Research Article

Eurypterygii caudal skeleton

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Abstract: The osteology of the caudal skeleton in representatives of 41 genera in 39 families of eurypterygian fishes was studied. 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). 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, 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 some Scorpaeniformes, all the elements are fused and the caudal cartilage is lost.

Keywords: Bones, Cartilage, Eurypterygians, Tail, Osteology, Skeleton.

Introduction

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.

Osteology still plays an important role in the systematic study of fishes (Keivany 1996, 2000, 2014a,b,c,d, 2017; Keivany & Nelson 1997, 1998, 2004, 2006; Nasri et al. 2014; Jalili et al. 2015). Eurypterygian fishes composed of several orders including Aulopiformes, Myctophiformes Lampridiformes, Polymixiiformes, Percopsiformes, Zeiformes, Holocentriformes, Trachichthyiformes, Beryciformes, Mugiliformes, Atheriniformes, Beloniformes, Cyprinodontiformes, Synbranchiformes, Syngnathtiformes, Perciformes, Scorpaeniformes, Caproiformes, Pleuronectiformes and Tetraodontiformes (Nelson et al. 2016). The diversity of caudal skeleton as the main locomotor apparatus is described in this study. Each section consists of a description of osteology of the families. The aims of these sections are to describe and illustrate the variable and significant features of the taxa at higher levels

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Table 1. Classification of the studied taxa based on Nelson et al. (2016).

No.	Order	Family	Species	Lot No.	Size (SL, mm)
1	Aulopiformes	Synodontidae	*Synodus synodus*	UAMZ 1806	147
2	Myctophiformes	Myctophidae	*Myctophum* sp.	UAMZ 2689	60
3	Lampridiformes	Veliferidae	*Velifer hypselopterus*	AMS 21839005	101
4		Trachipteridae	*Trachipterus altivelis*	CAS 24297	85
5	Polymixiiformes	Polymixiidae	*Polymixia lowei*	USNM 159300	115
6	Percopsiformes	Percopsidae	*Percopsis omiscomaycus*	UAMZ 2048	55
7	Zeiformes	Grammicolepididae	*Xenolepidichthys dalgleishi*	USNM 322673	68
8	Holocentriformes	Holocentridae	*Sargocentron vexillarium*	UAMZ 5075	44
9	Trachichthyiformes	Monocentridae	*Monocentris* sp.	UAMZ 7854	92
10	Beryciformes	Stephanoberycidae	*Stephanoberyx monae*	USNM 304353	92
11		Rondeletiidae	*Rondeletia loricata*	AMS 20523001	37
12	Insera Sedis	Pomacentridae	*Stegastes partitus*	UAMZ 3640	34
13	Mugiliformes	Mugilidae	*Mugil* sp.	UAMZ 5125	101
14	Atheriniformes	Melanotaeniidae	*Melanotaenia* sp.	UAMZ 3526	51
15		Atherinidae	*Allanetta harringotonensis*	UAMZ 2673	58
16	Beloniformes	Hemiramphidae	*Arrhamphus sclerolepis*	UAMZ 3523	103
17		Belonidae	*Pseudotylosurus* sp.	UAMZ 8165	173
18	Cyprinodontiformes	Aplocheilidae	*Rivulus hartii*	UAMZ 6660	47
19		Cyprinodontidae	*Cyprinodont nevadensis*	UAMZ 3114	34
20	Synbranchiformes	Mastacembelidae	*Macrognathus aculeatus*	UAMZ 1855	119
21	Syngnathiformes	Pegasidae	*Pegasus volans*	UAMZ 4616	99
22		Solenostomidae	*Solenostomus paradoxus*	AMS 17111002	51
23		Syngnathidae	*Syngnathus griseolineatus*	UAMZ 3469	272
24		Aulostomidae	*Aulostomus valentini*	CAS 11979	139
25		Fistulariidae	*Fistularia petimba*	UAMZ 6348	158
26		Macroramphosidae	*Macroramphosus scolopax*	USNM 344398	99
27		Centriscidae	*Aeoliscus strigatus*	UAMZ 4048	89
28		Dactylopteridae	*Dactylopterus volitans*	UAMZ 2633	74
29	Perciformes	Centrarchidae	*Lepomis gibbosus*	UAMZ 7715.4	40
30			*Elassoma zonatum*	UAMZ 6920	30
31		Percidae	*Perca flavescens*	UAMZ 1244	54
32		Cirrhitidae	*Amblycirrhitus pinos*	UAMZ 3640	45
33	Scorpaeniformes	Scorpaenidae	*Sebastes caurinus*	UAMZ 3142	75
34		Hypoptychidae	*Hypoptychus dybowskii*	UAMZ 5550	80
35		Aulorhynchidae	*Aulichthys japonicus*	UAMZ 5542	47
36		Gasterosteidae	*Gasterosteus aculeatus*	UAMZ 3894	58
37			*Spinachia spinachia*	UAMZ 6582	53
38		Indostomidae	*Indostomus paradoxus*	CAS 64017	25
39		Hexagrammidae	*Hexagrammos decagrammus*	UAMZ 3190	50
40		Agonidae	*Xeneretmus latifrons*	UAMZ 3196	95
41	Caproiformes	Caproidae	*Antigonia* sp.	USNM 266901	37

Materials and Methods
Some 100 specimens from representatives of the taxa were prepared 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 compari-son among the taxa. Some 42 genera represent-ing 41 families were studied. The specimens were mostly obtained from the University of Alberta Museum of Zoology (UAMZ), four lots from the Smithsonian Institution (United States National Museum, USNM), three from Califor-nia Academy of Sciences (CAS), and three from Australian Museum at Sydney (AMS) (Table 1). The standard length in millimeters of specimens and their depository numbers are given in the caption of each figure. All the scale bars indicate 1mm. For more details refer to

Keivany (2000, 2014a,b,c,d, 2017) and Keivany & Nelson (2004, 2006).

