Comments on the Development of Fin-supports in Fishes

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(Received May 25, 1983)

The cartilaginous-osteological development of teleostean fishes remained little studied largely because of technical difficulties. With the development of techniques for clearing and staining whole specimens through the works of Taylor (1967, for bone only) and Dingerkus and Uhler (1977, for both cartilage and bone), a great deal of knowledge has been accumulated concerning the cartilaginous-osteological development of fish larvae of various species by many workers, notably by Potthoff (see Table 1). This study is designed to discuss some topics raised through our previous study on the cartilaginous-osteological development of Pagrus major larvae (Kohno et al., 1983). This study concurrently reviews works of many researchers listed in Table 1. Supplemental observations were made in 24 species. Fin-supports of all fins except for the ventral are dealt with in this study.

Terminologies generally follow Starks (1930), Eaton (1945) and Monod (1968).


Dorsal and anal fin-supports. The structures of the dorsal and anal fin-supports were minutely studied by Bridge (1896) and Eaton (1945). Lindsey (1955) reviewed meristic relations in the dorsal and anal fins of teleosts. Anterior dorsal fin-supports and predorsal bones were examined by Smith and Baily (1961) and Kendall (1976) in relation to its phylogenetic significance within the percoids.

The distal and proximal radials were observed as originating from an elongate cartilaginous

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<td>1974</td>
<td>Houde et al.</td>
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pterygiophore during ontogeny in such genera as *Thunnus* (Potthoff, 1975), *Coryphaena* (Potthoff, 1980), *Scombrolabrax* (Potthoff et al., 1980) and *Xiphias* (Potthoff and Kelley, 1982). However, in our observations on *Pagrus major*, the distal radial was first seen in a 6.40 mm NL specimen, in which the radial is rather widely separated from the proximal radial (Kohno et al., 1983, figs. 2, 3). As development goes on, these two radials come in close contact. This suggests that both radials have their own cartilaginous center and they are connected by a connective tissue.

The anteriormost anal pterygiophore is originated from two cartilaginous pieces in *Thunnus* (Potthoff, 1975), *Morone americana* (Fritzsche and Johnson, 1980) and *Scombrolabrax* (Potthoff et al., 1980). We observed the same condition in *Tilapia nilotica* and *Auxis* sp. As to the anteriormost dorsal pterygiophore, however, Smith and Baily (1961) mentioned that it is not possible for the pterygiophore to originate from the fusion of two elements, and Potthoff (1975) found no evidence of this fusion during the ontogeny of *Thunnus*. Whereas, from observation of two parallel struts of bony tissues in the first dorsal pterygiophore, Kendall (1976) indicated the possible origin of the pterygiophore from a fusion of two elements. Fritzsche and Johnson (1980) directly observed the first dorsal pterygiophore originated from two elements in *Morone americana*, but it was not detected in the related species, *M. saxatilis*. They may have failed in observing it in the latter species, because, as mentioned by themselves, the elements remain separated for only a very short time.

In our observations of *Pagrus major*, in which the first dorsal pterygiophore supports two spines by secondary (non-serial) association, the pterygiophore of initial stages consists of two struts connected by thin cartilage stained palely, indicating its derivation from two cartilaginous pieces (Kohno et al., 1983, fig. 2). On *Scomber*, in which the first dorsal pterygiophore supports one spine by secondary association, Kramer (1960) mentioned that the pterygiophore is derived from two elements. However, in *S. japonicus* we could observe neither separated cartilaginous nor a two-strut condition as in *P. major* (cf., Kohno et al., in press, fig. 1). Thus our observations seem to support Kendall’s (1976) opinion that the pterygiophore supporting two spines by secondary association might have originated from two pieces of cartilage.

Usually one additional radial, the vestigial radial element of Bridge (1896) or stay of Weitzman (1962), is present posterior to the last dorsal and anal pterygiophores. The gempylids have two stays (Potthoff et al., 1980; present obs.) and *Coryphaena* has no stay (Potthoff, 1980; present obs.). On the origin of the stay, Potthoff (1975, 1980), Potthoff et al. (1980) and Potthoff and Kelley (1982) mentioned that it originated from the last cartilaginous proximal (-middle) radial and is not a vestige of fin-support. Our observations on *Pagrus major*, *Scomber japonicus*, *Oncorhynchus keta*, synodontid sp., *Tilapia nilotica* and two species of *Pempheris*, however, suggest that the stay is originally different from the last pterygiophore. In early stages, the two rays of the last double fin-ray are widely separated, the anterior ray attaches to the last pterygiophore and the

