

Corrections for Univ. Kansas Science Bulletin, vol. 48, no. 5 [Distler, D.A.
Distribution and variation of Etheostoma spectabile (Agassiz)]

1. Running heads on right-hand pages: for Etheostoma Spectabile,
read Etheostoma spectabile.
2. P. 144, Map 1: The symbol for the easternmost locality plotted, a
questionable record discussed on page 157, par. 4, is misplaced on
the Clinch River in Virginia; that symbol should be on the North
Fork of the **Holston** River, immediately below the position shown.
3. P. 149: Color plate is Figure 1. A, Etheostoma spectabile squamosum;
B. **E. s. pulchellum**; C, **E. s. spectabile**; D, **E. s. uniporum**;
E, E. s. fragi. All males.
4. P. 150, line 28: for pigment, read ... color;
P. 150, line 33: for ... vertical, not well ... read ... vertical
less well
5. P. 151, line 19: after ... 1/3 fin height; insert beneath this band a
narrow red basal band with color usually restricted to membranes;
P. 151, line 29: for paleblue ... read ...pale blue ...
6. P. 162, line 14: **for** ... supra basal ... read ... suprabaasal
7. P. 163, line 20: for bands larger than marginal and basal bands ...
read bands wider than marginal blue and basal red bands
8. P. 177, following line 20: Insert **ETYMOLOGY**. The name squamosum has
reference to the scaled anterior region (see diagnosis).
9. P. 182, line 27: for ... did nor force ... read ... did not force ...
10. P. 186, line 34: **for** ... E. stgmaeum .. **read** ... E. stigmaeum

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Distribution and Variation of *Etheostoma spectabile* (Agassiz) (Percidae, Teleostei)

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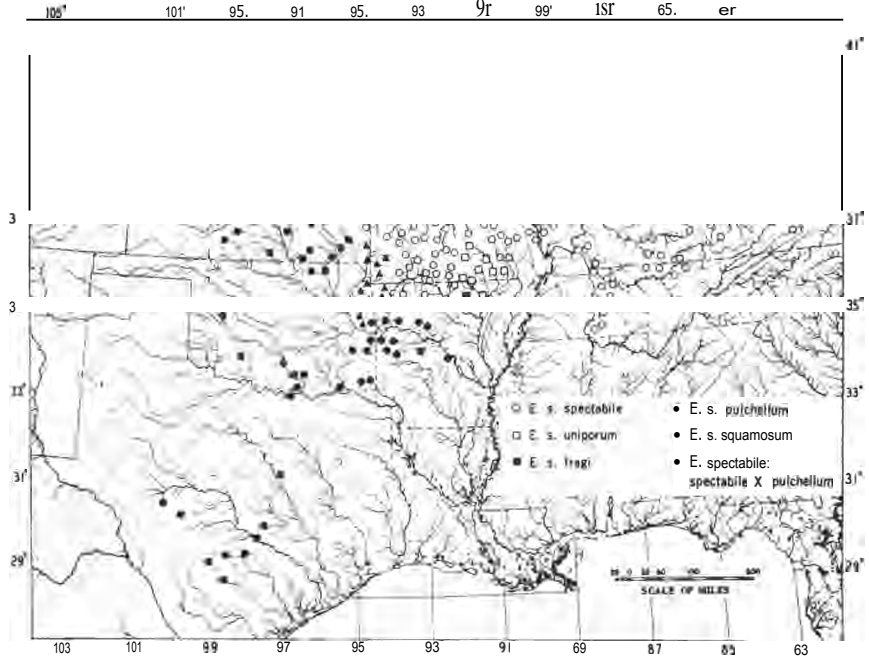
ABSTRACT

Etheostoma spectabile, the orangethroat darter, is a small, bottom-dwelling inhabitant of upland, hardwater streams in the Mississippi River System and western Coastal Province. This study has attempted to determine the present range and phenotypic variation of the species, to determine the fertility and character stability in progeny resulting from laboratory crosses between phenotypically distinct populations and within such populations, and to interpret the zoogeography of the species so far as it can be inferred from biological and geological evidence now available. Five subspecies are recognized: *E. s. spectabile*, *E. s. pukhellum*, *E. s. squamosum*, *E. s. fragi*, and *E. s. uniporum*. The distributions, areas of intergradation, and probable evolutionary histories of the taxa are discussed in relation to geologic changes that may have effected these phenomena.

INTRODUCTION

The orangethroat darter, *Etheostoma spectabile* (Agassiz), is a small percid fish inhabiting hardwater, gravelly streams of the Edwards, Ozark, and Interior Low plateaus and adjacent Central Lowlands of North America (Map 1). The tribe Etheostomatini, subfamily Percinae, to which the orangethroat belongs, is composed of about 100 species that are endemic to the Atlantic drainage of North America (one species in the Pacific drainage of Mexico; cf. Meek, 1904). The members of this tribe have the air bladder reduced or absent, and are thereby adapted to a bottom-dwelling mode of life. Most occur in parts of streams with weak to moderately strong currents. The orangethroat has posed systematic problems for ichthyologists since its description in 1854. Unfortunately, this species has been recognized in the

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MAP 1. Distribution of *Etheostoma spectabile*. Symbols indicate streams from which one or more collections of orangethroats have been examined or taken. Records in Indiana are partly from Gerking (1945:94) and in Ohio partly from Trautman (1957:597). Localities where intergrades and hybrids have been collected are omitted with the exception of the extensive zone of intergradation between *E. s. spectabile* and *E. s. pulchellum*.

literature and catalogued under various names. Early workers considered it to be conspecific with *Etheostoma caeruleum* Storer, the rainbow darter. This arrangement remained until Trautman (1930) established the specific distinctness of the two darters. Attention has been given the orangethroat in faunal studies and in keys for identification. Winn (1958) described its breeding behavior and ecology. Hubbs (1955) and Linder (1955) reported the occurrence of natural hybrids between the orangethroat and other darters. Clark Hubbs and his associates at the University of Texas have utilized this darter in studies of experimental hybrids. Collette (1965) commented on the phylogenetic significance of breeding tubercles on nuptial males of this and other species of percids.

Although much attention has been given the orangethroat in previous investigations, the relationships of populations throughout the range remain obscure. Hence a study of variation permitting refined diagnosis of the species is in order. At the time this study was begun, the orangethroat was considered in the literature to be composed of two subspecies: *E. s. spectabile*, the northern orangethroat, of the Ozark and Interior Low Plateaus and adjacent Central Lowlands, and *E. s. pulchellum*, the plains orangethroat, of the Great Plains and adjacent Central Lowlands. Hubbs and Lagler (1958),

in a comment on the range of *E. s. spectabile*, suggested the possibility of further subspeciation south of the Ohio River System. Two variants that I describe as the subspecies *E. s. squamosum* and *E. s. uniporum* from the Ozark region were recognized by earlier workers. Carl Hubbs was aware of both variants on the basis of specimens in the collections of the University of Michigan Museum of Zoology, and J. D. Black (unpublished doctoral dissertation, University of Michigan, 1940) mentions one of them.

The purposes of this report are to (1) determine the present range and investigate morphological variation of the orangethroat, (2) elucidate the evolutionary history of the species insofar as it can be inferred from geological and zoogeographic evidence now available, and (3) demonstrate the degree of interfertility, character-stability, and relationships of morphologically distinguishable forms as indicated by experimental crossings of individuals representing several populations.

ACKNOWLEDGEMENTS

I wish to thank Frank B. Cross, University of Kansas Museum of Natural History (KU), under whose guidance this study was initiated, and the following persons and their institutions for making specimens, facilities, or both, available to me: Reeve M. Bailey, University of Michigan Museum of Zoology (UMMZ); William M. Clay, University of Louisville (UL); Shelby D. Gerking, University of Indiana (UI); Clark Hubbs, University of Texas (TNHC); George A. Moore, Oklahoma State University (OAM); Edward C. Raney, Cornell University (CU); Philip W. Smith, Illinois Natural History Survey (INHS); Kirk Strawn, University of Arkansas (UARK); Arthur Witt Jr., University of Missouri (UMO); Loren P. Woods, Chicago Natural History Museum (CNHM). I am grateful to Leslie W. Knapp, United States National Museum, and Artie L. Metcalf, The University of Texas at El Paso, for examining types of *E. spectabile* for me at the U.S. National Museum (USNM) and to the following persons for assistance in collecting specimens of *E. spectabile*: William Berg, Branley A. Branson, Frank B. Cross, James E. Deacon, Jerry F. Downhower, Artie L. Metcalf, Wendell L. Minckley, Leonard J. Olund, Bill A. Simco, Milton Topping, Martin L. Wiley, and Larry A. Witt. For critical reading of the manuscript, I wish to thank Frank B. Cross, Raymond C. Jackson, and Robert M. Mengel.

I am indebted to the State Biological Survey of Kansas for providing laboratory facilities and most of the expenses of both the field and laboratory investigations, and to the Research Committee of Wichita State University for funds allowing me to continue this investigation at my present location.

METHODS

Characters studied included 32 morphometric and 25 meristic features

determined for small series (20-30) from localities throughout the range of the species. To minimize the effects of allometric growth on the data, only specimens larger than 30 mm in standard length were used. Counts and measurements were made by methods given in Hubbs and Lagler (1958) unless otherwise indicated. Data for each sex were analyzed separately and later combined unless there was significant difference between sexes.

Most morphometric data have scant diagnostic value because sexual dimorphism, breeding condition, state of preservation, and measuring error (large in proportion to the total length of these small fish) tend to mask differences between geographic variants. Therefore measurements are omitted from the descriptive accounts that follow.

Coloration and the following characters seem most useful for defining geographic variation and revealing trends within and between river systems. *Gill membranes* are indicated to be separate to moderately conjoined, based on the distance from the tip of the snout to their union. If this distance, measured with dividers, was less than the distance from the tip of the snout to the posterior orbital rim, an index of 0 was recorded; if the distance exceeded this, but terminated within the postocular sinus (Branson and Moore, 1962), a 1 was recorded; if the distance extended beyond the postocular sinus, a 2 was recorded. *Lateral line scales* were counted on the left side only. At first, counts from males and females were averaged separately; then, these counts were combined because only small series had means that were not within one scale of each other. *Pored lateral line scales* were counted as above. *Diagonal scales* were counted on the left side, beginning at the origin of the soft-dorsal fin and proceeding downward in the diagonal series to the anal fin. *Scales above the lateral line* were counted as above, except that the count was terminated in the scale row above the lateral line.

Anterior squamation is represented by indices 0 through 3 for each part of the fish under consideration. An index of 0 was recorded for any part devoid of scales. For the cheek, one scale of two rows of scales below or behind the orbit was considered "lightly scaled" and given an index number of 1; three or four rows, "moderately scaled," as index of 2; more than four rows, "well scaled," an index of 3. For opercle and nape, less than 50 per cent scaled, an index of 1; more than 50 per cent scaled, but not completely scaled, an index of 2; fully scaled, an index of 3. For the breast, when scaled before either the pectoral or pelvic fin but not both, an index of 1; before both fins but not covering the posterior portion of the breast, an index of 2; covering posterior portion of the breast, an index of 3. In all regions embedded scales were included if they were evident without dissection. These indices were summed and divided by four to obtain an *anterior scale index*.

The *infraorbital canal* is interrupted (rarely complete) in the orange-throat. There are usually four (sometimes three or five) anterior pores associated with the lachrymal bone, an interruption, then one to five pores

associated with the orbital series of bones from the dermosphenotic anteriorly. Because of the variable nature of the posterior set of pores, they are the only ones reported in this study. The supratemporal canal is often complete, having a single median and two dorsolateral pores, but may be widely to narrowly interrupted medially.

Lepidotrichs are of some diagnostic value and their number is discussed where dines appear in and between various river systems or geographic races. Counts reported are of dorsal spines, dorsal soft-rays, anal soft-rays, and pectoral rays. Breeding *tubercles* are variably present on males on the *ventro-lateral* surfaces posterior to the breast, during the height of the breeding season; however, they show considerable variation as to location and degree of development. The genital papilla of males is usually conical, but the shape of the apex and degree of pigmentation vary throughout the range.

An attempt was made to give a complete literature record. In literature prior to 1930, I have included only those reports with an adequate description of the species or reports from localities where *spectabile* now occurs; nevertheless, some of the citations may refer to *E. caeruleum* or to mixed collections of *caeruleum* and *spectabile*.

Material examined is listed in my doctoral dissertation (1966), The University of Kansas, Lawrence, Kansas and in University Microfilms (Dissertation Abstracts 28: 1267, 1967), Ann Arbor, Michigan.

DESCRIPTIONS

Etheostoma spectabile (Agassiz)

Figure 1

DIAGNOSIS. A species of *Etheostoma*, subgenus *Oligocephalus*, having an interrupted infraorbital canal, body depth greatest near origin of spinous dorsal fin, 11-12 pectoral rays, and, in nuptial males, bright orange branchiostegal membranes and usually absence of red on anal fin (when present, red in anal fin restricted to amorphous blotches, never the prevalent color).

DESCRIPTION. Body shape average to stout, oval in cross-section, back elevated, and caudal peduncle rather slender; head large, 3.0-3.8 in standard length; mouth average, subterminal to terminal, lower jaw included, upper jaw 3.1-4.0 in head-length; snout rather strongly decurved; eye average, 3.5-4.5 in head-length; gill membranes separate to moderately connected; dorsal spines 8-12, usually 9-10; dorsal rays 10-15, usually 12-13; branched caudal rays 10-15, usually 13-14; anal spines 2; anal soft-rays 4-8, usually 6-7; pelvic spine 1; pelvic soft-rays 5; pectoral rays 10-14, usually 11-12; infraorbital canal incomplete (usually 4 pores anteriorly and 1-5 posteriorly), rarely complete with 8-9 pores; lateral (temporal) canal with 5 pores; anterior nasal, posterior nasal, interorbital, coronal, and postorbital pores present; preoperculo-mandibular canal with 10 (rarely 9) pores; vertebrae 35-37, usually

36; top of head naked except for several small scales at junction of lateral and supratemporal canals; squamation of sides of head variable. Breast usually naked. If present, scales on head and breast often embedded and cycloid.

Base color brownish to olivaceous; dorsum and upper sides densely pigmented, variably lined or tessellated; males brightly colored with red or orange and blue or blue-green, base color of sides and ventrum often white; sides with 4-11 transverse bars from axil of pectoral fin to base of caudal fin, bars on postanal sides usually most prominent; in breeding males, bars dark blue or blue-green, spaces between bars bright orange or red; bars variably continuous or interrupted across ventrum; dorsum with 0-10 squarish, dark-brown saddles alternating and coalescent with or separate from lateral bars; spinous dorsal fin dark blue or green marginally, having a variably developed submarginal (and sometimes a basal) orange band; red or orange present in soft dorsal fin, often predominant color; caudal fin colorless to pale yellow, rays red in northern Ozarks; anal fin dark blue or green, anterior rays often colorless distally, ray-margins and breeding tubercles opaque white; pelvic fins blue- or green-black, margins and tubercles similar to those of anal fin; pectoral fins colorless to pale yellow.

Color in females more subdued than in males, pale reds and blues evident during breeding season; ventrum generally immaculate; anal and paired fins generally colorless.

Breeding tubercles variable in males; if present, appearing on one, several, or all of the following locations: anal spines and rays, pelvic spines and rays, lower rays of caudal fin, lower rays of pectoral fin, and ventral scales.

Genital papilla of males flattened, commonly subtriangular: distally may be acute, obtuse, rounded, emarginate, truncate, or acuminate; coloration variable. Papilla of adult females oblong and tubular, overlapping front of first anal ray, always immaculate.

HABITAT. Sluggish to moderately swift, shallow, hardwater streams with bottoms of sand, gravel, rubble, or bedrock. Inhabitant of riffles, raceways, shallow pools and backwater, occasionally in temperate springs.

***Etheostoma spectabile spectabile* (Agassiz)**

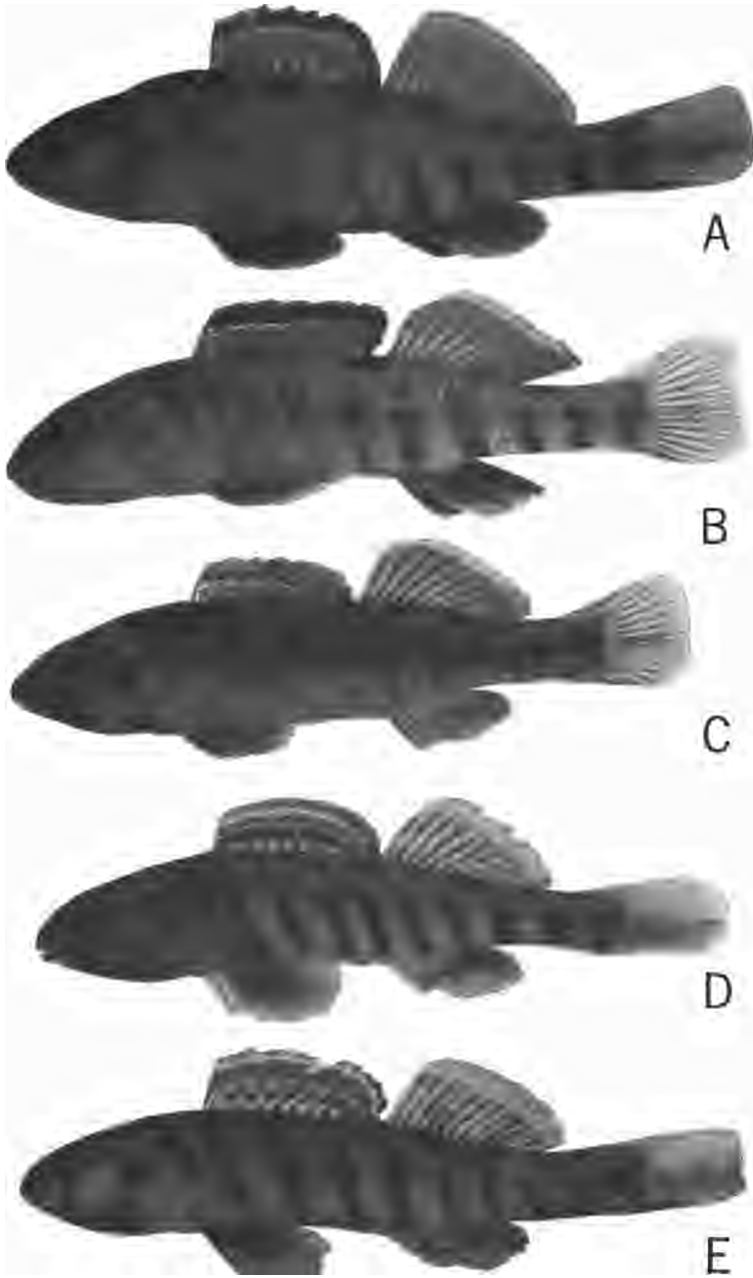
Northern Orangethroat Darter

Figure 1C

Poecilichthys spectabilis Agassiz, 1854, Amer. J. Sci. Arts, 17:304 (Osage River, Mo.).

Poecilichthys versicolor Agassiz, 1854, Amer. J. Sci. Arts, 17:304 (Quincy, Ill.). See Collette and Knapp (1967).

TYPES. Three sets of syntypes of *Poecilichthys spectabilis* Agassiz are extant; they are in the University of Michigan Museum of Zoology (UMMZ 86340, 8 specimens), the United States National Museum (USNM 120284,



5 specimens), and the Museum of Comparative Zoology, Harvard University (MCZ 24503, 24520, 24722; 21 specimens).

A lectotype, male, 47.5 mm in standard length, is herein designated from the Michigan series and retains the original catalog number. A lectotype is designated because one specimen of *E. caeruleum* was present in the original series. The remaining paralectotypes in the Michigan set have been recataloged as UMMZ 179528 and the specimen of *E. caeruleum* as UMMZ 179529.

I have not seen the other type specimens, but those at the U.S. National Museum were checked by Leslie Knapp and Artie Metcalf and those at the Museum of Comparative Zoology by Bruce Collette. All were confirmed to be *E. spectabile*. Knapp (per. comm.) also confirms specimens of *P. versicolor* to be *E. spectabile*. See Collette and Knapp (1967).

