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Author(s)	SHIRAI, Shigeru; 白井, 滋
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Identity of Extra Branchial Arches of Hexanchiformes
(Pisces, Elasmobranchii)

Shigeru Shirai*

Abstract

A hypothesis on the homology of branchial arches in living shark taxa is proposed. Based on the comparative anatomy, the branchial arches are composed of four types of units, the anteriormost (α-type), penultimate (γ-type), ultimate (δ-type), and other two or more arches (β-type). The extra branchial unit(s) of hexanchiforms should result from the duplication of the β-type arch (second or third arch of the original five-gilled condition). The first additional arch in the hexanchoids (cow sharks) is regarded as the fourth (*Hexanchus*) or the fifth arch (*Heptranchias* and *Notorynchus*). Homology of the extra arch in *Chlamydoselachus* (frill sharks) is uncertain, but it appears to be homoplasous with that of hexanchoids.

Most living elasmobranchs have five branchial arches supporting four holobranchs. In the order Hexanchiformes (Compagno, 1973) composed of *Chlamydoselachus* and the hexanchoids (*Notorynchus, Heptranchias*, and *Hexanchus*), six or seven branchial arches are present, and previous authors have been traditionally referred to the unit(s) behind the fifth branchial arch as the "sixth" or "seventh" arch (e.g., Garman, 1885, 1913; Goodey, 1910; Allis, 1923; Daniel, 1934). Such a convention is, however, primarily one of connvenience and does not mean that the sixth and/or seventh unit is not homologous with any branchial arches of five-gilled taxa. Recently, the extra gill unit(s) was considered as one of the synapomorphies of Hexanchiformes (Compagno, 1973, 1977; Maisey and Wolfram, 1984), but the homology of their extra arches was not discussed in detail.

In this paper, the identity of the extra branchial arches of hexanchiforms is evaluated based on the morphological comparisons of adult specimens. For this purpose, branchial skeletons and associated muscles of five-gilled species are described, and the similarities and differences of branchial arches among hexanchiforms are clarified.

Material and Method

Observations were made from dissections prepared using the method of Dingerkus and Uhler (1977). Illustrations were made using a camera lucida. In this paper, an ordinal number of branchial arch or its element is described as an Arabic numeral, for example, the "arch 1" (the first branchial arch) or "ceratobranchial 5" (ceratobranchial of the fifth arch).

Specimens examined are listed below. Five-gilled shark species including

* *Laboratory of Marine Zoology, Faculty of Fisheries, Hokkaido University*
　(北海道大学水産学部水産動物学講座)

many squaloids were examined for comparison.   Institutional abbreviations follow Leviton et al. (1985).

Chlamydoselachoidei
  Chlamydoselachus anguineus Garman, MSM-88-40, male, 1,392 mm TL.

Hexanchoidei
  Hexanchus griseus (Bonnaterre), HUMZ 95104, male, 698 mm TL.
  Notorynchus cepedianus (Peron), HUMZ 6749, female, 740 mm TL.
  Heptranchias perlo (Bonnaterre), HUMZ 40064, female, 559 mm TL ; HUMZ
      101712, male, 542 mm TL.

Squaloidei
  Echinorhinus brucus (Bonnaterre), HUMZ 113400, male, 1,100 mm TL.
  Etmopterus lucifer Jordan et Snyder, HUMZ 34580, female, 355 mm TL.
  Centrophorus acus Garman, HUMZ 101726, male, 714 mm TL.
  Centroscymnus coelolepis Bocage et Capello, USNM 206064 (1 of 8 specimens),
      male, 630 mm TL.
  Squaliolus laticaudus Smith et Radcliffe, HUMZ 74972, female, 250 mm TL.
  Oxynotus bruniensis (Ogilby), HUMZ 91383, male, 545 mm TL.
  Squalus acanthias Linnaeus, HUMZ 91533, male, 525 mm TL.

Squatinoidei
  Squatina japonica Bleeker, HUMZ 91670, male, 510 mm TL.

Pristiophoroidei
  Pristiophorus nudipinnis Günther, FSFL-EA735, male, 878 mm TL.

Heterodontoidei
  Heterodontus zebra (Gray), HUMZ 37666, male, 440 mm TL.

Orectoloboidei
  Chiloscyllium punctatum Müller et Henle, HUMZ 109476, male, 720 mm TL.

Carcharhinoidei
  Cephaloscyllium umbratile Jordan et Fowler, HUMZ 35479, male, 382 mm TL.

Lamnoidei
  Pseudocarcharias kamoharai (Matsubara), HUMZ 94348, male, 1,051 mm TL.

