DEVELOPMENT AND REPLACEMENT ORDER OF PHARYNGEAL TEETH IN THE GOLDEN SHINER, *NOTEMIGONUS CRYSOLEUCAS*[1]

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Abstract. Pharyngeal teeth and arches of larval, juvenile, and adult golden shiners were cleared and stained to determine development and replacement order. The first pharyngeal teeth ankylosed in the order 4–5–3–2–1, differing from that in *Catostomus* but similar to that in the Japanese cyprinid *Gnathopogon coerulescens*. The first 3 sets of replacement teeth differed in shape from their predecessors as has been reported in other cyprinids. The order of ankylosis of the first pharyngeal teeth differed from the replacement order in juveniles and adults. Of the arches examined, 52% showed the replacement order 4–2–5–3–1 and 16% showed the replacement order 4–2–5–1–3. Replacement order in the golden shiner was similar to that in *Semotilus*, *Clinostomus*, and *G. coerulescens*. A normal second row of pharyngeal teeth was not found in golden shiner larvae: the occurrence of a second row of teeth was considered to be an anomaly in the replacement pattern and not a recapitulation of multi-rowed ancestry.

In 1939, Vasnecov reported that certain cyprinids possessed 2 rows of pharyngeal teeth as larvae but only one row as adults. This finding formed part of his theory that the evolution of teeth in cyprinids began with multiple rows. The golden shiner, *Notemigonus crysoleucas*, possesses a single row of pharyngeal teeth as an adult. To determine whether or not a transitory second tooth row existed in larval shiners and therefore supported Vasnecov's (1939) theory, I studied the development of golden shiner pharyngeal teeth.

The replacement of pharyngeal teeth in cyprinids has been described by Evans and Deubler (1955), Schwartz and Dutcher (1962), and Nakajima (1979), and is believed to follow a specific pattern. Differing theories describing the replacement process have been presented by Edmund (1960, 1962) and Osborn (1971), particularly for reptiles. Nakajima (1979) applied these theories to the replacement of pharyngeal teeth in a Japanese cyprinid and supported the theory of Osborn (1971).

The present study was directed to determine if replacement of pharyngeal teeth in the golden shiner would support Osborn's theory.

MATERIALS AND METHODS

Material examined: larval and juvenile golden shiner (size range 5 mm to 27 mm standard length: SL) collected in Breon's Pond, Oak Hall, Centre Co., Pennsylvania, 12 June through 24 June 1964; and Benner Springs, 2 miles SW of Bellefonte, Centre Co., Pennyslvania, 29 May through 23 July 1964. Juveniles and adults (size range 44 mm to 124 mm SL) collected on 29 August 1960 at Martin's Creek, tributary to Delaware River, 8 miles N of Easton, Northhampton Co., Pennyslvania.

To determine development of the pharyngeal teeth and arches, 48 larval and juvenile golden shiners were cleared and stained with trypsin and alizarin red S according to Taylor (1967). The fish were placed in glycerin and alcohol and the number, size, and shape of the developing teeth and replacement caps were recorded. Terminology of fish developmental phases follows Snyder *et al* (1977).

The pharyngeal arches and their associated tissues were dissected from 78 juvenile and adult golden shiners, cleared and stained as above, and examined to determine the replacement order of the teeth. The replacement order was determined by the relative size of the tooth caps: the largest being more developed and first to replace a functional tooth (Nakajima 1979). Tooth replacement was determined only on those arches with at least 4

tooth caps and only those arches with 5 functional teeth, including any missing teeth, were used. A missing tooth was indicated by the presence of a pit on the dentigerous surface of the arch. One specimen had an arch with only three tooth caps and was not used; thus 155 arches were examined.

RESULTS

One pharyngeal tooth and two tooth caps were present in each arch in protolarvae 5.0 to 6.0 mm in length. The remaining teeth formed and ankylosed as shown in fig. 1. Ankylosis followed the sequence 4–5–3–2–1. In mesolarvae 10.5 mm to 11.0 mm in length, pharyngeal teeth in positions 3 and 2 became ankylosed to the arch at nearly the same time; however, a replacement cap had formed behind the tooth in position 3 and thus the tooth in position 3 was considered to have ankylosed before the tooth in position 2.

