# THE LATERAL LINE SYSTEM IN EXTINCT AMPHIBIA.

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The study of the system of canals and sense organs in the lower vertebrates, known as the lateral line system, has interested many anatomists. The existence of the lateral line system was first observed, of course, in the fishes where it is clearly marked, more especially on the body of the fish. According to Collinge (1), the lateral line organs were first observed on a species of skate by Stenonis in 1664, and in 1669 on some of the sharks. The term canal was first applied to this set of structures under the preconceived idea that there was an actual canal under the skin, as indeed there seems to be in some cases, and M'Donnell (2) tells us of his attempts to inject the system of canals with a syringe. Various means were devised for studying the anatomy of this peculiar set of structures and many theories were propounded as to its possible functions. The general opinion was that the lateral line structures were secreting organs and the grooves on the crania of fishes and on the skulls of the ancient Amphibia are almost universally spoken of as *slime canals* or *mucous canals* or *grooves.*

Through the recent embryological and anatomical studies of Allis, Pollard, Platt, Collinge, Cole, Parker, Takahashi, Harrison, and others, the full development and functions of the lateral line system have been made out in a few forms.

It is now generally admitted, especially since the excellent experiments of Parker (3) on the function of these organs in fishes, that the lateral line system is a set of sense organs intermediate in function between the organs of touch and those of hearing, but more delicate than either in some respects.

Parker ascertained that the lateral line organs in some of the fishes seemed to respond to slow wave vibrations. It is thus through the action of wave vibrations on the external lateral line organs that the animal is notified of a disturbance in the water near it, the wave vibrations of which were too slow to affect the organs of touch or hearing.

It is not our purpose to discuss here the functions of these organs, but to describe the manner of their occurrence in the ancient Amphibia, on the crania of which the canals are often clearly marked. Unfortunately there are but comparatively few skulls in existence and they are scattered far and wide in the museums of the world. The remains of the early Amphibia are represented in great part by fragments. Occasionally, however, a good skull is discovered and almost always the lateral line canals are well shown on such skulls. But there is another source of grievance. When such good skulls are described, the describer of the specimen either pays but scanty attention to the subject of the lateral line system, or omits a discussion of it altogether or describes the canals inadequately. We are indebted to the paleontologists of the world for the knowledge we have of the lateral line canals of the ancient Amphibia and more especially to von Meyer and Fraas.

The lateral line system, as preserved in the extinct Amphibia, is of a very peculiar character and is unlike anything with which I am acquainted among the fishes, although some degree of correlation is possible. The entire set of structures on the skull of the Stegocephala is usually spoken of as the *lyre* or *lyra,* the former being the more correct term. The system of organs is represented by canals of various forms and with varying directions. They are usually in the form of gutters with more or less vertical sides, although sometimes, especially among the Microsauria, the canal is represented by a row of elongate pits. The bottoms of the well-formed canals may be smooth or roughened by pits such as commonly occur in the crania of the Stegocephala. The smoothness of the bottoms of the canals is, I think, an indication either of age or of specialization, for I have observed that in the more generalized forms the line canals are roughened by the vascular pits, but in the highly specialized labyrinthodonts the bottoms of the canals are usually rather smooth, and this smoothness increases as the animal grows older. The canals of the lateral line organs are always open and never have the canals roofed over as is the case, according to Dean (4), in some of the Arthrognathid fish-like vertebrates.

Pollard (5), Baur (6), and Allis (7) have attempted some correlation of the cranial elements of the fishes and Stegocephala on the basis of the lateral line system. Baur's work had to deal with the stegocephalan side of the question and the others treated the question from the fish point of view. Allis' paper on the homologies of the squamosal and other elements is especially instructive. Pollard, according to Baur, did not fully understand the arrangement of the lateral line organs in the Polypterus which he was studying, having failed to comprehend the significance of the occipital cross-commissure. Baur did not complete the homologies of the crania of the fishes and stegocephalans, but carried the correlations as far as was then possible. In my studies on the Carboniferous Amphibia, I have been led to investigate the conditions of the lateral line system in the extinct forms to see if some definite idea might be formed as to the homology of the squamosal and supratemporal elements in the skull of the Stegocephala. The investigation was undertaken in the hopes of ascertaining just what the element which lies laterad to the parietal in most forms of the Stegocephala is, whether it is the squamosal, prosquamosal or supratemporal, all of which names have been applied to it by various authors.

An attempt has been made to correlate the lateral line canals in the Stegocephala with those of the fishes and recent Amphibia. In the accompanying diagram (Fig. 1), there are represented all of the canals which occur on the crania of the Stegocephala. They do not all occur in any one species nor indeed in any one group, but are all found in more or less well-developed form in some of the extinct Amphibia. The nomenclature here proposed, it is hoped, does not depart widely from that given by Allis for Amia (8). The supraorbital (Fig. 1 "d") and infraorbital (Fig. 1 "c") canals are readily correlated with the canals of the same name in the fishes. The anterior commissure (Fig. 1 "a") is also homologous with that of fishes, as is also the canal which is here called the

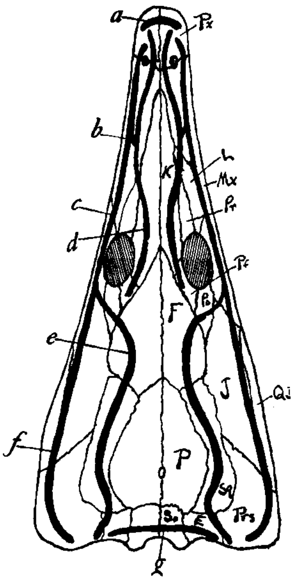
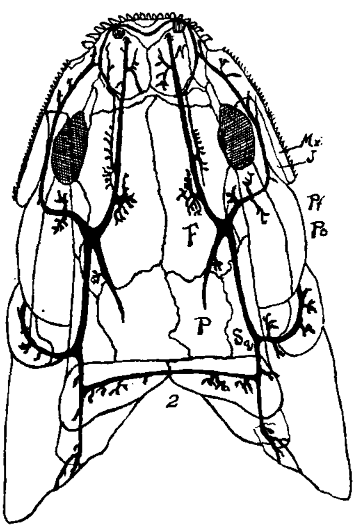



FIG. 1.—A diagram of the lateral line canals in the Stegocephala.

a, anterior commissure; b, antorbital commissure; c, infraorbital canal; d, supraorbital canal; e, temporal canal; f, jugal canal; g, occipital cross-commissure.

