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Demise of the Scorpaeniformes (Actinopterygii: Percomorpha): An Alternative Phylogenetic Hypothesis

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Abstract

The Scorpaeniformes has been defined by two synapomorphies, the presence of a suborbital stay and a bony parietal structure supporting the sensory canal, but monophyly for the order is still uncertain. Two monophyletic groups of scorpaeniform fishes are currently recognized: a scorpaenoid lineage, including the suborders Scorpaenoidei and Platycephaloidei; and a cottoid lineage, containing suborders Anoplopomatoidei, Zaniolepidoidei, Hexagrammoidei and Cottoidei. Synapomorphies that support the monophyly of these two lineages, four in the case of the scorpaenoid lineage and 13 for the cottoid lineage, are reviewed and reevaluated. Comparison of these two sets of synapomorphies with those that define percomorph taxa, provides evidence to support the following phylogenetic hypotheses: (1) the scorpaenoid lineage and percoid family Serranidae have a close relationship supported by two synapomorphies; and (2) the cottoid lineage and perciform suborder Zoarcoidei have a sister relationship supported by 13 synapomorphies. The order Scorpaeniformes as currently recognized is thus hypothesized to be polyphyletic. We propose reallocation of both lineages to the order Perciformes, recognizing a suborder Scorpaenoidei to contain the scorpaenoid lineage plus Serranidae, and a suborder Cottoidei closely aligned with the Zoarcoidei to contain the cottoid lineage.

Key words: Scorpaeniformes, Polyphyly, Synapomorphy, Scorpaenoid lineage, Cottoid lineage, Perciformes, Serranidae, Zoarcoidei

Introduction

The phylogenetic relationships of most families of the order Scorpaeniformes have been inferred by many ichthyologists (e.g., Gill, 1888; Taranetz, 1941; Matsubara, 1943; Bolin, 1947; Matsubara and Ochiai, 1955; Quast, 1965; Washington et al., 1984b; Yabe, 1985; Kido, 1988; Kanayama, 1991; Ishida, 1994; Shinohara, 1994; Imamura, 1996; Mandrytsa, 2001). These studies have resulted in an extensive array of morphological information on Scorpaeniformes, leading Imamura and Shinohara (1998) to propose two monophyletic groups among the Scorpaeniformes, i.e., the scorpaenoid lineage (sensu Imamura and Shinohara, 1998 = suborders Scorpaenoidei + Platycephaloidei sensu Eschmeyer, 1998) and the cottoid lineage (sensu Imamura and Shinohara, 1998 = suborders Anoplopomatoidei + Zaniolepidoidei + Hexagrammoidei + Cottoidei sensu Shinohara, 1994) (Fig. 1). The monophyly of the order Scorpaeniformes, however, is still uncertain (e.g., Quast, 1965; Johnson and Patterson, 1993; Nelson, 1994;

Imamura and Shinohara, 1998), although many authors have supported scorpaeniform monophyly by the presence of a suborbital stay (e.g., Gill, 1888; Matsubara, 1943; Washington et al., 1984b; Shinohara, 1994; Yabe and Uyeno, 1996; Mandrytsa, 2001) (Fig. 2). In addition to the suborbital stay, two putative synapomorphies, presence of a bony parietal structure associated with the sensory canal and the extrinsic muscle of the swimbladder, were suggested as further evidence for the monophyly of the order (Johnson, 1993; Shinohara, 1994; Mooi and Johnson, 1997). Imamura (1996), however, demonstrated that the extrinsic muscle in the scorpaenoid lineage is not homologous with that in the cottoid lineage. As for the suborbital stay and parietal sensory canal, it is well known that these two characters are not autapomorphic for scorpaeniform fishes. Several non-scorpaeniform taxa (e.g., the smegmamorph Aulorhynchidae, perciform Dactylopterinae and trachinoid Chiasmodontidae) also have a posterior extension or expansion of the third (or second) infraorbital (Regan, 1913; Pietsch, 1989; Imamura, 2000; pers. obs.).

Scorpaenoid lineage   **Cottoid lineage**

Backwardly-directed opercular spine

Extrinsic muscle
derived from obliquus superioris

Parasphenoid connected with pterosphenoid

Six branchiostegal rays

Third epibranchial without toothed plate

No supraneurals

Dorsal pterygiophores arranged singly in each interneural space

Absence of anal spines with robust pterygiophores

Extrinsic muscle derived from epaxialis

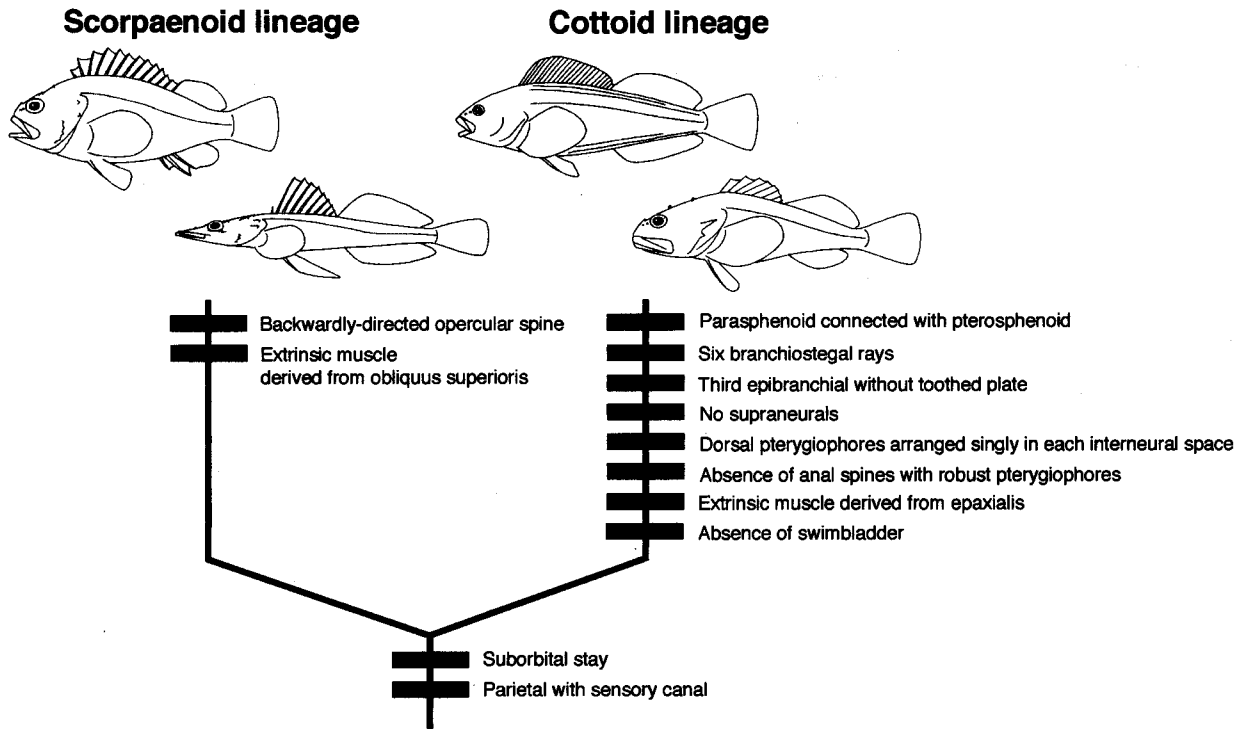Absence of swimbladder

Suborbital stay
Parietal with sensory canal

Fig. 1. Previously proposed phylogenetic relationships of Scorpaeniformes based on Shinohara (1994) and Imamura
(1996).

A   **Infraorbitals**   **Suborbital stay**
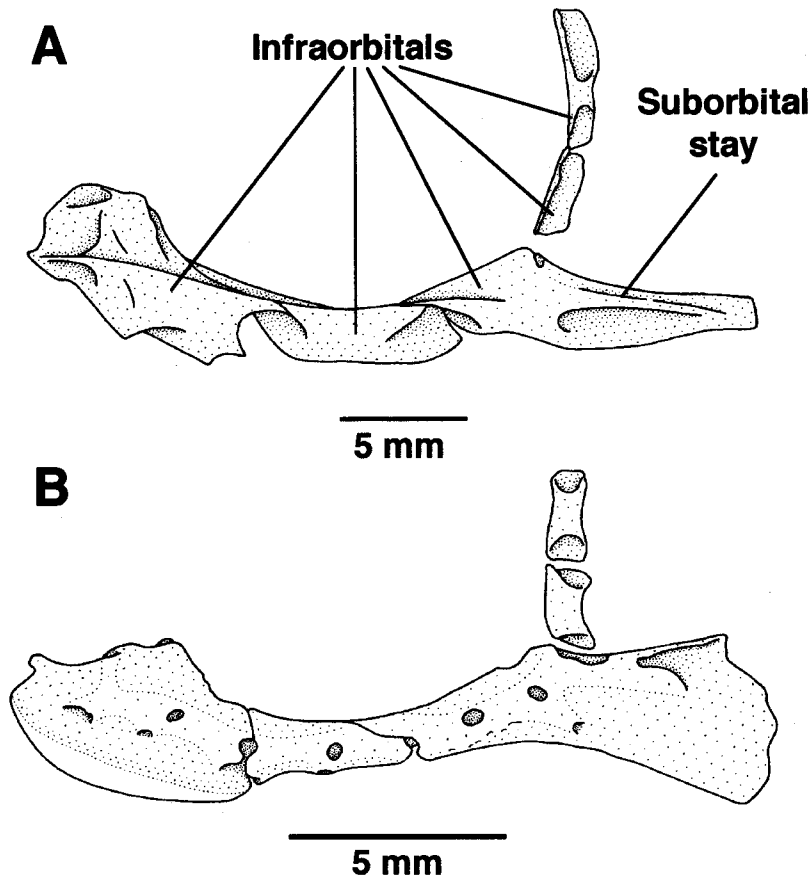
5 mm

B

5 mm

Fig. 2. Lateral view of infraorbital bones of *Helicolenus hilgendorfi* (scorpaenoid lineage), HUMZ 39743, 136 mm (A)
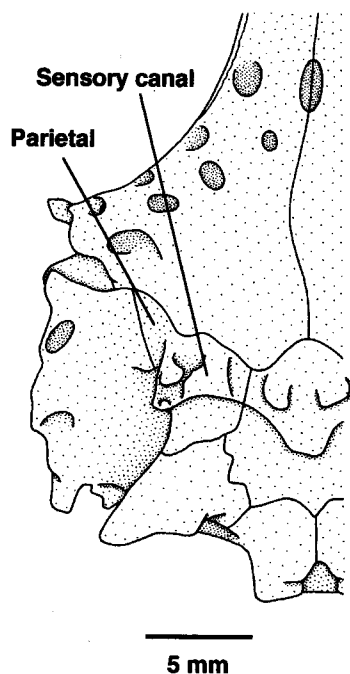and *Oxylebius pictus* (cottoid lineage), CAS 2010183, 124 mm (B).

5 mm

Fig. 3.   Dorsal view of the posterior portion of the cranium
of *Bathymaster signatus* (Zoarcoidei), HUMZ uncat.,
248 mm.

The bony parietal structure supporting the sensory canal
is also recognized in many perciforms (e.g., the serranid
Niphon, trachinoid Trichodontidae, all zoarcoids, except
for the ptilichthyid *Ptilichthys* and stichaeid *Lumpenella*,
and some blennioids and notothenioids) (Makushok,
1958; Eakin, 1981; Shinohara, 1994; Mooi and John-
son, 1997; pers. obs.) (Fig. 3).   In addition, as emphas-
ized in this study, the homology of the bony parietal
structure supporting the sensory canal among the Scor-
paeniformes has not been clearly explained.   When
recognizing the monophyly of the Scorpaeniformes
cladistically, *a priori* weighting must be provided for
these two synapomorphies, because as shown in this
study many synapomorphies that support the mono-
phyly of the scorpaenoid lineage and those of cottoid
lineage are also recognized in many perciform taxa.
However, we cannot justify this weighting in our parsi-
monious approach.

The purpose of this study was to test the monophyly
of the Scorpaeniformes parsimoniously, by considering
putative synapomorphies without *a priori* weighting, as
well as other derived characters, and comparing the
synapomorphies of two scorpaeniform lineages with
percomorph taxa, especially perciforms, so as to identify
the taxon most closely related to each lineage.

Methods

Definitions   of   the   scorpaenoid   (suborders   Scor-

paenoidei + Platycephaloidei *sensu* Eschmeyer, 1998)
and cottoid lineages (suborders Anoplopomatoidei +
Zaniolepidoidei + Hexagrammoidei + Cottoidei *sensu*
Shinohara, 1994) follow Imamura and Shinohara
(1998).   The order Scorpaeniformes (*sensu* Nelson,
1994 minus his Dactylopteridae) is tentatively used here,
despite Mooi and Gill (1995) and Mooi and Johnson
(1997) treating it as a perciform suborder.   The most
parsimonious character evolution in the scorpaenoid
and cottoid lineages (and also in Zoarcoidei) were
analyzed mainly by using MacClade ver. 4 (Maddison
and Maddison, 2000) to infer the condition at each
ingroup (IG) node, which represents the ancestor of
subsequent groups (Wiley et al., 1991).   For this ana-
lysis, we relied on the cladistic topology hypothesized by
Imamura (1996) for the scorpaenoid lineage (Fig. 4) and
that by Shinohara (1994) for the cottoid lineage (Fig. 5),
because they are the only studies hypothesize the com-
prehensive relationships of the scorpaenoid and cottoid
lineages.   When morphological variations were recog-
nized within the Congiopodidae, Gnathanacanthidae
and Pataecidae, families not included by Imamura
(1996) in his study, inference of the IG node of the
scorpaenoid lineage was referred to Ishida's (1994)
phylogenetic hypothesis of the suborder Scorpaenoidei,
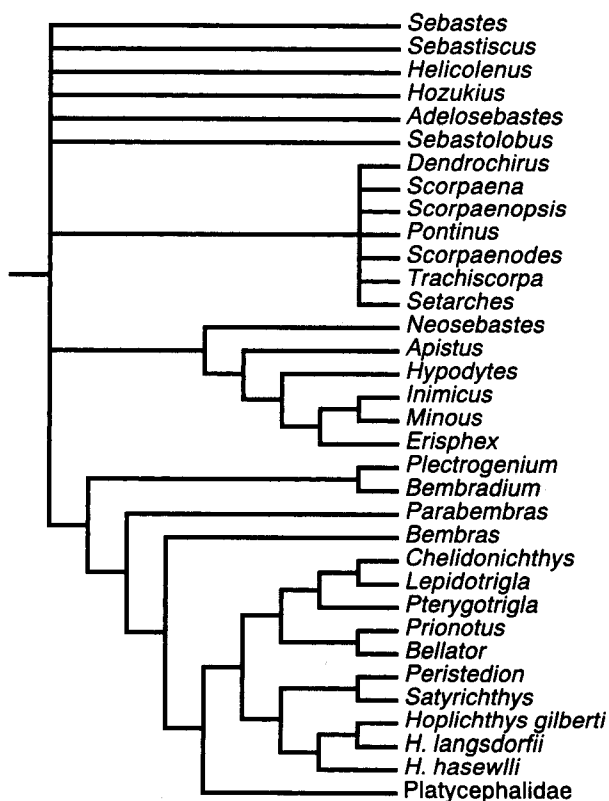in which the families were deeply nested.   The mono-

Fig. 4.   Phylogenetic relationships of the scorpaenoid line-
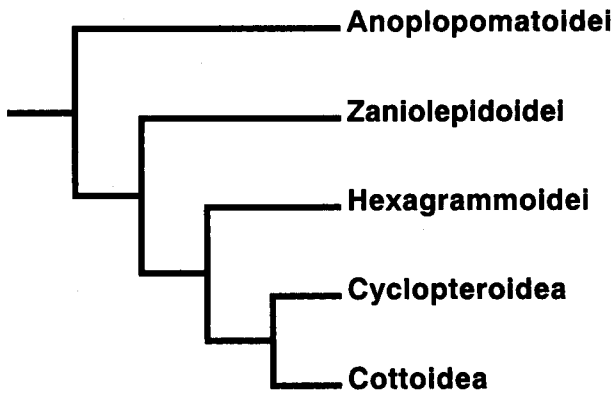age based on Imamura (1996).

