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Development of the Pharyngeal Teeth in the Big Head, *Aristichthys nobilis* (Cyprinidae)

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Abstract The development of pharyngeal dentition was observed in the big head, *Aristichthys nobilis*, which is one of the hypophthalmichthyines of the cyprinids. This fish has the C-type larval dentition, in which no teeth ever occur at the position An3, and in which the first tooth at the position An2 is on the third replacement wave. So the positions Po1, Ce0, An1 and An2 in the larval dentition correspond to the positions A4, A3, A2 and A1 in the adult dentition, respectively. The initial tooth at each position is a conical one. The conical teeth are then changed to ones bearing a narrow grinding surface with a hook at the tip and some denticles on the margins. These teeth are of the *Leuciscus* stage. In the following teeth, the grinding surface is expanded, and the denticles are increased in number and distributed on not only the margins but also the whole grinding surface. These teeth bearing a very broad grinding surface characterize the hypophthalmichthyines. At the positions A2 to A4, the teeth become the hypophthalmichthyine type in the larval period. But the tooth at the position A1 becomes the hypophthalmichthyine type in the juvenile period. The morphological change of teeth in this species is simple although their teeth are highly specialized. We think that this phenomenon gives a hint on their phylogeny.

The cyprinid fishes bear well-developed pharyngeal dentitions. The external features, numbers and arrangements of the teeth have often been studied as criteria for taxonomic classification. Adult cyprinids bear various pharyngeal dentitions, but the teeth in larvae are similar to each other in external features and arrangements (Nakajima, 1979, 1984).

Cyprinids continue to replace their teeth in the regular pattern throughout their life span. The replacement waves sweep alternately and cephalad in common cyprinids (Evans and Deubler, 1955; Nakajima, 1979; Nakajima et al., 1981, 1983). The pharyngeal dentition changes in tooth shape and arrangement through tooth replacements.

Vasnecov (1939) was the first to take notice that the cyprinid phylogeny was represented in the ontogeny of the pharyngeal dentition. He studied the development of pharyngeal dentitions in cyprinid and cobitid fishes. He found that *Abramis brama*, *Rutilus rutilus* and *Misgurnus fossilis*, bearing a single row of teeth in the adult phase, develop two rows during the larval period, and concluded that the multi-rowed dentition in cyprinids is primitive. Certainly, the evolution of cypriniform dentitions was initiated primarily with multiple rows (Nakajima, 1987). However, Vasnecov (1939) put a hasty interpretation on the evolution of the cypriniform dentition. That is because the multi-rowed larval dentition is quite different from the multi-rowed adult one. The minor row in the adult dentition of cyprinids is an apomorphic character within cypriniforms. The cobitid or catostomid dentition in a single row has not been evolved in the least from the multi-rowed dentition in the cyprinids (Nakajima, 1979, 1987).

The initial teeth in cypriniforms are conical, and they are changed to specialized forms (Vasnecov, 1939; Weisel, 1967; Nakajima, 1977, 1979, 1984, 1987; Kodera, 1982). Vasnecov (1939) used the changes in the tooth form as evidence of phylogenesis in the cyprinids. After that, some authors have suggested the possibility that the morphological change of pharyngeal teeth during successive replacements implies the phylogenesis of cypriniform fishes (Weisel, 1967; Nakajima, 1977; Kodera, 1982).

In hypophthalmichthyines dentition, four teeth are arranged in a row, and they are depressed and somewhat in the shape of a reversed slipper. The grinding surface of the teeth is broad and slightly concave. Their teeth represent one of the highest specializations attained by the cyprinid fishes

(Chu, 1935). The present study is undertaken to clarify the development of their specialized dentition, and describes the morphological change of teeth by replacements in the big head, *Aristichthys nobilis* (Richardson).

Materials and methods

Larvae and juveniles of *Aristichthys nobilis* were reared from eggs artificially fertilized in the laboratory, and sampled at random. Their parent fish were captured in East Lake (Lake Tong-hu), Hubei Province, China.

