THE UNIVERSITY OF MANITOBA

GILL RAKER CHARACTERISTICS IN TRANSPLANTED AND PARENT WHITEFISH (COREGONUS CLUPEAFORMIS), AND AN EXAMINATION OF THEIR HISTOLOGY AND REGENERATION CAPABILITIES

by

A. S. TRETIAK

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

WINNIPEG, MANITOBA

OCTOBER, 1975

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ABSTRACT

Gill raker morphology of adult lake whitefish (Coregonus clupeaformis) was compared between a parent Clearwater Lake population and a transplanted second-generation Lyons Lake population, and related to diet and food availability.

Significant differences ($P < .05$) between populations occurred for gill raker length, spacing, base length, angle between base and blade, blade width, number of teeth on both sides of raker blade, spacing of teeth, distal portion of raker without teeth, tooth socket succession patterns, tooth socket counts, and occurrence of teeth on posterior rakers. These differences are apparently correlated with the pelagic diet of Lyons fish and the benthic diet of Clearwater fish.

Histologic details of whitefish rakers are described. Gill rakers were found capable of limited regeneration. Regenerates were hypotypic, but similar in appearance.

The hypothesis of abrasion as the causal agent of the shorter Clearwater gill rakers is rejected. Gill raker differences may be attributable to a phenotypic response by the raker apparatus to changes in the environment, particularly diet, and possibly occurs throughout the development of the fish. Such developmental plasticity can account for the rapid adaptation to diet by transplanted whitefish.

ACKNOWLEDGEMENTS

The author expresses thanks to Dr. C. C. Lindsey for his supervision of this study, and valuable criticisms on the preliminary draft of this manuscript. The assistance and cooperation of staff members of the Department of Zoology, University of Manitoba, was sincerely appreciated, in particular the use of the animal holding facilities under Dr. K. W. Stewart and R. Hancock. Assistance for obtaining the Clearwater fish was provided by the staff at the Provincial Government Hatchery at Clearwater Lake. Whitefish fry specimens were generously provided by W. G. Franzin. Special thanks go to a most capable field assistant and typist, my wife, Marjorie.

Financial support for the author was provided by University of Manitoba graduate fellowships. This study was supported in part by grants from the National Research Council and the Aquatic Biology Research Unit of the University of Manitoba to Dr. C. C. Lindsey.

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INTRODUCTION

Numerous authors suggest that the gill rakers of fish serve to strain out small food particles from the water for consumption, and also to prevent particulate matter from damaging the delicate gill filaments (Alexander 1967; Norman and Greenwood 1963; Romer 1955; Weichert 1965). The former function is probably the most important, as raker structure has been shown to be related to diet. One can readily discover this relationship by examining the rakers of the pike, *Esox lucius*, and the cisco, *Coregonus artedii*. The former is piscivorous and has rakers that are reduced to denticulated plates; the latter is mainly a plankton feeder and has numerous long gill rakers.

The shape and number of rakers can generally be correlated with diet, and two studies on lake whitefish *Coregonus clupeaformis* (Mitchill) have added evidence for a correlation between raker length and diet. Kliewer (1970) found a strong negative correlation between relative gill raker length and the percentage of benthic food eaten. Loch's study (1974) of Clearwater and Lyons Lakes whitefish supports Kliewer's findings. Lyons Lake whitefish are offspring of transplanted Clearwater stock. Loch found that whitefish in Clearwater Lake, which are predominately benthic feeders, have short gill rakers. Whitefish in Lyons Lake are mainly pelagic feeders, and have long gill rakers. Diet in these groups of fish was shown to be correlated with the food that was available to the fish.

The diets of the Clearwater and Lyons whitefish have been determined to be different. This study further examines gill rakers of the two populations for correlations between diet and other raker parameters in addition to their length. Lyons whitefish are relatively recent offspring of Clearwater stock, and this study examines the possibilities of phenotypic origin of gill raker variation. Structures that are related to feeding often also have a sensory capacity, and this possibility is also examined.

This work includes a behavioral study in the manner of feeding of adult whitefish, gross examination of the rakers while on the arch, miscroscopic examination of single alizarin-stained rakers, histologic examination of prepared sections, and experiments on regeneration capabilities of the rakers of specimens held live in the lab.

REVIEW OF BRANCHIAL STRUCTURES IN TELEOSTS

SKELETAL ORIGIN

Fish possess a series of gill openings that are separated by cartilaginous or bony arches. These arches support and aid the movement of the gill apparatus, and form the major portion of the visceral skeleton of a fish.

Most endoskeletal structures are formed from mesenchyme that is derived from the mesoderm. Visceral arches are formed in the walls of the gut, and are believed to have developed from mesenchyme formed from neural crest cells that migrated downward (Romer 1955). This mesenchyme is sometimes referred to as mesectoderm (Romer 1955; Weichert 1965). The visceral skeleton has played an important role in the development of jaws. In higher vertebrates the number of visceral arches have been reduced, some of their parts modified, and the cartilage replaced by bone.

In modern fish such as the coregonids, five arches remain. Each arch consists of a series of elements that are articulated to provide limited movement. The arches of the coregonids bear a series of rakers on the inner surface and gill filaments on the outer surface, with the exception of the fifth arch which lacks gill filaments.

These arches are part of the visceral endoskeleton of the fish. The rakers, however, which are not fused to the arches, are considered to be dermal elements and are not of the same embryonic origin as the arches (Nelson 1969). According to Nelson, dermal elements arose by an assimilative process in certain regions of the visceral skeleton. In fish requiring a biting surface, this produced large teeth or tooth plates in localized areas; in fish specialized for a microphagous diet, a more uniform distribution of dermal elements produced a series of gill rakers along the arches. The whitefish is an example that exhibits this raker proliferation.

SKELETAL STRUCTURE

The skeletal elements comprising the branchial arches of Coregonus have been well documented by Norden (1961). The first three arches all have the same number of elements (Fig. 1). The most dorsal element is the pharyngobranchial, followed by the epibranchial and ceratobranchial bones. These latter two form the angle of arch. The most ventral element is the hypobranchial, which terminates the arch at the median row of basibranchial bones that lie along the floor of the branchial apparatus.

The fourth arch consists of only the epibranchial and ceratobranchial bones, and the fifth arch is further reduced, consisting of only the ceratobranchial. Pharyngeal plates are present on the third pharyngobranchial, fourth epibranchial, and fifth ceratobranchial bones (Norden 1961).

Gill filaments are carried along the outer posterior margins of the first four branchial arches. Gill rakers are arranged along the anterior and posterior borders of the inner margin of the arches (Figs. 2 & 3) with the exception of the fifth arch which has rakers only on the

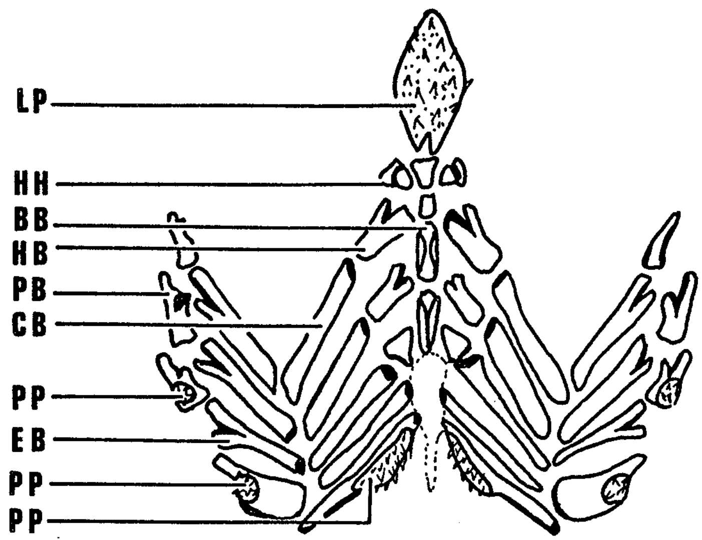


Fig. 1. Branchial skeleton of Coregonus clupeaformis, about 1.3X. Abbreviations: BB, basibranchial; CB, ceratobranchial; EB, epibranchial; HB, hypobranchial; HH, hypohyal; LP, lingual plate; PB, pharyngobranchial; PP, pharyngeal plate. Taken from Norden (1961).

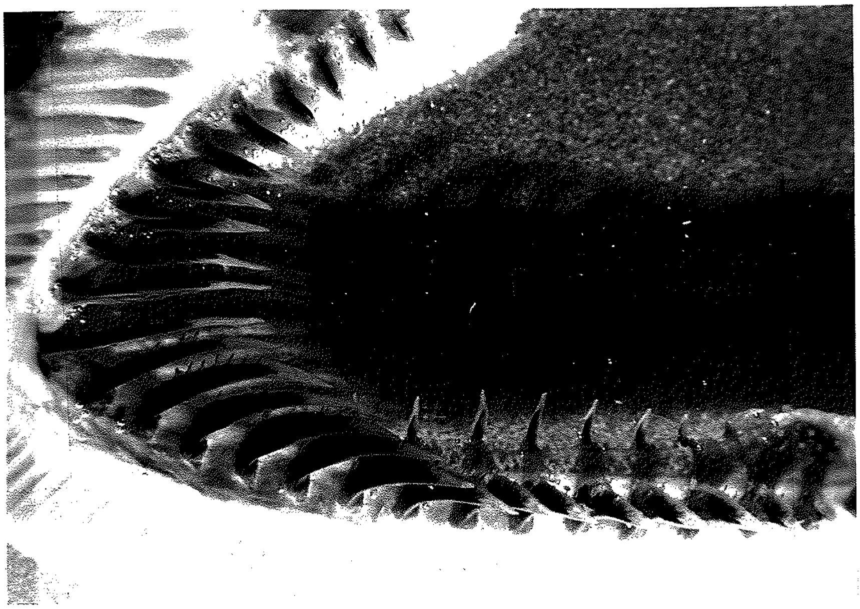


Fig. 2.

Fig. 3.

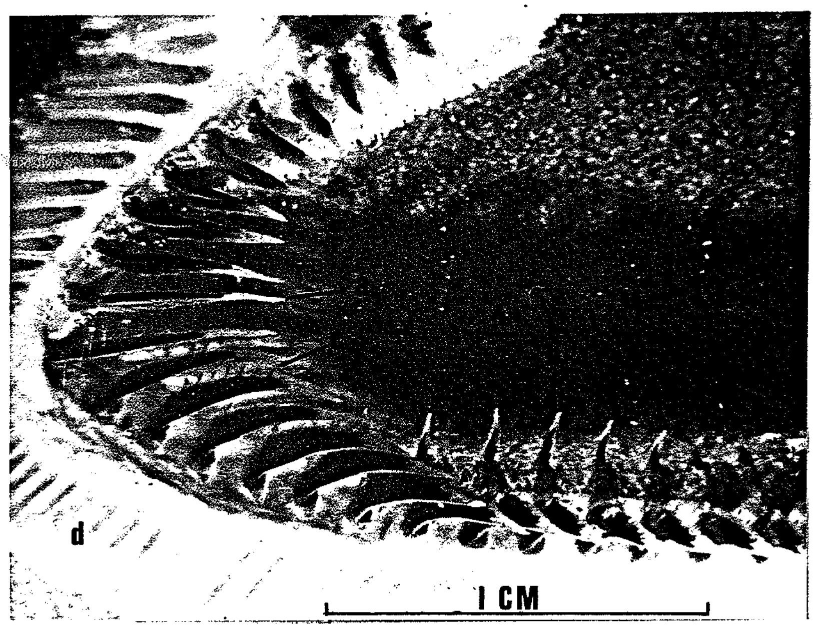


Fig. 2. Right first gill arch of a Lyons fish, lateral view, indicating outer anterior rakers (a), inner posterior rakers (b), and raker teeth (c). Alizarin stained. Gill filaments (d) clipped.

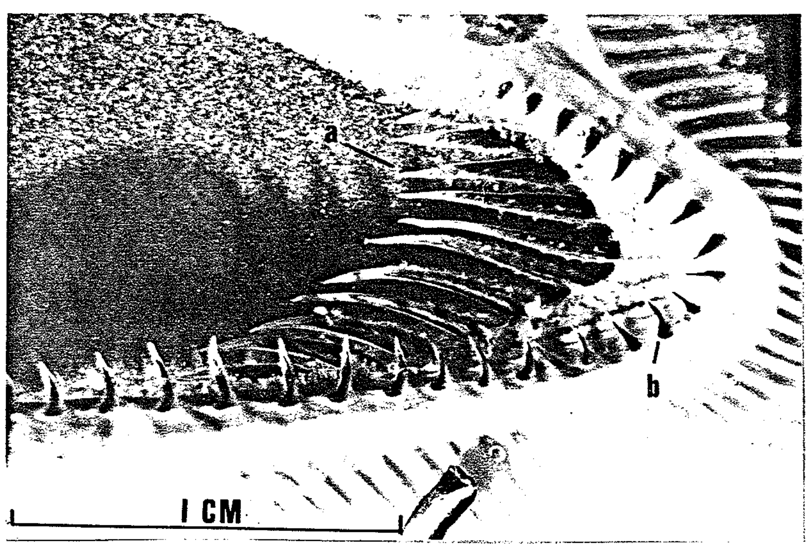


Fig. 3. Right first gill arch of a Lyons fish, medial view, indicating same structures as Fig. 2.

anterior border. The anterior gill rakers of Coregonus clupeaformis bear teeth (Fig. 2); posterior gill rakers may also bear teeth, which are usually less numerous than teeth of anterior rakers. The teeth are replaced as the raker grows, leaving behind socket patterns.

MUSCULATURE AND INNERVATION

The musculature of the branchial arches is not strongly developed in the bony fishes. According to Hughes and Shelton (1962), teleost branchial muscles usually form small bundles of muscle fibres capable of producing individual movements of the branchial arch skeleton and the gill filaments.

The musculature of these arches is striated and voluntary. Striated muscles usually are derived from myotomes, as they are part of the somatic musculature of the body. The branchial muscles, however, are derived from the splanchnic mesoderm of the hypomere (Romer 1955; Weichert 1965), hence their origin is similar to gut musculature, which is smooth and involuntary.

Although the branchial muscles are striated and voluntary, visceral branches of cranial nerves supply the gill arch region with sensory and motor fibres. Innervation of the first gill arch is provided by branches of the glossopharyngeal nerve (IX) and the vagus nerve (X) (Fig. 4). The remaining arches are innervated by branches of the vagus nerve. The major branch or ramus is the post-trematic, which is both visceral sensory and motor, while the smaller pre-trematic is sensory only. A small sensory branch, the pharyngeal, goes to receptors in the

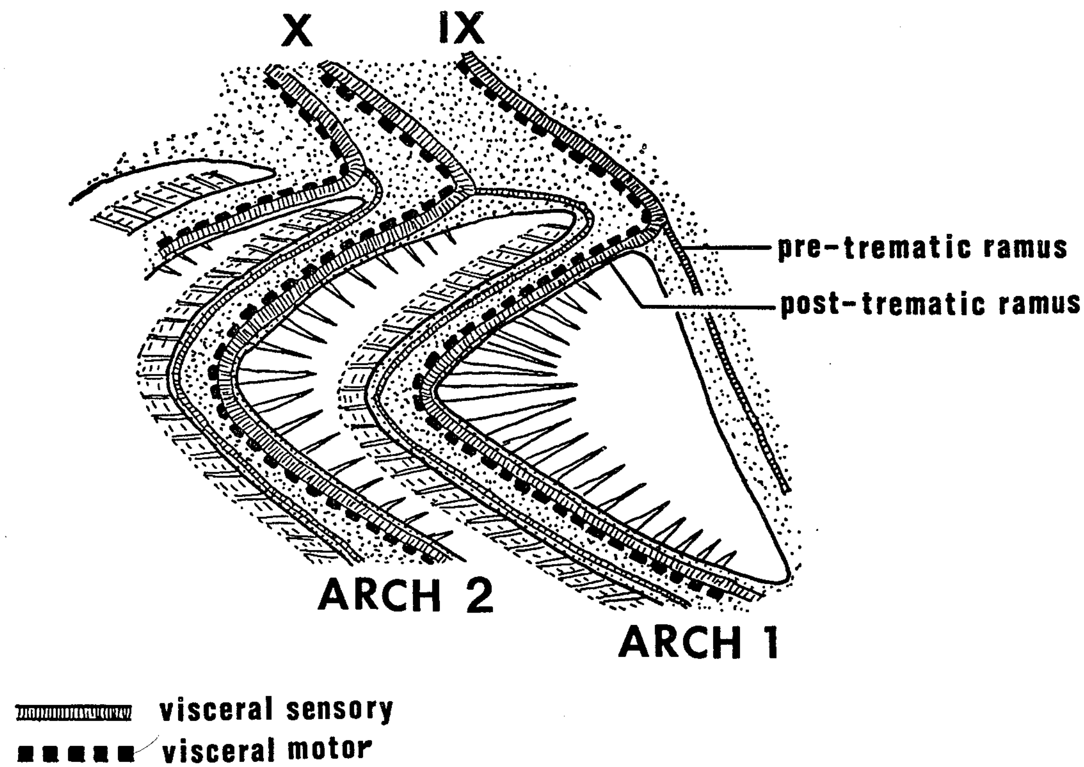


Fig. 4. Innervation of gill arches 1 & 2 of a teleost, by visceral branches of the cranial nerves IX (glossopharyngeal) & X (vagus). Diagramatic representation; no scale intended.

pharynx. A fourth small branch is found in some primitive aquatic vertebrates as a branch of the glossopharyngeal nerve, which innervates the anterior portion of the lateral line. This is the dorsal branch, a somatic sensory nerve (Romer 1955).

The first two gill arches of the white fish were the principal arches investigated in this study. According to the typical branching pattern of these nerves (Romer 1955; Weichert 1965) the first gill arch of modern fish is innervated by the post-trematic ramus of the glosso-pharyngeal nerve, and the pre-trematic ramus of the vagus nerve (Fig. 4).

MATERIALS AND METHODS

FEEDING BEHAVIOUR

Feeding of adult whitefish, Coregonus clupeaformis, was observed and photographed in a 350-gallon tank with glass observation windows, held in a controlled environment room. Dimensions of the tank were 72" by 36" by 36" (182.9 cm by 91.4 cm by 91.4 cm). Both 35 mm black and white still photography, and super 8 cinematography, were used to analyse feeding under flood lights.

Two groups of Lyons Lake whitefish were used. One group had been collected from Lyons Lake and held at the University since early 1970, and the second group was collected from Lyons Lake on May 1, 1971. Fork lengths of the fish ranged from approximately 35 to 40 cm. Feeding experiments were conducted from April 26, 1971 to October 26, 1971 in Room Z 111 of the Department of Zoology, University of Manitoba.

Three types of food were used: (1) the staple, pelleted salmon food, size 3, brand name EWOS F169 (Appendix); (2) live Daphnia; (3) diptera larvae of Chaoborus and Chironomus, in a mud bottom.

The colour of the tank floor and wooden portions of its sides was changed from light grey to dark green early in the feeding experiments (see Results).

Whitefish fry being raised by W. G. Franzin were also available for feeding observations; feeding behaviour of fry on live Daphnia was observed for a comparison with feeding of adults.

These feeding experiments were exploratory in nature, and yielded only observations of a qualitative nature before they were discontinued. The results are included as a guide for possible future studies.

RAKER MORPHOLOGY

Twenty whitefish (fork lengths 32 - 41 cm) were obtained from Lyons Lake, Manitoba on September 26, 1971, by gillnetting. A similar number (fork lengths 35 - 42 cm) were obtained from Clearwater Lake, Manitoba on October 20, 1971. The sample size chosen was considered the maximum that could be examined satisfactorily for the raker parameters, in the time period of this study.

Loch (1974), who provides locations and descriptions of both lakes, demonstrated that whitefish in Lyons Lake feed primarily on plankton, while those in Clearwater Lake feed primarily on benthic organisms.

In preparation for future histological work, the left branchial arches of three fish from each of the two samples were immediately removed and placed in Lavdowsky formalin-acetic acid-alcohol solution, a fixative that causes a minimum of tissue shrinkage while penetrating and fixing at a moderate rate (Galigher and Kozloff 1964).

All fish were then placed in 10% formalin. Once fixed, the right gill arches of all 40 fish were removed, rinsed, and soaked in several changes of water over two days. The arches were placed in a 2% KOH solution for four days to clear the tissues, stained for 24 hours in 1% KOH solution containing alizarin, rinsed, and placed in 50% ethyl alcohol.

Some of the arches were photographed on 35 mm black and white film before and after staining. Counts and measurements made in this study, following the methods of Hubbs and Lagler (1964), were fork length (FL), head length (HL) and gill raker number (GRN). A general examination was made of the first right gill arch of all specimens, and the distance occupied by ten rakers (10 RD) on the lower arch was measured (from L2 to L12 in Fig. 5).

Individual rakers were removed from the alizarin-stained arches and a number of counts and measurements were made with a Wild Stereo Microscope Model M5 equipped with a measuring micrometer eye disc. Specimens were measured under transmitted light at a magnification of 12X in a 5 cm diameter straight-sided dish in 50% ethyl alcohol maintained at a depth of approximately 7 mm. All raker measurements are expressed as units of the micrometer eyepiece scale. At 12X magnification, 10.0 units are equivalent to 8.33 mm. Manipulation of the raker was carried out with bent dissecting needles to avoid meniscus disturbance over the area of the fluid through which the reading was made. Magnification up to 50X was used to check features of the rakers.

All raker measurements are those of the osseous dimensions of the rakers which are stained with alizarin, except for raker length, which includes the connective tissue to the tip of the raker blade. The stratified squamous covering is not included in any of the measurements, as it had deteriorated from the KOH treatment.

Each raker may be distinguished by two sides (Figs. 5 & 6), the anterior side ('A'), with a row of teeth that face the opening of the

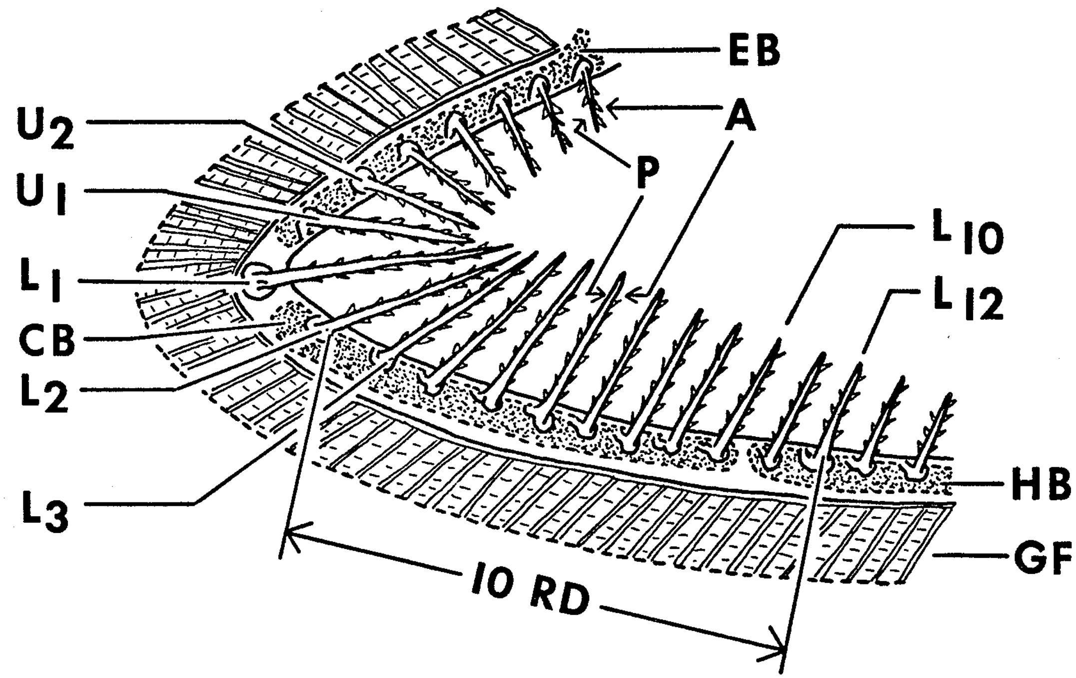


Fig. 5. Arrangement of gill rakers on first right arch. L_1, angle raker; L_2 - L_{12}, remaining rakers on lower arch counted forward; U_1 & U_2, upper rakers; 10 RD, distance along lower arch for 10 rakers, from L_2 to L_{12}; A, anterior side of raker blade; P, posterior side of raker blade; EB, epibranchial; CB, ceratobranchial; HB, hypobranchial; GF, gill filaments. Diagramatic; no scale intended.

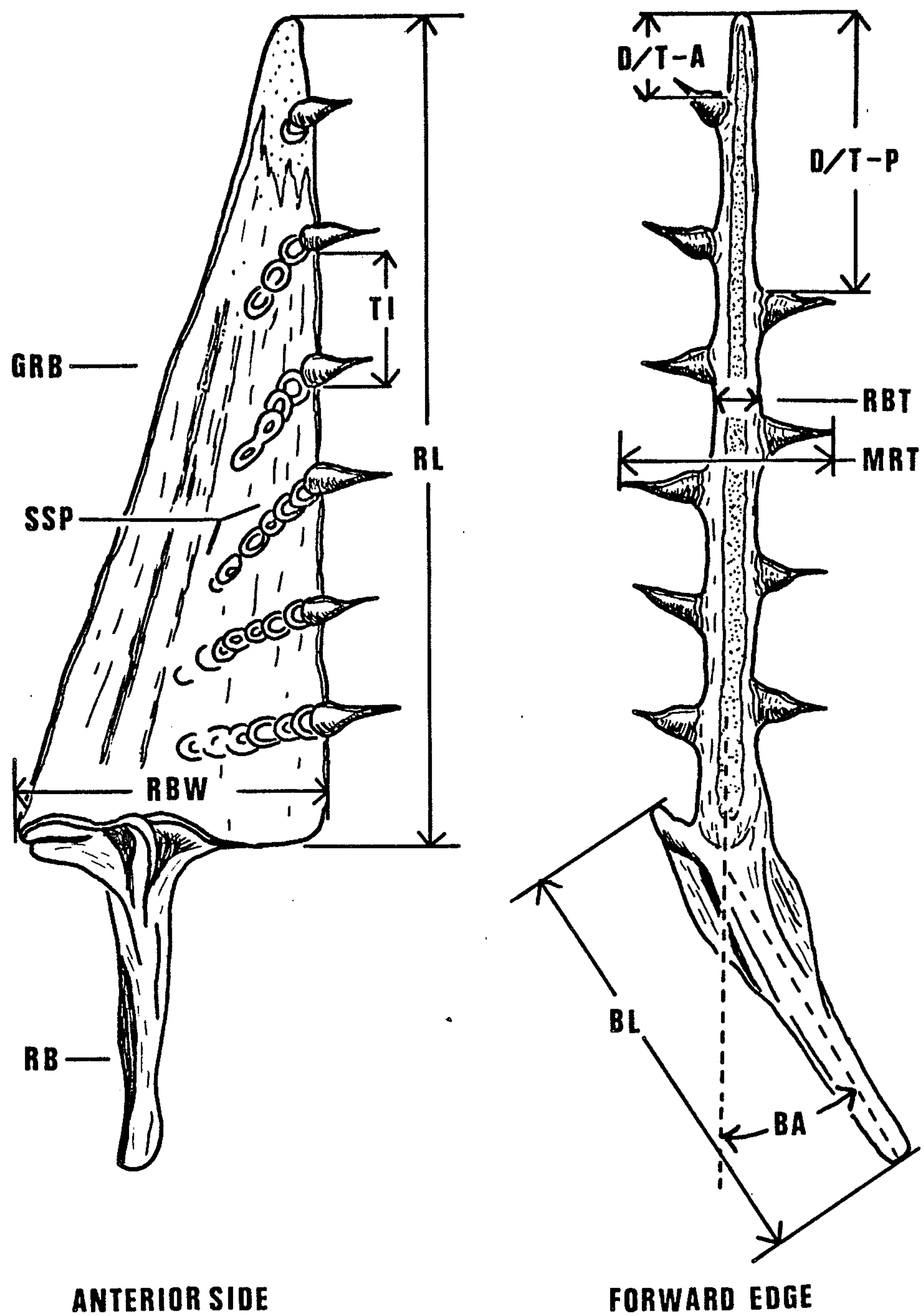


Fig. 6. Gill raker characteristics. Abbreviations: GRB, gill raker blade; SSP, socket succession pattern; RBW, raker blade width; RB, raker base; TI, tooth interval; RL, raker length; D/T-A & D/T-P, distance from most distal tooth to raker tip, anterior (A) & posterior (P) sides; RBT, raker blade thickness; MRT, maximum raker thickness; BL, base length; BA, base angle. Diagramatic; no scale intended.

mouth, and the posterior side ('P'), with the teeth facing the opening of the oesophagus.

