

TOPOGRAPHY OF THE CEPHALIC SENSORY CANAL
SYSTEM OF THE FAMILY CHANNICHTHYIDAE
(PERCIFORMES, NOTOTHENIOIDEI)

Tetsuo IWAMI¹, Akane MATSUO² and Hideki NUMANAMI¹

¹Laboratory of Biology, Tokyo Kasei Gakuin University,
2600 Aihara, Machida-shi, Tokyo 194-0292

²Kinryu Prefectural Protective Care School,
2339-2 Kinryu, Saga 849-0906

Abstract: Morphological peculiarities of cephalic sensory canals of 15 species of the family Channichthyidae are analyzed. Two species of the Bathydraconidae are also studied as the sister group of the Channichthyidae. The general structural plan of the cephalic sensory canal system in the Channichthyidae is considered to be the percoid type. Some morphological variations among channichthyid species are recognized in the connection between the preoperculo-mandibular and temporal canals, the pore numbers of the infraorbital, preoperculo-mandibular and supratemporal canals, and the development of prolonged canaliculi of the infraorbital canal. In comparison with the morphological variations in the cephalic sensory canal systems of the Nototheniidae, however, those of the Channichthyidae are not so conspicuous. Relationships among some channichthyid species are discussed based on the evaluation of these morphological features.

key words: Channichthyidae, cephalic sensory canal, systematics, Notothenioidei, lateral line

Introduction

The Channichthyidae is characterized most noticeably by having no circulating oxygen-carrier hemoglobin and is thought to be an evolutionary advanced group of the suborder Notothenioidei. This family is composed of 15 (IWAMI and KOCK, 1990) or 19 (BALUSHKIN, 1996a) species in 11 genera, and all channichthyid species are endemic to the Antarctic Ocean except for the Patagonian species *Champscephalus esox*.

Lateral line canals are used in taxonomic investigations of many fish groups. Notothenioid fishes also have shown remarkable changes in the lateral line canal system through their evolution (BALUSHKIN, 1996b). Although the relationships among structure, function and physiology of the lateral line systems of the Notothenioidei have been actively studied (COOMBS and MONTGOMERY, 1994; MONTGOMERY *et al.*, 1994; JANSSEN, 1996; MONTGOMERY, 1997; MONTGOMERY and SUTHERLAND, 1997), only a few morphological studies on the cephalic sensory canal system have been done on the family Nototheniidae (JAKUBOWSKI, 1970, 1971; ANDERSEN, 1984; BALUSHKIN, 1990, 1996b).

With regard to the Channichthyidae, morphological features of the lateral line canal

system, in particular the cephalic sensory canal system, have been little studied except for a descriptive species diagnosis (ANDRIASHEV and NEELOV, 1978; DEWITT and HUREAU, 1979). As suggested by BALUSHKIN (1990), the identification of elementary structural units of the cephalic sensory canal system by detailed positioning of neuromasts is indispensable for comparative morphological study of the cephalic sensory canal system. The aim of this paper is to describe the topography of the cephalic sensory canal system of the Channichthyidae as a preliminary work for discussing the evolutionary process of this family.

Materials and Methods

The fish used in the present study were taken from the collection of Tokyo Kasei Gakuin University except for 5 specimens of *Champocephalus esox* from the Natural History Museum, London and 6 specimens of *Dacodraco hunteri* from the Antarctic Division, Hobart. The number of specimens examined and the range of the standard length by species are as follows.

