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Pharyngeal Teeth and Masticatory Process of the Basioccipital Bone in Japanese Bitterlings (Cyprinidae)

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Abstract The pharyngeal teeth and the masticatory process of the basioccipital bone were compared in fifteen species and subspecies of Japanese bitterlings. *Acheilognathus lanceolata*, *A. limbata* and two subspecies of *Rhodeus ocellatus*, which are characterized by the absence of serrations on the side of the pharyngeal teeth, have reduced occlusal grooves on the pharyngeal teeth. In the larvae of these species, the occlusal grooves are fairly developed. The occlusal grooves of the adult pharyngeal teeth in herbivorous species are more developed than those in omnivorous species. The occlusal grooves seem to have developed in relation to the feeding habits.

On the basis of the combination of developmental degrees of the anterior part of the masticatory process, the occlusal grooves and the chewing area on the pharyngeal first tooth, Japanese bitterlings were classified into two groups and two types and/or five subtypes, suggesting phylogenetic relationships among them.

Cyprinid fishes have well developed pharyngeal dentition which is an important character for studying their phylogeny and taxonomy (Chu, 1935; Aoyagi, 1957; Kobayasi and Maeda, 1961; Arai, 1982, etc.). Kobayasi and Maeda (1961) used the external features of the pharyngeal teeth and bones as a criterion for the classification of Japanese bitterlings. Recently Nakajima (1982) studied the pharyngeal and masticatory processes of the basioccipital bone in Japanese bitterlings for analysis of the occlusal movement.

The purpose of this study is to describe the morphological characters of the pharyngeal teeth and the masticatory process of the basioccipital bone for studying the phylogenetic relationships among Japanese bitterlings.

Materials and methods

Adult specimens used for this study are shown in Table 1. All specimens were fixed in 10% formalin. Larval specimens used for this study were obtained by the method of artificial insemination (Suzuki and Hibiya, 1984). The specimens were fed only with commercial diets ("Tetramin") and reared in an aquarium of 30*l* in volume. They were sampled at randam and were fixed in 10% formalin, and then cleared in 1% KOH and stained with alizalin red S. The data from these specimens are shown in Table 2. The pharyngeal arch was taken from the head region together with the mucous membrane. After the mucous membrane was removed from the pharyngeal arch, the pharyngeal teeth and bone were fixed in cacodylate-buffered 2.5% glutaraldehyde for 24 hours and were dehydrated in a graded series of ethanol followed by isoamylacetate, and then subjected to critical point drying in liquid CO_2 using a critical dryer. The dried specimens were coated with gold by ionsputter and examined with a Hitachi S-450 scanning electron microscope. The pharyngeal and masticatory processes were cleared in 1% KOH and stained with alizarin red S to examine their morphological features under a binocular microscope. Figures of the processes are drawn by using micrographs. Identification of acheilognathine fishes followed Nakamura (1969). Terminology of the pharyngeal teeth and bone is adopted from Kodera (1982).

Results

Morphological character of the masticatory process. The horny pad adhering to the masticatory process of the basioccipital bone occludes directly the occlusal surfaces of the pharyngeal teeth (Fig. 1A). Among acheilognathine fishes examined here, difference is found in the developmental degree of the anterior part of the masticatory process of the basioccipital bone. The masticatory process in *Acheilognathus lanceolata* (Temminck et Schlegel) is horseshoe-shaped and straight at

Table 1. List of materials for pharyngeal element analysis of Japanese bitterlings.

Species	River system and locality	No. of specimens examined	Range of total length (mm)
Acheilognathus lanceolata	R. Yabe, Fukuoka Pref.	8	86.80–98.65
	L. Biwa, Shiga Pref.	5	76.30–82.25
	R. Asahi, Okayama Pref.	5	62.70–81.62
A. limbata	R. Yabe, Fukuoka Paref.	22	20.40–84.70
	R. Asahi Okayama Pref.	5	50.80–62.70
	L. Biwa, Shiga Pref.	5	32.40–52.80
A. tabira tabira	R. Asahi, Okayama Pref.	10	46.25–71.95
	L. Biwa, Shiga Pref.	5	63.10–77.10
A. tabira subsp (a)	R. Sakura, Ibaraki Pref.	12	43.30–55.00
A. tabira subsp (b)	R. Yabe, Fukuoka Pref.	20	53.80–83.60
A. moriokae	R. Sakura, Ibaraki Pref.	15	55.80–94.35
A. rhombea	R. Yabe, Fukuoka Pref.	20	67.00–80.50
	L. Biwa, Shiga Pref.	5	71.00–81.25
A. cyanostigam	L. Biwa, Shiga Pref.	20	45.40–66.20
A. longipinnis	R. Yodo, Osaka Pref.	11	41.60–94.00
Pseudoperilampus typus	L. Kasumigaura, Ibaraki Pref.	15	32.00–118.60
Tanakia tanago	Ciba Pref.	5	65.00–70.40
Rhodeus ocellatus smithi	R. Yabe, Fukuoka Pref.	40	24.30–58.60
R. ocellatus ocellatus	R. Sakura Ibaraki Pref.	20	45.50–67.50
R. atremius	R. Yabe, Fukuoka Pref.	30	37.05–49.55
R. suigensis	R. Asahi, Okayama Pref.	10	36.45–45.80

