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ON THE HEAD OF THE MACROPETALICHTHYIDS

WITH CERTAIN REMARKS ON THE HEAD OF THE OTHER ARTHRODIRES

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PREFACE

The Museum specimen (P 1154) on which the following paper by Dr. Stensiö is chiefly based, is from the Onondaga (Corniferous) Middle Devonian limestone of Leroy, Genesee County, New York. The original collector is not known to the Museum. The specimen together with another (P 1155), from the same locality, was obtained by the Museum from Ward's Natural Science Establishment, Rochester, New York, in 1894. Its remarkably complete preservation has enabled Dr. Stensiö to make the profound anatomical study that is presented in the following pages.

The matrix of this specimen when freshly broken is seen to be a dark brown, partially crystallized limestone. This limestone is somewhat argillaceous and bituminous, and slightly magnesian. Here and there it exhibits the inclusions of chert which are characteristic of Corniferous limestones. On weathered surfaces the matrix is chalk-white in color, upon which the dull black parts of the fossil fish stand out in contrast.

In specimen P 1155, only the dermal bones of the cranial roof of a *Macropetalichthys* are preserved. This head is larger than that of P 1154, being 19 centimeters in length as compared with 12 centimeters in P 1154. The width (12 centimeters) is about the same for both. The plates preserved in the larger specimen are of a dark, calcareous substance, about 1 mm. thick. Except for a black pigment, this substance dissolves readily in dilute hydrochloric acid. On removal of the remains of these plates, imprint of a pustulose external surface can be plainly seen on the overlying rock. In the limestone matrix of both specimens, numerous aggregates of more or less comminuted brachiopod shells and crinoid stems are visible. Among the brachiopods so preserved, individuals of the species *Leptaena rhomboidalis* and *Atrypa reticularis* can be identified.

Oliver C. Farrington.

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INTRODUCTION

As the holder of a scholarship from the University of Upsala and with support from the Palæontological Museum of Kristiania, I undertook in 1922 a journey to the United States of America for the study of certain groups of fossil vertebrates, especially Ostracoderms and Arthrodires.

In examining the collection of the Arthrodires in Field Museum of Natural History at Chicago I found a specimen of *Macropetalichthys rapheidolabis,* (Field Museum Cat. No. P 1154), that if prepared in a proper way was likely to show the primordial neurocranium rather completely preserved. Through the courteous assistance of Mr. H. W. NICHOLS, Associate Curator of Geology of the Museum, permission was secured for me to carry out the preparation of the specimen which I found necessary for my studies. While carrying on this work it soon became evident that the specimen was of much greater importance from the anatomical point of view than I at first thought; for most of the canals for nerves and vessels, the entire cavum cerebrale and a part of the labyrinth cavity were in such a good state of preservation that they could be examined in detail. I spent ten days working with the specimen and during this time the photographs reproduced in Pls. XIX-XXVI were made by the photographer of the Museum. (Cf. Annual Report of the Director, Field Museum of Nat. Hist., Publication 213. Report series, Vol. VI, No. 2, p. 121.)

The present paper is chiefly based on the specimen of *Macropetalichthys rapheidolabis,* in Field Museum of Natural History at Chicago, that has just been referred to. But as this specimen was imperfect regarding the occipital region, this was studied on certain specimens in the American Museum of Natural History in New York, a few of which—those figured in this paper—were sent to me in 1923 in Sweden for a re-examination in certain respects.

The specimen of the new, interesting form *Epipetalichthys wildungensis* described in the present paper was, in the most courteous way, placed at my disposal by Professor O. JAEKEL of Greifswald, and for the opportunity to examine the specimen described below under the name of *Macropetalichthys agassizi?* I am indebted to Mr. S. JUNKERMANN of Bielefeld.

It is a pleasant duty for me to express here my most sincere thanks to Mr. H. W. NICHOLS, of Field Museum of Natural History, for all the help I received from him and for the kindness he showed to me during my stay at Chicago. Further I wish to express hearty thanks to Dr. W. K. GREGORY and Dr. W. D. MATTHEW for their help in facilitating my studies at the American Museum of Natural History in New York, and for their great kindness in sending material to me in Sweden. Finally, I am also highly indebted to Professor O. JAEKEL of Greifswald, both for the material which I received from him for this paper and for important information concerning the Wildungen Arthrodires upon which he is working.

All the drawings for this paper were made by Mr. G. LILJEVALL, of Stockholm.

DESCRIPTION OF THE MACROPETALICHTHYIDS

MACROPETALICHTHYS RAPHEIDOLABIS

Norwood & Owen

(Pls. XIX-XXVII, Pl. XXVIII, figs. 3-5; Pl. XXX, fig. 2; Pl. XXXI, fig. 1)

PRIMORDIAL NEUROCRANIUM

GENERAL REMARKS. The primordial neurocranium is strikingly broad and low, its maximum width almost equalling the length and its maximum height constituting only about one-seventh of the length and between one-fifth and one-sixth of the maximum width (Figs. 1, 3, 5, 8; Pls. XIX-XXII; Pl. XXIV, figs. 1, 3). The maximum height is situated in the posterior and the maximum width in the anterior half of the labyrinth region.

As is seen from text figs. 4, 5, 8, 9, and Pl. XXIV, figs. 1, 3, the primordial neurocranium is so arched both in a transversal and longitudinal direction, that its dorsal surface is convex and its ventral surface correspondingly concave.

Concerning the shape of the different divisions of the primordial neurocranium, it may be especially pointed out in this connection that the occipital and ethmoidal regions have a considerable length, while the labyrinth and orbitotemporal regions are short. The latter region is even strikingly short and at the same time very broad, its length being only about one-half of the width, a condition which is due partly to the slight development of the orbits and partly to the considerable width of the skull as a whole. With regard to the orbits, it is in addition noteworthy that they have shifted some distance backwards and medially and that they are much directed upwards.

The primordial neurocranium consisted of cartilage and bone, the latter containing fairly numerous cell spaces. The bone occurs, however, only as thin layers, which covered the cartilage on the cerebral surface, within the labyrinth cavity, to a large extent on the external surface, and in addition also formed a lining membrane for all the canals for the vessels and nerves piercing the walls of the neurocranium. Accordingly, there may be distinguished an internal bone-layer, a labyrinth bone-layer, an external bone-layer and canal bone-layers. More closely defined, these different layers of bone, which evidently are perichondral, have the following extension and relations:

1. The *internal layer* forms a continuous covering of the cerebral surface of the primordial neurocranium. In other words, it lines the whole cavum cerebrale cranii.

2. The *labyrinth layer* forms a continuous lining membrane of the whole labyrinth cavity (cavities for the semicircular canals included).

3. The *external layer* covers the outside of the primordial neurocranium ventrally, laterally and posteriorly, but dorsally, on the contrary, only in the posterior narrow division of the occipital region and probably in a short anterior part of the ethmoidal region. The remaining parts of the dorsal side of the occipital and ethmoidal regions, as well as the whole dorsal side of the labyrinth and orbitotemporal regions, are destitute of a perichondral bone-layer, so that the cartilage must have appeared there to the extent shown in Fig. 3. The portion of the external layer covering the posterior side of the anterior broad part of the occipital region, is connected with the inner layer by a few, chiefly sagitally placed, laminæ of bone, which passed through the cartilage, and which naturally are enchondral.

4. The *canal layers* line all the canals traversing the cranial walls, even canals and branches of canals with a very narrow diameter. In those cases where the canals pass from the cavum cerebrale to the outside, the layers lining them are continuous with and connect the external and internal bone layers with one another. In a similar way the internal layer is continuous with the labyrinth layer by layers lining such canals which run from the cavum cerebrale to the labyrinth cavity.

The different layers of bone just described actually form by their connections with each other a single large bone extending throughout the length of the primordial neurocranium. That this large bone was formed by the coalescence of a few smaller ones seems not improbable, since vestiges of ossification centres perhaps occur in certain places.

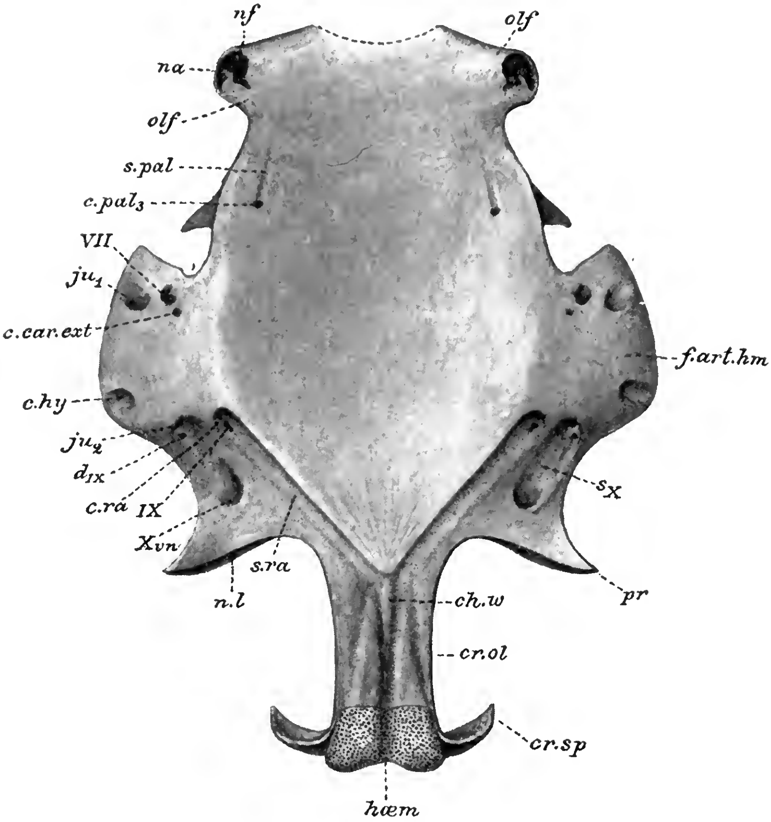

Fig. 1. Macropetalichthys rapheidolabis

Restoration of primordial neurocranium in ventral aspect. Occipital region after specimens in the American Museum of Nat. Hist., New York, other regions after a single specimen in Field Museum of Nat. Hist., Chicago. The dimensions of the occipital region probably not fully correct in relation to those of the other regions. Cartilage dotted. ×½.

c.car.ext, canal for the arteria carotis externa; *c.hy,* canal for the vena hyoidea; *ch.w,* ridge caused by the most anterior part of the notochord; $c.pal_3$, opening for the r. palatinus facialis; *c.ra,* canal for the radix aortæ; *cr.ol,* crista occipitalis lateralis; *cr.sp,* cranio-spinal process; d_{IX}, probable foramen for the dorsal branch (lateralis branch) of the n. glossopharyngeus; *f.art.hm,* probable place of articulation for the dorsal end of the hyoid arch; *hæm,* hæmal groove; *ju,* canal traversed in the anterior part by the vena mandibularis; in the longer posterior part by the v.jugularis (behind the confluence between this and the vena mandibularis); ju_1 and ju_2, anterior and posterior openings of the canal *ju,* the anterior one traversed by the vena mandibularis; *na,* nasal opening; *nf,* nasal fontanelle; *n.l,* canal for the n.lineæ lateralis; *olf,* olfactory capsule; *pr,* postero-lateral process of the anterior broad division of the occipital region; *s.pal,* groove for the r.palatinus facialis; *s.ra,* groove for the radix aortæ; s_x, groove leading some distance anteriorly from the external opening of the vagus canal; *IX,* canal for the n. glossopharyngeus; X_{vn}, canal for the n.vagus and the vena cerebralis posterior.

The position of these presumed centres is seen in Figs. 1 and 3, and will be further dealt with in the subsequent description of the different regions of the primordial neurocranium.

OCCIPITAL REGION

The occipital region is very long, its length probably being continued between two and three times into the length of the primordial neurocranium (Figs. 1, 3, 5; Pl. XXVII; Pl. XXVIII, figs. 4, 5). With regard to its shape otherwise it may be considered as composed of two divisions, an anterior one and a posterior one.

The posterior one of these divisions (Figs. 1, 3, 5; Pl. XXVII; Pl. XXVIII, figs. 3-5; Pl. XXX, fig. 2) is much longer than the anterior one but, on the other hand, considerably narrower and lower. With the longer anterior part it does not by far extend up to the cranial roof. At its posterior end it has a paired laterally and dorsally projecting process (*cr-sp*), which is coalesced with its fellow of the other side medially and so connected on the anterior side with a descending lamina from the posterior bones in the dermal cranial roof that it forms a support for these. The process much resembles the cranio-spinal process in *Acipenser, Polyodon* and *Saurichthys* (HUXLEY 1864, Fig. 82; PARKER 1882, Pl. 15, fig. 13; Pl. 16, figs. 1, 3; IWANZOW 1887, Pl. 1, fig. 2; GEGENBAUR 1912, pp. 319-325; STENSIÖ 1925) and may therefore be termed a cranio-spinal process although it obviously has evolved independently of that in the fishes enumerated.

The most postero-ventral part of the posterior division situated beneath that from which the cranio-spinal process issues is not found preserved in any of the specimens investigated, a fact which seems to indicate that it lacked the external bone layer and thus was entirely cartilaginous when seen from the outside (Figs. 1, 3, 5; Pl. XXVII; Pl. XXVIII, figs. 3-5; Pl. XXX, fig. 2). It probably had a paired condyle or a paired fossa for articulation with the vertebral column, as a cranio-vertebral joint might have been present as in ordinary Arthrodires.

Two transverse sections through the posterior division are shown in text fig. 2. As is understood from these and Fig. 5, the posterior division is much flattened in a dorso-ventral direction, its height being only about one-half of the width. As a consequence of the flattening, the external surface has no lateral fields, but only a dorsal and a ventral field separated from each other by a paired, well pronounced lateral crista, the crista occipitalis lateralis (*cr.ol*). The dorsal one of the two fields, which, as mentioned above, is situated deep below the dermal cranial roof except at the posterior end, is provided with a longitudinal unpaired crista, the crista occipitales dorsalis (*cr.od*), while the ventral field, on the contrary, has a wide and deep longitudinal groove. This groove (*hæm,* Figs. 1, 2; Pl. XXVIII, figs. 3, 4) constitutes undoubtedly an anterior, cephalic portion of the hæmal groove of the vertebral column, and may therefore properly be termed the hæmal groove. Towards the transition of the anterior division of the region, it becomes gradually shallower and seems to divide there into two shallow branches (Fig. 1; Pl. XXVII, fig. 4), a right and a left one, each of which is continued forwards by the groove *s.ra* which will be further dealt with below in another connection.

The part of the cavum cerebrale cranii situated within the posterior division is long and low and narrow in comparison with those in front of it. It is, however, somewhat narrower in its anterior, than in its posterior portions, as is well shown by Fig. 10 and Pl. XXVII, fig. 1. A transverse section through its posterior half is seen in Fig. 2.

The notochord extended into the basal part of the neuro-cranium, but was very slightly developed there (*ch,* Fig. 2) and reached forwards only to about the transition between the anterior and posterior divisions of the occipital region (Pl. XXVIII, fig. 4). It was, thus, in the neurocranium, limited to the posterior division of the occipital region, while the parts of it that originally existed further forward as far as to the dorsum sellæ have become reduced. The persistent part was surrounded by a thin bone layer of its own, and this bone layer, which is well preserved in the fossil, forms a fine longitudinal tube, a tube which is coalesced with the inner bone layer dorsally and the external bone layer (for explanation of these bone layers see p. 93 ventrally at the bottom of the hæmal groove (Fig. 2). In the anterior part of the hæmal groove the notochord has pressed the external bone layer downwards as a ridge, the notochordal ridge (*ch.w*), which is conspicuous when the hæmal groove is seen from below or in transverse section (Figs. 1, 2B; Pl. XXVIII, fig. 4).

The slight development of the cephalic portion of the notochord of the fish, forms, it seems to me, a support for the view advanced above, that there was a kind of articulation between the head and the body as in typical Arthrodires. (ADAMS 1919, pp. 123-127; DEAN 1901, Figs. pp. 116-117; EASTMAN 1908a, pp. 113-149; 1908b, pp. 158-205; JAEKEL 1902, p. 106; 1907, p. 171; 1919, pp. 96-108; etc.) Such an articulation required of course a considerable weakening of the notochord at the transition between the vertebral column and the occipital region of the neurocranium, and if such a weakening took place the cephalic portion of the notochord must evidently have lost its importance and decreased in width and extension, just as it has done in recent Chimæroids, which, as we know, have a sort of cranio-vertebral articulation.

From its very considerable length it would be expected that the posterior division of the region consisted of a rather large number of coalesced segments, and, accordingly, that it was pierced by numerous canals for spino-occipital nerves. No canals of this kind could, however, be found on the material investigated, and it is therefore impossible at present to decide anything with certainty concerning the number of segments composing the division.

The anterior division of the region, if we now proceed to this (Figs. 1, 3, 5; Pls. XIX-XXIV; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1, 2; Pl. XXVII, fig. 1), is, as already pointed out, much shorter, but, on the other hand, considerably higher and broader than the posterior one. Anteriorly, its dimensions are equal to those in the adjacent part of the labyrinth region, so that it is really in no way marked off from this. The postero-latero-dorsal corner of each side is produced backwards and laterally to a rather large process supporting the lateral parts of the dermal cranial roof.

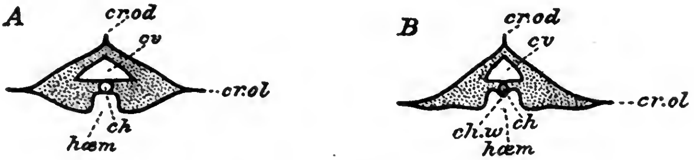

Fig. 2. MACROPETALICHTHYS RAPHEIDOLABIS

A. Transverse section through the anterior part of the posterior half of the posterior division of the occipital region.

B. Transverse section through the anterior half of the same division (accordingly taken posterior of A).

After specimens in the American Museum, New York. Bone layers with black, continuous lines. Cartilage dotted. ×1.

ch, cavity for the chorda dorsalis; *ch.w*, ridge in the hæmal groove caused by the chorda dorsalis; *cr.od*, dorsal occipital crista; *cr.ol*, lateral occipital crista; *cv*, cavum cerebrale cranii; *hæm*, hæmal groove.

For the detailed description we may conveniently consider that the anterior division of the region is composed of five walls, which are as follows: a ventral, a posterior, a right and a left lateral and a dorsal. Of these the ventral, the dorsal, and the two laterals are, as is evident from the figures, directly continuous with, and in no way marked off from, the correspondingly situated ones in the labyrinth region.

The ventral wall, which is the smallest one of the five, is as a whole narrow in comparison with the dorsal, although it rapidly increases in width forwards (Fig. 1; Pls. XXI-XXIII). As is well shown in Pl. XXIII; Pl. XXV, figs. 1, 2, and Pl. XXVI, figs. 1, 2, it is strikingly thin, especially in the median parts, and, as already pointed out, the notochord was entirely reduced in it. It is not pierced by any canals and has its external (ventral) surface, the shape of which may be understood from text fig. 1, well bounded along each lateral border by a sharp edge.

The posterior wall (Fig. 3; Pl. XXIV, fig. 3; Pl. XXV, fig. 2; Pl. XXVII, fig. 1) is large and mostly rather thick. Its ventro-median parts are coherent with the posterior division of the region, its dorso-median parts are a little inclined forwards and its lateral parts stand approximately vertical or may, most laterally, be inclined a little backwards. The wall is covered by the external bone layer on the outside and the internal bone layer on the inside, as are also the other walls, but, as mentioned above, it is, in addition, provided with a few sagittally running bone laminæ (*ls*, Pl. XIX; Pl. XXV, fig. 2), which connected the internal and external bone layers with one another. These bone laminæ in the fresh specimens traversed the cartilage.

The external surface of the posterior wall has, as is seen from Pl. XXIV, fig. 3, a considerable extension, which faces a little upward in the dorso-medial parts and straight backward or backward and a little downwards in the lateral parts. It is concave both in the transversal (Figs. 1, 3, 5; Pls. XIX-XXIV; Pl. XXVII, fig. 1) and dorso-ventral directions and by an anterior extension of the crista occipitalis dorsalis (*cr.od*) dorsally, and the posterior, narrow division of the region, vertically, it is divided into a right and a left half. The internal surface of the same wall, that is lower and narrower than the external one, faces forward and downward (Fig. 11; Pl. XX; Pl. XXIV, fig. 3; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1, 2) and, like the external one, is slightly concave both in transversal and dorso-ventral directions.

The posterior wall is perforated by a paired, rather wide, postero-laterally running canal (*n.l*, Figs. 1, 10, 11; Pl. XXIV, fig. 3; Pl. XXVII, fig. 1), which has its external opening rather far laterally on the external surface of the wall. This canal is, as will be evident from facts given below, a branch from the wide vagus canal (X_{vn}) and transmitted the n. lineæ lateralis.

The dorsal wall (Fig. 3; Pls. XIX, XX; Pl. XXIV, figs. 1, 3; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1, 2) has a very considerable breadth in relation to its length. In its median part it is rather thin, but grows rapidly thicker towards the lateral parts. It is much arched in transversal direction so that the convexity faces upwards. As has already been pointed out, it has no external bone layer (Fig. 3) and no definite external boundary. Despite this, it is, however, fully evident that its upper surface had no fossæ or depressions for portions of the trunk muscles penetrating from behind, beneath the dermal bones, for the external bone layer of the posterior wall has no emarginations in its upper border and reaches in all its breadth quite up to the lower surface of the dermal bones above it. (Pl. XXIV, fig. 3.) The sensory canals of the cranial roof being, as we shall see, situated in rather strongly developed ridges on the lower side of the dermal bones, the upper surface of the dorsal wall of the primordial neurocranium must have had grooves for these ridges in the way shown in text figs. 3 and 5. These grooves in the subsequent description will be referred to as sensory canal grooves. (In the Field Museum specimen (Pls. XIX, XX; Pl. XXIV, fig. 1) the dermal bones of the cranial roof with the exception of those parts situated deepest, namely, the sensory canal ridges, have weathered away, so that we can from the conditions there easily see that the sensory canal ridges must have been situated in grooves on the upper side of the primordial neurocranium).

The canal for the n. lineæ lateralis (*n.l.*), during its passage through the posterior wall of the division, gives off several fine branches in a more or less straight dorsal direction. These fine branches (ld_1-ld_6, Pls. XIX, XX; Pl. XXIV, fig. 3; Pl. XXVII), which number at least six and are surrounded in their total length by a thin bone layer, pass upward through the dorsal wall and open into an overlying portion of the sensory canal system, thus having a course that fully proves them to have transmitted lateralis fibres and that the canal from which they are given off was traversed by a thick lateralis nerve. As the latter canal is the only one that issues backward from the vagus canal, and, in addition, as we shall see, forms the sole possible way backward to the abdominal region for all the lateralis fibres that accompanied the vagus roots proper at the exit from the cavum cerebrale cranii, it undoubtedly transmitted the whole n. lineæ lateralis. The portion of the sensory canal system of the head innervated from it is thus the cephalic division of the main lateral line (Cf. the description of the sensory canal system below). In the Field Museum specimen, in which the dermal bones of the cranial roof have weathered away and certain parts of the underlying dorsal and posterior walls of the primordial neurocranium have split off, the canal for the n. lineæ lateralis and its dorsal branches are, as may be seen in the figures mentioned, beautifully displayed.

Some distance medially of these dorsal branches, a rather fine, paired canal (*cl*, Figs. 3, 5; Pls. XIX, XX) goes upward through the dorsal wall and, after arriving close to the upper surface of this, turns abruptly medially, continuing in this direction almost until it meets its fellow of the opposite side in the median line. During this superficial, medially directed, part of its course it sends out several branches both forward and backward. It could not be traced quite to its ventral end and hence a positive explanation of its function can not be given. It seems most probable, however, that it transmitted bundles of communis and general cutaneous fibres from the vagus to the cranial roof, and thus transmitted a ramus supratemporalis vagi. Besides this it may perhaps also have been traversd by vessels and, in addition, perhaps by a branch of lateralis fibres, as it communicated with the canal for the n. lineæ lateralis by a fine branch. The destination and morphological importance of this possible bundle of lateralis fibres will be discussed below in connection with the description of the sensory canal system.

The lateral walls of the division (Figs. 1, 5; Pls. XXI-XXIII; Pl. XXIV, figs. 1, 2; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1-4; Pl. XXVII, fig. 1) are thick throughout their extension, the thickness being, however, not equal in all parts but gradually increasing upwards. They are covered by the external bone layer on the outside and the internal bone layer on the inside. Each has its external surface directed laterally and much downwards and its internal surface almost straight medially. A distinct but rather narrow groove (*s.ra*) runs along the ventral edge of the external surface, a groove, which, as we shall see, continues forward on to the external surface of the lateral wall of the labyrinth region and backwards to the hæmal groove, at the anterior end of which it meets its fellow of the opposite side in the median line. This groove undoubtedly lodged the radix aortæ (lateral dorsal aorta) of its side, as will be evident from the account of the labyrinth region given below.

At the transition to the labyrinth region, each lateral wall is pierced by the vagus canal. This canal (X_{vn}, Figs. 5, 10, 11, 12, 13; Pls. XX, XXI; Pl. XXIV, fig. 2; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1-4; Pl. XXVII, fig. 1), which is wide and on account of the thickness of the lateral wall at this place has a fairly considerable length, runs almost straight laterally to the external surface of the lateral wall, where it opens with a wide, rather forward facing foramen (X_{vn}, Figs. 1, 5; Pls. XXII, XXIII; Pl. XXIV, figs. 1, 2). A proximal short part of it is much higher than broad (Pl. XXV, figs. 1, 2; Pl.

XXVI, figs. 1, 2) and exhibits no certain evidence of subdivision by longitudinal septa.

On the other hand the remaining distal, and by far longer, part, has a more circular section than the former and is subdivided into two incompletely separated divisions, a narrow and a wide one, by two longitudinal ridges, divisions which perhaps in the living animal were totally separated from each other by a membrane of connective tissue extending between the ridges. In the proximal part of the distal half of

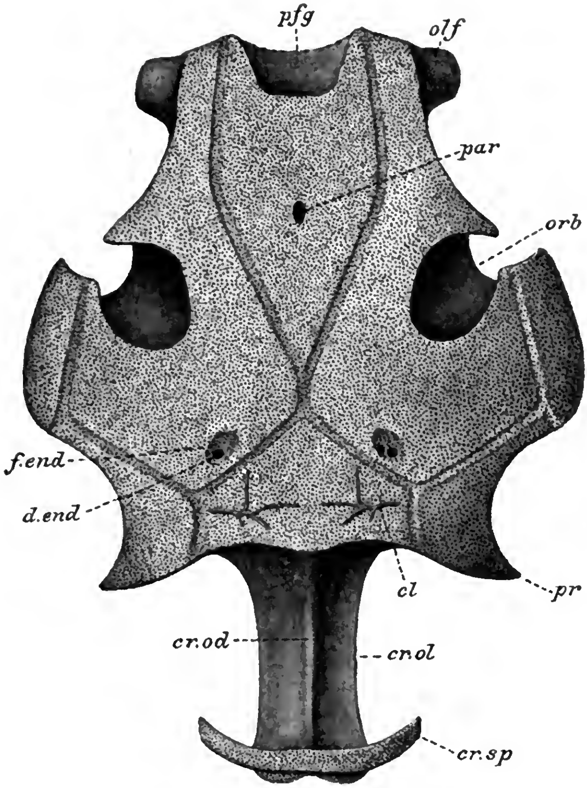

Fig. 3. MACROPETALICHTHYS RAPHEIDOLABIS

Primordial neurocranium in dorsal view. Occipital region after specimens in the American Museum, New York, and a specimen in Field Museum, Chicago; other regions after the latter specimen. Perichondral bone with a dark tone. Cartilage dotted. ×½.

cl, canal probably for a dorsal branch of the vagus and a bundle of lateralis fibres; *cr.od,* dorsal occipital crista; *cr.ol,* lateral occipital crista; *cr.sp,* craniospinal process; *d.end,* canal for the ductus endolymphaticus; *f.end,* fossa endolymphatica; *olf,* olfactory capsule; *orb,* orbit; *par,* pineal opening; *pfg,* cavum precerebrale; *pr,* postero-lateral process of the anterior broad division of the occipital region.

the canal the narrow division (X_v, Fig. 11; Pl. XXIV, fig. 2) is situated dorsally of the wide one (X_n, Pl. XXIV, fig. 2), but during the passage outwards they gradually change their mutual position so that the former finally lies behind the latter and occupies the posterior portion of the common external opening, which is distinctly broader than high. (Pl. XXIV, fig. 1.)

From conditions in other fishes we may conclude with great probability that in *M. rapheidolabis* the narrow one of the two divisions just described in the vagus canal transmitted the vena cerebralis posterior (v. encephalica posterior) and the wide one the vagus proper and in the proximal half the n. lineæ lateralis too. For the vena cerebralis posterior in all fishes which have been closely investigated with regard to this, arises by the confluence of anterior and posterior branches from the dorsal side of the medulla oblongata and enters the cranial wall dorsally of the vagus roots. It then within the cranial wall usually turns a little forward and crosses the vagus roots on the dorsal side so that when reaching the outer surface it is situated just in front of these roots and not as in *M. rapheidolabis* posterior to them. In certain forms it runs through the same canal with the vagus roots, in other forms it is more or less completely separated from them by a septum of bone, cartilage or connective tissue. (Cf. STENSIÖ 1922, p. 172; 1925, p. 21; GROSSER 1907, Fig. 4; O'DONOGHUE 1914, p. 442; POLLARD 1892a, Pl. XXIX, fig. 23; ALLEN 1905, pp. 87-89; REX 1891, Pls. 15, 16; etc.) Similar conditions were also found in a specimen of *Chimæra monstrosa,* which was dissected by me.

During the passage through the lateral wall, the vagus canal in *M. rapheidolabis* gives off from its proximal half two branches, one on the posterior and the other on the anterior side. The former of these (*n.l,* Figs. 10, 11; Pls. XXI, XXIII; Pl. XXIV, fig. 3; Pl. XXVII, fig. 1), which issues rather low, is the canal for the n. lineæ lateralis and has already been dealt with above in connection with the description of the posterior and dorsal walls. As pointed out there, it runs postero-laterally to the outer surface of the posterior wall, sending out several fine branches upwards to the cephalic division of the lateral line. The other branch (d_x, Figs. 10, 11; Pl. XXIV, fig. 2), which is much narrower and issues much higher up and more proximally, runs some distance almost straight dorsally, then not so very deep below the dorsal surface of the dorsal wall, bifurcating into an antero-lateral (d_{xa}, Pl. XXIV, fig. 2) and an antero-medial (d_{xb}, Pl. XXIV, fig. 2) ramus, each of which has a superficial course beneath a sensory canal division, to which fine ramuli are sent out in a dorsal direction (Pl.

XXIV, fig. 2). And, as it is fully evident that these ramuli must have transmitted nerves to the sensory canal organs, the anterior branch (d_x) from the vagus canal is consequently proved to have transmitted a dorsal branch from the n. lineæ lateralis. The relations of this dorsal lateralis branch will be treated also in the description of the sensory canal system below.

Into the proximal half of the vagus canal and, more exactly, into the dorsal part of this just as it leaves the cavum cerebrale, there opens a wide canal (*v.lb,* Figs. 10, 11; Pl. XX, XXIV, fig. 2; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1, 2, 3), which comes from the postero-dorso-medial corner of the labyrinth cavity. The function of this canal is not fully clear, but it seems very probable that it transmitted a vein from the labyrinth to the vena cerebralis posterior, because in the *Lorcati*—the only teleostomous fishes investigated in detail with regard to the veins of the head—there is a small vein which goes from the labyrinth in a similar way back to the v. cerebralis posterior (ALLEN 1905, Pl. III, figs. 23a, 23, 25). This vein in the *Loricati* receives blood, as it seems, merely from the ampulla posterior, while the presumed vein in question in *M. rapheidolabis,* to judge from the large width of the canal *v.lb,* must have received blood from the larger part or the whole of the membranous labyrinth.

At the transition between the anterior and posterior divisions of the region, the external bone layer on both the ventral and dorsal side seems to show a certain very faint radiation from a median unpaired centre. Hence, if this observation is true, there would be two unpaired, vestigial centres of ossification in the region, the dorsal one of which would correspond most closely to the centre of a supraoccipital bone, the ventral one to the centre of a basioccipital bone. Better preserved material than that investigated by the author is, however, needed for a positive decision in this case.

The part of the cavum cerebrale cranii enclosed in the anterior division of the region increases rapidly both in height and breadth forwards. Its shape is well shown by Figs. 10, 11, 12, 13, Pl. XX, Pl. XXIII, Pl. XXIV, fig. 3; Pl. XXV, figs. 1, 2 and Pl. XXVI, figs. 1, 2.

LABYRINTH REGION

The labyrinth region is very short and broad, its length being contained about two and a half times in the maximum breadth. It is also rather low, as its maximum height amounts only to between a fourth or a fifth of the maximum breadth. The maximum height is situated far back, almost at the transition to the occipital region, the maximum breadth, on the other hand, in the anterior half of the region (Figs. 1, 3, 4, 5; Pls. XIX-XXI, XXIII; Pl. XXIV, figs. 1, 3; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1, 2). As shown by the figures, the region is arched both transversally and longitudinally, so that the dorsal side is convex and the ventral side concave, the arching being, however, stronger in the former than in the latter direction. The antero-lateral corner of each side projects forwards as a large postorbital process, forming not only a posterior but also to a large extent a lateral boundary of the orbit, a disposal which is due to a postero-medial displacement of the orbit. The postorbital process is ventrally, throughout its length, continuous with the extensive orbital floor (Figs. 3, 8).

For the detailed description we may consider the region to be composed of four walls: a ventral, a dorsal and a paired lateral.

The ventral wall, if we first turn to it (Figs. 1, 4, 5; Pls. XXI, XXIII; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1, 2, 3), is comparatively thin throughout almost its entire extension, but is thinnest in the median parts. At the transition to the occipital region it is fairly narrow, but grows rapidly broader forwards, finally attaining a very considerable width. It is covered both by the internal and external bone layers and perforated by certain canals in the lateral parts at the transition to each lateral wall. These canals will, however, not be described here, but in connection with the lateral walls, which are also perforated by them.

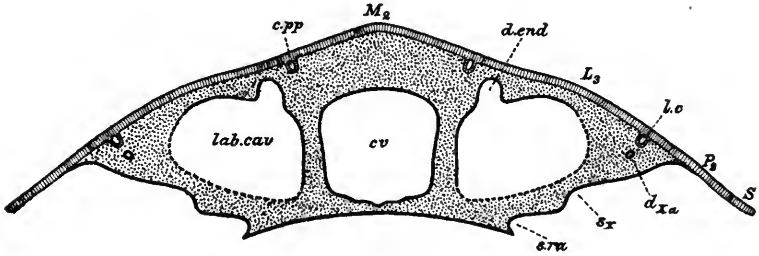

Fig. 4. MACROPETALICHTHYS RAPHEIDOLABIS

Transverse section through the posterior part of the labyrinth region. Dermal bones marked with vertical lines. Layers of substitution bone with continuous black lines. Cartilage dotted. ×¾.

M_2, L_3, P_2, S, bones of the dermal cranial roof (approximate extensions). For their position cf. text fig. 15. *c.pp,* sensory canal commissure, probably corresponding to the posterior head line of pit organs in fishes in general; *cv,* cavum cerebrale cranii; *d.end,* canal for the ductus endolymphaticus (ventral part); d_{xa}, the antero-lateral branch of the canal d_x, which transmitted a lateralis branch to the above-lying sensory canal; *lab.cav,* labyrinth cavity; *lc,* cephalic division of the lateral line; *s.ra,* groove for the radix aortæ (lateral dorsal aortæ); S_x, groove leading some distance forward from the external opening of the vagus canal.

The dorsal wall of the region (Figs. 3, 4, 5; Pls. XIX, XX, XXIV; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1-3) is broad throughout its extension, its breadth being, however, larger in the anterior than in the posterior half. With the exception of its lateral parts, situated above the labyrinth cavities, the wall must have been rather thick, and, as pointed out already in the general description of the neurocranium, it was covered only by the internal bone layer, so that the dermal bones of the cranial roof rested on its cartilage. The external (dorsal) surface must have had rather pronounced grooves for the sensory canal ridges on the lower sides of the dermal bones of the cranial roof, as indicated in text figs. 3, 4 and 5. Far back on the dorsal surface there may, in addition, have been a paired pit (*f.end*) at the bottom of which the canal for the ductus endolymphaticus (*d.end,* Fig. 3; Pl. XX; Pl. XXVI, fig. 3) opened, for this canal does not seem to extend fully up to the ventral side of the overlying dermal bones (Pls. XIX, XX). In other words, there seems to have been a fossa endolymphatica.

