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Phylogenetic relationships of Gasterosteiformes (Teleostei, Percomorpha)

by

Yazdan Keivany ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of **Doctor of Philosophy**

in

Systematics and Evolution

Department of Biological Sciences

Edmonton, Alberta

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University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Phylogenetic relationships of Gasterosteiformes (Teleostei, Percomorpha)** submitted by **Yazdan Keivany** in partial fulfillment of the requirements for the degree of **Doctor of Philosophy** in **Systematics and Evolution.**

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Abstract

The phylogenetic relationships of Gasterosteiformes were studied in an osteological examination of representatives of 48 genera in 41 families of eurypterygian fishes to hypothesize their systematic relationships within Acanthopterygii. The outgroup comparison method was used for polarizing characters and cladistic methods employing MacClade 3.08 and PAUP 4.0 computer programs were used for reconstructing systematic relationships of Gasterosteiformes.

Monophyly of Acanthomorpha, Acanthopterygii, Percomorpha, and Smegmamorpha is supported. Mugiliformes and Atherinomorpha are shown to be each other closest relatives and together form a monophyletic group. This study shows that Synbranchiformes is the sister group of Gasterosteiformes and that Elassomatiformes (Elassomatidae) is the sister group of Synbranchiformes and Gasterosteiformes. To reflect the new phylogeny in a classification of Percomorpha, it is suggested that the series Percomorpha be divided into two subseries: Smegmamorphei and Percomorphei. Smegmamorphei consist of two infraseries: Atherinomorphea (Mugiliformes, Atheriniformes, Beloniformes, and Cyprinodontiformes) and Gasteromorphea (Elassomatiformes, Synbranchiformes, and Gasterosteiformes). Percomorphei consist of four orders: Perciformes, Scorpaeniformes, Pleuronectiformes, and Tetraodontiformes. Although no unique synapomorphy was found to unite all Gasterosteiformes, support was provided that Gasterosteiformes (including Hypoptychidae and Indostomidae) is a monophyletic group. Based on the phylogenetic analysis and synapomorphies provided for the subgroups, three suborders in Gasterosteiformes are recognized: Hypoptychoidei, Gasterosteoidei, and Syngnathoidei. The family Dactylopteridae is shown to be a member of Scorpaeniformes and, within the taxa examined, the sister-group of Agonidae. Although monophyly of Scorpaeniformes is supported, it is nested within Perciformes and branch support indices do not strongly support its monophyly.

This work is dedicated to

my wife and children who made it possible

by their patience, encouragement, and moral support

Acknowledgments

This research could not be conducted without the guidance, supervision and inspiration of my respectful supervisor, Dr. J.S. Nelson. I express my deepest gratitude to him for being an excellent mentor and supporter. I thank my supervisory committee, Dr. P. R. Willoughby and Dr. M.V.H. Wilson for providing helpful comments and advice during the course of this study. I also thank Dr. B. S. Heming, Dr. G. Goss, and my external examiner Dr. L. R. Parenti for their comments and advice.

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1. Introduction

Gasterosteiformes, a diverse order of fishes of uncertain relationships, is currently recognized with two suborders and 11 families (Nelson, 1994). Gasterosteoidei, with three families (Hypoptychidae, Aulorhynchidae, and Gasterosteidae), is primarily a temperate marine group ranging widely in the Northern Hemisphere in the Atlantic and Pacific oceans. The family Hypoptychidae (sand eel) is monotypic, marine, and distributed around Japanese islands. The family Aulorhynchidae (tubesnouts) consists of two monotypic genera: *Aulichthys* and *Aulorhynchus*. Both its species are marine; *Aulichthys japonicus* is found in Japanese waters and *Aulorhynchus flavidus* in the eastern North Pacific. The family Gasterosteidae (sticklebacks) consists of a marine monotypic genus (*Spinachia*) in Atlantic of northern Europe, a marine-brackishwater monotypic genus (*Apeltes*) in Atlantic coast of central North America, one monotypic freshwater genus (*Culaea*) in North America, and two anadromous-freshwater genera (*Gasterosteus* and *Pungitius*) in Atlantic and Pacific coastal areas of North America and Eurasia.

The suborder Syngnathoidei, with three infraorders (Syngnatha, Indostomoida, and Aulostomoida), is a marine group widely distributed in temperate and tropical Atlantic, Pacific, and Indian oceans. The infraorder Syngnatha consists of two superfamilies: Pegasoidea with one family (Pegasidae) and Syngnathoidea with two families (Solenostomidae and Syngnathidae). The family Pegasidae (seamoths) is heavily armored, distributed in temperate to tropical Indo-West Pacific, and consists of two genera (*Pegasus* and *Eurypegasus*). The family Solenostomidae (ghost pipefishes) is distributed in tropical Indo-West Pacific and consists of one genus (*Solenostomus*). Syngnathids (pipefishes and seahorses) are the most speciose family of the order (52 genera and 215 species (Nelson, 1994)), heavily armored, and distributed in Atlantic, Pacific, and Indian oceans. The infraorder Indostomoida consists of the family Indostomidae (nailfishes, my suggestion as a common name), with one genus (*Indostomus*) and three species. *Indostomus spp.*, are tiny, heavily armored freshwater fish found in Southeast Asia. The infraorder Aulostomoida consists of two superfamilies, each with two families: Aulostomoidea (Aulostomidae and Fistulariidae) and Centriscoidea (Macroramphosidae and Centriscidae). The family Aulostomidae (trumpetfishes) is distributed in tropical Atlantic and Indo-Pacific and consists of one genus (*Aulostomus*). The family Fistulariidae (cornetfishes) is distributed in tropical Atlantic, Indian, and Pacific and consists of one genus (*Fistularia*). The family Macroramphosidae (snipefishes) is distributed in tropical and subtropical Atlantic, Indian, and Pacific and consists of three genera (*Macroramphosus*, *Notopogon*, and *Centriscops*). The family Centriscidae (shrimpfishes) is distributed in Indo-Pacific and consists of two genera (*Centriscus* and *Aeoliscus*).

The families contained in Gasterosteiformes have been brought together at different times and even under different names, and due to morphological diversity of these families, their placement in Gasterosteiformes and their systematic relationships have been subject to much disagreement. Before Bonaparte (1839) erected the family Gasterosteidae and Goodrich (1909) the order Gasterosteiformes for sticklebacks, Linnaeus (1758), on the basis of the position of their pelvic fins, placed Gasterosteidae (*Gasterosteus*) in the order Thoracic and all Syngnathoidei but Solenostomidae in the order Abdominal. Solenostomidae (Pallas, 1770) and Aulorhynchidae (Gill, 1861) were described later.

Gill (1884), based on the structure of gills and pectoral girdle, grouped all Gasterosteiformes except Syngnathoidea and Indostomidae (which was described later) in the order Hemibranchii. Bridge and Boulenger (1904) placed Hemibranchii close to Lamprididae in the order Cateostomi and Pegasidae at the end of Cateostomi. Regan (1913) placed them with scorpaenoids in the order Scleroparei on the basis of being physoclists, having an anterior pelvic fin, fewer pelvic fin soft rays than five and the third infraorbital stay. Jungerson (1915), on the basis of skull osteology, concluded that Pegasidae were not closely related to Gasterosteiformes and treated Pegasidae as a separate order (Pegasiformes). Jordan (1923), based on the structure of the gills, divided his Thoracostei into two suborders: Hemibranchii (including Gasterosteidae and Aulorhynchidae) and Lophobranchii (Solenostomidae and Syngnathidae). He also put Pegasidae in Hypostomides and other Gasterosteiformes in Aulostomi. Prashad and Mukerji (1929) described *Indostomus paradoxus* from Southeast Asia and considered it closely related to Solenostomidae and Syngnathidae. Berg (1947) classified Gasterosteidae, Aulorhynchidae, and Indostomidae in the order Thoracostei, and other gasterosteiforms in Syngnathiformes.

Greenwood et al. (1966) divided Gasterosteiformes into three suborders: Gasterosteoidei (Aulorhynchidae, Gasterosteidae, and Indostomidae), Aulostomoidei (Aulostomoidea and Macroramphosoidea), and Solenostomoidei (Solenostomidae and Syngnathidae), and treated Pegasidae as a separate order and placed it near Scorpaeniformes. McAllister (1968), based on the structure of hyoid and branchial arches, placed Syngnathiformes with his basal Acanthopterygii, Gasterosteiformes with his higher Acanthopterygii and Pegasiformes at the end of his Acanthopterygii. He also included Indostomidae as *inserta sedis* in Gasterosteiformes. Banister (1970) removed the family Indostomidae from Gasterosteiformes and placed it as a separate order within the Paracanthopterygii. Gosline (1971) recognized Syngnathoidei and Gasterosteoidei under the ordinal name Syngnathiformes and placed it in the intermediate teleostean group on the basis of several structural changes, for example, in the upper jaw, lateral line system, circumorbital bones, and attachment of the body musculature to the head. Nelson (1971) studied Aulorhynchidae and Gasterosteidae and concluded that Aulorhynchidae and Gasterosteidae were distinct families with *Spinachia* the primitive member of Gasterosteidae.

Ida (1976) removed Hypoptychidae from Ammodytoidei (Perciformes) and placed it within Gasterosteiformes. Pietsch (1978) argued that the family Pegasidae was the ancestor (herein interpreted as the primitive sister-group) of Gasterosteiformes and placed Pegasoidei (Pegasidae plus Ramphosidae) as the sister group of Syngnathoidei (Syngnathidae plus Solenostomidae), these together forming the sister group of Gasterosteoidei, in which he included Hypoptychidae. He did not identify synapomorphies for those three groups, but defended the monophyly of his Gasterosteiformes on the basis that Pegasidae was clearly intermediate between Gasterosteoidei and the typical Syngnathoidei. Although Pietsch (1978) did not include *Indostomus* in his new classification of Gasterosteiformes, he concluded that Banister's (1970) exclusion of *Indostomus* was unjustifiable considering several specialization's shared by Pegasidae and Indostomidae. Lauder and Liem (1983) followed Pietsch (1978) in including Pegasidae in Gasterosteiformes and placed it in a trichotomy with Dactylopteriformes and higher percomorphs (Fig. 1.1).

Nelson (1984) accepted Ida's placement of Hypoptychidae but retained Gasterosteiformes, Indostomiformes, Pegasiformes, and Syngnathiformes as separate orders. Bowne (1985) treated Hypoptychidae and Indostomidae as *inserta sedis* and excluded them from Gasterosteiformes, but she considered Dactylopteridae as a close relative of Pegasidae, and regarded Gasterosteiformes as an off-shot of the Cottoidei lineage of Scorpaeniformes. She placed her Gasterosteoidei (all Gasterosteiformes and Syngnathiformes, except Hypoptychidae, Indostomidae, and Pegasidae) and Dactylopteroidei (Dactylopteridae and Pegasidae) with Cottoidei in Scorpaeniformes. She reiterated her conclusions in a recent article (Bowne, 1994). Johnson and Patterson (1993) argued that Pietsch's Gasterosteiformes was monophyletic only with inclusion of the Indostomidae in his Syngnathoidei and proposed a new hypothesis of their relationships. They proposed the name Smegmamorpha for a group consisting of Synbranchiformes, Elassomatidae, Gasterosteiformes, Mugiloidei, and Atherinomorpha (Fig. 1.2). Nelson (1994) accepted some of Pietsch's (1978) and Johnson and Patterson's (1993) views and included Indostomiformes, Pegasiformes and Syngnathiformes in Gasterosteiformes, but did not accept the Smegmamorpha assemblage and placed Gasterosteiformes in a trichotomy with Synbranchiformes and higher percomorphs (Fig. 1.3).

Orr (1995) accepted the Smegmamorpha assemblage, but considered the word

Smegma offensive and replaced it with Gasteromorpha and disputed the placement of Hypoptychidae and Indostomidae within the Gasterosteiformes. He believed that Hypoptychidae was related to Atherinomorpha and considered Indostomidae as *inserta sedis*. Parenti and Song (1996), based on the pectoral-pelvic fin innervation pattern, found no evidence to reject a relationship between Gasterosteiformes and Atherinomorpha, but no synapomorphy for Smegmamorpha. Recently, Johnson and Springer (1997) proposed Elassomatidae as the possible sister group of Gasterosteiformes. Jones and Quattro (1999), using mitochondrial DNA sequences, found close relationships between Elassomatidae, Centrarchidae, and Pomacentridae. However, the systematic relationships of Gasterosteiformes are still unclear. Johnson (1993), Johnson and Patterson (1993), Bowne (1994), and Orr (1995) reviewed the systematic problems in Gasterosteiformes and other acanthomorphs.

The main objective of this study is to test the recent hypotheses of relationships of Gasterosteiformes and present my own hypothesis. My three subobjectives are to study the interrelationships of Gasterosteiformes *sensu* Nelson (1994), systematic position of Dactylopteridae (which is thought to be related to syngnathoids by Pietsch (1978)), and the evolution of phylogenetically significant osteological characters in Gasterosteiformes and related taxa. I use osteology to study the systematics of this group, emphasizing osteology of the visceral, opercular, pectoral, pelvic, and caudal skeletons, using the extensive literature on this group and my own work.

This work is organized into eleven sections, including this introduction, methods and materials, and literature cited. In sections three to eight, osteology of jaws, suspensorium and opercular series, hyoid and branchial arches, pectoral, pelvic, and caudal skeletons of Eurypterygii is presented, respectively, and variation in characters where noted in the cited literature is given. References made to other works are mostly based on their figures and tables, but I give my own descriptions and interpretations. Each section consists of a brief introduction followed by a description of osteology of the families. The aims of these sections are to describe and illustrate the variable and phylogenetically significant features of the taxa at higher levels. The systematic conclusion is not anticipated in these sections and classification of the taxa follows that of Nelson (1994). In section nine, phylogenetic relationships of Gasterosteiformes and related taxa are analyzed based on the information presented in the previous sections and available literature. In section ten, distribution and homology of characters and monophyly and phylogeny of the taxa are discussed.

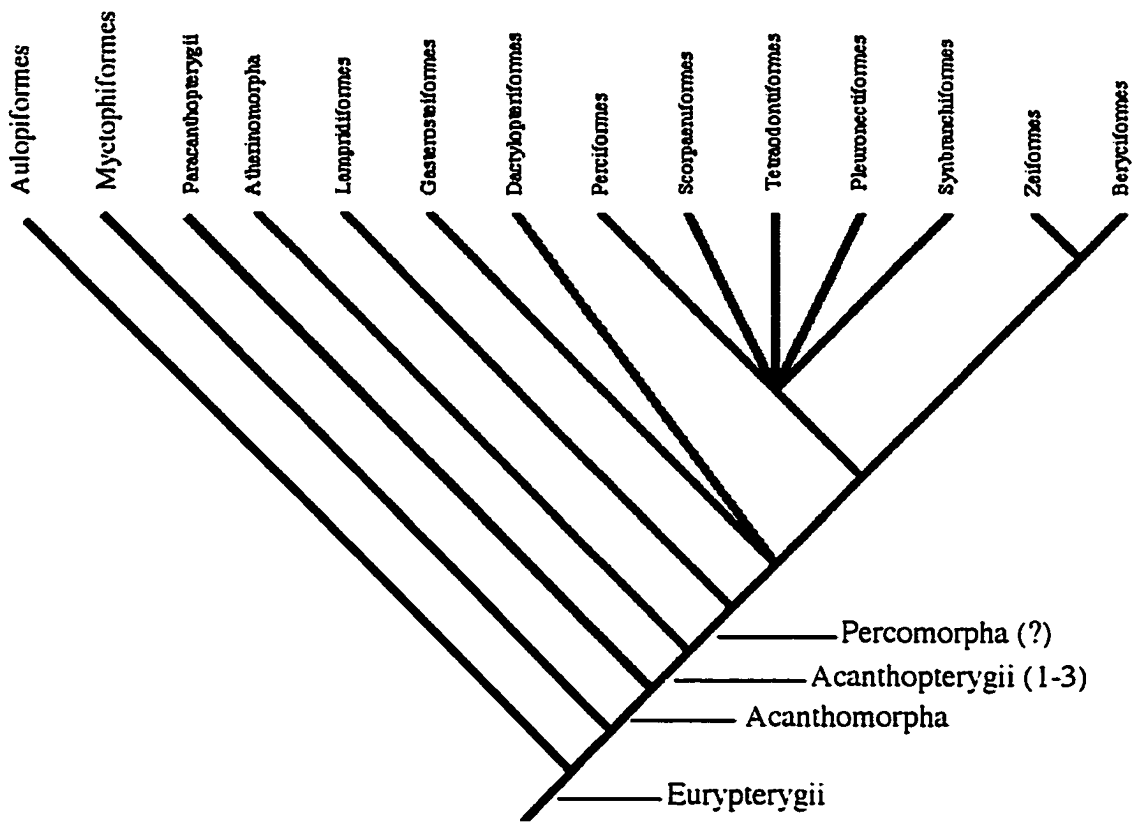

Fig. 1.1. Lauder and Liem's (1983) view on phylogenetic relationships of Eurypterygii.

1. Presence of an interarcual cartilage between the first and second pharyngobranchials.
2. Retractor dorsalis inserts primarily or entirely on the third pharyngobranchial.
3. Symphyseal and alveolar parts of the premaxilla are capable of significant downward and forward displacement.

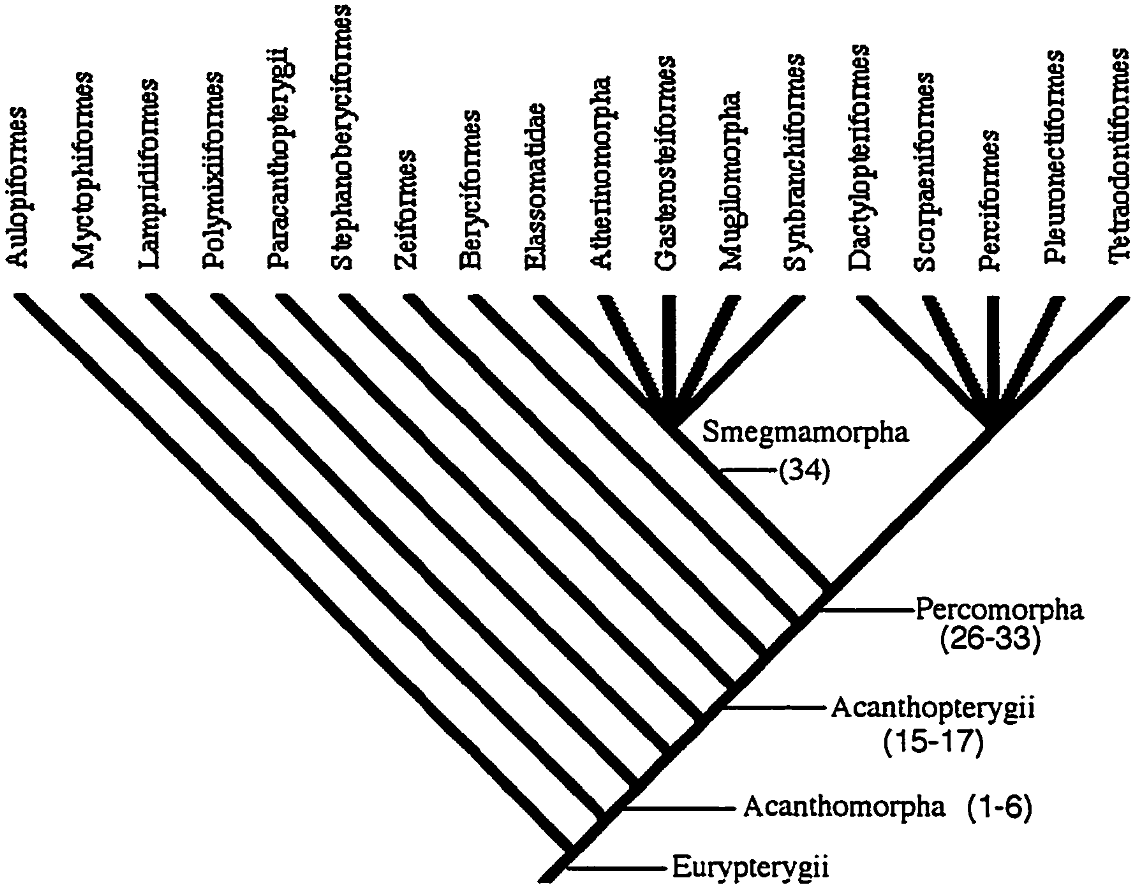

Fig. 1.2. Johnson and Patterson's (1993) view on phylogenetic relationships of Eurypterygii.

1. True dorsal and anal fin spines present.
2. Rostral cartilage present.
3. Medial caudal cartilage absent.
4. Anterior and medial infracarinales separate.
5. Dorsal limb of posttemporal firmly bounds to epioccipital.
6. Medial pelvic process ossified distally.

15. Pelvic spines present.
16. Free pelvic radials reduced in size and/or number.
17. Pelvic anteromedial process present.

26. Rod-like interarcual cartilage present.
27. Second ural centrum absent.
28. Five or fewer hypurals.
29. Fewer than six pelvic soft rays.
30. Transforming ctenoid scales present.
31. Free pelvic radials lost.
32. Points of origin of all but the first two epineurals displaced ventrally and the distal parts of all epineurals displaced ventrally into the horizontal septum.
33. Seventeen principal caudal fin rays in I,8,7,I pattern.
34. First epineural originates on the parapophysis or the lateral surface of the centrum.

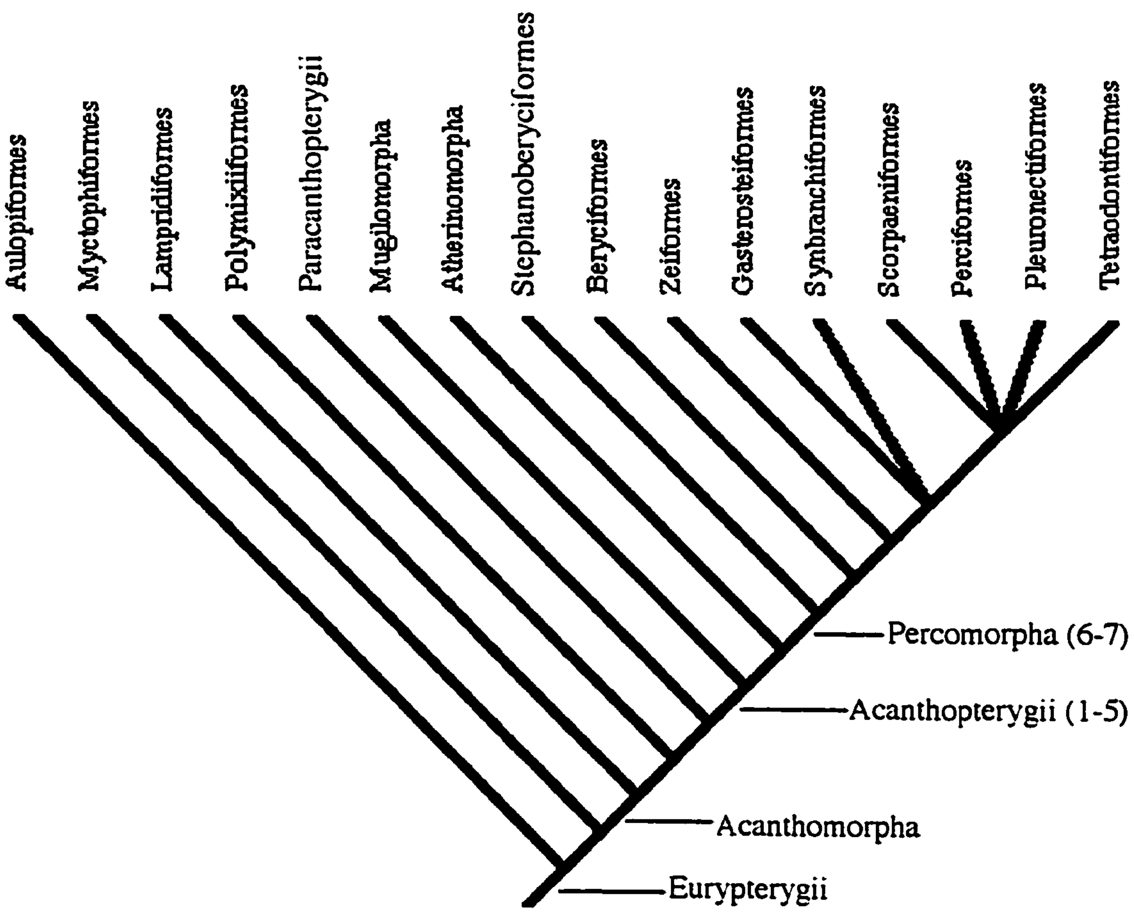

Fig. 1.3. Nelson's (1994) view on phylogenetic relationships of Eurypterygii.

1. Retractor dorsalis inserted on the third pharyngobranchial.
2. Articular surface of the fourth epibranchial reduced.
3. The second and third epibranchials enlarged as the principal support of the upper pharyngeal dentition.
4. A well developed ascending process present.
5. Baudelot's ligament originates on the basioccipital.

6. Pelvic girdle directly or ligamentously attached to the cleithrum or coracoid.
7. Anteromedial pelvic process displaced ventrally.

2. Methods and Materials

Methods

I prepared representatives of the taxa for dissection following Taylor and Van Dyke's (1985) method for clearing and staining bone and cartilage. A camera lucida attached to a Wild M5 dissecting microscope was used to prepare the drawings. The bones in the first figure of each anatomical section are arbitrarily shaded and labeled and in the others are shaded in a consistent manner (dark, medium, and clear) to facilitate comparison among the taxa. Forty nine genera representing 41 families (11 being Gasterosteiformes) were studied. The number of genera studied in each order is: Aulopiformes (1), Myctophiformes (1), Lampridiformes (2), Polymixiiformes (1), Percopsiformes (1), Mugiliformes (1), Atheriniformes (2), Beloniformes (2), Cyprinodontiformes (2), Stephanoberyciformes (2), Beryciformes (2), Zeiformes (2), Gasterosteiformes (18) Synbranchiformes (2), Scorpaeniformes (including Dactylopteridae) (5), and Perciformes (including Elassomatidae) (5).

Using cladistic (Hennig, 1966; Forey et al., 1992), parsimony, and outgroup comparison methods (Watrous and Wheeler, 1981; Maddison et al., 1984) for reconstructing phylogenetic relationships, I entered the osteological characters in MacClade 3.08a (Maddison and Maddison, 1992) and analyzed them in PAUP 4.0b4a (Swofford, 2000) and Winclada 0.9 (Nixon, 1999b) computer programs. All the characters were weighted equally and treated as unordered. Inapplicable data were coded as missing "?" as suggested by Strong and Lipscomb (1999). Many characters have more than one equally parsimonious reconstruction and the accelerated transformation (ACCTRAN) option of PAUP was used to optimize ambiguous characters. This method favors reversals over parallel acquisition of character states when both are equally parsimonious (Maddison and Maddison, 1992). Exhaustive and branch-and-bound search methods of PAUP, which yield the most possible parsimonious trees, were not usable in this analysis and heuristic search was used instead (closest addition sequence; TBR swapping algorithm). Different options of the heuristic search of PAUP (addition sequence: simple, closest, as is, random; swapping algorithm: no swapping, NNI, SPR, TBR) were tried, but they did not produce a shorter tree. The parsimony ratchet (Nixon, 1999a) was used as an alternate fast searching method in Winclada. Bootstrap (Felsenstein, 1985) and decay analysis (Bremer, 1988; Bremer, 1994) were used for estimating tree support. The AutoDecay computer program (Eriksson, 1998) was employed to calculate the decay values. However, the decay values are approximate, because PAUP and AutoDecay cannot do exhaustive or branch-and bound searches. The ingroup consists of the 11 families of Gasterosteiformes, the primary outgroups consist of all other acanthopterygians, and the secondary outgroups members of Percopsiformes, Polymixiiformes, Lampridiformes, Myctophiformes and Aulopiformes. The trees were rooted on Aulopiformes, which is considered the basal Eurypterygii by many authors (e.g., Johnson and Patterson (1993); Nelson (1994)).

Materials

Most of the specimens were obtained from the University of Alberta Museum of Zoology (UAMZ). Some were obtained from the Smithsonian Institution (United States National Museum) (USNM), California Academy of Sciences (CAS), and Australian Museum at Sydney (AMS). Numbers in parentheses indicate the standard length in millimeters of specimens; those in bold are specimens used for figuring osteology of the taxa.

Aulopiformes

Synodontidae (lizardfishes)

Synodus synodus UAMZ 1806 (**147**).

Synodus intermedius UAMZ 4889 (**78**).

Myctophiformes

Myctophidae (lanternfishes)

Myctophum sp. UAMZ 2689 (**60**, 77, 80).

Lampridiformes

Veliferidae

Velifer hypselopterus AMS 21839005 (**101**, 115).

Trachipteridae (ribbonfishes)

Trachipterus altivelis CAS 24297 (**85**), CAS 51177 (105).

Polymixiiformes

Polymixiidae (beardfishes)

Polymixia lowei USNM 159300 (81, **115**).

Percopsiformes

Percopsidae (trout-perches)

Percopsis omiscomaycus UAMZ 2048 (17, 19, 27, **55**, 60).

Mugiliformes

Mugilidae (mullets)

Mugil sp. UAMZ 5125 (55, 63, 63, **66**, 91).

Atheriniformes

Melanotaeniidae (rainbowfishes)

Melanotaenia sp. UAMZ 3526 (40, 42, **51**).

Atherinidae (silversides)

Allanetta harringtonensis UAMZ 2673 (47, **58**, 59, 60, 61).

Beloniformes

Belonidae (needlefishes)

Pseudotylosurus sp. UAMZ 8165 (**173**).

Hemiramphidae (halfbeaks)

Arrahamphus sclerolepis UAMZ 3523 (**103**).

Cyprinodontiformes

Aplocheilidae (rivulines)

Rivulus hartii UAMZ 6660 (44, **47**).

Cyprinodontidae (pupfishes)

Cyprinodon nevadensis UAMZ 3114 (24, **34**, 41).

Stephanoberyciformes

Stephanoberycidae (pricklefishes)

Stephanoberyx monae USNM 304353 (85, **92**).

Rondeletiidae (redmouth whalefishes)

Rondeletia loricata AMS 21141001 (88), AMS 20523001 (34, **37**), AMS 18813001 (53).

Beryciformes

Monocentridae (pinecone fishes)

Monocentris sp. UAMZ 7854 (**92**).

Holocentridae (squirrelfishes)

Sargocentron vexillarium UAMZ 5075 (34, 34, 40, **44**, 84).

Zeiformes

Grammicolepididae

Xenolepidichthys dalgleishi USNM 322673 (**68**, 75).

Caproidae (boarfishes)

Antigonia sp. USNM 266901 (**37**, 41).

Gasterosteiformes

Hypoptychidae (sand eel)

Hypoptychus dybowskii UAMZ 5550 (75, **80**, 81).

Aulorhynchidae (tubesnouts)

Aulorhynchus flavidus: UAMZ 3783 (104, 105, **109**).

Aulichthys japonicus UAMZ 5542 (**47**,48).

Gasterosteidae (sticklebacks)

Spinachia spinachia UAMZ 6582 (25, **53**, 55).

Apeltes quadracus UAMZ 7958 (34, **37**, 39).

Gasterosteus aculeatus UAMZ 3894 (32, 57, 58, **58**, 73, 77, 83).

Culaea inconstans UAMZ 3797 (21, 30, 49, 56, **57**, 58, 60).

Pungitius pungitius UAMZ 3049 (39, 43, **46**, 55).

Pegasidae (seamoths)

Pegasus volans UAMZ 4616 (**99**, 104).

Solenostomidae (ghost pipefishes)

Solenostomus paradoxus AMS 17111002 (**51**), AMS 17160002 (50), AMS 18852002 (52), AMS 18314001 (59).

Syngnathidae (pipefishes and seahorses)

Syngnathus scovelli UAMZ 3782 (**117**).

Syngnathus griseolineatus UAMZ 3469 (225, 240, **272**).

Hippocampus ingens UAMZ 3594 (170).

Indostomidae (nailfishes)

Indostomus paradoxus UAMZ 6700, CAS 64017 (23, 23, 24, **25**).

Aulostomidae (trumpetfishes)

Aulostomus valentini CAS 11979 (**139**).

Aulostomus sp. CAS 145550 (109, 125).

Aulostomus maculatus CAS 145176 (213), CAS 145549 (171).

Fistulariidae (cornetfishes)

Fistularia petimba UAMZ 6348 (125, **158**, 171).

Macroramphosidae (snipefishes)

Macroramphosus scolopax USNM 344398 (94, 99, **99**, 100).

Centriscidae (shrimpfishes)

Centriscus scutatus UAMZ 3480 (94, 107).

Aeoliscus strigatus UAMZ 4048 (79, **89**).

Synbranchiformes

Synbranchidae (swamp-eels)

Monopterus albus USNM 192939 (**193**, 245).

Mastacembelidae (spiny eels)

Macrognathus aculeatus UAMZ 1625 (120), UAMZ 1855 (**119**).

Scorpaeniformes

Dactylopteridae (flying gurnards)

Dactylopterus volitans UAMZ 2633 (61, **74**).

Dactyloptena sp. UAMZ 7519 (65).

Scorpaenidae (rockfishes)

Sebastes caurinus UAMZ 3142 (71, **75**).

Hexagrammidae (greenling)

Hexagrammos decagrammus UAMZ 3190 (47, **50**).

Agonidae (poachers)

Xeneretmus latifrons UAMZ 3196 (90, **95**, 143).

Perciformes

Percidae (perches)

Perca flavescens UAMZ 1244 (50, 51, 52, **54**, 55).

Cirrhitidae (hawkfishes)

Amblycirrhitus pinos UAMZ 3640 (24, 25, 26, **45**, 61).

Elassomatidae (pygmy sunfishes)

Elassoma zonatum UAMZ 6920 (26, 29, **30**).

Pomacentridae (damselfishes)

Stegastes partitus UAMZ 3640 (12,12, 13, 14, 25, **34**, 47).

Centrarchidae (sunfishes)

Lepomis gibbosus UAMZ 7715.4 (23, 24, 25, 31, **40**).

3. Osteology of the jaws in Eurypterygii

The upper jaw consists of the premaxilla, maxilla, and supramaxilla. The lower jaw consists of the dentary, anguloarticular, retroarticular, and sesamoid articular. In higher taxa, the premaxilla bears ascending, articular, and postmaxillary processes. The maxilla usually bears a ventral and a dorsal articular process. The supramaxilla is present only in some taxa. The dentary is usually toothed and bears coronoid and posteroventral processes. The retroarticular is small and located at the posteroventral corner of the anguloarticular. I follow the terminology of Rojo (1991) for the jaw skeleton, except that I use the term anguloarticular for the angular. In atherinomorphs, what is called the ascending process of premaxilla might be homologous to the articular process of other acanthomorphs, because the ascending process in other acanthomorphs is usually long, thin, pointed, and the rostral cartilage is tightly attached to it. In atherinomorphs the ascending process of the premaxilla is short, thick, round or blunt, like the articular process of other acanthomorphs, and the rostral cartilage is separate from the process. Mugiliformes have the same upper jaw configuration as atherinomorphs, except that the rostral cartilage is attached to the premaxilla.

Aulopiformes

Synodontidae (Fig. 3.1). The premaxilla is toothed and lacks the ascending and postmaxillary processes, but a small knob-like articular process is present. The maxilla is narrow, excluded from the gape by premaxilla, and lacks the articular processes. The dentary is toothed, triangular, well developed, and with a long coronoid process. The anguloarticular is bifurcated anteriorly and the dorsal fork is inserted into the dentary. In *Saurida* (Johnson et al., 1996) and *Bathysaurus* (Baldwin and Johnson, 1996), a small supramaxilla is present. In *Pseudotrichonotus*, the ascending and articular processes of the premaxilla, and the articular and posterior processes of the maxilla are present (Johnson et al., 1996).

Myctophiformes

Myctophidae. The premaxilla bears tiny teeth and small bud-like ascending and articular processes. The maxilla is narrow, excluded from the gape by premaxilla, and bears small ventral and dorsal articular processes. The dentary is thinner anteriorly and bears tiny teeth and equal coronoid and posteroventral processes. The anguloarticular is not bifurcated anteriorly.

Lampridiformes

Veliferidae (Fig. 3.2). The premaxilla is toothless and bears well developed ascending and articular processes. The maxilla is broad, not fully excluded from the gape, and bears well developed ventral, dorsal, and posterior articular processes. The dentary is toothless and bears a long posteroventral process. The anguloarticular is not bifurcated anteriorly.

Polymixiiformes

Polymixiidae (Fig. 3.3). The premaxilla bears tiny teeth and short ascending and articular processes. The maxilla is broad and hook-shaped distally, not excluded from the gape, and bears small ventral and dorsal articular processes. One large and one small supramaxilla are present on the dorsal margin of maxilla. The dentary bears tiny teeth and equal coronoid and posteroventral processes. The anguloarticular is not bifurcated anteriorly.

Percopsiformes

Percopsidae. The premaxilla is toothed and bears an ascending process. The maxilla is narrow, bears ventral and posterior articular processes, a posterior process, and contributes to the gape. The dentary is toothed, highly deep posteriorly, and bears small coronoid and posteroventral processes. The anguloarticular is bifurcated and weakly articulated with the dentary.

Mugiliformes

Mugilidae (Fig 3.4). The premaxilla is toothed and bears the articular and postmaxillary processes and a small caudad process. The maxilla is narrow, not fully excluded from the gape, and bears ventral and dorsal articular processes. The dentary is toothed and its posteroventral process is much longer than the coronoid process. The anguloarticular is not bifurcated and is weakly articulated with the dentary.

Atheriniformes

Melanotaeniidae (Fig. 3.5). The premaxilla is toothed and bears the articular and postmaxillary processes. The maxilla is narrow, not fully excluded from the gape, and bears ventral and dorsal articular processes and a posterior process. The dentary is toothed and bears equal coronoid and posteroventral processes. The anguloarticular is not bifurcated and is weakly articulated with the dentary.

Atherinidae. The premaxilla is toothed and bears the articular and postmaxillary processes. The maxilla is narrow, not fully excluded from the gape, and bears ventral and dorsal articular processes. The dentary is toothed and with equal coronoid and posteroventral processes. The anguloarticular is not bifurcated and is weakly articulated with the dentary.

Beloniformes

Belonidae (Fig. 3.6). The premaxilla is elongated, toothed, fused to its counterpart along most of its length, and bears no processes, but is expanded posteriorly. The maxilla is sutured to the premaxilla. The dentary is toothed and with a longer posteroventral process. The anguloarticular is not bifurcated and is tightly articulated with the dentary.

Hemiramphidae (Fig. 3.7). The premaxilla bears tiny teeth and a triangular articular process. The maxilla is narrow, not excluded from the gape, and bears a long ventral articular process and a dorsal articular process. The dentary is toothed and with a longer posteroventral process. The anguloarticular is not bifurcated and is tightly articulated with the dentary.

Cyprinodontiformes

Aplocheilidae (Fig 3.8). The premaxilla is toothed and bears the articular, postmaxillary, and caudad processes. The maxilla is narrow, not excluded from the gape, and bears ventral and dorsal articular processes. The dentary is toothed and with a longer coronoid process. The anguloarticular is bifurcated and weakly articulated with the dentary.

Cyprinodontidae (Fig 3.9). The premaxilla is sinusoid, with weakly attached teeth, and bears the articular and caudad processes. The maxilla is narrow, not excluded from the gape, and bears ventral and dorsal articular processes. The dentary is toothed, short and deep, and bears a short coronoid and posteroventral processes. The anguloarticular is slightly bifurcated and weakly articulated with the dentary.

Stephanoberyciformes

Stephanoberycidae (Fig. 3.10). The premaxilla bears tiny teeth and a short ascending, small articular, and deep postmaxillary process. The maxilla is broad posteriorly, not excluded from the gape, and bears ventral and dorsal articular processes. A broad supramaxilla is present. The dentary is toothed and bears a slightly longer coronoid process. The anguloarticular is not bifurcated and is weakly articulated with the dentary.

Rondeletiidae. The premaxilla bears very tiny teeth and a small bud-like articular process. The maxilla is broader posteriorly, not excluded from the gape, and bears short ventral and dorsal articular processes and a posterior process. A relatively large supramaxilla is present. The anguloarticular is highly incorporated into the dentary and hardly distinguishable from that.

Beryciformes

Monocentridae (Fig. 3.11). The premaxilla bears very tiny teeth and the ascending, articular, and postmaxillary processes. The maxilla is broader posteriorly and bears short ventral, dorsal, and posterior articular processes and a small posterior process. A large supramaxilla is present. The anguloarticular is not bifurcated anteriorly.

Holocentridae. The premaxilla is toothed and bears the ascending, articular, and postmaxillary processes. The maxilla is broad posteriorly, much longer than the premaxilla, and bears ventral and elongated dorsal and posterior articular processes. A large and a small supramaxilla are present. The dentary bears a longer coronoid process. The anguloarticular is not bifurcated anteriorly.

Zeiformes

Grammicolepididae (Fig. 3.12). The premaxilla is short, bears tiny teeth and a long ascending, an articular, and a posterior process. The maxilla is broad, longer than the premaxilla and bears a ventral and an enlarged dorsal and a posterior process. The dentary is triangular, toothed, and not distinctly bifurcated. The anguloarticular is not bifurcated and is fully inserted in the dentary.

Caproidae. The premaxilla is short, toothed proximally, and bears the ascending, articular, and postmaxillary processes. The maxilla is broad and bears the ventral and dorsal articular and posterior processes. The dentary bears a longer posteroventral process. The anguloarticular is not bifurcated and is fully coupled with the dentary. In *Capros aper*, the articular process of the premaxilla is not distinct (Rosen, 1984).

Gasterosteiformes

Hypoptychidae (Fig. 3.13). The premaxilla is toothed in males, but toothless in females, and bears a long cylindrical ascending and a postmaxillary process. The maxilla is longer than the premaxilla and bears the ventral and dorsal articular processes. The anguloarticular is not bifurcated and is fully inserted in the dentary.

Aulorhynchidae (Fig. 3.14). The premaxilla is well developed and toothed in males, but toothless or poorly toothed in females (Orr, 1995), and bears a long, strong, and pointed ascending process. The postmaxillary process of the premaxilla is present in *Aulichthys japonicus*, but absent in *Aulorhynchus flavidus*. The maxilla is longer than the premaxilla and bears the ventral and dorsal articular processes. The anguloarticular is not bifurcated and is fully inserted in the dentary.

Gasterosteidae (Fig 3.15). The premaxilla is toothed and bears a long and strong ascending process. In the ascending process of juveniles there is a line that might indicate the fusion of the articular and ascending processes, but there is no distinct articular process. The maxilla bears the ventral and dorsal articular processes. The anguloarticular is not bifurcated and is fully inserted in the dentary.

Pegasidae (Fig. 3.16). The terminology for the unusual jaws of Pegasidae follows that of Pietsch (1978). The premaxilla is toothless and bears a small articular process that connects it to the maxilla by a ligamental ossification. The maxilla is triradiate and its posterior process connected to the vomer by the ossified maxillovomerine cartilage and is longer than premaxilla. The dentary is not bifurcated posteriorly, the coronoid process is not distinct, the posteroventral process is long, and the symphyseal process is well developed. The anguloarticular is not bifurcated, but bears a large coronoid process and is tightly connected to the dentary. The retroarticular is relatively large.

Solenostomidae (Fig. 3.17). The premaxilla is toothless and bears a small articular process. The maxilla is much broader posteriorly, longer than the premaxilla, and bears small ventral and dorsal articular processes. The dentary is trifurcated posteriorly. The anguloarticular is bifurcated and tightly connected to the dentary.

Syngnathidae. The premaxilla is toothless and bears a small articular process. The maxilla is broad, longer than the premaxilla, and bears a small articular process. The dentary is broader posteriorly. The anguloarticular is not bifurcated and is tightly connected to the dentary.

Indostomidae (Fig. 3.18). The premaxilla is toothed and bears no distinct processes. The maxilla is thread-like and broader posteriorly, shorter than the premaxilla, not reaching the midline, and with a tiny ventral articular process. The dentary bears a longer posteroventral process. The anguloarticular is not bifurcated anteriorly.

Aulostomidae. The premaxilla is toothless and poorly developed and bears a small articular process. The maxilla is broader distally and bears small dorsal and ventral articular processes. The anguloarticular is bifurcated and tightly connected to the dentary and bears a posterocoronoid process.

Fistulariidae (Fig. 3.19). The premaxilla is toothed and poorly developed and bears small articular and postmaxillary processes. The maxilla is broad, much longer than the premaxilla, and bears small dorsal and ventral articular processes. The dentary is trifurcated posteriorly. The anguloarticular is bifurcated and tightly connected to the dentary.

Macroramphosidae (Fig 3.20). The premaxilla is toothless, poorly developed, and bears a small articular process. The maxilla is broad, longer than the premaxilla, and bears small articular processes. The dentary is deep and bears a well developed coronoid process. The anguloarticular is bifurcated and tightly connected to the dentary and bears a posterocoronoid process.

Centriscidae. The premaxilla is toothless and poorly developed and bears a small articular process. The maxilla is broad, longer than the premaxilla, and bears no distinct processes. The dentary bears an upright coronoid and a posteroventral process. The anguloarticular is upright, not bifurcated and is tightly connected to the dentary.

Synbranchiformes

Synbranchidae. The premaxilla is toothed, narrow, and bears only a small articular process. The maxilla is broader posteriorly, longer than the premaxilla, and bears no processes. The anguloarticular is not bifurcated, but fully coupled with the dentary.

Mastacembelidae (Fig. 3.21). The premaxilla is toothed but poorly developed and bears no processes. The maxilla is broader and hook shaped posteriorly, much shorter than the premaxilla, and bears no processes. The anguloarticular is not bifurcated and not fully coupled with the dentary.

Scorpaeniformes

Dactylopteridae (Fig. 3.22). The premaxilla is toothed and bears long ascending and articular processes. The maxilla is much longer than premaxilla and bears the ventral and dorsal articular processes. The coronoid and posteroventral processes of the dentary are widely separated from each other. The anguloarticular is not bifurcated anteriorly and does not bear a distinct coronoid process.

Scorpaenidae. The premaxilla is toothed and bears the ascending, articular, and postmaxillary processes. The maxilla is broader posteriorly, longer than the premaxilla, and bears the ventral and dorsal articular processes. The anguloarticular is not bifurcated and not fully coupled with the dentary.

Hexagrammidae. The premaxilla is toothed and bears the ascending, articular, and postmaxillary processes. The maxilla is broader posteriorly, much longer than the premaxilla, and bears ventral and dorsal articular processes. The anguloarticular is not bifurcated and not fully coupled with the dentary.

Agonidae (Fig. 3.23). The premaxilla is toothed and bears a short ascending and a well developed articular process. The maxilla is broader posteriorly, much longer than the premaxilla, and bears ventral and dorsal articular processes. The anguloarticular is not bifurcated and not fully coupled with the dentary and bears a large tube.

Perciformes

Percidae. The premaxilla is toothed and bears a small ascending, an articular, and a postmaxillary process. The maxilla is broader posteriorly, much longer than the premaxilla, and bears ventral and dorsal articular processes. The anguloarticular is not bifurcated and not fully coupled with the dentary.

Cirrhitidae. The premaxilla is toothed and bears the ascending, articular, and postmaxillary processes. The maxilla is broader posteriorly, longer than the premaxilla, and bears the ventral and dorsal articular processes and a posterior process. The anguloarticular is not bifurcated and not fully coupled with the dentary.

Elassomatidae (Fig. 3.24). The premaxilla is toothed and bears the ascending and articular processes. The maxilla is broader posteriorly, longer than the premaxilla and bears the ventral and dorsal articular processes and a posterior process. The anguloarticular is bifurcated but not fully coupled with the dentary.

Pomacentridae. The premaxilla is toothed and bears the ascending, articular, and postmaxillary processes. The maxilla is broader posteriorly and bears the ventral and dorsal articular processes and a posterior process. The dentary bears a longer posteroventral process. The anguloarticular is large and forms most of the ventral jaw, is not bifurcated and not fully coupled with the dentary.

Centrarchidae. The premaxilla is toothed and bears a long ascending, an articular, and a postmaxillary process. The maxilla is broad posteriorly, longer than the premaxilla, and bears ventral and dorsal articular processes and a posterior process. The anguloarticular is bifurcated anteriorly and not fully coupled with the dentary.

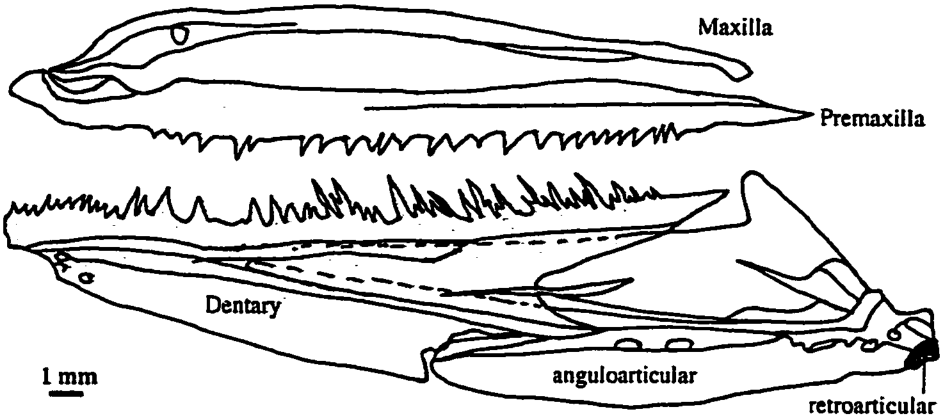

Fig. 3.1. Lateral view of the jaws in *Synodus synodus* (**Synodontidae**) (UAMZ 1806, 147 mm).

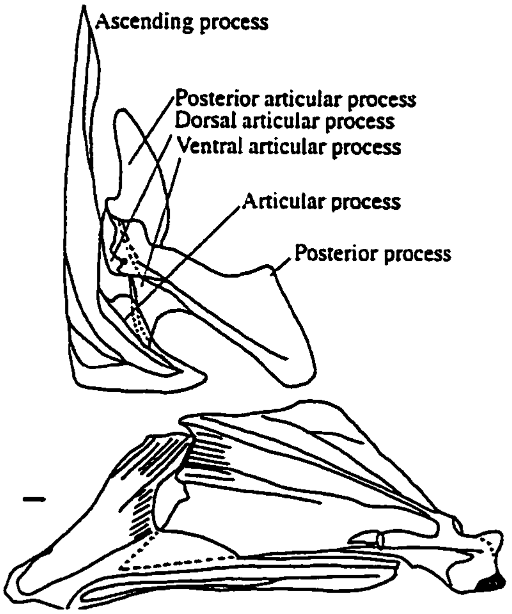

Fig. 3.2. Lateral view of the jaws in *Velifer hypselopterus* (**Veliferidae**) (AMS 21839005, 101 mm).

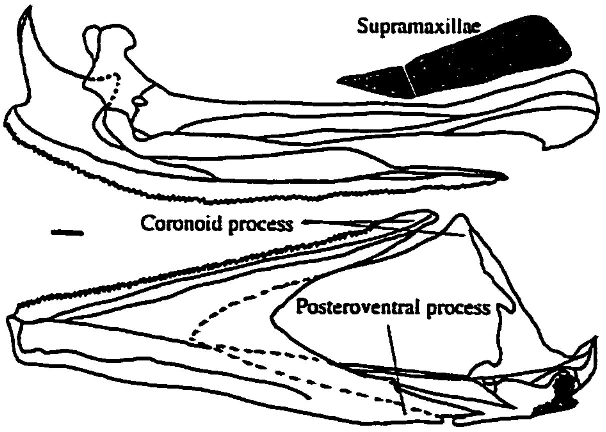

Fig. 3.3. Lateral view of the jaws in *Polymixia lowei* (**Polymixiidae**) (USNM 159300, 115 mm).

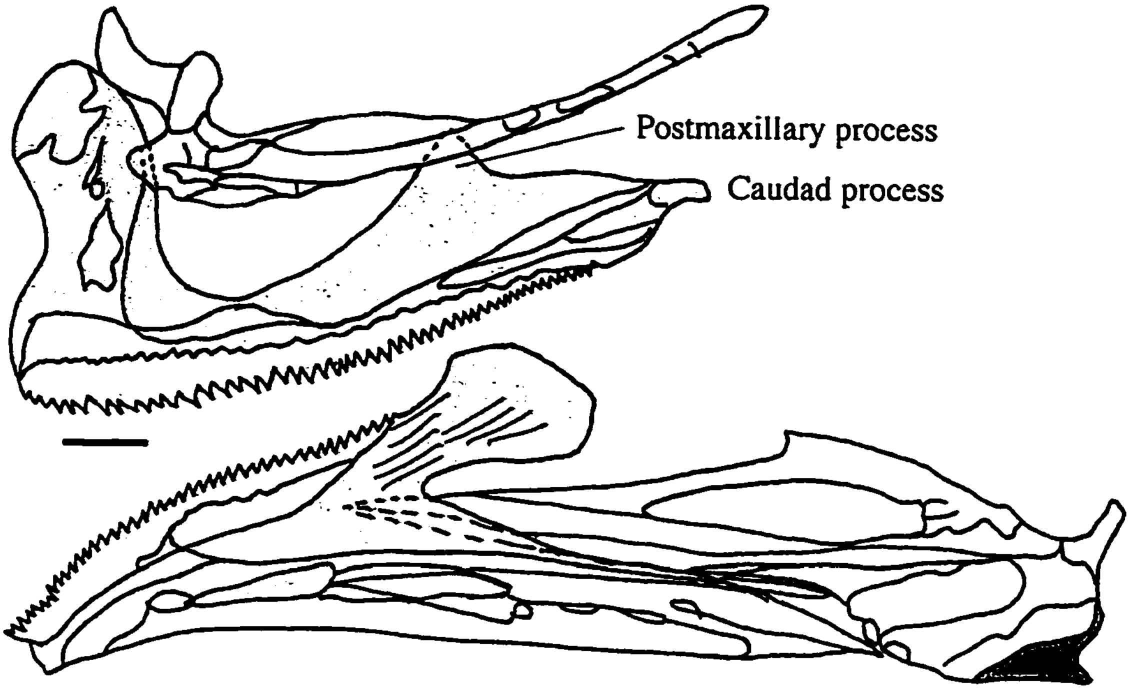

Fig. 3.4. Lateral view of the jaws in *Mugil sp.* **(Mugilidae)** (UAMZ 5125, 66 mm).

Fig. 3.5. Lateral view of the jaws in *Melanotaenia sp.* **(Melanotaeniidae)** (UAMZ 3526, 51 mm).

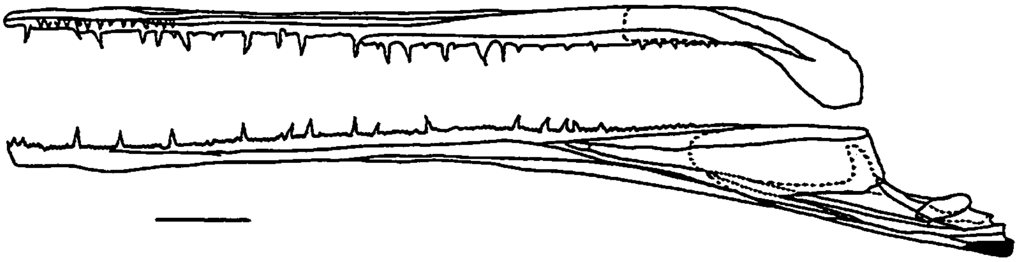

Fig. 3.6. Lateral view of the jaws in *Pseudotylosurus sp.* **(Belonidae)** (UAMZ 8165, 173 mm).

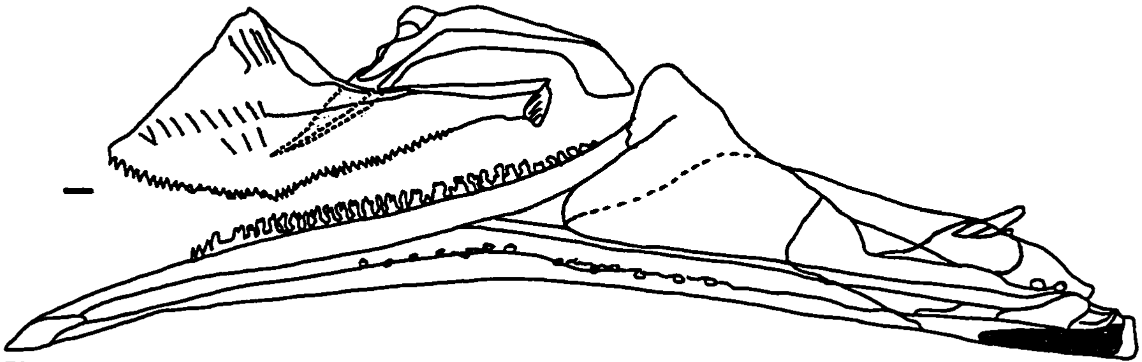

Fig. 3.7. Lateral view of the jaws in *Arrhamphus sclerolepis* (**Hemiramphidae**) (UAMZ 3523, 103 mm).

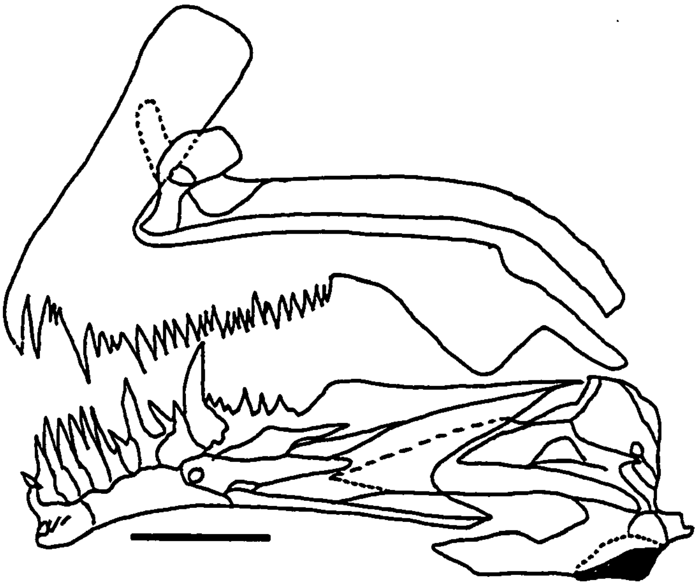

Fig. 3.8. Lateral view of the jaws in *Rivulus hartii* (**Aplocheilidae**) (UAMZ 6660, 47 mm).

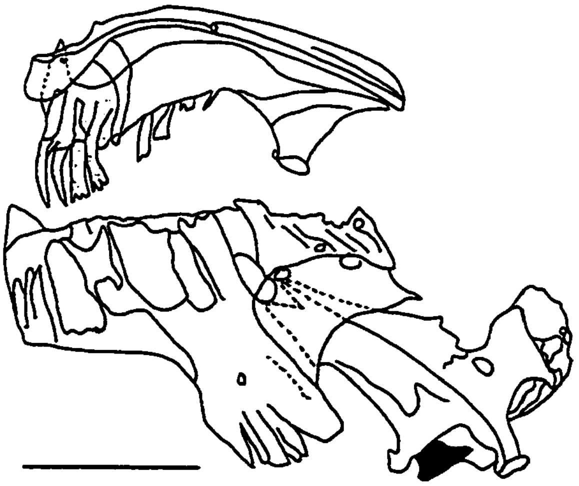

Fig. 3.9. Lateral view of the jaws in *Cyprinodon nevadensis* (**Cyprinodontidae**) (UAMZ 3114, 34 mm).

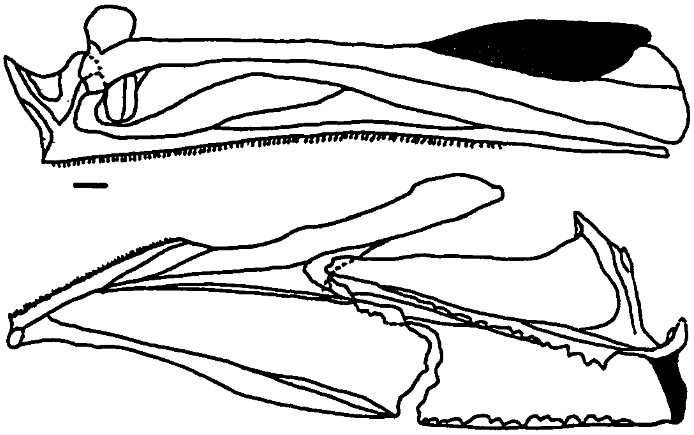

Fig. 3.10. Lateral view of the jaws in *Stephanoberyx monae* **(Stephanoberycidae)** (USNM 304353, 92 mm).

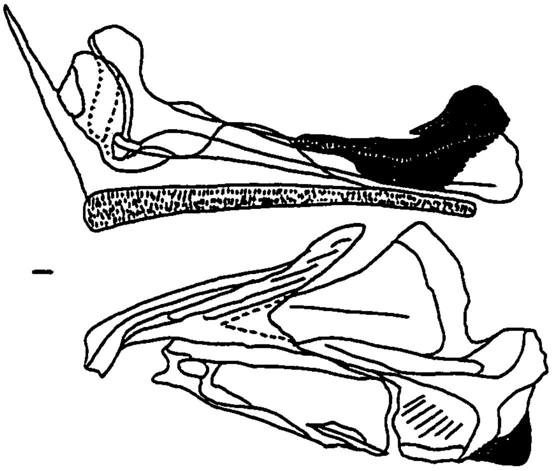

Fig. 3.11. Lateral view of the jaws in *Monocentris sp.* **(Monocentridae)** (UAMZ 7854, 92 mm).

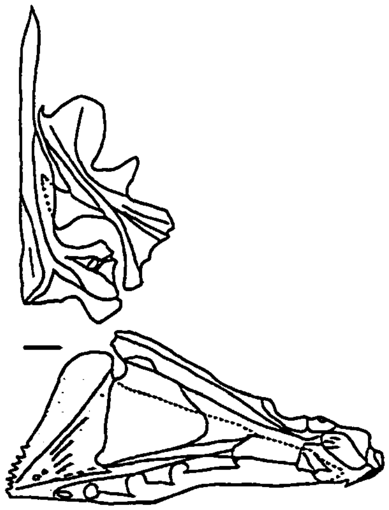

Fig. 3.12. Lateral view of the jaws in *Xenolepidichthys dalgleishi* **(Grammicolepididae)** (USNM 322673, 68 mm).

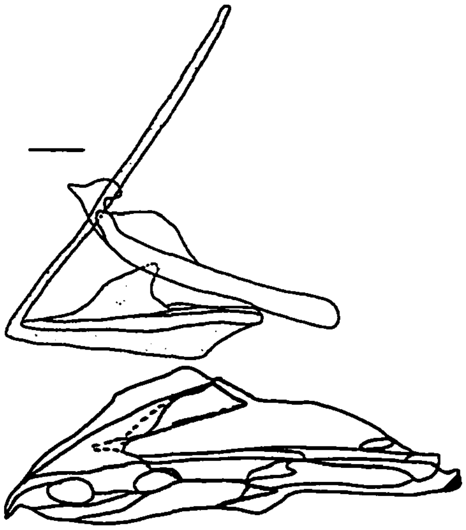

Fig. 3.13. Lateral view of the jaws in *Hypoptychus dybowskii* **(Hypoptychidae)** (UAMZ 5550, 80 mm).

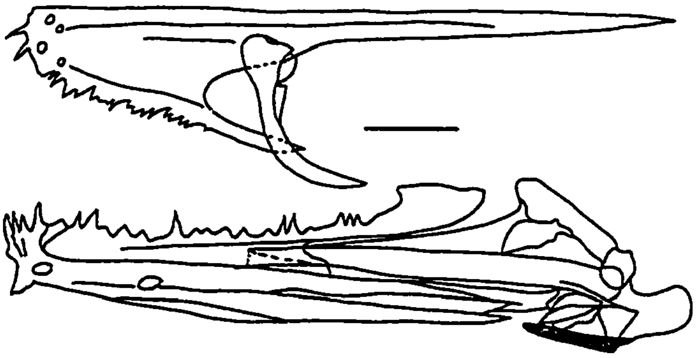

Fig. 3.14. Dorsal view of the upper jaw and lateral view of the lower jaw in *Aulorhynchus flavidus* **(Aulorhynchidae)** (UAMZ 3783, 109 mm).

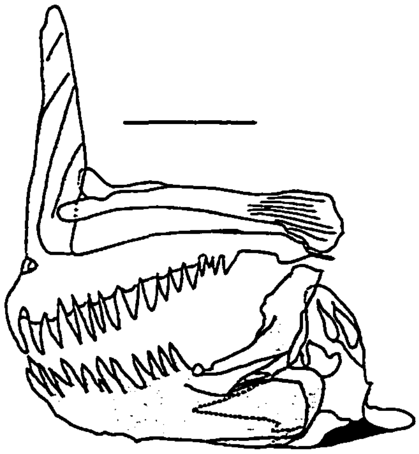

Fig. 3.15. Lateral view of the jaws in *Apeltes quadracus* **(Gasterosteidae)** (UAMZ 7958, 37 mm).

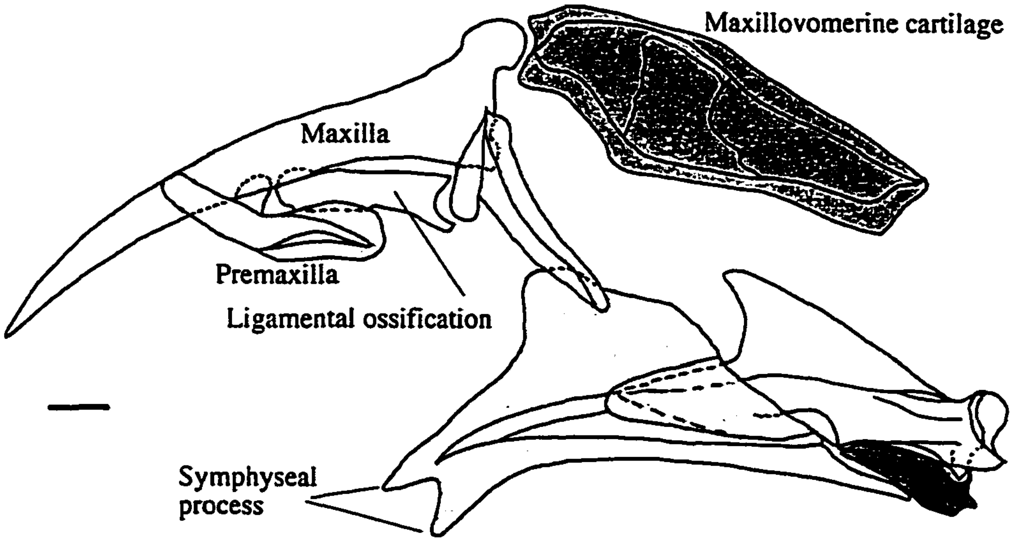

Fig. 3.16. Lateral view of the jaws in *Pegasus volans* (**Pegasidae**) (UAMZ 4616, 99 mm).

