

RYUKYUPERCIS, A NEW GENUS OF PINGUIPEDID FISH FOR THE SPECIES *PARAPERCCIS GUSHIKENI* (TELEOSTEI: PERCIFORMES) BASED ON THE PHYLOGENETIC RELATIONSHIPS OF THE FAMILY

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ABSTRACT. – A new pinguipedid genus, *Ryukyupercis*, was established based on *Paraperccis gushikeni* Yoshino, 1975, from the reconstructed phylogenetic relationships of the family Pinguipedidae. *Ryukyupercis* new genus is inferred to be nested within the Family Pinguipedidae and is the sister group of the monophyletic group comprising of the genus *Kochichthys* Kamohara, 1960 and *Paraperccis* Bleeker, 1863. The new genus is easily separable from the other five genera of Pinguipedidae (i.e., *Kochichthys*, *Paraperccis*, *Pinguipes* Cuvier, 1829, *Prolatilus* Gill, 1865 and *Pseudoperccis* de Miranda-Ribeiro, 1903) by having a combination of the following 25 characters: 6 dorsal fin spines; 23 - 24 pectoral fin rays; no iris lappet; 4 - 6 teeth on vomer, palatine and ectopterygoid; endopterygoid and ectopterygoid autogenous; posteroventral margin of opercle very concave; beryciform foramen absent; cartilage on posterior margin of lowermost actinost extending ventrally; cartilaginous tip of elongate anterior limb of coracoid connected with the inner portion of the lateral flange of the cleithrum; the lowermost pectoral fin ray branched or unbranched; a single supraneural (= first supraneural); first dorsal pterygiophore supporting two spines; hemal arch of anterior caudal vertebrae large; 4 or 5 anal fin pterygiophores anterior to first hemal spine; 3 epurals; posterior portion of adductor mandibulae section 2 (A2) connected to preopercle only; adductor mandibulae section w extending to medial surface of suspensorium; anterior element of levator operculi connected with hyomandibula; gill-arch adductores I - III absent; protractor pectoralis comprising sheet-like element only; extensor proprius inserted on pelvis; adductor dorsalis present and scaled area of dorsal surface of head reaching to interorbital region.

KEY WORDS. – *Ryukyupercis* new genus, Pinguipedidae, phylogenetic relationships, synapomorphy.

INTRODUCTION

Yoshino (1975) described a pinguipedid species, *Paraperccis gushikeni*, based on five specimens collected from Okinawa Island, Ryukyu Islands, Japan (Fig. 1). When describing *P. gushikeni*, he noted several differences between the species and other species of *Paraperccis* Bleeker, 1863 (e.g., 6 dorsal spines and 23 - 24 pectoral fin rays in *P. gushikeni* vs. 4 - 5 dorsal spines and 14 - 21 pectoral fin rays in other *Paraperccis* species). Although *P. gushikeni* has been mentioned subsequently by several authors (e.g., Gloerfelt-Tarp & Kailola, 1984; Yoshino, 1984; Allen & Swainston, 1990; Shimada, 2002; Shibukawa et al., 2003), none of them discussed its generic placement. In this study, we examined

the osteological and myological characters, as well as the external morphology of *P. gushikeni*. We recognized several morphological differences between *P. gushikeni* and other *Paraperccis* species. We examined morphological characters to determine the phylogenetic analysis of the family Pinguipedidae and results have shown that *P. gushikeni* is the sister group of a monophyletic clade that includes *Kochichthys* and *Paraperccis*. Thus, we conclude that it is cladistically reasonable to establish a generic rank for *P. gushikeni*.

The purpose of the present study is to establish a new pinguipedid genus based on *P. gushikeni*, to reconstruct the phylogenetic relationships of the Pinguipedidae and to

demonstrate the phylogenetic position of the new genus established in this study.

MATERIALS AND METHODS

Terminology generally follows recent perciform studies on osteology (e.g., Baldwin & Johnson, 1993) and follows Winterbottom (1974) for myology. Specimen lengths were expressed as standard length, SL (mm). The data were analyzed using Phylogenetic Analysis Using Parsimony (PAUP) version 4.0b10 (Swofford, 2002), including the exhaustive search option. Character evolution was assumed as “ordered” (Wagner parsimony), or “unordered” (Fitch parsimony) when multiple states within the transformation series (TS) were difficult to order. Materials examined for the present study are deposited in SMBL and URM. Institutional acronyms follow Leviton et al. (1985).

TAXONOMY

Ryukyupercis, new genus

(New Japanese name: Wani-toragisu zoku)

(Figs. 1 to 4, 5B, 6 to 9)

Type species. – *Parapercis gushikeni* Yoshino, 1975.

Material examined. – Holotype - 301 mm SL, SMBL F-73371, external examination only. Paratypes - SMBL F-73372-73375, 4 specimens, 241 - 297 mm, external examination only.

Non-types - URM-P 6476, 1 specimen, 277 mm, partially dissected; URM-P 20911, 23291, 25409, 25410, 29472, 37954, 6 specimens, 281-314 mm, external examination only; URM-P 25410, 1 specimen, 304 mm, dissected.

