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A Study of the Pattern of Scale Development in Salmo Clarkii Spilurus Cope

Josephine Hawrylko

Hawrylko — SALMO CLARKII SPILURUS COPE

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A STUDY OF THE PATTERN OF SCALE DEVELOPMENT IN <u>SALMO CLARKII SPILURUS</u> COPE

A Thesis
Presented to
the Faculty of the Biology Department
University of New Mexico

In partial Fulfillment
Of the Requirements for the Degree
Master of Science in Biology

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by
Josephine Hawrylko
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MASTER OF SCIENCE

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DEAN

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The writer wishes to acknowledge her indebtedness to Dr. William J. Koster for the specimens that he provided and for the help and many suggestions that he gave.

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INTRODUCTION

Statement of the problem. One of the phases of fish investigation is to determine the pattern of scale development in fishes. The problem deals with a study of the gross development of scales and their distribution over the body in *Salmo clarkii spilurus* Cope, Rio Grande Cut-throat trout. "This trout is known only from the upper Rio Grande basin and southward into the mountains of Chihuahua."[1] The Cut-throat trout is a member of the Family Salmonidae and often goes under such common names as black-spotted trout, mountain trout, New Mexico native trout, red-throat trout and various other titles.

Importance of the study. The study of fish scales has become an important phase of ichthyology for many reasons. In a single species the scale-pattern; that is

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CHAPTER I

INTRODUCTION

Statement of the problem. One of the purposes of this investigation is to determine the pattern of scale development in fishes. The problem deals with a study of the gross development of scales and their distribution over the body in Salmo clarkii virginalis Girard, the Rio Grande cut-throat trout. "This trout is known only from the upper Rio Grande basin and headwaters [illegible] of Colorado."[1] The cut-throat trout is a member of the family Salmonidae and other [illegible] brown trout, mountain trout, [illegible] trout, red-throat trout and various other fishes.

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the number, form, structure and distribution of scales is essentially constant and so of great aid in classification. Tims[2] points out that a knowledge of the structure and development of scales in fishes not only throws considerable light on the affinities between living groups of fishes but also aids in determining their evolutionary backgrounds. Scales are also an aid in interpreting the life-history of a single fish by furnishing an indication of age and of the growth rate. For this purpose the determination of the size of fish when the scales are first formed and the season of development are often of importance.

Definition of terms used. Since there is a diversity in the usage of terminology among the many authors writing on scales, a list of the terms as used in this paper follows.

Focus - the center of the scale.

Circuli - ridges arranged concentrically to the focus.

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Anterior field of the scale - that part of the scale from the focus to the anterior end of the scale which is largely embedded in the scale pocket.

Posterior field of the scale - that part of the scale from the focus to the posterior end of the scale. It projects out of the scale pocket and is visible on gross examination after the epidermis is removed.

Papilla - the first indication of scale activity, consisting of an aggregation of dermal cells before bone formation.

Platelet - a small, bony plate without ridges that corresponds to the focus in the fully developed scale.

Primordium - the first distinguishable stage in the development of a new structure.

Lateral line scale - a scale appearing directly on the lateral line, characterized by the presence of a lateral line pore.

Predorsal region - the region of the fish extending along the mid-dorsal line from the occipital region to the origin of the dorsal fin.

Nape - the area immediately behind the occiput, the anterior

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Nape - the area immediately behind the occiput, the anterior

most part of the predorsal region.

Caudal peduncle - the region of the fish extending from the posterior insertion of the anal fin to the base of the caudal fin.

Lateral line - a canal with many pores leading to the exterior and numerous sense organs responsive to pressure changes in the water. The canal has several branches on the head which unite at the pectoral girdle to form a single tube that runs along the side of the body to the base of the caudal fin. Over the lateral line on the body canal is a series of modified scales containing pores, the exterior openings of the canal.

Standard length - the length of a fish from the tip of the snout to the base of the caudal fin. Unless otherwise indicated this is the measurement referred to in the text.

Total length - the length of a fish from the tip of the snout to the tip of the caudal fin.

