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Development and Replacement of Upper Jaw Teeth in Gobiid Fish, *Sicyopterus japonicus*

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Abstract Upper jaw teeth of *Sicyopterus japonicus* are examined regarding their shape, development and replacement. The fish has a row of functional teeth and ca. 23 rows (31 mm SL) to ca. 40 rows (85 mm SL) of replacement teeth on their upper jaw. Replacement teeth shift their position in the gum with development, and at the last stage of their development a small bone is formed at the base of each tooth. Replacement teeth with the small basal bones completed move downward in the gum and set firmly on the premaxillary to become functional teeth. Old functional teeth replaced by new ones are gradually resorbed in the tissue of the upper jaw in the process of entering into a crevice of the premaxillary, and finally completely disappear. This resorption suggests that there is a possibility of the reuse of their components to produce new teeth. This replacement occurs every 9.2 days when the fish size (SL) increases 0.12 mm per one day (1.1 mm per 9.2 days). The fish probably needs tooth replacement frequently and resorption of the teeth because the upper jaw teeth wear out rapidly when feeding by scraping algae from the surface of stones with its teeth.

Sicyopterus japonicus (Tanaka) of the family Gobiidae is well known for the habit of amphidromous migration, and is also known for its peculiar habit, i.e., rock-climbing behavior (Fukui, 1979).

Juveniles of this fish appear in schools at the mouths of rivers in spring and early summer, and then run up river. When they reach midstream or upstream where rocks and/or pebbles fill in the bottom, their school breaks up and the fish set up separate home ranges. They scrape off diatoms, blue-green algae, etc., growing on the surface of stones with a row of upper jaw teeth to get food (Dôtu and Mito, 1955; Fukui, 1979).

This fish has numerous replacement teeth hidden in the gum on the upper jaw behind an outer visible row of functional teeth (Prince Akihito and Meguro, 1979; Fukui, 1979). These teeth have been considered to correlate with feeding habits, as mentioned above. Rows of functional teeth are replaced by replacement teeth. Herre (1927) wrote in his description of genus *Sicyopterus* that "as the teeth of the first row are worn out or broken they are replaced by the buds next in line". However, arrangement of the teeth and processes of their development and replacement are not known, and shapes of the teeth in some reports are considered to be insufficiently described (Dôtu and Mito, 1955; Prince Akihito and Meguro, 1979).

In the present paper, we report the shape, arrangement, development and replacement of the upper jaw teeth in *S. japonicus*.

Materials and methods

Five hundred and thirty-seven specimens, 25 ~ 104 mm in standard length (SL) were collected for this study in the Nagano River, Koza River, and Takada River (a branch of the Kumano River), Wakayama Pref., Japan (Fig. 1), for the period between May 22 and August 15, 1979. Most of the specimens were caught by small dip-nets when they were climbing rocks. Casting nets and spears were also used sometimes.

In addition to the specimens, small specimens which had still translucent bodies were also caught in brackish waters at the mouth of the rivers. However, they were not used in the present study because their upper jaw teeth were not completed yet. These teeth are completed when their body color changes to dark after the start of the river run.

Among the materials, 55 specimens were used for counting numbers of functional teeth and of replacement teeth in the first row just behind the row of functional teeth, and also for study-

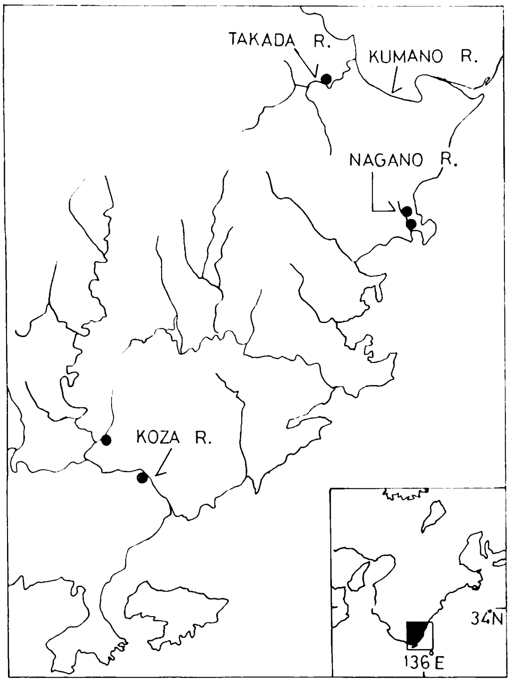

Fig. 1. A map of the collection localities.
●: collection sites.

