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Copeia, Vol. 1973, No. 1. (Mar. 5, 1973), pp. 45-53.

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Intraspecific Variation in the Pharyngeal Tooth Formulae of Some Cyprinid Fishes

JOSEPH T. EASTMAN AND JAMES C. UNDERHILL

Forty-two species of cyprinids were studied to determine the amount of intraspecific variation in their pharyngeal tooth formulae. Widely different degrees of variation were found to exist. The percentage of arches, in a given species, bearing variant half-formulae ranged from 0 to 49.2%. The 0,4-4,0 formula was almost invariable whereas most of the species with 0,5-5,0; 2,5-4,2; or 1,4-4,1 formulae exhibited small or intermediate amounts of variation. The 2,4-4,2 condition was the most variable with four species possessing high percentages (5.8% to 49.2%) of deviant half-formulae. Some of the variability in certain formulae was attributed to evolutionary trends tending to decrease the number of minor-row teeth or increase the number of major-row teeth. A functional mechanism influencing the trends was offered. Faulty tooth replacement was also thought to contribute to some of the variation encountered. Because of the variability in certain formulae, it is suggested that pharyngeal arch and tooth characteristics should also be included in species descriptions and keys.

THE use of cyprinid pharyngeal teeth as taxonomic characters requires, as a prerequisite, a thorough knowledge of intraspecific variation in tooth formulae. In most studies dealing with pharyngeal teeth sample sizes have been small and the data are therefore limited. The principles of tooth loss and replacement have not been understood, e.g., the "untrue" teeth of Holčik and Duyvené de Wit (1962), in spite of the existence of papers on the subject by Grieb (1932), Geyer (1937), Belogurov (1940), Evans and Deubler (1955), and Schwartz and Dutcher (1962). In this paper we examine the magnitude and speculate on the causes of intraspecific variation in the pharyngeal tooth formulae of 42 species of cyprinids inhabiting Minnesota waters.

Heincke (1892) was the first to explore intraspecific variation in a row of pharyngeal teeth and gave examples of deviant tooth counts for some Old World minnows. Eigenmann (1895) studied tooth variation in *Leuciscus* (= *Richardsonius*) *balteatus*, a cyprinid native to the western United States, and found eight deviant formulae in a sample of 36 fish. Tölg (1958) noted variability in tooth number in a population of *Abramis brama* and Miaskowski (1960) gave the percentage of tooth formula deviants in 15 species of Old World minnows. In 260 *Cyprinus carpio* from Korea, Yang (1964) found that 88.9% had the usual 1,1,3-3,1,1 formula.

Berinkey (1967; 1968) found many abnormal formulae in small populations of *Phoxinus phoxinus* and suggested that this variation was a prelude to speciation (1968). Shutov (1967) noted that 69 of 500 *Abramis brama* from Lake Seliger had formulae of 1,5-5,1; 1,5-5,0; or 0,5-5,1 instead of the usual 0,5-5,0. Penczak (1968) examined the pharyngeal teeth of 260 *Leuciscus leuciscus* and found that 83% were of the usual 2,5-5,2 arrangement.

Little work has been done on dental variation in the New World cyprinids. Evans and Deubler (1955) found that 150 *Clinostomus elongatus* all had the usual 2,5-4,2 arrangement whereas the same number of *Semotilus atromaculatus* showed 11 variations. In Schwartz and Dutcher's (1962) sample of 504 *Notropis cerasinus* from Virginia, only one individual departed from the expected tooth count of 2,4-4,2.

Bilateral asymmetry in pharyngeal tooth number among Old World minnows was mentioned by Von Martens (1896) and Ludwig (1932). Hubbs and Hubbs (1944) noted that, for some unknown reason, the greater number of teeth is usually found on the left arch in asymmetrical counts in American minnows.

MATERIALS AND METHODS

Study material consisted of specimens of 42 species of minnows found in Minnesota

waters. Specimens of *Carassius auratus* were donated by Dr. Jack Young of the Zoology Department at the University of Oklahoma in Norman. These were hatched and raised to a total length of about 50 mm in his breeding ponds at Noble, Oklahoma. Rare or uncommon species were borrowed from the collections of the James Ford Bell Museum of Natural History at the University of Minnesota.