  Abbreviations used in figures are listed below :

ab — adductor arcuum branchialium
acc— accessory cartilage (of basibranchial copula)
ad — arcualis dorsalis
bb — basibranchial
bh — basihyal
ccl — cucullaris
cb — ceratobranchial
cdb— cardiobranchial
ch — ceratohyal
eb — epibranchial

exb— extrabranchial cartilage
gr — gill ray
hb — hypobranchial
oes — constrictor oesophagi
pb — pharyngobranchial

Description and Comparison

Each gill arch is essentially composed of five skeletal elements. From dorsal to ventral, these are pharyngobranchial (pb), epibranchial (eb), ceratobranchial (cb), hypobranchial (hb), and basibranchial (bb). Several variations of branchial arches are found among living shark taxa, caused by the fusion and absence of these elements.

Five-gilled taxa (Fig. 1). — The arch 1 does not have the basibranchial, and the anterior end of the ceratobranchial 1 is articulated with the basihyal (bh) loosely or tightly. The hypobranchial 1 is also absent or is a reduced cartilage in the junction between the ceratobranchial 1 and basihyal (Fig. 1D). The other four arches have five elements, but there are specific fusions (or loss) at their ventral portion and the arches 4 and 5.
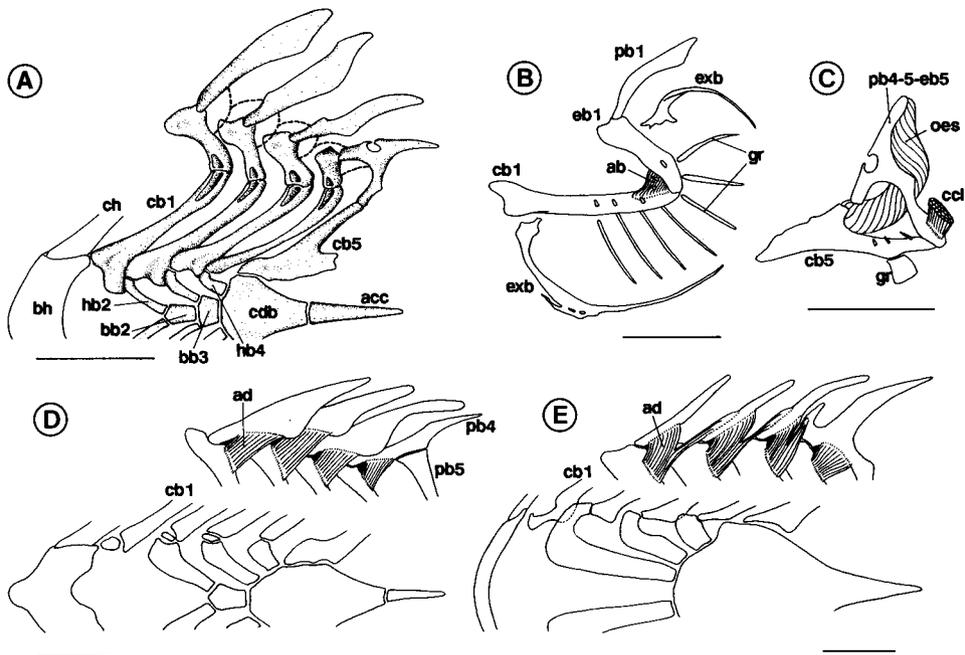

Fig. 1. Branchial arches of five-gilled sharks. A, *Etmopterus lucifer*, dorsal aspect of right half of whole arches unfolded. B-C, lateral aspect of first (B) and fifth arch (C) of same. D-E, dorsal aspects of left dorsal (upper) and basal portions (lower) of *Heterodontus zebra* (D) and *Pristiophorus nudipinnis* (E). A thick broken line in A shows the arcualis dorsalis, and the subspinalis and interpharyngobranchialis are removed. Scales = 10 mm.

The arches 2-5 are supported by the basibranchial copula that comprises hypobranchials and basibranchials at the floor of the throat. A pentagonal or octagonal large plate of the basibranchial copula, the cardiobranchial (cdb ; Gegenbaur, 1898), directly supports ceratobranchial 5 and hypobranchial 4, and thus this large cartilage is regarded as a fused plate of hypobranchial 5 and basibranchials 4 and 5. Behind the cardiobranchial, an accessory branchial cartilage (acc) is present, and it is sometimes fused with the cardiobranchial. Anterior to the cardiobranchial, there are typically two discrete unpaired elements (basibranchials 2 and 3) ; the third one or both of them are often absent (Fig. 1D-E). The arch 5 has a "Y" or "T"-shaped cartilage at the dorsal end, which is a fused cartilage of the epibranchial 5 and pharyngobranchials 4 and 5. This is termed the gill pickax ; in *Heterodontus* (Fig. 1D), the pharyngobranchial 5 is not fused with pharyngobranchial 4. The ceratobranchial 5 has a large lobe at the proximal terminus.

