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THE CRANIAL ROOF OF *DIPNORHYNCHUS SUSSMILCHI* (ETH. FIL.).

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(Plate ix and Figures 1–6.)

Introduction.

In 1933, the writer published a description of the cranial roofing-bones of *Dipnorhynchus sussmilchi* (Eth. fil.), based on an examination of the external features of the type and only specimen, which is preserved in the Australian Museum, Sydney (Reg. No. F.10813). This dipnoan skull was discovered by Mr. C. A. Süssmilch in the Middle Devonian limestones of Taemas, New South Wales, and was originally described as (?) *Ganorhynchus sussmilchi* by R. Etheridge, Jnr., in 1906. In 1927, Jaekel erected the new genus *Dipnorhynchus* for the specimen, the name being accompanied by an unlabelled original figure, but no written description. In view of the fact that the genus *Ganorhynchus* Traquair is not capable of precise definition and is applicable only to cosmine-covered dipnoan snouts (see Traquair, 1873; Newberry, 1889; Dutertre, 1929; Gross, 1933, 1937), it is undoubtedly preferable to designate the excellently preserved skull from Taemas as a new genus, the name *Dipnorhynchus* Jaekel being here regarded as valid (see also remarks in Hills, 1933, pp. 634–5).

Since the appearance of my earlier paper on *Dipnorhynchus* there has been much discussion about the homologies and nomenclature of the cranial roofing-bones in Devonian fishes, in the course of which the situation of the sensory canals of the lateral line system of the head has assumed considerable significance. As all statements in my previous description were based on examination of the external features only, no dissection having been attempted for fear of damaging the specimen, it was not possible to compare *Dipnorhynchus* in any detail with other dipnoans. The importance of the specimen in relation to the comparative anatomy of the group was, however, obvious, and it was therefore decided to make a partial dissection of the skull in order, if possible, to trace the sensory canals. My thanks are due to Dr. Charles Anderson, former Director of the Australian Museum, for kindly authorizing preparation of the specimen, and to the present Director, Dr. A. B. Walkom, for permission to complete the examination.

The cavity of the skull is filled with massive limestone that adheres strongly to the bones, and it was not until the specimen of *Coccosteus* from the Middle Devonian limestones of Buchan, Victoria, had been studied (Hills, 1936) that a satisfactory and fairly rapid technique for the dissection of such material was developed. Serial sectioning was not favoured for either specimen because each is unique of its kind, and it was desired to preserve them intact as far as possible. In *Dipnorhynchus* the sensory canals were traced by excavating the covering bone and the calcite infilling the canals with dental probes and fine needles, cleaning being carried out by the application of hydrochloric acid with a camel-hair brush. After this treatment the specimen was not suitable for photographic representation, but Figure 1 shows the structures actually observable on the left side of the skull, without any attempt at reconstruction. A few significant details were also obtained from the right side, particularly along the exposed edges of the bones.

Geological Horizon of Dipnorhynchus.

A recent study by Dr. Dorothy Hill (1941) of the rugose coral fauna of the Middle Devonian limestones in the neighbourhood of the Murrumbidgee and Goodradigbee Rivers, from which *Dipnorhynchus* was obtained, indicates that the age of the beds is Couvinian (lower Middle Devonian). I am indebted to Dr. Ida Brown for provisional confirmation of the field evidence that *Dipnorhynchus* was obtained from beds belonging to the Murrumbidgee Series, discussed by Dr. Hill in the above-mentioned paper.

The Sensory Canals of the Head.

The sensory canals of the lateral line system of the head of *Dipnorhynchus* are represented in Figures 1, 5, and 6. The canals lie within the dermal bones, being connected with the exterior by tubules leading to superficial pores.

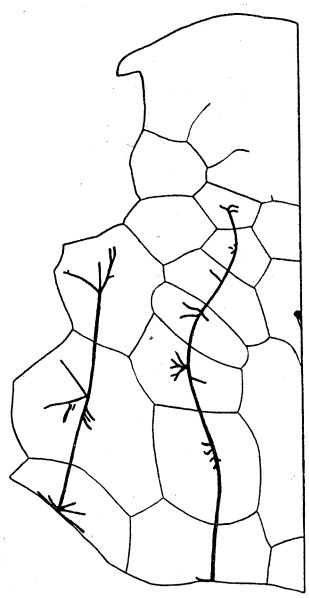

Fig. 1.—Outlines of the bones on the left side of the skull of *Dipnorhynchus sussmilchi*, showing the sensory canals and tubules as revealed by dissection. Drawn from a photograph taken normal to the side of the skull, to facilitate comparison with flattened dipnoan crania.

On the left side, the more mesially situated canal (o.b., Fig. 6) emerges posteriorly through the fractured edge of the cranial roof and is therefore incompletely represented, but on the right side the specimen extends further back, and the corresponding canal is seen to rise towards the outer surface of the bone, terminating within it. The anterior continuation of this canal is undoubtedly the supra-orbital canal (s.o.c.). As it passes forward, the supra-orbital canal, where dissected on the left side, gradually becomes more deeply embedded in the bone, and finally, as Säve-Söderbergh (1933) found in *Osteolepis*, it passes beneath the bone. The approximate course of the canal more anteriorly is, however, clearly indicated by the tracts of superficial pores on the snout (see Fig. 5, and Pl. ix, fig. 2). Its probable course is indicated in Figure 6. There are also, on the antero-lateral parts of the snout, tracts of pores that indicate the course of the anterior parts of the infra-orbital canals (i.f.c.).