Examination of the teeth of at least 50 individuals per collection of each species was attempted. In most cases enough specimens were available so that this number was exceeded. On occasion the goal of 50 was not reached because of the rarity of a few species. When a large number of arches was obtained from a certain species, the data summarized in Table 1 are for several collections, any one collection consisting of at least 50 specimens.

Terminology.—The large fifth ceratobranchials of cyprinids are called pharyngeal arches or pharyngeal bones. Chu (1935) is followed when mentioning regions of the pharyngeal arches.

Removal of Pharyngeal Arches.—Whenever possible, study specimens were not fixed in formalin but returned to the laboratory fresh for immediate dissection. The pharyngeal arches were easily loosened by repeatedly running the tips of needle-nosed forceps between the medial margin of the cleithrum and the lateral margin of the pharyngeal arch. A moderate amount of pulling with the forceps then freed the arch from the masticatory muscles and the anterior cartilagenous copula. Care was taken in extracting the arches since they were delicate and easily broken.

Rapid removal of arches of fixed specimens was more difficult because of the rigidity of the masticatory muscles and the brittleness of formalin-preserved bone. An additional hazard was the possibility that the arches had become decalcified, a condition rendering them useless for study since all that remains is a collagen matrix that is easily torn and deformed when removal is attempted.

Cleaning Pharyngeal Arches.—It was very important to clean all tissue from the pharyngeal arches and teeth in order to insure an accurate tooth count. Arches from

fresh specimens were placed in hot running water for several hours. This treatment eliminated most of the adhering pharyngeal arch muscles, the mucosa around and between the teeth, and the fat in the pitted surface of the arch. The periosteum and any other remaining bits of tissue were then removed under a dissecting microscope with the aid of needle-nosed forceps. Arches from fixed specimens were boiled for several hours and then allowed to soak in water for two weeks. Adhering tissue was then pulled from the arches. Subsequent treatment included dehydration of the arches in 95% ethanol, air-drying for 24 hr, and storage in small, screw-top glass vials.

Counting Pharyngeal Teeth.—Thorough cleaning (see above) permitted the detection of missing teeth (as evidenced by a pit, the former site of a tooth, on the dentigerous surface of the pharyngeal arch) and of teeth broken off below the mucosa; both were incorporated into the tooth count. Tooth crowns embedded in the mucosa around the arch and destined to replace presently ankylosed teeth were excluded from the tooth count; these crowns were removed in cleaning.

New World cyprinids usually have one or two rows of teeth on each pharyngeal arch; the introduced carp has three rows. The major row of each arch, also termed by various workers the greater or primary row, usually has four or five teeth. The minor (lesser or secondary) row, if present, has one or two teeth and is dorsal-lateral to and within the concavity of the curve of the major row when the arches are in position in the fish. Individual teeth in the major and minor rows are distinguished by a number; the most anterior-ventral tooth in both the major and minor rows is the first, and the other teeth, posterior-dorsal to the first, are assigned consecutively higher numbers.

The tooth count is expressed as the pharyngeal tooth formula. Hubbs and Lagler (1958) and Cross (1967) explain the interpretation of pharyngeal tooth formulae. The deviations in tooth formulae in Table 1 are presented in terms of half-formulae for the left and right arches. This was done for two reasons. Processing and tabulation of the pharyngeal arches was greatly facilitated when whole collections were handled at once.

It would have been an impractical task to keep some 4000 pairs of arches matched up during the course of the study. Secondly, since variation in the formulae of the two sides was found to be independent, half-formulae proved to be the most accurate method of expressing variation.

RESULTS

Examination of Table 1 reveals that widely different degrees of intraspecific variation exist in the pharyngeal tooth formulae of Minnesota cyprinids. The percentage of arches examined bearing variant half-formulae ranged from 0 to 49.2%. The variation was not distributed evenly throughout the various formulae but was more marked in some formulae. In other words, species possessing certain formulae showed more variation from the formula in question than did species with other, seemingly invariable, formulae. Because of the manner in which the arches and teeth were cleaned and counted (see Materials and Methods), the possibility of confusing tooth loss and replacement with true variation was virtually nonexistent. Nevertheless, tooth replacement was observed and tabulated. The percentage of pharyngeal arches examined that exhibited one or more tooth replacements ranged from 14% to 82% with a mean of 37% for the 42 species.