The specimens were fixed and preserved in 10% formalin, and cleared in 1% KOH, stained with alizarin red S, and stored in 80% alcohol. In every specimen, the pharyngeal arches with their mucous membrane were removed from the head and stored in 80% alcohol.

Some specimens, in which the attached teeth and tooth germs with the mucous membrane were left, were submerged in pure glycerine and examined under a binocular microscope. Other specimens were re-fixed in 2% osmic acid. Soft tissue was removed from them with the unattached tooth germs, and the attached teeth were left there. The bones and attached teeth were dried with a critical point dryer, coated with gold by an ion spatter, and examined under a scanning electron microscope.

The standard length (SL) was measured from the snout to the end of the notochord in larvae, and from the snout to the end of the hypurals in juveniles and adults.

Terminology. The pharyngeal teeth are replaced alternately and cephalad as if the waves swept. A replacement wave is a series of replacement teeth of the same generation. The teeth are ankylosed at even or odd positions on a single replacement wave. The waves permitting tooth ankylosis sweep alternately at even and odd positions. The initial tooth and its replacement teeth which appear at each position belong to a group of teeth, called tooth family (Table 1).

The larval dentition is defined as the multi-rowed dentition in which each tooth row consists of teeth on a single replacement wave. The tooth row in the adult dentition consists of teeth on some replacement waves. The tooth rows in the larval dentition are occupied alternately by the teeth which are ankylosed at even and odd positions in the larval dentitions. The period during which the larval dentition persists does not necessarily correspond to the larval period (Nakajima, 1984).

In the larval dentition, tooth positions and identified numbers of teeth are numbered according to Nakajima et al. (1986). The tooth at the position (r) on the replacement wave (n) is numbered $_{n-1}$[r]. However, the position of the initial tooth is numbered Ce0, the more anterior positions are numbered anteriorly An1, An2, and more posterior ones Po1 (Table 1).

Results

The type of larval dentition. The first tooth, $_0$[Ce0], is attached to the bone at the end of the pre-larval period, 7.0 mm SL. Then, the pharyngeal bone has not yet been stained in red without the basement of the tooth. At the early stage of the post-larval period, 8 mm SL, the pharyngeal bone is stained with alizarin red S, and three teeth, $_1$[Po1], $_0$[Ce0] and $_1$[An1], are ankylosed to the bone (Fig. 1a). After that, the larvae bear the larval dentition with their teeth arranged in multiple rows (Fig. 1). However, each tooth row consists of teeth on a single replacement wave, and is different from the tooth rows of the adult dentition.

In the post-larval period, about 12 mm SL, four teeth, $_5$[Po1], $_6$[Ce0], $_5$[An1], $_6$[An2], are arranged in a row. This row is a major row, A row, of the adult dentition. It consists of teeth on two replacement waves, the sixth and seventh waves.

Table 1. Appearance pattern or distribution of the teeth during the larval period in *Aristichthys nobilis*.

Replacement wave	Tooth family or tooth position in larval and adult dentition			
	Po1/A4	Ce0/A3	An1/A2	An2/A1
1st		$_0$[Ce0]		
2nd	$_1$[Po1]		$_1$[An1]	
3rd		$_2$[Ce0]		$_2$[An2]
4th	$_3$[Po1]		$_3$[An1]	
5th		$_4$[Ce0]		$_4$[An2]
6th	$_5$[Po1]		$_5$[An1]	
7th		$_6$[Ce0]		$_6$[An2]
8th	$_7$[Po1]		$_7$[An1]	
9th		$_8$[Ce0]		$_8$[An2]
10th	$_9$[Po1]		$_9$[An1]	

