INFORMATION TO USERS

The most advanced technology has been used to photograph and reproduce this manuscript from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book. These are also available as one exposure on a standard 35mm slide or as a 17" x 23" black and white photographic print for an additional charge.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

U·M·I

University Microfilms International
A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
313/761-4700 800/521-0600

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Order Number 8915580

Systematics of the centrarchidae (Perciformes: Percoidei) with notes on the haemal-anal-axial character complex

Chang, Chang-Hwa M., Ph.D.

City University of New York, 1988

U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

SYSTEMATICS OF THE CENTRARCHIDAE (PERCIFORMES: PERCOIDEI) WITH NOTES ON THE HAEMAL-ANAL-AXIAL CHARACTER COMPLEX

by

CHANG-HWA M. CHANG

A dissertation submitted to the
Graduate Faculty in Biology in
partial fulfillment of the requirements
for the degree of Doctor of Philosophy,
The City University of New York.

1988

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

Sept 23, 1988
date

C. Lavett Smith
Chairman of Examining Committee
Dr. C. Lavett Smith, American Museum of Natural History

Sept 27, 1988
date

Executive Officer
Dr. Peter C. Chabora

Gareth J. Nelson
Dr. Gareth Nelson, American Museum of Natural History

Janis Roze
Dr. Janis Roze, American Museum of Natural History

Jess Hanks
Dr. Jess P. Hanks, City University

George Dale
Dr. George Dale, Fordham University

Robert E. Schmidt
Dr. Robert Schmidt, Simon's Rock College

Supervisory Committee

The City University of New York

Abstract

SYSTEMATICS OF CENTRARCHIDAE (PERCIFORMES: PERCOIDEI) WITH NOTES ON THE HAEMAL-ANAL-AXIAL CHARACTER COMPLEX

by

Chang-hwa M. Chang

Advisor: Dr. C. L. Smith

The monophyly of the Centrarchidae is supported by the presence of prominent wing-like transverse processes on the first haemal spine and more than one anal pterygiophore united with the first haemal spine groove. Two subfamilies are recognized within the Centrarchidae. The Elassomatinae with one monophyletic genus Elassoma is characterized by numerous reductive characters. The Centrarchinae consists of eight monophyletic genera, Micropterus, Lepomis, Enneacanthus, Acantharchus, Ambloplites, Archoplites, Centrarchus, and Pomoxis based mainly on a combination of synapomorphies associated with the haemal-anal-axial character complex. A cladogram of the most parsimonious hypothesis of relationships for the genera of the Centrarchidae established by the present study is congruent with the previous phylogenetic relationships proposed by Smith and Bailey (1961) and Mok (1981). In an attempt to evaluate the potential utilization and understanding of the haemal-anal-axial character complex, representative taxa from major groups of teleosts are surveyed. The sister group relationship between the Centrarchidae and Percichthyidae is suggested and the systematic usefulness of the haemal-anal-axial character complex at different taxonomic levels is indicated.

ACKNOWLEDGEMENTS

I thank Dr. C. L. Smith for his valuable advice and continuous encouragement throughout the course of this study. I am grateful to my committee members Drs. Gareth Nelson, Bob Schmidt, George Dale, Jess Hanks, and Janis Roze for their support and constructive comments on this research. For helpful discussions on the various aspects of systematics, I thank Drs. C. L. Smith, Gareth Nelson, Hin-Kiu Mok, Lynne Parenti, Carl Ferraris, Mary Rauchenberger, Darrel Siebert, and John Waldman. I am indebted to the late Dr. Donn Rosen for his inspiration and his interest in Centrarchidae. Drs. Barbara Brown and Melanie Stiassny and Ms. Norma Feinberg provided technical advice and assistance. Ms. Loretta Stillman helped preparing this manuscript for which I am most appreciative. For loan of specimens, I thank Drs. Paula Mabee, Rich Vari, and John Waldman. For information on systematic literature I also thank Drs. James Atz and Bob Schmidt. My deepest gratitude to Grace, our parents, and families, and my sister-in-law Anne, whose constant encouragement, support, and love made this study possible, and I dedicate this work to them.

TABLE OF CONTENTS

Abstract..iii

Acknowledgements..v

Table of Contents...vi

List of Tables..viii

List of Figures...ix

Introduction..1

Historical Review...4

Materials and Methods.......................................8

Part I - Centrarchidae......................................27

Results...27

  Character analysis..27
    Defining characters of the Centrarchidae................28
      Transverse processes..................................28
      Anal-fin pterygiophores...............................30
    Interrelationships among the genera.....................33
      Posterior bifurcation of the swimbladder..............33
      Anal-fin osteology....................................38
        Number of anal-fin pterygiophores anterior to the first haemal spine........38
        Total number of anal-fin pterygiophores.............39
        Anal spines associated with first anal-fin pterygiophores.........40
        Total number of anal spines.........................40
        Anal soft rays......................................41
        Precaudal and caudal vertebrae......................41
        Position of the first anal-fin pterygiophore in the first haemal spine groove..........43
        Proximal radial of the first anal-fin pterygiophore...............44
      Anal fin morphology...................................45
      Haemal spine..47
        Length of first haemal spine........................47
        Arching pattern of the first haemal spine...........47
        Anterior face of the first haemal spine.............48
        Contact between the first and second haemal spine...............48
      Abdominal haemal arches...............................50

Opercular morphology....................................52
  Posterior opercular morphology..................52
  Ear spot...54
Ceratohyal foramen and epihyal-ceratohyal channel...57
Number of branchiostegal rays......................60
Gill rakers on the first branchial arch............61
Dorsal fin morphology..............................61
Apomorphic characters from previous studies........62
  Olfactory organs.................................63
  Dorsal fin supports..............................63
  Kidney morphology................................64

Discussion and Summary.................................65
  Monophyly and Intrarelationships of the Centrarchidae..65
  Systematic position of Elassoma........................70
  Sister group relationships.............................72

Conclusion (Part I)....................................75

Part II - The haemal-anal-axial character complex 77

Introduction...77

General results and discussion 79

General Summary..86

Percoids results and discussion........................87

Conclusion (Part II)...................................98

References..237

LIST OF TABLES

Table 1. Developmental characteristics of haemal arch, tranverse processes, swimbladder, and the anterior anal pterygiophore in larval Ambloplites rupestris (AMNH 43783) 102

Table 2. Most frequent number of anal spines (A), soft rays (B), pterygiophores anterior to the first haemal spine (C), the total anal pterygiophores (D), precaudal vertebrae (E), and caudal vertebrae (F), present in Centrarchidae. 104

Table 3. Anal-fin insertion in the Centrarchidae: a comparison between Bailey (1938) and Chang (present study). Bailey (1938) indicated anal fin insertion as the general location of the fin with reference to the body shape. Chang (present study) obtained the position of the anal-fin insertion by following a line from the articulation of the first anal spine on the pterygiophore vertically to the vertebral column. Caudal vertebrae indicated by CV; precaudal by PV, counting from the posteriormost precaudal first. 105

Table 4. Comparison of closed abdominal haemal arches commonly present in larval and adult Centrarchidae. 106

LIST OF FIGURES

Fig. 1. Relationships of vertebral column, haemal spine, and anterior anal-fin pterygiophore in *Ambloplites rupestris*, A) lateral view, B) detailed anterolateral view of the first haemal spine. 108

Fig. 2. Relationships of vertebral column, haemal spine, and anterior anal-fin pterygiophore in *Perca flavescens*, A) lateral view, 12 mm SL B) lateral view 51 mm SL. 110

Fig. 3. Posterior extension of the swimbladder in *Ambloplites rupestris* , (A) 9mm SL, (B) 12 mm SL, (C) 14 mm SL, (D) 21 mm SL, and *Micropterus salmoides* (E) 17 mm SL., (F) 24 mm SL. 112

Fig. 4. Relationships of vertebral column, haemal spine, and anterior anal-fin pterygiophore in *Elassoma evergladei*, A) lateral view, B) detailed anterior view of the first haemal spine. 114

Fig. 5. Relationships of vertebral column, haemal spine, and anterior anal-fin pterygiophore in *Micropterus salmoides* (A) detailed anterior view 45 mm SL, B) detailed anterior view 230 mm SL, (C) lateral view, and (D) *Micropterus dolomieui* lateral view. 116

Fig. 6. Relationships of vertebral column, haemal spine, and anterior anal-fin pterygiophore in *Lepomis macrochirus*, A) lateral view, B) detailed anterior view of the first haemal spine. 118

Fig. 7. Relationships of vertebral column, haemal spine, and anterior anal-fin pterygiophore in *Enneacanthus chaetodon*, A) lateral view, B) detailed anterior view of the first haemal spine. 120

Fig. 8. Relationships of vertebral column, haemal spine, and anterior anal-fin pterygiophore in *Acantharchus pomotis*, A) lateral view, B) detailed anterior view of the first haemal spine. 122

Fig. 9. Relationships of vertebral column, haemal spine, and anterior anal-fin pterygiophore in *Archoplites interruptus*, A) lateral view, B) detailed anterior view of the first haemal spine. 124

Fig. 10. Relationships of vertebral column, haemal spine, and anterior anal-fin pterygiophore in *Centrarchus macropterus*, A) lateral view, B) detailed anterior view of the first haemal spine. 126

Fig. 11. Relationships of vertebral column, haemal spine, and anterior anal-fin pterygiophore in *Pomoxis annularis*, A) lateral view, B) detailed lateral view of the first haemal spine. 128

Fig. 12. Supernumery anal spine association on the first anal pterygiophore in A) *Archoplites interruptus* 16 mm SL, B) *Pomoxis nigromaculats*, 14 mm SL, C) *Centrarchus macropterus* 13 mm SL, D) *Lepomis macrochirus* 10 mm SL. 130

Fig. 13. Lateral view of a 9 mm SL *Amblopiites rupestris* showing five bridged haemal arches in abdominal region and four separate anal pterygiophores anterior to the first haemal spine. 132

Fig. 14. Lateral view comparison of transverse processes in *Ambloplites rupestris*, A) ventrally directed processes 16 mm SL, B) laterally directed processes 43 mm SL. 134

Fig. 15. Morphology of posterior opercular margin in, A) *Acantharchus pomotis*, B) *Centrarchus macropterus*, C) *Elassoma zonatum*, D) *Ambloplites rupestris*, and E) *Pomoxis annularis*. 136

Fig. 16. Morphology of posterior opercular margin in, *Enneacanthus gloriosus*, B) *Enneacanthus chaetodon*, C) *Enneacanthus obesus*, D) *Archoplites interruptus* 62 mm SL and E) *Archoplites interruptus* 197 mm SL. 138

Fig. 17. Morphology of posterior opercular margin in *Lepomis*, A) *gibbosus*, B) *marginatus*, C) *auritus* D) *gulosus*, E) *cyanellus*, F) *humilis*, G) *macrochirus*, H) *symmetricus*, I) *punctatus* and J) *microlophus*. 140

Fig. 18. Ontogeny of posterior opercular margin in *Lepomis megalotis*, A) 13 mm SL, B) 19 mm SL and C) 47 mm SL. 143

Fig. 19. Morphology of posterior opercular margin in *Micropterus*, A) *punctulatus*, B) *salmoides*, C) *coosae*, and D) *dolomieui*. 145

Fig. 20. Morphology of ear spot in *Lepomis auritus* A) 36 mm SL, and B) 107 mm SL. 147

Fig. 21. Morphology of ear spot in A) *Pseudogramma polycanthus* AMNH 51733, B) *Fowleria auritus* AMNH 33775, and C) *Morone punctatus* AMNH 43094. 149

Fig. 22. Development of ceratohyal foramen in *Lepomis megalotis*, A) 13mm SL, B) 15mm SL, C) 15 mm SL, D) 19 mm SL, E) 26 mm SL, and *Micropterus salmoides*, F) 17 mm SL, G) 19 mm SL, H) 22 mm SL., I) 35 mm SL and J) 46 mm SL. 151

Fig. 23. Lateral view of the hyoid arch in *Micropterus* A) *coosae*, B) *salmoides*, C) *dolomieui* and D) *punctulatus*. 153

Fig. 24. Lateral view of the hyoid arch in *Lepomis* A) *cyanellus*, B) *humilis*, C) *punctatus* D) *gibbosus*, E) *megalotis*, F) *auritus* G) *symmetricus*, H) *macrochirus*, I) *microlophus* J) *marginatus*, and K) *gulosus*. 155

Fig. 25. Lateral view of the hyoid arch in *Enneacanthus* A) *gloriosus*, B) *obesus*, and C) *chaetodon*. 157

Fig. 26. Lateral view of the hyoid arch in A) *Pomoxis nigromaculatus*, B) *Pomoxis annularis*, C) *Centrarchus macropterus*, D) *Ambloplites rupestris*, and E) *Archoplites interruptus*. 159

Fig. 27. Lateral view of the hyoid arch in *Elassoma* A) *evergladei*, B) *zonatum*, and C) *okefenokee*. 161

Fig. 28. Dorsal fin morphology in A) *Micropterus salmoides*, B) *Lepomis cyanellus*, C) *Centrarchus macropterus*, and D) *Pomoxis annularis*. 163

Fig. 29. Cladogram of the most parsimonious hypothesis of relationships for the genera of the family Centrarchidae. Numbers correspond to synapomorphies: 1, transverse processes on the first haemal spine; 2, more than one anal-fin pterygiophore anterior to the first haemal spine; 2a, more than two anal-fin pterygiophors anterior to the first haemal spine; 2b, more than three anal-fin pterygiophores anterior to the first haemal spine; 2c, more than four anal-fin pterygiophores anterior to the first haemal spine; 2d, more than five anal-fin pterygiophores anterior to the first haemal spine; 3, posterior bifurcation of the swimbladder; 3a, swimbladder extends beyond second haemal spine; 3b, swimbladder extends beyond fifth haemal spine; 4a, thirteen anal-fin pterygiophores; 4b, fourteen anal-fin pterygiophores; 4c, twenty anal-fin pterygiophores; 4d, twenty-two anal-fin pterygiophores; 5, four spines on first anal-fin pterygiophore; 6, more than three anal spines; 7, 16-18 soft anal rays; 8a, 15-17 or 14-18 vertebral formula; 8b, 12-16 vertebral formula; 8c, 13-17 vertebral formula; 8d, 13-18 vertebral formula; 8e, 14-18 vertebral formula; 9, distal tip of anterior anal-fin pterygiophore reaches the middle of the first haemal spine groove; 10, proximal radial of the first anal-fin pterygiophore expanded; 11a, insertion of anal fin vertical; 11b, insertion of anal fin obtusely forward; 12, first haemal spine as long as the second one; 13, first haemal spine arched; 14, deep groove on first haemal spine; 15a, contact between first and second haemal spines; 15b, four haemal spines fused; 16a, single bridged abdominal arch; 16b, absence of bridged abdominal haemal arch; 17a, serrae on posterior opercular margin; 17b, posterior opercular margin rounded or fimbriate; 18, earspot; 19a, ceratohyal with deep notch; 19b, ceratohyal concave; 20, epi-ceratohyal channel reduced; 21, seven branchiostegal rays; 22, 25-40 long and slender gill rakers; 23a, shallow-notched dorsal fin; 23b, single dorsal fin; 24, olfactory organs; 25, dorsal fin supports; 26, thick tissue layer over posterior kidney; 27a, extreme posterior kidney; 27b, fusion of posterior kidneys behind the first haemal spine......................165

Fig. 30. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Osteoglossum bicihrrosum AMNH 38150SW. 167

Fig. 31. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Elops saurus AMNH 55346SW. 169

Fig. 32. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Brevoortia tyrannus AMNH 15495SW. 171

Fig. 33. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Notropis hudsonius. 173

Fig. 34. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Salmo gairdneri AMNH 40268. 175

Fig. 35. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of A) Fundulus similis AMNH 39167 and B) Menidia menidia AMNH 35924. 177

Fig. 36. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of A) Holocentrus poco AMNH 22925 and B) Gephyroberyx philippinus AMNH 49701SW. 179

Fig. 37. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Polymixia lowei AMNH 27413. 181

Fig. 38. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Zeus faber AMNH 29458SW. 183

Fig. 39. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of A) Eucalia inconstans AMNH 10181SW and B) Cottus bairdi AMNH 40281. 185

Fig. 40. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Trinectes maculatus AMNH 43047. 187

Fig. 41. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Monacanthus ciliatus AMNH 22214. 189

Fig. 42. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Centropomus robalito AMNH 32925SW. 191

Fig. 43. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Lates niloticus AMNH 55359. 193

Fig. 44. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Ambassis commersoni AMNH 37769. 195

Fig. 45. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Banjos typus AMNH 35845. 197

Fig. 46. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Haemulon sciurus AMNH 15484. 199

Fig. 47. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of A) Lateolabrax japonicus AMNH 14380 and B) Siniperca scherzeri AMNH 10506. 201

Fig. 48. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Bostockia porosa AMNH 31448. 203

Fig. 49. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Morone saxatilis. 205

Fig. 50. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Serranus trigrinus AMNH 43172. 207

Fig. 51. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of A) Lobotes surinamensis AMNH 22125 and B) Eucinostomus harengulus AMNH 21893. 209

Fig. 52. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Terapon butleri AMNH 35648. 211

Fig. 53. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Pristigenys alta AMNH 29378. 213

Fig. 54. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Nemipterus sp. AMNH 16676. 215

Fig. 55. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of A) Pseudochromis fuscus AMNH 16969 and B) Assessor mcneilli AMNH 49639. 217

Fig. 56. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Apogon binotatus. 219

Fig. 57. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Lethrinus ornatus AMNH 14916SW. 221

Fig. 58. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Kuhlia malo AMNH 9374. 223

Fig. 59. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Nannatherina balstoni. 225

Fig. 60. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of A) Caulolatilus affinis AMNH 49709 and B) Hoplolatilus starcki AMNH 38129. 227

Fig. 61. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of A) *Sillago bassensis* AMNH 31440 and B) *Pomatomus saltatrix* AMNH 18804. 229

Fig. 62. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Caranx crysos* AMNH 22026. 231

Fig. 63. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Scatophagus argua* AMNH 14614. 233

Fig. 64. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Acanthurus chirurgus* AMNH 21806SW. 235

INTRODUCTION

Perciformes (perch-like fishes) is the largest and most diverse order of teleostean fishes, containing about 20 suborders, 150 families and at least 6,900 species (Lauder and Liem, 1983). The suborder Percoidei includes the most generalized and several specialized perciforms. This suborder, the largest central mass of the Perciformes, includes such generalized members as the sunfishes, perches, darters, groupers, basses, etc., and such highly specialized fishes as the fast swimming dolphins and the wide-spread remoras in which the spinous dorsal fin is transformed into a sucking disc. The suborder Percoidei cannot be defined cladistically and its monophyly is doubtful (Johnson, 1984). Regan (1913) defined the Percoidei as "the most generalized suborder, defined by the absence of the special peculiarities which characterize the other suborders of the Percomorphii". Rosen (1973) concludes that there is uncertainty regarding the monophyly of the Perciformes and the phyletic validity of existing subordinal and familial classifications.

The Centrarchidae are a family of perciform fishes (suborder Percoidei) native to the freshwaters of North America. All of the extant species of the family range east of the Rocky Mountains, except the Pacific Coast species *Archoplites interruptus* (Girard).

A considerable amount of systematic literature is available concerning various members of the nine genera and thirty two species of this family. Recent attempts to determine phylogenetic relationships among genera of sunfish have been based on morphological counts and measurements (Schlaikjer, 1937; Bailey, 1938), dorsal fin supports (Smith and Bailey, 1961), the acoustico-lateralis system (Branson and Moore, 1962), chromosome cytology (Roberts, 1964), success of hybridization (Hester, 1970; West, 1970), biochemical genetics (Avise et al., 1977) and kidney morphology (Mok, 1981). Results of these studies are far from uniform and these variations offer opportunity for the present synoptic study. Furthermore, despite the fact that sunfish are one of the dominant elements of the ichthyofauna in North America there has been no comparative osteological study of the centrarchid family as a whole, and the monophyly of these assemblages has yet to be demonstrated.

The primary goals of this study are to resolve the question of monophyly for the Centrarchidae, to define the phylogenetic relations among the genera, to determine the affinities of Elassoma, and finally to determine the possible sister group relations of centrarchids among the percoids.

In addition preliminary study indicates a character complex associated with haemal-anal-axial region provides significant systematic information in the analysis of inter- and intra-relationships of Centrarchidae. Further exploration has been made in order to evaluate the potential utilization and understanding of this character complex among percoids.

HISTORICAL REVIEW

Cuvier and Valenciennes (1828-1849) and Gunther (1859) were among the first to attempt a natural arrangement of the centrarchids. Gill (1861) proposed seven new genera, of which three, *Acantharchus*, *Archoplites*, and *Enneacanthus* are still in current use. The family name Centrarchidae was first proposed by Gill (1872) who recognized sixteen genera and suggested a further division of the group into three subfamilies - Centrarchinae, Lepominae, and Micropterinae. Jordan (1877) on advise from Gill, followed the same subfamilial treatment but arranged them into nine genera: Micropterinae (*Micropterus*), Centrarchinae (*Centrarchus* and *Pomoxis*) and Lepominae (*Chaenobryttus*, *Ambloplites*, *Archoplites*, *Acantharchus*, *Lepomis* and *Enneacanthus*). Jordan had such a strong impact on centrarchid classification that eight of the nine genera he proposed are still accepted today. Boulenger (1895) was the first worker to include the genera *Elassoma* and *Kuhlia* in the Centrarchidae. Regan (1913) removed the latter group from the Centrarchidae because of several character conflicts. Bailey (1938) divided the centrarchids into two subfamilies with a total of eleven genera. Those with three anal spines were placed in the Lepominae and those with four or more spines in the Centrarchinae. In a series of papers dealing with the black basses, Bailey and Hubbs (1949) relegated Huro to a subgenus of Micropterus. Eddy (1967) included Mesogonistius chaetodon in the genus Enneacanthus and Bailey et al. (1970) placed Chaenobryttus in the synonymy of Lepomis. Although there is no general agreement on the interrelationships of the genera, the inclusion of each genus within the family is well supported except for Elassoma.

Jordan (1877) did not assign Elassoma to a family, but suggested it might belong among the cichlids. Based on the similar rudimentary condition of the pseudobranchiae in Elassoma and the Centrarchidae, Jordan and Everman, (1896) suggested close affinity but placed them in separate families. In a detailed acoustico-lateralis system study Branson and Moore (1962) agreed with the familial status of Elassoma based on twenty characters that distinguished them from the Centrarchidae. The results of electrophoretic variation in proteins among the centrarchid genera (Avise et al., 1977) also correlates strongly with the results of Branson and Moore's study. Johnson (1984) suggested that the affinities of Elassoma possibly lie outside the Perciformes.

It has been suggested that Elassoma is a neotenic sunfish (Moore and Sisk, 1963). The reduced posterior olfactory folds in Elassoma zonatum are equivalent to those found in juvenile sunfishes (Eaton, 1956). The majority of centrarchids frequently display an arrangement of three predorsal bones, but _Elassoma_ has lost two or all of the predorsals (Smith and Bailey, 1961). Loss of the predorsals also occurs in the Percidae. Smith and Bailey (1961) placed _Elassoma_ in one subfamily with a single genus _Elassoma_. Nelson (1984) placed the remaining genera under the subfamily Centrarchinae.

Fossil centrarchids have been reported from North Dakota, South Dakota, Nebraska, Colorado and Oregon - representing a geological range form early Eocene and late Miocene. Schlaikjer (1937) described a fossil centrarchid from Alaska, this suggests possible sister group relations between centrarchids and freshwater percoids in the Far East (e.g. _Siniperca_, _Coreoperca_). Close resemblances between the external characters of centrarchids and _Coreoperca_ indicate a possible relationship between them (Katayama, 1959). Because of similarities in scale morphology, McCully (1962) states that "the Centrarchidae came from an ancient freshwater group that was ancestral to the freshwater serranids". Many other workers have suggested that the Centrarchidae are closely related to serranids (Gill, 1861:Regan, 1913; Bailey, 1938, Bollman, 1891, Branson and Moore, 1962). Jordan (1896) states "There is reason to believe that from some such form the centrarchids were derived." It has also been suggested that they are closely allied to Kuhliidae (Jordan and Everman, 1896, Boulenger, 1895 and Bailey, 1938). However, without synapomorphies to define the common ancestry the sister group relations of Centrarchidae remain unknown.

MATERIALS AND METHODS

Specimens examined for this study were collected directly from local waters or obtained mainly from the collections of the American Museum of Natural History (AMNH) and the U.S. National Museum (USNM). Preserved specimens include both dry skeletons and alcohol preserved specimens, with a portion of the latter being cleared and stained following the methods of Dingerkus and Uhler (1977). Counts and measurements will follow the methods of Hubbs and Lagler (1958). Drawings were made with a Zeiss microscope camera lucida.

Osteological examinations were mainly based on cleared and stained specimens. Dry skeletons preparations were also used in studying certain features (particularly those of the opercular bones and vertebral column). However, difficulties exist when using dry skeletons to study the relationship between the anal fin supports and the axial skeleton because of the disarticulation and distortion caused by the preparation of the dry skeletons. Therefore, when examining the association between the anal fin supports and the axial skeleton cleared and stained specimens and x-ray radiographs were used.

Examination of the swimbladder could sometimes be made using cleared and stained specimens if the melanophores present on the body cavity had not bleached during the clearing and staining process. If observations could not be made on cleared and stained specimens then alconol specimens were used. All dissections done on alcohol specimens were done on the right side.

Relationships will be evaluated following the principals first proposed by Hennig (1966) and since further developed and discussed by a variety of authors (Nelson, 1971; Nelson and Plantnick, 1981).

This methodology is considered best suited to the objectives of the present study because the methodology is a phylogenetic approach, and is well defined in regard to character evolution. Other approaches currently used are not well suited to the objectives of the present study. Numerical taxomony, best described by Sneath and Sokol (1973), is a phenetic approach in which taxa are clustered by overall similarity. Evolutionary systematics as described by Mayr (1969) and Simpson (1961) is very subjective and no well-developed, repeatable method had been incorporated into this approach.

In using the Hennigian or cladistic methodology, certain principals are followed: recognized taxa must be monophyletic in that they include all descendants of a hypothetical common ancestor. Monophyletic groups are defined on the basis of the most parsimonious hypothesis of relationships from the distribution of shared derived (synapomorphic) characters rather than on their overall similarity. Those characters shared by a specific group are hypothesized to be uniquely derived for that group, thus uniquely defining it. The derived character information then can be summarized in the most parsimonious way possible by a cladogram. Cladistic data are records of the characters of the organisms being studied. Characters are defined as a feature that can be evaluated or a variable with two or more mutually exclusive and ordered states (Pimental and Riggins, 1987). Patterson (1982) equates homology and synapomorphy saying "the recognition of homologies and hence of monophyletic groups is directly comparable to discovering new species".

In estimation the plesiomorphic or apomorphic nature of various characters, two methods are used. The first method is outgroup comparison. The general occurrence of a character state among the surrounding taxa may indicate it is probably primitive at that level. The second method utilizes the ontogenetic information. In a character transformation, the more general state may be considered primitive and the less general derived (Nelson, 1978).

The usefullness of characters of larvae and juveniles in elucidating systematic relationships has been demonstrated in several groups (Kendall, 1979, Richardson, 1981, Johnson, 1984, Mabee, 1986). Results of these studies have indicated that ontogenetic characters provide an additional set of characters with which to evaluate phylogenetic relationships. Characters of larvae have been particularly helpful in analyzing problems associated with neoteny (Nelson, 1973). For purpose of ontogenetic information a series of cleared and stained specimens of different developmental stages of centrarchids have been examined.

Outgroups were chosen either from the literature where it has been suggested a possible interfamilial relationship may exist or randomly selected from both within or close to the suborder Percoidei. Included are at least one species from the following families: Holocentridae, Percichthyidae, Serranidae, Grammistidae, Teraponidae, Centropomidae, Kuhliidae, Percidae, Apogonidae, Lutjanidae, Gerreidae, Haemulidae, Sparidae, Sciaenidae, Chaetodontidae, Moronidae, Pomacanthidae, Nandidae, Cichlidae, Embiotocidae, and Pomacentridae.

TERMS

The following terms are defined as used in this study.

Anal fin pterygiophore - Terminology used is that of Eaton (1945), unless specified, anal-fin pterygiophore refers to the proximal radial of the anal-fin pterygiophore.

Basal percoids (sensu Gosline, 1966b)- Centropomidae, Percichthyidae, Kuhliidae, Centrarchidae, Percidae, and Nandidae.

Ceratohyal foramen - Terminology used is that of Rosen, 1973.

First caudal vertebrae - That vertebrae which shows the haemal spine developed.

Haemal-anal-axial character complex - Translated from "Complexe hemaxanal" of Blot (1968) who first used the term to express the relationships of anteriormost anal fin pterygiophores, first haemal spine, and the vertebral column as illustrated in Fig. 1.

Percichthyidae (sensu Johnson, 1984) - *Percalates*, *Plectroplites*, *Macquaria*, *Maccullochella*, *Percichthys*, *Percilia*, *Bostockia*, *Gadopsis*, *Nannoperca*, *Edelia*, and *Nannatherinia*.

Precaudal vertebrae - First anal pterygiophore is used to separate precaudal from caudal vertebrae; this pterygiophore is just anterior to the first haemal spine of the anteriormost caudal centrum.

Transverse process - Throughout the length of the trunk the bodies of the vertebral centrum often have lateral processes that bear ribs. These processes are termed transverse processes or parapophyses. I will follow the terminology used by most workers dealing with centrarchid osteology (Blair and Brown, 1961; Stokely, 1952; Dineen and Stokely, 1956; Sweeney, 1972) and use the term transverse process instead of parapophysis.

ABBREVIATIONS

Institutional:

AMS	Australian Museum, Sydney
AMNH	American Museum of Natural History, New York
GMBL	Grice Marine Biological Laboratory
UMMZ	University of Michigan, Museum of Zoology
USNM	National Museum of Natural History, Washington, D.C.
VPI	Virginia Polytechnic Institute

Individual Collectors:

C & W	Chang and Waldman
JP	Jerry Platt
PM	Dr. Paula M. Mabee
S	Dr. C. L. Smith
W	Dr. John Waldman

ANATOMICAL

AP1-6	Anal-fin pterygiophore 1 - 6
APAH	Anal -fin pterygiophore anterior to first haemal spine
AR	Anal-fin ray
AS	Anal-fin spine

BSR	Branchiostegal rays
CB	Cartilaginous bar
CH	Ceratohyal
CHD	Ceratohyal foramen deeply notched
CHF	Ceratohyal foramen
CHU	Ceratohyal foramen unroofed
CV1	Caudal vertebra 1
DN	Dorsal-fin notch
EP	Epihyal
ES	Earspot
EPR	Epipleural rib
HA1-5	Haemal arch 1 - 5
HAB	Haemal arch bridged
HAU	Haemal arch unbridged
HSG1-4	Haemal spine groove 1-4
HS1-4	Haemal spine 1 - 4
HHD	Dorsal hypohyal
HHV	Ventral hypohyal
NS	Neural spine
OP	Opercle
OPN	Opercular notch
OPS	Opercular spine
PR	Pleural rib
PRE	Proximal radial expanded
PV1	Precaudal vertebra 1
SER	Serrae

SOP	Subopercle
TP	Transverse processes
TPL	Lateral transverse processes on haemal spine
SB	Swimbladder
VC	Vertebral centrum

MATERIALS EXAMINED

Specimens examined for comparative anatomical study of Centrarchidae relationships are listed here. C refers to cleared and stained specimens; A - alcohol preserved specimens; S - dry skeletal specimens; X - radiographed specimens.

Taxa	Catalogue No.	No. of Specimens	Nature of Specimen
Centrarchidae			
<u>Acantharchus pomotis</u>	AMNH 64736	1	X
		1	A
	AMNH 55482SW	1	C
	AMNH 67235	5	X
	GMBL 75-67	3	X
		2	A
	GMBL 78-169	3	X
		1	C
	PM 16-86	2	C
	USNM 237607	3	X
		3	A
<u>Ambloplites ariommus</u>	AMNH 30258	2	A
	USNM 237622	1	A
	USNM 237629	3	A
	USNM 237634	1	A
<u>Ambloplites cavifrons</u>	AMNH 30260	1	A
	AMNH 63153	3	A
<u>Ambloplites constellatus</u>	USNM 237633	1	A
<u>Ambloplites rupestris</u>	AMNH 21536SD	1	S
	AMNH 43783	11	A
		9	C
	AMNH 55876SD	1	S
	AMNH 56644SD	1	S
	AMNH 65860	2	A
	AMNH 66829	1	A
	AMNH 68265	4	A
	S 81-42	2	C
	Uncatalogued	1	S
<u>Archoplites interruptus</u>	AMNH 21997SW	2	C
	AMNH 46681SD	1	S (disarticulated)
	AMNH 46683SD	1	S (disarticulated)
	AMNH 47024SD	1	S (disarticulated)
	PM PP-1	1	C

	USNM 106571	1	C
		23	X
Centrarchus macropterus	AMNH 62531	3	A
	AMNH 64123	6	A
	AMNH 64734	5	C
		14	A
	VPI 1349	3	C
Elassoma boehlkei	AMNH 55528	30	A
		2	C
Elassoma evergladei	AMNH 1848	6	C
	AMNH 52247	2	C
	AMNH 52268	1	A
	AMNH 55751	7	A
		10	A
	Florida State University Collection 200715	18	A
	GMBL 76-30	3	A
Elassoma okefenokee	AMNH 55752	2	C
	AMNH 55753	5	A
Elassoma zonatum	AMNH 21849SW	10	C
	AMNH 53386	1	C
		6	A
	AMNH 64753	60	A
	AMNH 67672	3	C
		25	A
	GMBL 72-64	3	A
	GMBL 73-131	3	A
Enneacanthus chaetodon	AMNH 33543	5	C
		28	A
Enneacanthus gloriosus	AMNH 38563	12	C
	AMNH 48066	3	C
		110	A
	AMNH 68119	18	A
Enneacanthus obesus	AMNH 33541	3	C
		20	A
	AMNH 62528	8	A
Lepomis auritus	AMNH 10152	1	S
	AMNH 22112	1	C
	AMNH 40748	2	C
		14	A
	AMNH 49294	1	A
	AMNH 53113	11	A
	AMNH 53467	3	A
	AMNH 53492	18	A
	AMNH 53494	9	A
	AMNH 53716	9	A
	AMNH 55977SD	1	S
	AMNH 56209	1	S
	AMNH 56213SD	1	S
	AMNH 56217SD	1	S

	AMNH 66349	3	A
	AMNH 67012	2	C
		7	A
Lepomis cyanellus	AMNH 46546SD	2	S
	AMNH 53492	6	C
	AMNH 53890	3	C
Lepomis gibbosus	AMNH 35443SD	1	S
	AMNH 45816	1	A
	AMNH 47265SD	8	S
	AMNH 69576	3	A
	S 581-42	3	C
	S 586-4	40	A
Lepomis gulosus	AMNH 40735	1	A
	AMNH 47120SD	3	S
	AMNH 64892	1	C
		11	A
	AMNH 66911	2	A
	AMNH uncatalogued	1	C
Lepomis humilis	AMNH 53397	2	C
	AMNH 53682	9	A
	AMNH 53773	19	A
	AMNH 53827	11	A
		7	A
	VPI 2941	2	C
Lepomis macrochirus	AMNH 101091	28	C
	AMNH 36396SD	1	S
	AMNH 51684SW	1	C
	AMNH 53404	2	C
		15	A
	AMNH 53561	8	C
	AMNH 55265	9	A
	AMNH 56228SD	1	S
	C & W 86-1	2	S
	S 81-42	1	C
	Uncatalogued	1	C
Lepomis marginatus	AMNH 67709SW	2	C
		56	A
Lepomis megalotis	AMNH 53506	9	A
	AMNH 53542	6	C
		41	A
	AMNH 53593	2	C
		34	A
	AMNH 66175	1	A
	AMNH 67977	2	A
	AMNH 68765	4	A
Lepomis microlophus	AMNH 471255SD	1	S
	AMNH 47126SD	1	S
	AMNH 67720	28	A
	VPI 2773	2	C
Lepomis punctatus	AMNH 52265	2	C
		14	A

	AMNH 65161	1	A
	AMNH 65218	10	A
Lepomis symmetricus	AMNH 38994	1	A
	North Louisiana State Collection 1086	3	C
	USNM 172587	13	A
	USNM 230908	9	A
Lepomis spp.	AMNH 53822	52	C
Micropterus coosae	AMNH 52715	2	C
		5	A
Micropterus dolomieui	AMNH 22202	1	S
	AMNH 22203	1	S
	AMNH 41047	3	A
	AMNH 42604	5	C
		10	A
	AMNH 51682	1	C
	AMNH 68402	14	A
	C & W 86-1	2	S
	JP 78-23	1	C
	S 81-42	1	C
	Uncatalogued	2	C
Micropterus punctulatus	AMNH 53518	4	C
		40	A
	AMNH 64644	1	A
	AMNH 65784	3	A
Micropterus salmoides	AMNH 22205	3	C
	AMNH 51681SW	1	C
	AMNH 53162	6	A
	AMNH 53296	4	A
	AMNH 55886SD	1	S
	AMNH 56215SD	1	S
	AMNH 71769	1	A
	C & W 83-7	4	C
	S 81-42	4	C
	Uncatalogued	2	C
Pomoxis annularis	AMNH 10156	1	S
	AMNH 42262	2	A
	AMNH 48415	2	C
		9	A
Pomoxis nigromaculatus	AMNH 10162	1	S
	AMNH 22430	6	C
	AMNH 22431	1	S
	AMNH 44673	2	C
		23	A
	AMNH 64894	8	A
	AMNH 68104	4	C
	C & W 86-1	1	S
	PM 18-85	2	C

