

## A New Subspecies of the Ayu, *Plecoglossus altivelis*, (Plecoglossidae) from the Ryukyu Islands

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**Abstract** A new subspecies of the ayu, *Plecoglossus altivelis ryukyuensis*, is described on the basis of specimens from Amami-oshima and Okinawa Islands, the Ryukyu Islands, Japan. This new subspecies is distinguished from *P. altivelis altivelis* by the fewer numbers of pectoral fin rays, longitudinal scales and scales above and below the lateral line, and also by the unique electrophoretic mobilities of several enzymes.

It has long been known that populations of the ayu *Plecoglossus altivelis* Temminck et Schlegel inhabit the Ryukyu Islands (Jordan and Tanaka, 1927; Kuroiwa, 1927; Okada and Ikeda, 1938). A few recent reports suggest that the ayu in the Ryukyus with characteristic fauna differ from those of the Japan Islands in behavior and certain morphological traits (Inoha and Sesoko, 1965; Kawanabe, 1972; Shokita et al., 1975). During the course of a detailed investigation on intra-specific variation in the ayu (Nishida and Takahashi, 1978; Nishida, 1985a, 1986; Nishida and Sawashi, 1987), the Ryukyuan populations were found to differ distinctly from those of other geographic regions in many morphological and biochemical-genetic characters and appeared to have a unique evolutionary history. The present paper describes these Ryukyuan populations as a new subspecies on the basis of the observations of the previous studies on geographic variation among populations in the Japan and Ryukyu Islands.

The methods of counting and measurements were those of Nishida (1985b, 1986) and Nishida and Sawashi (1987), being basically the same as those of Hubbs and Lagler (1958). Type specimens are deposited at the Department of Marine Sciences, College of Science, University of the Ryukyus (URM-P).

*Plecoglossus altivelis ryukyuensis* subsp. nov.

(Japanese name: Ryukyu-ayu)

(Fig. 1)

**Holotype.** URM-P18462, a male, 110.6 mm in standard length (SL), Sumiyo River (27°16'N, 129°24.5'E), Amami-oshima Island, the Ryukyu Islands,

July 29, 1981, caught by M. Nishida.

**Paratypes.** URM-P18463, 24 specimens, 75.5–113.2 mm SL, collected with holotype; URM-P18464, 31 specimens, 75.1–113.2 mm SL, Yona River (26°45.5'N, 128°13'E), Okinawa Island, the Ryukyu Islands, July 3, 1971, caught by R. Shimojo.

**Diagnosis.** This subspecies is distinguished from *P. altivelis altivelis* by the combination of the smaller numbers of the following characters: pectoral fin rays (11–13 mainly 12, instead of 12–15 mainly 14); longitudinal scales (104–131 instead of 121–176) to hypural end; scales above the lateral line (14–17 instead of 16–25); scales below the lateral line (8–11 instead of 10–17).

**Description.** Counts and proportional measurements are shown in Table 1. The following description is based on all the specimens.

Vertebrae 58–61. Pectoral fin rays 11–13, anal fin rays 14–18. Lateral line scales 59–63, longitudinal scales 104–131, scales above and below lateral line 14–17 and 8–11, respectively. Comb-like teeth on upper and lower jaws 12–15 and 11–13, respectively. Gillrakers 31–39.

Body relatively robust. Trunk at the posterior part and caudal peduncle deep. Tip of snout wide. Interorbital space wide. Gillrakers slightly short. Scales on body large. Both anterior and posterior rays of dorsal fin elongated in some individuals. Other counts and measurements largely representative of the species in general.

In life, body color similar to the nominotypical subspecies as represented by grayish olive on dorsum and pearl white on venter, sometimes with two yellow marks on each side near pectoral base. Membrane color of elongated dorsal fins grayish brown (holotype and topoparatypes). In formalin, the grayish olive area in life becomes



Fig. 1. Holotype of *Plecoglossus altivelis ryukyuensis* subsp. nov., URM-P18462, 110.6 mm in standard length, Sumiyo River, Amami-oshima Island, the Ryukyus, Japan.

grayish brown, and the yellow marks become pale yellow.

**Variation.** There is some variation between populations of this subspecies from Amami-oshima and Okinawa Islands (Table 1). The population from Amami-oshima Island has significantly fewer numbers of vertebrae, longitudinal scales, scales above and below lateral line and comb-like teeth on upper jaw than that from Okinawa Island ( $P < 0.05$ , t-test). Body robustness and other morphometric characteristics of this subspecies are, however, more pronounced in the latter than in the former.

