

Scorpaeniform Fish Phylogeny: An Overview

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Abstract The progress and present status of phylogenetic studies on the order Scorpaeniformes are reviewed by considering two major clades: the scorpaenoid lineage (Scorpaenoidei+Platycephaloidei) and the cottoid lineage (Anoplopomatoidei+Zanioleptoidei+Hexagrammoidei+Cottoidei). Continuing problems in scorpaeniform phylogeny are also outlined.

Key words: Scorpaeniformes, fishes, phylogeny, systematics, classification.

The order Scorpaeniformes, a member of the Acanthopterygii (Greenwood *et al.*, 1966; Lauder & Liem, 1983; Nelson, 1994), is characterized by a remarkable diagnostic character, the suborbital stay, formed by a posterior extension of the second suborbital (*sensu* Matsubara, 1943). Owing to this character, scorpaeniforms have been referred to as “mail-cheeked fishes.” The group includes more than 1,200 species, some, such as the cottoid abyssocottids and *Cottus* spp. inhabiting fresh water (Nelson, 1994). Depths inhabited by marine species range from shallow waters to 7,000 m (species of Liparidae) (Andriashev, 1955; Nelson, 1994). The order has been variously subdivided and classified by many investigators (Tables 1–4).

The first phylogenetic study of the Scorpaeniformes was presented by Gill (1888). Although his family-level relationships were unsubstantiated (Fig. 1), his methodology was based on apparent similarities, and relationships inferred subjectively by using characters such as head spines and condition of the dorsal fin ray. Subsequently, Matsubara (1943, 1955) and Washington *et al.* (1984 a) also provided comprehensive relationships of the order. Matsubara (1943) reconstructed phylogenetic relationships of his Scorpaenidae (=most similar to the recently-proposed Scorpaenoidei) on the basis of osteology, except for the jaws, gill arches and caudal skeleton, and the swimbladder and associated muscles. He also proposed relationships of the Scorpaeniformes, recognizing four major clades in the order: the Triglidae+Peristediidae+Dactylopteridae, which were derived initially from other groups; a second clade derived from a *Sebastes glaucus*-ancestor, such including generalized scorpaenids, such as *Sebastes glaucus*, plus the Anoplopomatidae and Hexagrammidae; a third clade derived from a *Plectrogenium*-ancestor, comprising the specialized scorpaenids, such as *Plectrogenium nanum*, plus the Bembridae, Platycephalidae and Ho-

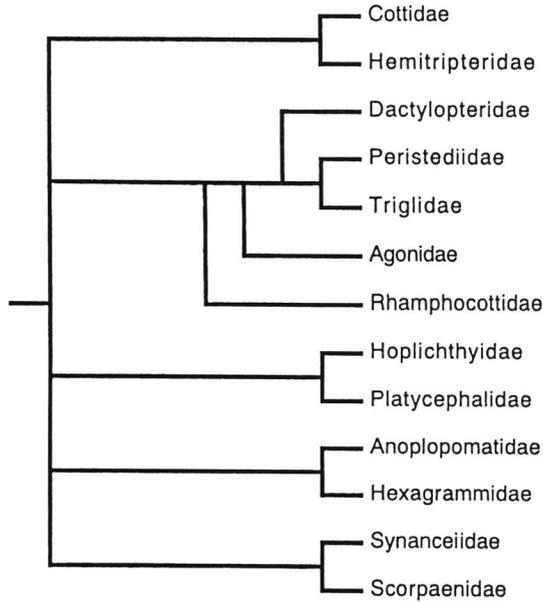


Fig. 1. Phylogeny of the order Scorpaeniformes, as proposed by Gill (1888).

plichthyidae; and a fourth clade containing the Agonidae, Cottidae, Cyclopteridae and Liparidae, all of which were derived from a *Setarches*-ancestor. Subsequently, Matsubara (1955) reworked his previously-proposed relationships of *Bembras*, Platycephalidae and Hoplichthyidae, based on the results of Matsubara & Ochiai (1955), although his other earlier-proposed relationships were retained (Fig. 2). Washington *et al.* (1984 a) followed much of Matsubara's (1943, 1955) proposals, presenting a revised phylogenetic hypothesis based on the latter's original osteological data, and also considered schemes proposed after Matsubara (1955).

The studies of Matsubara (1955) and Washington *et al.* (1984 a) were based mostly on that of Matsubara (1943), which used a precladistic methodology. However, the need for a more objective basis for phylogenetic hypotheses has become apparent following the initial proposal of cladistic methodology and its subsequent development by many authors (*e.g.*, Eldredge & Cracraft, 1980; Wiley, 1981; Maddison *et al.*, 1984), *via* the conflicting views in the 1970's–1980's of the evolutionary systematic and numerical taxonomic schools. In Ichthyology, the use of cladistics has become widespread. Accordingly, in recent years, many authors have inferred phylogenetic relationships of the Scorpaeniformes by using a cladistic approach to morphological characters (*e.g.*, Leipertz, 1985; Yabe, 1985; Kido, 1988; Begle, 1989; Kanayama, 1991; Ishida, 1994; Shinohara, 1994; Imamura, 1996). Additionally, allozyme electrophoresis and molecular data have been utilized for phylogenetic analysis, although only a few authors have applied such to the scorpaeniforms (*e.g.*,

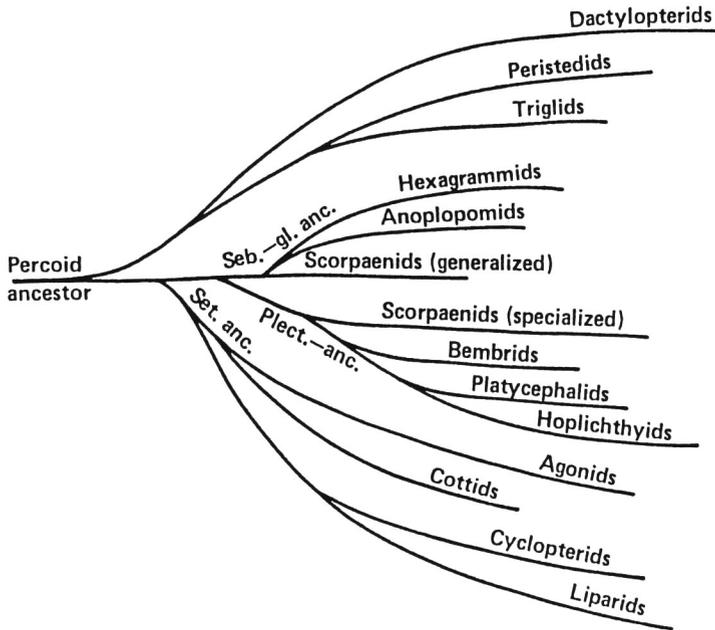


Fig. 2. Phylogeny of the order Scorpaeniformes, as proposed by Matsubara (1955) (from Washington *et al.*, 1984 a). Plect.-anc., *Plectrogenium*-ancestor; Seb.-gl.-anc., *Sebastes glaucus*-ancestor; Set.-anc., *Setarches*-ancestor.

Keenan, 1991). Much myological data for the order has also been presented, following the demonstration of its validity in phylogenetic analysis of the superfamily Cottoidea by Yabe (1985). At present, owing to the accumulation of considerable data and various phylogenetic proposals, a reconsideration of the monophyly and phylogenetic position of the order is due.

A recent review of the phylogenetic relationships, monophyly and phylogenetic position of the Scorpaeniformes, and remaining problematic issues (Imamura & Shinohara, 1997) (in Japanese), provided the basis of the present review, which includes additional information and presents an expanded and up-graded account.

In this review, for convenience, Scorpaeniformes is divided into two major clades, the scorpaenoid lineage (including the suborders Scorpaenoidei and Platycephaloidei, *sensu* Imamura, 1996) and the cottoid lineage (containing the Anoplopo-matoidei, Zaniolepidoidi, Hexagrammoidei and Cottoidei, *sensu* Shinohara, 1994), thus following the concept of Washington *et al.* (1984 a), except for the family Dactylopteridae, which is included under the section "Monophyly of the Scorpaeniformes." The above two lineages are regarded as monophyletic groups supported by synapomorphic characters, according to Imamura (1996) and Shinohara (1994), respectively.