DIAGNOSIS. This subspecies can be distinguished from those of the western or *pulchellum* complex by a combination of the following characters: anterior region lightly to moderately scaled, index 1.5 (0.8-2.2); scales usually large, mean number of lateral line scales usually less than 48, of pored scales usually less than 30, diagonal scale rows usually 12 or less, scale rows above lateral line usually 5 or less (scale characteristics will separate most populations from *pulchellum* complex with exception of those in upper White River, Arkansas); branchiostegal membranes separate to slightly connected, index 1; in breeding males, fewer than 9 vertical blue bars or blotches, not continuous across ventrum except near base of caudal fin; blackish longitudinal lines strongly developed in northern Ozarks, less so in southern and eastern portion of range; belly of breeding males usually with discrete patches of red; spinous dorsal fin having three or more longitudinal bands of color, the distal two separated by a narrow colorless or white line, predominant color of fin bluish; soft dorsal having much blue (as well as red) pigment; caudal rays with or without red, membranes colorless.

Distinguished from *E. s. uniporum* by having sensory canals better developed (usually 2 or more pores in posterior segment of infraorbital canal, supratemporal canal complete, and pored scales more numerous); pectoral rays more than 11, and transverse bars nearly vertical, not well developed.

Distinguished from *E. s. fragi* by having anterior region less well scaled, body scales larger (lateral line and diagonal scale rows fewer), gular region uncolored, transverse bars less well developed in brightly colored males, belly not chevron-marked with orange, humeral spot less conspicuous, breeding tubercles usually present on nuptial males.

COLORATION. *Breeding males:* The following composite account is based on specimens from the tributaries of the Osage River in Missouri, the type locality. Notable differences in coloration elsewhere in the range are discussed under river systems in which they occur.

Body scales, from dorsal midline to several scale rows below lateral line,

saturated basally with melanin, collectively producing pattern of continuous horizontal lines. Dorsum olive to reddish brown with 3-9 brownish black saddles from occiput to base of caudal fin, representing intensifications of melanin in horizontal lines. Upper sides reddish brown, lower sides pale blue to opaque white. Zero to 9 transverse bars representing intensifications of melanin in horizontal lines, usually suffused with blue on axilla and on post-anal sides; bars continuous across ventrum only near base of caudal fin. Interspaces between bars reddish orange, most intense posteriorly. Breast blue-gray changing to pink near insertion of pectoral fins, often saturated with fine melanophores. Belly having discrete, oblong salmon-red patches on each side of the ventral midline. Genital papilla blue-gray, saturated with fine melanophores. Cranial region blue-black; snout dark olive to reddish brown. Lips and anterior $\frac{1}{2}$ of cheek blue-gray; suborbital bar blue-black; posterior half of cheek, sides of head, and operculum reddish orange, darkened by underlying melanin on opercle. Branchiostegal membranes brilliant red or orange. Chin and gular region blue-gray. Marginal $\frac{1}{3}$ - $\frac{1}{2}$ of spinous dorsal fin blue-black; beneath marginal band a narrow white or colorless band often suffused with deep red basally; beneath submarginal band a suprabasal gray or gray-blue band about $\frac{1}{3}$ fin height; bands often separated by fine colorless or white lines. Soft dorsal fin also having 4 bands, but colors not so dense; marginal blue-gray, suprabasal blue-gray, and basal red bands usually narrow; submarginal red band usually wide; red best developed on membranes, blue on rays. Caudal rudimentary rays blue, principal rays usually red, occasionally alternating red and blue (barred appearance), rarely all blue; membranes usually colorless; base of fin with 2 orange or red spots in a vertical plane. Anal fin blue, occasionally with small red patches along base and more rarely along rays. Pelvic fins blue-black, having opaque whitish margins. Pectoral fins pink or pale yellow at base, rays occasionally paleblue, membranes colorless.

Non-breeding males: Chromatic colors subdued or lacking; melanins subdued. Pale blue persisting on suborbital bar, margin of spinous dorsal fin, base of anal fin, rudimentary caudal rays, and on caudal peduncle in association with transverse bars. Orange limited to branchiostegal membranes, interspaces on caudal peduncle, base of caudal fin, and thin submarginal band on dorsal fins. Transverse bars indistinct or absent. Horizontal lines often discontinuous.

Females: Mostly devoid of chromatic colors. In breeding specimens, branchiostegal membranes orange. Margin of spinous dorsal, base of posterior anal rays and vertical bars pale blue; bars more diffuse than in males. Branchiostegal membranes, gular region, and chin having fine, scattered melanophores. Soft dorsal and rays of caudal fin lightly barred with melanin. Ventrum immaculate, otherwise pattern of melanin like that of

males. Chromatic colors absent during non-breeding period except for faint red band in middle of spinous dorsal fin.

ADDITIONAL CHARACTERS (exclusive of populations in western Missouri River). The number following the character is the whole number nearest the mean. The range appears in parentheses. *Lateral line scales* (Table 2): 44 (35-59); lowest mean number (39) in lower Cumberland River and (40) in Tennessee River, highest (52) in upper White River, Arkansas; differences in mean number of scales within river systems often far exceeds differences among them. However, the mean number of scales increases somewhat in major rivers northward from Tennessee River to Ohio River (40-45) and westward from Interior Low Plateaus to Ozark Plateaus (43-47). *Pored lateral line scales* (Table 5): 26 (12-42); lowest mean number (21) in Tennessee and lower Cumberland rivers, highest (33) in upper White River, Arkansas; similar to lateral line scales, differences within often exceed differences between river systems, also, there is an increase in the mean number of pored scales northward from Tennessee River to Ohio River (21-26) and westward from Interior Low Plateaus to Ozark Plateaus (24-27). *Diagonal scales*: 12 (9-17); modal number 12 through most of range, 11 in Tennessee River, 13 in upper White River; slight increase in mean from east to west and from south to north in eastern part of range. *Scales above lateral line*: 5 (4-8); modal number 5 through most of range, 6 in upper White River. *Anterior squamation* (Table 8): Cheek naked to well scaled, usually lightly scaled, mean index 1; lowest mean (0.9) in upper White River, highest (1.6) in Tennessee River. Opercle naked to well scaled, usually moderately scaled, mean index 2; lowest mean (1.1) in upper Green River, highest (3.0) in lower Cumberland River. Nape naked to well scaled, usually moderately scaled, mean index 2; lowest mean (1.2) in upper White River and (1.3) in upper Green River, highest (3.0) in Tennessee and lower Cumberland rivers, and (2.9) in lower Green River. Breast naked to moderately scaled, usually naked, mean index 0; highest mean (1.8) in lower Cumberland River. Mean anterior scale index 1.5; lowest mean (0.8) in upper White River and (0.9) in upper Green River, highest (2.2) in Tennessee and lower Cumberland rivers; mean index between major river systems decreases northward from Tennessee River to Ohio River (2.2-1.1), southward from Missouri River to White River (1.6-1.2), and westward from Interior Low Plateaus to Ozark Plateaus (1.5-1.4); differences within river systems far exceed differences between them. *Posterior infraorbital pores* (Table 12): 3 (1-5); modal number 3 through most of range. *Supratemporal canal* (Table 12): Usually complete throughout range; about 10 per cent of individuals east and 12 per cent west of Mississippi River with incomplete canals. *Gill membranes*: Separate to moderately connected; index 1 through most of range; index 0 in Ohio River system exclusive of Green, Cumberland, and Tennessee rivers. *Lepidotrichs*: Spinous dorsal 10 (8-12); soft dorsal 13 (11-15); anal soft-rays

7 (4-8); pectoral rays 12 (11-13). *Breeding tubercles*: Usually absent in Ohio River system and northward and in direct tributaries of Mississippi River; when present, restricted to anal rays. In remainder of range, *tubercles* present on anal and pelvic rays; also on ventral scales in Cumberland River, Missouri River, and upper White River in Arkansas; also along lower caudal rays in upper White River. *Genital papilla of males*: Acute, rounded, or acuminate; often truncate in central White River of Missouri and Arkansas. Usually stippled with fine melanophores.

RANGE. Tributaries of upper Mississippi River in southeastern Iowa (populations now extirpated) and northeastern Missouri; eastward through Illinois and Indiana to southeastern Michigan and western Ohio; southern tributaries of Ohio River from Kinniconick Creek (Kentucky) westward to Tennessee River; Osage River system of Kansas and Missouri, eastward and southward in Gasconade, Meramec, St. Francis, upper Black, and White rivers of Missouri; White River system in Arkansas from Ozark escarpment westward. Absent from Coastal Plain, Mississippi Embayment, and Appalachian Plateaus.

INTERGRADES. With *E. s. pulchellum* in eastern tributaries of Kansas River and Missouri River eastward to mouth of Osage River; possibly with *E. s. squamosum* in tributaries of upper White River in Arkansas.

DISCUSSION. Unlike most other subspecies recognized herein, *E. s. spectabile* is a composite of weakly differentiated geographic races. Differences are significant among some populations, but variation is often clinal and zones of intergradation seem broad. In that part of the range east of the Mississippi River, my investigation was less intensive than in the Ozarks and western Central Lowlands; for some of the color descriptions in the eastern range, I have relied partly on notes and photographs by other investigators. A more thorough study of these eastern populations, especially in Kentucky and Tennessee, may reveal geographic races sufficiently distinct to be recognized as subspecies.

I use the terms race and subrace for populations less well defined than subspecies, but with diagnostic characters distinct enough to warrant mention.

Variation, particularly in color pattern, of characters which differ consistently from those of populations in the Osage River (the type locality) is discussed in the order of (1) streams draining the Ozark Plateaus east of the Missouri-Osage River confluence (generally north to south), and (2) streams east of the Mississippi River from north to south.

Variation west of the Mississippi River. Populations in the Gasconade River are generally like those in the Osage River. Eastward, in the Meramec and in small, immediate tributaries of the Mississippi River, specimens have less intense horizontal lining and better developed vertical bars posteriorly than do those in the Osage River; bands of the spinous dorsal fin are sub-

equal in width and usually the caudal rays lack red pigment. In the White-water, St. Francis, and Black river populations, horizontal lines are broken and diffuse; the dorsum and upper sides are often dark and tessellated; blue is reduced throughout; red ventral pigmentation is developed extensively from the branchiostegal membranes to the caudal base. This bright red ventrum is least developed in specimens from the Whitewater River, reaching maximum development in populations of Black River and St. Francis River. As in the Meramec River specimens, bands of the spinous dorsal fin are subequal in width. In the Black River watershed from Cane Creek southward through Strawberry River, populations of orangethroats are recognized herein as two distinct subspecies; these are discussed later.

Westward in the White River drainage, populations of orangethroats are considered to be a southwestern race of *E. s. spectabile* because they resemble that subspecies more than they resemble the two subspecies in the tributaries of Black River alluded to above. The White River race is not a homogenous population, but on the basis of coloration and squamation it is divisible into two subraces or variants, one in the headwaters of White River above its confluence with Roaring River and one in the tributaries of White River from Roaring River eastward to the Ozark escarpment (sparsely distributed in tributaries east of the confluence of White River with its North Fork). The eastern subrace in White River differs as follows from Osage River populations: horizontal lines reduced to rows of dots and usually suffused with orange or deep red in interspaces between transverse bars, sometimes throughout; transverse bars of melanin variable, usually no more than blotches along lateral line; transverse bars of blue usually present along entire sides of breeding males; interspaces on lower sides gray or blue-white, occasionally with flecks of orange posteriorly; spinous dorsal fin with marginal and suprabasal blue bands partially to completely fused, basal red band narrow and often incomplete; soft dorsal fin predominantly blue (two thirds or more), red pigment limited usually to a narrow submarginal band; mean number of lateral line scales (43) lowest in any Ozarkian population; genital papilla of males truncate or mucronate, rarely rounded or obtuse.

In the western or headwater subrace in White River, horizontal lining is not so strong as in Osage River populations, but it is more evident than elsewhere in the range of the subspecies. These lines appear on at least four scale rows below the lateral line. Transverse bars of blue or blue-gray are darkened by melanin posteriorly. Anteriorly the lower sides are blue-white or gray, but the belly usually has an extensive orange patch. The suprabasal and marginal blue bands of the spinous dorsal fin are usually separated by a narrow red or red and white band; the blue-black marginal band is widest. The soft dorsal fin has 4 bands, but either blue or orange may be the dominant color. The largest area of ~~tubercle-development~~ is found in the western White River subrace. The lower caudal and outer surface of lower pectoral

rays are often tuberculate, as are anal rays, pelvic rays and ventral scales. The anterior scale index is low (0.8) compared with Osage and lower White River populations (both 1.5). The mean number of lateral line scales (52) is higher in the upper White River than anywhere in the range of the species except for populations of *E. s. pulchellum* in the Brazos River (53). The mean number of pored scales (33) is higher than elsewhere, except for populations of *E. s. pulchellum* in the Republican River (33) and Brazos River (34) and *E. s. fragi* in the Strawberry River (34).

The intermediate color patterns, tuberculate ventral scales, and tuberculate lower pectoral rays suggest that the upper White River subrace may consist of intergrades of *E. s. spectabile* and *E. s. squamosum* of the Illinois River (Arkansas River drainage). On the other hand, the anterior scale index is lower than, and the lateral line and pored scale counts of the western subrace of *E. s. spectabile* are higher than the corresponding values in the eastern White River subrace and *E. s. squamosum*, the supposed parental forms. I doubt that heterotic effects of interbreeding are responsible for these extreme values; laboratory crosses of stock from White River and Arkansas River exhibit no heterosis in the F1 generation.

Barlow (1961) and others have suggested that slow embryonic development and/or low temperatures during formative periods increase meristic counts. Other environmental factors that influence meristic counts are summarized by Strawn (1961). Loren C. Hill (per. comm.) found an increase in the number of vertebrae in populations of *Etheostoma juliae* Meek from tributaries of upper White River. Gilbert Castro (per. comm.) found a similar increase in the number of lepidotrichs in populations of *Micropterus dolomieu* Lacépède from the same locality. Possibly low developmental temperatures are responsible for extreme meristic characters in upper White River.

Variation east of the Mississippi River. Orangethroats from streams in Illinois that flow directly into the Mississippi River closely resemble the Meramec-Big River populations in Missouri. Those from the upper Illinois and Kaskaskia rivers exhibit loss or reduction of horizontal lines (best developed in females). The transverse blue bars are variable. They may be restricted to the post-anal sides, or equally well developed on the trunk and caudal peduncle. Melanin associated with these bars, particularly on the post-anal sides, forms a subtriangular pattern, having the widest angle pointing anteriorly. Red is lacking on the caudal membranes, but they sometimes appear pale yellow or orange.

I have not examined live breeding males from Indiana, Michigan, and Ohio, but I surmise from preserved material that their coloration is similar to that of Illinois specimens. The marginal and suprabasal bands of the spinous dorsal fin are separated by a colorless or white band, a portion of which is usually suffused with red. There is a general decrease in the total

area of the body colored red and blue. Trautman (1957) mentions one difference in Ohio specimens in which the breast and ventral surface of the head are deep orange. Westward, the breast and underside of head (except for the branchiostegal membranes) are gray-white or blue-gray.

Reeve M. Bailey's field notes on specimens from Kentucky River agree generally with the description of Ohio specimens, but he notes that the distal portion of the caudal fin is tinged with orange, the pectoral fin with yellow-orange, and the anterior half of the breast is bright orange.

In specimens from Salt and Rolling Fork rivers in Kentucky, transverse bars are straplike and most evident on the post-anal sides. Orange is limited to the interspaces and best developed posteriorly. The breast and belly are usually immaculate, but orange is variably present on the belly (a few flecks to broad, oval patches). The submarginal red band of the spinous dorsal fin is reduced to a few red spots posteriorly, leaving the marginal and suprabasal bands separated by a white or colorless band; the basal red band is poorly developed. Horizontal lines are poorly developed on most specimens.

In my opinion, orangethroats from the Illinois and Kaskaskia rivers of Illinois, from the Lake Erie drainage, and from the entire drainage of the Ohio River with the exception of the Green, Cumberland, and Tennessee rivers of Kentucky and Tennessee represent a northeastern race of *E. s. spectabile*. I suspect that it originated from populations that found refuge in tributaries of the Ohio River during late Pleistocene glaciation. Members of this race seem more closely allied to each other than they do to populations in the Ozarks and populations in the Green, Cumberland, and Tennessee rivers.

Based on differences in coloration, anterior squamation, and body squamation, I recognize the orangethroats from Green (Barren), Cumberland, and Tennessee rivers of Kentucky and Tennessee as a southeastern race of *E. s. spectabile*. Populations in each of those three stream-systems seem distinctive also in some features of squamation and coloration, but I prefer not to recognize them taxonomically until a more thorough study can be made.

In the headwaters of Green River in Lincoln Co., Kentucky, orange-throats resemble those from Rolling Fork-Salt River except that the transverse bars are less well developed. The anterior scale index is low (0.9), the opercle and nape are usually sparsely scaled, and lateral line scales are usually 45 or more. Lower Green River (Barren River) populations have a high anterior scale index (1.9), the opercle and nape are well scaled, and the breast is lightly scaled; the lateral line scales average about 41. Adult males are often deep-bodied anteriorly. Transverse bars are represented by diffuse blotches of melanin along and slightly below the lateral line, from which pale, blue-gray bars extend dorsad and ventrad. Colored bars may appear from the axil of the pectoral fin to the base of the caudal fin but usually are best developed on the post-anal sides. The interspaces on the upper sides

are olivaceous with flecks of orange. Orange increases in extent posteriorly. Interspaces on the lower sides are gray-white and flecked with orange only on the caudal peduncle. Color radiates out of the orange spots at the base of the caudal fin along the principal rays. The rudimentary rays are pale green. The dorsum is often tessellated, contrasting sharply with the pallid base-color on the upper sides. The breast and belly are whitish except directly before the insertion of the pectoral fins, where the breast is cream-yellow. The principal evidence of horizontal lines is in the composition of the transverse blotches in females. The colored bands of the spinous dorsal fin, from the distal margin to the base, are as follows (numbers indicate approximate width of band as per cent of fin height) : blue-black, 50; colorless or white, 20 (submarginal band of red lacking); blue-black, 10, and red 20.

I have not seen living specimens from the upper Cumberland River, but preserved individuals have a color pattern like Kentucky River specimens, though less dark. Transverse bars are more straplike than angular and there are faint horizontal lines in most specimens. Some individuals approach Barren River patterns of pigmentation. Interspaces are suffused with orange, but the anterior lower sides seem to have been bluish or gray-white. The upper sides are plain or tessellated. A thin, red, submarginal band is present in the spinous dorsal fin, but the caudal fin seems to lack red except at its base. There are usually more than 25 pored and 40 total lateral line scales. The anterior scale index is 1.3.

Preserved orangethroats from the lower Cumberland resemble Barren River populations. The horizontal lines are usually lacking or faint. The transverse bars, if not blotchlike, are best developed along the lateral line and a few scale rows below it. A few specimens are well banded along the entire sides. The dorsum except for the saddles is pale, the upper sides mottled or tessellated. The lower sides and belly are usually immaculate. No colors were preserved well enough to ascertain if a submarginal red band is present in the spinous dorsal fin. There are usually less than 22 pored and 40 lateral line scales. The anterior scale index is 2.2 because of an increase in breast squamation.

Orangethroats in the Tennessee River drainage seem to be restricted to tributaries of the lower Duck River (Piney River and westward), and to direct tributaries to the Tennessee River west of Waynesboro, Tenn. A single individual has been cataloged at the University of Michigan (UMMZ 96877) from the North Fork of Holston River in Virginia. Robert E. Jenkins (per. comm.) apprised me of a possible mixing of collections at UMMZ that may have been responsible for the inclusion of *E. spectabile* in the upper Tennessee River drainage. In 1928, Herbert R. Becker made a total of 34 collections in Virginia, Kentucky, Tennessee, Georgia, and Alabama. Evidently, most of the collections were sent to C. L. Hubbs at Michigan. In a letter to Becker dated 30 September 1928, Hubbs implied that a summer as-

sistant at UMMZ may have mixed up labels for specimens from some of Becker's collections and that he would welcome Becker's help in straightening out the trouble. However, Hubbs considered the record of *E. spectabile* from Virginia good because he had no evidence that labels from this accession had been mixed. Other than the alleged Holston River specimen (UMMZ 96877), specimens of *E. spectabile* were collected only from the Barren River drainage of Kentucky (UMMZ 96314, 4 specimens and UMMZ 96346, 20 specimens). No additional specimens have been collected from this locality. Ross and Carico (1963) in a survey of the North, Middle, and South forks of the Holston River, report no orangethroats from this drainage. Robert D. Ross (per. comm.) informed me that he has collected in headwaters of the Tennessee River as far west as Oak Ridge, Tenn., but has never found *E. spectabile*. Because of the absence of records from intervening streams and the existence of only one specimen, I believe the specimen labelled as having come from the Holston River is either an introduced individual or an erroneous locality record.