**Distribution.** This new subspecies is distributed in Amami-oshima and Okinawa Islands, the Ryukyus, Japan.

**Etymology.** The name *ryukyuensis* refers to the Ryukyus where the types were collected.

**Remarks.** *Plecoglossus altivelis ryukyuensis* has, as in the case of *P. a. altivelis*, comb-like teeth considered characteristic of ayu, and its appearance is essentially the same as that of *P. a. altivelis*. However, it can be distinguished from the latter by the fewer numbers of pectoral fin rays, longitudinal scales and scales above and below the lateral line (Table 2). The two subspecies show a certain degree of variation in these meristic characters, but the variation is not clinal and the differences between the two subspecies in these characters are quite pronounced in comparison with the variation within each subspecies (Nishida, 1986; Nishida and Sawashi, 1987). Two multivariate analyses, cluster analysis and stepwise discriminant function analysis, of 12 meristic and 17 morphometric characters demonstrated that the populations of ayu in the Japan-Ryukyu Archi-

pelago are clearly separable into two subspecies groups (Nishida, 1986).

Dorsal fin elongation is found in some specimens of both subspecies but they differ with respect to the shape and color of their fins. The anterior and posterior rays of the dorsal fins are elongated and the membrane color is grayish brown in *P. a. ryukyuensis*, whereas only the posterior rays of the fins are elongated with the membrane color being black, particularly in the posterior part, in *P. a. altivelis* (Nishida, 1986). The elongated dorsal fins of ayu have a significant social meaning (Nishida, 1986; Tachihara and Kimura, 1988). According to Kawanabe (1972), the territorial behavior of *P. a. ryukyuensis* differs from that of *P. a. altivelis* in terms of fitful and interspecific chasing of intruders by the former. Whether shape and color differences in elongated dorsal fins are directly related to differences in territorial behavior is a matter awaiting clarification.

Other ecological characteristics of *P. a. ryukyuensis* have been observed. Compared to *P. a. altivelis*, the number of eggs from a mature female of *P. a. ryukyuensis* tends to be few, with egg and larva size being somewhat larger (Shokita et al., 1975; Nishida, 1986; Nishida and Uchimura, 1987).

The new subspecies is quite distinct from *P. a. altivelis* in biochemical-genetic characters. *P. a. ryukyuensis* in Amami-oshima Island is nearly or completely fixed for unique alleles at 5 loci which control glucosephosphate isomerase-2, isocitrate dehydrogenase-1, lactate dehydrogenase-2, phosphoglucomutase and superoxide dismutase (Nishida, 1985a, unpublished; Seki et al., 1988). The electrophoretic mobilities of these enzymes in

this subspecies clearly differ from those of *P. a. altivelis*, and accordingly, the allozyme patterns are highly diagnostic (Fig. 2). On the basis of the data for a total of 28 loci, the average of Nei's (1972) genetic identities between populations of both subspecies was determined as 0.78, indicating that both subspecies share in common only about 80% of the total structural genes (as detected electrophoretically) in their genomes on the average.

It is usually difficult to determine the taxonomic

statuses of geographically isolated allopatric populations, because the interbreeding community criterion of a species is not applicable (Mayr, 1969; but also see Wiley, 1981). However, recent developments in molecular techniques have made it possible to obtain data on the degree of genetic similarity between populations. It is thus possible and also desirable to assign subspecific statuses to geographical isolates that have genetically diverged to a considerable extent. Subspecies thus established would not be arbitrary but actual

Table 1. Counts and proportional measurements, expressed as the percent of standard length in *Plecoglossus altivelis ryukyuensis* subsp. nov. Ranges (and means) are presented for paratypes.