Results

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 the entire cartilages posterior to the caudal elements (postneural spine, posthaemal spine, postepural, posthypural, postparhypural cartilage), and caudal cartilages to refer to both intercaudal and postcaudal cartilages.

AULOPIFORMES

Synodontidae (Fig. 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 *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 uro-

style 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 & 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.
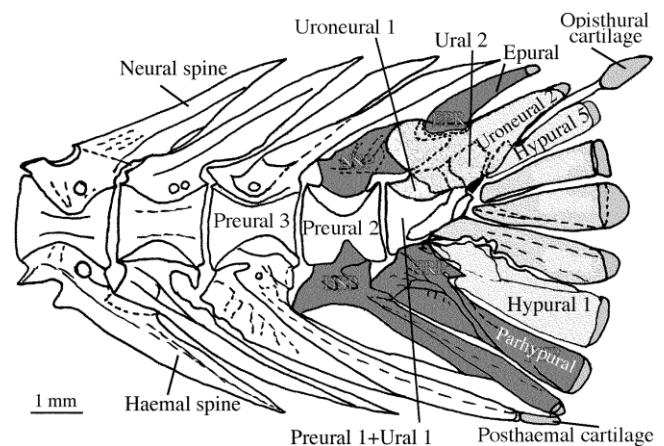

Fig. 1. Left lateral view of the caudal skeleton in *Synodus synodus* (UAMZ 1806, SL 147mm).

MYCTOPHIFORMES

Myctophidae (Fig. 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 cartilages and a pair of median caudal cartilages 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).
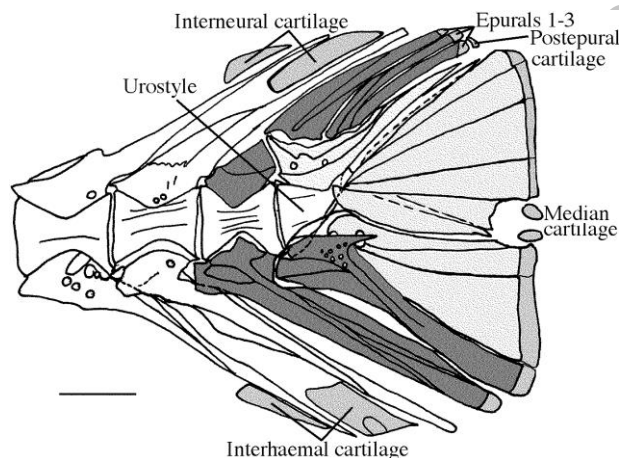
Fig. 2. Left lateral view of the caudal skeleton in *Myctophum* sp. (UAMZ 2689, SL 60mm).

LAMPRIDIFORMES

Veliferidae (Fig. 3). 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.
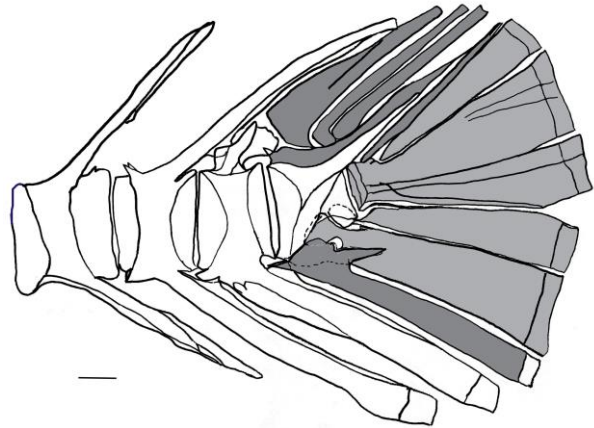

Fig. 3. Left lateral view of the caudal skeleton in *Velifer hypselopterus* (AMS 21839005, SL 101mm).

Trachipteridae (Fig. 4). 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

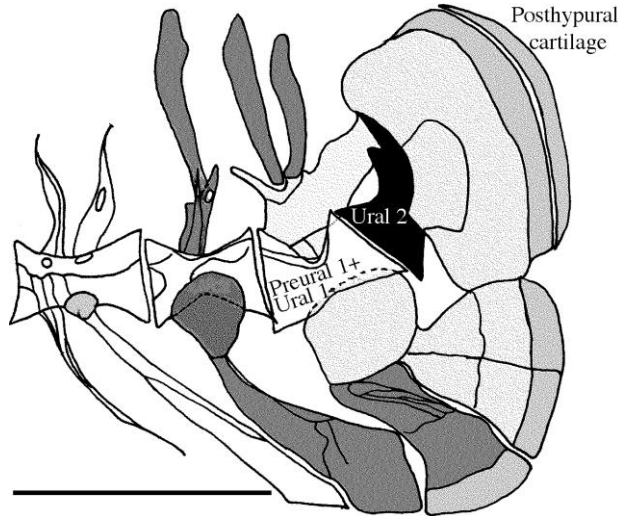parhypural are autogenous (Olney et al. 1993).

Fig. 4. Left lateral view of the caudal skeleton in *Trachipterus altivelis* (CAS 24297, SL 85mm).

