

Nomenclature of Cartilaginous Elements in the Caudal Skeleton of Teleostean Fishes

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Abstract Nomenclature and abbreviations are proposed for the cartilaginous elements of the caudal skeleton of teleostean fishes. These were developed on the basis of examination of 510 species within 198 families of 31 orders and the determination of the positional relationship between these structures and the bony elements. A review of the most important relative literature is also provided.

Within the last two decades, the caudal skeleton of teleostean fishes has been recognized to be of special value in studying relationships among fish groups. Simple techniques such as that of Dingerkus and Uhler (1977) for staining cartilage and bone of whole fish specimens have greatly facilitated these osteological studies. Terminology, nomenclature and abbreviations for caudal bony elements have been given notably by Gosline (1960, 1961a, b), Nybelin (1963) and Monod (1967, 1968), and were further used by Greenwood et al. (1966), Patterson (1968a, b), Rosen and Patterson (1969), and Rosen (1973, 1974) in their studies on the interrelationships of fishes.

Studies on caudal cartilaginous elements have been incomplete and various terms have arbitrarily used by researchers. For this reason, the author reviewed the osteological studies of past workers to discern the pertinent references concerning caudal cartilaginous structures in teleostean fishes (Table 1), examined 510 species to delineate these elements, and developed nomenclature based primarily on the positional relationships of this cartilage to bony components.

Materials and methods

The material studied comprised 510 species in 198 families of 31 orders of teleostean fishes (Fujita, 1987). Following the method of Dingerkus and Uhler (1977), all specimens were stained for bone with alizarin red S, for cartilage with alcian blue 8GX, and then cleared with an enzyme solution. Caudal parts of these specimens were also dissected under a dissecting microscope for more exact examination. Ob-

servations and illustrations were made by means of a Wild M-7A dissecting microscope equipped with a camera lucida.

The characters examined include bony elements, the presence or absence of cartilage structures, and the number and shape of free cartilage and their positions. Bony element terminology follows Nybelin (1963) and Monod (1968).

Historical review

Main literature concerning the cartilaginous elements in the teleostean caudal skeleton is listed in Table 1.

Kölliker (1860) is probably the first author to study these structures as he recognized two small free cartilaginous elements behind the last two haemal spines of *Cyprinus carpio*, and named them "freie Knorpel". Lotz (1864) found similar structures in *Salmo salar*, *S. fario*, *Thymallus vexillifer* (Salmonidae), *Barbus fluviatilis* (Cyprinidae) and *Perca fluviatilis* (Percidae), and called all of them "selbständiges Knorpelstück". Ryder (1885) reported in an early stage of *Amiurus*, a hypaxial cartilage which abutted the underside, and near the posterior tip, of the notochord, and conditionally gave it the name "opisthural (cartilage)-op". Cope (1890) distinguished two kinds of cartilage in the caudal skeletons examined by Lotz: the "basilar cartilage" behind the haemal spines, hypurals and epurals, and the "intercalary cartilage" between the haemal spines or hypurals.

In the early 19th century, Whitehouse (1910) reported an extensive similar free cartilage in a variety of fishes including *Acipenser*, *Polyodon*, *Serranus cabrilla*, *Box salpa*, *Labrus festivus*,

Gobius paganellus, and *Cristiceps argentatus*. He used the terms "distal segment of radials" for this cartilage in *Acipenser* and *Polyodon*, and "cartilage supporting finrays" for those in the teleosts. Totton (1914) referred to the dorsal and ventral caudal cartilage in the nototheniid *Pleuragramma antarcticum* as "cartilaginous elements (car), which later on give attachment to the anterior dorsal ventral procurent fin-rays".

According to Patterson (1968a), in *Pholidophorus bechei* (Pholidophoridae), the last three haemal spines and the first hypural each bear a small triangular or rhomboid distal element (ventral caudal radial), while three to five similar distal bones or cartilage are present in *Acipenser*, *Polyodon*, *Pteronisculus* and *Boreosomus*. He

suggested that the presence of free radials is one of the important primitive features peculiar to the caudal skeleton in chondrosteans.