Other pinguipedid materials, including five genera and 11 species, deposited in AMS, BSKU, CAS, HUMZ, MZUSP and UW were used for the phylogenetic analysis. The specimens used are listed in Imamura & Matsuura (2003).

Diagnosis. – A new genus of Pinguipedidae with the following 25 characters: 6 dorsal fin spines; 23 - 24 pectoral

fin rays; no iris lappet (sensu Matsubara & Ochiai, 1955); teeth on vomer, palatine and ectopterygoid (Figs. 2 & 7); endopterygoid and ectopterygoid autogenous (Figs. 2 & 7); posteroventral margin of opercle very concave (Fig. 2); beryciform foramen absent (Fig. 3); cartilage on posterior margin of lowermost actinost extending ventrally (Fig. 4); cartilaginous tip of anterior limb of coracoid connected to inner portion of lateral flange of cleithrum (Fig. 5B); lowermost pectoral fin ray branched or unbranched; hemal arch of anterior caudal vertebrae large, a single supraneural (= first supraneural); first dorsal pterygiophore supporting 2 spines; 4 or 5 anal fin pterygiophores anterior to first hemal spine; 3 epurals; posterior portion of adductor mandibulae section 2 (A2) connected to preopercle only (Fig. 6); adductor mandibulae section Aw extending to medial surface of suspensorium (Fig. 7); anterior element of levator operculi connected with hyomandibula (Fig. 6); gill-arch adductores I - III absent; protractor pectoralis comprised of a sheet-like element only; extensor proprius inserted on pelvis; adductor dorsalis absent and scaled area of dorsal surface of head reaching to interorbital region.

Etymology. – The new genus is named from the combination of the Ryukyu Islands (the locality of the type species) and generic name *Percis*, which was previously used for many pinguipedid species.

Remarks. – *Ryukyupercis* includes only *Parapercis gushikeni* at present.

PHYLOGENETIC POSITION OF RYUKYUPERCIS AMONG PINGUIPEDIDAE

Definition of the ingroup and outgroup for the phylogenetic analysis. – After anatomical examination of specimens of the genus *Ryukyupercis*, we reconfirmed that the genus belongs to the family Pinguipedidae. This is owing to the following 13 synapomorphies of the family identified by Imamura & Matsuura (2003): 7 infraorbitals (Fig. 8) (vs. 6 in basal percoids); supratemporal sensory canal on both sides

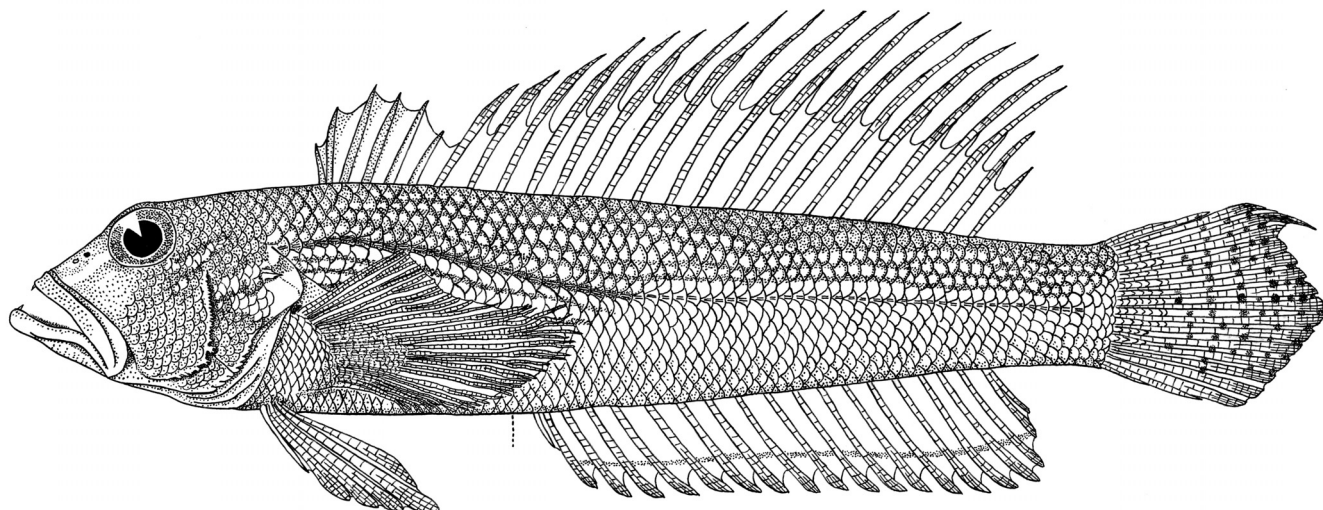


Fig. 1. *Ryukyupercis gushikeni*, SMBL F-73371, holotype, 301 mm SL. Lateral view.

continuous (vs. not continuous); hyomandibula with an oblique crest (Fig. 2) (vs. without); 6 branchiostegal rays (Fig. 3) (vs. 7); third epibranchial tooth plate absent (Fig. 9) (vs. present); scapula and coracoid partially overlapping (Fig. 4) (vs. separated); ventral portion of lateral flange of cleithrum very concave (Fig. 5B) (vs. not concave); anterior portion of epineurals (sensu Patterson & Johnson, 1995) expanded (vs. not expanded); 4 or 5 anal fin pterygiophores anterior to first hemal spine (vs. 1 or 2); serially associated element of first anal fin pterygiophore a soft ray (vs. the element is a spine); posterior portion of A1 nested within A2 (Fig. 6) (vs. not nested); levator operculi composed of 2 elements (Fig. 6) (vs. single element) and transversus dorsalis unbranched (vs. branched). Although the genus *Ryukyuperpis* lacks one synapomorphy of the family, which is the presence of adductores I - III, we recognize that the absence of these muscles is due to reversal of synapomorphy.