POLYMIXIIFORMES
Polymixiidae (Fig. 5). 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.
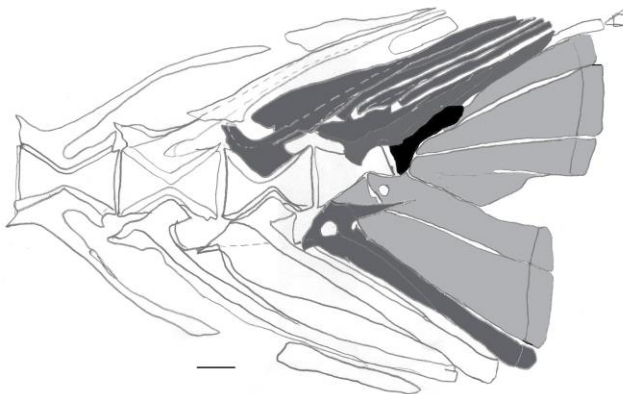
Fig. 5. Lateral view of the jaws in *Polymixia lowei* (USNM 159300, SL 115mm).

PERCOPSIFORMES
Percopsidae (Fig. 6). 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 & Patterson 1969).
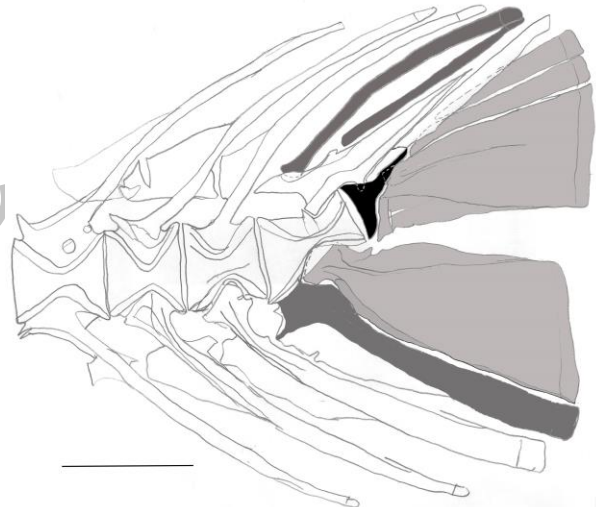

Fig. 6. Lateral view of the jaws in *Percopsis omiscomaycus* (UAMZ 2048, SL 55mm).

ZEIFORMES
Grammicolepididae (Fig. 7). 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.
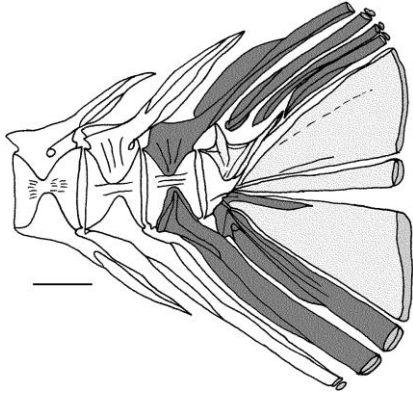
Fig. 7. Left lateral view of the caudal skeleton in *Xenolepidichthys dalgleishi* (USNM 322673, SL 68mm).

HOLOCENTRIFORMES

Holocentridae (Fig. 8). 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).

Fig. 8. Left lateral view of the caudal skeleton in *Sargocentron vexillarium* (UAMZ 5075, SL 44mm).

TRACHICHTHYIFORMES

Monocentridae (Fig. 9). 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.
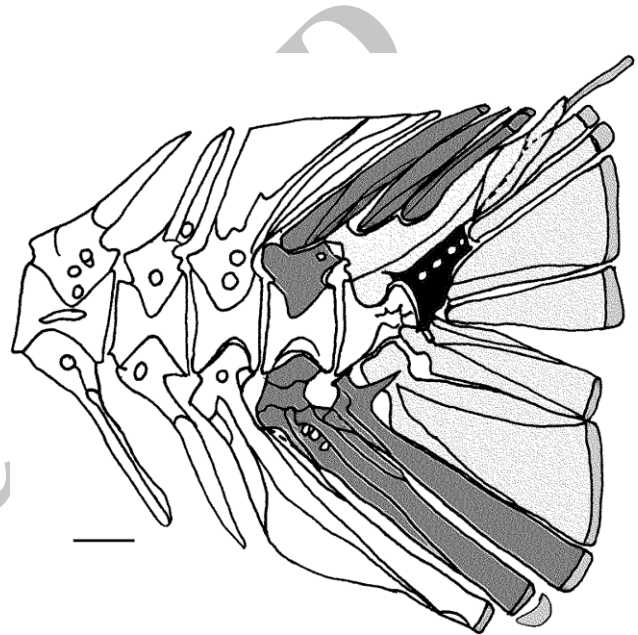

Fig. 9. Left lateral view of the caudal skeleton in *Monocentris* sp. (UAMZ 7854, SL 92mm).

BERYCIFORMES

Stephanoberycidae (Fig. 10). 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.

Fig. 10. Left lateral view of the caudal skeleton in *Stephanoberyx monae* (USNM 304353, SL 92mm).

Rondeletiidae (Fig. 11). 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).
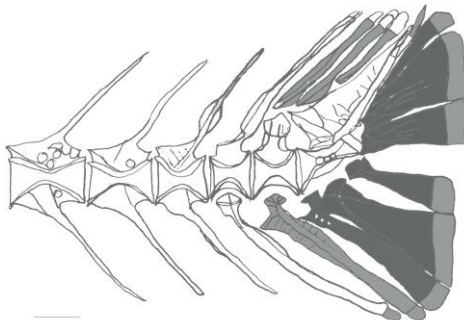
Fig. 11. Left lateral view of the caudal skeleton in *Rondeletia loricata* (AMS 20523001, SL 37mm).