Besides by the canal for the ductus endolymphaticus mentioned, which will be described more in detail below in the account of the labyrinth cavity, the dorsal wall must have been pierced by several fine canals for vessels and nerve branches. Two of these, both for lateralis branches to a portion of a sensory canal, are well seen in the Field Museum specimen (*in,* Pls. XX, XXII).

The lateral wall of each side is very thick, especially in its dorsal and anterior parts, and is covered by both the internal and external bone layers (Figs. 1, 3, 4, 5; Pls. XX, XXI, XXIII, XXIV). In its interior it contains the large labyrinth cavity (*lab.cav,* Fig. 4; Pl. XX; Pl. XXVI, figs. 3, 4; Pl. XXVII), which is completely separated from the cavum cerebrale cranii by a rather thick septum of cartilage, covered by the internal bone layer on the cerebral surface and the labyrinth bone layer on the labyrinth surface. The internal surface of the wall is directed almost straight medially. The external one consists of two fields, an anterior and a posterior one, the latter of which faces ventrally to a marked degree, while the former, which forms the posterior surface of the orbital cavity, faces mainly forwards. The two fields are separated from each other by a rounded edge running from the antero-dorsal corner of the postorbital process a short distance in a ventral direction. By another, although indistinct dorso-ventral edge the posterior field is in its turn subdivided into an anterior and a posterior part, the former of which is convex both in dorso-ventral and antero-caudal directions and faces almost straight downwards, while the latter, on the contrary, is concave in the same directions and faces much less downwards, but in addition a little backwards (Figs. 1, 4, 5; Pls. XXI, XXIII, XXIV). On the latter part we find along the ventral border the anterior continuation of the groove *s.ra* (Figs. 1, 4, 5; Pls. XXI-XXIV) already referred to above in the description of the lateral wall of the anterior division of the occipital region, and at the transition to the anterior part of the same field this groove deepens and is suddenly transformed into a closed canal (*c.ra*), which goes forward in the wall. We shall below return to this canal (*c.ra*) and the groove (*s.ra*) leading to it and try to make out what their functions were. Before doing this we must, however, examine the canals for cranial nerves that perforate the lateral wall, beginning with the glossopharyngeus canal and proceeding forwards.

The glossopharyngeus canal (IX, Figs. 1, 5, 7, 10, 11; Pls. XXI-XXIII; Pl. XXIV, figs. 1, 2; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1, 2, 4; Pl. XXVII), which is fairly narrow, has its internal opening situated rather far anterior of the vagus canal and much nearer to the floor than to the roof of the cavum cerebrale cranii. It seems to go almost straight laterally to the posterior lower part of the labyrinth cavity, continuing from this cavity with about the same direction as before to the external surface of the lateral wall, where it opens in the anterior part of the groove *s.ra,* and accordingly close to the ventral edge of the surface. The external opening is incompletely subdivided into two divisions (Figs. 1, 5; Pl. XXIV, fig. 1), an anterior and a posterior one, the latter of which is slightly smaller than the former.

Somewhat dorsally of the external opening of the glossopharyngeus canal there are traces of another, although finer, canal (d_{ix}, Fig. 1; Pls. XXI, XXIII; Pl. XXIV, figs. 1, 2; Pl. XXVII), which seems to run upwards to a portion of a sensory canal, piercing during its passage the dorsal part of the lateral wall and the overlying lateral part of the dorsal wall. Accordingly, this canal has a course which seems to indicate that it may have contained a lateralis nerve. And as it is situated almost straight above the external opening of the glossopharyngeus canal, we may conclude with a rather high degree of probability that this lateralis nerve arose from fibres which had their passage through the lateral wall, together with the n. glossopharyngeus, as is the case in several other recent and fossil fishes, e.g. *Selachii.* (EWART and COLE 1895, pp. 475-476; NORRIS and HUGHE 1920, p. 358, Figs. 51, 52, 53), *Polypterus* (POLLARD 1892a, p. 397, Pl. 28, fig. 13; LEHN 1918, pp. 395-396; ALLIS 1922a, pp. 283-284), *Lepidosteus* (VEIT 1907, p. 187; 1911, Pl. D, figs. 2, 6, 10), *Amia* (ALLIS 1897, p. 684), *Acipenser,* *Polyodon* (ALLIS 1920, pp. 138, 142; observations made by the author: cf. also STENSIÖ 1924), *Saurichthys* (STENSIÖ 1925) and certain Teleostei (HERRICK 1901, pp. 207-208, Pl. XIV). In other fishes in which the conditions are known, the corresponding lateralis fibres pass through the vagus canal associated with the n. lineæ lateralis.

The possible lateralis branch which has just been dealt with may perhaps be thought to have caused the bipartition of the external opening of the glossopharyngeus canal. And, if so, it seems probable that the n. glossopharyngeus proper passed through the larger anterior and the lateralis nerve through the smaller posterior division of the opening.

The canals for the n. acusticus (VIII) and the n. facialis (VII) begin proximally in a common, distinct recess (*afr,* Figs. 10, 11; Pl. XXIII; Pl. XXV, figs. 1, 2; Pl. XXVI, fig. 2) on the ventral part of the lateral side of the cavum cerebrale. This recess, which may be properly termed the acustico-facialis recess, communicates in the fossil freely with the cavum cerebrale, but was perhaps in the fresh specimens separated from this by a membrane belonging to the dura mater. For comparison, it may here be mentioned that a recess of a similar kind occurs in several recent fishes, but that in these it often has a larger extension forward so that not only the acusticus and facialis canals but also the trigeminus canal take their origins from it. On account of this fact it is called in such forms the acustico-trigemino-facialis recess, and it may further be noted that it sometimes is separated there from the cavum cerebrale by a thin lamina of connective tissue or bone, a lamina formed by the dura mater. (Cf. ALLIS 1909a, pp. 44, 46-47, 124; 1914a, pp. 232-236, 239, 240, 243, 246-248; 1914b; 1919a; 1922a, p. 228.)

The acusticus canal (VIII) of *M. rapheidolabis,* which is rather wide, goes from the posterior part of the acustico-facialis recess almost straight laterally to the labyrinth cavity, piercing the ventral part of the septum that separates the labyrinth cavity and the cavum cerebrale from one another. Its position in relation to the labyrinth cavity is shown by Pl. XXVI, fig. 3, in which the septum separating that cavity from the cavum cerebrale, however, has been almost entirely removed.

The facialis canal (VII), which is of about the same width as the acusticus canal, issues from the anterior part of the acustico facialis recess (Figs. 10, 11; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1, 2). On account of the thickness of the lateral wall at this place it gets a considerable length. It runs first for some distance forward and slightly laterally close to the antero-ventral part of the labyrinth cavity (Figs. 10, 11; Pl. XXV, fig. 1; Pl. XXVI, fig. 3), then at the antero-ventro-medial corner of this cavity it suddenly takes a more lateral and ventral direction (Figs. 10, 11; Pl. XXV, figs. 1, 3; Pl. XXVI, figs. 3, 4) and continues with this course to the external opening (text fig. 1; Pls. XXI-XXII; Pl. XXIV, fig. 1), close posterior to the antero-ventral corner of the posterior field of the external (lateral) surface of the lateral wall. The more laterally and ventrally running part is situated immediately anterior of the labyrinth cavity between this and the orbit. As may be understood from Pl. XXVI, fig. 3, the part of the lateral wall separating the orbit and labyrinth cavity from one another is rather thin.

Approximately at the place where it turns more laterally and downward, the facialis canal gives off from its antero-dorsal parts a rather wide branch in an antero-dorsal direction. This branch (*c.ophth.lat,* Figs. 8, 10, 11; Pl. XXIII; Pl. XXV, figs. 1-3) soon enters the orbitotemporal region, ascending there after a short distance to the dorsal wall and continuing forward into the ethmoidal region rather close below the upper surface of this. In almost the whole orbitotemporal region and throughout the ethmoidal region it goes rather straight beneath the supra-orbital sensory canal to which fine rami issue from it (*rm.ophth.lat,* Pls, XXI, XXIII), a fact which fully shows that it lodged the n. ophthalmicus lateralis. It may, therefore, properly be called the canalis n. ophthalmici lateralis. In the subsequent description we shall return to it and its importance for the understanding of the trigemino-facialis ganglionic complex.

Not far distally of the canalis n. ophthalmici lateralis, a second branch issues from the facialis canal, but on the antero-ventral side. This branch (*c.bucc.lat,* Figs. 10, 11), which has almost the same calibre as the canalis n. ophthalmici lateralis, goes forward and opens into the trigeminus canal, and, as the trigeminus and facialis canals lie close to each other at this place, it is rather short. As will be evident from my subsequent account of the trigemino-facialis ganglionic complex, the canal transmitted certain lateralis fibres, viz., those that formed the n. buccalis lateralis.

A third, wide, but short branch (*c.pal*[1], Figs. 10, 11) is given off from the facialis canal close to the external opening. This branch runs forward to the postero-ventro-lateral corner of the orbit, and, as will be shown below, the conditions are such that it must have been pierced by the r. palatinus facialis.

It has already been pointed out above, that the fine but pronounced

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[1] This branch was discovered by preparation after the photographs had been taken and is therefore not shown in the plates.

groove *s.ra,* along the ventral border of the external (lateral) surface of each lateral wall deepens and is transformed into a canal a short distance anterior to the external opening of the glossopharyngeus canal, the canal arising in this way (*c.ra,* Figs. 1, 5, 7; Pls. XXI-XXIII) being fairly narrow. Not far dorsally of this canal is found the posterior opening (ju_2) of another much wider canal (*ju,* Figs. 1, 5, 7; Pls. XX-XXIII). These two canals, which we, after their index letters in the previous figures, may refer to as *c.ra,* and *ju* respectively, go forward within the lateral part of the lateral wall, where they soon meet and join to a wide sinus (*si,* text fig. 7; Pls. XXI-XXIII). In this sinus there may be distinguished a wide, dorsal division corresponding to the canal *ju* and a narrow, ventral division corresponding to the canal *c.ra.* Although very imperfectly separated from one another, these divisions indicate that the structures traversing the two canals *ju* and *c.ra,* retained their independence and original positions in the sinus, *si.*

The ventral division of the sinus *si,* is continued forward by a canal which is lettered *c.com* in the figures (Fig. 7; Pls. XXI, XXIII) and which runs in an anterior and slightly medial direction at the transition between the lateral and ventral walls of the region. It is also noteworthy that this canal (*c.com*) has a very superficial position, as it is situated wholly within the external bone layer. After a short course forward it divides into two branches of about equal calibre, a lateral one (*c.car.ext*) and a medial one (*c.car.int*). The former of these runs latero-dorsally through the lateral wall and opens close to and postero-ventrally of the facialis canal (Figs. 1, 7; Pls. XXI, XXIII), while the latter takes a course forward and slightly medially to the orbitotemporal region. The former of these branches is throughout its extension situated within the external bone layer (Fig. 8), as is also the latter till it reaches the anterior end of the orbitotemporal region (Fig. 8), where it suddenly leaves the external bone layer and ascends into the cartilaginous interior of the ventral wall in the manner that will be described below in the account of the orbitotemporal region. As we shall find from its course, the latter branch (*c.car.int*) must have lodged the arteria carotis interna and is therefore termed the internal carotid canal. This being the case, it is easy to understand that the other branch (*c.car.ext*) must have been traversed by the arteria carotis externa. (Cf. ALLIS 1897, pp. 497-500; 1908a; 1908b; 1909a, pp. 51-55, 185-187; 1909b; 1911a; 1911b; 1912a, b, c, d; 1914a; 1914b; 1919a, 1922a, pp. 266-268; 1922b; ALLEN 1905, pp. 51-62; DANFORTH 1912, pp. 435-445; GREIL, 1913, Pl. LV, fig. 2.) Hence this may properly be termed the external carotid canal.

The branches of the canal *c.com,* having had these functions, it is evident that the canal *c.com* itself must have lodged the arteria carotis communis. From the canal *c.com,* the arteria carotis communis may have continued a short distance backwards into the ventral division of the sinus *si,* there probably, as we shall see, having received the arteria efferens hyoidea and having become the radix aortæ (lateral dorsal aorta). The radix aortæ must then have traversed the remaining posterior part of the ventral division of the sinus *si* behind this, continuing through the canal *c.ra,* and the groove *s.ra,* to the anterior end of the hæmal groove (*hæm*). At the anterior end of this it probably met its fellow of the opposite side and joined with it to the unpaired aorta dorsalis, which in its backward course occupied the hæmal groove. The efferent arteries from the two or three anterior branchial arches may probably have emptied into the radix aortæ of their side, while those from the remaining posterior branchial arches probably opened into the anterior portion of the aorta dorsalis. My view concerning the course and mutual relations of the arterial trunks mentioned is further elucidated by the diagrammatic sketch reproduced in Fig. 6, and as is evident from this the arterial system of the head seems to

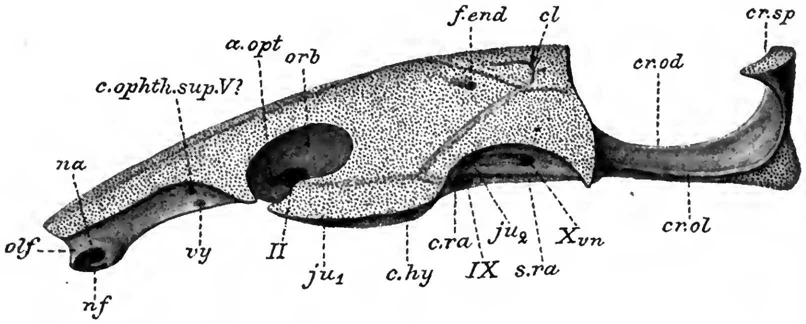

Fig. 5. MACROPETALICHTHYS RAPHEIDOLABIS

Primordial neurocranium in lateral view. Occipital region after specimens in the American Museum, New York, other regions after a specimen in Field Museum, Chicago. Bone dark, cartilage dotted. ×½.

a.opt, division of the distal part of the opticus canal, probably for the arteria optica; *c.hy,* canal for the v. hyoidea; *c.ophth.sup.V?,* canal probably for the r. ophthalmicus superficialis trigemini; *cr.od,* crista occipitalis dorsalis; *cr.ol,* crista occipitalis lateralis; *cr.sp,* cranio-spinal process; ju_1, anterior opening of the canal *ju.* The opening was traversed by the vena mandiburalis; ju_2, posterior opening of the canal *ju; na,* nasal aperture; *orb,* orbit; *s.ra,* groove for the radix aortæ; *vy,* canal of doubtful importance; either for vessel or nerves or for both; II, opticus canal; IX, glossopharyngeus canal; X_{vn}, canal for the n. vagus and the vena cerebralis posterior.

resemble mostly that in *Chimæra* (ALLIS 1912a). The arteria carotis interna will be further treated below in the description of the orbitotemporal region.

Turning again to the canal *ju*, we find that anterior to the sinus *si* (Fig. 7; Pls. XXI, XXIII) it takes a more lateral direction than in its posterior part. It opens with its anterior opening (ju_1) on the

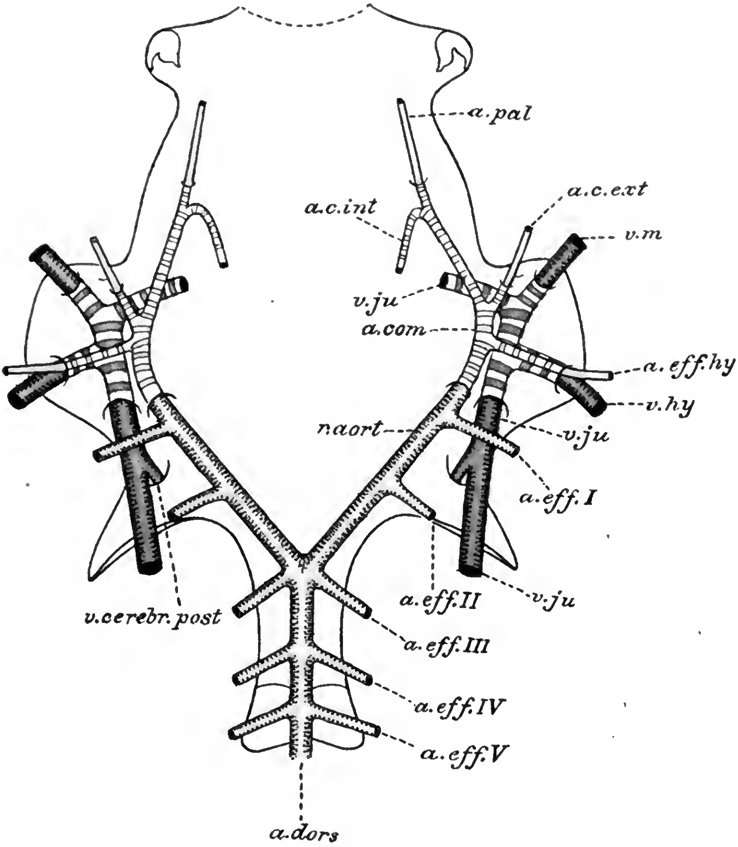

Fig. 6. MACROPETALICHTHYS RAPHEIDOLABIS

Diagrammatic sketch of the main, arterial and venous trunks of the primordial neurocranium. Outlines of neurocranium in ventral view. Arteries red, veins blue. The parts of the different vessels situated in canals or cavities indicated by transversal bands of color. ×½.

a.com, arteria carotis communis; *a.c.ext,* arteria carotis externa; *a.c.int,* arteria carotis interna; *a.eff.hy,* arteria efferens hyoidea; *a.eff.I-a.eff.V,* efferent arteries of the branchial arches I-V; *a.dors,* aorta dorsalis; *a.pal,* possible palatine branch of the a. carotis interna; *r.aort,* radix aortæ; *v.cerebr.post,* vena cerebralis posterior; *v.hy,* vena hyoidea; *v.ju,* vena jugularis; *v.m,* vena mandibularis (from the dorsal parts of the mandibular arch to the jugular vein).

external (lateral) surface of the lateral wall rather close laterally to the facialis canal. With the part situated anterior of the sinus *si,* it joins on the medial side a fairly wide canal *jg,* which comes from the postero-latero-ventral corner of the orbit, perforating in its course backwards the ventral portion of the postorbital process. This canal, *jg,* does not, however, run straight backwards but postero latero-ventrally and crosses in its course the distal part of the facialis canal on the dorsal side. Its position may be understood from Pl. XXI, Pl. XXII, Pl. XXV, figs. 1, 3, and Figs. 6, 7. (In Pl. XXIV is seen a section of it just after it has crossed the facialis canal; in Pl. XXV, fig. 1, it is seen crossing the facialis canal on the dorsal side, and it is also obvious that the bone layer lining it is continuous proximally with the part of the external bone layer that covers the posterior surface of the orbit; Pl. XXV, fig. 3, shows the same part of it as the preceding figure but from behind.)

From the conditions in recent fishes it is not difficult to conclude what the functions of the canals *ju* and *jg* were. Both must have been traversed by veins. The vein that traversed the canal *jg* evidently collected the blood from the eye bulb, the eye muscles and probably also from the anterior parts of the cavum cerebrale cranii. Hence it must have corresponded to the vena jugularis interna according to the terminology mostly employed hitherto. ALLIS has, however, recently proposed to call this vein simply the jugular vein, a term that I shall adopt here as I have done in my other works. (Cf. ALLEN 1905, pp. 78-90, Pl. I, figs. 1, 5; Pl. II, figs. 13, 15; Pl. III, figs. 23-25; ALLIS 1897, pp. 500-506; 1903, p. 93; 1908b, pp. 219-222; 1909a, pp. 40, 45, 50, 187, etc.; 1914a; 1914b; 1919a, p. 222, and in several other places throughout the paper; 1922a, pp. 260-264; 1922b, p. 153; GREIL 1913, Pl. 54, fig. 1; Pl. 55, figs. 2, 8 (vena capitis lateralis); GROSSER 1907; LEHN 1918, pp. 365-372; O'DONOGHUE 1914, pp. 438-443, anterior cardinal sinus + postorbital sinus; PARKER, T. J., 1887, pp. 711-713; STENSIÖ 1921, p. 178; 1923, pp. 1244, 1260-1268; 1925.)

A vein of a considerable size must have entered the canal *ju* through the anterior opening ju_1. As far as can be judged, this vein collected the blood from the palatoquadrate and perhaps also from certain parts of the ethmoidal region; in other words, it seems to have drained a large dorsal part of the mandibular arch and nearest surroundings. Hence it may be properly termed the vena mandibularis.

The vena mandibularis of the fish so defined, after a short passage backwards within the canal *ju,* met and joined the jugular vein to a common large stem which then passed backwards through the dorsal division of the sinus *si* and the posterior part of the canal *ju* behind this sinus, then continuing along the external surface of the lateral wall of the neurocranium received during this latter part of its course the vena cerebralis posterior as it passed the external opening of the vagus canal. Despite the fact that the vena mandibularis was much larger than the vena jugularis, the common stem described, that arose by its confluence with the latter, must for morphological reasons be considered as the backward continuation of this, and hence throughout its extension it must retain the name of jugular vein. The course and relations of the juglar vein, the mandibular vein and the vena cerebralis posterior seem to have been as indicated in the diagrammatic sketch in Fig. 6.

In the dorsal division of the sinus *si*—thus, after what we have just found, the division for the jugular vein—there opens on the lateral side a short but rather wide canal *c.hy* (Figs. 1, 5, 7; Pls. XX-XXIII; Pl. XXIV, figs. 1, 3), which leads from the external surface of the lateral wall of the region, or, to define it more closely, from the postero-dorsal corner of the anterior part of the posterior field of the lateral surface of the region. From its course and position we may conclude with a rather large degree of probability that it was traversed by a vein. This supposed vein must have come from the hyoid arch and emptied into the jugular vein, thus corresponding partly to the sinus hyoideus of Selachians. I call it here the vena hyoidea.

In Selachians the sinus hyoideus is a large vein which runs upward on the posterior side of the hyoid arch, receiving blood not only from this arch, but also from the dorsal and middle parts of the mandibular arch (PARKER, T. J., 1887, Pl. 35, fig. 10; O'DONOGHUE 1914, pp. 441-442), a condition which explains the fact that a mandibular vein is lacking. In *Polypterus* a hyoid vein seems also to occur (ALLIS 1922a, p. 264), but in *Ceratodus* (GREIL 1913, Pls. 54, 55) and the *Loricati* (ALLEN 1905, pp. 79-80), the dorsal parts of this vein seem to be lacking. At least in the *Loricati* the venous blood of the hyoid arch goes chiefly forward to the mandibular vein, arriving through this into the vena jugularis. In *Ceratodus* the conditions in this respect are not known with certainty. The venous system of other fishes besides those mentioned, is not known in detail and accordingly nothing can be said of the veins in the mandibular and hyoid arches there.

The occurrence of both the vena mandibularis and the vena hyoidea in *Macropetalichthys rapheidolabis* is, it seems to me, to be considered a primitive character, since we may presume that the venous system of fishes originally had a segmental arrangement.

If the interpretation given here of the canal *c.hy* of *Macropetalichthys rapheidolabis* is correct, and if the vena hyoidea during the passage to this canal went approximately as it does in Selachians, it is evident that the dorsal end of the hyoid arch must have articulated against the lateral wall of the region anterior to the external opening of the canal *c.hy*. What this means for views concerning the homologies of the hyomandibular in Selachians and Teleostomes will be dealt with below in the account of the visceral skeleton. It has been mentioned above that the arteria efferens hyoidea ought to have persisted in *M. rapheidolabis,* and if so, it probably, as in recent fishes in which it is found, went upwards along the posterior side of the hyoid arch and emptied into the anterior part of the radix aortæ, which, as we have seen, was situated here within the sinus *si.* After leaving the hyoid arch, the a. efferens in order to reach this sinus must have entered the external opening of the canal *c.hy,* as no other foramen can be found for it. Perhaps it did not, however, traverse the entire canal *c.hy,* but took near the proximal end of this a more anterior course, entering the rather fine canal *c.ef* (Fig. 7; Pls. XX, XXII), which, at least on the left side of the Field Museum specimen, runs from the proximal part of the canal *c.hy* forward, medially and downward to the anterior end of the sinus *si.* If well arrived into the sinus *si* in this way, the artery must have crossed the jugular vein and passed downwards to the ventral division of the sinus, joining there the radix aortæ at the transition to the arteria carotis communis. It may, however, be possible that the canal *c.ef,* instead of being traversed by the arteria efferens hyoidea, as here supposed, transmitted the truncus hyoideomandibularis facialis, and if this was the case, the a. efferens hyoidea must of course have traversed the entire canal *c.hy,* and have entered the sinus *si* much farther back. (ALLEN 1905, pp. 44-62; ALLIS 1908a, b; 1909a, pp. 51-52, 183-184; 1909b; 1911a, b; 1912a, b, c, d; 1922a, pp. 264-268; DANFORTH 1912, pp. 435-445.)

In most fishes in which there is a canal for the jugular vein in the lateral wall of the neurocranium, the jugular vein is generally during its passage through this canal accompanied for some distance by the truncus hyoideomandibularis, which enters the canal either from in front through the anterior opening or from the medial side. In the former case the truncus hyoidemandibularis has its exit through the cranial wall anterior to, in the latter case into the canal for the jugular vein. (Cf. ALLIS 1897, pp. 492-497; 1903, pp. 87-95, 266; 1908b, pp. 219-222; 1909a, pp. 44-45; 1911a, p. 291; 1914a; 1914b;

1919a; 1922a, pp. 263-264; 1922b; LEHN 1918, pp. 363-372; POLLARD 1892a, Pl. 30, figs. 27-30; STENSIÖ 1921, p. 178; 1923, pp. 1244, 1261, 1262-1268; 1925; etc.)

Concerning *M. rapheidolabis,* we cannot say at present whether the truncus hyoidemandibularis after its exit from the facialis canal definitely left the cranial wall or whether it again entered the cranial wall accompanying the vena jugularis for some distance. If the former of these alternatives were true, the truncus hyoidemandibularis would have left the cranial wall rather far anterior of the hyoid arch and would thus have reached this from in front in the same way as in Selachians. (Cf. RUGE 1897, Figs. 3, 12, 13, 14; GOODRICH 1909, Fig. 44; ALLIS 1915; 1918b; cf. also VAN WIJHE 1882, Pl. 15, figs. 1, 3, 4, 6; etc.) If, on the other hand, the latter were true, it is at once evident that the truncus hyoideomandibularis cannot have entered the anterior opening of the canal *jg* for the jugular vein, (as we have found, this opening is situated in the orbit, while the external opening of the facialis canal lies on the lateral surface of the lateral wall behind the orbit), but would, together with the vena mandibularis, have passed through the anterior opening (ju_1) of the canal *ju.* In other words, the truncus hyoideomandibularis would, with this alternative, have reached the vena jugularis in the anterior part of the canal *ju,* after traversing the part of this canal situated anterior to the canal *jg.*

Assuming that it did so, it may during its course further backward either have traversed the entire dorsal division of the sinus *si* and behind this the posterior part of the canal *ju,* or may soon after its entrance in the sinus *si* have turned latero-dorsally, entering and traversing the canal *c.ef* and the distal portion of the canal *c.hy.* If it took the former of these courses it would have left the cranial wall considerably behind its arch, the hyoid arch, which, as we have seen, articulated against the lateral wall of the region anterior to the external opening of the canal *c.hy.* It would thus have gone a considerably roundabout way to its destination, which seems rather improbable. If, on the contrary, it passed from the sinus *si* through the canal *c.ef* and the canal *c.hy,* it would, of course, have had its exit from the cranial wall in closer relation to its arch, although still behind this.

The conditions on the external surface of the lateral wall of the region between and around the external opening of the facialis canal and the anterior opening of the canal *ju,* would, perhaps, if they were known in detail, enable us to decide with considerable degree of probability what course the truncus hyoideomandibularis took after leaving the facialis canal[1]. But, unfortunately, the external surface of the wall is not sufficiently well preserved to enable me to determine this in any of the specimens so far investigated by me.

In dealing with the trigeminus and facialis canals below we shall see that the r. oticus lateralis must have originated in the proximal part of the facialis canal, which it left either through the external opening, or through a canal of its own. In the latter case it would have issued from the dorsal side of the distal part of the facialis canal. A few fine canals, which were traversed by rami from the r. oticus lateralis to a sensory canal portion in the dermal cranial roof are seen in the Field Museum specimen (*in,* Pls. XX, XXII). These fine canals could, however, not be traced downwards to their origin, and, therefore, we cannot say whether they come from a larger canal within the cranial wall or whether each of them went independently down and opened on the lateral surface of the lateral wall.

LABYRINTH CAVITY

The labyrinth cavity is completely preserved only in the Field Museum specimen. Traces of it are, however, seen also in one of the New York specimens (Pl. XXVII). It (*lab.cav,* Fig. 4; Pl. XX; Pl. XXVI, figs. 3, 4; Pl. XXVII) is large and, as pointed out, lined throughout by a thin layer of perichondral bone, the labyrinth bone layer. As has also been mentioned, it is completely separated from the cavum cerebrale cranii by a thick septum (Pl. XX) which consisted of cartilage lined by the labyrinth bone layer on the labyrinth side and by the internal bone layer on the cerebral side.

The division for the sacculus (*sac,* Pl. XXVI, fig. 3) is not well exposed, but, as far as can be judged, it cannot have been very large. It is not distinctly separated from the remaining divisions of the cavity. From its dorsal part a canal (*d.end,* Fig. 4; Pl. XX; Pl. XXVI, fig. 3) issues in a dorso-postero-lateral direction to the dorsal surface of the primordial neurocranium. This canal seems, however, to end some distance below the dermal bones of the cranial roof, a fact which probably indicates that the cartilage at this place did not reach quite up to the dermal bones, i.e., that there probably was a shallow fossa into which the canal had its dorsal opening

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[1] The presence of a groove between the two openings would of course have indicated that the r. hyoideomandibularis after its exit from the facialis canal went backward along the lateral surface and entered the canal *ju* through the anterior opening ju_1. The absence of such a groove would of course point in the opposite direction. If the two openings should be found situated in a common pit this must probably also indicate that the tr. hyoideomandibularis entered the canal *ju* through the anterior opening ju_1.

(Fig. 3; Pls. XIX, XX). From its course and relations it is evident that the canal in question must have lodged the ductus endolymphaticus, which, accordingly, opened on the dorsal surface of the primordial neurocranium in a fossa endolymphatica as in Selachians (RETZIUS 1881).

Slightly postero-ventrally of the canal for the ductus endolymphaticus, another, but much wider canal, issued from the division for the sacculus. This canal (*v.lb,* Figs. 10, 11; Pl. XX; Pl. XXIV, fig. 2; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1, 2, 3), which runs backward and somewhat dorsally to the dorsal division of the vagus canal, has already been described in another connection, and, as pointed out there, it probably transmitted a large vein, that drained the whole, or at least the main part, of the labyrinth.

The division for the utriculus (*utr,* Pl. XX; Pl. XXVI, figs. 3, 4) appears to be relatively very large, but as it is not distinctly marked off from the other divisions, its size may, perhaps, be over-estimated. As is seen from the plates, its largest extension is from above down-

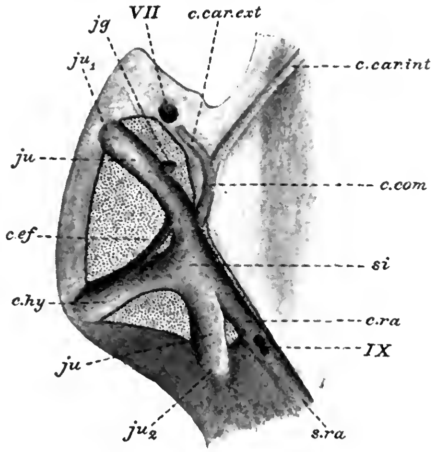

Fig. 7. MACROPETALICHTHYS RAPHEIDOLABIS

Diagrammatic sketch showing the position of certain canals in the lateral wall of the labyrinth region. Certain ventral parts of the lateral wall removed. Bone layers indicated with shading and when in cross section with black lines. Cartilage dotted. ×¾.

c.com, canal for the arteria carotis communis; *c.ef,* canal perhaps for the arteria efferens hyoidea; *c.hy,* canal for the vena hyoidea; *c.ra,* canal for the radix aortæ behind the sinus *si*; *jg,* canal for the vena jugularis through the postorbital process; *ju,* canal behind *jg,* for the vena jugularis, anterior of *jg,* for the vena mandibularis ju_1, ju_2, anterior and posterior openings of the canal *ju*; *si,* sinus arisen by confluence of the canals *ju* and *c.ra*; *s.ra,* groove for the radix aorta (lateral dorsal aorta); *VII,* canal for the n. facialis; *IX,* canal for the n. glossopharyngeus.

wards and forwards, which must mean that the utriculus did not have a horizontal position, but was inclined in the same way as in Selachians (cf. RETZIUS 1881). Just at the antero-ventral end, there is, immediately anterior of the place of entrance of the acusticus canal (VIII) a rather pronounced bulge (*ru,* Pl. XXVI, fig. 3), which, to judge from its position, probably contained the recessus utriculi. Immediately in front of this bulge lies the proximal portion of the facialis canal (VII).

The divisions for the semicircular canals are very imperfectly known, which is due partly to the fact that they could not be laid bare without danger to other important structures, and partly to the circumstance that they probably are not well differentiated from the other parts of the labyrinth cavity. It seems, however, not unlikely that the part designated with the letters *c.sem.ant,* in Pl. XX and Pl. XXVI, figs. 3, 4, was occupied by the canalis semicircularis anterior, and if this is true the canalis semicircularis anterior would have had a position almost transversal to the longitudinal axis of the head. This position would, as is easily understood, have been caused by the backward shifting of the orbit. What parts of the divisions for the other two semicircular canals are represented by the fragments denoted by *c.sem* in Pl. XXI and Pl. XXVI, fig. 4, is difficult to say with certainty, but at least what is seen in Pl. XXI seems most probably to be a part of the division for the canalis semicircularis externus, which thus would have been situated as in Elasmobranchs.

The n. acusticus, as is seen from the position of its canal (VIII), enters the labyrinth cavity at the very bottom, as in certain Elasmobranchs (*Scyllicum, Raja,* cf. RETZIUS 1881), and is rather short. The glossopharyngeus, as has already been mentioned, traversed the postero-ventral parts of the labyrinth cavity. The facialis went first for some distance along the antero-ventro-medial part of the labyrinth cavity, then turned laterally and passed along the antero-ventral part of the same cavity between it and the orbit. (Pl. XXV, figs. 1, 3; Pl. XXVI, figs. 3, 4.)

From the description now given of the labyrinth cavity it seems rather probable that this was larger than the membranous labyrinth enclosed in it, a condition which makes it difficult to conclude anything with certainty about the finer details of the latter. But what is, however, known so far of the larger divisions of the labyrinth cavity, indicates beyond doubt, as we have seen, that the membranous labyrinth, at least in certain of its general characters, was of the Elasmobranchian type.

A more detailed knowledge of the labyrinth cavity would seem evidently to be of great importance for the understanding of the affinites of *Macropetalichthys* to other fishes, and it is therefore to be hoped that new material, fit for a detailed investigation of the labyrinth cavity, will soon be found.

ORBITOTEMPORAL REGION

The orbitotemporal region (Figs. 1, 3, 5, 8; Pls. XIX-XXIII; Pl. XXIV, fig. 1; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1, 2) is strikingly short and broad, its breadth being almost three times as great as its length. The breadth is, however, much greater at the bottom of the region than higher up, a condition which is caused by the presence of the very extensive floors for the orbits (Figs. 3, 8; Pls. XIX, XXI, XXIII). The height is greatest at the posterior end of the region, where it is about equal to the length and a third of the breadth, decreasing slowly and gradually forwards throughout the region. On account of the orbital floors, the region is, at the bottom, not marked off from the adjacent regions, otherwise being, however, considerably narrower than these.