Preserved specimens from northern Duck River drainage exhibit moderately developed horizontal lines or rows of dots. The dorsum is pale except for saddles, and the upper sides are lined or tessellated. The transverse bars are blotch-like, having melanin best developed on the lower sides of the caudal peduncle. Some specimens are barred diffusely over the entire sides. The dark marginal and lighter suprabasal bands of blue on the spinous dorsal fin are often fused, at least posteriorly. The submarginal red band is lacking or poorly developed. There is evidence of an orange wash on the caudal fin. Except for the lined upper sides, these specimens resemble those from Barren River. The anterior scale index is 2.3. In specimens from Buffalo River (southern tributary of Duck River), horizontal lines are faint or absent. The transverse bars are diffusely blotched or subtriangular and often appear over the entire sides. The upper sides are pale in base color but mottled or tessellated and probably saturated with orange posteriorly. There is a progressive loss of scales on the cheek and breast from lower to upper Buffalo River (index 25 to 1.8). In Hardin Creek (an immediate tributary to Tennessee River with tributaries that interdigitate with those of the upper Buffalo River) specimens are similar to those of the upper Buffalo River in anterior squamation (1.8-2.0), but dusky, broken horizontal lines are evident on the upper sides.

PRIMARY LITERATURE RECORDS AND MISIDENTIFICATIONS. This subspecies has been reported under the following names:

Poecilichthys spectabilis Agassiz (1854) original description, Osage River, Missouri—Nelson (1876) northern Illinois; Jordan (1876) in part, Indiana and Kentucky; Jordan (1877a) in part, Ohio River Valley; Jordan (1877b) in part, upper Mississippi River Valley and Lake Erie; Jordan (1877c) in part, White River, Indiana; Jordan (1878) Mississippi River Valley; Jordan and Brayton (1878) in part, Ohio and Illinois river basins; Jordan (1880) characters; Jordan and Gilbert (1882) characters, Mississippi River Valley; Jordan (1882) characters, ecology, Ohio; Trautman (1930) specific characters; Kuhne (1939) Tennessee; Collette and Knapp (1967)

catalog of type specimens. *Poeciliichthys versicolor* Agassiz (1854) original description, Quincy, Illinois—Collette and Knapp (1967) catalog of type specimens. *Astacichthys coeruleus* (Storer)—Vailant (1873) in part, characters. *Astacichthys pulchellus* (Girard)—Vailant (1873) in part, characters. *Etheostoma varium spectabile*—Jordan and Meek (1885) characters, Lamine and Osage rivers, Missouri. *Etheostoma caeruleum spectabile*—Jordan (1885) Mississippi River Valley; Jordan and Gilbert (1886) White River, Arkansas; Meek (1891) in part, Missouri and White river basins in Missouri and Arkansas, characters; Meek (1892) Cedar River, Iowa; Meek (1894) White River, Arkansas; Hay (1894) in part, Indiana; Meek (1895) White River, Arkansas; Kirsch (1895a) Indiana; Kirsch (1895b) Ohio; Jordan and Evermann (1896) characters, Mississippi River Valley; Evermann and Cox (1896) in part, Missouri River Valley; Eigenmann and Beeson (1905) Indiana; Jordan (1916) in part, Indiana to Kansas. *Etheostoma caeruleum*—Kirsch (1892) in part, Tennessee River, Tennessee (2 specimens, UMMZ 61546, one is a male *E. s. spectabile*, the other, *E. caeruleum*); Hahn (1909) in part, Indiana (6 specimens, UMMZ 63003, 2 are *E. s. spectabile*, the remainder *E. caeruleum*); Forbes and Richardson (1920) in part, Illinois; Thompson and Hunt (1930) in part, Illinois. *Poeciliichthys coeruleus spectabilis*—Hubbs (1926) Great Lakes Region; Hubbs and Ortenburger (1929) in part, Missouri and Kansas. *Oligocephalus coeruleus spectabilis*—Jordan (1929) characters, Missouri to Kansas. *Oligocephalus caeruleus*—Jordan, Evermann, and Clark (1930) in part, check list. *Poeciliichthys spectabilis spectabilis*—Aitken (1940) Iowa; Hubbs and Lagler (1941) characters, distribution; Shoemaker (1942) characters, Wayne Co., Indiana; Gerking (1949) ecology, distribution, Indiana; Hubbs and Lagler (1949) characters, distribution; Shockley (1949) Boone Co., Indiana. *Etheostoma spectabile spectabile*—Harlan and Speaker (1951) characters, Iowa; Bailey (1951) characters, Iowa; Bailey and Gosline (1945) vertebral counts; Gerking (1955) characters, Indiana; Harlan and Speaker (1956) characters, Iowa; Bailey (1956) characters, Iowa; Trautman (1957) characters, ecology, distribution, Ohio; Hubbs and Lagler (1958) characters, distribution; Stegman and Minckley (1959) southern Illinois; Larimore and Smith (1963) distribution, Champaign Co., Illinois; Collette (1965) breeding tubercles; Collette and Knapp (1967) catalog. *Etheostoma spectabile*—Martin and Campbell (1953) Black River, Missouri; Eddy (1957) characters, distribution; Hubbs and Strawn (1957a) hybrid survival; Clark, Breukelman, and Andrews (1958) Lyon Co., Kansas; Hubbs (1958b) variation in egg complement; Winn (1958a) ecology, behavior; Winn (1958b) ecology, behavior; Hubbs (1959) hybrid combinations; Stegman (1959) southern Illinois; Bailey *et al.* (1960) common name; Larimore (1961) collecting success; Deacon (1961) eastern Kansas; Hubbs (1961b) gamete compatibility; Hubbs and Armstrong (1962) temperature tolerance; Fisher (1962) Missouri River near Rocheport, Missouri; Hubbs and Strawn (1963) temperature tolerance; Greeson (1963) Dix River, Kentucky; Dlinger (1966) habits of fry; Cross (1967) characters, habits, distribution in Kansas.

Etheostoma spectabile uniporum subsp. nov.

Current River Orangethroat

Figure 1D

TYPES. Holotype (KU 7478) an adult male 44.5 mm in standard length, collected by D. A. Distler and J. F. Downhower April 7, 1963, in Pigeon Creek, a headwater tributary of Current River, Sec. 8, T. 32 N, R. 7 W, Dent County, Missouri. Paratypes are 230 additional specimens (KU 7479, 7480) collected with the holotype.

DIAGNOSIS. *E. s. uniporum* differs from other subspecies of *E. spectabile* in possessing a unique combination of the following characters: usually a single pore in posterior section of infraorbital canal, an interrupted supratemporal canal, less than $\frac{1}{2}$ of lateral line scales pored, modal number of pectoral rays 11, and in coloration having transverse bars of equal intensity from axil of pectoral fin to base of caudal fin (anteriorly, bars slanting forward along plane of diagonal scale-rows, not subvertical as in other subspecies).

COLORATION. *Breeding males:* The following data were taken from the

holotype and paratypes. Dorsum with 7-8 squarish saddles usually of equal intensity, but occasionally the saddle at posterior insertion of spinous dorsal and one at posterior insertion of soft dorsal darker than others. Upper sides brown to brick-red, usually with fine, discontinuous lines extending length of body. Lower sides blue-gray, rusty gray, or off-white where not crossed by bars; horizontal lines lacking except near lateral line. Transverse bars bright blue intensified by dense melanin, 2-3 scale rows wide and weakly continuous across ventrum, less often across dorsum; Current River specimens extreme in forward-slant of bars, Spring River specimens having more nearly vertical and occasionally wider bars. Entire sides lightly stippled with melanin. Humeral spot small but distinct, often iridescent blue or green, largest in specimens from Spring River. Breast gray-blue, gray, or white. Belly (between bars) rusty gray, gray-blue, or gray; incidence of a reddish ventrum somewhat higher in Spring River than elsewhere. Genital papilla and peritroct white, sometimes with a few melanophores. Dorsum of head dark brown. Cheeks bright blue, darkened with melanin. Pre- and post-orbital bars narrow but distinct; suborbital bar diffuse in Current River, more distinct in Spring River. Lips, chin, and gular region gray or gray-blue; less blue in Spring River. Branchiostegal membranes bright orange, extending onto interopercle and subopercle, remainder of operculum brown or brownish orange. Spinous dorsal fin with 4 distinct bands generally separated from each other by narrow colorless or white lines: marginal blue, submarginal orange, suprabaasal blue, and basal orange (suprabaasal blue band generally widest); in Spring River, submarginal orange band much reduced, appearing only posteriorly or not at all, allowing variable fusion of marginal and suprabaasal blue bands. Soft dorsal also four-banded, similar to *E. s. spectabile*. Rudimentary rays of caudal fin blue or blue-green, principal rays pale gray-yellow or gray-green; membranes mostly colorless; base of fin with 2 orange spots in a vertical plane, often coalescing. Anal fin blue-gray, fading distally; random flecks of orange occasionally appearing on fin. Pelvic fin blue-black, margin of rays white. Base of pectoral fins pale yellow or pink; rays near base pale blue to colorless, membranes colorless distally; fleshy axilla of fin orange.

Non-breeding males: Blues subdued or absent; lateral bars represented only by melanin, most dense on lower sides. Paired fins colorless. Caudal fin finely barred with melanin. Orange subdued. Melanin reduced.

Females: Blues absent or appearing only faintly. Orange limited to a fine submarginal band on spinous dorsal fin. Soft dorsal fin and caudal fin weakly barred with melanin. Sides with fine, discontinuous, horizontal lines. Transverse bars indistinct or wanting, except in Spring River, where often distinct.

ADDITIONAL CHARACTERS. The number following the character is the whole number nearest the mean. The range appears in parentheses. *Lateral*

line scales (Table 3) : 45(39-52). *Pored scales* (Table 6) : 22 (10-32), less than in other subspecies except for populations of *E. s. spectabile* in the Tennessee and lower Cumberland rivers, which have an average of 21 pored scales. Specimens from Current and Eleven Point rivers have the lowest mean numbers within the range of *uniporum*. *Diagonal scales*: 12 (10-14), modal number 12 throughout range. *Scales above lateral line*: 5 (4-6), modal number 5 throughout range. *Anterior squamation* (Table 9) : Cheek naked to well scaled, generally lightly scaled, mean index 1.2. Opercle naked to well scaled, mean index 1.7, a clinal increase from north to south (0.9 in Cane Creek to 2.3 in Spring River). Nape naked to well scaled, usually moderately scaled, mean index 1.6; in northern part of range (Cane Creek and Current River) nape usually lightly scaled, in remainder of range moderately scaled. Breast naked to moderately scaled, generally naked, mean index 0.2; little variation throughout range. Mean anterior scale index 1.2; 0.7 in northern part of range to 1.4 in southern part. *Posterior infraorbital pores* (Table 13) : 1 (1-3), mean 1.4; modal number 1.0 in Cane Creek, Current and Eleven Point rivers; 2.0 in Fourche and Spring rivers. Lowest modal and mean number of subspecies complex. *Supratemporal canal* (Table 13) : About 1/3 of all specimens examined with a complete canal; highest number of specimens having complete canals in Fourche and Spring rivers (ca. 60 per cent). *Gill membranes*: Separate to slightly connected, index of 1. *Lepidotrichs*: Spinous dorsal 10 (9-11); soft dorsal 12 (11-14); anal soft-rays 7 (6-8); pectoral rays 11 (10-12), lowest modal and mean number of subspecies complex. *Breeding tubercles*: Present on anal and pelvic rays of breeding males. *Genital papilla of males*: Generally with acute apex, little variation in shape.

RANGE. Black River drainage from Cane Creek, Butler County, Missouri, southward to Flat Creek, Lawrence County, Arkansas, in upland streams. Major tributaries include Current, Eleven Point, and Spring rivers.

INTERGRADES. In some characters with *E. s. spectabile* to the west and with *E. s. fragi* to the south. See below.

DISCUSSION. In several respects, *uniporum* is the most neotenic member of the subspecies complex. The reduced infraorbital, supratemporal, and lateral line canals and a reduced number of pectoral rays probably are due to fixation of juvenile attributes. Collette (1962), in discussing populations of neotenic *Etheostoma fusiforme* (Girard), suggests that reduction of the number of pored scales, reduction of the number of infraorbital pores, and failure of the supratemporal canal to close probably is the result of the low productivity of lakes where these populations of neotenic darters occur. Productivity of a stream is largely dependent on the fertility of the soil over which it drains and composition of the channel in which it flows. The physicochemical properties of the Current and Eleven Point rivers seem no poorer than those of other streams draining the Ozarks. The Current and

Eleven Point rivers support a rich and varied fauna of both vertebrates and invertebrates and seem comparable to other Ozark streams where neoteny in the orangethroat is not evident. Within the range of *uniporum*, increase in the development of the acoustico-lateralis system southward may be due to the genetic influence of *E. s. fragi*, which has a better developed lateralis system than *uniporum*, or as Collette suggests, to an increase in productivity of the southern habitat.

Loss of scales from the opercle and nape may be a response to environmental conditions, but little experimental evidence for this is available. Of all members of the subspecies complex, only *E. s. pukhillum* has the anterior region more sparsely scaled.

Coloration of the spinous dorsal fin is somewhat like that of adjacent subspecies—*E. s. spectabile* in the upper Black River and *E. s. fragi* in the Strawberry River—except that the supra basal blue band is generally widest in *uniporum* and partially to completely fused to the marginal blue band in populations from Spring River. This fusion also is evidenced in populations of *E. s. spectabile* across the divide from Spring River in North Fork of White River. In males from Spring River the transverse bars are more nearly vertical and rarely slant as far forward as those in populations of *uniporum* from Eleven Point and Current rivers.

E. s. uniporum may have evolved from an Ozarkian stock of *E. spectabile* isolated in tributaries of Black River where *uniporum* now occurs. This probably occurred in post-Nebraskan time, after the Mississippi River shifted its course eastward from the Ozark highlands. Specimens reported as *EMeostoma coeruleum spectabile* by Meek (1891) from Spring River and its tributaries near Mammoth Spring, Fulton County, Arkansas, are referable to this subspecies.

ETYMOLOGY. The latin name *uniporum* is a substantive derived from *unus* (one) and *porus* (pore), and has reference to the single pore occurring modally in the posterior segment of the infraorbital canal.

***Etheostoma spectabile fragi* subsp. nov.**

Strawberry River Orangethroat

Figure 1E

TYPES. Holotype (KU 7481) an adult male 44.0 mm in standard length, collected by D. A. Distler and J. F. Downhower, April 10, 1963, in Spring Creek, a tributary of Big Creek, Sec. 36, T. 16 N, R. 5 W, Sharp County, Arkansas. Paratypes are 145 additional specimens (KU 7482, 7483) collected with the holotype.

DIAGNOSIS. *E. s. fragi* differs from other subspecies of *E. spectabile* by possessing the following characters in a distinctive combination: gular region red in males, occasionally in females; blue on head restricted to sharply out-

lined suborbital bar; humeral spot distinct, iridescent blue-green; transverse bars on sides of body having little melanin, orange interspaces often continuous across belly in a chevron-shaped pattern; cheek well scaled, opercle and nape generally well scaled, breast usually lightly scaled, mean anterior scale index 2.5; breeding tubercles absent.

COLORATION. *Breeding males:* Dorsum olivaceous to reddish brown, saddles narrow, usually indistinct. Sides with 10-12 transverse blue bars of equal density, little intensified by melanin; bars faintly continuous across belly, strongly so across post-anal ventrum; bars less often continuous across dorsum. Interspaces reddish brown or reddish gray on upper sides, paling ventrally and becoming orange on belly and ventrum of caudal peduncle. Horizontal lines fine, discontinuous, often indistinct, and generally limited to upper sides and a few scale rows below lateral line. Breast white, gray, or gray-orange. Dorsum of head brown; cheeks, sides of snout, and lips gray-yellow or white; suborbital bar bright blue, margins sharp; opercle brown fading to yellow ventrally; gular region, interopercle, ventral margin of opercle, and anterior $\frac{2}{3}$ of branchiostegal membranes bright orange (posterior $\frac{1}{3}$ colorless). Humeral spot distinct, often iridescent blue-green. Spinous dorsal fin 4-banded, with submarginal orange and suprabasal blue bands larger than marginal and basal bands; submarginal orange band usually widest, giving fin slight predominance of orange. Soft dorsal fin 4-banded, suprabasal blue band often well developed. Caudal rudimentary rays blue, usually most intense ventrally; principal rays gray-yellow or gray-blue; base of fin with 2 orange spots in a vertical plane; spots occasionally surrounded by a faint yellow ring, hence conspicuous. Anal fin gray-blue, blue fading distally; occasionally with flecks of orange on membranes or base of fin. Pelvic fins blue-black, with whitish margins. Base of pectoral fin gray to pale orange or blue, fleshy axilla of fin red, membranes generally colorless.

Non-breeding males: Blues subdued or lacking. Orange faded, but pattern distinct. Vertical bars most evident above and below lateral line. Ventrums often having orange bars or "chevrons." Horizontal lines somewhat more distinct than in breeding males.

Females: Dorsum and upper sides brownish yellow, having faint, discontinuous horizontal lines; lower sides, lips, cheek, throat, breast, and belly usually colorless except for suborbital bar on cheek (blue-gray). Sides occasionally with 10-11 pale blue-green, transverse bars, not intensified by melanin. Orange, if present, limited to narrow submarginal and basal bands on spinous dorsal fin, and on gular region. Rudimentary rays of caudal fin occasionally pale green. Soft dorsal and caudal fin weakly barred with melanin.

ADDITIONAL CHARACTERS. The number following the character is the whole number nearest the mean. The range appears in parentheses. *Lateral*

line scales (Table 3) : 50 (43-55), highest mean number in the species. *Pored scales* (Table 6) : 35 (26-42), highest mean number in the species. *Diagonal scales*: 13 (12-15), modal number 13 throughout range. *Scales above lateral line*: 6 (5-6), modal number 6 throughout range. *Anterior squamation* (Table 9) : Cheek lightly to well scaled, usually well scaled, mean index 2.9. Opercle lightly to well scaled, usually well scaled, mean index. 2.9. Nape lightly to well scaled, usually well scaled, mean index 2.7. Breast naked to well scaled, usually lightly scaled, mean index 1.4. Mean anterior scale index 2.5, highest in the species. *Posterior infraorbital pores* (Table 13) : 3 (2-5), about 6 per cent having complete canals. *Supratemporal canal* (Table 13) : Usually complete, about 6 per cent with incomplete canals. *Gill membranes*: Slightly to moderately connected; mean index 2. *Lepidotrichs*: Spinous dorsal 10 (8-12); soft dorsal 12 (11-14); anal soft-rays 7 (6-8); pectoral 12 (11-12), about 40 per cent of specimens with 11 rays. *Breeding tubercles*: Not evident in males in breeding condition; only member of species in which tubercles were not found. *Genital papilla of males*: Deltoid, with an acute apex.

RANGE. Strawberry River and its upland tributaries in northeastern Arkansas.

INTERGRADES. Possibly with *E. s. uniporum* in streams that interdigitate with tributaries of Spring River; in these streams, *E. s. fragi* has the anterior region least well scaled (index 2.1). Also *E. s. fragi* may intergrade with populations of *E. s. spectabile* in some lower tributaries of White River. Seven immature specimens (UMMZ 123615, *Poecilichthys s. spectabilis*) from Millers Creek, a tributary of White River near Batesville, Independence County, Arkansas possess patterns of pigmentation and head squamation suggesting intergradation between *E. s. spectabile* and *E. s. fragi*.