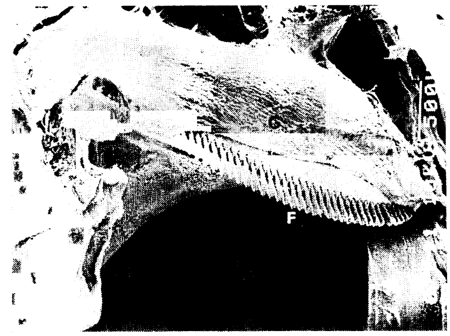

Fig. 2. Anterior view of head of *S. japonicus*, 28 mm SL, caught at the Nagano River. F: a row of functional teeth; G: gum on the left upper jaw, with derma removed to expose the gum; L: left lower jaw.

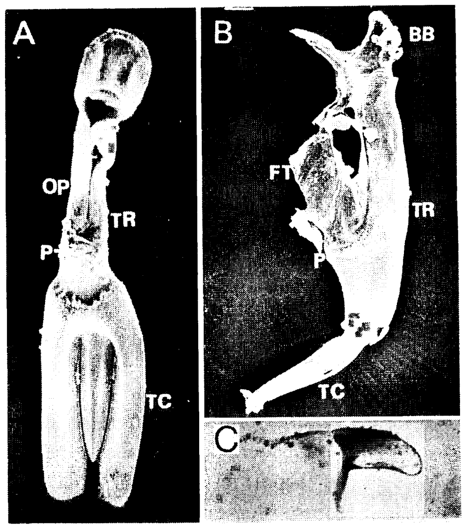

Fig. 3. Complete replacement teeth on upper jaw of *S. japonicus*. A: posterior view, without a small bone at the base of the tooth; B: lateral view; C: lateral view of the small bone at the base of tooth. BB: small bone at the base of tooth; FT: fibrous tissue connected between process of the root and premaxillary; OP: opening of the pulp cavity; P: process on the lateral side of root; TC: crown of tooth; TR: root of tooth.

ing the structure of the gum, arrangement of the teeth and processes of development and replacement of the upper jaw teeth.

Gums were observed after staining by Alizarin red-S. Some parts of the gums were kept in 3% KOH solution for 1～6 months in order to break down the tissues. Then, each tooth was observed by binocular microscope and/or SEM (Hitachi S-700). Critical drying method was used for observation of the upper jaw and the gum by SEM.

Other specimens were examined for their length composition to find out the growth of this fish.

Results

Functional teeth of upper jaw. Functional teeth of *S. japonicus* are found in line on the ventral margin of the upper jaw (Fig 2).

Each functional tooth consists of two parts; i.e., crown and root, with a small bone at the base of each tooth (Fig. 3).

The crown is brownish-yellow in color, and tricuspid, shovel-like in shape. Among the three projections, the middle one is shorter and pointed at the tip, and those on both sides are flattish and wide near the tip (Fig. 3A, B). The tip of the crown is generally observed to be shortened a greater or lesser degree since this part is worn out during feeding (Fig. 4C).

The root contains a process on the mid-posterior side (Fig. 3B:p). This process has many

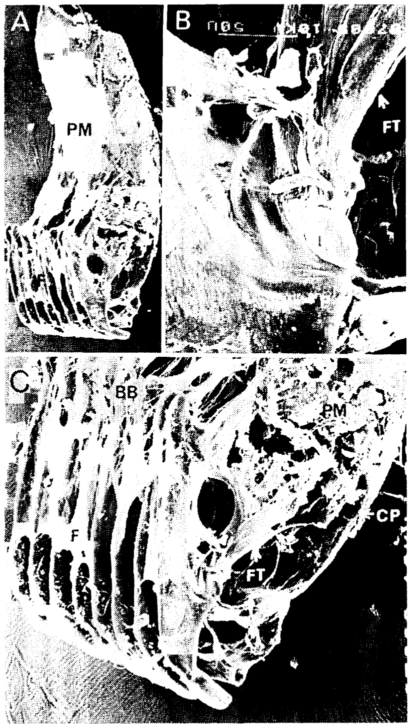

Fig. 4. A: relationship between functional teeth (F) and premaxillary (PM) in the specimens of 37 mm SL caught from the Nagano River. B: process of the root (P) and the fibrous tissue (FT) connected between the process and the premaxillary; the fibrous tissue is transformed artificially, usually straight shown in Fig. 3B; this photograph was enlarged from Fig. 4A. C: the functional teeth and the lower part of premaxillary; crowns of the teeth were about half worn out; enlarged from Fig. 4A. CP: crevice of premaxillary.