Family Channichthyidae

- Chaenocephalus aceratus* (LÖNNBERG), 12 specimens (201–540 mm SL)
- Chaenodraco wilsoni* REGAN, 2 specimens (178–219 mm SL)
- Champocephalus esox* (GÜNTHER), 5 specimen (142–194 mm SL)
- Champocephalus gunnari* LÖNNBERG, 9 specimens (270–395 mm SL)
- Channichthys rhinoceratus* RICHARDSON, 4 specimens (233–315 mm SL)
- Chionobathyscus dewitti* ANDRIASHEV and NEELOV, 2 specimens (189–245 mm SL)
- Chionodraco hamatus* (LÖNNBERG), 1 specimen (313 mm SL)
- Chionodraco myersi* DEWITT and TYLER, 2 specimens (285–295 mm SL)
- Chionodraco rastrispinosus* DEWITT and HUREAU, 8 specimens (255–352 mm SL)
- Cryodraco antarcticus* DOLLO, 5 specimens (217–355 mm SL)
- Dacodraco hunteri* WAITE, 6 specimens (168–214 mm SL)
- Neopagetopsis ionah* NYBELIN, 3 specimens (223–400 mm SL)
- Pagetopsis macropterus* (BOULENGER), 5 specimens (112–215 mm SL)
- Pagetopsis maculatus* BARSUKOV and PERMITIN, 2 specimens (127–155 mm SL)
- Pseudochaenichthys georgianus* NORMAN, 6 specimens (326–470 mm SL)

Family Bathydraconidae

- Gymnodraco acuticeps* BOULENGER, 4 specimens (250–312 mm SL)
- Parachaenichthys charcoti* (VAILLANT), 1 specimen (broken; ca 400 mm SL)

MAYER's hematoxyline was injected into the cephalic sensory canals according to the procedure of JAKUBOWSKI (1967) with slight modifications. Dehydration and clearing in xylen were not performed to avoid deterioration of the specimens. The lateral line was also traced with cyanin-blue (SARUWATARI *et al.*, 1997). Some specimens were cleared and stained mainly following the method of DINGERKUS and UHLER (1977) for osteological observation of the elements supporting the cephalic sensory canals. The terminology of the canals follows that of ANDERSEN (1984).

Canal Topography

General plan

In all members of the Channichthyidae, the cephalic sensory canal system is basically arranged in a common plan of the percoid type and its general structural plan is also found in the Nototheniidae (JAKUBOWSKI, 1970, 1971; BALUSHKIN, 1990) (Fig. 1a). The cephalic

