THE STRUCTURE AND GROWTH OF THE SCALES OF THE SQUETEAGUE AND THE PIGFISH AS INDICATIVE OF LIFE HISTORY

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Contribution from the United States Fisheries Biological Station, Beaufort, N. C.

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INTRODUCTION.

Since the invention of the microscope, fish scales have been the subject of numerous investigations and heated controversies [b] relating almost wholly to structure, phylogenetic relations, and taxonomic value. It was not until 1898 that scales were thought to bear evidences of the age and life history of the fish, when Hoffbauer (1898, 1900) observed on the scales of carp concentric rings which he supposed to be growth rings. The discovery of these rings and their supposed relation to age and life history has actuated a renewal of investigations in England, Germany, Scotland, Norway, and other countries.

These concentric rings (or annuli, as they are called in this paper) are supposed to be produced by varying rapidities of growth. This theory has been applied minutely to investigations of Atlantic salmon and English brook trout and, to some extent, to cod, flounder, sole, eel, halibut, smelt, herring, mackerel, and other fishes, and by it an elaborate life history of the salmon has been worked out.

The theory has been objected to, especially by Tims (1906) and Brown (1903). The uncertainty existing as to regeneration and constancy of growth has given rise to grave doubts as to the reliability of these indications of age and life history. The fact stands out, as Masterman (1913a) shows, that these indications of age have never been satisfactorily tested; the relation of the annuli to growth has been a supposition, and investigations have been limited to a small number of species.

In America Cockerell, only, has worked on the taxonomy of scales, Nickerson, Ryder and Cockerell on their phylogenetic relations, and it is only recently that work on life history has been begun by Gilbert and McMurrich on the Pacific coast salmon, and Thompson on the halibut.

It is the purpose of this paper to embody the results of investigations directed toward explaining the various scale characters employed in the determination of life history, their origin, constancy, bearing on life history, the various methods of detecting them,

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[a] The writer acknowledges with thanks the assistance in writing this paper and valuable suggestions as to illustrations by Dr. J. J. Wolfe.

[b] For an excellent review of the literature of fish scales, see Thomson (1906).

and a few other observations not closely allied to the main subject. These investigations have been carried on with *Cynoscion regalis* and *Orthopristis chrysopterus*, the scales of which have not been hitherto investigated, with the hope that the results might broaden the knowledge of scales, either by corroborating, modifying, or contradicting the extant theories.

There are also some observations of the radii with a discussion in which a conclusion is reached that is quite at variance with all previous theories of their origin. If this conclusion is sufficiently borne out by facts, it will either negative or seriously modify systems of classification employing the radii as characters.

A review of literature is necessary in order to bring out the investigations in the light of what has already been done.

REVIEW OF LITERATURE.

FASTENING TO INTEGUMENT.

Peters (1841) was the first to devote his attention to scales as a part of an integumental organization. He gives the following analysis of the skin: (1) Epidermis composed of squamous cells; (2) layer of pigmented cells; (3) skin proper, a layer composed of fibrous connective tissue and containing fatty globules; (4) an exceedingly thin membrane on the exterior surface of the scale, but distinct from the skin to which it is intimately fastened. In this are found the circuli and radii. He maintains that scales are not found on the epidermis, but in the skin itself.

Baudelot (1873) described scales as contained in sacs and more or less visible to the exterior, but in some cases (eels, etc.) covered entirely in the skin. The epidermis sometimes extends so far over the posterior field as to be pierced by the teeth in cases of ctenoid scales. The degree of firmness of anchorage to the scale pocket varies from species to species. In imbricated scales, the free portion has intimate connection with the skin. In saying that they are contained in dermal sacs, he implies an agreement with Peters as to their dermal origin.

Vogt (1842) advances an interesting theory as to the nature of the scale pocket. He regards it merely as a fold in the epidermal membrane. By this he implies that scales have their origin in the epidermis.

Leydig (1851) says: "The scales of most of our fresh-water fishes appear partly as ossifications of flattened skin continuations which are generally termed 'scale pockets.'" This is close to Vogt's theory, but he confuses "skin" with epidermal folds.

In considering the work of Klaatsch (1894), done on trout, *Esox*, and several cyprinoids for the younger stages, I can do no better than quote what he has to say about the fastening to the integument:

> Under the epidermis, which contains a large number of mucous cells, the dermis is seen to be raised in a series of projections, each of which corresponds with the posterior free end of the scale. Each scale lies in an oblique direction from behind forward and becomes inclosed in a compartment of the dermis, the so-called "scale pocket." In this scale pocket one distinguishes an outer and an inner wall. The outer wall consists, in its posterior part, of loose connective tissue containing numerous chromatophores; in the anterior part, the outer wall is composed of tense connective tissue which is similar to the inner wall of the adjoining anterior scale pocket. The fibrous projections of this connective tissue of the outer

wall of the scale pocket unite themselves at the anterior border of the scale with the deepest layer of the dermis in which the fibers have a course parallel with the surface of the body. The inner wall of the scale pocket at its posterior part unites with the outer wall of the adjoining posterior pocket. Farther forward it is built up of the fibrous processes of the deep epidermal layer. Near the scale its condition changes, as immediately toward the inside the same number of cells is found in a ground substance only slightly developed and not fibrillated. The fibers of the deep dermis layer have a similar arrangement to that of the ganoids and selachians.[a]

FORM AND MODE OF ORIENTATION.

Ryder (1893) worked on the arrangement of the scales on the body, seeking to account for their arrangement in rows and their imbrication. He shows that scales may lie in rows in three directions: (1) Downward and backward; (2) downward and forward; (3) along the long axis of the body.

He advances a most interesting opinion in explanation of this method of orientation, viz., that it is due to the segmentally arranged muscles of the body. In support of this he notices that in archaic types the number of scales corresponds with the number of somites in the body. He summarizes two important conclusions:

1. Scales of fishes bear a segmental relation to the remaining hard and soft parts of the body and are either repeated consecutively in oblique rows corresponding to the number of segments, or they may be repeated in rows corresponding to the number of somites, or segmental reduction may occur which may affect the arrangement of the scales so as to reduce the number of rows below the number of somites indicated by the other hard and soft parts.

2. The peculiar manner of interdigitation of the muscular somites as indicated by the sigmoid outline of the myocommata as seen from their outer faces and the oblique direction of the membrane separating the muscular cones has developed a mode of insertion of the myocommata upon the corium which has thrown the integument into rhombic areolæ during muscular contraction. These areolæ are in line in three directions and the folds separating them, particularly at their posterior borders, are inflected in such a manner by muscular tensions due to the arrangements of the muscular cones as to induce the condition of imbrication so characteristic of the squamation of many fishes.

Ryder seems to be the only scale investigator who takes into consideration the adaptation of the stiff scale to the movements of the fish's body—a subject which will be considered in connection with the function of the radii in another part of this paper.

Under the caption "Form and mode of orientation" in his paper, Baudelot (1873) takes notice only of the extreme variability, from genus to genus, from species to species, between individuals and even in the same individual. It is a well-known fact among modern taxonomists that the number of scales in longitudinal rows is constant enough within certain limits to be a valuable taxonomic character.

SIZE.

The basis of age determinations is the fact that the scales are constant throughout life, both in identity and number. Steenstrup (1861) noted that cycloid, ctenoid, and ganoid scales grow throughout life and increase in size proportionately to that of the fish, while placoid scales never exceed certain limits, but fall off, giving rise to others. The size and shape are agreed upon as constant within certain limits, and Cockerell and others use them as taxonomic characters. It is understood, however, that size is by no means constant.

[a] Thomson's translation.

CIRCULI.

The concentricity of the circuli suggested their connection with growth as early as 1716, when Réaumur said of them: "They occupy the borders of each layer and they represent different degrees in the growth of scales."

It seems that the difficulty in cutting cross sections has been largely responsible for the confusion as to the nature of the circuli. They have been variously regarded as the ends of laminæ, grooves for blood vessels, "cellular lines," growth rings, crossings of transverse fibers in the superior layer, etc.

Peters (1841) admits a difficulty with the circuli. He contends that they are not the ends of laminæ, because they are not always parallel with the outer edge of the scale, but are sometimes perpendicular, a condition that could never occur in the case of lamina edges. His only attempt at explanation was that "the crossing of the fibers in the superior layer seems to explain the circuli."

Agassiz (1834) thought that the number of circuli agreed with the number of laminæ in the inferior layer, but Peters was never able to bring himself to this opinion Blanchard (1866) rejected this theory because he found that in some species the number of circuli is the same in the young as in the old.

The "cellular lines" of Mandl (1840) are explained thus: "The laminæ are not superimposed layers, but have their origin in special cells in the superior layer and finally become lines"—a rather vague explanation.

Salbey (1868) attempted to show by vertical sections that they have no connection with the laminæ, but that they belong to the superior layer, and may disappear or be replaced, or new ones may be interposed between them.

Baudelot (1873) gives a thorough description of the circuli under the following scheme:

1. Presence: (*a*) May be present over the entire scale; (*b*) may be partially present (on the periphery); (*c*) may be absent.

2. Disposition: (*a*) Concentric; (*b*) regularly concentric at periphery, irregular at center.

3. On posterior field: (*a*) Sometimes appear; (*b*) sometimes very rare, losing their regularity and becoming enlarged at certain points or covered with tubercles.

4. Other modes of orientation: (*a*) Perpendicular with contour, but parallel with each other.

5. Number: (*a*) Greater in anterior than in lateral field; (*b*) greater in lateral than in posterior field

He finds the form of the circuli to be a ridge with its edge turned toward the focus Its edge is somewhat serrate, resembling the teeth of a saw. He notes zones where circuli appear to be closer together. He considers the circuli as having some relation to the moorings to the body, suggesting them as holdfasts. To show that they are not edges of laminæ he makes the following observations:

(1) The circuli very rarely effect a complete arrangement in the form of concentric lines; (2) the circuli may be perpendicular to the contour of the scale; (3) they may show the most irregular arrangement, become folded up against one another, entangled in all directions, or even form a sort of network of irregular meshes; (4) the circuli are appendages of the superficial layer of the scale; (5) they originate at the margin of the scale as points of isolated calcification; (6) they show a marked inclination to the focus.

To sum up his conclusions, he rejects Agassiz's idea that the circuli are the edges of laminæ. He considers them as related to the mooring of the scale to the integument and not as necessary organs of the scale. He finds the zones of apparently unequally distant circuli (annuli) which constitute the basis of the modern system of age determination. Variations in the number of ridges are not usually great on scales from similar positions on the bodies of fish of the same species. In fish of the same species but of different ages the number of ridges increases proportionately with age and consequently also with the diameter of the scale.

Klaatsch (1894) noticed that the concentric arrangement of the circuli is unusual for superficial reliefs. He says that in trout the cells arrange themselves so as to correspond exactly with the circuli. He further states:

> One might expect that the superficial scleroblast layer would cover the deeper cell layer with its product so that the constituent part of the ridges would be taken up in the interior substance of the scale. This does not, however, occur. The cells arrange themselves as they pass through the changes described, so that they come to lie in the external surface of the ridges and contribute to their enlargement. They elaborate, as it were, the upper relief surface of the scale, for which the deeper cells had only supplied the foundation.

Ussow (1897) noticed the same thing, but at a later stage when the ridges had entirely formed. At the stage when the reliefs occurred for the first time no such aggregations existed. It is possible that these cells later take part in the formation of the reliefs, but he believes that the commencement of their formation arises at the expense of the peripheral elements of the papilla.

Tims (1906), in his work on cod scales, arrives at very different conclusions. He describes the circuli as a series of scalelets with their peripheral borders turned up by the pull of the stretched pocket. He notes the lateral fusion of two or more scalelets which, if carried out completely, would result in the typical clupeoid scale which is composed of eccentric imbricated rings.

In the recent work of Miss Esdaile (1912) are found detailed statistics relating to the circuli (which she calls annuli), their number and disposition, and, especially, enumerations of their occurrence on scales of different parts of the body. She finds that there is a uniform variation in their occurrence, an observation of much importance in age determination. Her conclusions are:

> 1. A great variation in the number of annuli and in the lengths of the scales taken from different parts of the body of the same fish is clearly indicated. This was found on each of three fish [*Salmo salar*], but the results obtained seem to be in no way correlated.
>
> 2. It is to be noticed that in the three fish examined the number of annuli in each peronidium increases from the head to the adipose fin, and then diminishes toward the tail. A similar increase and decrease is found on both the dorsal and ventral sides of the lateral line.
>
> 3. In a comparison of scales taken from positions at corresponding distances from the head on both dorsal and ventral sides of the lateral line it is seen that, as a general rule, the scales on the dorsal side have fewer annuli in each peronidium.[a]

Masterman (1913a) regards the circuli as stiffening or supporting tissue of the scale. His discussion is, however, directed not so much toward the morphological significance of these structures as toward their bearing on age determination. Consequently his discussion of this subject is treated in this paper under the heading "Age determination."

[a] Miss Esdaile has adopted the word "peronidium" as meaning that part of the scale which represents the growth of a summer and a winter together.

SPINES.

Kuntzmann (1824) described what he regarded as two distinct kinds of spines: (1) Spines which molt, and (2) permanent spines, which are integral parts of the superior layer of the scale. Mandl (1840) thought spines were comparable to true teeth. Leydig (1851) regarded them as extensions of osseous corpuscles, a view shared also by Peters. Salbey (1868) considered them as integral parts of the superior layer appearing successively at the posterior margin of the scale and which constantly wear away.

Baudelot (1873) gives a detailed description of all the variations of spines, which is too long to reproduce. He concludes, among other things, that their number increases with age and on different parts of the body, and in places where they are rudimentary they may drop off, leaving cycloid scales. He advances the theory that the spines have their origin in the serræ on the edges of the posterior circuli. In support of this hypothesis he uses the following arguments:

> In many scales * * * the edges of the circuli present a series of very distinct microscopic indentations, and in some ctenoid scales the spines are so small as to appear only as indentations of the circuli of the posterior region which have become very prominent. In many cycloid scales the posterior region shows a series of tubercles arranged with as much regularity as the spines and presenting a striking analogy to these structures. These tubercles are, however, only partial thickenings of the concentric ridges (circuli). In the same fish the scales become altered and pass from the ctenoid to the cycloid condition, and in that case it frequently happens that the spines become replaced by simple ridges.[a]

This substitution is to him sufficient proof of the homology of the spines and the circuli.

Klaatsch (1890) makes the cycloid scale typical of teleosts, because "(1) it represents simple conditions, and (2) it supplies a suitable object for placing the skin covering of the teleosts in line with the selachians and ganoids." He regards the ctenoid scale as the result of still further specialization in the teleosts.

Ussow (1897) thinks that there is no relation whatever between placoid teeth and the spines of ctenoid scales, but that the similarity is purely accidental. He thinks that spines are formed of the same substance as the superior layer of the scale—the hyalodentine of Hofer.

Tims (1906) finds in the minute projections on the scalelets of the cod the antecedent form from which the spines of ctenoid scales are derived. If these projections (which he finds more prominent on the posterior field) be more pronounced and slightly more perpendicular, we have the spines of ctenoid scales.

Cockerell and Moore (1910) advanced a somewhat different theory, as follows:

> The teeth arise through the modification of the apical ends of the vertical circuli, i. e., circuli which in the apical region retain their vertical position. It is not evident that they have anything to do with the radii. In very highly specialized ctenoid scales * * * the teeth form a separate fringe which appears to have no intimate connection with the rest of the scale. It follows that a scale with completely transverse apical circuli can not be, and can not become, ctenoid. The reason why there are no ctenoid cyprinid scales seems to be that the group has advanced too far along the line of modification in regard to the circuli to be able to produce them.

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[a] Translation by Thomson.

RADII.

The first important hypothesis dealing with the nature of the radii was that of Agassiz (1840), who thought them "channels at the margin of the external surface which connect one layer with another and multiply during the growth of the scale." Mandl (1840) considered them as canals for transporting nutrition to the center of the scale. Peters, instead of giving them the function of connective canals, regarded them as sutures allowing growth in all directions. He also notes that they are sometimes concentric, as in *Ophidium*.

Williamson (1849) denied the existence of any such canals as Mandl described. He says that they are simply the absence of the superior tissue along their course. While they are not nutrient canals, neither do they pass through the entire calcareous portion of the scale and reach the soft portion, as Agassiz contended.

Salbey (1868) says that the radii are grooves in the superficial layer, but not through what he calls the conjunctive layer, and suggests that they are the channels for the continued calcification of the interior conjunctive substances which calcify slowly and are not in juxtaposition to any other nourishing parts. Tims considers the radii as adaptations to the increasing circumference.