Table 2. List of larval and juvenile specimens for pharyngeal element analysis.

Species	River system of parent fish	No. of specimens examined	Days after hatching (days)	Range of total length (mm)
Acheilognathus lanceolata	R. Yabe	5	40	9.55–11.75
		5	80	17.10–20.95
		6	160	29.80–40.60
A. limbata	R. Yabe	3	80	17.20–17.50
		6	160	27.10–47.50
A. tabira subsp. (b)	R. Yabe	6	40	8.20–11.50
		6	100	21.30–26.40
Rhodeus ocellatus smithi	R. Yabe	6	60	16.30–18.60
		6	100	20.23–24.58

its anterior edge (Fig. 2A). Although the masticatory process in *A. limbata* (Temminck et Schlegel) resembles that of *A. lanceolata*, the anterior part of the bone in this species is relatively underdeveloped (Fig. 2B). The masticatory process in *Tanakia tanago* (Tanaka) is also horseshoe-shaped and the roof of the pharyngeal process posteriorly fans out and widens (Fig. 2C). The masticatory process in *Rhodeus atremius* (Jordan et Thompson) and *R. suigensis* (Mori) is ovoid-shaped and slightly depressed anteriorly (Fig. 2D, E). Although the masticatory process in *R. ocellatus smithi* (Regan) and *R. ocellatus ocellatus* (Kner) resembles that of *R. atremius* and *R. suigensis*, the developmental degree of the anterior part of the bone in these subspecies is relatively high (Fig. 2F, G). The masticatory process in *A. tabira tabira* Jordan et Thompson, *A. tabira* subsp. (a), *A. tabira* subsp. (b) is ovoid-shaped (Fg. 2H, I, J). Although the masticatory process in *A. moriokae* Jordan et Thompson resembles that of three subspecies of *A. tabira*, the anterior part of the bone in this species is relatively developed (Fig. 2K). The masticatory process in *A. rhombea* (Temminck

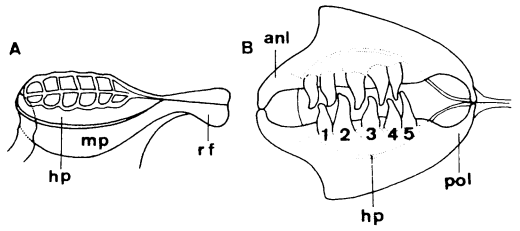

Fig. 1. The pharyngeal dentition in a bitterling. A, horny pad and masticatory process in *Rhodeus ocellatus smithi*. B, feature of pharyngeal dentition in *R. ocellatus smithi*. Pharyngeal teeth are shown with numerals. mp, masticatory process of the basioccipital bone; hp, horny pad; rf, roof of the pharyngeal process; anl, anterior limb of the pharyngeal bone.