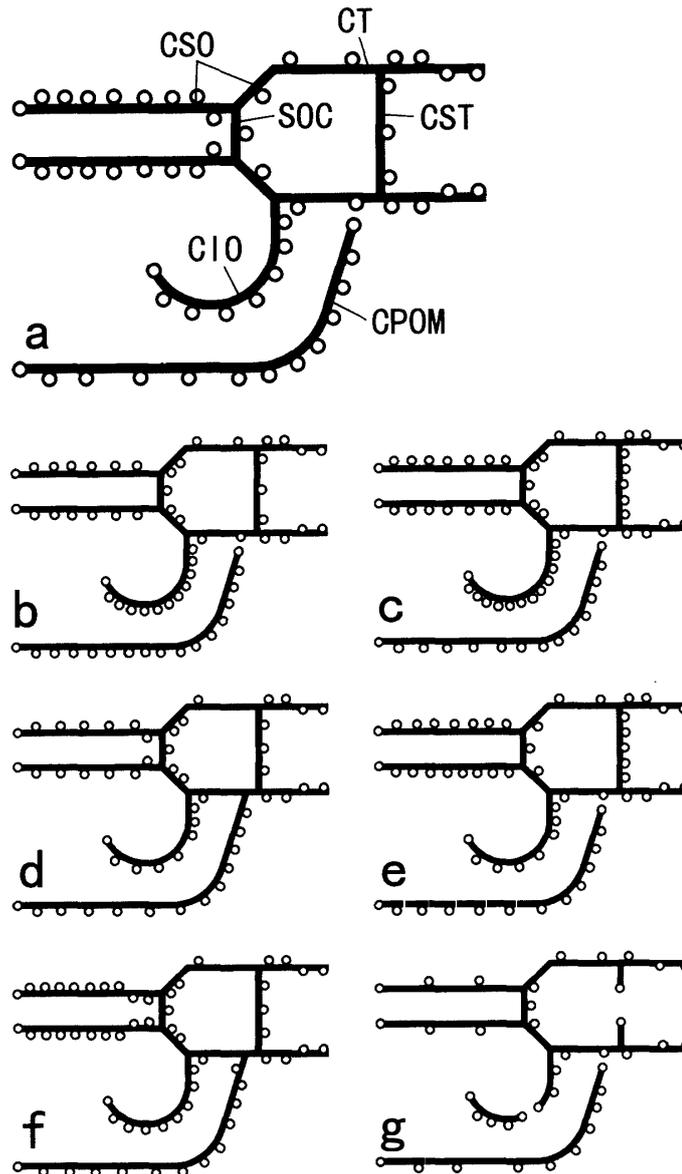


Fig. 1. Diagrammatic topography of the cephalic sensory canal systems in the Channichthyidae (a-f) and Bathydraconidae (g). a) *Chaenocephalus aceratus* (typical form of the Channichthyidae), b) *Champscephalus gunnari*, c) *Champscephalus esox*, d) *Pseudochaenichthys georgianus*, e) *Neopagetopsis ionah*, f) *Chiono-draco myersi* and g) *Gymnodraco acuticeps*. Open circles show the positions of the canal pores. CIO, infraorbital canal; CPOM, preoperculo-mandibular canal; CSO, supraorbital canal; CST, supratemporal canal; CT, temporal canal; and SOC supraorbital commissure.

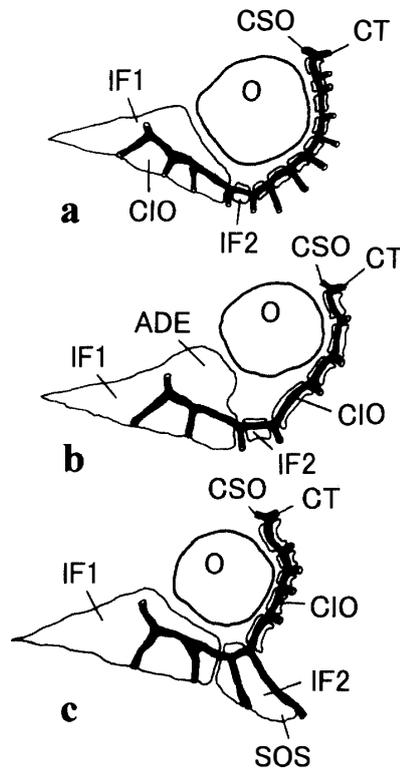


Fig. 2. Diagrams of the infraorbital canals and infraorbital bones (left side). a) *Champscephalus gunnari*, b) *Chaenocephalus aceratus* and c) *Pseudochaenichthys georgianus*. ADE, anterodorsal expansion; CIO, infraorbital canal; CSO, supraorbital canal; CT, temporal canal; IF1, 1st infraorbital bone; IF2, 2nd infraorbital bone; O, orbit; and SOS, suborbital stay.

sensory canals are composed of the four-paired elements and two transverse canals connecting the left and right elements. The four-paired elements include supraorbital (CSO), infraorbital (CIO), temporal (CT) and preoperculo-mandibular (CPOM) canals. The left and right CT's are connected by the supratemporal canal (CST) and also the CSO's on both sides are connected by the supraorbital commissure (SOC) with a single pore in the middle, namely the coronal pore. The CSO, CIO and CT are connected with each other. The CSO is connected to the CIO and CT behind the orbit, and the CT joins the lateral line canal above the pectoral girdle. The CPOM is not connected to the CT except for two species, *Pseudochaenichthys georgianus* and *Chionodraco myersi* (Fig. 1d and 1f). The prolonged canaliculi are developed in the CSO, CT, CST, SOC and especially in the CIO (Fig. 2). The number of pores of the cephalic sensory canals in each species of the Channichthyidae is listed in Table 1.

Supraorbital canals (CSO)

The CSO is derived from tubular structures developed on the dorsal surface of the frontal and also supported by the nasal anteriorly. In all channichthyid species examined, the CSO is continuous and not divided into any sections. This condition is common among notothenioid fishes except for the pelagic nototheniid species, *Pleuragramma antarcticum*, in which the CSO is split into two sections (ANDERSEN, 1984). In the

Table 1. List of the number of pores of the cephalic sensory canals in the Channichthyidae and Bathydraconidae (with asterisk).