DISCUSSION. *E. s. fragi* is distinctive in coloration, but resembles *uniporum* more closely than any other subspecies. In squamation and the lack of breeding tubercles on males, *fragi* resembles an oligocephalid relative of the Coastal Plain and Mississippi Embayment, *Etheostoma asprigene* (Forbes). The latter darter, however, has a complete infraorbital canal and a mean number of one more pectoral ray than *fragi*. To my knowledge, *asprigene* has not been collected on or above the Ozark Escarpment. In Arkansas it has been recorded from the St. Francis Basin in gravelly streams draining minor uplands such as Crowley's Ridge, from the Cache River Trough near its confluence with White River, and from tributaries of Red River below the Ouachita Escarpment. I have never collected *asprigene* while seining for *spectabile*.

E. s. fragi may have evolved from a population of White River *spectabile* isolated in Strawberry River throughout most of the Pleistocene; however, I think that *fragi* is too distinct to have developed in this manner. It is alternatively possible that hybridization could have occurred between popula-

tions of *E. spectabile* in the Strawberry River and populations of a lowland scaly-cheeked darter (*E. aspri gene*) before or shortly after the Mississippi River shifted eastward from the Ozark escarpment leaving an alluvial barrier to dispersal. The possibility exists also that *fragi* is really a neotenic *E. asprigene* that is undergoing reduction of the infraorbital canal. If so, I would expect a concomitant reduction of the supratemporal and lateral line canals, but this has not occurred.

Although *fragi* possesses characters common to several species, I judge that it is most closely related to *E. spectabile* populations (*uniporum*) of the lower Black River and that it has occupied the tributaries of the Strawberry River through much of the post-Kansan Pleistocene.

ETYMOLOGY. The name *fragi* has reference to the Strawberry River where this subspecies occurs. The noun *fra gum* (for Strawberry) is placed in the genitive singular modifying *Etheostoma*.

***Etheostoma spectabile pulchellum* (Girard)**

Plains Orangethroat

Figure 1B

Oligocephalus pulchellus Girard, 1859b, Proc. Acad. Nat. Sci. Phila., 11:102 (Gypsum Creek, a tributary of the Washita River, Indian Territory, now Custer Co., Okla.).

Etheostoma arcus-celestis Crevecoeur, 1903, Trans. Kansas Acad. Sci., 18:177 (Vermillion River near Onaga, Pottawatomie Co., Kan.).

TYPE. A single, juvenile specimen, 25.0 mm in standard length, on which Girard based his description of *Oligocephalus pulchellus*, is in collections of the Museum of Comparative Zoology, Harvard University (MCZ 32950). This specimen was examined by Carl Hubbs (Hubbs and Ortenburger, 1929) and by Leslie Knapp who kindly took counts and measurements for me in June, 1962. Both Hubbs and Knapp confirm its identity with the western, plains representative of *E. spectabile*, but Knapp informs me that the specimen is in poor condition (body distorted, bleached, and left pectoral fin missing).

Girard (18591) wrote that this specimen was captured in ". . . a tributary of Gypsum Creek, which empties itself into the Canadian River, by the party under Lieut. A. W. Whipple, while exploring the railroad along the 35th parallel." No tributary of the Canadian River, however, flows southward in the area concerned. Whipple (1856, pt. 2) in his log of the expedition writes, "Near Camp 30, we crossed Gypsum Creek, an affluent to the Washita, flowing south through bluff banks cut from an alluvial valley." Marcou (1856, pt. 4), geologist and mining engineer of the expedition, also places camps 30 and 31 in the Washita valley.

Grant Forman (1941), who edited and annotated Whipple's log of the survey, gives the Gypsum Creek locality (camp 30) as southeast of Arapaho, Custer County, Oklahoma. Streams draining this area are in the Washita

watershed; Beaver Creek, about 0.5 mile southeast of Arapaho, and Gyp Creek, about six miles southeast of Arapaho, are south-flowing tributaries of the Washita River that are now shallow. H. B. Möllhausen, topographer, artist, and naturalist of the expedition obscured the relationship of Gypsum Creek to the Washita River (established by Whipple and Marcou, and later confirmed by Forman) by stating in his diary of the journey (1858): "Scantily watered as the district was, we could manage every evening to reach a brook, which offered sufficient for our necessities, while our cattle found food on its banks. All these streams, including the most considerable of them, the Gypsum Creek, hastened in various windings to the Washita and Canadian. They were swarming with fish of many species, amongst which we particularly distinguished the *Chaetodon rostratus*, armed with its tremendous row of teeth: this creature appeared to share the dominion of the waters with the soft-shelled coriaceous turtle." In an account of *Moniana lutrensis*, Girard (1856) gave an accurate account of the locality ". . . Gypsum Creek, a tributary of the false Washita River . . ." (on maps available in 1856, the "false Washita" was the name used for the present Washita River in Oklahoma) but later (1859a, pt. 6) he reported an erroneous watershed-locality for *M. lutrensis* ("Tributary of Gypsum Creek, Canadian River") as he had for *O. pulchellus*.

On collecting trips in May, 1962, and May, 1964, to the headwaters of the Washita and southern tributaries of the Canadian along Whipple's route, I was unable to collect specimens of *E. s. pulchellum* in either drainage. The valley of Beaver Creek more closely resembles Whipple's description of the Gypsum Creek region than any tributary of the Canadian across the divide. The habitat in Beaver Creek seemed favorable for *E. s. pulchellum*. Because the Plains Orangethroat exists in similar habitat in tributaries of the lower Washita, it probably occupied Beaver Creek in times past. Prolonged drouths and recent excessive demands on groundwater have now reduced this and other tributaries of the Washita to streams of generally low flow or intermittency.

DIAGNOSIS. This subspecies can be distinguished from those of the eastern (*E. s. spectabile*) complex by its unique combination of the following characters: anterior region mostly naked, mean anterior index 0.6; scales small, mean number of lateral line scales usually more than 48, mean number of pored scales usually more than 30, diagonal scales usually 13, scales above lateral line usually 6, branchiostegal membranes moderately connected, index 2; in breeding males, 9 or more blue-green, transverse bars on sides of body from axil of pectoral fin to base of caudal fin, bars usually continuous across ventrum, especially posteriorly; horizontal lines poorly developed or absent; belly usually gray-blue or white, never with discrete red patches but sometimes with red pigment encroaching ventrally; spinous dorsal fin with 2 major longitudinal bands—a marginal, blue-black band

about 1/2 of fin-height and a broad basal brick-red band; soft dorsal fin predominantly orange; caudal fin rays never red, membranes pale yellow to transparent. Differs from *E. s. squamosum* by usually naked cheek, opercle, breast, and much of nape and in less conspicuous horizontal lines and more distinct vertical bars on upper sides.

COLORATION. *Breeding males*: Dorsum pale tan to brownish orange with 3-9 squarish dark saddles from occiput to base of caudal fin. Sides with 9 (6-11) vertical bars of melanin suffused with blue or blue-green, from axil of pectoral fin to base of caudal fin, most dark on lower and postanal sides; bars joining a single saddle dorsally or splitting to join two saddles dorsally, and ventrally either continuous or anastomosing with opposite bars. Interspaces on upper sides yellow, orange, or brownish orange; abdomen white, gray, or gray-blue (often orange or brick-red in Arkansas River drainage, from Poteau River eastward); interspaces of posterior lower sides mostly orange. Sides sometimes with poorly developed, broken, horizontal lines of melanin, best developed within vertical bars. Breast white, gray, or pale yellow. Genital papilla and peritroct grayish blue or green. Head brownish to dark olive dorsally. Snout, lips, and cheek anterior to suborbital bar pale yellow, orange or dark gray; suborbital bar short, rarely extending below preopercle, and often suffused with blue in Arkansas River drainage and southward; cheek posterior to suborbital bar colorless to yellow-gray. Operculum brownish orange. Branchiostegal membranes orange, paler than in eastern subspecies. Chin and gular region colorless to gray. Spinous dorsal fin with bluish or greenish black margin, about 1/2 of fin-height; lower $\frac{2}{3}$ of fin bright orange to brick-red, separated from marginal band by a narrow colorless to white line; occasionally a narrow, usually incomplete, basal or suprabaasal blue-green band best developed anteriorly; lower dark band seldom as dense as marginal band and seldom separated from orange by transparent or opaque areas. Soft dorsal fin mostly orange except for narrow, dusky-blue margin (best developed posteriorly) and a better developed, but often incomplete, basal or suprabaasal blue or blue-green band; marginal band separated from orange by fine transparent line; lower blue band usually separated from orange dorsally by transparent areas located on lower $\frac{1}{3}$ to $\frac{1}{2}$ of fin rays and a small portion of adjacent membranes. Rays of both dorsal fins often less saturated with orange than membranes, and these areas first to fade in post-breeding condition. Rudimentary rays of caudal fin blue or blue-green; principal rays dark gray, blue, blue-green, or pale yellow; base of fin with 2 orange spots in a vertical plane, membranes colorless to pale yellow. Anal fin blue or blue-green, anterior rays and membranes often gray to colorless distally; occasionally small, amorphic, orange blotches on anal fin; breeding tubercles and ridges on anal fin-rays opaque white. Pelvic fins black, suffused with blue or blue-green, margin of rays usually opaque white, margin of fin grayish. Pectoral fins colorless

to pale yellow. Chromatic colors, when present on pectoral, pelvic, anal and caudal fins, usually best developed on base of fin and fading distally.

Non-breeding males: Orange subdued, blues much subdued or lacking. Vertical bars variably contracted or diffuse but never lacking. Anterior region pale except for dark cranial portion. Branchiostegal membranes pale orange. Dorsum light olive or tan with subdued darker saddles. Anal and pelvic fins transparent. Faint melanin on caudal and soft dorsal rays sometimes producing a weak barred effect.

Females: Orange usually limited to basal band on spinous dorsal fin but occasionally appearing faintly on soft dorsal fin. Branchiostegal membranes sometimes orange, usually colorless. Blue-green limited to lower sides of caudal peduncle, in association with vertical bars. Barred effect on caudal and soft dorsal fin more distinct than in males. Non-gravid females lack all chromatic colors.

ADDITIONAL CHARACTERS. The number following the character is the whole number nearest the mean. The range appears in parentheses. *Lateral line scales* (Table 4): 50 (41-61), a slight increase in mean number from north to south for each major river system except Red River; no consistent east-west gradient, although individual streams in major river systems may exhibit variation from headwaters to mouth. *Pored lateral line scales* (Table 7): 31 (21-42), mean number highest in Republican River (33); increase in mean number (31-32) from east to west in Arkansas River. *Diagonal scales*: 13 (11-16), modal number 13 throughout range, although 14 not uncommon. *Scales above lateral line*: 6 (5-7), little variation in mean number. *Anterior squamation* (Table 10): Cheek naked to lightly scaled, mean index 0.7; lowest mean (0.2) in upper Kansas River, highest (1.0) in Brazos and Colorado rivers; slight increase in mean from upper to lower Kansas River (0.2-0.8). Opercle naked to lightly scaled, usually naked, some specimens in lower Kansas and lower Red rivers moderately to well scaled (see DISCUSSION), mean index 0.3; lowest mean (0.0) in Brazos, Colorado, and Guadalupe rivers, highest (1.5) in lower Kansas River. Nape naked to well scaled, usually lightly scaled, mean index 1.3; lowest mean (0.9) in Brazos and upper Arkansas rivers, highest (2.0) in lower Kansas River. Breast naked (occasional specimens in lower Kansas River having one to several scales), mean index 0.0. Mean anterior index 0.6; little difference in mean between major river systems; within river systems lowest mean (0.4) in upper Kansas and upper Arkansas rivers, highest (1.1) in lower Kansas River. *Posterior infraorbital pores* (Table 14) : 3 (1-4) modal number 2 in eastern Arkansas River. *Supratemporal canal* (Table 14) : Usually complete, but increase in per cent incomplete from south to north throughout range, and from east to west in Arkansas River. *Gill membranes*: Moderately connected, index 2, except in eastern Kansas River where index is 1. *Lepidotrichs*: Spinous dorsal 10 (8-12) except in Republican River (9) : soft

dorsal 13 (11-15); anal soft rays 7 (5-8) except in eastern Arkansas River (6); pectoral rays 12 (11-13). *Breeding tubercles*: Anal and pelvic lepidotrichs having ridges or tubercles (in specimens examined from Texas, not at peak of breeding condition, only anal rays tuberculate); tubercles on lower rays of pectoral fin and on ventral scales of specimens from eastern Kansas River and upper Mulberry River (eastern Arkansas River drainage). *Genital papilla of males*: Finely punctulated with melanin and suffused with blue or blue-green; usually deltoid in shape; apex obtuse, truncate, rounded, or acuminate.

RANGE. North Platte River of western Nebraska; Republican River of Colorado, Nebraska, and Kansas; Arkansas River from about Garden City, Kansas, to Ozark escarpment west of Little Rock, Arkansas, except in streams draining Springfield Plateau, where replaced by *E. s. squamosum*; Red River (mostly its northern tributaries) from Wichita Mountains eastward to Little River (southeast Oklahoma); Brazos, Colorado, Guadalupe-Medina rivers of Texas on Comanche and Edwards plateaus and southeastward to Balcones Escarpment.

INTERGRADES. With *E. s. spectabile* in southern tributaries of Kansas River eastward to confluence of Missouri and Osage rivers; with *E. s. squamosum* in lower tributaries of Neosho and Spring rivers in southeastern Kansas, in Illinois and Grand (Neosho) rivers near their confluence with Arkansas River, and in Sallisaw Creek (Arkansas tributary east of Illinois River confluence) in northeastern Oklahoma.

DISCUSSION. The Plains Orangethroat shows comparatively little phenotypic variation throughout its range, with the exception of populations in the eastern Kansas, eastern Arkansas, and eastern Red rivers.

Most specimens in tributaries of the eastern Kansas River resemble those to the west and south but possess some characteristics of the eastern subspecies, *E. s. spectabile* (more squamous anterior region). The westernmost evidence of intergradation in color pattern is in semi-isolated tributaries of the Wakarusa River (Lone Star Lake), Douglas County, Kansas. Here coloration strongly resembles that of *E. s. spectabile* and squamation that of *pulchellum*; or, in other specimens, both characteristics are intermediate between the subspecies. Less than ten per cent of specimens collected just below Lone Star Lake have anterior scale characters of *E. s. spectabile*; usually all possess the coloration of *pulchellum*. The color pattern of *pulchellum* generally is dominant eastward to the Lamine River of Missouri where the color pattern is again intermediate and squamation approaches that of the nominate subspecies. In the Petite Saline River, Missouri (next drainage east of Lamine River), the color pattern of *E. s. spectabile* is more evident, although the dense melanin of the western subspecies remains; most males have pink belly patches and horizontal lining is moderate to strong; vertical bars are less dense and often are interrupted ventrally;

squamation of the body commonly is like that of the eastern subspecies anteriorly and like that of the western subspecies posteriorly. In the Moniteau and Moreau drainages, Missouri, coloration usually is that of the eastern subspecies, but vertical bars and horizontal lines are about equal in density. Posterior squamation (scales above lateral line; diagonal scales) in the Moniteau usually is that of *pulchellum* and in the Moreau usually is that of *E. s. spectabile*.

In northern tributaries of the Missouri River, I found no orangethroats farther west than Ray and Caldwell counties, Missouri; these are intergrades resembling mostly *pulchellum* in coloration, but intermediate in squamation between *E. s. spectabile* and *pulchellum*. In Howard County and eastward, orangethroats resemble representatives from Lamine River more closely than specimens from streams more nearly opposite them to the south, especially with regard to color pattern; the spinous dorsal fin may be like that of either subspecies or intermediate, the soft dorsal fin generally is pigmented like that of *pulchellum*. Horizontal lining is diffuse or absent in 70 per cent, faint in 20 per cent, and intense in 10 per cent of the 54 specimens examined. Most males have tuberculate anal and pelvic fins. Vertical bars are strongly developed. Squamation is intermediate but nearer that of the nominate subspecies.

In a cursory examination of specimens from the zone of intergradation, I could assign less than 10 per cent to one subspecies or the other. A more thorough investigation revealed evidence of intergradation in these few individuals.

Slight influence of the eastern subspecies can be seen westward in the Blue, Republican, and Platte rivers; anterior scale indices are higher than elsewhere in the range of *E. s. pulchellum*, the highest values being in the eastern Kansas River. Specimens from the southwestern Kansas River drainage (Smoky Hill River) exhibit the low scale indices typical of representatives throughout the remainder of the range.

Whether genetic traits of *E. s. pulchellum* have entered populations east of the Osage-Missouri confluence is uncertain. I think that some of the color-pattern of the western subspecies (dark vertical bars that meet ventrally in breeding males, weakly developed horizontal lines, and predominantly red spinous dorsal fin) has been incorporated in populations of *E. s. spectabile* in tributaries of the Mississippi River in Missouri and Illinois and to a lesser degree in tributaries of the Ohio River in Illinois, Indiana, Ohio, and Kentucky exclusive of Cumberland, Green, and Tennessee rivers.

With the exception of Kansas River, where intergrades are responsible for most heterogeneity, the Arkansas River System has the most variation in populations of orangethroats of any river of the plains. *E. s. pulchellum* can be separated into three populations in the Arkansas Basin: (1) Populations west of the Neosho-Verdigris rivers are typical of the plains subspecies from

Nebraska to Texas; males have 10 or fewer vertical bars, are predominantly blue, have transparent, rarely pale yellow, caudal and pectoral fin-membranes, and have no red in the anal fin; (2) Those from the Neosho-Verdigris exclusive of tributaries draining the Springfield Plateau (range of *E. s. squamosum*) have 10 or more vertical bars, also are predominantly blue, but have pale yellow membranes in caudal and pectoral fins, and occasionally have red in the anal fin; (3) Those of the eastern Arkansas River from about Fort Smith to Little Rock, Arkansas, have fewer than 10 vertical bars, are predominantly reddish orange, have transparent, rarely pale yellow, membranes in caudal and pectoral fins, and rarely possess red in the anal fin. In the third region, breeding males are as deeply barred with blue or blue-green as in *pulchellum* elsewhere, but reddish orange pigment is more extensive on interspaces, anterior sides, and belly; the belly, rather than having one or two isolated, oblong, red blotches, as in *E. s. spectabile*, is colored by extension of reddish orange from sides of the body. The general post-breeding color is orange; blues fade and leave only underlying melanin. Meristically there is a small increase in the cheek- and nape-scale index, and a one-scale decrease in mean number of pored scales. Orangethroats in some southern tributaries (Poteau, Fourche La Pave, and Petit Jean rivers) are smaller than specimens from other parts of the range of *pulchellum*. Breeding males average 30 mm in standard length against an average of about 40 mm elsewhere. In other features, they differ little from populations in the remainder of the drainage. Tributaries in which the small orangethroats were collected drain the north slope of the Ouachita Mountains and seemed (at the time of collecting) to be intermittent in flow. The small size of specimens may be due to low productivity of the region (lack of limestones) and/or high mortality-rates in older age-classes when tributaries are dry.

Throughout the Arkansas Basin the anal and pelvic fins of breeding males are strongly tuberculate and many males have tuberculate ventral scales. A narrow, green or blue-green suprabasal band usually is present in the spinous dorsal fin from this drainage southward into Texas. Anal fin-rays average 6.6 west of the Poteau River and 6.3 east.

Occurrences of the orangethroat in the Red River are limited generally to its northern tributaries, from the Wichita and Arbuckle mountains eastward to Little River Drainage of southeastern Oklahoma. The only locality record for a southern tributary of Red River seems to be Rock Creek, Cook County, Texas (Riggs and Bonn, 1959). The greatest amount of variation in this drainage occurs in Blue River, where specimens are snub-nosed, deep-bodied, and have extensive red in the anal fin. The Blue River population represents a hybrid swarm between *E. radiosum cyanorum* Moore and Rigney and *E. s. pulchellum* (see Natural Hybridization). The easternmost collection from the Red River Basin I examined was taken from Mountain Fork River, a tributary of Little River, McCurtain County, Oklahoma.