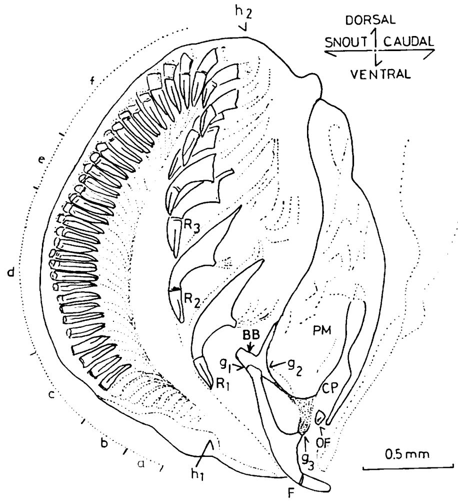

Fig. 5. Cross section of the gum of *S. japonicus*, 84 mm SL, collected from the Takada River. OF: old functional tooth which is being resorbed in tissue; R_1, R_2 and R_3: replacement teeth in the first, second and third rows respectively; a~f: stages of tooth development; g_1, g_2 and g_3: connections between tooth and small bone, between small bone and premaxillary and between process of the root and premaxillary by the fibrous tissue (FT) respectively; h_1: initiation of the toothgerm; h_2: the uppermost part of the gum; F, CP, BB and PM: see the explanations of Figs. 2, 3, 4.

minute tubercles at the tip. Each functional tooth is jointed to the premaxillary at the process by a long fibrous connective tissue (Fig. 4B, C: FT). It was found from materials soaked in 3% KOH solution for 4~6 months that the root contains an opening of the pulp cavity which is found at the posterior margin from near the process of the root to the basal end near the small bone (Fig. 3A).

The small bone at the base of each tooth is articulated to the basal end of the root and also fixed firmly to the premaxillary (Figs. 4C, 5).

Among the three connections, two, i.e., between the process of the root and the premaxillary (Fig. 5: g_3) and between the basal end of the root and the small bone (Fig. 5: g_1), are easily broken when pressed and these parts are separated. These connections are flexible and movable slightly because the former is connected by a fibrous tissue and because the articulation of the latter is not so firm. If the parts are soaked in 3% KOH solution for 2~3 months, the two connections are also broken and can be separated from the premaxillary and the small bone.

However, connection between the small bone and the premaxillary (Fig. 5: g_2) is so firm that it is difficult to break it and to separate the teeth without breaking the small bone down by pressing.

Development of upper jaw teeth. *S. japonicus* has many rows of replacement teeth hidden in the gum between the premaxillary and maxillary.