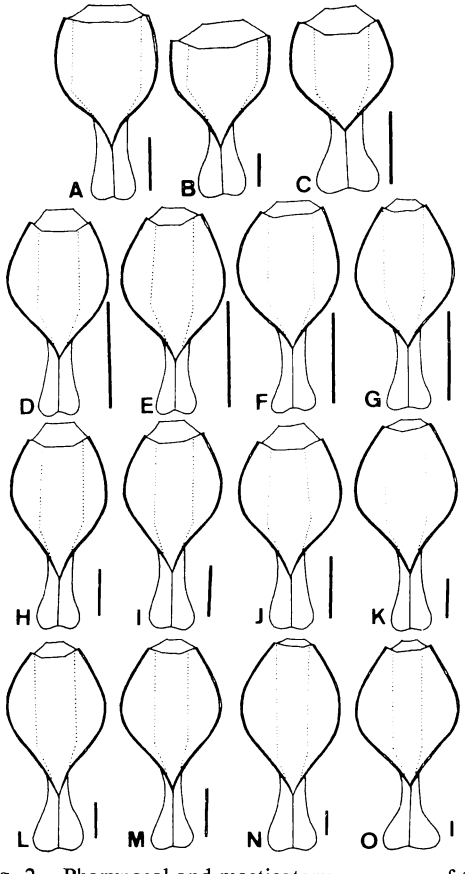

Fig. 2. Pharyngeal and masticatory processes of the basioccipital bone in bitterlings. A, *Acheilognathus lanceolata*. B, *A. limbata*. C, *Tanakia tanago*. D, *Rhodeus atremius*. E, *R. suigensis*. F, *R. ocellatus smithi*. G, *R. ocellatus ocellatus*. H, *A. tabira tabira*. I, *A. tabira* subsp. (a). J, *A. tabira* subsp. (b). K, *A. moriokae*. L, *A. rhombea*. M, *A. cyanostigma*. N, *A. longipinnis*. O, *Pseudoperilampus typus*. Scales indicate 1 mm.

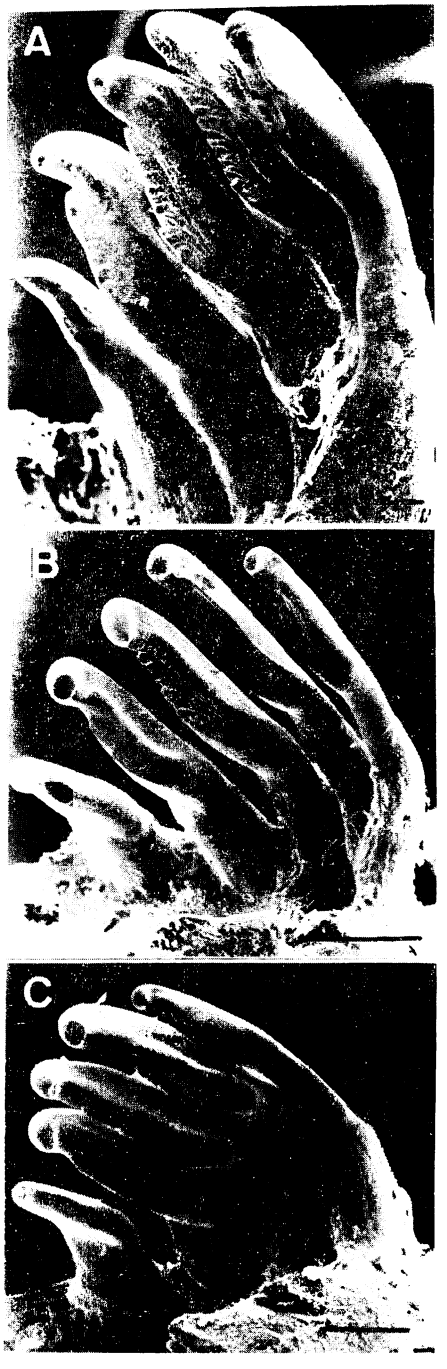

Fig. 3. Pharyngeal teeth of bitterlings belonging to Group I. A, *Acheilognathus lanceolata*. B, *A. limbata*. C, *Tanakia tanago*. Scales indicate 500 μm.

