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Development of the Bitterling, *Paracheilognathus himantegus* (Cyprinidae), with a Note on Minute Tubercles on the Skin Surface

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Abstract The development of the eggs and larvae and minute tubercles on the skin surface of *Paracheilognathus himantegus* larvae were observed. The egg began to hatch approximately 68 hours after insemination and the larvae reached the free-swimming stage 23 days after hatching at water temperature of 22±1°C. The larval development and minute tubercles on the skin surface of this species were similar to those of *Acheilognathus lanceolata*, *A. limbata*, *A. signifer* and *Tanakia tanago*. However, the shape of the ripe eggs of *P. himantegus* differed from those of the four species. As regards the shape of eggs, there was a common characteristic among *P. himantegus*, *Rhodeus uyekii* and *A. limbata* from Korea. As regards larval development, *P. himantegus* had two characters also found in *Rhodeus*. These facts seem to suggest that *P. himantegus* is closely related to *A. lanceolata*, *A. limbata*, *A. signifer* and *T. tanago* but is more specialized than these four species, except for *A. limbata* from Korea.

Paracheilognathus himantegus Günther, a common bitterling in the fresh water of China and Taiwan, is widely distributed in ponds, lakes, streams and mountain torrents (Wu et al., 1964; Tzeng, 1986). No detailed information on the embryonic and larval stages of this species has been hitherto available. It is well known that larvae of bitterlings have minute tubercles on the skin surface (Uchida, 1937; Nakamura, 1969). The morphology and distribution of minute tubercles in the larvae of *Acheilognathus*, *Pseudoperilampus*, *Tanakia* and *Rhodeus* have been reported (Fukuhara et al., 1982; Suzuki and Hibiya, 1984a, 1985a; Suzuki et al., 1985, 1986; Suzuki and Jeon, 1987, 1988a, b, c, d), but those of *P. himantegus* are still unknown.

The present paper deals with the development of eggs and larvae and the minute tubercles on the skin surface of larval *P. himantegus*. In addition, the phylogenetic relationship of this species among acheilognathine fishes is discussed.

Material and methods

Adult fish of *P. himantegus* were obtained from an aquarium dealer and reared in a water tank at Saitama Aquarium (Prefectural Station). Artificial inseminations were made several times from March to July using a pair (female, 50.30 mm in total length (TL) and male, 68.75 mm TL) of breeders. During this period the ovipositor elongated reaching its maximal length (ca. 12.7 mm) at intervals of 11 to 40 days. The number of the ripe eggs obtained artificially ranged from 33 to 46 (mean, 41 eggs) per spawning. Methods of artificial insemination and rearing of eggs and larvae followed those of Suzuki and Hibiya (1984a). The development of eggs and larvae was observed under a dissecting microscope. The total length of live larvae was measured with an ocular micrometer. Five specimens per larval stage were used for morphological observation of the minute tubercles on the skin surface. For electron microscopic observation, the specimens were fixed for 24 hours at 2°C in cacodylate-buffered 2.5% glutaraldehyde, dehydrated in a graded series of ethanol, dried to the critical point by ion sputtering, and then examined with a JEOL JSMT-20S scanning electron microscope.

Egg and larval development of *Paracheilognathus himantegus*

Embryonic stages. Sixteen stages (A–P) were found during the embryonic development (Fig. 1). Unfertilized eggs appeared nearly spindly in shape,

