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# Scales in the Permian Amphibian *Trimerorhachis*

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## INTRODUCTION

Scales have long been known in fossil and recent amphibians, and a considerable volume of literature has been published on amphibian scales. Among the recent amphibians, the caecilians (Apoda, Gymnophiona) are characterized by the presence of scales in many genera, and these have been studied and described by various authors. Among the fossil forms, scales have been recognized in the Labyrinthodontia, the Aistopoda, and the Microsauria (this last order is regarded by some authorities as containing the ancestors of the modern caecilians).[1] These have been described and figured by several authors, especially by Fritsch in his monumental work entitled "Fauna der Gaskohle und der Kalksteine der Permformation Böhmens." In spite of this, much remains to be learned about scales in fossil amphibians, and as new discoveries are made from time to time they add to our body of knowledge concerning scalation in the extinct Amphibia.

In the autumn of 1945, Mr. Robert V. Witter, then of the American Museum of Natural History, had the good fortune to discover in Texas a deposit containing many complete skeletons of the rhachitomous labyrinthodont genus *Trimerorhachis*. These were excavated by Witter and brought to the museum, where they were prepared by him. During the

[1] Genera here placed in the Labyrinthodontia and the Microsauria are assigned in much of the literature to the "branchiosaurs." The problem of the Phyllospondyli (whether the branchiosaurs are distinct forms or are larval stages of other amphibians) cannot be considered within the limits of the present paper. I here follow Romer in regarding the branchiosaurs as larval forms.

course of preparation it was discovered that in several instances not only was the skeleton preserved more or less completely, but in addition the body covering had been fossilized. As preparation of the material progressed it became evident that large areas of scales were present.

This was a most fortunate discovery. Scales in labyrinthodonts and other extinct amphibians are known mainly from fossils of Carboniferous age. The presence of scales in a Permian genus is unexpected and gives a welcome opportunity for a description and for comparison with the scales in other amphibians, both fossil and recent.

At this place I wish to acknowledge the aid I received from Mr. Witter in the prosecution of this study. It was because of his skillful work of collecting in the field and preparing the fossils in the laboratory that the *Trimerorhachis* scales were preserved for study. His interest in the problem of amphibian scales was responsible for the first recognition of their presence in the fossils at hand and for the subsequent work that resulted in the preservation of these fossils.

To Prof. Emmett Reid Dunn of Haverford College, our leading authority on the caecilians, and to Mr. Charles M. Bogert of the American Museum of Natural History, I am indebted for advice and constructive suggestions with regard to the scales in these modern amphibians. To Dr. Charles M. Breder, Jr., and to Dr. Bobb Schaeffer of the American Museum of Natural History I am grateful for some very fruitful conversations on the problem of scales in fishes and their possible homologies with amphibian scales.

The drawings illustrating this paper were made by Mrs. Lois Darling and Mr. M. Insinna.

## SCALES IN RECENT AMPHIBIA

Scales are found in some but not all genera of recent Apoda. "Bony cycloid scales are concealed beneath the skin anterior to both primary and secondary grooves in all Rhinatrema, all Gymnopis, and in most Caecilia. They are absent in all Siphonops, in all Chthonerpeton, and in all Typhlonectes" (Dunn, 1942, p. 448). In the primitive caecilians there are two or three complete rings of bony scales for each body segment, but in the more specialized genera this condition may be greatly modified. Moreover, as Dunn has pointed out, there is no overlapping of the scales of one ring by those of another. It has been stated by some authorities that scales are limited to the back region in most genera of caecilians, but Dunn has shown that this is not correct; indeed it is common for scales to be present on the belly as well as on the back of these amphibians.

From the above it is clear that even in the most primitive caecilians the scales are much reduced in their distribution from what must have been the truly primitive condition, in which the entire body probably was covered by overlapping scales. The reason for assuming such a condition for the as yet unknown ancestral caecilians is based on a comparison with some of the fossil amphibians in which scales are preserved over the entire body.