Progress and Present Situation

Monophyly of the scorpaenoid lineage

The scorpaenoid lineage comprises two suborders, the Scorpaenoidei (*sensu* Ishida, 1994 minus *Plectrogenium*), including the following twelve families: Sebastidae, Setarchidae, Neosebastidae, Scorpaenidae, Apistidae, Tetrarogidae, Synanceiidae, Congiopodidae, Gnathanacanthidae, Pataecidae, Aploactinidae and Caracanthidae, and the Platycephaloidei (*sensu* Imamura, 1996), including the following seven families: Plectrogeniidae, Parabembridgeae, Bembridgeae, Triglidae, Peristediidae, Hoplichthyidae and Platycephalidae. Although these suborders have long been regarded as closely related to each other (Matsubara, 1943, 1955; Matsubara & Ochiai, 1955; Washington *et al.*, 1984 a) (Fig. 2), no concrete synapomorphic characters, widely common to both suborders, had been presented until Imamura (1996). The latter demonstrated that the monophyly of the group was supported by an osteological apomorphy, a backwardly-directed opercular spine extending across the subopercle (=lower opercular spine *sensu* Moser & Ahlstrom, 1978). Although the spine is absent in adults of the Pteroinae (Matsubara, 1943; Imamura, 1996), it was recognized in the larvae of such by Kojima (1988) and Imamura & Yabe (1996). Accordingly, Imamura (1996) considered the absence of the spine in the adult Pteroinae as a secondary reduction. In addition, as a result of Imamura's (1996) analysis of the scorpaenoid lineage (=his "first step" analysis) (Fig. 3 A), a single myological character, presence of an extrinsic swimbladder muscle derived from the obliquus superioris, was also regarded as a synapomorphy for the group (absence of the muscle in some triglids was considered to be a character reversal).

Interrelationships of the scorpaenoid lineage

Many authors have variously classified the scorpaenoid lineage at the subordinal level (Tables 1–2). Although the suborders Congiopodoidei and Hoplichthyoidei have previously been proposed (Greenwood *et al.*, 1966; Nelson, 1976), it is reasonable at present to recognize only two suborders, the Scorpaenoidei and Platycephaloidei, following the phylogenetic analyses by Ishida (1994) and Imamura (1996).

Suborder Scorpaenoidei. Judging from Matsubara's (1955) phylogenetic relationships of the Scorpaeniformes (Fig. 2), his superfamily Scorpaenicae, which was similar to the more recently-recognized Scorpaenoidei (see Table 1), was a non-monophyletic group. On the other hand, Ishida (1994) regarded the Scorpaenoidei, excluding the cottoid lineage, Triglidae, Peristediidae and Platycephaloidei, as monophyletic. His subsequent cladistic analysis of relationships within the suborder (Fig. 3 B) recognized twelve families. On the other hand, Shinohara (1994) and Imamura (1996) could find no synapomorphies supporting monophyly of the suborder.

Sebastidae. — Although this group had been recognized as a subfamily (Sebastinae) of the Scorpaenidae (Table 1), Ishida (1994) ranked it as the family level.

Matsubara (1943, 1955) included his Sebastinae and Neosebastinae in a *Sebastes*-stem, which was regarded as a group which had separated initially from other scorpaenoids. Although he also recognized the above two subfamilies as having a sister relationship, Ishida (1994) considered only the Sebastidae to represent an initial separation from other scorpaenoids (Fig. 3 B). Ishida (1994) included eight genera in his Sebastidae: *Sebastes*, *Sebastiscus*, *Hozukius*, *Helicolenus*, *Adelosebastes*, *Sebastolobus*, *Trachyscorpia* and *Plectrogenium*. However, Imamura (1996) included *Plectrogenium* in his platycephaloid Plectrogeniidae and regarded *Trachyscorpia* as a member of a monophyletic group (=Imamura's [1996] clade A7), including other genera such as *Pontinus* and *Scorpaena* (Fig. 3A). In addition, Imamura (1996) was unable to find synapomorphies uniting Ishida's other sebastid genera (Fig. 3 A). Barsukov's (1981) account of the relationships of the Sebastinae followed a precladistic methodology. Matsubara (1955) considered *Sebastes* to be the most primitive group among the Scorpaeniformes, stating, "Among the scorpaeniforms, *Sebastes* is nearest to the origin of its evolution," owing to the weakly developed suborbital stay and body form resembling generalized perciforms. However, Eschmeyer & Hureau (1971) did not agree, stating, "The genus *Sebastes*, while retaining many generalized features, is not a good choice for a primitive scorpionfish as has been earlier presumed."

Setarchidae and Neosebastidae. — The family Setarchidae includes three genera, *Setarches*, *Lioscorpis* and *Ectreposebastes*, and the Neosebastidae, two, *Neosebastes* and *Maxillicosta* (Eschmeyer & Collette, 1966; Ishida, 1994; Nelson, 1994). Matsubara (1943, 1955) treated the two groups as scorpaenid subfamilies (Table 1), placing them into different clades; thus he considered that the Setarchinae was a member of the *Scorpaena*-stem and was a sister group of a monophyletic group, including Scorpaeninae and Pteroinae, and that the Neosebastinae was a derivative of the *Sebastes*-stem, being a sister group of the Sebastinae. In addition, he inferred that the Agonidae, Cottidae, Cyclopteridae and Liparidae were derived from a *Setarches*-ancestor (Fig. 2), because of their possessing common characters with the Setarchinae, such as absence of the basisphenoid. However, Eschmeyer & Collette (1966) found all four species of the Setarchinae did, in fact, possess that element, and consequently could not agree with Matsubara's hypothesis. Ishida (1994) inferred that the Setarchidae and Neosebastidae had a sister relationship and were secondarily divided from other scorpaenoids, following the initially diverged Sebastidae (Fig. 3 B). Recently, Imamura (1996) considered that *Setarches* was much more closely related to genera such as *Pontinus* and *Scorpaena* (Scorpaenidae), and that *Neosebastes* was a sister group of a clade comprising *Hypodytes* (Tetrarogidae), *Inimicus* and *Minous* (Synanceiidae), *Erisphex* (Aploactinidae) and *Apistus* (Apistidae) (Fig. 3 A).

Scorpaenidae. — The extent of the former Scorpaenidae was effectively reduced by Ishida (1994), who elevated some of the subfamilies contained therein to separate family status (Table 1). Matsubara (1943, 1955) considered that the Scor-

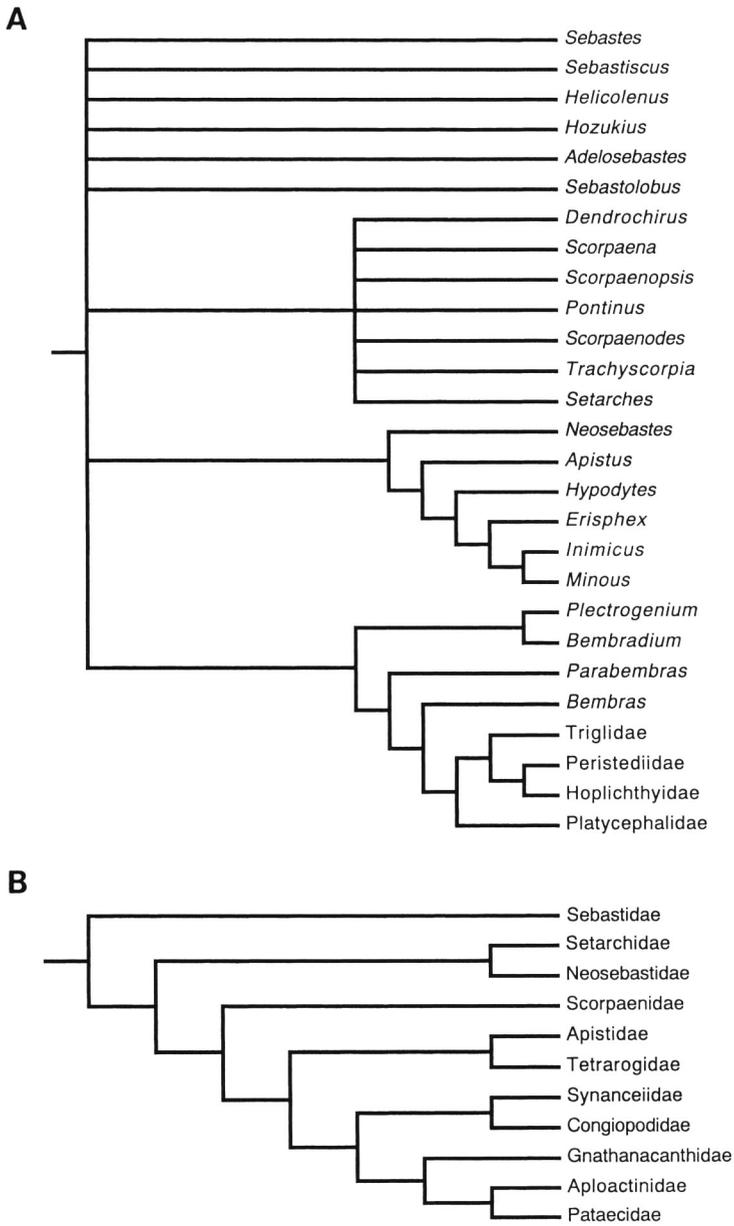


Fig. 3. Cladograms showing the relationships among (A) the scorpaenoid lineage, proposed by Imamura (1996), and (B) families of the suborder Scorpaenoidei, proposed by Ishida (1994).

