5-1978

Distribution of Etheostoma nigrum Rafinesque, Etheostoma olmstedi Storer, and their introgressive hybrid populations in the James River drainage

John Edward Clark

DISTRIBUTION OF *ETHEOSTOMA NIGRUM* RAFINESQUE, *ETHEOSTOMA OLMSTEDI* STORER, AND THEIR INTROGRESSIVE HYBRID POPULATIONS IN THE JAMES RIVER DRAINAGE

By

John Edward Clark

A Thesis

Submitted to the Graduate Faculty

of the University of Richmond

in Candidacy

for the Degree of

Master of Science

in Biology

May 1978

DISTRIBUTION OF *ETHEOSTOMA NIGRUM* RAFINESQUE, *ETHEOSTOMA OLMSTEDI* STORER, AND THEIR INTROGRESSIVE HYBRID POPULATIONS IN THE JAMES RIVER DRAINAGE

A Thesis

Presented to the Faculty of the Graduate School

of the University of Richmond

in Partial Fullfillment of the Requirements of the

Degree of Master of Science

William S. Woolcott

S. C. Schaefer

W. R. West Jr.

F. B. Leftwich

Nolan E. Rice

by

John Edward Clark

May 1978

John W. Bird

Wilton R. Tenney

David W. Towle

J. C. Strickland

R. Dean Decker

TABLE OF CONTENTS

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to the following people who not only made this study possible, but enjoyable: Dr. G. C. Schaefer, Dr. W. R. West, members of my committee, and Dr. J. W. Bishop for their criticisms, encouragement, and aid in the preparation of this manuscript; Dr. R. W. Jenkins, for suggesting the study, providing specimens from the Roanoke fish collection, and clarifying certain aspects of this problem; and the many friends who contributed their time, ideas, and encouragement in the collection of specimens and preparation of this thesis: T. Armstrong, J. Armstrong, J. Bazeman, T. Blair, M. Caldwell, E. Coppedge, B. Griggs, S. Jennings, B. Kohen, T. Lane, G. Maurakis, J. Maurakis, M. Pritchett, B. Pritchett, J. Sheridan, and P. Yerby.

Much more than my special thanks are due to Dr. W. S. Woolcott, chairman of my thesis committee. His help and criticism throughout the study, suggestions in the statistical analysis of data, and the vast amount of time and energy he devoted to the preparation of the manuscript was invaluble and deserves more than this brief recognition.

ABSTRACT

An analysis of proportional measurements and meristic characters of *Etheostoma nigrum* and *E. olmstedi* identified five populations within the James River drainage. *Etheostoma nigrum* inhabited the montane and piedmont areas through the Fall Line; *E. o. atromaculatum* was distributed throughout the tidal river and its lower tributaries; and *E. o. olmstedi* was restricted to creeks on the upper coastal plain. Appomattox River and Falling Creek contained introgressive hybrid populations with character frequency distributions intermediate to those of *E. nigrum* and *E. o. olmstedi*. It is proposed that *E. nigrum* probably entered these drainages through stream piracy on piedmont tributaries of the James and interbred with an established population of *E. o. olmstedi*.

INTRODUCTION

The darter subgenus *Boleosoma* (Percidae) is represented in the James River drainage system by the Johnny darter, *Etheostoma nigrum* Rafinesque, the longfin darter, *E. longimanum* Jordan, and two subspecies of the tesselated darter, *E. olmstedi olmstedi* Storer and *E. o. atromaculatum* Girard (Jenkins, 1971; Cole, 1967 and 1971). *Etheostoma longimanum*, endemic to the upper James, differs from the other two species by having two anal spines rather than one. The closely related species *E. nigrum*, a piedmont and montane form, and *E. olmstedi*, a coastal plain darter, can be distinguished from each other by the number of rays in the dorsal and pectoral fins and the number of infraorbital canal pores (Cole, 1965 and 1967). Zorach (1971) questioned the subspecific status of *E. o. olmstedi* (which occurs in creek headwaters) and *E. o. atromaculatum* (which occurs in lower creeks and rivers) after studying their distribution in the lower James River and Roanoke River tributaries.

Etheostoma olmstedi and *E. nigrum* occur sympatrically only in the Lake Ontario drainage. Stone (1947) found no evidence of hybridization in this zone of overlap; however Cole (1958 and 1965) reported hybrid swarms and possible massive intergradation between these populations. Cole (1958 and 1965) concluded that the direction of introgression was from *E. nigrum* into *E. olmstedi*. McAllister (1972), the only other investigator to report hybridization between the two species, found that hybrids constituted 7.6 per cent of the Ottawa River population with no clear evidence for intergradation. As E. nigrum and E. olmstedi occur allopatrically in the same river system in the Atlantic Coast drainages (Cole, 1971), the possibility of their hybridization was not considered; however, populations of E. nigrum in the Appomattox River drainage, a tributary of the lower James River, have a high percentage of complete infraorbital canals, an E. olmstedi characteristic (Jenkins, 1973. personal communication). The present study was initiated to determine the distribution of E. nigrum and E. olmstedi in the James River drainage and to define the extent of introgression between the two species.

MATERIALS AND METHODS

Specimens Examined

Eight hundred and ninety four specimens from 70 field collections were examined. The collections are listed in an upstream-downstream sequence of the James River and its tributaries. Collections designated as RC are from the Roanoke College museum. Other collections are in the University of Richmond fish collection and are designated by catalog number, number of specimens (in parenthesis), locality and date.

Upper James River: 3478 (3), Cowpasture R., Bath Co., 25 October 1975; 2990 (8), Craige Cr., Craige Co., 31 July 1968; 1888 (9), Catawba Cr., Roanoke Co., 5 July 1963; 2951 (3), Partridge Cr., Amherst Co., 16 December 1966; 2557 (4), Partridge Cr., Amherst Co., 9 April 1968; 2488 (1), Partridge Cr., Amherst Co., 6 April 1967; 2972 (2), Partridge Cr., Amherst Co., 5 May 1970; 3779 (1), James River at Bremo Bluff, Buckingham-Fluvanna Co., 16 September 1971; 3776 (1), James River at Bremo Bluff, Buckingham-Fluvanna Co., 18 October 1971; 3789 (1), James River at Bremo Bluff, Buckingham-Fluvanna Co., 29 August 1972; 3778 (1), James River at Bremo Bluff, Buckingham-Fluvanna Co., 3 January 1972; 3786 (1), James River at Bremo Bluff, Buckingham-Fluvanna Co., 26 September 1972; 3782 (3), James River at Bremo Bluff, Buckingham-Fluvanna Co., 21 February 1974; 3781 (1), James River at Bremo Bluff, Buckingham-Fluvanna Co., 2 March 1972; 3784 (2), James River at Bremo Bluff, Buckingham-Fluvanna Co., 11 September 1973; 3777 (1), James River at Bremo Bluff, Buckingham-Fluvanna Co., 20 September 1971; 3783 (1), James River at Bremo Bluff, Buckingham-Fluvanna Co., 30 November 1973; 3785 (1), James River at Bremo Bluff, Buckingham-Fluvanna Co., 17 August 1972; 1840 (88), Willis R., Buckingham Co., 25 June 1964; 2380 (8), Ohio Cr., Albemarle Co., 15 April 1965; 2296 (17), Rock Castle and Tolier Cr., Albemarle Co., 1 April 1965; 2010 (44), Rivanna R., Fluvanna Co., 16 October 1964; 2892 (6), Beavordam and Buffalo Cr., Goochland Co., 24 September 1969; 2908 (5), Beavordam and Buffalo Cr., Goochland Co., 17 October 1969; 3576 (2), Beavordam and Buffalo Cr., Goochland Co., 3 July 1976; 2898 (4), Beavordam and Buffalo Cr., Goochland, 17 October 1969; 1761 (28), Tuckahoe Cr., Goochland Co., 4 June 1964; 3522 (12), Tuckahoe Cr., Goochland Co., 6 June 1976; 2809 (33), Tuckahoe Cr., Goochland Co., 1 October 1969; 3764 (8), James River in City of Richmond, Chesterfield-Henrico Co., 18 August 1976.

Appomattox River: 2214 (45), Appomattox River, Appomattox Co., 20 October 1964; RC (13), Bush R., Prince Edward Co., 7 March 1974; RC (27), Rice Cr., Prince Edward Co., 23 May 1975; RC (17), Mountain

Cr., Prince Edward Co., 22 May 1975; RC (31), Nibbs Cr., Amelia Co., 8 March 1974; 3598 (41), Smacks Cr., Amelia Co., 7 August 1976; 3770 (31), Beavorpond Cr., Amelia Co., 17 March 1977; 3725 (49), Whipponock Cr., Dinwiddie Co., 17 March 1977; 3765 (3), Appomattox River at Appomattox Dam, Chesterfield-Dinwiddie Co., 28 March 1977; 3749 (22), Creek 2 km below Appomattox Dam, Dinwiddie Co., 28 March 1977.

Lower James River: 3769 (2), James River at bottom of Fall Line, Chesterfield-Henrico Co., 8 September 1976; 3766 (1), James River at Chesterfield Power Station, Chesterfield Co., 25 March 1977; 3767 (1), James River at Chesterfield Power Station, Chesterfield Co., 21 April 1977; 3605 (15), Bailey Cr., Henrico Co., 5 October 1976; 3505 (38), Bailey Cr., Henrico Co., 12 June 1976; 3775 (19), Swift Cr. at Rt. 1, Chesterfield Co., 11 May 1977; 3484 (46), Swift Cr. at Rt. 631, Chesterfield Co., 22 May 1976; 3773 (3), First Branch of Swift Cr., Chesterfield Co., 7 May 1977; 3774 (2), Second Branch of Swift Cr., Chesterfield Co., 7 May 1977; 3759 (11), Swift Cr. at Rt. 653, Chesterfield Co., 21 March 1977; 1872 (8), Swift Cr. at Rt. 667, Chesterfield Co., 11 July 1964; 3734 (23), East Run, Charles City Co., 23 March 1977; 3627 (17), Herring Cr., Charles City Co., 19 October 1976; 3763 (2), Herring Cr., Charles City Co., 31 October 1975; 3536 (2), Grassy Swamp Cr., Hanover Co., 13 June 1976; 3572 (4), Beavor dam Cr., Hanover Co., 17 July 1976; 3365 (2), Beavor dam Cr., Hanover Co., 8 April 1958; 178 (3), Millpond Cr., Henrico Co., 8 December 1956; 3590 (34), Crumps Swamp Cr., New Kent Co., 3 August 1976; 3770 (1), Jones Run, New Kent Co., 4 August 1976; 3767 (10), Collin's Run, Charles City Co., 29 March 1977; 3768 (5), Barrows Cr., Charles City Co., 29 March 1977; 187 (5), Diascund Cr., New Kent-James City Co., 30 December 1956.

Falling Creek: 3494 (2), Falling Cr. at Rt. 1, Chesterfield Co., 29 May 1976; 3514 (16), Falling Cr. at Rt. 638, Chesterfield Co., 29 May 1976; 3776 (5), Falling Cr. at Rt. 638, Chesterfield Co., 16 May 1977; 3768 (15), Pocoshock Cr. at Rt. 650, Chesterfield Co., 2 May 1977; 3771 (3), Falling Cr. at Rt. 651, Chesterfield Co., 2 May 1977; 3772 (6), Falling Cr. at Rt. 653, Chesterfield Co., 11 May 1977; 3762 (8), Falling Cr. at Rt. 667, Chesterfield Co., 21 March 1977.