E, epiotic; F, frontal; J, jugal; L, lachrymal; Mx, maxilla; P, parietal; Pf, postfrontal; Po, postorbital; Pr, prefrontal; Prs, supratemporal; Px, premaxilla; Qj, quadrato-jugal; So, supraoccipital.

"antorbital commissure" (Fig. 1 "b"). The others are not so readily homologized. The upper canal in the posterior part of the cranium is here designated the "temporal canal" (Fig. 1 "e"). It is, however, clearly a part of the infraorbital canal of the fishes. Its relations in the Stegocephala are such that a new name is deemed necessary, for otherwise the canal would have to be referred to by the circumlocution: "the upper posterior portion of the infraorbital canal." For the lower posterior portion of the infraorbital canal I propose the term "jugal canal" (Fig. 1 "f"), since it lies in great part on that element of the skull. The jugal canal is, I believe, a new formation in the Stegocephala. I am unable to homologize it with anything which I can find occurring in fishes. It may be composed of the infraorbital and a portion of the operculo-mandibular canal, but of this I am not sure. The most posterior canal of the stegocephalan skull is homologous with the



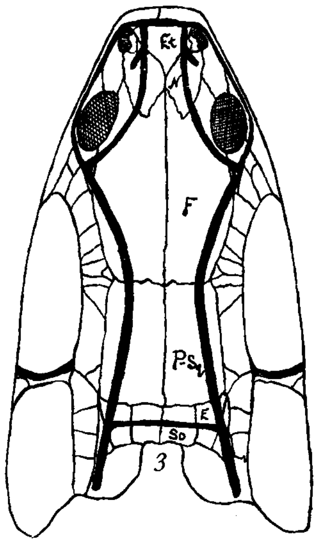




FIG. 2.—Outline of the lateral line canals on the skull of Amia calva. Lettering as in Fig. 1. After Allis.

FIG. 3.—Outline of the lateral line canals on the skull of Polypterus. After Baur and Traquair.

supratemporal cross-commissure of Amia as defined by Allis, and it is here designated the "occipital cross-commissure" (Fig. 1 "g"). Allis (1899) was doubtful as to whether this canal could be homologous with the same placed canal in Amia and Polypterus, and was inclined to correlate it with a canal which occurs in other fishes and which would distinctly change the correlations of the cranial elements. There can be no doubt, however, that the "occipital cross-commissure" is the same as the supratemporal cross-commissure of Amia. It will be noticed that the main canal in the Stegocephala is the infraorbital canal as it is in Amia and Polyterus (Figs. 2, 3). In the Stegocephala likewise, the main canal always, or almost always, cuts the epiotic as it does that element in the fishes which Baur would correlate with the epiotic.

There are five suborders of the extinct Amphibia (9) in nearly all of which there have been detected evidences of the lateral line system. The extinct Amphibia of the pre-Jurassic are known as the Stegocephala and the five suborders of this group may be designated: the Branchiosauria, the Microsauria, the Aistopoda, the Temnospondylia and the Stereospondylia. In all of these suborders, with the exception of the Aistopoda, the lateral line system has been observed. The canals are more clearly preserved on the skulls of the Stereospondylia than in any of the other groups, the reasons for which we will consider later.

The Branchiosauria are known by numerous individuals of several species found abundantly in Europe in the Upper Carboniferous and Permian, and by a single species founded on a single well-preserved specimen from the Carboniferous of Illinois. The Branchiosauria are the best preserved of all of the extinct Amphibia and not only is the complete skeletal anatomy known, but something of the soft parts, color markings, covering and habits. Credner (10) has been able to write an interesting paleontological embryology based on the Branchiosauria preserved in the Permian rocks of Saxony and adjacent regions. The European students of the Branchiosauria have not, unfortunately, paid any special attention to the study of the lateral line system as it is preserved in the Branchiosauria. Thevenin (11) barely mentions the occurrence of the lateral line on the specimens he studied from the Upper Carboniferous rocks of France. It is to be hoped that more may be added to our knowledge of this portion of the anatomy of the Branchiosauria.

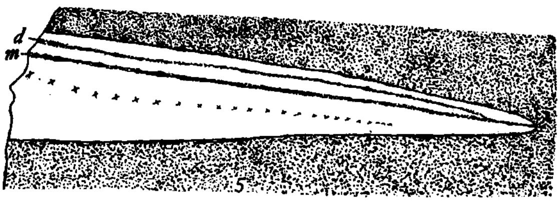
The form from Illinois, described elsewhere (9) as Micrerpeton caudatum gen. et. sp. nov. (Fig. 4), is a very small animal, apparently adult. It measures 49 millimeters in length or a little less than two inches. It is preserved, almost perfectly, in one of the nodules from Mazon Creek, Grundy County, Illinois; the collector in splitting the nodule lost the chips containing the hands and feet. From this specimen not a few new characters have been added to those already known for the Branchiosauria such as certain color markings on the body, the character of the dermal covering, and most important of all, the presence of a distinct type of lateral line preserved clearly and distinctly on the impression of the fleshy tail. This

FIG. 4.—Impression of Micrerpeton caudatum Moodie, from the Carboniferous of Illinois. Twice natural size.

has been fully described elsewhere, but it is deemed of such importance that a redescription is here given.

"The most interesting and important single structure discovered on the specimen is the impression of the lateral line system which is clearly evident as two dark lines on the impression of the fleshy part of the tail. The sense organs are represented by two longitudinal rows of pigmented scales. one beginning at the tip of the tail, the other taking its origin from the median line somewhat further forward (Fig. 5). I am indebted to Dr. Takahashi for calling my attention to the similarity of this arrangement to that found in the modern

Necturus (Fig. 6). The arrangement and disposition of the lines containing the sense organs is practically the same in the two forms. The median lateral line takes its origin from the extreme tip of the tail or rather it ends there, and is continued to the base where the impression is broken. The dorsal lateral line has its origin rather abruptly from the median line at a distance of six millimeters from the tip of the tail. The sense organs were undoubtedly located beneath specialized pigmented scales on the surface of the animal's body as in



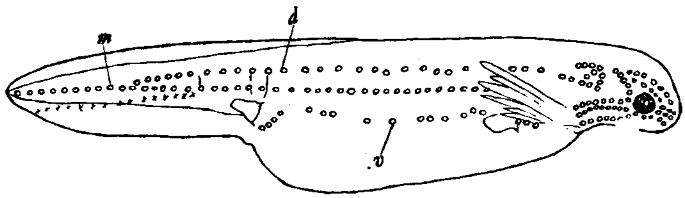




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FIG. 5.—Detail of lateral line on impresion of the tail of Micrerpeton caudatum. d, dorsal lateral line; m, median lateral line; xxx, impressions of cartilaginous vertebræ. X 4.

