GILL ARCHES OF FISHES OF THE SUBORDER NOTOTHENIOIDEI (PISCES, PERCIFORMES)

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Abstract: Gill-arch structures of 34 species belonging to five families of the suborder Notothenioidei were studied in detail. Remarkable differences among notothenioid gill arches were recognized mainly in the degree of ossification of basibranchials, the dentition on the epibranchial, and the shapes of the hypobranchial and pharyngobranchials.

On the basis of the character analyses of these osteological features, the relationships among notothenioid families were inferred. The family Bovichthyidae was recognized as the most primitive group among five families, while the Channichthyidae seemed to be the most advanced one. The Harpagiferidae was clearly identified as a distinct family from the Nototheniidae.

1. Introduction

Fishes of the suborder Notothenioidei of the order Perciformes, consisting of the Bovichthyidae, Nototheniidae, Harpagiferidae, Bathydraconidae and Channichthyidae, are mostly limited to the Antarctic and Subantarctic waters in distribution and are the most dominant group of the benthic ichthyofauna in the Southern Ocean (ANDRIASHEV, 1965; DEWITT, 1971). Therefore, the study on the relationships of the Notothenioidei is thought to provide important information on the evolution of the Antarctic biota. However, there have been only a few systematic studies on the notothenioid fishes (EAKIN, 1981; VOSKOBOYNIKOVA, 1982), and their relationships are still uncertain.

The present study deals with gill-arch structures and does not include detailed comparative study of whole osteological features of fishes which will be dealt with elsewhere. The purpose of the present study is to discuss the relationships among families of the Notothenioidei mainly based on osteological features of their gill arches.

2. Materials and Methods

Materials used in the present study were specimens of 34 species belonging to five families of the suborder Notothenioidei (Table 1). Most of these were collected by

Table 1. List of fishes examined in the present study.

Family and species	No. of specimens	Standard length (mm)
Family Bovichthyidae		
Bovichthys variegatus (RICHARDSON)	2	95, 99
Pseudaphritis urvilli (CUVIER and VALENCIENNES)	1	80
Cottoperca gobio (GÜNTHER)	2	202, 242
Family Nototheniidae		
Notothenia kempi NORMAN	2	250, 269
N. nybelini (BALUSHKIN)	1	138
N. gibberifrons LÖNNBERG	1	154
N. nudifrons LÖNNBERG	1	97
Patagonotothen ramsayi (REGAN)	2	160, 204
Pagothenia borchgrevinki (BOULENGER)	2	195, 198
Trematomus bernacchii BOULENGER	2	126, 163
T. hansoni BOULENGER	2	124, 242
T. scotti BOULENGER	1	108
Dissostichus mawsoni NORMAN	1	105
Pleuragramma antarcticum BOULENGER	2	146, 169
Aethotaxis mitopteryx DEWITT	2	102, 148
Family Harpagiferidae		
Harpagifer antarcticus (NYBELIN)	2	44, 60
Artedidraco orianae REGAN	1	101
Histiodraco velifer (REGAN)	1	119
Family Bathydraconidae		
Gerlachea australis DOLLO	2	183, 231
Vomeridens infuscipinnis (DEWITT)	1	149
Gymnodraco acuticeps BOULENGER	2	210, 235
Family Channichthyidae		
Champsocephalus gunnari LÖNNBERG	6	200–363
Pagetopsis macropterus (BOULENGER)	1	201
P. maculatus BARSUKOV and PERMITIN	1	156
Neopagetopsis ionah NYBELIN	1	440
Pseudochaenichthys georgianus NORMAN	6	333–434
Channichthys rhinoceratus RICHARDSON	1	482
Chaenocephalus aceratus (LÖNNBERG)	4	221–339
Cryodraco antarcticus DOLLO	3	210–419
Chionobathyscus dewitti ANDRIASHEV and NEELOV	2	205, 241
Chionodraco hamatus (LÖNNBERG)	1	352
C. myersi DEWITT and TYLER	3	154–206
C. rastrospinosus DEWITT and HUREAU	5	314–353
Chaenodraco wilsoni REGAN	3	181–222

Japan Marine Fishery Resource Research Center in the Ross Sea (1978–1979) (IWAMI and ABE, 1981) and off the South Shetland Islands (1980–1981 and 1981–1982) (IWAMI and ABE, 1982). Others were from the collection of the National Institute of Polar Research.

Gill arches were dissected as unit from a given specimen and were cleared and stained by the method of DINGERKUS and UHLER (1977) with a slight modification.

