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Phylogeny of the Family Pholididae (Blennioidei) with a Redescription of *Pholis* Scopoli

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Abstract A cladistic analysis of Pholididae was made on the basis of morphological characters and of color of all 14 species. Polarity of a character was determined by out-group comparison using *Bathymaster* and Stichaeoidea (excluding Pholididae) as out-groups. Four genera were accepted. *Rhodymenichthys* and *Apodichthys* are sister groups. *Allopholis* and *Pholis* are sister groups. *Enedrias* was synonymized with *Pholis*.

The family Pholididae is considered monophyletic due to the possession of hemonephrapophyses but its sister group relationship has not been demonstrated in the superfamily Stichaeoidea (Yatsu, 1981). This study is aimed to elucidate the phylogenetic interrelationships of Pholididae at species level by cladistic analysis (Hennig, 1966) on the basis of morphological differences. Makushok (1958) and Yatsu (1981) should be referred for the general morphology, distribution and taxonomy.

Fourteen or fifteen species are classified in Pholididae depending on the status of *Pholis nea* (Peden et Hughes, 1984). I examined all species including *P. nea*, and I tentatively regarded *P. nea* as an amphi-Pacific twin subspecies of *Pholis ornata*. The results would not be affected by this action because they are not different from each other in the present set of character states. Scientific names follow those of Yatsu (1981) except for *Enedrias*. *Enedrias* is synonymized with *Pholis* which is redescribed below.

Material

Osteological investigation was made on cleared and alizarin-stained material listed below. Data on external morphology, vertebral number and color were derived from Yatsu (1981). Comparative data of the superfamily Stichaeoidea and *Bathymaster* was taken mainly from Makushok (1958) and from an alizarin-stained specimen of *Bathymaster signatus* respectively. Cleared and alizarin-stained specimens of Stichaeoidea were also examined to corroborate or make up for the observations by Makushok (1958).

Pholis gunnellus, NMC (National Museum of Canada) 73-337, 110.5 mm in standard length (SL), off Newfoundland I., Canada. *Pholis ornata*, NSMT-P (National Science Museum, Tokyo) 18583, 3 specimens, 78.2–114.3 mm SL, off British Columbia, Canada; NSMT-P 10070 (*Pholis nea*), 83.3 mm SL, off Pacific coast of Hokkaido, Japan. *Pholis fasciata*, NMC 65-568, 146.0 mm SL, off Northwest Territories, Canada. *Pholis picta*, HUMZ (Laboratory of Marine Zoology, Faculty of Fisheries, Hokkaido University) 3883, 164.2 mm SL, off Kuril Is. *Pholis crassispina*, MTUF (Museum, Tokyo University of Fisheries) 24155, 2 specimens, 105.4 and 114.5 mm SL, off Hakodate, Japan. *Pholis nebulosa*, MTUF 24156, 2 specimens, 116.0 and 116.5 mm SL, off Yokohama, Japan. *Pholis fangi*, ZUMT (Department of Zoology, University Museum, University of Tokyo) 51484, 135.1 mm SL, northern East China Sea; NSMT-P 18656, 3 specimens, 136.3–153.7 mm SL, Pusan Fish Market, Korea. *Allopholis laeta*, NSMT-P 18528, 101.1 mm SL, off Pacific coast of Alaska, U.S.A. *Allopholis clemensi*, BCPM (British Columbia Provincial Museum) 976–1290, 2 specimens, 90.2 and 91.4 mm SL, off British Columbia. *Allopholis schultzi*, NSMT-P 18521, 93.3 mm SL, off California, U.S.A. *Rhodymenichthys dolichogaster*, ZUMT 16172, 108.1 mm SL, off Iwate Pref., Japan. *Apodichthys flavidus*, NSMT-P 18532, 67.2 mm SL, off California. *Apodichthys fucorum*, NSMT-P 18538, 97.1 mm SL, off California. *Apodichthys sanctaerosae*, NSMT-P 18535, 131.7 mm SL, off California.

Comparative material. *Bathymaster signatus*, MTUF 24595, Bering Sea. *Stichaeus nozawae*, *Stichaeopsis nana*, *Opisthocentrus ocellatus*, *Lumpenus sagitta*, *Alectrias benjamini*, *Cebidichthys violaceus*, *Dictyosoma burgeri*, *D. rubrimaculata*, *Ernogrammus hexagrammus*, *Phytichthys chirus*, *Xiphister atropurpureus*, *X. mucosus*.

Methods

Morphology. A camera lucida, Wild M-7A, was used for osteological observation and drawing. Measurements for the urohyal bone are shown in Fig. 1. Osteological terminology follows that of Monod (1968) for the caudal skeleton, and Springer (1968) for the other parts except for the infraorbitals. Terminology of the cephalic sensory canal system follows that of Yatsu (1981).