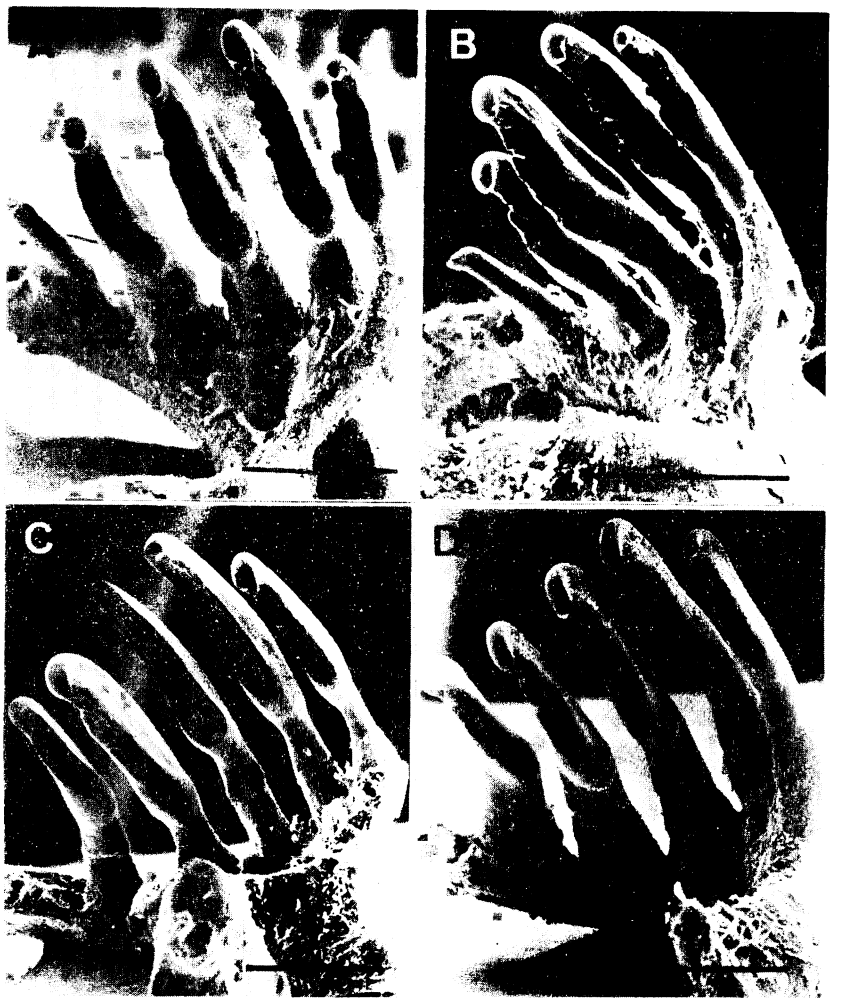

Fig. 4. Pharyngeal teeth of bitterlings belonging to Type A. A, *Rhode atremius*. B, *R. suigensis*. C, *R. ocellatus smithi*. D. *R. ocellatus ocellatus*. Scales indicate 500 μm.

et Schlegel), *A. cyanostigma* Jordan et Fowler, *A. longipinnis* Regan and *Pseudoperilampus typus* Bleeker is also ovoid-shaped and the roof of the pharyngeal process posteriorly fans out and widens (Fig. 2L, M, N, O).

Morphological characters of the occlusal grooves on the pharyngeal teeth and the chewing area on the pharyngeal first tooth. The dental formula of bitterlings is usually represented as 0, 0, 5–5, 0, 0 and five teeth are arranged in a row on the pharyngeal bone of each side (Fig. 1B). The dentition is polyphyodont and homodont. The crowns of the teeth have the occlusal grooves and the occlusal surfaces. Many serrated grooves are connected with each serrated tubercle on the occlusal surface. When the occlusal surface has excessively worn away, the occlusal grooves disappear from the occlusal surface.

In *A. lanceolata*, *A. limbata* and *T. tanago*, *R. atremius* and *R. suigensis*, the occlusal grooves on the pharyngeal teeth are relatively reduced and the chewing area on the pharyngeal first tooth is relatively underdeveloped. Their occlusal surface is narrow (Figs. 3A, B, C; 4A, B). The occlusal grooves in two subspecies of *R. ocellatus* are reduced but the chewing area on the pharyngeal first tooth is relatively developed (Fig. 4C, D). Three subspecies of *A. tabira* and *A. moriokae* have relatively developed occlusal grooves on the pharyngeal teeth and a developed chewing area on