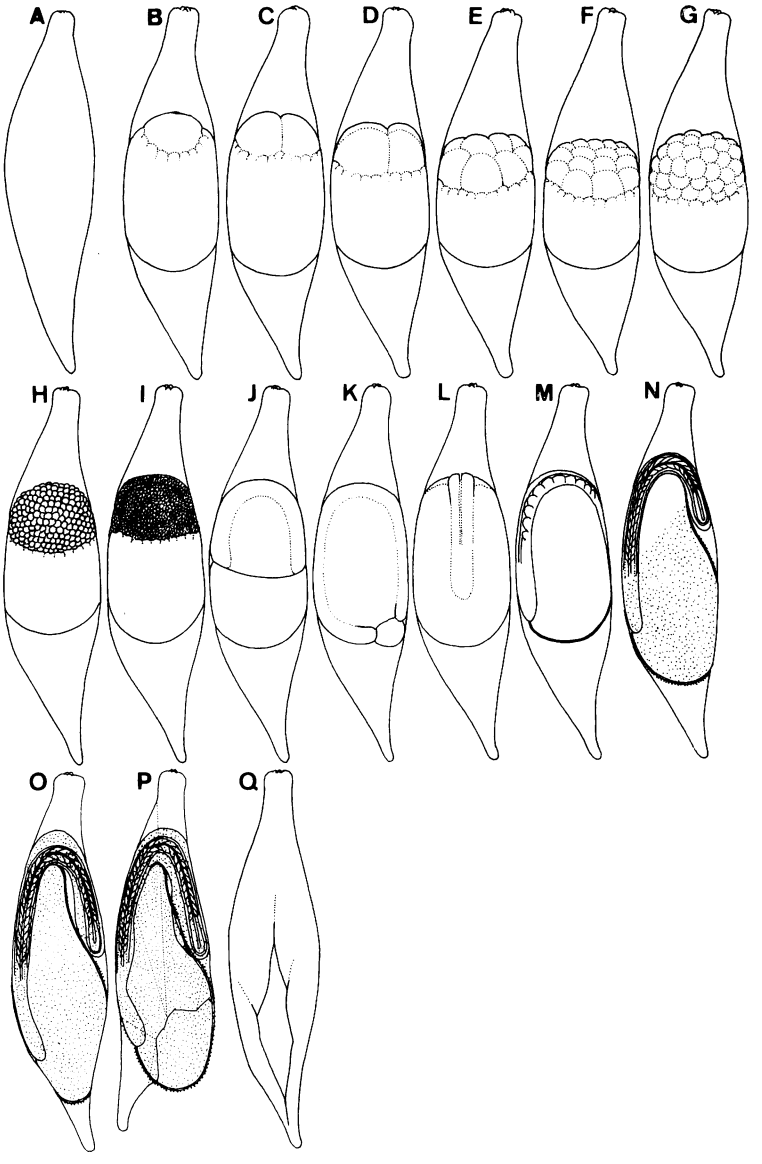

Fig. 1. Egg development of *Paracheilognathus himantegus*. Time required for each embryonic stage (A–Q) at 22±1°C of water temperature is shown in Table 1.

(averaging 4.11 mm in length with the range of 3.82 to 4.38 mm and 1.04 mm in breadth with the range of 0.96 to 1.11 mm for the 50 eggs measured), and opaque yellow in color (Fig. 1A). The time required for each embryonic stage of 22±1°C water temperature is shown in Table 1. After insemination and contact with water, the egg membrane began to swell and the eggs formed a mass. The inflation of the egg membrane ceased about 30 minutes after insemination. Therefore, the chorion separated from the plasma membrane to form a perivitel line space at both sides of the animal and vegetal poles after insemination. Usually the complete blastodisc is formed in an hour after insemination (Fig. 1B). The cleavage of *P. himantegus* was similar to that found in the egg of most bitterlings. About 42 hours after insemination, the embryonic body became evident, with a kell-like structure forming the central nervous system (Fig. 1L). About 52 hours after insemination, the

whole embryonic body had been re-orientated with the tail bud of the embryo usually situated at the side of the animal pole. At this stage the primitive minute tubercles appeared on the skin surface of the embryonic body (Fig. 1N). About 68 hours after insemination, most of the embryos began to hatch continuing for about 10 consecutive hours. All the embryos hatched out by rupturing the side of the vegetal pole of the egg membrane (Fig. 1P).

Larval development. 1) Immediately after hatching, 3.82–4.14 mm TL (Fig. 2A). Twenty-eight to twenty-nine myotomes were counted. The yolk sac contained a substantial amount of yolk. The dorsal part of the sac slightly developed to form a pair of hilly yolk projections and the anteriormost part elongated slightly forward (Fig. 4A). A few hours after hatching, when the primordial fin-fold at the caudal portion had relatively developed, the larvae began to move although they just usually lay on their trunk on the bottom of the petri-dish.