Baudelot (1873) thoroughly describes radii, both as to structure and disposition. Aside from numerous variations, all of which he records minutely, mention might be made of the three main modes of disposition. These are (1) divergent from the focus; (2) parallel with each other; and (3) parallel with the contour of the scale. Their form may be that of simple lines of fissures in which the scale appears to be broken; a ravine whose sides are perpendicular with the sides of the scale; a wide and shallow trench; a groove of varying width; a series of depressions, or, in some cases, a series of small cavities in the same straight line. In regard to number, he says, "The number of radii of an individual is capable of varying with age, and if the number increases with age it may also be reduced." The same conclusions apply to the transverse or concentric grooves.

Baudelot pointed out that up to his time no satisfactory explanation of the radii had been offered, and in his attempt to explain them he attributes them to irregular calcification. He says:

> Grooves are lines of noncalcification. The exterior layer has centers of calcification which later unite with one another as these centers extend. When the union takes place laterally the grooves will be radii; otherwise they will be transverse grooves, and when calcification takes place all over at the same time there will be no radii.

Cockerell (1911) finds radii on both the anterior and posterior fields, calling the former "basal" and the latter "apical" radii. He attaches enough importance to their number to make it a taxonomic character.

FOCUS.

The center of the scale would, to most observers, suggest a center of growth; nevertheless, it has been the subject of much conjecture. Vogt (1842) first noticed that the focus is larger in the adult than in the young, suggesting wear, unless the scale, in its entirety, increases in size—a supposition very difficult to substantiate. The comparatively large focus in some cases suggested to Agassiz (1834) that it might be the result of wearing down of the thickened center. Both Peters (1841) and Salbey (1868) disagree with this, holding that since the scale is covered with a membrane constantly lubricated with mucus the wear on the hard scale would not be enough to make a noticeable difference. They account for it by a difference of growth.

Baudelot (1873) admits his inability to give an adequate explanation of the focus. He describes it with minute detail in all its variations and concludes that it and the annuli are due to the same cause but he can not tell what that cause is.

Hoffbauer (1898, 1900) calls it the center of growth representing the oldest part of the scale and also notes that in some cases it is abnormally large, but that at other parts of the same fish it is normal—observations in perfect accord with Dahl's explanation.

According to Tims (1906) "it consists of a flattened plate of calcified tissue, elliptical in shape with an irregular margin. From its appearance in section and from a surface view I believe it to be formed of a fusion of a number of basal plates, the spines of which have entirely disappeared."

Dahl (1911) gives an explanation of abnormally large foci which seems to be adequate. Those scales with such foci are simply regenerated scales, the focus being composed of secreted matter which filled the empty scale pocket following the loss of the old scale. He illustrates this with a cut, which shows his evidence to be quite conclusive.

PERFORATING CANALICULI AND INTERNAL LACUNÆ.

The observation by Blanchard (1866) of certain very small perforations through which water might freely flow seems to be the origin of the theory that scales have a respiratory function. He noticed that they are especially prominent in the Cyprinidæ.

They were first described by Baudelot, who was able to make out their structure clearly. He describes them as extremely small canals perforating the scale from top to bottom. They are found on the posterior side and pass through the scale obliquely—i. e., from the exterior surface they incline toward the periphery on the posterior side and from the longitudinal axis of the scale. They are developed from notches that appear in the posterior margin and, as the scale grows in size, the notches are surrounded by newly secreted substance becoming canals which extend through the entire thickness of the scale. As to function Baudelot thinks that nerves pass through them, thus relating them to the supposed sensory function of the lateral line.

In the interior of the scale the canaliculi may become more or less expanded, forming a cavity which, in extreme cases, pervades almost the entire scale between the inferior and superior layers. He called these lacunæ. In the case of *Dactylopterus volitans* the lacunæ are very large and are filled with a bony tissue which he regards as a connecting link between scales and bones. He confesses that he is unable to conjecture any function for them.

STRUCTURE, FORMATION, AND GROWTH.[a]

Agassiz (1834) believed scales to be analogous to nails and hair and hence not living tissue. He explained growth as taking place by secretions from the floor of the scale pocket and by the increasing size of the scale pocket, which enlarges in proportion to the size of the body of the fish. The laminæ were different leaves or folia. As to calcification, he regarded it as nonhomogeneous—i. e., occurring in corpuscles or calcareous bodies—which he believed to occur only on the superior and inferior surfaces.

[a] For a review of the older literature on scales, see Thomson, 1904.

Mandl (1839), on the other hand, considered scales living tissue capable of growth by intussusception and consisting of two layers, the superior and the inferior. The inferior layer is laminate, while the superior layer is cartilaginous, the lower part being interspersed with calcareous corpuscles. The growth of the superior layer is peripheral, while that of the inferior layer takes place by the addition of secretions from the floor of the scale pocket. He described the corpuscles as separate elements or cells in the superior layer, in definite positions, and of a yellow color which disappears on acidulation.

Peters (1841) agreed with Mandl as to the laminate structure but with Agassiz as to the location of the corpuscles, with the exception that he was unable to find them on the surface of the superior layer.

Williamson (1849) followed, adopting the opinions of Agassiz, Mandl, and Peters, with modifications. He stated that there were three layers, the superior, the inferior, and the median. The superior layer differs both in structure and origin from the other two layers. In section it presents the appearance of an undulating outline with a very faintly laminate interior structure. It extends entirely to the periphery. In early stages it is a soft membrane which later calcifies. In substance it resembles the ganoin of *Lepidosteus* (*Lepisosteus*).

The median layer is built up of a mass of lenticular calcareous bodies which unite with one another as they increase in size, losing their shape in this coalescence. In thickness it decreases from the center to the periphery until it disappears, leaving the periphery flexible. After the fusion of the corpuscles the median layer splits up into horizontal laminæ which agree in direction with the membranous laminæ which exist previous to calcification.

The inferior layer consists of numerous membranous laminæ arranged in parallel horizontal lines more numerous at the center, only one appearing at the periphery. Each lamina is composed of fibers, all parallel with each other. They are the result of the calcification of the laminæ and have their origin as small centers of calcification which grow in size by the addition of layers to the outer surface, in section giving the appearance of concentric rings. Growth takes place by the successive increase in size of the laminæ of the inferior layer.

Salbey (1868) says that the inferior layer consists of thick lamellæ, separated by thinner ones. The thin lamellæ are conjunctive, while the thicker ones are calcareous. The thinner ones finally calcify and fuse with the thicker ones, giving the older scales the appearance of having fewer laminæ, while they really have more. According to him, the mode of growth is that the inferior lamina is fastened by a conjunctive substance which eventually calcifies, after which calcification another layer of the conjunctive substance is added, which in its turn calcifies, etc.

The work of Baudelot (1873) is in greater detail than that of any of the foregoing authors and probably of more value. He states that calcium phosphate and carbonate constitute the inorganic substance of the scale. He described the tissue of scales as being a striated substance separable into laminate folia. Corpuscles are more abundant in the exterior laminæ and comparatively rare in the inner ones. They increase in size with age and two or more may fuse. They represent products of a crystalline nature and exhibit a series of concentric lines from the center to the outer surface.

The origin of a scale is a calcified spot which slowly extends until it becomes a lamina. The scale always adheres by its inferior surface and periphery and always grows by the addition of layers to the internal face. On the superior surface it is loosely connected. Subsequent calcification is from the exterior toward the interior and from the periphery toward the center.

Nickerson (1893) says:

> Throughout the series of scale structures, beginning with the selachian type, there has been a constant tendency toward the reduction of the superficial parts (spines) and increase of the deeper parts which are independent of the epidermis. * * * In the higher teleosts the whole scale growth is within the dermis and the more superficial process is entirely lost.

Klaatsch (1894) divides the scale into the outer homogeneous layer and the inner fibrillar layer. The outer layer is bony tissue, entirely soluble in hydrochloric acid and having no special structure except a slight layering. It is formed from cells located chiefly in the lower surface of the overlying scale pocket. The scleroblasts (formative cells that give rise to scales) form the superficial reliefs. This exists for a long time before the inner layer appears.

The inner, less calcified layer consists of fibers in bundles, all the fibers in one bundle being parallel, and the bundles being parallel with each other but crossing those of the next higher and lower layers at acute angles. This is considered the connective tissue layer of the scale.

In the scleroblast layer there are polygonal elements between which there is a colorless network. The cells in this layer arrange themselves in groups whose nuclei come to lie closer together. Then those parts of the cells farthest from the nuclei separate and are added to the intercellular substance. This substance is added to the part of the cell already existing. The scale is thus an intercellular secretion which is eventually hardened by lime salts.

Ussow (1897) concludes his paper as follows:

> The scale of teleosteans is a plate consisting of two layers. The upper layer (including the relief) consists of a homogeneous tissue without any structure except a very slight striation parallel to the upper surface. This layer originates in the dermis at the expense of the so-called scleroblasts. * * * The tissue of this layer is a simple bony tissue. The lower layer also originates at the expense of the same elements. It is formed in part out of the indurated connective tissue.

Tims (1906) found that in the cod the calcareous material does not form an uninterrupted layer, but is in the form of minute isolated platelets the exterior surface of which bears a small spine resembling very small placoid scales.

CLASSIFICATION.

The first attempt at classification by means of scales was that of Heusinger (1823).[a] He devised the following plan:

1. Fishes with scales entirely hidden in the skin: *Anguilla*, etc.
2. Those with scales proper: *Esox*, *Salmo*, etc.
3. Those with strongly toothed scales: *Chætodon*.
4. Those with osseous scales: *Lepidosteus*, etc.
5. Those with osseous plates: *Acipenser*, etc.
6. Selachians.

[a] Thomson, 1904. This reference not verified by writer.

Kuntzmann's (1824) classification of scales, while artificial and crude, was far in advance of his time. It follows:

1. Membranous scales—those with concentric lines.
2. Semimembranous—membranous posterior field, but anterior field faintly marked, as in *Clupea*.
3. Simple scales—no radii or circuli; simple center.
4. Scales with a design.
5. Scales divided into regions.
6. Scales with prickles.
7. Spinous scales.

Agassiz (1834) gave great impetus to scale classification. He originated the four groups—ganoid, placoid, cycloid, and ctenoid. His system was abandoned on account of the great variability, but attempts are being made, it seems, to revive it. Cockerell and Miss Esdaile are working in this direction.

Mandl (1839) claimed to have found definite characteristics for each family and expressed his belief in their usefulness for distinguishing genera, and even species. Peters (1841) repudiated this statement when he found both cycloid and ctenoid scales in the same fish. Vogt (1842) was able to distinguish the different orders of ganoids by their scales.

Baudelot (1873) concludes that none of the characters can form a basis of classification, since the presence or absence of spines—the most important scale character—is too variable. Although the characters alone are of little value, yet taken together they ought not to be neglected in forming natural groups. Tims (1906) distinguishes the different groups of the Gadidæ but goes no further into classification.

The work of Cockerell (1910, 1911, 1913, 1915) and Cockerell and Callaway (1909) on classification is more elaborate than that of any other recent investigators. Cockerell says (1911):

> It has been possible to test rather thoroughly the value of scale characters and the result has been to show that while they are not rarely deceptive through convergence, they are, on the whole, of great taxonomic importance.

As indexes of classification he uses size, shape, spines, radii, and circuli.

AGE DETERMINATION.

The more important means of age determination is based on Steenstrup's (1861) observation that all scales except placoid grow throughout life proportionately to the size of the fish. Agassiz, however, believed that scales are laminate and that one lamina was added each year. Baudelot also took this view, with slight modifications.

By polarized light Carlet (1878) was able to distinguish old scales from young ones, the former being birefringent, while the latter were monorefringent. Further, by means of picrocarmine stain he was able to distinguish the newer lamina from the older ones, the uncalcified parts staining red, the calcified parts staining yellow.

Hoffbauer (1898, 1900) by observations on the hibernating habit of the carp, showed the supposition that the circuli were lamina edges was incorrect, since the number of laminæ is not the same as that of the circuli and the number of laminæ is greater than the number of years the fish has lived. He says that the number of circuli between annuli on scales from the same region of the same fish is approximately constant. He noticed that the number of circuli increases where the scale becomes smaller and also that there is a considerable difference between different specimens for the same year. In short, his theory is that during favorable seasons when the food supply is plentiful, the fish grows more rapidly than in seasons of poorer food supply, and that this difference of growth is indicated by the circuli, they being closer together during seasons of slow growth than in seasons of rapid growth.

Johnston (1905, 1906, 1907, 1909), in Scotland, undertook to work out the difficult life history of the salmon from its scales. He found the annuli and correlated them with the known facts of the life of the fish in such a way as almost to establish the conclusion that they are winter marks. He discovered the "spawning mark," which is the worn or absorbed part of the scale that was the periphery at the time that the fish went into fresh water to spawn.

Thomson (1904) and Tims (1902, 1906) worked independently at about the same time. The work of the former was done on the Gadidæ and Pleuronectidæ. Besides a splendid review of the literature up to his time, of which liberal use has been made in this paper, he gives many minute measurements to support the points he makes. He is convinced that the annuli represent years and finds that the number of circuli in a band of a given width varies but little. His statistics show that if the annuli do not represent years there is a remarkable coincidence.

Tims is skeptical of age determinations by this means. He admits that he is able to follow Thomson through the first summer and winter bands, but that he can detect no further alternations. In his reasons for his disbelief he points out Klaatsch's observation that scales do not appear simultaneously all over the body and not until the fish is 3 to 4 cm. long, an objection which he admits, however, to be of little consequence. He finds variations in the number of annuli on scales on different parts of the same fish. Furthermore, the number of circuli varies indefinitely. And more important than all, scales are lost and are replaced, and for this reason age determination by means of scales is impossible.

Thomson, referring to Tims's objections, admitted that age determinations in old fishes are difficult, and in some fishes, even in the young, probably more difficult than in others, but asserted that in the cod the evidence is both plain and conclusive. He includes in his paper many observations of variation, tending to corroborate his conclusions.

Brown (1904) raises further objections to the theory supported by Thomson and others. They are:

1. Gadoid fishes shed their scales immediately after spawning.

2. After the age limit of spawning no further shedding takes place.

3. The concentric rings of scales of fish do not represent annual increments, but must have other causes.

He finds scales on a 3-year-old cod with 30, 60, and 90 circuli, respectively, depending on the location on the body; hence this method of determining age is of no value.

Among other conclusions, Dahl (1911) says that injuries or adverse conditions, even in summer, will produce annuli. Further, he applied the method devised by Johnston of calculating the length of the fish for each year by the proportionate width of the several bands. By this means he shows that comparisons of fish of different localities can be made with much fewer fish. Suspecting that the scale-covered parts and the remaining parts of the body of the fish might not grow in the same proportion he made measurements to show that errors from such a source would be negligible.

Hutton (1909, 1910, 1914b, 1914c) wrote several papers popularizing and urging the economic importance of fish-scale examination. He also gave some notes on photographing scales.

Esdaile (1912) did a valuable work in determining the degree of variation of scales on different parts of the salmon, *Salmo salar*. She shows that within certain limits the circuli in each year band ("peronidium") is proportionate to the width of the scale, but different in absolute number on different parts of the body of the fish. Criticism of this part of her work is offered below in connection with the writer's observations on age determinations (q. v.). In her second paper (1913) Miss Esdaile gives the results of investigations of salmon scales devoted largely to points in the life history of that fish.

Gilbert (1913) worked on the salmon of the Pacific coast after essentially the same methods as those employed by Dahl, Hutton, Thomson, and others. His scale photography is brought to a high degree of perfection, and deserves special mention.

Milne (1913) in a work similar to Gilbert's, on salmon of the Pacific coast, offers a pertinent criticism of Dahl's (and Johnston's) method of calculating length. He was able to test this method by scales of two fishes captured, marked, measured, and recaptured by Johnston. On one, Milne points out, Johnston's calculation showed an error of only one-half inch for the kelt measurement of a 27-inch salmon; the other showed an error of 6 inches for a 26¼-inch fish, from which he concludes "either that the scale is abnormal, or that Dahl's system of measurement is not applicable to a fish that has spawned."

McMurrich (1912), in addition to the methods of Gilbert and Milne, made use of evidences found on otoliths. In these structures, zones or lines may be observed which are believed by McMurrich and others to represent growth periods.

Masterman (1913a) perceived that much of the work of recent investigators was based on assumptions rather than on definitely settled facts. He therefore undertook a careful critique of the work done on salmon, making an effort to decide whether it had been proved that summer and winter growth rings are invariably and indubitably formed in their respective seasons; and whether the spawning mark invariably records the spawning period; and whether its absence can be taken as denoting maiden fish.