The orbitæ are rather small and lie far apart. While in Arthrodires in general they are situated fairly far forward, and have the entrances facing almost straight laterally, they have here shifted a certain distance in a postero-medial direction and have their entrances directed much upwards (Figs. 3, 5, 8; Pls. XIX, XX; Pl. XXIV, fig. 1). On account of the shifting, they are much more completely bounded by the primordial neurocranium than is generally the case in fishes, for, in fact, they have not only a medial, a posterior and an anterior, but, in addition, a ventral and to a large extent a lateral wall formed by this. The ventral wall, which has been already referred to as the orbital floor, is a rather thin plate which is continuous laterally and posteriorly with the postorbital process, medially with the ventral part of the interorbital wall and anteriorly with the ethmoidal region. It consists of cartilage covered both on the upper (orbital) and lower surfaces by the external bone layer. The lateral wall, as far as it is present, is formed by the large postorbital process, which reaches so far forward that it leaves only a rather limited opening between its anterior end and the ethmoidal region (Figs. 3, 5; Pls. XIX, XX; Pl. XXIV, fig. 1). A transverse section through the posterior half of the region that shows the relations between the different walls of the orbit at this place as well as the shape of the orbit itself is seen in Figure 8. The orbital entrance is of an elliptical shape, with the largest axis directed so as to converge a little towards that of the other side in a postero-dorso-medial direction (Fig. 3; Pls. XIX, XX; Pl. XXIV, fig. 1).

For detailed description we may consider the region to be composed of four walls—a ventral, a dorsal, and a right and a left lateral —all of which, of course, are continuous with the correspondingly situated walls in the adjacent regions.

The ventral wall (Figs. 1, 5, 8; Pls. XXI, XXII, XXIII; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1, 2) is characterized in the first place by its very considerable breadth, which remains almost unchanged throughout the region. As a whole it is thin, and especially is this the case in the lateral (orbital floors) and median parts. Like the corresponding walls in the adjacent regions, it is covered by the internal bone layer dorsally and the external bone layer ventrally and is curved so that the ventral surface is concave in transversal direction. It has no fenestra hypophyseus or fenestration whatever and the fossa hypophyseus is only very slightly developed on its dorsal (cerebral) side.

The canal for the internal carotid artery of each side (*c.car.int*, Fig. 8; Pls. XXI-XXIII; Pl. XXV, fig. 2) enters the ventral wall of the region from behind and perforates the lateral part of this that forms the orbital floor. Its direction is forward and a little medially and, in the posterior larger part of its course, it is here, as in the labyrinth region, situated entirely within the external bone layer, thus very superficially. In the anterior part of the region it penetrates deeper into the wall, curving postero-dorso-medially. With this latter course it arrives up and into the lateral wall of the region, where it finally opens into the opticus canal (Pl. XXIII; Pl. XXV, fig. 2), its opening into this being situated on the anterior side close to the orbit. Just at the place where it curves from the anterior to the postero-dorso-medial direction, it lies somewhat anterior of the orbit, thus really in the basal part of the antorbital process, a fact which is certainly explained by the backward shifting of the orbits. We shall have the opportunity of returning to it again in connection with the description of the opticus canal.

The orbital floor of each side is perforated by a second canal (*c.pal*$_2$, Pls. XXI, XXII) which begins in the orbit and runs antero-ventrally through the floor, opening into the anterior portion of the suborbital part of the internal carotid canal. At the place where the latter canal curves dorso-postero-medially it has an opening (*c.pal*$_3$, Fig. 1), leading to the ventral surface of the neurocranium, and from this opening a shallow groove (*s. pal*, Fig. 1) goes forward. As we shall see from the description of the trigemino-facialis ganglionic complex below, it is not difficult to conclude that the canal $c.pal_2$ was traversed by the r. palatinus facialis, which passed down to the anterior portion of the suborbital part of the internal carotid canal, then left this and arrived at the ventral side of the neurocranium by the opening $c.pal_3$.

The dorsal wall (Figs. 3, 8; Pls. XIX, XX; Pl. XXIV, fig. 1; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1, 2) is broad and short like the ventral one, but on the other hand considerably thicker. As far as one can judge from its appearance in the fossil it had no fontanelle, and, as already pointed out, it is devoid of the external bone layer. Its upper (external) surface is slightly convex in transversal direction and provided with grooves for the ridges on the lower side of the dermal bones in which the sensory canals are enclosed. In its anterior part it is, as already mentioned above, traversed by the canal for the n. ophthalmicus lateralis, which arrives there from below from the lateral wall. Otherwise there are in it only several very fine canals, the most important of which issue from the canal for the n.ophthalmicus lateralis and pass upwards to the supraorbital sensory canal.

Finally, the lateral walls (Figs. 1, 5, 8; Pls. XXII-XXIV; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1, 2), although thick, are by no means as thick as those in the labyrinth region. Their thinnest place is situated around the opticus canal (II). They are covered both by the internal and external bone layers. Their external surface is concave both in dorso-ventral and antero-caudal direction. Their internal surface has a rather complicated appearance, as may be understood from the figures quoted and as will be further dealt with below.

Each lateral wall is perforated by several canals. We begin here with the most posterior one, the trigeminus canal, proceeding forward from this.

The trigeminus canal (V, $V_{2,3}$, Figs. 10, 11; Pl. XXIII; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1, 2) leaves the cavum cerebrale cranii a short distance anterior to the facialis canal and, as pointed out above, its internal opening has nothing to do with the acustico-facialis recess. It runs antero-laterally and somewhat ventrally to the postero-ventro-medial corner of the orbit, and, on account of the fact that the cranial wall is much thinner at this place than immediately behind the orbit, it naturally becomes considerably shorter than the facialis canal. The external opening, as is easily understood, is situated rather far medially of that of the facialis canal.

In the trigeminus canal there may properly be distinguished two parts, a proximal short and wide one (V) and a distal rather long and narrower one ($V_{2,3}$), the former of which actually forms a recess on the lateral side of the cranial wall, a recess which may be called the trigeminus recess.

From the antero-dorsal part of the trigeminus recess, as thus defined, there issues a rather wide canal (*c.ophth.sup.V*) which runs forward and a little upward, crossing the canal for the n. ophthalmicus lateralis (*c.ophth.lat*) on the ventro-medial side and opening into the postero-ventro-medial part of the orbit (Pl. XXIII; Pl. XXV, fig. 2; Pl. XXVI, figs. 1, 2). Slightly ventrally of this canal a second, but considerably narrower one, (*c.ophth.prof*), leaves the trigeminus recess, and taking its course ventro-medially of the canal for the n. ophthalmicus lateralis, goes almost straight forward to the orbit, where it opens somewhat postero-ventrally of the former.

With the knowledge we now possess of the conditions in recent fishes, it is easy to conclude what the functions of the canals just described were, and, in addition, to make out to a certain degree how the trigemino-facialis ganglionic complex and its roots were developed. For comparison the reader may be referred to the works of HERRICK (1899; 1900; 1901), JOHNSTON (1898; 1901), KINGSBURY (1897), ALLIS (1897; 1901; 1903; 1909a; 1918c; 1922), LANDACRE (1916), NORRIS and HUGHE (1920) and STRONG (1895), etc.

As mentioned in another connection, it is fully evident that the canal designated by the letters *c.ophth.lat* transmitted the n. ophthalmicus lateralis (cf. above) and as this canal does not communicate with the trigeminus canal or the fine canals issuing from the latter, we may also conclude with full certainty that it did not give passage to any general cutaneous fibres. These fibres to the orbit or dorsal side of the neurocranium must therefore undoubtedly have emerged into the orbit through the canals *c.ophth.prof* and *c.ophth.sup.V*, and it is easy to understand that those of them which passed through the canal *c.ophth.prof* formed the r. ophthalmicus profundus trigemini, or a somewhat equivalent nerve, while the others which passed through the canal *c.ophth.sup.V* formed the r. ophthalmicus superficialis trigemini. In other words, the general cutaneous fibres which formed the r. ophthalmicus profundus were transmitted to the orbit through the canal *c.ophth.-prof*, and those which formed the r. ophthalmicus superficialis trigemini through the canal *c.ophth.sup.V*, while the lateralis fibres which formed the n. ophthalmicus lateralis never entered the orbit but passed in the interorbital wall through a canal of their own which is given off from the facialis canal and has no connection with the trigeminus canal (including the trigeminus recess). A separate course of the r. ophthalmicus lateralis and r. ophthalmicus profundus trigemini is, besides in the form now under consideration, found in *Acipenser, Polyodon* (Stensiö 1925), *Saurichthys* (Stensiö 1925) and *Siluroids* (Workman 1900, pp. 403-407; Herrick 1901, pp. 201-203).

The r. ophthalmicus superficialis trigemini and the r. ophthalmicus profundus trigemini having issued from the trigeminus recess—the proximal part of the trigeminus canal—it is fully evident that this recess must have contained at least the main parts of the ganglion gasseri and the profundus ganglion, i.e., the main parts of the ganglia of the general cutaneous fibres. Only small parts of these ganglia may perhaps have reached into the cavum cerebrale cranii. From the origin of the r. ophthalmicus superficialis and the r. ophthalmicus profundus trigemini, we can further conclude that the distal narrower part of the trigeminus canal ($V_{2,3}$) transmitted the r. maxillaris and the r. mandibularis trigemini after their origin from the ganglion gasseri. That these two latter rami were accompanied by certain lateralis fibres and perhaps also by certain communis fibres, we shall see from the subsequent account.

During their passage through the cranial wall, the trigeminus roots proper (i.e., the general cutaneous roots and the motor root) of recent fishes are, as a rule, accompanied by a lateralis root, which leaves the medulla oblongata postero-dorsally of the trigeminus root proper running outward postero-dorsally or dorsally of these, and having its ganglion dorsally or postero-dorsally of the ganglion gasseri. From the ganglion of this lateralis root the n. ophthalmicus lateralis and n. buccalis lateralis take their origin.

In *Macropetalichthys rapheidolabis,* in which the canal for the n. ophthalmicus lateralis issues from the facialis canal and in which, as we have seen, there is no communication between the proximal parts of the latter canal and the trigeminus canal, the lateralis root which gave rise to the n. ophthalmicus lateralis and the n. buccalis lateralis must evidently have left the cranial cavity through the facialis canal, traversing the proximal part of this canal and having its ganglion there. The n. buccalis lateralis thus also arose within the facialis canal.

In order to reach the trigeminus canal, the n. buccalis lateralis in *M. rapheidolabis* must, soon after its origin, have turned forward, traversing the short canal *c.buc.lat,* described above (Figs. 10, 11), which leaves the facialis canal slightly distally and somewhat ventrally of the canal for the n. ophthalmicus lateralis and goes to the distal narrow part ($V_{2,3}$) of the trigeminus canal. The n. buccalis lateralis after arriving into this part of the trigeminus canal, probably joined more or less intimately the r. maxillaris trigemini and passed distally with this in the normal way.

From the considerations given the following is evident in *M. rapheidolabis* concerning the trigemino-facialis ganglionic complex and its roots: 1. Into the trigeminus recess there entered only the general cutaneous roots and the viscero-motor root of the mandibular arch. 2. The ganglion gasseri and the profundus ganglion must have been situated in a proximal wide part of the trigeminus canal, called here the trigeminus recess. 3. Into the facialis canal there entered all the lateralis fibres and all the communis fibres of the ganglionic complex and, further, the viscero-motor root of the hyoid arch. 4. The ganglia of the fibres entering the facialis canal, i.e., in this case the ganglion geniculi, the ganglion of the dorsal lateralis root and the ganglion of the ventral lateralis root, must have been situated in the proximal part of this canal and partly, perhaps, in the acustico-facialis recess.

The lateralis ganglion of the dorsal lateralis root (from which the n. ophthalmicus lateralis and n. buccalis lateralis arose) must in the facialis canal have had its position antero-dorsally of the two other ganglia, the ganglion geniculi and the ganglion of the ventral lateralis root. Although separated from the ganglion gasseri by a rather thick wall, it thus had, as far as can be judged, about its normal position in relation to this, and the fact that it was situated in the facialis canal is therefore of hardly any importance from a morphological point of view. Similar arrangements would certainly arise in many recent forms if the septa of connective tissue that there more or less completely separate the ganglia in question and their roots from each other developed more strongly and chondrified or ossified. Moreover, we find in certain recent forms that all the roots of the trigemino-facialis ganglionis complex may run close together through a single canal in the cranial wall, and that their ganglionic formations may be very intimately connected with each other. Thus the wall between the trigeminus and facialis canals in certain cases is reduced. That variations occur within certain bounds in the trigemino-facialis ganglionic complex of fishes is accordingly not so remarkable.

Whether in *M. rapheidolabis* any general cutaneous fibres went backward to the facialis branches and any communis fibres forward to the trigeminus branches it is not possible to say with certainty from the conditions in this fossil, but it is not impossible that this was the case, for these fibres can very well be thought to have traversed the canal *c.buc.lat*. Possible communis fibres to the n. ophthalmicus lateralis must have entered the canal for this nerve directly from the facialis canal.

The r. oticus lateralis, which, as is known, is a branch from the n. buccalis lateralis, certainly arose within the facialis canal, probably just as the n. buccalis lateralis on its way forward entered the canal *c.buc.lat*. Whether the r. oticus lateralis then traversed the entire remaining part of the facialis canal or sooner or later perforated its dorsal wall, entering a canal of its own, it is impossible to decide at present.

Apart from the r. oticus facialis, the distal part of the facialis canal (distally of the point of origin of the ophthalmicus lateralis canal) transmitted communis fibres—the viscero-motor fibres—for the hyoid arch, lateralis fibres for the n. mandibularis externus and possibly also a few general cutaneous fibres. All these fibres formed together a large facialis stem which, soon after its origin from the ganglia within the canal, must have branched into the r. palatinus and the truncus hyoidemandibularis.

The r. palatinus, after its origin in the facialis canal, must first have turned forward and traversed the canal $c.pal_1$ which leads from the facialis canal to the orbit (cf. above). Well within the orbit the nerve continued forward for some distance in a groove on the orbital floor, then penetrated downwards in the floor through the canal $c.pal_2$ to the suborbital part of the internal carotid canal. In the last mentioned canal it went only a short distance forward, leaving it through the opening $c.pal_3$ and arriving at the lower surface of the primordial neurocranium. When emerging from the opening $c.pal_3$ it was perhaps accompanied by a fine branch from the arteria carotis interna (Cf. text fig. 6).

The correctness of the course of the r. palatinus facialis of the fish as sketched here is proved by the conditions in recent fishes, in which the nerve in question also runs in a similar way and also often more or less closely accompanies the a. carotis interna for a corresponding distance. (ALLIS 1897, pp. 498, 685, Pl. XXXVI, fig. 61; Pl. XXXVII, figs. 62, 63; 1901, p. 182; 1909a, pp. 43-55; 88, 185-186; 1911a, p. 290; 1919a; 1922a, pp. 280-281; 1923, p. 213; ALLEN 1905, pp. 51-56; GREIL 1913, Pl. LV, fig. 2; etc.; cf. also STENSIÖ 1923, pp. 1241-1248; 1925.)

If in *M. rapheidolabis* there was an anastomosis between the r. palatinus facialis and the r. palatinus glossopharyngei, this anastomosis must have been situated in the anterior suborbital part of the internal carotid canal and the r. palatinus glossopharyngei must have arrived there through the canal *c.ra,* the sinus *si,* and the canal *c.com* (Cf. ALLIS 1897, Pls. XXXVI, fig. 61; Pl. XXXVII, figs. 62, 63; 1909a, p. 186; 1911a, p. 289-290). The canal for the n. ophthalmicus lateralis has already been dealt with, and I call attention here only to the fact that from its origin in the lateral wall of the labyrinth region it goes forward and upward to the lateral wall of the orbito-temporal region, from which it soon arrives up and into the dorsal wall, continuing into this through the entire ethmoidal region. It gives off several rami in dorsal direction to the sensory canal situated dorsally of it, i.e., the supraorbital sensory canal.

After having dealt with the trigeminus and facialis nerves and their roots and ganglionic complex, we can now understand better than before the relation between these structures and the jugular vein, and that my view of the course of the latter ought to be correct. As I suppose this vein to have run, it must, after its origin in the orbit, have passed backward below the r. maxillaris and the r. mandibularis trigemini. During its passage through the basal part of the postorbital process it then crossed the facialis canal on the dorsal side, thus passing ventrally of the trigeminus and dorsally of the facialis. Although it ran rather far laterally of the trigemino-facialis ganglionic complex and did not, as in most recent forms, traverse this, it had, however, obviously retained its normal relations to the trigeminus and facialis nerves. (Cf. ALLIS 1922a, pp. 260-264.)

Neither for the n. trochlearis nor for the n. abducens have canals so far been found. The trochlearis canal was probably very narrow, and may, therefore, have been overlooked, especially as the medial wall of the orbit is very imperfectly known in detail at the place where this canal ought to have been situated. That the abducens canal is not found may perhaps be explained by concluding that there was in reality no independent canal for the n. abducens, for this nerve may perhaps have emerged into the orbit more or less closely associated with the r. maxillaris and r. mandibularis trigemini, as it does in certain recent forms, for instance, certain Selachians. (ALLIS 1901, p. 132; etc.)

A rather wide canal for the n. oculomotorius opens into the orbit somewhat in front of the canals for the n. ophthalmicus profundus and the r. ophthalmicus superficialis (V, Figs. 8, 10, 11; Pl. XXIII; Pl. XXV, fig. 2; Pl. XXVI, figs. 1, 2). A short distance in front of that canal, the wide opticus canal (II, Figs. 5, 10, 11; Pl. XXIII; Pl. XXV, fig. 2) pierces the lateral wall in an antero-lateral direction, opening into the anterior half of the orbit not far above the floor. In its most distal (orbital) part it receives on the anterior side the canal for the arteria carotis interna (*c.car.int*), which, during its way upwards from the ventral wall, makes a long curve forward, so that for a short distance it even traverses a posterior part of the ethmoidal region.

We thus find that the arteria carotis externa entered the distal part of the opticus canal. From there it evidently must have traversed the canal in medial direction to reach the cavum cerebrale. But just as it turned medially to do this it probably gave off the branch known as the arteria optica, for the external opening of the opticus canal has on its anterior side distally of the confluence with the internal carotid canal a distinct emargination (*a.opt*), which cannot have had any other function than to transmit a vessel. (Cf. ALLEN 1905, pp. 56-57; ALLIS 1897, p. 498; 1908a, p. 258; 1908b, p. 223; 1909a, p. 186; 1911a, p. 290; 1911b, p. 518; 1912a; 1912b, pp. 489-490; 1912c, p. 586; 1914a; 1922a, p. 168; 1923, Pl. XIX; DANFORTH 1912, pp. 442-445 etc.)[1]

The way in which the arteria carotis interna of the fish entered the cavum cerebrale may perhaps at first glance appear rather strange, as this artery in fishes generally pierces the ventral wall of the primordial neurocranium so that it arrives immediately into the cavum cerebrale and not first into the opticus canal. But a closer study makes it clear that the difference is really not so important, for in certain forms, e.g., *Saurichthys* (STENSIÖ 1925), the canal for the internal carotid opens either in the proximal part of the opticus canal or at the transition between this and the cavum cerebrale cranii. We have there a stage intermediate between the one in *Macropetalichthys rapheidolabis* just described and the one generally occurring in fishes. In this connection it is also noteworthy that the arteria carotis interna in *Polypterus* (ALLIS 1908b, loc.cit; 1922a, loc.cit; LEHN 1918, p. 380) runs externally of the interorbital wall so far forward that it enters the cavum cerebrale either together with or close behind the n. opticus, and that in Elasmobranchs the same artery within the lateral wall of the neurocranium goes a long distance forward and upward in direction towards the opticus canal before entering the cavum cerebrale. (ALLIS 1912b, loc.cit; 1914a, pp. 229-230, 236, 238, etc.)

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[1] Another interpretation is possible, viz.:—that the arteria pseudobranchialis efferens reached the a. carotis interna just in the opticus canal, and that the a. ophthalmica magna was given off to the orbit through the emargination on the anterior side of the opticus canal. This emargination would consequently in this case have been traversed by both the a. ophthalmica magna and the a. pseudobranchialis efferens.

Whether a canal for the arteria pseudobranchialis efferens was present or not in the lateral wall could not be decided from the material available, and it is therefore not possible to conclude anything with certainty concerning the relations between the arteria pseudobranchialis efferens and the arteria carotis interna. (Cf. the footnote on the preceding page.)

As is seen from the description given of the trigeminus and facialis canals, there is no real trigemino-facialis chamber in *Macropetalichthys rapheidolabis.*

A posterior myodome also does not occur in *M. rapheidolabis,* and it does not seem probable that there was an anterior one either. A satisfactory decision in the latter respect is, however, not as yet possible, since the conditions of the anterior wall of the orbit are very imperfectly known.

Since the postero-ventro-medial corner of the orbit as well as the postero-ventral part of the interorbital wall were partly covered by matrix, which could not be removed without hurting the fossil as a specimen, the pituitary canal (canal for the pituitary vein) could not be observed, but I do not doubt that it actually exists, for it is, as far as I know, without exception found in all fishes, although in those forms which have a posterior myodome it is a part of this and has been much widened and transformed. (Cf. ALLIS 1909a, pp. 183-208;

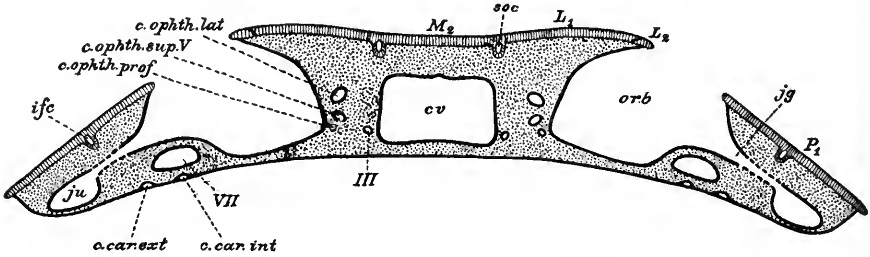

Fig. 8. MACROPETALICHTHYS RAPHEIDOLABIS

Transverse section through the posterior part of the orbitotemporal region and the antero-lateral parts (postorbital processes) of the labyrinth region. Layers of substitution bone drawn with black lines, dermal bones with vertical striation. Cartilage dotted. ×¾.

L_1, L_2, M_2, P_1, dermal bones of the cranial roof (boundaries approximately drawn); *c.car.ext,* canal for the arteria carotis externa; *c.car.int,* canal for the arteria carotis interna; *c.ophth.lat,* canal for the n. ophthalmicus lateralis; *c. ophth.prof,* canal for the r. ophthalmicus profundus trigemini; *c.ophth.sup.V,* canal for the r. ophthalmicus superficialis trigemini; *cv,* cavum cerebrale cranii; *ifc,* infraorbital sensory canal; *jg,* canal for the vena jugularis through the postorbital process (somewhat diagrammatically drawn as it really would not be visible to this extent on a single transverse section); *ju,* canal in the part seen in the section for the vena mandibularis, behind this place for the vena jugularis; *orb,* orbit; *soc,* supraorbital sensory canal; III, canal for the n. oculomotorius; VII, facialis canal.

1911a, p. 291; 1914a; 1918a; 1919a; 1922a, p. 228; 1922b; GEGENBAUR 1872, pp. 75-79, canalis transversus ALLEN 1905, p. 81; O'DONOGHUE 1914, pp. 440-441; STENSIÖ 1921, pp. 62, 177-180; 1922, p. 179; 1923, pp. 1244, 1262-1268; 1925, LEHN 1918, p. 380.)

Owing to reasons similar to those which prevented study of the pituitary canal, it was not possible to see any canal for the vena cerebralis anterior, which in fishes usually perforates the upper part of the interorbital wall and goes to the orbit. (Cf. ALLIS 1897, Pl. 21, figs. 9-11, *acvfr*; 1903, Pl. 4, fig. 9, *acvfr*; 1909a, p. 39; 1922a, pp. 261-262 LEHN 1918, p. 380, figs. 3, 4; STENSIÖ 1921, pp. 168-169; 1923, pp. 1246-1247; 1925.)

ETHMOIDAL REGION

As compared with the labyrinth and orbito-temporal regions the ethmoidal region is fairly long, its breadth being, however, also considerable, and even so considerable that it exceeds the length. On account of the presence of the extensive orbital bottom, the region is not marked off from the orbitotemporal region ventrally. Higher up above the bottom of the orbit it is, however, much broader than the latter region, forming the anterior wall of the orbits and projecting on each side as a preorbital process in the normal way (Figs. 1, 3, 5; Pls. XIX-XXI; Pl. XXIV, fig. 1; Pl. XXV, figs. 1, 2).

Both the height and breadth of the region decrease anteriorly, the latter, however, proportionally somewhat more than the former. The anterior end is imperfectly preserved, but it is probable that it was truncated, and, to judge from the conditions in *Epipetalichthys* described below, it is likely that it was, in addition, a little concave.

Close to the anterior end of the region there projects from the basal parts of each side a strong, broad process (*olf*, Figs. 1, 3, 5; Pls. XXI-XXIII; Pl. XXIV, fig. 1) in a lateral and somewhat ventral direction. This process has its distal end truncated and provided with a large oval opening (*na, nf*), which, as is evident from the description of *Epipetalichthys* below, must at least in part be the nasal opening. Accordingly, the process contains the nasal cavity and represents the olfactory capsule. We thus have here an olfactory capsule that, as in Elasmobranchs, is fairly independent and projects laterally in relation to the other internasal parts of the ethmoidal region. (Cf. ALLIS 1923, pp. 126-147.)

A closer examination of the nasal opening shows that this, by a process of bone that projected forwards from the posterior wall, is incompletely subdivided into a dorso-lateral (*na*) and a ventro-medial (*nf*) portion. Both of these portions are directed ventro-laterally, but the latter considerably more so than the former, so that it in fact is situated on the ventral side of the nasal capsule (Figs. 1, 5; Pl. XXI; Pl. XXIII; Pl. XXIV, fig. 1). I was at first inclined to consider them as corresponding to the two nasal apertures generally found in fishes, and to think that the process that separates them would be homologous with a part of the ala nasalis of Elasmobranchs (ALLIS 1923, pp. 126-147), and that the ala nasalis would be continuous with, and form an integral part of, the nasal capsule. But after having read the fine memoir on *Chlamydoselachus* recently published by ALLIS (1923) I arrived at the conclusion that what has been called above the ventromedial portion (*nf*) of the nasal opening, really represents a lateral part of the nasal fontanelle of *Chlamydoselachus* and certain other Selachians and that, accordingly, the other portion (*na*) alone is the nasal opening. The ala nasalis or its possible homologue, if there were one, was probably entirely without ossification. If this opinion is true, the vein commissure that in Selachians (ALLIS 1923, pp. 126-147), *Saurichthys* (STENSIÖ 1925), and probably in most fishes (ALLEN 1905, Pl. 1, fig. 1; Pl. III, figs. 17, 18), connects the orbito-nasal vein and the anterior facial vein with each other must, obviously, have traversed the posterior part of the nasal fontanelle. Whether this fontanelle was entirely occupied by a membrane of connective tissue or whether it was more or less occupied by cartilage it is not possible to decide.

From what has been set forth regarding the nasal capsule, it is clear that *M. rapheidolabis* in this regard much resembles the Elasmobranchs.

The cavum cerebrale cranii extends only a short distance into the posterior part of the region, which, therefore, apart from certain canals, in the whole of its interior consisted of cartilage. On account of this fact we cannot conveniently consider it to be composed of a number of walls, as in the case of the other regions, but will have to deal with it as a solid body with five external surfaces which are well bounded from each other. These surfaces are the following: a ventral, a posterior, a dorsal, and a right and a left lateral.

The ventral surface is broad and large and is posteriorly continuous with the ventral surface of the orbitotemporal region (Fig. 1; Pls. XXI-XXIII). Unfortunately it is not fully preserved in its anterior parts. As is seen from the figures (the transversal section reproduced in Fig. 9 and Pl. XXIV, fig. 1) it is slightly concave both in transversal and rostro-caudal direction. And, as has been pointed out above, it is covered by the external bone layer throughout its extension. Not far from each lateral border it has a distinct sulcus (*s.pal*, Figs. 1, 9; Pl. XXII), which leads forward for some distance from the opening $c.pal_3$ (Fig. 1; Pl. XXII). This sulcus was evidently developed for the r. palatinus facialis, and may, perhaps, in addition, also have lodged a small arterial branch given off from the arteria carotis interna through the foramen $c.pal_3$. So far as can be judged there is no indication of an articulation facet for the palatoquadrate on the ventral surface of the region.

Close, medially, to each groove for the r. palatinus just described, and about midway between the anterior end of the region and the foramen $c.pal_3$, the external bone layer seems to show faint indications of an ossification centre, a centre which, if it really exists, is so situated that the bone which it represents corresponds at least to the exethmoid (lateral ethmoid) of fishes in general, and perhaps, in addition, to the preëthmoid of certain fishes. (Cf. ALLIS 1897, Pl. 21, figs. 8-10, *SMX*; 1898, pp. 446-450; 1909a, pp. 17-22; STENSIÖ 1921, pp. 61, 93-94; 1922, pp. 184-186; 1923, pp. 1247-1248; 1925, etc.) A positive decision in this respect is, however, not possible until more and better preserved material is available for investigation.

The posterior surface of the region, if we next turn to this, is, by the anterior part of the orbitotemporal region above the orbital floor, subdivided into a right and a left half, each forming the anterior surface of the orbit of its side. As it could not be cleaned from matrix, I can state little concerning it. It may have had a foramen through which the r. ophthalmicus superficialis after traversing the orbit entered the region, but nothing can be said about the position of this foramen. As has already been pointed out above, there probably was no anterior myodome developed, but a positive decision in regard to this point is evidently not possible until material is found which will enable us to undertake a detailed examination of the posterior parts of the region. The olfactory nerve did not traverse the orbit and accordingly it had no foramen on the posterior surface of the ethmoidal region.

The dorsal surface, like the ventral one, is large and broad and posteriorly continuous with the dorsal surface of the orbitotemporal region (Figs. 3, 5, 9; Pls. XIX-XX; Pl. XXIV, fig. 1; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1, 2). It is slightly convex, both in transversal and rostro-caudal direction (Fig. 9), and slopes slightly forward. In its most anterior parts it is not preserved in the specimen examined, being either crushed together with the dermal cranial roof or destroyed in some other way. From the closely allied *Epipetalichthys* to be described below, we are, however, justified in concluding that the conditions were about as shown in Fig. 3, i.e., that there probably was a deep, broad, antero-dorsally directed depression (*pfg*) at the anterior end of the dorsal surface, and that this depression was lined throughout by a perichondral bone layer. A similar depression seems among adult fishes to occur only in Elasmobranchs (Cf. GEGENBAUR 1872, Pls. IV-VIII, etc.; ALLIS 1913; 1923, pp. 127-130; FRITSCH 1895, figs. 228, 230; WOODWARD 1916-1919, Pl. II, fig. 1, Pl. XXVI, fig. 3; DANIEL 1915, Pl. I, fig. 1, etc.), and we would accordingly have here a very remarkable agreement between *Epipetalichthys* and *Macropetalichthys* on the one hand, and the Elasmobranchs on the other. As we shall see from the account given below, a depression of the same sort probably occurred in all Arthrodires. In Elasmobranchs the depression, which is described by ALLIS under the name of cavum precerebrale, is filled by a fatty tissue and this was probably the case also in the Arthrodires, since the dermal bones in these do not bend down so that they could have been directly superimposed on the bottom of the depression, but are situated on a level with the upper borders of this. This relatively loose position of the dermal skeleton in relation to the primordial neurocranium at the anterior end of the ethmoidal region explains why the dermal skeleton is generally in a very imperfect state of preservation there. While in Elasmobranchs the cavum precerebrale is separated from the cavum cerebrale in most cases merely by membranous tissue, there was here in *Macropetalichthys rapheidolabis* and in *Epipetalichthys* certainly a thick wall of cartilage between them. In *Læmargus borealis* I have also found that the wall between the cavum precerebrale and the cavum cerebrale is to a large extent formed by cartilage. This is also partly shown in WHITE (1892, Pl. I, fig. 5).

From the dorsal side of the anterior part of the cavum cerebrale cranii a rather wide canal goes dorsally and forward to the upper surface of the region, where it opens with a large oval foramen (*par*, Fig. 3; Pls. XIX-XX; Pl. XXVI, fig. 1). This canal, as we shall see, lodged the pineal or parietal organ or both these structures.

Apart from this canal, several fine ones for vessels and nerve branches naturally opened on the dorsal surface of the region. In Pls. XXI and XXIII we can see one of this sort (*rm.ophth.lat*), that goes from the canal for the r. ophthalmicus lateralis (*c.ophth.lat*) a short distance upwards and forwards to the anterior part of the supraorbital sensory canal (*soc*). This sensory canal being, like the others, situated in a ridge on the lower side of the dermal bones, there must evidently have been a paired groove corresponding to the ridge, a groove running as is shown by text fig. 3.

Finally, the lateral surface of each side (Figs. 5, 9; Pls. XXI-XXIII; Pl. XXIV, fig. 1; Pl. XXV, figs. 1, 2) is strikingly long, but not particularly high. It faces laterally and slightly downwards and is somewhat concave in dorso-ventral direction. From its antero-ventral part projects the large nasal capsule (*olf*) already described, but, as is seen from text fig. 5 and Pl. XXIV, fig. 1, this does not occupy more than the ventral half of the height of the surface at this place. As far as can be seen, there is no articulation facet for the palatoquadrate, either on the surface itself or on the posterior or ventral parts of the nasal capsule. This, together with the fact pointed out above that there was no articulation facet on the ventral surface either, seems to indicate that the palatoquadrate actually did not articulate against the region, but was suspended beneath this with ligaments in about the same manner as in the Selachians.

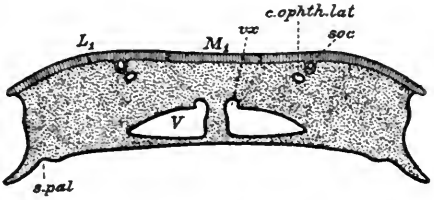

Fig. 9. Macropetalichthys rapheidolabis

Transverse section through the posterior half of the ethmoidal region, slightly anterior to the anterior end of the cavum cerebrale cranii. Layers of substitution bone denoted by strong black lines; cartilage dotted; dermal bones with vertical striation. ×¾.

L_1, M_1, dermal bones of the cranial roof (their boundaries not fully correct); *soc*, supraorbital sensory canal; *s.pal*, groove for the r. palatinus facialis and perhaps for an arterial branch too; *vx*, proximal part of a canal running upwards in the cartilage, probably for some venous vessel; I, canalis tractus olfactorii.

In this connection it may also be pointed out that the postnasal part of each lateral surface is very large, a condition probably caused by the insertion of a powerfully developed part of the musculus constrictor superficialis (I) homologous to the muscle of the Selachians and Teleostomes generally, known as the m. levator labii superioris (Vetter 1874, etc.), levator maxillæ superioris (Allis 1897, pp. 552-556), abductor B (Allis 1901, Pl. 11, fig. 4; Pl. 12, fig. 5) or preorbitalis (Luther 1909, pp. 36-39). If this were not the case, it would be very difficult to find a satisfactory explanation for the considerable post-nasal extension of the lateral surfaces.

On the posterior part of each lateral surface there are found the anterior openings of two fairly wide canals (*c.ophth.sup.V ?* and *vy,* Fig. 5; Pl. XXII; Pl. XXIII; Pl. XXIV, fig. 1) which evidently issue from the orbit. But as the position of the posterior openings of these canals and their course within the preorbital process are so far unknown, it cannot be positively decided what their functions were. The dorsal one (*c.ophth.sup.V?*) possibly transmitted the r. ophthalmicus superficialis trigemini, the ventral one either vessels or the r. maxillaris trigemini and the n. buccalis lateralis or both these nerves and vessels.