The terminology of the bones follows NELSON (1969).

3. Osteology

Endoskeletal elements of notothenioid gill arches are composed of one median basihyal, four median basibranchials, three pairs of hypobranchials, five pairs of ceratobranchials, four pairs of epibranchials and three (occasionally two) pairs of pharyngobranchials. These elements are numbered according to their respective arches. Dermal elements associated with these endoskeletal elements include gill rakers and tooth plates.

Among notothenioid fishes, there is no remarkable difference in morphological features of ceratobranchials. The number and shape of gill rakers are variable even between closely related species, *e.g.*, *Chionodraco hamatus* and *Chionodraco rastrospinosus* (DeWitt and Hureau, 1979), and are supposed to be not useful for discussing the relationships among genera and families of the Notothenioidei. Therefore, ceratobranchials and gill rakers were not shown in most of figures in the present study.

Family Bovichthyidae (Figs. 1A–D)

The shape of the basihyal varies among species of the Bovichthyidae. The basihyal of *Pseudaphritis urvilli* (Fig. 1A) is narrow and triangular and that of *Bovichthys variegatus* (Fig. 1B) is fan-shaped, while *Cottoperca gobio* (not shown) has the rod-like

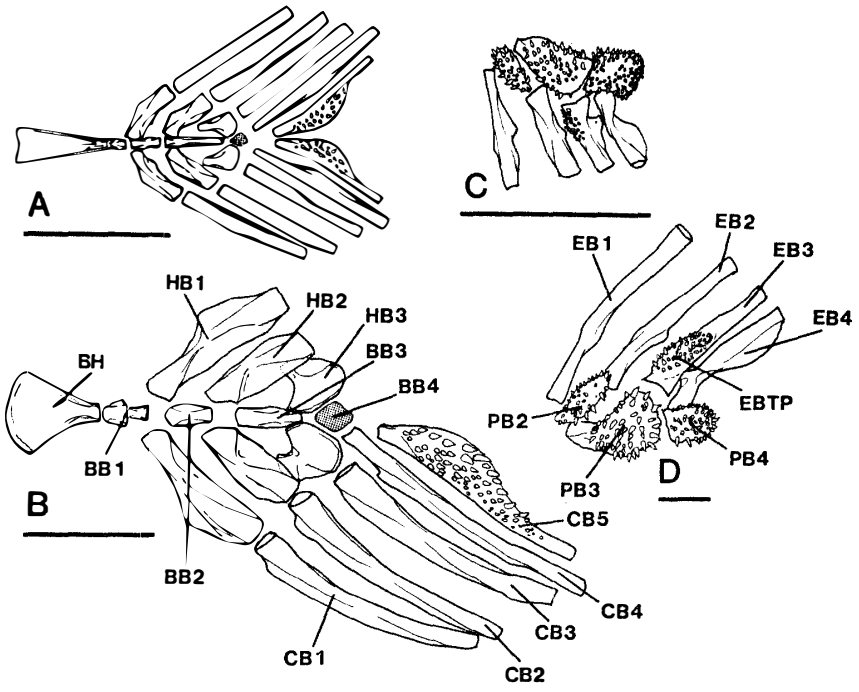

Fig. 1. Gill arches of fishes of the family Bovichthyidae. A, Pseudaphritis urvilli *(lower part, dorsal view); B,* Bovichthys variegatus *(lower part, dorsal view); C,* Pseudaphritis urvilli *(upper part, right side, ventral view); and D,* Cottoperca gobio *(upper part, left side, ventral view). Cartilaginous portions are shown by dots. Scales 5 mm. BB, basibranchial; BH, basihyal; CB, ceratobranchial; EB, epibranchial; EBTP, epibranchial tooth plate; HB, hypobranchial; and PB, pharyngobranchial.*

basihyal. The basibranchial series of *B. variegatus* seems distinctive in having four ossified elements between the basihyal and cartilaginous fourth basibranchial. The first basibranchial is divided into two bony elements. One of which is attached to the basihyal anterodorsally and is articulated with hypohyals laterally, and the other posterior element joins the second basibranchial posteriorly. The third and fourth ossified basibranchial bones correspond to the second and third basibranchials respectively. In all of three species of bovichthyids examined, the first, second and third basibranchials are recognized as ossified elements, and the fourth basibranchial is cartilaginous.

