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PRELIMINARY NOTE ON DEVONIAN STEGOCEPHALIANS FROM EAST GREENLAND

BY

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WITH 22 PLATES AND 22 FIGURES IN THE TEXT

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PREFACE

The highly interesting material described in this paper belongs to the Geological Survey of Greenland (Chief: Dr. LAUGE KOCH) and was collected by the Danish East Greenland Expedition in the summer of 1931. For being honoured with the pleasant task of its description I am greatly indebted to Doctor LAUGE KOCH, Chief of the Expeditions. To Professor E. STENSIÖ I am indebted in many respects: for his recommending me as a member of the Danish Expedition of 1931, for most valuable instruction in the methods and technique of modern vertebrate palaeontology, for constant help and much valuable advice, and finally for his very stimulating interest in this work.

For the performance of the by far greatest part of the extremely difficult preparation thanks are due to Mrs. A. STENSIÖ, and Miss A. BRASCH, and for the drawings and retouching to Mr. S. EKBLOM, Mrs. K. SILFVERSWÄRD, and Miss K. EKBLOM.

I. Introduction.

The Danish Expeditions to East Greenland have, during the last few years, brought home material that throws new light on several questions of palaeontology. One of the most important results of these expeditions was the discovery and exploration, in 1929 and 1931, of richly fossiliferous localities in the Upper Devonian of Mt. Celsius on Ymer Island (73°10′ N., 23° W.). The fish-fauna of these localities is clearly of Upper Devonian type and has already been partly described in an important paper by STENSIÖ (1931), and a new paper by the same author is in preparation. The localities have been described by KULLING (1930, 1931) and myself (1932 a). In the last-mentioned paper, which also contains a more precise discussion of the age of the fossils, were mentioned, from "a little above the very East Plateau", "some Crossopterygian and other non-Antiarch remains" (l. c., p. 11). Among the latter there are some rather well preserved remains of Stegocephalians; others not so well preserved, were found at the "Coulisses" and on the Central Part of the northern slope of Mt. Celsius (cf. SÄVE-SÖDERBERGH 1932 a). All come from the mainly red and blackish layers, corresponding to ORVIN's (1930) and KULLING's (1930, 1931) "Upper Red Sandstone Series" (cf. SÄVE-SÖDERBERGH, 1932 a, p. 26—28). Consequently these Stegocephalians are the oldest known Tetrapods.

This preliminary note is intended to describe only the dermal bones of some of the most clear and interesting specimens of the material. A more complete account of the whole material, dealing also with the endocranium and with the bearing of the finds on the morphology of other forms is to be prepared next winter, together with a description of the new material that, it is hoped, will be found during the Expedition of 1932.

II. Material and Methods.

The material dealt with in this preliminary note includes seven skulls or fragments of skulls, lettered A. 1—A. 7. The fossils are, on the whole, tolerably well preserved but some specimens are much crushed, others are preserved only as casts, and all are imbedded in an extremely

hard and tough matrix, which makes preparation exceedingly time-consuming and expensive.

Owing to the considerable difficulty often found in tracing the sutures between the dermal bones, all modern methods had to be used. Alcohol, xylol, and especially oil of aniseed and thick or diluted Canada balsam proved very suitable for clearing up the radiate structure in the dermal bones. The use of these media necessitated the use of strong illumination by the aid of a Pointolite lamp. The sutures were traced under a binocular microscope at different magnifications and marked off with red colour and then the colour of the bone was made more equal by thin wh te staining. The delicate work of colouring the bones after the sutures had been marked off was performed by Mrs. A. Stensiö. After photographing, the white colour was removed where it obscured the minute details of structure, and all details on the plates were retouched under the author's continuous supervision and control.

For clearing away the matrix a special dental mallet (constructed by Doctor H. Arnell) was used. All this work was carried out under binocular microscopes.

The photographs were taken on Ilford Special Rapid Panchromatic plates, practically all with an Ilford Gamma filter, and with the objectives: Zeiss Tessar 1:6,3, F 36 cm, Zeiss Tessar 1:6,3, F 25 cm and Zeiss Tessar 1:4,5, F 16,5 cm.

III. Terminology.

Since this is only a preliminary paper it is not necessary to discuss in it the extremely complicated questions of bone nomenclature. Because of the fish-like organisation of the primitive Tetrapods, described in this paper, it is possible to employ without difficulty the modern terminology worked out — in connection with studies by Allis and others on the lateral line system of fishes — by Stensiö in several important papers on Crossopterygians and other Teleostome fishes (see especially Stensiö 1921; 1922; 1932, pp. 32—38). Thus the bones will be denoted according to the following scheme:

A. Dermal bones of the skull-roof and cheeks.

1. Bones connected with the infraorbital canals[1]): the *rostrals* on the snout, connected with the ethmoidal part or anterior commissure of the infraorbital canals; the *antorbitals*, connected with the parts of the infraorbital canals, forming the postnasal connections with the supraorbital canals (or situated between the supraorbital and the infraorbital canals and in front of the orbits); the *lachrymals* antero-ventrally or antero-laterally,

[1]) For the terminology of the lateral line system here adopted see Säve-Söderbergh 1932 b.

the *jugals* postero-ventrally or postero-laterally, the *postorbitals* posterior to the orbits; the *dermosphenotics* at the postorbital connections of the infraorbital canals with the supraorbital canals and at the place where the infraorbital canal curves downwards towards the cheek; the *intertemporals* around the otic parts of the infraorbital canals.

2. Bones between each infraorbital and supraorbital canal: the *antorbitals* in front of the orbits, the *supraorbitals* above the orbits.

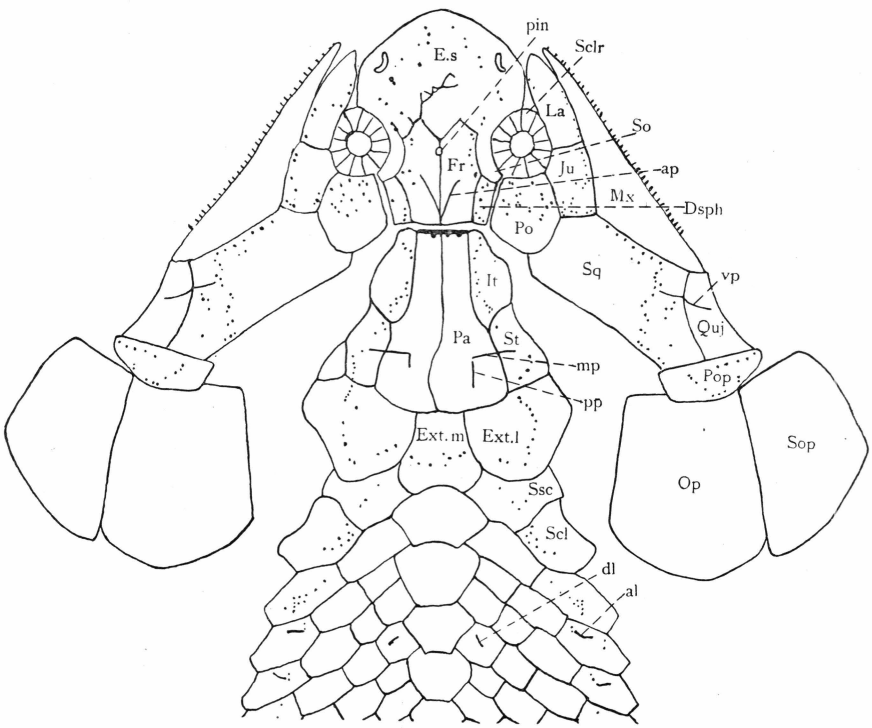


Fig. 1A.

Text-fig. 1. Scheme of dermal bones in primitive Crossopterygians. A. *Osteolepis macrolepidotus*. B. *Dictyonosteus articus*. A. after material belonging to the Palaeontol. Inst. of Uppsala (SÄVE-SÖDERBERGH 1932 b). B after STENSIÖ 1922. Lateral line canals dotted in B, indicated by the position of the pores in A. Ant_1, Ant_2, antorbitals; *Dsph*, dermosphenotic; *E.s*, ethmoidal shield; *Ext. l*, lateral extrascapular; *Ext. m*, median extrascapular; *Fr*, frontal; *Ir*, interrostral; *It*, intertemporal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary, Na_1, Na_2, Na_3, nasals; *Op*, opercular; *Pa*, parietal; *Pmx*, premaxillary; *Po*, postorbital; *Pop*, preopercular; *Ptr*, postrostral; *Quj*, quadratojugal; *R*, rostral; *Scl*, supracleithral (only partly shown in the figure)); *Sclr*, sclerotic ring; *So*, So_1, So_2, So_3, supraorbitals; *Sop*, subopercular; *Sq*, squamosal; *Ssc*, suprascapular (only partly shown in the figure); *St*, supratemporal; *al*, accessory lateral line of the trunk; *ap*, anterior pit-line; *dl*, dorsal lateral line of the trunk; *mp*, middle pit-line; na_1, anterior external naris; *pin*, pineal foramen; *pp*, posterior pit-line; *vp*, vertical pit-line of the cheek, *y* unpaired assymetrical bone of the postrostral series.

3. Bones connected with the supraorbital canals: the *nasals* on the snout; the *frontals* behind the nasals.

4. Bones between the supraorbital canals: the unpaired *interrostral* behind the rostrals; the *postrostrals* behind the interrostral.

5. Bones medial to the otic parts of the infraorbital canals and to the postotic canals[1]): the *parietals*, connected with the medial parts of the middle pit-lines of the head.

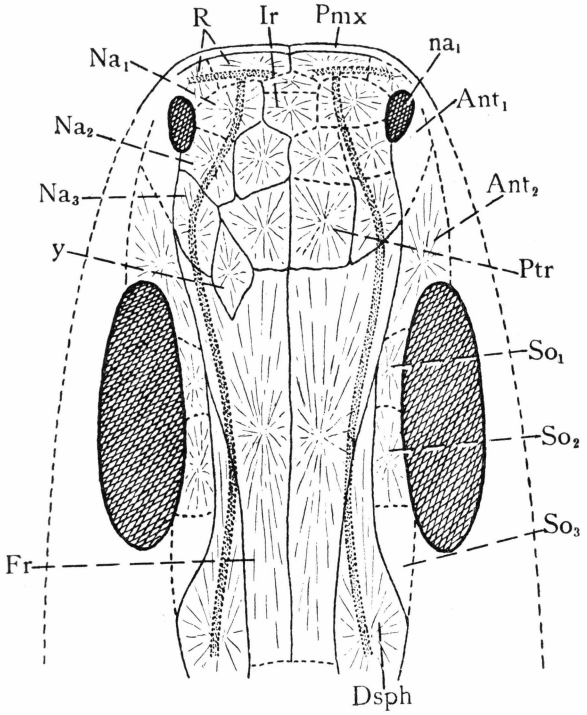


Fig. 1 B.

6. Bones connected with the postotic canals[1]): the *supratemporals*.

7. Bones connected with the cephalic divisions of the main lateral line canals and with the supratemporal canal: the *lateral extrascapulars* and the *median extrascapular*.

8. Bones connected with the hyomandibular group of the lateral line system: a) the *squamosals*, connected with the jugal canals (horizontal pit-lines of the cheek) and the dorsal parts of the vertical pit-lines of the cheek;

b) the *quadratojugals*, connected with the ventral parts of the vertical pit-lines of the cheek (quadratojugal canals[2]);

[1]) The canals, innervated through the nn. glossopharyngei (cf. SÄVE-SÖDERBERGH 1932 b).

[2]) For the terminology of the lateral line system here adopted see SÄVE-SÖDERBERGH 1932 b.

c) the *preopercular*s, connected with the preopercular canals.

9. The *maxillaries* behind, and the *premaxillaries* in front of the posterior external nasal openings[1]). These bones are formed as bases for teeth of the upper jaws.

B. Dermal bones of the palate.

1. An outer row on each side, originally tooth-bearing: *vomer*, *dermopalatine*, *ectopterygoid*.

2. an inner *entopterygoid* on each side.

3. a median *parasphenoid*.

C. Dermal bones of each mandible.

1. connected with the mandibular canal: the *supraangular*, *angular*, *preangular*, *postsplenial*, and *splenial*.

2. the tooth-bearing *dentary* (on the labial side), and *coronoids* (on the lingual side).

3. the *prearticular*, on the lingual side of the mandible.

IV. Description of the specimens.

Family *Ichthyostegidae* n. fam.

Diagnosis[2]): Primitive labyrinthodont Stegocephalians of various size, with the dermal bones of the skull-roof and palate arranged in many respects like those of Crossopterygians: with an unpaired parieto-extrascapular, an unpaired rostro-interrostral, premaxillaries wholly on the ventral side of the skull, fused with lateral rostrals to compound rostro-premaxillaries, narrow frontals, and (probably always) small preoperculars; with broad naso-postrostrals, large oblong posterior antorbitals and a small square anterior antorbital on each side between the rostro-premaxillary and the lachrymal; with large jugals, short fronto-parietals, and compound postorbito-dermosphenotics and supratemporo-intertemporals. Squamosals rigidly connected by suture with the supratemporo-intertemporals and with the large lateral extrascapulars. Maxillaries long, underlying with their posterior ends the anterior ends of the quadrato-jugals, and attached in front to special processes of the vomeres. — Palate extensively ossified, with very large entopterygoids meeting in a median suture, large vomeres, and tooth-bearing dermopalatines and ectopterygoids. — Lower jaw with large supraangulo-angulars and prearticulars.

Lateral line system, at least for the greater part, enclosed in the dermal bones in canals, connected with the surface by primary tubes and pores. A true jugal canal[3]) in the jugal and squamosal.

[1]) cf. below pp. 90—91, text-fig. 17.

[2]) For further discussion of the family I. see below pp. 72—105.

[3]) Homologue of the horizontal pit-line of the cheek and the jugal canal in Crossopterygians (cf. SÄVE-SÖDERBERGH 1932 b).

External nares situated on the ventral surface of the skull, between the maxillaries and the tooth-bearing parts of the rostro-premaxillaries. Palate with anterior palatal vacuity and very narrow interpterygoid vacuities.

Genus ***Ichthyostega*** n. g.

Diagnosis: Ichthyostegids with long, or at least not broad, skulls, with elongate, small to medium-sized orbits, situated with their greater parts in the posterior half of the skull. Each lachrymal and jugal meeting farther forward than the anterior margin of the orbit. Each posterior antorbital with a suture towards the jugal. Fronto-parietals probably only partially separated by a median suture, developed only in front of the pineal foramen. Internal nares wholly situated anterior to the anterior margin of the orbit.

Genotype: *Ichthyostega stensiöi* n. sp.

1. *Ichthyostega stensiöi* n. sp.

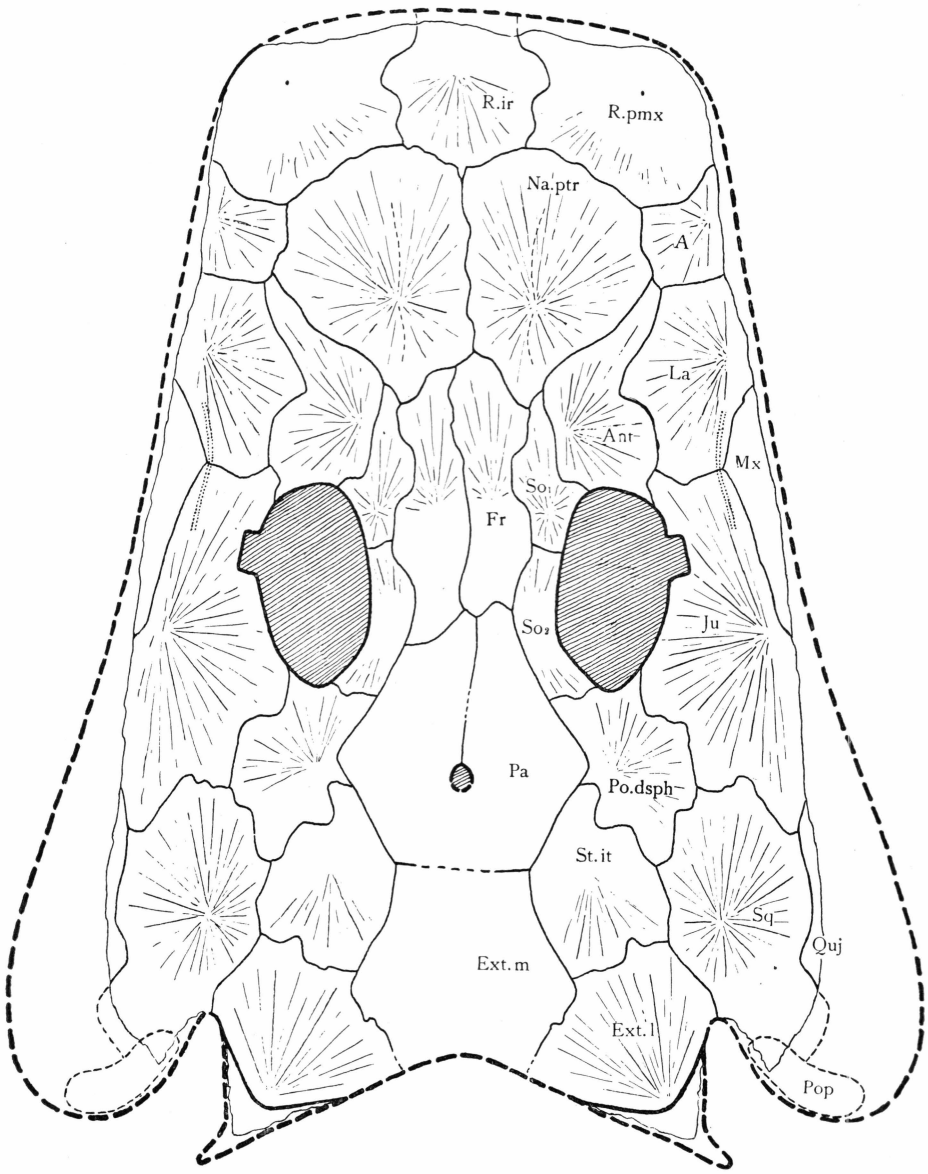
(Pls. I, II, III; pl. IV, figs. 1, 2; text-fig. 2).

Diagnosis: An *Ichthyostega* with a long skull and truncate snout. Dermal bones with fine external sculpture. Each anterior antorbital square, with a straight posterior margin and meeting a long and narrow antero-lateral process of the posterior antorbital, thus separating the naso-postrostral from the lachrymal. Posterior antorbitals with posterior and postero-medial orbital margins. Naso-postrostrals meet the frontals in sutures that have a direction from antero-medially towards postero-laterally. Jugals not excessively large.

Holotype and material. (A. 1) The right half of a skull-roof, exposed from within (A. 1. a), with a counterpart of the anterior half (A. 1. b) showing also part of the palate, as far back as the anterior end of the parasphenoid.

As will be seen from plates I—III and text-fig. 2, the dermal bones of the cranial roof more or less completely preserved in the holotype include: The right rostro-premaxillary, the right anterior antorbital posterior antorbital, naso-postrostral, frontal, anterior and posterior supraorbitals, fronto-parietal, postorbito-dermosphenotic, supratemporo-intertemporal, lateral extrascapular, lachrymal, jugal, squamosal, and the median rostro-interrostral. There are also preserved considerable parts of the left naso-postrostral and frontal, about half of the left fronto-parietal, and smaller parts of the right maxillary and quadratojugal, of the parieto-extrascapular, and of the left rostro-premaxillary, and possibly a part of the right preopercular.

In the palate there are preserved the almost complete right vomer and dermopalatine and parts of the right entopterygoid and ectoptery-



Text-fig. 2. *Ichthyostega stensiöi* n. g. n. sp. Attempted restoration of the skull-roof as seen from the ventral side. $^5/_7$ natural size.

The actually observed parts of the lateral line system indicated by dotted outlines. *A*, anterior antorbital; *Ant*, posterior antorbital; *Ext. l*, lateral extrascapular; *Ext. m*, parieto-extrascapular; *Fr*, frontal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na.ptr*, naso-postrostral; *Pa*, fronto-parietal; *Po.dsph*, postorbito-dermosphenotic; *Pop*, preopercular; *Quj*, quadratojugal; *R.ir*, rostro-interrostral; *R.pmx*, rostro-premaxillary; So_1, anterior supraorbital; So_2 posterior supraorbital; *Sq*, squamosal; *St.it*, supratemporo-intertemporal.

goid as well as of the left vomer and dermopalatine and the anterior tip of the parasphenoid.

Description.

General shape. The reconstruction (text-fig. 2) and the plates I—III show the skull-roof to be rather oblong and roughly rectangular owing to the truncate form of the snout. The restored median length of the skull is 1,18 times its restored maximum breadth, i. e. across its posterior quarter and nearly twice the restored breadth of the nasal region. The medium-sized orbits were situated a little behind the mid-length of the skull. They have their maximum length along a line running from postero-dorso-medially to antero-ventro-laterally. No trace of the external nares can be seen on the preserved part of the skull.

The skull-roof seems to have been rather high, owing to a marked bend along a longitudinal line passing through the most median part of the orbit. Accordingly the bones on each side of the median line of the skull-roof come to lie in two somewhat distinct planes: the more medially situated bones in a plane, horizontal in transverse section but slightly convex upward in longitudinal section; the more laterally situated bones in a slightly twisted plane, dipping ventrally at inner angles of 150—130° towards the plane of the medially situated bones, the former angle applying to the posterior, the latter to the anterior part of the skull. To the median plane belong the bones described below as the rostro-interrostral, the frontals, the posterior supraorbital, the fronto-parietals, the parieto-extrascapular, and half of each of the naso-postrostrals, intertemporo-supratemporals and lateral extrascapulars. The other halves of these bones, as well as the rostro-premaxillary, the anterior and posterior antorbital, the lachrymal, postorbito-dermosphenotic, jugal, squamosal, and quadratojugal on each side belong to the lateral plane.

To give a more exact idea of the proportions and size of the skull in *Ichthyostega stensiöi*, the following measurements from the holotype may be cited:

Restored median length	192 mm
Length from posterior angle of rostro-interrostral to anterior margin of parieto-extrascapular	126 mm
Restored breadth over posterior margins of anterior antorbital	103 mm
Restored breadth between the posterior ends of the lateral extrascapular-squamosal sutures	94 mm
Distance from anterior margin of otic notch to posterior margin of orbit	64 mm
Distance from posterior angle of rostro-interrostral to anterior margin of orbit	61 mm
Length of orbit	40 mm
Breadth of orbit	27 mm

Dermal bones of the skull-roof. The *rostro-interrostral* (*Ṙ. ir*, pls. I, II, III; pl. IV, fig. 1; text-fig. 2) lacks only its anterior marginal part. It is roughly pentagonal, with one angle directed backwards. Posteriorly it overlaps the naso-postrostrals, laterally it meets the rostro-premaxillaries. Its growth-centre falls within the median line; probably it was situated somewhat anterior to the mid-point of the bone. The radiate structure is clearly seen in the posterior half of the bone. Its anterior portion is traversed by numerous vertical canals, probably related, at least in part, to the infraorbital sensory canal. (cf. below p. 53, 86).