Phylogenetic inference. A character was defined as a suit of attributes that were presumed functionally and/or developmentally correlated. Polarity of a character was determined by outgroup comparison using an operational rule that "for a given character with 2 or more states within a group, the state occurring in related groups is assumed to be plesiomorphic state . . ." (Watrous and Wheeler, 1981). This rule was at first applied to Pholididae (in-group) and the other families of Stichaeoidea (related groups), as the sister group of Pholididae has not been known. When the plesiomorphic state of a character could not be determined by the rule due to the occurrences of two or more common states to Pholididae and the other stichaeoids, the rule was applied to Stichaeoidea (in-group) with *Bathymaster* as an outgroup. Then polarity of a character in Pholididae was determined along with the *Bathymaster*-stichaeoid polarity. *Bathymaster* was assumed to be a related group of Stichaeoidea according to my personal observations (cf. Table 1) and according to the opinion by Gosline (1968: 63) that ". . . it [Bathymasteridae] stands on the percoid side of the Zoarceoidae [sic] and, hence, may be considered the most generalized family in the group."

In constructing the cladogram, I preferred the cladogram with the least number of parallelisms.

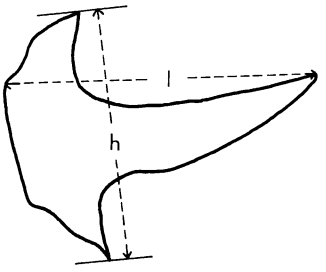

Fig. 1. Measurements of height (h) and length (l) of urohyal bone.

Genus *Pholis* Scopoli

Type species. *Blennius gunnellus* Linnaeus.

Diagnosis. Ito absent, ifo 6, first and second anal spines equal in size.

Description. Body prominently elongate (*P. fasciata* and *P. picta*) or not so elongate for this family. Head with or without scales. Vertebrae 76–101. Abdominal vertebrae less than 46. Cephalic sensory canal opening formula is generally: na 2, ito 0, ifo 6, apo+ppo 3+3, oc 1-1-1, mn+pop 4+5. *Pholis* contains seven species.

Polarity of characters

More or less clear morphological differences were found in the following eleven characters at species level of Pholididae. Polarity of eleven characters of Pholididae is described below.

1. Cephalic sensory pores. Interspecific variations in number of pores were observed in three pore series: presence or absence of an interorbital pore (ito), 3 or 4 mandibular pores (mn), 5 or 6 infraorbital pores (ifo). According to the reductive trend in number of cephalic sensory pores (Table 1), absence of ito, 3 mn and 5 ifo are all apomorphous, though the latter two have no information on phylogenetic inference as they are autapomorphous at the species level (3 mn occurs only in *Allopholis schultzi* and 5 ifo is found only in *Rhodymenichthys dolichogaster*). Thus there are only two informative character states, 1a (ito present) and 1b (ito absent), of which 1a represents the plesiomorphous condition. Loss of a pore is caused not only from the closure of a pore on the skin but also from the closure of an exit from canal-containing bones in the cases of ito and mn.

2. Infraorbital bones. Infraorbital bones are assumed, from Table 1, basically composed of a lacrymal, 4 infraorbitals (*sensu strict*) and a dermosphenotic (character state 2a, Fig. 2a). *Apodichthys* has totally 5 infraorbital bones probably caused from fusion of the uppermost infraorbital (*sensu strict*) to the dermosphenotic (character state 2b, Fig. 2d). A reductive trend in number of infraorbital bones is found in *Bathymaster*-stichaeoid polarity, where the causes of reduction probably include fusion of some parts and loss of infraorbital bones (see figs. 25 and 45 of Makushok, 1958). Although Makushok (1958) showed 5

infraorbital bones of *Pholis gunnellus* in his fig. 29b, the present material of *P. gunnellus* had 6 infraorbital bones on each side. Contrary to the reductional trend, total number of infraorbital bones increased to 7–12 in *Allopholis* and to 6–11 in *Pholis fangi* (Fig. 2b, c). Based on extensive material of *Pholis laeta* (sic) and *Pholis ornata* (excluding *P. nea*), Peden and Hughes (1984) showed the total number of infraorbital bones varied from 7 to 10 (usually 8) in *P. laeta* (sic) and from 5 to 7 (usually 6) in *P. ornata*. The increased number may be apomorphous and informative, however I refrain from establishing the third character state (more than 7 infraorbital bones) because variation of number in the other species of *Allopholis* has not been studied yet. Thus there remain two character states, 2a (6 or more infraorbital bones) and 2b (5 infraorbital bones), the former representing the plesiomorphous condition.

3. Skull. The skull is constructed more or less in a similar fashion in all species except for the

Table 1. Comparison of selected characters of *Bathymaster* and Stichaeoidea. Data for Stichaeoidea were taken mainly from Makushok (1958), partly from present observation. CP_2, second pre-ural centrum; HL, head length.