Methods

The methods of Hubbs and Lagler (1958) were followed to ascertain counts and proportional measurements from preserved specimens larger than 30 mm. Where applicable, only left side counts were made. Variations were examined on numbers of dorsal spines, dorsal soft rays, anal soft rays, pectoral rays, pelvic rays, caudal rays, lateral line scales, scales above lateral line, and scales below lateral line. The infraorbital, supratemporal, and preoperculomandibular canal pores were counted and the canals described as complete or incomplete if interrupted. Squamation was quantified by a modification of the squamation index of Cole (1967) which was later used by Zorach (1971). The nape, cheek, breast, and belly were initially described as either naked, partially scaled or fully scaled. A composite index was constructed by assigning the values 0 (naked), 1 (partially scaled) or 2 (fully scaled) to the nape, cheek, breast, and belly and summing the four values. Values range from 0 (no squamation) to 8 (complete squamation). The opercular shape, lip position relative to the snout, caudal fin shape, caudal fin bars, lateral markings, genital papillae, and various internal characteristics were examined. Body depth, depth of caudal peduncle, length of caudal peduncle, predorsal length, forehead length, length of anal base, length of depressed dorsal, length of depressed anal, height of first dorsal spine, length of pectoral fin, head length, depth of head, head width, snout length, suborbital width, length of cheek, orbit length, length of upper jaw, and width of gape were measured to the closest 0.1mm with dial caliper and expressed as a proportion of the standard length. In addition, the following proportions were calculated: pectoral fin length to head length, head depth to head length, snout length to length of upper jaw, length of upper jaw to gape width, length of cheek to gape width, anal fin length to anal fin base, anal fin length to caudal peduncle length, snout length to head length, upper jaw length to head length, gape width to head length, length of cheek to head length, predorsal length to pectoral fin length, head depth to pectoral fin length, anal fin length to caudal peduncle depth, anal base to caudal peduncle depth, upper jaw length to snout length, gape width to snout length, orbit length to snout length, gape width to upper jaw length, orbit length to upper jaw length, orbit length to gape width, and predorsal length to forehead length. Fifteen meristic characters had discriminatory value for separating populations: dorsal spines, dorsal soft rays, anal soft rays, pectoral rays, lateral line scales, scales above lateral line, scales below lateral line, infraorbital canal pores, preoperculomandibular canal pores; proportional measurements were length of dorsal fin, length of anal fin, and length of anal base. In addition to the squamation index, two character indices are presented. The first, that of Cole (1965), is a summation of the pectoral rays, infraorbital canal pores, and second dorsal rays. The second index was devised by summing values assigned to nine meristic characters that showed a difference of 70 per cent or greater between the populations of E. nigrum and E. olmstedi. The characters and assigned values are as follows: dorsal rays, 0 (10 or less), 1 (11), 2 (12), 3 (13), and 4 (14 or more); pectoral rays, 0 (11 or less), 1 (12), 2 (13), 3 (14 or more); anal rays, 0 (7 or less), 1 (8 or more); lateral line scales, 0 (39 or less), 1 (40-43), 2 (44-47), 3 (48 or more); scales above lateral line, 0 (3 or less), 1 (4), 2 (5), 3 (6 or more); scales below lateral line, 0 (5 or less), 1 (6), 2 (7), 3 (8 or more); pores in the infraorbital canal, 0 (6 or less), 1 (7), 2 (8 or more); pores in the preoperculomandibular canal, 0 (10 or less), 1 (11 or more); and the squamation index value.

Statistics were computed on a Wang Model 600 Series, and, unless stated otherwise, significant differences are at the 0.05 confidence level. Per cent of separation was determined by the method proposed by Ginsburg (1938). Proportional measurements are presented following the graphical design of Hubbs and Hubbs (1953). The populations were graphically analyzed using the methods outlined by Anderson (1949).

RESULTS

Five populations of E. nigrum and E. olmstedi in the James River drainage; E. n. nigrum, E. o. olmstedi, E. o. atromaculatum, and two populations which show introgression, were distinguished statistically. Characters of E. n. nigrum, which inhabits the piedmont and montane region of the James River and its tributaries, were analyzed and the results coincide with those of Cole (1967 and 1971). No significant differences were found among populations; therefore data were combined and the results used for comparison with populations of E. n. nigrum and E. olmstedi from other parts of the James River drainage. Character analysis of specimens from below the Fall Line support the conclusions of Cole (1967) that two subspecies, E. o. olmstedi (an upper tributary form) and E. o. atromaculatum (a lower tributary and river form) occupy the coastal plain drainage of the James River (Tables 1-13). The 75 per cent level of separation between populations is considered significant for recognizing subspecies (Ginsburg, 1938). That level was exceeded when a line was drawn between 47 and 48 lateral line scales (82.3 %; Table 1), between the 12 and 13 sum of scales above and below lateral line (75.1 %; Table 2), and between 20 and 21 character indices (93.9 %; Table 13). Also, a significant separation was attained when a line was drawn between partially scaled and naked breast (87.6 %; Table 10); between complete and partially scaled cheek (86.3 %; Table 9), nape (89.8 %; Table 8), and belly (92.8 %; Table 11) and between 4 and 5 squamation indices (92.2 %; Table 12).

Larger average character divergences values occured between E. n. nigrum and E. o. atromaculatum than between E. n. nigrum and E. o. olmstedi (Tables 14-24; 32-46). Values are presented first for E. n. nigrum vs E. o. atromaculatum and then for E. n. nigrum vs E. o. olmstedi for the following characters (line of best separation and per cent of separation in parenthesis): lateral line scales (43-44, 97.7 %; 41-42, 88.8 %; Tables 14 and 32); scales above lateral line (4-5, 94.3 %; 4-5, 90.2 %; Tables 15 and 33); scales below lateral line (6-7, 92.5 %; 6-7, 85.1 %; Table 34); sum of scales above and below lateral line (11-12, 92.5 %; 10-11, 87.8 %; Table 35); dorsal soft rays (12-13, 96.5 %; 12-13, 94.0 %; Tables 16 and 36); pectoral rays (11-12, 93.0 %; 11-12, 75.3 %; Tables 17 and 37); anal soft rays (7-8, 89.8 %; 7-8, 72.5 %; Tables 18 and 38); infraorbital canal pores (7-8, 95.0 %; 7-8, 92.5 %; Tables 20-21 and 39-40); preoperculomandibular canal pores (10-11, 79.0 %; 10-11, 71.4 %; Table 22); cheek squamation (naked-partially scaled, 96.5 %; naked-partially scaled, 95.8 %; Table 42); breast squamation (naked-partially scaled, 96.8 %; naked-partially scaled, 59.2 %; Table 43); nape squamation (partially scaled-fully scaled, 96.0 %; naked-partially scaled, 86.3 %; Table 41); belly squamation (partially scaled-fully scaled, 93.8 %; naked-partially scaled, 58.3 %; Table 44); squamation index (4-5, 98.0 %; 1-2, 86.3 %; Table 45); and the character index (12-13, 100 %; 10-11, 99.0 %; Tables 24 and 46).

There were no significant differences among the populations from the Appomattox River and its tributaries, therefore these data were combined and compared with those of E. n. nigrum from the James River above the Fall Line and the two subspecies of E. olmstedi from the coastal plain. The results indicate that the Appomattox population is more lake E. nigrum than E. olmstedi even though means of eight of nine meristic characters differ significantly. Counts of the lateral line scales, scales above lateral line, dorsal soft rays, pectoral rays, dorsal spines, infraorbital canal pores, and preoperculomandibular canal pores were significantly higher than corresponding counts of the upper James River drainage population and approached those of E. o. olmstedi (Tables 14-17 and 19-22). The anal ray count was significantly lower than E. n. nigrum (Table 18).

Additional comparisons of quanitative characters showed that the Appomattox River population differed from that of the upper James at the racial (average divergence 60-75 %) or subspecific level when a line was drawn between 6 and 7 infraorbital canal pores (77.2 %; Table 20), between 10 and 11 preoperculomandibular pores (64.1 %; Table 22), between 39 and 40 lateral line scales (64.6 %; Table 14) and between 8 and 9 dorsal spines (63.3 %; Table 19). An average divergence of 68.1 % separated the two populations when a line was drawn between 5 and 6 character indices (Table 24).

Fifty-five specimens from six sampling sites in the Falling Creek drainage were compared by an Analysis of Variance test for single variable of classification (Tables 25-31). Significant differences at the 0.01 confidence level were obtained between sampling locations in five of the meristic characters; scales above lateral line (F = 3.76; Table 25), sum of scales above and below lateral line (F = 4.48; Table 26), dorsal soft rays (F = 4.01; Table 27), and anal soft rays (F = 6.48; Table 28). At the 0.05 confidence level pectoral rays (F = 2.93; Table 29) were significantly different. The squamation index (F = 7.80; Table 30) and the character index (F = 13.78; Table 31) showed significant differences at the 0.01 level of confidence.

Small sample size and extreme variance precluded a definitive analysis of the Falling Creek population. A cursory examination indicated that an upstream-downstream introgression trend from E. n. nigrum to E. o. olmstedi characters existed; therefore, for further analysis, the populations were divided into upper Falling Creek (14 specimens), middle Falling Creek (18 specimens) and lower Falling Creek (21 specimens).

Meristic and proportional characters of the upper Falling Creek population were not significantly different from those of the James River (Tables 32-46). Middle Falling Creek darters were significantly different from E. n. nigrum in lateral line scales (Table 32), scales above lateral line (Table 33), scales below lateral line (Table 34), sum of scales above and below lateral line (Table 35), dorsal soft rays (Table 36), squamation index (Table 44) and character index (Table 46). Lower Falling Creek specimens differed significantly in lateral line scales (Table 32), scales above lateral line (Table 33), scales below lateral line (Table 34), sum of scales above and below lateral line (Table 35), infraorbital canal pores (Table 39), dorsal soft rays (Table 36), pectoral rays (Table 37), anal soft rays (Table 38), squamation index (Table 44), and character index (Table 46).

Proportional measurements were of relatively little value in distinguishing the Boleosoma populations because only two proportional measurements, length of the depressed anal fin to anal base and length of dorsal fin to body length, out of 20 examined showed significant differences among the five populations of the James River drainage (Figs. 2-4).

DISCUSSION

Many hybrid combinations are known throughout Teleostomi (Schwartz, 1972). Natural intrageneric and even intergeneric hybrids have been described in the family Percidae by Hubbs (1955) and in 1967 Hubbs demonstrated that virtually any hybrid combination can be made between any two darter species under artificial conditions. Most hybrid combinations have been sterile and introgression is extremely rare; however, interspecific introgression in darters was reported between Percina notogramma and P. peltata (Loos and Woolcott, 1969), Etheostoma spectabile and E. radiosum cyanorum (Branson and Cambell, 1969), and Etheostoma nigrum and E. olmstedi (Cole, 1965).

The Appomattox River and Falling Creek populations of Boleosoma exhibit many of the characteristics presented by Gilbert (1961) that distinguish introgressive populations. Analysis of the data reveals that 7 of 9 meristic characters of darters from the Appomattox River, 8 of 9 in lower Falling Creek and 5 of 9 in middle Falling Creek were significantly different from both E. n. nigrum and E. olmstedi and lie between the parental extremes. Figures 5-8 graphically depict the intermediacy of the two intergrade populations. The Appomattox River and middle Falling Creek populations show introgression from _E. n. nigrum_; which would imply that it is the recurrent parental species.

Swift Creek, which lies between the Appomattox River drainage basin and Falling Creek (Fig. 1), and flows from the Piedmont across the Fall Line to the coastal plain, contains _Boleosoma_ populations in its headwaters that do not differ significantly from other populations of coastal plain _E. o. olmstedi_. This supports the conclusion that the intermediate populations in the Appomattox River and Falling Creek, which resemble _E. n. nigrum_, are not the product of geographical variation but rather represent fishes that entered the two systems by upstream stream piracy from the James River. The location of Swift Creek precludes the possibility of stream capture of upstream James tributaries.

Environmental disruption has been proposed as one of the factors that lead to the formation of hybrid swarms (Anderson, 1949; Mayr, 1963). Falling Creek meets this requirement with a series of three dams and numerous conduits in the lower two-thirds of its drainage which have altered the habitat extensively. It is proposed that introduction of _E. n. nigrum_ into the headwaters of the Appomattox River united two previously allopatric species with hybridization resulting. Because character distributions of the Appomattox population resemble _E. n. nigrum_, perhaps the piedmont quality of this drainage system selectively favors _E. n. nigrum_ characters. No hybrids have been found between the two species in the James River proper which may be due to the extensive Fall Line and because the E. o. atromaculatum in the main stream have spawning habits that differ from those of E. n. nigrum.

