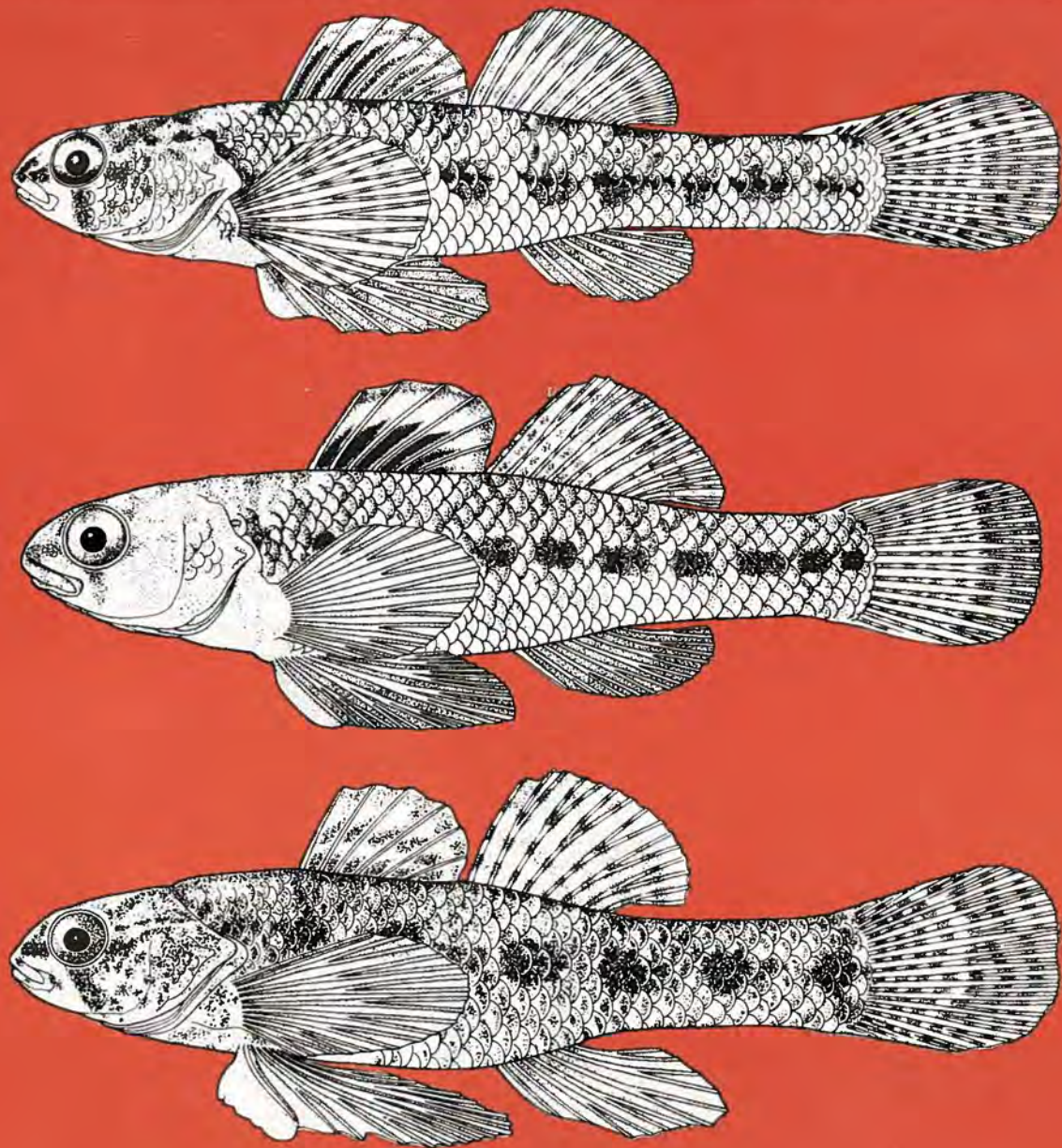


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Brooks M. Burr

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Systematics of the Percid Fishes of the Subgenus *Microperca*, Genus *Etheostoma*

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ABSTRACT: Burr, Brooks M., Systematics of the Percid Fishes of the Subgenus *Microperca*, Genus *Etheostoma*. Bulletin Alabama Museum of Natural History, Number 4, 53 pages, 19 figures, 11 tables, 1978. The objectives of this study are threefold: first, to describe the intraspecific variation of morphological characteristics in populations of the subgenus *Microperca*; second to map and discuss the distributions of the species; and third, to clarify both the intra- and interspecific relationships of the subgenus. More than 25 meristic characters were examined on approximately 1200 specimens of *E. proeliare* (Hay); 200 specimens of *E. fonticola* (Jordan and Gilbert); and 2000 specimens of *E. microperca* Jordan and Gilbert. Sixteen proportional measurements were taken from 40 to 70 specimens of each species. Spot distribution maps, and a figure of both sexes of each species are included. Information from life history studies (to be published separately) is included in the taxonomic analyses. The subgenus is diagnosed and its subgeneric status discussed. *Microperca* displays an array of derived morphological and life history characteristics that establish it as the most specialized group of darters. The three species in the subgenus inhabit heavily vegetated standing water bodies on the Coastal Plain, in the Mississippi Valley and/or the Great Lakes drainages where they are distributed mostly allopatrically.

E. proeliare is distinguished from the other two species by higher meristic values for several characters, different color pattern, more complete squamation, and a greater maximum standard length. Variation in the species is minor although notable geographic trends in squamation, maximum size, and some meristic characters were found. *E. proeliare* inhabits Coastal Plain streams and lakes from western Florida north to Illinois and southwest to the San Jacinto River, Texas.

E. fonticola, a nationally recognized endangered species, is presently restricted to the luxuriantly vegetated springs at San Marcos, Texas. It formerly occurred in Comal Spring at New Braunfels, Texas, but has recently been extirpated. This species is distinguished from the other two species by differences in color, squamation, body proportions, maximum standard length, and some meristic features. Specimens available from both populations are about 90 percent separable in number of pectoral rays and second dorsal fin pigmentation.

The most variable species, *E. microperca*, is distinguished from the other two species by numerous features, chief of which are cephalic lateral line characters, brighter colors, many meristic features and shape of the female genital papilla. The species is widespread in the upper Mississippi River valley and Great Lakes drainages and has disjunct populations in the Ozarks of Missouri, Kansas, Arkansas, and Oklahoma. It occurs syntopically with *E. proeliare* in one stream in Oklahoma. Throughout the Great Lakes populations the configuration of the infra-orbital canal is variable, but makes some geographic sense. Ozark populations of the species are the only North American percids known with tubercles developed on their dorsal fins. However, Ozark populations are in various stages of differentiation and no new taxa are recognized.

The subgenus *Microperca* is considered to be most closely related to the subgenus *Hololepis* based on similarities in morphology and life history. Within the subgenus *Microperca* there are two groups: one containing *E. proeliare* and *E. fonticola* and the other containing *E. microperca*. The former group shares a more completely developed lateralis system, bilobed genital papillae in females, tubercles well developed on anal and pelvic fins of breeding males, and similar fin pigmentation patterns. *E. microperca* has an extremely reduced lateralis system, conical female genital papilla, tubercle distribution usually reduced on anal fin of breeding males, and bright orange or red male pelvic and anal fin color.

E. proeliare and *E. fonticola* are the most primitive species in the subgenus since they have retained the greater number of ancestral character states. *E. microperca* is the most specialized member of the subgenus and probably the most specialized North American percid.

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Introduction

The subgenus *Microperca* consists of three darters in the genus *Etheostoma*, tribe Etheostomatini, family Percidae, and order Perciformes. They are the smallest darters and, as a group, among the smallest freshwater fishes in North America. Phylogenetically they are nearest the species in the subgenus *Hololepis*, from which they differ in a number of morphological features. *Microperca* is considered to be the most derived component in the evolution of *Etheostoma*, and the group displays a number of highly specialized characteristics.

The species of *Microperca* are primarily sluggish-stream inhabitants, often associated with cool waters and aquatic vegetation, although they are also found in lakes and springs of moderately high temperatures. Two of the species are primarily spring spawners, and all three have one-year to 18-month life cycles. Some populations of two of the species probably spawn almost the year around in the constant-temperature springs that they inhabit. The adult size is usually between 25 and 35 mm standard length.

The three species in the subgenus are *E. proeliare*, *E. fonticola* and *E. microperca*. In general they are distributed allopatrically from Ontario, Michigan, Minnesota, and Wisconsin south through the Great Lakes and Mississippi Valley to the panhandle of Florida and the Guadalupe River of Texas. However, sympatry occurs between two species in the Arkansas and Red rivers of Oklahoma.

Morphological information on the species of *Microperca* has been limited to surveys of a few characters such as vertebral counts (Bailey and Gosline, 1955); branchial apparatus (Branson and Ulrikson, 1967); breeding tubercles (Collette, 1965); and the lateralis system (Page, 1977). The distributional and interspecific relationships of the species have not been carefully studied.

The objectives of this study are: first, to describe the variation and distribution of morphological characteristics in populations of *Microperca*; second, to map and discuss the distributions of the species; and third, to clarify the relationships of these darters within the subgenus and to the other closely related subgenera of *Etheostoma*.

Acknowledgments

This study was completed under the direction of Philip W. Smith. In addition to numerous favors, Dr. Smith provided access to his library, encouragement, constructive criticism, and counsel on numerous matters. I am equally indebted to Lawrence M. Page who was always willing to discuss various problems with me, freely gave of his knowledge on darters, and greatly stimulated my interest. This paper is extracted from a dissertation submitted to the University of Illinois in partial fulfillment of the requirements for the PhD degree.

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I am grateful to the following curators, staff, or students and their institutions (abbreviations used throughout the text) for granting specimen loans, information concerning types, laboratory space and numerous other courtesies: Albert P. Blair (APB), University of Tulsa; Anthony A. Echelle, Baylor University (BU); Eugene C. Beckham, formerly at Cornell University (CU); Branley A. Branson, Eastern Kentucky University (EKU); Robert K. Johnson and Garrett S. Glodek, Field Museum of Natural History (FMNH); Ralph W. Yerger, Florida State University (FSU); Henry W. Robison (HWR), Southern Arkansas University; Lawrence M. Page and Philip W. Smith, Illinois Natural History Survey (INHS); Frank B. Cross, University of Kansas (KU); Robert Schoknecht, formerly at Museum of Comparative Zoology (MCZ); Max A. Nickerson, Milwaukee Public Museum (MPM); Glenn H. Clemmer, Mississippi State University (MSU); William M. Palmer, North Carolina State Museum (NCSM); Neil H. Douglas and John A. Harris, Northeast Louisiana University (NLU); Rudolph J. Miller, Oklahoma State University (OAM); Ted M. Cavender and Milton B. Trautman, Ohio State Museum (OSM); Loren G. Hill and William J. Matthews, University of Oklahoma (OUMZ); E. J. Crossman and formerly W. B. Scott, Royal Ontario Museum (ROM); Tomio Iwamoto, California Academy of Sciences including former Stanford University collection (SU); John D. McEachran, Texas A & M University (TCWC); Thomas M. Buchanan (TMB), Westark Community College; Robert F. Martin and Clark Hubbs, University of Texas Natural History Collection (TNHC); Royal D. Suttkus and Eugene C. Beckham, Tulane University (TU); Herbert T. Boschung, University of Alabama Ichthyological Collection (UAIC); Carter R. Gilbert, Florida State Museum (UF); William D. Pearson, University of Louisville (UL); James C. Underhill, University of Minnesota (UM); Reeve M. Bailey and Robert R. Miller, University of Michigan Museum of Zoology (UMMZ); Bruce B. Collette and Victor G. Springer, National Museum of Natural History (USNM); David A. Etnier, University of Tennessee (UT); Albert P. Blair and Hague Lindsay, University of Tulsa (UTULSAC); George C. Becker, University of Wisconsin at Stevens Point (UWSP); and Wayne C. Starnes (WCS), University of Tennessee.

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Methods and Materials

The general systematic methodology used in this study is similar to that of Smith (1966) as summarized in his revision of the sucker subgenus *Pantosteus*. Briefly, the traditional systematic procedure has consisted of measuring characteristics of samples of populations and interpreting the characters and/or character complexes in terms of biological units or phyletic lines. In Smith's study and the present one, the presumed biological units, based on morphology and life history data, were not always satisfactorily expressible in terms of the taxonomic units of species or subspecies, as they are presently defined. When geographic variation was somewhat extreme for certain populations, it seemed more judicious to think in terms of populations which may or may not belong to species or subspecies as rigidly defined. Unusual populations are therefore referred to in the text in terms of their geography, and names assigned subsequently.

Most characters were given equal treatment, except in a few cases where sample size varied according to the assumed importance of a character. Adults were used for the final analyses so as not to confound the data with differences due to allometry or ontogeny. When only one or two specimens were available from a highly disjunct locality (e.g. Richland Creek, Tennessee), the counts made were used for identification only and are not included in the analyses since a number of the "disjunct" populations have locality data of uncertain provenance (see Distribution sections).

All meristic characters were analyzed initially for sexual or geographic variation by minor drainage. When no significant sexual, intra- or interdrainage variation was apparent, the data were pooled into major drainages for presentation in the tables, figures, and text. The limits of sample pooling were decided after consideration of both geography and character uniformity. Drainages are arranged from east to west in *E. proeliare*; and from southwest to northeast in *E. microperca*. For certain comparisons, groups of population samples were lumped under one name. For example, the name "Ozark" or "Ozarkian" refers to all the population samples of *E. microperca* located in Arkansas, Missouri, and Oklahoma; the name "northern" refers to all the other populations of *E. microperca*.

U. S. Postal Service abbreviations are used for state names in the graphic presentations and tables. In addition

to standard compass directions, other abbreviations used are as follows: trib.=tributary; and uncat.=uncataloged.

Counts and measurements follow the procedures outlined by Hubbs and Lagler (1964), except for certain modifications which are indicated in the Analysis of Characters section. Statistical calculations of the mean (\bar{x}), standard deviation (SD), coefficient of variation (CV) and 95 percent confidence intervals were conducted according to standard procedures. Graphic presentations follow the revised method of Hubbs and Hubbs (1953), except that the standard error of the mean was converted to 95 percent confidence intervals (*vide* Smith, 1966).

To obtain as clear an interpretation as possible of the systematic position and intrasubgeneric relationships of *Microperca*, life history studies of *E. microperca* and *E. proeliare* were conducted at study sites in Illinois. Supplemented with life history information on *E. fonticola* presented by Schenck and Whiteside (1976; 1977 a, b) a substantial amount of ecological data is now available for *Microperca* and is used in the taxonomic analyses. The life history studies will be published separately.

The institutions from which material was examined are noted in the Acknowledgments section. Specimens studied are listed at the end of the account of each form treated. Collections are listed by drainage, state, county, and museum number. The number of specimens counted, measured, or used for other descriptive purposes are in parentheses. Only material actually studied is included. The many hundreds of specimens merely identified for use as distributional data are not included. Complete locality data are given only for important distributional records. More specific locality data for all specimens used in the study may be obtained from the author upon request.

Analysis of Characters

LATERAL LINE SYSTEM.—All populations of the subgenus *Microperca* have an extremely reduced lateral line on the body, the most reduced of all darters. There appears to be an orderly sequence to the reduction with *E. proeliare* having, on the average, the most pored scales; *E. microperca* usually with no or one pored scales; and *E. fonticola* intermediate between the two. Frequently adults of all three species may lack a lateral line on the body and none ever has more than nine pored scales.

Variation in the number of pored lateral line scales is also the result of sex. Both *E. proeliare* and *E. fonticola* have some populations that exhibit significant differences between sexes in the degree of development of pored lateral line scales. However, the usual lack of lateral line pores in *E. microperca* precluded any meaningful analysis in sexual differences for this character. Sexual dimorphism in the number of pored lateral line scales has been shown for some members of *Hololepis* (Collette, 1962) and *E. (Catonotus) kennicotti* (Page

and Smith, 1976). The biological or functional significance of these differences is enigmatic.

In examination of the cephalic lateral line, the terminology, abbreviations, and counting procedures of Hubbs and Cannon (1935), Collette (1962), and Page (1977) are followed with a few modifications. In pore count formulas, interruptions along the length of a canal are indicated by a (+) sign. Cephalic pores are easily discerned and counted in *Microperca*, the pores being extremely large in comparison with those on other darters.

The cephalic lateral line system of darters has recently been reviewed by Page (1977). The species of *Microperca* are the most extreme among darters in the number of cephalic lateral line reductions and are rivaled only by members of *Hololepis* and *Catonotus* in this respect. The reductions are presumably caused by incomplete or arrested development since many of the reductions observed are the last to develop in ontogeny. Features of the cephalic lateral line are among the most diagnostic characters for *Microperca* and other subgenera (e.g. *Hololepis*—Collette, 1962; *Catonotus*—Page and Braasch, 1976) and they are helpful in elucidating inter- and intrasubgeneric relationships and presumed evolutionary trends among the more advanced darter subgenera.

The supraorbital (SO) canal is complete with four pores in all three species of *Microperca* (Fig. 1) which is unlike four of the six members of *Hololepis*, which often have the interorbital pores missing (Collette, 1962). The lateral canal is complete with five pores and is only occasionally interrupted in certain populations of *E. microperca*. The coronal pore (CP) is a common pore connecting the two SO canals by two short SO commissures. The CP is usually present in *E. proeliare* and *E. fonticola* and there is always a median, posteriorly-projecting tube leading to the CP (Fig. 1). In *E. microperca* the CP may be present or absent. Many specimens have an intermediate condition in which the CP is interrupted leaving the two SO commissures unjoined in what may be termed two CP's as Ramsey and Suttkus (1965) have shown for *E. (Oligocephalus) ditrema*. There is never a median, posteriorly-projecting tube leading to the CP in *E. microperca* (Fig. 1). *E. microperca* exhibits geographic variation in CP development.

The supratemporal (ST) canal of all three species is usually broadly interrupted at the dorsal midline with a normal count of 2+2 (Fig. 1). Incomplete development of the ST canal rarely leaves secondary interruptions to one side or the other. The ST canal may rarely be complete with three pores in *E. proeliare* and *E. fonticola*.

The infraorbital (IO) canal is interrupted in all three species. *E. proeliare* and *E. fonticola* have three pores developed anteriorly and one pore with a tube developed posteriorly (Fig. 1). *E. microperca* has three pores developed anteriorly but the posterior tube and pore are wholly absent (Fig. 1). The count is therefore given as 0+3 to differentiate it from the count of 1+3 in the other two species. Geographic variation is exhibited by

E. microperca in the northeastern part of its range where the anterior segment of the IO canal is further reduced to two pores; the count is signified as 0+2.

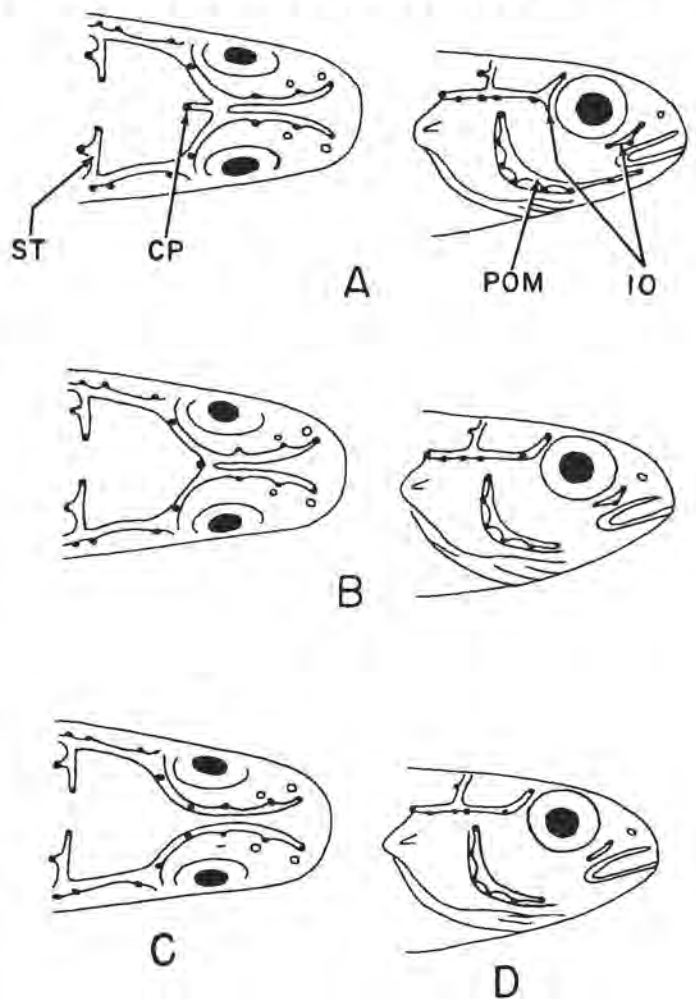


Fig. 1. Cephalic lateral line system in members of the subgenus *Microperca*. A, Canal and pore development typical of *E. proeliare* and *E. fonticola*. B, Canal and pore development typical of *E. microperca*. C, Absence of coronal pore typical of Ozark populations of *E. microperca*. D, Infraorbital canal condition typical of northeastern populations of *E. microperca*. ST=supratemporal canal; CP=coronal pore; POM=preoperculo-mandibular canal; and IO=infraorbital canal.

The preoperculo-mandibular (POM) canal is reduced to eight pores in *E. proeliare* and *E. fonticola* with only minor deviations in number either way (Fig. 1). *E. microperca* has a usual POM count of six pores, occasionally seven. All other darters have nine or more POM pores with only rare occurrences of eight.

Both the subgenera *Hololepis* (Collette, 1962) and *Catonotus* (Page and Braasch, 1976; 1977) exhibit extreme reductions in the lateral line system. Reductions in the lateral line system appear to follow phylogenetic lines in *Hololepis* and *Microperca* and may also be directly correlated with ecological parameters and behavior. The two groups are found in low gradient streams, lakes or springs where

vegetation is often abundant. In similarities between *Microperca* and *Catonotus*, reductions in the lateralis system apparently represent evolutionary convergence since there are ecological parameters that are commonly shared (e.g. low gradient streams) between the two groups. The reduction or obsolescence in sensory canals and pores on both the body and head in *Microperca* may not be critically needed in the reduction or absence of predation, which may be the case for some populations of all three species.

FIN RAY AND SPINE COUNTS.—The pelvic fins show no deviation from the count of one spine and five rays. The branched caudal fin rays rarely deviate from the usual count of nine to 11. The number of pectoral fin rays, counted only on the left side, show consistent patterns of geographic variation for *E. fonticola* and *E. microperca* but are of limited use in distinguishing between species. The group as a whole usually has nine or 10 pectoral rays. The total number of elements in the dorsal fins shows notable geographic patterns in *E. microperca*, and the count is valuable in separating the three species. The number of anal spines is consistently one in *E. fonticola* but is variable in the other two species. *E. proeliare* displays some unusual trends for this character with certain populations consistently having one or two anal spines. A similar variation in number of anal spines has also been shown for *E. (Hololepis) collis* (Collette, 1962). The total number of anal fin elements is similar in number for all three species with certain populations of *E. microperca* having the highest counts in the subgenus ($\bar{x}=8.05$).

SCALE COUNTS.—Scales in a lateral series were counted from the edge of the occiput beginning with the first scale where the lateral canal ends and continued along an imaginary line to the end of the hypural plate. The presence of one or a few pored scales indicates the scale row to follow. Transverse scale rows were counted in two ways: from the origin of the anal fin to the first dorsal fin; and from the origin of the anal fin to the second dorsal fin (Raney and Suttkus, 1964). The lack of a lateral line extending very far posteriad eliminated the often useful counts of scales above and below the lateral line.

The number of lateral scales is useful in separating *E. proeliare* from the other two species, but the character is subject to considerable variation in *E. fonticola* and *E. microperca* which modally have the same count. Both transverse scale row counts are virtually the same for all three species. Notable geographic trends do occur in *E. microperca* for transverse scale counts made to the first dorsal fin. The number of caudal peduncle scale rows was of little systematic value, and seemed to vary either discordantly or not at all. The character is modally different between the two populations of *E. fonticola*.

SQUAMATION.—*Microperca* has the most reduced squamation of any of the darter subgenera. The nape, cheek, breast, and anterior belly are usually naked. The opercle

is usually scaled to varying degrees in all three species. In *E. proeliare* the cheek and prepectoral area are almost always scaled, and the nape is partially to fully scaled in some large adult specimens from Lake Pontchartrain.

The areas covered by scales were estimated to the nearest 10 percent, similar to the methods described by Lagler and Bailey (1947). Scales were often embedded on the opercles of *E. fonticola* and *E. microperca* and were thus difficult to discern unless loosened with a needle. Definitions for the nape, breast, cheek, and opercle regions were made by Collette (1962). The prepectoral region is the triangular area just anterior to the pectoral fin base. Ontogenetically, the breast, belly, nape, and head are the last regions to develop scales. *E. proeliare* thus represents the primitive condition in the subgenus. The subgenera *Hololepis* and *Catonotus* both have species groups with the squamation reduced in all or several of the areas mentioned above (Collette, 1962; Page and Smith, 1976; Page and Braasch, 1976; 1977). With respect to *Catonotus* the similarity is probably due to convergence.

VERTEBRAE.—Vertebral numbers were determined from radiographs. The total count includes the urostylar vertebra. Radiographs were taken from disjunct populations of *E. microperca*, the two populations of *E. fonticola*, or those populations of all three species deemed unusual for other reasons. Counts from Bailey and Gosline (1955) are included in the totals for all three species. Variation was exhibited in the two populations of *E. fonticola* and certain Ozark populations of *E. microperca*. Among percids, *Microperca* have the fewest number of vertebrae (*E. fonticola* occasionally has only 31 vertebrae).

BRANCHIOSTEGAL RAYS.—Branchiostegal ray counts were made on both sides of the gill membrane and are expressed in the text in the following fashion: 5:5 or 6:6, indicating the count for both sides. Darters as a whole have been considered to exhibit the characteristic branchiostegal ray count of 6:6 with rare deviations of 5:5 or 7:7 (except in a few species). The other tribe in the subfamily Percinae characteristically has 7:7 or 8:8 branchiostegals (Collette, 1962; Scott and Crossman, 1973). Perusal of the literature indicates a rather cursory treatment of this character. A few exceptions are the studies of Bailey (1941), Collette (1962), and Tsai and Raney (1974) in which some quantitative data for the frequency of the counts was presented. *E. microperca* usually has 5:5 branchiostegals. The only other darters with a modal branchiostegal count of 5:5 are *E. (Etheostoma) zonale* (Tsai and Raney, 1974) and several members of the subgenus *Ulocentra* (Bouchard, 1977), a number of which are formally undescribed. The other two species of *Microperca* have a modal count of 6:6 with populations of *E. proeliare* exhibiting unusually high frequencies for the counts of 6:7 or 7:7.

GILL RAKERS.—The number of gill rakers was counted on the first arch; all rudiments were counted. The character was only cursorily examined, but it appears that

Microperca usually have five moderately long to short gill rakers on the first arch. Gill raker counts have been repeatedly used as systematic characters of high value in many groups of fishes. The character has been poorly investigated for darters, although the study by Branson and Ulrikson (1967) introduced reduction trends among some darter groups. For the 19 species they studied, *E. microperca* had the fewest gill filaments.

CONDITION OF PREOPERCLE.—The preopercle is smooth in all species of *Microperca* except in one population of *E. proeliare* wherein the preopercle was serrate. The condition of the preopercle is variable in some species of *Hololepis* (Collette, 1962) but was of little systematic value in *Microperca*. The significance of this isolated case is unknown since the character was not present in juveniles and was not sexually or seasonally variable.

TUBERCULATION.—Collette (1965) reviewed the systematic significance of breeding tubercles in the family Per-

cidae. In recent years the importance of tuberculation as a systematic character has been greatly appreciated for many groups of fishes (Wiley and Collette, 1970). As pointed out by Snelson (1972) the utility of tuberculation characters are limited by their ephemeral nature, developmental variation, and similarity to other sensory structures. Nonetheless, tuberculation has proved to be of significant value in determining species recognition and relationships.

The hundreds of collections made since Collette's study have enabled a more comprehensive treatment of tuberculation in *Microperca* to be made. Males of all three species have tubercles present on the anal and pelvic fins. *E. proeliare* and *E. fonticola* have similar tubercle distributions (Fig. 2), with tubercles present on the anal fin spines and rays. Most populations of *E. microperca* are divergent in only having tubercles present on the anal spines (Fig. 2).

As indicated above, geographic variation in tuberculation does exist. Ozark populations of *E. microperca* have tubercles developed on the anal rays as well as the spines, and tubercles were also found to be present on the anterior elements of both dorsal fins. The latter distribution is not known for any other North American percid (Collette, 1965).

The spawning behavior of all three species is similar (Strawn, 1955; Winn, 1958a; Burr and Page, 1978), and the tubercles probably function in stimulation of the female as well as maintaining close body contact to insure fertilization. The function of dorsal fin tubercles in *E. microperca* is a puzzle unless they are demonstrative of a different reproductive behavior characteristic of southwestern populations.

BREEDING COLORATION AND PIGMENTATION.—Color and most aspects of pigmentation are developed best in breeding males. In *Microperca*, males of each species have different degrees and configurations of red-orange color in their first dorsal fins. *E. proeliare* and *E. fonticola* males have melanistic pelvic and anal fins. *E. microperca* has intensely colored red-orange pelvic and anal fins, which are partly melanistic in Ozark populations. Coloration and pigmentation are very useful in separating the species and in determining intrasubgeneric relationships. The number of dorsal saddles (usually poorly developed) and lateral blotches were of little systematic value. An exception is the lateral pigment in *E. fonticola*, which is formed into stitchlike dashes rather than larger round or squarish blotches as in *E. proeliare* and *E. microperca*.