FIG. 6.—Outline of the larva of Necturus maculosus Raf., showing arrangement of lateral line organs. d, dorsal lateral line; m, median lateral line; v, ventral lateral line. After Platt. Enlarged.

many of the modern fishes, e. g., the Holocephali, and to this pigment is due the preservation of the lines in a visible form.

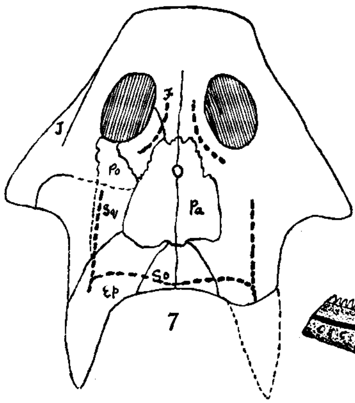
"The fact that the arrangement of the lines of the sense organs of Micrerpeton corresponds so exactly to the condition found in Necturus is of considerable interest. Necturus alone among the modern tailed Amphibia has the arrangement of the lateral lines above described for Micrerpeton. All other forms of the Caudata as also the larval forms of the Salientia have an arrangement of the lateral line system which is perfectly distinct from that found in Necturus, although the same general plan is observable in all. The Necturus is, I believe, a more generalized type of amphibian so far as the lateral line is concerned than any of the other modern forms. This preservation of the lateral line system so perfect is due, without doubt, to the constant water habitat of the animal. Kingsbury (12) has expressed it as his opinion that Necturus is a primitive form and bases his conclusions on other grounds than that of the lateral line system. In very few of the modern Amphibia is the median line present as far back as the tip of the tail and in none, so far as I can learn, are the median and dorsal lines both present on the tail except in the Necturus. Other forms have lost the line from the tail, and this but gives expression to the general law that structures present over the entire body are lost first in the posterior region. This finds another expression in the loss of stripes by the zebras where in the quagga the hind part of the animal is destitute of stripes. In Ambystoma, for instance, the median lateral line is not present on the tail at all and the dorsal line is but imperfectly developed (13). The close similarity of the arrangement of the sense organs in the two forms, Necturus and Micrerpeton, may be of genetic significance with regard to the former group.

"The interval of time which has elapsed from the age in which Micrerpeton lived to the present is reckoned by many millions of years. But since the lateral line organs are of fundamental significance and since they are subject to comparatively little variation, this system of sense organs in the Amphibia may have persisted through the ages unchanged as we know it has done in some of the fishes (14). The ancestors of the modern Caudata and Salientia must have originated somewhere in the Carboniferous or earlier ages. Among all of the extinct Amphibia there are none which could have given rise to the modern forms save the Branchiosauria. The Microsauria are too highly specialized when we first know them in the Carboniferous, and they are already tending toward the reptilian type, to some groups of which they probably gave rise. The other groups of extinct Amphibia are, of course, out of the question so far as being ancestral to the modern Amphibia is concerned. The Aistopoda, when we first know them, are highly specialized, snake-like Amphibia and could not have given rise to animals with legs since it is well-known that they are descended from forms with well-developed limbs as is evidenced by the vestigial pectoral girdle in Ptyonius. The Temnospondylia and Stereospondylia, which are closely related, were also highly specialized along their own line, and like the Pterodactyles went out of existence completely and, so far as we know, left no descendants. There is certainly nothing in the structure of the Branchiosauria to prevent their being ancestral forms to the modern Amphibia. There is much in favor of it. The idea is not a new one but has been suggested by Baur and others. We have here, however, for the first time, something definite on which to base our conclusions." This matter is discussed more fully elsewhere. The cranium of the Branchiosauria, like the modern Amphibia, is never grooved by the lateral line canals, but the system was undoubtedly present on the skull in the skin, much as it is in the modern forms.

In the Microsauria, although there are numerous forms known, there have been but few observations made on the lateral line system. There are evidences of the canals on a skull and mandibles of Diplocaulus, Andrews (15) has observed rows of pits on the skull of Ceraterpeton galvani Huxley from the Carboniferous rocks of Staffordshire, England, and the writer has recently detected them on an excellent skull of Tuditanus tabulatus Cope from the Linton, Ohio, beds and traces of the supraorbital canal have been observed on the skull of Stegops divaricata Cope from the same locality.

In the Ceraterpeton specimen (Fig. 7) there are evidences of the lateral lines on the posterior and upper portions of the skull only. They consist in the occipital cross-commissure, the temporal canal and a portion of the supraorbital canal.

The infraorbital, the anterior commissure, and the jugal canals were not detected. The presence of a well-developed occipital cross-commissure in the skull of Ceraterpeton is of interest because this structure is rarely present in the more highly specialized labyrinthodonts. This is a generalized character as may be seen by referring to the figures of the Actinopterygian, Amia, and the Crossopterygian, Polypterus, in both of which the occipital cross-commissure is well-developed. The

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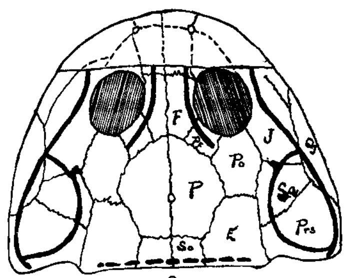


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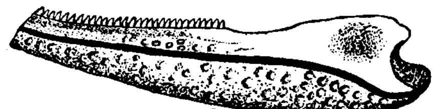

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FIG. 7.—Outline of the skull of Ceraterpeton galvani Huxley from the Carboniferous of England, showing the distribution of the lateral line canals. After Andrews. Natural size.

FIG. 8.—Outline of the skull of Tuditanus tabulatus Cope, showing the arrangement of the lateral line canals in their relations to the cranial elements. One and one-third natural size.

FIG. 9.—The mandible of Diplocaulus magnicornis Cope, showing operculo-mandibular canal from the side. One-half natural size.

temporal canal, which is a portion of the infraorbital, begins its course on the epiotic and crosses most of the squamosal when it is lost. The supraorbital canal occurs on the frontal and postfrontal and has the usual relations for that canal.