He states the usual assumptions of age determinations, but is doubtful of the reliability of this method beyond the fourth or fifth year of growth. Concerning the manner of growth of the circuli, he says: "They have an innate tendency to be produced roughly in lines equidistant from the center and at a certain distance from the preceding ridge * * *. The distance between neighboring ridges is determined by the rate of growth at the time." In addition to the accumulation of circuli in summer and winter bands, he notices other morphological arrangements of the circuli which may also help to indicate the seasons of active growth; but, to quote him on this point, "In the case of sea fish, at any rate, they may just as likely have reference to changes in food and temperature, with no direct reference to the calendar."

He divides the evidence necessary to prove the general theory of age determinations on scales into (*a*) morphological, (*b*) experimental, and (*c*) statistical. To summarize his conclusions:

(*a*) Morphological:

(1) The evidence necessary to prove that a broad band is formed in summer and a narrow one in winter has not yet been produced. On this point he cites the insufficiency of Dahl's and Johnston's evidence.

(2) "The scale can not be an accurate gauge of the lapse of time unless the zones, besides being produced in their respective seasons, are always produced in response to these seasons."

(3) "The formation of these two different series of growth—rings or zones—takes place in the winter half or summer half of the year, respectively" (quoting Dahl).

(*b*) Experimental: The evidence of fishes of known age and kept under artificial conditions is convincing as far as it goes (for the first two years), but can not be regarded as convincing through the entire term of life until more work is done.

(*c*) Statistical: "In studying the average sizes, average weights, and seasonal occurrence of the different age groups and numerous other statistical relations, the age data obtained from the scales give a rational and consistent result throughout."

Under the caption, "The morphology of salmonoid scales" he classifies the different circuli as complete circles, occurring in the earliest stages of the fish; crescentic or incomplete circles, occurring in normal summer growth, and incomplete seasonal crescentic ridges. These latter occur in the winter growth, and if his conclusions here are reliable, consideration of these short circuli should be a valuable addition to the methods already employed, but, of course, not necessarily applicable to any species other than the salmon studied by him.

In connection with his discussion of the "spawning mark," his conclusions may be summarized as follows:

1. It may be held as conclusive that the spawning mark is produced by changes incidental to the act of spawning.

2. The spawning mark is not caused by the mechanical vicissitudes of river life or the act of spawning, as assumed by Johnston, Dahl, and others. In support of this view he calls attention to the following points: (*a*) The spawning mark is produced prior to entering the river and in some cases, long prior to spawning; (*b*) the fact that the scale is imbedded deep in the dermal pocket would, alone, destroy the mechanical attrition theory; (*c*) since it is known that gonads are developed partly by the absorption of other tissues, it is not unreasonable to assume that the scales are among the tissues so absorbed.

3. It can not be taken as proved that the absence of the spawning mark is valid evidence that the fish has not spawned. In this connection he cites the case of salmon kept in aquaria at the Plymouth laboratory that were stripped for two successive seasons without the formation of a spawning mark. This, he admits, may possibly be due to the artificial conditions.

4. It seems impossible accurately to define the spawning mark. Consequently the personal element will enter into doubtful cases, and differences of opinion will result.

On the whole, Masterman's paper constitutes one of the most valuable contributions to scale literature. He suggests numerous researches on the subject that are needed and that might profitably be followed.

Calderwood (1914) takes up some of Masterman's criticisms of the spawning-mark doctrine. Referring to Masterman's theory that the mark is due to absorption incident to spawning he pointed out that the attrition is noted on the lateral, seldom on the anterior, margin. If Masterman's view is correct, the anterior margin ought to suffer most. It will be observed, however, that Masterman had taken this into consideration and suggested that this absorption of the lateral margin rather than the anterior margin might be in anticipation of the decreased girth after spawning. Calderwood also cites Milne's observation that the thickness of the scale is increased at the spawning mark which according to the latter observer is due to a continued secretion of the scale substance while the size of the body remains constant. Calderwood finds difficulty in seeing how absorption of scale substance and a deposition of more at one and the same time could take place; yet this must be true if Milne's contention is correct. Calderwood rather regards the attrition of the scale as necessary for the thickening and toughening of the skin, but fails to point out very clearly just how this is accomplished. He ends his paper by expressing the belief that the absence of the spawning mark is valid negative evidence.

In the application of the scale reading no more important work has been published than that of Hjort (1914). Since, however, no effort is made in this paper to review the general applications of the subject which are entirely too voluminous to permit it, further comment on his work may be omitted here. A great volume of work of this nature has been done not only by Hjort and his assistants, Lea and Dahl, but by McMurrich, Gilbert, Petersen, Johnston, Calderwood, Hutton, Esdaile, Masterman, Hoek, and a host of others.

The work of Winge (1915) on the cod supplies much of the evidence that Masterman found lacking in the salmon. He measured the "platelets" (Tims) or as he calls them "sclerites," each one individually from the focus to the periphery, constructed curves from these measurements, the maximal and minimal modes corresponding to the summer and winter growths, respectively. By comparing these scale measurements with the actual lengths of living fishes measured, marked and recaptured, he was able to show that these modes agree quite satisfactorily with the growth of the fish. These modes (the summer and winter growth bands) are, in the cod, formed in September and March, respectively.

Another division of his paper deals with the question whether the growth of the scale is exactly proportional to that of the fish. By measurements on four marked cod, he finds a surprisingly close agreement—altogether within the limits of experimental error. Furthermore, he was able to show that cod living under similar conditions will show similar curves when plotted in his manner. And, finally, he tests the otoliths as a means of determining age, using his data from scales as a check. Judging from his excellent technique, his results must be regarded as reliable. He concludes: "* * * in the cod examined a very high degree of uniformity exists between the growth of the scales and that of the otoliths. Both scales and otoliths exhibit growth rings by means of which the age of the cod can be determined."

Mention should be made here of the work of the investigators of the Kommission zur Untersuchung der deutschen Meere, Reibisch (1899), Jenkins (1902), Heincke (1905, 1908), Maier (1906), and Immermann (1908). These investigators worked chiefly on the sole, cod, and turbot, while Wallace (1907, 1909, 1911), in England, worked on the plaice, employing the otoliths and bones as means of age determination. The result of this work seems to show that not only are age indications to be found on scales, but on the otoliths, opercula, and bones. Since these structures reveal age only after they are prepared by special technique, it is evident that they can never be employed in the examination of large numbers of specimens, as can the scales. These structures have served the useful purpose of verifying, to a certain extent, the evidences found on scales.

In spite of all this work, there remain doubtful points. Heincke (1908) cites numerous instances of fishes that were very old, but undersized, along with examples of variation in size among fishes of this same age, but of different sex or from different localities. Yet he fails to show that these variations are in the number of age rings rather than in age. He concludes that the number of age rings is normal and correct and that growth in these cases is abnormal; but from his data he might as well have concluded that the size was normal but the number of rings abnormal.

APPLICATION OF SCALE CHARACTERS TO AGE DETERMINATION.

The idea that the age and life history of fishes may be determined by their scales has given rise to much investigation. Each method has been investigated and an attempt has been made to find other indications of age on scales.

The different means of determining age with more or less accuracy are:

(1) A count of the annuli aided by—

- (*a*) Polarized light.
- (*b*) The selective action of picrocarmine stains.
- (*c*) The origins of the radii.

(2) Identification of year groups by measurements of length and weight.

These methods may be used in combination.

COUNT OF ANNULI.

It has been contended that, at least for some species, growth does not proceed uniformly, but that during the winter and in other seasons, because of lack of food or because of injuries or other causes, growth takes place more slowly than in summer or in seasons of more abundant food supply or when conditions are otherwise more favorable. Such changes of conditions as well as certain peculiar habits are said to leave their marks on scales. From the investigations of Johnston, Gilbert, and Dahl on salmon and trout, and Hoffbauer on carp, it would seem that circuli appear at fairly regular intervals of time while the growth of the scale in width depends on the growth of the fish. The appearance of the circuli at regular intervals of time while the scale increases more rapidly in size in summer than in winter would produce concentric areas in which the circuli were close together alternating with areas in which they were farther apart. The earlier investigators considered these areas in which the circuli are not widely separated "winter bands," assuming that the fish grew less rapidly in winter than in summer, thus producing rings analogous to the annual rings in tree trunks.

When viewed under low magnification, these alternate bands appear, in most cases, clearly; and if they really represent winters, it is a simple matter to determine age by counting them. Hoffbauer seems to have demonstrated that these zones do represent winters by observations on the scales of carp kept in aquaria and under known conditions.

One is, however, confronted with many obstacles in relying entirely on this means of age determination. In very old fishes, as Tims points out, the annuli, through wear and diminished growth, become so indistinct and close together that it is almost, if not quite, impossible to arrive at a satisfactory conclusion as to age.

Investigating the scales of *Cynoscion regalis* and *Orthopristis chrysopterus*, the writer has not been able to verify all these observations, for the reason, possibly, that these investigations were made on English brook trout, salmon, and carp, the scales of which he has not had the opportunity to examine.

Miss Esdaile (1912) in the following language accepts and states very clearly the fundamental assumption of all the workers on age determination:

> Examination * * * shows that the annuli [circuli] are arranged in a definite manner, some far apart and others closer together. Those far apart are, according to Mr. Johnston, formed during the rapid growth of the fish in the summer, and those closer together during a time of slow increase in the winter.

This implies clearly that bands representing equal lengths of time ought to exhibit at least approximately equal numbers of circuli, and that scales of the same size ought to be sculptured with a similar number of circuli. But later in her paper she states that "there is no constant variation in the number of annuli in the different periods of the scales from the same position." In her table no. 2, scales from positions 4 and 5 have the third peronidia of the same width—0.48 mm.—yet one has 10 circuli, the other 7.8 circuli on the long axis. Again, scales from positions 6 and 7 have total lengths of 6.07 and 6.09 mm., respectively; yet one has a total of 107.8 circuli, the other of 118.2 circuli, a difference of 10.4 circuli, or 9.2 per cent variation from the mean. In no case where the widths of any two peronidia were the same, were the corresponding numbers of circuli identical.

A similar criticism can be made from the photographs in Gilbert's paper (1913); take, for example, plate VI, figure 10, of his paper: Judging from the width of the summer bands, the growth each year is less than that of the preceding, yet the separation of the circuli is greater each year than that of the preceding. There are more circuli per linear centimeter in the third band than in the fourth, yet the former is wider and is supposed to have grown more rapidly.

The following observations bear on the nature of the annuli:

1. The circuli on the scales of the *C. regalis* are almost equidistant. Figure 1 is a graph correlating the number of circuli and distance apart measured in tenths of a millimeter. Each ordinate unit represents one circulus and the units of the abcissa are tenths of a millimeter. If the annuli are uniformly one-tenth millimeter apart a 45° straight line would result. Barring very small fluctuations, this is true. Their separation does not vary in the vicinity of the annuli, nor does their separation vary with different distances from the periphery.

2. The direction of the annuli is not necessarily coincident with that of the circuli. This is more or less apparent on all the scales examined but is most strikingly demon-

strated on the scales of the Clupeidæ. On the scales of *Brevoortia tyrannus* and *Pomolobus mediocris* and others of the Clupeidæ the annuli cross the circuli at more or less acute angles—laterally at almost right angles—the annuli being coincident in direction with the scale contour while the circuli are arcs of concentric circles whose center is posterior to the scale, and are not coincident in direction with the contour. (Pl. LVII, fig. 22.) In these cases there seems to be no more than an accidental relation between the annuli and the circuli. It may be seen that this is also true for *C. regalis* in plate LVI, figure 19. Whether the annuli in these different genera are homologous characters is open to question, but their number, disposition, etc., suggest that they are.

3. On the scales of *Cynoscion regalis* the number of circuli between the last annulus and the periphery, is, in July and August [a] much less than half the number of circuli between any two adjacent annuli. The number of circuli between any two annuli is from 30 to 100. Between the last annulus and the periphery the number of circuli varied from 4 to 8 in July and August.

4. Measurements calculated from the annuli considered as summer bands agree with the length groups actually measured. The following method was employed: Three hundred and eighty-two specimens were measured at random.[b] Their lengths were found to fall in modes of 19.91, 26.31, etc., cm. (Tables 1, 2, 3.) Then the lengths of 28 specimens were divided into parts proportionate to the distances between the several annuli, and these lengths entered as the respective first, second, etc., years of the fish. (Table 1.) The averages of these lengths were then compared with the modal lengths of the 382 measured fish. (Table 2.) It will be seen that the averages agree remarkably.

5. Annuli are narrow areas parallel with the contour of the scale, in which the regularity of the circuli is interrupted, manifested as branches, breaks, or terminations.

6. The scale is separable into laminæ, the edges of which coincide with the annuli.

7. Annuli stain pink with picrocarmine.

8. Annuli have a refractive index different from that of the spaces between.[c] So far as the writer has been able to determine, the refractive index of scales has never been actually measured.

The conclusion of previous investigators that annuli are approximations of circuli and are caused by retarded growth is rendered questionable by the foregoing observations. If the annuli were approximations of circuli, the expected curve would be the dotted lines in figure 1, showing retarded growth at the time the annuli were formed. In the second place, if retardation of growth brought the circuli closer together, then in the fifth or sixth year of the life of the fish, when growth is much slower than in the earlier years (indicated by the narrowness of the bands), the circuli would be closer together, giving the scale the appearance to the unaided eye, or under low magnification, of having at the center widely separated circuli while, approaching the periphery, the circuli would appear closer together. The scale would then have a light inner part, growing darker toward the periphery. The writer did not find this to be the case on the scales

[a] This character is much less constant on the scale of the pigfish, *Orthopristis chrysopterus*, Linnæus, due, perhaps, to the more variable spawning time of the latter fish. Specimens 2 cm. long were taken as early as June 15 and as late as Sept. 1, 1913.

[b] The detailed measurements in the table cover only 65 specimens. However, in addition to these the lengths of 382 fishes measured by Hecht and Crozier were used in constructing the modes.

[c] Carlet (1878); Dahl (1910).

of *Cynoscion regalis*, nor, judging from the cuts in the papers of Hutton, Dahl, and others, does it appear to be true of other species. If each annulus represented a year and the circuli appeared at regular intervals of time, then the number of circuli could vary but little in each band. In the third place, that annuli and circuli have nothing in common is proved beyond doubt by the fact that the former may cross the latter. The suppositions referred to are negatived by these observations, and it remains that

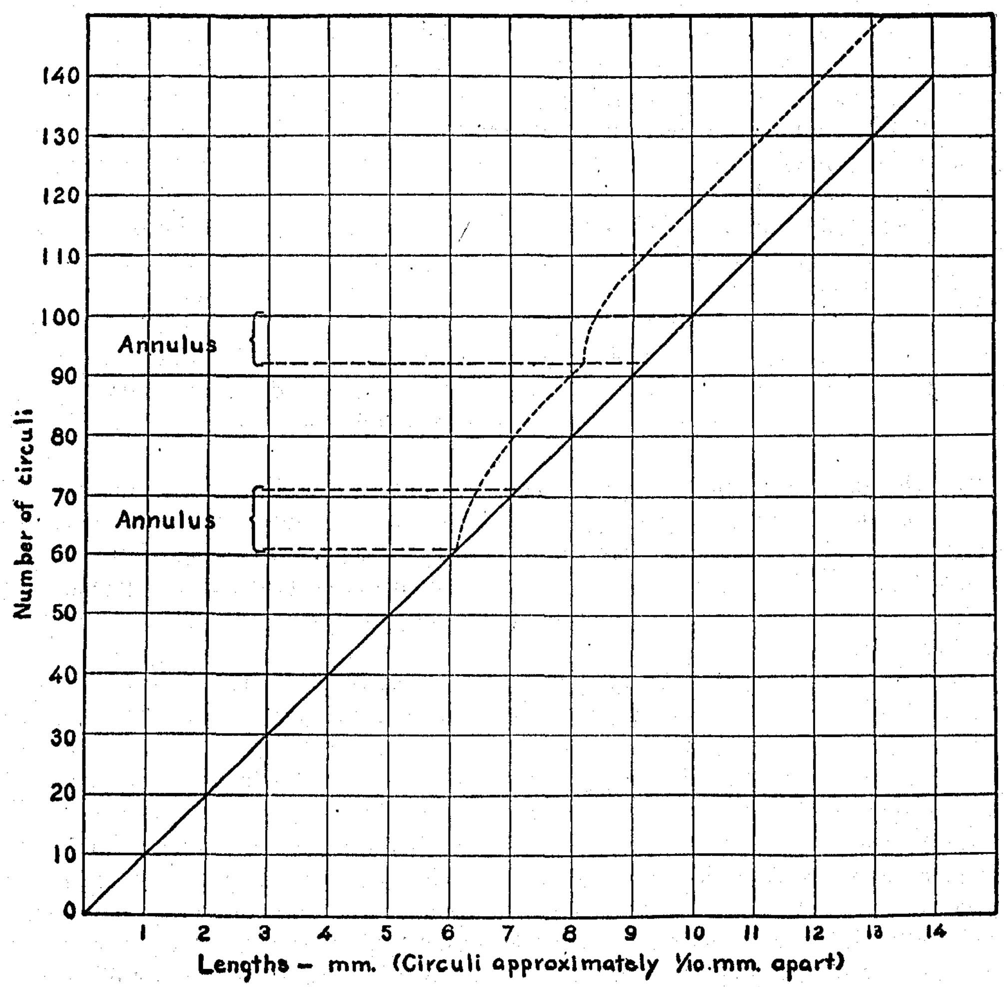

FIG. 1.—Showing number and distance apart of the circuli on a scale of the squeteague including two annuli. Dotted line represents the expected curve of such a correlation if the annuli were groups of approximated circuli.

one annulus may be produced each year, but that it is not produced by retarded growth, nor does it consist of approximated circuli.