2) 3 days after hatching, 5.68–5.72 mm TL (Fig. 2B). The number of the myotomes ranged from 31 to 32 (18+13–14). The tail elongated backwards and the caudal fin-fold became well-developed. The pair of hilly projections of the yolk sac gradually expanded toward both sides of the body. The anteriormost part of the sac ran gradually forward and became a slender projection. Blood vesicles on the caudal fin-fold appeared.

3) 5 days after hatching, 5.94–6.03 mm TL (Fig. 2C). The number of the myotomes ranged from 31 to 32 (17+14–15). The optic cups, still without lens, and auditory vesicles possessing two pairs of otoliths were clearly observed. The heart began to pulsate. The blood cells on the caudal fin-fold became reddish and increased in number. The notochord started to flex. The projection on the anteriormost portion of the yolk sac became reduced.

4) 7 days after hatching, 6.70–6.78 mm TL (Fig. 2D). The number of the myotomes ranged from 31 to 32 (16–17+15). The circulatory system was already established. The pair of hilly yolk projections became slightly reduced in size. A pair of small nasal sacs was evident in front of the eye cups. The dorsal portion of the head was raised slightly with the brain underneath. At this stage, the larvae sometimes moved actively while lying down on their side.

5) 9 days after hatching, 6.73–6.79 mm TL (Fig. 2E). The lenses became completely developed and melanin pigments began to form on the optic cups. The notochord became completely flex (45°) and cartilaginous hypural elements began to differentiate. Some incipient fin-rays were also visible. Rudiments of the pectoral fins appeared as small membranes. A small gas-bladder and a green gall bladder were easily seen beneath the pectoral fins. The part of the fin-fold comprising future dorsal and anal fins bulged considerably. The hilly projections of the yolk sac were considerably reduced in size. The mouth occasionally opened and closed.

6) 14 days after hatching, 6.80–6.86 mm TL (Fig. 2F). All caudal fin-rays started to develop. The posterior margin of the caudal fin changed from a rounded to a truncated shape. Some rays were formed in the dorsal and anal fins. Small melanophores appeared on the head region, caudal fin-rays, the dorsal part of the yolk sac and the lateral part of the body. Black pigments developed on the retinal layers. The optic cups appeared silvery blue due to the presence of guanine scattered on this organ. The hilly projections of the yolk sac were so diminished that they were not easily found.

Table 1. Time required for each embryonic stage of *Paracheilognathus himantegus* at 22±1°C water temperature. Stages A to Q correspond to those in Fig. 1.

Stage	Time after insemination (hr:min)	Remarks
A	0:00	unfertilized egg
B	1:00	blastodisc
C	2:00	two-celled egg
D	2:30	four-celled egg
E	3:00	eight-celled egg
F	3:30	sixteen-celled egg
G	4:00	thirty-two-celled egg
H	5:00	early morula
I	6:00	post morula
J	10:00	blastula
K	40:00	blastopore nearly closed
L	42:00	neurula
M	44:00	somites formation
N	52:00	embryo formed entirely
O	62:00	the last embryonic stage
P	68:00	hatching begins
Q	—	castoff chorion