Gill filaments are present on the anterior four arches. These arches also share usually many gill rays elongated radially (gr), adductor muscle (ab ; adductor arcuum branchialium), and dorsal and ventral extrabranchial cartilages (exb ; not the "extra arch") to support the gill filaments (Fig. 1B). The arcualis dorsalis (ad) arises from the pharyngobranchial and is inserted on the epibranchial in the first four arches. Gill filaments and these skeletons and muscles are absent in the fifth arch (Fig. 1C) ; the gill ray is one or a few modified skeletal elements if present. The cucullaris (ccl) suspends epibranchial 5, and the constrictor oesophagi (oes) are
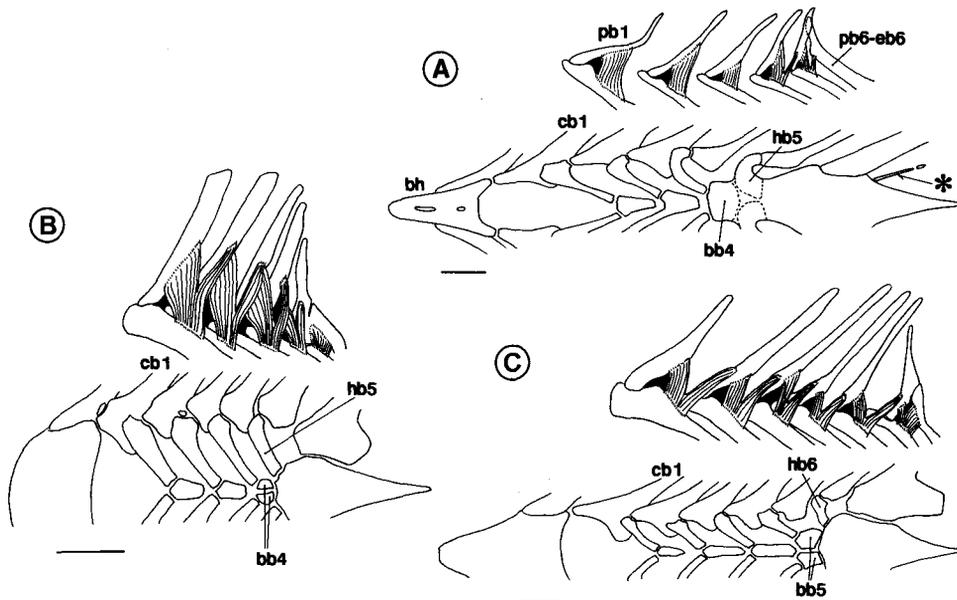

Fig. 2. Branchial arches of hexanchiform sharks. Dorsal aspects of left dorsal (upper) and basal portions (lower) of *Chlamydoselachus anguineus* (A), *Hexanchus griseus* (B), and *Heptranchias perlo* (C). In A, outlines of basibranchial 4 and hypobranchial 5 follows Goodey (1910) and Allis (1923), and the asterisk shows the remnant gill rays of ultimate arch. Scales = 10 mm.

inserted onto the gill pickax and ceratobranchial 5.

Hexanchiformes (Fig. 2). — The arch 1 is identical with that of five-gilled taxa in having the ceratobranchial-basihyal articulation and no basibranchial. The penultimate arch (arch 5 of *Chlamydoselachus* and *Hexanchus*, or arch 6 of *Notorynchus* and *Heptranchias*) has a discrete hypobranchial, gill filaments, an adductor muscle, elongate gill rays, and extrabranchial cartilages, but no discrete basibranchial. These are features of the arch 4 of five-gilled taxa. The ultimate arch is similar to the arch 5 of the latter in many characteristics as follows : the ceratobranchial has an expanded proximal terminus and is articulated with the cardiobranchial ; the pharyngobranchial is not differentiated from the epibranchial ; pharyngobranchial connects with the counterpart of the penultimate arch ; and, there are not gill filaments nor associated skeletons and muscles. In hexanchiforms, the cardiobranchial is composed of the basibranchials of penultimate and ultimate arches and hypobranchial of ultimate arches (in *Chlamydoselachus*, the hypobranchial 5 and the basibranchial 4 are often fused with the cardiobranchial irregularly like Figure 2A, but these are essentially a discrete element; Goodey, 1910 ; Allis, 1923). This is also the same as the cardiobranchial of the five-gilled taxa. Separate basibranchials in front of the cardiobranchial are three in six-gilled *Chlamydoselachus* and *Hexanchus* or four in seven-gilled other hexanchoids, and these are more than those of five-gilled taxa by one or two.