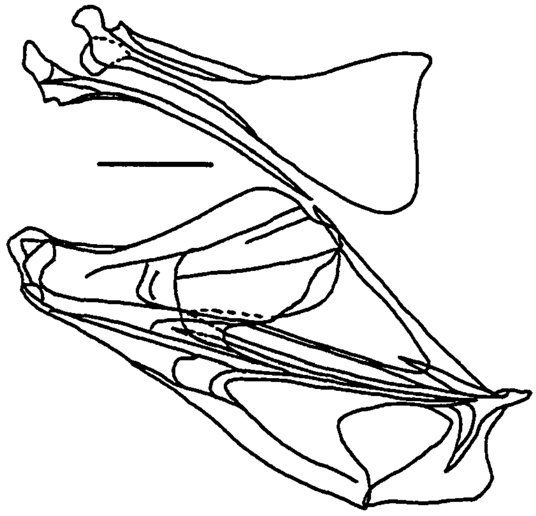

Fig. 3.17. Lateral view of the jaws in *Solenostomus paradoxus* (**Solenostomidae**) (AMS 17111002, 51 mm).

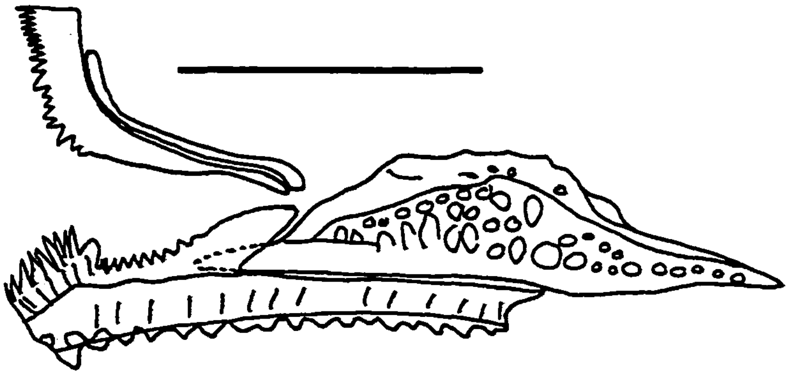

Fig. 3.18. Dorsal view of the upper jaw and lateral view of the lower jaw in *Indostomus paradoxus* (**Indostomidae**) (CAS 64017, 25 mm).

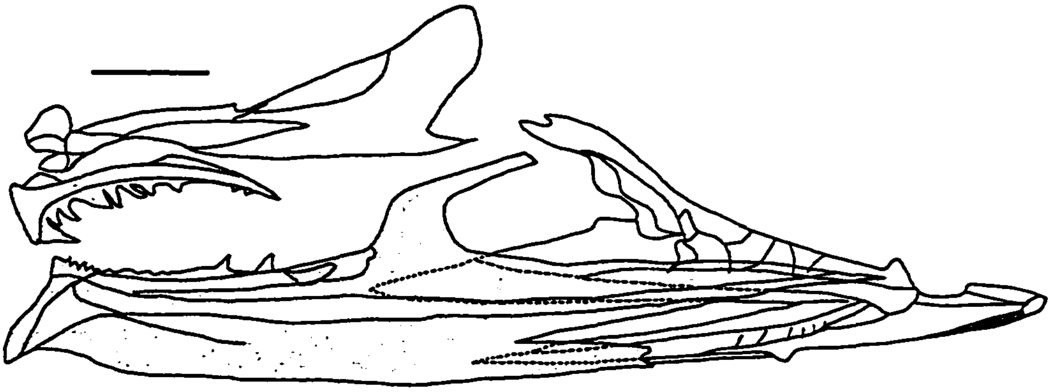

Fig. 3.19. Lateral view of the jaws in *Fistularia petimba* (Fistulariidae) (UAMZ 6348, 158 mm).

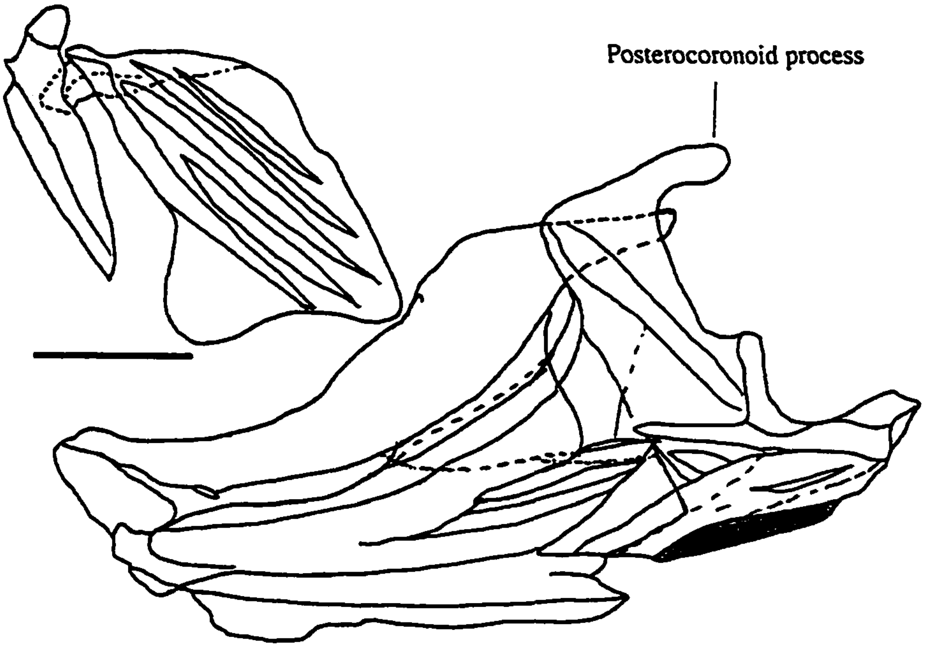

Fig. 3.20. Lateral view of the jaws in *Macroramphus scolopax* (Macroramphosidae) (USNM 344398, 99 mm).

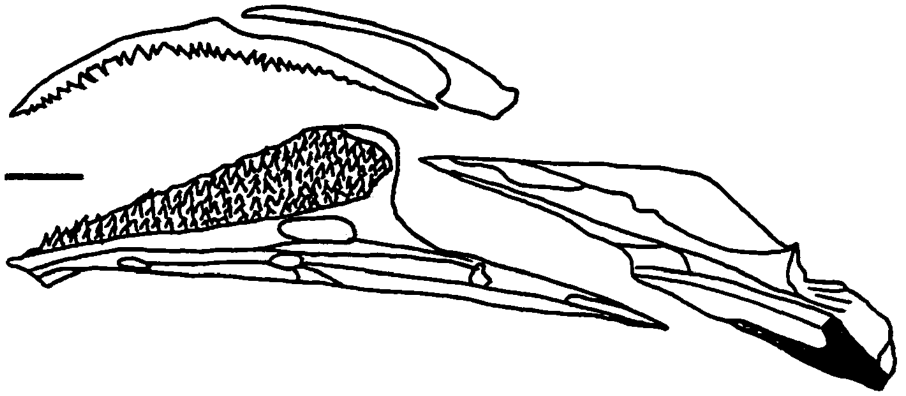

Fig. 3.21. Lateral view of the jaws in *Macrognathus aculeatus* (Mastacembelidae) (UAMZ 1855, 119 mm).

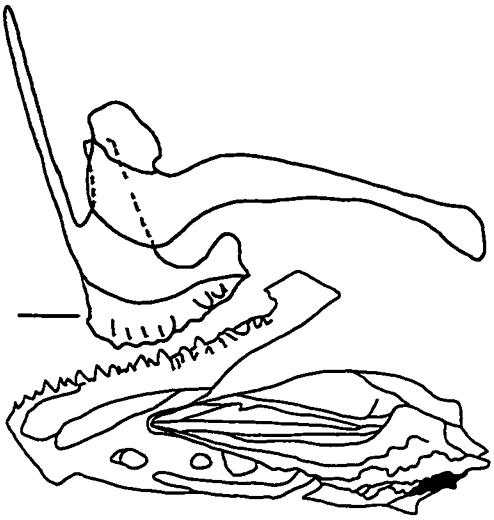

Fig. 3.22. Lateral view of the jaws in *Dactylopterus volitans* **(Dactylopteridae)** (UAMZ 2633, 74 mm).

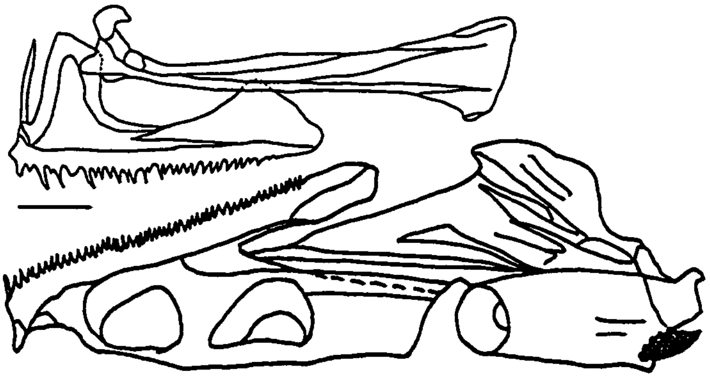

Fig. 3.23. Lateral view of the jaws in *Xeneretmus latifrons* **(Agonidae)** (UAMZ 3196, 95 mm).

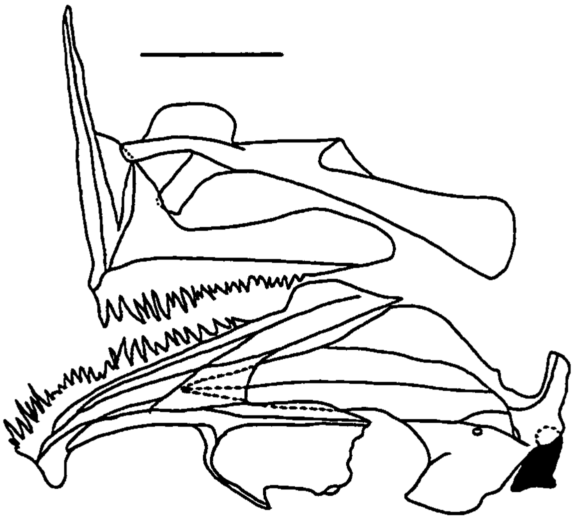

Fig. 3.24. Lateral view of the jaws in *Elassoma zonatum* **(Elassomatidae)** (UAMZ 6920, 30 mm).

4. Osteology of the suspensorium and opercular series in Eurypterygii

The suspensorium consists of the palatine, ectopterygoid, endopterygoid, metapterygoid, quadrate, symplectic, and hyomandibular bones. The hyomandibular has three dorsal articular heads. The anterior head articulates with the sphenotic, the middle head with the pterotic, and the posterior head with the opercle. The hyomandibular foramen is present at the base of the anterior head.

The opercular series consists of the preopercle, subopercle, interopercle, and opercle. In most Eurypterygii, the preopercle is L-shaped and bears an open or closed preoperculomandibular canal. I follow the terminology of Rojo (1991) for the suspensorium and opercular series, except that I use "ventral process" of the quadrate for the quadratojugal process.

Aulopiformes

Synodontidae (Fig. 4.1). The palatine is long, compressed, toothed, and with a medial cylindrical head. The ectopterygoid is L-shaped, autogenous and its posteroventral arm lies anterior to the quadrate anterior arm. The endopterygoid is narrow and connected to the medial surface of the palatine. The metapterygoid is large, triangular and autogenous. The quadrate is U-shaped, with ascending anterior and posterior arms, and a ventral process. The symplectic is short, rodlike, and fully inserted in the quadrate posterior arm. The hyomandibular bears distinct dorsal condyles and intercondyle, anterior and posterior flanges.

The preopercle is smooth, its ventral arm is indistinct, and bears a closed preoperculomandibular canal. The interopercle is triangular, large, and overlaps the subopercle. The subopercle bears a small anterior ascending process and its posterior margin is round. The subopercle is the largest element and covers most of the gill opening. The opercle is small and roughly square. In *Bathysaurus*, the quadrate is fanlike, but the symplectic is small and fully inserted in the quadrate (Baldwin and Johnson, 1996). In Pseudotrichonotidae, the quadrate is fanlike, the symplectic is large and not fully inserted in the quadrate, the ventral arm of preopercle is distinct, the opercle is triangular, and the interopercle is long (Johnson et al., 1996).

Myctophiformes

Myctophidae. The palatine is long, bears a laterally projected head with numerous tiny teeth, and is tightly connected to the ectopterygoid. The ectopterygoid is T-shaped, autogenous, and its posterodorsal arm overlies the quadrate medial surface. The endopterygoid is broad and connected to the medial surface of the ectopterygoid. The metapterygoid is large and autogenous. The quadrate is fanlike and with a distinct ventral process. The symplectic is short, rodlike, and fully inserted in the quadrate. The hyomandibular bears distinct dorsal condyles and intercondyle and anterior flanges.

The preopercle is smooth, its ventral arm is indistinct, and bears a preoperculomandibular canal and a thin broad posterior flange. The interopercle is triangular and large and overlaps the subopercle. The subopercle lacks a distinct anterior ascending process and its posterior margin is blunt. The opercle is roughly square and bears a dorsal strut.

Lampridiformes

Veliferidae (Fig. 4.2). The palatine is short, cylindrical, edentulous, with a laterally projected and bifurcated head, and abuts the ectopterygoid posteriorly. The ectopterygoid is slightly curved and autogenous. The endopterygoid is broad and connected to the medial surface of the ectopterygoid. The metapterygoid is large and autogenous. The quadrate is fanlike and with a ventral process. The symplectic is short, rodlike, and fully inserted in the quadrate. The hyomandibular is long and lacks distinct dorsal condyles, but bears a lateral lamina and a small anterior flange. In *Metavelifer*, the palatine and ectopterygoid are broad and the hyomandibular bears a distinct posterodorsal condyle (Olney et al., 1993).

The preopercle is smooth, with a distinct short ventral arm, and bears a closed preoperculomandibular canal. The interopercle is roughly ovoid and overlaps the subopercle. The subopercle bears a distinct ascending process and its posterior margin is pointed. The opercle bears an anterior strut.

Polymixiiformes

Polymixiidae (Fig. 4.3). The palatine is short, with tiny teeth, and a laterally projected cylindrical head. The ectopterygoid is L-shaped and autogenous. The endopterygoid is broad and connected to the medial surface of the palatine and ectopterygoid. The metapterygoid is large and autogenous. The quadrate is fanlike and without a distinct ventral process. The symplectic is short, rodlike, and fully inserted in the quadrate. The hyomandibular is long and bears distinct dorsal condyles, a lateral lamina, and intercondyle and anterior flanges.

The preopercle is toothed, without a distinct ventral arm, and bears a preoperculomandibular canal. The interopercle is roughly ovoid and abuts the subopercle posteriorly. The subopercle bears a distinct ascending process and its posterior margin is blunt. The opercle bears the anterior and dorsal struts.

Percopsiformes

Percopsidae (Fig. 4.4). The palatine is short, edentulous, and with a laterally projected cylindrical head. The ectopterygoid is slightly curved and autogenous. The endopterygoid is broad and connected to the medial surface of the ectopterygoid. The metapterygoid is large and autogenous. The quadrate is fanlike and with a highly expanded ventral process. The symplectic is long, rodlike, with dorsal and ventral flanges, and not fully inserted in the quadrate. The hyomandibular bears a distinct posterior dorsal condyle, a lateral lamina, and an anterior flange.

The preopercle is toothed, with a distinct long ventral arm, and bears a preoperculomandibular canal. The interopercle is long, broad, and abuts the subopercle posteriorly. The subopercle bears a distinct ascending process and its posterior margin is pointed. The opercle bears the anterior and dorsal struts.

Mugiliformes

Mugilidae. The palatine is short, toothed, and with a small laterally projected cylindrical head. The ectopterygoid is slightly curved and autogenous. The endopterygoid is broad and connected to the medial surface of the palatine and ectopterygoid. The metapterygoid is large and autogenous. The quadrate is fanlike and with a long ventral process. The symplectic is long, rodlike, with small dorsal and ventral flanges, and not fully inserted in the quadrate. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina and an anterior flange.

The preopercle is smooth, with a distinct long ventral arm, and bears a preoperculomandibular canal. The interopercle is triangular, long, and slightly overlaps the subopercle posteriorly. The subopercle bears a distinct ascending process and its posterior margin is pointed. The opercle bears an anterior strut.

Atheriniformes

Melanotaeniidae. The palatine is short, toothed, with a laterally projected cylindrical head, and lies on the lateral surface of the ectopterygoid. The ectopterygoid is slightly curved. The endopterygoid is broad and with a lateral wing that articulates with the quadrate. The metapterygoid is large and overlies the symplectic and hyomandibular. The quadrate is fanlike, with a distinct ventral process. The symplectic is long, rodlike, with small dorsal and ventral flanges, and not fully inserted in the quadrate. The hyomandibular bears a distinct posterodorsal condyle, a lateral lamina and an anterior flange.

The preopercle is smooth, with a distinct long ventral arm, and bears a preoperculomandibular canal. The interopercle is triangular, long, and slightly overlaps the subopercle posteriorly. The subopercle bears a distinct ascending process and its posterior margin is pointed. The opercle lacks an anterior strut.

Atherinidae (Fig. 4.5). The palatine is short, edentulous, with a laterally projected cylindrical head, and lies on the lateral surface of the ectopterygoid. The ectopterygoid is slightly curved. The endopterygoid is broad and with a lateral wing that articulates with the quadrate. The metapterygoid is large and overlies the symplectic and hyomandibular. The quadrate is fanlike and with a distinct ventral process. The symplectic is long, rodlike, with small dorsal and ventral flanges, and not fully inserted in the quadrate. The hyomandibular bears distinct dorsal condyles, a small lateral lamina, and an anterior flange.

The preopercle is smooth, with a distinct long ventral arm, and bears a preoperculomandibular canal. The interopercle is triangular, long, and slightly overlaps the subopercle posteriorly. The subopercle bears a distinct ascending process and its posterior margin is pointed. The opercle lacks struts.

Beloniformes

Belonidae. The palatine is short, edentulous, without a distinct head, and tightly articulated with the ectopterygoid. The ectopterygoid is long, straight, and rodlike. The endopterygoid is narrow and connected to the medial surface of the quadrate. The metapterygoid is large and overlies the symplectic and hyomandibular. The quadrate is fanlike, with a long anterior ascending process that extends along the ectopterygoid and reaches the palatine, and bears a distinct ventral process. The symplectic is long, rodlike, with small dorsal and ventral flanges, and not fully inserted in the quadrate. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina and an anterior flange.

The preopercle is smooth, with a distinct long ventral arm, and bears a closed preoperculomandibular canal. The interopercle is long and slightly overlaps the subopercle posteriorly. The subopercle bears a distinct ascending process and its posterior margin is pointed. The opercle lacks an anterior strut.

Hemiramphidae (Fig. 4.6). The palatine is long, edentulous, with a laterally projected cylindrical head, and tightly articulated with the ectopterygoid and quadrate. The ectopterygoid is short, straight, and rodlike. The endopterygoid is broad and connected to the medial surface of the quadrate. The metapterygoid is small and overlies the symplectic and hyomandibular. The quadrate is fanlike, with a long anterior ascending process that extends along the ectopterygoid and reaches the palatine, and bears a distinct ventral process. The symplectic is well developed, with expanded dorsal and ventral flanges, and not fully inserted in the quadrate. The hyomandibular bears a distinct posterodorsal condyle, a lateral lamina, and an anterior flange.

The preopercle is smooth, with a distinct long ventral arm, and bears a closed preoperculomandibular canal and a posteroventral process. The interopercle is broad and slightly overlaps the subopercle. The subopercle bears a distinct ascending process and a pointed posterior margin. The opercle lacks an anterior strut.

Cyprinodontiformes

Aplocheilidae (Fig. 4.7). The palatine is short, edentulous, with a laterally projected head, and articulated with the endopterygoid posteriorly. The ectopterygoid is not present as a distinct bone and may be fused to the palatine. The endopterygoid is expanded anteroventrally and lies over the quadrate. The metapterygoid overlies the symplectic and hyomandibular. The quadrate is fanlike and bears a long ventral process. The symplectic is well developed, with expanded dorsal and ventral flanges, and not fully inserted in the quadrate. The hyomandibular bears dorsal condyles, a lateral lamina, and the intercondyle and anterior flanges.

The preopercle is smooth, with a broad ventral arm, and bears a preoperculomandibular canal. The interopercle is broad and slightly overlaps the subopercle posteriorly. The subopercle bears a distinct ascending process and a pointed posterior margin. The opercle bears an anterior strut.

Cyprinodontidae. The palatine is edentulous, with a small medially projected head, and articulated with the ectopterygoid and endopterygoid posteriorly. The ectopterygoid is curved and reduced. The endopterygoid overlies the quadrate. The metapterygoid is absent. The quadrate is fanlike and bears a large ventral process. The symplectic is well developed, with dorsal and ventral flanges, and not fully inserted in the quadrate. The hyomandibular bears dorsal condyles, a lateral lamina, and the intercondyle and anterior flanges.

The preopercle is smooth, with a broad ventral arm, and bears a preoperculomandibular canal. The interopercle is broad and slightly overlaps the subopercle posteriorly. The subopercle bears a distinct ascending process and a pointed posterior margin. The opercle bears an anterior strut.

Stephanoberyciformes

Stephanoberycidae (Fig. 4.8). The palatine is short, edentulous, with a cylindrical head, and articulated with the ectopterygoid and endopterygoid posteriorly. The ectopterygoid is curved. The endopterygoid is broad. The metapterygoid is connected to the quadrate via cartilage. The quadrate is fanlike and bears a distinct ventral process. The symplectic is rodlike and mostly inserted in the quadrate. The hyomandibular bears a distinct posterodorsal condyle, a lateral lamina, and an anterior flange.

The preopercle is toothed, without a distinct ventral arm, and bears a closed preoperculomandibular canal. The interopercle is broad and short. The subopercle lacks a distinct ascending process and its posterior margin is blunt. The opercle is reduced and bears a strong anterior strut.

Rondeletiidae. The palatine is short, edentulous, with a laterally projected cylindrical head and a dorsomedial flange, and articulated with the ectopterygoid posteriorly. The ectopterygoid is L-shaped. The endopterygoid is absent. The metapterygoid is tightly connected to the hyomandibular and via cartilage to the quadrate. The quadrate is fanlike and bears a distinct ventral process. The symplectic is hourglass shaped and mostly inserted in the quadrate. The hyomandibular bears distinct dorsal condyles, a lateral lamina, and an anterior flange. The posterodorsal condyle is enlarged.

The preopercle is smooth, with a distinct ventral arm and a posterior flange, and bears a closed preoperculomandibular canal. The interopercle is highly reduced. The subopercle is triangular, lacks a distinct ascending process, and its posterior margin is pointed. The opercle bears anterior and dorsal struts.

Beryciformes

Monocentridae (Fig. 4.9). The palatine is short, with tiny teeth and a laterally projected head, and articulated with the ectopterygoid posteriorly. The ectopterygoid is curved. The endopterygoid is broad. The metapterygoid is connected to the quadrate via cartilage. The quadrate is fanlike and bears a distinct ventral process. The symplectic is hourglass shaped and mostly inserted in the quadrate. The hyomandibular lacks distinct dorsal condyles, but bears a small lateral lamina and an anterior flange.

The preopercle bears two posteroventral spines, a short distinct ventral arm, and a preoperculomandibular canal. The interopercle is toothed ventrally. The subopercle is toothed, lacks a distinct ascending process, and its posterior margin is pointed. The opercle bears strong struts.

Holocentridae. The palatine is short, toothed, with a laterally projected head, and articulated with the ectopterygoid posteriorly. The ectopterygoid is T-shaped, with a very small posterodorsal arm. The endopterygoid is broad. The metapterygoid is autogenous. The quadrate is fanlike and bears a distinct ventral process. The symplectic is rodlike, with a small ventral flange, and not fully inserted in the quadrate. The hyomandibular bears a distinct posterodorsal condyle, a small lateral lamina, and a large anterior flange.

The preopercle bears several small spines and a strong posteroventral spine, a short ventral arm, and a closed preoperculomandibular canal. The interopercle is small. The subopercle bears a small ascending process and its posterior margin is blunt. The opercle bears an anterior strut, several small posterior spines, and two long spines.

Zeiformes

Grammicolepididae. The palatine is short, edentulous, with a straight cylindrical head, and is articulated with the ectopterygoid posteriorly. The ectopterygoid is curved posterodorsally covering the anterior and dorsal margins of the quadrate. The endopterygoid is broad. The metapterygoid is small and attached to the medial surface of the endopterygoid. The quadrate is fanlike and bears a distinct ventral process. The symplectic bears the dorsal and ventral flanges and is not fully inserted in the quadrate. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina and an anterior flange.

The preopercle is toothed, with a distinct ventral arm, and bears a preoperculomandibular canal. The interopercle is broad. The subopercle bears a small ascending process and its posterior margin is pointed. The opercle bears an anterior strut.

Caproidae (Fig. 4.10). The palatine is short, edentulous, bears a laterally projected head, and articulated with the ectopterygoid and endopterygoid posteriorly. The ectopterygoid is triangular. The endopterygoid is broad. The metapterygoid bears a ventral process that via cartilage articulates with the symplectic-hyomandibular joint. The quadrate is fanlike and bears a distinct ventral process. The symplectic is simple and rodlike and not fully inserted in the quadrate. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina and a narrow anterior flange.

The preopercle is toothed, with a distinct ventral arm, angled distinctly, and bears a preoperculomandibular canal. The interopercle is long and broad posteriorly. The subopercle bears a small ascending process and its posterior margin is pointed. The opercle is reduced and bears an anterior strut.

Gasterosteiformes

Hypoptychidae (Fig. 4.11). The palatine is edentulous and bears a laterally projected cylindrical head. The ectopterygoid is elongated and posteriorly expanded into a triangle that lies on the lateral surface of the quadrate and extends to the metapterygoid. The endopterygoid is absent. Orr (1995) identified an endopterygoid in Hypoptychidae, but I argue that what he identified as an endopterygoid is the lateral ethmoid. The metapterygoid is reduced to a small splint over the symplectic. The quadrate is fanlike and bears a distinct ventral process. The symplectic is rodlike and not fully inserted in the quadrate. The hyomandibular bears distinct dorsal condyles, but lacks the lateral lamina and anterior flange.

The preopercle is smooth, with a distinct ventral arm, and bears a closed preoperculomandibular canal. The interopercle is long and broader posteriorly. The subopercle bears a small ascending process and its posterior margin is pointed. The opercle lacks an anterior strut.

Aulorhynchidae (Fig. 4.12). The palatine is edentulous and bears a straight conical head. The ectopterygoid is T-shaped with a long posterior arm and short anterior and ventral arms and posteriorly articulated with the symplectic. The endopterygoid is absent. The metapterygoid is reduced. The quadrate is fanlike and bears a highly elongated ventral process. The symplectic is cylindrical and with a bifurcated dorsal flange. The hyomandibular bears distinct dorsal condyles in *Aulorhynchus* (not distinct in *Aulichthys*) and a small lateral lamina.

The preopercle is smooth, with an elongated ventral arm, and bears a closed preoperculomandibular canal. The interopercle is elongated and broader posteriorly. The subopercle bears a distinct ascending process and its posterior margin is fimbriated. The opercle lacks an anterior strut.

Gasterosteidae (Fig. 4.13). The palatine is edentulous and bears a straight conical head. The ectopterygoid and endopterygoid are fused into a triradiate bone which embraces the anterior and dorsal margins of the quadrate. The metapterygoid is reduced. The quadrate is fanlike and bears a distinct ventral process. The symplectic is cylindrical and with bifurcated dorsal and ventral flanges. The hyomandibular bears distinct dorsal condyles, a small lateral lamina, and an anterior flange.

The preopercle is smooth, with an elongated ventral arm, and bears a closed preoperculomandibular canal. The interopercle is broader posteriorly. The subopercle bears a well developed ascending process and its posterior margin is fimbriated. The opercle is roughly triangular and lacks an anterior strut.

Pegasidae. The palatine, ectopterygoid, endopterygoid, and metapterygoid are absent. Bowne (1985) believed that the maxillovomerine ligament of Pietsch (1978) was the palatine and Jungerson (1915) argued that it was the fused palatine and ectopterygoid without giving evidence for compound origins (though I observed two centers of ossification in my specimens; one anterior and the other posterior). Orr (1995) followed Pietsch (1978) and I agree that these structures might not be homologous with the palatine and ectopterygoid. The quadrate is small and bears an expanded ventral process. The symplectic is cylindrical and bears a bifurcated dorsal flange and a ventral flange. The hyomandibular bears separate dorsal condyles and the posterior one is elongated. A large medial lamina reduces movement of the suspensorium.

The preopercle is toothed, without a distinct ventral arm, but highly enlarged, approaching its counterpart ventrally covering most of the ventral surface of the head, and bears a closed preoperculomandibular canal and a socket at its articulation with the interhyal. The interopercle is elongated and widely separated from the subopercle and opercle. The subopercle is reduced and bears a distinct ascending process. The opercle is also highly reduced and lacks struts.

Solenostomidae (Fig. 4.14). The palatine is edentulous, fused to the vomer and bears a laterally projected cylindrical head. The ectopterygoid is curved. The endopterygoid is narrow and elongated at the quadrate dorsal margin. The metapterygoid is fused to the symplectic in adults. The quadrate is fanlike and bears a long ventral process with a broad dorsal flange. The symplectic is cylindrical and with a ventral flange. The hyomandibular bears distinct dorsal condyles and a small lateral lamina. A large medial lamina reduces movement of the suspensorium.

The preopercle bears several small lateral spines, a long posteroventral spine, an elongated ventral arm, and a closed preoperculomandibular canal. The interopercle is elongated and widely separated from the subopercle and opercle. The subopercle is threadlike, curved around the opercle, and lacks a distinct ascending process. The opercle is concave and bears spiny anterior and dorsal struts. As Orr (1995) noted, the interhyal lamina is attached to the posteroventral corner of the preopercle.

Syngnathidae (Fig. 4.15). The palatine is edentulous and bears a bud-like head. The ectopterygoid is thin and curved at the anterior margin of the quadrate. The endopterygoid is narrow at the quadrate dorsal edge. The metapterygoid is fused to the symplectic in adults, but autogenous in young (Azzarello, 1989). The quadrate is fanlike and bears a long ventral process with a broad dorsal flange. The symplectic is cylindrical and with a ventral flange. The hyomandibular bears distinct dorsal condyles, a lateral lamina, and an anterior flange. A large medial lamina restricts movement of the suspensorium.

The preopercle bears a strong posteroventral process, an elongated, angled ventral arm, a preoperculomandibular canal, and a socket at its articulation with the interhyal. The interopercle is elongated and widely separated from the subopercle and opercle. The subopercle is thin, curved, mostly overlaps the opercle, and lacks a distinct ascending process. The opercle is concave and lacks the struts. The gill opening is reduced to a small pore on the top of the opercle.

Indostomidae (Fig. 4.16). There are no distinct palatine, ectopterygoid and endopterygoid bones. Instead, there is a single long bone that connects the quadrate to the ethmoid region and might be homologs of the above bones (Banister, 1970). The metapterygoid is small and located dorsal to the symplectic-hyomandibular. The quadrate is without a distinct ventral process. The symplectic is simple and without the flanges. The hyomandibular bears distinct dorsal condyles.

The preopercle is triangular and lacks a ventral arm. The interopercle is absent, as noted by Johnson and Patterson (1993) and Orr (1995). The subopercle is a threadlike bone inside the opercle and does not bear an ascending process. The opercle is concave, bears six conspicuous posterior spines, and lacks struts.

Aulostomidae (Fig. 4.17). The palatine is short and edentulous. The ectopterygoid is thin, T-shaped with a long posterodorsal arm and a short ventral arm at the anterior margin of the quadrate. The endopterygoid is absent. The metapterygoid is independent in juveniles, but fused to the symplectic in adults (Azzarello, 1989). The quadrate is fanlike and bears a long ventral process with a broad dorsal flange. The symplectic is cylindrical and with a dorsal flange. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina.

The preopercle bears an elongated ventral arm, and bears a preoperculomandibular canal. The interopercle is elongated and slightly broader posteriorly. The subopercle is thin, fimbriated posteriorly, and bears an enlarged triangular ascending process. The opercle is fimbriated posteriorly and lacks struts.

Fistulariidae. The palatine is short, edentulous and bears a laterally projected head. The ectopterygoid is thin, and T-shaped with a long posterodorsal arm and a short ventral arm at the anterior margin of the quadrate. The endopterygoid is elongated and its dorsal edge is spinous. The metapterygoid is fused to the symplectic in adults. The quadrate is fanlike and bears a long ventral process with a broad dorsal flange. The symplectic is cylindrical and with well developed flanges. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina.

The preopercle bears an elongated ventral arm and a preoperculomandibular canal. The interopercle is elongated and extended along the opercle. The subopercle bears an enlarged triangular ascending process. The opercle is fimbriated posteriorly and lacks struts.

Macroramphosidae (Fig. 4.18). The palatine is edentulous and bears a small laterally projected head with a tiny posteromedial process. The ectopterygoid is curved. The endopterygoid is elongated. The metapterygoid is triangular. The quadrate is fanlike and bears a long ventral process with a broad dorsal flange. The symplectic bears developed flanges. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina. A large medial lamina restricts movement of the suspensorium.

The preopercle bears an elongated ventral arm, a posteroventral process, a preoperculomandibular canal, and a socket at its articulation with the interhyal. The interopercle is elongated and slightly broader posteriorly. The subopercle bears a distinct ascending process. The opercle bears an anterior strut.

Centriscidae. The palatine is small, edentulous, and bears no distinct head but a tiny posteromedial process. The ectopterygoid is small and triangular. The endopterygoid is elongated. The metapterygoid is thin and triangular. The quadrate is fanlike and bears a long ventral process with a broad dorsal flange. The symplectic bears developed flanges. The hyomandibular is pointed and lacks distinct dorsal condyles. A large medial lamina restricts the movement of the suspensorium.

The preopercle bears an elongated ventral arm, a large posteroventral process, a preoperculomandibular canal, and a socket at its articulation with the interhyal. The interopercle is elongated and slightly broader anteriorly and widely separated from the subopercle. The subopercle bears a large ascending process. The opercle bears no struts.

Synbranchiformes

Synbranchidae (Fig. 4.19). The palatine is small, toothed, and without a head, but with a small lateral process. The ectopterygoid is toothed and highly enlarged. The endopterygoid is fused to the dorsolateral margin of the ectopterygoid. The metapterygoid is fanlike, broad, lies posterior to the quadrate, with which it interdigitates via bony struts. The quadrate is fanlike and has a distinct ventral process. The symplectic is rod-like. The hyomandibular is short and lacks distinct condyles.

The preopercle is lacks a distinct ventral arm, is evenly broad, obliquely positioned, and bears a closed preoperculomandibular canal. The interopercle is broad and widely separated from other elements. The subopercle bears a triangular ascending process and is fimbriated posteriorly. The opercle lacks the struts and is fimbriated posteriorly.

Mastacembelidae. The palatine is long, edentulous, and without a distinct head. The ectopterygoid is broad. The endopterygoid is narrow and autogenous at the dorsomedial margin of the ectopterygoid. The metapterygoid is fanlike, broad, and lies posterior to the quadrate. The quadrate is fanlike and with a distinct ventral process. The symplectic is rodlike, long, and has small dorsal and ventral flanges. The hyomandibular is short, bears distinct anterodorsal and posterodorsal condyles, a lateral lamina, and a small anterior flange.

The preopercle bears a ventral arm and a closed preoperculomandibular canal. The interopercle is long and broader posteriorly. The subopercle bears a triangular ascending process and is fimbriated posteriorly. The opercle lacks the struts and is fimbriated posteriorly.

Scorpaeniformes

Dactylopteridae (Fig. 4.20). The palatine is edentulous, fused to the ectopterygoid, and has a cylindrical head that bears a small lateral process. The ectopterygoid is large. The endopterygoid lies on the medial surfaces of the ectopterygoid. The metapterygoid is autogenous. The quadrate is fanlike and has a distinct ventral process. The symplectic lies perpendicular to the quadrate. The hyomandibular bears distinct dorsal condyles and well developed lateral and medial laminae.

The preopercle bears a distinct ventral arm, a long toothed posteroventral process, an anterior flange, and a closed preoperculomandibular canal. The interopercle is small and widely separated from the subopercle. The subopercle is highly reduced and has a long posterior process, but no ascending process. The opercle is also reduced and lacks struts.

Scorpaenidae. The palatine is long, toothed, and with a laterally projected cylindrical head. The ectopterygoid is L-shaped. The endopterygoid is broad and autogenous at the dorsomedial margin of the ectopterygoid. The metapterygoid is autogenous, fanlike, and lies posterior to the quadrate. The quadrate is fanlike and with a distinct ventral process. The symplectic is rodlike. The hyomandibular bears a large head without distinct condyles, but bears a small lateral lamina and an anterior flange.

The preopercle is with a ventral arm and a closed preoperculomandibular canal. The interopercle is broad and situated below the preopercle and only overlaps the spines. The subopercle bears a distinct ascending process and a long posterior process. The opercle bears the anterior and dorsal struts and three posterior spines.

Hexagrammidae (Fig. 4.21). The palatine is edentulous and has a laterally projected cylindrical head. The ectopterygoid is T-shaped. The endopterygoid is narrow and autogenous, lying at the dorsomedial margin of the ectopterygoid. The metapterygoid is autogenous, fanlike, and lies posterior to the quadrate. The quadrate is fanlike and with a distinct ventral process. The symplectic is rodlike. The hyomandibular bears a large head without distinct condyles, but bears a small lateral lamina and an anterior flange. The palatine is toothed in some specimens of *Hexagrammos*, *Oxylebius*, *Zaniolepis*, and *Ophiodon* (Shinohara, 1994).

The preopercle bears a ventral arm, a closed preoperculomandibular canal, and four lateral arches. The interopercle is broad and situated below the preopercle. The subopercle bears distinct ascending and posterior processes. The opercle lacks struts.

Agonidae (Fig. 4.22). The palatine is long, toothed, and with a cylindrical head. The ectopterygoid is curved. The endopterygoid is autogenous and reduced to a small splint. The metapterygoid is autogenous, fanlike, and lies posterior to the quadrate. The quadrate is fanlike and with a distinct ventral process. The symplectic is rodlike. The hyomandibular bears no distinct condyles, but bears a small lateral lamina and an anterior flange. In some genera (e.g., *Percis*, *Agnus*, and *Bathyagonus*), the palatine is edentulous and in *Hypsagonus*, the endopterygoid is relatively large (Kanayama, 1991).

The preopercle bears a ventral arm, a closed preoperculomandibular canal, and five large lateral arches. The interopercle is long and broader posteriorly. The subopercle bears a distinct ascending and a long posterior process. The opercle is triangular and bears the anterior and dorsal struts and three posterior spines.

Perciformes

Percidae. The palatine is short, toothed, with a laterally projected head, and lies ventral to the ectopterygoid. The ectopterygoid is triradiate and autogenous. The endopterygoid is broad and connected to the medial surface of the ectopterygoid. The metapterygoid is broad and autogenous. The quadrate is fanlike and with a distinct ventral process. The symplectic is rodlike. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina and an anterior flange.

The preopercle is toothed and has a broad ventral arm and a closed preoperculomandibular canal. The interopercle is broad. The subopercle bears a small ascending process. The opercle bears a dorsal strut.

Cirrhitidae. The palatine is short, with a few small teeth and a laterally projected head, and lies ventral to the ectopterygoid. The ectopterygoid is triradiate and autogenous. The endopterygoid is broad and connected to the medial surface of the ectopterygoid. The metapterygoid is broad and autogenous. The quadrate is fanlike, with a distinct ventral process. The symplectic is rodlike. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina and an anterior flange.

The preopercle is toothed, with a broad ventral arm, and a closed preoperculomandibular canal. The interopercle is broad. The subopercle bears a small ascending process and is fimbriated posteriorly. The opercle bears a dorsal strut.

Elassomatidae (Fig. 4.23). The palatine is edentulous and has a laterally projected head. The ectopterygoid and endopterygoid are absent. The metapterygoid is relatively broad and autogenous. The quadrate is fanlike and with a distinct narrow ventral process. The symplectic is rodlike. The hyomandibular bears a distinct posterodorsal condyle, a small lateral lamina, and an anterior flange.

The preopercle is smooth and with a distinct ventral arm and a preoperculomandibular canal. The interopercle is triangular. The subopercle bears a small ascending process. The opercle bears a dorsal strut.

Pomacentridae. The palatine is short, edentulous, with a laterally projected head, and lies on the lateral surface of the ectopterygoid. The ectopterygoid is triradiate, and tightly attached to the quadrate. The endopterygoid is broad and fused to the medial surfaces of the ectopterygoid and quadrate. The metapterygoid is broad and fused to the symplectic-hyomandibular. The quadrate is fanlike and its ventral process is confluent with the quadrate body. The symplectic is rodlike. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina and an anterior flange. There is a tendency in most of the elements to fuse together.

The preopercle is toothed, with a broad ventral arm, and a preoperculomandibular canal. The interopercle is broad. The subopercle bears a small ascending process. The opercle bears the anterior and dorsal struts.

Centrarchidae (Fig. 4.24). The palatine is edentulous, with a laterally projected head, and lies on the lateral surface of the ectopterygoid. The ectopterygoid is curved and tightly attached to the quadrate. The endopterygoid is broad. The metapterygoid is broad and cartilaginously connected to the quadrate. The quadrate is fanlike and without a distinct ventral process. The symplectic is rodlike. The hyomandibular lacks distinct dorsal condyles, but bears a lateral lamina and an anterior flange.

The preopercle is smooth, with a broad ventral arm and a closed preoperculomandibular canal. The interopercle is broad. The subopercle bears a small ascending process. The opercle bears an anterior and a dorsal strut.

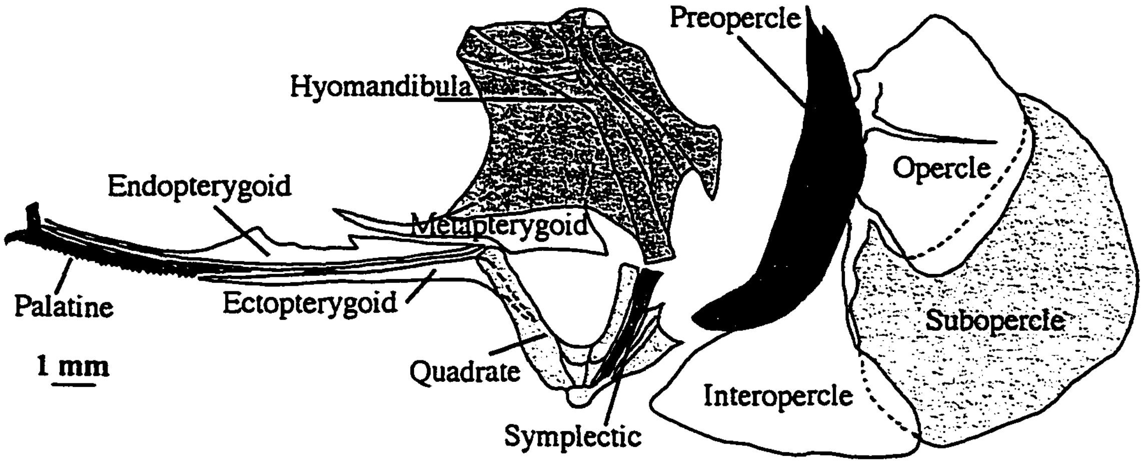

Fig. 4.1. Lateral view of the suspensorium and opercular series in *Synodus intermedius* **(Synodontidae)** (UAMZ 4889, 78 mm).

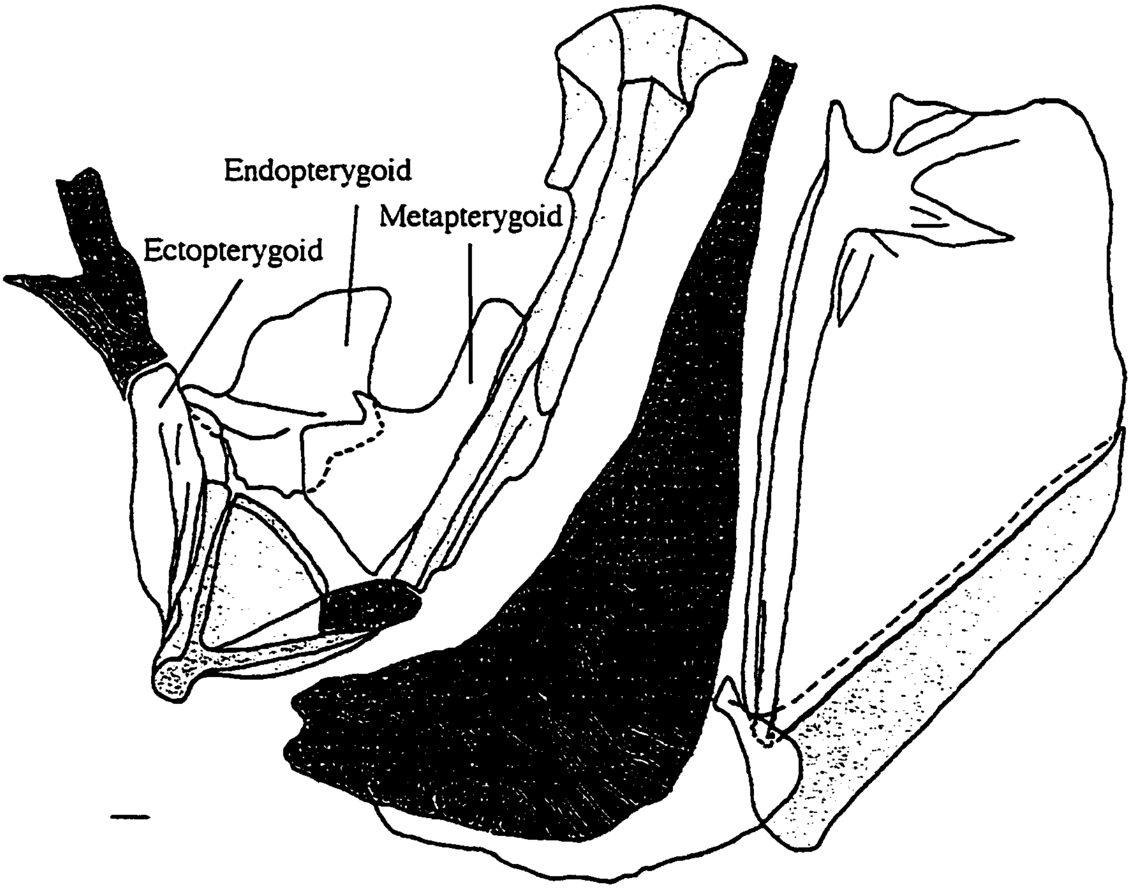

Fig. 4.2. Lateral view of the suspensorium and opercular series in *Velifer hypselopterus* **(Veliferidae)** (AMS 21839005, 101 mm).

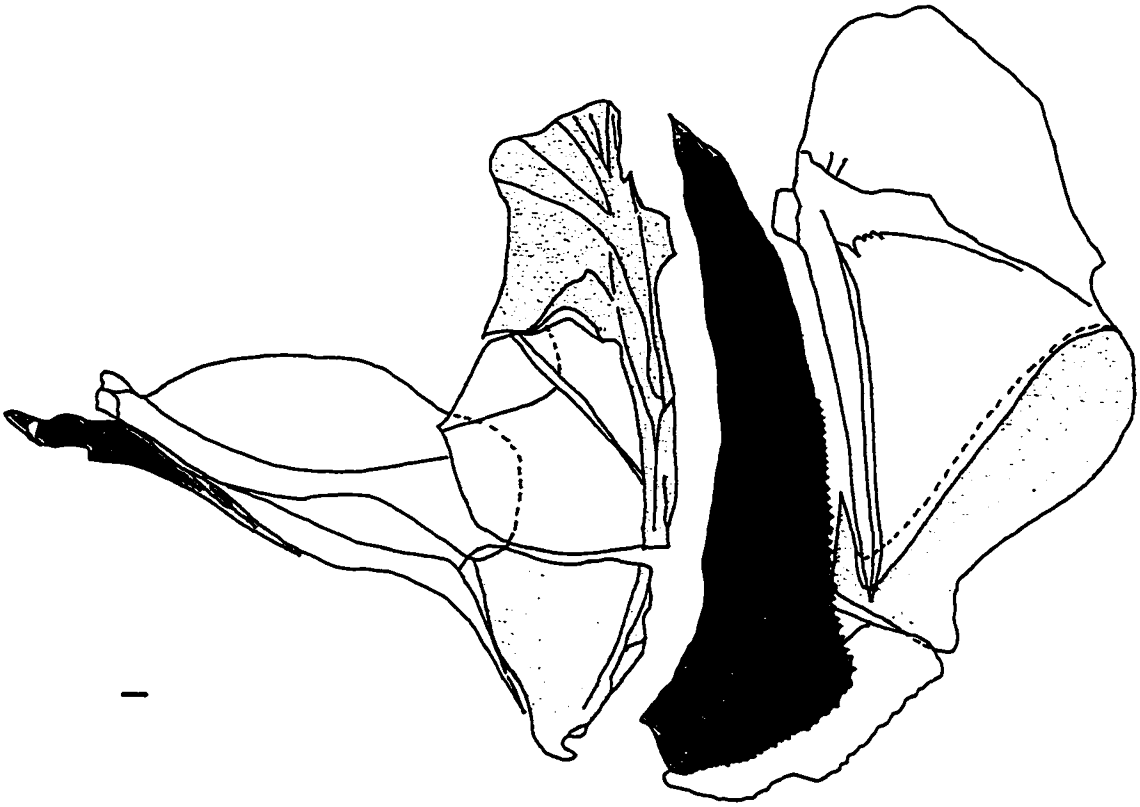

Fig. 4.3. Lateral view of the suspensorium and opercular series in *Polymixia lowei* **(Polymixiidae)** (USNM 159300, 115 mm).

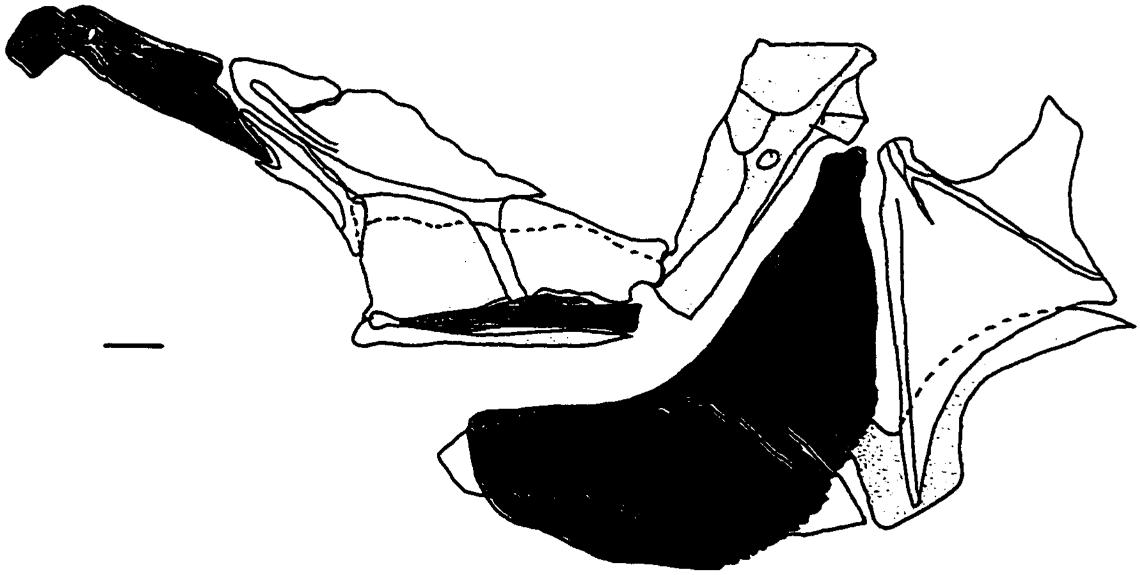

Fig. 4.4. Lateral view of the suspensorium and opercular series in *Percopsis omiscomaycus* **(Percopsidae)** (UAMZ 2048, 55 mm).

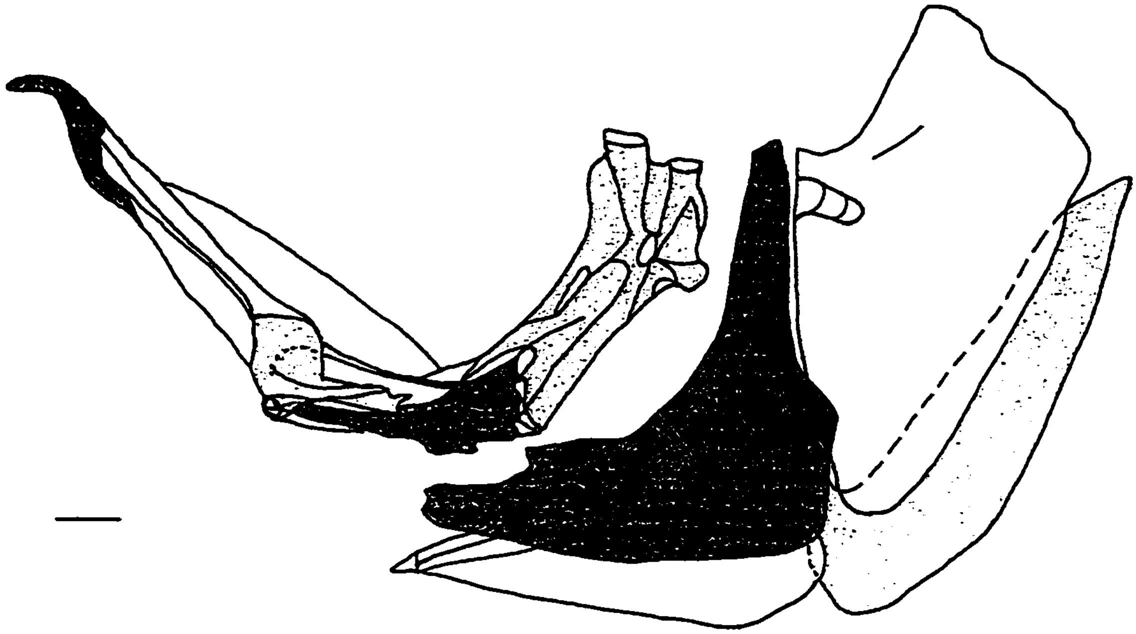

Fig. 4.5. Lateral view of the suspensorium and opercular series in *Allanetta harringtonensis* **(Atherinidae)** (UAMZ 2673, 58 mm).

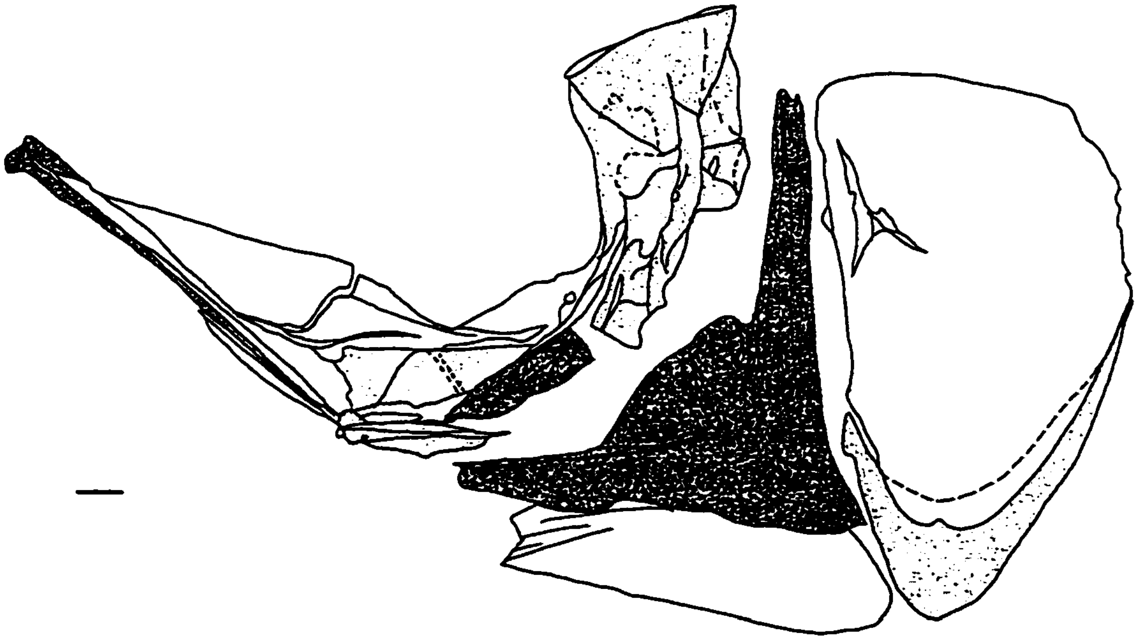

Fig. 4.6. Lateral view of the suspensorium and opercular series in *Arrhamphus sclerolepis* **(Hemiramphidae)** (UAMZ 3523, 103 mm).

Fig. 4.7. Lateral view of the suspensorium and opercular series in *Rivulus hartii* (**Aplocheilidae**) (UAMZ 6660, 47 mm).

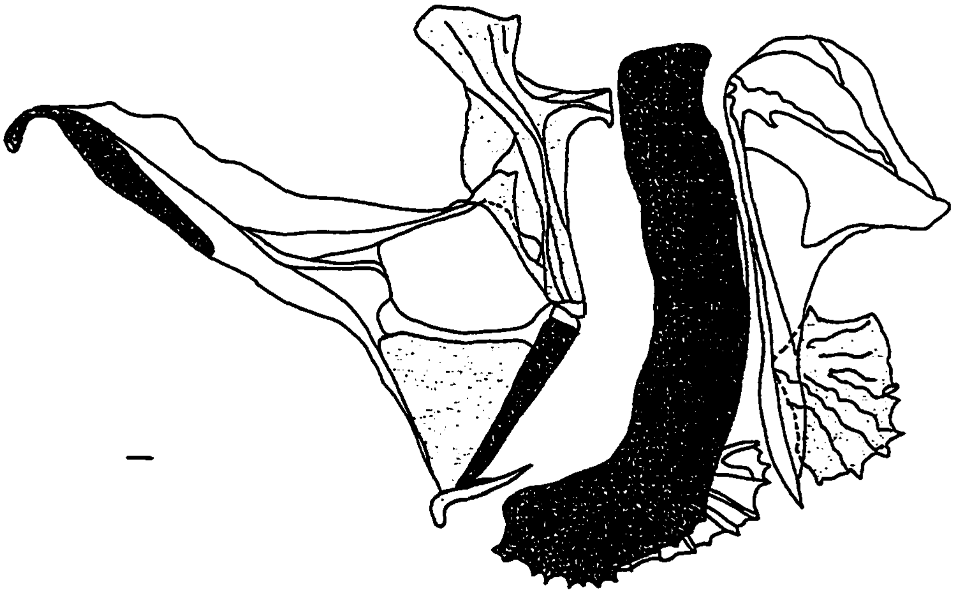

Fig. 4.8. Lateral view of the suspensorium and opercular series in *Stephanoberyx monae* (**Stephanoberycidae**) (USNM 304353, 92 mm).

Fig. 4.9. Lateral view of the suspensorium and opercular series in *Monocentris sp.* **(Monocentridae)** (UAMZ 7854, 92 mm).

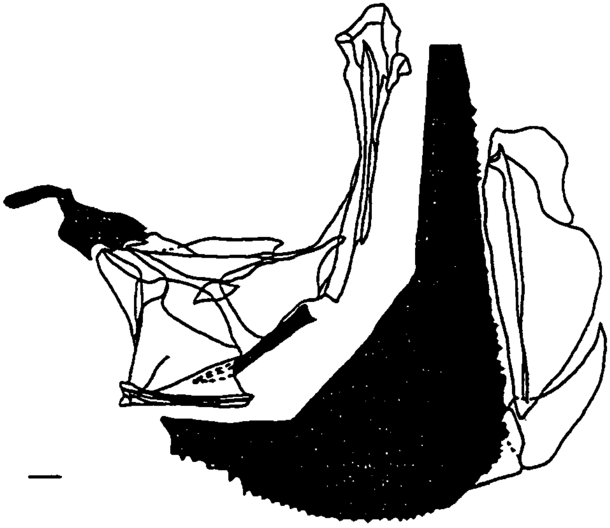

Fig. 4.10. Lateral view of the suspensorium and opercular series in *Antigonia sp.* **(Caproidae)** (USNM 266901, 37 mm).

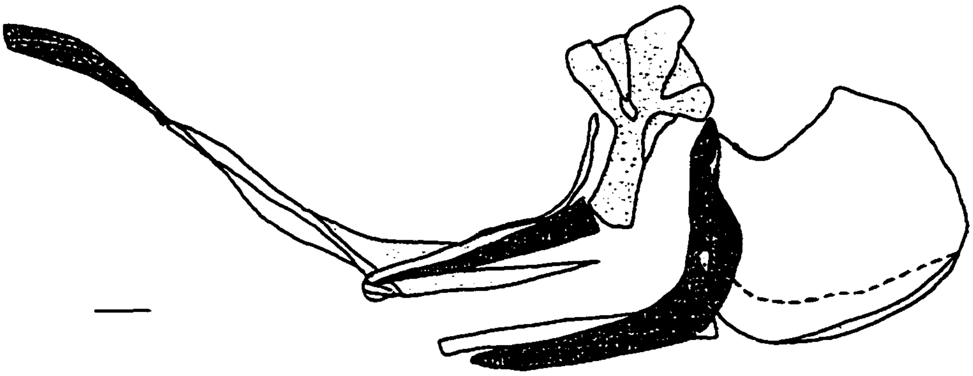

Fig. 4.11. Lateral view of the suspensorium and opercular series in *Hypoptychus dybowskii* **(Hypoptychidae)** (UAMZ 5550, 80 mm).

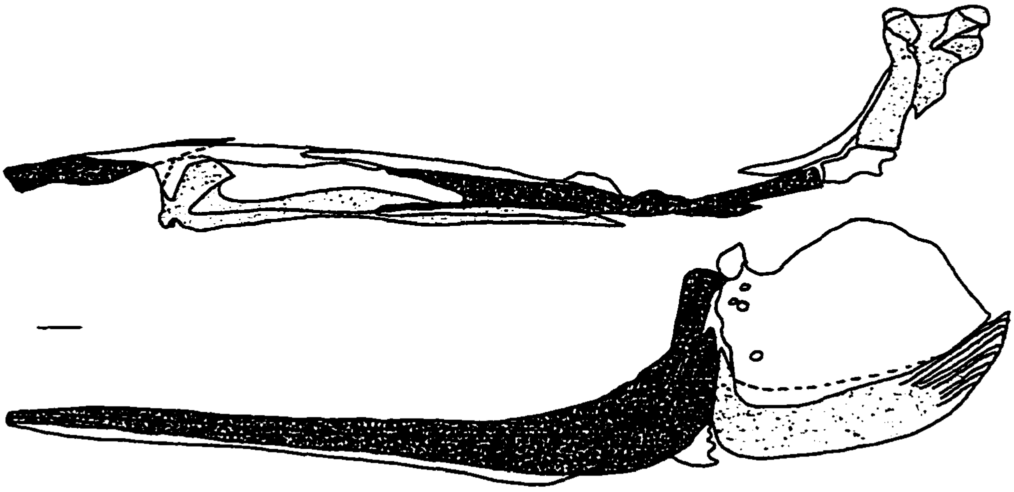

Fig. 4.12. Lateral view of the suspensorium and opercular series in *Aulorhynchus flavidus* **(Aulorhynchidae)** (UAMZ 3783, 109 mm).

Fig. 4.13. Lateral view of the suspensorium and opercular series in *Pungitius pungitius* **(Gasterosteidae)** (UAMZ 3049, 46 mm).

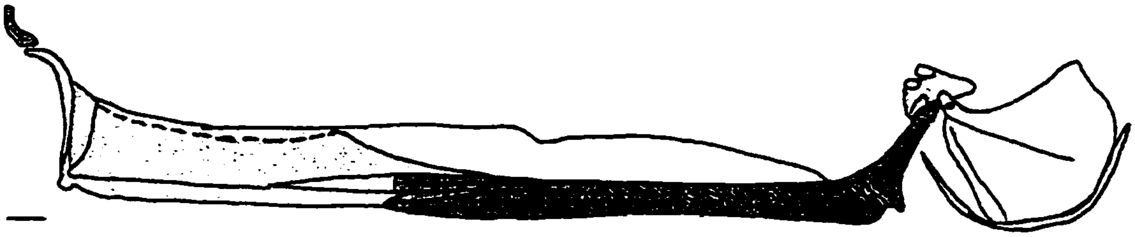

Fig. 4.14. Lateral view of the suspensorium and opercular series in *Solenostomus paradoxus* **(Solenostomidae)** (AMS 17111002, 51 mm).

Fig. 4.15. Lateral view of the suspensorium and opercular series in *Syngnathus scovelli* **(Syngnathidae)** (UAMZ 3782, 117 mm).

