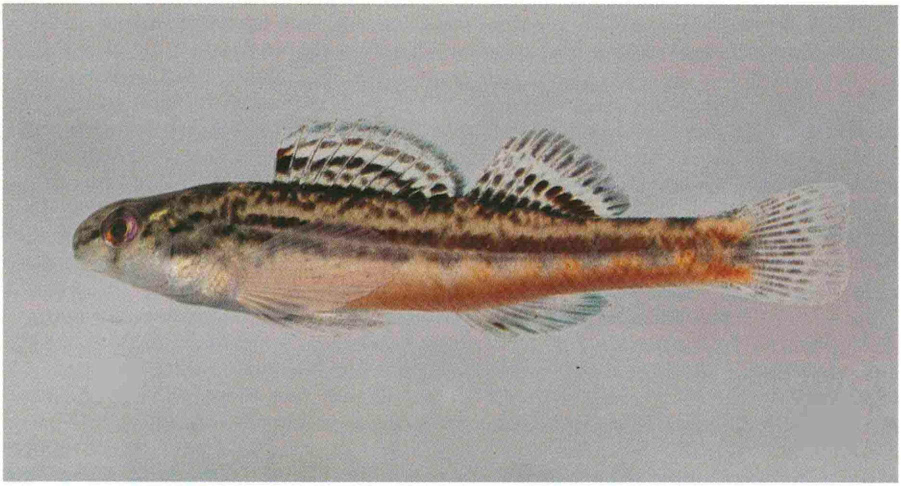
PLATE 1



Etheostoma pyrrhogaster, adult male, 45.5 mm SL. Sweetlips Creek, Forked Deer River system, Chester Co., TN, 1 March 1974.



Etheostoma zonistium, adult male, 47 mm SL. Clear Creek, tributary to Snake Creek, Hardin Co., TN, 1 March 1974.