The right *rostro-premaxillary* (*R. pmx*, pls. I, II, III; pl. IV, fig. 1; text-fig. 2) lacks its anterior and lateral marginal portions. It has an undulating medial suture towards the rostro-interrostral and a slightly curved postero-medial suture towards the anterior antorbital. It must obviously be composed of a tooth-bearing and a canal bone component. Near the postero-lateral corner of the preserved part of the bone there is left about half of the base of a great labyrinthine tooth (pls. I and II, just at the end of the broken line from *R. pmx*). But most of the tooth-bearing part has fallen away laying bare the more dorsal canal bone part, except in the mentioned postero-lateral part and in a minute part in the antero-medial corner of the bone. The greater, middle part of the bone consists of a postero-medial portion, showing a radiate structure, converging towards the mid-point of the bone, a middle portion traversed by about twenty vertical canals and horizontal anastomoses, and finally an antero-lateral portion, separated into two, as shown in the plates, by a repeatedly bent ridge of matrix which may possibly indicate the course of the infraorbital sensory canal (cf. pp. 22, 86). In the antero-lateral part there can also be seen in the specimen several broken inner ends of anteriorly directed tubules.

The right *naso-postrostral* (*Na. ptr*, pls. I, II, III; text-fig. 2) may be considered as roughly quadrangular with a short straight postero-medial, a very long curved antero-lateral, and long, mainly straight, median and postero-lateral sides. Thus the anterior breadth of the bone is a little longer than its length along the median line, which latter length is nearly twice the length of the postero-medial side of the bone. The long, slightly undulating median margin of the bone joins by suture with the left naso-postrostral; its slightly S-curved postero-medial margin has a suture with the frontals, its straight postero-lateral margin has sutures with the anterior supraorbital and the posterior antorbital, and its curved antero-lateral margin meets in sutures the rostro-premaxillary, the anterior antorbital and the rostro-interrostral, the suture with the last named bone bending postero-medially from the suture towards the rostro-premaxillary. The growth-centre of the right naso-postrostral lies in the posterior half of the bone, its distance from the nearest margin,

the straight postero-lateral one, being $^4/_5$ of the distance to the postero-medial, $^6/_7$ of the distance to the median and about $^3/_7$ of the distance to the curved antero-lateral margin. The radiate structure is very clear over the whole of the bone. The naso-postrostral is probably traversed by the supraorbital canal (see below p. 22).

The preserved part of the left naso-postrostral agrees in shape with the corresponding part of the right one, except that it seems to have a more acute angle between its sutures with the rostro-interrostral and rostro-premaxillary.

The right *frontal* (*Fr*, pls. I, II, III; text-fig. 2) is a long and narrow bone, its average breadth being $^1/_4$ of its length along the median line. Its anterior, sigmoid suture with the naso-postrostral runs postero-laterally from the median line. The two frontals meet in an almost straight median suture, which is not continuous with the median suture of the naso-postrostrals but terminates in front on the postero-medial margin of the right naso-postrostral, dividing this margin into a short medial and a longer lateral part. The well-known rule that in the skull-roof of Stegocephalians there are never four bones meeting in one point seems to hold good also for the Devonian forms. Another example of this can be seen in the region where the frontals and the fronto-parietals should meet, the right fronto-parietal having a short but distinct suture towards the left frontal, thus separating the right frontal from the left fronto-parietal. — The lateral margin of the right frontal joins by suture with the supraorbitals and is strongly undulating, showing one convexity and two concavities lateralwards. The posterior margin of the right frontal is bent in a slight anteriorly concave curve. The growth-centre of the right frontal lies a little in front of the mid-point of the bone. The radiate structure can only be seen in the anterior half and in the most antero-laterally situated part of the posterior half of the right frontal, the rest of the bone being preserved with the external, pitted sculpture only on the positive (A. 1. b).

The ventral side of the anterior half of the left frontal can be seen on A. 1. a (*Fr*, pls. I, II) and, as far as it is preserved, this bone agrees with the right frontal, except that its anterior margin is convex towards the posterior end of the median suture of the naso-postrostrals. The dorsal surface of the posterior half of the left frontal is seen on A. 1. b (*Fr*, pl. III).

The frontals were probably traversed by the supraorbital sensory canal (cf. below p. 22).

The right *anterior antorbital* (*A*, pls. I, II, III; pl. IV, fig. 1; text-fig. 2) is approximately square, its anterior suture towards the rostro-premaxillary being, however, distinctly concave forward and its medial suture towards the naso-postrostral and posterior antorbital slightly convex. The post-

erior suture of the anterior antorbital towards the lachrymal is almost straight. The lateral marginal part of the bone is not preserved, but the growth-centre must have been situated nearer to the lateral than to the medial margin of the bone. The radiate structure can be clearly seen in the whole preserved part of the bone. — The anterior antorbital was probably not traversed by the anterior, commissural part of the infraorbital canal, which must have passed ventrally to the external nares (cf. below p. 22, 39), and from a comparison with other Stegocephalians (see chapter VII, p. 100—102), it is clear that the anterior antorbital is not traversed by the supraorbital canal. The possibility, however, is not yet quite excluded that the anterior commissure of the infraorbital canal may have passed through the most anterior marginal part of the bone in question, which consequently may contain in its most anterior part a very small rostral component.

The *posterior antorbital* (*Ant*, pls. I, II, III; text-fig. 2) has a very characteristic form. It has a bent postero-lateral orbital margin and straight medial and antero-medial sutures towards the anterior supraorbital and the naso-postrostral, a very short antero-lateral suture towards the anterior antorbital, and a likewise short posterior suture with the anterior supraorbital. Its lateral suture, with the lachrymal and the jugal, is more complicated. From the point where the posterior antorbital meets the anterior antorbital and the lachrymal the suture in question runs first postero-medially, thus forming the postero-lateral margin of a long and narrow antero-lateral process of the posterior antorbital, extending between the naso-postrostral and the lachrymal. Then the lateral margin of the posterior antorbital makes a sharp bend and continues in a convex curve to the point where the posterior antorbital meets the lachrymal and jugal; and finally the most posterior part of this margin is formed by an anterior concave and a posterior straight part. The growth-centre of the posterior antorbital lies near the midpoint of the straight medial margin of the bone.

The *anterior supraorbital* (*So*$_1$, pls. I, II, III; text-fig. 2) is a long bone, wedged in between the posterior antorbital, the naso-postrostral, the frontal, the posterior supraorbital, and the orbit. Its lateral margin is suturally connected with the posterior antorbital and is bent laterally in its posterior quarter. The anterior supraorbital further has a short postero-lateral orbital margin, a very short posterior suture with the posterior supraorbital, and a long slightly bent medial suture with the frontal and the naso-postrostral.

The medial border of the anterior supraorbital is continuous with that of the long rectangular *posterior supraorbital* (*So*$_2$, pls. I, II, III; text-fig. 2), which is bounded by short anterior and posterior sutures towards the anterior supraorbital and the postorbito-dermosphenotic,

and by the orbit laterally. The middle part of this bone has been broken away and is restored in plaster in plates I and II. The ventral side of the posterior supraorbital is thickened to form a rounded swelling dorso-medially to the orbit. — The supraorbitals are probably not traversed by the supraorbital sensory canal; if they should prove to be so, they must, of course, be termed naso- or fronto-supraorbitals (cf. p. 76).

Of the *fronto-parietals* (*Pa*, pls. I, II, III; pl. IV, fig. 2; text-fig. 2) only small parts are preserved, mostly as negatives (A. 1. a), but the position of the foramen parietale or pineal foramen[1]) (*pin*, pl. I; pl. IV, fig. 2) is clearly seen and the general form of the bones can be restored without much uncertainty. As will be seen later on by comparison with other, allied species (cf. p. 28, p. 46), there was probably a median suture only as far back as the pineal foramen. Each fronto-parietal has a median length twice its maximum breadth and may be considered as having five margins: one anterior, suturally connected with the frontal, one lateral suturally connected with the posterior supraorbital and the postorbito-dermosphenotic, one postero-lateral, suturally connected with the supratemporo-intertemporal and, for a short stretch, with the postorbito-dermosphenotic, one posterior with a suture towards the parieto-extrascapular, and finally a median margin suturing with the corresponding one of the bone of the other side. The pineal foramen lies on an elevated part of the skull-roof, bounded postero-laterally by a broad, very shallow depression (see fig. 2, pl. IV). The sculptural elements radiate in each fronto-parietal from a point midway between the midpoint of the pineal foramen and the point where the lateral and the postero-lateral margins of the bone meet.

The *postorbito-dermosphenotic* (*Po. dsph*, pls. I, II; text-fig. 2) is an irregularly shaped, oblong bone, (maximum length about $^9/_7$ of the maximum breadth), with a sigmoid lateral suture towards the jugal, which bone it is seen to overlap, a zig-zag postero-lateral suture towards the squamosal, a postero-medial suture towards the supratemporo-intertemporal, consisting of a posterior straight and an anterior sigmoid part, a concave medial margin joined by suture to the fronto-parietal, and a more or less straight anterior margin partly joined by suture to the posterior supraorbital, and partly being a free orbital margin. — The postorbito-dermosphenotic is in part preserved only as an impression of the external, sculptured surface, but the portions of bony substance preserved in the specimen allow of a determination of the radiate structure which has a centre, situated three times nearer to the medial than to the lateral margin of the bone and about in the mid-length of the bone as shown in

[1]) Without wanting to express any opinion concerning the character of the organ once situated in this foramen, and only for the practical reason to avoid unnecessary repetition, I shall employ in the following the term pineal foramen.

the attempted restoration (text-fig. 2). No certain traces of the supraorbital or infraorbital sensory canal can be seen in the postorbito-dermosphenotic in its present state of preservation.

The *supratemporo-intertemporal* (*St. it*, pls. I, II; text-fig. 2) has a very characteristic form, a small anterior, somewhat antero-laterally directed process making it a little longer than broad. The supratemporo-intertemporal abuts by a gently curved convex medial suture on the fronto-parietal and the parieto-extrascapular, by an irregularly bent posterior suture on the lateral extrascapular, by an almost straight lateral suture on the squamosal, and by an antero-lateral suture on the postorbito-dermosphenotic, the last already described as the postero-medial suture of the latter bone. Only a part of the posterior half of the supratemporo-intertemporal is preserved as a bony substance, showing a clear radiate structure with its centre near the midpoint of the bone. The rest is preserved as an impression of the external sculptured surface. No certain trace of the otic part of the infraorbital canal or of the postotic canal could be found.

Of the *parieto-extrascapular* (*Ext. m*, pls. I, II; text-fig. 2) hardly anything is seen except a minute part, bounded by an anterior short, straight suture towards the right fronto-parietal and a slightly sigmoid lateral suture towards the supratemporo-intertemporal and the lateral extrascapular. To judge, however, from the conditions in all the nearly allied forms (cf. below pp. 36, 47, 65) the parieto-extrascapular must have been a roughly rectangular, unpaired bone. Its preserved part shows a sculpture consisting of tubercles in rows converging towards a point in the median line of the skull.

Of the *lateral extrascapular* (tabular) (*Ext. l*, pls. I, II; text-fig. 2) only the roughly square dorsal horizontal part and the dorsal beginning of a posterior more vertical part are preserved. The lateral extrascapular has a long lateral suture with the squamosal, thus excluding the supratemporo-intertemporal from the otic notch, further an anterior irregularly zig-zag suture with the supratemporo-intertemporal, and a medial, only partly preserved, suture with the parieto-extrascapular. In most of the preserved part of the lateral extrascapular the bony substance is left, but the lateral marginal part of the bone is only preserved as an impression of the external surface. The bony substance exhibits a radiate structure with a centre situated at the dorso-latero-posterior end of the bone. Just in the plane along which the lateral part of the bony substance is broken away, there are seen traces of a longitudinal canal, possibly representing a part of the cephalic division of the main lateral line canal.

The *lachrymal* (*La*, pls. I, II, III; pl. IV, fig. 1; text-fig. 2) is an oblong bone, its maximum length being about $^4/_5$ of its maximum breadth. It

has a straight anterior suture with the anterior antorbital, a medial margin which is formed by a suture towards the posterior antorbital and consists of an anterior straight antero-medially, and a posterior concave postero-medially directed part. Further the lachrymal has a sharply bent posterior suture with the jugal and a ventro-lateral, only partly preserved, suture with the maxillary. The radiate structure in the lachrymal can be easily seen: its centre is situated near the lateral margin of the bone, a little nearer to its anterior than to its posterior end. The lachrymal is traversed near its lateral margin by a part of the infraorbital sensory canal (cf. below pp. 21—22).

The *jugal* (*Ju*, pls. I, II, III; text-fig. 2) is a large, oblong, roughly pentagonal bone, with a sharply bent anterior suture towards the lachrymal and a curved and bent antero-medial suture towards the posterior antorbital, a straight orbital margin with a curious rectangular incisure, a sigmoid postero-medial suture towards the postorbito-dermosphenotic, and a similarly curved suture towards the squamosal. The lateral margin of the jugal was probably almost straight but is not preserved in its middle part. Its anterior part is formed by a suture with the maxillary, its posterior part by a suture with the quadratojugal. The radiate structure in the jugal is very clear; its centre is situated near the lateral margin and considerably in front of the mid-point of the bone. The jugal is clearly seen to be traversed by a part of the infraorbital canal (cf. below p. 21) and must have been traversed also by the anterior half of the jugal canal (cf. pp. 26, 53, 70).

The *squamosal* (*Sq*, pls. I, II; text-fig. 2) is roughly oval, its length being, at least, more than $^5/_3$ of its maximum breadth. The squamosal is seen to overlap the quadratojugal with its almost straight lateral margin, and probably its strongly bent anterior margin overlaps, at least partly, the posterior end of the jugal. Medially the squamosal meets the postorbito-dermosphenotic in a zig-zag and the supratemporo-intertemporal and the lateral extrascapular in a slightly curved suture. Only in the antero-lateral half of the squamosal is the bony substance preserved, showing a clear radiate structure with a centre situated a little behind and medial to the mid-point of the bone. No trace of the lateral line canals have been seen in the squamosal, which is, however, certainly traversed by the jugal canal (cf. below pp. 26, 70). At the very posterior end of the preserved part of the squamosal there is seen (pls. I, II) a small piece of bone, bounded by a straight antero-lateral and a strongly sigmoid anterior margin, along which latter it is overlapped in ventral view, i. e. it overlaps the posterior part of the squamosal. This piece may perhaps be the dorsal part of a *preopercular* (cf. below pp. 24—25) as given in the restoration, but may also be only a broken part of the squamosal. It was ascertained by further preparation that the piece of

bone in question continues dorsally to the squamosal, but its radiate structure and its form give no certain evidence of its nature.

Of the *maxillary* (*Mx*, pls. I, II; pl. IV, fig. 1; text-fig. 2) and the *quadratojugal* (*Quj*, pls. I, II; text-fig. 2) only fragments are preserved in the form of strips of bone below the lachrymal and jugal and the jugal and squamosal respectively.

The external sculpture of the dermal bones in this species is of a rather fine type. As an illustration to this a positive cast from specimen A. 1. a, of the region around the pineal foramen is shown in pl. IV, fig. 2.

Dermal bones of the palate. On the palatal surface of the specimen A. 1. b (pl. IV, fig. 1), there is, in the present state of preservation, a large anterior palatal vacuity (*apv*), showing parts of the endocranium and a long and slightly oval right internal naris (*n. i.*). The bony substance of the palate is much eroded, so that only the radiate structure in its dermal bones but not the place of the teeth-sockets can be made out.

Each *vomer* (*Vo*, pl. IV, fig. 1) has two longitudinal parallel sides, one transverse anterior, and two oblique posterior. The outer marginal parts of the vomeres in front of the internal nares are broken away on both sides. The preserved stretch of the lateral longitudinal margin of the bone anteriorly forms the anterior part of the inner margin of the internal naris, posteriorly a little more than the anterior quarter of the suture towards the dermopalatine. The main part of this suture forms the postero-lateral boundary of the vomer, whilst the suture between the vomer and the entopterygoid forms the postero-medial boundary of the former bone. The straight median suture between the vomeres is not continuous with the median suture between the entopterygoids, which latter terminates on the postero-medial margin of the left vomer. — The centre of the fairly clear radiate structure in each vomer is seen to lie pronouncedly antero-laterally to the midpoint of the bone, slightly postero-laterally to the anterior end of the internal naris.

The oblong *dermopalatine* (*Dpl*, pl. IV, fig. 1) is deficient laterally, but its maximum breadth seems to have been about half of its maximum length. The backward continuation of its suture with the vomer, described above, is formed by its suture with the entopterygoid. The latter suture runs first directly posteriorly but then turns laterally and is finally obscured at the hind margin of the preserved part of the palate. The sutures of the dermopalatine with the vomer and the entopterygoid form the medial and posterior margins of the bone. Its postero-lateral margin is formed by a partly preserved suture towards the ectopterygoid. The centre of the radiate structure in the dermopalatine lies equally near the anterior and posterior ends of the bone, but most probably nearer the lateral than the medial margin. It lies almost straight behind

the internal naris. A row of minute openings, probably for vessels to the teeth, are seen near the medial border of the dermo-palatine.

Of the *ectopterygoid* (*Ecpt*, pl. IV, fig. 1) there is only a very small fragment, just sufficient to show a radiate structure with a centre situated posterior to the dermo-palatine.

The *entopterygoids* (*Enpt*, pl. IV, fig. 1) are also fragmentary, the right one being better preserved than the left one. The fragment of the former is a roughly triangular piece of bone, with an almost straight medial margin and a roughly sigmoid lateral suture towards the vomer and the dermopalatine. In the median line the entopterygoid meets its fellow for a short distance anteriorly and leaves posteriorly a narrow, triangular interpterygoid space, partly occupied by the anterior end of the parasphenoid. The radiate structure in the preserved parts of the entopterygoid is mainly longitudinal. The same is the case in the rectangular fragment of the *parasphenoid* (*Psph*, pl. IV, fig. 1).

Finally it should be added that in the palate the left vomer is seen to overlap (i. e. lie dorsally to) the right one and both vomeres are seen to be overlapped by the entopterygoids and the right dermopalatine, the latter of which overlaps also the former.

Sensory canals of the head. As will be further demonstrated below (cf. pp. 26, 29, 40—41, 52—54, 59, 60—72, 82—87) the lateral line system in the Ichthyostegids was, at least in greater part, enclosed in narrow canals in the dermal bones, as it is in many fishes, for instance in the Crossopterygians (cf. Goodrich 1919; Stensiö 1921, 1922 etc.). Owing to this their course can only be ascertained by extensive preparation or in cases of exceptionally fortunate breaks or weathering. As such extensive preparation of the whole specimen would largely destroy the unique material, it was necessary to leave open many questions as to the course of the lateral line canals in the hope of getting new material. Moreover it is sometimes impossible to clear the stone cast of the canals, owing to weathering, that makes the once solid filling of the canals friable, or even quite loose in consistence.

Owing to these difficulties the only part of the lateral line system in the type-specimen of *I. stensiöi* that can be described with certainty is the part of the infraorbital canal, shown in plate I and II (*ifc*), and running from a point near the lateral margin of the jugal through the anterior quarter of this bone, parallel to the said margin, towards the most lateral part of the suture between the jugal and the lachrymal. In the latter bone the canal continues for a short stretch forward to disappear in the lateral, thickened and richly canalised part of the bone. In the anterior portion of that thickened part there are small pieces of canals, some of which may belong to the infraorbital canal. If it is true, as I strongly

incline to think, that the thickened part really lodged the forward continuation of the infraorbital canal, that canal seems to have left the lachrymal at the lateral margin of this bone and, consequently, to have passed ventrally to the anterior antorbital. Whether it rose again dorsally as soon as it reached the most anterior part of this bone, or remained wholly ventral to it, cannot be ascertained. If it rose dorsally to pierce the rostro-premaxillary, it is possible that the ridge of matrix across the antero-lateral part of that bone (see p. 14) really marks the place of the infraorbital canal (cf. p. 53).

There is no indication in this specimen of the course of the posterior half of the suborbital part or of the otic part of the infraorbital canal. The same is the case with the jugal and preopercular canals.

As to the supraorbital canal there are indications of its course on the right naso-postrostral. On the ventral side of this bone there are seen several openings to canals and traces of canals (*c*, pls. I, II, III) lying in a slightly curved line from the most posterior part of the postero-lateral towards the middle of the anterior margin of the bone. These canals probably do not belong to the supraorbital canal proper, but may conceivably have transmitted nerves and vessels to it. This somewhat slight indication of the possible course of the supraorbital canal is, however, strengthened by the fact that similar traces of probable canals for nerves and vessels occur in the same place in another specimen (cf. below pp. 40, 84), and similar canals in the frontals of a Crossopterygian, figured below (text-fig. 19) are clearly related to the supraorbital canal.

Traces of canals, seen in the section through the lateral extrascapular, (cf. p. 18, see pl. I), may possibly have a relation to the cephalic part of the main lateral line canal.

Remarks. This species is named in honour of Professor E. STENSIÖ, Stockholm.

Locality. The East Plateau, Mt. Celsius (cf. SÄVE-SÖDERBERGH 1932 a, pp. 10, 11, fig. 5).

2. *Ichthyostegid* sp. a.

(Pl. V; pl. VI, figs. 2, 3; text-fig. 3).

Material. I interrupt here the description of the determinable species of the genus *Ichthyostega* to describe, before the rest of them, a fragment (A. 6) which, although too scanty to allow of any determination of its species or even certain determination of its genus, is of paramount importance for the understanding of the morphology and phylogeny of the Devonian Stegocephalians. It consists of a detached postero-lateral part of a skull-roof and the posterior half of a right mandible in almost its natural position.

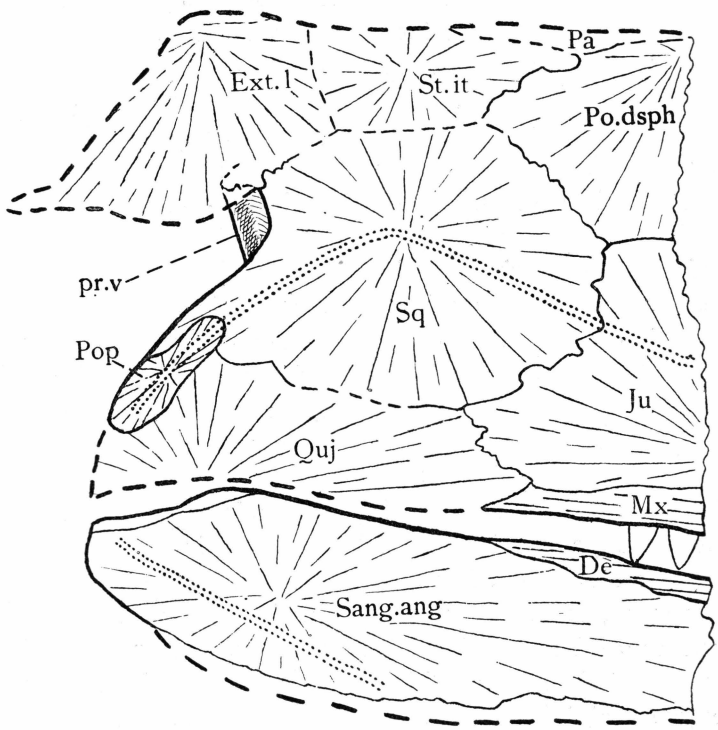
This specimen, although crushed flat from the sides, shows with

admirable clearness the sutures, the radiate structure of the dermal bones, and the sensory canals. The part preserved includes the right squamosal, preopercular, quadratojugal, and parts of the right postorbito-dermosphenotic, jugal, lateral extrascapular, maxillary, entopterygoid, supraangulo-angular, dentary, posterior coronoid, and prearticular.

Description.

Dermal bones of the skull roof (pl. V, fig. 2).

Of the *postorbito-dermosphenotic* (*Po. dsph*, pl. V, fig. 2; text-fig. 3) there is preserved only a small postero-lateral part showing two straight



Text-fig. 3. Attempted restoration of the posterior part of the skull-roof and mandible of the specimen A. 6 in lateral view. 1,5 times natural size. Lateral line canals with dotted outlines.

