Abstract

The osteological features of the Channichthyidae are described and their characteristics are discussed by means of the cladistic analysis. The osteological features of the suborder Notothenioidei which comprise the Bovichthyidae, Nototheniidae, Harpagiferidae, Bathydraconidae and Channichthyidae are also studied and compared with one another.

A total of 17 characters shows the systematic value in reconstructing the phylogenetic relationships in the Channichthyidae. Considering the relationships among the genera of the Channichthyidae, they are classified into seven groups as follows: (1) *Champsocephalus*, (2) *Pagetopsis-Neopagetopsis-Pseudochaenichthys*, (3) *Dacodraco*, (4) *Channichthys*, (5) *Cryodraco-Chionobathyscus-Chaenocephalus*, (6) *Chionodraco* and (7) *Chaenodraco*. Also judging from the fact that most channichthyid genera contain only one or two species, it may be certain that some of the groups mentioned above are treated as a proper genus, but each of seven groups is only represented as a "group" in the present study.

The phylogenetic relationships among the families of the Notothenioidei are discussed and a new phylogenetic cladogram is proposed based on the analysis of 26 characters. The survey of the various features shows that the Bathydraconidae and Channichthyidae are most closely related, and the Bovichthyidae were the earliest derived from the common ancestor of notothenioid fishes.

Evolutionary trends which occurred among notothenioid fishes include: the reduction of ossification, consolidation of bony elements, expansion of the oral cavity, development of the defense posture and pectoral girdle, and acquirement of the piscivorous, sit-and-wait feeding and benthic habits. The above mentioned evolutionary trends are correlated to each other, so they cannot be discussed independently. Morphologically speaking, the Channichthyidae are the most advanced group within the Notothenioidei for the benthic mode of life in the Southern Ocean.

1. Introduction

Distribution of the notothenioid family Channichthyidae, the icefishes, are limited to the Antarctic and Subantarctic waters, except for one species (*Champsocephalus esox*) which inhabits the Patagonian-Falkland waters. The family consist of 11 genera and 17 nominal species.

Most of the channichthyid species are deep-water sedentary predators which occur below a depth of 100 to 200 m (ANDRIASHEV, 1965; DEWITT, 1971), and are sometimes collected below a depth of 800 m (ANDRIASHEV and NEYELOV, 1978; IWAMI, unpublished data). They mainly feed on small fishes and crustaceans such as the Antarctic krill, *Euphausia superba* (PERMITIN and TARVERDIYEVA, 1972; ABE and SUZUKI, 1978; TARGETT, 1981; TAKAHASHI, 1983). On the other hand, some species are found at shallow depths and observed in the epipelagic layers (RICHARDSON, 1844; NYBELIN, 1947; OLSEN, 1955; ROBILLIARD and DAYTON, 1969; DANIELS and LIPPS, 1982). These channichthyids occurring in the upper layers of water are often taken along with the Antarctic krill (ABE and SUZUKI, 1978, 1981; REMBISZEWSKI *et al.*, 1978; TAKAHASHI, personal communication).

The channichthyid fishes are characterized most noticeably by the absence or a very small number of erythrocytes (RUUD, 1954; MARTSINKEVICH, 1964); therefore, they are also called the white-blooded fishes. Their haemoglobinless condition, which is unique among vertebrates, is thought to be compensated by a modified vascular system by which oxygen is transported (TWELVES, 1972; HEMMINGSEN and DOUGLAS, 1977).

The Channichthyidae, together with three other Antarctic families—the Nototheniidae, Harpagiferidae and Bathydraconidae and a non-Antarctic Bovichthyidae, constitute the suborder Notothenioidei. Of the coastal and benthic fishes found in the Antarctic waters, the Notothenioidei are the most dominant group, as they include over 60% (DEWITT, 1971) to 75% (ANDRIASHEV, 1965) of the species and over 90% of the individuals (DEWITT, 1971).

These notothenioid fishes exhibit an adaptive radiation in an isolated region where ecological niches have little or no competition. According to ANDRIASHEV (1965), they may be termed the ancient autochthonic element of the Antarctic fish fauna, and they have evolved in the cool waters of the southern hemisphere throughout the Tertiary period (REGAN, 1914; NORMAN, 1938; ANDRIASHEV, 1965; DEWITT, 1971). ANDERSEN (1984) also guessed that the notothenioids occurred in the Pacific Western Antarctic and Pacific South American regions prior to the opening of the Drake Strait, 30 to 25 million years ago.

Previous systematic studies of the notothenioid fishes were based on the small number of characters (DOLLO, 1904; REGAN, 1914), or were only concerned with the Nototheniidae (ANDERSEN, 1984) and Harpagiferidae (EAKIN, 1981). Consequently, a definitive systematic study of the Channichthyidae which shows the unique physiological feature, *e.g.* the haemoglobinless condition, is expected to be completed.

The purpose of the present study is (1) to describe and analyze the osteology of all of the currently recognized genera of the family Channichthyidae, (2) to discuss the relationships among the genera of the Channichthyidae, (3) to compare osteological features of the Channichthyidae with those of the other families of the suborder Notothenioidei, and (4) to discuss the interrelationships of the Notothenioidei.

2. Materials and Methods

Most of the specimens used in the present study were collected during the exploratory bottom trawl fishing carried out by Japan Marine Fishery Resource Research Center. Survey areas and years in parentheses were as follows: the eastern part of the Ross Sea (1979–1980) (IWAMI and ABE, 1981a) and the region adjacent to the South Shetland Islands in the Scotia Sea (1980–1981 and 1982–1983) (IWAMI and Abe, 1982). In these areas the bottom fishes were collected by the commercial bottom trawl.

Most of the fishes were frozen at about −40°C on board the research vessels and were preserved at about −20°C. Some of the specimens were fixed immediately in 10% formalin. For the use in the study, the specimens were thawed in running water, and were measured and weighed. Some of the specimens in good condition were cataloged and fixed in 10% formalin and were transferred into 70% ethanol after fixation for a period of two to four weeks.

Specimens borrowed or received from institutions and museums other than Japan Marine Fishery Resource Research Center were preserved in 70% ethanol.

The species examined in the present study are listed below. Sources of specimens used are abbreviated as follows: A, Dr. Tokiharu ABE's personal collection; SAM, South Australian Museum; BMNH, British Museum (Natural History); FRSKU, Fisheries Research Station, Kyoto University; IBUT, Institute of Biological Sciences, University of Tsukuba; NIPR, National Institute of Polar Research.

List of the cleared and stained specimens

Family Channichthyidae

Champsocephalus gunnari (LÖNNBERG): 4 specimens (IBUT 81–328, 442, 476, 82–801), 200–363 mm SL, South Shetland.

Pagetopsis macropterus (BOULENGER): 3 specimens (IBUT 81–409, 82–359, 786), 201–253 mm SL, South Shetland.

Pagetopsis maculatus BARSUKOV and PERMITIN: 2 specimens (A 19049′, 19099′), 152–189 mm SL, Ross Sea.

Neopagetopsis ionah NYBELIN: 2 specimens (uncataloged, IBUT 81–878), 175–440 mm SL, Ross Sea and South Shetland.

Pseudochaenichthys georgianus NORMAN: 3 specimens (IBUT 81–433, 435, 82–786), 224–434 mm SL, South Shetland.

Dacodraco hunteri WAITE: 1 specimen (IBUT 82–738), 105 mm SL, South Shetland.

Channichthys rhinoceratus RICHARDSON: 1 specimen (A 17689′), 423 mm SL, locality unknown (Kerguelen ?).

Cryodraco antarcticus DOLLO: 6 specimens (IBUT 78–267, 82–251, 294, 295, 298, 445), 210–419 mm SL, South Shetland.

Chionobathyscus dewitti ANDRIASHEV and NEYELOV: 2 specimens (IBUT 82–287, 521), 205–241 mm SL, South Shetland.

Chaenocephalus aceratus (LÖNNBERG): 3 specimens (IBUT 78–313, 81–411, 417), 221–339 mm SL, South Shetland.

Chionodraco hamatus (LÖNNBERG): 1 specimen (A 19102′), 235 mm SL, Ross Sea.

Chionodraco rastrospinosus DEWITT and HUREAU: 4 specimens (IBUT 81–025, 026, 82–430, 531), 314–353 mm SL, South Shetland.

Chionodraco myersi DEWITT and TYLER: 3 specimens (A 19075′, IBUT 82–096, 554), 154–206 mm SL, Ross Sea and South Shetland.

Chaenodraco wilsoni REGAN: 5 specimens (A 18974′, 18975′, 18990′, IBUT 81–819, 82–455), 181–222 mm SL, Ross Sea and South Shetland.

Family Bovichthyidae

Bovichthys variegatus (RICHARDSON): 2 specimens (SAM no catalog number), 95–99 mm SL, South Australia.

Pseudaphritis urvilli (CUVIER and VALENCIENNES): 1 specimen (SAM no catalog number), 80 mm SL, South Australia.

Cottoperca gobio (GÜNTHER): 2 specimens (FRSKU no catalog number), 202–242 mm SL, Patagonia.

Family Nototheniidae

Notothenia rossii marmorata FISCHER: 1 specimen (IBUT 82–140), 308 mm SL, South Shetland.

Notothenia coriiceps neglecta NYBELIN: 1 specimen (IBUT 81–297), 324 mm SL, South Shetland.

Notothenia kempi NORMAN: 2 specimens (IBUT 78–323, 325), 250–269 mm SL, South Shetland.

Notothenia nybelini BALUSHKIN: 1 specimen (IBUT 78–335), 138 mm SL, South Shetland.

Notothenia gibberifrons LÖNNBERG: 1 specimen (IBUT 81–706), 154 mm SL, South Shetland.

Notothenia nudifrons LÖNNBERG: 1 specimen (NIPR no catalog number), 97 mm SL, Antarctic Peninsula.

Patagonotothen ramsayi (REGAN): 2 specimens (FRSKU N53), 160–204 mm SL, Patagonia.

Pagothenia borchgrevinki (BOULENGER): 2 specimens (NIPR no catalog number), 195–198 mm SL, Lützow-Holm Bay.

Trematomus bernacchii BOULENGER: 2 specimens (NIPR no catalog number), 126–163 mm SL, Lützow-Holm Bay.

Trematomus hansoni BOULENGER: 2 specimens (NIPR no catalog number, IBUT 82–567), 124–242 mm SL, Lützow-Holm Bay and South Shetland.

Trematomus scotti (BOULENGER): 1 specimen (IBUT uncataloged), 108 mm SL, South Shetland.

Dissostichus mawsoni NORMAN: 1 specimen (IBUT uncataloged), 105 mm SL, South Shetland.

Pleuragramma antarcticum BOULENGER: 2 specimens (IBUT uncataloged), 146–169 mm SL, South Shetland.

Aethotaxis mitopteryx DEWITT: 2 specimens (IBUT 81–247, 440), 102–148 mm SL, South Shetland.

Family Harpagiferidae

Harpagifer antarcticus NYBELIN: 2 specimens (NIPR no catalog number), 44–60 mm SL, Antarctic Peninsula.

Artedidraco orianae REGAN: 1 specimen (A 18991′), 101 mm SL, Ross Sea.

Histiodraco velifer (REGAN): 1 specimen (A 19043′), 119 mm SL, Ross Sea.

Pogonophryne dolichobranchiata ANDRIASHEV: 1 specimen (IBUT 78–315), 208 mm SL, South Shetland.

Family Bathydraconidae

Vomeridens infuscipinnis (DEWITT): 1 specimen (A 19046′), 149 mm SL, Ross Sea.

Gerlachea australis DOLLO: 2 specimens (IBUT 81–419, 490), 183–231 mm SL, South Shetland.

Parachaenichthys charcoti (VAILLANT): 2 specimens (IBUT 82–329, 431), 165–325 mm SL, South Shetland.

Cygnodraco mawsoni WAITE: 1 specimen (A 17673′), 362 mm SL, locality unknown.

Gymnodraco acuticeps BOULENGER: 2 specimens (IBUT 81–024, 489), 210–235 mm SL, South Shetland.

Basically the methods for taking measurements and counts followed those given by HUBBS and LAGLER (1958). Osteological preparations were made of more than one specimen of each species or genus when possible. The method of DINGERKUS and UHLER (1977), with a slight modification, was utilized for staining cartilaginous and ossified parts of skeletons. To avoid disarticulation, alizarin red S staining was performed with 70% ethanol–0.6% KOH solution. After the staining procedures were completed, the specimen was transferred into 70% ethanol. Then, each stained skeleton was dissected as a unit and stored in pure glycerin for drawing with a camera lucida (Nikon SMZ-10). Radiographs were also used for the observation of osteological features.

The systematic methodology used in the present study basically follows that of HENNIG (1966). HENNIG's method, called cladistics, has been discussed by many taxonomists such as MASLIN (1952), MAYER (1969, 1974), NELSON (1970), CRACRAFT (1974), WILEY (1981) and SAWADA (1982); therefore, the theoretical dispute about this methodology is not treated in the present study.

Different sources of osteological terminology were used for different portions of the skeleton. The sources used for each section are indicated at the begining of the section.

Abbreviations used in the figures: ANG angular, ART articular, BB basibranchial, BH basihyal, BOC basioccipital, BST branchiostegal ray, CB ceratobranchial, CH ceratohyal, CL cleithrum, COR coracoid, CPR caudal principal rays, DEN dentary, DHH dorsal hypohyal, EB epibranchial, ECA ethmoid cartilage, ECP ectopterygoid, EH epihyal, EP epural, EPO epiotic, ESC extrascapular, ETH ethmoid, EXO exoccipital, FR frontal, GR gill raker, HB hypobranchial, HYO hyomandibular, HYP hypural, IH interhyal, IOB infraorbital, IOP interopercle, LEM lateral ethmoid, MSP mesopterygoid, MTP metapterygoid, MAX maxillary, NA nasal, OP opercle, OPO opisthotic, PAH parhypural, PAL palatine, PAR parietal, PAS parasphenoid, PB pharyngobranchial, PFR pectoral fin ray, PMX premaxillary, POP preopercle, PRO prootic, PT posttemporal, PTO pterotic, PTS pterosphenoid, PU preural centrum, Q quadrate, RAD radial, SC scapula, SCL supracleithrum, SOC supraoccipital, SOP subopercle, SPO sphenotic, SYM symplectic, TUB small tubercles, U ural centrum, UH urohyal, UN uroneural, VHH ventral hypohyal, VOR prevomer.

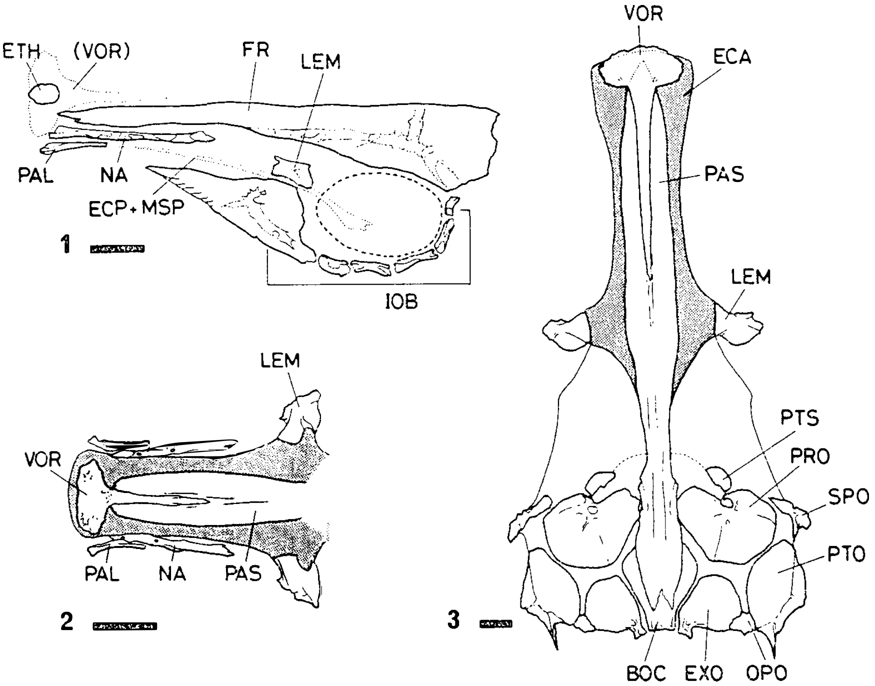
3. Osteology of the Family Channichthyidae

3.1. Neurocranium

3.1.1. Description

In channichthyid fishes, the ethmoid cartilage and 15 bones, ten paired and five median, constitute the neurocranium (Figs. 1–27). These bones include the following: the ethmoid (ETH), lateral ethmoids (LEM), frontals (FR), sphenotics (SPO), pterotics (PTO), parietals (PAR), epiotics (EPO), exoccipitals (EXO), supraoccipital (SOC), prevomer (VOR), parasphenoid (PAS), prootics (PRO), opisthotics (OPO) and basioccipital (BOC). The basisphenoid is absent in fishes of the Channichthyidae. This terminology follows that of WEITZMAN (1962).

Ethmoid region (Figs. 1–3): The greater part of the ethmoid region consists of the ethmoid cartilage. The ethmoid cartilage is covered dorsally by the ethmoid and laterally by the paired lateral ethmoids.



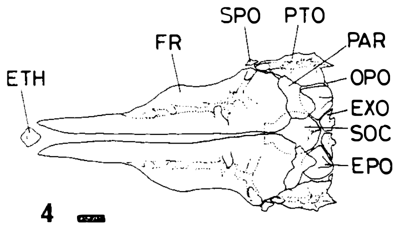
Figs. 1–3. Ethmoid region. Ventral view: (1) *Chaenocephalus aceratus*, (3) *Pagetopsis macropterus*; dorsal view: (2) *Chaenodraco wilsoni*. Shaded areas show the ethmoid cartilage. Scale 5 mm.

The ethmoid is bordered posterolaterally by the anterior tips of the frontals. This thin, round, roof-shaped bone is somewhat convex. In some genera, *Pagetopsis* (Fig. 6), *Pseudochaenichthys* (Fig. 7), *Neopagetopsis* (Fig. 9), *Channichthys*, *Chionodraco* (Fig. 21) except *Chionodraco myersi* (Fig. 19), and *Chaenodraco*, a median ridge of the ethmoid forms a spine namely the rostral spine. The ethmoid is not attached to any other bones directly and also not connected to a ligament.

Each lateral ethmoid borders on the anterior margin of the orbit. The lateral ethmoid is situated nearly along the midline of the snout. These paired bones are partially but firmly attached to the ethmoid cartilage. Each lateral ethmoid is connected with the posterodorsal portion of the first infraorbital bone and with the posterior tip of the palatine.

Prevomer (Figs. 1–3, 5, 8, 10, 14, 16, 18, 20, 22, 25–27): This median, teardrop-shaped and horizontally flattened bone is situated in the anteroventral region of the neurocranium. The head of the prevomer is wide, and is attached ventrally to the ethmoid cartilage. The tapered posterior end fits into a groove on the ventral surface of the parasphenoid. The anterior portion is not so thickened, and also lacks the anterodorsal process and vomerine teeth. In channichthyid fishes, this bone is not connected to the palatine by a strong ligament. The shape of the prevomer slightly varies with species.

Frontal (Figs. 1, 4, 6, 7, 9, 12, 13, 15, 17, 19, 21): These paired, triangular and thin bones constitute most part of the skull roof. The supraorbital canal and its connecting canal are supported by the tubular structures on the dorsal surface of the



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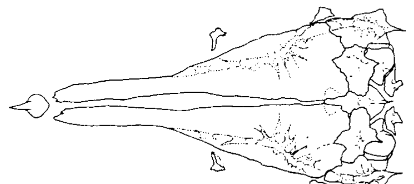

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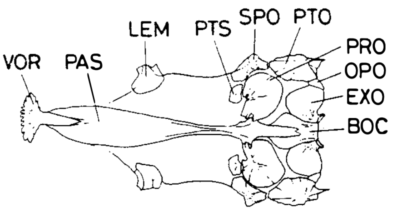

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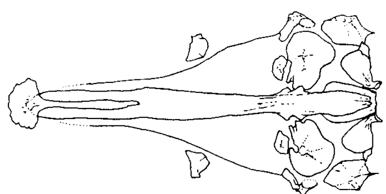

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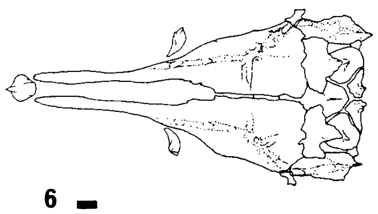

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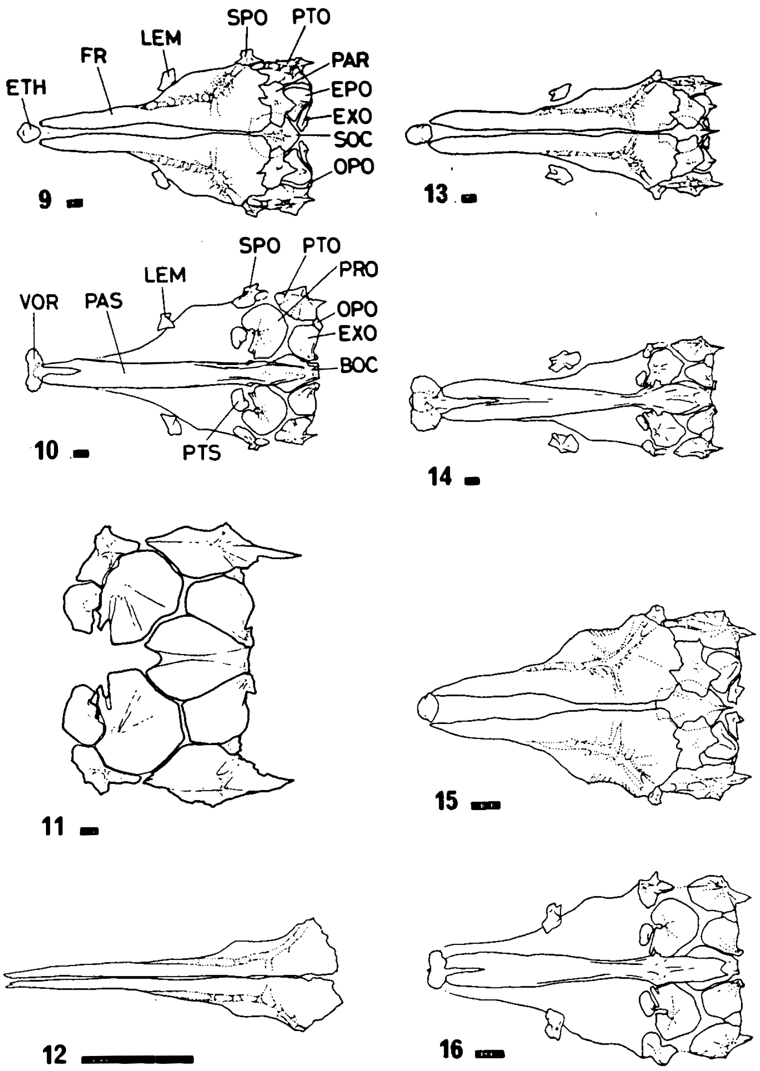
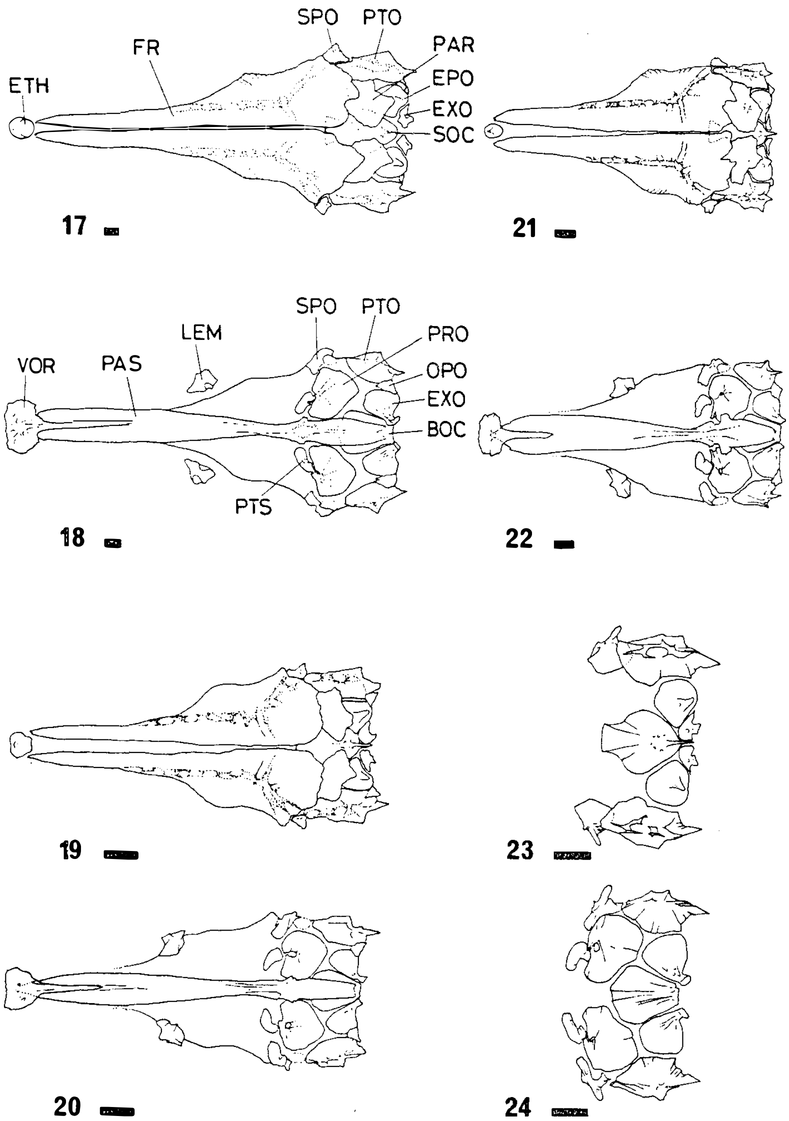
Figs. 4–8. Neurocranium. Dorsal view: (4) *Champsocephalus gunnari*, (6) *Pagetopsis macropterus*, (7) *Pseudochaenichthys georgianus*; ventral view: (5) *Champsocephalus gunnari*, (8) *Pseudochaenichthys georgianus*. Scale 5 mm.