Measurements and counts were made for six rakers on the first right gill arch of all specimens, and repeated for six rakers of the second right gill arch. These six rakers were U-1, U-2, L-1, L-2, L-3, and L-10, as designated in Fig. 5. Raker L-2 was also measured on the third and the fourth arches of all specimens. Measurements and counts were limited to these rakers due to the time-consuming procedure required to obtain the data. These particular rakers were chosen for detailed examination after consideration of which rakers would best represent possible variation between the two groups of whitefish.

Figure 6 illustrates the features that were measured and counted on each raker. The criteria used for determining the parameters are described in the Appendix. Measurements were made of raker length (RL), base length (BL), distance from the most terminal tooth to the tip of the raker on each side, 'A' side (D/T-A) and 'P' side (D/T-P), raker blade thickness halfway along length (RBT), maximum effective thickness of the raker using the greatest distance between a set of teeth on a raker (MRT), raker blade width at base (RBW), and the base-blade angle to the nearest 5° (BA). The angle was determined with an eyepiece protractor. Counts were made of the number of teeth on the 'A' and 'P' sides of the raker blade (TA and TP). Average spacing of teeth was calculated from the measurements and counts. Socket succession patterns (SSP) on the 'A' side of the rakers were examined, and classified as straight or curved (Fig. 7; Appendix). Socket counts (SC) were made for the longest

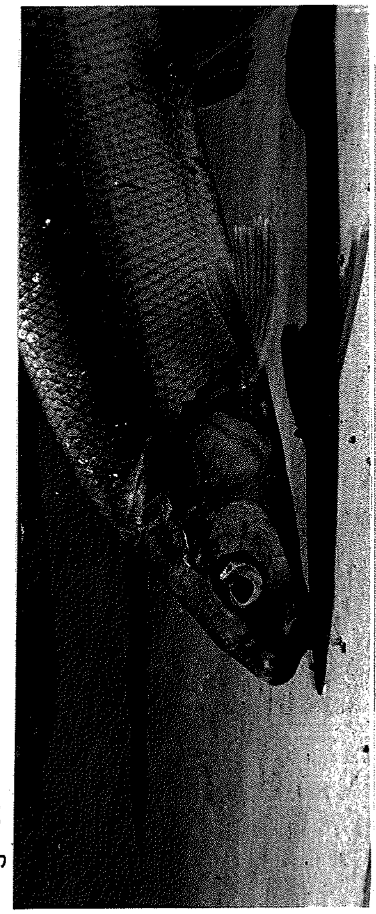


Fig. 8.

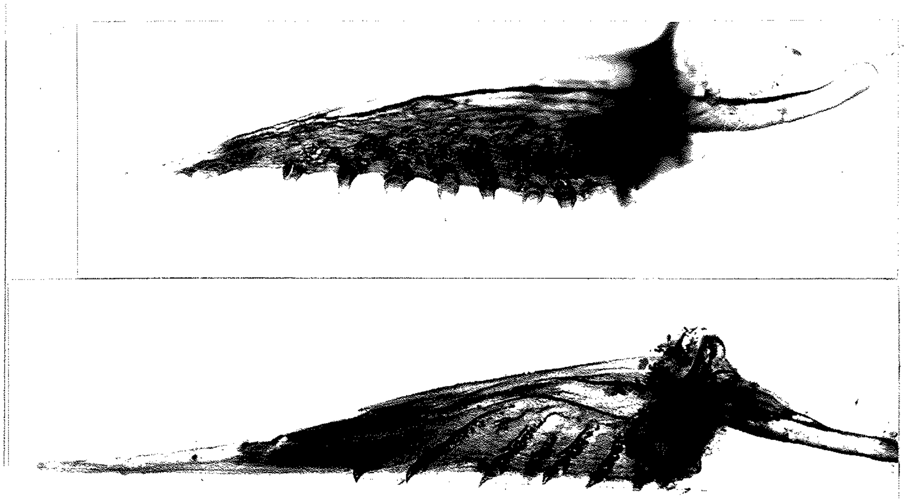


Fig. 7.

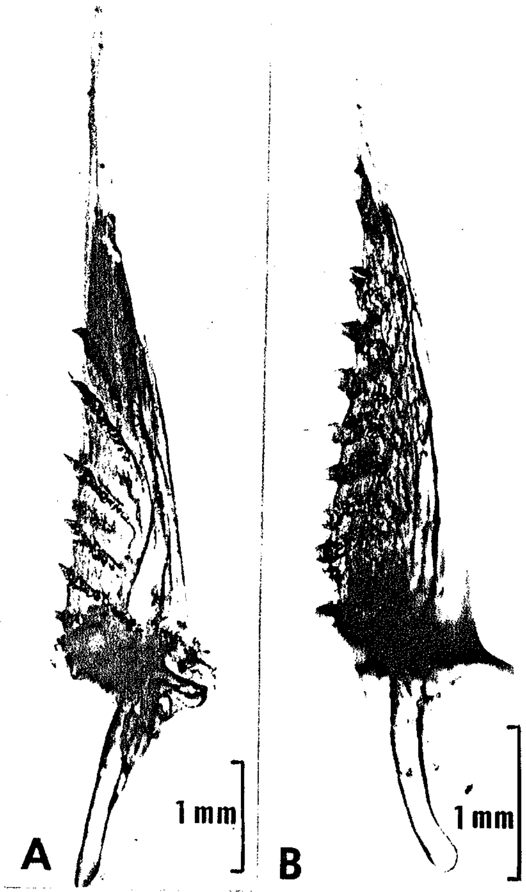


Fig. 7. Anterior side of (A) Clearwater raker with straight socket patterns (U_1, Arch 1) and (B) Lyons raker with curved and reversing socket patterns (U_2, Arch 2). See Fig. 5 for coding.

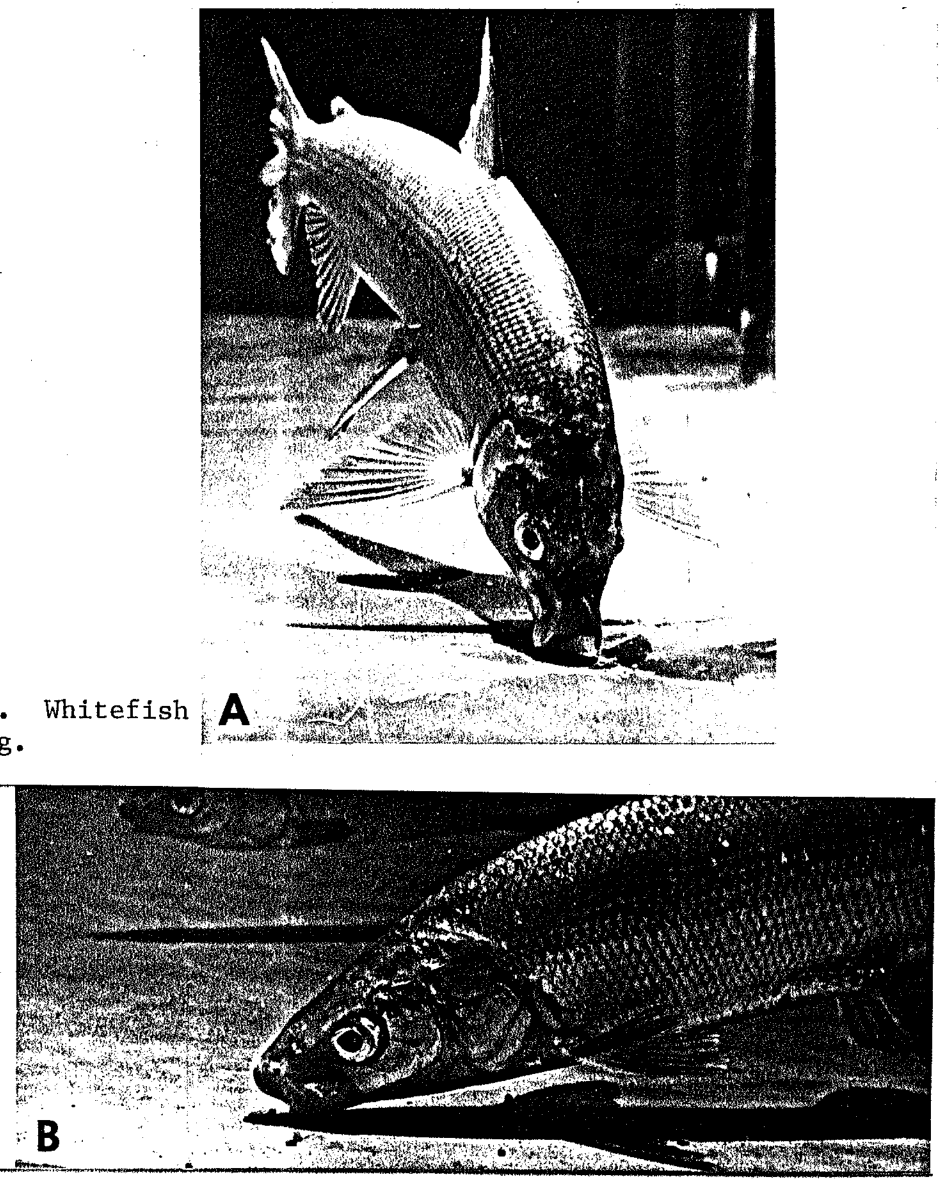


Fig. 8. Whitefish feeding.

succession pattern on the 'A' side of the rakers. Examples of raker structures were photographed on 35 mm black and white film.

A base length is not reported for the angle raker L-1. Its base structure is quite different from the other rakers as a result of its position at the junction of the epibranchial and ceratobranchial portions of the arch.

Because particular measurements were very time-consuming, the following were omitted from some of the specimens: RBT, MRT, BA, SSP, SC.

Counts of posterior rakers and the occurrence of teeth on these rakers were determined for all four arches in both groups of fish, and examples photographed.

No small specimens of whitefish were captured from Lyons or Clearwater Lakes. In order to examine raker measurements in a greater range in size of whitefish, specimens were collected from Steep Rock Lake in the Porcupine Hills of Manitoba (52°35'N, 101°20'W) in mid-September. Eight specimens representing the range of sizes collected (fork lengths 8.7 - 36.0 cm) were examined for the paramenters previously outlined.

Sample size for each of the parameters is 20, with a few exceptions. For each parameter, the pair of samples (Clearwater and Lyons) was subjected to an 'F' test for equality of variance (Snedecor and Cochran 1967). The samples of equal variance were then subjected to a Student 't' test using pooled variance for the hypothesis $U_1 = U_2$. The few samples with variances not equal were subjected to 't' test procedures according to Cochran (Snedecor and Cochran 1967), which tend to give more conservative results for 't'. Correlation coefficients were calculated for selected pairs of parameters.

The fish in both samples had a small and similar range of fork lengths (means not significantly different at P 0.05). Therefore, absolute rather than relative raker measurements were used for statistical and graphical interpretation. Analysis of covariance was employed for a limited amount of data to confirm the statistical significance of absolute measurements using Student 't' tests.

RAKER HISTOLOGY

Standard microtechniques were followed in preparation for histological sections of the rakers. Following fixation in Lavdowsky FAA (Galigher and Kozloff 1964) and upgrading to 70% ethyl alcohol, the left gill arches were placed in a decalcifying solution consisting of 3% concentrated HCl in 70% ethyl alcohol for three weeks. Fresh HCl was added daily, or if the solution became discolored it was replaced. This was followed with neutralization of the acid alcohol for one day, using 70% ethyl alcohol saturated with lithium carbonate.

The arches were then cut into small sections containing intact rakers. These specimens were passed through a series of increasing concentrations of alcohol, then to xylene-alcohol, xylene, xylene-paraffin, and finally embedded in paraffin blocks. The paraffin blocks were sectioned with a rotary microtome at a thickness of 8 microns, unless a particular block required a greater thickness in order to yield an intact section.

A thickness less than 8 microns usually did not produce a satisfactory section due to the differential hardness of inclusions within the specimen. Sections were floated on a heated water bath, removed on microscope slides and allowed to air dry. The slides were passed through a series of coplin jars containing xylene, alcohol, and water to the staining stage, followed by a water-alcohol-xylene series to the final step of the addition of coverslips.

Staining was done initially with Mallory's triple stain (Galigher and Kozloff 1964) and Koneef's stain(Gridley 1960). Both of these stains confirmed the presence of bone and cartilage, and subsequent staining was done with Mallory's triple stain, as this gave a suitable range of colours to relate to tissues.

A young whitefish fry obtained from W. G. Franzin was subjected to the same micro-technique series, and mounted slides were prepared of the gill arch region of the head. Raker structures were compared in fry and in adults. Structures were described, and photographed on 35 mm black and white, and on colour film.

RAKER REGENERATION

A number of Lyons Lake whitefish which had been collected by the author and previously engaged in feeding experiments were later used to investigate raker regeneration. On September 21, 1971, two fish were anaesthesized with tricaine methanesulphonate (MS222) at a concentration of one gram per twelve liters water. The anaesthesized fish were removed from the water and a gravity-fed anaesthetic solution irrigated the gills on the opposite side of the head during the operation. The rakers on the first gill arch were clipped with narrow dissecting scissors, and the fish returned to the holding tank. Water temperature was constant at 12 C.

These fish were examined two months later, and regeneration appeared to be taking place. At that time, seven additional fish each had several rakers clipped at various levels of the raker blade on the right and left first gill arch.

All fish recovered from the procedure and remained in the Department's holding facilities. Their staple diet remained unchanged as pellet salmon food, size 3, brand name EWOS F169. This food was examined with a set of standard sieve screens for particle size, to determine the average size of food particles that the fish were ingesting (Appendix).

Seven months later, on June 21, 1972, all the fish were killed and the first gill arches were removed, fixed and stained in alizarin as previously outlined.

A detailed examination of the stained rakers was carried out with a Wild M5 stereomicroscope, as previously outlined. The measurements and counts obtained from these specimens were RL, BL, D/T-A, D/T-P, regenerated portion of raker length (RGL), and counts of teeth (RTA and

RTP) and their sockets (RSC) on the regenerated portion. The results were subjected to limited graphical and statistical analysis, and various examples were described and photographed on 35 mm black and white film.

RESULTS

FEEDING BEHAVIOUR

The following general observations were made on the feeding behavior of adult whitefish held in the experimental tank.

1. The presence of a second fish frequently motivated a feeding response by a solitary fish.
2. The tank colour was light grey for the initial feeding experiments. During this period, the fish were easily frightened by any local movement. They swam excitedly in the tank, frequently colliding with the glass, and ignored food on the bottom. Slight irregularities on the walls of the tank elicited biting responses. The tank colour was changed to dark green, and this was followed by marked behavioural changes. The fish were no longer excitable and their response to the tank floor was an instant positive taxis, with feeding movements along the bottom despite the lack of food. Feeding was no longer a problem.
3. Ingestion of the staple particulate food (pelleted salmon food) most frequently occurred off the tank floor. Notable exceptions were particles with entrapped air, which rose from the floor to the surface. Fish immediately responded to such particulate movements, which would resemble the upward migration of one of their natural commond foods, the dipteran larva Chaoborus.
4. Feeding movements in adults include a presumed reduction of buccal pressure and the sucking in of the food particle(s) (Fig. 8).

Following a number of such movements, a fish would frequently expand the buccal cavity and open its mouth, extending the premaxilla far forward (Figs. 9). These movements may be cleaning actions to move food from along the gill rakers and/or gill arches towards the oesophagus.

5. When Daphnia of mixed sizes were provided, feeding occurred in mid-water and along the bottom. Bottom was preferred, although denser clouds of Daphnia were present in mid-water. Dense clouds of Daphnia on the bottom were not preferred over smaller clusters on the bottom. The feeding pattern was similar to that observed for particulate matter, although the sucking rate was greater. The adult whitefish did not appear to have separate and distinct feeding patterns for particulate and filter feeding, such as were reported for the anchovy (Leong and O'Connell 1969; O'Connell 1972).
6. Whitefish fry were observed to feed on Daphnia with very distinct biting activity. Mouth position in the fry is quite terminal compared to adults (Fig. 10).
7. Adult whitefish appear to feed discriminately. Small particles of grass or other foreign matter were immediately spit out. The vision of the adult fish appeared to be excellent, as single Daphnia were noticed and ingested.
8. An adult whitefish made only one feeding attempt over a mud bottom displaying the tubes of chironomidae larvae. The resulting cloud of sediment was avoided from then on by the fish, which moved to the upper portion of the tank.

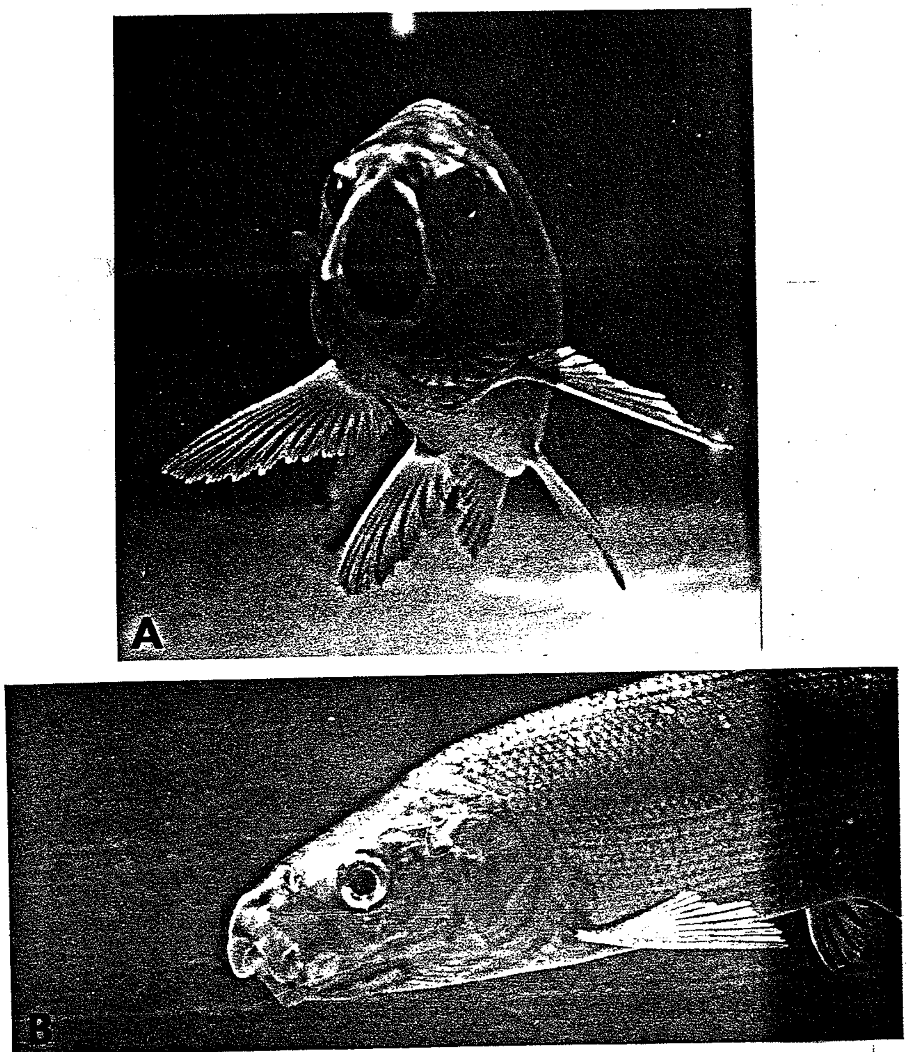


Fig. 9. Mouth extension following feeding by **adult** whitefish.

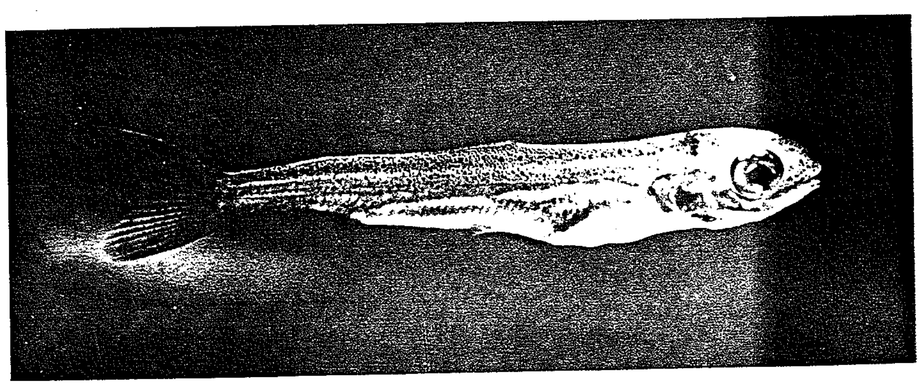


Fig. 10. Whitefish fry.

RAKER MORPHOLOGY

One of the most apparent features of the first gill arch in the majority of specimens of adult Clearwater whitefish is the distorted raker pattern near the angle of the arch. In contrast, Lyons Lake whitefish present a more uniform pattern of rakers with only minor abnormalities. Figure 11 illustrates the first arch of a typical Lyons specimen, and a normally developed first gill arch of a Clearwater fish. Figure 12 illustrates some examples of common localized anomalies of the first arch of Clearwater fish. The appearance of these latter rakers suggests localized and excessive contact through feeding on large and hard items.

According to Loch (1974), diets of whitefish in these two lakes appeared to be correlated with food availability in the respective lakes. The major components of the Lyons whitefish were Tendipedidae, Chaoborus and zooplankton, contrasted with snails, clams and amphipods in the Clearwater fish diet. It appears reasonable to assume that the diet of Clearwater fish may have contributed to the production of raker anomalies.

Analysis of Parameter Means

Tables 1, 2, and 3 list the means, 't' value and significance for each of the tested parameters. At the 5% level of significance, there are no differences between the means of fork length, head length, and gill raker numbers of the first two arches when Lyons and Clearwater fish are compared (Table 1). Loch (1971) indicated a difference in head length between the two populations, but the sample sizes and the size range of the specimens in the present study were considerably smaller.

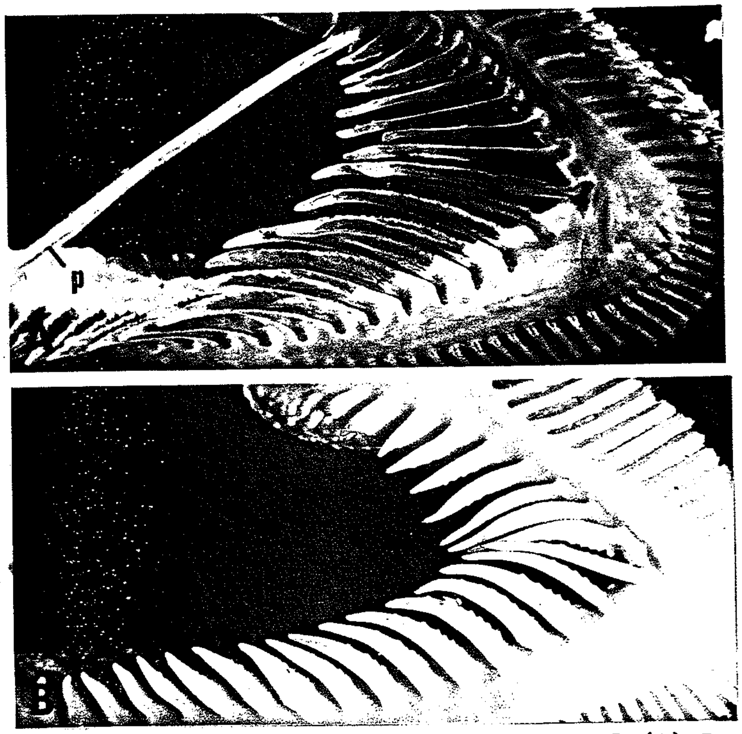


Fig. 11. Normal first left gill arches of (A) Lyons (alizarin stained) and (B) Clearwater (unstained) whitefish. Pin (p) spreading Lyons arch.

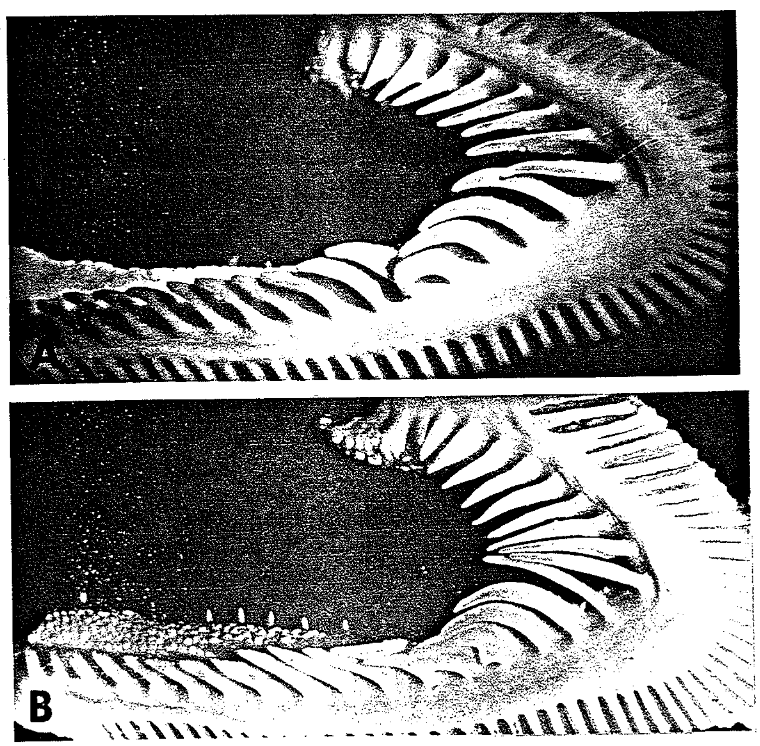


Fig. 12. Gill raker anomalies on lower portion of first left gill arches of Clearwater whitefish.

TABLE 1. Means of characteristics of Clearwater (CW) and Lyons (LY) fish, and levels of significance for difference between means. Characteristics are fork length (FL), head length (HL), gill raker number (FRN), and distance for 10 rakers along lower arch (10 RD).

	FL	HL	GRN (ARCH 1)	GRN (ARCH 2)	10 RD
CW	39.16 cm	8.09 cm	27.05	26.25	1.73 cm
LY	37.95	7.78	27.35	26.40	1.52
't'	1.86	1.98	0.91	0.44	5.89
Signif.	N.S.	N.S.	N.S.	N.S.	*

*** P<.001
** .01 - .001
* .05 - .01
N.S. >.05 (Not Significant)

P determined from 't' test Table A4, p. 549, Snedecor & Cochran (1967).

TABLE 2. Means of gill raker lengths and base lengths of Clearwater (CW) and Lyons (LY) fish, and levels of significance for difference between means. Mean values are expressed in micrometer units.

	ARCH 1						ARCH 2						ARCH 3	ARCH 4
	U_2	U_1	L_1	L_2	L_3	L_{10}	U_2	U_1	L_1	L_2	L_3	L_{10}	L_2	L_2
RAKER LENGTH														
CW	6.59	7.13	7.37	7.60	7.17	4.52	3.18	3.64	3.87	3.78	3.61	3.26	2.53	1.49
LY	7.76	8.53	9.15	9.19	8.93	5.94	3.98	4.48	4.74	4.61	4.41	4.06	3.11	1.63
't'	5.06	5.45	[4.53]	[3.49]	[4.10]	5.65	6.36	5.56	5.87	5.45	5.77	5.53	2.76	1.80
Signif.	***	***	***	**	***	***	***	***	***	***	***	***	**	N.S.
BASE LENGTH														
CW	2.99	3.07		3.36	3.34	2.50	2.40	2.51		2.98	2.79	1.87	2.82	1.71
LY	2.67	2.81		2.84	2.75	2.02	2.14	2.30		2.67	2.41	1.69	2.55	1.32
't'	4.11	2.84		5.36	6.76	5.23	3.87	2.80		3.42	4.23	2.13	3.44	4.30
Signif.	***	**		***	***	***	***	**		**	***	*	**	***

*** P<.001
** .01 - .001
* .05 - .01
N.S. >.05 (Not Signficant)

[ ] = modified 't' test (Snedecor and Cochran 1967)

U_2 - L_{10} raker coding according to Fig.5 .