FIGURE 1. Developmental changes and ankylosis of first pharyngeal teeth in golden shiner larvae. Original teeth are stippled. Size range in mm standard length and date collected are given on the vertical margin; tooth position is given on the horizontal margin.

The first three sets of replacement teeth differed in shape from their predecessors. The first teeth formed were conical with a slightly bent corona. These were replaced with a thicker tooth that had a hooked corona and

chewing furrow (fig. 1). Each succeeding replacement had serrated edges around the chewing furrow. This replacement sequence did not occur at tooth position 1; each replacement was conical, similar to the initial tooth.

Ossification of the arches began at fish lengths of 8.0 mm. At 10.5 mm, the arches had extended forward and were ossified to the extent shown in fig. 2. The arches were similar to that in the adult at fish lengths of 23 mm and ossification was nearly complete at the ventral tips of the arches. There was no evidence of a normal second row of teeth at any fish length examined in this study, but two larvae had a second row tooth ankylosed to the arch at positions 5, and 3, respectively.
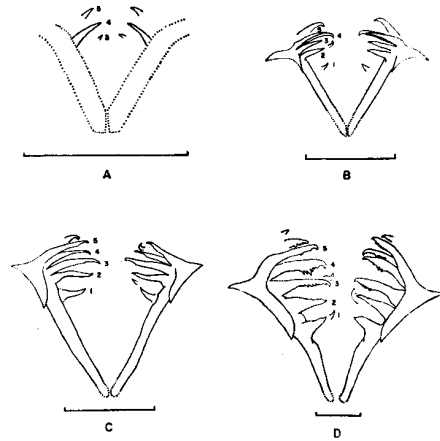

FIGURE 2. Anterior view of developing pharyngeal arches. Each scale bar equals 0.5 mm. (A) protolarva, 5.4 mm standard length (SL); (B) mesolarva, 10.5 mm SL; (C) metalarva, 11.5 mm SL; (D) juvenile, 23 mm SL.

The replacement order observed in juveniles and adults differed from the order of ankylosis of the first pharyngeal teeth. Of 155 arches examined, 80 showed the replacement order of 4–2–5–3–1 (table 1). The replacement order 4–2–5–1–3 occurred with the second highest frequency. The remaining 47 arches were divided accordingly:

(a) 23 arches with 5 tooth caps exhibited 12 variations of the replacement order 4–2–5–3–1: the

most numerous was 4–2–3–5–1 occurring 4 times; and

(b) 24 arches with 4 tooth caps not considered to be parts of either replacement orders 4–2–5–3–1 or 4–2–5–1–3.

TABLE 1

*Frequency distribution of successional tooth replacement in 155 arches of golden shiner with at least four tooth caps.**

Replacement order	No. arches
Full formula of 4–2–5–3–1	51 (52%)
2–5–3–1	12
4–2–5–3	7
3–1–4–2	5
5–3–1–4	4
1–4–2–5	1
Full formula of 4–2–5–1–3	20 (17%)
3–4–2–5	4
4–2–5–1	2
1–3–4–2	1
Other combinations	48 (31%)

*Those orders with 4 tooth caps are considered part of the respective full formula.

The normal tooth formula of the golden shiner is 0,5–5,0 (Scott and Crossman 1973). In my study, 11% of the arches examined had 4 teeth on the right arch. This condition was not observed on the left arch, following the account by Hubbs and Hubbs (1945) concerning bilateral asymmetry in fishes. Other apparently anomolous conditions were: 2 rows of teeth observed on eight arches and one arch had 3 rows; in one arch, 2 tooth caps were forming simultaneously, one behind the other, presumably to replace the tooth in position 5.

DISCUSSION

The sequence of ankylosis of the pharyngeal teeth in the golden shiner differed from that described by Weisel (1967) for larval *Catostomus*. The first 5 teeth that ankylosed in *Catostomus* followed the order 2–3–1–4–5. In the Japanese cyprinid *Gnathopogon coerulescens*, the first 3 teeth ankylosed in positions 4–5–3 (Nakajima 1979). The adult dentition of *G. coerulescens* (3,5–5,3) is more similar to that of the golden shiner than the dentition of Weisel's (1967) *Catostomus* (each arch has a single row of 45–65 teeth).