That the annuli do not represent winters, as contended by the previously mentioned investigators, is verified by the observations on *Cynoscion regalis* as already noted. If the annuli represented winters, then in July and August the number between the periphery and the last annulus ought to be at least half the average number of circuli between any two adjacent annuli. But the small number of circuli found points to May or June as the time of formation of the last annulus. In the case of the comparisons of measured and calculated lengths (table 2), if the annuli represented winters a discrepancy between the averages would be expected; for the fishes measured would be approximately an even number of years old (spawned in June and measured in July and August), while the winters represent points midway between birthdays. But the calculated and measured lengths agree remarkably (table 2; also fig. 2 and 7), suggesting the view that annuli are year-old marks, but not winter marks.

These observations seem to justify the opinion that the annuli are simply the margins of the laminæ composing the scale. Plate LI, figure 3, a photomicrograph of a part of a scale under high magnification, including two annuli in the field, shows clearly that the annuli are not circuli closer together, but simply branching circuli. This branching possibly may be explained by the disproportionate growth of the anterior and posterior fields.

It is seen that while several circuli are being formed across the anterior field, only one is formed on the lateral field, hence the branching. A glance at plate LVI, figure 19, will show that all the circuli on the anterior field are traced back to a point on the posterior field where they join the following circulus, and that an annulus is being formed continually. Thus the last circulus on the periphery is, at its posterior extremity, part of an annulus that will not be complete till the next year. The beginning of a new annulus appears to be determined by a sufficient lateral growth to permit the formation of another circulus.

But this does not explain the annulus on the anterior field. Here, as elsewhere, it seems to be the edge of a lamina. Just why these laminæ end at the ends of years is yet undetermined. It suggests that the fish passes through year cycles of growth, and that one lamina is formed each year. It has been suggested that the fish spawns every year from the first, and that the laminæ represent differences of calcification during spawning time.

Dahl proposes a unique theory. The scale is secreted by the floor of the scale pocket and the increasing size of the pocket explains the increasing size of the scale. The thickness of the scale is only dependent on continued secretion. Thus if the scale pocket remains constant in size, so will the scale; if it increases in size, a new ring will be added to the periphery, etc. But a contraction of the pocket will produce an upward fold in the thin edge. It is conceivable to him that during the spawning period the body is more or less distended and while it is in this condition a new layer is added from the floor of the scale pocket. Now a contraction of the body follows the spawning period and with it a contraction of the scale pocket, pulling the thin periphery upward. Such a process would produce structures similar to what we know the annuli to be, if we leave the interior structure out of consideration.

The evidence, however, does not point to this conclusion. That spawning has nothing to do with the formation of annuli is evidenced by four different points:

(1) Annuli are often found running in a direction contrariwise to that of the circuli.

(2) Spawning leaves a mark on scales of a character quite different from that of the annuli. (Masterman 1913a, Milne 1913, Calderwood 1911.)

(3) Expansions and contractions of the body of the fish consequent upon the spawning of the fish could not possibly affect the scales on the caudal peduncle, head, etc., yet

annuli are found on scales taken from these parts which correspond exactly to those on scales taken from parts of the body subject to expansion.

(4) The process of expansion and contraction could not produce the separable laminæ of which the annuli seem to be edges.

It seems to be explained by differences of calcification. The inferior layer, in which the laminæ occur, is the secreted product of the floor of the scale pocket. As the fish grows, both the scale pocket and its secreting floor increase in size proportionately. We thus get a scale constantly increasing in size and thickness, the lower lamina of which is always the newest part. This secretion on the inferior side is constantly being added and calcifies much more slowly as it is pushed outward. If calcification should vary, we would find layers of more and less calcification. In this case, if the scale were torn forcibly, the less calcified part would yield while the more calcified parts would adhere, giving the idea of separable laminæ. This was actually done; in one case six laminæ were easily separated. The scale, according to this view, is a solid mass, and the apparant layers are strata of slightly differing degrees of calcification. That mineral metabolism, at least, in some marine animals is dependent on temperature is indicated by investigations[a] in which it is shown that the magnesium content of crinoid skeletons is higher in tropical than in colder latitudes. It is quite possible that the same variation will be found in the calcium content of fish scales—not only in fishes from different regions, but in the different laminæ of the same scale.

Polarized light.—The utility of polarized light in age determinations is twofold: (1) When the scale is young—i. e., less than 1 year old—it is monorefringent to polarized light; when more than 1 year old—i. e., consisting of more than one lamina—it is birefringent (the writer was unable to verify this observation);[b] (2) when used with a selenite plate, the annuli stand out in colors different from those between. This is said to be due to the scarcity of mineral salts in the vicinity of the annuli. The chief value of polarized light is thus to bring out the annuli clearly in obscure cases. The refringency of light is of little value, since it only differentiates fishes less than 1 year old from those more than 1 year old, which usually in fishes so young is sufficiently indicated by the annuli alone.

The selective action of picrocarmine stain.—Picrocarmine is the most satisfactory selective stain for scales. Its value in age determinations depends, as shown by Carlet (1878), on the selection of the carmine by the uncalcified parts. By it the outer lamina—i. e., the youngest—which is deficient in mineral salts, is stained pink. The next inner lamina is an orange, while the older completely calcified laminæ stain yellow with the picric acid. The edges of the several laminæ up to three or four from the periphery also stain pink. The value of this stain in age determinations, then, is twofold: (1) It differentiates the last lamina, which is always the most difficult in old fishes; (2) it also stains the edges of the laminæ between this one and the first or second. Thus in most cases the age of a fish 5 or 6 years old may be easily deciphered.

The origins of the radii.—Like polarized light and picrocarmine stain, the radii are only supplementary to the annuli as a means of age determinations.

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[a] Clarke, F. W., and Wheeler, W. C.: Composition of crinoid skeletons. Professional Paper 90-D, U. S. Geological Survey. June 16, 1914.

[b] Carlet (1878).

As in the majority of teleosts, radii appear on the scale of *Cynoscion regalis* only on the anterior side. They begin, usually four to six in number (on the sides of the fish), at about the seventh circulus, counting from the focus. These usually continue to the periphery. As the scale increases in size, more radii are added on either side of those first appearing, beginning at various distances from the periphery. Proceeding laterally from the long axis, one finds that they extend diminishing distances from the periphery. They are usually symmetrically arranged—i. e., a radius beginning on one side of the axial radius will correspond with a similar radius beginning at the same distance from the periphery on the other side. The points at which radii begin in the main coincide with the annuli. It would, then, be a simple matter to count these points to determine age, but this rule is by no means infallible. Radii often begin between two annuli, and sometimes continue for a short distance only and then disappear. But radii beginnings, notwithstanding this variability, are sufficiently constant to afford a valuable means of verifying and supplementing the other methods.

In case we find an old fish on whose scales the annual rings are very obscure, the various aids in combination make it possible to determine accurately the age of the fish or, at least, to count the annuli. When the annuli near the periphery are so near and indistinct as to be indecipherable, the picrocarmine stain will clearly differentiate the last two laminæ and probably stain the edges of two or three more. The radii origins indicate the intermediate ones. These can be verified by color differentiations of polarized light through a selenite plate. We then have the following scheme:

First annulus: Usually clearly distinguishable.

Second, third, and fourth annuli: Stain red with picrocarmine; color differentiations by polarized light.

Fifth and sixth annuli: The last stains red; the next inner stains orange.

YEAR GROUPS IN LENGTH AND WEIGHT.

This is a statistical method of verifying the other means of age determinations and must be employed before the age characters of any one species can be settled definitely. Upon measuring a great number of squeteagues the writer found that they fall into groups of different lengths around 20, 26, 31, 37, etc., cm. (Table 1 and text fig. 2.) These are what Johnston (1904, 1905, 1907, 1909) called "year groups"—those falling around 20 cm. being probably 1 year old, around 26 cm., 2 years old, etc. If the other means of determination agree with these results, they may be taken as correct.

Another suggested means of age determination—probably of little importance—is based on the observation of Williamson that the calcareous corpuscles are also built in layers, so that when viewed in section they appear as concentric rings. This, it seems, is due to a difference of calcification, and the rings would probably represent years, but investigations of the structure of these corpuscles have not been sufficient to warrant an opinion as to their value in this connection. At any rate, it would be an extremely difficult method to apply.

INTERPRETATION OF THE RADII.

Various conjectures as to the function and importance of the radii appear in the literature on scales. They were an important item in the Agassiz-Mandl controversy. In some systems of classifications by scales they have been considered constant enough to be used in distinguishing genera and species. Observations recorded below point to conclusions differing from any that have been advanced hitherto.

In examining a large tarpon scale focussing was accomplished by bending the scale on the stage. While this was being done the radii were noticed, their edges coming closer together as the scale was bent (viewed from the distal side), and they seemed to be lines of most flexibility.

The number of radii on different parts of the body of the fish seems to vary as the mobility of the parts. (Text fig. 2.) On the caudal peduncle more radii were found than on any other part of the body. This number decreases (subject to the influence of size, shape, thickness, etc.) as one proceeds anteriorly. On all the inflexible parts—i. e., above the head, on the opercula, nape, etc.—the scales were entirely without radii; but proceeding posteriorly, on the parts where there is slight movement, a wave was found in the anterior field. (Pl. LII, fig. 4.) Proceeding farther posteriorly, the number of radii increases and there is a tendency toward an increase ventrally from the median line of the back. In no case were radii found on scales taken from inflexible parts of the body, and the other factors being equal, notably shape, their number varied directly as the flexibility of the part from which the scales were removed.

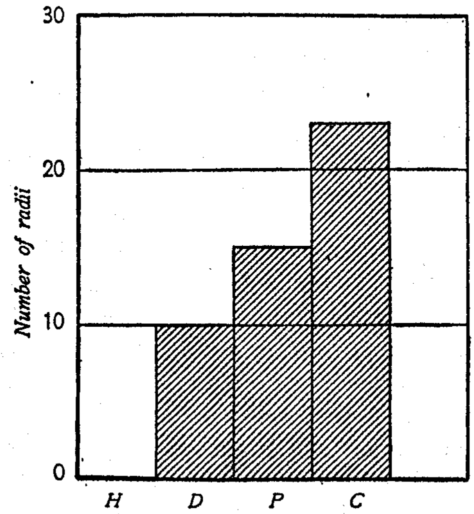

FIG. 2.—Polygon showing the occurrence of radii on scales taken from different parts of the body. H, scales from head; D, scales from a point below the anterior base of the spinous dorsal fin; P, scale from a point beneath pectoral fin; C, scales from caudal peduncle.

These facts suggested that radii might be hinges to permit the scale to bend in adaptation to the movements of the body of the fish. The fact that all degrees in the formation of radii, from total absence, then wavy folds, then a few to finally numerous radii, are found and that these correspond with the mobility of the part, which varies from zero, then slight, and finally to the maximum on the peduncle, is alone sufficient evidence to support the hypothesis that radii are simply hinges.

There are numerous other evidences to support this hypothesis. As was shown under the head of age determination, the uncalcified parts stain red with picrocarmine; the radii stain heavily with it. Plate LIII, figure 14, shows a cross section of a scale that will illustrate how the radii facilitate bending.

An examination of a scale will make this clear. It will be noticed that the radii do not begin at the focus, but the young scale must increase to a size that will interfere with the movement of the fish, i. e., the scale must become stiffened by calcification so as not to bend readily with the body of the fish before the radii begin to appear.

They then increase in number as the periphery is approached, the radii in most cases appearing late, beginning at the lamina edges. This is explained by the supporting effect of each lamina on the next following lamina. On the under side of the scale the radii do not appear, for the lower or uncalcified layer is flexible and does not break until it becomes calcified, when it leaves a fissure showing, in stained scales, the uncalcified, red-stained layer below.

All the other factors being constant, then, the radii might be expected to increase in a definite proportion as the periphery is approached. The number of radii varies with (1) the activity of the fish, (2) the size of the scale, (3) its shape, (4) its thickness, (5) its degree of calcification, (6) its curvature, and (7) the position of the fulcrum of the scale.

(1) Variations of activity may mean relative activity of the different parts of the body, or of the same parts of the body at different seasons of the life of the fish. By examining scales from all parts of the body of the same fish (pl. LII, LIII) it will be seen that there are no radii on the inflexible parts; on the very slightly movable parts very few are found; and on very movable parts the whole anterior field is sculptured with radii; but on certain scales, symmetrical in shape, and on flexible parts of the body, the number is found to increase to a certain extent as the periphery is approached, afterwards diminishing, until there are no more radii at the periphery than at the focus (pl. LIV, fig. 15). This is explained by the relative activity of the fish at different seasons. If this explanation is correct we have an index of the relative activity of the fish throughout life.

(2) As the scale increases in size the number of radii must increase proportionately if the extent of bodily movement remains constant; but if the radii are found to increase in number to a certain point, then remain the same in number where an increase would be expected, or decrease, and if we assume that the radii are caused by bodily movement, the probability is that the fish suffered a diminution in activity at this point. The number of radii at the several annuli on the scales of forty specimens were counted and tabulated (table 5), showing that the expected increase does not occur on *Cynoscion regalis*. Plate LIV, figure 15, shows a scale on which the radii thus decrease in number after the third year.

(3) Narrow scales have fewer radii than broad ones, the reasons for which are obvious. *Rachycentron canadus* has long narrow scales with very few radii; *Paralichthys albiguttus* has scales of a similar shape with one or two radii. The scales of *Istiophorus nigricans*, the extreme of this shape, have no radii at all. Scales around the vent of *Brevoortia tyrannus* or *Cynoscion regalis* are long and narrow, and have very few radii. On a scale taken from the top of the peduncle of *Cynoscion regalis*, one of the anterior angles was prolonged, and there were many more radii on the side of the prolonged angle than on the opposite side. Shape also determines the relative direction of the radii. When the anterior angles are both prolonged, the radii are seen to be parallel and not divergent, as usual. (Pl. LII, fig. 7.) The scales of *Fundulus majalis* normally possess this character, and here the radii are uniformly parallel.

(4) Thin scales have fewer radii than thicker ones. On the scale of *Urophycis earlli*[a] no radii were found, and the scales were extremely thin, although large. Thickness, however, varies little in the scales of the same fish, and, so far as the writer has found, in the same species.

[a] This is an interesting scale bearing evidence relating to Baudelot's theory of spines (see Review of Literature).

(5) Apparently the scales of some fish do not calcify so rapidly as those of others. *Synodus fœtens* has very thick and broad scales; nevertheless they are not marked with so many radii as might be expected. They are calcified very little in comparison with those of *Archosargus probatocephalus*. In fact, judging from the flexibility of these scales, one would expect still fewer radii were it not for convexity.

(6) Most scales are more or less meniscus in shape, the convex side being exterior. This is believed to be responsible for the radiate rather than a transverse direction of the radii. If a scale were perfectly flat, fewer radii would appear, and they would run perpendicular to the long axis of the body of the fish. The more depressed the body of the fish, the more convex the scale, and consequently the more sculptured with radii.

Brevoortia tyrannus furnishes an example of a scale that is nearly flat. On this scale the radii are irregular in direction and are generally perpendicular to the long axis of the scale.