Osteoglossiformes:			
Osteoglossum bicirrhosum	AMNH 38150SW	1	C
Hiodon alosoides	AMNH 23754	1	C
Elopiformes:			
Elops saurus	AMNH 55346SW	1	C
	AMNH 55801SD	1	S
	AMNH 56635SD	1	C
Clupeiformes:			
Brevoortia tyrannus	AMNH 15495SW	1	C
Cypriniformes:			
Notropis cornutus	AMNH 39539SW	1	C
Notropis hudsonius	AMNH 44686SW	1	C
Rhinichthys cataractae	AMNH 39592SW	1	C
Semotilus atromaculatus	AMNH 39536SW	1	C
Salmoniformes:			
Salmo gairdneri	AMNH 40268	1	C
Salvelinus namaycush	AMNH 39269	1	C
Gadiformes:			
Melanogrammus aeglefinus	AMNH 56658SD	1	S
Cyprinodontiformes:			
Cyprinodon nazas	UMMZ 196712	1	C
Fundulus similis	AMNH 39167	1	C
Girardinichthys viviparus	UMMZ 196678	1	C
Atheriniformes:			
Menidia menidia	AMNH 35924	1	C
Atherinopsis californiensis	AMNH 46006SD	1	S
Beryciformes:			
Gephyroberyx philippinus	AMNH 49701SW	1	C
Holocentrus ascensionis	AMNH 55445SD	1	S
	AMNH 56445SD	1	S
	AMNH 56453SD	1	S
Holocentrus poco	AMNH 22925	1	C
Holocentrus rufus	AMNH 22007	1	C
	AMNH 35437SD	1	S
Polymixia lowei	AMNH 27413	1	C
	AMNH 27452	1	C
Zeiformes:			
Antigonia capros	AMNH 55975	1	S
Capros aper	AMNH 482	1	C
Zenopsis conchifera	AMNH 56447SD	1	S
Zeus japonicus	AMNH 22707SD	1	S
Zeus faber	AMNH 29458SW	1	C

Gasterosteiformes:			
Eucalia inconstans	AMNH 10181SW	2	C
Scorpaeniformes:			
Cottus bairdi	AMNH 40281SW	1	C
Scorpaena sp.	AMNH 16874	1	S
Perciformes:			
Acanthuridae			
Acanthurus chirurgus	AMNH 21806SW	2	C
Acanthurus nigrosis	AMNH 72606	2	X
Ambassidae			
Ambassis agrammus	AMNH 38003	13	X
		12	C
Ambassis baculis	AMNH 21535SD	1	S
Ambassis commersoni	AMNH 37769SW	8	C
Apogonidae			
Apogon binotatus	AMNH 24042	2	C
Fowleria auritus	AMNH 33775	1	C
Banjosidae			
Banjos typus	AMNH 35845SW	3	C
Carangidae			
Caranx erysos	AMNH 22026	1	C
Caranx latus	AMNH 56632SD	1	S
Oligoplites saurus	AMNH 56654SD	1	S
Centropomidae			
Centropomus robalito	AMNH 32925SW	3	C
Lates calcarifer	AMNH 37836SW	1	C
	AMNH 37837	1	X
Lates niloticus	AMNH 55359	1	C
Chaetodontidae			
Chaetodon multicinetus	AMNH 50028	2	X
Chaetodon punctatofasciatus	AMNH 43440	1	C
Cichlidae			
Aequidens awani	AMNH 39952SD	1	S
Aequidens cf. itanyi	AMNH 54862	1	X
Cichlasoma champotonis	AMNH 25401	1	X
	AMNH 27847	1	C
Cichlasoma coerulora	AMNH 25465	1	X
Cichlasoma spilurum	AMNH 32296	4	X
Cichlasoma synspilum	AMNH 28072SD	1	S
Geophagus surinamensis	AMNH 54944	2	X
Haplochromis livingstonii	AMNH 31777	1	X

Heros severus	AMNH 52601	1	X
Tilapia mossambica	AMNH 3639SD	1	S
Coryphaenidae			
Coryphaena hippurus	AMNH 55850	1	S
Ephippididae			
Chaetodipterus faber	AMNH 56651SD	1	S
	AMNH 56637SD	1	S
Echeneididae			
Echeneis naucrates	AMNH 56597SD	1	S
Gerreidae			
Diapterus mexicanus	AMNH 25296	1	X
Eucinostomus narengulus	AMNH 21893	1	C
Eucinostomus havana	AMNH 34381	2	X
Gerres lineatus	AMNH 9328	1	X
Gerres cinereus	AMNH 5566	1	X
Grammistidae			
Pseudogramma polycanthus	AMNH 51733	1	C
Rypticus maculatus	AMNH 55824	1	C
Haemulidae			
Haemulon album	AMNH 56660SD	1	S
Haemulon sciurus	AMNH 15484SW	2	C
Howella			
Howella brodiei	AMNH 29790	2	A
Kuhliidae			
Kuhlia malo	AMNH 9374	1	C
	AMNH 17090	1	A
	AMNH 22068	1	S
	AMNH 22069	1	S
Kuhlia marginata	AMNH 20206SW	3	C
	AMNH 73120	17	A
Kuhlia sandwicensis	AMNH 18018SW	2	C
Labridae			
Tautoga onitis	AMNH 56653SD	1	S
Labrisomidae			
Labrisomus nuchipinnis	AMNH 73227	3	A
Lactariidae			
Lactarius lactarius	AMNH 32523	1	C
Lateolabrax incertae sedis			
Lateolabrax japonicus	AMNH 10508	2	X

	AMNH 14380	1	C
	AMNH 26805	1	X
Lethrinidae			
Lethrinus nebulosus	AMNH 8173	3	A
Lethrinus ornatus	AMNH 14916SW	3	C
Lobotidae			
Lobotes surinamensis	AMNH 22125	3	C
Lutjanidae			
Lutjanus apodus	AMNH 23096	1	X
Lutjanus aya	AMNH 55869SD	1	S
Lutjanus buccanella	AMNH 56820SD	1	S
Lutjanus griseus	AMNH 52341	6	A
Lutjanus synagris	AMNH 22166	1	S
Malacanthidae			
Branchiostegus japonicus	AMNH 37948SD	1	S
Caulolatilus affinis	AMNH 49709SW	1	C
Caulolatilus chrysops	AMNH 56664SD	1	S
Hoplolatilus starcki	AMNH 38129SW	1	C
Malacanthus plumieri	AMNH 30811SD	1	S
Moronidae			
Morone americana	AMNH 56668SD	1	S
	AMNH 101243	25	C
Morone chrysops	AMNH 56346SD	1	S
Morone punctatus	AMNH 56343SD	1	S
Morone mississippiensis	AMNH 56425SD	1	S
Morone saxatilis	AMNH 103829	4	C
	AMNH 56426SD	1	S
Mullidae			
Pseudupeneus maculatus	AMNH 22764	1	X
Nemipteridae			
Nemipterus sp.	AMNH 16676SW	3	C
Nandidae			
Badis buchanani	AMNH 13790	1	C
Polycentrus schomburgkii	AMNH 14366	1	C
Pristolepis fasiatus	AMNH 195545	1	C
Percichthyidae			
Bostockia porosa	AMNH 31443	1	C
		30	A
Edelia vittata	AMNH 31352	2	C
	AMNH 31354	2	C
	AMNH 31388	1	C

Gadopsis marmoratus	AMNH 9235	1	A
Maccullochella peeli	AMS I15806-001	1	A
Macquaria ambigua	AMS I21693-002	1	A
Nannatherina balstoni	AMNH 31349	11	A
	AMNH 31357	2	C
		14	X
Percalates colonorum	AMS I15413-001	2	X
Percalates novaemaculatus	AMS I16607-002	1	C
Percidae			
Ammocrypta pullicida	Uncatalogued	1	C
Etheostoma caeruleum	Uncatalogued	1	C
Etheostoma flabellare	Uncatalogued	1	C
Etheostoma nigrum	Uncatalogued	1	C
Etheostoma variatum	Uncatalogued	1	C
Etheostoma zonale	Uncatalogued	1	C
Perca flavescens	AMNH 42539	2	C
	AMNH 43887	1	C
Perca fluviatilia	AMNH 56284	1	S
Stizostedion vitreum	AMNH 35435	1	C
Stizostedion lucioperca	AMNH 56286	1	S
Plesiopidae			
Assessor mcneilli	AMNH 49637SW	3	C
Trachinops taeniatus	AMNH 49688SW	1	C
Pomacentridae			
Chromis cyanea	AMNH 25063	2	X
Dascyllus trimaculatus	AMNH 72259	2	X
Eupomacentrus arcifrons	AMNH 73405	2	X
Pomacentrus imperator	AMNH 38113SW	1	C
Pomacanthidae			
Holacanthus ciliaris	AMNH 35428SD	1	S
Pomacanthus sp.	AMNH 56388SD	1	S
Pomatomidae			
Pomatomus saltatrix	AMNH 18804	1	C
	AMNH 56577	1	C
Pricanthidae			
Pricanthus arenatus	AMNH 56603	1	C
Pricanthus cruentatus	AMNH 56639SD	1	S
Pristigenys alta	AMNH 55831	1	C
	AMNH 29378SW	1	C
Pseudochromidae			
Pseudochromis fuscus	AMNH 16969	1	C
Scatophagidae			
Scatophagus argus	AMNH 14614	1	C

Sciaenidae			
Micropogonias undulatus	AMNH 53079SW	6	C
Serranidae			
Anthias pleurotaenia	AMNH 38119SW	1	C
Centropristis striata	AMNH 56642SD	1	S
Cephalopholis fulva	AMNH 21713	1	S
Epinephelus adscensionis	AMNH 35460	1	S
Epinephelus drummondhayi	AMNH 21860	1	S
Mycteroperca tigris	AMNH 35487	1	S
Paralabrax maculatofasciatus	AMNH 17955	1	X
Paranthias furcifer	AMNH 8318	1	X
Serranus tigrinus	AMNH 33015	3	X
	AMNH 28697	13	A
	AMNH 43172	2	C
Serranus subligarius	AMNH 55827SD	1	S
Variola louti	AMNH 45018SD	1	S
Sillaginidae			
Sillago bassensis	AMNH 31440	1	C
Siniperca incertae sedis			
Siniperca scherzeri	AMNH 10506	1	X
	AMNH 10506	1	C
Siniperca chuatsi	AMNH 10504	1	S
	Uncatalogued	2	X
Sparidae			
Calamus bajonado	AMNH 35442SD	1	S
Calamus calamus	AMNH 21671SD	1	S
Calamus pennatula	AMNH 18948	1	X
Sparus ehrenbeigi	AMNH 45477	1	X
Sphyraenidae			
Sphyraena barracuda	AMNH 56530SD	1	S
Teraponidae			
Syncomistes jenkins	AMNH 35670	8	X
Terapon butleri	AMNH 35648	4	C
Terapon fuliginosus	AMNH 35670	8	X
Pleuronectiformes:			
Trinectes maculatus	AMNH 43047	1	C
Tetraodontiformes:			
Monacanthus ciliatus	AMNH 22214	1	C
Sphoeroides maculatus	AMNH 56623SD	1	C

PART I - CENTRARCHIDAE

RESULTS

CHARACTER ANALYSIS

The following character analysis is presented in two major parts. The first part consists of characters found to be useful in defining the family and delimiting the possible sister group relationships. The second part consists of the character states used in the reconstruction of the interrelationships among the genera within the Centrarchidae.

Following analysis of each character state, a number in square brackets [ ] is used to represent the hypothesized apomorphic characters in the establishment of the most parsimonious cladogram for the Centrarchidae. For characters having multiple character states within the family, a number plus a letter (a, b, c, etc.) will represent their cladistic sequence with the letter order coinciding with decreasing universality of the apomorphic characters in the family.

Defining characters of the Centrarchidae

Transverse processes [1]

The prominent wing-like transverse processes (first described by Boulenger, 1895) are located on the lower part of the first caudal centrum and unite with the haemal arch and the first haemal spine forming a crossbow shape, as illustrated in Ambloplites (Fig. 1). Several authors (Dobbin. 1941; Stokely, 1952; Dineen and Stokely, 1952) have noted that posterior bifurcation of the swimbladder in centrarchids seems to be associated with the presence of transverse processes on the caudal vertebrae, and possibly these processes support the posterior extension of the swimbladder.

Transverse processes on the precaudal vertebrae are located on the vertebra centrum. Transverse processes on the caudal vertebrae originate from the lateral sides of the haemal spine and are formed after the appearance of the precaudal transverse processes.

The majority of outgroups do not have transverse processes on the haemal spine of the first caudal vertebrae. In Lates, Lateolabrax and Perca this character state is superficially similar to that of the centrarchids but different in two respects. In these genera the transverse processes present on the first caudal vertebrae are ventrally oriented while in centrarchids these processes project laterally and slightly posteriorly. There is also a difference in the lengths of the first and second haemal spines. In Lates and Perca the first haemal spine is much shorter than the second while in centrarchids the first and second haemal spines are approximately equal.

Larval Perca show developmental differences in the modification of the first haemal spine. In specimens of 12mm SL the ventral tip of the first haemal spine appears as a single spine (Fig. 2A). At 51 mm SL the ventral tip of the first haemal spine becomes trifurcate and interdigitates with the first anal pterygiophore (Fig. 2B). There is no lateral expansion of the first haemal spine in Perca.

The percichthyids examined (Edelia, Maccullochella, Macquaria, Nannatherina, and Percalates) show a lateral expansion of the haemal spine similar to that of centrarchids. However the lateral expansion in percichthyids does not form wing-like structures on the transverse processes.

In larval centrarchids the lateral expansions on the first haemal spine start as protruding flanges much the same as percichthyids, then gradually the ventro-lateral sides of the flanges expand forming two distinctly pointed wing-like shapes (Fig. 5A,B). This condition is considered more derived than that seen in percichthyids.

Anal-fin pterygiophores [2]

Blot (1968, 1969) studied the relationship between the anal fin and the axial skeleton (the haemal-anal-axial character complex). He recognized three general types in teleosts. In type I (e.g. Esox, Elops, etc.) there is no connection between the first haemal spine and the first anal pterygiophore. In type II (e.g. Perca, Serranus, etc.) the connection is between the elongated first proximal anal pterygiophore and the distal end of the first haemal spine. In type III (e.g. Mene, Amphistius etc.) the extreme elongation of the first anal pterygiophore almost reaches the vertebral centrum and fuses with the front of the first haemal spine.

The majority of percoids show a type II condition. Most percoids having three anal spines (the primitive condition, Bailey, 1938) show a pattern in which only one anal pterygiophore (normally a large structure carrying two spines) attaches to or lies next to the first haemal spine. However, among the genera of centrarchids which have three anal spines two or three anal pterygiophores attach to the anterior face of the first haemal spine. The remaining genera of centrarchids have more than three anal spines and show a distinct pattern in which both the additional anal pterygiophores (from 3 to 6) and the anal spines (4 to 7) lie anterior to the first haemal spine.

Among outgroups a somewhat similar condition exists among the Cichlidae. In a survey (from x-rays) of cichlids with anal spines ranging from 2 to 9 the number of additional anal pterygiophores added anterior to the haemal spine is limited to two or three and the remaining additional spines lie posterior to the first haemal spine.

Among percoids more than 3 anal spines also occurs in Chaetodontidae, Gerreidae, Pentacerotidae, Pomacanthidae, Scatophagidae, and Nandidae. Information obtained either from literature or personal observation indicates that in these groups there is a general pattern of only one anal pterygiophore anterior to the first haemal spine.

The majority of Morone show the general pattern with the exception of Morone saxatilis where there may be 2 anal pterygiophores anterior to the first haemal spine. However there is no close attachment between the first haemal spine and the anteriormost anal pterygiophore.

The percichthyids examined show a derived condition similar to the centrarchids, there are generally 2 or 3 anal pterygiophores anterior to the first haemal spine.

The occurrence of the lateral expansions on the haemal spine and the unique attachment pattern of the anal pterygiophores and the haemal spine appears to be a continuous sequence of events when observed ontogenetically. Table 1 shows the ontogenetic changes seen in a series of cleared and stained Ambloplites rupestris ranging from 9mm SL to adult. This unique pattern starts as the posterior extension of the swimbladder reaches the dorsal tips of the anal pterygiophores anterior to the first haemal spine. The swimbladder presses the dorsal tips toward the first haemal spine groove, at about the same time the lateral transverse processes on the first haemal spine starts to develop. When the swimbladder reaches the first haemal spine the lateral expansions on the haemal spine becomes evident.

Centrarchidae form a distinctive group of perciform fishes that has been traditionally defined on the basis of a series of primitive characters which are shared with other groups of the suborder Percoidei. Johnson (1984) states that "I know of no morphological specification that defines the family" consequently, the monophyly of the group, that is, a common ancestry based on shared derived characters, has never been demonstrated for the Centrarchidae. The present study indicates that the Centrarchidae can be defined as a monophyletic group based on the following synapomorphies:

(I) presence of prominent wing-like transverse processes on the first haemal spine;

(II) unique pattern of anal pterygiophores attached anterior to the first haemal spine.

The above characters are cladisticaly significant in both inter- and intrafamilial relationships and will discussed in detail at various levels.

Interrelationships among the genera

Posterior bifurcation of the swimbladder [3]

Outgroup comparisons among the Perciformes indicates that the plesiomorphic condition in the Percoidei is an oval-shaped swimbladder restricted to the abdominal region.

With the exception of Elassoma, all centrarchids have the swimbladder penetrating into the caudal region in a bilobed conformation posterior to the first haemal spine.

Gunther (1859) noted the "swimbladder notched behind" in some centrarchids. Bailey (1938) recognized different degrees of swimbladder bifurcation. The most detailed study on the gross anatomy of centrarchid swimbladder structure was done by Dobbin (1941). I agree with most of Dobbin's observations except the report that in Acantharchus the swimbladder does not extend into the caudal region. In fact the swimbladder in Acantharchus does extends into the caudal region reaching the second haemal spine. Furthermore, Dobbin did not mention that in

Archoplites the swimbladder also extends to the second haemal spine.

Ontogenetic changes observed in centrarchids reveals a transition from the primitive to the more derived condition. In early larval stages centrarchids have a single chamber, oval-shaped swimbladder which occupies a space dorsal to the body cavity and anterior to the first haemal spine. In later stages the swimbladder invades the caudal region and forms two diverticula, one on each side of the haemal spines. The dorsal wall of the swimbladder lies close to the ventral surface of the vertebral column with the posterior dorsal margin lying underneath the transverse process on the first haemal spine. The posterior bifurcations extend into the caudal region and taper to a point.

Variations occur in the degree to which the swimbladder penetrates into the caudal region. In Micropterus only a shallow indentation is formed behind the first haemal spine. The most extreme condition is found in Centrarchus and Pomoxis [3b] where the swimbladder extends beyond the fifth haemal spine forming a deeply bilobed posterior margin. In the remaining genera the swimbladder penetrates to between the second to fourth haemal spine [3a].

The haemal spines are connected to each other by a thin membranous connective tissue in such a way that it appears as a vertical partition between the two diverticula on each side of the haemal spines.

The formation of the bifurcation and the degree of penetration into the caudal region is correlated with the developmental stage. In Micropterus the bifurcation develops at a late stage. At 40mm SL Micropterus has a slight indentation present anterior to the first haemal spine; in the adult the swimbladder reaches to just beyond the first haemal spine. However, in Pomoxis at 40mm SL the larvae is in a later stage of development with the swimbladder already extending beyond the fourth haemal spine. In adult Pomoxis the swimbladder extends beyond the sixth haemal spine.

Micropterus attains a maximum length of about 830mm (TL) while Elassoma at the other extreme is not known to exceed 40mm (TL) (Nelson, 1984). However, cleared and stained specimens of Elassoma zonatum at 12mm SL are seen to be as developed as adult specimens of 32 mm SL. Connor (1980) used the posterior position of the swimbladder as a diagnostic character for the generic separation of early mesolarvae of Elassoma and Micropterus. In Elassoma at 6-8 mm TL and Micropterus at 8mm or larger the swimbladder is confined to an area above and anterior to the gut coils, while in Pomoxis (8 mm TL) and Centrarchus (8 mm TL) the swimbladder extends posteriorly to or beyond the anus.

As mentioned by Anjard (1974), Micropterus is readily distinguished from Lepomis and Pomoxis by its thicker, massively coiled gut. Connor (1980) stated that "similar gut architecture is manifest in Elassoma and this feature, along with its robust head and trunk, relatively large eye, and anteriorly placed swimbladder, results in a strong superficial resemblance to protolarvae and mesolarvae of Micropterus.

Elassoma is the only centrarchid without a posterior bifurcation of the swimbladder. There are two possible explanations which could account for this difference. If Elassoma is not closely related to the other centrarchids then the absence of the bifurcation is not relevant to the systematic position of Elassoma, however, the bifurcation would serve as a familial defining character for the rest of the centrarchids. On the other hand, if as suggested here, Elassoma is more closely related to centrarchids than to other percoids, then the absence of the bifurcation would be considered a neotenic condition. Elassoma attains maturity while the swimbladder is still in the larval condition as seen in juvenile Micropterus. Furthermore, lateral transverse processes in Elassoma (Fig. 4) are well developed on the first haemal spine and there is more than one anal pterygiophore anterior to the first haemal spine providing evidence for its retention in Centrarchidae.

Available literature on the swimbladder structures in Percoidei (Marshall, 1962); Dobbin (1941); Katayama, 1958) and dissections on various groups show that the swimbladder extends into the caudal region in *Lethrinus nebulosus*, *Chaetodipterus faber* and *Kuhlia* (3 species). In both *L. nebulosus* and *C. faber* the posterior end of the swimbladder forms a distinct diverticula on each side of the haemal spines. However, the swimbladder walls are composed of thick tissue and are surrounded by epaxial muscles. In centrarchids the swimbladder walls are composed of very thin and fragile tissue and there is no muscle between the two diverticula.

The condition of the posterior swimbladder in all species of *Kuhlia* examined is similar to the derived condition found in *Pomoxis*. In adult *Kuhlia* the posterior swimbladder extends beyond the fifth haemal spine often to the eighth haemal spine. One major difference, however, is that in *Kuhlia* the position of the swimbladder follows the ventral contour posteriorly while in centrarchids the posterior swimbladder lies close to the vertebral column. Based on the different position of the swimbladder situated in the caudal region, it is hypothesized that they are independently derived in these taxa.

Anal fin osteology

The pattern of anal pterygiophore attachment anterior to the first haemal spine along with several characters (Table 2) associated with it are important and useful in determining the interrelationships within the Centrarchidae.

Number of anal-fin pterygiophores anterior to the first haemal spine [2]

As discussed previously the primitive pattern in Percoids is a single anal pterygiophore anterior to the first haemal spine. Among the genera of centrarchids there is a definite pattern in which the number of anal pterygiophores anterior to the first haemal spine continuously increases (Table 2). As illustrated in figure 1 and figures 3-11, *Elassoma*, *Lepomis*, and *Micropterus* usually have 2 (sometimes 3) anal pterygiophores anterior to the first haemal spine, *Enneacanthus* , and *Acantharchus* have 3 [2a], *Ambloplites* and *Archoplites* have 4 [2b], *Centrarchus* 5 [2c], and *Pomoxis* 6 [2d].

In a few specimens there may be variation in the number of anal pterygiophores anterior to the first haemal spine, however, the variation in very infrequent and limited to one element difference.

Total number of anal-fin pterygiophores [4]

In general the total number of anal pterygiophores present in Centrarchidae shows a continuous increase from 6 to 23 (Table 2).

Elassoma is unusual among centrarchids in having only 6 anal pterygiophores. All other genera have between 11-23. *Micropterus*, *Enneacanthus*, and *Lepomis* have either 11 or 12 total anal pterygiophores. The remaining genera display a pattern of continually increasing total number of anal pterygiophores, *Acantharchus* 13 [4a], *Ambloplites* 14, *Archoplites* 14 [4b], *Centrarchus* 20 [4c], *Pomoxis* 22 or 23 [4d].

The gradual increase in total number of anal pterygiophores seen in *Acantharchus*, *Ambloplites*, *Archoplites*, *Centrarchus*, and *Pomoxis* parallels the gradual increase seen in the number of anal pterygiophores anterior to the first haemal spine.

Anal spines associated with the first anal-fin pterygiophore [5]

As discussed by Johnson (1980), the general rule is that the first anal pterygiophore is larger than the succeeding pterygiophores and bears 2 spines in supernumerary association and the third spine in serial association. Most centrarchids have between 3 to 7 anal spines with the first 2 supernumerary and the succeeding in serial association.

Centrarchus and *Archoplites* (Fig. 12A) are an exception to this general, the first anal pterygiophore bears 4 spines of which 3 are supernumerary [5] and the fourth is serial. This condition is rare among the outgroups. In most taxa the ontogenetic development of the first anal pterygiophore shows a ventral aspect forming a bifurcation which associates with 2 supernumerary anal spines (e.g. *Lepomis*, Fig. 12D). In *Centrarchus* (Fig. 12C) and *Archoplites* the ventral aspect of the first anal pterygiophore forms a trifurcation and associates with 3 supernumerary anal spines.

Total number of anal spines [6]

As presented in Table 2 in *Elassoma*, *Enneacanthus*, and

Micropterus show the primitive condition of having 3 anal spines. The remaining 5 genera characteristically show an increase form the primitive number to 5 or 7 anal spines [6].

It is interesting to note that all anal spines and their supporting pterygiophores associate with the first haemal spine. Among outgroups, in those taxa which have more than 3 anal spines, generally the additional spines and their supporting pterygiophores do not associate with the first haemal spine but with the succeeding ones.

Anal soft rays [7]

Most genera of centrarchids have 10 or 11 soft anal rays. Elassoma has a very reduced number of anal soft rays, usually 5. Centrarchus and Pomoxis are unusual [7] in having a higher number of soft anal rays (16-18) than any other genera (Table 2).

Precaudal and caudal vertebrae [8]

Gosline (1966a) noted that the basal number in percoids is 24-25 (10 + 14-15). Vertebrae numbers range from 28-32 in Centrarchidae, with precaudal numbers between 12-15 and caudal between 16-18 (Table 2). Based on vertebral number alone the polarity of this character cannot be determined. However, when correlated with other characters associated with the anal fin supports the polarity can be hypothesized.

The primitive precaudal and caudal vertebrae arrangement in centrarchids is probably 12-17, as seen in Elassoma and Lepomis. Micropterus frequently possesses two states, either 15-17 or 14-18 [8a], as associated with its elongate body shape. Additional vertebrae may be added to the precaudal or caudal region. Lepomis consistently shows a 12-17 pattern which is hypothesized to be a general condition. Enneacanthus has a short rounded body with a 12-16 arrangement [8b] of vertebrae. It appears to be a reduction of one vertebrae in the caudal region. The remaining genera of the lineage appear to show a somewhat stable two directional modification. Acantharchus possesses a 13-17 arrangement [8c] with one additional vertebra being added onto the precaudal region. Ambloplites, Archoplites, and Centrarchus share a 13-18 [8d] arrangement with an extra vertebra added to the caudal region. Pomoxis has a 14-18 arrangement [8e], the most derived state, with one additional vertebra being added to the precaudal region.

Position of the first anal-fin pterygiophore in the first haemal spine groove [9].

The nature of the articulation between the anal fin and the vertebral column is such that the first pterygiophore lies in a channel on the anterior face of the first haemal spine. Additional reinforcement is usually provided by a connection between the ends of the posterior pleural ribs and the first pterygiophore-haemal junction. In the majority of percoids the first anal pterygiophore is typically a double structure (fusion of the first and second pterygiophores), and frequently its dorsal tip reaches almost to the vertebral centrum (e.g. percids, Fig 2). In centrarchids *Micropterus* appears to show this general condition, the dorsal tip extends to the upper part of the haemal spine, almost reaching the haemal canal. *Lepomis* and *Elassoma* display a similar character state, but in *Lepomis* the extension of the dorsal tip is slightly lower. In the remaining genera the dorsal tip of the first anal pterygiophore reaches only to the middle of the first haemal spine.

Ontogenetically in centrarchids the anal pterygiophores form as separate elements which do not contact the haemal arch. As the fish increases in size the progressive development of the air bladder and the anal pterygiophores is such that the posterior extension of the air bladder seems to force the anterior anal pterygiophores to migrate together and closer into the groove on the anterior face of the first haemal spine.

As more anal pterygiophores are added anteriorly to the first haemal spine the distance between the first anal pterygiophore and the first haemal spine increases to a point where the first anal pterygiophore can no longer reach the upper part of the haemal spine. The distal tip thus only reaches into the middle of the groove, a condition considered here as a derived state shared by the remaining genera, Enneacanthus, Acantharchus, Ambloplites, Archoplites, Centrarchus and Pomoxis [9].

Proximal radial of the first anal-fin pterygiophore [10]

The anterior face of the first anal pterygiophore in lower percoids generally has a smooth curved configuration with a medial-anteriorly directed bony ridge running along the lower half of the pterygiophore. This bony ridge may be narrow (e.g. Perca, Morone, Kuhlia), or wide (e.g. Epinephelus, Centropomus), but rarely shows any significant anterior expansion.

In Centrarchidae all the taxa (e.g. Fig. 1 & 6-11), except Elassoma (Fig. 4) and Micropterus (Fig. 5), share this apomorphic character - the distinct expansion of the bony ridge on the first anal pterygiophore [10].

However, a different modification of the first anal pterygiophore was noted by Katayama (1958) in surveying the swimbladder morphology in Serranidae. In Lateolabrax and Acropoma the anterior face of the first anal pterygiophore expands anteriorly and is formed into a pocket-shaped structure which receives the posterior end of the swimbladder. This apparently has been independently derived several times in different lineages (e.g. Elops, Polymixia, Calamus)

Anal-fin morphology [11]

In percoids, variation in anal fin morphology occurs mostly in the length of the base and the insertion position of the fin. Most percoids are fusiform and generally tend to have a short-based anal fin with a posterior orientation (e.g. Serranus, Centropomus), while deep bodied, compressed percoids normally tend to have a long-based anal fin with an anterior insertion (e.g. Chaetodon, Pomacanthus).

Bailey (1938) analyzed the insertion of the anal fin in centrarchids and found three general patterns, far back (posterior), intermediate, and far forward (anterior). Bailey's information showed that character states in Micropterus, Ambloplites, Acantharchus and Archoplites are of the "far back" type and Enneacanthus is an "intermediate" type.

A more informative and repeatable method for expressing the origin of the anal fin insertion can be obtained by following a line from the articulation of the first anal spine on the anal pterygiophore vertically to the vertebral column. A comparison of the results of this analysis (Table 3) shows significant differences between genera.

Centrarchids appear to show a continuum in this character ranging from Micropterus with insertion line below caudal vertebrae 2 to caudal vertebrae 4 (obliquely backwards), Lepomis and Elassoma insertion line below caudal vertebrae 1 to caudal vertebrae 4 , Enneacanthus, Acantharchus, Ambloplites and Archoplites [11a] with insertion line below precaudal vertebrae 1 to caudal vertebrae 1 (vertical) to Centrarchus, and Pomoxis [11b] with insertion line below precaudal vertebrae 2 to precaudal vertebrae 4 (obtusely forward).

Haemal spine

Length of the first haemal spine [12]

In percoids the first haemal spine is always situated behind the first anal pterygiophore and has a pointed ventral tip. It is a general characteristic of the percoids that the first haemal spine is shorter than the second haemal spine. It may be more than one half shorter (e.g. *Centropomus*, *Lates*, *Perca*, *Cichla*), or one third shorter (e.g. *Elassoma*, *Epinephelus*, *Serranus*, *Lutjanus*, *Siniperca*, *Edelia*, and many others). Very rarely it is about equal length (so far found only in *Apogon* and *Pricanthus*).

In contrast centrarchids (with the exception of *Elassoma*) all share the apomorphic condition that the first haemal spine is almost as long as the succeeding one [12].

Arching pattern of the first haemal spine [13]

An important modification associated with the first haemal spine appears only in *Micropterus*. As observed in *M. dolomieui*, the first haemal spine initially appears as a straight element oriented ventrally, identical to the second haemal spine. AT 17 mm the area of the haemal spine closest to the haemal canal arches posteriorly [13]. This character is very distinctive in juveniles but not so obvious is adult specimens.

Anterior face of the first haemal spine [14]

Most percoids have an elongate first anal pterygiophore which lies close to the anterior face of the first haemal spine. The anterior face of the first haemal spine ordinarily forms a shallow depression where the elongated pterygiophore arm lies proximal to it.

In centrarchids two character states are present. Elassoma displays a general type, the anterior face of the first haemal spine is indented only slightly. The remaining members of the family possess an advanced form, in which the anterior face of the first haemal spine has a notably deep groove [14].

Contact between the first and second haemal spines at the mid-region [15]

With the exception of Scatophagus (where the first 4 haemal spines contact each other) a wide range of percoids examined have the first two haemal spines completely separate. The anteriormost interhaemal space (the distance between the first and second haemal spines) may vary from about equal spacing in the majority of species to slightly less in a few species (e.g. Edelia, Nannatherina).

In Centrarchidae, except Pomoxis, at least the first two spines unite or are in contact. The pattern of the attachment seen ontogenetically is such that the lateral flanges of the second spine gradually expand toward the back face of the first haemal spine. The ontogenetic pattern of development of this character is similar in all genera. However the stage at which development occurs may differ.

For example in Micropterus dolomieui the first and second haemal spines have contacted each other [15a] at 95mm SL while in Centrarchus the fusion is complete at 20 mm SL.

Some variation exists in the number of spines fused together, 2 or 3 may be fused in Acantharchus, Enneacanthus, Ambloplites, and at least 4 are fused in Centrarchus [15b].

Based on the sum corroborated derived character states identified in the present study, the absence of contact between the haemal spines in Pomoxis is most parsimoniously interpreted as a secondary loss.

Although Elassoma does not show this specialization it shares a condition very similar to that of the juvenile

Micropterus. At early developmental stages of *Micropterus*, before the contact of the two spines is completed, the ventral tip of the first haemal spine bends posteriorly toward the second haemal spine. All *Elassoma* show this "juvenile" condition and in addition I have found several cases where the ventral tip of the first haemal spine contacts the second haemal spine.

Abdominal haemal arches [16]

The presence of bridged abdominal haemal arches is considered a primitive condition among the acanthopterygians (Rosen, 1973). Most percoid taxa examined showed the presence of bridged abdominal haemal arches. However, this character was found to be absent in *Edelia*, *Nannatherina*, *Perca*, and centrarchids.

Although absent in most adult centrarchids, larvae of *Elassoma*, *Micropterus*, *Enneacanthus*, *Lepomis*, and *Ambloplites* (Fig. 13) show the presence of bridged abdominal haemal arches (Table 4). The absence of bridged abdominal haemal arches is apparently associated with the development of transverse processes from a more ventral position in juveniles to the lateral position in adult (Fig. 14). The larvae of *Archoplites*, *Centrarchus*, and *Pomoxis* do not have bridged abdominal haemal arches in either the larval or adult stages. *Acantharchus* [16a] is exceptional among centrarchids in having a single bridged abdominal haemal arch on the last abdominal vertebrae of adults and 1-2 abdominal haemal arches present in the larval stage.

The general occurrence of bridged abdominal haemal arches in adult percoids suggests that this is a primitive condition and the absence of this character in adult centrarchids is considered derived. The absence of bridged abdominal haemal arches in the ontogeny of Archoplites, Centrarchus, and Pomoxis is hypothesized to be a further reduction [16b].

The absence of bridged abdominal haemal arches in adult centrarchids may be related to the presence of a well-developed swimbladder. Specimens of Perca flavescens have a swimbladder similar to centrarchids. They also show an absence of bridged abdominal haemal arches in the adult stage, and the presence of a single bridged abdominal haemal arch in the larval stage. In Etheostoma, which is a more derived percid with a vestigial swimbladder, 4 or 5 bridged abdominal haemal arches are commonly present. The retention of bridged abdominal haemal arches in Etheostoma may be correlated with the absence of a swimbladder.

Opercular morphology

Posterior opercular morphology [17]

The primary opercular spine projects from the posterior border of the opercle at the level of the hyomandibular-opercular articulation. A ridge generally passes along the inner surface of the opercle between the spine and the hyomandibular articulation. Broadening ventrally from the articulation, the opercle extends posteriorly to overlie the region of the supracleithrum and the dorsal portion of the cleithrum. Along its ventral and posterior-ventral margins the operculum overlies the dorsal portion of the subopercular.

The number of opercular spines (from 0 to 3 in Percoidei, McAllister, 1968) has been used as a significant character in some percoid fishes. One of the major features by which Gosline (1966a) distinguished his restricted family Serranidae from Percichthyidae is that all Serranids share the presence of an additional opercular spine below the primary spine, making a total of three spines on the opercle. In almost all other percoids there are only two opercular spines, the primary one and a small one above it. "A single innovative specialization, the presence of three spines on the opercle indicates that the Serranidae are monophyletic" (Johnson 1983).

The posterodorsal opercular margin varies among adult centrarchids. In the adult centrarchids 5 character states of the opercle are recognized:

1. notched posteriorly
2. rounded posteriorly
3. fimbriate posteriorly
4. weak serrae on dorsal edge only
5. strong serration on both dorsal and ventral edges.

Character state 1 is the primitive condition in which the opercular margin in notched and entire. It is present in the adults of *Acantharchus*, *Ambloplites*, *Centrarchus*, *Enneacanthus*, *Elassoma*, and *Pomoxis* (Fig. 15). Sweeney (1972) interpreted this condition in *Enneacanthus* (Fig. 16) as "...the opercle possesses a deep rounded notch.." which is unique among the Centrarchidae. The shape of the notch varies from shallow in *Elassoma* to deep in *Enneacanthus*, however the distinction is not clear and it overlaps among the genera. For this reason I identify both the shallow notch and the deep notch as a single character state.

Early stages of *Lepomis* shows a notched posterior opercular margin which in the adult becomes either rounded or fimbriate [17b]. In *Lepomis cyanellus*, *L. symmetricus*, *L. punctatus*, *L. gibbosus*, and *L. microlophus* the posterior dorsal margin is rounded posteriorly (Fig. 17). In L. megalotis the margin of the opercule is initially notched (Fig. 18A), passes through a rounded state (Fig. 18B) and later becomes posteriorly fimbriated (Fig. 18C). L. auritus also has a fimbriated opercular margin and presumably passes through similar ontogenetic stages.

Micropterus shows an unusual pattern with serrations (Fig. 19) consisting of 3 short (sometimes 2) serrae on the dorsal edge of the operculum [17a].

Archoplites is unique [17c] in having a posterior opercular margin heavily sculptured with numerous serrations which increase in number as the fish grows (Fig. 16D,E). The primary opercular spine has splayed out to form many smaller spines. A similar condition was noted in Howella (Gosline, 1966a) however Archoplites has numerous small spines but Howella (in a specimen 78 mm SL) has only 3 spines.

Ear spot [18]

Coloration patterns among fishes are important and have be suggested to be involved in reproduction, recognition and defense. Opercular flaps with conspicuous edging appear to be one of the key features by which male Lepomis megalotis recognize conspecific males during defense of there breeding territories (Keenley, 1971).