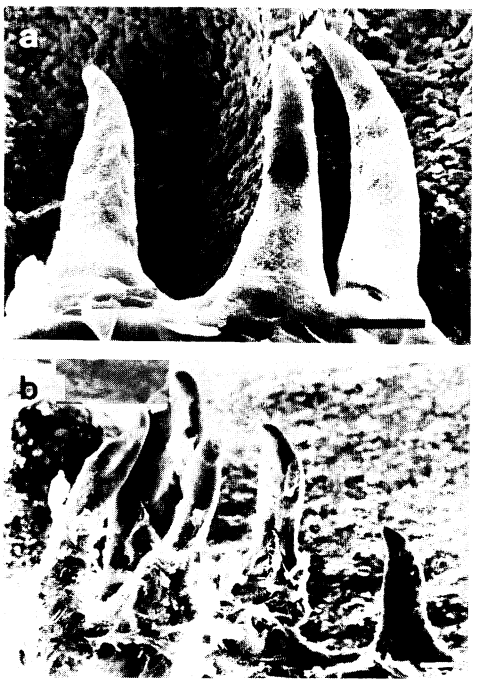

Fig. 1. Scanning electron microphotographs of the larval dentitions on the left pharyngeal bones of *Aristichthys nobilis*. The larval dentition is arranged in multiple rows. Scale bars show 20 μm. a: 8.4 mm SL. Teeth $_{1}$[Po1], $_{0}$[Ce0] and $_{1}$[An1], from left to right, are seen. b: 10.5 mm SL. Teeth $_{3}$[Po1], $_{4}$[Ce0], $_{2}$[Ce0], $_{3}$[An1] and $_{4}$[An2], from left to right, are seen.

Therefore, the adult dentition is completed in the post-larval period, about 12 mm SL. The persisting period of each tooth in the larval dentition is shown in Table 2.

Table 2. Persisting period of each tooth in the larval dentition in *Aristichthys nobilis*.

Tooth	Germ period (mm SL)	Functioning period (mm SL)
$_{0}$[Ce0]		7.0– 9.7
$_{1}$[Po1]	7.0– 7.7	7.3– 9.8
$_{1}$[An1]	7.0– 7.8	7.3–10.4
$_{2}$[Ce0]	7.8– 9.0	9.0–11.5
$_{2}$[An2]	8.4– 9.0	9.0–10.2
$_{3}$[Po1]	9.0– 9.9	9.8–11.5
$_{3}$[An1]	9.0–10.0	9.9–11.5
$_{4}$[Ce0]	9.9–10.4	10.0–11.5
$_{4}$[An2]	9.9–10.4	10.4–11.5
$_{5}$[Po1]	10.0–11.9	11.9–
$_{5}$[An1]	10.0–11.9	11.9–

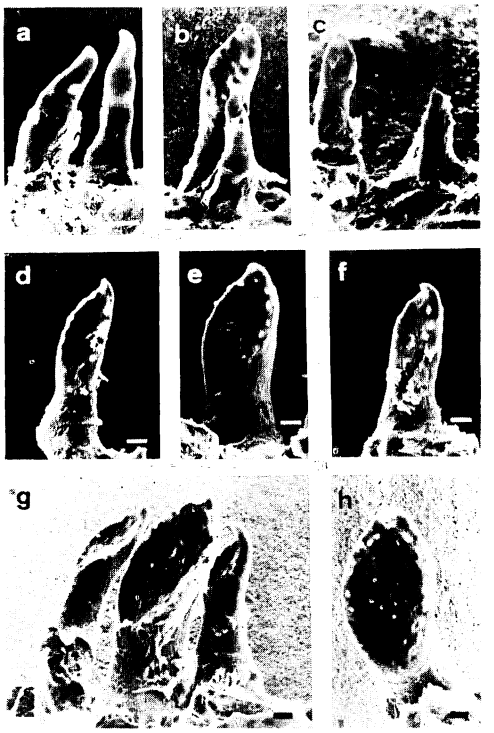

Fig. 2. Scanning electron microphotographs of the left teeth of larval *Aristichthys nobilis*. Scale bars show 20 μm. a, $_{3}$[Po1] (left) and $_{2}$[Ce0] (right); b, $_{4}$[Ce0] (left) and $_{2}$[Ce0] (right); c, $_{3}$[An1] (left) and $_{4}$[An2] (right); d, $_{5}$[Po1]; e, $_{6}$[Ce0]; f, $_{5}$[An1]; g, $_{7}$[Po1] (left), $_{8}$[Ce0] (middle) and $_{7}$[An1] (right); h, the tooth of the hypophthalmichthyine type, $_{8}$[Po1].