Figs. 9–16. Neurocranium. Dorsal view: (9) *Neopagetopsis ionah*, (12) *Dacodraco hunteri*, (13) *Chaenocephalus aceratus*, (15) *Chionobathyscus dewitti*; ventral view: (10) *Neopagetopsis ionah*, (11) *Channichthys rhinoceratus*, (14) *Chaenocephalus aceratus*, (16) *Chionobathyscus dewitti*. Scale 5 mm.

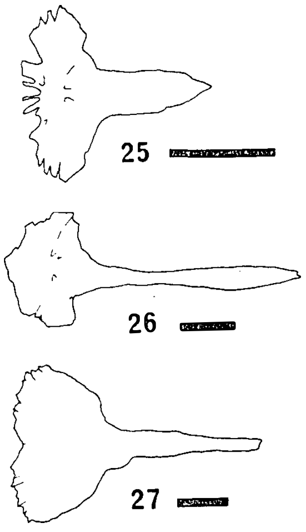
frontals. The supraorbital canals on the frontals connect to those on the nasals anteriorly, and join the connecting canals on the sphenotics and pterotics posteriorly. The frontals lie over the sphenotics, pterotics, parietals and supraoccipital posteriorly. The dorsal surface of the frontals is horizontally flattened and not strongly convex. Channichthyid fishes posess "the long anterior part" which is a part of the frontal without the tubular structure. The anteriormost opening of the supraorbital canal on the frontal is situated in the neurocranium and connects the ethmoid region with the orbital and otic ones. In *Champsocephalus* its anteriormost opening is situated at a point one-third of the way from the frontal's anterior end (Fig. 4). The part of the frontal forming the supraorbital roof of *Champsocephalus*, therefore, is larger than in any other channichthyid species. In some genera, *e.g.* *Channichthys*, *Chaenocephalus* and *Chionodraco*, each frontal bears radiating ridges extending to the lateroposterior



Figs. 17–24. Neurocranium. Dorsal view: (17) *Cryodraco antarcticus*, (19) *Chionodraco myersi*, (21) *Chionodraco rastrospinosus*, (23) *Chaenodraco wilsoni*; ventral view: (18) *Cryodraco antarcticus*, (20) *Chionodraco myersi*, (22) *Chionodraco rastrospinosus*, (24) *Chaenodraco wilsoni*. Scale 5 mm.

margin which appears crenulate.

Pterotic (Figs. 3–11, 13–24): These paired, elongate and somewhat triangular bones form a part of the lateral wall of the otic region. Each pterotic is fused to its dermal component which appears as a tubular canal, namely the temporal canal, on its dorsolateral edge. A lateral fringe is developed on each outer side, and also a triangular fringe is recognized posteriorly. Each pterotic has a ventrolateral facet for the middle strut of the hyomandibular. Anterodorsally the bone meets the sphenotic and sits under the frontal and parietal. Each pterotic meets the epiotic posteromedially, the sphenotic and prootic anteroventrally, and the exoccipital posteroventrally. The cartilaginous junction between the pterotic and exoccipital is capped with the opisthotic.



Figs. 25–27. Prevomer. Ventral view: (25) *Champsocephalus gunnari*, (26) *Pseudochaenichthys georgianus*, (27) *Chaenocephalus aceratus*. Scale 5 mm.

Prootic (Figs. 3, 5, 8, 10, 11, 14, 16, 18, 20, 22, 24): These paired and trapezoidal bones are the largest among the otic elements. They form the anterior and lateral walls of the brain case. Each prootic meets the sphenotic anterodorsally, at about the midpoint of this bone. In channichthyid fishes it does not meet the opisthotic. The anterior part of the prootics is noticeably separated.

Parietal (Figs. 4, 6, 7, 9, 13, 15, 17, 19): These paired, somewhat rectangular skull roofing bones slide under the frontals anteriorly and overlap the epiotics posteriorly, the sphenotics lateroposteriorly, and the supraoccipital posteromedially. Each parietal is separated by the supraoccipital and does not meet the other of the pair.

Sphenotic (Figs. 3, 5, 8, 10, 11, 14, 16, 18, 20, 22, 24): These paired, somewhat rectangular bones form the posterodorsal edge of the orbit and the anterolateral wall of the otic region. Each sphenotic slides under the frontal and pterotic dorsally, and is bordered by the prootic ventrally. It has a ventrolateral facet for the anterior strut of the hyomandibular. The last infraorbital is attached to this bone laterally. The suborbital and supraorbital canals are joined together by this connection.

In *Champsocephalus* and *Channichthys*, the sphenotic and pterotic meet (Figs. 5, 11). In the other nine genera, on the other hand, these two paired bones are clearly and widely separated by the cartilage.

Parasphenoid (Figs. 3, 5, 8, 10, 14, 16, 18, 20, 22): This long, median bone forms the greater part of the floor of the pterotic dorsoposteriorly, the pterosphenoid anterodorsally, the exoccipital posteriorly, and the basioccipital ventroposteriorly. Anteriorly it receives the posterior end of the prevomer in a groove on its ventral surface and posteriorly it narrows and thickens. The parasphenoid is narrowest at the portion between the orbital and otic regions, then expands laterally into two wing-like processes which overlie the prootics. These wing-like processes are not developed in this family. Posterior to the wing-like processes, the parasphenoid becomes wide and thin, overlapping the lateral parts of the prootics and basioccipital. This bone is not fused with the basioccipital, but the two bones are tightly attached together.

Opisthotic (Figs. 3–11, 13–24): The opisthotics are situated in the posteriormost portion of the otic region. This smallest bone of otic series is somewhat triangular and overlies the exoccipital-pterotic junction below the epiotic. It is connected to the lower limb of the posttemporal by a strong ligament. In channichthyid fishes, this bone is caducious and does not meet the prootic.

Epiotic (Figs. 4, 6, 7, 9, 13, 15, 17, 19, 21, 23): These paired, somewhat triangular, cap-like bones form the posterodorsal wall of the otic region. Each epiotic meets the parietal dorsoanteriorly, the supraoccipital medially, the pterotic laterally, and the exoccipital medially. The dorsal process projects posteriorly to receive the upper limb of the posttemporal.

Supraoccipital (Figs. 4, 6, 7, 9, 13, 15, 17, 19, 21, 23): This dorsoposterior, median bone forms the skull roof of the neurocranium. Its shape is slightly rounded and cap-like with a medial crest. This bone meets the frontal anteriorly, the parietal dorsolaterally, the exoccipital posteriorly, and the epiotic lateroposteriorly. In channichthyid fishes its crest is not so developed as in typical percoid fishes and does not extend posterior to the supraoccipital. The crest is not higher than the level of the dorsal surface of the neurocranium.

Basioccipital (Figs. 3, 5, 8, 10, 11, 14, 16, 18, 20, 22, 24): This fan-shaped median bone forms the ventroposterior floor of the neurocranium. The anterior portion is rounded and meets the prootics laterally. It meets the parasphenoid anteriorly and medially, and the exoccipitals posterolaterally. The posterior end of the basioccipital connects with the first vertebra via its concave, round condyle.

Exoccipital (Figs. 3–11, 13–24): These paired, flared bones form the posterior wall of the neurocranium. The exoccipitals surround the foramen magnum which accomodates the spinal cord. Two exoccipital condyles articulate with a pair of anteroventral condyles of the first vertebra. Each exoccipital meets the basioccipital ventromedially and the pterotic laterally. The exoccipital-pterotic junction is capped by the opisthotic. The exoccipital also meets the prootic anteriorly, the epiotic and supraoccipital dorsoanteriorly.

Pterosphenoid (Figs. 3, 5, 8, 10, 11, 14, 16, 18, 20, 22, 24): These paired, small and somewhat crescent-shaped bones form the anterior wall of the otic region. The pterosphenoids form the anterior border of the foramen for the cranial nerve. In *Champsocephalus* and *Channichthys*, each bone meets the pterotic (Figs. 5, 11). In the other nine genera, on the other hand, the two bony elements are noticeably separated by the wide cartilaginous area.

Basisphenoid: The basisphenoid is not recognized in the nuerocranium of the Channichthyidae. It can be concluded that the basisphenoid is absent in channichthyid fishes.

Remarks on this item: Most of junctions between the bony elements of the neurocranium form no sutured border and are separated by cartilaginous area.

Except for the tubular structures and ridges, most of the bones show a smooth surface, but the frontals, sphenotics, pterotics, parietals and supraoccipital of *Channichthys* bear many small tubercles on their surface. This feature is discussed in the next item.

3.1.2. Discussion

Ethmoid region: Features of the ethmoid slightly vary among species. The presence or absence of the rostral spine is able to show the differences of ethmoids and to be well recognized externally. However, this character is not thought to be conservative at the generic level in this family. In the three species of *Chionodraco*, *Chionodraco hamatus*, *C. myersi* and *C. rastrospinosus*, which are thought to be more closely related to each other than any other species of this family, *C. myersi* is obviously distinguished from the other two species by the absence of the developed rostral spine. In the character of the presence or absence of the rostral spine, *C. myersi* seems to bear a closer resemblance to *Champsocephalus* and *Cryodraco* than to the other two species, *Chionodraco hamatus* and *C. rastrospinosus*. Therefore, the morphological features of the ethmoid are not thought to be a useful character for the systematic studies of the Channichthyidae, and appear to be more effective for identifying species (REGAN, 1913, 1914; NORMAN, 1938).

Prevomer: The prevomer varies in shape among closely related channichthyid species. The differences in shape are supposed to be useful to distinguish and identify each species, but the morphocline or tendency in the morphological changes cannot be recognized in the shapes of the prevomers.

Frontal: Some morphological differences are observed in the shape of the frontals of this family. For example, the shape of the frontals of *Champsocephalus* is somewhat trapezoidal, while that of *Pseudochaenichthys* is triangular. However, the polarity in its features is hard to be recognized. In comparison with the other notothenioid fishes, the unconvex dorsal surface and elongated anterior part are recognized as the common and characteristic features of the frontal of the Channichthyidae. The frontal of *Champsocephalus* can be distinguished by the position of the anteriormost opening of the supraorbital canal from any other genera of the Channichthyidae. Although the anteriormost opening of the supraorbital canal is situated at the anterior tip of the frontal and the "anterior part" of the frontal is not obviously recognized in the other notothenioid families (the out-groups) (see Section 4), the anteriormost opening of the supraorbital canal is situated at about the mid-length of the frontal in most channichthyid fishes. In *Champsocephalus*, it is situated at a more anterior position than any other genera of this family and the character condition observed in *Champsocephalus* is thought to show the intermediate form between the conditions of the Channichthyidae and those of the other families of the Notothenioidei (the out-groups). Therefore, it is concluded that the character is synapomorphic for the ten genera of the Channichthyidae and the alternate is plesiomorphic.

Parietal: Except for the presence of the small tubercles observed only in *Channichthys*, considerable differences among the genera and species of this family are not recognized.

Sphenotic: The same as mentioned above.

Parasphenoid: No distinctive feature to each genus is observed in this bone.

Pterotic: Except for the presence of small tubercles on the pterotics of *Channichthys*, no distinct difference is recognized among the genera.

Opisthotic: This element is extremely reduced and its anterior tip never reaches the prootics in channichthyid fishes. The reduced opisthotics are also found in some notothenioid fishes. Among channichthyid fishes, no noticeable difference in the feature of this bone is recognized.

Epiotic: Except for the presence of small tubercles on this bone of *Channichthys*, no distinct difference is recognized among the genera.

Supraoccipital: The same as mentioned above.

Basioccipital: There is no noticeable difference in its feature among the genera of the Channichthyidae.

Exoccipital: The same as mentioned above.

Pterosphenoid: No obvious difference among the genera of this family is observed its feature. However, the channichthyid genera can be divided into two groups by the position of the pterosphenoid in relation to the surrounding elements. In most notothenioid fishes, the sphenotic and pterosphenoid are situated along the anterior margin of the prootic and are attached to each other. On the other hand, the sphenotic and pterosphenoid are separated by the wide cartilaginous area in the Channichthyidae excepting two genera of *Champsocephalus* and *Channichthys*. This condition which is caused by the reduction of ossification of bony elements is recognized only in channichthyids among notothenioids. Therefore, this character condition is thought to be a derived state or an apomorphy. The genera of the Channichthyidae other than *Champsocephalus* and *Channichthys* are concluded to share a synapomorphic condition in this character.

Basisphenoid: The absence of the basisphenoid is also recognized in the Harpagiferidae and Bathydraconidae (Eakin, 1981; see Section 4.1). Discussion on this character is given in the later section.

3.2. Superficial dermal bone

3.2.1. Description

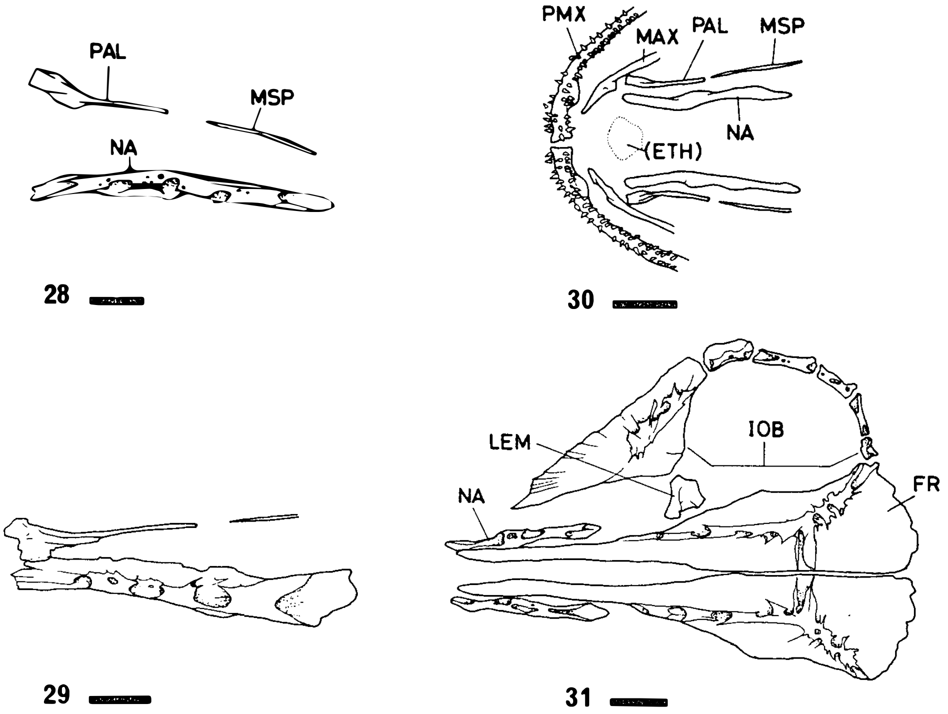
The superficial dermal bones consist of the nasals (NA), infraorbitals (IOB) and lateral line scales. The body scales which are a kind of the superficial dermal bone are not mentioned in this section, because all of channichthyid fishes are naked. This terminology follows that of Johnson (1974).

Nasal (Figs. 1, 2, 28–31): These paired, slender and tubular bones are situated along the anterior part of the frontals. The nasals place the ethmoid and anterior parts of the frontals between them. Each nasal shares the supraorbital canal with the frontal and forms the anteriormost part of the canal.

Infraorbitals (Figs. 31–42): The infraorbitals form the series of bones around the orbit. These basically paired bones support the suborbital canal with their tubular or troughlike structures. Each element of the infraorbitals is numbered from the anteriormost triangular bone as the first to the element attached to the sphenotic as the last. Each opening of the suborbital canal corresponds to the junction between the infraorbitals or an opening of tubular structure of this bone.

The number of the infraorbitals varies among not only the species but also individuals. In channichthyid fishes, six or seven infraorbitals are usually known. In *Champsocephalus*, the number increases to eight or nine (Fig. 32).

The first infraorbital is basically triangular in shape and meets the lateral ethmoid by a strong ligament internally. The posterodorsal expansion of the first infraorbital



Figs. 28–31. Nasal and related bones. (28) *Pagetopsis macropterus* (Left side, dorsal view); (29) *Champsocephalus gunnari* (right side, ventral view); (30) *Pagetopsis macropterus* (ventral view); (31) *Pagetopsis macropterus* (dorsal view). Scale 5 mm.

which excludes the second and third infraorbitals from the margin of the orbit is found in *Chaenocephalus* (Fig. 39).

The posteroventral expansion of the second infraorbital is observed in *Pagetopsis* (Figs. 33, 34), *Neopagetopsis* (Fig. 36) and *Pseudochaenichthys* (Fig. 37). The degree of expansion of the second infraorbital should be recognized in comparison with the size of the third and fourth infraorbitals. The expansion is most noticeable in *Pseudochaenichthys* and obviously recognized in a young fish (about 150 mm in standard length) of this species (not shown), while young ones of *Neopagetopsis* only show the small expansion. On the other hand, *Pagetopsis* which is composed of the small-sized species shows the moderately small expansion even in the adult.

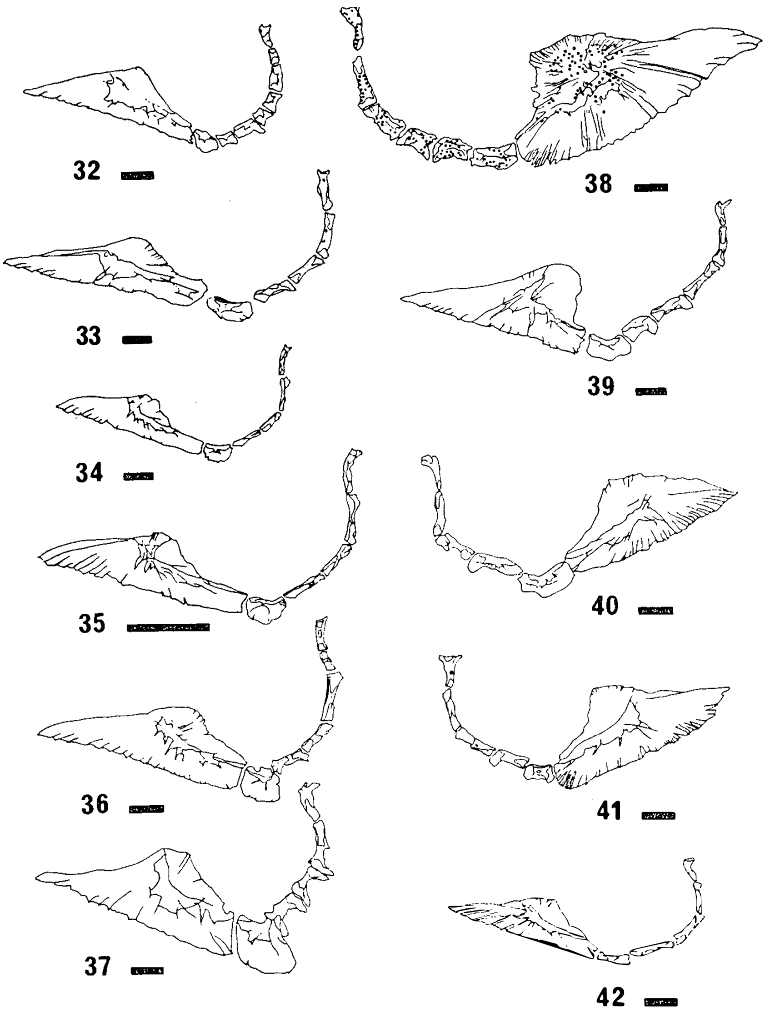
In *Channichthys*, the outer surface of the infraorbitals bears a large number of small tubercles.

In all channichthyid fishes, the infraorbitals never form the subocular shelf.

Lateral line scales: The body of channichthyid fishes is not covered with scales and the lateral line is also not supported by the tubular structures on scales in normal shape. In most channichthyid fishes, the lateral line is formed by the thin and small tubular bones which are not well ossified. Each tubular bone lines longitudinally and does not form the complex junction. Lateral line scales of *Channichthys* are developed into bony plates with small tubercles.

3.2.2. Discussion

Superficial dermal bones usually do not form a difinitive shape because of the lack of junctions with any other bony elements. As for the features of the nasals, infraorbit-



Figs. 32–42. Infraorbitals. Left side: (32) *Champsocephalus gunnari*, (33) *Pagetopsis macropterus*, (34) *Pagetopsis maculatus*, (35) *Neopagetopsis ionah* (young), (36) *Neopagetopsis ionah*, (37) *Pseudochaenichthys georgianus*, (39) *Chaenocephalus aceratus*, (42) *Chaenodraco wilsoni*; right side: (38) *Channichthys rhinoceratus*, (40) *Cryodraco antarcticus*, (41) *Chionodraco hamatus*. Scale 5 mm.

als and lateral line scales, their basic features are not much different among the genera of this family and their slight differences are within intraspecific variations. Therefore, most of the differences observed in superficial dermal bones are impossible to use for the systematic investigations. A few features which are thought to be available for the systematic studies are the presence or absence of small tubercles on superficial dermal bones, the number of the infraorbitals, the shape of the first and second infraorbitals, and the feature of the lateral line scales.

Small tubercles on superficial dermal bones: As mentioned in the former item, in *Channichthys* the dorsal surface of bony elements of the skull roof also shows the presence of small tubercles. These tubercles seem to be the same as those on the infraorbitals and lateral line scales, but their function is still uncertain.

As the presence of small tubercles is distinctive in *Channichthys* among notothenioid fishes which also include the out-groups for the Channichthyidae, it is thought to be a derived state.

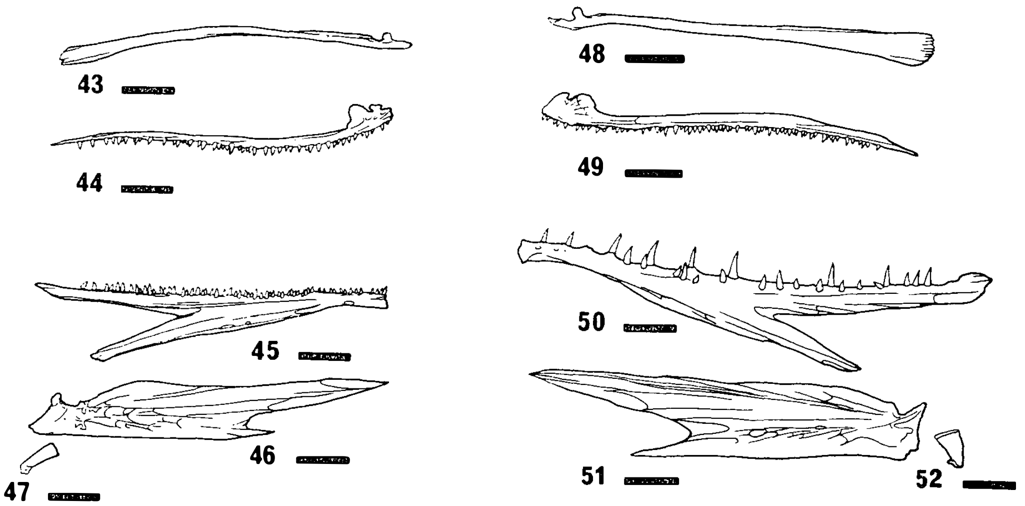
First infraorbital: The posterodorsal expansion of the first infraorbital which excludes the succeeding infraorbitals and the suborbital canal from the surrounding of the orbit is the characteristic of *Chaenocephalus*. As the first infraorbitals of the other channichthyids and notothenioids are triangular in shape and posess no posterodorsal expansion, the triangular infraorbitals without posterodorsal expansion which are also shared by the out-groups (the notothenioids other than the channichthyids) are assumed to be plesiomorphic.