Although distribution of the scales on the body in the modern caecilians is much reduced from the assumed ancestral condition, the structure of the individual scale itself remains primitive. In fact, the modern caecilian scale is essentially a fish scale, carried over into the amphibian level of evolutionary development. The scale of *Dermophis,* for instance, as described and figured by Ochoterena (1932) shows the essential characters that typify the fish scale. It is a cycloid scale, more or less rounded, but with the lateral fields expanded in the anterior portion of the scale. There is a focus placed anteriorly to the center of the scale and around this are arranged annular rings, similar to the annular rings in the scales of many fishes.

Not only is the scale of *Dermophis* similar to a fish scale, but the implantation of the scales in this amphibian can be compared with the implantation of fish scales. In the fishes the scales are arranged in oblique rows, directly beneath the epidermis. Each scale is enclosed within a pouch, the walls of which are formed in part by the epidermis, in part by

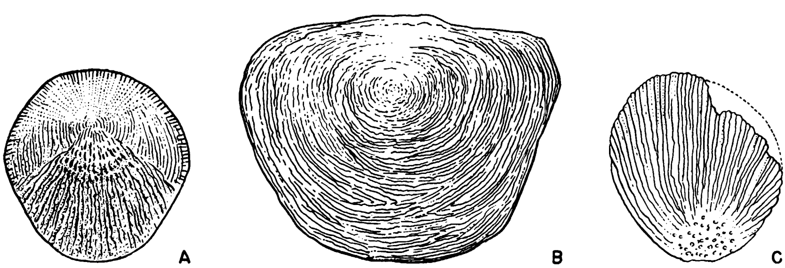


FIG. 1. Enlarged views of single scale of crossopterygian fish and two amphibians. A. *Eusthenopteron*, a crossopterygian of Devonian age, about $\times$ 2.5; after Jarvik. B. *Dermophis*, a recent caecilian, considerably enlarged; after Ochoterena. C. *Hylopesion*, a Pennsylvanian lepospondyl, about $\times$ 20; after Fritsch.

the corium. Consequently the individual scales do not touch one another, even though they are arranged in an overlapping fashion. Essentially the same relationships are found in the caecilian scales, as is well shown by Ochoterena's published microphotograph showing a sagittal section of the dorsal part of the skin in *Dermophis* (Ochoterena, 1932, fig. 4).

## SCALES IN FOSSIL AMPHIBIA

Because caecilians are unknown as fossils, it is necessary to turn to other amphibian groups and from an examination of them to draw what deductions we can as to the evolution of scales in the amphibians. Scales are known in a number of extinct genera, formerly generally classified as "branchiosaurs" but here placed in several orders in accordance with the recent classification published by Romer. Thus, as mentioned above, scales or the derivatives of scales are known in the Labyrinthodontia, in the Aistopoda, and in the Microsauria. In this last-named order the scales are particularly well developed.

It should be said here that scales are found well developed on both the dorsal and the ventral surfaces in these fossil amphibians. If anything, the ventral scales are more common in the fossil material than those of the dorsal surface. In this paper, however, particular attention is given to the dorsal scales, so that, unless otherwise indicated, the descriptions and discussions that follow are concerned primarily with the scales of the back.

Among the Labyrinthodontia, in the primitive Ichthyostegalia, the presence of scales is indicated in the genus *Erpetosaurus*. According to Steen the dorsal scales in this form are "fragile, showing a concentric radial ornament" (Steen, 1931, p. 872). Even in the more advanced labyrinthodonts, such as the Rhachitomi, dorsal scales are found, as recorded by Steen for *Stegops* and *Mytaras* and by Broili for *Archegosaurus*. With regard to this last genus, Broili says: "Diese rundlichen oder ovalen Schuppen, . . . sind bei *Archegosaurus* deutlich konzentrisch gestreift und zuweilen mit 'einem Knöpfchen oder Nabel und einigen radialen Eindrücken' versehen" (Broili, 1927, p. 380). In *Archegosaurus,* the dorsal scales do not form a regular pattern, but rather are scattered as separate elements, or are modified into appressed, roughly hexagonal scutes. Dorsal scales are particularly well developed in the genus *Dendrerpeton,* as was recognized years ago by Dawson. Figure 8 of the present paper illustrates the arrangement of the scales in *Dendrerpeton,* as drawn from a specimen in the British Museum, kindly lent by that institution for the purpose of this study. As is shown below, scales are very well developed in the genus *Trimerorhachis* of the Rhachitomi, a fact that was first recognized but not fully appreciated by Williston in 1916.