Chlamydoselachus differs from hexanchoid genera in its branchial skeletons and musculature. The basibranchial 4 in *Hexanchus* or the basibranchial 5 in other hexanchoids is paired, a condition not known in other living shark taxa including *Chlamydoselachus*. In hexanchoids, the dorsal end of the ultimate pharyngobranchial is tightly connected with the posterior margin of penultimate pharyngobranchial like *Heterodontus* (Fig. 1D). In *Chlamydoselachus*, the ultimate pharyngobranchial does not connect with the penultimate pharyngobranchial, not to form the gill pickax ; the dorsal end of ultimate pharyngobranchial is somewhat depressed and attached to the ventral side of penultimate pharyngobranchial via loose ligament. The arcualis dorsalis of hexanchoids has two heads of origin, connecting the epibranchial and the succeeding pharyngobranchial as in squaloids (Fig. 1A), *Squatina*, and pristiophorids (Fig. 1E), while this muscle is composed of a single slip binding the pharyngobranchial and epibranchial of the same arch in *Chlamydoselachus* like *Heterodontus* (Fig. 1D) and galeoids. In *Chlamydoselachus*, a few remnant cartilages are visible posterior to ceratobranchial 6 (asterisk in Fig. 2A). These have been described as elements of the seventh gill arch (e.g., Garman, 1885 ; Goodey, 1910), and similar cartilages are known in five-gilled sharks (e.g., *Heterodontus* and carcharhinoid *Galeocerdo* : Hamdy and Khalil, 1973 ; Maisey, 1982). However, these cartilages do not form an arch and are probably reduced gill rays as noted by Allis (1923).

Discussion

The presence of more than five gill arches has not been known in the related groups of living sharks and rays (fossil euselachians, xenacanthids, and holocephali ; Maisey, 1984b), and there is no evidence that five-gilled condition is derived among living euselachians as remarked by previous authors (Gregory, 1933 ; Romer, 1966 ;

Schaeffer, 1967 ; Maisey, 1982). Thus, one or two extra branchial arches of the hexanchiforms should have been added through the evolutionary change. So then, which arch is additional ? If the extra arch(es) has been added behind the original five gills as is implied by the traditional means of numbering branchial units, a series of modifications must be hypothesized through the morphological changes. In particular, the original arch 5 must have acquired gill filaments and associated skeletal elements and muscles, and the additional arch have all the features of arch 5. In seven-gilled taxa, this series of modification must be repeated. Such an evolutionary hypothesis seems unlikely.

Based on comparative anatomy of the branchial arches of living shark taxa, generally four patterns of arches can be distinguished. The arch 1, or α-type, is characterized by the ceratobranchial articulating with the basihyal and not support-ed by the hypobranchial and basibranchial. The ultimate arch, or δ-type, differs from the others in lacking gill filaments and associated skeletal elements and muscles. Also, the ceratobranchial has a lobe-like proximal terminus for articula-tion with the cardiobranchial, and the pharyngobranchial is fused with the epibran-chial. The cucullaris and constrictor oesophagi are inserted onto the δ-arch. The penultimate arch, or γ-type, has a discrete hypobranchial, but its basibranchial is always fused with the cardiobranchial. The pharyngobranchial of γ-arch makes the complete or incomplete gill pickax with the pharyngobranchial of δ-arch. The others (β-type) are second and third arches in five-gills, second to fourth arches in six-gills, or second to fifth arches in seven-gills, which are generally composed of the basic five elements, although the basibranchial tends to be reduced.

Arrangement of branchial arches can be formulated with these four types as follows :

five-gills $\{\alpha, \beta, \beta, \gamma, \delta\}$,
six-gills $\{\alpha, \beta, \beta, \beta, \gamma, \delta\}$, and
seven-gills $\{\alpha, \beta, \beta, \beta, \beta, \gamma, \delta\}$.

As is evident from the fomrulae, it is the addition of β-type arch that is responsible for increases in branchial arch number. This might have occurred through the duplication or insertion onto the original β-type arches in the actual course of evolution. The anteriormost, penultimate, and ultimate arches of hexanchiforms are thus homologous to the arches 1, 4, and 5 of five-gilled taxa respectively, and the same term must be given to these sets of arches.