De, dentary; *Ext. l*, lateral extrascapular; *Ju*, jugal; *Mx*, maxillary; *Pa*, frontoparietal; *Po.dsph*, postorbito-dermosphenotic; *Pop*, preopercular; *Quj*, quadratojugal; *Sang-ang*, supra-angulo-angular; *Sq*, squamosal; *St.it*, supratemporo-intertemporal; *pr.v*, ventral process of lateral extrascapular.

margins, one lateral, joined by suture to the jugal, and one postero-lateral, joined by suture to the squamosal. The growth-centre was situated medially to the preserved part of the bone.

The preserved posterior part of the *jugal* (*Ju*, pl. V, fig. 2; pl. VI, fig. 2; text-fig. 3) shows a straight medial suture towards the postorbito-

dermosphenotic, a mainly concave postero-medial margin with a suture towards the squamosal, an irregularly zig-zag postero-lateral margin with a suture towards the quadratojugal and a straight lateral margin joined by suture with the maxillary. The growth-centre of the jugal is seen to have been situated near the lateral margin of the bone, in front of the preserved part of it.

The *squamosal* (*Sq*, pl. V, fig. 1; pl. VI, fig. 2; text-fig. 3) is completely preserved except in its most medial parts. It must have had a fairly regular oval form, its length being about $^{7}/_{5}$ of its breadth. Antero-medially the squamosal has a mainly straight suture towards the postorbito-dermosphenotic, antero-laterally a convex suture towards the jugal, and laterally probably a mainly straight or slightly rounded suture towards the quadrato-jugal. In the region of the last-mentioned suture the specimen has been somewhat damaged by crushing, which has pressed in part of the lateral marginal part of the squamosal together with the medial marginal part of the quadratojugal. — Postero-laterally, the squamosal shows a deep notch for the preopercular, and descends postero-laterally in a narrow strip posterior to the medial half of that bone. The squamosal further has a straight postero-medial margin, forming the lateral margin of the otic notch and meeting the quadrate ramus of the entopterygoid, a shorter straight posterior margin, forming, with the posterior margin of the lateral extrascapular, the anterior margin of the otic notch, and finally a postero-medial suture with the lateral extrascapular to prove definitely the Stegocephalian character of the specimen. Of the important suture last mentioned there is only shown in the specimen a short part, stretching forward from the mid-point of the anterior margin of the otic notch. It is, however, clearly seen to be an interlocked suture, excluding every possibility of a movement of the squamosal in relation to the lateral extrascapular. The growth-centre of the squamosal is clearly seen to be situated much as in *Ichthyostega stensiöi*, but a little nearer to the medial margin of the bone.

Of the *lateral extrascapular* (tabular) (*Ext. l*, pl. V, fig. 2; pl. VI, figs. 2, 3; text-fig. 3) are preserved only the parts nearest to its above-described suture with the squamosal. Nothing is left of the dorsal lamina of the bone, but there is a curious ventral process of it (*Ext. l*, *pr. v*, pl. VI, figs. 2, 3; *pr. v*, text-fig. 3). This process is guttershaped with flattened sides and in the present state of preservation it has a vertical direction and is parallel to the palatal surface of the specimen. The gutter-shaped part is connected laterally with a thick, vertical, transverse lamina, forming the medial half of the anterior margin of the otic notch and joined by suture to the squamosal as described above.

The *preopercular* (*Pop*, pl. V, fig. 2; pl. VI, fig. 2; text-fig. 3) is very clearly shown in this specimen. It is an oblong bone (its length being

1.5 times its maximum breadth) with semicircular, somewhat broadened ends and a narrower middle part. The upper semicircular end of the preopercular fits into the above-described notch in the postero-lateral margin of the squamosal, which latter bone also connects by suture with a little more than the anterior half of the postero-medial margin of the preopercular. The posterior half of the preopercular overlaps the quadrate bone and meets the quadratojugal antero-laterally. The radiate structure of the preopercular is very clear and the centre of growth is situated near the mid-point of the bone, a little nearer to its antero-lateral than to its postero-medial margin.

The *quadratojugal* (*Quj*, pl. V, fig. 2; pl. VI, fig. 2; text-fig. 3) is a long bone (maximum length about 3.5 times its restored maximum breadth), roughly quadrangular, with a medial suture towards the squamosal, partly crushed in in this specimen, a zig-zag antero-medial suture towards the jugal, a short antero-lateral suture towards the hind end of the maxillary, and a faintly curved postero-medial suture towards the preopercular. The lateral marginal part of the bone is partially destroyed; the growth-centre, which was close to the lateral margin, and in the posterior third of the bone, falls within the destroyed area.

The *maxillary* (*Mx*, pl. V, fig. 2; text-fig. 3) is represented only by a fragment, forming a narrow triangular strip of bone at the ventro-lateral margin of the jugal and the quadratojugal. Half of a labyrinthine tooth and traces of another can be seen.

The sculpture of the dermal bones in this specimen is rather fine, at least as fine as in *I. stensiöi.*

Dermal bones of the palate (pl. V, fig. 2).

In the anterior broken plane of the specimen there is a transverse section of a bone of the lateral palatal row, conceivably the *ectopterygoid*, with the base of a tooth and a suture towards the jugal, concealed by the maxillary in lateral view.

The preserved most posterior part (quadrate ramus) of the *entopterygoid* (*Enpt*, pl. V, fig. 1) is divided by a longitudinal ridge into two planes, one ventral, probably originally horizontal, the other dorsal and vertical. The former shows the rounded margin of the bone towards the adductor fenestra ("subtemporal fossa", Watson 1926 a, p. 212; "fenestra basitemporalis", Abel 1919, p. 249; "adductor foramen", Stensiö 1925, p. 101) and exhibits a radiate structure with its centre situated at the anterior end of the longitudinal ridge. The vertical lamina of the entopterygoid meets the squamosal dorsally and covers the quadrate bone posteriorly. It shows a radiate structure with the same centre as that of the horizontal part. There is a fairly large foramen in the anterior part of the vertical lamina of the bone.

Dermal bones of the lower jaw.

On the outer side of the lower jaw (pl. V, fig. 2; text-fig. 3) the *supraangulo-angular* (*Ang*, pl. V, fig. 2; *Sang-ang* text-fig. 3) is preserved to a great extent, but lacks its ventral border, and its whole anterior part. The preserved part of its dorsal margin may be divided into a dorso-posteriorly facing margin overlying the articular, which it conceals in lateral view except most dorsally, and a more purely dorsal part, with suture towards the dentary. The radiate structure in the supra-angulo-angular has a centre in the posterior third of the preserved part of the bone, as shown in the figures.

Of the *dentary* (*De*, pl. V, fig. 2; text-fig. 3) there is preserved a long narrow posterior part, exactly facing the maxillary of the upper jaw. A labyrinthine tooth is seen in section in the broken anterior surface of the specimen. In this surface there is also a section of a second tooth, belonging to an inner row of teeth and conceivably situated on a *coronoid.*

The *prearticular* (*Pr. art*, pl. V, fig. 1) is preserved in a similar manner to the supraangulo-angular; posteriorly it is seen to overlap the articular (*Art*) with its rounded border, dorsally it has a rounded edge stretching anteriorly and conceivably somewhat antero-ventrally from the anterior end of the visible part of the articular. The centre of the radiate structure of the prearticular is clearly seen to be situated near the anterior, broken side of the specimen.

Sensory canals.

The course of the sensory canals is exceptionally clear in this specimen. The *jugal canal* (*juc*, pl. V, fig. 2), at least for the greater part enclosed in the middle layer of the dermal bones, runs through the posterior part of the jugal (probably originally from the growth-centre of that bone) in a straight line posteriorly towards the growth-centre of the squamosal and from this point its course is indicated in the present state of preservation by a groove, running to the suture between the squamosal and the preopercular. Here it apparently joined the preopercular canal.

The course of the *preopercular canal* (*poc*, pl. V, fig. 2) is, in the present state of preservation, partly indicated by a groove running ventro-laterally from the suture between the preopercular and the squamosal to the centre of the preopercular. It is probably enclosed in the postero-lateral half of that bone.

The *mandibular canal* (*mc*, pl. V, fig. 2) is clearly seen in the supra-angulo-angular, running from the dorso-posterior end of this bone antero-ventrally a little below the growth-centre of the bone and terminating in the present specimen on the middle third of the broken lower margin of this bone. In its present state of preservation the mandibular canal is

partially represented by a groove, but originally it must have been enclosed below the outer layer of bone, which is not preserved except in patches near the dorsal margin of the bone.

It may be added to the description of this specimen that the articular (*Art*, pl. V) and the quadrate (*Qu*, pl.V) bones are well ossified and shown to a great extent.

Remarks. This specimen, owing to the very partial knowledge that it affords as to the structure of the skull to which it belongs, cannot be referred with certainty to a definite species. The shape of the parts preserved does not fully agree with that of the corresponding parts in any of the species described in this paper. Identity with the species *Ichthyostega watsoni* described below seems wholly excluded by the shape of the posterior part of the maxillary. The form of the antero-medial margin of the squamosal is a point of difference from *Ichthyostega stensiöi*. On the other hand, in the convex anterior suture of the squamosal (towards the jugal) the specimen resembles *Ichthyostega stensiöi*, but differs from *I. watsoni*, *I. eigili* and *Ichthyostegopsis wimani*, all described below. The sculpture, as far as can be judged from the present specimen, may have been of about the same type as in *I. stensiöi*. A comparison with the species *Ichthyostega? kochi* is at present impossible, as the shape of the corresponding parts in that species is unknown. The sculpture in *Ichthyostega? kochi*, however, is not unlike that of this specimen. Finally it may be mentioned that in the same piece of rock as this specimen there are preserved plates of a small *Remigolepis*.

Locality. Above the East Plateau, Mt. Celsius, in débris, probably originating from the "emarginata"-horizon (see SÄVE-SÖDERBERGH 1932 a, p. 12).

3. *Ichthyostega*? sp. b.

(Pl. IV, fig. 3; pl. XVI, fig. 2).

Material. This is another fragment, indeterminable as to species and genus, but of great importance for the understanding of the structure of the more completely preserved specimens, as it shows the shape of the fronto-parietal, which is elsewhere well preserved only in the subsequently described *Ichthyostegopsis wimani* n. sp., where it has a shape different from that found in the present specimen. The fragment in question (A. 2) shows a part of the skull-roof with the complete left fronto-parietal and parts of the right fronto-parietal as well as parts of the frontals, parieto-extrascapular and left posterior supraorbital, postor-

bito-dermosphenotic, supratemporo-intertemporal, jugal, and squamosal. The greater part of the specimen is only an imprint of the external surface of the bones.

Description.

Dermal bones. The preserved parts of the *frontals* (*Fr*, pl. XVI, fig. 2) show these bones to have been rather narrow, with nearly straight median and posterior margins, the latter joined by suture to the fronto-parietal, and with a lateral suture towards the posterior supraorbital. The latter suture is nearly straight on the ventral surface of the skull-roof and is seen in the anterior, broken side of the specimen to be situated considerably more lateralwards on the dorsal than on the ventral side of the skull-roof.

The shape of the preserved part of the posterior *supraorbital* (*So*, pl. XVI, fig. 2) agrees well with that of the corresponding bone in *Ichthyostega stensiöi*. As seen by the course of the medial suture towards the frontal in the anterior broken end of the specimen, the supraorbital is rather narrow on the dorsal side of the skull-roof, but thick, forming a very pronounced, thick, rounded swelling along the dorso-medial margin of the orbit. Posteriorly the supraorbital connects by a curved suture with the postorbito-dermosphenotic, medially by an irregulary curved suture with the fronto-parietal, and by the above-described suture with the frontal.

The *fronto-parietals* (pl. IV, fig. 3; *Pa*, pl. XVI, fig. 2) are the most interesting bones in this specimen. They are clearly seen to be but partially separated by a median, interlocked suture, extending only forwards from the large, oval pineal foramen, behind which there is no trace of a median suture. The pineal foramen (*pin*, pl. IV, fig. 3) lies in an elevated part of the surface of the bone, this elevated part being bounded posteriorly by a rather pronounced V-shaped depression, the point of which extends back over the irregularly curved suture between the fronto-parietals and the parieto-extrascapular. This V-shaped depression is much more pronounced in specimen A. 2 than in *Ichthyostega stensiöi*. The irregularly curved lateral margin of the left fronto-parietal connects by suture with the postorbito-dermosphenotic and with the supratemporo-intertemporal. The course of the latter suture can not be distinguishd with certainty in its posterior half, where it runs over parts that are preserved only as imprints of the external sculpture. There are two possibilities: either the suture follows the more medial and anterior thicker line (pl. XVI, fig. 2), which looks perhaps more like a suture than the other possible suture, a more lateral and posterior finer line (same figure), or it follows the latter, in which case the fronto-parietal would have a form more comparable to that found in *Ichthyostega stensiöi* —

whereas it would in the other case be more similar to the same bone in *Ichthyostega eigili* described below.

The rather coarse external sculpture of the fronto-parietal is clearly shown in the positive cast (pl. IV, fig. 3).

Of the *parieto-extrascapular* (*Ext. m*, pl. XVI, fig. 2) there is only a small part preserved as a cast of its external sculptured surface, just enough to show that this bone was unpaired as in the other Ichthyostegids.

The sutures bounding the preserved parts of the *postorbito-dermosphenotic*, *supratemporo-intertemporal*, and *jugal* are a little difficult to make out in the present state of preservation, but the radiate structure in the preserved fragments of bony substance excludes errors of any importance in tracing the sutures.

The *postorbito-dermosphenotic* (*Po. dsph*, pl. XVI, fig. 2) is long and has in the main a similar shape to that of the same bone in *Ichthyostega stensiöi*. Thus, it has a short, curved anterior suture with the supraorbital, an orbital margin, an irregularly curved lateral suture with the jugal, and a straighter postero-lateral suture with the *squamosal* (of which latter bone there is preserved only a small strip nearest to the just described suture and that with the supratemporo-intertemporal). But the medial margin of the postorbito-dermosphenotic has a straight suture with the fronto-parietal and a similar, nearly straight suture with the supratemporo-intertemporal. The postorbito-dermosphenotic is traversed by the infraorbital sensory canal.

The *supratemporo-intertemporal* (*St. it*, pl. XVI, fig. 2) connects by a curved and bent medial suture with the fronto-parietal and parieto-extrascapular, and with the postorbito-dermosphenotic by an antero-lateral suture, probably much straighter than the corresponding suture in *Ichthyostega stensiöi*.

Of the *jugal* there is preserved only its most medial part with a slightly curved suture towards the postorbito-dermosphenotic. The jugal is traversed by the infraorbital sensory canal.

Sensory canals. Of the lateral line system there may be distinguished on this specimen only a short portion of the suborbital part of the *infraorbital canal* (*ifc*, pl. XVI, fig. 2) stretching from a little behind the growth-centre of the postorbito-dermosphenotic straight antero-ventro-laterally towards a point in the posterior half of the preserved part of the jugal.

Remarks. A reference of this fragment to any definite species is, of course, excluded. As pointed out in the description, it shows several points of agreement with *Ichthyostega stensiöi*, but several points of

disagreement too, among others, the much coarser sculpture of the dermal bones (cf. pl. IV, figs. 2 and 3). It seems very probable, but of course cannot be proved, that the specimen belongs to the genus *Ichthyostega*. It is true that the other specimens belonging to this genus and discussed in this paper are not preserved in the parts which would be most suited for comparison with the specimen A. 2 (especially the parts surrounding the pineal foramen), but the existing evidence (cf. p. 46) tends to show that the characteristic partial median suture between the fronto-parietals is found also in the other species of *Ichthyostega*.

Locality. Central part of the northern slope of Mt. Celsius (cf. SÄVE-SÖDERBERGH 1932 a, p. 15).

4. *Ichthyostega watsoni* n. sp.

(Pl. VI, fig. 1; pls. VII, VIII; text-figs. 4, 5).

Diagnosis. Skull broader than in *Ichthyostega stensiöi*. Dermal bones with coarse external sculpture. Naso-postrostrals with postero-lateral margins connected by suture with the frontals. Lachrymals with distinct sutures towards the naso-postrostrals, thus separating the posterior antorbitals from the anterior antorbitals. Posterior antorbitals wholly posterior to the anterior ones, without narrow antero-lateral processes. Medial part of the suture of each anterior antorbital towards the lachrymal running antero-medially to postero-laterally. Very large jugals.

Holotype and material. A rather well-preserved skull (A. 3), lacking the posterior part of its left half and the central part of the dermal cranial roof, the most anterior part of the snout and minor parts on the left side and in the dermal roof of the right otic and occipital region.

As will be seen from the figures, there are preserved on the dorsal side of this specimen, almost complete: the right anterior antorbital, the right naso-postrostral, the right frontal, posterior antorbital, lachrymal and jugal, the left naso-postrostral, posterior antorbital, and lachrymal, the greater part of the right squamosal, and minor parts of the rostro-interrostral, the right rostro-premaxillary, the left anterior antorbital and the left jugal, the right quadrato-jugal and lateral extrascapular, and the parieto-extrascapular. On the palatal side of the specimen are seen in part and counterpart the complete right and the anterior two-thirds of the left side of the palate and the complete right maxillary.

Description.

General shape. This specimen has been crushed to some extent, so that the general form of its right side is wholly distorted and the left side has probably been flattened out by the pressure. Therefore nothing

exact can be stated about its breadth, but it is conceivable that the skull-roof was, on the whole, broader than in *Ichthyostega stensiöi* and was not narrower than in text-fig. 4 A and not broader than in text-fig. 4 B. The orbits are clearly situated somewhat farther back than in *I. stensiöi*. The external nares are not seen in dorsal view; as emphasized below, they must have been situated below the anterior antorbital.

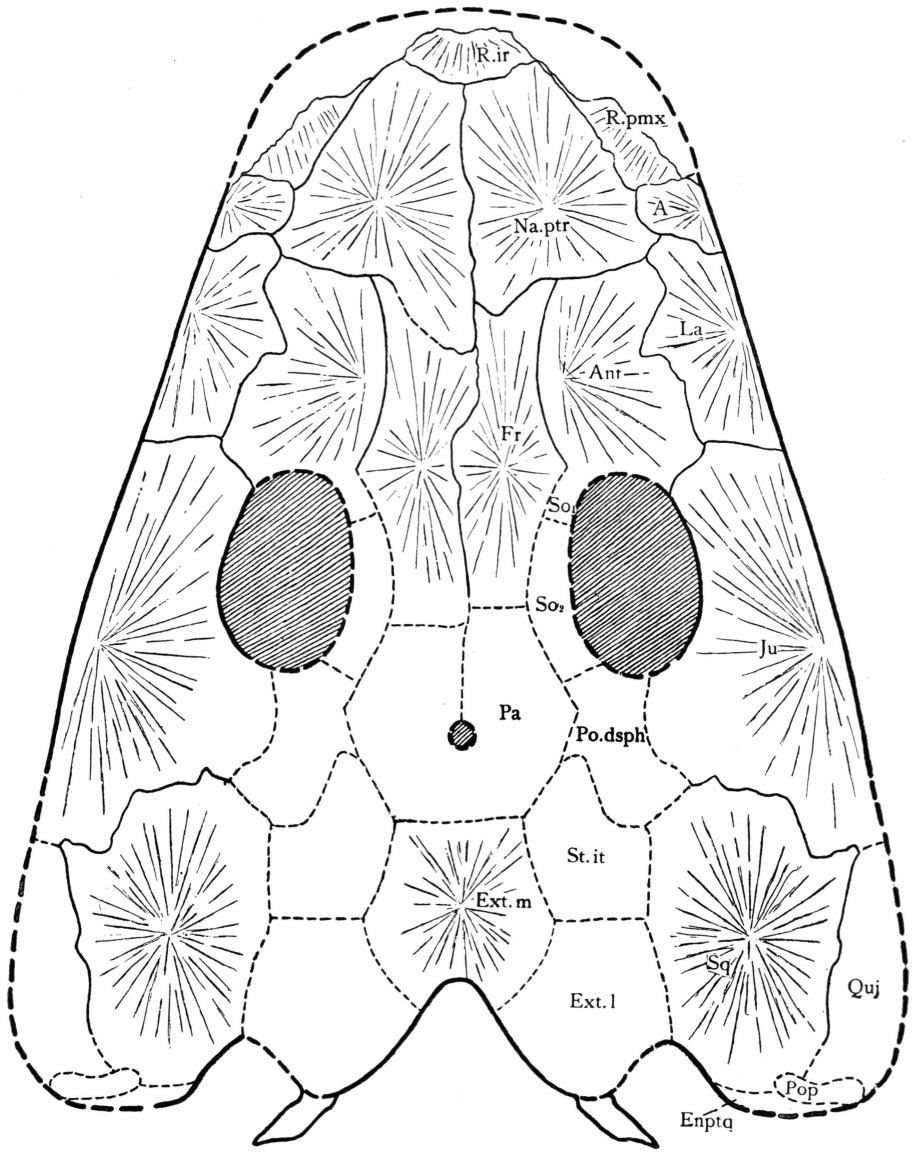
The following measurements may give an idea of the size and general shape of the holotype of *Ichthyostega watsoni:*

Restored median length ..... about 168 mm
Length from posterior margin of rostro-interrostral to posterior margin of parieto-extrascapular..... 163 mm
Distance from midpoint of posterior margin of parieto-extrascapular to posterior end of lateral extrascapular ..... 46 mm
Restored distance from posterior margin of rostro-interrostral to posterior end of the cheek ..... 185—190 mm
Restored posterior breadth, between the lateral margins of the quadratojugals ..... 157—167 mm
Anterior breadth, over posterior margins of anterior antorbitals 100 mm
Restored distance between the lateral extrascapular-squamosal sutures at the otic notches ..... between 75 and 85 mm

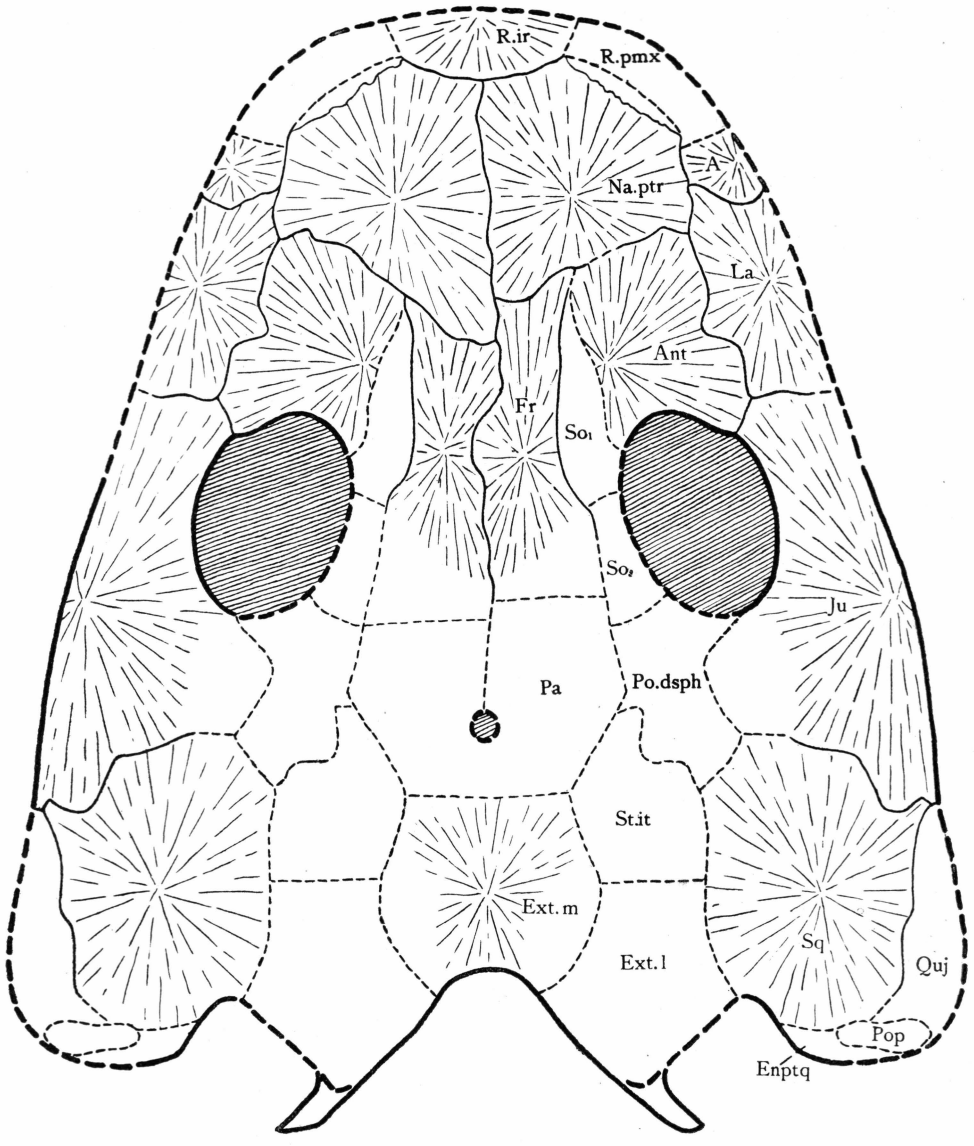
Of the *rostro-interrostral* (*R. ir*, pl. VI, fig. 1; pl. VIII; text-fig. 4) only a posterior marginal part is preserved, showing a slightly curved posterior margin and a radiate structure with a centre that must have been situated in the median line, farther forward than the preserved part of the snout.