paeninae and Pteroinae had a sister relationship, thus including the latter also in his Scorpaenidae. Ishida (1994) also included Matsubara's pteroine genera in the Scorpaenidae, but did not provide a formal category for them. According to Ishida (1994), Scorpaenidae constitutes the third branch from the scorpaenoids, following a clade including Setarchidae and Neosebastidae (Fig. 3 B).

Apistidae and Tetrarogidae. — Matsubara (1943, 1955) treated the family Apistidae as a scorpaenid subfamily (Apistinae) (Table 1), including it in the *Cocotropus*-stem. He also presumed that *Apistus*, the sole genus of his Apistinae, had branched off initially from all other members of the stem (Matsubara [1943] used the name Congiopinae for a group including *Neocentropogon*, *Ococia*, *Hypodytes*, *Synderina* and *Kanekonia*, all of which were members of his *Cocotropus*-stem. Subsequently, *Kanekonia* was included in the Aploactinidae and the other genera in the Tetrarogidae). Washington *et al.* (1984 a) inferred a close relationship among the Apistinae, Triglidae and Peristediidae, based on swimbladder and intrinsic muscle morphology. They also stated, "Apistinae may be the primitive sister group of the Triglidae and Peristediidae." Rejecting this hypothesis, Ishida (1994) considered the Apistidae and Tetrarogidae to have a sister relationship (Fig. 3 B), while Imamura (1996) considered the former to be a sister group of a monophyletic group, including *Hypodytes*, *Inimicus*, *Minous* and *Erisphex* (Fig. 3 A).

Synanceiidae and Congiopodidae. — Whereas the family Synanceiidae has been recognized by some as a scorpaenid subfamily (Synanceiinae) (Washington *et al.*, 1984 a; Nelson, 1994) (Table 1), the Congiopodidae has instead been elevated to a separate suborder, Congiopodoidei (Nelson, 1976; Lauder & Liem, 1983). Moreland (1960) stated that "the Congiopodidae show relationship with the Scorpaenidae...", and Ishida (1994) inferred that the Synanceiidae and Congiopodidae had a sister relationship, treating them as distinct families among the suborder Scorpaenoidei. Although Matsubara (1955) recognized four subfamilies (Minoinae, Synanceiinae, Inimicinae and Erosinae) in the Synanceiidae, Ishida (1994) did not recognize any, although his Synanceiidae included genera of Matsubara's four subfamilies.

Gnathanacanthidae. — The family Gnathanacanthidae was regarded as a pataecid subfamily (Gnathanacanthinae) by Nelson (1976, 1984) (Table 1). However, Ishida (1994) considered it to be a sister group of a monophyletic group, Aploactinidae + Pataecidae, thus regarding the former as a separate family (Fig. 3 B).

Pataecidae and Aploactinidae. — Mandrytza's (1991 b) examination of the suborbital bones of four pataecid species showed that they did not possess a suborbital stay. Thus, he considered that they should be excluded from the Scorpaeniformes, although the resulting phylogenetic position of Pataecidae among the Acanthopterygii was not determined. On the other hand, Ishida (1994) recognized the absence of a suborbital stay as a derived condition among the Scorpaenoidei, thus including the Pataecidae in that suborder. Mooi & Gill (1995) also determined that the pataecids

had a typical scorpaeniform (=their scorpaenoidei) arrangement of the epaxial musculature (Type 1 *sensu* Mooi & Gill, 1995). Matsubara (1943, 1955) did not examine the pataecids. However, Ishida (1994) presumed that the Pataecidae and Aploactinidae had a sister relationship (Fig. 3 B). Although Matsubara (1943) included the Aploactinae among the Scorpaenidae, he later included members of that subfamily in his Congiopodidae, to which he ascribed no subfamilies (Matsubara, 1955).

Caracanthidae. — The family Caracanthidae includes a single genus, *Caracanthus* (Eschmeyer, 1986 a; Ishida, 1994; Nelson, 1994). Although many authors have considered the group to be of family rank, within the Scorpaenoidei (Table 1), its sister group is still unclear.

Suborder Platycephaloidei. Many authors have regarded the suborder Platycephaloidei as being closely-related to *Plectrogenium* (Matsubara, 1943, 1955; Matsubara & Ochiai, 1955; Washington *et al.*, 1984 a). Matsubara & Ochiai (1955) presumed that a branch from a *Plectrogenium*-ancestor gave rise to *Plectrogenium*, *Parabembras* and *Bembras* in sequence, with a sister relationship between the remaining Platycephalidae and Hoplichthyidae. Washington *et al.* (1984 a) supported Matsubara & Ochiai's (1955) hypothesis, owing to the similarity of body scales and caudal skeletons in *Plectrogenium* and *Parabembras*. Imamura (1996) assessed the relationships of the Scorpaenoidei and Platycephaloidei cladistically (Fig. 3 A) and redefined the latter by a synapomorphy, the presence of a posterior pelvic fossa (see Imamura, 1996: 132).

Plectrogeniidae. — At present, the family includes two sister-related genera, *Plectrogenium* and *Bembradium* (Imamura, 1996) (Fig. 3 A). Previously, *Plectrogenium* had been included in the Scorpaenidae, and *Bembradium* in the platycephalid subfamily Bembrinae or family Bembridae (Nelson, 1984, 1994) (Tables 1–2). Plectrogeniidae was considered by Imamura (1996) to have been an initial branch from all other platycephaloids (Fig. 3 A).

Parabembridae. — Although the family Parabembridae, including only the genus *Parabembras*, was established by Jordan & Hubbs (1925), it had not been generally recognized until Imamura's (1996) reevaluation, *Parabembras* having been included in the Bembridae or platycephalid Bembrinae (*e.g.*, Greenwood *et al.*, 1966; Washington *et al.*, 1984 b; Nelson, 1994) (Table 2). Imamura (1996), however, considered that the genus was not closely related to the clade containing *Bembras*, type genus of Bembridae, and accordingly recognized the Parabembridae. Parabembridae represents a second branch, from all other remaining platycephaloids, according to Imamura (1996) (Fig. 3 A).

Bembridae. — Including a single genus, *Bembras* (Imamura, 1996), this family has been treated by some as a platycephalid subfamily, Bembrinae, although more recently, it has been recognized as a separate family (Table 2). Imamura (1996) also recognized Bembridae, based on platycephaloid interrelationships (Fig. 3 A).

Triglidae and Peristediidae. — Triglidae and Peristediidae have long been re-

Table 1. Prior placements of Ishida's (1994) twelve families in the suborder Scorpaenoidei

Ishida (1994)	Matsubara (1955)	Greenwood <i>et al.</i> (1966)	Nelson (1976)	Nelson (1984)	Washington <i>et al.</i> (1984 a)	Nelson (1994)
Scorpaenidae	placed in SFS*	placed in SS*	placed in SS	placed in SS	placed in SS	placed in SS
Sebastidae	placed in SFS as scorpaenid SB*		placed in SS as scorpaenid SB	placed in SS as scorpaenid SB	placed in SS as scorpaenid SB	placed in SS as scorpaenid SB
Setarchidae	placed in SFS as scorpaenid SB		placed in SS as scorpaenid SB	placed in SS as scorpaenid SB	placed in SS as scorpaenid SB	placed in SS as scorpaenid SB
Neosebastidae	placed in SFS as scorpaenid SB				placed in SS as scorpaenid SB	placed in SS as scorpaenid SB
Apistidae	placed in SFS as scorpaenid SB		placed in SS as scorpaenid SB	placed in SS as scorpaenid SB	placed in SS as scorpaenid SB	placed in SS as scorpaenid SB
Tetrarogidae						
Synanceiidae	placed in SFS	placed in SS	placed in SS	placed in SS	placed in SS	placed in SS
Congiopodidae	placed in SFS		placed in suborder Congiopodoidei	placed in SS	placed in SS	placed in SS
Gnathanacanthidae			placed in SS as patactid SB	placed in SS as patactid SB	placed in SS	placed in SS
Aploactinidae		placed in SS	placed in SS	placed in SS	placed in SS	placed in SS
Patactidae		placed in SS	placed in SS	placed in SS	placed in SS	placed in SS
Caracanthidae		placed in SS	placed in SS	placed in SS	placed in SS	placed in SS

*SB, subfamily; SFS, superfamily Scorpaenicae (*sensu* Matsubara, 1955); SS, suborder Scorpaenoidei.
Blank spaces indicate taxa not recognized or discussed.