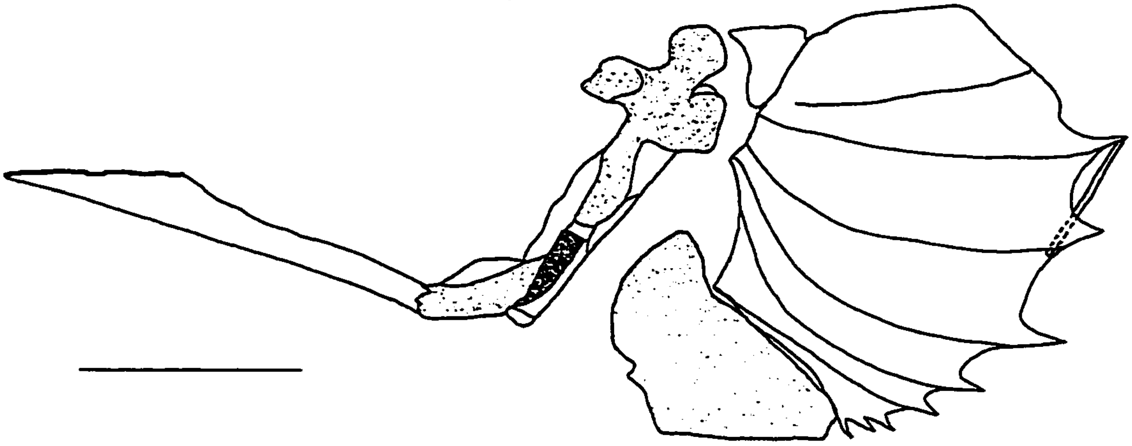

Fig. 4.16. Lateral view of the suspensorium and opercular series *in Indostomus paradoxus* **(Indostomidae)** (CAS 64017, 25 mm).

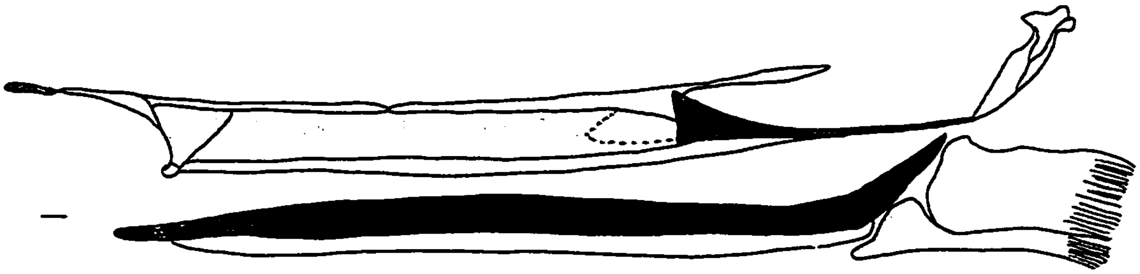

Fig. 4.17. Lateral view of the suspensorium and opercular series in *Aulostomus valentini* **(Aulostomidae)** (CAS 11979, 139 mm).

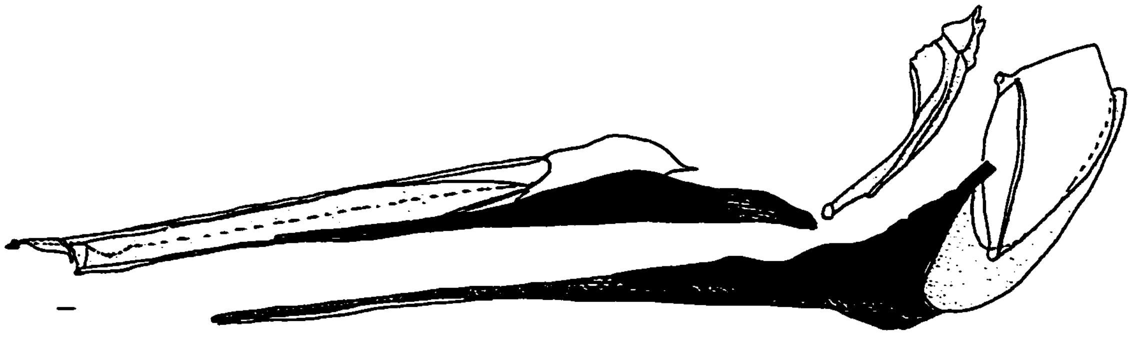

Fig. 4.18. Lateral view of the suspensorium and opercular series in *Macroramphosus scolopax* **(Macroramphosidae)** (USNM 344398, 99 mm).

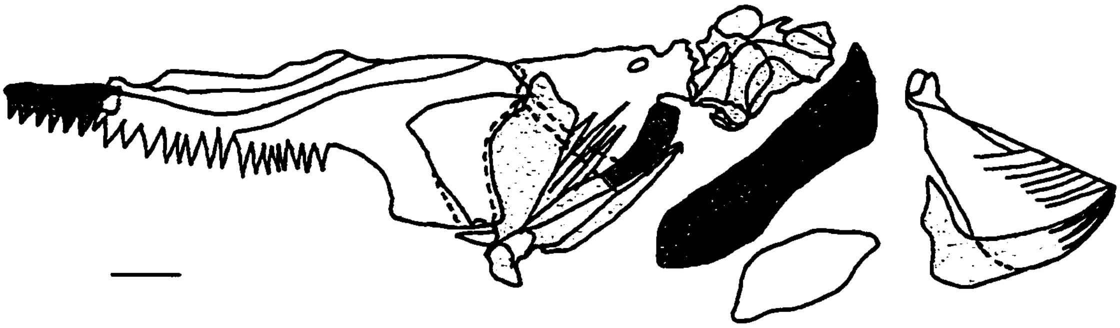

Fig. 4.19. Lateral view of the suspensorium and opercular series in *Monopterus albus* **(Synbranchidae)** (USNM 192939, 193 mm).

Fig. 4.20. Lateral view of the suspensorium and opercular series in *Dactylopterus volitans* **(Dactylopteridae)** (UAMZ 2633, 74 mm).

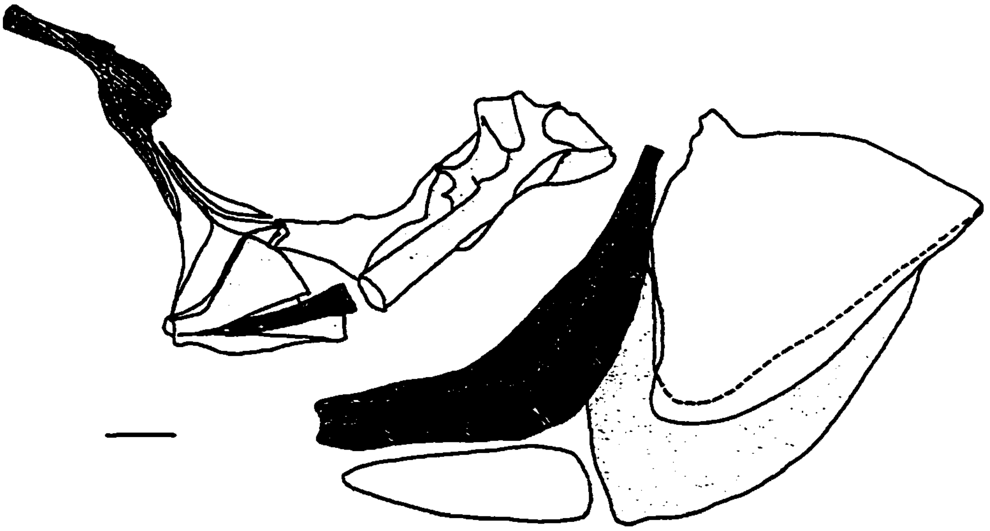

Fig. 4.21. Lateral view of the suspensorium and opercular series in *Hexagrammmus decagrammus* **(Hexagrammidae)** (UAMZ 3190, 50 mm).

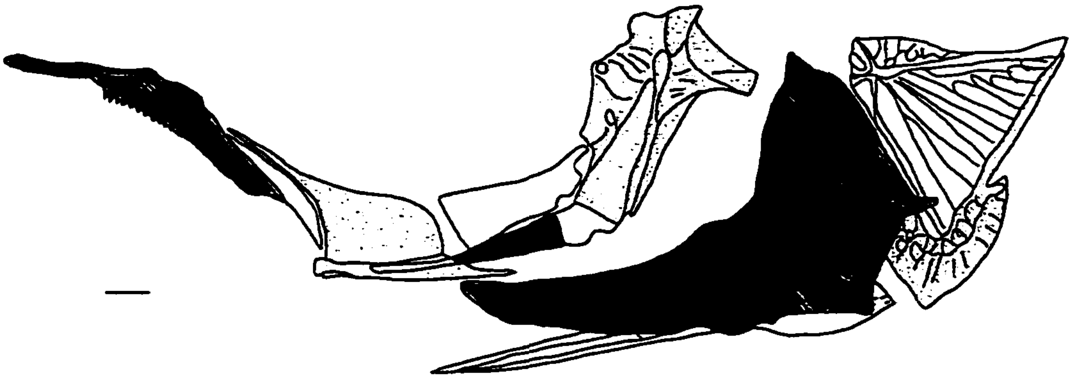

Fig. 4.22. Lateral view of the suspensorium and opercular series in *Xeneretmus latifrons* **(Agonidae)** (UAMZ 3196, 95 mm).

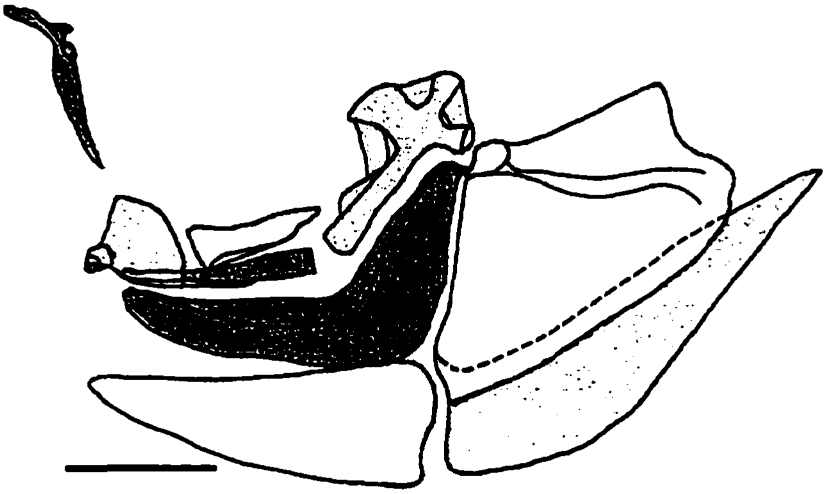

Fig. 4.23. Lateral view of the suspensorium and opercular series in *Elassoma zonatum* **(Elassomatidae)** (UAMZ 6920, 30 mm).

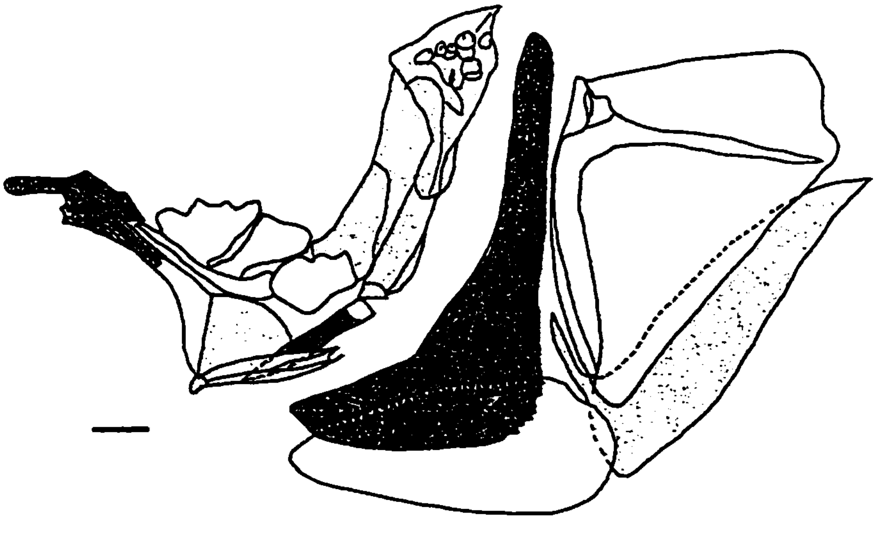

Fig. 4.24. Lateral view of the suspensorium and opercular series in *Lepomis gibbosus* **(Centrarchidae)** (UAMZ 7715.4, 40 mm).

5. Osteology of the hyoid and branchial arches in Eurypterygii

The hyoid arches consist of a single basihyal and urohyal, and the arch on each side consists of a dorsal and a ventral hypohyal, an anterior ceratohyal, a posterior ceratohyal, an interhyal, and branchiostegal rays that are borne on the ceratohyals. In some of the taxa, the anterior ceratohyal is connected to the posterior ceratohyal with medial, lateral, or dorsal struts.

The branchial arches consist of three single, separate, and ossified basibranchials, and in most taxa the arches on each side consist of three hypobranchials, five ceratobranchials, four epibranchials, four pharyngobranchials, and associated teeth and tooth plates. A cartilaginous fourth basibranchial is present in some taxa. The third hypobranchial is usually oblique and bears a cylindrical ventral process. Some epibranchials bear an uncinate process. The first pharyngobranchial is absent in some taxa, and when present lacks the pharyngeal tooth plate. The second and third pharyngobranchials usually bear toothplates. The fourth pharyngobranchial is absent or reduced in all the studied taxa, but the fourth pharyngeal tooth plate is usually present. Gill rakers and small toothplates are present on the branchial arches of most taxa. McAllister (1968) studied the branchiostegal rays and associated bones, Nelson (1969) studied gill arches, Kusaka (1974) provided a monograph on the urohyal, and Rosen and Patterson (1990) provided an atlas of percomorph dorsal gill arches. I follow the terminology of Rosen and Patterson (1990) for the hyoid and branchial arches.

Aulopiformes

Synodontidae (Fig. 5.1). The basihyal is short and toothed. The urohyal is blade-like, with a dorsal flange. The hypohyals are small and not incorporated in the anterior ceratohyal. The anterior and posterior ceratohyals are thin, deep, and widely separated from each other. The interhyal is cylindrical and relatively long. Eighteen branchiostegal rays are present.

The three basibranchials are fused into a single bone through a dorsal toothplate, and followed by a small cartilaginous element posteriorly. Hypobranchial 3 is much shorter than others. The third and fourth ceratobranchials bear ventral processes, and the fifth one is cylindrical and bears a dorsomedial toothplate. The first epibranchials bears an uncinate process that articulates cartilaginously with the uncinate process of pharyngobranchial 2 and the second bears an uncinate process that articulates with pharyngobranchial 3. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears an uncinate process that articulates with epibranchial 1. Pharyngobranchials 3 and 4 abut each other and bear toothplates.

In *Synodus variegatus*, the uncinate processes of the first epibranchial and the second pharyngobranchial are reduced and do not contact each other. The epibranchials 3 and 4 of *Scopelosaurus* (Notosudidae), epibranchial 3 of *Bathypterois* and *Bathysauropsis* (Ipnopidae), and epibranchial 4 of *Lestrolepis* (Paralepididae) and *Coccorella* (Evermannellidae) bear small uncinate processes (Baldwin and Johnson, 1996). In *Pseudotrichonotus* (Pseudotrichonotidae), the basihyal is large, hypohyals are attached to the anterior ceratohyal, branchiostegal rays are six, a fifth cartilaginous epibranchial is present, and pharyngobranchial 2 lacks an uncinate process (Johnson et al., 1996). *Alepisaurus* (Alepisauridae) lacks the first pharyngobranchial and the second pharyngeal toothplate, and some members of Aulopidae bear a fifth pharyngeal toothplate (Rosen, 1973).

Myctophiformes

Myctophidae (Fig. 5.2). The basihyal is absent. The urohyal is thin and broad. The hypohyals are separated from other elements and bear one branchiostegal ray. The anterior and posterior ceratohyals are thin and broad, and separated from each other. The interhyal is cylindrical. Eight branchiostegal rays are present.

The three basibranchials are followed by a cartilaginous element. Basibranchials 2 and 3 are elongated and bear anterior struts that articulate with the preceding basibranchial. Basibranchial 3 is toothed. The third pair of hypobranchials are tightly attached to basibranchial 3 and positioned obliquely ventral to that. The fourth and fifth ceratobranchials bear toothplates. The first epibranchial bears an uncinate process that articulates via cartilage with the uncinate process of pharyngobranchial 2, the second and the third bear dorsal flanges, and the fourth bears an uncinate process and a dorsal flange. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears an uncinate process that articulates with epibranchial 1. Pharyngobranchials 3 and 4 abut each other and bear toothplates. The third epibranchial of some Myctophiformes bear fused toothplates (Stiassny, 1996).

Lampridiformes

Veliferidae (Fig. 5.3). The basihyal is short. The urohyal is deep and thin. The hypohyals are relatively large and loosely attached to the anterior ceratohyal. The anterior and posterior ceratohyals are short, thin, deep, and separated from each other. The interhyal is cylindrical. Six branchiostegals are present.

The three basibranchials are followed by a cartilaginous element posteriorly. Basibranchial 2 is elongated and bears anterior and posterior struts that articulate with the basibranchials 1 and 3. The fourth ceratobranchial bears a ventral flange and the fifth bears a toothplate. The four short epibranchials, except epibranchial 2, bear uncinate processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears a short uncinate process that articulates with the first epibranchial uncinate process. Pharyngobranchial 4 is absent, but the fourth pharyngeal toothplate is present. The uncinate process of the fourth epibranchial is absent in Trachipteridae (Rosen, 1973). In Lamprididae, the first epibranchial lacks an uncinate process and pharyngeal toothplates are reduced (Olney et al., 1993).

Polymixiiformes

Polymixiidae. The basihyal is small. The urohyal consists of a bifurcated strut and flanges. The hypohyals are small and loosely attached to the anterior ceratohyal. The anterior and posterior ceratohyals are deep and separated from each other. The interhyal is cylindrical. Four large and two small branchiostegal rays are present.

The three basibranchials are tightly articulated together via cartilage, covered by a single toothplate, and followed by a posteriorly cartilaginous element. The fifth ceratobranchial bears a large toothplate. The four short epibranchials, except epibranchial 2, bear uncinate processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears an uncinate process that articulates with the first epibranchial uncinate process. Pharyngobranchial 4 is absent, but a toothplate is present.

Percopsiformes

Percopsidae. The basihyal is short. The urohyal consists of a blade and dorsal and ventral flanges. The dorsal hypohyal is incorporated in the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and narrower anteriorly and separated from the posterior ceratohyal. The interhyal is cylindrical. Six branchiostegal rays are present.

The three basibranchials are separated and followed by a cartilaginous element which is covered by a toothplate. The fifth ceratobranchial bears a large toothplate and abut its counterpart for its full length. The four short epibranchials, except epibranchial 2, bear uncinate processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears an uncinate process that articulates with the first epibranchial uncinate process. Pharyngobranchial 4 is absent, but a toothplate is present.

Mugiliformes

Mugilidae. The basihyal is small, but bears a large cartilaginous head anteriorly. The urohyal consists of a blade and a deep ventral and narrow lateral and medial flanges. The hypohyals are small and overlap the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and narrower anteriorly and connected to the posterior ceratohyal with lateral and medial struts. The interhyal is cylindrical. Six branchiostegal rays are present.

The three basibranchials are tightly articulated together cartilaginously, followed by a cartilaginous element posteriorly, and covered by several small toothplates. The fifth ceratobranchial bears gill rakers and a toothplate. The four short epibranchials bear uncinate processes. Pharyngobranchial 1 is present. An interarcual cartilage connects the second pharyngobranchial with the first epibranchial. Pharyngobranchials 3 and 4 and their toothplates are sutured together. Branchial arches are covered by triangular gill rakers.

Atheriniformes

Melanotaeniidae (Fig. 5.4). The basihyal is small, but bears a large cartilaginous head anteriorly. The urohyal consists of an anterodorsal process, a central blade, and ventral and narrow lateral flanges. The hypohyals are small and overlap the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly and connected to the posterior ceratohyal with dorsal struts. The interhyal is very short. Five branchiostegal rays are present.

The three basibranchials are tightly articulated together cartilaginously and followed by a cartilaginous element. The fifth ceratobranchial bears a large toothplate, and ventral and posterior processes. The four short epibranchials, except epibranchial 2, bear uncinate processes and epibranchial 4 is enlarged. An interarcual cartilage connects the second pharyngobranchial with the first epibranchial. Pharyngobranchial 1 is present, pharyngobranchials 3 and 4 are fused together and bear pharyngeal toothplates.

Atherinidae. The basihyal is small, but bears a large cartilaginous head anteriorly. The urohyal consists of a small anterodorsal process, a central blade, and ventral and narrow lateral flanges. The hypohyals are small and overlap the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly and connected to the posterior ceratohyal with dorsal struts. The interhyal is small. Six branchiostegal rays are present.

The three basibranchials are covered by thin toothplates and followed by a cartilaginous element. The fifth ceratobranchial bears a large toothplate, and ventral and posterior processes. The four short epibranchials bear uncinate processes and epibranchials 1 and 4 are enlarged. An interarcual cartilage connects the second pharyngobranchial with the first epibranchial. Pharyngobranchial 1 is present. Pharyngobranchial 3 and 4 and their toothplates are fused together. In Phallostethidae, hypohyals are absent or cartilaginous (Parenti, 1984) and epibranchials do not bear uncinate processes (Rosen and Parenti, 1981).

Beloniformes

Belonidae (Fig. 5.5). The basihyal is small, but bears a large cartilaginous head anteriorly. The urohyal is elongated and consists of a small anterodorsal process and a central blade which trifurcates posteriorly. The hypohyals overlap the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and gradually becomes narrower anteriorly and connected to the posterior ceratohyal with lateral and medial struts. The interhyal is absent. Eleven branchiostegal rays are present.

The three basibranchials are followed by a cartilaginous element. The hypobranchials are short and the third one is tightly connected to the ceratobranchial 3. The fifth ceratobranchials are fused together and toothed. Epibranchials 1-3 bear small processes at their bases and epibranchial 4 is simple and rodlike. Pharyngobranchial 1 is absent. Pharyngobranchial 2 is long and with its toothplate takes place of the epibranchials 3 and 4. Pharyngobranchials 3 and 4 and their toothplates are absent. Pharyngobranchials 2-4 and a small fourth pharyngeal toothplate are present in *Pseudotylosurus angusticeps, Potamorrhaphis,* and *Strongylura,* and pharyngobranchial 2 and its toothplate are present in *Belonion* (Collette, 1966).

Hemiramphidae (Fig.5.6). The basihyal is small, but bears a large cartilaginous head anteriorly. The urohyal is elongated and consists of a posteriorly bifurcated blade. The hypohyals overlap the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and gradually becomes narrower anteriorly and connected to the posterior ceratohyal with lateral and medial struts. The interhyal is absent. Twelve branchiostegal rays are present.

The three basibranchials are followed by a cartilaginous element. The hypobranchials are relatively short. The ceratobranchials are curved posteriorly functioning as epibranchials. The fifth ceratobranchials are fused together, toothed and bear a ventral process. Epibranchials 2-4 are triradiated and highly reduced, but epibranchial 4 is larger than 2 and 3. Pharyngobranchial 1 is absent. Pharyngobranchial 2 is enlarged and bears a large toothplate. Pharyngobranchials 3 and their toothplates are enlarged and fused together.

Cyprinodontiformes

Aplocheilidae (Fig. 5.7). The basihyal is short. The urohyal consists of a small anterodorsal process, a central blade, and dorsal, ventral, and lateral flanges. The hypohyals are small and incorporated in the anterior ceratohyal and positioned beside each other. The anterior ceratohyal is bifurcated anteriorly and each head articulates with one of the hypohyals. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly and connected to the posterior ceratohyal with dorsal struts. The interhyal is small. Seven branchiostegals are present.

The three basibranchials are roundish and followed by a cartilaginous element. The hypobranchials are small and relatively the same size. The fourth ceratobranchial is toothed anteriorly. The fifth ceratobranchial is toothed and bears ventral and posterior processes. The first epibranchial is reduced, the fourth is enlarged, and epibranchials 3 and 4 bear uncinate processes. An interarcual cartilage connects the second pharyngobranchial with the first epibranchial. Pharyngobranchial 1 is absent. Pharyngobranchials 3 and 4 and their toothplates are fused together. The basihyal of *Nothobranchius*, bears a large cartilaginous head, and epibranchial 4 of *Aplocheilus panchax* lacks an uncinate process (Parenti, 1981).

Cyprinodontidae. The basihyal is short. The urohyal consists of a small anterodorsal process, a blade, and dorsal and lateral flanges. The hypohyals are small and incorporated in the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly and connected to the posterior ceratohyal with dorsal struts. The interhyal is small. Six branchiostegal rays are present.

The two basibranchials are long and followed by a cartilaginous element. The hypobranchials are small and relatively the same size. The fourth ceratobranchial is toothed anteriorly and the fifth is toothed and bears ventral and posterior processes. The first epibranchial is reduced, the fourth is enlarged, and epibranchials 3 and 4 bear uncinate processes. An interarcual cartilage connects the second pharyngobranchial with the first epibranchial. Pharyngobranchial 1 is absent. Pharyngobranchial 3 is moved medially and its toothplate is fused to the fourth toothplate. Pharyngobranchial 4 is reduced, but bears a large fused toothplate. The basihyal of *Cubanichthys* bears a large cartilaginous head and Epibranchial 4 of *Procatopus* (Poeciliidae) lacks an uncinate process (Parenti, 1981).

Stephanoberyciformes

Stephanoberycidae (Fig.5.8). The basihyal is highly reduced to a small hardly recognizable cylindrical bone. The urohyal is highly reduced and consists of a bifurcated blade and a flange in between. The hypohyals are not incorporated in the anterior ceratohyal, but overlap the anterior ceratohyal, and are tightly connect to it cartilaginously. The anterior ceratohyal is deeper posteriorly and gradually becomes narrower anteriorly, separated from the posterior ceratohyal, and bears a small fenestra. The interhyal is cylindrical and relatively long. Eight branchiostegal rays are present.

The three basibranchials are long and followed by a cartilaginous element. The fifth ceratobranchial is reduced and toothless. Epibranchials 1 and 3 bear uncinate processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears an uncinate process that articulates with the uncinate process of the first epibranchial, but bears no toothplate. Pharyngobranchial 3 is thin, enlarged, and half of its surface covered by a toothplate. Pharyngobranchial 4 and its toothplate are reduced.

Rondeletiidae. The basihyal is reduced. The urohyal is highly reduced and consists of a bifurcated blade and a flange in between. The hypohyals are not incorporated in the anterior ceratohyal, but overlap the anterior ceratohyal, and are tightly connect to it cartilaginously. The anterior ceratohyal is deeper posteriorly and gradually becomes narrower anteriorly, separated from the posterior ceratohyal and bears a small fenestra. The interhyal is cylindrical and relatively long. Eight branchiostegal rays are present.

The three basibranchials are long and followed by a cartilaginous element. The third hypobranchial is smaller, oblique, and its cylindrical ventral process articulates with its counterpart ventrally. The fifth ceratobranchial is reduced and toothless. Epibranchials 1, 3, and 4 bear uncinate processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears an uncinate process that articulates with the uncinate process of the first epibranchial, but bears no toothplate. Pharyngobranchial 3 is thin, enlarged, and half of its surface covered by a toothplate. Pharyngobranchial 4 and its toothplate are reduced.

Beryciformes

Monocentridae. The basihyal is reduced. The urohyal consists of a blade and dorsal and ventral flanges. The hypohyals are not incorporated in the anterior ceratohyal, but overlap the anterior ceratohyal, and are tightly connect to it cartilaginously. The anterior ceratohyal is short and deeper posteriorly, and gradually becomes narrower anteriorly, separated from the posterior ceratohyal and bears a fenestra. The interhyal is cylindrical and relatively long. Eight branchiostegal rays are present.

The three basibranchials are long and followed by a cartilaginous element. The third hypobranchial is oblique, tightly connected to the third basibranchial, and its long cylindrical ventral process articulates with its counterpart ventrally. The fifth ceratobranchial is toothed. Epibranchials 1, 3, and 4 bear uncinate processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears an uncinate process that articulates with the uncinate process of the first epibranchial, but bears no toothplate. Pharyngobranchial 3 bears a toothplate, but epibranchial 4 and its toothplate are absent.

Holocentridae (Fig. 5.9). The basihyal is relatively long. The urohyal consists of a blade and a dorsal flange. The hypohyals are not incorporated in the anterior ceratohyal, but overlap the anterior ceratohyal, and are tightly connect to it cartilaginously. The anterior ceratohyal is short, deeper posteriorly and gradually becomes narrower anteriorly, separated from the posterior ceratohyal and bears a fenestra. The interhyal is cylindrical and relatively long. Eight branchiostegal rays are present.

The three basibranchials are long and followed by a cartilaginous element. The fifth ceratobranchial is toothed. Epibranchials 1, 3, and 4 bear uncinate processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears an uncinate process that articulates with the uncinate process of the first epibranchial, but bears no toothplate. Pharyngobranchial 3 is large and bears a toothplate. Pharyngobranchial 4 is absent, but a toothplate is present.

Zeiformes

Grammicolepididae (Fig. 5.10). The basihyal is enlarged and articulates with the second basibranchial. The urohyal consists of a blade and a dorsal flange. The hypohyals are relatively large, not incorporated in the anterior ceratohyal, but overlap the anterior ceratohyal, and are connect to it cartilaginously. The anterior ceratohyal is short, and deep, separated from the posterior ceratohyal and bears two fenestrae. The interhyal is cylindrical and relatively long. Seven branchiostegal rays are present.

The three basibranchials are long, the second is bent ventrally and at the bending point articulates with the basihyal and bears anterior and posterior struts that covers the first and third basibranchials. The first basibranchials is positioned ventral to the basihyal. The fifth ceratobranchial is reduced and toothless. Epibranchials 2-4 bear uncinate processes. Pharyngobranchial 1 is present. Pharyngobranchials 2 and 3 and their toothplates are reduced. Pharyngobranchial 4 and its toothplate are absent.

Caproidae (Fig. 5.11). The basihyal is moderate. The urohyal consists of a bifurcated blade, a dorsal flange, and a flange between the blades. The hypohyals are relatively large but not incorporated in the anterior ceratohyal. The anterior ceratohyal is short, deeper posteriorly and gradually becomes narrower anteriorly, bifurcated anteriorly and each fork receives a hypohyal. The anterior ceratohyal is connected to the posterior ceratohyal by lateral struts, and bears a fenestra. The interhyal is cylindrical and relatively long. Six branchiostegal rays are present.

The three basibranchials are long and followed by a small cartilaginous element. The fifth ceratobranchial is toothed. Epibranchials 1, 3 and 4 bear uncinate processes.

Pharyngobranchial 1 is present. Pharyngobranchials 2 and 3 and their toothplates are reduced. Pharyngobranchial 4 is absent, but a small toothplate is present. In *Antigonia capros*, a small fourth pharyngobranchial is present (Rosen, 1984).

Gasterosteiformes

Hypoptychidae (Fig. 5.12). The basihyal is elongated. The urohyal is long and consists of a blade, a posteriorly fimbriated dorsal flange, and ventrolateral flanges. The hypohyals are small and incorporated in the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and gradually becomes narrower anteriorly and separated from the posterior ceratohyal. The interhyal is small. Four branchiostegal rays are present.

The three basibranchials are long and cylindrical. The fifth ceratobranchial is toothless, cylindrical, and the same length as the others. Epibranchials 3 and 4 are reduced and bear uncinate processes. Pharyngobranchial 1 and 4 are absent. Pharyngobranchials 2 and 3 are long and cylindrical and bear few teeth.

Aulorhynchidae. The basihyal is elongated. The urohyal is long and consists of a blade, a dorsal flange, and posteriorly expanded (and fimbriated in *Aulorhynchus flavidus*) ventrolateral flanges. The hypohyals are small and incorporated in the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and gradually becomes narrower anteriorly and is separated from the posterior ceratohyal. The interhyal is present. Four branchiostegal rays are present.

The three basibranchials are long and cylindrical and followed by a cartilaginous element in *Aulorhynchus flavidus*. The fifth ceratobranchial is cylindrical and toothed. Epibranchial 4 is long and like 3 bears an uncinate process. Pharyngobranchial 1 is absent. Pharyngobranchials 2 and 3 and their toothplates are large. Pharyngobranchial 4 is absent, but a toothplate is present in *Aulorhynchus flavidus*.

Gasterosteidae (Fig. 5.13). The basihyal is elongated in *Spinachia spinachia* and moderate in others. The urohyal is long in *Spinachia spinachia*, moderate in others and consists of a blade, a dorsal flange, and ventrolateral flanges. The hypohyals are small and incorporated in the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly, and is connected to the posterior ceratohyal by dorsal struts. The interhyal is cylindrical. Three branchiostegal rays are present.

The three basibranchials are long and followed by a cartilaginous element. The hypobranchials are roundish and the third one is oblique. The fifth ceratobranchial is toothed. Epibranchial 4 is long and like 3 bears an uncinate process. Pharyngobranchial 1 is absent. Pharyngobranchials 2 and 3 bear toothplates. Pharyngobranchial 4 and its toothplate are absent.

Pegasidae (Fig. 5.14). The basihyal is moderate. The urohyal consists of a bifurcated blade, a flange in between, and narrow ventrolateral flanges. The hypohyals are relatively large and incorporated in the anterior ceratohyal. The anterior ceratohyal is deep and connected to the posterior ceratohyal by lateral struts. The interhyal is cylindrical. Five filamentous branchiostegal rays are present.

The two basibranchials are long. The third hypobranchial is absent. The fifth ceratobranchial is toothed. Epibranchial 4 is elongated and like 1-3 lacks an uncinate process. Pharyngobranchial 1 is absent. Pharyngobranchial 2 bears a toothplate. Pharyngobranchial 3 and 4 and their toothplates are absent. Gill filaments are lophobranch with skeleton fused basally as described by Johnson and Patterson (1993).

Solenostomidae (Fig. 5.15). The basihyal is absent. The urohyal is elongated and consists of a posteriorly bifurcated blade. The hypohyals are incorporated into the anterior ceratohyal. The anterior ceratohyal is elongated and separated from the posterior ceratohyal. The posterior ceratohyal is reduced. The interhyal is small, cylindrical, and located in a notch posterior to the posterior ceratohyal. One bifurcated, filamentous, and elongated branchiostegal ray is present.

Basibranchials and the third hypobranchial are absent. The fifth ceratobranchial is cylindrical and toothed. Epibranchials are absent. Pharyngobranchial 1 is absent. Pharyngobranchial 2 is absent, but a toothplate is present. Pharyngobranchial 3 bears a long toothplate. Pharyngobranchial 4 and its toothplate are absent. No gill rakers are present on the branchial arches, but few small teeth are present on the cartilaginous distal end of the ceratobranchials (epibranchials of Orr (1995)). Gill filaments are lophobranch with skeleton fused basally.

Syngnathidae. The basihyal is short and cylindrical. The urohyal is elongated and consists of a posteriorly bifurcated blade. The hypohyals are highly incorporated in the anterior ceratohyal and the ventral hypohyal is the largest element and embraces the anterior ceratohyal and articulates with the posterior ceratohyal. The anterior ceratohyal is tightly connected to the posterior ceratohyal. The interhyal is relatively large and round, and located in a notch posterior to the posterior ceratohyal. Two filamentous and elongated branchiostegal rays are present.

Basibranchials 2 and 3 are absent. Hypobranchial 1 and 2 are long and hypobranchial 3 is absent. Ceratobranchials 3-5 are angled and bear ventral processes at their angling point. The fifth ceratobranchial is cylindrical and toothless. Epibrancial 4 is absent. Pharyngobranchial 1 is absent. Pharyngobranchial 2 is cylindrical and pharyngobranchial 3 bears an uncinate process. All the toothplates are absent. Gill filaments are lophobranch with skeleton fused basally.

Indostomidae. The basihyal is enlarged. The urohyal consists of a posteriorly bifurcated blade and a dorsal flange. The hypohyals are highly incorporated in the anterior ceratohyal. The anterior ceratohyal is tightly connected to the posterior ceratohyal. The interhyal is small. Six branchiostegal rays are present.

The three basibranchials are followed by a large cartilaginous element. The hypobranchials are rectangular. Ceratobranchials 4 and 5 are toothed. Epibranchials bear no uncinate processes and epibranchial 4 is slightly enlarged. Pharyngobranchials 1 and 2 are absent. Pharyngobranchial 4 is absent, but a toothplate is present. Gill filaments are lophobranch with skeleton fused basally.

Aulostomidae (Fig. 5.16). The basihyal is elongated. The urohyal is an elongated and posteriorly deepened blade. The hypohyals are highly incorporated in the anterior ceratohyal and the ventral hypohyal is large and articulated with the posterior ceratohyal. The anterior ceratohyal is tightly connected to the posterior ceratohyal and bears a small fenestra. The posterior ceratohyal bears medial and lateral extensions that articulate with anterior ceratohyal and ventral hypohyal. The interhyal is large and triangular. Four branchiostegal rays are present.

Basibranchials 2 and 3 are absent. The hypobranchials are short, hourglass shaped, and the third hypobranchial consists only of a ventral cylindrical process. The fifth ceratobranchial is reduced, cylindrical, and bears a toothplate. Epibranchial 1 bears an uncinate process and epibranchial 4 is absent. Pharyngobranchial 1 is absent. Pharyngobranchials 2 and 3 are cylindrical, long, and bear toothplates. Pharyngobranchial 4 is absent, but a toothplate is present.

Fistulariidae. The basihyal is elongated. The urohyal is elongated and consists of a posteriorly bifurcated blade. The hypohyals are tightly articulated with the anterior ceratohyal and the ventral hypohyal articulates with the posterior ceratohyal. The anterior ceratohyal is tightly connected to the posterior ceratohyal by strong struts. The interhyal is fused to the posterior ceratohyal. Five branchiostegal rays are present.

Basibranchials 2 and 3 are absent. The hypobranchials are small. The fifth ceratobranchial is reduced, cylindrical, and toothless. Epibranchial 1 bears an uncinate process and epibranchial 4 is absent. Pharyngobranchial 1 is absent. Pharyngobranchial 2 is cylindrical, long, and bears a toothplate. Pharyngobranchial 3 and 4 are absent, but toothplates are present. No gill rakers are present on the branchial arches.

Macroramphosidae(Fig. 5.17). The basihyal is elongated. The urohyal is elongated and consists of a posteriorly trifurcated blade and a ventral flange. The hypohyals are tightly articulated with the anterior ceratohyal and the ventral hypohyal is enlarged. The anterior ceratohyal is separated from the posterior ceratohyal. The posterior ceratohyal is reduced. The interhyal is relatively large, round, and sutured in a notch posterodorsal to the posterior ceratohyal. Four short branchiostegal rays are present.

Basibranchial 1 is fused to the basihyal and a cartilaginous element follows the third basibranchial. Hypobranchials bear short ventral processes. The fifth ceratobranchial is reduced, cylindrical, and toothed. Epibranchial 1 is highly enlarged and epibranchials 1-4 bear uncinate processes. Pharyngobranchial 1 is absent. Pharyngobranchials 2-4 and their toothplates are reduced.

Centriscidae. The basihyal is elongated and depressed. The urohyal is elongated and consists of a posteriorly bifurcated blade and a dorsal flange. The hypohyals are tightly articulated with the anterior ceratohyal. The ventral hypohyal is the largest element, embraces the anterior ceratohyal, and articulates with the posterior ceratohyal. The anterior ceratohyal is tightly connected to the posterior ceratohyal. The interhyal is relatively large and round, and sutured in a notch posterior to the posterior ceratohyal. Four filamentous and elongated branchiostegal rays are present.

Basibranchial 1 is fused to the basihyal. The third hypobranchial bears a short ventral process. The fifth ceratobranchial is cylindrical and toothed. Epibranchials 3 and 4 bear uncinate processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 and 3 bear toothplates. Pharyngobranchial 4 is absent, but a toothplate is present.

Synbranchiformes

Synbranchidae (Fig. 5.18). The basihyal is cylindrical, long, and fused to the first basibranchial. The urohyal is long, anteriorly depressed, and consists of a strong blade. The hypohyals are incorporated in the anterior ceratohyal. The anterior ceratohyal becomes abruptly narrower anteriorly and is connected to the posterior ceratohyal by strong struts. The interhyal is long. Six branchiostegal rays are present.

The first basibranchial is fused to the basihyal and basibranchials 2 and 3 are absent. The hypobranchials are long and the third one consists of only a small cylindrical ventral process. The fifth ceratobranchial is cylindrical and toothed. An interarcual bone that connects epibranchial 1 to pharyngobranchial 2 is present. Epibranchial 3 bears an uncinate process and epibranchial 4 is enlarged. Pharyngobranchial 1 is absent. Pharyngobranchial 2 is small and cylindrical. Pharyngobranchials 3 and 4 are absent, but toothplates are present. No gill rakers are present on the branchial arches.

In *Macrotrema, Ophisternon* and *Synbranchus*, basibranchials 2 and 3 are present. In *Monopterus boueti, M. cuchia*, and some specimens of *M. albus*, a vestigial basibranchial 2 is present. In *Monopterus cuchia*, the first epibranchial is absent and others lack the uncinate processes. In *Ophisternon* and *Synbranchus*, the fourth epibranchial bears an uncinate process and pharyngobranchial 3 is present (Rosen and Greenwood, 1976).

Mastacembelidae. The basihyal is cylindrical and long. The urohyal is long and consists of a blade and a bifurcated dorsal flange. The hypohyals are incorporated in the anterior ceratohyal. The anterior ceratohyal becomes abruptly narrower anteriorly and is connected to the posterior ceratohyal by strong struts. The interhyal is small. Six branchiostegal rays are present.

The three basibranchials are followed by a cartilaginous element. The first basibranchial is fused to the basihyal. The hypobranchials are short and all bear cylindrical ventral processes. The fifth ceratobranchial is toothed. Epibranchials 3 and 4 bear uncinate processes. Pharyngobranchial 1 is absent. Pharyngobranchial 2 is absent, but a small toothplate is present. Pharyngobranchial 3 and a small pharyngobranchial 4 and their toothplates are present. No gill rakers are present on the branchial arches.

Scorpaeniformes

Dactylopteridae (Fig. 5.19). The basihyal is cylindrical. The urohyal is small and consists of a bifurcated blade and a flange in between. The hypohyals are incorporated in the anterior ceratohyal. The anterior ceratohyal is hourglass shaped and separated from the posterior ceratohyal. The interhyal is cylindrical and long. Six branchiostegal rays are present.

The three cylindrical basibranchials are followed by a cartilaginous element. The hypobranchials are short and all are oblique and bear cylindrical ventral processes. The fifth ceratobranchial is toothed. Epibranchials 1, 3, and 4 bear uncinate processes. Pharyngobranchial 1 is cartilaginous. Pharyngobranchial 2 bears a small toothplate. Pharyngobranchial 4 is absent, but a small toothplate is present.

Scorpaenidae (Fig. 5.20). The basihyal is cylindrical. The urohyal is shorter than the hyoid arch and consists of a blade and a dorsal flange. The hypohyals are not tightly articulated with the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly and is separated from the posterior ceratohyal. The interhyal is cylindrical and long. Seven branchiostegal rays are present.

The three cylindrical basibranchials are followed by a cartilaginous element. Hypobranchial 1 is angled and hypobranchial 3 is oblique and bears a cylindrical ventral process. The fourth ceratobranchial bears a ventral process. The fifth ceratobranchial is toothed and expanded anteroventrally. Epibranchials 1, 3, and 4 bear uncinate processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears a small toothplate, an uncinate process, and is connected to the first epibranchial by an interarcual cartilage. Pharyngobranchial 4 is absent, but a small toothplate is present.

Hexagrammidae. The basihyal is depressed. The urohyal is shorter than the hyoid arch and consists of a blade, an anterodorsal process, and a dorsal flange. The hypohyals are not tightly articulated with the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly, and is connected to the posterior ceratohyal by small medial struts. The interhyal is cylindrical and long. Six branchiostegal rays are present.

Three cylindrical basibranchials are present. The hypobranchials are short. The fifth ceratobranchial is cylindrical and toothed. The fourth epibranchial is slightly larger than 2 and 3. Epibranchials 1, 3, and 4 bear uncinate processes. Pharyngobranchial 1 is absent. Pharyngobranchial 2 bears a small toothplate. Pharyngobranchial 4 is absent, but a small toothplate is present.

Agonidae (Fig. 5.21). The basihyal is absent. The urohyal is shorter than the hyoid arch and consists of a blade, a dorsal flange, and broad ventrolateral flanges. The hypohyals are not tightly articulated with the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly and is separated from the posterior ceratohyal. The interhyal is cylindrical and long. Six branchiostegal rays are present.

The three tightly connected basibranchials are followed by a small cartilaginous element. The hypobranchials are short. The fourth ceratobranchial bears a ventral process. The fifth ceratobranchial is toothed. Epibranchials 1, 3, and 4 bear uncinate processes. Pharyngobranchial 1 is absent. Pharyngobranchial 2 bears a small toothplate. Pharyngobranchial 3 and 4 are absent. In *Anoplagonus*, the third and/or the second basibranchial are absent. In *Tilesina, Brachyopsis*, and *Pallasina*, the third basibranchial is absent (Kanayama, 1991).

Perciformes

Percidae. The basihyal is cylindrical. The urohyal consists of a blade, a dorsal flange, and narrow ventrolateral flanges. The hypohyals are not tightly articulated with the anterior ceratohyal and the dorsal hypohyal bears a fenestra. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly and is separated from the posterior ceratohyal, but tiny medial struts are present. The interhyal is cylindrical and long. Seven branchiostegal rays are present.

The three cylindrical basibranchials are followed by a small cartilaginous element. Hypobranchials are short and the first one is angled. The fifth ceratobranchial is toothed and bears a narrow ventral flange. Epibranchials 1, 3, and 4 bear uncinate processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears a small toothplate and is connected to the epibranchial 1 uncinate process by an interarcual cartilage. Pharyngobranchial 4 is reduced and bears a toothplate.

Cirrhitidae. The basihyal is cylindrical and relatively long. The urohyal consists of a blade, a dorsal flange, and narrow ventrolateral flanges. The hypohyals are incorporated in the anterior ceratohyal and dorsal hypohyal bears a fenestra. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly and is separated from the posterior ceratohyal. The interhyal is cylindrical and long. Six branchiostegal rays are present.

The three basibranchials are followed by a small cartilaginous element. Hypobranchials 1 and 2 are short, broad, and bifurcated proximally. The fourth ceratobranchial bears a small ventral flange and the fifth ceratobranchial is toothed and bears a ventral flange. Epibranchials 1, 3, and 4 bear uncinate processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears a small toothplate and is connected to the first epibranchial by an interarcual cartilage. Pharyngobranchial 4 is absent, but a toothplate is present.

Elassomatidae (Fig. 5.22). The basihyal is flattened. The urohyal consists of an anterodorsal process, a posteriorly bifurcated blade and a flange in between, and narrow ventrolateral flanges. The hypohyals overlap the anterior ceratohyal and the dorsal hypohyal bears a fenestra. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly, is separated from the posterior ceratohyal, but tiny medial struts are present. The interhyal is cylindrical. Five branchiostegal rays are present.

The three basibranchials are followed by a cartilaginous element. The hypobranchial are short. The fifth ceratobranchial is toothed and bears a small ventral flange. Epibranchial 3 bears an uncinate process. Pharyngobranchial 1 is absent. Pharyngobranchial 2 bears a small toothplate. Pharyngobranchial 4 is absent, but a small toothplate is present.

Pomacentridae (Fig. 5.23). The basihyal is flattened. The urohyal consists of an anterodorsal process, a posteriorly bifurcated blade, a flange in between, and narrow ventrolateral flanges. The hypohyals are incorporated in the anterior ceratohyal and the dorsal hypohyal bears a fenestra. The anterior ceratohyal is deeper posteriorly and gradually becomes narrower anteriorly, is connected to the posterior ceratohyal with medial and lateral struts, and bears a small fenestra. The interhyal is cylindrical. Six branchiostegal rays are present.

The three basibranchials are followed by a cartilaginous element and the first basibranchial is curved posteriorly and lies ventral to the second one. The hypobranchial are short. The fourth basibranchial bears a small ventral flange. The fifth ceratobranchials are fused together, toothed, and bear posterior extensions. Epibranchials 1, 3, and 4 bear uncinate processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears a small toothplate and is connected to the first epibranchial uncinate process by a rodlike interarcual cartilage. Pharyngobranchial 4 and its toothplate are absent.

Centrarchidae (Fig. 5.24). The basihyal is short. The urohyal consists of an anterodorsal process, a posteriorly bifurcated blade, a flange in between, and narrow ventrolateral flanges. The hypohyals are not tightly articulated with the anterior ceratohyal. The anterior ceratohyal is deeper posteriorly and abruptly becomes narrower anteriorly, is connected to the posterior ceratohyal with medial struts, and bears a large fenestra. The interhyal is cylindrical. Six branchiostegal rays are present.

The three basibranchials are followed by a cartilaginous element. Hypobranchials are short. The fourth basibranchial bears a small ventral flange. The fifth ceratobranchial is toothed and bears a ventral flange. Epibranchials 1, 3, and 4 bear uncinate processes. Pharyngobranchial 1 is present. Pharyngobranchial 2 bears a small toothplate and is connected with a rodlike interarcual cartilage to the first epibranchial uncinate process. Pharyngobranchial 4 is absent, but a toothplate is present.

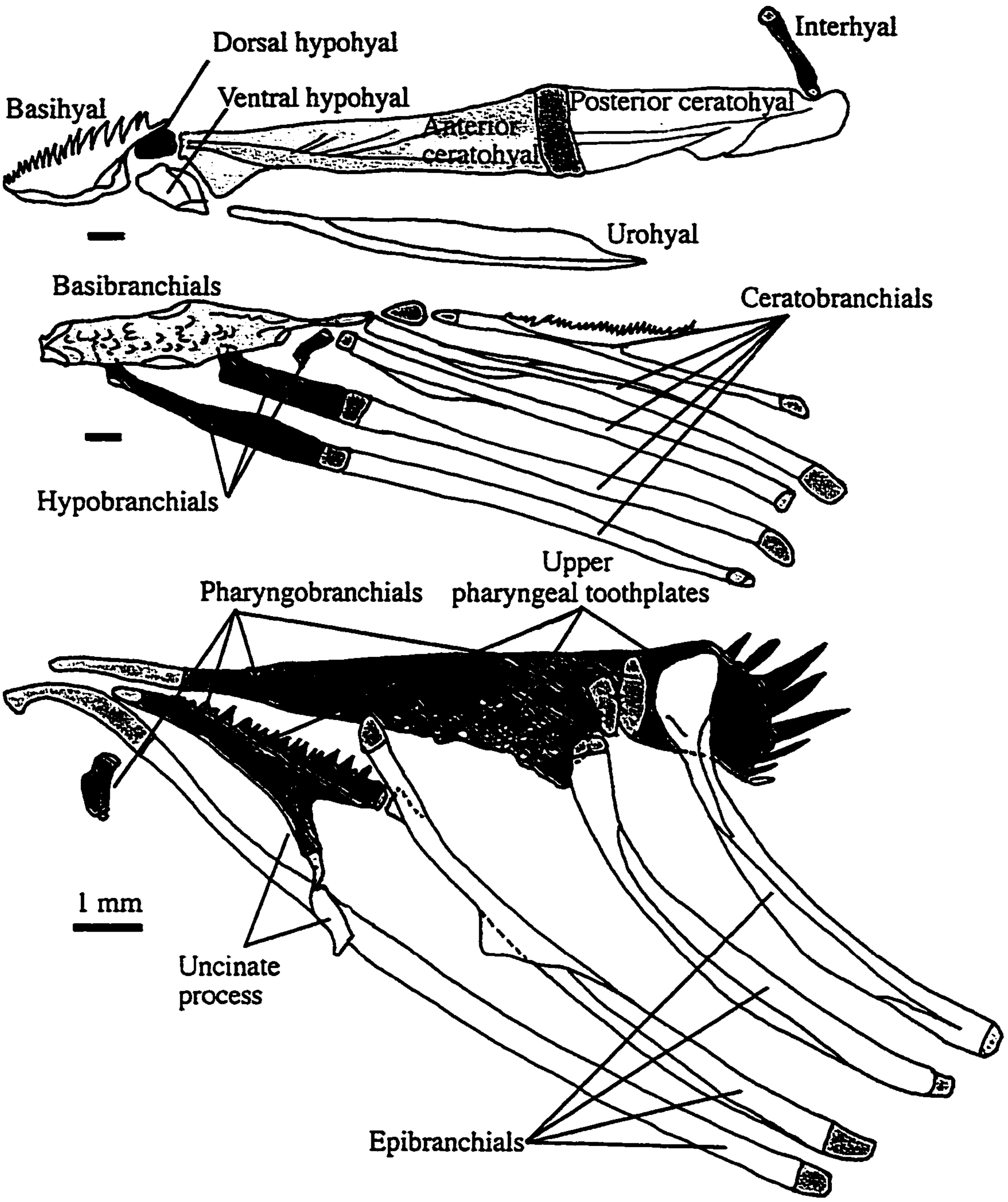

Fig. 5.1. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral (middle), and dorsal (bottom) branchial arches in *Synodus synodus* (**Synodontidae**) (UAMZ 1806, 147 mm).

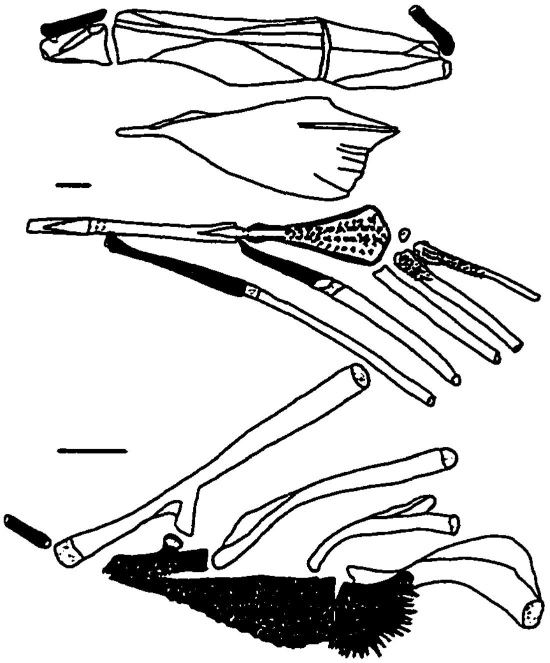

Fig. 5.2. Lateral view of the left hyoid arch (top), dorsal view of the left ventral branchial arches (middle), and ventral view of the dorsal branchial arches (bottom) in *Myctophum sp.* (**Myctophidae**) (UAMZ 2689, 60 mm).

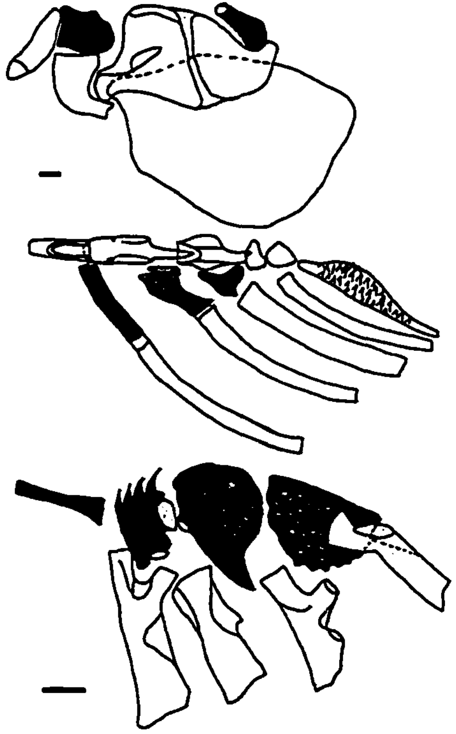

Fig. 5.3. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral (middle) and dorsal (bottom) branchial arches in *Velifer hypselopterus* (**Veliferidae**) (AMS 21839005, 101 mm).

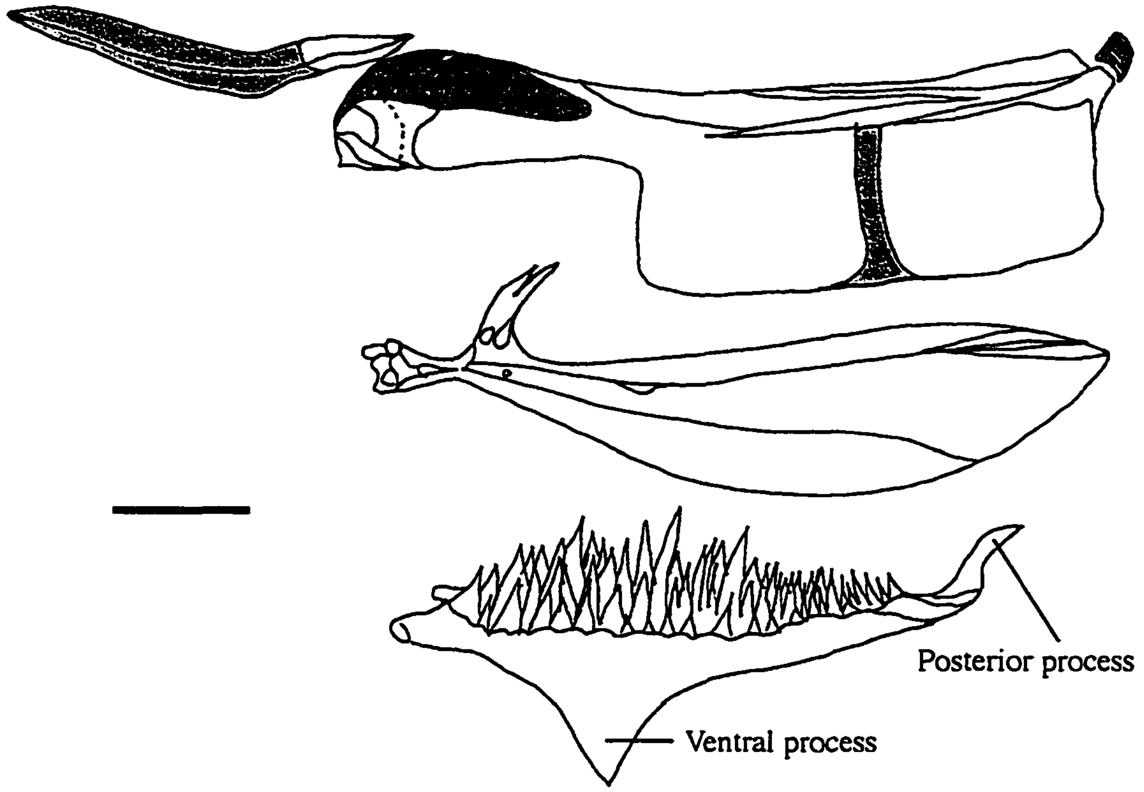

Fig. 5.4. Lateral view of the left hyoid arch (top) and the left fifth ceratobranchial (bottom) in *Melanotaenia sp.* **(Melanotaeniidae)** (UAMZ 3526, 51 mm).

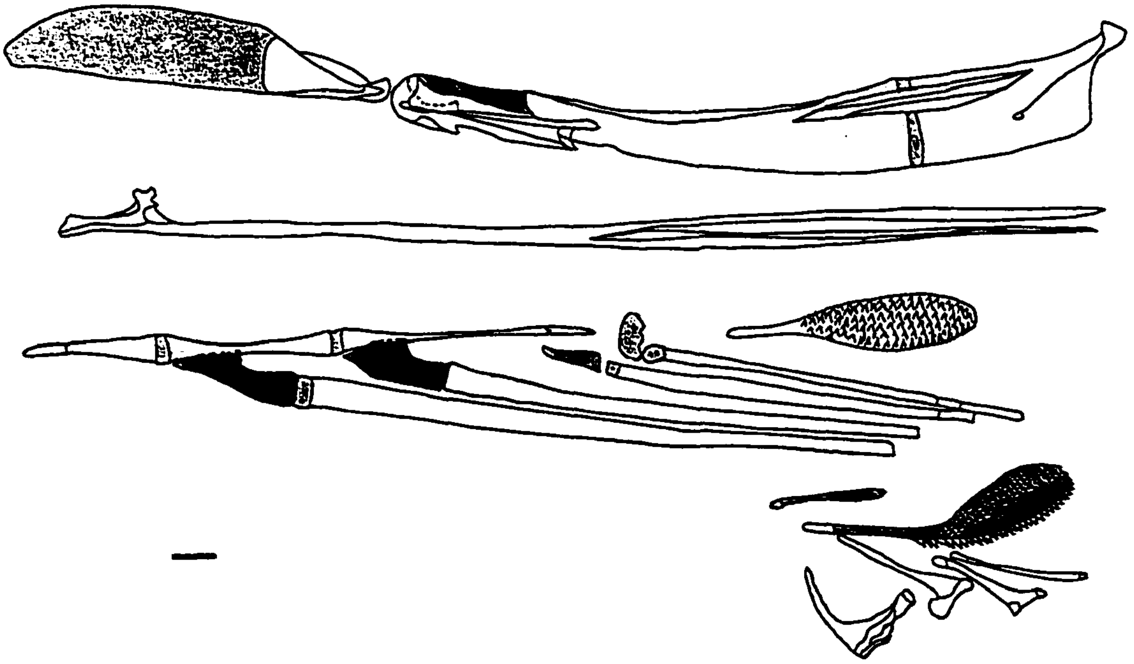

Fig. 5.5. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral (middle) and dorsal (bottom) branchial arches in *Pseudotylus sp.* **(Belonidae)** (UAMZ 8165, 173 mm).

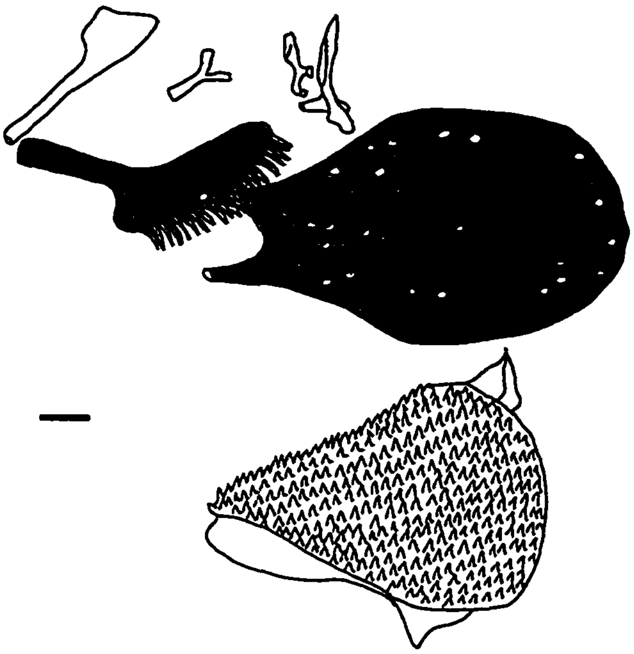

Fig. 5.6. Dorsal view of the right dorsal branchial arches (top) and the fifth ceratobranchials (bottom) in *Arrhamphus sclerolepis* **(Hemiramphidae)** (UAMZ 3523, 103 mm).

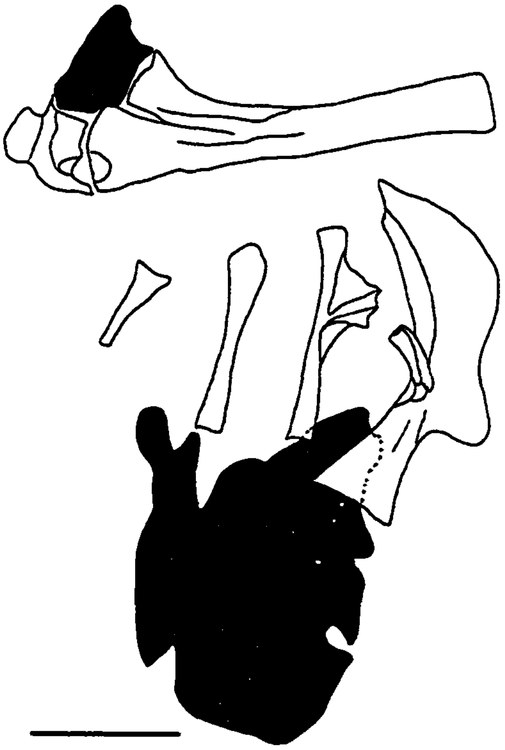

Fig. 5.7. Dorsal view of the left anterior ceratohyal and hypohyals (top) and the right dorsal branchial arches (bottom) in *Rivulus hartii* **(Cyprinodontidae)** (UAMZ 6660, 47 mm).

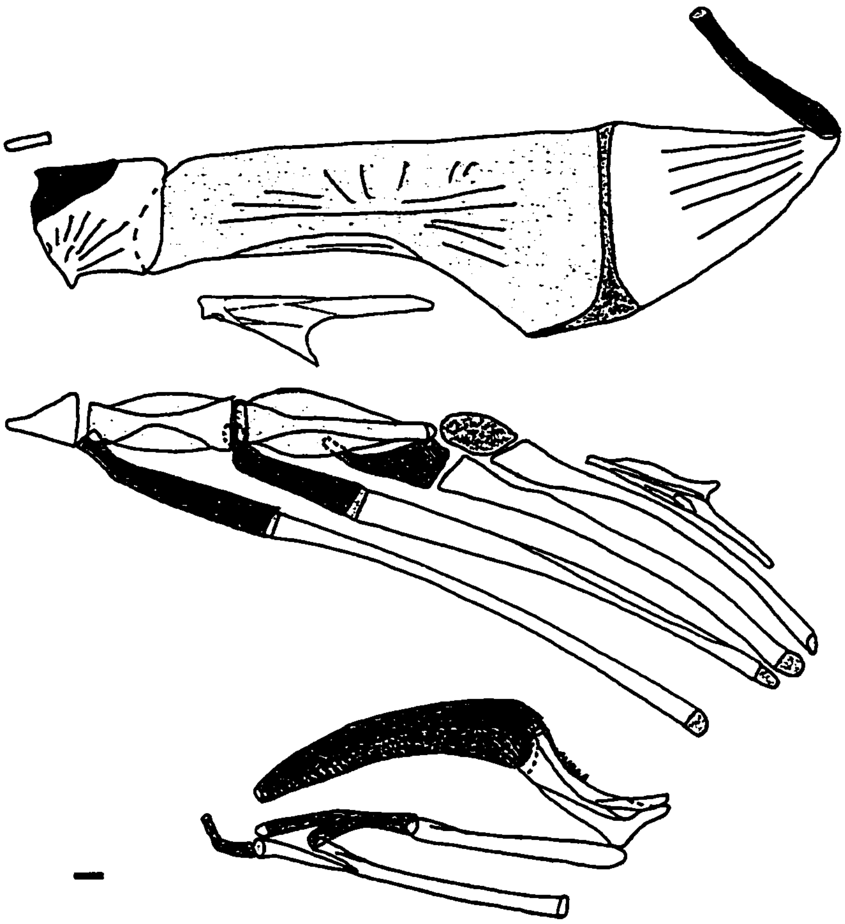

Fig. 5.8. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral (middle) and dorsal (bottom) branchial arches in *Stephanoberyx monae* **(Stephanoberycidae)** (USNM 304353, 92 mm).