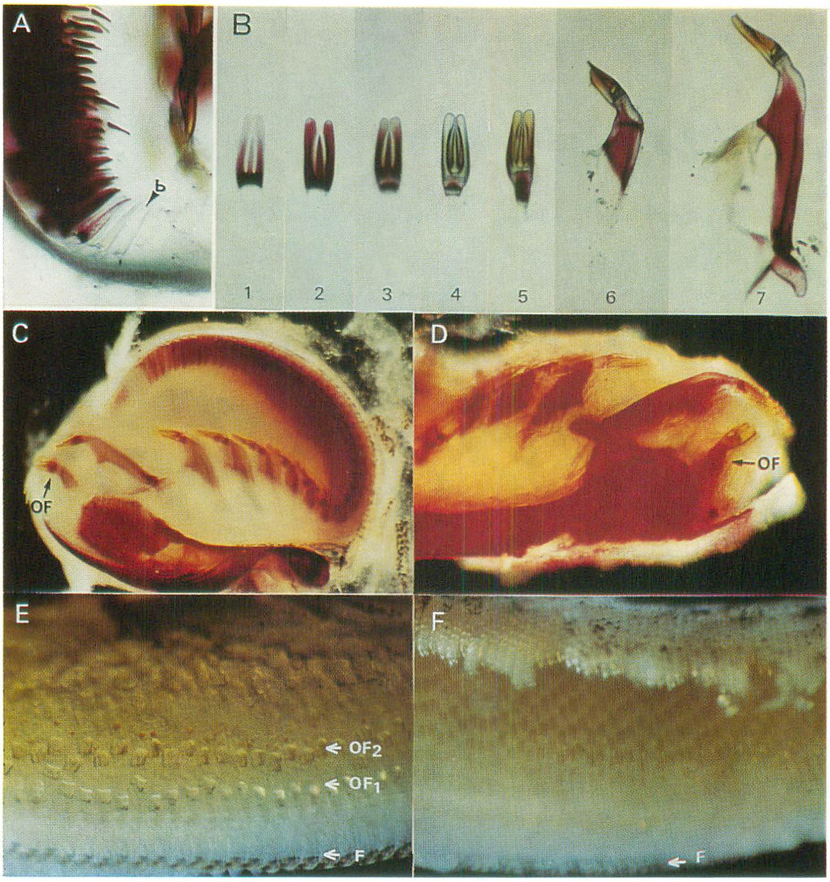

Fig. 6. A: toothgerms in the stage b shown in Fig. 5, which contain colorless, transparent and tricuspid materials. B: replacement teeth stained by Alizarin red-S; 1: stage c in Fig. 5; 2, 3: stage d in Fig. 5; 4: stage e in Fig. 5; 5, 6: stage f in Fig. 5; 7: complete tooth in the first row of replacement teeth. C: cross section of the posterior half part of the gum in the course of replacement; lower part of old functional tooth and the small bone are resorbed. D: cross section of gum in course of replacement; old functional tooth starts to sink into the tissue of the upper jaw. E: old functional tooth in the crevice of the premaxillary which is being resorbed; OF_1, OF_2: rows of old functional teeth in course being resorbed. F: arrangement of replacement teeth on the posterior part of the left gum (anterior view).

When cutting the gum at a right angle to its long axis, a functional tooth and many replacement teeth are found in a series of cross-rows (Fig. 5). This series consists of ca. 23 teeth (31 mm SL) to ca. 40 teeth (85 mm SL) at the middle part of the gum during different stages of growth. The number of the teeth in a cross-row increases with growth.

In a cross-row, several toothgerms at the earliest stage (Fig. 5: a) can not be stained by Alizarin red-S and dissolved in 3% KOH solution after soaking for 2～3 months.

In each of a few toothgerms at the second stage (Fig. 5: b), a colorless, transparent and tricuspid material is found, which is similar to a complete crown in shape. This is not stained in the dye (Fig. 6A: b) and easily changes its shape when it is dried. It is not dissolved in 3% KOH solution even after soaking for 5～6 months.

In each of the next several toothgerms (Fig. 5: c), the crown is closely similar to fully-developed ones in shape (Fig. 7A). It also changes its shape easily when dried. At first it is stained by the dye very slightly, and is gradually stained stronger as it progresses in development (*Fig. 6B: 1*). Its shape, however, does not change except for its basal part near the root, which develops slightly with growth.

The next ten or more crowns (Fig. 5: d) are closely similar in shape to the previous several ones. The anterior half of the crowns is wholly stained strongly by Alizarin red-S (Fig. 6B: 2). Each of these has a very small developing tooth root which is very strongly stained. However, the latter half of the crowns becomes gradually less stained at the tip and base (Fig. 6B: 3). Finally, all parts of the crown change to be stained very weakly. The next few crowns (Fig. 5: e) are colorless and transparent, not stained by Alizarin red-S, each with a strongly stained small part of the root (Fig. 6B: 4).

All crowns following these colorless and transparent ones (Fig. 5: f) are brownish-yellow in color and are not stained by Alizarin red-S (Fig. 6B: 5～7). They are all alike in shape.

In the stage where the crown is brownish-yellow in color, the root is additionaily developing from the part near the crown to the basal part near the small bone (Fig. 6B: 5～7; 7D, E, F). At the middle part of this stage the cross-row chain of teeth reaches to the uppermost part of the gum (Fig. 5: h_2) and then begins to go down in the posterior part of the gum. The root develops rapidly in the posterior part of the gum, and is completed near the lowest part of the gum where its position is just behind the functional tooth. The small bone at the base of the tooth is also formed at a position just behind the functional tooth after completion of the root in the same position.

Opening of the pulp cavity is found at the developing part of the root through all stages where crowns are brownish-yellow in color in materials soaked in 3% KOH solution for 5～6 months.