<u>**INSERA SEDIS**</u>

Pomacentridae (Fig. 12). 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).
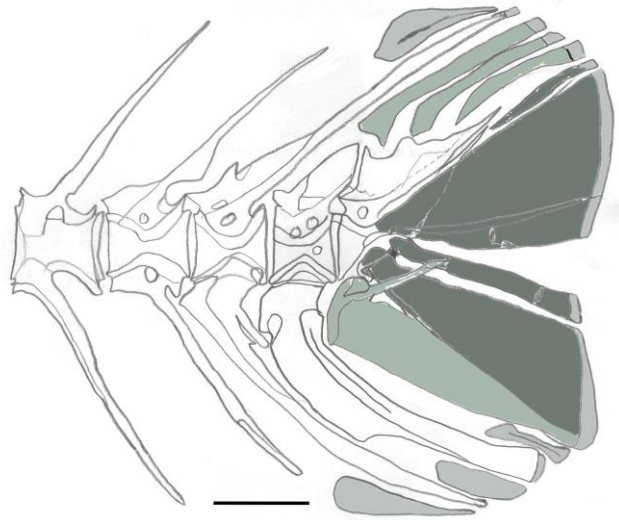

Fig. 12. Left lateral view of the caudal skeleton in *Stegastes partitus* (UAMZ 3640, SL 34mm).

<u>**MUGILIFORMES**</u>

Mugilidae (Fig. 13). 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 an urostyle. The hyporapophysis is well developed. The neural spine of preural 2 is short and fused. The haemal spine of preural 2 is autogenous. The intercaudal and postcaudal cartilages are present. In *Mugil cephalus* and *Liza carinata*, hypurals 3 and 4 are fused together and to urostyle (Fujita 1990).
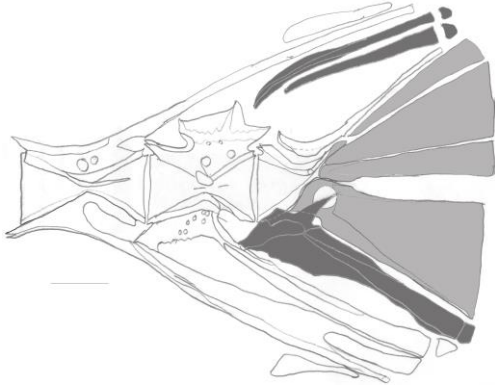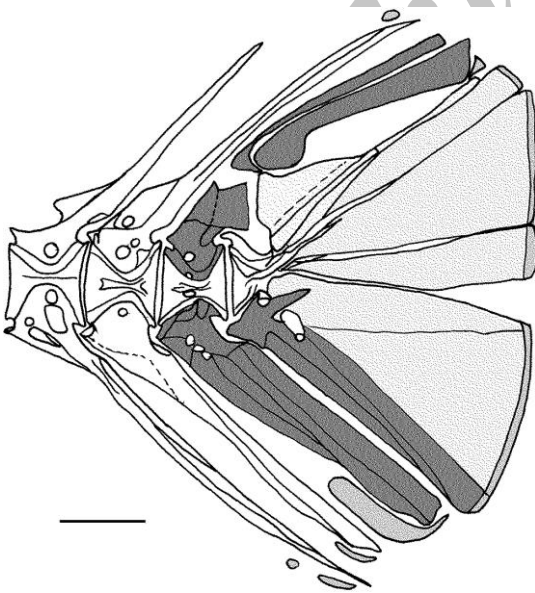
Fig. 13. Left lateral view of the caudal skeleton in *Mugil* sp. (UAMZ 5125, SL 101mm).

ATHERINIFORMES

Melanotaeniidae (Fig. 14). 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.

Fig. 14. Left lateral view of the caudal skeleton in *Melanotaenia* sp. (UAMZ 3526, SL 51mm).

Atherinidae (Fig. 15). 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).
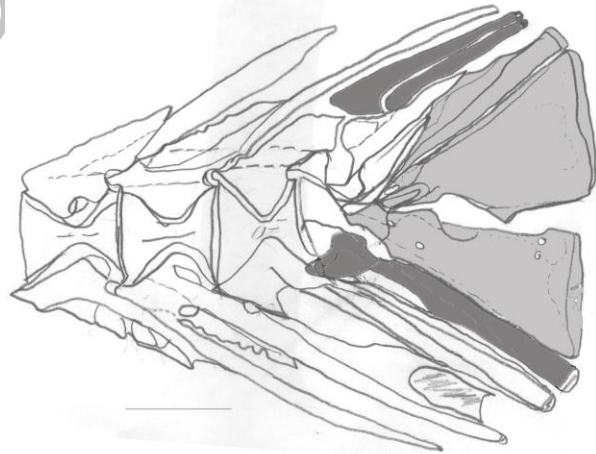

Fig. 15. Left lateral view of the caudal skeleton in *Allanetta harringotonensis* (UAMZ 2673, SL 58mm).

BELONIFORMES

Hemiramphidae (Fig. 16). 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 & 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).
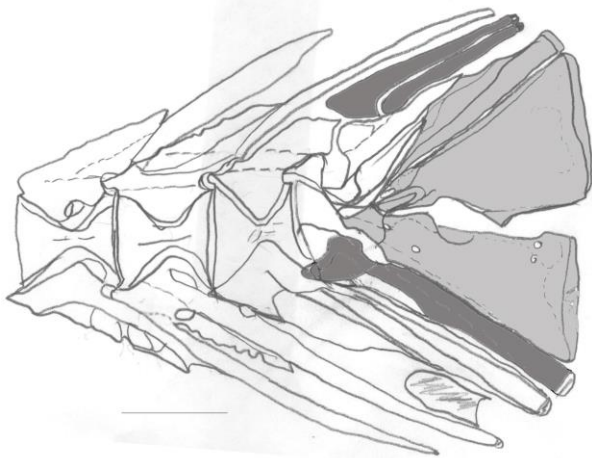

Fig. 16. Left lateral view of the caudal skeleton in *Arrhamphus sclerolepis* (UAMZ 3523, 103 mm).