The right *rostro-premaxillary* is preserved in two parts, one vertical, anterior, tooth-bearing part (*R. pmxd*, pl. VI, fig. 1; *Pmx*, pl. VII; *R. pmxd*, pl. VIII; text-fig. 5), and one more horizontal and posterior part (*R. pmxc*, pl. VI, fig. 1; pl. VIII; text-fig. 4). Originally the latter must have overlain the former, and thus its preserved part represents only part of the posterior half of the canal bone component of the compound rostro-premaxillary (cf. below p. 45).

Whether the tooth-bearing part originally had a further extension backward than in the present state of preservation is not so easy to ascertain, but it seems probable, from a comparison with the corresponding parts in the species *I. eigili*, described below, that this was the case and that consequently the part on the left side lettered *R. pmx?* on pl. VIII represents a part of the rostro-premaxillary in its natural position. Anyhow the two components of the rostro-premaxillary are easy to recognise on the right side. That they were originally fused is inferred by comparison with *I. stensiöi* and the species *Ichthyostega eigili*, described below.



Text-fig. 4 A. *Ichthyostega watsoni* n. sp. Attempted restoration of the dorsal side of the skull. After the right side of the specimen. $^3/_4$ natural size.
A, anterior antorbital; *Ant*, posterior antorbital; *Enptq*, quadrate ramus of entopterygoid; *Ext. l*, lateral extrascapular; *Ext. m*, parieto-extrascapular; *Fr*, frontal; *Ju*, jugal; *La*, lachrymal; *Na. ptr*, naso-postrostral; *Pa*, fronto-parietal; *Po. dsph*, postorbito-dermosphenotic; *Pop*, preopercular; *Quj*, quadratojugal; *R. pmx*, rostro-premaxillary; *R. ir*, rostro-interrostral; So_1 anterior supraorbital, So_2 posterior supra orbital; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.



Text-fig. 4 B. *Ichthyostega watsoni* n. sp. Attempted restoration of the dorsal side of the skull. Anterior half after the left side, posterior half modified after the right side of the specimen. $^3/_4$ natural size. Lettering as in text-fig. 4 A.

Of the canal bone (rostral) component of the rostro-premaxillary there is preserved a small fragment on the right side, but its anterior and lateral parts are lacking on both sides. The preserved part shows that the rostral component had a mainly straight posterior suture with the anterior antorbital and an interlocked, mainly straight medial suture with the naso-postrostral. The radiate structure in the preserved part

implies that the growth-centre was situated about as in the same bone in *Ichthystega stensiöi*. The rostral part of the rostro-premaxillary was in some way connected with the ethmoidal part (anterior commissure) of the infraorbital sensory canals (cf. below p. 53).

The tooth-bearing part of the rostro-premaxillary shows a lateral, vertical surface (see pl. VII), with external sculpture similar to that of the other dermal bones. This lateral surface has a straight posterior and a damaged ventral margin; its postero-ventral corner is rounded. The dorsal broken surface of the tooth-bearing part (pl. VI, fig. 1) has a very slightly concave medial margin and further shows the bases of three teeth and a large rounded vacuity between the two posterior teeth (probably a section through a pit for a replacing tooth; cf., for instance, WATSON 1926 a). Of the three teeth preserved, the posterior is apparently longer than the two anterior, from which it is separated by a larger space than that between the two anterior teeth.

The *naso-postrostrals* (*Na. ptr*, pl. VI, fig. 1; text-fig. 4) are relatively as well as absolutely larger than in *Ichthyostega stensiöi*. Their general shape is as in that species, but their curved postero-lateral sutures with the frontals continue without any bend into their straight sutures towards the posterior antorbitals and the lachrymals. The latter bones separate the posterior antorbitals from the anterior antorbitals as mentioned above. Further the suture of each naso-postrostral towards the anterior antorbital and the rostro-premaxillary in *Ichthyostega watsoni* has a more longitudinal direction than in *I. stensiöi*. The left naso-postrostral stretches farther back than the right one and has a short median suture with the right frontal, thus separating the right naso-postrostral from the left frontal.

The radiate structure can be more clearly seen in the left than in the right naso-postrostral. The growth-centres in the naso-postrostrals lie conceivably about in the corresponding places as in *Ichthyostega stensiöi*, i. e. nearest to the postero-lateral margins of the bones, but owing to the great backward extension of the posterior part of the left naso-postrostral, the growth-centre of this bone lies at about the same distance from the anterior as from the posterior end of the median suture between the naso-postrostrals. The naso-postrostrals were probably traversed by the supra-orbital sensory canals (see pp. 22, 40).

The *frontals* (*Fr*, pl. VI, fig. 1; text-fig. 4) are very imperfectly preserved posteriorly. They are long and narrow, with concave anterior and lateral margins. The median suture between the two frontals is sigmoid anteriorly, but is straighter posteriorly. The radiate structure is clearly seen in the anterior and medial parts of the frontals; the growth-centres were probably situated near the mid-points of the bones. The courses of the posterior parts of the lateral sutures towards the supra-

orbitals are doubtful, owing to crushing and weathering of the bone substance. Those conditions also make it impossible to state with certainty the shape and position of the probably independent *anterior supraorbitals*[1]).

The right *anterior antorbital* (*A*, pl. VI, fig. 1; pl. VIII; text-fig. 4) is roughly quadrangular, with a length along the lateral margin twice its length along the medial suture with the naso-postrostral. Contrary to the case in *Ichthyostega stensiöi*, the anterior antorbital in *I. watsoni* does not reach the posterior antorbital, conceivably because the region which in *I. stensiöi* is ossified as the postero-medial part of the anterior antorbital here takes part in the formation of the lachrymal. The posterior, slightly curved margin of the anterior antorbital consequently has an antero-medial–postero-lateral course. The anterior suture of the anterior antorbital with the rostro-premaxillary, is straight except for a forwardly directed bend in its most lateral part. The radiate structure of the anterior antorbital can be seen with some difficulty; its centre lies near the lateral margin of the bone, as in *Ichthyostega stensiöi*. Since in its lateral part this bone has the same extension as in *I. stensiöi* the discussion of the nature of the anterior antorbital in that species (p. 16) applies equally to the bone in *I. watsoni*.

Both posterior *antorbitals* (*Ant*, pl. VI, fig. 1; text-fig. 4) are deformed by the general crushing of the specimen, which also obscures their medial extension and the shape of their medial margins, but they still show a general form, suggestive of that of the same bones in *Ichthyostega stensiöi*, i. e., with probably straight medial sutures, most probably towards the anterior supraorbitals, as shown in text-fig. 4 B, and with characteristically bent lateral sutures towards the lachrymals. The narrow antero-lateral process, found in *Ichthyostega stensiöi*, is in *I. watsoni* short and somewhat broader than in the former species; it does not reach the anterior antorbital in *I. watsoni*. Accordingly the whole lateral margin of the posterior antorbital is formed by its suture towards the lachrymal. A suture on its very short postero-lateral margin connects the posterior antorbital with the jugal, as in *Ichthyostega stensiöi*. The posterior marginal part of the posterior antorbital is preserved only on the left side, where it shows a bent orbital margin as in *Ichthyostega stensiöi*. The antero-lateral margin of the posterior antorbital is joined by an almost straight suture with the naso-postrostral. The radiate structure can be clearly seen, especially in the right posterior antorbital; the growth-centre lies, as in *Ichthyostega stensiöi*, near the medial margin of the bone.

Of the *parieto-extrascapular* (*Ext. m*, pl. VI, fig. 1; text-fig. 4) only

[1]) This bone is possibly crushed in to a large extent on the right side. (So_1?, pl. VI, fig. 1).

the central part is preserved, and shows a radiate structure with its centre in the median line of the skull.

The *lateral extrascapular* (tabular) (*Ext. l*, text-fig. 4) is much damaged dorsally but still shows interesting features. Postero-medially it consists of a thick vertical lamina (*Ext. l, l. pm*, pl. VI, fig. 1; pl. VIII) with a marked bend in its posterior part. The process-like part (*Ext. l, pr. p*, pl. VI, fig. 1) posterior to this bend should probably be interpreted as a "tabular horn" (WATSON 1926 a, p. 203—204, 218; 1926 b, p. 226) for the attachement of the shoulder-girdle. Of the horizontal lamina of the lateral extrascapular there is only a slight fragment preserved (*Ext. l, l. d*, pl. VI, fig. 1). A gutter-shaped ventral process of the lateral extrascapular (*Ext. l, pr. v*) is seen on pl. VIII and it is situated and developed in a way that makes it closely comparable to the same process in the specimen A. 6 (p. 24; pl. VI, figs. 2, 3).

The *lachrymals* (*La*, pl. VI, fig. 1; text-fig. 4) have, like the posterior antorbitals, a general form not differing much from that of the same bones in *Ichthyostega stensiöi*, if allowance be made for a slight degree of distortion. The ossification from this bone, however, extends in *I. watsoni*, antero-medially over an area occupied in *I. stensiöi* by the antero-lateral process of the posterior antorbital and the postero-medial part of the anterior antorbital, so that the lachrymal in *I. watsoni* has a short antero-medial suture with the naso-postrostral. The medial margin of each lachrymal is bent in an angle, pointing medially, as in *Ichthyostega stensiöi*. The lachrymal also has a straight, rather long anterior or antero-lateral suture towards the anterior antorbital, and a similarly straight, a little shorter posterior suture towards the jugal. Laterally the lachrymal has a free margin, overlapping the anterior part of the maxillary. The right lachrymal is clearly traversed by the infraorbital sensory canal (see below p. 40).

The large right *jugal* (*Ju*, pl. VI, fig. 1; pls. VII, VIII; text-fig. 4) is somewhat damaged medially, where its exact form and extension cannot be determined[1]). It seems to have been roughly quandrangular with a very short anterior, a somewhat longer postero-medial, a rather long antero-medial and a still longer lateral side. Its straight anterior margin is suturally connected with the lachrymal and forms a forward pointing angle with the slightly curved short suture towards the posterior antorbital. The latter suture forms, together with the slightly concave orbital margin, and probably a part of the suture towards the postorbito-demosphenotic, the antero-medial side of the bone. The postero-medial side of the jugal is formed in its preserved part by a sharply sigmoid suture towards the

[1]) The uncertain parts of its margins are marked by broken lines in the attempted restoration (text-fig. 4).

squamosal and a short, curved suture towards the quadratojugal. The radiate structure in the jugal is very clearly shown. Its centre is situated near the lateral margin, midway between the anterior and the posterior end of the bone.

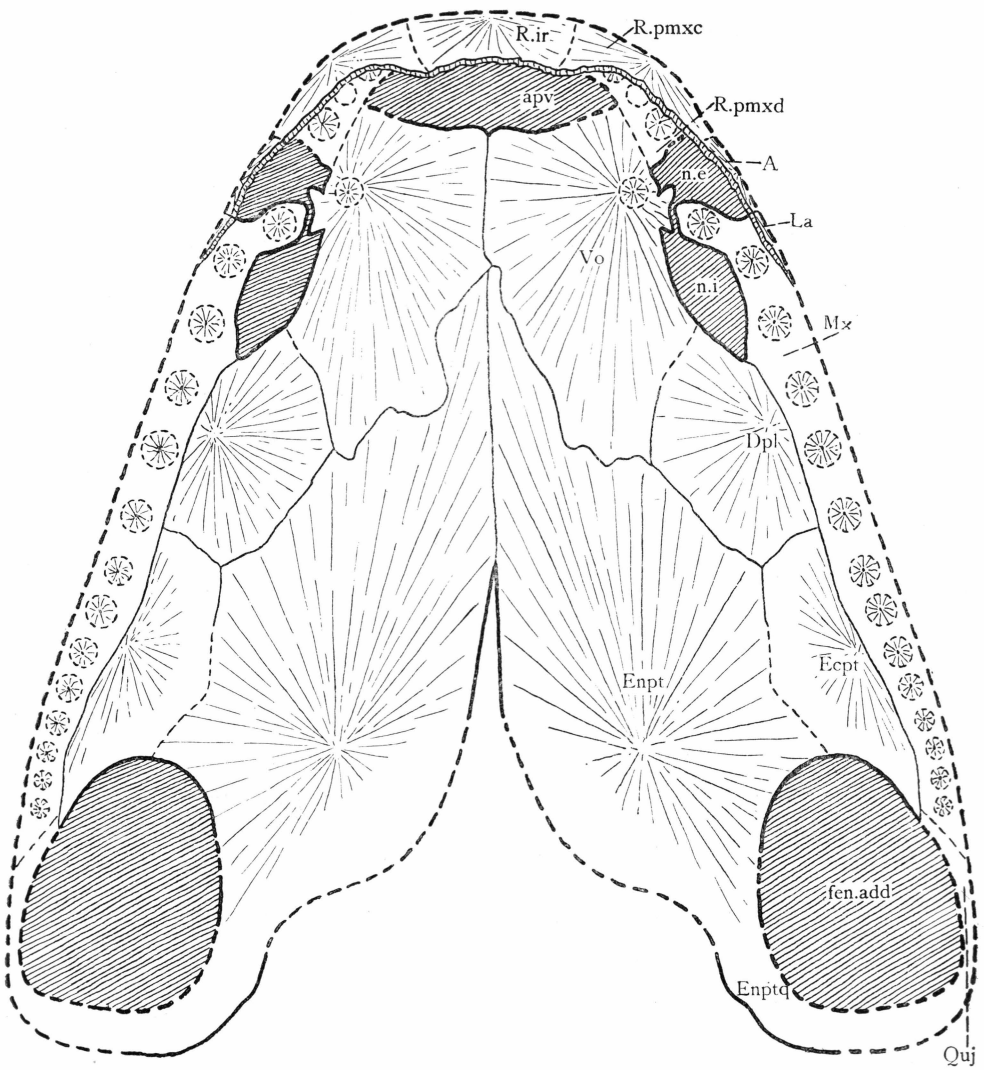
The jugal is without doubt traversed by parts of the infraorbital and jugal sensory canal (cf. below p. 40; cf. *Ichthyostega stensiöi*, pp. 19, 21; *Ichthyostega eigili*, pp. 48, 53; *Ichthyostegopsis wimani*, pp. 67, 70—71).

The *squamosal* (*Sq*, pl. VI, fig. 1; text-fig. 4) is preserved only in its lateral parts, showing a sigmoid antero-lateral suture with the jugal, and a rather straight lateral suture towards the quadratojugal. The radiate structure in the squamosal is clear; its centre is situated at the medial margin of the preserved part of the bone; probably it was situated nearest to the medial and the posterior margins of the bone. The squamosal is probably traversed by the jugal canal, though in the present state of preservation no certain traces of this canal can be distinguished. The crushing of the postero-lateral part of the skull also makes it impossible to ascertain, whether there was originally an independent *preopercular*, as indicated in text-fig. 4 (*Pop*).

Of the *quadratojugal* (*Quj*, pl. VI, fig. 1; pls. VII, VIII; text-figs. 4, 5) there are preserved the anterior and the posterior parts, but the central part has fallen away. The anterior and posterior parts, owing to crushing, actually lie in different planes, the anterior part being tilted in under the squamosal, the posterior part, on the contrary, probably flattened out laterally. In the present state of preservation the quadratojugal has an almost straight medial suture towards the squamosal.

The long *maxillary* (*Mx*) is shown in lateral view on the right side of the specimen (pl. VII), whereas its anterior part is shown on the left in dorsal view in plate VIII and text-fig. 5. Anteriorly the maxillary is smooth and fits to a spoon-like process of the vomer described below (p. 39). Then it curves round the lateral margin of the internal naris to join by a suture posterior to this with the dermopalatine. Further posteriorly the maxillary continues along nearly the whole of the side of the skull, lying wholly on the ventral surface of the skull, with a vertical lateral side, sculptured like the external surface of the other dermal bones. Most posteriorly the maxillary underlies the anterior end of the quadratojugal. The maxillary along its whole length bears teeth (pl. VII), which are considerably smaller in the posterior than in the anterior parts of the bone. All the teeth are clearly labyrinthine, pointed, and conical, or slightly compressed laterally. There are seen in the present state of preservation 13 teeth in the right maxillary. Along its dorsal margin the maxillary connects by suture with the lachrymal, jugal, and quadratojugal, and along its medial margin with the dermopalatine and ectopterygoid.

The external sculpture of the dermal bones in this species is best shown on parts of the left posterior antorbital and naso-postrostral (pl. VI, fig. 1) and on the maxillary and tooth-bearing part of the rostro-premaxillary (pl. VII). It is clearly of a much coarser type than that found in *I. stensiöi*.



Text-fig. 5. *Ichthyostega watsoni* n. sp. Restoration of the palate in dorsal view. $^{3}/_{4}$ natural size.

A, anterior antorbital; *Dpl*, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Enptq*, quadrate ramus of entopterygoid; *La*, lachrymal; *Mx*, maxillary; *Quj*, quadratojugal; *R. ir*, rostro-interrostral; *R. pmxc*, rostral part of rostro-premaxillary; *R. pmxd*, tooth-bearing part of rostro-premaxillary; *Vo*, vomer; *apv*, anterior palatal vacuity; *fen. add*, adductor fenestra; *n. e*, external naris; *n. i*, internal naris.

Dermal bones of the palate.

The palate of this specimen (pl. VIII) was completely laid bare by splitting off the dorsal parts of the skull, which covered the whole right and the anterior half of its left side. The radiate structure is now very clearly seen in all the bones of the complete right side of the palate.

The large *vomeres* (*Vo*, pl. VIII, text-fig. 5) with their rather thin, slightly curved anterior margins form the posterior boundary of the broad anterior palatal vacuity (*apv*, pl. VIII; text-fig. 5). Each vomer also joins by a short straight median suture with its fellow of the other side, by a long, irregularly sigmoid postero-medial suture with the entopterygoid, and by a short concave postero-lateral suture with the dermopalatine. The posterior half of its thickened lateral margin is developed as a vertical wall, which forms the anterior two-thirds of the medial margin of the small internal naris (*n. i*, pl. VIII; text-fig. 5). Most anteriorly the lateral margin of the vomer probably connects by suture with the rostro-premaxillary, as in *Ichthyostega eigili* (p. 50). Between its most anterior part and the anterior end of the internal naris the vomer exhibits a more or less vertical free lateral side and a curious spoon-like process for the attachment of the anterior end of the maxillary just in front of the internal naris, as shown on the left side on pl. VIII. The external nasal aperture (*n. e*, pl. VIII; text-fig. 5) must have been situated just in front of this process, and has been bounded medially by the mentioned free vertical side of the vomer. — By further preparation of the right side of the specimen it was found that, just below the anterior margin of the spoon-like process, there is a labyrinthine tooth of the same size as the larger of the teeth of the maxillary.

The growth-centres of the vomeres are situated near the lateral margins of the bones, slightly medial to the spoon-like processes described above.

The rather long *dermopalatines* (*Dpl*, pl. VIII; text-fig. 5) are roughly quadrangular, with curved antero-medial sutures towards the vomeres, mainly straight postero-medial sutures towards the entopterygoids, short, straight, posterior sutures towards the ectopterygoids and lateral margins, of which the anterior parts form the posterior third of the medial margin of each internal naris while the posterior parts form sutures with the maxillaries. The growth-centres of the dermopalatines are situated a little in front of, and only slightly medial to, the mid-points of the lateral margins of the bones.

The *ectopterygoid* (*Ecpt*, pl. VIII; text-fig. 5) (very fragmentary on the left but wholly preserved, yet somewhat crushed, on the right side) seems to be rather long and narrow; it has a short straight anterior suture towards the dermopalatine, an undulating postero-medial suture to-

wards the entopterygoid, a short[1]) curved free margin towards the adductor fenestra, and a nearly straight lateral suture towards the maxillary. Its growth-centre is situated, like that of the dermo-palatine, near the lateral margin and anterior to the mid-length of the bone.

The very large *entopterygoids* (*Enpt*, pl. VIII; text-fig. 5) meet in a median suture anteriorly. Posteriorly they are not very well preserved but probably left narrow interpterygoid vacuities between themselves and the processus cultriformis of the parasphenoid. Each entopterygoid has or had an antero-lateral margin, consisting of an irregularly sigmoid suture with the vomer, a mainly straight suture with the dermopalatine and an undulating suture with the ectopterygoid, also a concave free postero-lateral margin (somewhat broken in the specimen) towards the adductor fenestra. The powerful quadrate ramus of the entopterygoid (*Enptq*, pl. VIII; text-fig. 5) may bee seen also in section in plate VII (*Enptq*).

The growth-centres of the entopterygoids were situated as far back as at the transverse plane trough the anterior margins of the adductor fenestrae but considerably nearer to the median line of the skull than to these fossae.

Lateral line system of the head.

The difficulty in tracing the course of the sensory canals in this material has been already emphasized when treating of the lateral line system in *Ichthyostega stensiöi*. In the more crushed specimen of *Ichthyostega watsoni* this difficulty is of course still greater. Only the following parts of the system have been distinguished with a somewhat high degree of probability in the holotype of *I. watsoni*.

In the right lachrymal, near the posterior part of its lateral margin, there are a few rather large pores (*ifp*, pl. VI, fig. 1) and a little behind these, in the same bone, there is a small piece of canal, probably belonging to the infraorbital sensory canal.

In the anterior half of the right jugal there is a similar short piece of canal (*ifc*, pl. VI, fig. 1), continued forward by an imperfect narrow groove, conceivably once the inner surface of the canal.

The similar groove and canal on the posterior part of the jugal and the short piece of canal on the squamosal, both lettered *juc?* on pl. VI, fig. 1, possibly represent traces of the jugal canal.

On the left naso-postrostral there are seen, as in *Ichthyostega stensiöi*, traces of canals (*c*, pl. VI), probably related to the supraorbital sensory canal (cf. p. 22).

Remarks. This species is named in honour of Professor D. M. S.

[1]) This is possibly partly due to crushing, as may be easily gathered from pl. VIII.

WATSON, the author of several works (especially 1916, 1919, 1921, 1926 a, b) of fundamental importance for the study of the morphology of the Stegocephalians.