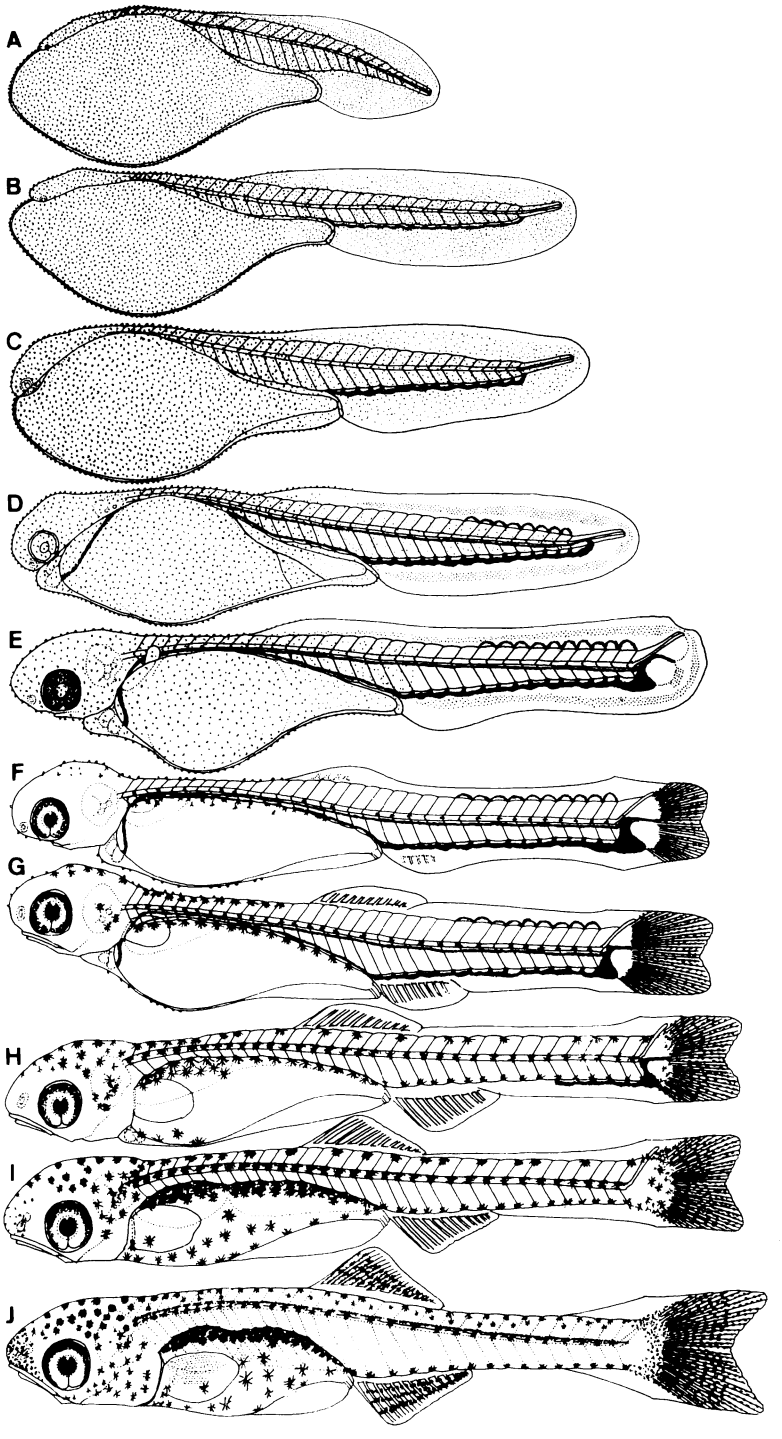

Fig. 2. Larvae of *Paracheilognathus himantegus*. A, immediately after hatching, 3.92 mm TL; B, 3 days after hatching, 5.71 mm TL; C, 5 days after hatching, 5.98 mm TL; D, 7 days after hatching, 6.75 mm TL; E, 9 days after hatching, 6.76 mm TL; F, 14 days after hatching, 6.83 mm TL; G, 17 days after hatching, 7.45 mm TL; H, 20 days after hatching, 7.62 mm TL; I, 23 days after hatching, 8.59 mm TL; J, 40 days after hatching, 8.42 mm TL.

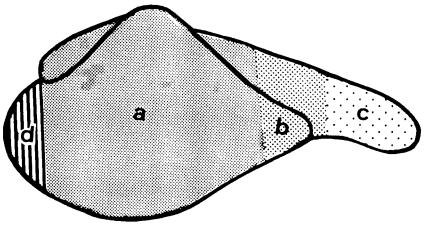

Fig. 3. Diagram showing division of the skin surface of larvae to facilitate description of the distribution of minute tubercles in larval *Paracheilognathus himantegus*. For details on parts a to d, see text.