Belonidae (Fig. 17). 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).

Fig. 17. Left lateral view of the caudal skeleton in *Pseudotylosurus* sp. (UAMZ 8165, SL 173mm).

CYPRINODONTIFORMES
Aplocheilidae (Fig. 18). 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).
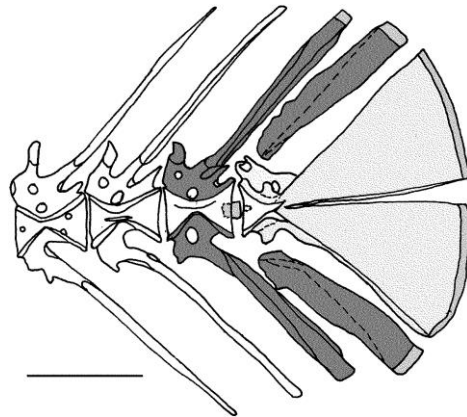

Fig. 18. Left lateral view of the caudal skeleton in *Rivulus hartii* (UAMZ 6660, SL 47mm).

Cyprinodontidae (Fig. 19). 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).
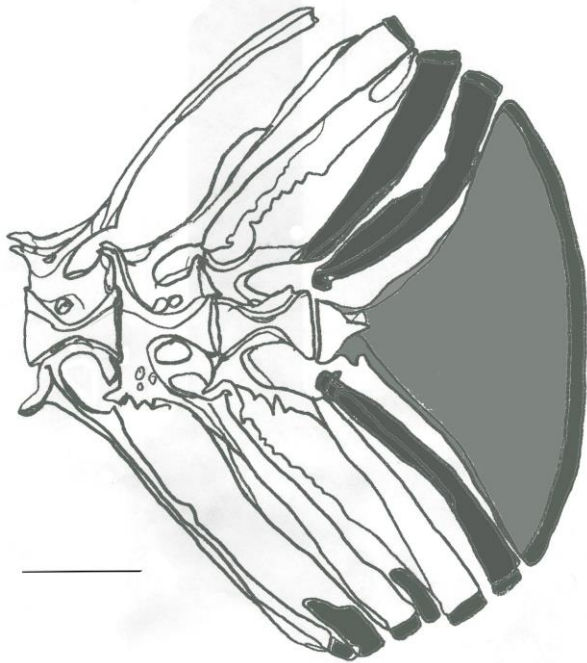
Fig. 19. Left lateral view of the caudal skeleton in *Cyprinodont nevadensis* (UAMZ 3114, 34mm).

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

Mastacembelidae (Fig. 20). 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, parhypural is fused to hypurals and uroneurals are one pair or absent (Travers 1984).
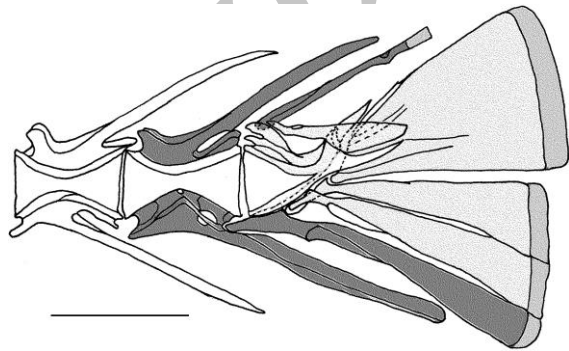

Fig. 20. Left lateral view of the caudal skeleton in *Macrognathus aculeatus* (UAMZ 1855, SL 119mm).

SYNGNATHIFORMES
Pegasidae (Fig. 21). 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.
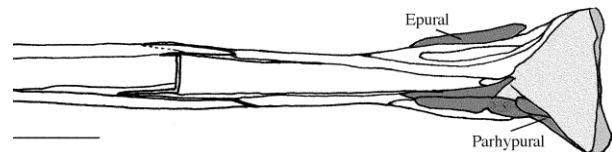

Fig. 21. Left lateral view of the caudal skeleton in *Pegasus volans* (UAMZ 4616, SL 99mm).

Solenostomidae (Fig. 22): 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.
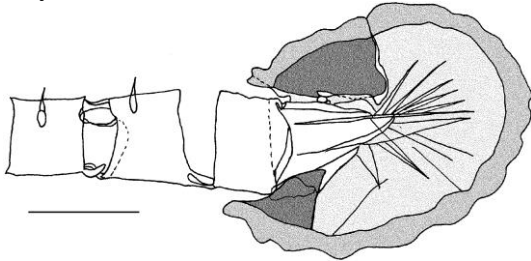

Fig. 22. Left lateral view of the caudal skeleton in *Solenostomus paradoxus* (AMS 17111002, SL 51mm).

Syngnathidae (Fig. 23): 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).
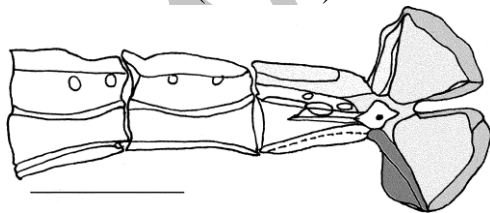

Fig. 23. Left lateral view of the caudal skeleton in *Syngnathus griseolineatus* (UAMZ 3469, SL 272mm).

Aulostomidae (Fig. 24). 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).
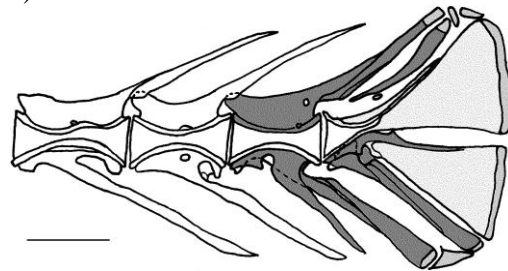

Fig. 24. Left lateral view of the caudal skeleton in *Aulostomus valentini* (CAS 11979, SL 139mm).