No teeth appear at the position An3, so the position An2 in the larval dentition becomes the position A1 in the adult dentition. At the position An2, the first tooth is on the third replacement wave. Therefore, this fish has the C-type of larval dentition (Nakajima, 1984). So the positions Po1, Ce0, An1 and An2 correspond to the positions A4, A3, A2 and A1 in the adult dentition, respectively (see Table 1).

Morphological change of teeth during the larval period. The first tooth at the position Po1, $_{1}$[Po1], is recurved and conical (Figs. 1a, 3a). The second tooth, $_{3}$[Po1], bears a narrow grinding surface with a hook. There are some denticles on the margins of the grinding surface of this tooth (Figs. 1b, 2a, 3b). In the third and fourth teeth, $_{5}$[Po1] and $_{7}$[Po1] respectively, the grinding surface is expanded. The denticles are increased

in number and are distributed not only on the margins but also on the grinding surface (Figs. 2d, g, 3c, d). The fifth tooth, $_{9}$[Po1], is similar to the preceding tooth in shape. However, they group up in size. The denticles are increased in number and are distributed on the whole grinding surface (Fig. 3e).

The first and second teeth at the position Ce0, $_{0}$[Ce0] and $_{2}$[Ce0] respectively, are recurved and conical (Figs. 1a, b, 2a, b, 4a, b). The third tooth, $_{4}$[Ce0], bears a broad grinding surface with a hook and denticles. The denticles are distributed on the margins of the grinding surface (Figs. 1b, 2b, 4c). The fourth and fifth teeth, $_{6}$[Ce0] and $_{8}$[Ce0] respectively, bear a very broad grinding surface with a hook and many denticles, and grow up in size. The denticles are distributed not only on the margins but also on the whole grinding surface (Figs. 2e, g, h, 4d, e).

The first tooth at the position An1, $_{1}$[An1], is recurved and conical (Figs. 1a, 5a). The second tooth, $_{3}$[An1], bears an obscure grinding surface that has some denticles on the margin (Figs. 1b, 2c, 5b). The third tooth, $_{5}$[An1], bears a grinding surface with a hook at the tip and some denticles on the margins (Figs. 2f, 5c). In the fourth tooth, $_{7}$[An1], the denticles are increased in number and are distributed on the whole grinding surface (Figs. 2g, 5d). The fifth tooth, $_{9}$[An1], bears a very broad grinding surface with a hook and many denticles (Fig. 5e).

The first and second teeth at the position An2, $_{2}$[An2] and $_{4}$[An2] respectively, are recurved and conical (Figs. 1b, 2c, 6a, b). The third to fifth teeth, $_{6}$[An2], $_{8}$[An2] and $_{10}$[An2] respectively, are conical, but the apex of the teeth are not recurved as in the preceding teeth (Fig. 6c, e).

The teeth which are of the adult dentition during the post-larval period can be identified on the basis of difference in shape on the fifth to eighth replacement wave. But the teeth on the following replacement waves are not changed obviously in shape and size, and hence it is difficult to identify these teeth.

The morphological change of teeth during the late larval period and the juvenile period. In the post-larval period, about 18 mm SL, A2–A4 teeth bear a very broad grinding surface with a hook and many denticles, but the grinding surface is worn. A1 tooth is left just as a conical tooth (Fig. 7a). It becomes a tooth with a narrow grinding surface in the juvenile period at 23 mm SL (Fig. 7b), and bears a broad grinding surface at 35 mm SL (Fig. 7c). At this stage, all the teeth become the hypophthalmichthyine type.