Imamura & Matsuura (2003) concluded that the genus *Prolatilus* Gill, 1865 is the basal clade within the family Pinguipedidae. They identified two derived characters of *Prolatilus*, the vomer and palatine without teeth, the former of which is an autapomorphy within the family. The latter is also found in several members of the genus *Paraperpis* (e.g., Cantwell, 1964; Rosa & Rosa, 1997; Imamura & Matsuura, 2003), but Imamura & Matsuura (2003) inferred that it evolved independently. In this study, we chose *Prolatilus* as the outgroup for the analysis to infer the phylogenetic position of *Ryukyuperpis*. We also omitted these two characters from the analysis.

On the other hand, Imamura & Matsuura (2003) found that *Pinguipes* Cuvier in Cuvier & Valenciennes, 1829, *Pseudoperpis* de Miranda-Ribeiro, 1903 and *Paraperpis* share the following four synapomorphies [and an additional character when accelerated transformation (ACCTRAN) is employed]: 1) posteroventral margin of opercle very concave; 2) lowermost pectoral fin ray branched; 3) adductor

mandibulae section Aw extending to medial surface of suspensorium; 4) adductor dorsalis present and 5) hemal arch of anterior caudal vertebrae large [when ACCTRAN is used]. *Ryukyuperpis* also has characters (1), (3), (4) and (5) (Figs. 2 & 7) while (2) are present or absent in the genus. Therefore, we selected *Paraperpis*, *Pinguipes*, *Pseudoperpis* and *Ryukyuperpis* as the ingroup for the phylogenetic analysis. In this study, we also included *Kochichthys* in the ingroup, although we could only examine some of its internal characters by using soft X-ray films. As pointed out by Imamura & Matsuura (2003), *Kochichthys* has at least four synapomorphies of the Pinguipedidae: a) supratemporal sensory canal on both sides continuous; b) hyomandibula with oblique crest (see also Rosa & Rosa, 1997); c) 6 branchiostegal rays and d) presence of a soft ray on the posterior portion of first anal fin pterygiophore. We have determined that it has 2 additional synapomorphies of the ingroup, namely posteroventral margin of opercle very concave and lowermost pectoral fin ray branched.

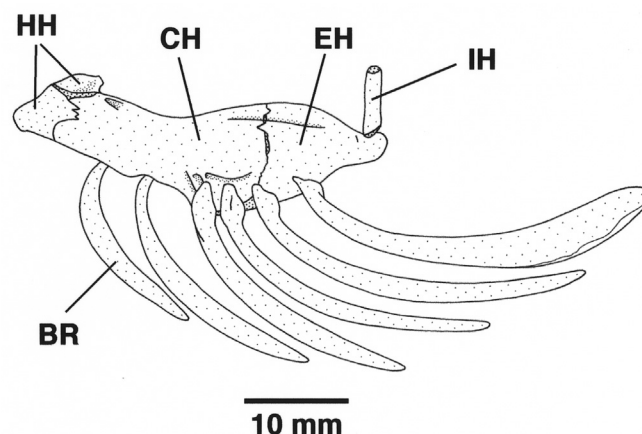


Fig. 3. Lateral view of hyoid arch of *Ryukyuperpis gushikeni*, URM-P 25410, 304 mm SL. BR = branchiostegal ray; CH = ceratohyal; EH = epihyal; HH = hypohyal; IH = interhyal.

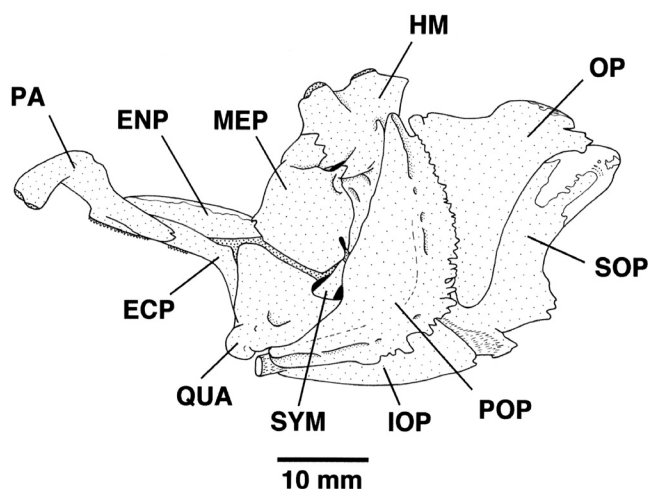


Fig. 2. Lateral view of suspensorium of *Ryukyuperpis gushikeni*, URM-P 25410, 304 mm SL. ECP = ectopterygoid; ENP = endopterygoid; HM = hyomandibula; IOP = interopercle; MEP = metapterygoid; OP = opercle; POP = preopercle; QUA = quadrate; SOP = subopercle; SYM = symplectic.