Lateral to the canals above referred to, there is, in that portion of the skull behind the eyes, a second pair of canals, traversing the bones adjacent to those in which the more median canals lie, but turning sharply downwards behind the eye. In this latter region the data from the left side were somewhat incomplete, but corroborative detail was obtained from the right. On the right side, this lateral canal emerges posteriorly through the edge of a bone that is preserved intact, so that this canal must be the continuation of the main lateral line of the body. The only indication of the presence

of an occipital cross-commissure is a short and indistinct remnant on the fractured posterior edge of bone 8, Figure 5. Moreover, there is no indication of any branches linking the lateral and mesial canals on either side, such as are present in *Dipterus platycephalus* and *D. valenciennesi* (Figs. 2a and 3a).

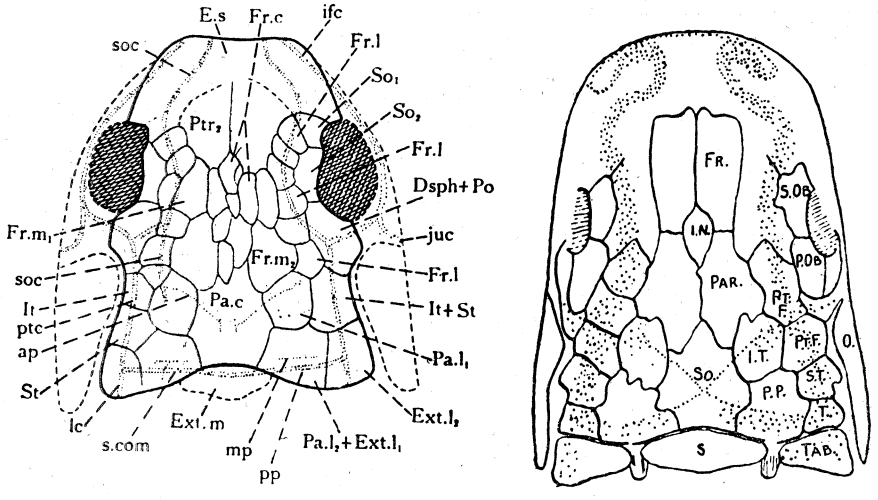

Fig. 2.—A. *Dipterus platycephalus*, after Stensiö. Dsph. + Po., fused dermo-sphenotic and post-orbital; E.s., ethmoidal shield; Ext. l., lateral extrascapular; Ext. m., median extrascapular; Fr. c., Fr. l., Fr. m., central, lateral, and median frontals; It., inter-temporal; Pa. c., Pa. l., central and lateral parietals; Ptr., post-rostral; So., supra-orbital; St., supra-temporal; ap., anterior pit line; ifc., infra-orbital canal; juc., jugal canal; lc., main lateral line canal; mp., middle pit line; pp., posterior pit line; s. com., occipital commissure; soc., supra-orbital canal.

B. *Dipterus platycephalus*, after Goodrich. Fr., frontal; I.N., inter-nasal; I.T., inter-temporal; O., operculum; Par., parietal; P.P., post-parietal; Pt.F., post-frontal; S., "median post-occipital"; So., dermo-supra-occipital; S.Ob., supra-orbital; S.T., supra-temporal; T., pretabular; Tab., tabular.

The sensory canals pass through the growth centres of the individual bones. In the neighbourhood of each growth centre, groups of tubules arise from the canals, and lead to pores on the exterior (see Fig. 1). This condition is similar to that in the only other dipnoan for which the tubules have been described, viz. *Fleurantia* (see Graham-Smith and Westoll, 1937), but is quite distinct from the arrangement in *Osteolepis* (see Säve-Söderbergh, 1933), in which the tubules, although showing a distinct organization in groups, arise at fairly regular intervals along the canals, within each group. As in *Fleurantia*, some of the tubules in *Dipnorhynchus* are long, others short; some are simple, others bifurcate; some, like the ribs of a fan, radiate from a centre, while others are spaced out along the canal near the growth centre of a bone.

Only one line of pit organs is discernible on the skull, this being situated on bone 16 (Fig. 5; Pl. ix, fig. 1).

On the snout, the course of the sensory canals can be judged only from the arrangement of the superficial pores. These are in clearly defined tracts, and it is possible to recognize that, on the antero-ventral surface of the snout, the two mesially situated canals are connected by a short commissure, the region enclosed within the canals and commissure being slightly raised above the general surface and forming the rostral prominence (7, Fig. 5).

The anterior parts of the infra-orbital canals are represented by pores on the antero-lateral margins of the snout on either side. There is, however, a well-defined gap between these pores and those belonging to the mesial canals, so that the

infra-orbital canals probably terminate anteriorly without making an anterior commissure.

