

MISCELLANEOUS PUBLICATIONS  
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 93

**Variation and Systematic Significance of Vertebral  
Counts in the American Fishes  
of the Family Percidae**

BY  
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AND  
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ANN ARBOR  
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN  
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# VARIATION AND SYSTEMATIC SIGNIFICANCE OF VERTEBRAL COUNTS IN THE AMERICAN FISHES OF THE FAMILY PERCIDAE\*

## INTRODUCTION

LONG and successfully used in racial studies of fishes, vertebral counts have also been employed frequently as a taxonomic character at higher systematic levels. Their use has been restricted, however, because of the techniques necessary for determination of vertebral numbers and the resultant damage to museum specimens. The adoption of Roentgen-ray photography, however, by avoiding specimen damage, makes possible extended use of vertebral counts (Gosline, 1948).

Knowledge of vertebral numbers in the American percids has been dependent chiefly on a survey of 20 species of darters by Jordan and Eigenmann (1885). These authors listed a range in counts of 30 to 44. Since no intraspecific variation was noted, it may be surmised that for most if not all species only a single skeleton was examined. Information on vertebral structure and numbers in various Eurasian species of percids was introduced by Boulenger (1895), wherein he repeated the counts of Jordan and Eigenmann. Counts have been reported also for a few additional species by Forbes and Richardson (1909: 300), Hubbs and Raney (1946: 20), and Bailey (1940: 535, and 1948: 82). Gosline (1947: 10) has dealt with vertebral variation within a single large sample of *Etheostoma exile*.

In the present study we have counted representatives of 99 known species of American percids here regarded as valid. Vertebrae have been tabulated for the geographic races of some species, but no attempt has been made to include all subspecies. In our study some 3675 counts were made from X-ray photographs. In addition are the 1000 individuals reported by Gosline (1947) and 188 specimens used in temperature-controlled experiments. In 1936 Hilary John Deason presented to the Graduate School of the University of Michigan his doctoral dissertation on "Morphometric and Life History Studies of the Pike-perches (*Stizostedion*) of Lake Erie." This investigation was carried out for the then U. S. Bureau of Fisheries and has not yet been published. It included a thorough assessment of vertebral numbers in *Stizostedion vitreum* in the lower Great Lakes, and Dr. Deason has generously made this information available for inclusion. Dr. Deason's 550 counts (Table III) were made by dissection. Thus, 5413 vertebral counts are included in the present inquiry.

The over-all range of variation is determined as 32 to 50. Jordan and Eigenmann (1885) recorded 30 vertebrae for *Etheostoma microperca* (as *Microperca punctulata*), a figure which has been frequently quoted. We believe the record to be erroneous since in 22 new counts for the species only

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two have as few as 32 vertebrae. The difficulty in accurate enumeration from a dissection of a small species is readily understandable. It is not unlikely that an undetected vertebral aberration was responsible for the low count. Our maximum count is 48, in *Stizostedion vitreum* and in *Ammocrypta asprella*. Dr. Deason's many counts of the former species have extended this range upward to 50.

This survey of vertebral numbers in the American percids was undertaken in order to (1) discover to what extent these counts are useful in the delimitation of systematic categories; (2) determine whether or not the analysis of counts may throw light on the evolution of the group; and (3) test the practicability of the X-ray method for obtaining large numbers of vertebral counts. As the project developed many unforeseen problems emerged, and it is now obvious that although the investigation yielded fairly satisfactory answers to the original objectives, it raises so many new complexities that it must stand as an introduction rather than an answer to the problem of vertebral variation in the American Percidae.

#### CLASSIFICATION

The generic classification used for darters in this paper follows that presented by Bailey (in Bailey, Winn, and Smith, 1954: 139-41). The other generic names (*Stizostedion* and *Perca*) are used in their conventional sense. The division of each of the three genera of darters into subgenera is original; it is based on otherwise unpublished studies by Bailey that will appear elsewhere. Many of the subgenera are equivalent to groups ranked as genera by recent workers. The composition by species of the several subgenera is clearly indicated in Table I and in the Appendix. Established names are available for most of the groups here designated subgenera. One species that seems not to be intimately allied with or properly placed in any of the other groups may best stand alone. Since no generic or subgeneric name is available it may be christened

#### *Allohistium* Bailey, new subgenus

Orthotype. — *Etheostoma cinerea* Storer.

Diagnosis. — Lateral line straight and complete; infraorbital and supra-temporal canals complete; preoperculomandibular pores 10; vomer with teeth; palatine edentulous; branchiostegal membranes separate; branchiostegal rays 6; preopercle entire; top of head scaleless; cheek and opercle fully covered with ctenoid scales, those of cheek much the smaller; nape, prepectoral area, and breast naked; belly covered with unspecialized, ctenoid scales; body scales moderate (56 to 61 in lateral line); flesh opaque; body rather elongate, slightly compressed; head of moderate length; vertebrae 42; snout considerably produced; premaxillary frenum broad; interorbital area rather narrow and slightly concave; fin rays: dorsal XI or XII-12, anal II, 8, pectoral 14 or 15; first dorsal fin high, the spines without fleshy tips; second dorsal much elevated and rounded distally, extending almost to caudal base in adult; anal spines moderately long and stiff; pelvic fins

separated by 65 to 68 per cent of pelvic fin base; anus not encircled with fleshy villi. The body is lined with brownish above; there are about a dozen blotches on the lateral line; the first dorsal is handsomely variegated with dark and has an orange-brown margin, and the high second dorsal has a prominent rusty brown streak in each interradiation membrane. *Allohistium* appears to be most nearly related to *Nothonotus* and *Oligocephalus*. From these subgenera *Allohistium* differs in the notably elevated second-dorsal fin (hence the name, ἄλλος, "another," and ἱστῖον, a "sail") with distinctive color pattern, the absence of palatine teeth, the more numerous vertebrae (Table I), and the longer snout. From *Nothonotus* it differs further in the presence of a well-scaled cheek, the more terete body, and many features of pigmentation. From *Oligocephalus*, *Allohistium* differs also in the complete lateral line (complete in only two or three species of *Oligocephalus*), and the prominently striped upperparts. A single species, *Etheostoma cinereum* Storer, is referred to *Allohistium*. (Diagnosis by Bailey.)

#### PROCEDURE

The project was initiated during the winter of 1947-48 and greatly extended in 1951-52. X-rays were taken of one or more series of specimens of each species. Vertebral counts were made from the X-ray negatives. As a measure of economy in X-ray film and operator time it was customary to photograph a rather large number of specimens placed in close-ranked rows. Several lots were commonly X-rayed simultaneously. Lead strips placed strategically between the various groups not only served for convenient separation of lots, but furnished clear areas on the film on which to ink permanent recognition data. After records were made the large X-ray sheets were cut up to isolate the lots prior to counting. During the first year's work photographs were taken on over-aged medical X-ray film. Although this film seemed satisfactory at the time we later learned that for X-rays of small fish it was vastly inferior to industrial X-ray film. (Kodak type A and type M alone were used for the work done in 1951-52.) Radiographs were taken at 10 milliamperes and approximately 68 kilovolts with the standard bedside X-ray machine mentioned by Gosline (1948).

Counting was accomplished by passing transmitted light through a ground-glass plate on the stage of a binocular dissecting microscope. In all counts the urostylar vertebra is included. The relatively few individuals with fused vertebrae or other obvious abnormalities are excluded from the tabulations. Counts were taken independently by both authors on each specimen; if either author regarded a specimen as too small or otherwise unsuited to accurate count, it was rejected. If the two counts for a fish were in disagreement they were repeated, and if concordance was still not possible the disputed specimen was eliminated. Failure to agree on counts was usually caused by the difficulty of designation of the anterior vertebra. Counts from nearly 5 per cent of the fish photographed during the first year's work were thrown out because of disagreement, but no warping of the data is believed to have resulted since neither author consistently counted higher than the other.

With the higher quality of the X-ray film during the second period of photographing very few fish were rejected because of failure of agreement in count.

The first vertebra varies considerably in size among the species, but is usually highly consistent in a single species. It usually bears a well-formed, neural spine, but this is typically much shorter than that of the second vertebra. In most species of darters, the first interneural spine lies between the neural spines of the fourth and fifth vertebrae. Though not to be relied on implicitly, since occasional fish deviate, this characteristic position provides a useful check on the proper determination of the first vertebra in fish X-rayed in lateral view — as most of ours were. The species of *Ammocrypta* normally have the first interneural spine farther back, as do a few species of *Percina*, and in *Etheostoma punctulatum* the first interneural usually lies between the neural spines of the third and the fourth vertebrae.

Specimens of two types of vertebral aberrations were discarded from our counts. In one type, a block of two or more adjacent vertebrae apparently had been badly injured in early life and had subsequently regenerated; centra are too few and neural spines too numerous for a normal area, and both spines and centra may be malformed and out of position. Such regions may occur anywhere along the column, and two or more of them may be present in the same fish. If such an aberration caused any doubt as to the normal vertebral number it was rejected. The second type has a normal column except that one of the three vertebrae preceding the urostyle is incomplete. All grades of incompleteness can be found, from vertebrae that are almost whole to ones that are rudimentary. We have eliminated counts as "abnormal" only if the aberrant vertebrae are approximately half-developed, i.e., those giving rise to a question in counting to the nearest whole number.

Experience adds to competence in identification of vertebral characters in fishes, for example in distinguishing the first vertebra, and in the detection of minor vertebral aberrations. By and large the vertebral count is a highly objective enumeration, basically more accurate than most fin-ray and scale counts. Usually, too, it is much less variable than other meristic characters.

As Gosline (1947: 4) has noted in *Etheostoma exile*, it is usually impossible to distinguish between precaudal and caudal vertebrae in X-rays of darters. An arbitrary segregation, such as that of rating as caudal vertebrae those in which the haemal spines lie posterior to the first anal interhaemal spine, has the obvious disadvantage that the definitive element is extrinsic and to some extent unrelated. In some species, for example those with very short and weak anal spines, the interhaemal spines are also short and do not extend as far as the tips of the haemal spines. In these species even the arbitrary definition mentioned above fails. For these and other reasons we have recorded only total vertebral counts.

Significance diagrams (Figs. 2-4) are used to portray the variation in vertebral number among various samples. The method is adapted with minor change from the proposal by Hubbs and Hubbs (1953). In each diagram the horizontal lines show ranges in vertebral count, the small inverted triangles indicate the means, the open plus the shaded rectangles

comprise one standard deviation on each side of the mean, and the shaded rectangles designate two standard errors on each side of the mean.

#### VERTEBRAL NUMBER AS A SYSTEMATIC CHARACTER

The data (Table I) demonstrate the value of vertebral counts in the taxonomy of the Percidae. Like most other structural features in the group, however, the variation in count from population to population, from species to species, and from genus to genus is gradual, more or less continuous or overlapping, and is noteworthy for the rarity of wide gaps. Thus, the pattern of variation in vertebral number lends support to the interpretation that the darters constitute a closely interrelated and relatively recent group.

The variation of vertebral numbers in the American genera is charted in Figure 1. *Stizostedion* and *Perca* (subfamily Percinae) are seen to differ notably from one another, normally having 44 to 49 and 39 to 42 vertebrae respectively, but these figures overlap broadly the counts for the other genera (subfamily Etheostomatinae). The individuals of *Stizostedion* having fewer than 43 or 44 vertebrae (Table III) are infrequent in number and possibly anomalous or teratological. The genus *Percina* has approximately the same range in vertebral numbers as do the slim, translucent sand darters, *Ammocrypta*, which may plausibly be regarded as derivatives of a *Percina*-like ancestor. *Ammocrypta* (*Crystallaria*) *asprella*, largest of the sand darters, has the maximum number of vertebrae (45 to 48) in the subfamily. The only overlap with any species of the subgenus *Ammocrypta* is at 45, the infrequently encountered maximum in *A. pellucida*. As might be expected, *Etheostoma*, the most varied genus of the Percidae and the largest, containing over 70 per cent of the American species, has the greatest range of vertebral count, 32 to 44. Few of the species (most of these in the nominate subgenus) ever have more than 40 vertebrae, and the majority have 38 or fewer, the minimum modal number in any species of the other genera.

Darters that appear to be generalized in most other characters are typified by having about 41 to 45 vertebrae. To be sure, a few species in this range are notably specialized in one or more other ways, but the conclusion seems obvious that this number closely approaches the starting point for the generalized ancestral darter. We shall return to this point.

*Percina*, with 20 described species, is second only to *Etheostoma* in number of forms. The eight subgenera when arranged in an attempted sequence of increased specialization (Fig. 1) show an irregular reduction from about 43 to 45 vertebrae in *Hypohomus* and *Alvordius* to 38 to 40 in the terminal groups. Reduction of vertebrae appears to be the more common direction of change in the subfamily. Rather high counts in four species of the subgenera *Swainia* and *Percina* (Table I) may be the result in part of a secondary increase or may indicate these subgenera to be generalized in this respect.