According to Fujii (1969) the color pigments contained in chromatophores of fishes have been commonly classified as melanophores (brown or black), xanthrophores (yellow), leucophores (white) and iridophores (reflecting). The leucophores contain colorless pigments which can move back and forth in the cytoplasm. Most pigments (except black and brown) are known to fade when specimens are stored in alcohol. Only alcohol specimens were used to evaluate the ear spot character.

Ear spots are present on all centrarchids (except Elassoma) and serve as very useful field and laboratory identification characters (Smith 1985). In centrarchids the ear spot is located in the dorsal posterior margin of the operculum and extends posteriorly toward the ear flap. The size, color, and shape of the ear spot varies from species to species and within species may vary with age and sex (Fig. 20).

In general the earspot consists of dense pigments which concentrate on the dorsal posterior margin of the operculum. A cross section of the ear spot examined under the compound microscope (60X to 400X) showed that melanophores are present in the dermis of both the outer and inner surfaces of the operculum [18]. The melanophores form a band in the dermis. The pigment band on the inner surface of the operculum is more dense and broader than the band on the outer surface. Where there is no bony element, on the posterior aspect of the ear spot, the two pigment bands merge. Among the centrarchids the degree of pigmentation varies from very distinctive in some adult male Lepomis to indistinct in Pomoxis.

Ear spots are present in certain perciform fishes. Morone punctatus (Fig. 21C), M. labrax, Percalates colonorum have ear spots superficially similar to the Centrarchidae. Cross-sectional examination under the microscope shows that the pigments are present only on the inner surface of the operculum. In addition the ear spot covered the areas both above and below the primary opercle spine whereas in Centrarchidae it is restricted to the area above the opercle spine.

In Pseudogramma polycanthus (Fig. 21A) and P. grammistidae of the family Grammistidae and in Labrisomus nucnipinnis of the Labrisomidae, the dense pigment cells in the ear region are only present on the outer surface of the operculum. There is no pigment located on the inner surface of the operculum and the ear spot does not extend to the edge of the ear flap.

In Apogon odorii and Fowleria auritus (Fig. 21B) of the family Apogonidae pigments are present mostly on the inner surface of the opercle and the location of the ear spot is limited to the area below the primary opercular spine.

Ceratohyal foramen [19] and epihyal-ceratohyal channel [20]

In Lepomis and Micropterus the anterior ceratohyal has a foramen bounded by a bar of cartiladge which eventually ossifies. This foramen was termed the "beryciform foramen" by McAllister (1968) in the belief that this hyoid feature of acanthopterygians is uniquely different from a similar "foramen" that is a primitive feature of all major groups of teleosts. Rosen (1973) argued that McAllister presented no convincing reasons for this belief and suggested the removal of the modifier "beryciform". The terminology used here is that of Rosen (1984).

Gosline (1966a) separated "Percichthyidae" from Serranidae by using the upper border of the ceratohyal. In the Percichthyidae the border of the ceratohyal is straight or has an oblong hollow excavated into it. In Serranidae the border is smoothly concave. Arratia (1982) noted that the "Percichthyidae" condition described by Gosline is present in some serranids too. For example, the upper margin of the ceratohyal of Percichthys is similar to that of the serranids Hemilutjanus and Acantnistius. Thus this character state cannot be used to separate Serranidae from Percichthyidae.

McDonald (1978) illustrated three character states in the most generalized genera of Australian percichthyid fishes. In the most primitive genus, *Percalates*, (also personal observation) there is a complete foramen, oblong in shape. *Macquaria* and *Plectroplites* have an oblong excavation on the upper margin of the ceratohyal and *Maccullochella* has a smooth, concave indentation. The most derived genera I have examined, *Edelia* and *Nannatherina* (sensu Johnson, 1984), show a condition similar to that of *Maccullochella*.

Another important character associated with the upper border of the ceratohyal is a prominent channel across the epi- and ceratohyal. Katayama (1959) examined both the upper boarder of the ceratohyal and the epi-ceratohyal channel and recognized three types.

Type I is represented by *Niphon*, *Stereolepis*, and *Siniperca*. In these fishes the channel runs longitudinally across the epi- and ceratohyal passing ventrally under an oblong foramen in the ceratohyal. This condition is also present in *Centropomus*, *Lates*, *Caranx*, *Holocentrus*, *Percalates*, *Chaetodipterus*, and *Kuhlia*.

In type II there is no completely formed foramen; the upper edge of the ceratohyal forms an oblong hollow. A continuous channel is present along the upper edge of the epi- and ceratohyal. This condition is present in *Lateolabrax*, *Epinephelus*, *Calamus*, *Priacanthus*, and *Lutjanus*.

In type III there is no foramen, the upper border of the ceratohyal is concave, and the channel is interrupted in the vicinity of the ceratohyal concavity. This condition is present in *Morone*, *Perca*, *Apogon*, *Centropristis*, *Haemulon*, *Bostockia*, and *Paralabrax*.

All lower percoids I have examined fall into one of Katayama's types and all show the presence of a prominent channel across the epi-ceratohyal junction.

In Centrarchidae the epi-ceratohyal channel is greatly reduced in *Micropterus* and absent in all the remaining genera [20], and this is considered a derived condition.

Ontogenetic observations in *Lepomis* and *Micropterus* (Fig. 22) show a similar developmental pattern in the formation of the ceratohyal foramen. Early in ontogeny a notch forms on the upper border of the ceratohyal. As ossification proceeds the anterior and posterior edges of the notch grow together forming an oval shaped foramen as the two edges meet. Later in development in *Micropterus* (Fig. 23) the foramen is transformed from an oval shape to a slit-like shape. In *Lepomis* (Fig. 24) and *Acantharchus* the foramen is transformed from an oval to a round shape.

A complete foramen is never formed in the remaining centrarchid genera. In *Enneacanthus* (Fig. 25) the dorsal ceratohyal foramen is only partially formed leaving a deep hollow notch in the margin of the ceratohyal [19a]. In

Pomoxis, Ambloplites, Centrarchus, and Archoplites (Fig. 26) remnants of the foramen remain in the shape of a shallow, slightly concave upper ceratohyal margin [19b]. In Elassoma the ceratohyal foramen is absent and the upper ceratohyal margin is not concave (Fig. 27).

The common occurrence of a foramen among outgroups indicates that it is a primitive condition. The absence of a foramen in some centrarchids is considered a derived condition which exists either as a deep notch or a slight concavity on the upper margin of the ceratohyal.

Number of branchiostegal rays [21]

Three character states can be described for the number of branchiostegal rays, 5, 6, or 7 rays present. McAllister (1968) found the distribution of these three character states showed a mosaic pattern within perciforms and evidently each has been derived repeatedly in different groups. He noted that in Centrarchidae the primitive genera have 7 rays, advanced genera 6 or 5. Mok (1983) suggests that 6 rays has the broadest distribution within the Perciformes, hence is the primitive state. In examining the lower percoids I found 7 rays to be common, but 6 are present in percids, percichthyids, and kuhliids.

Among the centrarchids Elassoma (Fig. 27) has 5 rays, Lepomis, Micropterus, Ambloplites, and Enneacanthus

(Fig. 23 - 25) have 6 rays and Archoplites, Centrarchus and Pomoxis (Fig. 26) have 7 branchiostegal rays [21]. Based on the congruence of this character with other characters in this study it is most parsimonious to hypothesize that 6 branchiostegal rays is primitive in Centrarchidae 5 and 7 rays are derived.

Gill rakers on the first branchial arch [22]

The number and shape of gill rakers can be separated into two distinct groups (Bailey 1938): 5-15 moderately long gill rakers and 25-40 long and slender gill rakers.

The polarity of this character is uncertain. However it appears that the low number and moderately long shape is more generalized. In the limited number of basal percoids examined the high number of gill rakers and long and slender shape present in Archoplites, Centrarchus, and Pomoxis seem to be derived [22].

Dorsal fin morphology [23]

In most percoids the dorsal fin consists of both spinous and soft rays. Most basal percoids, such as Centropomus, Perca, Morone, and Apogon, have a well developed notch in the dorsal fin and the spinous and soft rays of the fin appear to be separate. This condition is considered to be primitive for the basal percoids.

Three character states of dorsal fin shape are displayed in the Centrarchidae. A primitive type deep-notched dorsal is seen in all Micropterus (Fig. 28A), a shallow-notched condition is seen in Lepomis (Fig. 28B), Enneacanthus, Acantharchus, Ambloplites, and Archoplites [23a], and the most derived condition, shared by Centrarchus and Pomoxis (Fig. 28C, D), in which the notch is completely lost and only a single dorsal fin is displayed [23b].

Apomorphic characters from previous studies

In an attempt to evaluate the congruence of presumed apomorphic character states identified in the present study, previous published information on the phylogenetic relationships of the Centrarchidae were carefully evaluated and corroborate here in the belief that the most parsimonious cladogram can be further strengthened by incorporating synapomorphies from different studies.

Olfactory organs [24]

Eaton (1956) showed that in centrarchids, the olfactory epithelium supplied by branches of the olfactory nerve, is thrown into a series of folds. In *Archoplites*, *Pomoxis*, and *Centrarchus* the folds are paired, alternate ones are swollen [24]. In other sunfishes this pairing has not been found, and either the most posterior, or all, of the folds may be swollen. *Elassoma* has only three rudimentary folds.

Dorsal fin supports [25]

The study of Smith and Bailey (1961) on the dorsal fin supports of percoid fishes shows evidence that *Micropterus*, *Lepomis*, and *Enneacanthus* possess 10 dorsal spines but *Acantharchus*, *Ambloplites*, *Archoplites*, *Centrarchus*, and *Pomoxis* form a monophyletic group by sharing the apomorphic character state of an additional dorsal spine (total 11) with its supporting pterygiophore [25a]. Subsequent addition of another dorsal spine (total 12) on the fist pterygiophore are characteristic of *Archoplites* and *Centrarchus* [25b]. *Pomoxis* has a reduced number of dorsal spines (6) and is considered to have a reduced condition [25c].

Kidney morphology [26][27]

Mok (1981) studied kidney morphology among centrarchids. Although he did not find a synapomorphy for the whole family, he noted that the monophyly of Lepomis is indicated by the presence of a thick tissue layer over the extreme posterior kidney [26]. He also found that Centrarchus and Pomoxis form a monophyletic group by sharing the fused extreme anterior kidneys and fusion of the posterior kidneys behind the first haemal spine [27b]. Furthermore Mok demonstrated that all genera (except Elassoma and Micropterus) possess a unique extreme posterior kidney distinctively different from the outgroups [27a].

A cladogram of the most parsimonious hypothesis of relationships for the genera of the family Centrarchidae is presented in figure 29.

DISCUSSION AND SUMMARY

MONOPHYLY AND INTRARELATIONSHIPS OF THE CENTRARCHIDAE

The monophyly of the Centrarchidae is suggested by the following synapomorphies. First, the presence of the prominent wing-like transverse processes on the first haemal spine. Second the unique pattern of attachment between the anterior anal pterygiophores and the first haemal spines. The first and second haemal spines originate as separate elements with anterior directed flanges. Eventually the first and second haemal spines contact and the flange on the anterior haemal spine forms a deep groove. More than one anal pterygiophore unites with the first haemal spine groove.

Two subfamilies are recognized within the Centrarchidae, the Elassomatinae and the Centrarchinae. The Elassomatinae with one monophyletic genus have been suggested previously by Smith and Bailey (1961) and Nelson (1984). This subfamily is defined by numerous reductive characters (see discussion to follow).

The Centrarchinae include the remaining eight genera. The genera of this subfamily share the following apomorphic characters: prominent ear spot, first and second haemal spines united, elongation of the first haemal spine, and posterior bifurcation of the swimbladder.

Within the Centrarchinae the eight genera (Micropterus, Lepomis, Enneacanthus, Acantharchus, Ambloplites, Archoplites, Centrarchus, and Pomoxis) each form a monophyletic genus based on a series of apomorphic characters along a lineage of increasing derivation from the base taxon Micropterus.

Micropterus is identified by the presence of 2 to 3 serrae on the dorsal margin of the upper opercular spine and the arching pattern of the first haemal spine.

The remaining members of the Centrarchinae are united by sharing a greatly expanded proximal radial on the first anal pterygiophore, extreme posterior kidney, swimbladder extending beyond the first haemal spine, abdominal transverse processes laterally directed, dorsal fins with a shallow notch, and the absence of a channel across the ceratohyal and epihyal.

Lepomis is recognized by having a rounded (or fimbriate) posterior opercular margin and the presence of a thick tissue layer over the extreme posterior kidney.

The remaining six genera are united by the distal ends of the anterior pterygiophore reaching the middle of the first haemal spine groove and the vertical orientation of the anal fin supports with respect to the vertebral column.

Enneacanthus is unique in having a deeply rounded notch on the upper ceratohyal margin.

The remaining five genera are united by the possession of more than 3 anal spines.

Acantharchus is identified by having a single bridged abdominal haemal arch in adults.

The remaining four genera share the following synapomorphies: 4 or more anal pterygiophores anterior to the first haemal spine, olfactory sac with paired folds alternate ones swollen, and the absence of a ceratohyal foramen.

Archoplites, *Centrarchus*, and *Pomoxis* a closely related assemblage in the Centrarchinae. The synapomorphies uniting this group include the absence of bridged abdominal haemal arches in larvae and adults, 7 branchiostegal rays, and numerous long and slender gill rakers.

Archoplites is unique in having numerous opercular spines.

Centrarchus and *Pomoxis* form a closely related sister group based on 5 or more anal pterygiophores anterior to the first haemal spine, swimbladder extending beyond the fifth haemal spine, posterior kidney fused behind the base of the first haemal spine, no notch in the dorsal fin, insertion of anal fin far forward and more than 20 soft anal rays.

Centrarchus is unique in having 5 anal pterygiophores anterior to the first haemal spine and the anterior 4 haemal spines fused at mid-region.

Pomoxis, the most derived genus of the Centrarchinae, is unique in having 6 anal pterygiophores anterior to the first haemal spine, 0 to 1 predorsal bones, and the presence of 4 transverse processes on the anterior 4 haemal spines.

Various phylogenetic relationships proposed previously show certain congruence or incongruence with the present study. The major differences are due mainly to results obtained through different systematic approaches and character analysis.

The studies of Smith and Bailey (dorsal fin supports), Mok (kidney morphology) and Eaton (olfactory organs) revealed arrangements of groups within the Centrarchidae that are congruent with interpretations based on the present study, and serve to reinforce the systematic conclusions obtained in the present study.

Findings incongruent with the present study were found by Branson and Moore (1962). The failure of these authors to recognize that 3 anal spines is a primitive character state resulted in two false conclusions. First they united Lepomis and Micropterus on the basis of 3 anal spines being apomorphic. Second they proposed Ambloplites as the basal taxon in the Centrarchidae based on a high number of anal spines being primitive. These conclusions were erroneous since 3 anal spines is a primitive and not an apomorphic character. As discussed previously a 3 anal spine count is so widely distributed in Perciformes that to suggest it is apomorphic is misleading.

One of the major differences between the detailed ontogenetic study done by Mabee (1987) and the present study is the monophyletic grouping of *Lepomis* and *Enneacanthus*. One of the characters Mabee based this grouping on is the presence of a rounded ceratohyal foramen in adults. A rounded ceratohyal foramen is always present in *Lepomis* however in *Enneacanthus* the foramen is either absent or formed by the presence of a partially ossified cartilaginous bar. The presence of the foramen is dependent upon the formation of a cartilaginous bar during development. Based on outgroups, the presence of this bar is considered a primitive condition. A shared primitive condition (symplesiomorphy) is not a sound basis for expressing a sister taxa relationship.

My interpretation is different from Mabee's. I treat the partially ossified ceratohyal foramen as a deeply notched form and consider it to be a more derived condition than that of *Lepomis*.

SYSTEMATIC POSITION OF ELASSOMA

Numerous reductive features have been reported in Elassoma. These include reduction in laterosensory system (Branson and Moore, 1962); reduced dorsal spines, pterygiophores and predorsal bones (Smith and Bailey, 1961); rudimentary olfactory organs (Eaton, 1956); absence of basisphenoid, endopterygoid and reduced number of principal caudal rays (Johnson, 1984); cycloid scales (Bailey, 1938) and absence of intercranial cartilage (pers. observation).

Based on reductive characters Branson and Moore (1962) suggested family status for Elassoma. Johnson (1984) suggested that the affinities of Elassoma may even be outside the Perciformes. He noted that "...the ossified portion of the ethmoid consists of two, closely applied, disc-like bones, a condition listed as one of the defining characteristics of the Atherinomorpha by Rosen and Parenti (1981)." However Parenti (pers. communication) points out that the ethmoid bones of Atherinomorpha are overlapping and parallel while those of Elassoma overlap at an angle. She further suggests that the condition found in Elassoma resembles the early developmental Percoid condition.

All Centrarchids exhibit a similar mode of nest-building and parental-care (Breeder and Rosen, 1966) and Johnson (1984) suggested that this behavioral "synapomorphy" is not shared by *Elassoma*. However, although members of *Elassoma* are not known to construct nests during spawning (Mettee, 1974; Walsh and Burr, 1984) it has been shown that *E. evergladei* (Robison, 1971) and *E. zonatum* (Walsh and Burr, 1984) guard eggs and defend the developing embryos.

Neoteny, or pedomorphosis, has regularly troubled discussions of ontogeny and its relevance for systematics (Nelson, 1985). Whether or not *Elassoma* is neotenic, the use of reductive or "absence" characters does not provide a sound basis for separating them from the Centrarchidae.

SISTER GROUP RELATIONSHIPS

The results of this study indicate that the Centrarchidae and Percichthyidae are sister groups. Two synapomorphies were found to unite Centrarchidae and Percichthyidae, the lateral expansion of the first haemal spine and the number of anal pterygiophores anterior to the first haemal spine. McCully (1962) also proposed a possible relationship between the Centrarchidae and the subfamily Percichthyinae Which is composed of the basal members of Johnson's (1984) restricted Percichthyidae. He based this relationship on scale morphology in which the posterior field of the scale has monodont scalelets which are slightly amputate.

Several other derived characters also suggest a close relationship between these two taxa. These characters include the unbridged abdominal haemal arches, the first haemal spine forming a medial-anteriorly directed groove, higher vertebral counts (25-33) than basal percoids, and pleural ribs attached close to the centrum rather than on the transverse process as seen in most basal percoids.

These two linages can be distinguished by the way in which the anterior anal pterygiophores contact the first haemal spine groove. In Percichthyidae the dorsal tip of the first anal pterygiophore reaches into the haemal spine groove. In Centrarchidae the dorsal tips of all anal pterygiophores anterior to the first haemal spine unite and migrate into the haemal spine groove.

As mentioned previously, different workers have hypothesized the Centrarchidae to also be related to Serranidae, Siniperca or Kuhliidae. On the basis of the haemal-anal-axial characters (prominent wing-like transverse processes on the first haemal spine and the unique pattern of anal pterygiophores anterior to the first haemal spine) the condition found in Centrarchidae does not appear to be approximated in any of these three groups. None of the apomorphic characters which define these groups (Gosline, 1966a, with respect to Serranidae) has been found to be present in Centrarchidae.

As discussed previously, the extreme bifurcation of the posterior swimbladder in Kuhlia is considered independently derived and different from that of the Centrarchidae. No synapomorphy was found to unite these two taxa. Furthermore Kuhlia retains a well-developed not concealed pseudobranch (Bailey, 1938)(rudimentary condition and concealed in the Centrarchidae), procurrent spur (Johnson, 1975) (absent in Centrarchidae), and a different pattern of Ramus Lateralis Accessorius innervation (Freihofer, 1963).

Due to the absence of information on the ontogeny of percichthyids questions remain as to whether the ontological development of the lateral expansion on the first haemal spine and the attachment of the anal pterygiophores to the first haemal spine are similar to that seen in centrarchids. Nevertheless, the occurrence of lateral transverse processes on the first haemal spine and more than one anal pterygiophore attached to the first haemal spine in centrarchids and percichthyids is consistent and is treated as a synapomorphous feature subject, like all other synapomorphies, to reinterpretation with additional information.

CONCLUSIONS (PART I)

Among Centrarchidae there is a general trend from fusiform body shape to a shorter more rounded shape. These changes correlate with changes in the morphology of the swimbladder. More generalized centrarchids (Micropterus) show only a slight extension of the swimbladder into the caudal region. More derived taxa (e.g. Pomoxis) show an extreme extension of the swimbladder into the caudal region. The modification of the swimbladder seems to be a response to the change of body shape. By increasing the extension of the swimbladder round bodied fish are able to maintain their stability in the water column.

Modifications of the swim bladder are associated with osteological changes seen in the haemal-anal-axial complex and associated characters. Ontogenetically the progressive extension of the swimbladder into the caudal region is associated with the migration of the anterior anal pterygiophores into the first haemal spine groove.

Another consequence of swimbladder extension is a loss of muscle mass in the caudal region. It is hypothesized that this loss of muscle mass is possibly compensated for by the stregthening of the connection between the anal pterygiophores and the haemal spines.

The more derived taxa possess more laterally directed abdominal transverse processes which are apparently modified in response to the extreme penetration of the swimbladder. In addition the prominant wing-like transverse processes on the haemal spines provide protection for the posterior extension of the swimbladder.

This unique pattern of modifications associated with the haemal-anal-axial character complex is hypothesized to correlate with the phylogeny of the Centrarchidae.

Percoid evolution has been characterized by considerable adaptive modifications, and it is only through comprehensive group studies that we can come to recognize the evolutionary significance of various character complexes. In conclusion, I agree with Johnson's (1980) opinion that "valid phylogeny in the percoids will result from the family and family complex approach, wherein numerous aspects of the anatomy of all recognized genera can be evaluated, integrated, and compared".

PART II

THE HAEMAL-ANAL-AXIAL CHARACTER COMPLEX

INTRODUCTION

I became interested in the character complex of the anterior anal pterygiophores, first haemal spines, and axial skeleton during the course of an investigation into the interrelationships of several percoid fishes, but further exploration has shown it to be significant at different taxonomic levels. Blot (1968) surveyed the relationships between the anal fin and the axial skeleton (complexe hemaxanal), among some fossil teleosts. He recognized three general types: TYPE I there is no connection between the first haemal spine and the first anal pterygiophore; Type II connection is made by the elongation of the first anal pterygiophores with the haemal spine; Type III the extreme elongation of the first anal pterygiophore and fusion with the first haemal spine.

The morphology of the anterior anal fin pterygiophore has been used by some fish biologists to provide useful systematic information (Fritzsche and Johnson 1980; Smith-Vaniz 1984; Potthoff et al. 1987; and Gushiken 1988). The shape of haemal arches of vertebral column in several species of South American atherinids have been compared and showed significant taxonomic values as an aid to determining the complex relationships within the family of Atherinidae (Piacentino and Torno 1987). The diagnostic potential of pterygiophore interdigitation patterns in the genus Morone was recognized by Woolcott (1957) in an examination of adult osteology. Recently, Olney et al. (1983) demonstrates that the number and position of anal pterygiophores relative to interhaemal spaces are characters useful for identifying larvae of Morone species.

The interrelationships of the anterior anal pterygiophore, the first haemal spine, and the vertebral column however, are often not considered. Johnson (1984) stated that for percoids the anal fin is less variable in form and composition than the dorsal fin, but when the relationships are examined in detail, certain phylogenetically significant patterns are revealed. I have examined representative taxa from each major group of teleosts in order to evaluate the potential utilization and understanding of this character complex and major efforts have been concentrated on the percoid fishes.

GENERAL RESULTS AND DISCUSSION

Osteoglossomorpha

Osteoglossoidei

Osteoglossidae

Osteoglossum bicirrhosum - Type I (Fig. 30)

Osteoglossum shows no contact between the first anal pterygiophore and the first haemal spine. The distal tip of the first anal pterygiophore extends into the interhaemal space. There is only one anal pterygiophore anterior to the first haemal spine but in Hiodon (suborder Notopteroidei) there are five anal pterygiophores anterior to the first haemal spine and the anal pterygiophores do not reach into the interhaemal space.

Elopormorpha

Suborder Elopoidei

Elopidae

Elops saurus - Type I (Fig. 31)

There is no contact between the first anal pterygiophore and the first haemal spine. The distal tip of the first anal pterygiophore does not extend into the interhaemal space. The anal pterygiophore is uniquely modified being enlarged into a pocket shape probably to accommodate the posterior end of the swimbladder.

Clupeomorpha

Clupeoidei

Clupeidae

Brevoortia tyrannus - Type I (Fig. 32)

There is no contact between the anal pterygiophores and the haemal spines and the anal pterygiophores do not extend into the interhaemal space. Numerous intermuscular bones were observed in the caudal region. Judging from x-rays presented in Grande (1985) the number of anal pterygiophores anterior to the first haemal spine in the clupeomorph fishes he surveyed varies between 1 and 5, with 1 being the most common.

Euteleostei

Ostariophysi

Cypriniformes

Cyprinidae

Notropis hudsonius - Type I (Fig. 33)

There is no contact between the anal pterygiophores and the haemal spines and the anal pterygiophores do not extend into the interhaemal space. There is a slight enlargement of the ventral tip of the anal pterygiophores.

Protacanthopterygii

Salmoniformes

Salmonidae

Salmo gairdneri - Type I (Fig. 34)

There is no contact between the anal pterygiophores and the haemal spines and the anal pterygiophores do not extend into the interhaemal space. The first anal pterygiophore is greatly reduced in size.

Paracanthopterygii

Gadiformes

Gadidae

Melanogrammus aeglefinus - Type I

There is no contact between the anal pterygiophores and the haemal spines and the anal pterygiophores do not extend into the interhaemal space. There are 8 anal pterygiophores anterior to the first haemal spine.

Acanthopterygii

Cyprinodontiformes

Fundulidae (Parenti, 1981)

Fundulus similis - Type I (Fig. 35A)

There is no contact between the anal pterygiophores and the haemal spines. The anterior anal pterygiophore reaches into the interhaemal space. The anal pterygiophores are slightly enlarged.

Atheriniformes

Atherinidae

Menidia menidia - Type I (Fig. 35B)

There is no contact between the anal pterygiophores and the haemal spines. The anterior anal pterygiophores do not extend into the interhaemal space. There are 5 anal pterygiophores anterior to the first haemal spine. The anal pterygiophores are slightly enlarged.

Beryciformes

Holocentridae

Holocentrus poco - Type II (Fig. 36A)

H. rufus

H. ascensionis

This order may come closest to representing the ancestral stock from which the Perciformes evolved (Nelson, 1984). There are 2 anal pterygiophores anterior to the first haemal spine. The first anal pterygiophore is elongate and extends into the interhaemal space. The second anal pterygiophore is also enlarged, a condition not seen in the basal percoids. The orientation of the anal pterygiophores with respect to the vertebral column is distinctly oblique, a condition which is very common in the basal percoids.

Trachichthyidae

Gephyroberyx philippinus -Type II (Fig. 36B)

The pattern seen in Gephyroberyx is similar to Holocentrus except that there are 3 anal pterygiophores anterior to the first haemal spine.and the orientation of the anterior anal pterygiophores with respect to the axial skeleton is more vertical.

Polymixiidae

Polymixia lowei - Type II (Fig. 37)

The first anal pterygiophore is greatly enlarged (possibly a fusion of two elements), and modified into a pocket shape.

Zeiformes

Zeidae

Zenus faber - Type III (Fig. 38)

Z. japonicus

Zenopsis conchifera

The condition seen in this taxon of fishes is unique. The anteriormost anal pterygiophores are greatly enlarged and strongly fused together. This unique fusion pattern involves not only the first haemal spine but also fusion with 2 abdominal haemal arches. In Zenus japonicus 3 abdominal haemal arches are fused to the anteriormost anal pterygiophores and in Zenopis there are 4 involved.

Gasterosteiformes

Gasterosteidae

Eucalia inconstans - Type III (Fig. 39A)

The first anal pterygiophore is greatly modified into a single enlarged structure and extends into a groove on the first haemal spine.

Scopraeniformes

Cottidae

Cottus bairdi - Type I (Fig. 39B)

There is one slightly enlarged anal pterygiophore anterior to the first haemal spine. The distal tips of the anal pterygiophores do not extend into the interhaemal space.

Perciformes (see separate discussion)

Pleuronectiformes

Soleidae

Trinectes maculatus - Type III (Fig. 40)

This taxon is unique in that the first anal pterygiophore is greatly elongated and curved posteriorly to contact the first haemal spine. There are 7 anal pterygiophores anterior to the first haemal spine.

Tetraodontiformes

Balistidae

Monacanthus aliatus - Type III (Fig. 41)

The condition seen in this taxa is somewhat similar to that seen in the Zeiformes. The anteriormost anal pterygiophores are elongate and fused together. This fusion patter involves 2 abdominal haemal arches and the first haemal spine.

Traditionally Zeiformes are placed close to the Beryciformes. Based on the specialized morphology of the otoliths, Patterson (1964) suggested the order Zeiformes is a sister group of the Beryciformes and both groups are the sister group of the perciform assemblage. Recently, Rosen (1984) included the Zeiformes in the order Tetraodontiformes based on 11 synapomorphies. Although Rosen's proposed new relationship is subject to reinterpretation with additional data, the anal pterygiophore patterns of the two taxa seem to support his suggestion.

In both Zeus of the Beryciformes (Fig. 38) and Monacanthus of the Tetraodontiformes the first anal pterygiophore fuses with three abdominal haemal arches. Judging from radiographs of skeletons among several clades in Rosens' new Tetraodontiformes (In Rosen, 1984, Fig. 17, 18, 19, and 20, p. 17-20) this character seems to occur frequently. This condition has never been found anywhere else. Further study using an extensive survey of this character complex possibly can provide additional information.

GENERAL SUMMARY

Cursory investigation of the three general types of haemal-anal-axial character complex reveals that transitional structural changes reflect the evolutionary trend in teleosts towards spiny finned fishes.
This survey has provided understanding of the evolution of this character complex. Within each general pattern various modification related to the character complex are displayed. The number of anterior anal pterygiophore to the first haemal spine, the modifications of the anterior pterygiophore, the degree of contact between the anal pterygiophore and the haemal spine, the orientation of anal pterygiophore with respect to the vertebral column, and the elements involved in the fusion of the first anal pterygiophore and the first haemal spine, are informative and can be useful in searching the relationships among the groups under study.

As proposed here the specialized fusion pattern involving the abdominal haemal arches, the first anal pterygiophore, and the first haemal spine in Zeus may support the inclusion of Zeiformes in Tetraodontiformes.

PERCOIDS RESULTS AND DISCUSSION

Suborder Percoidei
Centropomidae
subfamily Centropominae
Centropomus robalito (Fig. 42)

The first anal pterygiophore is hypertrophied and elongate (type II) and the orientation of the anal pterygiophores with respect to the vertebral column is extremely oblique. The distal tip of the first anal pterygiophore articulates with the haemal arch of the first precaudal vertebrae.

subfamily Latinae
Lates niloticus (Fig. 43)
L. calcarifer

The first anal pterygiophore is elongated and enlarged (type II). The distal tip of the first anal pterygiophore articulates with the first haemal spine. The orientation of the anal pterygiophores with respect to the vertebral column is oblique.

subfamily Ambassinae
Ambassis commersoni (Fig. 44)

The first anal pterygiophore almost reaches the vertebral centrum and the orientation with the vertebral column is almost vertical. The anterior tip of the first anal pterygiophore has been greatly expanded into a prominent flange.

Generally Ambassis is considered to be a subfamily of Centropomidae (Berg, 1940; Greenwood et. al., 1966; Nelson, 1984). However, this taxa has also been placed in its own family, Ambassidae (Johnson, 1975).

Based on my examination of this character complex the condition seen in Ambassis is considered autapomorphic whereas Centropomus and Lates share a more generalized type II condition. Therefore Johnson's proposal of the placement of Ambassis is not supported at this time.

The following taxa show a generalized type II condition (with modifications as noted).

Banjosidae
  Banjos typus (Fig. 45)

Lutjanidae
  Lutjanus apodus

Haemulidae
  Haemulon sciurus (Fig. 46)

Siniperca scherzeri (Fig. 47B)

Lateolabrax japonicus (Fig. 47A)

The anterior face of the first anal pterygiophore is modified into a pocket shape.

Percichthyidae

Bostockia porosa (Fig. 48)

The first haemal spine has a medial-lateral expansion.

Moronidae

Morone saxatilis (Fig. 49)

Generally 1, but occasionally 2 anal pterygiophores anterior to the first haemal spine.

Serranidae

Serranus trigrinus (Fig. 50)
Serranus subligarius
Centropristis striata
Epinephelus adscensionis
Cephalopholis fulva
Mycteroperca tigris

There is only one anal pterygiophore anterior to the first haemal spine. It is enlarged and elongated and articulates with the first abdominal haemal arch. The orientation of the anal pterygiophores is oblique. All the Serranid genera examined were found to have an almost identical pattern. This pattern is commonly found among the percoids, and is hypothesized to be the primitive condition.

Percidae

Percinae

Perca flavescens (Fig. 2)

In adult specimens the ventral tip of the first haemal spine is trifurcate and articulates with the dorsal tip of the first anal pterygiophore.

Etheostoma nigrum

E. flabellare

E. variatum

E. caeruleum

E. zonale

Ammocrypta pullicida

Percina caprodes

The first anal pterygiophore is not elongated or enlarged (this may possibly be secondarily reduced). Two or 3 anal pterygiophores are usually present anterior to the first haemal spine.

Luciopercinae

Stizostedion vitreum

The first anal pterygiophore is not elongated or enlarged. The first haemal spine forms a distinct posterior arch which in adults articulates with the second haemal spine.

Based mainly on the characteristics of the anteriormost anal pterygiophore, Collette (1963) recognized two subfamilies within the Percidae. The Percinae in which the first anal pterygiophore is much larger than the posterior ones, and the Luciopercinae in which the first anal pterygiophore is poorly developed.

Gerreidae

Eucinostomus harengulus (Fig. 51A)

The first anal pterygiophore is expanded anterioventrally.

The following taxa display a more derived type II condition in which the angle of orientation between the first anal pterygiophore and the vertebral column becomes increasingly vertical (with modifications as noted).

Lobotidae

Lobotes surinamensis (Fig. 51B)

Teraponidae

Terapon butleri (Fig. 52)

Pricanthidae

Pristigenys alta (Fig. 53)

Nemipteridae

Nemipterus sp. (Fig. 54)

Pseudochromidae

Pseudochromis fuscus (Fig. 55A)

The dorsal tip of the first anal pterygiophore articulates with a groove in the first haemal spine.

Plesiopidae

Assessor mcneilli (Fig. 55B)

Trachinops taeniatus

The first haemal spine has a slight lateral expansion.

Apogonidae

Apogon binotatus (Fig. 56)

Generally the enlarged first anal pterygiophore is composed of two fused elements. In Apogon there are 2 anal pterygiophores anterior to the first haemal spine which are not enlarged and unfused.

Lethrinidae

Lethrinus ornatus (Fig. 57)

Pomacanthidae

Pomacanthus imperator

Holacanthus sp.

Chaetodontidae

Chaetodon punctatofasciatus

The posterior face of the first anal pterygiophore lies closely against the anterior surface of the first haemal spine, and nearly fused with each other (a condition approaching Type III).

Kuhliidae

Kuhlia malo (Fig. 58)

Percichthyidae

Nannatherina balstoni (Fig. 59)

Edelia sp.

The distal tip of the first anal pterygiophore articulates with a groove on the anterior face of the first haemal spine. There is also lateral expansion of the first haemal spine.

Nannatherina and Edelia are generally placed with Kuhlia in the family Kuhliidae (Nelson, 1984) however additional evidence for the separation was gathered in an examination of the swimbladder. In Kuhliids (3 species examined) show an extreme extension of the posterior swimbladder into the caudal region (extending beyond the 7th haemal spine) following the ventral contour of the body. This is unique in percoids and not present in Nannatherina or Edelia.

The following taxa have what is considered a derivation of a generalized type II condition in which the anterior anal pterygiophores are not enlarged (with modifications as noted).

Malacanthidae

Latilinae

Caulotilus affinis (Fig. 60A)

Branchiostegeus japonicus

The first haemal spine is distinctly arched posteriorly. There are 5 anal pterygiophores anterior to the first haemal spine in Caulotilus , and three in Branchiostegeus .

Malacanthinae

Hoplolatilus starcki (Fig. 60B)

The first anal pterygiophore is greatly reduced.

Malacanthus plumieri

There are 15 reduced anal pterygiophores anterior to the first haemal spine. The *Branchiostegeus* and *Malacanthus* have been variously united and separated in past classification.

Dooley (1978) recognized *Branchiostegeus* as a separate family, Branchiostegidae. Robins et al. (1980) suggested a close affinity between the two groups by treating them as subfamilies of the Malacanthidae (as preferred here). Several modifications of haemal-anal-axial complex as noticed in this family suggesting a source of worth investigation for the Malacantnidae.

Pomatomidae

Pomatomus saltatrix (Fig. 61B)

Sillaginidae

Sillago bassensis (Fig. 61A)

The anal pterygiophores are greatly reduced in size and length.

Coryphaenidae

Corypnaena hippurus

There are three anal pterygiophores anterior to the first haemal spine.

Echeneididae

<u>Echeneis naucrates</u>

There are 3 reduced anal pterygiophores anterior to the first haemal spine.

Rachycentridae

<u>Rachycentron canadum</u>

There are 4 or 3 reduced anal pterygiophores anterior to the first haemal spine. As discussed by Johnson (1984) the Coryphaenidae, Echeneididae, and Rachycentridae form a monophyletic group. One of the specialized features in this group is the presence of several anal pterygiophores anterior to the first haemal spine.

The following taxa are a highly modified derivation of the type III condition where the first anal pterygiophore is tightly fused to the first haemal spine. The angle of orientation between the first anal pterygiophore and the vertebral column is almost vertical.

Carangidae

<u>Caranx crysos</u> (Fig. 62)

<u>C. latus</u>

<u>Scomberoides tolooparah</u>

<u>Selene setapinnis</u>

<u>Selar crumenophthalmus</u>

The first anal pterygiophore is tightly fused to the first haemal spine. The anterior face of the first anal pterygiophore is curved anteriorly. Smith-Vaniz (1984) used the extended distance between the second and third anal spine as a synapomorphous feature for the family.