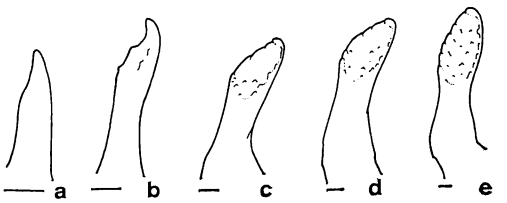

Fig. 3. Morphological changes of the teeth at the position Po1. Scale bars show 20 μm. a, $_{1}$[Po1]; b, $_{3}$[Po1]; c, $_{5}$[Po1]; d, $_{7}$[Po1]; e, $_{9}$[Po1].

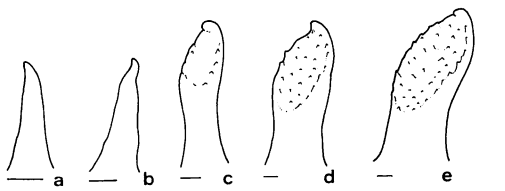

Fig. 4. Morphological changes of the teeth at the position Ce0. Scale bars show 20 μm. a, $_{0}$[Ce0]; b, $_{2}$[Ce0]; c, $_{4}$[Ce0]; d, $_{6}$[Ce0]; e, $_{8}$[Ce0].

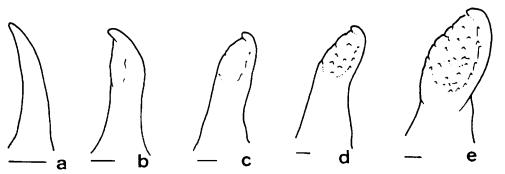

Fig. 5. Morphological changes of the teeth at the position An1. Scale bars show 20 μm. a, $_{1}$[An1]; b, $_{3}$[An1]; c, $_{5}$[An1]; d, $_{7}$[An1]; e, $_{9}$[An1].

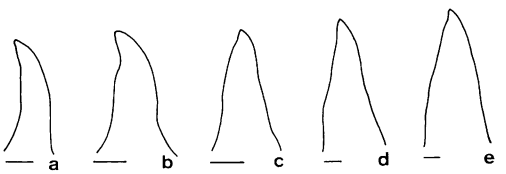

Fig. 6. Morphological changes of the teeth at the position An2. Scale bars show 20 μm. a, $_{2}$[An2]; b, $_{4}$[An2]; c, $_{6}$[An2]; d, $_{8}$[An2]; e, $_{10}$[An2].

Discussion

The initial teeth are conical and are later changed to specialized teeth during successive