7) 17 days after hatching, 7.35–7.47 mm TL (Fig. 2G). The head raised slightly. The caudal fin-rays began to fork. The dorsal and anal fins were clearly observed. Eye pigments, both melanin and guanine, were heavily concentrated. Melanophores newly appeared on the auditory visicles and the dorsal part of the body. The melanophores in this stage were larger than those in the former larval stages.

8) 20 days after hatching, 7.58–7.65 mm TL (Fig. 2H). The upper and lower jaws were approximately equal in size. The pectoral fins commenced to move. Melanophores newly appeared on the ventral parts of the yolk and the body, and increased slightly in number. The gas-bladder, which was not yet divided into lobes, grew larger. At this stage, the larvae swam with well-balanced orientation. However, they were unable to swim vigorously for more than a few seconds.

9) 22–24 days after hatching, 8.26–8.61 mm TL (Fig. 2I). This marked the beginning of the free-swimming stage. The gas-bladder divided completely into anterior and posterior lobes. The larvae were now able to swim actively with well-balanced orientation for much longer periords than before. Yellow pigments were found on the dorsal parts of both the head and the body. At this stage, the melanophores never increased remarkably in number compared with the former stage, and unlike in larvae of other bitterlings, no melanophores appeared on the dorsal and anal fin-rays. Although the yolk still remained, the larvae began to feed on commercial diets ("Tetramin").

10) 40 days after hatching, 8.39–10.21 mm TL (Fig. 2J). Rudiments of the ventral fins emerged as small membranes on the breast. Guanine was sparsely distributed on the belly. Some rays were formed in the pectoral fins. The larvae at this stage became light in color due to less intensive pigmentation by melanophores on both sides of the body. All dorsal and anal fin-rays were completed in number. Melanophores began to appear on the dorsal and anal fin-rays. However, the melanophores on the former did not aggregate towards the anterior region of the dorsal fin to form a black spot as in the larvae of *Rhodeus*.

Minute tubercles on the skin surface of *Paracheilognathus himantegus* larvae

The skin surface of *P. himantegus* larvae was divided into the following four parts (a–d) to facilitate description of the distributional patterns of the tubercles (Fig. 3): a) most part of the yolk sac, composed of a pair of hilly yolk projections and the mid-yolk sac, and the mid-body region, b) posterior parts of both the yolk sac and the body, c) the caudal fin-fold, and d) the anteriormost part of the yolk sac. The larvae of this species possessed minute tubercles on the skin surface of parts a, b and d, which developed from single cells of the free surface of the epidermis (Fig. 4A–F). Their distribution and development altered with larval growth. Immediately after hatching, minute scale-like tubercles (ca. 15–25 μm in height), shaped like circular cones that tilted posteriorly, were observed on parts a and d (Fig. 4B). Also, many hemispheric minute tubercles (ca. 5–10 μm in height) and vestigial minute tubercles were found on part b (Fig. 4C). There were hardly any tubercles on part c (Fig. 4D). In 3-day-old larvae the minute scale-like tubercles on parts a and d increased in height to ca. 30–35 μm (Fig. 4E). In 14-day-old larvae, the minute scale-like tubercles on parts a and d changed from circular cone shape to hemispheric shape and decreased in height to ca. 10 μm (Fig. 4F). From about 17 days after hatching, all minute tubercles started to reduce in size as the larvae began to swim actively. In the free-swimming stage, as in larvae of other bitterlings, the minute tubercles on most parts of the body had almost completely diminished except for the ones sparsely present on ridges, such as the eye cups and the dorsal part of the head.