MEASUREMENTS.—Measurements were taken with dial calipers to the nearest 0.1 mm. Most of the measurements followed Hubbs and Lagler (1964) except that postdorsal length was taken from the insertion of the second dorsal fin (D_2 fin) to the caudal base. D_2 fin length was the greatest transverse distance from the D_2 fin insertion to the longest fin ray. The first dorsal fin is hereafter referred to as D_1 fin. Body proportions varied little over the range of a species, although some measurements in

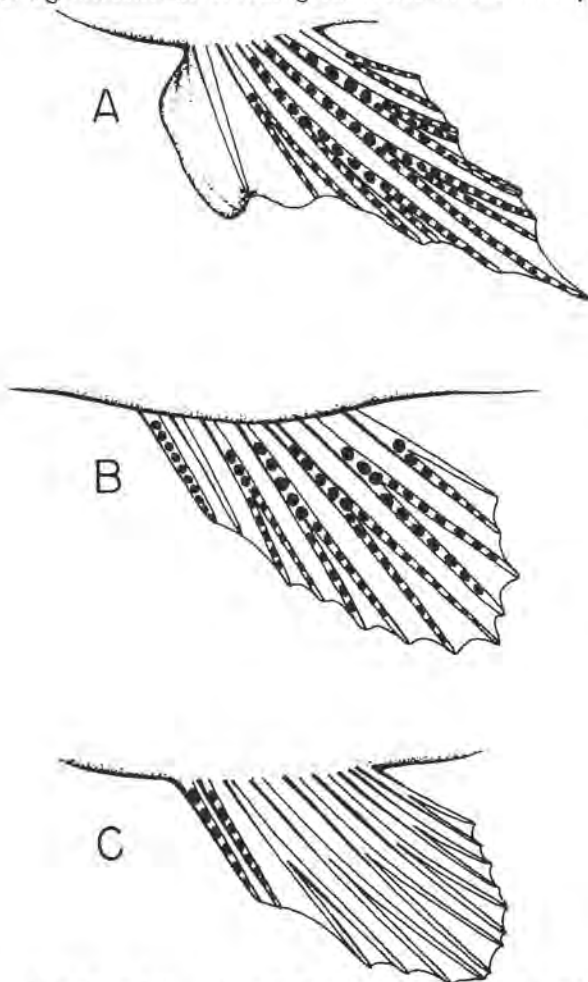


Fig. 2. Male pelvic and anal fins of members of the subgenus *Microperca* illustrating maximum tubercle development. A, Pelvic fin flaps characteristic of all three species during breeding periods. Pelvic fin tuberculation is similar for all three species. B, Anal fin of *E. proeliare* showing maximum tubercle development. The pattern is also characteristic of *E. fonticola*. C, Anal fin of *E. microperca* showing maximum tubercle development for northern populations and often for Ozark populations.

E. proeliare may average somewhat larger from the more southern parts of its range (e.g. Lake Pontchartrain drainages).

The use of morphometric data in *Microperca* is complicated by several factors: most conspicuous are allometric, sexual, and seasonal components. Allometric variation was not investigated. The effect of seasonal variation was minimized by measuring only breeding specimens. Measurements were made on both sexes, and the data were tabulated separately in order to eliminate sexual variation and demonstrate sexual dimorphism.

MAXIMUM SIZE.—The standard length (SL) was taken for all specimens examined to the nearest 0.1 mm. In addition all specimens were sexed in order to show significant differences in sizes between the sexes as well as between species. Statistical significance of sizes was determined by the Kolmogorov-Smirnov two-sample test (Siegel, 1956). *Microperca* contains the smallest darters: *E. microperca* and *E. fonticola* reach a maximum SL of about 36 or 37 mm, *E. proeliare* is somewhat larger and probably reaches at most 40 mm SL. Significant geographic variation in size was noted for *E. proeliare* and *E. microperca*; populations from more southern latitudes attaining the largest maximum size.

Other darters in the genus *Etheostoma* showing extreme reduction in size are *E. (Nothonotus) tippecanoe* with a maximum SL of 35 mm (Zorach, 1969); *E. (Holepis) zoniferum* with a maximum SL of 36.6 mm (Collette, 1962); and *E. (Oligocephalus) nuchale* with a maximum SL of 39.8 mm (Howell and Caldwell, 1965). This reduction in size contrasts to the largest darter known, *Percina (Hadropterus) lenticula* with a maximum SL of 168 mm (Douglas, 1968). Evolutionary trends toward reduction in size cross several phyletic lines, and several major groups have one or two species with a small maximum size.

Sexual differences in size have been investigated for relatively few species of darters. Females attaining a larger size than males has been interpreted as a generalized or primitive character in darters (Winn, 1958a). In both *E. proeliare* and *E. microperca*, females are larger than males but probably only because they live longer (Burr and Page, 1978); the growth curves of both sexes are not significantly different. In *E. fonticola*, males are larger than females, but this may only be an artifact due to biased samples. The validity of Winn's interpretation of sexual differences in size is questionable, since in the majority of what have been considered to be the more primitive darters males are larger than females.

SEXUAL DIMORPHISM.—Sexual variation has been poorly investigated in most darter groups, although recent papers by Page and Smith (1976); Page and Braasch (1976; 1977); and Denoncourt (1976) have clearly demonstrated a number of characteristics that are significantly variable as a result of sexual differences. The species of *Microperca* exhibit pronounced sexual dimorphism; insufficient data for many darters prevent meaningful com-

parisons. As is typical for many darters of the genus *Etheostoma*, the more striking differences involve coloration. The breeding colors of female *Microperca* are more subdued than males and perhaps could even be considered nonexistent. Tubercles are always absent in females. Melanism is also sexually dimorphic. Only breeding males develop pigmented or melanistic dorsal, pelvic, and anal fins whereas these fins in females are usually devoid of definite pigmentation patterns or melanism. Sexual dimorphism in the number of pored lateral line scales has already been noted.

Large numbers of both male and female specimens were examined from all months of the year for the physiognomy of their genital papillae. Males of all three species are similar in having a small, slightly swollen anal area with a partially pigmented, slender tube posterior to the anus present during the breeding season, which is much less evident at other times of the year.

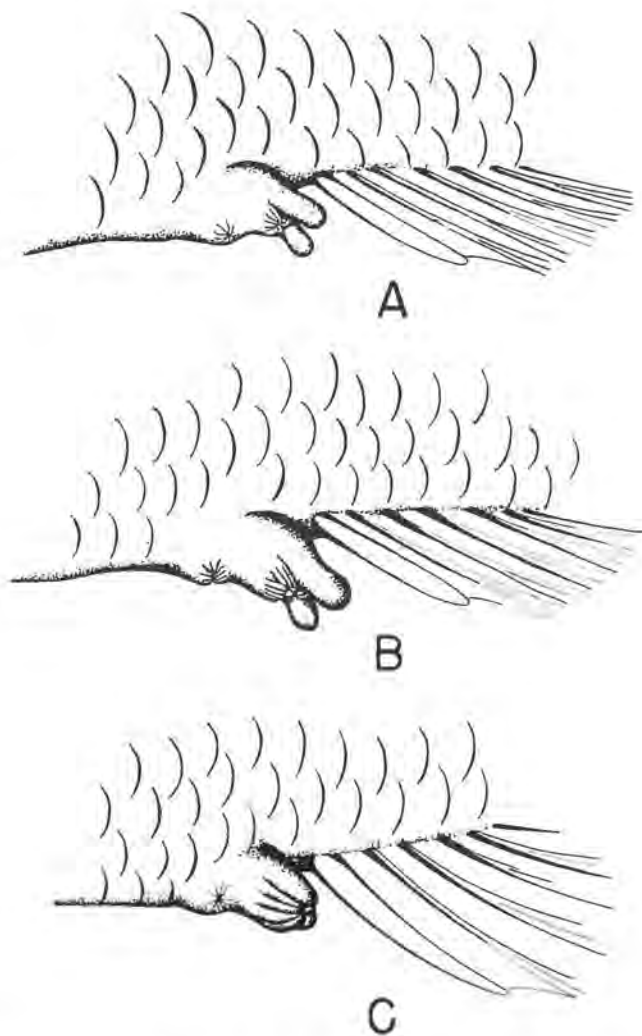


Fig. 3. Genital papillae of female members of the subgenus *Microperca*. A, Bilobed papilla of *E. proeliare* (INHS 75701). B, Bilobed papilla of *E. fonticola* (INHS 75668). C, Conical papilla of *E. microperca* (INHS 75817).

Among females of the three species, the shape and structure of the papillae is of systematic significance. *E. proeliare* and *E. fonticola* both have a strongly forked, bilobed papilla, which becomes swollen and bulbous during the breeding season (Fig. 3). In contrast, *E. microperca* has a swollen conical papilla (Fig. 3). The female papillae of all three species are evident during non-breeding periods and facilitate external sexing throughout all months of the year. Collette (1962) discussed and illustrated the "bilobed" genital papilla of *E. (Hololepis) serriferum*. The female papilla of *E. serriferum* is not as bilobed or bulbous as in the two species of *Microperca* (see Collette, 1962; fig. 1e).

Hubbs and Cannon (1935) first recognized the utility of genital papillae as a systematic character. Although a number of systematic studies on darters have appeared since that time, the character has not been adequately studied for many species. From the genital papillae that have been figured or described, there are none similar to *E. proeliare* and *E. fonticola*.

All three species are sexually dimorphic for a number of body proportions. Only breeding adults were measured for the analyses. Means for each measurement were compared statistically with Student's *t*-test. Levels of probability (*P*) greater than 0.1 were considered not significant (*ns*). In *E. microperca* as many as 14 out of 16 body proportions had a significantly greater value in males; in *E. proeliare* 11 of 16; and in *E. fonticola* only seven of 16. In general, males of all three species have deeper caudal peduncles and longer D_1 , anal, and pelvic fins. D_2 fin length divided by postdorsal length has been shown to average significantly greater in males of the subgenus *Catonotus* (Page and Braasch, 1976; 1977; Page and Smith, 1976) but was not significantly greater for males in any of the species of *Microperca*. Lachner et al. (1950) showed that in three species of the subgenus *Etheostoma*, males usually have longer pelvic, anal, and dorsal fins. Sexual dimorphism in maximum size was discussed earlier. Nothing has been published on significant differences in body proportions within the subgenus *Hololepis*. The highly evolved barcheck members of the subgenus *Catonotus* are sexually dimorphic usually for only two or at most three body proportions (Page and Braasch, 1976; 1977).

The significance, if any, of sexual dimorphism in certain body proportions (e.g. head length, fleshy interorbital width) is poorly understood. One proportion always well developed is the length and shape of the pelvic fins (larger in males). *Microperca* is unique in having exceptionally long pelvic fins, the longest in relation to body size of any darter. It is further unique in the development of expanded cuplike webs of skin on the pelvic fins of males (Fig. 2) that facilitate better contact with the female during spawning (Petravicz, 1936; Winn, 1958a; Burr and Page, 1978). The larger anal fin of males is also of functional significance since it is in contact with the caudal peduncle region of the female during the spawn-

ing act. It also helps maintain close contact with the female presumably to insure maximum fertilization of the eggs.

Subgeneric Status

Bailey in Bailey et al. (1954) reduced the number of recognized darter genera to three: *Percina*, *Ammocrypta*, and *Etheostoma*. Many of the former genera were downgraded to subgeneric rank and Bailey's nomenclature has been followed by most modern workers. This action was executed primarily on the basis that the characters used to delimit the genera were highly variable, overlapping, or the product of convergent evolution (Bailey et al., 1954). A detailed rationale for this action has never been published. Moreover, the criteria employed to define and delimit the taxon "subgenus" have never been critically evaluated.

Systematic treatments of the genera *Percina* (Page, 1974a) and *Ammocrypta* (Williams, 1975) have recently appeared. However, no one has yet attempted a critical analysis of the largest genus *Etheostoma*, which contains about 106 species in 16 subgenera. Linear phylogenies for *Etheostoma* (*s.l.*) have been arranged by Bailey and Gosline (1955), Collette (1965), and Page (1977) based on vertebral counts, breeding tubercles, and the lateralis system, respectively. The three treatments are similar in their placement or ranking of most of the primitive and advanced subgenera but are in disagreement with the several intermediate groups.

Evolutionary trends within the tribe Etheostomatini have been established and are presented in Table 1. Some are original, others are taken from Hubbs and Cannon (1935), Bailey and Gosline (1955) and Winn (1958a). The presumed "primitive" characteristic of females attaining a larger maximum size than males is of dubious validity and is not included. Of the 16 subgenera of *Etheostoma*, at least three are considered to be highly specialized based on their morphological attributes and life history characteristics. These are *Catonotus*, *Hololepis*, and *Microperca*. Of all the subgenera, *Microperca* has been considered to display the largest number of derived characters and thus has been allocated to the most advanced position among the darters (Bailey and Gosline, 1955; Collette, 1965; Page, 1977). Evidence from this study supports that conclusion.

The specialized features exhibited by some members of the subgenus *Catonotus* are similar to those of *Microperca* but are not indicative of close relationship and are evidently the product of convergent evolution. Thus the relationship between the two is not intimate and will not be considered further. The subgenus *Hololepis* has been considered to be most closely allied to the subgenus *Microperca* (Hubbs and Cannon, 1935; Bailey and Gosline, 1955; Collette, 1962, 1965; Page, 1977).

Collette (1962) stated that *Hololepis* could be distinguished from *Microperca* by "a more complete lateral line; more lateral line scales; the presence of a premaxil-

lary frenum; and the absence of the peculiar flap on the pelvic fins of breeding male *Microperca*." Actually, *Microperca* has a well-developed premaxillary frenum. In addition to the above features *Microperca* can be further distinguished from *Hololepis* by the following combination of characters: red-orange breeding colors in D₁ fin of males; melanistic or red-orange pelvic and anal fins of breeding males; \bar{x} pelvic fin length/SL > .250 mm; naked nape; interorbital pores present; unique physiognomy of female papillae; smaller maximum body size; and mature ova shape.

The close relationship between members of the subgenera *Microperca* and *Hololepis* is demonstrated largely by the reduction trends in a number of morphological features that the two groups share as well as similar life history characteristics. These are primarily the following: reduced squamation, reduced lateralis system, reduced meristics, similar body shape, similar habitat, and similar reproductive behavior. Insufficient data on the life histories of most of the species of *Hololepis* preclude any meaningful comparisons between the two groups in this respect.

The two most advanced species of *Hololepis*, *E. saludae* and *E. collis*, appear to be somewhat intermediate between *Hololepis* and *Microperca* in several meristic features but share more characters with *Hololepis* than with *Microperca*. Moreover, they do not exhibit any of the unique features of *Microperca* such as their lack of bright fin colors, small pelvic fins without the lateral flaps, structurally different female genital papillae, larger maximum size, and round, symmetrical mature ova. There is no natural hybridization between the two subgenera and the present ranges of *E. saludae* and *E. collis* on the central Atlantic Coast (Collette, 1962; fig. 3) are far removed from the present distributions of any *Microperca* and would thus present complex zoogeographic problems.

The species that make up what is presently called *Microperca* clearly form a natural group, which are separated by a decided gap (Mayr, 1969) from *Hololepis*, but there is little doubt that the relationship between the two groups is close. Arguments could be made for lumping *Hololepis* and *Microperca* and perhaps other dubiously placed species such as *E. (Oligocephalus) exile*. The resolution of the question of subgeneric status is a difficult one, but the recognition of monophyletic, morphologically definable species groups is favored over the formal recognition of the evolutionary closeness of *Hololepis* and *Microperca*. In summation, the existing morphological data suggest that the relationship of *Hololepis* and *Microperca* can best be expressed as subgenera within *Etheostoma*.

SYSTEMATIC ACCOUNTS

Subgenus *Microperca* Putnam

Microperca Putnam, 1863:4 (original description; type-species *Microperca punctulata* Putnam [now *Etheostoma microperca* Jordan and Gilbert, in Gilbert, 1887, see below] by monotypy).

Microperca Castelnau, 1872:48 (original description; type-species *Microperca Yarrae* Castelnau [preoccupied by *Microperca* Putnam, 1863; replaced by *Percamia* Bleeker, 1876] a synonym of *Nannoperca* Gunther, 1861 [family Kuhlidae]).

NOMENCLATURE AND HISTORICAL RESUME.—When Jordan (1888) reduced the number of nominal darter genera to a single genus *Etheostoma* Rafinesque, a replacement name for *Microperca punctulata* was in order since the name then became preoccupied in *Etheostoma* by *Poecilichthys punctulatus* Agassiz (1854). Evidently Jordan and Gilbert had decided upon a substitute name at an earlier date since *Etheostoma microperca* Jordan and Gilbert first appeared in use as a footnote in Gilbert (1887) rather than in Jordan (1888) as has been frequently cited as the correct date for the substitute name (e.g. Jordan and Everman, 1896a; Jordan et al., 1930; Collette and Knapp, 1966).

Putnam (1863) originally described *Microperca* as a genus and included *Microperca punctulata* as the only species known at the time. The major features Putnam used to distinguish his new genus from other related genera were small size, compressed body, large scales, absence of lateral line, reduced dorsal fin spine count, length of pectoral and pelvic fins, and a slightly rounded caudal fin. Putnam's original description also included material from Alabama, a locality far out of the range of *Etheostoma microperca*. It is possible that the original description was based in part on the related *E. proeliare* which is common in Alabama, but the specimen(s) from Alabama have never been located.

Nominal species were added to the group by Hay (1881) and Jordan and Gilbert (1886), although in the latter work *E. fonticola* was described under the genus *Alvarius* Girard and compared with the nominal *Alvarius lateralis* Girard (1859). Jordan and Gilbert (1886) also stated that the new species was very similar to *Alvarius (Microperca) punctulatus*. Jordan later expressed in several papers the view that *Alvarius* and *Microperca* were probably identical (e.g. Jordan, 1887) and he and Evermann cautiously remarked that the three species of *Microperca* "may all be varieties of *Microperca punctulata*." (Jordan and Evermann, 1896a).

Jordan and his co-workers vacillated between calling *Microperca* a genus (Jordan and Eigenmann, 1886) and a subgenus (Gilbert, 1887). However, in Gilbert's (1887) careful redescription of *Alvarius fonticola*, the *Microperca* group was constituted in essentially modern terms, except for the erroneous inclusion of *Alvarius lateralis*. Since no one was sure of the identity of *A. lateralis* (= *Gobiomorus dormitator* Lacépède [an eleotrid]) until Bailey and Richards (1963) determined its identity, the generic position of *E. fonticola* vacillated from *Microperca* to *Alvarius* until as late as 1930 (Jordan et al., 1930). Any further instability surrounding *Microperca* was dispelled by Bailey in Bailey and Gosline (1955) with his placement of all three species within the subgenus *Microperca*.

SUBGENERIC DIAGNOSIS.—The subgenus *Microperca* is recognizable as a phylogenetic unit on the basis of a number of diagnostic characters. In general the group is characterized by small body size and the loss or reduction in number of several meristic features.

Lateral line on body greatly reduced (arching within 2 to 4 scale rows of D, fin), from 0 to 9 pored scales, usually 0 to 6; lateral body scales 30 to 38, usually 32 to 36. Lateralis system on head degenerate, POM canal with 5 to 9 pores, usually 6 to 8; IO canal always interrupted, usually with a count of 1+3 or 0+3; ST canal usually interrupted; SO canal complete, interorbital pores present. Dorsal fins small, dorsal fin spines 5 to 9, usually 6 to 8; anal fin spines 1 or 2; anal fin rays 4 to 8, usually 5 to 7; branched caudal fin rays usually 10; pectoral rays 8 to 11; usually 10. Branchiostegal membranes moderately conjoined across isthmus, branchiostegal rays usually 5:5 or 6:6. Vertebrae 31 to 37, usually 32 to 36.

Squamation reduced, scales usually absent on nape, breast, and anterior belly; scale development on cheek and opercles variable (small ctenoid scales usually present on cheek, opercles, and prepectoral areas in *E. proeliare*). Snout blunt and rounded to somewhat produced; premaxillary frenum present; mouth small, lower jaw included; preopercle smooth. Teeth in brushlike bands on upper and lower jaws; outer teeth enlarged and widely spaced, inner teeth smaller and more crowded; teeth present on prevomer and palatine, size of teeth and spacing decreases toward rear of tooth band.

Pelvic fins exceedingly long in males (\bar{x} pelvic fin length/SL > .250 mm), usually reaching to anus or past anal fin origin; pelvic fins of breeding males developing expansive, cup-like webs of skin between the pelvic spine and first two or three pelvic rays during the breeding season. Tubercles present on males only; tubercles small, round, and white; developed to varying degrees on anal fin, all rays of pelvic fins, usually concentrated most heavily on distal seven-eighths of the fin elements. Genital papillae bilobed or conical. Breeding colors red or orange in some combination; subdistal band or blotches of red-orange in D, fin of breeding males; pelvic and anal fin membranes red-orange or with heavy concentrations of melanophores; melanophores sharply outlining pectoral fin rays; females generally not developing breeding colors. Humeral spot absent. Sexual dimorphism well developed in several body proportions. Mature ova indented on one side, appearing as a half donut. Adult maximum size to 40 mm SL.

Etheostoma proeliare (Hay)

Cypress Darter

Figure 4

Microperca proeliaris Hay, 1881:496-497, 514 (original description; branch of Tusculumbia River, Corinth, Mississippi).—Hay, 1883 (Big Black River, Edwards, Mississippi [USNM 10113]; Pearl River, Jackson, Mississippi [USNM 32205]; Memphis, Tennessee [USNM 32179]).—Jordan and Gilbert, 1883 (redescription; range).—Jordan and Evermann, 1896a (in key; redescription; range).—Jordan and

Evermann, 1896b (list; range).—Hubbs and Ortenburger, 1929 (trib., Black Fork, 6 mi S Heavener, Oklahoma).—Jordan et al., 1930 (list; range).—Schrenkeisen, 1938 (characters; range).—Baker and Parker, 1938 (Reelfoot Lake; Bayou de Chien).—Baker, 1939a (in Reelfoot Lake key).—Kuhne, 1939 (Tennessee list).—Bangham and Venard, 1942 (parasites; Reelfoot Lake).—Gerking, 1945 (probable in Indiana).—Lincicome and Van Cleave, 1949 (parasites *fide* Bangham and Venard, 1942).—Moore and Rigney, 1952 (Kiamichi River, SE Clayton, Pushmataha County, Oklahoma).—Cross and Moore, 1952 (Poteau River, Oklahoma localities; abundant).
Microperca punctulata.—Putnam, 1863 (Alabama).—Jordan, 1875 (Alabama).—Jordan and Copeland, 1876 (Alabama).—Jordan, 1878a (Drury Creek, Union County, Illinois).—Forbes, 1887 (Union County, Illinois). Large, 1903 (Skillet Fork, Wayne County, Illinois; Drury Creek, Union County, Illinois).—Forbes and Richardson, 1908 (same records as Large, 1903).—Forbes, 1909 (Cairo district, Illinois).—O'Donnell, 1935 (same records as Large, 1903).—Fowler, 1945 (listed for several Gulf Coast drainages).

Alvarius fonticola.—Jordan and Gilbert, 1886 (Washita River, Arkadelphia, Arkansas).—Jordan et al., 1930 (same record as Jordan and Gilbert, 1886).

Etheostoma proeliare.—Gilbert, 1887 (comparisons).—Boulenger, 1895 (in key; partial synonymy; redescription; range).—Moore, 1952 (Oklahoma list).—Cook, 1953 (type-locality in Mississippi).—Knapp, 1953 (in Texas key; range; figure).—Bailey et al., 1954 (Escambia River, Alabama and Florida localities; common in tidal freshwater).—Hubbs, 1954 (mentioned).—Eddy, 1957 (in key; range).—Hubbs, 1957a (Austro-riparian zone, Texas).—Hubbs, 1957b (Texas list).—Moore, 1957 (in key; characters; range).—Briggs, 1958 (W Florida to Mississippi).—Hubbs, 1958a (Texas list).—Blair, 1959 (NE Oklahoma records; map).—Boudreaux et al., 1959 (mentioned).—Cook, 1959 (in Mississippi key; redescription; localities).—Hubbs, 1959 (artificial hybrid combinations with several species of darters).—Riggs and Bonn, 1959 (Limestone Creek, Oklahoma).—Bailey et al., 1960 (list).—Hubbs, 1961 (Texas list; range).—Collette, 1962 (most primitive *Microperca*).—Collette, 1963 (cleared and stained for study).—Burton and Douglas, 1965 (Bayou de Siard, Louisiana).—Norden, 1965 (Little River drainage, Louisiana).—Walker, 1965 (Bayou D'Arbonne, Louisiana).—Smith, 1965 (sporadic in S Illinois).—Pflieger, 1966 (Missouri list; key).—Douglas and Davis, 1967 (Louisiana list).—Distler, 1968 (artificial hybridization with *E. spectabile*).—Whitaker, 1968 (in key; map, in part).—Moore, 1968 (in key; characters; range).—Smith-Vaniz, 1968 (in Alabama key; range; stream capture; figure).—Eddy, 1969 (in key; range).—Bailey et al., 1970 (list).—Pflieger, 1971 (Missouri distribution; habitat; zoogeography).—Hubbs, 1972 (Texas list; range).—Jenkins et al., 1972 (lower Tennessee River; probable in lower Cumberland River).—Schwartz, 1972 (list of artificial hybrid combinations).—Buchanan, 1973a (in Arkansas key; distribution).—Buchanan, 1973b (Arkansas list).—Miller and Robison, 1973 (in Oklahoma key; redescription; habitat).—Moore, 1973 (first recorded in Oklahoma by Hubbs and Ortenburger, 1929).—Sisk, 1973 (ponds near Hickman County, Kentucky).—Smith, 1973 (in Illinois key; range).—Cloutman and Olmstead, 1974 (Cossatot River, Arkansas).—Douglas, 1974 (in Louisiana key; figure; redescription; distribution).—Green and Beadles, 1974 (trib., Current River, Arkansas).—Pigg and Hill, 1974 (Kiamichi River, Oklahoma; uncommon).—Robison and Beadles, 1974 (Machine Creek, Smithville, Arkansas).—Robison et al., 1974 (reference to Cross and Moore, 1952).—Burr and Page, 1975 (Ohio River oxbows, Kentucky).—Pflieger, 1975 (in Missouri key; figure; characters; distribution; habitat).—Webb and Sisk, 1975 (absent from Bayou de Chien, Kentucky).—Clay, 1975 (in Kentucky key; brief description; localities; habitat).—Bounds and Beadles, 1976 (Fourche River, Arkansas).—Hubbs, 1976 (Texas list).—Yeager and Beadles, 1976 (Cane Creek, Missouri and Arkansas).

Alvarius proeliaris.—Jordan, 1887 (list; *Alvarius* and *Microperca* probably identical).

Etheostoma microperca.—Gilbert, 1889 (trib., Poteau River, 7 mi W Waldron, Scott County, Arkansas).—Meek, 1891 (Little Red River, Judsonia, Arkansas [USNM 42837]).—Meek, 1894a (Little Red River, Heber, Arkansas; Illinois River, Russellville, Arkansas

[USNM 59186]; Sallisaw River, Makeys, Arkansas; Gilbert's 1889 record).—Meek, 1894b (Arkansas localities repeated).—Meek, 1896 (Walnut Creek, Kiamichi Indian Territory, Oklahoma [SU 1250]; Poteau River, Fort Smith, Arkansas; Old River, 10 mi E Greenway, Arkansas; St. Francis River, Big Bay, Arkansas [SU 1940]; St. Francis River, Marked Tree, Arkansas).—Pigg and Hill, 1974 (Kiamichi River, Oklahoma *vide* Meek, 1896).—Geisler et al., 1975 (Illinois River, Arkansas *vide* Meek, 1894a).

Etheostoma procliaris.—Gilbert, 1891 (Little Escambia River, Pollard, Alabama).

Etheostoma fonticola.—Meek, 1894a (Washita River, Arkadelphia, Arkansas *vide* Jordan and Gilbert, 1886).

Microperca fonticola.—Jordan and Evermann, 1896a (Washita River record).—Jordan and Evermann, 1896b (Washita River record).

Microperca procliaris.—Pratt, 1923 (in key; characters; range).—Alice, 1942 (food habits in Reelfoot Lake).

Microperca procliaris.—Baker, 1939b (Reelfoot Lake).

Microperca procliaris.—Hubbs, 1951 (records from E. Texas).

Microperca microperca.—Cross and Moore, 1952 (listed from Poteau River, Arkansas *vide* Gilbert, 1889; Meek, 1891; 1894a).

Etheostoma proliare.—Jürgens and Hubbs, 1955 (Texas list).

Etheostoma (Microperca) proliare.—Bailey and Gosline, 1955 (vertebral counts).—Collette, 1965 (tubercle distribution; sexual dimorphism).—Collette and Knapp, 1966 (location of holotype).—Page and Whitt, 1973a (isozyme patterns).—Page and Whitt, 1973b (isozyme patterns).

Etheostoma proliare.—Hoffman, 1967 (parasites).

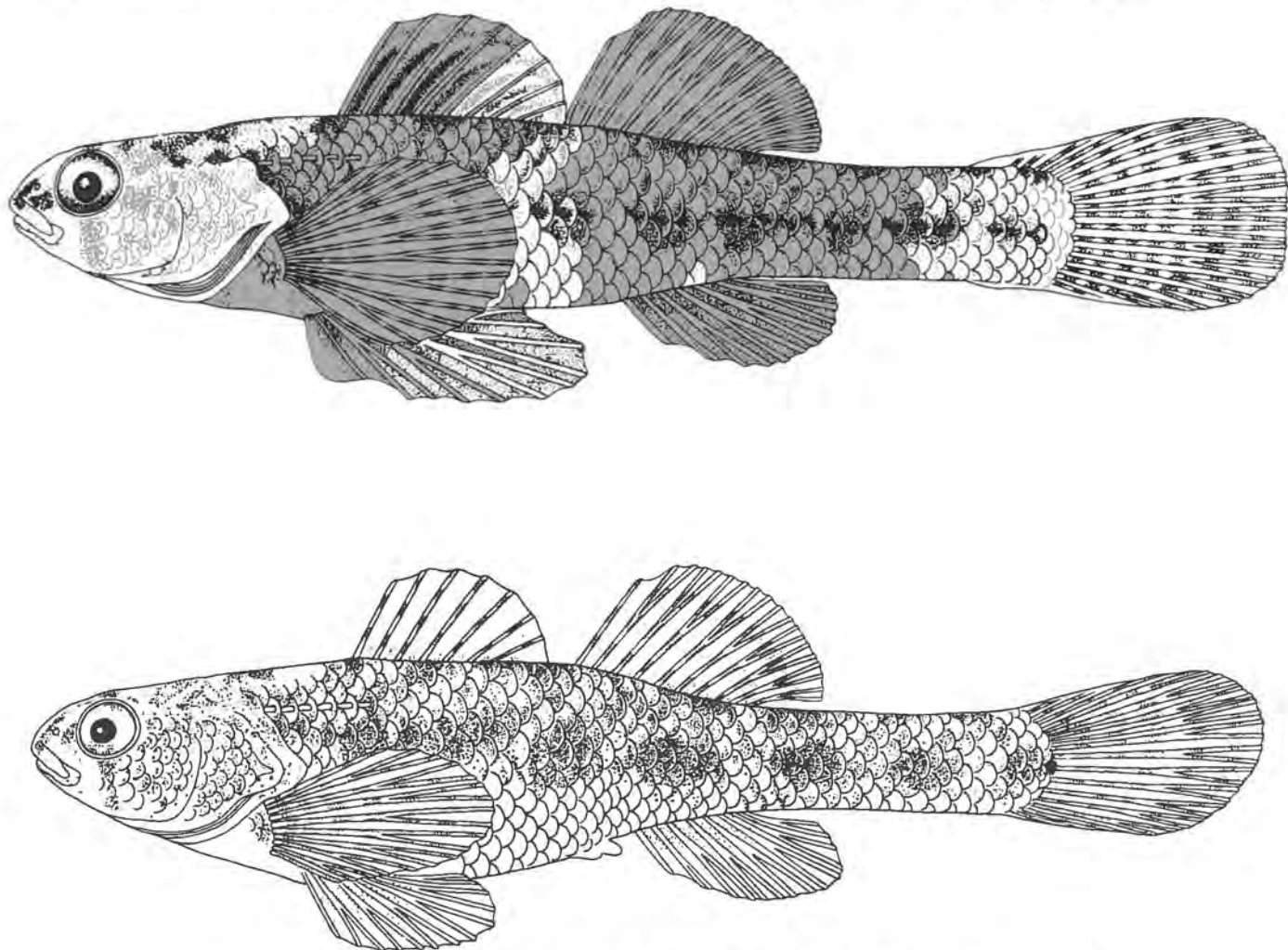


Fig. 4. Breeding adults of *E. proliare*: INHS 26925, Max Creek, Johnson County, Illinois, 10 March 1976. Top) Male, 33 mm SL. Bottom) Female, 31 mm SL. Nuptial tuberculation not shown. Drawing by Alice A. Prickett.