Character	*Bathymaster*	Stichaeoidea excl. Pholididae	Pholididae
Cephalic sensory canal system:			
canal	well developed	well developed or partly reduced	well developed
number of pores	ca. 200	8 to ca. 150	48, 49 or 50
ito (an interorbital pore)	present	present or absent	present or absent
Number of infraorbital bones	6	1, 2, 3, 5 or 6	5, 6 or 7–10
Position of pterosphenoid	pterosphenoid separates frontal from parasphenoid to form a part of posterior wall of orbit	pterosphenoid is excluded from posterior wall of orbit	
Caudal fin and its supporting skeleton:			
neural process of CP_2	reduced	reduced or well developed	reduced or well developed
haemal process of CP_2	autogenous to CP_2	autogenous or fused to CP_2	autogenous or fused to CP_2
hypural 5	present	present or absent	present or absent
caudal procurrent rays	not extend to dorsal and anal fins	not extend to dorsal and anal fins	not extend or extend to dorsal and anal fins
Pectoral fin and shoulder girdle:			
number of rays	19–20	8–9 to 20–23 or absent	7–17
interspace between coracoid and cleithrum	present	present or absent	present or absent
Pelvic fin	present (I, 5)	I, 1–4 or absent	I, 1 or absent
1st and 2nd anal spines	1st spine smaller than 2nd spine	1st spine smaller or larger than 2nd or 1st spine lost	1st spine smaller or larger than 2nd spine
Number of vertebrae	54–55 in total	precaudal 14–59 mostly 14–31	precaudal 35–53
		caudal 29–209 mostly 29–60	caudal 37–59
Shape of urohyal bone	almost oblong	almost oblong or various	various

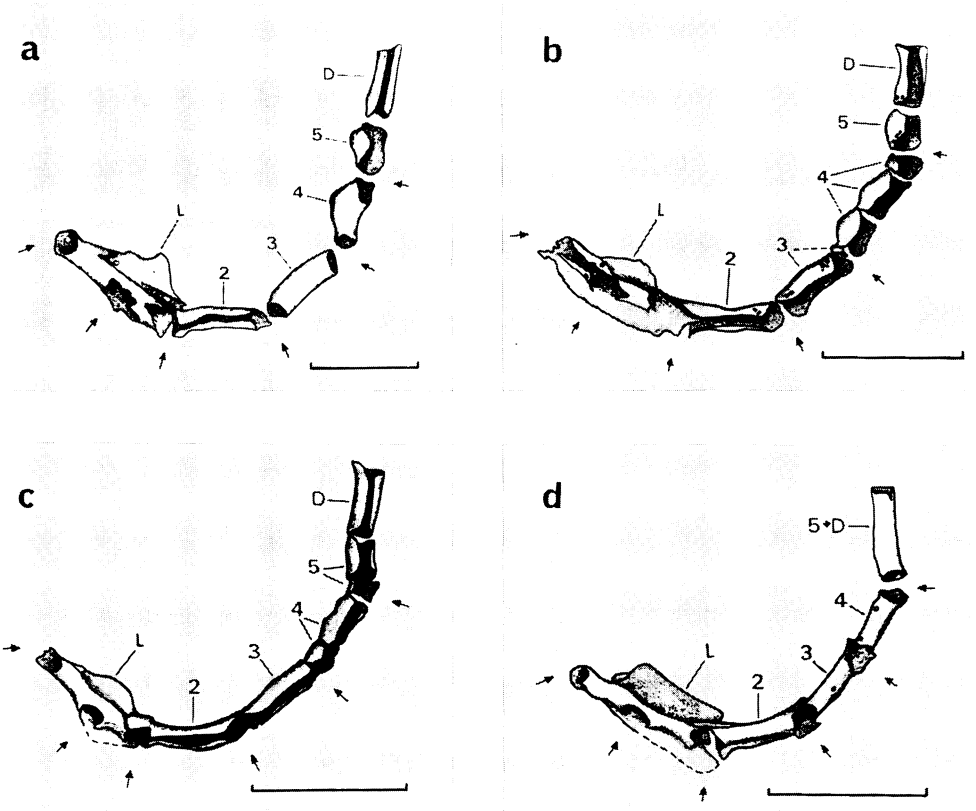

Fig. 2. Infraorbital bones in four species of Pholididae. a, *Pholis picta*, HUMZ 3883; b, *Allopholis laeta*, NSMT-P 18528; c, *Al. clemensi*, BCPM 976–1290; d, *Apodichthys fucorum*, NSMT-P 18538. D, dermosphenotic; L, lacrymal; 2–5, infraorbitals 2–5. Arrows indicate infraorbital openings of cephalic sensory canal system. Scales indicate 1 mm.

topographical relationship among the sphenotic, pterosphenoid and parasphenoid. The sphenotic is separated from the parasphenoid by the pterosphenoid which occupies the antero-dorsal edge of the trigemino-facialis opening (character state 3a, Fig. 3b) or the sphenotic meets the parasphenoid to exclude the pterosphenoid from the edge of the trigemino-facialis opening (state 3b, Fig. 3d). The character state 3a is an assumed plesiomorphic condition because the state 3b is not known from other stichaeoids and because there is a trend of diminishing the laterally exposed area of the pterosphenoid by contact of the frontal with the parasphenoid (Table 1).