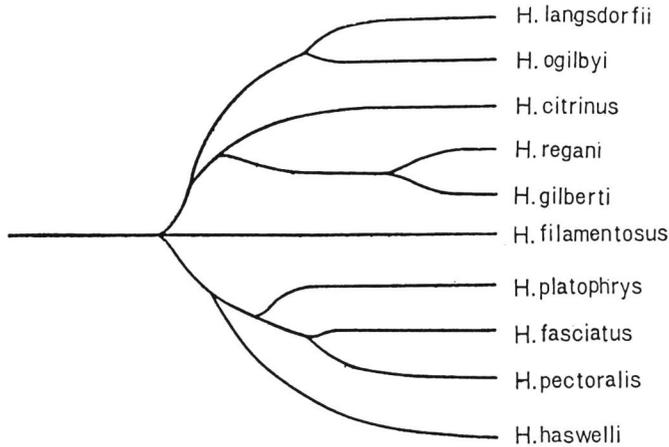


Fig. 4. Phylogeny of the family Hoplichthyidae (from Matsubara, 1955).

garded as closely-related groups (Gill, 1888; Matsubara, 1943, 1955; Washington *et al.*, 1984 a) (Figs. 1–2). Matsubara (1955) considered them to be “a specialized group branched off from an ancestor not much differing from the scorpaenid-ancestor at a very early age, and passed through a specialized evolutionary process,” because they had specialized characters such as “protector-like suborbital bones expanded abnormally” and also primitive characters such as “sensory canal supported by the suborbital bones.” Greenwood *et al.* (1966) and Nelson (1984, 1994) included both families in the suborder Scorpaenoidei, without giving reasons (Table 1), whereas Washington *et al.* (1984 a) suggested that they were related to the Apistinae (see above). Imamura (1996) recently suggested that the Peristediidae and Hoplichthyidae comprise a monophyletic group, being a sister group of the Triglididae (Fig. 3 A).

Hoplichthyidae. — The family Hoplichthyidae has previously been regarded as a sister group of the Platycephalidae (Matsubara & Ochiai, 1955; Matsubara, 1955; Washington *et al.*, 1984 a). Although Winterbottom (1993), attempting to determine a sister group for the perciform suborder Gobioidae, suggested Hoplichthyidae as a candidate, Imamura (1996) instead proposed Hoplichthyidae as a sister group of the Peristediidae (Fig. 3 A). Mooi & Gill (1995) also failed to support Winterbottom’s suggestion, following their examination of the relationship between the dorsal fin pterygiophores and epaxial musculature. A precladistic analysis of the relationships of ten hoplichthyids, made by Matsubara & Ochiai (1950), was subsequently reassessed and partially changed by Matsubara (1955) (Fig. 4). Imamura (1996) also inferred hoplichthyid phylogenetic relationships, although his materials were restricted to only three species.

Platycephalidae. — Matsubara & Ochiai (1955) investigated platycephalid generic interrelationships using osteological characters of ten Japanese species, in ad-

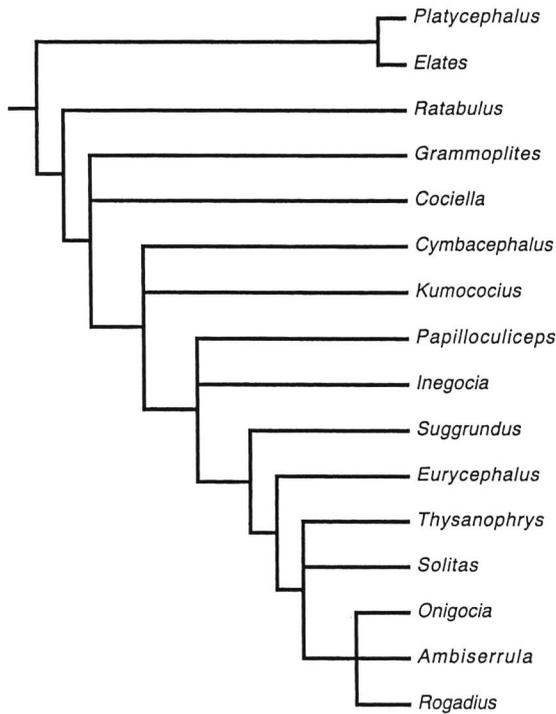


Fig. 5. Cladogram showing generic interrelationships in the family Platycephalidae, proposed by Imamura (1996).

dition to literature information on other genera. Taniguchi *et al.* (1972) compared electropherograms of muscle proteins, *LDH** and *MDH**, of ten Japanese platycephalids in an analysis of their relationships and Keenan (1991) constructed the relationships of twenty-four Australian species in eleven genera using allozyme analysis, classifying them at subfamilial and generic levels, in addition to recognizing paraphyletic groups. Imamura's (1996) cladistic analysis of the relationships of thirty-eight platycephalids using morphological (osteology and myology) characters (Fig. 5) agreed with that of Keenan (1991) at many points, although the interpretation differed, Imamura (1996) not recognizing paraphyletic groups.

Monophyly of the cottoid lineage

The cottoid lineage comprises the Anoplopomatoidei (including Anoplopomatiidae), Zaniolepidoidaei (Zaniolepididae), Hexagrammoidei (Hexagrammidae) and Cottoidaei (Rhamphocottidae, Ereuniidae, Cottidae, Hemitripterae, Agonidae, Psychrolutidae, Cyclopteridae, Liparidae, etc.) (Washington *et al.*, 1984a; Shinohara, 1994). Although close relationships among the members of the cottoid lineage have been suggested by many ichthyologists (*e.g.*, Gill, 1888; Matsubara, 1943, 1955; Yabe,

Table 2. Prior placements of Imamura's (1996) seven families in the suborder Platycephaloidei

Imamura (1996)	Matsubara (1955)	Greenwood <i>et al.</i> (1966)	Nelson (1976)	Nelson (1984)	Washington <i>et al.</i> (1984 a)	Nelson (1994)
Platycephalidae	placed in SFP*	placed in SP* (including subfamily Bembrinae)	placed in SP (including subfamily Bembrinae)	placed in SP (including subfamily Bembrinae)	placed in SS*	placed in SP
Bembridae	placed in SFP (including <i>Bembradium</i>)	placed in SP (including <i>Bembradium</i> and <i>Parabembras</i>)	placed in SP as platycephalid subfamily	placed in SP as platycephalid subfamily	placed in SS (including <i>Bembradium</i> and <i>Parabembras</i>)	placed in SP (including <i>Bembradium</i> and <i>Parabembras</i>)
Parabembridae	placed in SFP					
Hoplichthyidae	placed in SFP	placed in suborder Hoplichthyoidei	placed in suborder Hoplichthyoidei	placed in SP	placed in SS	placed in SP
Triglidae	placed in superfamily Triglidae	placed in SS	placed in SS	placed in SS	placed in SS	placed in SS
Peristediidae	placed in superfamily Triglidae	placed in SS as triglid subfamily	placed in SS as triglid subfamily	placed in SS as triglid subfamily	placed in SS	placed in SS as triglid subfamily
Plectrogoniidae	placed in superfamily Scorpaenidae as scorpaenid subfamily (excluding <i>Bembradium</i>)				placed in SS as scorpaenid subfamily (excluding <i>Bembradium</i>)	placed in SS as scorpaenid subfamily (excluding <i>Bembradium</i>)

*SFP, superfamily Platycephalidae (*sensu* Matsubara, 1955); SP, suborder Platycephaloidei; SS, suborder Scorpaenoidei. Blank spaces indicate taxa not recognized or discussed.