TYPES.—The holotype (USNM 27418) was collected March–April 1880 by O. P. Hay from a tributary of Tusculumbia River [Hatchie drainage] at Corinth [Alcorn County], Mississippi (Hay, 1881). The following counts for the holotype are taken from the original description and other counts made by Bruce B. Collette (pers. comm.): a male, 26 mm SL with 2 pored lateral line scales, 34 lateral scales (=36); dorsal fins with 8 spines

and 10 rays; anal fin with 1 spine and 6 rays; branchiostegal rays ?;6; IO pores 1+?; POM pores 8; ST canal interrupted at midline; nape and breast naked; cheeks and opercles completely scaled.

ETYMOLOGY.—The name *proliare* pertains to battle, in reference to its having been found near the Civil War battlefield of Corinth, Mississippi.

DIAGNOSIS.—A species of the subgenus *Microperca* distinguished from other members by combinations of the following characters: 1 or 2 anal spines, modally 2; usually 18 to 20 total dorsal fin elements; IO pores 1+3; POM pores 8; usually 35 or 36 lateral scales (modally 35), usually 2 to 4 pored; branchiostegal rays modally 6:6, vertebrae usually 35 or 36; cheeks, opercles and prepectoral area usually fully scaled; genital papilla of female bilobed; lateral pigment usually forming 9 or 10 blotches on sides of adults. In breeding males, median spots of red-orange color present in anterior membranes of D₁ fin; basal one-third of first two dorsal fin membranes black in D₁ fin; pelvic and anal fins melanistic; tubercles present on full length of all anal fin elements. Maximum adult size 39.6 mm SL.

DESCRIPTION.— Certain counts and measurements are presented in Tables 2-5. General body shape (Fig. 4), tuberculation patterns, features of the cephalic lateral line, and shape of the female genital papilla are illustrated in Figs. 1-4.

Scales in a lateral series (including pored scales) number 34 (64 specimens); 35 (370); 36 (321); 37 (75); and 38 (19); \bar{x} =35.55. Transverse scale rows (from anal fin origin to D fin number 8 (23 specimens); 9 (231); 10 (414); 11 (142); and 12 (9); \bar{x} =9.86. Transverse scale rows from anal fin origin to D₂ fin number 8 (16 specimens); 9 (61);

10 (66); and 11 (14); \bar{x} =9.50. Caudal peduncle scale rows number 13 (31 specimens); 14 (159); 15 (447); 16 (187); 17 (19); and 18 (3); \bar{x} =15.02.

Dorsal fin spines number 7 (202 specimens); 8 (573); and 9 (74); \bar{x} =7.85. Dorsal fin rays number 10 (239 specimens); 11 (507); 12 (98); and 13 (8); \bar{x} =10.89. Total dorsal fin elements number 17 (55 specimens); 18 (277); 19 (398); 20 (102); 21 (15); and 22 (2); \bar{x} =18.71. Branched caudal fin rays number 9 (119 specimens); 10 (246); 11 (133); and 12 (1); \bar{x} =9.98. Anal fin spines number 1 or 2 (Table 2). Anal fin rays number 4 (6 specimens); 5 (468); 6 (346); and 7 (22); \bar{x} =5.46. Total anal fin elements number 6 (33 specimens); 7 (600); 8 (214); and 9 (5); \bar{x} =7.31. Left pectoral rays number 9 (66 specimens); 10 (674); and 11 (106); \bar{x} =10.05. Pelvic fins always with 1 spine and 5 rays.

Branchiostegal rays number 5:5 (6 specimens); 5:6 (9); 6:6 (532); 6:7 (46); and 7:7 (32) (Table 3). Gill rakers on first arch moderately long and number 5 (8 specimens); 6 (3); and 7 (1); \bar{x} =5.58. Vertebrae number 34 (7 specimens); 35 (36); 36 (37); and 37 (1); \bar{x} =35.40 (Bailey and Gosline, 1955).

Lateral line on body always incomplete with 0 to 9 pored scales (Fig. 5), modally 2 to 4. Cephalic lateral line reduced, with most canals showing arrested or incomplete development. ST canal usually broadly interrupted at

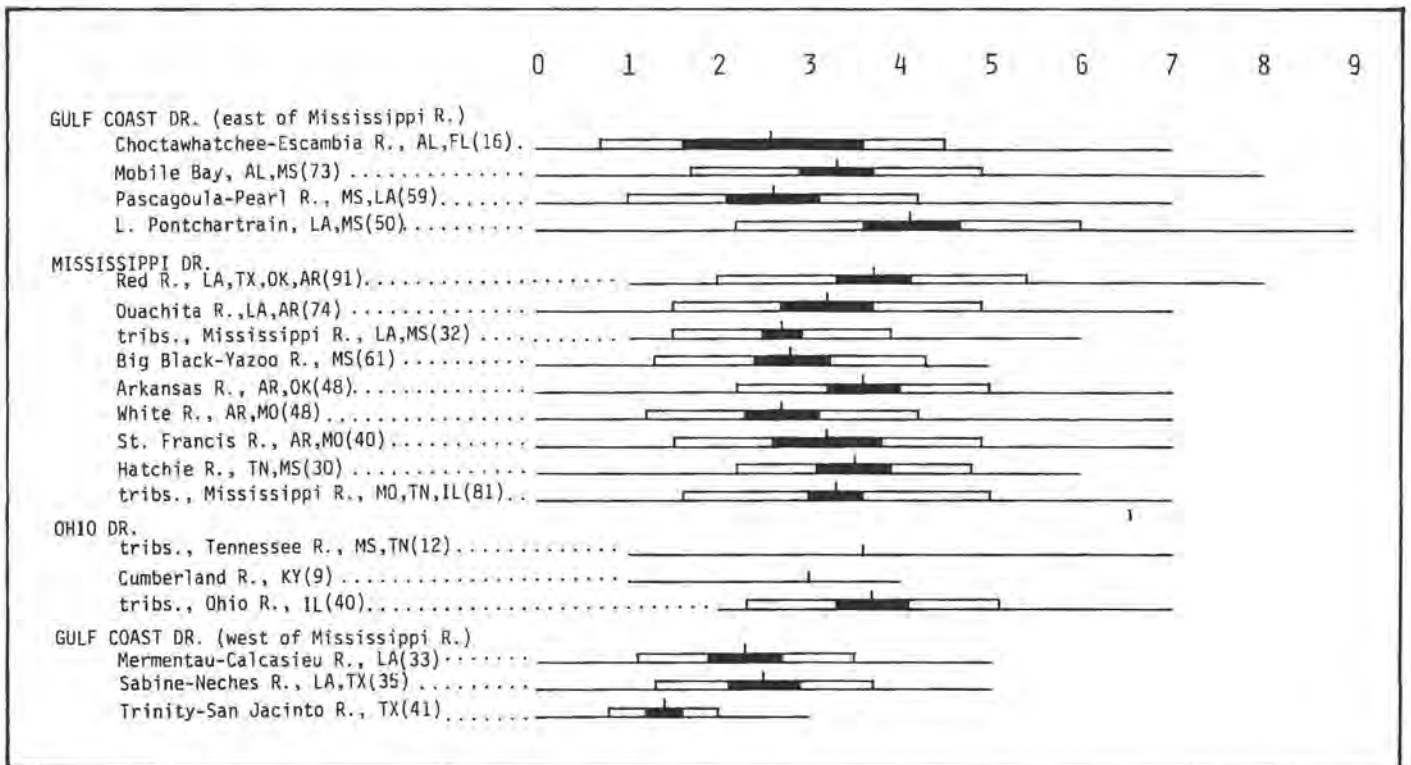


Fig. 5. Variation in the number of pored lateral line scales in populations of *E. procliare*. The diagrams indicate the mean (center point), 95 percent confidence limits of the mean (black rectangle), one standard deviation on either side of the mean (outer limits of open rectangle), and sample range (basal line). State name abbreviations follow U. S. Postal Service abbreviations. The sequence of populations is based on geographic propinquity between and within drainage basins, where possible.

dorsal midline, ST canal formulae number 1+2 (1 specimen); 2+2 (423); and complete with 3 pores in 39 specimens. SO canal complete and always with 4 pores. CP always present, CP with median, posterior-leading tube in 432 specimens, without tube in 7 specimens. CP connected to SO canals by SO commissures. POM canal reduced, POM pores number 7 (12 specimens); 8 (453); and 9 (17); $\bar{x}=8.01$. IO canal always interrupted, IO pores number 0+2 (1 specimen); 0+3 (2); 1+2 (10); 1+3 (435); and 1+4 (3). Lateral canal complete with 5 pores. Head canal pores large, exceeding those of *E. fonticola* in size, but smaller than those of *E. microperca*.

Scales ctenoid, large, and of relatively same size on body. Head, nape, and breast always unscaled. Belly squamation highly variable within a given population. Percent of belly scaled is as follows: 10-20% (16 specimens); 30-40% (56); 50-60% (234); 70-80% (85); and 90-100% (37). Belly naked along complete midline in 72 specimens. Generally half the belly is scaled in both sexes. Opercle scaled in all specimens. Cheek fully scaled in almost all specimens. Percent of cheek scaled is as follows: 0% (6 specimens); 10-20% (12); 30-40% (4); 50-60% (15); 70-80% (9); and 100% (428). Scales on cheek and opercles more often exposed than embedded, usually easily observed. Opercular spine well developed.

The general body shape of breeding males and females is shown in Fig. 4. The body is small, laterally compressed and somewhat slender (most slender in the subgenus). The snout is usually bluntly rounded. The premaxillary is non-protractile and is connected to the snout by a narrow frenum. The mouth is small, the maxillaries extend posteriorly beyond the front margin of the eye. The gill membranes are moderately connected, free from the isthmus, and form an obtuse angle. The eye is small and situated high on the head. Vertical fins small, pectoral fins fanlike and rounded to somewhat pointed; posterior margin of caudal fin straightedged or rounded. Pelvic fins reaching anus or beyond in breeding males, developing extra flaps of skin on both sides of the pelvic spine and between pelvic rays one to three during breeding periods.

The general body coloration of both sexes is olivaceous brown or various shades of brown. Three basic caudal spots usually lacking. Upper lip more heavily pigmented than lower; fine, discrete melanophores evenly spaced on chin, throat, breast and belly of males; females unlike males may have a few randomly scattered melanophores on lower lip and breast but otherwise are free from dark pigment. Posterior edge of dorsal body scales dark-edged with melanophores, remainder of scale lighter tan. Body pigment forming distinct lateral blotches in both sexes. Lateral blotches number 7 (10 specimens); 8 (50); 9 (116); 10 (117); 11 (43); and 12 (15); $\bar{x}=9.51$. Below lateral blotches are several larger concentrations of melanin often forming rows of spots. Caudal and D_2 fin of both sexes distinctly barred. D_2 fin usually with 5 or 6 amber colored bands. Caudal fin usually with 6 or 7 amber colored bands. Well-defined dark teardrop

present beneath eye; dark line or blotch of pigment usually present anterior and posterior to margins of eye. Humeral spot absent. Dorsal saddles usually well defined and number 6 (24 specimens); 7 (76); 8 (110); and 9 (15); $\bar{x}=7.52$.

Breeding coloration: The following color description is based on color transparencies of breeding individuals, and specimens seen in life from many parts of the range of the species.

The general body coloration of males is light tan to dusky brown with specks of iridescent yellow laterally along the body. A creamish iridescence is present on the bases of the opercle and pectoral fin. Well-developed amber or reddish-orange bands are present in the D_2 and caudal fins. The lateral blotches are dark brown, and in the most intensely marked individuals are elongate and form vertical bars. Some males develop nearly a uniform dark color over all parts of the body.

The most striking color changes take place in the fins of males. The head, D_2 , and caudal fins become thickened with a milky-white appearance. The D_1 fin has red or orange blotches of color developed medially in the first one or two membranes; red or orange is suffused in the most posterior membranes with occasional orange in the middle of the fin but never forming discrete blotches as in the anterior membranes. Basally the D_1 fin is solid black or nearly so in the first one to three membranes. The pigment is concentrated entirely on the membranes, never on the spines; the melanophores are progressively less concentrated in the posterior membranes. Distally the fin is gray edged with melanophore concentration rarely becoming as dark as the basal portion of the fin. Both the anal and pelvic fins become melanistic with the melanophores concentrated most heavily on the distal portions of the fins. The melanophores rarely occur on the rays of the anal fin but occur both radially and interradially on the pelvic fins. The pectoral rays are distinctly outlined by melanophores with rarely any melanin present on the membranes. The black preorbital, suborbital, and postorbital bars are intense. The iris of the eye is bright red or orange with hints of iridescent green and gold.

Breeding colors are poorly developed in females and their coloration is much the same year around. Some females develop a suffuse orange color in the anterior membranes of the D_1 fin, otherwise the fin is clear or has scattered traces of melanin. The D_2 and caudal fins have the amber-orange bands as in males. The pectoral fins are outlined with black melanophores. The pelvic and anal fins are generally clear with only random spots of melanin. The iris of the eye is orange. The general body coloration is like that described for the male.

Tuberculation: Tubercle distribution in *E. proeliare* has been briefly described by Collette (1965:606); the following is an amplification of his description based on the many hundreds of tuberculate specimens now available in collections.

Tubercles occur on the anal and pelvic fins of males only and are present in maximum development from collections made during mid-January through very early June. One collection made 2 August 1963 (KU 9276) from the St. Francis drainage in Missouri contained several males with maximally developed tubercles. Tubercle size varies with body size. Small males (25-30 mm SL) have smaller tubercles, whereas larger males (>30 mm SL) have the largest tubercles. Tubercles are also largest on the central portions of the anal fin elements becoming progressively smaller basally and distally. At maximum development, moderate-sized, round, white tubercles are present in a single file on the anal fin and the ventral surfaces of the pelvic fins. Pelvic fin tubercles at maximum development are distributed as follows: distal tip of first ray; full length of rays two through four; and distal half of ray five. Tubercles do not develop on the pelvic fin spines. Anal fin tubercles at maximum development are distributed as follows: full length of anal spine; distal seven-eighths of all the anal rays except the final element of the last branched ray in which tubercles do not develop.

By counting the number of tubercles from the base of a fin element to the tip of a single ray branch the following variation in numbers of tubercles was observed at maximum development: tubercles on first pelvic ray number 1 to 5; second ray 6 to 15; third ray 8 to 17; fourth ray 5 to 17; fifth pelvic ray usually 4 or 5 tubercles, often altogether absent; tubercles on first anal spine number 1 to 10; second anal spine absent; first anal ray 6 to 9; second anal ray 9 to 12; third ray 9 to 14; fourth ray 6 to 12; fifth ray 5 to 9; sixth anal ray 4 or 5 tubercles, often absent. At minimum development, tubercles may be present only on the central elements of the pelvic fins and wholly lacking on the anal fin. Thus tubercles apparently develop first on the middle rays and then spread to the other rays as first suggested by Collette (1965).

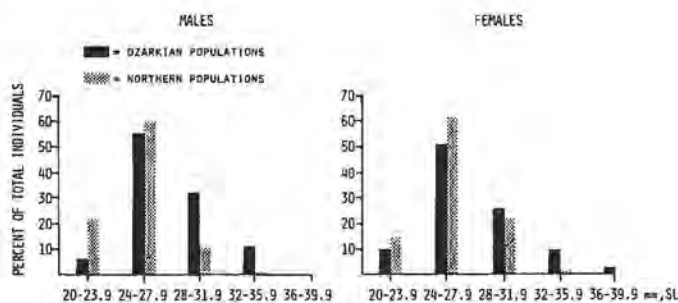


Fig. 6. Frequency distribution by size class and sex of adult *E. procliare* showing geographic variation in maximum size between Lake Pontchartrain and Ohio drainage populations. Based on 80 males and 71 females.

GEOGRAPHIC VARIATION.—*E. procliare* exhibits the least amount of variation in the subgenus but displays several characteristics which are believed to be of importance

and merit discussion. No significant geographic variation in body proportions was observed. The majority of the meristic variation fits into one of three patterns: (1) variation slight and random; (2) unusual variation in populations of certain drainages; (3) Gulf Coast populations in Texas somewhat divergent.

The following characters fall into pattern 1 above: lateral scales, transverse scale rows, caudal peduncle scale rows, dorsal spines, dorsal rays, total dorsal fin elements, pectoral rays, caudal fin rays, anal rays, total anal fin elements, features of the cephalic lateral line, most squamation characters, pigmentation, tuberculation, and breeding coloration. Inasmuch as the variation in these characters is apparently insignificant, the counts are lumped and placed in the Description.

Several characters fit pattern 2: branchiostegal rays (Table 3), condition of the preopercle, maximum SL attained (Fig. 6) and nape squamation. Most darters have been observed to exhibit the characteristic Etheostomatine branchiostegal ray count of 6:6. A few exceptions are *Percina nasuta* (Bailey, 1941) which has a modal count of 7:7, and *P. tanasi* (Etnier, 1976), *P. oxyrhyncha* (Bailey, 1941), some species of *Nothonotus* (Zorach, 1972), some species of *Hololepis* and *E. edwini* (Collette, 1962), all of which very rarely have 7 branchiostegal rays on a side. A branchiostegal ray count of 7:7 has further been considered a primitive feature characteristic of the ancestral Percinae (Bailey, 1941). Several populations of *E. procliare* (Table 3) have a rather high incidence of a 6:7 or 7:7 branchiostegal ray count, and most other populations except those from the Cumberland, Tennessee, and Ohio Rivers have some incidents of a 6:7, 7:7 frequency. For instance, 37 percent of the specimens from the Sabine-Neches rivers have 6:7 or 7:7 branchiostegals. For such a highly evolved group of darters this is a remarkable characteristic. If anything the variation would be expected to have been toward a more reduced number of rays. In the more specialized members of *Hololepis*, such as *E. collis*, less than 1 percent of the individuals have a count of 7 branchiostegals (Collette, 1962: table 44). The variation in this character does not appear to fit any geographical pattern and the adaptive significance of an additional ray is difficult to imagine considering the shortness of the branchiostegal membrane and the habitat of the species.

One feature that was not expected to vary was the condition of the preopercular margin. In only one collection (CU 37538) from the upper Pearl River, a breeding male has a serrate preopercle, two other ripe females in the lot have a slightly serrate preopercle. The serrations are extremely fine. In many other collections from the Pearl River at TU including a nonbreeding series from the same locality the preopercular margins are entirely smooth. A serrate preopercle was not found in any other collection from throughout the range of the species. A serrate preopercle is characteristic of *E. serriferum*, the most primitive member of *Hololepis* and is variously developed in other members of the subgenus (Collette, 1962). Preopercle serrations are ontogenetically variable

in *Percina sciera* (Hubbs and Black, 1954) but this fact does not seem applicable to the case at hand. The significance of the individual case in *E. proeliare* is obscure and is considered to be of little importance.

Two characters from the Lake Pontchartrain drainages and elsewhere at southern latitudes seem to be positively correlated with each other. These are maximum SL attained and extent of nape squamation. The maximum size in *E. proeliare* does not appear to vary clinally or in consistent geographic patterns. However, most specimens from southern latitudes such as the lower Ouachita River populations and especially those from the Lake Pontchartrain region attain a greater maximum size in SL than do those populations from more northern latitudes such as the upper Mississippi River and Ohio River populations. A comparison of the largest adults (breeding males and females) from Lake Pontchartrain to those from tributaries of the Ohio River illustrates the point (Fig. 6). The differences between Lake Pontchartrain and Ohio River populations are highly significant when tested with the Kolmogorov-Smirnov two-tailed test ($P < .001$). Larger size at southern latitudes is somewhat contrary to Bergman's Rule and for what has been found for other fishes in which the more northern representative of a species is usually larger than that to the south (Hubbs, 1926a).

The extent of nape squamation is correlated with the above. All populations of *E. proeliare* consistently have a naked nape except those from the Lake Pontchartrain region where maximum body size is attained. For example, in a collection containing 29 adults (NLU 4317) 83 percent have as much as half of the nape scaled and the remaining specimens have 70 to 80 percent of the nape scaled. Two females have the nape completely covered with exposed scales. Squamation of the nape is one of the last features to appear during the ontogeny of many fishes (Barlow, 1961). The larger maximum size attained and the partially scaled napes in populations from Lake Pontchartrain are probably a result of the longer growing season in this region. These features are therefore regarded as being environmentally induced rather than indicative of genetic divergence.

Two characters examined fall into pattern 3 in which the Gulf Coast populations west of the Mississippi River are divergent from other populations. These are the number of pored lateral line scales (Fig. 5) and the number of anal fin spines (Table 2). The number of pored lateral line scales in *E. proeliare* varies from 0 to 9 throughout the range with most individuals from most drainages having from 2 to 4 pored scales, and often as many as 6 or 7 pored scales. All of the drainages where large enough sample sizes are available are rather uniform in this respect except the Gulf Coast drainages west of the Mississippi River (Fig. 5). Specimens from the Trinity-San Jacinto rivers never have more than 3 pored scales ($\bar{x} = 1.42$). The 95 percent confidence intervals from this population do not overlap with other populations. There appears to be an erratic cline in these Gulf Coast popula-

tions with lower values (mean and ranges) in the Trinity-San Jacinto samples and higher values in the Mermentau-Calcasieu samples.

The above populations are further divergent in number of anal fin spines. Most populations of *E. proeliare* have individuals with 1 or 2 anal spines (Table 2). The Gulf Coast populations are consistent in always having 2 anal spines. Variation throughout the range in number of anal spines is discordant with all 12 specimens from the Tennessee River tributaries consistently having 1 spine and all specimens from the Big Black River consistently having 2 spines. The combination of two divergent characters for Gulf Coast samples is perhaps the result of their isolation from the main body of populations. Isolated Gulf Coast populations east of the Mississippi River, particularly those in the Escambia and Choctawhatchee rivers are more like the majority of populations. In totality of characters, the Gulf Coast populations west of the Mississippi River do not differ decidedly from Mississippi Valley - Mobile Bay populations. Most of the differences are minor and overlap is broad. Since several important characters are either uniform or vary discordantly, formal taxonomic recognition does not seem warranted or desirable.

SEXUAL DIMORPHISM.—Sexual dimorphism in breeding coloration, pelvic fin shape, tuberculation, and genital papilla shape was discussed elsewhere in this paper. Sexual dimorphism in the number of pored lateral line scales in selected populations of *E. proeliare* is shown in Table 4. Significance levels vary from low to not significant in one population (Lake Pontchartrain). The low significance levels perhaps indicate that the differences observed are artificial and may only be a result of small sample size or some other artifact. A more involved discussion can be found in the Sexual Dimorphism section of the *E. fonticola* account. *E. proeliare* shows highly significant differences in several body proportions (Table 5) but is not as sexually dimorphic in morphometric ratios as *E. microperca*. Males display significantly greater values for head length, predorsal length, postdorsal length, caudal peduncle depth, eye diameter, D, base length, pelvic fin length, pectoral fin length, anal fin length, and D₂ fin length. Females display a significantly greater value for body depth due to their egg-swollen condition.

In most large samples females are larger than males. The largest specimen examined is a female 39.6 mm SL; the largest male is 37.8 mm SL. The larger maximum size attained in females is probably real and not biased by sample size or some other factor (Burr and Page, 1978).

DISTRIBUTION.—The distribution of *E. proeliare* is plotted in Fig. 7. To determine possible historical changes in the range of the species locality records from 1880-1908 were plotted with large open circles, whereas more modern records (1940 to present) were plotted with small solid circles. The solid black line represents the Coastal Plain boundary.

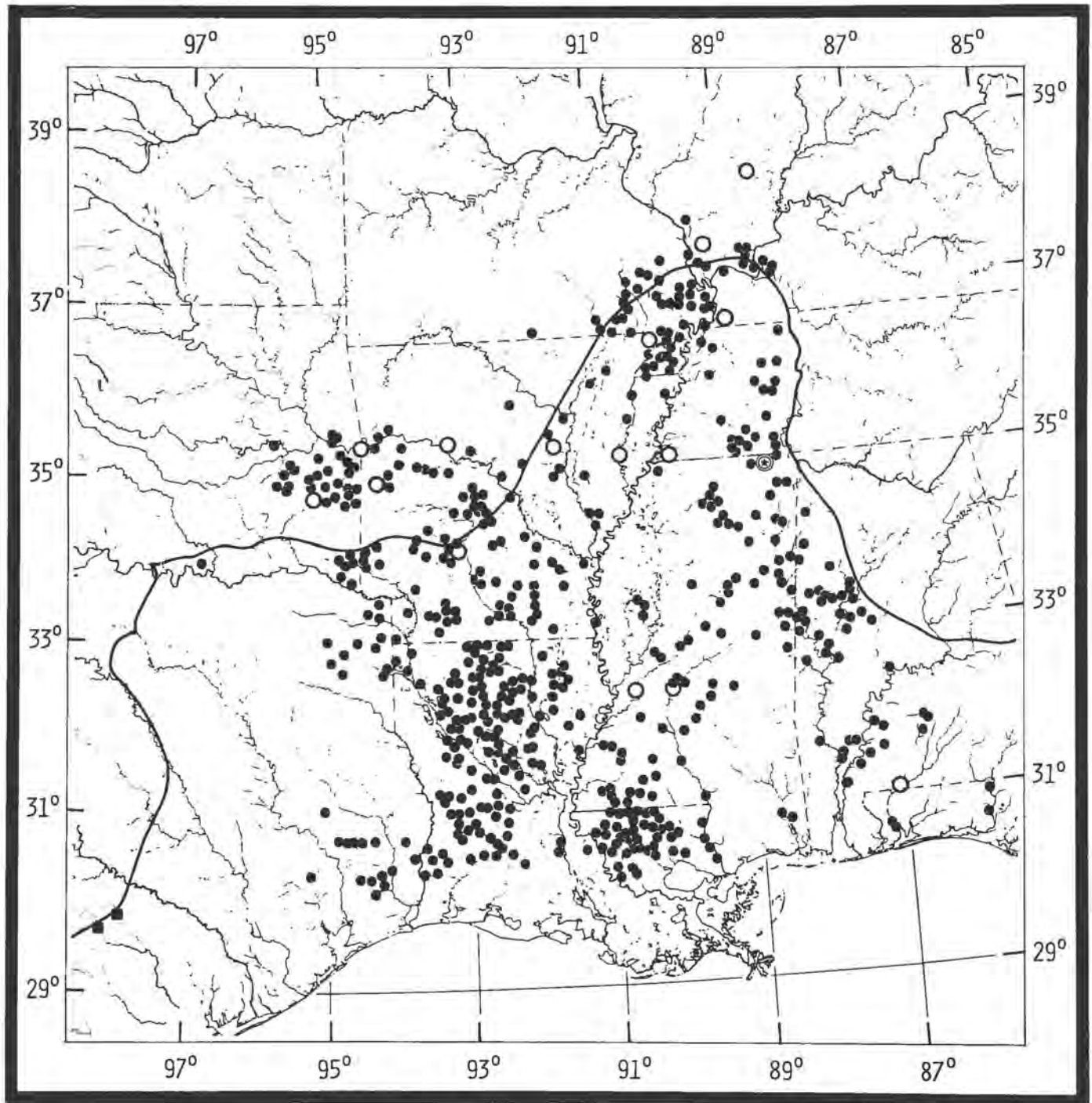


Fig. 7. Distribution of *E. proeliare* (circles) and *E. fonticola* (squares). The solid black line represents the Coastal Plain boundary. Large open circles represent record stations where *E. proeliare* was collected from 1880 to 1908. Small solid circles represent modern localities for *E. proeliare* (1940 to present). The circled star is the type locality of *E. proeliare*.

E. proeliare is primarily a Coastal Plain species extending east to the Choctawhatchee River, Florida, southwest to the San Jacinto River, Texas, and north through lowland areas to the Big Muddy River (Mississippi River) in Illinois. The record for Limestone Creek (Red River), Oklahoma, reported by Riggs and Bonn (1959) is the westernmost locality known for the species. Although the specimen could not be found at OAM, OUMZ, or UTULSAC, the record is considered valid since it is within the probable range of the species. Its suggested occurrence in the lower Cumberland River by Jenkins et al. (1972) is verified by two separate localities from the drainage (INHS 75839; 75841).

E. proeliare traverses the Coastal Plain boundary in Arkansas, Oklahoma, Missouri, Illinois, and Kentucky. Although it is primarily a lowland species, it apparently tolerates more upland conditions present above the boundary line where suitable habitat is available. Several other primarily Coastal Plain fishes also show a tolerance for sluggish waters above the boundary line such as *E. gracile* (Collette, 1962) and *Notropis fumeus* (Snelson, 1973).

The most northern locality tentatively accepted for the species is from Skillet Fork (Wabash River), Wayne County, Illinois, where it was reported by Large (1903) as *Microperca punctulata*. The specimen(s) are no longer extant and the record could possibly be based on a juvenile *E. gracile* or some other darter species. However, it is difficult to believe that Large could have confused *E. gracile* with a *Microperca* since both species were familiar to him. It is probably gone from the locality in Big Muddy River, Illinois, which is now impounded by Lake Kincaid reservoir. Similarly, the species has not been collected in Bayou de Chien, Kentucky, in recent years (Webb and Sisk, 1975) where A. J. Woolman collected it in 1890 (UMMZ 198980).

E. proeliare is rare in the Pascagoula River, Mississippi, but is common in the drainages both to the east and west of the Pascagoula. Reasons for this are difficult to determine. The drainage has been well collected and presumably suitable habitat is present. The species is also rare farther east in the Choctawhatchee River, Florida, where it is known from a few individuals. In the San Jacinto River, Texas, it is known from one specimen. It is uncertain whether the lack of records for east-central Texas is real or just an artifact due to inadequate collecting. Otherwise, the species shows a predilection for the Austroriparian zone in Texas as pointed out by Hubbs (1954).

E. proeliare and *E. microperca* are syntopic in Sansbois Creek (Arkansas River), Pittsburg County, Oklahoma. This is the only known locality where the two species have been taken together. Two *E. microperca* and six *E. proeliare* were present in the collection. No evidence of hybridization or introgression was apparent. Recent collecting at this locality revealed only the presence of

E. proeliare (Jim Pigg, pers. comm.) perhaps suggesting some competitive interaction between the two species.

The distribution of *E. proeliare* has evidently changed very little since the turn of the century. The species was, however, often confused with *E. microperca* in the Arkansas and Red rivers of Arkansas and Oklahoma by Gilbert (1889) and Meek (1891, 1894a, 1894b, 1896). Fowler (1945) also reported *E. microperca* (as *Microperca punctulata*) from several Gulf Coast drainages. Most of Meek's specimens are extant (USNM, SU) and clearly represent *E. proeliare*. The inclusion of *E. microperca* in later studies from the Poteau River, Oklahoma, and Arkansas (Cross and Moore, 1952) the Kiamichi River, Oklahoma, (Pigg and Hill, 1974) and the Illinois River, Oklahoma, (Geihslar et al., 1975) are all based on Meek's and Gilbert's original misidentifications.