TABLE 3. Means of gill raker base angle (BA), raker blade thickness (RBT), maximum raker thickness (MRT) and raker blade width (RBW) for Clearwater (CW) and Lyons (LY) fish, and levels of significance for difference between means. Mean values of RBT, MRT, and RBW are expressed in micrometer units.

	BA-ARCH 1		RBT-ARCH 1		MRT-ARCH 1	
	L_2	L_3	L_2	L_3	L_2	L_3
CW	51.2°	55.5°	0.875	0.865	1.805	1.855
LY	22.0°	34.7°	0.870	0.855	1.935	1.935
't'	9.03	6.87	0.14	0.28	1.92	1.23
Signif.	***	***	N.S.	N.S.	N.S.	N.S.

RAKER BLADE WIDTH

	ARCH 1						ARCH 2						ARCH 3	ARCH 4
	U_2	U_1	L_1	L_2	L_3	L_{10}	U_2	U_1	L_1	L_2	L_3	L_{10}	L_2	L_2
CW	1.56	1.69	1.81	1.63	1.59	1.43	1.36	1.38	1.62	1.47	1.48	1.41	1.24	0.95
LY	1.63	1.76	1.83	1.70	1.66	1.63	1.43	1.50	1.73	1.61	1.58	1.68	1.35	1.05
't'	[1.02]	[0.85]	0.44	1.37	1.23	3.29	1.56	2.39	2.28	2.83	[1.67]	4.32	[1.58]	1.95
Signif.	N.S.	N.S.	N.S.	N.S.	N.S.	**	N.S.	*	*	**	N.S.	***	N.S.	N.S.

*** P <.001
** .01 - .001
* .05 - .01
N.S. >.05 (Not Significant)

[ ] = modified 't' test (Snedecor and Cochran 1967)

U_2 - L_{10} raker coding according to Fig. 5.

The distance covered by ten rakers along the lower arch (Table 1) is significantly greater for Clearwater fish than Lyons fish ($P<0.001$). As there are no significant differences in the thickness of the rakers (RBT and MRT, Table 3), the greater distance occupied by ten rakers in Clearwater fish must be a result of greater spacing between rakers. This method of comparing spacing provides a more accurate method than measuring distance with hand calipers between a single pair of rakers, a procedure which results in variation between readings with very slight changes in pressure against the rakers by the caliper points.

Table 2 gives means and 't' values for the raker lengths and base lengths of the fourteen rakers examined. All 't' values indicate significant differences between the means with the exception of the raker length of L_2 on the fourth gill arch. In most cases the differences are highly significant ($P<0.001$). This significance is confirmed by analysis of covariance on a limited amount of the data. 'F' ratios for the difference between adjusted means of fork length and raker length, and fork length and base length, are listed in Table 4. Thus, raker lengths, and also base lengths, differ significantly between the two samples, whether expressed in absolute measurements or as proportions of the body length.

Raker lengths and base lengths of each of the rakers U_2 to L_{10} are represented in Figures 13 & 14, following the method of Hubbs & Hubbs (1953), which compares the mean, range, standard deviation and standard error. For the first and second arches, all Lyons raker lengths have a greater standard deviation and range than the corresponding Clearwater values. Although the mean raker lengths are significantly longer for all

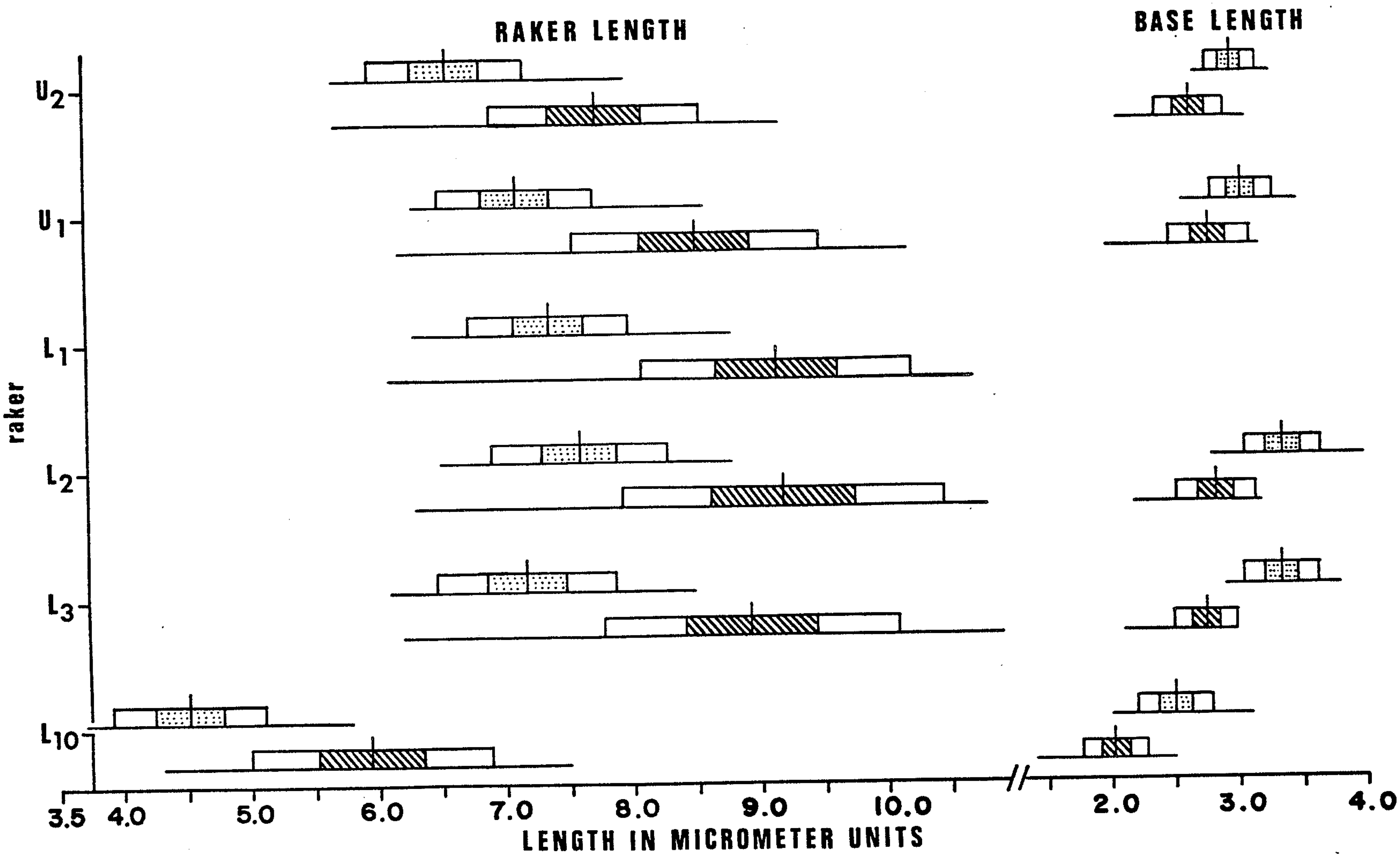
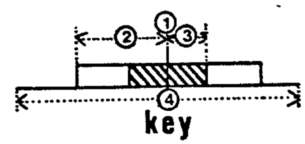


Fig. 13. Raker length and base length plots of gill rakers U_2-L_{10}, Arch 1, for Clearwater (stippled) and Lyons (hatched) fish. Key: 1) mean, 2) standard deviation, 3) two standard errors, 4) range. Method after Hubbs-Hubbs (1953). Raker coding according to Fig. 5.



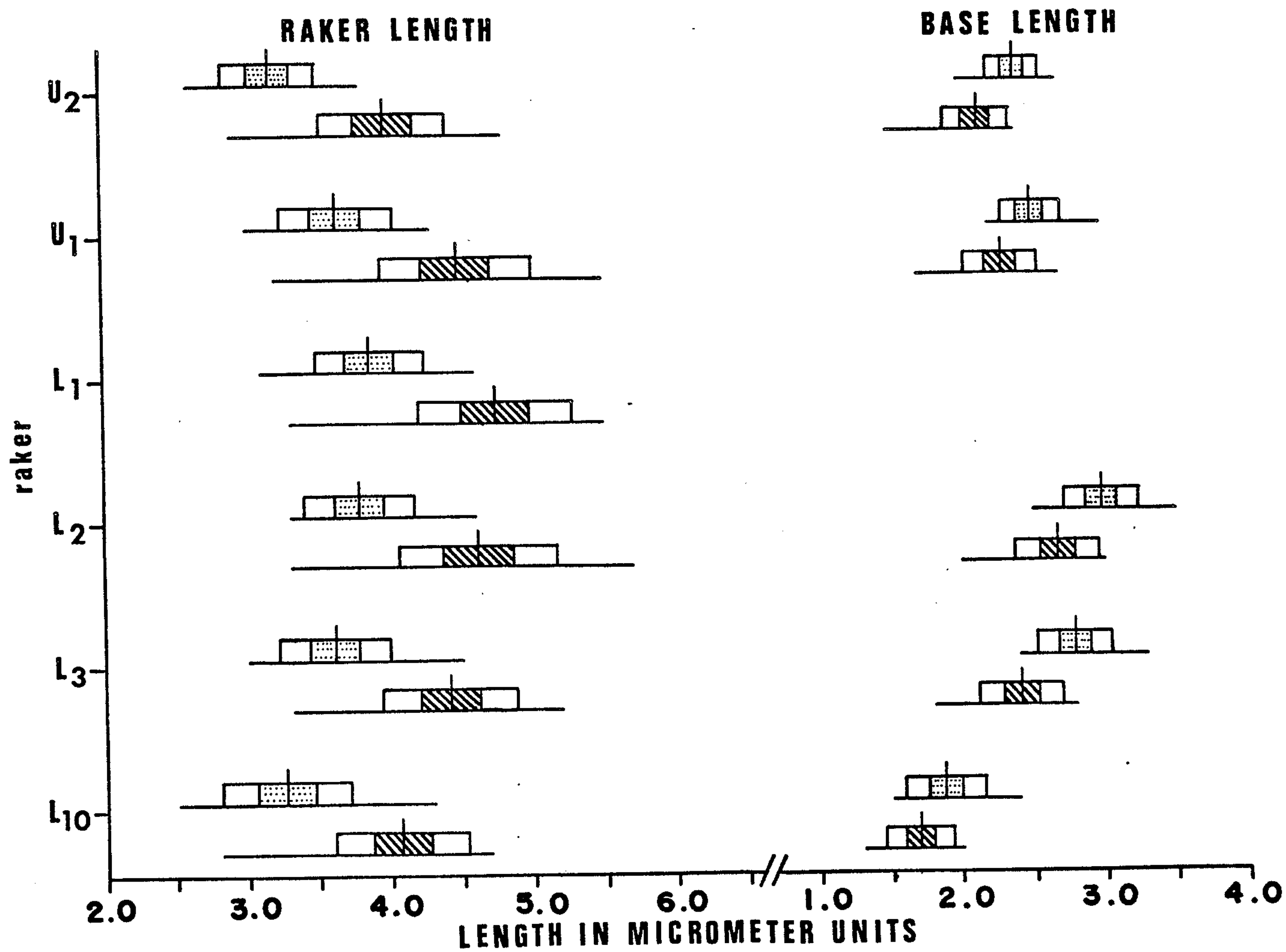


Fig. 14. Raker length and base length plots of gill rakers U_2-L_{10}, Arch 2, for Clearwater (stippled) and Lyons (hatched) fish. Method after Hubbs & Hubbs (1953); refer to Key, Fig. 13 , for interpretation. Raker coding according to Fig. 5.

TABLE 4. Analysis of Covariance of fork length to gill raker parameters between Clearwater (CW) and Lyons (LY) fish. 'F' values are for differences between adjusted means of fork length (FL) and raker length (RL), and fork length and base length (BL). Raker coding according to Fig. 5.

Significance *** = P<.001.

CLEARWATER & LYONS PARAMETERS	'F'	SIGNIFICANCE
FL and RL of U_2, Arch 1	39.97	***
FL and RL of L_2, Arch 1	46.04	***
FL and RL of L_{10}, Arch 1	37.58	***
FL and RL of L_2, Arch 2	64.13	***
FL and BL of L_2, Arch 1	30.38	***

the Lyons fish, the difference is not as great for the second as for the first arch. In addition, the ranges of the Lyons raker lengths are so great as to include the majority of the ranges for Clearwater lengths. A striking pattern exists regarding the position of the means on the range. In Lyons Lake almost all raker length means are located well to the right of the center of the ranges, while in Clearwater Lake they are located well to the left of the center of the ranges in all examples for the first arch, and three of the six examples in the second arch.

Base lengths have a similar pattern for the Lyons fish, with all the means located well to the right of center of the ranges. Clearwater base length means, however, are quite centrally positioned on the ranges.

Correlation of Values

Correlations were calculated to examine the relationship of raker length and base length, to head and fork length, for the two groups of fish. In particular, correlations between raker lengths of the first arch and head and fork length, are compared to correlations between raker lengths of the second arch and head and fork length for each group of fish. Lower correlations for the first arch than the second arch suggest environmental factors may have had a greater influence on the development of rakers of the first arch than those of the second arch.

Table 5 lists the 'r' values for correlation between fork length and raker length. In Lyons fish, correlations for lengths of all rakers on the second arch are greater than correlations for lengths of corresponding rakers on the first arch. All 'r' values are highly significant for Lyons rakers on both arches ($P<.001$) with the exception of L_{10} on the

TABLE 5. Correlation between fork length and raker length for Clearwater (CW) and Lyons (LY) fish.

	ARCH 1						ARCH 2						ARCH 3	ARCH 4
	U_2	U_1	L_1	L_2	L_3	L_{10}	U_2	U_1	L_1	L_2	L_3	L_{10}	L_2	L_2
CW	.15	.15	.10	.40	.15	.15	.39	.35	.12	.42	.56	.36	.68	-.01
Signif.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	*	N.S.	***	N.S.
LY	.65	.62	.75	.64	.68	.37	.69	.75	.77	.74	.73	.76	.71	.33
Signif.	**	**	***	**	***	N.S.	***	***	***	***	***	***	***	N.S.

TABLE 6. Correlation between head length and raker length for Clearwater (CW) and Lyons (LY) fish.

	ARCH 1						ARCH 2						ARCH 3	ARCH 4
	U_2	U_1	L_1	L_2	L_3	L_{10}	U_2	U_1	L_1	L_2	L_3	L_{10}	L_2	L_2
CW	.17	.16	.10	.34	.07	.18	.59	.51	.30	.49	.57	.52	.72	.00
Signif.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	**	*	N.S.	*	**	*	***	N.S.
LY	.79	.71	.85	.67	.78	.41	.79	.78	.80	.80	.78	.84	.77	.30
Signif.	***	***	***	**	***	N.S.	***	***	***	***	***	***	***	N.S.

*** P.<.001
** .01 - .001
* .05 - .01
N.S. >.05 (Not Significant)

U_2 - L_{10} raker coding according to Fig. 5.

P for correlation coefficient determined from Table V, p. 426, Simpson, Roe & Lewontin (1960).

first arch.

In Clearwater fish, most correlations are low. Correlation between fork length and raker length is significant at the 5% level only with raker L_3 of the second arch, and increases to the 0.1% level with raker L_2 of the third arch.

Table 6 indicates the 'r' values for correlation between head length and raker length. For almost all rakers, correlations with head length are higher than with fork length. Five of the six rakers on the second arch of Clearwater fish are now significant at the 5% level. However, none of the Clearwater rakers on the first arch approaches being significant.

Correlations between raker lengths on the first and the second arches are provided in Table 7. Five of the six Lyons values are significant at the 0.1% level and one at the 1% level; Clearwater figures are lower, with two of the six values significant at the 0.1% level, two significant at the 1% level, and one at the 5% level.

Correlations for Lyons fish between the base lengths and the head or fork lengths in Table 8 are higher than correlations between raker lengths and head lengths (Table 6). Correlations for Clearwater fish between the base lengths and the head or fork lengths (Table 8) are also higher than correlations between raker lengths and head lengths (for the first and second arch), with the values for L_2 significant at the 0.1% level. The Clearwater correlation between raker length and head length for L_2 of the first arch (Table 6) was not significant at the 5% level.

TABLE 7. Correlation between raker lengths on Arch 1 and raker lengths on Arch 2, for Clearwater (CW) and Lyons (LY) fish.

	RAKER					
	U_2	U_1	L_1	L_2	L_3	L_{10}
CW	.53 *	.56 **	.72 ***	.58 **	.38	.62 **
LY	.95 ***	.89 ***	.91 ***	.71 ***	.76 ***	.58 **

TABLE 8. Correlation between (1) head length (HL) and base length of raker L_2 (Arch 1), and (2) fork length (FL) and base length of raker L_2 (Arch 1), for Clearwater (CW) and Lyons (LY) fish.

		ARCH 1	ARCH 2	ARCH 3	ARCH 4
HL	CW	.64 **	.58 **	.48 *	.22
	LY	.80 ***	.92 ***	.81 ***	.41
FL	CW	.64 **	.61 **	.58 **	.23
	LY	.80 ***	.87 ***	.73 ***	.37

TABLE 9. Correlation between raker base lengths on Arch 1 and raker base lengths on Arch 2, for Clearwater (CW) and Lyons (LY) fish.

	RAKER	
	L_2	L_{10}
CW	.72 ***	.66 **
LY	.87 ***	.68 ***

*** P<.001
** .01 - .001
* .05 - .01
N.S. >.05 (Not Significant)

U_2 - L_{10} raker coding according to Fig. 5.

TABLE 10. Correlation between raker length and base length for rakers L_2 and L_{10} on Arches 1 and 2, Clearwater (CW) and Lyons (LY) fish.

	ARCH 1		ARCH 2	
	L_2	L_{10}	L_2	L_{10}
CW	.42	.26	.57 **	.08
LY	.50 *	.42	.79 ***	.59 **

TABLE 11. Correlations between characteristics of 8 Steeprock Lake whitefish (fork lengths 8.7-36.0 cm). Characteristics are head length (HL), fork length (FL), and raker length (RL).

CORRELATION BETWEEN	'r'	SIGNIFICANCE
HL and FL	.992	***
HL and RL	.987	***
FL and RL of L_2, Arch 1	.987	***
RL of L_2, Arch 1, and RL of L_2, Arch 2	.997	***

*** P.<.001
** .01 - .001
* .05 - .01
N.S. >.05 (Not Significant)

U_2 - L_{10} raker coding according to Fig. 5

In fish from both lakes, correlations between base lengths on the first and the second arch (Table 9) are higher than those for the corresponding raker lengths (Table 7). The 'r' values of Table 9 are significant to at least the 1% level.

Correlations between raker length and base length (Table 10) are higher in Lyons than in Clearwater fish, and higher for the second arch than for the first (except for L_{10} of Clearwater which is not significant at the 5% level for either the first or second arches).

In order to check the raker length relationship in a wide size range of whitefish, eight specimens from Steep Rock Lake (fork lengths 8.7-36.0 cm) provided the data for the correlations in Table 11. All the 'r' values are significant at the 0.1% level, and the results are in closer agreement with Lyons than with Clearwater fish. Steep Rock data is also included in the Appendix.

The main results that have emerged from correlation treatment are:

1. The considerable difference between the two groups of fish in correlation between raker lengths of the first arch and head lengths. There was no significant correlation at the 5% level for the Clearwater fish.
2. The higher correlation between raker length and head length for rakers on the second arch than on the first arch, in both groups of fish.
3. The highest correlation between raker length and head length for Clearwater fish was for raker L_2 on the third arch.
4. Correlations between base length and head length were generally

higher than between raker length and head length. For Clearwater fish, there was correlation between base length and head length at the 1% level for the first arch, while there was no significant correlation for raker length to head length for this arch.

Raker Teeth

Raker teeth are very numerous on all the anterior rakers of Lyons fish, and although less numerous on Clearwater fish, they are still abundant. Figure 15 illustrates the variations that can occur in raker teeth. Tooth attachment is not rigid; a gap in the bone occurs between the tooth and its socket (Fig. 16), which is presumably occupied by fibrous connective tissue (see Histology Results).

The teeth are located along the leading edge of the raker blade, but do not extend to the tip of the raker (Fig. 7). Figure 17 illustrates the extent of raker teeth occurrence along rakers of the first two arches. The raker teeth in both groups of fish extend closer to the tip on the 'A' side of the blade, which would be most frequently in contact with incoming food or other particulate matter. However, the teeth extend closer to the tip on 'A' and 'P' sides for Lyons fish than Clearwater fish, on all the rakers for both arches. It is assumed some interdigitation would occur between the teeth of adjacent rakers, such as 'A' side of L_2 and 'P' side of L_3.

The total numbers of teeth are considerably higher on all the rakers of Lyons fish, usually at least twice the number found on Clearwater fish. This is mainly the result of a larger portion of the (longer) Lyons raker possessing teeth (Fig. 7). An additional factor is

Fig. 15.

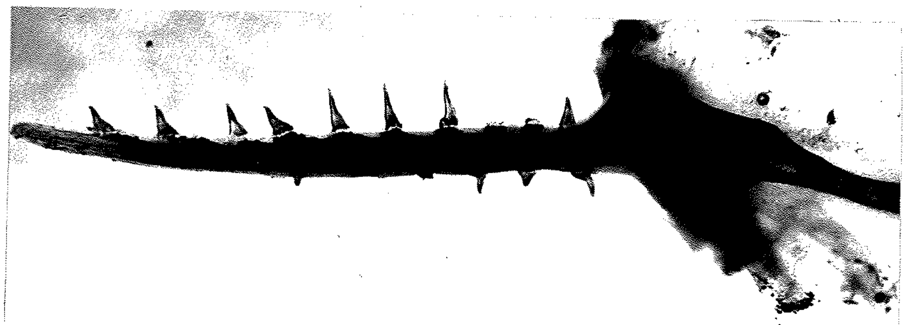


Fig. 16.

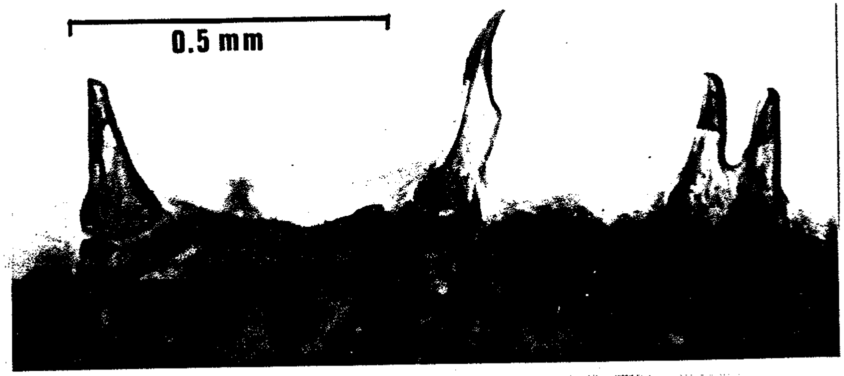


Fig. 15. Variations in raker tooth structure. Lyons specimen, raker L_{10} of the first right gill arch.

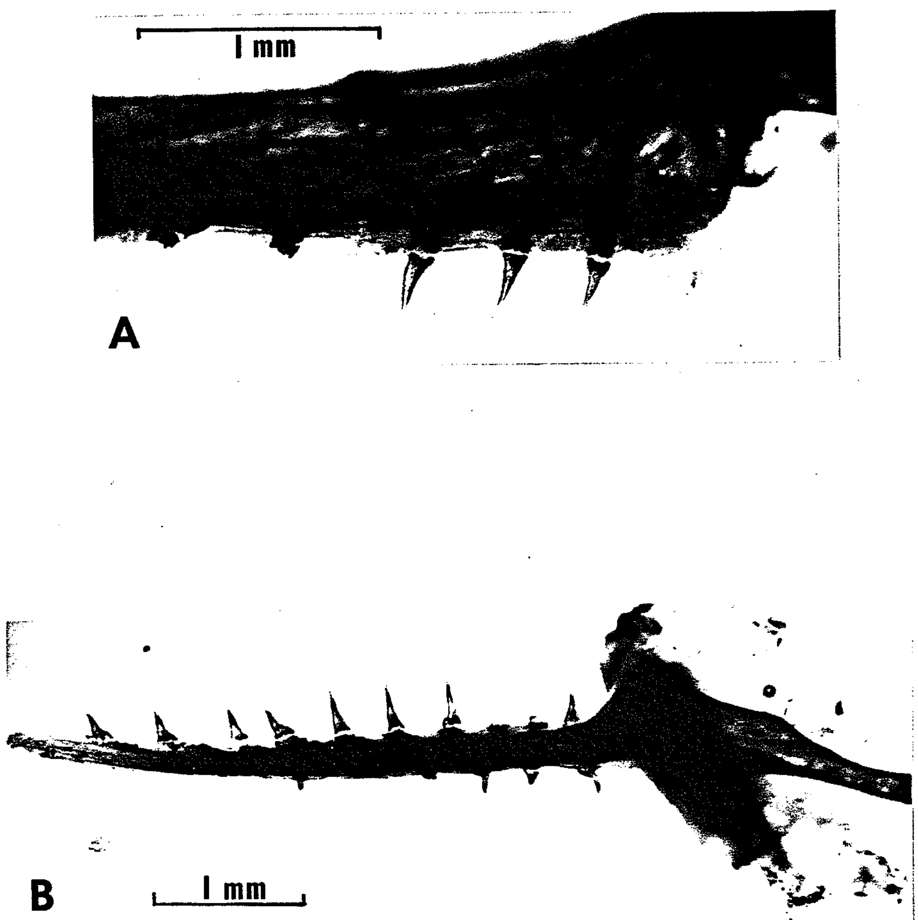


Fig. 16. Raker tooth attachment. Space between tooth and socket indicates bone is not continuous.

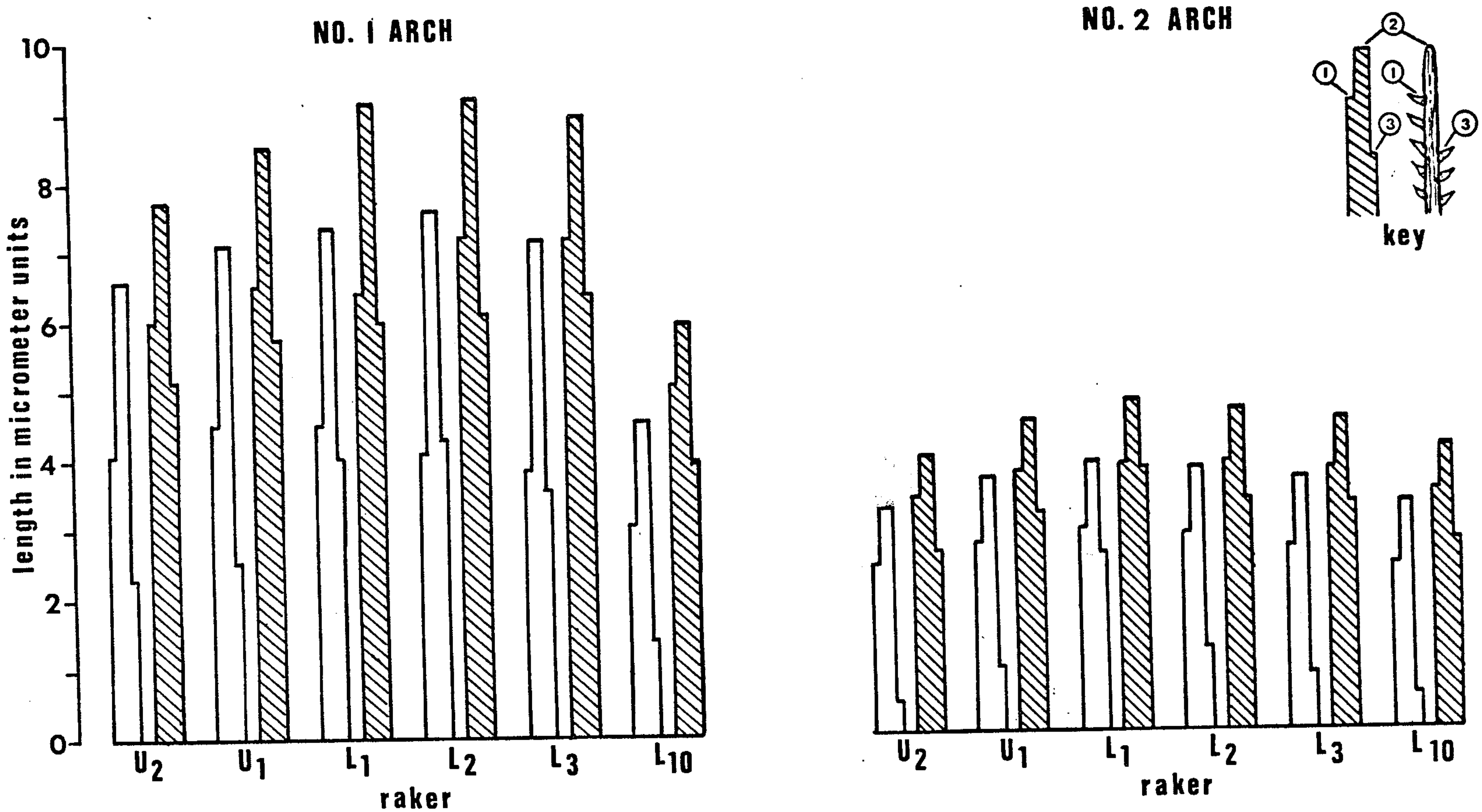


Fig. 17. Extent of raker teeth occurrence along rakers U_2-L_{10}, Arches 1 & 2, for Clearwater (clear) & Lyons (hatched) fish. Key: 1) position of most distal tooth on 'A' side of raker, 2) length of raker, 3) position of most distal tooth on 'P' side of raker. Raker coding according to Fig. 5.

spacing of the teeth on the raker.