CHAPTER II

HISTORICAL BACKGROUND

Although our more important works on scale study commenced in the nineteenth century, it is interesting to note that as far back as the sixteenth century work had been done by Petrus Borellus, on the features of the scale. The discovery of lenses fostered an interest in scale structures and greatly facilitated their study. In 1667 Robert Hooke, one of the pioneers of microscopy examined a representative series of fish scales and made notes on their structure. At the end of the seventeenth century Leeuwenhoek wrote on the work he had done on various members of the animal kingdom among which he refers to his work on fish scales. Besides describing the mode of growth of fish scales, he is accredited as being the first to intimate that they might furnish an index of age.

Creaser[3] points out that many men did significant

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[3] Charles W. Creaser, "The structure and growth of the scales of fishes in relation to the interpretation of their life-history, with especial references to the Sunfish (Eupomotis Gibbosus)." University of Michigan Museum, Zoological Miscellaneous Publications, 17:5, 1926.

scale work on fish in the nineteenth century. Agassiz published his "Recherches sur les Poissons Fossiles" in 1834, which helped to get classification with scale anatomy as a basis under way. Just a few years after Agassiz's work, Mandl (1839-40) published his contribution on the histological structure of the scale. Others such as Williamson (1851), Baudelot (1873), Hofer (1889), and Klaatsch (1890) added to our knowledge of the histogenesis of scale structure of the Teleosts.

In the twentieth century, especially in the last twenty five years, many scientists have engaged in fish scale study. Among these several have worked out the pattern of scale development in different species of trout. Parrott did work on Salmo trutta (brown trout), Elson on Salvelinus fontinalis (brook trout), Paget on Salmo irideus (rainbow trout), Salmo fario (brown trout) and Salmo salar (atlantic salmon) and Neave on Salmo gairdnerii Richardson (steelhead trout), Salmo clarkii Richardson (cut-throat trout), Salmo trutta Linnaeus (brown trout) and Salmo gairdnerii kamloops Jordan (kamloops rainbow trout). Ferris Neave seems to be the

only one that has done work on the development of the scale-pattern in Salmo clarkii Richardson.

Development of scales in different species of closely related fish varies to some degree. A little further along in this paper the findings of the different men and the modifications displayed in various species will be brought out.

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CHAPTER III

MATERIALS AND METHODS USED

Source of specimens. All the specimens used were wild fish provided from Dr. Koster's personal collections. The material was collected from Rio la Junta, a typical Rio Grande cut-throat trout stream in the town of Tres Ritos in Taos County, New Mexico. The fish were caught by Dr. William J. Koster, M. A. Gee and F. W. Johnson. The three series examined were taken in 1941, 1944 and 1945. The series of forty four fish ranged in size from thirty two to seventy nine millimeters in standard length. This range was selected because it covers all stages of scale development from the earliest beginnings to the time when the fish is fully scaled.

Preparation of specimens. Flat mounts of the skin were used from which the epidermis was removed because it does not play a role in scale formation and its presence interferes with observations of the scales in the deeper lying dermis. The specimens had been preserved in formalin and stored in seventy per cent alcohol. The skins

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were passed down from seventy per cent alcohol to thirty per cent. According to Paget[4] (1920), the epidermis will slough off if the skin is kept in thirty per cent alcohol for a day or so. After two days in thirty per cent alcohol, the epidermis was still intact but its removal was facilitated by the preliminary treatment. The skins were stained with Delafield's haemotoxylin and both the epidermis and the pigment layer of the dermis were scraped off with a teasing needle. In the flat mounts of skin, the dermis stained a light purple with Delafield's haemotoxylin. The papillae stood out against this background because they stained a deeper purple. The specimens were observed under binocular dissecting and compound microscopes.

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[4] Geoffrey W. Paget, "Report on the scales of some teleostean fish with special references to their method of growth." Ministry of Agriculture and Fisheries, Fish Investigation, 4:3, 1920.

were passed down from seventy per cent alcohol to forty per cent. According to Paget[4] (1920), the epidermis will slough off if the skin is kept in thirty per cent alcohol for a day or so. After two days in thirty per cent alcohol, the epidermis was still intact but its removal was facilitated by the preliminary treatment. The scales were stained with Delafield's haematoxylin and then the epidermis and the pigment layer of the dermis were scraped off with a teasing needle. In the first months of study, the dermis stained a light purple with Delafield's haematoxylin. The papillae stood out against the background because they stained a deeper purple. The specimens were observed under binocular dissecting and compound microscopes.