CONSERVATION STATUS.—*E. proeliare* is not in danger of extinction. It is, however, rather uncommon in the panhandle of Florida and the Coastal Plain of Illinois and Kentucky. Sisk (1973) suggested that it should be placed on Kentucky's rare and endangered species list. Otherwise the species is common and often one of the most abundant lowland darters in many parts of its range.

Material Examined

Choctawhatchee River Drainage. Florida: HOLMES COUNTY: TU 46278 (1) Choctawhatchee River 2 mi N of Pitman, 1 May 1967. WALTON COUNTY: FSU 351 (1) Bruce Creek 2.4 mi N of Redbay, 27 May 1951.

Escambia River Drainage. Florida: SANTA ROSA COUNTY: UMMZ 165174 (5). Alabama: BUTLER COUNTY: UMMZ 88729 (3); 128778 (4); 139158 (3).

Alabama River Drainage. Alabama: BIBB COUNTY: UAIC 1288 (1). MONROE COUNTY: USNM 251937 (1).

Tombigbee River Drainage. Alabama: CLARKE COUNTY: UAIC 1839 (1); 1840 (5); 2027 (1); 2321 (2). MARENGO COUNTY: UAIC 4507.08 (7). MARION COUNTY: UAIC 4400 (1). PICKENS COUNTY: FSU 15350 (1). SUMTER COUNTY: UAIC 1890 (3). Mississippi: LOWNDES COUNTY: MSU 5931 (5); 5999 (5). OKTIBBEHA COUNTY: MSU 156 (9).

Black Warrior River Drainage. Alabama: GREENE COUNTY: CU 21898 (10); INHS 76250 (70). HALE COUNTY: CU 21888 (10). TUSCALOOSA COUNTY: CU 33218 (5); KU 10948 (6).

Pascagoula River Drainage. Mississippi: GEORGE COUNTY: TU 100184 (6) Pascagoula River 14 mi SW of Lucedale, 29 Oct. 1976. NEWTON COUNTY: CU 33796 (9) trib. to Leaf River between Lawrence and Lake, 25 Oct. 1958.

Pearl River Drainage. Louisiana: WASHINGTON PARISH: MSU 1313 (2); INHS 75844 (2). Mississippi: ATTALA COUNTY: CU 37538 (3); TU 28673 (10). COPIAH COUNTY: FSU 10643 (2). HINDS COUNTY: FSU 10676 (1); UMMZ 161136 (3). SCOTT COUNTY: NLU 20766 (10). SIMPSON COUNTY: TU 26790 (7). SMITH COUNTY: NLU 21007 (4).

Lake Pontchartrain Drainage. Louisiana: EAST FELICIANA PARISH: NCSM 5314 (4). ST. HELENA PARISH: BU 306 (3); NLU 1635 (10). TANGIPAHOA PARISH: BU uncat. (5); 234 (2); NLU 1371 (10); 4317 (10). Mississippi: LINCOLN COUNTY: UMMZ 161177 (1). WILKINSON COUNTY: UMMZ 146617 (8); USNM 59820 (8).

Red River Drainage. Louisiana: CADDO PARISH: NLU 7989 (10). Texas: BOWIE COUNTY: TNHC 522 (3). CASS COUNTY: TNHC 4045 (10). HARRISON COUNTY: TCWC 4068.8 (10). MARION COUNTY: BU 213 (10). Arkansas: COLUMBIA COUNTY: HWR uncat. (10). SEVIER COUNTY: HWR 72-11 (10); 72-12 (3). Oklahoma: MCCURTAIN COUNTY: APB uncat. (10); OUMZ 37979 (7); 41069 (1). PUSHMATAHA COUNTY: OAM 5629 (4); SU 1250 (2).

Ouachita River Drainage, Louisiana: OUACHITA PARISH: INHS 75701 (60). UNION PARISH: BU 1561 (6). ARKANSAS: BRADLEY COUNTY: HWR 74-25 (10); TMB 74-59 (3). CLARK COUNTY: HWR 72-22 (10); 73-4 (6). COLUMBIA COUNTY: HWR uncat. (9). DREW COUNTY: TMB 74-58 (2). SALINE COUNTY: NLU 15185 (10); TMB 72-38 (5); 72-39 (10); 74-16 (4).

Lower Mississippi River Drainage, Louisiana: CONCORDIA PARISH: NLU 3539 (7). FRANKLIN-TENSAS PARISH: USNM 172848 (5). MADISON PARISH: USNM 172733 (20).

Big Black River Drainage, Mississippi: CHOCTAW COUNTY: FSU 10554 (10); MSU 228 (10). CLAIBORNE-HINDS COUNTY: NLU 12890 (3). HOLMES COUNTY: FSU 9404 (10); UMMZ 161110 (2). RANKIN COUNTY: USNM 32205 (1). WEBSTER COUNTY: USNM 165959 (4).

Yazoo River Drainage, Mississippi: DESOTO COUNTY: USNM 195886 (10). LAFAYETTE COUNTY: UMMZ 162916 (5). MARSHALL COUNTY: UMMZ 161062 (3). MONTGOMERY COUNTY: INHS 75845 (1). YAZOO COUNTY: USNM 195885 (3).

Arkansas River Drainage, Arkansas: CRAWFORD COUNTY: TMB 74-15 (3). FRANKLIN-LOGAN COUNTY: KU 6208 (1). POPE COUNTY: USNM 59186 (1). PULASKI COUNTY: USNM 165891 (3). SCOTT COUNTY: KU 6191 (10). YELL COUNTY: TMB 73-81 (2); UMMZ 177142 (5). OKLAHOMA: LATIMER COUNTY: UTULSAC 1254 (2). LEFLORE COUNTY: KU 2423 (5); SU 16085 (3). PITTSBURG COUNTY: OUMZ 34072 (3); 35848 (10).

White River Drainage, Arkansas: FAULKNER COUNTY: KU 9826 (2). INDEPENDENCE COUNTY: TMB 73-78 (3). MONROE COUNTY: TMB 72-3 (6). PRAIRIE COUNTY: NLU 8555 (10); 8568 (10). PHILLIPS COUNTY: FSU 14498 (3). WHITE COUNTY: USNM 42837 (1). MISSOURI: HOWELL COUNTY: KU 15232 (10).

St. Francis River Drainage, Arkansas: CRAIGHEAD COUNTY: KU 16079 (1). CROSS COUNTY: NLU 12106 (10). POINSETT COUNTY: INHS 75843 (3). ST. FRANCIS COUNTY: FSU 14342 (10). MISSOURI: DUNKLIN COUNTY: KU 9276 (10). WAYNE COUNTY: FMNH 60731 (6).

Hatchie River Drainage, Mississippi: ALCORN COUNTY: MSU 2670 (10). TENNESSEE: HARDEMAN COUNTY: MSU 6058 (10); TU 89327 (1); 89345 (5); USNM 190789 (2). MCNAIRY COUNTY: TU 88721 (2).

Middle Mississippi River Drainage, Tennessee: CARROLL COUNTY: FMNH 77440 (4); UT 91.461 (3). DYER COUNTY: UT 91.1163 (2). LAKE COUNTY: UT 91.132 (7). MISSOURI: MISSISSIPPI COUNTY: INHS 75838 (10). NEW MADRID COUNTY: CU 42298 (3); INHS 75832 (10); 75833 (10). SCOTT COUNTY: INHS 75838 (10). KENTUCKY: HICKMAN COUNTY: UMMZ 198980 (1) Bayou de Chien, 29 July 1890. ILLINOIS: JACKSON COUNTY: INHS 22594 (1); UMMZ 105937 (6); 130277 (3).

Lower Ohio River Drainage, Illinois: ALEXANDER COUNTY: INHS 6042 (10). JOHNSON COUNTY: INHS 26918 (10); 26925 (2). POPE COUNTY: INHS 1358 (10). KENTUCKY: LIVINGSTON COUNTY: INHS 75840 (10) Bayou Creek 1 mi N of Burna, 3 March 1973.

Cumberland River Drainage, Kentucky: LIVINGSTON COUNTY: INHS 75839 (3) Sugar Creek 2 mi SW of Tiline, 27 July 1971; INHS 75841 (6) Richland Creek 2 mi N of Iuka, 30 Jan. 1964.

Tennessee River Drainage, Tennessee: HENDERSON COUNTY: KU 9811 (1); UT 91.723 (3). MCNAIRY COUNTY: TU 88690 (2); UT 91.1063 (2). MISSISSIPPI: ALCORN COUNTY: TU 87969 (6).

Mermentau-Calcasieu River Drainage, Louisiana: ALLEN PARISH: NLU 2910 (10); TU 43298 (10); 50225 (10). EVANGELINE PARISH: TU 44565 (3).

Sabine-Neches River Drainage, Texas: HARDIN COUNTY: INHS 75667 (2); TNHC 899 (3). NEWTON COUNTY: TCWC 4025.4 (10). POLK COUNTY: TNHC 2434 (1); 2578 (1). TRINITY COUNTY: NLU 30130 (8). TYLER COUNTY: TU 21839 (10).

Trinity-San Jacinto River Drainage, Texas: MONTGOMERY COUNTY: TNHC 1515 (1) Peach Creek 14 mi E of Conroe, 23 March 1951. POLK COUNTY: TCWC 4001.19 (10). TNHC 1348 (24); 2723 (6).

Etheostoma fonticola (Jordan and Gilbert)

Fountain Darter

Figure 8

Alvarius fonticola Jordan and Gilbert, 1886:23 (original description; Rio San Marcos at San Marcos, Texas).—Jordan, 1887 (list; *Alvarius* and *Microperca* probably identical).—Jordan, 1929 (southern Texas).—Jordan et al., 1930 (list; range, in part).—Driver, 1942 (in key; range, in part).

Etheostoma (Alvarius) fonticola.—Gilbert, 1887 (redescription; comparisons).

Etheostoma fonticola.—Evermann and Kendall, 1894 (Rio Grande fauna, Texas; 43 specimens from Comal River, New Braunfels, Texas; range, in part; figure).—Boulenger, 1895 (in key; partial synonymy; redescription; range).—Hubbs et al., 1953 (restricted to Comal and San Marcos springs, Texas; habitat).—Jurgens and Hubbs, 1953 (Texas list).—Bailey, 1954 (name modified improperly by Knapp, 1953).—Hubbs, 1954 (restricted to Comal and San Marcos springs, Texas).—Strawn, 1955 (coloration; range; habitat; hard water darter; never free swimming).—Kuehne, 1955 (Comal and San Marcos springs, Texas).—Strawn, 1956 (spawning temperatures; spawns year around; egg deposition sites; eggs not guarded; photograph of breeding male).—Strawn and Hubbs, 1956 (stripping milt and eggs).—Eddy, 1957 (in key; range; figure).—Hubbs, 1957a (Comal and San Marcos springs, Texas).—Hubbs, 1957b (Texas list).—Hubbs and Strawn, 1957 (males produce little milt; small eggs; artificial hybridization with several species of darters; hybrid survival).—Moore, 1957 (in key; characters; range).—Hubbs, 1958a (Texas list).—Huobs, 1958b (non-visible milt).—Hubbs, 1959 (artificial hybrid combinations with several species of darters).—Bailey et al., 1960 (list).—Hubbs, 1961 (Texas list; range).—Hubbs and Laritz, 1961 (improbable hybrid parent).—Collette, 1962 (most advanced *Microperca*).—Breder and Rosen, 1966 (breeding habits *vide* Strawn, 1955; 1956).—Hubbs, 1967 (artificial hybrid survival).—Distler, 1968 (artificial hybrid cross with *E. spectabile*).—Moore, 1968 (in key; characters; range).—Eddy, 1969 (in key; range; figure).—Bailey et al., 1970 (list).—Hubbs, 1972 (Texas list; range).—Miller, 1972 (nationally recognized endangered species from Texas).—Schwartz, 1972 (list of artificial hybrid combinations).—Anonymous, 1973 (threatened status).—Hubbs, 1976 (Texas list).—Schenck and Whiteside, 1976 (distribution; habitat; population size; extirpation from Comal River, Texas; endangered status).—Anonymous, 1977 (in endangered species list).—Berger, 1977 (in endangered species list).—Schenck and Whiteside, 1977a (food habits; feeding behavior).—Schenck and Whiteside, 1977b (fecundity; sex ratio; sexual dimorphism).

Microperca fonticola.—Jordan and Evermann, 1896a (in key; redescription; range, in part; figure in 1900 edition).—Jordan and Evermann, 1896b (list; range, in part).—Cockerell and Elder, 1914 (scales like *M. punctulata*).—Baughman, 1950 (Texas list).

Etheostoma fonticulum.—Knapp, 1953 (in Texas key; range; figure).

Etheostoma (Microperca) fonticola.—Bailey and Gosline, 1955 (vertebral counts).—Collette, 1965 (tubercle distribution; sexual dimorphism).—Collette and Knapp, 1966 (lectotype designation for *Alvarius fonticola*).

TYPES.—The type-series was collected September, 1884 by D. S. Jordan and C. H. Gilbert from the San Marcos River [Guadalupe drainage], just below the mouth of the Blanco River [Hays County], Texas (Jordan and Gilbert, 1886). This locality is actually about 2 miles south of the town of San Marcos, although the type-locality is now referred to as being near or within the town of San Marcos. The specimen collected from the Washita River at Arkadelphia, Arkansas, and referred to in Jordan and Gilbert (1886:13) was presumably based on a misidentification of *E. proeliare*. The species was redescribed from the original type-series in more detail and compared with

related species by Gilbert as *Etheostoma (Alvarius) fonticola* Jordan and Gilbert sp. nov. (Gilbert, 1887:63).

Jordan and Evermann (1896a-1900:plate 177, fig. 470) designated USNM 36523 as lectotype by virtue of the illustration drawn from the "type" by E. Copeland (Jordan and Evermann, 1896a-1900:3271). This was the same figure used in Evermann and Kendall (1894:plate 36), although no mention of its being drawn from the "type" was made. Evidently the "type" referred to by Jordan and Evermann was actually a series of syntypes (four specimens) since Collette and Knapp (1966:10) selected a lectotype from USNM 36523, the number originally referred to by Gilbert (1887) and Jordan and Evermann (1896a-1900). Because the figure was of a male and included a size scale, it is assumed that Collette and Knapp selected the lectotype on the basis of sex and size. The following counts for the lectotype are from Collette and Knapp (1966:10). A male, 27 mm SL with 2 pored lateral

line scales; 30 lateral scales (=32); dorsal fins with 7 spines, and 10 rays; anal fin with 1 spine and 6 rays; IO canal pores 1+3; POM canal pores 8; ST canal interrupted at midline; nape, cheeks, and breast naked; breeding tubercles on posterior anal rays. The other three syntypes (21-24 mm SL) removed from USNM 36523 are now paralectotypes USNM 198004.

ETYMOLOGY.—The name *fonticola* comes from the latin *fons*, fountain and *cola*, to inhabit, in reference to its occurrence in the large spring at San Marcos, Texas.

DIAGNOSIS.—A species of the subgenus *Microperca* distinguished from other members by combinations of the following characters: 1 anal spine; usually 17 to 18 total dorsal fin elements; IO pores 1+3; POM pores 8; usually 32 to 34 lateral scales (modally 33), usually 2 or 3 pored; branchiostegal rays modally 6;6; vertebrae usually 32 or 33; opercles usually scaled, cheeks and prepectoral

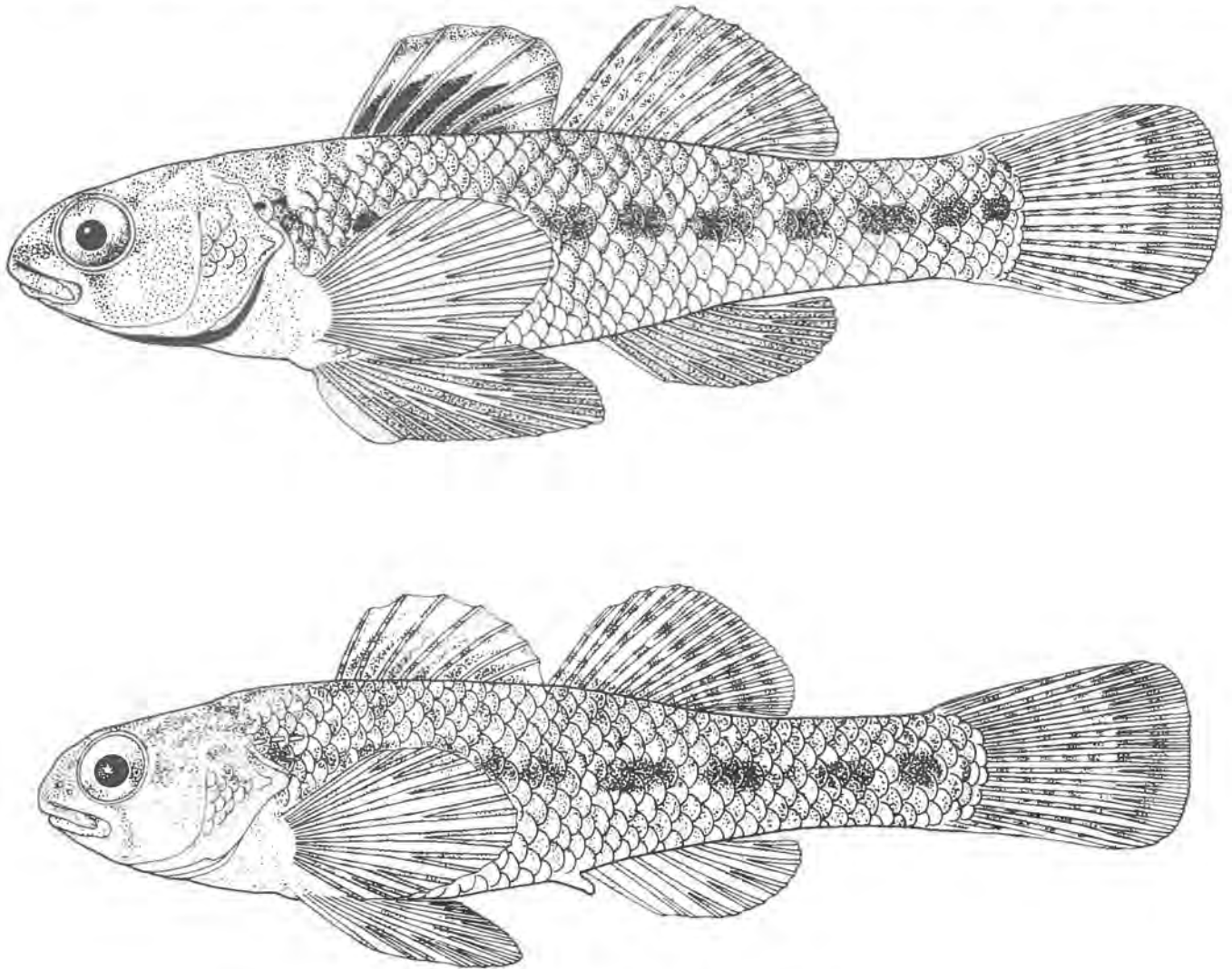


Fig. 8. Breeding adults of *E. fonticola*: INHS 75562, San Marcos River, Hays County, Texas, 22 April 1965. Top) male, 29 mm SL. Bottom) female, 27 mm SL. Nuptial tuberculation not shown. Drawing by Alice A. Prickett.

area naked; genital papilla of female bilobed; lateral pigment usually forming 11 stitchlike dashes on sides of adults rather than blotches along side. In breeding males, solid, broad, subdistal band of red-orange color present in all membranes of D_1 fin; basal one-third of D_1 fin solid black; pelvic and anal fins melanistic; tubercles present on full length of all anal fin elements. Maximum adult size 35.5 mm SL.

DESCRIPTION.—Certain counts and measurements are presented in Tables 6-8. General body shape (Fig. 8) tuberculation patterns, features of the cephalic lateral line, and shape of the female genital papilla are illustrated in Figs. 1, 2, 3, and 8.

Scales in a lateral series (including pored scales) number 31 to 37 (Table 6), modally 33. Transverse scale rows (from anal fin origin to D_1 fin) number 9 to 12 (Table 6), modally 11. Transverse scale rows (from anal fin origin to D_2 fin) number 8 (2 specimens); 9 (16); 10 (15); 11 (11); and 12 (1); \bar{x} =9.84. Caudal peduncle scale rows number 14 to 17 (Table 6), modally 16.

Dorsal fin spines number 6 (20 specimens); 7 (100); and 8 (11); \bar{x} =6.93. Dorsal fin rays number 10 (45 specimens); 11 (82); 12 (3); and 13 (1); \bar{x} =10.69. Total dorsal fin elements number 16 (5 specimens); 17 (47); 18 (51); and 19 (8); \bar{x} =17.56. Branched caudal fin rays number 8 (3 specimens); 9 (18); 10 (58); and 11 (31); \bar{x} =10.06. Anal fin spines usually number 1 (108 specimens); rarely 2 (3). Anal fin rays number 5 (1 specimen); 6 (61); 7 (68); and 8 (1); \bar{x} =6.53. Total anal fin elements number 6 (1 specimen); 7 (61); 8 (69); and 9 (2); \bar{x} =7.54. Left pectoral rays number 8 to 11 (Table 6), modally 9 or 10. Pelvic fins always with 1 spine and 5 rays.

Branchiostegal rays number 5:5 (2 specimens); 5:6 (5); 6:6 (67); 6:7 (7); and 7:7 (1). Gill rakers on first arch short and stout and number 4 (2 specimens); 5 (4); and 6 (4); \bar{x} =5.20. Vertebrae number 31 to 34 (Table 6), modally 33.

Lateral line on body always incomplete with 0 to 6 pored scales (Table 7). Cephalic lateral line reduced, with most canals showing retarded or incomplete development. ST canal usually broadly interrupted at dorsal midline (ST count formula 2+2), except in three specimens with canal complete and pore count three. SO canal complete with 4 pores. CP with median, posterior-leading tube, present in all but three specimens. CP connected to SO canals by SO commissures. POM canal reduced, POM pores number 7 (6 specimens); 8 (101); and 9 (4); \bar{x} =7.98. IO canal always interrupted, IO pores number 1+3, except in three specimens with pore count of 1+4. Lateral canal complete with 5 pores. Head canal pores large but exceeded in size by the other species of *Microperca*.

Scales ctenoid, large, and of relatively same size on body. Head, nape, breast, cheeks, and prepectoral area always unscaled. Belly squamation highly variable on an individual basis. Percent of belly scaled is as follows: 0% (11 specimens); 10-20% (1); 30-40% (18); 50-60% (56); 70-80% (19); and 90-100% (3). Usually, about half the

belly is scaled in both sexes. Opercle scaled in 95 specimens, with from one to 16 scales present; unscaled in 16 specimens. Scales often embedded and difficult to discern. Opercular spine well developed.

The general body shape of breeding males and females is shown in Fig. 8. The body is small, laterally compressed and rather robust. The snout is usually rounded. The premaxillary is non-protractile and is connected to the snout by a narrow frenum. The mouth is small, the maxillaries extend posteriorly beyond the front margin of the eye. The gill membranes are moderately connected, free from the isthmus, and form an obtuse angle. The eye is moderately large (largest in the subgenus) and is situated high on the head. Fleishy interorbital width is roughly equal to snout length. Vertical fins small, pectoral fins small, fanlike, and rounded; posterior margin of caudal fin usually rather straight-edged, sometimes rounded. Pelvic fins reaching anus or beyond in breeding males, developing extra flaps of skin on both sides of the pelvic spine, and between pelvic rays one to three during breeding periods.

The general coloration of the body of both sexes is olivaceous or green. Unlike the other species of *Microperca*, the lateral pigment forms a series of stitchlike dashes rather than blotches. Lateral stitches number 9 (4 specimens); 10 (16); 11 (37); 12 (19); and 13 (4); \bar{x} =11.04. Three distinct basicaudal spots are often present. The upper lip is more heavily pigmented than the lower; tiny discrete melanophores are evenly spaced on the chin, breast, and belly of males. Females may have large, randomly spaced melanophores on lower lip and chin but have no pigment on the breast or belly. The posterior edges of the body scales are broadly margined by melanophores, appearing dusky on the upper parts of the body, somewhat laterally and including scales around the caudal peduncle. D_2 and caudal fins of both sexes distinctly barred. Well-defined dark teardrop present beneath eye; dark line or blotch of melanin usually present anterior and posterior to margins of eye. Humeral spot absent. Dorsal saddles usually vague or nonexistent, when present number 7 or 8.

Breeding coloration: The following color description is based on color photographs of breeding individuals, specimens seen in life during February at San Marcos, and from the field notes of Reeve M. Bailey and Carl L. Hubbs made on specimens collected in April and June respectively.

The general body coloration of males is dusky overall, plain green to reddish olive with metallic green present on the opercle, prepectoral area, and lateral portions of the stomach. Amber or brown bands are intense on the D_2 and caudal fins. The lateral stitches are very dark and distinct, and in the most intensely marked individuals they become elongated and form dusky vertical bars.

Most breeding color changes take place in the fins of males rather than on the body. The head, D_2 , and caudal fins become thickened and milky white. The D_1 fin is the most brightly marked region and may be described as

follows: milky blue-black on basal one-third, except melanin not present on the white spines; distal margin of fin a deep dusky green or gray-black; subdistally a broad band of red-orange color traverses the entire fin interradially. The black pigment in the basal one-third of the fin is most intense on the membranes between the first five or six spines becoming more subdued posteriorly. The anal and pelvic fins are very dusky overall with melanophores evenly distributed on the membranes of the fins usually not on the rays. The pectoral rays are clearly outlined by melanophores with little pigment on the ray membranes and none on the rays themselves.

Females are more or less colored as they are when juvenile or in nonbreeding condition. The anal and pelvic fins are generally clear with some random scattering of pigment blotches. The pectoral fins are outlined with black melanophores. The D_1 fin has the basal portion marked with diffuse dark spots and is occasionally margined with a thin, dusky band. Some scattered pigment occurs in a random fashion medially. Occasionally a light wash of orange is present subdistally. The iris of the eye is usually orange.

Tuberculation: Tubercle distribution in *E. fonticola* has been described by Collette (1965:605-606); the following is intended to amplify his description with additional observations on the variation and number of tubercles in the species.

Tubercles occur on the anal and pelvic fins of males only, and are present in varying degrees of development from collections made during February, March, April, May, June, and September. No tubercles were present on December-collected specimens. Tubercle size varies with body size. Small males (<21 mm SL) have the smallest tubercles, whereas larger males (>25 mm SL) have somewhat larger tubercles.

At maximum development small to moderate-sized, round, white tubercles are present in a single file on the anal fin and the ventral surfaces of the pelvic fins. Pelvic fin tubercles at maximum development are distributed as follows: distal tip of first ray; full length of rays two through four; and distal half of ray five. Tubercles do not develop on the pelvic fins spines. Anal fin tubercles at maximum development are distributed as follows: full length of anal spine; distal seven-eighths of all the anal rays except the final element of the last branched ray in which tubercles do not develop.

By counting the number of tubercles from the base of a fin element to the tip of a single ray branch the following variation in numbers of tubercles was observed at maximum development: tubercles on first pelvic ray number 4 to 9; second ray 5 to 12; third ray 7 to 18; fourth ray 9 to 14; fifth pelvic ray usually 4 or 5 tubercles; tubercles on anal spine number 7 to 10; first anal ray 8 to 13; second ray 9 to 15; third ray 9 to 18; fourth ray 6 to 16; fifth ray 7 to 13; sixth anal ray usually 5 or 6 tubercles. Tubercles on pelvic fins of males from February, March, June, and September are developed only on

the middle rays, whereas in April they are at maximum development. There seems to be only individual variation in anal fin tubercle development; at least some males from all the months mentioned display maximum development. As in *E. proeliare*, tubercles evidently develop first on the middle rays and then spread to the other rays as first suggested by Collette (1965).

GEOGRAPHIC VARIATION.—Fortunately, a few collections of *E. fonticola* were made from Comal River before the presumed extirpation of the species from the site. When the San Marcos and Comal River populations are compared, *E. fonticola* exhibits rather clear-cut character shifts in several features (Tables 6-7).

The character differing most saliently was the number of left pectoral rays (Table 6). In the Comal River population 90 percent of the individuals have nine or fewer pectoral rays; in the San Marcos population 88 percent have 10 or more pectoral rays. Likewise, there are average differences between the two populations in number of lateral scales, number of transverse scale rows, number of caudal peduncle scale rows, and number of vertebrae (Table 6). The Comal River population also shows highly significant sexual differences in the number of pored lateral line scales (see Sexual Dimorphism section) whereas this character did not differ between the sexes from the San Marcos River. In the Comal River sample, 85 percent of the individuals have 33 or fewer lateral line scales; in the San Marcos River 47 percent have 34 or more lateral line scales. Differences between the two populations for the other characters listed above are not as great. No significant differences between the two populations were found for other meristic characters or body proportions.

The pigmentation pattern of the breeding male D_2 fin was observed to be different between the two populations. Males from the San Marcos River display the typical amber-colored banding pattern in the D_2 fin, with the bands of pigment occurring both radially and interradially. Most breeding males from Comal River deviate in having the bands absent with the melanophores evenly distributed throughout the fin. Some lighter colored males have very irregular, wavy bands that approach the San Marcos pattern.

The two populations are isolated from each other by approximately 18 airmiles and about 100 river miles. Apparently the isolation between the two localities has contributed to the degree of differentiation noted between the two populations. Modification of structural characters of fishes (e.g. scales, vertebrae) has been experimentally demonstrated by differences in temperature during development (Hubbs, 1926a). The temperatures in the headwaters of San Marcos River and Comal Spring differ by about 2.2° C on the average (Schenck and Whiteside, 1976). In most cases the experimental modification of fish structures to a significant level is produced with greater temperature differences involved. Therefore, it is difficult to imagine that the slight temperature dif-

ferences between the two localities could produce a near 90 percent separation between the two populations in number of left pectoral rays.

The isolation of the two springs, the magnitude of the differences observed, the fact that the region is well documented as an area of aquatic endemism, and the small differences in temperature between the two springs argues for real genetic differentiation between the two populations rather than just a morphological response to the temperature conditions of the environment. It is highly probable that genetic drift has been responsible for the divergence of the two populations and that the high temperatures of the springs and the numerous generations produced each year have influenced and accelerated the rate of evolution of this species (Miller, 1948).

E. fonticola has differentiated sufficiently in number of pectoral rays and second dorsal fin pigmentation to allow taxonomic breakdown into subspecies, at least according to the criteria of Mayr (1969). However, the 93 percent separation for subspecies suggested by Bailey et al. (1954) is not met. Even if individuals from Comal River still exist naturally, the present introduction of individuals from San Marcos River (Schenck and Whiteside, 1976) will surely obscure the character shifts observed. If the Comal River population is indeed extinct, it should be noted that it was clearly part of an evolutionary unit separate from the San Marcos population.