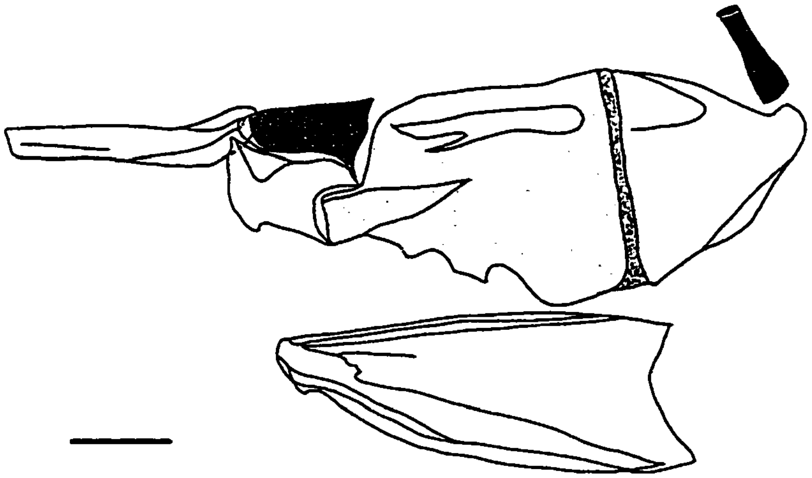

Fig. 5.9. Lateral view of the left hyoid arch in *Sargocentron vexillarium* **(Holocentridae)** (UAMZ 5075, 44 mm).

Fig. 5.10. Lateral view of the left hyoid arch (top), basihyal and basibranchials (middle), and ventral view of the left dorsal branchial arches (bottom) in *Xenolepidichthys dalgleishi* **(Grammicolepididae)** (USNM 322673, 68 mm).

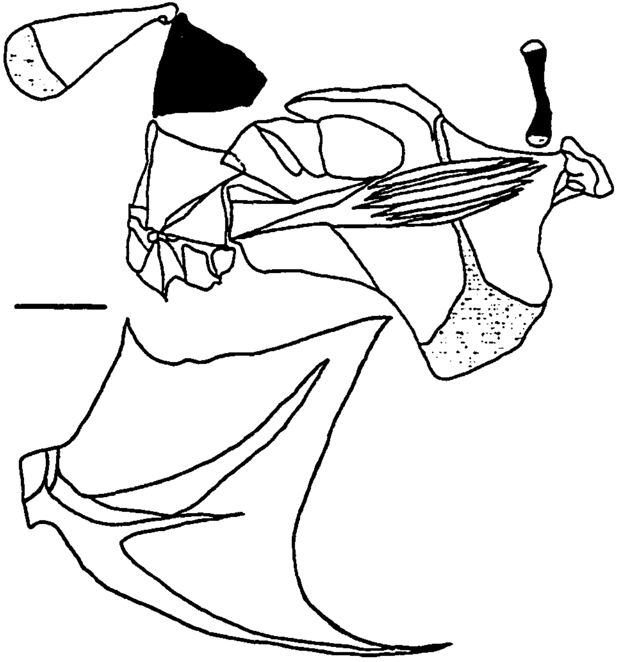

Fig. 5.11. Lateral view of the left hyoid arch in *Antigonia sp.* **(Caproidae)** (USNM 266901, 37 mm).

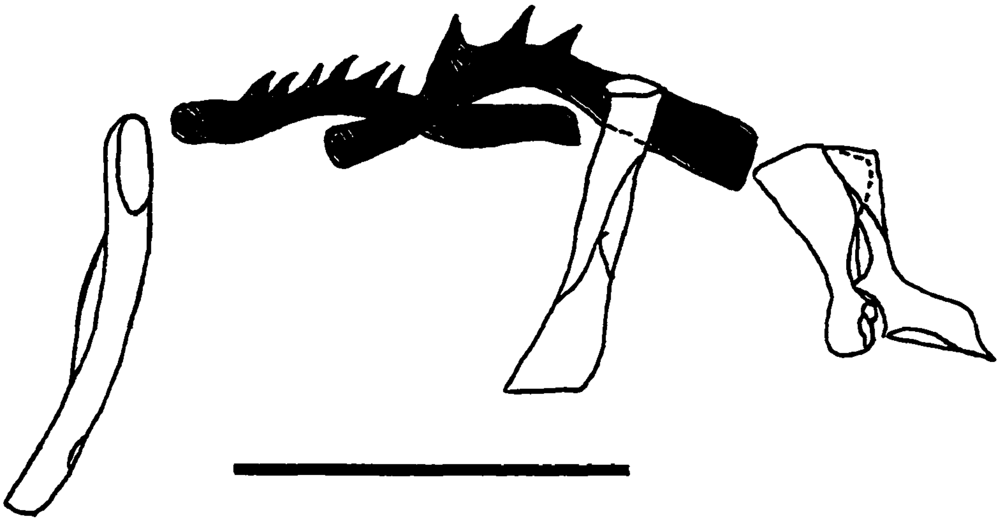

Fig. 5.12. Dorsal view of the left dorsal branchial arches in *Hypoptychus dybowskii* **(Hypoptychidae)** (UAMZ 5550, 80 mm).

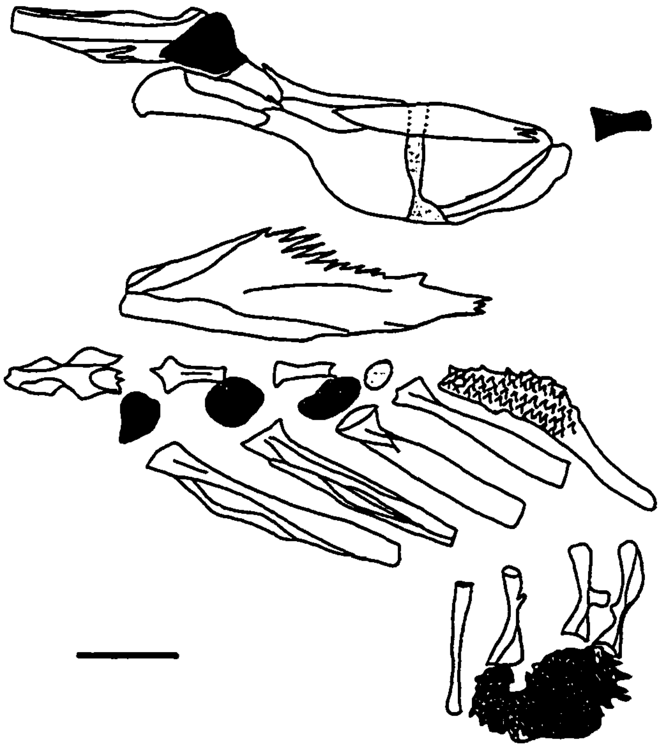

Fig. 5.13. Lateral view of the left hyoid arch (top), dorsal view of the left ventral branchial arches (middle), and ventral view of the left dorsal branchial arches (bottom) in *Apeltes quadracus* **(Gasterosteidae)** (UAMZ 7958, 37 mm).

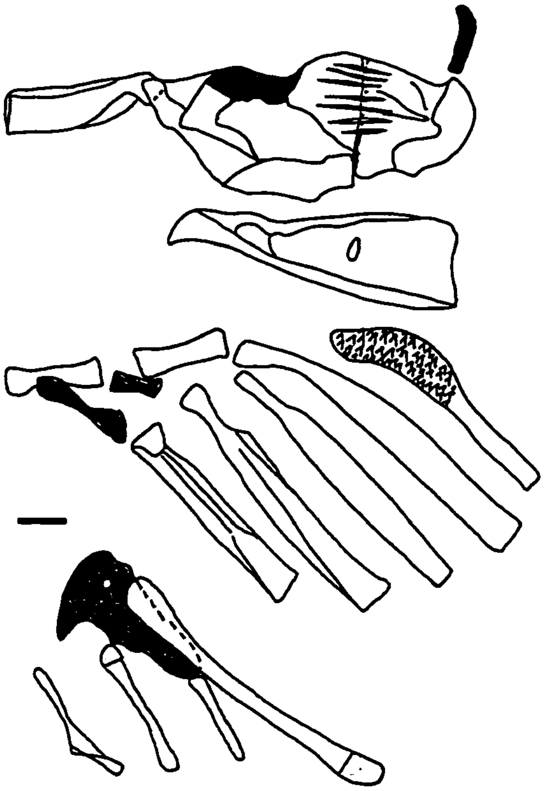

Fig. 5.14. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral (middle) and dorsal (bottom) branchial arches in *Pegasus volans* **(Pegasidae)** (UAMZ 4616, 99 mm).

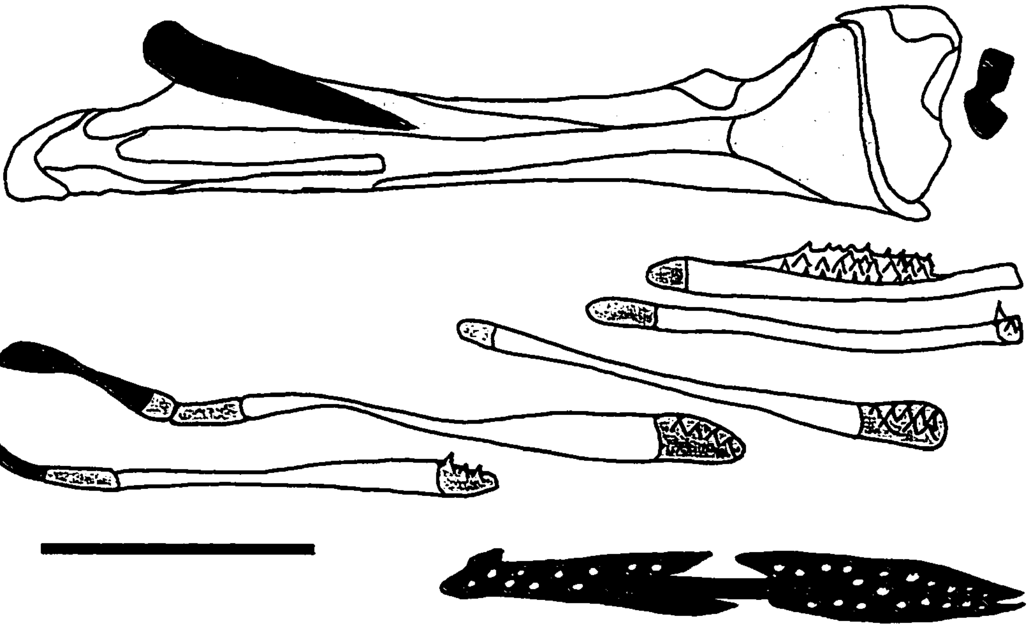

Fig. 5.15. Lateral view of the left hyoid arch (top), and dorsal view of the left ventral (middle) and the dorsal (bottom) branchial arches in *Solenostomus paradoxus* **(Solenostomidae)** (AMS 17111002, 51 mm).

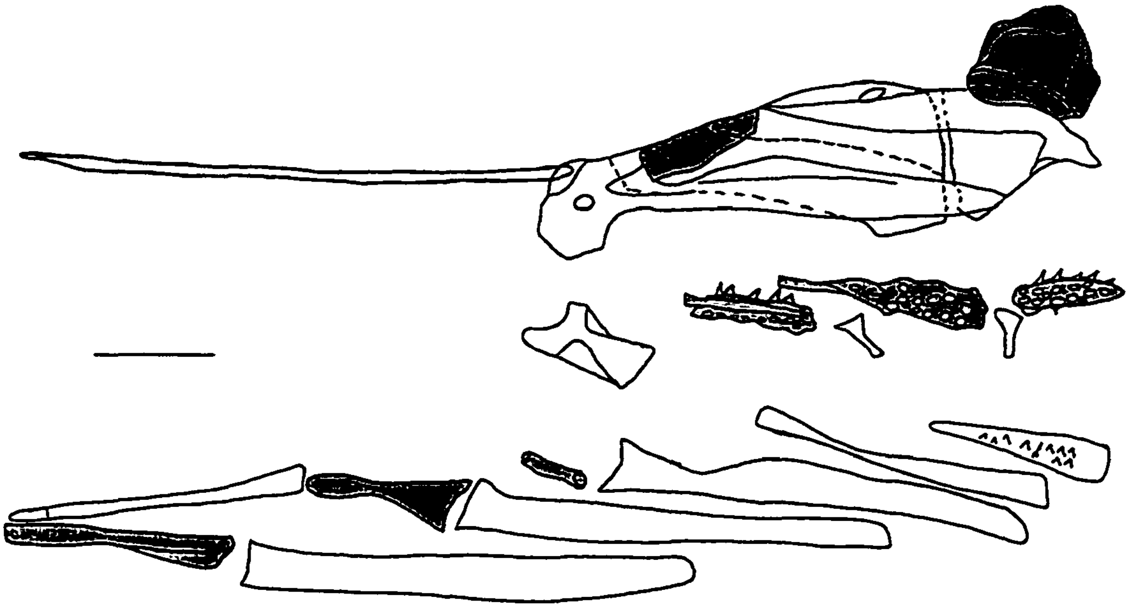

Fig. 5.16. Lateral view of the left hyoid arch (top), and dorsal view of the left dorsal (middle) and ventral (bottom) branchial arches in *Aulostomus valentini* (**Aulostomidae**) (CAS 11979, 139 mm).

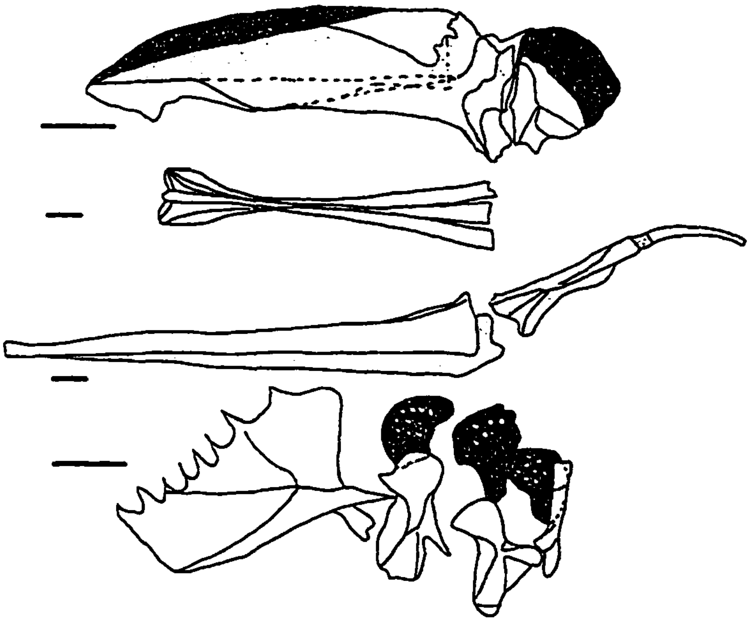

Fig. 5.17. Lateral view of the left hyoid arch and dorsal view of the urohyal (top), lateral view of the basihyal and basibranchials (middle), and dorsal view of the left dorsal branchial arches (bottom) in *Macroramphosus scolopax* (**Macroramphosidae**) (USNM 344398, 99 mm).

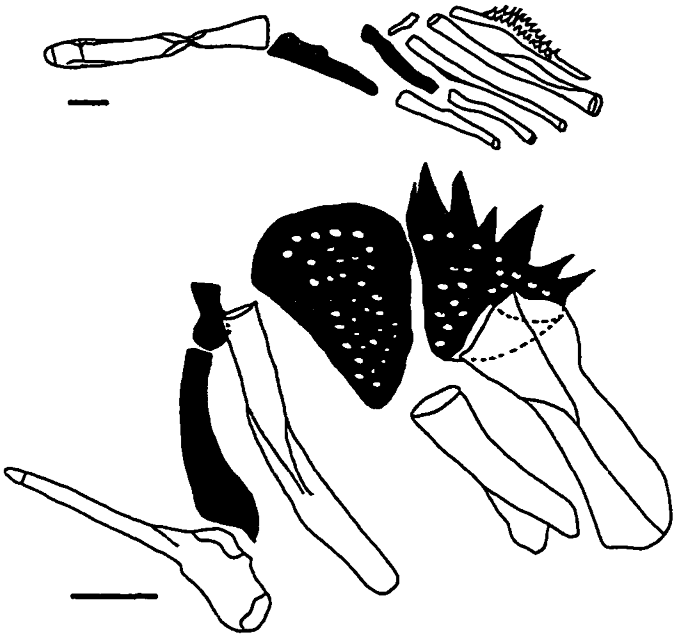

Fig. 5.18. Dorsal view of the left ventral branchial arches (top) and dorsal branchial arches (bottom) in *Monopterus albus* (**Synbranchidae**) (USNM 192939, 193 mm).

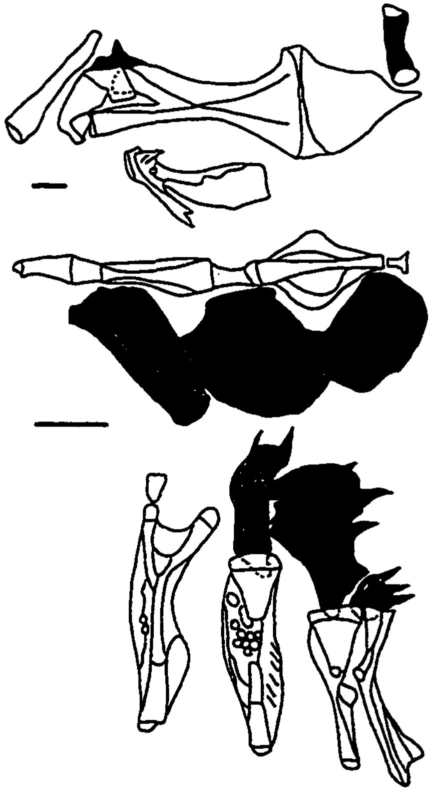

Fig. 5.19. Lateral view of the left hyoid arch (top), dorsal view of the basibranchials and left hypobranchials (middle), and dorsal view of the dorsal branchial arches (bottom) in *Dactylopterus volitans* (**Dactylopteridae**) (UAMZ 2633, 74 mm).

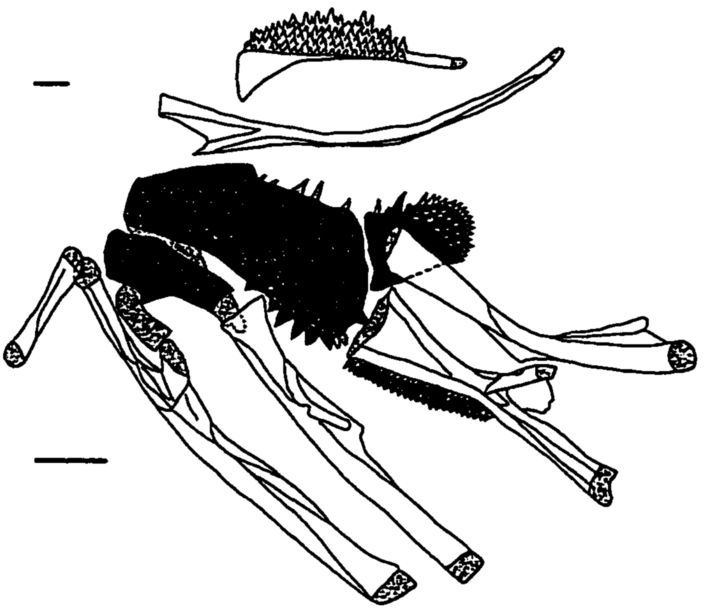

Fig. 5.20. Lateral view of the left fourth and fifth ceratobranchials (top) and dorsal view of the left dorsal branchial arches (bottom) in *Sebastes caurinus* **(Scorpaenidae)** (UAMZ 3142, 75 mm).

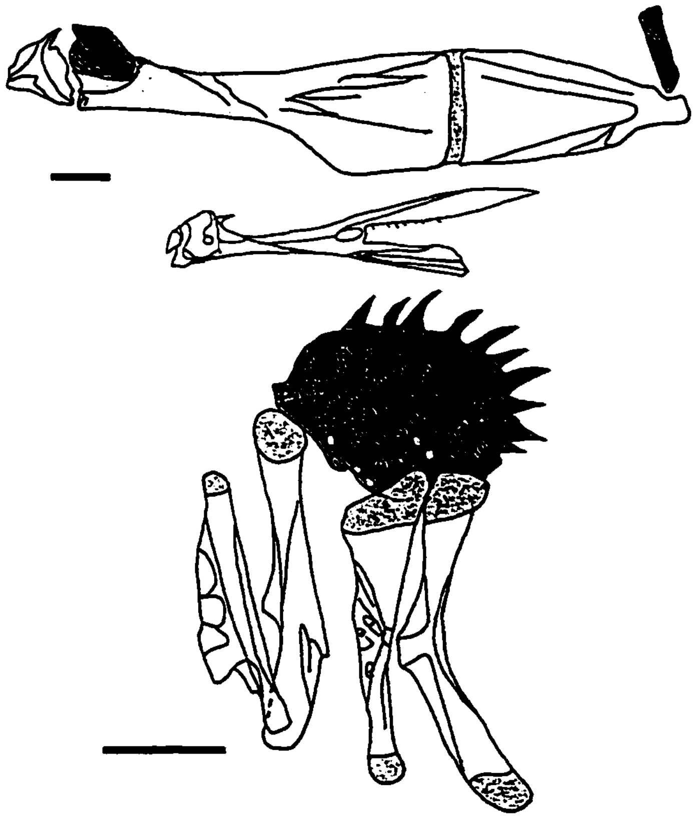

Fig. 5.21. Lateral view of the left hyoid arch (top) and dorsal view of the left dorsal branchial arches (bottom) in *Xeneretmus latifrons* **(Agonidae)** (UAMZ 3196, 95 mm).

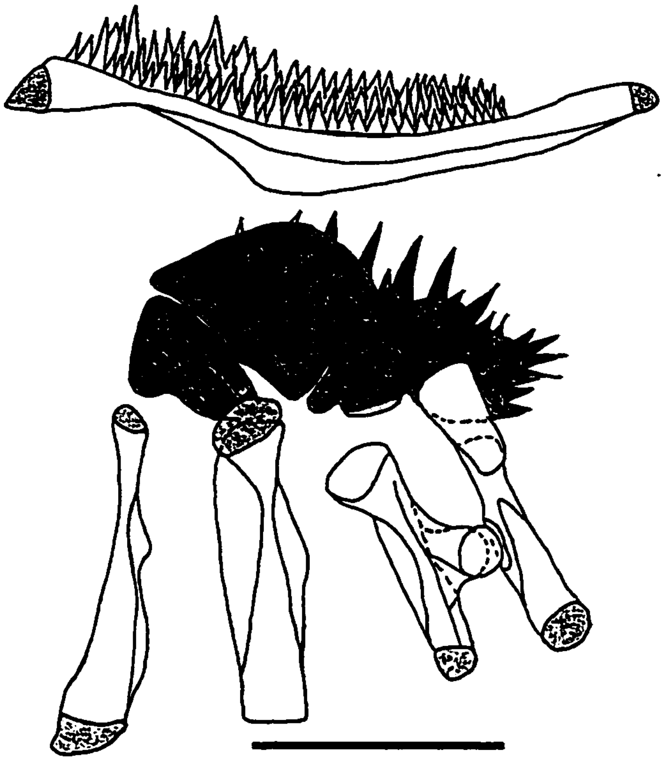

Fig. 5.22. Lateral view of the left fifth ceratobranchial (top) and dorsal view of the left dorsal branchial arches (bottom) in *Elassoma zonatum* (**Elassomatidae**) (UAMZ 6920, 30 mm).

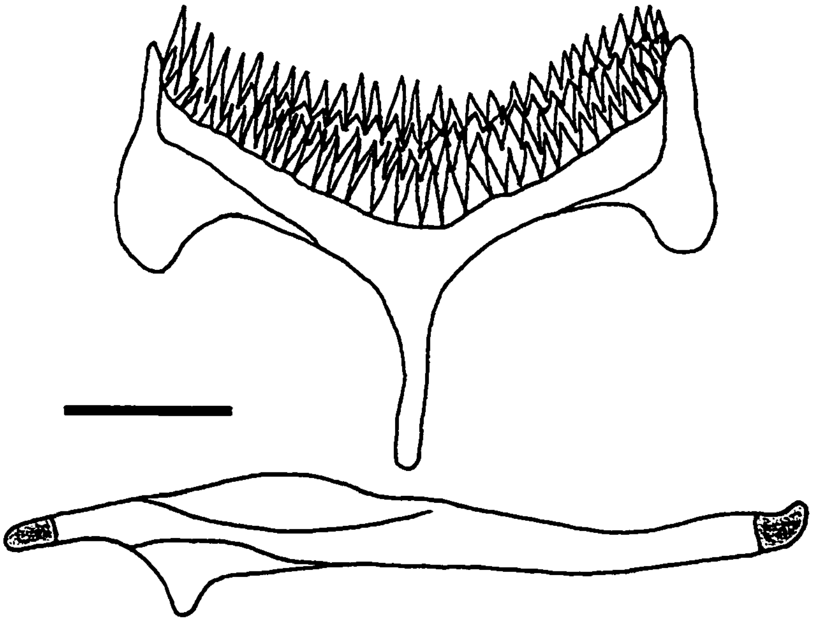

Fig. 5.23. Anterior view of the fifth ceratobranchials (top) and lateral view of the left fourth ceratobranchial (bottom) in *Stegastes partitus* (**Pomacentridae**) (UAMZ 3640, 34 mm).

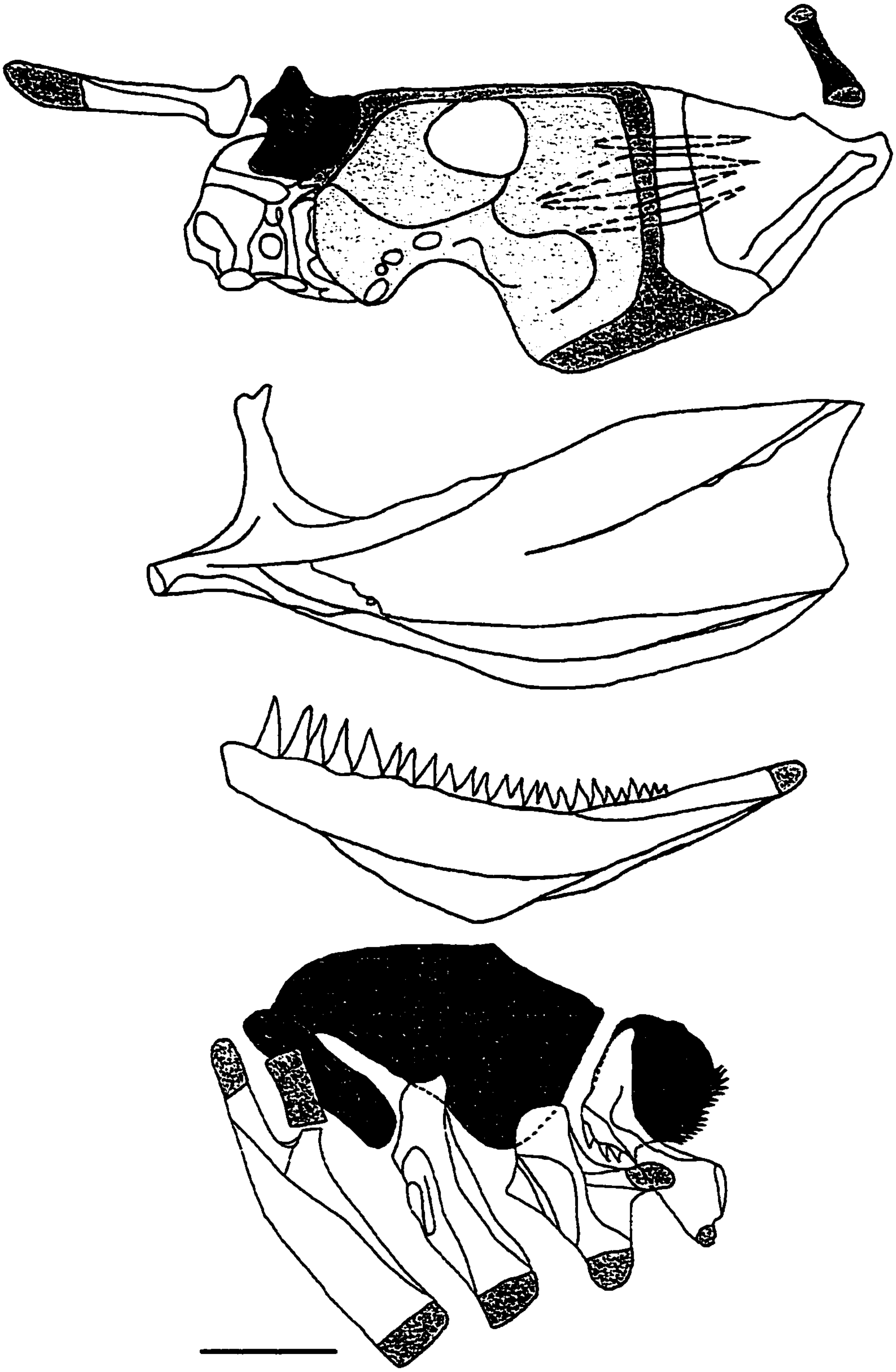

Fig. 5.24. Lateral view of the left hyoid arch (top) and the left fifth ceratobranchial (middle), and dorsal view of the left dorsal branchial arches (bottom) in *Lepomis* **(Centrarchidae)** *gibbosus* (UAMZ 7715.4, 40 mm).

6. Osteology of the pectoral girdle in Eurypterygii

The structure and position of the pectoral girdle is relatively stable in eurypterygian fishes. It consists of the extrascapula, posttemporal, supracleithrum, cleithrum, postcleithrum, scapula, coracoid, actinosts, and fin rays. An ectocoracoid is present in some Gasterosteiformes. The extrascapula, posttemporal, supracleithrum, cleithrum, postcleithra, and ectocoracoid are dermal bones, but the scapula, coracoid, and actinosts are endochondral (Rojo, 1991). Most eurypterygians have a posttemporal with distinct dorsal and ventromedial processes. The dorsal process ligamentously articulates with the epioccipital and the ventromedial process with the intercalary when present, and when absent, with the posteroventral margins of the pterotic and exoccipital. In most taxa, the supracleithrum bears a sensory canal and articulates with the posttemporal anteriorly and with the cleithrum posteriorly. The cleithrum is Y-shaped consisting of the anterodorsal, posterodorsal, and ventral rami. A lamina fills the space between the two dorsal rami. The ventral ramus may bear lateral, medial, posteromedial, and anterolateral flanges. The posteromedial flange provides an articulation surface for the scapula and coracoid. Dorsal and ventral postcleithra are present in some Eurypterygii. The scapula articulates with the cleithrum and bears a foramen which is complete or open anteriorly and bordered by the cleithral ventral ramus. The coracoid is a broad plate consisting of a shaft and dorsal and ventral flanges and articulates with the cleithrum anteriorly and with the scapula dorsally by scapulocoracoid cartilage. Most taxa have four autogenous actinosts that increase in size gradually from the first to the fourth, but in some, the first actinost is fused. The dorsalmost ray is rudimentary in some taxa. Nelson (1971) studied the anatomy of the pectoral girdle in sticklebacks, Vorkhvardt (1987) reviewed the origin of the pelvic girdle, Borkhvardt (1992) studied the development of the paired fins in fishes, and Parenti and Song (1996) studied the pectoral-pelvic fin association in acanthomorphs. I follow the general terminology of Johnson et al. (1996) for the pectoral girdle.

Aulopiformes

Synodontidae (Fig. 6.1). A relatively large extrascapular is present. The dorsal and ventromedial processes of the posttemporal are distinct. The dorsal process is loosely attached to the epioccipital by a relatively long ligament. The supracleithrum is large and overlaps the cleithrum and postcleithrum posteriorly. The cleithrum is tapered and its anterodorsal ramus is short and blunt. The posterodorsal ramus extends well beyond the scapula. The ventral ramus of the cleithrum bears perpendicular lateral and posteromedial flanges. The dorsal postcleithrum is flat and bears an anteroventral extension. The ventral postcleithrum is flat and narrow. The two postcleithra are situated behind the cleithral dorsal portion and actinost. The scapula bears a short dorsal shaft that is tipped with cartilage anteriorly and articulates with the cleithral angle. The scapula also articulates with the cleithrum dorsally and anteriorly and bears a complete small foramen. The coracoid is a broad plate consisting of a shaft tipped with cartilage and dorsal and ventral flanges that anteriorly articulates with the cleithrum cartilagenously. The actinosts are autogenous and the fourth one is highly enlarged.

Myctophiformes

Myctophidae. Two round extrascapulars are present. The dorsal and ventromedial processes of the posttemporal are distinct. The dorsal process is loosely attached to the epioccipital by a relatively long ligament. The supracleithrum is large and bears a sensory canal. The anterodorsal ramus of cleithrum is short and pointed. The posterodorsal ramus is not distinct. The ventral ramus of cliethrum bears a lateral flange that overlies the scapula and coracoid. The dorsal postcleithrum is flat and ovoid and the ventral postcleithrum is flat and narrow. The scapula bears a complete small foramen. The coracoid consists of a shaft and dorsal and ventral flanges. The actinosts are autogenous and their size increases gradually from the first to the fourth.

Lampridiformes

Veliferidae. A relatively large extrascapular is present. The dorsal and ventromedial processes of the posttemporal are distinct. The supracleithrum is large. The cleithrum is tapered and its anterodorsal ramus is long and pointed. The posterodorsal ramus is not distinct. The ventral ramus of the cliethrum bears perpendicular lateral and posteromedial flanges. The dorsal postcleithrum is broad and bears an anterior strut and the ventral postcleithrum is elongated. The scapula articulates with the posterodorsal shaft of the cleithrum dorsally, but it is free anteriorly and bears a complete foramen. The coracoid consists of a shaft and a dorsal flange. The actinosts are autogenous, hourglass shaped, and their size increases gradually from the first to the fourth. The dorsalmost ray is rudimentary and spiny.

Trachipteridae (Fig. 6.2). The extrascapulars are absent. The posttemporal bears a long dorsal and a very short ventromedial process. The supracleithrum is long and bears a sensory canal and overlaps the cleithrum posteriorly. The cleithrum is long and roughly sinusoid. The ventral ramus of the cliethrum bears very narrow lateral and posteromedial flanges. The postcleithrum is elongated, originated on the cleithrum, and oriented posteriorly passing behind the fourth actinost. The small, rectangular scapula articulates with the ventral shaft of the cleithrum, but it is free anteriorly and bears no foramen. The coracoid consists of a shaft and a dorsal flange. The actinosts are autogenous, hourglass shaped, and their size increases gradually from the first to the fourth. The dorsalmost ray is rudimentary and spiny.

Polymixiiformes

Polymixiidae. A relatively large extrascapular is present. The dorsal and ventromedial processes of the posttemporal are distinct. The supracleithrum is large. The anterodorsal ramus of the cleithrum is short and pointed, but the posterodorsal ramus is not distinct. The ventral ramus of the cliethrum bears medial, lateral, and posteromedial flanges. The dorsal postcleithrum is broad and bears an anterior strut and ventral postcleithrum is elongated. The scapula articulates with cleithrum dorsally and anteriorly and bears a complete foramen. The coracoid is a broad plate consisting of a shaft tipped with cartilage and a dorsal flange, and cartilagenously articulates with the cleithrum anteroventrally. The actinosts are autogenous, hourglass shaped, and their size increases gradually from the first to the fourth. The dorsalmost ray is rudimentary and spiny.

Percopsiformes

Percopsidae (Fig. 6.3). A small extrascapular is present. The dorsal and ventromedial processes of the posttemporal are distinct. The supracleithrum is large. The anterodorsal ramus of the cleithrum is long and pointed, but the posterodorsal ramus is not distinct. The ventral ramus of the cliethrum bears median, lateral, and posteromedial flanges. The postcleithrum is very broad and bears an anteroventral extension. The scapula articulates with the cleithrum dorsally and bears a complete foramen. The coracoid consists of a shaft tipped with cartilage and a dorsal flange, and cartilaginously articulates with the cleithrum anteroventrally. The actinosts are autogenous, hourglass shaped, and their size increases gradually from the first to the fourth. The dorsalmost ray is rudimentary.

Mugiliformes

Mugilidae. Three extrascapulars are present. The dorsal and ventromedial processes of posttemporal are distinct. The supracleithrum is relatively small. The anterodorsal ramus of the cleithrum is short and pointed, but the posterodorsal ramus is not distinct. The ventral ramus of the cliethrum consists of lateral and posteromedial flanges. The dorsal postcleithrum is broad and bears an anterior strut and the ventral postcleithrum is elongated.

The scapula articulates with the cleithrum dorsally and anteriorly and bears a complete foramen. The coracoid consists of a shaft and dorsal and ventral flanges, and articulates with cleithrum anterodorsally and anteroventrally. The coracoid is highly notched to receive the fourth actinosts. The actinosts are autogenous, with hourglass shaped cores and dorsal and ventral lamina, and their size slightly increases from the first to the fourth. The dorsalmost ray is rudimentary.

Atheriniformes

Melanotaeniidae (Fig. 6.4). The extrascapulars are absent. The dorsal and ventromedial processes of posttemporal are distinct. The supracleithrum is small and lacks a sensory canal. The anterodorsal ramus of cleithrum is short and pointed, but the posterodorsal ramus is not distinct. The ventral ramus of cliethrum consists of anterolateral, lateral, medial, and posteromedial flanges. The medial flange bends laterally and articulates with the coracoid. The dorsal postcleithrum is small and round, but ventral postcleithrum is elongated. The scapula articulates with the cleithrum dorsally and anteriorly and bears a complete foramen. The coracoid consists of a shaft and dorsal and ventral flanges and articulates with the cleithrum anteriorly. The coracoid is much larger than the scapula and highly notched to receive the third and fourth actinosts. The first actinost is fused to the scapula, but the other three are autogenous, with hourglass shaped cores and dorsal and ventral lamina, and their size slightly increases from the first to the fourth. The dorsalmost ray is rudimentary.

Atherinidae. The extrascapulars are absent. The dorsal and ventromedial processes of posttemporal are distinct. The supracleithrum is small and lacks a sensory canal. The anterodorsal ramus of the cleithrum is short and blunt, but the posterodorsal shaft is not distinct. The ventral ramus of the cliethrum consists of posterolateral, lateral, medial, and posteromedial flanges. The dorsal postcleithrum is elongated and the ventral postcleithrum is relatively broad. The scapula bears an incomplete foramen. The coracoid consists of a shaft and dorsal and ventral flanges and articulates with the cleithrum anteriorly. The coracoid is much larger than the scapula and receives the third and fourth actinosts. The actinosts are autogenous, with hourglass shaped cores and dorsal and ventral lamina, and their size increases from the first to the fourth. The dorsalmost ray is rudimentary. The extrascapulars are present in *Atherinops* and *Melanorhinus*, but absent in Bedotiidae (Stiassny, 1993).

Beloniformes

Belonidae (Fig. 6.5). The extrascapulars are absent. The dorsal and ventromedial processes of posttemporal are distinct. The supracleithrum is small. The dorsal rami of cleithrum are not distinct. The ventral ramus of the cliethrum consists of lateral and posteromedial flanges. The postcleithrum is elongated. The scapula bears a complete foramen. The coracoid consists of a shaft and dorsal and ventral flanges and articulates with the cleithrum anterodorsally and anteroventrally. The coracoid is much larger than the scapula and highly notched to receive the fourth actinost. The actinosts are autogenous, with hourglass shaped cores and dorsal and ventral lamina, and their size increases from the first to the fourth. The dorsalmost ray is rudimentary.

Hemiramphidae. The extrascapulars are absent. The ventromedial process of the posttemporal is not distinct. The supracleithrum is small. The dorsal rami of the cleithrum are not distinct. The ventral ramus of the cleithrum consists of lateral, medial, and posteromedial flanges. The postcleithrum is elongated and positioned vertically. The scapula articulates with the cleithrum dorsally and anteriorly and bears a complete foramen. The coracoid consists of a shaft and dorsal and ventral flanges, and articulates with the cleithrum anterodorsally and anteroventrally. The coracoid is much larger than the scapula and highly notched to receive the fourth actinost. The first and second actinosts strongly articulate with the scapula and the third and fourth ones with the coracoid. The dorsalmost ray is rudimentary.

Cyprinodontiformes

Aplocheilidae. The extrascapulars are absent. The dorsal and ventromedial processes of posttemporal are distinct. The supracleithrum is small. The posterodorsal ramus of the cleithrum is not distinct. The ventral ramus of the cleithrum consists of lateral, medial, anterolateral, and posteromedial flanges. The postcleithrum is elongated. The scapula articulates with the cleithrum dorsally and anteriorly and bears a complete, small foramen. The coracoid consists of a shaft and dorsal and ventral flanges, and articulates with the cleithrum anterodorsally and anteroventrally. The coracoid is the same size as the scapula and highly notched posteriorly. The actinosts are autogenous, with hourglass shaped cores and dorsal and ventral lamina, and their size increases from the first to the fourth. In *Aplocheilus panchax* the ventromedial process of posttemporal is just a bud and a small round dorsal postcleithrum is present (Parenti, 1981).

Cyprinodontidae (Fig. 6.6). The extrascapulars are absent. The dorsal and ventromedial processes of posttemporal are distinct. The supracleithrum is small. The posterodorsal ramus of the cleithrum is not distinct. The ventral ramus of the cleithrum consists of lateral, medial, anterolateral, and posteromedial flanges. The dorsal postcleithrum is broad and the ventral postcleithrum is elongated. The scapula is twisted anteriorly and articulated with the cleithrum dorsally and anteriorly and bears a complete small foramen. The coracoid consists of a shaft and dorsal and ventral flanges and articulates with the cleithrum anterodorsally and anteroventrally. The coracoid is the same size as the scapula and both are highly notched posteriorly. The actinosts are autogenous, with hourglass shaped cores and dorsal and ventral lamina, and their size increases from the first to the fourth. The first actinost is sutured to the scapula. In representatives of *Fundulus* and *Cubanichthys*, the posttemporal anteromedial process is not distinct (Costa, 1998).

Stephanoberyciformes

Stephanoberycidae. The extrascapular is large and tightly connected to the cranium. The ventromedial process of the posttemporal is distinct. The supracleithrum is large. The posterodorsal ramus of the cleithrum is long and pointed. The ventral ramus of the cleithrum consists of lateral and medial flanges. The dorsal postcleithrum is broad and bears an anterior strut, but the ventral postcleithrum is elongated. The scapula articulates with the cleithral posterodorsal ramus and bears a complete small foramen. The coracoid consists of a shaft and dorsal and ventral flanges and articulates with the cleithrum anteriorly. The actinosts are autogenous, with hourglass shaped cores and dorsal and ventral lamina, and their size increases gradually from the first to the fourth..

Rondeletiidae (Fig. 6.7). The extrascapulars are absent. The posttemporal is large and roughly pyramidal and its dorsal and ventromedial processes are not distinct. The supracleithrum is relatively small. The posterodorsal ramus of the cleithrum is not distinct. The ventral ramus of the cleithrum is highly expanded and bears a huge posteroventral extension and consists of a broad lateral and small medial and posteromedial flanges. The postcleithrum is elongated. The scapula is highly reduced and does not bear a foramen. The coracoid is also highly reduced and consists of a shaft and a dorsal flange. The actinosts are tiny and autogenous, with hourglass shaped cores and dorsal and ventral laminae.

Beryciformes

Monocentridae. A large extrascapular is tightly attached to the cranium. The dorsal and ventromedial processes of the posttemporal are distinct. The supracleithrum is relatively small. The posterodorsal ramus of the cleithrum is long and pointed. The ventral ramus of the cleithrum consists of lateral, medial, and posteromedial flanges. The postcleithrum is relatively broad and with an anterior strut. The scapula bears a complete small foramen. The coracoid consists of a shaft and dorsal and ventral flanges and articulates with the cleithrum anterodorsally and anteroventrally. The coracoid is larger than the scapula and bears a posterior process. The actinosts are autogenous, with hourglass shaped cores and dorsal and ventral lamina, and their size increases from the first to the fourth. The dorsalmost ray is rudimentary.

Holocentridae (Fig. 6.8). A large extrascapular is tightly attached to the cranium. The dorsal and ventromedial processes of the posttemporal are distinct. The supracleithrum is broad. The posterodorsal ramus of the cleithrum is pointed. The ventral ramus of the cleithrum is divided into three struts ventrally and consists of lateral, medial, and posteromedial flanges. The postcleithrum is relatively broad and bears an anterior strut. The scapula articulates with the cleithrum anteriorly and bears a complete foramen. The coracoid consists of a shaft and dorsal and ventral flanges, and articulates with the cleithrum anterodorsally and anteroventrally. The actinosts are autogenous, with hourglass shaped cores and dorsal and ventral lamina, and their size increases from the first to the fourth. The dorsalmost ray is rudimentary.

In *Ostichthys* the extrascapular is large, the dorsal postcleithrum is broad, and the ventral postcleithrum is long. In Anomalopidae, postcleithrum is broad and with a long anteroventral extension. In Diretmidae, the actinosts are located on the dorsal margins of the scapula and coracoid (Zehren, 1979). In Trachichthyidae, the extrascapular is large (Kotlyar, 1992; Zehren, 1979).

Zeiformes

Grammicolepididae (Fig. 6.9). The extrascapulars are absent. The dorsal and ventromedial processes of posttemporal are not distinct. The supracleithrum is elongated. The anterodorsal ramus of the cleithrum is long and pointed, but the posterodorsal ramus is not distinct. The ventral ramus of cliethrum consists of lateral, medial, and posteromedial flanges. The postcleithrum is elongated and strongly articulated with the cleithrum. The scapula articulates with the cleithrum anteriorly and bears a complete small foramen. The coracoid consists of a shaft and a dorsal flange and articulates with the cleithrum anterodorsally and anteroventrally and bears a posterior process. The actinosts are autogenous, with hourglass shaped cores and dorsal and ventral laminae, and their size increases from the first to the fourth.

Caproidae. The extrascapulars are absent. The dorsal and ventromedial processes of the posttemporal are not distinct. The supracleithrum is elongated. The posterodorsal ramus of the cleithrum is pointed. The ventral ramus of the cleithrum consists of lateral, medial, and posteromedial flanges. The postcleithrum is relatively broad dorsally, but elongated ventrally. The scapula articulates with the cleithrum anteriorly and bears a complete foramen. The coracoid consists of a shaft and a dorsal flange and weakly articulates with the cleithrum anterodorsally and bears a posterior process. The actinosts are autogenous, with hourglass shaped cores and dorsal and ventral lamina, and their size increases from the first to the fourth. In Diretmidae, the ventral flange of coracoid is very large and all the actinosts are fused (Olney et al., 1993), although, in representatives of *Diretmoides* only the first actinost is fused (Moore, 1993).

Gasterosteiformes

Hypoptychidae (Fig. 6.10). Two small extrascapulars are present. The dorsal and ventromedial processes of the posttemporal are distinct. The supracleithrum is relatively small. The posterodorsal ramus of the cleithrum is pointed. The ventral ramus of the cleithrum is broad ventrally and consists of narrow lateral, medial, and posteromedial flanges. Postcleithra are absent. The scapula bears a complete foramen. The coracoid is broad and bears an incomplete foramen. The actinosts are autogenous and rectangular.

Aulorhynchidae (Fig. 6.11). The extrascapulars are absent in *Aulorhynchus*, but a small triradiate extrascapular is present in *Aulichthys*. The posttemporal is elongated, bifurcated anteriorly, and its dorsal and ventral processes are not distinct. In *Aulichthys*, the posttemporal is broad and bears distinct dorsal and ventral processes. The supracleithrum is absent in *Aulorhynchus*, but a small supracleithrm is present in *Aulichthys*. The anterodorsal ramus of the cleithrum is short and pointed and the ventral ramus is divided into two parts ventrally and consists of narrow lateral, medial, and posteromedial flanges. The scapula articulates with the cleithrum dorsally and bears an incomplete foramen. The coracoid is broad and bears an anteroventral extension that articulates with the cleithrum anteriorly and with the ectocoracoid ventrolaterally. The ectocoracoid which is known only in Aulorhynchidae, Gasterosteidae, and Aulostomoidea, is a superficially ornamented bone which extends along the coracoid and reaches posterior end of the actinosts. The actinosts are autogenous and with almost the same size, cuboidal in *Aulorhynchus*, but hourglass shaped with foramina in between in *Aulichthys*, and are cartilage filled. The fourth actinost bears an anteroventral strut that articulates with the coracoid.

Gasterosteidae (Fig. 6.12). The extrascapulars are absent. In *Spinachia*, dorsal and ventromedial processes of the posttemporal are absent. In *Apeltes*, the ventromedial process is absent. In *Gasterosteus*, *Culaea*, and *Pungitius*, the dorsal and ventromedial processes are distinct. The supracleithrum is relatively small. The anterodorsal ramus of the cleithrum is strongly pointed. The ventral ramus of the cleithrum bears lateral, medial, and posteromedial flanges. The scapula articulates with the cleithrum dorsally and bears an incomplete foramen and posteriorly notched to receive the actinosts. The coracoid is broad and bears a foramen and an anteroventral shaft that articulates with the cleithrum anteriorly and with the ectocoracoid ventrolaterally. The ectocoracoid reaches the posterior end of the actinosts. The actinosts are autogenous, cuboidal, almost the same size, and are cartilage filled. The fourth actinost bears an anteroventral strut that articulates with the coracoid. The posttemporal and supracleithrum are absent in *Gasterosteus wheatlandi* (Nelson, 1971).

Pegasidae (Fig. 6.13). The pectoral girdle is rotated laterally so that the original lateral surface becomes ventral. The extrascapulars are absent. The posttemporal is firmly sutured to the cranium and bears the dorsal and anteromedial processes. The supracleithrum is small. The posterodorsal ramus of the cleithrum is blunt. The ventral ramus of the cleithrum consists of lateral, medial, and posteromedial flanges and it is divided ventrally. Postcleithra are absent. The scapula bears an incomplete foramen. The coracoid consists of a shaft and dorsal, ventral, and lateral flanges, sutured to the scapula, and bears a posterior process. The actinosts are square and the same size. The first actinost is fused to the scapula and others are autogenous, but firmly connected to each other and to the coracoid.

Solenostomidae (Fig. 6.14): The extrascapulars are absent. The posttemporal is pyramidal and its dorsal and ventromedial processes are distinct. The supracleithrum is flat and relatively small. The posterodorsal ramus of the cleithrum is horizontal and sends a flange over the scapula. The ventral ramus of the cleithrum consists of lateral, medial, and posteromedial flanges. A spike borders the posteromedial flange which articulates with the coracoid. Postcleithra are absent. The scapula is indistinguishable from the actinosts and articulates with the cleithrum anterodorsally and anteroventrally. The coracoid consists of a shaft and a dorsal flange and weakly articulates with the cleithrum anterodorsally and anteroventrally and bears a long posterior process. The actinosts are autogenous, hourglass shaped, cartilage filled, and almost the same size.

Syngnathidae. The extrascapulars are absent. The posttemporal is convex and its dorsal and ventromedial processes are not distinct. The supracleithrum is absent. The dorsal rami of the cleithrum are horizontal. The ventral ramus of the cleithrum is bifurcated ventrally and consists of lateral, medial, and posteromedial flanges. The postcleithra are absent. The scapula is indistinguishable from the actinosts and articulates with the cleithrum. The coracoid consists of a shaft and dorsal and ventral flanges and weakly articulates with the cleithrum. The actinosts are autogenous, hourglass shaped, and relatively the same size.

Indostomidae (Fig. 6.15). The extrascapulars are absent. The posttemporal is scute like and with a distinct anteromedial process. The supracleithrum is small. The cleithrum is fused to body scutes. The ventral ramus of the cleithrum consists of lateral, medial, and posteromedial flanges. The postcleithra are absent. The scapula is rectangular and similar to the actinosts. The coracoid is funnel shaped and articulated with the cleithrum anteriorly and with the actinosts posteriorly. The actinosts are large, rectangular, and cartilaginously articulated together and to the coracoid, and except the first one which is smaller and fused to the scapula, are the same size. The fourth actinost sends a posteroventral extension to the coracoid. I agree with Banister (1970) and Bowne (1994) that the ectocoracoid-like scutes are not homologous with the ectocoracoid in sticklebacks, but disagree with them in the number of actinosts.

Aulostomidae. The extrascapulars are absent. The posttemporal is laterally broad. The supracleithrum is absent. The posterodorsal ramus of the cleithrum is horizontal and articulated with the postcleithrum. The ventral ramus of the cleithrum bears lateral and posteromedial flanges which send a strut to the coracoid. The large sinusoidal postcleithrum originates on the posterodorsal end of the cleithrum and touches the ectocoracoid and extends posteriorly beyond it. The scapula articulates with the cleithrum dorsally and bears a complete foramen. The coracoid is broad and bears an anteroventral shaft that articulates with the cleithrum anteriorly and with the ectocoracoid laterally. The ectocoracoid is very long. The first actinost is smaller and tightly connected to the scapula, but others are autogenous, hourglass shaped, the same size, and cartilage filled.

Fistulariidae (Fig. 6.16). The extrascapulars are absent. The posttemporal is fused to the cranium and bears distinct dorsal and anteroventral processes. A dorsolateral extension connects the posttemporal to the cranium. The supracleithrum is very small. The anterodorsal ramus of the cleithrum is short and blunt. The posterodorsal ramus is horizontal and articulated with the postcleithrum. The ventral ramus of the cleithrum bears the lateral and posteromedial flanges which send a strut to the coracoid. A large postcleithrum originates on the posterodorsal end of the cleithrum and touches the ectocoracoid posteriorly. The scapula is indistinguishable from the actinosts and articulates with the cleithral posterodorsal ramus dorsally and with the posteromedial flange anteroventrally, making a foramen in between. The coracoid is broad and bears an anteroventral shaft that articulates with the cleithrum anteriorly and with the ectocoracoid ventrolaterally. The ectocoracoid is long and expanded posteriorly. The first actinost is small and articulated with the scapula, but others are autogenous, hourglass shaped, the same size, and cartilage filled.

Macroramphosidae (Fig. 6.17). The extrascapulars are absent. The posttemporal is fused to the cranium. The supracleithrum is relatively small and entirely lies on the cleithrum. The anterodorsal ramus of the cleithrum is short and blunt and the posterodorsal ramus is horizontal and articulates with the postcleithrum. The ventral ramus of the cleithrum bears lateral and posteromedial flanges. The broad postcleithrum originates on the posterodorsal end of the cleithrum and is oriented posteriorly. The scapula articulates with the cleithrum anteriorly and bears a complete foramen. The coracoid is broad and bears an anteroventral extension that articulates with the cleithrum anteriorly and for its entire length with its counterpart ventrally. The ectocoracoid is absent. The actinosts are small and tightly articulated with the scapula, with hourglass shaped cores and dorsal and ventral laminae, and all the same size. The fourth actinost sends an anteroventral strut to the coracoid. The dorsalmost ray is rudimentary.

Centriscidae (Fig. 6.18). The extrascapulars are absent. The posttemporal is sutured to the cranium. The supracleithrum is sutured to the body plates and lies entirely on the cleithrum. The anterodorsal ramus of the cleithrum is short and blunt and the posterodorsal ramus is horizontal. The ventral ramus of cleithrum is divided into anterolateral and posteromedial struts and bears lateral and posteromedial flanges. The sinusoidal postcleithrum originates on the posterodorsal end of the cleithrum and is oriented posteriorly. The scapula articulates with the cleithrum anteriorly and bears a tiny foramen. The coracoid is broad and bears an anteroventral extension that articulates with the cleithrum anteriorly and bears a posterior process. The ectocoracoid is absent. The actinosts tightly articulate with the scapula and consist of hourglass shaped cores and dorsal and ventral laminae. Distally, actinosts are bend 90° laterally. The fourth actinost is larger and sends an anteroventral strut to the coracoid. The dorsalmost ray is rudimentary.

Synbranchiformes

Synbranchidae (Fig. 6.19). The extrascapulars are absent. The posttemporal bears distinct dorsal and anteromedial processes. The supracleithrum is present. The cleithrum is a simple curved bone with a small lateral flange. The postcleithra, scapula, coracoid, actinosts, and rays are absent.

Mastacembelidae (Fig. 6.20). The extrascapulars are absent. The posttemporal is small and cylindrical. The supracleithrum is elongated. The cleithrum is broad laterally and its dorsal rami are not distinct. The ventral ramus of the cleithrum consists of lateral and medial flanges. The postcleithra are absent. The scapula articulates with the cleithrum anteriorly and bears a complete foramen. The coracoid consists of a shaft and a dorsal flange, articulates with the cleithrum anteriorly, and bears a posterior process. The actinosts are autogenous, with hourglass shaped cores and dorsal and ventral laminae, and their size increases from the first to the fourth. Similar pectorals are found in specimens of *Mastacembelus*, but some have an extra element before the posttemporal that might be homologous to the extrascapula, however, Travers (1984) called it the posttemporal.

Scorpaeniformes

Dactylopteridae (Fig. 6.21). The pectoral girdle is rotated laterally so that the original lateral surface becomes ventral. The extrascapulars are absent. The posttemporal is firmly sutured to the cranium and bears a distinct anteromedial process. The supracleithrum is small and does not articulate with the posttemporal. The anterodorsal ramus of the cleithrum is long and pointed and articulates with the posttemporal. The ventral ramus of the cleithrum consists of lateral, medial, and posteromedial flanges. The postcleithrum is elongated and bears a small triangular head. The scapula articulates with the cleithrum dorsally and anteriorly, and bears a complete foramen and sends spikes to the coracoid posteriorly. The coracoid consists of a shaft and dorsal and ventral flanges and bears a posterior process. The actinosts are tipped with cartilage from both sides, autogenous, hourglass shaped, and their size increases from the first to the fourth. The dorsalmost ray is rudimentary.

Scorpaenidae. Two autogenous extrascapulars are present. The dorsal and ventromedial processes of the posttemporal are distinct. The supracleithrum is relatively large. The anterodorsal ramus of the cleithrum is short and pointed, but the posterodorsal ramus is not distinct. The ventral ramus of the cleithrum consists of lateral, medial, and posteromedial flanges. The dorsal postcleithrum is broad and bears an anterior strut, but the ventral postcleithrum is elongated. The scapula articulates with the cleithrum dorsally, and anteriorly, and bears a complete foramen. The coracoid consists of a shaft and dorsal and ventral flanges and articulates with the cleithrum anterodorsally and anteroventrally. The first actinost is fused to the scapula and the other three are autogenous, hourglass shaped, and their size increases from the first to the fourth.

Hexagrammidae. Two autogenous extrascapulars are present. The dorsal and ventromedial processes of posttemporal are distinct. The supracleithrum is broad and overlaps the cleithrum and postcleithrum posteriorly. The anterodorsal ramus of the cleithrum is long and pointed, but the posterodorsal ramus is not distinct. The ventral ramus of the cleithrum consists of lateral, medial, and posteromedial flanges. The dorsal and ventral postcleithra are elongated. The scapula bears an incomplete foramen. The coracoid consists of a shaft and dorsal and ventral flanges and articulates with the cleithrum anteriorly. The actinosts are autogenous, hourglass shaped, and their size increases from the first to the fourth.

Agonidae (Fig. 6.22). An extrascapular is present. The posttemporal is firmly sutured to the cranium and does not bear a distinct anteromedial process. The supracleithrum is small. The anterodorsal ramus of the cleithrum is pointed. The ventral ramus of the cleithrum consists of lateral, medial, and posteromedial flanges. Both postcleithra are relatively broad. The scapula articulates with the cleithrum dorsally and anteriorly and bears an incomplete foramen. The coracoid consists of a shaft and dorsal and ventral flanges and bears a posterior process. The first actinost is smaller and fused to the scapula, but others are autogenous, square, and the same size.

The same conditions are found in other agonids, but in members of some genera the first actinost is not fused (Kanayama, 1991). In Cottoidea, scapula and coracoid are reduced, but actinosts enlarged and constitute most of the pectoral girdle (Yabe, 1981; Yabe, 1985; Yabe, 1983; Yabe, 1991; Jackson and Nelson, 1998).

Perciformes

Percidae. A triradiate extrascapular is present. The dorsal and ventromedial processes of posttemporal are distinct. The supracleithrum is broad and overlaps the cleithrum posteriorly. The anterodorsal ramus of the cleithrum is pointed. The ventral ramus of the cleithrum consists of lateral, medial, and posteromedial flanges. The dorsal postcleithrum is broad and bears an anterior strut, but the ventral postcleithrum is elongated. The scapula articulates with the cleithrum anteriorly, and bears a small, complete foramen. The coracoid consists of a shaft and dorsal and ventral flanges, bears a posterior process, and articulates with the cleithrum anterodorsally and anteroventrally. The actinosts are autogenous, hourglass shaped, and their size increases from the first to the fourth.

Cirrhitidae. A triradiated extrascapular is present. The dorsal and ventromedial processes of the posttemporal are distinct. The supracleithrum is broad and overlaps the cleithrum posteriorly. The anterodorsal ramus of the cleithrum is pointed. The ventral ramus of the cleithrum is widely divided and consists of lateral, medial, and posteromedial flanges. The dorsal postcleithrum is broad and bears an anterior strut, but the ventral postcleithrum is elongated. The scapula articulates with the cleithrum anteriorly and bears a small complete foramen. The coracoid consists of a shaft and dorsal and ventral flanges, bears a posterior process, and articulates with the cleithrum anterodorsally and anteroventrally. The actinosts are autogenous, hourglass shaped, and their size increases from the first to the fourth.

Elassomatidae (Fig. 6.23). A triradiated extrascapular is present. The dorsal and ventromedial processes of the posttemporal are distinct. The supracleithrum is broad and overlaps the cleithrum posteriorly. The anterodorsal ramus of the cleithrum is long and pointed. The ventral ramus of the cleithrum consists of narrow lateral, medial, and posteromedial flanges. The dorsal postcleithrum is broad and bears an anterior strut. The ventral postcleithrum is broad but smaller and bears an elongated ventral extension. The scapula articulates with the cleithrum anteriorly and bears a small complete foramen. The coracoid consists of a shaft and dorsal and ventral flanges, bears a small posterior process, and articulates with the cleithrum anterodorsally and anteroventrally. The actinosts are autogenous, consists of hourglass shaped cores and dorsal and ventral laminae, and their size increases from the first to the fourth.

Pomacentridae. A triradiated extrascapular is present. The dorsal and ventromedial processes of the posttemporal are distinct. The supracleithrum is broad. The anterodorsal ramus of the cleithrum is pointed. The ventral ramus of the cleithrum consists of lateral, medial, and posteromedial flanges. The dorsal postcleithrum is broad and bears an anterior strut, but the ventral postcleithrum is elongated. The scapula articulates with the cleithrum anteriorly and bears a small complete foramen. The coracoid consists of a shaft and dorsal and ventral flanges, bears a posterior process, and articulates with the cleithrum anterodorsally and anteroventrally. The actinosts are autogenous, hourglass shaped, and their size increases from the first to the fourth. The dorsalmost ray is shorter than the next ray.

Centrarchidae (Fig. 6.24). A triradiated extrascapular is present. The dorsal and ventromedial processes of the posttemporal are distinct. The supracleithrum is broad. The anterodorsal ramus of the cleithrum is pointed. The ventral ramus of the cleithrum consists of lateral, medial, and posteromedial flanges. The dorsal postcleithrum is broad and bears an anterior strut, but the ventral postcleithrum is elongated. The scapula articulates with the cleithrum anteriorly, and bears a small complete foramen. The coracoid consists of a shaft and dorsal and ventral flanges, bears a posterior process, and articulates with the cleithrum anterodorsally and anteroventrally. The actinosts are autogenous, hourglass shaped, and their size increases from the first to the fourth. The dorsalmost ray is shorter than the next ray.

In general, perciforms have extrascapulars, a posttemporal with distinct processes, a medium size supracleithrum, a cleithrum with medial, lateral, and posteromedial flanges, a broad dorsal postcleithrum and an elongated ventral postcleithrum, well developed scapula and coracoid, and four autogenous actinosts (Ida, 1976; Gill and Mooi, 1993; Bellwood, 1994; Matsuoka, 1985; Pietsch, 1989; Sasaki, 1989; Simons, 1991; Simons, 1992). However, there are some variations in the number, shape and size of the extrascapulars and postcleithra and shape and size of the actinosts and supracleithra (Doyle, 1998; Mok, 1983; Springer, 1993).