Character	Holotype	Paratypes	
	Amami-oshima Is. URM-P18462	Amami-oshima Is. URM-P18463 (N=24)	Okinawa Is. URM-P18464 (N=31)
Standard length (mm)	110.6	75.5-113.2 (92.5)	75.1-113.2 (97.9)
Vertebrae	60	58-60 (59.3)	58-61 (60.0)
Dorsal fin rays	11	10-11 (10.6)	10-11 (10.5)
Pectoral fin rays	13	11-13 (12.4)	12-13 (12.1)
Ventral fin rays	8	8-8 (8.0)	8-8 (8.0)
Anal fin rays	16	14-18 (16.6)	15-18 (16.0)
Caudal fin rays	19	19-19 (19.0)	18-19 (18.8)
Lateral line scales	60	59-63 (60.8)	59-63 (60.7)
Longitudinal scales	117	104-122 (113.9)	109-131 (122.5)
Scales above lateral line	15	14-15 (14.3)	15-17 (16.1)
Scales below lateral line	9	8-10 (9.4)	9-11 (10.1)
Comb-like teeth on upper jaw	14	13-15 (13.5)	12-14 (13.1)
Comb-like teeth on lower jaw	13	12-13 (12.5)	11-13 (12.3)
Gillrakers	38	33-39 (35.1)	32-38 (34.9)
Predorsal length	47.7	47.8-50.7 (49.1)	48.5-52.0 (50.5)
Preventral length	49.9	49.7-52.0 (50.7)	49.0-52.4 (50.8)
Preanal length	72.1	71.0-73.6 (72.6)	72.4-76.6 (74.1)
Body depth	21.3	18.5-22.2 (20.1)	20.5-24.8 (23.0)
Body depth at anus	17.0	13.3-17.5 (15.9)	16.5-20.0 (18.6)
Length of caudal peduncle	12.5	12.9-14.9 (13.7)	11.9-14.7 (13.3)
Depth of caudal peduncle	9.4	8.3-9.5 (8.9)	8.8-10.5 (9.5)
Length above lateral line	13.9	11.0-14.2 (12.4)	12.6-16.4 (14.7)
Length below lateral line	9.5	8.0-10.5 (9.3)	9.5-11.2 (10.4)
Head length	25.0	24.4-26.8 (25.8)	24.0-26.8 (25.3)
Snout length	9.1	8.4-10.0 (9.2)	7.7-9.3 (8.7)
Length of upper jaw	13.5	12.8-14.5 (13.8)	12.5-14.4 (13.7)
Snout width	5.1	4.5-5.7 (5.2)	4.5-5.7 (5.2)
Interorbital width	8.3	7.7-8.6 (8.1)	7.7-8.6 (8.3)
Length of 2nd dorsal ray	21.2	16.3-21.4 (18.7)	15.3-24.2 (20.0)
Length of depressed dorsal	36.1	20.5-35.5 (26.1)	18.8-40.2 (30.7)
Length of pectoral fin	17.9	15.7-18.6 (17.5)	15.6-18.6 (17.5)
Length of ventral fin	15.0	12.9-14.8 (13.9)	13.1-16.6 (14.5)
Length of longest caudal ray	23.5	21.2-26.0 (23.7)	21.8-25.9 (24.4)

Table 2. Comparison of 10 meristic characters of two subspecies of *Plecoglossus altivelis*. Data for *P. a. ryukyuensis* were based on the type series; data for *P. a. altivelis* were based on 150 specimens from various localities in the Japan Islands (Nishida, 1986; Nishida and Sawashi, 1987).

	Vertebrae						Pectoral fin rays					Anal fin rays										
	58	59	60	61	62	63	11	12	13	14	15	13	14	15	16	17	18					
<i>P. a. ryukyuensis</i>	3	17	30	5			1	41	14				1	6	31	13	4					
<i>P. a. altivelis</i>			9	68	61	6		1	25	91	33	1	34	86	23	4						
	Longitudinal scales																					
	100– 104	105– 109	110– 114	115– 119	120– 124	125– 129	130– 134	135– 139	140– 144	145– 149	150– 154	155– 159	160– 164	165– 169	170– 174	175– 179						
<i>P. a. ryukyuensis</i>	2		14	12	19	7	1															
<i>P. a. altivelis</i>					2	9	11	18	30	21	19	8	11	8	3	2						
	Lateral line scales							Scales above lateral line														
	59	60	61	62	63	64	65	66	14	15	16	17	18	19	20	21	22	23	24	25		
<i>P. a. ryukyuensis</i>	8	15	20	10	3				16	13	21	6										
<i>P. a. altivelis</i>		1	4	38	38	46	13	6			1	22	38	27	22	13	18	8		1		
	Scales below lateral line										Comb-like teeth on upper jaw											
	8	9	10	11	12	13	14	15	16	17	12	13	14	15	16	17						
<i>P. a. ryukyuensis</i>	2	14	35	5							3	36	16	1								
<i>P. a. altivelis</i>			6	25	51	35	22	7	3	1		11	36	83	19	1						
	Comb-like teeth on lower jaw						Gillrakers															
	11	12	13	14	15	16	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
<i>P. a. ryukyuensis</i>	1	32	23				2	12	11	9	8	8	5	1								
<i>P. a. altivelis</i>		5	42	86	14	3				1	3	7	6	9	25	31	29	20	9	3	2	1