SEXUAL DIMORPHISM.—Sexual dimorphism in breeding coloration, pelvic fin shape, tuberculation, and genital papilla shape was discussed elsewhere in this paper.

Significant sexual dimorphism in the number of pored lateral line scales was noted for the Comal River population of *E. fonticola* (Table 7). Other species showing significant sexual differences in this character are some members of *Hololepis* (Collette, 1962), and *E. hennicotti* (Page and Smith, 1976). The biological significance of this difference is unknown. Lateral line canals are better developed in more active forms (Hoar, 1975) and thus the more completely developed canals in male *E. fonticola* suggests that there may be differences in activity between the sexes of this species. The detection of prey, enemies, and sexual partners as a result of local water displacement are some biological functions of the lateral line. The better developed lateral line in males perhaps reflects the more active role of the male in at least some of the above categories. This line of reasoning is substantiated among darters by the fact that males are generally the more active and aggressive of the two sexes at least during reproductive periods (Page, 1974b; 1975). The San Marcos River population did not exhibit sexual dimorphism in the number of pored lateral line scales.

E. fonticola shows the least amount of sexual dimorphism among the several morphometric characters measured (Table 8). Males of *E. fonticola* display significantly greater values for fleshy interorbital width, caudal peduncle depth, D_1 fin basal length, D_2 fin basal length, pelvic fin length, and anal fin length. Body depth in females

averages significantly greater than males, but this is probably due to their egg-swollen condition.

In both populations males are larger than females. Of 12 collections, a male is the largest specimen in eight collections, a female in four. Of the five largest specimens of both sexes measured from these 12 collections the mean SL of males is 29.2 mm; whereas for females the mean SL is 28.2 mm. The largest male recorded is 35.5 mm SL; the largest female is 31.0 mm SL.

DISTRIBUTION.—The distribution of *E. fonticola* is plotted in Fig. 7. The range of *E. fonticola* is within the Coastal Plain boundary lying on the edge of the Edwards Plateau and the Balcones Escarpment fault line. *E. fonticola* has the most restricted range of the subgenus *Microperca* and has one of the most restricted ranges of all darters known.

The species is at present known to occur only in the San Marcos River at or near the city of San Marcos, Hays County, Texas. Formerly, it occurred in the Comal River, Comal County, Texas where 43 specimens were first captured by Evermann and Kendall (1894). The species has been reported from the Washita River, Arkadelphia, Arkansas, (Jordan and Gilbert, 1896) and Dickinson Bayou, Texas, (Evermann and Kendall, 1894). These specimens have not been located at FMNH, SU, UMMZ, or USNM and the records are almost certainly erroneous. They were probably based on the superficially similar *E. proclivare*. Collections made at numerous other springs along the Balcones Escarpment have not revealed the presence of *E. fonticola*.

The recently described freshwater shrimp, *Palaemonetes texanus* (Strength, 1976) is the only other endemic animal known to naturally occur in both the San Marcos and Comal Rivers at the above same localities. This region of Texas also harbors other endemic vertebrates such as several brook or cave salamanders of the genus *Eurycea* (Conant, 1975), the Guadalupe bass, *Micropterus treculi* (Hubbs and Peden, 1968), the largespring Gambusia, *Gambusia geiseri* (Hubbs, 1954) and the San Marcos Gambusia, *Gambusia georgei* (Hubbs and Peden, 1969).

The last reported collection of *E. fonticola* from the Comal River was made in 1954 (Hubbs and Strawn, 1957). Rotenone poisoning in 1951, the ceasing of flow from Comal Springs in 1956, and flooding of the area in 1971 were marshalled as evidence contributing to the elimination of the species from the Comal River (Schenck and Whiteside, 1976). Schenck and Whiteside spent over 300 man hours collecting throughout the Comal River and were unable to reveal the presence of the species. Individuals from the San Marcos River population were re-introduced into the Comal River in March, May, and June, 1975 (Schenck and Whiteside, 1976).

CONSERVATION STATUS.—*E. fonticola* is nationally recognized as an endangered species (Miller, 1972; Berger, 1977), and is listed as rare for the state of Texas (Miller, 1972). In a recent study of its population size in the San

Marcos River, Schenck and Whiteside (1976) estimated the total number of fish at 103,000. The species was considered endangered by these authors only because of its limited habitat. Control of development along the Comal and San Marcos rivers and limiting the pumping of water from the Edwards Aquifer were recommendations for management of the species.

Material Examined

San Marcos River Drainage. Texas: HAYS COUNTY: BU 1886 (10); INHS 75560 (10); 75562 (10); 75668 (20); KU 2284 (10); 5989 (10); UF 9305 (6); UL 12299 (4); UMMZ 120264 (10); 166045 (30).

Comal River Drainage. Texas: COMAL COUNTY: CU 38493 (17); FMNH 6847 (4); SU 5181 (4); TNHC 2336 (2); TU 4746 (30); UMMZ 86348 (1); USNM 166101 (35).

Etheostoma microperca Jordan and Gilbert

Least Darter

Figure 9

Microperca punctulata Putnam, 1863:4 (original description; from various points in Michigan, Wisconsin, Illinois, and Alabama).—Jordan, 1875 (list; range, in part).—Jordan, 1876 (White River, Indiana).—Jordan and Copeland, 1876 (range, in part).—Nelson, 1876 (Fox River, Geneva, Illinois; tribs., Lake Michigan, Waukegan, Illinois; not common in Wabash Valley).—Jordan 1877a (Indiana records).—Jordan, 1877b (not noticed by Rafinesque; White River, Indiana).—Jordan, 1877c (list; range).—Jordan and Gilbert, 1877 (Indiana list).—Klippart, 1877 (frequent for Indiana *vide* Jordan's papers).—Jordan, 1878a (Illinois records, in part).—Jordan, 1878b (list; range).—Jordan, 1878c (frequent in Indiana).—Jordan and Brayton, 1878 (Ohio; Illinois).—Jordan, 1879 (Fox River, Wisconsin; Rock River, Wisconsin; Wolf River, Wisconsin; White River, Indiana).—Forbes, 1880 (food habits).—Cope, 1881 (characters; western states [?]).—Hay, 1881 (comparisons).—Jordan, 1882 (range; Wabash River, Indiana [USNM 17846]).—Cope, 1883 (characters; western states [?]).—Jordan and Gilbert, 1883 (redescription; northwestern states [?]).—Forbes, 1884 (habitat; Illinois range).—Jordan and Eigenmann, 1886 (cranial description; vertebral number; *Microperca* a distinct genus).—Forbes, 1887 (range, in part; habitat).—Evermann and Cox, 1896 (Jones Creek, Dixon, Missouri, *vide* Meek, 1891).—Jordan and Evermann, 1896a (in key; redescription; range).—Jordan and Evermann, 1896b (list; range).—Cox, 1897 (redescription; Pine Creek, Crow Wing County, Minnesota; Grand Rapids, Minnesota).—Blatchley, 1901 (Lake Maxinkuckee, Indiana; Lost Lake, Indiana).—Ramsey, 1901 (Winnona Lake, Indiana).—Evermann, 1902 (Great Lakes list).—Eigenmann and Beeson, 1905 (Indiana list).—Jordan, 1905 (most degraded of all darters).—Michael, 1905 (Ecorse, Michigan [USNM 35031]; Port Huron, Michigan [USNM 73606]).—Fowler, 1906 (in synonymy of *E. fusiforme*).—Jordan, 1907 (most degraded of all darters).—Forbes and Richardson, 1908 (in Illinois key; redescription; food habits; range, in part; figure=*E. exile*).—Hankinson, 1908 (Walnut Lake, Michigan; presumed spawning in May).—Meek, 1908 (Indiana list; habitat; range).—Evermann and Clark, 1910 (Fletcher Lake, Indiana).—Meek and Hildebrand, 1910 (redescription; range; Hickory Creek, Marley, Illinois; New Lenox, Illinois; figure=*E. exile*).—Halkett, 1913 (perhaps in Canada).—Shelford, 1913 (records near Chicago, Illinois).—Cockerell and Elder, 1914 (scale shape and size).—Jordan, 1919 (orthotype).—Evermann and Clark, 1920 (redescription; coloration; figure; habits; parasites; habitat; range; Lake Maxinkuckee, Indiana; Lost Lake, Indiana).—Surber, 1920 (characters; Minnesota records *vide* Cox, 1897).—Pratt, 1923 (in key; characters; range).—Jordan, 1925 (most degraded of all darters).—Hubbs, 1926b (Great Lakes list).—Cahn, 1927 (Bark River, N Rome, Waukesha County, Wisconsin; predation; food habits).—Greene, 1927 (Wisconsin list).—Potter and Jones, 1927 (Iowa records).—Hubbs and Greene, 1928 (Great Lakes list).—Dymond et al., 1929 (Credit River, Ontario).—Hubbs and

Brown, 1929 (Ontario localities; habitat).—Jordan, 1929 (redescription; range).—Jordan et al., 1930 (list; range; name preoccupied).—Osburn et al., 1930 (Turkeyfoot Lake, Ohio).—Hankinson, 1933 (Michigan lakes; habitat).—Ricker, 1934 (mentioned).—Greene, 1935 (Wisconsin distribution and dispersal).—Hubbs and Cannon, 1935 (pelvic fin description; Forbes and Richardson's, 1908 figure of *M. punctulata*=*P. exilis*).—O'Donnell, 1935 (range, in part).—Aitken, 1936 (Iowa list).—Petravicz, 1936 (sexual dimorphism; coloration; behavior; spawning; incubation).—Blatchley, 1938 (characters; Indiana localities; habits).—Schrenkeisen, 1938 (characters; range).—Bangham and Hunter, 1939 (no parasites).—Greeley, 1940 (not in Lake Ontario tribs. of New York).—Aitken, 1941 (Iowa list).

Poecilichthys punctulata.—Hoy, 1877 (common in Racine County, Wisconsin).

Alvarius (Microperca) punctulata.—Jordan and Gilbert, 1886 (compared with *A. fonticola*).

Alvarius punctulatus.—Jordan, 1887 (list; *Alvarius* and *Microperca* probably identical).—Forbes, 1888 (food habits).

Etheostoma microperca Jordan and Gilbert in Gilbert, 1887:63-64 (substitute name for *M. punctulata* preoccupied in *Etheostoma*; comparisons).—Jordan, 1888 (in key; characters; range).—Meek, 1891 (Jones Creek, Dixon, Missouri [USNM 42578]).—Meek, 1892a (Cedar River and tribs., West Liberty, Iowa [USNM 174834]; Maquoketa River, Delhi, Iowa; rare at Manchester, Iowa).—Meek, 1892b (scarce in Cedar River, Iowa).—Eigenmann and Beeson, 1894 (Indiana records).—Hay, 1894 (in Indiana key; redescription; localities; food *vide* Forbes, 1880; 1884).—Kirsch, 1894 (Blue Lake, Indiana [SU 6287]; Round Lake, Indiana).—Boulenger, 1895 (in key; partial synonymy; redescription; range).—Kirsch, 1895 (Fish Lake, Indiana).—Eigenmann, 1896 (Turkey Lake, Indiana; Tippecanoe River, Indiana).—Garman, 1896 (Kentucky record *vide* Woolman, 1892).—Hay, 1896 (Water Valley, Lake County, Indiana [FMNH 334]; Momence, Illinois [FMNH 310]).—Blatchley and Ashley, 1901 (Indiana lake records).—Blatchley, 1902 (Indiana lake records).—Hay, 1902 (Indiana records; range).—Bailey, 1951 (Iowa list; key).—Harlan and Speaker, 1951 (characters; rare in Iowa).—Moore, 1952 (Oklahoma list).—Linder, 1953 (reference to Petravicz, 1936).—Hall, 1954 (Spring Creek, 2 mi E Camp Garland, Mayes County, Oklahoma).—Cleary, 1954 (rare in lower Cedar River, Iowa *vide* Meek, 1892a, b).—Hubbs, 1954 (reference to Fowler's 1945 erroneous records).—Taylor, 1954 (records for upper peninsula, Michigan).—Gerking, 1955 (in Indiana key).—Linder, 1955 (Blue River, Oklahoma).—Bailey, 1956 (Iowa list; key).—Eddy, 1957 (in key; range).—Hubbs and Lagler, 1957 (Great Lakes list).—Moore, 1957 (in key; characters; range, in part).—Trautman, 1957 (in Ohio key; figure; redescription; distribution; habitat).—Underhill, 1957 (Minnesota distribution; zoogeography).—Hubbs and Lagler, 1958 (in key; range; SW populations probably distinct subspecies; figure).—Linder, 1958 (reference to Petravicz, 1936).—Scott, 1958 (Ontario list).—Slattenenko, 1958a (in Canada key; partial synonymy; redescription; range; habitat).—Slattenenko, 1958b (Great Lakes basin).—Becker, 1959 (Plover River, Wisconsin).—Blair, 1959 (NE Oklahoma records; habitat; abundance; species associates).—Hallam, 1959 (species associates).—Bailey et al., 1960 (list).—Dickinson, 1960 (in Wisconsin key; figure).—Becker, 1961 (changing distribution in Wisconsin).—Blair and Windle, 1961 (habitat; associate of *E. cragini*).—Eddy et al., 1963 (above and below St. Anthony Falls, Minnesota).—Scott, 1963 (Ontario list).—Branson, 1964 (first Kansas record).—Smith, 1965 (occasional in NE Illinois).—Becker, 1966 (absent from SW Wisconsin).—Breder and Rosen, 1966 (breeding habits summarized).—Copes and Tubbs, 1966 (not taken in Red River, North Dakota).—Pflieger, 1966 (Missouri list; key).—Braasch and Smith, 1967 (reproductive behavior similar to *E. gracile*).—Branson, 1967 (Neosho River, Oklahoma records; habitat).—Branson and Ulrikson, 1967 (gill raker counts; gill filament counts; branchial skeleton).—Cross, 1967 (in Kansas; redescription; locality; habits).—Hubbs, 1967 (artificial hybrid survival).—Phillips and Underhill, 1967 (new Minnesota records).—Distler, 1968 (artificial hybridization with *E. spectabile*).—Moore, 1968 (in key; characters; range, in part).—Nelson, 1968 (Crooked Lake, Indiana).—Nelson and Gerking, 1968 (in Indiana key; range).—Whitaker,

1968 (in key; map, in part).—Eddy, 1969 (in key; range).—Scott and Crossmann, 1969 (in Ontario key; Atlantic watershed basin).—Bailey et al., 1970 (list).—Branson et al., 1970 (Spring River records; habitat; breeding on June 30; not common).—Van Meter and Trautman, 1970 (tribs., Lake Erie).—Pflieger, 1971 (Missouri distribution; habitat; zoogeography).—Eddy et al., 1972 (Ottetail River, Minnesota; zoogeography).—Miller, 1972 (threatened in Pennsylvania and Kansas).—Buchanan, 1973a (in Arkansas key; distribution, in part).—Buchanan, 1973b (Arkansas list).—Hine et al., 1973 (changing status in Wisconsin).—Miller and Robison, 1973 (in Oklahoma key; redescription; distribution; habitat).—Moore, 1973 (relict in part of Oklahoma).—Platt et al., 1973 (peripheral in Kansas).—Scalet, 1973 (reference to Petravic, 1936; Winn 1958a).—Scott and Crossman, 1973 (in Canada key; redescription; coloration; distribution; biology; relation to man; partial synonymy; figure).—Smith, 1973 (in Illinois key; range).—Buchanan, 1974 (vulnerable in Arkansas; habitat; range, in part).—Eddy and Underhill, 1974 (in Minnesota key; figure; redescription; habitat; range; Minnesota records).—Pflieger, 1974 (abundant in W Ozark springs).—Robison, 1974 (Arkansas range, in part; rare).—Balon, 1975 (phytophil reproductive guild).—Clay, 1975 (in Kentucky key; redescription, in part; records, in part).—Cross and Collins, 1975 (Kansas range; characters; habitat; biology).—Lutterbie, 1975 (in Wisconsin key; figure; range).—Pflieger, 1975 (in Missouri key; figure; characters; distribution; habitat; biology).—Seeburger, 1975 (some Wisconsin records).—Becker, 1976 (Lake Michigan distribution; habits; value; status).—Crossman, 1976 (mentioned).—Richards, 1976 (Au Sable River, Michigan).—Hubbs and Pigg, 1976 (Oklahoma distribution reduced by reservoir flooding).—Balon et al., 1977 (phytophil guild).—Collette and Bănărescu, 1977 (nomenclature).—Tramer, 1977 (Tenmile Creek, Ohio; mortality due to stream dessication).

Etheostoma microperca.—Woolman, 1892 (Little Barren River, Osceola, Barren County, Kentucky; rare).

Microperca punctulata.—Large, 1903 (Mackinaw Creek, Woodford County, Illinois).—Evermann, 1918 (Kentucky record *vide* Woolman, 1892).

Microperca punctulata.—Hankinson, 1911 (predation).

Microperca microperca microperca.—Hubbs and Lagler, 1939 (in Great Lakes key).—Hubbs and Lagler, 1941 (in key; range; habitat; SW populations probably a distinct subspecies).—Carlander, 1941 (in key; Pug Hole Creek, Crow Wing County, Minnesota; Rum River, near Anoka, Minnesota; Crystal Lake, Minnesota).—Haas, 1943 (localities in McHenry County, Illinois).—Eddy and Surber, 1943 (in key; figure; redescription; range; Minnesota localities).—Radforth, 1944 (SW Ontario; zoogeography; map).—Gerking, 1945 (Indiana distribution; habitat).—Hubbs, 1945 (only Mississippi River system in Minnesota).—Hubbs and Lagler, 1947 (in key; range; habitat; southwestern populations probably a distinct subspecies).—Eddy and Surber, 1947 (in key; figure; redescription; range; Minnesota localities).—Leonard and Leonard, 1949 (Birch Lake, Michigan).

Microperca microperca.—Eddy, 1945 (smallest fish in Minnesota).—Dymond, 1947 (Ontario range; habitat).—Paden, 1948 (Oklahoma records; Blue River, N Tishomingo, Oklahoma).—Moore and Rigney, 1952 (associate of *P. spectabilis* and *P. r. cyanorum*).—Scott, 1954 (figure; characters; Canada range).

Etheostoma (Microperca) microperca.—Bailey and Gosline, 1955 (vertebral counts).—Winn, 1958a (spawning dates; size of females; sex dimorphism; territory defense; spawning position; egg site deposition; number eggs laid; migration).—Winn, 1958b (spawning; territoriality; egg laying).—Collette, 1965 (tubercle number, placement).—Collette and Knapp, 1966 (location of syntypes of *M. punctulata*; discussion of replacement name).—Page and Whitt, 1973a (isozyme patterns).—Page and Whitt, 1973b (isozyme patterns).

TYPES.—*Microperca punctulata* was described from a large series of syntypes from several localities in Illinois, Wisconsin, Michigan, and Alabama. Those from Alabama are apparently no longer extant and probably rep-

resented *E. proeliare* or juveniles of another similar appearing species. A number of the original syntypes were transferred from MCZ to USNM or UMMZ (Collette and Knapp, 1966) and only their present catalogue numbers are given.

Collette and Knapp (1966) located the following syntypes; USNM 1377, MCZ 24566, Calumet R., near Chicago, Illinois, R. Kennicott (4, 22-24 mm SL); USNM 1283, MCZ 24570, UMMZ 86457, Oconomowac R., Lac la Belle, Wisconsin, July, 1853, S. F. Baird (32, 23-31 mm SL); USNM 1288, MCZ 24690, UMMZ 86316, Port Huron, Michigan, August, 1853, S. F. Baird (42, 15-30 mm SL); MCZ 24582, Detroit R., Michigan, August, 1853, S. F. Baird (1, 19 mm SL); and USNM 1276, tribs., Fox R., Vienna, Wisconsin, August, 1853, S. F. Baird (1, ?), not found.

A lectotype of *Microperca punctulata* is herein selected from UMMZ 86457. The lectotype now bears the following number and data: UMMZ 200216, Oconomowac River [Rock drainage], Lac la Belle [Waukesha County], Wisconsin, July, 1853, S. F. Baird. The lectotype is a male, 24 mm SL, with no pored scales and 31 or 32 lateral scales; dorsal fins with 6 spines and 9 rays; anal fin with 1 spine and 5 rays; branchiostegal rays 5:5, IO pores 0+3; POM pores 6; ST canal interrupted at midline, nape, cheeks, and breast naked. The other syntypes now become paralectotypes bearing their original catalogue numbers.

The lectotype was chosen from the above locality for the following reasons. The species is apparently gone from the Calumet River, Illinois, and the localities in Michigan are from within the region of geographic variation in the number of IO pores (see Geographic Variation section). The type-locality, now in Wisconsin, is from a drainage wherein the species is still common and where variation in most characters is insignificant.

ETYMOLOGY.—The name *microperca* means small (*micro*) perch (*perca*) in reference to its adult size in relation to other percids.

DIAGNOSIS.—A species of the subgenus *Microperca* distinguished from other members by combinations of the following characters: 1 or 2 anal spines, modally 2; usually 14 to 17 total dorsal fin elements; IO pores 0+3 or 0+2; POM pores modally 6; usually 32 to 34 lateral scales (modally 33), usually with 0 or 1 pored; branchiostegal rays modally 5:5, vertebrae usually 32 or 33; opercles usually with embedded or exposed scales, cheeks and prepectoral area naked; genital papilla of female conical; lateral pigment usually forming 8 to 10 blotches on sides of adults. In breeding males, subdistal spots of red-orange color present in all membranes of D, fin; basal one-third of D, fin charcoal gray; pelvic and anal fins brick red or orange; tubercles usually present on full length of anal spines only. Maximum adult size 36.9 mm SL.

DESCRIPTION.—Certain measurements are presented in Table 9. General body shape (Fig. 9), tuberculation pat-

terns, features of the cephalic lateral line, and shape of the female genital papilla are illustrated in Figs. 1, 2, 3, and 9.

Scales in a lateral series (including pored scales) number 30 to 36 (Fig. 10), modally 33. Transverse scale rows (from anal fin origin to D_1 fin) number 8 (54 specimens); 9 (294); 10 (290); 11 (109); and 12 (10); \bar{x} =9.64. Transverse scale rows (from anal fin origin to D_2 fin) number 7 (12 specimens); 8 (69); 9 (81); 10 (116); and 11 (24); \bar{x} =9.24. Caudal peduncle scale rows number 12 to 16 (Fig. 11), modally 14.

Dorsal fin spines number 6 (48 specimens); 7 (123); and 8 (10); \bar{x} =6.79 in Ozark populations, 5 (30 specimens); 6 (357); 7 (253); and 8 (5); \bar{x} =6.36 in northern populations. Dorsal fin rays number 8 (2 specimens); 9 (69); 10 (95); and 11 (15); \bar{x} =9.68 in Ozark populations, 7 (3 spe-

cimens); 8 (187); 9 (399); and 10 (56); \bar{x} =8.79 in northern populations. Total dorsal fin elements 13 to 18 (Fig. 12), modally 16 in Ozark populations; modally 15 in northern populations. Branched caudal fin rays number 9 (82 specimens); 10 (343); 11 (256); and 12 (9); \bar{x} =10.28. Anal fin spines number 1 (187 specimens); or 2 (649); \bar{x} =1.78. Anal fin rays number 4 (12 specimens); 5 (451); 6 (365); and 7 (17); \bar{x} =5.46. Total anal fin elements 6 to 9 (Fig. 13), modally 8 in Ozark populations, modally 7 in northern populations. Left pectoral rays number 9 to 12 (Fig. 14), modally 10. Pelvic fins always with 1 spine and 5 rays.

Branchiostegal rays number 5:5 (134 specimens); 5:6 (25); and 6:6 (10) in Ozark populations, 5:4 (1 specimen); 5:5 (203); 5:6 (6); and 6:6 (5) in northern populations. Gill rakers on first arch moderately long and number 4

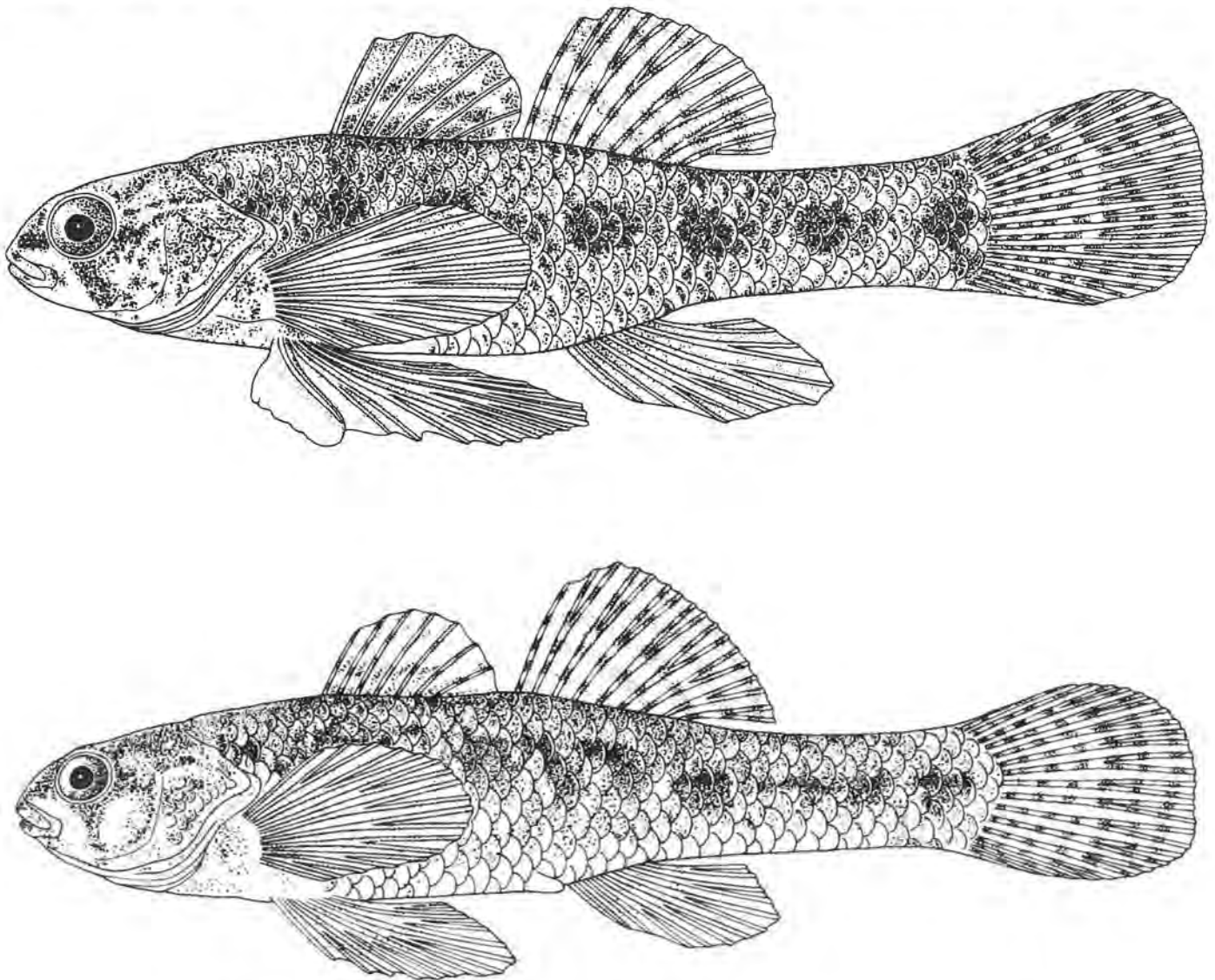


Fig. 9. Breeding adults of *E. microperca*: INHS 26932, trib., Iroquois River, Iroquois County, Illinois, 23 May 1976. Top) male, 30 mm SL. Bottom) female, 30 mm SL. Nuptial tuberculation not shown. Drawings by Alice A. Prickett.

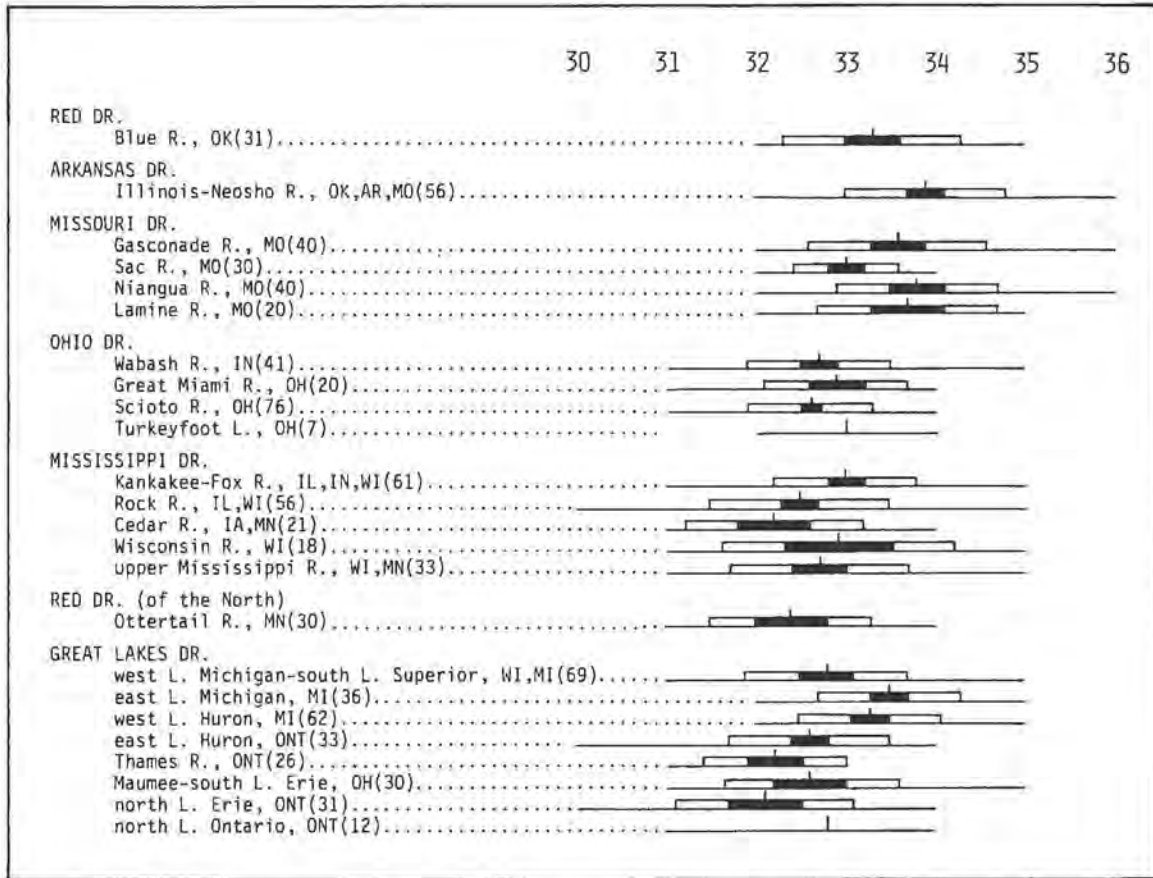


Fig. 10. Variation in the number of lateral scales in populations of *E. microperca*. See legend for Fig. 5 for explanation of the diagrams.