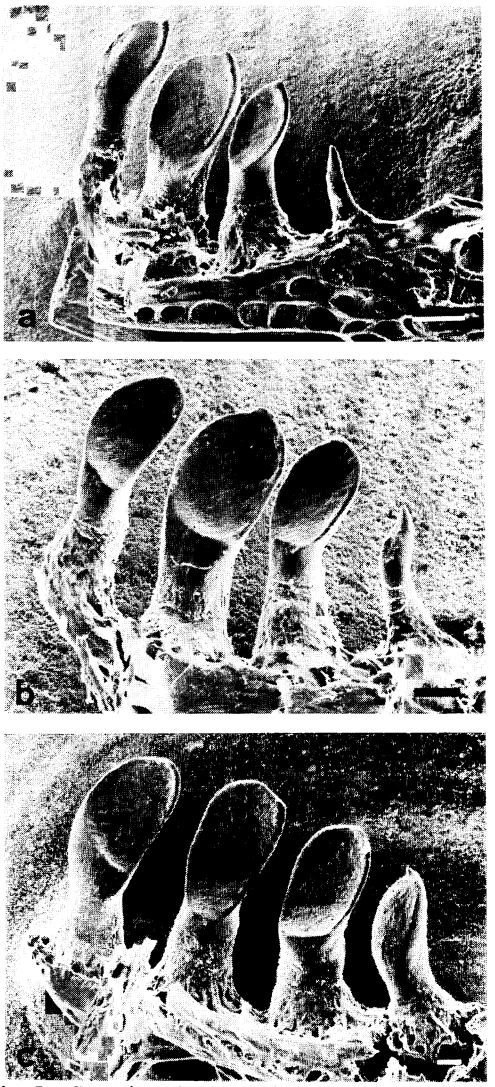

Fig. 7. Scanning electron microphotographs of the adult dentition during the late post-larval to early juvenile period in *Aristichthys nobilis*. Scale bars show 20 μm. a, 18.2 mm SL; b, 23.0 mm SL; c, 34.0 mm SL.

replacements in cyprinids (Vasnecov, 1939; Nakajima, 1977, 1979, 1984; Kodera, 1982). Vasnecov (1939) observed the morphological change of the teeth in eight cyprinids and one cobitid, and has made it clear that the teeth are changed from conical to specialized ones through ones bearing a narrow grinding surface with a hook at the tip and some denticles on the margins of the grinding surface, which is called *Leuciscus* stage. He used the changes in tooth form as evidence of phylogenesis in the cypriniforms.

In *Aristichthys nobilis*, too, some initial teeth at each position are conical, and the following teeth have the narrow grinding surface with a hook at the tip and some denticles on the margins. The conical tooth and the tooth of the *Leuciscus* stage appear at the early stages of its ontogeny. But A1 tooth is left just as a conical tooth during the larval period, and it gets into the *Leuciscus* stage in the juvenile period. The tooth of the *Leuciscus* stage is followed by teeth bearing a very broad grinding surface with a hook and many denticles at each position. This type of teeth represents hypophthalmichthyines.

In *Cyprinus carpio*, whose adult teeth are very specialized, the teeth are changed from conical teeth through a complex way. The morphological changes in the teeth of *Cyprinus carpio* resemble those of some fish groups, for example, barbines and gobionines (Kodera, 1982). In *Aristichthys nobilis*, however, the teeth are changed directly from the *Leuciscus* stage to the hypophthalmichthyine type, and their teeth become highly specialized. The morphological change of teeth in this species is simple although their teeth are highly specialized.

We think that this phenomenon gives a hint on the evolution of the hypophthalmichthyine teeth. Their teeth were evolved directly from some leuciscine type and become highly specialized. Their teeth do not have affinity to gobionine and barbine teeth. This is also supported by the evidence that their larval dentition is of the C-type. This type of the larval dentition occurs in cyprinines, leuciscines and danionines, and never in gobionines and barbines (Nakajima, 1984).

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コイ科魚類コクレンにおける成長にともなう咽頭歯の形態変化

中島経夫・楽　佩琦

コクレンの咽頭歯系の個体発生を観察すると，位置 An3 に歯がまったく出現せず，位置 An2 の第 1 世代の歯が第 3 交換波のものである．このことから，本種の仔魚歯系は，C型である．したがって，最初の歯が現われる位置，Ce0 は，成魚歯系の位置 A3 に対応する．各位置の最初の歯は，円錐歯である．その後歯は交換によって，小突起が縁どる狭い咬合面をもつ歯に変わる．この歯は，ロイシスカス段階と呼ばれ，コイ科魚類の仔魚に普遍的に見られるものである．さらに，歯は咬合面が拡大し，小突起の数が増してゆく．この小突起は，咬合面の縁ばかりではなく，咬合面全体に見られる．この歯は，レンギョ亜科魚類特有のものである．高度に特殊化しているにもかかわらず，コクレンの歯は，単純な過程をへて形態形成が進む．このことは，レンギョ亜科魚類の系統発生を暗示しているように思える．

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