The problem of subspecific recognition of E. o. olmstedi and E. o. atromaculatum was not considered an objective of this study, however the 75 per cent or greater average divergence in the frequency distributions of six meristic characters of E. o. olmstedi and E. o. atromaculatum indicates that the two populations are subspecies and that the zone of intergradation between E. o. olmstedi and E. o. atromaculatum is not as large as that described by Zorach (1971) for the lower tidewater James.

Cole (1971) postulated that E. nigrum and E. olmstedi evolved in isolation from common stock in geological times predating Pleistocene glaciation. Etheostoma olmstedi then moved into the James River basin within the early Pliestocene and utilized expanded coastal plain drainages during periods of sea level decline. The Fall Line probably limited E. olmstedi to the lower piedmont and coastal streams. The E. nigrum population represents an intrusion from the west as a result of stream capture between the James River headwaters and the New River.

In summary; greater similarities in habitat preference and morphological counts between E. n. nigrum and the tributary form from the lower James River, E. o. olmstedi, than those between E. n. nigrum and E. o. atromaculatum suggest that E. o. olmstedi and E. n. nigrum form the parental populations of the hybrids in the Appomattox River and Falling Creek. I postulated that the *E. n. nigrum* of the Appomattox River and the headwaters of Falling Creek entered these systems by stream piracy from piedmont tributaries of the James River and the cohabitation of this species with *E. o. olmstedi* was conducive to hybridization.

LITERATURE CITED

Anderson, E. 1949. Introgressive hybridization. John Wiley and Sons, Inc. New York. 199 p.

Branson, B. A. and J. B. Campbell. 1969. Hybridization in the darters *Etheostoma spectabile* and *Etheostoma radiosum cyanorum*. Copeia 1969: 70-75.

Cole, C. F. 1958. The taxonomy of the percid fishes of the genus *Etheostoma*, subgenus, *Boleosoma*, of the eastern United States. Diss. Abstr. 18: 1155-1156.

____. 1965. Additional evidence for separation of *Etheostoma olmstedi* Storer from *Etheostoma nigrum* Rafinesque. Copeia 1965. 8-13.

____. 1967. A study of the eastern Johnny darter, *Etheostoma olmstedi* Storer (Teleostei, Percidae). Chesapeake Sci. 8: 28-51.

____. Status of the darters, *Etheostoma nigrum*, *E. longimanum* and *E. podostemone* in Atlantic drainages (Teleostomi, Percidae, subgenus *Boleosoma*). p. 119-138. In P. C. Holt (ed.) The distributional history of the biota of the southern Appalachians. Part III. Va. Polytech. Inst. and State Univ. Res. Div. Monogr. 4: 306 p.

Gilbert, C. R. 1961. Hybridization versus intergradation: an inquiry into the relationship of two cyprinid fishes. Copeia 1961: 181-192.

Ginsburg, I. 1938. Arithmetic definition of the species, subspecies and race concept, with a proposal for a modified nomenclature. Zoologica 23: 253-286.

Hubbs, C. L. 1955. Natural hybridization in fishes. Syst. Zool. 4: 1-20.

____ and Clark Hubbs. 1953. An improved graphical analysis and comparison of series samples. Syst. Zool. 2: 49-56.

____ and K. F. Lagler. 1958. Fishes of the Great Lakes Region. Cranbrook Inst. Sci. Bull. (26): 1-27.

Hubbs, Clark. 1967. Geographic variation in survival of hybrids between etheostomatine fishes. Bull. Tex. Mem. Mus. 13: 1-72.

Jenkins, R. E., E. A. Lachner, and F. J. Schwartz. 1971. Fishes of the central Appalachian drainages: their distribution and dispersal. p. 43-117. In P. C. Holt (ed.) The distributional history of the biota of the southern Appalachians. Part III. Va. Polytech. Inst. and State Univ. Res. Div. Monogr. 4: 306 p.

Loos, J. J. and W. S. Woolcott. 1969. Hybridization and behavior in two species of Percina (Percidae). Copeia 1969: 374-385.

Mayr, E. 1963. Animal species and evolution. The Belknap Press. Harvard University Press, Cambridge Mass. 797 p.

McAllister, D. E., P. Jolicoiur, and H. Tsuyuki. 1972. Morphological and myogen comparison of Johnny and tessellated darters and their hybrids, genus Etheostoma, near Ottawa, Canada. J. Fish. Res. Bd. Canada 29: 1173-1180.

Schwartz, F. J. 1972. World literature to fish hybrids with an analysis by family, species, and hybrid. Gulf Coast Research Laboratory. Ocean Springs, Miss. 328 p.

Stone, F. L. 1947. Notes of two darters of the genus Boleosoma. Copeia 1947: 92-96.

Zorach, T. 1971. Taxonimic status of the subspecies of the tessellated darter, *Etheostoma olmstedi* Storer, in southeastern Virginia. Chesapeake Sci. 11: 254-263.

Table 1. Frequency distribution of lateral line scales in <u>Etheostoma olmstedi atromaculatum</u> and <u>Etheostoma olmstedi olmstedi</u>.

Location	No.	Lateral Line Scales																										
		37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	58	60	61	x̄	S.D.
<u>E. o. atromaculatum</u>																												
James R.	4										1								1	2							52.5	4.4
Bailey Cr.	53							2	3	3	5	3	5	5	8	9	5		3	1	1						49.1	3.1
Lower Herring Cr.	19										2		2	2	1	4	1			2	3	1			1		51.9	4.0
Diascund Cr.	5												1	1			2			1							51.2	2.8
Lower Swift Cr.	19									1	1	2	3	4	2		2			1	2					1	50.4	4.1
<u>E. o. olmstedi</u>																												
East Run	23					1	3	1	6	4	2	2	3			1											45.0	2.4
Grassy Swamp	2											1	1														47.5	0.7
Crumps Swamp	34					1	1	3	7	6	7	3	3	3													45.4	2.0
Beavordam Cr.	6							1	1		2			1	1												46.3	2.7
Millpond Cr.	3						2		1																		42.7	1.2
Jones Run	1											1															47.0	-
Collins Run	10					1	2		1	1	1	1	1		1		1										45.7	3.6
Barrows Cr.	5							2		2		1															44.6	1.7
Upper Swift Cr.	70	1		3	6	4	16	10	16	7	2	2	1	1	1												43.0	2.3

Table 2. Frequency distribution of sum of scales above and below lateral line in *Etheostoma olmstedi atromaculatum* and *Etheostoma olmstedi olmstedi*.

Location	No.	Sum of Scales Above and Below Lateral Line									
		9	10	11	12	13	14	15	16	$\bar{x}$	S.D.
E. o. atromaculatum											
James R.	4					2		1	1	14.2	1.5
Bailey Cr.	53			4	9	18	18	2	2	13.2	1.1
Lower Herring Cr.	19				1	9	7	2		13.5	0.8
Diascund Cr.	5				1	3	1			13.0	0.7
Lower Swift Cr.	19		2	2	10	2	3			12.1	1.2
E. o. olmstedi											
East Run	23		4	8	6	4	1			11.6	1.1
Grassy Swamp	2				2					12.0	-
Crumps Swamp	34		2	5	14	8	4	1		12.3	1.1
Beavordam Cr.	6			3	3					11.5	0.5
Millpond Cr.	3				2		1			12.7	1.2
Jones Run	1				1					12.0	-
Collins Run	10		1	1	4	4				12.1	1.0
Barrows Cr.	5			1	1	2	1			12.6	1.1
Upper Swift Cr.	70	1	12	29	22	4	1	1		11.3	1.0

Table 3. Frequency distribution of dorsal rays in Etheostoma olmstedi atromaculatum and Etheostoma olmstedi olmstedi.

Location	No.	Dorsal Rays 12	13	14	15	16	x̄	S.D.
E. o. atromaculatum								
James R.	4			4			14.0	-
Bailey Cr.	53		18	29	6		13.8	0.64
Lower Herring Cr.	19		6	9	3	1	14.0	0.85
Diascund Cr.	5		2	3			13.6	0.55
Lower Swift Cr.	19		9	6	4		13.7	0.81
E. o. olmstedi								
East Run	23	1	13	8	1		13.4	0.66
Grassy Swamp	2		1	1			13.5	0.71
Crumps Swamp	34		16	17	1		13.6	0.56
Beavordam Cr.	6	1	4	1			13.0	0.63
Millpond Cr.	3	1	2				12.7	0.58
Jones Run	1		1				13.0	-
Collins Run	10		5	4	1		13.6	0.70
Barrows Cr.	5		3	2			13.4	0.55
Upper Swift Cr.	70	12	38	20			13.1	0.67

Table 4. Frequency distribution of pectoral rays in Etheostoma olmstedi atromaculatum and Etheostoma olmstedi olmstedi.

Location	No.	Pectoral Rays					
		11	12	13	14	$\bar{x}$	S.D.
E. o. atromaculatum							
James R.	4			4		13.0	-
Bailey Cr.	53		4	45	4	13.0	0.39
Lower Herring Cr.	19		3	9	7	13.2	0.71
Diascund Cr.	5		1	3	1	13.0	0.71
Lower Swift Cr.	19	1	3	13	2	12.8	0.69
E. o. olmstedi							
East Run	23		12	10	1	12.5	0.59
Grassy Swamp	2		1	1		12.5	0.71
Crumps Swamp	34		9	25		12.7	0.45
Beavordam Cr.	6		3	3		12.5	0.55
Millpond Cr.	3		2	1		12.3	0.58
Jones Run	1			1		13.0	-
Collins Run	10		4	5	1	12.7	0.68
Barrows Cr.	5		3	2		12.4	0.55
Upper Swift Cr.	70	3	36	30	1	12.4	0.60

Table 5. Frequency distribution of anal rays in _Etheostoma olmstedi atromaculatum_ and _Etheostoma olmstedi olmstedi_.

Location	No.	Anal Rays 6	7	8	9	10	11	$\bar{x}$	S.D.
E. o. atromaculatum									
James R.	4			2	1		1	9.0	1.4
Bailey Cr.	53		3	25	20	5		8.5	0.7
Lower Herring Cr.	19			8	10	1		8.6	0.6
Diascund Cr.	5			3	2			8.4	0.5
Lower Swift Cr.	19		2	6	11			8.5	0.7
E. o. olmstedi									
East Run	23	5	8	10				7.2	0.8
Grassy Swamp	2			1	1			8.5	0.7
Crumps Swamp	34	2	19	12	1			7.4	0.7
Beavordam Cr.	6		2	2	2			8.0	0.9
Millpond Cr.	3			2	1			8.3	0.6
Jones Run	1			1				8.0	-
Collins Run	10	1	3	6				7.5	0.7
Barrows Cr.	5		1	3	1			8.0	0.7
Upper Swift Cr.	70	2	18	46	4			7.7	0.6

Table 6. Frequency distribution of infraorbital canal pores in *Etheostoma olmstedi atromaculatum* and *Etheostoma olmstedi olmstedi*.

Location	No.	Infraorbital Canal Pores						
		6	7	8	9	10	$\bar{x}$	S.D.
E. o. atromaculatum								
James R.	4			1	3		8.8	0.50
Bailey Cr.	53		4	43	5	1	8.1	0.50
Lower Herring Cr.	19		2	13	4		8.1	0.57
Diascund Cr.	5			5			8.0	-
Lower Swift Cr.	19	1	1	17			7.8	0.50
E. o. olmstedi								
East Run	23		3	19	1		7.9	0.42
Grassy Swamp	2		1	1			7.5	0.71
Crumps Swamp	34		2	32			7.9	0.24
Beavordam Cr.	6			6			8.0	-
Millpond Cr.	3			3			8.0	-
Jones Run	1			1			8.0	-
Collins Run	10		2	7	1		7.9	0.24
Barrosw Cr.	5			4	1		8.2	0.45
Upper Swift Cr.	70	3	9	56	2		7.8	0.55

Table 7. Frequency distribution of preoperculomandibular pores in *Etheostoma olmstedi atromaculatum* and *Etheostoma olmstedi olmstedi*.