(1 specimen); 5 (8); and 6 (1); \bar{x} =5.00. Vertebrae number 32 (7 specimens); 33 (22); and 34 (6); \bar{x} =33.97 in Ozark populations, 32 (14 specimens); 33 (25); and 34 (4); \bar{x} =33.77 in northern populations.

Lateral line on body always incomplete, pored scales number 0 (513 specimens); 1 (282); 2 (56); and 3 (3); \bar{x} =0.42. Cephalic lateral line reduced with most canals showing retarded or incomplete development. ST canal always broadly interrupted at dorsal midline, ST formulae number 1+1 (2 specimens); 1+2 (3 specimens; and 2+2 (659 specimens). SO canal complete and always with 4 pores. CP present or absent; if present always without median, posterior-leading tube. Excluding Ozark populations CP present in 472 specimens, absent in 130 specimens. (Condition of CP in Ozark populations discussed in Geographic Variation section). POM canal greatly reduced, POM pores number 5 (23 specimens); 6 (558); and 7 (45); \bar{x} =6.04. IO canal always interrupted with posterior tube lacking. Excluding northeastern populations IO pores number 0+2 (2 specimens); 0+3 (246); and 0+4 (8). (Condition of IO canal in northeastern populations discussed in Geographic Variation section.) Lateral canal usually complete with 5 pores, sometimes a pore missing anteriorly in Ozark populations. Head canal

pores largest in subgenus and probably largest of all darters.

Scales ctenoid, large, and of relatively same size on body. Head, nape, breast and prepectoral area always unscaled. Belly squamation somewhat variable. Percent of belly scaled is as follows: 10-20% (9 specimens); 30-40% (80); 50-60% (425); 70-80% (109); and 90-100% (46). Belly naked along complete midline in 3 specimens. Generally half of the belly is scaled in both sexes. Opercle more often scaled than not. Percent of opercle scaled is as follows: 0% (276 specimens); 10-20% (81); 30-40% (39); 50-60% (59); 70-80% (38); and 90-100% (129). Scales on opercle often embedded and difficult to discern. Opercular spine well developed.

The general body shape of breeding males and females is shown in Fig. 9. The body is small, laterally compressed and relatively deep (Table 9). The snout is usually rounded, the premaxillary is protractile and is connected to the snout by a narrow frenum. The mouth is small (smallest in subgenus) and usually does not extend posteriorly beyond front margin of eye. The gill membranes are moderately connected, free from the isthmus, and form an obtuse angle. The eye is small and situated high on the head. Vertical fins small, pectoral fins fanlike and rounded; posterior margin of caudal fin straightedged

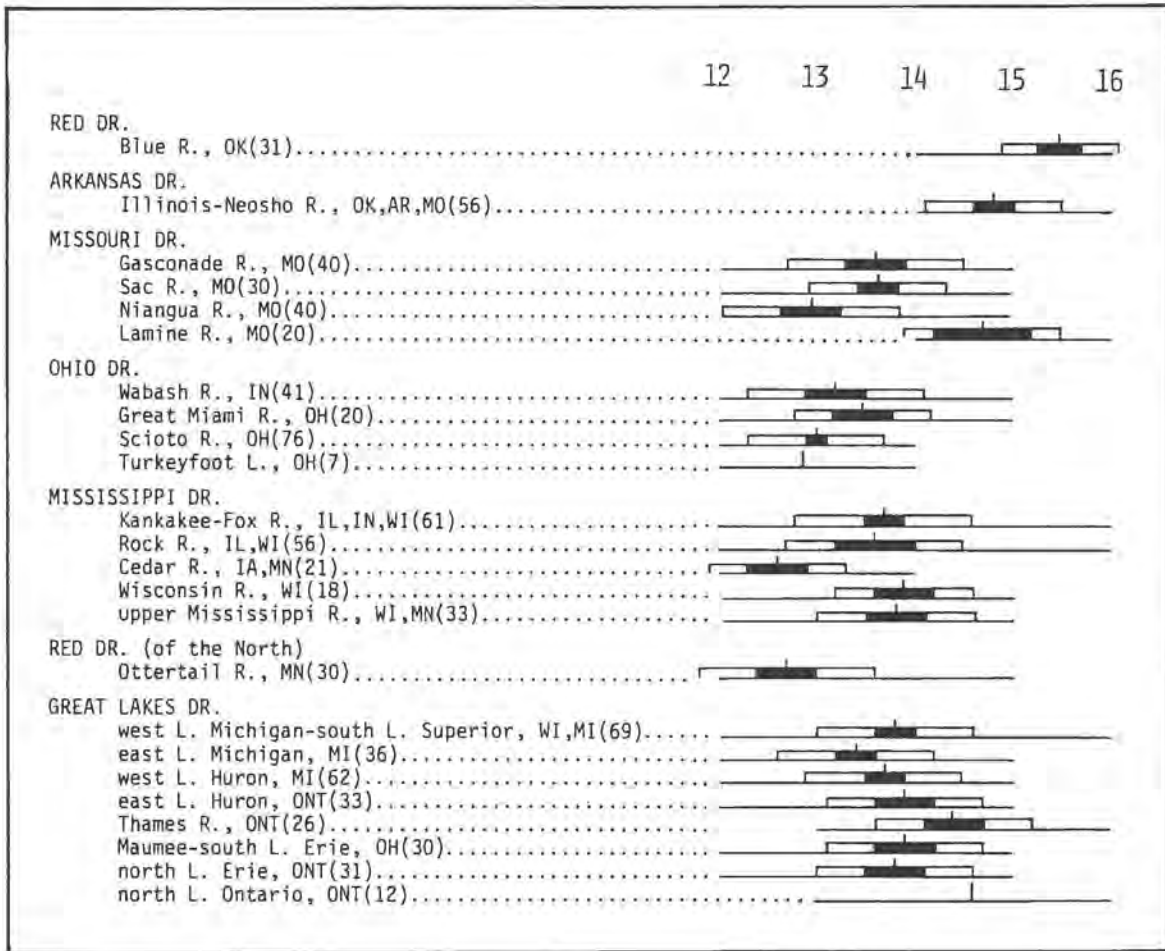


Fig. 11. Variation in the number of caudal peduncle scales in populations of *E. microperca*. See legend for Fig. 5 for explanation of the diagrams.

or rounded. Pelvic fins reaching anus or beyond in breeding males, developing extra flaps of skin on both sides of the pelvic spine and between pelvic rays one to three during breeding periods.

The general body coloration of both sexes is green to olive-green. Three basicaudal spots may be present or absent. Upper and lower lips pigmented to about the same degree. Melanophores on chin, throat, breast, and belly forming large irregular blotches in both sexes as opposed to the fine evenly sprinkled tiny melanophores of the other two species. Usually a large blotch of pigment on chin and often one on throat. Dorsal half of body sometimes uniformly dark, often just posterior edges of scales dark edged. Melanophores usually forming distinct lateral blotches in both sexes. Lateral blotches number 7 (22 specimens); 8 (137); 9 (219); 10 (126); and 11 (27); \bar{x} =9.00. Below lateral blotches are random spots of melanin smaller than the lateral blotches. Caudal and D_2 fins of both sexes distinctly barred. D_2 fin usually with 4 or 5 charcoal gray bands. Caudal fin usually with 6 or 7 charcoal gray bands. Pelvic and anal fins of males washed with orange year around. Well-defined, dark teardrop

present beneath eye; dark line or blotch of melanin usually present anterior to front margin of eye; post-orbital blotch vague or absent. Humeral spot absent. Dorsal saddles vague, poorly defined or absent; when present number 6 (36 specimens); 7 (45); 8 (24); and 9 (10); \bar{x} =7.14.

Breeding coloration: The following color description is based on color transparencies of breeding individuals, and specimens seen in life from all the major populations in the Ozarks as well as from several localities from more northern populations. Pigmentary differences exist between the Ozark populations and those from northern regions. The differences will be described below and discussed in more detail in the Geographic Variation section.

In males, the general body coloration is green to varying degrees, often with a suffusion of ochre on the body. Well-developed charcoal gray bands present in the D_2 and caudal fins which are creamy yellow or white. The opercles, belly and spaces between the lateral blotches are mist green with a metallic sheen. The lateral blotches are dark green-black.

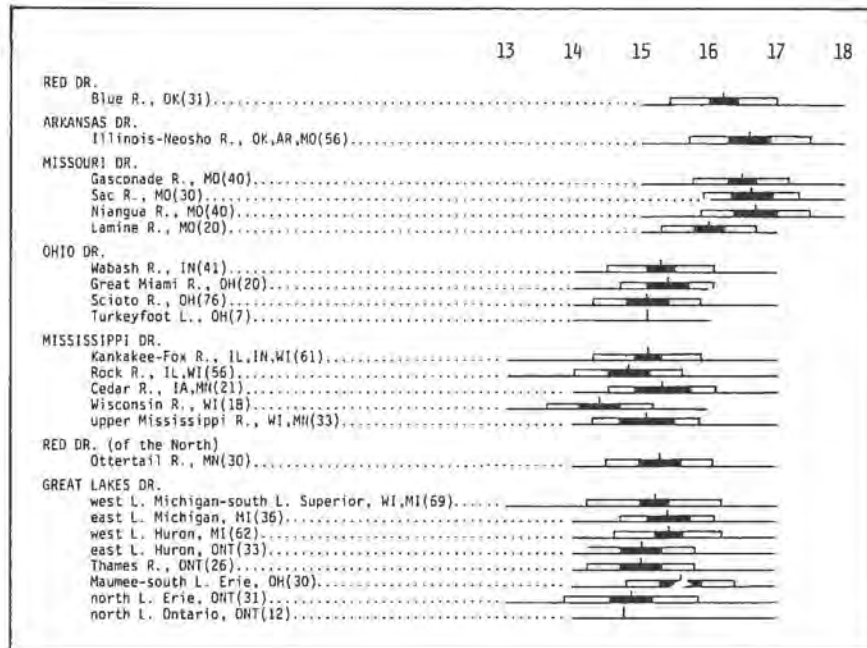


Fig. 12. Variation in the number of total dorsal fin elements in populations of *E. microperca*. See legend for Fig. 5 for explanation of the diagrams.

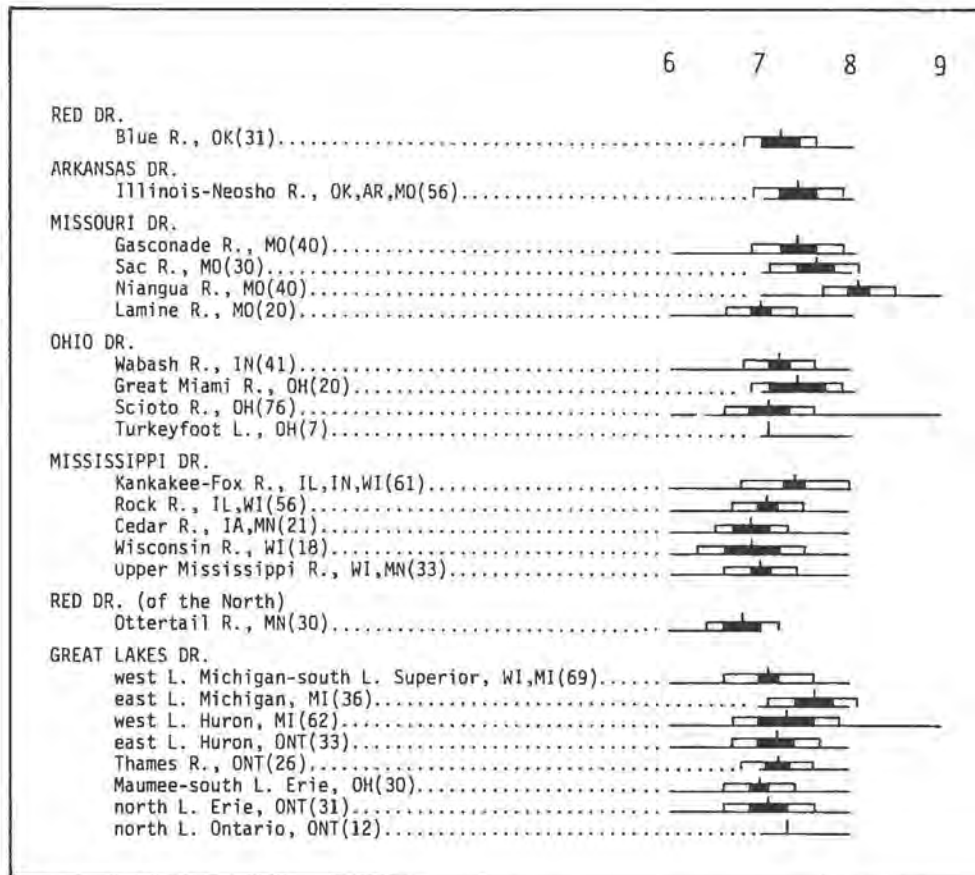


Fig. 13. Variation in the number of total anal fin elements in populations of *E. microperca*. See legend for Fig. 5 for explanation of the diagrams.

The most striking color changes take place in the fins of males. The D_2 and caudal fins become only slightly thickened and milky white, whereas the head region often is swollen and milky white in appearance. The D_1 fin has a subdistal series of blotches of red-orange color traversing through all of its membranes. The red-orange color being almost entirely restricted to the membranes and not on the spines. Some spots of mist green surround the red blotches. Basally and distally the D_1 fin has fairly heavy concentrations of melanophores which form charcoal gray horizontal bands of about equal intensity. In northern populations, both the anal and pelvic fins become solid red-orange with the pigment present both radially and interradially. In Ozark populations both the pelvic and anal fins are more brick red and distally have a distinctly demarcated band of gray to jet black caused by a heavy concentration of melanophores. After the melanophores continue basally giving the fins an overall dark red-black appearance.

The pectoral fins are usually clear, but the rays are sharply outlined by black melanophores. There is also a heavy concentration of melanin around the pelvic fin bases. Pre- and postorbital bars are intense, the teardrop

is jet black and runs through the eye. The iris of the eye is bright red or orange.

Breeding colors are poorly developed in females and their coloration is much the same year around. The pelvic and anal fins are sometimes amber in color and often develop a light yellow or orange wash. The pectoral fins are outlined with black melanophores and the D_2 and caudal fins develop the charcoal gray bands. The iris of the eye is orange. The general body coloration is like that described for the male.

Tuberculation: Tubercle distribution in *E. microperca* was briefly described by Collette (1965). The examination of many more samples containing breeding males has resulted in a modification of Collette's description. Tubercles are geographically variable in their number and distribution and were discovered to be present on the dorsal fins of breeding males from the Ozark region. The development of tubercles on the dorsal fins is not known for any other North American percid (Collette, 1965), but tubercles do occur on the dorsal fins of the European percid genera *Zingel* and *Romanichthys* (Collette, 1965).

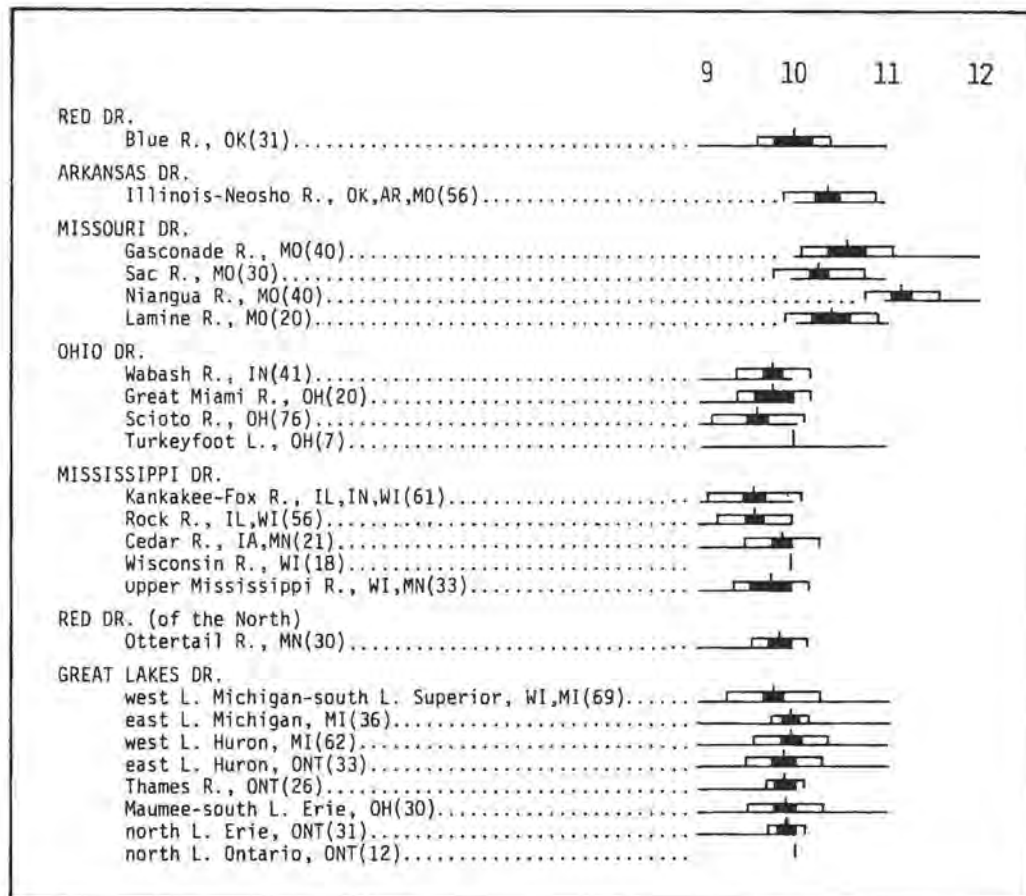


Fig. 14. Variation in the number of left pectoral rays in populations of *E. microperca*. See legend for Fig. 5 for explanation of the diagrams.

Tubercles occur on the anal, pelvic, and dorsal fins of males only and are present in maximum development from collections made during mid-March to early July. Tuberculate males from July come from constant temperature springs where the species presumably breeds over a protracted period. Specimens from 1 February and late July have only sparsely or weakly developed tubercles. Tubercles are largest on the central portions of the anal fin rays and diminish in size both basally and distally. At maximum development, northern populations have small, round, white tubercles present in a single file on the anal fin spines (never on the rays) and the ventral surfaces of the pelvic fins. Pelvic fin tubercles at maximum development are distributed as follows: full length of rays one through four; and distal half of ray five. Tubercles were not found on the pelvic fin spines. Anal fin tubercles at maximum development are distributed as follows: full length of first anal spine; distal seven-eighths of second anal spine. At maximum development, Ozark populations have a similar tubercle distribution on the pelvic fins but have a more extensive tubercle distribution on the anal fin which may be described as follows: full length of both anal spines; distal seven-eighths of anal rays one through three; medial portion of ray four; and basal portion of ray five. Most males have tubercles on the anal spines and only the first two anal rays.

Three collections from the Neosho River, Oklahoma, (APB uncat.; UTULSAC 1016, 2571) have tubercles present on one or both of the dorsal fins of males during March, April, and May. Tubercles on the dorsal fins are distributed as follows: distal seven-eighths of first two dorsal spines; and distal seven-eighths of first dorsal ray. The tubercles are small and evenly spaced. As many as seven tubercles are present per element.

By counting the number of tubercles from the base of a fin element to the tip of a single ray branch the following variation in numbers of tubercles was observed at maximum development in northern populations: tubercles on first pelvic ray number 3 to 7; second ray 10 to 15; third ray 15 to 18; fourth ray 4 to 8; fifth pelvic ray usually 2 to 4 tubercles, often altogether absent; tubercles on first anal spine number 2 to 7; second anal spine 3 to 7. In Ozark populations, the maximum number of tubercles on an anal fin ray is 10. At minimum development tubercles are present only on the central rays of the pelvic fins and are lacking on the anal spines.

GEOGRAPHIC VARIATION.—*E. microperca* is the most variable species in the subgenus with certain populations nearly differentiated to subspecies levels of recognition. No significant geographic variation in body proportions was observed. Almost every character investigated showed some geographically variable trends. The majority of the variation falls largely into the following three categories: (1) variation slight and random; (2) northeastern populations sharply divergent in one character; and (3) Ozark populations in various stages of differentiation.

The following characters investigated fall into pattern 1 above: number of pored lateral line scales, branched caudal fin rays, anal fin spines, features of the cephalic lateral line (except development of the IO canal) and all squamation characters. Variation in the number of pored lateral line scales appears to be of little significance. However, only three individuals had as many as three pored scales which is important to note inasmuch as Bailey (1951) and Trautman (1957) reported counts as high as eight pored scales for the species.

Northeastern populations of *E. microperca* are sharply set off from all other populations of the species in one characteristic. The IO canal is frequently reduced further (see Description) to a count of 0+2; of the usual three anterior pores the second one is most often missing. The area in which this type of variation occurs is shown in Fig. 15. Throughout the remainder of the range of the species the IO canal is consistent in always having a count of 0+3. Samples from the White River, Indiana, Great Miami and Maumee rivers, Ohio, and most of Michigan are intermediate for the two IO counts. That is, roughly half of the individuals from a given collection site within the area described above have the 0+2 IO count and half have the 0+3 IO count. Samples from the Scioto River and Turkeyfoot Lake, Ohio, and most of Ontario are usually 90 to 100 percent "pure" for the 0+2 IO count. However, the intermediate condition (both 0+2 and 0+3 counts) frequently appears within the otherwise "pure" zone of 0+2 counts in Ontario. This suggests that the differentiation noted for these northeastern populations is not yet complete. The broad area of intergradation between the two types of IO counts, the lack of strong differentiation in other independent character sources, and the lack of complete differentiation within the zone of "pure" 0+2 counts argues against the recognition of the populations as a separate taxonomic unit.

Several meristic characters, pigmentation features, tubercle patterns and maximum SL attained are all divergent in most Ozark populations. In general, the trend is toward greater numbers in the meristic features, tuberculation more extensive, and SL greater in the Ozark populations when compared to all other more northern and eastern populations combined. The variation is not clinal for most of these characters but is rather sharply deviate as demonstrated by several features: number of left pectoral rays (Fig. 14), total dorsal fin elements (Fig. 12), and maximum SL attained (Fig. 16). To a lesser extent the number of branchiostegal rays and the number of transverse scales to the D₁ fin show a similar trend toward greater values in the Ozark samples studied.

The divergence of Ozark populations is clearly illustrated by comparing the number of left pectoral rays (Fig. 14) and the total number of dorsal fin elements (Fig. 12) with other populations of the species. The ranges and means for these characters in the Ozarks are consistently higher and the 95 percent confidence intervals do not overlap with any other populations except in one in-

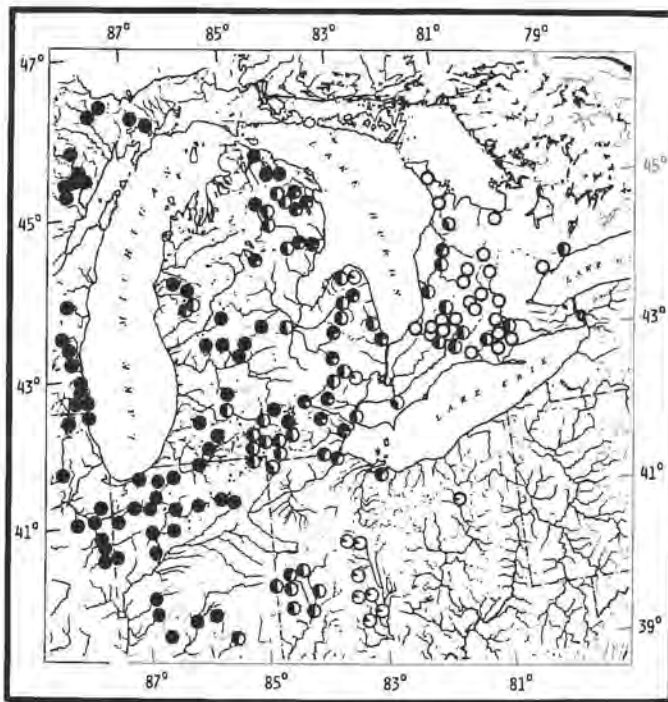


Fig. 15. Percent composition of 0+2 and 0+3 IO canal counts in northeastern populations of *E. microperca*. Solid black circles represent 100 percent of individuals from a particular site with a 0+3 IO count; open white circles represent 100 percent of individuals from a particular site with a 0+2 IO count. Partially filled circles represent localities where a certain percentage of the individuals from a particular site have a 0+2 IO count and a certain percentage have a 0+3 IO count (e.g. in Scioto River, Ohio samples 90 percent of the individuals have a 0+2 IO count; 10 percent have a 0+3 IO count). Based on a total of 1,447 specimens.

stance. In other characteristics, variation is discordant within the Ozarks. For example, in number of caudal peduncle scales (Fig. 11), number of lateral scales (Fig. 10) and total number of anal fin elements (Fig. 13) the overall variation is more random but with higher values for some Ozark populations. In number of caudal peduncle scales, three of the Missouri River samples are more like northern populations than like other Ozark samples. Only Neosho River samples show a greater frequency for the branchiostegal ray count of 5:6 or 6:6.

In other instances, divergence in the Ozark populations is complex and confounding. Individuals from the Blue River, Oklahoma, the most disjunct southwestern population of *E. microperca*, are often more like northern populations than like other Ozark populations in number of left pectoral rays and number of lateral scales. Blue River samples have the greatest mean number of caudal peduncle scales (Fig. 11). In pigmentation of the male pelvic and anal fins, Blue River samples are again more similar to northern populations. They lack the extensive melanophore concentrations on the distal edges of these fins so characteristic of other breeding males from the Ozarks.

Like the Blue River samples, individuals from Hahatonka Spring, Camden County, Missouri, are especially noteworthy for their strong divergence from other Ozark populations, primarily in having greater mean values for several characteristics. The most salient features are number of left pectoral rays (Fig. 14) and total number of anal fin elements (Fig. 13). The 95 percent confidence intervals do not overlap with any other populations for these two characteristics. In number of left pectoral rays individuals always have 11 or 12 elements ($\bar{x}=11.15$), the highest recorded for the species. Indeed, the SD bars barely overlap with other Ozark populations. Hahatonka Spring is one of the 15 largest springs in Missouri (Vineyard and Feder, 1974) where the water temperature is presumably constant. Whether the greater number of elements for the above fin counts is genetic or environmentally produced is unknown.

In maximum SL attained for both sexes, Ozark populations average greater (Fig. 16). The difference between Ozark and northern populations is highly significant when tested with the Kolmogorov-Smirnov two-tailed test ($P<.001$). The length frequencies also demonstrate that females attain a greater maximum length than males probably because they live longer. The greater size reached in the Ozarks may possibly be due to a longer, more favorable growing season, especially in springs or spring-fed streams where temperature fluctuates little and conditions are presumably optimal during most times of the year. Another character which may also be correlated with southern latitude is the development of more tubercles. At maximum development breeding males from Ozark populations frequently have tubercles present on the anal rays. Collette (1965) found that three other species of darters also have more extensive tuberculation in the southern parts of their ranges. Of unknown function and significance is the development of tubercles on the dorsal fins of breeding males from Spring Creek (Neosho drainage), Mayes County, Oklahoma. Many other collections of ripe males from this drainage and the other Ozark drainages did not reveal the presence of tubercles on the dorsal fins. Reproductive behavior of the species from this region has not been studied, and it is, therefore, unknown whether or not the tubercles function in different behavior patterns that are unique to Ozark populations.

The only feature of the cephalic lateralis system that varied significantly in the Ozarks was the development of the CP. In all but one of the Ozark samples the CP was absent or the supraorbital commissures leading to the pore were interrupted in at least some individuals. A number of populations were from 90 to 100 percent constant for the absence of the CP and others were variously intermediate (Fig. 17). In the final analysis, variation in CP development was largely random in the Ozarks. The larger size of specimens from the Ozarks would be expected to be correlated with the presence of a CP, but this was not the case. There is some variation in the presence or absence of the CP in northern populations,

but it is even more random than what takes place in the Ozarks.

As indicated in the Description, pigmentation of breeding male pelvic and anal fins is different in Ozark specimens. Fresh samples from all the major drainages have a heavy concentration of melanophores on the distal edges of the otherwise red-orange pelvic and anal fins which almost forms a gray band. Melanophores are never developed to that degree or pattern in northern samples where the pelvic and anal fins are a solid red-orange.

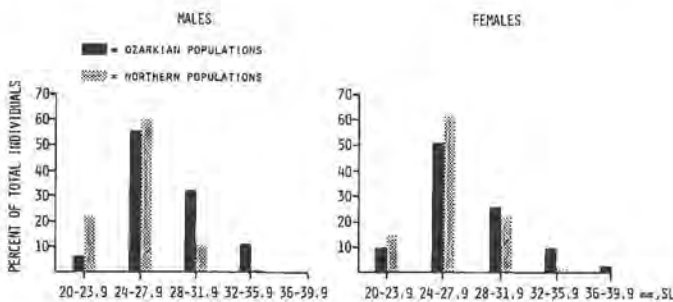


Fig. 16. Frequency distribution by size class and sex of adult *E. microperca* showing geographic variation in maximum size between Ozark and northern populations. Based on 418 males and 453 females.

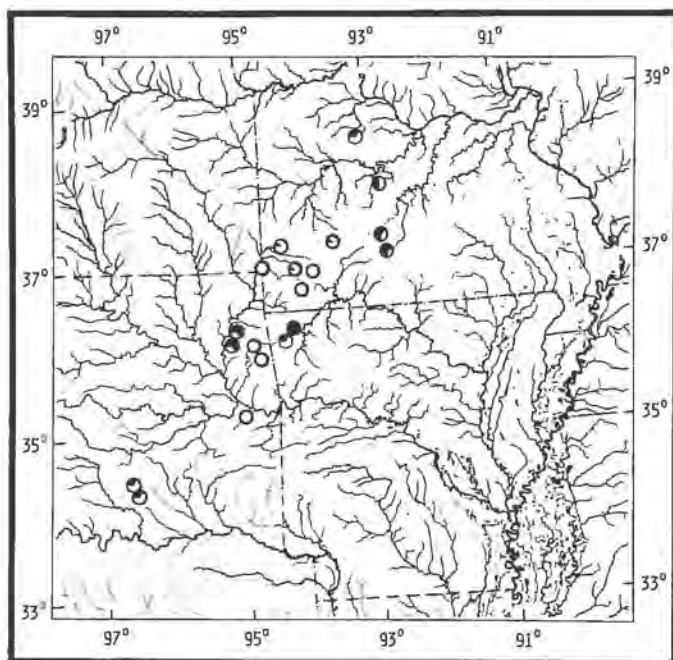


Fig. 17. Percent composition of the presence of a CP in Ozark populations of *E. microperca*. The solid black circle represents a locality where 100 percent of individuals have a CP. Open white circles represent localities where 100 percent of individuals lack a CP. Partially filled circles represent localities where a certain percentage of individuals from a particular site have a CP and a certain percentage lack one (e.g. in Hahatonka Spring, Missouri, samples 50 percent of the individuals have a CP; 50 percent lack a CP). Based on 261 specimens.