Other osteological features of gill-arch structures are relatively similar among bovichthyid species examined. Some tooth plates are fused with endoskeletal supports such as the fifth ceratobranchial (Figs. 1A, B), third epibranchial (Figs. 1C, D) and three pharyngobranchials (Figs. 1C, D). Among notothenioid families, the presence of the tooth plate on the epibranchial is a character restricted to this family. The thrid hypobranchial is flattened and triangular as that of the other notothenioid fishes except for channichthyids. The first pharyngobranchial is absent (Figs. 1C, D). The second, third and fourth pharyngobranchials with fused tooth plates are similar

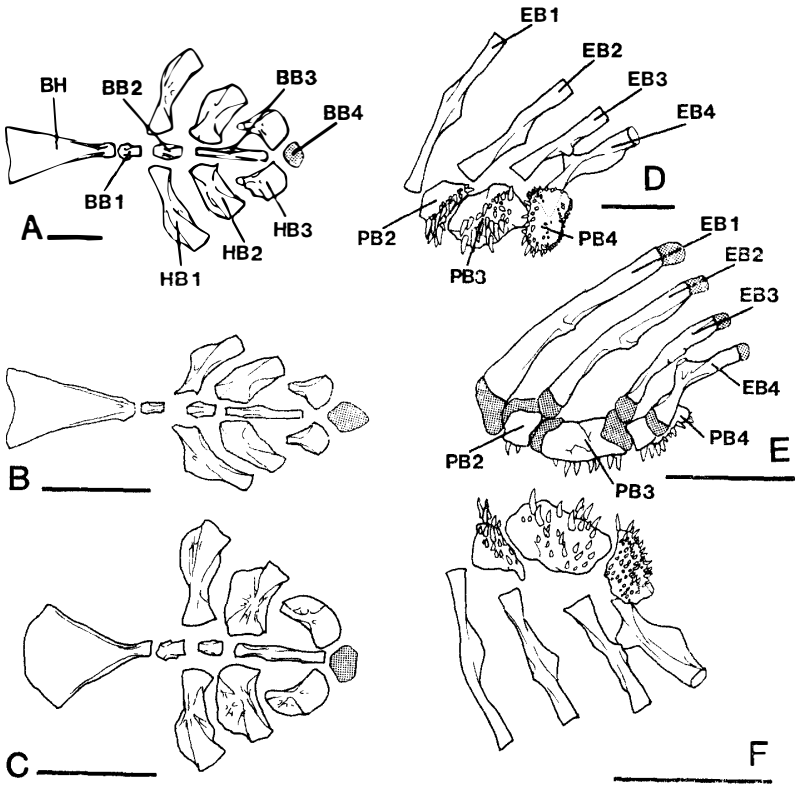

Fig. 2. Gill arches of fishes of the family Notothenidae. A, Notothenia kempi *(lower part, dorsal view); B,* Patagonotothen ramsayi *(lower part, dorsal view); C,* Trematomus bernacchii *(lower part, dorsal view); D,* Notothenia kempi *(upper part, left side, ventral view); E,* Aethotaxis mitopteryx *(upper part, right side, dorsal view); and F,* Trematomus bernacchii *(upper part, right side, ventral view). Cartilaginous portions are shown by dots. Scales 5 mm. Abbreviations follow those in Fig. 1.*

to those of notothenioids except for channichthyids in shape.

Family Nototheniidae (Figs. 2A–F)

Arches of the Nototheniidae are organized in much the same manner as those of the Bovichthyidae, except that there is no tooth plate on the third epibranchial (Figs. 2D–F). The basihyal which is relatively similar among nototheniid species examined is triangular and fan-shaped (Figs. 2A–C). The first, second and third basibranchials are recognized as ossified elements, and the posteriormost one is the longest (Figs. 2A–C). As mentioned above, there is no tooth plate on the epibranchial and it occurs only on the fifth ceratobranchial and three pharyngobranchials (Figs. 2D–F). The third hypobranchial of nototheniid fishes is basically presented as a triangular bony element (Figs. 2A–C).

Family Harpagiferidae (Figs. 3A–C)

Most of osteological features of this family agree with those of the Nototheniidae. Gill-arch structures of *Harpagifer*, *Artedidraco* and *Histiodraco* show a close resemblance among the three and no specific feature in the shape of the element.