![Fig. 1. Development of the last dorsal fin elements in *Tilapia nilotica* (top) and the last anal fin elements in *Pempheris japonica* (bottom). Larval sizes in SL are, starting from the left, 9.50 and 19.75 for top, and 10.35, 14.55 and 35.70 for bottom. All elements excepting the last double fin-ray are cartilage. AF, anterior fin-ray of last double fin-ray; DR, distal radial; MR, middle radial; PF, posterior fin-ray of last double fin-ray; PR, proximal radial; St, stay. Scale bars: 0.1 mm.](image-url)
Fig. 2. Development of the primary shoulder girdle in *Engraulis japonica* (top) and *Oncorhynchus keta* (bottom). Larval sizes in SL are 25.85 (left) and 30.40 (right) for top, and 22.30 and 29.70 for bottom. All elements are cartilage. Ac, actinost (blade-like cartilage); CS, coraco-scapular cartilage; PrP, propterygium. Scale bars: 0.2 mm.

posterior one is situated close to the stay (Fig. 1). With growth the proximal (=middle) radial and stay fuse together, and the posterior ray moves forward, thus forming a double fin-ray on the last pterygiophore (Fig. 1). From this the stay is considered to be a vestige of a fin-support. This view agrees with the opinions of Bridge (1896) and Potthoff (1974) in the respect that the stay is a reduced proximal radial.

**Pectoral girdle.** The cartilaginous-osteological development of the pectoral skeleton was studied by Swinnerton (1905) for *Salmo salar* and *Gasterosteus aculeatus*. Starks (1930) described the primary shoulder girdle of a large number of fish in detail.

The coracoid and scapula originated from a cartilaginous plate, or the coraco-scapular cartilage, through ossification in each part. Saksena and Richards (1975) reported the appearance of an unstained Y-shaped coracoid, which was judged by Potthoff (1980) as a coraco-scapular cartilage. Our observations on all species support Potthoff's (1980) judgement. The actinosts (=proximal radials) are derived from a blade-like cartilage. Both the coraco-scapular and blade-like cartilages remain as they are in adult *Dallia* (Starks, 1930) and adult sundasaranids (Roberts, 1981). The propterygium (Jessen, 1973) is derived from the blade-like cartilage in *Engraulis japonica* and *Oncorhynchus keta* (Fig. 2). The possibility was suggested by Starks (1930) that the pectoral condyle supporting the uppermost fin-ray may be an ankylosed actinost. Potthoff and Kelley (1982), on the other hand, mentioned that the condyle originated from the upper part of the coraco-scapular cartilage, i.e., the scapular cartilage. However, the condyle develops neither from the scapular cartilage nor from the blade-like cartilage in our observations. The condyle may have its own cartilaginous center, and may possibly be homologous with the distal radials (cf., Kohno et al., 1983, fig. 5).

**Caudal complex.** The caudal complex occupies an important position in phylogenetic studies. A great deal of knowledge concerning its structure has accumulated on various groups of fishes, and phylogenetic relationships have been induced from its features (e.g., Hollister, 1936; 1937a, b; Gosline, 1961b; Monod, 1968; Rosen and Patterson, 1969; Rosen, 1973).

The urostyle of primitive fishes is composed of three or more centra which are separated even in adults (e.g., Gosline, 1961a). Though such a separate condition is not seen in all adult higher fishes, their urostyle is considered to have originated from three centra, the preural centrum 1 and ural centra 1 and 2 (Nybelin, 1973; Ahlstrom in Potthoff, 1975). We observed in larval *Pangrus major* a urostyle containing two separate elements, most probably the ural centra 1 and 2 (Kohno et al., 1983, fig. 4C). This agrees with the above view as to the origin of the urostyle of higher fishes. These centra were stained light blue by alcian blue, and hence Kohno et al. (1983) considered them to be cartilage. However, this view is mistaken since the centrum of teleostean fishes develops probably directly from a notochord (Takashima, 1982). Alcian blue is specific for mucopolysaccharides (Dingekus and Uhler, 1977), and in the above case it may have stained those in the second chorda sheath. According to our observations and Roberts (1981), alcian blue stains uncalcified bone or bone in early stage larvae. Setting aside this misinterpretation, it is interesting from a phylogenetic viewpoint that the separate ural centra 1 and 2 were observed, even though momentarily. Yabumoto (1980) reported the presence of the
preural centrum 1 and ural centrum 1 in Leio-
ognathus larvae, but these centra appear to be the
urostyle and relic of the notochord, respectively.
Leiby (1981) described separate ural centra in
the ophichthid Bascanichthys bascanium, though
all other ophichthids possess a fused ural centrum
(Leiby, 1979a, b, 1981). An urostyle with
two-separated parts was described without any
comment in Archosargus larvae by Mook (1977).