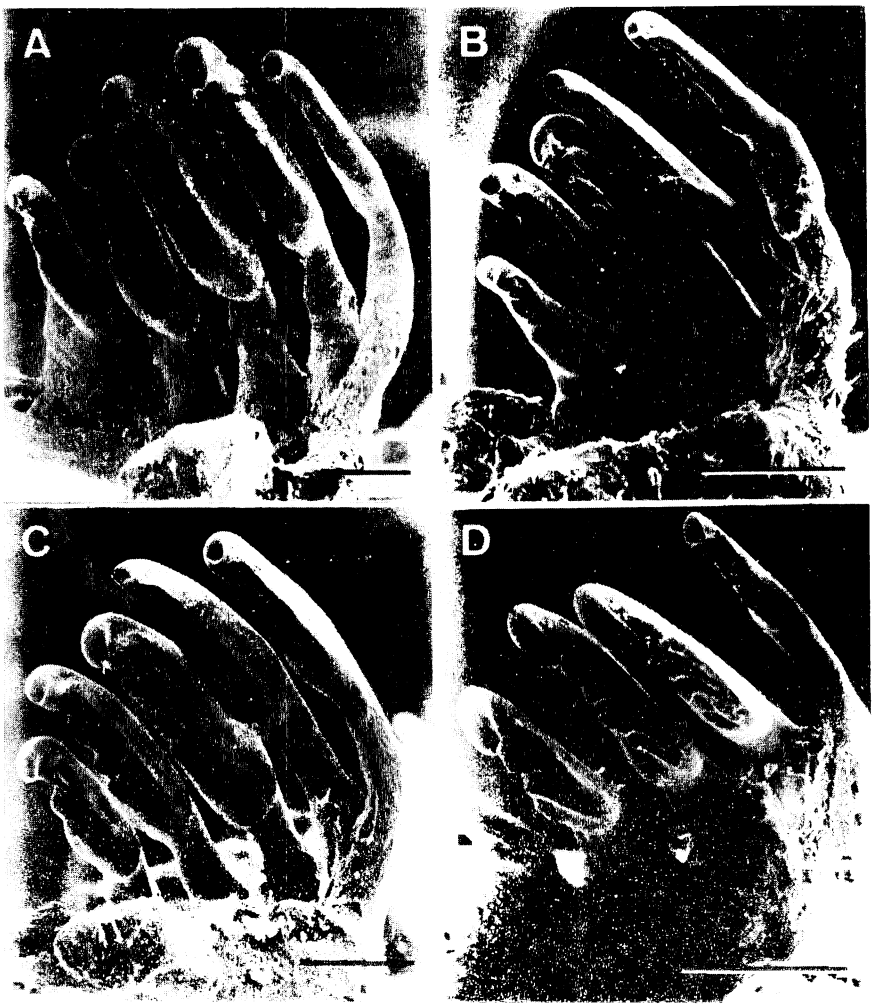

Fig. 5. Pharyngeal teeth of bitterlings belonging to Subtype c. A, *Acheilognathus tabira tabira*. B, *A. tabira* subsp. (a). C, *A. tabira* subsp. (b). D, *A. moriokae*. Scales indicate 500 μm.

the pharyngeal first tooth (Fig. 5A, B, C, D). In *A. rhombea*, *A. cyanostigma*, *A. longipinnis* and *P. typus*, the occlusal grooves on the pharyngeal teeth are well developed and the chewing area on the pharyngeal first tooth is developed (Fig. 6A, B, C, D).

In addition, larval and juvenile pharyngeal teeth were examined in several species (Table 2). In *A. lanceolata*, some serrated tubercles are arranged on the outside occlusal margin of the larvae of 40 days after hatching (Fig. 7A) and the occlusal grooves are connected with each serrated tubercle on the occlusal surface in the larvae of 80 days after hatching (Fig. 7B). The occlusal grooves of this species become reduced in adults at 160 days after hatching (Fig. 7C). The occlusal grooves are also connected with each serrated tubercle on the occlusal surface in *A. limbata* at 80 days after hatching (Fig. 7D) and in *R. ocellatus smithi* at 60 days after hatching (Fig. 7E). The occlusal grooves are developed in *A. tabira* subsp. (b) at 100 days after hatching (Fig. 7F). In these larvae, the occlusal grooves on the pharyngeal teeth are fairly developed and the chewing area on the pharyngeal first tooth is underdeveloped and the occlusal surface is narrow.

Discussion

Kobayasi and Maeda (1961) reported that *A. lanceolata*, *A. limbata* and *R. ocellatus* have no ser-