In *Etheostoma* as in *Percina* the more generalized species usually have more vertebrae (about 39 to 43) than do the presumably derivative species. However, because of the complex arborescence of the phyletic descent no simple linear trend can be depicted (Fig. 1). Those forms of the subgenera *Boleosoma* and *Etheostoma* with 39 to 43 vertebrae appear to be the least

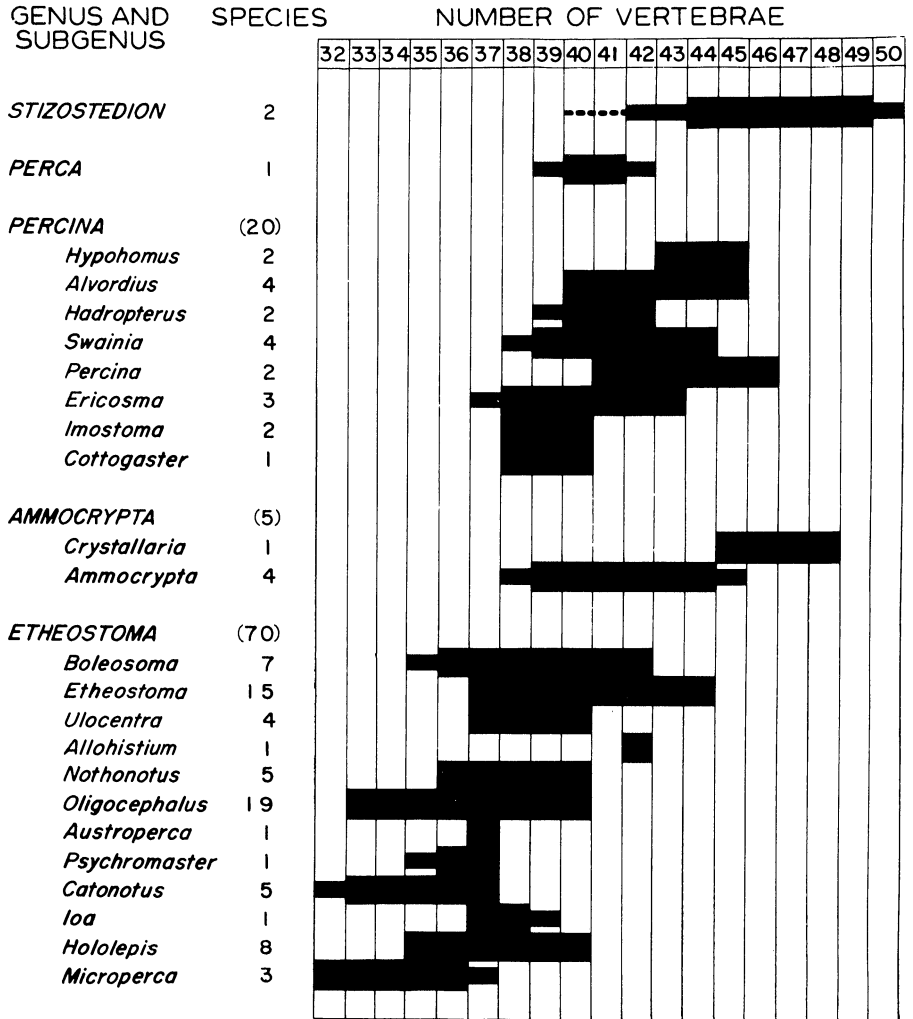


Fig. 1. Vertebral numbers in the genera and subgenera of American percids. Broad bars indicate normal or frequent counts in any species; narrow bars signify infrequent numbers, i.e., those encountered in no more than 10 per cent of any sample studied. A dashed line is employed for rare counts that are perhaps abnormalities.

modified members of the genus, though even in these subgenera there are some species [i.e., *Etheostoma (Boleosoma) chlorosomum* and *E. (Etheostoma) blennioides*] that are much specialized in certain characters. The subgenera *Oligocephalus*, *Catonotus*, *Hololepis*, and *Microperca* include many of the most highly modified darters, and in these groups vertebral numbers have been reduced to the minimum for the subfamily.

Within subgenera there is marked cohesion among the constituent species. Though often not of high value as a specific character, the counts are of evident utility in helping to assess relationships, to decipher phylogeny, and to corroborate or to contradict findings based on other structures or criteria.

One of the primary motivating stimuli for this study was the expectation that vertebral count would yield another and presumably valuable tool to the taxonomist in the discrimination of species, a hope that seemed to be fulfilled at the time of our preliminary work on this study in 1948, when we had already made over 1600 counts. Our earlier confidence has now largely vanished for the following reason. The initial procedure was to take X-rays and compare counts usually of single series of each species. The many marked differences found were misinterpreted as being reliable specific distinctions. Through the prior work of Gosline (1947) we were cognizant of the limited extent of individual and sexual variation, and despite our preliminary study of geographic variation in *Percina caprodes* and *Etheostoma flabellare*, in both of which marked geographic differences were detected, we failed to appreciate the extent to which specific differences are masked by this type of variation. This is not to say that vertebral count has no value in the identification of species. Careful scrutiny of Table I reveals a number of examples of related species (i.e., *Ammocrypta clara* and *A. pellucida*; *Etheostoma proeliare* and *E. microperca*) that can be distinguished with confidence on the basis of vertebral count. But geographic variation is so pronounced in most if not all of the wide-ranging species (see pp. 24-32), that the character should be employed with great caution at the species level.

#### BODY FORM, SIZE, AND VERTEBRAL NUMBER

Attenuation of the body may be correlated with an increase in vertebral number, as in those fishes that employ a sinuous method of locomotion (e.g., eels), or by a relative elongation of the vertebrae (e.g., *Fistularia*). The most attenuate darters are the species of *Ammocrypta*, one of which (*asprella*) has the maximum vertebral count in the subfamily. Other rather slender species such as *Percina caprodes* and *P. squamata* also may have many vertebrae (41 to 46). However, the slimmest of all percids, *Ammocrypta beani*, has only 40 or 41 vertebrae, and a rather slender species such as *Etheostoma kennicotti* averages 34. Several relatively stocky species commonly have 40 or more. A few slender darters (e.g., *Etheostoma chlorosomum*) have more vertebrae than closely related species that are more generalized. Although, on the average, slender species probably exceed robust ones slightly in vertebral number, little causal significance is attached to this relationship. The form of the vertebrae, however, bears a

TABLE I  
FREQUENCY DISTRIBUTION OF VERTEBRAL COUNTS  
IN THE AMERICAN SPECIES OF PERCIDAE

Taxon	Catalogue Number <sup>1</sup>	State	Number of Vertebrae														No.	Mean	S. D.		
			36	37	38	39	40	41	42	43	44	45	46	47	48						
<i>Stizostedion vitreum vitreum</i>	UM 101531	Iowa															1	14	46.79	.70	
	UM 110367	Mich.															10	13	46.77	.44	
<i>vitreum glaucum canadense</i>	UM 112186	Mich.															2	5	46.40		
	UM 115964	Ohio															2	4	45.75		
	UM 157232	Ohio															1	3	47.33		
	UM 100906	Iowa																3	3	45.00	
<i>Perca flavescens</i>	UM 139849	Ind.																2	4	44.50	
	UM 139943	Ind.																2	2	45.00	
	UM 139955	Ind.																1	2	44.67	
	UM 122547	Ala.																2	3	44.33	
	UM 126979	Maine																1	17	40.94	.43
	UM 67239	Mich.				1	2	14	1									1	27	40.00	.28
<i>Percina (Hypohomus) aurantiaca</i>	UM 103446	Va.																	1	44.00	
	UM 129300	Tenn.																1	1	45.00	
<i>cymatotaenia</i>	UM 129431	Tenn.																1	1	45.00	
	UM 156985	N. C.																3	5	44.60	
	UM 151955	Mo.																1	1	44.00	
	UM 111335	Mo.																1	1	44.00	
	UM 102529	Mo.																1	1	43.00	
<i>(Alvordius) macrocephala maculata notogramma</i>	UM 152214	Mo.																	1	44.00	
	UM 142315	Mo.																	1	44.00	
	UM 142322	Mo.																1	1	44.50	
	UM 152366	Mo.																1	1	45.00	
	UM 96879	Va.																3	3	45.00	
<i>maculata</i>	US 63778	Ky.																	2	44.00	
	UM 60034	Mich.																11	16	42.81	.54
<i>notogramma</i>	UM 104450	Mich.																1	6	42.83	
	UM 160879	Ala.																6	7	43.14	
	UM 144697 and CU 9708	Va.																1	10	43.40	.84
	CU 8324	Va.																3	4	43.25	
	UM 102326	Va.																12	13	41.08	.28
	CU 10528	Va.																2	2	41.00	



	CU 10527	Va.				1	1						2	40.50	
	CU 10193	Va.						3	1				4	42.25	
<i>peltata peltata</i>	UM 109755	N. Y.						6	11	2			19	42.79	.63
<i>peltata nevisensis</i>	CU 11928	Va.							5	3			8	43.38	
	CU 20765	Va.							6	2			8	43.25	
( <i>Hadropterus</i> )															
<i>sciera</i>	UM 137916	Okla.				2	13	3					18	41.06	.54
<i>nigrofasciata</i>	UM 146616	Miss.		1		11	7						19	40.32	.58
( <i>Swainia</i> )															
<i>phoxocephala</i>	UM 81385	Ind.			7	3							10	39.30	.48
	UM 149382	Mo.	1	21		6							28	39.18	.48
<i>nasuta</i>	UM 137133	Ark.				3	1						4	40.25	
	UM 137914	Okla.				4							4	40.00	
<i>oxyrhyncha</i>	UM 118482	Va.						2	1				3	42.33	
	UM 131829	W. Va.						1					1	42.00	
	UM 131830	W. Va.						1					1	42.00	
<i>squamata</i>	UM 156239	N. C.							1				1	43.00	
	UM 156980	N. C.								1			1	44.00	
( <i>Percina</i> )															
<i>caprodes semifasciata</i>	UM 146739	Iowa					11	13					24	41.54	.51
	UM 78038	Wis.					4	14	7	1			26	42.19	.75
	UM 133368	Mich.						14	16	1			31	42.58	.56
	UM 81622	Mich.						20	1				21	42.05	.22
	UM 81612	Mich.					3	20	1				24	41.92	.41
	UM 87740	Mich.					5	20	3				28	41.93	.54
	UM 81731	Mich.					2	25	1				28	41.96	.33
	UM 81665	Mich.					6	22	5				33	41.97	.59
	UM 98611	Mich.						1	15	15	3		34	43.59	.70
	UM 59574	Mich.					1	5	9	1			16	42.63	.72
	UM 111880	Mich.						3	15	5	2		25	43.24	.78
	UM 145071	Mich.						1	4	1			6	43.00	
	UM 67184	Mich.						2	14	9			25	43.28	.61
	UM 92219	Mich.					1	4	14	6			25	43.00	.76
	UM 81976	Mich.					1	..	5	10	8		24	44.00	.98
	UM 98078	Mich.							15	12			27	43.44	.51
	UM 99065	N. Y.							10	5			15	43.33	.49
	UM 104590	Ont.						9	23	1			33	42.76	.50
	UM 158976	Md.					1	5					6	41.83	
<i>caprodes; caprodes x semifasciata</i>	UM 63049	Ind.							7	14	5		26	43.92	.69
	UM 118508	Ohio					1	..	5	3	1		10	43.30	1.06
<i>caprodes caprodes</i>	UM 105434	Tenn.								7	7	2	16	44.69	.70
	UM 154611	and													
	UM 154612	Tenn.									2		2	45.00	
	CU 20686	Va.										1	1	46.00	

TABLE I (Continued)

Taxon	Catalogue Number	State	Number of Vertebrae													No.	Mean	S. D.
			36	37	38	39	40	41	42	43	44	45	46	47	48			
<i>caprodes carbonaria</i>	UM 123064	Ark.									4	14				18	43.78	.43
	UM 160878	Ala.									1	10	1			12	44.00	.43
<i>rex</i>	CU 8453	Va.											1	1		2	45.50	
	US 154653	Va.												3		3	45.00	
	CU 11560	Va.												1		1	45.00	
	CU 20766	Va.												2		2	45.00	
	CU 16910	Va.										1	1			2	44.50	
<i>(Ericosma) palmaris</i>	UM 111233	Ala.					4	3								7	40.43	
	UM 160896	Ala.					2	2								4	40.50	
<i>evides</i>	UM 157978	Ga.					1	11								12	40.92	.29
	UM 167077	Ind.			3	7										10	38.70	.48
<i>crassa crassa</i>	CU 14084	N. C.					2	19	10							31	41.26	.58
	CU 10994	N. C.							2	1						3	42.33	
	CU 10881	N. C.							2	3						5	42.60	
<i>crassa roanoka</i>	CU 8541	N. C.		1	8	6										15	38.33	.62
	UM 156665	N. C.			1	4										5	38.80	
	CU 18631	N. C.			2	4										6	38.67	
	CU 16915	Va.			1	13	1									15	39.00	.38
	CU 11631	Va.				27	23	1								51	39.50	.54
	UM 158999	Va.					3	1								4	40.25	
	CU 18627	Va.					20	3								23	40.13	.36
	<i>(Imostoma) shumardi</i>	UM 76804	Wis.			1	13	3									17	39.12
UM 81563		Mich.			1	3	1									5	39.00	
<i>uranidea</i>	UM 122637	Ala.			2	3										5	38.60	
	UM 122707	Ala.			1	1										2	38.50	
	UM 153134	Mo.				2										2	39.00	
	UM 153259	Mo.			1	2										3	38.67	
	<i>(Cottogaster) copelandi</i>	UM 85919	Ont.			12	9	1									22	38.50
UM 91349		Mich.			2	4	1									7	38.86	
<i>Ammocrypta (Crystallaria) asprella</i>	UM 76823	Wis. Minn.												1	3	4	47.75	
	UM 113449	Miss.													1	1	48.00	
	UM 128481	Ark.											3	3		3	46.00	
	UM 167598	La.											3	1		4	45.25	
												1			1	45.00		

<i>(Ammocrypta)</i> <i>vivax</i>	UM 111226	Ala.							3	2						5	42.40	
	UM 157816	Miss.						5	14	1						20	41.80	.52
<i>pellucida</i>	UM 117429	Mo.							1	7		1				9	43.00	
	UM 66562	Ind.							2	4		3				9	43.11	
	UM 104381	Mich.							1	1		1				3	43.00	
<i>clara</i>	UM 146691	Que.								5	12			1		18	43.78	.55
	UM 76089	Wis.				12	14									26	39.54	.51
	UM 148570	Mo.		1		11										12	38.92	.29
<i>beani</i>	UM 149952	Mo.				1										2	39.50	
	UM 134623	Fla.														5	40.00	
	UM 155484	Fla.														6	40.33	
	UM 155344	Miss.							16	10						26	40.39	.50