Fistulariidae (Fig. 25): 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.
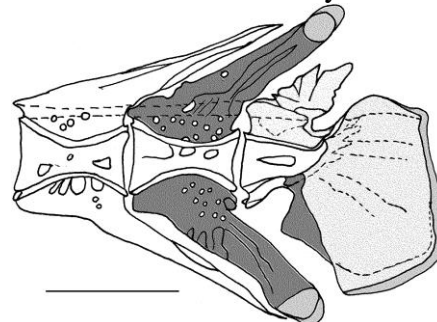

Fig. 25. Left lateral view of the caudal skeleton in *Fistularia petimba* (UAMZ 6348, SL 158mm).

Macroramphosidae (Fig. 26). 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.

Fig. 26. Left lateral view of the caudal skeleton in *Macroramphosus scolopax* (USNM 344398, SL99mm).

Centriscidae (Fig. 27). 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.
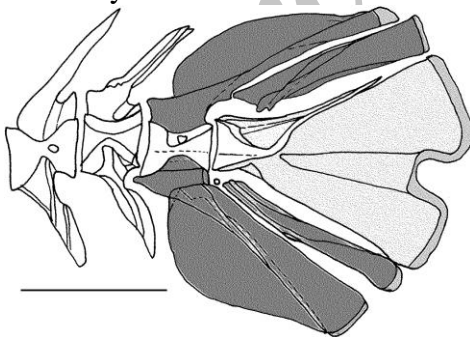

Fig. 27. Left lateral view of the caudal skeleton in *Aeoliscus strigatus* (UAMZ 4048, SL 89mm).

Dactylopteridae (Fig. 28). 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).
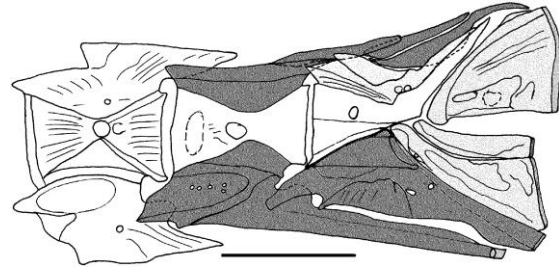

Fig. 28. Left lateral view of the caudal skeleton in *Dactylopterus volitans* (UAMZ 2633, SL 74mm).

PERCIFORMES
Centrarchidae (Fig. 29). 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.
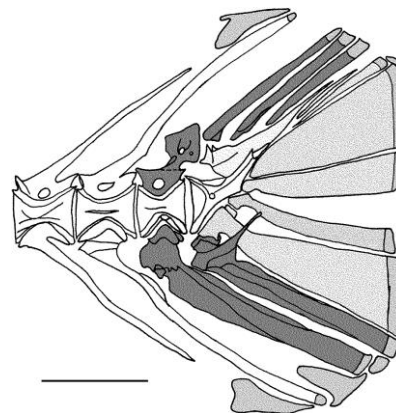

Fig. 29. Left lateral view of the caudal skeleton in *Lepomis gibbosus* (UAMZ 7715.4, SL 40mm).

In *Elassoma zonatum* (Fig. 30), 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.
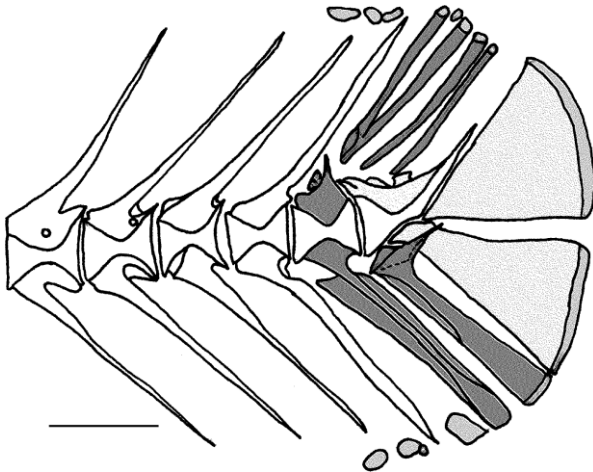

Fig. 30. Left lateral view of the caudal skeleton in *Elassoma zonatum* (UAMZ 6920, SL 30mm).

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 (Greenwood 1976; Mok 1983; Sasaki 1989; Fujita 1990; Hoese & Gill 1993; Gill & Mooi 1993; Westneat 1993; Gomon 1997; Doyle 1998).

Percidae (Fig. 31). 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.
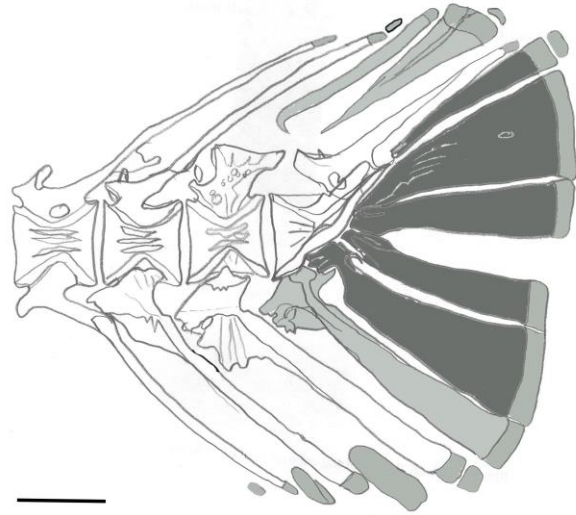

Fig. 31. Left lateral view of the caudal skeleton in in *Perca flavescens* (UAMZ 1244, SL 54mm).