Second infraorbital: The posteroventral expansion of the second infraorbital is restricted to the following three genera: *Pagetopsis*, *Neopagetopsis* and *Pseudochaenichthys*. The degree of expansion of the second infraorbitals in the Channichthyidae shows the ontogenetic character precedence from the tubular and unexpanded second infraorbital to the expanded and trapezoidal second infraorbital. The former character state is found in the channichthyid fishes other than those belonging to *Pagetopsis*, *Neopagetopsis* and *Pseudochaenichthys*, while the latter character state is found in adults of *Neopagetopsis* and in *Pseudochaenichthys*. An intermediate character state between the above-mentioned two character states is recognized in adults of *Pagetopsis* and young of *Neopagetopsis*. Judging from the ontogenetic character precedence, the character, the posteroventral expansion of the second infraorbital, found in *Pagetopsis*, *Neopagetopsis* and *Pseudochaenichthys*, is considered to be apomorphic.

3.3. Mandibular arch

3.3.1. Description

The mandibular arch is composed of the upper and lower jaws. All of the elements of the mandibular arch are paired and are as follows: the premaxillaries (PMX), maxillaries (MAX), dentaries (DEN), articulars (ART), angulars (ANG), Meckel's



Figs. 43–52. Mandibular bones. Maxillary: (43) *Pagetopsis macropterus* (right), (48) *Chionobathyscus dewitti* (left); premaxillary: (44) *Pagetopsis macropterus* (right), (49) *Chionobathyscus dewitti* (left); dentary: (45) *Pagetopsis macropterus* (right), (50) *Chionodraco myersi* (left); articular: (46) *Pagetopsis macropterus* (right), (51) *Chionodraco myersi* (left); angular: (47) *Pagetopsis macropterus* (right), (52) *Chionodraco myersi* (left). Scale 5 mm.

cartilage and sesamoid articulars. The last two of these elements are not discussed in the present study. This terminology follows that of WEITZMAN (1962) and TOMINAGA (1965).

Premaxillary (Figs. 44, 49): These slender and toothed bones are situated under the maxillaries and are bordered by the maxillaries. The anterior head of each premaxillary which bears a triangular ridge is connected with that of the maxillary by a strong ligament. No prominent dorsal process is recognized in the maxillaries of all channichthyid fishes.

Maxillary (Figs. 43, 48): These slender, slightly curved and toothless bones meet the palatines and premaxillaries anteriorly. The posterior portion is tapered and blade-shaped, and reaches the posteriormost angle of the upper jaw. The premaxillary and maxillary border the ventral margin of the upper jaw, and the upper jaw length, upper jaw width and size of the mouth are limited by the premaxillary and maxillary.

Dentary (Figs. 45, 50): The dentary is the largest bone among the elements of the lower jaw. This complex, triangular and toothed bone forms the anterior portion of the lower jaw. It meets its fellow anteriorly in a median symphysis and the articular posteriorly, and its posterior portion is bifid. The upper limb bears conical teeth dorsally for about anterior three-fourths to four-fifths in length. The lower limb supports the mandibular canal connecting to the articular.

Articular (Figs. 46, 51): Each articular is slightly slender and borders the posteroventral margin of the lower jaw. The anteroventral portion of this bone is bifurcated by the V-shaped notch. The upper limb is longer than the lower one and is inserted between the two posterior limbs of the dentary. This articulation between the dentary and the articular is supported internally by the Meckel's cartilage. The lower limb of this bone is shorter and does not reach the posterior margin of the dentary. The articular bears the tubular structure on its lateral surface. A part of the mandibular canal supported by this tubular structure is leading posteriorly from the anterior part of the mandibular canal on the dentary to the preopercular canal on the preopercle. On the posteroventral surface, it is attached by the angular, and on the posterodorsal surface it forms a facet for the articulation with the quadrate.

Angular (Figs. 47, 52): These small, cap-like and triangular bones are firmly attached to the posteroventral margin of the articular.

3.3.2. Discussion

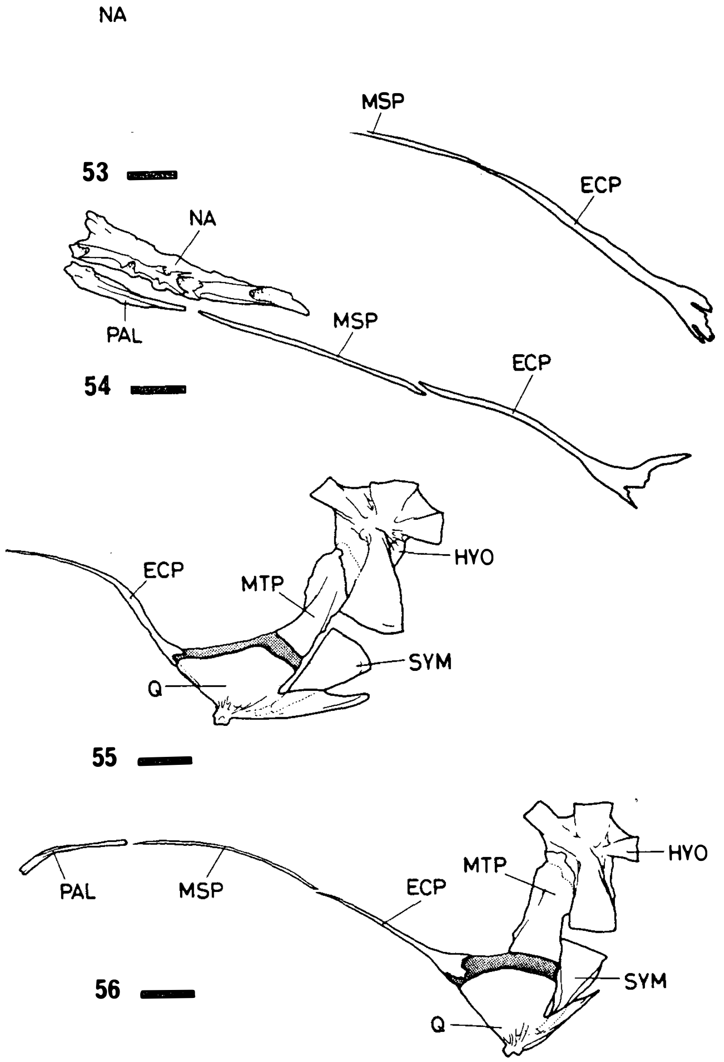
Some features of each of bony elements vary among species, but the qualitative differences which are useful for the definition of each genus cannot be recognized in the osteological features of the bony elements of the mandibular arch.

On the presence or absence of the premaxillary process, the Channichthyidae are clearly distinguishable from any other families of the Notothenioidei. Therefore, this character is thought to be useful for the investigation of the familial taxa and is mentioned later in detail (see Section 4.3).

3.4. Palatine arch

3.4.1. Description

The palatine arch is composed of bony elements which connect the hyoid arch with the upper jaw. All of the elements are paired and comprise the following: the



Figs. 53–56. Palatine arch and suspensorium. Left side: (53) *Cryodraco antarcticus*, (54) *Chionodraco rastrospinosus*, (55) *Champsocephalus gunnari*, (56) *Cryodraco antarcticus*. Shaded areas indicate cartilaginous junctions. Scale 5 mm.

palatines (PAL), ectopterygoids (ECP) and metapterygoids (MTP). In channichthyid fishes, the mesopterygoid (MSP) "has been" thought to be absent. The problem on the identification of the mesopterygoid will be discussed later. This terminology follows that of Weitzman (1962) and Voskoboynikova (1982).

Palatine (Figs. 53, 54, 56): The palatines of channichthyid fishes are extremely characteristic among those of notothenioid fishes. The palatine is weakly ossified, slender and filamentous. The anterior portion which is somewhat thick and cylindrical meets the anterior part of the maxillary with a strong ligament. It tapers posteriorly to a point which joins the succeeding pterygoin bone with the cartilaginous filament. There are no palatine teeth.

Ectopterygoid (Figs. 53–56): See discussion below.

Metapterygoid (Figs. 55, 56): These relatively large and flat cheek bones are basically triangular. Each metapterygoid overlaps the hyomandibular dorsally, and meets the quadrate ventrally with the cartilaginous part. Its posterior margin with the fringe is attached to the ventral limb of the hyomandibular and the symplectic.

3.4.2. Discussion

The extremely elongated feature of the palatine arch reflects the long snout and large mouth of channichthyid fishes. The reduction of ossification of each element is the common feature of this family.

VOSKOBOYNIKOVA (1982) suggested that a correlation between elongation and thinning of the palatine and reduction of the mesopterygoid can be clearly seen in the Nototheniidae. Considering the morphological features of the palatine and pterygoid bones of channichthyid fishes, it can be concluded that the Channichthyidae show the extreme condition of this tendency suggested by VOSKOBOYNIKOVA (1982).

Palatine: Any noticeable differences in the palatine are not recognized among channichthyid fishes.

Ectopterygoid and mesopterygoid: GILL (1862), REGAN (1913, 1914) and NORMAN (1938) stated that the mesopterygoid was lacking in the Channichthyidae. In the Channichthyidae, the portion which is usually shared by the two elements such as the ectopterygoid and mesopterygoid consists of only one bony element and this bony element has been currently identified as the ectopterygoid. Therefore, GILL (1862) and others concluded that the loss of the mesopterygoid occurred in the Channichthyidae. Judging from the feature of the pterygoid bone of *Champsocephalus* identified as the ectopterygoid which overlies the anterior edge of the quadrate, the identification of the bony element seems to be reasonable.

Neverthless, there is a problem with the identification of another ossified part which is situated between the palatine and the ectopterygoid. The boundary between the palatine and the ossified part is clearly recognized, and the posterior tip of the ossified part meets the bony element previously identified as the ectopterygoid. The above-mentioned features are inconsistent with those of the common ectopterygoid and it is thought to be proper that the ossified part between the two bony elements is identified as the remnant of the mesopterygoid. The modification of the mesopterygoid in channichthyid fishes might be expected due to the feature of the elongated mesopterygoid of the Bathydraconidae (see Section 4.4). The modification of the pterygoid bones is also mentioned by VOSKOBOYNIKOVA (1982) as a manifestation of the general process of reduction of these bones within the suborder which is completed with the fusion between the ecto- and mesopterygoids and then their fusion with the palatine. Therefore, VOSKOBOYNIKOVA (1982) names the fused pterygoid bones "mesopterygoid+ectopterygoid" or "palatine+ectopterygoid+mesopterygoid". However, the present study proves that these three bones, the palatine, ectopterygoid and mesopterygoid, are clearly separated and form the series of the three filamentous ossified elements. It is concluded for the first time that the Channichthyidae posess the mesopterygoid as the reduced ossified element.

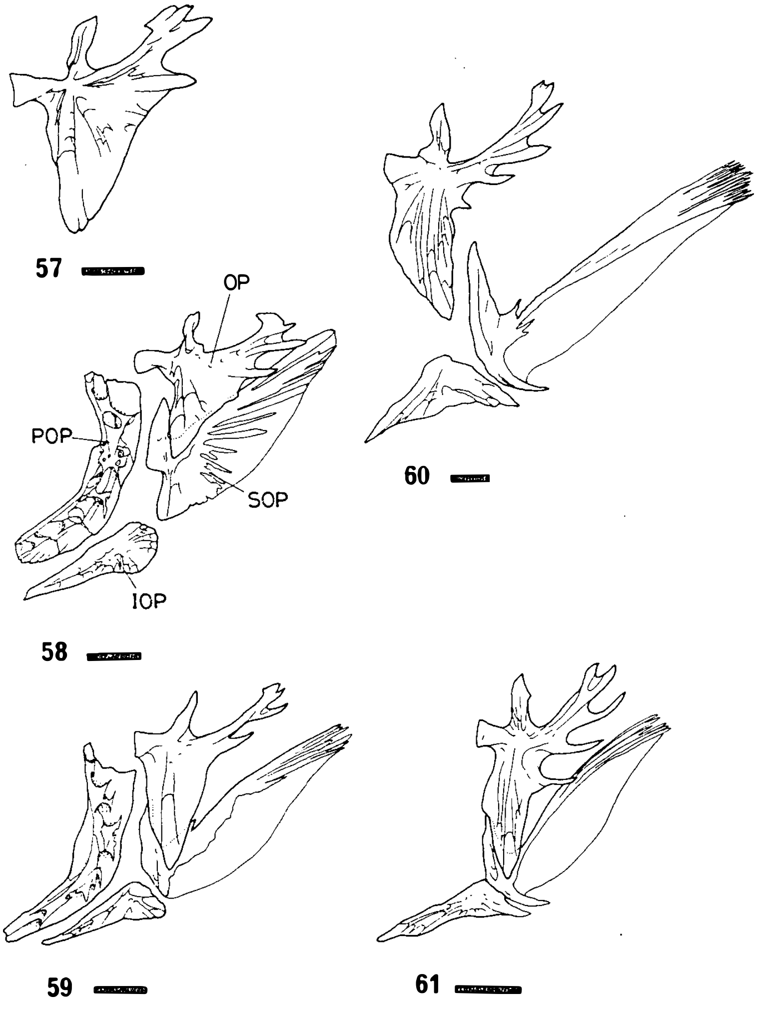
In notothenioid fishes, except most of channichthyids, the ectopterygoids overlap the anterior margin of the quadrate (see Section 4.4 and also VOSKOBOYNIKOVA, 1980, 1982). The ectopterygoids of channichthyid fishes, except the fishes belonging to *Champsocephalus*, are never attached to the quadrates. From the evidence mentioned above, the character state represented by *Champsocephalus* is thought to be a primitive state.

Metapterygoid: There are no noticeable differences among the genera of the Channichthyidae.

3.5. Opercular apparatus

3.5.1. Description

The opercular apparatus of channichthyid fishes consists of four paired bones as follows: the opercles (OP), subopercles (SOP), preopercles (POP) and interopercles (IOP). This terminology follows that of Weitzman (1962).



Figs. 57–61. Opercular apparatus. Left side: (57) *Champsocephalus gunnari*, (58) *Pagetopsis macropterus*, (59) *Cryodraco antarcticus*, (60) *Chionodraco rastrospinosus*, (61) *Chaenodraco wilsoni*. Scale 5 mm.

Opercle (Figs. 57–61): These slightly triangular bones are flattened and convex externally. Each opercle joins to the hyomandibular with the anterior limb, overlaps the subopercle ventrally, and forms spines at the posterodorsal angle. The number and shape of the opercular spines vary according to the species and individuals. Basically, the spines are dorsally and posteriorly pointed.

In *Champsocephalus* (Fig. 57), *Pagetopsis* (Fig. 58), *Neopagetopsis* and *Pseudo-*

chaenichthys, the fringe develops between the posterior and ventral limbs as a web, while in the other channichthyid genera (Figs. 59–61) the fringe between the two limbs is reduced to small spines which look like umbrella ribs.

Subopercle (Figs. 58–61): Each triangular, thin bone consists of the dorsally pointed process and the dorsoposteriorly pointed membraneous portion. It slides under the ventral part of the opercle and meets the interopercle anteriorly. The membraneous portion of *Pagetopsis* (Fig. 58), *Neopagetopsis* and *Pseudochaenichthys* is ossified, but those of the other genera are shown as the transparent portion by means of the alizarin staining (Figs. 59–61).

In *Chionodraco* (Fig. 60) and *Chaenodraco* (Fig. 61), the subopercle and interopercle bear a pair of spines at the angle where they meet.

Preopercle (Figs. 58, 59): These large, crescent-shaped bones form tubular canal structures. On each side of the body, this tubular structure which supports the preopercular canal connects the temporal canal with the mandibular canal. It partially overlaps the posteroventral portion of the hyomandibular, the anterodorsal portion of the subopercle, and the posteroventral portion of the interopercle.

Interopercle (Figs. 58–61): Each interopercle is a small triangular and blade-shaped element. It is attached to the anterior edge of the subopercle, is situated under the preopercle anteriorly, and joins to the interhyal with the cartilaginous articulation internally.

In *Chionodraco* (Fig. 60) and *Chaenodraco* (Fig. 61), the posteroventral angle of the interopercle forms a spine as described before.

3.5.2. Discussion

Opercle: The number of opercular spines is variable among the species and individuals. Therefore, this character is not available for systematic study at the generic level.

The shape of the fringe between the posterior and ventral limbs divides the channichthyid genera into two groups. One group, consisting of *Champsocephalus*, *Pagetopsis*, *Neopagetopsis* and *Pseudochaenichthys*, posesses the web-like fringe, while the other group, consisting of most channichthyid genera except the above-mentioned four genera, has the spine or reduced fringe. The opercle of fish is originally a cover of the gill chamber, and its shape is generally flat (or slightly convex) and enlarged as in that of the Nototheniidae and the other general percoid fishes. Therefore, the opercles of *Champsocephalus*, *Pagetopsis*, *Neopagetopsis* and *Pseudochaenichthys* appear to be plesiomorphic in contrast with those of the other channichthyid genera.

Subopercle: The ossified membraneous parts of subopercles are known only in *Pagetopsis*, *Neopagetopsis* and *Pseudochaenichthys*. In the other eight genera, membraneous parts are not ossified and are shown as the transparent area by means of the alizarin staining. Judging from the fact that most of notothenioid fishes generally bear the fully ossified subopercles, the feature of the channichthyid genera such as *Dacodraco*, *Channichthys*, *Chaenocephalus*, *Chionobathyscus*, *Cryodraco*, *Chionodraco*, *Chaenodraco* and *Champsocephalus* is thought to be a derived character state.

The subopercle (and interopercle) which forms a spine is observed in *Chionodraco* and *Chaenodraco* and shows a derived feature.

Preopercle: Some minor differences are recognized in the preopercle of the channichthyid species. However, they cannot be used as the distinguishing feature among the genera of this family.

Interopercle: The shape of the interopercle is simple and not different enough to draw a sharp line among the genera. The character analysis of the interopercular spine is mentioned above.

3.6. Hyoid arch

3.6.1. Description

The neurocranium, palatine arch, opercular apparatus, mandibular arch and gill arch are connected with one another by the hyoid arch as an intermediary. The hyoid arch includes the basihyal (BH), ceratohyals (CH), hypohyals (HH), epihyals (EH), hyomandibulars (HYO), interhyals (IH), quadrates (Q), symplectics (SYM) and urohyal (UH). Some branchiostegal rays (BST) are attached to the epihyal and ceratohyal. Within the bony elements mentioned above, the basihyal and urohyal are median and the others are paired. This terminology follows that of McAllister (1968) and Johnson (1974). The terminology of the urohyal parts follows that of Kusaka (1974).

Hyomandibular (Figs. 55, 56): The hyomandibular is composed of four main rods of bone which roughly form an "X". It is attached to the sphenotic fossa with the anterodorsal rod, to the pterotic fossa with the dorsal rod, to the anterior articulating head of the opercle with the posterior rod, to the symplectic with the ventral rod, and to the preopercle laterally. The hyomandibular also meets the metapterygoid anteriorly and the interhyal internally. The fringe develops between the rods as a web.

Symplectic (Figs. 55, 56): These slightly triangular bones connect the hyomandibular to the quadrate. Each symplectic overlaps the posterior process of the quadrate laterally and joins to the angle where the quadrate and articular meet each other. Its anterodorsal margin borders the posteroventral edge of the metapterygoid.

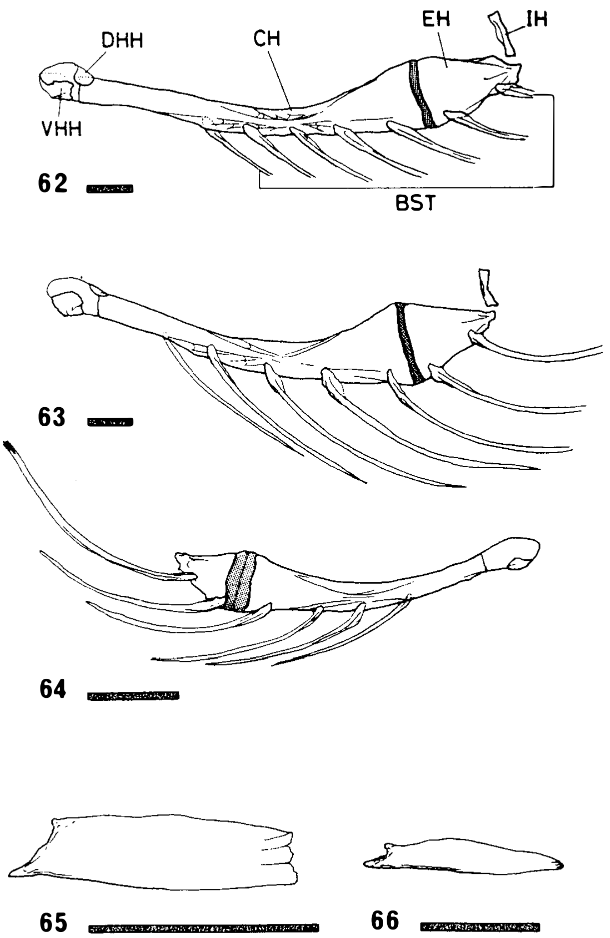
Quadrate (Figs. 55, 56): These triangular, fan-shaped bones connect the hyoid arch to the mandibular one. The ventral head of the quadrate is articulated tightly to the articular, and the posterior process of the quadrate receives the lower part of the symplectic laterally. In each quadrate, the dorsal edge is bordered by the developed cartilaginous area. It meets the ectopterygoid anteriorly and the metapterygoid posteriorly.

In most channichthyid fishes other than *Champsocephalus* (Fig. 55), the posterior portion of the ectopterygoid does not overlie the anterior margin of the quadrate.

Interhyal (Figs. 62–64): The interhyal is a rod-like bone which connects the upper end of the epihyal and the ventral edge of the ventral rod of the hyomandibular.

Epihyal (Figs. 62–64): Each epihyal is a flat, triangular bone with the two largest branchiostegal rays on its posteroventral margin. It is articulated to the interhyal posteriorly and the ceratohyal anteriorly without sutured junctions.

Ceratohyal (Figs. 62–64, 77): The ceratohyal is a paddle-like bone without the beryciform foramen. It consists of a cylindrical anterior portion and a tapered posterior portion. This bone is articulated to the hypohyals anteriorly and the epihyal posteriorly without sutured junctions. Four to seven branchiostegal rays are attached to the ceratohyal laterally.



Figs. 62–66. Hyoid arch and urohyal. Hyoid arch: (62) *Champsocephalus gunnari* (leftt side, outer view), (63) *Pagetopsis macropterus* (left side, outer view), (64) *Chaenocephalus aceratus* (right side, outer view); urohyal (left side): (65) *Champsocephalus gunnari*, (66) *Chionodraco myersi*. Scale 5 mm.

Branchiostegal rays (Figs. 62–64): All of the branchiostegal rays are acinaciform as stated by McAllister (1968). The anteriormost one or two rays are attached to the ceratohyal internally and the others are articulated externally. These branchiostegal rays increase in size posteriorly. The largest or posteriormost one is tapered and branched distally. Branchiostegals support the membrane which is lying between the opercle and the isthmus.

The number of branchiostegal rays, shown as "the number of rays on the epihyal + the number of rays on the ceratohyal", is as follows: *Champsocephalus* (Fig. 62), *Pagetopsis* (Fig. 63) and *Pseudochaenichthys* =2+5; *Neopagetopsis*=2+5—7; and the other genera =2+4 (Fig. 64).

Hypohyals (Figs. 62–64, 67–77): The hypohyals consist of dorsal (DHH) and ventral hypohyals (VHH). Each hypohyal is a small, cap-like bone which is articulated to the ceratohyal and to each other by a cartilaginous junction. The ventral hypohyal receives a ligament which is connected to the anterior tip of the urohyal and is attached medially to the basihyal and first hypobranchial.

The dorsal hypohyal is recognized as an ossified element in *Champsocephalus*

(Figs. 62, 67), *Pagetopsis* (Figs. 63, 68, 69), *Neopagetopsis* (Fig. 70) and *Pseudochaenichthys* (Fig. 71). On the other hand, the dorsal hypohyals of the other seven genera are never ossified (Figs. 64, 72–77).

Urohyal (Fig. 65, 66): This small, blade-like thin bone is situated under the second or third basibranchial. Its anterior tip (hypohyal attachment) is connected to the ventral hypohyals with a strong ligament. The dorsal and ventral spread is absent, and the ventral edge does not form the keel structure.

Basihyal (Figs. 67–77): This median and triangular bone is the anteriormost element of the basibranchial series. It tapers anteriorly and forms the cylindrical articulating head posteriorly. The basihyal meets the ventral hypohyals posteroventrally and the first basibranchial posteriorly. The shape varies among the genera; however, it is hard to classify the shape into several groups.