Location	No.	Preoperculomandibular Pores						
		8	9	10	11	12	$\bar{x}$	S.D.
E. o. atromaculatum								
James R.	4			2	2		10.5	0.58
Bailey Cr.	53		3	12	37	1	10.7	0.61
Lower Herring Cr.	19			3	14	2	11.0	0.52
Diascund Cr.	5			1	3	1	11.0	0.71
Lower Swift Cr.	19			6	13		10.7	0.48
E. o. olmstedi								
East Run	23		1	11	11		10.4	0.59
Grassy Swamp	2			1	1		10.5	0.71
Crumps Swamp	34	1	1	5	27		10.7	0.68
Beavordam Cr.	6				6		11.0	-
Millpond Cr.	3			3			10.0	-
Jones Run	1				1		11.0	-
Collins Run	10			6	4		10.4	0.52
Barrows Cr.	5			1	3	1	11.0	0.71
Upper Swift Cr.	70		5	30	33	2	10.5	0.67

Table 8. Frequency distribution of nape squamation in *Etheostoma olmstedi atromaculatum* and *Etheostoma olmstedi olmstedi*.

Location	No.	Nape Squamation		
		Naked	Partially Scaled	Fully Scaled
E. o. atromaculatum				
James R.	4		1	3
Bailey Cr.	53		2	51
Lower Herring Cr.	19		2	17
Diascund Cr.	5			5
Lower Swift Cr.	19		3	16
E. o. olmstedi				
East Run	23	7	16	
Grassy Swamp	2		2	
Crumps Swamp	34		25	9
Beavordam Cr.	6	1	5	
Millpond Cr.	3		3	
Jones Run	1			1
Collins Run	10		8	2
Barrows Cr.	5			5
Upper Swift Cr.	70	11	57	2

Table 9. Frequency distribution of cheek squamation in *Etheostoma olmstedi atromaculatum* and *Etheostoma olmstedi olmstedi*.

Location	No.	Cheek Squamation		
		Naked	Partially Scaled	Fully Scaled
E. o. atromaculatum				
James R.	4			4
Bailey Cr.	53		10	43
Lower Herring Cr.	19		3	16
Diascund Cr.	5			5
Lower Swift Cr.	19		2	17
E. o. olmstedi				
East Run	23	2	21	
Grassy Swamp	2		2	
Crumps Swamp	34		29	5
Beavordam Cr.	6		5	1
Millpond Cr.	3		3	
Jones Run	1			1
Collins Run	10		5	5
Barrows Cr.	5			5
Upper Swift Cr.	70		68	2

Table 10. Frequency distribution of breast squamation in *Etheostoma olmstedi atromaculatum* and *Etheostoma olmstedi olmstedi*.

Location	No.	Breast Squamation		
		Naked	Partially Scaled	Fully Scaled
E. o. atromaculatum				
James R.	4	2		2
Bailey Cr.	53	1	13	39
Lower Herring Cr.	19	2	9	8
Diascund Cr.	5			5
Lower Swift Cr.	19	1	3	15
E. o. olmstedi				
East Run	23	21	2	
Grassy Swamp	2	2		
Crumps Swamp	34	27	7	
Beavordam Cr.	6	6		
Millpond Cr.	3	2	1	
Jones Run	1	1		
Collins Run	10	8	1	1
Barrows Cr.	5	2	3	
Upper Swift Cr.	70	56	12	2

Table 11. Frequency distribution of belly squamation in *Etheostoma olmstedi atromaculatum* and *Etheostoma olmstedi olmstedi*.

Location	No.	Belly Squamation		
		Naked	Partially Scaled	Fully Scaled
E. o. atromaculatum				
James R.	4		1	3
Bailey Cr.	53		1	52
Lower Herring Cr.	19	2	1	16
Diascund Cr.	5			5
Lower Swift Cr.	19			19
E. o. olmstedi				
East Run	23	7	16	
Grassy Swamp	2		2	
Crumps Swamp	34	4	24	6
Beavordam Cr.	6	2	4	
Millpond Cr.	3	3		
Jones Run	1	1		
Collins Run	10		4	6
Barrows Cr.	5		2	3
Upper Swift Cr.	70	44	22	4

Table 12. Frequency distribution of squamation index in <u>Etheostoma olmstedi atromaculatum</u> and <u>Etheostoma olmstedi olmstedi</u>.

Location	No.	Squamation Index									
		1	2	3	4	5	6	7	8	$\bar{x}$	S.D.
<u>E. o. atromaculatum</u>											
James R.	4					2			2	6.5	1.7
Bailey Cr.	53				1	1	4	13	34	7.5	0.9
Lower Herring Cr.	19		1	1		1	1	7	8	6.8	1.7
Diascund Cr.	5								5	8.0	-
Lower Swift Cr.	19		1			1	2	3	12	7.2	1.5
<u>E. o. olmstedi</u>											
East Run	23	3	9	10	1					2.4	0.8
Grassy Swamp	2			2						3.0	-
Crumps Swamp	34		3	17	8	2	1	3		3.7	1.3
Beavordam Cr.	6	1	1	4						2.5	0.8
Millpond Cr.	3		2	1						2.3	0.6
Jones Run	1			1						3.0	-
Collins Run	10			2	5		2		1	4.6	1.6
Barrows Cr.	5					1	2	2		6.2	0.8
Upper Swift Cr.	70	11	26	19	10	2	1		1	2.6	1.3

Table 13. Frequency distribution of the character index in *Etheostoma olmstedi atromaculatum* and *Etheostoma olmstedi olmstedi*.

Location	No.	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	$\bar{x}$	S.D.
										Character Index												
E. o. atromaculatum																						
James R.	4														1	1		2			24.8	1.5
Bailey Cr.	53											2	3	4	10	10	11	8	3	2	24.2	1.9
Lower Herring Cr.	19											1	1	2	1	3		7	4		24.7	2.2
Diascund Cr.	5														1		2		2		25.4	1.7
Lower Swift Cr.	19					1	1					2	3	2		6	3		1		22.2	3.3
E. o. olmstedi																						
East Run	23			1	5	3	2	3	4	1	3	1									15.6	2.4
Grassy Swamp	2							1			1										17.5	2.1
Crumps Swamp	34				1	1	1	7	3	5	7	6		2		1					18.1	2.3
Beavordam Cr.	6				1			1	2	1	1										16.7	2.1
Millpond Cr.	3				1		1		1												15.0	2.0
Jones Run	1									1											18.0	-
Collins Run	10						1	1		2	3	1	1	1							18.7	2.1
Barrows Cr.	5									1	1		1	1			1				21.0	2.7
Upper Swift Cr.	70	1	3	4	14	7	15	10	5	6	4	1									14.9	2.2

Table 14. Frequency distribution of the lateral line scales in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the Appomattox River population.

Population	No.	Lateral Line Scales																											x̄	S.D.
		35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61		
E. nigrum	299	4	10	41	51	76	52	30	19	8	7		1																39.2	1.9
Appomattox River	286		3	13	33	41	61	45	39	30	15	4	1		1														40.5	2.0
E. o. olmstedi	154			1		3	6	7	24	17	32	20	14	11	9	5	3	1	1										44.3	2.6
E. o. atromaculatum	100									2	3	4	9	5	11	12	11	13	10		4	7	6	1			1	1	50.1	3.7

Table 15. Frequency distribution of the scales above lateral line in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the Appomattox River population.

Population	No.	Scales Above Lateral Line						
		3	4	5	6	7	$\bar{x}$	S.D.
E. nigrum	299	53	236	9	1		3.86	0.45
Appomattox R.	286	13	260	13			4.00	0.30
E. o. olmstedi	154		25	103	26		5.01	0.58
E. o. atromaculatum	100		8	72	18	2	5.14	0.57

Table 16. Frequency distribution of the dorsal soft rays in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the Appomattox River population.

Population	No.	Dorsal Soft Rays								
		10	11	12	13	14	15	16	$\bar{x}$	S.D.
E. nigrum	299	17	162	113	7				11.4	0.63
Appomattox R.	286	4	110	153	19				11.6	0.62
E. o. olmstedi	154			15	83	53	3		13.3	0.66
E. o. atromaculatum	100				35	51	13	1	13.8	0.70

Table 17. Frequency distribution of the pectoral rays in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the Appomattox River population.

Population	No.	Pectoral Rays						
		10	11	12	13	14	x̄	S.D.
E. nigrum	299	5	122	166	6		11.6	0.56
Appomattox R.	286	2	88	193	3		11.7	0.50
E. o. olmstedi	154		3	70	78	3	12.5	0.57
E. o. atromaculatum	100		1	11	74	14	13.0	0.54

Table 18. Frequency distribution of the anal soft rays in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromacualtum* and the Appomattox River population.

Population	No.	Anal Rays 3	4	5	6	7	8	9	10	11	$\bar{x}$	S.D.
E. nigrum	299	1		4	67	181	42	4			6.9	0.72
Appomattox R.	286			2	98	163	23				6.7	0.61
E. o. olmstedi	154				10	51	83	10			7.6	0.71
E. o. atromaculatum	100					5	44	44	6	1	8.5	0.73

Table 19. Frequency distribution of the dorsal spines in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the Appomattox River population.

Population	No.	Dorsal Spines						
		7	8	9	10	11	$\bar{x}$	S.D.
E. nigrum	299	13	121	151	14		8.6	0.66
Appomattox R.	286	3	49	207	27		8.9	0.55
E. o. olmstedi	154	1	11	117	25		9.1	0.50
E. o. atromaculatum	100		19	69	11	1	8.9	0.58

Table 20. Frequency distribution of the infraorbital canal pores in Etheostoma nigrum, Etheostoma olmstedi olmstedi, Etheostoma olmstedi atromaculatum and the Appomattox River population.

Population	No.	Infraorbital Canal Pores							
		5	6	7	8	9	10	$\bar{x}$	S.D.
E. nigrum	299	37	180	76	6			6.2	0.66
Appomattox R.	286	4	48	128	93	13		7.2	0.83
E. o. olmstedi	154		3	17	129	5		7.9	0.46
E. o. atromaculatum	100		1	7	79	12	1	8.1	0.52

Table 21. Frequency distribution of the completeness of the infraorbital canals in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the Appomattox River population.

Population	No.	Infraorbital Canal		
		Incomplete	Complete	Percentage Complete
E. nigrum	299	297	2	0.7%
Appomattox R.	286	193	93	32.5%
E. o. olmstedi	154	15	139	90.0%
E. o. atromaculatum	100	4	96	96.0%

Table 22. Frequency distribution of the preoperculomandibular canal pores in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the Appomattox River population.

Population	No.	8	9	10	11	12	$\bar{x}$	S.D.
		Preoperculomandibular Canal Pores						
E. nigrum	299	14	105	135	43	2	9.7	0.79
Appomattox R.	286		19	143	122	2	10.4	0.62
E. o. olmstedi	154	1	7	57	86	3	10.5	0.65
E. o. atromaculatum	100		3	24	69	4	10.7	0.58

Table 23. Frequency distribution of the sum of the pectoral rays, dorsal soft rays, and infraorbital canal pores in <u>Etheostoma nigrum</u>, <u>Etheostoma olmstedi olmstedi</u>, <u>Etheostoma olmstedi atromaculatum</u> and the Appomattox River population.

		Sum of Pectoral Rays, Dorsal Soft Rays and Infraorbital Canal Pores															
Population	No.	26	27	28	29	30	31	32	33	34	35	36	37	38	39	$\bar{x}$	S.D.
<u>E. nigrum</u>	299	2	18	62	101	91	22	2	1							29.1	1.1
Appomattox R.	286		2	8	45	84	83	49	15							30.6	1.3
<u>E. o. olmstedi</u>	154						4	18	39	53	37	3				33.7	1.1
<u>E. o. atromaculatum</u>	100						1	1	5	33	34	19	6		1	34.9	1.2

Table 24. Frequency distribution of the character index in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the Appomattox River population.

Population	No.	Character Index																												$\bar{x}$	S.D.
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28		
E. nigrum	299	3	11	41	53	67	51	31	28	8	2	4																		5.28	1.9
Appomattox R.	286		3	12	18	31	49	48	59	34	17	10	4	1																7.06	2.1
E. o. olmstedi	154										1	3	5	22	11	20	23	15	17	20	9	2	4		1	1				16.31	2.8
E. o. atromaculatum	100														1	1					5	7	8	13	20	16	17	10	2	23.99	2.4

Table 25. Frequency distribution of scales above lateral line in Falling Creek by sampling site.