(7) The scale acts as a lever. When the posterior side is raised, the center rests against the upper edge of the scale pocket as a fulcrum, and the anterior edge is pressed inwardly. It is easily seen, then, that the more posterior the fulcrum—i. e., the more deeply inserted the scale—the more numerous the radii. As a further substantiation of this theory, it has been possible to tear the several laminæ apart. The segments between two radii of the upper laminæ were completely separable from the surrounding tissue, indicating that they were not held in place by the tissue of the laminæ from which they were taken, but by the stratum below. In the upper laminæ the scale being stiffened by calcification, broke into separable segments, while the uncalcified stratum below yielded when the scale was bent.

There are probably numerous other factors influencing the presence, number, and character of the radii. Among these might be mentioned the elasticity of the scale pocket. This is probably less in older fish than in young, with a concomitant increase in the number of radii. The shape of the body of the fish, its length, comparative activity, and habits may be more or less important influences.

With this large number of variants contributing to the production or nonproduction of radii, their value as taxonomic characters appears very doubtful. For instance, it is certain that the scale grows more anteriorly than posteriorly, being forced deeper and deeper into the pocket, throwing the fulcrum posteriorly, tending to produce more radii. It also increases in size, again necessitating more radii. At the same time, calcification is going on, making the scale less flexible, and its thickness is increasing by the constant addition of secretions from below, the shape remaining practically constant throughout life. All these conditions tend to a geometrical increase in the number of radii. But while the fish is growing older, its activity is possibly declining, tending to reduce the number of radii. Distention consequent upon spawning may be another factor, increasing or diminishing the number of radii. These variants may conflict and neutralize, or may work together to increase the number of radii. From all this we may conclude that by simply counting the radii without taking the contributing factors into consideration, fallacious conclusions may be reached.

Some of these factors are, however, taken into consideration in taxonomy. The shape of the fish is always noted. The size (number of scales in a line) and shape of scales are also noted. If now, instead of counting the radii, the other factors of elasticity and thickness were considered, we would have much more reliable additions to ordinary characters in classification.

LIFE HISTORY OF THE SQUETEAGUE (CYNOSCION REGALIS) AS INDICATED BY THE SCALES.

Unlike the salmon, which spends a life of widely varying conditions, and which, by its various markings, first attracted the attention of scale investigators to the possibility of determining age by this means, the squeteague leaves only obscure evidences of its life history on its scales. Since it spends its entire life under fairly constant conditions, the sculpturings on its scales are rather uniform.

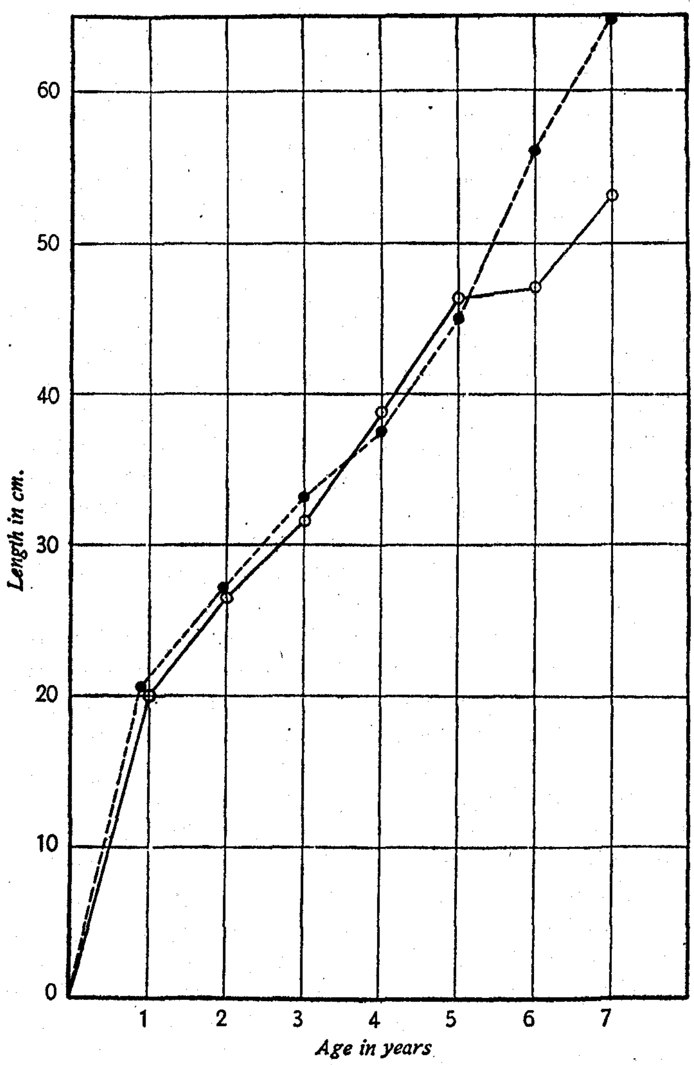

FIG. 3.—Comparison of calculated and measured lengths. Continuous line, lengths calculated from width bands on scales; broken line, length groups measured. *Cynoscion regalis.* (See table 3.)

Effort has been made to determine: (1) The age of the fish of average size; (2) the rapidity of growth; (3) the age at first spawning; (4) the maximum age and length; (5) winter habits.

(1) The average length of all the fish measured[a] is 32 cm.; of the 38 specimens the age of which were computed (see table 6 and text fig. 4), 94.7 per cent survive till the third year.

(2) The rapidity of growth during the first year of the life of the fish is remarkable. The average length of the squeteague at the completion of its first year is 20 cm. It is very rare for a fish to grow more during any subsequent year than in the first. (Text fig. 3.)[b] However, there is here the possibility of a slight error. In fishes of 4 or 5 cm. in length the scales do not overlap, but must grow proportionately more rapidly than the body in order to do so. In addition to this, it is also noted that the proportion of the exposed part to the unexposed part

[a] Including 382 fish measured by Hecht and Crozier and the 65 specimens represented in table 2, total of 447. It will be noticed that there are very few one-year fish in the table. This accounts for the high average of total length, 38 cm., which agrees well with the calculated length for the average age (4.1 yr.), which is in the fourth-year column, 38.48. (Table 1.)

[b] Carl H. Eigenmann (Investigations into the history of the young squeteague: Bulletin, U. S. Fish Commission, vol. XXI, 1901, p. 47) concludes from measurements that a fish may reach the adult length of 400 mm. in 7 months. It will be noted that this is at wide variance with the conclusions in this paper based on evidences found on scales. It will also be noted that some of Eigenmann's measurements were made on young fish kept in an aquarium, while those of the larger fish were made on fish taken at a later time, with apparently no means of determining age.

is constantly diminishing, indicating a more rapid growth of scales than of the body. Hence, the proportionate distance apart of the several annuli does not represent the correct proportion of growth of the fish. This is probably compensated for by the late appearance of the scales (Vogt, 1845). The fish is from 3 to 4 cm. long before any scales appear. That any error here is negligible is testified to by the close agreement of the "calculated" and "measured" lengths. (Table 2.) After the fourth or fifth year, growth probably takes place very slowly, although the writer's data on very old fish are too meager to afford definite conclusions.

(3) Age at first spawning has been the subject of much conjecture. The opinion seems to have prevailed generally, probably on account of the rapid growth during

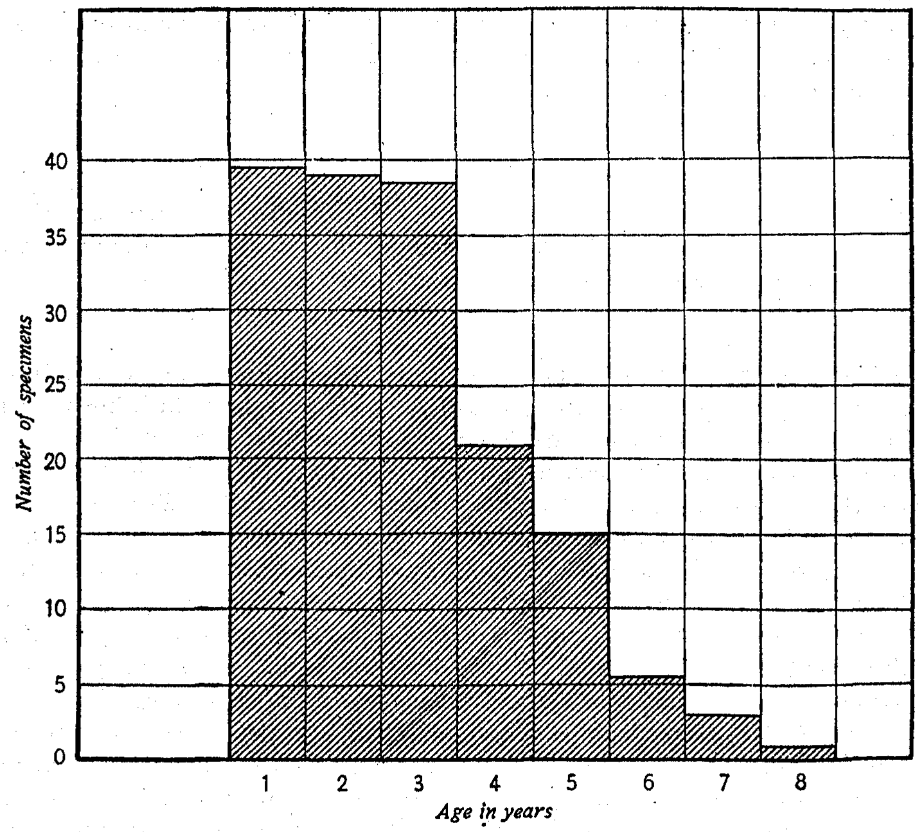

FIG. 4.—Polygon showing the occurrence of *Cynoscion regalis* at different ages.

the first year, that spawning takes place at the end of the first year. With the evidences afforded by scales, the writer is not prepared to accept this conclusion, unless the annuli represent spawnings and they occur every year of the life of the fish. There are two evidences which lead to the conclusion that spawning takes place for the first time in the third year: (*a*) The survival of 94.7 per cent of all fishes through three years. (See table 6.) As they increase in age and length after this point, their numbers decrease remarkably. (Text fig. 4.) (*b*) The relative activity, as indicated by the radii. (Table 5.)

If the ratio of the number of radii present to the number expected represents relative activity, a speculation may be ventured that activity decreases the third year. (See table 5.) It is at least possible that the activity, if variable at all, drops at first spawning, and decreases with age. This sudden decrease, followed by a continued decrease points to the third year as maturity, or the time of first spawning. If this is true, market fish ought to agree in size with fish of this age.

(4) The oldest fish caught was 8 years old, and at this age the annuli were so close together as to make their enumeration very difficult. It is likely that they seldom exceed this age, although fish of much greater size and probably greater age are reported from more northern waters.[a]

(5) It may be inferred from observations of the scales that winter habits do not differ greatly from those of summer, the annuli alone not being sufficiently pronounced to warrant such a belief. At any rate, very little evidence has been gathered from scales bearing on this point.

CONCLUSIONS.

AGE DETERMINATION.

Age may be determined in two ways: (1) By counting the annuli, the count being facilitated by (*a*) polarized light, (*b*) picrocarmine stain, (*c*) beginnings of radii; (2) by year groups in length and weight.

RADII.

The following observations support the theory that radii are hinges permitting the scale to bend: (1) Scales on inflexible parts of the body have no radii, while their number when present is proportionate to the degree of flexibility. (2) In thick scales the radii are seen to close when the scale is flattened. (3) In broad scales the radii are more numerous than in narrow scales. (4) Very young (uncalcified) scales have no radii; in older scales they appear to begin at some distance from the focus. (5) In cross section they appear as ridges of calcified matter on the flexible uncalcified substratum; when these ridges approach each other the scale is so bent as to make it more nearly flat. (6) Scales whose anterior angles are prolonged and acute have parallel radii; those with rounded anterior peripheries have divergent radii. (7) Radii stain as uncalcified parts with picrocarmine, the stained uncalcified layer below being visible through the radii fissures. (8) Those radii which do not begin at a point near the focus usually have their beginning at an annulus which is explained by the tendency of a lamina to crease without the support of the next superior lamina. (9) The radii on the several laminæ are in straight line one with another. This is explained by the support of the inflexible parts between the radii, i. e., the newly formed laminæ will bend in lines coincident with those of the next superior lamina. (10) No previous theory explains them.

CIRCULI.

(1) The number, distance apart, and mode of growth of the circuli afford no evidence as to the cause or periodicity of the annuli; (2) they are of uniform distance apart, regardless of the rate of growth, hence they do not represent definite periods of time; (3) their function is probably that of anchoring the scale in the pocket.

[a] Gill, Theodore: Natural history of the weakfish. Transactions of the American Fisheries Society, p. 269–276. Washington, 1910.

ANNULI.

(1) Annuli are edges of laminæ, and are not composed of circuli occurring closer together; (2) they do not represent periods of retarded growth; (3) they probably represent differences in degree of calcification.

CLASSIFICATION.

(1) Spines, not being permanent, have little classificatory value; (2) radii have none; (3) shape, alone, has none; (4) size has none; (5) the foregoing characters, collectively, may be of some value in classification; (6) circuli, appearing as the most constant character, are probably of some classificatory value.

LIFE HISTORY.

(1) If the squeteague grows more in summer than in winter, it leaves no trace of such a difference on its scales; (2) this fish probably spawns in its third year; (3) the maximum age is not less than 8 years, the oldest fish caught being of this age; (4) an average adult fish of this species is 32 cm. long; (5) little has been learned of winter habits from scales.

TABLE 1.—SHOWING GROWTH EACH YEAR OF CYNOSCION REGALIS, LENGTHS CALCULATED FROM GROWTH BANDS ON SCALES.[a]

Number.	First year.	Second year.	Third year.	Fourth year.	Fifth year.	Sixth year.	Seventh year.	Eighth year.	Sex.	Age.	Weight.	Total length.
	cm.	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*		*Years.*	*gm.*	*cm.*
1	24.44	31.77	38.09	......	......	......	......	......	♀	3	489.0	38.3
2	22.10	......	......	......	......	......	......	......	♀	1	75.9	22.1
3	19.80	30.80	38.50	......	......	......	......	......	♀	3	524.5	38.5
4	13.44	23.52	28.00	......	......	......	......	......	♀	3	198.0	28.0
5	16.01	18.08	20.45	25.20	29.35	31.72	......	......	♀	6	273.0	31.4
6	19.44	23.50	26.74	31.61	34.86	42.97	48.65	56.00	♀	8	1,370.0	56.0
7	19.85	30.30	36.57	42.84	45.98	......	......	......	♀	5	822.0	46.0
8	13.97	20.61	24.63	27.31	......	......	......	......	♀	4	191.0	27.4
9	16.33	22.87	30.40	......	......	......	......	......	♀	3	248.0	30.5
10	32.37	40.81	47.85	55.59	56.99	......	......	......	♀	5	1,788.0	57.0
11	19.43	23.33	29.17	31.11	......	......	......	......	♂	4	270.0	31.0
12	22.16	28.69	31.30	......	......	......	......	......	♀	3	299.0	31.3
13	17.68	24.00	30.31	32.84	40.41	42.94	45.45	......	♀	7	795.0	45.5
14	18.70	27.12	33.66	50.50	......	......	......	......	♀	4	1,176.0	50.5
15	26.71	34.95	40.09	47.35	56.61	......	......	......	♂	5	1,602.0	56.5
16	26.77	34.88	39.34	46.63	57.99	......	......	......	♀	5	1,900.0	58.0
17	26.86	33.97	41.08	48.10	55.12	60.65	65.50	......	♀	7	2,635.0	65.5
18	15.75	18.38	21.00	......	......	......	......	......	♀	3	85.0	21.1
19	18.34	24.45	27.50	......	......	......	......	......	♀	3	184.0	27.5
20	22.30	28.50	......	......	......	......	......	......	♂	2	184.0	28.5
21	23.05	27.32	31.59	36.71	......	......	......	......	♀	4	510.0	38.0
22	13.77	18.37	26.02	......	......	......	......	......	♀	3	163.0	26.0
23	21.96	26.23	29.47	31.13	36.79	38.02	......	......	♀	6	445.0	38.0
24	14.49	21.43	25.18	29.47	33.50	......	......	......	♂	5	340.0	33.5
25	21.39	27.93	31.59	......	......	......	......	......	♂	3	298.0	31.5
26	19.87	25.39	26.50	......	......	......	......	......	♀	3	170.0	26.5
27	11.67	17.51	23.35	28.53	30.50	......	......	......	♀	5	270.0	30.5
28	21.71	28.95	38.26	43.48	50.60	......	......	......	♀	5	1,135.0	50.5
29	24.04	30.77	37.50	45.19	50.00	......	......	......	♀	5	1,361.0	50.0
30	17.41	26.11	32.64	38.08	......	......	......	......	♂	4	426.0	38.0
31	22.06	26.47	29.80	......	......	......	......	......	♂	3	227.0	30.0
32	13.60	21.76	26.29	......	......	......	......	......	♂	3	163.0	26.3
33	22.03	26.37	30.71	......	......	......	......	......	♂	3	799.0	30.5
34	17.67	22.56	25.38	27.50	......	......	......	......	♀	4	184.0	27.5
35	20.41	25.78	29.00	......	......	......	......	......	♂	3	227.0	29.0
36	18.57	22.28	26.00	......	......	......	......	......	♂	3	142.0	26.0
37	15.86	25.55	35.24	46.69	55.50	......	......	......	♀	5	1,580.0	55.5
38	24.82	32.36	37.32	42.28	59.15	65.50	......	......	♀	6	2,260.0	65.5
Average	19.91	26.31	31.84	38.48	46.22	46.96	53.20	56.00	......	4.1	......	38.0

[a] The measurements of length in this paper are from tip of snout to the end of the shortest rays, middle of the caudal fin.