Species	N	CSO		CIO		CPOM	
		Range	Average	Range	Average	Range	Average
<i>Chaenocephalus aceratus</i>	12	9-12	10.6	8-9	8.1	12-15	13.1
<i>Chaenodraco wilsoni</i>	2	9	9.0	8-9	8.8	12-14	13.0
<i>Champocephalus esox</i>	5	8-10	9.5	11-14	12.8	15-17	15.8
<i>Champocephalus gunnari</i>	9	8-10	9.2	11-13	11.9	15-18	16.6
<i>Channichthys rhinoceratus</i>	4	7-10	8.5	8-10	8.4	11-14	12.7
<i>Chionobathyscus dewitti</i>	2	9-12	10.5	7-9	8.0	13	13.0
<i>Chionodraco hamatus</i>	1	11-13	12.0	8-9	8.5	12	12.0
<i>Chionodraco myersi</i>	2	10-12	11.3	8-9	8.5	13-14	13.5
<i>Chionodraco rastrispinosus</i>	8	9-13	10.7	8-11	9.3	12-14	13.2
<i>Cryodraco antarcticus</i>	5	8-13	10.2	6-9	7.6	13-14	13.3
<i>Dacodraco hunteri</i>	6	6-9	7.2	8	8.0	11-13	12.2
<i>Neopagetopsis ionah</i>	3	10-12	10.5	7-10	8.3	12-14	13.2
<i>Pagetopsis macropterus</i>	5	8-10	9.2	8-9	8.5	11-14	12.6
<i>Pagetopsis maculatus</i>	2	7-10	8.5	8-9	8.3	12-13	12.5
<i>Pseudochaenichthys georgianus</i>	6	8-9	8.6	7-10	8.2	12-13	12.9
<i>Gymnodraco acuticeps*</i>	4	4-5	4.1	5-6+3	5.1+3.0	9-10	9.7
<i>Parachaenichthys charcoti*</i>	1	7	7.0	8-9	8.5	9-10	9.5

Species	CST		CT		SOC	
	Range	Average	Range	Average	Range	Average
<i>Chaenocephalus aceratus</i>	3	3.0	6	6.0	1	1.0
<i>Chaenodraco wilsoni</i>	3	3.0	6	6.0	1	1.0
<i>Champocephalus esox</i>	4-6	5.0	6	6.0	1	1.0
<i>Champocephalus gunnari</i>	3	3.0	6	6.0	1	1.0
<i>Channichthys rhinoceratus</i>	3	3.0	6	6.0	1	1.0
<i>Chionobathyscus dewitti</i>	3	3.0	6	6.0	1	1.0
<i>Chionodraco hamatus</i>	3	3.0	6	6.0	1	1.0
<i>Chionodraco myersi</i>	3	3.0	5	5.0	1	1.0
<i>Chionodraco rastrispinosus</i>	3	3.0	6	6.0	1	1.0
<i>Cryodraco antarcticus</i>	3	3.0	6	6.0	1	1.0
<i>Dacodraco hunteri</i>	3	3.0	6	6.0	1	1.0
<i>Neopagetopsis ionah</i>	4-7	5.3	6	6.0	1	1.0
<i>Pagetopsis macropterus</i>	3	3.0	6	6.0	1	1.0
<i>Pagetopsis maculatus</i>	3	3.0	6	6.0	1	1.0
<i>Pseudochaenichthys georgianus</i>	3-4	3.5	5	5.0	1	1.0
<i>Gymnodraco acuticeps*</i>	1+1	1+1	5	5.0	1	1.0
<i>Parachaenichthys charcoti*</i>	3	3.0	5-6	5.5	1	1.0

CIO, infraorbital canal ; CSO, supraorbital canal ; CST supratemporal canal ; CT, temporal canal ; CPOM, preoperculo-mandibular canal ; N, number of specimens examined ; SOC, supraorbital commissure ; +, the canals are divided into a number of sections.