Nomenclature of the Sensory Canals.

The nomenclature of the sensory canal system in fishes is based on topography and innervation. Säve-Söderbergh (1933, pp. 5–10) has made a detailed analysis of the canal system, and proposed a consistent nomenclature which it seems advisable to use as far as possible in the interpretation of *Dipnorhynchus*. The innervation of the various canals in *Dipnorhynchus* cannot, of course, be studied, and one is forced to rely on purely topographic data in the homologization of the canals with those of other fishes. Two illustrations of *Dipterus* are particularly useful for comparative purposes, and are reproduced in Figures 2a and 3a. These are of *D. platycephalus* by Stensiö (in Säve-Söderbergh, 1932, p. 96) and of *D. valenciennesi* by Westoll (in Graham-Smith and Westoll, 1937, pp. 244, 251). The general resemblance between the sensory canal systems in these two species and *Dipnorhynchus* is at once obvious. One may recognize in all three the supra-orbital canals. The plan of these canals is remarkably constant,

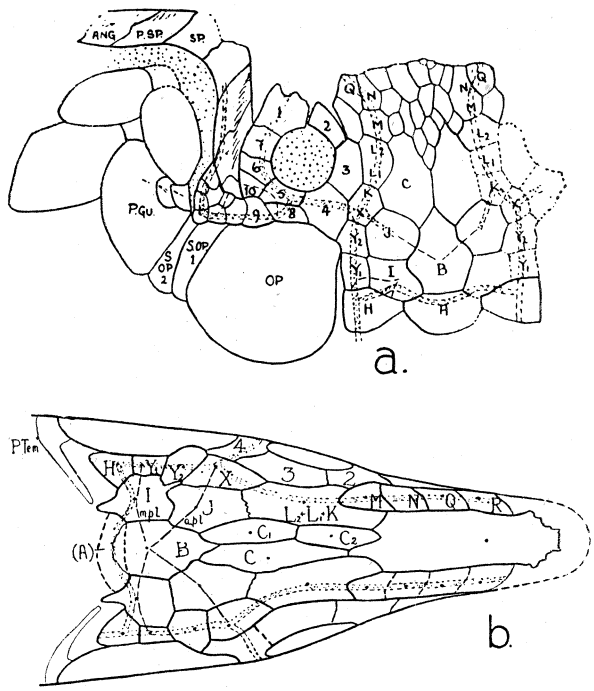

Fig. 3.—A. *Dipterus valenciennesi*, after Westoll. Lettering and numbering of cranial roofing bones based on an arbitrary system by Foster-Cooper.

B. *Fleurantia denticulata*, after Graham-Smith and Westoll. Lettering and numbering correspond with Fig. 3*a*.

so far as is known, among the Dipnoi. Not only in the above-mentioned illustrations of *Dipterus*, but also in Goodrich's figures of *D. platycephalus* and of *Epiceratodus forsteri* (see Figs. 2b and 4 herewith), also Foster-Cooper's illustration of *Protopterus* (1937, p. 234), the supra-orbital canals exhibit characteristic flexures. In all these forms there is a mesially convex flexure between the eyes, followed anteriorly by a laterally directed convexity, and then by a sweeping inward flexure that brings the canals quite close together. In *Epiceratodus* and *Protopterus* there is a short rostral commissure joining the two branches of the supra-orbital canal on the front of the snout in a similar manner to that in *Dipnorhynchus*. Illustrations of this region in other fossil dipnoans are not available for comparison, but there can, in view of the

above-mentioned topographic similarities, be no doubt about the identification of the supra-orbital canals in *Dipnorhynchus*. They are at least the anterior parts of the more mesially situated pair of canals. In *Dipterus* and *Dipnorhynchus*, however, these canals extend well back behind the orbits, and Westoll's figures of *Dipterus valenciennesi* indicate their posterior portions to be somewhat divergent from the course of the supra-orbital canals proper. Moy-Thomas remarks that the posterior branch represents the anterior pit-line developed in part as a canal, and the arrangement in *Dipterus valenciennesi* is not inconsistent with this view. The equivalent canals in *Dipterus platycephalus* and *Dipnorhynchus*, however, are clearly an integral part of the supra-orbital canal system. In *Dipterus platycephalus* the anterior pit-lines are divergent from the canals in question, and there is a short extension of the canals behind the contiguous ends of the pit-lines. I therefore believe that the anterior pit-lines and the canals are distinct structures. Although the canals are part of the supra-orbital canal system, as indicated by Stensiö, their length in the region behind the orbits in *Dipnorhynchus* suggests that they are probably differently innervated and should be distinguished from the supra-orbital canals. Owing to their apparently close connection with the anterior pit-lines, which in many dipnoans lie partly within the median unpaired bone that has been called the median occipital, they will be referred to as the occipital parts or branches of the supra-orbital canals.

With regard to the lateral pair of canals, it is clear that the part turning downwards behind the eyes is the vertical portion of the infra-orbital canal. The canal extending backwards from this vertical portion in *Dipnorhynchus* is clearly homologous with the similarly situated canal in *Dipterus*, and contains the otic canal in front, with the post-otic canal (so named by Säve-Söderbergh) behind. The latter is continued posteriorly as the main lateral line of the trunk.