Nybelin (1971) recognized in the three species of *Elops* a cartilage and ossification at the tips of the last three haemal spines and the first hypural, and also described them as "distal caudal radials," the hemispherical cartilage occurring behind the posterior ends of the 5th, 6th, 7th hypurals and the third epural. Distal caudal radials were also recognized in *Megalops cyprinoides*, *Albula vulpes*, *Chirocentrus dorab*, *Alosa fallax*, *Osmerus eperlanus*, *Coregonus lavaretus*, *C. albula*, *Thymallus thymallus*, *Argentina silus*, *Esox lucius*, *Alestes nurse* and *Bathylagus antarcticum*. He suggested that the distal caudal radials served as some kind

Table 1. Main literature on the cartilaginous elements of the caudal skeleton of teleostean fishes, shown in chronological order with family names studied by the authors. Numbers in parentheses show the number of species studied.

Year	Author	Family	Year	Author	Family
1860	Kölliker	Cyprinidae (1)			Characidae (1)
1864	Lotz	Salmonidae (3)	1973	Rosen	Sternoptychidae (1)
		Cyprinidae (1)			Cetomimidae (1)
		Percidae (1)			Megalomycteridae (1)
1885	Ryder	Ictaluridae (1)	1974	Weitzman	Sternoptychidae (4)
1890	Cope	Salmonidae (3)	1975	Videler	Cichlidae (3)
		Cyprinidae (1)		Birdsong	Gobiidae (1)
		Percidae (1)	1976	Markle	Alepocephalidae (14)
1910	Whitehouse	Acipenseridae (1)	1977	Barel et al.	Cichlidae (1)
		Polyodontidae (1)	1980	Markle	Alepocephalidae (1)
		Serranidae (1)		Markle and	
		Sparidae (1)		Merrett	Alepocephalidae (1)
		Labridae (1)		Fritzsche and	
		Gobiidae (1)		Johnson	Percichthyidae (2)
		Blenniidae (1)	1981	Peters	Blenniidae (1)
1914	Totton	Nototheniidae (1)	1982	Fink and	
1956	Marathe and Bal	Polynemidae (1)		Weitzman	Gonostomatidae (1)
1968	Patterson	Pholidophoridae (1)		Stiassny	Cichlidae (44)
	Monod	Clupeidae (2)		Lau and	
		Salmonidae (1)		Shafland	Centropomidae (1)
		Percichthyidae (1)		Matsuoka	Sparidae (1)
		Apogonidae (1)	1983	Kohno et al.	Sparidae (1)
		Rachycentridae (1)		Springer	Gobiidae (2)
1971	Nybelin	Elopidae (3)		Peters	Gobiidae (1)
		Megalopidae (1)	1984	Potthoff et al.	Haemulidae (1)
		Albulidae (1)	1985	Murdy	Gobiidae (1)
		Salmonidae (3)		Whitehead and	
		Bathylagidae (1)		Teugels	Clupeidae (1)
		Osmeridae (1)	1986	Lindeman	Haemulidae (1)
		Esocidae (1)		Taki et al.	Chanidae (1)
		Clupeidae (1)	1988	Kullander	Cichlidae (1)
		Chirocentridae (1)		Potthoff et al.	Lutjanidae (1)

of buffer or intermediary between the lepidotrichia and the central skeletal elements, that the presence of cartilaginous structures was a rather common phenomenon in teleosts, and that their presence could hardly be regarded as primitive features.

Rosén (1973) figured and called the free cartilage supporting procurrent rays between neural or haemal spines of the last two or three vertebrae in *Maurollicus muelleri*, *Cetomimus* sp., *Eutaenio-phorus* sp. and *Ataxolepis apus*, "accessory cartilage", the same structures which Totton had termed "cartilaginous elements".

Markle (1976) reported cartilaginous elements behind the tips of the haemal spines of the second or third preural centrum in the alepocephalid fishes, including *Leptochilichthys agassizii*, *Nerces stomias*, *Bajacalifornia carcaratus*, *Bathylaco nigricans*, *Bathyprion danae*, *Talasma oregoni*, *Bathyroctes microlepis* and *Alepocephalus agassizii*, called them "cartilaginous ventral caudal radials", and also noted a cartilaginous pair between the second and third hypurals, the "median caudal radials". The latter was also found to be present in *Asquamiceps hjorti*, *Mentodus rostratus*, *Micrognathus normani*, *Rouleina maderensis*, *Einara edentulus* and *Alepocephalus bicolor*.