Fig. 5. Phylogenetic relationships of the cottoid lineage based on Yabe (1985) and Shinohara (1994).

phyly and relationships of Zoarcoidei as presented by Anderson (1994) were supported in this study (see "Relationship of cottoid lineage and Zoarcoidei" below), and his hypothesis of relationships of the suborder was also accepted by our analysis. The evolutionary interpretation was examined by both DELTRAN and ACCTRAN optimizations in the relationships of the cottoid lineage. However, such optimizations could not be selected for the scorpaenoid lineage and Zoarcoidei owing to polytomies. For the determination of character polarity in Scorpaeniformes, the Percoidei (sensu Nelson, 1994), which have been considered as the most primitive group within the

Perciformes, were employed, their typical characters being taken as the primitive condition for the former (although the monophyly of the Percoidei is unclear; see e.g., Nelson, 1994). In addition, it has been recognized that scorpaeniforms and generalized perciforms have many similarities and are very comparable (e.g., Yabe, 1985; Ishida, 1994; Imamura, 1996). When the typical percoid condition was difficult to determine, the lower acanthomorph taxa (i.e., Beryciformes, Polymixiiformes and Stephanoberyciformes sensu Johnson and Patterson, 1993) were used to confirm the primitive percoid condition, such being interpreted also as the primitive scorpaeniform condition. Terminology generally follows recent scorpaeniform studies (e.g., Yabe, 1985; Shinohara, 1994; Imamura, 1996) for osteology, except for the infraorbitals and lateral extrascapular, which follow Imamura (2000) and Eakin (1981), respectively, and Winterbottom (1974) for myology, except for the extrinsic swimbladder muscles, which follow Hallacher (1974). Institutional abbreviations follow Leviton et al. (1985).

Possibility of Non-homology of the Bony Parietal Structure Supporting the Sensory Canal between the Scorpaenoid and Cottoid Lineages

Most scorpaeniforms have a bony parietal structure supporting the sensory canal, whereas it is absent in the Cyclopteroidea (Shinohara, 1994; pers. obs.). Shino-
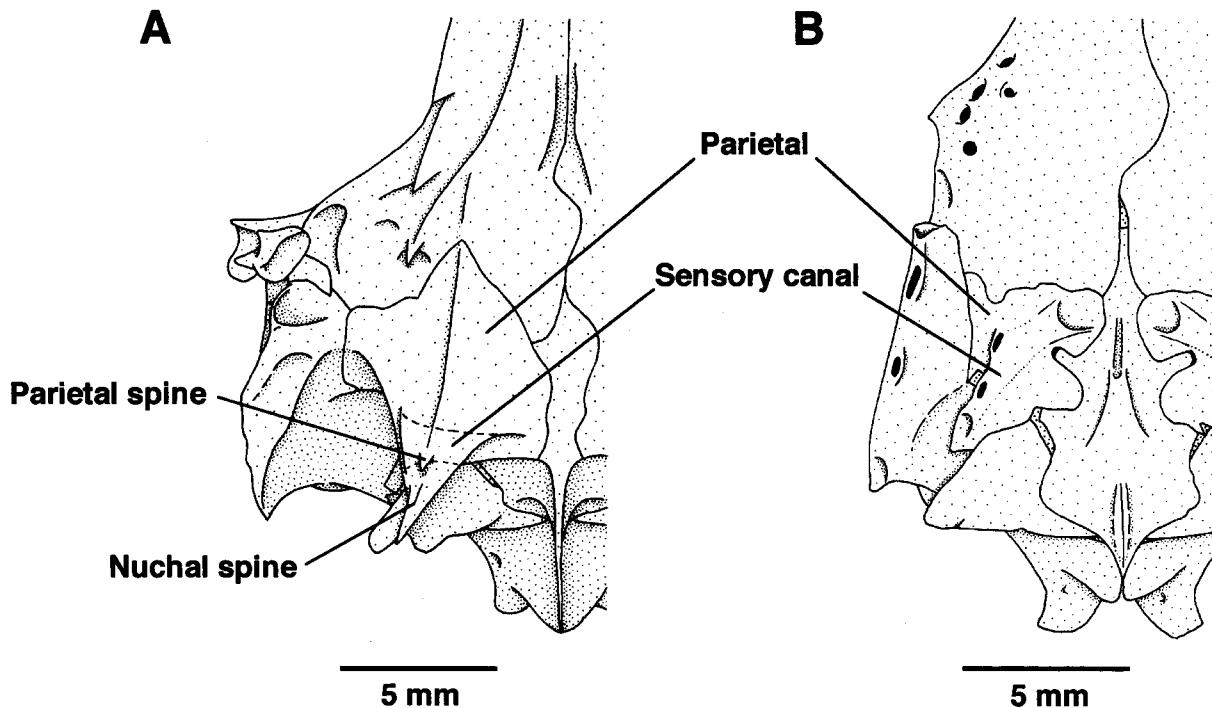

Fig. 6. Dorsal view of the posterior portion of the cranium of Helicolenus hilgendorfi (scorpaenoid lineage), HUMZ 39743, 136 mm SL (A) and Hexagrammos lagocephalus (cottoid lineage), HUMZ 104878, 152 mm SL (B).

A

Parietal spine   Posterior projection of   Anterior projection of
                     parietal spine   nuchal spine

Nuchal spine   Sensory canal
                  with spines

B

Anterior ridge   Posterior ridge   Sensory canal
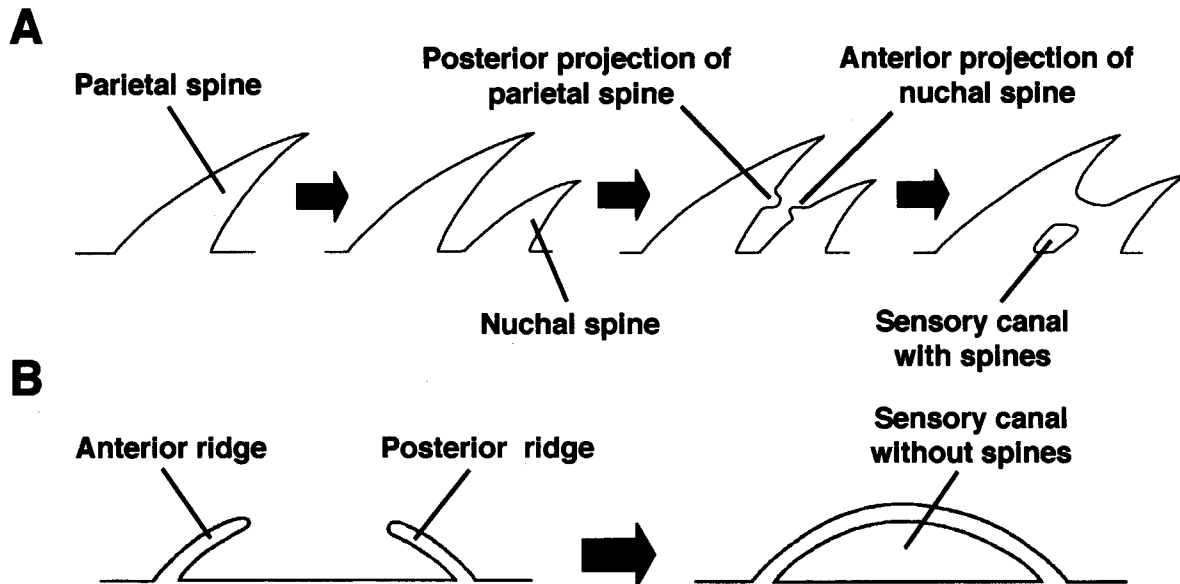   without spines

Fig. 7. Diagrammatic illustration of ontogenetic development of parietal sensory canal in the scorpaenoid lineage (A) and cottoid lineage (B).

hara (1994) considered the parietal supporting a sensory canal to be a synapomorphy of the Scorpaeniformes, the absence of the structure in Cyclopteroidea being a secondary loss by reason of the epaxial-muscle extending forward to that region. Subsequently, Mooi and Johnson (1997) indicated that the canal-bearing parietal spine corroborated scorpaeniform (=their scorpaenoid) monophyly, several families having lost the spine secondarily, or that it was evidence of the monophyly of the scorpaeniform subgroup sharing it. These hypotheses were based on the perceived homology of the bony parietal structure supporting the sensory canal in Scorpaeniformes, the different structures in that group belonging to a single transformation series. In the present study, the condition of the bony parietal structure supporting the sensory canal at the IG node of the scorpaenoid lineage and that of the cottoid lineage of the Scorpaeniformes are inferred, and the osteological development of this character in the IG node of both lineages is also examined to test their homology.

The bony parietal structure for the sensory canal has two spines (parietal and nuchal spines) in the scorpaenoid lineage (Fig. 6A), except in Congiopodus, Tetrarogidae, Gnathanacanthidae and Pataecidae (pers. obs.), which are deeply nested within Scorpaenoidei, according to Ishida (1994) and Imamura (1996). In addition, larval tetrarogids (e.g., Hypodytes rubripinnis and Gymnapistes marmoratus) have both parietal and nuchal spines (e.g., Okiyama, 1988; Neira, 1989), and it can be inferred that these spines reduce in size with fish growth in that family. Thus, it is considered that the IG node of this lineage is also characterized by the

sensory canal having two spines, analyzing the parietal sensory canal evolution based on the phylogenetic relationships of this lineage proposed by Imamura (1996) (Fig. 4) and those of the Scorpaenoidei by Ishida (1994). Ontogenetically, the condition follows the following process: (1) the parietal spine develops initially, followed by the nuchal spine (e.g., Moser et al., 1977; Washington et al., 1984a; Okiyama, 1988; Imamura and Yabe, 1998); (2) two projections develop on the posterior portion of the parietal spine and anterior portion of the nuchal spine; and (3) the tubular structure for the sensory canal is completed by the fusion of the spine projections, as observed in Inimicus and Suggrundus (Fig. 7A) (see also Imamura and Yabe, 1998: figs. 3-4).

In the cottoid lineage, three morphotypes of bony parietal structure supporting the sensory canal (=cranial arch 6 sensu Nelson, 1982) exist: (1) sensory canal without spines in the suborders Anoplopomatoidei, Zaniolepidoidei and Hexagrammoidei, and some members of superfamily Cottoidea (e.g., cottid genera Gymnocanthus, Bero and Pseudoblennius) (Fig. 6B); (2) sensory canal with spine(s) in many members of the Cottoidea; and (3) sensory canal and spines absent in the superfamily Cyclopteroidea (e.g., Ueno, 1970; Nelson, 1982; Yabe, 1985; Kido, 1988; Shinohara, 1994; pers. obs.). After the analysis of character evolution of the parietal sensory canal, it was inferred that the IG node of the cottoid lineage is characterized by the sensory canal lacking spines, subsequent spine(s) being a secondary development among the Cottoidea with the canal being secondarily lost in the Cyclopteroidea (these characters were unordered). From an ontogenetic

A

Anterior ridge   **Parietal**

Posterior ridge

1 mm

B

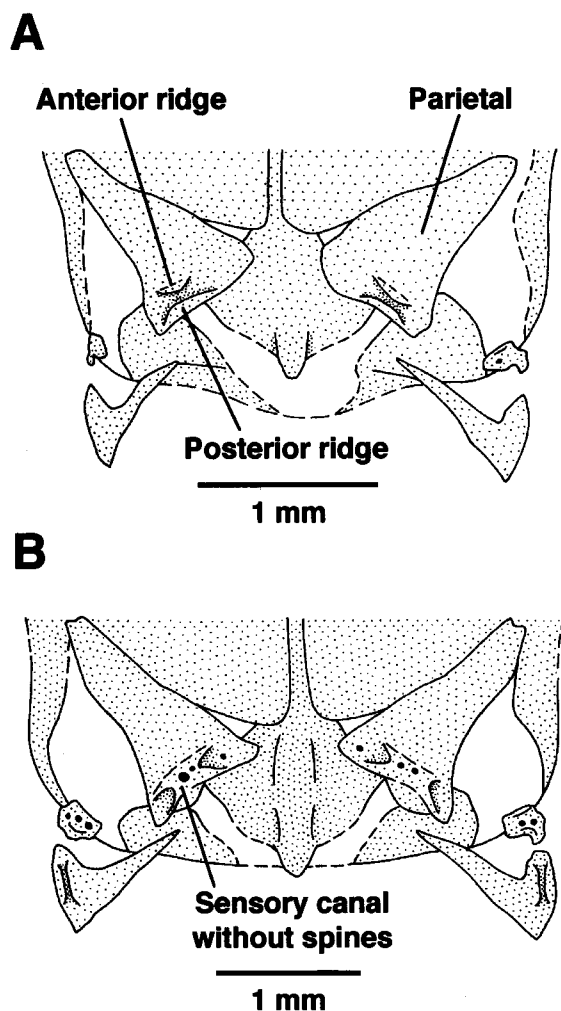**Sensory canal
without spines**

1 mm

Fig. 8. Dorsal view of the posterior portion of the cranium of *Hexagrammos decagrammus* (cottoid lineage), HUMZ-L 2469, 26.8 mm (A) and 33.7 mm (B).

examination of *Anoplopoma* and *Hexagrammos*, it appears that a sensory canal without spines has formed by the fusion of anterior and posterior ridges developed on the parietal, spines as such not being present during the ontogenetic process (Figs. 7B, 8).

As the result of above comparison, we conclude that the estimated character condition at the IG node and the development sequence of the bony parietal structure supporting the sensory canal in the scorpaenoid lineage are different from those in the cottoid lineage.   Therefore, the possibility of non-homology of the parietal sensory canal between the scorpaenoid and cottoid lineages is suggested, although the parietal sensory canal is regarded here as one of two synapomorphies of the Scorpaeniformes.

Synapomorphies Supporting the Monophylies of the Scorpaenoid and Cottoid Lineages

In this section, we propose two sets of synapomorphies, one that supports the monophyly of the scorpaenoid lineage, and the other that of the cottoid lineage.   Each character is analyzed at the IG node for each lineage, and each is regarded as the derived condition by our determination of the polarity.