Taxon	Catalogue Number	State	Number of Vertebrae													No.	Mean	S. D.	
			32	33	34	35	36	37	38	39	40	41	42	43	44				
<i>Etheostoma</i> <i>(Boleosoma)</i> <i>nigrum olmstedii</i> <i>nigrum nigrum</i> <i>nigrum eulepis</i> <i>perlongum</i> <i>chlorosomum</i>	UM 158978	Md.						5	21	6							32	38.03	.60
	UM 82364	Mich.						4	18	6							28	38.07	.60
	UM 77054	Wis.						12	19	1							32	37.66	.55
	UM 138476	N. C.								3		10	1	1			15	40.00	.76
	UM 110543	Tex.										5	5				10	39.50	.53
	UM 130081	Ill.								3	29	8					40	39.13	.52
	UM 103591	Tenn.										4	3				7	40.43	
	UM 104339	Tenn.										13	39	2			54	40.80	.49
	UM 154704	and											10	25	4		39	40.85	.59
	UM 154705	Ky.										6	7	1			14	39.64	.63
UM 139667	Mo.										2	10	5			17	40.18	.64	
UM 137865	Okla.											4	14	1		19	38.84	.50	
UM 155359	Miss.											1	3			4	39.75		
UM 111231	Ala.											2	3			5	39.60		
UM 124039	Ala.											7	16	1		24	38.75	.53	
UM 139154	Ala.											1	5	2		8	39.13		
UM 155483	Fla.											2	3			5	37.60		
<i>longimanum</i>	UM 95164	Va.						2	3							5	37.60		
	UM 95179	Va.						7	12	1						20	37.70	.57	
<i>podostemone</i>	UM 135399	Va.								2						2	38.00		
	UM 95321	Va.					3	14	2							19	36.95	.52	
	UM 159000	Va.				1	5	14	2							22	36.77	.69	





TABLE I (Continued)

Taxon	Catalogue Number	State	Number of Vertebrae												No.	Mean	S. D.
			32	33	34	35	36	37	38	39	40	41	42	43			
<i>swaini</i>	UM 155375	Miss.					7	9							16	36.56	.51
	UM 155453	Miss.					6	7							13	36.54	.52
	UM 155246	Ga.					2	1							3	36.33	
	UM 110973	Fla.				2	2								4	35.50	
	UM 158205	Fla.				2									2	35.00	
<i>mariae</i>	UM 156983	N. C.					1	53	16						70	37.21	.45
<i>juliae</i>	UM 152018	Mo.				1	10								11	35.91	.30
	UM 152095	Mo.				2	8								10	35.80	.42
<i>punctulatum</i>	UM 151096	Mo.						7		2					9	37.22	
	UM 160396	Kan.					2	3							5	36.60	
	UM 137866	Okla.					8	5							13	36.39	.51
<i>parvipinne</i>	UM 88336	Ga.					1	4		1					6	37.00	
	UM 161055	Miss.					1	1							2	36.50	
	UM 161109	Miss.					1	2		1					4	37.00	
	UM 113867	Miss.					1	..		2					3	37.33	
	UM 161217	Miss.					2	2							4	36.50	
<i>caeruleum</i>	UM 66539	Mich.					14	11							25	36.44	.51
	UM 103284	Mich.				1	14	19		1					35	36.57	.61
<i>cragini</i>	UM 151432	Mo.			2	3	1								6	34.71	
	UM 156694	Kan.		7	16	2									25	33.80	.58
	UM 160409	Kan.		2	5										7	33.71	
<i>pottsi</i>	UM 161675	Mex.			1	4	13								18	35.67	.59
	US 38245	Mex.				1									1	35.00	
	US 125107	Mex.				1									1	35.00	
	US 55855	Mex.				4	4		2						10	35.80	.79
<i>exile</i>	UM 159978	Wyo.							5	8					13	37.62	.51
	UM 137775 <sup>2</sup>	Mich.			1	3	55	435	445	56	5				1000	37.51	.73
<i>luteovinctum</i>	UM 121123	Tenn.					3	15	2						20	36.95	.51
	UM 132708	Tenn.					1	5	1						7	37.00	
<i>grahami</i>	UM 120322	Tex.					2	4							6	36.67	
	UM 162135	Mex.					14	5							19	36.26	.45
<i>spectabile spectabile</i>	UM 159858	Ohio				4	27	4							35	36.00	.49
	UM 152930	Mo.				4	25	6							35	36.06	.54
<i>spectabile pulchellum</i>	UM 160459	Kan.				12	14	2							28	35.64	.62



TABLE I (Continued)

Taxon	Catalogue Number	State	Number of Vertebrae													No.	Mean	S.D.	
			32	33	34	35	36	37	38	39	40	41	42	43	44				
( <i>Hololepis</i> )																			
<i>edwini</i>	UM 107047	Fla.								2							2	38.00	
	UM 158182	Fla.						1	1								1	37.00	
	UM 158204	Fla.					1	1	1								2	36.50	
	UM 110972	Fla.					1	1	1								3	37.00	
	UM 155506	Fla.			1		1	5									7	36.57	
<i>serriferum</i>	UM 107055 and																		
	UM 107067	N. C.								1	5						6	39.83	
	UM 107063	N. C.								1	4						5	38.80	
	UM 94658	N. C.								1							1	38.00	
<i>zoniferum</i>	UM 124012	Ala.					1	3	4	2							10	37.70	.95
<i>gracile</i>	UM 154781	Ky.					1	4	5								10	37.40	.70
<i>fusiforme fusiforme</i>	UM 107087	Mass.											7	1			8	39.13	
<i>fusiforme erochroum</i>	UM 109565	N. J.							4	16	2						22	37.91	.53
<i>barratti</i>	UM 155201	S. C.							2	7	9	1					19	38.47	.77
	UM 107083	S. C.							1	2	3						6	38.33	
<i>saludae</i>	UM 109104	S. C.						1									1	36.00	
<i>collis</i>	UM 94546	S. C.						1									1	36.00	
( <i>Microperca</i> )																			
<i>proeliare</i>	UM 146493	La.				2	2										4	35.50	
	UM 146617	Miss.					3										3	36.00	
	UM 152995	Mo.			6	15	1										22	34.77	.53
	UM 153258	Mo.			1	19	31	1									52	35.62	.57
<i>microperca</i>	UM 88956	Mich.	2	11	1												14	32.93	.47
	UM 88966	Mich.		7	1												8	33.13	
<i>fonticola</i>	UM 111007	Tex.	4	4													8	32.50	
	UM 160752	Tex.	1	6													7	32.86	

<sup>1</sup> Specimens in Cornell University are indicated by CU, those in the University of Michigan Museum of Zoology by UM, those in the United States National Museum by US.

<sup>2</sup> In his counts of *Etheostoma exile*, Gosline (1947) excluded the urostylar vertebra; we here adjust his figures to agree with our method of enumeration.



clear dependence on body shape. This phenomenon is seen to best advantage in *Ammocrypta*, the species of which are interpreted, figuratively, as attempting to stretch their bodies. They are also characterized by the most attenuate vertebral centra in the subfamily. The foremost vertebra, or atlas, in particular is long, in sharp contrast to its foreshortened condition in such chunky, shortheaded darters as *Etheostoma simoterum*.

In the American percids a highly significant relationship seems to exist between vertebral count and adult size. Of the larger percids *Stizostedion vitreum* usually has 46 to 48 vertebrae, *S. canadense* has 44 or 45, and *Perca flavescens* 40 or 41; these are in direct proportion to the size of the fishes. The largest darters include *Percina caprodes* and *P. rex* (usually 42 to 45 vertebrae), *Ammocrypta asprella* (45 to 48), *Percina aurantiaca* (44 or 45), and *Etheostoma blennioides* (41 to 43). At the other extreme are *Etheostoma tippecanoe* (36), *E. cragini* (33 to 35), *E. pottsi* (35 or 36), *E. kennicotti* (34), *E. proeliare* (35 or 36), *E. microperca* (33), and *E. fonticola* (33). If it were possible to devise an adequate expression of average size, this figure plotted against mean vertebral count would depict clearly the high positive correlation, though there would be frequent notable deviations.

Those percids, especially darters, believed to be generalized are relatively large and moderately slender. Evolution in the group is characterized by apparent size reduction along all major phyletic lines and by seemingly random modification of body form. Decreased size is apparently, and probably causally, correlated with reduction in vertebral number. Increase in attenuation within the group appears to be primarily or entirely associated with elongation of the vertebral centra, rather than with increase in vertebral number; deepening of the body is marked by some foreshortening of the vertebrae.

#### VARIATION WITHIN SAMPLES

Significant sexual differences in vertebral numbers among darters are probably nonexistent. In the sample of *Etheostoma exile* examined by Gosline (1947: 5), 495 males had a mean of 37.51 vertebrae, 505 females 37.50. In other species no critical analysis has been made, but we have no evidence that there is any difference.

All of our 143 samples with more than 9 specimens show some variation in vertebral count; the minimum standard deviation obtained is 0.22 (Table I). On the other hand, the variability is never great. Two consecutive units account for a large majority of the enumerations in any homogeneous sample, and our maximum standard deviation is only 1.06. Between 0.22 and 1.06 the samples fluctuate erratically.

Several reasons for these fluctuations may be considered. One is that certain species may have a consistently higher variability than others. But since both our maximum and minimum standard deviations come from samples of the same species (*Percina caprodes*), this possibility does not seem to have much validity. In general, there is a slight tendency for those samples and those species with higher average vertebral counts to have greater variability, but this tendency is badly obscured by other factors.

Second, it is possible that samples derived from a very few parents may show less variability than those derived from larger parental populations. The offspring of the three pairs of parents of *Etheostoma nigrum* raised experimentally (Table II, matings 177, 181, and 183) give some check on this. The average standard deviation for a progeny of these brothers and sisters raised at a single temperature is 0.48. Yet the average standard deviation of three wild-population samples of the same species (Table I) is only 0.58; the average standard deviation of all wild samples of the subgenus *Boleosoma* (to which *E. nigrum* belongs) is also 0.58 and for all wild samples of *Etheostoma*, 0.55. Thus the progeny of a single parental pair shows roughly five-sixths as much variability as the average wild-population sample; indeed the variability in 22 out of our 95 samples of *Etheostoma* is less than that shown between siblings in these experimentally-raised broods.

Matings 177, 181, and 183 (Table II) were made between six individuals taken at the same place and time. Yet the combined offspring of these six parents grown at 60°F. give a standard deviation of 0.58 (those raised at 70°F. also give 0.58), which is equal to the average variation of wild samples of the subgenus *Boleosoma*. The conclusion seems to follow that only a few parents may provide the amount of variation found in the usual wild population. (This does not mean that the progeny of every pair of parents has a roughly similar mean count. Indeed, the offspring of matings 177 and 183 show an average difference of about 0.8 vertebrae.)

A third factor which may affect the amount of sample variation is selection pressure. If we assume that an optimum number of vertebrae is selected by the environment, then the amount of variation will decrease with increased selection pressure. Certain data seem to bear on this question. The sample of 1000 specimens of *Etheostoma exile* (Gosline, 1947) came from a hatchery pond in which, because of the apparently optimum environmental conditions prevailing and because of the relatively large number of deformed specimens surviving, selection pressure was thought to have been unusually low. This sample had a standard deviation of 0.73. For our 26 samples of the subgenus *Oligocephalus* (to which *E. exile* belongs), the average standard deviation is 0.52, and for all samples of *Etheostoma* 0.55, as already stated. Thus, this sample did have a higher than average variability; in fact only 8 of 95 *Etheostoma* samples show greater variation. It is possible, however, that some factor other than low selection pressure caused this high variability even though no such factor is apparent.

Finally, when two populations with different mean vertebral counts become lumped in a sample the variability of that sample will go up. Though such lumping did not seem evident in our samples (which are all homogeneous), it is presumably at least one of the factors causing the high variability in Deason's *Stizostedion* data.

The average percentage of counts discarded as "aberrant" from 1952 samples with more than nine normal specimens is 4.9, or about one in 20. The samples fluctuated from no discards in a sample of 70 (*Etheostoma mariae*) to 10 "abnormal" specimens out of 35, or 29 per cent (*Etheostoma cragini*).

The possibility that samples with a mean count half way between two units may have more abnormal vertebrae than those with a mean count

about at a unit, say at 38.01, was briefly investigated and rejected. Nor could any relationship be found between either the mean or the standard deviation and the number of "abnormal" specimens. The possibility that some subgenera or genera might have a greater tendency to produce abnormal specimens than others was also investigated. However, no clear relationship was apparent. Both the highest and the lowest amount of "abnormality" was observed in samples of the same subgenus of *Etheostoma* (*Oligocephalus*). Nevertheless, most of the samples with an unusually high percentage of abnormalities do come from *Oligocephalus*. Possible correlation between geography and the number of aberrations was checked. Though lots with a high percentage of abnormal specimens are from widely scattered areas, a high concentration of these is from Oklahoma, Kansas, and Mexico. Some relationship between regional hydrography and the formation of abnormal vertebrae may be indicated. Whether pollution or other local aspects of hydrography have any relation to the development of vertebral abnormalities in American percids is impossible to determine from our data.

TABLE II  
 FREQUENCY DISTRIBUTION OF VERTEBRAL COUNTS  
 IN SPLIT SIBSHIPS OF *ETHEOSTOMA NIGRUM\**

Subspecies and Mating Number	Temperature (F.)	Uncounted because of vertebral aberrations	Number of Vertebrae				No.	Mean	S. D.	P†
			37	38	39	40				
<i>E. n. nigrum</i> 59	60°	2	1	12	7	..	20	38.30	0.57	
	70°	0	..	14	1	..	15	38.07	0.27	
	Combined	2	1	26	8	..	35	38.20		
177	60°	1	..	2	6	..	8	38.75	0.46	
	70°	1	..	5	5	1	11	38.64	0.67	
	Combined	2	..	7	11	1	19	38.68		
181	60°	4	..	6	9	..	15	38.60	0.51	
	70°	1	..	7	2	..	9	38.22	0.44	
	Combined	5	..	13	11	..	24	38.46		
183	60°	3	2	13	1	..	16	37.94	0.44	
	70°	0	5	22	..	..	27	37.81	0.40	
	Combined	3	7	35	1	..	43	37.86		
<i>E. n. eulepis</i> 138	60°	2	2	27	6	..	35	38.11	0.46	
	70°	4	12	18	2	..	32	37.69	0.59	
	Combined	6	14	45	8	..	67	37.91		

\*See Appendix for source of parental stocks.

†Probability that the vertebral differences between the two temperature lots from a mating should have occurred by pure chance.