From the anterior end of the cavum cerebrale cranii, a paired, rather low but wide canal (I, Figs. 9, 10, 11, 12, 13; Pls. XXIII, XXVII) issues in a forward and somewhat lateral direction to the nasal fossa of its side, being during the entire length situated very low in the region. This canal, which narrows anteriorly, lodged, as far as I can judge, the tractus olfactorius and, at the most anterior, probably somewhat widened end, the lobus olfactorius. It may, therefore, be called the canalis tractus olfactorii. That it would lodge a long olfactory nerve and that the lobus olfactorius would have been situated at the front end of the telencephalon is not, as will be set forth below, in accordance with what we know concerning the features of the brain otherwise. From its dorso-medial side there are given off in the Field Museum specimen two canals of finer calibre which run antero-dorso-laterally within the interior of the region (*vx, vx*$_1$, Pl. XXVI, fig. 1), and which probably were traversed by veins draining the cartilage and dorsal surface.

Close below the groove for each supraorbital sensory canal, we find the canal for the r. ophthalmicus lateralis (*c.ophth.lat,* Fig. 9; Pls. XXI, XXIII), from which, as already pointed out, branches (*rm.ophth.lat*) run upward to the supraorbital sensory canal.

CAVUM CEREBRALE CRANII AND BRAIN

Although being partly much narrower than the primordial neurocranium, the cavum cerebrale cranii (*cv,* Figs. 2, 4, 8, 10, 11; Pls. XX, XXI, XXIII; Pl. XXIV, fig. 3; Pl. XXV figs. 1, 2; Pl. XXVI, figs. 1, 2; Pl. XXVII) has nevertheless a rather considerable size. Observing its shape, it may be considered to consist of three divisions, which in the subsequent description are called the posterior, middle and anterior divisions respectively.

The posterior division is limited entirely to the posterior narrow division of the occipital region, and, in accordance with this, it is much narrower and lower than the other two (*pd,* Figs. 10, 11; Pl.

XXVII). Its narrowest part is situated anteriorly, just at the transition to the middle division. Behind this place it grows slowly and gradually broader and a little lower backwards, but whether it did so quite to the posterior end or not is unknown. Two transverse sections through its posterior half somewhat anterior to the cranio-spinal processes are seen in text fig. 2.

The middle division (*md,* Figs. 10, 11) extends through the anterior division of the occipital region, the whole labyrinth region and a short posterior part of the orbitotemporal region (Cf. also Figs. 2, 4, 8; Pls. XX, XXIII; Pl. XXIV, fig. 3; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1, 2), and is the largest one of the three with regard to height and breadth, but its length is about equal to that of the posterior division. Its maximum height is situated approximately at the transition between the occipital and labyrinth regions, decreasing from there both forward and backward, although only very slightly forward. The bulge caused by the vagus and the other nerves, not taking into consideration the width, attains its maximum in the front end of the division, in the most anterior part of the orbitotemporal region, from which it narrows slightly both backward and forward.

The anterior division (*ad,* Figs. 10, 11) extends through the anterior larger part of the orbitotemporal region and a very short posterior part of the ethmoidal region, where, at the very anterior end, it divides into a right and a left half, each of which anteriorly is continued by the canalis tractus olfactorii (Figs. 10, 11; Pl. XXIII; Pl. XXVI, figs. 1, 2). It is well bounded from the middle division, being both lower and narrower than the anterior part of this. The height gradually diminishes forward throughout the length of the division, finally becoming equal to that of the posterior end of the canalis tractus olfactorii, while the breadth, on the contrary, increases slightly in the same direction. The length is only about half as great as in the other two divisions.

The floor of the middle division is slightly convex, that of the posterior division slightly concave, and so is also that of the anterior division, although the concavity is somewhat larger there (Figs. 10, 13; Pl. XXVI, figs. 1, 2) and forms a shallow, indistinct fossa. In the median parts, this fossa has, in its turn, a small, very slightly indicated depression (*fhy,* Fig. 10), which is so situated that it must have lodged at least the most ventral part of the hypophysis. The lobi inferiores probably had their position laterally of this depression, which may represent the last remnant of an originally more pronounced and large fossa hypophyseos.

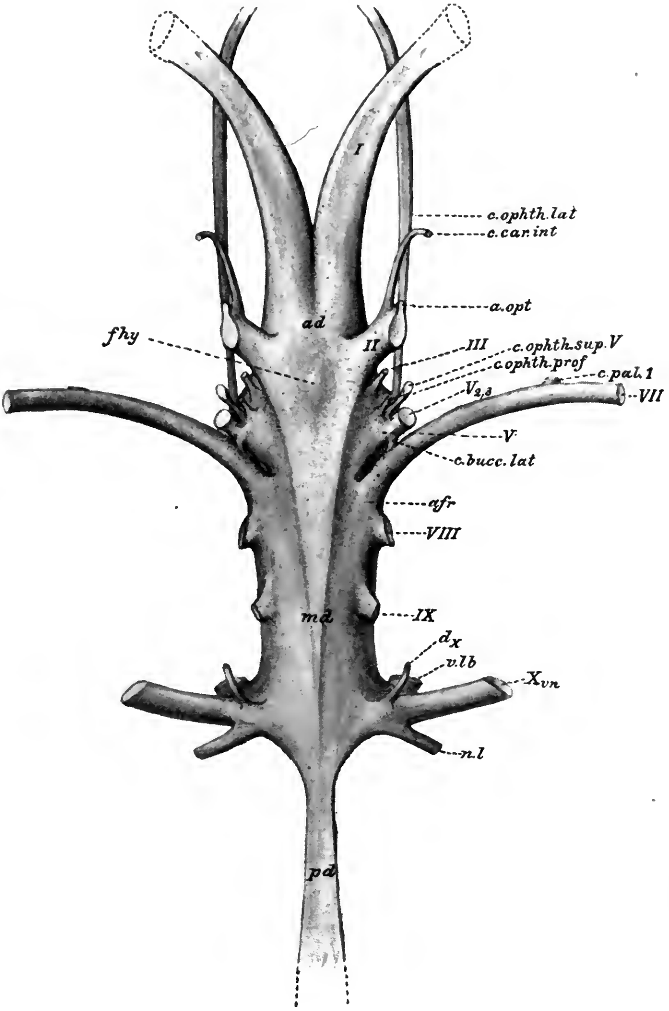

Fig. 10. Macropetalichthys rapheidolabis

Shape of the cavum cerebrale cranii in ventral view. With the exception of the posterior division, which is restored from specimens in the American Museum, entirely after the Field Museum specimen. ×¾.

ad, anterior division of the cavum cerebrale cranii; *afr,* acustico-facialis recess; *a.opt,* division of the external opening of the opticus canal, probably for the arteria optica; *c.bucc.lat,* canal for the lateralis fibres, representing the n. buccalis lateralis and possibly also for certain general cutaneous fibres to the n. facialis; *c.car.int,* canal for the arteria carotis interna; *c.ophth.lat,* canal for the n. ophthalmicus lateralis; *c.ophth.prof,* canal for the r. ophthalmicus profundus; *c.ophth.sup.V,* canal for the r. ophthalmicus superficialis trigemini; *c.pal*$_1$, canal for the r. palatinus facialis from the facialis canal to the orbit; *dx,* canal for a dorsal branch from the n. lineæ lateralis; *fhy,* depression probably for the hypophysis; *md,* middle division of the cavum cerebrale; *n.l,* canal for the n. lineæ lateralis; *pd,* posterior division of the cavum cerebrale cranii; *v.lb,* canal leading from the labyrinth cavity to the vagus canal, probably for a large vein; I, canalis tractus olfactorii; II, division of the opticus canal for the n. opticus; III, canal for the n. trochlearis; V, proximal wide part of the trigeminus canal, forming a trigeminus recess; $V_{2,3}$, distal narrow part of the trigeminus canal traversed by the r. maxillaris, r. mandibularis trigemini and the n. buccalis lateralis; VII, facialis canal; VIII, acusticus canal; IX, glossopharyngeus canal; X_{vn}, vagus canal transmitting the n. vagus and the v. cerebralis posterior.

In the posterior part of the roof of the anterior division, there is, in the Field Museum specimen, a median, unpaired diverticle (*ep*) situated as shown by Fig. 11, i.e., it extends a short distance upward into the dorsal wall of the orbitotemporal region. Somewhat in front of this diverticle, the canal *par* to which reference has already been made issues from the same division in an antero-dorsal direction to the dorsal surface of the posterior part of the ethmoidal region, opening there with a rather large, oval foramen (*par,* Figs. 3, 11-13; Pls. XIX, XX; Pl. XXVI, fig. 1).

According to the observations recently made by WOODWARD (1922, p. 31, fig. 3) the pit that regularly occurs on the lower side of the pineal plate in non-Macropetalichthyid Arthrodires is paired in *Titanichthys,* a fact which causes WOODWARD to consider that the epiphysis there was a paired, symmetrically situated organ. We are thus in *Titanichthys* concerned with a form in which the parietal and pineal organs probably were situated beside one another (Cf. GOODRICH 1909, p. 25; PLATE 1923, pp. 743-753) and it seems to be a matter of course that in all typical non-Macropetalichthyid Arthrodires, as, for instance, *Dinichthys* and *Coccosteus,* they must have been situated exactly as in *Titanichthys.*

In *Macropetalichthys rapheidolabis* the bone-plate M_1 (text fig. 15) of the dermal cranial roof with its posterior part evidently corresponds to the pineal plate (*Pi,* Fig. 14) of *Titanichthys* and other typical non-Macropetalichthyid Arthrodires. The canal by which it is said by EASTMAN (1908a, p. 104; 1908b, p. 169) to be perforated seems to have such a position that it must form the distal continuation of the canal *par,* and at least ventrally correspond to the pit on the lower side of the pineal plate in the non-Macropetalichthyid Arthrodires. These facts, together with the circumstance that *Macropetalichthys rapheidolabis* in most other respects is fairly closely allied to the other Arthrodires, make it highly probable that the parietal and pineal organs in it were situated as in these. If, therefore, these organs in the other Arthrodires occupied a position beside one another, they would obviously in *M. rapheidolabis* both have been situated in the canal *par,* and the diverticle *cp* would thus have lodged no part of the brain and might in such a case very well be thought to be occasionally developed in the Field Museum specimen. That the diverticle *ep* cannot probably have lodged the pineal organ is also, as kindly pointed out to me by Professor N. HOLMGREN of Stockholm, indicated by its position very far back.

Leaving this question, we turn to the canals that issue from the three divisions of the cavum cerebrale cranii, beginning posteriorly and proceeding forward.

It would be expected that several canals for spino-occipital nerves had left the posterior division of the cavum cerebrale cranii, but, as pointed out above, no such canals could be observed in the material so far investigated, a fact which of course does not necessarily imply that they are lacking, for the possibility is to be taken into consideration that they are very minute and on that account can only exceptionally be distinctly seen, and then only in especially well-preserved specimens.

From the middle division of the cavum cerebrale issues most posteriorly the wide vagus canal (X_{vn} Figs. 10, 11, Pl. XX; Pl. XXIII; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1, 2). Some distance anterior of this appears the glossopharyngeus canal (IX) and most anteriorly, rather close to each other, the acusticus canal (VIII), the facialis canal (VII) and the trigeminus canal (V). The acusticus and facialis canals take their origin from a common recess on the side of the division, a recess which I have termed the acustico-facialis recess (*afr*). All the canals enumerated leave the basal parts of the division. Besides these there are, however, three other canals situated higher up, all of which must have been traversed by vessels. The most posterior one of these, (*v.lb*, Fig. 11; Pl. XX; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1, 2), which is very wide and goes from the postero-dorso-medial parts of the labyrinth cavity to the dorsal part of the vagus canal at the transition between this canal and the division in question of the cavum cerebrale, probably transmitted a vein that drained the labyrinth. The two remaining canals (v_1, v_2, Fig. 11; Pl. XX; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1, 2, 3) are both narrow, connect the dorsal parts of the division above the acustico-facialis recess with the labyrinth cavity and most probably may have been traversed by arteries.

From the anterior division of the cavum cerebrale cranii, the oculomotorius canal (III, Fig. 11; Pl. XXIII; Pl. XXV, figs. 1, 2; Pl. XXVI, figs. 1, 2), the opticus canal (II) and the canal for the tractus olfactorius (I) take their origin, the one last mentioned from the anterior end and the one first mentioned far posteriorly, not so very far from the middle division. Besides these canals there issue from the anterior division, as we have already seen, the canal *par* and the diverticle *ep*.

Guided by the detailed knowledge we possess of the canals for the cranial nerves, we are to a certain extent able to draw conclusions concerning the brain and its position in the cavum cerebrale. From the place of exit and direction of the acusticus facialis and trigeminus canals, it is obvious that the roots of the n. acusticus, n. facialis and n. trigeminus must have left the medulla oblongata in the anterior half of the middle division of the cavum cerebrale and, accordingly, that the medulla oblongata reached far forward in the middle division (*myl*, Figs. 12, 13). The most anterior part of this division was, however, certainly occupied by the whole, or, at least, the larger posterior portion of the mesencephalon (*mes*, Figs. 12, 13). Dorsally of the mesencephalon and the anterior portion of the medulla, there probably existed a rather well-developed cerebellum (*met*, Figs. 12, 13) and the anterior half of the middle division may accordingly have been rather well filled, while the posterior half of the same division, which lodged only the posterior longer portion of the medulla oblongata, cannot have been filled by this. The conditions there must have been about as seen in Figs. 12, 13. The medulla was undoubtedly long, but it is impossible to say with certainty how far back it extended.

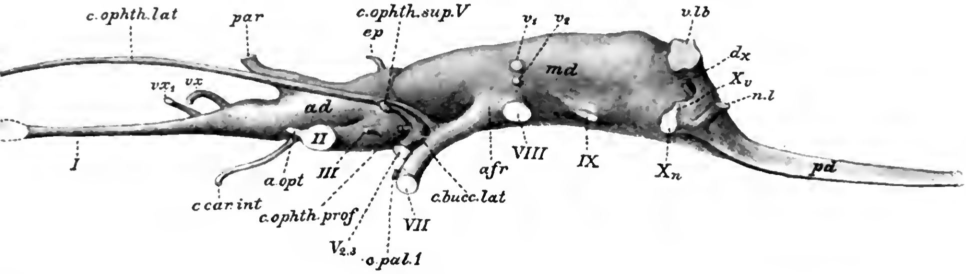

Fig. 11. Macropetalichthys rapheidolabis

Shape of the cavuum cerebrale cranii in lateral view. After the Field Museum specimen, with the exception of the posterior division, which is restored after a specimen in the American Museum. ×¾.

ep, canal of doubtful importance, probably an occasional structure; *par*, pineal canal, probably for both the parietal and pineal organs (at least in the basal half); v_1, v_2, canals probably for arteries from the cavum cerebrale cranii to the labyrinth cavity; vx, vx_1, canals probably for veins. Other letters of reference as in text fig. 10.

The anterior division of the cavum cerebrale must, as is easily understood, have lodged the telencephalon and diencephalon (Figs. 12, 13), and in addition probably a short anterior portion of the mesencephalon. The diencephalon (*dic*) seems to have been long, probably reaching forward to about the middle of the division, but, may as far as can be judged, not have been so high as this. The hypophysis, and, if they were developed, the saccus vasculosus and the lobi inferiores as well, may have been situated in the shallow concavity in the floor of the anterior division approximately in the way shown in text fig. 13. The hypophysis occupied, however, a small depression of its own in the middle part of the concavity (*fhy,* Fig. 10). The canal *par,* probably lodged both the parietal and pineal organs, while the importance of the diverticle *cp* is still doubtful.

The telencephalon (*tel,* Figs. 12, 13) probably occupied about the anterior half of the anterior division of the cavum cerebrale. It must have been comparatively broad and low and anteriorly it was probably bilobated, a portion of it on each side extending into the proximal part of the canalis tractus olfactorii of its side. From each of the two anterior lobes the tractus olfactorius (I) went through its long canal anteriorly and laterally to the lobus olfactorius (*l.olf*), which, as far as can be judged, was situated close to the nasal pit.

From what has now been said it will be evident that the cavum cerebrale cranii only to a certain extent reflects the shape of the brain. But despite this it seems to be rather clear that the brain cannot have resembled that in *Dipnoi, Crossopterygii* or *Actinopterygii,* but that it may have been Elasmobranchian-like. At least with regard to certain anterior parts it probably was much as in *Heptanchus* (Cf. GEGENBAUR 1898, Fig. 455) and *Chalmydoselachus* (ALLIS 1923, Pl. 22, fig. 59).

The restoration of the brain given in text figs. 12 and 13 is based chiefly on the conditions in *Heptanchus* and is of course to a large extent rather arbitrary.

DERMAL BONES OF THE PRIMORDIAL NEUROCRANIUM

The ventral side of the primordial neurocranium was entirely without dermal bones, the parasphenoid of COPE'S (1891, p. 453, Pl. 29, fig. 2; Pl. 30, fig. 1) and EASTMAN'S (1908a, pp. 108-109; 1908b, pp. 174-175) descriptions being simply the external bone layer on the ventral side of the primordial neurocranium.

The dorsal side of the primordial neurocranium, on the contrary, is, as known, completely covered by a cuirass of dermal bones, a cuirass, which, in this paper, is generally referred to as the dermal cranial roof. On account of the postero-medial displacement of the eyes, the orbital openings have become entirely encircled by the dermal cranial roof.

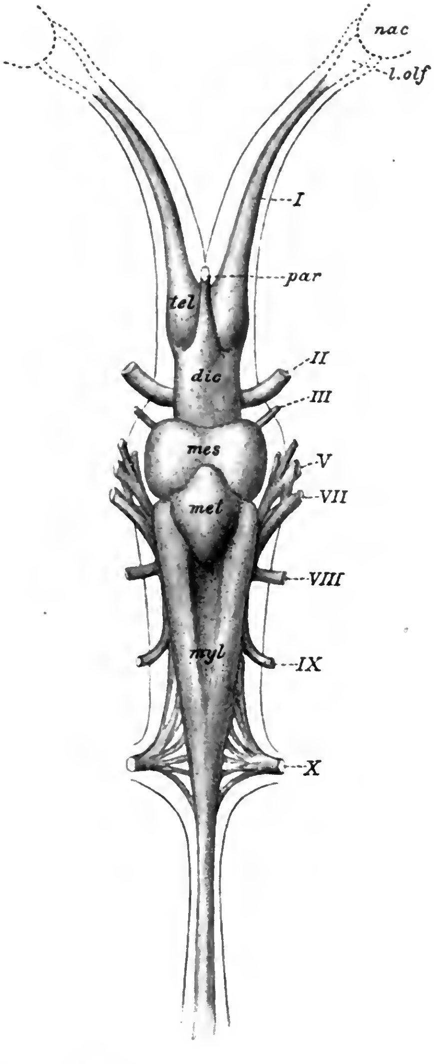

Fig 12. MACROPETALICHTHYS RAPHEIDOLABIS

Hypothetical shape of brain from above in relation to the cavum cerebrale cranii. Brain with a dark tone, outlines of the cavum cerebrale indicated by a continuous line. ×¾.

dic, diencephalon; *l.olf*, lobus olfactorius; *mes*, mesencephalon; *met*, cerebellum; *myl*, medulla oblongata; *nac*, nasal pit; *par*, parietal or pineal organs or both; *tel*, telencephalon; I, tractus olfactorius; II, n. opticus; III, n. oculomotorius; V, roots of the trigeminus proper; VII, facialis roots + lateralis roots of the entire trigemino-facialis complex; VIII, root of the n. acusticus; IX, root of the n. glossopharyngeus; X, roots of the n. vagus and the n. lineæ lateralis.

The general shape of the dermal cranial roof may be seen in Fig. 15. The restoration given of it by Dean (1901, Fig. 12, p. 116) is almost correct, while the one published six years later by Eastman is wrong with regard to its general proportions (Eastman 1908a, Fig. 19), as becomes evident by comparing Eastman's restoration with the specimen he figured in Pl. II of his description.

Concerning the number of bones composing the dermal cranial roof, I have nothing new to add here to what is known from earlier descriptions. The boundaries between the various bones, on the other hand, I have in certain places found to be somewhat different from those shown in Dean's (1901) and Eastman's (1908a) restorations. But my own restoration (Fig. 15) does not claim to be fully accurate in this respect, as the material investigated by me was both very limited and imperfectly preserved with regard to the dermal cranial roof.

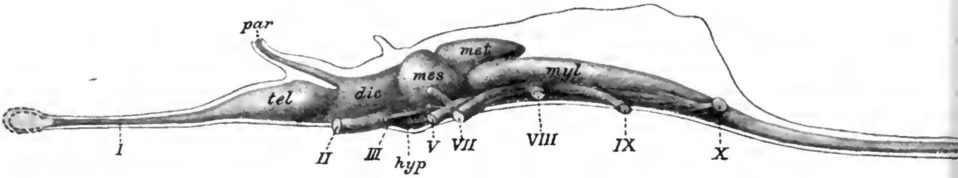

Fig. 13. Macropetalichthys rapheidolabis

Hypothetical shape of brain from the left side in relation to the shape of the cavum cerebrale cranii. Brain with a dark tone, outlines of the cavum cerebrale indicated by a continuous line. ×¾.

hyp, hypophysis and other ventral parts of the diencephalon. Other letters of reference as in text fig. 12.

As in a paper which I expect to publish later, I think I can show that the dermal bones of the cranial roof in Arthrodires have evolved independently of those in the *Teleostomi,* or, to put it differently, that they are not directly comparable to those in the *Teleostomi,* I have lettered them here in text fig. 15 with indifferent letters.

Each plate *S* has, posteriorly, close to the posterior border, a vertically descending lamina which is rigidly fixed to the cranio-spinal process of its side. In the specimens investigated by me, this lamina is unfortunately very imperfectly preserved, so that its extension and relations could not be established with certainty. In *M. pelmensis* it is, however, well-preserved, and it seems there to cover the posterior surface of the cranio-spinal process and to be very large and meet its fellow of the opposite side in the median line.

HENNIG in his description of *M. pelmensis,* did not perceive the true nature of this lamella, but considered it to be a paired lateral occipital (HENNIG 1907, pp. 585-586, Fig. 3, *OL*)[1]. This ventral lamella is necessary for the support of the much lengthened, posterior parts of the dermal cranial roof. A parallel to this is found in sturgeons (both Polyodontids and Acipenserids) in which a lamella issues from each extrascapular bone downwards in such a way that it covers and is fixed to the anterior surface of the cranio-spinal process of its side. Accordingly, it is not homologous with that in *Macropetalichthys.* In *Saurichthys,* in which also a strong cranio-spinal process, very similar to that in sturgeons, occurs, a descending lamina from the dermal cranial roof is, on the contrary, entirely lacking (STENSIÖ 1925).

The plate *M* is said by EASTMAN (1908a, p. 104; 1908b, p. 169) to be pierced by a fine canal just above the canal *par* in the roof of the primordial neurocranium. The material investigated by me was not satisfactorily preserved at this place, and I have therefore not been able to verify the correctness of EASTMAN's statement as to this point.

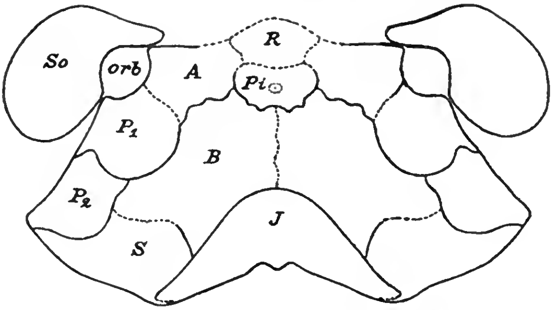

Fig. 14. TITANICHTHYS AGASSIZI, NEWB.

Dermal cranial roof and infraorbital plate. After EASTMAN (1908a, fig. 29). Sensory canal grooves omitted. Much diminished. *Pi,* pineal plate; R, rostral plate; *orb,* orbital opening.

DERMAL BONES OF THE CHEEK

No remains of dermal bones were found which, with certainty, belonged to the cheek, and it is rather probable that these bones were either much reduced or entirely lacking in the fish. That the plate P_1, situated latero-ventrally of the orbital opening, is no infraorbital bone, is evident both from the fact that the eye has shifted a rather considerable distance postero-medially and from the course of the sensory canals, as we shall understand from the account of these given below.

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[1] The description which HENNIG (1907) gives of *M. pelmensis* is also in most other respects very incorrect, the anatomical features of the fish having been for the most part entirely misunderstood.

VISCERAL SKELETON

Remains of the visceral skeleton have hitherto not been found. Despite this we are, however, able to draw certain conclusions about it.

The palatoquadrate was not coalesced with the primordial neurocranium, but was an independent element. As far as we can judge, it did not articulate with the primordial neurocranium, either anteriorly or posteriorly, and, if this be true, it must have been suspended merely by ligaments below the ethmoidal region and by means of the hyoid arch below the labyrinth region. Accordingly, its relations to the primordial neurocranium seem to have been about as in sturgeons and recent sharks (except the *Notidanidc*, in which, as known, there exists a postorbital articulation between the palatoquadrate and primordial neurocranium).

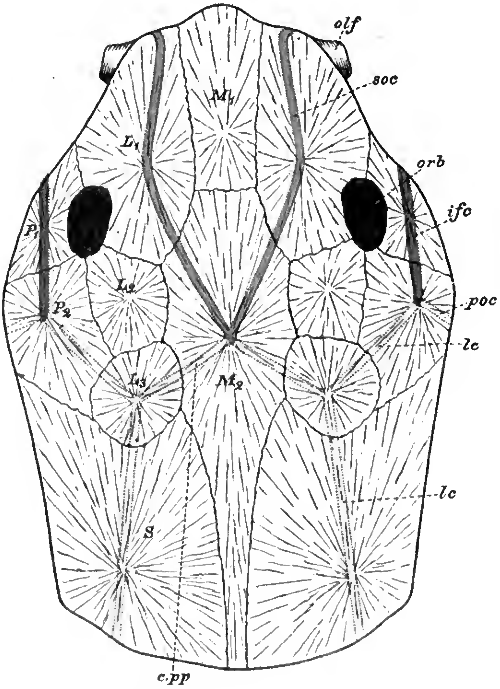

Fig. 15. MACROPETALICHTHYS RAPHEIDOLABIS

Restoration of the dermal cranial roof. Course of the sutures probably in places not fully correct. Sensory canals marked with double dotted lines and colors. Ornament of the bones omitted. ×⅜.

L_1, L_2, L_3, M_1, M_2, P_1, P_2, S, dermal bones of the cranial roof; *c.pp*, sensory canal commissure, probably corresponding to the posterior head lines of pit origin in recent fishes (red); *ifc*, infraorbital sensory canal (blue); *lc*, cephalic division of the lateral line(red); *olf*, nasal capsule; *orb*, orbital opening; *poc*, preopercular sensory canal (yellow); *soc*, supraorbital sensory canal (green).

Probably there was in relation to the palatoquadrate, a large musculus preorbitalis (Cf. the description of the ethmoidal region above).

If my interpretation of the canal *c.hy* as the canal for the vena hyoidea is correct, it is obvious that the hyoid arch articulated against the primordial neurocranium closely anterior to the external opening of this canal, or, at least that the hyoid arch, if it did not articulate against the primordial neurocranium, had its dorsal end situated closely anterior to this place, for it must of course have been situated anterior to the hyoid vein. Or to express it in another way, the hyoid vein must have passed upward to the jugular vein along the posterior side of the hyoid arch. Whether the dorsal end of the hyoid arch was situated ventrally of the vena jugularis, as in Selachians, or dorsally of the same vein as in the *Teleostomi*, it is impossible to decide from the specimens investigated (Cf. ALLIS 1915, 1918b).

Of much interest in this connection is the fact that the jugular vein as well at the upper end of, as anterior and posterior to the hyoid arch, went within the lateral wall of the primordial neurocranium and that, accordingly, a shifting of the place of articulation of the dorsal end of the hyoid arch against the primordial neurocranium could take place in a dorsal or ventral direction without affecting the jugular vein. As the jugular vein in *Eusthenopteron*[1] also passed within the lateral wall of the primordial neurocranium to about the same extent as in *Macropetalichthys* and probably did also in other Crossopterygians (Cf. STENSIÖ 1922, p. 201, the long intramural course of the truncus hyoidemandibularis facialis) one suspects that this was originally the case in all fishes.

If this suspicion be true, the mainly extramural course of the jugular vein in most fishes would be due to reduction of certain lateral parts of the lateral walls of the primordial neurocranium. And, moreover, it would be very easy to understand how the place of articulation of the hyoid arch could have shifted upwards to the dorsal side of the jugular vein in the *Teleostomi*. Finally, the hyomandibular of the *Teleostomi*, would not, as ALLIS (1915, 1918b) supposes, have incorporated at its dorsal end certain parts lacking as such in the hyomandibular of the Elasmobranchs. The conditions found in *Macropetalichthys* and *Eusthenopteron* with regard to the vena jugularis and the vena hyoidea thus seem to make certain of the views recently advanced by ALLIS (1915, 1918b) concerning the homologies of the hyomandibular of fishes very doubtful.

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[1] Observation made on a well preserved specimen in the collection of the Palæontological Institution of Upsala.

The first branchial arch followed not very far behind the hyoid arch. On account of the cranio-vertebral articulation found in most or all Arthrodires, there is no reason to believe that the branchial basket extended backwards into the abdominal region of the trunk, but was limited to the suboccipital part of the head.

DENTITION

Unfortunately the dentition is so far entirely unknown.

SENSORY CANALS OF THE HEAD

The sensory canals are found preserved on the head only in the dermal cranial roof. They consist there of tubes which are situated within the bones, or, more exactly, in ridge-like thickenings on the lower side of the bones (Figs. 4, 8, 9). Accordingly they have a very deep position (Cf. KAER 1915, p. 12), a fact which explains that there are frequently traces of them preserved even in specimens in which the dermal bones have almost entirely weathered away, as, for instance, in the specimen reproduced in Pls. XIX, XX. At least in the larger parts of their extension they open outwards with a double series of fine tubuli. These tubuli occur in great number and are situated fairly close to each other, conditions which seem to indicate that they were much more numerous than the sensory canal organs. In any case they are much more numerous than the nerve-canals leading to the sensory canals.

On account of the fortunate circumstance that the fine canals for the nerve branches to the sensory canal organs are lined by a thin layer of bone, they could be preserved, and thus enable us to get a rather complete knowledge of the manner in which the sensory canals were innervated. With the help of this knowledge it is not difficult to homologize the sensory canals in *Macropetalichthys rapheidolabis* with those in recent fishes, as will be evident from the subsequent account. With regard to the terminology, I shall follow ALLIS (1889; 1900; 1901; 1903; 1905; 1923) with the exception only that in accordance with EWART (1892), EWART and COLE (1895), EWART and MITCHELL (1892), and COLE (1896a, b; 1898) I limit the infraorbital sensory canal to those parts innervated by the n. buccalis lateralis and n. oticus lateralis.

The *supraorbital sensory canal* (*soc.* Figs. 8, 9, 15; Pls. XIX. XX, XXI, XXIII) has in its present state of preservation its anterior end at the anterior border of the bone-plate L_1, but in the living fish it continued forward into the soft tissue anteriorly and laterally to this plate. How it may have passed in this soft tissue it is of course not possible to say positively, but it seems to me most probable that it was there as in *Coccosteus,* and forms allied to this (Cf. JAEKEL 1902 fig. to page 107; 1906a, text figs. 2, 3), i.e., that it very soon turned backwards and went dorsally and behind the nasal opening down to the infraorbital canal. It would thus, if I am right, have had the same course in its anterior parts as in Elasmobranchs. (Cf. GARMAN 1888; ALLIS 1901, pp. 104-107, 118-128; 1905, p. 419, pp. 470-478; 1923; EWART 1892, pp. 66-74; HAWKES 1906, pp. 960-961, Pl. 68; cf. also COLE 1896 a, b.) Within the bone-plate L_1 it runs first backward and slightly laterally to about the center of the ossification of the plate, then fairly suddenly curves and takes a backward and slightly medial direction. With this direction it continues backward to the plate M_2, which it traverses to about the center of ossification, and here joins its fellow of the opposite side and a cross comissural sensory canal between the cephalic division of the lateral lines in the way shown in text fig. 15. No anastomosis is found between it and the posterior part of the infraorbital canal of its side.

To the supraorbital sensory canal go several fine branches from the canal for the n. ophthalmicus lateralis. The number of these branches could not, however, be established. The posterior ones issue dorso-postero-medially, the anterior ones antero-dorso-laterally. In Pls. XXI and XXIII one anterior branch (*rm.ophth.lat*) is clearly seen issuing from the canal for the n. ophthalmicus lateralis (*c.ophth. lat*) to the supraorbital sensory canal (*soc*).

Its considerable extension backwards and its direction in the posterior parts, indicate with certainty that the supraorbital sensory canal comprises not only the supraorbital sensory canal as found, for instance, in *Amia* and many other fishes, but also the homologue of the anterior head line of pit organs of these fishes. (Cf. ALLIS 1889, pp. 505-506; 1900, pp. 445; 1903, p. 187; 1905; HERRICK 1901, pp. 222-223; STENSIÖ 1921, pp. 218, 263; 1922, p. 192; 1923, p. 1258; 1925.)

The *infraorbital sensory canal* (*ifc,* Figs. 8, 15; Pls. XIX, XX, XXII; Pl. XXIV, fig. 1) has its posterior end situated at about the ossification center of the plate P_2; being there continuous with the cephalic division of the lateral line of its side. From this place it runs forward and slightly medially into the plate P_1, retaining the same direction as behind this and being during this part of its course situated latero-ventrally of the orbital opening. It does not, however, traverse the bone-plate P_1, in the entire length, but goes to the lateral border of this some distance behind the anterior end as is shown in text fig. 15. After leaving the cranial roof at this point, it must have passed forward and downward on the cheek, probably through soft tissue, and it is likely that it extended as far forward as to the rostrum, and, that it, as pointed out, anastomized with the supraorbital canal behind the nasal opening.

To the part of the infraorbital canal situated within the bone-plates P_1 and P_2 lead a few fine canals which pierce the lateral parts of the postorbital process and which very probably transmitted lateralis branches from a nerve corresponding to the r. oticus lateralis of recent fishes. Two of these branches (*in*) are partly seen in Pls. XX, XXII, and it is easy to understand from their direction that they in any case must have been traversed by lateralis branches that were given off from a proötic nerve, i.e., a nerve that had its exit through the cranial wall anterior to the labyrinth.

Before leaving the infraorbital canal, it is finally necessary to point out that its course in the dermal cranial roof is incorrect in the restoration published by DEAN (1901, text fig. 12).

The *cephalic division of the lateral line* (*lc,* text figs. 4, 15; Pls. XIX, XX, XXIV) enters the dermal cranial roof at the posterior border of the bone-plate *S,* traverses this bone-plate in anterior and slightly medial direction, and continues with the same direction to the ossification center of the bone-plate L_3. There it suddenly takes an antero-lateral course and goes with this to the ossification center of the bone-plate P_2, joining there, as already mentioned, the infraorbital canal.

At the place in the bone-plate L_3, where the cephalic division of the lateral line turns laterally, it gives off an antero-medial branch which goes to the ossification center of the plate M_2, joining there with its fellow of the opposite side and forming in this way an angulated transverse commissure (*c.pp,* text figs. 4, 15; Pls. XIX, XX; Pl. XXIV, fig. 3). At the angle in the median line this commissure anastomozes with the posterior end of the supraorbital sensory canals just after these have joined one another.

A short anterior portion of the cephalic division of the lateral line just behind the infraorbital sensory canal was probably innervated by the presumed lateralis branch that traversed the cranial wall, together with the n. glossopharyngeus. The remaining part of the division anterior of the transverse commissure, as well as the adjacent half of this commissure, was supplied by a nerve that issued from the n. lineæ lateralis already within the vagus canal and from there went upward through the canal d_x, (Pl. XXIV, fig. 2), and its branches d_{xa} and d_{xb} (Pl. XXIV, fig. 2), thus by a ramus supratemporalis from the n. lineæ lateralis. Finally, the part of the division behind the transverse commissure was innervated by a number of fine branches which independently of each other issued from the n. lineæ lateralis, each of them probably supplying only a single sense organ. In the anterior division of the occipital region where these nerve branches pierced the primordial neurocranium, six of these canals are seen in the Field Museum specimen (*ld_1-ld_6*, Pls. XIX, XX; Pl. XXIV, fig. 3).