Synapomorphies of the scorpaenoid lineage

Monophyly for the scorpaenoid lineage has been supported by two synapomorphies, the presence of a backwardly-directed opercular spine and the extrinsic swimbladder muscle derived from the obliquus superioris (Imamura, 1996; Imamura and Shinohara, 1998) (Fig. 1).   These two characters plus two newly recognized scorpaenoid-lineage synapomorphies (SS), the presence of a single postocular spine in larval stage and an adductor dorsalis muscle, are discussed as follows:

SS 1.   Single postocular spine in larval stage.—In the larvae of most members of the scorpaenoid lineage, a single postocular spine (*sensu* Moser and Ahlstrom, 1978) is present on the supraorbital region, whereas this region is serrated in Hoplichthyidae (Okiyama, 1988; Leis and Carson-Ewart, 2000; pers. obs.), a family that is deeply nested within the scorpaenoid lineage (Fig. 4). A single spine on that region is present in the larvae only of some anthiine and epinepheline serranids, the monotypic Lobotidae, and monophyletic Coryphaenidae, Rachycentridae and Echeneididae in the percoids (Johnson, 1984; Baldwin and Johnson, 1993). This condition is considered to be a synapomorphy of the scorpaenoid lineage, with a secondarily-modified condition in the Hoplichthyidae, owing to an analysis of the larval postocular spine evolution based on the phylogenetic relationships of the scorpaenoid lineage (Fig. 4).   Although such a spine is present in the larvae of some members of the superfamily Cottoidea (e.g., the ereuniid *Marukawichthys*, rhamphocottid *Rhamphocottus*, cottids *Astrocottus* and *Enophrys*, and agonid *Agonomalus*) (e.g., Okiyama, 1988), the IG node of the cottoid lineage is inferred as being characterized by the supraorbital region lacking postocular spines based on the phylogenetic relationships of the cottoid lineage (Fig. 5).

SS 2.   Backwardly-directed opercular spine (Fig. 9). —Imamura (1996) hypothesized that the backwardly-directed opercular spine, crossing the subopercle, is a synapomorphy of the scorpaenoid lineage, owing to the secondary reduction of this condition in the Pteroinae (*sensu* Matsubara, 1943).   Within the Perciformes, the spine is restricted to Serranidae, *Sphyraenops*
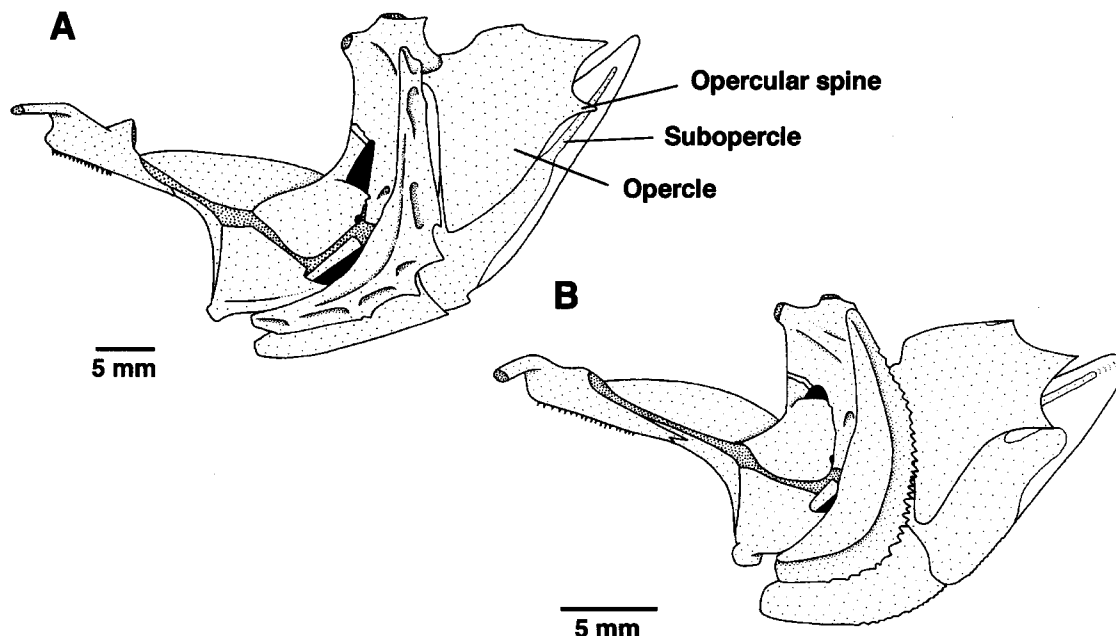
Fig. 9. Lateral view of suspensorium of *Sebastes owstoni* (scorpaenoid lineage), HUMZ 42641, 183 mm (A) and *Chelidoperca hirundinacea* (Serranidae), HUMZ 36481, 102 mm (B).

(Epigonidae), the trachinoid *Bembrops* (Percophidae) and Trachinidae, and the notothenioid Channichthyidae (Johnson, 1983; Iwami, 1985; pers. obs.).

SS 3. Extrinsic swimbladder muscle derived from obliquus superioris.—This derived character was not found in other taxa examined in this study and is considered to be an autapomorphy of the lineage (see Imamura, 1996).

SS 4. Adductor dorsalis.—A caudal muscular element, adductor dorsalis, was inferred as a character of the IG node of the scorpaenoid linage following consideration of the evolution of this muscle based on the scorpaenoid-lineage relationships (Fig. 4), despite its absence in several members of the lineage (e.g., Synanceiidae, Aploactinidae, Triglidae, Peristediidae, Hoplichthyidae and Platycephalidae) (Yabe, 1985; Ishida, 1994; Imamura, 1996). Adductor dorsalis was also recognized in many perciform taxa [e.g., Serranidae, except for *Niphon* and *Diploprion*, the callanthiid *Grammatonotus*, centrarchid *Lepomis*, kuhliid *Kuhlia*, lutjanid *Lutjanus*, Terapontidae and Sparoidea, the trachinoid *Parapercis* (Pinguipedidae) and notothenioid *Patagonotothen* (Nototheniidae)], but was not common in Perciformes overall. This muscular element is also absent in lower acanthomorphs (Shinohara, 1994; pers. obs.). Therefore, it is reasonable to infer that the presence of the muscle is a derived character for both Perciformes and Scorpaeniformes. It is concluded here that the presence of adductor dorsalis is a synapomorphy of the scorpaenoid lineage. The muscle is absent in all members of the cottoid lineage (Yabe, 1985; Shinohara,

1994; pers. obs.).

Equivocal character.—The cleithral spine, situated posterodorsally on the cleithrum and backwardly-directed, is commonly found in the scorpaenoid lineage, except for *Dendrochirus* and *Sebastolobus*, whereas it is absent in all members of the cottoid lineage (Shinohara, 1994, see his fig. 28). Shinohara (1994) believed that presence of the spine was a synapomorphy of Scorpaeniformes, secondary loss of the spine having occurred in *Dendrochirus* and *Sebastolobus*, and in the cottoid lineage. However, it is here inferred that the cleithral spine condition is an equivocal character at the IG node of the scorpaenoid lineage, the spine having been acquired by a common ancestor of either the scorpaenoid lineage or subgroup of this lineage (thus this character was omitted from Fig. 1). A cleithral spine is present in several perciform taxa (e.g., Trachinidae and Uranoscopidae).

Synapomorphies of the cottoid lineage

The cottoid lineage was regarded by Shinohara (1994) to be a monophyletic group on the basis of seven synapomorphies, including one reversal character (= presence of cleithral spine, which is here recognized to be an equivocal character for the IG node of the scorpaenoid lineage) (Fig. 1). Imamura (1996, 2000) pointed out that the presence of the extrinsic muscle derived from the epaxial muscle is a synapomorphy of this lineage. Imamura (2000) also considered the absence of the swimbladder to be a synapomorphy of the cottoid lineage. In this study, we found the IG node of

Table 1. Characters in four suborders, including two superfamilies, among the cottoid lineage and inferred ingroup node of the lineage.

Taxa and node	Characters												
	1	2	3	4	5	6	7	8	9	10	11	12	13
INGROUP NODE	+	6	—	2	0	+	—	+	2	+	+	—	+
Anoplopomatoidei	+	6	—	2	0	+/—	—	+	2	+	+	—	+
Zaniolepidoidei	+	6	—	1/2	0	+	+	+	2	+	+	—	+
Hexagrammoidei	+	6	+/—	1/2	0/1	+	—	+	2	+	+	—	+
Cottoidei													
Cottoidea	+/—	6/7	+/—	1/1H/2	0	+	—	+	2	+/—	+/—	—	+
Cyclopteroidea	—/0	5/6	—	0/1L	0	+	—	—/0	1/2	—	—	—	+

1) Presence (+) or absence (—) of parasphenoid and pterosphenoid connection, or absence of pterosphenoid (0). 2) Numbers of branchiostegal rays. 3) Presence (+) or absence (—) of toothed plate on third epibranchial. 4) Numbers of lateral extascapular elements: 1, a single element with three openings; 1H, a single horizontal element with two openings; 1L, a single longitudinal element with two openings. 5) Number of supraneurals. 6) Relationships of dorsal pterygiophores and neural spines: arranged singly (+) or not (—). 7) Presence (+) or absence (—) of anal spines with robust pterygiopores. 8) Presence (+) or absence (—) of insertion of adductor mandibulae section 3 (A3) into medial surface of levator arcus palatini, or absence of A3 (0). 9) Number of levator operculi elements. 10) Presence (+) or absence (—) of circular element of transversus dorsalis anterior. 11) Presence (+) or absence (—) of adductores I-III. 12) Presence (+) or absence (—) of swimbladder. 13) Presence (+) or absence (—) of extrinsic swimbladder muscle derived from epaxialis. Data mainly from Yabe (1985), Kido (1988), Kanayama (1990), Shinohara (1994), Imamura (2000) and present study. Slashes indicate polymorphisms.

the cottoid lineage to be supported by five additional synapomorphies. In total, the following 13 cottoid-lineage synapomorphies (CS) were recognized in this study.

CS 1. Parasphenoid connected with pterosphenoid. —This character has been recognized as important in the phylogeny of Scorpaeniformes (e.g., Gill, 1888; Quast, 1965; Yabe, 1985; Shinohara, 1994). Quast (1965) considered the condition to be a reliable taxonomic character separating scorpaenoid fishes from the hexagrammids, zaniolepidids and cottids. More recently, Shinohara (1994) recognized the connection of the parasphenoid and pterosphenoid as a synapomorphy of the cottoid lineage. Although some taxa of the suborder Cottoidei lack this derived connection (Ereuniidae, Psychrolutidae, most hemitripterids, the liparids Liparis and Nectoliparis, and Cyclopteridae) or the pterosphenoid is absent (Liparidae, except for Liparis and Nectoliparis) (Yabe, 1985; Kido, 1988), the validity of the connection of these bones as a synapomorphy of the cottoid lineage was supported in this study, owing to the evolutionary analysis of the parasphenoid-pterosphenoid connection (Table 1). The condition is not common in percoids (Sasaki, 1989; Shinohara, 1994; Imamura, 2000), although several perciform suborders also have the derived condition (e.g., Zoarcoidei, except for the zaprorid Zaprora, the notothenioids Nototheniidae and Bovichthyidae, blennioid Blenniidae, and trachinoids Trachinidae and Uranoscopidae) (e.g., Starks, 1923;

Makushok, 1958; Springer, 1968; Anderson, 1994; pers. obs.). In the scorpaenoid lineage, such a connection is restricted only to several taxa (i.e., Alertichthys, Pataecus, Bembradium and several platycephalids) (pers. obs.), which are nested within the lineage according to Ishida (1994) and Imamura (1996) (Fig. 4). It is assumed here that the IG node of the scorpaenoid lineage has the primitive condition, the parasphenoid separated from the pterosphenoid.

CS 2. Six branchiostegal rays.—In percoids, the presence of seven branchiostegal rays is regarded as the primitive condition (Johnson, 1984; Sasaki, 1989; Imamura, 1996, 2000), although six or fewer rays are recognized in other perciform suborders (e.g., Zoarcoidei, except for Anarhichadidae with six or seven rays and several zoarcids with seven or eight rays, some notothenioids, Blennioidei and trachinoids Trichodontidae, Pinguipedidae, Trachinidae and Uranoscopidae) (e.g., McAllister, 1968; Eakin, 1981; Springer, 1993; Anderson, 1994; pers. obs.). Shinohara (1994) regarded six branchiostegal rays as a synapomorphy of the cottoid lineage with a reversal in the Psychrolutidae having seven rays. This study shows that the IG node of the cottoid lineage has six branchiostegal rays, the psychrolutid condition is a reversal, and the presence of five branchiostegal rays in the liparids Paraliparis nanus and Nectoliparis (Kido, 1988) is a further derived condition among the family (characters ordered as five-six-seven) based on the cottoid-lineage phylogenetic rela-
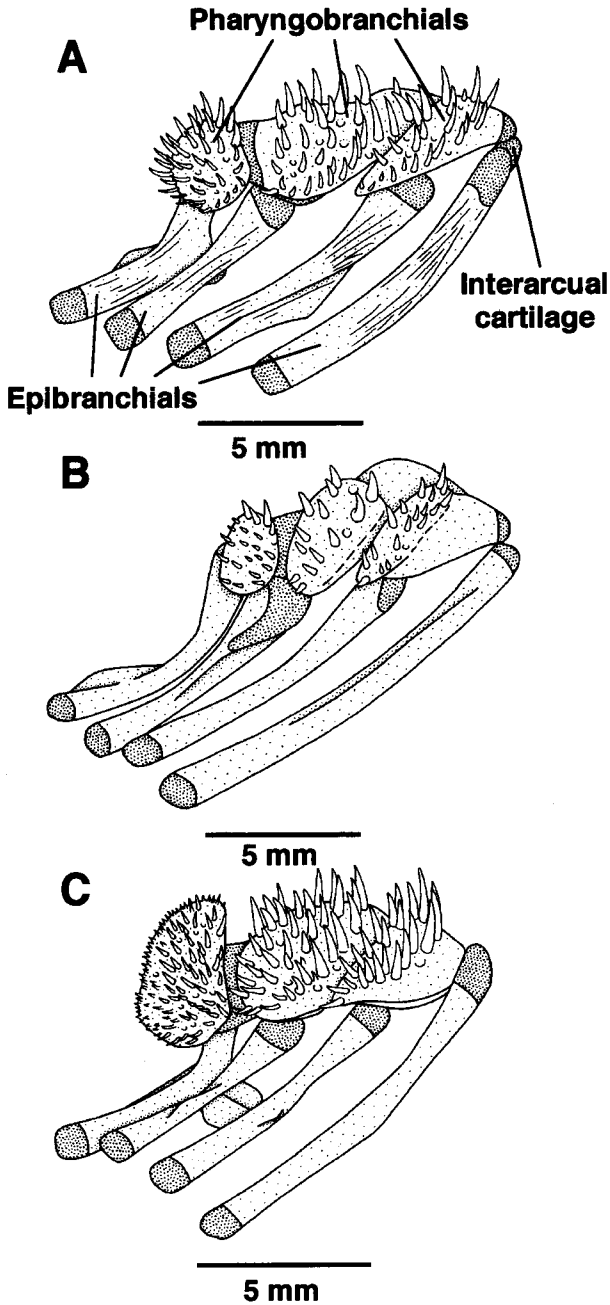
Fig. 10. Medial view of upper gill arch of *Anoplopoma fimbria* (cottoid lineage), HUMZ 130803, 240 mm (A), *Bathymaster signatus* (Zoarcoidei), HUMZ uncat., 248 mm (B) and *Patagonotothen ramsayi* (Notothenioidei), HUMZ 30575, 211 mm (C).
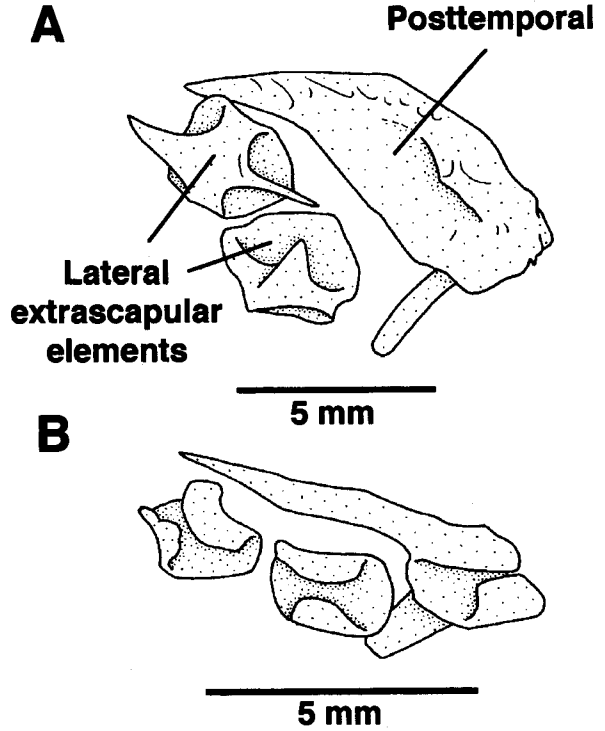