## EXPERIMENTAL MODIFICATION OF VERTEBRAL NUMBER

The influence of temperature on vertebral number has been shown for several nonpercid fishes by Gabriel (1944), Tåning (1944 and 1952), and included references. Though no extensive experiments have been carried out on percids, the following preliminary data have been made available to us by Dr. Karl F. Lagler. For each of five matings of *Etheostoma nigrum* the eggs were separated into two groups as soon as possible after oviposition and exposed to temperatures of  $60 \pm 2^{\circ}$  F. ( $15.5^{\circ}$  C.) and  $70 \pm 2^{\circ}$  F. ( $21.1^{\circ}$  C.), respectively, until or after hatching. The eggs of mating 159 were less than 3 hours old (time since last previous examination) when separated; those of mating 183 less than 5 hours, of mating 138 less than 8 hours, and of matings 177 and 181 less than 12 hours old. (Tåning, 1946, has reported that in sea trout, and supposedly in teleosts generally, the number of vertebrae is determined early in ontogeny, prior to hatching. In fact most of the tangible effect of modification occurred during the first half of the incubation period, or within 170 day-degrees (C.), when hatching takes place at about 400 day-degrees.) Vertebral counts for the five sibships in *E. nigrum* are given in Table II. The number of young reared is regrettably low; nevertheless, in all five sibships those fish which developed at the lower temperature have the higher mean count. In the several broods the mean differences range from 0.11 to 0.42 vertebra, of which only that for mating 138 is statistically significant. The fact, however, that the five vertebral differences are consistently in the same direction adds up to a virtual certainty that temperature does affect the number of vertebrae in these samples of *Etheostoma nigrum*. Indeed, when all five samples are combined in an analysis of variance, the probability that the vertebral differences between the  $60^{\circ}$  and  $70^{\circ}$  samples occurred by pure chance is less than one in a thousand.

Thus, temperature differentials during early ontogeny may modify the number of vertebrae in darters. Within the framework of the experiment here reported, the amount of modification is not great. Under conditions obtaining in nature perhaps greater influence may at times be exerted, and quite possibly, additional contributory environmental factors remain to be identified.

GEOGRAPHIC VARIATION WITH A DISCUSSION OF ITS  
POSSIBLE CAUSES

That the geographical variation in vertebral number within species of darters is so great as to minimize the usefulness of the vertebral count as a distinguishing character between species has been alluded to above. Indeed, by selecting certain geographically separated samples within species we could demonstrate a more significant statistical difference in count than usually occurs between related species (Figs. 2-4).

This geographical variation is presumably in part an expression of genetic differentiation between populations, but also in part due to differences between the environments in which the eggs of the various populations develop. We are unable to say how much of this geographic variation is due to environ-

mental and how much to inherited causes, nor are we able to demonstrate exactly how the environmental influences affect the phenotype. We have, however, examined our data for possible correlations between vertebral number and geography and have tried to use these to set up certain working hypotheses concerning the biological causes of geographic variation.

An examination of the counts in certain species indicates a south to north increase in vertebrae. Thus, in *Ammocrypta asprella* 8 specimens from Mississippi, Louisiana, and Arkansas have 45 or 46 vertebrae, whereas 5 specimens from Wisconsin and Minnesota have 47 or 48 vertebrae (Table I). By carefully choosing samples from other species the same sort of trend may be demonstrated. On the other hand, our samples of other species almost equally often indicate an increase in vertebrae from north to south. For example, a sample of 10 specimens of *Percina evides* from Indiana has a mean count of 38.7 whereas 11 specimens from Georgia have a mean of 40.9. Again, a series of 20 specimens of *Etheostoma blennioides* from Ontario has an average vertebral number of 41.2; 18 specimens from Tennessee have a mean of 43.3. Obviously, any attempt to associate changes in vertebral count with latitude alone would fail.

A somewhat more consistent geographical trend is toward an increased number of vertebrae from west to east (perhaps more correctly from southwest to northeast). Forms for which our data show a definite increase of this sort (Table I) are: *Perca flavescens* (average count of 40.0 from a Michigan sample, 40.9 from Maine); *Percina caprodes semifasciata* (lowest average of 41.5 from Iowa, mean sample counts ranging from 41.9 to 44.0 from Michigan, and 43.3 in New York); *Ammocrypta pellucida* (average 43.1 in Indiana, 43.8 in Quebec); and *Etheostoma flabellare flabellare* (with the lowest count of 34.0 from Indiana and the highest of 35.9 from West Virginia). Other species showing a similar geographic trend but less well-marked vertebral differentiation are *Percina phoxocephala*, *Etheostoma nigrum*, and *E. proeliare*. Only in *Etheostoma maculatum*, in which the lowest average count is from Pennsylvania and the highest from Tennessee, do our data suggest a reverse trend, i.e., an increase in vertebrae from east to west. In this species, however, the gradient is more strictly north to south than east to west. In sum, then, there appears to be a real increase in the number of vertebrae in many darter species from west (or southwest) to east (or northeast). A similar southwest to northeast increase in the number of vertebrae was found in preliminary investigations of the cyprinid *Notemigonus crysoleucas* by Gosline (1948). The biological significance, if any, of this gradient remains unknown.

One of the features that obscures any simple, over-all geographic pattern is the large variation in vertebral count that often occurs within areas, e.g., within a state. Our means of 14 samples of *Percina caprodes semifasciata* from Michigan range from 41.9 to 44.0 and only one of four samples from Iowa, Wisconsin, New York, and Ontario has a mean outside this range. Again, Virginia samples of *Percina notogramma* differ from one another in average count by as much as 2.3 vertebrae, North Carolina samples within *P. crassa crassa* by 1.3 vertebrae, and Missouri lots of *Etheostoma tetrazonum* by 1.4. Obviously, some relatively local phenomenon is acting to differentiate the various populations of darters.

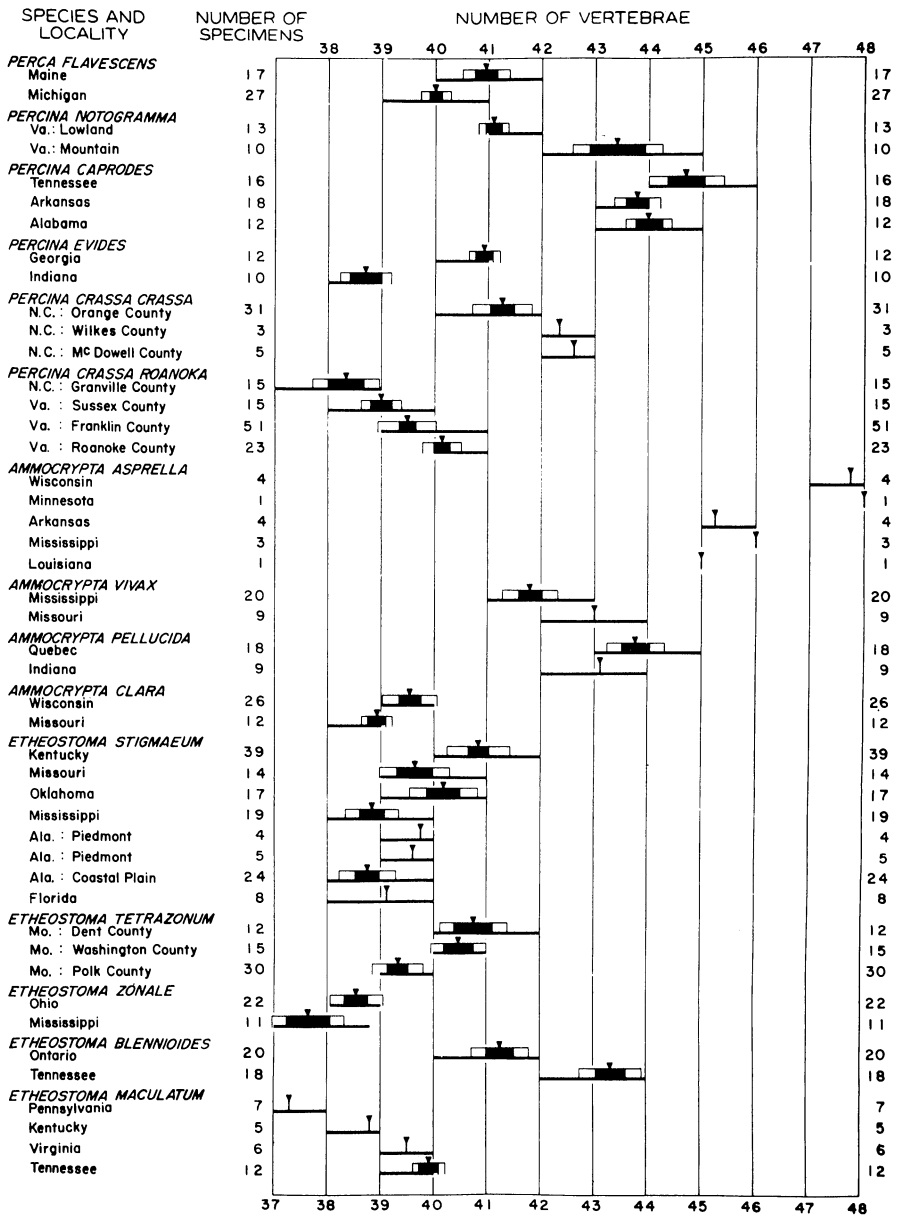


Fig. 2. Geographic variation in number of vertebrae in selected species of American percids. (For explanation see pp. 24 to 27.)

Several environmental factors that might have such a local effect could be postulated, but one that it seems especially profitable to investigate is altitude. In general, a good positive correlation between altitude and vertebral count exists. For example, among the Virginia samples of *Percina notogramma*, that from Spotsylvania County near the coast (Table I) has an average vertebral count of 41.08, whereas that from Rockbridge County in the Appalachian Mountains has a mean of 43.40. In *P. crassa crassa* the sample from the Carolina Piedmont has a mean of 41.26, whereas two small lots from the mountains of the same state each have over 43 vertebrae.

Our data which permit the most intensive analysis of the relationship between altitude and vertebral count are those of *Etheostoma f. flabellare*. If average vertebral number is assessed against altitude, a positive relationship appears within areas (Fig. 3). Thus, the sample from 2000 feet in Tennessee has slightly more vertebrae than those taken at 1000 and 1100 feet. Again there are strong indications of an increase in vertebral number with increase in altitude among the seven samples taken in the Upper Kanawha system.

The inclusion of samples from various scattered localities in Figure 3, however, obscures in part the correlation with altitude noted above. Indeed, the two samples from 700 feet or less in New York have nearly as high mean vertebral counts as the mountain populations. The explanation for this phenomenon may depend on local conditions and perhaps in part on a geographic trend. We believe that within areas there is a real but erratic tendency for higher vertebral number with increase in altitude.

Nevertheless, that altitude is not the only feature causing variation within areas is shown by the variations in our samples of *Percina caprodes semifasciata*, all of which come from approximately the same height above the sea (Table I). In this subspecies, as previously mentioned, the sample means from Michigan alone vary by as much as 2.1 vertebrae. Nor does geographic variation offer an explanation here, for the highest count (44.00) comes from southern Michigan and the lowest (41.92) from the Upper Peninsula.

In an attempt to explain some of the vagaries noted in the preceding paragraphs, the following hypothesis is suggested. We start with the as yet unproved assumptions that, whatever the mechanism leading to the ripening of adults, temperature provides at least the trigger mechanism for actual spawning and the temperature requirements for the initiation of spring spawning are uniform throughout the various populations of a species, at least within areas. We make the further assumption that there is an increase in the number of vertebrae among percid eggs developed at colder temperatures. If these assumptions are correct, then observed differences in vertebral count between genetically similar populations depend upon environmental differences that obtain between the stimulation for spawning and the time the eggs pass the sensitive period of vertebral formation; i.e., eggs in rapidly warming water should have a low vertebral count and those in slowly warming water a relatively high one. In line with this hypothesis the following facts may be marshaled.

In the data on vertebral number in the subspecies of *Stizostedion vitreum* assembled by Dr. Deason (Table III), *S. v. vitreum* from Saginaw Bay (farther north and somewhat cooler) has a slightly, though perhaps not signifi-

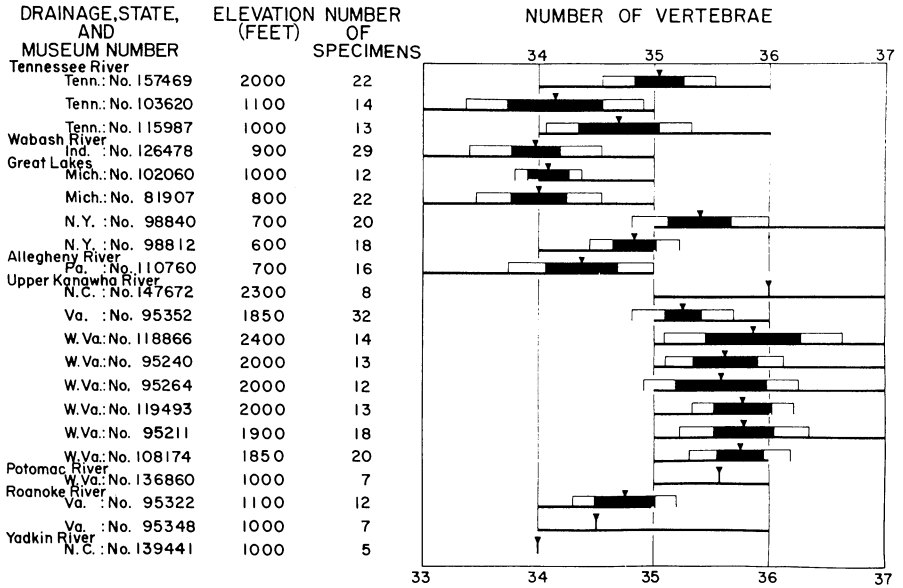


Fig. 3. Geographic variation in number of vertebrae in *Etheostoma flabellare flabellare*. (For explanation see p. 27.)