Scatophagidae

Scatophagus argua (Fig. 63)

The first anal pterygiophore is tightly fused to the first haemal spine and fused with the second and third anal pterygiophores. The second and third haemal spines fuse medially with the first haemal spine.

suborder Acanthuroidei

Acanthuridae

Acanthurus chirurgus (Fig. 64)

The first anal pterygiophore is tightly fused to the first haemal spine.

CONCLUSIONS (PART II)

Percoids generally display a type II condition with a major trend towards type III involving various modifications associated with this character complex. Such as:

1. Reinforcement of the first anal pterygiophore (by enlargement and elongation of the first anal pterygiophore.)
2. Articulation of first anal pterygiophore with first haemal spine.
3. Orientation of the anterior anal pterygiophore with respect to the vertebral column (from extremely oblique towards vertical or obtuse position).
4. Fusion of first anal pterygiophore with first haemal spine.
5. Increase in the number of anal pterygiophores anterior to the first haemal spine.
6. Secondary reductions toward type I.
7. Fusion of abdominal haemal arches with the first haemal spine.

Most basal percoids share a primitive type II condition (e.g. Serranus, Centropomus, Siniperca, Lates, and many others); specialized percoids however share either a reductive type II (e.g. Sillago, Pomatomus, Caulotilus, Branchiostegeus, Malacanthus) or advanced type III conditions (e.g. Caranx, Scatophagus). Furthermore, in many cases the determination of types are difficult. For example, Chaetodon and Pomacentrus can be placed in either advanced type II or a general type III. The resolution of this problem may be reached by two approaches; a.) ontogeny - observe the patterns and elements in the fusion, and b.) morphometrics - measure the angle, size ratios, and distance related to the haemal-anal-axial character complex.

The value of this character complex can be illustrated by considering its shared specialization in relation to some current concepts of teleost relationships at different levels. As discussed in Part I, the monophyly of the Centrarchidae is evidenced, in part, from the presence of the unique pattern of haemal-anal-axial character complex among percoids. Further, based on this character complex, the sister group relationship between Centrarchidae and Percichthyidae is indicated. The above discussion and specific examples demonstrate the potential value of this character complex.

Because there are indications that this character complex has been modified independently several times, one should not draw any definite inferences concerning relationships solely from the pattern of this character complex. Once more comprehensive information becomes available and phylogenetic relationships of the group under study becomes better understood, then the haemal-anal-axial complex can function as corroborating evidence.

TABLES

TABLE 1 Developmental characteristics of haemal arch, transverse processes, swimbladder, and anterior anal pterygiophore in larval *Ambloplites rupestris* (AMNH43783).

Standard Length in mm	# of Closed Abdominal Haemal Arches	Development of Transverse Processes on CV 1	Migration of Anteriormost Anal Pterygiophores	Position of Posterior End of Swimbladder	Formation of Haemal Spine Groove
8.0	1 -5	—	4 separate elements	Below PC 2	—
10.5	1 - 3	—	Anterior 2 elements contact	Below PC 1	—
11.0	1 - 3	—	Anterior 3 elements contact	Approach to 1st haemal spine	Start formation
12.0	1 - 4	—	Migration towards 1st haemal spine	Same	1st haemal spine with lateral flange
13.0	1 - 3	—	Contact 1st haemal spine groove	1st haemal spine	Same

TABLE 1 Continued:

Standard Length in mm	# of Closed Abdominal Haemal Arches	Development of Transverse Processes on CV 1	Migration of Anteriormost Anal Pterygiophore	Position of Posterior End of Swimbladder	Formation of Haemal Spine Groove
15.0	1 - 3	Lateral expansion developing	Migrate into haemal spine groove	Same	1st haemal spine groove completely formed
16.0	1 - 2	Distal tips developed	Same	Between 1st & 2nd haemal spine	2nd haemal spine begins lateral expansion
18.0	1 - 2	Wing-like structure developed	Same	2nd haemal spine	1st & 2nd haemal spines contact
20.0	1	Wing-like structure well developed	Same	2nd haemal spine	1st & 2nd haemal spines contact
Adult	—	Wing-like structure prominent	Fused in groove	4th haemal spine	1st, 2nd & 3rd haemal spines contact

TABLE 2 Most frequent number of anal spines (A), soft rays (B), pterygiophores anterior to the 1st haemal spine (C), the total anal pterygiophores (D), precaudal vertebrae (E), and caudal vertebrae (F), present in Centrarchidae.

Genera	A	B	C	D	E	F
Elassoma	3	5	2	8	12	17
Micropterus	3	11	2 or 3	12	15 or 14	17 or 18
Lepomis	3	10	2	11	12	17
Enneacanthus	3	10	3	11	12	16
Acantharchus	5	10	3 or 4	13	13	17
Ambloplites	5 or 6	11	4	14	13	18
Archoplites	7	10	4	14	13	18
Centrarchus	7 or 8	16	5	20	13	18
Pomoxis	6 or 7	18	6	22	14	18

TABLE 3 Anal fin insertion in the Centrarchidae: a comparison between Bailey (1938) and Chang (Present study). Bailey (1938) indicated anal fin insertion as the general location of the fin with reference to the body shape. Chang (Present study) obtained the position of the anal fin insertion by following a line from the articulation of the first anal spine on the pterygiophore vertically to the vertebral column. Caudal vertebrae indicated by CV; precaudal by PV, counting from the posteriormost precaudal first.

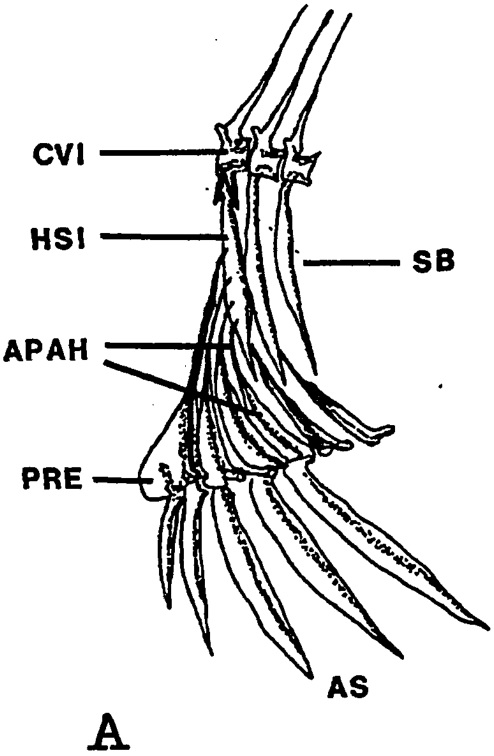
Genera	CHANG (Present study)	BAILEY 1938
Elassoma	CV-1 to CV-2 (Obliquely backward)	-----
Micropterus	CV-2 to CV-4 (Obliquely backward)	Far back
Lepomis	CV-1 to CV-4 (Obliquely backward)	Far back to intermediate
Enneacanthus	PC-1 to CV-1 (Vertical)	Intermediate
Acantharchus	PC-1 to CV-1 (Vertical)	Far back
Ambloplites	PC-1 to CV-1 (Vertical)	Far back
Archoplites	PC-1 to CV-1 (Vertical)	Far back
Centrarchus	PC-3 to PC-4 (Obtusely forward)	Far forward
Pomoxis	PC-2 to PC-3 (Obtusely forward)	Far forward

TABLE 4 Comparison of closed abdominal haemal arches commonly present in larval and adult Centrarchidae.

Genera	No. of Closed Haemal Arches Observed	
	Larval	Adult
Elassoma	2, 1	0 (but frequently show remnants on last abdominal haemal arch)
Micropterus	3, 2, 1	0
Lepomis	3, 2, 1	0
Enneacanthus	3, 2, 1	0
Acantharchus	2, 1	1
Ambloplites	5, 4, 3, 2, 1	0
Archoplites	0	0
Centrarchus	0	0
Pomoxis	0	0

FIGURES

Fig. 1. Relationships of vertebral column, haemal spine, and anterior anal-fin pterygiophore in *Ambloplites rupestris*, A) lateral view, B) detailed anterolateral view of the first haemal spine.


CVI
HSI
SB
APAH
PRE
AS
A

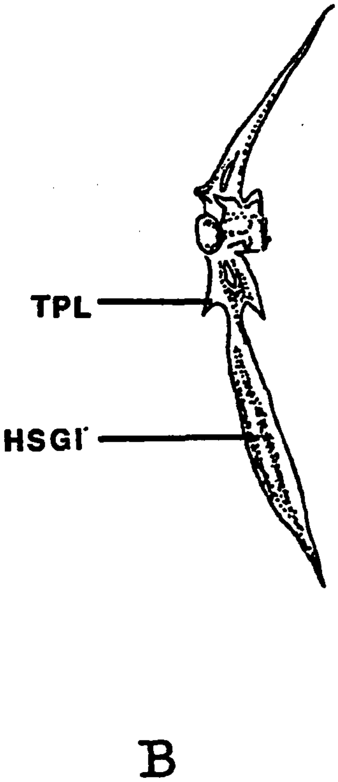
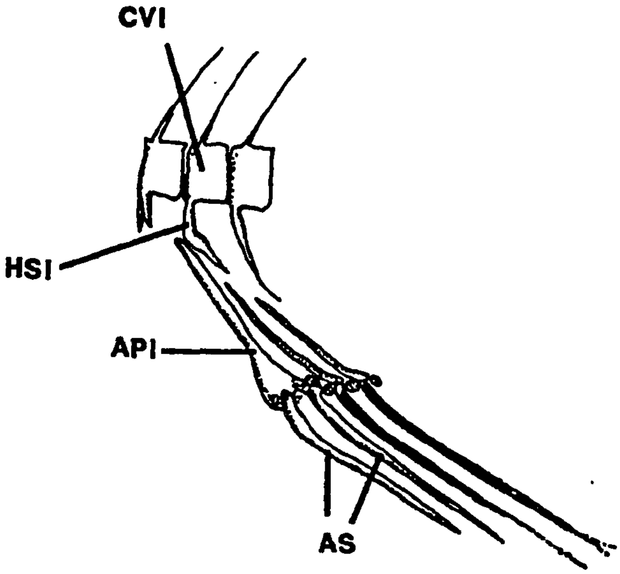
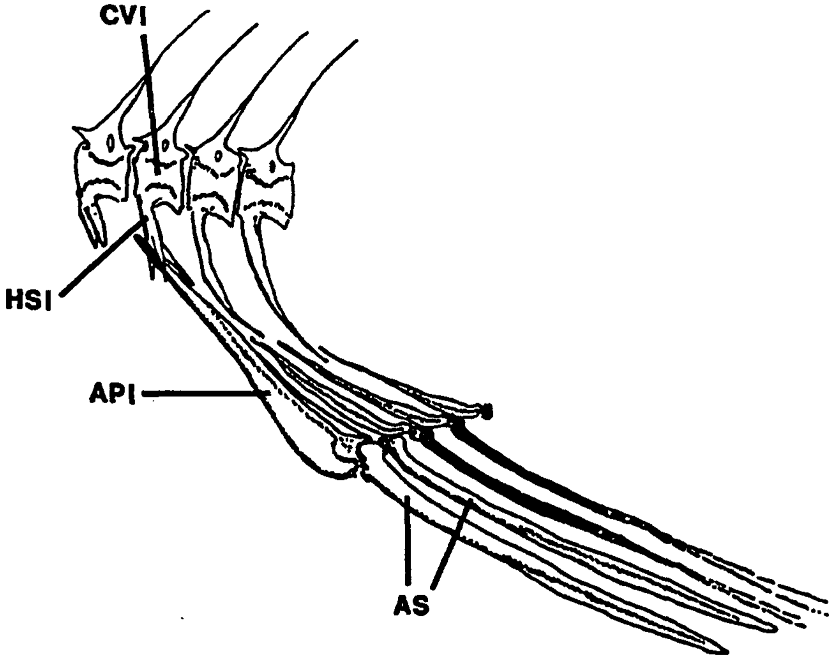

TPL
HSGI'
B

Fig. 2. Relationships of vertebral column, haemal spine, and anterior anal-fin pterygiophore in *Perca flavescens*, A) lateral view, 12 mm SL B) lateral view 51 mm SL.



A



B

Fig. 3. Posterior extension of the swimbladder in *Ambloplites rupestris* , (A) 9mm SL, (B) 12 mm SL, (C) 14 mm SL, (D) 21 mm SL, and *Micropterus salmoides* (E) 17 mm SL., (F) 24 mm SL.

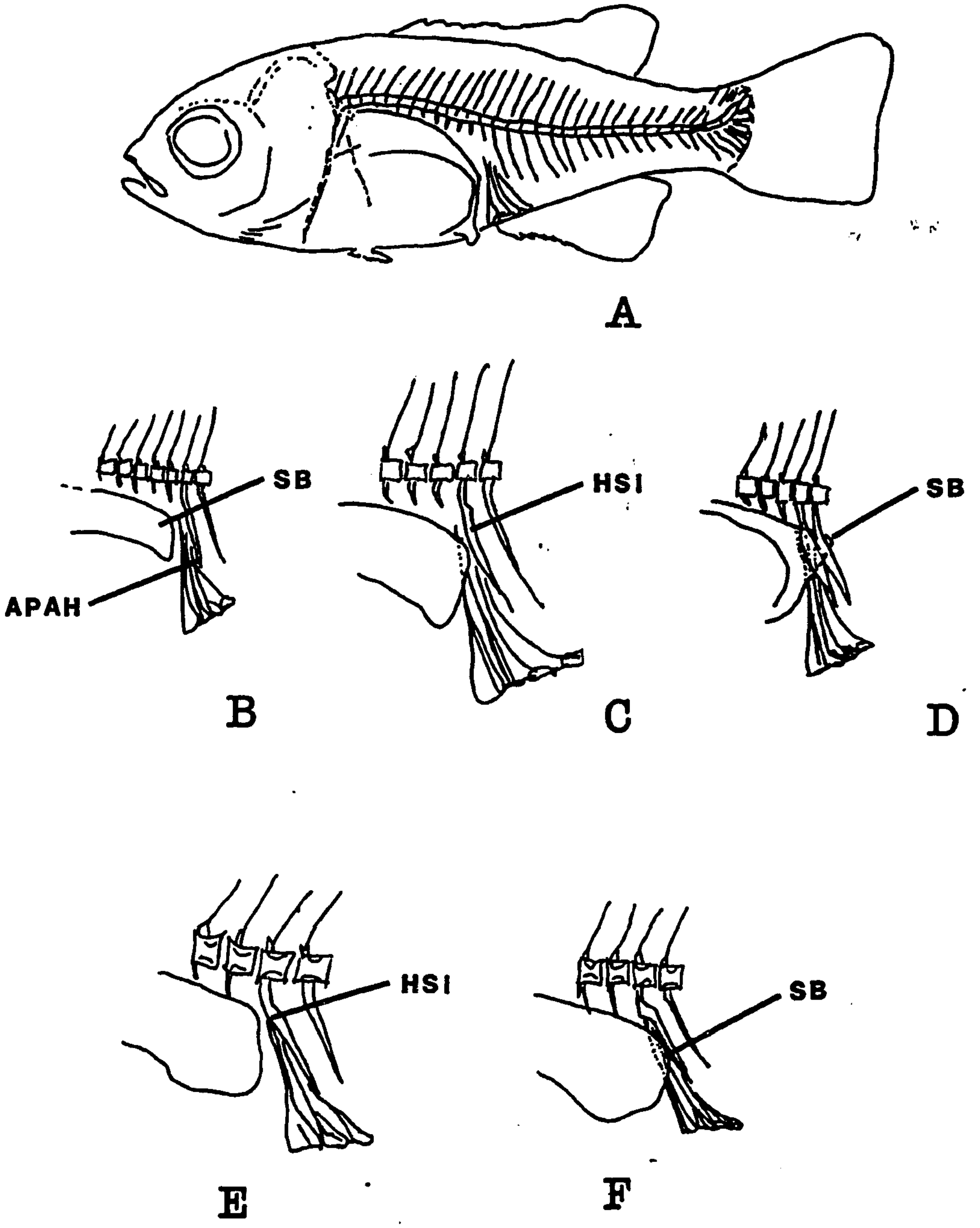
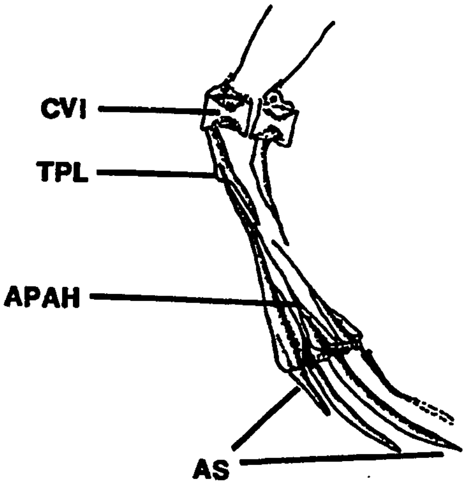
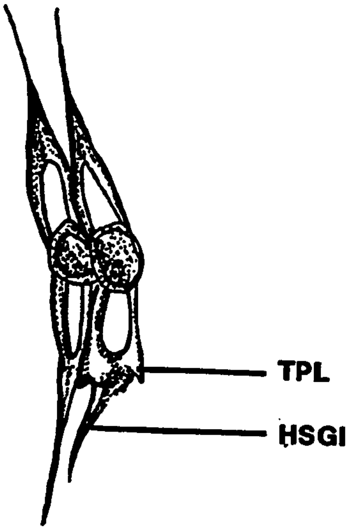

A
SB
APAH
B
HSI
C
SB
D
HSI
E
SB
F

Fig. 4. Relationships of vertebral column, haemal spine, and anterior anal-fin pterygiophore in *Elassoma evergladei*, A) lateral view, B) detailed anterior view of the first haemal spine.



A



B

Fig. 5. Relationships of vertebral column, haemal spine, and anterior anal-fin pterygiophore in *Micropterus salmoides* (A) detailed anterior view 45 mm SL, B) detailed anterior view 230 mm SL, (C) lateral view, and (D) *Micropterus dolomieui* lateral view.

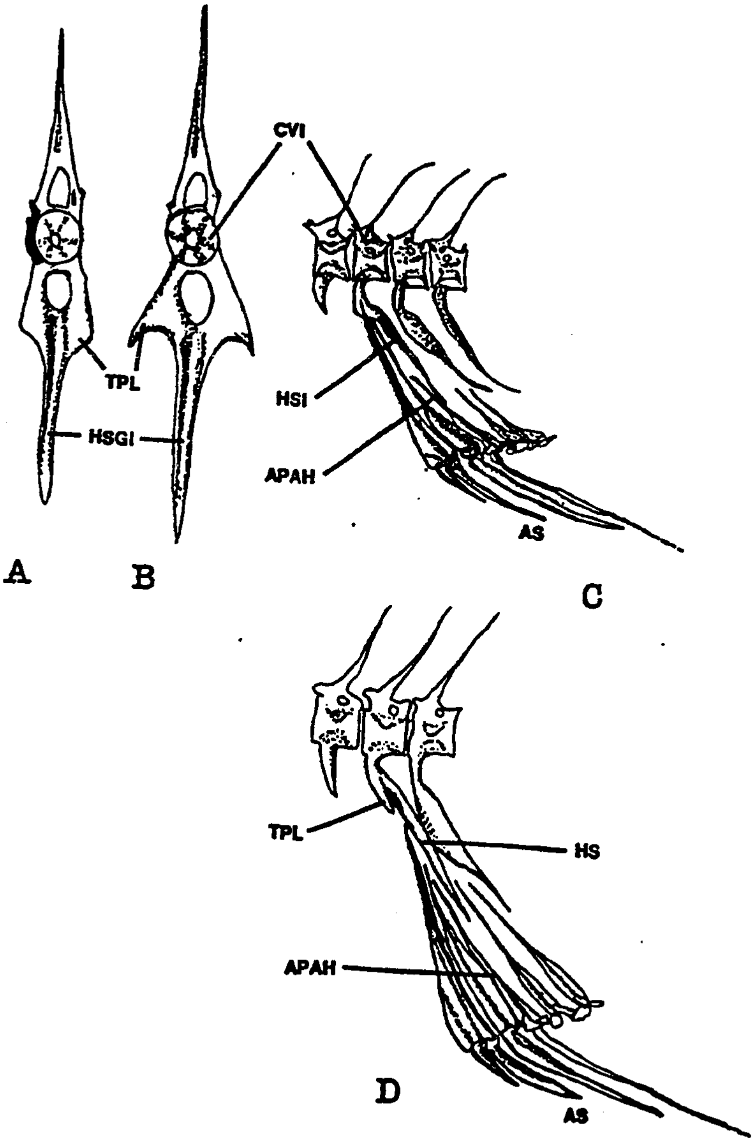

CVI
TPL
HSGI
HSI
APAH
AS
A
B
C
TPL
HS
APAH
D
AS

Fig. 6. Relationships of vertebral column, haemal spine, and anterior anal-fin pterygiophore in *Lepomis macrochirus*, A) lateral view, B) detailed anterior view of the first haemal spine.

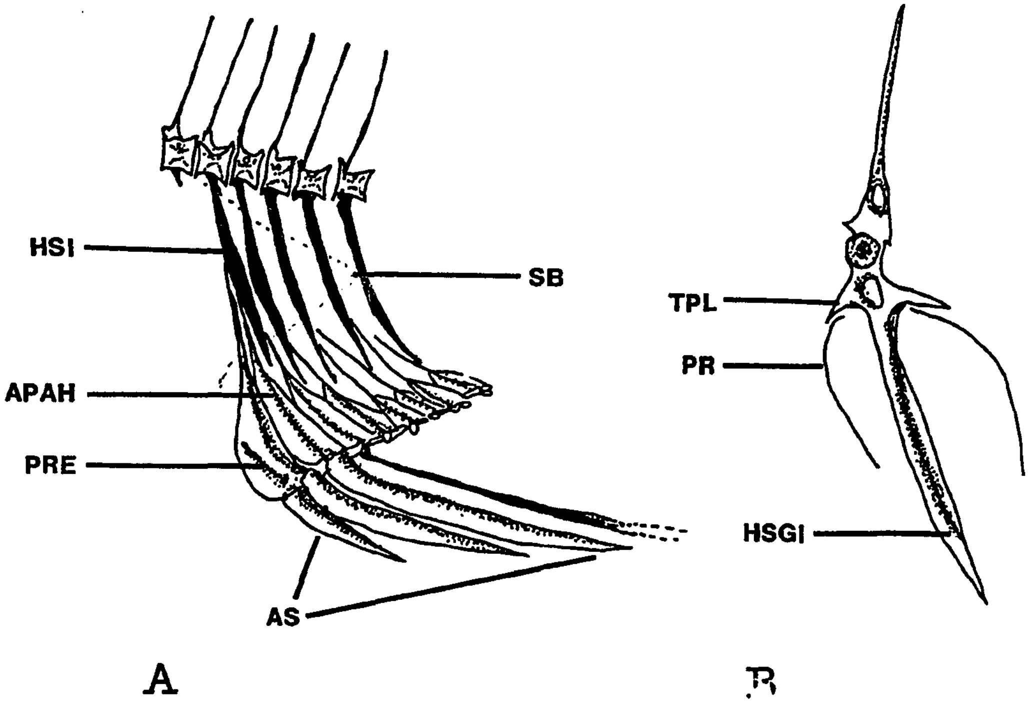

HSI
SB
APAH
PRE
AS
A
TPL
PR
HSGI
B

Fig. 7. Relationships of vertebral column, haemal spine, and anterior anal-fin pterygiophore in Enneacanthus chaetodon, A) lateral view, B) detailed anterior view of the first haemal spine.

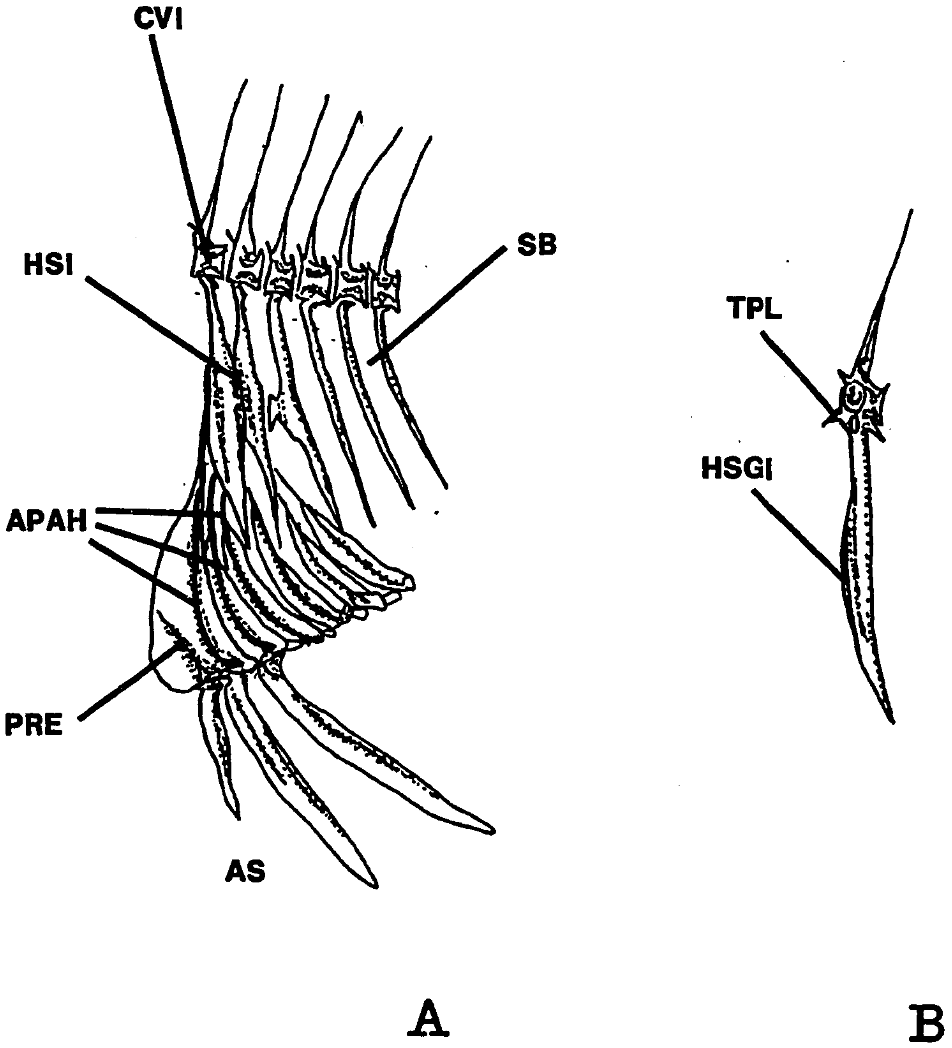

CVI
HSI
SB
APAH
PRE
AS
TPL
HSGI
A
B

Fig. 8. Relationships of vertebral column, haemal spine, and anterior anal-fin pterygiophore in *Acantharchus pomotis*, A) lateral view, B) detailed anterior view of the first haemal spine.

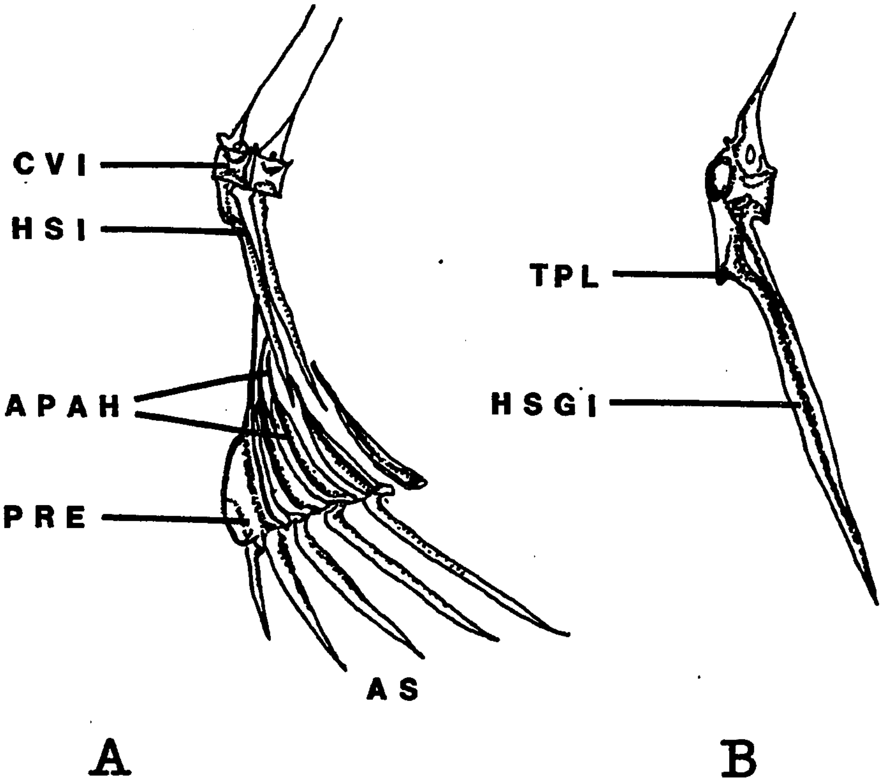

CVI
HSI
APAH
PRE
AS
A
TPL
HSGI
B

Fig. 9. Relationships of vertebral column, haemal spine, and anterior anal-fin pterygiophore in Archoplites interruptus, A) lateral view, B) detailed anterior view of the first haemal spine.

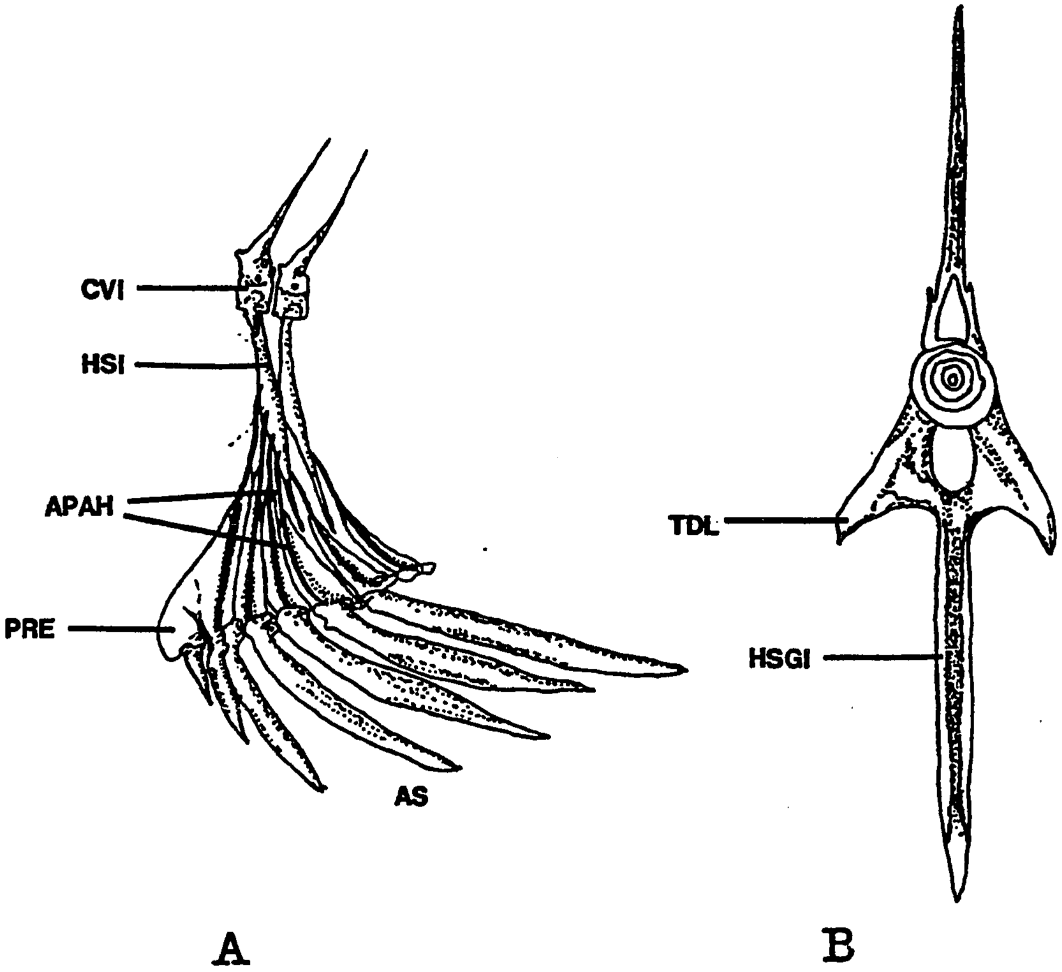

CVI
HSI
APAH
PRE
AS
A
TDL
HSGI
B

Fig. 10. Relationships of vertebral column, haemal spine, and anterior anal-fin pterygiophore in *Centrarchus macropterus*, A) lateral view, B) detailed anterior view of the first haemal spine.

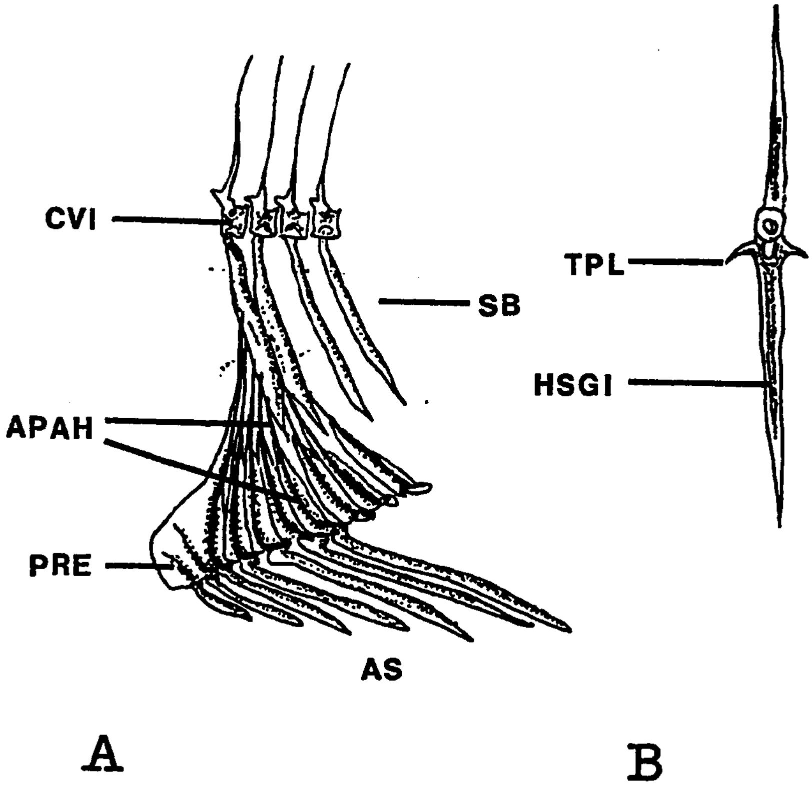

CVI
SB
APAH
PRE
AS
TPL
HSGI
A
B

Fig. 11. Relationships of vertebral column, haemal spine, and anterior anal-fin pterygiophore in *Pomoxis annularis*, A) lateral view, B) detailed lateral view of the first haemal spine.

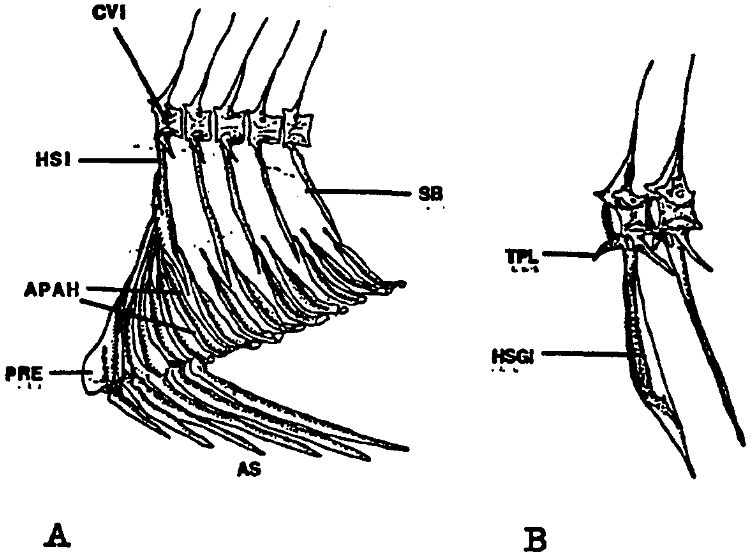

CVI
HSI
SB
APAH
PRE
AS
A
TPL
HSGI
B

Fig. 12. Supernumery anal spine association on the first anal pterygiophore in A) Archoplites interruptus 16 mm SL, B) Pomoxis nigromaculats, 14 mm SL, C) Centrarchus macropterus 13 mm SL, D) Lepomis macrochirus 10 mm SL.