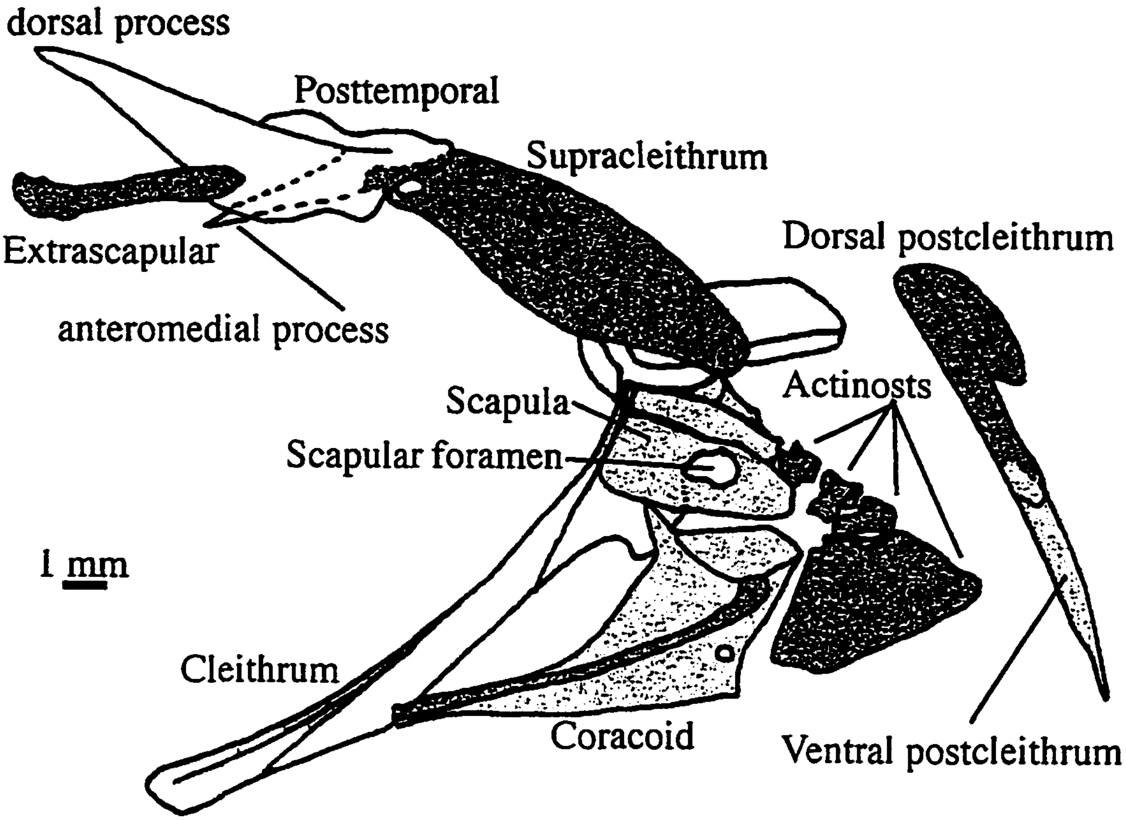

Fig. 6.1. Lateral view of the left pectoral girdle in *Synodus synodus* (**Synodontidae**) (UAMZ 1806, 147 mm).

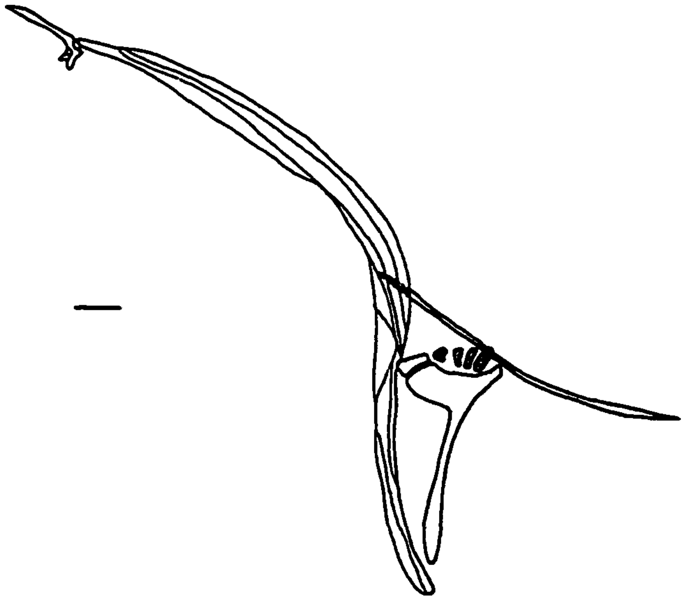

Fig. 6.2. Lateral view of the left pectoral girdle in *Trachipterus altivelis* (**Trachipteridae**) (CAS 24297, 85 mm).

Fig. 6.3. Lateral view of the left pectoral girdle in *Percopsis omiscomaycus* (Percopsidae) (UAMZ 2048, 55 mm).

Fig. 6.4. Lateral view of the left pectoral girdle in *Melanotaenia sp.* (Melanotaeniidae) (UAMZ 3526, 51 mm).

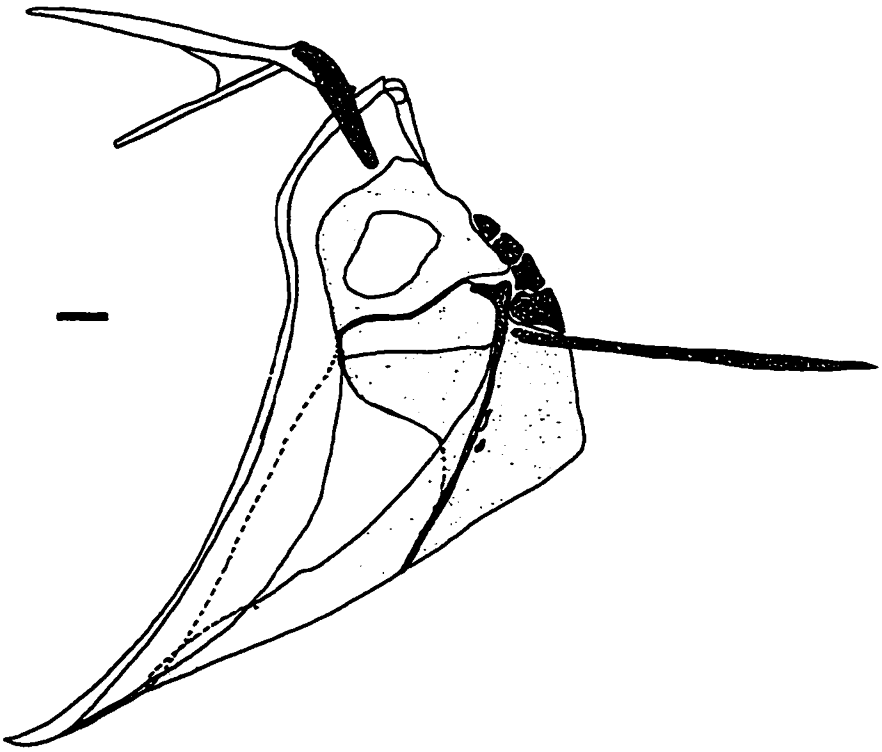

Fig. 6.5. Lateral view of the left pectoral girdle in *Pseudotylosurus sp.* **(Belonidae)** (UAMZ 8165, 173 mm).

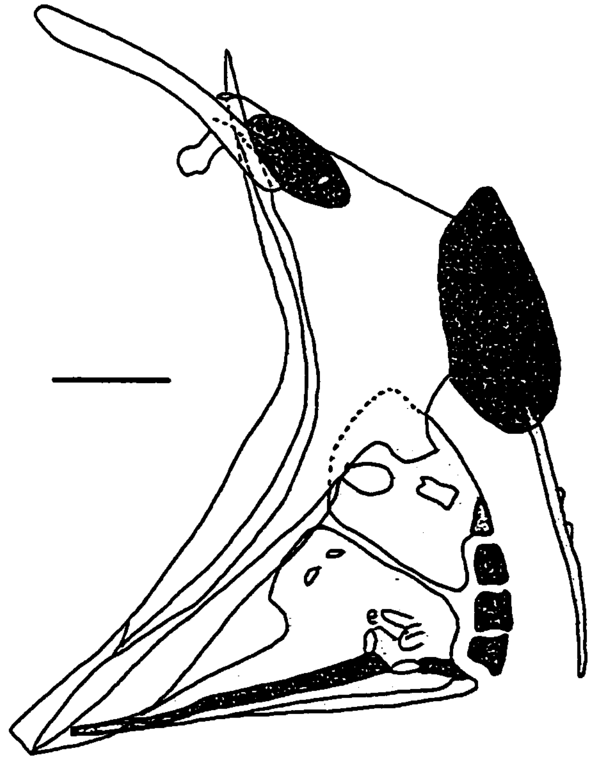

Fig. 6.6. Lateral view of the left pectoral girdle in *Cyprinodon nevadensis* **(Cyprinodontidae)** (UAMZ 3114, 34 mm).

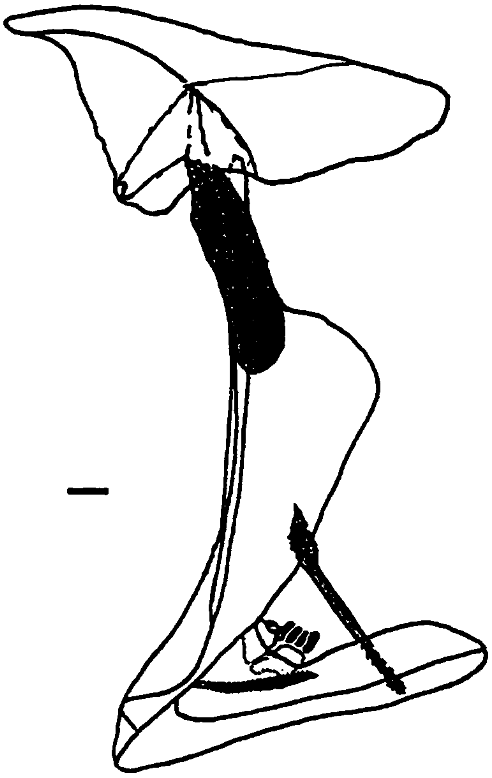

Fig. 6.7. Lateral view of the left pectoral girdle in *Rondeletia loricata* (**Rondeletiidae**) (AMS 20523001, 37 mm).

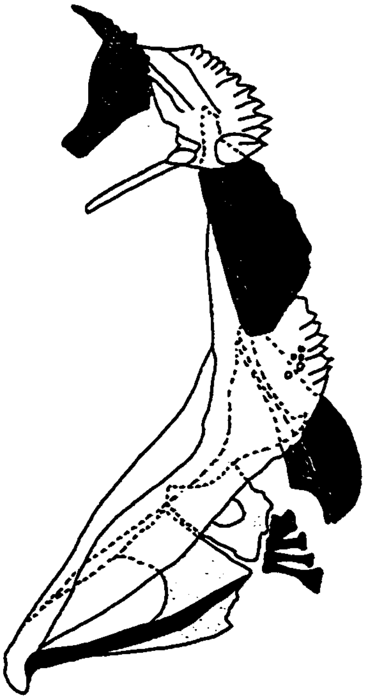

Fig. 6.8. Lateral view of the left pectoral girdle in *Sargocentron vexillarium* (**Holocentridae**) (UAMZ 5075, 44 mm).

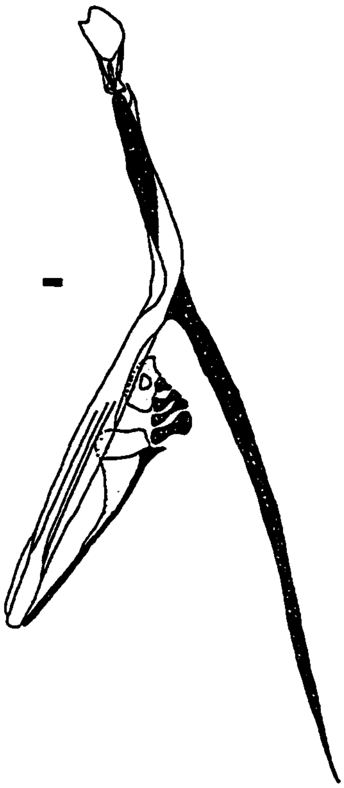

Fig. 6.9. Lateral view of the left pectoral girdle in *Xenolepidichthys dalgleishi* **(Grammicolepididae)** (USNM 322673, 68 mm).

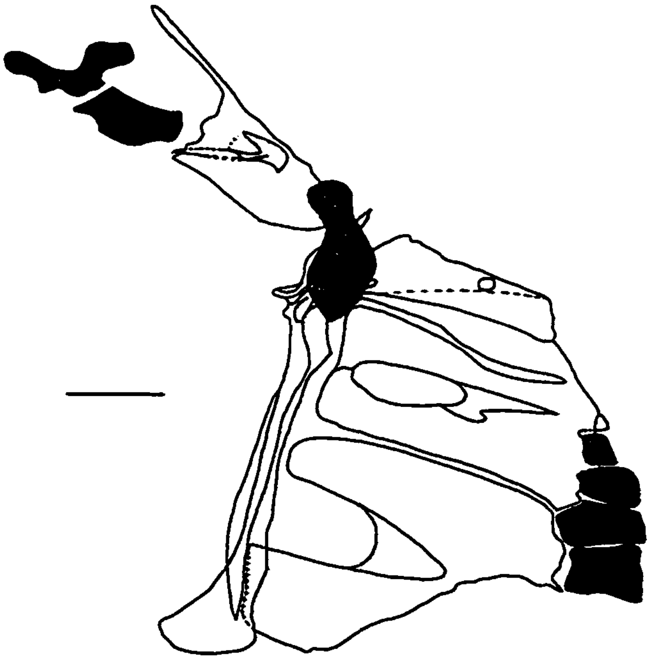

Fig. 6.10. Lateral view of the left pectoral girdle in *Hypoptychus dybowskii* **(Hypoptychidae)** (UAMZ 5550, 80 mm).

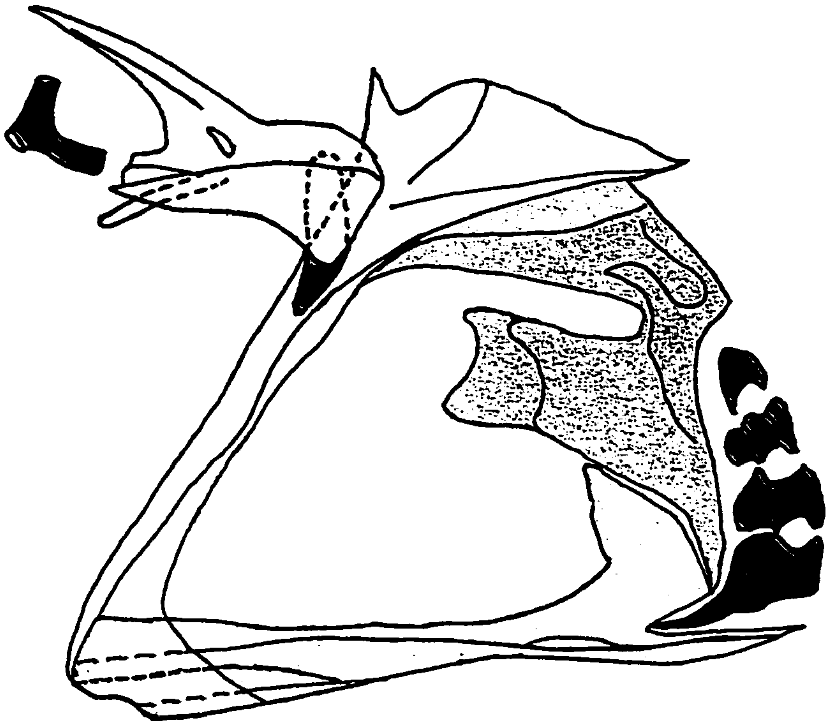

Fig. 6.11. Lateral view of the left pectoral girdle in *Aulorhynchus flavidus* **(Aulorhynchidae)** (UAMZ 3783, 109 mm).

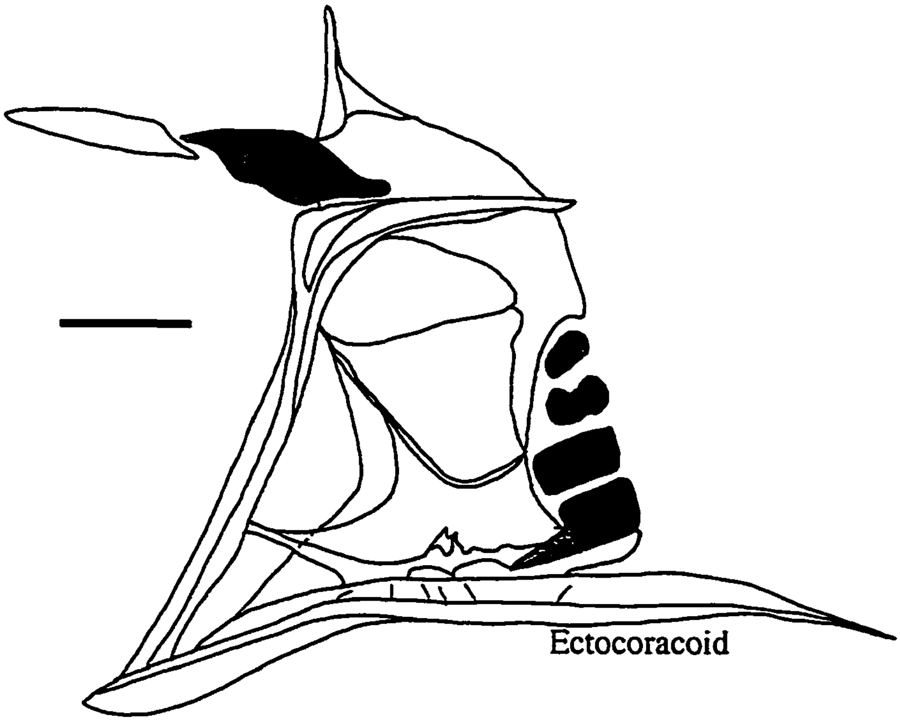

Fig. 6.12. Lateral view of the left pectoral girdle in *Spinachia spinachia* **(Gasterosteidae)** (UAMZ 6582, 53 mm).

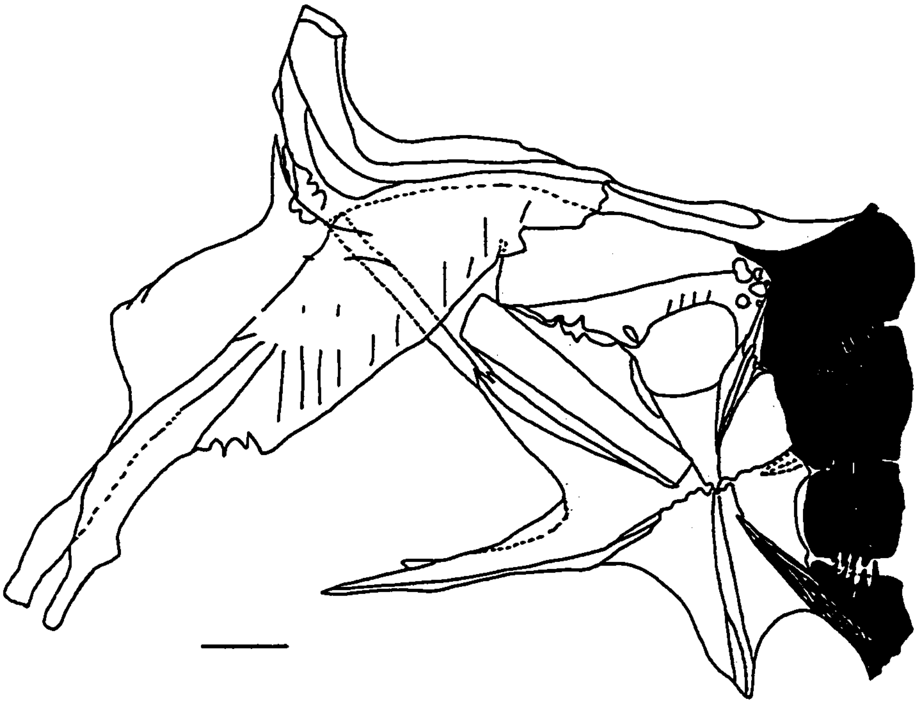

Fig. 6.13. Lateral view of the left pectoral girdle in *Pegasus volans* (**Pegasidae**) (UAMZ 4616, 99 mm).

Fig. 6.14. Lateral view of the left pectoral girdle in *Solenostomus paradoxus* (**Solenostomidae**) (AMS 17111002, 51 mm).

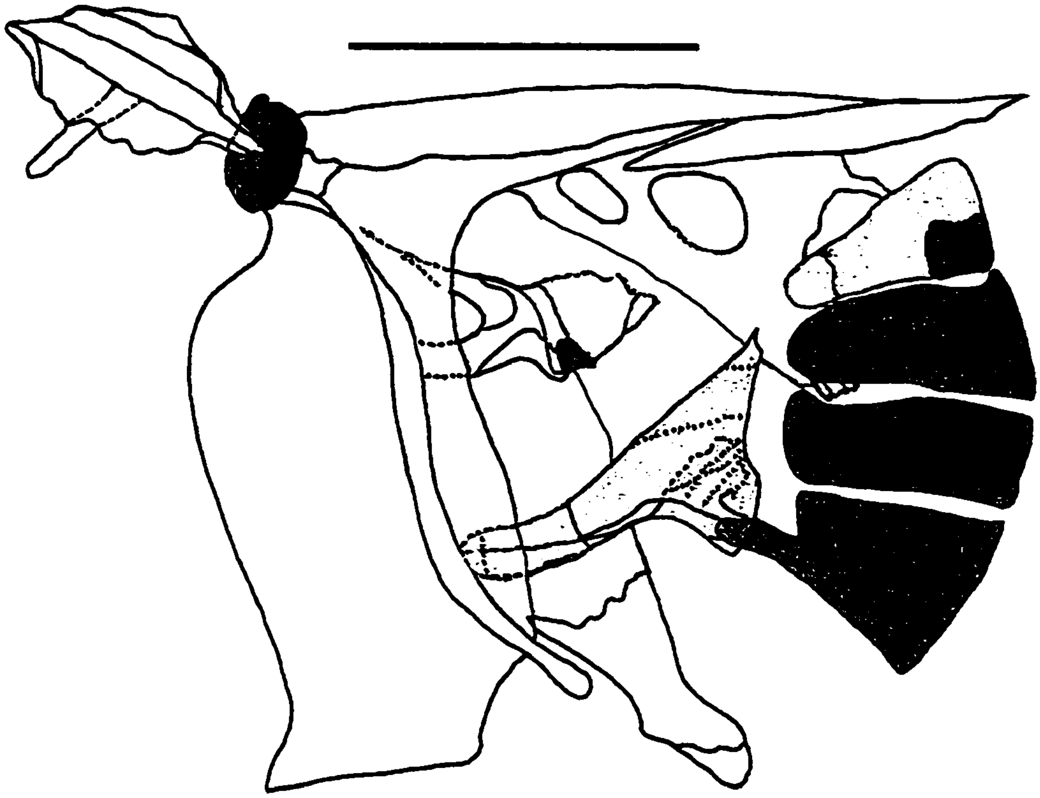

Fig. 6.15. Lateral view of the left pectoral girdle in *Indostomus paradoxus* **(Indostomidae)** (CAS 64017, 25 mm).

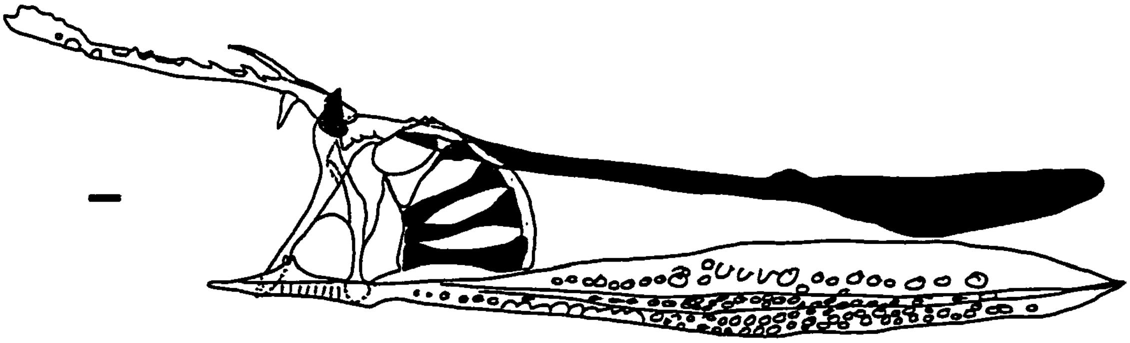

Fig. 6.16. Lateral view of the left pectoral girdle in *Fistularia petimba* **(Fistulariidae)** (UAMZ 6348, 158 mm).

Fig. 6.17. Lateral view of the left pectoral girdle in *Macroramphosus scolopax* **(Macroramphosidae)** (USNM 344398, 99 mm).

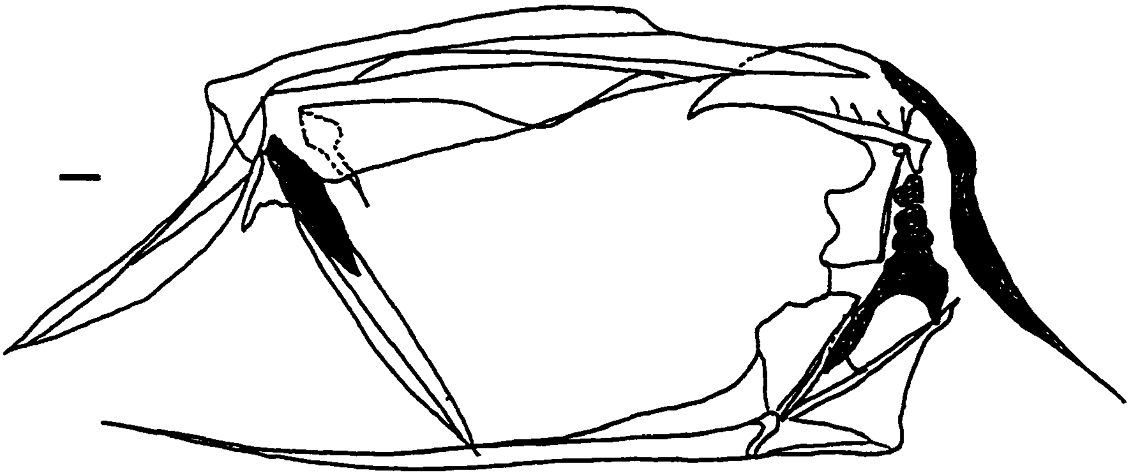

Fig. 6.18. Lateral view of the left pectoral girdle in *Aeoliscus strigatus* **(Centriscidae)** (UAMZ 4048, 89 mm).

Fig. 6.19. Lateral view of the left pectoral girdle in *Monopterus albus* **(Synbranchidae)** (USNM 192939, 193 mm).

Fig. 6.20. Lateral view of the left pectoral girdle in *Macrognathus aculeatus* **(Mastacembelidae)** (UAMZ 1855, 119 mm).

Fig. 6.21. Lateral view of the left pectoral girdle in *Dactylopterus volitans* **(Dactylopteridae)** (UAMZ 2633, 74 mm).

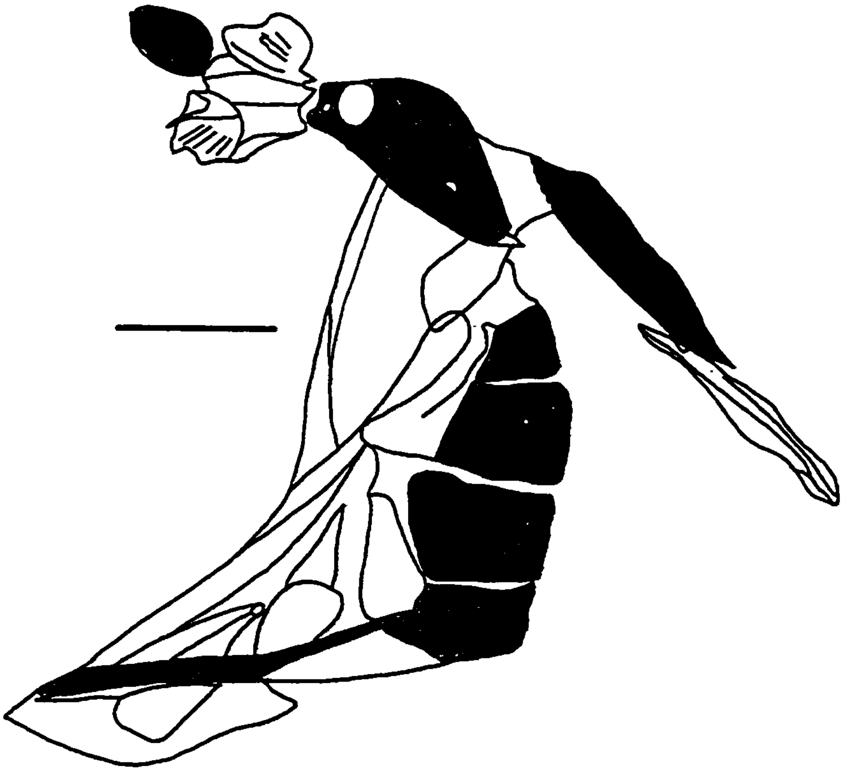

Fig. 6.22. Lateral view of the left pectoral girdle in *Xeneretmus latifrons* **(Agonidae)** (UAMZ 3196, 95 mm).

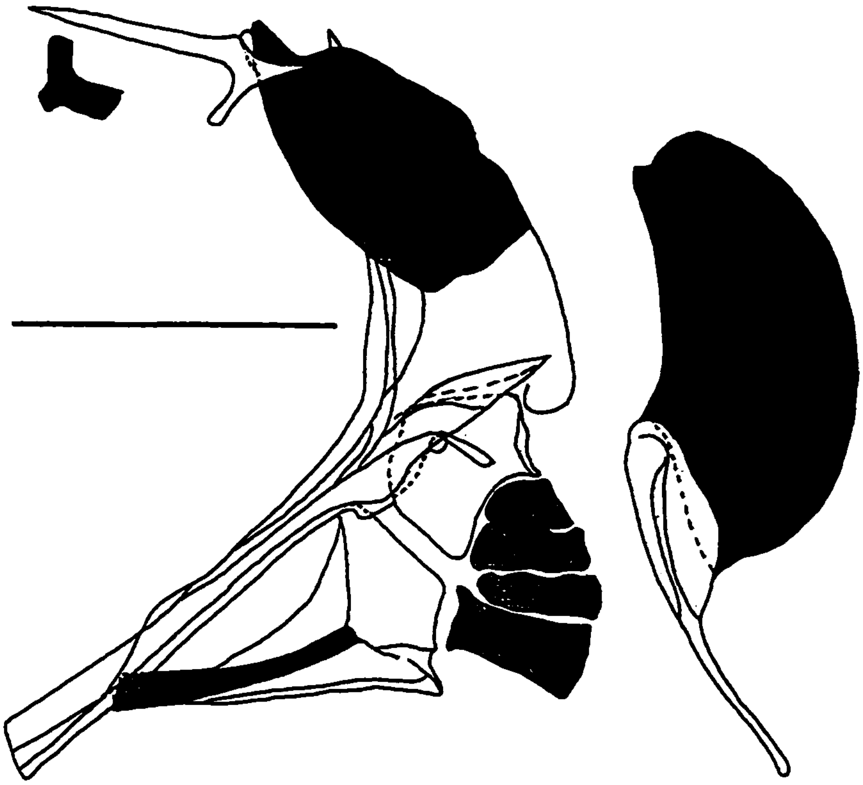

Fig. 6.23. Lateral view of the left pectoral girdle in *Elassoma zonatum* **(Elassomatidae)** (UAMZ 6920, 30 mm).

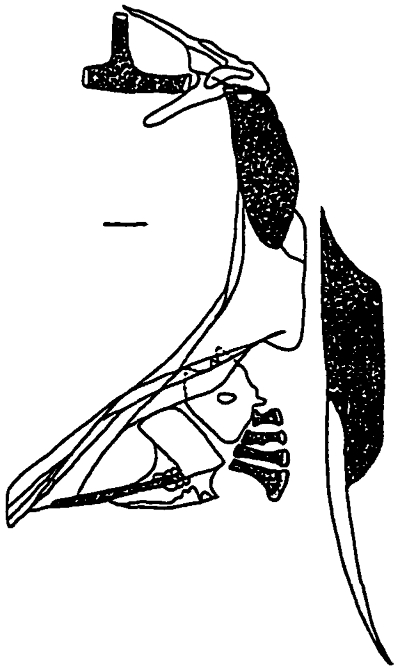

Fig. 6.24. Lateral view of the left pectoral girdle in *Lepomis gibbosus***(Centrarchidae)** (UAMZ 7715.4, 40 mm).

7. Osteology of the pelvic girdle in Eurypterygii

The pelvic girdle of fishes has been used since the earliest fish classifications. Linnaeus, (1758) used pelvic girdle position as the main feature to classify fishes. Because of its apparent similarity in fishes, there has been little attempt to give a detailed description of the pelvic girdles. Nelson (1971) provided terms for different parts of the pelvic girdle in sticklebacks. Stiassny and Moore (1992) modified the terminology of Potthoff (1980) and synonymized different terminologies for the pelvic girdle and gave a new analysis of the pelvic girdle in acanthomorph fishes.

The pelvic girdle is made up of a pair of ventral plates (basipterygia). Each plate consists of a central part, a median process, a membranous anterior process, an endochondral posterior process, wings, radials, and pelvic spines and rays. Splints are present in some primitive taxa. The central part is an ossification of the original pelvic cartilage that usually anteriorly retains a cartilage tip and posteriorly forms an articulation surface for the fin radials and rays. The membranous wings constitute an internal, an external dorsal, an external ventral, and a ventral wing. Not all the processes and wings are present in all eurypterygian fishes. It is the elaboration and orientation of wings that leads to its complexity in higher fishes. Primitively, in euteleosts, there are a number of autogenous radials. The medialmost radial is the largest and associated or fused to the base of the innermost ray and other radials are autogenous (Stiassny and Moore, 1992). In adults of higher taxa, the autogenous radials are lost although they may be present in juveniles. I follow the terminology of Stiassny and Moore (1992) for the pelvic girdle.

Aulopiformes

Synodontidae (Fig. 7.1). The pelvic girdle consists of a pair of cartilaginously connected plates. The connecting cartilage resembles the anterior process in members of higher taxa. Each plate consists of a central part, internal and external ventral wings, a long posterior process with a threadlike extension, a short cartilaginous lateral process, and three autogenous and one fused radial to the medialmost ray. The internal wings of the plates are perpendicular anteriorly. The anterior process and external dorsal and ventral wings are absent. There is no spine, but there are eight soft rays. The pelvic girdle is subthoracic and not associated with the pectoral girdle and the ribs.

The same conditions are found in members of *Pseudotrichonotus* (Johnson et al., 1996) and *Saurida* (Bowne, 1985), except that the posterior process is not threadlike. In Chlorophthalmidae and Notosudidae, the posterior process is thickened and tightly connected together cartilaginously and the lateral process is well developed. In Ipnopidae, the posterior process is elongated and threadlike. In Scopelarchidae the posterior process is blunt and indistinct and the lateral process is small. In Evermannellidae and to some extent in Paralepididae the posterior process is cartilaginous (Baldwin and Johnson, 1996).

Myctophiformes

Myctophidae (Fig. 7.2). The pelvic girdle consists of a pair of separate but adjacent plates. Each plate consists of a central part, an internal wing, narrow external dorsal and external ventral wings, a well developed cartilaginously tipped median process, a short cartilaginous lateral process, two autogenous cartilaginous radials and one fused radial to the medialmost ray, a very small posterior process, and a splint. The anterior process and ventral wing are absent. There is no spine, but there are eight soft rays. The pelvic girdle is abdominal and its lateral processes are cartilagenously associated with the sixth rib. In *Lampanyctus* and Neoscopelidae, the posterior process is well developed (Stiassny and Moore, 1992).

Lampridiformes

Veliferidae. The pelvic girdle consists of a pair of separate but adjacent and vertically positioned plates. Each plate consists of a central part, a narrow internal wing, external dorsal and external ventral wings, and a posterior process. Anterior, median, and lateral processes are absent. There is no spine, but there are eight soft rays. The pelvic girdle is thoracic and ligamentously connected to the postcleithra with its posterior process and to the coracoid with the anterior tip of its central part.

Trachipteridae (Fig. 7.3). The pelvic girdle consists of a pair of separate but adjacent and vertically positioned plates. Each plate consists of a central part, an internal wing, an external dorsal wing, and a long posterior process. Plates are bent anterodorsally between the cleithra and connected together through their anterior cartilaginous tips. Rays articulate in the middle with the cartilaginous ventral side of the plate. Anterior, median, and lateral processes are absent. There is no spine, but there are six soft rays. The pelvic girdle is thoracic and ligamentously connected to the postcleithra with its posterior process, and to the coracoid with the anterior tip of its central part. In *Zu* (Olney et al., 1993) and Lamprididae (Stiassny and Moore, 1992) the posterior process is not distinct.

Polymixiiformes

Polymixiidae. (Fig. 7.4). The pelvic girdle consists of a pair of plates that connect together with cartilage anteriorly and overlap medially with their median processes. Each plate consists of a central part, a long posterior process, a median process, an internal wing, external dorsal and external ventral wings, and three autogenous radials. Anterior and lateral processes and ventral wing are absent. There is no pelvic spine, but there are seven soft rays. The pelvic girdle is subthoracic and separated from the pectoral girdle, but is associated with the posterior tip of the postcleithrum.

Percopsiformes

Percopsidae. The pelvic girdle consists of a pair of plates that connect together with a triangular cartilage anteriorly and overlap with their median processes medially. Each plate consists of a central part, a posterior process, a median process, an internal wing, narrow external dorsal and external ventral wings, a splint, and three autogenous radials and a fused radial to the medialmost soft ray. Anterior and lateral processes and ventral wing are absent. There is no pelvic spine, but there are eight soft rays. The pelvic girdle is abdominal and separated from the ribs and pectoral girdle, but the postcleithrum reaches the pelvic plates. In Aphredoderidae a strong ligamentous postcleithral-pelvic association is present. In Amblyopsidae the pelvic girdle is abdominal (Stiassny and Moore, 1992).

Mugiliformes

Mugilidae. The pelvic girdle consists of a pair of posteromedially sutured plates. Each plate consists of a central part, an internal wing, a narrow external dorsal wing, a ventrally displaced anterior process, and a relatively short posterior process. The median process, external ventral wing, and ventral wing are absent. There is one pelvic spine and 4 soft rays. The pelvic girdle is thoracic and separated from the ribs, coracoid and cleithrum, but cartilaginously connected to the postcleithra with its small lateral processes.

Atheriniformes

Melanotaeniidae. The pelvic girdle consists of a pair of posteromedially abutting plates. Each plate consists of a central part, an internal wing, external dorsal and external ventral wings, a ventrally displaced anterior process, and a short posterior process. The external wings of the plate are perpendicular. The medial process and ventral wing are absent. One pelvic spine and five soft rays are present. The pelvic girdle is subthorasic and associated with the postcleithrum and the third rib through its small lateral processes.

Atherinidae (Fig. 7.5). The pelvic girdle consists of a pair of plates which connect together anteriorly and their median processes overlap medially. Each plate consists of a central part, an internal wing, an external dorsal wing, a ventrally oriented anterior process, a short posterior process, and a median process. A ventral wing is absent. One pelvic spine and five soft rays are present. The pelvic girdle is associated with the fourth to sixth ribs through its small lateral processes.

Beloniformes

Belonidae (Fig. 7.6). The pelvic girdle consists of a pair of widely separated plates. Each plate consists of a central part, an internal wing, and a dorsally oriented lateral process. The anterior, posterior, and medial processes, and other wings are absent. The pelvic spine is absent, but six soft rays are present. The pelvic girdle is abdominal and associated with the ribs through its lateral processes. The medialmost ray tipped with cartilage.

Hemiramphidae. The pelvic girdle consists of a pair of separate but adjacent plates. Each plate consists of a central part, a dorsally oriented lateral process, a ventrally oriented median process, and incomplete internal and external dorsal wings. An anterior process is present, but the posterior process and other wings are absent. The pelvic spine is absent, but six soft rays are present. The pelvic girdle is abdominal and widely separated from the pectoral girdle, but associated with the ribs through its lateral processes.

Cyprinodontiformes

Aplocheilidae (Fig. 7.7). The pelvic girdle consists of a pair of medially overlapping plates. Each plate consists of a central part, a medial process, and incomplete internal and external dorsal wings. Anterior and posterior processes and other wings are absent. The pelvic spine is absent, but seven soft rays are present. The pelvic girdle is abdominal and widely separate from the pectoral girdle and ribs. In members of *Aphyosemion* the posterior processes is distinct and medial processes completely overlap each other (Costa, 1998).

Cyprinodontidae. The pelvic girdle consists of a pair of medially overlapping plates. Each plate consists of a central part, angled internal and external dorsal wings, and long median and posterior processes. The anterior process and other wings are absent. A pelvic spine is absent, but six soft rays are present. The pelvic girdle is abdominal and widely separated from the pectoral girdle and ribs.

In Poeciliidae, as in Aplocheilidae, the posterior process is not distinct (Rauchenberger, 1989). The posterior process may or may not be distinct in Anablepidae (Ghedotti, 1998; Parenti, 1981).

Stephanoberyciformes

Stephanoberycidae (Fig. 7.8). The pelvic girdle consists of a pair of posteriorly abutting plates. Each plate consists of a central part, very narrow internal and external dorsal wings, a small median process, a large posterior process, and a small lateral process. The anterior process and other wings are absent. The pelvic spine is absent, but five soft rays are present. The pelvic girdle is abdominal and very small relative to body size and is separated from the pectoral girdle and ribs.

Rondeletiidae (Fig. 7.9). The pelvic girdle consists of a pair of separate plates. Each plate consists of a cartilagenously tipped central part, and very narrow and incomplete internal and external dorsal wings. Anterior, median, and posterior processes, and other wings are absent. A pelvic spine is absent, but five soft rays are present. The pelvic girdle is abdominal and very small relative to body size. It reaches the coracoid, but there is no apparent association with the pectoral girdle and ribs. In Melamphaidae, the anterior and posterior processes and internal and external dorsal wings are well developed (Kotlyar, 1991).

Beryciformes

Monocentridae. The pelvic girdle is a three dimensionally complex structure. Each plate consists of a central part, posterior process, an internal wing, and external dorsal and external ventral wings. The external dorsal and external ventral wings are connected laterally making a foramen which is apparent in the anterior view. The plates are firmly united making a foramen posteriorly. The medial process, anterior process, and ventral wing are absent. One pelvic spine and four soft rays are present.

Holocentridae (Fig. 7.10). The pelvic girdle is a three dimensionally complex structure. Each plate consists of a central part bifurcated into a dorsal and a ventral struts, an internal wing, an external dorsal wing, an external ventral wing, a ventrally displaced anterior process, and an enlarged posterior process. The internal wings of the dorsal struts are displaced dorsomedially and sutured together dorsally. The pelvic plates are firmly sutured. The medial process and ventral wings are absent. One pelvic spine and seven soft rays are present. The dorsal strut of the central part is connected to the coracoid and cleithrum, the anterior process to the ventral tip of the cleithrum, and the posterior process to the posterior tip of the postcleithrum.

In *Ostichthys*, the anterior process is not distinct, but a small lateral process is present (Zehren, 1979). In Trachichthyidae, the anterior process is not distinct in some genera and the internal wing is simple. In Caproidae, conditions are similar to that of Holocentrids, but the internal wing is simple (Stiassny and Moore, 1992). In Anoplogastridae, the plates are located vertically and are separate, a posterior process is present, but the anterior process is absent. In Diretmidae, there is a small anterior process and long posterior process. In Berycidae, both the anterior and posterior processes are distinct and a very short medial process is present, wings are not complex. In Anomalopidae, the posterior and anterior processes are not distinct but a medial process is present (Zehren, 1979).

Zeiformes

Grammicolepididae (Fig. 7.11). The pelvic girdle consists of a pair of anteriorly bent upward plates. The plates are connected cartilagenously anteriorly. Each plate consists of a long central part, very narrow internal, external dorsal, external ventral and ventral wings, and a dorsally displaced posterior process. The medial, lateral, and anterior processes are absent. One pelvic spine and six soft rays are present. The postcleithrum passes the pelvic girdle and connects to the pelvic posterior process. In Zeidae, the anterior process is not distinct, but posterior a process is well developed (Stiassny and Moore, 1992).

Caproidae (Fig. 7.12). The pelvic girdle consists of a pair of posteriorly articulated, anteriorly oriented upward plates. Each plate consists of a long central part, internal, external dorsal and external ventral wings, and anterior and posterior processes. The medial and lateral processes and ventral wing are absent. One pelvic spine and five soft rays are present. The central part passes between the coracoid shafts and postcleithra, but has no connection to them.

Gasterosteiformes

Hypoptychidae. The pelvic girdle is absent in members of this family.

Aulorhynchidae (Fig. 7.13). The pelvic girdle consists of a pair of posteriorly articulated plates. Each plate is a flat, broad, and ovoid bone in *Aulorhynchus flavidus* and an elongated bone in *Aulichthys japonicus*. The central part and posterior process are distinct in *Aulichthys japonicus* and the medial process is absent. A posteriorly directed lateral process is present. One pelvic spine and four soft rays are present. In adults, the pelvic girdle is separated from the pectoral girdle and radials are absent. In juveniles, the pelvic girdle overlaps the ectocoracoid and a small cartilaginous distal radial is present at the base of the first soft ray (Orr, 1995).

Gasterosteidae (Figs. 7.14 - 7.16). The pelvic girdle consists of a pair of sculptured and posteriorly articulated plates. The central part and medial process are not distinct except in *Culaea inconstans*. In *Spinachia* (Fig. 7.14) the pelvic plate is flat, long and weakly interdigitated posteriorly, but separated anteriorly. The lateral process is long and directed posterodorsally and the posterior process is short. In *Apeltes quadracus* (Fig. 7.15) the plates are broad and short without the anterior extension and posterior process and strongly interdigitate. The lateral process is long and directed posteriorly. In *Gasterosteus*, *Culaea*, and *Pungitius* (Fig. 7.16), the plates strongly interdigitate in the middle, the posterior process is long, and the lateral process is broad and directed dorsally. The pelvic overlaps the ectocoracoid anteriorly and is attached to it by connective tissue. There is one spine and 1-3 soft rays in *Gasterosteus*, 1-2 in *Culaea*(Orr, 1995), and 0-4 in *Pungitius* (Keivany, 1996; Keivany and Nelson, 1998).

Pegasidae (Fig. 7.17). The pelvic girdle consists of a pair of posteriorly abutting plates. The pelvic plate is highly folded ventrolaterally. Each plate consists of a central part, an internal wing, an external dorsal wing, a short posterior process, and a broad, ventrally folded lateral process. One short spine and two very long and one very short soft rays are present. The anterior process and other wings are absent. There is no attachment to the pectoral girdle.

Solenostomidae (Fig. 7.18) The pelvic girdle consists of a pair of broad anteromedially twisted and perpendicular plates. The central part, anterior, posterior, lateral, and median processes, and wings are not distinct. The anterior, ventral, and posterior edges of the plate are filled with cartilage. The pelvic plates abut anteriorly and articulate with scutes laterally and ventrally. Seven filamentous soft rays are present. There is no attachment to the pectoral.

Syngnathidae. The pelvic girdle is absent in members of this family.

Indostomidae (Fig. 7.19). The pelvic girdle consists of a pair of widely separated plates. Each plate consists of a rodlike central part. All wings and processes are absent. Five soft rays are present. There is no attachment to the pectoral girdle, but it is connected to the scutes.

Aulostomidae. The pelvic girdle consists of a pair of separated plates. Each plate is a flat triangular and posteriorly broad bone consisting of a central part, internal and external dorsal wings, and a very small medial process. Six soft rays are present. The pelvic girdle is abdominal and there is no attachment to the pectoral girdle. The anterior tip and posterior edge of the plate is filled with cartilage at the articulation with rays.

Fistulariidae (Fig. 7.20). The pelvic girdle consists of a pair of separated plates. Each plate is a flat ovoid, and posteriorly broad bone, consisting of a central part, internal and external dorsal wings, and a very small medial process. Six soft rays are present. The pelvic girdle is abdominal and there is no attachment to the pectoral girdle. The anterior tip and posterior edge of the plate are filled with cartilage at the articulation with rays. Other processes and wing are absent.

Macroramphosidae (Fig. 7.21). The pelvic girdle consists of a pair of anterodorsally bent and tightly attached plates. Each plate consists of a central part, external dorsal and external ventral wings, and a long posterior process. The external ventral wings are folded anteroventrally making a short tube between the plates. The internal wings are displaced mediodorsally and are perpendicular to each other. A foramen is present at the bending point. One pelvic spine and five soft rays are present. There is no connection with the ectocoracoid, but tip of the postcleithrum is attached to the lateral surface of the plate.

Centriscidae. The pelvic girdle consists of a pair of abutting and anterodorsally oriented plates. Each plate consists of a long central part and a broad head that articulates with the soft rays. The pelvic plate which is filled with cartilage at the dorsal tip and articulation surface with rays, extends and passes the postcleithrum and touches the body plates. One spine and four soft rays are present. Length of rays is sexually dimorphic (Mohr, 1937).

Synbranchiformes

The pelvic girdle is absent in members of this order.

Scorpaeniformes

Dactylopteridae (Fig. 7.22). The pelvic girdle is a tridimensionally complex structure consisting of a pair of firmly united plates. Each plate consists of a central part, the external ventral and internal wings, a ventrally displaced anterior process, a ventrally displaced lateral process, and a posterior process. The internal wing is twisted and medially connected perpendicularly to its counterpart, making a roof and ventrolaterally connected perpendicularly to the ventral wing, making a keel. One pelvic spine and five soft rays are present. The central part and internal wing are connected to the cleithrum.

Scorpaenidae. The pelvic girdle consists of a pair of posteriorly sutured plates. Each plate consists of a central part tipped with cartilage, a ventrally displaced anterior process, an internal wing, narrow external dorsal and external ventral wings, and a short posterior process. The central parts anteriorly connect together cartilagenously and connect to the cleithrum. One spine and five soft rays are present.

Hexagrammidae. The pelvic girdle consists of a pair of posteriorly sutured plates. Each plate consists of a central part tipped with cartilage, a very small ventrally displaced anterior process, an internal wing, narrow external dorsal and external ventral wings, and a short posterior process. The central parts anteriorly connect together cartilagenously and connect to the cleithrum. The posterior edge is highly notched to receive one weak spine and five soft rays. Other processes and wings are absent. The same conditions are found in specimens of *Pleurogrammus, Ophiodon, Oxylebius,* and *Zaniolepis* except that the posterior process is not distinct (Shinohara, 1994).

Agonidae (Fig. 7.23). The pelvic girdle consists of a pair of relatively broad, posteriorly sutured, and anteriorly abutted plates with a foramen in the middle. Each plate consists of a central part tipped with cartilage, a ventrally displaced anterior process, an internal wing, and narrow external dorsal and external ventral wings. The central parts anteriorly connect to cleithra. One weak spine and two soft rays are present.

In *Bothragonus* the posterior process is distinct (Kanayama, 1991). In Cottoidea, the posterior process may be or may not be distinct, the anterior process small in some but well developed in most and articulates with the ventromedial surface of the cleithra (Yabe, 1984; Yabe, 1991). In Normanichthyidae, the pelvic girdle is ligamentously attached to the coracoid, the anterior process is well developed, the posterior process is blunt, and only the internal wing is present (Yabe and Uyeno, 1996). In Ereuniidae wings are not distinct and spine is reduced or lost on one side in some specimens of *Ereunias*(Yabe, 1981; Yabe, 1983).

Perciformes

Percidae. The pelvic girdle consists of a pair of posteriorly sutured plates. Each plate consists of a central part tipped with cartilage, a ventrally displaced anterior process, an internal wing, narrow external dorsal and external ventral wings, and a short posterior process. The central parts anteriorly connect together cartilagenously and to the cleithra.

Cirrhitidae. The pelvic girdle consists of a pair of posteriorly sutured plates. Each plate consists of a central part tipped with cartilage, an internal wing, and narrow external dorsal and external ventral wings. Anterior and posterior processes are not distinct. The central parts anteriorly connect together cartilagenously and to the cleithra. One spine and five soft rays are present.

Elassomatidae (Fig. 7.24). The pelvic girdle consists of a pair of posteriorly sutured plates. Each plate consists of a central part tipped with cartilage, a ventrally displaced anterior process, an internal wing, narrow external dorsal and external ventral wings, and a short posterior process. The central parts anteriorly connect together cartilagenously, but unlike other Perciformes, is not connected to the cleithra. One week spine and five soft rays are present.

Pomacentridae. The pelvic girdle consists of a pair of posteriorly sutured plates. Each plate consists of a central part tipped with cartilage, a ventrally displaced anterior process, an internal wing, narrow external dorsal and external ventral wings, a ventral wing, and a short posterior process. The central parts anteriorly connect together cartilagenously and to the cleithra. One spine and five soft rays are present.

Centrarchidae. The pelvic girdle consists of a pair of posteriorly sutured plates. Each plate consists of a central part tipped with cartilage, a ventrally displaced anterior process, an internal wing, narrow external dorsal and external ventral wings, and a short posterior process. The central parts anteriorly connect together cartilagenously and to the cleithra. One spine and five soft rays are present.

In most perciforms, the pelvic girdle is connected to the cleithra, the posterior and anterior processes are distinct and external dorsal and external ventral wings are present (Bellwood, 1994; Mok, 1983; Mooi, 1993; Sasaki, 1989; Stiassny, 1990; Stiassny and Moore, 1992; Stiassny, 1993).

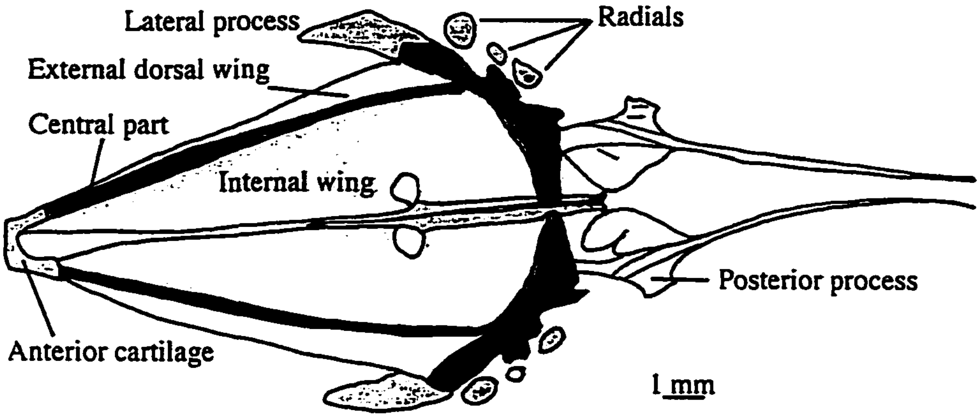

Fig. 7.1. Ventral view of the pelvic girdle in *Synodus synodus* **(Synodontidae)** (UAMZ 1806, 147 mm).

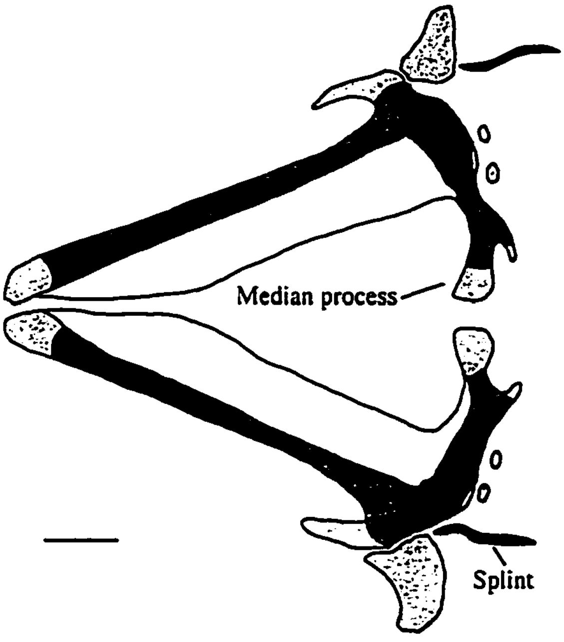

Fig. 7.2. Ventral view of the pelvic girdle in *Myctophum sp.* **(Myctophidae)** (UAMZ 2689, 60 mm).

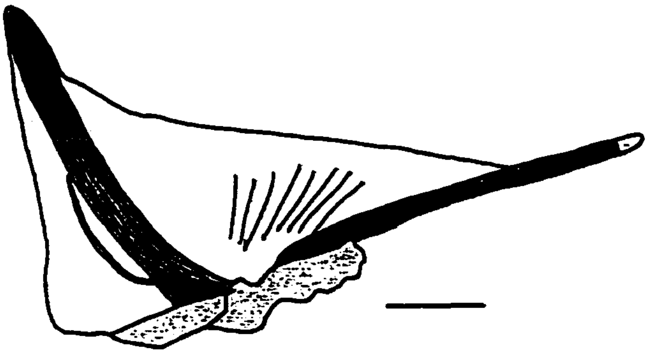

Fig. 7.3. Lateral view of the left pelvic plate in *Trachipterus altivelis* **(Veliferidae)** (CAS 24297, 85 mm).

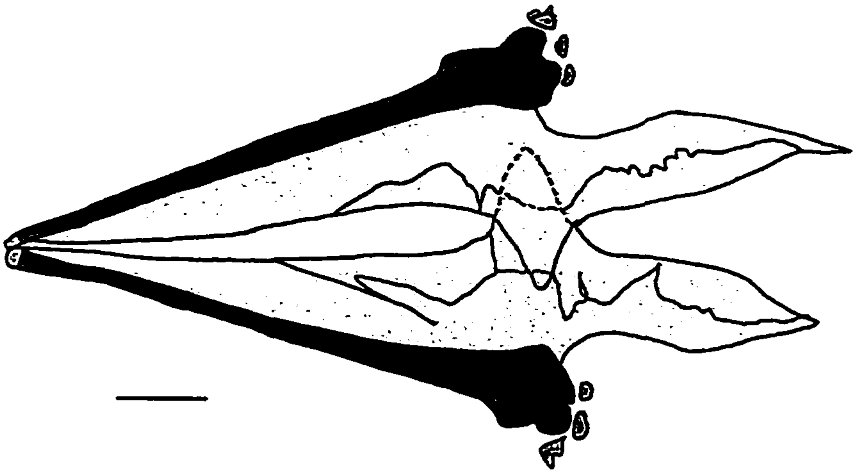

Fig. 7.4. Ventral view of the pelvic girdle in *Polymixia lowei* (**Polymixiidae**) (USNM 159300, 115 mm).

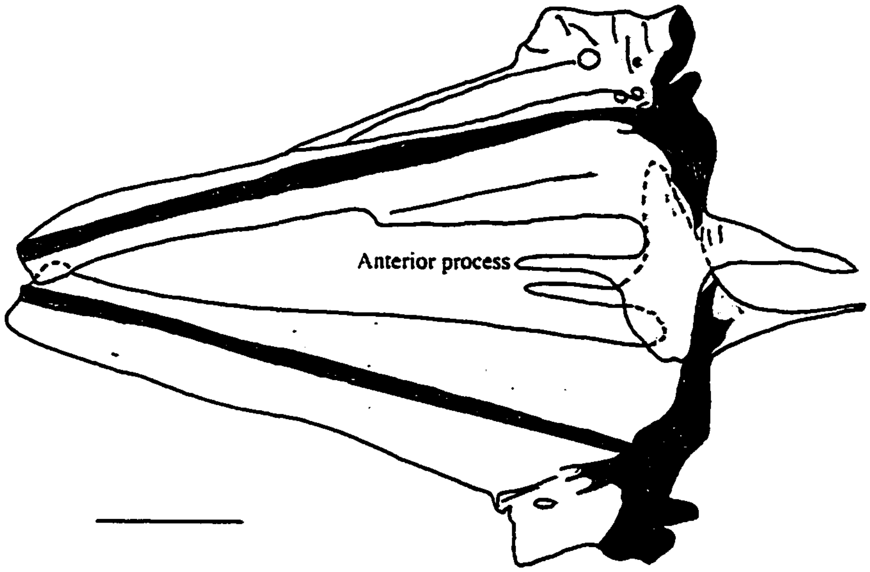

Fig. 7.5. Ventral view of the pelvic girdle in *Allanetta harringtonensis* (**Cyprinodontidae**) (UAMZ 2673, 58 mm).

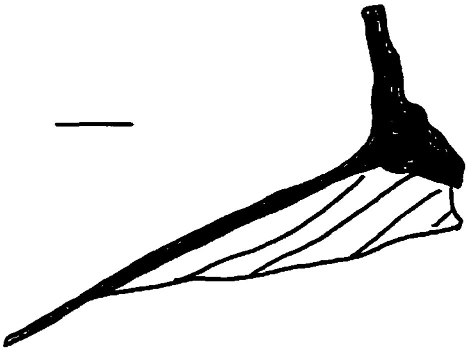

Fig. 7.6. Ventrolateral view of the left pelvic plate in *Pseudotylosurus sp*. (**Belonidae**) (UAMZ 8165, 173 mm).

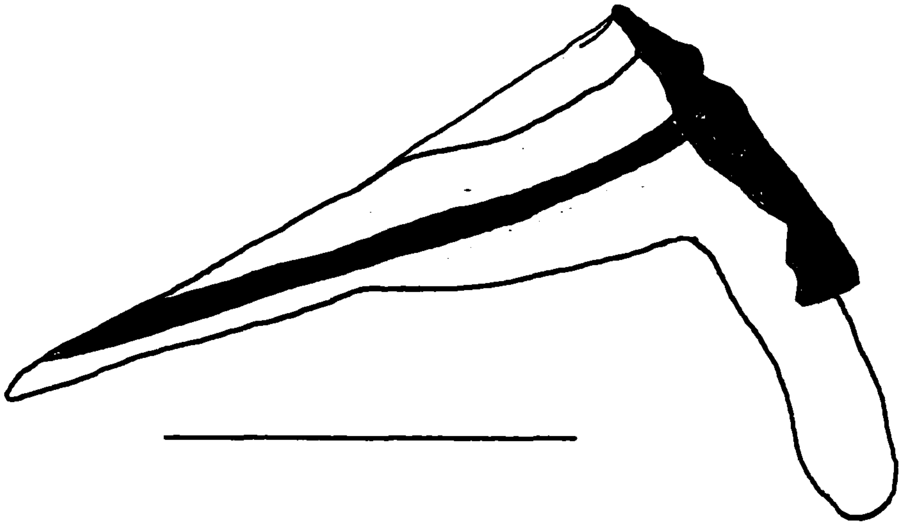

Fig. 7.7. Ventral view of the left pelvic plate in *Rivulus hartii* (**Aplocheilidae**) (UAMZ 6660, 47 mm).

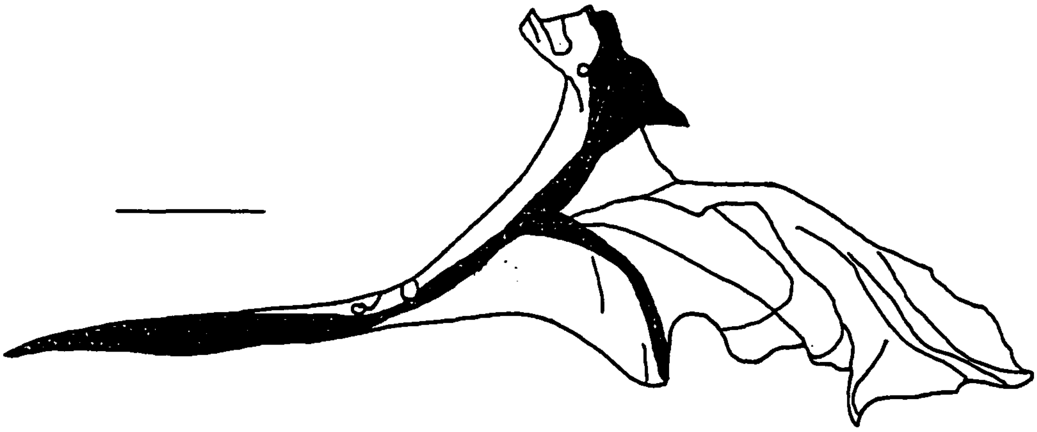

Fig. 7.8. Ventral view of the left pelvic plate in *Stephanoberyx monae* (**Stephanoberycidae**) (USNM 304353, 92 mm).

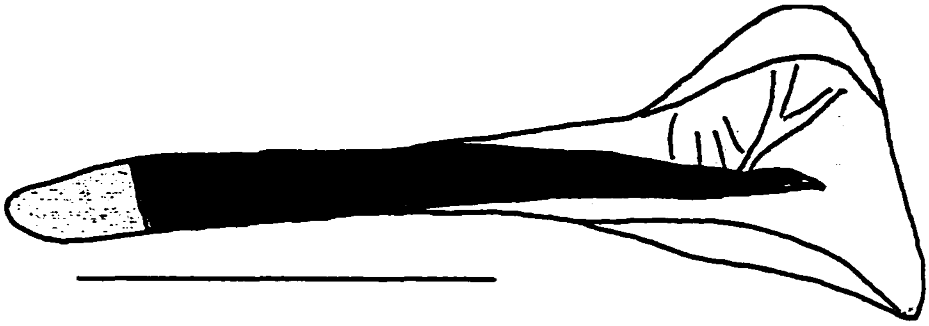

Fig. 7.9. Ventral view of the left pelvic plate in *Rondeletia loricata* (**Rondeletiidae**) (AMS 20523001, 37 mm).

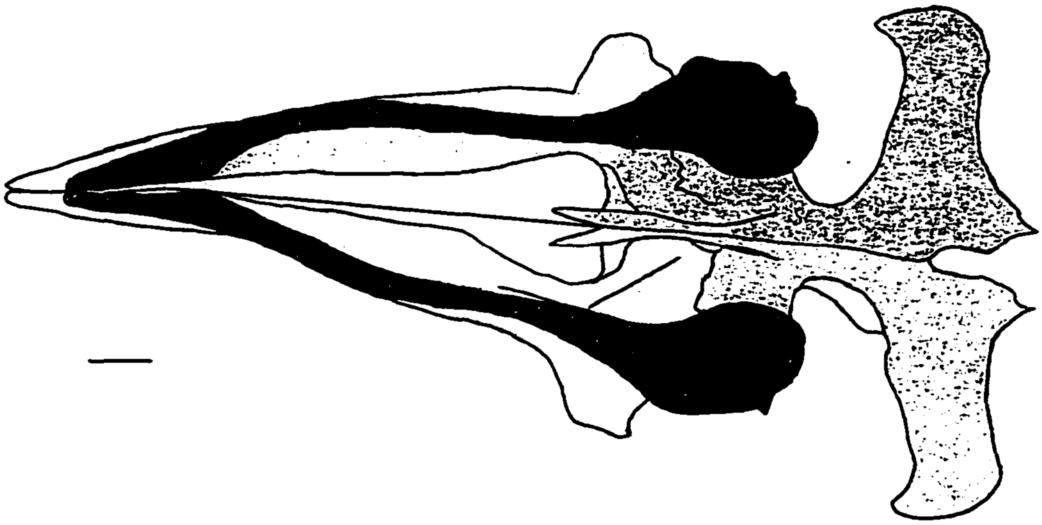

Fig. 7.10. Ventral view of the pelvic girdle in *Sargocentron vexillarium* **(Holocentridae)** (UAMZ 5075, 44 mm).