3.6.2. Discussion

Hyomandibular: The angle formed by each rod of the hyomandibular varies among species, but its character analysis and the determination of polarity are difficult.

Symplectic: No morphological feature of the symplectics shows any noticeable differences in this family.

Quadrate: A distinctive feature observed in *Champsocephalus*, where the quadrate and ectopterygoid are overlapping, was mentioned in the former item.

Interhyal, epihyal and ceratohyal: In each of these elements, there is no noticeable difference among the genera of the Channichthyidae.

Branchiostegal rays: The shape of branchiostegal rays of all channichthyid fishes is classified as acinaciform, and any features worthy of special mention are not known among them.

By the number of branchiostegal rays the channichthyid genera can be divided into two groups as follows: the six-rayed genera such as *Dacodraco*, *Channichthys*, *Chaenocephalus*, *Chionobathyscus*, *Cryodraco*, *Chionodraco* and *Chaenodraco*; and the seven(or more)-rayed genera such as *Champsocephalus*, *Pagetopsis*, *Neopagetopsis* and *Pseudochaenichthys*.

The posterior two branchiostegal rays are always situated on the epihyal in both groups. Therefore, the difference in the number of branchiostegal rays is supposed to be caused by the increase or decrease in the number of the anteriormost branchiostegal rays on the ceratohyal.

In not a few teleostean groups, a larger number of branchiostegal rays is supposed to indicate a more primitive character (MATSUBARA, 1943; HAEDRICH, 1967; MCALLISTER, 1968; PRINCE AKIHITO, 1969; OKAMURA, 1970). Therefore, it is concluded that the seven(or more)-rayed group shows the primitive state in this character.

Hypohyals: Based on the ossification of the dorsal hypohyal, the eleven channichthyid genera can be divided into two groups. MCALLISTER (1968) stated that "primitive teleostomes have only a single hypohyal; advanced ones have two (but some advanced ones lose one or both)." In the case of the primitive bony fishes such as *Amia* or *Lepisosteus*, their hypohyals are recognized as a single element, but this feature differs qualitatively from that of channichthyid fishes. Compared with the other notothenioid fishes in which the dorsal and ventral hypohyals are fully ossified, the Channichthyidae, in which only the ventral hypohyal is ossified, is thought to be a more advanced form.

Basihyal: In some specimens of *Champsocephalus*, *Pagetopsis*, *Neopagetopsis* and *Pseudochaenichthys*, each basihyal is somewhat triangular with a straight anterior edge and a shallower posterior angle. On the other hand, the basihyals of the other genera of this family are rather fan-shaped, with a rounded anterior margin and a deeper posterior angle. However, it is difficult to determine the boundary between the two morphological features, and the character distinctions among the genera cannot be presented clearly.

Urohyal: The reduced form and low ossification are common features in urohyals of the Channichthyidae, but there are no major differences in this feature among the channichthyid fishes.

3.7. Branchial arch

3.7.1. Description

Endoskeletal components include the following: the basibranchials (BB), ceratobranchials (CB), epibranchials (EB), hypobranchials (HB) and pharyngobranchials (PB). Dermal elements associated with the endoskeletal bones mentioned above include gill rakers and tooth patches. The basibranchials are median components and the others are paired elements. Gill-arch structures of the Channichthyidae and other notothenioid families are also given by IWAMI and ABE (1984). This terminology follows that of NELSON (1969) and ROSEN (1973).

Basibranchials (Figs. 67–77): These four basically median bones lie in the floor of the pharynx between right and left hypobranchials. The anteriormost one, termed the first basibranchial, lies between the basihyal and the hypobranchials and is usually recognized as an unossified element.

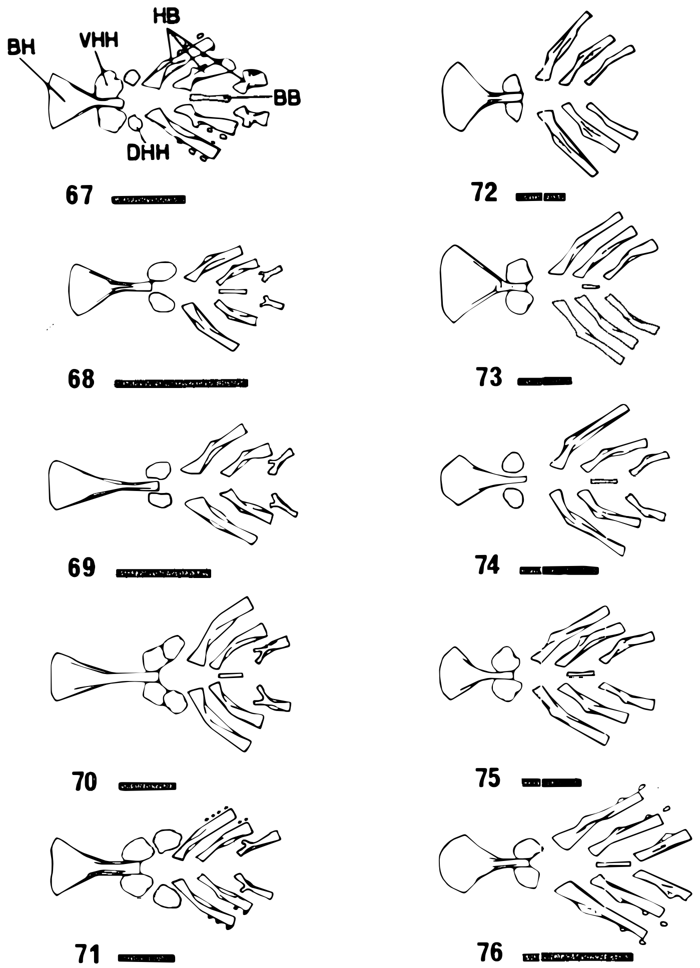
The second basibranchial, situated between the first and second hypobranchials, is also a cartilaginous element.

The third basibranchial, which is situated in the posterior portion of the basibranchial series, is the only ossified element among the basibranchial bones in most genera of this family. In *Pagetopsis maculatus* (Fig. 69), *Pseudochaenichthys georgianus* (Fig. 71) and *Channichthys rhinoceratus* (Fig. 72), the third basibranchial is also cartilaginous. The shape of the third, ossified basibranchial is slender and cylindrical.

The fourth, cartilaginous basibranchial is found in the posteriormost portion of the basibranchial series. It connects to the anterior tips of the fifth ceratobranchials posteriorly.

Hypobranchials (Figs. 67–77): The hypobranchials are composed of three paired elements which connect the basibranchial series with the ceratobranchials. Near the junction with the ceratobranchials, they sometimes bear gill rakers, but no tooth patch.

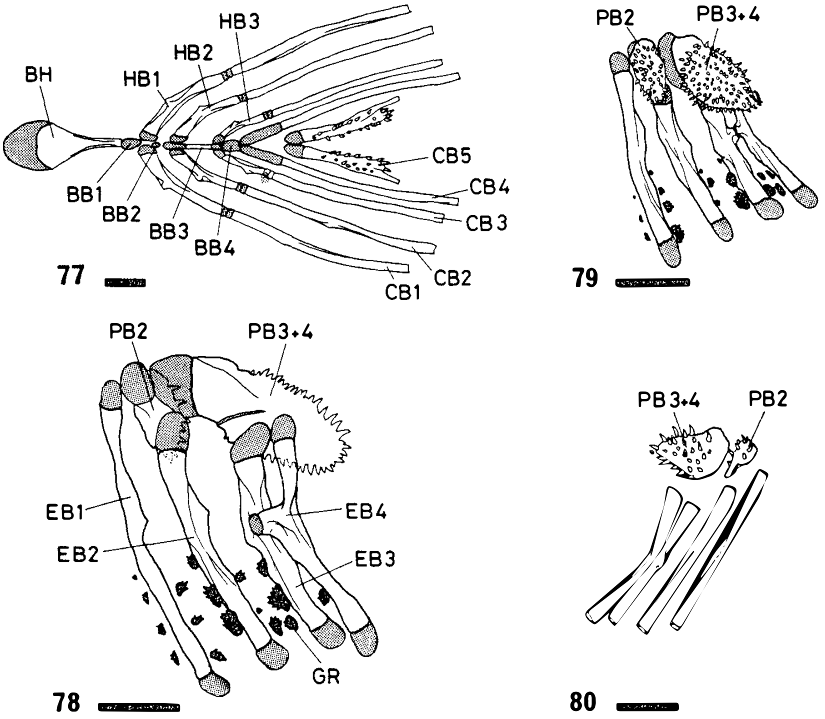
The feature of the posteriormost, third hypobranchial varies among channichthyid genera. It can be classified into three groups as follows: (1) The slender rod-like shape as in *Channichthys* (Fig. 72), *Chaenocephalus* (Fig. 73), *Chionobathyscus*, *Cryodraco* (Fig. 74), *Chionodraco* (Fig. 75) and *Chaenodraco* (Fig. 76); (2) the slender rod-like shape with the anterior pointed process as in *Pagetopsis* (Figs. 68 and 69), *Neopagetopsis* (Fig. 70) and *Pseudochaenichthys* (Fig. 71); and (3) the flattened Y-shape as in *Champsocephalus* (Fig. 67).



Figs. 67–76. Lower branchial arch. (67) *Champsocephalus gunnari*, (68) *Pagetopsis macropterus*, (69) *Pagetopsis maculatus*, (70) *Neopagetopsis ionah*, (71) *Pseudochaenichthys georgianus*, (72) *Channichthys rhinoceratus*, (73) *Chaenocephalus aceratus*, (74) *Cryodraco antarcticus*, (75) *Chionodraco myersi*, (76) *Chaenodraco wilsoni*. All figures are dorsal views. Scale 5 mm.

Ceratobranchials (Fig. 77): Ceratobranchials are the longest elements among those of the ventral part of the branchial arches, and consist of five paired elements. The posteriormost or fifth ceratobranchials are distinctive from the other ceratobranchials in having numerous conical teeth on their dorsal surface, no gill rakers and no associated epibranchials. The first three elements are long, slender, innercurved bones and each element respectively joins the epibranchial distally and the hypobranchial proximally. The fourth ceratobranchial is the longest and has no associated basibranchial and hypobranchial. These four paired elements bear gill filaments externally and gill rakers internally.

Epibranchials (Figs. 78–80): Epibranchials are four paired elements which construct the dorsal portion of the branchial arches. Each epibranchial joins its respective ceratobranchial. The first epibranchial, bearing no uncinate process, is longest and has no associated pharyngobranchial. The second one meets the second pharyngobranchial via a cartilaginous junction. The uncinate processes on the dorsomedian



Figs. 77–80. Branchial arch. Lower part: (77) *Chionodraco rastrospinosus* (dorsal view); upper part: (78) *Champsocephalus gunnari* (left side, dorsal view), (79) *Champsocephalus gunnari* (right side, ventral view), (80) *Pseudochaenichthys georgianus* (left side, ventral view). Dotted areas indicate cartilaginous junction. Scale 5 mm.

surface of the third and fourth epibranchials are connected to one another by a ligament, and these processes are also attached to the bottom of the skull.

The last two epibranchials meet the posterior pharyngobranchial medially. All elements bear gill rakers internally and gill filaments externally. Epibranchials have no associated tooth patch structure.

Interarcual cartilage cannot be observed in all specimens of channichthyid fishes examined.

Pharyngobranchials (Figs. 78–80): These two paired and somewhat oval bones are attached to the skull floor and bear numerous conical teeth on their ventral surface. The anterior pharyngobranchial, termed the second pharyngobranchial, is slightly smaller than the posterior one, and joins with the second epibranchial.

The posterior one is larger and articulated with the third and fourth epibranchials. This posterior pharyngobranchial may be formed by the fusion between the third and fourth pharyngobranchials (see Section 4.7).

The first pharyngobranchial is absent.

Gill rakers (Figs. 78–80): In channichthyid fishes, gill rakers are not well developed and their features are small dentigerous bony plates or vestigial knobs.

The fishes of *Champsocephalus* (Figs. 78, 79), *Pseudochaenichthys* (Fig. 80), *Chaenodraco* and *Chionodraco rastrospinosus* bear the dentigerous gill rakers. In the other channichthyid fishes, gill rakers are reduced to small knobs at the angle of the gill arches.

3.7.2. Discussion

Basibranchials: The feature of low ossification is also found in these elements. In *Pagetopsis maculatus*, *Pseudochaenichthys georgianus* and *Channichthys rhinoceratus*, even the third basibranchial is cartilaginous. 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 it shows that the third basibranchial exhibits the different features, ossified and cartilaginous, 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 at least in the family Channichthyidae.

Hypobranchials: As mentioned above, the shape of the third hypobranchials is classified into three groups as follows; the slender rod-like shape, the slender rod-like one with the anterior pointed process, and the flattened Y-shape. The other notothenioid fishes have the flattened and triangular one (see Section 4.7). The anterior pointed process found in *Pagetopsis*, *Neopagetopsis* and *Pseudochaenichthys* is supposed to be the remnant of the anterior angle of triangular hypobranchials in most notothenioid fishes. Judging from the polarity recognized in this character, slender rod-like elements are thought to be more advanced ones.

Ceratobranchials, epibranchials and pharyngobranchials: There is no remarkable differences among the genera of the Channichthyidae.

Gill rakers: Two kinds of gill rakers, dentigerous and vestigial, are known in channichthyid fishes. However, the both features are observed in one and the same genus such as *Chionodraco*. Judging from these evidences, it would not be proper to think that fishes having similar gill rakers are closely related to one another. Therefore, the character, the shape of gill rakers, is concluded not to be useful for the systematic study of this family at the generic level.

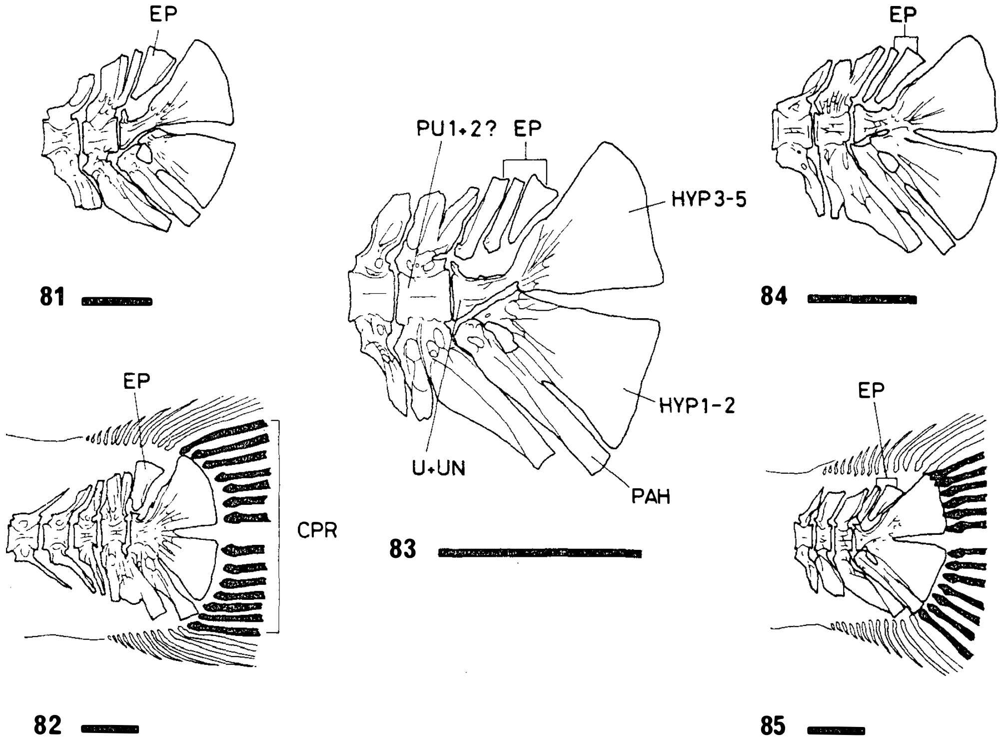
3.8. Axial skeleton

3.8.1. Description

Axial skeletons include vertebrae and caudal skeletons which are considered to be modified vertebral elements. The caudal skeletons consist of the ural centra (U), hypurals (HYP), parhypural (PAH), epurals (EP) and uroneurals (UN). In the Channichthyidae, uroneurals are fused to the ural centra and impossible to be recognized as a separate element. The terminology used in this item follows that of NYBELIN (1963), ROSEN (1973) and ANDERSEN (1984).

Ural centra (Figs. 81–85): The ural centra are posteriormost vertebral elements and fused into a single half-centrum in channichthyid fishes. This half-centrum is basically composed of two bony elements such as the first and second ural centra. The posteroventral surface of the fused ural centra is slightly flattened and is articulated with the proximal ends of the first and second hypurals and parhypural. Ural centra, parhypural and hypurals are often consolidated into a single bony plate in channichthyid fishes. Uroneurals are also always fused to ural centra dorsolaterally and are not recognized as separate elements.

Hypurals (Figs. 81–85): These triangular and flattened bones support caudal fin rays distally. In channichthyid fishes, hypurals basically consist of five bony ele-



Figs. 81–85. Caudal skeleton. (81) *Champsocephalus gunnari*, (82) *Pseudochaenichthys georgianus*, (83) *Chaenocephalus aceratus*, (84) *Cryodraco antarcticus*, (85) *Chionodraco rastrospinosus*. All figures are left side views. Scale 5 mm.

ments (ANDERSEN, 1984). The first two hypurals (HYP 1 and HYP 2) are fused into a single plate, namely the lower hypural plate, and the rest three elements (HYP 3, HYP 4 and HYP 5) are fused into the upper hypural plate. The proximal end of the lower hypural plate is articulated to the posteroventral surface of the ural centra and forms a foramen between the posterobasal margin of the parhypural and the anterobasal margin of the lower hypural plate. Hypurals of the channichthyids are sometimes consolidated with the ural centra.

Parhypural (Figs. 81–85): This flattened and elongate rectangular bone without a proximal caudally directed spine, a hypurapophysis, is articulated to the anteroventral surface of the consolidated ural centrum proximally and meets the first hypural posteriorly. The fringe-like structure developed along the anterior edge of the parhypural borders the posterior margin of the haemal spine of the first preural centrum.

Epurals (Figs. 81–85): These small and flattened bones are situated between the neural spine of the first preural centrum and the anterior margin of the upper hypural plate. The number of epurals varies from one to three within the same species of this family.

Vertebrae (Table 1): Morphological features of vertebrae are not mentioned in the present study. The number of vertebrae of channichthyid species is shown in Table 1. Most of genera of this family have about 60 vertebrae, while *Pagetopsis*, *Pseudochaenichthys* and *Dacodraco* are recognized as the genera having fewer vertebrae (49–55). On the other hand, *Cryodraco* has the largest number of vertebrae (67–70) among the genera of the Channichthyidae.

Table 1. The range of the number of vertebrae of all channichthyid species.

Species	Number of vertebrae																							
	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71
Champsocephalus esox													×											
Champsocephalus gunnari											×	×	×	×	×	×								
Pagetopsis macropterus						×																		
Pagetopsis maculatus		×	×																					
Neopagetopsis ionah													×	×										
Pseudochaenichthys georgianus				×	×	×	×	×																
Dacodraco hunteri						×																		
Channichthys rhinoceratus								×	×	×														
Channichthys velifer									×															
Chaenocephalus aceratus													×	×	×	×	×							
Chionobathyscus dewitti												×	×											
Cryodraco antarcticus																				×	×	×	×	
Chionodraco hamatus											×	×	×	×	×	×								
Chionodraco rastrospinosus													×	×	×	×								
Chionodraco myersi									×	×	×	×	×											
Chaenodraco wilsoni													×	×	×									

3.8.2. Discussion

Ural centra: No distinctive feature to each genus is observed in this bony element.

Hypurals: The number and mode of fusion of the hypurals are not much different among the channichthyid genera. ANDERSEN (1984) stated the type of the channichthyid caudal skeleton as the 2+3 type. The 2+3 type caudal skeleton is characterized by the fusion of the hypurals 1 and 2 (the lower hypural plate) and that of the hypurals 3, 4 and 5 (the upper hypural plate). ANDERSEN (1984) also assumed that the hypurals of channichthyid fishes are fully fused to the ventral edge of the consolidated ural centrum. However, this feature, the consolidation of the hypurals and ural centra, is not found in some of the channichthyid caudal skeletons examined. The consolidation of the two bony components is irregular in its appearance among species and even individuals. Therefore, this character is supposed not to be useful for the systematic study on the genera of this family.

Parhypural: No distinctive feature to each genus is observed in this bony element.

Epurals: The number of epurals varies from one to three among species and even individuals, and this is considered as a variable character. Therefore, the conclusions of EAKIN (1981) and ANDERSEN (1984) stating that only two epurals are found in the

Channichthyidae should be eliminated as an erroneous conclusion. This indicates that the systematic value of the number of epurals cannot be evaluated easily.

Vertebrae: The frequency distribution of the vertebral number shows that most channichthyid species have a somewhat large number of vertebrae such as 60 vertebrae. The Channichthyidae also contain the groups with the smaller number of vertebrae (49–55) and with the larger number (67–70), but it is difficult to decide the polarity in the change of the vertebral number. ANDERSEN (1984) suggested that the large number of abdominal vertebrae (20 or more) may be considered advanced or apomorphic. However, judging from the frequency distribution of the vertebral number of the Channichthyidae, the number of abdominal vertebrae is assumed to indicate a plesiomorphic condition and two different and opposite polarities (more and fewer) are supposed. At any rate, the polarity of change in the number of vertebrae is hard to certify.

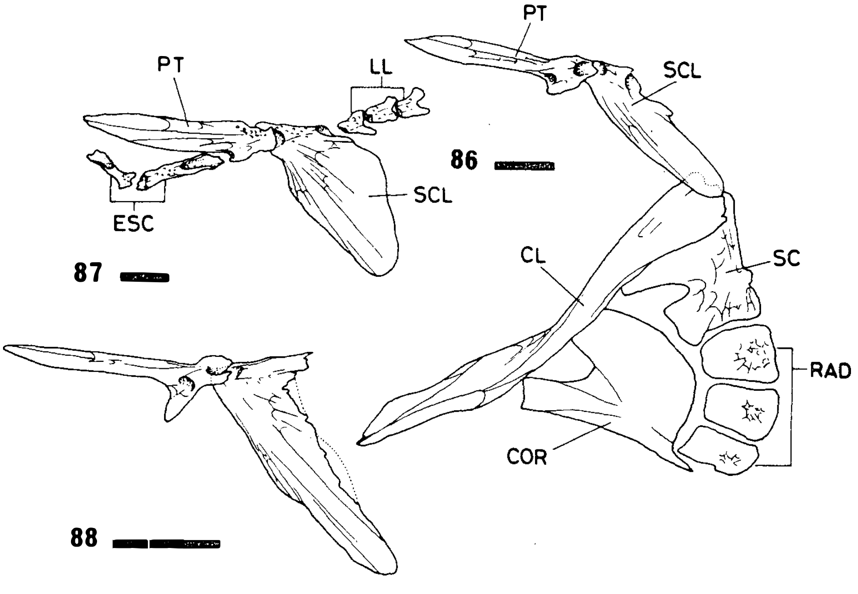
3.9. Pectoral girdle

3.9.1. Description

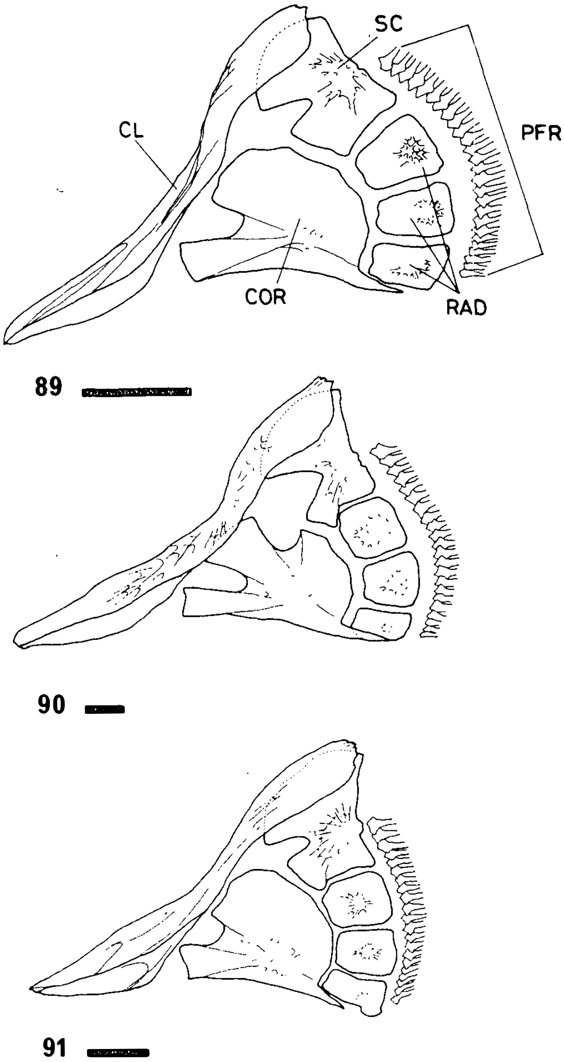
The pectoral girdle consists of the bony elements which support the pectoral fin. All elements are paired and as follows; the posttemporals (PT), supracleithra (SCL), cleithra (CL), scapulae (SC), coracoids (COR) and radials (RAD). Channichthyid fishes have no postcleithrum. This terminology follows that of WEITZMAN (1962).