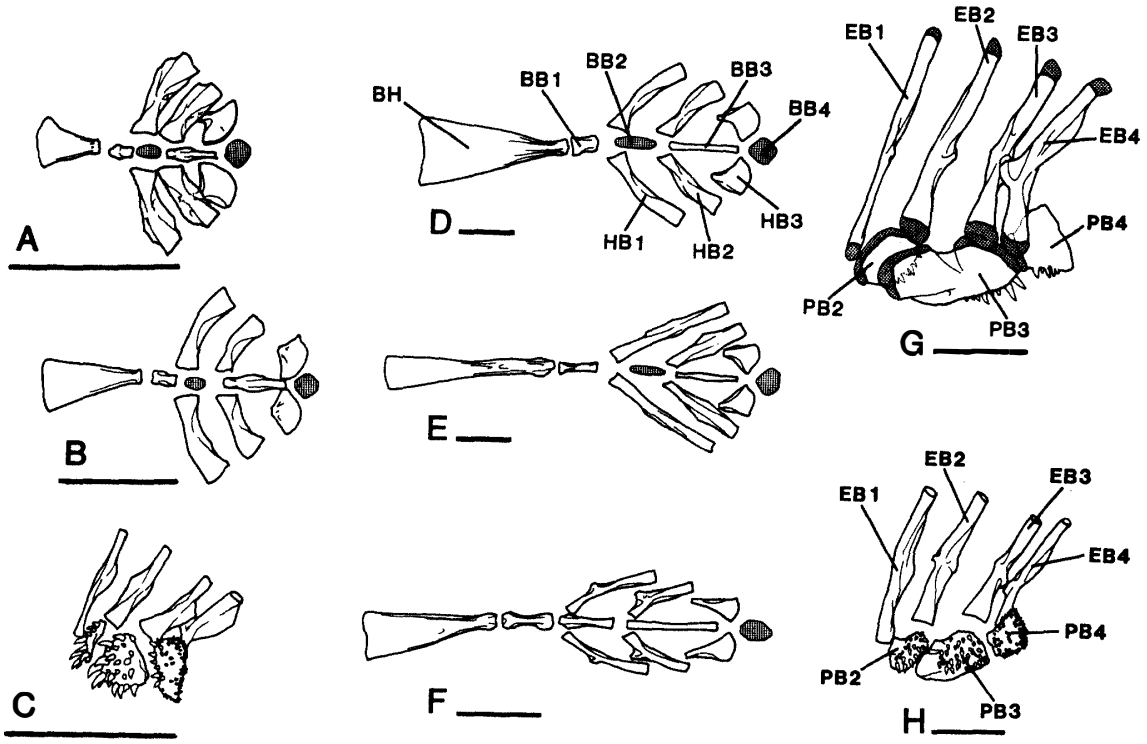

Fig. 3. Gill arches of fishes of the families Harpagiferidae and Bathydraconidae. A, Harpagifer antarcticus (*lower part, dorsal view*); *B,* Artedidraco orianae (*lower part, dorsal view*); *C,* Harpagifer antarcticus (*upper part, left side, ventral view*); *D,* Gymnodraco acuticeps (*lower part, dorsal view*); *E,* Gerlachea australis (*lower part, dorsal view*); *F,* Vomeridens infuscipinnis (*lower part, dorsal view*); *G,* Gymnodraco acuticeps (*upper part, right side, dorsal view*); *and H,* Gerlachea australis (*upper part, left side, ventral view*). *Cartilaginous portions are shown by dots. Scales 5 mm. Abbreviations follow those in Fig. 1.*

The member of this family seems distinctive in having the cartilaginous second basibranchial (Figs. 3A, B) which also occurs in bathydraconids and channichthyids.

Family Bathydraconidae (Figs. 3D–H)

Arches of bathydraconids are organized in relatively the same manner as those of harpagiferids. The major exception which is found in the basibranchial series of *Vomeridens infuscipinnis* is the presence of the well-developed and ossified second basibranchial (Fig. 3F). In the other bathydraconid fishes examined, *Gymnodraco acuticeps* (Fig. 3D) and *Gerlachea australis* (Fig. 3E), the second basibranchial is usually fully cartilaginous. The third hypobranchial and basihyal of bathydraconid fishes are also slightly narrower and longer than those of nototheniid and harpagiferid fishes (Figs. 3D–F).

Family Channichthyidae (Figs. 4A–E)

This family is distinctive in having the cartilaginous first and second basibranchials, the third hypobranchial with a slender rod-like shape (Figs. 4A–C) and only two pharyngobranchials (Figs. 4D, E).