In some of the more advanced Rhachitomi, the scales have been modified considerably. Thus, Romer and Witter in 1941 described dermal ovals with a thin epidermal covering over a part of the body surface of the genus *Eryops*. These authors show that the dermal ovals in *Eryops* are formed by groups of squamulae, which are small flat plates of bony tissue.

"These groups of squamulae may be reasonably interpreted as bony scales which have undergone partial phylogenetic reduction so that much of the originally solid scale is here represented by fibrous connective tissue" (Romer and Witter, 1941, p. 823).

Similar dermal ossifications are found in the skin of *Discosaurus* or *Discosauriscus,* a genus now placed in the Seymouriamorpha.

In the Order Aistopoda, scales are found in the genus *Ophiderpeton,* according to Steen. "In the dorsal and lateral surface of the animal small oval scales of various sizes occur; these lie scattered over the vertebral column" (Steen, 1931, p. 876).

But it is in the Order Microsauria that the most abundant evidence as to scales in fossil Amphibia is found. Fritsch, in his great monograph on the "Fauna der Gaskohle," described and figured a series of microsaurian genera in which well-developed scales are preserved. In these genera, particularly *Sparodus, Limnerpeton, Hyloplesion, Orthocosta, Seeleya, Microbranchis,* and *Ricnodon,* cycloid dorsal scales are present, frequently modified by radial ornamentation. Moreover, enough scales are preserved in a number of genera to show that they had a regular, overlapping pattern.

In a review of the above list of genera in which scales or modified scales have been found, it becomes apparent that with but one exception a dorsal body covering consisting of overlapping scales is present only in amphibians confined to the Mississippian and Pennsylvanian periods of earth history. The one exception is the Permian genus *Trimerorhachis,* in which, as is shown below, there is a well-defined pattern of overlapping scales. In the other Permian forms there has been a modification of the original scale pattern; to clusters of isolated scales, as in *Archegosaurus,* or to bony scutes or squamulae, also as in *Archegosaurus,* as well as in *Discosauriscus* and *Eryops. Trimerorhachis* is therefore of particular interest, as it has preserved a primitive amphibian character somewhat longer than have other upper Paleozoic amphibians.

## SCALES IN *TRIMERORHACHIS*

In 1916 Williston described what he thought was a peculiar type of dermal covering in the labyrinthodont genus *Trimerorhachis.* His description is as follows:

"A dermal covering of peculiar type in *Trimerorhachis* has been several times observed by Cope, Case, and myself, but it was assumed that it covered the ventral region only, and its nature was ill understood. The present specimens show very conspicuously that it covered the whole body, with the exceptions mentioned; in the preparation of the skull not a trace of it was seen, but it closely connected with its hind margins. In no place in these specimens does it appear to have been more than a millimeter in thickness. It is composed of slender and delicate bony fibrillae, in short pieces, and apparently in several layers. In another specimen transverse sections show that the bony rods were in numerous layers. As these fibrillae lie in this specimen they extend through a thickness of 6 or 8 mm., and are separated from each other by intervals greater than their own thickness. It seems hardly possible that postmortem causes could have separated them so uniformly, and one must conclude that they were imbedded in a considerable thickness of integument, at least a fourth of an inch. How long any of the rods were I cannot say; the longest connected piece that I trace is scarcely a fourth of an inch. It is still possible that the sections represent the ventral skin, since nothing of their character is visible in the connected skeleton.