The numbers of teeth on opposite sides of each raker were compared by expressing the values as a ratio of the mean number of teeth on 'P' side to the mean number on 'A' side. This method eliminates the effect of the longer Lyons rakers. A ratio of 0.5 indicates there are only half as many teeth on 'P' side as 'A' side, and 1.0 indicates there is an equal number of teeth on both sides, regardless of the absolute number of teeth. Figure 18 illustrates this comparison. There is a considerable decrease in the number of teeth on the 'P' side compared to 'A', for the second arch of the Clearwater fish. Lyons fish maintain a high number of teeth on the 'P' side of rakers of the second arch. Actual values of teeth totals and ratios are included in the Appendix.

Spacing of raker teeth along the forward edge of the blade was determined by an indirect method. The distance occupied by the teeth, (RL)-(D/T-A) and (RL)-(D/T-P), was divided by the number of teeth on the 'A' and 'P' sides, respectively. The value obtained represents the tooth interval (TI), which is the mean distance occupied by one tooth and the adjacent space. Figure 6 illustrates these parameters. Values were determined for 'A' and 'P' sides of rakers which possess at least two teeth.

Figure 19 illustrates the tooth interval for 'A' and 'P' sides of the rakers of the first two arches for both groups of fish. The mean spacing values for Lyons fish are fairly uniform for all the rakers examined, and considerably less than the values for Clearwater fish. Values for 'A' side are similar to those for 'P' side, for Lyons fish,

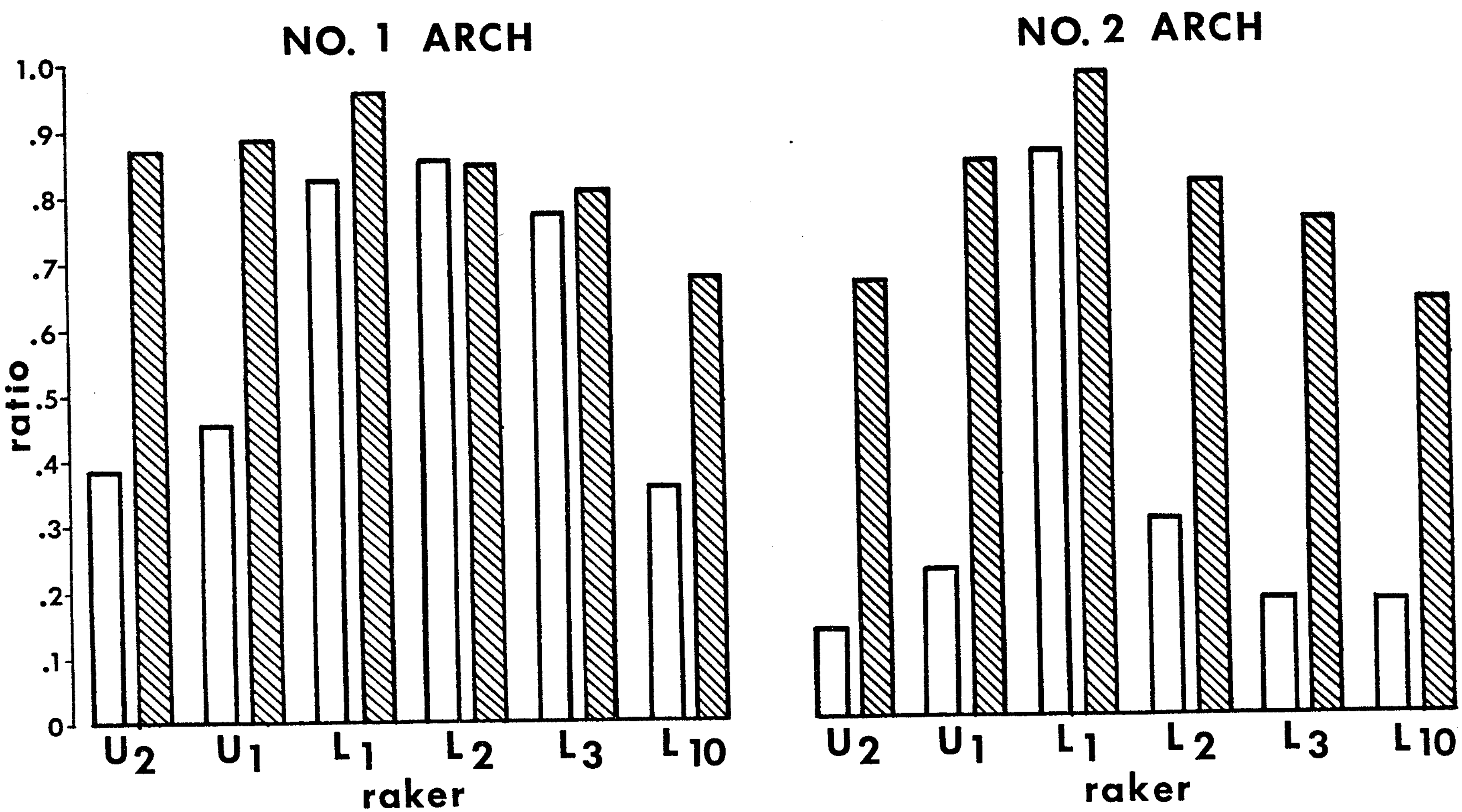


Fig. 18. Ratio of mean number of teeth on 'P' side of raker to mean number of teeth on 'A' side, Arches 1 & 2, for Clearwater (clear) & Lyons (hatched) fish. Raker coding according to Fig. 5.

but a considerable disparity exists between 'A' and 'P' values for the Clearwater fish. Tables of teeth totals and mean spacing values are included in the Appendix.

Examples of socket patterns are illustrated in Figures 20 & 21, and described in the Appendix. Table 12 summarizes the occurrence of straight and curved socket succession patterns on the 'A' side of the rakers. Over one half of the Clearwater rakers examined had straight succession patterns, while approximately one quarter of the Lyons patterns were straight. There appears to be a tendency for straight succession patterns to diverge as they approach the forward edge of the blade. This indicates that as the gill raker increases in length, the distance between adjacent teeth also increases. The curved socket pattern which is more common for Lyons fish indicates the distance between adjacent teeth tends to be more uniform as the raker increases in length.

The socket patterns indicate the tooth spacing in the past. Presumably this spacing was an adaptation to diet at that time. Figures 20 & 21 provide examples of socket pattern details.

Socket counts for the longest succession pattern on the 'A' side of the rakers are significantly higher in Clearwater than in Lyons fish ('t' test, $P<.05$). Table 13 summarizes the data. The mean socket counts for Clearwater and Lyons fish are 9.71 and 9.08, respectively. The distinctiveness of the sockets varied, some being clearly discernible while others were difficult to distinguish even under 50X magnification.

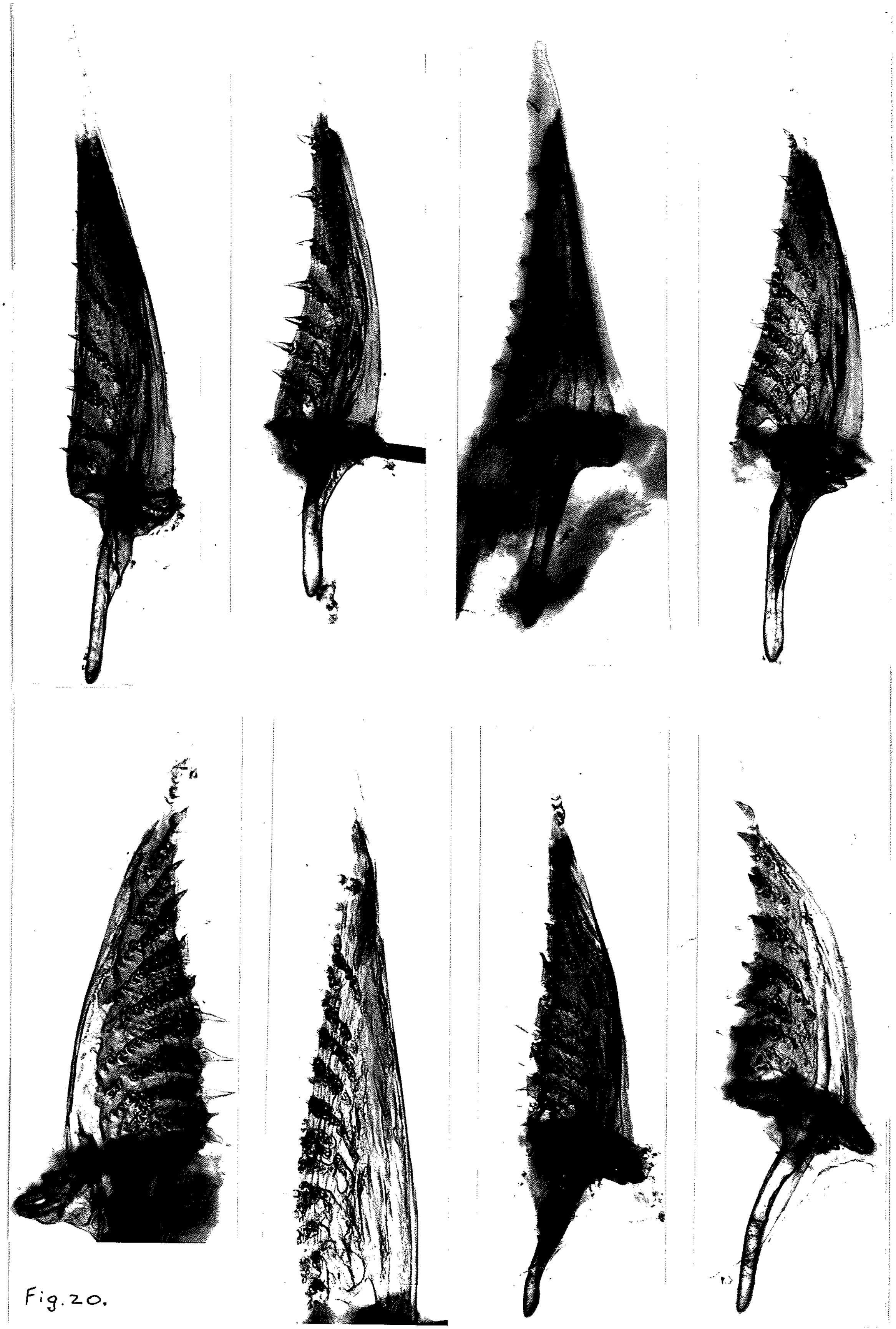


Fig. 20.

Fig. 20. Socket succession patterns on Clearwater (A - D) and Lyons (E - H) rakers. Examples A & B have straight succession patterns, C retains its layer of stratified squamous tissue, and D has some curved patterns in the lower portion of the blade. E, F, G and H all have predominately curved patterns, but the most distal patterns are straight. Lower patterns in E have curved and become parallel to the raker base and lower patterns in H have reversed direction from towards the tip to the base. G has strong linear patterns in the distal half of the blade, but this increase in spacing has been compensated by the appearance of an additional tooth at (a). In some photographs (i. e. F), teeth on both the 'A' and 'P' sides are visible, and make it difficult to locate the correct tooth for a particular socket pattern. This difficulty does not exist when rakers are viewed through a stereomicroscope. Raker identification follows: A, U_1; B, U_2; C, U_1; D, U_2; E, L_2; F, L_1; G, U_2; H, U_2. All rakers are from the first arch, with the exception of E & H from the second arch. The anterior side of the blade is illustrated in all examples except F. The indicated scale is 1 mm. All rakers are at the same magnification except for E and H.

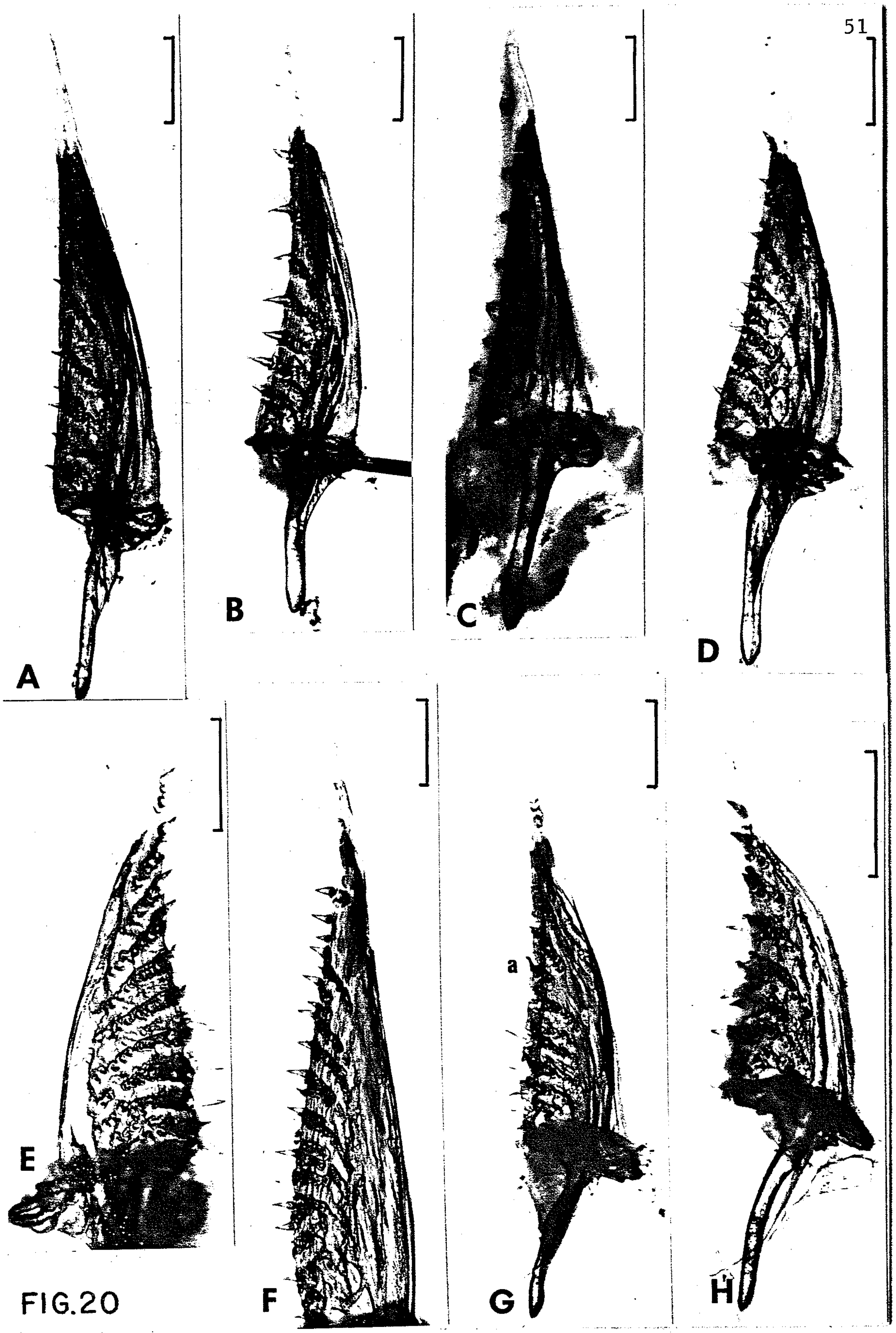


FIG.20

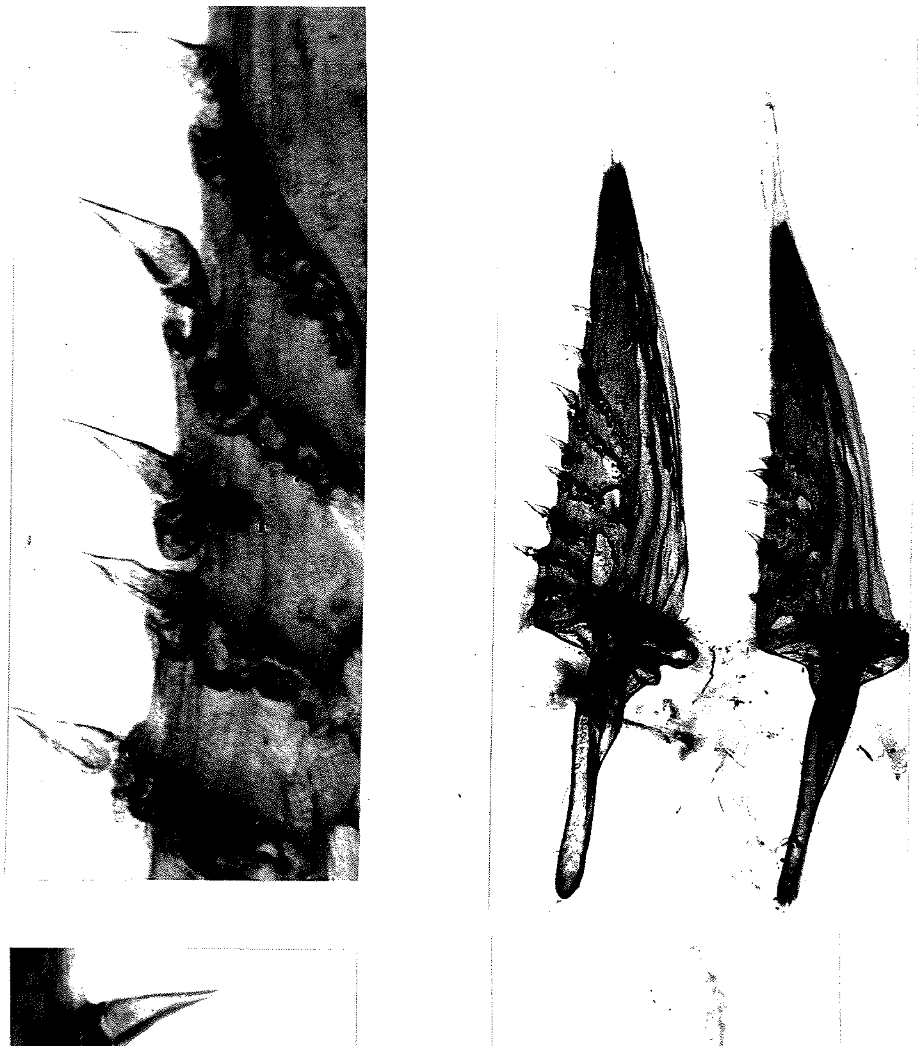


Fig. 21.

Fig. 21. Socket succession patterns on Clearwater (A, B & C) and Lyons (D) rakers. A illustrates a sudden increase in pattern slope with the addition of a tooth at (a), for raker U_1 on the first arch. B compares this raker with its adjacent one, U_2. A similar inflection has occurred in the socket pattern of U_2, with the addition of a new tooth. Socket patterns may converge on a single tooth, indicating a reduction in the number of teeth; (b) in example C (L_1 of Arch 1) and in D (L_2 of Arch 3). Indicated scale is 0.5 mm for A and C; 1 mm for B and D.

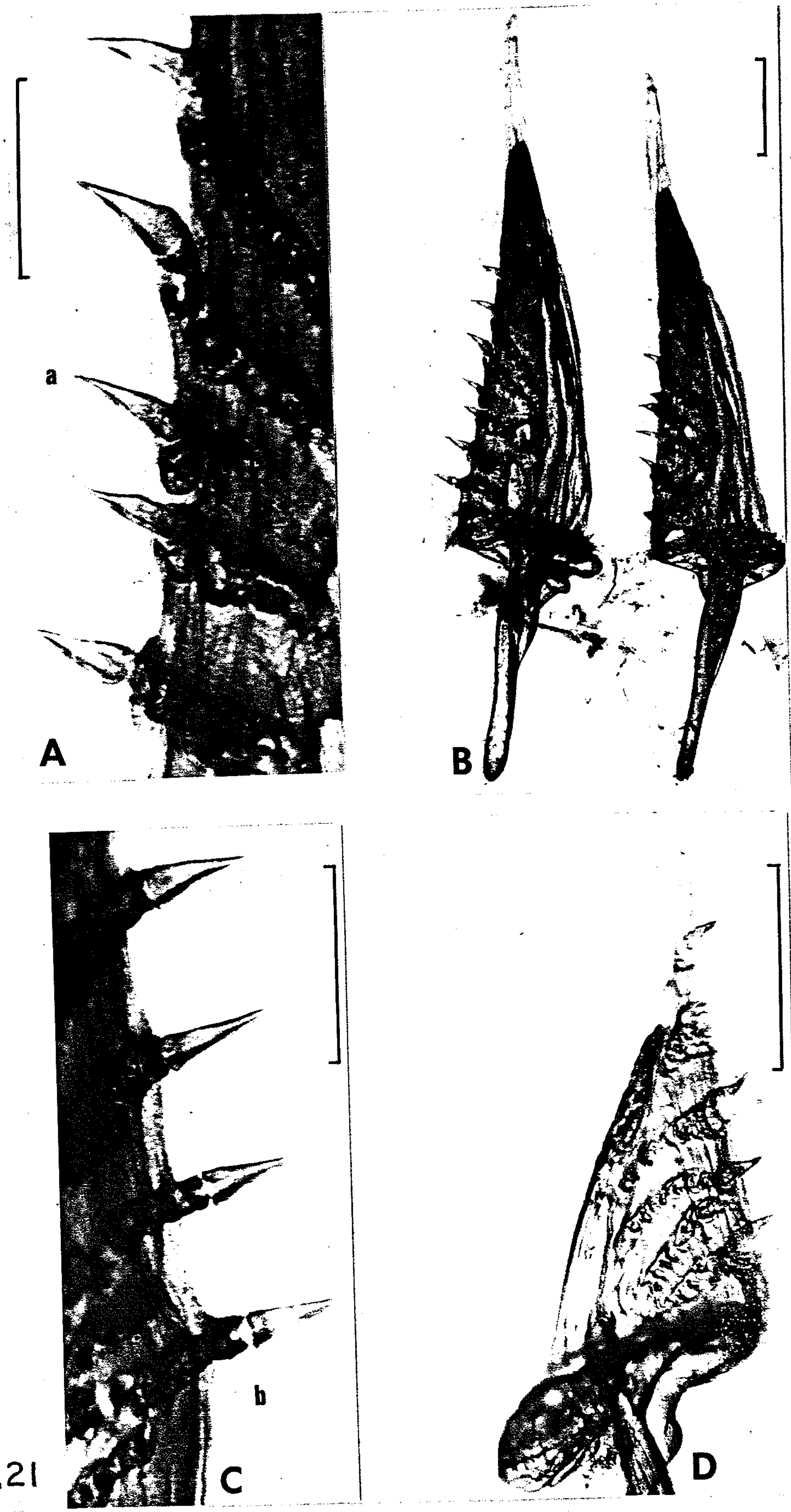


FIG.21

TABLE 12. Socket succession patterns (SSP) for 'A' side of rakers, Classified as straight (S) or curved (C). Examples in Figs. 20 and 21. Results are from approximately 100 rakers from each group of seven Clearwater (CW) and seven Lyons (LY) whitefish. Criteria in Appendix.

	ARCH 1		ARCH 2		ARCHES 3 & 4		TOTAL	
SSP	S	C	S	C	S	C	S	C
CW	30	12	20	22	10	2	60 (62.5%)	36 (37.5%)
LY	13	29	6	36	6	7	25 (25.8%)	72 (74.2%)

TABLE 13. Mean socket counts for longest socket succession pattern on 'A' side of rakers. Results are from the same rakers examined in Table 12. Criteria described in Appendix. Significant difference between Clearwater (CW) and Lyons (LY) means (* = P<.05).

	ARCH 1	ARCH 2	ARCHES 3 & 4	TOTAL *
CW	9.62	10.05	9.08	9.71
LY	9.14	9.17	8.77	9.08

The higher socket count in Clearwater fish appears compatible with the succession patterns. A row of raker teeth progressing on a straight pattern would require more replacements to maintain an edge position than a row of teeth following a curved pattern. Figure 20 illustrates examples of socket patterns and the apparently greater distance between some Clearwater sockets on a particular succession pattern.

A fish restricted to a microphagous diet would have an improved food gathering capacity if it possessed long rakers and many closely spaced teeth on both sides of the blade, both of which characteristics were found in Lyons fish.

Posterior Rakers

Posterior gill rakers are present on the upper portions of the first three arches and on the lower portions of all four gill arches of Clearwater and Lyons fish. The posterior rakers on the first arch are narrow, and not as well developed as those on the remaining arches (Fig. 22). The posterior rakers were counted and examined for the presence of teeth on all four left arches on ten Lyons and fourteen Clearwater fish. Mean counts of posterior rakers on the upper and lower portions of each arch are indicated in Table 14.

Figure 23 provides a general size relationship between anterior and posterior rakers of all four arches. Figure 24 illustrates the degree of interdigitation of the posterior and anterior rakers of adjacent arches.

Posterior rakers in Clearwater fish were found to have higher counts than Lyons fish, mainly due to the incidence of extra or accessory rakers

TABLE 14. Mean counts of posterior rakers for Clearwater (CW), (n = 14) and Lyons (LY) fish (n = 10), by upper (U), lower (L) & total (T) counts for each arch.

	ARCH 1			ARCH 2			ARCH 3			ARCH 4			TOTAL		
	U	L	T	U	L	T	U	L	T	U	L	T	U	L	T
CW	8.6	18.8	27.4	9.2	15.6	24.8	6.7	13.1	19.8	-	14.5	14.5	24.5	62.0	86.5
LY	8.7	16.1	24.8	8.8	14.5	23.3	6.8	12.2	19.0	-	12.6	12.6	24.3	55.4	79.7

TABLE 15. Percent of posterior rakers bearing teeth for Clearwater (CW) (n - 14) and Lyons (LY) fish (n = 10), by upper (U), lower (L) and total (T) arch.

	ARCH 1			ARCH 2			ARCH 3			ARCH 4			TOTAL		
	U	L	T	U	L	T	U	L	T	U	L	T	U	L	T
CW	0	0	0	0	0	0	0	0	0	-	2.0	2.0	0	0.5	0.3
LY	19.5	23.6	22.2	38.6	51.0	46.4	30.9	47.5	41.6	-	38.9	38.9	29.6	39.5	36.5

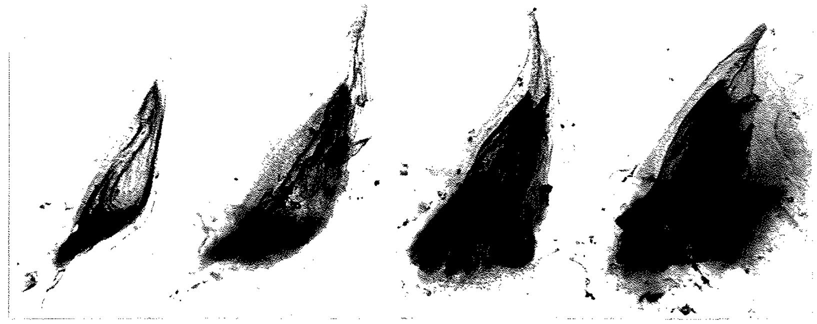


Fig. 22.