4. Caudal fin and its supporting skeleton. Interspecific variations were observed in the following four parts. 1) Neural process of second preural centra (CP_2) reduced being lower than that of preceding centra (sub-character state 1α) or well developed being as high as that of preceding centra (state 1β). 2) Haemal process of CP_2 autogenously attached to CP_2 (state 2α) or fused to CP_2 (state 2β). 3) Hypural 5 present (state 3α) or absent (state 3β). 4) Caudal procurrent rays do not extend to the ends of dorsal and anal fins (state 4α) or extend anteriorly to form a more or less continuous series of vertical fin rays (state 4β). Four different combinations of these sub-characters were actually distributed in Pholididae:

character state 4a; 1β, 2α, 3α, 4α (Fig. 4a)

character state 4b; $1\alpha/\beta$, 2α, $3\alpha/\beta$, 4β (e.g. Fig. 4b)

character state 4c; 1α, 2α, 3α, 4β (Fig. 4c)

character state 4d; 1α, 2α, 3β, 4β (Fig. 4d)

character state 4e; 1α, 2β, 3β, 4β (Fig. 4e)

According to the trends in Table 1, sub-character

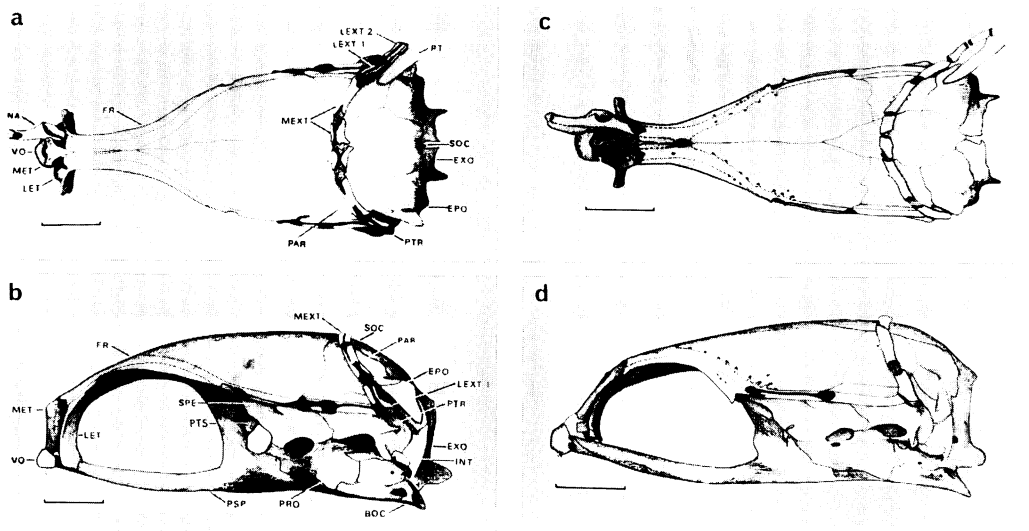

Fig. 3. Skull in two species of Pholididae. a and b, dorsal and lateral views of skull of *Pholis gunnellus*, NMC 73-337; c and d, dorsal and lateral views of skull of *Apodichthys sanctaerosae*, NSMT-P 18535. BOC, basioccipital; EPO, epiotic; EXO, exoccipital; FR, frontal; INT, intercalar; LET, lateral ethmoid; LEXT 1–2, lateral extrascapulars 1–2; MET, median ethmoid; MEXT, median extrascapular; NA, nasal; PAR, parietal; PRO, prootic; PSP, parasphenoid; PT, posttemporal; PTR, pterotic; PTS, pterosphenoid; SOC, supraoccipital; SPE, sphenotic; VO, vomer. Scales indicate 1 mm.

states 1α, 2α, 3α and 4α represent plesiomorphous conditions. In addition to the actual four character states, a hypothetical set of sub-character states (state 4x), all of which represent plesiomorphous conditions, is needed to express the polarity. Three different trends are parsimoniously assumed in this character:

$$\begin{array}{l} \nearrow 4a \\ 4x \rightarrow 4b \\ \searrow 4c \rightarrow 4d \rightarrow 4e \end{array}$$

5. Pectoral fin and shoulder girdle. There are four different character states combining two sub-characters, the length of pectoral fin (PL) with the presence or absence of the interspace between the coracoid and cleithrum: PL more than 25% of head length (HL) and the interspace present (character state 5a, Fig. 5a); PL more than 25% of HL and the interspace absent (state 5b, Fig. 5b); PL 10–20% of HL and the interspace present (state 5c, Fig. 5c); PL less than 5% of HL and the interspace present (state 5d, Fig. 5d). Because *Bathymaster* has a large pectoral fin and the interspace, plesiomorphous condition is the state 5a and two extremes of apomorphy are represented by the state 5b on the one hand and the state 5d via 5c on the other hand.