"Notwithstanding this thickness, the skin must have been flexible to have followed every inequality of the bones below it. It was doubtless covered by a smooth epidermis" (Williston, 1916, p. 293).

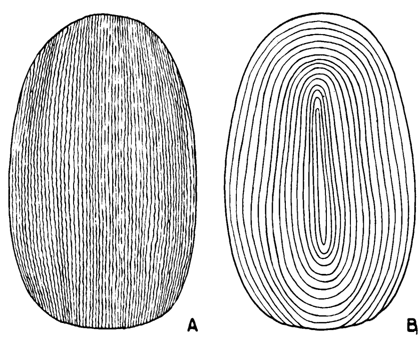


FIG. 2. Two views of complete scale of *Trimerorhachis*. A. Superficial layer of longitudinal ridges or striations. B. Underlying pattern of concentric growth rings. Both × 5.

On the evidence of our new material it seems quite obvious that what Williston saw were not "bony fibrillae," as he called them, but the remnants of bony scales. This is shown in his figure 3 in which the bare outlines of the scales as seen from above and the cross sections of superimposed scales can be recognized. These new specimens indicate that the dorsal surface of *Trimerorhachis* was covered with comparatively large and elongated scales. The individual scale is commonly about 10 mm. in length and about 5 mm. to 7 mm. in width—a large scale, especially in comparison with the size of the animal with which it is associated, for *Trimerorhachis,* though of medium size, is not a large labyrinthodont.

Figures 2 and 5 of the present paper show the shape of the scale in *Trimerorhachis,* which, as can be seen, is not only elongated, but is also somewhat wider at the lower or distal end than it is at the upper or proximal end. This elongated scale is somewhat different in shape from the scales in most of the Carboniferous scaled amphibians, in which the scales are more rounded in outline. It greatly resembles, however, the shapes of some scales from the Pennsylvanian of Canada, figured by Dawson and designated by him as belonging to the genus *Hylonomus.* Of course a long scale such as this gives a considerable degree of overlap, thereby increasing the protective value of the body covering, and this is considered below in the discussion of the pattern of squamation.

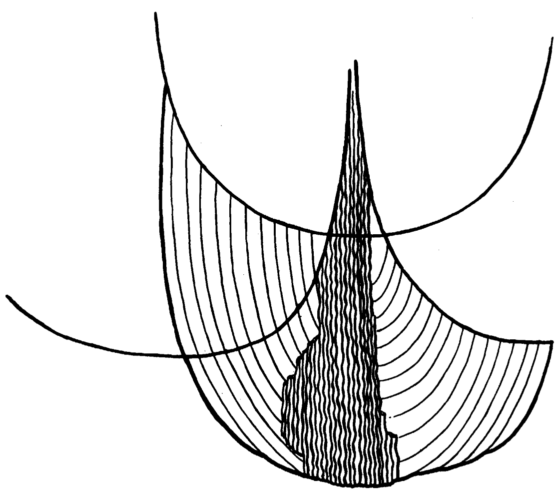

FIG. 3. Diagrammatic drawing showing segment of superficial layer of longitudinal ridges overlying basic concentric pattern of growth rings, and relationship of overlapping scales; about × 10.

According to the present interpretation, the scale in *Trimerorhachis* consists essentially of two layers, both seemingly well calcified. The upper layer is composed of rather wavy, parallel, closely appressed longitudinal ridges or striae, which make a corrugated surface. Below this ridged surface is a lower bony layer that shows a concentric pattern. It consists of rings, rather broad and dense, with pronounced sulci between them. It is to be supposed that these correspond to the annular rings in a fish scale. Frequently the entire surface of the scale consists of this layer of concentric rings, but often the scale is seen to consist of a combination of concentric and longitudinal patterns, the result of partial loss of the upper ridged surface.