Seven of nine specimens have one to several scales on the opercle (mean anterior index 0.7), all have a complete supratemporal canal, and the number of posterior infraorbital pores varies from one to four. Unlike the Blue River hybrids, the general body shape is that of *pulchellum*. The above characters may suggest introgression with a related darter (*E. aspri* gene or *E. radiosum*), but a more thorough study of this region is necessary before the variation found here is explicable.

Though variation of scale size and minor variation in color exists among populations in the Brazos, Colorado, and Guadalupe river systems in Texas, all orangethroats there are representatives of the plains subspecies.

PRIMARY LITERATURE RECORDS AND MISIDENTIFICATIONS. This subspecies has been reported under the following names:

Oligocephalus pulchellus Girard (1859b) original description—Collette and Knapp (1967) catalog of type specimens. *Astaitichthys pulchellus*—Vaillant (1873) in part, description, figure, incorrect type locality "Indiana River." *Poecilichthys lepidus*—Jordan and Gilbert (1882) in part, synonymy by implication in footnote; Ortenburger and Hubbs (1927) Oklahoma. *Poecilichthys coeruleus* (Storer)—Gilbert (1884) Ellis Co., Kansas. *Etheostoma varietum* Kirtland—Gilbert (1885b) Ellis Co., Kansas; Cragin (1885) Ellis Co., Kansas. *Etheostoma varietum spectabile*—Graham (1885) Kansas River. *Etheostoma coeruleum*—Evermann and Fordice (1886) Timber Creek, Winfield, Kansas. *Etheostoma lepidum*—Jordan and Gilbert (1886) characters, Brazos River, Texas; Hay (1887) northwestern Kansas; Jordan (1891) Wichita, Kansas; Meek (1895) Arkansas River, Arkansas; Evermann and Cox (1896) Kansas River; Meek (1896) in part, Arkansas, Oklahoma, and Texas; Jordan and Evermann (1896) in part, synonymy, characters, distribution. *Etheostoma caeruleum lepidum*—Gilbert (1886) characters, Kansas; Gilbert (1889b) Poteau River, Arkansas; Meek (1894) Waldron, Arkansas. *Etheostoma coeruleum spectabile*—Evermann and Cox (1896) Kansas River basin. *Etheostoma arcus-celestis*—Crevecoeur (1903) original description. *Etheostoma arcus-celestis*—Crevecoeur (1908) Mound Creek a tributary of Vermillion River, Onaga, Kansas. *Oligocephalus coeruleus lepidus*—Jordan (1929) in part, characters, distribution. *Poecilichthys coeruleus pulchellus*—Hubbs and Ortenburger (1929) characters, distribution, systematics. *Oligocephalus lepidus*—Jordan, Evermann, and Clark (1930) in part, check list. *Poecilichthys spectabilis pulchellus*—Breukelman (1940) distribution, northwestern Kansas; Jennings (1942) Blue River, Kansas; Cross and Moore (1942) Poteau River of Arkansas and Oklahoma; Simon (1946) provisionally included in Wyoming; Baughman (1950) Texas; Bailey (1948) characters. *Boleichthys fusiformes* (Girard)—Breukelman (1940) inferred reference to *pulchellum*, Logan and Scott Cos., Kansas. *Poecilichthys spectabilis*—Moore and Cross (1950) comparison to *P. jessiae*; Moore and Rigney (1952) southeastern Oklahoma. *Etheostoma spectabile pulchellum*—Bailey (1951) possible occurrence in Iowa; Beckman (1952) characters, Colorado; Knapp (1953) Texas; Cross (1954) Cottonwood River, Kansas; Bailey and Gosline (1955) vertebral counts; Bailey (1956) possible occurrence in Iowa; Schelske (1957) Fall and Verdigris rivers, Kansas; Metcalf (1959) Caney, Walnut, and Elk rivers, Kansas; Minckley (1959) Blue River, Kansas; Deacon and Metcalf (1961) Wakarusa River, Kansas; Collette (1965) breeding tubercles; Metcalf (1966) Kansas River System; Collette and Knapp (1967) catalog. *Etheostoma spectabile*—Moore (1952) Oklahoma; Jurgens and Hubbs (1953) Texas; Hubbs, Kuehne, and Ball (1953) Guadalupe River, Texas; Hubbs (1954) distribution, Texas; Linder (1955a) Verdigris River, Oklahoma; Linder (1955b) Blue River, Oklahoma; Kuehne (1955) Guadalupe and San Antonio rivers, Texas; Moore and Buck (1955) Chikaskia River, Kansas; Strawn (1955) Colorado and Guadalupe rivers, Texas, behavior; Minckley (1956) Deep Creek, Riley Co., Kansas; Strawn and Hubbs (1956) stripping; Hubbs (1957a) check list, Texas; Hubbs (1957b) distribution patterns, Texas; Hubbs (1957c) sperm viability; Hubbs and Strawn (1957a) hybrid survival; Hubbs and Strawn (1957b) hybrid variability; Clark, Breukelman, and Andrews (1958) Lyon Co., Kansas; Hubbs (1958a) hybrid fertility; Linder (1958) behavior, hybrids; Hubbs (1958b) variation in egg complement; Minckley and Cross (1959) Kansas River Basin; Hubbs (1959) hybrid combinations; Riggs and Bonn (1959) Red River, Oklahoma and Texas; Hubbs and Hettler (1959) Colorado River, Texas, ecology; Blair (1959) northeastern Oklahoma; Hubbs, Littlejohn, and Littlejohn (1960) survival of young; Hubbs and Delco (1960) egg size; Hubbs (1960) functional duration of sperm; Hubbs (1961a) temperature tolerance; Hubbs (1961b) gamete compatibility; Hubbs and Laritz (1961) natural intergeneric hybrid;

Deacon (1961) Neosho River, Kansas; Strawn (1961) meristic variation; Hubbs and Armstrong (1962) temperature tolerance; Jones, Hettler, and Hubbs (1962) egg survival; Hubbs and Strawn (1963) temperature tolerance; Metcalf (1966) Kansas River System. Cross (1967) characters, habits, distribution in Kansas; Summerfelt (1967) Smoky Hill River, Kansas.

***Etheostoma spectabile squamosum* subsp. nov.**

Arkansas River Scaly Orangethroat

Figure 1A

TYPE. Holotype (KU 7476) an adult male 45.4 mm in standard length, collected by D. A. Distler and B. A. Simco, April 23, 1961, in Indian Creek, a tributary of Elk River, 2.5 miles southwest of Sweetwater, Newton Co., Missouri, on State Road D. Paratypes are 33 additional specimens (KU 7477) collected with the holotype.

DIAGNOSIS. *E. s. squamosum* differs from other subspecies of *E. spectabile* by having the anterior region moderately scaled (anterior index 2) and coloration resembling that of *E. s. pulchellum* except that horizontal lines are more conspicuous and vertical bars less distinct on upper sides.

COLORATION. *Breeding males:* Generally like that of *E. s. pulchellum* but vertical bars most dense on lower sides and across ventrum, especially on caudal peduncle; bars rarely confluent with dorsal saddles. Spinous and soft dorsal fins predominantly orange but with a narrow suprabaasal, green band. Often, amorphic blotches of orange on membranes of anal fin, principal rays of caudal fin, and distal margin of pectoral and pelvic fins. Dorsal saddles most prominent at origin of spinous dorsal fin, between spinous and soft dorsal fins, and at posterior end of soft dorsal fin.

Non-breeding males: Chromatic colors subdued or wanting. Faint orange on posterior sides, dorsal fins, and branchiostegal membranes. Faint blue-green on banded area of caudal peduncle.

Females: Often devoid of chromatic colors even at peak of breeding season; occasionally having a pale submarginal band of orange on dorsal fins. Broken horizontal lines more conspicuous than in males.

ADDITIONAL CHARACTERS. Within the range of the subspecies are two major river systems draining the western Ozarks: the lower Grand (Neosho) River (eastern tributaries) and the Illinois River system. Color patterns seem not to differ greatly between the two drainages, but some meristic characters vary both between and within the two systems. The number following the character is the whole number nearest the mean. The range appears in parentheses. *Lateral line scales* (Table 4) : 48 (40-56), no significant variation of mean number from headwaters to mouth in either river system but an increase of 1 in mean number from Grand to Illinois river. *Pored lateral line scales* (Table 7) : 30 (20-41), variation as above but with an increase of about 2 (29.0-30.8) in mean number from Grand River to Illinois River. *Diagonal scales:* 13 (11-16), modal number 13 throughout range but a small

increase in mean number (13-13.5) from Grand River to Illinois River. *Scales above lateral line*: 6 (5-7), modal number 6 throughout range but increase in mean number (0.3) from Grand River to Illinois River. Anterior squamation (Table 11) : Cheek naked to well scaled, usually moderately scaled, mean index 2.2 in Grand River, 1.9 in Illinois River. *Opercle* naked to well scaled, usually moderately scaled, mean index 2.0 in Grand River, 1.9 in Illinois River. Nape naked to well scaled, usually well scaled, mean index 2.8 in Grand River, 2.8 in Illinois River. Breast naked to well scaled, usually lightly scaled, mean index 1.4 in Grand River, 0.7 in Illinois River. Mean anterior index 2.1 in Grand River, 1.8 in Illinois River. *Posterior infraorbital pores* (Table 15) : 3 (2-5), infraorbital canal complete in 2 per cent of individuals from Grand River, 3 per cent from Illinois River. *Supratemporal canal* (Table 15) : Usually complete, 11 per cent from Illinois River and 23 per cent from Grand River having incomplete canals. *Gill membranes*: Moderately connected, mean index 2 throughout range. *Lepidotrichs*: Spinous dorsal 10 (8-11) ; soft dorsal 13 (11-15); anal soft rays 7 (6-8) ; pectoral 12 (11-13). *Breeding tubercles*: Anal and pelvic lepidotrichs tuberculate; lower pectoral rays sometimes ridged in Elk River (Grand River drainage); pectoral rays and ventral scales tuberculate in headwaters of Illinois River. *Genital papilla of males*: Generally ovate in shape; apex acuminate, obtuse, truncate, or rounded.

RANGE. Southeastern Kansas, southwestern Missouri, northwestern Arkansas, and northeastern Oklahoma in streams draining the Springfield Plateau west and southwest into the Arkansas River.

INTERGRADES. With *E. s. pulchellum* in lower tributaries of Neosho River in southeastern Kansas, in lower tributaries of Spring River near confluence with Neosho (Grand) River, in Illinois River of Oklahoma near confluence with Arkansas River, and in Sallisaw Creek; intergradation may occur with *E. s. spectabile* in headwaters of Illinois River.

DISCUSSION. The range of *E. spectabile squamosum* lies mainly within the Ozark biotic district of Blair and Hubbell (Blair, 1959). Intergrades with *E. s. pulchellum* are found in the northern part of the range near the junction of the Ozark and Cherokee Prairie biotic districts, and in the southern part of their range near the junction of the Ozark and Osage Savanna biotic districts, but mostly within the latter.

Its restriction to a single biotic zone suggests that *squamosum* may be an ecophenotype. However, the characters that distinguish it from the other subspecies are stable in specimens hatched and reared in the laboratory; there is no loss of anterior squamation or changes in the pattern of pigmentation.

Past isolation of populations of *pukhellum*, perhaps as we know it today, in streams draining the Springfield Plateau probably occurred during the extensive pluvial periods of the Pleistocene when the silt- and sand-loaded

Arkansas River was even more a barrier to dispersal than at present. Such populations could have evolved into *squamosum*.

Alternative means of origin of this subspecies exist. *E. spectabile squamosum* may have evolved through introgression with one or more related species. The density of anterior squamation, presence of three well developed dorsal saddles, and high percentage of complete infraorbital canals (when compared with the plains subspecies) suggest introgression with a darter or darters having those characters. *Etheostoma whipplei* (Girard), a related darter, is partly sympatric with *squamosum* and throughout most of its range is sympatric with *E. s. pulchellum*. In the area of sympatry, *E. s. pulchellum* and *E. whipplei* occasionally hybridize when both are compelled to spawn in the same area because of drouth or other adverse conditions. If such hybrids are fertile, however, their progeny usually do not survive in competition with normal offspring, or are swamped by backcrossing with the parental species. Hubbs (1955), in a discussion of hybridization among fishes, suggests that when two related species are sympatric, and one is much more abundant than the other, hybridization is likely. *E. whipplei* is found only rarely in the Ozark biotic districts but is abundant in the Osage Savanna and Cherokee Prairie biotic districts (Blair, 1959, Fig. 4). If hybridization between *E. whipplei* and *squamosum* has occurred, it is reasonable to assume that some of the genome of the less abundant species (*E. whipplei*) has been incorporated into that of the more abundant species because backcrossing would tend to be unidirectional. *E. whipplei*, although possessing some of the characters that distinguish *squamosum* from other subspecies of orangethroats (moderately scaled anterior region, complete infraorbital and supratemporal canals, extensive red in the fins) does not possess the **tri-saddle** pattern characteristic of *squamosum*.

Another related species is *Etheostoma caeruleum* Storer, the rainbow darter, in which the **tri-saddle** dorsal pattern does occur. Among the subspecies of *Etheostoma spectabile*, *squamosum* is unique (except for populations of *E. s. pulchellum*, in the Neosho River) in sharing the **tri-saddle** pattern with *E. caeruleum*. *E. s. squamosum* also resembles *E. caeruleum* in being moderately scaled anteriorly (but unlike *caeruleum*, *squamosum* has a moderately to well scaled cheek). Also, *squamosum* resembles *E. caeruleum* in having less red in the fins than does *E. whipplei*.

E. caeruleum, while it is sympatric with most subspecies of *E. spectabile*, it is not so with *squamosum* (and *E. s. pulchellum*) because *E. caeruleum* is not indigenous west of the Ozark Plateaus in tributaries of the Arkansas River. However, *E. caeruleum* is abundant in tributaries of White River immediately adjacent to the area drained by the Illinois and Grand rivers of southwestern Missouri and northwestern Arkansas, where *squamosum* occurs.

The divides between the Arkansas and White river drainages are narrow

and there is evidence that these have been crossed by various aquatic organisms during the Pleistocene (Williams, 1954; Branson, 1963). Moreover, Branson (1963) states that "... it would appear that the Neosho has captured the Spring River-Shoal Creek System, and possibly the Elk River as well, from the White River Drainage." Bretz (1965), however, in a study of the geomorphic history of the Missouri Ozarks, indicates that there is a lack of geologic evidence for stream piracy across the Springfield Plateau and that "... the more favored streams of the steeper eastern slope have captured nothing more from the western slope than additional runoff areas."

Also in northwestern Arkansas, the surfaces of the divides, which are narrow between the Illinois and White rivers (Quinn, 1958), may not be a barrier to small aquatic organisms. Both of these streams drain the Springfield Plateau. Western drainage is effected by tributaries of the Illinois River and eastern drainage by tributaries of White River. The Springfield Plateau is underlain by cherty limestone of Mississippian age; however, much of the limestone has weathered away, leaving a porous mantle of resistant chert up to 150 feet in thickness in the uplands (Thornbury, 1965). This porous mantle accounts for reduced surface runoff of the region and rapid diversion of surface water to the subsurface where it then emerges as springs or seeps usually at the level of the water table. A combination of narrow divides and extremely porous substrate suggests to me that the barriers for small aquatic organisms are lower in elevation than the surface of the divides of the dissected plateau. The bedrock underlying the chert perhaps serves as an effective divide during all but pluvial periods when these subsurface divides are breached by water both above (vadose) and at level of the water table (phreatic). Indirect evidence of such phenomena was brought to my attention while I was collecting fish in northwestern Arkansas (western drainage of the Springfield Plateau). A resident informed me that a large spring on his property became muddy periodically after heavy rains in the White River watershed just across the divide. Emphasis was made that no rain had fallen on his (Illinois River) side of the divide. This suggests to me that not only was his spring sustained by ground water from the Illinois River watershed, but that the spring was also connected, if only periodically, to surface drainage and vadose water across the divide (White River watershed).

An adult male rainbow darter (*E. caeruleum*) was collected from the headwaters of the Illinois River near Savoy, Washington County, Arkansas, by members of an ichthyology class at the University of Arkansas. To my knowledge, this is the first record of the rainbow darter from Arkansas River drainage, although it is abundant in tributaries of White River. The specimen collected from the Illinois River was in peak breeding condition and if it spawned, it probably did so with females of *E. spectabile squamosum*. Several hundred specimens of *squamosum* were collected with the single

specimen of the rainbow darter. The latter, of course, could have arrived in a bait bucket. Introduction, by this or by natural means, of an occasional specimen or small numbers of *E. caeruleum* into the range of *squamosum* would enhance the chance of unidirectional hybridization. Although back crossing (again unidirectional) would tend to swamp most characters of the least abundant species, some characters might in time become incorporated into the population. The characters which *squamosum* shares with *E. caeruleum* seem to me to be sufficiently constant so that their acquisition is unlikely to date from a time after the arrival of Caucasian man.

In general the orangethroat is less streamlined in shape than either *E. caeruleum* or *E. whipplei* and seems to prefer less swift currents than the latter two species. *E. spectabile squamosum*, on the contrary, is found in currents as strong as those preferred by *E. caeruleum*, particularly in the Elk and Illinois rivers. In these drainages, *squamosum* occupies habitats equivalent to those of *E. caeruleum* and possibly also *E. whipplei*.

Natural selection alone or natural selection and introgression of the genome of *E. whipplei* and/or *E. caeruleum* with the plains orangethroat may be responsible for the evolution of *squamosum* in western drainages of the Springfield Plateau. Continuous unidirectional hybridization is possible considering the distribution of these darters.

PRIMARY LITERATURE RECORDS AND MISIDENTIFICATIONS. This subspecies has been reported under the following names:

Etheostoma caeruleum Storer—Gilbert (1889a) characters, northeastern Oklahoma. *Etheostoma caeruleum spectabile* (Agassiz)—Meek (1891) Shoal Creek, southwestern Missouri; Meek (1894) Illinois River at Prairie Grove, Arkansas; Meek (1895) tributaries of Arkansas River in northwestern Arkansas. *Poecilichthys coeruleus pulchellus x spectabilis*—Hubbs and Ortenburger (1929) characters, distribution in northeastern Oklahoma. *Poecilichthys spectabilis*—Moore and Paden (1950) Illinois River in Oklahoma. *Etheostoma spectabile*—Hall (1952) northeastern Oklahoma; Moore (1952) Oklahoma; Blair (1959) distribution in northeastern Oklahoma; Cross (1967) scale characters, Spring River, Kansas.

KEY TO THE SUBSPECIES OF *ETHEOSTOMA SPECTABILE*

This key is based on the coloration and anterior squamation of breeding males. For a comparison of subspecies based on characters other than coloration, see Table 1.

- A. Orange prevalent color of dorsal fins, suprabasal blue band of spinous dorsal thin and incomplete or absent. Blue usually absent from sides of head **B.**
- B. Transverse bars of melanin usually of equal density on upper and lower sides; horizontal lines discontinuous and indistinct, mostly evident near lateral line and several scale rows below; dorsal saddles usually of equal density; suprabasal band of spinous dorsal fin usually absent; head usually naked. *E. s. pulchellum*
- BB. Transverse bars of melanin of unequal density on upper and lower sides, less dense or lacking on upper sides; horizontal lines more continuous and distinct than above, developed on upper and lower

- sides; dorsal saddles of unequal density (cranial, midpterygial, and caudal saddles most dense); suprabasal blue band of spinous dorsal fin usually lightly developed; head scaly. *E. s. squamosum*
- AA. Blue prevalent color of dorsal fins or blue and orange equal in area of development. Blue variably present on sides of head (often absent east of Mississippi River) C.
- C. Transverse bars of equal density from axilla to caudal base; humeral spot small but distinct; belly white, blue-gray, or rusty, usually barred by extension of melanin from sides; genital papilla without chromatic colors, immaculate or lightly stippled with fine melanophores. D.
- D. Transverse bars dense, often forward-slanting; suprabasal blue band of spinous dorsal fin wider than submarginal orange band; cheek blue, rarely well scaled; genital papilla immaculate, occasionally having a single submarginal row of fine melanophores. *E. s. uniporum*
- DD. Transverse bars of melanin faint, usually subvertical; submarginal orange band of spinous dorsal fin wider than suprabasal blue band; cheek cream-colored, usually well scaled. *E. s. fragi*
- CC. Transverse bars most dense on posterior sides, often subtriangular on caudal peduncle; humeral spot indistinct or wanting; belly with two oblong, orange patches on each side of midline or with patches confluent, uninterrupted by crossbars; genital papilla often blue-gray, saturated with fine melanophores. *E. s. spectabile*

ZOOGEOGRAPHY

No fossil remains of *E. spectabile* are known. The evolutionary history of the species can be surmised only from its present distribution, what is known of the history of changes in drainage throughout the range, and the present location and characteristics of geographic variants.