1981; Kido, 1988; Kanayama, 1991), the monophyly of the lineage has not been investigated. Quast (1965), however, suggested that the Anoplopomatidae had evolved along a different lineage from the other members (see under “Monophyly of the Scorpaeniformes”) and, recently, Shinohara (1994) confirmed the monophyly of the cottoid lineage on the basis of seven synapomorphies.

Interrelationships of the cottoid lineage

Interrelationships among the suborders of the cottoid lineage were first investigated by Shinohara (1994) (Fig. 6 A), who advocated a new classification comprising the following four suborders: Anoplopomatoidei, Zaniolepidoidi, Hexagrammoidei and Cottoidei.

Suborder Anoplopomatoidei. The Anoplopomatoidei comprises a single family, Anoplopomatidae, with two species: *Anoplopoma fimbria* and *Erilepis zonifer* (Nelson, 1984, 1994; Shinohara, 1994). *Anoplopoma fimbria* has been suggested as being closely-related to the Hexagrammidae (e.g., Gill, 1888; Berg, 1940; Matsubara, 1955) and historically has been included in the suborder Hexagrammoidei or superfamily Hexagrammicae (Table 3). However, Quast (1965) questioned such placements, after finding osteological differences between the Anoplopomatidae and Hexagrammidae (e.g., degree of fusion of caudal skeleton), and was followed by Nelson (1984, 1994), who placed the Anoplopomatidae into a distinct suborder, Anoplopomatoidei (Table 3). Shinohara (1994) subsequently inferred a sister relationship of the Anoplopomatidae to the monophyletic group comprising Hexagrammidae, Zaniolepididae and Cottoidei (Fig. 6 A), and adopted Nelson’s (1984, 1994) Anoplopomatoidei.

Suborder Zaniolepidoidi. The Zaniolepidoidi includes the family Zaniolepididae (Shinohara, 1994), treatment of which has varied over the years, with some authors including it as a subfamily (Zaniolepidinae) of Hexagrammidae (Regan, 1913; Berg, 1940; Rutenberg, 1962; Hart, 1973; Nelson, 1994) (Table 3). The generic composition has also been an issue, *Zaniolepis* having been regarded by some as the sole genus in the family (Quast, 1965; Greenwood *et al.*, 1966; Nelson, 1976, 1984). Quast (1965) considered the Cottidae as likely to be closely-related to the Zaniolepididae on the basis of osteological similarities and Shinohara (1994) inferred *Oxylebius*+*Zaniolepis* as having a sister relationship with a monophyletic group comprising the Hexagrammoidei and Cottoidei (Fig. 6 A). Shinohara (1994) also established a new suborder (=Zaniolepidoidi) for *Oxylebius* and *Zaniolepis* (Table 3).

Suborder Hexagrammoidei. The Hexagrammoidei includes only the family Hexagrammidae (Nelson, 1994; Shinohara, 1994), which Gill (1888) supposed to be more primitive than the Scorpaenidae, being closer to the Cottidae by way of a close relationship with the ancestor of the latter. However, Matsubara (1943, 1955) thought that the Hexagrammidae originated from a *Sebastes glaucus*-ancestor, together with the Anoplopomatidae (Fig. 2). Rutenberg (1962) described hexagrammid osteologi-

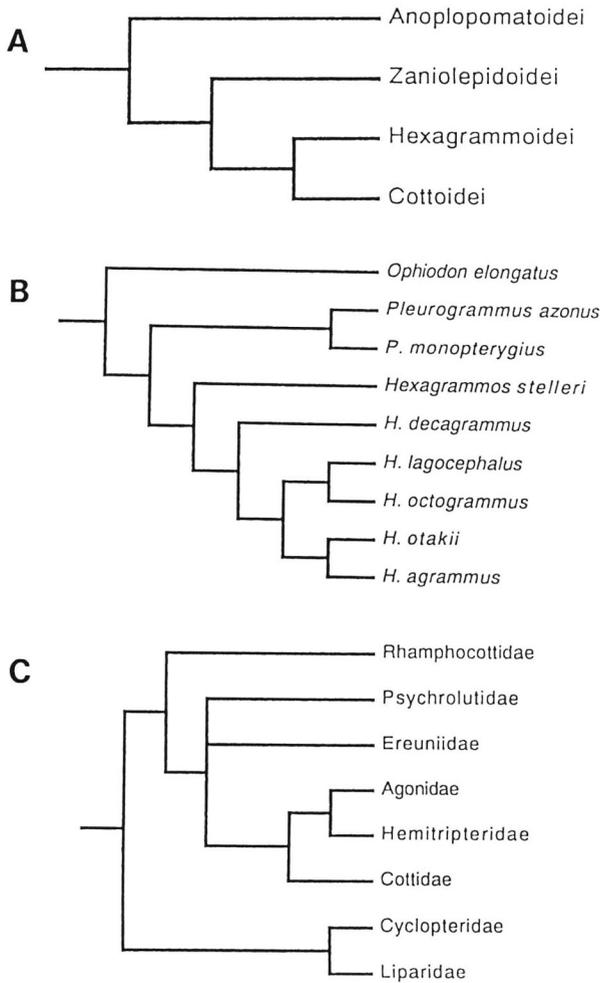


Fig. 6. Cladograms showing the relationships among (A) the suborders Anoplopomatoidei, Zaniolepidoidae, Hexagrammoidei and Cottoidei and (B) species of the family Hexagrammidae (proposed by Shinohara, 1994), and (C) families of the suborder Cottoidei (based on Yabe [1985] and Kido [1988]).

cal and external characters in detail and suggested the subfamily Zaniolepidinae as the most primitive higher group in the Hexagrammidae. Subsequently, Quast (1965) argued that the Hexagrammidae was closest to the Cottidae and questioned a close relationship of the former with the Anoplopomatidae. Although Yabe (1985) discovered several derived conditions shared by both the Hexagrammidae and Cottoidea, he refrained from suggesting a particularly close relationship of the two groups. Recently, Shinohara (1994) reexamined the monophyly and phylogenetic position of the Hexagrammidae and clarified the monophyly of the three component genera (*Hexa-*

Table 3. Prior placements of Shinohara's (1994) three families in the suborders Anoplopomatoidei, Zaniolepidoidae and Hexagrammoidei

Shinohara (1994)	Matsubara (1955)	Greenwood <i>et al.</i> (1966)	Nelson (1976)	Nelson (1984)	Washington <i>et al.</i> (1984 a)	Nelson (1994)
Anoplopomatidae (Anoplopomatoidei)	placed in SFH*	placed in SOH*	placed in SOH	placed in suborder Anoplopomatoidei	placed in SO*	placed in suborder Anoplopomatoidei
Zaniolepididae (Zaniolepidoidae)		placed in SOH (excluding <i>Oxylebius</i>)	placed in SOH (excluding <i>Oxylebius</i>)	placed in SOH (excluding <i>Oxylebius</i>)		placed in SOH as hexagrammid subfamily (excluding <i>Oxylebius</i>)
Hexagrammidae (Hexagrammoidei)	placed in SFH	placed in SOH (excluding <i>Oxylebius</i>)	placed in SOH (excluding <i>Oxylebius</i>)	placed in SOH (excluding <i>Oxylebius</i>)	placed in SO (including <i>Oxylebius</i> and <i>Zaniolepis</i>)	placed in SOH

*SO, suborder Cottoidei; SFH, superfamily Hexagrammiceae (*sensu* Matsubara, 1955); SOH, suborder Hexagrammoidei.

Blank spaces indicate taxa not recognized or discussed.

grammos, *Pleurogrammus* and *Ophiodon*), in addition to investigating specific-level relationships (Fig. 6 B).

Suborder Cottoidei. This suborder includes the superfamilies Cottoidea and Cyclopteroidea (Nelson, 1994; Yabe & Uyeno, 1996). Under the Cottoidea, Yabe (1985) recognized the following nine families: Rhamphocottidae, Ereuniidae, Cottidae, Hemitripteridae, Agonidae, Psychrolutidae, Comephoridae, Abyssocottidae and Normanichthyidae, Nelson (1994) subsequently adding the Bathylutichthyidae. The superfamily Cyclopteroidea includes two families, the Cyclopteridae and Liparidae (Nelson, 1994; Yabe & Uyeno, 1996). Yabe (1985) and Kido (1988) demonstrated the monophyly of this superfamily and assumed a sister relationship with the Cottoidea.