Fig. 11. Lateral view of lateral extrascapular elements and posttemporal of *Malacocottus zonurus* (cottoid lineage), HUMZ 83016, 158 mm (A) and *Eumesogrammus praecisus* (Zoarcoidei), HUMZ 103295, 173 mm (B).

tionships (Fig. 5, Table 1). On the other hand, the IG node of the scorpaenoid lineage is shown in this study to bear seven branchiostegal rays based on the relationships of the lineage (Fig. 4), although some members of the lineage have six or fewer rays (e.g., Aploactinidae and Congiopodidae) (Matsubara, 1943; Ishida, 1994; pers. obs.).

CS 3. Absence of a toothed plate on third epibranchial (Fig. 10).—Shinohara (1994) recognized the

absence of a toothed plate on the third epibranchial as a synapomorphy of the cottoid lineage, although the plate is present in the hexagrammid *Ophiodon* and hemitripterid *Hemitripterus villosus* (Yabe, 1985; Shinohara, 1994). Shinohara's assumption was supported here by an analysis of toothed plate evolution in the cottoid lineage (Table 1), based on its phylogenetic relationships (Fig. 5). Imamura (1996) used this derived character (his character 27-1), which he found in several taxa (e.g., *Hypodytes*, *Inimicus*, *Minous*, *Erisphex* and Peristediidae), in a phylogenetic analysis of the scorpaenoid lineage, but he assumed that it was not synapomorphous for the lineage. Thus, the IG node of the scorpaenoid lineage has the third epibranchial with a toothed plate. The derived character is also recognized in many perciform suborders (e.g., Zoarcoidei, Notothenioidei, except for Bovichthyidae, Blennioidei and the trachinoids Trichodontidae, Pinguipedidae and Uranoscopidae) (Iwami, 1985; Anderson, 1994; pers. obs.).

CS 4. Lateral extrascapular comprised of two elements (Figs. 11-12).—In the cottoid lineage, five morphotypes of lateral extrascapular occur: (1) the latter was comprised of a single element with three sensory openings on the right side of a specimen of zaniolepidoid *Oxylebius* (CAS 45609) and also in Hexagrammoidei, except for *Ophiodon*, and cottoid

A

Posttemporal

Lateral extrascapular elements
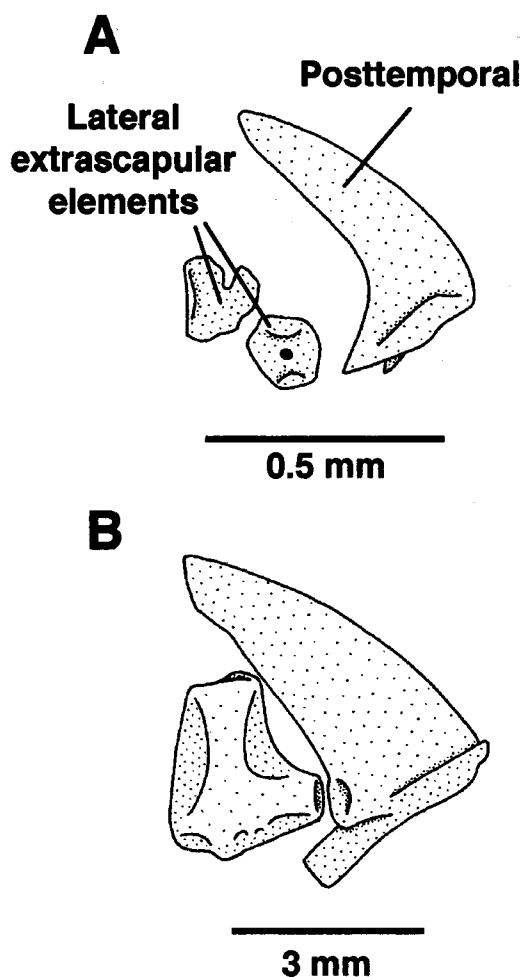
0.5 mm

B

3 mm

Fig. 12. Lateral view of lateral extrascapular elements and posttemporal of *Pterois volitans* (scorpaenoid lineage), HUMZ-L 6887, 11.0 mm (A) and NSMT-P 54350, 93 mm (B).

Rhamphocottidae, Agonidae and the hemitripterid *Hemitripterus bolini*; (2) two elements (horizontal and longitudinal tubes) with two sensory openings, respectively, in Anoplopomatoidei, Zaniolepidoidei, except on the right side of a specimen of *Oxylebius* (CAS 45609), the hexagrammoid *Ophiodon*, cottoid Ereuniidae, the psychrolutids *Dasycottus* and *Eurymen*, Hemitripteridae, except for *Hemitripterus bolini*, and Cottidae (Fig. 11A); (3) a single horizontal element with two openings in Psychrolutidae, except for *Dasycottus* and *Eurymen*; and (4) a single longitudinal element with two openings or (5) no elements in Cyclopteroidea (Yabe, 1985; Kido, 1988; Kanayama, 1991; Shinohara, 1994; pers. obs.). The lateral extrascapular is a single element with three sensory openings in typical percoids (Sasaki, 1989; pers. obs.). In addition, the ontogenetic development of the lateral extrascapular in the scorpaenoid *Pterois volitans* is characterized by two elements that develop initially (by 11.0 mm SL) and their subsequent fusion into a single bone with three openings (in adults)

(Fig. 12). Therefore, it can be interpreted that a lateral extrascapular comprising a single element with three openings is the primitive character, and the other four conditions are derived characters. It was inferred that the IG node of the cottoid lineage is characterized by the lateral extrascapular comprising two elements (characters unordered) (Table 1). On the other hand, the IG node of the scorpaenoid lineage was inferred as having a single lateral extrascapular with three openings, owing to the present analysis of the lateral extrascapular evolution, although some members have the alternate conditions (e.g., *Inimicus*, *Minous* and *Erisphex*, having a single horizontal element with two openings). Two separate lateral extrascapulars are also present in some perciform suborders (e.g., Zoarcoidei, except for the stichaeid *Lumpenella* with no elements and the zoarcid *Zoarces* with a single element with three openings, some notothenioids and trachinoid Trichodontidae) (Eakin, 1981; pers. obs.) (Fig. 11B).

CS 5. Absence of supraneurals.—Three supraneurals constitute the basic condition in percoids (Johnson, 1980, 1984; Sasaki, 1989; pers. obs.), the absence of such being regarded as a synapomorphy of the cottoid lineage (see also Shinohara, 1994), the single supraneural in *Ophiodon* being considered a reversal (Table 1). The number of supraneurals at the IG node of the scorpaenoid lineage was equivocal, being either zero or one, owing to the presence of two supraneurals in *Parabembras*, one in Sebastidae (*sensu* Ishida, 1994 minus *Plectrogenium*), the scorpaenid *Pontinus*, and setarchid *Setarches*, and a single specimen of *Bembras* (HUMZ 49409), and none in remaining taxa (ordered as two-one-zero). Supraneurals are absent in several perciform suborders (e.g., Zoarcoidei, Notothenioidei and Blennioidei) (Makushok, 1958; Anderson, 1994; pers. obs.).

CS 6. Dorsal pterygiophores arranged singly in each interneural space.—In the percoids, two major patterns exist for the dorsal-pterygiophore insertion: two pterygiophores inserted into a space between the second and third neural spines (e.g., Sparidae); and two between the third and fourth neural spines (e.g., Serranidae) (Johnson, 1984; pers. obs.). Shinohara (1994) inferred that dorsal pterygiophores arranged singly in each interneural space is a synapomorphy of the cottoid lineage, with a reversal in the anoplopomatoid *Erilepis*, which has two pterygiophores inserted into the space between the fifth and sixth neural spines. His assumption for this character was supported in this study, following an analysis of the dorsal pterygiophore arrangement evolution (Table 1). No member of the scorpaenoid lineage has the single pterygiophore arrangement (Ishida, 1994; Imamura, 1996; pers. obs.). However, pterygiophores are inserted singly into consec-

utive spaces between the neural spines in several perci-
form suborders, such as the Zoarcoidei, except for the
zoarcid *Lycodes tanakae*, Blennioidei and some tra-
chinoids (e.g., Springer, 1993; pers. obs.).

*CS 7. Absence of anal spines with robust pterygio-
phores.*—This character was considered as a synapomor-
phy of the cottoid lineage by Shinohara (1994). He
recognized a reversal in Zaniolepidoidei, with three anal
spines all having robust pterygiophores. This reversal
was also supported here; the IG node of the cottoid
lineage was inferred to lack anal spines with robust
pterygiophores (Table 1). Although both anal spines
and robust pterygiophores are absent in some members
of the scorpaenoid lineage (e.g., *Bembras*, Triglidae,
Peristediidae, Hoplichthyidae and Platycephalidae)
(Shinohara, 1994; pers. obs.), the IG node of the scor-
paenoid lineage, with anal spines supported by robust
pterygiophores, was here inferred to represent the primi-
tive condition. The derived character is also recognized
in several perciforms (e.g., all zoarcoids, notothenioids
and blennioids examined).

*CS 8. Adductor mandibulae section 3 located on
medial surface of levator arcus palatini* (Fig. 13).
—Adductor mandibulae section 3 (A3) is well devel-
oped and either separable from or somewhat continuous
with adductor mandibulae section 2 (A2) in the cottoid
lineage, except for the Liparidae, in which A3 is absent.
The posterior portion of A3 is located on the medial
surface of levator arcus palatini, except in Cyclopteridae,
in which A3 is not associated with the latter. In the
percoids, no adductor mandibulae elements are located
on the medial surface of levator arcus palatini. A3
located on the medial surface of levator arcus palatini
was assumed as a synapomorphy of the cottoid lineage
following an analysis of the evolution of the A3 condi-
tion (characters unordered) (Table 1). In the scor-
paenoid lineage, A3 is not clearly separated from A2,
forming a single large bundle, A2-3 (Ishida, 1994;
Imamura, 1996; pers. obs.). A2-3 is not usually locat-
ed on the medial surface of levator arcus palatini, its
posterior portion being partially or entirely located on
the medial surface of the muscle in the Apistidae,
Tetrarogidae, Synanceiidae, Congiopodidae, Pataecidae
and Gnathanacanthidae (Ishida, 1994; pers. obs.). It
was hypothesized here that the IG node of the scor-
paenoid lineage is characterized by the primitive condi-
tion, no parts of A2-3 being located on the medial
surface of levator arcus palatini. As noted by Ander-
son (1994), the similar condition of the A3 element in
the cottoid lineage was confirmed in all zoarcoids
examined in this study and is recognized as a
synapomorphy of Zoarcoidei. This condition was also
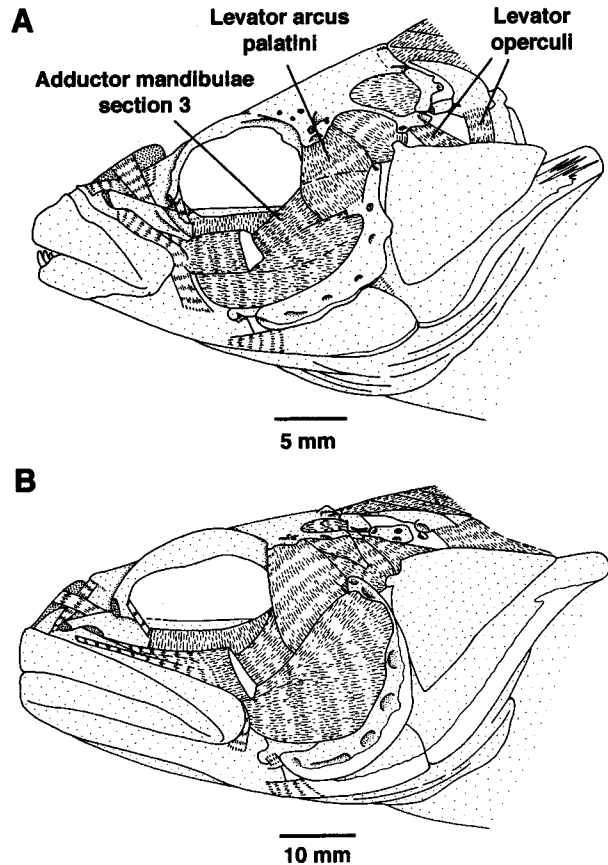found in some perciforms, such as the notothenioid

Fig. 13. Lateral view of head region of *Oxylebius pictus*
(cottoid lineage), CAS 2010183, 124 mm (A) and
Bathymaster signatus (Zoarcoidei), HUMZ uncat., 248
mm (B).

Channichthyidae, blennioids Tripterygiidae and Blen-
niidae, and the trachinoid Trichodontidae.