Preglacial and Glacial Drainage

The history of drainage as presented herein rests variously upon the evidence and arguments presented by: Bayne and Fent, 1963; Bretz, 1965; Fenneman, 1938; Flint, 1961; Frye and Leonard, 1952, 1963; Heim and Howe, 1963; Lueninghoener, 1947; Lugn, 1935; Quinn, 1957, 1958; SeEVERS and Jungmann, 1963; Stricklin, 1961; Thornbury, 1965; Ver Stegg, 1946; and Wayne, 1952.

Knowledge of late Tertiary drainage is incomplete, especially in the western part of the present range of the species, but there seems to be sufficient geologic evidence to make reasonably clear the major history of drainage.

In the late Pliocene, at least two south-flowing drainages existed between the Rocky Mountain System and Appalachian Highlands. A minor western river system (Ancestral Plains Stream System of Metcalf, 1966) drained

much of the southern one-half of the Great Plains Province, and a major eastern river system (Teays-Mississippi) drained the lower one-half of the northern Great Plains, the southern Central Lowlands, the Interior Low Plateaus, the southwestern Appalachian Plateaus, and the Ozark Plateaus. At present there is insufficient geologic evidence to ascertain whether the Ancestral Plains System flowed directly into the Gulf of Mexico or joined the Teays-Mississippi via the preglacial Arkansas River or Red River.

During the Pleistocene, multiple glaciation, changes in stream regimen, and regional tilting altered Tertiary drainage considerably to form the present Mississippi River System.

WESTERN REGION. Nebraskan ice had little effect on the Ancestral Plains System. Valleys were deepened, but drainage was still southward.

Kansan ice initiated changes in drainage that continued throughout the epoch. According to Frye and Leonard (1952), the southwestern lobe of this glacier overrode the Flint Hills upland in what is now northeastern Kansas. This upland formed a divide between the Ancestral Plains and the Teays-Mississippi river systems. Meltwaters from south of the lobe and east of the divide flowed eastward along the Wakarusa Valley into the Teays-Mississippi system. Meltwaters from the western edge of the glacier and west of the divide flowed southwestward into the Ancestral Plains system, greatly increasing its watershed (Frye and Leonard, 1952, Fig. 13). In early Yarmouth time the enlarged Plains drainage was partially beheaded by tributaries of the developing Mississippi River; plains drainage from the Saline River of Kansas northward flowed east via the Missouri River Valley.

By (or during) Illinoian time the Ancestral Plains System seems to have been altered further. According to Quinn (1958) the ancestral lower Arkansas River breached the divide near Magazine Mountain in Arkansas and captured a large part of the Ancestral Plains System to form the present Arkansas River Basin. To the south, a tributary of the Brazos shifted its course westward and was captured by the Red River (Stricklin, 1961). To the north, the Smoky Hill River was captured by a tributary of the Kansas River by late Illinoian or early Wisconsin time.

Little information is available concerning Pleistocene drainage between the present Red and Arkansas rivers and in the region south of the Brazos. Frye and Leonard (1952) describe a minor southward flowing drainage in southwestern Kansas that was present in late Nebraskan time; much of this drainage was aggraded during Kansan time and the remainder was integrated into the Arkansas River. Whether this drainage originally flowed into the Red River is unknown, but I judge that this or some other southern tributary of the present Arkansas River flowed south into the valley of Red River prior to its capture by the Arkansas River. Quinn (1957) describes the region of central Texas in Nebraskan time as a surface of little relief and considerable elevation. During the following glacial periods this area

was alternately degraded and aggraded by the action of streams. During Sangamon time, valleys below the Balcones Escarpment were filled completely with gravel. This fact suggests to me that divides between these valleys were breached by the waters that carried this gravel; hence, faunal interchange may have occurred between such rivers as the Brazos and Colorado and between the Colorado and Guadalupe below the Balcones Escarpment.

EASTERN REGION. Thornbury (1965) illustrates and discusses various interpretations of the Teays-Mississippi preglacial and glacial drainage. The major features that could have influenced dispersal of the orangethroat are as follows. The preglacial Mississippi River was joined by the Teays River in what is now central Illinois, and flowed southward along the present Illinois River Valley. Instead of meeting the Ohio River at the present confluence (Cairo, Illinois), the Mississippi River turned southwestward and flowed along the edge of the Salem Plateau in a valley near that now occupied by Black River and lower White River. The preglacial Ohio River probably originated near the present site of Madison, Indiana, and flowed southwestward along much of its present course; but, south of Golconda, Illinois, the river flowed westward through the Cache Lowland to Cape Girardeau, Missouri, then southwestward along the eastern edge of Crowley's Ridge (present St. Francis Basin), and united with the Mississippi River either below present Helena, Arkansas, or farther south near Simmesport, Louisiana. An alternate interpretation is that the preglacial Ohio originated east of present Cincinnati, Ohio, and included as tributaries the Kentucky, Licking, and Miami rivers; in the former interpretation, these rivers were part of the Teays Drainage. Opinions differ as to the preglacial course of the Tennessee River. It and the Cumberland River may have united with the Ohio before flowing through the Cache Lowland, or may have followed a course south of this lowland (along the western edge of the Interior Low Plateaus Province) before uniting with the Ohio River southeast of Crowley's Ridge.

Drainage changes in the Teays-Mississippi System were initiated by Nebraskan ice. The lower Teays was blocked and the upper course ponded until waters spilled over low divides into the Ohio River. Not until late Kansan time, however, was the present drainage of the Ohio River established by integration of former Teays and Lake Erie drainage. Illinoian ice continued to aggrade valleys and divert water to the developing Ohio River. By late Illinoian or early Wisconsin time the channel of the Mississippi River shifted eastward from the Salem Plateau to a lower level, through several gaps in Crowley's Ridge, and joined the Ohio on the eastern flank of this highland. Wisconsin ice aggraded most of the remaining Teays and lower Mississippi valley with sediment from the region of glacial Lake Agassiz and the Great Lakes. Changes following Wisconsin glaciation are evident

in the present drainage. The major changes were shift of the upper Mississippi River westward from the Illinois River Valley, diversion of the Ohio River southward from the Cache Lowland to unite with the Tennessee River near Paducah, Kentucky, a further shift eastward of the lower Mississippi River to its present channel, and loss of Great Lakes drainage to the Mississippi River System, culminating in the present Mississippi Basin.

ORIGIN AND DISPERSAL

The orangethroat darter may have originated in one of the following regions; north of the Teays-Mississippi (Hudson Bay), upper Mississippi, Teays, eastern drainage of the lower Mississippi (Interior Low Plateaus), or western drainage of the lower Mississippi (Ozark Plateaus). The least likely centers of origin will be discussed first.

If the orangethroat darter originated north of the Teays-Mississippi System, no evidence to that effect remains; the species is absent from the northern drainage that was not affected by glaciation (upper Missouri River). No evidence would be expected from the St. Lawrence System because this region was heavily glaciated. Populations present in the western Lake Erie drainage probably arrived via post-glacial routes. Specimens in this region resemble those in the Wabash River of Indiana, indicating that they entered the Lake Erie Basin in late Wisconsin time or subsequently via the glacial Lake Maumee outlet. Gerking (1945) indicated that the divide between the upper Wabash and Lake Erie is low, and that connections across this divide were observed during a period of high water in 1914. Perhaps this low divide had been crossed frequently by orangethroats during pluvial conditions.

Either the preglacial Teays or upper Mississippi may have been the center of origin, but here again the evidence is weak. Orangethroats are absent from the Driftdess Area of Wisconsin and populations now present in the Platte River could have arrived there as late as mid-Pleistocene. The species is present in the Kentucky, Licking, Miami, and Scioto rivers (presumably all tributaries of the preglacial Teays), but absent in eastern tributaries of the Teays having suitable habitat (Muskingum, Sandy, and Kanawha rivers.) If the orangethroat or its oligocephalid ancestor occurred or originated in the Teays or upper Mississippi, Pleistocene glaciation would have forced populations into southern refugia in the Ozark and Interior Low plateaus where secondary centers of dispersal developed.

Evidence for origin in the preglacial Ohio (Wabash through Tennessee rivers) is somewhat stronger than for origin in the above regions. The occurrence of endemic populations in the lower Green (Barren River), Cumberland, and Tennessee rivers suggests that the orangethroat occupied this region throughout much of the Pleistocene. Dispersal westward into the

Ozarks may have occurred early in the epoch before the course of the Mississippi shifted eastward from the Ozark highlands.

I think that the most likely center of origin lies in the Ozark Plateaus. The greatest amount of racial diversity occurs in that region. From there, also, preglacial pathways of dispersal extended east, north, and westward into the Teays-Mississippi and probably westward into the Ancestral Plains system. The cold, torrential waters of the Mississippi would have isolated populations of orangethroats in the southeastern Ozarks during Nebraskan time. By late Nebraskan or early Aftonian time, however, populations could have dispersed northward into the developing Mississippi River System via the mainstream along the eastern edge of the highland and/or across divides (discussed by Bretz, 1965) between the White and Missouri rivers. Later, Kansan glacial ice doubtless isolated populations in the northern Salem and Interior Low plateaus, and the Mississippi again isolated populations in the southeastern Ozarks. By late Kansan or early Yarmouth time, the course of the lower Mississippi shifted eastward, leaving an alluvial plain as a barrier to further dispersal from the southeastern Ozarks. Illinoian ice, which achieved the greatest southward advance in the east, probably had the greatest effect east of the Mississippi River, again isolating populations in southern tributaries of the developing Ohio River as well as separating them from populations in the Ozarks. By late Illinoian or early Sangamon time, the course of the lower Mississippi shifted east of Crowley's Ridge leaving a still wider alluvial plain. Populations of orangethroats in the Missouri and Ohio rivers dispersed northward as sufficient habitat became available. Meltwaters of the Wisconsin glacier (which underwent a series of four to six advances and retreats) again probably separated eastern and western populations, but doubtless did not force populations in the Ohio so far southward as the previous glacier had done, thus allowing for dispersal northward into the south-flowing tributaries of the Ohio River.

Etheostoma spectabile may have dispersed into the Missouri-Platte System in early Pleistocene and then have been isolated by either Nebraskan or Kansan ice in the Platte, where it evolved into *E. s. pukhellum*; southward dispersal over the Plains could have occurred from late Kansan to early Sangamon time. The similarity of now disjunct populations of *pukhellum* suggests that these populations have not been isolated from each other long. The subspecies *pukhellum* must have evolved from Teays-Mississippi stock no later than Kansan time to take advantage of routes of dispersal through the Ancestral Plains System available to it in late Kansan and early Yarmouth time. When the Kansas River captured a portion of the Ancestral Plains System, it not only isolated certain populations of *E. s. pukhellum* from others farther south, but it also brought the plains subspecies in contact with populations of *E. s. spectabile* of the Kansas-Missouri System. Evidence of intergradation between *pukhellum* and *spectabile* at

present occurs in some specimens from the Platte-Republican rivers and becomes progressively more common eastward in the Kansas and Missouri rivers. Lack of intergradation in the Smoky Hill River seems to reinforce evidence for the late capture of this stream by the Kansas River (late Illinoian or early Wisconsin).

Other possible interpretations for the origin of *pulchellum* are that it evolved from stock autochthonous in tributaries of the upper White River (in Missouri and Arkansas) that were pirated by the Arkansas River (Spring-Neosho) in the early Pleistocene. According to Bretz (1965), there is little geologic evidence of headwater exchange between the Arkansas and White rivers in Missouri. However, Williams (1954), in discussing the distribution of the crayfish *Orconectes neglectus* (Faxon), suggests that this species dispersed from the Ozarkian center of origin (White River) across divides into the Spring-Neosho System and northward through the Plains to the Platte River via the Pleistocene stream connections proposed by Frye and Leonard (1952). If such a capture did occur, it would suggest that the orangethroats now found on the west side of the Springfield Plateau (*squamosum*) descended from, or their ancestors gave rise to, "*pro*"-*pulchellum* stock.

Alternatively, *pulchellum* may have evolved from Teays-Mississippi stock isolated in highland tributaries of the lower Arkansas River Valley (drainage of the Ouachita and Boston mountains) by meltwaters of the Nebraskan glacier. However, evidence for dispersal of Teays-Mississippi stock to this region is weak. Although *pulchellum* occurs in this region at present as a population having color patterns distinct from those in the remainder of the range (suggesting some isolation), no orangethroats have been found in tributaries of Little Red River which drain the southeastern Ozarks between the valleys of the Arkansas and White rivers. The failure of "*pro*"-*pulchellum* to reach the Little Red and Arkansas rivers from the White River via the Mississippi River may perhaps be explained by lowland barriers to dispersal in the preglacial Mississippi Valley (see Thornbury, 1965, Fig. 3.17). Near its confluence with the White River, the course of the preglacial Mississippi turned eastward away from the Ozark highland and flowed in an alluvial valley more than 50 miles east of where the Arkansas River cuts into the highland. The course of the preglacial Arkansas River did not join the Mississippi River at this point, however, but flowed southward parallel to the course of the Mississippi before joining it more than 170 miles south of their present confluence. Assuming the Mississippi Alluvial Plain and the western Gulf Coastal Plain were as much a barrier to dispersal then as they are today, it is unlikely that *E. spectabile* invaded streams draining the Ozark and Ouachita provinces south of White River via these alluvial valleys. The western subspecies probably invaded the eastern Arkansas River Basin (Fort Scott to Little Rock, Arkansas) from a more western center (Ancestral Plains System).

NATURAL HYBRIDIZATION

Hybridization between *Etheostoma spectabile* and other species is not common, but has been reported with *E. radiosum* (Hubbs and Black) and *E. whipplei* (Girard) by Linder (1955b), with *E. caeruleum* (Storer) by Knapp (per. comm.), and with *Percina sciera* (Swain) by Hubbs and Strawn (1957) and Hubbs and Laritz (1961).

I have examined specimens that seem to be hybrids from one locality in Kansas (with *E. whipplei*) and two localities in Kentucky (with *E. caeruleum*).

Hubbs (1955) suggests several conditions or circumstances that are conducive to hybridization in nature. Particularly applicable to darters having similar breeding habits are: (1) disturbance of the habitat causing the two species to breed in a habitat intermediate to that preferred by each, (2) one species, for lack of adequate spawning sites, is forced to spawn in the area of another, (3) abundance of one species and scarcity of another in a spawning area induces individuals of the less numerous species to breed with members of the more numerous one because mates of its own kind are unavailable. Linder (1958) concluded that the latter circumstance was responsible for two hybrid specimens he described in 1955 (*E. radiosum* X *E. spectabile*); *E. radiosum* was much more abundant than *E. spectabile* at the collection site in Blue River, Johnson County, Oklahoma. Linder (1955b) noted that the Blue River orangethroat was unlike *E. s. pulchellum* from northern Oklahoma, and suggested that it might be an undescribed subspecies. I examined the series of orangethroats (UMMZ 163876, 163877, 163878) used by Linder to compare with specimens of *E. radiosum cyanorum* (Moore and Rigney), and concluded that these, as well as the two specimens Linder described as hybrids, are members of a hybrid swarm. I compared Linder's data on color pattern and squamation with similar data from representative *E. s. pulchellum* collected at Turner Falls, Murray County, Oklahoma (KU 5249). Both his two hybrids and specimens of the Blue River orangethroat are intermediate in coloration and scale counts between *E. r. cyanorum* and *E. s. pulchellum*. Scale counts are tabulated below; listed are the means of 20 specimens (10 of each sex) from each group, with exception of Linder's hybrids (one of each sex).

Character	<i>E. r.</i> <i>cyanorum</i> *	Linder's hybrids*	Blue R. o'throat*	<i>E. s.</i> <i>pulchellum</i> (KU 5249)
Total lateral line scales	56	53	53	48
Pored lateral line scales	48	40	38	32
Scales above lateral line	8	7	7	6
Scales below lateral line	12	9	8	7

*Data from Linder (1958).

Variation of orangethroat populations in Blue River has been studied by James B. Campbell, Kansas State College of Pittsburg, and he (per. comm.) concurs that these populations are hybrids between *E. r. cyanorum* and *E. s. pulchellum*.

Perhaps experimental hybridization of *E. r. radiosum* with *E. s. pulchellum* may provide evidence for the origin of *E. r. paludosum* and *E. r. cyanorum*. Possibly both *E. r. paludosum* and *E. r. cyanorum* arose by hybridization with and periodic isolation from populations of *E. s. pulchellum*.

With regard to the hybrid combination *E. whipplei* X *E. s. pulchellum*, Linder (1955b) reported predominance of the orangethroat (82 per cent, of which 61 per cent were females) at the hybrid locality. F. B. Cross (per. comm.) took only one specimen of *E. whipplei* at the locality in Verdigris River where the hybrid (KU 3165) was obtained; *E. s. pulchellum* was abundant at this locality. When the specimens were collected (April 1, 1954), Kansas was in the third year of a severe drouth and most tributaries of the Verdigris River were dry. The collection was made in the mainstream at Altoona, Kansas, on a riffle only a few inches deep.

Hubbs and Laritz (1961) suggest that the natural hybrid *P. sciera* X *E. spectabile* resulted from great abundance of *P. sciera* and scarcity of *E. spectabile* at the locality of capture, and from alteration of the habitat because of extensive collecting.

I am aware of the nature of the habitat at only one location where specimens of *E. caeruleum* X *E. s. spectabile* were collected. The bed of upper Knob Creek in the Salt River Drainage, Bullitt County, Kentucky is composed of a gravel substrate (stones less than egg-size) over which flows a shallow, braided stream. Few fish could be observed in the clear water before collecting, but deep agitation of gravel in the narrow channels yielded an abundance of specimens. The total collection was composed of about 50 per cent *E. s. spectabile*, 40 per cent *E. caeruleum*, and 10 per cent *E. flabellare* Rafinesque. About 10 per cent of the 60 specimens of ostensible *E. s. spectabile* and *E. caeruleum*, I consider to be hybrids between the two. The width of the channel of Knob Creek indicates that the stream often has much greater volume than it did when I seined there. Decreased precipitation seemingly reduced this stream to near-intermittency, forcing several species into similar habitat. Winn (1958b) observed that *E. s. spectabile* and *E. caeruleum* often breed on the same riffle, and have no obvious differences in breeding behavior; nevertheless, Winn never observed interspecific matings under laboratory or field conditions. Winn (1958a) also found that *E. s. spectabile* breeds most often near the heads of small riffles whereas *E. caeruleum* tends to breed in deeper, swifter water at the base of these riffles, and that *E. caeruleum* preferred a coarser substrate than *E. s. spectabile*. I observed, in the laboratory, that males of *E. s. spectabile* and *E. s. pulchellum* will breed readily with females of *E. caeruleum* when no other mates are

available. Males of *E. caeruleum* were not observed breeding with females of *E. spectabile*, even after the females lay half buried in the sand (which generally initiated mounting-response in males). They obviously did breed, however, because hybrids were produced in aquaria containing only male *E. caeruleum* and female *E. spectabile*. Additional hybrids were examined from Bay's Fork, Barren-Green River Drainage, Allen County, Kentucky. Of a mixed collection of 31 ostensible *E. caeruleum* and *E. spectabile*, I consider 29 per cent to be hybrids between the two species.

Intrinsic mechanisms may minimize hybridization under normal environmental conditions. Hubbs (1960) indicates that darter eggs possess a factor that reduces the chance of fertilization by foreign sperm from sympatric populations of related species but not from allopatric populations, and that the duration of sperm function is greatly reduced in a population of darters sympatric to related species. This may partly explain the rarity of natural hybrids between *E. spectabile* and sympatric congeners that have similar reproductive behavior. Mate selection undoubtedly is a strong factor in maintaining the integrity of related, sympatric species.