Location	No.	Scales Above Lateral Line					
		3	4	5	6	$\bar{x}$	S.D.
Rt. 1	2		2			4.0	-
Rt. 638	21		9	11	1	4.6	0.59
Pocoshock Cr.	15		11	4		4.3	0.46
Rt. 651	3		2	1		4.3	0.58
Rt. 653	6	1	5			3.8	0.41
Rt. 667	8		8			4.0	-

Table 26. Frequency distribution of sum of scales above and below lateral line in Falling Creek by sampling site.

Location	No.	Sum of Scales Above and Below Lateral Line						
		9	10	11	12	13	$\bar{x}$	S.D.
Rt. 1	2		1		1		11.0	1.4
Rt. 638	21		2	7	8	4	11.7	0.9
Pocoshock Cr.	15	2	2	8	1	2	10.9	1.2
Rt. 651	3				3		12.0	-
Rt. 653	6	2	3	1			9.8	0.8
Rt. 667	8	1	4	1	2		10.5	1.1

Table 27. Frequency distribution of dorsal soft rays in Falling Creek by sampling site.

Location	No.	Dorsal Soft Rays					
		10	11	12	13	$\bar{x}$	S.D.
Rt. 1	2			1	1	12.5	0.71
Rt. 638	21		5	7	9	12.2	0.81
Pocoshock Cr.	15		3	8	4	12.1	0.70
Rt. 651	3		1	2		11.7	0.58
Rt. 653	6	2	1	3		11.2	0.98
Rt. 667	8		7	1		11.1	0.35

Table 28. Frequency distribution of anal soft rays in Falling Creek by sampling site.

Location	No.	Anal Soft Rays					
		5	6	7	8	$\bar{x}$	S.D.
Rt. 1	2			2		7.0	-
Rt. 638	21		1	7	13	7.6	0.60
Pocoshock Cr.	15	2	7	5	1	6.3	0.82
Rt. 651	3		1	1	1	7.0	1.00
Rt. 653	6		2	2	2	7.0	0.89
Rt. 667	8	1	2	5		6.5	0.76

Table 29. Frequency distribution of pectoral rays in Falling Creek by sampling site.

Location	No.	Pectoral Rays 11	12	13	$\bar{x}$	S.D.
Rt. 1	2		2		12.0	-
Rt. 638	21	5	13	3	11.9	0.63
Pocoshock Cr.	15	4	10	1	11.8	0.56
Rt. 651	3	1	2		11.7	0.58
Rt. 653	6	5	1		11.2	0.41
Rt. 667	8	6	2		11.2	0.46

Table 30. Frequency distribution of the squamation index in Falling Creek by sampling site.

Location	No.	Squamation Index 0	1	2	3	4	5	6	7	x̄	S.D.
Rt. 1	2				1				1	5.0	2.8
Rt. 638	21	3	2	7	3	2	3		1	2.6	1.9
Pocoshock Cr.	15		5	6	2	1	1			2.1	1.2
Rt. 651	3	1	2							0.7	0.6
Rt. 653	6	4	2							0.3	0.5
Rt. 667	8	7	1							0.1	0.3

Table 31. Frequency distribtuion of the character index in Falling Creek by sampling site.

Location	No.	Character Index 2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	$\bar{x}$	S.D.
Rt. 1	2												1				1			15.0	2.8
Rt. 638	21							1	6	3	2	2	1		2	1	1	1	1	11.9	3.5
Pocoshock Cr.	15						1	4	3	3	1		1	2						9.9	2.2
Rt. 651	3				1					2										8.3	2.9
Rt. 653	6	1			4		1													4.8	1.6
Rt. 667	8			4	1	2	1													5.0	1.2

Table 32. Frequency distribution of lateral line scales in Etheostoma nigrum, Etheostoma olmstedi olmstedi, Etheostoma olmstedi atromaculatum and the populations of Falling Creek.

Population	No.	Lateral Line Scales																												
		35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	$\bar{x}$	S.D.
E. nigrum	299	4	10	41	51	76	52	30	19	8	7		1																39.2	1.9
Upper Falling Cr.	14			1	1	4		3	3	2																			40.4	1.9
Middle Falling Cr.	18				1	3	7	2	1	1		1	1		1														41.2	2.7
Lower Falling Cr.	23					2	2	5	6	1	5		1	1															42.2	2.0
E. o. olmstedi	154			1		3	6	7	24	17	32	20	14	11	9	5	3	1	1										44.3	2.6
E. o. atromaculatum	100									2	3	4	9	5	11	12	11	13	10		4	7	6	1			1	1	50.1	3.7

Table 33. Frequency distribution of scales above lateral line in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the populations of Falling Creek.

Population	No.	Scales Above Lateral Line						
		3	4	5	6	7	$\bar{x}$	S.D.
E. nigrum	299	53	236	9	1		3.9	0.45
Upper Falling Cr.	14	1	13				3.9	0.27
Middle Falling Cr.	18		13	5			4.3	0.46
Lower Falling Cr.	23		11	11	1		4.6	0.59
E. o. olmstedi	154		25	103	26		5.0	0.58
E. o. atromaculatum	100		8	72	18	2	5.1	0.57

Table 34. Frequency distribution of scales below lateral line in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the populations of Falling Creek.

Population	No.	Scales Below Lateral Line								
		4	5	6	7	8	9	10	$\bar{x}$	S.D.
E. nigrum	299	4	131	131	30	3			5.7	0.72
Upper Falling Cr.	14		2	8	2	2			6.3	0.91
Middle Falling Cr.	18		2	3	9	4			6.8	0.92
Lower Falling Cr.	23			7	8	8			7.0	0.82
E. o. olmstedi	154		1	28	77	40	6	2	7.2	0.84
E. o. atromaculatum	100			4	25	45	24	2	8.0	0.86

Table 35. Frequency distribution of sum of scales above and below lateral line in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the populations of Falling Creek.

Population	No.	Sum of Scales Above and Below Lateral Line											
		7	8	9	10	11	12	13	14	15	16	x	S.D.
E. nigrum	299	5	41	100	119	29	4	1				9.5	1.0
Upper Falling Cr.	14			3	7	2	2					10.2	0.9
Middle Falling Cr.	18			2	2	8	4	2				11.1	1.1
Lower Falling Cr.	23				3	7	9	4				11.6	0.9
E. o. olmstedi	154			1	19	47	55	22	8	2		11.7	1.1
E. o. atromaculatum	100				2	6	21	34	29	5	3	13.1	1.2

Table 36. Frequency distribution of dorsal soft rays in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the populations of Falling Creek.

Population	No.	Dorsal Soft Rays							x̄	S.D.
		10	11	12	13	14	15	16		
E. nigrum	299	17	162	113	7				11.4	0.63
Upper Falling Cr.	14	2	8	4					11.1	0.66
Middle Falling Cr.	18		4	10	4				12.0	0.69
Lower Falling Cr.	23		5	8	10				12.2	0.80
E. o. olmstedi	154			15	83	53	3		13.3	0.66
E. o. atromaculatum	100				35	51	13	1	13.8	0.70

Table 37. Frequency distribution of pectoral rays in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the populations of Falling Creek.

Population	No.	Pectoral Rays						
		10	11	12	13	14	$\bar{x}$	S.D.
E. nigrum	299	5	122	166	6		11.6	0.56
Upper Falling Cr.	14		11	3			11.2	0.43
Middle Falling Cr.	18		5	12	1		11.8	0.55
Lower Falling Cr.	23		5	15	3		11.9	0.60
E. o. olmstedi	154		3	70	78	3	12.5	0.57
E. o. atromaculatum	100		1	11	74	14	13.0	0.54

Table 38. Frequency distribution of anal rays in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the populations of Falling Creek.

Population	No.	Anal Rays										
		3	4	5	6	7	8	9	10	11	$\bar{x}$	S.D.
E. nigrum	299	1		4	67	181	42	4			6.9	0.72
Upper Falling Cr.	14			1	4	7	2				6.7	0.83
Middle Falling Cr.	18			2	8	6	2				6.4	0.86
Lower Falling Cr.	23				1	9	13				7.5	0.59
E. o. olmstedi	154				10	51	83	10			7.6	0.71
E. o. atromaculatum	100					5	44	44	6	1	8.5	0.73

Table 39. Frequency distribution of infraorbital canal pores in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the populations of Falling Creek.

Population	No.	Infraorbital Canal Pores							
		5	6	7	8	9	10	$\bar{x}$	S.D.
E. nigrum	299	37	180	76	6			6.2	0.66
Upper Falling Cr.	14		8	6				6.4	0.51
Middle Falling Cr.	18		13	3	2			6.4	0.70
Lower Falling Cr.	23		10	11	2			6.7	0.65
E. o. olmstedi	154		3	17	129	5		7.8	0.46
E. o. atromaculatum	100		1	7	79	12	1	8.1	0.52

Table 40. Frequency distribution of the completeness of the infraorbital canal in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the population of Falling Creek.

Population	No.	Infraorbital Canal		
		Incomplete	Complete	Percentage complete
E. nigrum	299	297	2	0.7%
Upper Falling Cr.	14	14	0	0.0%
Middle Falling Cr.	18	16	2	11.1%
Lower Falling Cr.	23	21	2	8.7%
E. o. olmstedi	154	15	139	90.0%
E. o. atromaculatum	100	4	96	96.0%

Table 41. Frequency distribution of the nape squamation in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the population of Falling Creek.

Population	No.	Nape Squamation		
		Naked	Partially Scaled	Fully Scaled
E. nigrum	299	254	45	0
Upper Falling Cr.	14	11	3	0
Middle Falling Cr.	18	6	11	1
Lower Falling Cr.	23	6	15	2
E. o. olmstedi	154	19	116	19
E. o. atromaculatum	100	0	8	92

Table 42. Frequency distribution of the cheek squamation in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the population of Falling Creek.

Population	No.	Cheek Squamation		
		Naked	Partially Scaled	Fully Scaled
E. nigrum	299	278	21	0
Upper Falling Cr.	14	14	0	0
Middle Falling Cr.	18	4	13	1
Lower Falling Cr.	23	4	12	7
E. o. olmstedi	154	2	133	19
E. o. atromaculatum	100	0	15	85

Table 43. Frequency distribution of the breast squamation in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the population of Falling Creek.

Population	No.	Breast Squamation		
		Naked	Partially Scaled	Fully Scaled
E. nigrum	299	298	1	0
Upper Falling Cr.	14	14	0	0
Middle Falling Cr.	18	17	1	0
Lower Falling Cr.	23	18	4	1
E. o. olmstedi	154	125	26	3
E. o. atromaculatum	100	6	25	69

Table 44. Frequency distribution of the belly squamation in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the population of Falling Creek.

Population	No.	Belly Squamation		
		Naked	Partially Scaled	Fully Scaled
E. nigrum	299	168	109	22
Upper Falling Cr.	14	13	1	0
Middle Falling Cr.	18	13	3	2
Lower Falling Cr.	23	12	3	8
E. o. olmstedi	154	61	74	19
E. o. atromaculatum	100	2	3	95

Table 45. Frequency distribution of the squamation index in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the Falling Creek populations.

Population	No.	Squamation Index										
		0	1	2	3	4	5	6	7	8	$\bar{x}$	S.D.
E. nigrum	299	151	95	35	15	3					0.74	0.92
Upper Falling Cr.	14	11	3								0.21	0.43
Middle Falling Cr.	18	1	7	6	2	1	1				1.89	1.23
Lower Falling Cr.	23	3	2	7	4	2	3		2		2.83	1.99
E. o. olmstedi	154		15	41	56	24	5	6	5	2	3.07	1.46
E. o. atromaculatum	100			2	1	1	5	7	23	61	7.27	1.25

Table 46. Frequency distribution of the character index in *Etheostoma nigrum*, *Etheostoma olmstedi olmstedi*, *Etheostoma olmstedi atromaculatum* and the Falling Creek populations.