Among the Minnesota cyprinids, 0,4-4,0 was the most invariable formula. Of the 17 species having this formula, 13 had no variant formulae. Three of the 0,4-4,0 species with deviant formulae had low percentages of variants; *Hybognathus hankinsoni*, 0.8% (2 deviant half-formulae among the 247 arches examined), *Notropis anogenus*, 0.9% (1 of 115) and *N. stramineus*, 0.6% (1 of 147). In all three, the deviation consisted of the addition of a single tooth to the major row of the left arch resulting in a 0,5-4,0 formula. Whether the 0,4-4,0 formulae were inherited intact, were the result of previous minor-row reduction, or were a sequel to tooth loss during recent speciation, the final consequence was the same: a static formula with little variance.

The only 0,4-4,0 species with any great degree of variance was *Notropis lutrensis* at 7.4% (16 of 215). Examination of the deviants revealed that 15 of the 16 were caused by the presence of a single tooth, in a minor-row position, resulting in 1,4- or -4,1

half formulae. The nature and incidence of the variation of *N. lutrensis* suggested that this species probably had, at some previous time in its phylogeny, at least one minor-row tooth and that, at the present time, the evolutionary loss of the minor-row teeth has almost been completed in Minnesota specimens. However, if it was examined throughout its range, it might be that tooth formula variation resulted partially from specific differences since *N. lutrensis* probably will prove to be a complex of several species, some of which may have 0,4-4,0 and others 1,4-4,1 teeth.

The 0,5-5,0 formula, characteristic of four Minnesota species, was not as static as the 0,4-4,0. Ninety-four *Opsopoeodus emiliae* pharyngeal arches showed no deviants but 155 *Notemigonus crysoleucas* had deviants; two were 0,6- and one was -5,1 for a total of 1.9% (3 of 155). There was, in addition, variation in the formulae of *Phoxinus erythrogaster* and *P. eos* amounting to 2.0% (5 of 246) and 8.0% (11 of 137) respectively. The majority of variants resulted in a 0,4-5,0 (*P. erythrogaster*) or a 0,5-4,0 (*P. eos*) formula. Some of these species (especially *P. erythrogaster* and *P. eos*) may have added a tooth (the first) to the major row, yielding the 0,5-5,0 formula, at some time in their recent phylogenetic histories. The following evidence supported this contention: the tooth was smaller with a less specialized crown than the other four teeth and the anterior edentulous process of the arch was shorter because of the addition of the tooth, thus giving the process a disproportionate appearance when compared to that of species with four major-row teeth. The fact that most of the *P. erythrogaster* and *P. eos* variants were forms with only four major-row teeth further supported this conclusion and indicated that a small percentage of individuals have not, as yet, added the extra tooth to one or the other of the pharyngeal arches.

The 2,5-4,2 formula may also be cited as illustrative of the trend, among some cyprinids, toward an increase in the number of major-row teeth. The added tooth in these species was similar to that in the 0,5-5,0 species in that it was smaller and less specialized than the other major-row teeth. Pharyngeal teeth of four Minnesota species were of the 2,5-4,2 arrangement. The percentage of arches showing variant formulae in these species were: *Phoxinus neogaeus*, 1.4% (1

TABLE 1. INTRASPECIFIC VARIATION IN THE PHARYNGEAL TOOTH FORMULAE OF THE MINNESOTA CYPRINIDS.