CS 9. Levator operculi comprised of two elements
(Fig. 13).—Levator operculi is comprised of two ele-
ments, originating from the pterotic and posttemporal,
respectively, in the cottoid lineage, except in Liparidae,
which has only a single element originating from the
pterotic (Yabe, 1985; pers. obs.). Typical percoids
have a single levator operculi originating from the
pterotic (Sasaki, 1989; Imamura, 1996, 2000). Accord-
ingly, the muscle composed of two elements can be
considered to be a derived character for the Scor-
paeniformes. The IG node of the cottoid lineage is
characterized by the derived condition, with a reversal in
Liparidae (Table 1). Although Imamura (1996) recog-
nized two levator operculi elements as a derived charac-
ter for several members of the scorpaenoid lineage (e.g.,
Pterois, *Scorpaenodes*, Apistidae, Tetrarogidae, Synan-
ceiidae and Aploactinidae), this feature is most likely
not synapomorphous for the scorpaenoid lineage.
Thus, the IG node of the scorpaenoid lineage has s single
levator operculi. The derived condition was also pres-
ent in all zoarcoids examined, as well as in Cheimar-

A   **Transversus dorsalis anterior**

B

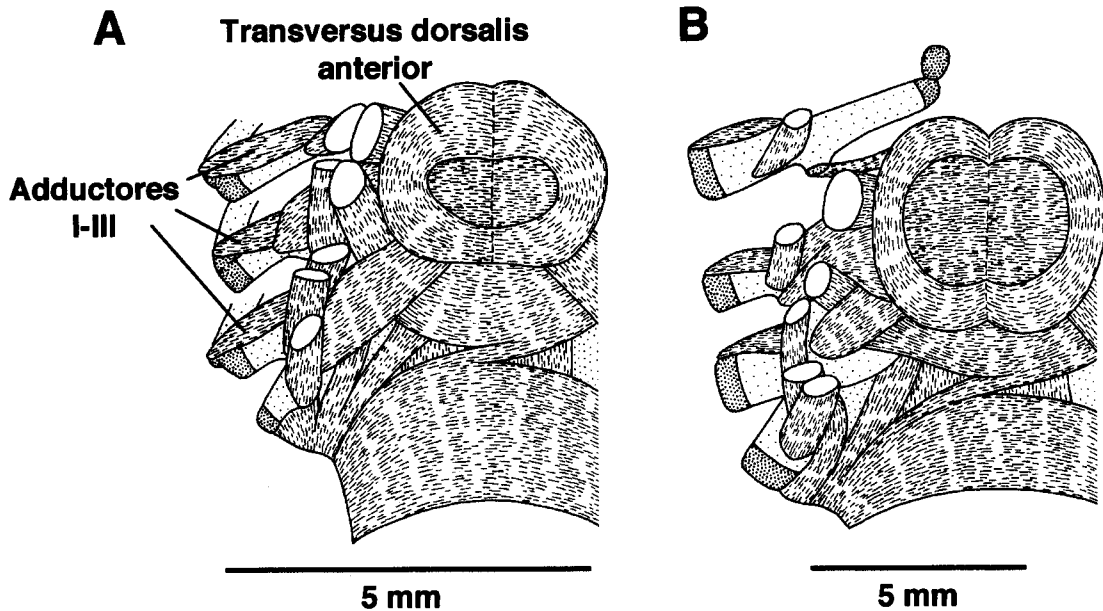**Adductores I-III**

5 mm   5 mm

Fig. 14. Dorsal view of upper gill arch muscles of *Hexagrammos lagocephalus* (cottoid lineage), HUMZ104878, 152 mm (A) and *Pholis nebulosa* (Zoarcoidei), HUMZ 92281, 201 mm (B).

richthyidae, Trichodontidae and Pinguipedidae, but was absent in Notothenioidei.

CS 10. Presence of circular element of transversus dorsalis anterior (Fig. 14).—The circular element of transversus dorsalis anterior has been recognized as a derived character in the percoids (Imamura, 2000). This condition was found in all members of the cottoid lineage, except for the Cyclopteroidea and several cottoids (e.g., the cottid *Enophrys* and psychrolutid *Malacocottus*). It was assumed, therefore, that the IG node of this lineage is characterized by the circular element (Table 1). The character is restricted only to Congiopodidae and Gnathanacanthidae in the scorpaenoid lineage, but cannot be inferred as a synapomorphy of this lineage, because those families are both deeply nested within the Scorpaenoidei (Ishida, 1994). Although all zoarcoids examined, except for the Stichaeidae and Zoarcidae, had the circular element of transversus dorsalis anterior, most perciforms, including Notothenioidei and Trachinoidei, typically did not have the element.

CS 11. Presence of adductores I-III (Fig. 14).—In the percoids examined, adductores I-III were absent in Percichthyidae and Serranidae, as well as in the symphysanodontid *Symphysanodon*, epigonid *Epigonus*, nemipterid *Parascolopsis* and terapontid *Terapon*. They are present in the callanthiid *Grammatonotus*, centrarchid *Lepomis*, gerreid *Gerres*, kuhliid *Kuhlia*, and sparoids *Evynnis* and *Lethrinus*. Although the typical condition for percoids could not be confirmed, the lower acanthomorphs examined in this study commonly did not have these elements. There-

fore, it can be considered that the presence of the adductores I-III is a derived character for both Perciformes and Scorpaeniformes. The members of the cottoid lineage, except for some cottoids (e.g., the hemitripterid *Hemitripterus*) and Cyclopteroidea, had distinct adductores I-III. It is inferred that the IG node of this lineage is characterized by the derived condition (Table 1). Among the scorpaenoid lineage, these elements occur only in Congiopodidae (Ishida, 1994; pers. obs.), the condition being a synapomorphy of the family, according to Ishida (1994). Adductores I-III were also recognized in other perciforms, such as the Zoarcoidei, notothenioids Nototheniidae and Channichthyidae, Blennioidei, and the trachinoids Cheimarrichthyidae and Pinguipedidae (pers. obs.).

CS 12. Absence of swimbladder.—All members of the cottoid lineage lack a swimbladder, the absence being regarded as a synapomorphy of the lineage (Table 1) (see also Imamura, 2000). The swimbladder condition at the IG node of the scorpaenoid lineage was considered as equivocal, owing to the absence of a swimbladder in *Helicolenus, Adelosebastes, Sebastolobus, Trachyscorpia, Scorpaena, Scorpaenopsis, Inimicus*, Plectrogeniidae, Parabembridae, Bembridae, Hoplichthyidae and most platycephalids, whereas it is present in others. A swimbladder is also absent in many perciform taxa, including Zoarcoidei and Notothenioidei (Iwami, 1985; pers. obs.).

CS 13. Extrinsic swimbladder muscle derived from epaxialis.—Imamura (1996, 2000) pointed out that the presence of the extrinsic muscle derived from the epaxial muscle is a synapomorphy of the cottoid lineage,

although the muscle in *Anoplopoma fimbria* is not well differentiated (Imamura, 1996). We also support his recognition (Table 1). The character has been found neither in the scorpaenoid lineage (Imamura, 1996) nor in the perciforms examined in this study, and is therefore regarded as an autapomorphy of the cottoid lineage.

Equivocal character (Fig. 10).—The first epibranchial is a simple, unbranched rod-like bone in the Anoplopomatoidei, whereas the bone has two processes in other scorpaeniforms, one (=uncinate process) being connected with the second pharyngobranchial and, primitively, the interarcual cartilage between them, and the other being associated with the first pharyngobranchial (if present). In the Anoplopomatoidei, *Anoplopoma* has the medial tip of the first epibranchial connected with the second pharyngobranchial, with a small cartilage, identical with the interarcual cartilage, present between them (but cartilage and first epibranchial fused in *Erilepis*) (Fig. 10A). Accordingly, it is regarded that the uncinate process is retained and the other process, associated with the first pharyngobranchial, absent in the Anoplopomatoidei. The condition of the first epibranchial at the IG node of the cottoid lineage was inferred as being equivocal after an analysis

of epibranchial evolution. In the Perciformes, such a condition as in the Anoplopomatoidei is restricted only to the Zoarcoidei, Notothenioidei, and the trachinoids Creediidae, Leptoscopidae and Percophidae (e.g., Iwami, 1985; Rosen and Patterson, 1990; Anderson, 1994; pers. obs.) (Fig. 10B, C). Therefore, this character can be interpreted as a rare derived condition among the Perciformes and Scorpaeniformes.

Polyphyly of the Order Scorpaeniformes

In the recent past, monophyly for the Scorpaeniformes has been supported by two derived characters, the presence of a suborbital stay and a parietal sensory canal. In this study, however, we concluded that monophyly of the scorpaenoid lineage is supported by a combination of four synapomorphies and that of the cottoid lineage by a combination of 13 synapomorphies. At the same time, however, we recognized that most of these same characters are also found in many perciform taxa. We treated two putative synapomorphies of the Scorpaeniformes as characters without *a priori* weighting, and searched taxa presumably closely related to the scorpaenoid and cottoid lineages, parsimoniously, if
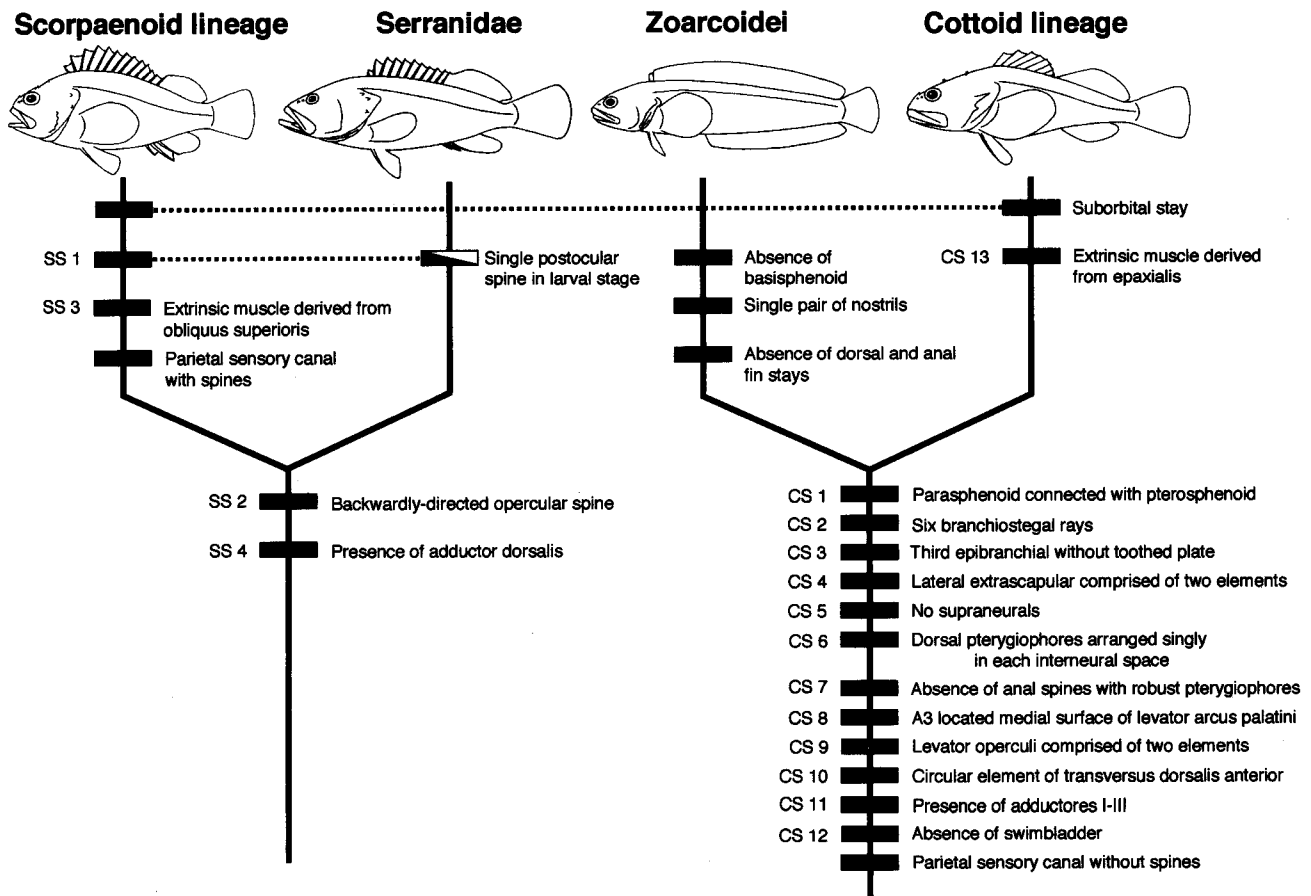

Fig. 15. Proposed phylogenetic relationships of the former Scorpaeniformes and related taxa.

such taxa exist. As a result, we concluded that the scorpaenoid lineage and family Serranidae had two synapomorphies (SS 2 and 4), and the cottoid lineage and suborder Zoarcoidei bore 12 synapomorphies (CS 1-12). In addition, the IG node of the cottoid lineage and most zoarcoids commonly had a spineless parietal sensory canal. No other taxa, having many derived characters shared with the scorpaenoid and cottoid lineages, were recognized in this study.

Conflicting hypotheses of monophyly for the Scorpaeniformes on one hand, and that for the scorpaenoid lineage plus the Serranidae on the other are each supported by two unrelated derived characters (presence of a suborbital stay and a parietal sensory canal vs. presence of a backwardly-directed opercular spine and an adductor dorsalis). It seems that both hypotheses are equivocal when considering these four characters by themselves, but no less than 12 synapomorphies (as well as a spineless parietal sensory canal; see discussion below) of the cottoid lineage and Zoarcoidei must be treated as homoplasies if the hypothesis of scorpaeniform monophyly is accepted. Because it is a more parsimonious interpretation to recognize a close relationship between the scorpaenoid lineage and Serranidae, and the cottoid lineage and Zoarcoidei, respectively, rather than to link the scorpaenoid and cottoid lineages as a monophyletic group based on two derived characters, we propose that the order Scorpaeniformes is a polyphyletic group (Fig. 15). We conclude further that the suborbital stay and the bony parietal structure supporting the sensory canal are derived features acquired independently in the scorpaenoid and cottoid lineages (Fig. 15).

The close relationships of the scorpaenoid lineage and Serranidae, and the cottoid lineage and Zoarcoidei, are each discussed below.

Relationship of scorpaenoid lineage and Serranidae

As concluded above, the scorpaenoid lineage is supported by a combination of four synapomorphies, including a single autapomorphy, presence of the extrinsic swimbladder muscle derived from obliquus superioris (SS 3). Among these synapomorphies of the scorpaenoid lineage, Serranidae has two synapomorphies, presence of a backwardly-directed opercular spine (SS 2) (Fig. 9) and presence of a caudal muscular element, the adductor dorsalis (SS 4). Johnson (1983) redefined the family Serranidae on the basis of four derived characters, the presence of three opercular spines (additional lowermost spine crossing the subopercle), and the absence of the posterior uroneural, procurrent spur and inter-hemal spine cartilage of the fourth preural centrum (CIHPU4 *sensu* Fujita, 1990). He regarded the first character as

the most important supporting the monophyly of the family. All four characters are also found in most members of the scorpaenoid lineage, the condition of the opercular spine, in particular, being consistent with a synapomorphy of the scorpaenoid lineage (SS 2), although the other three characters are also found in the cottoid lineage (Johnson, 1975; Fujita, 1990; pers. obs.). Although some members of the genus *Sebastes* (*S. owstoni* and *S. oblongus*) have CIHPU4, a distinct CIHPU4 condition has not been recognized in *S. matsubarae* and *S. thompsoni* (Fujita, 1990; pers. obs.). The analysis of CIHPU4 evolution revealed that the IG node of the scorpaenoid lineage was not characterized by CIHPU4, a reversal having occurred among *Sebastes*. In addition to these characters, a Type 1 epaxial muscle (*sensu* Mooi and Gill, 1995) is also shared by the scorpaenoid lineage and Serranidae, although it is also recognized in most members of the cottoid lineage and in many perciforms (Mooi and Gill, 1995).