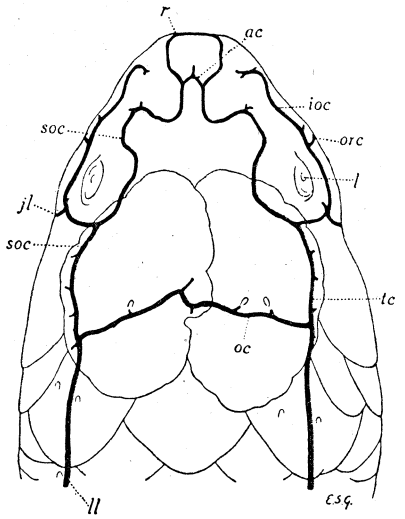

Fig. 4.—*Epiceratodus forsteri*, after Goodrich, showing the sensory canal system of the head. ac., anterior commissure; ioc., infra-orbital canal; jl., jugal canal; l., eye; ll., main lateral line of the trunk; oc., occipital commissure; orc., oral canal; r., rostral commissure; soc., supra-orbital canal; tc., temporal canal.

Anteriorly, the infra-orbital canal traverses the lateral edges of the snout, but there is no evidence of any ethmoidal part (anterior commissure) linking the infra-orbital canals of the right and left sides. The arrangement of the pore tracts suggests rather that the horizontal portions of these canals terminate on either side of the rostral prominence, in a condition similar to that illustrated in *Epiceratodus* by Goodrich and in *Protopterus* by Foster-Cooper.

It may be remarked that Watson (1926) has illustrated the sensory canal system in the head of *D. valenciennesi* in a way differing considerably from that shown for the

same species by Jaekel (1929) and by Westoll (in Graham-Smith and Westoll, 1937). This illustration was the only one available to me when the previous account of *Dipnorhynchus* was written, and it appeared to agree with the canals in *Dipnorhynchus* in so far as these were deducible from the pore tracts. The infra-orbital, otic, and post-otic canals were not discovered until dissection was carried out. In the light of recent investigations of Palaeozoic Dipnoi and the present work on *Dipnorhynchus*, it seems preferable to omit Watson's figure from further discussions until the material on which it was based is re-examined.

Bone Homologies.

The concept originally proposed by Goodrich (1909), that there is a very close connection between the localization of dermal bones and the sensory canals of the head of primitive fishes, has now met with general acceptance (see especially Moy-Thomas, 1938; Romer, 1936; Säve-Söderbergh, 1933; Westoll, 1936, 1938), and is regarded as of major importance in the homologization of the cranial roofing bones. The general principles involved have been dealt with by Moy-Thomas, while Säve-Söderbergh and Westoll have both advocated radical revision of former ideas concerning the nomenclature and evolution of the dermal bones in primitive fishes. Final agreement has not yet been achieved on many points, the Dipnoi having proved particularly difficult to deal with, so much so that a scheme of lettering the dermal bones has been employed by some authors as a preliminary stage in the derivation of homologies with the Osteolepids on the one hand and the Tetrapods on the other. In order to avoid verbal confusion in this paper, the bone-nomenclature used in the description of *Dipnorhynchus* will be that of the Osteolepids, no attempt being made to apply Westoll's revised tetrapod-fish homologies as outlined in his papers of 1936 and 1940.

The species that most closely resembles *Dipnorhynchus* is *Dipterus platycephalus*. As will be seen by reference to Figures 2a and 5 herewith, the following points of comparison may be recognized: the lateral series of bones, traversed by the post-otic and otic canals and the vertical portion of the infra-orbital canal, is well defined. Stensiö's figure shows three bones in this series on the right, with four on the left. In *Dipnorhynchus* there are three bones preserved on the left, and four on the right, but the division of the central bone is by a longitudinal suture and not a transverse one as in *Dipterus platycephalus*. This subdivision in *Dipnorhynchus* is believed to be of no anatomical significance. It is clear that the anterior bone in this series, in which the sensory canal changes its course, is the homologue, wholly or in part, of the bone occupying a similar position in *Dipterus platycephalus*. This bone must contain a dermo-sphenotic element (see definition by Säve-Söderbergh, 1933, pp. 8–9), and may also, as indicated by Stensiö,[1] contain the post-orbital, since its posterior border extends well down at the back of the orbit. Comparison with *D. valenciennesi* also indicates that this bone is correctly identified (see Fig. 3a). The other bones normally represented in this series are, from front to back, the inter-temporal, supra-temporal, and lateral extra-scapular. Of these, the supra-temporal is usually connected with the lateral parts of the middle pit lines, as in *Osteolepis* and *Dipterus valenciennesi*. It is, therefore, probable that the bone on which the short pit line is situated in *Dipnorhynchus* is the supra-temporal. The bone on the left and the two bones on the right, anterior to the supra-temporal, are thus regarded as the inter-temporal. All the bones of this series so far identified in *Dipnorhynchus* are firmly attached together as integral parts of the skull roof. The lateral extra-scapulars, which normally follow behind the supra-temporals, are usually rather loosely attached to the skull. They contain the cephalic division of the main lateral line, and also the junction of this canal with the occipital cross-commissure (see Fig. 6). It is, therefore, necessary to add these bones to the skull of *Dipnorhynchus* in the restoration. This is also in accord with the fact that there is no indication of the cross-commissure in any more anterior bone of this series.