Species	Usual Tooth Formula	No. Arches Examined	No. Arches Showing Variant Tooth Formulae	% Arches Showing Variant Tooth Formulae	Variant Formula (e)	N
<i>Cyprinus carpio</i>	1,1,3-3,1,1	380	22	5.8	1,2,3-	6
					0,1,3-	2
					1,1,1,3-	2
					1,1,2,3-	1
					-3,2,1	7
-3,1,1,1	4					
<i>Carassius auratus</i>	0,4-4,0	172	0	0.0	—	—
<i>Pimephales promelas</i>	0,4-4,0	285	0	0.0	—	—
<i>Pimephales notatus</i>	0,4-4,0	356	0	0.0	—	—
<i>Pimephales vigilax</i>	0,4-4,0	100	0	0.0	—	—
<i>Hybognathus hankinsoni</i>	0,4-4,0	247	2	0.8	0,5-	2
<i>Hybognathus nuchalis</i>	0,4-4,0	123	0	0.0	—	—
<i>Campostoma anomalum</i>	0,4-4,0	199	0	0.0	—	—
<i>Dionda nubila</i>	0,4-4,0	190	0	0.0	—	—
<i>Phoxinus erythrogaster</i>	0,5-5,0	246	5	2.0	0,4-	4
					0,6-	1
					0,6-	1
					2,5-	1
					-4,0	8
-4,1	1					
<i>Phoxinus eos</i>	0,5-5,0	137	11	8.0	0,6-	1
					2,5-	1
					-4,0	8
					-4,1	1
					3,5-	1
<i>Phoxinus neogaeus</i>	2,5-4,2	71	1	1.4	3,5-	1
					2,4-	19
<i>Clinostomus elongatus</i>	2,5-4,2	170	19	11.2	2,4-	19
<i>Semotilus atromaculatus</i>	2,5-4,2	130	5	3.9	2,6-	1
					-5,2	4
					1,5-	2
					1,4-	1
					-4,1	4
<i>Semotilus margarita</i>	2,5-4,2	134	7	5.2	1,4-	1
					-4,1	4
					1,4-	1
					-4,1	1
					—	—
<i>Rhinichthys cataractae</i>	2,4-4,2	219	2	0.9	1,4-	1
					-4,1	1
					—	—
<i>Rhinichthys atratulus</i>	2,4-4,2	119	0	0.0	—	—
<i>Couesius plumbeus</i>	2,4-4,2	53	1	1.9	-4,3	1
<i>Nocomis biguttatus</i>	1,4-4,1	141	2	1.4	2,5-	1
					-4,2	1
					1,5-	1
<i>Hybopsis storeriana</i>	1,4-4,1	104	3	2.9	2,4-	1
					-4,0	1
					—	—
<i>Hybopsis aestivalis</i>	0,4-4,0	115	0	0.0	—	—
<i>Hybopsis x-punctata</i>	0,4-4,0	19	0	0.0	—	—
<i>Phenacobius mirabilis</i>	0,4-4,0	83	0	0.0	—	—
<i>Notemigonus crysoleucas</i>	0,5-5,0	155	3	1.9	0,6-	2
					-5,1	1
<i>Opsopoeodus emiliae</i>	0,5-5,0	94	0	0.0	—	—
<i>Notropis anogenus</i>	0,4-4,0	115	1	0.9	0,5-	1
<i>Notropis heterolepis</i>	0,4-4,0	231	0	0.0	—	—
<i>Notropis lutrensis</i>	0,4-4,0	215	16	7.4	1,4-	9
					-4,1	6
					0,5-	1
<i>Notropis stramineus</i>	0,4-4,0	174	1	0.6	0,5-	1
<i>Notropis topeka</i>	0,4-4,0	108	0	0.0	—	—
<i>Notropis volucellus</i>	0,4-4,0	240	0	0.0	—	—
<i>Notropis amnis</i>	1,4-4,1	34	1	2.9	2,4-	1