The first and second basibranchials are not ossified even in a large adult. The only ossified element, the third basibranchial, is slender and cylindrical in shape. In

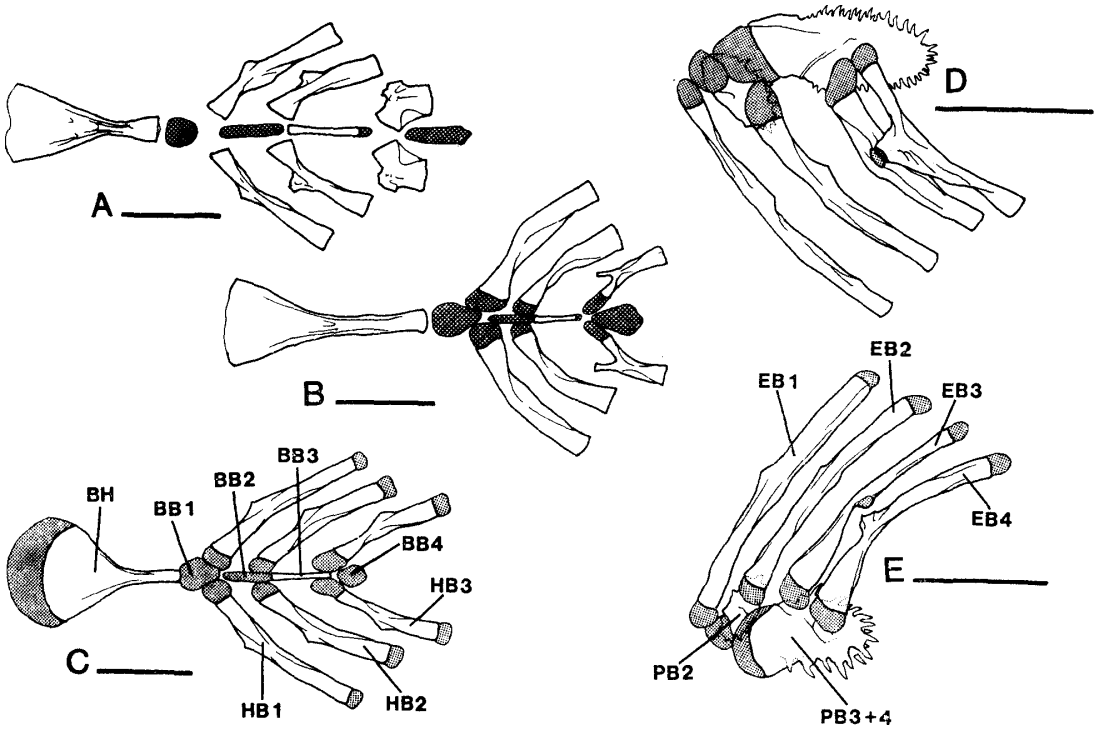

Fig. 4. Gill arches of fishes of the family Channichthyidae. A, Champsocephalus gunnari *(lower part, dorsal view); B,* Neopagetopsis ionah *(lower part, dorsal view); C,* Chionodraco rastrospinosus *(lower part, dorsal view); D,* Champsocephalus gunnari *(upper part, left side, dorsal view); and E,* Chionodraco rastrospinosus *(upper part, right side, dorsal view). Cartilaginous portions are shown by dots. Scales 10 mm. Abbreviations follow those in Fig. 1.*

some species, *e.g.*, *Pagetopsis maculatus*, *Pseudochaenichthys georgianus* and *Channichthys rhinoceratus*, even the third basibranchial is cartilaginous (not shown). However, *Pagetopsis macropterus* which is thought to be most closely related to *P. maculatus* in the Channichthyidae appears to have the ossified third basibranchial, and the third basibranchial exhibits different features, ossified and unossified, between the closely related species. This indicates that the systematic value and conservativeness of the osteological feature of the third basibranchial cannot be evaluated easily. The shape of the third hypobranchial slightly varies among genera of this family. *Champsocephalus* has the flat and short hypobranchial (Fig. 4A), while *Channichthys*, *Chaenocephalus*, *Cryodraco*, *Chionobathyscus*, *Chionodraco* and *Chaenodraco* have the long and rod-like hypobranchial which resembles the first and second hypobranchials in shape (Fig. 4C). The third hypobranchial of *Pagetopsis*, *Neopagetopsis* and *Pseudochaenichthys* bears an anterior-pointed process at about the midpoint of its outer margin. All channichthyids share the same condition of the osteological feature of the pharyngobranchial (Figs. 4D, E). The first pharyngobranchial is absent. The anterior element with fused tooth plate, which joins the second epibranchial, is supposed to be the second pharyngobranchial. The posterior element is articulated with the third and fourth epibranchials and is obviously larger than the third or fourth pharyngobranchials of the other notothenioids. Therefore, it seems to be reasonable that the posterior one is formed by the fusion between the third and fourth pharyngobranchials.