Through all stages of development, each crown is wrapped in a column of soft connective tissue, which is elongated in a string-like shape from the crown to the lowest part of the anterior part of the gum (Fig. 5: h_1). Each root is also wrapped by soft tissue, which is elongated to the uppermost part of the gum (Fig. 5: h_2). Therefore, no replacement tooth is fixed to another hard tissue, and all of the replacement teeth are easily movable. Each replacement tooth can be considered to be hung up from two parts of the gum (Fig. 5: h_1, h_2 respectively).

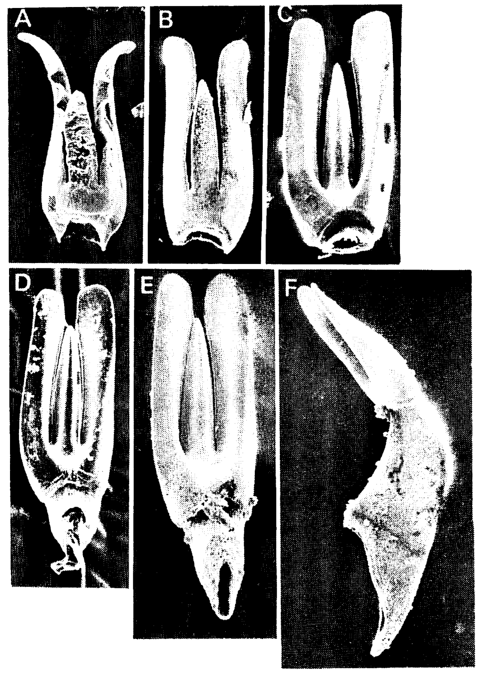

Fig. 7. Replacement teeth in various stages of development. A: stage c in Fig. 5, transformed artificially when this was dried; B: stage d in Fig. 5, stained strongly by Alizarin red-S wholly; C: stage e in Fig. 5, colorless and transparent; D～F: stage f in Fig. 5, complete crown, and root in development.

Arrangement of replacement teeth. Removing the anterior part of the gum near the tip of the snout, many replacement teeth are observed, which are arranged orderly in each lateral row in addition to the row of functional teeth.

The functional tooth row (F) is found on the ventral margin of the gum. The first row of replacement teeth (R_1) is found just behind F; the second (R_2) is found just behind R_1; the third (R_3) just behind R_2; etc. (Fig. 8).

R_1 is arranged orderly in a straight line, as is F. R_2 gets slightly out of order. In general, R_3 and the following rows are not arranged in straight lines but in zigzag lines which resemble many jointed V-letters. Arrangement of these zigzag lines appears as parallel oblique lines or oblique check patterns (Fig. 6F).

In younger fish, there are fewer rows of replacement teeth and R_1 and R_2 as well as R_3 are arranged in zigzag lines.

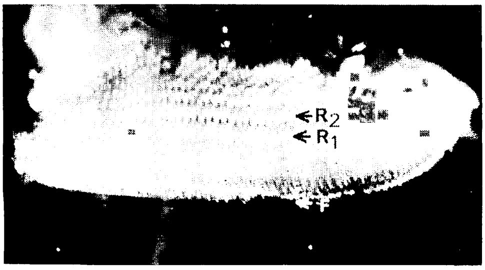

Fig. 8. Arrangement of teeth in the posterior half of gum just after replacement (anterior view) in a fish of 48 mm SL caught from the Koza River. F, R_1 and R_2: see the explanations of Figs. 2, 5.

Replacement of teeth. Crowns of functional teeth are worn out at their tip in various degrees. In some cases, less than half of each tooth remains (Fig. 4C). In such samples, replacement teeth are completed in R_1 already, and in some of these samples teeth in R_1 have started to move forward.

In the first stage of replacement, some teeth in R_1 start moving forward, and functional teeth in front of these become movable simultaneously. At this time, movable functional teeth are severed at the two connections with the premaxillary and the small bone at the base of the tooth. Then, the teeth are gradually resorbed from their basal parts including the small bone (Fig. 6C).

Functional teeth gradually turn at the tip according to the progress of replacement and resorption. When replacement teeth become nearly functional, the former functional teeth turn at approximately right angles, and the small bone and about two-thirds of the root near the small bone disappear.

In the next stage, "old" functional teeth start sinking into the tissue of the upper jaw and "new" functional teeth become set on the premaxillary (Fig. 6D). Resorption of the old functional teeth progresses as they fall into a crevice of the premaxillary. When they reach the crevice, only the crown remains. A row of these crowns of old functional teeth can be observed through a thin layer of the premaxillary. Sometimes zero or two rows of these crowns are observed in the premaxillary. (Fig. 6E). Finally the crowns are resorbed completely.