The lateral line canals are but weakly developed in the cranial region of Diplocaulus. On a nearly perfect skull and mandibles of the species D. magnicornis Cope in the collection of the University of Chicago, there are traces of only three of the canals. On the mandibles, the operculo-mandibular canal is well-marked (Figs. 9, 9a). The canal, apparently, has a course completely around the mandibles, although the anterior portion of each mandibular ramus has been broken and lost. However, at the point where the ramus is broken the canal is still strongly marked. The canal has its course, for the most part, near the middle of the rami, but as it approaches the posterior angle of the mandible it suddenly changes its course and drops down to the lower edge only to rise again and to come out strongly marked near the median plane on the posterior angle of the mandible. On the dorsal surface of the skull (Fig. 10) there are faint traces of the canals and on the

FIG. 9a.—The mandibles of Diplocaulus magnicornis Cope as seen from below. The operculo-mandibular canal at the arrow. One-half natural size.

edges the infraorbital is clearly marked. The arrows on the skull indicate the positions where the canals were detected. The long arrow points to a doubtful indication of the supraorbital canal. The infraorbital is clearly marked where it is preserved, but the premaxillary region of the skull is lost so the entire extent of the canal cannot be determined.

On the skull of Tuditanus tabulatus Cope (in the Zoological collection of Columbia University, New York City) there are evidences of a nearly complete system of canals (Fig. 8). The fore part of the skull anterior to the transverse line has been lost so that portion is unknown since the species is represented by a single specimen. The occipital cross-commissure is represented on the posterior border of the skull by elongate pits such as Andrews has described for Ceraterpeton. I fail to detect any pores in connection therewith such as Andrews describes for the lines in Ceraterpeton, and indeed I would be surprised if there were any since there is no evidence that the lateral line system in the Stegocephala was other than superficial. The temporal canal forms with the jugal canal a complete ring in this form much as in Trematosaurus, only in Tuditanus the temporal canal does not touch the epiotic. I think there are evidences of a former connection of the tem-

FIG. 10.—Photograph of the skull of Diplocaulus magnicornis Cope. The arrows indicate the regions where the canals occur. One-third natural size.

poral canal with the supraorbital, but am not sure of it. It is so represented tentatively in the diagram (Fig. 8). The temporal canal cuts the supratemporal (prosquamosal), the squamosal and the jugal. The jugal canal lies for the most part on the supratemporal and quadratojugal. It joins the infraorbital on the jugal. A portion only of the infraorbital is preserved and the remainder, i. e., its connection with the jugal canal, is restored. There is a portion of the supraorbital canal preserved. It seems not to be connected with the temporal canal, although there is a possible indication of this connection as has been stated above. The supraorbital crosses the frontal, prefontal and a part of the nasal. The squamosal element in Tuditanus tabulatus Cope is peculiar in that it is excluded from the parietal by the extension of the epiotic and postorbital. This condition is found in several other species of the Microsauria. It will be noticed that with the changed condition of the position of the squamosal, the temporal canal has changed also and this is further proof of the close connection between the cranial elements and the lateral line canals.

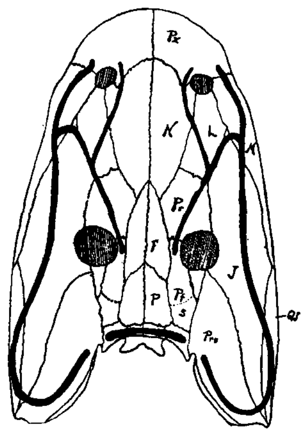

FIG. 11.—The cranium of Eryops megacephalus Cope with the cranial elements and the associated lateral line canals. Modified after Branson. One-ninth natural size.

Among the Temnospondylia the lateral line canals are well-developed on some of the skulls, such as Cricotus, Eryops, and Archegosaurus. I have had the opportunity of studying only one of these forms, that of Eryops megacephalus Cope (Fig. 11), from the Permian of Texas, represented by an almost perfect skull in the collection of the University of Chicago. This skull presents very striking characters as to the lateral line canals. The entire surface of the cranial elements in Eryops as in other of the Stegocephala is covered with coarse pits. The fossæ are present even in the bottoms of the grooves which represent the lateral line system. This character is more marked in Eryops than in the Stereospondylia, a matter of considerable importance as we shall see.

The occipital cross-commissure is well-developed in Eryops. It is short and ends abruptly within the limits of the epiotics. Its ends are occupied by large pits. The cross-commissure, as in Amia, grooves the supraoccipital and epiotic elements. There is no evidence of an anterior commissure. I think there is an evidence of a temporal canal on the left side of the skull, but am not sure. This part of the skull is imperfect on the right side. The jugal and infraorbital canals are well-developed and strongly connected. The jugal canal starts far back on the supratemporal (prs), and after curving around over the quadratojugal joins the infraorbital somewhere on the jugal. There is nothing unusual in the characters of the infraorbital. The antorbital commissure is well developed in Eryops. It is longer and better developed in this form than in any other known to the writer. The supraorbital canal starts anterior to the nostril and makes a decided bend downwards to meet the antorbital commissure. It ends abruptly on the postfrontal bone. The squamosal is apparently not grooved in this form. The position of this element is a little doubtful as Branson has stated and the diagram of the cranial elements given is based on his studies of the skull. The antorbital commissure is primitively a branch of the supraorbital. It is such in the fishes and Dr. Takahashi informs me it is the same in Necturus. It would be an interesting matter if we could determine the points of origin of the lateral line canals in Eryops, and some day this may be known when we get material representing the youthful stages of the form. The peculiarly specialized condition of the lateral line canals bears witness to the specialization of the form. This is borne out by its osteology. Branson has shown that in its vertebral structure it is approaching the Stereospondylia, the most highly specialized of all of the Stegocephala.

There are faint traces of the lateral line canals on a poorly preserved mandible of Eryops in the collection of the University of Chicago. It does not differ greatly from that described below for the mandible of Anaschisma.

Although Archegosaurus (16) has been known for nearly sixty-five years, we have had as yet no adequate discussion of the manner of occurrence of the lateral line canals on the cranium of this form, where they assuredly occur. Burmeister, it is true, gave a figure of the canals as he thought they occurred on the cranium, but von Meyer states (16) that his representation is incorrect and seemed to be based in large part on the cranium of Trematosaurus. Although von Meyer criticised Burmeister's representation of the canals, yet he himself does not give any representation except in patches here and there on the skulls. Surely among the nearly two hundred specimens which von Meyer had at his disposal when he wrote on Archegosaurus there was sufficient information to have given such a restoration. There are two poorly preserved skulls of Archegosaurus decheni Goldfuss in the Field Museum. I have studied these specimens, which are preserved in the characteristic nodules much like those from the Mazon Creek region, but was unable to make out anything definite in regard to the lateral line canals on account of the poor state of preservation. The only other well-known form of the Temnospondylia with which I am acquainted, is that of Gondwanosaurus. This is represented by an almost entire cranium, but the cranial elements have almost all disappeared and have left only the sandstone cast.