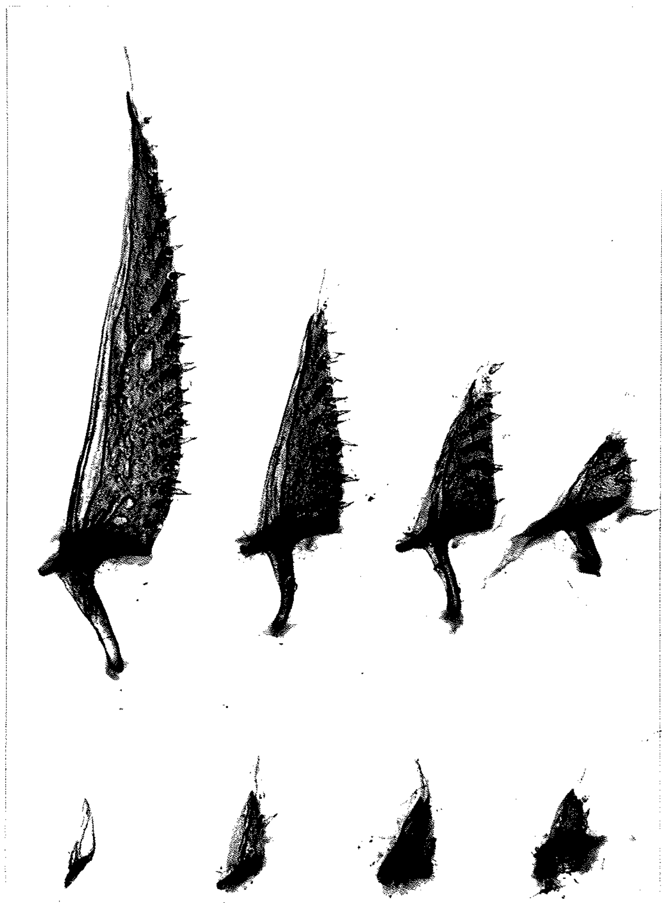


Fig. 23.

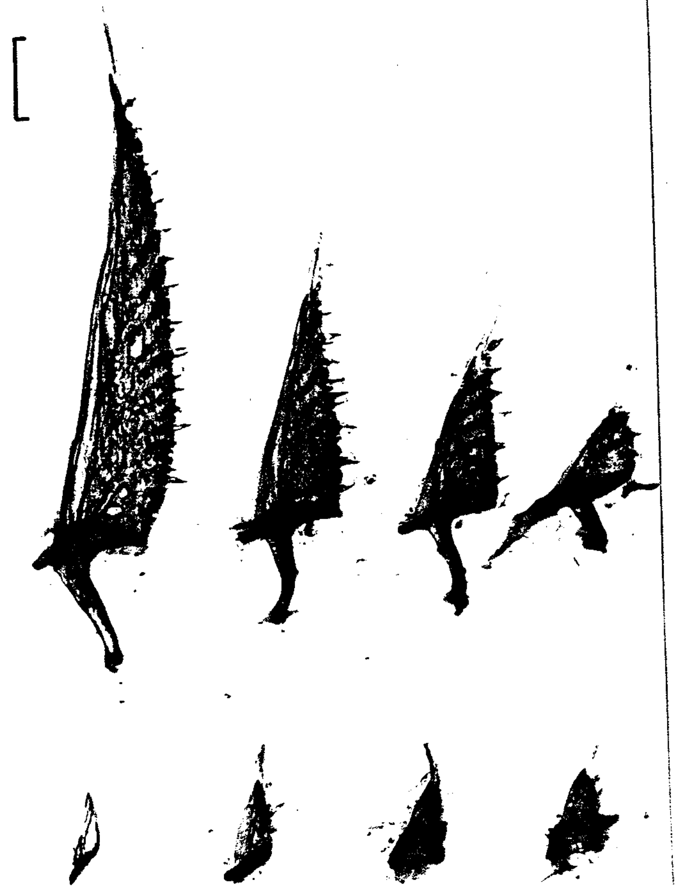


Fig. 23. Anterior Lyons rakers (L_3 from Arches 1 - 4) compared to posterior rakers which occupy a similar position on each arch. Longest anterior raker (top row) is from the first arch; shortest anterior raker is from the fourth arch. Posterior rakers on bottom row. Indicated scale 1 mm.

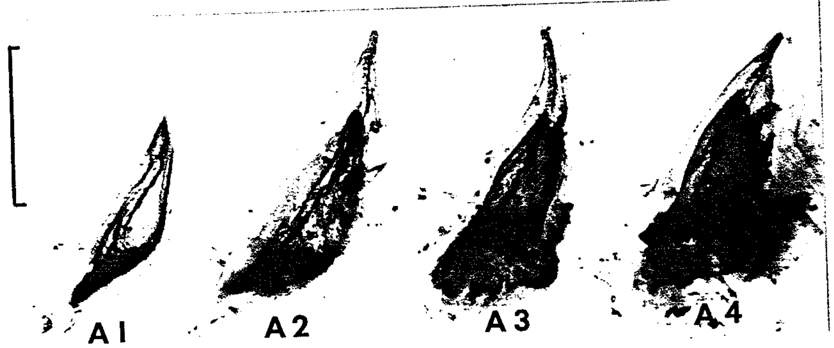


Fig. 22. Posterior rakers of Lyons whitefish from gill arches (A) 1 to (A) 4, which occupy a similar position on each arch. Indicated scale 1 mm.

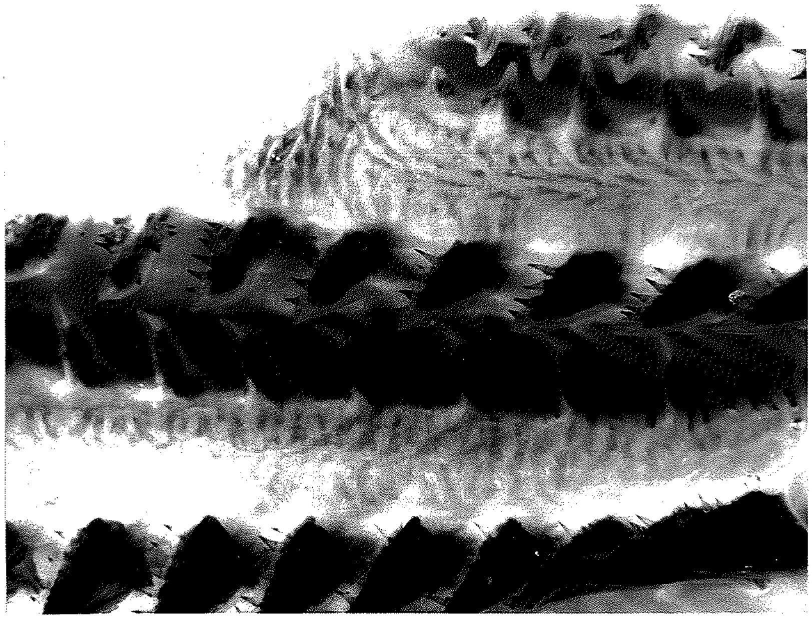


Fig. 24.

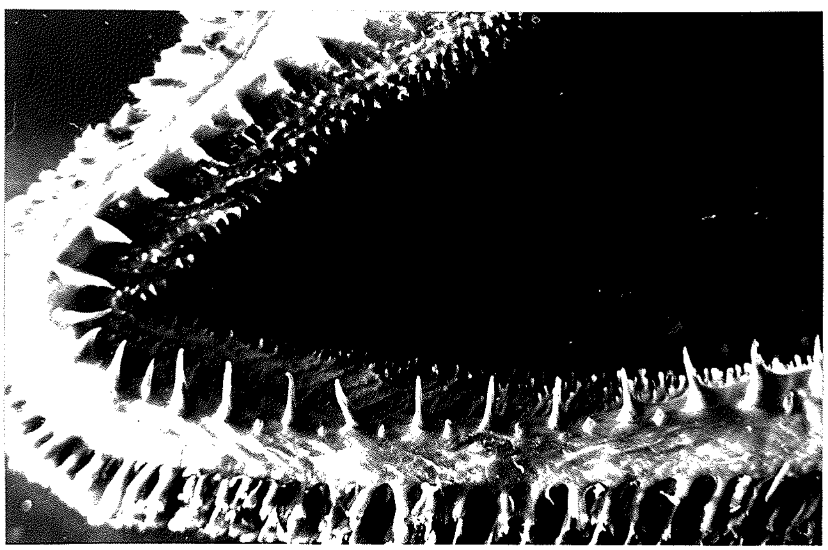


Fig. 25.

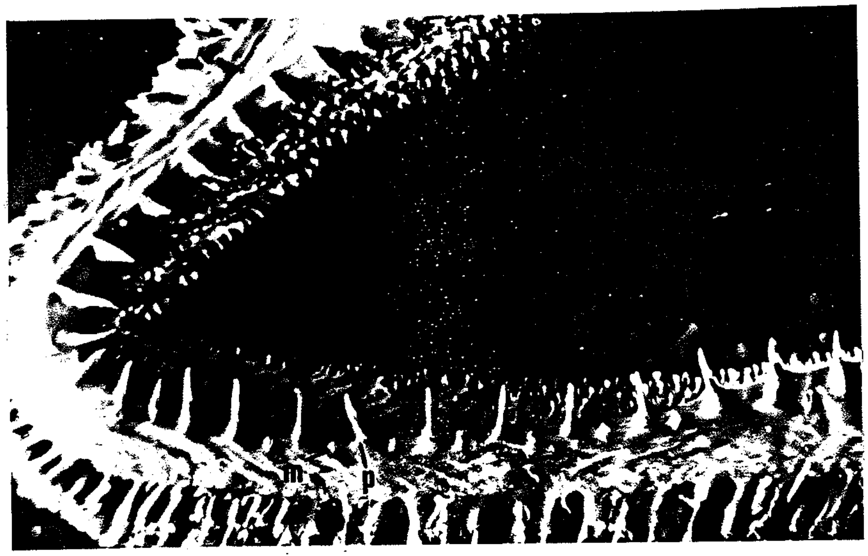


Fig. 25. Rudimentary accessory rakers (m) between posterior rakers (p) of first gill arch of Clearwater fish.

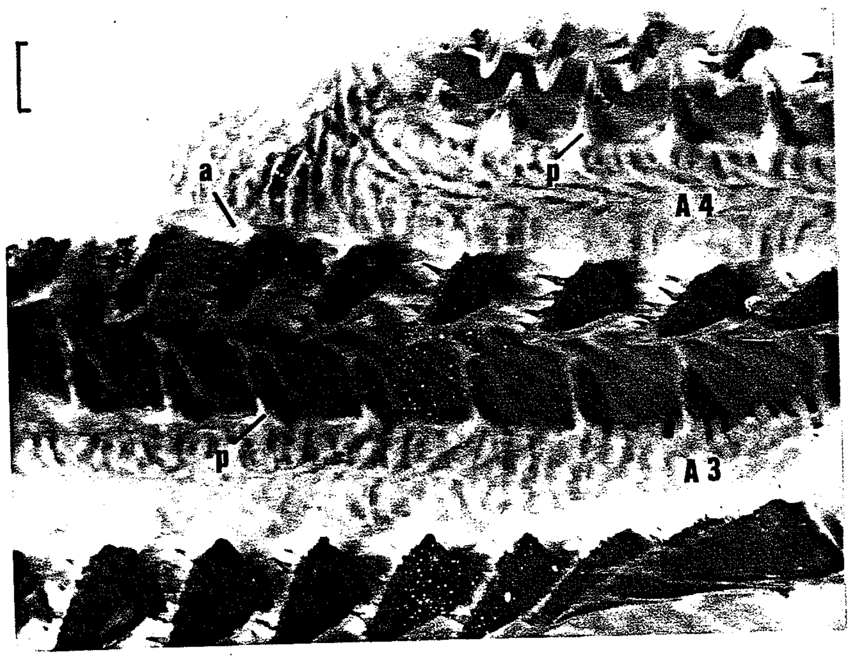


Fig. 24. Interdigitation between posterior rakers (p) on third arch (A3) and anterior rakers (a) on fourth arch (A4) of Lyons fish. Indicated scale 1 mm.

between the main posterior rakers of the lower portion of the arch. These accessory rakers are small and poorly developed (Fig. 25).

There is a sharp contrast in the occurrence of teeth on posterior rakers between the two groups of fish. All Lyons fish had teeth on some posterior rakers. The number of posterior rakers with one or more teeth that each Lyons fish possessed ranged from 4 to 62 rakers, for the 10 specimens examined. This represents 3.8% to 80.5% of all the posterior rakers of these fish. Approximately 800 Lyons posterior rakers were examined, and 36.5% possessed one or more teeth. Table 15 indicates the percent of posterior rakers bearing any teeth for the upper and lower portions of each arch. For Lyons fish, there are only about half as many posterior rakers bearing teeth on the first arch as there are bearing teeth on each of the remaining arches (Table 15). Some of the Lyons posterior rakers possess as many as four or five teeth, which considerably improve the "net" formed by the adjacent rows of rakers.

Teeth on the posterior rakers of Clearwater fish are rare. Only three of the fourteen specimens had one or more posterior rakers with a single tooth. Two fish had a single raker with one tooth, and a third fish had two rakers with a single tooth. The occurrence of teeth for all the posterior rakers examined (approximately 1200) on Clearwater fish was only 0.3% (Table 15).

HISTOLOGY

Identification of histological elements was assisted by the following references: Andrew & Hickman 1974; Bloom & Fawcett 1962; Di Fiore 1963; Freeman & Bracegirdle 1967.

Whitefish gill rakers were found to contain a matrix of dermal bone with a hollow core. This is surrounded by a layer of loose connective tissue, which is then followed by an outer layer of stratified squamous. The stratified squamous contains taste buds and mucous cells.

The dermal bone matrix of the raker is arranged as a double-sided blade, open to the forward edge, and closed at the opposite edge. A thin portion of blade extends out from the closed edge of the raker matrix. In transverse section, the matrix is in the shape of a tuning fork (Figs. 26 A, B, C & D). Figures 26 B & D illustrate the persistence of this double-sided pattern along the length of the raker blade of adult and fry whitefish. Raker teeth emerge from the forward edge of the raker blade, and previous sockets are retained (Figs. 26 A, B & C).

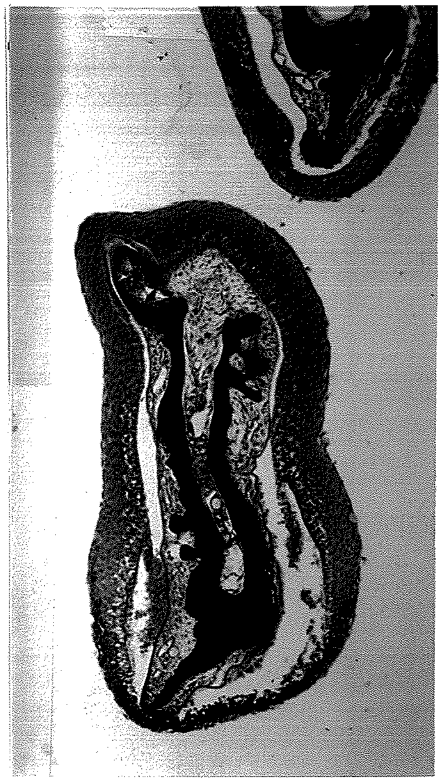
The hollow central region contains loose connective tissue, blood vessels, and small nerve fiber bundles (Figs. 26 A, B & C; Figs. 28 A & E), protected by this bone channel. The nerves are assumed to be involved in sensory functions as the rakers possess taste buds. The hollow core of the matrix is continuous through tooth sockets (Fig. 28 D) and raker teeth (Fig. 28 C). Tooth development is illustrated in Figure 28 B.

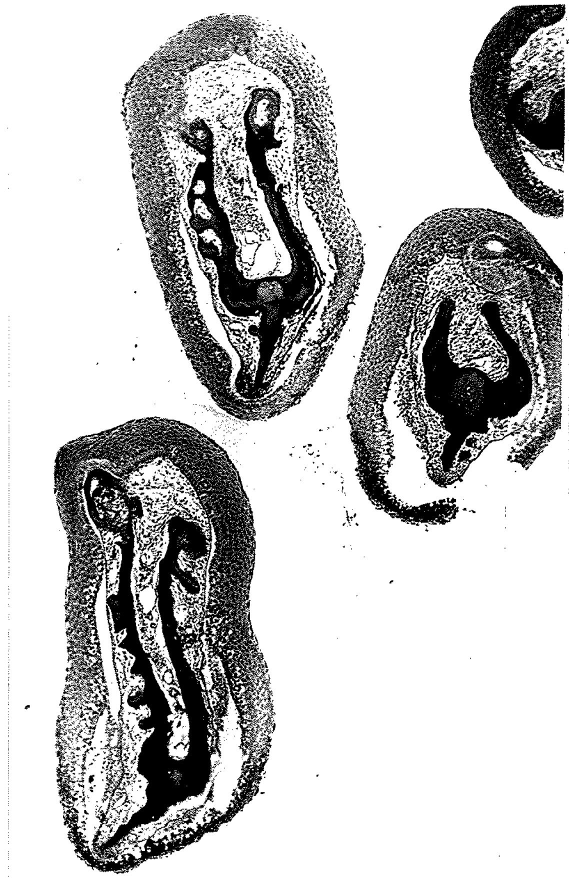
Taste buds are very abundant along the forward edge (Fig. 27 G) and distal end (Fig. 27 C) of the whitefish gill raker. The taste buds are bulbiform, with a tapering long axis of sensory cells extending to the surface of the stratified squamous. These sensory cells possess basal nuclei (Figs. 27 B & F) and appear to be ringed by support cells (Figs. 27 C & E). Figure 27 D illustrates the tip of a bud at the epithelial surface. No sensory hairs were detected on the taste buds, although these may have been present, but torn off or damaged during histological procedures.

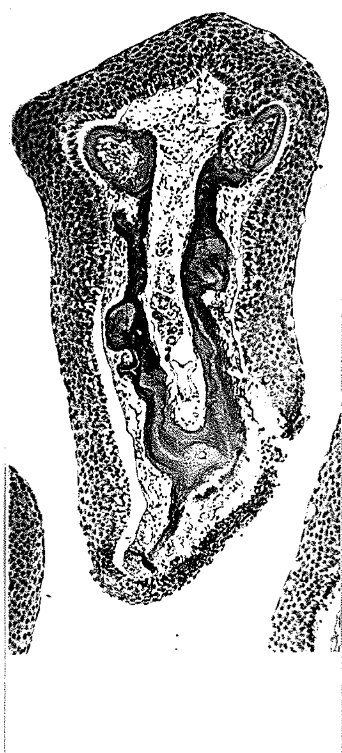
Iwai (1964) conducted a comparative study on gill raker taste buds of 24 species of fish, and describes two types of taste buds; those with short sensory hairs on the distal edges, and those without sensory hairs. He reports that size and shape of buds are closely related to the thickness of the epithelial layer. This study found that the forward edge of a whitefish raker generally has the thickest epithelium (Figs. 26 A, B, C & D) and that this region is abundantly provided with taste buds (Fig. 27 G).

Papillary eminences of connective tissue appear to contact the base of taste buds, and an extension from the eminences may contain a nerve fiber which enters the bud. When the stratified squamous of an intact raker is removed, papillary eminences with fine 'hairs' are prominent along the forward edge of the blade (Figure 26 E). These can be identified in longitudinal section in Figures 26 B, C and 28 C.

Histological results indicate whitefish gill rakers possess a sensory system. The abundance of structures which resemble taste buds suggest a gustatory function.







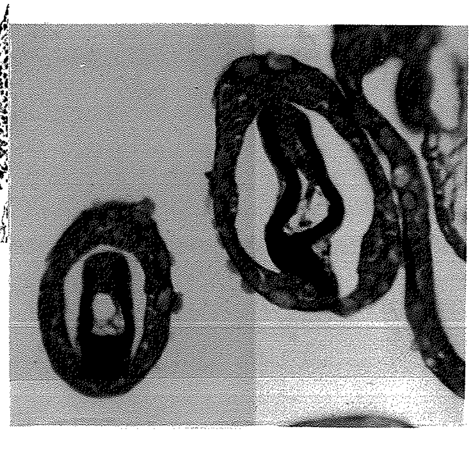


Fig. 26.

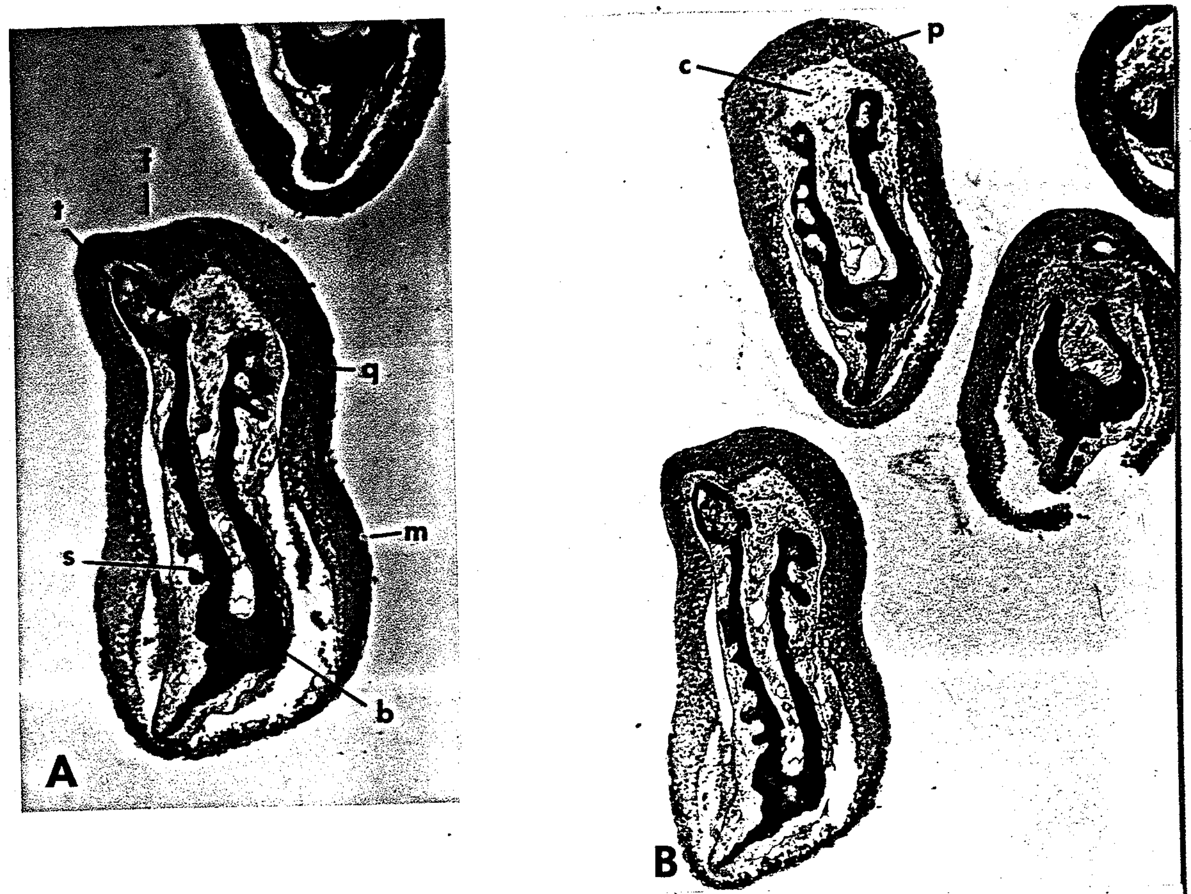


FIG. 26

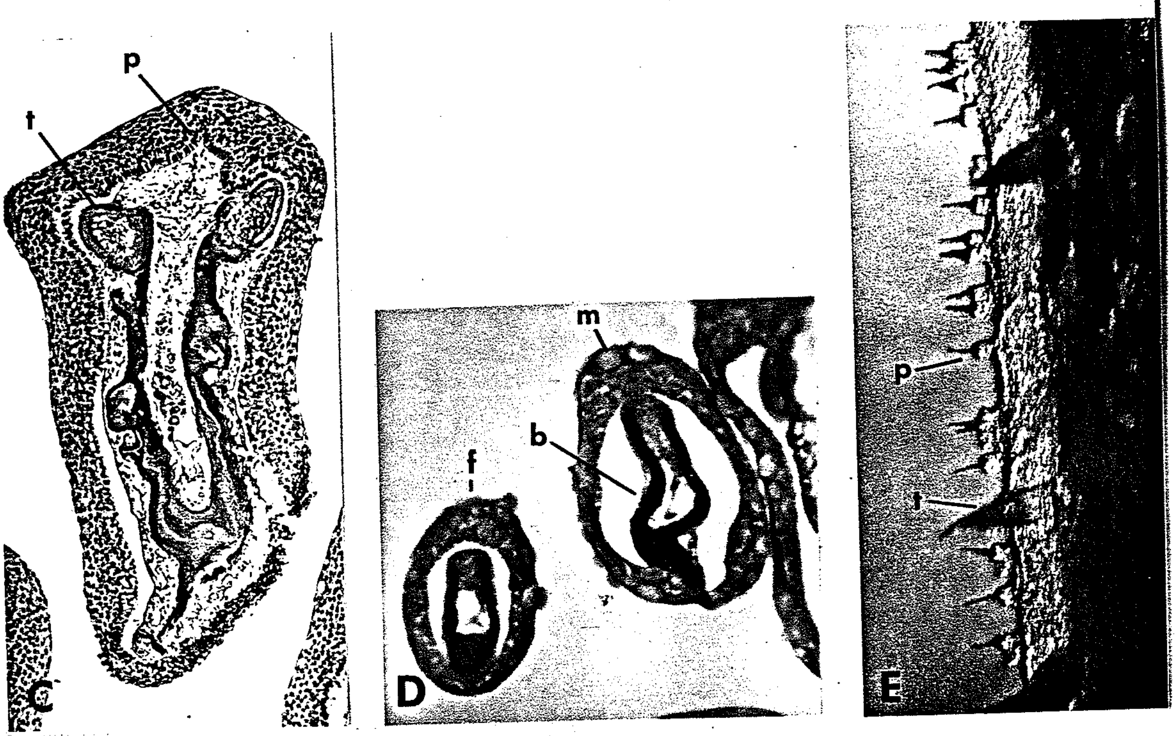


Fig. 26. A, transverse section (ts) of adult gill raker, Mallory's triple stain (mts). B, ts of 4 gill rakers at different levels along blade. The smallest raker section is most distal along the blade (mts). C, ts of raker (mts). D, ts of whitefish fry gill rakers, Koneef's stain (ks). E, forward edge (f) of intact raker with stratified squamous (q) removed, alizarin stained.

Additional abbreviations for Figs. 26, 27, & 28: b, bone matrix; c, loose connective tissue; d, taste bud; dt, developing tooth; m, mucous cell; n, nerve fiber; nb, nerve bundle; p, papillary eminences; s, socket; sc, sensory cells; se, sensory cell endings; ss, support cells; t, tooth; v, blood vessels.

