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Cartilage and related tissues in the trunk and fins of teleosts

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ABSTRACT

The structure and distribution of cartilage and related tissues in the dorsal fin, caudal fin and vertebrae of teleosts were studied in 11 species. With the exception of Zellknorpel, all the tissues previously described in teleost heads were present in the trunk and fins, although they were found in smaller quantities. The distribution of the supporting tissues indicates that they serve different functions. Hyaline cartilage was restricted to vertebral and fin bones undergoing endochondral ossification, fibro/cell-rich cartilage acted as an articular tissue, and hyaline-cell cartilage and its subtypes formed flexible and resilient supports in the caudal fin. Mucous connective tissue was packed as a space-filler around neurovascular bundles in fin rays, and chondroid bone was found beneath articular surfaces. The differences between cranial, and trunk and fin supporting tissues may reflect developmental as well as functional differences between the cranial and postcranial skeleton.

INTRODUCTION

There is a variety of different types of cartilage in the heads of teleosts (Benjamin, 1990). In addition to hyaline cartilage, there are several others of distinctive histological structure that are rarely present in higher vertebrates. These are hyaline-cell cartilage, which is common in the oromandibular region; Zellknorpel which supports gill filaments; elastic/cell-rich cartilage, which is found in barbels; and fibro/cell-rich cartilage, a common articular tissue. The related tissues, mucous connective tissue (mucochondroid) and chondroid bone are also present. Mucous connective tissue is common beneath the skin (Benjamin, 1988) and chondroid bone beneath articular surfaces (Huysseune & Verraes, 1986). The different tissues have different extracellular matrices (Benjamin & Ralphs, 1991). In the present study, we survey the supporting tissues found in the trunk, dorsal and caudal fins of teleosts.

MATERIALS AND METHODS

One or 2 fish were examined from each of 11 species of teleosts. The selection of fish ensured that those with a wide variety of skeletal tissues in the head were examined, notably Cypriniformes, and that several other orders of teleosts were represented. The species were the sucking loach *Gyrinocheilus aymonieri* (standard lengths 35 mm, 36 mm), the red-tailed black shark *Labeo bicolor* (34 mm, 42 mm), the rosy barb *Barbus conchonius* (24 mm, 36 mm), the white cloud mountain minnow *Tanichthys albonubes* (17 mm, 21 mm), the skunk botia *Botia horae* (28 mm, 29 mm), and the horse-faced loach *Acanthopsis choirorhynchus* (50 mm) from the Cypriniformes, the catfish *Pangasius sutchi* (41 mm) from the Siluriformes, the guppy *Poecilia reticulata* (31 mm, 31 mm) from the Atheriniformes, and the convict cichlid *Cichlasoma nigrofasciatum* (23 mm, 24 mm) and the earth eater *Geophagus jurupari* (40 mm) from the Perciformes. The heads of these fish were used in previous studies on cranial skeletal tissues (Benjamin, 1988, 1990). Portions of the body were removed that included the dorsal or caudal fins and the material was prepared for routine histology as described previously (Benjamin, 1990). Transverse sections were cut at 8 μm and collected at 50 μm intervals. The sections were stained with haematoxylin and eosin, Masson's trichrome or with Weigert's and van Gieson's connective tissue stains. The skeletal elements seen in the sections were identified by reference to alizarin red and Alcian blue preparations of whole fish (Dingerkus & Uhler, 1977).