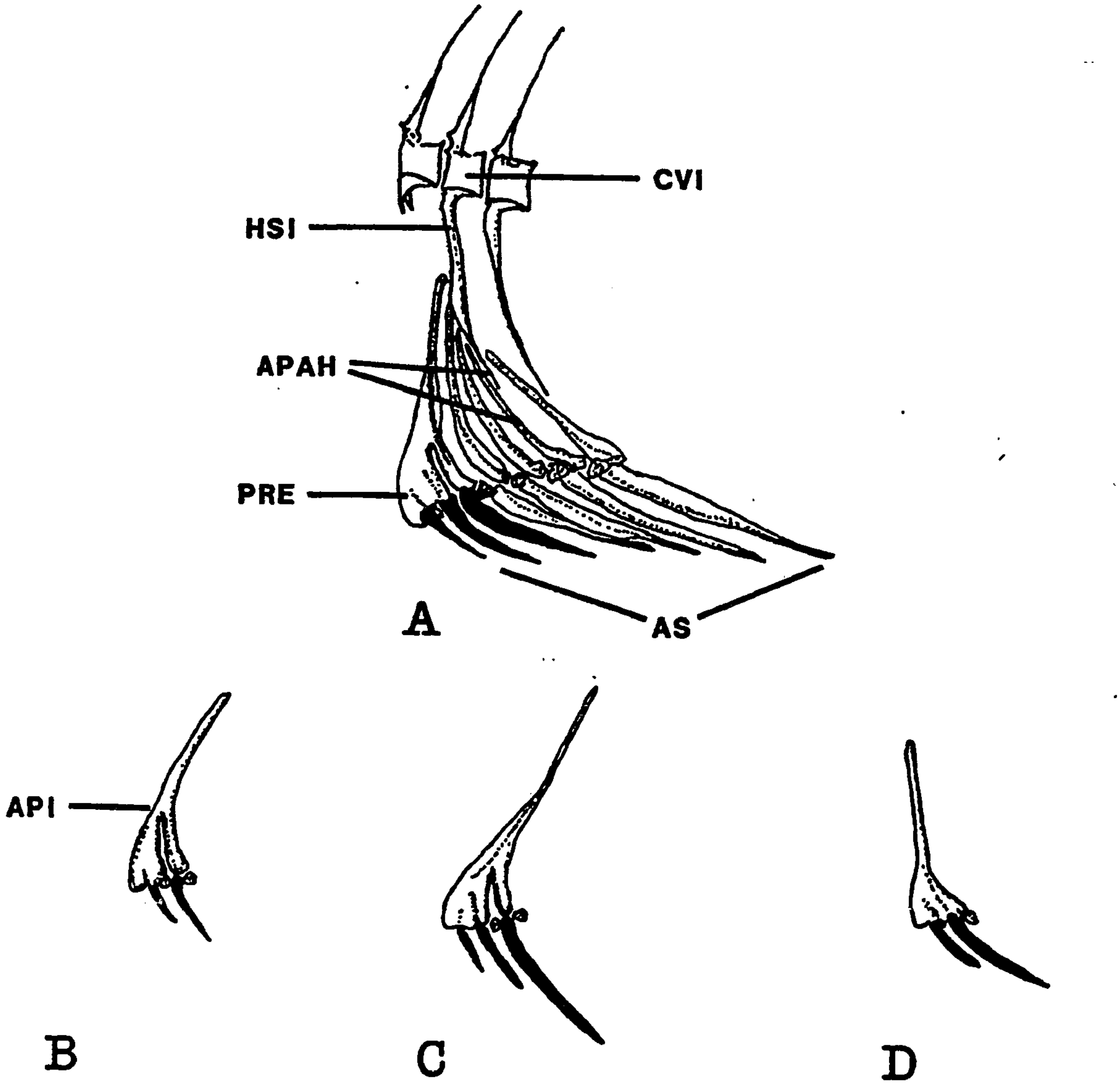

CVI
HSI
APAH
PRE
A
AS
API
B
C
D

Fig. 13. Lateral view of a 9 mm SL *Ambloplites rupestris* showing five bridged haemal arches in abdominal region and four separate anal pterygiophores anterior to the first haemal spine.

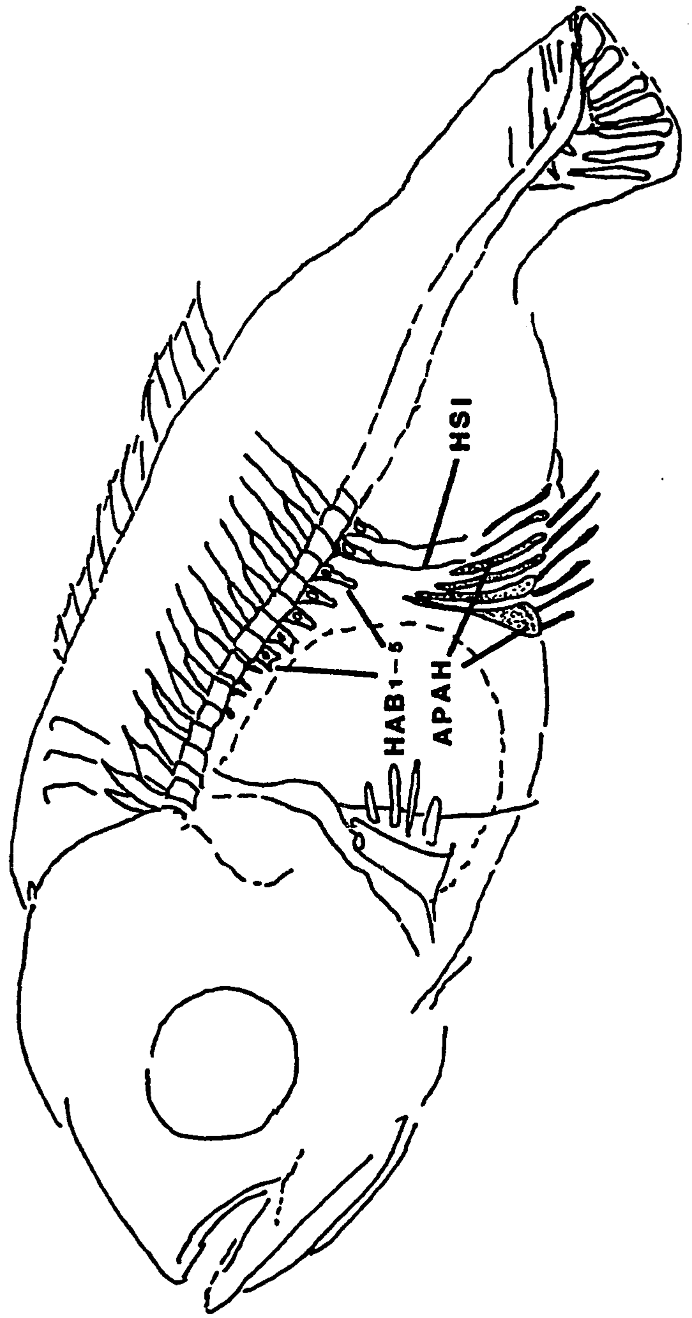
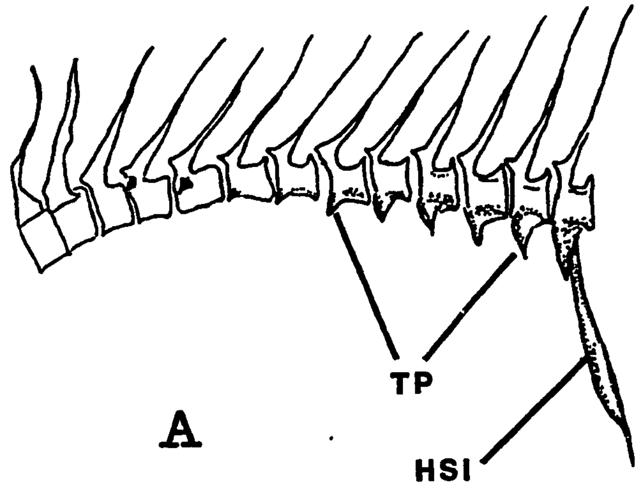

HSI
HAB1-5
APAH

Fig. 14. Lateral view comparison of transverse processes in *Ambloplites rupestris*, A) ventrally directed processes 16 mm SL, B) laterally directed processes 43 mm SL.


TP
A
HSI

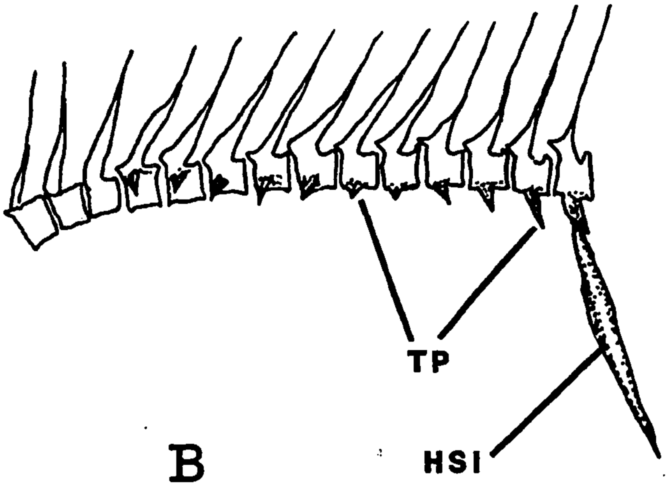

TP
B
HSI

Fig. 15. Morphology of posterior opercular margin in, A) *Acantharchus pomotis*, B) *Centrarchus macropterus*, C) *Elassoma zonatum*, D) *Ambloplites rupestris*, and E) *Pomoxis annularis*.

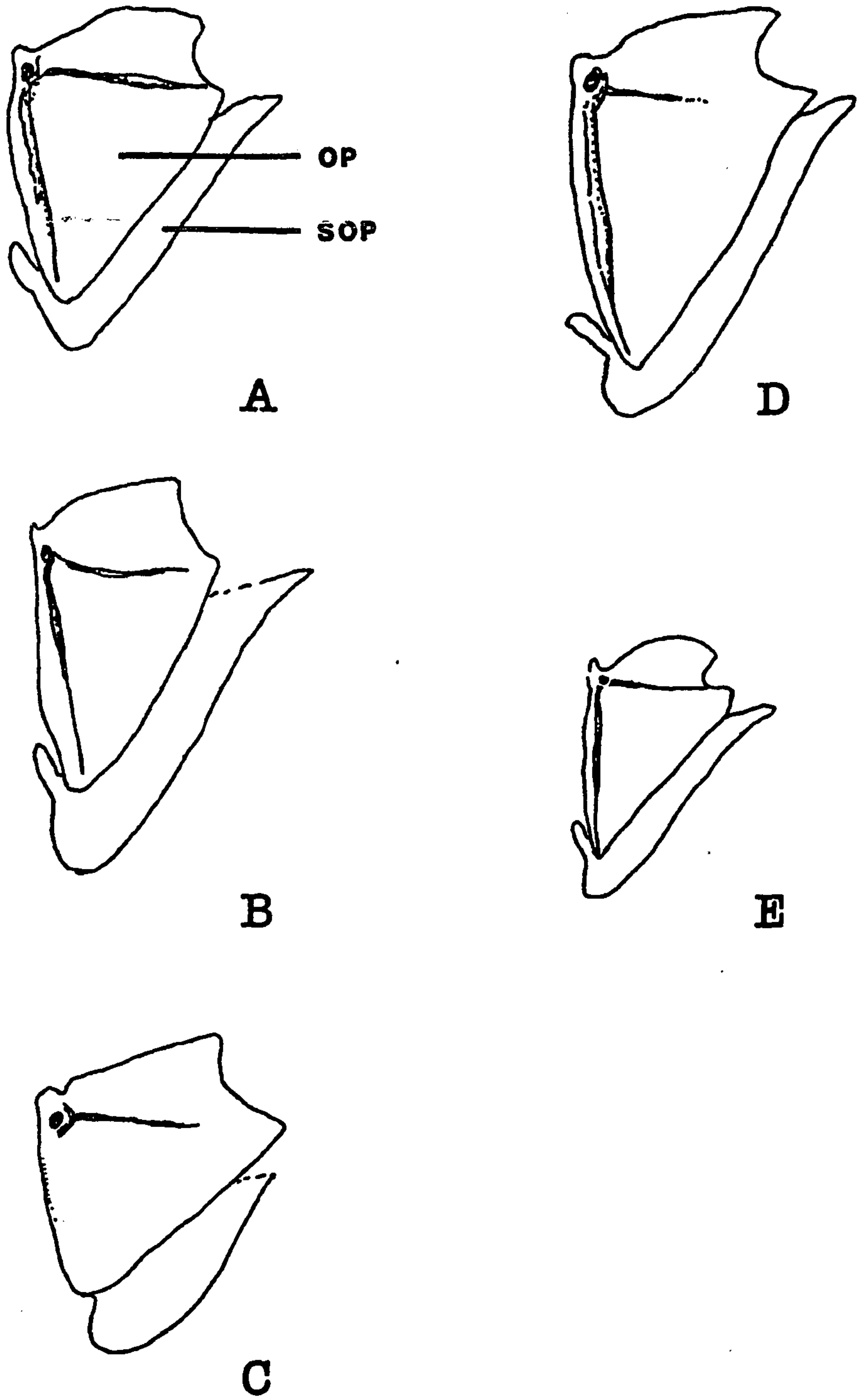

OP
SOP
A
D
B
E
C

Fig. 16. Morphology of posterior opercular margin in, *Enneacanthus gloriosus*, B) *Enneacanthus chaetodon*, C) *Enneacanthus obesus*, D) *Archoplites interruptus* 62 mm SL and E) *Archoplites interruptus* 197 mm SL.

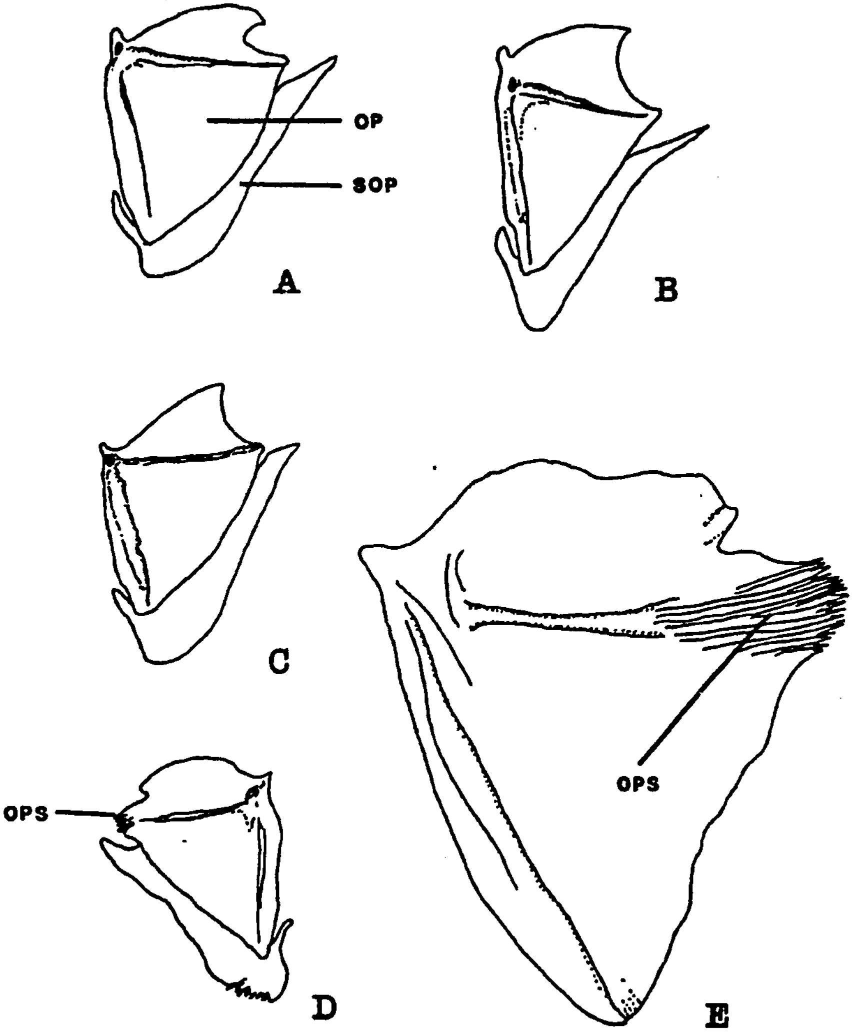
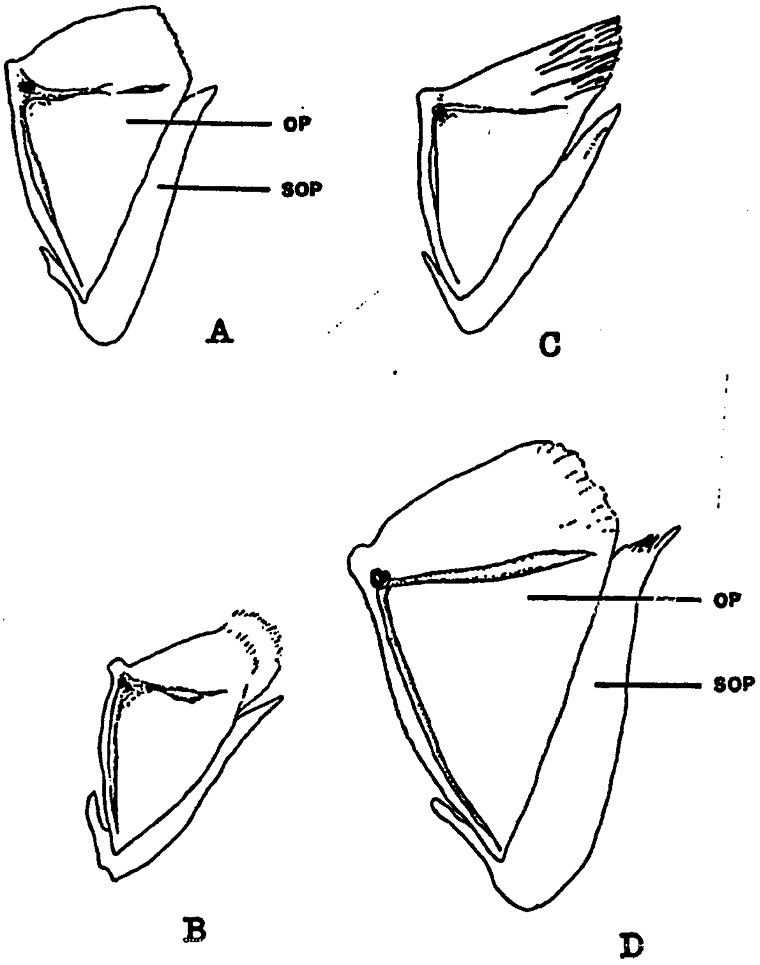
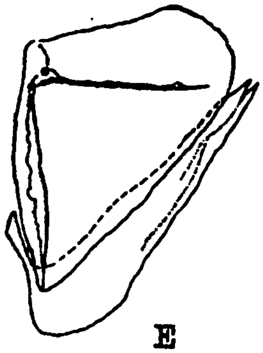
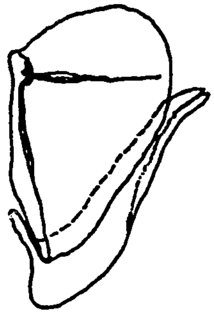
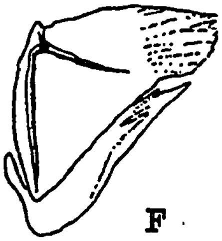

OP
SOP
A
B
C
OPS
D
OPS
E

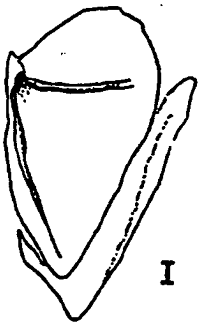
Fig. 17. Morphology of posterior opercular margin in *Lepomis*, A) *gibbosus*, B) *marginatus*, C) *auritus* D) *gulosus*, E) *cyanellus*, F) *humilis*, G) *macrochirus*, H) *symmetricus*, I) *punctatus* and J) *microlophus*.

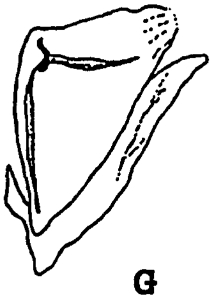

OP
SOP
A
C
OP
SOP
B
D


E


H


F


I


G

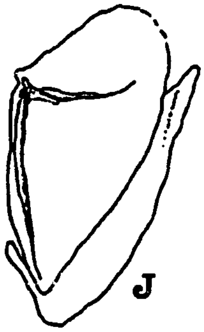

J

Fig. 18. Ontogeny of posterior opercular margin in *Lepomis megalotis*, A) 13 mm SL, B) 19 mm SL and C) 47 mm SL.

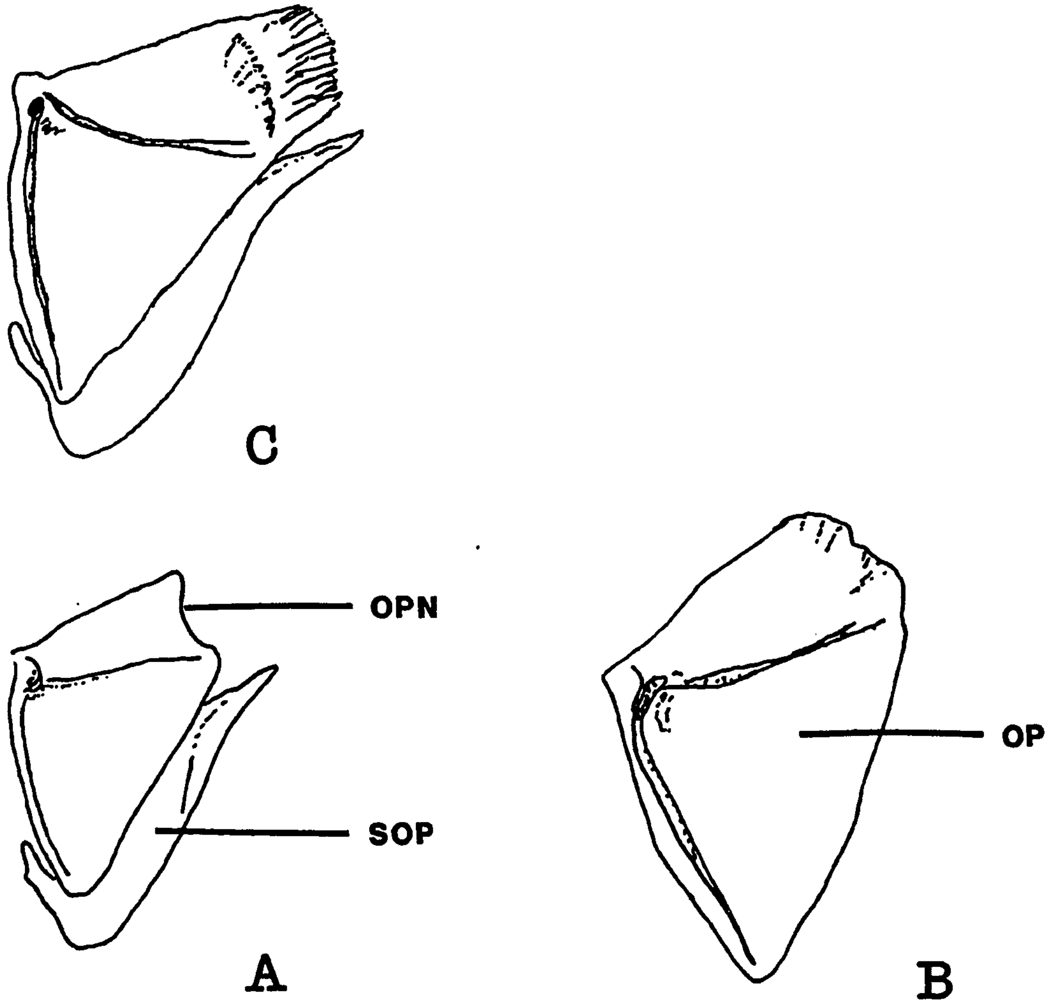
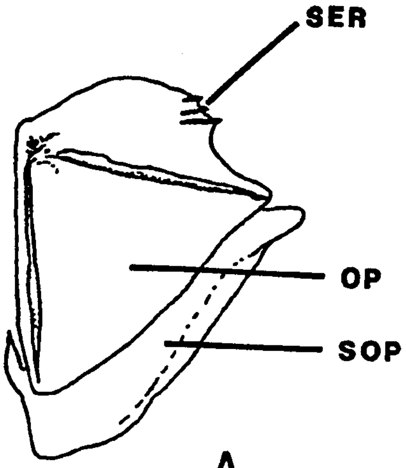
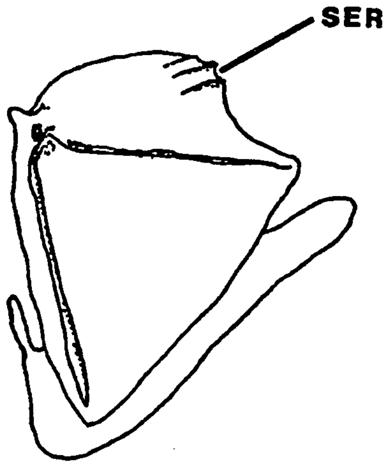

C
OPN
SOP
A
OP
B

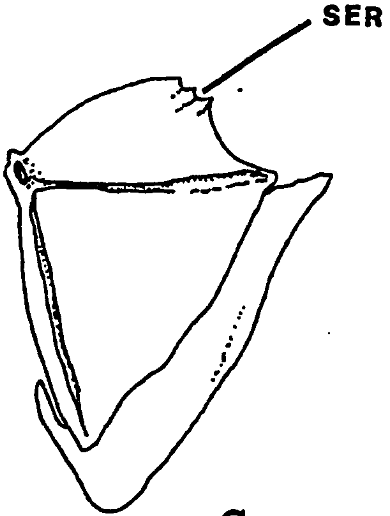
Fig. 19. Morphology of posterior opercular margin in *Micropterus*, A) *punctulatus*, B) *salmoides*, C) *coosae*, and D) *dolomieui*.



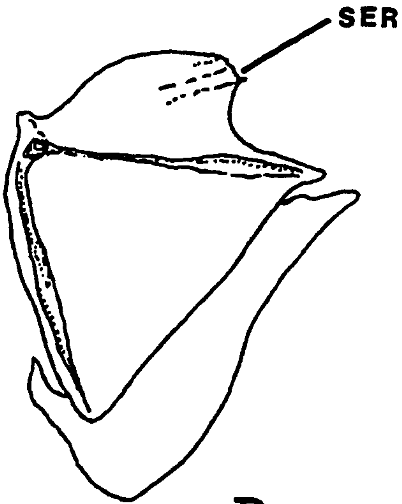
A



B

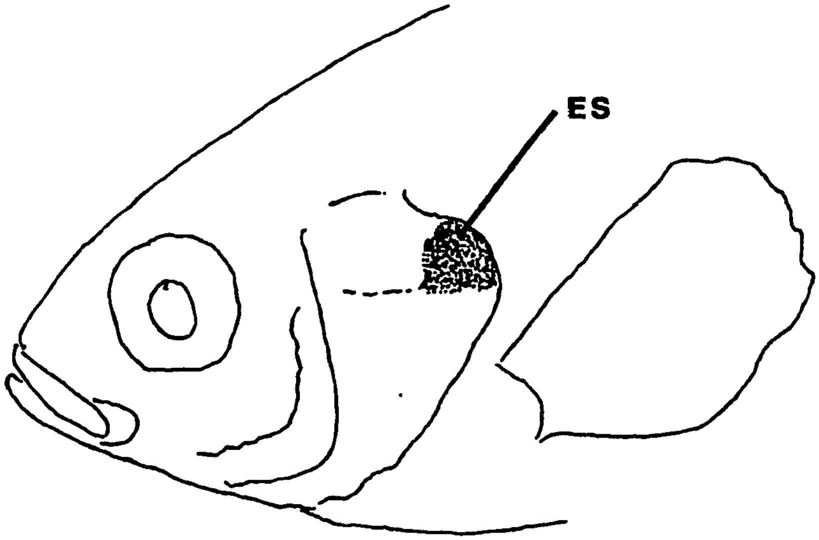


C

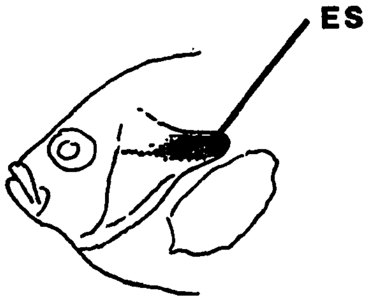


D

Fig. 20. Morphology of ear spot in Lepomis auritus
A) 36 mm SL, and B) 107 mm SL.



A



B

Fig. 21. Morphology of ear spot in A) *Pseudogramma polycanthus* AMNH 51733, B) *Fowleria auritus* AMNH 33775, and C) *Morone punctatus* AMNH 43094.

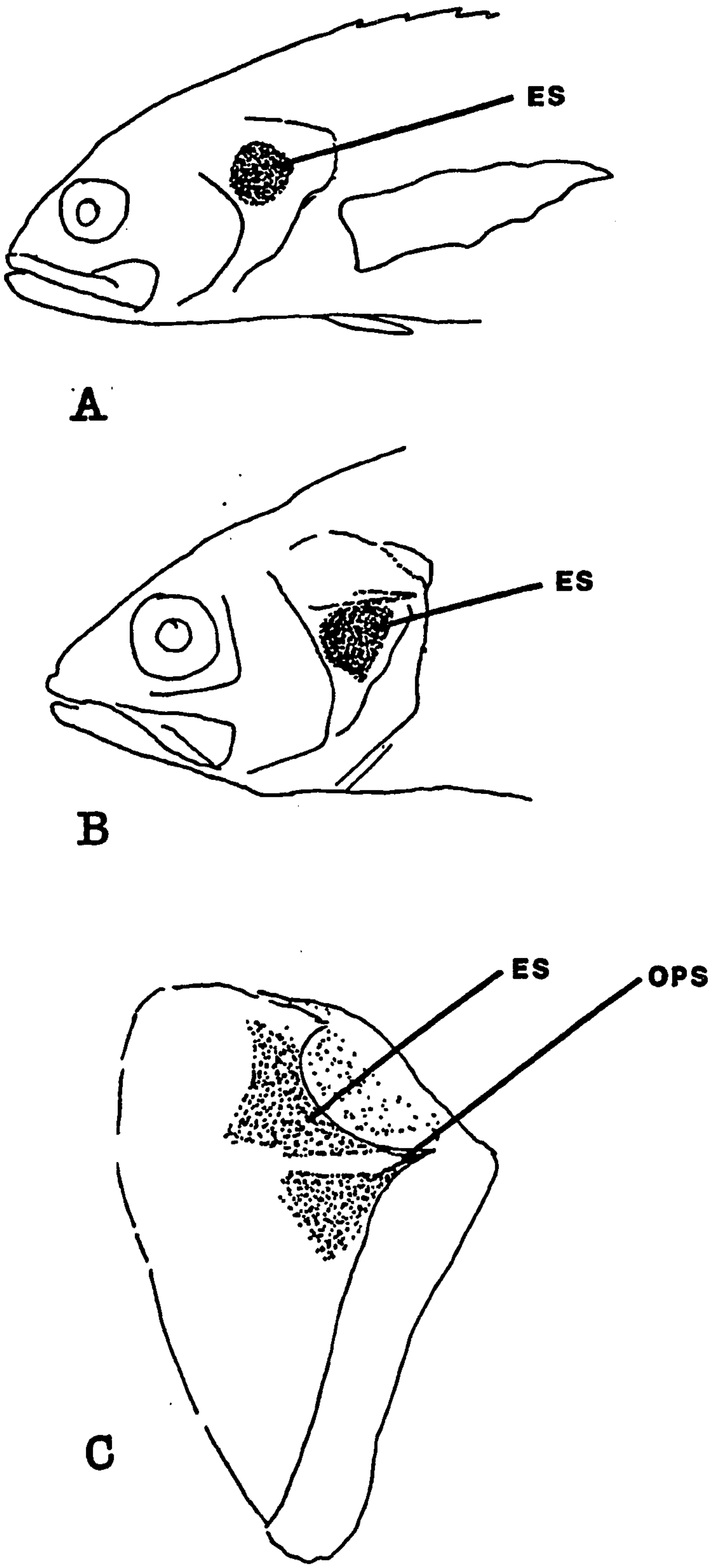
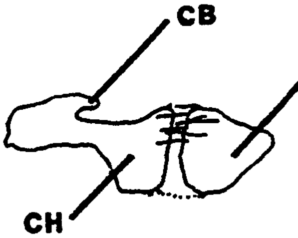
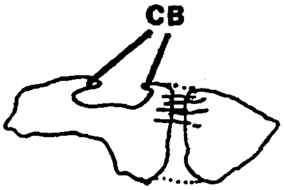

ES
A
ES
B
ES
OPS
C

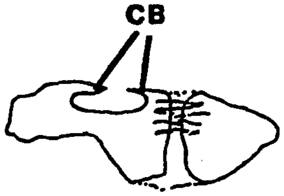
Fig. 22. Development of ceratohyal foramen in *Lepomis megalotis*, A) 13mm SL, B) 15mm SL, C) 15 mm SL, D) 19 mm SL, E) 26 mm SL, and *Micropterus salmoides*, F) 17 mm SL, G) 19 mm SL, H) 22 mm SL., I) 35 mm SL and J) 46 mm SL.



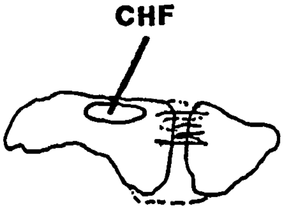
A



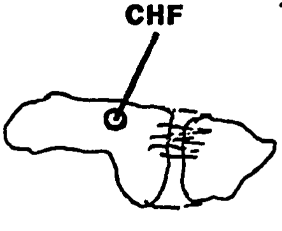
B



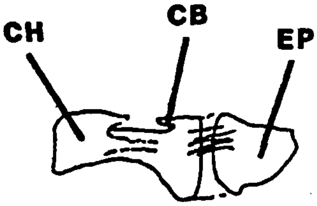
C



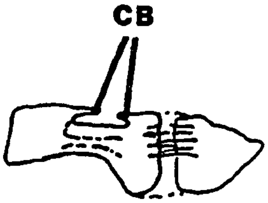
D



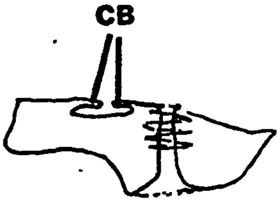
E



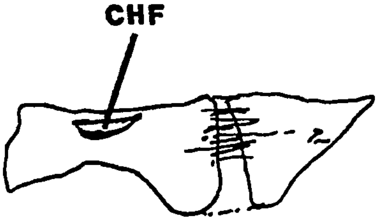
F



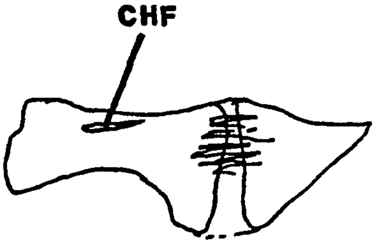
G



H



I



J

Fig. 23. Lateral view of the hyoid arch in *Micropterus* A) *coosae*, B) *salmoides*, C) *dolomieui* and D) *punctulatus*.

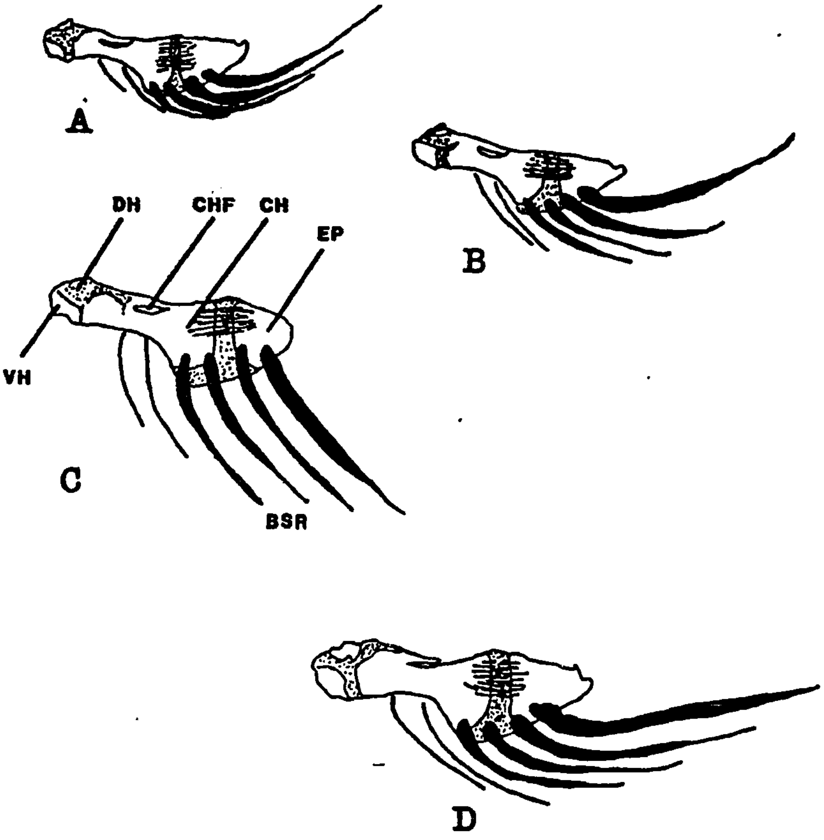

A
B
DH
CHF
CH
EP
VH
C
BSR
D

Fig. 24. Lateral view of the hyoid arch in Lepomis
A) cyanellus, B) humilis, C) punctatus
D) gibbosus, E) megalotis, F) auritus
G) symmetricus, H) macrochirus, I) microlophus
J) marginatus, and K) gulosus.