This scale structure, notably the presence of two layers, one striated and one concentric, is similar to the structure seen in many fishes, especially the teleosts. One should not suppose that the scale of *Trimerorhachis* is therefore closely related to the teleost scale, but perhaps it can be maintained that the amphibian scale is essentially a fish scale that has followed a line of evolutionary development rather like that in the advanced fishes. Certain crossopterygian and dipnoan scales, such as those found in the genera *Glyptolepis, Holoptychius, Eusthenopteron,* and *Scaumenacia*, show a combination of striated and concentric patterns on the surface of the scales, the former commonly being limited to the areas

FIG. 4. Photomicrograph of portion of body surface in *Trimerorhachis* (A.M.N.H. No. 7116) showing several scales, in which both superficial layer of longitudinal striations and basal layer of concentric rings are apparent; about × 10.

that are overlapped, the latter to the exposed portions of the scales, and from scales such as these the *Trimerorhachis* scale may have evolved.

Because each scale in *Trimerorhachis* is elongated, it is evident that a considerable overlap of the scales is to be expected, and the rather large areas of scales preserved in our material shows that such is the case. In fact, the scales in this amphibian are so arranged that at certain points there is a superposition of four scales, one on top of the other, as can be seen in figure 9, which is a diagrammatic analysis of the scale pattern in *Trimerorhachis*.

From figure 9 it is evident that the scales in *Trimerorhachis* are arranged in such a way that the scales in any particular transverse row do not touch one another laterally; rather they are separated along their

FIG. 5. Photomicrograph of single scale of *Trimerorhachis* (A.M.N.H. No. 7116) with superficial layer eroded away; about × 10.

FIG. 6. Photomicrograph of portion of body covering in *Trimerorhachis* (A.M.N.H. No. 7116) showing superficial longitudinal ridges and underlying concentric growth rings of scales; about × 20.