[1] I assume that the nomenclature of the bones, as well as their outlines, is due to Stensiö in the figure published by Säve-Söderbergh (1933), though this is not expressly stated.

Turning to the median bones, lying between the supra-orbital canals, it is clear that the most posterior bone preserved, which is an unpaired element, cannot be the median extra-scapular because it is an essential and firmly fixed part of the architecture of the skull roof, whereas the median extra-scapular is loosely connected with the remainder of the cranial roof, and contains the central portion of the occipital cross-commissure. A median extra-scapular has therefore been added in the reconstruction. In other dipnoans, the unpaired bone in front of the median extra-scapular is the so-called "median occipital" (to use Goodrich's non-committal term) and it lies between the posterior ends of the occipital branches of the supra-orbital canals, being normally

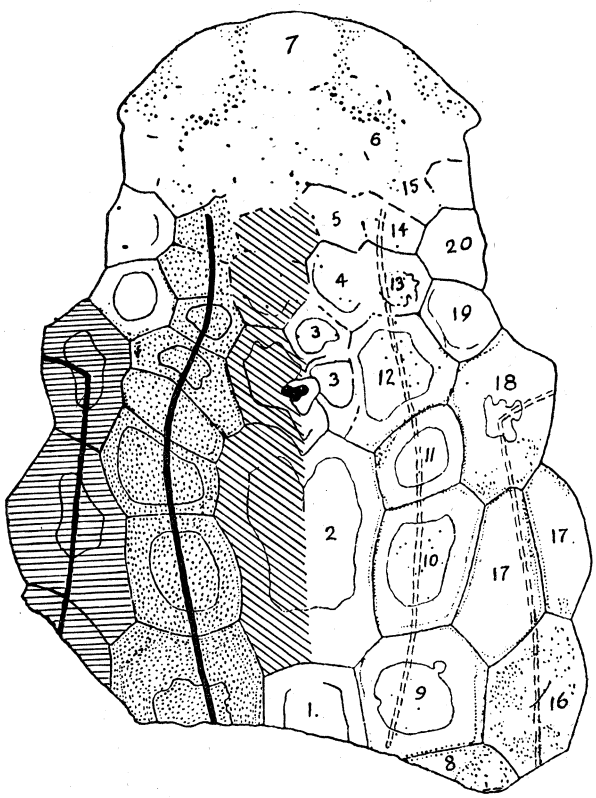

Fig. 5.—*Dipnorhynchus sussmilchi*, showing the outlines of the cranial roofing bones, the course of the sensory canals, and the pore tracts on the snout. On the left side the three longitudinal bone series are indicated by distinctive shading. On the right the bones are numbered to correspond with references in the text.

associated with the inner ends of the anterior pit lines. In *Dipnorhynchus* the anterior pit lines are not represented, but the bone in question does lie between the ends of the occipital branches of the supra-orbital canals, as in *Dipterus platycephalus* and *Dipterus valenciennesi*. In front of the "median occipital", there are in most Palaeozoic Dipnoi two bones, meeting in a longitudinal suture along the middle line. In *Dipnorhynchus* there can be no doubt that these bones are represented by a single element (2, Fig. 5), which, however, is subdivided along the middle line anteriorly. In Stensiö's figure of *Dipterus platycephalus* these two bones are probably represented by the large bones labelled Fr.m_2 (see Fig. 2a), which are separated by irregular small ossifications.

More anteriorly, paired bones junctioning along the middle line are recognizable in *Dipterus platycephalus* (after Goodrich; see Fig. 2b), *Dipterus valenciennesi* (after Jaekel), an unnamed species of *Dipterus* figured by Romer (1936), and in *Dipnorhynchus*. There is, however, in both genera, a notable tendency towards the distintegration of

the median paired bone series by the development of somewhat irregularly arranged small ossicles.

With regard to the homologies of these median paired bones, *Dipnorhynchus* presents one notable feature that is absent from other dipnoans, the presumed pineal foramen (p.f., Fig. 6). Romer (1936, p. 252) has taken the view that though the presence of the pineal body may be a stimulus to bone development, there is no evidence that the associated elements need necessarily be always the same, since the position of the pineal is dependent upon the position of the brain. In his interpretation of the skull of *Dipnorhynchus*, therefore, he sees no incongruity in identifying the bones penetrated by the pineal foramen as nasals. Westoll (1938, 1940), on the other hand, has advocated bone homologies for the Rhipidistra and for primitive tetrapods, in which the pineal foramen is always situated within the equivalents of the tetrapod parietals, regarded by him as the equivalents of the frontals in the old Rhipidistran (Osteolepid) terminology. There are, therefore, some grounds for assuming, as I originally did, that the bones penetrated by the pineal foramen in *Dipnorhynchus* are the homologues of the Osteolepid frontals, and much greater incongruity in calling them nasals, situated as they are behind the eyes, whereas the nasals are normally situated on the snout. In view of other evidence discussed below, however, it seems preferable to regard the pineal foramen as indicating in a general way only, the position of a region which contains the equivalents of the Osteolepid frontals.