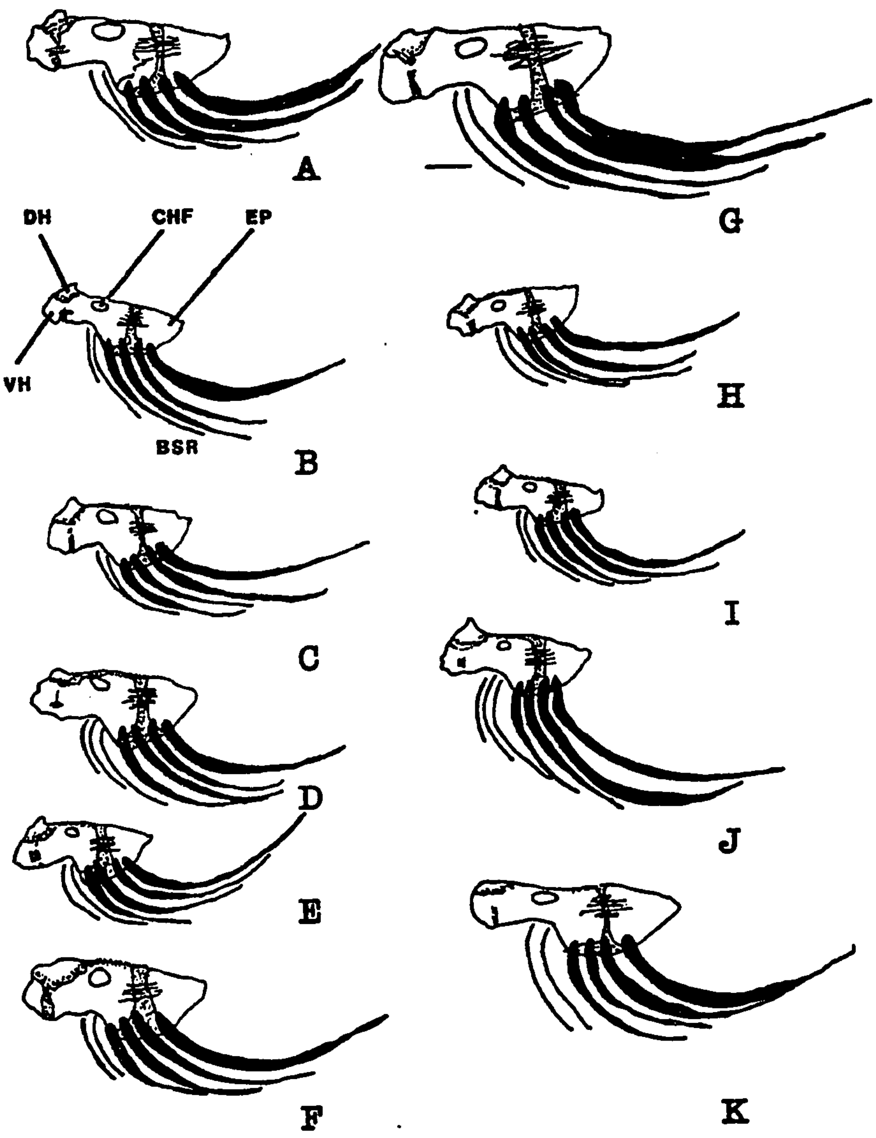
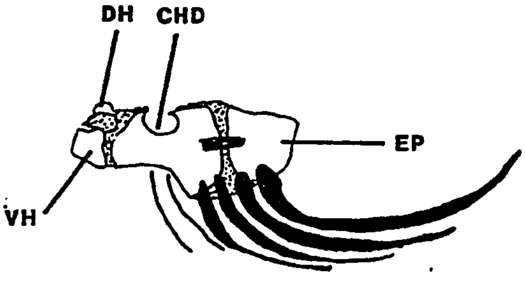
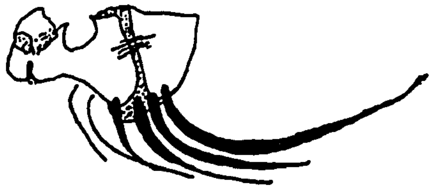

A
G
DH
CHF
EP
VH
BSR
B
H
C
I
D
J
E
F
K

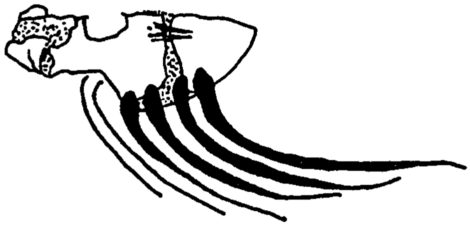
Fig. 25. Lateral view of the hyoid arch in Enneacanthus A) gloriosus, B) obesus, and C) chaetodon.



A



C



B

Fig. 26. Lateral view of the hyoid arch in A) *Pomoxis nigromaculatus*, B) *Pomoxis annularis*, C) *Centrarchus macropterus*, D) *Ambloplites rupestris*, and E) *Archoplites interruptus*.

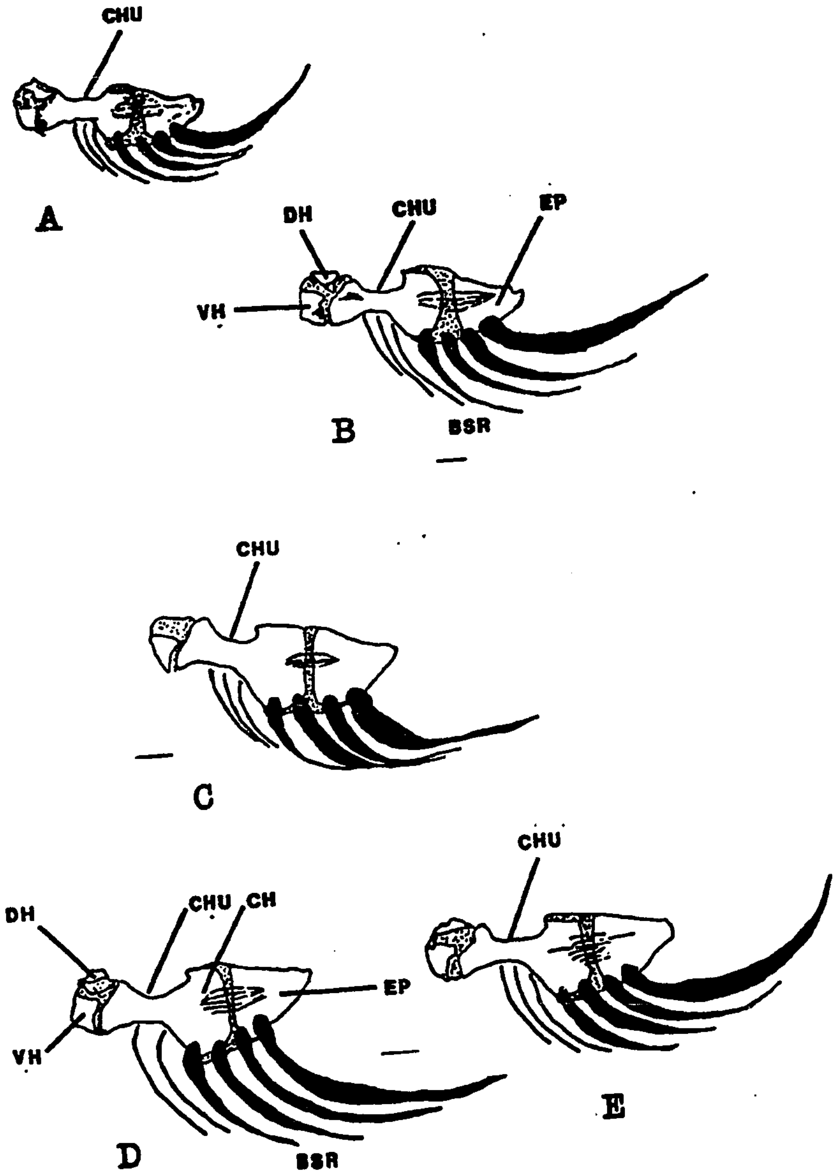

CHU
A
DH
CHU
EP
VH
B
BSR
CHU
C
DH
CHU
CH
EP
VH
D
BSR
CHU
E

Fig. 27. Lateral view of the hyoid arch in *Elassoma* A) *evergladei*, B) *zonatum*, and C) *okefenokee*.

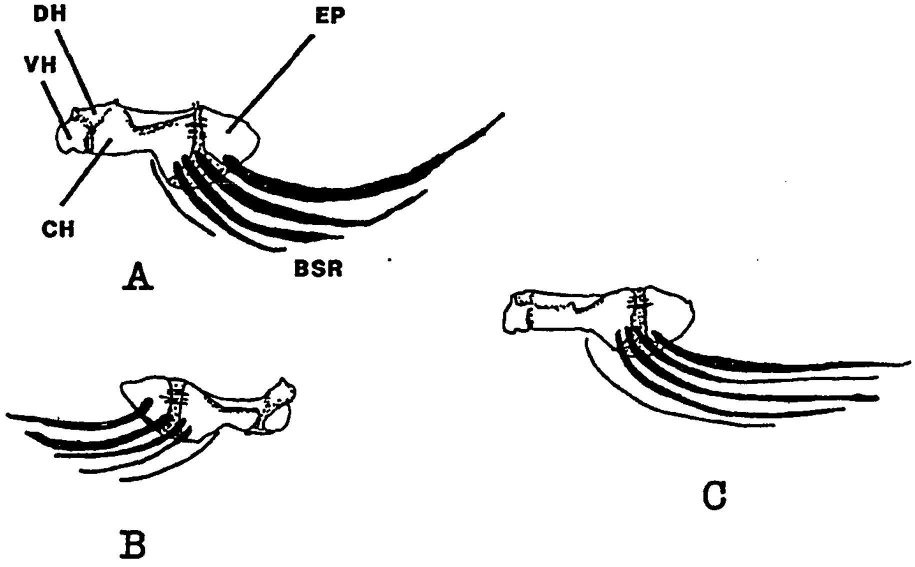
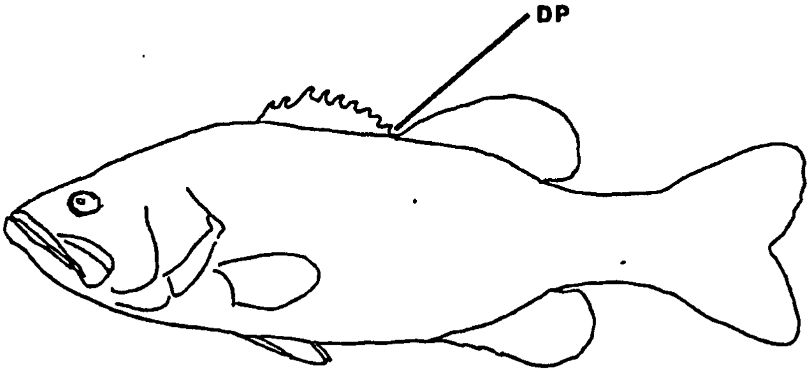
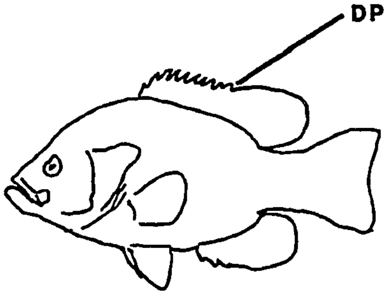

DH
VH
EP
CH
A
BSR
B
C

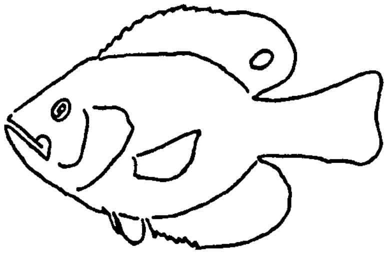
Fig. 28. Dorsal fin morphology in A) *Micropterus salmoides*, B) *Lepomis cyanellus*, C) *Centrarchus macropterus*, and D) *Pomoxis annularis*.



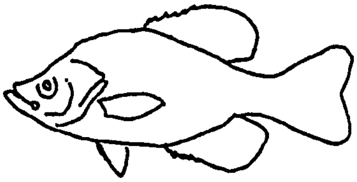
A



B



C



D

Fig. 29. Cladogram of the most parsimonious hypothesis of relationships for the genera of the family Centrarchidae. Numbers correspond to synapomorphies: 1, transverse processes on the first haemal spine; 2, more than one anal-fin pterygiophore anterior to the first haemal spine; 2a, more than two anal-fin pterygiophors anterior to the first haemal spine; 2b, more than three anal-fin pterygiophores anterior to the first haemal spine; 2c, more than four anal-fin pterygiophores anterior to the first haemal spine; 2d, more than five anal-fin pterygiophores anterior to the first haemal spine; 3, posterior bifurcation of the swimbladder; 3a, swimbladder extends beyond second haemal spine; 3b, swimbladder extends beyond fifth haemal spine; 4a, thirteen anal-fin pterygiophores; 4b, fourteen anal-fin pterygiophores; 4c, twenty anal-fin pterygiophores; 4d, twenty-two anal-fin pterygiophores; 5, four spines on first anal-fin pterygiophore; 6, more than three anal spines; 7, 16-18 soft anal rays; 8a, 15-17 or 14-18 vertebral formula; 8b, 12-16 vertebral formula; 8c, 13-17 vertebral formula; 8d, 13-18 vertebral formula; 8e, 14-18 vertebral formula; 9, distal tip of anterior anal-fin pterygiophore reaches the middle of the first haemal spine groove; 10, proximal radial of the first anal-fin pterygiophore expanded; 11a, insertion of anal fin vertical; 11b, insertion of anal fin obtusely forward; 12, first haemal spine as long as the second one; 13, first haemal spine arched; 14, deep groove on first haemal spine; 15a, contact between first and second haemal spines; 15b, four haemal spines fused; 16a, single bridged abdominal arch; 16b, absence of bridged abdominal haemal arch; 17a, serrae on posterior opercular margin; 17b, posterior opercular margin rounded or fimbriate; 18, earspot; 19a, ceratohyal with deep notch; 19b, ceratohyal concave; 20, epi-ceratohyal channel reduced; 21, seven branchiostegal rays; 22, 25-40 long and slender gill rakers; 23a, shallow-notched dorsal fin; 23b, single dorsal fin; 24, olfactory organs; 25, dorsal fin supports; 26, thick tissue layer over posterior kidney; 27a, extreme posterior kidney; 27b, fusion of posterior kidneys behind the first haemal spine.

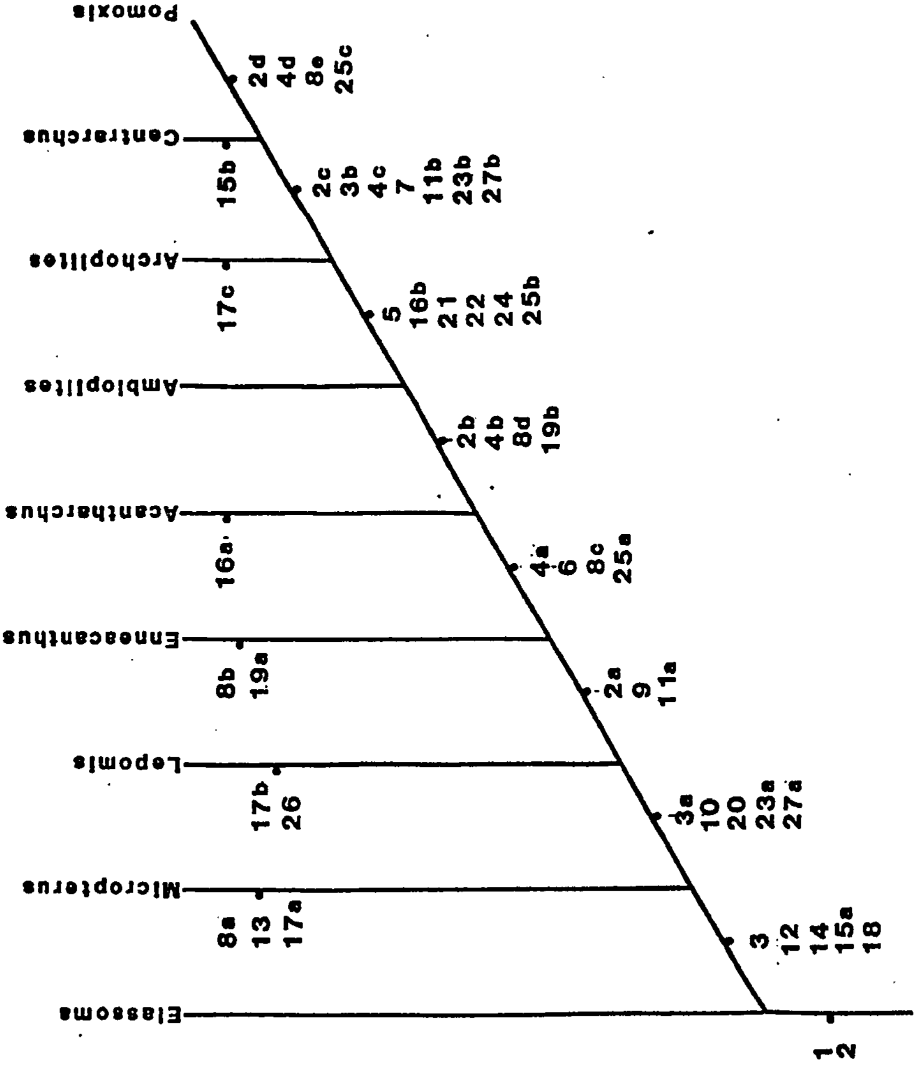

Pomoxis
2d
4d
8e
25c
Centrarchus
15b
2c
3b
4c
7
11b
23b
27b
Archoplites
17c
5
16b
21
22
24
25b
Ambloplites
2b
4b
8d
19b
Acantharchus
16a
4a
6
8c
25a
Enneacanthus
8b
19a
2a
9
11a
Lepomis
17b
26
3a
10
20
23a
27a
Micropterus
8a
13
17a
3
12
14
15a
18
Elassoma
1
2

Fig. 30. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Osteoglossum bicihrrosum* AMNH 38150SW.

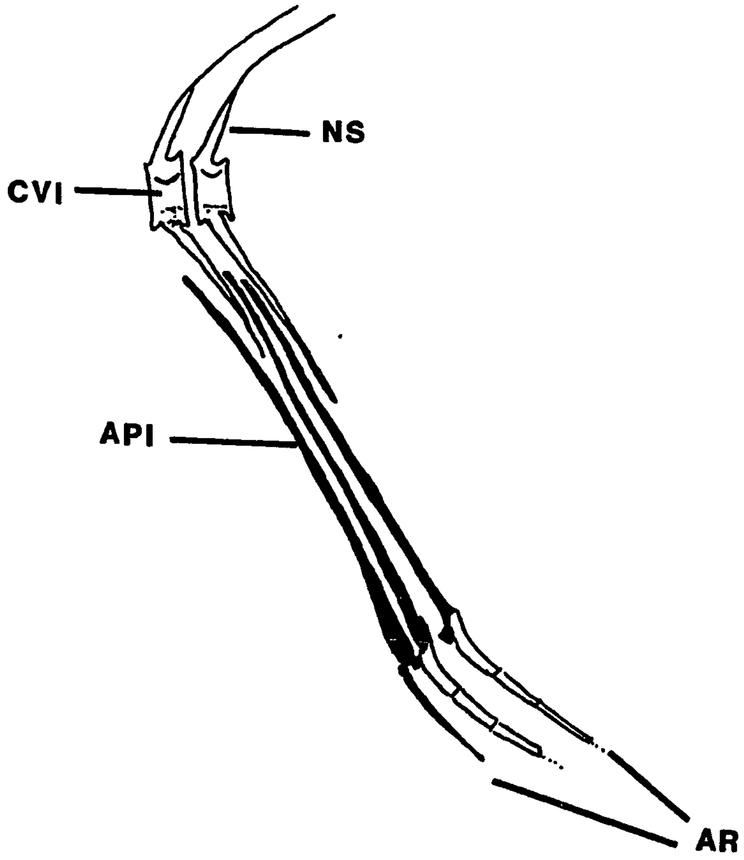

NS
CVI
API
AR

Fig. 31. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Elops saurus AMNH 55346SW.

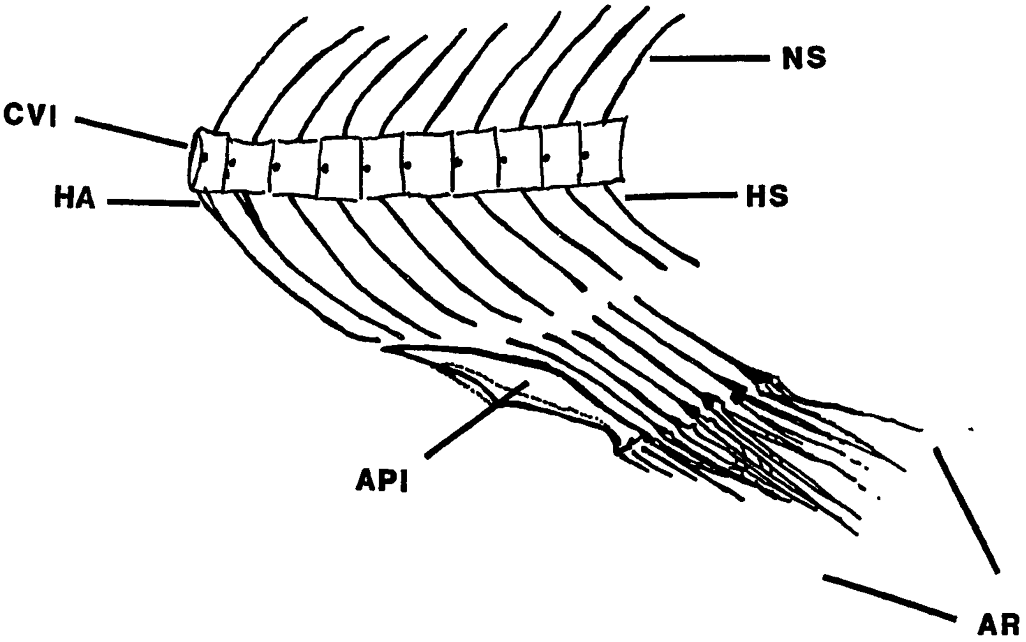

CVI
HA
NS
HS
API
AR

Fig. 32. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Brevoortia tyrannus* AMNH 15495SW.

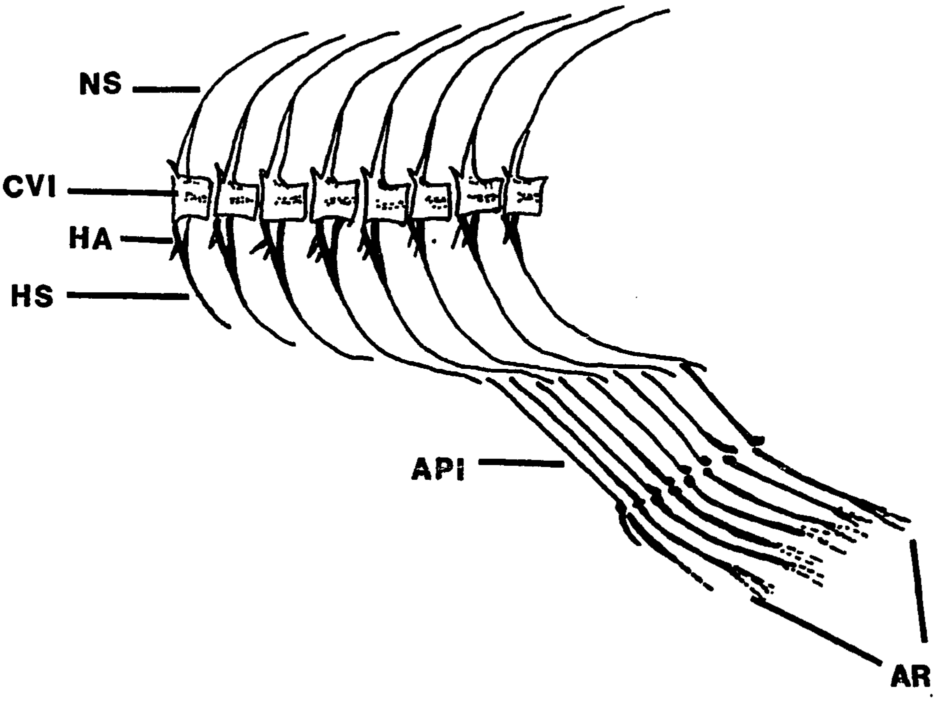

NS
CVI
HA
HS
API
AR

Fig. 33. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Notropis hudsonius*.

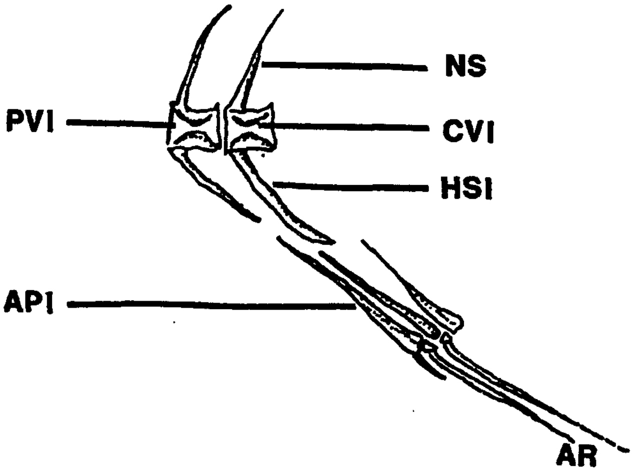

NS
PVI
CVI
HSI
API
AR

Fig. 34. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Salmo gairdneri AMNH 40268.

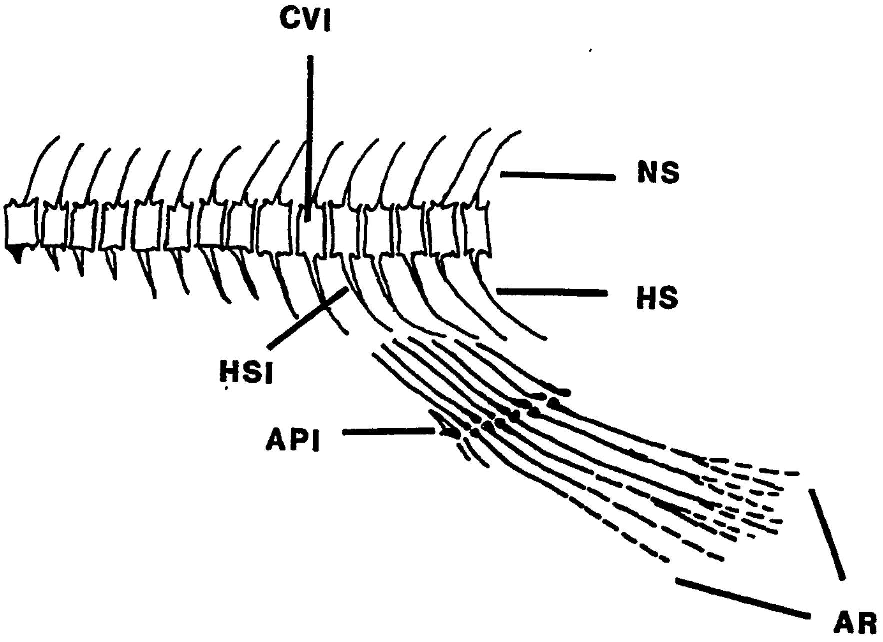
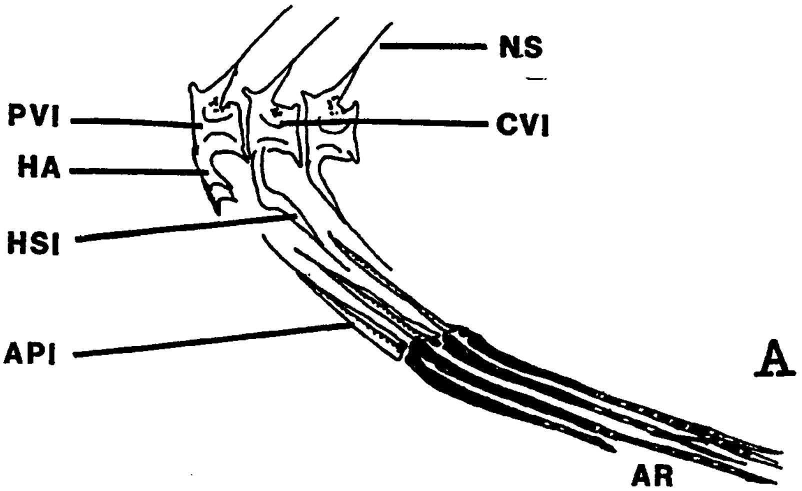

CVI
NS
HS
HSI
API
AR

Fig. 35. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of A) *Fundulus similis* AMNH 39167 and B) *Menidia menidia* AMNH 35924.


NS
PVI
CVI
HA
HSI
API
A
AR

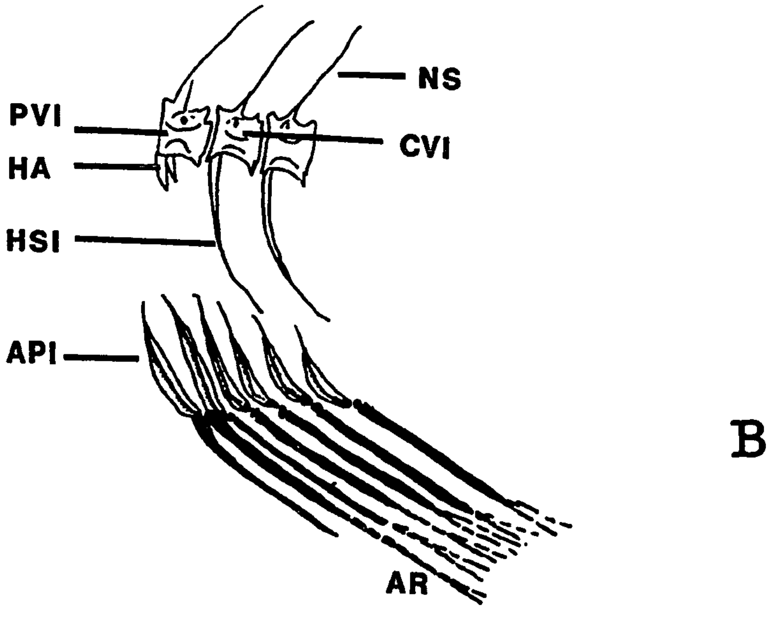

PVI
NS
CVI
HA
HSI
API
B
AR

Fig. 36. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of
A) *Holocentrus poco* AMNH 22925 and
B) *Gephyroberyx philippinus* AMNH 49701SW.

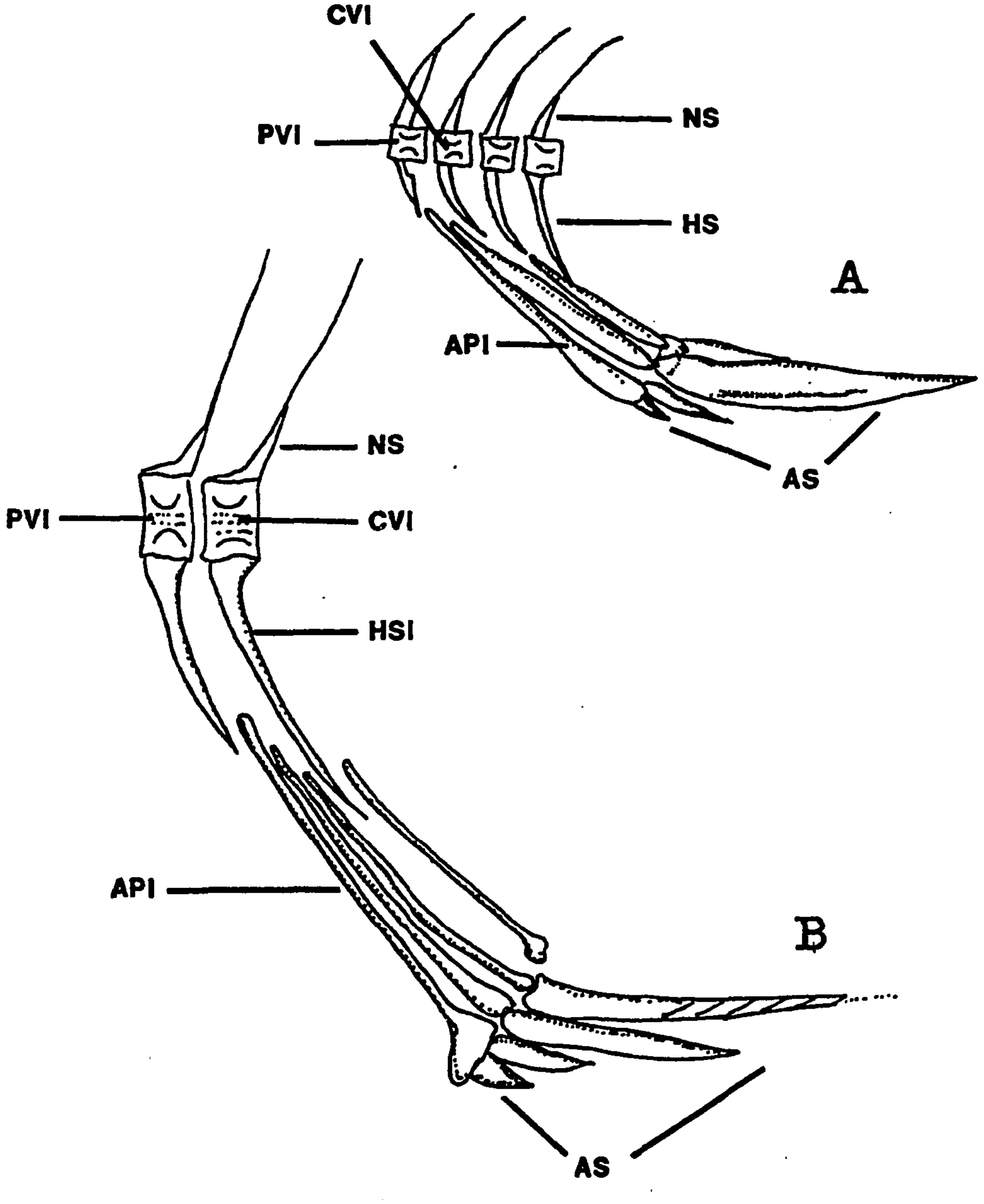

CVI
PVI
NS
HS
A
API
AS
NS
PVI
CVI
HSI
API
B
AS

Fig. 37. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Polymixia lowei* AMNH 27413.

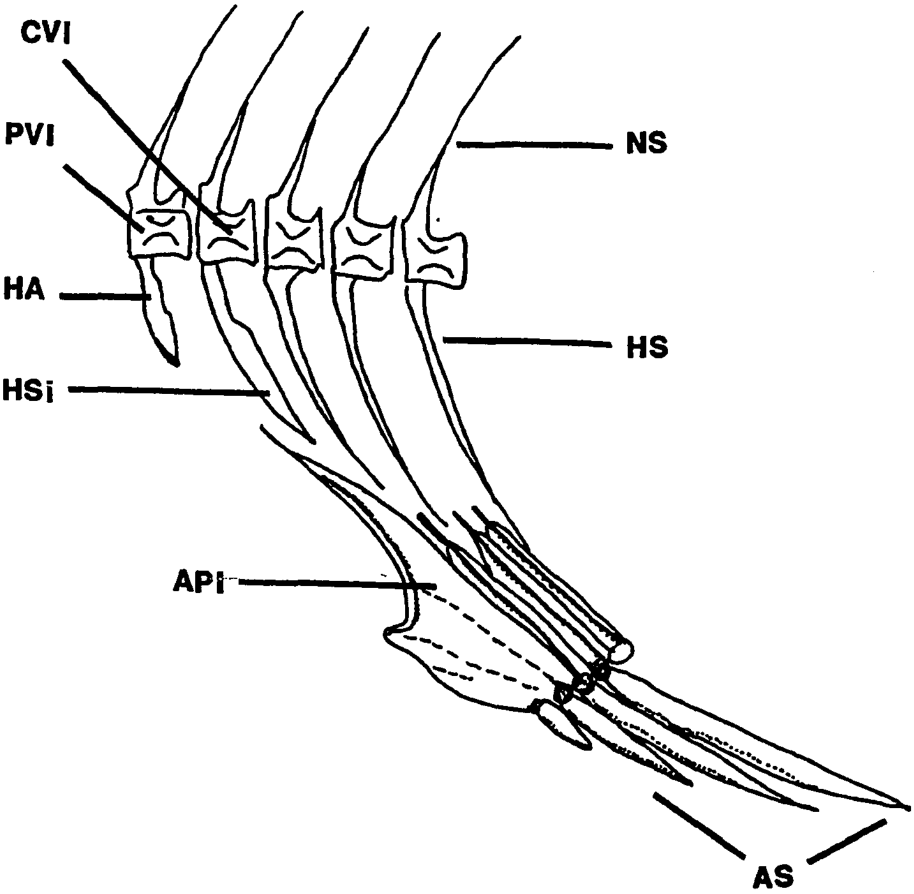

CVI
PVI
HA
HSi
NS
HS
API
AS

Fig. 38. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Zeus faber* AMNH 29458SW.

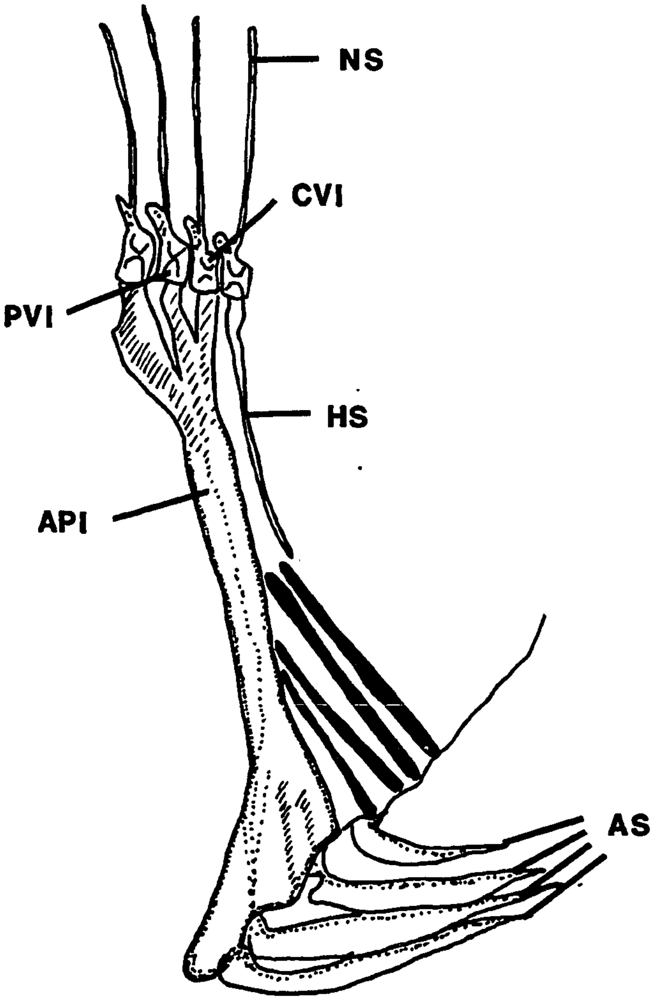
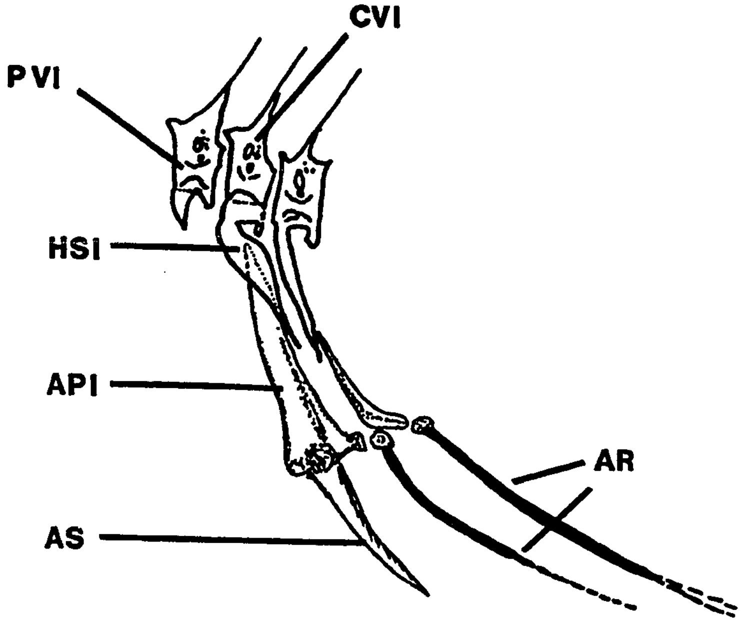
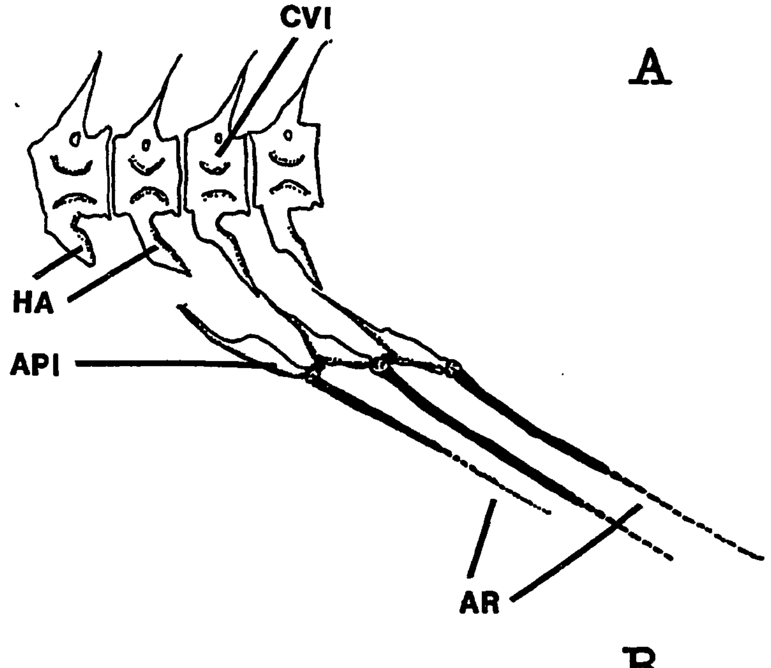

NS
CVI
PVI
HS
API
AS

Fig. 39. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of A) *Eucalia inconstans* AMNH 10181SW and B) *Cottus bairdi* AMNH 40281.