As may be gathered from the above description, *Ichthyostega watsoni* markedly differs in several respects from *I. stensiöi*. A striking difference between the present species and *Ichthyostega stensiöi* is among others the large jugal in the former. (The length of this bone is very nearly 0,5 of the length between the posterior margin of the rostro-interrostral and the posterior margin of the parieto-extrascapular in *Ichthyostega watsoni*, but the same relation in *I. stensiöi* is a little less than 0.45. The absolute length of the jugal is greater in *Ichthyostega watsoni*, which has an absolute distance between the rostro-interrostral and the posterior margin of the parieto-extrascapular of less length than in *I. stensiöi*). The differences seen in the preorbital region of the skull may be in part due to the crushing of this region in the specimen of *Ichthyostega watsoni*. The general type and arrangement of the dermal bones of the skull in both species are, however, obviously the same; among common features may be cited the occurrence of a median rostro-interrostral, a median parieto-extrascapular and the little quadrangular anterior antorbital, the typically bent suture between the lachrymal and the posterior antorbital, the short suture between the jugal and posterior antorbital, the large, forwardly broadening naso-postrostrals, the narrow frontals etc., and the similar shape of the anterior part of the palate.

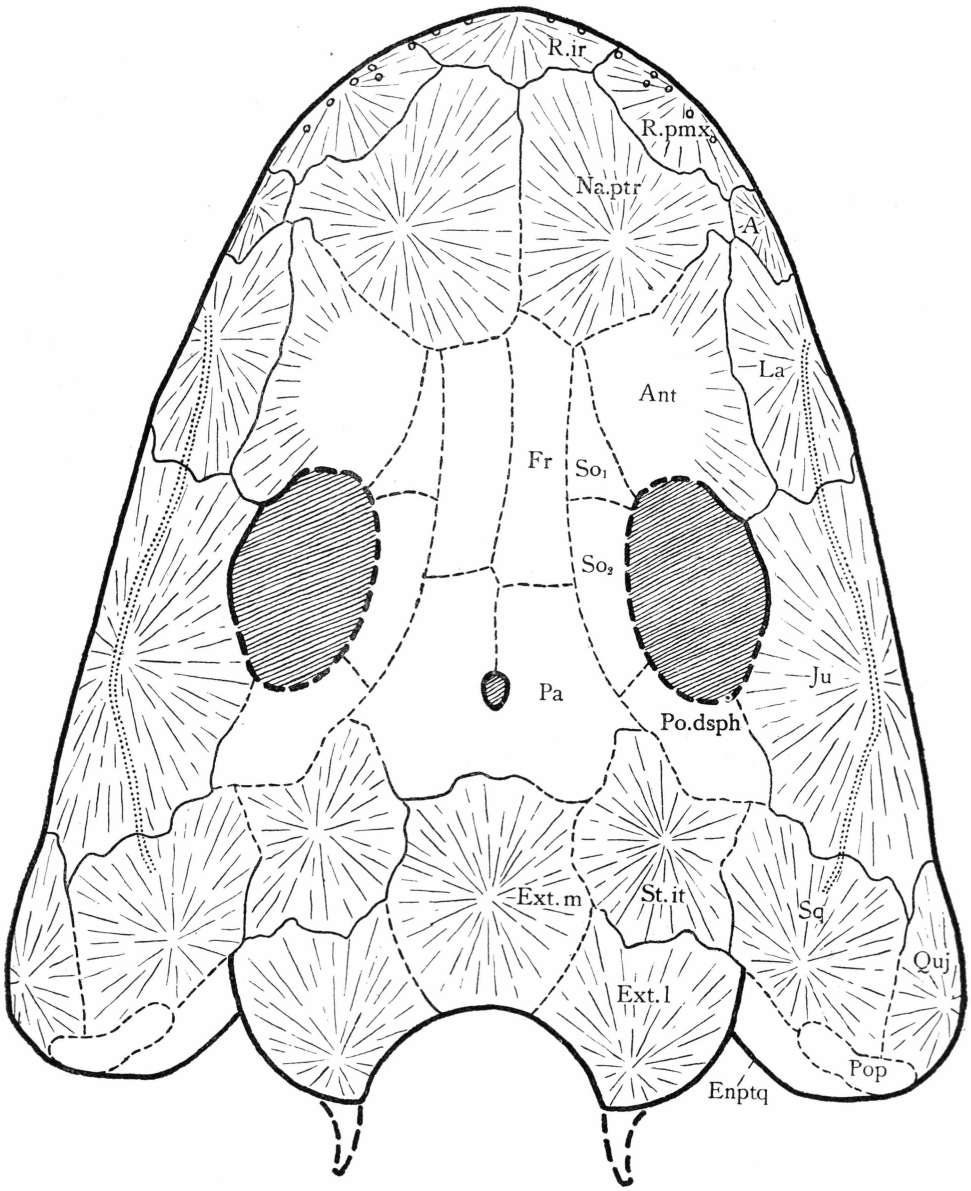
All this tends to show a close relationship between the two forms, and, if I am right, the resemblances justify no more than a specific separation of the two forms. Of course, as in all systematic conclusions in this preliminary note, a reservation is to be made for the possibility of greater differences in the parts not preserved or not yet studied.

Locality. The East Plateau, Mt. Celsius (cf. SÄVE-SÖDERBERGH 1932 a, pp. 10, 11; fig. 5).

5. *Ichthyostega eigili* n. sp.

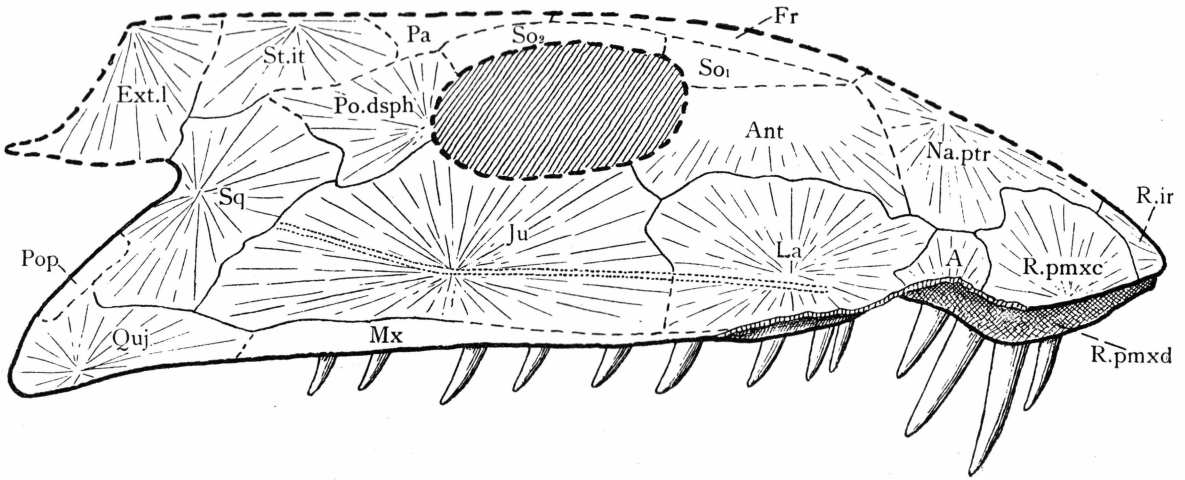
(Pls. IX, X, XI, XII, XIII, XIV, XV; text-figs. 6, 7, 8, 9).

Diagnosis: Skull higher and broader than in *I. watsoni* and *I. stensiöi*. Dermal bones with coarse external sculpture. Lachrymals with distinct sutures towards the naso-postrostrals, thus separating the posterior antorbitals from the anterior antorbitals. Posterior antorbitals with narrow antero-lateral processes stretching as far forward as the middle of the anterior antorbitals. Medial part of the suture of each anterior antorbital towards the lachrymal running antero-medially to postero-laterally. Very large jugals.



Text-fig. 6. *Ichthyostega eigili* n. sp. Attempted restoration of the skull in dorsal view. $^{7}/_{8}$ natural size. The parts of the lateral line system discovered thus far denoted with dotted outlines.

A, anterior antorbital; *Ant*, posterior antorbital; *Enptq*, quadrate ramus of entopterygoid; *Ext. l*, lateral extrascapular; *Ext. m*, parieto-extrascapular; *Fr*, frontal; *Ju*, jugal; *La*, lachrymal; *Na. ptr*, naso-postrostral; *Pa*, fronto-parietal; *Po. dsph*, postorbito-dermosphenotic; *Pop*, preopercular; *Quj*, quadratojugal; *R. ir*, rostro-interrostral; *R. pmx*, rostro-premaxillary; So_1, anterior supraorbital; So_2, posterior supraorbital; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.



Text-fig. 7. *Ichthyostega eigili* n. sp. Attempted restoration of the skull in lateral view. $^{7}/_{8}$ natural size. The parts of the lateral line system discovered thus far denoted with dotted outlines. Ventro-lateral parts of the rostral part of the rostro-premaxillary, of the anterior antorbital, and of the lachrymal removed in order to show the posterior part of the rostro-premaxillary.

A, anterior antorbital; *Ant*, posterior antorbital; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na. ptr*, naso-postrostral; *Pa*, fronto-parietal; *Po. dsph*, postorbito-dermosphenotic; *Pop*, preopercular; *Quj*, quadratojugal; *R. ir*, rostro-interrostral; *R. pmxc*, rostral part of rostro-premaxillary; *R. pmxd*, tooth-bearing part of rostro-premaxillary; So_1, anterior supraorbital; So_2, posterior supraorbital; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

Holotype and material. A fairly well-preserved skull (A. 4), showing the dermal bones of the skull-roof with the exception mainly of the supraorbitals, frontals and greater parts of the fronto-parietals, and showing also the complete palate, as well as the maxillaries of both sides. The specimen has been crushed so that the top of the skull forms with the right side of it a more or less continuous plane, sloping slightly ventro-laterally, at nearly right angles to the steeply sloping left side. Of the skull-roof there are preserved in this specimen the complete anterior antorbitals, right lachrymal, left jugal, squamosal and quadratojugal, the maxillaries, the greater parts of the rostro-premaxillaries, left naso-postrostral, left posterior antorbital, left lachrymal, right jugal, squamosal, quadratojugal, parieto-extrascapular, lateral extrascapulars, the left supratemporo-intertemporal and postorbito-dermosphenotic, and fragments of the rostro-interrostral, right naso-postrostral and posterior antorbital, fronto-parietals and right postorbito-dermosphenotic and supratemporo-intertemporal. The palate is completely preserved in part or counterpart, but has not been laid bare on the lateral half of the right side.

Description.

General shape. In spite of the crushing it can still be determined that the skull of *Ichthyostega eigili* must have been relatively high, short, and broad, its maximum breadth, restored from the right side, being slightly greater than its length along the median line. The following measurements from the holotype may give an idea of the size and general shape of this species:

Length along the median line ..... 150 mm
From anterior margin of rostro-interrostral to extreme posterior preserved end of lateral extrascapular..... 173 mm
From anterior margin of rostro-interrostral to posterior end of the cheek ..... between 171[1]) and 180[2]) mm
Restored breadth over posterior margins of anterior antorbitals about 85 mm
Breadth between posterior ends of lateral extrascapular-squamosal sutures ..... 77 mm
Restored breadth between lateral margins of quadratojugals about 144 mm
Maximum height .....about 50 mm

Dermal bones of the skull-roof.

The preserved part of the *rostro-interrostral* (*R. ir*, pls. IX, X, XI; pl. XII, fig. 1; pls. XIII, XIV; text-figs. 6, 7) shows that this bone was

[1]) Left side.
[2]) Right side.

very broad, its length being about half its breadth. The rostro-interrostral has a rounded anterior free margin, overlapping the most anterior parts of the rostro-premaxillaries (tooth-bearing parts), a finely zig-zag lateral suture on each side towards the rostral part of the rostro-premaxillary, and a rounded irregularly curved posterior suture towards the naso-postrostrals. The growth-centre of the rostro-interrostral is in the median line of the skull, near the anterior margin of the bone.

The *rostro-premaxillary* is damaged and distorted by crushing on the left, but well preserved on the right side of the skull. Its dorsal, rostral part (*R. pmxc*, pls. IX, X, XI; pl. XII, fig. 1; pls. XIII, XIV, XV; text-figs. 6, 7, 8) is rather short and roughly quadrangular, with nearly straight antero-medial and postero-lateral sides, formed by finely zig-zag sutures towards the rostro-interrostral and the anterior antorbital, a slightly convex free lateral margin, and an irregularly curved medial suture with the naso-postrostral. Its growth-centre is near the mid-point of the lateral margin of the bone. The tooth-bearing part of the rostro-premaxillary (*R. pmxd*, pl. XI; pl. XII, fig. 1; pl. XIII; text-figs. 7, 8, 9) is seen only in lateral or ventral view. It is overlapped dorsally by the free lateral and anterior margins of the rostral part of the rostro-premaxillary and the rostro-interrostral. These free margins project a little more laterally than the dorso-lateral edge of the tooth-bearing part of the rostro-premaxillary, forming in this way a groove (*ifg*?, pl. XII, fig. 1), which runs round the snout, ventral to the lateral and anterior edges of the rostro-interrostral and rostral parts of the rostro-premaxillaries. It is very probable that this groove lodged the anterior, commissural part of the infraorbital sensory canal (see below pp. 53—54). The tooth-bearing part of each rostro-premaxillary extends as far back as the middle of the anterior antorbital, which it underlies, and has a rather high, vertical, lateral side with an external pitted sculpture like that of the other dermal bones. There may be counted four long pointed, conical or slightly compressed and curved teeth on the left, and six on the right, rostro-premaxillary. The most posterior tooth on the left and the two teeth in front of the most posterior one on the right side are very much larger and longer than the others.

The *naso-postrostral* (*Na. ptr*, pls. IX, X, XI, XIV; text-figs. 6, 7) is best preserved on the left side, but here its antero-lateral part is damaged, this part being, on the other hand, well preserved on the right side of the skull. The posterior end of the naso-postrostral is lacking on both sides. The shape of this bone, as restored from both sides (text-fig. 6), is roughly pentagonal with a short, irregularly curved antero-medial margin, connecting by suture with the rostro-interrostral, a long, mainly sigmoid antero-lateral margin formed by the short straight suture with the anterior antorbital and the long, irregularly curved suture with the

rostro-premaxillary, a zig-zag postero-lateral margin with a suture towards the posterior antorbital, and a straight posterior or postero-medial margin with a suture towards the frontal. The growth-centre of the naso-postrostral can be seen on the left side, where it is situated rather far back as in *Ichthyostega stensiöi*, but probably relatively a little more laterally than in that species.

Of the *frontals* nothing is left on either side.

The *anterior antorbital* (*A*, pls. IX, X, XI; pl. XII, fig. 1; pls. XIII, XIV; text-figs. 6, 7, 8) is well preserved on both sides. It is a small, broad, pentagonal bone, with a long straight lateral margin, a long straight anterior suture with the rostro-premaxillary, a short straight medial suture with the naso-postrostral, and a bent suture towards the lachrymal, forming the long, concave postero-medial and the very short, straight posterior side of the bone. The radiate structure, as in the rostro-premaxillaries and the rostro-interrostral, is clear and its centre is situated near the free lateral margin of the bone.

The *posterior antorbital* (*Ant*, pls. IX, X, XI, XIV; text-figs. 6, 7) is fairly well preserved on the left side and the parts lacking there are preserved on the right side, so that its shape may be restored without much uncertainty. It is a rather long bone, owing principally to a narrow antero-lateral process which extends far forward between the naso-postrostral and the lachrymal. In *Ichthyostega eigili*, however, this process does not reach the anterior antorbital, as it does in *I. stensiöi*. It lies wholly medially to that bone, from which it is separated by the meeting of the naso-postrostral and lachrymal. Another important point in the shape of the posterior antorbital is that it has a short, curved posterior suture with the jugal. The posterior antorbital is further bounded by a slightly curved orbital margin, a long, slightly curved, lateral suture with the lachrymal, a short straight anterior and a long, bent antero-medial suture with the naso-postrostral. The medial boundary of the posterior antorbital is not clear in this specimen. The growth-centre of the posterior antorbital is situated, as in the two species of *Ichthyostega* already described, nearest to the medial margin of the bone.

The *supraorbitals* are totally lacking on both sides.

Of the *fronto-parietals* (*Pa*, pl. IX; text-fig. 6) there are only two small fragments of the posterior part, mainly of the left one with a posterior suture towards the parieto-extrascapular extending a little over the median line of the head without bending forwards or joining any forwardly directed suture, thus indicating that there was probably in *Ichthyostega eigili*, as in the specimen A. 2, described above (p. 28), an incomplete separation of the two fronto-parietals by a median suture extending only as far back as the pineal foramen.

The *postorbito-dermosphenotics* (*Po. dsph*, pls. IX, XI, text-figs. 6, 7) are imperfectly preserved but must have been rather broad, as seen on the left side (pl. IX). Each of these bones has a slightly bent lateral suture towards the jugal, a more or less curved orbital margin, an irregularly curved and bent posterior suture with the squamosal and supratemporo-intertemporal, and a medial with the fronto-parietal. The growth-centre of the postorbito-dermosphenotic was probably situated in the dorsal and medial part of the bone.

The *supratemporo-intertemporal* (*St. it*, pls. IX, XI; text-figs. 6, 7), preserved somewhat completely only on the left side, is a little longer than broad. It has a sharply sigmoid posterior suture (preserved only on the right side) towards the lateral extrascapular, a sigmoid medial margin, formed by sutures with the parieto-extrascapular and the fronto-parietal, a sigmoid anterior suture with the fronto-parietal and post-orbito-dermosphenotic, and an undulating lateral suture with the squamosal. The centre of the fairly clear radiate structure in the supratemporo-intertemporal is near the mid-point of the bone.

The *parieto-extrascapular* (*Ext. m*, pl. IX; text-fig. 6) is well preserved anteriorly but partly worn off posteriorly. It must have been relatively long, at least a little longer than its maximum breadth. The well-preserved parts of this bone show a slightly curved anterior suture with the fronto-parietal, gently curved, finely zig-zag lateral sutures with the supratemporo-intertemporals and, at least mainly, straight postero-lateral sutures with the lateral extrascapulars. The growth-centre of the parieto-extrascapular is situated in the median line of the head, distinctly behind the mid-point of the bone.

The *lateral extrascapular* (*Ext. l*, pls. IX, XI; text-fig. 6, 7) is damaged on both sides of the skull, but evidently is built up mainly by one dorsal horizontal, one lateral, and one posterior or postero-medial lamina, the dorsal one (*Ext. l*,*l. d*, pl. IX) being bounded antero-medially by a probably straight suture from the parieto-extrascapular, and anteriorly by a bent suture from the supratemporo-intertemporal, whilst laterally and posteriorly the margin of the dorsal lamina probably passed over gradually by a rounded bend into the lateral and postero-medial laminae of the bone. The anterior suture of the dorsal lamina with the supratemporo-intertemporal is continued as the anterior margin of the lateral lamina of the bone. This lateral lamina (*Ext. l*, *l.l*, pls. IX, XI) is further bounded by a lateral suture from the squamosal. The postero-medial lamina (*Ext. l*, *l. pm*, pl. IX) of the lateral extrascapular is imperfectly preserved; its anterior part is shown on the left, its posterior part on the right side. Its posterior part is imperfect most posteriorly even on the right side, but shows indications of a posterior process (*Ext. l*, *pr. p*) as in *Ichthyostega watsoni*. The growth-centre of the lateral extrascapular evidently lay

at the meeting point of the three above-described laminae of the bone, and as shown in the restorations text-figs. 6 and 7.

The *lachrymal* (*La*, pls. IX, X, XI; pl. XII, fig. 1; pl. XIV; text-figs. 6, 7, 8) is most complete on the right side, where it has, however, been somewhat distorted by pressure. Each lachrymal is an elongate bone (proportions length-breadth about 3:2) and may be considered as having five margins: one slightly curved medial joined by suture with the posterior antorbital and naso-postrostral, one short antero-lateral and one still shorter anterior, both joined by suture with the anterior antorbital, one free lateral margin, overlapping the maxillary, and one posterior bent and curved margin, suturally connected with the jugal. The growth-centre of the lachrymal is situated nearest to the lateral margin of the bone and considerably in front of the mid-point of this margin. The lachrymal is traversed by the infraorbital sensory canal (see below).

The *jugals* (*Ju*, pls. IX, X, XI, XIV; text-figs. 6, 7, 8) are very large, as in *Ichthyostega watsoni*. They are preserved on both sides, but the lateral marginal part is damaged on both sides by pressure and weathering. On the right this margin is probably complete, but its pressured condition makes it impossible to ascertain its exact relation to the maxillary, which latter it conceivably overlies, as in *Ichthyostega watsoni*. Each jugal has a bent anterior suture with the posterior antorbital and the lachrymal, a concave orbital margin, a curved medial suture with the postorbito-dermospenotic, and a postero-medial bent suture with the squamosal. Its lateral margin is joined by suture posteriorly with the quadratojugal.

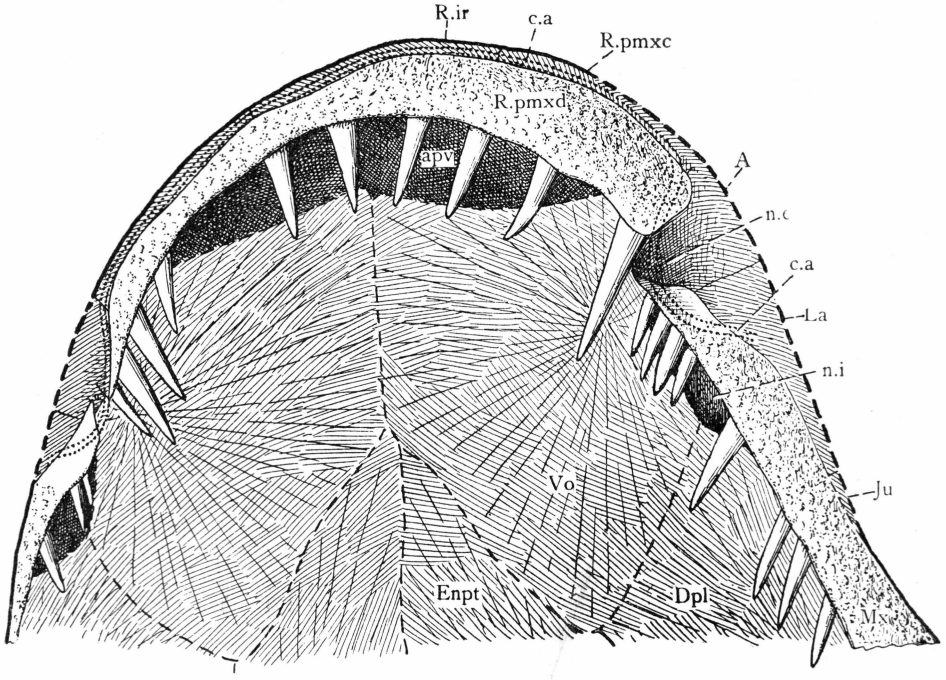
The growth-centre of the jugal is situated near the lateral margin of the bone, about equally distant from the anterior and posterior ends.

The jugal is traversed by the jugal and infraorbital sensory canals (see below p. 53).