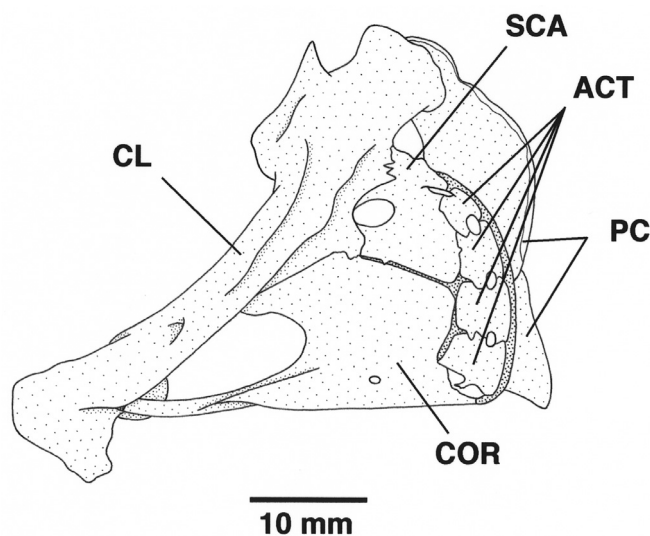


Fig. 4. Lateral view of shoulder girdle of *Ryukyuperpis gushikeni*, URM-P 25410, 304 mm SL. ACT = actinosts; CL = cleithrum; COR = coracoid; PC = postcleithrum; SCA = scapula.

Table 1. Matrix of characters used for the phylogenetic analysis of Pinguipedidae. Numbers of transformation series and characters correspond to those in the text and Fig. 10. Characters in parentheses indicate polymorphism.

Genus	Transformation Series	
	1 - 5	6 - 10
<i>Prolatilus</i> (outgroup)	0 0 0 0 0	0 0 0 0 0
<i>Kochichthys</i>	? ? ? 1 1	0 2 ? ? 1
<i>Parapercis</i>	1 1 2 (01) (01)	0 2 (012) 1 (12)
<i>Pinguipes</i>	0 0 0 1 0	1 0 0 0 1
<i>Pseudopercis</i>	0 1 0 1 0	1 0 1 1 1
<i>Ryukyuperpis</i>	1 1 1 (01) 0	1 1 0 1 1

Character argumentation. – In this study, we recognized the following characters in 10 transformation series, which vary within the ingroup and are informative for inferring the phylogenetic intrarelationships. The character matrix is shown

in Table 1. All characters, except for those in TS 3 and 10, were discussed in Imamura & Matsuura (2003). Only

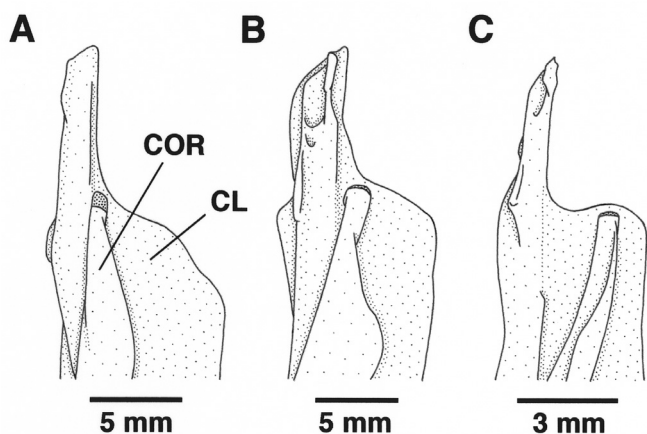


Fig. 5. Ventral view of shoulder girdle of A) *Prolatilus jugularis*, HUMZ 82279, 240 mm SL. CL = cleithrum; COR = coracoid. B) *Ryukyuperpis gushikeni*, URM-P 25410, 304 mm SL. C) *Parapercis multifasciata*, HUMZ 131744, 116 mm SL.