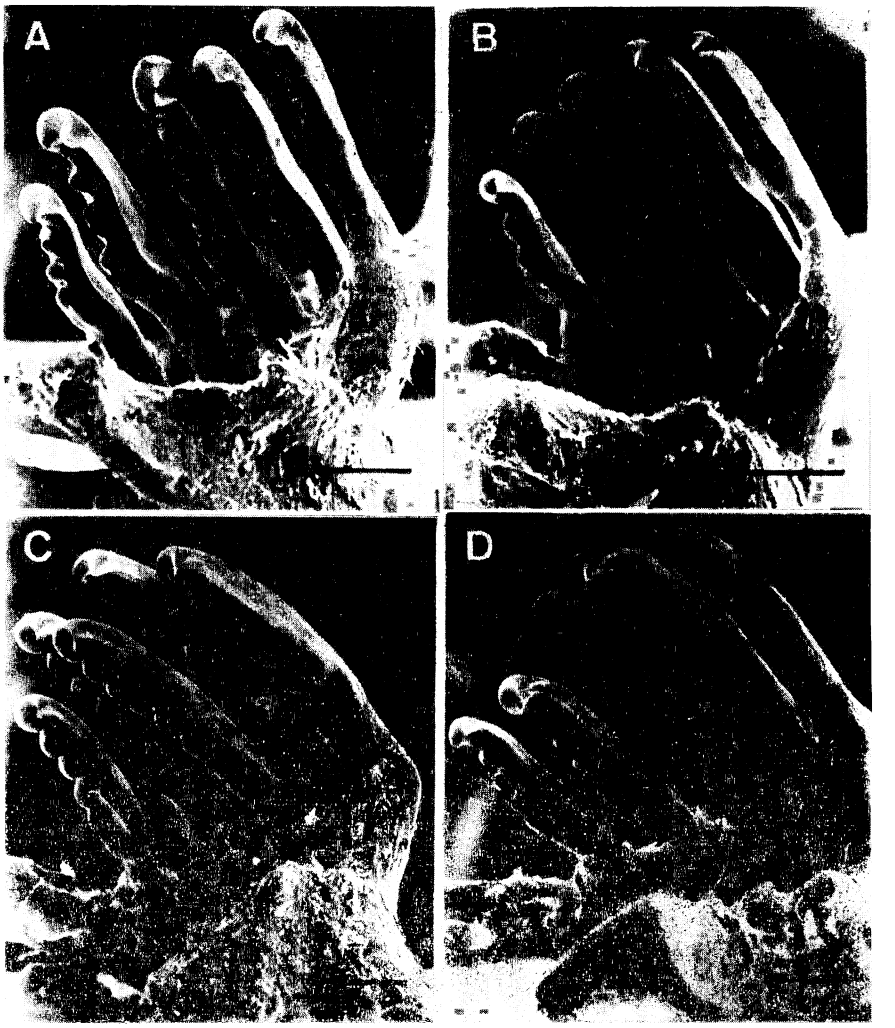

Fig. 6. Pharyngeal teeth of bitterlings belonging to Subtype d. A, *Acheilognathus rhombea*. B, *A. cyanostigma*. C, *A. longipinnis*. D, *Pseudoperilampus typus*. Scales indicate 500 μm.

rated grooves on the side of the pharyngeal teeth. Our observations show that in these species the phayrngeal teeth have reduced grooves on the occlusal surfaces. The occlusal grooves on the pharyngeal teeth in two subspecies of *R. ocellatus* are more reduced than those in *A. lanceolata* and *A. limbata*. However, the occlusal grooves are rather developed in the larvae of these four species and subspecies. It is found in larvae of some cyprinid fishes that the pharyngeal teeth have serrated grooves on the occlusal surface, which change morphologically with growth of the fish (Vasnecov, 1939; Kodera, 1982). In *A. lanceolata*, *A. limbata* and *R. ocellatus*, the occlusal grooves on the pharyngeal teeth seem to become reduced with growth.

In acheilognathine fishes, the masticatory process of the basioccipital bone has scarcely been used for the analysis of phylogenetic relationships, although it has been described (Nakajima, 1982). Among Japanese bitterlings, differences are found in the developmental degrees of the anterior part of the masticatory process, the occlusal grooves on the pharyngeal teeth and the chewing area on the pharyngeal first tooth. On the basis of the combination of these characters, Japanese bitterlings are divided into two groups (Table 3).