A



B

Fig. 40. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Trinectes maculatus* AMNH 43047.

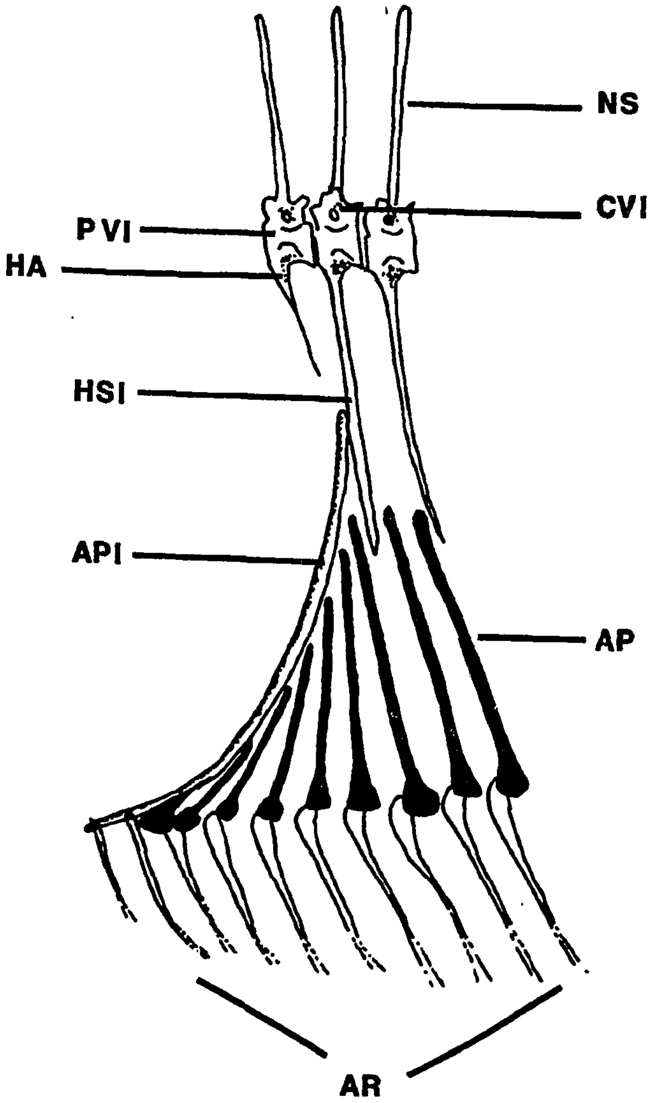

NS
CVI
PVI
HA
HSI
API
AP
AR

Fig. 41. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Monacanthus ciliatus* AMNH 22214.

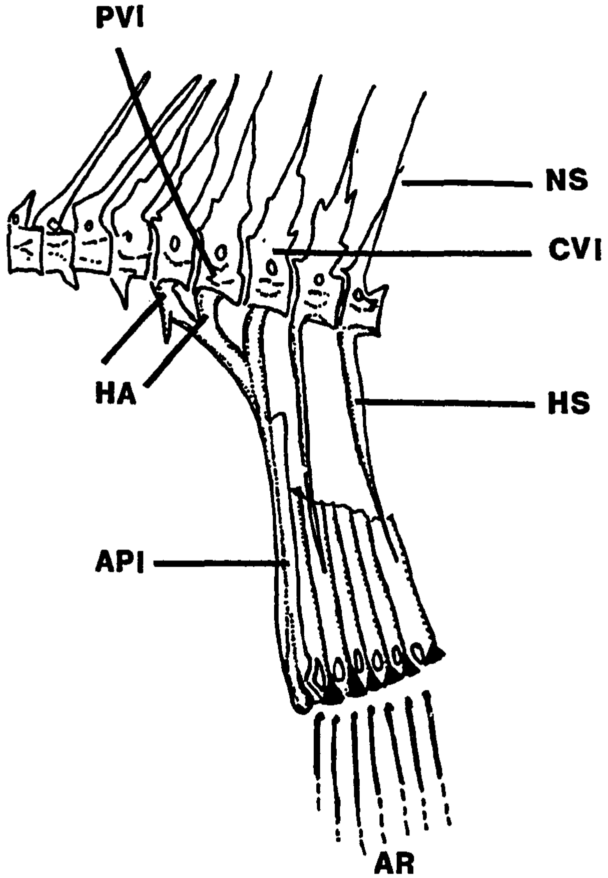

PVI
NS
CVI
HA
HS
API
AR

Fig. 42. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of <u>Centropomus robalito</u> AMNH 32925SW.

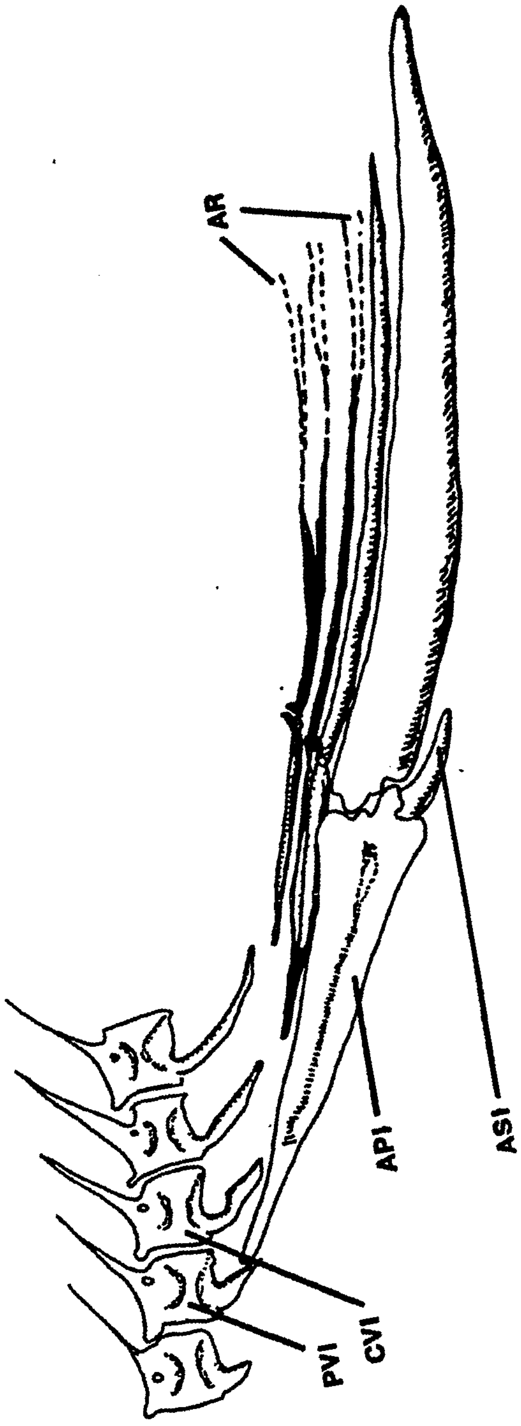

AR
API
ASI
PVI
CVI

Fig. 43. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Lates niloticus* AMNH 55359.

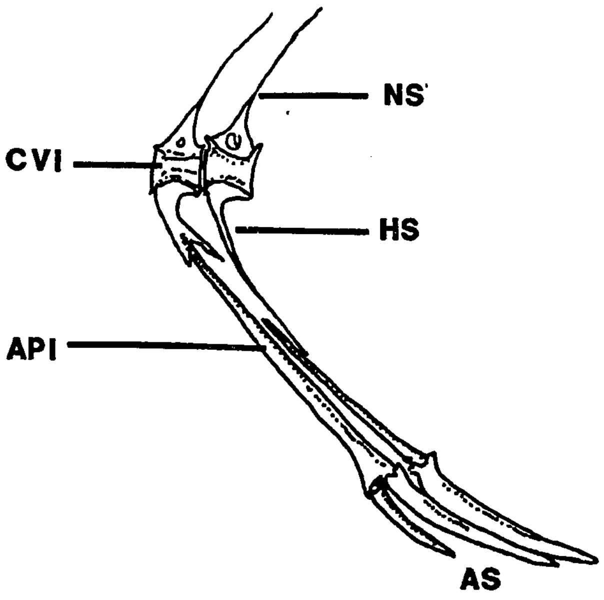

NS
CVI
HS
API
AS

Fig. 44. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Ambassis commersoni* AMNH 37769.

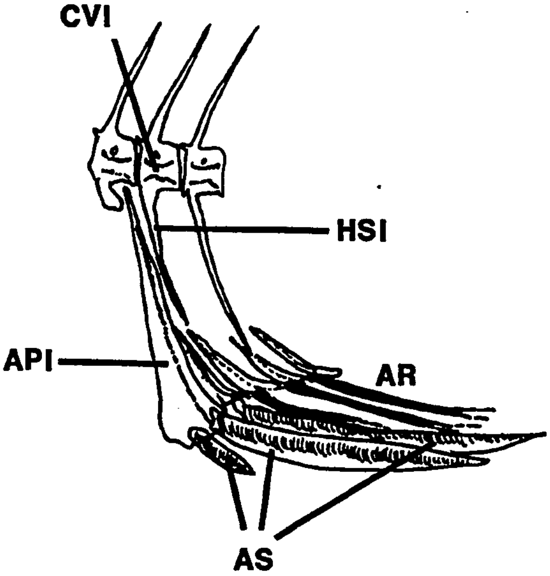

CVI
HSI
API
AR
AS

Fig. 45. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Banjos typus* AMNH 35845.

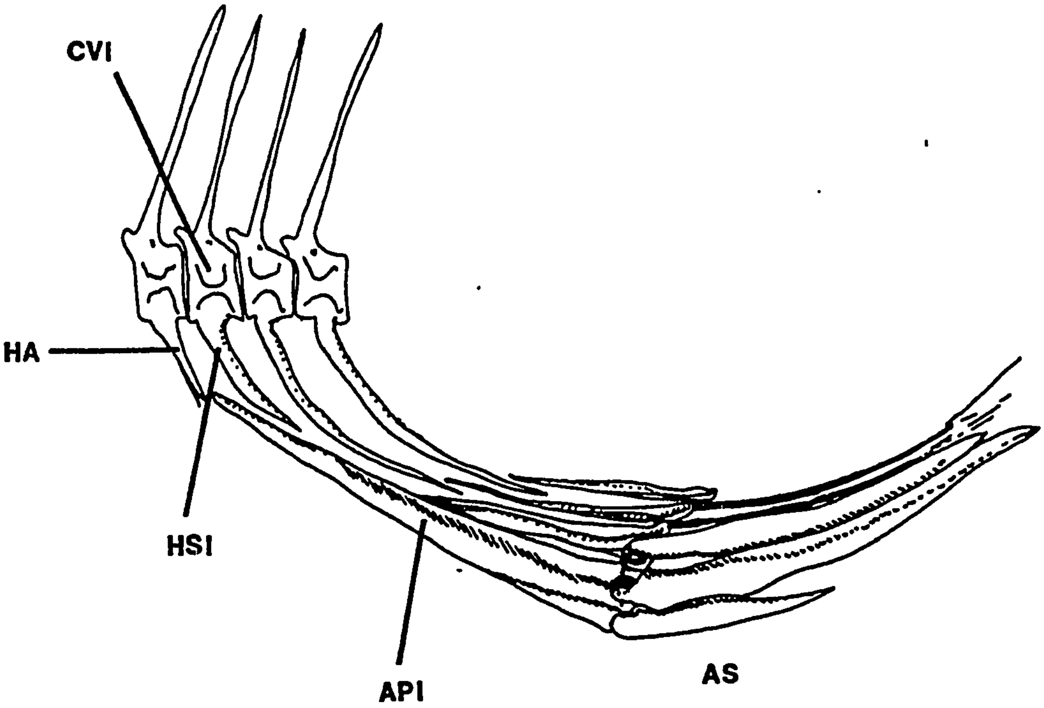

CVI
HA
HSI
API
AS

Fig. 46. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Haemulon sciurus* AMNH 15484.

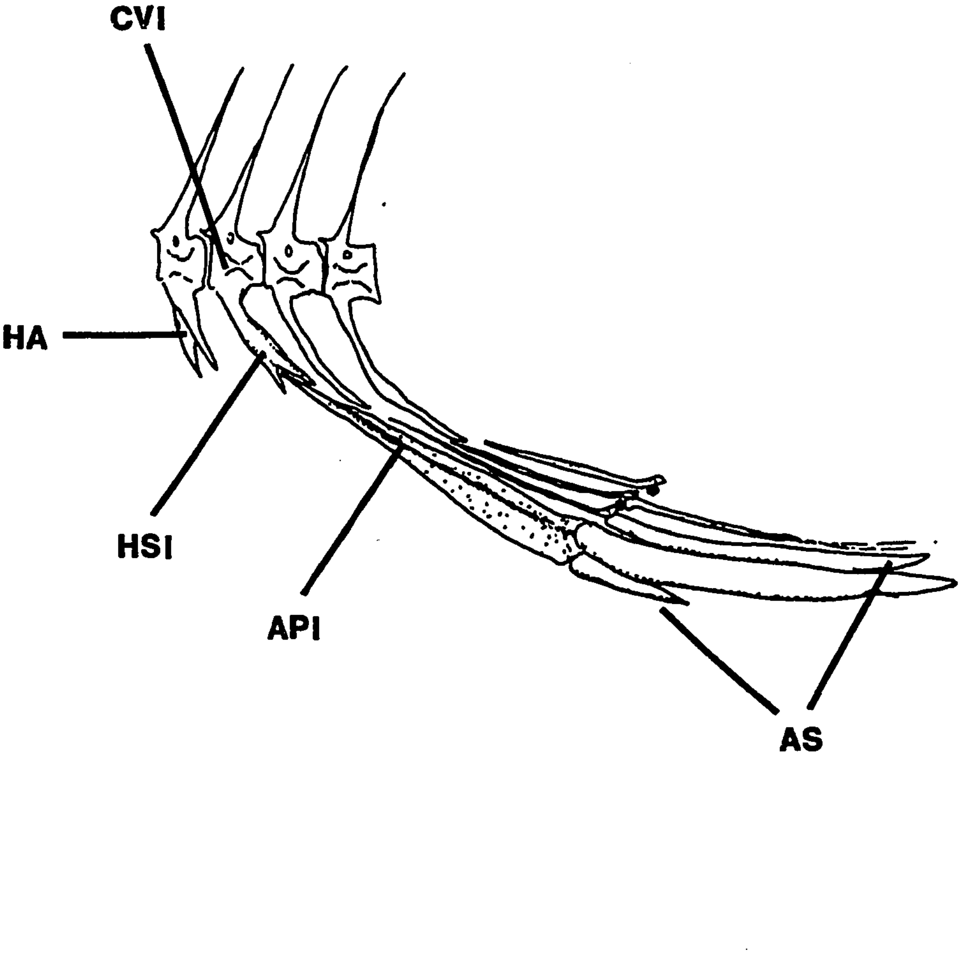
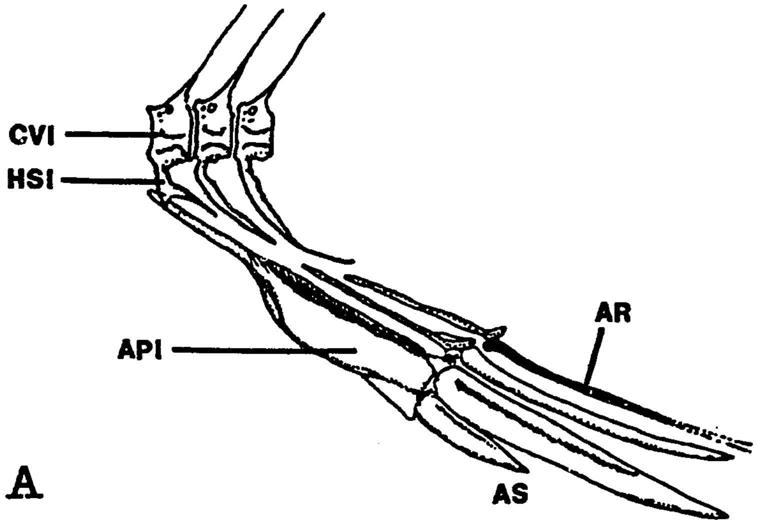

CVI
HA
HSI
API
AS

Fig. 47. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of
A) *Lateolabrax japonicus* AMNH 14380 and
B) *Siniperca scherzeri* AMNH 10506.


CVI
HSI
AR
API
A
AS

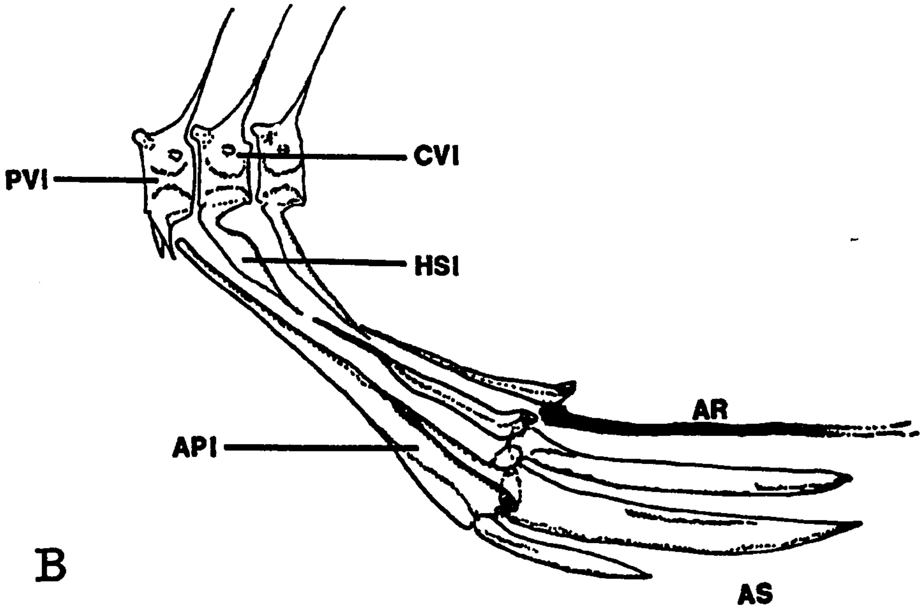

PVI
CVI
HSI
AR
API
B
AS

Fig. 48. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Bostockia porosa* AMNH 31448.

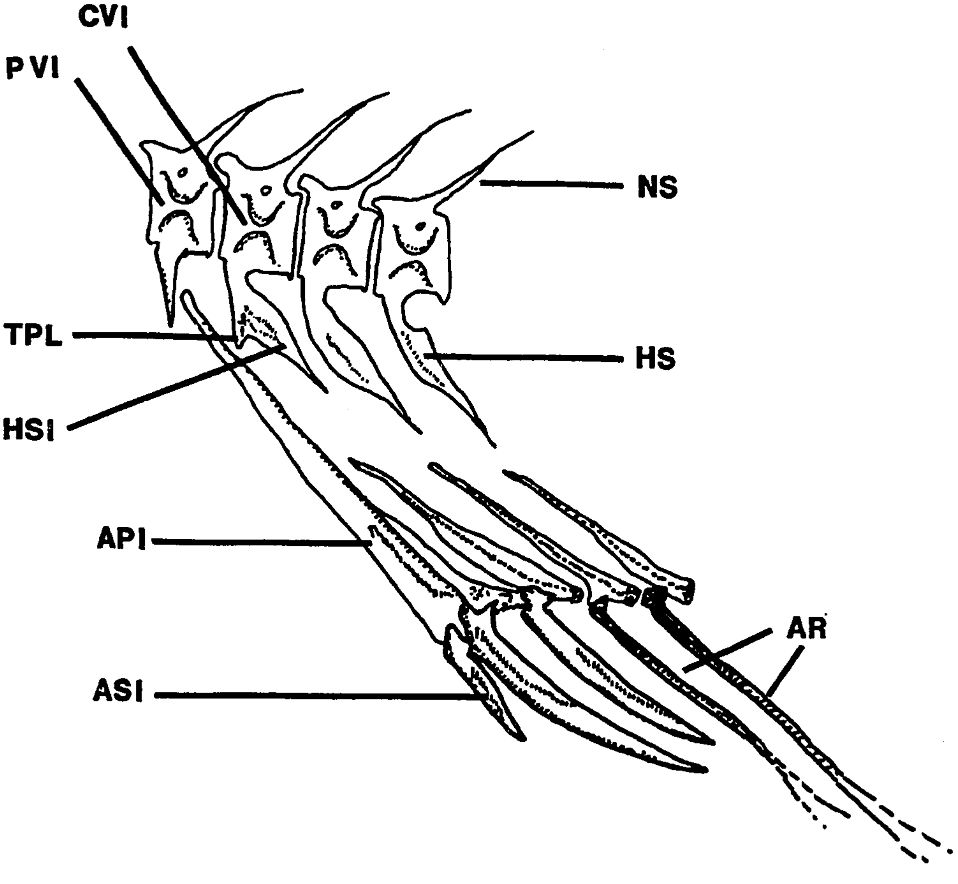

CVI
PVI
NS
TPL
HS
HSI
API
AR
ASI

Fig. 49. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Morone saxatilis*.

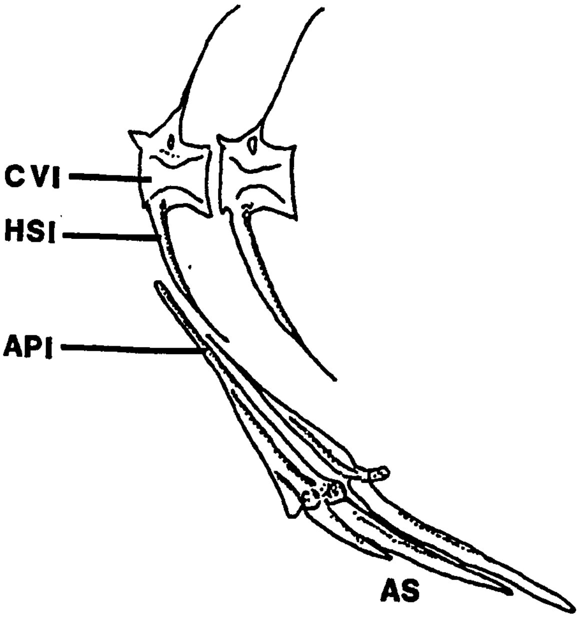

CVI
HSI
API
AS

Fig. 50. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Serranus trigrinus* AMNH 43172.

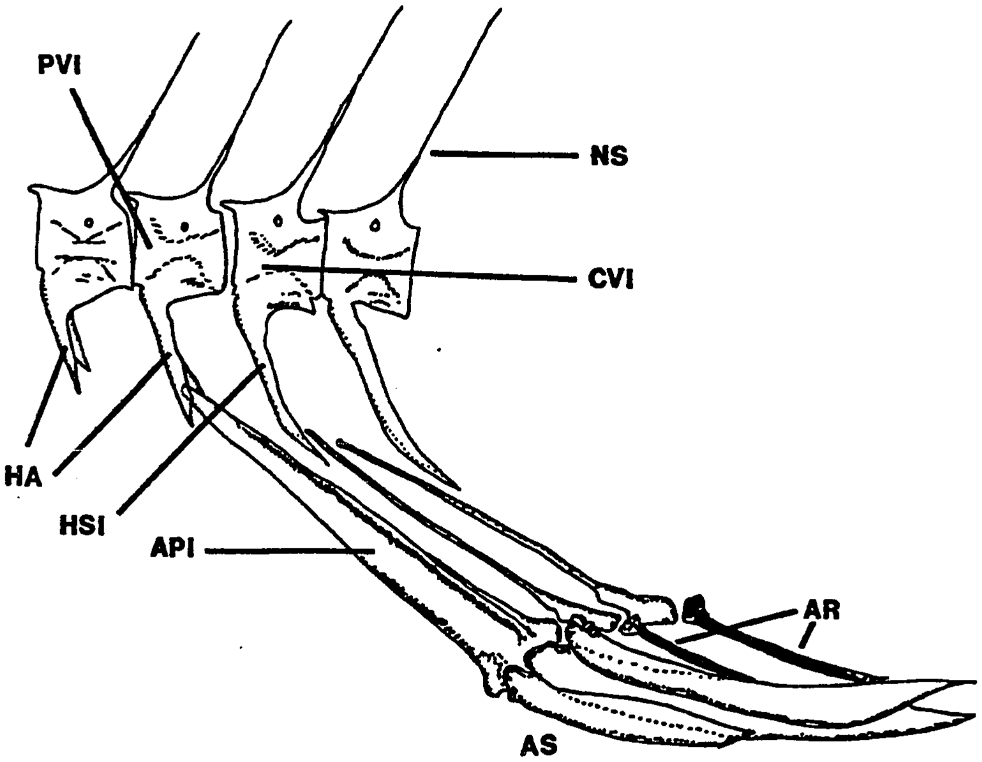

PVI
NS
CVI
HA
HSI
API
AR
AS

Fig. 51. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of A) *Lobotes surinamensis* AMNH 22125 and B) *Eucinostomus harengulus* AMNH 21893.

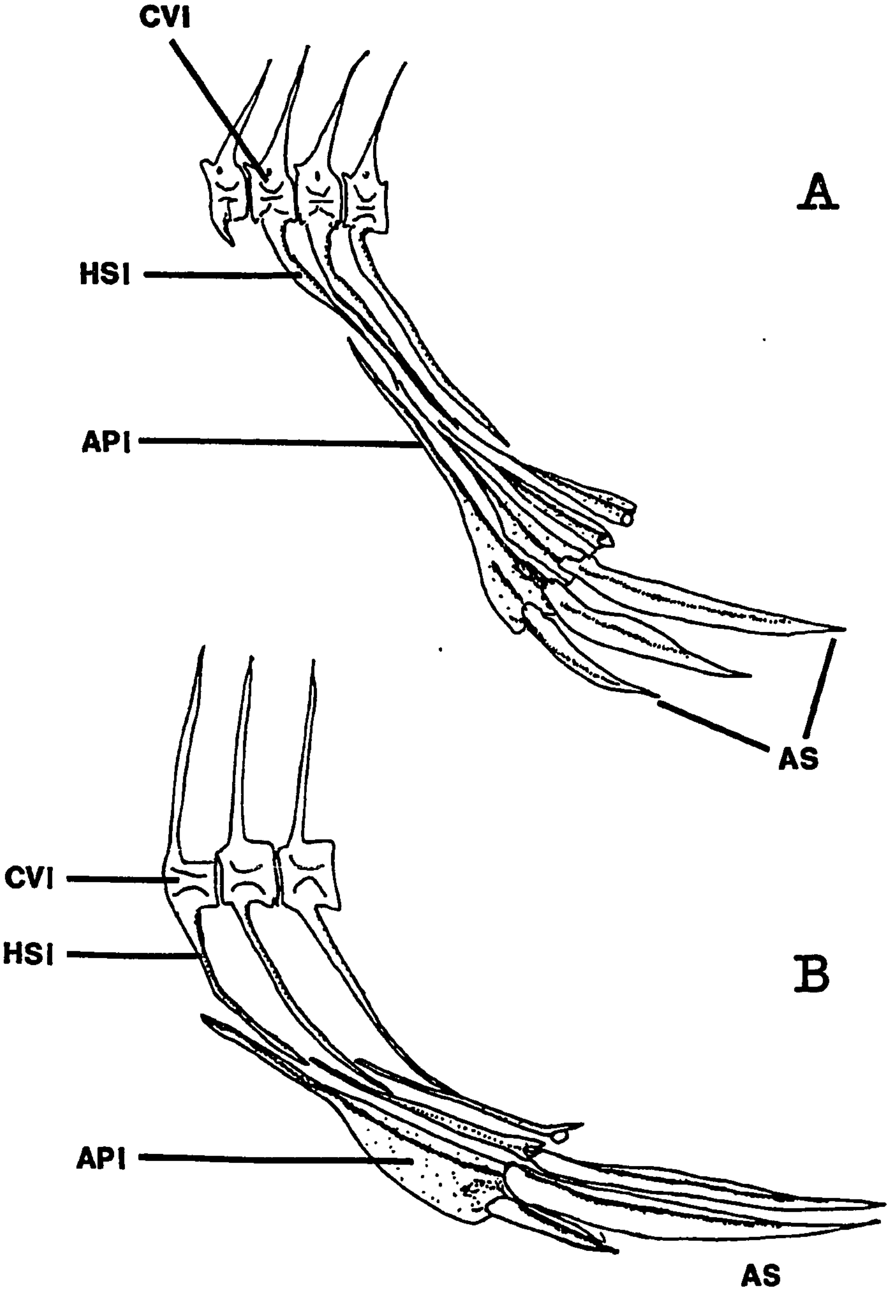

CVI
A
HSI
API
AS
CVI
HSI
B
API
AS

Fig. 52. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Terapon butleri* AMNH 35648.

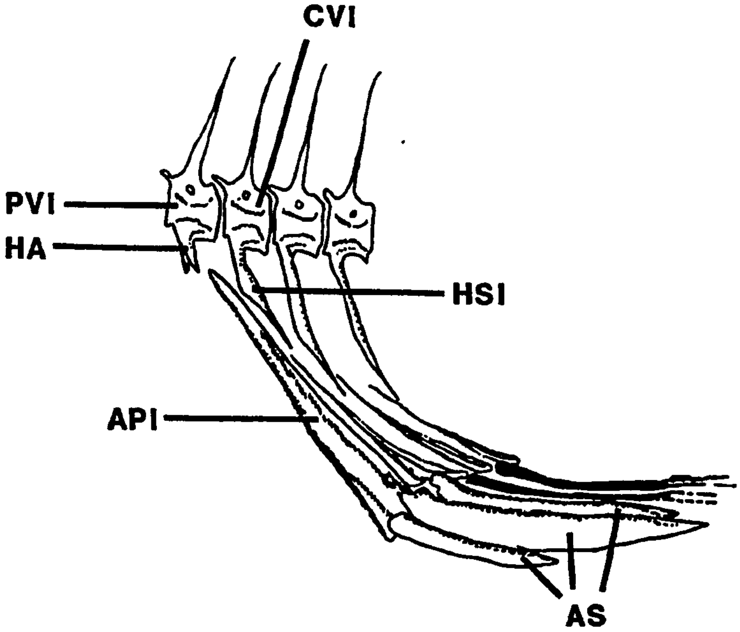

CVI
PVI
HA
HSI
API
AS

Fig. 53. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of Pristigenys alta AMNH 29378.

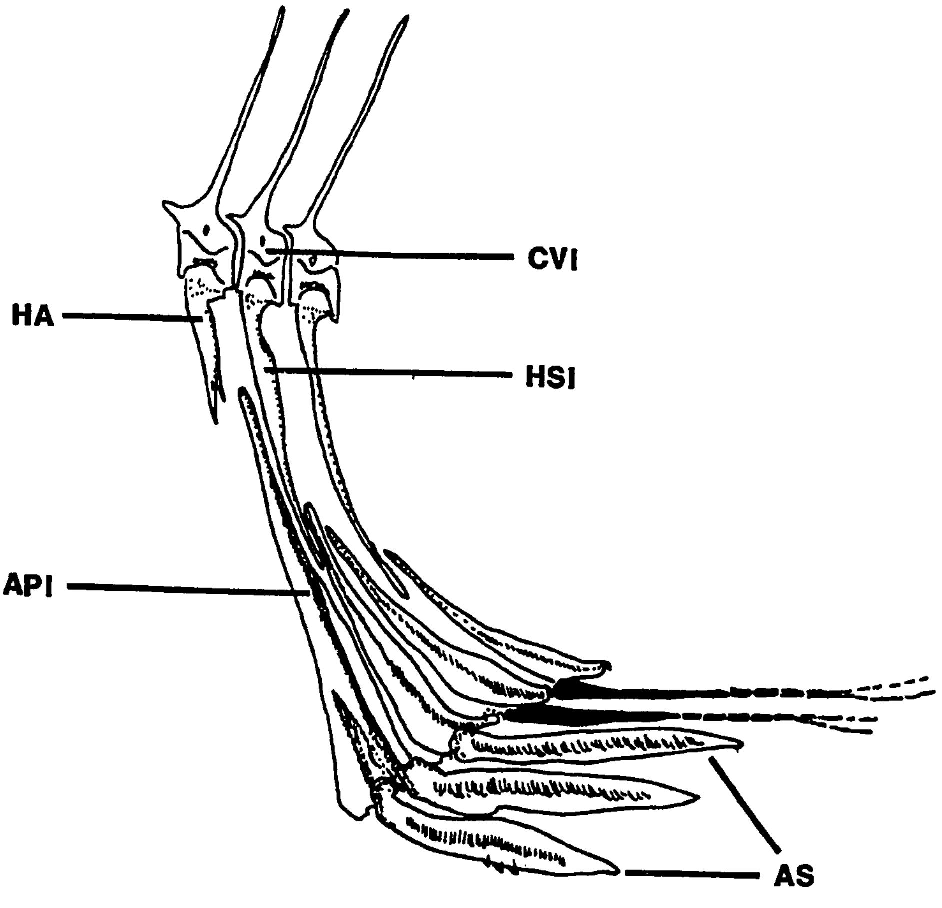

CVI
HA
HSI
API
AS

Fig. 54. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Nemipterus* sp. AMNH 16676.

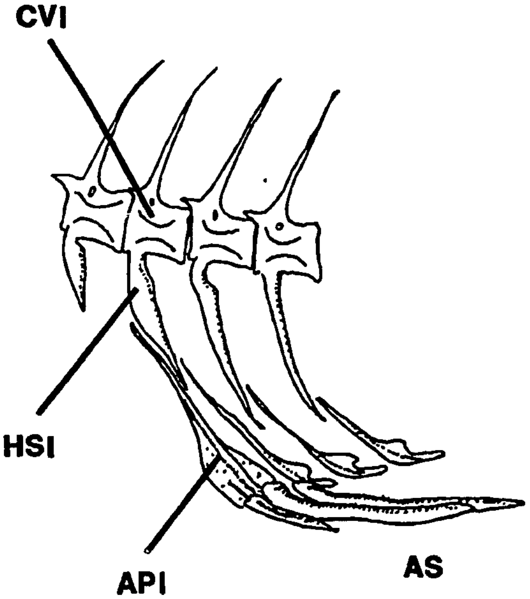
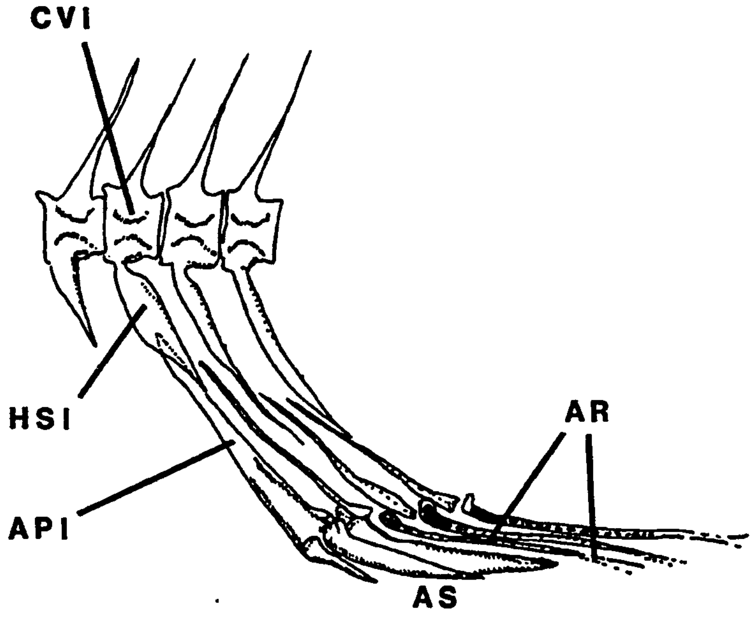
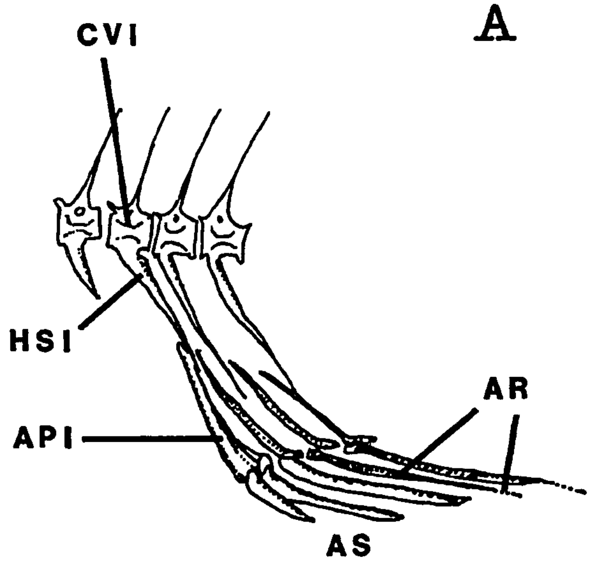

CVI
HSI
API
AS

Fig. 55. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of A) *Pseudochromis fuscus* AMNH 16969 and B) *Assessor mcneilli* AMNH 49639.