4. Discussion

A summary of osteological data of five notothenioid families mentioned above is presented in Table 2. Judging from these data, variations in gill-arch structures of

Table 2. Distinctive osteological features of gill arches of five notothenioid families.

Characters	Bovichthyidae	Nototheniidae	Harpagiferidae	Bathydraconidae	Channichthyidae
1st basibranchial	Ossified	Ossified	Ossified	Ossified	Cartilaginous
2nd basibranchial	Ossified	Ossified	Cartilaginous	Cartilaginous	Cartilaginous
3rd hypobranchial	Triangular	Triangular	Triangular	Triangular	Rod-like
3rd epibranchial	Toothed	Untoothed	Untoothed	Untoothed	Untoothed
3rd and 4th pharyngobranchials	Divided	Divided	Divided	Divided	Fused

notothenioid fishes mainly involve the degree of ossification of basibranchials, the dentition on the epibranchial, and the shape of the hypobranchial and pharyngobranchial.

It is supposed that the primitive percoid branchial skeleton consists of three ossified and one cartilaginous basibranchials (JOHNSON, 1980). This condition (three ossified and one cartilaginous basibranchials) is recognized in all bovichthyid and nototheniid fishes examined, and exceptionally in one bathydraconid species of *V. infuscipinnis*. In comparison with osteological features of the Harpagiferidae and Channichthyidae, the basibranchial series of the Bathydraconidae is fundamentally thought to show "two ossified and two cartilaginous" condition as observed in *G. acuticeps* and *G. australis*. Therefore, if the cartilaginous second basibranchial is not

acquired independently in each of the harpagiferid, bathydraconid and channichthyid, the condition observed in the basibranchial series of *V. infuscipinnis* is supposed to be the secondarily derived form rather than the primitive form as recognized in the bovichthyid and nototheniid.

The family Harpagiferidae created by GILL (1862) had been involved in the family Nototheniidae (LÖNNBERG, 1905; REGAN, 1913, 1914; WAITE, 1916; NORMAN, 1937) until NORMAN (1938) treated the harpagiferid as a distinct family again. Recently, GREENWOOD *et al.* (1966) and NELSON (1976) included harpagiferids in the family Nototheniidae, and NELSON (1976) placed them in the subfamily Harpagiferinae under the family Nototheniidae as proposed by REGAN (1914). However, the present result suggests their classification improbable because harpagiferids share a derived condition (the cartilaginous second basibranchial) with bathydraconids and channichthyids and are thought to be more closely related to these two groups than to nototheniids.

The Channichthyidae differ most noticeably from the other notothenioid fishes in having two pharyngobranchials, the cartilaginous first basibranchial and the third hypobranchial with a slender rod-like shape.

It is usually thought that the separation of the third and fourth pharyngobranchials appears to be rather widespread condition (ROSEN, 1964). Therefore, the third and fourth pharyngobranchials of channichthyids which are joined together are supposed to show an advanced feature. The reduction of the ossification of the first basibranchial may be considered to be the derived condition such as reduction of the ossification of the second basibranchial. The slender rod-like hypobranchial of channichthyids is easily guessed as a derived form from the triangular condition, since the anterior-pointed process on the third hypobranchial of some channichthyids (*Pagetopsis*, *Neopagetopsis* and *Pseudochaenichthys*) is supposed to be a remnant of the anterior angle of the triangular hypobranchial in most notothenioid fishes.

On the basis of the character analyses mentioned above, the relationships among five families of the suborder Notothenioidei are inferred, but the small number of useful characters make the proposed relationships unstable. In the present study, the following considerations can be suggested: (1) The Bovichthyidae and Nototheniidae show the typical percoid condition in their gill-arch structure; (2) the harpagiferid appears not to belong to the Nototheniidae and forms a distinctive family, namely the Harpagiferidae; and (3) the Channichthyidae shows the autapomorphic feature on the three out of five osteological characters examined, and this indicates the Channichthyidae is the most advanced group in the suborder Notothenioidei. The reconstruction of the phylogenetic relationships or cladograms, which should be investigated based on a larger number of more useful characters and more detailed character analyses, is left for the future study.

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