The lateral line canals are well developed on the skulls of the Stereospondylia. Like the majority of the Stegocephala the cranial elements are strongly pitted and grooved. The sutures between the elements of the skull are usually clearly marked by smooth, narrow grooves. The lateral line canals can always be distinguished from the sutural grooves by the shape of the bottom, being U-shaped in the former, and V-shaped in the latter. The lateral line canals also at times have their bottoms roughened by pits occurring in them, the sutural grooves always have smooth bottoms. The lateral line canals are usually rather shallow and sometimes broad with the edges of the grooves more or less perpendicular, but in Metoposaurus the canals are deep and the borders are sharply incised.

Why the lateral line canals are more deeply incised on the skulls of the Stereospondylia is not easy to determine. This suborder is the most highly specialized of all of the Stegocephala and it is a part of this specialization that the canals are deeply incised. The canals become more strongly marked as the individual grows older, and it is possible that the same will hold for the suborder. This suborder began, or at least we find the first evidences of it, in the Carboniferous at the same time that all of the other groups are represented by well-developed forms. All of the other groups, however, died out or became modified into other forms, so far as our present knowledge goes, before the Triassic or at least we know nothing of them after the close of the Permian. The Stereospondylia, however, did not become extinct until the latter part of the Trias or the early Jurassic. It is thus the longest lived of any of the groups of the Stegocephala as such, and for this reason we may consider that the lateral line canals are strongly developed. In Eryops, attention has already been called to the coarse pits occurring in the bottoms of the canals, and it must be stated that the canals in Eryops are not so well-developed as in the labyrinthodonts. It is thus evident, if we take Eryops to be a primitive form, that the primitive characters of the lateral line canals are the occurrence of deep coarse pits in the bottoms and their broad character and weakness of development. In other words the lateral line canals in the Stegocephala are, in their earliest development, rows of pits which later become developed into well-defined grooves. Whether the condition described for Eryops will hold for other of the Temnospondylia remains to be determined. In the Stereospondylia the canals, as stated, are usually clearly marked and often have smooth bottoms.

In the collection of the University of Chicago, there are two perfect skulls of labyrinthodonts, collected some years ago by Mr. N. H. Brown, of Lander, Wyoming, in the Triassic rocks some eight miles southwest of Lander. These skulls were described in 1905, by Dr. Branson (17), as two species, Anaschisma browni for the larger specimen (Figs. 12, 14), and A. brachygnatha for the smaller skull. From my own study of the type specimens, I believe that the latter is but a youthful form of the former species. This is evidenced in several

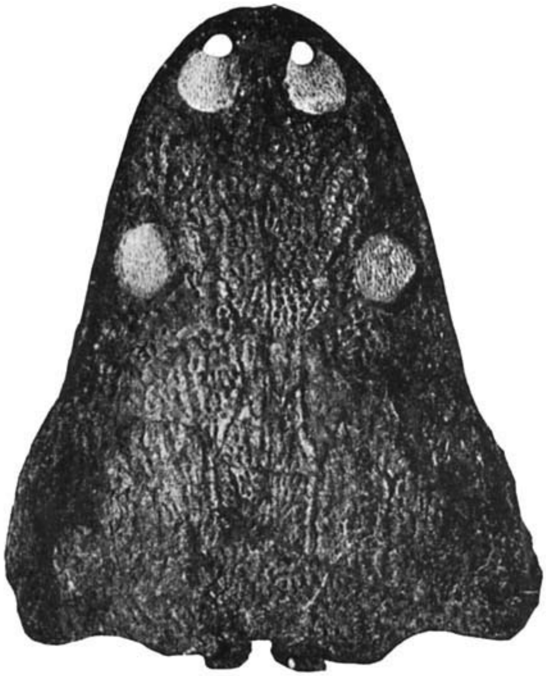

FIG. 12.—The larger skull of Anaschisma browni Branson, showing distribution of canals. After Branson. One-fourth natural size.

particulars. The skull designated A. brachygnatha is narrower and shorter than the skull designated by A. browni. The broadening and lengthening of the skull would, of course, come with age. The vascular pits on the upper surface of the smaller skull are weaker and their borders are not so clearly defined as in the large skull. The position of the orbits is slightly different in the two skulls, but not enough to be of specific importance, and the difference is, in all probability, an individual variation since it is very slight. But it is the lateral line canals that the chief points of resemblance lie. The general plan of the canals is identical in the two skulls. The only difference is this: the connection between the temporal and supraorbital canals is absent in the younger skull while in the adult it is well developed. The pits in the bottoms of the

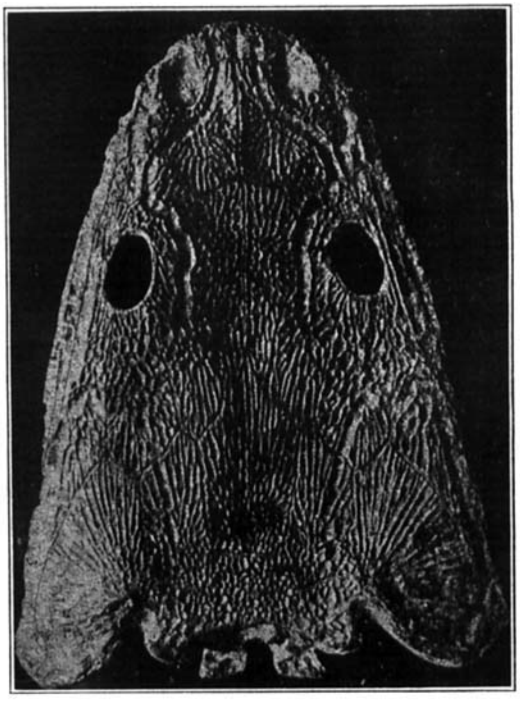

Fig. 13.—The skull of Metoposaurus diagnosticus von Meyer, showing the manner of distribution and occurrence of the canals. After Fraas. One-fifth natural size.

canals are more clearly marked in the younger than in the adult skull, and this is an indication of youth. There is another factor which tends to corroborate the statement as to the specific identity of the two skulls. They were found to be slightly overlapping each other in the rocks. This might not be of importance were there remains of other species of labyrinthodonts known from these deposits. There are literally millions of fragments of labyrinthodont skeletons scattered along the exposures of the Popo Agie beds of Wyoming for a distance of more than thirty miles, but all of the fragments are of the same character and these two skulls represent the sum total of skulls, save fragments, from the Triassic deposits of the West. It is, I believe, therefore safe to assume that A. brachygnatha is a youthful form of A. browni, and that the lateral line canals really do become more deeply incised with age, lose the pits from the bottoms of the canals and become more clearly marked and more closely connected.