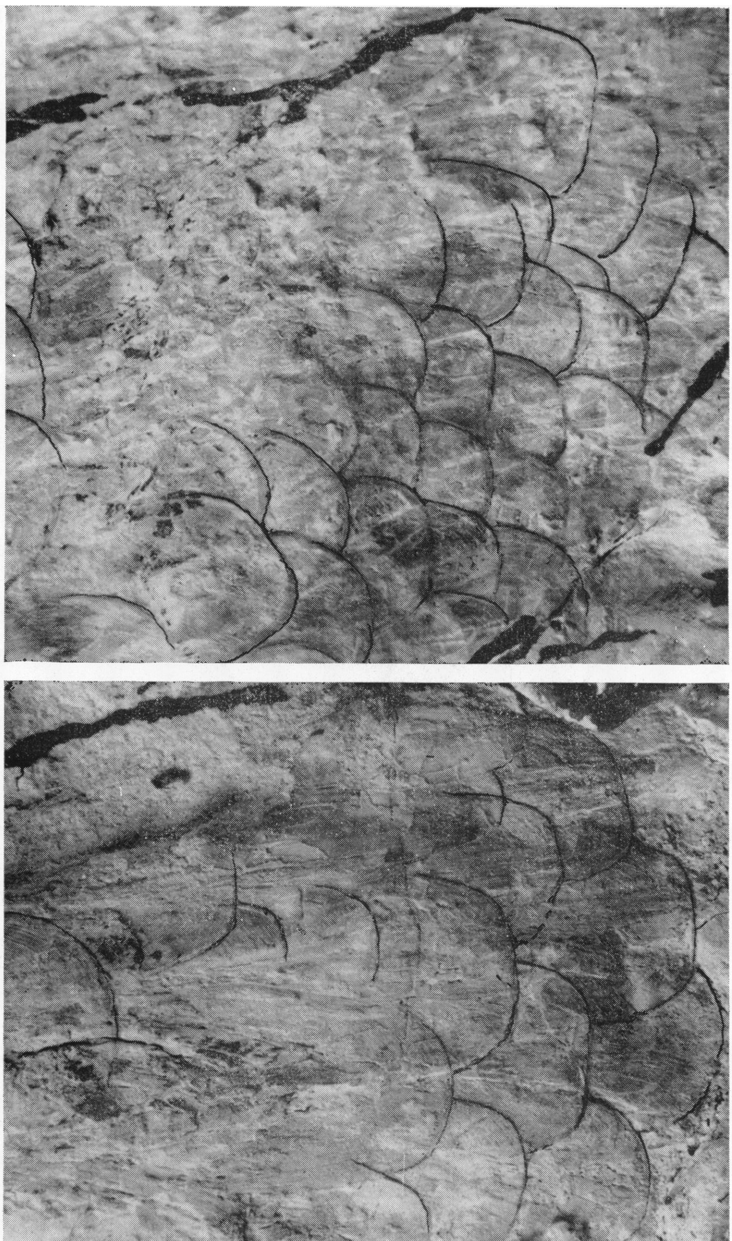

FIG. 7. Photomicrographs of two sections of body covering in *Trimerorhachis* (A.M.N.H. No. 7116) showing patterns of scale overlap. There has been some displacement of scales. About × 5.

lateral margins by small but distinct gaps. As might be expected, the scales are arranged shingle-fashion, so that the gap separating two laterally adjacent scales is immediately beneath the median portion of the next overlapping scale. Because of the elongation and the large overlap of the scales only a small fraction of the area of any one scale is exposed. The

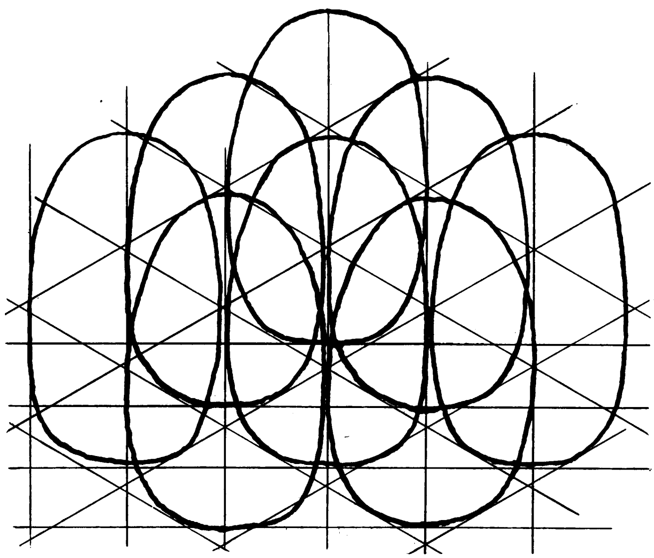

FIG. 8. Patterns of scale overlap in *Trimerorhachis*; about × 5.

lateral portions of each scale are covered distally by two scales of the next overlapping row; proximally the lateral areas of the scale as well as its median portion are covered, not only by the two scales of the next overlapping row, but also by a scale of the second overlapping row; finally, a small area in the proximal-lateral portion of the scale is covered on either side by the two scales of the third overlapping row.

It seems probable that the labyrinthodont scale pattern was derived from the scale pattern as developed in certain crossopterygian fishes, particularly the osteolepids. The crossopterygian fish *Osteolepis* shows a distinct 60-degree grid arrangement of rhombic scales, while the genus *Eusthenopteron* has a somewhat similar arrangement of cycloid scales. No significant change would be involved in the development of the *Trimerorhachis* arrangement from the crossopterygian scale pattern, as exemplified by the genera mentioned above.

It is significant that the scales in *Trimerorhachis* are thin and rounded, as is shown above in the description of the individual scale. The heavy,