6. Pelvic fin and girdle. Pholididae have a pelvic fin composed of a spine and a ray and a pelvic girdle (character state 6a) except for *Apodichthys*. The pelvic fin and girdle are lost in *Apodichthys* (state 6b). Loss of these elements is an apparent specialization. Several specimens of *Pholis fasciata* from Greenland lack pelvic fins (Jensen, 1942), but *P. fasciata* was given the state 6a because specimens without the pelvic fin were expected to be rare.

7. Anal spines. Two different changes had probably occurred in this character. One is the enlargement of the first anal spine and its proximal pterygiophore in *Apodichthys* compared with the nearly equal size of the first and second spines in the other genera. Another change is the development of a groove on the ventral surface of the enlarged first spine in *Apodichthys flavidus*. The latter condition is not known from other stichaeoids. Along the presumed evolutionary sequence, three actual character states are arrayed

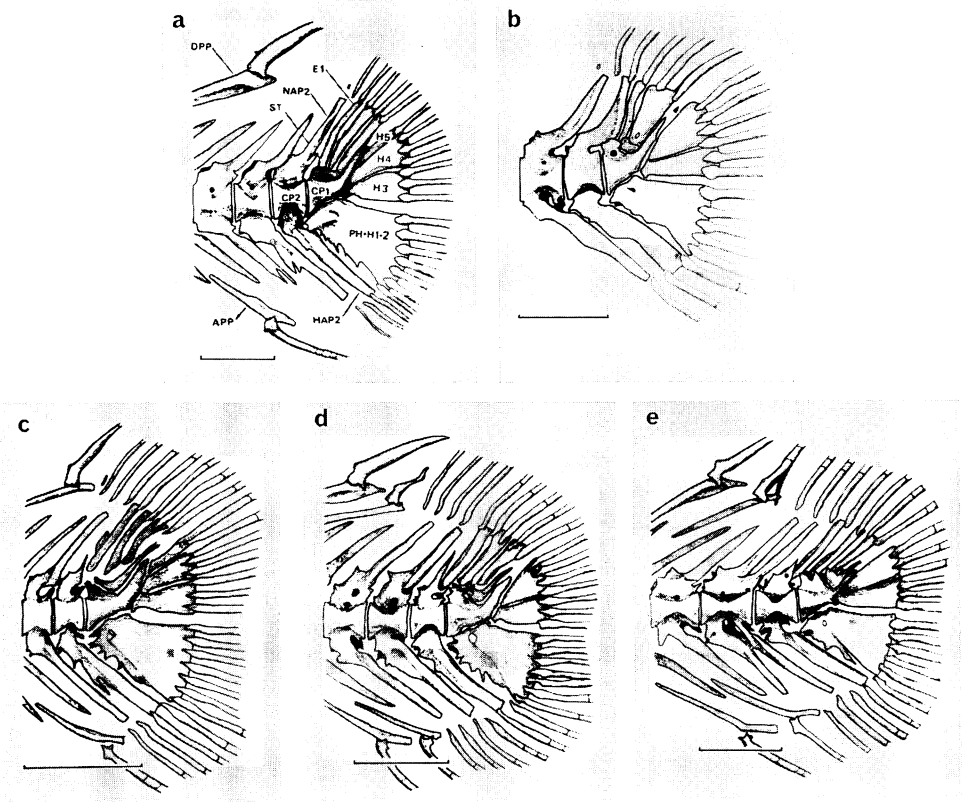

Fig. 4. Caudal skeleton and vertical fins of caudal region in five species of Pholididae. a, *Pholis crassispina*, MTUF 24155; b, *Rhodymenichthys dolichogaster* (vertical fins omitted), ZUMT 16172; c, *Apodichthys flavidus*, NSMT-P 18532; d, *Ap. fucorum*, NSMT-P 18538; e, *Ap. sanctaerosae*, NSMT-P 18535. APP, posteriormost anal proximal pterygiophore; CP1 and CP2, first and second pre-ural centra; DPP, posteriormost dorsal proximal pterygiophore; E1, first epural; H1–H5, hypurals 1–5; HAP2, haemal process of second pre-ural centrum; NAP2, neural process of second pre-ural centrum; PH, parhypural; ST, stegural. Scales indicate 1 mm.

as follows: normally-shaped first anal spine as large as the second spine (state 7a), normally-shaped first anal spine more than twice as thick as the second spine (state 7b), the first spine with a ventral groove much larger than the second spine (state 7c).

8. Vertebral number. Total vertebral number varies from 80 to 105 within the Pholididae (Yatsu, 1981). Although no clear gap was found in total number, the precaudal vertebral number distinctly separates *Apodichthys* from other genera: precaudal vertebrae 49–53 in *Apodichthys* (character state 8b), or 35–46 in the other genera (state 8a). According to a trend of increase in both caudal and precaudal vertebrae (Table 1), character state 8a is plesiomorphous.