The first group, Group I, including *A. lanceolata*,

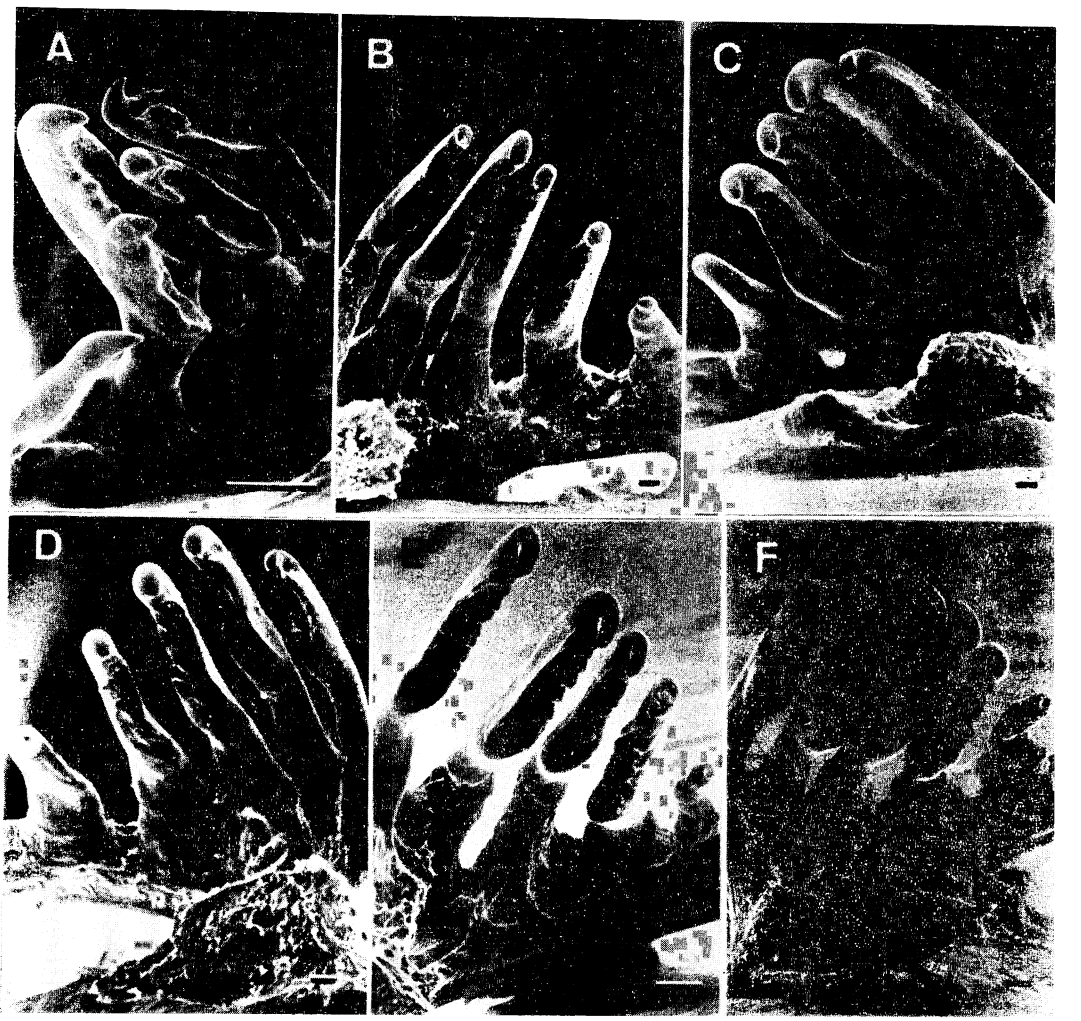

Fig. 7. Pharyngeal teeth of larval and juvenile bitterlings, A, *Acheilognathus lanceolata*, 40 days after hatching. B, *A. lanceolata*, 80 days after hatching. C, *A. lanceolata*, 160 days after hatching. D, *A. limbata*, 80 days after hatching. E, *Rhodeus ocellatus smithi*, 60 days after hatching. F, *A. tabira* subsp. (b), 100 days after hatching. Scales indicate 50 μm.

A. limbata and *T. tanago*, is characterized in that the anterior part of the masticatory process is relatively underdeveloped, the occlusal grooves on the pharyngeal teeth are reduced and the chewing area on the pharyngeal first tooth is relatively underdeveloped.

The second group, Group II, consisting of *R. atremius*, *R. suigensis*, *R. ocellatus smithi*, *R. ocellatus ocellatus*, *A. tabira tabira*, *A. tabira* subsp. (a), *A. tabira* subsp. (b), *A. moriokae*, *A. rhombea*, *A. cyanostigma*, *A. longipinnis* and *P. typus*, is different from Group I in that the anterior part of the masticatory process is relatively developed. According to the degree of the development of the occlusal grooves, this group is subdivided into two types. The first type, Type A, which includes fishes of the genus *Rhodeus*, is characterized in having reduced occlusal grooves on the pharyngeal teeth. This type is classified into two subtypes based on the developmental degree of the chewing area on the pharyngeal first tooth. The first subtype, Subtype a, including *R. atremius* and *R. suigensis*, has a relatively underdeveloped chewing area on the pharyngeal first tooth. The second subtype, Subtype b, includes two subspecies of *R. ocellatus*. Although this subtype resembles Sub-

Table 3. Relationship between three pharyngeal elements and classification among Japanese bitterlings.