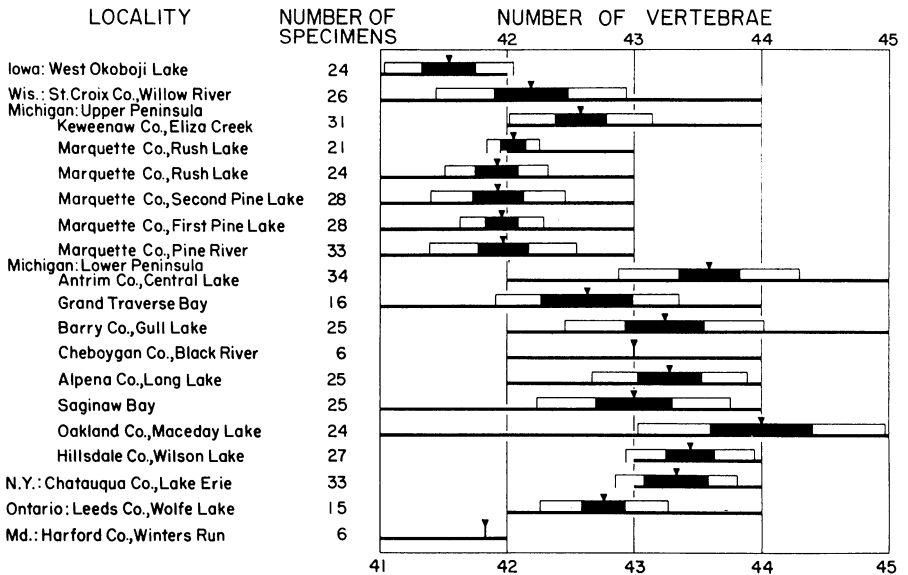


Fig. 4. Geographic variation in number of vertebrae in *Percina caprodes semifasciata*. (For explanation see pp. 29 to 31.)



TABLE III  
 FREQUENCY DISTRIBUTION OF VERTEBRAL COUNTS  
 OF *STIZOSTEDION VITREUM VITREUM* AND *S. V. GLAUCUM*  
 FROM THE GREAT LAKES. DATA FROM DEASON

Number of Vertebrae	<i>S. v. vitreum</i>		<i>S. v. glaucum</i>	
	Lake Erie	Lake Huron	Lake Erie	Lake Ontario
40	...	...	...	1
41	...	...	...	1
42	...	...	2	...
43	...	1	3	...
44	2	2	17	3
45	2	5	52	7
46	32	10	73	12
47	66	28	53	20
48	48	35	22	5
49	19	20	4	...
50	4	1	...	...
Number	173	102	226	49
Mean	47.32	47.47	46.03	46.12
S. D.	1.08	1.27	1.26	1.56

cantly, higher vertebral number than does the same form in Lake Erie. But in Lake Erie the population of *S. v. vitreum*, although it inhabits the shallower and warmer western end, has a notably higher vertebral average (1.29 vertebrae) than does *S. v. glaucum*, which is a characteristic inhabitant of the deeper and cooler eastern part. In his dissertation Dr. Deason comments that *vitreum* spawns, on the average, from April 10 to April 30; *glaucum*, on the average, from May 10 to June 1. In view of the great temperature differential of the shoal water [where this species spawns] between these periods, it seems probable that the cooler water is primarily responsible for the higher vertebral number of *S. v. vitreum*.

That a genetic difference controls time of spawning in these subspecies jointly inhabiting Lake Erie is possible. But an alternative interpretation seems to us more acceptable. It may be surmised that early warming in the shallow western waters first stimulates *vitreum* to spawn. Prevailing temperatures during the ensuing developmental period are then relatively low. The same temperature for stimulation reaches *glaucum* later, sending these fish from the deeper, cooler water onto the shoals which are now relatively warmer. Thus, an ecological rather than a genetic difference may result in the later spawning of *glaucum*, which in turn is responsible for a reduction in number of vertebrae. The more rapid rate of early development would likely also result in the larger eye (Martin, 1949: 47-49), a characteristic feature of this form.

We may now turn to *Percina caprodes* to see whether or not the variation in this species is concordant with the foregoing hypothesis. Judged on a purely geographic basis the counts appear at first to run counter to expectation. Mean vertebral numbers at or near the minimum for the species occur in northwestern Iowa, in the Upper Peninsula of Michigan, and in eastern Maryland. High counts are encountered in southern Michigan, Tennessee,

Alabama, and Arkansas. *Percina caprodes* differs notably in habitat from the other darter species here studied. Instead of living primarily in streams it is found commonly also in lakes, and many of our samples come from each habitat. Probably a more important factor involves the very late spawning which is delayed until well into July at some northern localities. It seems apparent that the ecological complexities created by these factors are responsible for the seeming irregularity of pattern in vertebral variations.

If we consider those collections obtained in streams only (Fig. 4) it is seen that minimal counts are at low elevations (Winters Run, Maryland; Willow River, Wisconsin), intermediate counts are in Michigan and Ohio, and high counts (Table I; Fig. 2) are in the plateau or mountainous areas of the Appalachian upland. Thus, stream populations of *Percina* follow the pattern established for other darters: as usual, lower temperature during development, a concomitant of increased elevation, results in more vertebrae.

In lakes (Figs. 2 and 4) minimal vertebral counts in *Percina caprodes* are found in or near the northern periphery of the range (northwestern Iowa, 41.5; upper Michigan, 42.0; Ontario, 42.8). Most localities in the Great Lakes area have mean vertebral numbers of 43.0 to 43.5. Maximum counts of 43.8 to 44.0 are found in Arkansas, southern Michigan, and northern Indiana. An irregular decrease from south to north is apparent. That the cause is environmental rather than intrinsic is strongly indicated by the absence of a consistent geographic pattern and by the appreciable differences between some adjacent populations.

In lakes thermal gradients introduce a regime different from that encountered in streams, and vertical movement by the fish may substantially alter their thermal environment. In small streams essentially isothermal conditions prevail at any given time, so temperature preceding spawning differs from that during the critical stages of embryonic development only to the extent that it is modified by atmospheric factors. By contrast it has been found (Reighard, 1913) that in Douglas Lake, Michigan, *Percina caprodes* remains in deeper water before breeding, at which time it moves into shallow sandy shoals at depths of from four to twelve inches (other observations extend the range to a depth of at least six feet). Variations in latitude, lake morphometry, exposure to wind action, and meteorological conditions all probably contribute to thermal differences among lakes. Thus, the hypothesis drawn for populations of *Stizostedion vitreum* in Lake Erie may be applied and extended in dealing with lacustrine samples of *Percina caprodes*, which represent dissimilar environments varying greatly in size, depth, configuration, thermal characteristics, and geography.

Minimal average vertebral counts of *Percina caprodes* (Table I; Fig. 4), from West Okoboji Lake in northwestern Iowa (41.5) and lakes in Marquette County, Upper Michigan (42.0), are from areas with a short growing season and in waters that are slow to warm in the spring. The lakes concerned vary from moderate to great depth (273 feet in Rush Lake). One apparently common characteristic is a rather shallow thermocline. *Percina caprodes* breeds late in these waters, a delay which we attribute to the late warming of the deep waters where logperch await the spawning period. On July 1, when the Marquette County lakes were sampled, water temperatures on the shoals (the breeding grounds for *P. caprodes*) were warm, varying from

25.5° to 30.5° C., and the fish had not yet completed spawning. The logperch from West Okoboji, taken on July 9 when the water temperature was 26.7°, were nearly all spent, marking the approximate end of the breeding season. The high temperatures of the breeding waters are interpreted as the probable cause of the low vertebral numbers in these samples.

Samples from Central Lake (43.6 vertebrae) and Maceday Lake (44.0), both in the Lower Peninsula of Michigan, are among those with the highest counts. Morphometrically these lakes are dissimilar; Central Lake is rather large (1515 acres), with a gently sloping bottom and a maximum depth of about 70 feet, whereas Maceday Lake is smaller (417 acres) but beyond the shoals has a steep bottom extending to a depth of 117 feet. Neither lake was sampled during the breeding season of *Percina caprodes*, but on May 10, when Maceday Lake was examined, prespawning logperch were abundant on a very wide (800 feet), shallow (less than 5 feet) shoal area; the temperature was 14.4° C. These limited limnological data seem consistent with the surmise that conditions favored the early warming of water occupied by *P. caprodes* and that spawning occurred at a relatively early date, when the shallow water bathing the eggs was still substantially cooler than in those lakes discussed in the preceding paragraph. Thus, a high number of vertebrae was formed.

The circulation of large deep lakes prevents sudden fluctuations in temperature and eliminates striking thermal gradients. Thus, if very high or very low temperatures during early development are responsible for the production of extremes in vertebral count, we should expect intermediate numbers in *Percina caprodes* from Great Lakes waters. Our samples from East Bay of Grand Traverse Bay, Lake Michigan (42.6), Saginaw Bay of Lake Huron (43.0), and eastern Lake Erie (43.3) fulfill this expectation. The progressively higher counts to the south may indicate earlier spawning at lower shoal temperatures, conditioned by an earlier warming of subsurface waters. The Grand Traverse Bay fish, taken only a few miles from Central Lake, have an average of 1.0 vertebrae fewer than do the specimens from the smaller lake.

Most smaller inland lakes have thermal characteristics that are not extreme; hence, predictably they should produce *Percina caprodes* with intermediate vertebral averages, but these need not be uniform from lake to lake. Thus, the populations from Gull, Long, and Wilson Lakes, Michigan, and Wolfe Lake, Ontario (Fig. 4), are similar in vertebral count to those from the Great Lakes. We have not inquired into the limnological characteristics of these lakes.

On the basis of the available information it is not certain that the interplay of thermal factors alone permits full explanation of the observed variations in vertebral number in *Percina caprodes*. The picture is complex, and we believe merits a much extended investigation, which should include variations among year classes at a single locality, to be correlated with careful field observations and temperature records. We feel confident, however, that environmental modification will prove of vital importance in a final exposition of the problem. Fundamentally, *P. caprodes* appears to respond to temperature in the same way as do other percids.

The hypothesis erected seems to permit satisfactory explanation of the

directional and altitudinal gradients in vertebral counts noted for several species. If all samples of a species are from the lowlands (e.g., *Ammocrypta asprella*), maximum vertebral count can be anticipated to the north. But if some populations come from high elevations and other samples are from nearer sea level (e.g., *Percina evides*, *Etheostoma blennioides*), it appears that altitude outweighs latitude or longitude in its effect on water temperature, and thus, indirectly, on vertebral number.

The data at hand are insufficient more than to indicate the hypothesis discussed above. Indeed, the problems dealt with in such an hypothesis are outside the primary scope of the paper. We would feel remiss in the use of our rather extensive data, however, if we were merely to draw the conclusion that variation in samples occurs. We feel that the presentation of the hypothesis will be justified if it leads others into more thorough investigations regarding the causes of vertebral variation in fish populations.

### SUMMARY

Vertebral counts have been previously used in racial work and to some extent as a systematic character for differentiating families. The present paper is an attempt to determine the value of vertebral number as a taxonomic character at specific, subgeneric, and generic levels in the Percidae.

The vertebrae have been counted in some 5413 specimens, representing 315 samples of 99 species of American percids.

From our data we conclude that there are certain average differences in vertebral number between genera and most subgenera and between many species within a subgenus. An analysis of these differences indicates vertebral number to be a powerful adjunct to phylogenetic interpretation, for in the American percids our vertebral counts fit very well with a classification of these fishes (Bailey, ms) established on the basis of other criteria.

In the matter of differentiating genera, subgenera, and species, however, the vertebral number is of limited use in darters. This is because of the extensive overlapping in counts. A primary source of this overlap arises from the tremendous variation from sample to sample, even within subspecies.

Since this sample variability in darters was one of our most unexpected and perplexing findings, we have devoted considerable effort to analyzing its possible causes. Preliminary experiments with darters show that (1) progenies from different parents of *Etheostoma nigrum* grown under the same environmental conditions can and do have different mean vertebral numbers, but also that (2) parts of progenies from the same parents grown at different temperatures differ in vertebral number. Thus, the differences in vertebral number between our samples from natural conditions may have been genetically or environmentally induced, or both.

By comparing these aquarium specimens with hatchery and field data we have also come to the conclusions that (1) very few wild parents would be necessary to provide the variability found in our wild samples, and that (2) selection operates in such a way as to cut down the amount of variability found within wild samples.

When samples within any one species are compared, there seems to be something of a southwest to northeast increase in vertebral number. Superimposed on this weak geographic gradient there is a more consistent trend within any one area for the fishes taken at higher altitude to have more vertebrae. Nevertheless, both of these gradients are insufficient to account for the local and geographic variations that occur in such a subspecies as *Percina caprodes semifasciata*.

As an attempt to find a more fundamental and consistent explanation for the variations that occur in samples of American percid species, we hypothesize that it is the amount of change (warming) in water temperature that occurs between spawning and the end of the sensitive period for vertebral formation that determines, at least in part, whether a sample will have a relatively high or low mean vertebral count. According to this hypothesis eggs laid in rapidly warming waters should have fewer vertebrae than genetically similar eggs spawned in more gradually warming waters. In lacustrine populations, thermal stratification may result in stimulation to breed at a given temperature with the resultant spawning occurring at a substantially different vertical and thermal level. Variations in spawning temperatures from lake to lake are reflected in average vertebral number, which is high when early development is in cool water, low if in warm water. Thus directional, altitudinal, and ecological gradients in vertebral numbers are all believed to result, at least in large part, from variations in temperature.

#### ACKNOWLEDGMENTS

Any merit that this paper may have accrued in large part from the contributions of various colleagues. Dr. Hilary J. Deason, formerly of the U. S. Fish and Wildlife Service, has placed at our disposal the material in Table III, for which he has our sincere gratitude. Several years ago Dr. Karl F. Lagler, operating with the support of the Laboratory of Vertebrate Biology (a division of the Institute of Human Biology), of the University of Michigan, undertook an investigation on the morphological consequences of splitting batches of darter (*Etheostoma nigrum*) eggs and permitting their development at different temperatures. We are indebted to Dr. Lagler for turning over to us those (unpublished) materials that are pertinent to our inquiry (Table II). Howard E. Winn has assisted freely in taking X-ray photographs and has our sincere thanks. We appreciate also the co-operation of Dr. Edward C. Raney of Cornell University and of Dr. Ernest A. Lachner and Dr. Leonard P. Schultz of the U. S. National Museum, who have aided through the loan of specimens in those institutions. Dr. Lachner also provided radiographs of a few specimens in the National Museum. Mrs. Margaret Hinson and Mr. William Cristanelli assisted in the drafting of the figures; to them we are grateful.