The temporal canal in Anaschisma browni (Fig. 14) is represented by broken furrows. The portions preserved exhibit the usual downward tendency of the canal to unite with the infraorbital on the postorbital element. In its course forward from the epiotic the temporal canal cuts the squamosal; a matter of considerable importance to be referred to later on. The supraorbital canal has an unusually deviating course in Anaschisma, but aside from the minor twists and curves it does not differ essentially from the same canal in other forms. It ends abruptly at the anterior end of the muzzle. In its course it gives off the vestige of an antorbital commissure which tends to join a vestige from the infraorbital canal. The jugal canal begins broadly at the very posterior edge of the skull as though it were continued, as it undoubtedly was, to the body of the animal. In its course forward it joins the infraorbital canal on the jugal. The course of the infraorbital is not unusual in any respect. There is no anterior commissure on the skull nor is the occipital cross-commissure developed in either of the specimens. There are distinct indications of the operculo-mandibular canal on the mandibles of Anaschisma. Each skull has a mandibular ramus preserved and the canals are identical on the two rami. The canal enters the mandible on the surangular and passes forward around the mandible as described for Diplocaulus.

Whether or not the canal completed the course around the mandibles is not to be determined from the specimens at hand.

The close resemblance between the arrangement of the lateral line canals of Metoposaurus (18), and that already described for Anaschisma is made evident by a glance at the figures (Figs. 12, 15). This is indicative of the affinity which the osteology of the two genera exhibits. The forms are, however, generically distinct as Branson has pointed out, by the absence of the characteristic ear slit in the latter genus. The arrangement of the lateral line canals would separate the forms generically if other characters were lacking. Since the canals have such a similar arrangement in the two forms only the differences need be pointed out and the detailed description given for Anaschisma will serve for Metoposaurus. There are no traces of an occipital cross-commissure in either form, nor indeed have I been able to detect traces of this canal in but one of the stereospondylous forms. The main difference between the two forms lies in the absence of connection between the temporal and supraorbital canals (Fig. 15), and in the more direct course of the latter canal in Metoposaurus. Other characters are almost identical in the two groups. The skull of Metoposaurus shows its specialized characters in the smoothness of the bottoms of the canals in the anterior part of the skull, and in the canals all over the skull, being more sharply defined than they are in Anaschisma.

The skull of Mastodonsaurus giganteus Jæger, fragments of which were first discovered by Dr. Jæger, in 1824, is the largest and first known of all of the extinct Amphibia. The skull reaches, at times, enormous proportions for an amphibian, often attaining a length of four feet with a posterior breadth of two and one-half feet. The lateral line canals are clearly marked on all of the skulls known or at least on all which have been figured (Fig. 16). There are no evidences of the occipital cross-commissure in an excellent photograph, published by Fraas (18, Pl.I), nor does that author indicate such a canal in the figure (18, p. 44), he gave of which the accompanying cut is a copy. The skull of Mastodonsaurus differs greatly from the other skulls described in the large size and posterior position of the orbits. This has had an effect on the arrangement of the lateral line canals. The temporal canal is deflected strongly downwards and its union with the infraobital takes place to the side of the eye. The jugal canal according to Fraas's figure does not touch the supratemporal. In fact the canal is not represented in its most posterior portion. It may have had the course indicated in Fig. 16. The supraorbital is weakly connected with the jugal and with the temporal canal. It has the usual course forward and ends near the nares. The only character of interest in connection with the infraorbital canal is the distinct bend near the anterior termination as though it were a remnant of the former connection between the infra- and supraorbital canals through the intervention of the antorbital commissure. It is to be noticed that the temporal barely cuts the outer edge of the squamosal.

The skull of Trematosaurus brauni Burmeister (16) has already been figured and described in this connection by Baur and Miall, although the figures given by both of these authors are inaccurate in detail when compared with the original drawing of von Meyer. Fritsch in his translation of the report published by Miall also copies his figure and thus continues the inaccuracies. There is nothing unusual in the Trematosaurus (Fig. 17) except the strong development of canals. The occipital cross-commissure is well developed and is contained within the borders of the epiotics. The temporal has no connection with the supraorbital and the antorbital commissure is well developed. There is no anterior commissure. It is to be noticed that the squamosal element is clearly cut by the temporal canal which ends at the ear slit. It was stated above that there was rarely any evidence of an occipital cross-commissure in the Stereospondylia but Trematosaurus seems to be an exception to this rule. There may be others.

The skull of Anthracosaurus from the Carboniferous of

Great Britain has been figured and described by Atthey (19). In regard to the lateral line canals he says: "The mucous-grooves are two pairs. The anterior pair run backwards and inwards along the inner side of the naso-lachrymal suture as far as the posterior margin of the nasals; the posterior are deeper, and appear in two disconnected portions along the outer margins of the jugal and quadratojugal bones. The anterior pair of grooves are less deep and less distinct than those of Loxomma; the posterior are deeper, wider and rougher than those of that labyrinthodont." The skull studied by Atthey was in rather poor state of preservation, but it is evident that he detected the anterior portions of the supra-orbital canals and the jugal canal on one side, with possibly a portion of the infra-orbital. He does not indicate the "mucous-grooves" on his drawing of the skull.

The skull of Loxomma allmanni Huxley (20) is of peculiar interest in connection with the study of the lateral line system of the extinct Amphibia on account of the presence of a distinct anterior commissure which extends, clearly marked, according to the figure given by Embleton and Atthey (20), between the anterior extremities of the supraorbital canals. The antorbital commissure is also clearly preserved. The occipital cross-commissure is not represented in the drawing of Embleton and Atthey nor in that given by Miall (21). Miall's representation of the canals of Loxomma is manifestly inaccurate in regard to the antorbital commissure. In the skull of Gonioglyptus, Huxley (22) has figured the lateral line canals as more strongly developed than usual. Unfortunately only fragments of the skull remain. Huxley's restoration of the lateral line canals in this form is, so far as I can learn, conjectural. The manner in which the supraorbital canals curl around the nostril, if such is their normal course in Gonioglyptus, is without parallel among the other labyrinthodonts.