Rhamphocottidae. — This family includes *Rhamphocottus richardsonii* (e.g., Nelson, 1994). Following his cladistic analysis of adult morphology, Yabe (1985) considered the family to be an early offshoot within the Cottoidea (Fig. 6 C).

Ereuniidae. — Yabe (1981) investigated the osteology of three genera, *Icelus*, *Marukawichthys* and *Ereunias*, in order to reevaluate Berg's (1940) Icelidae, in which they had been included. He demonstrated a close relationship between *Icelus* and the typical cottid genus *Hemilepidotus*, supported by seven osteological characters. Yabe (1981) subsequently recognized the family Ereuniidae, which included only *Marukawichthys* and *Ereunias*, thus supporting Rass & Lindberg (1971). Although Yabe (1981) considered the Cottidae to be a sister group of the Ereuniidae, he did not indicate a close relationship of these families in a subsequent paper (Yabe, 1985) (Fig. 6 C).

Cottidae. — This family is a well-studied member of the cottoid lineage. Taranetz (1941) investigated osteological characters and showed the interrelationships of cottid genera using precladistic methodology. Similarly, Bolin (1947) estimated the evolutionary lines of Californian Cottidae (Fig. 7). Subsequent notable studies included those of Watanabe (1958) (Japanese cottids), Cowan (1972) (*Myoxocephalus*), Peden (1977) (subfamily Hemilepidotinae) and Neyelov (1979) (subfamilies Myoxocephalinae and Artediellinae). Whereas all of the above studies were based on adult specimens, Richardson (1981) analyzed larval characters phenetically in a study of the interrelationships of six genus-groups. The cladistic analysis by Washington *et al.* (1984 a) of larval characters, in a study of the interrelationships of the Cottidae and allies, was followed by a similar analysis of adult osteology and myology by Yabe (1985), who examined cottid phylogeny. The latter recognized a sister relationship between the Cottidae and a monophyletic group comprising the Hemitripteridae and Agonidae (Fig. 6 C). Several recent studies have considered the Cottidae inhabiting shallow waters of the Pacific region. For example, Washington (1986) proposed the monophyly of two genus-groups, *viz.* *Artedius*+*Clinocottus*+*Oligocottus* (ACO-monophyly hypothesis *sensu* Strauss, 1993) and *Clinocottus*+*Oligocottus* (CO-monophyly hypothesis *sensu* Strauss, 1993), on the basis of larval morphology, and Begle (1989) demonstrated the interrelationships of *Artedius*

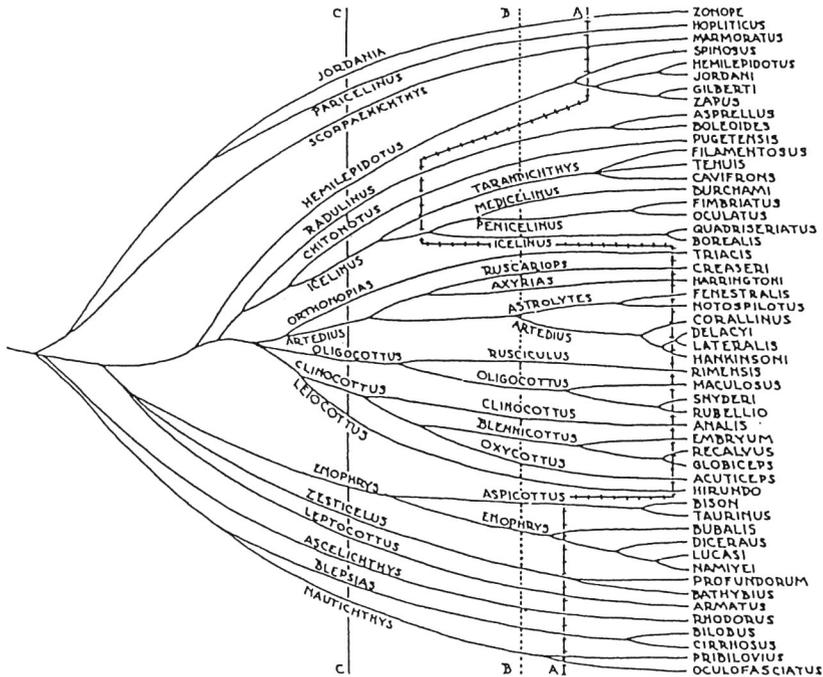


Fig. 7. Phylogeny of the family Cottidae from California (from Bolin, 1947).

species and related genera in his review of the taxonomy of the former. According to Begle (1989), Bolin's (1947) *Arte dius*, which comprised seven species, was not itself monophyletic, but constituted two monophyletic groups, one with five species, being a sister group of *Clinocottus*+*Oligocottus*, and the other with two, a sister group of *Clinocottus*. Strauss (1993) reexamined both the ACO- and CO-monophyly hypotheses on the basis of revised characters of Washington (1986) and Begle (1989) by using parsimony analysis. Using both larval only and larval+adult characters, that approach supported the ACO-monophyly hypothesis. On the other hand, the CO-monophyly hypothesis was supported by the use of larval+adult characters only. Strauss (1993) recommended leaving the matter of the interrelationships of the three genera unresolved pending further information.

Hemitripteridae. — The phylogenetic relationships of the family Hemitripteridae were investigated by Yabe (1985). The family includes three genera, *Hemitripterus*, *Blepsias* and *Nautichthys*, the latter two sharing a sister relationship (Fig. 8 B). Yabe (1985) showed the Agonidae to be a sister group of the Hemitripteridae on the basis of a single synapomorphy (Fig. 6 C).

Agonidae. — Nishimura's (1974) precladistic analysis of the interrelationships of the subfamilies Percidinae, Barchyoposinae and Tilesininae was an attempt to explain the diversity of the endemic species of Agonidae in the Sea of Japan. Using a

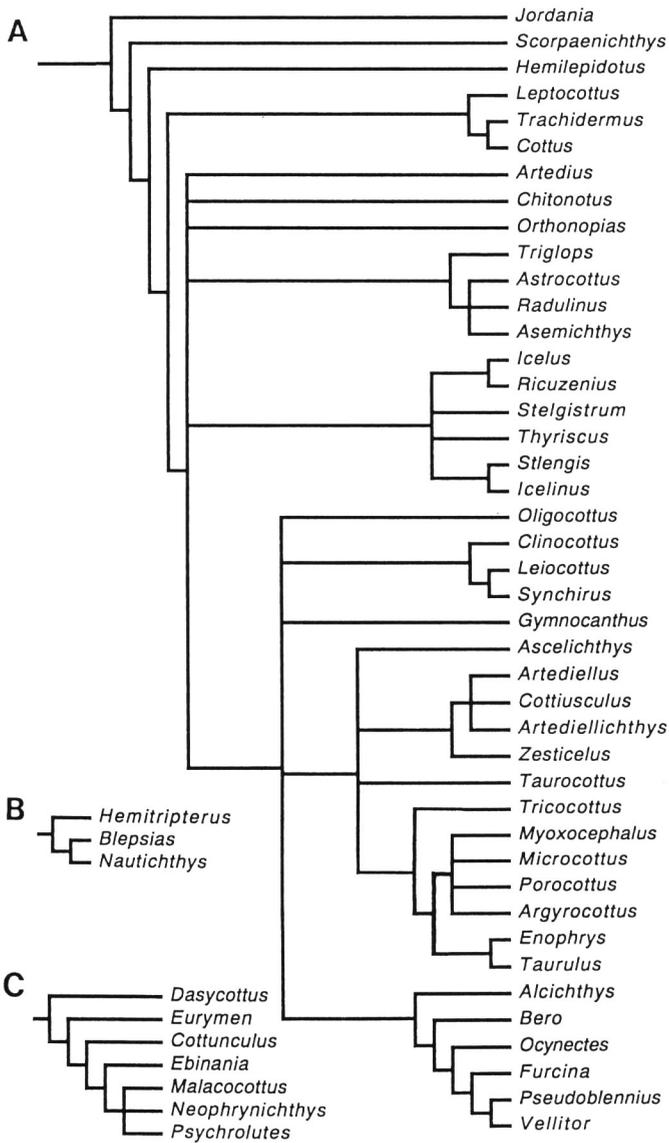


Fig. 8. Cladograms showing generic interrelationships in the families Cottidae (A), Hemitripteriidae (B) and Psychrolutidae (C) (based on Yabe, 1985).