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CHAPTER IV

AN OUTLINE OF SCALE DEVELOPMENT

Scales arise from the integument of fishes which consists of two distinct parts, the epidermis and the dermis. Each, in turn, is composed of several layers of cells. The epidermis forms the outer covering of the body and is highly glandular. The dermis is usually much thicker than the epidermis and is comprised largely of connective tissue. In each layer of the integument there is a variety of pigment cells or chromatophores which gives color to the skin.

Several investigators have undertaken histological work to determine whether one or both layers of the skin are involved in cycloid scale production. It is generally agreed upon by recent writers such as Tims,[5] Creaser[6] and

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5 H. W. Marett Tims, op. cit., p.61.

6 Charles W. Creaser, op. cit., p.14.

Neave[7] that teleost scales of the cycloid type are wholly a product of the dermis and remain as such throughout their existence. These scales are thus different in origin from the placoid scales of the Elasmobranchs which are formed by the secretory activity of cells in both the epidermis and the dermis.

Although the fundamental phases of scale development are essentially the same along the lateral line and over the rest of the body surface, there is a variation in the method of formation of the two kinds of scales. The following description of the phases involved in scale formation applies to both the lateral line scales and to the body scales. The differences in development displayed by each are described in more detail later.

The development of cycloid scales may be divided into three arbitrary phases. A small, round papilla that expands chiefly in diameter comprises the first stage.

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[7] Ferris Neave, "Origin of the teleost scale-pattern and the development of the teleost scale." Nature (London), 137:1034, April, 1936.

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[7] Ferris Neave, "Origin of the teleost scale-pattern and the development of the teleost scale," Nature (London), [illegible], 1943.

Neave[8] says that a papilla results from a local increase of dermal cells and that the aggregation lies just beneath the epidermis. He indicates that similar accounts have been given by men who have made histological studies of the subject such as Paget (1920), Goetsch (1921) and Setna (1934). When a papilla attains a certain size, bony material is deposited in the form of a platelet. This constitutes the second phase of development. The platelet is without ridges, and corresponds to the focus of the definitive scale. In a very short time the platelet acquires ridges and the structure is considered a scale.

Most authors, amongst whom are Paget,[9] Parrott[10] and Neave,[11] are in agreement that the first indications of

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[8] Ferris Neave, "The development of the scales of *Salmo*." *Transactions of the Royal Society of Canada*, 30: 57, 1936.

[9] Geoffrey W. Paget, *op. cit.*, p.4.

[10] Arthur W. Parrott, "The variability and growth of the scales of brown trout (*Salmo trutta*) in New Zealand." *Transactions and Proceedings of the New Zealand Institute*, 63(64):499, 1933(1934).

[11] Ferris Neave, *op. cit.*, p.57.

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[9] Geoffrey V. [illegible], op. cit., p. [illegible].

[10] Arthur [illegible]. Everhart, "The variability and growth of the scales of brown trout (Salmo trutta) in New Zealand," Transactions and Proceedings of the New Zealand Institute, 83(64):409, 1953(1954).

[11] Ferris Neave, op. cit., p. 67.

papillae are to be sought on or near the lateral line. In the Rio Grande cut-throat trout the first indications of papillae are along the lateral line. The first papillae are called lateral line papillae to distinguish them from other papillae that develop into body scales. The lateral line papillae are formed first in the anterior and median regions of the lateral line and last along the caudal peduncle. Each lateral line scale is formed by the fusion of two primordia. In this respect the lateral line scales are different from other scales of the body which are formed from a single primordium.

Soon after the lateral line papillae are formed, body scale papillae arise. Above and below the lateral line, oblique rows of developing body scales progress rapidly across the underlying myotomes toward the cephalic end of the body until the entire body is scaled.

In the two succeeding chapters scale development along the lateral line and the general body surface will be discussed in more detail. Since the lateral line papillae are the first to appear, scale development on the lateral line will be discussed foremost.

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Soon after the lateral line papillae are formed, body scale papillae arise, above and below the lateral line, oblique rows of developing body scales progress rapidly across the underlying myotomes toward the cephalic end of the body until the entire body is covered.

In the two succeeding chapters scale development along the lateral line and the general body surface will be discussed in more detail. Since the lateral line papillae are the first to appear, scale development on the lateral line will be discussed first.