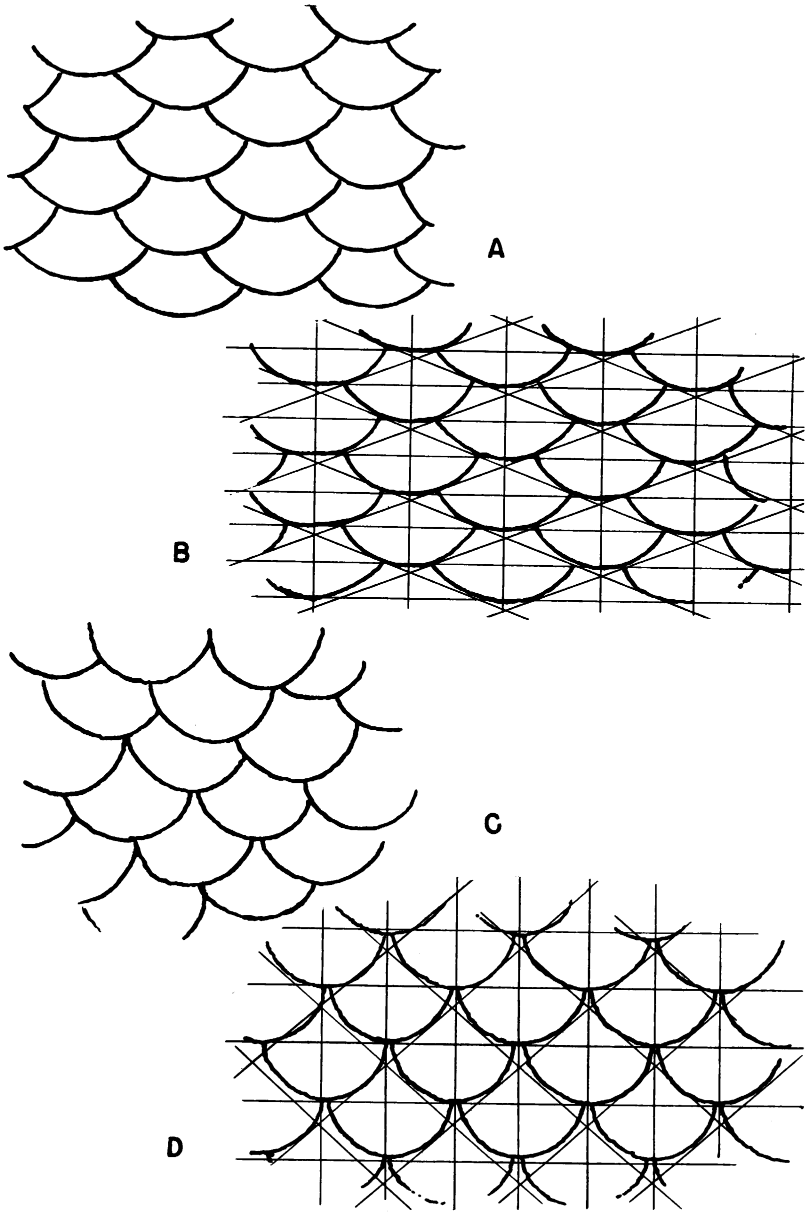


FIG. 9. Patterns of scale overlap in crossopterygian fish and amphibian. A, B. *Eusthenopteron*, a crossopterygian fish of Devonian age; about × 2.5. C, D. *Dendrepeton?*, a labyrinthodont amphibian of Pennsylvanian age, British Museum (Natural History) No. R4167; about × 10.

rhombic scales of a central osteolepid fish, such as *Osteolepis,* were probably in time transformed into the superficially teleost-like scales and scale pattern of *Trimerorhachis,* but such a transformation was obviously quite independent of the evolution of the teleosts. In both cases, however, the factors bringing about the evolutionary development of the scales were much the same, and these can be summed up as a phylogenetic trend requiring protection for the body combined with lightness and flexibility.

*Trimerorhachis* obviously lived in and out of the water, as do many modern amphibians. Fish scales would be a protection to the animal in both media, but for a partly terrestrial animal the heavy, rhombic scales of the generalized osteolepid fish would be much too heavy and inflexible for successful adaptations to land life. Light scales arranged in a flexible pattern were necessary to allow for the free movements required of this animal when it was out of the water. Therefore there were the transformations that brought about the cycloid type of scales and the teleost-like arrangement of scale pattern characterizing *Trimerorhachis.* Here we see an interesting example of convergence between the active, land-living amphibian, descended from crossopterygian ancestors with rhombic "ganoid" scales, and the active, marine teleost, descended from palaeoniscid ancestors, also with rhombic "ganoid" scales.