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## APPENDIX

Locality data are presented here for fish listed in Tables I and II. Specimen lots not otherwise indicated are in the University of Michigan Museum of Zoology; those indicated as CU are in Cornell University, and those designated USNM are in the United States National Museum. In this list Bailey assumes responsibility for the sequence and nomenclature.

*Stizostedion vitreum vitreum* (Mitchill). — No. 101531: Spirit Lake, Dickinson Co., Iowa. No. 110367: Bear Lake, T. 26 N., R. 15 W., sec. 33, Manistee Co., Mich. No. 112186: Houghton Lake, 1.5 mi. nw. of Houghton Lake Village, Roscommon Co., Mich.

*Stizostedion vitreum glaucum* Hubbs. — No. 115964: Lake Erie, 29 mi. ne. of Vermilion, Ohio. No. 157232: Lake Erie, Sandusky, Erie Co., Ohio.

*Stizostedion canadense* (Smith). — No. 100906: Mississippi R., midway between Lansing and mouth of Upper Iowa R., Allamakee Co., Iowa. No. 139849: Footh Pond, Gibson Co., Ind. No. 139943: Wabash R., 6.5 mi. w. of Mt. Vernon, Posey Co., Ind. No. 139955: Grassy Pond, near Wabash R., Gibson Co., Ind. No. 122547: Mulberry Cr., Pickwick Lake, T. 3 S., R. 13 W., sec. 28, Lauderdale Co., Ala.

*Perca flavescens* (Mitchill). — No. 126979: Buff Brook, 2.5 mi. n. of Ross Corner, Waterboro Twp., York Co., Maine. No. 67239: Roe Lake, in Sucker R., T. 28 N., R. 8 E., sec. 35, Alcona Co., Mich.

*Percina (Hypohomus) aurantiaca* (Cope). — No. 103446: Powell R., at mouth of Station Cr., U. S. hwy. 58, e. of Jonesville, Lee Co., Va. No. 129300: Middle Prong, Little Pigeon R., Richardsons Cove, Sevier Co., Tenn. No. 129431: Little R., just above Kinzel Springs, 4 mi. below Townsend, Blount Co., Tenn. No. 156985: Watauga R., 2 mi. above mouth of Cove Cr., Watauga Co., N. C.

*Percina (Hypohomus) cymatotaenia* (Gilbert and Meek). — No. 151955: Niangua R., 2 mi. e. of Charity, Dallas Co., Mo. No. 111335: Big Niangua R., at mouth of Greasy Cr., 6 mi. se. of Buffalo, Dallas Co., Mo. No. 102529: Big Piney R., 6 mi. s. of Houston, Texas Co., Mo. No. 152214: Big Piney R., 2.5 mi. w. of Houston, Texas Co., Mo. No. 142315: Big Piney R., T. 32 N., R. 10 W., sec. 24, 6 mi. e. of Success, Texas Co., Mo. No. 142322: Gasconade R., 1 mi. e. of Competition, at Bowens Mill, La Clede Co., Mo. No. 152366: Gasconade R., 8 mi. s. of Richland, Pulaski Co., Mo.

*Percina (Alvordius) macrocephala* (Cope). — No. 96879: North Fork of Holston R., above Saltville, Smyth Co., Va. USNM No. 63778: Redbird Cr. at town of Big Creek, Clay Co., Ky.

*Percina (Alvordius) maculata* (Girard). — No. 60034: Denton Cr., Muskegon R. system, Mich. No. 104450: Manistee R., Wexford Co., Mich. No. 160879: Duck Cr., 12.7 mi. ne. of Cullman, hwy. 31, Cullman Co., Ala.

*Percina (Alvordius) notogramma* (Raney and Hubbs). — No. 144697 and CU No. 9708: North River, Lexington Quadrangle, Rockbridge Co., Va. CU No. 8324: Catawba Cr., 2 mi. n. of Fincastle, hwy. 220, Botetourt Co., Va. No. 102326: Ni R., about 10 mi. s. of Fredericksburg, Spotsylvania Co., Va. CU No. 10528: trib. to South Anna R., 2.5 mi. n. of Gum Springs, Louisa Co.,

Va. CU No. 10527: Rapidan R., Madison Mills, Madison Co., Va. CU No. 10193: Rappahannock R., Fredericksburg, Stafford Co., Va.

*Percina (Alvordius) peltata peltata* (Stauffer). — No. 109755: Unadilla R., at mouth of Wharton Cr., New Berlin, Chenango and Otsego cos., N. Y.

*Percina (Alvordius) peltata nevisensis* (Cope). — CU No. 11928: Great Cr., Mekerrin R. drainage, 4 mi. sw. of Alberta, U. S. hwy. 1, Brunswick Co., Va. CU No. 20765: Stony Cr., Chowan R. system, 1.2 mi. s. of Dinwiddie on U. S. hwy. 1, Dinwiddie Co., Va.

*Percina (Hadropterus) sciera* (Swain). — No. 137916: Slate Ford, Poteau R., near Shady Point, Le Flore Co., Okla.

*Percina (Hadropterus) nigrofasciata* (Agassiz). — No. 146616: cr. 1.5 mi. s. of Centreville, Wilkinson Co., Miss.

*Percina (Swainia) phoxocephala* (Nelson). — No. 81385: Patoka R., Patoka, Gibson Co., Ind. No. 149382: Salt R., 6 mi. n. of Center on county road H, Ralls Co., Mo.

*Percina (Swainia) nasuta* (Bailey). — No. 137133: White R., 6 mi. ne. of Fayetteville, Washington Co., Ark. No. 137914: Slate Ford, Poteau R., near Shady Point, Le Flore Co., Okla.

*Percina (Swainia) oxyrhyncha* (Hubbs and Raney). — No. 118482: New R., just above Jacksons Ferry, Wythe Co., Va. No. 131829: New R., 1 mi. above Gauley Bridge, Fayette Co., W. Va. No. 131830: New R., at Round Bottom Cr., about 5 mi. below Virginia line, Summers Co., W. Va.

*Percina (Swainia) squamata* (Gilbert and Swain). — No. 156239: French Broad R., Hot Springs, Madison Co., N. C. No. 156980: Cane R., 3 mi. above junction with Toe R., Yancey Co., N. C.

*Percina (Percina) caprodes semifasciata* (DeKay). — No. 146739: West Okoboji Lake at Haywards Bay, Dickinson Co., Iowa. No. 78038: Willow R. and mill pond, Hudson, St. Croix Co., Wis. No. 133368: Eliza Cr., T. 58 N., R. 30 W., sec. 6, Keweenaw Co., Mich. No. 81622: Rush Lake, T. 52 N., R. 28 W., sec. 19, Marquette Co., Mich. No. 81612: Rush Lake, T. 52 N., R. 28 W., sec. 19, Marquette Co., Mich. No. 81740: Second Pine Lake, T. 52 N., R. 28 W., sec. 28, Marquette Co., Mich. No. 81731: First Pine Lake, T. 52 N., R. 28 W., sec. 21, Marquette Co., Mich. No. 81665: Pine R., first one-fourth mi. below Pine Lake, T. 52 N., R. 28 W., sec. 21, Marquette Co., Mich. No. 98611: Central Lake, T. 30 N., R. 7 and 8 W., Antrim Co., Mich. No. 59574: East Bay of Grand Traverse Bay, Grand Traverse Co., Mich. No. 111880: Gull Lake, T. 1 N., R. 9 W., sec. 31, Barry Co., Mich. No. 145071: Black R., 2 mi. above Black Lake, T. 35 N., R. 1 E., sec. 5, Cheboygan Co., Mich. No. 67184: Long Lake outlet, T. 32 N., R. 8 E., sec. 23, Alpena Co., Mich. No. 92219: Saginaw Bay, Lone Tree Island, Huron Co., Mich. No. 81976: Maceday Lake, T. 3 N., R. 9 E., sec. 7, Oakland Co., Mich. No. 98078: Wilson Lake, T. 7 S., R. 3 W., secs. 5 and 8, Hillsdale Co., Mich. No. 99065: mouth of Chautauqua Cr., at Barcelona Beach, near Westfield, Chautauqua Co., N. Y. No. 104590: outlet of Wolfe Lake, near Sand Lake, Leeds Co., Ont. No. 158976: Winters Run, 9 mi. sw. of Aberdeen, Harford Co., Md.

*Percina (Percina) caprodes: caprodes x semifasciata*. — No. 63049: Turkey Lake, Steuben Co., Ind. No. 118508: Ten Mile Cr., at University of City of Toledo, sec. 32, Washington Twp., Lucas Co., Ohio.



*Percina (Percina) caprodes caprodes* (Rafinesque). — No. 105434: Cove Cr., Campbell Co., Tenn. No. 154611-2: Wolf R., along hwy. 28, near Pall Mall, 8 mi. n. of Jamestown, Fentress Co., Tenn. CU No. 20686: North Fork Holston R., 2.3 mi. sw. of Broadford on hwy. 91, Smyth Co., Va.

*Percina (Percina) caprodes carbonaria* (Baird and Girard). — No. 123064: Lake Hamilton, T. 3 S., R. 20 W., Garland Co., Ark. No. 160878: Duck Cr., 12.7 mi. ne. of Cullman, Cullman Co., Ala.

*Percina (Percina) rex* (Jordan and Evermann). — CU No. 8453, UMMZ No. 162299, and USNM No. 154653: Mason Cr., 1 mi. e. of Salem, Roanoke Co., Va. CU No. 11560: Roanoke R., 2 mi. w. of Salem, Roanoke Co., Va. CU No. 20766: Roanoke R., at Glenvar, Roanoke Co., Va. CU No. 16910: Sappony Cr., 2.5 mi. w. of Stony Cr., hwy. 40, Sussex Co., Va.

*Percina (Ericosma) palmaris* (Bailey). — No. 111233: Sougahatchee Cr., Ala. No. 160896: Sougahatchee Cr., about 3 mi. nw. of Loachapoka, Lee Co., Ala.

*Percina (Ericosma) evides* (Jordan and Copeland). — No. 157978: Notala R., 5 mi. se. of Blairsville, Union Co., Ga. No. 167077: Tippecanoe R., Marshland, Ind.

*Percina (Ericosma) crassa crassa* (Jordan and Brayton). — CU No. 14084: Morgans Cr. at Masons Farm, Cape Fear R. drainage, 1 mi. below Chapel Hill, Orange Co., N. C. CU No. 10994: trib. to Yadkin R., 1.2 mi. w. of Moravian Falls, Wilkes Co., N. C. CU No. 10881: Catawba R., 4 mi. w. of Marion, McDowell Co., N. C.

*Percina (Ericosma) crassa roanoka* (Jordan and Jenkins). — CU No. 8541: Tar R., 2 mi. n.w. of Berea on hwy. 158, Granville Co., N. C. No. 156665: Little R., 2 mi. n.w. of Orange Factory, Durham Co., N. C. CU No. 18631: Eno R., Neuse R. system, 2 mi. e. of Efland, Orange Co., N. C. CU No. 16915: Sappony Cr., 2.5 mi. w. of Stony Cr. on hwy. 40, Sussex Co., Va. CU No. 11631: Pigg R., 0.5 mi. s. of Rocky Mount on hwy. 220, Franklin Co., Va. No. 158999: Mason Cr., 2 mi. e. of Salem, Roanoke Co., Va. CU No. 18627: Roanoke R., 2 mi. w. of Salem, Roanoke Co., Va.

*Percina (Imostoma) shumardi* (Girard). — No. 76804: Mississippi R. at Cassville, Grant Co., Wis. No. 81563: Au Sable R., below Foote Dam, Iosco Co., Mich.

*Percina (Imostoma) uranidea* (Jordan and Gilbert). — No. 122637: Swan Cr., T. 4 S., R. 4 W., sec. 19, Wheeler Reservoir, Limestone Co., Ala. No. 122707: Round Island Cr., T. 4 S., R. 5 W., sec. 10, Wheeler Reservoir, Limestone Co., Ala. No. 153134: Little River Floodway, 4 mi. se. of Gideon, New Madrid Co., Mo. No. 153259: drainage ditch, 1 mi. e. of Anniston, Mississippi Co., Mo.

*Percina (Cottogaster) copelandi* (Jordan). — No. 85919: Fish Point, Pelee Island, Lake Erie, Ont. No. 91349: Point Lookout, Saginaw Bay, Arenac Co., Mich.

*Ammocrypta (Crystallaria) asprella* (Jordan). — No. 76823: Mississippi R. at Cassville, Grant Co., Wis. Minnesota Conservation Department: Mississippi R., below railroad bridge at Winona, Winona Co., Minn. No. 113449: Trim Cane Cr., trib. to Tombigbee R., Oktibbeha Co., Miss. No. 128481: White R., 1 mi. ne. of DeValls Bluff, Prairie Co., Ark. No. 167598: Bogue Chitto R., hwy. 35, Franklinton, Washington Parish, La.

*Ammocrypta (Ammocrypta) vivax* Hay. — No. 111226: along Columbus Road, 3 mi. e. of Tuskegee, Macon Co., Ala. No. 157816: trib. to Big Bogue Homo R., 3.5 mi. nne. of Sandersville, Jasper Co., Miss. No. 117429: Black R., T. 25 N., R. 6 E., sec. 8, Clark National Forest, Butler Co., Mo.

*Ammocrypta (Ammocrypta) pellucida* (Baird). — No. 66562: Tippecanoe R. between Talma and Rochester, Fulton Co., Ind. No. 104381: Rouge R., Rouge Park, Wayne Co., Mich. No. 146691: Chateauguay R., Chateauguay Village, near Montreal, Que.

*Ammocrypta (Ammocrypta) clara* Jordan and Meek. — No. 76089: Black R., about 5 mi. s. of Black River Falls, Jackson Co., Wis. No. 148570: Salt R., 8 mi. nw. of Louisiana, Pike Co., Mo. No. 149952: Mississippi R., 3 mi. w. of Winfield, Lincoln Co., Mo.