The adductor dorsalis was found in all of the serranids examined, except *Niphon* and *Diploprion*. It was inferred by Baldwin and Johnson (1993) that the latter genera are nested within the family, the subfamilies Serraninae and Anthiinae, having the adductor dorsalis, being initially and secondarily branched off from other serranids, respectively. Therefore, judging from serranid relationships, it is reasonable to consider that the IG node of this family is characterized by the adductor dorsalis, the muscle having been secondarily lost in *Niphon* and *Diploprion*.

As pointed out by Johnson (1983), the trachinoid Trachinidae bears all four synapomorphies of Serranidae. However, this family has only a single synapomorphy of the scorpaenoid lineage, presence of a backwardly-directed opercular spine (SS 2) (Johnson, 1983; Watson et al., 1984; pers. obs.). Pietsch (1989) and Pietsch and Zabetian (1990), while considering the phylogenetic relationships of the Trachinoidei, regarded the Trachinidae and Uranoscopidae as sister families based on nine shared derived characters. In addition to these synapomorphies, the sister relationship of the Trachinidae and Uranoscopidae was supported in this study by a single autapomorphic character, the lateral and medial aspects of the two lower actinosts being expanded anteriorly and sandwiching the coracoid. A backwardly-directed opercular spine and adductor dorsalis are absent in Uranoscopidae (Pietsch, 1989; pers. obs.). Accordingly, we concluded that the Trachinidae does not have a close affinity with the scorpaenoid lineage or with the Serranidae, the former family having acquired the opercular spine independently.

Thus, the highly possible hypothesis, monophyly of the scorpaenoid lineage and Serranidae, is proposed on

the basis that they share two scorpaenoid-lineage synapomorphies (SS 2 and 4) and three reductive serranid synapomorphies (absence of the posterior uroneural, procurrent spur and CIHPU4) and a Type 1 epaxial muscle.

The scorpaenoid lineage has a single postocular spine in the larval stage (SS 1), which is consistent with a putative synapomorphy of the serranid subfamilies Anthiinae and Epinephelinae, as shown by Baldwin and Johnson (1993). Recognition of a sister relationship of the scorpaenoid lineage and Serranidae implies that the spine is a synapomorphy of the scorpaenoid lineage and Serranidae, owing to the secondary reduction in the subfamily Serraninae, or, equally likely, that the character is a synapomorphy of the scorpaenoid lineage, and also of the Anthiinae plus Epinephelinae. On the other hand, it is also possible that the scorpaenoid lineage and Anthiinae plus Epinephelinae are a monophyletic group supported by the larval spine condition. The family Serranidae must be recognized as a paraphyletic group in the last case, whereas the monophyly of the scorpaenoid lineage is consistently supported by three synapomorphies (SS 3, and the homoplasic suborbital stay and parietal sensory canal with spines). A comprehensive phylogenetic analysis of the scorpaenoid lineage and Serranidae is a necessary "next step".

Relationship of cottoid lineage and Zoarcoidei

According to this study, the monophyly of the cottoid lineage is supported by a combination of 13 synapomorphies, including a single autapomorphy, presence of the extrinsic muscle derived from the epaxialis (CS 13). Following a comparison of these characters with those of percomorph taxa, we consider the cottoid lineage to have a sister relationship with the suborder Zoarcoidei.

Anderson (1994) considered the Zoarcoidei to be a monophyletic group, owing to three synapomorphies: (1) loss of the basisphenoid; (2) a single pair of nostrils; and (3) the medial portion of the adductor mandibulae section 2-3 (A2-3) extending medial to levator arcus palatini. In addition, we recognized another eight derived characters found in all zoarcoids examined, regarding them as synapomorphies of the suborder (see below). We therefore agree with Anderson's (1994) conclusion that the suborder is monophyletic. The last zoarcoid synapomorphies of Anderson (1994) is considered here to be similar to the condition of adductor mandibulae section 3 (A3) of the cottoid-lineage synapomorphy (CS 8). Among our eight synapomorphies, the following six synapomorphies were also consistent with the cottoid-lineage synapomorphies: (1) absence of a toothed plate on the third epibranchial (CS 3) (Fig. 10B); (2) absence of supraneurals (CS 5); (3)

absence of anal spines with robust pterygiophores (CS 7); (4) levator operculi comprised of two elements (CS 9) (Fig. 13B); (5) presence of adductores I-III (CS 11) (Fig. 14B); and (6) absence of the swimbladder (CS 12). As for the two remaining synapomorphies of the Zoarcoidei, the first epibranchial with a single process associated medially with the second pharyngobranchial (Fig. 10B) is regarded as an equivocal character of the cottoid lineage, and the absence of dorsal and anal fin stays is not a synapomorphy of the cottoid lineage.

Although other cottoid-lineage synapomorphies were not commonly found in all zoarcoids examined here, we analyzed the IG node condition of each character in the suborder. Anderson (1994) regarded that the Bathymasteridae initially branched off from the other zoarcoids, on the basis of three synapomorphies (scales minute, cycloid, embedded or absent; pelvic bone small, rod-like or absent; and pelvic fin absent or reduced). In this study, an additional derived character, absence of a pelvic fin muscle (extensor proprius), was recognized in all zoarcoids, except the Bathymasteridae. Accordingly, we follow Anderson's (1994) phylogenetic assessment of the Zoarcoidei (Fig. 16), although the relationships among the other families remain unresolved. Following Anderson's (1994) proposal, we considered whether or not the IG node of the Zoarcoidei was characterized by the remaining synapomorphies of the cottoid lineage. The following five characters at the IG node of the Zoarcoidei were consistent with the synapomorphies of the cottoid lineage: (1) parasphenoid connected with the pterosphenoid (CS 1); (2) six branchiostegal rays (CS 2) (ordered as three-four-five-
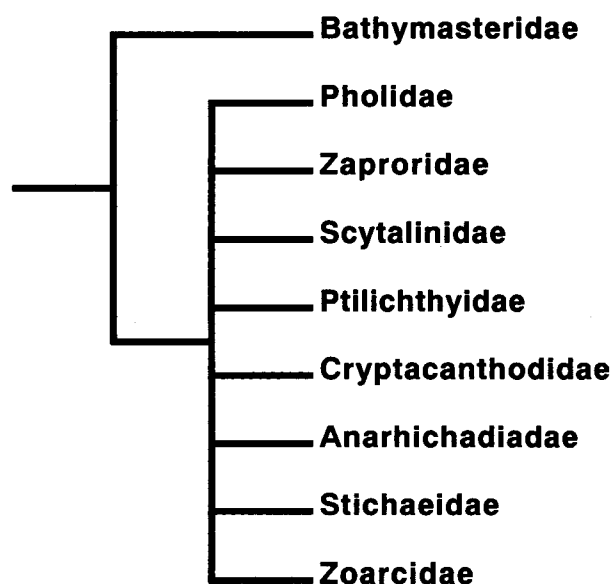

Fig. 16. Phylogenetic relationships of the suborder Zoarcoidei based on Anderson (1994).

Table 2. Characters in nine families among the suborder Zoarcoidei and inferred ingroup node of the suborder.

Taxa and node	Characters												
	1	2	3	4	5	6	7	8	9	10	11	12	13
INGROUP NODE	+	6	−	2	0	+	−	+	2	+	+	−	−
Bathymasteridae	+	6	−	2	0	+	−	+	2	+	+	−	−
Pholidae	+	5/6	−	2	0	+	−	+	2	+	+	−	−
Zaproridae	−	6	−	2	0	+	−	+	2	+	+	−	−
Scytalinidae	?	6	?	?	?	?	?	?	?	?	?	?	?
Ptilichthyidae	+	3/5/6	?	?	?	?	?	?	?	?	?	?	?
Cryptacanthodidae	?	6	?	?	?	?	?	?	?	?	?	?	?
Anarhichadidae	+	6/7	−	2	0	+	−	+	2	+	+	−	−
Stichaeidae	+	6	−	0/2	0	+	−	+	2	−	+	−	−
Zoarcidae	+	4/5/6/7/8	−	1/2	0	+/−	−	+	2	−	+	−	−

Data mainly from Makushok (1958), McAllister (1968), Yatsu (1985), Anderson (1994) and present study. Question marks indicate data unavailable. Character numbers and slashes as in Table 1.

six-seven-eight); (3) lateral extrascapular comprised of two elements (CS 4) (unordered) (Fig. 11B); (4) dorsal pterygiophores arranged singly in each interneural space (CS 6); and (5) presence of a circular element of the transversus dorsalis anterior (CS 10) (Fig. 14B) (Table 2). In addition, the IG node of the cottoid lineage and that of Zoarcoidei are inferred commonly having the parietal sensory canal without spines (Figs. 3, 6B), owing to an analysis of the sensory canal evolution in these groups based on these relationships (Figs. 5, 16). Accordingly, the IG nodes of the cottoid lineage and Zoarcoidei share 13 derived characters in total.

Therefore, we concluded that the cottoid lineage and Zoarcoidei together form a monophyletic group designated by 13 synapomorphies (CS 1-12 plus the parietal sensory canal without spines), and further that they share a sister relationship, each with their own synapomorphies: presence of the extrinsic swimbladder muscle derived from the epaxialis (CS 13) and homoplasic suborbital stay in the cottoid lineage; and presence of a single pair of nostrils, and absence of a basisphenoid and dorsal and anal fin stays in the Zoarcoidei (vs. two pairs of nostrils, and basisphenoid and stays present in typical percoids; pers. obs.).

Nelson (1994) noted that the Notothenioidei and Zoarcoidei might be closely related, with both having some affinity with the Trachinoidei. Subsequently, Stepien et al. (1997) indicated a sister relationship of the Notothenioidei and Zoarcoidei based on an analysis of mitochondrial 12S rDNA. Hastings (1993) supported the monophyly of the Notothenioidei, recognizing the following four synapomorphies: (1) absence of the swimbladder; (2) presence of a single pair of nostrils; (3) presence of three actinosts; and (4) posterior pleural ribs floating. Among them, the first character is

consistent with a synapomorphy of the cottoid lineage (CS 12) and also that of the Zoarcoidei. In addition, we found another five derived characters in all of the notothenioids examined here: (1) absence of supraneurals; (2) absence of anal spines with robust pterygiophores; (3) cartilages on the anterior tip of the pelvis fused on both sides (vs. not fused in typical percoids, see Imamura, 1996); (4) posterior portion of the pelvis cartilaginous (vs. not cartilaginous) (see Iwami, 1985: figs. 92-95); and (5) first epibranchial with a single process associated medially with the second pharyngobranchial (Fig. 10C). Therefore, we also support the monophyly of the Notothenioidei. Of these five characters, the first two agree with the cottoid-lineage synapomorphies (CS 5 and 7). However, the Notothenioidei lacks two synapomorphies of the cottoid lineage and Zoarcoidei: levator operculi comprised of two elements (CS 9) (vs. only a single element in Notothenioidei) and presence of a circular element of transversus dorsalis anterior (CS 10) (absent). In addition, a derived character, A3 located on the medial surface of levator arcus palatini (CS 8), is absent in Bovichthyidae and Nototheniidae, which have the primitive condition (A3 not located on the medial surface of that muscle). However, CS 8 is found in the Channichthyidae. Although information on myological characters is particularly limited in this suborder, the Channichthyidae has been inferred to be nested within the suborder (e.g., Eakin, 1981; Iwami, 1985; Eastman, 1991; Bargelloni et al., 2000), thus CS 8 in the family can be assumed to be independently derived. The remaining synapomorphies of the cottoid lineage are present or absent among the Notothenioidei (e.g., Eakin, 1981; Iwami, 1985; pers. obs.). We consider the Zoarcoidei to be more closely related to the cottoid lineage than the latter is to

the Notothenioidei.

On the other hand, the last notothenioid synapomorphy listed above (first epibranchial with a single process associated medially with the second pharyngobranchial) is also present in the Zoarcoidei (Anderson, 1994; pers. obs.) (Fig. 10B). A rare derived character among Perciformes, this character is found in the Anoplopomatoidei among the cottoid lineage (Fig. 10A). In addition, the suborder Notothenioidei was inferred as being closely related to the Zoarcoidei by Stepien et al. (1997). Therefore, it is probable that the Notothenioidei is a sister group for a monophyletic group including the cottoid lineage and Zoarcoidei. Acceptance of this hypothesis recognizes that a monophyletic group comprising the cottoid lineage, Zoarcoidei and Notothenioidei is supported by the first epibranchial with a single process being associated medially with the second pharyngobranchial (and also CS 5, 7 and 12), the presence of two first epibranchial processes in the monophyletic Zaniolepidoidei, Hexagrammoidei and Cottoidei (see Shinohara, 1994) being regarded as a reversal.

Nelson (1994) provisionally recognized 13 families in the suborder Trachinoidei, although Mooi and Johnson (1997) cast doubt on the monophyly of this suborder as tentatively proposed by Pietsch and Zabetian (1990). Mooi and Johnson (1997) subsequently moved the Champsodontidae from the suborder to their Scorpaenoidei. Our examination of these families (except Pholidichthyidae) showed none to have (at least) a cottoid-lineage synapomorphy, a circular element of transversus dorsalis anterior (CS 10). In addition, none of the trachinoid families (except Trachinidae and Uranoscopidae) shared the parasphenoid-pterosphenoid connection (CS 1). The Trichodontidae has the bony parietal structure for the sensory canal without spines (Mooi and Johnson, 1997; pers. obs.), but has neither the above-mentioned characters (CS 1 and 10), nor adductores I-III (CS 11) and the extrinsic swimbladder muscle derived from the epaxialis (CS 13).

Mooi and Gill (1995) suggested a possible relationship of the Scorpaeniformes (=their Scorpaenoidei) and Blennioidei, owing to the latter having the supratemporal sensory canal enclosed by the parietal (=the bony parietal structure for the sensory canal without spines in this study), although the canal in most tripterygiids is not enclosed by the parietal (i.e., sensory tube separated from parietal). The former character is consistent with a synapomorphy of the cottoid-lineage and Zoarcoidei. However, the Blennioidei examined in this study lacked at least four synapomorphies of the cottoid lineage (and also those of Zoarcoidei): (1) parasphenoid connected with pterosphenoid (CS 1) (the Blenniidae, inferred as

nested within the suborder by Stepien et al., 1993, has this connection); (2) lateral extrascapular comprised of two elements (CS 4) (single element with three openings in Blennioidei); (3) levator operculi comprised of two elements (CS 9) (single element); and (4) presence of a circular element of transversus dorsalis anterior (CS 10) (absent) (Springer, 1968 ; pers. obs.).

Finally, in an examination of numerous perciform taxa, none were found to have all synapomorphies of the cottoid lineage plus Zoarcoidei. For example, the benthic Gobioidei lacks CS 4, 6, 8, 10 and 12 (Miller, 1973; Birdsong et al., 1988; pers. obs.), the Callionymoidei lacks at least CS 6, 9 and 10 (Nakabo, 1983; pers. obs.) and the Gobiesocioidei lacks CS 6, 8, 9, and 10 (Hayashi et al., 1986; pers. obs.). All of these taxa further lack the parietal sensory canal.