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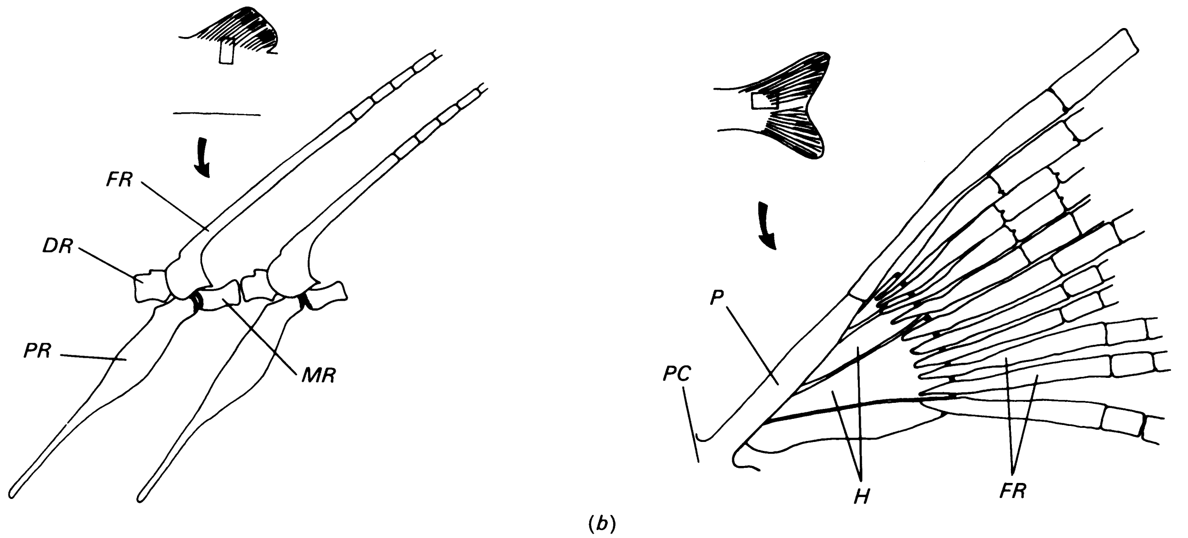

Fig. 1. Osteology of the dorsal (*a*) and caudal (*b*) fins in *Botia horae* drawn from an alizarin red/Alcian blue preparation. In the dorsal fin, each fin ray (*FR*) was supported by a series of pterygiophores. These consisted of a dorsal (*DR*), proximal (*PR*) and medial radial (*MR*). In the caudal fin, the fin rays were supported by a series of elongated and flattened hypural bones (*H*). *P*, pleurostylar process; *PC*, first preural centrum.

OBSERVATIONS

Basic fin structure

In all species examined in this study, the dorsal fin supports consisted of a series of longitudinally-arranged bones (pterygiophores) embedded in the dorsal musculature, that articulated with the fin rays. This structure is illustrated in Figure 1*a* for *Botia horae* and further details are given in Sawada (1982). The fin rays were usually bifurcated proximally and articulated either side of the pterygiophores. In *Geophagus jurupari* and *Cichlasoma nigrofasciatum*, the first dorsal fin rays were spiny. The spines were simply thickened and stronger versions of the more flexible fin rays. In the caudal fins, the principal fin rays were supported by a series of flattened hypural bones (Fig. 1*b*).

Descriptions of tissues

Several types of supporting tissues were found in the trunk and fins (Figs 2, 3). *Hyaline cartilage* was cell-rich (CRHC) or matrix-rich (MRHC) according to whether the cells or the extracellular matrix occupied more than 50% of the tissue volume. The remaining cartilages were all highly cellular. In *hyaline-cell cartilage* (HCC), the cells were chromophobic (and thus hyaline in appearance), not shrunken within lacunae and separated by thin layers of weakly-staining matrix. This tissue was only seen as an expansion of the periosteum. Two subtypes of this cartilage were present: *fibro/hyaline-cell cartilage* (FCC) where the extracellular matrix was coarsely fibrous and *elastic/hyaline-cell cartilage* (ECC) where the matrix contained many elastic fibres. *Fibro/cell-rich cartilage* (FCRC) is a highly cellular fibrocartilage that often forms articular tissue. Its matrix contains much collagen and its cells are not hyaline. *Mucous connective tissue* is a gelatinous loose connective tissue that was present in small quantities. *Chondroid bone* is a tissue with properties intermediate between those of cartilage and bone and was always present in association with parallel-fibred bone.