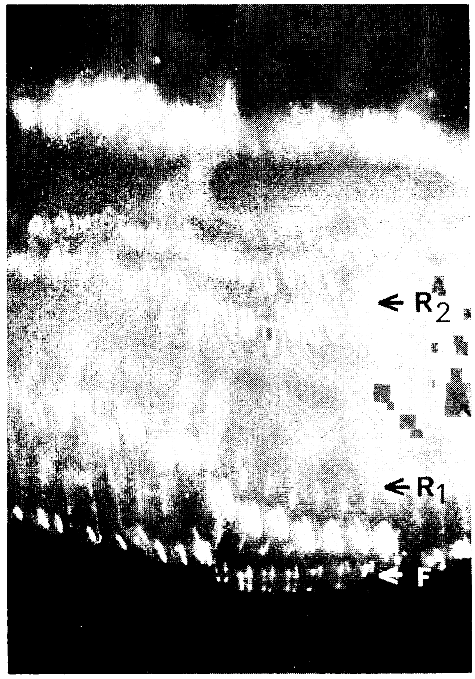

Fig. 9. Arrangement of teeth in course of replacing (anterior view of the posterior half part of gum). F, R_1 and R_2: see the explanations of Figs. 2, 5.

This replacement is done almost simultaneously in a row of teeth. However, in general, part of the replacement teeth precede other parts. Therefore, the teeth line on the replacement row is not straight. In some cases, the last several teeth start moving forward when some of the teeth in the line approach old functional teeth very closely (Fig. 9).

Each tooth in R_2, R_3, etc., also starts to move forward after moving of the tooth in front of it.

Increase in number of functional teeth with growth. The number of the functional teeth (N_F) as well as that of the first replacement teeth (N_{R1}) increases with growth (Fig. 10). Relationships between both N_F and N_{R1} on the left upper jaw and standard length (SL in mm) are fitted to straight lines by the least square method as follows;

$$N_F = 18.89 + 0.818SL$$
$$N_{R1} = 19.95 + 0.814SL$$
$$(27\ \text{mm} \leqq SL \leqq 104\ \text{mm})$$

These two lines are nearly parallel, and the dif-

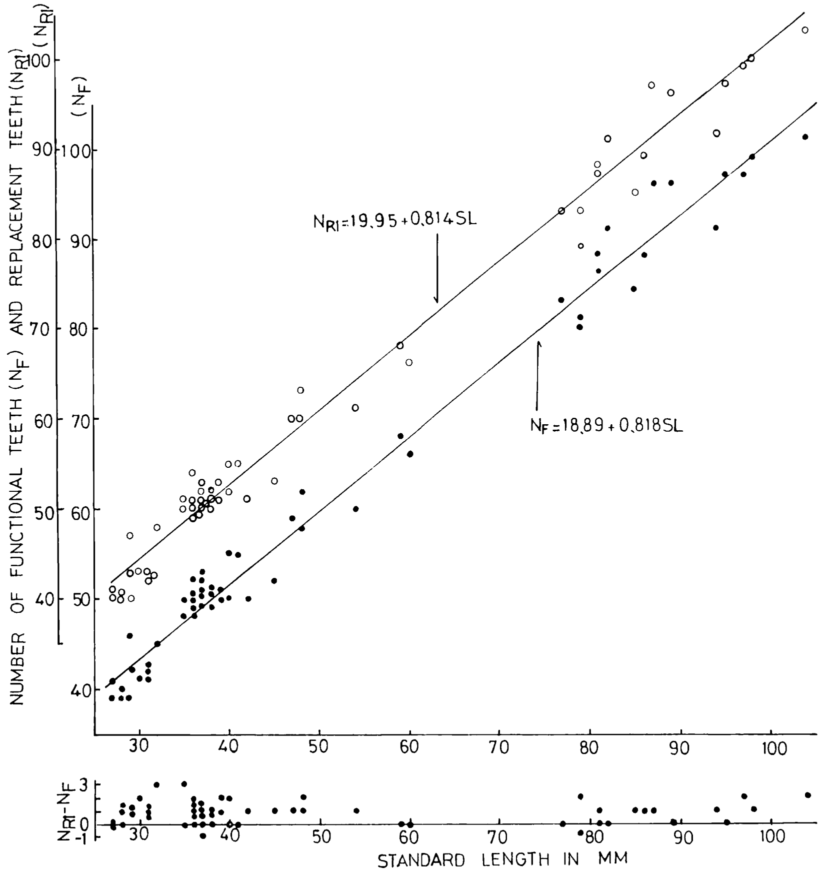

Fig. 10. Relationships between numbers of functional teeth and replacement teeth in the first row and standard length (N_F, N_{R1} and SL respectively), and the difference between the numbers of N_{R1} and N_F. ●: number of the functional teeth (upper) and the difference between N_{R1} and N_F (lower); ○: number of replacement teeth.