One of the main points to be brought out in this discussion of the lateral line canals of the extinct Amphibia is the correlation of the cranial elements with those of the fishes so far as is possible. Professor Thyng (23), in his study of the squamosal bone in the tetrapodous Vertebrata, reached the conclusion that the element usually called squamosal in the Stegocephala is not that element, but is the supratemporal. Baur had made the same statement many years previously when he says: "Das sogenannte 'Squamosum' der Stegocephalen (Huxley, Miall, Fritsch, Credner, etc.) ist aber nicht dieses Element, sondern in Wirklichkeit das supratemporale, während das 'supratemporale' dieser Forscher das Squamosum repräsentirt" (Baur, Anat. Anz., I, p. 349). He afterward withdrew from this position (Anat. Anz., Bd. XI, p. 660) and concluded that the squamosal really was that element. Thyng now revives this idea and bases his conclusions on embryological studies of several forms. His major thesis is not, however, well taken since he assumes it to be an accepted fact that the quadrate of the lower vertebrates is represented in the mammals by an element of the ear, the incus. This is by no means so generally accepted as he would have us think. His conclusions are briefly these: since the incus of the mammals represents the quadrate of the lower vertebrates and since there is an intimate relation between the incus and the squamosal bone in certain embryos, ergo the so-called squamosal of the Stegocephala is the supratemporal. Whatever the element lying next to the parietal may be in other forms, I am fairly well convinced that in the Stegocephala it is the true squamosal and not the supratemporal (prosquamosal).

This position is sustained by the study of the lateral line canals on the crania of the extinct Amphibia and their correlation with those of the fishes. In the skull of Amia the temporal canal, in its course forward, cuts the squamosal as it does in all of the Stegocephala examined where the lateral line canals are preserved. I take the conclusion of Allis, Pollard and van Wijhe that this element in the fishes is really the squamosal and the reader is referred to them for their reasons. In Polypterus according to van Wijhe, when in his discussion of the lateral line system he says: "Bedenkt man, dass ein Theil des Hauptastes, nämlich der, welcher bei andern Fischen dem Squamosum zukommt, durch das Parietale geht, dass dieser Knochen auch an der Begrenzung der Gelenkpfanne für das Hyomandibulare theilnimmt, was bei andern Fischen ebenfalls das Squamosum thut, und endlich dass das Schädeldach keinen besonderen Knochen besitzt, der auf den Namen Squamosum Anspruch erheben kann, so ist es kaum zu bezweifeln, dass der bis jetzt als Parietale bei Polypterus beschriebene Knochen ein Squamoso-parietale ist," the so-called parietal is the squamoso-parietal. He is followed in this by Pollard.

I do not find that the arrangement of the canals on the skull of Polypterus has ever been given in an accurate diagram. Tranquair gives a verbal description of their course (24). Van Wijhe remarks: "Ihren Verlauf (i. e. die Schleimkanäle in Polypterus) habe ich nicht verfolgt, er ist aber von Traquair beschrieben" (25). Pollard's representation is modified after Wiedersheim and Baur's figure is modified after Pollard. According to Traquair's description of the course of the canals, all of these figures are inaccurate in regard to the course of the main canal. Traquair says the infraorbital gives off the supraorbital canal on the postfrontal and I have represented it thus in the diagram (Fig. 3). In Polypterus according to Traquair the main canal is the infraorbital as it is in the Stegocephala.

The course taken by the lateral line canals is not subject to great change. This is suggested by the condition described for Micrerpeton and Necturus. If the temporal canal, which is the posterior part of the infraorbital canal, cuts a certain element in one form and cuts the same element with the same relations in another and related form, it is safe to assume that the element is identical in the two forms. We have thus a definite basis for conclusions regarding the homologies of the cranial elements in the two groups; fishes and stegocephalans. It is easy to understand the correlations of the premaxillaries, maxillaries, nasals, frontals, prefontals and parietals of the fishes with the same elements in the

Stegocephala but the correlation of the other elements is not so definite. Pollard is of the opinion that the post-suborital (postorbital) of fishes is homologous with that of the Stegocephala and it probably is. Baur was inclined to correlate the epiotics and supraoccipital of the Stegocephala with the supratemporal elements of the fishes and the arrangement of the lateral line canals substantiates his suggestion. He also would correlate the supratemporal (prosquamosal) with the preoperculum of the Amiadiæ and the quadratojugal with the suboperculum. The lateral line canals of the Stegocephala offer nothing which would contradict this view, so far as I am aware. The squamosal has been shown above to be the squamosal of the fishes, so that we have a nearly complete correlation of the elements of the Stegocephala with those of the fishes and more especially the Amia.

Maggi has offered some interesting suggestions with regard to the correlations of the elements of the stegocephalan skull with those of the higher forms and he would even go so far as to correlate the epiotics of the Stegocephala with the interparietal of man (26). While I have no reasons to doubt his conclusions in regard to some of the correlations yet I doubt his statements in regard to the cranial structure of Archegosaurus and Loxomma. If I understand Maggi correctly his homologies are, in large part, based on the assumption of the fusion of several of the cranial elements in the Stegocephala. I doubt very much if there has ever been a true case of the fusion of the cranial elements of the stegocephalans proved. Jaekel (27) thought he had a case of such a fusion in the skulls of Diceratosaurus punctolineatus Cope from the Carboniferous of Ohio, but in a perfect skull of a closely allied species of this genus I find the elements all clearly separated, as one would expect. Maggi is also inclined to doubt, according to Allis, the correlation of the occipital cross-commissure in the fishes and stegocephalans. It has been definitely shown above, I believe, that the canals are homologous in the two groups.

## Summary.

1. There are present on the skulls of the extinct Amphibia seven distinct lateral line canals, all more or less connected.

2. These canals may be partly homologized with those of fishes. They may be termed: the anterior commissure, homologous with the same canal in fishes; the antorbital commissure, homologous with the similarly placed canal in fishes; the infraorbital canal, homologous with that of fishes; the supraorbital canal, homologous with that of fishes; the temporal canal, homologous with the posterior portion of the infraorbital canal of fishes; the jugal canal, homologous with the operculo-mandibular (?) and the posterior portion of the infraorbital (?) canal of fishes; and the occipital cross-commissure, homologous with the supra-temporal cross-commissure of fishes.