TABLE 2.—LENGTHS AT DIFFERENT AGES OF 65 EXAMPLES OF CYNOSCION REGALIS AS CALCULATED FROM THE SCALES AND AS AVERAGES OF MEASURED YEAR CLASSES, WITH THE NUMBER OF FISH MEASURED IN EACH CASE.

Year.	Length.		Number of fish.		Year.	Length.		Number of fish.	
	Calculated.	Measured.	Calculated.	Measured.[a]		Calculated.	Measured.	Calculated.	Measured.
	cm.	cm.				cm.	cm.		
1	19.91	20.5	38	1(+10)	6	46.96	56.0	6	3
2	26.31	26.6	37	1(+13)	7	53.20	65.5	3	2
3	31.84	32.3	36	15(+ 1)	8	....	56.0	....	1
4	38.48	37.0	21	6(+ 3)					
5	46.22	45.2	15	9	Total	....	....	156	65

[a] As the number 1, 2, 3, and 4 year-old fish used in table 1 was small the present table includes 27 additional specimens employed for length measurements, their distribution is indicated by the numbers in parentheses.

TABLE 3.—VARIATIONS IN LENGTH AT DIFFERENT AGES OF CYNOSCION REGALIS.

Year.	Maximum.	Minimum.	Difference.	Average.[a]	Year.	Maximum.	Minimum.	Difference.	Average.[a]
	cm.	cm.	cm.	cm.		cm.	cm.	cm.	cm.
First	32.37	11.67	20.70	19.91	Fourth	55.59	25.20	30.39	38.48
Second	40.81	17.51	23.30	26.31	Fifth	59.15	29.35	29.80	46.22
Third	47.85	21.00	26.85	31.84	Sixth	65.50	31.72	33.78	46.96

[a] Average not of the maximum and minimum in class, but of entire class.

TABLE 4.—RELATIVE DISTANCE APART OF THE ANNULI (ARBITRARY STANDARD), AND THE NUMBER OF CIRCULI BETWEEN EACH TWO.

Band.	Width.	Number of circuli.	Ratio.
1	19	78	4.01
2	10	40	4.00
3	6	21	3.50
4	6	20	3.33
5	3	10	3.33

TABLE 5.—NUMBER OF RADII IN EACH YEAR OF THE LIFE OF 40 FISH, COUNTED ON THE ANNULI.[a]

Number.	First year.	Second year.	Third year.	Fourth year.	Fifth year.	Sixth year.	Seventh year.	Number.	First year.	Second year.	Third year.	Fourth year.	Fifth year.	Sixth year.	Seventh year.
1	18	28	.....	.....	.....	.....	.....	22	11	15	19	.....	.....	.....	.....
2	9	13	16	.....	.....	.....	.....	23	11	20	18	.....	.....	.....	.....
3	13	13	10	10	8	8	.....	24	12	13	13	14	17	.....	.....
4	38	46	49	52	75	.....	.....	25	14	18	20	22	22	20	18
5	17	18	19	27	.....	.....	.....	26	18	20	21	.....	.....	.....	.....
6	7	15	11	13	10	.....	.....	37	7	14	15	.....	.....	.....	.....
7	16	26	33	29	.....	.....	.....	28	18	32	35	.....	.....	.....	.....
8	13	20	20	.....	.....	.....	.....	29	12	13	13	11	11	.....	.....
9	12	15	17	16	18	18	.....	30	12	22	.....	.....	.....	.....	.....
10	14	23	32	34	40	42	.....	31	16	24	26	28	.....	.....	.....
11	9	12	13	17	.....	.....	.....	32	10	20	21	.....	.....	.....	.....
12	12	25	27	31	.....	.....	.....	33	12	15	15	.....	.....	.....	.....
13	15	20	18	24	.....	.....	.....	34	16	21	21	23	28	31	.....
14	13	17	17	18	.....	.....	.....	35	13	18	21	22	28	.....	.....
15	13	19	15	15	12	.....	.....	36	12	21	24	23	28	.....	.....
16	14	25	28	.....	.....	.....	.....	37	10	14	15	13	6	3	1
17	13	21	21	17	.....	.....	.....	38	12	11	11	10	.....	.....	.....
18	11	16	17	.....	.....	.....	.....	39	22	32	42	53	62	.....	.....
19	13	17	19	.....	.....	.....	.....	40	11	14	16	16	15	.....	.....
20	13	17	17	8	5	1	.....								
21	13	15	21	28	23	23	.....	Average	13.5	19.5	20.7	22.1	25.5	18.2	9.5

[a] Different series from table 1. The fortuity that the small number of scales more than three years old includes, No. 4, 10, and 39 which have an unusually large number of radii, serves in a measure to obscure the purpose of the table; with these abnormal figures omitted throughout, the averages corroborate the fact that it is otherwise obvious to one who examines the scales.

TABLE 6.—NUMBER OF FISH (CYNOSCION REGALIS) ATTAINING THE DIFFERENT AGES.[a]

Year.	Sex. Male.	Sex. Female.	Total.	Year.	Sex. Male.	Sex. Female.	Total.
1	11	27	38	5	2	13	13
2	11	26	37	6	0	6	6
3	10	26	36	7	0	3	3
4	4	17	21	8	0	1	1

[a] This table shows that 36 out of originally 38 specimens, or 94.7 per cent survived till the third year (see text, p. 314).

SUPPLEMENTARY OBSERVATIONS ON THE PIGFISH, ORTHOPRISTIS CHRYSOPTERUS.

The foregoing investigations on the scales of the squeteague were done during the summer of 1912. The writer undertook a similar work on the scales of the pigfish in the summer of 1913. Besides bringing out some points in the life history of this fish, the investigation also throws additional light on the nature of the annuli.

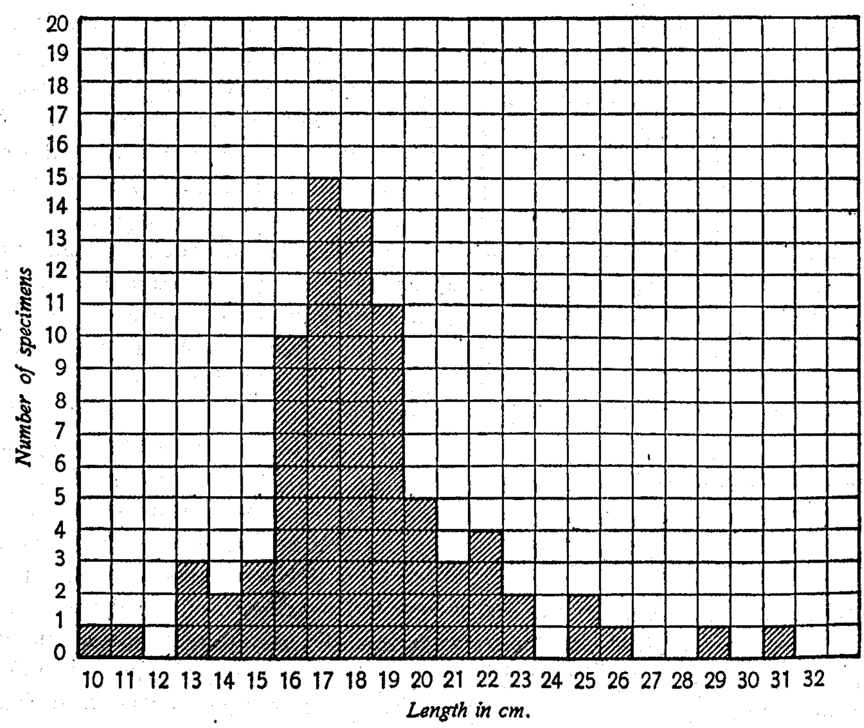

FIG. 5.—Occurrence of pigfish of different lengths, one year old and upward. The 10 cm. class consists of specimens 10 to 11 cm. in length, etc.

The scales of the pigfish are similar in type to those of the squeteague, i. e., they are ctenoid, radiate, and characterized by circuli, annuli, etc., and they have the same general shape as those of the squeteague.

The radii found on the scales of the pigfish are similar to those of the squeteague in structure, but are much more regular in arrangement. Branching is not common inside the second annulus and as the annuli seldom exceed two in number, branching bears a much less important relation to age determination on the pigfish than on the squeteague. At the focus the radii are usually from six to nine in number, and more often than not continue to the periphery without branching.

The radii on the pigfish scales corroborate the evidence found on the squeteague and make even more convincing the probability that radii are adaptations to bodily movement. A cross section of the pigfish scale shows a very characteristic structure strongly supporting the proposed explanation. Immediately under, and coincident with, the radii are corrugations, in the upper layer of whose summits are the radii. These corrugations stain rose pink in picrocarmine (Hoyer), while the superior layer stains hardly any.

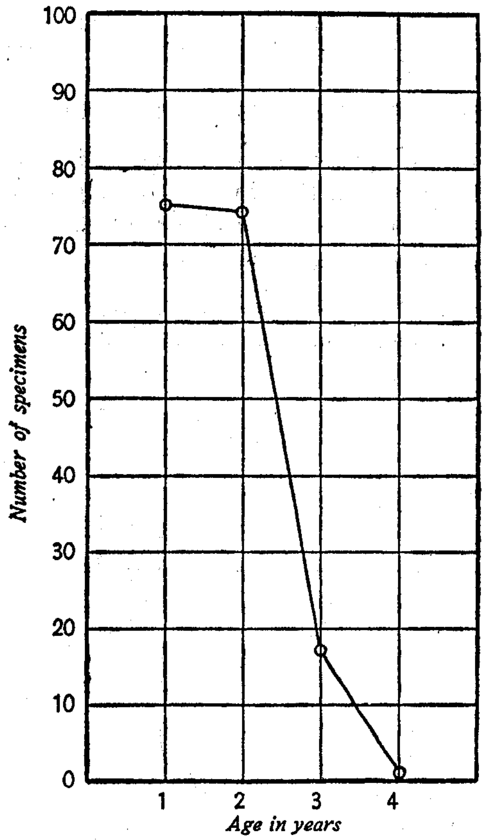

FIG. 6.—Occurrence of pigfish at different ages.

Scales taken from the opercula of the pigfish offer still further corroboration of the conclusions drawn from observations on the scales of the squeteague. They present in cross section a sinuous outline suggesting the view that they are stages intermediate between those that bend and have the regular radii and those occupying inflexible parts and having no radii.

A series of experiments was carried on directed toward determining what influence food supply has on the formation of the annuli. Two aquaria were kept. (See feeding record, table 7.) In aquarium no. 1 four fish were placed, ranging from 14 to 18 cm. in length; in aquarium no. 2 seven fish of lengths ranging from 14 to 22 cm. were placed. All were started in aquaria on June 24. From June 27 the feeding record shows their treatment till they died or were taken out, August 22. In the beginning the fish in aquarium no. 2 were fed sparingly, but as it was learned that they could live on very little, feeding was practically abandoned during the month of August. In all cases the fish in aquarium no. 1 were fed daily all they would eat, while those in no. 2, even when fed, were never satisfied. For some unaccountable reason all of the "well-fed" fish died on August 6, while one of the "starving" fish died August 5.

Careful watch was kept on the growth of the scales, but no difference whatever was noticeable in the formation of annuli. Any difference in growth was so small as not to be reckoned with. (Pl. LVIII, fig. 25, 26.)

These results appear to offer conclusive evidence that feeding habits have no influence upon the formation of annuli. Other possible factors yet untested are the influence of temperature and the presence of lime salts in the food and water.

The method of determining the probable length of life and spawning time of the pigfish was the same as that pursued for the squeteague. The survival of the great majority of pigfish through two years, followed by a sudden and great diminution in number, suggests the conclusion arrived at by Gilbert (1913) for the Pacific coast salmon, i. e., that this is the age of sexual maturity and that as a general rule they perish after this time. A glance at text figure 6 shows that out of 167 fish observed, only one reached the fourth year; 17 reached the third year, while 75 and 74 reached the ages of 1 and

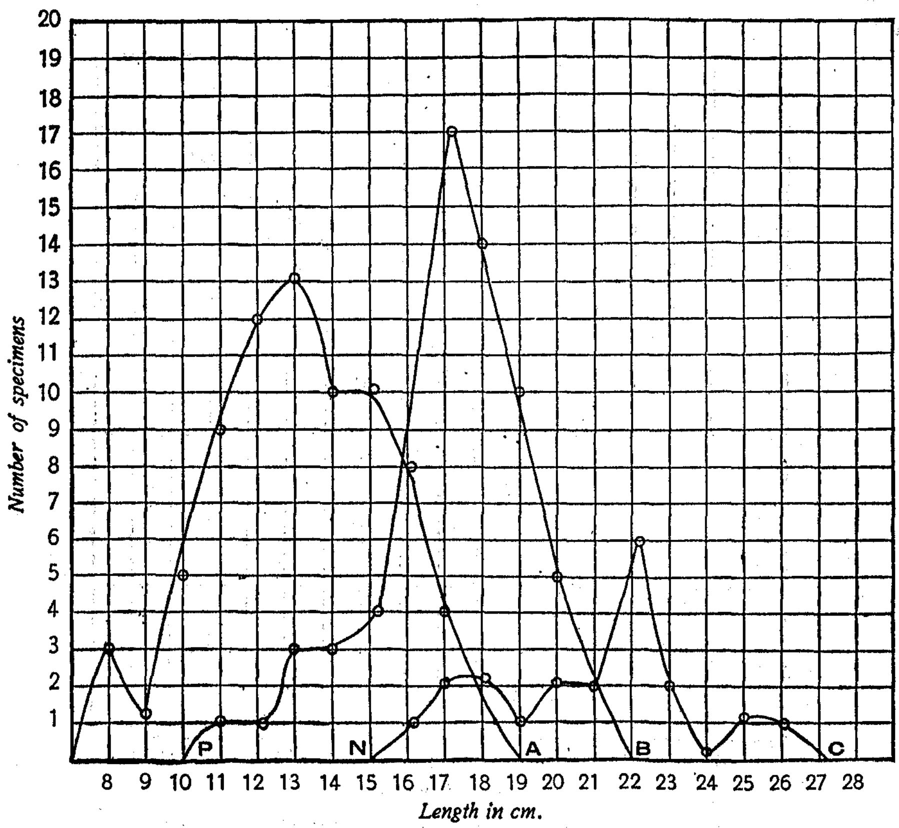

FIG. 7.—Occurrence of pigfish of one, two, and three years old. OA, fishes one year old; PB, two years; NC, three years. The 8 cm. class consists of specimens 8 to 9 cm. long, etc.

2 years, respectively. At all events, if the pigfish ever lives over four years it is extremely exceptional, since out of the total of 337 fish examined only one was found of that age, and none exceeded it. (Text figure 8.) Reasoning then from the small number of fish upon which perpetuation of the species would depend if spawning did not take place before the fourth or third year, we are forced to the assumption that the pigfish spawns in the second year if not in the first. There is no evidence on the scales to indicate whether or not spawning occurs in the first year, unless we regard the almost universal survival through the second year and the unripe condition of the ovaries and testes in July in 1-year-old fish as evidence that spawning does not occur the first year.

There seems to be greater latitude in the spawning time of the pigfish than in that of the squeteague. Not only was the length of individuals of the various age groups much more variable, but through the entire summer fry of all sizes from 1 cm. up were taken in great numbers in dragnets, while during the summer of 1912 the writer was led to believe that the squeteague had a very definite spawning time by the uniformity of length and the absence of small fry.