Substantial arguments could be made for the recognition of subspecies in *E. microperca*. In totality of characters the Ozark populations differ decidedly from northern populations. However, when considered individually the differences are discordant in the Ozarks, and overlap is sometimes broad. Furthermore the recognition of the Missouri-Oklahoma-Arkansas populations as subspecies would raise the question of how to treat the Blue River, Oklahoma, population. Its geographic position makes it illogical to consider it comprised of intergrades between the Ozarks and northern populations. Moreover, the most distinctive Ozark population is that from Hahatonka Spring. This population is as distinctive from other Ozark populations as they are from the remaining northern populations. Comparing specimens from Hahatonka Spring alone with northern populations in number of left pectoral rays reveals a 92 to 100 percent separation. Its geographic location and overlap in many other characters with the other Ozark samples makes taxonomic recognition of the population too arbitrary.

Subspecific partitioning of certain populations of *E. microperca* hardly seems justified from a pragmatic viewpoint especially if the categorization does not result in some sort of ordering of the variation. Taxonomic breakdown would be subjective and actual identification of a subspecies 90 percent of the time would be impossible. Inasmuch as the variation is known and described herein it seems sufficient to recognize the species as monotypic while noting that several populations are in the process of genetic differentiation.

SEXUAL DIMORPHISM.—Sexual dimorphism in breeding coloration, tuberculation, pelvic fin shape, and genital papilla shape was discussed elsewhere in this paper. No sexual dimorphism in any meristic character examined was observed.

In body proportions, *E. microperca* is the most sexually dimorphic species in the subgenus. Males display significantly greater values for head length, snout length, fleshy interorbital width, postdorsal length, caudal peduncle depth, upper jaw length, eye diameter, D_1 base length, D_2 base length, pelvic fin length, pectoral fin length, anal fin length, and D_2 fin length (Table 11). Females display a significantly greater value for body depth presumably due to their egg-swollen condition.

Although there is considerable geographic variation in size, females appear to reach a greater maximum SL than males in most populations. In Ozark populations the largest female is 36.9 mm SL; the largest male is 33.0 mm SL. In northern populations the largest female is 33.6 mm SL; the largest male is 33.3 mm SL.

DISTRIBUTION.—The distribution of *E. microperca* is plotted in Fig. 18. To determine historical changes in the range of the species, locality records between the years 1853-1908 were plotted with large hollow circles and more modern records (1920 to present) were plotted with small solid circles. The map is based largely on specimens ex-

amined with some literature records included that are believed to be valid.

The species distribution extends northeast to the Moira River in eastern Ontario, then westward throughout the Great Lakes, northwest to the Red River of the North in northwestern Minnesota, and south through northern Indiana, Illinois, and Ohio to Beargrass Creek, Kentucky; disjunct populations extend into the Ozark regions of Missouri, Kansas, Arkansas, and Oklahoma and continue as far south as the Blue River in southeastern Oklahoma. The presumed occurrence of the species in North Dakota (Moore, 1968) has not been verified. Copes and Tubb (1966) did not record the species from Red River (of the North) tributaries in North Dakota, although it occurs in that drainage in Minnesota. Miller (1972) listed the species as threatened in Pennsylvania but no valid records are known from the state.

The distribution of *E. microperca* is thus widely disjunct with populations in the Ozarks separated by over 200 miles from the nearest northern and eastern populations. The present disjunct pattern is interpreted as a glacial displacement. The species occurrence in the Ozarks and Blue River, Oklahoma, probably dates from one or more of the Pleistocene ice advances, when a cooler and moister climate favored southward dispersal across regions where the species cannot now survive. Persistence of relict populations in southern regions is favored by the numerous cool springs and spring-fed streams which provide conditions like those of more northern waters (Ross, 1965). Several other primarily northern fishes have relict populations in the Ozarks similar to *E. microperca* such as *Nocomis biguttatus* (Lachner and Jenkins, 1971), *Notropis heterolepis* (Cross, 1970) and *Phoxinus erythrogaster* (Cross, 1970). In fact, *Notropis pilsbryi*, *Nocomis asper*, and *P. erythrogaster* all have small remnant populations in Blue River, Oklahoma (Gilbert, 1964; Lachner and Jenkins, 1971; Robison and Miller, 1973).

Throughout its range *E. microperca* is sporadic in occurrence. The map used to illustrate its distribution is somewhat misleading in that the scale used is small enough to make the species' spotty pattern appear more continuous than it may be in reality. An examination of the distribution of *E. microperca* in several state ichthyofaunal works (e.g. Trautman, 1957; Pflieger, 1975) demonstrates more accurately the spottiness of the species. Thus certain parts of the range of the species are presently reduced to several small remnant populations. These include Moira River, Ontario; Turkeyfoot Lake, Ohio; Beargrass Creek, Kentucky; and the headwaters of the Cedar River, Minnesota. These remnant populations may in part be the result of recent modifications in the habitat of the species. The alteration of certain ecological parameters through extensive ditching, dredging, draining, and polluting of streams has undoubtedly played a role in the extirpation or reduction in population size of the species in several regions.

Two examples of presumed recent extirpation will serve to illustrate the above point. While Professor of

Biology at Coe College, Cedar Rapids, Seth E. Meek collected intensively in Iowa between the years 1889 and 1891. Meek (1892a) listed three localities for *E. microperca* in Iowa. In the Maquoketa River in Delaware County, he recorded the species as rare at Manchester and common at Delhi; in the Cedar River in Cedar County he also listed the species as rare at West Liberty. The collection from the Cedar River at West Liberty is extant (USNM 174834) thus verifying the species one-time occurrence in Iowa. *E. microperca* has not been taken in Iowa since 1890; Cleary (1954) did not find the species during his extensive surveys of the Iowa and Cedar rivers. Phillips and Underhill (1967) recently reported *E. microperca* from Cedar River drainage near Lyle, Minnesota, just across the Iowa border. This is presumably a relict of the larger population that must have existed in the late nineteenth century. The presumed extirpation of *E. microperca* from Iowa is not surprising since agricultural practices have long been the state's mainstay economy. Several other species which like *E. microperca* have an affinity for aquatic vegetation, soft bottom and slow water habitats have also disappeared from Iowa since Meek's time (Harlan and Speaker, 1956).

A somewhat parallel situation is presumably occurring in parts of Illinois. *E. microperca* is no longer present in the Calumet and Du Page rivers, Illinois, where it was recorded by Putnam (1863) and Forbes and Richardson (1908). A recent survey of Illinois fishes by Philip W. Smith did not include records of this species for these rivers.

Buchanan (1973a, 1974) plotted and discussed the distribution of *E. microperca* in Arkansas, noting several localities for the species in the upper Saline River (Ouachita River tributary) in Saline and Grant counties. Re-examination of the material (NLU, TMB, TNHC, TU) indicates that the Saline River records of *E. microperca* are based on the related *E. proeliare*. Therefore, the species is known with certainty in Arkansas only from the Illinois River drainage in Benton and Washington counties. Similarly, Clay (1975) recorded *E. microperca* from Guist Creek (Salt River tributary), Shelby County, and Rough Creek (Green River tributary), Jefferson County, Kentucky. These records are based on misidentifications of *E. (Catonotus) flabellare* (UL 5370) and *E. (Catonotus) kennicotti* (UL 7070), respectively. The only certain Kentucky record of *E. microperca* is that from Beargrass Creek, (Ohio River tributary), Jefferson County, Kentucky (UL 6479). Additional collecting in the Beargrass system has failed to reveal further specimens.

Three questionable records for *E. microperca* have also been plotted in Fig. 18. Woolman (1892) recorded the species as rare from Little Barren River (Green River tributary), 5 or 6 miles from its mouth near Osceola, Kentucky. The town Osceola could not be located on several Kentucky maps examined, nor is the town listed in a Kentucky Place Names book. Specimens from this locality were not present among those examined from CAS, FMNH, MCZ, UMMZ, or USNM. It is therefore uncer-

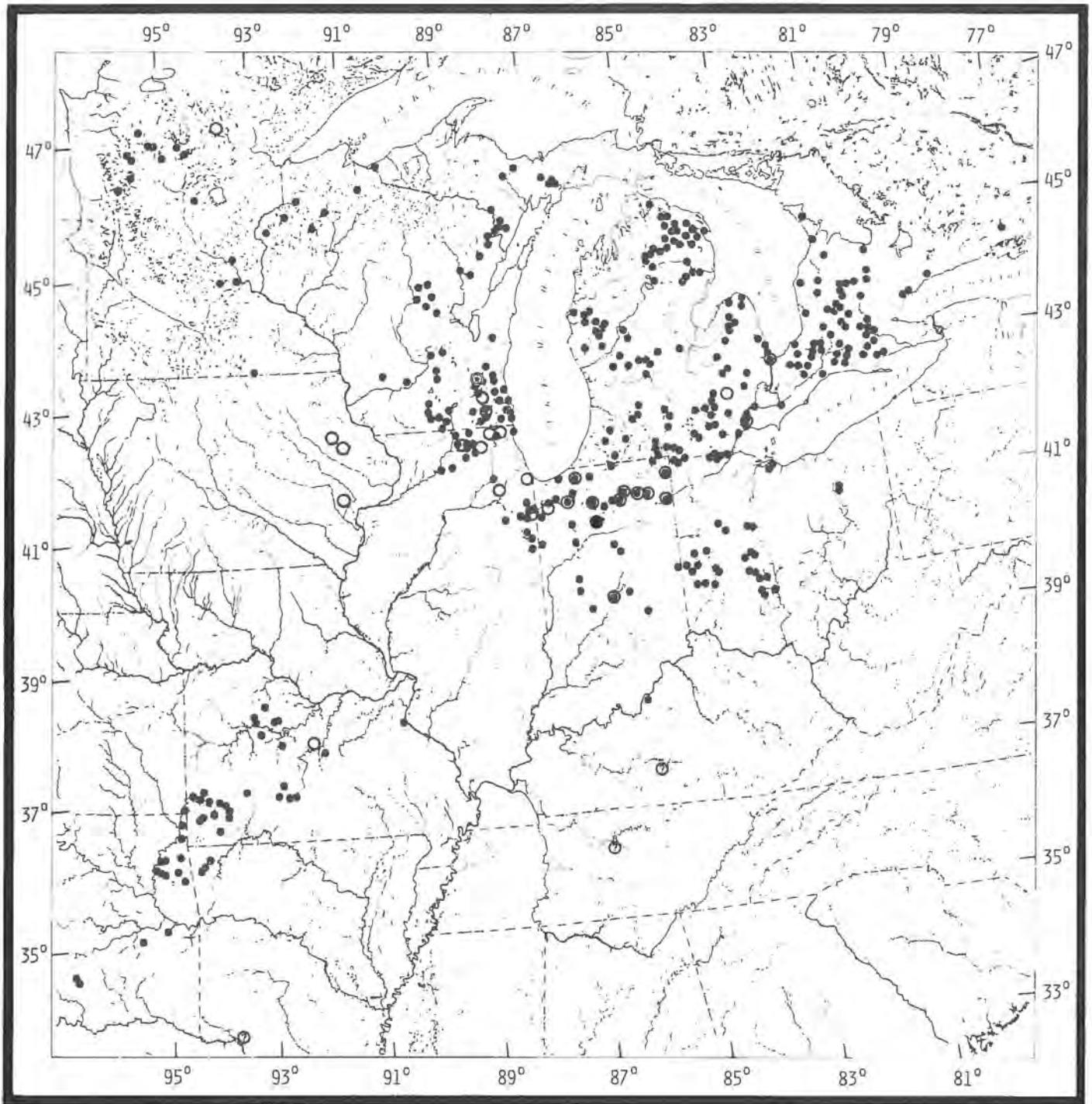


Fig. 18. Distribution of *E. microperca*. Large open circles represent record stations where the species was collected from 1853 to 1908. Small solid circles represent modern localities (1920 to present). The circled star is the type locality. Open circles with question marks represent localities of questionable validity.

tain whether the record is valid. A single female specimen of *E. microperca* from Richland Creek (Cumberland River tributary), Davidson County, Tennessee (OAM 5021) is the only record for the state. The possibility of

the species occurring naturally in this area is questionable and the provenance of the specimen is therefore suspect. A final questionable record is that of a juvenile *E. microperca* from Bois de Arc Creek (Red River tributary),

Hempstead County, Arkansas (UMMZ 123168). This locality is now inhabited by *E. proeliare* and a mistake in labeling or cataloging is suspected.

CONSERVATION STATUS.—*E. microperca* has been placed on the rare or threatened list of Kansas (Miller, 1972; Platt et al., 1973); Arkansas (Buchanan, 1974; Robison, 1974); and Oklahoma (Robison et al., 1974). It was placed on the endangered list for Pennsylvania (Miller, 1972) although no specimens are known from the state. It is also on the list of animals with a changing status in Wisconsin where it has been found infrequently in recent years (Hine et al., 1973). In addition it should be placed on a threatened list for Iowa where it has not been collected in over 75 years. The adjacent population of the species just across the Iowa border in Minnesota confirms its presence in the Cedar River and its possible presence in Iowa. The species is of questionable status in Tennessee where it is known from only one specimen and locality data of uncertain origin. Most of the above areas are on the periphery of the range. In other parts of its range *E. microperca* is often common to abundant in its preferred habitat.

Material Examined

Red River Drainage. Arkansas: HEMPSTEAD COUNTY: UMMZ 123168 (1) trib. to Bois de Arc Creek 4 mi W of Hope, 22 June 1938. Oklahoma: JOHNSTON COUNTY: CU 17878 (2); ECU 471 (2); 614 (5); INHS 75678 (27); KU 2421 (3); 12924 (4); NCSM 5088 (3); OAM 1597 (3); 7157 (7); UMMZ 147544 (1).

Arkansas River Drainage. Oklahoma: CHEROKEE COUNTY: APB uncat. (1). HASKELL COUNTY: OUMZ 33676 (2) Sansbois Creek 2 mi W of Keota, 3 Aug. 1963. MAYES COUNTY: APB uncat. (5); UTULSAC 1016 (3); 1171 (3); 2522 (4); 2571 (10); UMMZ 11979 (3); WCS AK/NSI-1 (3). PITTSBURG COUNTY: OUMZ 34071 (2) Featherston Creek 2 mi NE of Featherston, July 1963. Arkansas: BENTON COUNTY: NLU 25892 (9) Osage Creek 1.5 mi N of Cave Springs, 6 Feb. 1973; UMMZ 123459 (2) Wildcat Creek 12 mi W of Springdale, 1 July 1938. WASHINGTON COUNTY: CU 35568 (1) Clear Creek at Savoy, 17 April 1960. Missouri: BARRY COUNTY: UMMZ 116421 (1). JASPER COUNTY: KU 10735 (7). LAWRENCE COUNTY: FMNH 60706 (1); KU 10749 (10); UMMZ 103031 (20).

Osage River Drainage. Missouri: CAMDEN COUNTY: INHS 75817 (30) Hahatonka Spring at Hahatonka, 20 March 1977; UMMZ 108728 (7); 150283 (30). GREENE COUNTY: INHS 75822 (30) Spring 6 mi N of Springfield, 18 March 1977.

Gasconade River Drainage. Missouri: PULASKI COUNTY: USNM 42578 (1). WEBSTER COUNTY: INHS 75828 (40); KU 8029 (7). WRIGHT COUNTY: INHS 75819 (20); KU 10989 (17); UT 91.979 (9).

Lamine River Drainage. Missouri: MORGAN COUNTY: KU 16496 (20) Haw Creek 6 mi NW Stover, 27 Aug. 1962.

Cumberland River Drainage. Tennessee: DAVIDSON COUNTY: OAM 5021 (1) Richland Creek, 18 April 1954.

Wabash River Drainage. Indiana: HANCOCK COUNTY: OSM 29771 (3). HOWARD COUNTY: OSM 26130 (6). KOSCIUSKO COUNTY: OSM 25678 (2); UMMZ 66634 (5). MARSHALL COUNTY: USNM 65279 (4); 65284 (10). MONTGOMERY COUNTY: OSM 27171 (7). MORGAN COUNTY: OSM 29955 (1). RUSH COUNTY: OSM 27945 (1). WHITLEY COUNTY: UMMZ 167917 (1).

Middle Ohio River Drainage. Kentucky: JEFFERSON COUNTY: UL 6479 (1) Beargrass Creek, no date.

Great Miami River Drainage. Ohio: DRAKE COUNTY: OSM 2280 (10). MIAMI COUNTY: OSM 7604 (2); 14218 (1). SHELBY COUNTY: OSM 14219 (10). Indiana: RANDOLPH COUNTY: OSM 5733 (53).

Scioto River Drainage. Ohio: DELAWARE COUNTY: OSM 14896 (7); 15547 (62). FAYETTE COUNTY: OSM 1339 (4); 1361 (8). MADISON COUNTY: OSM 13272 (51); 21167 (9). PICKAWAY COUNTY: OSM 7188 (7); 13682 (24); 16617 (5); 16945 (5); 16983 (2); 16988 (2); 17017 (4); 17063 (2); UMMZ 159856 (10). UNION COUNTY: OSM 12503 (2); 15727 (1); 22893 (1); 22980 (10).

Muskingum River Drainage. Ohio: SUMMIT COUNTY: OSM 564 (2) Turkeyfoot Lake in Franklin Township, 14 Aug. 1927; 9956 (5).

Illinois River Drainage. Illinois: IROQUOIS COUNTY: INHS 7235 (10); 26932 (10). KANKAKEE COUNTY: INHS 5491 (10). WILL COUNTY: INHS 5020 (10). Indiana: LAKE COUNTY: FMNH 334 (1). PORTER COUNTY: FMNH 42447 (1); OSM 29247 (18).

Fox River Drainage. Illinois: DUPAGE COUNTY: INHS 5143 (4). LAKE COUNTY: INHS 4168 (12). MCHENRY COUNTY: INHS 26903 (1); 26904 (1). Wisconsin: WALWORTH COUNTY: UMMZ 78442 (2).

Rock River Drainage. Illinois: KANE COUNTY: INHS 4772 (10). MCHENRY COUNTY: INHS 3201 (10); 3248 (10); 26782 (10). OGLE COUNTY: INHS 22449 (10). Wisconsin: ROCK COUNTY: MPM 7932 (3). WAUKESHA COUNTY: MPM 9886 (7).

Cedar River Drainage. Iowa: MUSCATINE COUNTY: USNM 174834 (5) Cedar River at West Liberty, no date. Minnesota: MOWER COUNTY: UM 19684 (18) Otter Creek E of Lyle, 10 Oct. 1964.

Wisconsin River Drainage. Wisconsin: GREEN LAKE COUNTY: UMMZ 73872 (1). MARQUETTE COUNTY: UMMZ 73926 (1). PORTAGE COUNTY: UWSP 1095 (2); 1098 (7); 5199 (1). RICHLAND COUNTY: UMMZ 77649 (2). SAUK COUNTY: UMMZ 77382 (1).

Upper Mississippi River Drainage. Wisconsin: ASHLAND COUNTY: UMMZ 78564 (1). SAWYER COUNTY: UMMZ 95953 (2). BURNETT COUNTY: UMMZ 77939 (5); UWSP 4592 (3). WASHBURN COUNTY: UMMZ 96127 (2). Minnesota: HENNEPIN COUNTY: UMMZ 95001 (3). BECKER COUNTY: INHS 75831 (10). HUBBARD COUNTY: UF 21046 (10).

Red River of the North Drainage. Minnesota: OTTERTAIL COUNTY: INHS 75847 (20); 75848 (10).

Lake Superior Drainage. Michigan: GOGEBIC COUNTY: UMMZ 84088 (3); 185405 (2).

Western Lake Michigan Drainage. Wisconsin: MARINETTE COUNTY: UMMZ 74843 (1). MILWAUKEE COUNTY: UMMZ 64651 (1); 64685 (2). OCONTO COUNTY: MPM 6672 (5). RACINE COUNTY: UMMZ 64708 (2); 64873 (2). WAUKESHA COUNTY: UF 14641 (10). PORTAGE COUNTY: UWSP 1092 (10). WAUPACA COUNTY: UWSP 3816 (10). MARINETTE COUNTY: UMMZ 64091 (10); 74811 (3). Michigan: DICKINSON COUNTY: UMMZ 164180 (9). MENOMINEE COUNTY: UMMZ 85346 (10). DELTA-SCHOOL-CRAFT COUNTY: UMMZ 79205 (1).

Eastern Lake Michigan Drainage. Michigan: LAKE COUNTY: UMMZ 113142 (3); 164123 (6). MARQUETTE COUNTY: UMMZ 84222 (3). MASON COUNTY: UMMZ 11038 (1). NEWAYGO COUNTY: UMMZ 88956 (16); 88966 (10); 164496 (4). OCEANA COUNTY: UMMZ 139002 (7); 164398 (4). MECOSTA COUNTY: UMMZ 145088 (9). ROSCONIMON COUNTY: UMMZ 112254 (15). BARRY COUNTY: INHS 75846 (1). IONIA COUNTY: UMMZ 136460 (2). JACKSON COUNTY: UMMZ 79865 (1); 137744 (10); 137756 (1). KENT COUNTY: UMMZ 90380 (7). CALHOUN COUNTY: UMMZ 164208 (11); 164289 (1); 164356 (1). KALAMAZOO COUNTY: UMMZ 56093 (4); 56770 (2). BRANCH COUNTY: UMMZ 90033 (17); 90123 (10); 90150 (11). HILLSDALE COUNTY: UMMZ 97950 (2); 97958 (1); 97994 (1); 98008 (1); 98018 (1); 98028 (1); 98057 (1); 98229 (2); 98236 (1); 164349 (1). VAN BUREN COUNTY: UMMZ 82012 (8); 82716 (1). Indiana: STEUBEN COUNTY: OSM 25494 (5).

Western Lake Huron Drainage. Michigan: CHEROYGAN COUNTY: UL 5521 (1); 5530 (1); UMMZ 114688 (4). ALPENA COUNTY: UMMZ 67544 (6); 67916 (15); 67986 (10); 68001 (10); 68109 (16). MONTMORENCY COUNTY: UMMZ 68991 (17) 69031 (10); 69114 (10). CRAWFORD COUNTY: UMMZ 65702 (2). IOSCO COUNTY: UMMZ 66702 (10); 73187 (10). AGEMAW COUNTY: UMMZ 98415 (3). OTSEGO COUNTY: UMMZ 61723 (5); 82603 (3). GENESSEE COUNTY: UMMZ 82134 (2); 82142 (9); 82171 (7). GRATIOT COUNTY: UMMZ 56213 (1). SAGINAW COUNTY: UMMZ 136999 (10). SANILAC COUNTY: UMMZ 117021 (8). SHIAWASSEE COUNTY: UMMZ 136791 (3). TUSCOOLA COUNTY: UMMZ 116315 (3); 116349 (10); 116368 (8). HURON COUNTY: UMMZ 116948 (24); 116967 (10). LENAWE COUNTY: UMMZ 89872 (7); 89961 (6). MACOMB COUNTY: UMMZ 82618 (5); 103285 (6). MONROE COUNTY: UMMZ 117111 (1);

138090 (13). OAKLAND COUNTY: UMMZ 159498 (4); 159991 (2); 159994 (5); 159996 (5); 160000 (6); 160207 (1); 162222 (6). SANILAC COUNTY: UMMZ 117058 (2). ST. CLAIR COUNTY: UMMZ 116837 (4); 116855 (10). WASHTENAW COUNTY: UMMZ 56269 (14); 72248 (7); 139765 (12). WAYNE COUNTY: UMMZ 61305 (10); 162974 (12).

Thames River Drainage, Ontario: MIDDLESEX COUNTY: ROM 30996 (10). OXFORD COUNTY: ROM 30618 (5). PERTH COUNTY: ROM 24451 (1); 30135 (6); 30138 (4); UMMZ 85567 (16); 85824 (1).

Eastern Lake Huron Drainage, Ontario: BRUCE COUNTY: ROM 18515 (20); 22513 (11); 24798 (18); 30505 (5). GREY COUNTY: ROM 17914 (5); 17915 (5); 17919 (5); 17923 (2). HURON COUNTY: ROM 18068 (6); 30017 (6). LAMBTON COUNTY: ROM 24768 (5). MIDDLESEX COUNTY: UMMZ 85530 (10). PERTH COUNTY: ROM 26803 (4); 29969 (4). WELLINGTON COUNTY: ROM 25749 (10); 30250 (3).

Maumee River Drainage, Ohio: ERIE COUNTY: UMMZ 87504 (20). LUCAS COUNTY: OSM 9958 (1); UMMZ 118501 (15); UF 7357 (2). WILLIAMS COUNTY: OSM 9955 (10); 9957 (10); 9959 (9); UMMZ 87533 (2).

Northern Lake Erie Drainage, Ontario: ELGIN COUNTY: ROM 30380 (6); UMMZ 56858 (10). HALDIMAND COUNTY: ROM 18091 (1). NORFOLK COUNTY: ROM 18093 (6); 18243 (5); 24950 (5); 25905 (5). OXFORD COUNTY: ROM 17908 (3); 18121 (6); 30581 (10); 30657 (6); 30843 (5); UMMZ 89070 (7). BRANT COUNTY: ROM 8650 (1); 24849 (17). WATERLOO COUNTY: ROM 30636 (1); UMMZ 85585 (1).

Lake Ontario Drainage, Ontario: ONTARIO COUNTY: ROM 24454 (4). YORK COUNTY: UMMZ 60606 (4). HASTINGS COUNTY: ROM 24215 (4) Moira River, Aug. and Sept. 1947.

Comparisons

The distinguishing characters of species in the subgenus *Microperca* are summarized in Tables 10-11. *E. proeliare* clearly attains the greatest maximum SL of the three species. Only one male specimen of *E. fonticola* is over 35 mm SL, the majority of adults are three or four mm less in SL. *E. microperca* averages one or two mm larger than *E. fonticola*.

E. microperca differs consistently from the other two species in pigmentation. In addition to what is noted in Table 10, the chin, throat, and breast of males (sometimes females) have large blotches of black pigment not found on the other two species. In *E. proeliare* and *E. fonticola* pigment in these areas consists of tiny, discrete, evenly spaced melanophores.

When body proportions are compared, the three species show several differences (Tables 5, 8, 9). Compared with the other two species, *E. fonticola* exhibits significantly greater mensural values for head length, head width, snout length, predorsal length, upper jaw length, eye diameter, D_1 and D_2 fin basal lengths, and D_2 fin length. *E. fonticola*, however, has the smallest mean pelvic fin length, pectoral fin length, and postdorsal length values. When compared with the other two species, *E. microperca* shows the greatest mean values for pelvic, pectoral, and anal fin lengths. In the majority of body proportions measured *E. proeliare* and *E. microperca* have similar mean values.

When compared to the other two species, the array of significant characteristics exhibited by *E. fonticola* is of particular interest. Miller (1948) pointed out marked trends that are characteristic of warm spring fishes. These are (1) general reduction in number of meristic segments; (2) dorsal fin more posterior; (3) head and

eye, and in general, anterior parts of body enlarged; (4) fins more expansive and; (5) smaller size. *E. fonticola* shows similar trends in all of these categories as evidenced by its larger head, eye, snout and predorsal length, longer D_2 fin, smaller size and only one anal spine.

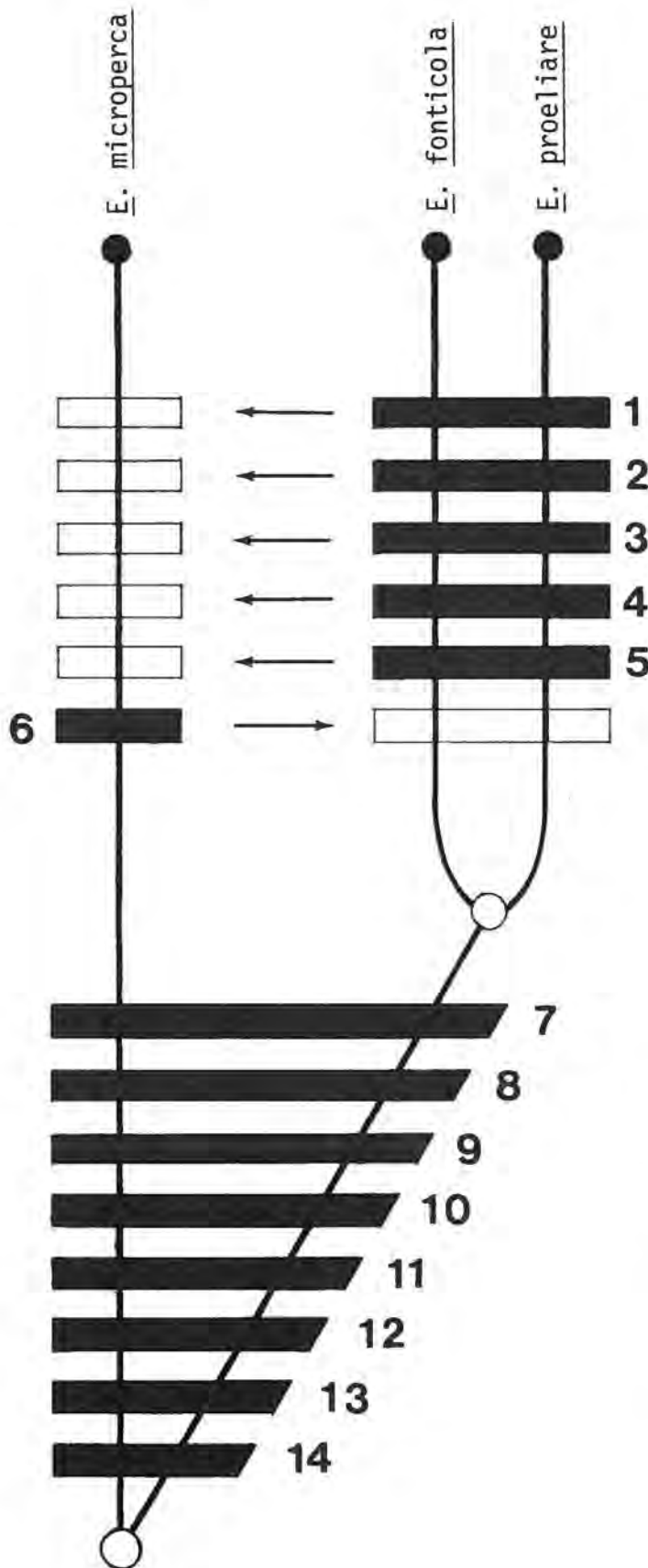
Summary counts of several distinctive meristic features are presented in Table 11. For some comparisons the count frequencies for Ozark and northern populations of *E. microperca* are tabulated separately. As with many closely related groups of animals none of the meristic features is 100 percent different for the three species. Frequencies for other less distinctive characters counted may be found under Description of the species.

Intrasubgeneric Relationships

The interpretation of phylogeny in the subgenus *Microperca* is based on morphology, coloration, zoogeography, and life history. In the following discussion the most primitive taxon is the one with the greatest number of primitive character states. Primitive character states are those from which others are derived (e.g. the presence of a lateral line precedes its absence). Determining advanced character states is more subjective. For the purposes of this discussion the most advanced taxon is the one with the largest number of "most advanced" characteristics.