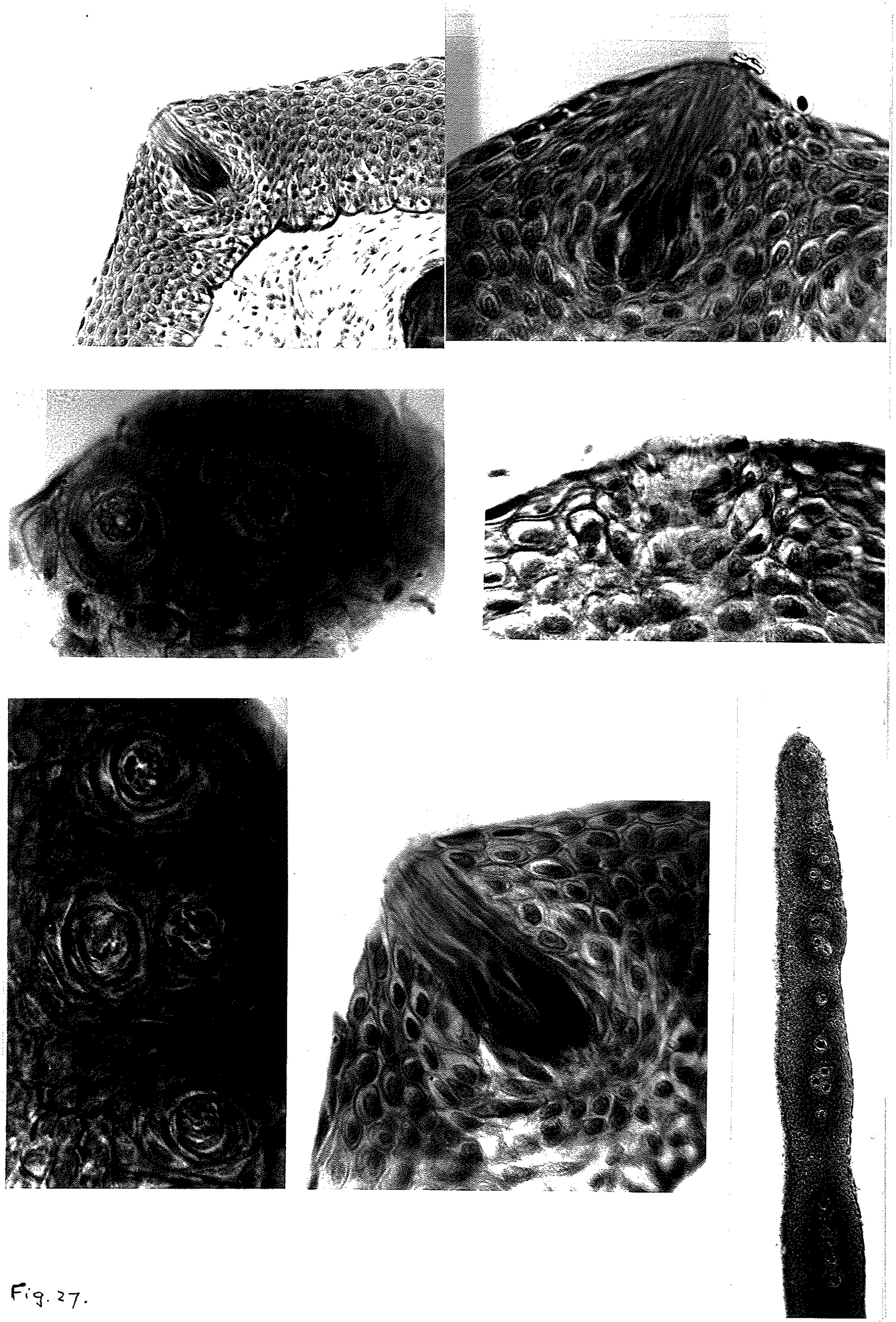


Fig. 27.

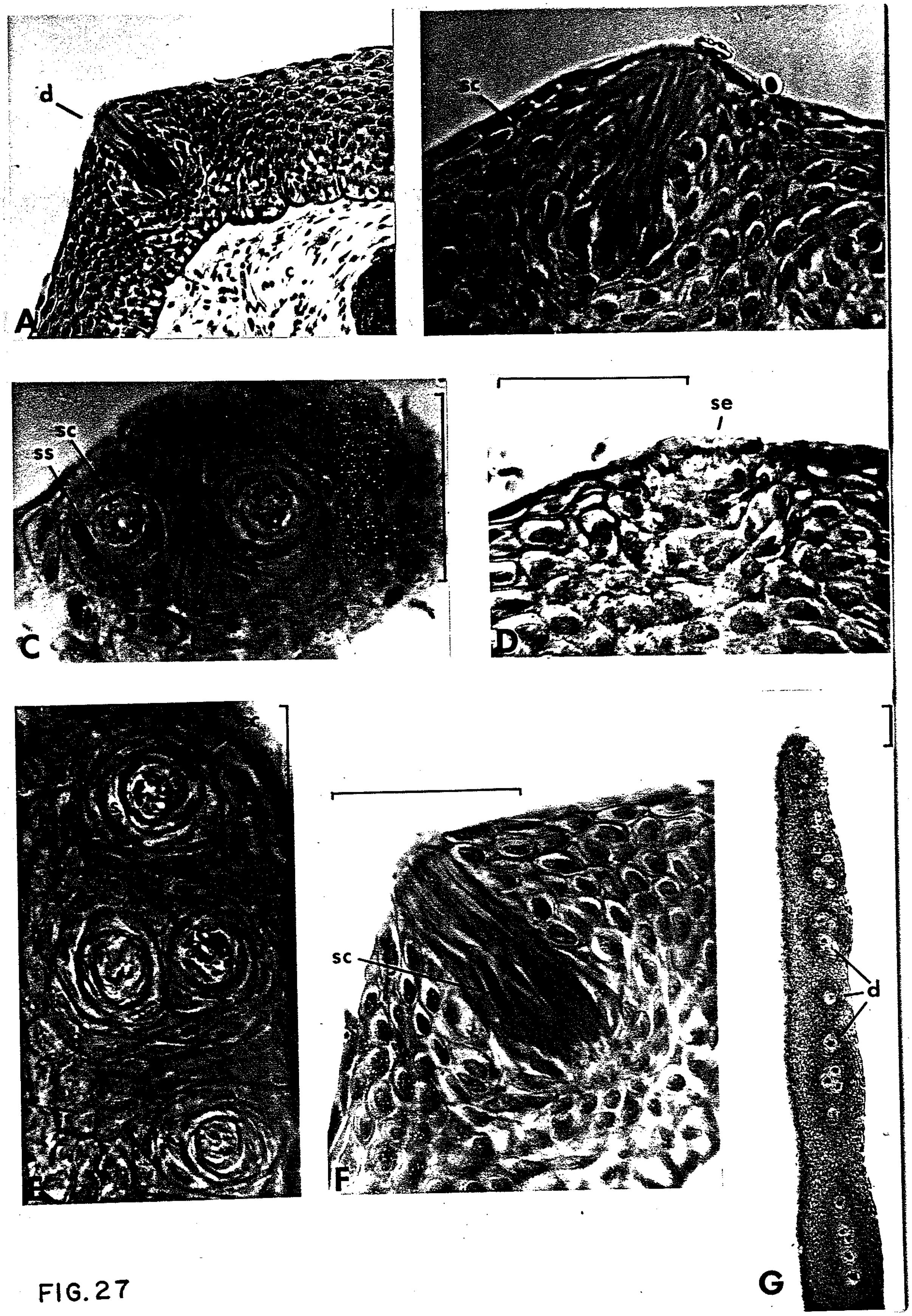
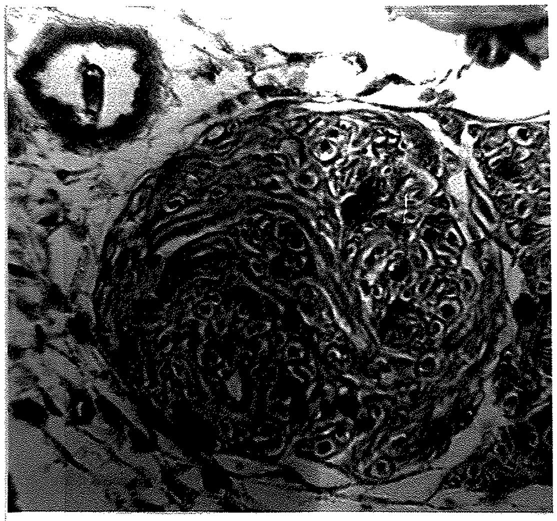
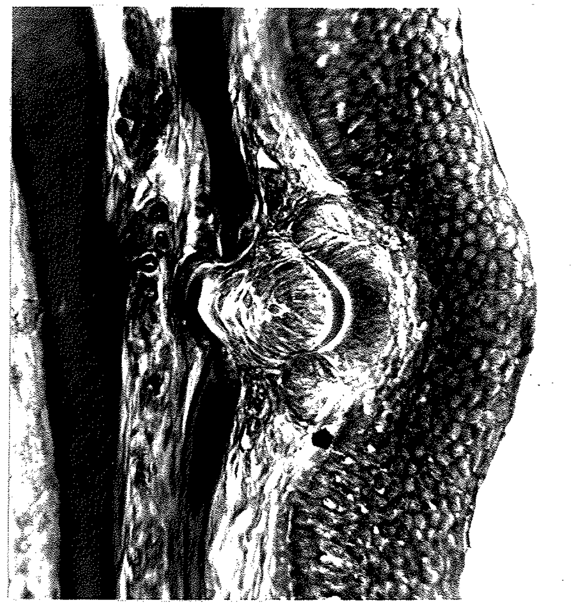
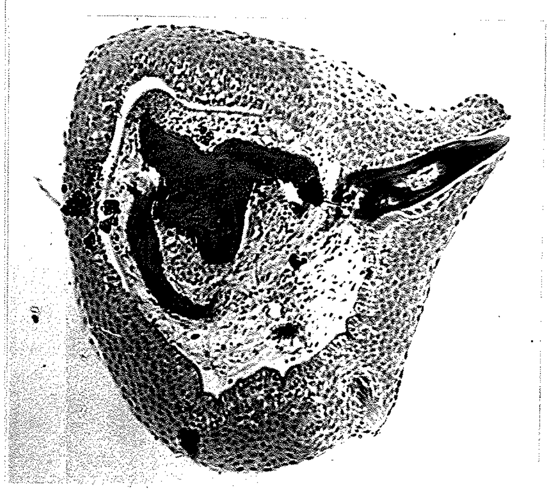


FIG. 27

Fig. 27. A, B & F, longitudinal sections (ls) of taste buds (d) (mts). C & E, ts of d (mts). D, sensory cell endings. G, ls of forward edge of raker. Additional abbreviations according to Fig. 26. Scale: C, D, E & F, 50 microns; G, 100 microns.







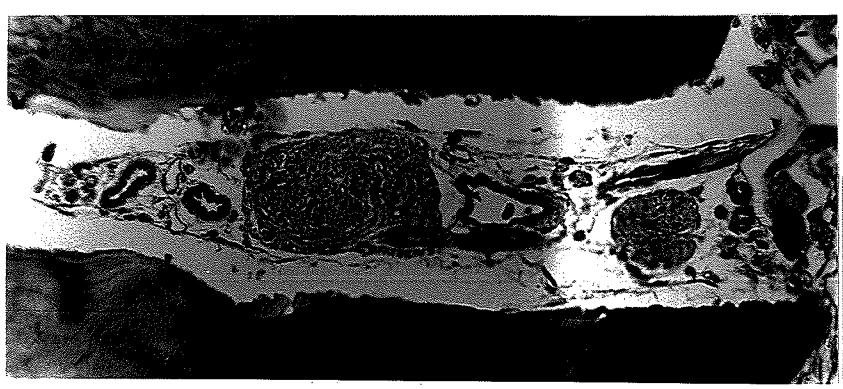
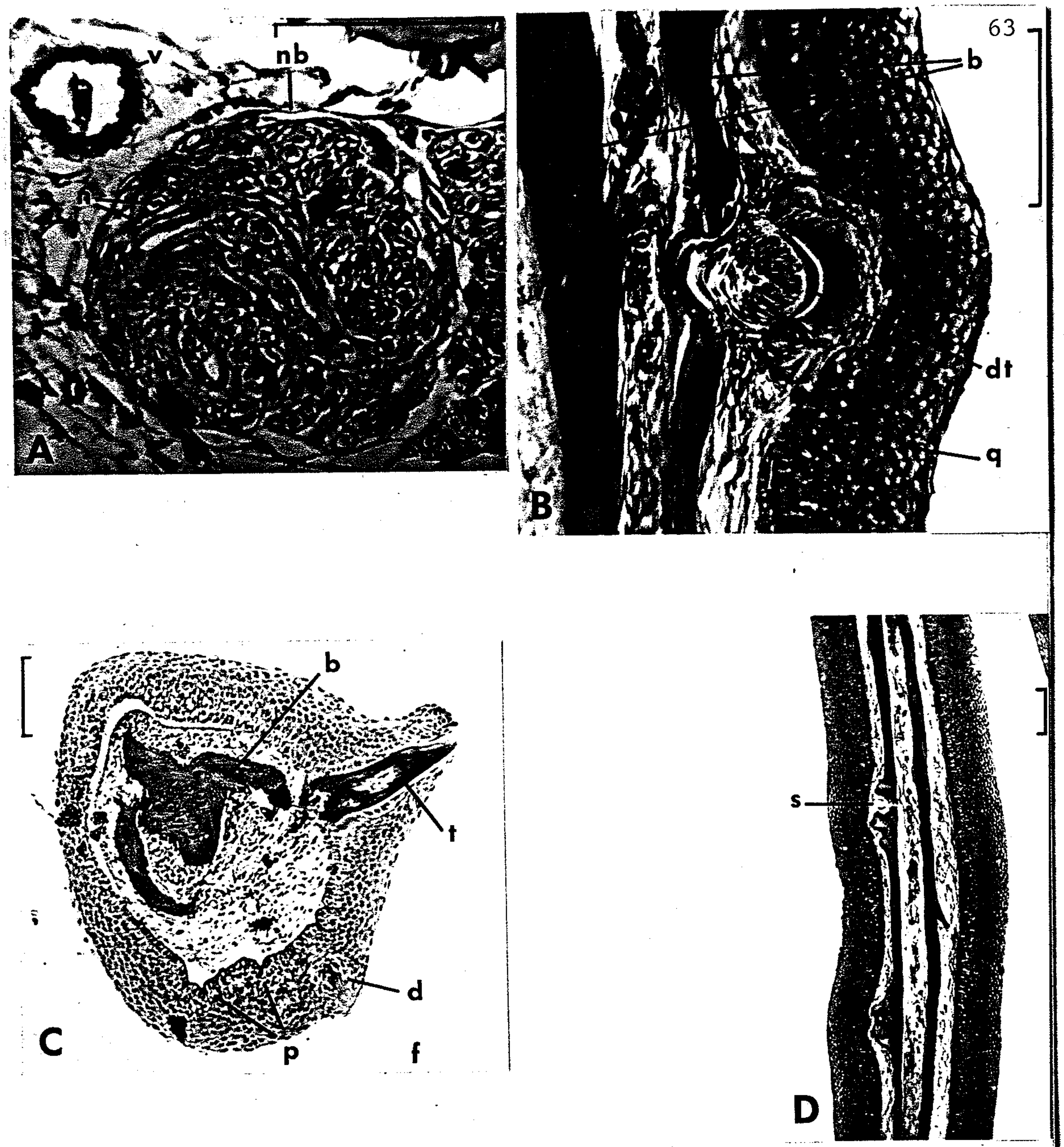


Fig. 28.

Fig. 28. A, ts of nerve bundle (nb) in raker core. B, ls of raker, with developing tooth (dt). C, ts of raker. D, ls of raker, with open socket. E, ts of core of matrix. Additional abbreviations according to Fig. 26. Scale: A, 50 microns; B, C. D & E, 100 microns.



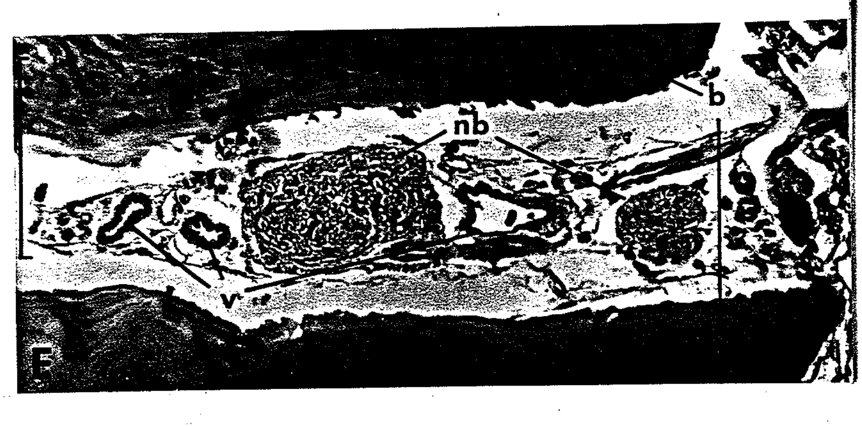


FIG.28

REGENERATION

Regeneration experiments indicate that rakers possess the capacity for limited replacement of lost parts. The degree of regeneration appears to be related to the level of amputation of the rakers. In all cases, the regenerated portion was shorter than the amputated length of the raker. Figure 29 illustrates the amount of regeneration that took place for each of the amputated rakers and the number of teeth present on the regenerated portion. Table 16 summarizes the data for five different rakers which showed appreciable regeneration. The mean regeneration length was significantly greater ($P<.001$) for base-cut rakers than for rakers cut at the midpoint or close to the tip. The mean regeneration for base-cut rakers was 2.7 micrometer units, and 2.0 for the latter.

Figure 30 illustrates a normal raker, and regenerated rakers that were amputated near the base. The original line of amputation is indicated. The regenerated raker is shorter, but possesses the component parts of the normal raker a distinct forward edge, bony core, raker teeth, and sockets from tooth succession. The 'A' side of the regenerated portions possesses more teeth than the 'P' side, and the teeth are closer to the raker tip.

Figure 31 illustrates regenerated rakers that were amputated near the tip. A number of these failed to regenerate, and those that were successful did not regenerate as much as rakers amputated near the base. Raker teeth were few, and those present were generally on the 'A' side of the blade.

Base-cut regenerates were well provided with teeth, with more than

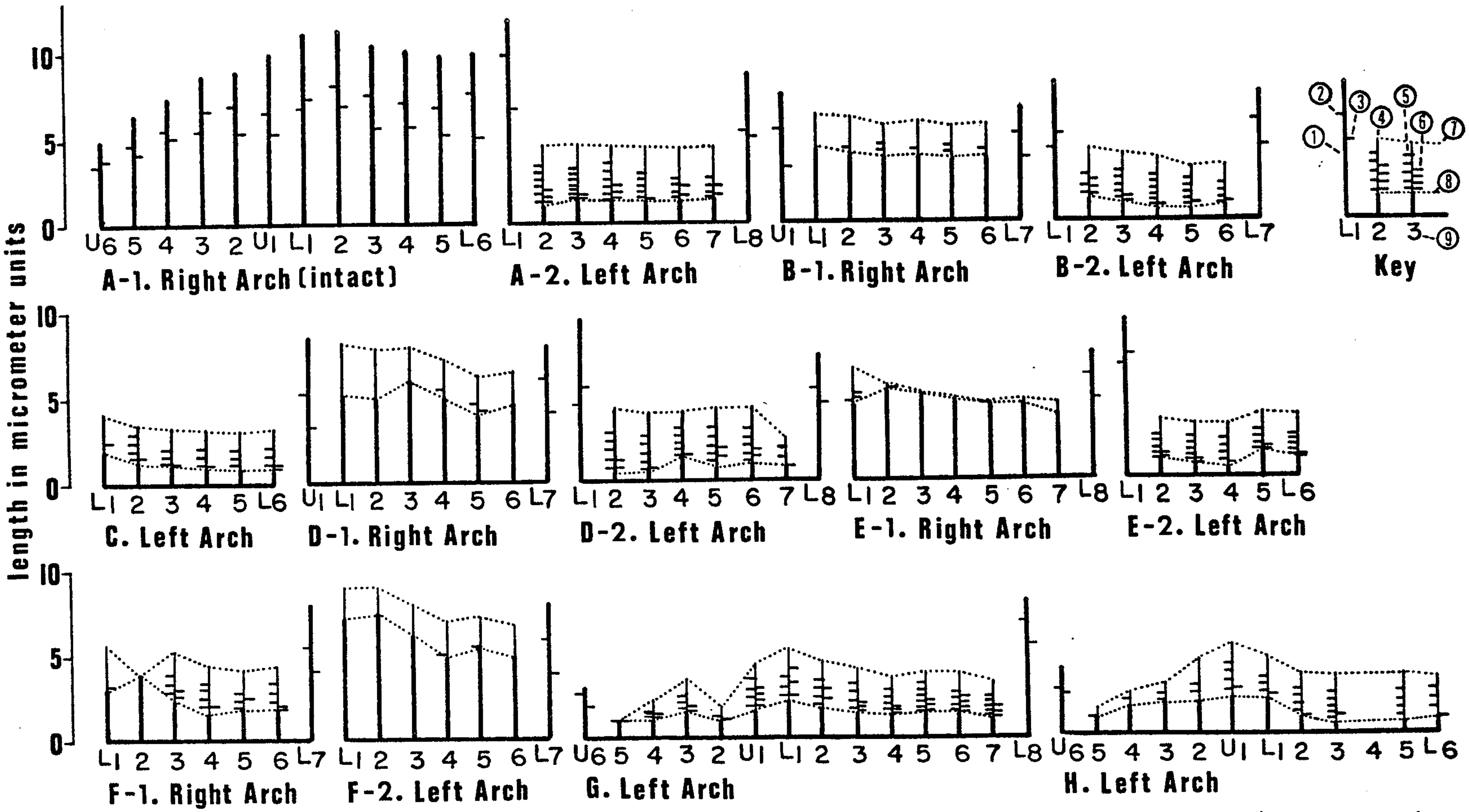


Fig.29 . Raker regeneration on first gill arch of Lyons fish, specimens A-H. Key: 1) intact raker (IR), 2) most distal tooth (MDT) on 'A' side of IR, 3) MDT on 'P' side of IR, 4) regenerated raker (RR), 5) MDT on 'A' side of RR, 6) MDT on 'P' side of RR, 7) level of regeneration attained, 8) level of amputation prior to regeneration, 9) raker code according to Fig. 5. Teeth indicated below 5) & 6) represent number present on regenerated portion, but not their precise position.

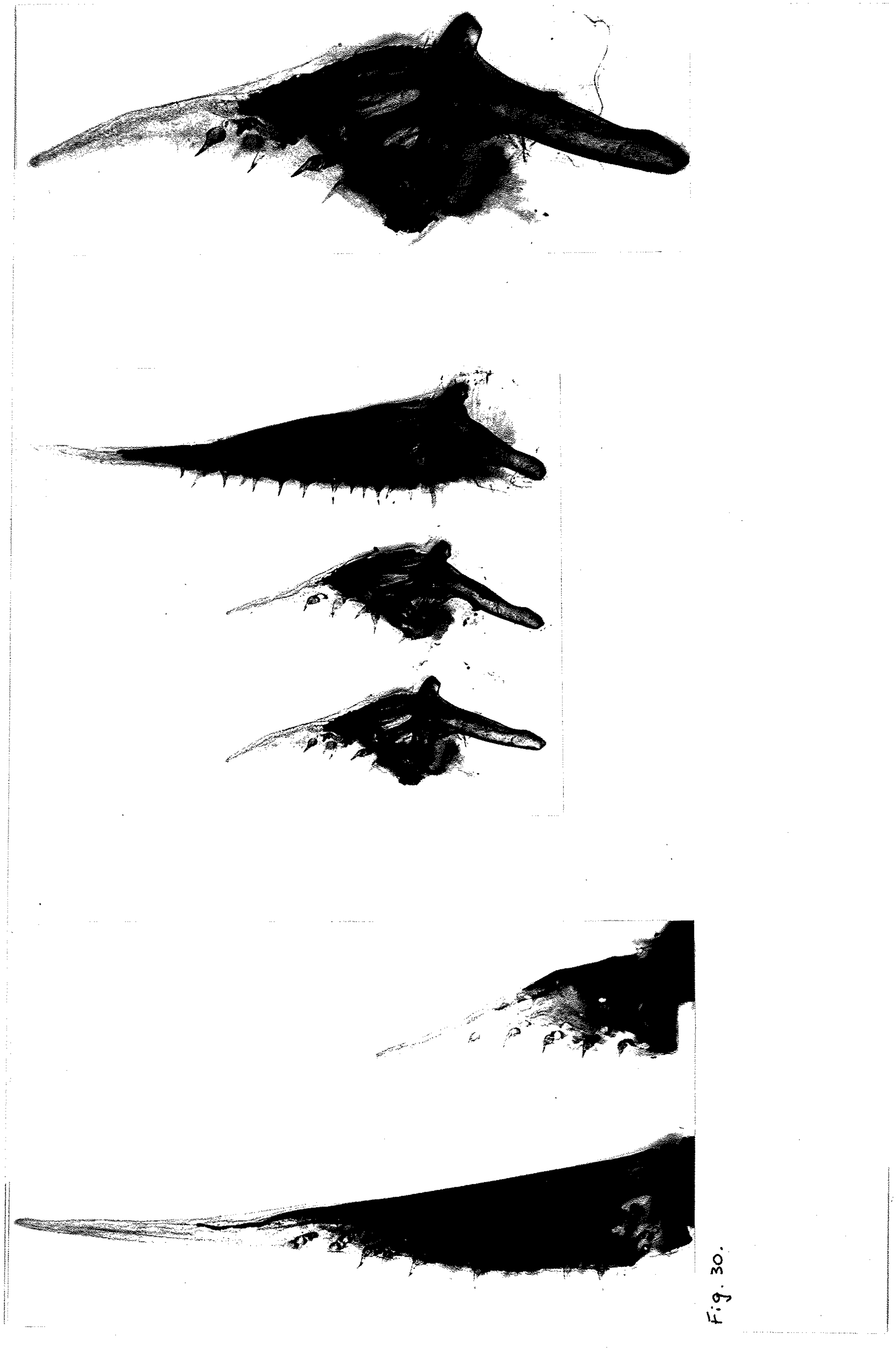


Fig. 30.

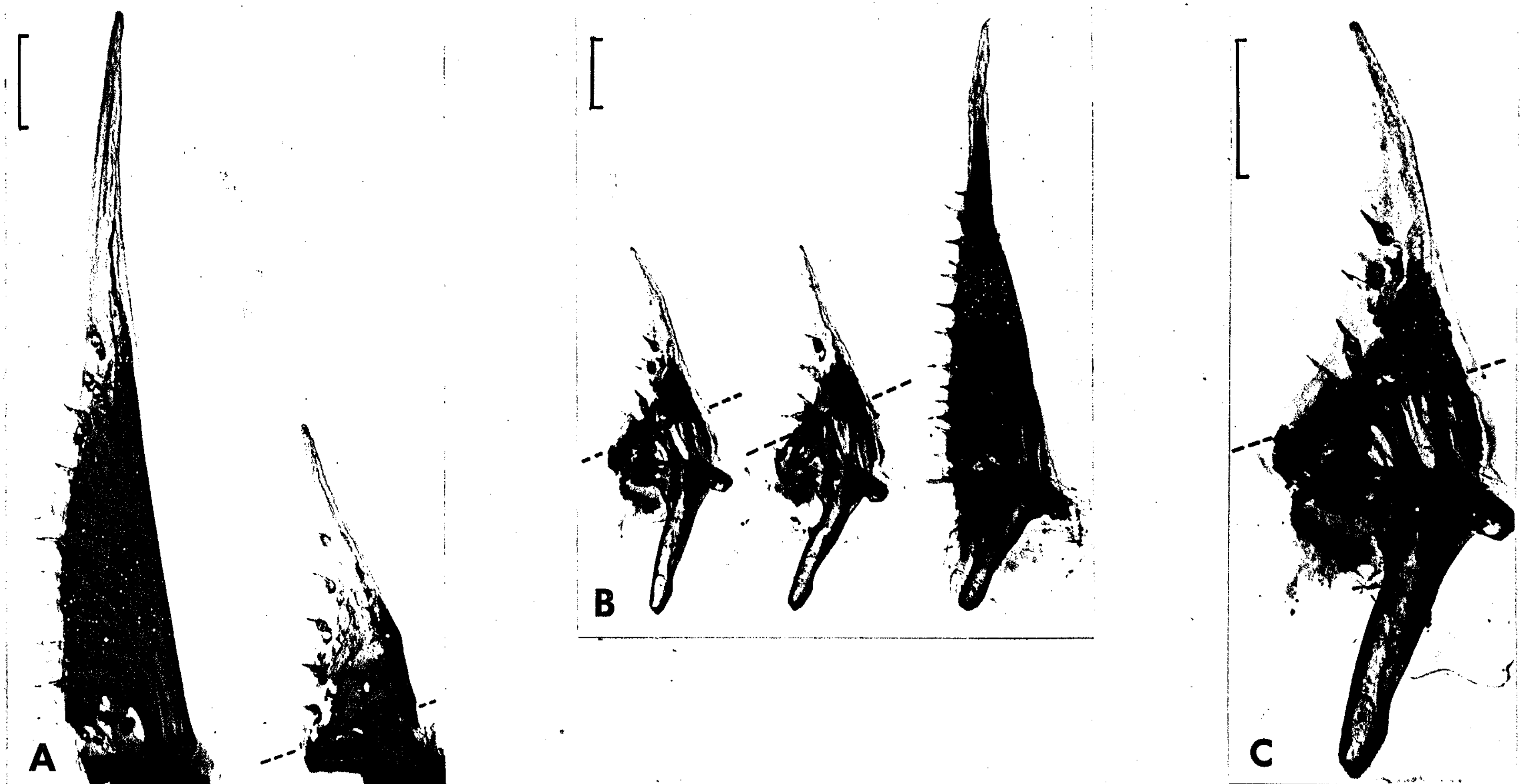


Fig. 30. Regeneration of base-cut rakers. Regenerates in A and B are compared to the adjacent uncut rakers. Dashed line indicates original level of amputation. Indicated scale 1 mm.