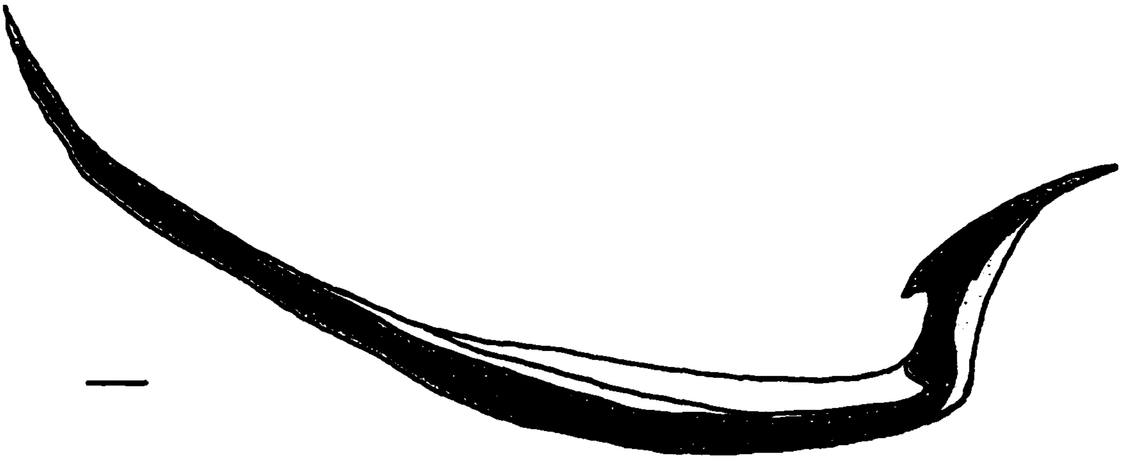

Fig. 7.11. Lateral view of the left pelvic plate in *Xenolepidichthys dalgleishi* **(Grammicolepididae)** (USNM 322673, 68 mm).

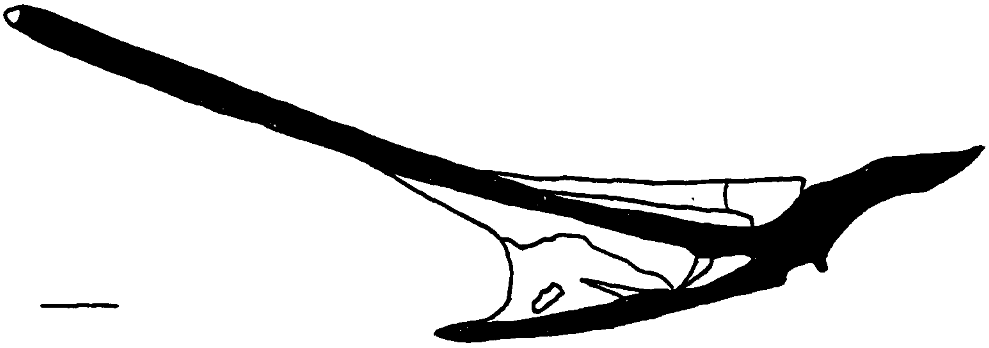

Fig. 7.12. Lateral view of the left pelvic plate in *Antigonia sp.* **(Caproidae)** (USNM 266901, 37 mm).

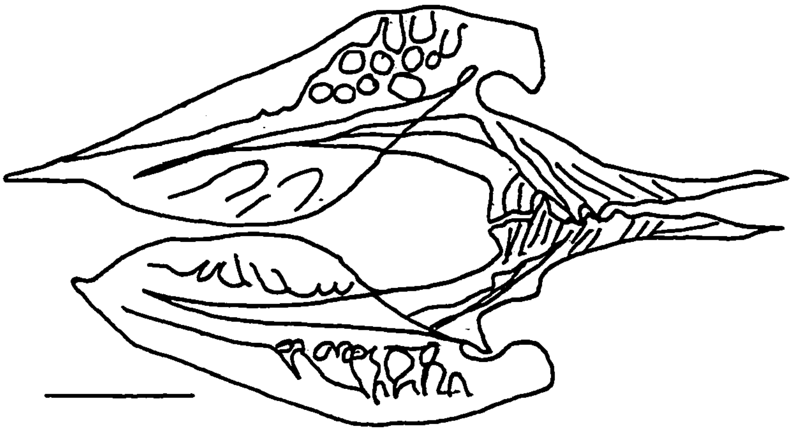

Fig. 7.13. Ventral view of the pelvic girdle in *Aulorhynchus flavidus* (**Aulorhynchidae**) (UAMZ 3783, 109 mm).

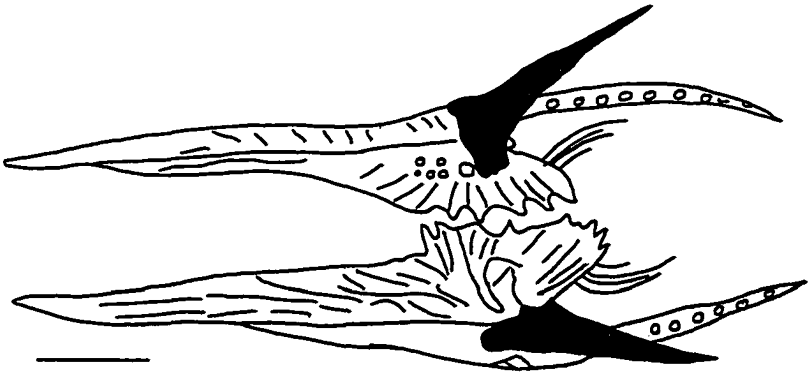

Fig. 7.14. Ventral view of the pelvic girdle in *Spinachia spinachia* (**Gasterosteidae**) (UAMZ 6582, 53 mm).

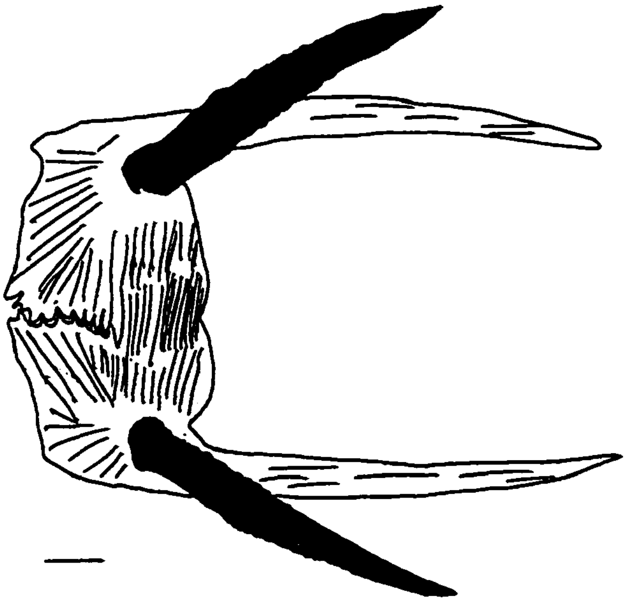

Fig. 7.15. Ventral view of the pelvic girdle in *Apeltes quadracus* (**Gasterosteidae**) (UAMZ 7958, 37 mm).

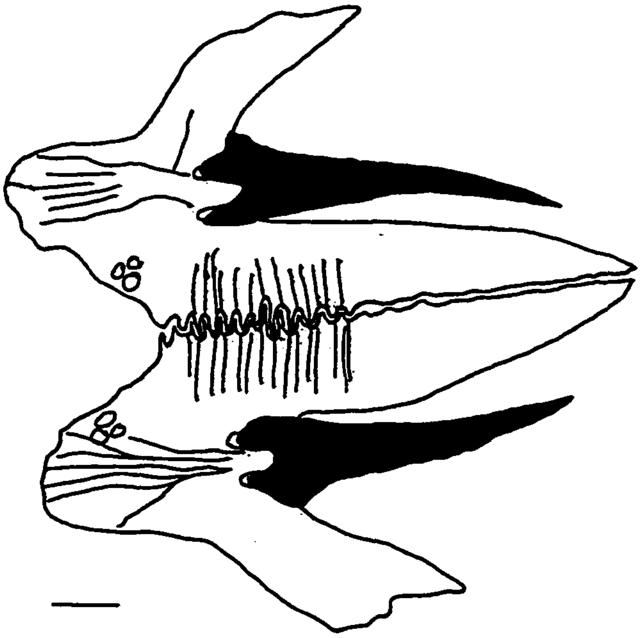

Fig. 7.16. Ventral view of the pelvic girdle in *Pungitius pungitius* (Gasterosteidae) (UAMZ 3049, 46 mm).

Fig. 7.17. Dorsal view of the pelvic girdle in *Pegasus volans* (Pegasidae) (UAMZ 4616, 99 mm).

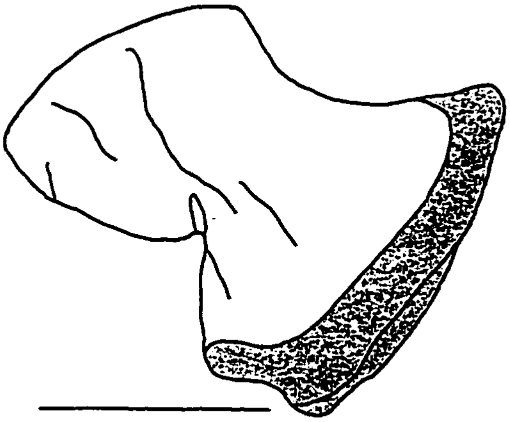

Fig. 7.18. Lateral view of the left pelvic plate in *Solenostomus paradoxus* **(Solenostomidae)** (AMS 17111002, 51 mm).

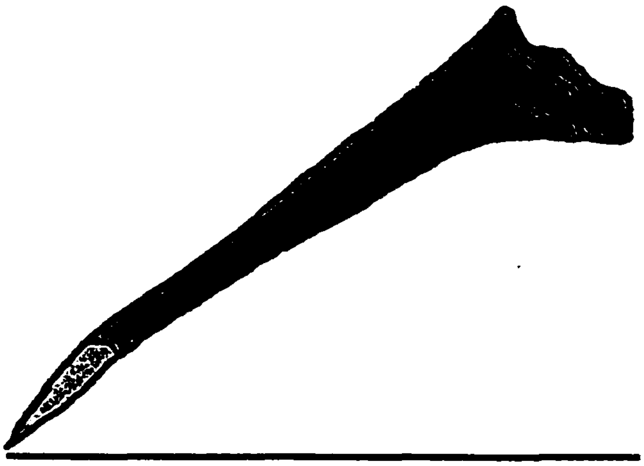

Fig. 7.19. Ventral view of the left pelvic plate in *Indostomus paradoxus* **(Indostomidae)** (CAS 64017, 25 mm).

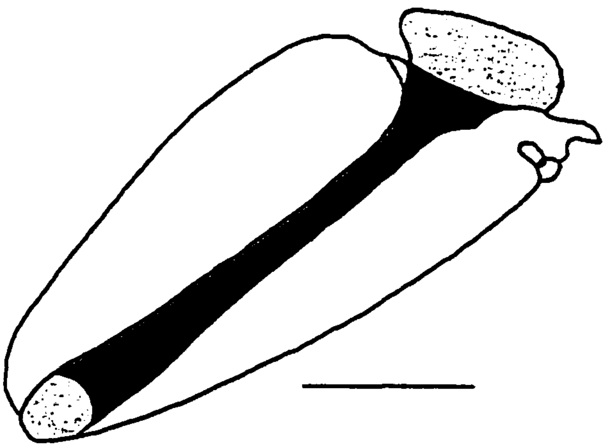

Fig. 7.20. Ventral view of the left pelvic plate in *Fistularia petimba* **(Fistulariidae)** (UAMZ 6348, 158 mm).

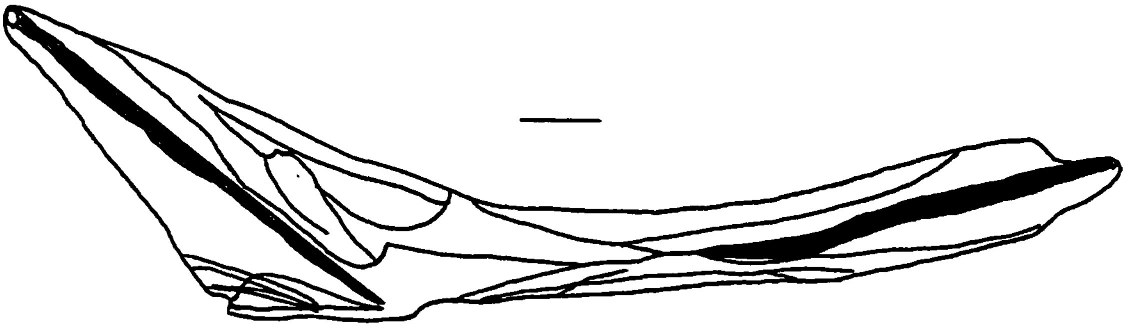

Fig. 7.21. Lateral view of the left pelvic plate in *Macroramphosus scolopax* **(Macroramphosidae)** (USNM 344398, 99 mm).

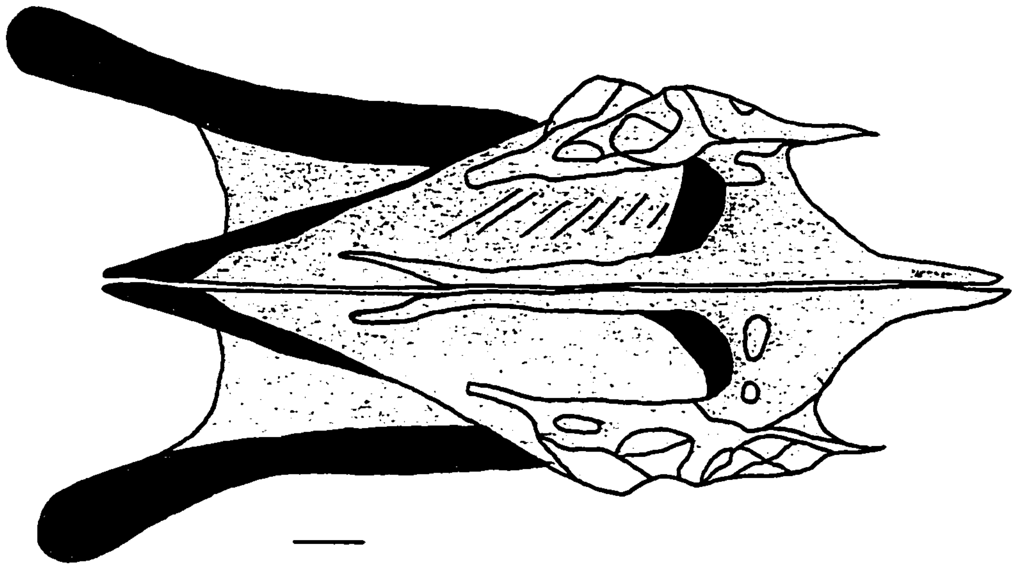

Fig. 7.22. Ventral view of the pelvic girdle in *Dactylopterus volitans* (**Dactylopteridae**) (UAMZ 2633, 74 mm).

Fig. 7.23. Ventral view of the pelvic girdle in *Xeneretmus latifrons* (**Agonidae**) (UAMZ 3196, 95 mm).

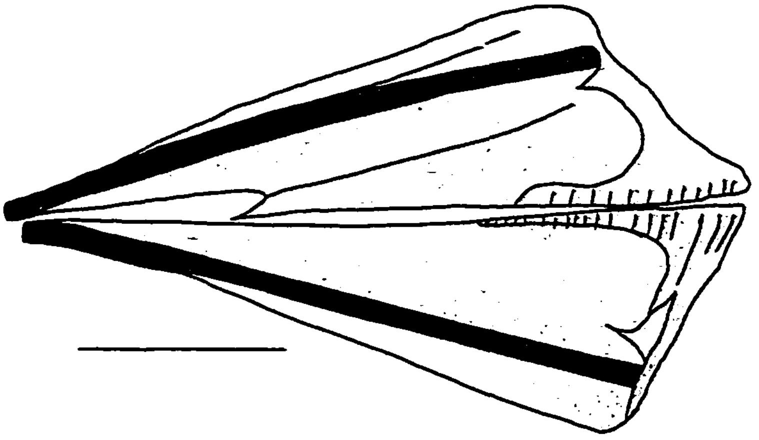

Fig. 7.24. Ventral view of the pelvic girdle in *Elassoma zonatum* (**Elassomatidae**) (UAMZ 6920, 30 mm).

8. Osteology of the caudal skeleton in Eurypterygii

The caudal skeleton of fishes has been used for taxonomic studies since about 150 years ago, when researchers such as Heckel (1850) used the caudal skeleton to define teleosts (de Pinna, 1996). Later, it was used by workers such as Kölliker (1860), Lotz (1864), Cope (1890), Whitehouse (1910), and Regan (1910). Hollister (1936) showed the importance of caudal skeleton for fish classification (Fujita, 1990) and Gosline (1960, 1961) and Nybelin (1963) gave detailed contemporary studies (de Pinna, 1996). Monad (1968) and Fujita (1990) provided the major monographic works on the caudal skeleton of teleostean fishes.

The caudal skeleton of eurypterygian fishes consists of five or six hypurals, a parhypural, one to three epurals, one or two pairs of uroneurals, ural centra 1 and 2, last preural centra and associated neural and haemal spines, and procurrent and principal rays. Eurypterygians like other teleosts have a diural caudal skeleton (two ural centra) . The ural and preural centra are distinguished by the branching point of the caudal artery; vertebrae posterior to that point are urals and those anterior to that point are preurals. The epurals are unpaired independent bones which are the remnants of the neural spines of the last vertebrae (Rojo, 1991). Schultze and Arratia (1989) in the light of ontogenetic studies proposed that not all the structures in actinopterygians called epurals are homologous. The uroneurals are paired bone remnants of the neural arches. The parhypural is a modified haemal spine of the first preural centrum and the last haemal arch crossed by the dorsal aorta (Rojo, 1991).

I follow the terminology of Fujita (1990) for the caudal skeleton. I use "intercaudal cartilage" to refer to both the interneural and interhaemal spines cartilage, postcaudal cartilage to refer to all the cartilage posterior to the caudal elements (postneural spine, posthaemal spine, postepural, posthypural, postparhypural cartilage), and caudal cartilage to refer to both intercaudal and postcaudal cartilage.

Aulopiformes

Synodontidae (Fig. 8.1). The caudal skeleton consists of five autogenous hypurals, an autogenous parhypural, one epural, and two autogenous uroneurals. Preural 1 and ural 1 are fused together. The hyporapophysis is well developed. The neural spine of preural 2 is short and autogenous. The haemal spines of preurals 2 and 3 are autogenous. The posthaemal and opisthural cartilages are present.

The same conditions are found in representatives of *Trachinocephalus*, another genus of Synodontidae (Fujita, 1990), but different conditions are found in those of other subfamilies of Synodontidae and of other families of the order. In Harpadontinae, the ural and preural centra are fused into a urostyle and two epurals and six hypurals are present (Bowne, 1985; Fujita, 1990). In Scopelarchidae, the ural and preural centra are fused into a urostyle and three epurals and six hypurals are present. Bathysaurinae, Omosudidae (Fujita, 1990), and Pseudotrichonotidae (Johnson et al., 1996) bear three epurals, but five hypurals. Aulopodidae, Ipnopidae, Paralepididae, and Chlorophthalmidae bear three epurals and six hypurals. In Evermannellidae, urals 1 and 2 and preural 1 are fused into a urostyle, and one epural, one pair of autogenous uroneurals, and six hypurals are present (Rosen, 1973). Alepisauridae bear two epurals, but five hypurals. Some species of Aulopodidae, Chlorophthalmidae, and Bathysaurinae bear a pair of urodermals. Members of many taxa bear a pair of median caudal cartilage. In some species uroneural 1, haemal spine of preural 2 or 3, and parhypural are fused. In all taxa, the neural spine of preural 2 is short (Fujita, 1990) except in Giganturidae which also have only one epural, one pair of fused uroneurals and their hypurals are fused into two dorsal and ventral plates which are fused to the urostyle (Rosen, 1973).

Members of more primitive Aulopiformes, Synodontoidei (Baldwin and Johnson, 1996), bear six autogenous hypurals, an autogenous ural centrum 2, an autogenous parhypural, three epurals, two pairs of autogenous uroneurals, autogenous haemal spines on preurals 2 and 3, a short neural spine on preural 2, an urodermal, a median caudal cartilage, and an opisthural cartilage.

Myctophiformes

Myctophidae (Fig. 8.2). The caudal skeleton consists of six autogenous but tightly attached hypurals, an autogenous parhypural, three epurals, and two pairs of autogenous uroneurals. Preural 1 and ural 1 and 2 are fused into a urostyle. The hyporapophysis is well developed. The neural spine of preural 2 is short and fused. The haemal spines of preurals 2 and 3 are autogenous. The intercaudal and postepural cartilage and a pair of median caudal cartilage are present.

There is a tendency in the caudal skeleton of myctophids to fuse and in some species, it consists of two upper and lower halves. Members of some genera have only two epurals, some have a fused haemal spine on preural 3, and some have a pair of urodermals. Neoscopelidae, as the more generalized Myctophiformes (Stiassny, 1996), have an autogenous ural centrum 2, two autogenous uroneurals, three epurals, and six autogenous hypurals (Fujita, 1990).

Lampridiformes

Veliferidae. The caudal skeleton consists of six hypurals, an autogenous parhypural, three epurals, and two pairs of autogenous uroneurals (one is tightly bound to the centrum). Hypurals 3 and 4 are fused together and to the ural centrum 2, but the others are autogenous. Ural centrum 2 is separated from the ural centrum 1. The hyporapophysis is well developed. The neural spine of preural 2 is short and fused. The haemal spines of preurals 2 and 3 are autogenous. The caudal cartilage is absent.

Trachipteridae (Fig. 8.3). The caudal skeleton consists of five hypurals organized into a dorsal plate (hypurals 3-5) and a ventral plate (hypurals 1-2) with a parhypural fused to its base, two epurals in one specimen and three in another one, and a pair of autogenous uroneurals. Preural centrum 1 and ural centrum 1 are fused together and ural centrum 2 is separated from them, but fused to the dorsal hypurals. The hyporapophysis is absent. The neural spine of preural 2 is long and fused. The haemal spine of preural 2 is autogenous, but of preural 3 is fused. The intercaudal and postcaudal cartilage, except posthypural cartilage, are absent. The procurrent rays are absent. Caudal rays are dentitioned and lacking the lateral processes at their bases.

In a specimen of *Trachipterus trachipterus*, hypurals 1 and 2 are separate from each other and only fused at their base. In *Desmodema*, parhypural and hypurals 1 and 2 are fused together and hypurals 3-5 are fused together and to the centrum, and only a very small epural is present (Fujita, 1990). In Lampridae, hypurals 1 and 2 and hypurals 3 and 4 are fused together and hypural five is autogenous. They bear two epurals and two pairs of autogenous uroneurals. In Radiicephalidae, all five hypurals and the parhypural are autogenous (Olney et al., 1993).

Polymixiiformes

Polymixiidae. The caudal skeleton consists of six autogenous hypurals, an autogenous parhypural, three epurals, and two pairs of autogenous uroneurals (one is tightly bound to the centrum). Ural centrum 2 is autogenous. The hyporapophysis is well developed. The neural spine of preural 2 is long and fused. The haemal spines of preurals 2 and 3 are autogenous. The intercaudal, and opisthural cartilage are present, but median caudal cartilage is absent. The procurrent rays are spiny.

Percopsiformes

Percopsidae. The caudal skeleton consists of six hypurals, an autogenous parhypural, two epurals, and two pairs of autogenous uroneurals. All hypurals, except 3 and 4, are separate from centra and hypurals 1 and 2 are fused together. In some specimens, hypurals 3 and 4 are fused together posteriorly. Ural centrum 2 is separate from ural centrum 1, but fused to hypurals 3 and 4. The hyporapophysis is small. The neural spine of preural 2 is long and fused. The haemal spines of preural 2 is autogenous. The intercaudal and median caudal cartilage are absent, but opisthural cartilage is present. In Amblyopsidae, there are two plates consisting of probably 5 hypurals and there is one epural in *Chologaster* and *Typhlichthys*, but two in *Amblyopsis* (Rosen and Patterson, 1969).

Mugiliformes

Mugilidae. The caudal skeleton consists of five hypurals, an autogenous parhypural, two epurals, and one pair of autogenous uroneurals. All hypurals are separate from the urostyle and hypurals 1 and 2 are fused together. Preural centrum 1 and ural centra 1 and 2 are fused into a urostyle. The hyporapophysis is well developed. The neural spine of preural 2 is short and fused. The haemal spines of preural 2 is autogenous. The intercaudal and postcaudal cartilage are present. In *Mugil cephalus* and *Liza carinata*, hypurals 3 and 4 are fused together and to urostyle (Fujita, 1990).

Atheriniformes

Melanotaeniidae (Fig. 8.4). The caudal skeleton consists of five hypurals, a fused parhypural, two epurals, and one pair of autogenous uroneurals. Hypurals 1 and 2 are fused together and with hypural 4 are fused to the urostyle, but hypurals 3 and 5 are autogenous. The parhypural is fused to hypural 1, but is separate from the urostyle. The hyporapophysis is well developed. The neural spine of preural 2 is short and fused. The haemal spines of preurals 2 and 3 are fused to the centra. The intercaudal and postcaudal cartilage are present.

Atherinidae. The caudal skeleton consists of five hypurals, an autogenous parhypural, two epurals, and one pair of fused uroneurals. Hypurals 1 and 2 are fused together and with hypural 5 are fused to the urostyle, hypurals 3 and 4 are fused together, but separate from urostyle. The hyporapophysis is well developed. The neural spine of preural 2 is short and fused. The haemal spines of preurals 2 and 3 are fused to the centra. The intercaudal cartilage is present.

In *Odontesthes*, hypurals 3, 4 and 5 are autogenous (Fujita, 1990). In *Menidia*, hypurals 1 and 2 and hypurals 3-5 are fused together and to the urostyle (Parenti, 1981). In

Notocheiridae (Isonidae), hypurals 3-5 are fused together, but separate from the urostyle and parhypural is fused to the urostyle and hypurals (Fujita, 1990). In Bedotiidae, all the hypurals and uroneurals are fused to the urostyle (Stiassny, 1990). In Phallostethidae hypurals 1 and 2 and hypurals 3-5 are fused together and to the urostyle (Parenti, 1984).

Beloniformes

Belonidae (Fig. 8.5). The caudal skeleton consists of five hypurals, an autogenous parhypural, three epurals, and one pair of autogenous uroneurals. Hypurals 1 and 2 are fused together and to the urostyle, hypurals 3-5 are fused together and tightly attached to the urostyle, but not fused to it. The hyporapophysis is well developed. The neural spine of preural 2 is short and fused. The haemal spines of preurals 2 and 3 are fused to the centra. The intercaudal and postcaudal cartilage are present. In *Strongylura*, uroneurals are fused and hypural 5 is autogenous (Fujita, 1990).

Hemiramphidae. The caudal skeleton consists of five hypurals, an autogenous parhypural, three epurals, and one pair of fused uroneurals. Hypurals 1 and 2 are fused together and to the urostyle, hypurals 3 and 4 are fused together, but separate from the urostyle, hypural 5 is autogenous. The hyporapophysis is well developed. The neural spine of preural 2 is short and fused. The haemal spines of preurals 2 and 3 are fused to the centra. Postcaudal cartilage is present.

The same conditions are found in *Hyporhamphus*, but intercaudal cartilage is present. In Adrianichthyidae, hypural 5 is fused to hypural 4, but is separate from the urostyle and intercaudal cartilage is present, but postcaudal cartilage is absent (Parenti, 1993). In Scomberesocidae, the parhypural is fused to the urostyle and the first hypural, hypural 5 is fused to the urostyle, and intercaudal and postcaudal cartilages are absent (Fujita and Oozeki, 1994). In Exocoetidae, the parhypural is separate from hypurals, but fused to the urostyle, hypural 5 is fused to hypural 4, but not to the urostyle, and intercaudal and postcaudal cartilage are absent (Fujita, 1990).

Cyprinodontiformes

Aplocheilidae (Fig. 8.6). The caudal skeleton consists of five hypurals, an autogenous parhypural, one epural, and one pair of fused uroneurals. Hypurals 1 and 2 and hypurals 3-5 are fused together and to urostyle. The hyporapophysis is small. The neural spine of preural 2 is long and fused. The haemal spines of preurals 2 and 3 are fused to centra. The intercaudal and postcaudal cartilage are absent. The same conditions are found in *Aphyosemion*, but in *Aplocheilus* hypural 3 is separate from others (Parenti, 1981).

Cyprinodontidae. The caudal skeleton consists of a single fused hypural plate, an autogenous parhypural, and one epural. Uroneurals are absent. All hypurals are fused to the urostyle. The hyporapophysis is small. The neural spine of preural 2 is long and fused. The haemal spines of preurals 2 and 3 are fused to centra. The intercaudal and postcaudal cartilage are present.

There is a notch in the hypural plate of some Anablepidae (Ghedotti, 1998). In *Gambusia* (Poeciliidae) the condition is similar to that of Aplocheilidae, but intercaudal cartilage is present. In the other poeciliid genus, *Poecilia*, the condition is the same as Cyprinodontidae, but intercaudal cartilage is present (Fujita, 1990).

Stephanoberyciformes

Stephanoberycidae (Fig. 8.7). The caudal skeleton consists of six autogenous hypurals, an autogenous parhypural, three epurals, and two pairs of autogenous uroneurals. The ural centrum 2 is autogenous. The hyporapophysis is small. The neural spine of preural 2 is short and fused. The haemal spines of preurals 2 and 3 are autogenous. The intercaudal and postcaudal cartilage are present. Caudal rays are dentitioned.

Rondeletiidae. The caudal skeleton consists of six autogenous hypurals, an autogenous parhypural, three epurals, and two pairs of autogenous uroneurals. Ural centrum 2 is autogenous. The hyporapophysis is very small. The neural spine of preural 2 is short and fused. The haemal spines of preurals 2 and 3 are autogenous. Intercaudal and postcaudal cartilage are absent.

In Barbourisiidae (Rosen, 1973) and Gibberichthyidae (Kotlyar, 1991b), there are six autogenous hypurals, three epurals and two pairs of uroneurals. In Melamphaidae there are five autogenous hypurals, three epurals and one pairs of uroneurals (Kotlyar, 1991a). In Mirapinnidae, Megalomycteridae, and Cetomimidae, there are only four autogenous hypurals, one pair of autogenous uroneural, and the neural spine of preural 2 is long and intercaudal cartilage is present (Rosen, 1973; Fujita, 1990).

Beryciformes

Monocentridae (Fig. 8.8). The caudal skeleton consists of six autogenous hypurals, an autogenous parhypural, three epurals, and two pairs of autogenous uroneurals. The ural centrum 2 is autogenous. The hyporapophysis is well developed. The neural spine of preural 2 is short and autogenous. The haemal spines of preurals 2 and 3 are autogenous. The postcaudal and opisthural cartilage are present. Caudal rays are dentitioned.

Holocentridae. The caudal skeleton consists of five autogenous hypurals, an autogenous parhypural, three epurals, and two pairs of uroneurals; one pair are fused. Ural centrum 2 is autogenous. The hyporapophysis is well developed. The neural spine of preural 2 is short and fused. The haemal spines of preurals 2 and 3 are autogenous. The intercaudal and opisthural cartilage are present.

In *Sargocentron lacteoguttatum*, *S. ittodai*, and in Berycidae the preural centrum 1 and ural centra 1 and 2 are fused into a urostyle. In Anoplogasteridae, the second pair of uroneurals is absent and a sixth hypural is present, and hypurals 3 and 4 are fused to the centra (Zehren, 1979). In Trachichthyidae (Kotlyar, 1992) and Anomalopidae, the sixth hypural is present and both pairs of uroneurals are autogenous (Fujita, 1990).

Zeiformes

Grammicolepididae (Fig. 8.9). The caudal skeleton consists of five hypurals, an autogenous parhypural, two epurals, and one pair of fused uroneurals. Hypurals 1 and 2 are fused together and with hypural 3 to the urostyle. Hypurals 4 and 5 are autogenous. The hyporapophysis is absent. The neural spine of preural 2 is long and fused. The haemal spines of preurals 2 and 3 are fused to the centra. The postcaudal cartilage is present.

Caproidae. The caudal skeleton consists of five autogenous hypurals, an autogenous parhypural, three epurals, and one pair of autogenous uroneurals. The hyporapophysis is well developed. The neural spine of preural 2 is short and fused. The haemal spines of preurals 2 and 3 are autogenous. Remnants of a possibly ural centrum 2 is present. The intercaudal and postcaudal cartilage are present.

In Parazenidae, there are two epurals, uroneurals are fused, the neural spine of preural 2 is long and fused, haemal spines of preurals 2 and 3 are fused, hypurals 1 and 2 are fused together and to the urostyle, and hypurals 3 and 4 are fused together, but separate from the urostyle. In some Macrurocyttidae and Oresomatidae, there are two epurals, uroneurals are fused, neural spine of preural 2 is long and fused, haemal spines of preurals 2 and 3 are fused, hypurals 1 and 2 and hypurals 3 and 4 are fused together and to the urostyle. In Zeidae, uroneurals are fused, neural spine of preural 2 is long and fused, haemal spines of preurals 2 and 3 are fused, hypurals 1 and 2 are fused together and to the urostyle and hypurals 3 and 4 are fused to the urostyle and either fused together or separate from each other (Fujita, 1990).

Gasterosteiformes

Hypoptychidae (Fig. 8.10). The caudal skeleton consists of a fused hypural plate with a notch in the middle, a fused parhypural, two epurals, and one pair of fused uroneurals. The hyporapophysis is absent. The neural spine of preural 2 is long and fused. The haemal spines of preurals 2 and 3 are fused. The caudal cartilage is absent.

Aulorhynchidae (Fig. 8.11). The caudal skeleton consists of a single fused hypural plate which is fused to the urostyle, a fused parhypural, two epurals in *Aulichthys*, but absent in *Aulorhynchus* that has an the urostyle with a full neural arch and spine, and one pair of fused uroneurals. A low hyporapophysis is present. The neural spine of preural 2 is long and fused. The haemal spines of preurals 2 and 3 are fused. The caudal cartilage is absent. In larvae there is a deep notch between the dorsal and ventral hypural plates (Orr, 1995), but in adults it is present only in *Aulichthys japonicus*. In some specimens of *Aulichthys* there is only one epural (Bowne, 1985).

Gasterosteidae. The caudal skeleton consists of a single fused hypural plate which is fused to the urostyle, a fused parhypural, two epurals (in *Spinachia*, but one in other genera), and one pair of fused uroneurals. A low hyporapophysis is present. The neural spine of preural 2 is long and fused. The haemal spines of preurals 2 and 3 are fused. The caudal cartilage is absent.

In *Gasterosteus*, the hypural plate is deeply cleft in adults; in larvae dorsal and ventral plates are autogenous, separated from each other and urostyle. Two autogenous epurals are present in *Spinachia* and in juveniles of other genera (Orr, 1995).

Pegasidae (Fig. 8.12). The caudal skeleton consists of a single fused hypural plate which is fused to the urostyle, a fused parhypural, one epural, and one pair of fused uroneurals. The hyporapophysis is absent. The neural spine of preural 2 is long and fused. The haemal spines of preurals 2 and 3 are fused. The caudal cartilage is absent. The procurrent rays are absent.

Solenostomidae (Fig. 8.13): The caudal skeleton consists of a single fused hypural plate, a fused parhypural, and a broad epural. The hyporapophysis is a low ridge in the center of the plate. *Solenostomus paradoxus* lacks the haemal spine on preural 2, but *S. cyanopterus* has expanded spines on preural 2 (Orr, 1995). A strong lateral process is present at the base of the rays.

Syngnathidae (Fig. 8.14): The caudal skeleton consists of a ventral hypural plate (hypurals 1 and 2) and a dorsal hypural plate (hypurals 3-5), and a fused parhypural. The plates are separated by a notch and ventral and dorsal plates are fused to the urostyle. Epurals and uroneurals are absent. The hyporapophysis is low. The vertebral arches are short. The procurrent rays are absent. A strong lateral flange is present at the base of the rays. The caudal fin is lost in Hippocampinae. The hypural plate might be entire in some specimens of *Syngnathus griseolineatus* (Bowne, 1985), but it is notched in my specimens, and it is with a small notch in *Heraldia nocturna* (Orr, 1995).

Indostomidae (Fig. 8.15). The caudal skeleton consists of a single fused hypural plate which is fused to the urostyle and a fused parhypural. Epurals, uroneurals, and hyporapophysis are absent. The full neural spine on preural 2 is fused. The haemal spines of preurals 2 and 3 are fused. The caudal cartilage is absent.

Aulostomidae (Fig. 8.16): The caudal skeleton consists of a ventral hypural plate (hypurals 1 and 2), a dorsal hypural plate (hypurals 3-5), an autogenous parhypural, two epurals; the second is very tiny at the base of the first one, and a pair of fused uroneurals. The ventral plate is autogenous, but the dorsal plate is fused to the urostyle. The two middle caudal rays are thickened at their base and support the end of the lateral line. The hyporapophysis is low. The only gasterosteiform family with intercaudal and postcaudal cartilage. The same conditions are found in *Aulostomus chinensis*, except that the parhypural is fused to the urostyle (Bowne, 1985) or to the base of the hypural plate (Orr, 1995).

Fistulariidae (Fig. 8.17): The caudal skeleton consists of a single fused hypural plate, including a parhypural, which is fused to the urostyle. The hyporapophysis is formed at the central part of the urostyle. No autogenous epurals are present. The neural and haemal spines of preurals 3 and 4 are tipped with cartilage. The neural and haemal spines of preural 2 are elongated and fused to the centra. The two middle rays are thickened and elongated, bearing the extended lateral line. Strong lateral processes are present at the base of the rays.

Macroramphosidae. The caudal skeleton consists of a fused hypural plate which is divided into two halves by a notch, one autogenous epural tipped by cartilage, and a pair of fused uroneurals. The hyporapophysis is well developed. The neural and haemal spines of preural 2 are distally tipped with cartilage and expanded anteriorly. Strong lateral processes are present at the base of the rays.

Centriscidae (Fig. 8.18). The caudal skeleton consists of a single fused hypural plate, an autogenous parhypural tipped with cartilage, one autogenous epural tipped with cartilage, and a pair of fused uroneurals. The plates are separated by a notch and dorsal and ventral plates are fused to the urostyle. The hyporapophysis is low. The neural and haemal spines of preural 2 are long, fused, and tipped distally with cartilage. Strong lateral processes are present at the base of the rays.

Synbranchiformes

Synbranchidae: Except in *Macrotremus* (Rosen and Greenwood, 1976), the caudal fin is absent in this family.

Mastacembelidae (Fig. 8.19). The caudal skeleton consists of a ventral plate (hypurals 1 and 2) that are fused together posteriorly, a dorsal plate (hypurals 3- 5), an autogenous parhypural, one epural, and two pairs of uroneurals; one is fused, and the other is autogenous. The hyporapophysis is low. The neural spine of preural 2 is long and fused. The haemal spine of preural 2 is autogenous, but of preural 3 is fused to the centrum. The caudal cartilage is absent. The same conditions are found in *Mastacembelus*, except that members of some species have one uroneural and one epural (Travers, 1984; Fujita, 1990). In Chaudhuriidae, the parhypural is fused to the hypurals and there is one pair of uroneurals or they are absent (Travers, 1984).

Scorpaeniformes

Dactylopteridae (Fig. 8.20). The caudal skeleton consists of a ventral (hypurals 1 and 2), a dorsal plate (hypurals 3- 5), and an autogenous parhypural which is tightly attached to the first hypural, two epurals, and two pairs of uroneurals; one is fused, the other is autogenous.

The hyporapophysis is well developed. The neural spine of preural 2 is short and fused. The haemal spines of preurals 2 and 3 are autogenous. The caudal cartilage is absent. The same conditions are found in *Dactyloptena gilberti*, except that one uroneural is present, and the parhypural is fused to the hypural (Fujita, 1990).

Scorpaenidae (Fig. 8.21). The caudal skeleton consists of a ventral plate (hypurals 1 and 2), a dorsal plate (hypurals 3 and 4), an autogenous hypural 5, an autogenous parhypural, three epurals, one pair of autogenous uroneurals, and probably remnants of a pair of fused uroneurals. The neural spine of preural 2 is short and fused. The haemal spines of preurals 2 and 3 are autogenous. The hyporapophysis is well developed. The caudal cartilage is present.

In representatives of *Plectrogenium* all the hypurals are autogenous. In those of *Parapterois*, hypurals 3 and 4 are autogenous. In those of *Minous*, parhypural 3 and 4 are fused to the urostyle and the parhypural is fused to the hypurals, neural spine 2 is long and the haemal spine of preural 3 is fused to the centrum. In members of *Erosa*, there are only two epurals and parhypural and hypural 5 are fused to the other hypurals (Fujita, 1990).

Hexagrammidae. The caudal skeleton consists of a dorsal plate (hypurals 3-5), a ventral plate (hypurals 1 and 2) and a parhypural, a urostyle, three epurals, and a pair of uroneurals. Both hypural plates are separated from the urostyle. The neural spine of preural centrum 2 is short and fused. The haemal spines of preurals 2 and 3 are autogenous. The hyporapophysis is absent. The intercaudal and postcaudal cartilages are present.

The lower hypural plate is free in members of all the genera, but the upper plate is fused to the urostyle in *Zaniolepis*. The parhypural is fused to the hypural plate in *Hexagrammos*, *Oxylebius*, *Pleurogrammus*, and *Zaniolepis*, but is autogenous in those of *Ophiodon* and *Anoplopoma*. Although the upper hypural is composed of two plates in members of *Anoplopoma*, it is one element in the other genera. A narrow hyporapophysis is present in *Oxylebius* and *Zaniolepis* (Shinohara, 1994).

Agonidae (Fig. 8.22). The caudal skeleton consists of a notched hypural plate fused to the urostyle, a fused parhypural, a urostyle, one broad epural, and a pair of fused uroneurals. The neural spine of preural centrum 2 is long and fused. The haemal spines of preurals 2 and 3 are fused. The hyporapophysis is well developed. The caudal cartilage is absent. There are two epurals in representatives of *Agonomalus* (Fujita, 1990), *Hypsagonus*, *Percis* and *Bothragonus*, and one in other agonids (Kanayama, 1991).

In Aploactinidae there are two epurals, hypurals 3 and 4 are fused together and to the urostyle, parhypural and hypurals 1 and 2 are fused together, the neural spine of preural 2 is long, and haemal spine of preural 3 is fused to the centrum. In Congiopodidae and Liparidae (Stein et al., 1991; Balushkin, 1996), parhypural and hypural 1 and 2, and hypurals 3 and 4 are fused together, but all are separate from the urostyle. In Triglidae, hypurals 3 and 4 are fused to the urostyle. In some Platycephalidae, all the hypurals are autogenous. In Hoplichthyidae, haemal spines of preurals 2 and 3 are fused to the centra, the parhypural is fused to hypural 1, and hypurals 3 and 4 are fused to the urostyle. In Normanichthyidae, haemal spine of preural 3 is fused to the centrum , uroneurals are fused and hypurals 3-5 are autogenous. In most Cottidae all the hypurals are fused to the urostyle, haemal spines of preural 2 and 3 are fused to the centra, and the neural spine of preural 2 is long. The uroneural is either autogenous or fused (Yabe, 1984; Yabe, 1991). In Cyclopteridae, the uroneurals are fused, neural spine of preural 2 is long, hypurals 3-5 are fused together and to the urostyle, and parhypural and hypurals 1 and 2 are fused together, but separated from the urostyle (Fujita, 1990).

Perciformes

Percidae. The caudal skeleton consists of five autogenous hypurals, a urostyle, an autogenous parhypural, three epurals, and a pair of autogenous uroneurals. The neural spine of preural centrum 2 is short and fused. The haemal spines of preurals 2 and 3 are autogenous. The hyporapophysis is small. The intercaudal and postcaudal cartilages are present.

Cirrhitidae. The caudal skeleton consists of five autogenous hypurals, a urostyle, an autogenous parhypural, three epurals, and a pair of autogenous uroneurals. The neural spine of preural centrum 2 is short and fused. The haemal spines of preurals 2 and 3 are autogenous. The hyporapophysis is well developed. The intercaudal and postcaudal cartilage are present.

Elassomatidae (Fig. 8.23). The caudal skeleton consists of a dorsal (hypurals 3-5) and a ventral (hypurals 1 and 2) plate, a urostyle, an autogenous parhypural, three epurals (four in one specimen), and a pair of fused uroneurals. The neural spine of preural centrum 2 is short and fused. The haemal spines of preurals 2 and 3 are fused. The hyporapophysis is well developed. The intercaudal and postcaudal cartilages are present.

Pomacentridae. The caudal skeleton consists of five hypurals, a urostyle, an autogenous parhypural, three epurals, and a pair of fused uroneurals. Hypurals 3 and 4 are fused to the urostyle. The neural spine of preural centrum 2 is short and fused. The haemal spines of preurals 2 and 3 are autogenous. The hyporapophysis is well developed. The intercaudal cartilage is present. In members of *Amphiprion* and *Pomachromis,* parhypural and hypurals 1 and 2 are fused together (Fujita, 1990).

Centrarchidae (Fig. 8.24). The caudal skeleton consists of five autogenous hypurals, a urostyle, an autogenous parhypural, three epurals, and two pairs of autogenous uroneurals. The neural spine of preural centrum 2 is short and fused. The haemal spines of preurals 2 and 3 are autogenous. The hyporapophysis is well developed. The intercaudal and postcaudal cartilages are present.

Perciformes usually have a urostyle, one or two uroneurals (the first one is autogenous or fused) and 1-3 epurals (mostly 3). Most Perciformes have a short neural spine on preural 2, an autogenous parhypural, autogenous haemal spines on preurals 2 and 3, an autogenous hypural 5 or separate from other hypurals, and caudal cartilage. In many Perciformes hypurals 1-4 are autogenous, but also in many are fused, either together, to the urostyle or both (Doyle, 1998; Fujita, 1990; Gomon, 1997; Greenwood, 1976; Hoese and Gill, 1993; Mok, 1983; Mooi, 1993; Sasaki, 1989; Westneat, 1993)

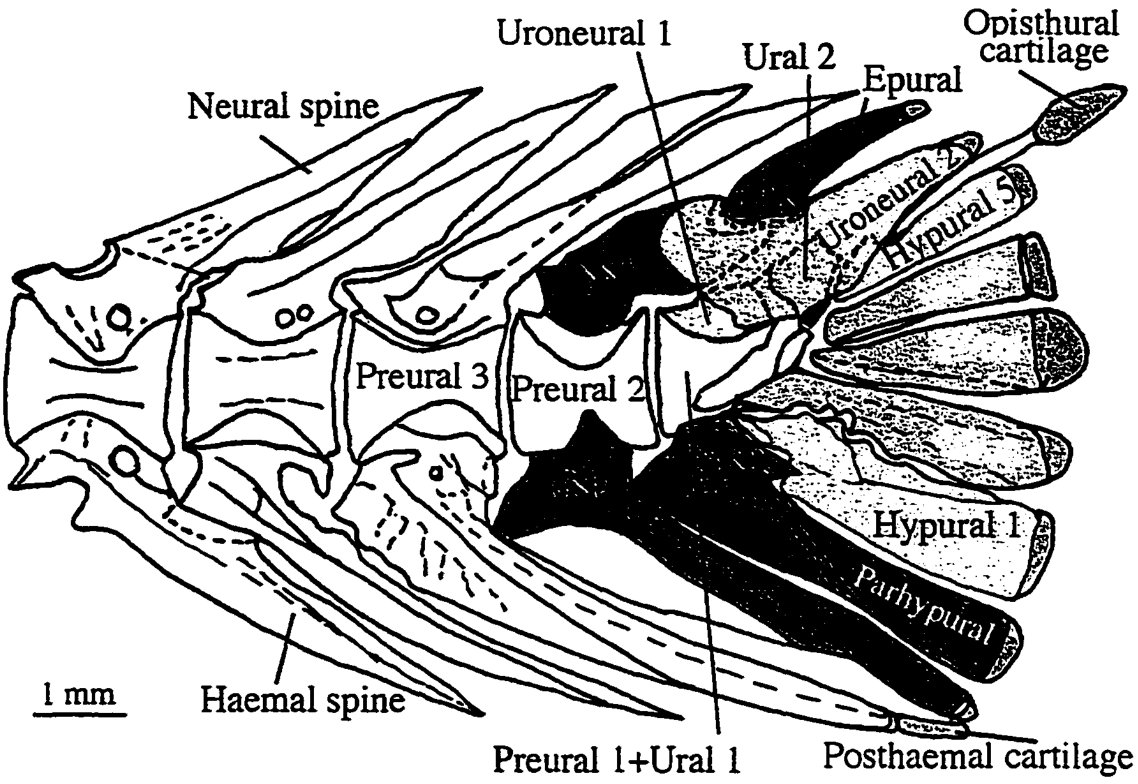

Fig. 8.1. Left lateral view of the caudal skeleton in *Synodus synodus* **(Synodontidae)** (UAMZ 1806, 147 mm).

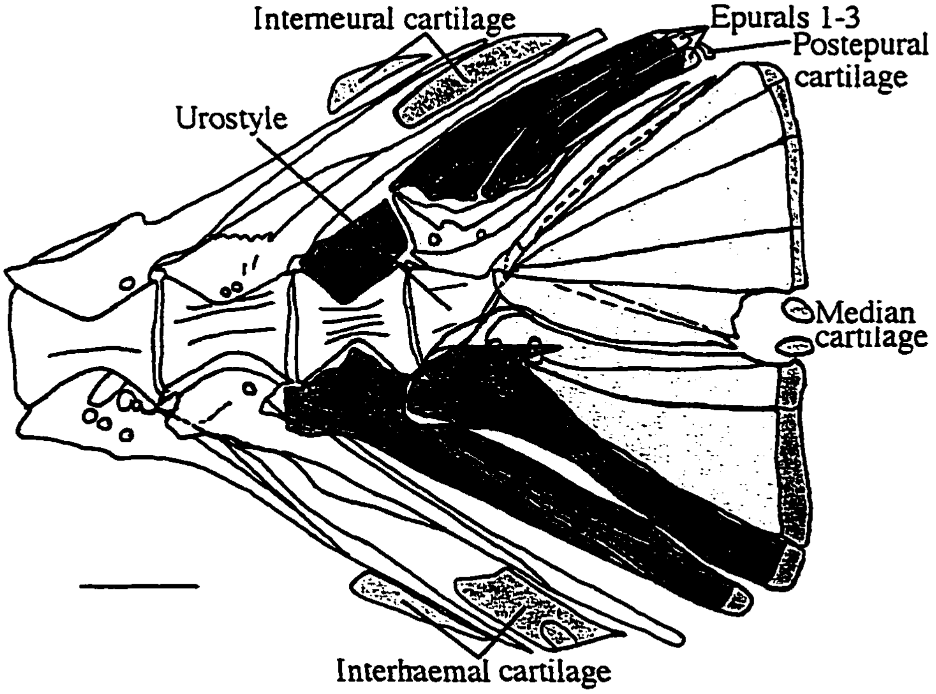

Fig. 8.2. Left lateral view of the caudal skeleton in *Myctophum sp.* **(Myctophidae)** (UAMZ 2689, 60 mm).

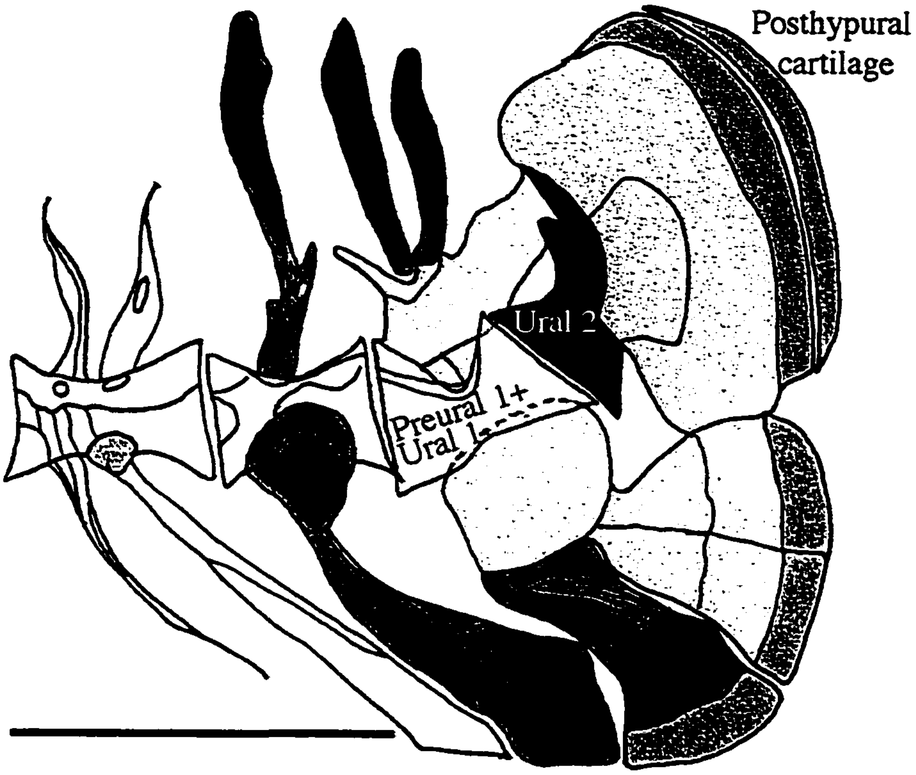

Fig. 8.3. Left lateral view of the caudal skeleton in *Trachipterus altivelis* **(Veliferidae)** (CAS 24297, 85 mm).

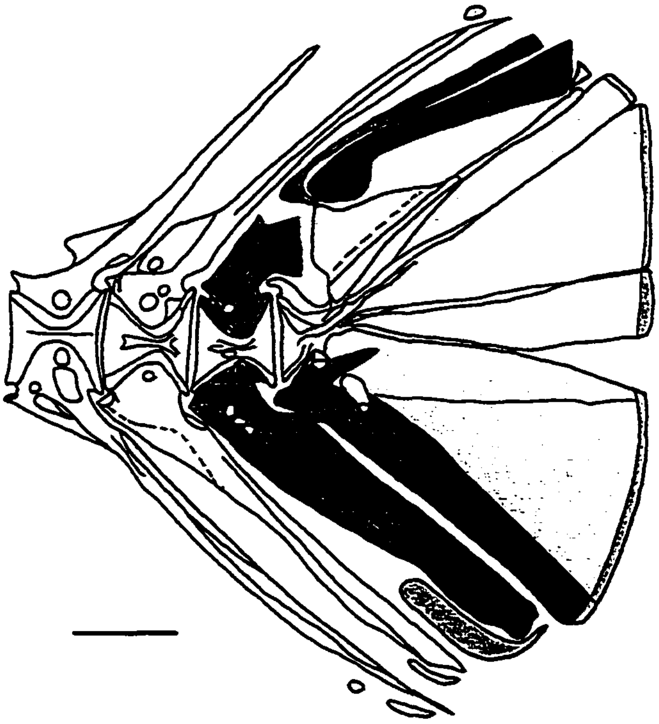

Fig. 8.4. Left lateral view of the caudal skeleton in *Melanotaenia sp.* **(Melanotaeniidae)** (UAMZ 3526, 51 mm).

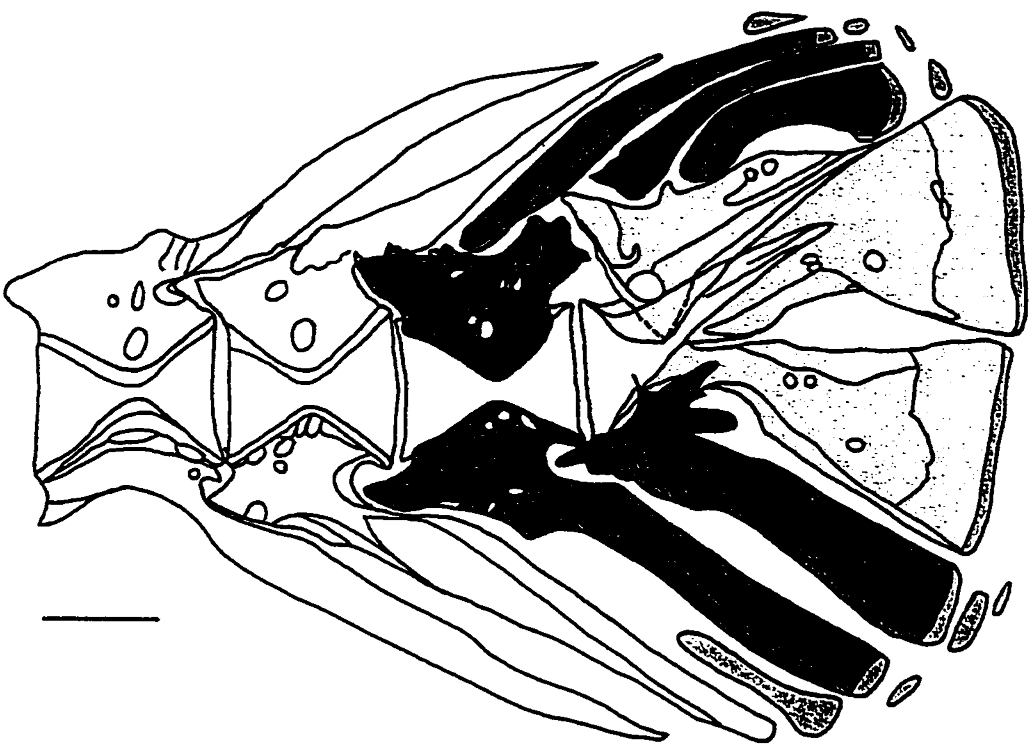

Fig. 8.5. Left lateral view of the caudal skeleton in *Pseudotylosurus sp.* (Belonidae) (UAMZ 8165, 173 mm).

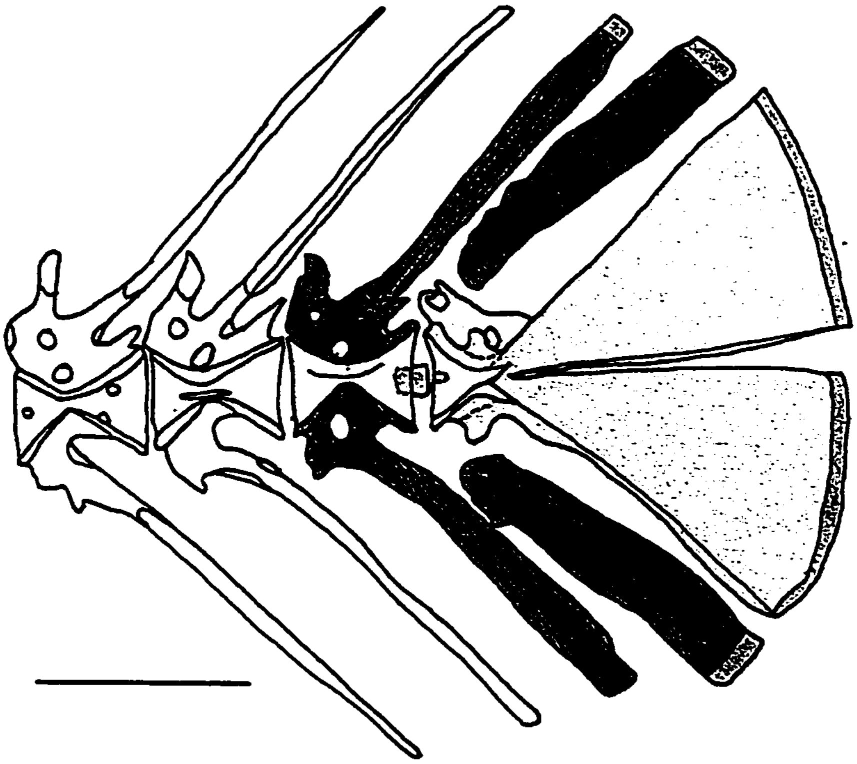

Fig. 8.6. Left lateral view of the caudal skeleton in *Rivulus hartii* (Aplocheilidae) (UAMZ 6660, 47 mm).

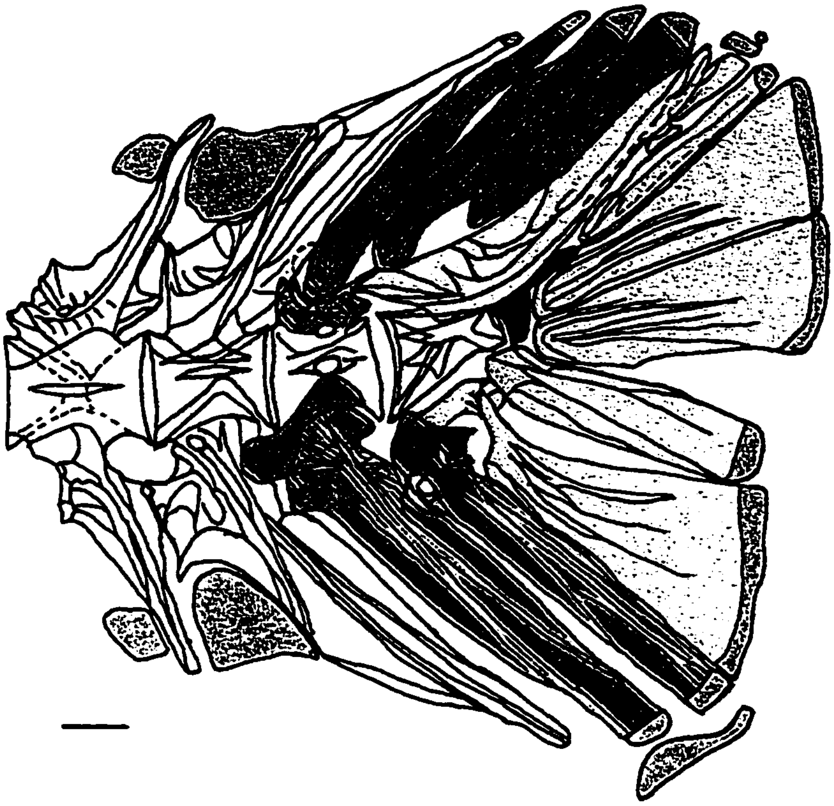

Fig. 8.7. Left lateral view of the caudal skeleton in *Stephanoberyx monae* **(Stephanoberycidae)** (USNM 304353, 92 mm).

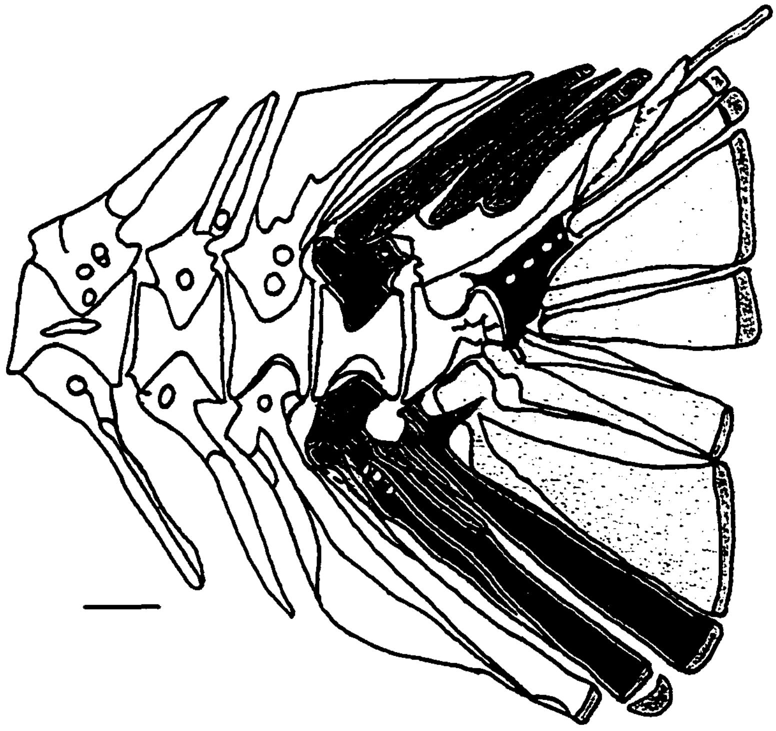

Fig. 8.8. Left lateral view of the caudal skeleton in *Monocentris sp.* **(Monocentridae)** (UAMZ 7854, 92 mm).

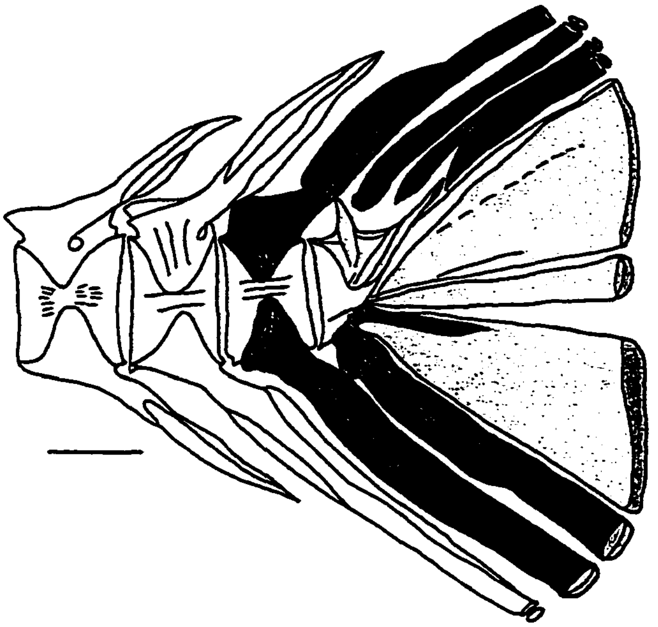

Fig. 8.9. Left lateral view of the caudal skeleton in *Xenolepidichthys dalgleishi* (Grammicolepididae) (USNM 322673, 68 mm).