TABLE 1. *Continued*

Species	Usual Tooth Formula	No. Arches Examined	No. Arches Showing Variant Tooth Formulae	% Arches Showing Variant Tooth Formulae	Variant Formula(e)	N
<i>Notropis dorsalis</i>	1,4-4,1	258	5	1.9	-4,0	5
<i>Notropis heterodon</i>	1,4-4,1	122	1	0.8	1,5-	1
<i>Notropis spilopterus</i>	1,4-4,1	245	13	5.3	0,4-	3
					2,4-	1
					1,4,1-	1
					-4,0	4
					-4,2	2
					-5,1	1
					-1,4,1	1
<i>Notropis atherinoides</i>	2,4-4,2	181	6	3.3	1,4-	3
					-4,1	1
					-4,3	1
					-4,0	1
<i>Notropis blennioides</i>	2,4-4,2	147	10	6.8	1,4-	4
					3,4-	1
					2,5-	1
					-4,1	2
					-4,3	2
<i>Notropis cornutus</i>	2,4-4,2	556	8	1.4	2,5-	3
					0,4-	2
					3,5-	1
					-4,1	1
					-4,0	1
<i>Notropis hudsonius</i>	2,4-4,2	1663	818	49.2	1,4-	367
					2,5-	12
					1,5-	8
					3,5-	2
					2,6-	1
					0,4-	1
					3,4-	3
					2,4,1-	1
					2,4,3-	1
					2,4,2-	1
					2,2,4-	1
					2,2,4,3-	1
					-4,1	404
					-5,2	7
					-5,1	3
					-4,0	2
					-4,3	1
					-1,5,3	1
					-2,4,2	1
<i>Notropis rubellus</i>	2,4-4,2	174	10	5.8	1,4-	8
					-4,1	2
<i>Notropis texanus</i>	2,4-4,2	156	15	9.6	1,4-	7
					0,4-	1
					2,5-	1
					-4,1	4
					-4,0	2
<i>Notropis umbratilis</i>	2,4-4,2	115	4	3.5	2,4,1-	1
					-4,1	2
					-3,2	1

of 71), *Semotilus atromaculatus*, 3.9% (5 of 130), *S. margarita*, 5.2% (7 of 134), and *Clinostomus elongatus*, 11.2% (19 of 170). Nothing conclusive can be said about the variation in *P. neogaeus*, *S. atromaculatus*, and *S. margarita* other than that the addition of the extra tooth to the left major row appears, based on the relatively low incidence and types of variation, to be essentially completed. In *Clinostomus elongatus*, however, the high (11.2%) percentage of deviants were all of the same type, 2,4-, indicating that the 2,5-4,2 formula has possibly not been attained by all populations of the species.

Among the six species with the 1,4-4,1 formula, only one, *Notropis spilopterus*, showed any marked amount of variation. Thirteen arches in a sample of 245 (5.3%) had a total of seven different deviant half-formulae. No trends or patterns were apparent in the deviants. The only conclusion we could draw was that *N. spilopterus* is a species that has a variable tooth formula.

The 2,4-4,2 formula was characteristic of 10 Minnesota species. Six of these (*Rhinichthys cataractae*, *R. atratulus*, *Couesius plumbeus*, *Notropis atherinoides*, *N. cornutus*, and *N. umbratilis*) were considered to have relatively invariant formulae although the amount of variation, 1.4% to 3.5% in the *Notropis* species, was higher than in species of the same genus with 0,4-4,0 teeth. We did not interpret the higher incidence of deviant formulae in these species as evolutionary change, but rather as a consequence of the inherently greater capacity for variation in the 2,4-4,2 formula because of the larger number of teeth among which deviation can occur.

The four 2,4-4,2 species with greater degrees of variation were: *Notropis rubellus*, 5.8% (10 of 174), *N. blennioides*, 6.8% (10 of 147), *N. texanus*, 9.6% (15 of 156), and *N. hudsonius*, 49.2% (818 of 1663). The greatest percentage of variants in each of these species were those missing one minor row tooth, thus giving the half-formulae of 1,4- and -4,1. In *N. hudsonius* this was probably indicative of, among other things, the trend toward the loss of minor row teeth and, although not as marked, the same was probably true for the other three species as well. *Notropis hudsonius* was by far the most variable of the species examined. Eight hundred eighteen of 1663 arches showed a total of 19 different deviant half-formulae. However, 775 of the

818 deviants were either 1,4- or -4,1. Thus it appears that *N. hudsonius* is evolving toward the 1,4-4,1 condition with almost half of the specimens examined having reached this state. The high percentage of *N. hudsonius* deviants cannot be attributed to a sampling disparity since the results represented the pooled data for over 800 individuals from 13 collections; 12 were from widely scattered areas in Minnesota and one was from South Dakota.

DISCUSSION

It appears that in some of the cyprinid species examined pharyngeal tooth formulae are not, by themselves, taxonomically reliable because of marked intraspecific variation. Although considerable interspecific variation exists in the morphology of the pharyngeal arches and teeth (Eastman, 1970), these structures are uniform within a species. Because of the intraspecific variation in tooth formulae and since several species may possess the same formula, we feel that brief descriptions of the form and relative dimensions of the pharyngeal arches and of the shape of the teeth are important components of species descriptions and keys.