The *squamosal* (*Sq*, pls. IX, X, XI, XIV; text-figs. 6, 7) is much damaged by crushing on both sides, especially on the right. Its sutures can not be determined with absolute certainty on the left, owing to weathering so extensive that it has mostly left only the innermost bone layer, which does not show any radiate structure, or even only the impression of this layer. As far as can be judged from the present specimen, each squamosal in *Ichthyostega eigili* is an irregularly shaped, elongate bone, with a short anterior suture with the postorbito-dermosphenotic, a bent antero-lateral suture with the jugal, a curved lateral suture with the quadratojugal, and a long medial suture with the entopterygoid (quadrate ramus), the lateral extrascapular, and the supratemporo-intertemporal. The growth-centre of the squamosal seems to have been situated near the medial margin of the bone. Nothing certain can be stated about the lateral line canals in the squamosal owing to the crushing and weathering of the specimen. The same factors make it impossible

to ascertain whether there is or is not an independent *preopercular* in this species.

The *quadratojugal* (*Quj*, pls. IX, X, XI, XIV; text-figs. 6, 7, 8) is most clearly shown on the left side. It is rather high (height more than half the length of the bone) and if there is no preopercular (cf. above) it is curved posteriorly to wrap round the posterior end of the quadrate bone. The quadratojugal probably has a short anterior suture with the maxillary. Further it has a short antero-medial suture with the jugal,



Text-fig. 8. *Ichthyostega eigili* n. sp. Restoration of a part of the skull seen obliquely from the anterior, ventral and left side to show position of external naris in relation to the dermal bones. $^{6}/_{5}$ natural size.

A, anterior antorbital; *Dpl*, dermopalatine; *Enpt*, entopterygoid; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *R. ir*, rostro-interrostral; *R. pmxc*, rostral part of the rostro-premaxillary; *R. pmxd*, tooth-bearing part of the rostro-premaxillary; *Vo*, vomer; *apv*, anterior palatal vacuity; *c. a*, probable course of anterior commissure of the infraorbital canals; *n. e*, external naris; *n. i*, internal naris.

a long curved medial suture with the squamosal, and with the preopercular or the entopterygoid, and finally a long curved free ventro-lateral and ventro-posterior margin, bounding the adductor fenestra laterally and posteriorly. The growth-centre of the quadratojugal is situated near the posterior half of the ventro-lateral margin of the bone.

The long *maxillary* (*Mx*, pls. IX, X, XI; pl. XII, fig. 1; pls. XIII, XIV; text-figs. 7, 8, 9) is crushed together with the bones dorso-medial to it

on the right side of the specimen (pl. XI) but better preserved on the left side (pl. XII, fig. 1; pl. XIII), where it is seen to have its anterior end situated ventro-medially to the anterior antorbital, below which conceivably it articulated with a process from the vomer as in *Ichthyostega watsoni* (cf. p. 39). The most anterior part of the vertical lateral side of the left maxillary, as far back as below the anterior half of the lachrymal, seems to have been smooth and devoid of external sculpture. At the ventral edge of this part, which forms the posterior margin of the external naris (*n. e*, pl. XII, fig. 1; pl. XIII; text-figs. 8, 9), there are seen fragments of four small teeth, placed close together. The posterior larger part of the left maxillary has a vertical lateral side with the usual pitted sculpture of the dermal bones, and further shows three large, long, conical and slightly posteriorly curved, pointed teeth, fragments of at least four other relatively large teeth, and finally two very small, conical teeth near the posterior end of the bone. The maxillary joins by suture dorsally with the lachrymal, jugal, and quadratojugal, and medially with the dermopalatine and ectopterygoid. — On the right maxillary there are fragments of at least 10 teeth, of which the most anterior and posterior are clearly of minor size than the other.

The sculpture of the external surface of the dermal bones in this species is coarse and similar to that in *I. watsoni*.

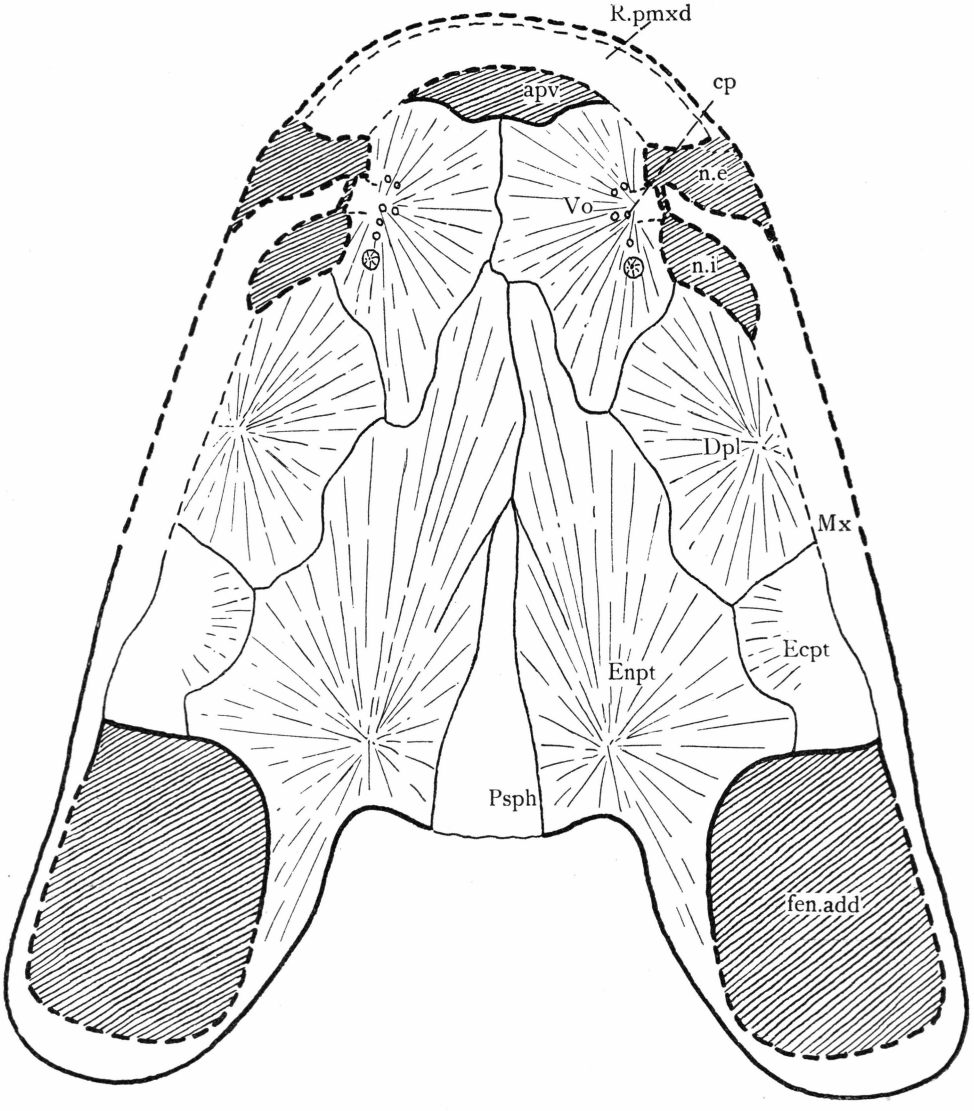
Dermal bones of the palate (pls. XIV, XV; text-fig. 9).

The palate is most completely shown in pl. XV, in ventral view. The lateral parts of the left side of the palate are also seen on pl. XIV, in dorsal view. On plate XIV are also seen the broad anterior palatal vacuity (*apv*), the small internal naris (*n. i.*), its communication (*n. ec*) with the still smaller narrow external naris, and finally the rather large adductor fenestra ("subtemporal fossa", *fen. add.*).

Each *vomer* (*Vo*, pls. XIV, XV; text-fig. 9) is a large bone with a somewhat thickened anterior margin towards the anterior palatal vacuity, a zig-zag median suture, an undulating postero-medial suture with the entopterygoid, an irregularly curved posterior suture towards the dermopalatine, and a lateral margin, which forms the anterior half of the medial margin of the internal naris, joins by suture with the rostropremaxillary and probably gives attachment to the maxillary anterior to the internal naris as it does in *Ichthyostega watsoni* (cf. above p. 39). The growth-centre of each vomer is situated near the lateral margin of the bone, in front of the middle of this margin. The base of a tooth is seen on the left vomer, near the posterior part of its lateral margin, just medial to the internal naris. Near the lateral margin of the left vomer there are further two rows of foramina (*cp*, pl. XIV; text. fig. 9), probably for vessels and nerves to the anterior part of the palate (branches of the

arteria palatina and vena palatina medialis and the n. palatinus (cf. Rr. mucosi praepalatini art. palatinae, ECKER-WIDERSHEIM-GAUPP 1899, p. 296).

The *dermopalatine* (*Dpl*, pls. XIV, XV; text-fig. 9) is shown on the left side. It is an elongate bone, roughly quadrangular in shape, with



Text-fig. 9. *Ichthyostega eigili* n. sp., Restoration of the palate in dorsal view. $^{7}/_{8}$ natural size.

Dpl, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Mx*, maxillary; *Psph*, parasphenoid; *R. pmxd*, tooth-bearing part of the rostro-premaxillary; *Vo*, vomer; *apv*, anterior palatal vacuity; *cp*, canals probably for branches of the art. palatina, the vena palatina medialis, and the n. palatinus; *fen. add*, adductor fenestra; *n. e.* external naris; *n. i.* internal naris.

an irregularly curved anterior suture towards the vomer, an undulating postero-medial suture with the entopterygoid, and a mainly straight posterior suture towards the ectopterygoid. The lateral margin of the dermopalatine is divided into an anterior part, forming the posterior half of the medial margin of the internal naris, and a posterior part, forming a suture with the maxillary. The growth-centre of the dermopalatine is situated near the middle of the lateral margin of the bone.

The *ectopterygoid* (*Ecpt*, pls. XIV, XV; text-fig. 9) is shown only on the left side. It is rather long, as in *Ichthyostega watsoni*, and has four sides, one anterior, with a suture towards the dermopalatine, one lateral, with a suture towards the maxillary, one postero-medial with a sigmoid suture towards the entopterygoid, and one posterior forming the lateral part of the anterior margin of the adductor fenestra ("subtemporal fossa"). The growth-centre of the ectopterygoid is situated near the lateral margin and in the anterior half of the bone.

The very large *entopterygoids* (*Enpt*, pls. X, XIV, XV; text-fig. 9) meet in a slightly curved median suture (pl. XV), which terminates in front on the most anterior part of the postero-medial margin of the left vomer. Posterior to this median suture the entopterygoids leave very narrow interpterygoid vacuities between themselves and the narrow processus cultriformis of the parasphenoid. The left entopterygoid shows an undulating, long antero-lateral side, joined by suture with the vomer, dermopalatine, and ectopterygoid, and a strongly concave postero-lateral margin towards the adductor fenestra. Laterally to this fenestra the entopterygoid is curved upwards to form a vertical quadrate ramus (*Enptq*, pls. X, XIV) which builds up the medial wall of the adductor fossa (subtemporal fossa) and joins by suture with the squamosal and with the quadratojugal or the preopercular.

The growth-centre of each entopterygoid is situated medial to the anterior third of the adductor fenestra, nearest to the medial margin of the bone.

The *parasphenoid* (*Psph*, pl. XV; text-fig. 9) has a narrow gutter-shaped processus cultriformis, which continues forward to be concealed in a ventral view by the median parts of the two entopterygoids (pl. XV). Posteriorly the parasphenoid has been greatly damaged by crushing.

Lateral line system of the head.

Owing to the same difficulties as in the species previously described our knowledge of the lateral line system of *Ichthyostega eigili* is as yet very partial. Moreover the extensive weathering to which the anterior and middle part of the top of the skull have been subjected makes it impossible to state anything about the supraorbital canal or the most posterior part of the suborbital part of the infraorbital canal. No traces

of the otic part of the infraorbital canal, of the postotic canal, supratemporal canal, or main lateral line canal have been detected.

Traces or indications of the suborbital part of the infraorbital canal have been detected in the right jugal and lachrymal, in the rostro-premaxillaries, and in the rostro-interrostral. In the right jugal the matrix filling the sensory canals is much weathered and there are traces left only of that part of the infraorbital canal (*ifc*, pls. IX, X, XI, XIV; text-fig. 6) which lies in the forward continuation of the jugal canal (*juc*, pls. IX, X, XI, XIV; text-fig. 6; see below). The crushing of the specimen has here contributed to show the course of the canals in the jugal, as there is a fissure just along the canals.

In the right lachrymal it was possible to prepare and expose clearly a part of the suborbital part of the infraorbital canal (text-fig. 6; *ifc*, pls. X, XI; pl. XII, fig. 2 pl. XIV). It lies in the forward continuation of the canal in the jugal and stretches from near the posterior margin of the lachrymal to the growth-centre of that bone, where it disappears in a group of tubules. Posterior to this group the preserved part of the canal in the lachrymal gives off three very clear tubules (*ift*, pl. XII, fig. 2). The most posterior tubule of the group of tubules round the growth-centre of the lachrymal can also be followed down to the canal, whereas the more anterior tubules are clear only in their terminal parts. Several of the tubules are preserved completely, out to their pores (*ifp*, pls. IX, X; pl. XII, fig. 2; pl. XIV). The pores of the part of the infraorbital canal now described, as they looked before the preparation are shown in pl. IX (*ifp*). The continuation of the infraorbital canal in the anterior part of the lachrymal is not so easy to follow and conceivably the canal must have turned down somewhere in the antero-lateral part of the lachrymal to pass ventral to the external naris, or it may have finished in the anterior part of the lachrymal, possibly giving off a post-nasal commissure to the supraorbital canal. In the latter case, which seems, however, less probable, the ethmoidal canal or anterior commissure was wholly independent of the rest of the infraorbital canal, as it may perhaps also have been for instance in *Tertrema* (Wiman 1914, pl. VII; Stensiö 1921, p. 145) and *Orthosaurus* (Watson, 1926 a, fig. 6, 7).

The anterior commissural part of the infraorbital canal was probably situated in the groove round the snout, between the tooth-bearing parts of the rostro-premaxillaries and the anterior and lateral edges of the rostro-interrostral and rostral parts of the rostro-premaxillaries (*ifg*?, pl. XII, fig. 1; *c. a*, text-fig. 8). Tubules and pores, probably appertaining to the anterior commissure of the infraorbital canal, are seen in the rostro-premaxillaries (*ifp*, pl. IX, X, XIV) and in the rostro-interrostral (see text-fig. 6!), but especially clearly in the left rostro-premaxillary. Several of the tubules have been followed ventrally far enough to ascertain that their matrix

filling is in direct communication with the matrix left in parts of the groove, in which the canal is supposed to have been situated.

The course of the jugal canal (text-fig. 6) is indicated by the posterior part of the above-mentioned fissure in the jugal (p. 53) and by two tubules at the posterior end of the fissure (*jut*, pls. X, XI). In the squamosal it is obscured by crushing.

Remarks. This species is named in honour of my friend Mr. EIGIL NIELSEN, who assisted me in a very valuable way during the whole work of collection in the summer of 1931.

Ichthyostega eigili is most nearly allied to *I. watsoni* in several respects. Among others there may be pointed out the relatively broad form of the skull and the similar form of the anterior antorbitals, which are, in both species, excluded from contact with the posterior antorbitals by the meeting of the lachrymals and naso-postrostrals. The relative length of the jugal is also very nearly the same in *Ichthyostega eigili* as in *I. watsoni*. But there are also several points of difference between the two species. The skull of *Ichthyostega eigili* is probably still broader and higher than that of *I. watsoni*. There are several differences in the shape and extension of the various dermal bones; e. g. the posterior antorbital in *Ichthyostega eigili* has a narrow antero-lateral process, stretching further forward than the anterior end of the same bone in *I. watsoni*, and lying as far forward as the growth-centre of the anterior antorbital.

Owing to the great agreement in the main features between *Ichthyostega eigili* and *Ichthyostega watsoni*, the discussion of the relation of the latter to *Ichthyostega stensiöi* (p. 41) holds good in the main when comparing *Ichthyostega eigili* to *Ichthyostega stensiöi*. This seems to justify the reference of *Ichthyostega eigili* to the same genus as the two species previously described.

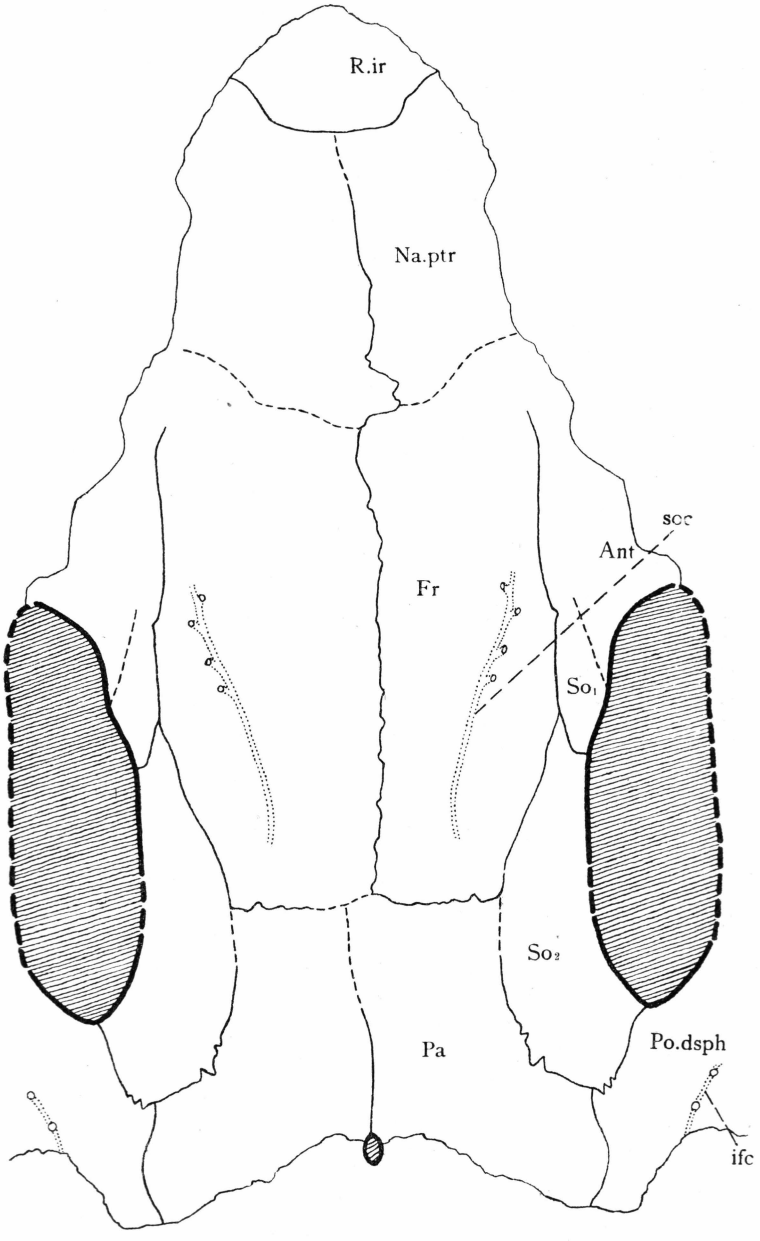
Locality. Above the East Plateau, Mt. Celsius (see SÄVE-SÖDERBERGH 1932 a, p. 11).

6. *Ichthyostega*? *kochi* n. sp.

(Pls. XX, XXI, XXII; text-fig. 10).

Diagnosis: Skull rather long. Internal nares far anterior to the whole orbits. Orbits very long. Dermal bones with fine external sculpture. Posterior antorbitals with postero-lateral orbital margins.

Material and holotype. The greater part of the right half of a skull (A. 7), showing in section large portions of the endocranium and further the following dermal bones: the complete right frontal and supra-orbitals, the greater parts of the right naso-postrostral, fronto-parietal



Text-fig. 10. *Ichthyostega? kochi* n. sp. Attempted restoration of part of the skull roof in dorsal view. $^{5}/_{4}$ natural size.

Ant, posterior antorbital; *Fr*, frontal, *Na. ptr*, naso-postrostral; *Pa*, fronto-parietal; *Po. dsph*, postorbito-dermosphenotic; *R. ir*, rostro-interrostral; So_1, anterior supraorbital; So_2, posterior supraorbital; *ifc*, infraorbital sensory canal; *soc*, supraorbital sensory canal.

and postorbito-dermosphenotic, vomer and entopterygoid, and parts of the rostro-interrostral, left naso-postrostral and frontal, right posterior antorbital, jugal, squamosal and supratemporo-intertemporal, and of the right dermopalatine. The posterior part of the specimen has been crushed into the anterior part and the lateral parts of the specimen are also damaged by crushing.

Description.

Dermal bones of the skull-roof.

The sculpture of the dermal bones in this species is of a type, most closely resembling that of the specimen A. 6, *Ichthyostega* sp. a., i. e. it is much finer than that of *Ichthyostega watsoni* and *Ichthyostega eigili*, and at least as fine as that of *Ichthyostega stensiöi*.

The *rostro-interrostral* (*R. ir*, pl. XX; text-fig. 10) shows a rounded postero-lateral suture with the right naso-postrostral. The radiate structure in this bone can not be made out in its present state of preservation.

The right *naso-postrostral* (*Na. ptr*, pl. XX; pl. XXI, fig. 1; text-fig. 10) is preserved in its medial parts and shows a mainly straight median suture with its fellow of the other side, a concave antero-medial suture with the rostro-interrostral, and a slightly curved postero-lateral suture towards the frontal. The place of the growth-centre of the naso-postrostral cannot be determined on the present specimen, which is preserved with the outermost, sculptured bone-layer.

The right *frontal* (*Fr*, pls. XX, XXI; text-fig. 10) is a rather long bone, roughly rectangular in shape, with a long, straight median suture towards the left frontal, a curved antero-medial suture towards the left and right naso-postrostral, a long, curved lateral suture with the supraorbitals, and a short, straight posterior suture towards the right frontoparietal. The growth-centre of the frontal is situated rather far back, at one-third the length of the bone. The frontal is traversed by the supraorbital sensory canal (see below p. 59).

The *posterior antorbital* (*Ant*, pl. XX; pl. XXI, fig. 1; text-fig. 10) is preserved only in its medial parts, where it shows a medial suture towards the frontal, and probably towards an anterior supraorbital, and a rather long postero-lateral orbital margin. At the anterior suture of the posterior antorbital towards the naso-postrostral the specimen is too crushed to allow of a more exact description. The radiate structure is clearly seen in the posterior antorbital and the growth-centre is situated near the medial margin of the bone.

The *anterior supraorbital* (So_1, pls. XX, XXI; text-fig. 10) cannot be determined with certainty as an independent element in this specimen, owing to its state of preservation, which prevents any exact statement as to the course of the radiate structure in the area under question. If it be not developed as an independent element, there is in this specimen

a compound antorbito-supraorbital, but it seems more probable that there is really a small, triangular, independent anterior supraorbital, wedged in between the frontal and the medial margin of the posterior antorbital, as indicated in the restoration (text-fig. 10). This bone then would have a short, concave orbital margin.

The *posterior supraorbital* (*So*$_2$, pl. XX; pl. XXI, fig. 1; text-fig. 10) has been broken into two pieces, the posterior of which has been pressed in, together with the fronto-parietal, below the parts in front of it. The restored posterior supraorbital (text-fig. 10) is a long bone, narrow anteriorly and broadening posteriorly. It has a short, curved antero-lateral suture with the anterior supraorbital (or antorbito-supraorbital), a long curved medial and postero-medial margin, with suture towards the frontal, the fronto-parietal, and, for a very short stretch, towards the postorbito-dermosphenotic, also a short postero-lateral suture with the postorbito-dermosphenotic and a lateral, orbital margin with a low vertical, orbital surface. The posterior supraorbital, as seen in pl. XX and text-fig. 10, has a farther backward extension in this species than in *Ichthyostega stensiöi*, a difference that may, however, be only apparent, as in *Ichthyostega stensiöi* the suture is exposed on the ventral surface of the skull roof, but in *Ichthyostega? kochi* on the dorsal surface.