Comparison with previous studies

Regan (1913: 169) stated "the most generalized family, Scorpaenidae, is not very remote from generalized percoids, such as the Serranidae." Freihofer (1963) examined the nervous system, ramus lateralis accessorius (RLA), of many teleostean fishes, finding that Scorpaenidae and Synanceiidae (Pattern 11) and Serranidae (Pattern 9) (except for Epinephelinae, in which the nerve is absent) commonly had an orbital entrance, a passage through the sphenotic crossing beneath the pterotic canal to its medial aspect. He also commented that the resemblance of Patterns 11 and 9 was consistent with the view of Regan (1913). The present study also supports Regan's (1913) hypothesis.

Freihofer (1963) demonstrated that Anoplopomatoidei was characterized by RLA Pattern 7(?), other members of the cottoid lineage having Pattern 12. Therefore, he recognized three morphological patterns of RLA in the Scorpaeniformes, commenting that the pattern in Anoplopoma resembled that in some other taxa, including Zoarcidae, although the bathymasterid genus Ronquilus had pattern 9 (Freihofer, 1963). Although Freihofer (1963) did not treat the Scorpaeniformes as a polyphyletic group, his RLA patterns were consistent with the subsequent findings of Quast (1965), who examined scorpaeniform osteological characters. Quast (1965) commented that the suborbital stay appeared to be the sole character uniting at least three seemingly distinct evolutionary lines (anoplopomatoid, scorpaenoid and cottoid) within the Scorpaeniformes (=his Cottoidei) and speculated that the suborbital stay had originated independently in at least two groups, the Scorpaeniformes being a polyphyletic assemblage. Such is supported in this study, which recognizes that the monophyletic scorpaenoid and cottoid lineages have acquired a suborbital stay indepen-
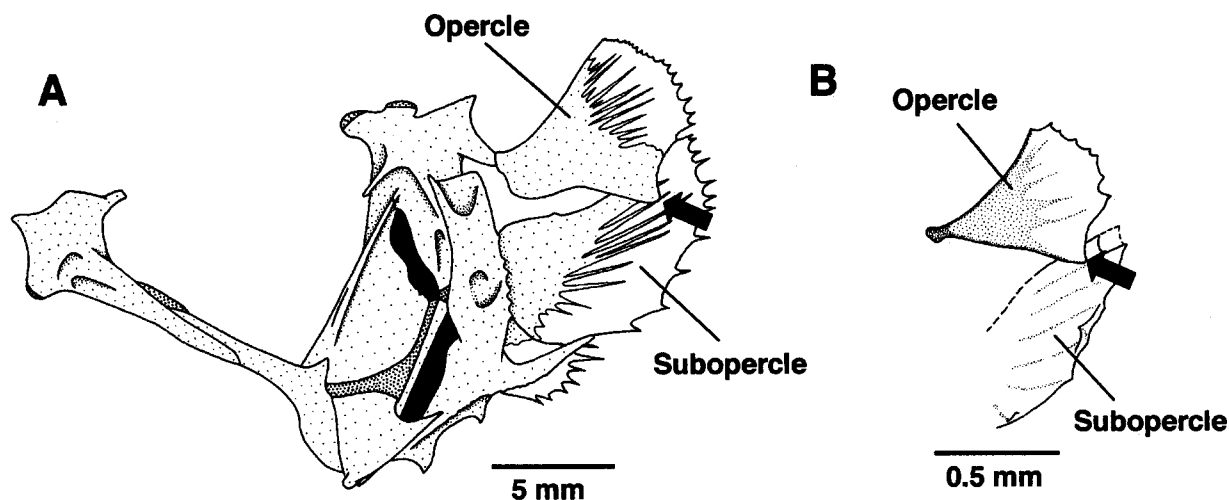
Fig. 17. Lateral view of suspensorium of *Champsodon guentheri*, HUMZ 79439, 88 mm SL (A) and *C.* sp. (larva), AMS I. 26192-002, 7.4 mm SL (B). Arrows indicate posteroventral angle of opercle.

dently. Shinohara (1994) supported the monophyly of the cottoid lineage, including Anoplopomatoidei, on the basis of seven synapomorphies, disagreeing with Quast's (1965) grouping. Shinohara's (1994) hypothesis is followed in this study, because Anoplopomatoidei bears all 13 synapomorphies supporting the monophyly of the lineage and Zoarcoidei.

Nelson (1994) recognized two further suborders, Dactylopteroidei (including a single family, Dactylopteridae) and Normanichthyioidei (including only Normanichthyidae), in his Scorpaeniformes. More recently, Mooi and Johnson (1997) included Champsodontidae in the Scorpaeniformes as *incertae sedis*. Among these taxa, Imamura (2000) proposed a new phylogenetic position of Dactylopteridae, while comments on the Champsodontidae and Normanichthyidae are provided below.

Champsodontidae.—The champsodontid opercle bears a serrated posterior margin, a prominent projection crossing the subopercle and a blunt projection anteroventrally (Fig. 17A). In a larval specimen of *Champsodon* sp. (AMS I. 96192-002, 7.4 mm), the opercle also had a posterior serration and prominent projection, but a blunt projection was not developed (Fig. 17B). Therefore, the projection crossing the subopercle can be identified in relation to the posteroventral angle of the opercle, the Champsodontidae lacking the opercular spine found in the scorpaenoid lineage and Serranidae (SS 2) (Fig. 9). In addition, Champsodontidae lacks two scorpaenoid-lineage and serranid synapomorphies, a single postocular spine in the larval stage (SS 1) and the adductor dorsalis (SS 4), whereas a serration present above the eye is a broadly recognized character of perciform larvae (e.g., Okiyama, 1988). The parietal sensory canal having a spine in the Champsodontidae is

the strongest evidence for Mooi and Johnson's (1997) hypothesis (above). However, the homology of the canal between Champsodontidae and the scorpaenoid lineage is unclear because two prominent parietal and nuchal spines are associated with the development of the canal in the scorpaenoid lineage (Fig. 7A) (see also Imamura and Yabe, 1998), whereas such spines are absent and serrations only present on the parietal in larval Champsodontidae (Okiyama, 1988; Mooi and Johnson, 1997; Leis and Carson-Ewart, 2000; pers. obs.), even though adult Champsodontidae has a prominent parietal spine (*sensu* Mooi and Johnson, 1997). Of 13 synapomorphies of the cottoid lineage and Zoarcoidei cited above, only two, absence of the supraneurals and anal spines with robust pterygiophores (CS 5 and 7), are recognized in the Champsodontidae (Mooi and Johnson, 1997; pers. obs.). Although character reversals or transformations may have occurred in the Champsodontidae, no evidence of such was found during the present study. Therefore, Champsodontidae is included neither in the monophyletic group composed of the scorpaenoid lineage and Serranidae, nor that of the cottoid lineage and Zoarcoidei.

Normanichthyidae.—The family Normanichthyidae, comprising a single species, *Normanichthys crockeri*, has been included in the order Scorpaeniformes on the basis of the former having a suborbital stay (e.g., Nelson, 1994). Yabe and Uyeno (1996), who considered normanichthyid osteological and myological characters, included Normanichthyidae in Scorpaeniformes as *incertae sedis* for lack of a better hypothesis of sister relationship. It is apparently not a member of the scorpaenoid lineage, because *Normanichthys* bears neither all four scorpaenoid-lineage synapomorphies (SS 1-4) nor bony parietal structure supporting the sensory

canal with spines (Washington et al., 1984a; Yabe and Uyeno, 1996; pers. obs.). Furthermore, Normanichthyidae differs from the cottoid lineage, because it does not have the following synapomorphies of the cottoid lineage and Zoarcoidei: (1) lateral extrascapular comprised of two elements (CS 4) (a single element with three openings in *Normanichthys*); (2) presence of a circular element of the transverses dorsalis anterior (CS 10) (absent); and (3) absence of the swimbladder (CS 12) (present). The absence of the extrinsic swimbladder muscle derived from the epaxialis in Normanichthyidae also supports the exclusion of the family from the cottoid lineage.

Taxonomic recommendations

The scorpaenoid lineage is considered here to be closely related group to the perciform family Serranidae (Fig. 15). Consequently, we recommend that the scorpaenoid lineage be placed within the order Perciformes, where it would appropriately constitute a newly defined perciform suborder, the Scorpaenoidei to contain a monophyletic group composed of the scorpaenoid lineage plus Serranidae, thus establishing two superfamilies, the Scorpaenoidea and Serranoidea.

The cottoid lineage is recognized here as the sister group of the perciform suborder Zoarcoidei (Fig. 15). We therefore further propose that this lineage be included in the Perciformes and provided a subordinal rank as the Cottoidei, to contain five superfamilies, the Anoplopomatoidea, Zaniolepidoidea, Hexagrammoidea, Cyclopteroidea and Cottoidea.

Materials Examined

We re-examined 162 "scorpaeniforms" listed in Yabe (1985) and Imamura (1996). Additional specimens, including larvae, are listed below. Normanichthyid specimens examined are listed in Yabe and Uyeno (1996).

Scorpaeniformes.—Agonidae: *Podothecus veternus*, HUMZ 58924 (153 mm). Aploactinidae: *Aploactis aspera*, HUMZ 37483 (55 mm). Congiopodidae: *Alertichthys blacki*, HUMZ 66621 (161 mm); *Congiopodus coriaceus*, HUMZ 91192 (142 mm). Cottidae: *Enophrys diceraus*, HUMZ uncat. (122 mm). Cyclopteridae: *Eumicrotremus birulai*, HUMZ 67949 (101 mm). Synanceiidae: *Choridactylus multibarbus*, CAS 15067 (71 mm); *Erosa erosa*, HUMZ 64250 (63 mm); *Synanceia horrida*, CAS 15073 (106 mm SL). Ereuniidae: *Marukawichthys ambulator*, HUMZ uncat. (123 mm). Gnathanacanthidae: *Gnathanacanthus goetzeei*, AMS I. 20188-001 (47 mm). Hemitripteridae: *Hemitripterus villosus*, HUMZ uncat. (101 mm). Liparidae: *Liparis*

agassizii, HUMZ 80745 (150 mm). Pataecidae: *Pataecus fronto*, AMS I. 38479-002 (110 mm). Psychrolutidae: *Malacocottus zonurus*, HUMZ 83016 (158 mm). Rhamphocottidae: *Rhamphocottus richardsonii*, HUMZ uncat. (59 mm). Scorpaenidae: *Pterois volitans*, NSMT-P 54350 (93 mm); *Taenianotus triacanthus*, USNM 106917 (60 mm). Sebastidae: *Sebastes matsubarae*, HUMZ 90303 (114 mm); *S. thompsoni*, HUMZ 92291 (156 mm). Setarchidae: *Ectreposebastes imus*, HUMZ 75112 and one uncatalogued specimen (2, 85-1,113 mm). Zaniolepididae: *Oxylebius pictus*, CAS 2010183 (124 mm).

Larval materials.—Anoplopomatidae: *Anoplopoma fimbria*, HUMZ-L (larval collection of HUMZ) 3774, 3779, 3784, 3787-3788 and 2 uncatalogued specimens (7, 16.6-34.8 mm, cleared and stained [CS]). Cottidae: *Porocottus allisi*, HUMZ-L 1178, 1180, 2700, 2732, 2913, 2995 (6, 8.9-16.5 mm, CS). Hexagrammidae: *Hexagrammos decagrammus*, HUMZ-L 2469, 2474-2475 (8, 15.4-33.7 mm, CS). Platycephalidae: *Suggrundus meerdervoortii*, HUMZ-L 6733-6743 (11, 12.9-35.5 mm, HUMZ-L 6734 and 6739 were cleared and stained). Scorpaenidae: *Pterois volitans*, HUMZ-L 6886-6887 (5, 3.8-11.0 mm, CS). Synanceiidae: *Inimicus japonicus*, HUMZ-L 4443-4445, 4448, 4451 (9, 4.2-10.1 mm, CS).

Comparative materials. *Beryciformes.*—Anoplogasteridae: *Anoplogaster cornuta*, HUMZ 40410 (72 mm). Berycidae: *Beryx splendens*, HUMZ 79840 (122 mm). Holocentridae: *Sargocentron diadema*, HUMZ 40258 (122 mm). Monocentrididae: *Monocentris japonica*, HUMZ 49798 (120 mm). Trachichthyidae: *Hoplostethus japonicus*, HUMZ 51824 (103 mm).

Champsodontidae.—*Champsodon guentheri*, HUMZ 79439 (117 mm); *C. longipinnis*, HUMZ 149645 (114 mm); *C. snyderi*, HUMZ 109313 (88 mm); *C. spp.*, AMS I. 25470-013, I. 26192-002 (3 larvae, 3.7-7.4 mm, CS).

Gasterosteiformes.—Gasterosteidae: *Gasterosteus aculeatus aculeatus*, HUMZ 98965 (73 mm).

Perciformes.—Ammodytidae: *Ammodytes personatus*, HUMZ 131165 (167 mm). Anarhichadidae: *Anarhichas orientalis*, HUMZ 33552 (184 mm). Bathymasteridae: *Bathymaster signatus*, HUMZ 46589 (250 mm) and one uncatalogued specimen (248 mm). Blenniidae: *Istiblennius enosimae*, HUMZ 63170 (90 mm). Bovichthyidae: *Cottoperca gobio*, HUMZ 82217 (174 mm). Chaenopsidae: *Neoclinus bryope*, NSMT-P 32728 (65 mm). Cheimarrichthyidae: *Cheimarrichthys fosteri*, USNM 198509 (87 mm). Channichthyidae: *Champsocephalus gunneri*, HUMZ 69281 (237 mm). Channidae: *Channa argus*, HUMZ 44272 (118 mm). Chiasmodontidae: *Chiasmodon boulengeri*, HUMZ 124516 (154 mm). Creediidae: *Limnichthys fasciatus*,

AMS I. 17363-002 (33 mm). Grammatidae: *Gramma loreto*, USNM 283741 (49 mm). Gobiesocidae: *Aspasmichthys ciconiae*, HUMZ uncat. (50 mm). Gobiidae: *Suruga fundicola*, HUMZ uncat. (66 mm). Labridae: *Halichoeres poecilopterus*, HUMZ uncat. (159 mm). Leptoscopidae: *Lesueurina platycephala*, AMS I. 15731-014 (45 mm). Notograptidae: *Notograptus guttatus*, AMS I. 200773003 (73 mm). Nototheniidae: *Patagonotothen ramsayi*, HUMZ 30575 (211 mm). Opistognathidae: *Opistognathus darwinensis*, USNM 328178 (43 mm). Percophidae: *Bembrops curvatura*, HUMZ 37322 (134 mm). Pholidae: *Pholis nebulosa*, HUMZ 92281 (201 mm). Pinguipedidae: *Parapercis multifasciata*, HUMZ 131744 (116 mm); *Pinguipes brasilianus*, UW 21232 (106 mm). Plesiopidae: *Plesiops caeruleolineatus*, HUMZ 37147 (57 mm). Stichaeidae: *Eumesogrammus praecisus*, HUMZ 103295 (173 mm); *Lumpenella longirostris*, HUMZ uncat. (244 mm). Trachinidae: *Trachinus draco*, USNM 198840 (114 mm). Trichodontidae: *Arctoscopus japonicus*, HUMZ 45194 (142 mm). Trichonotidae: *Trichonotus setiger*, AMS I. 34318-043 (54 mm). Tripterygiidae: *Enneapterygius etheostomus*, NSMT-P 45532 (37 mm). Uranoscopidae: *Uranoscopus bicinctus*, HUMZ 131756 (90 mm). Zaproridae: *Zaprora silenus*, HUMZ uncat. (204 mm). Zoarcidae: *Lycodes tanakae*, HUMZ 58127 (161 mm); *Zoarces gilli*, HUMZ 106561 (206 mm).