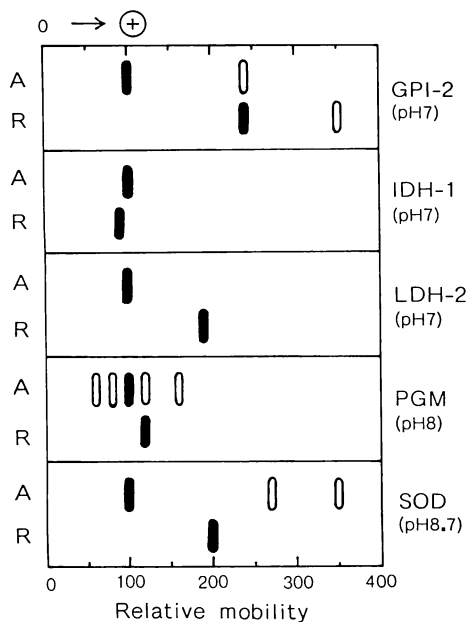


Fig. 2. Diagrammatic representation of electrophoretic mobilities of glucosephosphate isomerase-2 (GPI-2), isocitrate dehydrogenase-1 (IDH-1), lactate dehydrogenase-2 (LDH-2), phosphoglucumutase (PGM) and superoxide dismutase (SOD) in *Plecoglossus altivelis altivelis* (A) and *P. a. ryukyuensis* (R). Solid symbols represent homopolymers by predominant alleles (frequencies  $\geq 0.95$ ) and hollow symbols represent those by rare alleles ( $< 0.05$ ). Heteropolymers are not shown. For a detailed explanation of electrophoretic methods see Nishida (1985a).

entities (Smith and White, 1956; Inger, 1961).

In the case of sympatric populations, however, no upper limit of genetic similarity can be established for determining taxonomic status, since even slight genetic differences would be sufficient to decide that they are different species when the differences or other biological evidence prove their reproductive isolation. Indeed, speciation with little genetic change has been reported for various fishes (Avisé et al., 1975; Kirkpatrick and Selander, 1979; Echelle and Echelle, 1984; Humphrie, 1984; Sage et al., 1984). For allopatric populations, however, data on the degree of genetic difference may provide useful guidelines for determining taxonomic status.

Though genetic identity values for a wide variety of fish well exceed 0.90 between conspecific popula-

tions, these values between subspecies are usually in the range 0.75–0.95 (mostly 0.80–0.90). The value is 0.75–0.94 for the cutthroat trout *Salmo clarki* (Loudenslager and Gall, 1980), 0.84 for the bluegill *Lepomis macrochirus* (Avisé and Smith, 1977), 0.84 for the cyprinid *Camptostoma anomalum* (Buth and Burr, 1978), 0.87–0.93 for the flatfish *Platichthys flesus* (Galleguillos and Ward, 1982) and 0.89 for the brook trout *Salvelinus fontinalis* (Stoneking et al., 1981). Ayu in the Ryukyus are treated as a subspecies in the present study in view of their allopatry, as well as their considerable genetic divergence. It should be pointed out, however, that the genetic identity value of 0.78 in the present case of ayu is at the lowest limit of the above range. Seki et al. (1988) emphasize that the level of genetic divergence of ayu in the Ryukyus from those in other regions is within the range of differentiation observed between the full species of certain other fishes.

The new subspecies is geographically isolated from *P. a. altivelis* in the Japan Islands by the Tokara Channel, which separates Amami-oshima and Okinawa Islands from the main islands of Japan. This channel has been there since the middle Pleistocene period, though other regions such as the Japan Islands and the Korean Peninsula (and thus the Chinese Continent) were virtually connected by lowering of the sea level during the recent glacial ages (Kizaki and Oshiro, 1977). The low value of genetic identity, and particularly allelic substitution at several loci, indicate that essentially no gene exchange has occurred between the two subspecies for a considerable period of time. The origin of this new subspecies may possibly bear a close relation to the geological history of the Ryukyu Islands.

On the basis of available information, Nishida (1986) has suggested that the range of *P. a. ryukyuensis* is restricted to the Ryukyu Islands. The results of recent electrophoretic analysis of populations of ayu from the Korean Peninsula and the Japan-Ryukyu Archipelago by Seki et al. (1988) provide some support for this view. That is, the Korean populations have been found genetically quite similar to *P. a. altivelis* in the Japan Islands, but not at all to *P. a. ryukyuensis* in the Ryukyus. Preliminary results from the analysis of morphological variation in populations from Taiwan and the Chinese Continent also support the above suggestion.

At present, this new subspecies cannot be found at all in the waters of Okinawa Island, and its range of distribution in Amami-oshima Island is diminishing (Nishida and Uchimura, 1987).

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#### 琉球列島より得られたアユの新亜種

西田 睦

日本・琉球列島産アユの地理的変異の分析の結果、琉球列島に生息するアユは他と明瞭に異なる独自の集団であることが分かったので、奄美大島および沖縄島から得られた標本に基づき、これを新亜種 *Plecoglossus altivelis ryukyuensis* (和名: リュウキュウアユ) として記載した。本亜種は、縦列鱗数、側線上・下方横列鱗数および胸鰭条数が少ないことにより、基亜種と区別される。また、本亜種は、いくつかの酵素分子が、電気泳動的に他とは明瞭に異なることによって特徴づけられる。

(903-01 沖縄県西原町千原1 琉球大学理学部海洋学科)