The bones associated with the supra-orbital canals and their occipital branches in *Dipnorhynchus* form well-defined longitudinal series on either side of the skull. The regular progression of the numerous bones in these series is a unique feature of the skull, which is approached only by *Dipterus platycephalus* as figured by Stensiö. In other dipnoans the bones associated with the infra-orbital and supra-orbital canals are aligned in a smooth curve, but in *Dipnorhynchus* there is no link between these two canals, and the bone series associated with them must be regarded as distinct.

Anterior to the dermo-sphenotics, the bones normally connected with the supra-orbital canals on the snout and between the eyes in Rhipidistra are the nasals in front and the frontals behind them. Stensiö accordingly labels the small bones traversed by the supra-orbital canal in this region in *Dipterus platycephalus* "lateral frontals" (Fr.l., Fig. 2a), regarding the more centrally situated adjacent bones as "central and medial frontals". In other dipnoans, the supra-orbital canal in the region under discussion lies within one or more relatively large bones, and in *Fleurantia* Westoll and Graham-Smith have demonstrated that one such pair of large bones has developed by the fusion of three smaller elements on either side, represented by separate ossifications in *Dipterus valenciennesi*. They regard these composite bones as the equivalents of the Osteolepid frontals, the small ossifications situated between them in *Fleurantia* being regarded as not represented in the Osteolepids. Moy-Thomas (1937) regards the numerous bones penetrated anteriorly by the supra-orbital canal in *Dipterus* as "fronto-nasal ossifications", the centrally situated bones between them being "post-rostrals".

I believe that *Fleurantia* affords a definite clue to the real nature of the bones in the central region of the skull in Palaeozoic Dipnoi. The lateral line bone ($L_2 + L_1 + K$) in that genus (see Fig. 3b), which has been formed from the fusion of three smaller elements, appears to be developing into a transversely broader bone than the neighbouring elements of the supra-orbital canal series. In doing so, the roughly paired central elements (C, Cl, Fig. 3b) which probably correspond to somewhat larger bones in *Dipnorhynchus* (3, Fig. 5), have been rendered narrow and may readily be imagined as disappearing with further development of ($L_2 + L_1 + K$) as a unit. The evidence therefore suggests that the narrow median bones in *Fleurantia* are purely anamestic (i.e. filling in a space—term proposed by Westoll, 1936), and that ($L_2 + L_1 + K$) is the true homologue of the Osteolepid frontal. The extent and mode of development of the anamestic bones in any species may be correlated with three factors: firstly, that in primitive forms they are represented by two longitudinal bone series, contacting along the mid-dorsal line as advocated by

Romer and substantiated in *Dipnorhynchus*; secondly, that in the course of evolution the lateral line bones have tended to fuse and expand, assuming dominance in the skull roof as major structural elements at the expense of the anamestic bones; and, thirdly, that in forms at an intermediate stage of evolution the presence or absence of anamestic bones will be determined by the anatomical needs of the fish (broad, narrow, or average skull width) and the ability of the large organized lateral line bones to cover the area necessary. I therefore regard the numerous lateral line bones along the course of the supra-orbital canals in *Dipnorhynchus* as fronto-nasal ossifications, and the median, roughly paired elements as anamestic bones without strict homologues among the Osteolepids. Of these ossifications, I regard the nasals as being situated along the strong mesially concave flexure of the supra-orbital canal on the snout (6, Fig. 5), since, as formerly suggested (Hills, 1933, p. 639), the nasal capsules probably lay beneath this region. The more posterior bones (11–14, Fig. 5; Fr., Fig. 6) are regarded as frontals, though there may be some doubt as to the anterior and posterior limits of the frontal region.

On the above interpretation, the parietals should be situated in the posterior parts of the same bone series. In *Dipterus platycephalus*, according to Stensiö, the posterior ends of the occipital branches of the supra-orbital canals lie within the lateral parietals, the "median occipital" being regarded as the "central parietal", as it is also by Moy-Thomas (1937). It may be noted that in the Palaeoniscid fishes the supra-orbital canals also usually end in the parietals, and, as in *Dipnorhynchus*, the supra-orbital and infra-orbital canals in those fishes are not normally linked with each other. (The latter condition also obtains in the Acanthodii, according to Watson (1937).) Therefore, the bones labelled 9 in Figure 5 are regarded as parietals. If these bones are correctly identified, then those immediately anterior to them must also be regarded as parietals, on the following grounds: firstly, they lie too far back on the skull to be consistently regarded as frontals; secondly, as figured by Säve-Söderbergh (1932, p. 95), Stensiö has observed a specimen of *Eusthenopteron* in which there are two pairs of parietals separated by a transverse suture, so that it is probable that the normal parietals are developed from two primitive elements; thirdly, the parietals in *Osteolepis* extend over the same longitudinal range as the two bones in question in *Dipnorhynchus*, i.e., mesial to the supra-temporals and the inter-temporals.