Distributions of tissues

The distribution of skeletal tissues in the vertebrae, dorsal and caudal fins is summarised in the Table. In all species, the vertebrae were endochondral bones that contained hyaline cartilage (Fig. 2*a*, *b*). Chondroid bone was found in the vertebrae of *B. conchonius* and *B. horae*. There was a greater variety of skeletal tissues associated with the fins (Fig. 3). Hyaline cartilage (usually CRHC) was present in all fin supports (Fig. 3*a–d*). It formed the cartilaginous precursor of the pterygiophores and was eroded to form a marrow space. Chondroid bone was found in the dorsal fin supports of cypriniforms (Fig. 3*a*) and also in the perciform, *G. jurupari*. It was found in small quantities beneath the articular surfaces of both the pterygiophores and fin rays. In the dorsal fin, FCRC formed an articulating surface between pterygiophores and the fin rays (Fig. 3*a*, *b*) in all species

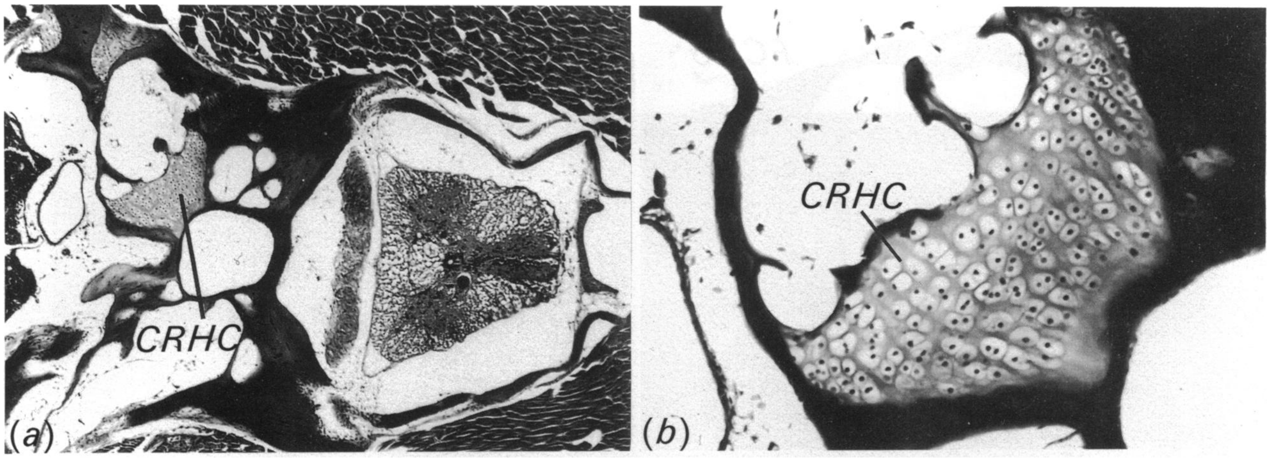

Fig. 2(*a*, *b*). Transverse section through a vertebra of *Botia horae* showing low and high power views (magnifications × 80 and × 300) of cell-rich hyaline cartilage (*CRHC*). Dorsal aspect is on the left of the figure. Masson's trichrome.

except *B. conchonius*. In this fish, the articular tissue was HCC. The only other site in which HCC was seen was in *G. aymonieri*, where it was on the deep surface of a ligament which ran between the bifurcations of each fin ray near their articulation with the pterygiophores.

In the caudal fin, the hypural bones contained hyaline cartilage surrounded by perichondral bone (Fig. 3*c*, *d*). HCC and its subtypes (ECC and FCC) were often present. In *P. reticulata*, HCC formed a series of rods of tissues (expansions of the periosteum) connected to each other by fibrous tissue and attached to the hypurals. The fin rays lay in the grooves between the rods (Fig. 3*c*, *d*). In several teleosts, including *B. horae* (Fig. 3*e*,*f*), ECC formed a small strip at the dorsal and ventral extremities of the hypural/parhypural complex. The tissue was continuous with a fibrous band that wrapped around the hypurals on the inner aspect of the fin rays. A rod of HCC lay between the ECC and the most dorsal and ventral hypurals. However in *G. jurupari*, each fin ray was linked individually to the hypurals by a series of ligaments and there was no fibrous band, or strip of ECC. The only skeletal tissue in the fins themselves, other than the bone of the fin rays, was mucous connective tissue (Fig. 3*g*, *h*). It surrounded a neurovascular bundle that courses through the middle of each ray.