CHAPTER V

SCALE DEVELOPMENT ON THE LATERAL LINE

Development of the lateral line. The lateral line on the body first appears as a shallow groove. As a fish develops, the groove becomes transformed into a canal by the development of scales and other tissues over the depression. The completed lateral line canal opens to the exterior by way of a pore in each lateral line scale.

Development of an individual lateral line scale. Shortly after the appearance of the lateral line groove, papillae, roughly circular in shape, are formed. These are arranged in pairs at regular intervals along the line, one member of each pair being on either side of the groove. Each papilla increases in size and changes from circular to crescentic in outline. The pairs of crescent-shaped papillae appear as a series of parentheses laid end to end along the lateral line with short spaces intervening between each pair. (Figure 1 illustrates this).

The anterior ends of each pair of crescent-shaped papillae grow toward one another until they meet and fuse

over the lateral line groove. After the two primordia have united, osseous material is laid down and a lateral line scale comes into being.

At first the lateral line scale is a U-shaped structure with the arms of the U directed caudally. (This is illustrated in Figure 3). These two arms or processes grow toward one another and eventually fuse leaving a small opening for the pore of the lateral line canal. The circular outline of the lateral line scale is complete with the convergence of the two processes. As a lateral line scale continues to grow it comes to overlap the scale immediately posterior to it.

Sequence of development. Circular lateral line papillae first appear in the anterior and middle regions of the trunk along the lateral line when fish are about thirty five to thirty six millimeters in length. When such papillae appear on the caudal peduncle in fish of thirty seven millimeters, the other papillae are already crescent-shaped.

Lateral line papillae apparently grow rapidly for, in specimens thirty eight millimeters in length, the two

over the lateral line groove. [illegible] the [illegible] have united, ectoderm material [illegible] over the lateral line would come into being.

At first the lateral line [illegible] contact with the [illegible]. This is illustrated in Figure [illegible]. These [illegible] grew toward one another [illegible] small opening for the pore of the lateral line canal. The circular outline of the lateral line canal [illegible] the convergence of the [illegible] lateral line would continue to [illegible] mediately posterior to it.

Sequence of development. [illegible] papillae first appear [illegible] of the trunk along the lateral line [illegible] thirty-five to thirty-six millimeters [illegible] each papillae appear [illegible] in fish of thirty seven millimeters, the [illegible] papillae are [illegible] crescent-shaped.

Lateral line papillae [illegible] in specimens thirty-eight millimeters in length. [illegible]

primordia immediately behind the pectoral girdle are joined in approximately the center of the line. By the time a length of forty one millimeters has been reached all the lateral line primordia have united.

Bony material is laid down in the fused primordia to form a lateral line scale when the fish measures about forty one to forty two millimeters. Such scales are at first present only in the anterior part of the trunk. Bony material is deposited in all of the fused primordia by the time fish are about forty four millimeters in length.

In fish of forty five millimeters lateral line scales with two posterior processes are present throughout the line. (Figure 4 shows lateral line scales with two posterior processes). These protrusions are beginning to unite in the scales directly behind the pectoral girdle when fish are about forty eight millimeters in length. All the lateral line scales have their posterior processes united when fish are about sixty five millimeters.

Growth on the lateral line takes place in an anterior-posterior direction. The first few stages of scale development progress rapidly but the fusion of the two pos-

primordia immediately behind the pectoral girdle are joined in approximately the center of the limb. By the time a length of forty one millimeters has been reached all the lateral line primordia have united.

Bony material is laid down in the basal membrane to form a lateral line scale when the fish measure about forty one to forty two millimeters, with scales not first present only in the anterior part of the trunk. Bony material is deposited in all of the canal primordia by the time fish are about forty three millimeters in length.

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Growth on the lateral line scale takes place in an antero-posterior direction. The first few stages of scale development progress rapidly but the scales of the sub-

terior excrescences requires a long time for completion. The entire process of lateral line scale development takes place from the time the fish are about thirty five millimeters until the fish are sixty five millimeters in length. By this time almost all the rest of the body surface is covered with scales.

CHAPTER VI

SCALE DEVELOPMENT OVER THE GENERAL BODY SURFACE

Body-scale papillae are formed later than the lateral line papillae. However, the first body scales develop bony material before any of the lateral line scales.