Identification of the parietals in this way means that bone 8, Figure 5, corresponds to bone I (a lateral extra-scapular) in Westoll's figure of *Dipterus valenciennesi* (see Fig. 3a) and in part to the bone labelled $Pa.l_2 + Ext.l_1$ (fused lateral parietal and lateral extra-scapular) in *Dipterus platycephalus* (Fig. 2a). Moy-Thomas figures it as a lateral extra-scapular in *Dipterus* (1937, p. 311), and this is the interpretation adopted herein for *Dipnorhynchus*. It is, therefore, quite normal that a remnant of the occipital cross-commissure should occur within this bone in *Dipnorhynchus*, as mentioned above.

The unpaired "median occipital" (1, Fig. 5) has no homologue in the Osteolepids, nor has the bone 2, anterior to it. The name median occipital (or dermo-supra-occipital) used by Goodrich (1925, 1930) may therefore be retained for the posterior bone (1), so characteristic of the dipnoan cranial roof.

On the basis of the above arguments, the reconstruction and bone nomenclature shown in Figure 6 have been arrived at.

In adding a lateral margin to the skull in the reconstruction, and indicating the probable approximate position and outlines of the jugal, squamosal, and operculum, consideration has been given to the general form of the preserved portions, the geometry of the bones, the presumed course of the lateral line canals, and to the published reconstruction of *Dipterus valenciennesi* by Westoll (in Graham-Smith and Westoll, 1937).

It will be seen that *Dipnorhynchus*, though comparable in many respects with other dipnoans, especially with *Dipterus platycephalus* and *Dipterus valenciennesi*, differs from these and all others in several important regards. Among these are the great development of the occipital branches of the supra-orbital canals, the lack of a connection between these and the infra-orbital canals, the presence of a presumed

pineal foramen, and the large number of bones in the region posterior to a line joining the orbits. The dermal cranial bones in *Dipnorhynchus* are, more clearly than in any other dipnoan genus, arranged in longitudinal series, affording strong support for Romer's suggestion that such an arrangement was probably present in the ancestral dipnoan. The details of Romer's hypothetical bone series are not, however, borne out by *Dipnorhynchus*, nor are they by Stensiö's figure of *Dipterus platycephalus*. Thus between Romer's C series (associated with the supra-orbital and the main lateral line canals on the head) and the more mesially situated A and B series, there is, in both these forms, a further series associated with the occipital branches of the supra-orbital

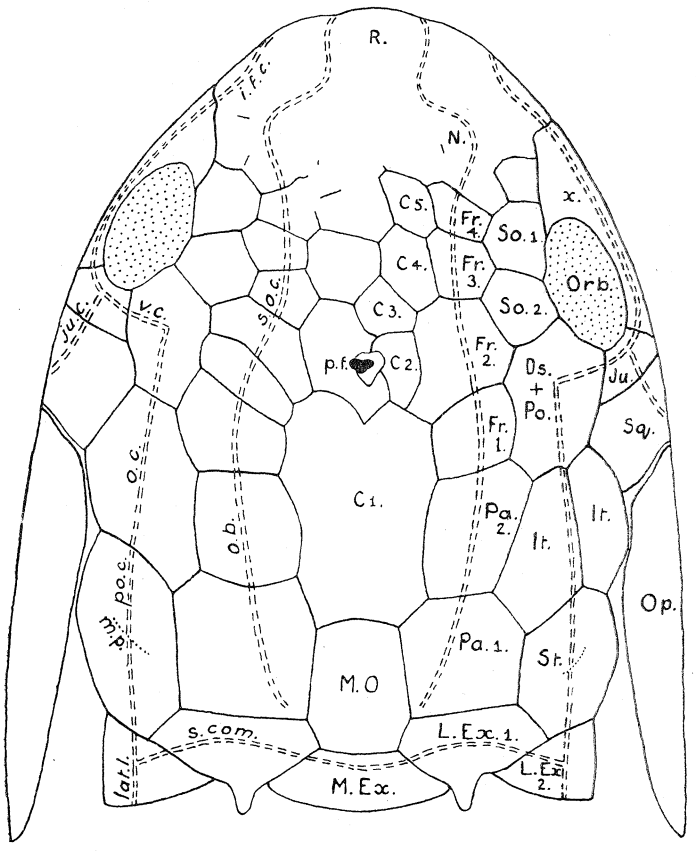

Fig. 6.—Reconstruction of the head of *Dipnorhynchus sussmilchi*, with the mid-dorsal line horizontal, based on a photograph. C 1, 2, 3, 4, 5, bones not represented in the Osteolepids; Ds. + Po., fused dermo-sphenotic and post-orbital; Fr. 1, 2, 3, 4, frontals; It., inter-temporal; Ju., jugal; L. Ex. 1, 2, lateral extra-scapulars; M. Ex., median extra-scapular; M.O., median occipital; N., nasal region; Orb., orbit; Op., operculum; Pa. 1, 2, parietals; R., rostral prominence; So. 1, 2, supra-orbitals; St., supra-temporal; Sq., squamosal; x., restored region, no subdivision attempted; ifc., infra-orbital canal; ju.c., jugal canal; lat. l., main lateral line; m.p., middle pit line; o.c., otic canal; o.b., occipital branch of the supra-orbital canal; p.f., pineal foramen; s. com., occipital commissure; s.o.c., supra-orbital canal; v.c., vertical portion of the infra-orbital canal.