EXPERIMENTAL BREEDING

When I began work with *E. spectabile*, I knew of no intergrading populations nor sympatric occurrences of recognized subspecies. Breeding experiments were undertaken to test character stability in progeny of intra-subspecific matings, intersubspecific matings, interspecific matings and various backcrosses reared under similar environmental conditions.

Artificial hybridization (stripping) of *E. spectabile* with other darters has been reported by Hubbs (1959) and Hubbs and Strawn (1957a and b); crosses were with *Percina caprodes* (Rafinesque), *Etheostoma lepidum* (Baird and Girard), *E. grahami* (Girard), *E. caeruleum*, *E. fonticola* (Jordan and Gilbert), *E. whipplei* (Girard), *E. radiosum* (Hubbs and Black), *E. gracile* (Girard), *E. parvipinne* Gilbert and Swain, *E. blennioides* Rafinesque, a hybrid *Etheostoma (spectabile X lepidum)*, and the centrarchid *Lepomis punctatus*. In addition, Clark Hubbs (per. comm.) has successfully reared hybrids of *E. spectabile* and the following darters: *Percina sciera* (Swain), *P. phoxocephala* (Nelson), *P. shumardi* (Girard), *P. copelandi* (Jordan), *Etheostoma chlorosomum* (Hay), *E. stgmaeum* (Jordan), *E. tetrazona* (Hubbs and Black), *E. euzona* (Hubbs and Black), *E. zonale* (Cope), *E. juliae* Meek, *E. punctulatum* (Agassiz), *E. flabellare* Rafinesque, *E. proeliare* (Hay), and *E. microperca* Jordan and Gilbert. Linder (1958) allowed *E. spectabile* and *E. radiosum* to hybridize under laboratory conditions.

REARING METHODS

About 50 aquaria of 5 to 25 gallon capacity were set up with grade 2

aquarium gravel and sub-gravel filters. Small slabs of limestone and clamshells were added for cover and establishment of territories, and to help maintain hard-water conditions. Dechlorinated tapwater was added and maintained at a depth of 6 to 10 inches. Continuous aeration was provided by a single large compressor which also operated filters. Favorable temperatures, 15° to 21° C., were maintained by means of two 10,000 B.T.U. air conditioners (room-size 20 x 8 x 8 feet). During the first year of experimentation (1959), fishes in spawning condition were brought from streams and placed in the aquaria. Males and females were stocked and allowed to remain for one week. Parental stock was then removed and the sexes separated in 5-gallon aquaria, to be held for other crosses. In subsequent years, procedures were similar except that most of the breeding stock was reared in the laboratory.

FOOD. The fish were fed living microcrustacea and mosquito larvae. Newly-hatched fry were fed infusoria, brine shrimp, and the smaller instar stages of zooplankton. An abundance of food was available to the fish at all times.

In nature, the aquatic larvae of insects make up the bulk of the diet of the orangethroat. The plankton that I used as food varied in species composition, but copepods usually predominated, giving way to cladocera in the spring and fall. Deficiency of carotenoids discussed by Hubbs and Stravnhagen (1958) was not apparent in my fish. Darters kept on this diet for three years produced viable offspring, without apparent defects, each year.

REPRODUCTION. In the laboratory, the peak of breeding occurred in late March, April, and May which is the approximate peak in nature at this latitude. Small hatches occurred in aquaria in September, and the earliest hatches occurred in January. Most females seemed spent by early June, but males continued to produce sperm through most of the year (based on microscopic examination of gonad smears). However, the intense colors of males began to fade in late May or early June. During the first winter (1959-60) temperatures in the aquaria were allowed to drop near the freezing point. Colors of males began to deepen and females developed large eggs in December. Darters maintained at 12° C. were not observed to spawn. Spawning was observed when temperatures rose to 15° or 16° C. and the greatest spawning activity seemed to occur between 16° and 20° C.

GROWTH. Fry were observed usually within two days after adults were removed. As the young fish grew, the brood-tanks were thinned at intervals of several weeks in an attempt to prevent stunting from overcrowding. Only 12 to 14 fish could be raised to sexual maturity in 10 to 12 months in a 25 gallon aquarium (432 sq. in. of substrate), and 3 or 4 darters in a 5 gallon aquarium (108 sq. in. in bottom-area). The number of individuals could be increased about 50 per cent if the water was filtered every 3 or 4 weeks, using a motor-driven charcoal filter. Fish hatched in the laboratory grew more

slowly than those hatched in nature—possibly because of dietary deficiency, lower developmental temperatures, crowding and accumulation of metabolic wastes, or a combination of these factors.

PARASITES. *Hydra* sp. was often introduced into aquaria with food; when abundant, *Hydra* could deplete a tank of fry in less than one week. In tanks of older fishes, *Hydra* consumed enough crustaceans to make it difficult to maintain a sufficient food supply for the darters. This coelenterate was easily controlled by adding 0.05 ml of a saturated solution of copper sulfate per gallon of aquarium water. The only important parasite was the crustacean *Mesocyclops edax*. This copepod seemed harmless in small numbers, and was utilized as food. When abundant, usually in late fall, it often attached to the epidermis of fishes of any size. The reactions of fish to heavy infections of this organism were fast erratic swimming and rubbing against the sides and bottom of the aquarium. When dead or dying fish were removed to a watch glass for observation under magnification, *Mesocyclops* poured off the fish into the water. Copepods tended to leave the host when fish were netted and placed in clean aquaria. Little mortality occurred among infected fish handled in the manner above. Fish allowed to remain in tanks containing large populations of *Mesocyclops* succumbed rapidly to these parasites. True parasitic lernaeid copepods were observed attached to darters in the wild, but no infected individuals were used as brood stock.

RESULTS

E. s. pulchellum

PARENTAL STOCK. Five males and 10 females from Kansas, Douglas Co., Deer Creek, a tributary of the Wakarusa River, T. 12 S, R. 8 E, Sec. 31 were used. All members of this population had the normal color pattern of *pulchellum*. One member of each sex had a few opercular scales.

F1 GENERATION. All of 117 specimens possessed the normal color pattern of *pulchellum* and had the opercle free of scales. Four males and five females were used for parental stock of the second filial generation.

F2 GENERATION. All of the 91 specimens had the normal color pattern of *pulchellum* and the opercle free of scales.

E. s. spectabile

PARENTAL STOCK. Two males and 11 females from Kansas, Franklin Co., Hickory Creek, a tributary of the Marais des Cygnes River, T. 16 S, R. 21 E, Sec. 29 were used. All had the normal color pattern of *spectabile* from the Osage River. The opercle was moderately to well scaled, index 2.7.

F1 GENERATION. Only 24 specimens were reared from this hatch; I overlooked a small adult when the breeding stock was removed, and it probably consumed most of the young. The remaining 13 males and 11 females had the normal color pattern of *spectabile*. The opercle was naked to well scaled,

having an index of 2.6. The same 24 specimens were used as parental stock of the second filial generation.

F2 GENERATION. All of 78 specimens had the normal color pattern of *spectabile* and the opercle sparsely to well scaled, index 2.7.

***E. s. pulchellum* ♂ X *E. s. spectabile* ♀**

PARENTAL STOCK. Five males from the *pulchellum* X *pulchellum* cross and 19 females from Hickory Creek were used. One male *pulchellum* had the opercle sparsely scaled. The opercle of females was lightly to well scaled (index 2.8). Each sex had the color pattern normal to its subspecies.

F1 GENERATION. Most of the 110 specimens had body color patterns intermediate between *pulchellum* and *spectabile*, with sides tessellated; specimens smaller than 22 mm in standard length usually resembled *pulchellum* in coloration. The first dorsal fin was banded like that of *spectabile*. The opercle was naked to well scaled, usually sparsely scaled, index 1.1. Three members of each sex were used as parental stock of the second filial generation; the opercle of these was sparsely scaled (in two males and two females) to moderately scaled (in one male and one female).

F2 GENERATION. Of 49 specimens reared, 15 resembled *spectabile* more than *pulchellum*, 18 were intermediate, and 14 resembled *pulchellum* more than *spectabile* in color pattern of the body. The opercle was naked to well scaled, index 1.3. In 31 specimens, one or both pelvic fins were abnormally developed. Fin-rays were either distorted, short or absent.

***E. s. spectabile* ♂ X *E. s. pulchellum* ♀**

PARENTAL STOCK. Four males from the Hickory Creek collection and 9 females from the *pulchellum* X *pulchellum* cross were used. Three males had the opercle well scaled and one had it moderately scaled. One female had the opercle sparsely scaled, but the remaining eight had naked opercles. Both sexes had color patterns normal for their subspecies.

F1 GENERATION. Most of the 88 specimens had body-color patterns intermediate between *pulchellum* and *spectabile*; the sides were tessellated as in the reciprocal cross, and the first dorsal fin was banded like that of *spectabile*. The opercle was sparsely to well scaled usually sparsely scaled, index 1.3 (1.5 in the largest specimens). The squamation differed from that in the reciprocal cross in that the scales were usually embedded in the flesh of the opercle and were difficult to locate in small specimens. Eight males and 10 females were used as parental stock of the second filial generation. The opercle-scale index of this breeding population was 1.6.

F2 GENERATION. Of 49 specimens reared, 18 resembled *spectabile*, 26 were intermediate, and 5 resembled *pulchellum* in color pattern of the body. The opercle was naked to well scaled, index 1.4. Scales on the opercle were often embedded. No teratological development was observed.

ADDITIONAL CROSSES. Matings were made between progeny of intersub-specific hybrids (reciprocal only), progeny of similar subspecies and progeny of intersubspecific hybrids, and wild stock of the following subspecies: *squamosum* X *squamosum*, *squamosum* X *spectabile*, *pulchellum* X *squamosum*, and *pulchellum* X *spectabile* from White River, Missouri.

No differences in coloration were detected between reciprocal crosses. The progeny of each mating were essentially intermediate between the parental kinds. This, of course, in crosses between pure parental strains, could result from incomplete dominance in several or many factors; but such seems not to be the case here as shown by the fact that, in every instance, backcross progeny were rather uniformly intermediate (showing no evidence of Mendelian segregation) between the F₁ and the parental type to which they were backcrossed. Involvement of a large number of characters regulated by multiple factors is suggested as a genetic mechanism controlling these characters.

Data other than those on coloration are presented in Table 16 for all laboratory crosses.

DISCUSSION. Decrease in length of the cephalic (posterior infraorbital and supratemporal canals) portion of the acoustico-lateralis system occurred in almost all laboratory crosses. Branson and Moore (1962) review the literature on correlation of lateral-line morphology with species ecology. Active swimmers or bottom-dwelling species inhabiting swift currents possess a better developed acoustico-lateralis system than do sluggish swimmers or bottom-dwelling species inhabiting slow currents. There is no doubt that the laboratory environment was more lentic than that in which the orangethroat is normally found. Currents under laboratory conditions would be mainly vertical and produced by stand-tubes of the under-gravel filters. Whether these mild currents were responsible entirely for decrease in canal lengths (reduction of posterior infraorbital pores) is questionable. Collette (1962) relates decrease in the number of infraorbital pores and incompleteness of the supratemporal canal, in the darter *Etheostoma fusiforme* (Girard), to low productivity of the habitat in which these darters occur. In the original intrasubspecific breeding experiment (A X A, B X B; for identification of symbols, see legend of Table 16), the mean number of posterior infraorbital pores decreased progressively in the F₁ and F₂ progeny. F₁ progeny (AB, BA) of original intersubspecific crosses (A X B and B X A) and F₂ progeny (ABAB) also demonstrate a decrease in the mean number of pores, but in F₂ progeny (BABA) the mean number of pores again is that of the parental female (A). Results with backcrossing demonstrate that the mean number of infraorbital pores is greater than that of either parent population in the progeny of two crosses (AABA and BABB), is intermediate to those of the parent populations in the progeny of four crosses (AAAB, BAAB, ABAB, and BBBA; the mean number of pores of the latter is equal

to that of the parental male, BB), and is less than that of either parent generation in the progeny of two crosses (BBAB and ABBA). The progeny (BC) of another intersubspecific cross (B X C) demonstrates an increase over that of either parent in the mean number of pores, while the progeny (BD) of yet another cross (B X D) have a mean number of pores equal to that of the parental male.

If the development of posterior infraorbital pores was under direct influence of the environment, I would expect progressive decrease in number of pores with each succeeding laboratory cross, but because the mean number of pores increased or remained intermediate in the progeny of two F_1 , one F_2 , and most backcross generations, I suspect that this character like that of coloration is regulated by multiple genetic factors.

Factors influencing squamation of the cheek, opercle, nape, and breast seem to be chiefly hereditary. Progeny usually are intermediate in anterior scale index between the parental forms. In only one cross were the progeny (BB) less scaly than either parent. Scale exposure, however, seems to depend on the characteristics of the female parent. The progeny (AB) of male *spectabile* and female *pulchellum* have the opercle scales mostly embedded; in progeny of the reciprocal cross (BA) the opercle scales are well exposed.

Developmental malformations appeared rarely in the experimental crosses, but when they did they appeared in such numbers as to remove chance as a factor for their presence. The first malformations appeared during the second year of experimentation in the F_2 progeny BABA, backcross progeny BBAB, and F_1 progeny CA and BD. In the BABA progeny, 63 per cent of all the specimens reared had one or both pelvic fins malformed; all BBAB and BD progeny had one or both dorsal fins malformed; about one-half the CA progeny had the dorsal fins and/or the operculum malformed. Factors responsible for these teratologies only can be surmised because of the meager evidence at hand. Dietary deficiencies could lead to eggs of poor "quality," hence low survival and anomalous development. Even though all darters were fed the same diet in abundant quantities, it is conceivable that some tanks of darters may not have benefited from this diet, especially if a tank harbored a large population of hydra. Close watch was kept on the fry-tanks to keep this coelenterate in check, but less attention was paid to tanks containing juvenile and adult fishes, because hydra seemed to have no direct effect on larger fishes. Consequently, brood stock of some crosses may have not been as well fed as others.

The small number of anomalous F_1 progeny (CA and BD) suggests that more information is needed about the reciprocal crosses (AC and DB) before any conclusions can be drawn. About 24 DB progeny are being reared currently; these show no obvious fin abnormalities.

Differences do exist, however, among the gametes of geographic variants of *E. spectabile* which may account for some of the anomalies observed in

laboratory crosses. Hubbs and Strawn (1957a) report that eggs of *E. s. spectabile* from Arkansas (White River) are smaller, more delicate, and have a far lower survival rate than eggs of *E. s. pulchellum* from Texas. Additional matings are necessary to ascertain the effects genetic differences have on progeny of matings between geographic variants of *E. spectabile*.

SUMMARY AND CONCLUSIONS

Etheostoma spectabile is a darter inhabiting upland, hardwater streams of the Mississippi Valley and western Coastal Province.

Three subspecies are described as new and several proposed races and subraces are based on one or more of the following characters: coloration (primarily on color and pigmentation, especially of the male), squamation, development of the acoustico-lateralis system, and number of rays in the pectoral fin.

Etheostoma spectabile spectabile is the most variable member of the subspecies complex and, as here restricted, is composed of five races, several of which are comprised of subraces. The northern Ozark race includes orangethroats in tributaries of the Missouri River from its confluence with the Osage River eastward, in tributaries of the Mississippi River from southern Iowa south to its confluence with the Ohio River, and in tributaries of the upper Black and St. Francis rivers. The southern Ozark race includes orangethroats from White River of Missouri and Arkansas, from the headwaters to the confluence with Black River. The northeastern race includes populations from tributaries of western Lake Erie and the Ohio River, exclusive of the Tennessee, Cumberland, and Green rivers of Kentucky and Tennessee. The southeastern race includes orangethroats of the Tennessee, Cumberland, and Green rivers. *E. s. spectabile* intergrades with *E. s. pulchellum* in tributaries of the Missouri River west of its confluence with the Osage River to its confluence with the Kansas River and in some eastern tributaries of the Kansas River.

Etheostoma spectabile uniporum (a new subspecies) is separated from the range formerly attributed to *E. s. spectabile*. *E. s. uniporum* inhabits the western tributaries of Black River from Butler County, Missouri (Cane Creek) to Lawrence County, Arkansas (Flat Creek); the major tributaries occupied are Current, Eleven Point, and Spring rivers. *E. s. uniporum* resembles *E. s. spectabile* in coloration of the fins and is somewhat similar to *E. s. pulchellum* in coloration of the body. Scale characteristics, however, most closely resemble those of *E. s. spectabile*. In addition *E. s. uniporum* possesses a less well developed acoustico-lateralis system and a lower number of pectoral fin rays than other members of the subspecies complex. This subspecies probably differentiated from Ozarkian stock in the western tributaries of Black River where it now occurs.

Etheostoma spectabile fragi (a new subspecies) is separated from the range formerly assigned to *E. s. spectabile*. *E. s. fragi* inhabits the tributaries of Strawberry River, a western tributary of Black River immediately south of Spring River alluded to above. *E. s. fragi* is the most scaly-headed member of the subspecies complex and resembles *E. s. uniporum* most closely in coloration. *E. s. fragi* may have evolved from autochthonous stock in Strawberry River; alternatively it may have arisen by hybridization between "pro"-*uniporum* and a lowland scaly-cheeked darter (possibly *E. asprigene*).

Etheostoma spectabile pulchellum, as restricted herewith, ranges from the North Platte River of Nebraska to the Guadalupe River of Texas. It varies little in coloration throughout its range, the most variation being in the eastern portion of the Kansas River (intergrades with *E. s. spectabile*), eastern Arkansas River (red color prevalent), and some eastern tributaries of Red River (hybridizes with *E. radiosum*). *E. s. pulchellum* differs from other members of the subspecies complex in having the anterior region largely free of scales and distinctive coloration. This subspecies may have evolved from "pro"-*pulchellum* stock isolated in the northwestern tributaries of the Teays-Mississippi System (early Platte River or a more southern tributary) by Kansan glacial ice, and spread southward via the Ancestral Plains System after retreat of the glacier.

Etheostoma spectabile squamosum (a new subspecies) most closely resembles *E. s. pulchellum*, but differs from it by having a more scaly anterior region and distinctive coloration. *E. s. squamosum* inhabits streams draining the western slope of the Springfield Plateau and is separated from the range formerly attributed to *E. s. pulchellum*. This subspecies possibly evolved from a *pulchellum*-like ancestor in the tributaries where it now occurs, but in addition, by means of unidirectional hybridization, it may have incorporated some of the genome of related species (*E. caeruleum* or *E. whipplei*) with whom *E. s. squamosum* shares several characteristics.

Etheostoma spectabile probably evolved in the Ozark Highlands not later than late Pliocene or early Pleistocene, and dispersed via preglacial pathways into much of the Teays-Mississippi River System. Multiple glaciation must have forced the orangethroat southward and isolated populations in the Plains, Ozark Plateaus, and Interior Low Plateaus long enough for populations to differentiate but not long enough for these isolated populations to establish biological barriers. Interglacial periods allowed some populations previously isolated to make contact and intergrade. Drainage changes concomitant with Pleistocene climatic change also isolated some populations, while allowing others to expand their range and intergrade with populations from which they were isolated previously.

Natural hybrids occur between *E. spectabile* and other darters with similar mating habits when two species are either forced to spawn in the immediate area or when the number of individuals of one species greatly exceeds that

of the other at the spawning site; however, hybrid swarms occur rarely throughout the range of the species.

Breeding experiments between morphological variants of *E. spectabile* yielded progeny intermediate in most characters between the parental stock, with the exception of the degree of development of the acoustico-lateralis system. Anomalous progeny of some matings may indicate gametic differences between some populations or abnormal conditions under which matings were made or progeny were reared in the laboratory.

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TABLE 1. Comparison of the five subspecies of *Etheostoma spectabile*. Values given are means (to two decimal places) or modal numbers (integers).