Development of an individual body scale. Shortly after the lateral line papillae are formed, the first body-scale primordia appear close to those of the lateral line scales. In the anterior region of the trunk posteriorly to approximately the origin of the dorsal fin, body-scale papillae are about twice as numerous as the lateral line papillae, being arranged two to every one lateral line papilla. One papilla is found directly opposite a lateral line papilla while the other is found over the gap between two consecutive lateral line papillae. (This is shown in Figure 2). Over the middle and caudal portions of the body, they are arranged one to each lateral line papilla. Here only the papillae opposite the lateral line primordia are present.

Each papilla grows and bony material is deposited in

the form of a platelet. After further growth, the platelet acquires circuli and is considered a scale. Each scale is embedded in a scale pocket, in which it remains throughout life. As a scale continues to grow in length and in width it comes to overlap the scales immediately posterior and toward the lateral line. This holds true for the scales both dorsal and ventral to the lateral line. Scales continue to grow and to acquire more circuli throughout life.

Sequence of development. The first body-scale primordia appear next to the lateral line papillae in the middle and posterior regions of the trunk when fish are from thirty six to thirty seven millimeters in length and in the anterior region of the trunk at about thirty eight millimeters. Most scale activity proceeds from these original body-scale papillae in oblique rows that are directed anteriorly both dorsal and ventral to the lateral line. The rows are inclined at about a 60° angle to the lateral line. In a single oblique row all phases of scale development are represented, papillae, platelets and scales with the most advanced stages nearest the lateral line.

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For example, a typical row in a forty two millimeter specimen presents this picture. Starting at the lateral line the row has five scales, two platelets and three papillae. The first four scales overlap one another but the scale nearest to the platelet lies parallel to the skin. The scale next to the lateral line has five circuli while the scale furthest from the line has only two circuli. The platelets also lie parallel to the skin surface. The size of the three papillae varies from a dot to a structure about the size of a platelet. Growth of each structure in the oblique rows seems to be initiated by the one immediately behind it. This seems to be the case because in the same region of the trunk some rows are longer than others. The longest rows are those below the dorsal fin. However, the caudal peduncle is the first region of the body to become completely scaled because there is less surface area there. Over the body, development of the scales proceeds most rapidly in this order median, posterior and last anterior. In these regions activity advances faster dorsal to the lateral line than ventral to it. The only deviation from the

For example, a typical row in a forty-two milli-meter specimen presents this picture. Starting at the lateral line the row has five scales, two platelets and three papillae. The first four scales overlap one another but the scale nearest to the platelet lies parallel to the skin. The scale next to the lateral line has five circuli while the scale farthest from the line has only two circuli. The platelets also lie parallel to the skin surface. The size of the above papillae varies from a dot to a structure about the size of a platelet. Growth of each structure in the [illegible] [illegible] is indica-ted by the one immediately behind it. This would be the case because in the [illegible] region of [illegible] rows are longer than others. The [illegible] rows are [illegible] below the dorsal fin. However, the [illegible] [illegible] is the first region of the body to become completely scaled because there is less surface area there. From the high development of the scales present here rapidly in these order median, posterior and last anterior. In these regions activity advances faster dorsal to the lateral line than ventral to it. The only deviation from the

general pattern of development of oblique rows of papillae that start from the lateral line at nearly the same time is shown by fish in a later stage of development, about fifty millimeters, which have a single row of large papillae that starts ventral to the lateral line and extends along the posterior margin of the pectoral girdle. The entire caudal peduncle is scaled when fish are forty six to forty seven millimeters in length.

When a length of sixty three millimeters has been reached the trunk is scaled except for the predorsal region and the breast between the pectoral and pelvic fins. In fish of sixty eight millimeters only the nape remains unscaled. Scalation of the body is complete earlier in some fish than in others but usually occurs when fish are sixty nine to seventy millimeters in length. The head and fins do not become scaled.

On any given fully scaled fish there is a variation in the size of the scales and in the number of circuli present. The scales nearer the dorsal and ventral margins are more rounded in shape and smaller in size than the scales close to the lateral line. The marginal scales also con-

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When a length of sixty three millimeters has been reached the trunk is scaled except for the pectoral region and the breast between the pectoral and pelvic fins. In fish of sixty eight millimeters only the throat remains unscaled. Squamation of the body is completed earlier in some fish than in others but usually occurs when fish are sixty nine to seventy millimeters in length. The head and fins do not become scaled.