canals. This point is clearly brought out in Romer's interpretation of *Dipnorhynchus* (1936, p. 243), where bone C4 is followed immediately (posteriorly) by B2, while in front of C3 is a bone of the D series (circum-orbital and cheek elements) which in actual fact is associated with the infra-orbital canal. It should be pointed out that Romer's interpretation was based on the author's earlier account of *Dipnorhynchus*, in which, although the cranial bones were accurately represented, the lateral line system was incompletely described, for reasons given above.

Conclusion.

Re-examination of the cranial roofing bones of *Dipnorhynchus sussmilchi* (Eth. fil.) has necessitated an entirely different interpretation of the skull from any formerly attempted. In conformity with its geological antiquity, the fish presents many primitive anatomical features which indicate that it is probably closer to the ancestral dipnoan than any other species yet discovered.

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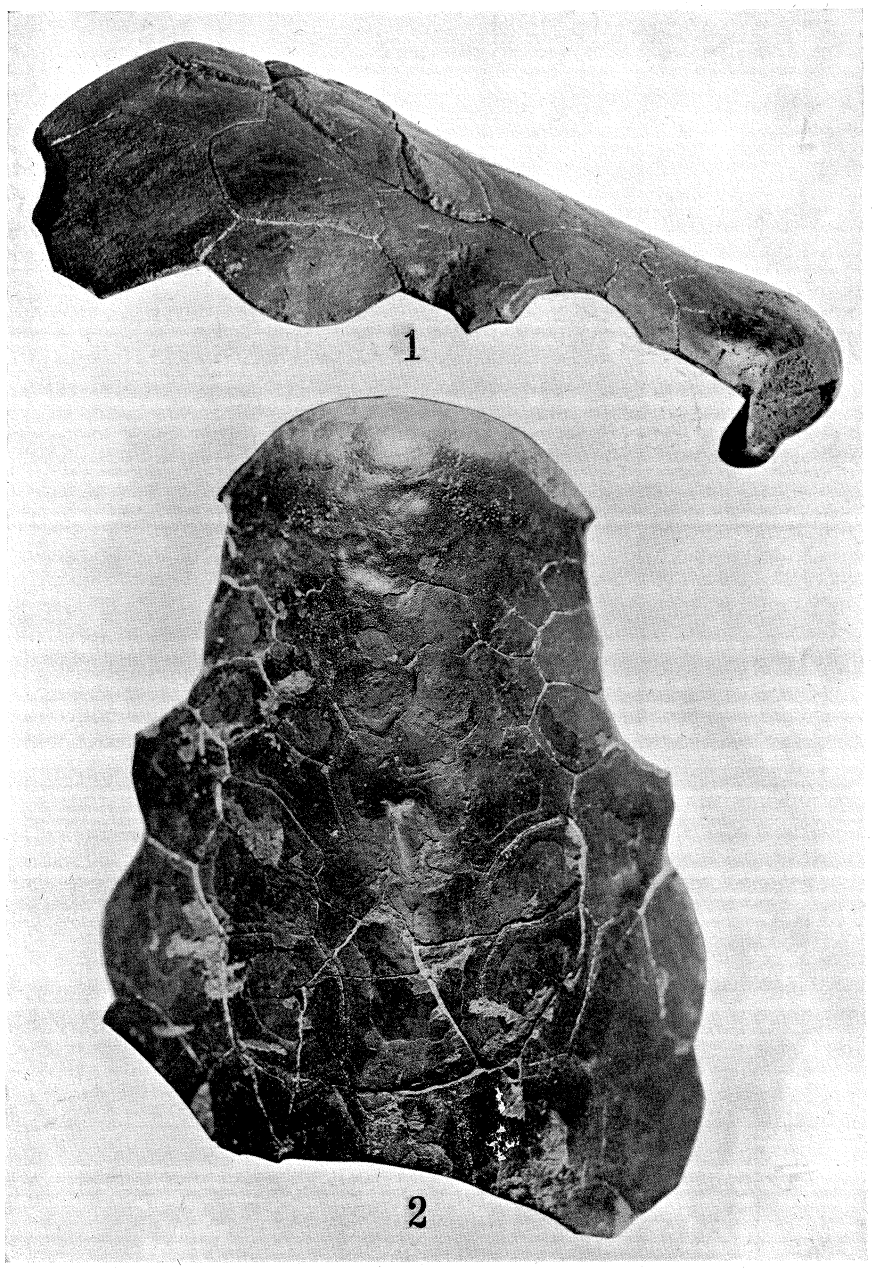
EXPLANATION OF PLATE IX.

Dipnorhynchus sussmilchi (Eth. fil.).

Middle Devonian, Taemas, N.S.W.

1. Lateral view of the skull.
2. Vertical view, with the mid-dorsal line horizontal.

(Both × 1 approx.)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