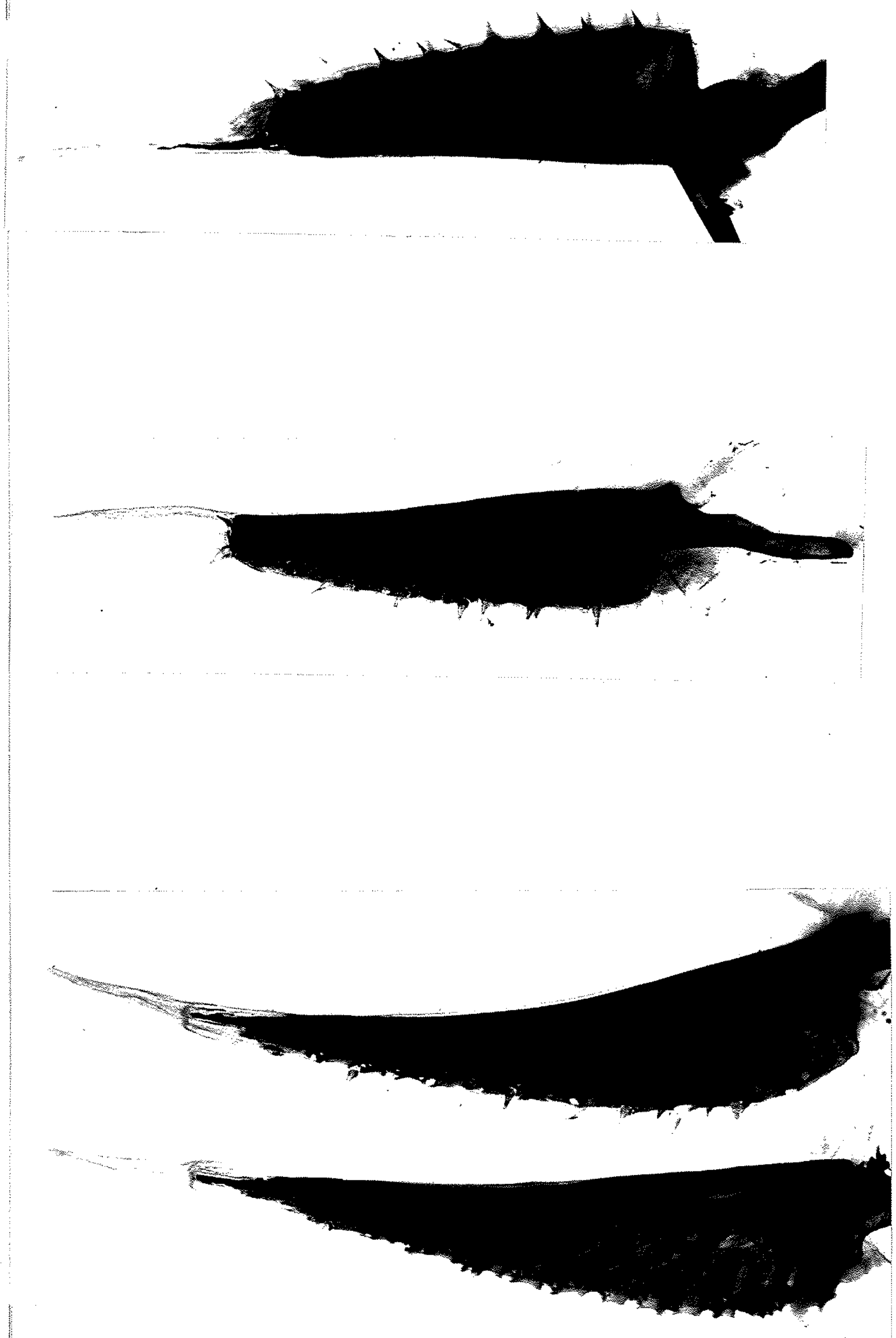


Fig. 31.

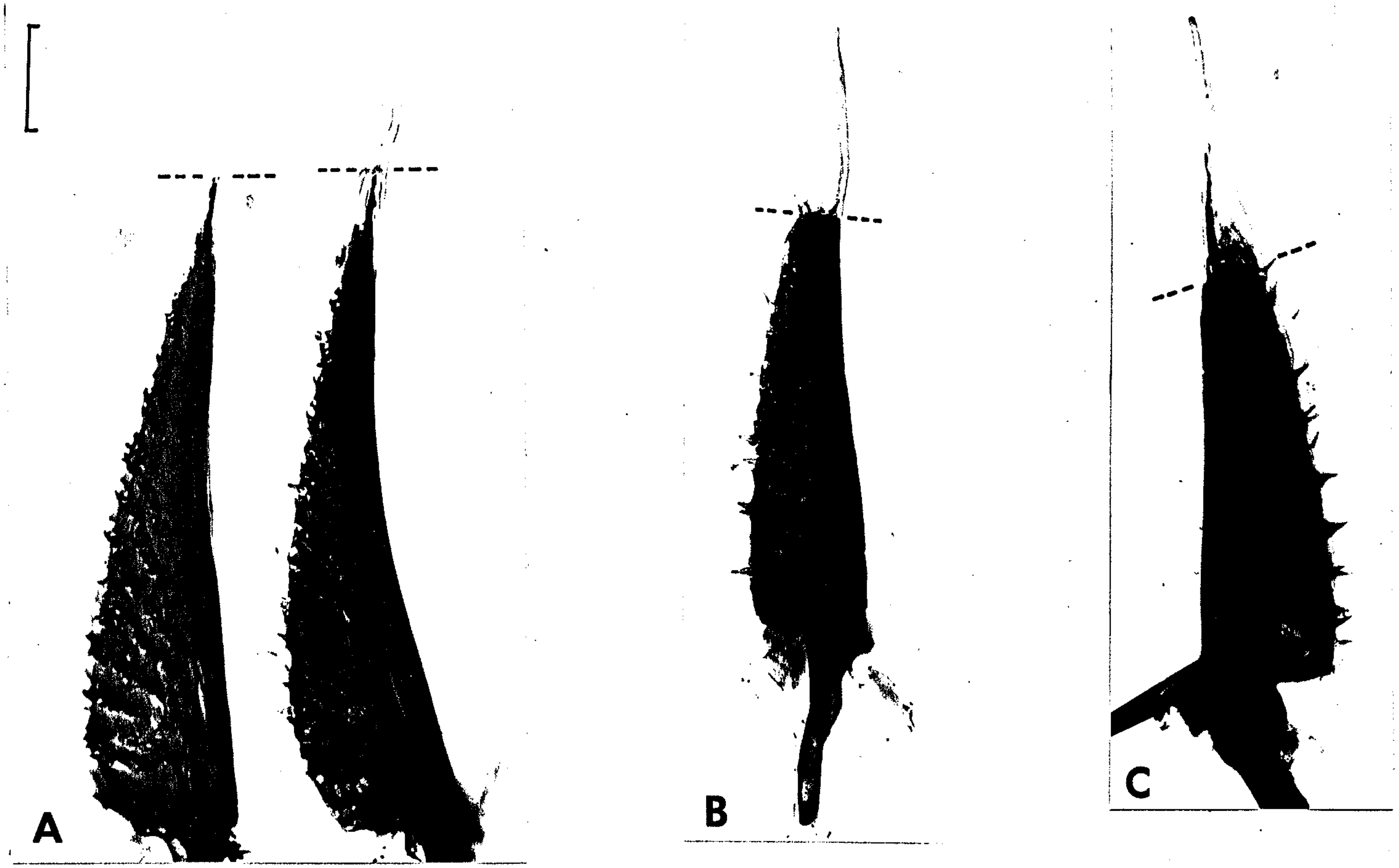


Fig. 31. Regeneration of tip- and mid-cut rakers. Dashed line indicates original level of amputation. Indicated scale 1 mm for all rakers.

twice as many on the 'A' side as the 'P' side. Teeth on mid- and tip-cut regenerates were scarce. The ratios of the mean number of teeth on 'P' side to the mean number on 'A' side, for base-cut regenerates, are included in Table 16. These values are considerably lower than the ratios of the wild Lyons fish (Fig. 18; Appendix). Clearwater fish, however, have lower ratios, particularly for rakers on the second arch. Ratios of teeth on the regenerated rakers more closely resemble those of the Clearwater fish.

The oldest tooth on each regenerated portion possesses a socket pattern with an average of two to three sockets behind its present position. A few teeth have four or five sockets behind them.

Raker Deformities

Some of the amputations resulted in deformities, such as curved and twisted regenerates, or stumps of scar tissue (Fig. 32). Possibly operational technique contributed to these results. Rakers were clipped with scissors, and portions of tissue may have been adhering to the remaining raker stump. This could lead to an uneven proliferation of cells during the regeneration process. A second possible cause may have been the angle of the cut. It has been shown that the rate of regeneration of pelvic fins depends on the level of amputation, with the fastest growth rate occurring with the most proximal level of amputation (Goss 1969). If the amputation occurred on a bias, different growth rates would occur for each of the rays in the fin. Some of the rakers possibly were amputated on a bias, and a differential growth rate along the cut on a single raker could produce a deformed regenerate.

TABLE 16. Regeneration summary of amputated rakers (base-cuts and mid/tip-cuts) L_2-L_6. Data provided are: mean regenerated lengths (RGL) in micrometer units; mean counts of teeth on 'A' (RTA) and 'P' (RTP) sides of regenerated portion of raker; ratios of RTP to RTA (Ratio). Raker coding according to Fig. 5. Significant difference between mean regenerated lengths (RGL) of base-cut and mid/tip-cut rakers; (* = P<.05).

Raker	L_2	L_3	L_4	L_5	L_6	L_2-L_6 Mean
BASE-CUT RAKERS						
n	7	8	7	8	8	
RGL	2.86	2.84	2.66	2.65	2.63	2.72 *
RTA	4.43	4.63	4.57	4.38	3.88	4.37
RTP	2.00	1.75	1.57	1.25	2.00	1.71
Ratio	0.452	0.378	0.344	0.286	0.516	0.391
MID/TIP-CUT RAKERS						
n	3	3	3	3	3	
RGL	2.20	1.87	2.10	1.93	1.90	2.00 *
RTA	0.33	0.67	1.00	1.33	0.33	0.73
RTP	0.00	0.00	0.00	0.33	0.00	0.07
Ratio	--	--	--	0.248	--	0.096

Fig. 32.

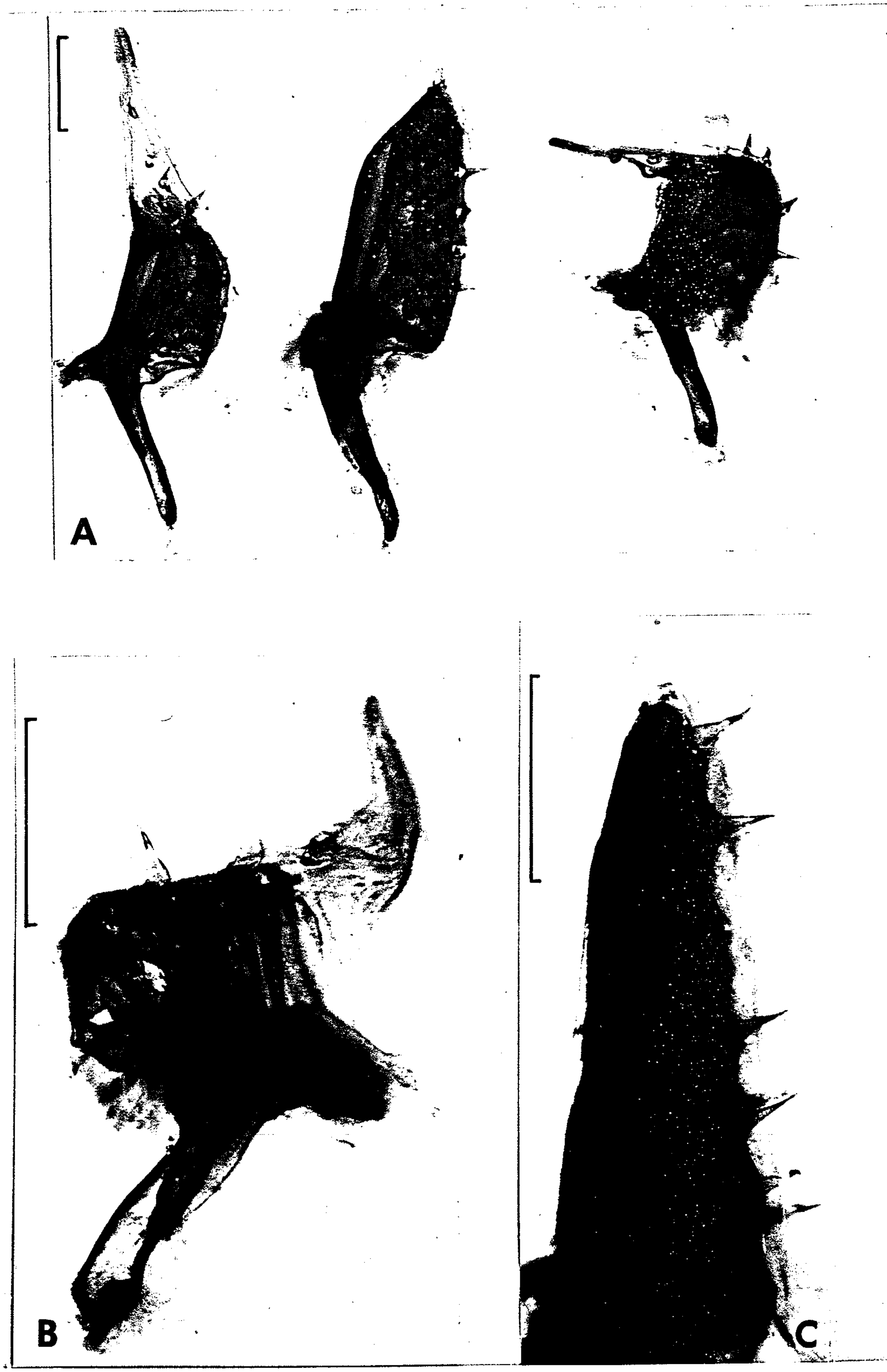


Fig. 32. Raker deformities resulting from amputation. Note sudden socket pattern change at (a) for raker C. Indicated scale 1 mm.

DISCUSSION

ADAPTATIONS FOR FEEDING

"Feeding is one of the most important functions of an organism. The basic functions of an organism--its growth, development, reproduction--all take place at the expense of energy which enters the organism in the form of its food. All the other energy processes within the organism of the fish also proceed at the expense of the food" (Nikolsky 1963).

The role of gill rakers in food gathering has been referred to earlier in this report. In numerous species of fish, a close relationship has been found between diet and the morphology of the raker apparatus. Kliewer (1970) and Loch (1974) found a relationship between raker length and diet for whitefish. Kliewer has reviewed several authors who conclude "fish with fewer and shorter rakers and larger spaces between them feed on larger and mainly benthic organisms, while fish with more and longer rakers and smaller spaces between them feed on smaller and mainly pelagic organisms." Kliewer has pointed out some exceptions to this rule.

Magnuson and Heitz (1971) found that the gill raker gaps of several marine species were correlated with the quantity of smaller organisms in their stomachs. Kliewer (1970) found in whitefish that such a correlation occurred with relative gill raker space, but not with absolute raker space.

Gill rakers have been described as a filtering mechanism or strainer (Alexander 1967; Norman & Greenwood 1963). In addition to direct filtering, rakers may serve as a sorting apparatus, such as that described for the cichlid Lethrinops furcifer in Lake Nyasa (Fryer 1959). This fish fills its mouth with sand and potential food items, and then discharges most of the sand through the opercular apertures. Chironomid larvae and large sand grains, which are normally found in the alimentary tract, presumably are trapped and ingested. A closely related species with more numerous and closely set gill rakers feeds on smaller chironomid larvae.

The relationship between raker spacing and the dimensions of potential food items may be complicated by behavioral selectivity. Galbraith (1967) showed that when Daphnia of a particular size range are not available for rainbow trout, the fish are forced to find an alternate source of food, and possibly compete with other species. Galbraith has observed that schools of trout feed in areas with concentrations of mainly large Daphnia. This would limit the size range available for filtering, although the filtering apparatus could accommodate smaller food items. Possibly the utilization of smaller food items by the trout is not an efficient method of obtaining adequate food.

Studies have been done on the relationship between feeding behaviour and food concentration for the anchovy, Engraulis mordax (Leong and O'Connell 1969; O'Connell 1972). This fish has two distinct feeding patterns, filtering and biting, that were related to the relative concentrations of adults and of nauplii of the brine shrimp, Artemia salina. This behaviour probably ensures the fish a maximum amount of food relative to the energy expended in feeding.

Ivlev (1964) has studied in detail the relationship between the abundance and distribution of food, and the selection and rate of consumption by several species of fish. Selection, or electivity, is influenced by many behavioural and physical factors. The preference by a predator fish for a particular ingredient of a food complex may be influenced by its abundance, the ease with which it can be obtained, and the intra- and interspecific competition for the food source.

The physical features of the feeding mechanism will limit the choice of food objects. Aleev (1969) has reviewed studies on the ontogeny of the shape, position and relative size of the mouth, and states "that the larvae of most species initially have a terminal or subterminal mouth, which best lends itself to capturing the relatively large (as compared with their size) and mobile plankton organisms which form their diet." Changes in the mouth occur during development which are dependent on the method of feeding as an adult. The relative size of the mouth is dependent primarily on the size of the food items.

Ontogenetic changes in the gill arches and rakers are also related to feeding. Shen (1969) has described the development of the feeding mechanism and feeding habits of the anchovy *Engraulis japonica*. He found diet to be related to the development of gill rakers. In the larval stage, the anchovy has a low number of rakers, with small protuberances which later develop into denticles or raker teeth. The diet at this stage is zooplankton. In the juvenile stage, the rakers are more numerous, longer, and possess teeth. The diet is then almost exclusively phytoplankton, presumably collected by a well-developed filtering apparatus. Nikolsky (1963) reports a similar ontogenetic feeding sequence from planktonic crustaceans to planktonic algae, by the Amur bighead, Hypophthalmichthys molitrix; Blaxter (1969) relates a correlation between phytoplankton in the intestines and formation of gill rakers in the anchovy, Engraulis anchoita.

The economy of feeding, therefore, depends on the nature of the feeding apparatus, available food items, and the behaviour of the fish. Presumably feeding behaviour and feeding apparatus have evolved mutually and offer the fish the most economical means of utilizing food through the various stages of development.

A review of the literature did not locate precise details on how gill rakers trap, transfer and concentrate plankton prior to swallowing. Information is available, however, on specific features of rakers that relate to their operation. Mucus is believed to play a role in concentrating phytoplankton into aggregates to prevent their passage through the rakers (Greenwood 1953); it may serve a similar function with zooplankton, and assist in transporting food along the arches to the oesophagus. According to Iwai (1964), the epithelium covering the gill rakers of teleosts is generally "studded with mucous cells." This study has found that the stratified squamous covering the rakers is well supplied with mucous cells.

Iwai has found the arrangement of taste buds in gill rakers to be well adapted to the filter-feeding mechanism. Whitefish rakers were found to have taste buds in the stratified squamous, and nerve fibres in the core of the raker blade. Proprioceptors have been reported in the rakers of some teleosts (Sutterlin and Saunders 1969). The sensory and food-gathering roles of the rakers of planktophagous fishes are probably closely related (Iwai 1964).

ADAPTIVE FEATURES OF LYONS LAKE RAKERS

Numerous significant differences exist between the gill rakers of the two groups of whitefish studied here which live in different lakes and possess distinctly different diets. The differences in the Lyons rakers appear very favourable for the microphagous diet of the fish. Loch (1974) has found good correlation between the diet of Lyons fish, and food availability in the lake. The differences in Lyons rakers could, therefore, be considered as adaptations of the food-gathering apparatus to the food resources available in the lake. The significant differences (adaptations) in Lyons rakers over Clearwater rakers, which may improve the efficiency of the food-gathering apparatus, are:

1. The lengths of the anterior rakers on the first two arches are greater, and provide an increase in the surface area of the filtering apparatus.
2. The increased raker length and base width increases the surface area of each blade, with its numerous mucous cells. This should increase the opportunity for zooplankton to become entangled with mucus.

3. The spaces between anterior rakers are reduced, improving the effectiveness of the net for zooplankton.
4. Longer Lyons rakers have more teeth, and these extend closer to the tip of the rakers on both the anterior and posterior sides of the blade. More teeth form a finer filtering apparatus.
5. The posterior sides of Lyons rakers have more teeth than Clearwater rakers, in absolute values, or expressed as a ratio of teeth on the posterior to teeth on the anterior sides, for the first two arches. For Clearwater fish, there is a considerable reduction in the number of teeth on the posterior sides of rakers on the second arch.
6. Teeth are closer together on rakers of both arches, improving the net. Socket succession patterns suggest that there is a tendency for the tooth interval to be maintained as the Lyons raker grows in length, while the tooth interval in Clearwater fish increases as the raker increases in length.
7. Posterior rakers of Lyons fish frequently possess teeth, which improve the interdigitation between posterior rakers of a forward arch and the anterior rakers of the arch behind it. Teeth on the posterior rakers of Clearwater fish occur rarely.

Some results from Lyons whitefish are in contrast to the findings of Norden (1970). He found posterior rakers poorly developed in Lake Michigan *Coregonus clupeaformis*, and gill teeth absent from posterior rakers. Norden has used such evidence to strengthen the separation of the genus *Prosopium* from *Coregonus*. However, this does not appear to be a valid morphological trait for such a separation. Incidence of raker teeth on posterior rakers may be useful within the Coregonus clupeaformis species complex for separation between populations.

There is some variance in the literature regarding the terminology for posterior gill rakers. In this study, the terms "anterior" and "posterior" gill rakers have been chosen according to Norden (1961), who made a comparative osteology study of various salmonids including Coregonus clupeaformis and Salvelinus namaycush. Martin and Sandercock (1967) have studied the feeding habits, and the development of pyloric-caeca and gill rakers of S. namaycush. They reported the presence of a row of gill rakers on the medial surface of the first gill arch, and referred to these structures as "accessory" gill rakers, to differentiate from the primary (or anterior, according to Norden) gill rakers. They found a correlation between the number and development of these rakers and the proportion of plankton eaten by the lake trout.

In his description of the branchial arches of the salmonid fishes, Norden (1961) refers to these "accessory" rakers as "posterior" rakers. For the trouts, according to Norden, these rakers, when present, are on the posterior surfaces of the arches, much smaller than anterior rakers, and are irregular in occurrence. He also verified the presence of posterior rakers for some specimens of S. namaycush.

This study on whitefish has followed the "anterior" and "posterior" raker terminology, and has used "accessory" to describe additional but rudimentary rakers which occur between posterior rakers (Fig. 25).

Although the occurrence of teeth suggests an improvement in the filtering efficiency of the rakers, there are only about half as many posterior rakers with teeth on the first arch of Lyons fish as there are on each of the remaining arches. This marked reduction in teeth, and the narrow shape of these rakers, may be related to the feeding sequence. The anterior rakers of the first arch are long, and probably are capable of movement in order to trap, clear, and transport food to the adjacent arches. The anterior rakers of the second arch, although shorter, are still relatively long and may have a similar capacity. Teeth on the posterior rakers of the first arch could then be a hindrance to movement by the anterior rakers of the second arch.

Two additional significant differences are raker base length and base angle. The adaptive nature of these differences are considerably more speculative. Possibly there is a relationship between these two features. In Clearwater fish, the sharper angle between the base and blade of the raker possibly positions the blade at a greater angle to the inflow of water and materials (that is, more to the perpendicular of the arch), and the force exerted by the inflowing materials is opposed by a substantial base. In Lyons fish, although the rakers are longer, the shallower angle suggests that the rakers tend to point more into the inflow, which would then exert less force at the reduced base. In addition, large food items of Clearwater fish may increase the force on the larger raker base, while small food items of Lyons fish would have a minimal effect on the smaller base. A simple analogy to this suggestion is to place a paddle directly forward into the current from a forward-moving boat, and then place the paddle at right angles to the current.

The force at the end of the handle is considerably greater in the latter case.

ORIGIN OF GILL RAKER ADAPTATIONS

Significant differences exist in the gill raker apparatus between the two groups of whitefish. These differences relate well to the differences in diet, hence they are considered adaptive. The question now considered is whether these adaptations are the results of genetic or nongenetic change. The ultimate origin of adaptations, however, is genetic, and as Kinne (1962) explains, "...the ability to adapt and the mechanisms involved must be considered evolutionary products. In this sense, then, nongenetic and genetic adaptation are different aspects of the same phenomenon."

This study considers further the origin of variations in Lyons gill rakers, and evaluates whether the factor responsible is (i) genotypic variation between the two groups of fish, (ii) a different phenotypic response to environmental differences by a common genotype, or (iii) a combination of both these factors.

Genetic Origin of Adaptations

(1) Natural Selection

Loch (1974) considers natural selection an unlikely source of major genetic changes, due to the limited number of generations (approximately 3) in Lyons Lake since stocking in 1960. Lyons Lake was poisoned out prior to stocking with whitefish fry. Under such circumstances, the initial selection pressure would probably be reduced considerably. There would be reduced interspecific competition for food, a minimum of predation pressure, and a relatively abundant plankton population. Intraspecific competition for food would probably have been the major selection pressure, but this should have been minimal for a new population yet to expand in numbers. It would appear that natural selection has had little opportunity to become effective in altering the genotypes of Lyons fish.

(2) Recombination and Mutation

These factors can introduce new variations into a gene pool. However, many generations would be required to establish the favourable genotype, which makes this an unlikely influence on the Lyons fish in this study.

(3) Gene Flow

Lyons Lake is not accessible to whitefish from adjoining lakes due to a fine steel grate obstructing the connecting waterway (Loch 1974). There would not be another whitefish gene pool to contribute genetic variation to the Lyons stock.

(4) Founder Principle

The possibility of the Lyons population carrying only a portion of the total genetic variation of the parent population in Clearwater is considered unlikely by Loch (1974). Random methods of fertilization and fry selection at the hatchery on Clearwater Lake should have ensured a varied gene pool in the transplanted fish.

(5) Selective Mortality

There is the possibility that selective mortality in Lyons Lake could have occurred among the new transplants and produced a limited gene pool. The physical and chemical factors in Lyons are quite different from Clearwater Lake (Loch 1974). Selective mortality due to these factors would most likely have occurred in the fry stage, when the food-filtering apparatus is not required and is not fully developed. The factors which presumably favoured survival at this time would have to coincide with the factors which provide an improved filtering apparatus. This latter feature would then have to coincide with the available food that forms the diet of the fish later in its life cycle. In addition, initial selection pressures for feeding are believed to have been low, hence this possibility appears remote.