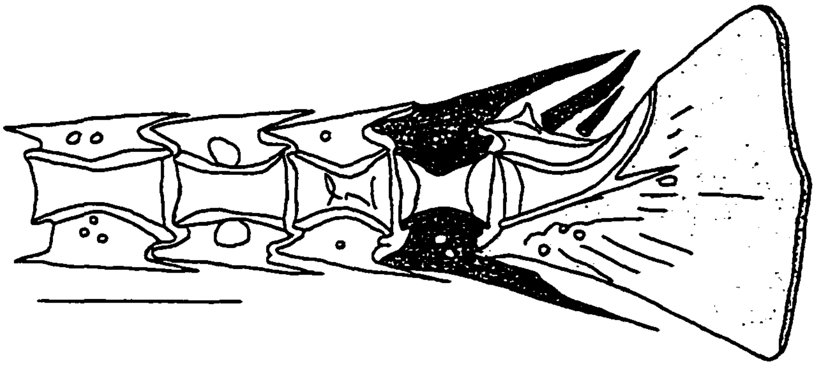

Fig. 8.10. Left lateral view of the caudal skeleton in *Hypoptychus dybowskii* (Hypoptychidae) (UAMZ 5550, 80 mm).

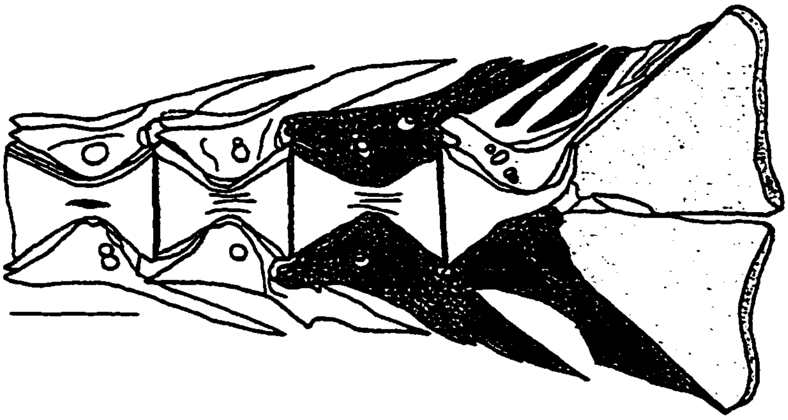

Fig. 8.11. Left lateral view of the caudal skeleton in *Aulichthys japonicus* (Aulorhynchidae) (UAMZ 5542, 47 mm).

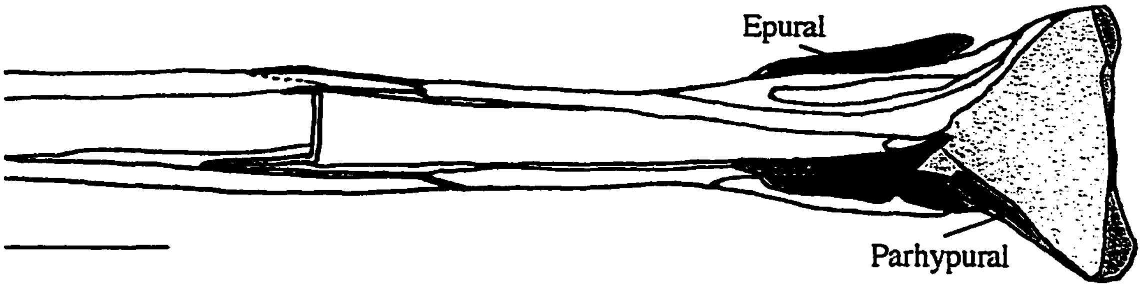

Fig. 8.12. Left lateral view of the caudal skeleton in *Pegasus volans* (Pegasidae) (UAMZ 4616, 99 mm).

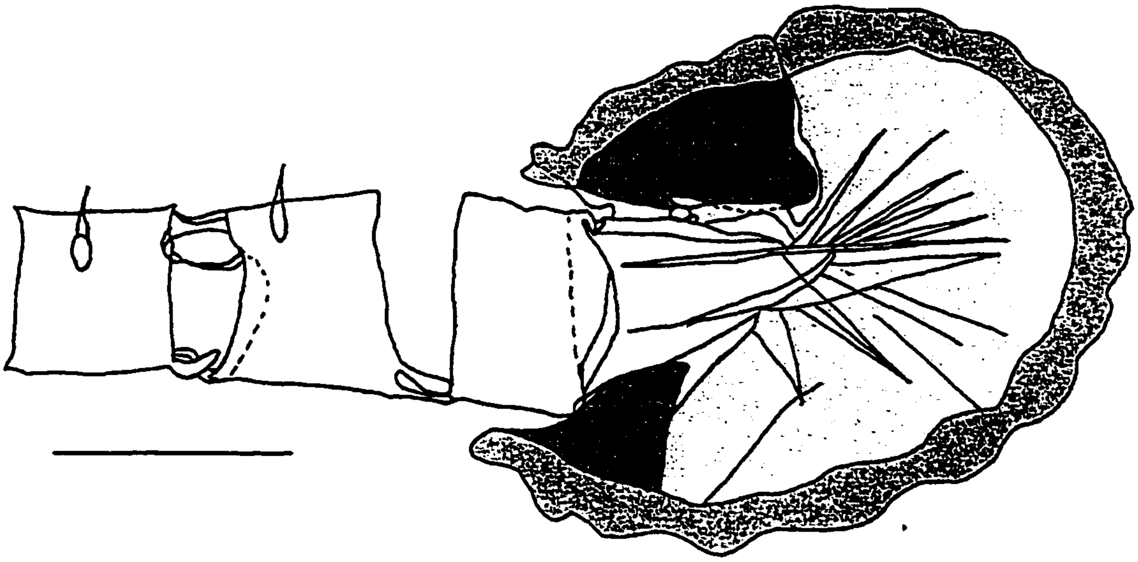

Fig. 8.13. Left lateral view of the caudal skeleton in *Solenostomus paradoxus* (Solenostomidae) (AMS 17111002, 51 mm).

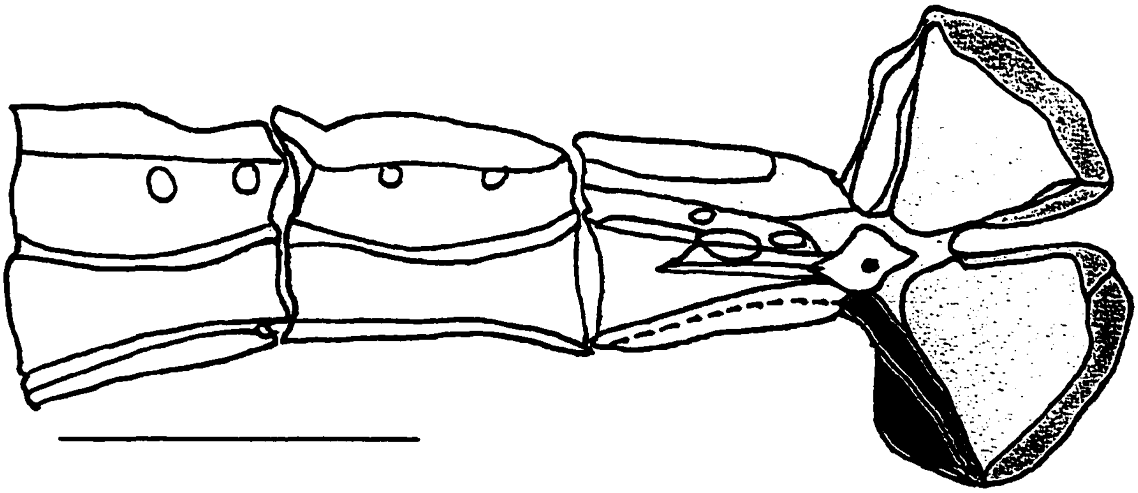

Fig. 8.14. Left lateral view of the caudal skeleton in *Syngnathus griseolineatus* (Syngnathidae) (UAMZ 3469, 272 mm).

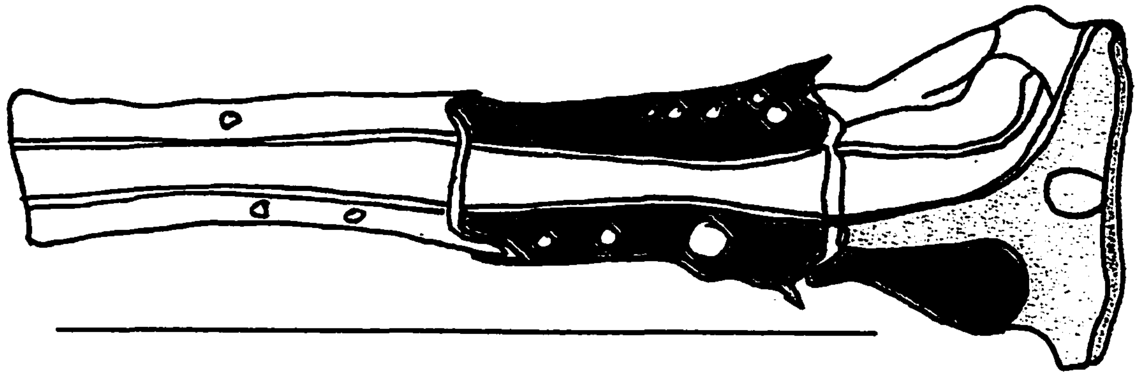

Fig. 8.15. Left lateral view of the caudal skeleton in *Indostomus paradoxus* (Indostomidae) (CAS 64017, 25 mm).

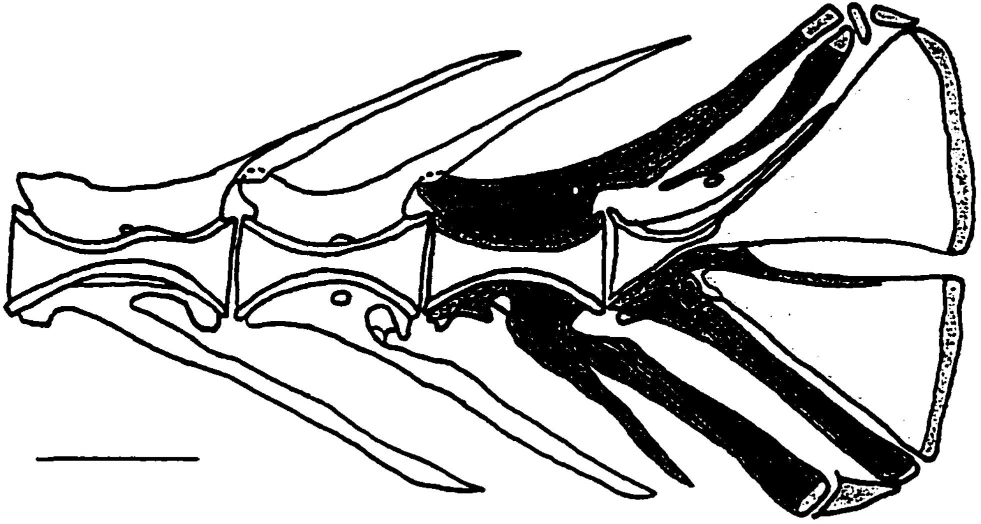

Fig. 8.16. Left lateral view of the caudal skeleton in *Aulostomus valentini* (Aulostomidae) (CAS 11979, 139 mm).

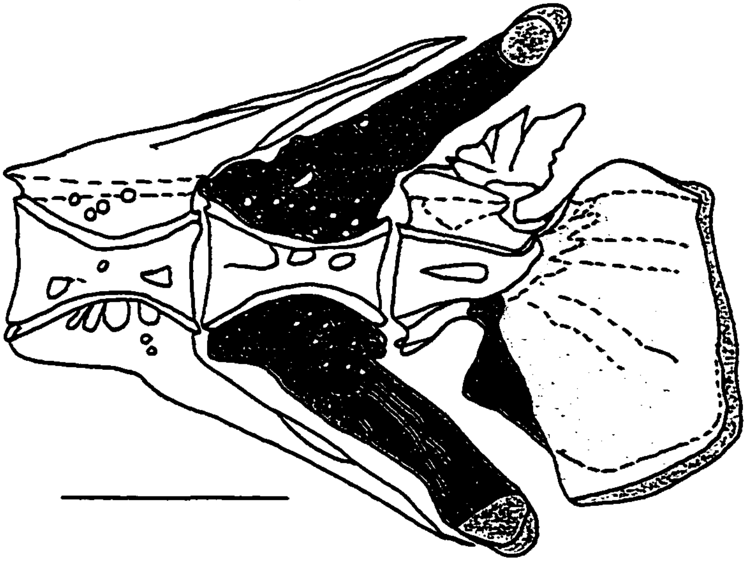

Fig. 8.17. Left lateral view of the caudal skeleton in *Fistularia petimba* (Fistulariidae) (UAMZ 6348, 158 mm).

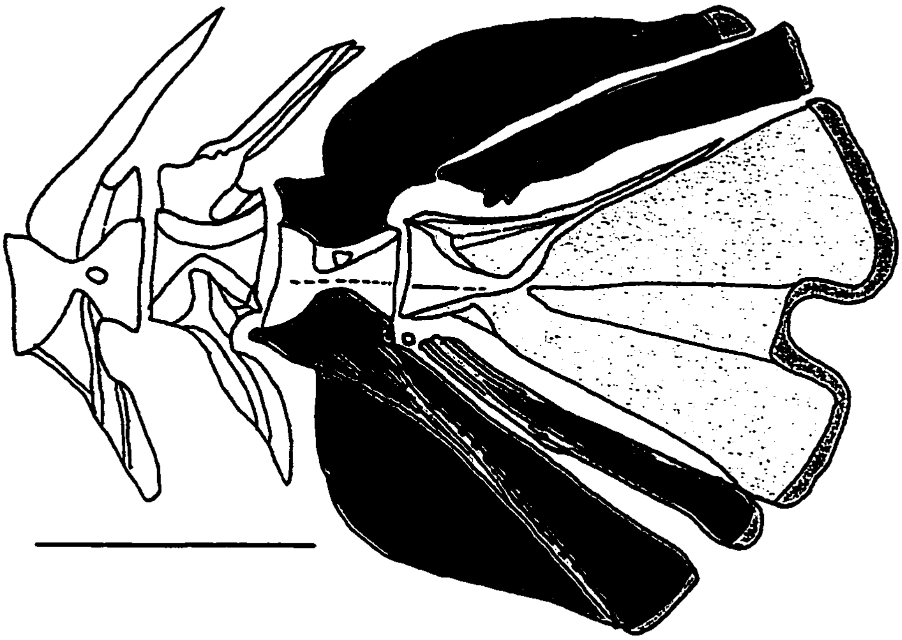

Fig. 8.18. Left lateral view of the caudal skeleton in *Aeoliscus strigatus* **(Centriscidae)** (UAMZ 4048, 89 mm).

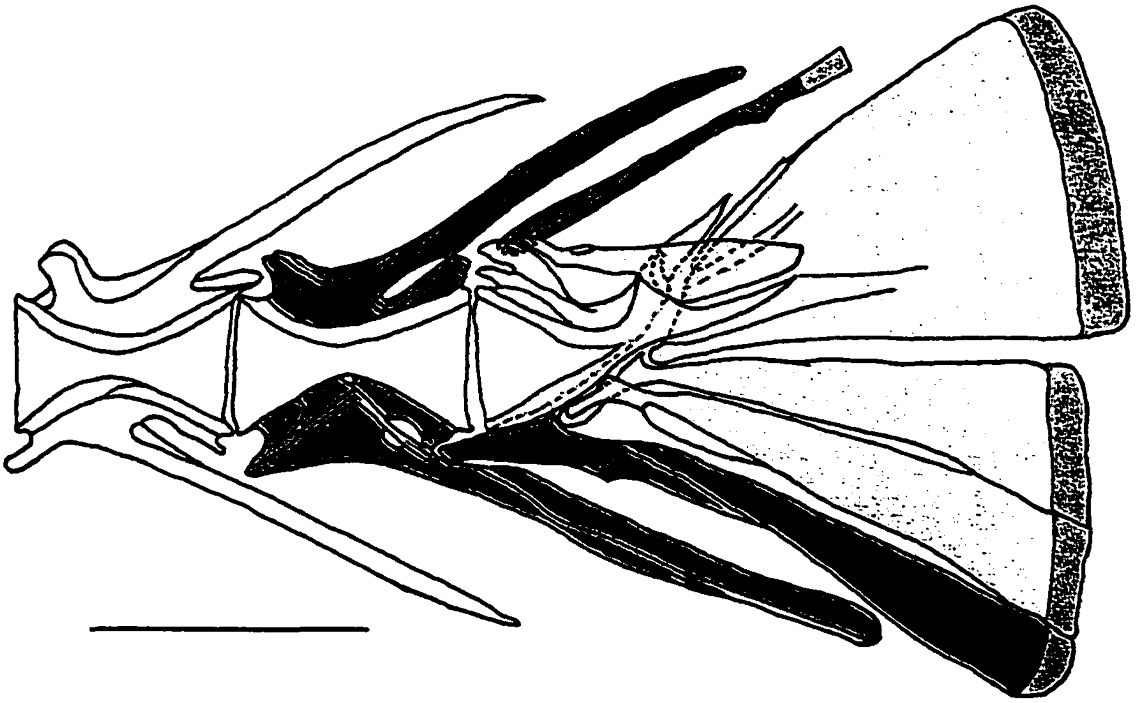

Fig. 8.19. Left lateral view of the caudal skeleton in *Macrognathus aculeatus* **(Mastacembelidae)** (UAMZ 1855, 119 mm).

Fig. 8.20. Left lateral view of the caudal skeleton in *Dactylopterus volitans* **(Dactylopteridae)** (UAMZ 2633, 74 mm).

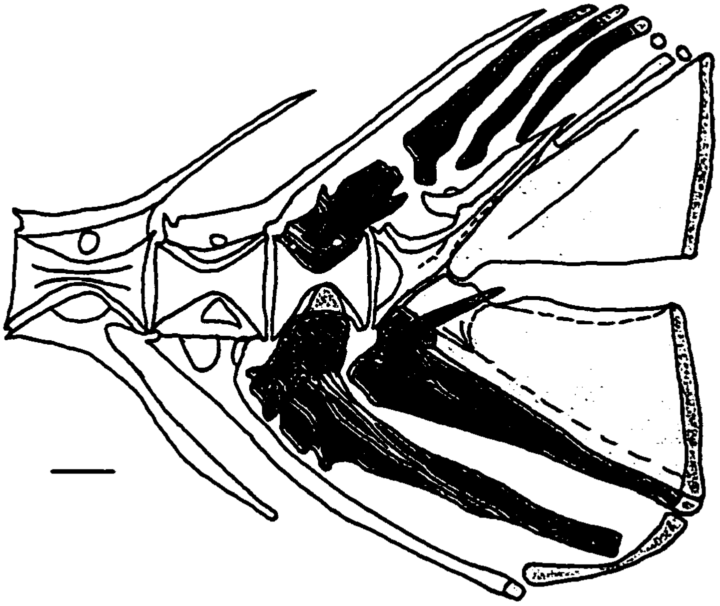

Fig. 8.21. Left lateral view of the caudal skeleton in *Sebastes caurinus* **(Scorpaenidae)** (UAMZ 3142, 75 mm).

Fig. 8.22. Left lateral view of the caudal skeleton in *Xeneretmus latifrons* **(Agonidae)** (UAMZ 3196, 95 mm).

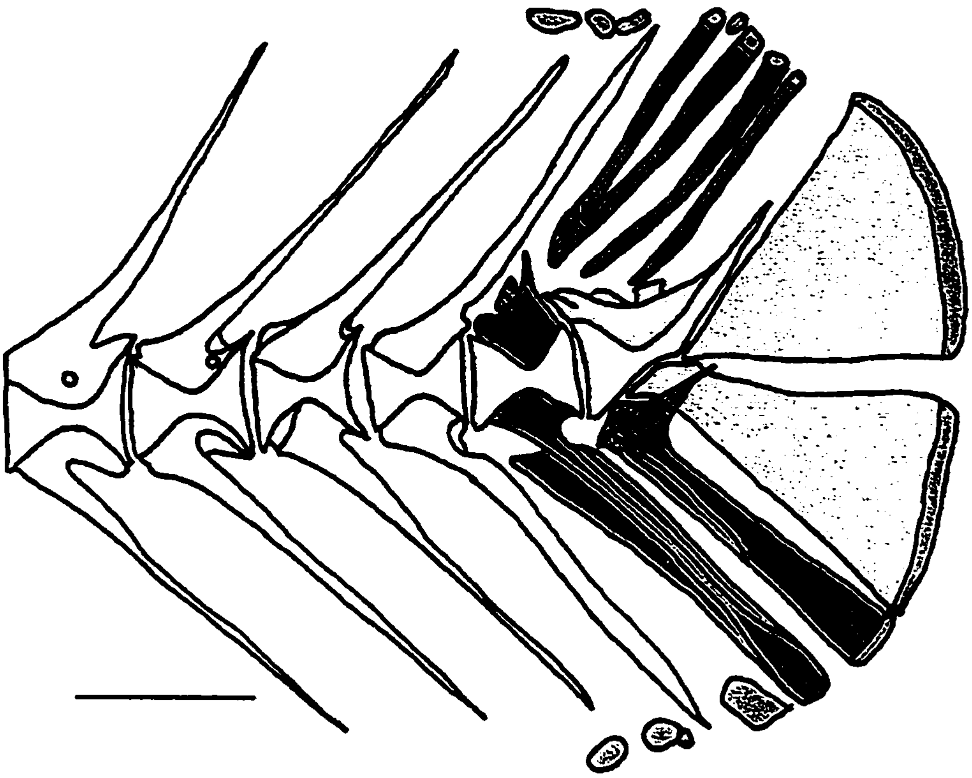

Fig. 8.23. Left lateral view of the caudal skeleton in *Elassoma zonatum* (Elassomatidae) (UAMZ 6920, 30 mm).

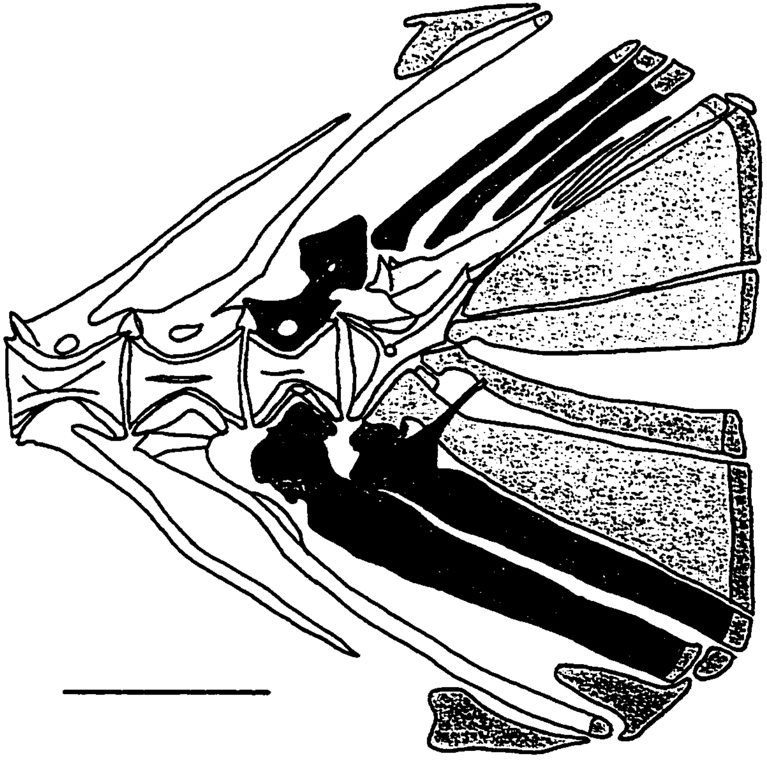

Fig. 8.24. Left lateral view of the caudal skeleton in *Lepomis gibbosus* (Centrarchidae) (UAMZ 7715.4, 40 mm).

9. Phylogenetic relationships of Gasterosteiformes

In this section, I first give the character states of the osteological features studied and briefly give the distribution of the states. Then, the results of the phylogenetic analyses of Gasterosteiformes and related taxa using these characters are presented. Many of these characters are described and illustrated in the previous sections. Finally, a classification of Gasterosteiformes is presented, based on results of the phylogenetic analyses.

Character description

One hundred and fifty one osteological characters are listed by 13 regions for convenience (six regions are described and illustrated in chapters three to five). For all characters, the primitive state is indicated by "0" and derived states by "1" or "2" based on the outgroup comparison method (a priori character polarization). Since characters 2, 59, and 84 are inferred to follow a trend, I polarize them according to my hypothesis. Most characters are binary, but a few are multistate (18 characters). A telegraphic sentence indicates different states of a character and is followed by a brief description and distribution of the characters in Gasterosteiformes and outgroups. Most of the characters listed here are used by other authors and are modified after them. For example, characters 1, 7, 14, 15, 16, 17, 21, 22, 25, 33, 41, 44, 48, 52, 53, 63, 69, 85, 96, 97, 90, 99, 120, 123, and 125 are among those used by Orr (1995). Characters 16, 18, 24, 86, 107, 115, 124, 130-137, and 142 are among those used by Johnson and Patterson (1993). Characters 2, 5, 9, 66, 75, 76, 87, 111, and 127 are among those used by Parenti (1993). Characters 139, 140, and 142-151 are among those used by Fujita (1990). Characters 26-28, 31, 92, 102,103, 104-109, and 112 are among those used by Stiassny (1986, 1992, 1993). Characters 4, 6, 11, 13, 18, 19, 46, 57 93, 94, 100, and 101 are among those used by Bowne (1985).

Ethmoid region

1. Nasal simple (0) / with an anterior lamina (1) / absent (2). The nasal is absent in Solenostomidae, Syngnathidae, and Fistulariidae. In Aulorhynchidae, Gasterosteidae, Pegasidae, Indostomidae, and Macroramphosidae, the nasal bears an anterior lamina that bends posteromedially and articulates with the ethmoid. In Pegasidae nasals are elongated and fused together and the anterior lamina is extended posteriorly. The condition of nasals in Pegasidae might not be homologous to other syngnathoids. In Indostomidae, the nasal is fused to the frontal, and the anterior lamina is less developed. In all primary and secondary outgroups, the nasal is simple.

2. Rostral cartilage attached to ethmoid (0) / separate (1) / attached to premaxilla (2). In Atherinomorpha, the rostral cartilage is separate from the premaxilla. In Aulopiformes, and Myctophiformes, the cartilage is attached to the ethmoid and in other taxa, including Gasterosteiformes, it is connected to the ascending process of the premaxilla.
3. Lateral ethmoid simple (0) / with extensions (1). In Gasterosteiformes, Scorpaeniformes (except Hexagrammidae), Synbranchiformes, Beryciformes, Atherinomorpha, and Aulopiformes, the lateral ethmoid bears medial or lateral extensions. Other taxa bear a simple lateral ethmoid.
4. Lateral ethmoid does not extend to the orbit (0) / extends to the orbit (1). In Gasterosteiformes (except Solenostomidae) and some outgroups, the lateral ethmoid extends to the orbit.
5. Ethmoid without (0) / with disc-like ossifications (1). In Atherinomorpha, one or two small, circular ossifications on the ethmoid are present. They are absent in other taxa.
6. Vomer toothless (0) / toothed (1). Polymixiiformes, Mugiliformes, Atheriniformes, Beryciformes, and most of the Perciformes and Scorpaeniformes bear a toothed vomer. Gasterosteiformes, Synbranchiformes, and Elassomatidae bear a toothless vomer.
7. Vomer located between ethmoids (0) / superficially anteriorly (1). In Syngnathoidei (except Pegasidae and Indostomidae), the vomer is prominent dorsally on the anterior tip of the snout, providing some of the superficial surface of the snout and excluding the ethmoid from its typical articulation with the upper jaw. In Pegasidae, the vomer is not superficial but excludes the ethmoid from the jaw. In all other taxa, the vomer is covered by ethmoids and nasals.

Orbital series

8. Lachrymal short (0) / elongated (1). In Gasterosteiformes (except Hypoptychidae and derived Gasterosteidae: *Apeltes, Gasterosteus, Culaea*, and *Pungitius* (McLennan, 1993)), the lachrymal is elongated anteriorly.
9. Infraorbitals more than three (0) / three or fewer (1). In Gasterosteiformes (except Aulorhynchidae), Synbranchiformes, Atherinomorpha, and Elassomatidae, infraorbitals are three or fewer.
10. Infraorbitals continuous (0) / discontinuous (1): In Gasterosteiformes (except Aulorhynchidae and Pegasidae), Synbranchiformes, Mugiliformes, Atherinomorpha, and Elassomatidae, infraorbitals are discontinuous.

11. Infraorbital 3 without (0) / with a posterior strut to preopercle (1): In Scorpaeniformes, the third infraorbital bears a posterior strut which extends to the preopercle.
12. Subocular shelf absent or reduced (0) / well developed (1): The subocular shelf is well developed in Myctophiformes, Polymixiiformes, and some Beryciformes, Scorpaeniformes, and Perciformes. It is absent or reduced in other taxa.

Cranium

13. Frontal lateral postorbital process absent (0) / present (1): Gasterosteiformes (except Gasterosteoidei, Syngnathidae, and Indostomidae), and some outgroups lack the frontal lateral postorbital process.
14. Frontal does not meet (0) / meets parasphenoid lateral process (1): In Aulorhynchidae, Gasterosteidae, Hexagrammidae, and Agonidae, the frontal meets the parasphenoid lateral process. In other taxa, they do not touch each other.
15. Parietal present (0) / absent (1): The parietal is absent in all Syngnathoidei (except Pegasidae and Centriscidae) and in some derived Atherinomorpha (Rosen, 1964; Parenti, 1981; Rosa and Costa-Wilson, 1993).
16. Intercalar present (0) / absent (1): The intercalars are absent in *Aulorhynchus*, Syngnathoidei, Synbranchiformes, Dactylopteridae, and Cyprinodontiformes.
17. Prootic and exoccipital connected (0) / widely separated by pterotic (1): In Syngnathoidei (except Pegasidae and Indostomidae), the pterotic is enlarged and separates the prootic and exoccipital from each other. In Pegasidae, pterotic enlarged, but do not separate those from each other.
18. Basisphenoid present (0) / absent (1): The basisphenoid is absent in Syngnathoidei, Elassomatidae, and Agonidae.
19. Pterosphenoid present (0) / absent (1): The pterosphenoid is absent in Aulorhynchidae (vestigial in *Aulorhynchus*), Gasterosteidae, and Pegasidae.
20. Parasphenoid narrow (0) / expanded between the lateral ethmoids (1): In Hypoptychidae, Syngnathoidei (except Indostomidae), Beloniformes, Dactylopteridae, and Myctophiformes, the parasphenoid is expanded between the lateral ethmoids.
21. Parashenoid shaft entire (0) / divided posteriorly (1). In Indostomidae, Aulostomidae, Fistulariidae, Synbranchiformes, and some other outgroups, the parasphenoid shaft is divided posteriorly.
22. Occipital condyle concave (0) / convex (1). In Macroramphosidae and Centriscidae, the occipital condyle is convex. In other taxa, it is concave.

23. Exoccipital elongated posterior process absent (0) / present (1). A long, separate process articulates with exoccipital in Solenostomidae, Aulostomidae, and Fistulariidae.
24. Spina occipitalis present (0) / absent(1). Solenostomidae, Syngnathidae, Indostomidae, and some outgroups, lack the spina the occipitalis. In Aulopiformes, the spina occipitalis is reduced.

Jaw skeleton

25. Jaws toothed (0) / toothless (1). Female *Hypoptychus*, Syngnathoidei (except Indostomidae) and some outgroups lack teeth on their jaws.
26. Premaxillary ascending process well developed (0) / absent or reduced (1). In Syngnathoidei, Rondeletiidae, Myctophiformes, and some Aulopiformes, the ascending process is reduced and indistinct. In Mugiliformes and Atherinomorpha, there is no distinct ascending process, but it might be confluent with the broad articular process.
27. Premaxillary articular process present (0) / absent (1): In Indostomidae, Belonidae, and Mastacembelidae, the ascending process is absent or highly reduced. In Hypoptychidae, Aulorhynchidae, Gasterosteidae, and Percopsiformes, a distinct process is absent, but it might be confluent with the ascending process.
28. Premaxillary postmaxillary process absent (0) / present (1). Gasterosteiformes (except Hypoptychidae and *Aulichthys japonicus*), lack a distinct premaxillary postmaxillary process, but it is present in most outgroups.
29. Maxillary shaft uniform (0) / expanded ventrally (1). In Gasterosteiformes (except Solenostomidae, Aulostomidae, and Fistulariidae), Atherinomorpha, and some outgroups, the maxillary shaft is narrow and expanded ventrally.
30. Maxillary posterior process absent (0) / present (1). This process is present in Aulostomidae and some outgroups.
31. Supramaxillary absent (0) / present (1). The supramaxillary is present in some Aulopiformes, Polymixiiformes, Stephanoberyciformes, and Beryciformes.

Suspensorium

32. Palatine toothed (0) / toothless (1). Gasterosteiformes and some outgroups bear a toothless palatine.
33. Palatine separate (0) / united at the midline and to vomer (1). In Solenostomidae and Aulostomidae, the palatine is united at the midline and to vomer.

34. Palatine head cylindrical /(0) / conical (1). In Aulorhynchidae and Gasterosteidae, unlike other taxa, the palatine head is conical.
35. Ectopterygoid curved (0) / triradiate (1): In Solenostomidae and some outgroups, the ectopterygoid is triradiate and T-shaped. In others, it is L-shaped or curved.
36. A separate endopterygoid present (0) / absent (1): A separate endopterygoid is absent in Hypoptychidae, Aulorhynchidae, Gasterosteidae, Pegasidae, Indostomidae, Aulostomidae, and some outgroups. In Gasterosteidae, it is probably fused to the ectopterygoid and palatine.
37. Metapterygoid separate (0) /fused to hyomandibula or symplectic (1). The metapterygoid is fused to the symplectic-hyomandibula in Gasterosteiformes (except Hypoptychidae, Aulostomidae, Macroramphosidae, and Centriscidae). It is also fused in Atheriniformes, and Centrarchidae and absent in Cyprinodontidae. Contrary to Orr's (1995) observation, in Pegasidae, a metapterygoid is present and fused to the symplectic-hyomandibula.
38. Metapterygoid posterior (0) / anterior to the orbit (1). The metapterygoid is anterior to the orbit in Solenostomidae, Syngnathidae, Aulostomidae, Fistulariidae, Macroramphosidae, and Centriscidae. It is also anterior to the orbit in derived Mastacembeloidei (Travers, 1984).
39. Quadrate shaft lacks (0) / bears a deep dorsal flange (1): Syngnathoidei (except Pegasidae and Indostomidae), bear a broad flange between the quadrate body and ventral process.
40. Quadrate shaft about the same length (0) / much longer than quadrate body (1). In Gasterosteiformes (except Hypoptychidae, derived Gasterosteidae, Pegasidae, and Indostomidae), the quadrate shaft is much longer than the quadrate body.
41. Quadrate articulates with the lower jaw below (0) / in front of orbit (1). In Gasterosteiformes (except Pegasidae), the quadrate articulates with the lower jaw far in front of the orbit.
42. Symplectic lacks (0) / bears a dorsal or a ventral flange (1) / bifurcated anteriorly (2). In Aulorhynchidae, and Gasterosteidae, the dorsal flange and to some extent the ventral flange of symplectic is bifurcated anteriorly. Other Gasterosteiformes (except Indostomidae), Macroramphosidae, and Centriscidae, bear a flange. In some outgroups also the symplectic bears a dorsal or a ventral flange.
43. Symplectic fully (0) / partially inserted in the quadrate (1). In the secondary outgroups (except Percopsiformes), the symplectic is short and fully inserted in the quadrate. In other taxa, it is partially inserted in the quadrate.

44. Hyomandibula lacks (0) / bears a large medial lamina (1). In Pegasidae, Syngnathoidea, Centriscoidea, and Dactylopteridae, a broad lamina extends from hyomandibula to the prootic and restricts mediolateral movement of hyomandibular.
45. Hyomandibular bears (0) / lacks a lateral lamina (1). Hypoptychidae, Aulorhynchidae, and some outgroups, lack the hyomandibular lateral lamina.
46. Hyomandibular with (0) / without distinct cranial condyles (1). In Gasterosteoidei, Indostomidae, and some outgroups, the hyomandibular bears distinct cranial condyles.

Opercular Series

47. Opercle bears (0) / lacks a distinct anterior marginal strut (1). In Gasterosteiformes and some outgroups, the opercle lacks a distinct anterior marginal strut.
48. Preopercle without (0) / with a socket at its articulation with interhyal (1): In Syngnathidae, the interhyal articulates with a socket on the ventromedial margin of preopercle. In Macroramphosidae and Centriscidae, the preopercle supports the articulation of the interhyal with the medial lamina. In Pegasidae, the interhyal articulates with a socket between symplectic and hyomandibular. In Solenostomidae, the interhyal articulates with a interhyal lamina on the ventromedial margin of preopercle. In other taxa, the interhyal articulates with the cartilage between symplectic and hyomandibular.
49. Preopercle without (0) / with distinct dorsal and ventral arms (1). In secondary outgroups (except Percopsiformes), Stephanoberyciformes, Pegasidae, and Synbranchiformes, the ventral arm of the preopercle is short and indistinct from the dorsal arm.
50. Preopercle bears an enclosed (0) / open preoperculomandibular canal (1). In Gasterosteiformes (except Syngnathidae), and most other taxa, the preopercle bears a preoperculomandibular tube. In others, it is open ventrally and makes a canal.
51. Subopercle bears (0) / lacks a distinct ascending limb (1) / bears a posterior process (2). In Solenostomidae, Syngnathidae, Indostomidae, and some outgroups, the subopercle lacks a distinct ascending process. In Scorpaeniformes, the subopercle bears a narrow posterior process which is absent in other taxa.
52. Subopercle and interopercle close together (0) / widely separated from each other (1). In Pegasidae, Solenostomidae, and Syngnathidae, the interopercle is separated from subopercle.
53. Interopercle short (0) / elongated (1). In Gasterosteiformes (except derived Gasterosteidae and Pegasidae), the interopercle is elongated. In the other taxa, the interopercle is roughly triangular and short.

54. Interopercle without (0) / with posteroventral expansion (1). In Aulorhynchidae, Gasterosteidae, Pegasidae, and Agonidae, the interopercle is narrow, but expanded posteroventrally. In other taxa, the interopercle is triangular or without the expansion.

Hyoid arches

55. Basihyal small (0) / elongated (1) / with enlarged anterior cartilage (2): Gasterosteiformes bear an elongated basihyal. Mugiliformes, Atheriniformes, and Beloniformes bear a small basihyal with a large anterior cartilage.
56. Urohyal without (0) / with ventrolateral flanges (1). In Syngnathidae, Aulostomidae, and Fistulariidae, the urohyal lacks the ventrolateral flanges. In other Gasterosteiforms, most of the primary outgroups and Percopsiformes, the urohyal bears ventrolateral flanges.
57. Urohyal blade entire (0) / incised posteriorly (1). In Solenostomidae, Fistulariidae, Macroramphosidae, Centriscidae, and Beloniformes, the urohyal blade is incised posteriorly. In other taxa, the urohyal is entire.
58. Urohyal without (0) / with a distinct anterodorsal process (1). In Hypoptychidae, *Aulichthys japonicus*, and some outgroups, a distinct anterodorsal process is present.
59. Hypohyals separate (0) / overlap anterior ceratohyal (1) / articulate with posterior ceratohyal (2). In Aulopiformes and Myctophiformes, hypohyals are in front of the anterior ceratohyal without any overlap. In Syngnathidae, Fistulariidae, and Centriscidae, the ventral hypohyal is highly enlarged and articulates with the posterior ceratohyal. In other taxa, hypohyals are incorporated in or overlap the anterior ceratohyal.
60. Anterior ceratohyal anteriorly even or gradually becomes narrower (0) / abruptly becomes narrower (1). In Gasterosteidae, Indostomidae, and Aulostomidae, and some outgroups, the anterior ceratohyal is distinctly rectangular posteriorly and abruptly narrows anteriorly.
61. Anterior ceratohyal lacks (0) / bears a fenestra (1). Among Gasterosteiformes, only in Aulostomidae the anterior ceratohyal bears a fenestra.
62. Struts that connects anterior and posterior ceratohyals absent (0) / present (1). In most Gasterosteiformes and primary outgroups dorsal, lateral or medial struts connect the anterior ceratohyal to the posterior ceratohyal. In secondary outgroups, anterior and posterior ceratohyals are widely separated by a cartilage.
63. Interhyal cylindrical and free (0) / round and sutured to posterior ceratohyal (1). In Syngnathidae Macroramphosidae and Centriscidae, the interhyal is round and sutured to the posterior ceratohyal. In other taxa, interhyal is cylindrical and autogenous.

64. Branchiostegal rays more than four (0) / four or fewer (1). Gasterosteoidei, Solenostomidae, Syngnathidae, and Aulostomidae bear four or fewer branchiostegal rays. Polymixiiformes also bear four branchiostegal rays.
65. Gill membrane free from isthmus (0) / united (1). In Gasterosteidae, Pegasidae, Aulostomoidea, Centriscidae, and some outgroups, the gill membrane is united to the isthmus, though the degree of attachment is variable.

Branchial skeleton

66. Ossified basibranchials three (0) / fewer than three (1). In Syngnathoidei (except Indostomidae and Centriscoidea) and Cyprinodontidae, there are fewer than three ossified basibranchials. In other taxa, there are three ossified basibranchials.
67. Basibranchial 2 without (0) / with spikes (1). In Myctophiformes and Lampridiformes, the second basibranchial bears anterior and posterior spikes that articulate with the first basibranchial anteriorly and with the third posteriorly.
68. A fourth cartilaginous basibranchial present (0) / absent (1). The fourth cartilaginous basibranchial is absent in most Syngnathidae, and some of the outgroups. Some authors refer to this as a fifth cartilage at the base of the fifth ceratobranchials (e.g., Johnson and Patterson, 1993). My observations indicate that the cartilaginous element between basibranchial 3 and the cartilaginous basibranchial 4, is in fact the unossified posterior portion of basibranchial 3. Ceratobranchials 4 are attached to the cartilaginous basibranchial 4 and in some taxa, ceratobranchial 5 is also attached to it.
69. Hypobranchials three (0) / fewer than three (1). In Pegasidae, Solenostomidae, and Syngnathidae, hypobranchials are fewer than three. In other taxa, there are three hypobranchials.
70. Ceratobranchial 5 without (0) / with ventral and posterior processes (1). In Atherinomorpha the fifth ceratobranchial bears a ventral and a posterior process. The ventral process is also present in some Perciformes.
71. Epibranchial 1 with (0) / without uncinate process (1). An uncinate process is absent in Gasterosteiformes (except Aulostomidae), Synbranchiformes, Cyprinodontiformes, and some Zeiformes.
72. Epibranchial 1 separate (0) / attached to pharyngeal toothplate 2 (1). In Gasterosteiformes (except Macroramphosidae), Elassomatidae, and Synbranchiformes, epibranchial 1 is cartilaginously attached to pharyngeal toothplate 2. In other taxa, it is free from the toothplate.

73. Epibranchial 3 and 4 with (0) / without uncinate process (1). Syngnathoidei (except Centriscoidea), and some outgroups lack the uncinate processes on epibranchials 3 and 4.
74. Epibranchial 3 and 4 not associated (0) / associated with their processes or heads (1). In Aulopiformes, Myctophiformes, Lampridiformes, Centriscoidea, and Synbranchidae, epibranchials 3 and 4 which normally are associated through their uncinate processes or heads, are not associated with each other.
75. Epibranchial 4 normal (0) / enlarged (1) / absent (2). In Syngnathoidea and Aulostomoidea, epibranchial 4 is absent. In Atherinomorpha, epibranchial 4 is enlarged.
76. Epibranchial 4 head larger than three (0) / normal (1). In Indostomidae and some outgroups, epibranchial 4 bears a larger head compared to epibranchial three.
77. Pharyngobranchial 1 present (0) / absent (1). Pharyngobranchial 1 is absent in Gasterosteiformes (except Centriscidae) and some outgroups.
78. Pharyngobranchial 2 with (0) / without an uncinate process (1). In Secondary outgroups and some primary outgroups, pharyngobranchial 2 bears an uncinate process.
79. Pharyngeal toothplate 2 present (0) / absent (1). Pharyngeal toothplate 2 is present in Pegasidae, Syngnathidae, and some outgroups.
80. Pharyngeal toothplate 4 present (0) / absent (1). Gasterosteoidei, Syngnathoidea, Indostomidae, and some outgroups, bear pharyngeal plate 4.
81. Interarcual cartilage absent (0) / present (1). Interarcual cartilage is absent in Gasterosteiformes (except Aulostomoidea). In Synbranchidae, the interarcual cartilage is ossified.
82. Gill filaments normal (0) / lophobranch with skeleton fused basally (1). As Johnson and Patterson (1993) described, in Pegasidae, Solenostomidae, Syngnathidae, and Indostomidae, gill filaments are lophobranch and bases of the filaments are fused.
83. Toothplates present (0) / absent (1). In Gasterosteiformes (except Aulorhynchidae and Aulostomidae), the small toothplates on the branchial arches are absent.

Pectoral skeleton

84. Posttemporal dorsal process loosely attached with a long ligament (0) / tightly attached with a short ligament to epioccipital (1) / ossified to cranium (2). In Aulopiformes and Myctophiformes, the posttemporal dorsal process is loosely attached to the epioccipital with a long ligament. In Pegasidae, Syngnathidae, Fistulariidae, Macroramphosidae, and Centriscidae, the posttemporal is incorporated in the skull. In

other taxa, the posttemporal dorsal process is tightly attached to epioccipital with a short ligament.

85. Posttemporal sensory canal absent (0) / present (1). In Aulorhynchidae, Aulostomoidea, and some outgroups, a posttemporal canal is present.
86. Extrascapular present (0) / absent (1). Gasterosteiformes, (except Hypoptychidae and *Aulichthys japonicus*) and some outgroups lack the extrascapulars.
87. Supracleithrum normal (0) / reduced (1) / absent (2). In Gasterosteiformes, Atherinomorpha, Mugiliformes, and Dactylopteridae, the supracleithrum is reduced. In some Gasterosteiformes and Atheriniformes, it is absent.
88. Cleithrum with (0) / without a pointed anterodorsal ramus (1). Some Gasterosteiformes and outgroups bear a blunt anterodorsal ramus.
89. Cleithrum entire (0) / divided into two struts ventrally (1). In some Gasterosteiformes and outgroups, the ventral ramus of the cleithrum is divided into two struts.
90. Cleithrum without (0) / with posteromedial extension to the coracoid (1). Some Gasterosteiformes and outgroups bear a posteromedial extension to coracoid.
91. Postcleithrum numbers: two (0) / one (1) / absent (2). Aulostomoidea and Centriscoidea bear one postcleithrum, but other Gasterosteiformes lack the postcleithra. Most outgroups bear two postcleithra.
92. Ventral postcleithrum separate (0) meets lateral process of pelvic girdle (1). In Macroramphosidae and some outgroups, the tip of the ventral postcleithrum meets the lateral margin of the pelvic plate.
93. Scapular foramen complete (0) / incomplete (1). In Gasterosteiformes (except Centriscoidea), the scapular foramen is open anteriorly and bordered by the ventral ramus of the cleithrum. In outgroups, the foramen is closed anteriorly.
94. Scapula and first actinost separate (0) / fused together (1). In Aulostomidae, Indostomidae, Centriscoidea, and some outgroups, the scapula and the first actinost are fused together.
95. Coracoid ventral flange present (0) / absent (1). In some Gasterosteiformes and outgroups, the ventral wing of the coracoid is absent.
96. Ectocoracoid absent (0) / present (1). An ectocoracoid is present only in Aulorhynchidae, Gasterosteidae, and Aulostomoidea.
97. Actinost normal (0) / strongly hourglass-shaped (1). In Solenostomidae, Syngnathidae, and Centriscoidea, the actinosts are strongly hourglass-shaped. In other taxa, they are cylindrical or rectangular.

98. Actinost with different sizes (0) / with the same size (1). In Gasterosteiformes and Agonidae, all the actinosts are more or less the same size. In other taxa, usually the first actinost is the smallest and the fourth is the largest.
99. Actinosts normal (0) / rotated laterally (1). In Centriscoidea, actinosts are rotated laterally.
100. Actinost 4 without / with a spike anteroventrally (1). In Gasterosteiformes (except Syngnathoidea, and Centriscoidea), the fourth actinost sends a spike to coracoid. The spike is absent in all other taxa.
101. Actinost 4 separate (0) / sutured to coracoid (1). In Gasterosteidae, Pegasidae, and Centriscoidea, Agonidae, and Hemiramphidae, the fourth actinost is sutured to coracoid.

Pelvic skeleton

102. Pelvic spines absent (0) / present (1). Aulorhynchidae, Gasterosteidae, Pegasidae, and Centriscoidea bear a pelvic spine. All secondary outgroups lack the spine.
103. Medial process present (0) / absent (1). The medial process of the pelvic plate is absent in Gasterosteiformes and primary outgroups (except some Atherinomorpha).
104. Lateral cartilaginous process absent (0) / present (1). In Aulopiformes and Myctophiformes, a cartilaginous lateral process is present. In Gasterosteidae, a well developed bony lateral process is present. In Atherinomorpha, a small lateral process is present that articulates with the ribs via a ligament.
105. Pelvic plates separate (0) / joined by a suture (1). In Aulorhynchidae, Gasterosteidae, Pegasidae, Macroramphosidae, Mugiliformes, Beryciformes, Caproidae, Scorpaeniformes, and Perciformes, the pelvic plates are sutured together. In other taxa, the pelvic plates are separate, abut each other, or their medial process overlap.
106. Posterior process present (0) / absent (1). Most Gasterosteiformes and primary outgroups bear a distinct posterior process.
107. Pelvic radials present (0) / absent (1). Secondary outgroups, Beryciformes, some Zeiformes and Stephanoberyciformes (Johnson and Patterson, 1993), and Indostomidae, bear 1-3 autogenous cartilaginous or ossified pelvic radials. Radials are lost in all other taxa.
108. Pelvic girdle separate (0) / meets cleithrum (1). In Zeiformes, Scorpaeniformes, and Perciformes (except Elassomatidae), the anterior tip of the pelvic girdle extends to the cleithrum and articulates with the pectoral girdle between the cleithra. In other taxa, the pelvic girdle is widely separated from the cleithrum.

109. Pelvic plate lacks (0) / bears an anterior process (1). Gasterosteiformes, secondary outgroups, Stephanoberyciformes, Cyprinodontiformes, and Belonidae, lack the anterior process of the pelvic plate. In Atherinidae and Hemiramphidae, the process lies in the plane of the girdle, in other taxa, it is displaced ventrally..

110. Pelvic splint absent (0) / present (1). In Myctophiformes and Percopsiformes, a splint is present at the lateral side of the plates. The splint is absent in all other taxa.

111. Pelvic does not articulate (0) / articulates with ribs cartilaginously (1) / ligamentously (2). In Myctophiformes, ribs articulate with the small lateral cartilaginous process of the pelvic. In Atherinomorpha, the ribs ligamentously articulate with the small lateral process of the pelvic. In other taxa, there is no association between the ribs and the pelvic girdle.

112. External ventral wing present (0) / absent (1). In Gasterosteiformes (except Macroramphosidae), Elassomatidae, Atherinomorpha (except Melanotaeniidae), Mugiliformes, Stephanoberyciformes, and Aulopiformes, the external ventral wing is absent.

Unpaired fins

113. Dorsal spines present (0) / absent (1). Some Gasterosteiformes, Perciformes, Scorpaeniformes, and some other outgroups bear dorsal spines. Dorsal spines are isolated and not connected by a membrane in Gasterosteiformes and Mastacembelidae.

114. Posterior basals absent (0) / present (1). In Aulorhynchidae and Gasterosteidae, some rayless posterior basals (distal pterygiophores) are present.

115. Dorsal spine distal pterygiophores autogenous (0) / fused (1). In secondary outgroups and some primary outgroups, the dorsal spine distal pterygiophores are autogenous.

116. Dorsal spine distal pterygiophores not expanded (0) / expanded (1). In Aulorhynchidae, Gasterosteidae, and Indostomidae the dorsal spine distal pterygiophores are expanded.

117. Adipose fin present (0) / absent (1). In Aulopiformes, Myctophiformes, and Percopsiformes, an adipose fin is present, but absent in others.

118. Anal fin origin placed posteriorly (0) / more anteriorly (1). In the secondary outgroups (except Polymixiiformes), the origin of the anal fin is posterior to the origin of the soft dorsal fin. In other taxa, the origin of the anal fin is anterior to the origin of the soft dorsal fin or beneath it.

119. Anal spines absent (0) / one (1) / more than one (2). Gasterosteiformes (except Aulorhynchidae and Gasterosteidae), lack an anal spine. Usually Perciformes and some other outgroups bear more than one spine.

Vertebral columns

120. Dorsal part of occipital condyle is made of exoccipitals and the first centrum bears a dorsal facet that articulates with the exoccipital condyles (0) / occipital condyle consists only of basioccipital and the first vertebra lacks the dorsal facet, but bears lateral facets that articulate with exoccipital (1) / the first vertebra directly connects only to the basioccipital (2). In Gasterosteiformes, Synbranchiformes, Agonidae, and Atherinomorpha, the first centrum lacks the dorsal facet that articulates with the exoccipital condyle. In Gasterosteiformes (except Aulorhynchidae and Gasterosteidae), Atherinomorpha, and Agonidae, the parapophyses or neurapophyses are expanded making lateral facets for the articulation of exoccipitals. In Aulorhynchidae and Gasterosteidae, the parapophysis is not expanded and the first vertebra connects only to the basioccipital.
121. First neural arch complete (0) / reduced (1). In Gasterosteiformes, the first vertebra bears a complete neural arch. In some outgroups, the arch is reduced.
122. First neural arch autogenous (0) / fused to centrum (1). In Gasterosteiformes and some outgroups, the first neural arch is fused to the centrum.
123. Anterior centra separate (0) / sutured together (1). In Aulostomoidea and Centriscidae, the first four vertebrae are tightly sutured together. In Aulorhynchidae, Beloniformes, and Dactylopteridae, neural arches of the vertebrae are weakly interdigitating, but never sutured together.
124. Transverse process on the first two vertebrae absent (0) / present (1). In Gasterosteoidei, some Syngnathoidei, and some outgroups, transverse processes (parapophyses) of the first two vertebrae are present.
125. Anterior vertebrae short (0) / elongated (1). In Pegasidae, Solenostomidae, Aulostomoidea, and Centriscoidea, the anterior vertebrae are distinctly longer than the others.
126. Anterior vertebrae lack (0) / bear lateral processes to scutes (1). In *Aulichthys japonicus*, Syngnathidae, Indostomidae, and Centriscoidea, the anterior vertebrae bear lateral processes to scutes.
127. Anterior neural spines narrow (0) / expanded (1). In Mugiliformes and Atherinomorpha, several anterior neural spines are expanded.

128. Neural arch of precaudal vertebra not pierced (0) / pierced by foramina (1). Some Gasterosteiformes and some outgroups bear some foramina on the neural arch of their precaudal vertebrae.
129. Neurohypophyses present (0) absent (1). In Pegasidae, Solenostomidae, Syngnathidae, Indostomidae, and Centriscidae, neurohypophyses of the vertebrae are absent.
130. Number of supraneural bones: three (0) / one or two (1) / absent (2). In Gasterosteiformes, there are two or no supraneural bones.
131. Anterior epineurals distal parts are not (0) are displaced into horizontal septum (1). In Aulostomidae, epineurals distal part are not displaced into the horizontal septum. In other epineural bearing Gasterosteiformes, and most primary outgroups (except some Monocentridae (Johnson and Patterson, 1993)), anterior epineural distal parts are displaced into the horizontal septum.
132. Anterior epineurals placed on the neural arches (0) are displaced ventrally (1). In Gasterosteiformes and most of the primary outgroups, anterior epineurals are displaced ventrally. In all the secondary outgroups, anterior epineurals are placed on the neural arches.
133. Anterior epicentral ligaments present (0) / absent (1). In Gasterosteiformes and all primary outgroups and Percopsiformes, anterior epicentral ligaments are absent (1). In Aulopiformes, anterior epicentral ligaments are present in some genera and absent in some others (Patterson and Johnson, 1995).
134. Pleural ribs present (0) / absent (1). In Syngnathoidei, pleural ribs are lost or reduced in number.
135. Epineurals and epipleurals present (0) / only epineurals present (1) / both absent (2). In Aulorhynchidae and Syngnathoidei (except Indostomidae and Aulostomidae), epineurals and epipleurals are absent. In other Gasterosteiformes, all primary outgroups and Percopsiformes, only epineurals are present. In other secondary outgroups (except Lampridiformes), both epineurals and epipleurals are present. Lampridiformes only have the epineurals. I follow terminology of Patterson and Johnson (1995) for intermuscular bones, but Gemballa and Britz (1998) interpret them differently.
136. First epineural on a neural arch (0) / a transverse process or lateral surface of a vertebrae (1). The first epineural originates on the transverse process or lateral surface of a vertebra in Gasterosteiformes, Atherinomorpha (except Cyprinodontidae), Mugiliformes, Elassomatidae, and Stephanoberycidae. In other taxa, it originates on the neural arch.

137. Baudelot's ligament originates on the first vertebra (0) / on exoccipital (1) absent (2). Baudelot's ligament is absent in Gasterosteiformes, Synbranchiformes, and Dactylopteridae. In primary outgroups (except Stephanoberyciformes), Agonidae and Grammicolepididae, it originates on exoccipital. In secondary outgroups (except Lampridiformes), it originates on the first vertebra.

138. Bony scutes absent (0) / present (1). In Gasterosteiformes (except Hypoptychidae and Aulostomoidea), the body is covered by bony scutes. In Aulorhynchidae and Gasterosteidae, scutes are reduced.

Caudal skeleton

139. Parhypural autogenous (0) / fused to centrum or hypurals (1). In Gasterosteiformes (except Aulostomidae and Centriscidae), the parhypural is fused to the hypurals and centrum. In most outgroups, it is autogenous.

140. Hypurals autogenous (0) / all fused to centrum (1). In Gasterosteiformes (except Aulostomidae), all the hypurals are fused to the centrum. In most outgroups, they are autogenous.

141. Hypurals organized into three or more (0) / into two plates (1) into a single plate (2). In Gasterosteiformes (except Hypoptychidae, and Aulostomidae), all the hypurals are fused into a single plate, although a notch is present in some genera. In Hypoptychidae, Aulostomidae, and some outgroups, hypurals are fused into dorsal and ventral plates. In all secondary outgroups and most of primary outgroups, hypurals are autogenous.

142. Hypural 6 present (0) / absent (1). The sixth hypural is present in some Aulopiformes, Myctophiformes, Lampridiformes, Polymixiiformes, Percopsiformes, Stephanoberyciformes, and Monocentridae.

143. Hyporapophysis distinct (0) / indistinct (1). In Gasterosteiformes and some outgroups, the hyporapophysis is not distinct and is confluent with parhypural and hypural plates.

144. Neural spines of preural 2 short (0) / long (1). In Gasterosteoidei, Aulostomoidea, and Centriscoidea, and some outgroups, the neural arch of preural 2 is long.

145. Haemal spine of preural 2 or 3 autogenous (0) / both fused to centrum (1). In Gasterosteiformes and some outgroups, haemal spine of preural 2 and 3 are fused to the centrum.

146. Ural centrum 2 independent (0) / fused (1). In Gasterosteiformes and primary outgroups (except Stephanoberyciformes and Beryciformes), ural centrum 2 is fused

to ural centrum 1 and preural centrum 1. In Myctophidae, the ural centrum 2 is fused, but in basal Myctophiformes (Neoscopelidae) it is autogenous.

147. Uroneural 1 independent (0) / fused (1). In Gasterosteiformes (except Aulostomidae) and some outgroups, uroneural 1 is fused to the centrum, but autogenous in others.
148. Number of epurals: three (0) / two (1) / one or absent (2). Gasterosteiformes (except Hypoptychidae, Aulorhynchidae, Gasterosteidae, Fistulariidae, and Indostomidae), have one epural. Hypoptychidae have two epurals. *Aulichthys japonicus* has two epurals, but *Aulorhynchus flavidus* has no epurals. Among Gasterosteidae, *Spinachia* has two epurals, but others have only one. Secondary outgroups and some primary outgroups have three epurals.
149. Caudal cartilage present (0) / absent (1). Gasterosteiformes (except Aulostomidae), lack the intercaudal and postcaudal cartilage. Most outgroups have intercaudal or postcaudal cartilage.
150. Opisthural cartilage present (0) / absent (1). Opisthural cartilage is present in secondary outgroups (except Lampridiformes) and Beryciformes.
151. Caudal median cartilage absent (0) / present (1). Caudal median cartilage is present in Aulopiformes and Myctophiformes, but absent in all the other taxa. In Synodontidae the median cartilage is absent, but in some other Aulopiformes it is present (Fujita, 1990).

Phylogenetic analysis

A data matrix of the above 151 informative characters (Table 9.1) was analyzed using heuristic search of PAUP and distribution of character states was explored in MacClade. All the characters were weighted equally and treated as unordered. Multistate characters within a taxon are treated as polymorphic. The accelerated transformation (ACCTRAN) option was used to optimize equivocal characters. Different options of the heuristic search of PAUP (addition sequence: simple, closest, as is, random; swapping algorithm: no swapping, NNI, SPR, TBR) were tried, but they did not produce a shorter tree. Characters were also treated and analyzed as ordered, but since most multistate characters occurred within the Gasterosteiformes, the same tree was produced. The data matrix was also analyzed in WinClada using parsimony ratchet to ensure the minimality of the most parsimonious trees obtained in the heuristic search of PAUP, but after 1000 reiterations WinClada did not find a shorter tree than that of PAUP. Thus I base my discussion on the results obtained from PAUP and MacClade. Bootstrap and decay analyses were used for estimating the tree support.

The single most parsimonious tree found by PAUP is shown in Fig. 9.1 (length:

727, consistency index: 0.41, retention index: 0.61, rescaled consistency index: 0.25, homoplasy index: 0.77). In this analysis, the monophyly of Gasterosteiformes is supported and Synbranchiformes is shown as the sister group of Gasterosteiformes. Monophyly of Acanthomorpha, Acanthopterygii, Percomorpha *sensu* Johnson and Patterson (1993), Smegmamorpha, and Atherinomorpha is also supported. The main clades of this tree are well supported by the strict consensus trees of the heuristic search of decay analysis in AutoDecay computer program (Fig. 9.2). The majority-rule consensus tree of 1000 bootstrap replicates does not support the whole tree, but it does support the monophyly of Acanthomorpha, Gasterosteiformes and Atherinomorpha, and the sister-group relationship of Agonidae and Dactylopteridae (Fig. 9.3). The bootstrap analysis also supports the monophyly of Gasterosteoidei, Aulostomoidea, Centriscoidea, basal position of Hypoptychidae within Gasterosteiformes and the basal position of Indostomidae and Pegasidae within Syngnathoidei.

The sister-group relationship of Gasterosteiformes and Synbranchiformes is supported by four characters. 1. Epibranchial 1 without an uncinate process (character 71). 2. Absence of postcleithrum (character 91). 3. Absence of Baudelot's ligament (character 137). 4. Absence of caudal cartilage (character 149).

Monophyly of Gasterosteiformes is supported by six synapomorphies. 1. Absence of basisphenoid (character 18). 2. Elongation of basihyal (character 55). 3. Actinosts of the same size (character 98). 4. Presence of a spike on the fourth actinost (character 100). 5. Fusion of parhypural to centrum and hypurals (character 139). 6. Fusion of hypurals to centrum (character 140).

Monophyly of Gasterosteoidei (Aulorhynchidae and Gasterosteidae) is supported by eight synapomorphies. 1. Frontal touches parasphenoid lateral process (character 14). 2. Palatine head is conical (character 34). 3. Quadrate shaft is much longer than quadrate body (character 40). 4. Symplectic bears an anteriorly bifurcated flange (character 42). 5. Ectocoracoid present (character 96). 6. Posterior basals present (character 114). 7. One anal spine present (character 119). 8. Exoccipital condyle consists only of basioccipital and the first centrum lacks any facets that articulate with exoccipital (character 120).

Monophyly of Syngnathoidei is supported by seven characters. 1. Loss of intercalar (character 16). 2. Loss or reduction of premaxillary ascending process (character 26). 3. Loss of uncinate process of epibranchials 3 and 4 (character 73). 4. Lophobranch gill filament with skeleton fused basally (character 82). 5. Loss of neurohypophyses (character 129). 6. Loss of pleural ribs (character 134). 7. Epurals absent or only one (character 148).

Monophyly of Centriscoidea (Macroramphosidae and Centriscidae) is supported by five synapomorphies. 1. Convex occipital condyle (character 22). 2. Preopercle with a socket at its articulation with interhyal (character 48). 3. Interhyal round and sutured to posterior ceratohyal (character 63). 4. Actinosts rotated laterally (character 99). 5. Vertebrae bear lateral processes to scutes (character 126).

Monophyly of Syngnathoidea (Syngnathidae and Solenostomidae) is supported by two synapomorphies. 1. Subopercle and interopercle widely separated from each other (character 52). 2. Hypobranchials fewer than three (character 69). Monophyly of Aulostomoidea is supported by four synapomorphies. 1. Hypohyals articulate with posterior ceratohyal (character 59). 2. Interarcual cartilage present (character 81). 3. An elongated ectocoracoid present (character 96). 4. Anterior centra sutured together (character 123).

Monophyly of Syngnathoidea + Aulostomoidea is supported by four synapomorphies. 1. Absence of nasals (character 1). 2. Presence of the exoccipital elongated posterior process (character 23). 3. Absence of epibranchial 4 (character 75). 4. Actinost strongly hourglass-shaped (character 97).