As to the winter habits of the pigfish the scales bear no evidence, since the experiments described above indicate that feeding habits have no influence upon the formation of the annuli.

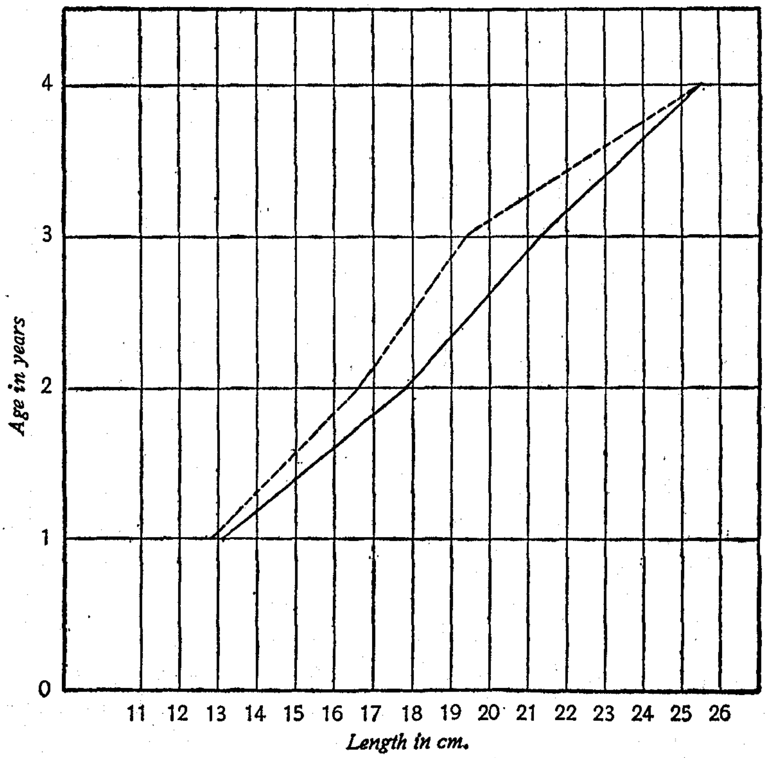

FIG. 8.—Comparison of calculated and measured lengths of the pigfish.

Numerous efforts were made to fix upon some method of marking individual scales for comparison of growth, and of paralyzing parts of the body to observe the formation of radii, but these efforts were uniformly without very encouraging results. To mark scales the writer tried $AgNO_3$, india ink, slips of tinfoil inserted under the scales, various aniline dyes, etc., but in all cases the mark was sloughed off or had impressed itself only on the mucous secretion covering the body of the fish. In order to determine empirically the growth of scales, the writer removed with a pair of fine-pointed scissors a segment of a scale, leaving the remainder in the scale pocket for comparison. It appears that such a segment in the scale pocket is partly or completely absorbed and almost entirely regenerated.

TABLE 7.—FEEDING RECORD.[a]

Date.	Aquarium no. 1.	Aquarium no. 2.
June 27	4 anchovies	4 anchovies.
June 28	2 shrimps	2 shrimps.
June 29	do	No food.
June 30	Fed well on anchovies.	2 anchovies.
July 1	Fed well on cut fish	No food.
July 2	do	Do.
July 3	do	Anchovies sparingly.
July 4	do	No food.
July 5	do	Well fed.
July 6–7	do	No food.
July 8	do	4 small anchovies.
July 9–13	Fed well on cut fish	No food.
July 14	do	Anchovies sparingly.
July 15–27	Anchovies daily	No food.
July 28	Anchovies	Full meal anchovies.
July 29–Aug. 6.[b]	Anchovies daily	No food.[c]
Aug. 7		Anchovies sparingly.
Aug. 8–10		No food.
Aug. 11		Do.
Aug. 12–22		Do.

[a] This feeding record embraces a period of 57 days. In aquarium no. 1 the fish were fed daily between June 27 and Aug. 6, when they died; while the fish in aquarium no. 2 were fed in the 57 days covered by the record only 9 times. This total for aquarium no. 2 includes 2 days well fed, July 5 and 28; the remaining feeding days they were fed very sparingly, the amount varying from 1 to 4 anchovies for 7 fishes.
[b] All fish in aquarium no. 1 died; reason unknown.
[c] One fish died.

TABLE 8.—TOTAL LENGTH AND TOTAL WEIGHT OF PIGFISH.

[Lengths for each year calculated from the annuli.]

No.	Total length.	Total weight.	Length first year.[a]	Length second year.[a]	Length third year.[a]	Length fourth year.[a]
	cm.	gm.	cm.	cm.	cm.	cm.
1	4.3	3.0				
2	1.5	2.0				
3	1.8	1.0				
4	20.0	184.0	9.33	8.82	2.05	
5	20.0	184.0	14.48	4.21	2.10	
6	20.0	189.0	16.23	3.77		
7	13.0	47.0	11.37	1.62		
8	15.0	55.0	14.44	.56		
9	13.0	52.0	11.70	1.30		
10	14.0	50.0	13.12	.87		
11	11.5	32.0	8.75	2.73		
12	16.0	82.0	13.27	2.92		
13	13.2	4.8	10.80	2.40		
14	18.0	102.0	15.15	2.87		
15	5.5	2.0				
16	16.8	52.0	13.44	3.36		
17	26.2	207.2	13.42	8.63	4.15	
18	23.0	125.1	15.23	3.54	4.13	
19	25.5	200.8	14.16	4.25	4.25	2.83
20	17.5	57.6	16.26	1.23		
21	20.2	89.8	15.08	5.12		
22	17.2	62.6	13.18	2.87	1.16	
23	17.2	60.2	15.05	2.15		
24	18.3	75.3	14.42	3.91		
25	16.3	50.5	12.86	3.43		
26	19.2	80.7	15.51	3.69		
27	17.1	63.5	12.38	4.73		
28	19.8	88.2	16.53	3.15		
29	21.5	115.4	11.06	8.35	2.09	
30	19.1	77.4	15.28	3.82		
31	16.6	51.2	11.80	4.79		
32	23.6	150.6	16.48	5.24	1.87	
33	16.4	46.1	14.21	2.19		
34	16.8	60.3	10.50	3.97	2.33	
35	17.0	56.7	8.09	7.69	1.21	
36	18.6	74.5	13.66	4.94		
37	15.7	42.5	13.08	2.62		
38	18.5	72.1	17.13	1.35		
39	22.7	132.9	15.45	5.52	1.69	
40	18.4	76.2	11.67	6.73		
41	19.4	92.8	12.56	6.82		
42	22.6	209.5	12.36	9.27	.97	
43	18.2	74.5	8.43	4.02	5.75	
44	19.6	94.1	14.70	4.90		
45	19.6	94.1	13.48	6.13		
46	16.1	52.3	12.21	3.89		
47	19.5	84.8	16.09	3.40		
48	17.2	63.4	12.61	4.58		
49	17.1	55.3	15.50	1.60		
50	16.1	51.6	12.15	3.95		
51	14.7	41.4	10.83	3.87		
52	22.0	145.7	12.97	4.51	4.51	
53	17.3	57.2	12.68	4.61		
54	19.4	90.5	17.00	2.40		
55	15.7	48.9	11.57	4.13		
56	17.8	74.1	13.35	4.45		
57	21.1	123.3	11.51	5.75	3.84	
58	20.6	99.7	18.30	2.29		
59	21.8	109.3	18.17	3.63		
60	18.1	78.0	16.16	1.94		
61	19.0	81.0	12.67	6.33		
62	17.9	64.9	16.89	.99		
63	17.3	67.1	14.57	2.85		
64	19.2	81.2	15.81	3.38		
65	17.7	65.2	14.90	2.79		
66	10.5	13.8	10.50			
67	19.5	97.0	14.73	1.73		
68	18.1	73.4	14.29	3.18		
69	18.2	83.1	13.23	4.96		
70	17.7	63.3	13.48	4.21		
71	17.6	70.2	15.84	1.76		
72	17.8	77.0	13.45	4.45		
73	16.3	54.8	11.15	5.15		
74	18.5	77.5	13.70	4.82		
75	18.0	67.8	12.24	4.32	1.44	
76	16.6	55.7	10.38	6.23		
77	18.4	71.6	11.50	6.90		
78	18.5	77.8	16.32	2.18		
79	25.8	205.5	10.32	10.32	5.16	
Average			12.8	3.85	2.86	

[a] Figures in these columns represent amount added for the respective years; the total length for any year may be found by adding the increment for one year to the preceding total.

TABLE 9.—PIGFISH.—COMPARING THE AVERAGE LENGTHS MEASURED FOR THE DIFFERENT YEAR GROUPS WITH THE LENGTHS CALCULATED, AND THE NUMBER OF SPECIMENS MEASURED AND CALCULATED IN EACH CASE.

Year.	Length.		Number of fish.	
	Measured.	Calculated.	Measured.	Calculated.
	cm.	*cm.*		
1.....	13.1	12.8	77	78
2.....	17.8	16.7	58	78
3.....	21.3	19.5	20	17
4.....	25.5	25.5	1	1
Total	....	....	156	174

SYNONYMY OF TERMS.

Owing to the great number of terms applied to the different structures of scales and the confusion resulting from it, this synonymy has been arranged to specify the terms employed in this paper.

The exterior surface of scales is marked with numerous, more or less distinct relieved lines, concentric, or nearly so, in most cases, with the periphery. They are variously known as annuli (Esdaile), circuli (Cockerell), striæ, fibrillæ, concentric rings, and growth-rings. Such lines are here denoted as *circuli*. (Pl. L, *C*.)

For their common center, usually somewhat posterior to the center of the scale, the term *focus* adopted by Cockerell is used in this paper. It has also been called the center, centrum, center of growth, and nucleus. (Pl. L, *F*.)

Concentric with the circuli are bands or zones, which are here denominated *annuli*. They are darker than the space between them and have been regarded as zones in which the circuli are closer together. They appear in some cases to be regions in which the regularity of the circuli is interrupted. They are variously known as annuli, peronidia, annual rings, winter bands, and growth-rings. (Pl. L, *A*.)

Radii, as they are called in this paper, are lines found usually on the anterior side of the scale, perpendicular to the circuli, directed from the focus to the periphery and usually increasing in number as the latter is approached. They have been known as grooves, radiating grooves, and radii. (Pl. L, *R*.)

The outer edge of the scale is called in this and other papers the *periphery*. It has been called the margin. (Pl. L, *P*.)

In some scales the posterior field is found to be covered with spines, barbs, or teeth. The author uses the term *spines* for these. They have been called denticles, spinules, and teeth. (Pl. L, *Sp*.)

A scale may be divided into four areas or fields. They are referred to in this paper as the *anterior field* or that portion covered in the scale pocket and directed toward the head of the fish; the *posterior field* or that part opposite the anterior field and in ctenoid scales covered with spines; and the *lateral fields* or those on either side of the scale. In connection with areas of the scale surface the words apical and basal have been used for posterior and anterior, respectively.

The *inferior* side is that nearest the body. The *exterior* or superior side is the sculptured side.

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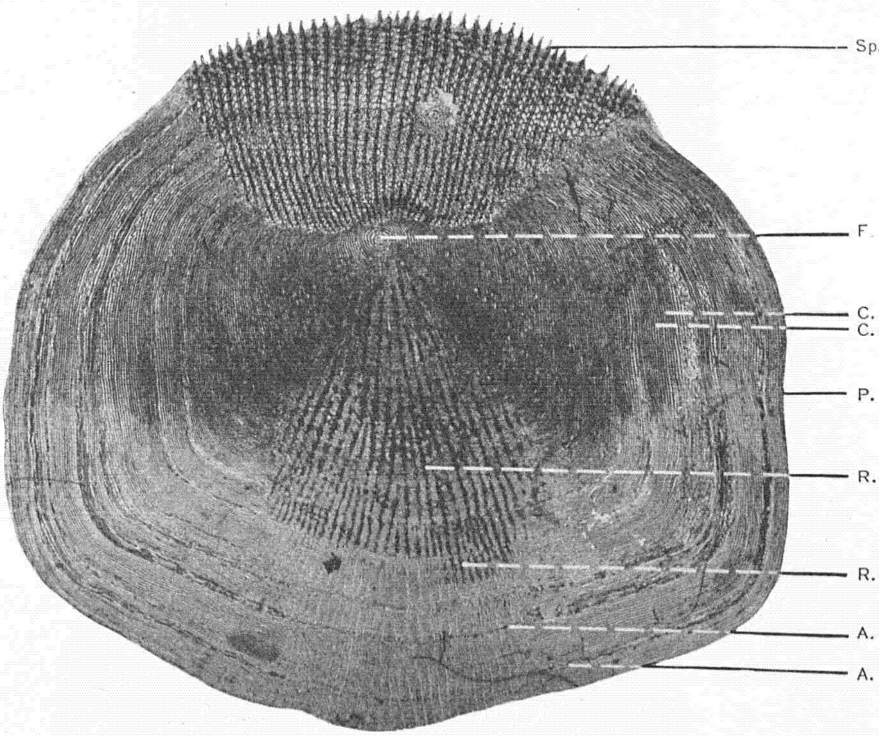

FIG. 1.—*Cynoscion regalis*. Typical scale showing all the terms used in this paper: F, focus; C, circuli; P, periphery; R, radii; A, annuli; Sp., spines. × 10.

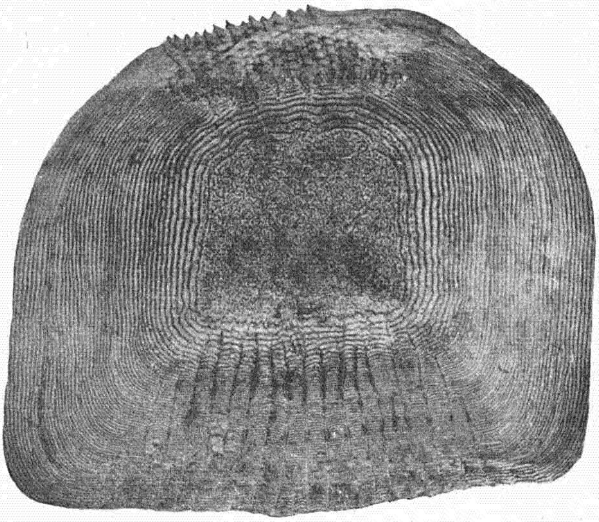

FIG. 2.—*Cynoscion regalis*. Regenerated scale showing unusually large focus marked with fine sculpturing. × 12.

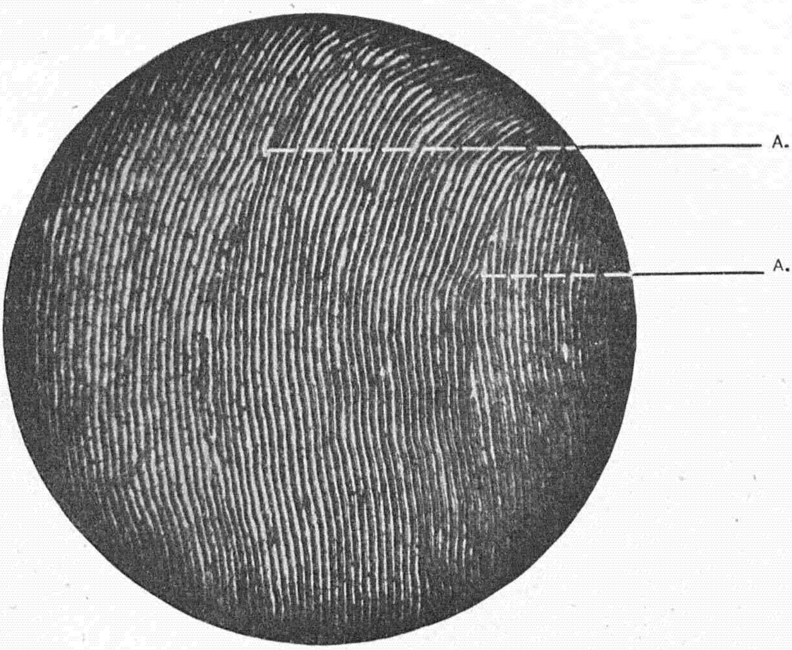

FIG. 3.—*Cynoscion regalis*. Photomicrograph of two annuli, A, showing that the annuli are not in reality bands in which the circuli are closer together. × 40.

FIG. 4.—Scale taken from the head of the fish directly above the eye and slightly off the median line. × 12.

FIG. 5.—Scale taken from above the eye and on the median line. × 14.