As a correlative to this study we hoped that examination of pharyngeal tooth formulae would provide some insight into the evolutionary trends in tooth number and number of tooth rows in cyprinids. Each pharyngeal arch of the species in this family bears one, two, or three rows of teeth. All New World species have one or two rows and presumably the East Asian stocks, from which they were derived, had the same number. Three rows predominate in many Old World groups. The works of Vladykov (1934) and Chu (1935) provide information concerning the worldwide distribution of cyprinids relative to the number of rows of teeth. Their findings indicate that genera with three rows are more common in Africa, India, and eastern Asia whereas one and two rowed genera predominate in Europe and North America. Regan (1911), Chu (1935), Vasnecov (1939), Brittan (1961), and Holčík and Duyvené de Wit (1962) all think that two or three rows of teeth represent the primitive condition in the Cyprinidae and that evolution has led to a reduced number of rows in some species.

Our studies on the pharyngeal tooth formulae of cyprinids of the subfamily Leuciscinae tended to support the above theory.

This trend was evident, and probably still continuing, in certain species of the genera *Notropis* and *Hybopsis* (especially if *Couesius* and *Nocomis* are included). These genera are polyphyletic; thus one ancestral tooth formula, from which reduction occurred, cannot be postulated although 2,4-4,2 or 1,4-4,1 or a close variant thereof may have been the ancestral formula for certain monophyletic groups undergoing reduction within these genera. Both genera have species with formulae of 2,4-4,2; 1,4-4,1; or 0,4-4,0. The closely related species *Notropis stramineus*, *N. volucellus*, and *N. dorsalis* have formulae of 0,4-4,0; 0,4-4,0; and 1,4-4,1 respectively. The 0,4-4,0 formulae in *N. stramineus* and *N. volucellus* could be the result of the loss of the minor-row tooth from a suspected 1,4-4,1 ancestral condition. *Notropis dorsalis* has not lost the minor row tooth.

Opposed to the loss of minor-row teeth is the constancy, or even gain, in the number of major-row teeth in some species. When a tooth has been added, as in *Semotilus atromaculatus*, *S. margarita*, *Clinostomus elongatus*, *Phoxinus neogaeus*, *P. eos*, and *P. erythrogaster*, resulting in a 2,5-4,2 or a 0,5-5,0 formula, the adjunct tooth has become ankylosed anterior to the original first tooth in the major row thereby decreasing the length of the anterior edentulous process. As mentioned earlier, the additional tooth was usually slightly smaller and less specialized (i.e., not as hooked as the other teeth in the row). No explanation can be offered why the addition always seems to be to the left arch in 2,5-4,2 species. It is theoretically possible that an additional tooth will eventually be added to the right arch.

The absence of significant types of tooth formula deviation in *Notemigonus crysoleucas* and *Opsopoeodus emiliae* indicated that teeth may not have been added in these two 0,5-5,0 species. They may have arrived in North America with this formula and have neither added to nor subtracted from it in the intervening time. It must be mentioned, however, that the structure of the first tooth in these species was similar to that of the added tooth in *Semotilus*, *Clinostomus*, and *Phoxinus*.

We agree with Chu (1935) concerning the trend, correlated with feeding adaptations, toward a reduction in the number of rows of teeth in cyprinids. We also support his contention (1935) that the one and two-rowed

East Asian forms that came across the Bering Sea connection to populate North America have, since arriving, undergone further reduction in number of tooth rows. Chu (1935) regarded five as the primitive number of major-row teeth in Chinese cyprinids and felt that specialization led to a reduced number in most members of the family with the exception of the Chondrostominae. Our hypothesis concerning the addition of a major-row tooth in some North American species was based on the assumption that many North American minnows were derived from ancestral stocks with four major-row teeth. These stocks presumably reached this reduced number before populating North America. It seems possible that certain of the feeding habitats encountered by some of these newly arrived species favored the addition of a fifth tooth to the major row. We also accept the possibility, mentioned by Lachner and Jenkins (1967), that a few North American minnows, such as *Nocomis leptocephalus*, are undergoing a reduction in the number of major row teeth.