Changes in the shape of golden shiner

pharyngeal teeth were similar to those illustrated by Nakajima (1979) for *G. coerulescens*. Weisel (1967) described similar changes in *Catostomus*, *Ptychocheilus oregonensis*, and *Richardsonius balteatus* except that the tooth in position one in these species also underwent various changes in shape. The changes in shape of the pharyngeal teeth in golden shiner follow that postulated by Vasnecov (1939) as indicating the recapitulation of the original cyprinoid form. The results of Weisel (1967) and Nakajima (1979) also support Vasnecov's theory.

A multi-rowed condition of the pharyngeal teeth has been considered to be more primitive than a single row (Vasnecov 1939). If a transitory double row is formed in cyprinoids that have a single row as adults, it may be a recapitulation of a multi-rowed ancestor. Weisel (1967) reported a double row of ankylosed teeth in 10% of his larval catostomids having a single row of teeth as adults. Weisel did not accept this as evidence of a multi-rowed ancestor but explained it as an anomaly. In the present study, two of 48 larvae exhibited a second row of ankylosed teeth. This was considered to be similar to the anomaly reported by Weisel (1967) in that the occurrence did not appear at a particular fish length or at a constant tooth position.

Vasnecov (1939) reported multiple rows of developed and rudimentary teeth in certain cyprinids. It was not clear whether these teeth were replacement teeth that improperly ankylosed or were a transitory second row. Only in *Misgurnus fossilis* (Family Cobitidae), did there appear a well-defined second row of ankylosed teeth that were lost in the adult.

Nakajima (1979) interpreted the presence of a row of replacement teeth and another row of ankylosed teeth as a recapitulation of an ancestral character. This interpretation differs from that of Vasnecov (1939), Weisel (1967), and that used in my study, namely that recapitulation of the multi-rowed ancestral character would be a second row of ankylosed teeth that are lost in the adult. It would seem more likely that

the normal replacement process is represented by Nakajima's interpretation.

Edmund (1960, 1962) and Osborn (1971) have presented separate theories to explain the replacement of jaw-teeth. Both theories incorporate the occurrence of a replacement wave that alternates in tooth position. This replacement has been supported by Evans and Deubler (1955), Nakajima (1979), and my study for pharyngeal teeth.

Conflicting aspects of the proposed theories lie in the relationships of the teeth to each other. Edmund's (1960, 1962) theory requires that a tooth occur at every tooth position and that teeth develop sequentially from the front to the back of the jaw. Additionally, groups of teeth are related to different tooth positions. Osborn (1971) applied these requirements to his data on *Lacerta* and found that 35 more teeth were required to support Edmund's theory than were present. Nakajima (1979) and the present study have found similar results in pharyngeal teeth but the 6 teeth required by Edmund's theory were not present. Osborn's (1971) theory describes the relationships of the teeth in "tooth families" where teeth within each family are related to a single tooth position and the replacement wave moves from the back of the jaw to the front. The pattern of development of pharyngeal teeth reported by Nakajima (1979) and the present study generally supports the theory of Osborn (1971).

The observed replacement order in the golden shiner was similar to that of *G. coerulescens* (Nakajima 1979) and of the left arch in *Semotilus* and *Clinostomus* (Evans and Deubler 1955). The replacement order of the right arch of *Semotilus* and *Clinostomus*, which has only 4 teeth in the major row, was 3-1-4-2. This order was observed in those golden shiner arches that had only 4 functional teeth.

Deviations in adult pharyngeal tooth formulae have been reported in many cyprinids (Evans and Deubler 1955, Eastman and Underhill 1973). In my study, 8 golden shiners had 2 rows of teeth on at least one arch and one had 3 rows of teeth on one arch. The extra

rows were apparently formed when a replacement tooth ankylosed to the arch without the loss of a functional tooth, similar to that found in golden shiner larvae. Eastman and Underhill (1973) reported 1.9% of their golden shiners had counts that deviated from the normal formula and felt that faulty tooth replacement may have contributed to the variations. Deviations in pharyngeal tooth formulae may also be indicative of evolutionary trends in loss or gain of teeth in the cyprinoids (Eastman and Underhill 1973).

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