Videler (1975) described "marginal cartilaginous plates" in the caudal peduncle of the cichlids *Tilapia nilotica*, *T. mossambica* and *Aequidens portalegrensis*. Each of these dorsal and ventral cartilaginous plates was connected to the skin by a double verge of collagenous fibers. Stiassny (1982) extended her findings by stating that these marginal cartilaginous plates were present in all the cichlid taxa she studied including twenty-five neotropical, one Asian, two Madagascan and sixteen African species. She also wrote that only in *Cichla*, there was an additional cartilaginous plate situated between the second and third hypurals, and that its presence could be interpreted as an autapomorphy of the genus. Additionally, she noted that a similar cartilage was widely distributed among the perciform taxa, and that the size and positional variation of this cartilage might prove to be of value in interfamilial phylogenetic analysis.

Matsuoka (1982) reported on the ontogeny of accessory cartilage in the caudal skeleton of *Pagrus major*. He suggested that the number

and arrangement of these cartilaginous elements might be of value in fish classification because they seemed to be characteristic features.

In the osteological study of *Microgobius signaps*, Birdsong (1975) defined many osteological characteristics of the Gobioidae including cartilaginous plates supporting procurrent caudal rays. Springer (1983) described similar procurrent cartilage in the caudal skeleton of the gobioid fishes *Xenisthymus clarus* and *Tyson belos*. This cartilage was widely distributed in various relatively unspecialized preperciforms and perciforms such as the percichthyids and apogonids. He noted that in some perciformes (viz., the serranids) only the ventral plate was present, and that there were however, no perciforms with only the dorsal plate present.

In the haemulid fish *Anisotremus virginicus*, Potthoff et al. (1984) distinguished two kinds of cartilage: radial and articular. Three radials were present ventrally and one dorsally in the caudal skeleton throughout ontogeny. In larvae, the anteriormost one was the largest, positioned proximally between the tips of the haemal spines of the second (PU2) and third preural (PU3) centra, the smallest one at the tip of the haemal spine of PU2 and the posteriormost one between the proximal tips of the haemal spine of PU2 and the parhypural. During development this radial cartilage gradually shifted to the region between the haemal spines of PU2 and PU3, while the dorsal one remained at the distal tip of the fifth hypural. An articular cartilage was formed at two points: the distal tips of the haemal spine of PU2 and the parhypural.

Whitehead and Teugels (1985) described dorsal and ventral caudal radials in the West African pigmy herring *Sierrathrissa leonensis*. The small, ball-shaped, dorsal caudal radial was situated between the tips of the neural spines of PU2 and PU3. There were three ventral caudal radials (VCR): VCR1 between the tips of the haemal spines of PU3 and PU4, VCR2 at the tips of the haemal spines of PU2 and PU3, and VCR3 at the tip of the parhypural. They also found an opisthural cartilage between the last procurrent ray and the first upper principal ray.

As seen above, there are no comprehensive works covering caudal skeletal cartilaginous structures throughout the wide range of teleostean fishes.

Nomenclature of cartilaginous elements in the caudal skeleton

The positional variation of cartilaginous elements in the caudal skeleton of representative teleostean fishes is shown in Fig. 1. The nomenclature of cartilaginous elements is as follows:

Inter-neural spine cartilage (CINPUØ): The free cartilage situated between the neural spines of the preural centra is named with reference to the anterior neural spine. For example, the cartilage between the second and third preural neural spines (NPU2 and NPU3) is called the "inter-neural spine cartilage of PU3 (CINPU3)" (Fig. 1a). Cartilage between the third preural neural spine (NPU3) and the first epural (EP1), due to the shortening of the second preural spine, is also regarded as CINPU3 (Fig. 1e, h, i). Likewise, CINPU4 represents the cartilage between the third and fourth preural neural spines (Fig. 1a, e, f, g, i).

Inter-haemal spine cartilage (CIHPUØ): The free cartilages between the preural haemal spines are named like the above. For instance, the cartilage between the second and third preural haemal spines (HPU2 and HPU3) is called the "inter-haemal spine cartilage of the third prural centrum (CIHPU3)" (Fig. 1a).

Inter-epural cartilage (CIEPØ): Similarly, the free cartilage between two epurals is named with reference to the anterior one, e.g. that between the first and second epurals (EP1 and EP2) is called the "inter-epural 1 cartilage (CIEP1)", while CIEP2 represents the cartilage between the second and third epurals (Fig. 1e).