Channichthyidae the maximum number of pores in the CSO is 13, which is found in *Cryodraco antarcticus*, *Chionodraco hamatus* and *Chionodraco rastrispinosus*. In contrast, the number of pores in the CSO is relatively low in *Pseudochaenichthys georgianus*, *Dacodraco hunteri*, *Channichthys rhinoceratus* and *Chaenodraco wilsoni*, and there are not more than 10 pores in these four species. In the posterior part of the CSO, which is defined as the section from the connection with the CIO and CT to that with SOC, most channichthyids have some prolonged canaliculi directed to the center of the occiput region. However, no trace of canaliculus is found in the posterior part of the CSO of *Dacodraco hunteri* or *Channichthys rhinoceratus*. In eight of the 11 channichthyid genera, *Pagetopsis*, *Pseudochaenichthys*, *Neopagetopsis*, *Chaenocephalus*, *Chionobathyscus*, *Cryodraco*, *Chionodraco* and *Chaenodraco*, well developed canaliculi are usually associated with the frontal part of the CSO just anterior to the joint with the SOC.

Infraorbital canals (CIO)

The CIO is supported by tubular or trough-like structures of the infraorbitals that form a series of separated bones around the orbit, but the CIO itself is not divided into any sections in any of the channichthyid species examined. The number of pores basically depends on the number of the infraorbitals and varies from 6 to 14. In *Champocephalus*, the number of pores in the CIO varies from 11 to 14, with an average of 12.3 (Figs. 1b, c and 2a). In *Chionodraco rastrispinosus*, there are 8 to 10 pores in its CIO, which is relatively high among channichthyids. The rest of the channichthyid species have almost the same average number of pores, varying from 7.6 to 8.8 (Fig. 3). In *Chaenocephalus aceratus*, the anterior part of the CIO runs far below the orbit because the anterodorsal

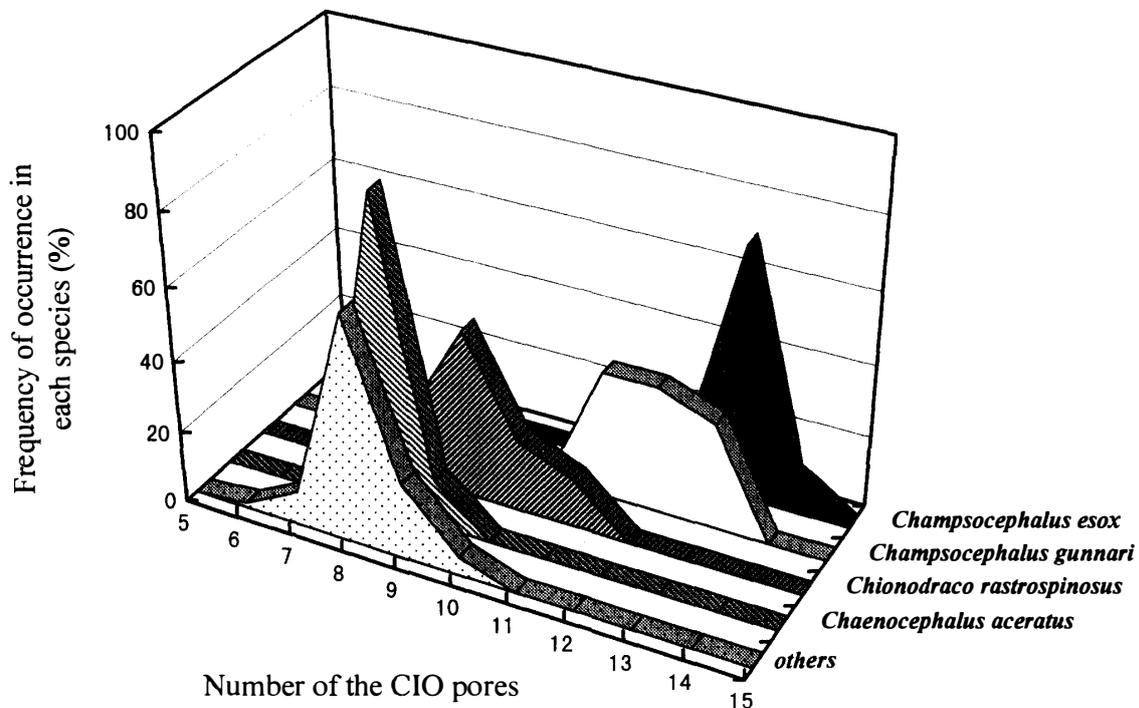


Fig. 3. Frequency distribution of the number of pores of the infraorbital canal (CIO) in the Channichthyidae.