DISCUSSION

The skeletal tissues seen in the fins, fin supports and vertebrae could be classified into the same categories as those in the head (Benjamin, 1988, 1990). However, Zellknorpel as seen in the gill filaments was absent in the postcranial skeleton.

The positions of the different supporting tissues suggest that they have different functions. Hyaline cartilage (CRHC or MRHC) was seen only in cartilage models of bones that were undergoing endochondral ossification. Articular surfaces between bones were usually covered with FCRC as in the head (Benjamin, 1990). It is known that, in the head, HCC is resilient and highly flexible (Benjamin, 1986). In the caudal fin, it is found in 2 positions where such properties may be functionally significant. In *P. reticulata*, HCC fixes the proximal end of the fin rays in flexible tracks that maintain an appropriate position of the rays relative to the hypurals. Dorsally and ventrally to the hypurals in *B. conchonius* and *B. horae*, HCC is associated with ECC (see Fig. 3*e*, *f*). It may be that these tissues are important in protecting the fin supports at extremes of dorsoventral fin movements. ECC may allow stretch in the fibrous band enclosing the hypurals, and the underlying HCC could provide a resilient cushion protecting the hypurals. Mucous connective tissue formed a space-filler packed around the neurovascular bundle between the 2 parts of bifurcated fin rays. Chondroid bone was common beneath articular surfaces as in the head, where it may provide for rapid growth (Huysseune & Verraes, 1986).

In all species, the tissues were similar to those in the head, but their structure was less clearly defined and they were present in smaller quantities. For example, in *G. aymonieri*, there are large amounts of HCC in the oral sucker (Benjamin, 1986), but much smaller quantities were seen in the caudal fin supports. In the oromandibular region of cyprinids, the cells are frequently aligned in rows (Benjamin, 1989). No such orderly arrangement characterised HCC in cyprinid dorsal or caudal fins. This is probably related to