Median caudal cartilage (CMC): This free cartilage occurs between or near the distal tips of the second and third hypurals (HY2 and HY3), usually appearing as two separate or fused elements, but sometimes as a single one (Fig. 1a, b, c). Markle's "median caudal radial" of the Alepocephalidae is synonymous with this.

Post-neural spine cartilage (CPNPUØ): Elements of the free cartilage just behind the tips of the preural neural spines are named accordingly. For instance, the one behind the tip of the third preural neural spine (NPU3) is called the "post-neural spine cartilage of PU3 (CPNPU3)" (Fig. 1d).

Post-haemal spine cartilage (CPHPUØ): Nam-

ing of the free cartilage just behind the tips of the preural haemal spines follows suit; the elements at the tip of the preural haemal spine (HPU2) being called the "post-haemal spine cartilage of PU2 (CPHPU2)" (Fig. 1d, f, g, h, i).

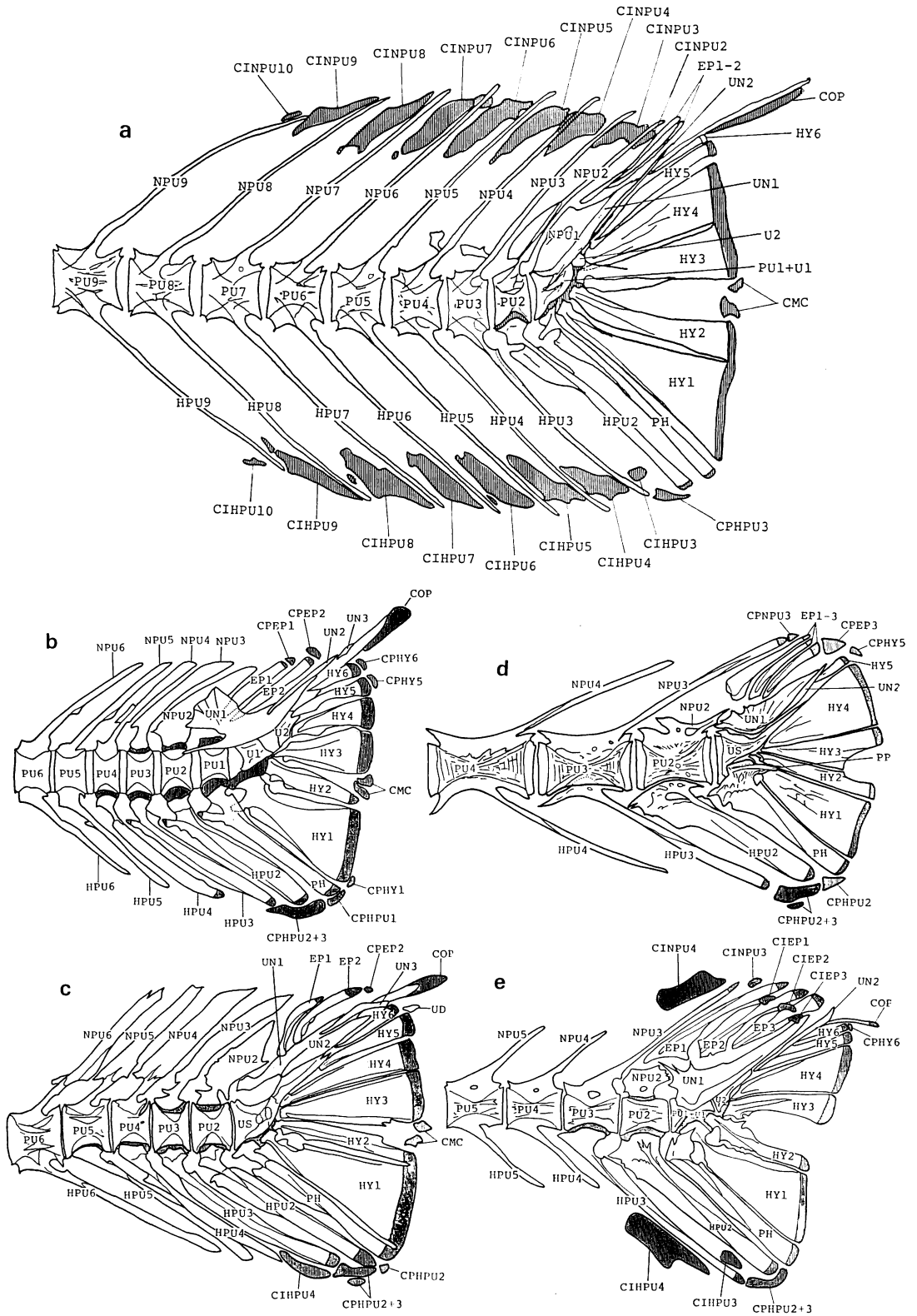
When a free cartilage extends behind the tips of two contiguous haemal spines, it is regarded as a possibly fused element, and named with reference to both spines; e.g. a cartilage extending over HPU2 and HPU3 is abbreviated as CPHPU2+3 (Fig. 1b, e). The same notation (CPHPU2+3) is also used for two cartilaginous elements in cases where they both occur essentially in parallel to each other (Fig. 1c, d).