A



B

Fig. 56. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Apogon binotatus*.

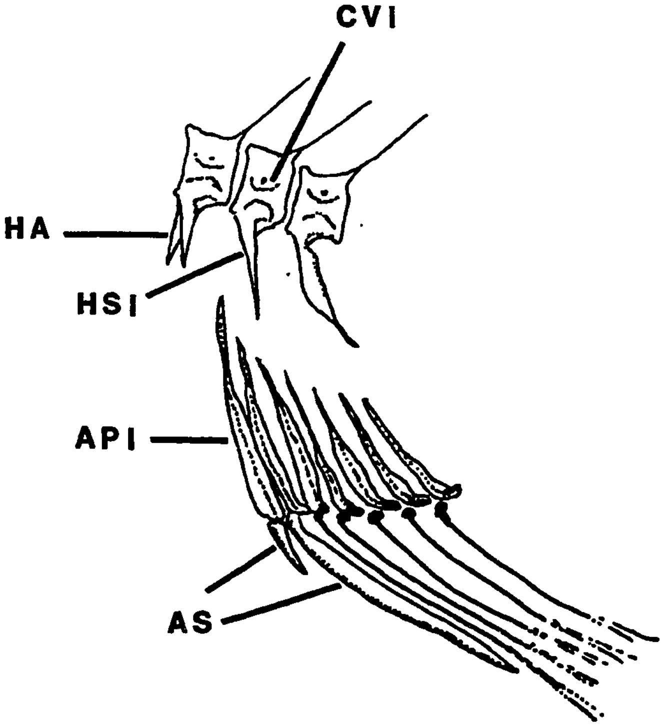

CVI
HA
HSI
API
AS

Fig. 57. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Lethrinus ornatus* AMNH 14916SW.

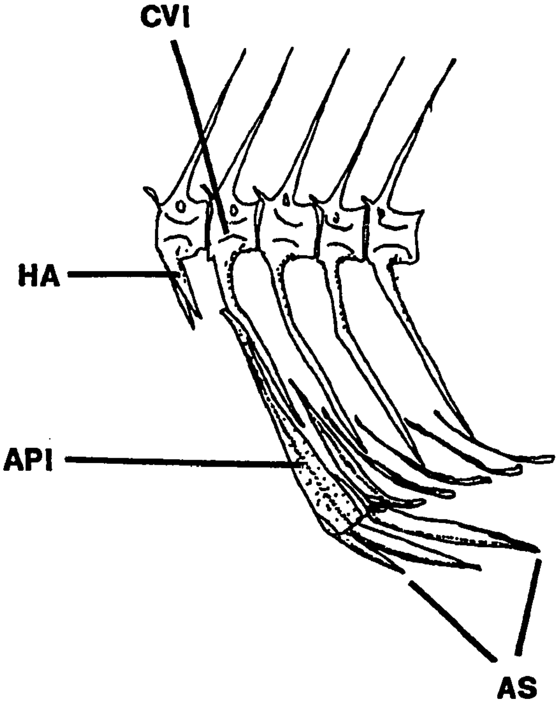

CVI
HA
API
AS

Fig. 58. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Kuhlia malo* AMNH 9374.

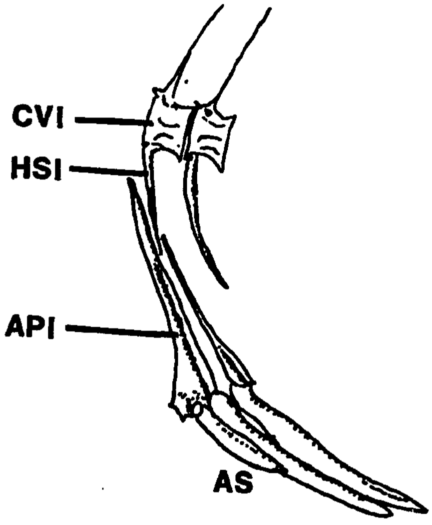

CVI
HSI
API
AS

Fig. 59. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of *Nannatherina balstoni*.

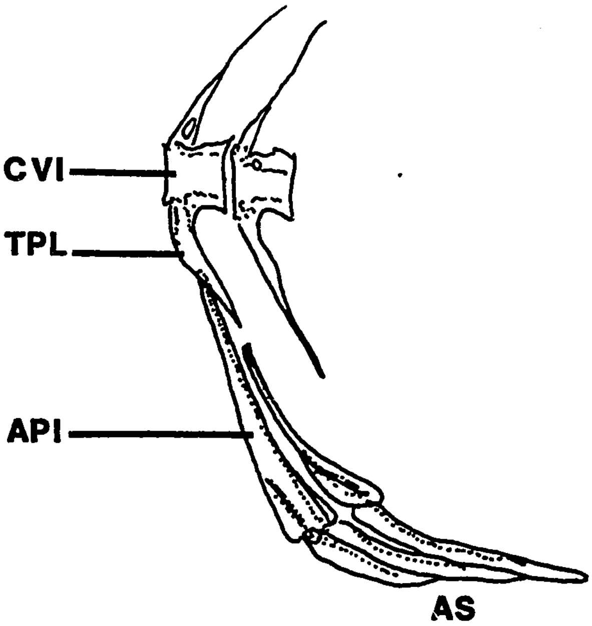

CVI
TPL
APl
AS

Fig. 60. Relationships of vertebral column, haemal spine, and anal-fin pterygiophores of A) *Caulolatilus affinis* AMNH 49709 and B) *Hoplolatilus starcki* AMNH 38129.

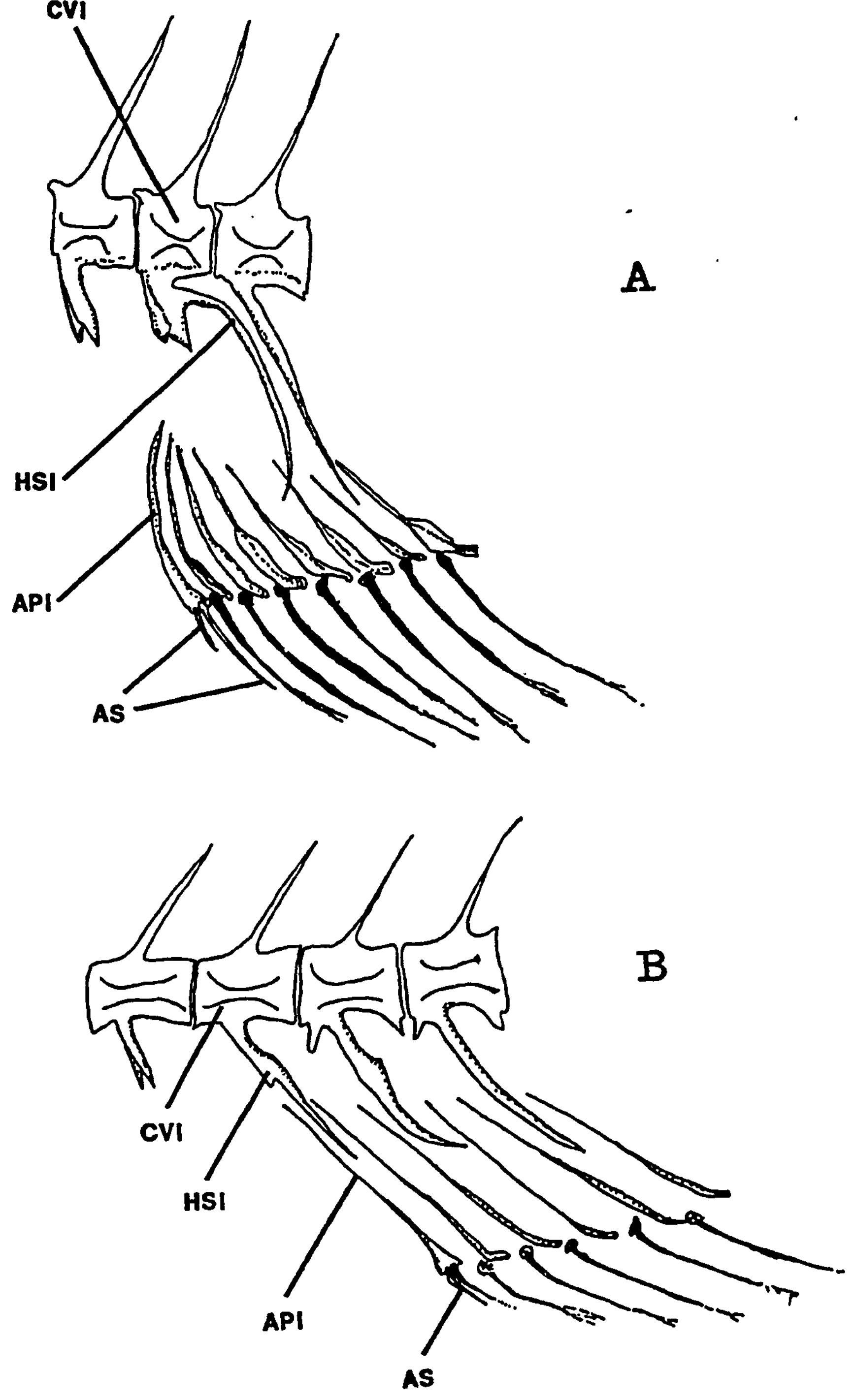

CVI
A
HSI
API
AS
B
CVI
HSI
API
AS

Fig. 61. Relationships of vertebral column, haemal spine, and anal-fin pterygiophore of
A) *Sillago bassensis* AMNH 31440 and
B) *Pomatomus saltatrix* AMNH 18803.

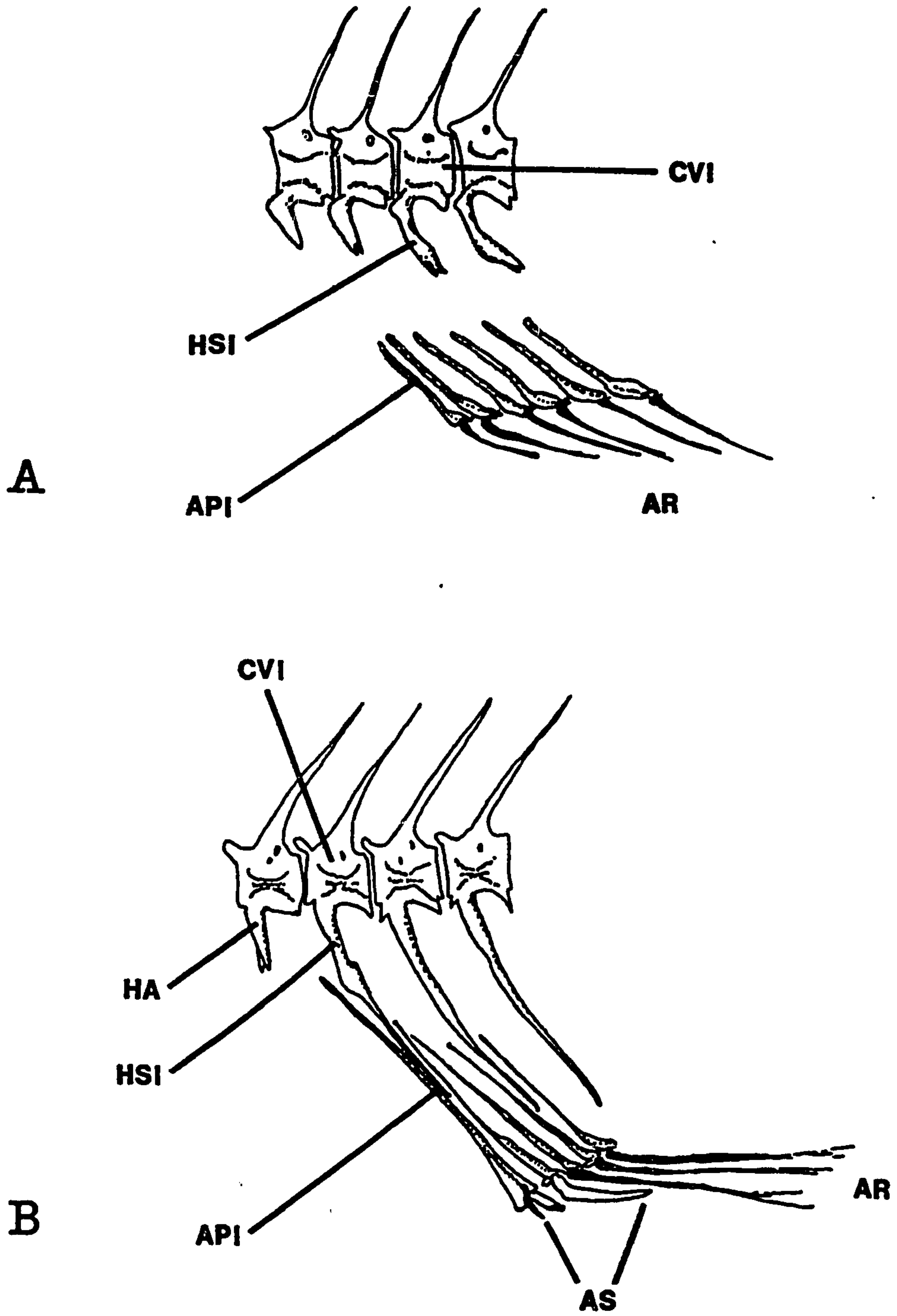

CVI
HSI
A
API
AR
CVI
HA
HSI
B
API
AR
AS

Fig. 62. Relationships of vertebral column, haemal spine, and anal-fin pterygiophore of *Caranx crysos* AMNH 22026

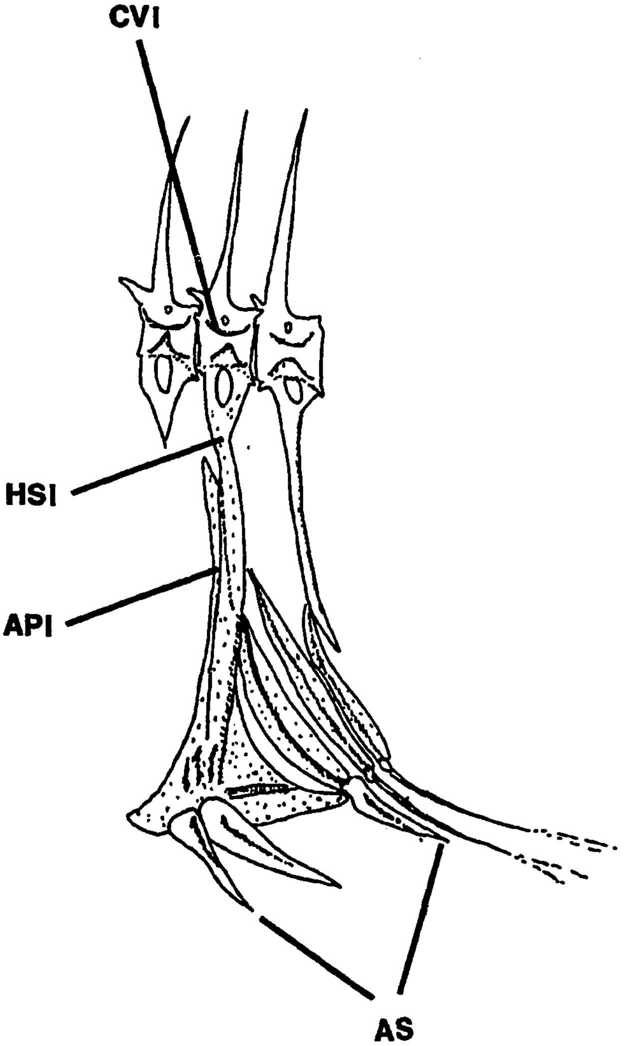

CVI
HSI
API
AS

Fig. 63. Relationships of vertebral column, haemal spine, and anal-fin pterygiophore of <u>Scatophagus</u> <u>argua</u> AMNH 14614.

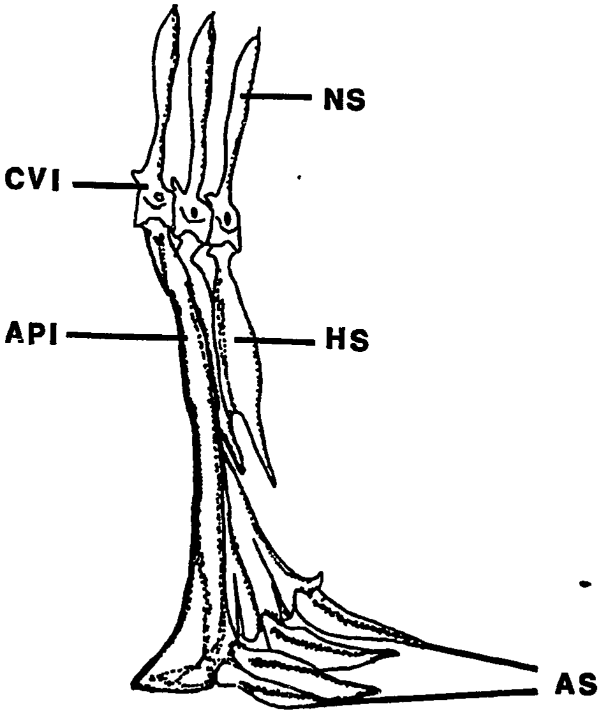
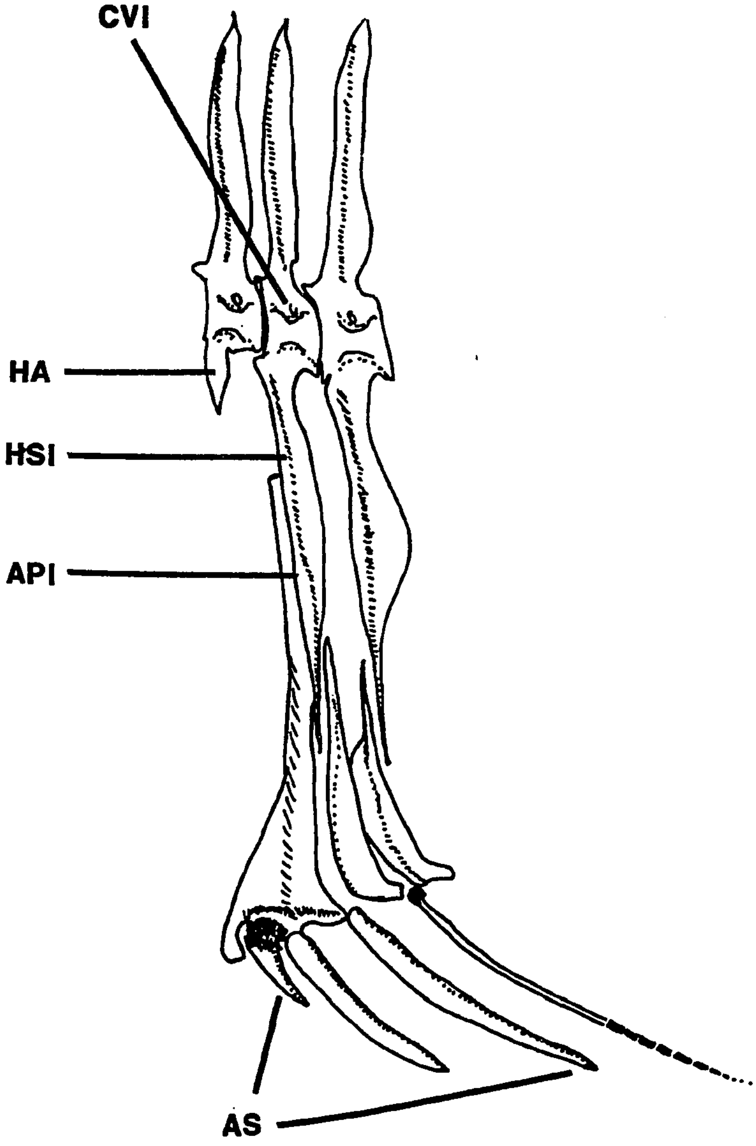

NS
CVI
API
HS
AS

Fig. 64. Relationships of vertebral column, haemal spine, and anal-fin pterygiophore of *Acanthurus chirurgus* AMNH 21806SW


CVI
HA
HSI
API
AS

REFERENCES

Anjard, C.A. 1974. Centrarchidae - sunfishes. In A.J. Lippson and R.L. Moran (eds.). Manual for identification of early developmental stages of fishes of the Potomac River estuary. Envi. Tech. Center, Baltimore, Maryland. pp.178-195.

Arratia, G.F. 1982. A review of freshwater percoids from South America (Pisces, Osteichthyes, Perciformes, Percichthyidae, and Perciliidae). Abh. senckenb. naturforsch. Ges. No. 540:1-52. Frankfurt a.M., 15.9.1982.

Avise, J. C., et al. 1977. Biochemical genetics of sunfish IV. Relationships of centrarchid genera. Copeia 1977 (2):250-258.

Bailey, R.M. 1938. A systematic revision of the centrarchid fishes, with a discussion of their distribution, variation, and probable interrelationships. Unpublished Ph.D. dissertation Univ. of Mich., Ann Arbor, 256pp.

Bailey, R.M. and C.L. Hubbs. 1949. The black basses of Florida, with a description of a new species. Mus. Zool. Univ. Mich., Misc. Pub. 516:1-40.

Bailey, R.M., and W.A. Gosline. 1955. Variation and systematic significance of vertebral counts in the American fishes of the family Percidae. Misc. Publ. Mus. Zool. Univ. Mich. 93:44pp.

Bailey, R.M., et al. 1970. A list of common and scientific names of fishes from the United States and Canada. Amer. Fish. Soc. Spec. Pub. 6.

Berg, L.S. 1940. Classification of fishes, both recent and fossil. Trav. Inst. Zool. Acad. Sci. URSS, 5(2):87-517. Also lithoprint, J.W. Edwards, Ann Arbor, Michigan, 1947.

Blair, C.B. Jr. and W.N. Brown. 1961. The osteology of the red eye bass, Micropterus coosae (Hubbs and Bailey) [sic] J. Morph. 109:19-36.

Blot, J. 1968. Le squelette interne de la nageoire anale et ses relations avec Le squelette axial. C.R. Seanc. Acad. Sci. Serie D, 266(19):1943-1946.

Blot, J. 1969. Les Poissons Fossiles, Du Monte Bolca Museo Civico Di Storia Nationale Di Verona Memorie Fuori Serie N.2, 525pp.

Bollman, C.H. 1891. A review of the Centrarchidae, or fresh water sunfishes of North America. Rept. U.S. Comm. Fish and Fisheries For 1888:557-589.

Boulenger, G.A. 1895. Catalogue of the Perciform fishes in the British Museum. British Museum (Natural History) London, 2nd Ed. 1:394 pp.

Branson, B.A. and G.A. Moore. 1962. The lateralis components of the Acoutico-Lateralis System in the sunfish family Centrarchidae. Copeia 1962 (1):1-108.

Breder, C.M. Jr. 1936. The reproductive habits of the North American Sunfishes (Family Centrarchidae). Zoologica 21:1-48.

Cashner, R.C. 1974. A systematic study of the Genus Ambloplites, with comparisons to other members of the Tribe Ambloplitini (Pisces: Centrarchidae). Ph. D. Dissertation, Tulane University, 378pp.

Childers, W.F. 1967. Hybridization of four species of sunfishes (Centrarchidae). Bull. Illinois Nat. Hist. Surv. 29:159-214.

Collette, B.B. 1963. The subfamilies, tribes and genera of the Percidae (Teleostei). Copeia 1963 (4):615-623.

Conner, J.V. 1980. Identification of larval sunfishes from southern Louisiana. Fourth larval fish conference, University of Mississippi, 1980. Proceedings U.S. Fish and Wildlife Service, Biological Services Proogram Ann Arbor, Michigan. pp.17-52.

Cuvier, M. and M. Valenciennes. 1828-1849. Histoire naturelle des poissons. 22 Volumes, Vol. 2.

Dineen, C.F. and P.S. Stokely. 1956. The osteology of the Sacramento perch, Archoplites enterruptus (Girard). Copeia 1956 (4):217-230.

Dingerkus, G., and L. Uhler. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Tech. 52(4):229-232.

Dobbin, C. N. 1941. A comparative study of the gross anatomy of the air bladders of ten families of fishes of New York and other eastern states. J. Morph. 68(1):1-25.

Dooley, J.K. 1978. Systematics and biology of the tilefishes (Perciformes: Branchiostegidae and Malacanthidae), with descriptions of two new species. NOAA Tech Rept. NMFS Circ. 411. 78pp.

Eaton, T. H. 1945. Skeletal supports of the median fins of fishes. J. Morph. 76:193-212.

Eaton, T.H. 1956. Notes on the olfactory organs in Centrarchidae. Copeia. 1956 (1):196-199.

Eddy, S. 1967. How to know the fresh water fishes. Wm. C. Brown Co., Dubuque, Iowa. 286 pp.

Freihofer, W.C. 1963. Patterns of the ramus lateralis acessorius and their systematic significance in teleostean fishes. Stanford Ichthyol. Bull., 8:81-189.

Fritzsche, R.A., and G.D. Johnson. 1980. Early osteological development of white perch and striped bass with emphasis on identification of their larvae. Trans. Am. Fish. Soc. 109:387-406.

Fujii, R. 1969. Chromatophores and pigments. In Hoar, W.S., and D.J. Randall (eds.), Fish Physiology, Vol. III:307-353. Academic Press, New York and London 485pp.

Gill, T. 1861. Notes on some genera of fishes of the Western coast of North America. Proc. Acad. Nat. Sci. Phil. 13:164-168.

Gill, T. 1872. Arrangement of the families of the fishes or classes Pisces Marsipebranchii and Leptocardi. Smiths. Misc. Coll. pp. 1-49.

Gosline, W.A. 1966a. The limits of the fish family Serranidae, with notes on other lower percoids. Proc. Calif. Acad. Sci. (ser. 4) 33:91-112.

Gosline, W.A. 1966b. Comments on the classification of the percoid fishes. Pac. Sci. 20:409-418.

Grande, L. 1985. Recent and fossil Clupeomorph fishes with materials for revision of the subgroups of clupeoids. Bull. Am. Mus. Nat. Hist. Vol. 181(2):235-307.

Greenwood, P.H., D.E. Rosen, S.H. Weitzman, and G.S. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Am. Mus. Nat. Hist. 131:339-456.

Gunther, A. 1859 Catalogue of the fishes in the British Museum. 1:1-524.

Gushiken, S. 1988. Phylogenetic Relationships of the Perciform Genera of the family Carangidae. Japanese J. Ichthyology 34(4): 443-461.

Hennig, W. 1966. Phylogenetic Systematics. Univ. Illinois Press., Urbana, 263 pp.

Hester, F.E. 1970. Phylogenetic relationships of sunfishes as demonstrated by hybridization. Trans. Amer. Fish. Soc. 1:100-104.

Hubbs, C.L., and K.F. Lagler. 1958. Fishes of the Great Lakes Region. Cranbrook Institute of Sci. Bull. 26, 213 pp.

Johnson, G.D. 1975. The procurrent spur: An undescribed perciform candal character and its phylogenetic implications. Occas. Pap. Calif. Acad. Sci. 121:23 pp.

Johnson, G.D. 1980. The limits and relationships of the Lutjanidae and associated families. Bulletin of the Scripps Institution of Oceanography of the Univ. of California, LA Jolla, Ca. 24:114 pp.

Johnson, G.D. 1983. *Niphon spinosus*: A primitive Epinepheline serranid, with comments on the monophyly and intrarelationships of the serranidae. Copeia 1983 (3):777-787.

Johnson, G.D. 1984. Percoidei: Development and Ralationships, In: Onogeny and Systematics of Fishes, H.G. Moser (Ed.). Sp. Publ. No. 1, A.S.I.H. pp. 464-498.

Johnson, R. H. 1907. The individuality and variation of the pyloric caeca of the Centrarchidae. The Transactions of the Wisconsin Acad. of Sci., Arts & Letters XV(2):713-732.

Jones, F.R.H., and N.B. Marshall. 1953. The structure and function of the teleostean swim bladder. Biol. Rev., 28:16-83

Jordan, D.S. 1877. Contributions to North American Ichthyology and review of Rafinesque's memoirs. Bull. U.S. Natl. Mus. 9:1-53.

Jordan, D.S., and B.W. Evermann. 1896. The fishes of North and Middle America. Bull. U.S. Natl. Mus. 47:1240 pp.

Katayama, M. 1959. Studies on the serranid fishes of Japan, Bull. Faculty of Education, Yamaguchi Univ. Japan. 8(2):103-181.

Kaufman, L., and K.F. Liem. 1982. Fishes of the suborder Labroidei (Pisces: Perciformes): Phylogeny, ecology, and evolutionary significance. Breviora Mus. Comp. Zool. 472:1-19.

Kendall, A.W. 1979. Morphological comparisons of North American sea bass larvae (Pisces: Serranidae). U.S. Dept. Comm., NOAA Tech. Rep. NMFS Circ. 428:509p.

Lauder, G.V., and Kard F. Liem. 1983. The evolution and interrelationships of the Actinopterygian fishes. Bull. Mus. Comp. Zoo. V.150, No. 3, 197 pp.

Lindsey, C.C. 1955. Evolution of meristic relations in the dorsal and anal fins of teleost fishes. Trans. Roy. Soc. Can., Ser. 3, 49:35-49.

Llewellyn, L.C. 1980. Family Kuhliidae pigmy perches. In: Fresh water Fishes of South-Eastern Australia. Ed. by R.M. McDowall pp. 153-155.

Llewellyn, L.C., and M.C. MacDonald. 1980. Family Percichthyidae Australian freshwater basses and cods. In: Freshwater Fishes of South-Eastern Australia. Ed. by R.M. McDowall pp. 142-149.

Mabee, P.M. 1987. Phylogenetic change and ontogenetic interpretation in the Family Centrarchidae (Perciformes: Centrarchidae). Dissertation, Duke University, 428 pp.

MacDonald, C.M. 1978. Morphological and Biochemical Systematics of Australian Freshwater and Estuarine Percichthyid Fishes. Aust. J. Marine Freshwater Res. 29:667-98.

Marshall, N.B. 1962. Swimbladder structure of deep-sea fishes in relation to their systematics and biology. Discovery Rept. 31:1-122.

Mathews, S. B. 1965. Reproductive Behavior of the Sacramento Perch, Archoplites interruptus. Copeia 1965 (2):224-228.

Mayr, E. 1969. Principles of Systematic Zoology. McGraw-Hill, Inc. New York, 428 pp.

McAllister, D.E. 1968. Evolution of branchiostegals and classification of Teleostome fishes. National Museum of Canada, Bull. 221 Bio. Series 77, 239 pp.

McCully, H.H. 1961. The comparative anatomy of the scales of the serranid fishes. Dissertation Abstracts, Vol. 22, No. 5, 248 pp.

McCully, H.H. 1962. The relationship of the Percidae and the Centrarchidae to the Serranidae as shown by the anatomy of their scales. Am. Zool. 2(3):430.

McKay, C.L. 1882. A review of the genera and species of the family Centrarchidae, with a description of one new species. U.S. National Museum Proceedings 4:87-93.

Mettee, M.F. Jr. 1974. A study on the reproductive behavior, embryology, and larval development of the pygmy sunfishes of the genus Elassoma. Unpubl. Ph.D. dissertation, Univ. of Alabama, 130pp.

Miller, H. 1963. The behavior of the pumpkinseed sunfish, Lepomis gibbosus (Linnaeus), with notes on the behavior of other species of Lepomis and the pygmy sunfish, Elassoma evergladei. Behavior 22(1-2):88-151.

Mok, H. 1981. The phylogenetic implications of centrarchid kidneys. Bull. Inst. Zool. Academia Sinica. 20(2): 59-67.

Mook, D. 1977. Larval and osteological development of the sheepshead Archosargus probatocephalus (Pisces: Sparidae) Copeia 1977(1):126-133.

Moore, G.A., and M.E. Sisk. 1963. The spectacle of Elassoma zonatum, Jordan. Copeia. 1963 (2):347-350.

Nelson, G.J. 1968. Review of "Evolution of branchiostegals and classification of teleostome fishes." Copeia 1968 (4):888-889.

Nelson, G.J. 1971. Paraphyly and polyphyly: Redifinitions. Syst. Zool. 20:471-472.

Nelson, G.J. 1978. Ontogeny, Phylogeny, Paleontology and the Biogenetic Law. Syst. Zool. 27(3):324-345.

Nelson, G.J., and N. Platnick. 1981. Systematics and Biogeography. Columbia Univ. Press, New York. 567 pp.

Nelson, G.J. 1985. Outgroups and ontogeny. Cladistics 1(1):29-45.

Nelson, J.S. 1984. Fishes of the world. Second Ed. Wiley Interscience Publ. 523 pp.

Olney, J.E., G.C. Grant, F.E. Schultz, C.L. Cooper, and J. Hageman. 1983. Pterygiophore - Interdigitation patterns in larvae of four Morone species. Tran. Am. Fish. Soc. 112:525-531.

Patterson, C. 1964. A review of Mesozoic acanthopterygian fishes, with special reference to those of the English chalk. Phil. Trans. Roy. Soc. London, ser. 3, Biol. Sci. 247:213-482.

Patterson, C. 1982. Morphological Characters and Homology. In: K.A. Joysey and A.E. Friday (Eds.), "Problems of Phylogenetic Reconstruction, Systematics Association Special Volume No. 21, pp. 21-74, Academic Press, London.

Piacentino, G.L., and A.E. Torno. 1987. Osteological observations of the vertebral column in some species of South American atherinids (Osteichthyes, Atheriniformes). Studies on Neotropical Fauna and Environment, 2:93-98.

Pimentel R.A., and R. Riggins. 1987. The Nature of Cladistic data. Cladistics 3(3):201-209.

Potthoff, T., S. Kelley, V. Saksena, M. Moe, and F. Young. 1987. Description of larval and juvenile yellow-tail Damselfish, Microspathodon chrysurus, Pomacentridae, and their osteological development. Bull. Marine Sci. 40(2):330-375.

Regan, C.T. 1913. The classification of Percoid fishes. Ann. Mag. Nat. Hist., Ser. 8, 12:111-145.

Richardson, S.L. 1981. Current knowledge of northeast Pacific sculpin larvae (Family Cottidae) with notes on relationships within the family. Fish. Bull., U.S. 79:(1)103-121.

Roberts, F.L. 1964. A chromosome study of twenty species of Centrarchidae. J. Morph. 115:401-418.

Robins, C.R., et. al. 1980. Common and scientific names of fishes from the United States and Canada. Am. Fish Soc. Spec. Publ. 12, 4th ed., 174 pp.

Robison, H.W. 1971. The everglades pygmy sunfish, Elassoma evergladei. Tropical Fish Hobbyist 19(10):30-33.

Rosen, D.E. 1973. Interrelationships of higher euteleostean fishes. In Greenwood, P.H., R.S. Miles, and C. Patterson (eds.), Interrelationships of fishes. Academic Press, London, pp. 397-513.

Rosen, D.E. 1984. Zeiforms as primitive Plectognath fishes. Amer. Mus. Novitates, No. 2782, pp. 1-45.

Rosen, D.E., and L.R. Parenti. 1981. Relationships of Oryzias, and the groups of Atherinomorph fishes. Amer. Mus. Novitates, No. 2719 pp. 1-25.

Rubenstein, D.I. 1981. Combat and communication in the everglades pygmy sunfish. Anim. Behav. 29(1):249-258.

Rubenstein, D.I. 1981. Population density, resource patterning and territoriality in the everglades pygmy sunfish. Anim. Behav. 29(1):155-172.

Rubenstein, D.I. 1981. Individual variation and competition in the everglades pygmy sunfish. J. Anim. Ecol. 50:337-350.

Schlaijker, E.M. 1937. New fishes from the continental tertiary of Alaska. Bull. Amer. Mus. Nat. Hist. 74:1-23.

Simpson, G.G. 1961. Principles of animal taxonomy. Columbia Univ. Press, New York, 247 pp.

Smith, C.L., and R.M. Bailey. 1961. Evolution of the dorsal-fin supports of percoid fishes. Papers Mich. Acad. Sci., Arts., and Letters, 46:345-363.

Smith, C.L., and R.M. Bailey. 1962. The subocular shelf of fishes. J. Morph. 110(1):1-17.

Smith, C.L. 1985. The inland fishes of New York State. New York State D.E.C., Albany, N.Y. 522pp.

Smith-Vaniz, W.F. 1984. Carangidae: relationships In: Ontogeny and Systematics of Fishes, H.G. Moser (Ed.). Sp. Publ. No. 1, A.S.I.H. pp. 522-530.

Sneath, P.H. and R.R. Sokal. 1973 Numerical taxonomy. W.H. Freeman and Company, San Francisco, California. 259 pp.

Stacey, P.B., and D. Chiszar. 1978. Body color pattern and the aggressive behavior of male pumpkinseed sunfish (Lepomis gibbosus) during the reproductive season. Behavior 64:271-297.

Stokely, Paul S. 1952. The vertebral axis of two speceis of Centrarchid fishes. Copeia 1952(4):255-261.

Sweeney, E.F. 1972. The systematics and distribution of the Centrarchid fish tribe Enneacanthini. Boston U. Ph.D. Dissertation, 205pp.

Travers, R.A. 1981. The interarcual cartilage; a review of its development distribution and value as an indicator of phyletic relationships in euteleostean fishes. J. Nat. Hist. 15:853-871.

Waldman, J. R. 1986 Systematics of Morone (Pisces: Moronidae) with notes on the lower percoids. The City U. of New York, Ph.D. Dissertation 150pp.

Walsh, S.J. and B.M. Burr. 1984 Life history of the banded pygmy sunfish Elassoma zonatum Jordan (Pisces: Centrarchidae) in Western Kentucky. Bull. Alabama Mus. Nat. Hist. 8:31-52.

West, J.L. 1970. The gonads and reproduction of three intergeneric sunfish (family Centrarchidae) hybrids. Evol. 24:378-394.

Woolcott, W.S. 1957. Comparative Osteology of Serranid fishes of the Genus Roccus (Mitchill). Copeia 1957 (1):1-10.