In the description of the anterior division of the occipital region it was pointed out that a fine branch from the n. lineæ lateralis probably went up to the dorsal surface of the primordial neurocranium through the canal *cl* (text fig. 3; Pls. XIX, XX). This fine lateralis branch thus had, if it really existed, such a course that it must have innervated one or a few sensory canal organs situated medially of the cephalic division of the lateral line posterior to the cross commissural canal *c.pp,* but, as it is not a closed sensory canal there, the presumed sensory canal organs supplied by it would have formed a short, transverse pit-line. Unfortunately the material investigated did not enable me to decide whether there was a groove for such a pit-line on the dorsal side of the dermal bones. The possible non-existence of the groove need not, however, indicate absolutely the absence of the pit-line, for this may in such a case very well be thought to have been situated entirely in the skin and thus to have been wholly unrelated to the underlying dermal bones.

If the pit-line in question really could be shown to exist, it would, according to its position and innervation, evidently be homologous with the supratemporal commissure in recent fishes, while the cross commissural canal *c.pp* would represent the posterior head line of pit organs in these, a view which is also supported by the position and direction of each half of the latter canal. (Cf. ALLIS 1889, Pl. 42; 1901, pp. 101-103, 116-117, Pl. 10; 1903, pp. 186-187, Pl. III; 1905, pp. 471, 474; EWART 1892, Pl. II, fig. 2; STENSIÖ 1923, p. 1258, fig. 4.) Below, in the description of *Epipetalichthys,* we shall find additional facts which point in the same direction.

According to the restoration published by DEAN (1901, text fig. 12) a canal, which, in its position, corresponds very well to the preöpercular canal, issues in latero-ventral and slightly posterior direction from the point where the infraorbital canal joins the cephalic division of the lateral line. This canal is not found in EASTMAN's restorations in 1908 (EASTMAN 1908a, text fig. 19; 1908b, text fig. 24), and the material investigated by me was not preserved sufficiently well to show with certainty whether DEAN or EASTMAN is right in this respect. As the canal in question is found in a specimen described as *Macropetalichthys agassizi?* below, and also occurs in most other Arthrodires, it seems very likely that it is not missing in *Macropetalichthys rapheidolabis.* On account of this it was drawn in text fig. 15, in which it is designated by the letters *poc.* If it really was present, it must have continued down to the cheek, where it chiefly, or, perhaps, even entirely, had its passage through soft tissue.

REMARKS

On account of the flat, broad shape of the primordial neurocranium as a whole and the position and direction of the orbital openings, there can be no doubt that *M. rapheidolabis,* like other species of *Macropetalichthys* must have been a decided benthonic form.

The description given here makes it fully evident that many of the strange anatomical features which EASTMAN thought he had observed in *M. rapheidolabis* are mistakes.

MACROPETALICHTHYS AGASSIZI? (H. v. Meyer)

(Pl. XXIX, figs. 1, 2)

Through the courtesy of Mr. S. JUNKERMANN of Bielefeld, Germany, I had the opportunity of examining an imperfectly preserved neurocranium of a Macropetalicthyid, which, as far as it is preserved, agrees so well with *M. rapheidolabis,* that it at least provisionally seems correct to refer it to the genus *Macropetalichthys.* Among the species described so far of this genus it seems to resemble most closely *M. agassizi,* and on this account I have, with some hesitation given it this specific name.

The primordial neurocranium is imperfectly preserved, being represented only by certain parts of the occipital region (Pl. XXIX, fig. 1), which are much fractured and crushed. As far as can be seen, it seems to have been less ossified than that of *M. rapheidolabis,* but at least in the posterior, narrow division of the occipital region, I found both the internal and external bone layers. Further forward the internal bone layer appears to have been entirely lacking. With regard to its general shape, the primordial neurocranium seems to have considerably resembled that in *M. rapheidolabis.*

In text fig. 16 we see two transversal sections through the most anterior part of the posterior narrow division of the occipital region. As is evident from these sections, the hæmal groove did not extend so far forward as in *M. rapheidolabis,* and it is further worthy of notice, that, contrary to what is the case in that species, there was no bone tube around the notochord. In the anterior one of the two sections figured, the postero-lateral-dorsal corners of the anterior broad division of the region are seen in section, as they are extended considerably in postero-lateral direction (*pr,* text fig. 16a). Of the dermal cranial roof we find the plates M_2, L_3, P_2 and S (text fig. 16a; Pl. XXIX, fig. 2) more or less well-preserved. Their ornaments consist of small, numerous, rather densely placed tubercles, which are stellate at their bases.

The sensory canals are closed tubes situated deeply in the dermal bones, as in *M. rapheidolabis.* They open outward with numerous, straight, unbranched tubuli, but while these tubuli in *M. rapheidolabis* are arranged in a double series, they form here only a single one from each canal (Pl. XXIX, fig. 2). It is quite probable that the canals for nerves leading from below to the sensory canals were much fewer in number than the tubuli, a fact which enables us to conclude with a rather great degree of probability, that the sensory canal organs did not correspond in number to the tubuli but were much less numerous than these.

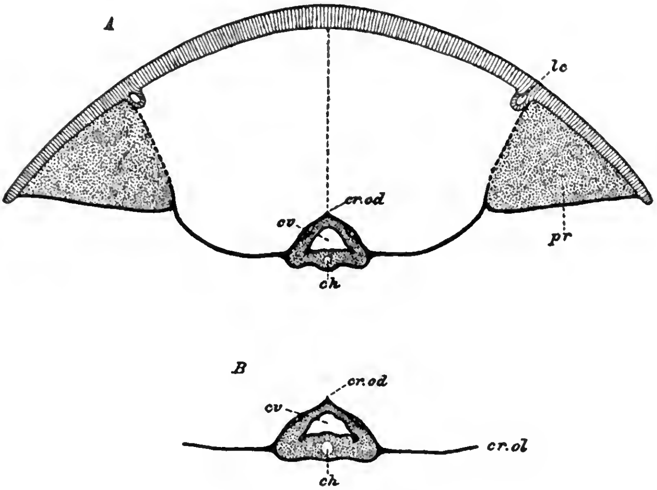

FIG. 16. MACROPETALICHTHYS AGASSIZI?

Transverse section through the most anterior part of the posterior narrow division of the occipital region. The section *A* taken only a short distance anterior to the section *B*. Cartilage dotted, layers of substitution bone with strong black lines, dermal bones of the cranial roof with vertical striation. $\times {}^3/_2$

cr.od, crista occipitalis dorsalis; *cr.ol,* crista occipitalis lateralis; *ch,* probable position of the space for the notochord; *cv,* cavum cerebrale cranii; *lc,* cephalic division of the lateral line; *pr,* postero-laterally projecting corner of the anterior broad division of the occipital region.

MACROPETALICHTHYS PELMENSIS, Hennig

The description given by HENNIG (1907) of this species is, as I found by examination of his type specimen, in several respects very incorrect.

What HENNIG (1907, pp. 585-586) takes to be a paired lateral occipital seems in fact to be a ventral, paired process from the bone-plate *S*, of the dermal cranial roof, according to the terminology employed by me in the present paper. This process, which meets its fellow of the opposite side in a median suture and extends very low downwards, covers the posterior surface of the probably very large cranio-spinal process of its side.

The structure of the dermal cranial roof was also in other respects very much misinterpreted by HENNIG, a circumstance which is, however, so obvious that it will not be necessary to deal with it here.

EASTMAN'S description of the species in 1908 (1908b, pp. 176-177) is, with regard to the posterior parts of the neurocranium, also very erroneous, as EASTMAN on that occasion did not even correctly recognize the main divisions of the neurocranium, a fact which lead him to certain very strange conclusions about the position of the ductus endolymphaticus and the relations between this and the sensory canal system (Cf. KAER 1915, pp. 11-12).

It may finally be emphasized in this connection that the primordial neurocranium probably is preserved in the specimen, and that a further preparation of it would therefore be very desirable.

EPIPETALICHTHYS WILDUNGENSIS, Jaekel, gen. nov., sp. nov.

Pl. XXVIII, figs. 1, 2; Pl. XXIX, figs. 3, 4; Pl. XXX, fig. 1; Pl. XXXI, fig. 2.

This species, which is a new one and also represents a new genus, is from the upper Devonian of Wildungen, Germany. It was placed at my disposal by Professor O. JAEKEL of Greifswald. On the labels accompanying it Professor JAEKEL had named it *Epipetalichthys wildungensis*. So far, only a single specimen, represented by the imperfectly preserved neurocranium, has been found of it. To judge from this specimen, the species must have attained about the same size as *Macropetalichthys rapheidolabis*.

PRIMORDIAL NEUROCRANIUM

General remarks. The primordial neurocranium, if we first turn to this, is partly rather badly crushed and fractured, and, in addition, also, weathered in places, so that it is not by far as well adapted for a detailed examination as that in the Field Museum specimen of *Macropetalichthys rapheidolabis.* In its general shape it must obviously have resembled that of the last-mentioned species, but, as we shall see, it differs distinctly from this in certain details.

Its degree of ossification was considerably less than that in *M. rapheidolabis* and less also than in *M. agassizi?,* a fact which deserves a special attention, as we are here concerned with an upper Devonian form, while the other two just mentioned specimens are both from earlier divisions of the Devonian. At least this is beyond question the case with *M. rapheidolabis,* which occurs only in middle Devonian strata.

On account of the imperfect state of preservation in which the primordial neurocranium is found, it is not possible to make out with full exactness the extension of its different layers of substitution bone, but the following may give an idea of the most important differences from *M. rapheidolabis* in this respect.

1. There is no evidence of the labyrinth bone layer. 2. The inner bone layer seems to be entirely lacking, except in the posterior, narrow division of the occipital region (text fig. 17). 3. The external bone layer surrounds the posterior, narrow division of the occipital region, and extends from this forward also on to the lateral and ventral sides of the anterior division of the same region and the ventral side of the labyrinth region. Whether, however, it continued from the latter region to the ventral side of the orbitotemporal region, cannot be decided, as the ventral parts of this region have been destroyed. On the ethmoidal region it is, however, found again on the ventral side and, in addition, at least partly, on the lateral sides and probably also on the anterior end. Accordingly, it is lacking on the larger anterior part of the dorsal side, quite as in *M. rapheidolabis,* but, contrary to what is the case in that form, also probably on the lateral sides of the entire labyrinth and orbitotemporal regions and the posterior side of the ethmoidal region. If it was lacking on the ventral side of the orbitotemporal region, this region would obviously have consisted entirely of cartilage. 4. The canal layers seem to have become entirely reduced.

As far as I can see, there are no traces of ossification centers either in the occipital region or in the ethmoidal region.

MICROSCOPIC STRUCTURE OF THE BONE

The substitution bone of *M. rapheidolabis* has generally been much infiltrated by a dark bitumen that is difficult to remove, and, accordingly, no good microscopic sections can be made from it. I could, however, see rather distinctly that it has numerous cell spaces (Pl. XXXI, fig. 1). In the species under consideration the bone tissue is also not favorably preserved for microscopic investigation, but it is fully obvious that it there too contained cell-spaces in fairly large number. In the posterior division of the occipital region we can further see that from the external and internal bone layers, numerous, irregular trabeculæ (Pl. XXXI, fig. 2) extend a short distance into the parts of the cranial walls that were occupied by cartilage, so that there really is certain evidence of cancellous bone, although this bone was very slightly developed. By means of short bone trabeculæ of about the same kind as those just mentioned, the bone layer surrounding the notochordal space (*ch.l,* Pl. XXXI, fig. 2) is connected with the internal and external bone layers. Otherwise, no details can be observed.

OCCIPITAL REGION

As in *M. rapheidolabis* and *M. agassizi?* the occipital region is composed of two divisions, a posterior, long and narrow one, and an anterior, short and broad one.

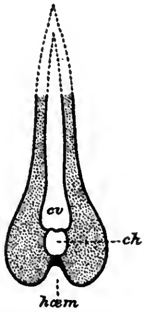

Fig. 17. EPIPETALICHTHYS WILDUNGENSIS Jaekel

Transverse section through the anterior half of the posterior division of the occipital region. Layers of substitution bone with strong black lines, cartilage dotted. The trabeculæ of substitution bone penetrating inwards into the cartilage from the bone layers not drawn. $\times {}^3/_2$

hæm, hæmal groove; *ch,* space for the notochord; *cv,* cavum cerebrale cranii.

The posterior one (text fig. 18; Pl. XXVIII, fig. 2) is represented merely by an anterior part, and no certain statement can therefore be given of its length. It is narrow and, contrary to that in *M. rapheidolabis* and *M. agassizi?,* it equals the other divisions of the primordial neurocranium in height. Further, it differs from that in the two species mentioned in the fact that it does not have the slightest traces of the crista occipitalis lateralis, which in them is such an important feature. The hæmal groove (*hæm,* text figs. 17, 18; Pl. XXVIII, fig. 2) is rather distinct and it is noteworthy that we find in the part of it preserved two rather shallow depressions (seen in text fig. 18), which, perhaps, may be segmentally arranged. Otherwise I only wish to emphasize that the division was narrowest anteriorly at the transition to the anterior division, gradually increasing somewhat in breadth backward from this place.

A transverse section through the part of the division present (text fig. 17) shows that the cavum cerebrale cranii (*cv*) within this part was very high and narrow and that there was below the cavum cerebrale a space for the notochord (*ch*). This space is, like that in *Macropetalichthys rapheidolabis,* bounded by a bone layer of its own, a bone layer that is continuous dorsally with the inner bone layer (bottom of the cranial cavity), and ventrally with the external bone layer (bottom of the hæmal groove), as already pointed out above (Pl. XXXI, fig. 2).

No traces of canals for spino-occipital nerves could be seen in the part of the division present.

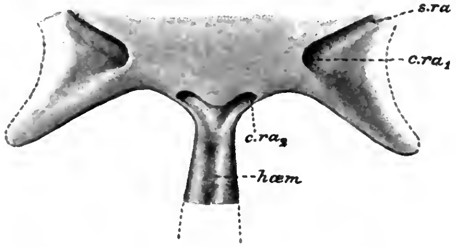

Fig. 18. EPIPETALICHTHYS WILDUNGENSIS

A posterior part of the primordial neurocranium from the central side. ×¾. *$c.ra_1$, $c.ra_2$,* anterior and posterior openings respectively of the canal for the radix aortæ (lateral dorsal aorta); *hæm,* hæmal groove; *s.ra,* groove for the radix aortæ lateral dorsal aorta, anterior of the canal *c.ra.*

Of the anterior broad division of the region only the ventral parts are accessible for investigation (text fig. 18; Pl. XXVIII, fig. 2). As far as can be seen from these its shape must have been very much the same as in *Macropetalichthys rapheidolabis.*

With regard to the details, we find that in this division the posterior part of the groove for the radix aortæ forms a closed canal in the primordial neurocranium. This canal has its anterior and posterior openings ($c.ra_1$, $c.ra_2$) situated as shown by text fig. 18 and Pl. XXVIII, fig. 2.

Nothing is so far known concerning the vagus canal and its branches.

LABYRINTH AND ORBITOTEMPORAL REGION

The labyrinth region (Pl. XXVIII, fig. 2) is somewhat longer than in *M. rapheidolabis.* It is very fragmentarily preserved, only parts of the external bone layer of its ventral side being left.

The orbitotemporal region is still more imperfectly preserved, and the only statement that can be made about it is that it certainly was rather short and that the orbits are situated far apart and in such a way that the eyes must have been directed much upwards, quite as in *M. rapheidolabis.*

ETHMOIDAL REGION

On account of the fact that, as pointed out, it has the external bone layer persisting to a considerable extension, the ethmoidal region has been fairly well preserved. A large part of its ventral side, an anterior part of its lateral side, an anterior part of its dorsal side and the anterior end are available for investigation (text fig. 19; Pl. XXVIII, fig. 1; Pl. XXIX, fig. 3; Pl. XXX, fig. 1).

From its broad, posterior end, it becomes rapidly narrow forward, but does not taper to a point, its anterior end being truncated and rather concave. The breadth at this end is about one-third of that at the posterior end.

From the antero-ventral part of each lateral side the olfactory capsule (*olf,* text fig. 19; Pl. XXIX, fig. 3; Pl. XXX, fig. 1) projects laterally exactly as in *M. rapheidolabis.* Unfortunately it is not so well preserved as in that species, its anterior and external parts being practically destroyed, and on account of this nothing can be said with certainty about its external opening and whether there was any nasal fontanelle on the ventral side of its lateral part.

The ventral surface of the region (Pl. XXIX, fig. 3) is rather concave in transversal direction and has in the postero-lateral part somewhat medially of the lateral margin a longitudinal, shallow groove (*s.pal*) for the r. palatinus facialis, quite as in *M. rapheidolabis.* Each one of the lateral surfaces (Pl. XXVIII, fig. 1), is concave in dorsoventral direction, and has a long post-nasal portion as in *M. rapheidolabis.* The dorsal surface (text fig. 19; Pl. XXX, fig. 1) is exposed only most anteriorly, the most anterior of the bones in the dermal cranial roof being weathered away. We find in this part of it a very deep, anteriorly and dorsally open depression (*pfg*), which, as far as can be judged from the conditions in the fossil, seems to have been lined by the external bone layer.

This depression, which, as already pointed out in the description of *M. rapheidolabis,* is obviously the homologue of the similarly situated depression in the skulls of Elasmobranchs, and which therefore may be properly called the cavum precerebrale, was, contrary to that in these fishes, separated from the cavum cerebrale by a thick septum of cartilage, presumably lined with the external bone-layer on the anterior side. There is thus no fenestra precerebralis. Laterally the cavum cerebrale is also well separated from the nasal capsules. Its floor is not perforated by any foramina.

CAVUM CEREBRALE

Since the internal bone layer, as pointed out, is lacking, except in the posterior division of the occipital region, the shape of the cavum celebrale is known merely in this, where it, as seen from text fig. 17, is very high and narrow.

The canal for the pineal and parietal organs seems not to have perforated the dermal bones of the cranial roof. At least no traces of such a perforation could be seen in the parts of the dermal bones preserved.

DERMAL BONES OF THE CRANIAL ROOF

Parasphenoid or other dermal bones were not present on the ventral side of the primordial neurocranium.

The dermal bones of the dorsal side of the primordial neurocranium (text fig. 19; Pl. XXX, fig. 1) are the same as in *M. rapheidolabis,* and their extensions and relations, too, are about the same as in this, with the exception, however, that the plates M_1 and M_2 do not meet, but are separated by the plates L_1, which extend to and suture with one another in the median line.

The plate L_3 is, in the posterior part, perforated by a rather large, oblong foramen (*d.end*), which certainly must be the external opening of the canal for the ductus endolymphaticus. This foramen lies definitely behind the place where in *M. rapheidolabis* the fossa endolymphatica is situated, and it seems therefore, rather probable that the ductus endolymphaticus from this fossa extended somewhat backward beneath the dermal cranial roof, thus making a bend and continuing backward quite as it does in *Chlamydoselachus* (GOODEY 1910, Pl. 43, figs. 7, 8) and several other Elasmobranchs (RETZIUS 1881). In this connection it deserves also to be emphasized that the position of the external opening of the ductus endolymphaticus in the form under consideration has, in relation to the sensory canal system, exactly the same position as in *Chlamydoselachus* (Cf. ALLIS 1923, Pl. II).[1]

The ornament on the dermal bones of the cranial roof consists of short, rather low, but nevertheless distinct, ridges, which, on the plates S and M_2, seem to lie with their longitudinal axis about parallel with

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[1] In *Chlamydoselachus* the ductus endolymphaticus has its external opening posterior of the supratemporal commissure of the main lateral lines; in *Acanthias, Mustelus* and others, on the contrary, it has this opening anterior of the same commissure (Cf. ALLIS 1901, Pl. 10).

the longitudinal axis of the head. On the other bones, excepting the plate M_1, on which their arrangement is unknown, the ridges are, on the contrary, arranged concentrically with the edges of the bones (Pl. XXIX, fig. 4). In the *Macropetalichthys* species known so far, the ornament consists of fairly sparse tubercles, which are, in the main, irregularly scattered.

THE SENSORY CANALS OF THE HEAD

The sensory canals of the head are known merely in the bones of the dermal cranial roof, in which they form closed canals. They are finer than in *M. rapheidolabis,* and the ridges for them on the lower

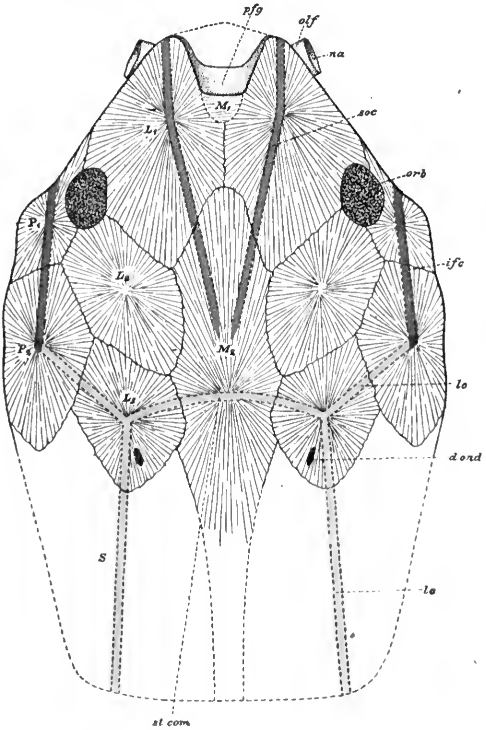

Fig. 19. EPIPETALICHTHYS WILDUNGENSIS

Head in dorsal view with the anterior parts of the bone plate M_1 removed to show the cavum precerebrale. The sensory canals marked with dotted outlines and colours. ×½.

L_1, L_2, L_3, M_1, M_2, P_1, P_2, S, dermal bones of the cranial roof (the anterior larger part of the plate M_1, removed); *d.end,* external opening of the canal for the ductus endolymphaticus; *ifc,* infraorbital sensory canal (blue); *lc,* cephalic division of the main lateral line (red); *na,* nasal aperture; *olf,* nasal capsule; *orb,* orbital entrance; *pfg,* cavum precerebrale; *st.com,* supratemporal commissure between the cephalic division of the main lateral lines (red); *soc,* supraorbital sensory canal (green).

sides of the bones are also less strong than in that species. They open outwards with numerous short and generally unbranched tubuli (Pl. XXX, fig. 1), which, however, contrary to the case in *M. rapheidolabis* are arranged like those in *M. agassizi?* and *M. pelmensis* in a single series.

The *supraorbital sensory canal* (*soc,* Fig. 19; Pl. XXX, fig. 1) does not extend as far backwards as in *M. rapheidolabis,* and, on this account, does not meet its fellow of the opposite side in the median line nor does it anastomose with the commissure (*s.com*) between the cephalic divisions of the main lateral lines, but ends some distance anterior of this. Behind the part where it ends as a closed canal it may, however, probably have continued a short distance further backwards as a pit line. Its anterior parts are not known, but it seems very probable that anterior of the most anterior part preserved in the fossil it curved strongly backwards and went first dorsally and then posteriorly of the nasal opening down to the infraorbital sensory canal, as it does in *Coccosteus* and Elasmobranchs. All the tubuli of the preserved portion of the canal issue in lateral direction, as is clearly shown by Pl. XXX, fig. 1.

The *infraorbital sensory canal* (*ifc,* Fig. 19; Pl. XXX, fig. 1) is, in the main, as in *M. rapheidolabis.*

The *cephalic division of the lateral line* (*lc,* Fig. 19); Pl. XXX, fig. 1) has also the same course as in *M. rapheidolabis,* and is, as in this, in communication with its fellow of the opposite side by a transversal commissure (*st.com,* Fig. 19; Pl. XXX, fig. 1), which traverses the plate L_3 and the plate M_2 to the plate L_3 of the opposite side. This commissure is, however, contrary to that in *M. rapheidolabis,* almost straight, and, as already mentioned, it does not communicate with the posterior ends of the supraorbital canals. It seems even to be situated behind the point in which the prolongations of these canals appear to meet each other. Consequently it has such a position and shape that in *M. rapheidolabis* it would seem to correspond to the presumed line of pit organs behind the cross commissural canal and not to this canal, and it thus appears to really represent the true supratemporal commissure of fishes. If this opinion is true, the homologue of the commissural canal of *M. rapheidolabis* would either be entirely lacking or be represented by a paired line of pit organs corresponding to the posterior head line of pit organs in recent fishes. (Cf. ALLIS 1889, pp. 505-506; 1903, p. 187; 1905; 1923, pp. 195-201; HERRICK 1901, pp. 222-223; STENSIÖ 1921, pp. 218, 263; 1922, p. 192; 1923, p. 1258; 1925; etc.)

The most anterior portion of the cephalic division of the lateral line situated between the supratemporal commissure and the infraorbital canal, does not open outward and has no tubuli at all. The remaining portion, on the contrary, is provided with numerous short tubuli, which issue on the lateral side and in lateral direction (Pl. XXX, fig. 1). The supratemporal commissure also has numerous tubuli, but these seem, as a rule, to perforate the bones in a straight upward direction (Pl. XXX, fig. 1).

Whether there was a preöpercular canal or not, it is at present impossible to decide.

REMARKS

As is obvious from this description, the form described here as *Epipetalichthys wildungensis* is well separated from other Macropetalichthyids known hitherto, and the erection for it of a new genus and species is therefore fully justified.

SOME GENERAL REMARKS ON THE MACROPETALICHTHYIDS

With the facts previously known, it has not been possible to arrive at any certain conclusion concerning the relationships of the Macropetalichthyids, but from what has now been determined some deductions may be made. Thus, there cannot be the slightest doubt that the Macropetalichthyids are true fishes, and, moreover, it is also clear that among recent forms they most resemble the Elasmobranchs. The most important characters which they have in common with these are the following: (1) The general shape of the primordial neurocranium, especially the tendency to broadening of the ventral surface, partly at the expense of the lateral surfaces. (This is especially the case in the labyrinth region in which the sacculus and perhaps the canalis semicircularis externus had about the same relation to the ventral surface as in *Chlamydoselachus* and most other Selachians). (2) The position and relations of the olfactory capsule. (3) The presence of a nasal fontanelle on the lower side of the nasal capsule as in *Chlamydoselachus* and certain other Selachians. (4) The presence of the cavum precerebrale. (5) The general shape of the labyrinth, especially with regard to the position of certain of its main parts, as, for instance, the utriculus. (6) The presence of the ductus endolymphaticus and the fact that there probably was a distinct fossa endolymphatica on the dorsal surface of the primordial neurocranium beneath the dermal bones. (7) The fact that the ductus endolymphaticus perforated the dermal cranial roof and had an external opening situated as in certain primitive Selachians (*Chlamydoselachus*). (8) The general shape of the brain as far as this can be restored from the exit of the nerve canals and the shape of the cavum cerebrale. (9) To a certain extent the course and arrangement of the blood-vessels and the presence of certain important trunks, as, for instance, the vena hyoidea. (10) The fact that the palatoquadrates as far as can be judged did not articulate with the ethmoidal region but must have been suspended below this by ligaments. (11) The probable course of the anterior part of the supraorbital sensory canal. (It should also be mentioned that the sensory canals must have had rather numerous sense organs and that they opened outward with very many tubuli.)

There are, of course, many differences between the Macropetalichthyids and Elasmobranchs, but these differences seem in general from the morphological point of view to be of much less importance than the agreements. The fact that bone occurs to a considerable extent in the Macropetalichthyids, while it is, as we know, totally lacking in recent Elasmobranchs, ought at first perhaps to be considered as an important difference, but from what is now known of the occurrence of bone in the vertebrate series, even this must be considered to be a character of minor importance. In order to illustrate this the following facts are given:

Typical bone tissue is found in the Cephalaspids, which, according to my recent investigations not yet published, are lowly organized vertebrates, without jaws, with three distinct proötic branchiomeres (hyoid segment, mandibular segment, and premandibular segment) and indications of still more. Further, there are in them also certain evidences that there were two segmentally arranged nerves anterior to the facialis, and we are able to conclude that they were in these respects much more primitive even than the recent Cyclostomes. As, in addition, more or less osteoid tissues occurs in a number of other very lowly organized Ostracoderms, we conclude that bone must be a tissue that appeared very early and very low down among the vertebrates, in fact already in the common stem of fishes and Cyclostomes. It is also well worthy of notice in this connection that in the Cephalaspids both the brain and the ears were situated in the bone of the cephalic shield, which means that there is in them no difference between dermal bone and substitution bone.

In the earliest appearing Dipnoans, Crossopterygians and Actinopterygians the primordial neurocranium and primordial skeleton in general are regularly well ossified, but the degree of ossification gradually decreases during the course of the geological periods, the substitution bone in many forms being finally entirely lost. We thus find that the primordial neurocranium in the Devonian Dipnoi *Scaumenacia* (my own observations) and *Dipterus* (TRAQUAIR 1878, p. 5; WATSON and DAY 1916, p. 33; observations made by the author in the Royal Scottish Museum, Edinburgh) is very well ossified, while it is not found to be ossified in any of the Carboniferous or post-Carboniferous forms, if we except the small ossification in the most posterior part of the occipital region of the recent *Ceratodus* (Cf. WATSON and GILL 1923; K. FURBRINGER 1904, Pl. 38, fig. 7; TELLER 1891; etc.). Among the Crossopterygians the process of reduction of the bone tissue is especially well displayed in the *Coelacanthidæ,* in which the Devonian form *Diplocercides* has the primordial neurocranium comparatively well ossified (STENSIÖ 1922; 1923, pp. 1259-1269), while the post-Devonian forms all have it to a very considerable extent consisting of cartilage, the bone being limited only to certain spots (STENSIÖ 1921, pp. 53-61, 91-94, 120-122; WATSON 1921; cf. also STENSIÖ 1923, pp. 1241-1259). According to information which I have received from Professor D. M. S. WATSON of London, the primordial neurocranium is, further, much more ossified in the Carboniferous Palæoniscids than in the Triassic ones *Birgeria* and *Acrorhabdus* (STENSIÖ 1921, pp. 152-175, 182-186, 187-198, 211, 224, etc.; pp. 238-250). Similar conditions are also met with in the Saurichthyids, in which those from the lower Triassic have their primordial skeleton very completely ossified, while primordial bone seems to be almost entirely lacking in those from the lower Jurassic (STENSIÖ 1925). In the Chondrosteids, Acipenserids and Polyodontids, which are very closely related to the Palæoniscids and Saurichthyids, the primordial neurocranium, as we know, is, as a rule, without bone. (We find bones only in very old specimens which indicates that the bone has lost its importance and that the parts still remaining therefore develop onto-genetically very late.) Finally, in a newly discovered ganoid from China, which with regard to its cranial anatomy much resembles *Amia,* the primordial skeleton is much more ossified than in *Amia.*

A similar reduction affects in several forms also the dermal bones. In the Dipnoi from the Devonian the dermal bones all lie superficially, are ganoine-covered and well developed (Cf. WATSON and GILL 1923). In many post-Devonian Palæozoic Dipnoans on the contrary, we see that, for instance, the most anterior and posterior bones of the dermal cranial roof sink down beneath the surface of the dermis, lose their ganoine covering and the grooves for head lines of pit organs, and, in the recent *Ceratodus,* this procedure has gone so far that the anterior and posterior parts of the dorsal side of the primordial neurocranium are uncovered by dermal bones (Cf. TELLER 1891, Figs. 2-4; cf. also K. FURBRINGER 1904, pp. 498-500, who strangely enough arrives at a quite opposite conclusion). The same procedure as the one described in the *Dipnoi* has taken place in several other Teleostomes, as, for instance, in the Chondrosteids, the Acipenserids and Polyodontids, which all are certainly descendants from forms with a very completely developed dermal skeleton.

From the facts now given we thus find that most groups of Teleostomous fishes in which the skeleton has been investigated in detail, undoubtedly appear to be degenerating with regard to the degree of ossification. And in this connection it is worthy of notice that the Macropetalichthyids themselves too seem to represent a degenerative series in this respect, as the primordial neurocranium of the middle Devonian *Macropetalichthys rapheidolabis* is much more completely ossified than that of the upper Devonian *Epipetalichthys wildungensis.*

If we turn to the Elasmobranchs, it has generally been considered that these do not have real bone tissue. This may be true for the more typical later forms, but if we go back to the Acanthodians the conditions seem to be different. REIS (1896, pp. 179-184, Pl. VII, fig. 1) and with him most other authors certainly say that in these too there is no bone, but that the primordial skeleton is calcified. But, as is evident from REIS' description and figures, the manner of "calcification" is there of quite another kind from that in the typical Elasmobranchs and in reality everything indicates that in the so-called calcified cartilage of Acanthodians we are concerned with true bone. That REIS[1] did not recognise it as bone is probably due simply to the fact that he expected to find the bones of fishes with the structure occurring in higher vertebrates, i.e., throughout, or almost throughout, with a lamellary structure and the lamellæ in the interior of the skeletal elements surrounding Haversian canals. This, however, is often not the case, the bone of lower vertebrates generally being entirely without Haversian canals and lamellæ and even rather often without cells. Unfortunately the knowledge of the microscopic structure of bone in

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[1] According to REIS the primordial skeleton of the Acanthodes consists peripherally of a rather lamellary layer containing numerous cell spaces. Internally to this follows a cancellous layer and most centrally a vacuity occupied in the fossil by stone but which in the living animal certainly consisted of cartilage. In the cancellous layer there are, if REIS is correct, no cell spaces. A microscopic investigation of the primordial skeleton of the Acanthodians, from the new points of view advanced here would be very desirable, but unfortunately I had no material with which to undertake one myself.

lower vertebrates is still very imperfect. The conditions in several other Elasmobranchs from the Palæozoic also seem to indicate that the Elasmobranchs in general originally had an osseous skeleton (Cf. WOODWARD 1924). Finally, it ought, in connection with this also, to be pointed out that, according to the recent interesting investigations by WEIDENREICH (1923, pp. 415-419, 461-462), there is really no fundamental difference between calcification and ossification.

From what we now know of the occurrence of bone in the vertebrate series, we must evidently presume that bone must have occurred also in the ancestors of and in the most primitive Elasmobranchs and the fact that it is to be found in the Acanthodes is therefore only a matter of course.

That the Macropetalichthyids cannot be closely related to any Teleostomous fishes so far known is thus, despite the presence of bone in their skeleton, beyond question. The development of the dermal bones in their cranial roof and the lacking of dermal bones on the ventral side of the primordial neurocranium, together with the Elasmobranchian characters, show definitely that they are not specialized Teleostomes at all but forms that among fishes known hitherto are in some way most closely related to the Elasmobranchs. In fact the indications as far as we can judge at present seem to be that the Macropetalichthyids evolved from some early, very primitive Elasmobranchian form soon after the Elasmobranchian stem had separated from the stem of Teleostomous fishes.

CERTAIN REMARKS CONCERNING THE OTHER NON-MACROPETALICHTHYID ARTHRODIRES

The increased knowledge that we now possess of the anatomy of the Macropetalichthyids throws of course new light on the other Arthrodires too, and it is therefore of importance to give here some remarks on these. I shall begin with the Phlyctenaspids, which, as JAEKEL has pointed out (1911, p. 46) seem to be most nearly related to the Macropetalichthyids. I shall then turn to the Coccosteids, Homosteids, Mylostomids, Ptyctodontids and, finally, to a form which has not hitherto been recognized as an Arthrodire.[1]

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[1] A satisfactory classification of the Arthrodires into families is difficult to give at present on account of the imperfect knowledge we still possess of the various forms, and because the opinions of different authors are widely at variance in this respect. The subdivisions given by me here are merely intended to simplify the account of certain anatomical features and not to give positive conclusions as to the mutual relations of all the forms.

THE PHLYCTENASPIDS

To the Phlyctenaspids are here referred among others the genera *Phlyctenaspis* and *Acanthaspis* (*Arctolepis,* EASTMAN 1908 b; KAER 1916).

PRIMORDIAL NEUROCRANIUM

Of the primordial neurocranium no remains have been found so far, a fact which indicates that it was either entirely cartilaginous or at least very slightly ossified. Despite this, it is, however, possible with the help of the configuration of the dermal cranial roof and the conditions in the Macropetalichthyids, to obtain an idea of its general shape, at least in the anterior parts. (See Fig. 20.) It is thus obvious that the ethmoidal and labyrinth regions must both have been very short and broad and that the labyrinth region was rather long, in any case several times as long as the two first-mentioned regions. It seems probable also that the occipital region was rather long, too. The differences with regard to general extent of the various regions from those in *Macropetalichthys rapheidolabis* can be clearly seen by comparing Fig. 20 with Figs. 1, 3, 5, etc.