cladistic analysis of osteological characters, Leipertz (1985) investigated the interrelationships of four species of *Xeneretmus*, and later (Leipertz, 1988) used a similar approach in his consideration of the phylogenetic position of the agonid, *Bothragonus swanii*. Kanayama's (1991) investigation of the interrelationships of the Agonidae

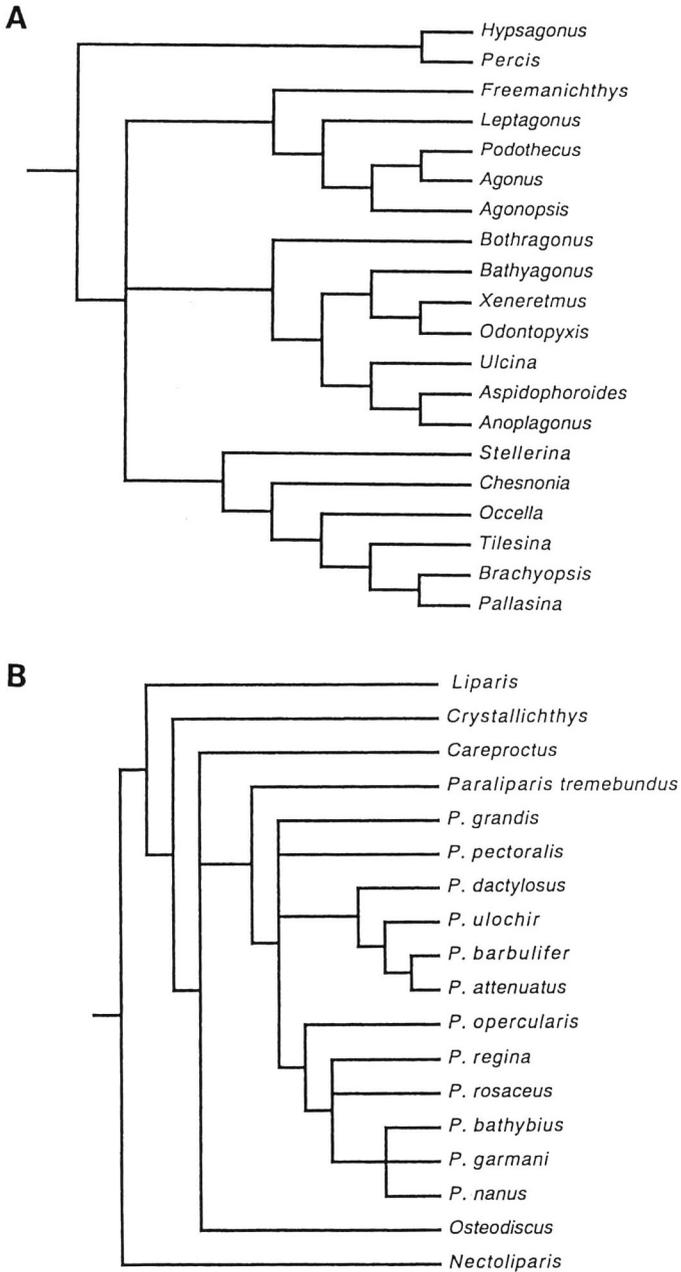


Fig. 9. Cladograms showing interrelationships within the families Agonidae (A) (based on Kanayama, 1990) and Liparidae (B) (based on Kido, 1988).

(Fig. 9 A) recognized the following four subfamilies: Agoninae, Anoplagoninae, Brachyopsinae and Percidinae. Although his conclusions partly disagreed with those of Leipertz (1985, 1988), Kanayama (1991) did not consider the reasons for such.

Psychrolutidae. — This family has been considered a key taxon connecting the Cottidae to the Cyclopteridae+Liparidae by several ichthyologists (*e.g.*, Taranetz, 1941; Matsubara, 1955; Ueno, 1970). However, Yabe (1985) demonstrated the Psychrolutidae to be a monophyletic group and showed trichotomical relationships with the Ereuniidae and a monophyletic group of Agonidae+Cottidae+Hemitripteridae (Fig. 6 C). He also investigated the interrelationships of seven psychrolutid genera (Fig. 8 C).

Abyssocottidae and Comephoridae. — Both families are endemic to Lake Baikal, the Abyssocottidae including twenty species belonging to six genera, and the Comephoridae, two, in the single genus *Comephorus* (Sideleva, 1982). Taliev (1955) considered the phylogenetic relationships of the Abyssocottidae and Comephoridae using precladistic methodology, proposing the ancestor (monophyletic) of both families to have been in the Myoxocephalinae+Cottinae assemblage. On the other hand, Sideleva (1982), who studied the morphology of the head lateral line system in both families, concluded a polyphyletic origin of the cottoids in Lake Baikal, the Comephoridae comprising a different lineage from the others. Yabe (1985) did not investigate either family, but tentatively included them in his Cottoidea (Table 4). Yabe's (1986) examination of the myology of *Comephorus dybowskii* led him to include the Comephoridae in the Cottoidea on the basis of shared derived conditions of the extrinsic and other muscles. However, he did not clarify the phylogenetic position of the family.

Cyclopteridae. — The interrelationships within the Cyclopteridae have been examined only by Ueno (1970). Yabe (1985) determined a sister relationship of this family with the Liparidae and was supported by Kido (1988), who demonstrated further synapomorphies shared by the two families (Fig. 6 C).

Liparidae. — Burke (1930) discussed the interrelationships among genera of the Liparidae on the basis of the similarity of external characters and Kido (1988) studied the interrelationships of northern hemisphere Liparidae using cladistic methodology (Fig. 9 B). Andriashev (1986) discussed character phylogeny in the genus *Paraliparis* in the southern hemisphere and supported Burke's (1930) polyphyletic origin hypothesis for the genus.

Normanichthyidae and Bathylutichthyidae. — The Normanichthyidae includes a single species, *Normanichthys crockeri* (Nelson, 1984, 1994; Washington *et al.*, 1984 a). Although Clark (1937), who originally proposed the family Normanichthyidae for *N. crockeri*, could not clarify its ordinal position, the family has been included in the Cottoidei by many authors (Table 4), including Mandrytza (1991 a), following an investigation of the head lateral line system. On the other hand, Nelson (1994) included the family in a new suborder, Normanichthyoidei. Recently, Yabe & Uyeno

Table 4. Prior placements of Nelson's (1994) eleven families in the suborder Cottoidei

Nelson (1994)	Matsubara (1955)	Greenwood <i>et al.</i> (1966)**	Nelson (1976)**	Nelson (1984)**	Washington <i>et al.</i> (1984 a)**	Yabe (1985)**
Rhamphocottidae						
Ereuniidae	placed in SCO* as cottid SB*		placed in SO* as cottid SB	placed in SO	placed in SO	placed in SCO placed in SCO
Cottidae	placed in SCO	placed in SO	placed in SO	placed in SO	placed in SO	placed in SCO
Comephoridae	placed in SO	placed in SO	placed in SO	placed in SO	placed in SO	placed in SCO
Abyssocottidae			placed in SO as cottocomephorid SB	placed in SO as cottocomephorid SB		placed in SCO
Hemiripieridae	placed in SCO as cottid SB					placed in SCO
Agonidae	placed in SFA*	placed in SO	placed in SO	placed in SO	placed in SO	placed in SCO
Psychrolutidae	placed in SCO	placed in SO	placed in SO	placed in SO	placed in SO	placed in SCO
Bathylutichthyidae						
Cyclopteridae	placed in SCY*	placed in SO	placed in SO	placed in SO	placed in SO	placed in SCO
Liparidae	placed in SCY		placed in SO as cyclopterid SB	placed in SO	placed in SO	placed in SCO

*SB, subfamily; SFA, superfamily Agoniceae (*sensu* Matsubara, 1955); SCO, superfamily Cotticeae (*sensu* Matsubara, 1955) or Cottoideae; SCY, suborder Cyclopterina (*sensu* Matsubara, 1955); SO, suborder Cottoidei.

**Authors included the family Normanichthyidae (included in the suborder Normanichthyoidei by Nelson, 1994) in the suborder Cottoidei or the subfamily Cottoideae.