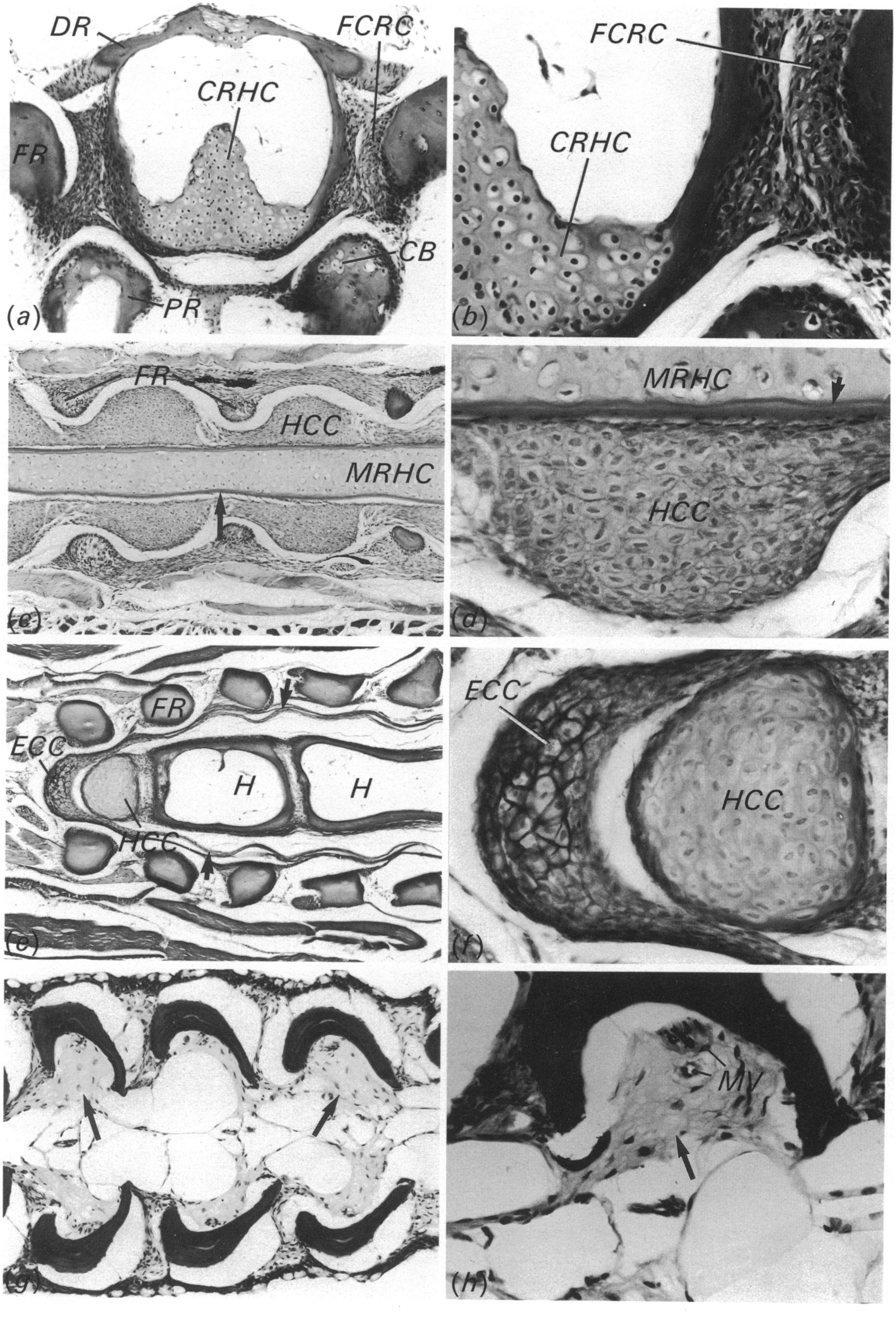
DR
FCRC
CRHC
FR
CB
PR
(a)
FCRC
CRHC
(b)
FR
HCC
MRHC
(c)
MRHC
HCC
(d)
FR
ECC
H
H
HCC
(e)
ECC
HCC
(f)
(g)
MV
(h)

Table. *The distribution of supporting tissues in the dorsal fin, caudal fin and vertebrae of teleosts*

	Dorsal fin		Caudal fin		
	fin supports	Fin	fin supports	Fin	Vertebra
Order Cypriniformes	CRHC	MC	CRHC	MC	CRHC
Gyrinocheilus aymonieri					
	CB		FCRC		
	FCRC		HCC		
	HCC				
Labeo bicolor	CRHC	MC	CRHC	MC	CRHC
	CB		FCRC		MRHC
	FCRC		ECRC		
			FCC		
Barbus conchonius	CRHC	MC	CRHC	MC	CRHC
	CB		HCC		CB
	FCC		FCC		
			ECRC		
Tanichthys albonubes	CRHC	MC	CRHC		CRHC
	CB		ECRC		
	FCRC		FCRC		
Botia horae	CRHC	MC	CRHC	MC	CRHC
	CB		ECC		CB
	FCRC				
Acanthopsis choirorhynchus	MRHC	MC	CRHC	MC	
	CRHC		MC		
	CB				
	FCRC				
Order Siluriformes					
Pangasius sutchi	MRHC	MC	CRHC	MC	MRHC
	CRHC		HCC		
	FCRC		FCC		
Order Atheriniformes					
Poecilia reticulata	CRHC	MC	CRHC	MC	CRHC
	FCRC		HCC		
Order Perciformes					
Geophagus jurupari	CRHC		MRHC	MC	CRHC
	FCC		HCC		
	FCRC		FCC		
	CB				
Cichlasoma nigrofasciatum	CRHC		CRHC	MC	CRHC
	FCRC		FCRC		