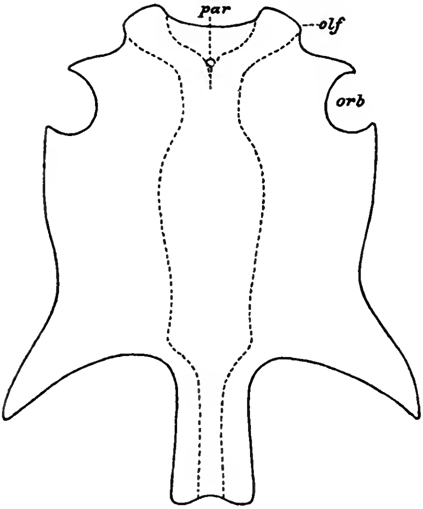

Fig. 20. PHLYCTENASPIS ACADICA

Restoration of the outlines of the primordial neurocranium with the guidance of the shape of the dermal cranial roof (Cf. Fig. 21) and the conditions in *Macropetalichthys rapheidolabis.* Shape of the cavum cerebrale indicated by broken lines. ×¾.

Olf, olfactory capsule; *orb,* orbit; *par,* pineal opening.

By the use of broken lines I have tried in Fig. 20 to indicate the possible shape and extension of the cavum cerebrale cranii, which if my view is correct ought to have been fairly like that in *Macropetalichthys* except that the canals for the tractus olfactorii must have diverged very strongly and rapidly from each other. As the anterior median dermal bone plate *M* (Fig. 21) has on the lower side close to its posterior border a pronounced pit corresponding to the pineal pit in *Titanichthys,* we are quite sure of the position of the dorsal part of the canal *par,* and from this we are of course able to conclude approximately where the anterior end of the cavum cerebrale cranii was situated. Whether there was any distinct cavum precerebrale or not it is not possible to decide, and, finally, it may be added that no external opening of the canal for the ductus endolymphaticus has hitherto been observed.

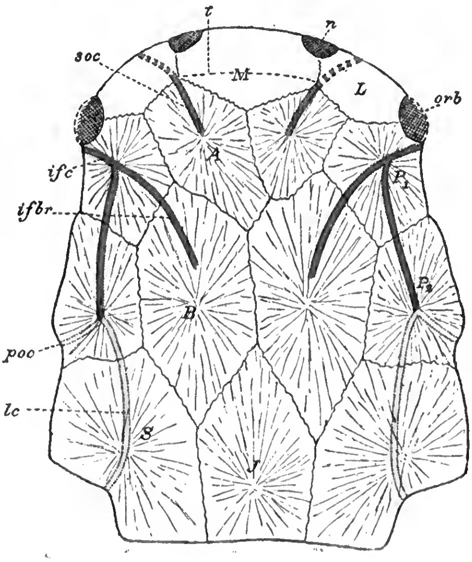

Fig. 21. PHLYCTENASPIS ACADICA

Dermal cranial roof. Sensory canal grooves with dotted outlines. Ornament not drawn. Sketch made after specimen *P. 6555* in the British Museum, London. ×¾.

A, B, I, L, M, P_1, P_2, *S,* dermal bones of the cranial roof *ifc,* infraorbital sensory groove (blue); *lc,* cephalic division of the lateral line (red) *n,* nasal aperture; *orb,* orbital entrance; *poc,* preopercular sensory groove (yellow); *soc,* supraorbital sensory groove (green), *t,* line on the plate *M,* perhaps a vestigial suture.

DERMAL CRANIAL ROOF

The plates P_1, P_2, and S (Fig. 21) correspond, at least in the main, to the plates in Macropetalichthyids lettered P_1, P_2, and S (Figs. 15, 19), while the plate J certainly represents a posterior part of the plate M_2 of the latter. The plate B (Fig. 21) seems to include the homologues of the plates L_2 and L_3, in the Macropetalichthyids, together with a part of the plate M_2 in these. The plate A (Fig. 21) is, as far as can be seen at present, represented in the Macropetalichthyids by the plate L_1, and an anterior part of the plate M_2. The plate L and the most anterior part of the plate M, seem to be without homologues in Macropetalichthyids and that in this case we are concerned with reductions in the last-mentioned forms is highly probable from the conditions in the other Arthrodires. The plate M has probably arisen by the coalescence of two plates, an anterior and a posterior one, homologous to the rostral and pineal plates respectively of the Coccosteids (Fig. 24) as it is crossed by a fine transverse line which seems to be the vestigial suture between the presumed two components.

As far as can be judged at present from the different conditions of their dermal cranial roofs, the Macropetalichthyids and Phlyctenaspids must both have descended from primitive Arthrodires in which the medial parts of the cranial roof were occupied by a larger number of bone plates than in any Arthrodire known hitherto.

Between the plates L and P_1 there is in the fish a rounded notch (*orb*, Fig. 21) indicating the position of the certainly very small orbital entrance, which is thus in relation to the dermal cranial roof situated in another manner than in the Macropetalichthyids and which in addition appears to be directed much more laterally than in these. Concerning the ventral boundaries of the orbital entrance nothing certain is known at present. Between the antero-medial border of the plate L and the postero-lateral border of the plate M, there is found another notch in the outline of the dermal cranial roof, a notch, which as far as I can see, must be the external nasal aperture (*n*, Fig. 31).

Most of the dermal bones are ornamented with tubercles and must have had a superficial position. Only the most anterior bones L and M seem to have been situated somewhat deeper in the skin, as at least their anterior parts usually seem to be without ornament and the supraorbital sensory canal anterior of the plate A probably passed entirely externally of the plate L.

SENSORY CANAL SYSTEM OF THE HEAD

The sensory canals are known only on the dermal cranial roof, on which they form open grooves. These grooves are, however, at least in several cases, deep and narrower at their external opening than further inwards (Fig. 22), so that they in fact open outwards only with a narrow slit. Concerning the number of sense organs in the grooves nothing can be said at present.

The *supraorbital groove* (*soc,* Fig. 21), which is very short, has its posterior end at about the ossification centre of the plate *A*. From this point it passes forward and laterally to the antero-lateral corner of the plate. On the plate *L,* there are no traces of it, but it certainly continued still further forwards, although situated there entirely externally of the plate *L* in the most external layers of the skin. From the direction of the part known of the groove it seems, as is obvious from text fig. 21, certain that the other hitherto unknown part of the same groove passed, as has already been emphasized above, antero-latero-ventrally posterior of the nasal aperture as it does in the Coccosteids and Elasmobranchs.

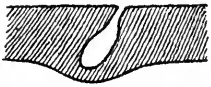

Fig. 22. Sketch of a sensory canal groove of a Phlyctenaspid in transversal section. Magnified.

The *infraorbital groove* (*ifc,* Fig. 21) is, with its posterior end, which is situated approximately at the ossification centre of the plate P_2, continuous with the cephalic portion of the lateral line groove. It goes forward to about the ossification center of the plate P_1, where it suddenly bends latero-ventrally and leaves the cranial roof posterior to the orbital entrance.

Just at the bend, it is continuous with a groove (*ifbr,* Fig. 21) which goes in an arch postero-medially to near the centre of the plate *B*. This groove must, as is easily understood, have been innervated either from the n. ophthalmicus lateralis and represent a posterior part of the supraorbital sensory canal, or from the r.oticus lateralis, in which case it must be considered as a branch from the infraorbital groove. Which one of these two alternatives is the true one it is difficult to decide from the conditions in the Phlyctenaspids, but when we come to the Coccosteids we find there, as we shall see, certain facts which seem to be much in favour of the latter. I have therefore called the groove in question the postero-medial branch of the infraorbital groove. A further support for this view is given perhaps by the conditions in *Læmargus*. In this form the infraorbital canal with its posterior part on the dorsal side of the head, turns abruptly medially and continues in this direction till it almost meets its fellow of the opposite side in the median line (EWART 1892, Pl. I, fig. 1).

A groove issuing in postero-medial direction from the infraorbital groove quite in the same manner as the postero-medial branch of the infraorbital groove in the Phlyctenaspids occurs in many Stegocephalians (WIMAN 1914, Pl. I, figs. 1, 2, 3; Pl. III, fig. 2; Pl. IV, figs. 2, 6, 7; PL. V, fig. I; Pl. VII, in the form figured on this plate the branch in question is double; 1916, Pl. XV, cf. MOODIE 1908; 1915). A homologue to it is also found in larval forms of *Triton*, in which, however, like the whole sensory canal system, it is represented merely by isolated pits arranged in a line.

The *cephalic division of the lateral line* (*lc*, Fig. 21) is, as already pointed out, like the other sensory canals, an open groove. Its anterior end is situated as the ossification centre of the plate P_2, in which it is continuous with the infraorbital groove. It goes backward to the postero-lateral edge of the plate *S*, its farther course backward being unknown. There is no cross commissural groove, which connects it with its fellow of the opposite side and, as far as known, there is not even any pit line representing a commissure of this kind.

The *preopercular groove* (*poc*, Fig. 21) is represented by a dorsal part which issues in a postero-latero-ventral direction from the point at which the infraorbital groove and the lateral line groove (*lc*) meet one another.

Nothing is known of pit lines, but this may perhaps be due to the unfavorable state of preservation in which remains of Phlyctenaspids are generally found.

DERMAL COVERING OF THE TRUNK

The anterior parts of the trunk of the *Phlyctenaspids* are, as we know, enclosed in a strong armour, which, as it follows immediately behind the head, obviously, at least with its anterior parts, occupies the position of the dermal shoulder girdle of the Teleostomous fishes. A further support for this view is the fact that, as set forth in the description of *M. rapheidolabis*, the branchial basket cannot have extended backward into the abdominal armour, but must have been limited entirely to the head. The powerful Elasmobranchian-like spine that in all Phlyctenaspids is rigidly attached to the antero-lateral edge of the antero-ventro-lateral and the lateral edge of the inter-lateral of each side, thus has in fact the approximate position of the pectoral fin of ordinary fishes and seems to me to represent either the entire dermal skeleton of this fin or to be a spine that was attached to its anterior border while the other parts of the fin have become reduced.

THE COCCOSTEIDS

To the Coccosteids in the broad sense in which they are taken here are referred not only *Coccosteus, Pachyosteus, Rhinosteus, Pholidosteus, Chelyophorus,* and others, but also such genera as *Dinichthys, Titanichthys,* and *Selenosteus,* the chief reason for this being the characters of their dermal cranial roof.

PRIMORDIAL NEUROCRANIUM

In *Chelonichthys primigenius* (EICHWALD 1860, pp. 1526-1527 Pl. 57, figs. 1, 2) the primordial neurocranium was partly well ossified, but unfortunately no details are known of it. In other forms it seems as a rule to have been entirely cartilaginous or at least almost entirely so, for no certain remains of it have been found so far.

Turning first to *Coccosteus decipiens* and the forms closely allied to it, we can at once understand from the proportions of the dermal cranial roof that the ethmoidal and occipital regions of the primordial neurocranium in them must have been short, while the remaining two regions, the orbitotemporal and labyrinth regions, had a rather considerable length. It deserves also to be mentioned in this connection that the primordial neurocranium must have been fairly high, in any case higher than in the dorso-ventrally much flattened *Macropetalichthys rapheidolabis*. That this was the case is easily understood if we look at the head, for instance, of *Pholidosteus friedelii* (JAEKEL 1919, Fig. 2) from the lateral side. In Fig. 23 A, the general shape of the primordial neurocranium has been drawn as I suppose it to have appeared. In this figure also the outlines of the cavum cerebrale cranii and the canals for the olfactory tracts have been put in mainly with the guidance of the conditions in *M. rapheidolabis* and the positions of the nostrils and the pineal pit on the lower side of the pineal plate (*Pi,* Fig. 24). We see from this that the canals for the olfactory tracts cannot have diverged quite so strongly forward as in the Phlyctenaspids.

While in *Coccosteus* and its nearest allies the lower side of the dermal cranial roof is rather smooth, or in any case without prominent ridges or formations of this kind, it has in *Dinichthys* a paired lamella, which extends some distance downwards. The position of this lamella, which in places is thickened or is provided with downward directed processes or is irregular in other ways, is shown by Fig. 2, Pl. IV, and Fig. 1, Pl. LII of NEWBERRY's description in 1889, and by Fig. 4 D of WOODWARD's description in 1922, and, as we understand from these figures, it must have covered a dorsal portion of the outer surface of each lateral wall of the primordial neurocranium. Accordingly it shows the outlines of the dorsal side of the primordial neurocranium, a fact that was recently pointed out by WOODWARD (1922, p. 33).

With the guidance of this lamella and the conditions in the Macropetalichthyids, the restoration shown in Fig. 23 B was made. As we see from it, the primordial neurocranium of *Dinichthys* agrees in several points with that in the Phlyctenaspids and *Coccosteus* but differs, however, distinctly at least from that in the former by the greater length and comparatively less considerable breadth of its orbitotemporal region. Further, it is also worthy of notice that the orbitotemporal region probably was not definitely bounded from the labyrinth region, but that the anterior parts of this were rather narrow too, while its posterior parts were very broad. Whether the short occipital region had an anterior broad division as in the Macropetalichthyids it is not possible to say, as we do not know how the vagus canal had its course.

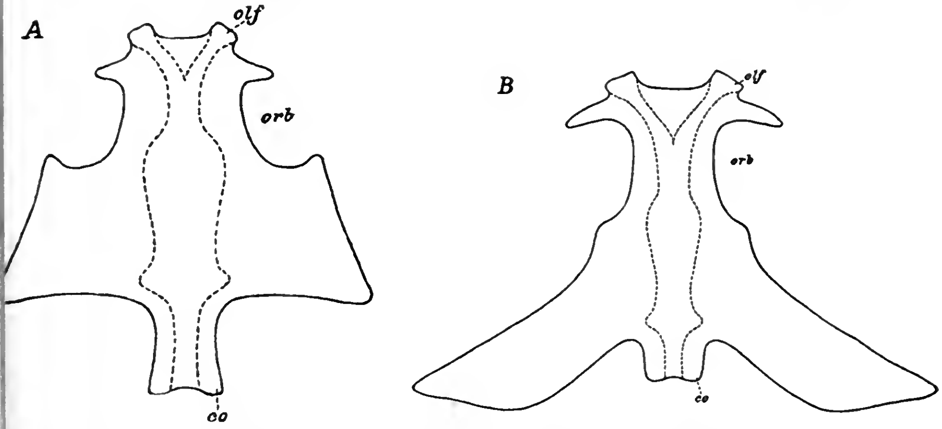

Fig. 23. Restoration of the outlines of the primordial neurocranium. *A*, of *Coccosteus*; *B*, of *Dinichthys*. The possible extension of the cavum cerebrale cranii and the olfactory tracts is indicated by broken lines. *co*, occipital condyles; *olf*, olfactory capsule; *orb*, orbit.

According to the opinion advanced by WOODWARD (1922, p. 33) the primordial neurocranium in *Dinichthys* would not have extended farther back beneath the dermal cranial roof than approximately to the transversal plane through the posterior ends of the supraorbital sensory canals (cf. Fig. 24 B). In the Macropetalichthyids the posterior ends of the supraorbital canals are, as is seen from Pl. XX in the present paper situated at a place about midway between the labyrinth cavities. In other fishes, too, they do not reach much farther back, even in those cases when they with certainty include the anterior head lines of pit organs. This fact in connection with the circumstance that the paired lamella on the lower side of the dermal cranial roof distinctly continues postero-laterally of this place to the very postero-lateral corner of the dermal cranial roof, seems to me to indicate with almost absolute certainty that the primordial neurocranium of *Dinichthys* extended backward as far as the dermal cranial roof and that the posterior parts of the labyrinth region were as broad as shown by my restoration in Fig 23 B.

The paired bony lamella on the lower side of the dermal cranial roof in *Dinichthys* is held by WOODWARD to be an ossified dorso-lateral part of the lateral wall of the primordial neurocranium and we would thus have here a primordial component coalesced with the dermal cranial roof. That this perhaps is the case seems probable to me especially from the conditions in the Coelacanthids, in which a part of the primordial skeleton in certain specialized Triassic forms has coalesced with an overlying dermal bone, while in the other forms it has retained its original primitive relations (STENSIÖ 1921, pp. 53, 93, 97, 124; 1923, p. 1269; cf. ALLIS 1899; 1909a). In the Coelacanthids this coalescence between dermal bone and primordial bone has, however, obviously taken place in connection with a process of reduction of the bone of the primordial neurocranium, and, from what has been emphasized above there is every reason to believe that this is also the case in *Dinichthys.* What the paired bone is that NEWBERRY (1889, pp. 147-148) describes from the interior of the head in *Dinichthys terelly,* it is not possible to decide. Perhaps it may be an ossified part of the primordial neurocranium.

A common character for all the Coccosteids is the fact that their orbit usually was large and that the eyes must have been directed straight or almost straight laterally.

DERMAL CRANIAL ROOF

The dermal cranial roof of *Coccosteus decipiens* (Fig. 24 A; 25) is rather similar to that in *Phylyctenaspis* (Fig. 21), but differs from this by the somewhat different shape of the various bones and the fact that the rostral plate (*R*) and the pineal plate (*Pi*) are always independent. Further, it is also to be noticed that the orbital entrance is bounded dorsally by the plate *A*, while in *Phlyctenaspis* it is bounded there by the plates *L* and P_1, the plate *A* there lying medially of the two just-mentioned plates. The external nasal aperture is paired, situated rather close to its fellow of the opposite side and directed almost straight forward. It is bounded medially by the rostral plate (*R*), laterally by the plate L.

The upper Devonian Coccosteids are generally more specialized than *Coccosteus decipiens*. (Cf. JAEKEL 1906a; 1907; DEAN 1901, figs. 14-18; EASTMAN 1908a, pp. 89-156; 1908b, pp. 152-205; BRYANT 1918, pp. 26-105; WOODWARD 1922, fig. 4, pp. 30-36.) The ornament of the bones in them is generally fine or is even in certain cases lacking; the bones have become firmly united to one another and in the American forms, as, for instance, *Dinichthys, Titanichthys* and *Stenosteus,* the plate *L* has hitherto not been found. This indicates either that it had sunk deep down in the skin and lost its connections with the neighbouring plates or that it had become entirely reduced, as in the Macropetalichthyids (Cf. WOODWARD 1922, p. 35).

In the restorations of the *Dinichthys*-species exhibited in various American museums, no consideration seems to have been given either to the absence of the paired plate *L* or to the circumstance that the primordial neurocranium with the olfactory capsules must have extended somewhat forward beyond the anterior margin of the plates *A* (Fig. 24 B) of the dermal cranial roof. (Cf. the restoration of DEAN 1909, Pls. 38-39; and by BRYANT 1918, Pl. 1, both of which are incorrect in this respect.)

DERMAL BONES OF THE CHEEK

In *Coccosteus decipiens* and its nearest allies, the cheek is regularly occupied by two bones, a large, anterior infraorbital (*So,* Fig. 24), which forms the ventral boundary of the orbital entrance and a small plate (*Ps,* Figs. 24, 25)[1], which is situated behind the infraorbital and occupies the most posterior part of the cheek. (Cf. TRAQUAIR 1890, Pl. 10, figs. 1, 2; JAEKEL 1902, Fig. on p. 107; 1919, Fig. 2, *Qj*.) In the American forms from the upper Devonian the last mentioned plate is, as far as I know, always lacking, a fact which probably indicates that it has become reduced. (Cf. EASTMAN 1908a, Figs. 23, 24, 29; 1908b, Figs. 27, 31; HUSSAKOF 1906, Figs. 1B, 12; DEAN 1909, Fig. 56, Pls. 38-40, etc.)

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[1] In certain cases this plate may probably be subdivided into two (JAEKEL 1902, Fig. on p. 107).

VISCERAL SKELETON

The primordial visceral skeleton seems generally to have consisted chiefly of cartilage, but in *Pholidosteus* (JAEKEL 1907, pp. 176-186; 1919, pp. 77-87, Figs. 4, 8) and *Erromenosteus* (JAEKEL 1919, pp. 84-86, Fig. 9) it is certainly at least partly ossified.

In *Dinichthys intermedius* WOODWARD has found a bone (WOODWARD 1922, p. 35) which seems to belong to the palatoquadrate, but whether this bone was an ossification in the palotoquadrate cartilage itself or whether it is simply a dermal bone developed in relation to this, it is at present not possible to decide. The occurrence is, however, of much interest, because it shows that there was in the upper jaw of the Arthrodires a palatoquadrate medially of the two external elements, and that the latter two elements on account of this must really be most nearly comparable with the premaxillary and maxillary respectively. An additional support for this interpretation of the two external elements in the upper jaw is the fact that the anterior one of these elements in certain species is tuberculated on the external surface (WOODWARD 1922, p. 33; EASTMAN 1908a, Pl. 7, figs. 4-6) and accordingly appears to be a superficial dermal bone.

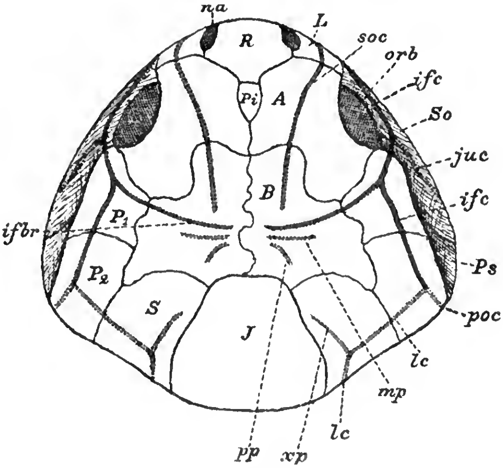

FIG. 24a. DERMAL CRANIAL ROOF

A. *Coccosteus decipiens* (sketch drawn by the author from specimens in the Royal Scottish Museum, Edinburgh). For explanation of lettering see next page.

The Meckelian cartilage has in *Pholidosteus* and *Erromenosteus* (JAEKEL 1907, pp. 176-184; 1919, Figs. 4, 8, 9) its pars articularis ossified, but seems, as far as we know, generally to have been entirely cartilaginous.[1] On the medial side it was almost entirely covered by the large, well-known bone (*Mix,* Fig. 25) which has been termed by various authors mandibular, gnathal, infero-gnathal, dentary, and splenial. This bone, on account of its extent and relations, obviously corresponds to all the dermal bones on the medial side of the mandible in the Teleostomes and would therefore if named from this point of view get a very complex title. For the sake of brevity we may call it simply the mixicoronoid (Cf. STENSIÖ 1921, p. 244). On the outside of the postero-ventral part of the Meckelian cartilage, there is in *Pholidosteus* (JAEKEL 1907, Fig. 5; 1919, Fig. 4) a small dermal bone which is ornamented with tubercles and which, as pointed out by

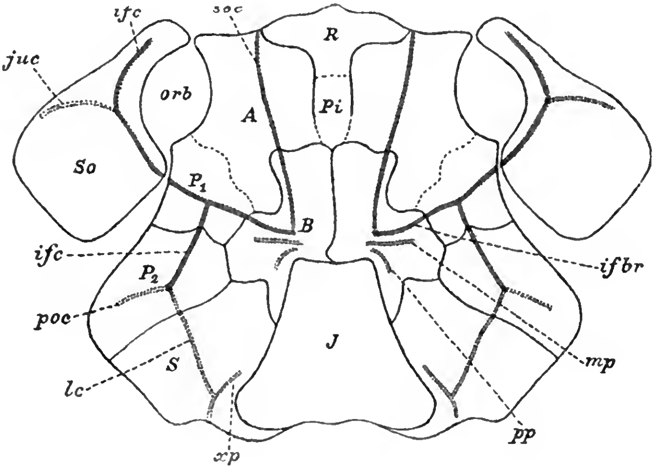

FIG. 24b. DERMAL CRANIAL ROOF

B. *Dinichthys halmodeus* (Bones after EASTMAN 1908a, Fig. 21, and 1908b, Fig. 24). Sensory grooves according to observations made by the author on a specimen in Albany, N. Y. Much diminished.

Sensory canal grooves in both *A* and *B,* indicated by a double dotted line and colours.

A, B, J, L, Pi, P_1, P_2, *R, S,* bones in the dermal cranial roof; *Ps, So,* bones of the cheek; *ifc,* infraorbital sensory groove (blue); *ifbr,* postero-medial branch of the infraorbital sensory groove (blue); *juc,* jugal groove (yellow); *lc,* lateral line groove (red); *mp,* groove, probably for the middle head line of pit organs (red); *na,* nasal aperture; *orb,* orbital entrance; *poc,* preopercular groove (yellow); *pp,* groove probably for the posterior head line of pit organs (red): *soc,* supraorbital groove (green); *xp,* branch from the cephalic division of the lateral line (groove), probably corresponding to a part of the superatemporal cross commissure (red).

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[1] I have had the opportunity of investigating *Pholidosteus friedelii* in the collection of Professor O. JAEKEL at Greifswald and I fully agree with him in his interpretations of the elements in the lower jaws of Arthrodires.

JAEKEL, apparently is comparable to the angular of the *Teleostomi*. The term angular may therefore properly be employed for it.

As is fully evident from the facts now known, the jaws in the Arthrodires must have been homologous with those in other fishes, and their movements, as emphasized by WOODWARD (1922, p. 35), have been as normally up and down. (For the previous views on this subject see: DEAN 1901, pp. 105-107; HUSSAKOF 1906; JAEKEL 1919, pp. 96-108; ADAMS 1919, pp. 123-127.)

In *Erromenosteus* (JAEKEL 1919, Fig. 9) the ventral parts of the hyoid arch and perhaps also a basibranchial element appear to have been ossified.

DENTITION

Teeth are found in all young specimens of Coccosteids, but while in certain forms, as for instance, *Coccosteus* and *Diplognatus,* they are retained throughout life, they are in adult specimens of several other forms such as *Dinichthys, Titanichthys* etc., entirely abraded by use, the labial edges of the jaws becoming in these forms transformed to cutting edges or adapted for crushing.

It is generally maintained (Cf. WOODWARD 1922, p. 35) that the teeth occur in a single series on the labial margins of the jaws, but the investigations undertaken by the author[1] show that on the mixicoronoid of certain forms there is at least a second and perhaps also a third or more series of lower teeth medially of the labial ones. All the teeth are ankylosed to the jaw bones with their bases and generally have the central parts occupied by a rather large pulp-cavity. In the dorsal parts this pulp-cavity is generally surrounded by ortho-dentine, in the basal parts by trabecular-dentine, but in certain teeth the trabecular-dentine may extend almost to the apex. This seems especially to be the case in one category of large teeth which belong to the labial series and are characterized by the fact that they have on their medial side one, two or three, small, bluntly conical cusps. Basally the trabecular-dentine gradually turns into the bone of the mixicoronoid.

Externally of the dentine there is in the distal parts of the teeth a layer of bright, shining enamel, which is perforated by the distal extensions of the dentine tubules, these tubules leading to and opening on the outside of the enamel. Also, the cusps on the medial side of the large external teeth are provided with an enamel layer of the same sort. Besides the cusps on the medial side, several of the larger teeth of the external series have also a small cusp on the anterior and pos-

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[1] The investigations have been made on the mixicoronoid of a Coccosteid from the Devonian of Spitzbergen.

terior side, so that, when seen from the lateral or medial side, they have the appearance of shark teeth (also teeth of Acanthodians).

The occurrence of at least two or three longitudinal series of teeth in their jaws, together with the circumstance that certain of the teeth in the external one of these series are shark-like in shape, indicates that the dentition in the Coccosteids probably has arisen from an Elasmobranchian-like one.[1] An additional support for this view is the fact that the medial side of the mixicoronoid ventrally of the longitudinal series of teeth appears to consist mainly of a dentine-like tissue.

SENSORY CANALS OF THE HEAD

The sensory canal system of the Coccosteids is, as in that of the Phlyctenaspids, represented merely by grooves on the external surfaces of certain of the external dermal bones. The course of these grooves is best known in *Coccosteus decipiens* (Figs. 24 A, 25) and in the *Dinichthys* species (Fig. 24 B). The subsequent account is based chiefly on *C. decipiens.*

The *supraorbital groove* (*soc,* Figs. 24 A, B; 25) goes from the plate *B* forward and somewhat laterally to the plate *A,* which it crosses to the antero-lateral corner. From this point it continues downward anterior of the eye and posterior to the nasal aperture on the plate *L,* on which it probably anastomized with the infraorbital groove. It is thus fully evident that with its anterior part it had the same course as in the recent Elasmobranchs (Cf. ALLIS 1901, pp. 104-107; 1905).

The *infraorbital groove* (*ifc,* Figs. 24 A, B, 25) has on the dermal cranial roof exactly the same course as in the Phlyctenaspids and has also a postero-medial branch (*ifbr*), as in these. We can here see quite clearly from its transverse course that this branch cannot represent a part of the supraorbital groove as one might perhaps be inclined to think merely from its position in the Phlyctenaspids (Cf. POLLARD 1892b, pp. 546-548). From the dermal cranial roof the infraorbital groove turns latero-ventrally to the cheek, on which it is first situated on the infraorbital bone. On this it passes first downwards and then anteriorly in the normal way, posterior and ventrally of the orbital entrance. After leaving the infraorbital it continues forward on the plate *L,* probably anastomizing there with the supraorbital groove and probably passing anterior of this commissure ventrally of the nasal aperture. What its relations were at the very anterior end is not known.

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[1] The only description that I have found of the microscopic structure of the teeth in Coccosteids was published by AGASSIZ 1844 (p. 26). What AGASSIZ describes there is probably merely a basal part of a tooth.

The *cephalic division of the lateral line groove* (*lc*, Figs. 24 A, B, 25) has the same course as in the Phlyctenaspids. Close to its posterior end there issues from its medial side a branch (*xp*) in anterior and somewhat medial direction. This branch, which goes close to the medial edge of the bone-plate *S* and which, contrary to what is shown in most restorations, is rather short and does not reach the plate *B*, may perhaps correspond to a lateral part of the supratemporal cross commissure.

The *preopercular groove* (*poc*, Figs. 24 A, B, 25) issues in the plate P_2 from the point where the infraorbital groove and the lateral line groove meet each other, quite as it does in the Macropetalichthyids and Phlyctenaspids. It goes to or close to the postero-lateral corner of the cranial roof, its passage on the cheek being unknown, as it probably passed there entirely in soft tissue.

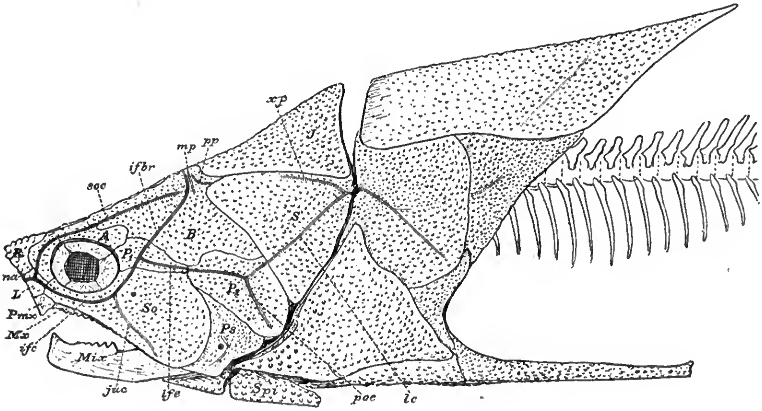

Fig. 25. COCCOSTEUS DECIPIENS

Head and abdominal armour, chiefly from JAEKEL (1902). Sensory canal grooves indicated by double dotted lines and colors.

A, B, J, L, P_1, P_2, R, S, bones of the dermal cranial roof; *Ps, So,* bones of the cheek (*So,* infraorbital bone); *Mx,* maxillary; *Pmx,* premaxillary; *Mix,* mixicoronoid; *Spi,* spinal; *ifc,* infraorbital groove (blue); *ifbr,* postero-medial branch of the infraorbital (blue); *juc,* jugal groove (yellow); *lc, cephalic* division of the lateral line (red); *mp,* groove probably corresponding to the middle head-line of pit organs (red) *poc,* preopercular groove (yellow); *pp,* groove probably corresponding to the posterior head-line of pit organs *xp,* groove probably corresponding to a lateral part of the supratemporal cross commissure.

About at the place in the infraorbital plate (*So*) at which the infraorbital groove turns forward from its downward direction, there issues from it a posteriorly and somewhat ventrally running branch (*juc,* Figs. 24 A, B; 25) which obviously is the homologue of the horizontal cheek canal of the Elasmobranchs (ALLIS 1923, pp. 199-201), the horizontal part of the jugal canal of Crossopterygians (STENSIÖ 1921, pp. 76-77; 1923, p. 1258), the horizontal cheek line of several Teleostomous fishes (ALLIS 1889, p. 506, Pl. 42; 1900, p. 445; 1905, pp. 406-407; 1923 p. 201, POLLARD 1892b, p. 548) and the jugal groove of the Stegocephalians (MOODIE 1908, p. 515; 1915, p. 320).

Whether there was any mandibular canal is not known.

Behind the postero-medial branch of the infraorbital groove, too, paired, short grooves (Figs. 24, 25) are regularly found on the bone plate *B* in most of the Coccosteids examined by the author. The anterior one (*mp*) of these grooves is situated transversally to the longitudinal axis of the head and seems to correspond to the middle head-line of pit organs in the *Elasmobranchii* and *Teleostomi,* while the posterior one (*pp*) which is situated obliquely so that its anterior end is nearer to the median line than the posterior one, probably is homologous with the posterior head-line of pit organs in the same fishes. (Cf. ALLIS 1889, pp. 502-509, Pl. 42; HERRICK 1901, pp. 222-223, Pl. 14; STENSIÖ 1921, p. 218; 1923, p. 1258; etc.)

SOME REMARKS ON THE TRUNK AND THE FINS[1]

A pectoral spine (*Spi,* Fig. 25) although much smaller than in the Phlyctenaspids, occurs at least in most of the Coccosteids, and it is beyond question that the paired plate found in *Coccosteus decipiens* and *Dinichthys gouldi* somewhat behind the abdominal armour, really represents the pelvic girdle (Cf. WOODWARD 1891, pp. 282, 289; 1922, p. 35; DEAN 1896, p. 162; 1909, pp. 282-287). There are also in *C.decipiens* a few endoskeletal radials in connection with the pelvic girdle. The lateral line was, on the trunk at least, partly surrounded by lime-bearing tissue, but whether this tissue was bone or not it is not possible to say. There are also in certain well-preserved specimens reliable evidences of very delicate dermal tubercles behind the abdominal armour.

Contrary to what is generally maintained, I feel inclined to think that the pelvic girdle, as well as all other endoskeletal elements that are found preserved in Coccosteids, consists of true bone. A more detailed microscopic examination of these elements has, however, so far not been made, a fact which is much to be regretted.

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[1] The remarks given here on the skeleton of the pelvic girdle and fins of Coccosteus are based on observations made by the author in the Royal Scottish Museum, Edinburgh and the British Museum, London. I fully agree with WOODWARD (1891) in his interpretation of the specimens in the latter museum (DEAN 1909, p. 285).

SOME GENERAL REMARKS ON THE COCCOSTEIDS

From what we know at present of the Coccosteids, it seems as if they degenerated during the Devonian with regard to the degree of ossification both in the exo- and endo- skeleton, a fact which to a certain degree was emphasized by JAEKEL in 1906 (1906a p. 82). In connection with this also a reduction of the pectoral spines took place.

THE HOMOSTEIDS

The Homosteids, represented by the genus *Homosteus,* are certainly closely related to the Coccosteids.

The bones of the dermal cranial roof are the same as in the Coccosteids, but the dermal cranial roof as a whole differs from that in these by the considerable lengthening of the occipital region and by the fact that the orbital entrance is directed upwards and entirely situated in it. It thus approaches in these respects that of the Phlyctenaspids on the one hand and that of the Macropetalichthyids on the other.

The plate *L* is not found in TRAQUAIR's restoration (TRAQUAIR 1889) of the fish, a circumstance which probably indicates that it had become entirely reduced. The anterior parts of the plates P_1, *A* and *R* lack both ornament and sensory canal grooves and must obviously have been situated deep in the skin and are probably in an early stage of reduction. The other parts of the dermal cranial roof are provided with a faint ornament, and this, in connection with the fact that certain of the sensory canal grooves are lacking, while the remaining ones are rather shallow and indistinct, seems to indicate that the dermal cranial roof as a whole had commenced to sink down into the deeper layers of the skin.

The skeleton of the cheek and the visceral skeleton are very imperfectly known and nothing can therefore be said of them here.