ference between N_F and N_{R1} is nearly constant. Relationship between the difference (D) and SL is calculated by the least square method:

$$D=N_{R1}-N_F=0.994-0.0034SL$$

By test of significance of regression coefficient, there is no correlation between D and SL at the 95% significant level, and this result means that D is constant within the range of the fish size examined in this study. In other words, mean increment of functional teeth in number is constant, 0.89, in each replacement through size from 27 mm SL to 104 mm SL. The mean increment of N_F is 63.0 from 27 mm SL to 104 mm SL, and times of the replacement corresponding to this mean increment of N_F is 70.8. Mean increment of SL corresponding to each replacement is 1.1 mm. Therefore, each replacement of functional teeth occurs when fish size increases 1.1 mm in standard length.

Frequency of replacement of teeth. In the present study, we could not get sufficient data concerning the growth of this species, and a tentative length frequency of young fish which were running up the Nagano River (0+ years old) was used to examine the growth.

Length frequency of the materials which were caught during May 22 and August 15, 1979, is considered to be able to fit a straight line (Fig. 11). This equation by the least square method is as follows;

$$SL=25.5+0.12d$$

Where d is the number of days counted from

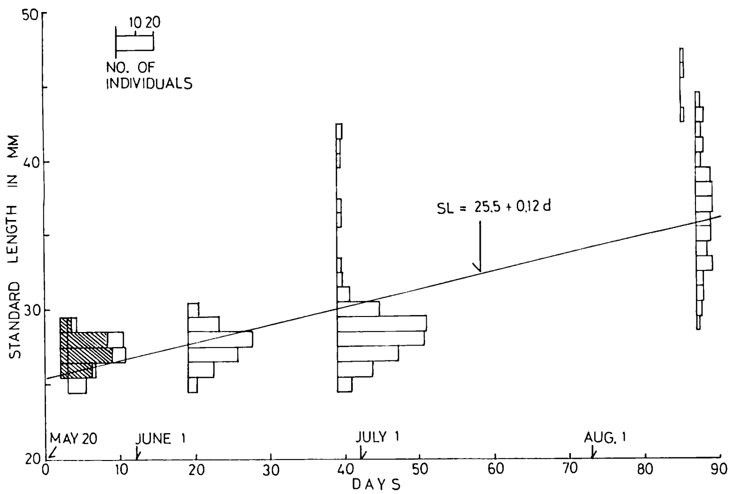

Fig. 11. Growth of 0+ years old fish in the Nagano River for the period from May 22 to August 15, 1979, based on length frequency. d: number of days counted from May 20, 1979.

May 20, 1979. This equation shows that mean increment of SL was 10.4 mm during 87 days of this period. Therefore, mean times of replacement corresponding to this growth was 9.5, and each replacement of functional teeth occurred at every 9.2 days on the average during the period. In other words, replacement of the teeth occurs every 9.2 days and the fish size (SL) increases 0.12 mm per one day.

Discussion

S. japonicus is different from many other vertebrates in having so many replacement teeth on its upper jaw. However, the process of the development is essentially identical with those of many fishes, mammals, etc., in the following points; 1) similarity in shape of the crown through its development (Figs. 6B, 7), 2) changing of staining condition of the crown and root by Alizarin red-S through process of the development (Fig. 6B), 3) crowns with brownish-yellow color in the later stages of its development (Fig. 6B: 5～7), 4) additional development of the root (Figs. 6B: 5～7; 7: D～F), 5) existence of an opening of the cavity considered as pulp cavity in the root (Figs. 3A, 7E), 6) existence of soft connective tissues which cover and can be considered to hang up each crown and root. These points suggest that "teeth" in the upper jaw of *S. japonicus* are teeth and that crown and root are enameloid and dentine respectively. The brownish-yellow color of the crown is probably caused by iron as in many other fishes that have yellow, brown or black colored teeth (Suga and Ogawa, 1980).