(6) Clearwater Lake Whitefish Sample

Clearwater Lake is a relatively large body of water with an area of 295 km^2 (Loch 1974). Opportunities would exist in such a large lake for subpopulations to develop, with slightly different gene pools. The 20 Clearwater fish used in this study were obtained by one visit to a single pound net on Clearwater Lake. The morphometric and meristic data from these fish may be representative of only a subpopulation in Clearwater that is not representative of the original parent stock of Lyons fish. The Clearwater fish in Loch's study (1971) were obtained on three dates between June 14 and October 24. The first two collections were obtained from gill nets, and the third, collected from a poundnet, for a total of 281 specimens. However, both this study and Loch's study (1974) indicate a significant difference in raker length between the two populations. As the remaining raker parameters examined in this study were not examined by Loch, they cannot be compared. The additional raker data indicate further differences exist between the rakers of the two populations.

The possibility cannot be excluded of a significant difference in genotype existing between this Clearwater sample, and the original parent stock. However, as the results for raker length are similar to the findings by Loch (1974), this study has proceeded on the basis that the Clearwater sample is representative.

The genetic origin of gill raker adaptations, although a possibility, appears to be an unlikely explanation of the rapid appearance of phenotypic differences between the two groups of fish.

Non-genetic Origin of Adaptations

(1) Environmental Modifications

There is a considerable amount of information concerning the influence of the environment on the morphology of an animal. The majority of these studies have dealt with meristic features of animals, as they provide more discrete results than nonmeristic variation. The characters studied have included vertebrae, myotomes, scales, fin rays and gill rakers.

Blaxter (1969) has reviewed numerous authors on the effects of various factors on meristic characters. The most frequently studied characteristics have been fin ray and vertebral count under the influence of temperature. Additional environmental factors investigated for meristic influence include salinity, oxygen, carbon dioxide, and light. The most sensitive exposure period usually occurs very early in the development of an animal. This period may occur from gastrulation stage to shortly after hatching, depending on the animal.

The results of several authors indicate contrasting responses of vertebrae to an increase in temperature, for several species of fish (Table XIV, Blaxter 1969). Vertebral counts either increased, decreased, or the distribution of counts became altered.

It is difficult to determine the functional value of such meristic lability in wild populations. Nikolsky (1963) suggests that "the changes in vertebral and fin-ray counts are adaptations to swimming in waters of different densities." Morris & Scheer (1957) have found that meristic characters in cottid fishes appear to be correlated with others having survival value.

The principal raker characteristics investigated for environmental influence have been raker number, length, and space between rakers. Gill raker number has been regarded as a fairly stable character for white-fish taxonomy. Svardson (1951) states, "The number of gill rakers is regulated by polygenes and is the only character so far used in Coregonid taxonomy, whose variation is proved to have a hereditary basis. The capacity for environmental non-genetic modification is very slight or non-existent." Kliewer's (1970) review of work done by a number of authors concludes that gill raker number may be influenced by extreme environmental changes.

Raker length and spacing are both considered to be environmentally alterable characteristics as they are consequences of growth, which is alterable by the physical, chemical and biological factors in the environment. Authors reviewed by Kliewer (1970) found, for *Coregonus* nasus and Salvelinus namaycush, that a linear relation between raker length and standard length occurs in the major portion of the size range, followed with a decelerated growth in raker length when the fish reach the upper limit of the size range. The humpback whitefish and sockeye salmon, however, maintained a linear relation between these characteristics. Fish reared in aquaria were reported to have shorter rakers than those raised in lakes; however, in another study, tank-reared fish retained parental raker lengths (Kliewer 1970).

It would seem reasonable to consider that several factors may be responsible for the variations tht occur in gill raker characteristics. In some cases, correlations between raker characteristics and environmental factors have been strong, yet for other populations similar relationships are lacking. From his study of whitefish in adjacent lakes, Kliewer (1970) considers natural selection to be the most important factor to have contributed to the variations in raker length, space and number. He found raker length to exhibit the most prominent difference, and to be related to diet. Loch (1974) found a similar relationship in Clearwater and Lyons whitefish, but considers raker length differences to be attributed mainly to phenotypic variation.

(2) Abrasion Theory

Loch (1974) suggests that the short gill rakers of Clearwater fish may be the result of abrasion by ingested food organisms and substrate material; long Lyons rakers may be the result of a lack of abrasion. The results of this study failed to provide any evidence to support Loch's hypothesis. The results suggest abrasion or contact may have caused damage to some rakers, but no "wear" on the raker blades was observed (Figs. 20 & 21).

As the raker grows in length, it grows at its leading edge, with teeth being replaced towards this edge. Figure 20 indicates a very straight edge has developed up to the tip of the blade. If abrasion was a factor affecting its length, there should be a worn portion at the tip.

Intact raker teeth extend to the edge of the blade, and are more common on the anterior side of the blade than the posterior. If abrasion was a factor, teeth should be worn or broken off near the edge on the anterior side. Socket patterns from previous teeth are orderly, with no indication of replacement teeth needed for worn or broken teeth (Fig. 20).

Raker length appears to be one of several characteristics that are modifiable by the environment. From detailed observations of Clearwater rakers, it appears unlikely that shorter rakers are the result of a wearing-down process by hard ingested matter. Developmental plasticity is suggested as the main contributing factor, and although genetic differences between the two populations cannot be discounted, they are considered to be a less likely source of the phenotypic variation in this study.

(3) Phenotypic Response to Diet

Numerous examples of nongenetic variation have been described in a preceding section. A range of phenotypic responses may be possible from a genotype exposed to different environmental conditions. "Natural selection favours (or discriminates against) phenotypes, not genes or genotypes " (Mayr 1963). This includes the phenotypic range of a genotype. Phenotypic expression may be behavioural, physiological, or developmental (morphological); according to Kinne (1962), the first two are classed as functional and the latter structural.

Freshwater environments in the northern latitudes undergo transitions in the course of their existence. They are generally recent features of our landscape, which have reappeared following the Pleistocene period. Whitefish occupy many of these freshwater environments, and their distribution throughout the cooler areas of the northern hemisphere is wide (McPhail and Lindsey 1970). As the physical, chemical and biological conditions can vary considerably between lakes, the food availability can differ significantly. Loch's (1974) study of Clearwater and Lyons Lakes demonstrates this variability.

Whitefish are unusually responsive to changes in the environment. According to Mayr (1963) "certain groups of freshwater fish (for instance Coregonus, Leucichthys) display a plasticity of the phenotype that far exceeds what is usual in animals." Plasticity in feeding habits of whitefish young has been reported by Lindstrom (1962), with diet varying strongly with the food offered. In adult whitefish, correlation occurs between diet and food availability (Loch 1974), and between diet and gill raker length (Kliewer 1970; Loch 1974). Scott and Crossman (1973) have reviewed the wide range of diet for this species, but note that primary foods are aquatic insect larvae, molluscs and amphipods. With a lack of the latter two food items in Lyons Lake, the increased utilization of the insect larvae and zooplankton component possibly influenced the development of the raker. The adaptive response may have been an increase in raker length, and the development of more raker teeth. These features would improve the feeding apparatus for a microphagous diet. Such a phenotypic change may have been manifested by genetic factors that were influenced by the environment. The genetic factors may have been influenced by information provided by the sensory receptors of whitefish rakers, the presence of which was confirmed in the histological study.

The short rakers of Clearwater fish may be attributed to such a response. In this case, poor correlation between raker length and head length on the first arch may indicate raker development in Clearwater fish is more independent of head length than in Lyons fish. The greatest influence of ingested food and substrate material should occur on the first arch of Clearwater fish, possibly providing higher sensory response than in Lyons fish. The phenotypic response may then have been a shorter raker with a larger base, and fewer teeth. The second arch would receive less impact, and the third arch with still less influence from ingested matter. This may account for the highest Clearwater correlation between raker length and head length, which occurs on the third arch. Table 6 indicates this pattern of correlations for Clearwater.

This speculative origin of raker variation in whitefish is based on the appearance of statistically significant and apparently functional features of Lyons gill rakers, in a very short (evolutionary) time. Developmental plasticity of the gill raker apparatus would be a most appropriate feature of a fish that is indigenous to such a large and diverse area. When considered among phenotypic adaptive responses of other animals, it appears as a plausible hypothesis. Waddington (1953) has described the response of newt larvae to low oxygen content in the water. The gills grow larger, and the tissues in the walls become thinner, providing a more rapid diffusion of gas. Gee (1974) has conducted studies on the behavioural and developmental plasticity of buoyancy in the longnose and blacknose dace. He found these fish show developmental plasticity in swimbladder length, volume and weight of tissue, that is determined by the velocity of water in which they are reared. Whitefish gill rakers may develop in response to the diet that is available, within the range determined by the genotype. "The ecological and evolutionary significance of developmental and behavioral plasticity is related to the resulting potential to occupy a variety of environments " (Gee 1974).

An important feature for phenotypic plasticity of the gill raker apparatus would be the ability of the structure to respond at different stages of the life cycle of the animal. Diet obviously varies through the life of a fish. Aleev(1969) has reviewed mouth morphology in relation to diet during the development of a fish, and Shen (1969) has described the ontogenetic development of the raker apparatus of the anchovy. Stages in the development of the raker apparatus should have a range of phenotypic plasticity that is compatible with food availability.

Experiments on meristic variation indicate the most sensitive period is in the prehatching stage, or shortly following hatching (Blaxter 1969). It is unlikely that a prehatching environmental exposure would coincidentally provide the future adult whitefish with appropriate long rakers well supplied with teeth for a planktonic diet. Similarly, future swim bladder "needs" in dace would not be "predetermined" by embryonic exposure.

Developmental plasticity appears to offer a reasonable explanation for gill raker variation between Clearwater and Lyons populations. Such plasticity appears operative well beyond the sensitive period reported for meristic characteristics.

GILL RAKER REGENERATION

Regeneration in Fishes and its Significance to Gill Rakers

The ability for restoration of lost parts by organisms is highly variable between different groups and during development stages in certain groups. This reparative regeneration is considered to be more prevalent in aquatic than terrestrial animals (Needham 1952). Most work on regeneration in fishes has been conducted on fins, barbels, and tails (Schmidt 1968) and limited or conflicting results are reported for jaws, operculum, gill arches and gill filaments (Goss 1969; Hay 1966). The results of various authors suggest that regenerative power is very limited in the head region. Size is believed to play a role in regeneration in fishes, with large size and regenerative power probably negatively correlated (Needham, 1952). Regenerative powers of gill rakers, however, were not commented on in the current literature.

Vorontsova (1960) reviews various authors on regeneration who describe the process as an adaptive faculty for certain organs and tissues which are vulnerable to injury. Goss (1969) stresses the return to functional competence by the injured part. Regenerative efforts should not lead to the production of useless structures.

The feeding apparatus is one of the most important parts of an organism. If it does not function adequately, the organism starves. Gill rakers are more vulnerable to injury than most structures of fish as they receive considerable physical contact. Ingestion of particulate matter may cause damage to rakers, as was suggested for the Clearwater fish. Loss of rakers by fish on a microphagous diet would result in less efficient utilization of the food resources.

The histologic elements of whitefish rakers include an enveloping layer of stratified squamous containing taste buds, and nerve fibers and blood vessels in the core of the raker blade (Figs. 26, 27, & 28). Nerves are believed to play an important role in regeneration. Rose (1970) discusses the role of nerves in limb regeneration. Sensory and motor nerves can function with equal efficiency in promoting regeneration. The ratio of nerve fibers to the amount of tissue to be controlled is thought to be important. The role of nerves may be their provision of a polarized bioelectrical field or limb field originating from the remaining stump (Schmidt 1968; Rose 1970). A similar "raker field" may emanate from the stump and be reinforced by the fields provided by adjacent rakers.

The bone core of the raker is considered to be of dermal origin (Nelson 1969). Fin rays also consist of dermal bone. During normal or regenerative growth, rays increase in length by the formation of new ray segments onto the ends of those already formed (Goss 1969). The raker core, however, lacks segmentation.

Factors of Possible Influence on Raker Regeneration

Raker regeneration achieved only limited success, as the structures did not attain their original size. The structures did, however, develop into rakers, and possessed raker teeth and sockets. A number of factors may have influenced this development. Future investigators may pursue this line of research; hence speculation would appear justified, on the possible influence of various factors on raker regeneration.

(1) Environmental factors such as water temperature and photo periodism are known to influence regeneration (Vorontsova, 1960). Voronstova provides an indication of the rate of regeneration in fish. Almost one month at 18 C was required for the regeneration of a fin of the wrasse, *Labrus bergylta*. Regeneration of the whitefish rakers took place at 12 C in the seven-month experimental period. The fish originally experienced temperature ranges in Lyons Lake. Loch (1974) reports a range of 26 C to 4 C between surface and bottom in July. The temperature range for Clearwater Lake was 18 C to 9 C between surface and bottom in August.

Oxygen content in Lyons Lake during the summer is reported to be high (10 ppm) at the surface in relatively warm water, and very low (1 ppm) at the bottom, where the coolest temperatures are encountered. The water in the holding facilities was aerated continuously.

In the wild, fish experience ranges in the physical and chemical factors of their environment. The animal has natural adaptations for change. The lack of change, and the possible stress created by the holding facilities, may have been contributing factors to the regeneration results.

(2) Carbohydrate, lipid and protein shifts in biochemical composition of tank-held fish have been reported (Love 1970) and may have influenced the regeneration results. Love has found that hatchery-reared fish contain less protein and more lipid than wild fish, although natural food has only one half the protein of hatchery food.

The diet provided in the holding facilities is physically artificial and feeding occurs on an artificial periodicity. In the wild, food type may vary through the year, and its daily time of availability may change. Food availability may determine the temperature and oxygen content of the water which the fish will encounter.

(3) Regeneration results that are smaller than the original are described as hypotypic (Needham 1952). According to Goss (1969), the regenerate is usually a duplicate of the original. When differences appear, these may be attributed to different histologic conditions present for regeneration than the original embryonic development.

The regenerating rakers possibly would have achieved their original lengths if allowed a sufficient length of time. This proposal would have to assume that raker regeneration rate is quite slow, compared to the rate of regeneration of a wrasse fin (Vorontsova 1960). Table 14 indicates the ratio of the number of teeth on the 'P' side to the number of teeth on the 'A' side. This ratio is similar to that of young whitefish obtained from Steeprock Lake (Appendix). A whitefish of approximately 9 cm had only one or two teeth on the 'A' side, and none on the 'P' side. Larger specimens (16 cm and 18 cm) had teeth on both sides, with 'A' side having about twice as many as 'P' side. A specimen of 36 cm had additional teeth, with only slightly fewer teeth on the 'P' side than the 'A' side. The acceptance of an ontogenetic explanation of the distribution of teeth on the regenerate would have to include acceptance of a slow rate of regeneration for a feeding structure.

(4) The final suggestion, which is the most speculative, is that the resulting regenerate is an adaptive response by a structure that possibly has considerable phenotypic plasticity.

Whitefish have a considerable capacity (compared to other fish) for phenotypic plasticity (Mayr 1963), which contributes to their wide distribution. Correlations have been demonstrated between raker characteristics and diet (Kliewer 1970; Loch 1974), and between diet and food availability (Loch 1974). Contrasting food availability in different lakes has also been demonstrated by Loch. Raker structures would be vulnerable to injury as a consequence of their role, and regenerative repair of vulnerable structures would be an adaptive faculty (Vorontsova 1960). The injured part would then be returned to functional competence (Goss 1969).

Possibly the regenerated rakers that were clipped near the base may have achieved a satisfactory level of functional competence for the new conditions. This may have been a developmental response to the available food and/or other environmental factors in the holding facilities. Should this be the limit of regeneration, there is a resemblance between these regenerated Lyons rakers and Clearwater rakers. These short regenerates have tooth ratios which resemble Clearwater fish (Table 14; Appendix). The implication is that the resemblance of regenerated rakers to Clearwater rakers reflects the parental origin of the Lyons fish. Although highly conjectural, this hypothesis invites future experimentation on developmental plasticity in which the regeneration of rakers might be studied under two or more different diets.

Adaptive Response Mechanisms

Rakers that had been cut midway or near the tip of the blade did not regenerate as much as base-cut rakers. In some cases, there was very little regeneration of tip- and mid-cut rakers (Fig. 29, E-1). If the regenerated base-cut rakers have achieved the optimum size (Fig. 29, A-2; B-2), there must be an explanation for the significant regeneration that has occurred on some mid- or tip-cut rakers (Fig. 29, B-1).

If the environment is to influence development at any stage of the life of an animal, there must be a system of physiological communication to detect changes and transmit the information to the appropriate target organs, tissues or cells. Neural and hormonal factors may be involved. The sensory capacity of gill rakers has been examined, (Iwai 1964; Sutterlin and Saunders 1969) and these neural mechanisms may be involved in stimulating and directing developmental plasticity. Specimens with rakers clipped only part way along the blade also had rakers on the opposite arch clipped close to the base. Possibly the base amputations stimulated regeneration at a level determined by the maximum amount of amputation. A general regeneration rate may then have influenced the degree of regeneration on the mid- or tip-cut rakers on the opposite arch.

Future Investigations

The ability for limited regeneration of whitefish rakers suggests an importance in the maintenance of these structures. It also suggests a method of evaluating the possible developmental plasticity of gill rakers.

A series of investigations on fish with amputated rakers can explore this adaptive capacity. Two groups of fish could be provided with the same diet, but of different dimensions and hardness. The regenerated rakers would then be examined for any association with the physical features of the diet. Investigations may be conducted on the influence of other environmental factors on raker regeneration. The possibilities for investigation are considerable; some examples are amputation levels, physical and chemical nature of the diets, environmental factors such as light, temperature, oxygen, carbon dioxide and dissolved solids, and the age of the fish.

Regeneration studies may determine if there is a range of phenotypic plasticity of whitefish gill rakers for various environmental factors.

SUMMARY

There were significant differences in a number of morphological characteristics of whitefish gill rakers between two populations, that are resident in two separate lakes which differ in physical and chemical parameters, and food availability. The raker differences are closely related to the diets of the whitefish and are considered to be adaptive.

In contrast to Clearwater fish, the Lyons fish, which are restricted by food availability to a microphagous diet, possess the following adaptations: longer rakers with a wider blade; closer spacing between rakers; more teeth along rakers; closer spacing between teeth; teeth closer to distal portion of the raker on both sides of the blade; frequent occurrence of teeth on posterior rakers. These characteristics would improve the food-gathering apparatus.

In contrast to Lyons fish, Clearwater fish, which feed on large and hard benthic organisms, possess rakers with larger bases which are at a sharper angle to the blade. It is suggested that these features are adaptive to larger and harder items entering the branchial cavity. Teeth are generally absent on the posterior rakers. It is suggested that the occurrence of posterior raker teeth may be used as a characteristic for separation of populations within the *Coregonus clupeaformis* species complex.

Socket patterns from previous teeth provide a temporal record in the life of the fish; they indicate the tooth spacing in the past and may serve as indicators of adaptations to previous diet or other environmen-

tal factors. Straight socket patterns were predominant on Clearwater rakers; curved socket patterns occurred on most of the Lyons rakers.

Histologic examination of the rakers indicates the presence of nerve fibers and taste buds, presumably to function in a sensory role related to feeding.

Whitefish gill rakers possess the capacity for at least limited regeneration. Although smaller than the original rakers, regenerates have a similar appearance and possess teeth in a specific distribution on each side of the raker blade, with socket succession patterns. The P/A ratios of teeth resemble those of young whitefish, and those of the large Clearwater specimens. The latter resemblance leads to speculation that the P/A teeth ratio of the regenerated Lyons rakers reflect their parental origin from Clearwater Lake. Gill raker regeneration in whitefish may provide future experimenters with a useful method of studying developmental plasticity in adult animals.

The marked phenotypic differences in gill rakers between the two populations in such a short period of time indicate that a rapid adaptation to food availability has occurred in Lyons whitefish. The short time that has transpired since the transplant of fish makes genetic change a highly improbably cause of gill raker variation between the two populations. The evidence does not support the suggestion that Clearwater fish have shorter rakers due to abrasion by a harder diet. Instead, this variation in raker characteristics is considered to be an adaptive phenotypic response of the gill raker apparatus to changes in the environment, possibly mediated via sensory input to the filtering apparatus by the food ingested.

APPENDIX

1. STAPLE FOOD DATA

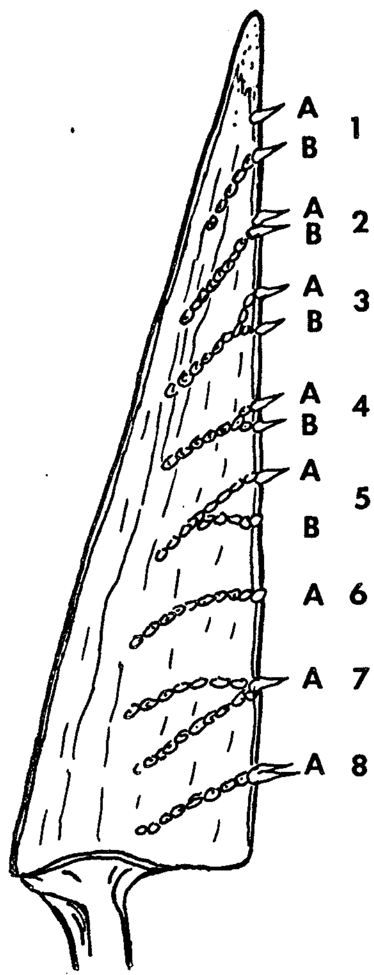
Product name: Ewos F 169, size 3, pelleted salmon food, Sodertalje, Sweden.

Particle Size	
< .25 mm	1.5%
.25 - .50 mm	1.4
.50 -1.00 mm	2.4
1.00 -2.00 mm	55.7
2.00 -4.00 mm	39.0
	100.0%

Content (taken from label)	
Crude protein	52 %
Fat	6
Carbohydrates	22
Cellulose	2
Ash	11
Water	7
	100.0%

2. CRITERIA FOR COUNTS OF RAKER TEETH

The normal structure of a raker tooth has been illustrated in this manuscript. However, some raker teeth varied in structure and in their method of appearance on the raker edge. The following hypothetical raker illustrates these discrepancies and their interpretations for this study:



(1) Counted as 2 teeth, as A is not a replacement for B, but an addition to the blade as it increases in length.

(2) Counted as 1 tooth, as A is the replacement tooth for B.

(3) Counted as 2 teeth with diverging socket patterns.

(4) Counted as 2 teeth with diverging patterns just commencing.

(5) Counted as 2 teeth with diverging socket patterns, with B tooth broken off.

(6) Counted as 1 tooth, which is broken off.

(7) Counted as 1 tooth, resulting from converging socket patterns.

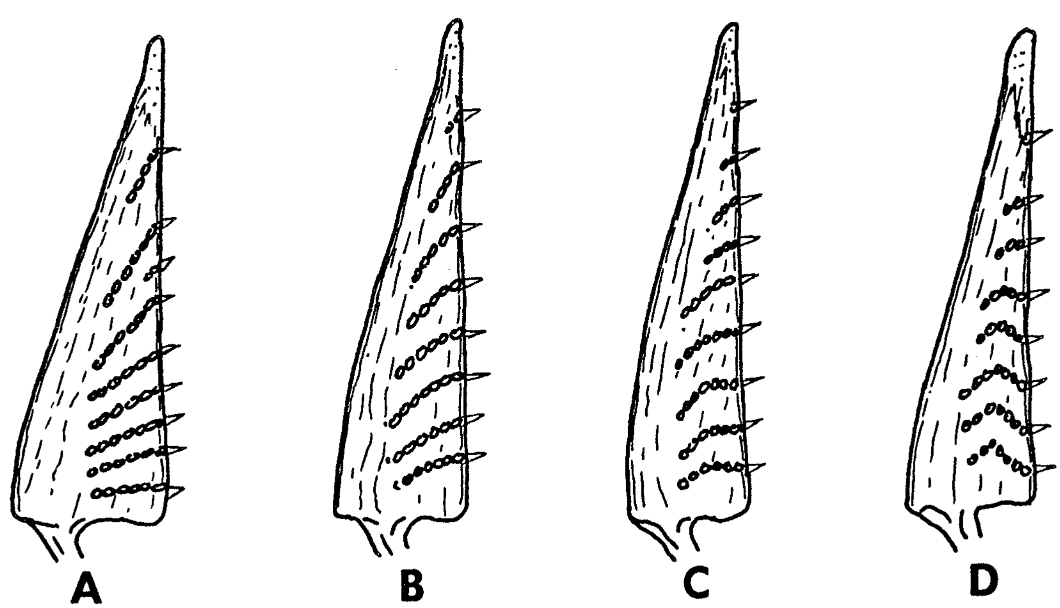
(8) Counted as 1 tooth, with twin cusps, but still a single base.

3. CRITERIA FOR TOOTH SOCKET COUNTS AND PATTERNS

Seven fish from each group had 14 rakers examined for socket counts and succession patterns: U_2, U_1, L_1, L_2, L_3, & L_{10} on arches 1 and 2; and L_2 on arches 3 & 4.

Socket counts of the longest pattern include an overlapping socket as a single socket. Some teeth are replaced in a socket distinctly separate from the previous socket, while others 'crowd' the old socket. Some old sockets are barely discernible, and appear grown in; other old sockets stand out distinctly. Therefore, counts in the former case would tend to be conservative. Another difficulty sometimes encountered when viewing sockets is the visibility of sockets on the side of the blade opposite to the side being viewed. The alizarin-stained blade is quite translucent in transmitted light.

Usually at least 4 sockets (including the tooth) were required before a succession pattern was determined. The pattern categories of straight and curved provided the most convenient method of classification. The straight pattern category indicates that all the socket patterns on the observed side (in this case, 'A') of the raker blade are straight; a curved pattern category indicates that all the socket patterns are not straight, and one or more patterns are curved. The diagrams below illustrate some examples:



Example A is classified as straight, and B, C, and D are curved. Occasionally a single raker may possess features of all of these examples. The significance of the two categories is to identify between rakers with socket patterns that diverge, hence the distance between teeth increases, and rakers that have some curved socket patterns, which indicates there has been some maintenance of tooth spacing.

4. RAKER TOOTH INTERVAL IN MICROMETER UNITS

Abbreviations according to previous tables & text.

	U_2		U_1		L_1		L_2		L_3		L_{10}	
	A	P	A	P	A	P	A	P	A	P	A	P
ARCH 1												
CW	.645	1.093	.644	.915	.710	.842	.661	.858	.698	.902	.693	.946
LY	.522	.519	.494	.496	.510	.498	.503	.491	.489	.533	.510	.603
ARCH 2												
CW	.565	.757	.566	.906	.613	.629	.570	.800	.637	.900	.689	.882
LY	.416	.494	.441	.440	.436	.437	.432	.462	.433	.511	.447	.565

5. MEAN NUMBER OF TEETH ON 'A' AND 'P' SIDES OF RAKERS

Abbreviations according to previous tables and text.

	U_2		U_1		L_1		L_2		L_3		L_{10}	
	A	P	A	P	A	P	A	P	A	P	A	P
ARCH 1												
CW	6.35	2.45	7.05	3.20	6.30	5.20	6.40	5.45	5.65	4.35	4.50	1.60
LY	11.90	10.35	13.35	11.85	12.70	12.15	14.60	12.35	14.90	12.00	10.25	6.90
ARCH 2												
CW	4.40	0.60	4.95	1.10	4.85	4.15	5.05	1.50	4.25	0.75	3.50	0.60
LY	8.25	5.45	8.55	7.20	8.95	8.70	9.05	7.30	8.75	6.55	7.85	4.90

6. RATIO OF MEAN NUMBER OF TEETH ON 'P' SIDE TO 'A' Side

Abbreviations according to previous tables and text.

	ARCH 1						ARCH 2					
	U_2	U_1	L_1	L_2	L_3	L_{10}	U_2	U_1	L_1	L_2	L_3	L_{10}
CW	.386	.454	.825	.852	.770	.356	.136	.222	.856	.297	.176	.171
LY	.870	.888	.957	.846	.805	.673	.661	.842	.972	.807	.749	.624

7. STEEP ROCK LAKE WHITEFISH. HL & FL in cm, RL in micrometer units.

Abbreviations according to previous tables and text.

SPECIMEN	1	2	3	4	5	6	7	8
HL	2.00	3.38	3.80	4.67	4.86	5.74	8.53	9.36
FL	8.7	15.8	18.2	21.7	23.5	28.8	34.8	36.0
RL(L_2, Arch 1)	2.1	3.9	4.0	5.0	6.0	6.1	7.8	7.8
RL(L_2, Arch 2)	0.9	1.6	1.7	2.2	2.6	2.8	3.6	3.7

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