Posttemporal (Figs. 86–88): These elongate, forked bones connect the pectoral girdles with the neurocranium. The upper limb rests on the posteriorly directed facet of the epiotic, and the lower one meets the opisthotic via a ligamentous attachment. It meets the supracleithrum posteriorly. This bone contains a part of the sensory canal ventrolaterally which forms the temporal canal.

Supracleithrum (Figs. 86–88): The supracleithrum is a thin, flattened and blade-like bone. It connects the cleithrum posteroventrally with the posttemporal anterodorsally. The anterior portion is slender and forms the canal connecting the temporal



Figs. 86–88. Pectoral girdle. (86) *Pagetopsis macropterus*, (87) *Channichthys rhinoceratus*, (88) *Chionodraco myersi*. All figures are left and outer views. Scale 5 mm.



Figs. 89–91. Pectoral girdle. (89) *Champsocephalus gunnari*, (90) *Channichthys rhinoceratus*, (91) *Chaenodraco wilsoni*. All figures are left and outer views. Scale 5 mm.

canal with the lateral line.

Cleithrum (Figs. 86, 89–91): These concave and arch-like bones border the anterior margin of the pectoral girdle. The dorsal portion of the cleithrum is flattened and meets the supracleithrum anteroexternally and the scapula posterointernally. Below this portion, the cleithrum bears a crest and joins the coracoid on its median and posterior surface.

The lower tip of the cleithrum extends anteroventrally and medially to meet its fellow just anterior to the pelvic girdle via a cartilage. A forked depression on the dorsal margin of the cleithrum which is usually recognized in the cleithrum of other notothenioid fishes (see Section 4.9) is not observed in channichthyid fishes.

Scapula (Figs. 86, 89–91): The scapula is a somewhat fan-shaped and flattened bone. This bone meets the upper portion of the cleithrum anteriorly, the dorsal edge of the coracoid ventrally and the dorsal margin of the uppermost radial posteroventrally. It also supports the uppermost pectoral fin rays on its posterior edge. The scapular foramen lies between the scapula and the coracoid, and forms the distinctive V-shape notch on the anteroventral portion of the scapula.

Coracoid (Figs. 86, 89–91): These flattened and semicircular bones share most of the medial portion of the pectoral girdle. Anteriorly each coracoid bears the notch which divides the bone into the upper and lower arms. The upper arm meets the cleithrum anteromedially. The lower arm is articulated to the inner surface of the cleithrum and to the anterior portion of the pelvic girdle via a cartilage. It also meets the scapula dorsally and the radials posteriorly. Its posterior-directed process borders the anteroventral edge of the lower radial.

In *Channichthys*, there is a notch forming a part of the scapular foramen on the dorsal edge of the coracoid, while in the other genera the dorsal edge of the coracoid is round and without notch.

Radials (Figs. 86, 89–91): These three paired, flattened and slightly rectangular bones meet each other and border the posterior margin of the pectoral girdle. They support pectoral fin rays on their posterior edge. The lowest radial is the smallest and its lower edge meets the dorsal margin of the posterior-directed process of the coracoid. The series of three radials borders the scapula dorsally and the coracoid anteriorly and ventrally.

Extrascapulars (Fig. 87): Extrascapulars (ESC) are associated with the anterodorsal portion of the pectoral girdle, but these bones are not thought to be a component of the pectoral girdle. There are two extrascapulars in all channichthyid fishes. They are tubular and troughlike bones of somewhat irregular shapes. The posterior extrascapular is slightly larger than the anterior one, but the shape is not much different between the two. The supratemporal, temporal and preoperculo-mandibular canals are joined to each other by the canal structure of these bones.

3.9.2. Discussion

Posttemporal and supracleithrum: In these two elements, there is no noticeable difference among the genera of the Channichthyidae.

Cleithrum: Absence of a forked depression on the dorsal margin of the cleithrum is a characteristic feature of this family (see Section 4.9). However, no distinctive feature useful for the analysis of the generic relationship is recognized.

Scapula and coracoid: The scapular foramen is formed by the V-shape notches of nearly an equal size in the scapula and coracoid. The position of the scapular foramen has been discussed as the distinguish character of the two genera *Trematomus* and *Notothenia* (BOULENGER, 1902; PAPPENHEIM, 1912; REGAN, 1913, 1914; NORMAN, 1938; HUREAU, 1962, 1970; ANDERSEN, 1984). In most notothenioid fishes except for most channichthyids and fishes belonging to *Trematomus*, *Pagothenia*, *Dissostichus*, *Pleuragramma*, *Cryothenia* and *Aethotaxis*, the foramen is formed by the V-shape notch on the ventral edge of the scapula and that on the dorsal edge of the coracoid. ANDERSEN (1984) concluded that the small foramen found in some genera of the Notothenidae (the above-mentioned six genera) is most likely the primitive condition. Therefore, in the present study the notched coracoid observed in *Channichthys* is concluded to be advanced.

Radials: No distinctive feature is recognized among the channichthyid genera.

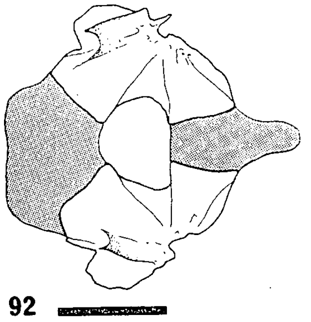
Extrascapulars: The same as mentioned above.

3.10. Pelvic girdle

3.10.1. Description

The pelvic girdle includes the paired pelvic bones which support the ventral fin rays. This terminology follows that of WEITZMAN (1962).

Pelvic bone (Figs. 92–95): The pelvic bones are slightly covex, triangular elements, and situated between the pectoral fins ventromedially. Each pelvic bone meets its fellow medially and forms the pelvic girdle in a lozenge shape. The pelvic bones meet the anteroventral tips of the cleithra anteriorly and support the ventral fins posteriorly.



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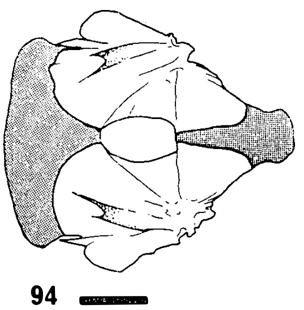

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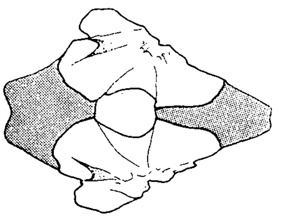

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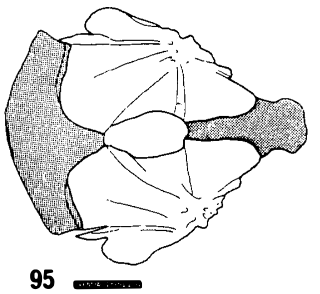

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Figs. 92–95. Pelvic bone. Ventral view: (92) *Pseudochaenichthys georgianus*, (93) *Chionobathyscus dewitti*, (94) *Chaenodraco wilsoni*; dorsal view: (95) *Chaenodraco wilsoni*. Shaded areas show cartilaginous parts. Scale 5 mm.

3.10.2. Discussion

The morphological features of the pelvic girdle are extremely conservative among the genera of the Channichthyidae. Therefore, these features cannot be used for the systematic study of this family.

3.11. Fins

3.11.1. Description

Channichthyid fishes have four median fins such as the first dorsal, second dorsal, anal and caudal fins, and also two paired fins such as the pectoral and ventral fins as in the case of the general percoid fishes. The fin ray number of each species is not represented in the present study.

Dorsal fins: Channichthyid fishes have the spiny first dorsal fin and the soft rayed second one. In *Champsocephalus*, *Pagetopsis*, *Neopagetopsis* and *Pseudochaenichthys*, the first dorsal fin is well developed, and has a larger number of fin rays and a greater basal length in comparison with those of the other seven genera. In the abovementioned four genera, the distance between the two dorsal fins is short and the fin membrane of the last spine of the first dorsal fin is often attached to the first ray of the second dorsal fin. In *Dacodraco* and *Cryodraco*, their first dorsal fins consist of a small number of fin rays, and their basal length is also short. The first and second dorsal fins of both genera are widely separated from each other. The height of the first dorsal fin shows the remarkable sexual dimorphism in the following species; *Champsocephalus gunnari*, *Chaenocephalus aceratus*, *Chionodraco myersi*, *Chionodraco rastrospinosus* and *Chionodraco hamatus* (OLSEN, 1955; DEWITT and HUREAU, 1979; IWAMI and ABE, 1981a). The fin membrane of the first dorsal fin is usually blackish or dusky. *Chaenodraco wilsoni* has a distinct dark blotch on its first dorsal fin.

The second dorsal fin has a long base opposite the anal fin. The length of each fin ray of the second dorsal fin is nearly the same, except the anteriormost and posteriormost rays which are somewhat shorter than the other fin rays. The last two rays are clearly separated at the base and this feature being common to notothenioid fishes is distinct from the other general percoid fishes. The fin membrane of the second dorsal fin is dusky, pale or transparent.

Anal fin: It has a long base, opposite the second dorsal fin. It is composed only of soft rays and the distal tip of each ray tends to be thickened. The last two rays are distinctly spaced at the base. The fin membrane of the anal fin is transparent or pale.

Pectoral fin: The pectoral fin of the channichthyid fishes is well developed, large, round and fan-shaped, and contains soft rays only. The uppermost fin ray is unbranched and unsegmented, and attains only to a half of the second pectoral fin ray. The short ray is attached to the second one tightly without the fin membrane between them.

Ventral fin: The ventral fin is situated at the thoracic position and consists of one spine and five soft rays except for *Chaenodraco* which has one spine and four soft rays. The ventral fins of other four notothenioid families are normal in shape, and their third rays are the longest. This morphological feature is shared also by two genera of the Channichthyidae, *Champsocephalus* and *Channichthys*. Ventral fins of *Pagetopsis*, *Neopagetopsis* and *Pseudochaenichthys* are fan-shaped with well-developed fin membrane and the third rays are the longest. In *Chaenocephalus*, *Chionobathyscus*, *Cryodraco*, *Chionodraco* and *Chaenodraco*, each ventral fin is elongated in a cane-like shape and its second ray is the longest. The ventral fin of *Dacodraco* is somewhat fan-shaped and its second and third rays are nearly of the same length. The distal tips of the fan-shaped and elongated ventral fins tend to be enveloped in the thick skin.

Caudal fin (Figs. 82, 85): The number and shape of the procurrent rays which vary with individuals and growth stages are not studied in the present study. All of the channichthyid genera except *Champsocephalus* have a rounded or subtruncate caudal fin. The number of caudal principal rays clearly divides the channichthyid genera into two groups as follows: the 14 rays (i+6+6+i) group comprising *Champsocephalus*, *Pagetopsis*, *Neopagetopsis* and *Pseudochaenichthys*; and the 13 rays (i+5+6+i) group comprising *Dacodraco*, *Channichthys*, *Chaenocephalus*, *Chionobathyscus*, *Cryodraco*, *Chionodraco* and *Chaenodraco*.

3.11.2. Discussion

Dorsal, anal and pectoral fins: Some morphological differences in the dorsal, anal and pectoral fins are thought to be valuable for the identification of species. However, the polarities of the morphological changes of these fins are hard to be clarified.

Ventral fin: The general feature of the ventral fin which is observed in the typical percoid fishes and most of notothenioid fishes is also found in *Champsocephalus* and *Channichthys*. Consequently, the fan-shape and the elongation of the ventral fins respectively show the differently derived states. Especially in the genus *Cryodraco*, the extreme elongation of the ventral fins is recognized and this peculiarity is supposed to be one of the most advanced states of the ventral fin.

The number of ventral fin rays is usually six (one spine and five soft rays) in the general percoid fishes and most of notothenioid fishes. Therefore, the ventral fin with five rays (one spine and four soft rays) in *Chaenodraco* is assumed to show a derived condition.

Caudal fin: The number of caudal principal rays is thought to be a conservative character which usually does not vary within the same genus and species. Therefore, the fact that the channichthyid genera can be divided into two groups by this character indicates its significant systematic value. Generally speaking, the number of caudal principal rays of the advanced teleosts is fewer than that of the primitive ones. Judging from the above-mentioned tendency, the seven genera, *Dacodraco*, *Channichthys*, *Chaenocephalus*, *Chionobathyscus*, *Cryodraco*, *Chionodraco* and *Chaenodraco*, are supposed to share a derived condition in this character.

4. Osteology of the Suborder Notothenioidei

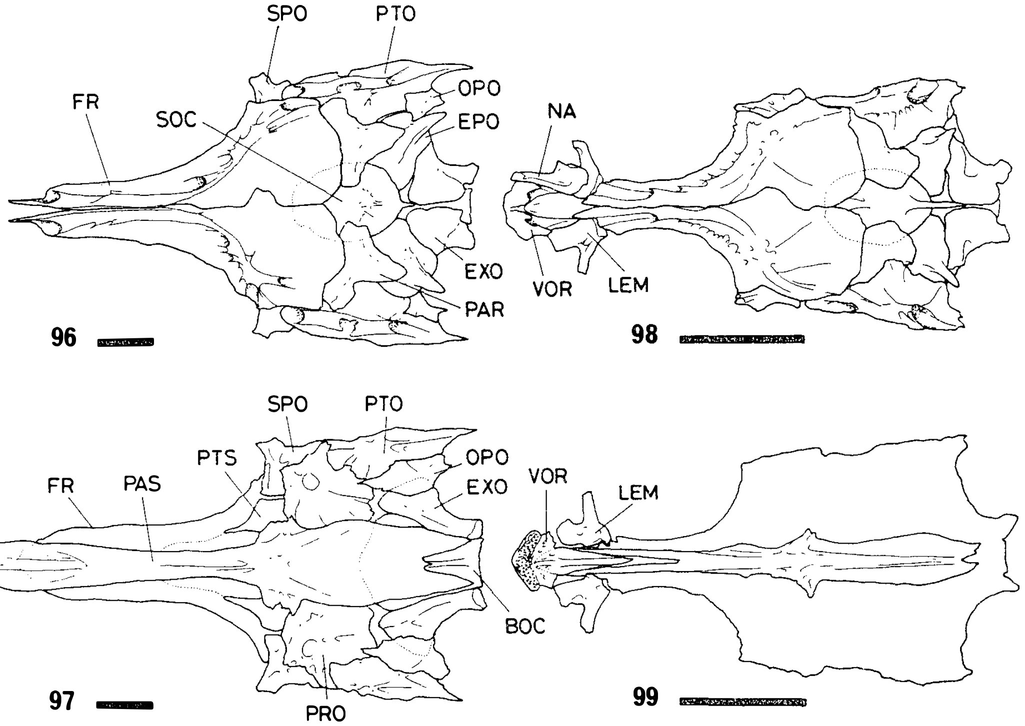
Most of the osteological features of the Channichthyidae described in the preceding section agree with those of other notothenioid families. Therefore, only the osteological features which differ from those of channichthyids and are distinct among the families are mentioned below.

4.1. Neurocranium

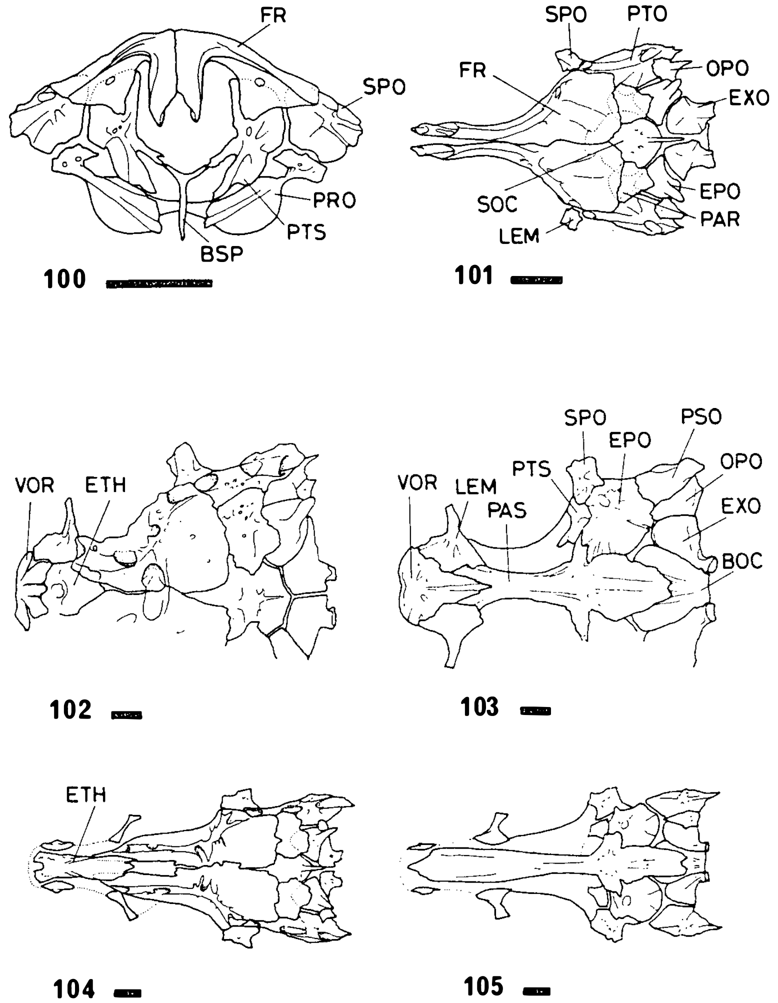
4.1.1. Description

A pair of bones which is attached to the anterolateral region of the ethmoid cartilage is recognized in bathydraconid fishes (Figs. 104, 105). These bones are never observed in the other notothenioid families. The identification of these ossified element is left for the future study.

Frontal (Figs. 96–98, 100–102, 104): In channichthyids, the frontal is flattened



Figs. 96–99. Neurocranium. Dorsal view: (96) *Cottoperca gobio*, (98) *Pseudaphritis urvilli*; ventral view: (97) *Cottoperca gobio*, (99) *Pseudaphritis urvilli*. Scale 5 mm.

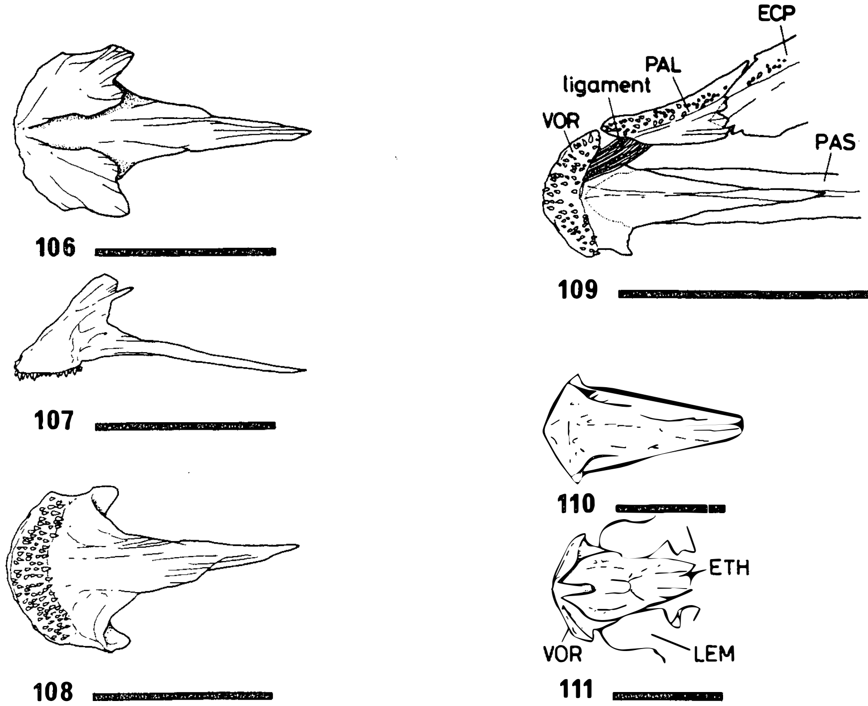


Figs. 100–105. Neurocranium. Front view: (100) *Notothenia gibberifrons*; dorsal view: (101) *Notothenia gibberifrons*, (102) *Pogonophryne dolichobranchiata*, (104) *Gymnodraco acuticeps*; ventral view: (103) *Pogonophryne dolichobranchiata*, (105) *Gymnodraco acuticeps*. Scale 5 mm.

and elongated, and has a remarkable "anterior part" which bears no tubular structure. In the other four families, each anteriormost opening of the supraorbital canal is situated at the distal end of the frontal. The frontals of the Bovichthyidae, Nototheniidae, Harpagiferidae and Bathydraconidae are dorsally convex and bear developed ridges.

Prevomer (Figs. 98, 99, 102, 103, 106–111): In channichthyids, the prevomer is flattened and bears no dorsal process nor tooth, while in the Nototheniidae, Harpagiferidae and Bathydraconidae, each prevomer bears the dorsoposteriorly pointed process. However, there is no tooth on its thickened head except for one bathydraconid species, *Vomeridens infuscipinnis*. The prevomer of the Bovichthyidae also bears the dorsal process, and further, small conical teeth forming the tooth patch on the anteroventral surface of this bone (Figs. 99, 107–109).

Prootic (Figs. 97, 100, 103, 105): The distinctive shape of the prootic is not recognized in each family of the Notothenioidei, but the relative position of the left and right prootics differs between the following two groups; the Bovichthyidae-



Figs. 106–111. Prevomer and adjacent bones. Dorsal view: (106) *Bovichthys variegatus*, (111) *Notothenia gibberifrons*; lateral view: (107) *Bovichthys variegatus* (left side); ventral view: (108), (109) *Bovichthys variegatus*, (110) *Notothenia gibberifrons*. Scale 5 mm.

Nototheniidae group and the Harpagiferidae-Bathydraconidae-Channichthyidae group. In the former group, the left and right prootics meet ventromedially, while in the latter group the prootics are clearly spaced from each other.

Pterosphenoid and sphenotic (Figs. 97, 100, 103, 105): In most of notothenioid fishes, the pterosphenoid and sphenotic are attached to each other along the outer edge of the pterosphenoid and the inner edge of the sphenotic. The pterosphenoid and sphenotic are obviously separated by the cartilaginous area in the Channichthyidae except for the two genera, *Champsocephalus* (Fig. 5) and *Channichthys* (Fig. 11) (see Section 3.1).

Basisphenoid (Fig. 100): The presence or absence of the basisphenoid is one of the most noticeable differences among families of the Notothenioidei. The basisphenoid is not recognized as an ossified and independent element in the Harpagiferidae, Bathydraconidae and Channichthyidae. However, in the other two families, Bovichthyidae and Nototheniidae, the ossified basisphenoid is situated at the normal position and is attached to the parasphenoid anteroventrally and prootics posteriorly.

4.1.2. Discussion

Frontal: The characteristic features observed in the frontals of channichthyid fishes which are assumed to reflect the enlargement of the head and the elongation of the snout are supposed to be autapomorphic for the Channichthyidae.

Prevomer: In the typical percoid fishes including most of notothenioids, the ethmoid region is fully covered with the lateral ethmoid, ethmoid and dorsal process of the prevomer. While in channichthyids, those three bony elements do not meet each other, and are spaced by the cartilaginous area. This feature which is related to the reduction of ossification is observed also in the other bony elements of the Channichthyidae. It is concluded that the flattened prevomer is one of the derived features of the Channichthyidae.

Nelson (1969) mentioned the general evolutionary trends in the gill arch structure as the decrease in the number of bony elements and tooth patches. Consequently, the prevomer without the tooth patch, the condition shared by the Nototheniidae, Harpagiferidae, Bathydraconidae and Channichthyidae, is thought to be a derived character state.

Prootic: In the general percoid fishes including the Bovichthyidae and Nototheniidae, the left prootic borders the right, but in the rest of the notothenioid families they are clearly spaced by the cartilaginous area. The loose junction between the prootics is assumed to develop in coordination with the formation of the depressed head. The reduction of ossification which is thought to be one of the general trends observed in the Notothenioidei also enables the changes of the shape of the head. The spaced prootics are assumed to have been derived from the united ones, and to be apomorphic.

Pterosphenoid and sphenotic: See discussion of the pterosphenoid of the Channichthyidae in the former Section 3.1.