9. Scales on head. Two distinct conditions are reported in this character (Yatsu, 1981): small scales present on the head anterior to the occipital sensory canal (character state 9b) and scales absent from the head (state 9a). The state 9a represents plesiomorphous condition within Stichaeoidea.

10. Urohyal bone. Shapes of the urohyal in 14 species of Pholididae (Fig. 6) seem more or less distinct from those of Stichaeidae which show considerable variation by genera (personal observation). The proportion of the urohyal expressed by the percent of height by length (see Fig. 1) is different by species and it allowed me to distinguish

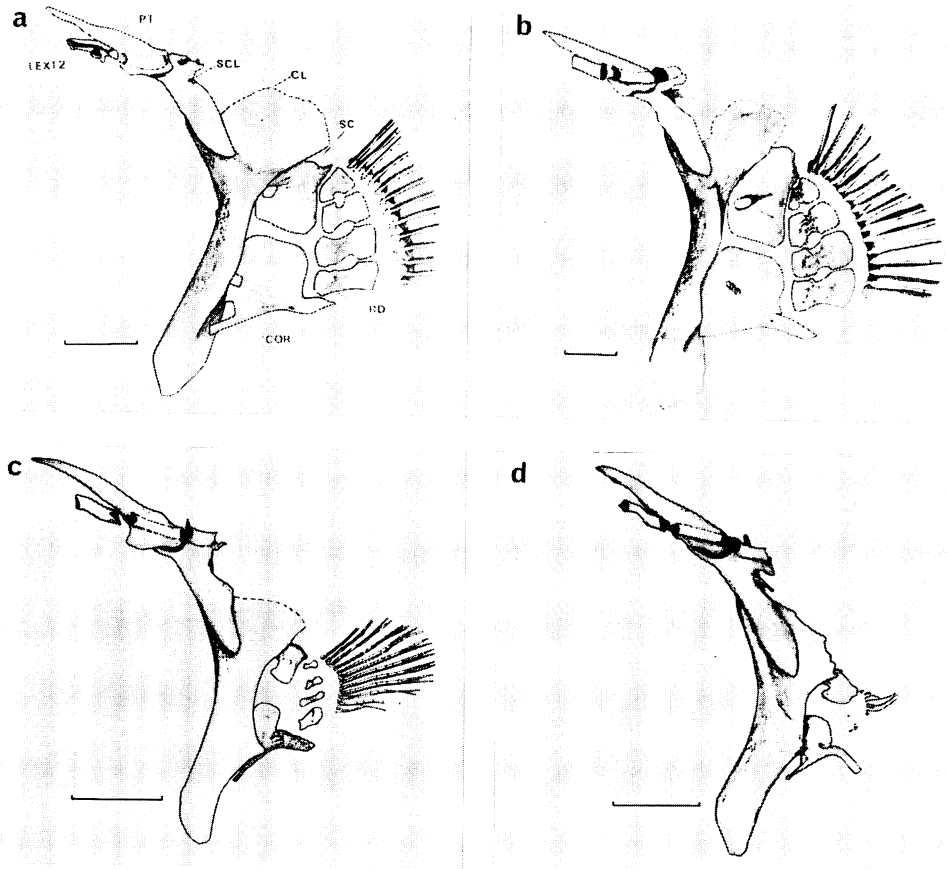

Fig. 5. Shoulder girdle and pectoral fin in four species of Pholididae. a, *Pholis gunnellus*, NMC 73-337; b, *Pholis fangi*, ZUMT 51484; c, *Apodichthys fucorum*, NSMT-P 18538; d, *Ap. sanctaerosae*, NSMT-P 18535. CL, cleithrum; COR, coracoid; LEXT2, lateral extrascapular 2; PT, posttemporal; RD, radial; SC, scapula; SCL, supracleithrum. Scales indicate 1 mm.

two character states: height is 125–136% of length in *Allopholis* and *Pholis ornata* (character state 10b) and 81–93% of length in the other species (state 10a). Since oblong urohyals are known from both *Bathymaster* and Stichaeoidea (Table 1), and such high urohyals are expected rare from my personal observation on Stichaeidae, the state 10a is assumed to be plesiomorphous.

11. Color. Compared with the other genera in which each species is variously, but specifically, ornamented by bars, blotches and spots (character state 11a), *Rhodymenichthys* and *Apodichthys* are uniformly olive (*R. dolichogaster* with a dark streak on head) in preserved conditions or polychromatic when alive (e.g., dark brown, bright-green, tan, red) (state 11b). Since a polychromatic condition has not been reported from other stichaeoids, the state 11a represents the plesiomorphous condition.

Figure 7 summarizes the distribution of character states in 14 species of Pholididae.

Since several polarities were determined by the condition of *Bathymaster signatus*, discovery of different character states in the other two genera of Bathymasteridae would force me to reconsider the polarities. If two or more common states are observed both in Pholididae and Bathymasteridae as well as the other Stichaeoidea, the polarity can not be immediately determined. Meanwhile, as internal structures (or phylogenetic interrelationships) of Stichaeoidea are established, many of the present assumption of polarities should be tested.