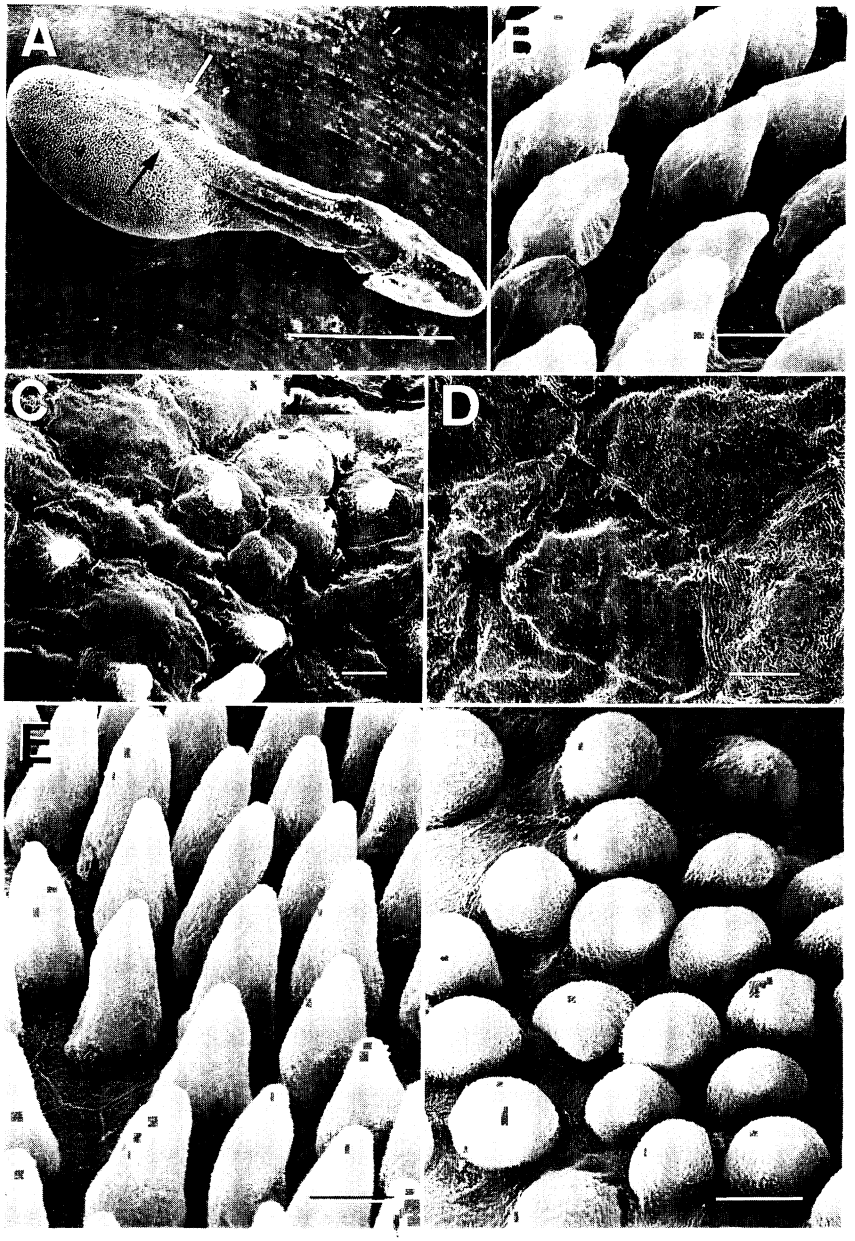

Fig. 4. The hilly yolk projections (arrows) (A), minute scale-like tubercles on parts a and d (B, E and F), hemispheric minute tubercles on part b (C) and vestigial minute tubercles on part c (D) on the body surface of larval *Paracheilognathus himantegus*. A–D, larva immediately after hatching, 3.92 mm TL; E, 3 days old larva, 5.71 mm TL; F, 14 days old larva, 6.83 mm TL. Scale bars, 1,000 μm (A) and 10 μm (B–F).

Discussion

There is no report on the spawning season of *Paracheilognathus himantegus*. Judging from our present study, it is considered that the spawning period of this species continues from early March to the end of July, and during this long period they spawn at least 5 times at intervals of 11 to 40 days.