Polymixiiformes.—Polymixiidae: *Polymixia japonica*, HUMZ 79394 (146 mm).

Stephanoberyciformes.—Melamphaidae: *Poromitra crassipes*, HUMZ 124120 (114 mm).

A further 36 percoid species, including nine species in the family Dactylopteridae, were listed in Imamura (2000).

Acknowledgments

Literature cited

Anderson, M.E. (1994) Systematic and osteology of the Zoarcidae (Teleostei: Perciformes). *Ichthyol.*

Bull. J.L.B. Smith Inst. Ichthyol., (**60**), 1-120.

Baldwin, C.C., Johnson, G.D. (1993) Phylogeny of the Epinephelinae (Teleostei: Serranidae). *Bull. Mar. Sci.*, **52**, 240-283.

Bargelloni, L., Marcato, S., Zane, L., Patarnello, T. (2000) Mitochondrial phylogeny of notothenioids: a molecular approach to Antarctic fish evolution and biogeography. *Syst. Zool.*, **49**, 114-129.

Birdsong, R.S., Murdy, E.O., Pezold, F.L. (1988) A study of the vertebral column and medial fin osteology in gobioid fishes with comments on gobioid relationships. *Bull. Mar. Sci.*, **42**, 174-214.

Bolin, R.L. (1947) The evolution of the marine Cottidae with a discussion of the genus as a systematic category. *Stanford Ichthyol. Bull.*, **3**, 1-135.

Eakin, R.R. (1981) Osteology and relationships of the fishes of the Antarctic family Harpagiferidae (Pieces, Notothenioidei). *Biol. Antarc. Seas 9. Antarc. Res. Ser.*, **31**, 81-147.

Eastman, J.T. (1991) Evolution and diversification of Antarctic notothenioid fishes. *Amer. Zool.*, **31**, 93-109.

Eschmeyer, W.N. (1998) Part IV. Genera in a classification. pp. 2449-2499, Eschmeyer, W.N. (ed), *Catalog of fishes. Vol. 3*, Calif. Acad. Sci., San Francisco.

Freihofer, W.C. (1963) Pattern of the ramus lateralis accessorius and their systematic significance in teleostean fishes. *Stanford Ichthyol. Bull.*, **8**, 80-189.

Fujita, K. (1990) *The caudal skeleton of teleostean fishes* (in Japanese). Tokai Univ. Press, Tokyo.

Gill, T. (1888) On the classification of the mail-cheeked fishes. *Proc. U.S. Nat. Mus.*, **11**, 567-592.

Hallacher, L.E. (1974) The comparative morphology of the extrinsic gasbladder musculature in the scorpionfish genus *Sebastes* (Pisces: Scorpaeniformes). *Proc. Calif. Acad. Sci.*, **15**, 59-84.

Hastings, P.A. (1993) Relationships of the fishes of the perciform suborder Notothenioidei. pp. 99-107, Miller, R.G. (ed), *A history and atlas of the fishes of the Antarctic Ocean*, Foresta Institute, Carson City.

Hayashi, M., Hagiwara, K., Hayashi, H. (1986) Osteology of the cling fishes in Japan (Family: Gobiesocidae) (in Japanese). *Sci. Rep. Yokohama City Mus.*, (**34**), 39-66.

Imamura, H. (1996) Phylogeny of the family Platycephalidae and related taxa (Pisces: Scorpaeniformes). *Spec. Div.*, **1**, 123-233.

Imamura, H. (2000) An alternative hypothesis on the phylogenetic position of the family Dactylopteridae (Pisces: Teleostei), with a proposed new classification. *Ichthyol. Res.*, **47**, 203-222.

Imamura, H., Shinohara, G. (1998) Scorpaeniform fish phylogeny: an overview. *Bull. Nat. Sci. Mus. Tokyo Ser. A*, **24**, 185-212.

Imamura, H., Yabe, M. (1998) Osteological development of the lumpfish, *Inimicus japonicus* (Pisces: Scorpaeniformes). *Ichthyol. Res.*, **45**, 53-67.

Ishida, M. (1994) Phylogeny of the suborder Scorpaenoidei (Pisces: Scorpaeniformes). *Bull. Nansei Nat. Fish. Res. Inst.*, **27**, 1-112.

Iwami, T. (1985) Osteology and relationships of the family Channichthyidae. *Mem. Nat. Inst. Polar Res. Ser. E, Biol. Med. Sci.*, **36**, 1-69.

Johnson, G.D. (1975) The procurrent spur: an undescribed perciform caudal character and its phylogenetic implications. *Occas. Pap. Calif. Acad. Sci.*, (**121**), 1-23.

Johnson, G.D. (1980) The limits and relationships of the Lutjanidae and associated families. *Bull. Scripps Inst. Oceanog. Univ. Calif.*, **24**, 1-114.

Johnson, G.D. (1983) *Niphon spinosus*: a primitive epinepheline serranid, with comments on the monophyly and intrarelationships of the Serranidae. *Copeia*, **1983**, 777-787.

Johnson, G.D. (1984) Percoidei: development and relationships. pp. 438-447, Moser, H.G., Richards, W.J., Cohen, D.M., Fahay, M.P., Kendall Jr., A.W. and Richardson, S.L. (eds), *Ontogeny and systematics of fishes*, Allen Press Inc, Lawrence.

Johnson, G.D. (1993) Percomorph phylogeny: progress and problems. *Bull. Mar. Sci.*, **52**, 3-28.

Johnson, G.D., Patterson, C. (1993) Percomorph phylogeny: a survey of acanthomorphs and a new proposal. *Bull. Mar. Sci.*, **52**, 554-626.

Kanayama, T. (1991) Taxonomy and phylogeny of the family Agonidae (Pisces: Scorpaeniformes). *Mem. Fac. Fish. Hokkaido Univ.*, **38**, 1-199.

Kido, K. (1988) Phylogeny of the family Liparididae, with the taxonomy of the species found around Japan. *Mem. Fac. Fish. Hokkaido Univ.*, **35**, 125-256.

Leis, J.M., Crason-Ewart, B.M. (eds) (2000) *Fauna Malesiana handbook 2. The larvae of Indo-Pacific coastal fishes: an identification guide to marine larvae*. Brill, Leiden, Boston and Köln.

Leviton, A.E., Gibbs Jr., R.H., Heal, E., Dawson, C.E. (1985) Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia*, **1985**, 802-832.

Maddison, W.P., Maddison, D.R. (2000) *MacClade, ver. 4*. Sinauer Associates Inc, Sunderland.

Makushok, V.M. (1958) The morphology and classification of the northern blennioid fishes (Stichaenoidae, Blennioidei, Pisces) (in Russian). *Tr. Zool. Inst. Akad. Nauk. SSSR*, **25**, 3-129.

Mandrytsa, S.A. (2001) *Seismosensory system and classification of scorpionfishes (Scorpaeniformes: Scorpanoidei)* (in Russian). Perm State Univ. Press, Perm.

Matsubara, K. (1943) Studies on the scorpaenoid fishes from Japan. Anatomy, phylogeny and Taxonomy (I). *Trans. Sigenkagaku Kenkyusyo*, **1**, 1-170.

Matsubara, K., Ochiai, A. (1955) A revision of the Japanese fishes of the family Platycephalidae (the flatheads). *Mem. Coll. Agr. Kyoto Univ.*, (**68**), 1-109, 3 pls.

McAllister, D.E. (1968) Evolution of branchiostegals and classification of teleostome fishes. *Nat. Mus. Canada Bull.*, (**221**): i-xiv+1-239.

Miller, P.J. (1973) The osteology and adaptive features of *Rhyacichthys aspro* (Teleostei: Gobioidei) and the classification of gobioid fishes. *J. Zool., London*, **171**, 397-434.

Mooi, R.D., Gill, A.C. (1995) Association of epaxial musculature with dorsal-fin pterygiophores in acanthomorph fishes, and its phylogenetic significance. *Bull. Nat. Mus. Lond. (Zool.)*, **61**, 121-137

Mooi, R.D., Johnson, G.D. (1997) Dismantling the Trachinoidei: evidence of a relationship for the Champsodontidae. *Ichthyol. Res.*, **44**, 143-176.

Moser, H.G., Ahlstrom, E.H. (1978) Larvae and pelagic juveniles of blackgill rockfish, *Sebastes melanostomus*, taken in midwater trawls off southern California. *J. Fish. Res. Board. Can.*, **35**, 981-996.

Moser, H.G., Ahlstrom, E.H., Sandknop, E.M. (1977) Guide to the identification of scorpionfish larvae (family Scorpaenidae) in the eastern Pacific with comparative notes on species of *Sebastes* and *Helicolenus* form other ocean. *NOAA Tech. Rep. NMFS Circ.*, **402**, i-v+1-71.

Nakabo, T. (1983) Comparative osteology and phylogenetic relationships of the dragonets (Pisces: Callionymidae) with some thoughts of their evolutionary history. *Publ. Seto Mar. Biol. Lab.*, **28**, 1-73.

Neira, F.J. (1989) Larval development of the Australian devilfish, *Gymnapistes marmoratus* (Teleostei: Scorpaenidae). *Fish. Bull.*, **87**, 889-898.

Nelson, J.S. (1982) Two new south Pacific fishes of the genus *Ebinania* and contributions to the systematic of Psychrolutidae (Scorpaeniformes). *Can. J. Zool.*, **60**, 1470-1504.

Nelson, J.S. (1994) *Fishes of the world. Third edition*. John Wiley and Sons, New York.

Okiyama, M. (ed) (1988) *An atlas of the early stage fishes in Japan* (in Japanese). Tokai Univ. Press, Tokyo.

Pietsch, T.W. (1989) Phylogenetic relationships of trachinoid fishes of the family Uranoscopidae. *Copeia*, **1989**, 253-303.

Pietsch, T.W., Zabetian, C.P. (1990) Osteology and interrelationships of the sand lances (Teleostei: Ammodytidae). *Copeia*, **1990**, 78-100.

Quast, J.C. (1965) Osteological characteristics and affinities of the hexagrammid fishes, with a synopsis. *Proc. Calif. Acad. Sci. Ser. 4*, **31**, 563-600.

Regan, C.T. (1913) The osteology and classification of the teleostean fishes of the order Scleroparei. *Ann. Mag. Nat. Hist. Ser. 8*, **11**, 169-184.

Rosen, D.E., Patterson, C. (1990) On Müller's and Cuvier's concepts of pharyngognath and labyrinth fishes and the classification of percomorph fishes, with an atlas of percomorph dorsal gill arches. *Novitates*, **2893**: 1-57.

Sasaki, K. (1989) Phylogeny of the family Sciaenidae, with notes on its zoogeography (Teleostei, Perciformes). *Mem. Fac. Fish. Hokkaido Univ.*, **36**, 1-137.

Shinohara, G. (1994) Comparative morphology and phylogeny of the suborder Hexagrammoidei and related taxa (Pisces: Scorpaeniformes). *Mem. Fac. Fish. Hokkaido Univ.*, **41**, 1-97.

Springer, V.G. (1968) Osteology and classification of the fishes of the family Blenniidae. *Bull. U. S. Nat. Mus.*, **284**, 1-85, 11 pls.

Springer, V.G. (1993) Definition of the suborder Blennioidei and its included families (Pisces: Perciformes). *Bull. Mar. Sci.*, **52**, 472-495.

Starks, E.C. (1923) The osteology and relationships of the uranoscopoid fishes. *Stanford Univ. Publ. Univ. Ser. Biol. Sci.*, **3**, 258-290.

Stepien, C.A, Dixon, M.T., Hills, D.M. (1993) Evolutionary relationships of the blennioid fish families Clinidae, Labrisomidae and Chaenopsidae: congruence between DNA sequence and allozyme data. *Bull. Mar. Sci.*, **52**, 496-515.

Stepien, C.A., Dillon, A.K., Brooks, M.J., Chase, K.L., Hubers, A.N. (1997) The evolution of blennioid fishes based on an analysis of mitochondrial 12S rDNA. pp. 245-270, Kocher, T.D. and Stepien, C.A. (eds), *Molecular systematics of fishes*, Academic Press, San Diego.

Taranetz, A.Y. (1941) On the classification and origin of the family Cottidae. *Inst. Fish. Univ. British Columbia Mus. Contr.*, **5**, 1-28.

Ueno, T. (1970) *Fauna Japonica: Cyclopteridae (Pisces)*. Acad. Press Japan, Tokyo.

Washington, B.B., Moser, H.G., Laroche, W.A., Richards, W.J. (1984a) Scorpaeniformes: development. pp. 405-428, Moser, H.G., Richards, W.J., Cohen, D.M., Fahay, M.P., Kendall Jr., A.W. and Richardson, S.L. (eds), *Ontogeny and systematics of fishes*, Allen Press Inc, Lawrence.

Washington, B.B., Eschmeyer, W.N., Howe, K.M. (1984b) Scorpaeniformes: relationships. pp. 438-447, Moser, H.G., Richards, W.J., Cohen, D.M., Fahay, M.P., Kendall Jr., A.W. and Richardson, S.L. (eds), *Ontogeny and systematics of fishes*, Allen Press Inc, Lawrence.

Watson, W., Matarese, A.C., Stevens, E.G. (1984) Trachinoidea: development and relationships. pp. 554-561, Moser, H.G., Richards, W.J., Cohen, D. M., Fahay, M.P., Kendall Jr., A.W. and Richardson, S.L. (eds), *Ontogeny and systematics of fishes*, Allen Press Inc, Lawrence.

Wiley, E.O., Siegel-Causey, D., Brooks, D.R., Funk, V.A. (1991) *The compleat cladist. A primer of phylogenetic procedures*. Univ. Kansas, Mus. Nat. Hist., Lawrence.

Winterbottom, R. (1974) A descriptive synonymy of the striated muscles of the Teleostei. *Proc. Acad. Nat. Sci. Philad.*, **125**, 225-317.

Yabe, M. (1985) Comparative osteology and myology of the superfamily Cottoidea (Pisces: Scorpaeniformes), and its phylogenetic classification. *Mem. Fac. Fish. Hokkaido Univ.*, **32**, 1-130.

Yabe, M., Uyeno, T. (1996) Anatomical description of *Normanichthys crockeri* (Scorpaeniformes, *incertae sedis*: family Normanichthyidae). *Bull. Mar. Sci.*, **58**, 494-510.

Yatsu, A. (1985) Phylogeny of the family Pholididae (Blennioidei) with a redescription of *Pholis scopoli*. *Japan. J. Ichthyol.*, **32**, 273-282.