expansion of the first infraorbital excludes the CIO from the margin of the orbit (Fig. 2b). All of the CIO pores, especially the first to fifth, possess developed canaliculi. In *Pseudochaenichthys georgianus*, the canaliculi of the fourth and fifth (rarely the fifth and sixth) pores are prolonged posteroventrally, of which the longest one is associated with a tubular structure on the second infraorbital bone (Fig. 2c). The second infraorbital bone of *P. georgianus* has a posteroventral expansion forming a suborbital stay as seen in the third infraorbital bone of scorpaeniform fishes. A suborbital stay is also found in the second infraorbital of *Neopagetopsis ionah*, however, an extremely prolonged canaliculus is not developed.

Temporal canals (CT)

The CT is not divided into several sections in the Channichthyidae. The number of pores in the CT is mostly conservative and is six except for two species, *Pseudochaenichthys georgianus* and *Chionodraco myersi*, which have five pores in the CT (Fig. 1d and 1f). As the CPOM of the two species is connected to and occludes one pore of the CT, the number of pores in the CT is thought to decrease from 6 to 5. The pores in the anterior part of the CT have canaliculi elongating outward, and the last pore usually has little canaliculus.

Preoperculo-mandibular canals (CPOM)

In all channichthyid species, the CPOM is not divided into several sections. The two species of *Champocephalus* have a larger number of pores in the CPOM, ranging from 15 to 18, with an average of 16.3 (Fig. 1b and 1c). The number of pores of the CPOM of the rest of the family varies from 11 to 14, with a modal number of 13. In all channichthyid species, the CPOM of preopercular region that is supported by developed ridges on the preoperculum is relatively complex, as shown by MONTGOMERY *et al.* (1994) in *Chionodraco hamatus*.

Supratemporal canal (CST)

In all channichthyid species examined, the CST is continuous and runs across the occipital region, not divided as seen in several species of the Nototheniidae (ANDERSEN, 1984) and Bathydraconidae (Fig. 1g). There are three pores in all channichthyids except for *Champocephalus esox* (Fig. 1c), *Neopagetopsis ionah* (Fig. 1e) and occasionally *Pseudochaenichthys georgianus*. Among the three species, the number of pores in the CST is largest in *N. ionah* and ranges from 4 to 7 with an average of 5.3. In *C. esox*, the average number of pores in the CST is 5.0, while in *P. georgianus*, three specimens out of six examined have three pores in their CST as in the case of other channichthyid species. In all specimens examined, one pore is always situated in the middle of the CST, and the middle pore divides the CST into two lateral sections with one pore each. In *N. ionah* with seven pores in the CST, the right and left lateral sections have three pores each. In some specimens having an even number of CST pores, these pores are arranged asymmetrically and the number of pores in each lateral section is different. All pores in the CST have canaliculi elongating posteriorly. In *P. georgianus* and *N. ionah*, the middle part of the CST curves convexly, but in the rest of the family, the CST nearly runs straight.

Supraorbital commissure (SOC)

The SOC is supported by a trough-like structure on the posterior region of the frontal. The number of pores in the SOC is invariably one in all channichthyid species (Fig. 1). The pore, named the coronal pore, is situated in the middle of the SOC and has a prolonged canaliculus directed posteriorly.

Discussion

The general structural plan of the cephalic sensory canal system in the Channichthyidae is considered to be the percoid type, which is characterized by having the SOC, the CSO connected with the CT, and no frontal-parietal canal (BALUSHKIN, 1990). In the Nototheniidae, interruption and partial reduction of the cephalic sensory canals are usually found in species more adapted to the pelagic mode of life (JAKUBOWSKI, 1971; ANDERSEN, 1984). In comparison with the morphological variations of the cephalic sensory canal systems of the Nototheniidae, those of the Channichthyidae are not so conspicuous. This shows two possibilities: (1) there is no remarkable difference in the ecological features among channichthyid fishes; and (2) the channichthyid species are more closely related phylogenetically to one another than the nototheniid species.