Classification			Developmental degree of pharyngeal elements			Species and subspecies
Group	Type	Subtype	Anterior part of masticatory process	Occlusal grooves on pharyngeal teeth	Chewing area on the first tooth	
I			underdeveloped	reduced	relatively underdeveloped	*Acheilognathus lanceolata* *A. limbata* *Tanakia tanago*
II	A	a	relatively developed			*Rhodeus atremius* *R suigensis*
		b			relatively developed	*R. ocellatus smithi* *R. ocellatus ocellatus*
	B	c		relatively developed		*A. tabira tabira* *A. tabira* subsp. (a) *A. tabira* subsp. (b) *A. moriokae*
		d			well developed	*A. rhombea* *A. cyanostigma* *A. longipinnis* *Pseudoperilampus typus*

type a in the feature of the occlusal grooves, it is distinguished from Subtype a in having a relatively developed chewing area on the pharyngeal first tooth.

The second type, Type B, consisting of fishes of the genera *Acheilognathus* and *Pseudoperilampus* is characterized by having relatively developed occlusal grooves on the pharyngeal teeth. This type is subdivided into two subtypes based on the developmental degree of the chewing area on the pharyngeal first tooth. The first subtype, Subtype c, including three subspecies of *A. tabira* and *A. moriokae*, has the relatively developed chewing area on the pharyngeal first tooth. The second subtype, Subtype d, which includes *A. rhombea*, *A. cyanostigma*, *A. longipinnis* and *P. typus*, is distinguishable from Subtype c in having the well developed chewing area on the pharyngeal first tooth.

Nakamura (1969) suggested that the fishes included in Group I and Type A in the present study are omnivorous species and those in Type B are herbivorous species. The occlusal grooves on the pharyngeal teeth in the species belonging to Type B are more developed than those in the species belonging to Group I and Type A. The pharyngeal and masticatory processes of the basioccipital bone in cyprinid fishes are considered to make efficent in feeding (Estiman, 1971; Nakajima, 1982; Nakajima *et al.*, 1982). Thus, it is naturally considered that the developmental degre of the occlusal grooves on the pharyngeal teeth seems to be related to the feeding habits.

We consider that the differences between Group I and Group II are larger than those between Type A and Type B. In other words, the morphological characters of the masticatory process of the basioccipital bone should be more important than the occlusal grooves on the pharyngeal teeth. Arai (1978, 1982) suggested that *Acheilognathus* species including Group I and Type B should be divided into two different fish groups based on karyotypes, the dorsal-fin ray formula and embryological data. From these facts, the characters of Group I examined here seem to be the most primitive. The classification based on the combination of the developmental degrees of the anterior part of the masticatory process, the occlusal grooves on the pharyngeal teeth and the chewing area on the pharyngeal first tooth suggests the phylogenetic

relationships among Japanese bitterlings.

Acknowledgments

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日本産タナゴ亜科魚類における咽頭歯と咀嚼突起の比較形態学的研究

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日本産タナゴ亜科魚類全種類の咽頭歯における咬合溝と第1歯咀嚼面ならびに基底後頭骨の咀嚼突起の形態的比較を行った．

従来，咽頭歯に咬合溝がないとされていた種類にも縮小的な咬合溝が存在することが明らかになった．また，仔魚は咬合溝の比較的発達した咽頭歯をもっており，咬合溝は仔魚の発育に伴ってそれぞれの成魚にみられる形態へと変化するものと考えられた．

成魚において，基底後頭骨にある咀嚼突起の形態は，その前縁部が未発達なものと比較的発達するものに，咽頭歯の咬合溝は縮小的なものと比較的発達するものとにそれぞれ区別された．また，第1歯の咀嚼面は比較的未発達なものおよび比較的発達するものとよく発達しているものとに分けられた．この3つの形態的特徴を組み合せて，日本産タナゴ亜科魚類は，2つのグループおよび2つのタイプまたは5つのサブタイプに区分された．この類型区分は，日本産タナゴ亜科魚類の系統類縁に関連しているものと推察された．

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