Post-epural cartilage (CPEPØ): This free cartilage occurs just behind the tips of the epurals; as an example, the element behind the tip of the first epural (EP1) is called the "post-epural 1 cartilage (CPEP1)" (Fig. 1b, h). CPEP1+3 indicates the cartilage extending from behind the first to third epurals (Fig. 1i).

Post-hypural cartilage (CPHYØ): When a cartilage occurs just behind the tips of the hypurals, it is named accordingly, e.g. that just behind the tip of the fifth hypural (HY5) is called the "post-hypural 5 cartilage (CPHY5)" (Fig. 1b, d, f, g, h, i).

Opisthural cartilage (COP): The attached cartilage at the posterior tip of the notochord in some fishes has been given this name. Ryder (1885) correctly called it the "opisthural" a century ago, but in the present paper, the name is expanded to "opisthural cartilage" and the notation revised from "OP" to COP to conform with the other abbreviations proposed for teleostean caudal cartilage nomenclature (Fig. 1a, b, c, e).

Remarks. Examination of the large number of teleostean fishes studied revealed that, except for the opisthural cartilage which is attached, the free cartilaginous structures in the caudal skeleton exist in most species of the following fish orders: Osteoglossiformes (Mormyridae), Elopiformes, Clupeiformes, Gonorynchiformes, Cypriniformes, Characiformes, Siluriformes, Salmoniformes, Stomiiformes, Myctophiformes, Percopsiformes, Lophiiformes, Beloniformes, Cyprinodontiformes, Atheriniformes, Lampriformes, Beryciformes, Zeiformes, Dactylopteriformes, Scorpaeniformes, Perciformes and Tetraodontiformes (Triacanthodidae and Triacanthidae). These structures