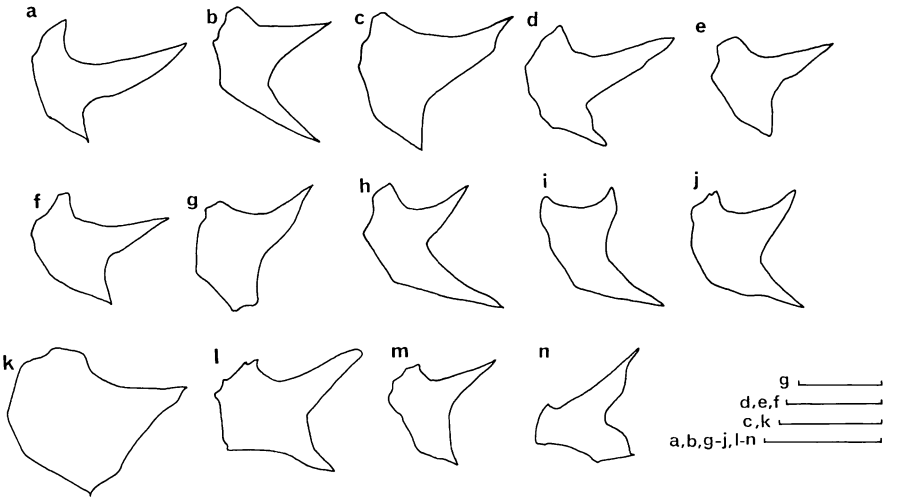

Fig. 6. Urohyal in fourteen species of Pholididae. a, *Pholis gunnellus*, NMC 73-337; b, *P. ornata*, NSMT-P 10070; c, *P. fasciata*, NMC 65-568; d, *P. picta*, HUMZ 3883; e, *P. crassispina*, MTUF 24155; f, *P. nebulosa*, MTUF 24156; g, *P. fangi*, ZUMT 51484; h, *Allopholis laeta*, NSMT-P 18528; i, *Al. schultzi*, NSMT-P 18521; j, *Al. clemensi*, BCPM 976-1290-2; k, *Rhodymenichthys dolichogaster*, ZUMT 16172; l, *Apodichthys flavidus*, NSMT-P 18532; m, *Ap. fucorum*, NSMT-P 18538; n, *Ap. sanctaerosae*, NSMT-P 18535. Scales indicate 1 mm.

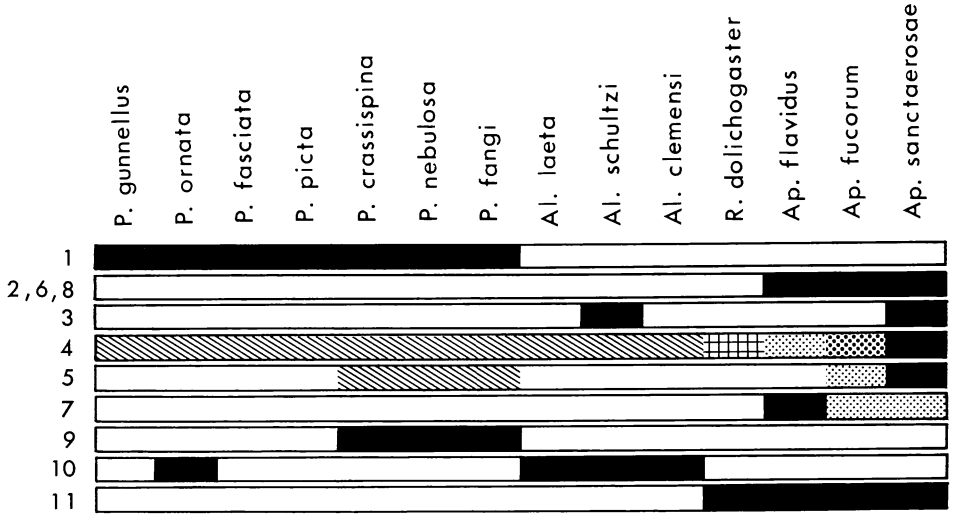

Fig. 7. Summary of character states of 14 species of Pholididae. Open areas represent plesiomorphous conditions. For character number, see text and Table 1. Black, striped and latticed areas represent most apomorphous conditions whose polarities are different from each other within a character. Dotted areas represent the intermediate condition between plesiomorphous and most apomorphous (black areas) states. In character 4, for example, there are three different extremes of a polarity among which an extreme represented by black area is accompanied by two intermediate states (dotted areas). Note that the most plesiomorphous state of character 4 is not discovered in living species.