On any given fully scaled fish there is a variation in the size of the scales and in the number of circuli present. The scales nearer the dorsal and ventral margins are more rounded in shape and smaller in size than the scales close to the lateral line. The marginal scales also are-

tain fewer circuli. As the body of the fish lengthens, the scales increase in size and add more concentric ridges.

The three series examined include specimens hatched in three different years. The series were taken in June, 1941, September, 1944 and April and October, 1945. The 1940 brood was caught June, 1944, the 1944 brood in September 1944 and April 1945 and the 1945 brood in October 1945. The results given in the text are based on the 1944 and 1945 series. These two broods are essentially identical in the time when various stages of development occur. The 1941 series shows lateral line papillae occuring in fish of thirty three millimeters and body-scale papillae in fish of thirty five millimeters which is slightly earlier than the results given in the text. Throughout the 1941 series growth in each phase of development takes place a little sooner than the results given. The difference is not great, however, as the most extreme variations were less than four millimeters.

CHAPTER VII

SUMMARY OF LITERATURE

As already noted, several men have worked on the pattern of scale development in several closely related species of *Salmo*. In most respects scale development in these various species correlates but, in others they differ. In the following discussion the extent of the research of these men and their findings will be brought out.

Geoffrey Paget (1920) worked with specimens of rainbow trout (*Salmo irideus*), brown trout (*Salmo fario*) and the atlantic salmon (*Salmo salar*). Although he does not state the size range of the series used, he indicates that brown trout ranging in size from twenty nine to seventy five millimeters exhibit all stages from first indications to complete investment. His materials were fixed in Bles' fluid and Bouin's Picroformal and stained with Delafield's haemotoxylin.

Arthur W. Parrott (1933) also worked with a series of formaldehyde preserved specimens of brown trout (*Salmo*

trutta) ranging in size from twenty to eighty millimeters.

Ferris Neave worked largely with a series of Bouin or formalin fixed specimens of the kamloops rainbow trout (*Salmo gairdnerii kamloops* Jordan). The series ranged in size from twenty to fifty five millimeters. He also extended his examination to a series of formalin-fixed steelhead (*Salmo gairdnerii* Richardson), cut-throat (*Salmo clarkii* Richardson) and brown trout (*Salmo trutta* Linnaeus). Flat mounts of the skin, whole mounts of individual scales and transverse sections of the whole body and of the skin were used.

Paget found that in brown trout (*Salmo fario*), papillae appear when the fish are between twenty seven to thirty millimeters in length. Parrott's results on brown trout (*Salmo trutta*) agree with those of Paget. He found the first signs of papillae in specimens from twenty four to twenty eight millimeters. In the four varieties of *Salmo* that Neave examined he found that the stages in the development of papillae appear to be precisely similar. There are however, variations in the different species as to the body

size at the time of papilla formation. In the kamloops rainbow trout and brown trout (*Salmo trutta*) papillae appear when fish are twenty five millimeters in length. This checks with the findings of Paget and Parrott on brown trout. In the steelhead (*Salmo gairdnerii*) and cut-throat trout (*Salmo clarkii*) papillae appear slightly later, in fish of about thirty one to thirty two millimeters in length. This is slightly earlier than the present results which indicate that papillae are first formed in fish of thirty five to thirty six millimeters.

These men differ as to the place where papillae are first observed, along the lateral line. Paget states, "it is in the posterior and median region that scale papillae may first be noted, and that from this region their development extends posteriorly and anteriorly."[12] Parrott's results are similar to those of Paget on this point. Whereas, Neave found that the papillae first appear in the anterior and median regions of the trunk and from there spread caudally. Thus, Neave's statement disagrees with the

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[12] Geoffrey Paget, *op. cit.*, p.4.

also at the time of papilla formation. In the rainbow trout and brown trout (*Salmo trutta*) papillae appear when fish are twenty two millimeters in length. This checks with the findings of Fagot and Parrott on brown trout. In the steelhead (*Salmo gairdnerii*) and cut-throat trout (*Salmo clarkii*) papillae appear slightly later, in fish of about thirty one to thirty two millimeters in length. This is slightly earlier than the present results which indicate that papillae are first formed in fish of thirty five to thirty six millimeters.