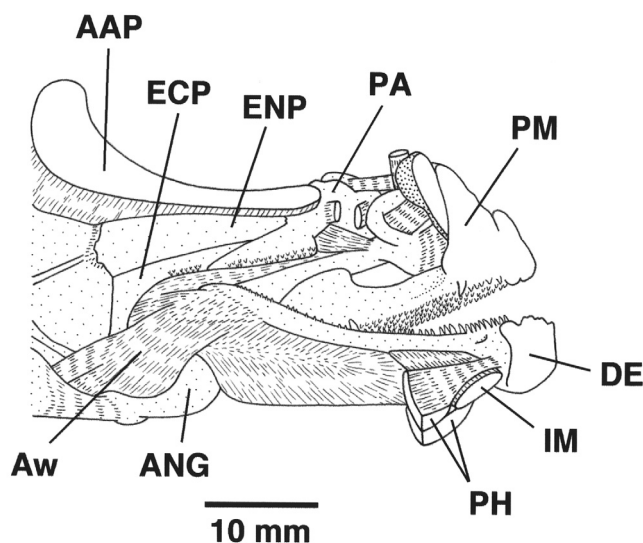


Fig. 7. Lateral view of jaws, suspensorium and associated muscles of *Ryukyuperpis gushikeni*, URM-P 25410, 304 mm SL. AAP = adductor arcus palatini; ANG = anguloarticular; Aw = adductor mandibulae section w; DE = dentary; ECP = ectopterygoid; ENP = endopterygoid; IM = intermandibularis; PH = protractor hyoidei; PA = palatine; PM = premaxilla.

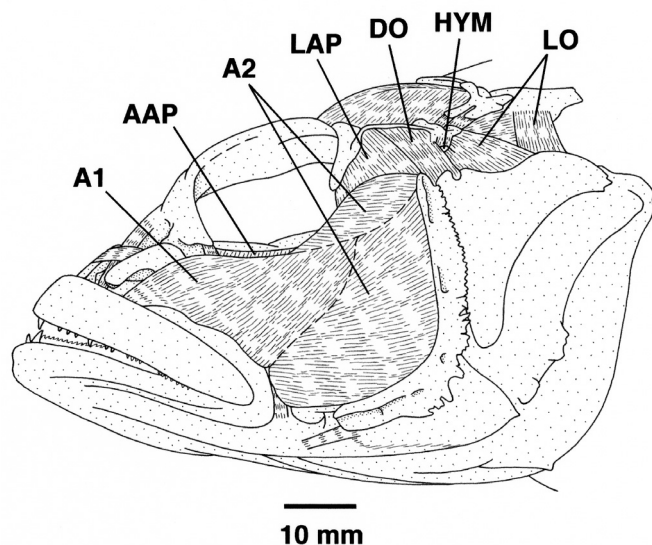


Fig. 6. Lateral view of head of *Ryukyuperpis gushikeni*, URM-P 25410, 304 mm SL. A1 = adductor mandibulae section 1; A2 = adductor mandibulae section 2; AAP = adductor arcus palatini; DO = dilatator operculi; HYM = hyomandibula; LAP = levator arcus palatini; LO = levator operculi.

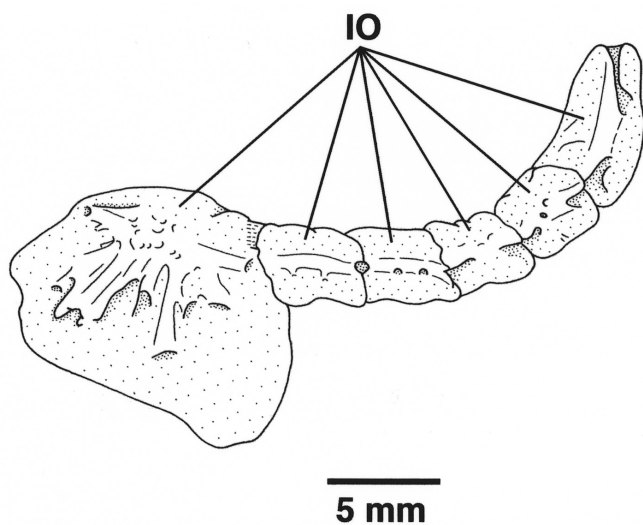


Fig. 8. Lateral view of infraorbital (IO) of *Ryukyuperpis gushikeni*, URM-P 25410, 304 mm SL. Uppermost infraorbital, which is firmly associated with the cranium, is not shown.

characters in TS 4, 5, 6, 7 and 10 could be examined in the genus *Kochichthys*.

TS 1. Bercyiform foramen (Fig. 3) - 0: absent; 1: present. The bercyiform foramen is absent in *Prolatilus*, *Pinguipes* and *Pseudoperca* but present in *Ryukyuperca* and *Paraperca*.

TS 2. Cartilage on posterior margin of lowermost actinost (Fig. 4) - 0: not extending ventrally; 1: extending ventrally. The cartilage on the posterior margin of the lowermost actinost was found to extend ventrally only in *Ryukyuperca*, *Pseudoperca* and *Paraperca*.

TS 3. Cartilaginous cap of elongate anterior limb of coracoid (Fig. 5) - 0: connected to lateral aspect of medial portion of cleithrum; 1: connected to inner portion of lateral flange of the cleithrum; 2: connected to outer portion of lateral flange of cleithrum (ordered). The cartilaginous cap of the elongate anterior limb of the coracoid is connected to the lateral aspect of the medial portion of the cleithrum in *Prolatilus* (Fig. 5A), *Pinguipes* and *Pseudoperca*. Whereas it is connected to the inner portion of the lateral flange of the cleithrum in *Ryukyuperca* (Fig. 5B) and to the outer portion of the lateral flange of the cleithrum in *Paraperca* (Fig. 5C).