Cirrhitidae (Fig. 32). 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.
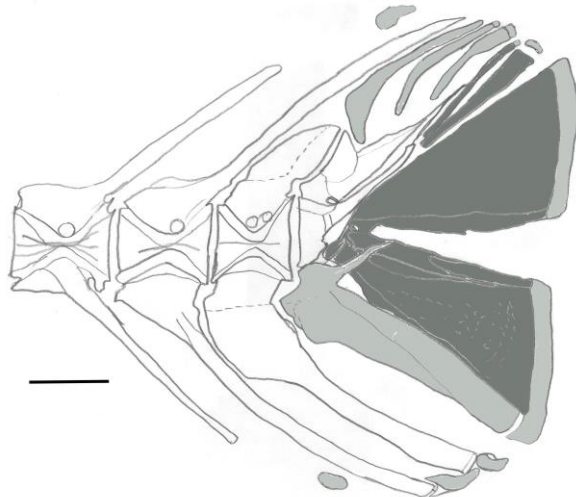

Fig. 32. Left lateral view of the caudal skeleton in *Amblycirrhitus pinos* (UAMZ 3640, SL 45mm).

SCORPAENIFORMES
Scorpaenidae (Fig. 33). 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).
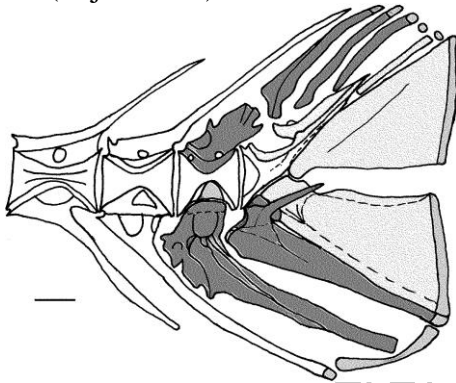

Fig. 33. Left lateral view of the caudal skeleton in *Sebastes caurinus* (UAMZ 3142, SL 75mm).

Hypoptychidae (Fig. 34). 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.

Fig. 34. Left lateral view of the caudal skeleton in *Hypoptychus dybowskii* (UAMZ 5550, SL 80mm).

Aulorhynchidae (Fig. 35). 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 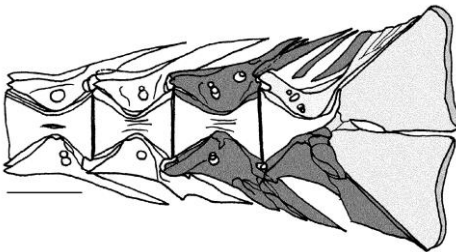preurals 2 and 3 are fused. The caudal cartilage is absent. In larvae there is a deep notch between the dorsal and ventral hypural plates (Orr 1995), but in adults it is present only in *Aulichthys japonicus*. In some specimens of *Aulichthys* there is only one epural (Bowne 1985).
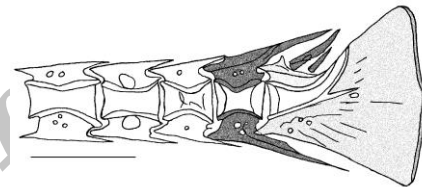

Fig. 35. Left lateral view of the caudal skeleton in *Aulichthys japonicus* (UAMZ 5542, SL 47mm).

Gasterosteidae (Figs. 36 & 37). The caudal skeleton consists of a single fused hypural plate which is fused to the urostyle, a fused parhypural, one epural (two in *Spinachia*, **Fig. 23**), 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 the urostyle. In *Spinachia* and juveniles of other genera two autogenous epurals are present (Orr 1995).
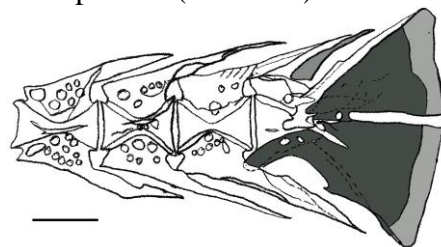

Fig. 36. Left lateral view of the caudal skeleton in *Gasterosteus aculeatus* (UAMZ 3894, SL 58mm).
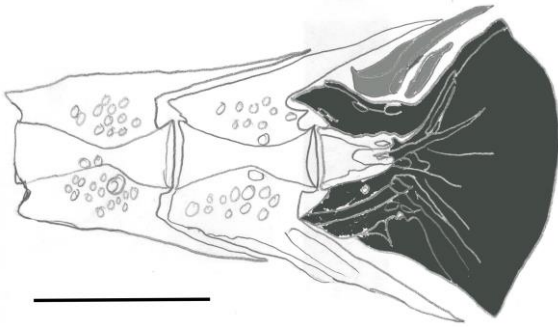
Fig. 37. Left lateral view of the caudal skeleton in *Spinachia spinachia* (UAMZ 6582, SL 53mm).

Indostomidae (Fig. 38). 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.
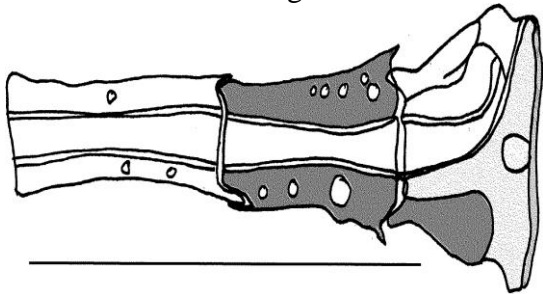

Fig. 38. Left lateral view of the caudal skeleton in *Indostomus paradoxus* (CAS 64017, SL 25mm).