One of the most remarkable features in the cephalic sensory canal systems of the Channichthyidae is found in the morphological condition of a connection between the CPOM and CT. Among 16 channichthyid species, only two species, *Pseudochaenichthys georgianus* and *Chionodraco myersi*, have the CPOM connected with the CT. In most nototheniids, the CPOM is not connected to the CT except for the following species: *Paranotothenia microlepidota*, *Paranotothenia angustata*, *Dissostichus mawsoni*, *Dissostichus eleginoides* and *Eleginops maclovinus* (JAKUBOWSKI, 1971; ANDERSEN, 1984). The fact that the CPOM of *Paranotothenia magellanica*, the other species of the genus *Paranotothenia*, is not connected to the CT casts doubt on the systematic value of the connection between the CPOM and CT. According to JAKUBOWSKI (1971), *Notothenia coriiceps* is also characterized by the presence of a connection between the CPOM and CT. Based on detailed comparative study on *Dissostichus* species and *N. coriiceps*, he concluded that the connection was evidently the result of a convergence. The systematic value of the connection between the CPOM and CT is still obscure, because this character is not well associated with the generic relationships not only in the Channichthyidae but also in the Nototheniidae. At least in some cases, the same condition of the connection between the two canals may be formed in species of different genera as a result of a convergence. In *Gymnodraco acuticeps* and *Parachaenichthys charcoti* of the Bathydraconidae, that are thought to be most closely related to the Channichthyidae in the suborder Notothenioidei (IWAMI, 1985; EASTMAN, 1993), the CPOM is not connected to the CT. On the basis of character polarity determined by outgroup comparison, the presence of a connection between the CPOM and CT found in *P. georgianus* and *C. myersi* is considered to be apomorphic. And phylogenetic relationships among the channichthyid genera proposed by IWAMI (1985) strongly imply that the above mentioned characteristic found in *P. georgianus* and *C. myersi* had been developed independently in the respective lineage.

In the CIO, pores are situated between the adjacent infraorbital bones except in the anterior part of the CIO supported by the first infraorbital, and the number of pores of the

CIO nearly corresponds to that of the infraorbitals. In fact, all of the channichthyids except for *Champscephalus* usually have only 6 infraorbitals (IWAMI, 1985) and about 8 pores in the CIO. However, there are 8–9 infraorbital bones in *Champscephalus* (IWAMI, 1985) which has on average 12 pores in the CIO. In *G. acuticeps* and *P. charcoti* of the Bathydraconidae, the number of the CIO pores is 8 or 9 as in the case of most channichthyid species. Judging from these observations, the most primitive number of CIO pores in the Channichthyidae may be considered to be 8. The increase of number of pores in the CIO is assumed to be apomorphic in the Nototheniidae (ANDERSEN, 1984). In the Channichthyidae, the same condition found in *Champscephalus* is also considered to be an autapomorphy of this genus.

Pseudochaenichthys georgianus is characterized by having extremely prolonged canaliculus in the CIO. The second infraorbital bone with a suborbital stay supports this characteristic canaliculus. A suborbital stay is also found in *Neopagetopsis ionah*; however, it is not so expanded posteroventrally as in *P. georgianus* (IWAMI, 1985). In *N. ionah*, therefore, the canaliculi of the fourth and fifth pores are slightly longer, but their distal ends do not extend to the posteroventral corner of the cheek. In a young specimen of *N. ionah*, a suborbital stay of the second infraorbital is reduced to a fringe-like structure associated with a tubular infraorbital bone. This condition is also found in the two species of *Pagetopsis* (IWAMI, 1985). In relation to these morphological features, the canaliculi on the second infraorbital are not elongated in *Pagetopsis* or in a young *Neopagetopsis*.

Acknowledgments

We thank Dr. M. TAKAHASHI, Japan Marine Fishery Resource Research Center, for kindly providing materials. Thanks are also due to Dr. T. HOSHIAI, former Director of the National Institute of Polar Research, Tokyo for his continuous advice. We are indebted to Dr. N. MERRETT of the Natural History Museum, London and Dr. D. WILLIAMS of the Antarctic Division, Hobart for the loan of valuable specimens. This work was supported in part by a Grant-in-Aid (No. 08640896) from the Ministry of Education, Science, Sports and Culture, Japan, Nippon Life Insurance Foundation and FUJIWARA Natural History Foundation.