It appears, then, that the evolutionary trend in the New World cyprinids with plastic tooth formulae is toward a decrease in the number of minor rows (from two to one or zero) by the loss of minor-row teeth. As far as the major row is concerned, the trend is toward preservation of the existing teeth or addition to their number. It must also be mentioned that these trends are mutually exclusive and, in a family as diverse as the Cyprinidae, neither universal nor relentless. Several Minnesota species have formulae that seem to be stabilized at 2,4-4,2 or 1,4-4,1. Furthermore, many species have not added, nor do they give any indication of adding, major-row teeth.

Another fact emerging from the study of intraspecific variation was that variation in the half-formula of one arch was independent of that in the arch of the other side although, in the samples upon which this study was based, the left arches showed more variants than the right. When addition of a major row tooth has resulted in an asymmetrical formula (e.g., 2,5-4,2) the left arch has always received the extra tooth.

It appears, then, that the tooth formulae of some species, because of continuing evolutionary trends adding to or subtracting from the number of teeth, are much more variable than those of other species that

possess, at the present time, more or less static formulae. Why, among species with plastic formulae, are minor-row teeth lost while the number of major-row teeth remains constant or increases? This phenomena can perhaps be explained by examining the function of the major and minor rows in mastication (Eastman, 1970; 1971). The position and size of the cyprinid chewing pad and pharyngeal arch modifications, a result of its transition from a ceratobranchial, combined to leave the minor-row teeth lateral to the main occlusal area in most New World minnows and hence less involved in masticatory activity. Major-row teeth, on the other hand, are in a better position to serve the masticatory needs of the species and the same is true for any teeth added to the major row. It seems to be a matter of utility; the minor-row teeth are not functionally essential and therefore are not maintained by selection pressure in some species. Major-row teeth are functional and it is not surprising that some species have, by genetic means, increased the number of these teeth.

Explanations other than those with a functional and evolutionary basis can also be offered to account for certain types of tooth formula variations encountered in our study. The presence of one or more extra rows of teeth on an arch (e.g., 2,4,2, or 2,2,4, etc.) and even the presence of a single extra tooth in the major or minor row could be indicative of faulty tooth replacement. In other words, a tooth destined to be replaced has not been shed even though its replacement has become ankylosed to the arch. Evans and Deubler (1955) and Weisel (1967) considered such disturbances in the replacement process to account for the deviant tooth counts found in their material. We feel this hypothesis also explains many of the sample additions and subtractions (e.g., 0,5- instead of 0,4, or 0,4- instead of 1,4-) we encountered in our samples. Additions were much more common than subtractions, giving credence, we think, to our hypothesis regarding the usefulness of extra major-row teeth. Any subtraction from the number of major-row teeth might impair the efficiency of the masticatory apparatus.

There are several mechanisms that could possibly govern permanent additions to or subtractions from the count of a species. Tooth buds (enamel organs) originate from the dental lamina by a process that has been

summarized for lower vertebrates (especially reptiles) by Edmund (1960). Tooth buds are produced throughout the life of the individual in vertebrates with polyphyodont dentition. Each definitive crown ankylosed to the pharyngeal arch has, in the surrounding mucosa, tooth buds that are destined to form its replacement caps. There would, presumably, be four anlagen on the dental lamina producing tooth buds in species with four major-row teeth. In order for a tooth to be permanently added to the complement of a species, a new bud-forming anlage would have to be initiated or an existing anlage would have to divide yielding two functional anlagen. Subtraction from the formula would require failure of an anlage to develop, fusion of two existing anlagen or continual fusion of buds produced by two adjacent anlagen. Selection probably acts at the level of the bud anlagen rather than at the level of the ankylosed teeth since tooth number would be regulated at this developmental point rather than at the level of the transitory definitive teeth that merely reflect the activity of the dental lamina. The actual mechanism controlling the number of bud anlagen remains obscure although it is possible that mesectoderm, of neural crest origin and forming the tooth papillae, induces the dental lamina to produce buds. If this is true, selection for definitive tooth number may be acting very early in development at the stage of the differentiation and migration of neural crest tissue.

ACKNOWLEDGMENTS

This work was supported by funds (C1160309 and C1160300) from the General Research Support Grant Subcommittee of the University of Oklahoma Health Sciences Center.

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