The Chinese bitterlings belonging to the genus

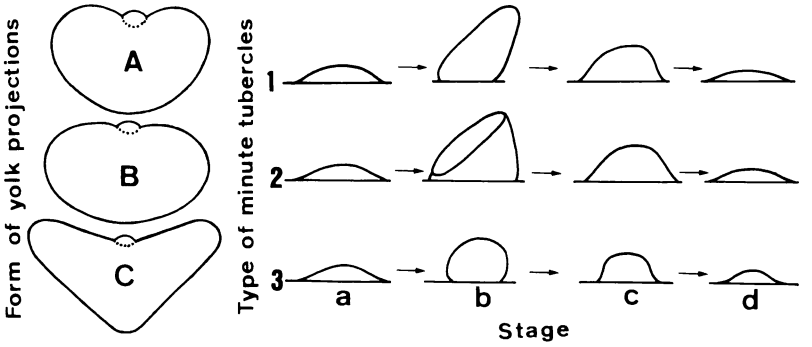

Fig. 5. Diagrams showing the forms (A, B, C) and types (1, 2, 3) of minute tubercles on the skin surface of the larvae of acheilognathine fishes. Forms (A, B, C) are based on the changes in the projections of yolk sac of larvae immediately after hatching. Stages a–d showing morphological changes of the tubercles during larval growth. a, embryonic stage; b, well-developed minute scale-like tubercles; c, degenerated minute tubercles; d, vestigial minute tubercles. Types (1, 2, 3) are based on the minute tubercles in Stage b.

Table 2. Comparison of the form of yolk projections, and distribution and types of minute tubercles on the skin surface in acheilognathine fishes. Form of yolk projections (A, B, C) and types of minute tubercles (1, 2, 3) are shown in Fig. 5. v, vestigial minute tubercles; —, vestigial minute tubercles almost disappeared. For parts of the body, see Fig. 3.

Group		Form of yolk projections	Types of minute tubercles in parts of the body				References
			a	b	c	d	
1	*Acheilognathus lanceolata*	A	1	3	v	1	Suzuki and Hibiya (1985a)
	A. limbata (from Japan)	A	1	3	v	1	Suzuki and Hibiya (1985a)
	A. limbata (from Korea)	A	1	3	v	3	Suzuki and Jeon (1988c)
	A. signifer	A	1	3	v	3	Suzuki and Jeon (1988b)
	Tanakia tanago	A	1	3	v	3	Suzuki et al. (1986)
	Paracheilognathus himantegus	A	1	3	—	1	Present paper
2	*A. yamatsutae*	A	2	3	v	2	Suzuki and Jeon (1987)
	A. moriokae	B	2	2	v	2	Suzuki and Hibiya (1985a)
	A. tabira tabira	B	2	2	v	2	Suzuki and Hibiya (1985a)
	A. tabira subsp. (a)	B	2	2	v	2	Fukuhara et al. (1982); Suzuki, unpublished data
	A. tabira subsp. (b)	B	2	2	v	2	Suzuki and Hibiya (1985a)
	A. cyanostigma	B	2	2	v	2	Suzuki and Hibiya (1985a)
	A. rhombea	B	2	2	2	2	Suzuki and Hibiya (1985a)
	Pseudoperilampus typus	B	2	2	2	2	Suzuki and Hibiya (1985a)
	A. longipinnis	B	2	?	?	?	Fukuhara et al. (1982)
3	*Rhodeus uyekii*	C	3	v	v	—	Suzuki et al. (1985)
	R. ocellatus smithi	C	3	—	—	—	Suzuki and Hibiya (1984a)
	R. ocellatus ocellatus	C	3	—	—	—	Suzuki and Hibiya (1984a); Suzuki and Jeon (1988a)
	R. atremius atremius	C	3	—	—	—	Suzuki and Hibiya (1984a)
	R. atremius suigensis	C	3	—	—	—	Suzuki and Hibiya (1984a); Suzuki and Jeon (1988d)