Fujita: Caudal Cartilage Nomenclature

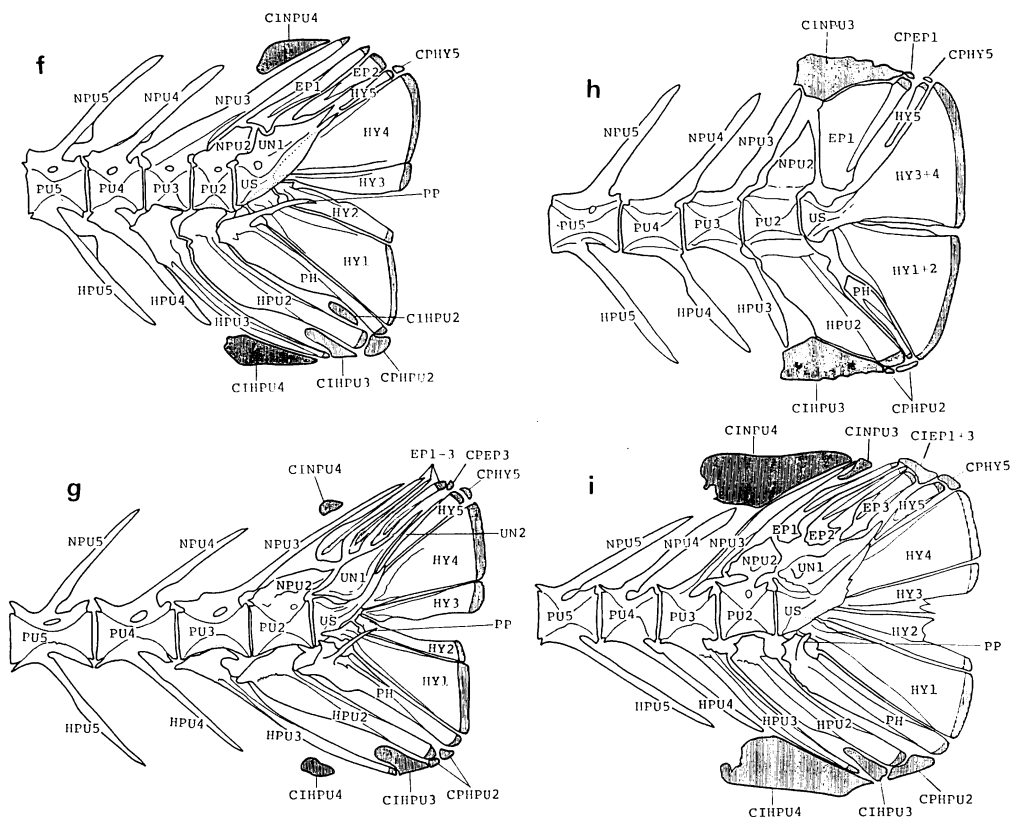


Fig. 1. Distribution of bony and cartilaginous elements in the caudal skeleton of representative teleostean fishes. a, *Bathylagus ochotensis* (Bathylagidae); b, *Oncorhynchus rhodurus* (Salmonidae); c, *Hypomesus japonicus* (Osmeridae); d, *Promethichthys prometeus* (Gempylidae); e, *Hoplostethus mediterraneus* (Trachichthyidae); f, *Plectroglyphidodon leucozona* (Pomacentridae); g, *Eryniscus japonica* (Sparidae); h, *Eviota abax* (Gobiidae); i, *Neoditrema ransonneti* (Embiotocidae). Bony and cartilaginous elements are outlined and shaded, respectively. Letter 'C' in the abbreviations stands for cartilage, while 'Ø' represents a numeric digit. Cartilaginous elements: C1EPØ, inter-epural cartilage; C1NPUØ, inter-neural spine cartilage; CMC, median caudal cartilage; COP, opisthural cartilage; CPEPØ, post-epural cartilage; CPHPUØ, post-haemal spine cartilage; CPHYØ, post-hypural cartilage; CPNPUØ, post-neural spine cartilage. Bony elements: EP, epural; HPU, preural haemal spine; HY, hypural; NPU, preural neural spine; PH, parhypural; PP, hypurapophysis; PU, preural centrum; U, ural centrum; UD, urodermal; UN, uroneural; US, urostyle.

were absent in Osteoglossiformes (Osteoglossidae and Notopteridae), Anguilliformes, Gadiformes, Ophidiiformes, Batrachoidiformes, Gobiesociformes, Gasterosteiformes, Syngnathiformes, Synbranchiformes, Pleuronectiformes and Tetraodontiformes (Balistidae, Monacanthidae, Ostraciidae and Tetraodontidae).

It was found very interesting that the occurrence of the opisthural cartilage and the median caudal cartilage was mainly restricted to rather primitive

fish groups which also possessed independent ural centra. The opisthural cartilage was found in Elopiformes, Clupeiformes, Salmoniformes (except Esocoidei), Stomiiformes, Myctophiformes, Percopsiformes and Beryciformes. Of these, Salmoniformes, Stomiiformes, Myctophiformes and Beryciformes (*Beryx* and *Anomalops*) also had the median caudal cartilage. In many fish groups, the number and position of free cartilages in the caudal skeleton appeared to be stable within

the families, or sometimes even at the suborder level. Details will be published in papers under preparation.

This terminology for cartilaginous elements in the caudal skeleton may be applicable to other species of teleosteans and other fishes. It is hoped that this paper will facilitate standardization in the terminology used in comparative studies among and within various fish groups.

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真骨魚類の尾部骨格に見られる軟骨の命名法

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真骨魚類 510 種 (31 目, 198 科) の魚類について、軟骨、硬骨二重染色法によって透明標本を作成し、尾部を構成する硬骨要素と軟骨の有無を調べた。その結果、尾部に存在する軟骨の存在場所がほぼ把握できたので、尾部骨格を構成する諸硬骨との位置関係に基づいた統一的な軟骨の命名法を提唱した。また、関連の主要業績についても再検討を加えた。この命名法は大多数の魚種に適応でき、それによって尾部の軟骨要素を種々の魚種間で比較しうる形質として捉えることが可能となった。

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