4.2. Superficial dermal bone

4.2.1. Description

In this item, the body squamation which differs noticeably among the families of the Notothenioidei is mentioned.

Body squamation: The nototheniid fishes are generally covered with the ctenoid scales, whereas the harpagiferid and channichthyid fishes are naked except for the lateral line scales. Within the Bovichthyidae and Bathydraconidae, different conditions of this character, naked and scaled, are recognized. In the Bovichthyidae, the two genera *Bovichthys* and *Aurion* are naked, while the other two genera, *Pseudaphritis* and *Cottoperca*, are scaled as in the case of the Nototheniidae. In the Bathydraconidae, the fishes of six out of the ten genera (*Bathydraco*, *Akarotaxis*, *Gerlachea*, *Vomeridens*, *Racovitzia* and *Prionodraco*) are covered with ctenoid scales or serrated bony plates (DeWitt and Hureau, 1979).

4.2.2. Discussion

It appears that the naked body was secondarily derived from the scaled body which is a general and primitive condition. However, the reduction of the body scales takes place independently in many groups of the bony fishes. Therefore, the case which is considered to be the convergence should be eliminated carefully. The naked condition observed in *Bovichthys* and *Aurion* is supposed to be a result of the convergence within the narrow taxonomic limits and does not show a close relationship with the other naked families such as the Harpagiferidae and Channichthyidae. The naked genera of the Bathydraconidae are also assumed to have been derived from the scaled bathydraconid. Therefore, it can be concluded that the reduction of the body scales observed in the harpagiferids, channichthyids and some bovichthyids and bathydraconids is a derived condition acquired independently in each family.

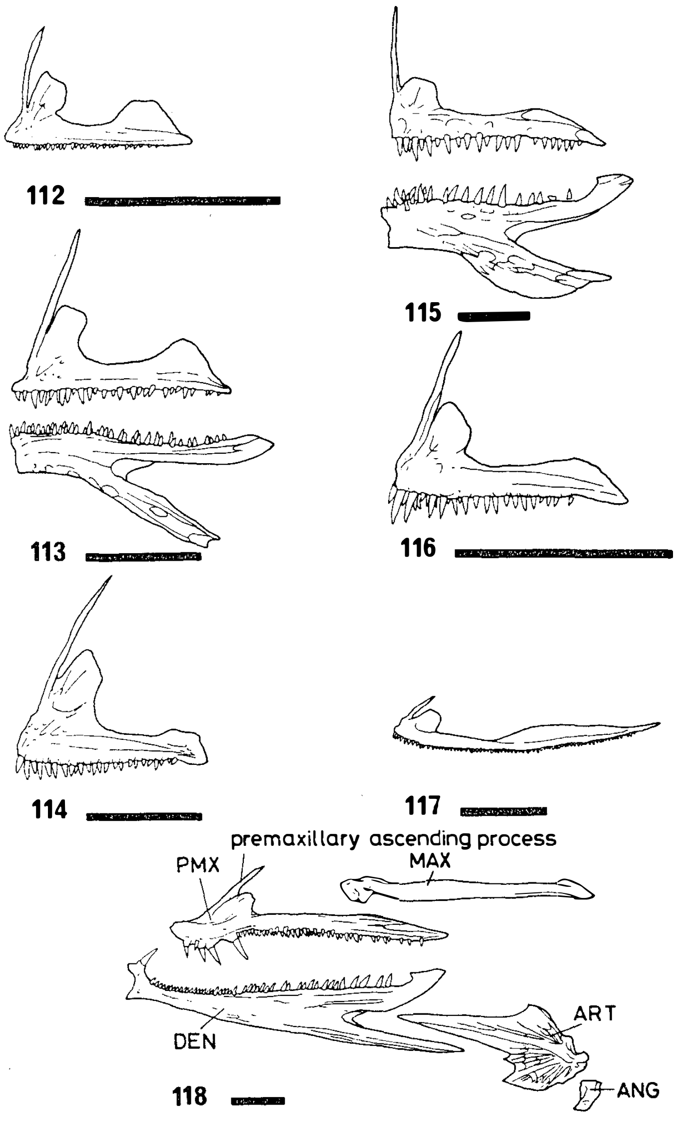
4.3. Mandibular arch

4.3.1. Description

Premaxillary (Figs. 112–118, 123): The premaxillaries of the general percoid fishes bear a pair of the processes, namely the ascending process, which slide over the groove formed by the lateral ethmoid, prevomer and ethmoid. Most of the nototheniioid fishes except channichthyids also have the ascending process at the anterior tip of the premaxillary. The process of the bathydraconids (Figs. 117, 118) is rather shorter than that of fishes of the other three families, the Bovichthyidae, Nototheniidae and Harpagiferidae. The peculiarity of the premaxillary of the Bathydraconidae rather resembles that of the Channichthyidae than that of the other three families.

4.3.2. Discussion

The fact that the length of the premaxillary ascending process has a close relationship to the food habit of fishes is represented in macrouroids (OKAMURA, 1970). This process enables its mouth to protract toward the bottom. Therefore, fishes with the developed ascending process have a great advantage in feeding on benthic organisms.



Figs. 112–118. Mandibular bone. Premaxillary: (112) *Pseudaphritis urvilli*, (113) *Bovichthys variegatus*, (114) *Notothenia gibberifrons*, (115) *Pagothenia borchgrevinki*, (116) *Harpagifer bispinis*, (117) *Vomeridens infuscipinnis*; dentary: (113) *Bovichthys variegatus*, (115) *Pagothenia borchgrevinki*; mandibular arch: (118) *Gymnodraco acuticeps*. Scale 5 mm.

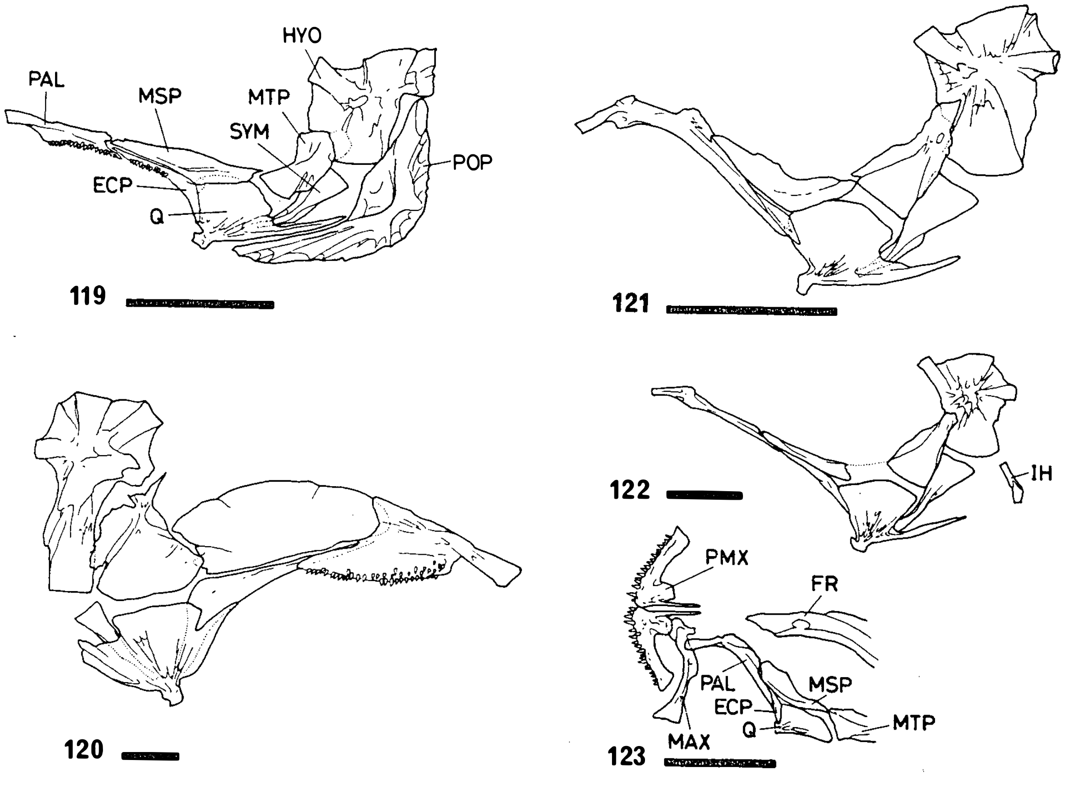
For example, *Notothenia gibberifrons* (Fig. 114) which has a long premaxillary ascending process feeds on a wide range of benthic and benthopelagic organisms, while channichthyids are predators of fishes and euphausids rather than benthic organisms (Targett, 1981; Takahashi, 1983).

Considering the low mobility of the channichthyid fish (Robilliard and Dayton, 1969), their food habits are thought to be acquired in association with the need of taking organisms with low activity. Therefore, the reduction of the premaxillary ascending process found in the channichthyid fish is assumed to have been derived from the other notothenioid and percoid conditions.

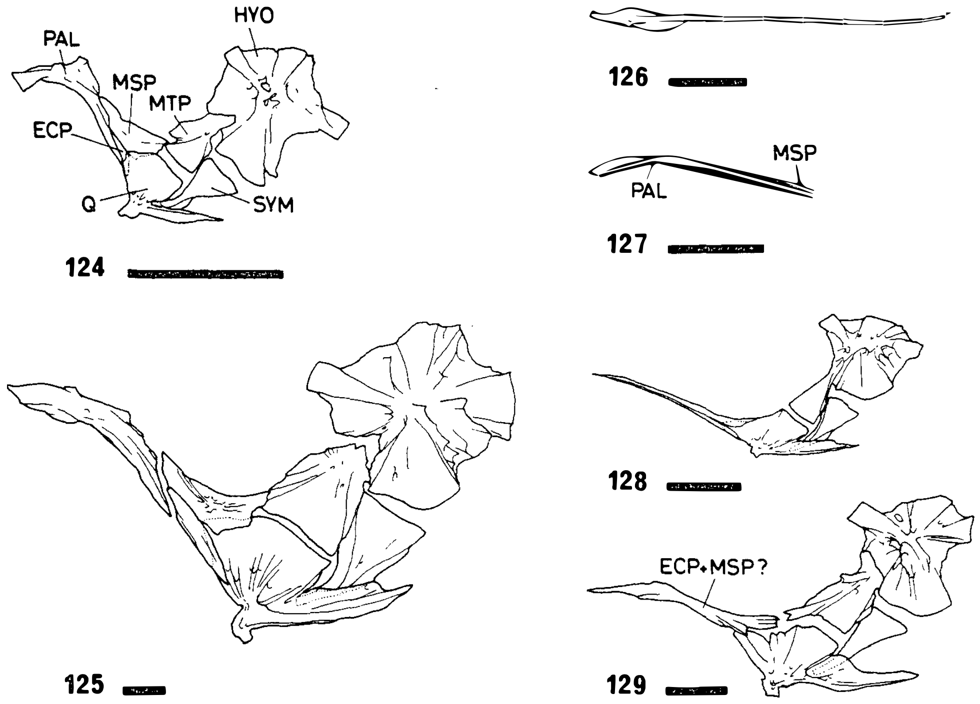
4.4. Palatine arch

4.4.1. Description

Ectopterygoid and mesopterygoid (Figs. 119–125, 127–129): The elongated and filamentous pterygoids of channichthyids are stated in the former section. In the Bovichthyidae, Nototheniidae and Harpagiferidae, each palatine meets the mesopterygoid posterodorsally and ectopterygoid posteroventrally. In the Bathydraconidae (Fig. 128), these bony elements are normal in position, but they are rather elongated as in the case of the Channichthyidae than those of the above-mentioned three families. In some genera of the Bathydraconidae (Fig. 129), the bony element referred to the mesopterygoid is hard to be recognized as a separate element. The ectopterygoid of



Figs. 119–123. Suspensorium. Right side: (119) *Pseudaphritis urvilli* (inner view), (120) *Cottoperca gobio* (outer view), (122) *Aethotaxis mitopteryx* (inner view); left side: (121) *Trematomus hansoni* (outer view); dorsal view: (123) *Ttematomus hansoni.* Scale 5 mm.



Figs. 124–129. Suspensorium. Left side: (124) *Harpagifer bispinis* (outer view), (125) *Pogonophryne dolichobranchiata* (outer view), (126) *Gerlachea australis* (palatine) (dorsal view), (129) *Parachaenichthys charcoti* (outer view); right side: (127), (128) *Vomeridens infuscipinnis* (inner view). Scale 5 mm.

Pseudaphritis urvilli (Fig. 119) bears numerous conical teeth on its ventral surface. The ectopterygoid teeth are not known in the other notothenioids examined in the present study.

Palatine (Figs. 119–127): The palatine of the bovichthyid fishes bears the tooth patch on its ventromedial surface (Figs. 119, 120). The other notothenioid fishes have no tooth on the palatine.

4.4.2. Discussion

Ectopterygoid and mesopterygoid: The reduction of ossification of the pterygoid bones found in the Channichthyidae appears to be a distinct and derived feature among notothenioid fishes (Balushkin and Voskoboynikova, 1979; Voskoboynikova, 1980, 1982). The channichthyid fishes indicate an autapomorphic condition in the ectopterygoid and mesopterygoid. The tooth patches on the ventral surfaces of the ectopterygoid and palatine are essentially of the same (Nelson, 1969). Therefore, the character analysis of the ectopterygoid teeth is discussed below.

Palatine: Nelson (1969) suggested that one of the most noticeable evolutionary trends of the branchial arches was the reduction of the tooth patch structures, and he concluded that the toothed palatine and ectopterygoid as in the case of the bovichthyid fishes indicate the primitive condition of these bony elements. Consequently, the other four families, the Nototheniidae, Harpagiferidae, Bathydraconidae and Channichthyidae, share synapomorphies in the features of the palatine and ectopterygoid.

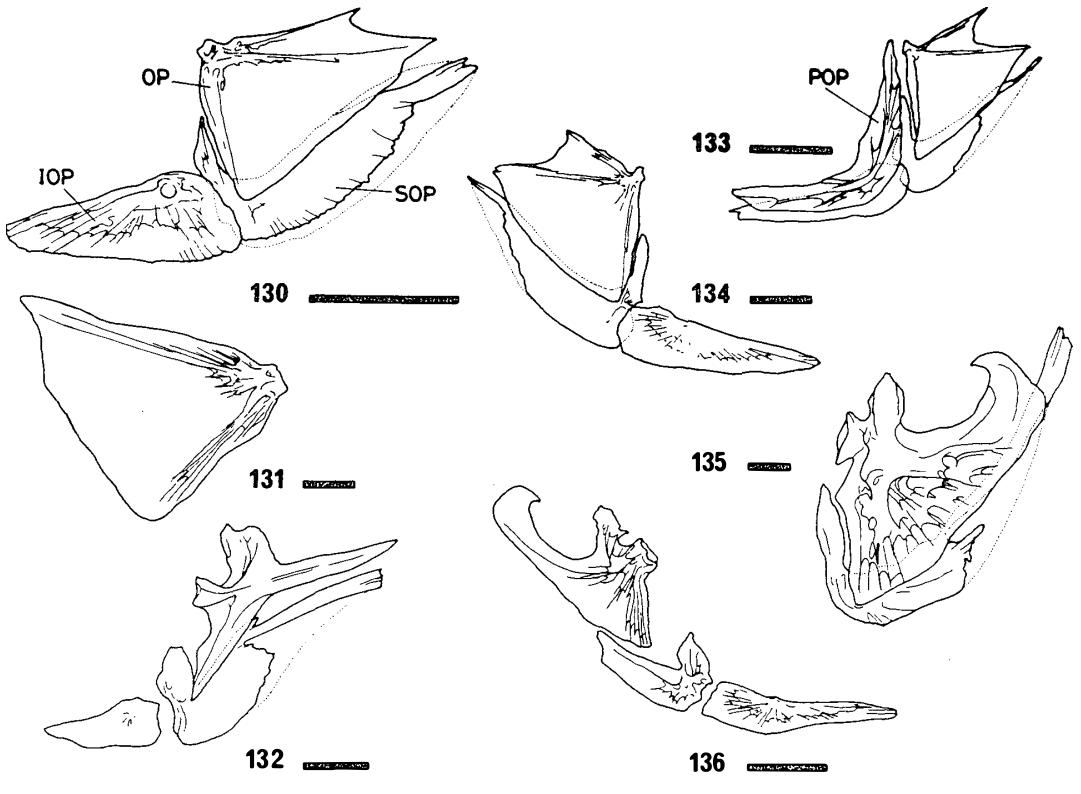
4.5. Opercular apparatus

4.5.1. Description

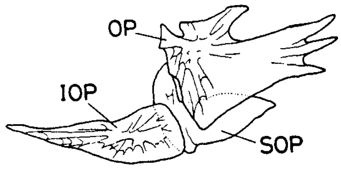
Opercle (Figs. 130–138): The spiny or hooked opercle occurs in the representatives of all notothenioid families except the Nototheniidae. The well-branched opercular spines are found in all channichthyid fishes and some of bathydraconids such as *Parachaenichthys* (Fig. 137) and *Cygnodraco* (Fig. 138), while fishes referred to the Harpagiferidae (Figs. 135, 136) have rather hooked opercles than spiny ones. In the Nototheniidae and Bovichthyidae excepting *Bovichthys* (Fig. 132) and *Aurion*, their spineless opercles bear the developed ridges which point to the posterodorsal and posterior edges.

4.5.2. Discussion

Opercle: The opercular spines or hooks are apparently derived from the structures of ridges observed in the opercles of most bovichthyids and nototheniids. It is thought that the considerable resemblance between the spined *Bovichthys* and spineless *Cottoperca*, which is accepted among taxonomists, indicates the highly peculiar opercle of *Bovichthys* is supposed to have been derived secondarily within narrow taxonomic limits. It is true that there are some "noises" as the convergence in the distinctive features of the opercles, and also it is hard to distinguish the results of the convergence from those of inheritance. In the present study, it is concluded that the spiny



Figs. 130–136. Opercular apparatus. Left side (outer view): (130) *Pseudaphritis urvilli*, (132) *Bovichthys variegatus*, (133) *Trematomus hansoni*, (135) *Pogonophryne dolichobranchiata*; right side (outer view): (131) *Cottoperca gobio*, (134) *Patagonotothen ramsayi*, (136) *Artedidraco orianae*. Scale 5 mm.



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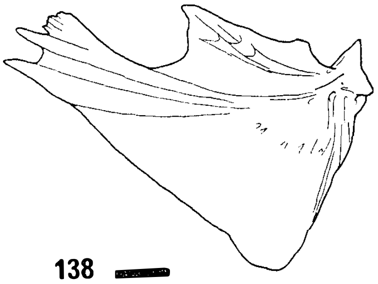

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Figs. 137–138. Opercular apparatus. (137) *Parachaenichthys charcoti* (left side, outer view), (138) *Cygnodraco mawsoni* (opercle) (right side, outer view). Scale 5 mm.

opercle found in the Bovichthyidae, Bathydraconidae and Channichthyidae and the hooked opercle in the Harpagiferidae are derived forms which were acquired independently in each family.

4.6. Hyoid arch

4.6.1. Description

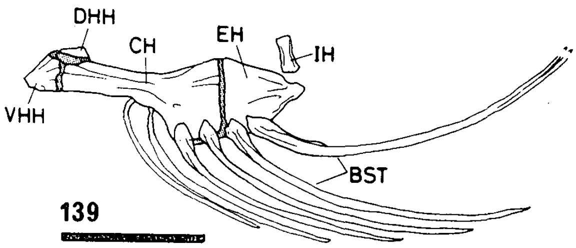
Hypohyals (Figs. 139–144, 146, 148, 150, 152, 154): In channichthyid fishes except *Champsocephalus*, *Pagetopsis*, *Neopagetopsis* and *Pseudochaenichthys*, the dorsal hypohyal is not ossified, while that in the Bovichthyidae, Nototheniidae, Harpagiferidae and Bathydraconidae is ossified and is attached to the anterior end of the ceratohyal.

Ceratohyal (Figs. 139–143): The ceratohyal is articulated to the epihyal posteriorly via a cartilage. In the Bathydraconidae (Figs. 142, 143) and Channichthyidae (Figs. 62–64), the posterior articulated cartilage of the ceratohyal is restricted to the area between the anterior edge of the epihyal and the posterior margin of the ceratohyal and it forms an I-shape cartilage. In the other three families, their ceratohyals show a hatchet shape and bear the articulating cartilage even on their posteroventral margin, and this articulating cartilage is recognized as an L-shape cartilage.

4.6.2. Discussion

Hypohyals: McAllister (1968) made mentions of the number of hypohyals as "(1) primitive teleostomes have only a single hypohyal, (2) advanced ones have two, and (3) some advanced ones lose one or both." The feature observed in the Channichthyidae fits with the last principle mentioned above and is thought to be a derived feature.

Ceratohyal: The hatchet-shape ceratohyal is known not only in the Bovichthyidae, Nototheniidae and Harpagiferidae, but also in the Mugiloididae, Callionymidae, Blennidae and so on (McAllister, 1968). Judging from the evidence mentioned above, the distinct features of the ceratohyals of bathydraconids and channichthyids



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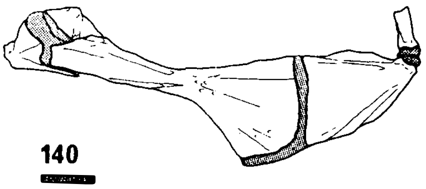

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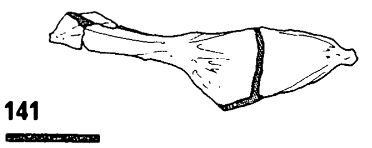

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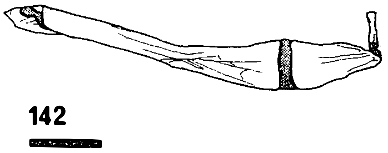

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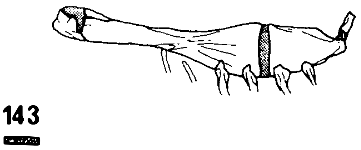

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Figs. 139–143. Hyoid arch. (139) *Pseudaphritis urvilli*, (140) *Notothenia kempi*, (141) *Artedidraco orianae*, (142) *Vomeridens infuscipinnis*, (143) *Gymnodraco acuticeps*. All figures are left and outer views. Shaded areas show cartilaginous junctions. Scale 5 mm.

are associated with the elongation of the snout, and are referred to a derived condition.

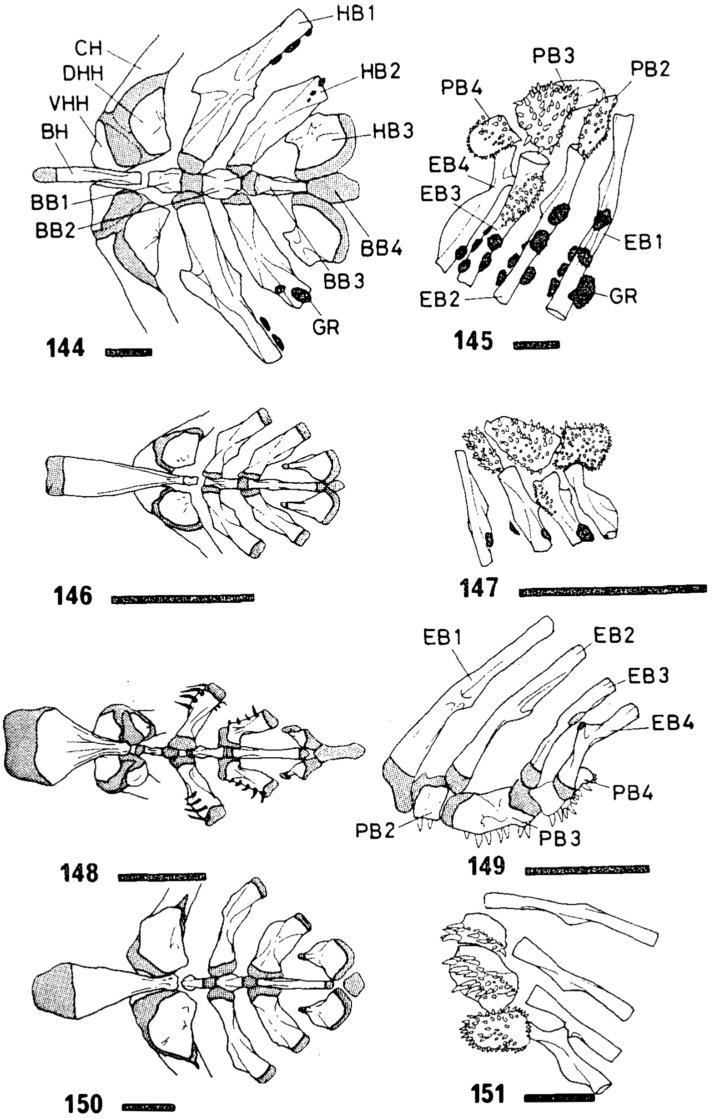
4.7. Branchial arch

4.7.1. Description

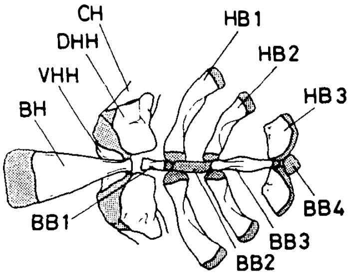
The gill-arch structures of notothenioid fishes have been studied and discussed by Iwami and Abe (1984). Therefore, only the typical condition of the gill arch of each family and the conclusion of the character analysis are represented below.