CB, chondroid bone; CRHC, cell-rich hyaline cartilage; ECC, elastic/hyaline-cell cartilage; FCC, fibro/hyaline-cell cartilage; FCRC, fibro/cell-rich cartilage; HCC, hyaline-cell cartilage; MC, mucous connective tissue; MRHC, matrix-rich hyaline cartilage.

differences in the stresses experienced by the tissue in the different regions. HCC stiffens the lips and tends to be subject to directional forces; in the fins, HCC seems to be deployed purely as a resilient buffer. Its constant association with the periosteum suggests that it may have developed as a secondary cartilage. Although cranial HCC is generally associated with periosteum, it can also form separate menisci (Benjamin, 1989). Hyaline cartilage was also present in greater quantities in the head than the body. It forms both a permanent part of the neurocranium and acts as a model for bones developing by endochondral

Fig. 3. Transverse sections through dorsal and caudal fins to show cartilage and related tissues. (*a*, *b*) Low and high power views (magnifications × 190 and × 480) of cell-rich hyaline cartilage (*CRHC*), fibro/cell-rich cartilage (*FCRC*) and chondroid bone (*CB*) in the pterygiophores of *Botia horae*. *CRHC* is being eroded to form a marrow cavity, *FCRC* forms articular surfaces and *CB* lies beneath the articular surface of the proximal radial. *DR*, distal radial; *FR*, fin ray; *PR*, proximal radial. Masson's trichrome. (*c*, *d*) Low and high power views (magnifications × 120 and × 480) of a transverse section of a hypural bone in *Poecilia reticulata*. Dorsoventral axis is horizontal. The hypural has a core of matrix-rich hyaline cartilage (*MRHC*) surrounded by perichondral bone (arrow) and large periosteal cushions of hyaline-cell cartilage (*HCC*) that separate the hypural from the fin rays (*FR*). Haematoxylin and eosin. (*e*, *f*) Low and high power views (magnifications × 120 and × 480) of a transverse section through the caudal fin of *Botia horae*. Dorsoventral axis is horizontal. Note the elastic hyaline-cell cartilage (*ECC*) at the dorsal extremity of the hypurals (*H*). This was continuous with a fibrous band (arrows) that wrapped around the inner aspect of the fin rays (*FR*). There is a piece of *HCC* adjacent to the *ECC*. Weigert's and van Gieson's stains. (*g*, *h*) Low and high power views (magnifications × 190 and × 480) of mucous connective tissue (arrows) between the bifurcations of the caudal fin rays in *Gyrinocheilus aymonieri*. *NV*, neurovascular bundle. Masson's trichrome.

ossification. In the trunk and fins, hyaline cartilage was always a model on which bone was formed. It is noteworthy that none of the other types of cartilage in any part of the fish underwent endochondral ossification. Mucous connective tissue was structurally similar in the fin rays and head, but the thick subdermal layer as seen in the head of *A. choirorhynchus* (Benjamin, 1988), was absent in its trunk and fins. Its presence in this position in bottom living fish suggests that it may serve as a protective buffer during burrowing or probing of the substrate. It may also serve a protective function in fin rays, protecting neurovascular bundles during fin bending. In Perciformes, this tissue was absent. This could be associated with the heavily bony nature of the spiny fin rays, rendering them less flexible.

The differences between cranial, and trunk and fin supporting tissues may reflect developmental as well as functional differences between the cranial and postcranial skeleton. It is known that the cartilaginous components of the cranial skeleton are derived from the neural crest (Langille & Hall, 1988). It seems likely that as in higher vertebrates, those of the postcranial skeleton of teleosts are mesodermal in origin.

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