The right *fronto-parietal* (*Pa*, pl. XX; pl. XXI, fig. 1; text-fig. 10) is preserved in its anterior portion, as far back as the pineal foramen (*pin*, pl. XX). The most anterior part that is preserved is pressed in below the frontal; the restored shape of the anterior part of the fronto-parietal may be seen in text-fig. 10. The fronto-parietal is rather long and narrow anteriorly and much broader posteriorly, laterally to the pineal foramen. The anterior suture of the fronto-parietal towards the frontal is at present concealed by the posterior part of the latter bone, and the median suture between the fronto-parietals is not clear in the specimen. The antero-lateral, strongly concave margin of the fronto-parietal shows an interlocked suture with the posterior supraorbital; its slightly convex lateral margin has a suture with the postorbito-dermosphenotic.

The *postorbito-dermosphenotic* (*Po. dsph*, pl. XX; pl. XXI, fig. 1; text-fig. 10) is well preserved in its medial and anterior parts. It shows a medial margin, consisting of two concave parts, the anterior of which forms a suture with the posterior supraorbital, the posterior with the fronto-parietal, also a slightly concave orbital margin, partly with an orbital surface at right angles to the main part of the outer surface of the bone. The postorbito-dermosphenotic surrounds a part of the suborbital part of the infraorbital sensory canal (see below p. 59).

A postero-lateral part of the right fronto-parietal is concealed by a crushed fragment (*St. it*, pl. XX; pl. XXI, fig. 1), conceivably of the *supratemporo-intertemporal.*

The *squamosal* is probably represented by a fragment (*Sq*, pl. XX,

XXI, fig. 1) that has been pressed in below the postorbito-dermosphenotic and appears in the hole left by the weathering off of the postero-lateral part of this bone.

A crushed fragment of the *jugal* (*Ju*, pl. XX; pl. XXI, fig. 1) is likewise pressed in below the postorbito-dermosphenotic.

Dermal bones of the palate. The palate is clearly of the same type as that of the previously described species of *Ichthyostega*, i. e. with the internal nares situated far more forward than the anterior margins of the orbits, and further with large vomeres and entopterygoids. In the present state of preservation of the specimen the adductor fenestra (*fen. add*, pl. XXII) has an antero-medial margin at right angles to its postero-medial margin, but this may be due to crushing.

The left *vomer* (*Vo*, pl. XXII) is a large bone, not preserved most laterally and most medially but still showing an anterior margin towards the anterior palatal vacuity, a curved, rounded lateral margin towards the internal naris, and a postero-lateral suture with the dermopalatine. The growth-centre of the vomer is situated near the lateral margin of the bone, probably just a little in front of the internal naris. Near the posterior part of the lateral margin of the vomer, medially to the anterior part of the internal naris, there are two rather large foramina (*cp*, pl. XXI), connected by a horizontal canal, and which probably transmitted branches of the arteria palatina, vena palatina medialis and the n. palatinus (*cf.* Rr. mucosi praepalatini art. palatinae, ECKER-WIEDERSHEIM-GAUPP, 1899, p. 296).

The *dermopalatine* (*Dpl*, pl. XXII), is preserved only medially, and is seen to have a suture towards the vomer antero-medially and to overlap the entopterygoid postero-medially. It seems to have been rather long, but its suture towards the *ectopterygoid* can not be found in the present specimen, so that a posterior part of the area lettered as a dermopalatine in the figure (*Dpl*, pl. XXII) conceivably belongs to the ectopterygoid.

The *entopterygoid* (*Enpt*, pl. XXII) is a very large and long bone with a long, undulating antero-lateral suture towards the vomer, the dermopalatine, and the ectopterygoid, and a sharply bent (cf. above) lateral margin towards the adductor fenestra. The posterior, vertical quadrate ramus of the entopterygoid (*Enptq*, pl. XXII) is, in this specimen, concealed to a large extent by fragments of other bones. The growth-centre of the entopterygoid is situated just medial to the bend in its margin towards the adductor fenestra.

Lateral line system of the head.

The present specimen is of extreme importance as being the only one in which the course of a part of the *supraorbital canal* can be de-

termined with certainty. The supraorbital canal (*soc*, pl. XX; pl. XXI, fig. 2) has been followed in the frontal of this specimen from near the lateral third of the posterior margin of that bone to its centre of growth and further towards the anterior third of the lateral margin of the bone. In its anterior part the canal is exceptionally clear and shows the tubules (*sot*) and pores (*sop*, pl. XX). The best preserved part of the supraorbital canal is shown in a prepared longitudinal section in pl. XXI, fig. 2. In its posterior part the canal is preserved only as small pieces of the ventral half of its matrix filling (*soc*, pl. XX). It is mainly on the structures shown in this specimen that the determination of the frontals and supraorbitals is based.

Of the suborbital part of the *infraorbital canal* there is preserved a short piece (*ifc*, pl. XX, XXII, fig. 1) in the postorbito-dermosphenotic, showing two pores (*ifp*, pl. XX; pl. XXI, fig. 2) with their short tubules. This and the part found in the specimen A. 2 (p. 29), are the most posterior parts of the infraorbital canal as yet demonstrated in any of the Devonian Stegocephalians.

Remarks. This highly interesting species, of which we must hope to find still more material during the coming expeditions, is named in honour of the distinguished Chief of the Danish expeditions and of the Geological Survey of Greenland, Doctor Lauge Koch.

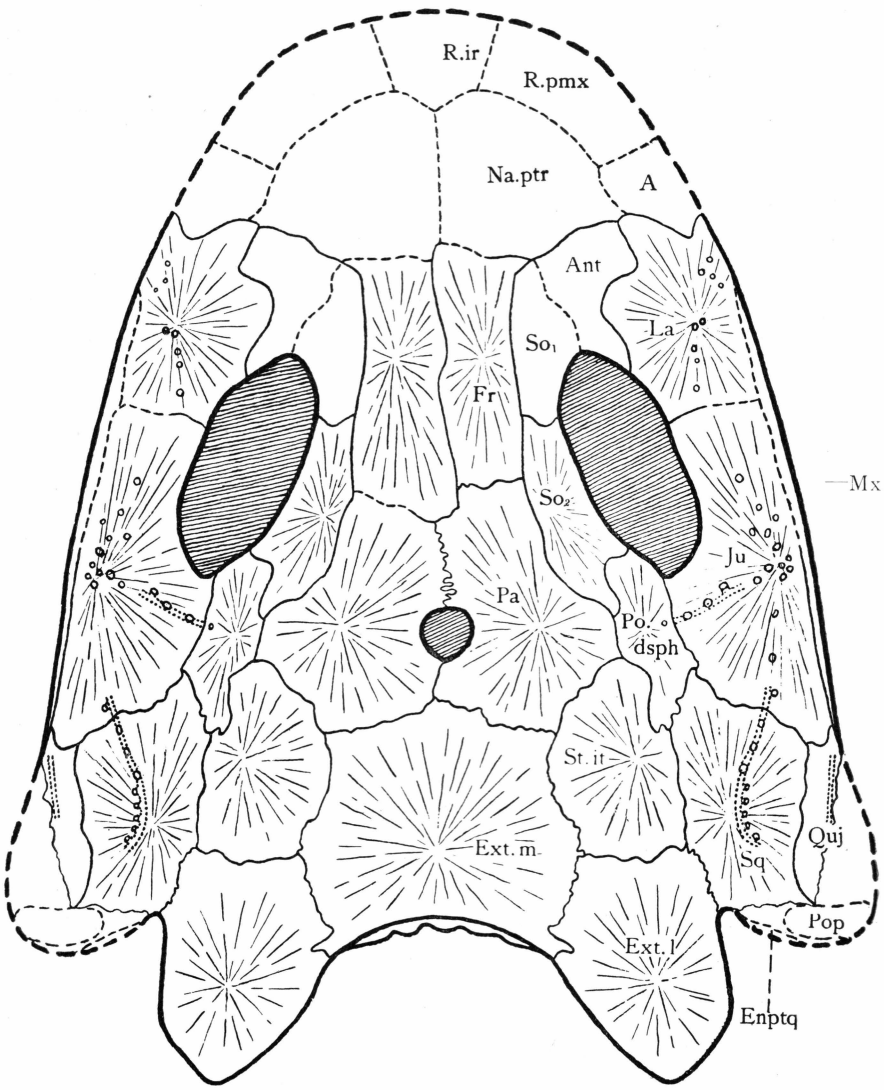
Ichthyostega? kochi shows in certain features a close resemblance to the genus *Ichthyostega*. The most important of these features are the position of the internal naris very markedly farther forward than the anterior margin of the orbit and the relatively long and narrow shape of the skull, as far as can be judged from the present specimen. But it is well distinguished from the other species of *Ichthyostega* by the forward extension of the orbit (contra *Ichthyostega stensiöi*) and by the fine sculpture of its dermal bones (contra *Ichthyostega watsoni* and *Ichthyostega eigili*). The former character is especially interesting as a possibly intermediate stage between the small orbits in *Ichthyostega* (or at least in *I. stensiöi*), and the very large and far forwardly extending orbits in the new genus *Ichthyostegopsis* described below.

Locality. The East Plateau, Mt. Celsius (see Säve-Söderbergh 1932 a, pp. 10, 11, fig. 5).

Genus ***Ichthyostegopsis*** n. g.

Diagnosis: Ichthyostegids with short and broad skulls, with large, rounded orbits, probably situated with their greater parts in the anterior half of the skull. Lachry-

mal and jugal meeting laterally to the orbit. Posterior antorbital not meeting the jugal. Fronto-parietals separated



Text-fig. 11. *Ichthystegopsis wimani* n. g. n. sp. Attempted restoration of the skull in dorsal view. $^5/_4$ natural size. The parts of the lateral line canals discovered thus far denoted with dotted outlines. *A*, anterior antorbital; *Ant*, posterior antorbital; *Enptq*, quadrate ramus of entopterygoid; *Ext. l*, lateral extrascapular; *Ext. m*, parieto-extrascapular; *Fr*, frontal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na. ptr*, naso-postrostral; *Pa*, fronto-parietal; *Po. dsph*, postorbito-dermosphenotic; *Pop*, preopercular; *Quj*, quadrato-jugal; *R. ir*, rostro-interrostral; *R. pmx*, rostro-premaxillary; So_1, anterior supraorbital; So_2, posterior supraorbital; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

by a complete median suture. Internal nares ventral to the anterior parts of the orbits.

Genotype: *Ichthyostegopsis wimani* n. sp.

Ichthyostegopsis wimani n. sp.

(Pl. XVI, fig. 1; pls. XVII, XVIII, XIX; text figs. 11, 12, 13).

Holotype and material. The greater part of a skull (A. 5) preserved in part (A. 5. a) and counterpart (A. 5. b, c), and representing the most median parts of the right and the whole left side of the skull, except its most anterior and postero-lateral parts. A. 5. a originally lacked parts of several bones, which parts were transferred from the more complete specimen A. 5. b so that now each bone of the skull is represented by an outer layer on A. 5. b or A. 5. c and an inner layer on A. 5. a. Specimen A. 5. b is however still much better than A. 5. a and shows very clearly most of the sutures of the dermal bones of the cranial roof, whereas on A. 5. a the sutures can in part be traced only with very great difficulty.

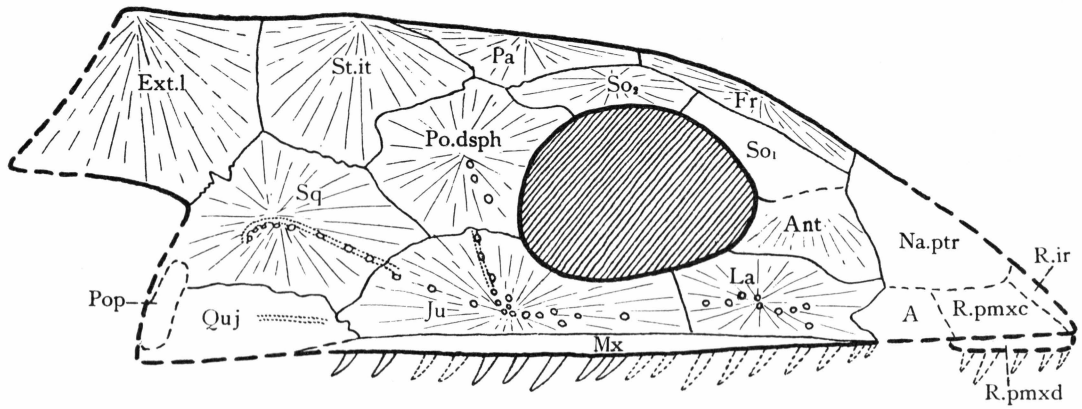
The dermal bones preserved in the specimen include the complete left posterior antorbital (A. 5. b), supraorbitals, fronto-parietal, post-orbito-dermosphenotic, supratemporo-intertemporal, lachrymal, jugal, and parieto-extrascapular, the greater parts of the left frontal, right fronto-parietal, left lateral extrascapular, squamosal and maxillary and fragments of the left naso-postrostral and anterior antorbital, right frontal and supratemporo-intertemporal and left quadratojugal.

Description.

General shape. As may be gathered from the figures and the attempted restoration, this species has a much shorter and relatively much broader skull than any of the species of the genus *Ichthyostega*. It is also very high and the sides of the skull-roof form an average inner angle of about 115° towards the median parts of it. The very sharply marked bend between the median and the lateral parts of the skull-roof passes from the growth-centre of the lateral extrascapular through the lateral extrascapular and supratemporo-intertemporal, then between the postorbito-dermosphenotic laterally and the fronto-parietal and posterior supraorbital medially, along the medial margin of the orbit, and finally between the anterior supraorbital laterally and the posterior supraorbital and frontal medially.

The median, dorsal part of the skull is not curved upward in transverse section but instead forms as a whole a depressed area behind the pineal foramen. — The posterior part of the cheek, lateral to the otic notch must have been strikingly short and slender in relation to the stout and high part of the skull roof, lying between the two otic notches.

The orbits are large and relatively broader than in *Ichthyostega*



Text-fig. 12. *Ichthyostegopsis wimani* n. g. n. sp. Attempted restoration of the skull in lateral view. $^{5}/_{4}$ natural size. The parts of the lateral line canals discovered thus far denoted with dotted outlines.

A, anterior antorbital; *Ant*, posterior antorbital; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na. ptr*, naso-postrostral; *Pa*, fronto-parietal; *Po. dsph*, postorbito-dermosphenotic; *Pop*, preopercular; *Quj*, quadratojugal; *R. ir*, rostro-interrostral; *R. pmxc*, canal bone part of rostro-premaxillary; *Rpmxd*, tooth-bearing part of rostro-premaxillary; So_1, anterior supraorbital; So_2, posterior supraorbital; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

stensiöi. Their maximum length is along a line, running from postero-ventro-laterally to antero-dorso-medially.

The following measurements from the specimen A. 5. b may give an idea of the size and proportions of the skull in *Ichthyostegopsis wimani*.

Restored median length of the skull	97 mm
Restored breadth over posterior margins of anterior antorbitals	56 mm
Restored breadth over anterior ends of quadratojugals	83 mm
Restored breadth between lateral extrascapular-squamosal sutures at the otic notches	60 mm
Maximum height of the skull	about 35 mm
Maximum length of orbit	27 mm
Breadth of orbit	22 mm

Dermal bones of the skull roof.

The *rostro-interrostral* (*R. ir*, text-figs. 11, 12), *rostro-premaxillaries* (*R. pmx*, text-figs. 11, 12), *naso-postrostrals* (*Na. ptr*, text-figs. 11, 12), and anterior antorbitals (*A*, text-figs. 11, 12) of which nothing or very little is preserved on the specimen, have been restored after the same bones in *Ichthyostega*, only broadened on account of the much broader form of the posterior parts of the skull in *Ichthyostegopsis*.

The *frontals* (*Fr*, pl. XVII, fig. 1; pl. XVIII; text-fig. 11) are long and rather narrow, though, of course, broader than in the representatives of the genus *Ichthyostega*. The better preserved left frontal retains a short part of its anterior suture towards the naso-postrostral. Further it has a mainly straight median suture with the right frontal, a short straight posterior suture with the left fronto-parietal, and a similarly straight lateral suture with the posterior and anterior supraorbitals and possibly with the posterior antorbital too. The radiate structure of the frontal is seen to have its centre approximately in the mid-point of the bone. The right frontal has a posterior suture with both fronto-parietals, the median suture between these two bones terminating in front at the posterior margin of the right frontal.

No certain traces of the supraorbital sensory canal have been found in the frontals in *Ichthyostegopsis wimani*.

The *anterior antorbital* (pl. XVIII; text. figs. 11, 12) has a bent posterior suture towards the lachrymal and seems to have been rather of the type met in *Ichthyostega watsoni* and *I. eigili* than of that found in *I. stensiöi*.

The present state of preservation does not allow of an absolutely certain statement whether there is an independent *anterior supraorbital* between the frontal and posterior antorbital or a compound antorbito-supraorbital that extends to meet the frontal medially. But the former seems more probable from what may be seen of the radiate structure in the doubtful part, and an extension of the anterior supraorbital as in the

restorations text-figs. 11 and 12 seems the more possible. There is in the posterior antorbital or lateral part of the antorbito-supraorbital (*Ant*, text-figs. 11, 12), a radiate structure with its centre near the boundary between this and the doubtful area medial to it (anterior supraorbital or medial part of the antorbito-supraorbital, So_1, text-figs. 11, 12). In the latter the radiate structure is not clear.

The large *antorbito-supraorbital* or, more probably, the *posterior antorbital* and the *anterior supraorbital* (*Ant*, pl. XVI, fig. 1; pl. XVII, fig. 1; pl. XVIII), are bounded by a straight medial suture towards the frontal, a short posterior suture towards the posterior supraorbital, a concave orbital margin, a sigmoid lateral suture towards the lachrymal, and a straight anterior suture towards the naso-postrostral.

The *posterior supraorbital* (*So*, pl. XVI, fig. 1; XVII, fig. 1; pl. XVIII; So_2, text-figs. 11, 12) is a long and narrow bone, slightly curved and following also with its medial margin the configuration of the orbital margin. Consequently it is bounded by a short anterior suture towards the anterior supraorbital (or antorbito-supraorbital), a long, curved medial suture towards the frontal and fronto-parietal, a somewhat shorter, curved orbital margin, and a posterior suture towards the post-orbito-dermosphenotic. The last suture, as seen in ventral view on the specimen A. 5. b (pl. XVIII) consists of a short, transverse, medial part, a longer, longitudinal, middle part and a short transverse, lateral part. The middle part of the suture lies along a longitudinal ridge, which continues forward over the whole posterior supraorbital and is formed by the meeting, at a wide angle, of the orbital surface of the bone and the more medial parts of its lower surface.

The broad *fronto-parietals* (*Pa*, pl. XVII, fig. 1; pl. XVIII; text-figs. 11, 12) have narrower anterior and very broad posterior halves. They are completely separated by an interlocked, mainly straight median suture, developed also behind the very large pineal foramen. Each fronto-parietal is further bounded by a short curved anterior suture towards the frontal, a roughly straight postero-medial suture towards the parieto-extrascapular, a slightly concave postero-lateral suture towards the supratemporo-intertemporal, a very short lateral suture towards the postorbito-dermosphenotic, and a long, curved antero-lateral suture with the posterior supraorbital. The growth-centre of each fronto-parietal is situated laterally to the pineal foramen, midway on the direct line between it and the lateral margin of the bone. The anterior narrower parts of the fronto-parietals form with the frontals a plane, which is horizontal in transverse section, but slightly convex upward in longitudinal section, whereas on the posterior parts of the fronto-parietals and on the parieto-extrascapular there is behind the pineal foramen a broadly V-shaped depression with the limbs of the V

extending onto the two fronto-parietals, and with its posteriorly directed angle on the parieto-extrascapular.

The *postorbito-dermosphenotic* (*Po. dsph*, pl. XVI, fig. 1; pl. XVII, fig. 1; pl. XVIII; text-figs. 11, 12) is rather broad and its medial half shows two distinct surfaces (except the dorsal one, which is not shown in the present state of preservation): one orbital surface, facing antero-ventrally, continuous with and meeting by suture antero-dorsally with the orbital surface of the posterior supraorbital, and one medially facing main inner surface. The latter has a short anterior suture towards the medial part of the posterior supraorbital, a short medial suture with the fronto-parietal, a sigmoid postero-medial suture with the most anterior part of the supratemporo-intertemporal, a short posterior suture with the lateral part of the last-named bone, a probably straight postero-lateral suture with the squamosal and a curved lateral suture with the jugal. The growth-centre of the postorbito-dermosphenotic cannot be determined accurately in the present state of preservation of the bone, but probably lies as shown in text-figs. 11 and 12. — The postorbito-dermosphenotic is traversed by the suborbital part of the infraorbital sensory canal (see below p. 70).

The large *supratemporo-intertemporal* (*St. it*, pl. XVI, fig. 1; pl. XVII, fig. 1; pl. XVIII; text-figs. 11, 12) has a form rather suggestive of that of the corresponding bone in *Ichthyostega stensiöi* i. e. with a curved medial margin, connected by suture with the fronto-parietal and parieto-extrascapular, a more straight posterior margin in suture with the lateral extrascapular, a straight lateral margin, connected by suture with the squamosal, and a sigmoid antero-lateral margin with a suture towards the postorbito-dermosphenotic. This makes the bone consist of a broader posterior and a narrower anterior part; the latter however is much broader in *Ichthyostegopsis wimani* than in *Ichthyostega stensiöi*. — The growth-centre of the supratemporo-intertemporal is situated about in the middle of the length and breadth of this bone just in the junction between the medial dorsal horizontal, and the lateral, nearly vertical part of the bone. There have as yet been observed no certain traces of any sensory canals in the supratemporo-intertemporal.

The *parieto-extrascapular* (*Ext. m*, pl. XVII, fig. 1; pl. XVIII; text-fig. 11), is roughly square but has a bent anterior margin, in suture with the two fronto-parietals, sigmoid lateral margins, divided into concave anterior parts, in suture with the supratemporo-intertemporals, and convex posterior parts with sutures towards the lateral extrascapulars, and finally a concave, mainly free, posterior margin connected, however, most laterally by suture with the lateral extrascapular. The growth-centre of the parieto-extrascapular is situated in the median line of the skull and in the posterior third of the bone.

The *lateral extrascapular* (*Ext. l*, pl. XVI, fig. 1; pls. XVII, XVIII; text-figs. 11, 12) is a rather short and high bone. It may be considered as made up mainly by one dorsal horizontal square and two more vertical laminae, one lateral rather vertical and one oblique posterior, the latter divided into one part facing postero-laterally and one facing postero-medially. All these laminae meet in a rounded knob which is situated at the most postero-dorso-lateral point of the whole skull.

The dorsal and smallest lamina of the lateral extrascapular (*Ext. l*, *l.d*, pl. XVII, fig. 1) has towards the parieto-extrascapular a medial suture mainly straight but most posteriorly somewhat curved, and a short anterior suture with the dorsal horizontal part of the supratemporo-intertemporal. The large, lateral lamina of the lateral extrascapular (pl. XVI, fig. 1; *Ext. l*, *l. l*, pl. XVII, fig. 1; pl. XVIII) has a mainly straight anterior suture with the vertical part of the supratemporo-intertemporal, a deeply interlocked antero-lateral suture with the squamosal (see A. 5. b, pl. XVIII; the suture on A. 5. a is uncertain), and a straight free postero-lateral margin towards the otic notch. The large posterior lamina of the lateral extrascapular (*Ext. l*, *l. p*, pl. XVII, fig. 1) consists of a concave smaller, triangular part facing postero-laterally and a larger part facing postero- medially, with a dorsal suture towards the most lateral part of the posterior margin of the parieto-extrascapular. The postero-ventral marginal part of the lateral extrascapular, seen on the right side of the specimen (pl. XVII, fig. 1) appears to have lacked any process for the attachment of the shoulder-girdle, which was possibly attached to the concave lateral part of the posterior lamina. On the ventral side of specimen A. 5. a, there are seen the ventral ends of two vertical, gutter-shaped ventral processes (*Ext. l*, *pr. v*, pl. XVII, fig. 2) situated ventrally to the lateral lamina of each lateral extrascapular, and conceivably homologues of the ventral processes of the lateral extrascapular, described above in the Ichthyostegid sp. a (p. 24) and in *Ichthyostega watsoni* (p. 36).