Basibranchials (Figs. 144, 146, 148, 150, 152, 154): The ossified first basibranchial is found in four families, Bovichthyidae, Nototheniidae, Harpagiferidae and Bathydraconidae. All of the channichthyid species have the cartilaginous first basibranchial. The second basibranchial is ossified in bovichthyids and nototheniids, while in the other three families they are recognized as cartilaginous elements. The third basibranchial of all notothenioids is ossified and cylindrical in shape. The fourth basibranchial is cartilaginous in all notothenioid fishes and its shape is nearly lozenge or rectangular.

Hypobranchials (Figs. 144, 146, 148, 150, 152, 154): Features of the third hypobranchial are noticeably different between the Channichthyidae and the other four families, Bovichthyidae, Nototheniidae, Harpagiferidae and Bathydraconidae. The third hypobranchial of the latter four families is flat and triangular and quite unlike that of the Channichthyidae. The posterior margin of the flattened and triangular hypobranchial found in most notothenioid fishes is fully bordered by the cartilage which meets the posterior tip of the third basibranchial, the proximal end of the third ceratobranchial and the anterior side of the fourth basibranchial. The proximal end of the cane-like third hypobranchial of channichthyids is articulated to the posterior tip of the



Figs. 144–151. Branchial arch. Lower part (dorsal view): (144) *Cottoperca gobio*, (146) *Pseudaphritis urvilli*, (148) *Aethotaxis mitopteryx*, (150) *Notothenia kempi*; upper part: (145) *Cottoperca gobio* (left side, ventral view), (147) *Pseudaphritis urvilli* (right side, ventral view), (149) *Aethotaxis mitopteryx* (right side, dorsal view), (151) *Notothenia kempi* (left side, ventral view). Shaded areas indicate cartilaginous parts. Scale 5 mm.



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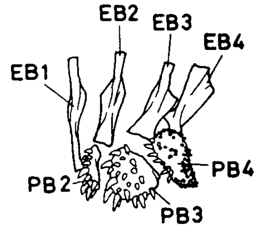

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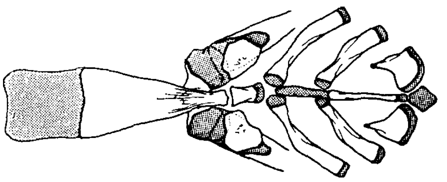

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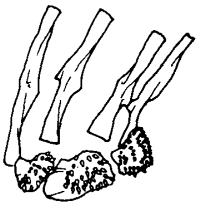

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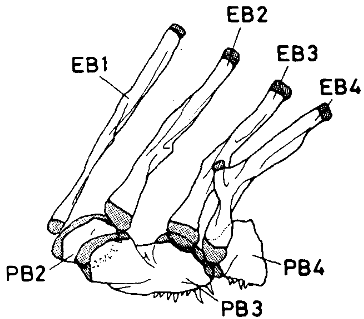

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Figs. 152–156. Branchial arch. Lower part (dorsal view): (152) *Artedidraco orianae*, (154) *Gymnodraco acuticeps*; upper part: (153) *Harpagifer bispinis* (left side, ventral view), (155) *Parachaenichthys charcoti* (left side, ventral view), (156) *Gymnodraco acuticeps* (right side, dorsal view). Shaded areas show cartilaginous parts. Scale 5 mm.

third basibranchial, and the distal end of this third hypobranchial meets only the third ceratobranchial.

Epibranchials (Figs. 145, 147, 149, 151, 153, 155, 156): Each of bovichthyid fishes bears a single tooth patch on the ventral surface of the third epibranchial. No other fishes of the Notothenioidei have the toothed structure on the epibranchials.

The interarcual cartilage cannot be observed in all families of the Notothenioidei (see also TRAVERS, 1981).

Pharyngobrancials (Figs. 145, 147, 149, 151, 153, 155, 156): There are three pharyngobranchials, namely, the second, third and fourth, in the Bovichthyidae, Nototheniidae, Harpagiferidae and Bathydraconidae. The first or suspensory pharyngobranchial is absent in all notothenioids. In notothenioid fishes excepting channichthyids, the proximal ends of the third and fourth epibranchials are attached to the junction between the third and fourth pharyngobranchials. Channichthyid fishes have only two pharyngobranchials, and the third and fourth epibranchials meet in the central position of the posterior and larger pharyngobranchial proximally.

4.7.2. Discussion

Basibranchials: The primitive percoid branchial skeleton consists of three ossified and one cartilaginous basibranchials (Johnson, 1980). This condition is found also in the Bovichthyidae and Nototheniidae. Therefore, the cartilaginous first basibranchial of the Channichthyidae and the unossified second basibranchial observed in the gill arches of the Harpagiferidae, Bathydraconidae and Channichthyidae are concluded to be derived conditions (Iwami and Abe, 1984).

Hypobranchials: The flat and triangular third hypobranchial is a common feature of the general percoid fishes (Nelson, 1967, 1969; Rosen and Patterson, 1969; Johnson, 1980), and it is thought that the cane-shape hypobranchial found in channichthyid fishes indicates its derived condition among notothenioids.

Epibranchials: The reduction of the tooth patch structure in the oral cavity is suggested to be a general trend (Nelson, 1969). Therefore, the presence of the fused tooth plate on the third epibranchial of the bovichthyid fish is supposed to represent a primitive condition.

Pharyngobranchials: In comparison with the features of the third and fourth pharyngobranchials of notothenioid fishes excepting channichthyids, the posterior and larger pharyngobranchial of channichthyids is proved to be formed by the consolidation of the two pharyngobranchials (Iwami and Abe, 1984).

During the evolution of the advanced teleosts, these bony elements are apparently modified through some processes involving the consolidation among the initially separated elements (Rosen, 1964, 1973; McAllister, 1968; Rosen and Patterson, 1969; Nelson, 1969). Therefore, the fused pharyngobranchials of channichthyid fishes are thought to be autapomorphic.

4.8. Caudal skeleton

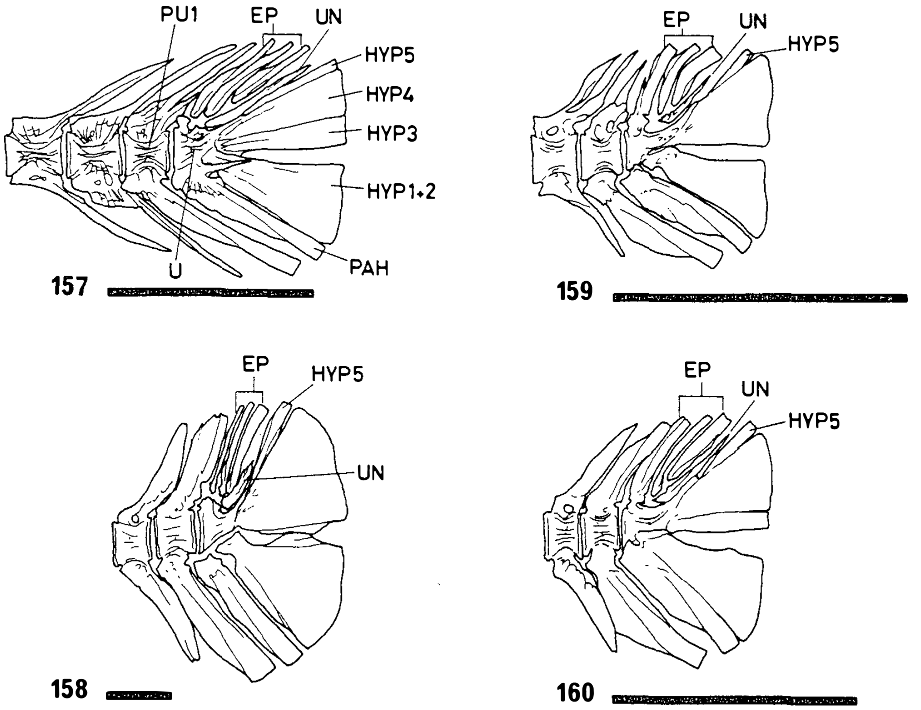
4.8.1. Description

The caudal skeleton of some notothenioid fishes was studied by Andersen and Hureau (1979) and Andersen (1984). In the present study, the common osteological features of each family are mentioned and discussed.

Hypurals (Figs. 157–164): In channichthyid fishes, the first and second hypurals are consolidated into the lower hypural plate and the third to fifth hypurals are fused into the triangular upper plate. In the other families of the Notothenioidei, the fifth hypural is not fully fused to the fourth one and is recognized obviously as an independent bony element. In the Bovichthyidae and some species of the Nototheniidae, the third hypural is not fused with the fourth. In *Bovichthys variegatus*, all hypurals are clearly separated from each other as in the case of the caudal skeletons of *Eleginops* and *Dissostichus* (Andersen and Hureau, 1979; Andersen, 1984).

Uroneural (Figs. 157–164): In the caudal skeletons of the Harpagiferidae, Bathydraconidae and Channichthyidae, the uroneural is attached to the anterodorsal surface of the uppermost hypural and is united to it. In those of the Bovichthyidae and Nototheniidae except some genera such as *Pleuragramma* and *Aethotaxis* (Andersen, 1984), the uroneural is clearly separated from the uppermost hypural.

Epurals (Figs. 157–164): The number of epurals is constantly three in the Bovichthyidae and Nototheniidae, while it varies among species and individuals in the other three families, Harpagiferidae, Bathydraconidae and Channichthyidae.

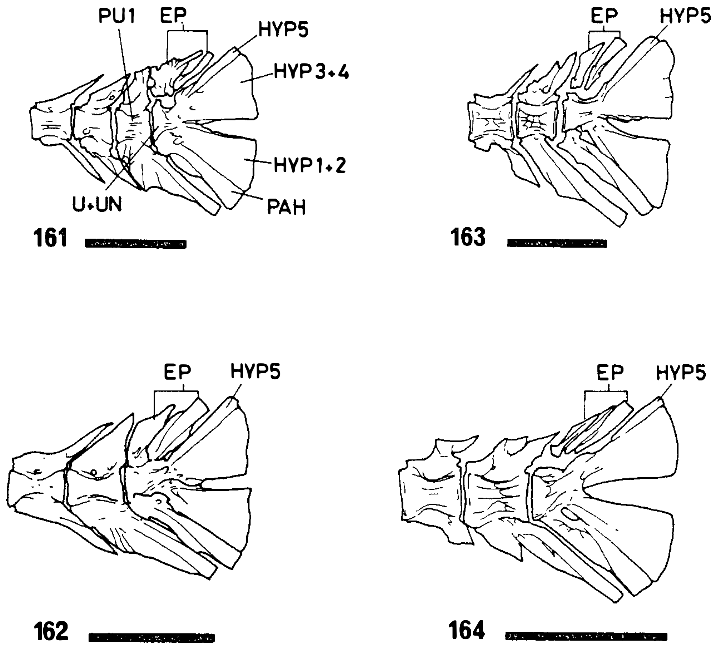


Figs. 157–160. Caudal skeleton. (157) *Pseudaphritis urvilli*, (158) *Notothenia rossii marmorata*, (159) *Trematomus hansoni*, (160) *Notothenia nudifrons*. All figures are left and lateral views. Scale 5 mm.

4.8.2. Discussion

Hypurals and uroneural: In the euteleostean fishes, the caudal skeleton is basically composed of six hypurals, two uroneurals, two ural centra, three epurals and one parhypural (Rosen and Patterson, 1969; Rosen, 1973), and the caudal skeleton of the advanced fishes is assumed to have resulted from the consolidation of the bony elements (Rosen and Patterson, 1969; Rosen, 1973; Nybelin, 1973). Therefore, the consolidations among the hypurals and uroneural are thought to be derived features. In other words, the channichthyid fishes show an autapomorphy in the features of the hypurals, and the harpagiferid, bathydraconid and channichthyid fishes also share a derived condition of the uroneurals. Some modes of the consolidation of the hypurals should be used at the intrafamilial level (Andersen, 1984).

Epurals: The problem on the number of epurals is discussed in the former section. Andersen (1984) described the epurals of *Notothenia rossii* and mentioned that its third epural (EP 3) was reduced in size. However, the specimen of *Notothenia rossii marmorata* examined in the present study possesses three epurals of a normal size. Therefore, the number and size of the epurals are thought to show the individual variation and cannot be utilized for the systematic study easily. These erroneous con-



Figs. 161–164. Caudal skeleton. (161) *Histiodraco velifer*, (162) *Artedidraco orianae*, (163) *Gerlachea australis*, (164) *Vomeridens infuscipinnis*. All figures are left and lateral views. Scale 5 mm.

clusions may be caused by the scarcity of materials examined.

4.9. Pectoral girdle

4.9.1. Description

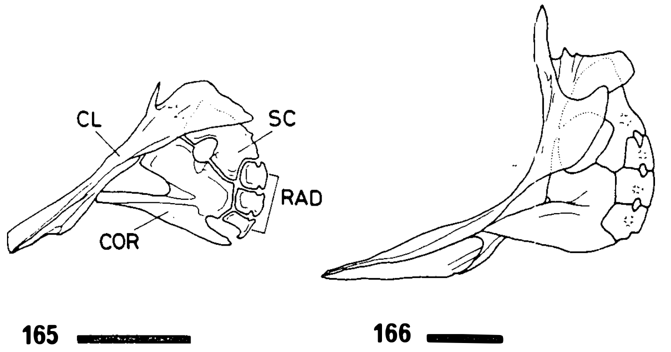
Cleithrum (Figs. 165–172): The cleithrum of *Bovichthys variegatus* (Fig. 166) is distinct and strongly curved outward, but its basic features agree with those of other notothenioids. The cleithrum of most notothenioid fishes except channichthyids bears a forked depression on its dorsal edge.

Radials (Figs. 165–172): The typical percoid fishes have four radials (Gosline, 1968), but all of the nototheniod species have only three radials. The radials of notothenioid fishes are noticeably larger than those of other percoid fishes. In the Bovichthyidae, the uppermost radial is excluded from the posterior edge of the coracoid and it meets only the scapula and the second radial. The features of the radials of the other notothenioid fishes agree well with those of channichthyids mentioned in the former section.

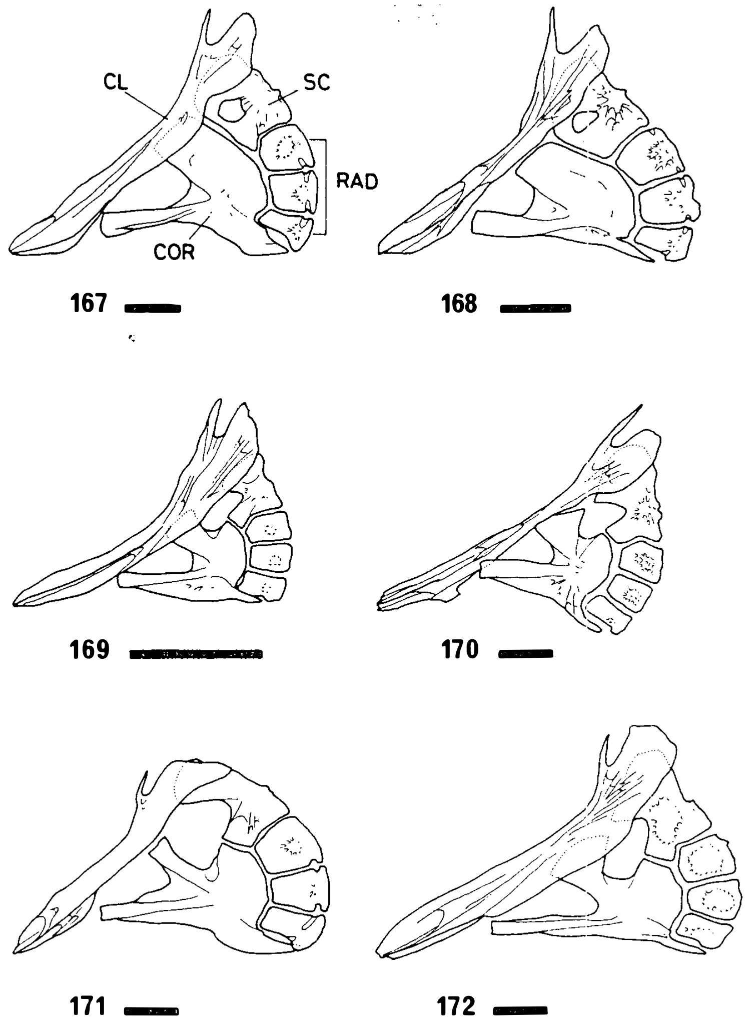
4.9.2. Discussion

Cleithrum: The functional value of the process which is formed by the forked depression on the dorsal margin of the cleithrum is obscure. However, the systematic value of this feature is impressed with the fact that the structure is restricted to the four families, Bovichthyidae, Nototheniidae, Harpagiferidae and Bathydraconidae. Although more detailed studies are needed for the character analysis of the cleithrum, it is proper that the absence of the forked depression, the condition restricted to the Channichthyidae, is assumed to be a derived condition.

Radials: In comparison with the character condition of the radials of the general



Figs. 165–166. Pectoral girdle. (165) *Pseudaphritis urvilli*, (166) *Bovichthys variegatus*. Both figures are left and outer views. Scale 5 mm.



Figs. 167–172. Pectoral girdle. (167) *Trematomus eulepidotus*, (168) *Aethotaxis mitopteryx*, (169) *Harpagifer bispinis*, (170) *Histiodraco velifer*, (171) *Gerlachea australis*, (172) *Parachaenichthys charcoti*. All figures are left and outer views. Scale 5 mm.

percoid fishes, the fewer number and larger size of radials of notothenioid fishes are thought to be derived features. In the Bovichthyidae, the uppermost radial is excluded from the posterior margin of the coracoid, and this feature is common among the general percoid fishes. Therefore, the condition observed in the Bovichthyidae seems to be plesiomorphic.

4.10. Pelvic girdle

Except for the distinctive feature of the pelvic girdle observed in *Bovichthys variegatus*, where the left and right pelvic bones are connected by the stiff rods, the morphological features of the pelvic bones do not vary basically among the families of the Notothenioidei.

4.11. Fins

4.11.1. Description

Dorsal fins: In the typical percoid fishes and most of notothenioid fishes except bathydraconid fishes, the dorsal fin consists of the first and second fins, while bathydraconid fishes have only one dorsal fin composed only of soft rays.

4.11.2. Discussion

The bathydraconid condition of the dorsal fin is brought about by the reduction of the first dorsal fin. Therefore, the feature of the absence of the spiny dorsal fin observed in the Bathydraconidae is supposed to be a derived condition.

5. General Discussion and Conclusion

5.1. Phylogenetic relationships among the genera of the family Channichthyidae

The character analysis of each of the osteological features was mentioned in the respective parts of the discussion on the bony elements. The character used for the present systematic study and the derived and primitive conditions of these characters are arranged in Table 2. Distributions of these character conditions among the channichthyid genera are shown in Table 3.

Table 2. States of 17 characters recognized as useful characters for elucidating the relationships among the genera of the Channichthyidae.

Characters	Primitive state	Derived state
1. Origin of supraorbital canal	Anterior region	Orbital region
2. Sphenotic-pterosphenoid	Bordered	Separated
3. Tubercles on dermal bones	Absent	Present
4. 1st infraorbital (dorsal expansion)	Absent	Present
5. 2nd infraorbital (ventral expansion)	Absent	Present
6. Number of infraorbitals	6 or 7	8 or 9
7. Lateral line bony plate	Absent	Present
8. Ectopterygoid-quadrate	Overlapped	Separated
9. Opercular spine	Unbranched	Well branched
10. Interopercular and subopercular spines	Absent	Present
11. Branchiostegal rays	More than 7	6
12. Dorsal hypohyal	Ossified	Cartilaginous
13. 3rd hypobranchial	Flat and triangular	Elongate and cane-like
14. Coracoid notch	Absent	Present
15. Ventral fin	Normal	Fan or cane-like shape
16. Ventral fin rays	1 spine and 5 soft rays	1 spine and 4 soft rays
17. Caudal principal rays	i+6+6+i	i+5+6+i

Reconstruction of the phylogenetic relationships in the Channichthyidae: The genus *Champsocephalus* shows the primitive features in 16 out of the 17 characters examined in the present study. This result indicates that *Champsocephalus* may resemble more closely the ancestral type, and it is supposed that this genus descended directly from the common ancestore of channichthyid fishes and has preserved the primitive features until the present.

The genera *Pagetopsis*, *Neopagetopsis* and *Pseudochaenichthys* maintain the same

Table 3. States of 17 characters exhibited by channichthyid genera.

Genera	Characters																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Champsocephalus	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−
Pagetopsis	+	+	−	−	+	−	−	+	−	−	−	−	+	−	+	−	−
Neopagetopsis	+	+	−	−	+	−	−	+	−	−	−	−	+	−	+	−	−
Pseudochaenichthys	+	+	−	−	+	−	−	+	−	−	−	−	+	−	+	−	−
Dacodraco	+	?	−	−	−	−	−	?	+	−	+	?	?	−	−	−	+
Channichthys	+	−	+	−	−	−	+	+	+	−	+	+	+	+	−	−	+
Chaenocephalus	+	+	−	+	−	−	−	+	+	−	+	+	+	−	+	−	+
Chionobathyscus	+	+	−	−	−	−	−	+	+	−	+	+	+	−	+	−	+
Cryodraco	+	+	−	−	−	−	−	+	+	−	+	+	+	−	+	−	+
Chionodraco	+	+	−	−	−	−	−	+	+	+	+	+	+	−	+	−	+
Chaenodraco	+	+	−	−	−	−	−	+	+	+	+	+	+	−	+	+	+

− Primitive state, + derived state.

character state in 17 characters examined. In two of the 17 characters, these three genera share the apomorphic conditions and they also share the primitive states in the four characters only with *Champsocephalus.*

Only two specimens of the genus *Dacodraco* could be examined. The lack of available specimens of *Dacodraco* makes the detailed study on the above-mentioned characters difficult. Referring to the literature, the osteological features of the juvenile and the external morphology of the paratype specimen, the 11 character conditions can be inferred. Four out of the 11 characters are assumed to be apomorphic. However, the exact systematic position of *Dacodraco* cannot be determined due to the lack of character analyses on the other five characters.

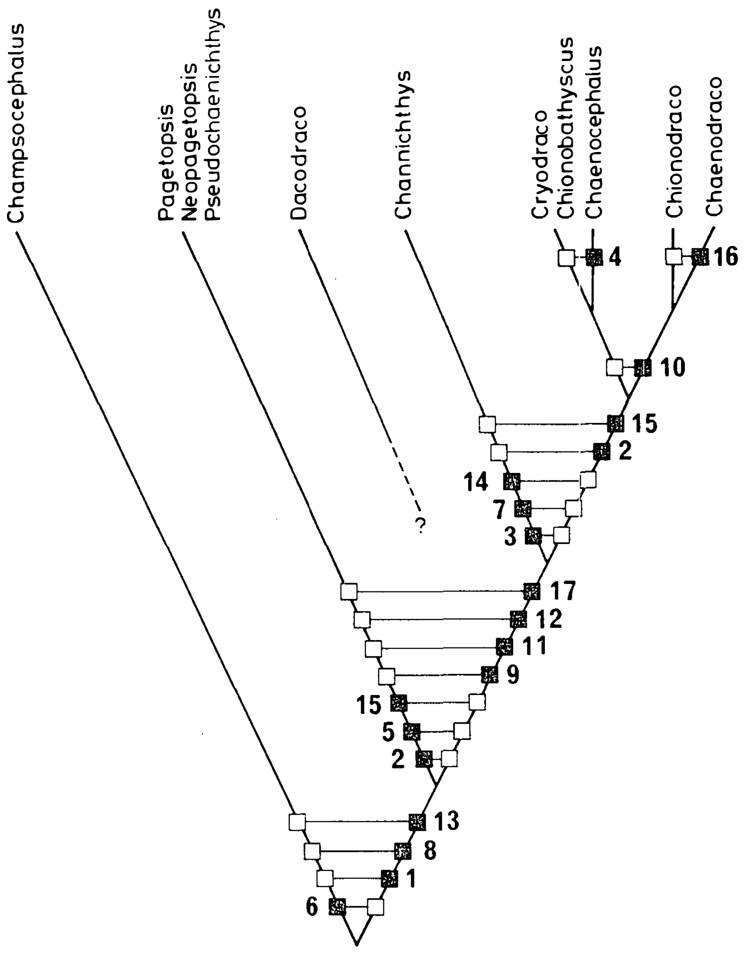
The genus *Channichthys* has two autapomorphic conditions within the 17 characters. The fishes of the genus *Channichthys* are distributed only in the regions adjacent to Kerguelen Island lying remote from the Antarctic continent (ANDRIASHEV, 1965; HUREAU, 1962; DEWITT, 1971; PERMITIN, 1977), and their distribution indicates a possibility that *Channichthys* has evolved in the different environments from those of the other channichthyid fishes. It is assumed that these autapomorphic characters are acquired in the isolated region independently. In the four characters, this genus shares the derived condition with the following five genera: *Chaenocephalus*, *Chionobathyscus*, *Cryodraco*, *Chionodraco* and *Chaenodraco.* Consequently, it is thought that *Channichthys* was first derived from the common ancestor of the above-mentioned six genera.