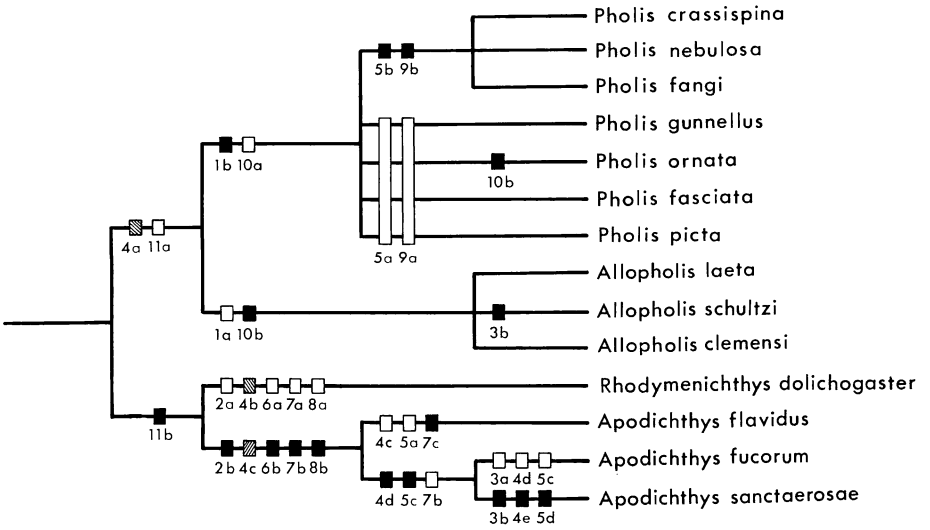

Fig. 8. Cladogram of Pholididae. Hollow and solid boxes represent plesiomorphous and apomorphous conditions respectively. Codes next to each boxes indicates a character state described in text and summarized in Fig. 7.

Phylogeny and classification

A synthesis of the present cladistic analysis appears in Fig. 8. A branching sequence was fully established for the *Rhodymenichthys-Apodichthys* group but unresolved are the intrageneric relationships in *Pholis* and in *Allopholis*. Monophyly of each four genera was proved. Intergeneric relationships are expressed as follows. *Rhodymenichthys* and *Apodichthys* are sister groups to form a higher category although here unnamed. *Allopholis* and *Pholis* are sister groups forming an unnamed higher category that is comparable to the preceding.

Parallelisms were found in character 3 (skull) and 10 (urohyal), though the proportion of the urohyal still serves as information on monophyly of *Allopholis*.

Some of the evolutionary trends seem to be correlated with the environment. A polychromatic condition matching to the color of sea weeds where they live (cf. Burgess, 1978) and the elongation of body (increased vertebral number) accompanied by the reduction of paired fins and by the modification of caudal fin probably has special correlation with their life-style and locomotion in weedy intertidal and subtidal environments. Although members of the *Pholis-Allopholis* group also live in the similar environments (table 1 of Yatsu, 1981), they are not polychromatic. This fact leaves an interesting question on the origin and meanings of polychromatic color. Also interesting is the relationship between phylogeny and geographical distribution. Zoogeography of Pholididae will be dealt with elsewhere in the future.

The generic classification of Yatsu (1981) is compatible with the interrelationships of Pholididae except for the separation of *Enedrias* from *Pholis*. Subfamilies and genera classified by Makushok (1958) are not acceptable from the present phylogenetic point of view. Makushok (1958) recognized two subfamilies, Pholinae (sic) and Apodichthyinae. The former is composed of one genus, *Pholis*, with ten species. The latter contained *Apodichthys flavidus, Xererpes fucorum* (sic) and *Ulvicola sanctaerosae* (sic). The subfamily Pholinae (sic) is paraphyletic (*sensu* Nelson, 1971) because of the inclusion of *Pholis dolichogaster* (sic). Three monotypic genera in Apodichthyinae were apparently over-split. Makushok's (1958) classification was presumably based on the degree of morphological differences rather than monophyly, though his fig. 33 indicates monophyly of the Pholinae (sic). The branching sequence in Apodichthyinae in fig. 33 of Makushok (1958) also seems to be based on the great morphological differences between *Ulvicola sanctaerosae* (sic) and

the other two species.

Acknowledgments

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ニシキギンポ科の系統およびニシキギンポ属の再記載

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ニシキギンポ科の全 14 種の外部形態，骨格系および色彩に基づき，分岐分類学の手法により種の系統的関係を推論した．形質の進化の方向(極性)は out-group を用いる方法によった．ニシキギンポ科の out-group として同科を除くタウエガジ上科を用いたが，これにより極性が決定できない場合は，ソコメダマウオ属 *Bathymaster* をタウエガジ上科の out-group として推定した上科内の極性に基づいてニシキギンポ科内の極性を決定した．分岐図の構築は，並行進化が最少となるように行った．その結果，単系統群として 4 属を認めるのが妥当であり，それらの系統的関係は次のように表現される：1) *Rhodymenichthys* と *Apodichthys* は姉妹関係にあり高次の単系統群を形成する，2) *Allopholis* と *Pholis* は姉妹関係にあり 1) と同レベルの単系統群を形成する．ギンポ属 *Enedrias* はニシキギンポ属 *Pholis* のジュニアシノニムとし，ニシキギンポ属の再記載を行った．

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