THE MYLOSTOMIDS

The Mylostomids, which probably are to be considered as an highly specialized offshoot of the Coccosteids, differ from them mainly in the characters of their dentition, the teeth, as we know, being in them transformed to strong tritoral plates.

The dermal cranial roof is, at least in *Mylostoma,* said to be thin and devoid of ornament and lacks most of the sensory canal grooves, all of which conditions indicate that it was situated deep in the skin and probably was in an initial stage of reduction. It may further be mentioned that the plates homologous with *L* and *Ps* of *Coccosteus* are lacking and that the infraorbital plate (*So*) is narrow. The orbital opening is not directly limited by any part of the dermal cranial roof.

In the lower jaw of *Dinomylostoma,* the Meckelian cartilage is ossified in the pars articularis (WOODWARD 1922, p. 34; EASTMAN 1906, pp. 25-26). EASTMAN'S view that the tritoral dentition of the Mylostomids would be more primitive than that in the Coccosteids (EASTMAN 1906, p. 6; 1907; 1908a, p. 95; 1908b, p. 163) must, as is easily understood, be incorrect (Cf. WOODWARD 1922, p. 35), for the Mylostomids not only do not pertain to the latest Arthrodires (they are from the upper Devonian), but they appear in most respects to be more specialized than the Coccosteids from the lower Devonian. Moreover it would be very difficult to explain from EASTMAN'S point of view how the tritoral plates of the Mylostomids could be transformed into teeth of the type found in the more primitive Coccosteids, as, for instance, in *Coccosteus.*

THE PTYCTODONTIDS

The primordial neurocranium of *Rhamphodus* is said by JAEKEL (1906b, p. 183) to consist of calcified cartilage, and if I understand JAEKEL'S account correctly this would also have been the case with the visceral skeleton. I am not inclined to accept this view, however, but rather think that we are in this case as in the Macropetalichthyids concerned with true bone-tissue. Probably this bone-tissue, as in *Macropetalichthys,* appeared chiefiy or exclusively as thin perichondral layers without evidence of sutures and distinct centres, conditions which of course without microscopic investigation make the detection of its true nature difficult.

I have more reason to suspect that the primordial skeleton of *Rhamphodus* was, at least in part, actually ossified, since the primordial neurocranium in a form pertaining to the family dealt with below after the Ptyctodontids, as far as I could find by a macroscopic examination of it, was to a considerable extent ossified, although it is said by JAEKEL in a recent paper (1921, p. 217) to consist of calcified cartilage (cf. the Jagorinids below)[1].

JAEKEL further mentions a "Schädeldach" in *Rhamphodus,* which, if I understand him correctly, must mean that there is in this fish a dermal cranial roof (JAEKEL 1906b, p. 183).

Concerning the dentition, I have nothing new to add here. It must, however, be emphasized that it is highly specialized. On account of its agreements with that of the Chimæroids, the Ptyctodontids have, as is well known, been considered by several authors to be closely allied to the Chimæroids (Cf. EASTMAN 1908b, pp. 120-123).

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[1] In another place in the same paper JAEKEL is, however, obviously aware that it was ossified (JAEKEL 1921, p. 218).

Rhamphodus has behind the head a dermal armour on the anterior part of the trunk, an armour that, as is clearly shown by JAEKEL, is of the Arthrodiran type (JAEKEL 1906b, Figs. 3, 5) although it has become more reduced than is generally the case in the Arthrodires. In fact this armour is represented merely by certain of the anterior plates and the pectoral spine, which latter occupies its ordinary position. Its agreements with a dermal shoulder girdle are obvious from JAEKEL'S account, and from this it seems to be beyond question that the armour of the trunk in the Arthrodires, at least in its anterior parts, really is homologous with the dermal shoulder girdle of the Telostomi and Tetrapods.

The trunk armour of the Ptyctodontids, as is seen from JAEKEL'S figure of it, obviously formed part of the posterior boundary of the branchial chamber and we thus have here an additional support for my view that this chamber in Arthrodires did not extend backward into the trunk. (Cf. JAEKEL 1906b, Figs. 3-6; 1907, p. 184; the homologue of the spinale also clearly understood from JAEKEL'S figures 3-6 in 1906a.)

THE JAGORINIDS

In a paper published in 1921, JAEKEL described under the name of *Jagorina pandora*, certain remains of an upper Devonian fish, which in this connection has a special interest. Through the courtesy of Prof. JAEKEL, I had, during a visit at Greifswald in 1922, the opportunity to examine the material so far available of this fish and the account given below is therefore in part based on my personal observations.

PRIMORDIAL NEUROCRANIUM

The primordial neurocranium is said by JAEKEL in one part of his paper, as already pointed out above, to consist of calcified cartilage, while in another part it is said to have its outer and inner walls feebly ossified. From the detailed account given by JAEKEL and from my own observations it is, however, fully evident to me that we are concerned here with a primordial neurocranium that consisted chiefly of cartilage, but which had the outside and inside (cerebral side) of this cartilage provided with a thin, perichondral layer of bone exactly as in *Macropetalichthys rapheidolabis*. There were, also, as in this species, a labyrinth layer of perichondral bone and, at least, to a certain extent, canal layers too.

Unfortunately the single specimen that exhibits the primordial neurocranium is preserved so that the primordial neurocranium is available for examination chiefly from the ventral side. The shape from this side is shown by Fig. 26, which has been copied after JAEKEL.

As is seen from this figure the ethmoidal region is very short and broad, with a truncated, concave anterior margin and a large anterolaterally projecting process on each side, a process (*olf*, Fig. 26), which obviously is so situated and has such a shape, that it agrees completely with the olfactory capsule of the Macropetalichthyids, and is therefore undoubtedly to be interpreted as the olfactory capsule. The orbits are very large and imperfectly bounded and the long orbitotemporal region is consequently not distinctly marked off from the labyrinth region, which probably also is rather long. The labyrinth region is further characterized by the circumstance that it is broadest in its posterior parts, quite as the one in *Dinichthys* (Cf. Fig. 23 B). The occipital region is short and its posterior end is provided with a paired condyle for articulation with the vertebral column.

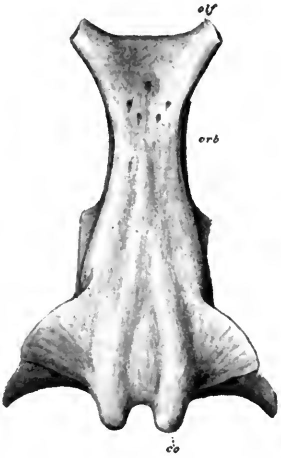

Fig. 26. JAGORINA PANDORA JAEKEL

Primordial neurocranium in ventral view. After JAEKEL (1921). ×½. *co*, occipital condyle (paired); *olf*, nasal capsule; *orb*, orbit.

As a bottom for the orbit does not occur in the fish and the interorbital wall is fairly narrow in comparison with that in the Macropetalithyids, we must expect that the carotis interna passed forward along the lateral edge of the ventral side of the primordial neurocranium and not in the orbital bottom as in *Macropetalichthys rapheidolabis*. Consequently it is probable that this artery when it turned medially to ascend through the ventral wall of the primordial neurocranium to the cavum cerebrale, entered a canal which opened in one of the pits situated on the ventral side of the anterior part of the primordial neurocranium at about the transition between the orbitotemporal and ethmoidal regions. (As these pits had not been cleaned from matrix in their deeper parts at the time I examined the specimen, I cannot, however, say with certainty whether there were among them any that really formed ventral openings for canals of this sort.)

The labyrinth cavity is well preserved and is evidently entirely separated from the cavum cerebrale, quite as in *M. rapheidolabis* and Selachians. The separating wall, which consisted of cartilage, was lined by the internal bone layer on the cerebral surface and the labyrinth bone layer on the labyrinth surface. A division for the sacculus, divisions for semicircular canals and a dorsally ascending canal for the ductus endolymphaticus are clearly distinguishable. The canal for the ductus endolymphaticus opened on the dorsal side of the primordial neurocranium and it seems probable also that in the living fish it continued out to and opened on the external surface of the skin, as it does in *Epipetalichthys wildungensis,* Selachians and Chimæroids. The canal for the n. acusticus issues from the cavum cerebrale very low down, almost at the bottom and goes outward to the ventral parts of the labyrinth cavity, probably almost as in *M. rapheidolabis.*

The shape of the cavum cerebrale is imperfectly known, but, as far as can be judged at present, it appears to have resembled that in *M. rapheidolabis.*

What function is to be ascribed to the wide canal that opens on the posterior side of the labyrinth region (Fig. 26) it is not possible to decide at present, as its course inside the lateral wall is very imperfectly known. It appears most probable that it may have transmitted the jugular vein, and perhaps, also, in its posterior parts, the vagus nerve as well.

It is fully evident that the palatoquadrate cannot have been fused with the primordial neurocranium, but must have been an independent element.

Despite the fact that the primordial neurocranium of *Jagorina pandora* is still in several points imperfectly known, we see, however, that it is clearly of the Arthrodiran type (Cf. Fig. 23). It is therefore beyond question that *Jagorina pandora* cannot be a sturgeon, as maintained by JAEKEL, but that it must be referred to the Arthrodires.

DERMAL CRANIAL ROOF

The dermal cranial roof is, as far as is known, represented merely by feebly developed isolated tubercules (called "Dornen" in the description given by JAEKEL 1921, p. 219). The microscopic structure of these tubercles is not known and it is therefore impossible to say whether they consist of bone or whether they are most comparable to the dermal denticles of the sharks.

This fish thus has no real dermal cranial roof of bones united with each other by sutures. The lack of a cranial roof of this kind must, however, as far as we can judge, be due to reduction, since a real dermal cranial roof occurs in all the other Arthrodires and is generally even most complete in the forms from the lower Devonian.

DERMAL BONES OF THE CHEEK

No dermal structures belonging to the cheek have been observed hitherto.

VISCERAL SKELETON

Associated with the primordial neurocranium are found several remains of the visceral skeleton, which was partly ossified. Among these remains are surely parts of the palatoquadrates and the mandibles. It is worthy of notice that the primordial neurocranium, as far as can be seen, has no articulating surfaces for the anterior ends of the palatoquadrates, and it therefore seems as if these had been suspended by ligaments beneath the ethmoidal region, as in the Elasmobranchs.

DENTITION

The dentition is, as JAEKEL pointed out to me during my visit at Greifswald, very interesting, as it consists of numerous, small, independent[1] Selachian-like teeth, thus teeth with several cusps. The shape of these teeth is in fact of such a nature that they undoubtedly would have been taken for shark teeth if they had been found detached from the specimen, a fact which in this connection is of much importance, as it forms a strong additional support for the view advanced by me in this paper that the Arthrodires are really closely related to the Elasmobranchs. The microscopic structure of the teeth is not known.

It is worthy of notice in this connection that WOODWARD already in 1921 shortly after JAEKEL had published his description of the primordial neurocranium of *Jagorina pandora,* without any knowledge of the character of the dentition, arrived at the conclusion that *J. pandora* was a primitive shark (WOODWARD 1921, p. 33).

SENSORY CANALS

Nothing is known of the sensory canals of the head.

ABDOMINAL ARMOUR

Close behind the head there is a girdle of dermal plates that evidently represents the shoulder girdle. It is not known in detail, but

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[1] Not ankylosed with the jaws

JAEKEL says of it (1921, p. 218) that it is sturgeon-like, which may mean very little, since he says the same of that in *Rhamphodus* (1906b, pp. 183-185).

SOME GENERAL REMARKS ON THE NON-MACROPETALICHTHYID ARTHRODIRES

From what has been set forth in the account given above the following ought to be obvious:

1. There is strong reason to believe that the primordial skeleton of the non-Macropetalichthyid Arthrodires originally was rather well ossified and that accordingly, a reduction of the degree of ossification took place during the course of the Devonian period.

2. It is fully clear that the dermal skeleton of the non-Macropetalichthyid Arthrodires was also during the Devonian period in process of reduction. In certain, especially upper Devonian, forms the reduction has gone rather far and in *Jagorina* even so far that practically the entire dermal skeleton of the head has been lost.

3. The reduction of the dermal skeleton in the non-Macropetalichthyid Arthrodires takes place in this manner: The bones sink deeper into the skin, become thinner and lose their ornament and the external sensory canal grooves. The sensory canals obviously must retain their superficial relations to the skin and they become on this account situated totally externally of the bones.

4. From the facts so far known it is beyond doubt that the non-Macropetalichthyid Arthrodires with regard to the degree of ossification represent a degenerating series.

5. There are so many common points of agreement between the non-Macropetalichthyid Arthrodires and the Macropetalichthyids that we cannot doubt that they are closely related to each other and that they must, as has generally been done hitherto, be referred to the same group of fishes.

6. From the structure of the primordial neurocranium, from the development of the labyrinth cavity, from the character of the dentition in certain forms, and from the course and development of the sensory canals, it is clear that the non-Macropetalichthyid Arthrodires, like the Macropetalichthyids, must be closely related to the Elasmobranchs. In the case of *Jagorina pandora* this is even so clear, that we should almost feel inclined to take it for a primitive Elasmobranch if we did not know that it had a shoulder girdle of dermal bones.

CONCLUDING REMARKS ON THE AFFINITIES OF THE ARTHRODIRES

After having dealt in detail with the head of the Macropetalichthyids and also given a short account of the head in the other Arthrodires, I shall here briefly summarize the results obtained and add certain remarks of interest otherwise.

With the comparatively good knowledge we now possess of their anatomy it is quite clear that the Arthrodires are true fishes and that as recently pointed out by WOODWARD (1922, p. 35) they have nothing to do with Ostracoderms, which as I have been able to make out, are much more lowly organized agnathous vertebrates.

We have seen that the Arthrodires from the oldest divisions of the Devonian generally have the dermal skeleton more complete and stronger than those from the youngest division of the same formation, and we have also found that the primordial skeleton is more or less ossified in several of their representatives. Concerning the primordial skeleton there have been advanced several facts which indicate that it must have been rather completely ossified in all primitive Arthodires. Accordingly we find that the Arthrodires like the *Dipnoi*, the *Crossopterygii*, the *Palæoniscidæ*, the *Saurichthyidæ*, the sturgeon fishes, the *Amiadæ* and several other fishes, form a degeneration series with regard to their degree of ossification.

In their general organization the Arthrodires have, as recently emphasized by WOODWARD (1922, p. 35), little in common with the *Dipnoi* and *Crossopterygii*, and it is equally evident that they are not *Actinopterygii*. From the investigation made here they were, however, found to be at the stage of the Elasmobranchs and in fact everything seems to indicate that they are really closely related to these. Their Elasmobranchian characters are as follows:

1. The general characters of the primordial neurocranium, especially the tendency to broadening of the ventral surface, partly at the expense of the lateral surfaces. (This is above all the case in the labyrinth region, the sacculus having occupied about the same position in relation to the ventral surface as in *Chlamydoselachus* and most other Selachians.) 2. The position and relations of the olfactory capsule. 3. The presence of a nasal fontanelle on the lower side of the olfactory capsule (*Macropetalichthys*) as in *Chlamydoselachus* and certain other Selachians. 4. The presence of the cavum precerebrale (*Epipetalichthys*). 5. The general shape of the labyrinth, especially with regard to the position of certain of its main parts, for instance, the utriculus. 6. The persistence of the ductus endolymphaticus (*Macropetalichthys*,

Epipetalichthys, Jagorina) and the fact that there was probably, at least in certain forms (*Macropetalichthys*), a fossa endolymphatica on the dorsal side of the primordial neurocranium beneath the dermal bones. 7. The fact that the ductus endolymphaticus, at least in certain forms (*Epipetalichthys*), perforated the dermal cranial roof and had an external opening situated about as in *Chlamydoselachus*. 8. The general shape of the brain as far as this can be restored from the position and course of the nerve canals through the cranial walls and from the shape of the cavum cerebrale. 9. To a certain extent the development of the blood vessels. 10. The fact that the palatoquadrate did not articulate with the ethmoidal region but must have been suspended beneath this merely by ligaments. 11. The dentition, which in certain forms, as *Jagorina*, consists of multicuspidated shark-like teeth. 12. The course and development of the sensory canal system.

The opinion now advanced of the close relationship between the Arthrodires and Elasmobranchs of course implies either that bone has arisen independently in different groups of vertebrates or that it is a very old sort of tissue that was present already among the most primitive vertebrates and from these was bequeathed to the common ancestors of the Arthrodires and Elasmobranchs. As has been pointed out, the conditions in the Cephalaspids and Ostracoderms in general as well as in the Acanthods and oldest *Teleostomi* indicate that the latter alternative ought to be the true one, and accordingly that the Elasmobranchs as far as can be understood at present must have lost the bone-tissue. In other words they too would represent a degenerating series with regard to the degree of ossification. In full accordance with this view is obviously the occurrence of large bone-like plates (or perhaps true bone-plates) in the earliest known true forms of the *Holocephali* (*Myriacanthus* and *Chimæropsis*) and the fact that among the Cochliodontids there is found a form (*Menaspis*) with evidence of armour on the head and anterior part of the trunk (Cf. WOODWARD 1924).[1]

Except by the presence of bone-tissue in their skeleton, a character which, as we have found, is of very slight importance from a morphological point of view, the Arthodires seem, as far as we know, to differ in no essential points from the Elasmobranchs. The different shape of the vertebral column in them as compared with the recent Elasmobranchs might perhaps be considered very insignificant, but if we consider the fossil Elasmobranchs this difference becomes less ap-

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[1] It is also of interest to note that *Menaspis* has paired lateral spines, which perhaps are identical with the pectoral spines of Arthrodires. In fact it seems not impossible that the Cochliodontids will reveal themselves as highly specialized Arthrodires (for Menaspis see Zittel's Grundzüge der Palæontologie, 1923; DEAN 1904, and JAEKEL 1891).

parent, for in the Palæozoic forms and certain earlier Mesozoic forms of these the neural arches are almost like those in the Arthrodires (Cf. DEAN 1909, *Clamydoselache;* FRITSCH 1895, *Xenacanthus* and *Pleuracanthus;* BROWN 1900 *Hybodus;* KOKEN 1907, *Hybodus*).

In addition to their general Elasmobranchian-like characters above enumerated the Arthrodires have also certain special Holocephalian characters the following of which deserve to be specially mentioned here. 1. The joint between the head and the vertebral column. 2. The structure of the branchial apparatus, inasmuch as this is covered externally by a sort of gill-cover. 3. The character of the dentition in the more specialized forms. 4. The dorsal extension of the pelvic girdle. 5. The general shape of the body. 6. Certain characters of the arterial system.

Of these characters, No. 3 is quite certainly simply a parallelism and it seems highly probable that this is the case with No. 5 too. Concerning the remaining four it is difficult to say at present how much stress ought to be laid on them, and it is consequently difficult to conclude whether the Arthrodires among the Elasmobranchs were most closely allied to the *Holocephali* or to the *Selachii* or whether they represent an independent branch from the Elasmobranchian stem. Since, as we have seen, they seem to have the pectoral fins much transformed or perhaps represented merely by an anterior spine, it is not probable that they could have given rise to the *Holocephali.* If it should appear that they are most closely allied to these the Arthrodires would have descended from the same primitive ancestors or, if we want to express it more exactly, from the primitive forms of the Holocephalian branch of the Elasmobranchian stem. Under the present conditions we can, however, with assurance only say that they are to be considered as *an offshoot of the Elasmobranchian stem of fishes* and that besides their Elasmobranchian characters they have retained a few primitive ones at the same time that they by specialization have acquired certain new ones.

Their main primitive characters must, as far as we understand, be the presence of bone-tissue in their skeleton and the occurrence of a postero-medial branch for the infraorbital sensory groove on the dermal cranial roof.

As in another paper I shall give a detailed account of the relationship between the *Arthrodira* and the *Antiarcha,* I shall here only mention that, as far as I can see from the investigations of material in the chief American and European Museums, as well as from material recently obtained from Scaumenac Bay, the *Antiarcha* seem to be a highly specialized group of fishes closely related to the *Arthrodira.*

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EXPLANATION OF PLATES

All the photographs here shown of the specimen of *Macropetalichthys rapheidolabis* in the possession of Field Museum of Natural History at Chicago were made by the photographic department of that Museum. The other specimens figured here were photographed by myself in the photographic laboratory of the Palæozoological Department of the Royal State Museum at Stockholm.

In those cases in which no special statements as to the scale of the figures are given the figures have been reproduced in natural size or have been slightly diminished.

In Fig. 4, Pl. XXIX and Fig. 2, Pl. XXXI, the bone is brighter than the stone; in all the other figures the bone is black or, in any case, darker than the stone. Sections through cavities and canals or external openings of canals are generally shown in a very bright, sometimes even an almost white tone. Fig. 1, Pl. XXX is an exception to this however, the sensory canals and their tubuli and the external opening of the canal for the ductus endolymphaticus being black.

EXPLANATION OF PLATE XIX

Macropetalichthys rapheidolabis. The specimen in Field Museum of Natural History at Chicago (Museum No. P 1154) in dorsal view. The dermal bones of the cranial roof being weathered away with the exception of the sensory canal ridges, the outlines of the primordial neurocranium are rather clearly exhibited. The specimen lacks the posterior narrow division of the occipital region, and the most anterior part of the ethmoidal region is imperfectly preserved. The ridge for the hindmost part of the cephalic division of the lateral line has become so abraded that the canals for nerve branches to it from the canal for the n. lineæ lateralis are clearly seen.

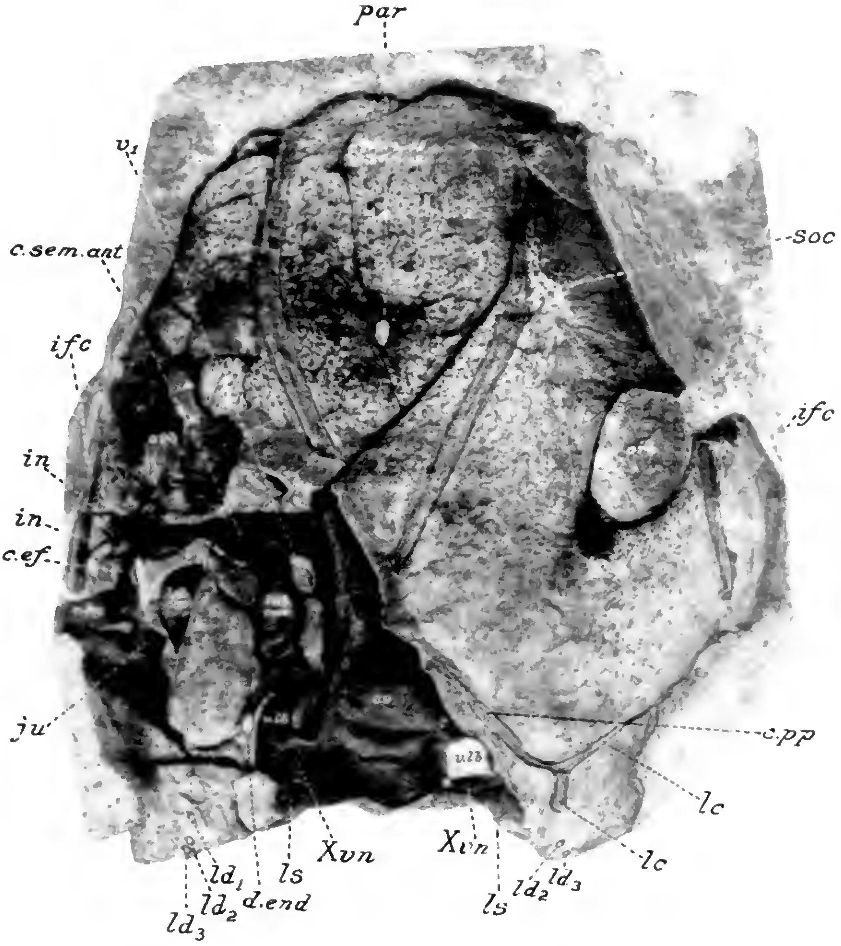
cl, fine canal coming from below; the canal probably transmitted a vagus branch, a fine branch from the n. lineæ lateralis and perhaps in addition some vessel; *c.pp,* sensory canal commissure, probably corresponding to the posterior head line of pit organs in fishes in general; *ifc,* infraorbital sensory canal; *lc,* cephalic division of the lateral line; ld_1-ld_8, dorsally ascending canals for nerve branches to the lateral line; the canals issue from the canal (*n.l*) for the n. lineæ lateralis; *orb,* orbital entrance; *par,* pineal foramen; *soc,* supraorbital sensory canal.


par
soc
orb
ifc
lc
lc
ld₁
ld₂
ld₃
cl
c.pp
ld₃
ld₂

EXPLANATION OF PLATE XX

Macropetalichthys rapheidolabis. Same specimen as in the preceding plate but with a postero-lateral part of the cranial roof removed to show in dorsal view the labyrinth cavity, a part of the cranial cavity and certain canals. As all these structures are lined by a thin, perichondral bone layer, which is black from infiltration by bitumen, they consequently appear black in the figures except when there are sections through them.

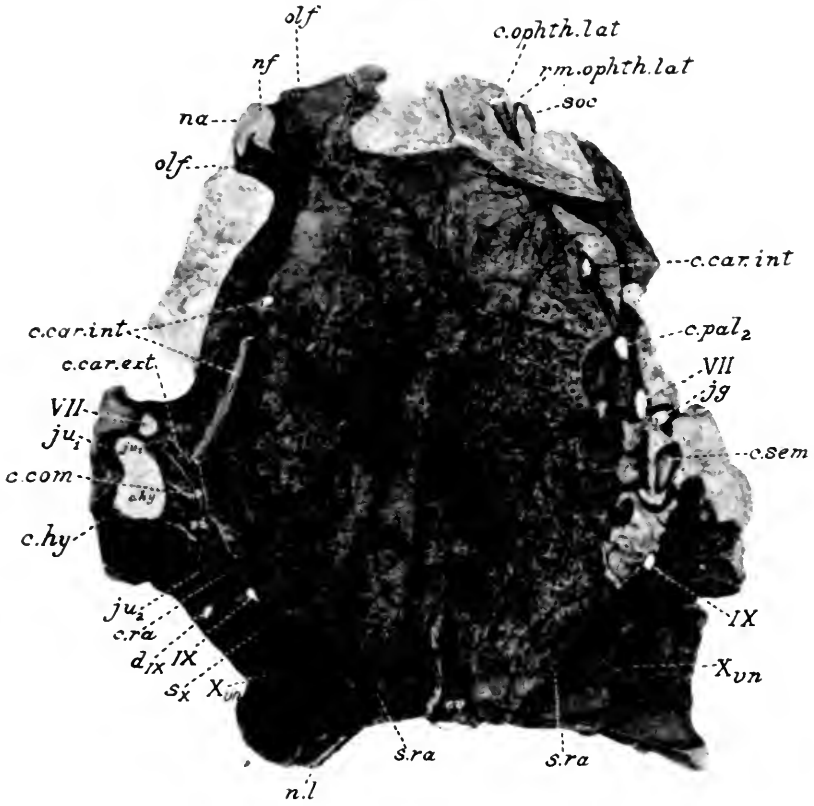
c.ef, canal perhaps traversed by the arteria efferens hyoidea on its way to the radix aortæ (lateral dorsal aorta); *c.hy,* canal for the vena hyoidea (probably, in the external part, for the arteria efferens hyoidea too); *c.pp,* sensory canal commissure, probably corresponding to the posterior head line of pit-organs in fishes in general; *c.sem.ant,* division of the labyrinth cavity for the canalis semicircularis anterior; *cv,* cavum cerebrale cranii (with its lining bone membrane); only a posterior part of it is seen; *d.end,* canal for the ductus endolymphaticus, *ifc,* infraorbital sensory canal; *in,* two canals for nerve branches to the infraorbital sensory canal. The direction of the two canals makes it fully obvious that the nerve-branches transmitted by them must have come from a prootic nerve, probably the r. oticus lateralis or its equivalent; *ju,* the canal for the jugular vein; only the posterior part behind the sinus *si* (see Pl. XXII), shown; *lab.cav,* labyrinth cavity (partly exposed. Like the cavum cerebrale it has its lining bone membrane preserved and is therefore black in the figure); *lc,* cephalic division of the lateral line; ld_1-ld_3, canals ascending from the canal *n.l.* for the n. lineæ lateralis to the cephalic division of the lateral line; *ls,* lamella of bone connecting canals transmitting lateralis branches for the innervation of the posterior part of the internal and external bone layers with each other; *orb,* orbital entrance; *par,* pineal foramen; *soc,* supraorbital sensory canal; *v.lb,* canal from the labyrinth; cavity to the dorsal part of the proximal portion of the vagus canal. The canal probably transmitted a vein. On the right side the canal is partly seen in section close to its posterior end; X_{vn}, the canal for the vagus and the vena cerebralis posterior (proximal part).


par
v₁
c.sem.ant
ifc
in
in
c.ef
ju
ld₁
ld₂
ld₃
d.end
ls
Xvn
ulb
Xvn
ls
ld₂
ld₃
lc
lc
c.pp
ifc
soc

EXPLANATION OF PLATE XXI

Macropetalichthys rapheidolabis. Same specimen as in Pls. XIX and XX. Primordial neurocranium in ventral view. Certain parts of the left side (right in the figure) and of the anterior end removed.

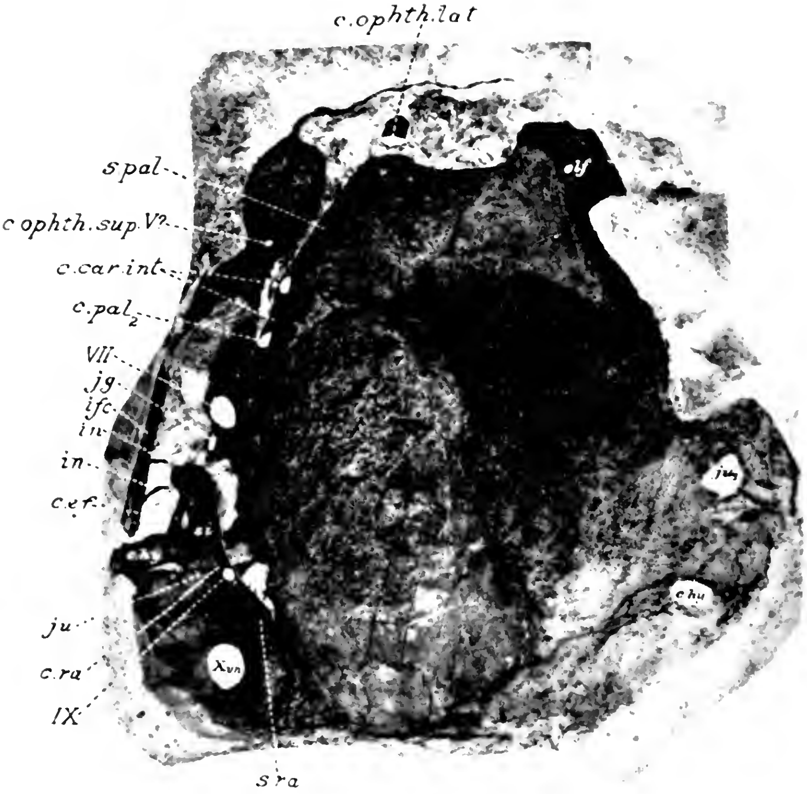
c.car.ext, canal for the arteria carotis external (represented merely by a groove, as its filling of stone and its external wall have been destroyed by weathering); *c.car.int,* canal for the arteria carotis interna (represented to a large extent by its filling of stone, as its external wall has been abraded). The most anterior white spot marks the place at which the internal carotid curved upward to the cavum cerebrale; *c.com,* canal for the arteria carotis communis (its external wall and in part also its stone filling destroyed. In the anterior part, in which the stone filling is lost, it appears as a groove); *c.hy,* canal for the vena hyoidea (merely the proximal part completely preserved in the figure, the distal part being, as is well seen, represented there by a groove); *c.ophth.lat,* canal for the n. ophthalmicus lateralis (anterior part); *c.pal*$_2$ the canal for the r. palatinus facialis through the orbital floor (dorsal opening); *c.ra,* canal for the radix aortæ (lateral dorsal aorta). The canal is imperfectly preserved, being represented merely by a groove in the figure; *c.sem,* division of the labyrinth cavity for a semicircular canal, probably the c. semicircularis externas; *cv,* cavum cerebrale cranii (merely a small posterior part is shown); d$_{ix}$, indication of a canal, perhaps for the lateralis branch that accompanied the n. glossopharyngeus from the cavum cerebrale; *jgx,* canal for the jugular vein from the orbit to the mandibular vein (section); *ju,* canal, which through its anterior opening transmitted the vena mandibularis (the anterior part not fully preserved. The anterior opening was situated more laterally than in the figure); *ju*$_1$ and *ju*$_2$, anterior and posterior opening of the canal *ju; na,* nasal aperture; *nf,* nasal fontanelle; *n.l.,* canal for the n. linæ lateralis; *olf,* olfactory capsule; *rm, ophth. lat,* branch for a lateralis nerve from the canal for the n. ophthalmicus lateralis to the supraorbital sensory canal; *si,* sinus formed by the confluence of the canal *ju* and the canal *c.ra* (its ventral wall has been removed, so that its stone filling covered by the lining membrane of bone is visible); *soc,* supraorbital sensory canal (a small anterior part); *s.ra,* groove for the radix aortæ (lateral dorsal aortæ); *S*$_x$, groove anterior of the external opening of the vagus canal; VII, canal for the n. facialis on the left side—right in the figure—the external part in section; IX, canal for the n. glossopharyngeus (external opening); X$_{vn}$, external opening of the canal for the vagus and the vena cerebralis posterior.


olf
c.ophth.lat
nf
rm.ophth.lat
soc
na
olf
c.car.int
c.car.int
c.pal$_2$
c.car.ext.
VII
VII
jg
VII
ju$_1$
ju$_1$
c.sem
c.com
c.hy
c.hy
IX
ju$_2$
c.ra
d$_{IX}$ IX
X$_{vn}$
s$_X$ X$_{vn}$
s.ra
s.ra
n.l

EXPLANATION OF PLATE XXII

Macropetalichthys rapheidolabis. Same specimen as in the three preceding plates. Imperfect impression of the ventral surface of the primordial neurocranium with certain lateral parts of this remaining in their original position on the left side.