These men differ as to the place where papillae are first observed, along the lateral line. Fagot says, "It is in the posterior and median region that the papillae may first be noted, and that from this region their expansion extends posteriorly and anteriorly."[12] Present results are similar to those of Fagot on this point. Whereas, Beave found that the papillae first appear in the anterior and median regions of the trunk and from there spread caudally. Thus, Beave's statement disagrees with the

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[12] Godfrey Fagot, *op. cit.*, p.4.

other two on this phase of development in brown trout. In the Rio Grande cut-throat trout the results of papillae formation are similar to the findings of Neave.

Parrott found that in brown trout (Salmo Trutta) the rows that start from the lateral line proceed more rapidly dorsally than ventrally. In this respect brown and cut-throat trouts are similar in their development. Parrott[13] noted that scales in different regions of the body vary in length and in the number of circuli that they contain. In this aspect of scale study Parrott[14] points out that his findings are similar to those of Esdaile. A similar condition also exists in the Rio Grande cut-throat trout.

Neave is the only author that offers an explanation as to the agent that starts the whole process resulting in scale formation. He says,

> In considering the general course of scale development it becomes more and more apparent that the lateralis branch of the vagus nerve is

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[13] Arthur W. Parrott, op. cit., p.514.

[14] Loc. cit.

> a prime agent in initiating a series of developments resulting in the complete scalation of the body.[15]

The lateralis branch of the vagus nerve would seem to start the activity of dermal cells to form papillae.

Neave indicates that although the individual scale development is similar in the species of *Salmo* that he observed, one distinct difference in the pattern of scale development was noted in brown trout (*Salmo trutta*). Neave says,

> Examination of brown trout about 3.6 to 4.5 centimeters in length shows that a small patch of papillae (and subsequently scales) develops independently of the other body scales on the mid-dorsal line a little behind the supratemporal canal.[16]

Both Paget and Parrott seem to have overlooked this phenomenon.

Neave makes no mention of the single row of papillae along the pectoral girdle that occurs in out-throat trout when specimens are about half scaled.

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15 Ferris Neave, *op. cit.*, p.67.

16 *Ibid.*, p.60.

CHAPTER VIII

SUMMARY AND CONCLUSION

A series of forty four specimens of Salmo clarkii spilurus Cope were examined to determine the general pattern of scale development and the size of fish when scales are first formed. The fish ranged in size from thirty two to seventy nine millimeters in standard length and included specimens without signs of scale formation as well as those with scalation complete. Individuals hatched in three different years were included in the series. Although the fish in the three year groups were essentially similar, the 1940 year class shows the first signs of papillae at thirty three rather than at thirty five or thirty six millimeters as in the 1944 and 1945 year classes.

Each scale passes through three phases in its development, papilla, an aggregation of dermal cells, platelet, a bony plate without circuli and finally a scale with circuli. The lateral line scale differs in formation from the body scale in that, it originates from two pri-

mordia rather than one.

Lateral line papillae appear simultaneously along the middle and anterior regions of the line and later along the caudal peduncle. This agrees with Neave's findings on kamloops rainbow trout, steelhead, cut-throat and brown trout and is in contrast with Paget's and Parrott's findings on brown trout. Bony material is laid down first in the lateral line scales at the anterior end of the lateral line and then in the scales along the remainder of the line.

Soon after the lateral line papillae are formed, body-scale papillae arise dorsal and ventral to each lateral line primordium. Some papillae are found directly opposite a lateral line papilla while others are found over the gaps between consecutive lateral line papillae. Starting from these papillae, oblique rows of body-scale papillae develop above and below the lateral line. These rows progress anteriorly and are inclined at about a 60° angle. A single row of papillae and subsequently scales develops immediately behind the pectoral girdle, ventral to the lateral line. None of the other workers mention

series rather than one.

Lateral line papillae appear simultaneously along the middle and anterior regions of the trunk and later along the caudal peduncle. This agrees with the similar findings of Landacre [illegible] and brown trout and is in contrast with [illegible] and Parrott's findings on brown trout. [illegible] down first in the lateral line anterior to the [illegible] of the lateral line and then in the [illegible] along the remainder of the line.