No cartilaginous fusion of the caudal complex
takes place in lower fishes, such as the clupeids
(Houde et al., 1974) and engraulids (present
obs.). During development, bony fusion is
seen centering on the uroneurals in lower fishes
(Hollister, 1936; Gosline, 1961a).

In hypurals, cartilaginous and bony fusions
occur in various ways. Our observations show
that cartilaginous fusion at proximal ends takes
place between hypurals 1 and 2 in Oncorhynchus
keta (Fig. 3A) and between the parhypural and
hypural 1 in Rhodeus ocellatus ocellatus (Fig.
3B). However, cartilaginous fusion takes place
more commonly in such a manner in which the
proximal ends of the parhypural and hypurals
1 and 2 are fused to form a cartilaginous bar
lying ventral to the urostyle (cf., Kohno et al.,
1983, fig. 4). With growth, the ossification of
these elements goes on, and the cartilaginous bar
is lost. In addition to the above-mentioned
typical cartilaginous fusion, the distal ends of
the hypurals 1 and 2 are fused in Atherion elymus
(Fig. 3C). In the ophichthids, on the other
hand, the hypurals 1 and 2, which are fused at
both the proximal and distal ends, are not fused
with the parhypural but with the hypural 3 at the
proximal end (Leiby, 1979a, b 1981). The carti-
laginous hypurals 1 and 2 form a cartilaginous
plate from early stages in the cottids, and the
cartilaginous parhypural comes to fuse with the
plate at both the proximal and distal ends with
growth (Matarese and Marliave, 1982). In
Mugilogobius abei the hypural plate 1+2 shows
the same condition as that of the cottids, but no
fusion takes place between the plate and parhy-
pural (Fig. 3D). In the bothids (Futch, 1977;
Hensley, 1977; Tucker, 1982) and the pleuronect-
ids (Richardson et al., 1980) the hypurals 1 and
2 and the hypurals 3 and 4 are not separated,
but they form the hypural plates 1+2 and 3+4
respectively, at their incipient stages. Similarly,
the hypural plates 1+2 and 3+4+5 are formed
in early stages in the gadids (Matarese et al.,
1981; Markle, 1982). Whereas, in the scombrids
such cartilaginous fusion comes during early
development in the following patterns: the
hypurals 1 and 2 are fused into a hypural plate
1+2 with which the proximal end of the parhy-
pural is fused, and the hypurals 3 and 4 are also
fused together at a later stage (Potthoff, 1975;
present obs.). It is interesting to compare the
scombrids with Coryphaena (Potthoff, 1980) and
Xiphias (Potthoff and Kelley, 1982) in which
cartilaginous fusion does not occur with the
exception of aforementioned typical cartilaginous
fusion, but bony fusion takes place in later
stages to form a hypural plate as in the scombrids.

Adults of Coryphaena have one epural. This
epural originates from a bony fusion of two
epurals during ontogeny (Potthoff, 1980).
Adults of Trachurus japonicus possess two
epurals, of which the anterior one results from a
bony fusion of two epurals in the same way as

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in *Coryphaena* (present obs.).

The relation between the specialized neural arch on the preural centrum 2 and the anterior epural in the scombrids shows an interesting case from a phylogenetic viewpoint. Both elements originated from a cartilaginous state, and no cartilaginous fusion occurs. In advanced scombrids, e.g., *Thunnus*, bony fusion occurs in considerably advanced stages (Potthoff, 1975). On the other hand, in adult primitive scombrids, e.g., *Scomber*, the anterior epural is never fused with the specialized neural arch.

Fusion of various parts of the caudal complex observed in the course of ontogeny was discussed by Potthoff (1975, 1980) and Potthoff and Kelley (1982). Gosline (1961b) emphasized the necessity of studies on the ontogenetic fusion of the caudal complex. Important clues for interpretation of higher-level phylogenetic relationships seems to be found in the developmental pattern of the caudal complex.

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魚類の鰭支持骨の形成過程

河野 博・多紀保彦

マダイの研究途中で生じた鰭支持骨の形成過程に関する問題について、他の24種の仔稚魚の観察を補足して考察した。

その結果、以下のことが示唆された：背・臀鰭の近担鰭骨と遠担鰭骨は別々の軟骨から生じる；最前部の近担鰭骨は、2本の鰭と2次的に関節している場合には、2つの近担鰭骨から出来する；stayは担鰭骨のこも跡である；鳥口骨と肩甲骨は単一の軟骨から発達する；輻射骨は1枚の軟骨板から分化する；特化した魚類の尾部棒状骨は2個の尾鰭椎と1個の尾鰭椎前椎体からなる；尾骨のゆちは魚種によって、そのパターンが異なる。

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