Population	No.	Character Index																												$\bar{x}$	S.D.
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28		
E. nigrum	299	3	11	41	53	67	51	31	28	8	2	4																		5.3	1.9
Upper Falling Cr.	14		1		4	5	2	2																						4.9	1.3
Middle Falling Cr.	18					1		1	4	3	5	1		1	2															9.6	2.3
Lower Falling Cr.	23								1	6	3	2	2	2		2	1	2	1	1										12.2	3.4
E. o. olmstedi	154										1	3	5	22	11	20	23	15	17	20	9	2	4		1	1				16.3	2.8
E. o. atromaculatum	100														1	1					5	7	8	13	20	16	17	10	2	24.0	2.4

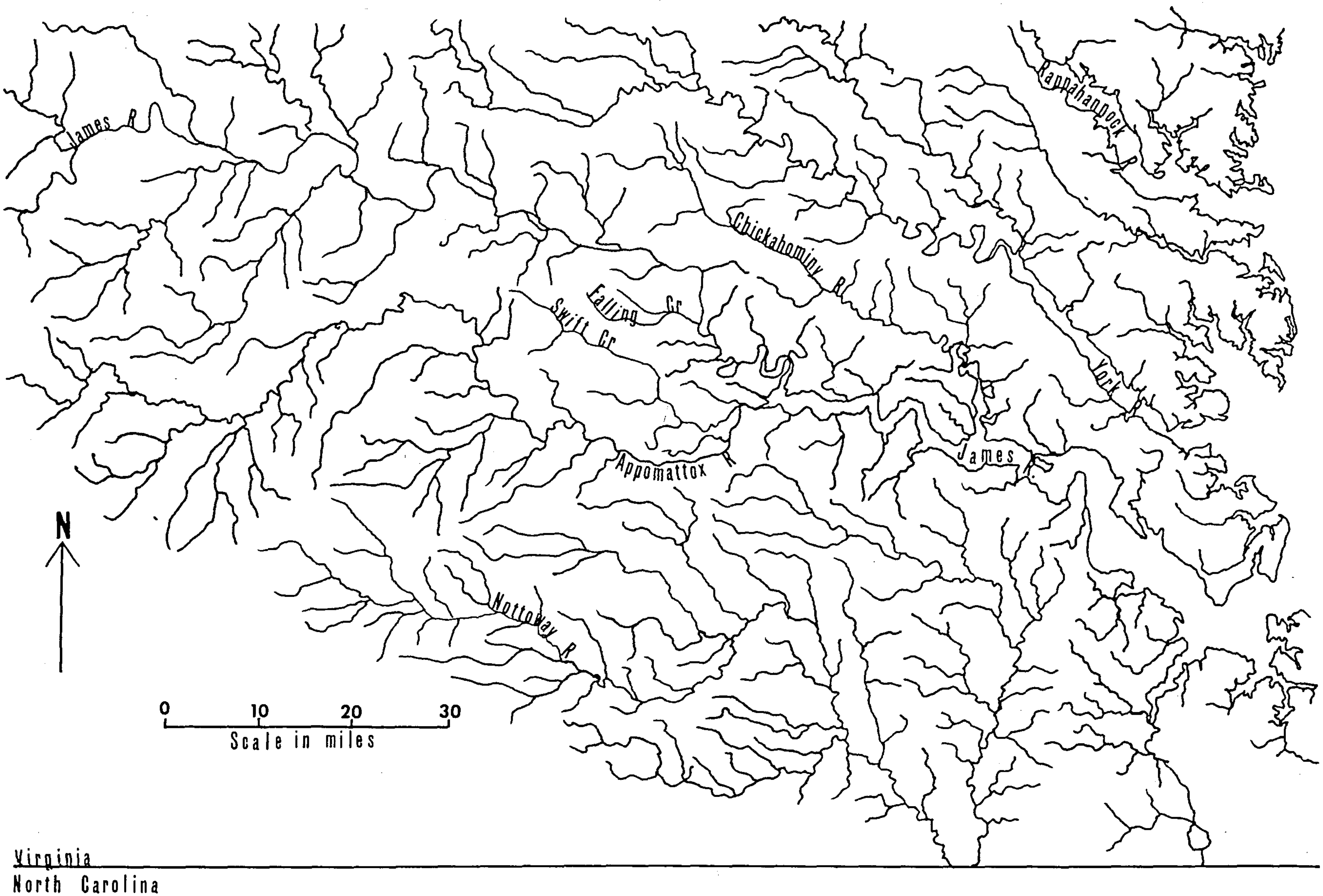

James R
Rappahannock R
Chickahominy R
Falling Cr
Swift Cr
York
James R
Appomattox R
Nottoway R
N
0
10
20
30
Scale in miles
Virginia
North Carolina

Figure 1. Map of the James River drainage showing the Falling Creek, Swift Creek, and Appomattox River drainages.

Figure 2. A comparison of the proportion of length of depressed dorsal fin to body length of male *Boleosoma* populations in the James River drainage.

A. *Etheostoma nigrum nigrum*

B. Appomattox River population

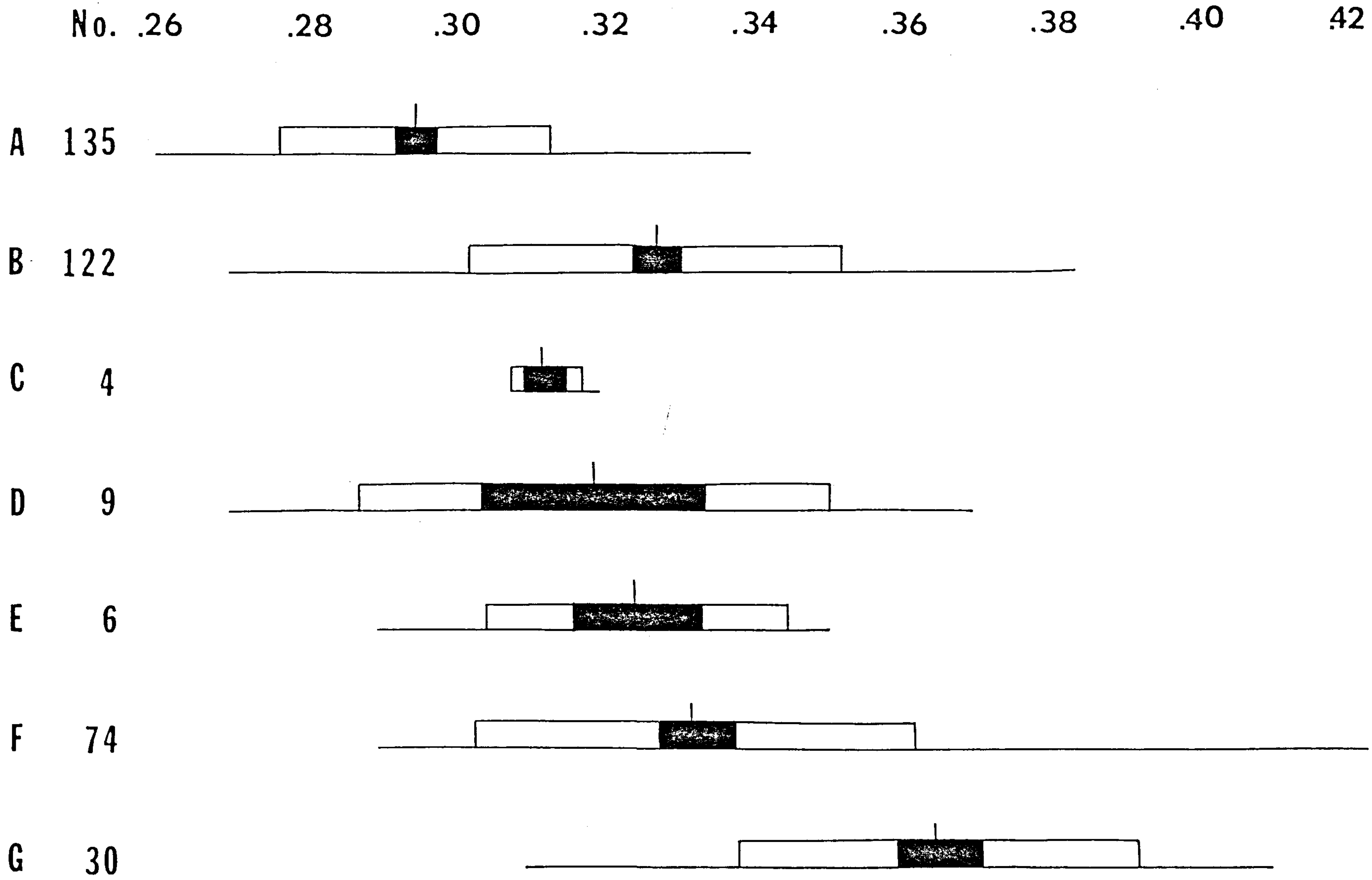
C. Upper Falling Creek population

D. Middle Falling Creek population

E. Lower Falling Creek population

F. *Etheostoma olmstedi olmstedi*

G. *Etheostoma olmstedi atromaculatum*



No.
.26
.28
.30
.32
.34
.36
.38
.40
42
A 135
B 122
C 4
D 9
E 6
F 74
G 30

Figure 3. A comparison of the proportion of length of depressed dorsal fin to body length of female *Boleosoma* populations in the James River drainage.

A. *Etheostoma nigrum nigrum*

B. Appomattox River population

C. Upper Falling Creek population

D. Middle Falling Creek population

E. Lower Falling Creek population

F. *Etheostoma olmstedi olmstedi*

G. *Etheostoma olmstedi atromaculatum*

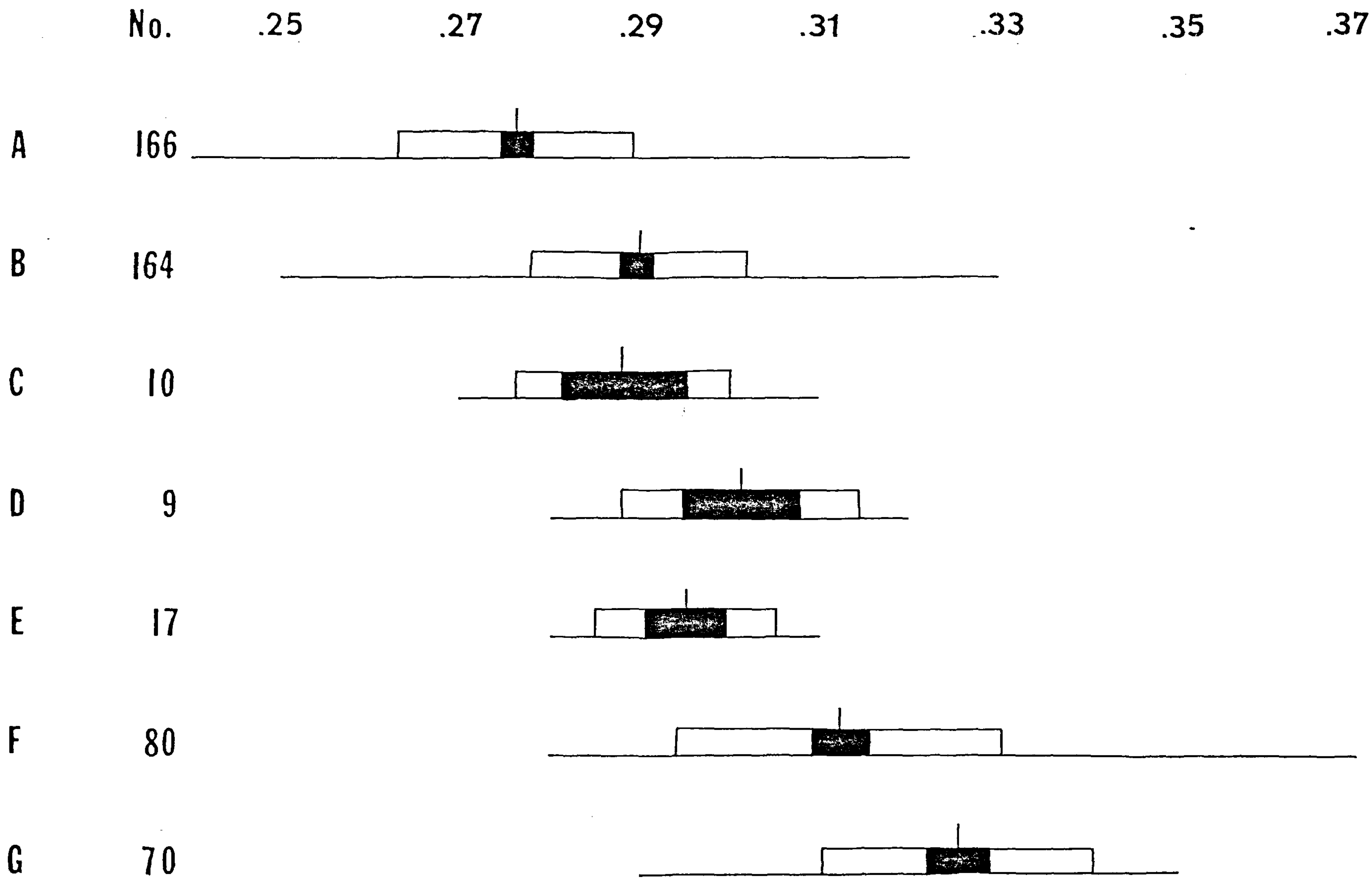

No.
.25
.27
.29
.31
.33
.35
.37
A
166
B
164
C
10
D
9
E
17
F
80
G
70

Figure 4. A comparison of the proportion of length of depressed anal fin length to anal fin base in *Boleosoma* populations in the James River drainage.