References

- ANDERSEN, N.C. (1984): Genera and subfamilies of the family Nototheniidae (Pisces, Perciformes) from the Antarctic and Subantarctic. *Steenstrupia*, **10**, 1–34.
- ANDRIASHEV, A.P. and NEELOV, A.V. (1978): The new white-blooded fish (*Chionobathyscus dewitti*, gen. et sp. n.) from the continental slope of the East Antarctica. *Morfologiya i Sistematika Ryb*, Akad. Nauk SSSR, 5–12.
- BALUSHKIN, A.V. (1990): Morphological bases of the systematics and phylogeny of the nototheniid fishes. Rotterdam, A. A. Balkema, 153 p.
- BALUSHKIN, A.V. (1996a): Similarity of fish of family Channichthyidae (Notothenioidei, Perciformes), with remarks on the species composition of the family and the description of a new species from the Kerguelen Archipelago. *J. Ichthyol.*, **36**, 1–10.
- BALUSHKIN, A.V. (1996b): Structure and evolution of the trunk lateral lines of the Notothenioidei

- (Perciformes). *J. Ichthyol.*, **36**, 419-429.
- COOMBS, S. and MONTGOMERY, J. (1994): Function and evolution of superficial neuromasts in an Antarctic notothenioid fish. *Brain Behav. Evol.*, **44**, 287-298.
- DEWITT, H.H. and HUREAU, J.C. (1979): Fishes collected during "Hero" cruise 72-2 in the Palmer Archipelago, Antarctica, with the description of two new genera and three new species. *Bull. Mus. natn. Hist. nat., Paris*, 4e ser., 1, sec. A, **3**, 775-820.
- DINGERKUS, G. and UHLER, L.D. (1977): Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Technol.*, **52**, 229-232.
- EASTMAN, J.T. (1993): Antarctic fish biology: Evolution in a unique environment. San Diego, Academic Press, 322 p.
- IWAMI, T. (1985): Osteology and relationships of the family Channichthyidae. *Mem. Natl Inst. Polar Res., Ser. E*, **36**, 1-69.
- IWAMI, T. and KOCK, K.H. (1990): Channichthyidae. *Fishes of the Southern Ocean*, ed. by O. GON and P.C. HEEMSTRA. Grahamstown, J.L.B. Smith Institute of Ichthyology, 381-399.
- JAKUBOWSKI, M. (1967): A method for the manifestation of lateral-line canals and their neuromasts in fishes. *Copeia*, **1967**, 234-235.
- JAKUBOWSKI, M. (1970): Morphological features of the lateral line organs in members of the Antarctic genus *Trematomus* BOUL. (Nototheniidae, Pisces). *J. Ichthyol.*, **10**, 268-271.
- JAKUBOWSKI, M. (1971): Morphological features of the lateral-line organs in members of the genus *Notothenia* RICH. and other genera of the family Nototheniidae (Pisces). *J. Ichthyol.*, **11**, 493-499.
- JANSSEN, J. (1996): Use of the lateral line and tactile senses in feeding in four Antarctic nototheniid fishes. *Envir. Biol. Fish.*, **47**, 51-64.
- MONTGOMERY, J.C. (1997): An ontogenetic shift in the use of visual and nonvisual senses in Antarctic notothenioid fishes. *Antarctic Communities—Species, Structure and Survival*, ed. by B. BATTAGLIA *et al.* Cambridge, Cambridge Univ. Press, 217-220.
- MONTGOMERY, J.C. and SUTHERLAND, K.B.W. (1997): Sensory development of the Antarctic silverfish *Pleuragramma antarcticum*: A test for the ontogenetic shift hypothesis. *Polar Biol.*, **18**, 112-115.
- MONTGOMERY, J.C., COOMBS, S. and JANSSEN, J. (1994): Form and function relationships in lateral line systems: Comparative data from six species of Antarctic notothenioid fish. *Brain Behav. Evol.*, **44**, 299-306.
- SARUWATARI, T., LOPEZ, J.A. and PIETSCH, T.W. (1997): Cyanine blue: A versatile and harmless stain for specimen observation. *Copeia*, **1997**, 840-841.

(Received August 24, 1998; Revised manuscript accepted October 28, 1998)