We identified the small bone at the base of each tooth as bone because of the process of its development. However, further examination is needed to reach a final conclusion.

Prince Akihito and Meguro (1979) reported shape of upper jaw teeth of *S. japonicus*. They drew a figure of the tooth based on a small specimen, 41 mm SL, where three projections of the crown are almost all the same size (Prince Akihito and Meguro, 1979: fig. 3H). However, we found all teeth have shorter middle projection except for worn teeth in the functional tooth row. The tooth in their report was probably a functional tooth with a greatly worn crown. Dôtu and Mito (1955) described upper jaw teeth of this fish as bicuspid, but it was probably based on misobservation.

Herre (1927) reported, in his description of the genus *Sicyopterus*, that upper jaw teeth of members of the genus were replaced when worn out or broken because of existence of many replacement teeth on the upper jaw.

Our observation of the upper jaw teeth of *S. japonicus* shows all processes of the replacement. "Old" functional teeth, replaced by new ones, are resorbed as they sink into a crevice of the premaxillary, and finally are completely resorbed in it. This complete resorption of teeth suggests a possibility of the reuse of their components to produce new teeth. If this is true, such reuse is probably more economical than to continuously produce teeth.

It is also shown in the present study that replacement of teeth occurs every 9.2 days on the average when fish size increases 0.12 mm in standard length per one day (1.1 mm SL per 9.2 days) and that the interval will be shortened more when increment of the fish size is greater. Therefore, many replacement teeth must be prepared to correspond to the short interval in order to maintain frequent replacement.

Existence of many replacement teeth is possibly caused by the facts that functional teeth are extremely worn out over a short period, such as the interval mentioned above. This wearing of teeth is caused by the fish's feeding habit. They scrape off diatoms, blue-green algae, etc., which grow on the surface of stones using functional teeth on the upper jaw to get food. In other words, the fish must grind their functional teeth against stones frequently. Therefore, they must prepare many replacement teeth and must frequently replace their teeth at intervals of short periods.

Ebeling (1957) reported that *Chaenomugil proboscideus*, family Mugilidae, has many replacement teeth in its jaws. According to his figures (figs. 3, 6), the shape of the teeth is very similar to that of the present fish except for the absence of a small bone at the base of each tooth. Arrangement of the teeth in a cross-row in *C. proboscideus* is also similar to the present species, though the teeth of the former do not hold firmly on the premaxillary. These similarities between the two fishes are probably explained by convergence because their phylogenetic relationship is not close; i.e., the system of the jaw teeth in the mugilid fish may have developed from their habit of scraping food materials off the surfaces of many things.

Roberts (1967, 1973) also reported two fishes which have many replacement teeth; *Distichodus fasciolatus* and *Ichthyoelephas humeralis*. These results probably suggest that fishes with many replacement teeth are not rare, including some members of the subfamily Sicydiaphiinae. However, *S. japonicus* is peculiar in characters of mechanism of replacement of the teeth, existence of a small bone at the base of each tooth, and resorption of "old" functional teeth.

Acknowledgments

We wish to express our sincere thanks to Prof. Shoichi Suga, the Nippon Dental University, who presented us with very important information of teeth. We also acknowledge Dr. Tyson R. Roberts, who informed us about jaw teeth of some fishes.

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ボウズハゼの上顎歯の成長・更新

望月賢二・福井正二郎

ボウズハゼ *Sicyopterus japonicus* の上顎歯の形態・成長・更新等について調べた．予備歯は歯槽 (gun) 内部に発生し，内部を移動しながら成長する．この成長の最後の段階において，各歯の基部に1小骨が形成される．その後，下方に移動し，前上顎骨に固定され，作用歯として用いられる．歯の更新において脱落した歯は，上顎組織内で吸収されながら，前上顎骨下端の腔所に引き込まれ，ここで完全に吸収される．このこと

から，歯の成分を再利用する可能性があることが示唆された．この更新は体長の増加に比例して起り，標準体長が 1.1 mm 増加するごとに 1 回の割合である．またその頻度は，標準体長が 1 日当り 0.12 mm 増加する場合には平均 9.2 日に 1 回の割合である．歯がこのような短い周期で絶えず更新するのは，餌として岩の表面で育つ付着藻類を掻き取るため，上顎歯の損耗が著しいためと思われる．

(望月：113 東京都文京区本郷 7-3-1　東京大学総合研究資料館水産動物部門；福井：649-53 和歌山県那智勝浦町宇久井)