*Ammocrypta (Ammocrypta) beani* Jordan. — No. 134623: Escambia R., w. of Jay, Escambia Co., Fla. No. 155484: Pond Cr., 1.8 mi. sw. of Milton, Santa Rosa Co., Fla. No. 155344: Brushy Cr., 1 mi. above mouth in Homochitto R., T. 4 N., R. 2 E., sec. 14, Amite Co., Miss.

*Etheostoma (Boleosoma) nigrum olmstedii* Storer. — No. 158978: Winters Run, 9 mi. sw. of Aberdeen on U. S. hwy. 40, Harford Co., Md.

*Etheostoma (Boleosoma) nigrum rafinesquei*. — No. 82364: Houghton Lake, T. 22 N., R. 4 W., sec. 3, Roscommon Co., Mich. Nos. 162486; 162487; 162488 (mating Nos. 177, 181, and 183): Mill Cr., 6 mi. sw. of Dexter, Washtenaw Co., Mich. No. 162485 (mating No. 59): Saline R., 3 mi. w. of Saline, Washtenaw Co., Mich.

*Etheostoma (Boleosoma) nigrum eulepis* (Hubbs and Greene). — No. 77054: Crawfish R., 2 mi. nw. of Fall R., Columbia Co., Wis. No. 162490 (mating No. 138): Detroit R., n. end of Belle Isle, Wayne Co., Mich.

*Etheostoma (Boleosoma) perlongum* (Hubbs and Raney). — No. 138476: Lake Waccamaw, n. shore, Columbus Co., N. C.

*Etheostoma (Boleosoma) chlorosomum* (Hay). — No. 110543: San Jacinto and Trinity river systems, Tex. No. 130081: Clear Cr. drainage ditch e. of Reynoldsville, T. 13 S., R. 2 W., sec. 20, Union Co., Ill.

*Etheostoma (Boleosoma) jessiae* (Jordan and Brayton). — No. 103591: pond opposite Doaks Dam, Campbell Co., Tenn. No. 104339: Bull Run Cr., between Hales Crossroads and Norris, Knox Co., Tenn.

*Etheostoma (Boleosoma) stigmaeum* (Jordan). — Nos. 154704 and 154705: Peters Cr., lower 0.5 mi. of course, U. S. hwy. 31E, 10 mi. ne. of Scottsville, Barren Co., Ky. No. 139667: Black R., 2 mi. above Poplar Bluff, T. 25 N., R. 6 E., sec. 24, Butler Co., Mo. No. 137865: Illinois R., near mouth of Swimmers Cr., Sequoyah Co., Okla. No. 155359: Bogue Chitto R., T. 2 N., R. 10 E., 7 mi. w. of Tylertown, Walthall Co., Miss. No. 111231: Loachapoka Cr., Lee or Macon Co., Ala. No. 124039: Opintlocco Cr., 3 mi. se. of Tuskegee, Macon Co., Ala. No. 139154: Rocky Cr., 1 mi. n. of Georgiana, Butler Co., Ala. No. 155483: Pond Cr., 1.8 mi. sw. of Milton, Santa Rosa Co., Fla.

*Etheostoma (Boleosoma) longimanum* Jordan. — No. 95164: Buffalo Cr., 6 mi. s. of Lexington, Rockbridge Co., Va. No. 95179: Catawba Cr., near Fincastle on hwy. 17, Botetourt Co., Va. No. 135399: Johns Cr., trib. to Craig Cr., Captain P. O., Craig Co., Va.

*Etheostoma (Boleosoma) podostemone* Jordan and Jenkins. — No. 95321:

Tinker Cr., just above Cloverdale, Botetourt Co., Va. No. 159000: Mason Cr., 2 mi. e. of Salem, Roanoke Co., Va.

*Etheostoma (Etheostoma) sellare* (Radcliffe and Welch). — USNM Nos. 74346 [holotype] and 74347 [paratype]: Swan Cr., Havre de Grace, Harford Co., Md.

*Etheostoma (Etheostoma) variatum* Kirtland. — No. 118358: West Fork of Little Beaver Cr., sec. 11, Wayne Twp., Columbiana Co., Ohio.

*Etheostoma (Etheostoma) tetrazonum* (Hubbs and Black). — No. 149516: Meramec R., 2 mi. nw. of Short Bend, Dent Co., Mo. No. 149774: Big R., trib. to Meramec R., 4 mi. n. of Caledonia, Washington Co., Mo. No. 150094: Little Sac R., 0.5 mi. sw. of Aldrich, T. 32 N., R. 24 W., sec. 4, Polk Co., Mo. No. 150922: Clear Cr., trib. to Sac R., 4 mi. n. of Willard, T. 30 N., R. 24 W., sec. 18, Greene Co., Mo.

*Etheostoma (Etheostoma) euzonum erizonum* (Hubbs and Black). — No. 124595: Current R., T. 26 N., R. 1 E., secs. 11 and 12, Carter Co., Mo.

*Etheostoma (Etheostoma) euzonum euzonum* (Hubbs and Black). — No. 151229: Big Indian Cr., trib. to White R., 1 mi. sw. of Baxter, Stone Co., Mo. No. 152121: Little North Fork, trib. to White R., Theodosia, Ozark Co., Mo.

*Etheostoma (Etheostoma) kanawhae* (Raney). — No. 131836: South Fork, New R., Index, Ashe Co., N. C. No. 131838: North Fork, New R., Crumpler, Ashe Co., N. C. No. 147673: New R. at Virginia state line, 5 mi. nw. of Sparta, Alleghany Co., N. C.

*Etheostoma (Etheostoma) osburni* (Hubbs and Trautman). — No. 118800: Indian Cr., Greenville, Monroe Co., W. Va.

*Etheostoma (Etheostoma) blennius* Gilbert and Swain. — No. 132640: Second Cr., trib. to Tennessee R., Lauderdale Co., Ala.

*Etheostoma (Etheostoma) thalassinum* (Jordan and Brayton). — No. 138493: trib. to Catawba R., 6 mi. ne. of Lincolnton on hwy. 150, Lincoln Co., N. C.

*Etheostoma (Etheostoma) inscriptum* (Jordan and Brayton). — No. 88305: Little Towaliga Cr., Ocmulgee R. system, near Barnesville, Lamar Co., Ga.

*Etheostoma (Etheostoma) swannanoa* Jordan and Evermann. — No. 138482: Swannanoa R., 1 mi. w. of Black Mountain, Buncombe Co., N. C.

*Etheostoma (Etheostoma) rupestre* Gilbert and Swain. — No. 111217: 3 mi. e. of Tuskegee, along Columbus road, Macon Co., Ala. No. 124013: Opintlocca Cr., 3 mi. se. of Tuskegee, Macon Co., Ala.

*Etheostoma (Etheostoma) histrio* Jordan and Gilbert. — No. 139655: Black R., at Arkansas state line, T. 22 N., R. 6 E., sec. 33, Butler Co., Mo. No. 153001: Floodway ditches 81 and 1, 4 mi. E. of Kennett on hwy. M 84, Dunklin Co., Mo. No. 161424: Lobitubby Cr., 10-12 mi. nw. of Oxford, Lafayette Co., Miss.

*Etheostoma (Etheostoma) zonale zonale* (Cope). — No. 159885: Deer Cr. at hwy. 104, 3.5 mi. s. of Yellowbud, Ross Co., Ohio. No. 103441: Powell R., at mouth of Station Cr., U. S. hwy. 58, e. of Jonesville, Lee Co., Va.

*Etheostoma (Etheostoma) zonale lynceum* Hay. — No. 155343: Brushy Cr., 1 mi. above mouth in Homochitto R., T. 4 N., R. 2 E., sec. 14, Amite Co., Miss.

*Etheostoma (Etheostoma) gutselli* (Hildebrand). — No. 156510: Cartoogechaye Cr., above mouth of Mill Cr., 5 mi. w. of Franklin, Macon Co., N. C. No. 156564: Tuckasegee R., 2 mi. ne. of Cullowhee, on hwy. 107, Jackson Co., N. C. No. 156601: West Fork Tuckasegee R., and Trout Cr., 3 mi. n. of Glennville, Jackson Co., N. C.

*Etheostoma (Etheostoma) blennioides* Rafinesque. — No. 85545: North Branch of Thames R., St. Marys, Perth Co., Ont. No. 138143: Huron R., New Boston, T. 4 S., R. 9 E., sec. 7, Wayne Co., Mich. No. 157448: Roan Cr., trib. to Watauga Reservoir, 2.5 mi. ese. of Doeville, Johnson Co., Tenn.

*Etheostoma (Ulocentra) coosae* (Fowler). — No. 88225: trib. to Coosa R., 3 mi. w. of Coosa, Floyd Co., Ga. No. 88188: Cedar Cr., trib. to Coosa R., 1 mi. n. of Cedartown, Polk Co., Ga. No. 88270: Spring Cr., at Spring Creek, about 10 mi. se. of Rome, Floyd Co., Ga. No. 96774: Cove (?) Cr., Coosa R. system, about 5 mi. from Gadsden, Etowah Co., Ala.

*Etheostoma (Ulocentra) simoterum* (Cope). — No. 103619: 6.6 mi. e. of Lafollette, Tennessee R. system, Campbell Co., Tenn. No. 157616: South Fork of Holston R., 1 mi. below Virginia state line, Sullivan Co., Tenn.

*Etheostoma (Ulocentra) atripinne* (Jordan). — No. 96351: branch of Stone R., Cumberland R. system, near Nashville, Davidson Co., Tenn.

*Etheostoma (Ulocentra) duryi* Henshall. — No. 132577: Spring Branch, trib. to Dry Cr., Tennessee R. system, Hardin Co., Tenn.

*Etheostoma (Allohistium) cinereum* Storer. — No. 121708: Pryor Bend, Obey R., Cumberland R. system, Pickett Co., Tenn. No. 125382: Obey R. at mouth of Eagle Cr., 2.2 mi. w. of hwy. bridge on Livingston-Byrdstown Road, Pickett Co., Tenn.

*Etheostoma (Nothonotus) maculatum* Kirtland. — No. 109092: French Cr., at Carlton, Mercer Co., Pa. No. 110753: Shenango R., probably Mercer or Lawrence Co., Pa. No. 102900: Shenango R., Delaware Grove, 6 mi. n. of Mercer, Mercer Co., Pa. No. 139053: Rockcastle R., just above Livingston on U. S. hwy. 25, Rockcastle and Laurel Co. line, Ky. No. 104319: Powell R., at mouth of Station Cr., U. S. hwy. 58, e. of Jonesville, Lee Co., Va. No. 104320: North Fork Holston R., above Saltville, Smyth Co., Va. Nos. 157581 and 159011: South Fork Holston R., one-fourth mi. above South Holston Dam — prior to impoundment, 7 mi. se. of Bristol, Sullivan Co., Tenn.

*Etheostoma (Nothonotus) camurum* (Cope). — Nos. 160641 and 160642: Big Darby Cr., 1 mi. s. of Fox, se. Jackson Twp., Pickaway Co., Ohio.

*Etheostoma (Nothonotus) rufilineatum* (Cope). — No. 157482: Watauga R., 4.5 mi. se. of Butler — before impoundment, 1.5 mi. below North Carolina line, Johnson Co., Tenn. No. 157546: South Fork Holston R., near mouth of Fish Dam Cr., 2 mi. ene. of South Holston Dam — before impoundment, Sullivan Co., Tenn.

*Etheostoma (Nothonotus) jordani* Gilbert. — No. 139107: trib. to Conasauga R., 7.3 mi. s. of Dalton, U. S. hwy. 41, Whitfield Co., Ga. No. 128768: Line Cr. [= Oakfuskee Cr.], near Montgomery, Macon and Montgomery cos., Ala.

*Etheostoma (Nothonotus) tippecanoe* Jordan and Evermann. — No. 160640: Big Darby Cr., 1 mi. s. of Fox, se. Jackson Twp., Pickaway Co., Ohio. No. 160644: Deer Cr., at hwy. 104, 3.5 mi. s. of Yellowbud, Ross Co., Ohio.

*Etheostoma (Oligocephalus) nianguae* Gilbert and Meek. — No. 152703:

Barren Fork, trib. to Tavern Cr., trib. to Osage R., 7 mi. se. of Tuscumbia, Miller Co., Mo.

*Etheostoma (Oligocephalus) spilotum* Gilbert. — USNM No. 125360: Hector Cr., 5 mi. w. of Big Creek, Clay Co., Ky. USNM No. 63778: Redbird Cr., 1 mi. w. of Big Creek, Clay Co., Ky.

*Etheostoma (Oligocephalus) sagitta* (Jordan and Swain). — No. 144492: Little Wolf Cr., trib. to Clear Fork R., Upper Cumberland R. system, 2.5 mi. w. of Pleasant View, Whitley Co., Ky.

*Etheostoma (Oligocephalus) radiosum radiosum* (Hubbs and Black). — No. 123256: Ten Mile Cr., 10 mi. ne. of Malvern, U. S. hwy. 67, T. 15 W., R. 3 S., Saline Co., Ark. No. 127853: bayou, trib. to Hudgin Cr., 2 mi. sw. of Star City, Lincoln Co., Ark.

*Etheostoma (Oligocephalus) radiosum cyanorum* (Moore and Rigney). — No. 161367: Blue R. on hwy. 99, s. of Ada, T. 1 S., R. 6 E., Johnston Co., Okla.

*Etheostoma (Oligocephalus) radiosum paludosum* (Moore and Rigney). — No. 161369: Bois d'Arc Cr., trib. to Clear Boggy Cr., T. 2 N., R. 6 E., Pontotoc Co., Okla.

*Etheostoma (Oligocephalus) whipplei whipplei* (Girard). — No. 110864: pools along Brushy Cr., trib. to Big Cr. of Black Fork of Poteau R., Le Flore Co., Okla. No. 127312: Poteau R. at Slate Ford, near Shady Point, Le Flore Co., Okla. No. 155103: Crooked Cr., hwy. 26, 3.5 mi. n. of River-ton, Cherokee Co., Kan.

*Etheostoma (Oligocephalus) whipplei montanum* (Hubbs and Black). — No. 123802: Blue Hole Cr., 1.5 mi. s. of Winslow, T. 13 N., R. 30 W., Wash- ington Co., Ark.