Blank spaces indicate taxa not recognized or discussed.

(1996) examined the internal morphology of *N. crockeri* with that of other Cottoidei and tentatively included Normanichthyidae in the Scorpaeniformes. Being unable to determine its relationships within the Scorpaeniformes, apart from not belonging to the Cottoidei, Yabe & Uyeno (1996) considered that the Normanichthyidae should be treated as *incertae sedis* within the Scorpaeniformes, pending the resolution of its sister group.

The Bathylutichthyidae includes *Bathylutichthys taranetzi* only (Balushikin & Voskoboynikova, 1990; Nelson, 1994). Following examination of both external and osteological characters of *B. taranetzi*, Balushikin & Voskoboynikova (1990) included the Bathylutichthyidae in the Cottoidei, recognizing its close relationship with the Psychrolutidae. Nelson (1994) followed Balushikin & Voskoboynikova's (1990) subordinal placement. However, Mooi & Gill (1995) questioned the inclusion of Bathylutichthyidae in the Scorpaeniformes because of the dissimilarity of the epaxial-dorsal pterygiophore pattern between the former and other scorpaeniform families.

Monophyly of the Scorpaeniformes

Although the Scorpaeniformes have been characterized by a single apomorphy, the presence of a suborbital stay, the monophyly of the order has been doubted (Quast, 1965; Johnson & Patterson, 1993; Nelson, 1994). Despite Regan's (1913) inclusion of the gasterosteiforms Gasterosteidae and Aulorhynchidae in the Scorpaeniformes, owing to the presence of a stay in the former families, Matsubara (1955) regarded the stays in the latter and the scorpaeniforms as an example of homoplasy. There has been no subsequent evidence to support the belief that the suborbital stay in Scorpaeniformes is homologous.

Freihofer (1963) determined three different patterns of the ramus lateralis accessorius in the scorpaeniforms and Quast (1965) recognized at least three distinct "evolutionary lines" in Berg's (1940) Cottoidei (=Scorpaeniformes) (*viz.* anoplopomatoid, scorpaenoid and cottoid), which corresponded to Freihofer's three groups. The latter stated, "It might be speculated that the suborbital stay originated independently in at least two of the groups and that the Cottoidei (=Scorpaeniformes) are a polyphyletic assemblage." On the other hand, Shinohara (1994) considered the monophyly of the Scorpaeniformes to be supported by three synapomorphies: presence of the suborbital stay, a sensory canal on the parietal and the swimbladder muscle. As a result, the different patterns of the ramus lateralis accessorius in the Anoplopomatoidei and other members of the cottoid lineage were regarded as independently-derived apomorphic characters. Recently, Imamura (1996) pointed out that the extrinsic muscle seen in the scorpaenoid lineage was not homologous with its counterpart in the cottoid lineage, owing to the different origins and directions of the muscle fiber. However, the homologies of the remaining synapomorphic characters of the Scorpaeniformes, listed by Shinohara (1994), including the suborbital stay, have not yet been verified.

Phylogenetic position of the Dactylopteridae. Two major hypotheses have been proposed concerning the taxonomic position of the Dactylopteridae; placement within the Scorpaeniformes (Gill, 1888; Jordan & Richardson, 1908; Allis, 1909; Regan, 1913; Matsubara, 1943, 1955; Washington *et al.*, 1984 a; Eschmeyer, 1986 b, 1990; Nakabo, 1993; Nelson, 1994), and treatment as an independent order (Berg, 1940; Nelson, 1976, 1984; Lauder & Liem, 1983; Johnson, 1993; Johnson & Patterson, 1993; Mooi & Gill, 1995). Several authors have considered the Dactylopteridae to be related to the Triglidae and Peristediidae (Gill, 1888; Matsubara, 1943, 1955; Washington *et al.*, 1984 a). However, Johnson (1993) and Mooi & Johnson (1997) pointed out that the dactylopterids do not possess a sensory canal on the parietal, recently regarded as a scorpaeniform synapomorphy (see above), and considered the former to be distinct from the Scorpaeniformes. Nevertheless, as pointed out by Eschmeyer (1997), the component bones of the dactylopterid suborbital stay remain poorly understood and any homology with that of the Scorpaeniformes is still unclear. The possibility presented by Pietsch (1978) that the Dactylopteridae had an origin among the Gasterosteiformes (based on six osteological similarities) was rejected by Johnson & Patterson (1993), who pointed out that the Dactylopteridae differed from the gasterosteiformes in lacking several derived characters found in the latter and concluded that the two groups were not closely related.

Phylogenetic position of the Scorpaeniformes

The Scorpaeniformes have been thought to be close to the Perciformes by many authors (*e.g.*, Gill, 1888; Regan, 1913; Matsubara, 1943, 1955). For example, Gill (1888) considered the Cirrhitidae (=his Cirritidae) as the ancestral position of the Scorpaeniformes, whereas Matsubara (1955) placed the percoid ancestor in that position, considering that the morphology of typical Scorpaeniformes was very similar to that of typical Perciformes, except for the suborbital stay. Greenwood *et al.* (1966) included the Scorpaeniformes in the superorder Acanthopterygii, recognizing the origin of the Scorpaeniformes in a pre-perciform position. Subsequently, Lauder & Liem (1983) showed a close relationship of the Scorpaeniformes to the Perciformes, Tetraodontiformes, Pleuronectiformes and Channiformes supported by three shared derived characters (*e.g.*, 17 principal caudal fin rays). In order to determine character polarities, Yabe (1985), Ishida (1994) and Imamura (1996) chose the Percoidei for comparison with the superfamily Cottoidea, suborder Scorpaenoidei and suborder Platycephaloidei, respectively. Following SEM observation of scales, Roberts (1993) suggested the monophyly of the three orders Scorpaeniformes, Pleuronectiformes and Perciformes. Although Johnson & Patterson (1993) stressed the inclusion of the Scorpaeniformes as a suborder of the Perciformes (the two being closely related), commenting on the lack of evidence supporting a pre-perciform position of the former, and their recommendation was followed by Mooi & Gill (1995) and Mooi & Johnson (1997). Shinohara (1994) made a point of not determining a closely-related

group within the superorder Acanthopterygii, judging that the hypothetical ancestor of Scorpaeniformes could be close to that of the superorder following reevaluation of morphological characters. Thus, a consensus exists concerning the inclusion of the Scorpaeniformes in the Acanthopterygii, although uncertainty continues regarding the former's closest affinities.

Problems

Although the phylogeny of the scorpaeniforms has been studied by many authors since the end of last century, many areas of study remain. For example, the phylogenetic positions of some groups, such as the Caracanthidae, Normanichthyidae and Bathylutichthyidae, have not been evaluated and the relationships of the Triglidae and Peristediidae at the genus- and species-levels are still poorly known. In addition, reevaluations of some taxa are also needed (*e.g.*, Cyclopteridae), although the phylogenetic relationships have perhaps been resolved.

One of the difficulties in solving the problems of monophyly and phylogenetic position of scorpaeniforms is related to the many members of the Acanthopterygii or Percomorpha with which comparisons should be made. Recently, Johnson (1993) pointed out a close relationship between the scorpaeniforms and champsodontids, owing to the similarity of the sensory canal on the parietal, the first time that the Champsodontidae has been considered as being related to the Scorpaeniformes. This hypothesis was supported by the connection between the dorsal pterygiophores and epaxial musculature, determined by Gill & Mooi (1995). Subsequently, Mooi & Johnson (1997) expanded Johnson's (1993) study and proposed that the Champsodontidae be included within the Scorpaenoidei, as *incertae sedis*. Although the validity of this hypothesis should be tested carefully, since the authors did not comment on most of the synapomorphies which support the monophyly of the cottoid and scorpaenoid lineages, as presented by Shinohara (1994) and Imamura (1996), respectively, it is noteworthy that the study has provided a new perspective on the phylogeny of the order.

Most of the phylogenetic studies referred to above were based on adult morphology, whereas Washington *et al.* (1984 a) inferred relationships by using larval characters. Although difficulties sometimes exist in larval and juvenile identification, and the preparation of a continuous ontogenetic series, the characters found in early life stages are valuable for both testing the homologies, as pointed out by Johnson (1993), and also for reconstructing more realistic relationships in combination with adult characters (*e.g.*, Baldwin & Johnson, 1993). On the other hand, molecular phylogenetic analyses using DNA data are also valuable and positive approaches from this discipline are needed.

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