There is a close resemblance among *Chaenocephalus*, *Chionobathyscus* and *Cryodraco*, because they share the same derived features which are recognized in nine out of the 17 characters. Most of the derived features are also found parallelly in *Chionodraco* and *Chaenodraco.* Therefore, the three genera are assumed to have been derived from the common ancestor of the five genera, *Chaenocephalus*, *Chionobathyscus*, *Cryodraco*, *Chionodraco* and *Chaenodraco.* There is no noticeable difference in the 16 characters among *Chaenocephalus*, *Chinobathyscus* and *Cryodraco.* Only one character, the shape of the first infraorbital, is recognized as an autapomorphy for *Chaenocephalus.*

Two genera, *Chionodraco* and *Chaenodraco*, which are specialized in 10 of the 17 characters are recognized as the most advanced genera in the Channichthyidae. As stated above, these two genera resemble more closely the group of *Chaenocephalus*, *Chionobathyscus* and *Cryodraco*. Therefore, *Chionodraco* and *Chaenodraco* seem to have been derived from the advanced channichthyid fishes which are supposed to be the common ancestor of the above-mentioned five genera.

Chaenodraco is specialized in the character of the number of ventral fin rays, but the functional value of this unique feature is obscure.

The proposed phylogenetic relationships constructed by the results of the character analyses mentioned above are represented in Fig. 173.



Figs. 173. Proposed relationships among the genera of the family Channichthyidae. Arabic numerals in the figure correspond to those in Tables 2 and 3. Open squares, primitive states; closed squares, derived states.

Phylogenetic classification of the Channichthyidae: From the results of the character analyses in the present study, the 11 genera of the Channichthyidae can be arranged in eight groups as follows; (1) *Champsocephalus*, (2) *Pagetopsis-Neopagetopsis-Pseudochaenichthys*, (3) *Dacodraco*, (4) *Channichthys*, (5) *Chaenocephalus*, (6) *Chionobathyscus-Cryodraco*, (7) *Chionodraco* and (8) *Chaenodraco*.

The *Champsocephalus* group is characterized by the larger number of remains of the plesiomorphic conditions.

The *Pagetopsis-Neopagetopsis-Pseudochaenichthys* group shares autapomorphic conditions in two out of the 16 characters. This indicates that these genera are closely related to each other and probably a natural group.

As mentioned above, the systematic position of the genus *Dacodraco* is uncertain due to the lack of materials. Therefore, the definitive systematic position among the genera is left for the future study.

In the *Chaenocephalus* and *Chionobathyscus-Cryodraco* groups, the difference between the two groups is based on the autapomorphic condition of *Chaenocephalus*, that is, the presence of the posterodorsal expansion of the first infraorbital. It is certain that this morphological feature shows a derived character state, but its significance on the generic relationships is obscure. Judging from the resemblance between *Chaenocephalus* and *Cryodraco* in the other osteological characters, the above-mentioned three genera should be dealt with as a single group rather than two different groups.

Chaenodraco is specialized only in the number of ventral fin rays, and most of the derived features agree well with those of *Chionodraco*. It is supposed that *Chionodraco* and *Chaenodraco* have a close relationship to each other, although there are a few differences between them. The number of ventral fin rays is rather conservative among the general percoid fishes. Therefore, this peculiar feature (one spine and four soft rays) seems to show a significant systematic value.

Considering the relationships among the eight groups enumerated previously, they can be classified into seven groups as follows: (1) *Champsocephalus*, (2) *Pagetopsis-Neopagetopsis-Pseudochaenichthys*, (3) *Dacodraco*, (4) *Channichthys*, (5) *Chaenocephalus-Chionobathyscus-Cryodraco*, (6) *Chionodraco* and (7) *Chaenodraco*.

Judging from the many common features observed within each group and the fact that most of the channichthyid genera contain only one or two species, it may be certain that some of the groups mentioned above should be treated as a proper genus. However, it needs more detailed studies on the external and internal morphology for determining the taxonomic rank to which the seven groups belong. The revisional study of the family Channichthyidae will be represented in the near future.

5.2. Phylogenetic relationships among the families of the suborder Notothenioidei

As stated in the foregoing item, the character analysis of each of the osteological features is mentioned in the respective parts of the discussion on the bony elements and is not discussed in this section.

The 22 osteological characters used in the present study on the relationships of the Notothenioidei, and their derived and primitive features are shown in Table 4. The distribution of the states of these 22 characters in each family is also represented in Table 5.

Other than the osteological characters, four features, namely the number of nostrils, presence or absence of mental barbel, swim bladder and haemoglobin, which seem to have a systematic value are recognized. These four characters are discussed below.

Nostril: All of notothenioid fishes differ noticeably from the typical percoid

Table 4. States of 26 characters recognized as useful characters for the relationships among the families of the Notothenioidei.

Characters	Primitive state	Derived state
1. Frontal	Convex dorsally	Flat, elongate
2. Vomerine teeth	Present	Absent
3. Prootics	Attached	Separated
4. Sphenotic-pterosphenoid	Bordered	Separated
5. Basisphenoid	Present	Absent
6. Premaxillary process	Present	Absent
7. Mesopterygoid	Developed	Filamentous
8. Ectopterygoid teeth	Present	Absent
9. Palatine teeth	Present	Absent
10. Dorsal hypohyal	Ossified	Cartilaginous
11. Epi-ceratohyal junction	L-shaped	I-shaped
12. 1st basibranchial	Ossified	Cartilaginous
13. 2nd basibranchial	Ossified	Cartilaginous
14. 3rd hypobranchial	Triangular	Rod-like
15. Epibranchial teeth	Present	Absent
16. Pharyngobranchial	3	2
17. 5th hypural	Separated	Fused
18. Uroneural	Separated	Fused
19. Forked depression on cleithrum	Present	Absent
20. Pectoral radial	4	3
21. Coracoid-uppermost radial	Separated	Bordered
22. 1st dorsal fin	Present	Absent
23. Nostril	2 pairs	1 pair
24. Mental barbel	Absent	Present
25. Swim bladder	Present	Absent
26. Haemoglobin	Present	Absent

Table 5. States of 26 characters exhibited by notothenioid families.

Families	Characters																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Bovichthyidae	−	−	−	−	−	−	−	±	−	−	−	−	−	−	−	−	−	−	−	+	−	−	+	−	+	−
Nototheniidae	−	+	−	−	−	−	−	+	+	−	−	−	−	−	+	−	−	−	−	+	+	−	+	−	+	−
Harpagiferidae	−	+	+	−	+	−	−	+	+	−	−	−	+	−	+	−	−	−	−	+	+	−	+	+	+	−
Bathydraconidae	−	+	+	−	+	−	−	+	+	−	+	−	+	−	+	−	−	+	−	+	+	+	+	−	+	−
Channichthyidae	+	+	+	±	+	+	+	+	+	±	+	+	+	+	+	+	+	+	+	+	+	−	+	−	+	+

− Primitive state, + derived state.

fishes in having a single nostril on each side of the head. However, in this character a high degree of convergence (*e.g.*, callionymids, cichlids, zoarcids and so on) is also suggested (EAKIN, 1981). Within the suborder Notothenioidei, it is considered that this characteristic feature was derived from the morphological change that occurred in the common ancestor of notothenioid fishes, and each family of this suborder shares an apomorphic condition in this character.

Mental barbel: In the family Harpagiferidae but one genus *Harpagifer*, the development of the mental barbel at the anteromedial tip of the lower jaw is recognized.

According to ANDRIASHEV (1967), the mental barbel is assumed to be used in searching for food. WYANSKI and TARGETT (1981) who do not mention the functional aspect of the mental barbel believe that most harpagiferids use a sit-and-wait method of predation, darting off the bottom to capture preys rather than active searching for food. The elucidation of the exact function of the mental barbel is needed for the histological study and underwater observation. Since the development of the mental barbel is found only in the Harpagiferidae, this feature indicates the advanced state of harpagiferids in the Notothenioidei.

Swim bladder: Most of the bony fishes have a swim bladder except for many benthic fishes which lost it secondarily. All of notothenioid fishes also have no swim bladder, although the suborder include several epipelagic or cryopelagic species, such as *Pleuragramma antarcticum*, *Aethotaxis mitopteryx*, *Dissostichus mawsoni*, *Dissostichus eleginoides*, *Eleginops maclovinus*, *Trematomus nicolai*, *Pagothenia borchgrevinki*, *Pagothenia brachysoma* and *Notothenia magellanica* (EASTMAN, 1980). EAKIN (1981) pointed out the possibility of the convergence in this character and he also suggested that this character is likewise of little systematic value. However, all members of the suborder Notothenioidei lack the swim bladder out of relation to their habitats. Therefore, it can be assumed that the swim bladder was absent in the common ancestor of notothenioid fishes.

Haemoglobin: Channichthyid fishes evidently differ from all other vertebrates in the characteristics of their blood which is nearly transparent and colorless due to the lack of erythrocytes, haemoglobin or any other respiratory pigment (RUUD, 1954; WALVIG, 1958, 1961; TWELVES, 1972; SUZUKI, 1980), while MARTSINKEVICH (1964) and DEARBORN *et al.* (1972) believe that an extraordinary small number of erythrocytes are present in their blood. MARTSINKEVICH (1964) and DEARBORN *et al.* (1972), however, concluded that the erythrocytes apparently do not play a significant role in the gaseous change.

This unique feature in channichthyid fishes is well discussed by TWELVES (1972) as follows: "Channichthyidae have evolved a haemoglobinless condition, compensated by a modified vascular system (see STEWART and DOUGLAS, 1973) and oxygen transport in physical solution, and it is possible that the precursors of the present day Antarctic nototheniiformes had haemoglobin which was not low-temperature efficient and adaptations." For the reasons mentioned above, it is clear that the haemoglobin-free condition of the blood in the Channichthyidae is one of the derived features.

Reconstruction of the phylogenetic relationships in the Notothenioidei: The Notothenioidei differ most noticeably from the general percoid conditions in having (1) three large plate-like radials, (2) a single nostril on each side of the head and (3) no swim bladder. Further, EAKIN (1981) gave the five peculiarities, such as (1) jugular pelvic fins, (2) nonpungent fin spines, (3) multiple lateral line, (4) usually fewer than 15 principal caudal rays and (5) an unusual rib pattern with well-developed epipleurals attached to parapophyses and degenerate, floating pleurals. He also pointed out the problem of separating convergences from true relationships, and concluded that most of the above-mentioned features are of little value in determining relationships. In the present study, it is considered that the endemic distribution, adaptations to cold environments and the morphological resemblance given above show their close relationships rather than the convergence, and it is concluded that the Notothenioidei are a monophyletic group derived from the percoid-like ancestor with several specializations as stated above.

Antarctic families of the Notothenioidei differ from the non-Antarctic family Bovichthyidae in the following features: (1) no vomerine teeth, (2) no palatine teeth, (3) no ectopterygoid teeth, (4) no epibranchial teeth and (5) the upper pectoral radial meeting both the scapula and coracoid. These differences represent that the Bovichthyidae conserve the most primitive conditions at least in their osteological features among the notothenioid families and this family may have been derived first from the common ancestor of the Notothenioidei.

Three notothenioid families, Harpagiferidae, Bathydraconidae and Channichthyidae, can be distinguished from the Nototheniidae and the Bovichthyidae by (1) the prootic separated from its fellow, (2) no basisphenoid and (3) the unossified second basibranchial. These three families apparently specialized in the above-mentioned three characters indicate that the Nototheniidae may have been derived from the common ancestor of the four Antarctic families, namely the Nototheniidae, Harpagiferidae, Bathydraconidae and Channichthyidae.

The Harpagiferidae except for one genus *Harpagifer* have an autapomorphic condition, the presence of the mental barbel, and differs from the Bathydraconidae and Channichthyidae in having (1) the L-shape cartilage between the epihyal and ceratohyal and (2) the separate uroneural. The two peculiarities of the Harpagiferidae show the plesiomorphic conditions, and so it is assumed that the common ancestor of the Bathydraconidae and Channichthyidae was derived from the common ancestor of the Harpagiferidae and the above-mentioned two families. EAKIN (1981) pointed out the naked body, reductions of epipleural and pleural ribs and fewer number of the epurals as the characteristic features shared with the Harpagiferidae and Channichthyidae. As the naked condition is observed in the Harpagiferidae, Channichthyidae and some genera of the Bathydraconidae, and the Bathydraconidae and Channichthyidae share some advanced features, the naked body of the Harpagiferidae is the result of the convergence rather than that of the close relationships with the Channichthyidae. The number of epurals varies among species and individuals, so it should not be used for the systematic study without the observations on the relative number of specimens.

Between the advanced families, such as the Bathydraconidae and Channichthyidae, the Channichthyidae are characterized by (1) the flat and elongate frontal, (2) the pterosphenoid and sphenotic not attached to each other, (3) no premaxillary ascending process, (4) the filamentous mesopterygoid, (5) the unossified first basibranchial, (6) the elongate and cane-like third hypobranchial, (7) two pharyngobranchials, (8) the unossified dorsal hypohyal, (9) no forked depression on the dorsal edge of the cleithrum, (10) the fused uppermost hypural, (11) no haemoglobin and (12) the presence of the first dorsal fin. Only the last feature, the presence of the first dorsal fin, is a primitive state for the Channichthyidae, and the Bathydraconidae show a derived state in this character (loss of the first dorsal fin). The survey of the various characters shows that the Bathydraconidae and Channichthyidae have the closest relationships between them. Consequently, the Bathydraconidae and Channichthyidae were derived independently from the common ancestor of the two families, and this common ancestor may have been formed after the branching of the three other families, Bovichthyidae, Nototheniidae and Harpagiferidae.

The proposed phylogenetic relationships among the five families of the Notothenioidei are shown in Fig. 174.

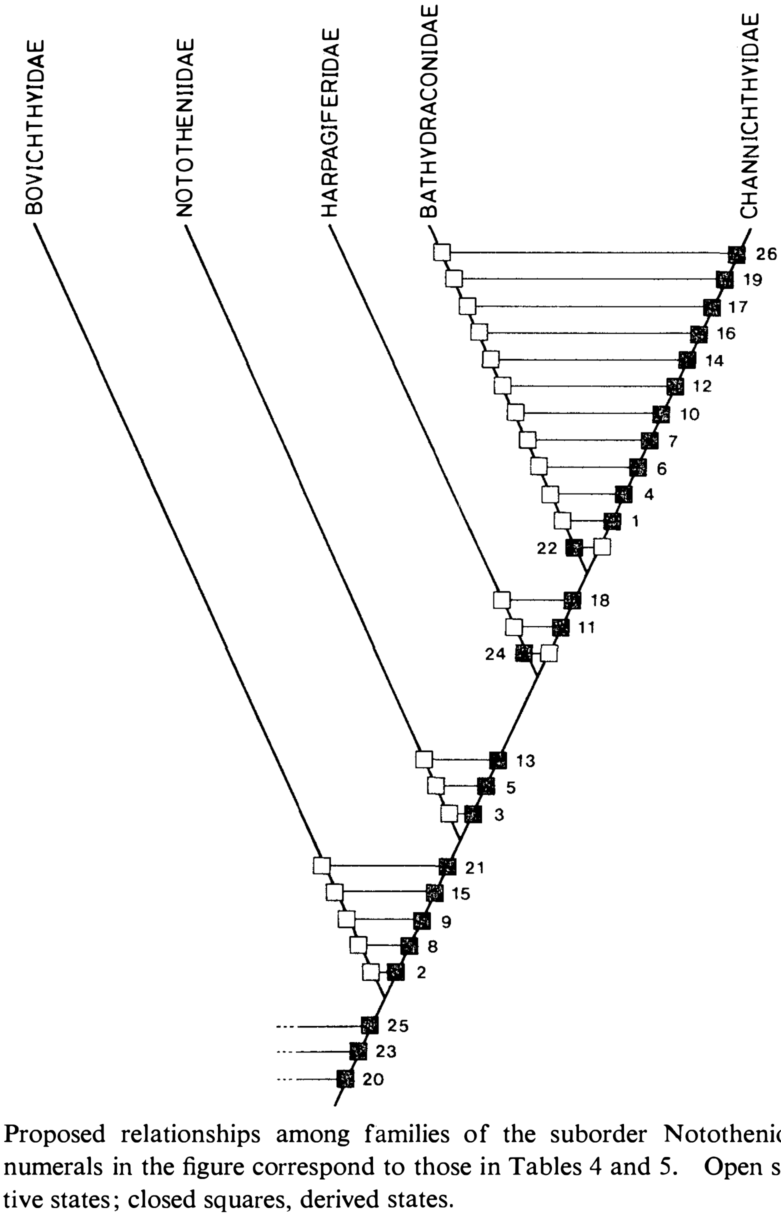


Fig. 174. Proposed relationships among families of the suborder Notothenioidei. Arabic numerals in the figure correspond to those in Tables 4 and 5. Open squares, primitive states; closed squares, derived states.

In comparison with the three previously proposed relationships (Dollo, 1904; Regan, 1914; Eakin, 1981), the present cladogram given by the author almost agrees with that of Eakin (1981). Dollo's dendrogram (1904) cannot be accepted because of his confusion of the channichthyid genera with those of the Bathydarconidae. Regan's dendrogram (1914) is too simple to discuss in detail. His dendrogram shows only that the Channichthyidae and Bathydraconidae were descended from the Nototheniidae and Bovichthyidae. Eakin (1981) presented the reasonable relationships of the five families of the Notothenioidei, but the degree of the kinship between the families is too diagrammatical to infer the familial relationships from his dendrogram.

5.3. Evolutionary trends of the Channichthyidae

The evolutionary trends recognized among notothenioid fishes basically involve the loss or reduction of some structures. There are many features which progress from the bovichthyid condition through the conditions shared by the Nototheniidae and Harpagiferidae, and to the derived conditions of the Bathydraconidae and Channichthyidae.

The Bovichthyidae differs most noticeably from the other notothenioid families in having many toothed elements in the oral cavity. NELSON (1969) stated that the reduction of toothed elements as "the loss of these tooth plates doubtless has functional significance, perhaps a different significance in each of the lineage in which it occurred; and these are problems deserving future study." The basic functions of this dentition are apparently to seize foods in the oral cavity and to pass them along to the gut (GOSLINE, 1971). However, the merit which compensates for the lack of the tooth structure is uncertain. The similar feature such as the reduction of the bony elements by the consolidations is also observed in (1) the uppermost hypural, (2) the uroneural and (3) the pharyngobranchial. At present, it can be suggested only that the reduction and consolidation of the toothed or bony elements is one of the aspects concerning the general trend of the euteleostean fishes. In the lineage of the Notothenioidei, the reduction of the ossification occurring in (1) the ethmoid region, (2) the prootic, (3) the basisphemoid, (4) the pterygoid arch and (5) the basibranchial series is also clearly pointed out.

These reductions of the ossification enable the fishes to expand their oral cavities laterally as well as vertically, and this expansion permits the fishes to swallow the larger preys and larger amount of water. The expansion of the oral cavity is also supported by the following modifications; (1) the elongate and cane-like third hypobranchial and (2) the slender ceratohyal with the I-shape articulating cartilage.

The problem of protection which is brought by the reduction of the ossification may be solved by developing the spiny or hooked opercle with which the fishes of the Harpagiferidae, Bathydraconidae and Channichthyidae are equipped. ROBILLIARD and DAYTON (1969) observed the defence posture of *Pagetopsis macropterus* and described it as follows: "the mouth was opened wide, the corners of the mouth and opercle were expanded laterally, the dorsal fin was erected, the pectoral fins were flared and held at right angle to the body, and the body was vented in a semicircle." In expanding the opercle laterally, the opercular spine and hook seem to be erected, and protect the head portion. Some of channichthyid fishes have not only the well branched opercular spine, but also the subopercular and interopercular spines. Consequently, it can be concluded that the channichthyid fish bears the extreme condition in this evolutionary trend in the development of the defence posture.

The evolutionary trend in the pectoral girdle is traced well from the benthic percoid condition to the notothenioid one. In the typical percoid fishes, the pectoral girdles contain four, split-like radials, and the pectoral fins are used to govern the vertical plane of forward movement, for stopping, turning and sometimes for forward locomotion.

In contrast with the typical percoid fishes, blennioid fishes, which are thought to be closely related with the notothenioids (GOSLINE, 1968; EAKIN, 1981), have rounded and broad base pectoral fins. The broad pectoral fins act as props against the bottom and provide a fast standing start from the normal stationary position (GOSLINE, 1971). The pectoral girdles in blennioid fishes tend to have four broad radials rigidly attached to the scapula, coracoid and to each other. In notothenioid fishes, the pectoral fins show a very close resemblance to those of blennioid fishes, but the pectoral girdle of notothenioids consists of three broad radials which meet the scapula and coracoid tightly.

Morphologically speaking, the reduction of the number of radials may be caused by the consolidation of the uppermost radial with the scapula. The functional value of the broad radials and consolidated ones is considered to be a strong support of the pectoral fin rays. These changes are apparently correlated with the sluggish and benthic modes of life in which the modified pectoral girdle is used more effectively. Not only the features mentioned above, but also the flattened head, dorsal position of eyes and dorsally pointed spine of the opercle are the features associated with the sluggish and benthic habits.

The morphological changes of the premaxillary ascending process are thought to be reflected in the feeding habits of fishes. The relationships between the length of the premaxillary ascending process and the diet composition is pointed out by OKAMURA (1970). In macrourioid fishes, the species with the shorter premaxillary ascending process feed on the nektonic animals such as small fishes, squids and euphausids, while the species with the longer premaxillary ascending process feed on the benthic animals such as polychaetes, molluscs and ophiuroids (OKAMURA, 1970). Notothenioid fishes also show the similar relationships between the length of the premaxillary ascending process and the diet composition. For example, channichthyid fishes which have no premaxillary ascending process noticeably show their piscivorous feature, while nototheniid fishes which have the longer process mainly feed on the benthic invertebrates (PERMITIN and TARVERDIYEVA, 1972; TARGETT, 1981; DANIELS, 1982; TAKAHASHI, 1983). The fact that few number of channichthyids are caught by traps baited with fish meat (HEMMINGSEN and GRIGG, 1967; IWAMI and NAITO, 1983) and the results of the underwater observation (ROBILLIARD and DAYTON, 1969) show that channichthyid fishes sit on the bottom of the sea, and wait preys such as small fishes and euphausids near enough to be caught by quick snapping movements. Therefore, the acquirement of the piscivorous feature in channichthyid fishes may be associated with their low activity which is also associated with their haemoglobinless condition. As mentioned above, this distinctive feature, the haemoglobinless condition, is perhaps an alternative to low temperature haemoglobin which maintains its function under the low temperature environment and is acquired by the nototheniid and bathydraconid. These phenomena represent that at least two divergent physiological mechanisms have evolved in the past.

The loss of the swim bladder in all families of the Notothenioidei is a common adaptive feature associated with the sluggish and benthic habits, while there is also an evolutionary trend toward the pelagic mode of life as found in some nototheniid fishes (EASTMAN, 1980; EASTMAN and DEVRIES, 1981).

These above-mentioned evolutionary trends are correlated to each other so that they cannot be discussed independently. Morphologically speaking, the Channichthyidae is the most advanced group within the Notothenioidei for the benthic mode of life in the Southern Ocean.

The relationships between the Notothenioidei and the other suborders of the order Perciformes were discussed by Greenwood *et al.* (1966), Gosline (1968, 1971), Fraser (1972), Eakin (1981) and Andersen (1984). Their discussions, however, are based on the results of studies on a small number of the systematic characters of a small number of specimens. In the present study, no detailed examinations of the percoid fishes are performed. Therefore, the origin of the notothenioid stock cannot be discussed and the aspects of the ancestor stock of the Notothenioidei and the relationships among the suborders of the Perciformes are left for the future studies.

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