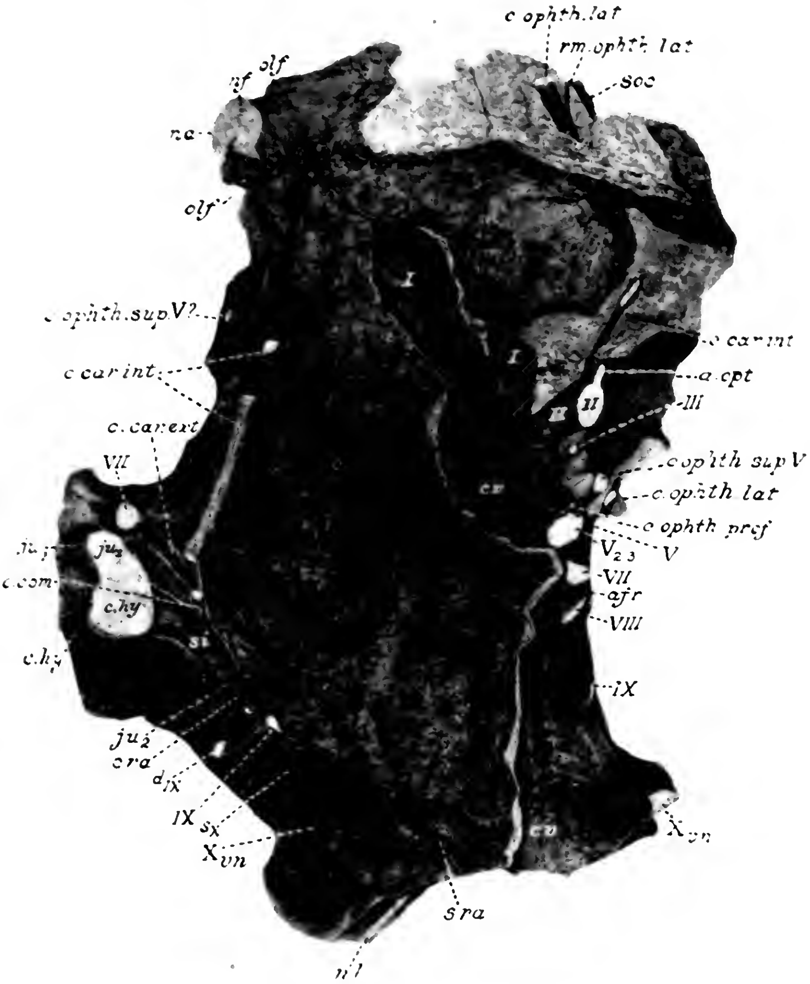
c.car.int, canal for the arteria carotis interna (the white opening denoted is the place at which the artery turned upwards and ascended to the cavum cerebrale); *c.hy,* canal for the venal hyoidea (on the right side is the external opening shown as impression); *c.cf,* canal perhaps for the arteria efferens hyoidea on its way to the radix aortæ (lateral dorsal aorta); *c.ophth.lat,* canal for the n. ophthalmicus lateralis; *c.ophth.sup.V?,* canal perhaps for the r. ophthalmicus superficialis V through the antorbital process (merely the anterior opening seen as impression in the figure); *c.pal*$_2$, canal for the r. palatinus facialis through the orbital floor (merely the ventral opening into the internal carotid canal is seen here); *c.ra,* canal for the radix aortæ (lateral dorsal aorta); *ifc,* infraorbital sensory canal; *in,* two canals for nerve branches to the infraorbital sensory canal. The direction of the canals makes it fully evident that the nerve branches transmitted by them must have come from a proötic nerve, probably the r. oticus lateralis or its equivalent; *jg,* canal for the vena jugularis from the orbit to the mandibular vein (section); *ju,* canal for the jugular vein posterior of the sinus *si; ju*$_1$, anterior opening of the canal *ju.* The opening was traversed by the mandibular vein (impression); *olf,* olfactory capsule (impression of ventral side); *si,* sinus arisen by the confluence of the canals *ju* and *c.ra; s.pal,* groove for the r. palatinus facialis on the lower side of the primordial neurocranium (seen as impression here and therefore appearing as a ridge); *s.ra,* groove for the radix aortæ (lateral dorsal aorta). The groove is preserved as an impression and has therefore the shape of a ridge; VII, canal for the n. facialis (section); IX, canal for the n. glossopharyngeus (section close at the external opening into the groove *s.ra;* X$_{vn}$, canal for the vagus and the vena cerebralis posterior (abraded impression of the left external opening).


c.ophth.lat
s.pal
c.ophth.sup.V?
c.car.int
c.pal$_2$
VII
jg
ifc
in
in
c.ef
ju
c.ra
IX
s.ra
olf
c.hy
sl
Xvn
ju
chu

EXPLANATION OF PLATE XXIII

Macropetalichthys rapheidolabis. Same specimen as in the preceding plates. The primordial neurocranium in ventral view with certain parts removed on the left side (right in the figure) to show the cavum cerebrale and the exits of the canals for the cranial nerves from this.

afr, acustico-facialis recess; *a.opt,* division of the external opening of the opticus canal traversed by the arteria optica; *c.car.ext,* canal for the arteria carotis externa (as its filling of stone and ventral wall have been destroyed, it appears as a groove in the figure); *c.car.int,* canal for the arteria carotis interna. On the right side (left in the figure) the suborbital part is in almost the entire extension represented by the filling of stone, as the ventral wall has been destroyed. The foramen somewhat in front of the stone filling is the place at which the artery curved upward to ascend to the cavum cerebrale. On the left side (the right in the figure) is seen the ascending part of the same canal; *c.com,* canal for the arteria carotis communis (in its anterior part, in which the ventral wall and stone filling have been destroyed, it appears as a groove, in its posterior part, in which merely the external wall is lacking, the filling of stone is clearly seen); *c.hy,* canal for the vena hyoidea (the distal part destroyed and represented in the figure merely as a groove); *c.ophth.lat,* canal for the n. ophthalmicus lateralis (merely an anterior part and a posterior part discernible); *c.ophth.prof,* canal for the r. ophthalmicus profundus (proximal part); *c.ophth. sup.V,* canal for the r. ophthalmicus superficialis trigemini to the orbit (entire canal with the external opening); *c.ophth. sup. V?,* canal probably for the r. ophthalmicus superficialis trigemini through the preorbital process; *c.ra,* canal for the radix aortæ (lateral dorsal aorta). Its external wall and filling being destroyed it appears merely as a groove; *cv,* cavum cerebrale cranii (with its lining membrane of bone—the inner bone layer); d_{IX}, indication of a canal to the dorsal side of the cranial roof, probably for a lateralis branch that accompanied the n. glossopharyngeus from the cavum cerebrale; ju_1, anterior opening of the canal *ju* (as the lateral parts are broken off the actual anterior opening of the canal *ju* was situated more laterally than in the figure. We are there in fact concerned with a section through the part of the canal *ju* situated anterior of the sinus *si*); ju_2, position of the posterior opening of the canal *ju* (the external wall and the filling of stone being destroyed, only a groove is seen at this place in the figure); *na,* nasal aperture; *nf,* nasal fontanelle; *n.l,* canal for the n. lineæ lateralis; *olf,* olfactory capsule; *rm.ophth.lat,* fine canal for a branch from the n. ophthalmicus lateralis to the supraorbital sensory canal; *si,* sinus in the lateral wall arisen by confluence of the canals *ju* and *c.ra; soc,* supraorbital sensory canal (anterior part); *s.ra,* groove for the radix aortæ (lateral dorsal aorta); S_X, groove leading from the vagus canal; I, canal for the tractus olfactorius; II, canal for the n. opticus (entire canal with external opening); III, canal for the n. oculimotorius; V, trigeminus recess; $V_{2,3}$ canal for the r. maxillaris and r. mandibularis trigemini (section through the proximal part); VII, canal for the n. facialis (proximal part in section); VIII, canal for the n. acusticus; IX, canal for the glossopharyngeus (proximal part); X_{vn}, canal for the n. vagus and the vena cerebralis posterior.


c ophth. lat
rm. ophth. lat
soc
olf
nf
na
olf
c ophth. sup. V?
c car int
c. car. ext
VII
ju_1
ju_2
c. com
c. hy
si
c. hy
ju_2
cra
d_{IX}
IX
s_X
X_{vn}
nl
sra
I
I
II
II
cv
cv
c car int
a opt
III
c ophth sup V
c ophth lat
c ophth prof
$V_{2\,3}$
V
VII
afr
VIII
IX
X_{vn}

EXPLANATION OF PLATE XXIV

Macropetalichthys rapheidolabis. Same specimen as in the preceding plates.

Fig. 1. Primordial neurocranium seen from the right side.

Fig. 2. A transversal section through the lateral part of the primordial neurocranium, along the canal for the n. vagus and the vena cerebralis posterior. The impression of the anterior side of this canal is shown in black. In one place a part of its filling of stone remains (with white external end).

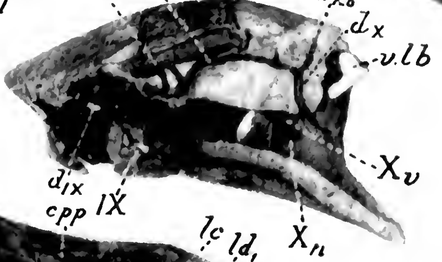
Fig. 3. Primordial neurocranium in posterior aspect. The place from which the posterior narrow division of the occipital region issues is well shown. Further, we can see at this place the posterior end of the middle division of the cavum cerebrale and a section through the cavum cerebrale at the transition to the posterior narrow division (white). The canal for the n. lineæ lateralis is exposed during a rather large part of its course, as the cranial wall has been destroyed at this place.

c.hy, canal for the vena hyoidea (the septum between it and the anterior opening of the canal *ju,* partly destroyed); *c.ophth.sup.V,* canal through the preorbital process, probably for the r. ophthalmicus superficialis trigemini; *c.pp,* sensory canal commissure, probably corresponding to the posterior head line of pit organs in fishes in general; *cv,* cavum cerebrale cranii (a section of it at the transition to the posterior narrow division is shown in white); d_{ix}. indication of a canal to the dorsal side of the primordial neurocranium. The canal probably transmitted a lateralis branch that might have accompanied the n. glossopharyngeus from the cavum cerebrale; d_x, dorsal branch from the vagus canal for a lateralis nerve; d_{xa}, and d_{xb}, branches of the canal d_x, the former of which lodged the nerve to the antero-laterally running part of the cephalic division of the lateral line, while the latter lodged the nerve to the sensory canal commissure *c.pp; ifc,* infraorbital sensory canal; ju_1, anterior opening of the canal *ju* (the septum between it and the external part of the canal *c.hy,* partly destroyed); *lc,* cephalic division of the lateral line; ld_1-ld_6, canals for branches from the n. lineæ lateralis to the most posterior part of the cephalic division of the lateral line; *na,* nasal aperture; *nf,* nasal fontanelle; *n.l,* canal for the lineæ lateralis (exposed in the distal part owing to the incomplete state of preservation of the posterior cranial wall; *orb,* orbit; *v.lb,* canal from the postero-dorso-medial part of the labyrinth cavity to the proximal dorsal part of the vagus canal. The canal probably transmitted a vein (section); *vy,* opening of a canal of doubtful importance (perhaps for some vessel); VII, canal for the n. facialis; XV, canal for the n. glossopharyngeus; X_{vn}, canal for the n. vagus and the vena cerebralis posterior (the two divisions are clearly shown).

1


lc
if.c
c.ophth.sup.V?
X_v
X_n
d_{IX}
IX
c.hy
ju_1
VII
vy
nf
na

2


lc
d_{Xa}
d_{Xb}
d_X
v.lb
d_{IX}
IX
X_v
X_n

3


cr.od
cpp
lc
ld_1
ld_2
ld_3
ld_4
ld_2
ld_1
ld_3
n.l
cv
n.l
ld_6
ld_5
c.hy

EXPLANATION OF PLATE XXV

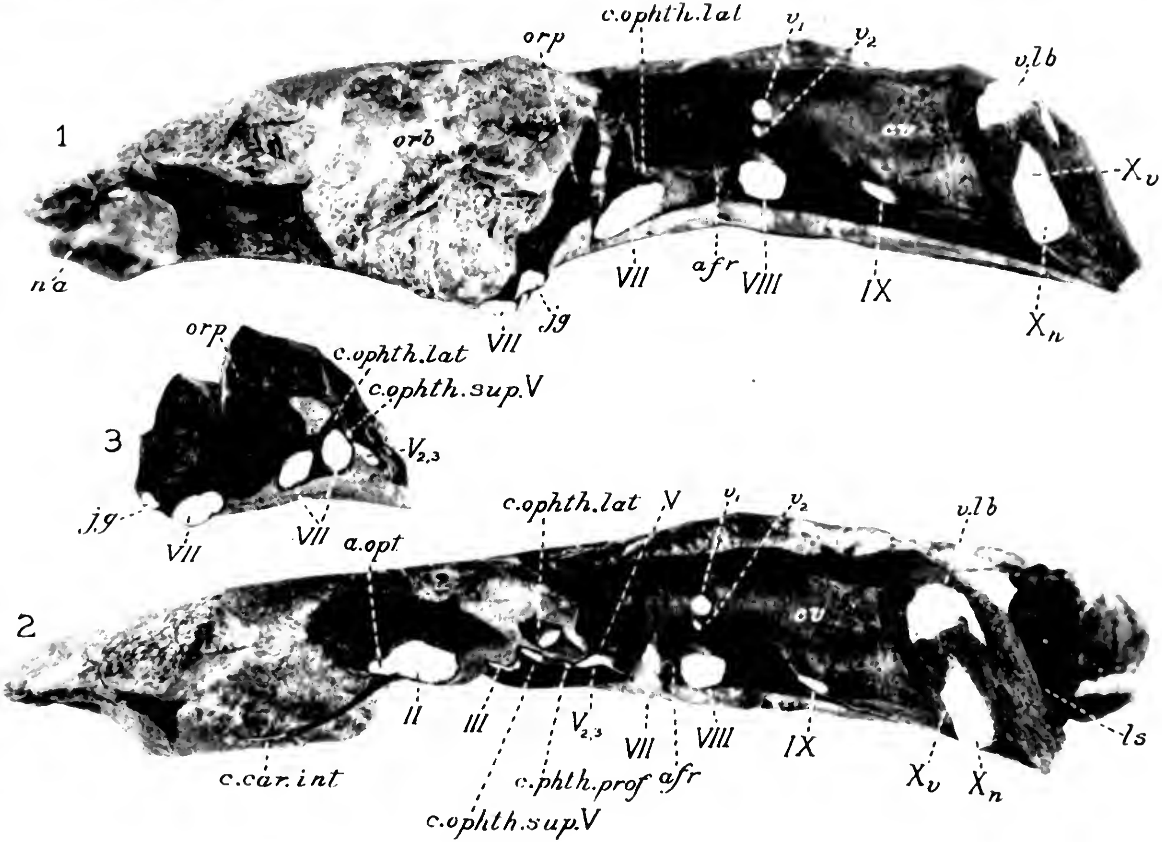
Macropetalichthys rapheidolabis. Same specimen as in the preceding plates.

Fig. 1. Primordial neurocranium from the left side with certain lateral parts removed to show parts of the cavum cerebrale.

Fig. 2. Primordial neurocranium in the same aspect as in the preceding figure but with still another lateral part removed to show the interorbital wall.

Fig. 3. The surface *orp* in fig 1, seen from behind. This surface is the impression of the posterior surface of the orbit.

afr, acustico-facialis recess; *a.opt,* division of the external opening of the opticus canal for the arteria optica; *c.car.int,* canal for the arteria carotis interna (the ascending portion); *c.ophth.lat,* canal for the n. ophthalmicus lateralis (proximal part); *c.ophth.prof,* canal for the r. ophthalmicus profundus to the orbit (proximal part); *c.ophth.sup.V,* canal for the r. ophthalmicus superficialis trigemini to the orbit; *cv,* cavum cerebrale (middle division, which is covered by its lining layer of bone—the inner bone layer); *jg,* canal for the jugular vein from the orbit to the confluence with the mandibular vein; *na,* nasal aperture; *orb,* orbit. In fig. 1 it is filled with stone, in fig. 2 this filling has been removed so that its medial wall is seen partly with its external surface preserved (black, as it is covered by the external bone layer) and partly in section (bright, with nerve canals in it); *orp,* posterior surface of the orbit preserved as an impression (to a large extent with the external bone layer adherent to it and therefore black in the figure); *v.lb,* canal from the postero-dorso-medial part of the labyrinth cavity to the proximal dorsal part of the vagus canal. The canal probably transmitted a vein (here is merely seen a section through the posterior part); v_1, v_2, two canals leading from the cavum cerebrale to the labyrinth cavity, probably for vessels; II, canal for the n. opticus (external opening); III, canal for the n. oculomotorius; V, trigeminus recess; $V_{2,3}$, canal for the r. maxillaris trigemini and the r. mandibularis trigemini (section through the proximal part); VII, facialis canal (several parts of it are seen). Figs. 1 and 2 show that it is crossed on the dorsal side by the canal *jg;* VIII, canal for the n. acusticus; IX, canal for the n. glossopharyngeus (proximal part); X_{vn}, canal for the n. vagus and the v. cerebralis posterior.


1
orp
orb
n'a
c.ophth.lat
v_1
v_2
v.lb
X_v
X_n
IX
VIII
afr
VII
jg
VII
3
orp
c.ophth.lat
c.ophth.sup.V
$V_{2,3}$
jg
VII
VII
2
a.opt
c.ophth.lat
V
v_1
v_2
v.lb
ls
X_v
X_n
IX
VIII
afr
VII
$V_{2,3}$
c.phth.prof
c.ophth.sup.V
III
II
c.car.int

EXPLANATION OF PLATE XXVI

Macropetalichthys rapheidolabis. Same specimen as in the preceding plates.

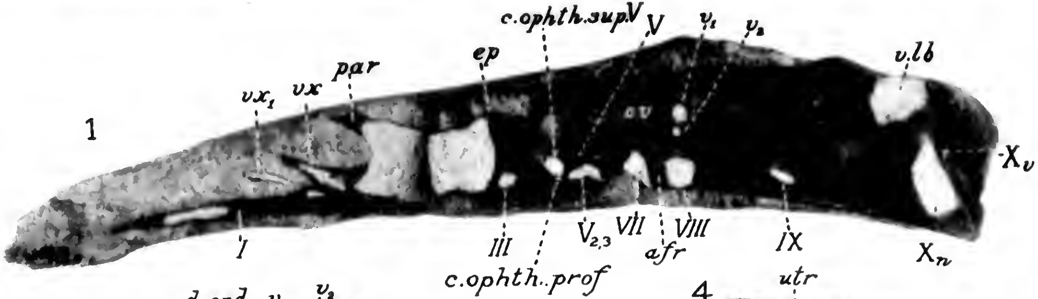
Figs. 1, 2. The cavum cerebrale seen from the left side (partly in section).

Fig. 3. The labyrinth cavity seen from the medial side with the wall separating it from the orbit (the posterior surface of the orbit denoted by *orp*) and the vagus canal (X_{vn},) shown in their positions and with their real thickness.

Fig. 4. The labyrinth cavity shown from the lateral side (imperfectly exposed).

afr, acustico-facialis recess; *c.ophth.prof,* canal for the r. ophthalmicus profundus to the orbit (proximal part); *c.ophth.sup.V,* canal for the r. ophthalmicus superficialis trigemini to the orbit proximal part); *c.sem,* divisions of the labyrinth cavity for a semicircular canal, perhaps the c. semicircularis externas; *c.sem. ant,* division of the labyrinth cavity for the canalis semicircularis anterior; *cv,* cavum cerebrale (with its lining bone layer—the inner bone layer—where it is shown in black; sections through it are shown in white); *d.end,* canal for the ductus endolymphaticus; *ep,* diverticle from the posterior part of the roof of the anterior division of the cavum cerebrale (not seen in its entire length in the figures); *orp,* posterior surface of the orbit; *par,* pineal canal; *ru,* division of the labyrinth cavity occupied by the recessus utriculi; *utr,* division of the labyrinth cavity occupied by the utriculus; *sac,* division of the labyrinth recess occupied by the sacculus (partly seen); *v.lb,* canal from the labyrinth cavity to the dorsal proximal part of the vagus canal (probably for a vein); v_x, v_x^1, canals probably for vessels; v_1, v_2, canals probably for vessels from the cavum cerebrale to the labyrinth cavity; I, canal for the tractus olfactorius; III, canal for the n. oculomotorius (proximal part); V, trigeminus recess; $V_{2,3}$, canal for the r. maxillaris trigemini and the r. mandibularis trigemini (proximal part in section); VII, canal for the n. facialis (in fig. 3 a considerable part of it is seen in the wall between the labyrinth cavity and the orbit, as the ventral part of this wall has been removed); VIII, canal for the n. acusticus; IX, canal for the n. glossopharyngeus; X_{vn}, canal for the n. vagus and the vena cerebralis posterior (in figs. 1, 2, section through its proximal part, in figs. 3, 4, impression of its anterior side. In fig. 4 also, a part of its stone filling is seen, the anterior end of which is white).

1


vx₁
vx
par
ep
c.ophth.supV
V
v₁
v₂
v.lb
ov
X_v
I
III
V₂,₃
VII
VIII
afr
IX
Xₙ
c.ophth.prof

3


v.lb
d.end
v₁
v₂
c.sem.ant
orp
X_vn
sac
VIII
VII
VII

4


c.sem.ant
orp
X_v
Xₙ
VII
c.sem
c.sem
s.ra
IX

2

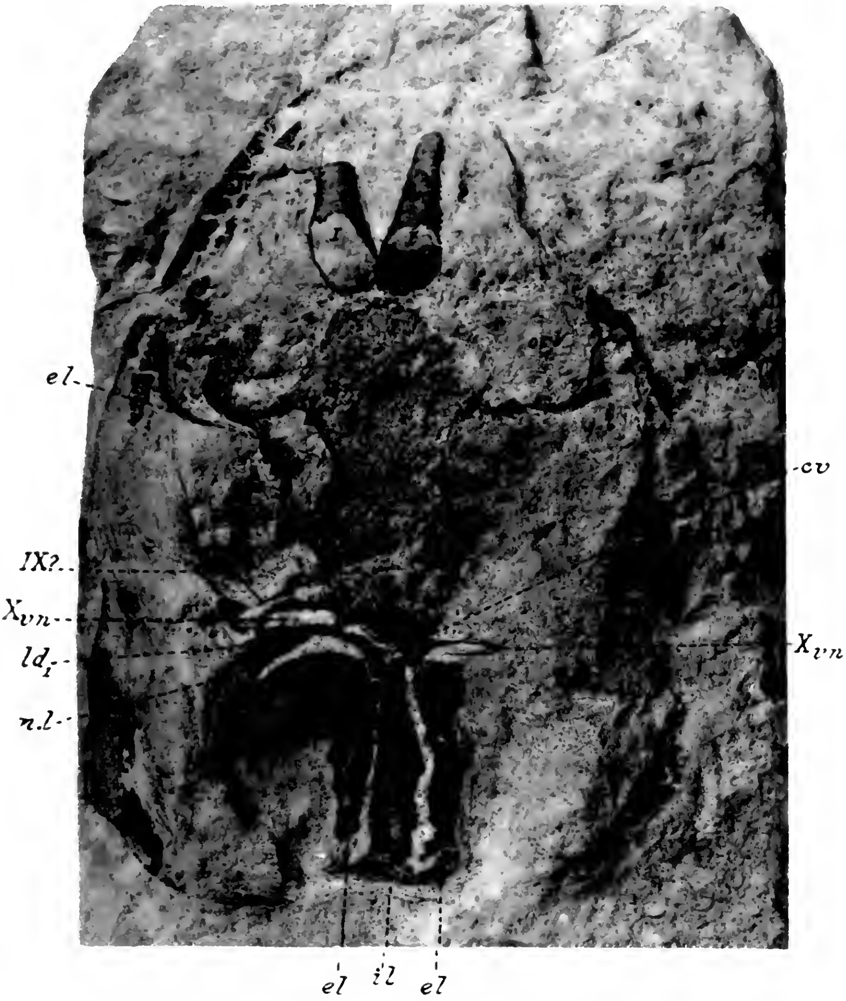

ep
c.ophth.supV
V
v₁
v₂
v.lb
ov
X_v
I
III
V₂,₃
VII
VIII
afr
IX
Xₙ
c.ophth.prof

EXPLANATION OF PLATE XXVII

Macropetalichthys rapheidolabis. Specimen 710 F in the American Museum of Nat. Hist., New York. About ¾ of the nat. size.

The specimen exhibits certain basal parts of the primordial neurocranium.

cv, cavum cerebrale cranii, the posterior narrow division (in section at the place denoted. Behind this place covered by the internal bone layer *il*) ; *el,* the external bone layer (the part of it on the ventral surface of the occipital labyrinth and orbitotemporal regions and a part of it on the dorsal side of the occipital region preserved. The latter part has, however, been partly removed by preparation) ; *il,* internal bone layer (surrounding the posterior narrow division of the cavum cerebrale) ; *lab.cav,* labyrinth cavity (in horizontal section) ; ld_1, canal for a nerve branch from the n. lineæ lateralis to the posterior part of the cephalic division of the lateral line; *n.l,* canal for the n. lineæ lateralis (its origin from the vagus canal clearly seen here) ; *orb,* orbit (its floor partly preserved on the left side) ; I, canal for the tractus olfactorius; IX?, perhaps the canal for the n. glossopharyngeus; X_{vn}, canal for the n. vagus and the vena cerebralis posterior.


I
el
cv
IX?
X_{vn}
ld_1
n.l
X_{vn}
el
il
el

EXPLANATION OF PLATE XXVIII

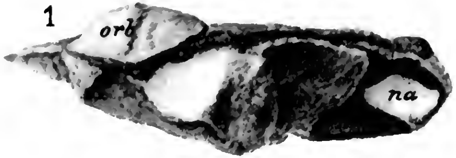
Figs. 1, 2. *Epipetalichthys wildungensis.* Specimen belonging to the Geological Institution of the University of Greifswald, Germany. Fig. 1 shows the parts preserved of the ethmoidal region of the primordial neurocranium from the right side; fig. 2 shows the parts preserved of the occipital and labyrinth regions in ventral aspect.

Figs. 3, 4. *Macropetalichthys rapheidolabis.* Specimen 4445 G of the American Museum of Nat. Hist., New York. Fig. 3 is in posterior, fig. 4 in ventral view. The specimen displays the posterior narrow division of the occipital region of a rather large animal.

Fig. 5. *Macropetalichthys rapheidolabis.* Specimen 280 G of the American Museum of Nat. Hist. New York. Portion of the posterior narrow division of the occipital region in ventral view. The ventral parts of the division and the cavum cerebrale have been removed so that merely certain dorsal parts remain. What is lettered *el* is here the anterior part of the external bone layer of the dorsal side of the division. The bone piece lettered *il* is a posterior part of the inner bone layer on the dorsal side of the cavum cerebrale.

ch, space for the notochord (just at the anterior end); *ch.w,* ridge in the anterior part of the hæmal groove caused by the notochord; $c.ra_1$, $c.ra_2$, anterior and posterior opening of a canal for the radix aortæ (lateral dorsal aorta). The canal corresponds to a posterior part of the groove *s.ra* in *M. rapheidolabis; cr.ol,* crista occipitalis lateralis; *cr.sp,* craniospinal process (impression of its anterior surface; fragments in fig. 3); *el,* external bone layer; *hæm,* hæmal groove; *il,* internal bone layer; *na,* nasal aperture; *orb,* orbital entrance; *pr,* postero-laterally projecting process of the anterior broad division of the occipital region.

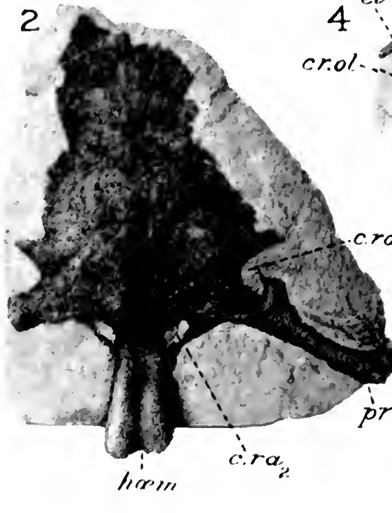
1


orb
na

3


cr.sp
e'l
hœm
el

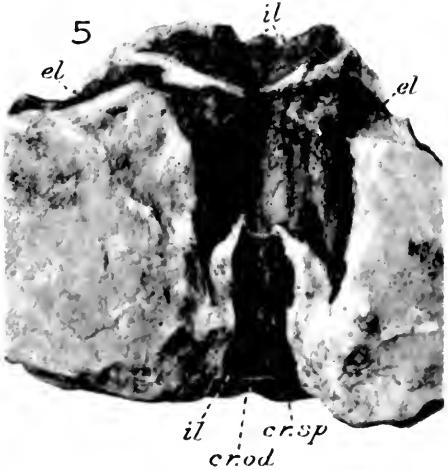
2


c.ra₁
pr
hœm
c.ra₂

4


el
cr.ol
il
ch
ch.w
el
e'l
il
hœm

5


il
el
el
il
cr.sp
cr.od

EXPLANATION OF PLATE XXIX

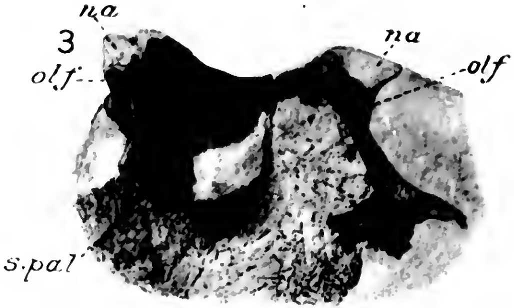
Figs. 1, 2. *Macropetalichthys agassizi?* Specimen in the possession of Mr. S. Junkermann of Bielefeld, Germany. Fig. 1 shows much crushed posterior parts of the primordial neurocranium in ventral view; fig. 2 a posterior part of the dermal cranial roof with a number of sensory canal pores.

Figs. 3, 4. *Epipetalichthys wildungensis.* Specimen belonging to the Geological Institution of the University of Greifswald, Germany. Same specimen as in figs. 1, 2, Pl. XXVIII. Fig. 3 shows the part preserved of the ethmoidal region in ventral view, fig. 4 the ornament on a part of the dermal cranial roof (impression with the bone tissue of the tubercles adhering to the stone and appearing brighter than this).

c.pp, sensory canal commissure probably corresponding to the posterior head line of pit organs in fishes in general; *cr.od,* crista occipitalis dorsalis (impression); *d.end,* dorsal opening of the canal for the ductus endolymphaticus; *lc,* cephalic division of the lateral line; *na,* nasal aperture; *olf,* olfactory capsule; *pr,* postero-laterally projecting process of the broad anterior division of the occipital region; *s.pal,* groove for the r. palatinus facialis.

1

3



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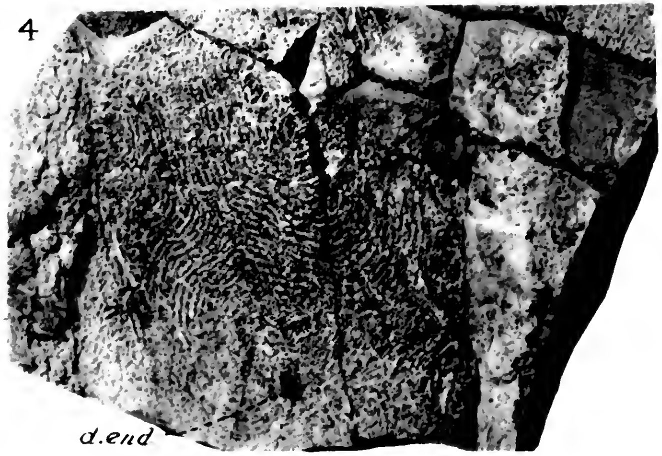

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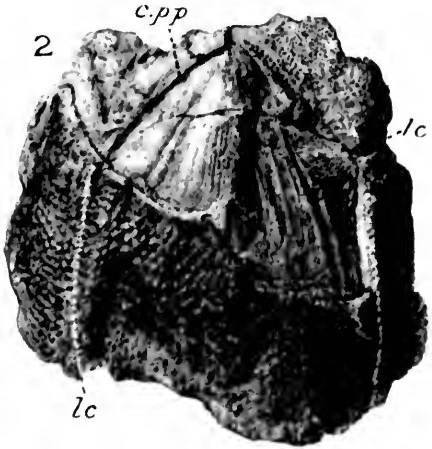


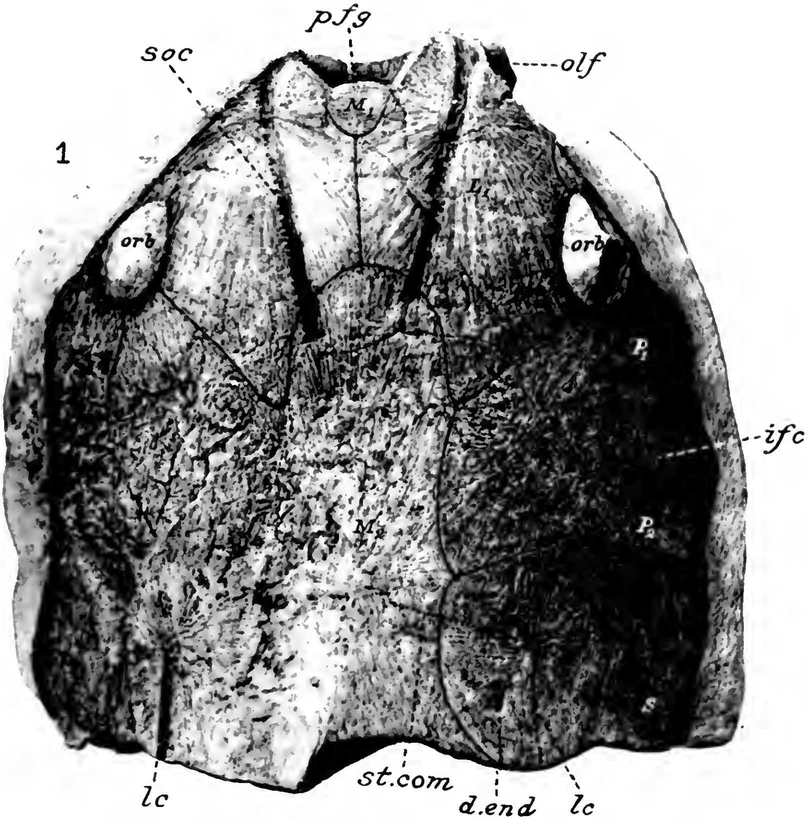
EXPLANATION OF PLATE XXX

Fig. 1. *Epipetalichthys wildungensis.* Specimen belonging to the Geological Institution of the University of Greifswald, Germany. Same specimen as in figs. 1, 2, Pl. XXVIII and figs. 3, 4 in Pl. XXIX. Head in dorsal view. The head lacks a large posterior part. Anteriorly it shows the cavum precerebrale and the olfactory capsule. The approximate position of the sutures between the bones of the dermal cranial roof is indicated with black lines.

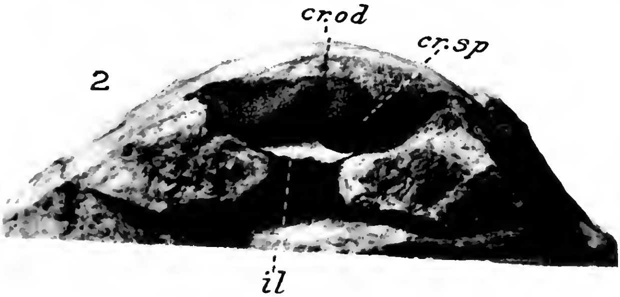
Fig. 2. *Macropetalichthys rapheidolabis.* Specimen 280 G of the American Museum of Nat. Hist., New York. The posterior end of the occipital region in posterior views. The cranio-spinal process (*cr.sp*) is well shown, but is represented only by the impression of its anterior side.

M_1, M_2, L_1, L_2, L_3, P_1, P_2, S, dermal bones of the cranial roof; M_1 imperfect anteriorly; *cr.od,* crista occipitalis dorsalis (its posterior continuation on the anterior surface of the cranio-spinal process); *cr.sp,* cranio-spinal process (represented merely by the impression of its anterior surface); *d.end,* the canal for the ductus endolymphaticus (dorsal opening); *ifc,* infraorbital sensory canal (its position indicated by its pores); *il,* internal bone layer; *lc,* cephalic division of the lateral line (its posterior part indicated by pores; its anterior part does not open outwards); *olf,* olfactory capsule; *orb,* orbital entrance; *pfg,* cavum precerebrale; *soc,* supraorbital sensory canal (exposed to a large extent by weathering) *st.com,* cross-commissural sensory canal, probably representing the true supratemporal commissure of fishes in general.

1


pfg
soc
olf
M_1
L_1
orb
orb
P_1
ifc
P_2
S
M_2
lc
st.com
d.end
lc

2


cr.od
cr.sp
il

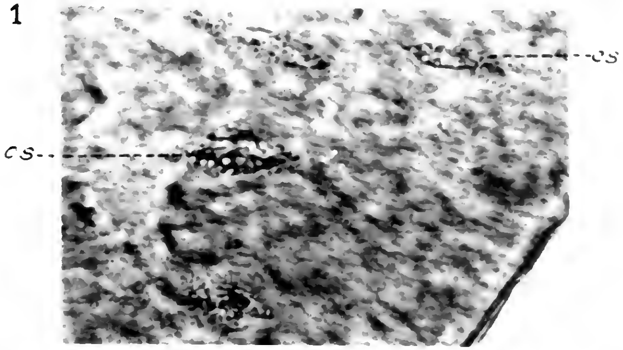
EXPLANATION OF PLATE XXXI

Fig. 1. *Macropetalichthys rapheidolabis.* Microscopic section through the external bone layer of the primordial neurocranium. Magnification 700/1.

Fig. 2. *Epipetalichthys wildungensis.* Specimen belonging to the Geological Institution of the University of Greifswald, Germany. Part of a section through the anterior part of the posterior narrow division of the occipital region. Note the trabecles on the inside of the external bone layer (*el*) and on the outside of the notochordal layer (*ch.l*). Magnification about 30/1.

ch, space for the notochord (partly seen); *ch.l,* bone layer surrounding the notochordal space; *cs,* cell space; *el,* external bone layer; *hæm,* hæmal groove.

1



2