In the morphological research with adult specimens, I failed to find which β-arch has been actually duplicated or inserted. The unique paired basibranchial of hexanchoid genera, however, should be homologous each other, and the arch including this particular element should be additional. Thus, the first additional (sixth) arch in hexanchoids is regarded as the arch 4 of *Hexanchus* and arch 5 of *Notorynchus* and *Heptranchias* ; for distinction, this arch is called the β'-type. The second additional (seventh) arch of the latter two genera is one of the other β-arches. This particular paired basibranchial was not found in *Chlamydoselachus* in my analysis nor in previous anatomical works (Garman, 1885 ; Fürbringer, 1903 ; Goodey, 1910 ; Allis, 1923). This fact suggests that the addition of branchial arch in *Chlamydoselachus* occurred independently of hexanchoids. This idea is support-ed by other differences between the two ; hexanchoids differs from *Chlamydoselachus*
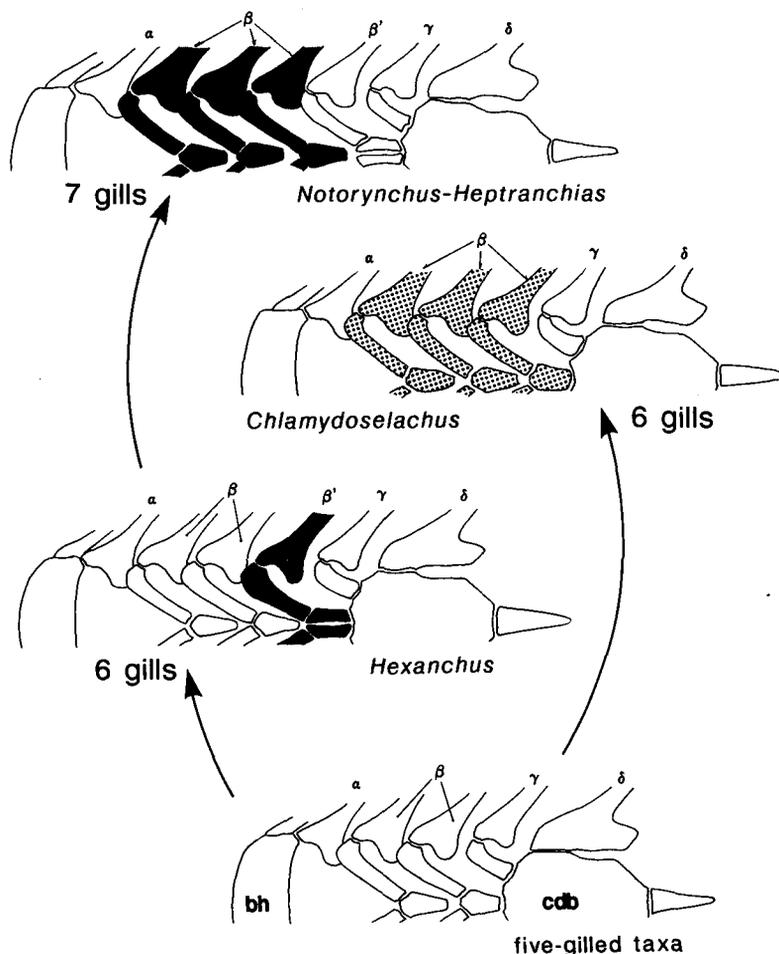
Fig. 3. A preliminary hypothesis of the increase of branchial arches in the Hexanchiformes. The arch with half tone shows the probable additional arch; in *Chlamydoselachus* and seven-gilled hexanchoids, the additional arch is one of three β-type arches.

by the presence of gill pickax (absent in the latter) and the two-headed origin of arcualis dorsalis (one-headed). These conditions of hexanchoids are should be derived and are common to squaloids, *Squatina*, and pristiophorids, which might be allied to hexanchoids (Maisey, 1984a).

Figure 3 shows the present hypothesis on the extra branchial arch discussed above. Identification of β-type arches must be further evaluated through examination of embryos. This hypothesis also reflects the hexanchiform relationships. Extra branchial arch was often considered as one of common features of *Chlamydoselachus* and hexanchoids (Compagno, 1977; Maisey and Wolfram, 1984). However, the present hypothesis agrees with the opposite idea that denies the monophyly of these two lineages (e.g., Holmgren, 1941; Schaeffer, 1967; Thies,

1987).

Acknowledgments

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