A. *Etheostoma nigrum nigrum*

B. Appomattox River population

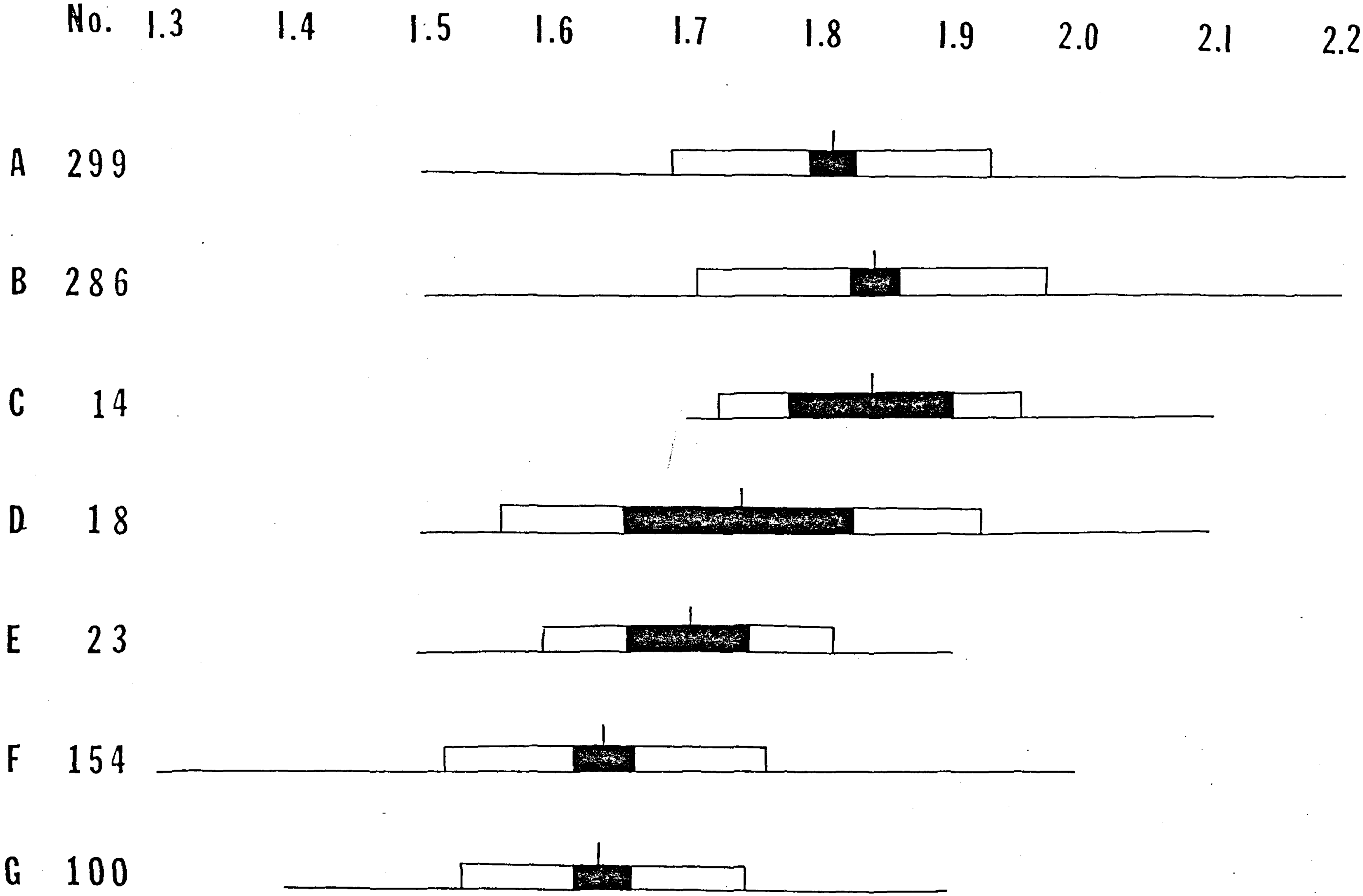
C. Upper Falling Creek population

D. Middle Falling Creek population

E. Lower Falling Creek population

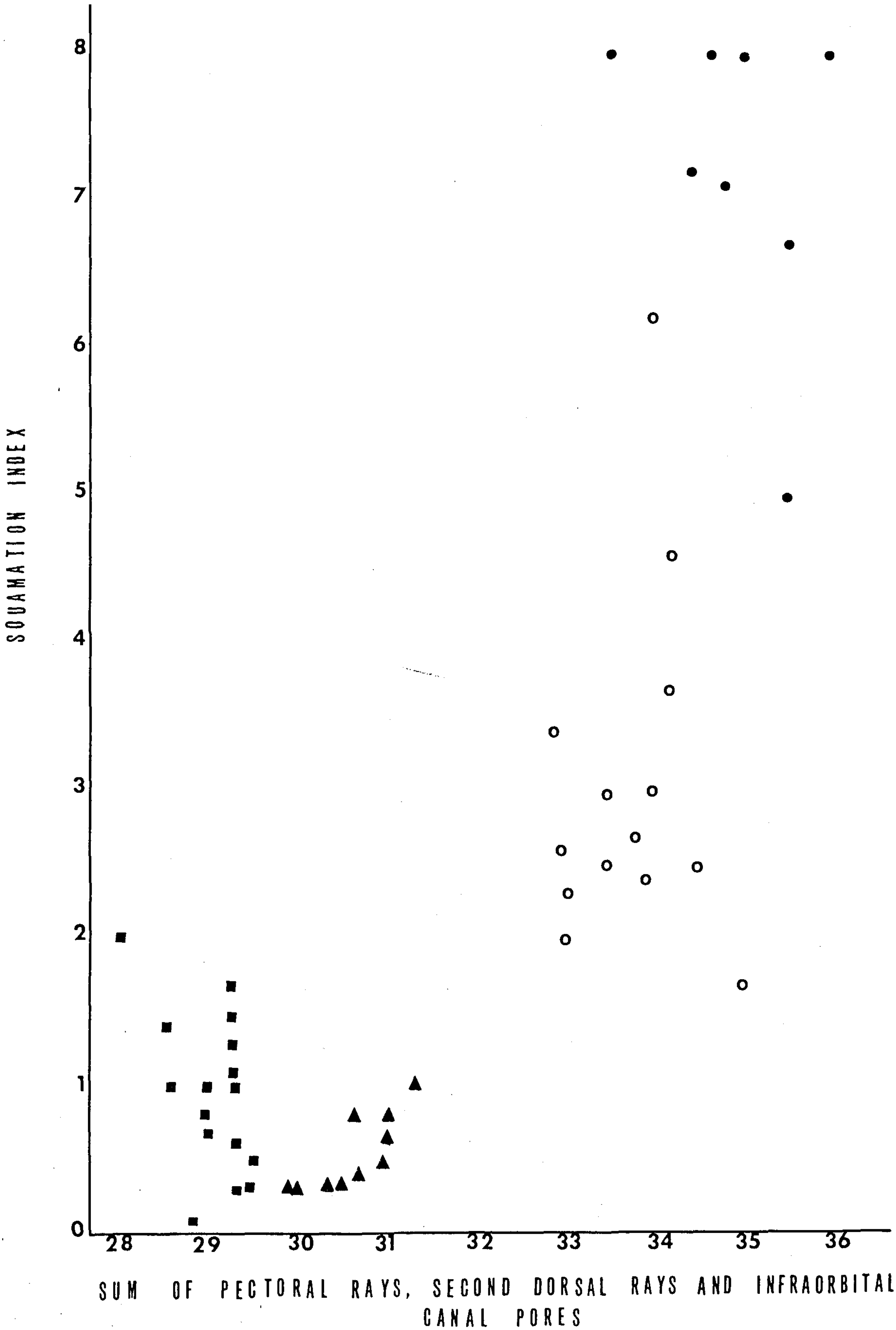
F. *Etheostoma olmstedi olmstedi*

G. *Etheostoma olmstedi atromaculatum*



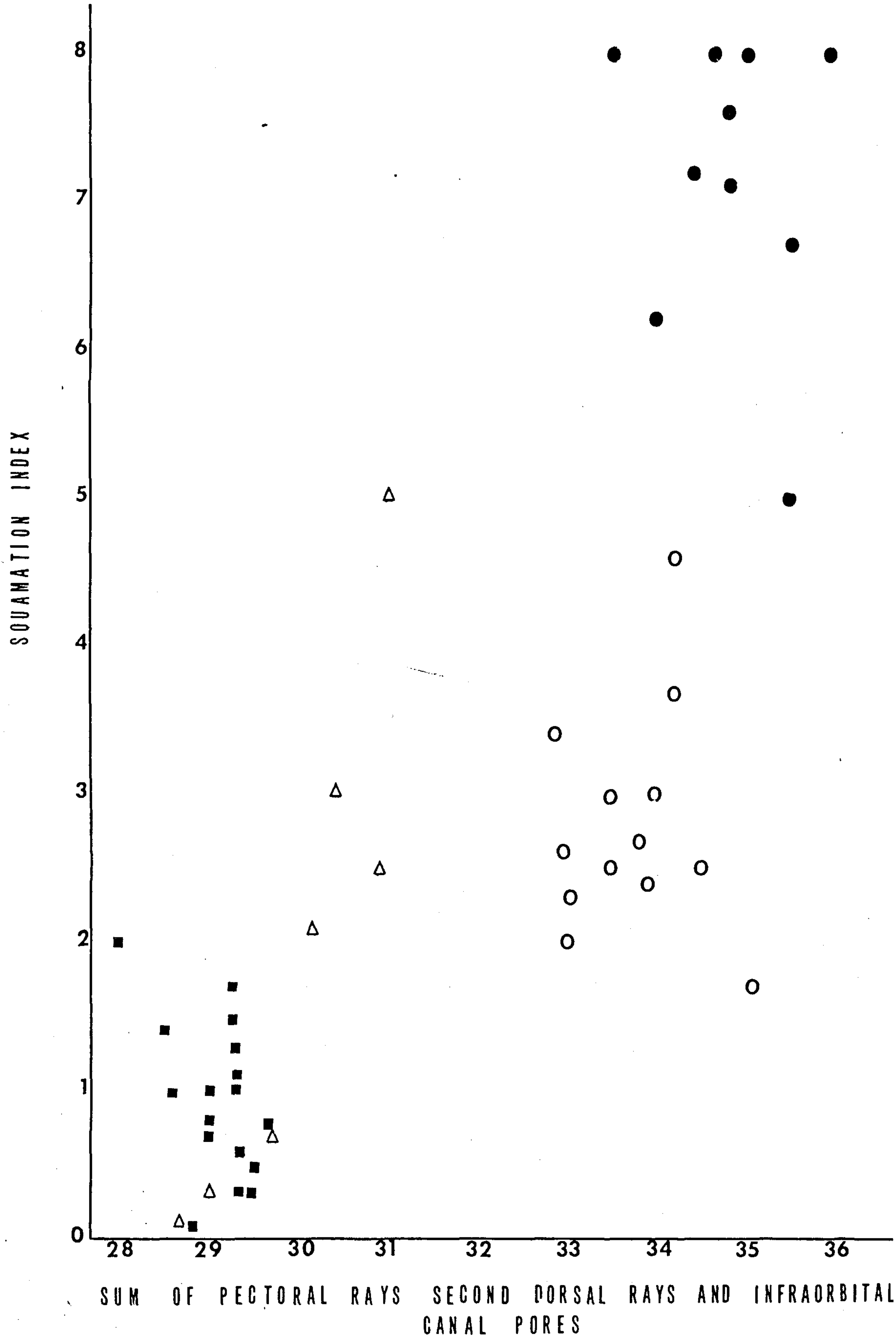
No.
1.3
1.4
1.5
1.6
1.7
1.8
1.9
2.0
2.1
2.2
A 299
B 286
C 14
D 18
E 23
F 154
G 100

Figure 5. Squamation index plotted against sum of pectoral rays, second dorsal rays and infraorbital canal pores for populations of *Etheostoma nigrum nigrum* (■), *Etheostoma olmstedi olmstedi* (○), *Etheostoma olmstedi atromaculatum* (●), and the Appomattox River population (▲). Each point represents the coordinant of the mean of the squamation index and the mean of the sum of the pectoral rays, second dorsal rays and infraorbital canal pores of specimens from a sampled population.