## EVOLUTION OF THE INTEGUMENT IN EARLY TETRAPODS

In the evolution of the body covering within the amphibians and reptiles several lines of adaptation can be discerned, developed during the transition from an aquatic to a terrestrial mode of life. In the first and undoubtedly the most primitive adaptational line, the original fish scales, inherited from fish ancestors, were retained. This condition is characteristic of various Carboniferous amphibians, and persisted into the Permian, in the genus *Trimerorhachis.* Among some of the Permian labyrinthodonts the primitive covering of fish scales was continued in the modified form of bony squamulae or scutes, as seen in *Archegosaurus* and *Eryops.* This primitive form of body armor seemingly does not reach the reptiles.

In another adaptational line the fish scales were lost, to be replaced by a covering of skin. This condition is typical of such modern amphibians as the urodeles and the anurans, and of course it is found in many reptiles. In the Gymnophiona, however, there is some retention of the more primitive condition, for these amphibians retain "fish scales," although not a complete covering of such scales. Thus the modern caecilians probably represent a condition intermediate between that characteristic of *Tri-*

*merorhachis* and that of the modern salamanders, frogs, and toads. In still another instance the original fish scales were lost, to be replaced by new scales such as those typical of the Squamata among the reptiles. It must be remembered, however, that in the lizards and snakes and their relatives the scales are not scales in the true sense of the word but rather folds in the skin that take the form of scales. Therefore the scales in such reptiles are not in any sense to be compared with the true scales as seen in the amphibians.

In the fishes the scales lie in connective tissue pouches of the dermis and are formed by ossification of the dermis. In the higher fishes these bony scales are covered by the epidermis, which may become cornified. This scale structure and these relationships of epidermis and dermis are carried over into the amphibian stage of evolution, as seen so well exemplified by *Trimerorhachis*. In the reptiles, on the other hand, the epidermis is strongly stratified, and it becomes secondarily cornified and folded. It is the folding of this stratified and cornified epidermis in the Squamata that leads to the formation of papillae that come to resemble the scales in lower vertebrates. However, it seems probable that the papilla, or epidermal fold, in the reptile that so resembles a fish scale is by homology actually that part of the body covering *between* the scales in the fishes and amphibians. One might say that as the scales were lost in the lower vertebrates, the skin folds between them became accentuated to form neomorphic structures resembling scales.

Of course in many reptiles such skin folds were never developed, and the body covering took the form of a thick, leathery skin, often reënforced by scutes or nodules.

It was of course a natural development in the evolutionary transition of the vertebrates from an aquatic to a terrestrial mode of life that profound changes took place in the body covering. The fish is constantly bathed by the watery medium in which it lives, so there is no problem of desiccation. Moreover, as the fish is buoyed up by the dense water in which it floats or swims, it is not subjected to serious problems of gravitational pull. But when the fish began to venture out on the land, thereby to become an amphibian, it was faced with many new and complex problems, not the least of which were those of desiccation and gravitational pull. The tetrapod must be able to guard itself constantly against the drying effects of the air, and it must be able to support its own body on the land against the constant downward pull of gravity.

This fact led to the gradual elimination of the scales as a body covering and the substitution of skin, well adapted for the protection of the evolving tetrapod. Scales have the disadvantage of adding considerable weight to an animal in which weight reduction is of great importance. In addition to this, the adaptational advantages of a moist skin that served as a large respiratory surface may have been an important factor in the elimination of the primitive scales among the Amphibia. The late Paleozoic amphibians were, one might say, caught in the middle of this process, so we find among them various degrees of scale reduction. It seems likely that in the more completely terrestrial amphibians of late Paleozoic times the scales were largely or completely lost. Such were the large and powerful rhachitomes of the Permian. But in the more aquatic forms it seems likely that the scales were retained in varying degrees. Such were the amphibians that are discussed in this study—the microsaurs, the aistopods, and some of the labyrinthodonts, of which latter group *Trimerorhachis* is a striking example.

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