TS 4. Lowermost pectoral fin - 0: unbranched; 1: branched. The lowermost pectoral fin ray is unbranched in *Prolatilus*, whereas it is branched in *Pinguipes* and *Pseudoperca*. The ray is usually branched in *Paraperca*, but Imamura & Matsuura (2003) mentioned that a few specimens of *Paraperca xanthozona* have an unbranched lowermost ray. The lowermost ray is branched or unbranched in *Ryukyuperca*.

TS 5. First supraneural - 0: present; 1: absent. The first supraneural is absent in *Kochichthys*, *Paraperca ramsayi* and *Paraperca multifasciata*, whereas it is present in the remaining taxa.

TS 6. Hemal arch of anterior caudal vertebrae - 0: small; 1: large. The hemal arch of the anterior caudal vertebrae is large in *Pinguipes*, *Pseudoperca* and *Ryukyuperca*, but it is small in *Prolatilus*, *Kochichthys* and *Paraperca*.

TS 7. Number of anal fin pterygiophores anterior to first hemal spine - 0: > 5 pterygiophores; 1: 4 - 5 pterygiophores; 2: 3 pterygiophores (ordered). There are more than 5 anal fin pterygiophores anterior to the first hemal spine in *Prolatilus* (6), *Pinguipes* (7), *Pseudoperca* (9 in *Pseudoperca numida* and 8 in *Pseudoperca semifasciata*), 4 or 5 in *Ryukyuperca* and only 3 in *Kochichthys* and *Paraperca*.

TS 8. Posterior portion of A2 (Fig. 6) - 0: connected to preopercle only; 1: connected to preopercle and levator arcus palatini; 2: connected to preopercle and posterodorsal portion of hyomandibula (unordered). The posterior portion of A2 is connected to the preopercle and levator arcus palatini in *Pseudoperca* and *Paraperca pulchella* and *Paraperca schauinslandi*. It is connected to the preopercle and posterodorsal portion of the hyomandibula in *Paraperca multifasciata* and *Paraperca cylindrica* and only to the preopercle in the remaining taxa.

TS 9. Anterior element of levator operculi (Fig. 6) - 0: not connected with hyomandibula; 1: connected with hyomandibula. The anterior element of the levator operculi interconnects the opercle and pterotic, but does not connect with the hyomandibula in *Prolatilus* and *Pinguipes*, whereas it also connects with the hyomandibula in *Pseudoperca*, *Ryukyuperca* and *Paraperca*.

TS 10. Scaled area of dorsal surface of head - 0: reaching to snout; 1: reaching to interorbital region; 2: restricted to occipital region (ordered). In *Prolatilus*, the dorsal surface of the head is mostly covered by scales and the scaled area reaches to the snout region. The scaled area reaches to the interorbital region in *Pinguipes*, *Pseudoperca*, *Ryukyuperca*, *Kochichthys* and *Paraperca haackei*, whereas it is restricted to the occipital region in *Paraperca*, except for *Paraperca haackei* (see Cantwell, 1964).

Phylogenetic relationships. - Our analysis of the phylogenetic relationships of the ingroup, produced a single most parsimonious tree, with a consistency index of 0.93 and tree length of 13 (Fig. 10).

Clade A - Includes all ingroup members. Clade A is unambiguously supported by characters 4-1, 6-1 and 10-1. The members of this clade also commonly possess three derived characters: posteroventral margin of opercle very concave (Fig. 2); adductor mandibulae section Aw extending to medial surface of suspensorium (Fig. 7) and adductor dorsalis present (Imamura & Matsuura, 2003).

Clade B - Includes *Pinguipes*. Although no characters support our analysis, *Pinguipes* autapomorphically has 2 epurals (vs. 3 in others) (Imamura & Matsuura, 2003).

Clade C - Includes all ingroup members except *Pinguipes*.

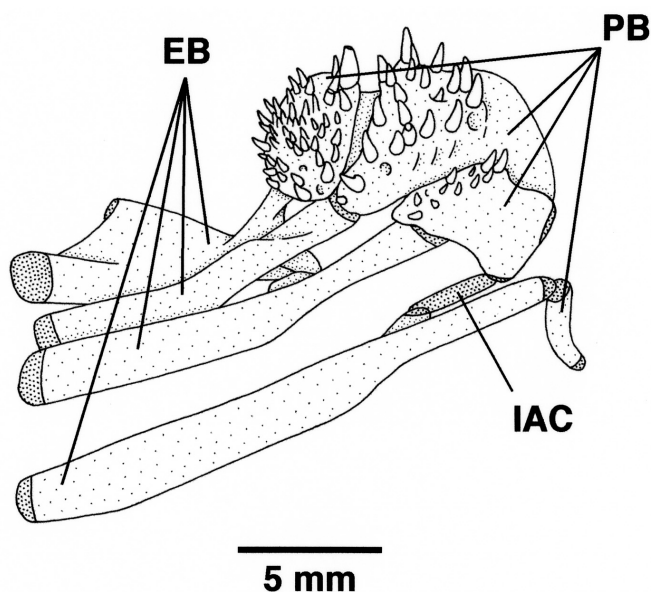


Fig. 9. Medial view of upper gill arch of *Ryukyuperca gushikeni*, URM-P 25410, 304 mm SL. EB = epibranchial; IAC = interarcual cartilage; PB = pharyngobranchial.