Character	<i>spectabile</i>	<i>uniporum</i>	<i>fragi</i>	<i>pulchellum</i>	<i>squamosum</i>
Dorsal spines	9.92	10.12	10.29	9.79	9.73
Dorsal rays	12.69	12.14	12.30	12.77	13.05
Soft anal rays	6.97	6.71	6.63	6.73	6.60
Left pectoral rays	12.01	11.44	11.57	11.96	11.98
Lateral line scales	44.36	45.51	49.72	49.95	48.50
Pored scales	25.67	22.43	34.50	31.24	29.86
Diagonal scales	12	12	13	13	13
Scales above lat. line	5	5	6	6	6
Cheek scale index	1.08	1.21	2.91	0.74	2.04
Opercle scale index	2.24	1.72	2.90	0.27	1.96
Nape scale index	2.22	1.59	2.74	1.30	2.84
Breast scale index	0.37	0.17	1.39	0.00	1.03
Anterior scale index	1.48	1.17	2.48	0.58	1.97
Posterior infraorbital pores	2.94	1.45	2.88	2.82	3.42
Complete supratemporal canal	88%	32%	94%	85%	84%
Junction gill membrane index	1	1	2	2	2

TABLE 2. Frequency distribution of lateral line scales in populations of *Etheostoma spectabile spectabile* in several major rivers, and in intergrades' with *Etheostoma spectabile pulchellum*.

Drainage	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	n	\bar{x}	
Tennessee	1	1	6	8	17	15	8	6	4	..	2	68	39.74
Cumberland (upper)				2	2	9	10	18	12	6	3	2	2														66	42.14
Cumberland(lower)		2	5	12	12	11	3	3	1	49	39.04
Green (upper)										1	3	3	4	1	2	1	1	1									17	47.29
Green (lower)		1	7	9	18	17	16	11	4	5						89	41.19
Ohio (S) ¹						5	4	13	9	28	20	15	15	10	4	1	1	125	45.81
Ohio (N) ²			2	4	6	18	32	39	31	28	11	8	2	2	1											..	184	43.38
Missouri (E) ³						3	3	6	12	25	18	26	28	34	20	14	7	8	5	1						..	210	47.84
Missouri (W)'							1	16	21	24	34	34	13	28	12	12	7	1	2		1					..	206	47.01
Mississippi ⁴				2	14	10	12	19	15	24	18	13	4	9	4		..		1							..	145	44.38
Black-St. Francis ⁵			1	..	1	4	..	5	7	6	6	1	5		1	1										..	38	45.68
White (upper)											1	1	1	2	5	11	11	16	15	9	10		4	1	1	88	52.25	
White (lower)	1	1	5	5	15	16	18	22	22	18	21	9	8	3	3	2	1									..	170	43.64

¹Southern tributaries east of Green River. ²Northern tributaries and Lake Erie. Osage River eastward. West of Osage River (intergrades). Tributaries from Iowa to Kentucky exclusive of Missouri and Ohio Rivers. ³Upper Black River (Poplar Bluff, Mo. northward).

TABLE 3. Frequency distribution of lateral line scales in populations of *Etheostoma spectabile uniporum* in several stream systems, and in *Etheostoma spectabile fragi* (Strawberry River).

Drainage	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	n	X
Cane Creek						1	1	1	4	6	2	3	1	1				20	48.10
Current River		2	4	8	6	5	9	10	6	7	5	4		1				67	45.34
Fourche River		1	3	3	1	4	7	3	5	1	1	2						31	44.94
Eleven Point River	1		4	3	9	11	6	5	5	1	..	2						47	44.32
Spring River		2	5	2	4	7	11	7	6	4	2	1						51	44.86
Strawberry River				..	3		5	4	6	12	19	16	17	15	5	4	3	109	49.72

TABLE 4. Frequency distribution of lateral line scales in populations of *Etheostoma spectabile pulchellum* in several major rivers, and in *Etheostoma spectabile squamosum* (Grand and Illinois rivers).

Drainage	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	n	X	
Kansas (upper)			1	2	8	8	18	24	39	29	28	30	16	7	2	3	1	216	47.85
Kansas (lower)				1	1	3	6	10	12	14	18	23	8	6	4	4		..	1	111	48.83
Arkansas (upper)						2	4	5	9	13	18	29	16	13	12	9	3	2					..	135	50.13
Grand River		1		5	3	11	18	19	22	32	21	28	10	4	1	2	1						..	178	47.64
Illinois River				1	3	..	5	12	23	40	53	48	30	22	6	7	3	1				254	49.36
Arkansas (lower)				..	2	10	14	23	23	23	46	32	31	26	8	6	6	1		1		1	1	253	50.16
Red (upper)				1		2	2	4	8	9	14	15	9	4	4	1	..	1					..	74	50.15
Red (lower)				1	3	1	2	3	7	6	4	8	3	1							..	39	47.77
Brazos							..		1	2	4	4	4	5	4	1	6	1	1	33	52.88
Colorado						2	1	3	6	10	4	2	5	4	1	38	49.55
Guadalupe						1			5	4	22	12	14	4	13	4	1						..	80	51.39

TABLE 5. Frequency distribution of pored scales in populations of *Etheostoma spectabile spectabile* in several major rivers, and in intergrades⁴ with *Etheostoma spectabile pulchellum*.*

	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42		
T	1	1	2		3	4	4	10	7	17	8	2	6	2	1														68	21.18
Cu					1					2	1	6	5	5	8	8	7	5	8	3	1						1					66	27.17
Cl		1			2	4	8	8	8	6	6	2	2	1	1																	49	20.84
Gu								1	2	2	4	2	2	2	..	2											17	25.18
GI							3	4	4	3	13	5	11	18	10	12	2	2												89	25.11
OS		2					1	5	5	5	10	19	25	17	15	9	2	2	2	125	25.06
ON							3	4	3	7	13	29	19	26	20	18	17	11	3	4	2	3	2			2		..				184	27.24
ME								2	6	1	14	17	22	16	20	24	24	17	14	16	4	6	2	3	2			..				210	27.79
MW ⁴								1	5	9	7	7	18	19	29	26	19	25	19	11	6	2	1	1	1		..					206	27.78
M						1	2	2	6	6	8	14	15	25	13	20	12	12	2	2	1								145	25.27
BSF			1		2			2	1	5	5		4	5	3	3	1	2	1	1												38	24.92
Wu													1	3	2	6	2	10	8	5	14	8	5	3	5	4	2	2	1			88	33.19
Wl					1	2		7	8	12	18	21	9	14	18	11	12	9	14	5	7	1	..				1					170	25.13

*For explanation of abbreviated drainage (stub) refer to Table 2 including footnote.

TABLE 6. Frequency distribution of pored scales in populations of *Etheostoma spectabile uniporum* in several stream systems, and in *Etheostoma spectabile fragi* (Strawberry River).

Drainage	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	n		
Cane Creek	-----						2	1	1	1	3	1	3	1	2	2	..	2						20	22.80	
Current River	--1--	1	1	2	2	5	5	5	9	7	10	9	2	3	1	1	3			67	19.66	
Fourche River					1					3	..	4	2	4	1	7	1	2	1	2	2	1	..	31	24.16
Eleven Point River	-----	1	..				2	2	7	4	..	11	2	6	6	6	47	21.00	
Spring River	-----											1	5	5	8	9	9	7	1	1	1	1	2	51	24.53	

Drainage	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	n	X	
Strawberry River	1	1	2	1	5	9	7	18	15	11	8	9	10	6	2	3	1					..	109	34.50

DIS T R I B U T I O N D I V A R I A N T N O O f e o s m a S p e c i e

TABLE 7. Frequency distribution of pored scales in populations of *Etheostoma spectabile pukhellum* in several major rivers, and in *Etheostoma spectabile squamosum* (Grand and Illinois rivers).

Drainage	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	n	X
Kansas (upper)				1	2	..	8	7	12	20	23	32	34	32	21	14	5	3	2		..			216	31.38
Kansas (lower)	-----			2	3	4	6	10	13	11	11	6	22	8	5	2	2	4	..	1	..	1		111	30.19
Arkansas (upper)	-----					2	2	7	3	15	11	20	14	17	12	11	9	5	4	2	..		1	135	32.17
Grand River		1		3	3	7	7	12	22	29	18	23	17	18	19	4	1	2	2			178	28.90
Illinois River		1		1	2	1	1	7	12	28	38	34	28	28	28	24	5	7	4	2		2	1	254	30.81
Arkansas (lower)	-----		1		1	6	13	13	17	18	22	31	29	32	14	23	19	8	3	..	1	1	1	253	30.56
Red (upper)	-----			3	..	1	5	3	10	15	9	10	6	3	4	2	3			74	31.80
Red (lower)	-----		1	1	2	2	3	4	4	5	5	2	4	..	1			39	28.77
Brazos	-----			1	1	..	1	1	3	4	3	3	4	4	2	2	1	2	1			33	34.18
Colorado	-----			1	3		6	4	7	10	2	1	2	1	1		..			38	31.95
Guadalupe	-----		1	1	1	4	6	4	6	8	7	10	15	8	4	..	3	2	..					80	30.19

TABLE 8. Frequency distribution of indices of anterior squamation in populations of *Etheostoma spectabile spectabile*, and in intergrades⁴ with *Etheostoma spectabile pulchellum*.

Drainage*	Cheek						Opercle					
	0	1	2	3	n	X	0	1	2	3	n	X
Tennessee -----		34	20	10	64	1.62		1	9	54	64	2.83
Cumberland (U)		66	5		71	1.07	¶	28	21	21	71	1.87
Cumberland (L) --		55	1	1	57	1.05		57	57	3.00
Green (U) -----		19	..		19	1.00		17	2	..	19	1.10
Green (L) -----		80	7		87	1.08		2	12	73	87	2.82
Ohio (S) ¹ ■■■■■	1	121	2		124	1.01	11	65	24	24	124	1.49
Ohio (N) ² ■■■■■		159	5		164	1.03		37	71	56	164	2.12
Missouri (E) ³ ■■■■		186	18		204	1.09		8	26	170	204	2.79
Missouri (W) ¹ ----	25	146			171	0.85	7	86	49	29	171	1.58
Mississippi ⁵	1	155	2		158	1.01		10	41	107	158	2.61
Black-St. Francis ²	35	3		38	1.08		7	13	18	38	2.29
White (U)	6	57			63	0.90		45	15	3	63	1.33
White (L) -----		128	2		130	1.02		14	25	91	130	2.59

Drainage*	Nape						Breast					
	0	1	2	3	n	X	0	1	2	3	n	X
Tennessee -----		..	1	63	64	2.98	16	19	29		64	1.20
Cumberland (U)		22	24	25	71	2.04	46	24	1		71	0.37
Cumberland (L) --		..	57	57	57	3.00	2	10	45		57	1.75
Green (U) -----		13	6	..	19	1.32	18	1	..		19	0.05
Green (L) -----			6	81	87	2.93	15	65	7		87	0.91
Ohio (S) ¹ ■■■■■	1	83	33	7	124	1.37	124	..			124	0.00
Ohio (N) ² ■■■■■	2	31	100	31	164	1.98	163	1			164	0.01
Missouri (E) ² ■■■■		12	52	140	204	2.63	201	3			204	0.01
Missouri (W) ⁴ .	29	101	24	17	171	1.17	171				171	0.00
Mississippi ⁵		7	55	96	158	2.56	158				158	0.00
Black-St. Francis ² ...		9	11	18	38	2.24	36	1	1		38	0.08
White (U) -----		53	10		63	1.16	63				63	0.00
White (L) -----	1	14	35	80	130	2.49	124	6			130	0.05

*For explanation of drainage refer to Table 2 including footnote.

TABLE 9. Frequency distribution of indices of anterior squamation in populations of *Etheostoma spectabile uniporum*, and in the Strawberry River population of *Etheostoma spectabile fragi*.

Drainage	Cheek						Opercle					
	0	1	2	3	n	X	0	1	2	3	n	X
Cane Creek -----	1	19	..		20	0.95	4	14	2		20	0.90
Current River ----		57	14	8	79	1.38	6	60	10	3	79	1.13
Fourche River		26	4		30	1.13		..	30	..	30	2.00
Eleven Point River .	1	59	14		74	1.18	13	30	31		74	2.24
Spring River -----		31	20		51	1.39	9	16	26		51	2.33
Strawberry River --		1	8	101	110	2.91	2	7	101	110		2.90

Drainage	Nape						Breast					
	0	1	2	3	n	X	0	1	2	3	n	X
Cane Creek -----	3	14	3	..	20	1.00	18	2			20	0.10
Current River ----	4	46	18	11	79	1.46	62	14	3		79	0.25
Fourche River ----	3	3	5	19	30	2.33	27	3			30	0.10
Eleven Point River ..	3	29	34	8	74	1.64	62	11	1		74	0.18
Spring River	4	21	22	4	51	1.51	41	10	..		51	0.20
Strawberry River --	..	3	22	85	110	2.74	19	42	36	13	110	1.39

TABLE 10. Frequency distribution of indices of anterior squamation in populations of *Etheostoma spectabile pulchellum*.

Drainage	Cheek						Opercle					
	0	1	2	3	n	X	0	1	2	3	n	X
Kansas (U) -----	166	36			202	0.18	175	27	202	0.13
Kansas (L) -----	24	82	3		109	0.81	29	25	22	33	109	1.54
Arkansas (U) ----	50	89			139	0.64	137	2			139	0.01
Arkansas (L) ---	34	192			226	0.85	224	2			226	0.01
Red (U)	14	70			84	0.83	77	7			84	0.08
Red (L)	23	16			39	0.41	30		1	8	39	0.67
Brazos		33			33	1.00	33				33	0.00
Colorado		37	1		38	1.03	38				38	0.00
Guadalupe	10	70			80	0.88	80				80	0.00

Drainage	Nape						Breast					
	0	1	2	3	n	X	0	1	2	3	n	X
Kansas (U) -----	31	83	84	4	202	1.30	202			..	202	0.00
Kansas (L)	2	30	45	32	109	1.98	107	2		..	109	0.02
Arkansas (U) ---	26	101	9	3	139	0.92	139			..	139	0.00
Arkansas (L)	13	184	29	..	226	1.07	226			..	226	0.00
Red (U)	2	72	10	..	84	1.10	84			..	84	0.00
Red (L)	2	11	18	8	39	1.82	39				39	0.00
Brazos	2	31		..	33	0.94	33				33	0.00
Colorado	5	25	4	4	38	1.18	38				38	0.00
Guadalupe	53	25	2	80	1.36	80				80	0.00

TABLE 11. Frequency distribution of indices of anterior squamation in major populations of *Etheostoma spectabile* squamosum.

Drainage	Cheek						Opercle				
	0	1	2	3	n	X	0	1	2	n	X
Grand	1	43	67	78	189	2.17	13	52	45	189	2.00
Illinois	4	83	99	66	252	1.90	13	80	72	252	1.92

Drainage	Nape						Breast				
	0	1	2	3	n	X	0	1	2	n	X
Grand	1	..	30	158	189	2.82	28	83	59	189	1.36
Illinois	1	35	216	252	2.85	114	105	28	252	0.70	

TABLE 12. Frequency distribution of posterior infraorbital pores and condition of supratemporal canal in populations of *Etheostoma spectabile spectabile* and intergrades with *Etheostoma spectabile pulchellum*.

Drainage*	Posterior infraorbital pores							Supratemporal canal			
	1	2	3	4	5	com.	n	X	com.	n	% com.
Tennessee		12	46	6			64	2.91	57	64	89
Cumberland	1	23	77	18	1	3	123	2.96	110	123	89
Green		5	54	17	1	10	87	3.18	81	87	93
Ohio (S) [†]	1	29	82	12			124	2.85	100	124	81
Ohio (N)		22	107	22	2	1	154	3.03	131	154	85
Missouri (E) [‡]		77	150	24			251	2.79	155	164	94
Missouri (W) [†]		3	137	31			171	3.16	144	171	84
Mississippi [¶]	3	79	67	8		1	158	2.51	141	158	89
Black-St. Francis [¶]		9	18	11			38	3.05	33	38	87
White		27	123	65	3	1	219	3.20	196	219	89

*For explanation of drainage refer to Table 2 including footnote.

TABLE 13. Frequency distribution of posterior infraorbital pores and condition of supratemporal canal in major populations of *Etheostoma spectabile uniporum* and in the Strawberry River population of *Etheostoma spectabile fragi*.

Drainage	Posterior infraorbital pores							Supratemporal canal			
	1	2	3	4	5	com.	n	X	com.	n	% com.
Cane Creek	52	3					55	1.05	4	20	20
Current River	74	5					79	1.06	9	79	81
Fourche River		30					30	2.00	19	30	63
Eleven Point River	58	16	..				74	1.22	4	74	83
Spring River	5	45	1				51	1.92	31	51	61
Strawberry River	..	21	74	7	1	7	110	2.88	104	110	94

TABLE 14. Frequency distribution of posterior infraorbital pores and condition of supratemporal canal in populations of *Etheostoma spectabile pukhellum*.

Drainage	Posterior infraorbital pores							Supratemporal canal		
	1	2	3	4	corn.	n	X	com.	n	% corn.
Kansas (U)		64	126	19	2	211	2.78	125	211	59
Kansas (L)	1	25	60	23		109	2.96	84	109	77
Arkansas (U) ---		41	68	15	1	125	2.79	101	125	81
Arkansas (L) ---	5	124	78	17	2	226	2.48	216	226	96
Red (U) -----	2	11	51	19	1	84	3.05	74	84	88
Red (L) -----	2	17	16	4*		39	2.59	9	9	100
Brazos		11	18	3		32	2.75	25	32	78
Colorado		7	21	8	2	38	3.03	32	38	84
Guadalupe		18	46	16		80	2.98	79	80	99

*One specimen with five pores.

TABLE 15. Frequency distribution of posterior infraorbital pores and condition of supratemporal canal in populations of *Etheostoma spectabile squamosum*.

Drainage	Posterior infraorbital pores							Supratemporal canal		
	2	3	4	5	corn.	is	X	corn.	n	com.
Grand -----	12	97	66	10	4	189	3.40	146	189	77
Illinois -----	5	132	102	6	7	252	3.44	226	252	90

TABLE 16. Results of experimental crosses between subspecies of *Etheostoma spectabile* (IO=number of pores in the posterior segment of the infraorbital canal, the range followed by the mean; CST=percentage of specimens having a complete supratemporal canal; ASI=anterior scale index; N=number of specimens from which data were taken; T=teratologic development, number of specimens, op=operculum, df=dorsal fins, pvf=pelvic fins; A=*spectabile* from Osage River, Kansas; B=pukhellum from Kansas River, Kansas; C=squamosum from Spring River, Kansas; D=spectabile from James River, Missouri; AB=F₁ generation or progeny of *spectabile* ♂ X *pukhellum* ♀; ABAA=progeny of F₁ ♂, [*spectabile* ♂ X *pukhellum* ♀] X F₁ ♀, [*spectabile* ♂ X *spectabile* ♀],

	A ♂	♀	9	♂	A	AAA	♀	B ♀	♂	BB	BBB	♂	9	♂	B	BAB
IO	2-2:2.0	2-4:2.8	2-3:2.2	1-3:2.1	3-4:3.2	2-4:3.2	2-3:2.3	2-3:2.1	2-4:3.2	2-4:3.2	2-3:2.5	1-4:2.3				
CST	0	2	5	12	8	5	3	0	3	5	3	0				
ASI	5	9	9	7	8	8	4	7	7	8	2	4				
N	2		9	5	3		1		1	7	9	9				
T																

	B ♂	♀	9	♂	A	BABA	AAAB	AABA	BBAB	BBBA	BABB	ABBB	BAAB	ABBA
IO	3-4:3.2	2-3:2.5	2-3:2.1	2-3:2.5	1-3:2.4	2-3:2.8	2-2:2.0	2-3:2.3	2-3:2.4	2-3:2.4	2-3:2.3	1-3:2.0		
CST	3	2		3	3	0	0	0	5	5	0	5		
ASI	8	7	2	3	5	6	9	8	0	0	0	9		
N	5		3	4	9		7	9	9	9	6	9		
T					31, pvf		5, df							

	C ♂	♀	C	♂	9	♂	9	C	♂	D9	D	
IO	3	4:3.7	3-4:3.3	3	2	3:2.9	3	3	3-4:3.5	3	2	3-3:3.0
CST	0	7	0	0	0	0	0	100	50	100	0	40
ASI	8	8	8	8	8	1	9	3.0	1.8	0.5	1.5	1.4
N	1	3	1		1	7		1	2	1	1	5
T								3df:2op				5df