Paracheilognathus consist of three species, *P. himantegus*, *P. imberbis* (Günther) and *P. meridianus* Wu (Wu et al., 1964). Recently, Arai et al. (1988) stated that *P. himantegus* was more closely related to *Acheilognathus lanceolata* (Temminck et Schlegel), *A. limbata* (Temminck et Schlegel) and *A. signifer* Berg than to *P. imberbis* on the basis of the karyotype and four morphological characters in adults. In addition, Arai and Akai (1988) suggested that *P. himantegus* be included in the genus *Tanakia* with four species, *A. lanceolata*, *A. limbata*, *A. signifer* and *Tanakia tanago* (Tanaka). The larvae of *P. himantegus* possess a pair of hilly projection of the yolk sac and minute circular cone-shaped and scale-like tubercles on part a and minute hemispheric tubercles on part b as in the larvae of the four species (Fig. 5; Table 2). These facts suggest that they are closely related species, because these characters are the important markers for determining phylogenetic relationships among acheilognathine fishes (Fukuhara et al., 1982; Suzuki and Hibiya, 1984a, 1985a; Arai, 1988).

As regards the embryonic stages, the time required for the embryonic development of *P. himantegus* resembles those of *A. lanceolata*, *A. limbata*, *A. signifer* and *T. tanago* compared with those of other species of *Acheilognathus*, *Rhodeus* and *Pseudoperilampus* (Suzuki and Hibiya, 1984b; Suzuki et al., 1986; Suzuki and Jeon, 1987, 1988a, b, c). On the other hand, in point of the shape of ripe eggs, *P. himantegus*, *Rhodeus uyekii* (Mori) and *A. limbata* from Korea share the following two characters which are not shared by the four species of the genus *Tanakia*: i.e., 1) fertilized eggs are nearly spindly shaped, and 2) the perivitelline space is wide on both sides of the animal and vegetal poles (Suzuki et al., 1985; Suzuki and Jeon, 1988d). As redgards the larval development, *P. himantegus* shares the following two characters with *A. limbata* from Korea, *R. uyekii*, *R. atremius atremius* (Jordan et Thompson), *R. atremius suigensis* (Mori), *R. atremius notatus* (Nichols), *R. ocellatus ocellatus* (Kner) and *R. ocellatus smithi* (Regan) (Suzuki and Hibiya, 1984b, 1985b; Suzuki et al., 1985; Suzuki and Jeon, 1988a, c, d): 1) the anteriormost part of the yolk sac elongates forward to form a projection and 2) there are hardly any tubercles on part c.

These characters of the egg and larval development in *P. himantegus* seem to suggest that this species is closely related to Suzuki and Hibiya's (1985a) Group 1 which includes *A. lanceolata*, *A. limbata*, *A. signifer* and *T. tanago* although it is more specialized than these species except for *A. limbata* from Korea.

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タイワンタナゴの卵発生と仔魚の発育ならびに仔魚の表皮上突起

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タイワンタナゴ *Paracheilognathus himantegus* の卵発生と仔魚期の発育について経時的に観察し併せて，これらの仔魚の表皮上に存在する突起の形態も観察した．22℃の飼育下では受精後 68 時間から孵化を開始し，浮上期に達するのにほぼ 23 日を要した．これらの時間的経過は，ヤリタナゴ・アブラボテ・ミヤコタナゴ・チョウセンボテのそれに類似している．本種の仔魚は，孵化直後にすでに尾部仔魚膜鰭（鰭褶）がやや発達していること，孵化後数時間で仔魚が動き始めること，卵黄嚢背面が上方へ低く隆起して 1 対の丘状突起を形成することならびに卵黄嚢の表皮上には高さ約 15–25 μm の斜円錐状の鱗状突起を備えており，系統発生上重要な形質をこれら 4 種と共有している．しかし，本種は完熟卵の形が紡錘型であり，孵化仔魚の卵黄嚢前端が前方へやや細長く突出することでは韓国産のアブラボテやウエキゼニタナゴに類似しており，体の後部および鰭褶の表皮上にほとんど小突起が存在しないなどバラタナゴ属 *Rhodeus* の仔魚の形質も共有している．以上のことから，本種はアブラボテ属 *Tanakia* のヤリタナゴ・日本産アブラボテ・韓国産アブラボテ・ミヤコタナゴ・チョウセンボテと近縁な関係にあるものと考えられるが，韓国産アブラボテを除くこれらよりもやや特化しているものと判断される．

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