3. The lateral system has been discovered in four of the five suborders of the Stegocephala.

4. The Branchiosauria have a type of lateral line on the tail which is similar to that on the tail of the modern Necturus. The branchiosaurian skull is not grooved by the lateral line canals.

5. In the Microsauria, so far as known, the system of the lateral line canals is well developed. The occipital cross-commissure is present on the skulls of at least two genera.

6. In the Temnospondylia the lateral line canals are of a peculiar type, especially so in the form described, Eryops. The occipital cross-commissure is well developed.

7. The Stereospondylia always have the lateral line canals well developed. This character is an indication of age and specialization. The occipital cross-commissure is present in a single species of the Stereospondylia.

8. The so-called squamosal bone in the skull of the Stegocephala is really that element and not the supratemporal.

9. The following elements of the stegocephalan cranium are homologous with the same elements in fishes: the premaxillæ, maxillæ, nasals, frontals, prefrontals, parietals, squamosals, and postfrontals. The epiotics and supraocci-

pitals of the Stegocephala are homologous with the supratemporal elements of the fishes. The quadratojugal is homologous with the subopercular of fishes. The supratemporal (prosquamosal) is homologous with the preoperculum of fishes.

I am indebted to Dr. Katashi Takahashi for several interesting suggestions in regard to the lateral line system of the modern Amphibia and more especially Necturus. Dr. S. W. Williston has, with his usual kindness, read the manuscript and has offered interesting suggestions. I am indebted to him likewise for the use of the material on which the greater part of this discussion is based. To Dr. Bashford Dean I am grateful for the loan of the large part of the Newberry collection of Carboniferous Amphibia belonging to the American Museum.

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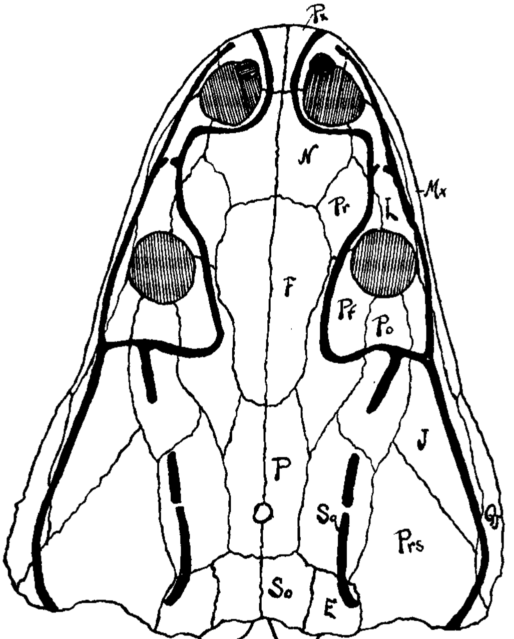
FIG. 14.—Outline of the larger skull of Anaschisma browni Branson, showing the distribution of the lateral line canals. Modified after Branson. A little less than one-fifth natural size.

FIG. 15.—Outline of the cranial elements and lateral line canals of the skull of Metoposaurus diagnosticus von Meyer. Modified after Fraas. One-fifth natural size.

FIG. 16.—Diagram of the cranial elements and the associated lateral line canals of Mastodonsaurus giganteus Jaeger. After Fraas. One-tenth natural size.

FIG. 17.—Outline of the arrangement of the lateral line canals and the cranial elements on the skull of Trematosaurus brauni Burmeister. After H. von Meyer. Paleontographica, Bd. VI, Pl. XXVII. Two-fifths natural size.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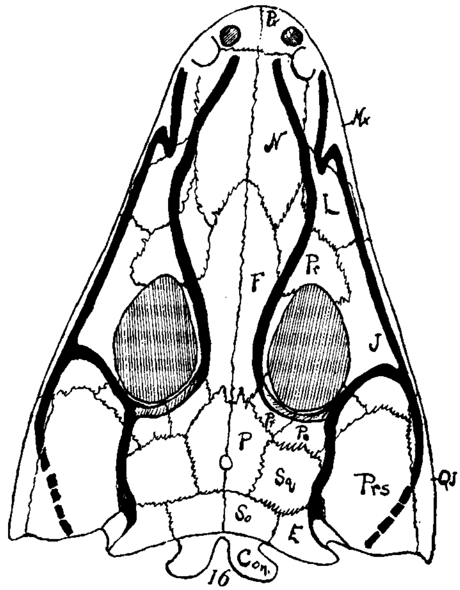
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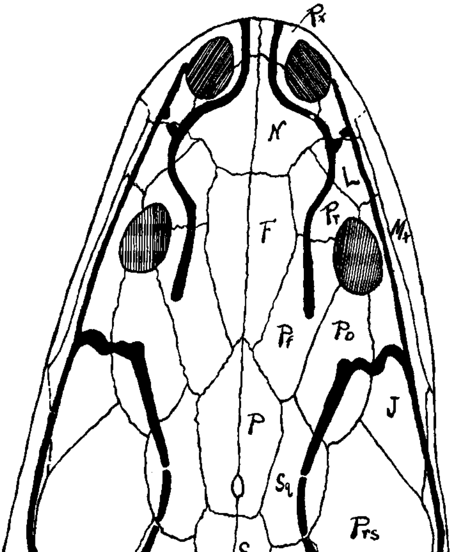
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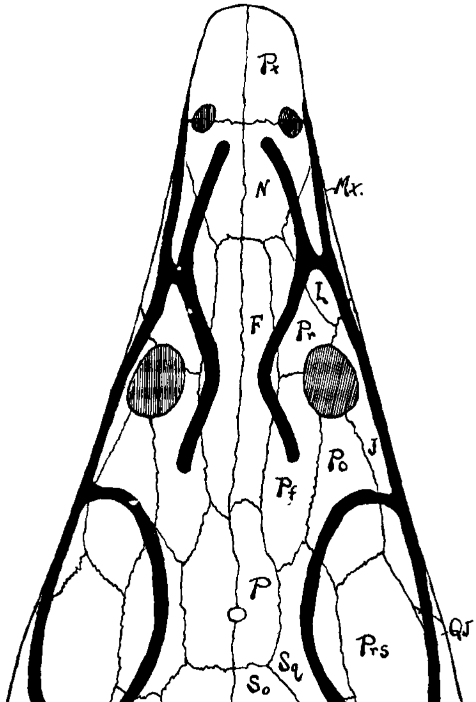
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