SQUAMATION INDEX
0
1
2
3
4
5
6
7
8
28
29
30
31
32
33
34
35
36
SUM OF PECTORAL RAYS, SECOND DORSAL RAYS AND INFRAORBITAL CANAL PORES

Figure 6. Squamation index plotted against sum of pectoral rays, second dorsal rays and infraorbital canal pores for populations of *Etheostoma nigrum nigrum* (■), *Etheostoma olmstedi olmstedi* (○), *Etheostoma olmstedi atromaculatum* (●), and the populations of Falling Creek (Δ). Each point represents the coordinant of the mean of the squamation index and the mean of the sum of the pectoral rays, second dorsal rays and infraorbital canal pores of specimens from a sampled population.



SQUAMATION INDEX
0
1
2
3
4
5
6
7
8
28
29
30
31
32
33
34
35
36
SUM OF PECTORAL RAYS SECOND DORSAL RAYS AND INFRAORBITAL CANAL PORES

Figure 7. Lateral line scales plotted against sum of pectoral rays, second dorsal rays and infraorbital canal pores for populations of *Etheostoma nigrum nigrum* (■), *Etheostoma olmstedi olmstedi* (○), *Etheostoma olmstedi atromaculatum* (◉), and the Appomattox River population (▲). Each point represents the coordinant of the mean of the lateral line scales and the mean of the sum of the pectoral rays, second dorsal rays and infraorbital canal pores of specimens from a sampled population.

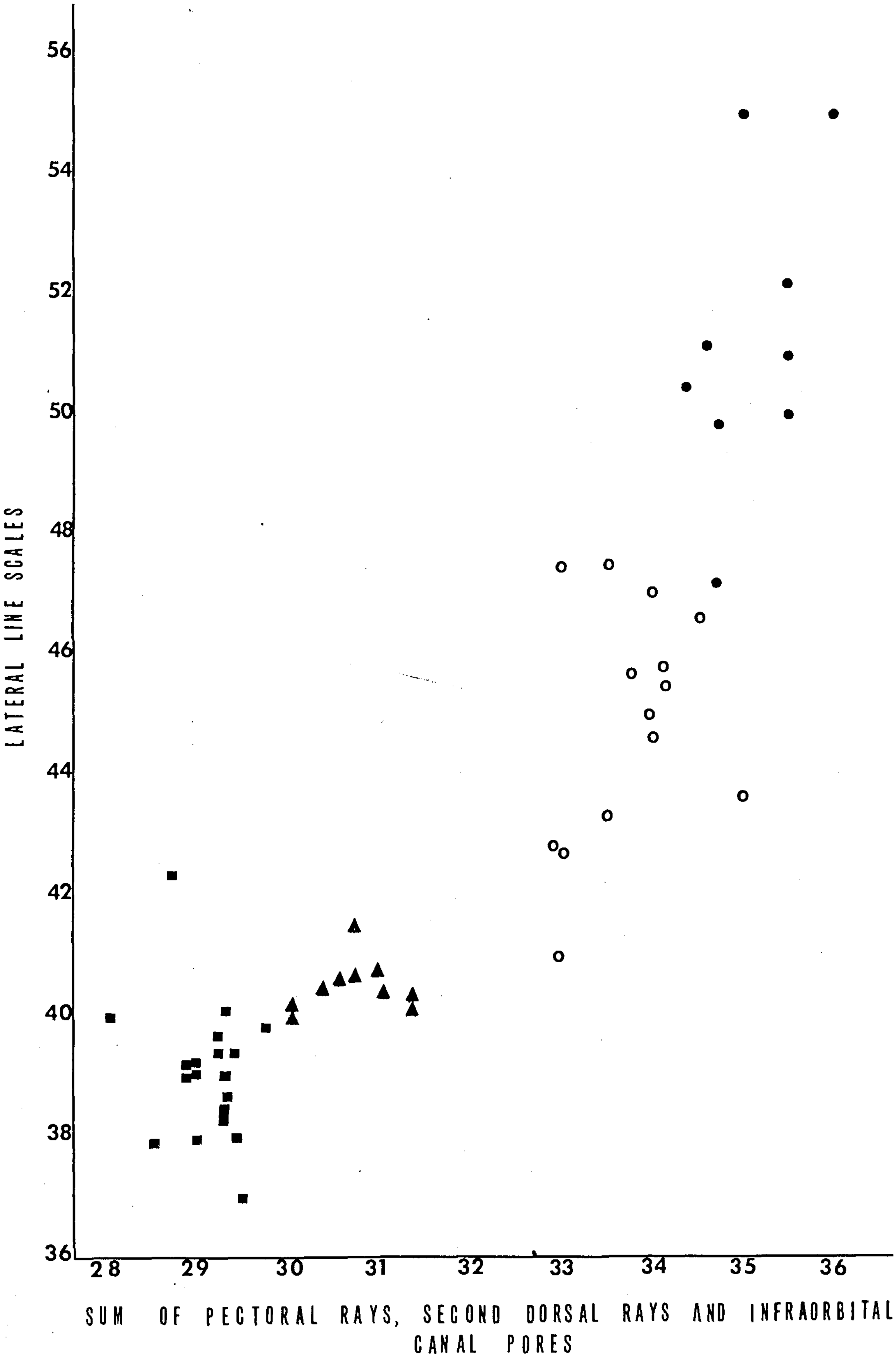
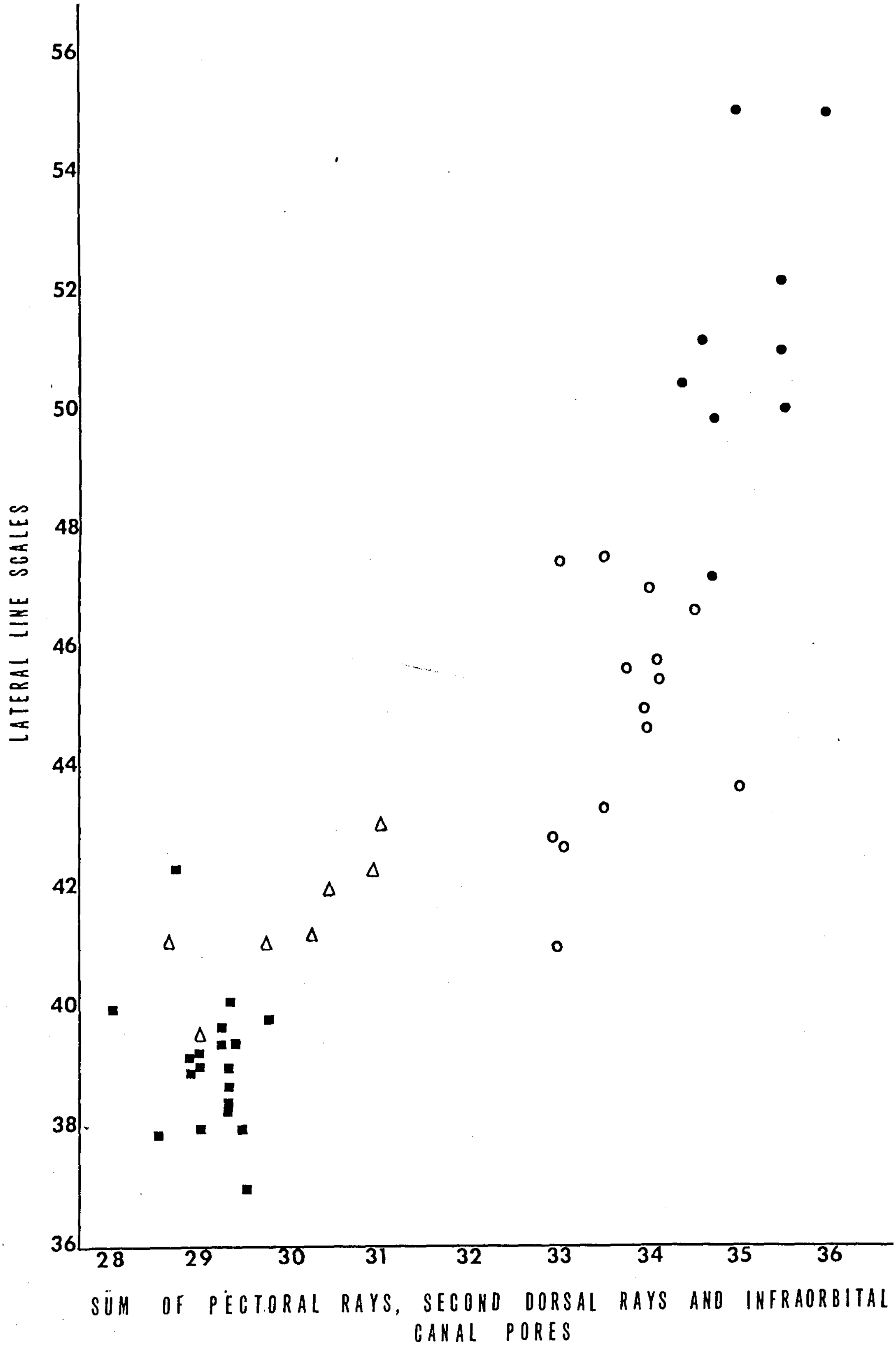

LATERAL LINE SCALES
56
54
52
50
48
46
44
42
40
38
36
28
29
30
31
32
33
34
35
36
SUM OF PECTORAL RAYS, SECOND DORSAL RAYS AND INFRAORBITAL CANAL PORES

Figure 8. Lateral line scales plotted against sum of pectoral rays, second dorsal rays and infraorbital canal pores for populations of *Etheostoma nigrum nigrum* (■), *Etheostoma olmstedi olmstedi* (○), *Etheostoma olmstedi atromaculatum* (●), and the populations of Falling Creek (Δ). Each point represents the coordinant of the mean of the lateral line scales and the mean of the sum of the pectoral rays, second dorsal rays and infraorbital canal pores of specimens from a sampled population.


LATERAL LINE SCALES
56
54
52
50
48
46
44
42
40
38
36
28
29
30
31
32
33
34
35
36
SUM OF PECTORAL RAYS, SECOND DORSAL RAYS AND INFRAORBITAL CANAL PORES

VITA

John Edward Clark was born January 11, 1950 in Danville Virginia. After graduation from George Washington High School he attended the University of Richmond for three years and the State University College of New York at Brockport for one year, graduating with a B. S. degree in biology in August, 1972. From September, 1972 to October, 1974, he taught Math and Science in Peru as a Peace Corps volunteer. After a few months of traveling in Central and South America he returned to Richmond and entered the Graduate School of the University of Richmond in August, 1975. He is expecting to receive his M. S. degree in May, 1978 and continue his education in a Ph. D. program.