Soon after the lateral line papillae [illegible], body-scale papillae which later [illegible] the lateral line primarily [illegible] directly opposite a lateral line papilla [illegible] over the gaps between successive lateral line papillae. Starting from these papillae, [illegible] papillae develop above and below the lateral line. These rows progress anteriorly and are inclined at about a [illegible] angle. A single row of papillae [illegible] develops immediately below the [illegible], ventral to the lateral line. [illegible]

this phenomenon.

Although growth of the oblique rows is most rapid in the middle of the body, the posterior portion is the first to become completely scaled. Scalation of the predorsal and breast regions occurs last, taking place long after the remainder of the body is covered. Complete scalation occurs in fish of sixty nine to seventy millimeters.

this phenomenon.

Although [illegible]

in the middle of the [illegible]

first to become completely [illegible]

dermal and [illegible] region [illegible]

after the remainder of the body [illegible]

exclusion occurs [illegible]

pattern.

PLATES

EXPLANATION OF PLATES

Figure 1. Shows the arrangement of lateral line papillae along the lateral line. The figure was made from a fish of thirty five millimeters in length.

Figure 2. Shows the arrangement of papillae in the anterior half of the body. The figure was made from a fish of thirty seven millimeters in length.

Figure 3. Shows two lateral line primordia joined in approximately the center of the lateral line. The figure was made from a fish of thirty eight millimeters in length.

Figure 4. Shows the lateral line scales with two posterior processes. The figure was made from a fish of fifty millimeters in length.

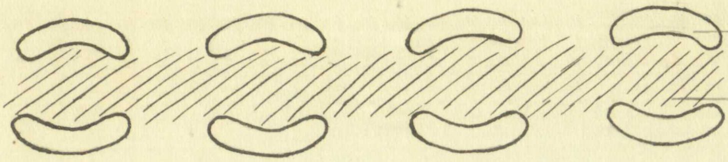

FIGURE 1

FIGURE 2

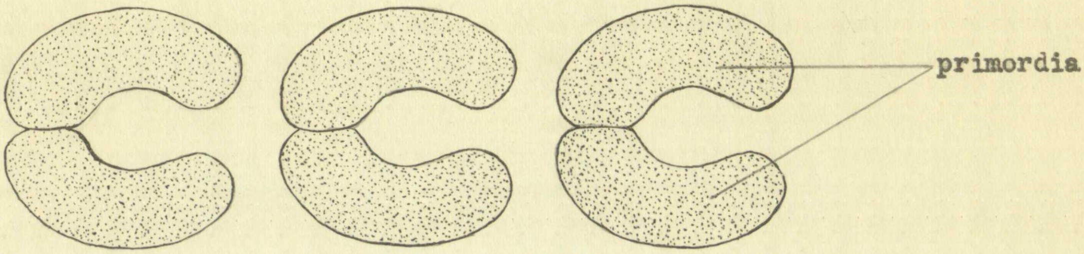

FIGURE 3

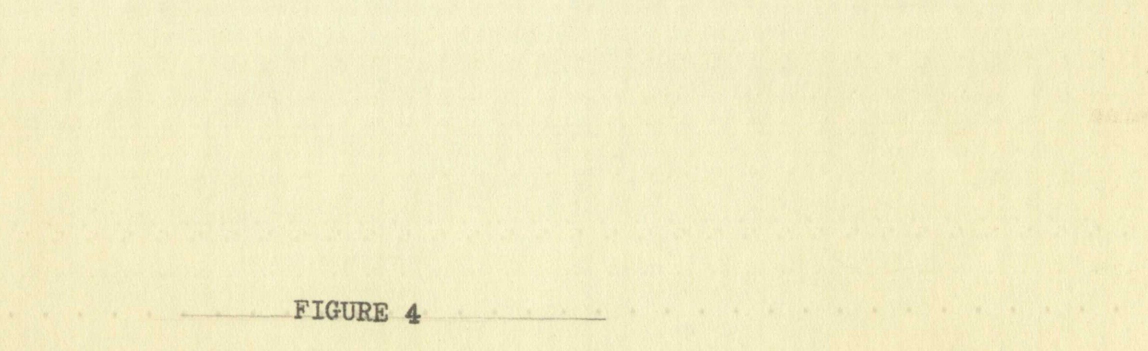

FIGURE 4

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