FIG. 6.—Scale taken from cheek. × 14.

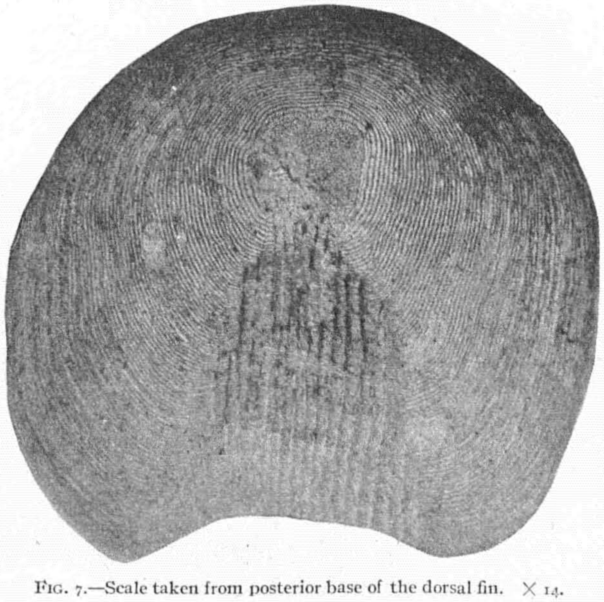

FIG. 7.—Scale taken from posterior base of the dorsal fin. × 14.

Cynoscion regalis.—Scales taken from different parts of the body showing the influence of movement and shape on the presence and number of radii.

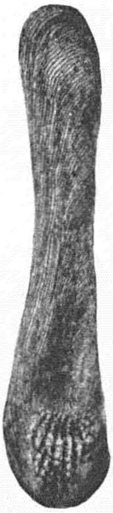

FIG. 8.—Scale taken from side of vent. × 12.

FIG. 9.—Scale taken from point near the vent. × 12.

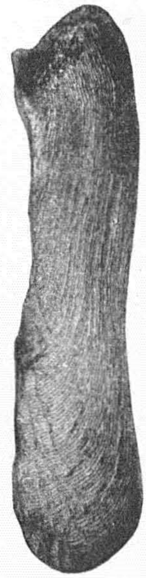

FIG. 10.—Scale taken from side of vent. × 12.

FIG. 11.—Scale taken from point near the vent. × 10.

FIG. 12.—Scale taken from slightly below the anterior base of the dorsal fin. × 10.

FIG. 13.—Scale taken from base of first dorsal fin on median line. × 10.

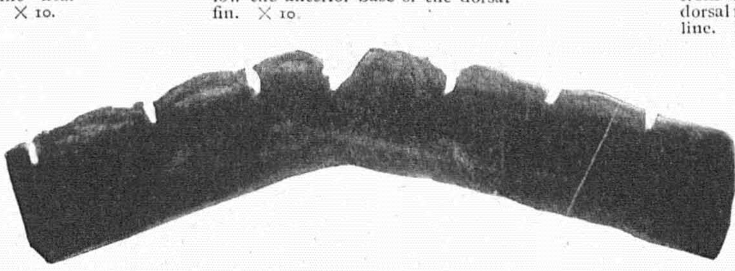

FIG. 14.—Cross section of scale bent to show opening of radii. × 40.

Cynoscion regalis.—Scales taken from different parts of the body showing the influence of movement of the fish and shape of the scale on the presence and number of radii.

FIG. 15.—Scale showing the diminution of the number of radii after the third year. × 12.

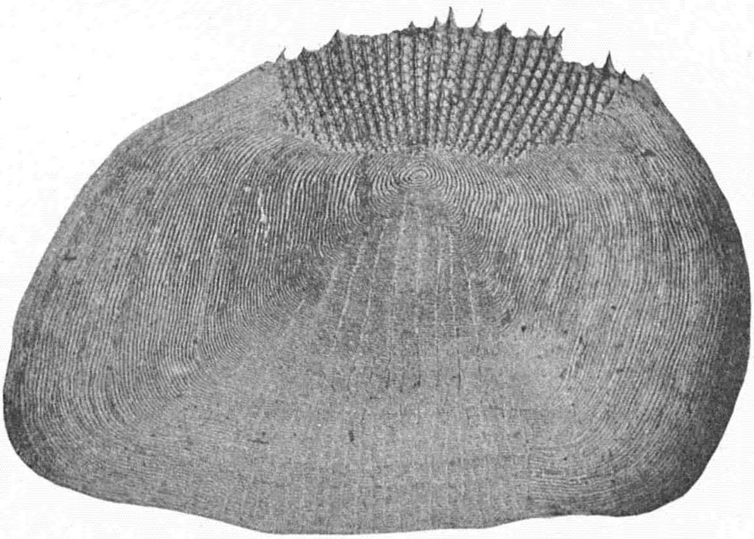

FIG. 16.—Scale taken from anterior base of caudal fin. × 14.

Cynoscion regalis.—Scales taken from different parts of the body showing the influence of movement of the fish and shape of the scale on the presence and number of radii.

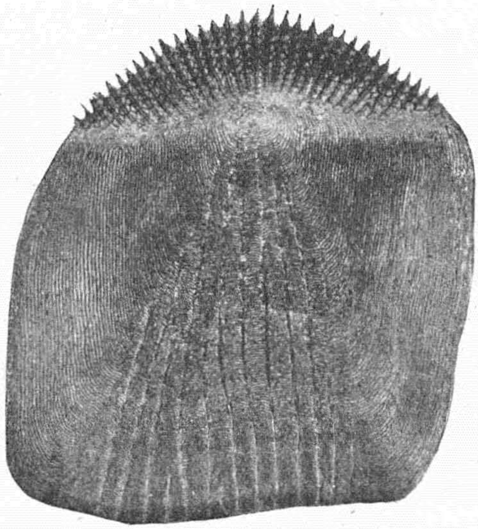

FIG. 17.—*Cynoscion regalis.* Scale from a fish beginning its second year. × 15.

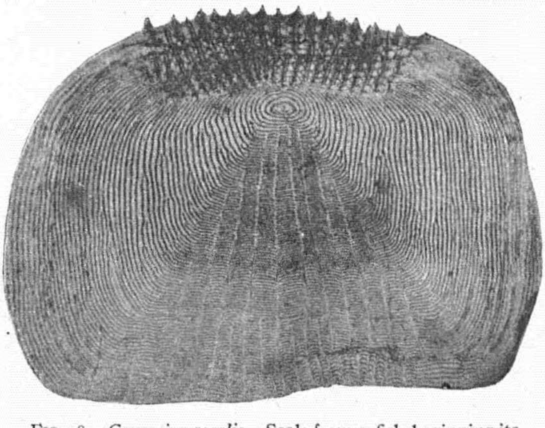

FIG. 18.—*Cynoscion regalis.* Scale from a fish beginning its third year. × 14.

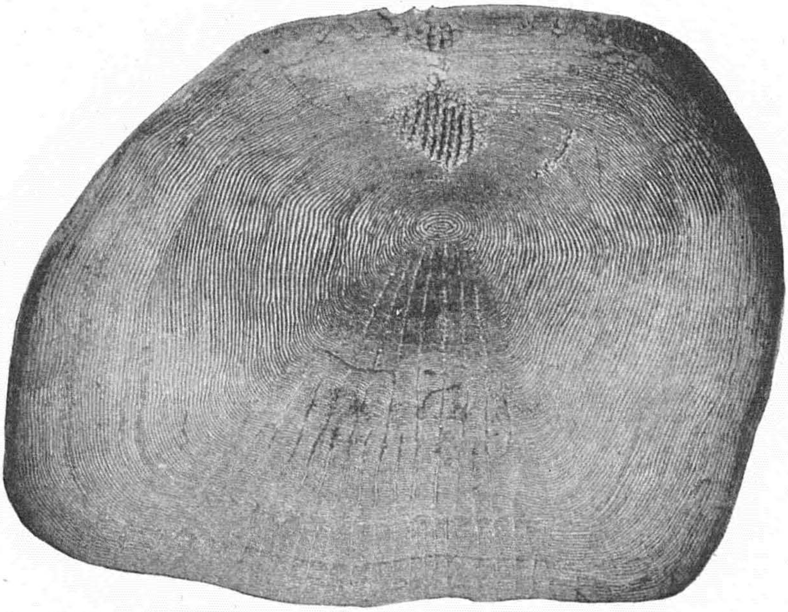

FIG. 19.—*Cynoscion regalis.* Scale from a fish beginning its fourth year. × 12.

FIG. 20.—*Cynoscion regalis.* Scale from a fish beginning its fifth year. × 12.

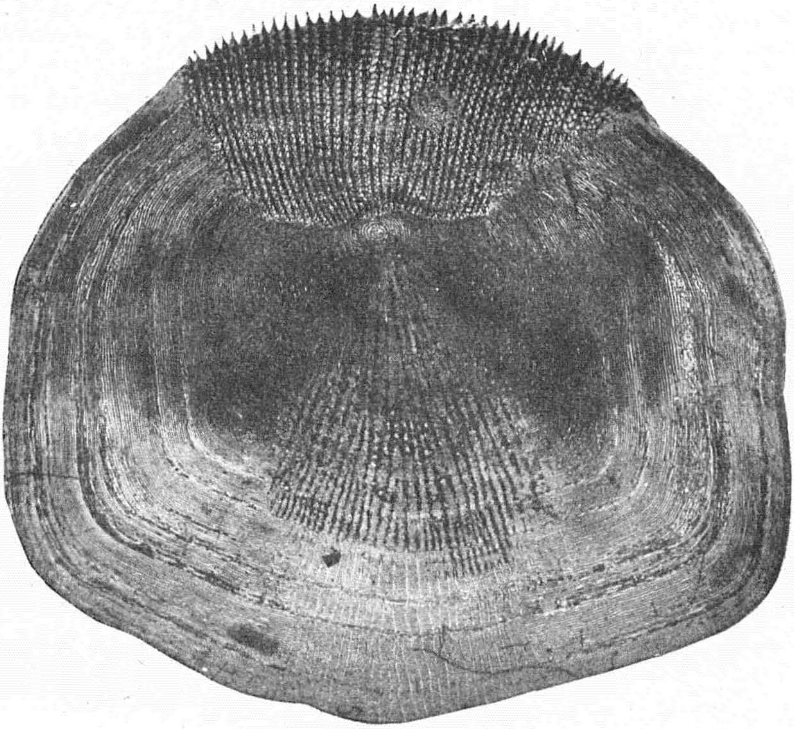

FIG. 21.—*Cynoscion regalis*. Scale from a fish beginning its sixth year. × 10.

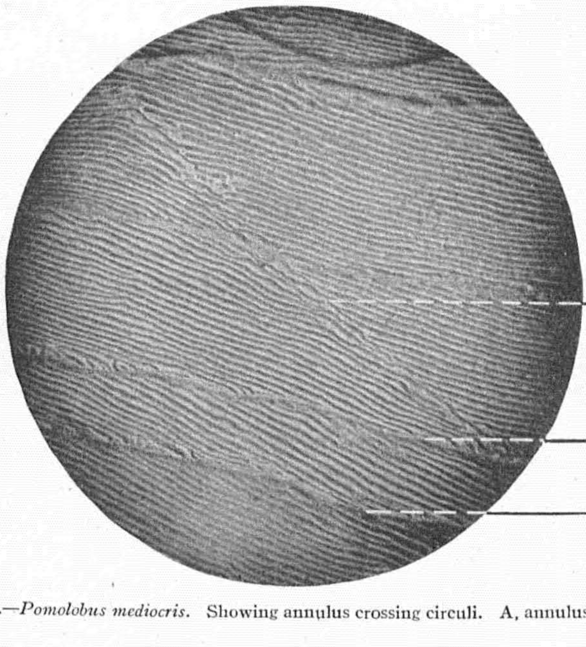

FIG. 22.—*Pomolobus mediocris*. Showing annulus crossing circuli. A, annulus; R, radii. × 40.

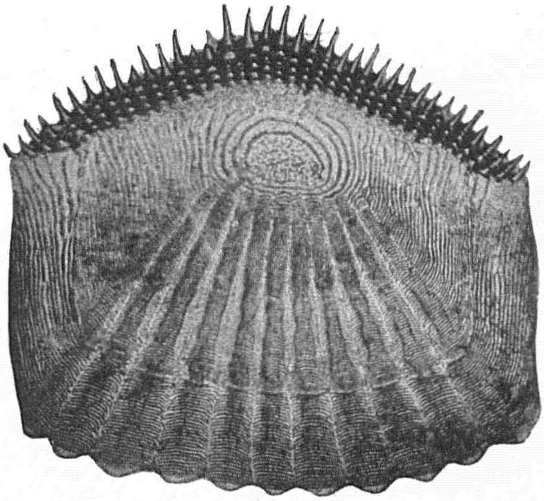

FIG. 23.—*Orthopristis chrysopterus.* Scale from a fish 1 year old. × 35.

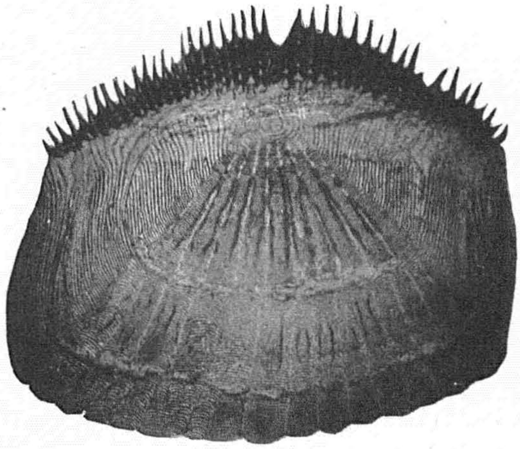

FIG. 24.—*Orthopristis chrysopterus.* Scale from a fish 2 years old. × 12.

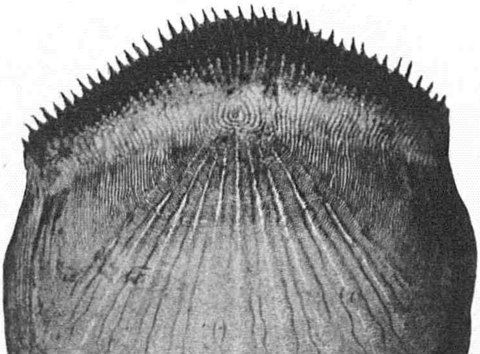

FIG. 25.—*Orthopristis chrysopterus.* Scale from a well-fed fish in aquarium no. 1. × 12. (See table 7.)

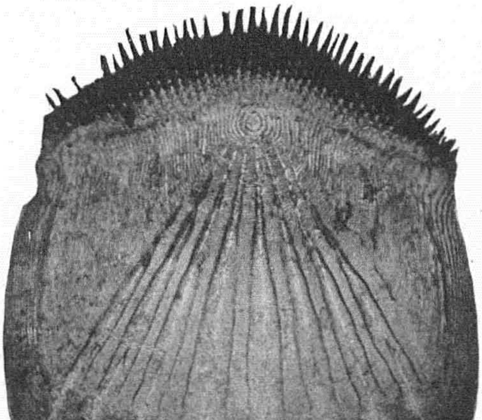

FIG. 26.—*Orthopristis chrysopterus.* Scale from a sparingly fed fish in aquarium no. 2. × 12.

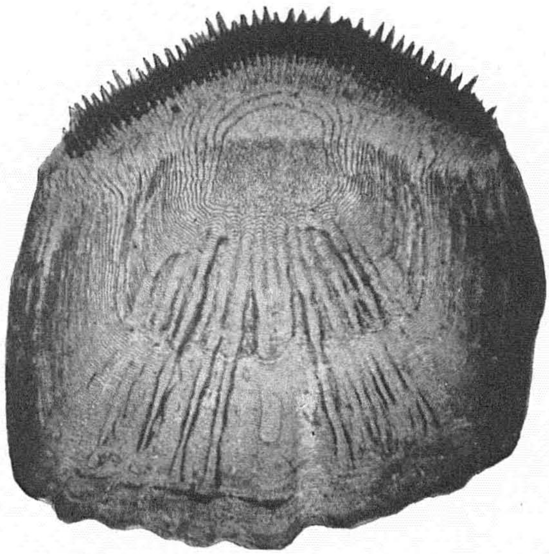

FIG. 27.—*Orthopristis chrysopterus*. Scale from a fish 4 years old. × 12.

FIG. 28.—*Orthopristis chrysopterus*. Scale from a fish 14 cm. long but with no annuli. × 12.

FIG. 29.—*Orthopristis chrysopterus*. Scale from a fish 3 years old. × 12.