Clade C is supported unambiguously by characters 2-1 and 9-1.

Clade D - Includes *Pseudoperca*. Clade D is unambiguously supported by character 8-1.

Clade E - Includes *Ryukyuperca*, *Kochichthys* and *Paraperca*. Clade E is unambiguously supported by characters 1-1, 3-1 and 7-1.

Clade F - Includes *Ryukyuperca*. Although *Ryukyuperca* has no character support in our analysis, it autapomorphically has teeth on the ectopterygoid (vs. dentulous in others) (Fig. 2) and a single character reversal, the absence of adductores I - III, as mentioned above.

Clade G - Includes *Kochichthys* and *Paraperca*. Clade G is supported unambiguously by characters 6-0 (reversal) and 7-2 (and also 3-2 and 5-1 according to ACCTRAN).

Clade H - Includes *Kochichthys*. *Kochichthys* has character 5-1 when delayed transformation (DELTRAN) is accepted. *Kochichthys* also possesses an autapomorphic character, the first dorsal fin pterygiophore supporting a single spine (vs. two in others) (Imamura & Matsuura, 2003).

Clade I - Includes *Paraperca*. Clade I is supported by character 3-2 according to DELTRAN. In addition,

Paraperca has the following four autapomorphic characters: 1) a simple and broad iris lappet present (vs. absent in others); 2) endopterygoid and ectopterygoid fused (vs. autogenous) (Fig. 2); 3) protractor pectoralis composed of sheet-like anterior and robust posterior elements (sheet-like element only) and 4) extensor proprius inserted on cleithrum (on pelvis) (see also Imamura & Matsuura, 2003).

DISCUSSION

Our phylogenetic analysis of the family Pinguipedidae indicates that the monotypic *Ryukyuperca* is a distinct clade (Clade F) and is the sister group to the monophyletic Clade G, which comprises *Kochichthys* and *Paraperca*. Therefore, it is cladistically reasonable to separate *R. gushikeni* from the other species of *Paraperca*, in which *R. gushikeni* was previously classified (e.g., Yoshino, 1975, 1984; Gloerfelt-Tarp & Kailola, 1984; Allen & Swainston, 1990; Shimada, 2002) and to recognize a generic rank for the former to avoid paraphyly of *Paraperca*. *Ryukyuperca* is distinguished from all other pinguipedids in having autapomorphically, the ectopterygoid with teeth (Fig. 2) (vs. without teeth in others) and 23 - 24 pectoral fin rays [vs. 14 - 22 in others (according to Cantwell, 1964, Yoshino, 1975 and Rosa & Rosa, 1997)].

Ryukyuperca is also easily distinguished from *Paraperca* in having the following eight plesiomorphic characters relative