Monophyly of Syngnathoida (Syngnathoidea + Aulostomoidea + Centriscoidea) is supported by six synapomorphies. 1. Vomer located superficially anteriorly (character 7). 2. Prootic and exoccipital widely separated by pterotic (character 17). 3. Metapterygoid located anterior to orbit (character 38). 4. Quadrate shaft with a deep dorsal flange (character 39). 5. Quadrate shaft much longer than quadrate body (character 40). 6. Urohyal blade is incised posteriorly (character 57).

Classification of Gasterosteiformes

Based on the phylogenetic analysis (Fig. 9.1) and synapomorphies presented above, I recognize three suborders, three infraorders, and three superfamilies in the ingroup, Gasterosteiformes.

- Order Gasterosteiformes
  - Suborder Hypoptychoidei (new suborder)
    - Hypoptychidae
  - Suborder Gasterosteoidei
    - Aulorhynchidae
    - Gasterosteidae
  - Suborder Syngnathoidei
    - Infraorder Indostomoida
      - Indostomidae
    - Infraorder Pegasoida

        Pegasidae
Infraorder Syngnathoida (new infraorder)
    Superfamily Centriscoidea
        Macroramphosidae
        Centriscidae
    Superfamily Syngnathoidea
        Syngnathidae
        Solenostomidae
    Superfamily Aulostomoidea
        Aulostomidae
        Fistulariidae

Table 9.1. Data matrix of the 151 osteological characters analyzed for phylogenetic reconstruction of Gasterosteiformes relationships. Polymorphic characters are shown by symbols: "*" for (0/1), "+" for (0/2), and "$" for (1/2)."?" indicates inapplicable data.

Characters	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40
Aulopiformes	00110	00000	00100	00000	00000	*0000	*0000	00000
Myctophiformes	00000	00000	01000	00001	10010	10100	00001	00000
Lampridiformes	02000	00000	00100	00000	00001	00001	01000	00000
Polymixiiformes	02000	10000	01000	00000	10000	00110	10000	00000
Percopsiformes	02000	00000	00000	00000	00000	01001	01000	00000
Mugiliformes	02110	10001	00100	00000	00000	10100	00000	00000
Atheriniformes	01101	10011	00100	00000	10000	10101	00000	01000
Beloniformes	011*1	00011	00*00	00001	*0010	1*100	01000	00000
Cyprinodontiformes	01101	00011	00000	10000	10000	10000	01000	10000
Stephanoberyciformes	02000	00000	00000	00000	100**	*0110	11000	*0000
Beryciformes	021*0	10000	0*100	00000	*000*	00110	1000*	00000
Zeiformes	02000	00000	00100	00000	00000	00110	01000	00000
Hypoptychidae	02110	00011	00100	00101	0001*	01100	01000	10000
Aulorhynchidae	12110	00100	00110	*01*0	00000	01*00	01010	11001
Gasterosteidae	12110	00111	00110	00110	00000	01000	01010	11001
Pegasidae	12110	00110	00000	10111	00001	10000	0????	11000
Solenostomidae	22100	01111	?0001	11101	00111	10010	01101	01111
Syngnathidae	22110	01111	00111	11101	00011	10000	01000	01111
Indostomidae	12110	00111	001?1	10100	10010	11000	01000	11000
Aulostomidae	02110	01111	00001	11101	10101	10011	01100	10111
Fistulariidae	22110	01111	00000	11101	10101	10010	01000	01111
Macroramphosidae	12110	01111	00001	11101	01001	10000	01000	01111
Centriscidae	02110	01111	00000	11101	01001	10000	01000	01111
Synbranchiformes	02110	00011	?0000	10000	10010	0*010	0*000	*0000
Dactylopteridae	02110	10000	11000	10001	10010	00000	01000	00000
Scorpaenidae	02110	10000	10000	00000	00000	00110	00001	00000
Hexagrammidae	02000	10000	10010	00000	00010	00011	01001	00000
Agonidae	02110	10000	11110	00100	00010	10010	00000	00000
Percidae	02000	10000	00100	00000	00000	00111	00001	00000
Cirrhitidae	02000	10000	01100	00000	00000	00111	01001	00000
Elassomatidae	02000	00011	00000	00100	00000	00011	0100?	10000
Pomacentridae	02000	00000	01000	00000	00000	00111	01000	01000
Centrarchidae	02000	10000	00000	00000	00000	00111	01000	01000

Table 9.1. Continued...

Characters	41-45	46-50	51-55	56-60	61-65	66-70	71-75	76-80
Aulopiformes	00001	01001	10000	00000	00000	00000	00100	00000
Myctophiformes	00001	01000	1000?	00000	00000	01000	00000	00000
Lampridiformes	00000	10001	00000	00010	10001	01000	00000	10000
Polymixiiformes	00000	00000	00000	00010	10010	00000	00010	10000
Percopsiformes	01100	10010	00000	10011	00001	00000	00010	00000
Mugiliformes	01100	00010	00002	10011	01000	00000	00010	10101
Atheriniformes	01100	01010	00002	10*11	01000	00001	00011	00101
Beloniformes	01100	1*011	00002	01*10	01?00	00001	00*1*	*1101
Cyprinodontiformes	01100	10010	00000	10111	*1000	*0001	10011	0110*
Stephanoberyciformes	00100	00001	10000	10010	*0000	00000	00*10	10011
Beryciformes	0*100	1001*	10000	10010	*0000	00000	00010	0000*
Zeiformes	01100	*0010	10000	10010	1*000	00*00	*0010	1010*
Hypoptychidae	01101	01011	00001	10110	0001?	00100	11010	11101
Aulorhynchidae	12101	*1011	00111	10*10	01010	00A00	11010	1110*
Gasterosteidae	12100	01011	00111	10011	01011	00000	11010	11101
Pegasidae	01110	11001	01010	10010	01001	10110	1?110	11?11
Solenostomidae	11110	11011	1110?	11010	00010	1?110	????2	?1101
Syngnathidae	11110	11110	11100	00020	01111	1?110	111?2	?1111
Indostomidae	10100	01011	1???1	10011	00000	00000	11110	01101
Aulostomidae	11100	11011	00101	00021	11011	1?100	011?2	?1100
Fistulariidae	11100	11011	00101	01020	01001	1?100	111?2	?1100
Macroramphosidae	10110	11111	00101	11010	00100	00000	10000	11100
Centriscidae	10110	11111	00101	11020	00101	00100	11000	10100
Synbranchiformes	0*100	*1001	10000	*0*11	01001	*0*00	1*0*0	*1110
Dactylopteridae	00111	11011	20000	10110	00000	00000	00010	10100
Scorpaenidae	00100	10011	20000	10011	00000	00000	00010	10000
Hexagrammidae	00100	11011	20000	10111	01000	00100	00010	10101
Agonidae	00101	10011	2001?	10011	00001	00000	0?010	11?11
Percidae	00100	11011	00000	10011	01000	00000	00010	10100
Cirrhitidae	00101	11011	00000	10011	10000	00000	00010	10100
Elassomatidae	00100	01010	00000	10011	00000	00000	01010	11100
Pomacentridae	00100	10010	00000	10011	11000	00000	00010	10100
Centrarchidae	00100	10011	00000	10111	11000	00000	00010	10100

Table 9.1. Continued...

Characters	81-85	86-90	91-95	96-100	101-105	106-110	111-115
Aulopiformes	00001	00100	00000	00000	00110	00000	0110?
Myctophiformes	00000	00000	00000	00000	00010	00001	1010?
Lampridiformes	00010	00000	01000	00000	00100	00000	0000?
Polymixiiformes	00011	00000	01001	00000	00000	00000	00000
Percopsiformes	00010	00000	10001	00000	00000	00001	00000
Mugiliformes	10110	01000	01001	00000	01101	01010	01001
Atheriniformes	10010	1$0*1	****0	00000	01*00	01010	2*001
Beloniformes	00010	11100	100*0	00000	*0*00	110*0	2110?
Cyprinodontiformes	10*10	11001	*00*0	00000	00000	*1000	2110?
Stephanoberyciformes	00110	*0000	10*00	00000	00100	**000	0110?
Beryciformes	00010	000*0	10000	00000	01101	00010	00001
Zeiformes	00010	10001	1*001	00000	0110*	0*110	00001
Hypoptychidae	00110	01100	2?000	00101	0????	??0??	??101
Aulorhynchidae	00011	*$010	2?101	10101	01101	01000	01011
Gasterosteidae	00110	11000	2?101	10101	11101	01000	01011
Pegasidae	01120	12001	2?100	00101	11101	11000	0110?
Solenostomidae	01110	11011	2?100	01100	00100	11000	0110?
Syngnathidae	01120	12100	2?100	01100	0????	?????	??10?
Indostomidae	01110	110?0	2?110	00101	00100	10000	010?1
Aulostomidae	10011	12110	10111	11100	00100	11000	0110?
Fistulariidae	10121	11010	10101	11100	00100	11000	0110?
Macroramphosidae	00120	11101	11010	00111	11101	01000	00001
Centriscidae	00120	11100	10010	00111	11100	11000	01001
Synbranchiformes	*011*	10100	2?001	00000	0????	?????	??*01
Dactylopteridae	00010	11101	10010	00000	01101	01110	00001
Scorpaenidae	10011	00010	00010	01000	01101	01110	00001
Hexagrammidae	00011	00000	01000	01000	01101	01110	00000
Agonidae	00011	00001	00010	00100	11101	11110	00001
Percidae	10011	00010	00000	00000	01101	01110	00000
Cirrhitidae	10011	00011	00000	00000	01101	11110	00001
Elassomatidae	00110	00001	00000	00000	01101	11010	01001
Pomacentridae	10011	00011	00000	00000	01101	01110	00001
Centrarchidae	10011	00001	00000	00000	01101	01110	00001

Table 9.1. Continued...

Characters	116-120	121-125	126-130	131-135	136-140	141-145	146-151
Aulopiformes	?0000	00000	00000	00*00	00000	0*000	000001
Myctophiformes	?0000	00000	00100	00000	00000	00000	000001
Lampridiformes	?1100	11000	00001	00000	01000	01000	000110
Polymixiiformes	01020	10010	00000	00000	00000	00010	010000
Percopsiformes	00010	00000	00102	10101	00000	00110	001000
Mugiliformes	01120	01010	01100	11101	11000	01000	101010
Atheriniformes	01111	01010	01*02	11101	110**	01001	1*1010
Beloniformes	01101	01010	01*02	11101	1100*	*1001	1*0*10
Cyprinodontiformes	01101	01010	01102	11101	*1001	$1111	111*10
Stephanoberyciformes	01100	11000	00**0	1110*	*0000	00100	010*10
Beryciformes	011+0	1*000	00*01	*110*	01*00	0*000	0*0100
Zeiformes	01121	**000	0010$	11101	0*000	010**	1**010
Hypoptychidae	?1101	01010	00102	1?101	12011	11111	111110
Aulorhynchidae	11112	01010	*010$	??1*2	12111	21111	11$110
Gasterosteidae	11112	01010	00101	11101	12111	21111	111110
Pegasidae	?1101	01001	00012	??112	?2111	21101	112110
Solenostomidae	?1101	01001	00012	??112	?2111	21101	112110
Syngnathidae	?1101	01010	10112	??112	?2111	21101	112110
Indostomidae	11101	01010	10011	11111	12111	21101	112110
Aulostomidae	?1101	01101	00002	01111	12000	11111	112010
Fistulariidae	?1101	01101	00002	??112	?2011	21111	102110
Macroramphosidae	01101	01011	10001	??112	?2111	21111	112110
Centriscidae	?1101	01101	10112	??112	?2101	21111	112110
Synbranchiformes	011+1	11010	00002	111*1	*2000	011**	102110
Dactylopteridae	01100	01000	00002	11111	?21*0	110*0	101110
Scorpaenidae	01120	10000	00101	11101	01000	01000	100010
Hexagrammidae	01100	10000	00102	11101	01010	11100	100010
Agonidae	01101	10000	00102	10111	00111	21111	111110
Percidae	01120	10000	00101	11101	01000	01100	100010
Cirrhitidae	01120	10000	00100	11101	01000	01000	100010
Elassomatidae	01120	01010	00002	11101	11000	11001	110010
Pomacentridae	01120	10000	00100	11101	01000	01000	110010
Centrarchidae	01120	10000	00000	11101	01000	01000	100010

Note: The thickest lines separate the secondary outgroups at the top of the table, the medium size lines delimit an order, and the thin triple lines separate Gasterosteiformes from other primary outgroups.

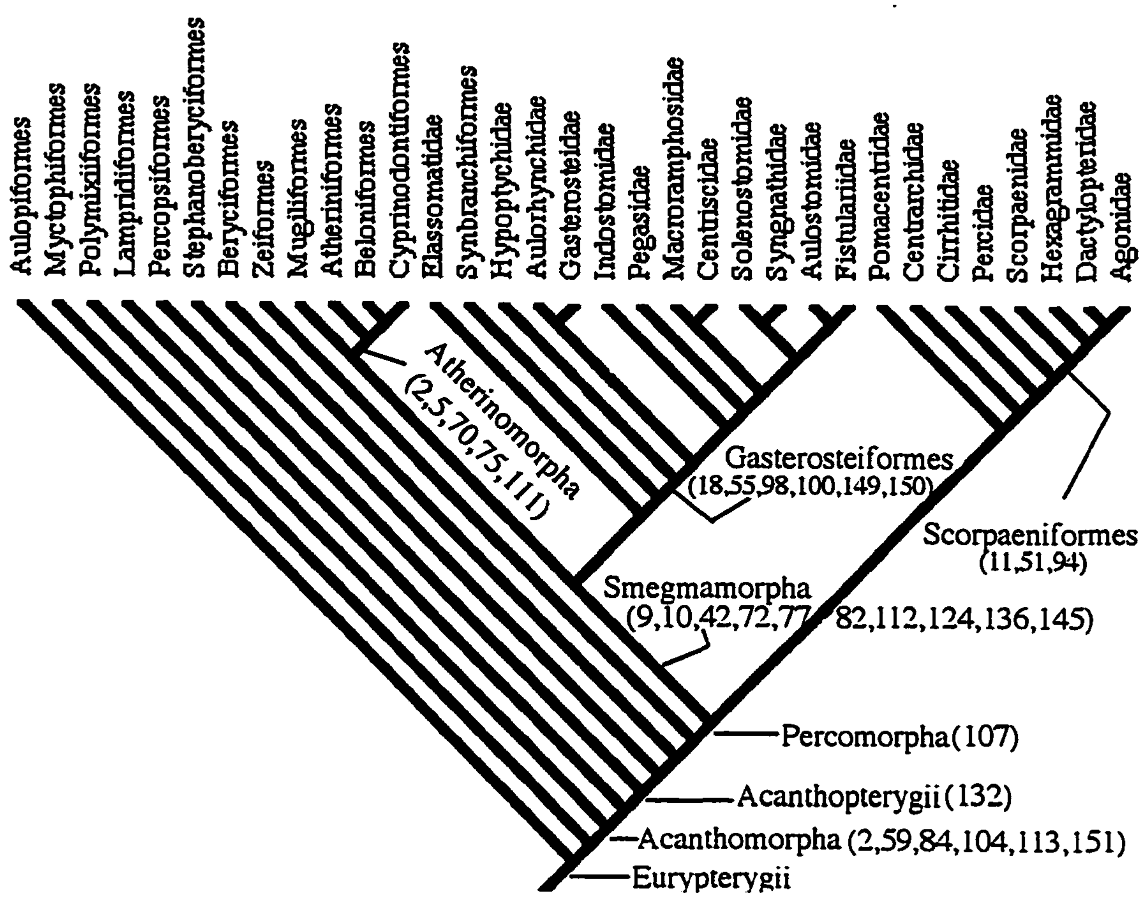

Fig. 9.1. The single most parsimonious tree obtained from analyzing 151 osteological characters in PAUP 4.0 (L: 727, CI: 0.41, RI: 0.61, RC: 0.25, HI: 0.77). Numbers in the parentheses indicate the synapomorphies for each group. Nomenclature follows that of Johnson and Patterson (1993).

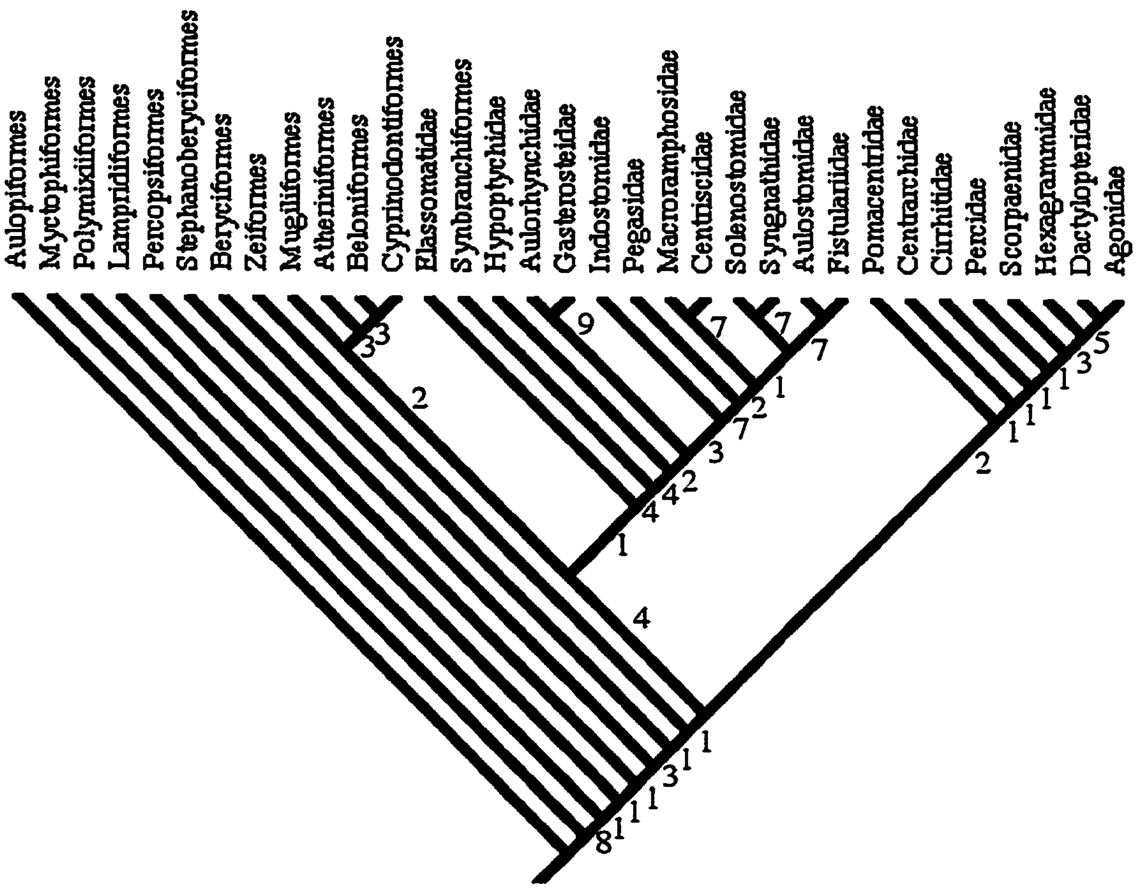

Fig. 9.2. Decay or Bremer support for major clades of the tree. Numbers indicate the support for each branch. Number of the trees for the lengths of up to 5 steps longer (738-732) is as follows: 20, 198, 1289, 6468, and 27337, respectively.

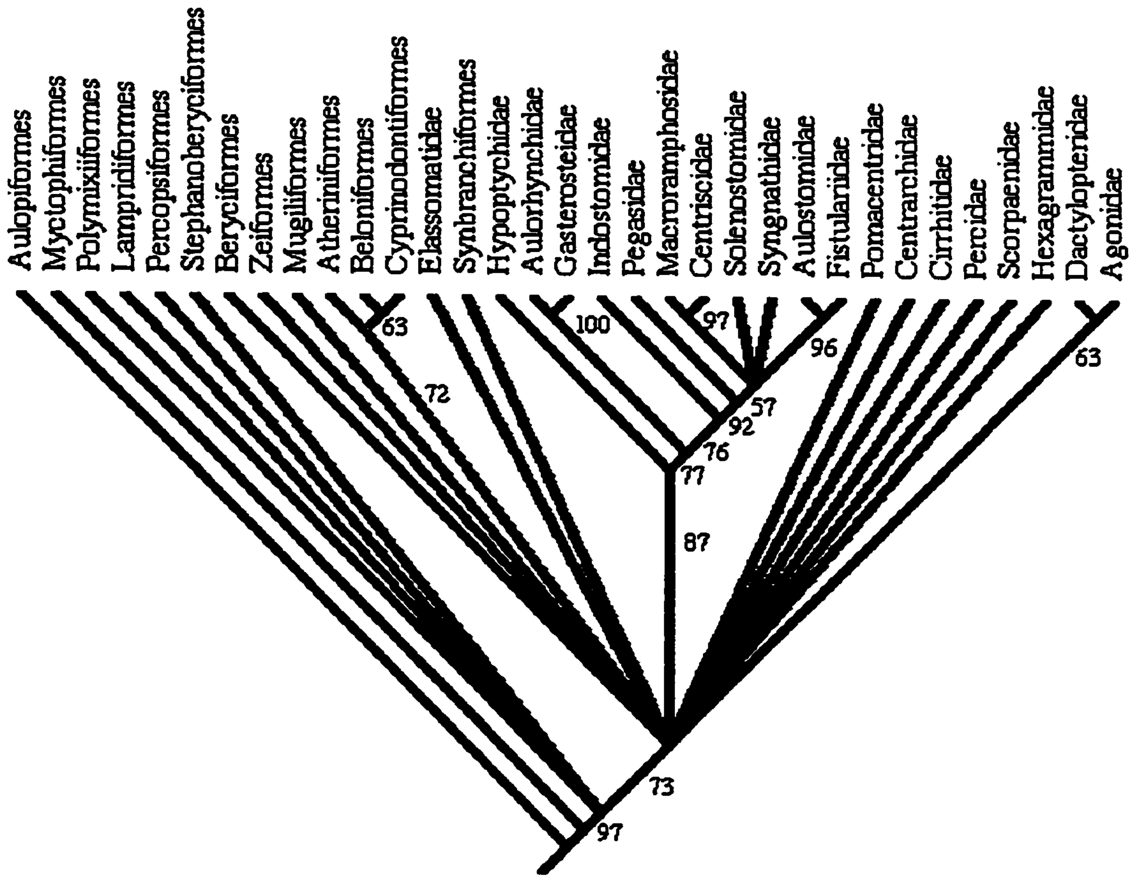

Fig. 9.3. The fifty percent majority-rule consensus tree of 1000 bootstrap replicates and the percentage of support for each branch.

10. Discussion and Conclusions

To hypothesize the systematic position of a group such as Gasterosteiformes, it is necessary to establish the monophyly of the group. Ideally, monophyly of a taxon is convincingly accepted when all members of a taxon possess many derived characters not possessed by members of any other group. Sister-group relationship of two taxa is unequivocal when all the members of both taxa share more uniquely derived characters with one another than with those of any other taxon. However, in practice, due to specialization of some members and homoplastic evolution of characters, few unequivocal synapomorphies are found. Johnson and Patterson (1993) reviewed and summarized the status of Acanthomorpha and proposed a list of synapomorphies for Acanthomorpha and its subgroups. In the following section, their review will serve as a basis for discussing the monophyly of some higher groups, their proposed synapomorphies, and distribution and variation of those characters in Gasterosteiformes as a member of these taxa. I finally discuss the sister group relationships and interrelationships of Gasterosteiformes, monophyly of Atherinomorpha plus Mugilomorpha, the position of Dactylopteridae, and evolution of some phylogenetically significant characters.

Gasterosteiformes within Acanthomorpha

Monophyly of Acanthomorpha is supported by six synapomorphies in this study (Fig. 9.1). Many of these characters have been proposed by previous authors (e.g., Stiassny and Moore (1992); Johnson and Patterson (1993)). 1. Presence of a rostral cartilage which is strongly attached to the premaxillary ascending process (character 2). In all Gasterosteiformes, even in Syngnathoidei which have a vestigial ascending process, the rostral cartilage is attached to the premaxilla. In Atherinomorpha, the rostral cartilage is not directly and tightly attached to the premaxilla. In Aulopiformes and Myctophiformes, the cartilage is attached to the ethmoid, but it is highly variable in non-acanthomorphs (Hartel and Stiassny, 1986). 2. Incorporation of the hypohyals into the anterior ceratohyal (character 59). In all Gasterosteiformes hypohyals are incorporated in the anterior ceratohyal and in Syngnathidae, Aulostomoidea, and Centriscidae, the ventral hypohyal is enlarged and strongly articulated with the posterior ceratohyal. 3. Dorsal limb of the posttemporal is tightly attached to the epioccipital (character 84). In all acanthomorphs, including gasterosteiforms, the dorsal process of the posttemporal is tightly connected to the exoccipital with a short ligament. In Pegasidae, Syngnathidae, Fistulariidae, and Centriscoidea, the posttemporal is fused to the cranium. 4. Absence of the lateral cartilaginous process (character 104). All gasterosteiforms lack a lateral cartilaginous process, but gasterosteoids bear a well developed ascending lateral process which is obviously different from that of Aulopiformes and Myctophiformes. 5. Presence of true dorsal fin spines (character 113). Hypoptychids and members of Syngnathoidei, except indostomids and centriscoids, lack dorsal spines. Gasterosteoids bear dorsal spines. Also, Beloniformes, Cyprinodontiformes, Stephanoberyciformes, and Trachipteridae (Lampridiformes) lack dorsal spines. 6. Absence of a caudal median cartilage (character 151). Caudal median cartilage is absent in all acanthomorphs, including Gasterosteiformes.

Johnson and Patterson (1993) in addition to characters 1, 3, 5, and 6, proposed four other synapomorphies for Acanthomorpha. 1. Presence of true dorsal and anal fin spines. This character is comparable to character 3 discussed above, although dorsal and anal spines do not correlate in all cases (e.g., Indostomidae, Centriscoidea, and Veliferidae bear dorsal spines, but no anal spines). 2. Anterior and medial infracarinales separate. This character was originally proposed by Stiassny (1993). 3. Medial pelvic process ossified distally. All gasterosteiforms and primary outgroups, except some atherinomorphs, percopsiforms, and polymixiiforms, lack the medial process. The condition in Aulopiformes, which lack a distinct medial process, is not homologous to that of myctophiforms which have a distinct cartilaginously tipped medial process. Thus within Eurypterygii, the presence of a cartilaginously tipped medial process is an autapomorphy of Myctophiformes. 4. First centrum with anterior surface bearing distinct facets that articulate with the exoccipital condyle. This character originally was proposed by Rosen (1985) and is comparable to character 120 and is correlated with the presence of the transverse process (character 124). However, I am not convinced that the condition is different in Aulopiformes and Myctophiformes compared to Lampridiformes. In the six basal eurypterygians I studied, the occipital condyle is tripartite, with the exoccipital forming the dorsal portion of the condyle, and the first vertebra bearing dorsal facets that articulate with the exoccipital condyles. In Gasterosteiformes, Atherinomorpha, Zeiformes, and Agonidae, the occipital condyle consists only of the basioccipital and the first vertebra connects to the exoccipital with facets on the enlarged neurohypophyses or the transverse processes.

Stiassny (1986) also suggested three other synapomorphies for Acanthomorpha. 1. The maxillo-rostroid ligament originates from the inner face of the maxillary median process. Though the description is correct, this character might be correlated with development of the articular and ascending processes of the premaxilla and maxilla in Acanthomorpha. 2. A spina occipitalis extends ventrally between the epioccipital and exoccipital to form the dorsal margin of the foramen magnum. This character was so variable that I could not objectively distinguish it the way Stiassny did, but I coded it as present or absent (character 24). However, the spina occipitalis is distinctly smaller in Aulopiformes and its size might be correlated with skull depth. Johnson and Patterson (1993) regarded the large spina occipitalis in Veliferidae as non-homologous to that of higher acanthomorphs and listed this character as a synapomorphy for their Euacanthomorpha (Acanthomorpha minus Lampridiformes). 3. The ethmoid cartilage is reduced and there is a close approximation (often sutural union) of the lateral ethmoids with the vomer. In Syngnathoidei, except Indostomidae and Pegasidae, the vomer is prominent dorsally, excludes the ethmoid from its typical articulation, and has no association with the lateral ethmoid.

Regarding the tree in Fig. 9.1, of particular interest is the basal position of Polymixiiformes in Acanthomorpha. This is contrary to Stiassny and Moore (1992), Johnson and Patterson (1993), and Nelson (1994), who placed Lampridiformes as the basal acanthomorph. Lampridiformes share at least three synapomorphies with Acanthopterygii not found in other eurypterygians I studied. 1. Fusion of the first neural arch to the centrum (character 122). 2. Origination of the Baudelot's ligament on the exoccipital (character 137). 3. Absence of the opisthural cartilage (character 150). Polymixiiformes share three synapomorphies with at least some Acanthopterygii. 1. Maxillary shaft expanded ventrally (character 29). 2. Presence of a supramaxilla (character 31). 3. Fusion of uroneural 1 (character 147). However, the position of Polymixiiformes and Lampridiformes is not well resolved in this study, and further research is necessary to resolve the conflict in the position of these taxa.

Percopsiforms share eight synapomorphies with Acanthopterygii not found in other eurypterygians I studied. 1. Symplectic partially inserted in the quadrate (character 43). 2. Preopercle with distinct dorsal and ventral arms (character 49). 3. Urohyal with ventrolateral flanges (character 56). 4. Anterior ceratohyal with a posteriorly distinct rectangular part that abruptly becomes narrower anteriorly (character 60). 5. Presence of one postcleithrum (character 91). 6. Anterior epineural distal parts displaced into horizontal septum (character 131). 7. Absence of anterior epicentral ligaments (character 133). 8. Absence of epipleurals (character 135).

Johnson and Patterson (1993), in addition to the spina occipitalis character, provided three characters to support their Euacanthopterygii. 1. First epineural displaced ventrally into horizontal septum. In all Gasterosteiformes with epineurals, the first epineural is displaced ventrally. One might interpret the condition in Veliferidae as a displaced epineural. 2. Posterior pelvic process ossified distally. In all Gasterosteiformes with a pelvic posterior process, the process is ossified distally. In the specimens of *Velifer hypselopterus* that I examined, the posterior process of the pelvic girdle is closed in bone. Thus, this character might be a synapomorphy for Acanthomorpha. 3. Point of origin of epineurals displaced ventrally on to centra or parapophyses. In all Gasterosteiformes with epineurals, the point of origin of epineurals is displaced ventrally on to the centra or parapophyses. In specimens of *Polymixia lowei* that I examined, all epineurals originate on the neural arch. Johnson and Patterson (1993) also listed three synapomorphies for Holacanthopterygii (Acanthomorpha minus Lampridiformes and Polymixiiformes) that are found at least in some Gasterosteiformes.

Gasterosteiformes within Acanthopterygii

Monophyly of Acanthopterygii is supported only by one unequivocal character, anterior epineurals displaced ventrally (character 132). This character is reversed in Agonidae, but is present in all Gasterosteiformes with epineurals and in other Acanthopterygii. Another possible synapomorphy is the fusion of uroneural 1 (character 147). Uroneural 1 is also fused in Polymixiiformes. Johnson and Patterson (1993) proposed three synapomorphies for Acanthopterygii. 1. Pelvic spine present. The pelvic spine is absent in Stephanoberyciformes that I studied, but may be present in others and their loss in Stephanoberycidae and Rondeletiidae is interpreted as secondary. The pelvic spine is also absent in Beloniformes, Cyprinodontiformes, and Agonidae. All Gasterosteiformes, but indostomids, aulostomoids, and members of Syngnathoidea bear a pelvic spine. 2. Free pelvic radials are reduced in size and/or number. I coded this character as absence or presence of the free radials (character 107). In Gasterosteiformes, only indostomids have a free ossified radial which I interpret as a reversal. 3. Presence of an anteromedial process (anterior process of Stiassny and Moore, 1992) of the pelvic bone. The anterior process is absent in all Gasterosteiformes, some Beloniformes, Cyprinodontiformes, and Stephanoberyciformes. Among Zeiformes, grammicolepidids (Fig. 6.11) bear a dorsomedially displaced process and caproids (Fig. 6.12) bear a ventrally displaced anterior process that might be homologous to the anterior process. Since the process is absent in Stephanoberyciformes, this character might be a synapomorphy of Euacanthopterygii (Acanthopterygii less Stephanoberyciformes), as mentioned by Johnson and Patterson (1993).

Another interesting issue is the position of Zeiformes as the sister-group of Percomorpha and the position of Beryciformes as the basal Euacanthopterygii (Percomorpha plus Beryciformes and Zeiformes). This view of relationship of Beryciformes, Zeiformes, and Percomorpha is in agreement with Nelson (1994) and in disagreement with Johnson and Patterson (1993) who placed Beryciformes as the sister-group of Percomorpha. Lauder and Liem (1983), based on otolith morphology, treated

Beryciformes and Zeiformes as the sister-groups of each other and both as the sister-group of higher percomorphs. However, reinterpreting Beryciformes as the sister-group of Percomorpha is only three steps longer, and sister-group relationship of Percomorpha and Zeiformes is supported only by a decay value of 1 in the present study. Zeiforms share two characters with percomorphs; absence of an uncinate process on pharyngobranchial 2 (present in Scorpaenidae), and fusion of the ural centrum 2 to the preceding centra. None of my characters unequivocally and uniquely supports the sister-group relationships of Percomorpha and Beryciformes. Johnson and Patterson (1993) listed five characters uniting Percomorpha and Beryciformes. 1. Complex pelvic spine. 2. Chain-like articulation of dorsal fin-spines. 3. Supraneurals ossified distally. 4. Second ventral procurrent caudal fin ray shortened proximally. 5. Myoseptal ligament from postcleithrum to posterolateral corner of pelvic girdle. They also listed three synapomorphies for the Zeiformes-Euacanthopterygii group; advanced dorsal fin, displacement of epineurals on to pleural ribs, and origination of the Baudelot's ligament on the exoccipital. Since the sister-group relationship of Zeiformes and Percomorpha is not well supported here, further research would be in order to resolve the conflict in the position of Zeiformes and Beryciformes.

Gasterosteiformes within Percomorpha

Monophyly of Percomorpha is weakly supported by a decay value of 1 and only one unequivocal synapomorphy, absence of the free pelvic radials (character 107). This character is reversed in Indostomidae and in several perciform families (Winterbottom, 1993). The connection of the anterior and posterior ceratohyals via struts (character 62) shared by percomorphs is reversed in many taxa. Johnson and Patterson (1993), in addition to the above character (107), proposed seven synapomorphies for Percomorpha. 1. Presence of a rod-like interarcual cartilage. In Gasterosteiformes, only aulostomoids bear an interarcual cartilage. This character is also absent in Beloniformes, Dactylopteridae, Agonidae, Hexagrammidae, Elassomatidae, and Mastacembelidae. The interarcual cartilage is ossified in Synbranchidae. 2. Second ural centrum absent. The second ural centrum is also absent in Zeiformes and unites them with percomorphs. 3. Five or fewer hypurals. All gasterosteiforms bear five fused hypurals. However, synodontids (Aulopiformes) and holocentrids (Beryciformes), also have five hypurals. 4. Pelvic fins with fewer than six soft rays. All gasterosteiforms, except aulostomoids and solenostomids, bear five or fewer pelvic soft rays. Stephanoberyciforms and monocentrids also bear five pelvic soft rays. 5. Presence of transforming ctenoid scales (originally proposed by Roberts (1993)). All gasterosteiforms, except aulostomids, lack scales and bear bony scutes. Transforming ctenoid scales are also absent in Atherinomorpha, Synbranchiformes, and

Tetraodontiformes (Roberts, 1993). 6. Points of origin of all but the first two epineurals are placed ventrally and the distal part of all epineurals displaced ventrally into the horizontal septum. In Gasterosteiformes with epineurals, points of origin of all but the first two epineurals are placed ventrally. In all Gasterosteiformes, except *Aulorhynchus flavidus* and Aulostomidae, the distal part of all epineurals are displaced ventrally into the horizontal septum. 7. Seventeen principal caudal fin rays in I,8,7,I pattern. All gasterosteiforms have fewer than 17 principal caudal rays.

Gasterosteiformes within Smegmamorpha

Monophyly of Smegmamorpha is well supported by a decay value of 4 and nine synapomorphies. 1. Infraorbitals three or fewer (character 9). This character is reversed in Mugilidae and Aulorhynchidae. 2. Infraorbitals discontinuous (character 10). This character is reversed in Aulorhynchidae and Pegasidae. 3. Symplectic bears dorsal or ventral flanges (character 42). This character is also found in Percopsiformes and Zeiformes that I interpret as independent gain in these groups. 4. Absence of pharyngobranchial 1 (character 77). This character is independently lost in Agonidae and reversed in Centriscidae, Atheriniformes and Mugiliformes. 5. Absence of toothplates (character 83). This character is reversed in Aulostomidae and Atherinomorpha and independently lost in Stephanoberyciformes. 6. Absence of ventral wing of pelvic plate (character 112). This character is reversed in Macroramphosidae and independently lost in Aulopiformes and Stephanoberycidae. 8. Presence of transverse processes on the first two vertebrae (character 124). This character is independently gained in Polymixiiformes and reversed in Syngnathoidei and again independently gained in Macroramphosidae and Syngnathidae. 9. First epineural on a transverse process or lateral surface of vertebra (character 136). Johnson and Patterson (1993) originally proposed this character as the only unequivocal synapomorphy of Smegmamorpha. This character is reversed in Cyprinodontidae and Mastacembelidae and independently gained in Stephanoberycidae, some species of Carangidae and Gobiidae (Johnson and Patterson, 1993). 10. Haemal spine of preurals 2 and 3 fused to centrum (character 145). This character is reversed in Mugiliformes and independently gained in Agonidae.

Johnson and Springer (1997) proposed Elassomatidae as the sister group of Gasterosteiformes, but my hypothesis (Fig. 9.1) is that the order Synbranchiformes is the sister group of Gasterosteiformes, and that the family Elassomatidae is the sister group of both. Placing Elassomatidae as the sister group of Gasterosteiformes and Synbranchiformes as the sister group of both requires seven more steps. Placing Elassomatidae as the sister group of Gasterosteiformes and Mugiliformes-Atherinomorpha as the sister group of both, requires nine more steps. Placing Mugiliformes-Atherinomorpha as the sister group of Gasterosteiformes and Synbranchiformes as the sister group of both, requires four more steps. Placing Mugiliformes-Atherinomorpha as the sister group of Gasterosteiformes and Elassomatidae as the sister group of both, requires seven more steps.

Elassomatids, as one of the proposed sister groups of Gasterosteiformes, share three characters with Gasterosteiformes: Absence of the basisphenoid which is also absent in Agonidae, absence of an endopterygoid which is also absent in Cyprinodontiformes, and attachment of the epibranchial 1 head with pharyngeal toothplate 2. Mugiliformes and Atherinomorpha share three characters with Gasterosteiformes. 1. Absence of the fourth pharyngeal toothplate which is also absent in Stephanoberyciformes, Hexagrammidae, and Agonidae. 2. Reduction of the supracleithrum which has also happened in Dactylopteridae. 3. Presence of two epurals, which is also found in Percopsiformes, Dactylopteridae, and Agonidae. In derived gasterosteids, there is only one epural and in Syngnathoidei, there is one or no epural.

Synbranchiformes share four synapomorphies with Gasterosteiformes. 1. Epibranchial 1 without an uncinate process (character 71). This character is independently lost in Cyprinodontiformes. 2. Absence of the postcleithrum (character 91). 3. Absence of the Baudelot's ligament (character 137). Dactylopterids also lost the Baudelot's ligament, but in Dactylopteridae pectoral attachment to the cranium and nature of the lost is different from Gasterosteiformes and Synbranchiformes and non-homologous to it. In Dactylopteridae, the pectoral girdle is attached to the cranium by body scutes, but in Synbranchiformes and basal Gasterosteiformes, no scute fill the gap between the pectoral girdle and the cranium. 4. Absence of caudal cartilage (character 149). Caudal cartilage is also independently lost in Lampridiformes, Beryciformes, Dactylopteridae and Agonidae. Among the synapomorphies Gosline (1982) listed for Synbranchiformes, four are present in Gasterosteiformes: body elongation, absence of the pelvic girdle (in Hypoptychidae and Syngnathidae), absence or reduction of the endopterygoid, and loss of the premaxillary ascending process (in Syngnathoidei).

Gasterosteiforms, synbranchiforms, and elassomatids share two synapomorphies. 1. Loss of the endopterygoid (character 36) which is also lost in Cyprinodontiformes and reversed in Syngnathoidei. 2. Attachment of the first epibranchial to the second pharyngobranchial or pharyngeal toothplate (character 72) with a reversal in macroramphosids.

Monophyly of atherinomorphs is supported by five characters. 1. Rostral cartilage separate from the premaxilla (character 2). 2. Ethmoid with disc-like ossifications (character

5). 3. Ceratobranchial 5 with a ventral and posterior process (character 70). 4. Epibranchial 4 enlarged (character 75). Epibranchial 4 is not enlarged in Belonidae. 5. Pelvic girdle articulates with pleural ribs ligamentously through its small lateral processes (character 111). In addition to the above synapomorphies, five reproductive, one myological and one histological synapomorphies, Parenti (1993) listed three osteological characters as synapomorphies of atherinomorphs. 1. Reduction of infraorbital bones. 2. Reduction of supracleithrum. 3. Absence of supraneurals. The first two characters are synapomorphies of Smegmamorpha as discussed above and the third character is widely found in Gasterosteiformes, Synbranchiformes, Elassomatidae, Hexagrammidae, Agonidae, Dactylopteridae, Caproidae, and Percopsiformes. These characters were highlighted and discussed as evidence for relationships of Gasterosteiformes and Atherinomorpha by Johnson and Patterson (1993), but subsequently Orr (1995) disputed some of these characters.

The sister-group relationship of Mugiliformes and Atherinomorpha is supported by three synapomorphies. 1. Basihyal with a large cartilaginous head (character 55). This character is reversed in Cyprinodontiformes. 2. Presence of interarcual cartilage (character 81). This character is reversed in Beloniformes and independently gained in Aulostomoidea, Scorpaenidae and Perciformes. 3. Anterior neural spines expanded. Parenti (1993) proposed eight characters as potential synapomorphies for sister group relationship of Atherinomorpha and some Paracanthopterygii, but this relationship has not been supported (Johnson and Patterson, 1993; Stiassny, 1993). Parenti (1993) proposed that the presence of these characters in some but not all Paracanthopterygii is an indication of paraphyly of Paracanthopterygii. Stiassny (1993) discussed and proposed several other synapomorphies to support the sister-group relationship of Mugiliformes and Atherinomorpha. Ontogenetic studies of osteological characters, such as the jaws of Mugiliformes and Atherinomorpha, will cast more light on the phylogeny of these groups.

Interrelationships of Gasterosteiformes

Although the monophyly of subgroups of Gasterosteiformes is relatively well defined, Gasterosteiformes lack unique diagnostic characters. All the synapomorphies proposed to date for Gasterosteiformes are absent or modified in some major groups of Gasterosteiformes and no unique synapomorphy is found for this order. In this study, monophyly of Gasterosteiformes is supported by six synapomorphies. 1. Absence of basisphenoid (character 18). The basisphenoid is lost in all Gasterosteiformes and also it is independently lost in Elassomatidae and Agonidae. 2. Elongation of basihyal (character 55). All gasterosteiforms, except derived gasterosteids, pegasids, and members of Syngnathoidea have an elongated basihyal. 3. Actinosts with the same size (character 98). In Gasterosteiformes actinosts are relatively the same size, but in outgroups, size of the actinosts increases gradually from the first to the last. In Agonidae and Cottoidei (Yabe, 1985) actinosts are also the same size; however in Cottoidei all actinosts are enlarged and comprise a large portion of the pelvic girdle, while in most Gasterosteiformes actinost are of normal size. 4. Presence of a spike on the fourth actinost (character 100). Gasterosteiforms bear a spike on the fourth actinost that inserts in the coracoid. This character is reversed in Syngnathoidea and Aulostomoidea. 5. Fusion of parhypural to centrum and hypurals (character 139). In Gasterosteiformes, the parhypural is fused to the centrum and hypurals. This character is reversed in Centriscidae and Aulostomidae. 6. Fusion of hypurals to centrum (character 140). In Gasterosteiformes, all the hypurals are fused to each other and to the centrum. This character is reversed in Aulostomidae. The last two characters are widely found in other percomorphs, e.g., Cyprinodontiformes, Cottoidei, Callionymidae, Creedidae, and Triacanthidae (Fujita, 1990).

Pietsch (1978) argued that hypoptychids are closer to aulorhynchids than aulorhynchids to gasterosteids and placed Hypoptychidae and Aulorhynchidae in the superfamily Aulorhynchoidea. Ortei et al. (pers. com., 1992, cited in Nelson (1994)), based on molecular data suggested that *Aulichthys japonicus* and Gasterosteidae form a monophyletic group with their sister group being *Aulorhynchus flavidus*. Some authors (e.g., Eschmeyer, 1990) combine Aulorhynchidae and Gasterosteidae. Johnson and Patterson (1993) stated that with the inclusion of Hypoptychidae, there is little evidence to support monophyly of Gasterosteiformes. However, they retained Hypoptychidae with Gasterosteiformes and argued that it is closer to *Aulichthys japonicus* and concluded that Aulorhynchidae and probably Gasterosteoidei are paraphyletic groups. Orr (1995) also believed that there was little evidence to support monophyly of Gasterosteiformes with the inclusion of Hypoptychidae and removed Hypoptychidae from Gasterosteiformes and regarded it as a relative of atherinomorphs. However, his study showed that *Aulorhynchus flavidus* and *Aulichthys japonicus* are the closest relatives and aulorhynchids are the sister group of gasterosteids. I accept his conclusion and treat Aulorhynchidae as a monophyletic group. Based on the phylogenetic analysis (Fig. 9.1) and synapomorphies listed above, I believe Hypoptychidae should be included in Gasterosteiformes. However, Gasterosteoidei will be polyphyletic with the inclusion of Hypoptychidae, thus Hypoptychidae should be treated as a basal gasterosteiforms in its own suborder, Hypoptychoidei.

Gasterosteoidei and Syngnathoidei share eight synapomorphies (characters 1, 8, 37, 41, 53, 54, 93, and 138 in the previous section). Orr (1995) defended the monophyly of his Gasterosteiformes (Hypoptychidae and Indostomidae excluded) by one presumably unambiguous character, condition of the occipital condyle. According to him only the basioccipital facet forms the articular surface of the condyle and exoccipital condyles are absent, but exoccipital facets are present, to which ligaments from the first vertebral articulating processes are attached. This condition differs from that of other taxa such as Cyprinodontiformes in that, in these taxa, the articulating processes are ventrolateral to the exoccipital, whereas it is dorsomedial in Gasterosteiformes. Although this is true for Syngnathoidei (except Indostomidae), the condition is different in Gasterosteoidei as discussed in character 120. Thus this character is another synapomorphy of Syngnathoidei with a reversal in Indostomidae.

Monophyly of Gasterosteoidei (Aulorhynchidae and Gasterosteidae) is supported by nine synapomorphies. 1. Frontal meets parasphenoid lateral process (character 14). This character is also independently gained in Syngnathidae, Hexagrammidae, and Agonidae. 2. Palatine head is conical (character 34). Among the studied taxa, this character is unique to this group. 3. Quadrate shaft is much longer than quadrate body (character 40). This character is reversed in derived Gasterosteidae and independently gained in Syngnathoida. 4. Symplectic bears an anteriorly bifurcated flange (character 42). Among the studied taxa, this character is unique to this group. 5. Ectocoracoid is present (character 96). An ectocoracoid is also present in Aulostomoidea, however, the ectocoracoid of Aulostomoidea is elongated and different from that of Gasterosteoidei and I interpret it as an independent gain. 6. Pelvic plates are joined by a suture (character 105). This character is also independently gained in Mugiliformes, Hexagrammidae, and Agonidae. 7. Posterior basals present (character 114). Among the studied taxa, this character is unique to this group. 8. One anal spine present (character 119). Atherinomorphs and percopsiforms also bear one anal spine. 9. Exoccipital condyle consists only of basioccipital and the first centrum lacks any facets that articulate with exoccipital (character 120). Among the studied taxa, this character is unique to this group.

Monophyly of Syngnathoidei is supported by seven characters. 1. Absence of intercalar (character 16). The intercalar is also lost independently in Cyprinodontiformes, Synbranchiformes and Dactylopteridae. 2. Absence or reduction of the premaxillary ascending process (character 26). The premaxillary ascending process is also independently reduced or lost in Myctophiformes, Stephanoberyciformes, Atherinomorpha Mugiliformes, and Agonidae. In Atherinomorpha and Mugiliformes there is no distinct ascending process, but the condition is different from others and the broad articular process might represent fused ascending and articular processes. 3. Absence of the uncinate process on epibranchials 3 and 4 (character 73). The uncinate process on epibranchials 3 and 4 are also independently lost in Aulopiformes. 4. Lophobranch gill filament with skeleton fused basally (character 82). This character is reversed in Macroramphosidae and Aulostomoidea. 5. Absence of the neurohypophyses (character 129). This character is reversed in Macroramphosidae and Aulostomoidea. 6. Absence of the pleural ribs (character 134). Pleural ribs are also lost independently in Dactylopteridae and Agonidae. 7. Epurals are absent or only one (character 148). Synbranchiforms also have one or no epural.

There is a general agreement on the monophyly of Syngnathoidea (Syngnathidae and Solenostomidae), Aulostomoidea (Aulostomidae and Fistulariidae), and Centriscoidea (Macroramphosidae and Centriscidae) (Johnson and Patterson, 1993; Nelson, 1994; Orr, 1995; Pietsch, 1978). However, monophyly, relationships, and composition of Syngnathoida are subject to disagreement. Pietsch (1978) regarded Pegasidae as the sister group of Syngnathoidea and defended his placement on the basis of Pegasidae being clearly intermediate between Gasterosteoidei and Syngnathoidei. He listed seven characters to support his conclusion. 1. Snout development and condition of the nasal. 2. Retention of parietal. 3. Retention of three infraorbitals. 4. Presence of a dorsal strut joining anterior and posterior ceratohyals. 5. Reduction in branchial arches. 6. Presence of two pairs of pleural ribs. Johnson and Patterson (1993) argue that these are intermuscular bones, not pleural ribs. 7. Retention of support for a spinous dorsal fin. Johnson and Patterson (1993), on the basis of structure of gill filaments, argued that indostomids and pegasids are most closely related to Syngnathoidea. Orr (1995) excluded Indostomidae from Gasterosteiformes, but placed Pegasidae as the sister group of Syngnathoidea. My analysis indicates that the lophobranch structure of gill filaments is a plesiomorphic feature in Syngnathoidei and its presence in Syngnathoidea is a reversal. Placing Pegasidae as the sister group of Syngnathoidea requires three more steps, and placing Indostomidae as the sister Group of Syngnathoidea requires 16 more steps. Thus I believe that Indostomidae and Pegasidae are best interpreted as basal Syngnathoidei.

Monophyly of Syngnathoida is supported by a decay value of 2 (Fig. 9.2), bootstrap (Fig 9.3), and the following six synapomorphies. 1. Vomer located superficially anteriorly (character 7). 2. Prootic and exoccipital widely separated by pterotic (character 17). 3. Metapterygoid located anterior to the orbit (character 38). 4. Quadrate shaft bears a deep dorsal flange (character 39). Among the studied taxa, these four characters are unique to this group. 5. Quadrate shaft much longer than quadrate body (character 40). This character in also independently gained in Gasterosteoidei. 6. Urohyal blade incised posteriorly (character 57). This character is reversed in syngnathids and aulostomids and independently gained in Beloniformes.

Monophyly of Syngnathoidea + Aulostomoidea is also well supported by decay analysis (decay value of 7), bootstrap (96%), and the following four synapomorphies. 1.

Absence of nasals (character 1). This character is reversed in Aulostomidae. 2. Presence of the exoccipital elongated posterior process (character 23). This character is reversed in Syngnathidae. 3. Absence of epibranchial 4 (character 75). Among the studied taxa, this character is unique to this group. 4. Actinosts are strongly hourglass-shaped (character 97). This character is independently gained in Scorpaenidae and Hexagrammidae.

Systematic position of Dactylopteridae

The family Dactylopteridae was placed with Scorpaeniformes at its inception by Lacepéde (1803), Regan (1913) treated it as a suborder, and Berg (1947) as an order close to Pegasiformes. Pietsch (1978), based on several similarities between dactylopterids and gasterosteiforms, suggested the possibility of relationship of dactylopterids and gasterosteiforms. Lauder and Liem (1983) treated Dactylopteridae as an order and placed it in a trichotomy with Gasterosteiformes and their higher Percomorpha. Washington et al. (1984) and Eschmeyer (1990) considered the family Dactylopteridae as a member of Scorpaeniformes. Johnson and Patterson (1993) reevaluated the position of the family Dactylopteridae and concluded that it did not belong to either Gasterosteiformes or Scorpaeniformes and placed it in its own order in a polychotomy with Scorpaeniformes, Perciformes, Pleuronectiformes, and Tetraodontiformes. Orr (1995) reviewed different hypotheses of relationships for Dactylopteridae and based on the configuration of occipital-vertebral articulation, suborbital stay, presence of a parietal sensory canal, and similarity of caudal skeleton, concluded that Dactylopteridae should remain in Scorpaeniformes. My study confirms his conclusion (Fig. 9.1); the family Dactylopteridae is shown as a member of Scorpaeniformes and sister group of Agonidae. Monophyly of Scorpaeniformes is supported by three Synapomorphies. 1. Infraorbital 3 with a posterior strut (suborbital stay) to preopercle (character 11). 2. Subopercle with a posterior process (character 51). 3. Fusion of scapula and the first actinost (character 94). This character is also independently gained in some Syngnathoidei. The sister group relationship of Dactylopteridae and Agonidae is highly supported by branch support indices (Figs. 9.2 and 9.3) and two synapomorphies: Absence of pleural ribs and presence of bony scutes. These two characters are also found in Syngnathoidei. Other possible synapomorphies are characters 12, 45, 90, 148, and 149 (section 9). However, phylogenetic relationships of Dactylopteridae within Scorpaeniformes and its sister-group relationship with Agonidae and Cottoidei need further research. Monophyly and phylogenetic relationships of Scorpaeniformes and Perciformes also need more detailed studies.

Character evolution and implications of the new phylogeny

Gasterosteiformes, especially Syngnathoidei, are highly specialized fishes. Among the 151 studied characters, 35 character states (23%) are found only in this order among the studied taxa (characters 1, 7, 8, 15, 17, 19, 22, 23, 33, 38, 39, 40, 41, 48, 52, 53, 55, 63, 66, 69, 75, 82, 84, 93, 96, 99, 100, 114, 116, 120, 123, 125, 126, 129, and 135). Most of these characters are unambiguously resolved on the phylogenetic tree, but some are equivocal and need further discussion as follows. It takes the same number of steps to lose the parietal (character 15) in basal Syngnathoidei and gain it independently in Pegasidae, Centriscidae, and Fistulariidae or to lose it independently four times in Indostomidae, Macroramphosidae, Syngnathoidea, and Aulostomidae. Since a loss may occur under selection pressure alone (verses selection pressure and genetic rearrangement for a gain), it may be more likely than a gain, and I assume these groups independently lost the parietal. The exoccipital elongated posterior process (character 23) is gained in Syngnathoidea and Aulostomoidea and lost in Syngnathidae, though it would be as parsimonious to assume independent gains in Aulostomoidea and Solenostomidae, I accept the former hypothesis. Although it is equally parsimonious to assume independent losses of the basibranchials (character 66) in Pegasidae and Syngnatha or a gain in the common ancestor of Pegasidae and Syngnatha and a reversal in Centriscoidea, I assume the former prevailed. Lophobranch gill filament with skeleton fused basally (character 82) is restricted to Syngnathoidei and is plesiomorphic for this group. However, it is equally parsimonious to assume three independent gains in Indostomidae, Pegasidae, and Syngnathoidea or a gain in the ancestor of Syngnathoidei and two losses in Aulostomoidea and Centriscoidea; I assume the former prevailed. In the following, character evolution in some phylogenetically significant character complexes of Acanthomorphs and Gasterosteiformes are discussed.

Jaws- Euteleosts are characterized by a protrusible jaw, which is intensified by development of the premaxillary process in members of higher taxa (Rosen, 1985). However, the ascending process is secondarily reduced or lost in several groups including Syngnathoidei. Most Syngnathoidei have an elongated snout and a small mouth at the end of the tube-like snout. The elongated vomer extends forward superficially and fills most of the space in the ethmoid region and leaves little or no space for a well developed ascending process. This modification of the jaws caused a secondary reduction or loss of the process in this group. In Mugiliformes and Atherinomorpha, probably due to the mode of feeding and shortening of the snout, the ascending process is lost or fused to the articular process. However, there is a disagreement on the homology of the premaxillary process. The ascending process is generally defined as the process that is in contact with rostral cartilage and the articular process as the one in contact with the maxilla (Parenti, 1984). Greenwood et al. (1966) believed that atherinomorphs do not bear a true ascending process and alternatively, Alexander (1967) believed that the process is the ascending process. Parenti (1984), based on presence of distinct ascending and articular processes in some primitive atherinomorphs such as Bedotiidae and Melanotaeniidae, argued that the process is the ascending process and the articular process is secondarily lost in other atherinomorphs. In Melanotaeniidae (Fig. 3.5) and Bedotiidae (Stiassny, 1990: fig. 6), there are large postmaxillary and articular processes but not any other distinct process. In Phallostethidae (Parenti, 1984: fig. 2), there is a relatively distinct long process but as in Atherinopsinae (Dyer, 1997), it is not positioned at the proximal end of the premaxilla (unlike in other acanthopterygians) and it is in contact with the maxilla, not the rostral cartilage. Besides, this process in Phallostethidae, as derived atheriniforms (Dyer and Chernoff, 1996), might be secondary. Although differentiated ascending and articular process are not found in the ontogeny of atherinomorphs (Langille and Hall, 1987), it is conceivable that the ascending and articular processes are fused together in some atherinomorphs; however, the configuration of the upper jaw in Mugiliformes and Atherinomorpha is different from that of other acanthopterygians.

Paired fins- Position and connection of the pelvic bones to each other and to the pectoral girdle is another significant feature of Acanthomorpha. Presence of a ventrally displaced anterior process is a diagnostic character for Acanthopterygii less Stephanoberyciformes; however, in Gasterosteiformes and most Atherinomorpha the process is lost. In Gasterosteidae, probably the process is absorbed in the main plate, but in other Gasterosteiformes the process is obviously lost. In some atherinomorphs, a medial process is developed and the anterior process is borne on that and it is not displaced ventrally. Based on the general configuration of these processes, the anterior process of Atherinomorpha might not be homologous to that of other Acanthopterygii. Presence of a pelvic spine is also a characteristic of acanthopterygians, but it is lost in more derived Gasterosteiformes and Atherinomorpha. In Gasterosteiformes, spine loss is probably related to elongation of the body and the general trend in reduction of the pelvic girdle. Stiassny and Moore (1992), Stiassny (1993), and Parenti (1993), proposed the presence of a ligamentous attachment between the ventral postcleithrum and the pelvic girdle as a synapomorphy for Acanthomorpha. In Atherinomorpha, the postcleithrum does not connect to the abdominally displaced pelvic girdle, but a pleural rib connects to the small lateral process of the pelvic girdle. This feature is considered a synapomorphy for Atherinomorpha. In Mugiliformes, the ventral postcleithrum ligamentously connects to the pelvic lateral process. Stiassny (1993) regarded this feature as a uniting character for Mugiliformes and Atherinomorpha and argued that if abdominal displacement of the pelvic girdle is secondary in atherinomorphs, then primitively the primary association of the pelvic lateral process was to the ventral postcleithrum. In Myctophiformes, the pleural ribs are associated with the pelvic girdle cartilaginously and is different from the ligamentous attachment of ribs in Atherinomorpha. In Gasterosteiformes, only in Macroramphosidae does the ventral postcleithrum come in close contact with the pelvic girdle and ligamentously connects to the posterior surface of the bent anterior part. All other Gasterosteiformes either lack the postcleithra or the pelvic girdle is abdominal and widely separated from the pectoral girdle. In derived gasterosteids, the pelvic girdle is ligamentously bound to the ectocoracoid. I interpret the loss of the connection between the pelvic girdle and postcleithra as secondary and the association of those in Macroramphosidae as an autapomorphy. In higher percomorphs, the central part of the pelvic girdle is inclined dorsally and directly or ligamentously attached to the cleithrum or coracoid. In Zeiformes, the pelvic girdle is bent dorsally and positioned between the cleithra, but unlike higher percomorphs, it is not strongly bound to the cleithra. There is also a tendency to lose the extrascapula and to lose or reduce the supracleithrum in Smegmamorpha.

Caudal skeleton- Primitively in basal Acanthomorpha and Acanthopterygii, the caudal elements are autogenous and several intercaudal and postcaudal cartilages support these isolated elements. Basal groups usually have six autogenous hypurals, three epurals, two pairs of autogenous neurals, autogenous ural centrum 2, and autogenous haemal and neural spines on the last centra. In some basal groups such as Myctophidae, many of the caudal elements are fused, because of the presence of primitive conditions in related taxa (Neoscopelidae), the fusion in such a groups should be regarded as secondary and independent from that in higher taxa. In higher groups, there is a tendency for the elements to fuse together and to the centra and caudal cartilage are lost due to lack of function. In specialized groups such as Gasterosteiformes and some Scorpaeniformes, all the elements are fused and the caudal cartilage is lost.

Implications and classification- If the monophyly of Smegmamorpha and its interrelationships as depicted in Fig. 9.1 is accepted, has several implications for zoogeography, behavior, paleontology, and classification. Mugiliformes are mainly marine or brackish water and distributed in coastal areas of all tropical and temperate seas. Atherinomorphs are mostly freshwater but some are brackish or marine and distributed around the globe. Synbranchiformes are mostly freshwater and are distributed in tropical and subtropical regions of Africa, Asia, and Central and North America. Gasterosteiformes are freshwater, brackishwater or marine and are distributed in coastal areas of all continents. However, elassomatids are freshwater and restricted to the eastern United States. This implies that ancestor of synbranchiforms and gasterosteiforms was freshwater and that secondarily basal gasterosteiforms became marine. The basal gasterosteiforms (hypoptychoids) are marine and primarily distributed around Japanese islands. Within gasterosteoids, aulorhynchids are marine and *Aulichthys japonicus* is found in Japanese waters and *Aulorhynchus flavidus* in the eastern North Pacific. However, gasterosteids include marine (*Spinachia spinachia* in Atlantic of northern Europe), marine-brackishwater (*Apeltes quadracus* in Atlantic coast of central North America), anadromous-freshwater (*Gasterosteus spp.* and *Pungitius spp.* in Atlantic and Pacific coastal areas of North America and Eurasia), and freshwater fishes (*Culaea inconstans* in North America). Thus it should be assumed that gasterosteiforms are basically marine and secondarily some members such as sticklebacks and Indostomids penetrated the freshwater.

Reproductive behaviors such as nest guarding in Gasterosteoidei might be another feature gained in the common ancestor of Elassomatidae, Synbranchiformes, and Gasterosteiformes. The fossil record for Elassomatidae and Synbranchidae is recent, but fossil Gasterosteiformes are known from the Eocene (Carroll, 1988); with the phylogenetic relationships of Elassomatidae, Synbranchiformes, and Gasterosteiformes as presented (Fig. 9.1), it is expected to find older fossils for Elassomatidae and Synbranchiformes.

A new classification is needed to reflect the new phylogeny. Although Johnson and Patterson (1993) presented a relatively similar phylogenetic scheme (Fig. 1.2) and proposed the name Smegmamorpha for the clade consisting of Mugiliformes, Atherinomorpha, Elassomatidae, Synbranchiformes, and Gasterosteiformes, they did not propose a new classification for other Percomorpha and subgroups of Smegmamorpha. I propose the following classification for Percomorpha (see Fig. 9.1).

- Series Percomorpha
  - Subseries Smegmamorphei (Smegmamorpha of Johnson and Patterson (1993))
    - Infraseries Atherinomorphea
      - Order Mugiliformes
      - Order Atheriniformes
      - Order Beloniformes
      - Order Cyprinodontiformes
    - Infraseries Gasteromorphea
      - Order Elassomatiformes
      - Order Synbranchiformes
      - Order Gasterosteiformes
  - Subseries Percomorphei
    - Order Perciformes

Order Scorpaeniformes
Order Pleuronectiformes
Order Tetraodontiformes

Conclusions

1. Monophyly of Acanthomorpha, Acanthopterygii, Percomorpha, and Smegmamorpha is supported.

2. To reflect the new phylogeny in the classification of Percomorpha, it is suggested to divide the series Percomorpha into two subseries; Smegmamorphei and Percomorphei. Smegmamorphei consist of two infraseries: Atherinomorphea (Mugiliformes, Atheriniformes, Beloniformes, and Cyprinodontiformes) and Gasteromorphea (Elassomatiformes, Synbranchiformes, and Gasterosteiformes). Percomorphei consists of four orders: Perciformes, Scorpaeniformes, Pleuronectiformes, and Tetraodontiformes.

3. Mugiliformes and Atherinomorpha are sister-groups.

4. The family Elassomatidae, which should be recognized at ordinal level (Elassomatiformes), are the sister group of Synbranchiformes and Gasterosteiformes.

5. Synbranchiformes are the sister group of Gasterosteiformes.

6. Monophyly of Gasterosteiformes (including Hypoptychidae and Indostomidae) is supported.

7. Based on the phylogenetic analysis and synapomorphies provided for the subgroups, I recognize three suborders in Gasterosteiformes: Hypoptychoidei, Gasterosteoidei, and Syngnathoidei.

8. Dactylopteridae is a member of Scorpaeniformes and, within the studied taxa, the sister-group of Agonidae. Although monophyly of Scorpaeniformes is supported, it is nested within Perciformes and branch support indices do not strongly support its monophyly.

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