*Etheostoma (Oligocephalus) whipplei artesia* (Hay). — No. 158275: trib. to Locust Fork, 0.5 mi. e. of Cleveland at hwy. 38, Blount Co., Ala.

*Etheostoma (Oligocephalus) fricksium* Hildebrand. — No. 145325: Savan- nah R. drainage, between Appleton and Martin, Allendale Co., S. C. No. 137768: trib. to McBean Cr., 2 mi. se. of Hepzibah, 15 mi. s. of Augusta, Richmond Co., Ga. CU No. 18459: trib. to Oconee R., 1.5 mi. ene. of Glen- wood, Wheeler Co., Ga. CU Nos. 17616 and 18458 [topotypes of *Poecilichthys hopkinsi* Fowler, which appears to be a synonym]: Oscewickee Springs, 10 mi. se. of Abbeville, 2 mi. e. of Forest Glen, Wilcox Co., Ga.

*Etheostoma (Oligocephalus) asprigene* (Forbes). — No. 78098: Missis- sippi R. at Buffalo, Buffalo Co., Wis.

*Etheostoma (Oligocephalus) swaini* (Jordan). — No. 155375: trib. to McGee Cr., trib. to Bogue Chitto R., 4.3 mi. ssw. of Tylertown, hwy. 27, Walthall Co., Miss. No. 155453: cr. trib. to Rocky Cr., trib. to Escatawpa R., 5.6 mi. ese. of Lucedale, T. 1 S., R. 5 W., sec. 33, George Co., Miss. No. 155246: Big Cypress Cr., at Newton-Colquit hwy. [route 91], Baker Co., Ga. No. 110973: Spring Cr., 1 mi. below dam, 3 mi. se. of Marianna, Jackson Co., Fla. No. 158205: Chipola R., 6 mi. nnw. of Marianna, Jack- son Co., Fla.

*Etheostoma (Oligocephalus) mariae* (Fowler). — No. 156983: outlet of Watsons Lake, Cape Fear drainage, 3 mi. e. of Southern Pines, Moore Co., N. C.

*Etheostoma (Oligocephalus) juliae* Meek. — No. 152018: James R., trib.

to White R., 6 mi. s. of Marshfield, Webster Co., Mo. No. 152095: North Fork of White R., on hwy. M-30 at Tecumseh, Ozark Co., Mo.

*Etheostoma (Oligocephalus) punctulatum* (Agassiz). — No. 151096: Shoal Cr., trib. to White R., at creek ford near Protem, along hwy. M-125, Taney Co., Mo. No. 160396: Spring Cr., at U. S. hwy. 166, 5.5 mi. e. of Baxter Springs, Cherokee Co., Kan. No. 137866: Illinois R., near mouth of Swimmers Cr., Sequoyah Co., Okla.

*Etheostoma (Oligocephalus) parvipinne* Gilbert and Swain. — No. 88336: trib. to Indian Cr., Ocmulgee R. system, 2 mi. from Perry on hwy. 11, Houston Co., Ga. No. 161055: stream on U. S. hwy. 78, 2 mi. nw. of Victoria, 9 mi. nw. of Holly Springs, Marshall Co., Miss. No. 161109: stream along U. S. hwy. 51, 4.9 mi. n. of Pickens, Holmes Co., Miss. No. 113867: Ponta Cr., trib. to Sucarnoochee Cr., Tombigbee R. system, 12 mi. s. of Electric Mills, U. S. hwy. 45, Lauderdale Co., Miss. No. 161217: stream, 2.5 mi. se. of Meadville, Franklin Co., Miss.

*Etheostoma (Oligocephalus) caeruleum* Storer. — No. 66539: Upper River Rouge, Northville, Wayne Co., Mich. No. 103284: Cougles Cove, at mouth in Clinton R., 3 mi. nw. of Utica, T. 3 N., R. 12 E., sec. 19, Macomb Co., Mich.

*Etheostoma (Oligocephalus) cragini* Gilbert. — No. 151432: Shoal Cr., trib. to Spring R., 7 mi. w. of Purdy on hwy. M-97, Barry Co., Mo. No. 156694: small stream, 1.5 mi. n. of Fowler, Meade Co., Kan. No. 160409: Artesian spring and bog, 1.5 mi. n. of Fowler, Meade Co., Kan.

*Etheostoma (Oligocephalus) pottsii* (Girard). — No. 161675: Rio Trujillo [= Rio Florido], 1 mi. w. of Rancho Grande, Zacatecas, Mexico. USNM No. 38245 [holotype of *Etheostoma micropterus* Gilbert]: Chihuahua, Mexico. USNM No. 125107: Rio Conchos, Chihuahua, Mexico. USNM No. 55855: Durango, Mexico.

*Etheostoma (Oligocephalus) exile* (Girard). — No. 159978: Pathfinder Reservoir, near dam, Natrona Co., Wyo. No. 137775: Wolf Lake Hatchery, Pond 4, Van Buren Co., Mich.

*Etheostoma (Oligocephalus) luteovinctum* Gilbert and Swain. — No. 121123: Little Flat Cr., Duck R. drainage, hwy. 16, Bedford Co., Tenn. No. 132708: Cortner Branch, trib. to Sinking Cr., Duck R. drainage, Bedford Co., Tenn.

*Etheostoma (Oligocephalus) grahami* (Girard). — No. 120322: Devil R., U. S. hwy. 90, nw. of Del Rio, Val Verde Co., Tex. No. 162135: San Pedro, Nuevo Leon, Mexico.

*Etheostoma (Oligocephalus) spectabile spectabile* (Agassiz). — No. 159858: Yellowbud Cr., 5 mi. se. of Williamsport, sw. Wayne Twp., Pickaway Co., Ohio. No. 152930: Bais Brick Cr., trib. to Osage R., 3 mi. s. of Carnegie, Cole Co., Mo.

*Etheostoma (Oligocephalus) spectabile pulchellum* (Girard). — No. 160459: Rose Cr. and South Fork Smoky Hill R., 3 mi. sw. of Wallace, Wallace Co., Kan.

*Etheostoma (Austroperca) australe* Jordan. — No. 86349: Chihuahua R. or trib., Mexico. No. 136124: Rio San Pedro, San Lucas, Chihuahua, Mexico.

*Etheostoma (Psychromaster) tuscumbia* Gilbert and Swain. — No. 104244: Harris Spring Pond, about 3 mi. n. of Decatur, Limestone Co., Ala.

*Etheostoma (Catomotus) squamiceps* Jordan. — No. 96363: Hurricane Cr.,

branch of Stone R., Cumberland R. system, near Nashville, Davidson Co., Tenn. No. 121270: North Fork Cr., Duck R. drainage, n. of Shelbyville, Bedford Co., Tenn. No. 121546: Rutherford Cr., Duck R. drainage, Williamson Co., Tenn.

*Etheostoma (Catonotus) kennicotti* (Putnam). — No. 144500: Little Wolf Cr., trib. to Clear Fork R., upper Cumberland R. drainage, 2.5 mi. w. of Pleasant View, Whitley Co., Ky. No. 104222: Johns Cr., Tennessee R. drainage, Anderson Co., Tenn.

*Etheostoma (Catonotus) flabellare flabellare* Rafinesque. — No. 157469: Little Doe Cr., trib. to Watauga Reservoir, just above hwy. 67, Doeville, Johnson Co., Tenn. No. 103620: stream 6.6 mi. e. of Lafollette, Tennessee R. system, Campbell Co., Tenn. No. 115987: Johns Cr., Tennessee R. system, Anderson Co., Tenn. No. 126478: Tippecanoe R., 1 mi. s. of Leesburg on hwy. 15, Kosciusko Co., Ind. No. 102060: Tiffin R., outlet of Devils Lake, T. 6 S., R. 1 E., sec. 7, Lenawee Co., Mich. No. 81907: Huron R., T. 3 N., R. 8 E., sec. 3, Oakland Co., Mich. No. 98840: Ellicott Cr., Lake Erie drainage, near Mill Grove, Erie Co., N. Y. No. 98812: Murder Cr., Lake Erie drainage, near Akron, Erie Co., N. Y. No. 110760: Shenango R., 6 mi. n. of Mercer, Mercer Co., Pa. No. 147672: New R. at Virginia state line, 5 mi. nw. of Sparta, Alleghany Co., N.C. No. 95352: Radford Brook, about 2 mi. above mouth, trib. to New R., near Radford, Montgomery Co., Va. No. 118866: Second Cr., trib. to Greenbriar R., Gap Mills, Monroe Co., W. Va. No. 95240: Turkey Cr., trib. to Indian Cr., trib. to New R., s. central Monroe Co., W. Va. No. 95264: Camp Cr., at Camp Cr. P. O., trib. to Bluestone R., Kanawha R. system, Mercer Co., W. Va. No. 119493: Spring Cr., trib. to Greenbriar R., 2 mi. sw. of Renick, Greenbriar Co., W. Va. No. 95211: trib. to Greenbriar R., s. edge of White Sulphur Springs, Greenbriar Co., W. Va. No. 108174: Muddlety Cr., trib. to Gauley R., about 5 mi. n. of Summerville, on U. S. hwy. 19, Nicholas Co., W. Va. No. 136860: Moores Run, Cacapon R. and Potomac R. drainages, 2 mi. n. of Wardensville, Hardy Co., W. Va. No. 95322: Tinker Cr., trib. to Roanoke R., just above Cloverdale, Botetourt Co., Va. No. 95348: Roanoke R., Salem, Roanoke Co., Va. No. 139441: Stewart Cr., trib. to Fisher R., U. S. hwy. 52 between White Plains and Mt. Airy, Surry Co., N. C.

*Etheostoma (Catonotus) flabellare lineolatum* (Agassiz). — No. 96133: outlet of Long Lake, 15 mi. se. and 2 mi. e. of Spooner, Washburn Co., Wis. No. 103075: Hickory Cr. [= Elm Spring Run], 3 mi. above U. S. fish hatchery, Neosho, Newton Co., Mo. No. 116776: Saline Cr., trib. to Grand R., T. 21 N., R. 20 E., sec. 26, Moyes Co., Okla. No. 120907: Eaton Branch, Duck R. drainage, n. of Manchester, Fredonia Road, Coffee Co., Tenn.

*Etheostoma (Catonotus) obeyense* Kirsch. — No. 125463: Sewell Cr., southern trib. to Wolf R., e. of Millers Chapel, Pickett Co., Tenn.

*Etheostoma (Catonotus) virgatum* (Jordan). — No. 96942: Parker Branch and Rockcastle R., n. tip of Laurel Co., Ky.

*Etheostoma (Ioa) vitreum* (Cope). — No. 89390: Patuxent R., 24 mi. e. of Washington, 2.5 mi. n. of Defense hwy., Prince Georges and Arundel cos., Md.

*Etheostoma (Hololepis) edwini* (Hubbs and Cannon). — No. 107047: Santa Fé R., Poe Springs, Alachua Co., Fla. No. 158182: Taluga R., 3 mi. se. of Bristol, hwy. 19, Liberty Co., Fla. No. 158204: Chipola R., 6 mi. n. of

Marianna, Jackson Co., Fla. No. 110972: Spring Cr., 1 mi. below dam, 3 mi. se. of Marianna, Jackson Co., Fla. No. 155506: cr. on hwy. 87 and 89, at Milton, Santa Rosa Co., Fla.

*Etheostoma (Hololepis) serriferum* (Hubbs and Cannon). — Nos. 107055 and 107067: Mingo Cr., Cumberland and Sampson cos., N. C. No. 107063: Buffalo Cr., Johnston Co., N. C. No. 94658: Little R., Neuse R. system, near Wendell, Wake Co., N. C.

*Etheostoma (Hololepis) zoniferum* (Hubbs and Cannon). — No. 124012: Slough Lake, East Opintlocco Cr., 5 mi. se. of Tuskegee, Macon Co., Ala.

*Etheostoma (Hololepis) gracile* (Girard). — No. 154781: Murphys Pond near Clinton, trib. to Mississippi R., Hickman Co., Ky.

*Etheostoma (Hololepis) fusiforme fusiforme* (Girard). — No. 107087: Bennett Brook and Pond, trib. to Stony Brook, 2 mi. e. of Ayer on hwy. 2, Merrimack R. system, Middlesex Co., Mass.

*Etheostoma (Hololepis) fusiforme erochromum* (Cope). — No. 109565: Cranberry bog ditch, Lakehurst, Ocean Co., N. J.

*Etheostoma (Hololepis) barratti* (Holbrook). — No. 155201: Savannah Migratory Waterfowl Refuge, Jasper Co., S. C. No. 107083: Wassamassaw Swamp, hwy. 31, Berkeley Co., S. C.

*Etheostoma (Hololepis) saludae* (Hubbs and Cannon). — No. 109104: Slatestone Cr., 8 mi. from Columbia, Richland Co., S. C.

*Etheostoma (Hololepis) collis* (Hubbs and Cannon). — No. 94546: Steele Cr., Rock Hill, Catawba R. system, York Co., S. C.

*Etheostoma (Microperca) proeliare* (Hay). — No. 146493: Bayou de Siard, near Monroe, Ouachita Parish, La. No. 146617: small cr., trib. to Comite and Amite rivers, 1 to 2 mi. s. of Centreville, Wilkinson Co., Miss. No. 152995: Floodway ditches 81 and 1, 4 mi. e. of Bennett on hwy. M-84, Dunklin Co., Mo. No. 153258: Drainage ditch, trib. to Mississippi R., 1 mi. e. of Anniston on road DD., Mississippi Co., Mo.

*Etheostoma (Microperca) microperca* Jordan and Gilbert. — No. 88956: Railroad Lake, Pere Marquette R. system, at Bitely, sec. 27, Lilley Twp., Newaygo Co., Mich. No. 88966: Mill Lake, Pere Marquette R. system, sec. 27, Lilley Twp., Newaygo Co., Mich.

*Etheostoma (Microperca) fonticola* (Jordan and Gilbert). — No. 111007: San Marcos R., at San Marcos, Hays Co., Tex. No. 160752: San Marcos R., near State Fish Hatchery, Hays Co., Tex.







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