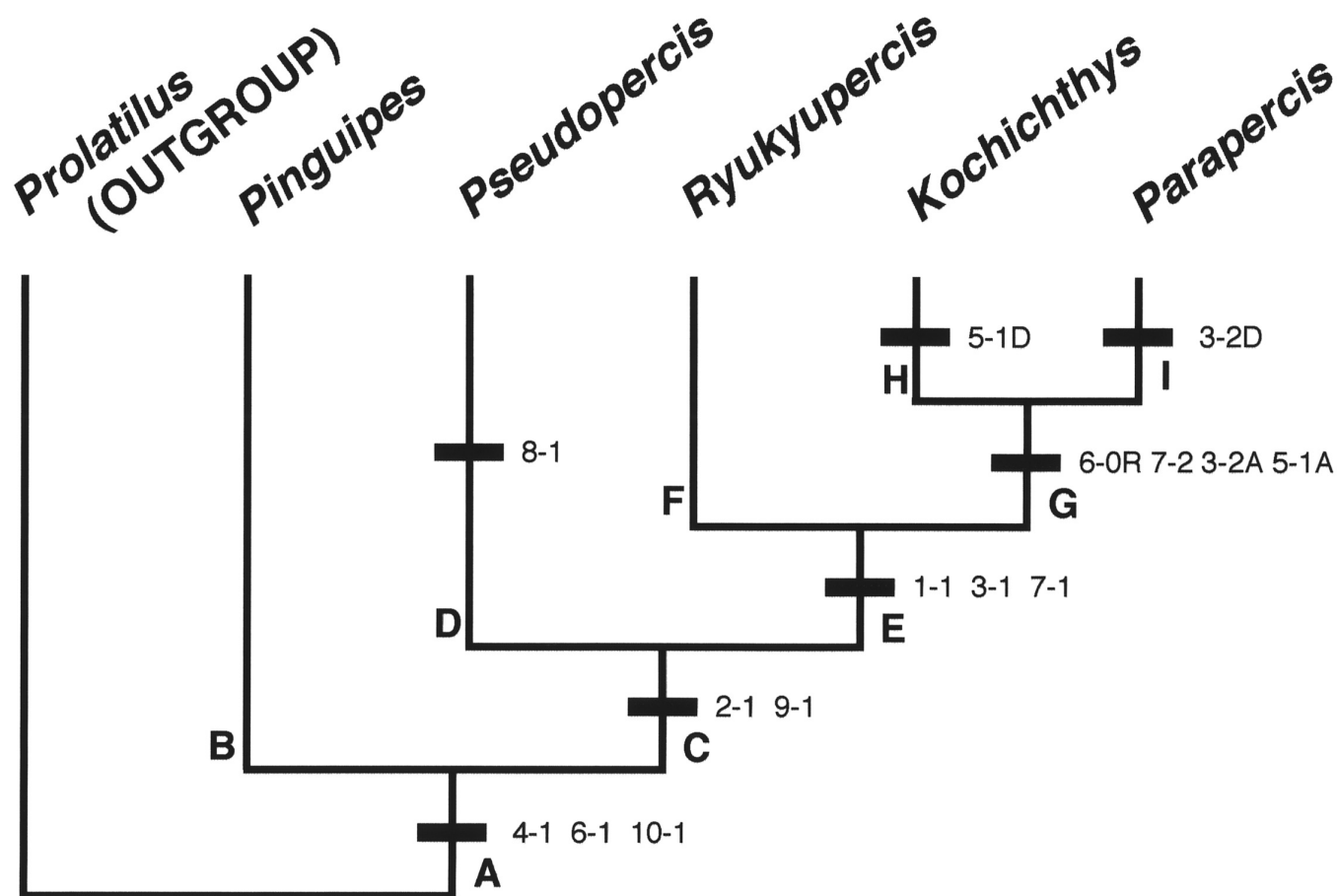


Fig. 10. Phylogenetic relationships of Pinguipedidae, showing phylogenetic position of *Ryukyuperca* from Clade A to I. Character numbers correspond to those in the text and Table 1. Character numbers with A and D indicate characters recognized when ACCTRAN or DELTRAN is used, respectively. Character number with R indicates reversal. Other characters are unambiguous.

to the latter: iris lappet absent (vs. simple and broad iris lappet present in *Parapercis*); endopterygoid and ectopterygoid autogenous (Fig. 2) (vs. fused); cartilaginous tip of elongate anterior limb of coracoid connected to the inner portion of lateral flange of cleithrum (Fig. 5B) (vs. connected to the outer portion of lateral flange of cleithrum (Fig. 5C); hemal arch of anterior caudal vertebrae large (vs. small); 4 or 5 anal fin pterygiophores anterior to the first hemal spine (vs. 3); protractor pectoralis composed of sheet-like element only (vs. sheet-like anterior and robust posterior elements); extensor proprius inserted on pelvis (vs. on cleithrum) and scaled area extending to the interorbital region (vs. restricted to the occipital region in all but one species).

The number of anal fin pterygiophores anterior to the first hemal spine is also useful to separate *Ryukyuperis* from *Kochichthys* (4 or 5 in *Ryukyuperis* vs. 3 in *Kochichthys*), as well as the numbers of spines supported by first dorsal pterygiophore (2 vs. 1) and supraneurals (1 vs. 0). In addition, *Ryukyuperis* is separable from these two genera in having 6 dorsal fin spines (vs. usually 4 or 5 in *Parapercis* and 2 in *Kochichthys*) (Cantwell, 1964; Rosa & Rosa, 1997; Imamura & Yoshino, this study).

Ryukyuperis differs from *Prolatilus*, *Pinguipes* and *Pseudoperis* in having three apomorphic characters: beryciform foramen absent (Fig. 3) (vs. present in *Prolatilus*, *Pinguipes* and *Pseudoperis*); cartilaginous tip of elongate anterior limb of coracoid connected to the inner portion of lateral flange of cleithrum (Fig. 5C) (vs. connected to the lateral aspect of medial portion of cleithrum (Fig. 5A) and 4 or 5 anal fin pterygiophores anterior to first hemal spine (vs. > 5).

The genus is also distinguished from *Prolatilus* in having the vomer and palatine with teeth (Fig. 2) (vs. without teeth in *Prolatilus*), the adductor dorsalis present (vs. absent) and the scaled area of the dorsal surface of the head reaching to the infraorbital region (vs. reaching to snout). It differs from *Pinguipes* in having 3 epurals (vs. 2 in *Pinguipes*) and from *Pseudoperis* in having the posterior portion of A2 connected to the preopercle only (Fig. 6) (vs. connected to the preopercle and levator arcus palatini in *Pseudoperis*). The cartilage on the posterior margin of lowermost actinost extending ventrally and the anterior element of the levator operculi connected to the hyomandibula in *Ryukyuperis* (Figs. 4 & 6) are also useful to separate the genus from *Prolatilus* and *Pinguipes* (where the cartilage does not extend ventrally and the anterior element of the levator operculi is not connected to the hyomandibula).

In conclusion, the family Pinguipedidae includes the following six genera at present, namely *Kochichthys*, *Paraperis*, *Pinguipes*, *Prolatilus*, *Pseudoperis* and *Ryukyuperis*.

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