The most primitive *Microperca* is probably *E. proeliare*. This species exhibits the greatest number of primitive character states such as larger size, more complete squamation, higher meristic values, and a more completely developed lateralis system. *E. fonticola* shares several primitive character states with *E. proeliare* such as the similarly developed lateralis system, and 6:6 branchiostegal ray count. In addition, the two species share the melanistic anal and pelvic fins of breeding males and the distinctly bilobed papillae of breeding females. Tubercle distribution is virtually identical and the present geographic propinquity of the two species also suggests intimacy. *E. fonticola* displays a few derived character states such as its smaller size, loss of scales on the cheek, reduction in number of anal spines to one, and reduced number of vertebrae.

Comparing a number of features of *E. proeliare* and *E. fonticola* with *E. microperca* reveals a derived condition for nearly every character (Table 10). *E. microperca* has the lowest values for most of the meristic characters examined and, similar to *E. fonticola*, has a more reduced squamation than *E. proeliare*. The body and cephalic lateral line show several reductions. The presence of red-orange color in the anal and pelvic fins of breeding males, the more expansive pelvic fin flaps and the greater degree of sexual dimorphism in body proportions are all interpreted as derived or specialized conditions. The presence of a conical papilla in female *E. microperca* is presumably a primitive condition. The bilobed papillae in the other two species are structurally more specialized and apparently represent a derived condition. In this feature *E. microperca* has undergone little change



from the assumed ancestral condition. Within *E. microperca* the Ozark populations retain more primitive character states than the northern populations. For example, Ozark populations have higher meristic values for several characters, more extensive tuberculation on the anal fin and attain a larger size. Some of these characteristics may be environmentally induced (e.g. larger size) but enough other characters indicate that the Ozark populations of *E. microperca* are the most primitive extant representatives of the species.

The relationship among members of the subgenus *Microperca* is corroborated by following principles similar to those outlined by Hennig (1966). According to Hennig's major principles species or groups of species are related by recency of common ancestry. Taxa that share an immediate common ancestor are termed sister groups. Only those characters of taxa that indicate immediate common ancestry are used to interpret relationships between sister groups. Characters intending to demonstrate immediate common ancestry are termed apomorphous (derived) characters. Characters purporting to show a phylogenetic relationship but not a sister group relationship are termed plesiomorphous (ancestral) characters. Taxa must be monophyletic, that is, descended from a single ("stem") species and including all descendants of that stem species. Ancestral (stem) species are hypothetical.

A summary of the relationships of the subgenus *Microperca* using Hennig's principles is shown in Fig. 19. The monophyly of the subgenus is corroborated by seven characters (7-14). That *E. fonticola* is most closely related to *E. proeliare* and that the two form a species pair (sister group) is corroborated by six characters (1-6). Fig. 19 also indicates that *E. microperca* is placeable in a group by itself.

Bailey and Gosline (1955) and Collette (1962) presented phylogenetic rankings for the subgenus *Microperca* based on one or a few characteristics. In each case *E. fonticola* was considered to be the most advanced *Microperca*. The present analysis of numerous other characters clearly indicates that these former rankings were superficial and the correct phylogenetic placement of *E. fonticola* is with its closest relative *E. proeliare*.

Fig. 19. A phylogenetic analysis of three species of *Etheostoma*, subgenus *Microperca*. Open circles are hypothetical ancestors. Black rectangles are ancestral (plesiomorphous) character states and open rectangles are derived (apomorphous) character states. Arrows are inferred directions of evolutionary change. Numbers refer to character states as listed below: 1, POM pores 8; 2, IO pores 1+3; 3, CP with median, posterior-leading tube; 4, Branchiostegal rays 6:6; 5, Melanistic anal and pelvic fins of breeding males; 6, Conical papilla of female; 7, Expanded pelvic fin flaps on breeding males; 8, x pelvic fin length/SL $>$.250 mm; 9, Sexual dimorphism well developed in coloration, tuberculation, body proportions, and shape and size of the genital papillae; 10, Body lateral line reduced to 0-9 pores; 11, Extreme reduction in numerous meristic features; 12, Red-orange band or blotches in D₁ fin of breeding males; 13, Virtually identical breeding behavior; 14, Mature ova indented on one side appearing as a half donut.

In summary, the analysis of numerous characters indicates that *E. proeliare* is the most primitive *Microperca*, that *E. fonticola* is most closely allied to *E. proeliare*, and that the two form a species pair. *E. microperca* is placeable in a separate species group with certain populations in various stages of differentiation, but most of the populations displaying the largest number of "most advanced" character states. *E. microperca* is the most advanced *Microperca* and probably the most advanced percid.

Zoogeography

There are no fossil darter remains known and the percid family is represented in the American fossil record only by Pleistocene deposits of *Perca flavescens* (Miller, 1965). As a group, darters occur largely in habitats poorly suited for fossilization and their geological age is thus unknown. Their diversification into nearly 150 species is, however, assumed to be a relatively recent event. The following discussion of distribution and dispersal of the subgenus *Microperca* is based on the present distributional patterns of the species involved, and past geological events. In some cases routes of dispersal have been conjectured only from biological evidence.

The origin of *E. proeliare* was probably in the lowlands of the Mississippi Valley where the species is now widely distributed and abundant. Its presence in the larger tributaries of the Mississippi River (Fig. 7) suggests that its dispersal into those drainages was of a direct route moving from one drainage system to another through past and existing interconnecting main rivers. The species may have used portions of the Ancestral Plains system and/or the lower Teays-Mississippi system (Metcalf, 1966: fig. 3; Pflieger, 1971: fig. 14) for entrance into the Red, Arkansas, and possibly Tennessee rivers.

The occurrence of *E. proeliare* in coastal drainages east of the Mississippi River might be explained by stream capture or lowland transfer. A stream capture could have taken place between the Pearl and Big Black drainages due to their close proximity and low relief of the divides between them (Snelson, 1972). During the history of the Mississippi River its lower reaches have had varying courses (Russell, 1940). At one recent stage the mouth of the Mississippi was very near the mouth of the Pearl River (see Snelson, 1972) and probable connections between the two rivers would have afforded ample opportunity for *E. proeliare* to enter the Pearl drainage from the Mississippi drainage via a lowland route. Entrance of the species from the Pearl River to the Mobile Bay drainage could have been by stream capture between eastern tributaries of the Mississippi River and western tributaries of the Tombigbee River (Smith-Vaniz, 1968).

As noted by Bailey et al. (1954), the Perdido, Escambia, and Choctawhatchee rivers form a common faunal block. Entrance of the species into the Escambia and Choctawhatchee rivers probably took place when mean sea levels were lowered during the Pleistocene presumably producing freshwater connections between the mouths of these

rivers. Bailey et al. (1954) also mentioned that *E. proeliare* was common in tidal fresh water.

Entrance of *E. proeliare* into Gulf Coastal streams west of the Mississippi River was again probably by lowland transfer. The Sabine, Neches, and Trinity rivers in their more ancient form were composed of large deltas in their lower reaches. These series of deltas were closely approximated and were probably interconnected from time to time by distributaries and cut-off channels characteristic of active deltas (Barton, 1930). The species is presently known from only the lower portions of these drainages and transfer of populations through these former lowland deltas seems likely.

E. fonticola, the closest relative of *E. proeliare*, is restricted to the San Marcos and Comal springs in the Guadalupe drainage (Fig. 7). The two species come within close proximity in Texas, separated by the Brazos and Colorado drainages. The present allopatry of the two species indicates that *E. fonticola* has probably long inhabited the springs in the upper Guadalupe River. Perhaps a dispersal route was at one time open along the edge of the Balcones Escarpment where numerous springs now exist from near Austin, Texas, southwestward. Stock(s) of *E. fonticola* could have entered this spring-rich region and dispersed to their present locations. The species may have at one time been more widespread in the several springs along the fault line but was extirpated by the constant fluctuation in water discharge from the springs and the periodic dry spells characteristic of the smaller springs (Meinzer, 1927). Evidence for extirpation from the large Comal Spring has been demonstrated (Schenck and Whiteside, 1976). Whatever the case, the species evidently found optimal conditions in the two largest escarpment springs at San Marcos and for a time at New Braunfels.

The present distribution of *E. microperca* (Fig. 18) makes speculation concerning its origin difficult. Its preglacial distribution may have been more extensive, but it almost surely included the preglacial Laurentian system and/or perhaps the northern portion of the Teays-Mississippi system (Pflieger, 1971: fig. 14). The broadly disjunct populations in the Ozarks of Missouri, Arkansas, and Oklahoma and the Blue River, Oklahoma, perhaps represent glacial relicts. With the onset of the Pleistocene Epoch, the species was probably displaced to a glacial refugium in the Ozark Uplands where suitable temperatures and habitat were available. The presence of isolated populations in the Neosho River is evidence for a former stream connection between the Arkansas and middle Missouri rivers (Metcalf, 1966; Pflieger, 1971).

The most disjunct population in the Blue River, Oklahoma, may have been present since one of the earlier glacial advances. This remnant population suggests that *E. microperca* may have been formerly more widespread when presumably more optimal conditions were present. A preference for cool temperatures and shallow streams stable enough to support aquatic vegetation suggests that the distributional history of the species may be inter-

puted "relative to changing atmospheric temperatures" as Cross (1970) has proposed for several other freshwater fishes. Cross (1970) stated that southward dispersal during glacial advance may have been favored by cooler air and water temperatures and that subsequent extirpation of most southern populations was a consequence of warmer air and water temperatures causing many of the shallow streams to dry, but leaving relict populations of species near springs. This explanation applies to the Ozark and Blue River populations of *E. microperca* which are now found only in springs, spring seeps/runs, or spring-fed streams and rivers.

Postglacial redispersal from an Ozark refugium was assisted by several post-glacial routes. *E. microperca* may be assumed to have moved northward via the Mississippi River following ice retreat. Opportunity for early crossing of the Mississippi-Great Lakes watershed toward the north and east appears to have been provided by the outlets of the Great Lakes (Greene, 1935). Re-entry into the Great Lakes and adjacent waters was probably afforded by the Chicago glacial outlet which formed at the foot of Lake Michigan and emptied into the Illinois River and eventually the Mississippi River.

It reached the Lake Erie drainage via the Maumee (or Fort Wayne) glacial outlet which connected the present-day Maumee River with the Wabash River and Lake Erie. According to Trautman (1957) *E. microperca* unquestionably invaded Ohio by using the Maumee outlet, gaining entrance into Lake Erie and subsequently entering the glaciated portion of the Ohio drainage (Scioto, Great Miami, and Muskingum rivers) before or during establishment of the prairies.

Dispersal into Ontario was probably also by the Chicago and Maumee glacial routes, which would have provided access to both the Lake Huron and Lake Erie drainages. The Lake Ontario drainage could have been reached from a route made possible by the glacial Lake Lundy stage which provided a wide channel into the Lake Ontario drainage basin (Radforth, 1944).

The occurrence of *E. microperca* both above and below St. Anthony Falls, Minnesota, a barrier to dispersal of many species near Minneapolis, could have been bypassed in immediate post Pleistocene time by a presumably free passage around the edge of glacial Lake Grantsburg draining into the St. Croix River (Underhill, 1957; Eddy et al., 1963). It evidently reached the Red River of the North through glacial River Warren (present Minnesota River) which at one time connected glacial Lake Agassiz with the Mississippi River (Underhill, 1957; Eddy et al., 1972). Its occurrence in the headwaters of the Red River may possibly represent a more recent arrival into the drainage with sufficient time not having accrued for expansion of its range. The fact that the river is a slow, turbid, silt-laden stream may now serve as a barrier to dispersal (Eddy et al., 1972).

There is some indication that the northern limits of *E. microperca* in Ontario, Wisconsin, Minnesota, and Michigan where no geological barriers exist are deter-

mined by temperature. More specifically the northern line of demarcation is probably the 65 or 70° July isotherm (Radforth, 1944). The species may be unable to exist in waters which do not attain a certain summer temperature possibly for breeding and development.

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Table 1. Evolutionary trends in the darter genera *Percina* and *Etheostoma*.

Primitive character states	Derived character states of <i>Microperca</i>
Serrate preopercle	Smooth preopercle
Conical genital papilla	Conical and bilobed papillae
Tubercles lacking	Tubercles developed on pelvic and anal fins of breeding males
Large body size	As a group, smallest darters known
Body mostly covered with scales	Body squamation greatly reduced
10 POM pores	6 to 8 POM pores
IO canal complete with 8 pores	IO canal interrupted with 1+3, 0+3, or 0+2 pores
ST canal complete	ST canal interrupted at midline
Lateral line complete	Lateral line extremely incomplete or wholly lacking
2 anal spines	1 or 2 anal spines
41 to 45 vertebrae	31 to 37 vertebrae
High meristic values	Most reduced meristic values
Sexual dimorphism weakly developed	Sexual dimorphism well developed
Eggs scattered over wide area of gravel	1 to 3 eggs deposited (per spawning act) on aquatic vegetation
Reproductive habitat of large streams or lake shores	Reproductive habitat of small, slow-moving streams, lakes or springs
Life cycle of 2 to 4 years	Life cycle of 1 year to 18 months
Mature ova round and symmetrical	Mature ova indented on one side appearing as a half donut
Spawning season late spring or summer	Spawning season very early spring to late spring (sometimes year around)
Neither a territory nor parental care is manifested	Some territorial behavior manifested by at least two species

Table 2. Counts of anal fin spines in populations of *E. proeliare*.

Population	1	2	N	\bar{X}	SD	% with 1 anal spine
GULF COAST DR. (east of Mississippi R.)						
Choctawhatchee-Escambia R., AL, FL	2	14	16	1.88	.342	12.5 %
Mobile Bay, AL, MS	10	63	73	1.86	.346	13.7 %
Pascagoula-Pearl R., MS, LA	4	55	59	1.93	.254	6.7 %
L. Pontchartrain, LA, MS	5	45	50	1.90	.303	10.0 %
MISSISSIPPI DR.						
Red R., LA, TX, OK, AR	10	81	91	1.89	.314	10.9 %
Ouachita R., LA, AR	32	42	74	1.57	.499	43.2 %
tribs., Mississippi R., LA, MS	2	30	32	1.94	.246	6.3 %
Big Black-Yazoo R., MS		61	61	2.00	.000	0.0 %
Arkansas R., AR, OK	3	45	48	1.94	.245	6.3 %
White R., AR, MO	11	35	44	1.75	.438	25.0 %
St. Francis R., AR, MO	12	28	40	1.70	.464	30.0 %
Hatchie R., TN, MS	22	8	30	1.27	.450	73.3 %
tribs., Mississippi R., MO, TN, IL	22	52	74	1.70	.460	29.7 %
OHIO DR.						
tribs., Tennessee R., MS, TN	12		12	1.00	.000	100.0 %
Cumberland R., KY	3	6	9	1.67	.500	33.3 %
tribs., Ohio R., IL	12	28	40	1.70	.464	30.0 %
GULF COAST DR. (west of Mississippi R.)						
Mermentau-Calcasieu R., LA		33	33	2.00	.000	0.0 %
Sabine-Neches R., LA, TX		35	35	2.00	.000	0.0 %
Trinity-San Jacinto R., TX		21	21	2.00	.000	0.0 %

Table 3. Counts of total branchiostegal rays in populations of *E. proeliare*.

Population	10	11	12	13	14	N	\bar{X}	SD	CV
GULF COAST DR. (east of Mississippi R.)									
Choctawhatchee-Escambia R., AL, FL			15	1		16	12.06	.250	2.0
Mobile Bay, AL, MS			67	3	1	71	12.07	.308	2.4
Pascagoula-Pearl R., MS, LA	1		34	1	7	43	12.30	.832	6.8
L. Pontchartrain, LA, MS			34	3		37	12.08	.277	2.3
MISSISSIPPI DR.									
Red R., LA, TX, OK, AR	2	2	65	8	1	78	12.05	.532	4.4
Ouachita R., LA, AR		3	34	5	3	45	12.17	.650	5.3
tribs., Mississippi R., LA, MS		1	29	1	1	32	12.06	.435	3.6
Big Black-Yazoo R., MS	1	1	51	4	2	59	12.08	.535	4.4
Arkansas R., AR, OK			34			34	12.00	.000	0.0
White R., AR, MO			29	4	3	36	12.28	.615	5.0
St. Francis R., AR, MO	2	1	24	5	1	33	12.06	.747	6.2
Hatchie R., TN, MS		1	26	2	1	30	12.10	.481	4.0
tribs., Mississippi R., MO, TN, IL			32	1	7	40	12.38	.774	6.3
OHIO DR.									
tribs., Tennessee R., MS, TN			12			12	12.00	.000	0.0
Cumberland R., KY			9			9	12.00	.000	0.0
tribs., Ohio R., IL		2	18	1		21	11.95	.384	3.2
GULF COAST DR. (west of Mississippi R.)									
Mermentau-Calcasieu R., LA			23	2		25	12.08	.277	2.3
Sabine-Neches R., LA, TX			17	5	5	27	12.56	.801	6.4
Trinity-San Jacinto R., TX			20	1		21	12.05	.218	1.8

Table 4. Sexual dimorphism and variation in numbers of pored lateral line scales in selected populations of *E. proeliare*.

Population	0	1	2	3	4	5	6	7	8	9	N	\bar{X}	SD	t value	P
GULF COAST DR.															
L. Pontchartrain, LA, MS															
Males			5	6	10	8	5	2			36	4.22	1.416		
Females		2	4	6	9	4	7	3	1	1	37	4.43	1.923	.6961	ns
Totals		2	9	12	19	12	12	5	1	1					
MISSISSIPPI DR.															
Red R., LA, TX, OK, AR															
Males		3	5	12	15	2	6	4			47	3.89	1.618		
Females		3	13	10	10		3	3	2		44	3.50	1.861	1.4079	<.1
Totals		6	18	22	25	2	9	7	2						
Ouachita R., LA, AR															
Males			11	16	14	17	5	5	2		70	3.11	1.620		
Females		3	16	17	17	13	2	2			70	2.50	1.370	2.4111	<.01
Totals		3	27	33	31	30	7	7	2						
Arkansas R., AR, OK															
Males			7	2	7	10	10	2			38	3.53	1.538		
Females		3	5	6	12	11	2	1	2		42	3.02	1.660	1.8085	<.05
Totals		3	12	8	19	21	12	3	2						
tribs., Mississippi R., MO, TN, IL															
Males		3	9	8	9	12	9	2	1		53	3.09	1.713		
Females			6	12	17	10	11	6	2		64	3.53	1.583	1.5771	<.1
Totals		3	15	20	26	22	20	8	3						

Table 5. Proportional measurements (expressed in thousandths of SL) for breeding *E. proeliare* from several areas summarizing sexual dimorphism. Specimens measured were 27-39 mm SL. Mean SL for the 25 males was 31.6 mm; mean SL for the 25 females was 31.4 mm. The significance of differences between means was determined by Student's *t*-test. Levels of probability (P) greater than 0.1 were considered not significant (ns).

Character	Sex	Range	\bar{X}	SD	<i>t</i> value	P
Head length	M	268-305	279	9.21	4.4944	<.005
	F	251-288	267	9.74		
Head width	M	92-134	117	9.43	0	ns
	F	99-138	117	12.12		
Snout length	M	39-68	49	8.03	1.4085	ns
	F	36-64	46	7.05		
Fleshy interorbital width	M	30-60	42	7.78	0	ns
	F	30-58	42	8.42		
Predorsal length	M	291-350	313	17.13	1.8450	<.05
	F	265-351	304	17.45		
Postdorsal length	M	434-509	470	15.57	2.7291	<.005
	F	429-484	458	15.69		
Body depth	M	148-198	173	11.88	4.8155	<.005
	F	163-216	189	11.71		
Caudal peduncle depth	M	81-109	96	7.23	3.9858	<.005
	F	74-99	87	8.74		
Upper jaw length	M	42-82	67	8.65	1.0842	ns
	F	43-81	64	10.89		
Eye diameter	M	52-74	62	5.73	1.9621	<.05
	F	50-68	59	5.12		
Base D ₁ fin length	M	154-230	191	20.56	2.0747	<.025
	F	138-233	177	26.87		
Base D ₂ fin length	M	155-221	173	13.92	1.2285	ns
	F	125-194	168	14.94		
Pelvic fin length	M	237-313	270	19.69	10.1235	<.005
	F	195-253	219	15.76		
Pectoral fin length	M	226-283	255	14.15	4.1418	<.005
	F	206-269	239	13.23		
Anal fin length	M	199-262	234	15.78	6.9212	<.005
	F	177-229	205	14.01		
D ₂ fin length	M	239-290	268	13.45	3.6036	<.005
	F	214-287	252	17.76		

Table 6. Counts of five meristic characters in the two populations of *E. fonticola*.

Population	Number of lateral line scales							N	\bar{X}	SD	CV	
	31	32	33	34	35	36	37					
San Marcos R., TX		9	44	30	14	2	1	100	33.59	.975	2.9	
Comal R., TX	6	25	29	10	1			71	32.59	.888	2.7	
		Number of transverse scale rows to D ₁ fin										
		9	10	11	12	N		\bar{X}	SD	CV		
San Marcos R., TX		5	26	39	10	80		10.68	.776	7.3		
Comal R., TX		13	19	23	1	56		10.21	.825	8.1		
		Number of caudal peduncle scale rows										
		14	15	16	17	N		\bar{X}	SD	CV		
San Marcos R., TX		4	37	56	3	100		15.58	.623	4.0		
Comal R., TX		16	32	23		71		15.10	.740	4.9		
		Number of left pectoral rays										
		8	9	10	11	N		\bar{X}	SD	CV		
San Marcos R., TX			12	84	4	100		9.92	.394	4.0		
Comal R., TX		9	81	10		100		9.01	.437	4.9		
		Number of vertebrae										
		31	32	33	34	N		\bar{X}	SD	CV		
San Marcos R., TX			12	15	1	28		32.61	.567	1.7		
Comal R., TX		8	26	3		37		31.86	.536	1.7		

Table 7. Sexual dimorphism and variation in numbers of pored lateral line scales in the two populations of *E. fonticola*.

Population	0	1	2	3	4	5	6	N	\bar{X}	SD	t value	P
San Marcos R., TX												
Males	3	9	20	9	6	2	1	50	2.32	1.301	.3596	ns
Females	7	8	16	10	5	3	1	50	2.22	1.475		
Totals	10	17	36	19	11	5	2					
Comal R., TX											2.8525	<.005
Males	2	5	7	11	7	3	1	36	2.81	1.431		
Females	7	10	14	10	1	3		45	1.93	1.338		
Totals	9	15	21	21	8	6	1					

Table 8. Proportional measurements (expressed in thousandths of SL) for breeding *E. fonticola* from Texas, summarizing sexual dimorphism. Specimens measured were 23-31 mm SL. Mean SL for the 20 males was 27.5 mm; mean SL for the 20 females was 26.6 mm. The significance of differences between means was determined by Student's *t*-test. Levels of probability (P) greater than 0.1 were considered not significant (ns).

Character	Sex	Range	\bar{X}	SD	<i>t</i> value	P
Head length	M	267-314	295	10.93	.2890	ns
	F	275-328	296	11.62		
Head width	M	111-153	128	9.79	0	ns
	F	116-145	128	8.22		
Snout length	M	47-68	55	5.58	1.1834	ns
	F	46-62	53	5.57		
Fleshy interorbital width	M	43-71	53	8.66	2.0576	<.025
	F	34-63	48	7.14		
Predorsal length	M	306-387	341	19.05	.5566	ns
	F	309-374	339	15.93		
Postdorsal length	M	420-472	443	12.81	.6652	ns
	F	411-475	446	16.32		
Body depth	M	186-222	201	9.80	7.6576	<.005
	F	196-240	218	2.85		
Caudal peduncle depth	M	98-122	106	5.74	3.0487	<.005
	F	93-113	101	4.93		
Upper jaw length	M	60-88	77	6.95	.4405	ns
	F	61-89	76	7.84		
Eye diameter	M	65-81	71	4.41	1.2739	ns
	F	57-78	69	5.72		
Base D ₁ fin length	M	168-236	198	19.93	3.5413	<.005
	F	137-221	177	18.63		
Base D ₂ fin length	M	171-218	191	12.54	3.7837	<.005
	F	160-195	177	11.56		
Pelvic fin length	M	236-294	260	14.47	8.0092	<.005
	F	200-250	225	14.08		
Pectoral fin length	M	231-270	251	9.89	1.4409	ns
	F	225-271	246	12.62		
Anal fin length	M	214-259	238	12.21	3.5941	<.005
	F	187-268	221	18.05		
D ₂ fin length	M	244-305	275	17.76	1.1561	ns
	F	240-301	269	16.02		

Table 9. Proportional measurements (expressed in thousandths of SL) for breeding *E. microperca* from several areas summarizing sexual dimorphism. Specimens measured were 23-33 mm SL. Mean SL for the 35 males was 27.4 mm; mean SL for the 35 females was 28.5 mm. The significance of differences between means was determined by Student's *t*-test. Levels of probability (P) greater than 0.1 were considered not significant (ns).

Character	Sex	Range	\bar{X}	SD	<i>t</i> value	P
Head length	M	252-299	275	12.55	2.8944	<.005
	F	246-297	267	10.96		
Head width	M	93-132	113	11.23	0	ns
	F	92-135	113	10.10		
Snout length	M	39-58	47	5.33	1.6949	<.05
	F	37-55	45	4.51		
Fleshy interorbital width	M	41-60	50	5.36	3.2520	<.005
	F	37-56	46	5.07		
Predorsal length	M	303-371	330	14.77	.7371	ns
	F	291-368	327	19.10		
Postdorsal length	M	446-507	473	17.15	3.0612	<.005
	F	415-508	458	23.43		
Body depth	M	169-213	189	11.08	5.9801	<.005
	F	174-243	207	14.02		
Caudal peduncle depth	M	83-120	104	8.53	4.1451	<.005
	F	80-111	96	7.61		
Upper jaw length	M	46-77	60	7.47	2.2346	<.025
	F	39-70	56	7.65		
Eye diameter	M	50-71	63	4.76	1.8762	<.05
	F	51-70	61	4.23		
Base D ₁ fin length	M	117-196	154	17.14	2.4129	<.01
	F	120-181	145	13.93		
Base D ₂ fin length	M	125-179	150	15.42	1.9074	<.05
	F	118-175	143	15.35		
Pelvic fin length	M	262-344	312	17.37	18.6352	<.005
	F	218-270	241	14.48		
Pectoral fin length	M	249-303	275	15.89	3.7791	<.005
	F	243-298	262	12.87		
Anal fin length	M	228-316	280	21.53	9.7713	<.005
	F	196-269	233	18.66		
D ₂ fin length	M	221-301	255	17.12	4.6272	<.005
	F	206-271	237	15.49		

Table 10. Summary of primary differences distinguishing the three species of the subgenus *Microperca*. The term "usually" indicates that over 90 percent of the observed counts are within the range given.

Character	<i>E. proeliare</i>	<i>E. fonticola</i>	<i>E. microperca</i>
Maximum size			
Males	37.8 mm SL	35.5 mm SL	33.3 mm SL
Females	39.6 mm SL	31.0 mm SL	36.9 mm SL
Female genital papilla	Bilobed	Bilobed	Conical
Check squamation	Usually fully scaled	Naked	Naked
POM pores	Usually 8	Usually 8	Usually 6
IO pores	Usually 1+3	Usually 1+3	Usually 0+3 or 0+2
Coronal pore	Present w/tube	Present w/tube	Absent or present w/o tube
Branchiostegal rays	Modally 6:6	Modally 6:6	Modally 5:5
Anal spines	1 or 2	1	1 or 2
Total dorsal fin elements	17 to 22, usually 18 to 20	16 to 19, usually 17 or 18	13 to 18, usually 14 to 17
Pored lateral line scales	0 to 9, usually 1 to 6	0 to 6, usually 1 to 3	0 to 3, usually 0 or 1
Lateral line scales	34 to 38, usually 35 to 36	31 to 37, usually 32 or 33	30 to 36, usually 32 to 34
Vertebrae	34 to 37, usually 35 or 36	31 to 34, usually 32 or 33	32 to 34
Breeding color of male pelvic fins	Melanistic	Melanistic	Orange to brick red
Breeding color of male D ₁ fin	Medial red-orange blotches in anterior membranes of fin	Solid, subdistal red-orange stripe on all membranes of fin	Medial red-orange blotches in all membranes of fin
Pigment at base of breeding male D ₁ fin	First two or three membranes black	Solid black	Gray
Lateral body pigment	Usually 8 to 10 blotches	Usually 9 to 11 stitchlike dashes	Usually 8 to 10 blotches
Tubercles on anal fin rays	Present	Present	Usually only on anal fin spines

Table 11. Counts of seven differentiating characters for the subgenus *Microperca*.

Species	Number of lateral line scales										N	\bar{X}
	30	31	32	33	34	35	36	37	38			
<i>E. proeliare</i>					64	370	321	75	19		849	35.55
<i>E. fonticola</i>		6	38	69	40	15	2	1			171	33.18
<i>E. microperca</i>	4	55	206	359	145	54	3				826	32.92

Species	Number of pored lateral line scales										N	\bar{X}
	0	1	2	3	4	5	6	7	8	9		
<i>E. proeliare</i>	26	125	181	187	185	86	45	23	4	1	873	3.10
<i>E. fonticola</i>	19	32	57	40	19	11	3				181	2.29
<i>E. microperca</i>	513	262	28	3							806	.41

Species	Number of total dorsal fin elements										N	\bar{X}
	13	14	15	16	17	18	19	20	21	22		
<i>E. proeliare</i>					55	277	398	102	15	2	849	18.71
<i>E. fonticola</i>				5	47	51	8				111	17.56
<i>E. microperca</i> (northern)	10	137	266	202	30						645	15.16
(Ozarkian)			20	74	69	18					181	16.47

Species	Number of total branchiostegal rays							N	\bar{X}
	9	10	11	12	13	14			
<i>E. proeliare</i>		6	9	532	46	25		618	12.12
<i>E. fonticola</i>		2	5	67	7	1		82	12.00
<i>E. microperca</i> (northern)	1	203	6	5				215	10.07
(Ozarkian)		134	25	10				169	10.27

Species	Number of POM pores					N	\bar{X}	
	5	6	7	8	9			
<i>E. proeliare</i>				12	453	17	482	8.01
<i>E. fonticola</i>				6	101	4	111	7.98
<i>E. microperca</i>	23	558	45				626	6.04

Species	Number of anal spines				N	\bar{X}
	1	2				
<i>E. proeliare</i>		163	679		842	1.81
<i>E. fonticola</i>		128	3		131	1.02
<i>E. microperca</i>		187	649		836	1.78

Species	Number of vertebrae							N	\bar{X}	
	31	32	33	34	35	36	37			
<i>E. proeliare</i>					7	36	37	1	81	35.40
<i>E. fonticola</i>		8	38	18	1				65	32.18
<i>E. microperca</i>			21	47	10				78	32.86