Hexagrammidae (Fig. 39). 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).
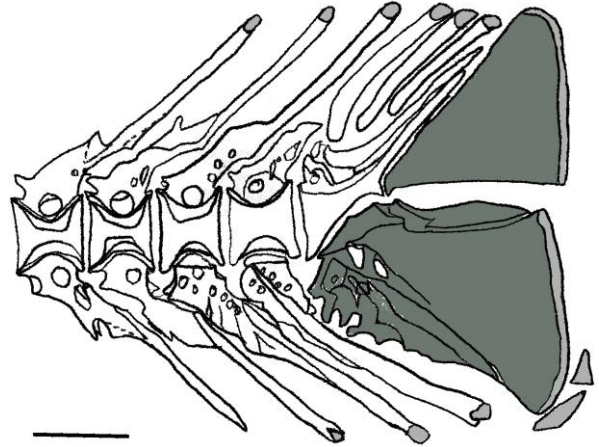

Fig. 39. Left lateral view of the caudal skeleton in *Hexagrammos decagrammus* (UAMZ 3190, SL 50mm).

Agonidae (Fig. 40). The caudal skeleton consists of a notched hypural plate fused to the urostyle, a fused parhypural, an 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 1985; 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).
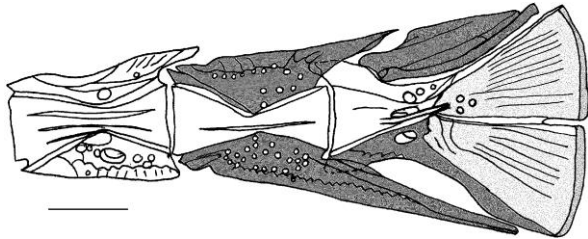

Fig. 40. Left lateral view of the caudal skeleton in *Xeneretmus latifrons* (UAMZ 3196, SL 95mm).

CAPROIFORMES
Caproidae (Fig. 41). 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).
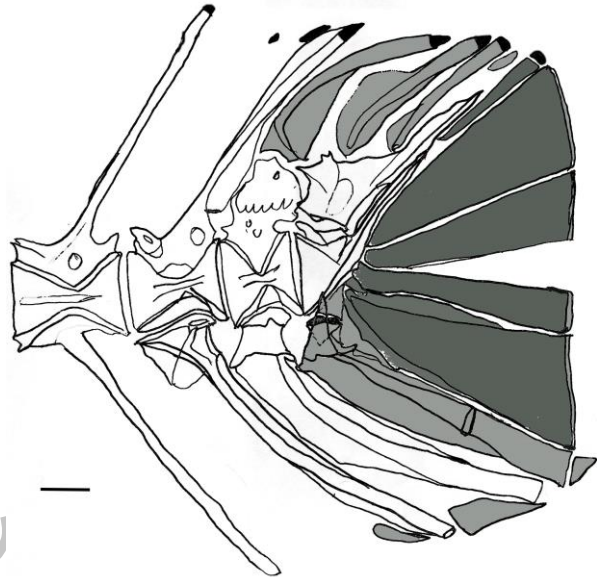

Fig. 41. Left lateral view of the caudal skeleton in *Antigonia* sp. (USNM 266901, 37mm).

Discussion & Conclusions
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 some Scorpaeniformes (Gasterosteidae) and Syngnathiformes, all the elements are fused and the caudal cartilage is lost.

Acknowledgements

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مقاله پژوهشی

اسکلت استخوانی باله دمی پهن‌بالگان (Eurypterygii)

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چکیده: استخوان‌شناسی اسکلت باله دمی نمایندگان ۴۱ جنس از ۳۹ خانواده پهن‌بالگان مورد بررسی قرار گرفت. اسکلت باله دمی پهن‌بالگان شامل پنج یا شش دمپره، زیردمپره، یک تا سه رودمپره، یک یا دوجفت دمکمانک، جسم دم‌مهره ۱ و ۲، آخرین جسم مهره پیش‌دمی و خارهای عصبی و خونی مرتبط و شعاع‌های اصلی و فرعی می‌باشد. پهن‌بالگان همانند سایر ماهیان استخوانی عالی دارای اسکلت دمی دوگانه (دو جسم دم‌مهره) هستند. به صورت ابتدایی، در خارباله‌ماهی‌مانندان ابتدایی و خاربالگان اجزای باله دمی از هم مجزا هستند و چندین غضروف بین‌دمی و پس‌دمی این اجزا را نگهداری می‌کند. گروه‌های قاعده‌ای معمولاً دارای شش دمپره مجزا، سه رودمپره، دو جفت دمکمانک مجزا، جسم دم‌مهره ۲ و خارهای عصبی و خونی مجزا بر روی آخرین جسم مهره هستند. در برخی از گروه‌های قاعده‌ای همچون فانوس‌ماهیان، بسیاری از اجزای باله دمی به هم جوش خورده‌اند که به خاطر وجود شرایط ابتدایی در آرایه‌های خویشاوند، جوش خوردگی در این گروه‌ها باید یک امر ثانویه و مستقل از آرایه‌های عالی در نظر گرفته شود. در گروه‌های عالی تمایل به جوش خوردن اجزا به یکدیگر و به جسم مهره است و غضروف‌های دمی به خاطر عدم کارایی از بین رفته‌اند. در گروه‌های تخصصی، همچون برخی از عقرب‌ماهی‌شکلان، تمام اجزا به هم جوش خورده و غضروف‌ها از بین رفته‌اند.

کلیدواژه‌ها: استخوان، استخوان‌شناسی، اسکلت، پهن‌بالگان، دم، غضروف.