The *lachrymal* (*La*, pl. XVI, fig. 1; pl. XVII, fig. 1; pl. XVIII; text-figs. 11, 12) is an irregularly formed bone, overlying the maxillary postero-laterally. It has a sigmoid anterior margin, with a very short straight suture towards the naso-postrostral, and a long strongly curved suture by which it meets the anterior antorbital, further a straight posterior suture with the jugal, a sigmoid medial suture with the posterior antorbital, and a short orbital margin. Conceivably the lachrymal, as in *Ichthyostega watsoni* and *Ichthyostega eigili*, has incorporated with it the area in which, in *Ichthyostega stensiöi*, the postero-medial part of the anterior antorbital meets the antero-lateral end of the posterior antorbital. — The lateral marginal part of the lachrymal is broken off. The growth-centre of this bone was clearly situated somewhat laterally to the mid-point of the bone.

The lachrymal is traversed by the suborbital part of the infraorbital sensory canal (see p. 70).

The *jugal* (*Ju*, pl. XVI, fig. 1; pl. XVII, fig. 1; pls. XVIII, XIX; text-figs. 11, 12) is a rather long bone, narrower anteriorly but broadening behind the orbit. It has a strongly concave antero-medial orbital margin, a straight anterior suture with the lachrymal, a long convex postero-medial margin with a suture towards the postorbito-dermosphenotic and squamosal and a very short postero-lateral margin with a suture towards the quadratojugal. The jugal further overlaps the maxillary laterally. The growth-centre of the jugal is situated near the lateral margin of the bone, midway between its anterior and posterior ends. The jugal is traversed by the suborbital part of the infraorbital canal and by the anterior part of the jugal canal (see below pp. 70—71).

The *squamosal* (*Sq*, pl. XVI, fig. 1; pl. XVII, fig. 1; pls. XVIII, XIX; text-figs. 11, 12) in its present state of preservation is longer than broad and roughly hexagonal, bounded by a concave antero-lateral margin with a suture towards the jugal, a probably straight antero-medial margin, with a suture towards the postorbito-dermosphenotic, a straight medial margin joined by suture with the supratemporo-intertemporal, a postero-medial margin with a deeply interlocked suture towards the lateral extrascapular (see pl. XVIII), a broken posterior side, and finally a slightly concave postero-lateral margin, with a suture towards the quadratojugal. The growth-centre of the squamosal is situated, as far as can be judged in the present state of preservation, rather near the postero-medial margin of the bone, and consequently in the posterior third of the preserved part of the bone.

The squamosal is traversed by the posterior part of the jugal canal (see below p. 71).

Whether there was or was not an independent *preopercular* in *Ichthyostegopsis wimani* cannot be determined in the present specimen. The possible shape and place of such an element is denoted in the restoration (*Pop*, text-figs. 11, 12).

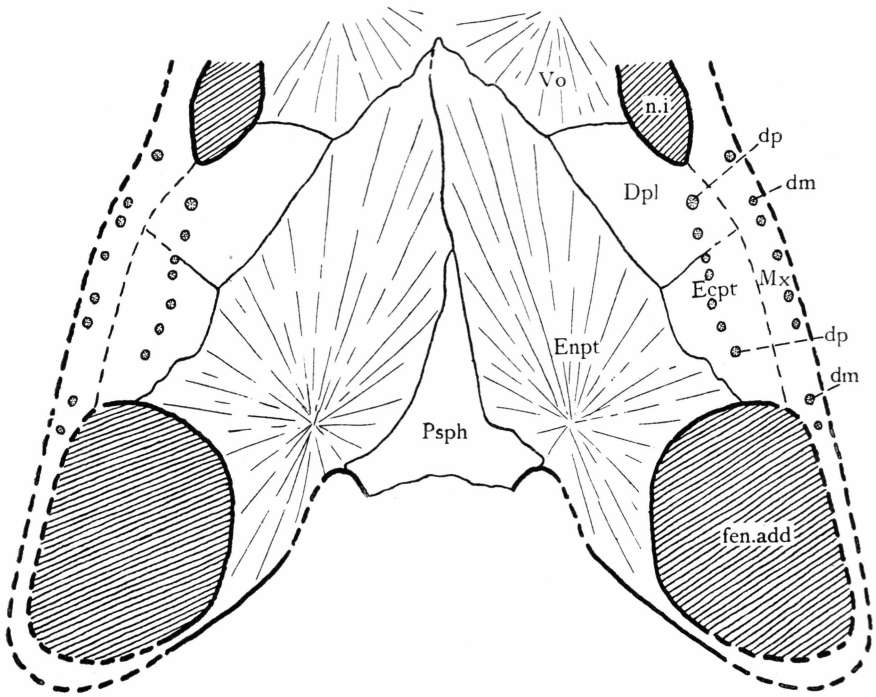
The *quadratojugal* (*Quj*, pl. XVI, fig. 1; pl. XVII, fig. 1; pls. XVIII, XIX; text-figs. 11, 12) is fragmentarily preserved in the specimen. All but its antero-medial marginal part, connected by suture with the jugal, squamosal, and maxillary, is broken off. Its growth-centre must have been situated near the lateral margin of the bone. The quadratojugal is probably traversed by a quadratojugal sensory canal (see below p. 71).

The long and narrow *maxillary* (*Mx*, pl. XVI, fig. 1; pl. XVIII, text-figs. 11, 12) is mainly vertical but has also a long triangular horizontal part, overlapped by the lachrymal and the anterior half of the jugal. In front of those bones the maxillary is broken off, farther posteriorly it underlies the posterior half of the jugal and the quadratojugal. In the

most anterior part of the maxillary there is seen the base of a labyrinthine tooth (pl. XVIII) and farther back there are, more or less well preserved, at least seven more teeth (pl. XVI, fig. 1; *dm*, pl. XVII, fig. 2; pl. XVIII; text-fig. 13) all small and pointed and, at least in the present state of preservation, directed with their points somewhat backwards.

Dermal bones of the palate.

Of the palate the left side is better preserved, lacking only its anterior and antero-lateral portions. The preserved parts of the palate are



Text-fig. 13. *Ichthyostegopsis wimani* n. g. n. sp. Restoration of posterior parts of the palate in ventral view. — $^5/_4$ natural size.
Dpl, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Mx*, maxillary; *Psp*, parasphenoid; *Vo*, vomer; *dm*, teeth of the maxillary; *dp*, teeth of the palate; *fen. add*, adductor fenestra; *n. i*, internal naris.

seen mainly on A. 5. a (pl. XVII, fig. 2), but a small part of it is preserved in counterpart on A. 5. c.

The rather narrow internal naris (*n. i.*, pl. XVII, fig. 2; text-fig. 13), as stated in the generic diagnosis (p. 61) lies ventral to the anterior half of the orbit. — In the left side of the palate there is seen a medium-sized oval adductor fenestra (*fen. add*, text-fig. 13).

The left *vomer* (*Vo*, pl. XVII, fig. 2; text-fig. 13) is preserved only in its postero-medial parts, where it shows long undulating postero-medial

sutures towards the entopterygoid and dermopalatine, and a short part of its margin towards the internal naris. The radiate structure in the preserved parts of the vomer indicates a position of the growth-centre about as in *Ichthyostega watsoni*.

The left *dermopalatine* (*Dpl*, pl. XVII, fig. 2; text-fig. 13) forms a straight anterior suture with the vomer, a straight long postero-medial suture with the entopterygoid and a short postero-lateral suture towards the ectopterygoid; its lateral margin forms with its anterior part the posterior half of the postero-medial boundary of the internal naris; its posterior part is in suture with the maxillary. There can be observed on the dermopalatine at least two small teeth (*dp*, pl. XVII, fig. 2 and text-fig. 13) of the same size as those of the maxillary and lying in a row posterior to the internal naris.

The *ectopterygoid* (*Ecpt*, pl. XVII, fig. 2; text-fig. 13) is a little shorter than the dermopalatine. It forms a short, straight antero-medial suture with the latter bone, a curved postero-medial suture with the entopterygoid, a short posterior margin towards the adductor fenestra, and conceivably a lateral suture with the maxillary. In a row, lying in the direct continuation of the row of teeth on the dermopalatine, there are found on the ectopterygoid traces of at least five teeth (*dp*, pl. XVII, fig. 2; text-fig. 13) all of the same shape as those of the maxillary and dermopalatine.

The large and long *entopterygoid* (*Enpt*, pl. XVII, fig. 2; text-fig. 13) has an anterior palatal ramus, covering in the present state of preservation the whole space between the parasphenoid and the lateral elements of the palate, and a slender quadrate ramus, forming the medial and postero-medial boundary of the adductor fenestra. The palatal ramus of each entopterygoid is triangular in shape, and its straight medial margin is connected by suture along its anterior part with the entopterygoid of the other side. The posterior part of the medial margin of each entopterygoid is overlapped by the parasphenoid. Along its mainly straight antero-lateral margin the palatal ramus of each entopterygoid is suturally connected with the vomer, dermopalatine, and ectopterygoid.

The *parasphenoid* (*Psph*, pl. XVII, fig. 2; text-fig. 13) is partly concealed by the entopterygoids in its anterior part (processus cultriformis). Posteriorly it exhibits lateral processes, probably surrounding the basipterygoid processes of the endocranium. The posterior part of the skull-base will be fully discussed when describing the endocranium of the Ichthyostegids.

Lateral line system of the head. (Pl. XVI, fig. 1; pl. XVII, fig. 1; pls. XVIII, XIX).

In this species there has been observed more of the lateral line system than in any other of the forms described in this paper. Even here

however, we have attained only a very partial knowledge of the system owing to the difficulties mentioned above (p. 21).

No certain traces of the *supraorbital canal* have as yet been found in *Ichthyostegopsis wimani*. There is, however, just in front of the suture between the left frontal and the left fronto-parietal a short portion of a canal (seen on pl. XVIII, fig. 2), which may belong to the supraorbital canal, and it is probable that there is a more posterior part of this canal just at, and slightly medially to, the suture between the left fronto-parietal and posterior supraorbital.

The suborbital part of the *infraorbital* canal has been traced in the postorbito-dermosphenotic, jugal, and lachrymal.

In the lateral part of the postorbito-dermosphenotic there are seen in A. 5. b (pl. XVIII; text-fig. 12) several pores, and just at the suture between this bone and the jugal is the upper end of a preserved portion of the suborbital part of the infra-orbital canal (*ifc*, pls. XVIII, XIX). From this point the canal has been followed in the jugal more than two-third the distance to the growth-centre of this bone. Then it is broken and its continuation is to be found on A. 5. a, where it is concealed in bony substance traversed by tubules which open in a group of pores round the growth-centre of the jugal (*ifp*, pl. XVI, fig. 1; pl. XVII, fig. 1; pl. XVIII). The portion of canal shown on A. 5. b (*ifc*, pl. XIX) is composed of at least three slightly curved parts and from their points of junction arise tubules (the tubule marked *ift*, and two more dorsal tubules, pl. XIX) which lead to pores on the external surface. In the group of pores around the growth-centre of the jugal (pl. XIX) there are two pores, clearly belonging to the vertical portion of the suborbital part of the infraorbital canal; four small pores very near the growth-centre belong either to the junction between the vertical and horizontal portions of the suborbital part of the infraorbital canal or to the anterior end of the jugal canal; and anterior to the growth-centre there are two tubules (*ift*) and two pores, clearly belonging to the horizontal portion of the suborbital part of the infraorbital canal. Further forward on the jugal there are seen two very distinct pores (pl. XVIII) of the suborbital part of the infraorbital canal. On the lachrymal there is a row of probably nine pores of the infraorbital canal, beginning at the suture with the jugal, just medially to the most medial point of the horizontal lamina of the maxillary, and continuing towards the anterior half of the lateral margin of the lachrymal. Thus, the infraorbital canal most probably left the skull-roof at the lateral margin of the lachrymal to pass ventral to the external naris.

On the posterior half of the jugal there is further found the anterior part of the *jugal canal* (*juc*, pls. XVIII, XIX). The most anterior part of this nearest to the infraorbital canal, is concealed by bony substance and

tubules on A. 5. a. A very distinct pore, clearly appertaining to this part of the jugal canal, is seen on A. 5. b (pls. XVIII, XIX) posterior to the group of four small pores, nearest to the growth-centre of the jugal. Some of these four pores may also belong to the jugal canal. A part of the jugal canal itself (*juc*, pl. XIX) is preserved near the postero-medial margin of the jugal, beginning 3 mm from the mid-point of the suture towards the squamosal and running directly towards this suture, in which it is concealed for a short stretch. The part of the jugal canal nearest to the broken anterior end of the preserved portion is swollen and conceivably marks the place of origin of a tubule (cf. below, see pl. XIX). — After having traversed the suture between the jugal and the squamosal, the jugal canal (*juc*, pls. XVIII, XIX) enters the squamosal, in which it runs first postero-medially towards the growth-centre of this bone for a stretch of some 12 mm, but does not reach this centre, as it now curves to a posterior, and finally to a postero-lateral direction to terminate at a point 7 mm antero-laterally to the posterior end of the suture between the lateral extrascapular and the squamosal. Especially in the posterior curved part of the jugal canal the tubules to the pores are very clearly shown (*jut*, pl. XIX). The portion of the canal between each two consecutive tubules is slightly curved and conceivably lodged one primary canal organ (cf. ALLIS 1889), as the rather short and clearly undivided tubules must be compared with the primary tubes leading to the primary pores in *Amia*. The curved shape of the portions of canal between the tubules indicates a cessation of the embryonic development (see ALLIS 1889, p. 523) at a stage when the primordial canals, formed around the primary organs, have just united and formed common primary tubes but have not yet wholly lost their individuality and become straight to form a straight compound canal. The parts first invaginated, nearest to each primary organ, still lie more deeply than the later enclosed parts of the canal. (See also below p. 83, text-fig. 14.) — Along the preserved part of the jugal canal in the squamosal there may be counted at least eight tubules, all directed laterally or antero-laterally. At its posterior end the jugal canal seems to have left the squamosal and to have been more superficially situated or to have joined a more superficially situated preopercular canal.

On the quadratojugal there are seen traces of canals situated as indicated in text-figs. 11 and 12, and probably belonging to a *quadratojugal canal* (see SÄVE-SÖDERBERGH 1932 b) homologue of the vertical pit-line of the cheek in fishes. Nothing is seen of this on the photographs, which were all taken and retouched before a fortunate preparation revealed these interesting traces of canals. They are, however, by no means so clear and undoubted as the remains of the jugal and infraorbital canals, described above.

Of the posterior (otic and most posterior part of the suborbital)

parts of the infraorbital canal and of the postotic canal, main lateral line canal, and supratemporal canal nothing is shown in this specimen in its present state of preservation.

Remarks. This species is named in honour of my respected teacher and friend, Professor C. WIMAN, Uppsala.

Ichthyostegopsis wimani is very well separated from the above described species of the genus *Ichthyostega* by important differences in the general shape and the topographical relations of the large orbits to the internal nares and the bones of the lateral orbital margin. The difference may perhaps be expressed most simply as a very important general broadening of the skull and a considerable forward extension of the orbit in *Ichthyostegopsis*, invading the area, in which, in *Ichthyostega*, the jugal meets the posterior antorbital in a short suture, and consequently cutting away the antero-medial end of the jugal and somewhat more than the posterior third of the posterior antorbital. — Since in regard to the topographical relations discussed the three described species of the genus *Ichthyostega*, as far as can be judged from the present material, show considerable uniformity, their generic separation from the species last described is thought to be well founded, with, of course, all due reservation for our present incomplete knowledge of the forms in question.

Locality. The East Plateau, Mt. Celsius (see SÄVE-SÖDERBERGH, 1932 a, p. 10, 11, fig. 5).

V. Summary of present knowledge of the organisation of the Ichthyostegids.

The foregoing special descriptions permit of a fairly full account of the general organisation of the *Ichthyostegidae* as far as it concerns the dermal bones and the greater part of the lateral line system of the head.

Dermal cranial roof.

The only openings in the dorsal side of the skull-roof in the *Ichthyostegids* are the two orbits, of varying shape and extension, and the rather large pineal foramen. The external nares, as shown in *Ichthyostega watsoni* (pp. 31, 39) and *Ichthyostega eigili* (p. 50) must have been situated ventral to the skull-roof, and have opened ventro-laterally, between the anterior ends of the maxillaries and the posterior ends of the tooth-bearing parts of the rostro-premaxillaries.

The dermal bones on the dorsal side of the skull are most completely shown in the specimens of *Ichthyostega stensiöi* (pp. 14—20) and *Ichthyo-*

stegopsis wimani (pp. 63—68) but several parts are better displayed in the other material. The dermal bones of the cranial roof comprise:

1. an unpaired median *rostro-interrostral*, covering the most anterior and median part of the dorsal side of the snout. The rostro-interrostral is approximately square in shape and most often has a rounded posterior margin (*Ichthyostega watsoni*, pl. VI, fig. 1; *I. eigili* pl. IX; *Ichthyostega? kochi*, pl. XX) but in *Ichthyostega stensiöi* (pls. I, II) it has a posterior angle, at least on the ventral side of the skull-roof. The growth-centre of the rostro-interrostral is always situated near the anterior margin of the bone.

The rostro-interrostral must obviously have been connected with the median part of the anterior commissure (ethmoidal part) of the infraorbital sensory canals, if such a commissure was at all developed; and it seems most probable (cf. p. 86), that such a commissure of the infraorbital canals was situated just below the most anterior marginal part of the rostro-interrostral and that its tubules traversed this part of the bone to end in pores on the dorsal surface of the skull-roof. Traces of such tubules have been found in *Ichthyostega stensiöi* (p. 14) and in *Ichthyostega eigili* (p. 53).

Thus the name of the rostro-interrostral is obviously justified in regard to its rostral component. The latter half of the name will be seen, by comparison of the dermal cranial roof of *Ichthyostega stensiöi* with that of the Crossopterygian *Dictyonosteus articus* Stensiö (see text-figs. 1 B, 16 B), to be justified at least in the mentioned species of *Ichthyostega*. In the two other species of that genus the bone termed by me rostro-interrostral is markedly shorter and may be only a median rostral. It is, of course, sometimes difficult to make out the exact homologue of a dermal bone that is, like the interrostral in the Crossopterygians, characterized by its topographical relations alone, and not by any connection with a definite part of the lateral line system. One argument for using the term rostro-interrostral also for the bone in *Ichthyostega watsoni* and *Ichthyostega eigili* is the absence of any median element posterior to it on the snout.

2. On each side postero-laterally to the rostro-interrostral there is an elongate, roughly rectangular lateral rostral element, fused with the premaxillary to a *rostro-premaxillary*, in which it is, however, still easy to distinguish the tooth-bearing component from the rostral, canal-bone component, at least when the bone is somewhat completely preserved, as in *Ichthyostega watsoni* (p. VI, fig. 1) and *Ichthyostega eigili* (pls. IX, X, XI; pl. XII; fig. 1; pl. XIII). — The rostral component of the rostro-premaxillary (*R. pmxc*, pl. VI, fig. 1; pl. IX) shows the growth-centre to be situated near the lateral margin of the bone and is traversed, in *Ichthyostega eigili*,

by several vertical canals, originating from a groove running below the most lateral marginal part of the rostral component, between this and the tooth-bearing component, of the rostro-premaxillary. This groove conceivably lodged the lateral parts of the anterior commissure or ethmoidal part of the infraorbital sensory canal, the tubules of which were apparently situated in the above-mentioned vertical canals.

The tooth-bearing component of the rostro-premaxillary is best shown in *Ichthyostega eigili* (*R. pmxd*, pl. XI; pl. XII, fig. 1; pl. XIII). It lies entirely on the ventral side of the skull-roof and has a vertical lateral side with a pitted sculpture, like that of the external surface of the dermal bones of the cranial roof. With its most anterior part the tooth-bearing component of each rostro-premaxillary underlies the rostro-interrostral in the same way as it underlies, farther postero-laterally, the canal-bone component of the rostro-premaxillary. The teeth of the rostro-premaxillary are only partially preserved in our material, but are evidently long, pointed and conical or slightly compressed from their labial and lingual sides. There seem to be two different types of teeth in the rostro-premaxillary, one smaller, at least often slightly curved, and more slender type, and another larger, straighter, and apparently stouter type. To the latter type belong a few of the more posterior teeth in the rostro-premaxillary.

3. Posterior to the rostro-interrostral and rostral components of the rostro-premaxillaries, the snout is covered by a paired large *naso-postrostral*, much broader anteriorly than posteriorly and with a long postero-lateral side. The growth-centre of each naso-postrostral is situated in the posterior half of the bone.

As the two naso-postrostrals meet in a median suture, it is certain that each of them contains a medial postrostral component. In *Ichthyostega watsoni* and *I. eigili* they also possibly contain in their most anterior parts the homologue of the interrostral of the Crossopterygians, if that element does not enter into the bone called rostro-interrostral in the descriptions (cf. above p. 73). — But the term naso-postrostral also presupposes that a part of the bone in question is traversed by the supraorbital sensory canal. This supposition depends upon the discovery, in *Ichthyostega stensiöi* (p. 22) and *I. watsoni* (p. 40), of a row of ventral openings to canals and pieces of canals (*c*, pl. I; pl. VI, fig. 1), situated in the naso-postrostrals near the ventral surface of those bones, in a slightly antero-laterally directed line from the posterior to the anterior margin of each bone and nearly along the middle of its breadth. These canals, as emphasized on p. 22, may most naturally be supposed to have transmitted vessels and nerves to an anterior part of the supraorbital canal.

4. The central parts of the dorsal side of the skull are covered by two long and narrow, roughly rectangular *frontals* (*Fr*, pls. I, II, III;

pl. VI, fig. 1; pl. XVIII) meeting the naso-postrostrals anteriorly. The median suture between the frontals is not directly continous with the median suture between the naso-postrostrals. The growth-centre of each frontal seems to have been situated near the mid-point of the bone.

In the specimen of *Ichthyostega? kochi* the lateral half of the right frontal is seen to be traversed by a part of the supraorbital canal (see pl. XX and Pl. XXI, fig. 1!).

5. Posterior to the rostral component of each rostro-premaxillary and laterally to each naso-postrostral there is a square or pentagonal small *anterior antorbital* (*A*, pls. I, II; pl. IV, fig. 1; pl. VI, fig. 1; pls. IX, X, XI; pl. XII, fig. 1; pl. XIII). The growth-centre of this bone is situated near the lateral margin of the bone.

The anterior antorbital lies dorsal to the external naris (see pl. XIII) and consequently the greater part of it can not have been connected with the anterior commissure of the infraorbital canals, which must have passed ventral to the external naris. However, (as mentioned on p. 16) it is not quite impossible (though rather improbable) that the most anterior part of the bone may have been connected in some way with a short part of the anterior commissure of the infraorbital canals in front of the external naris, and may thus comprise a very small rostral component. But at least the greater part of the bone is made up by a component from the more dorso-medially situated series, and the comparison with younger Stegocephalians (pp. 100—102) will show that it is an anterior antorbital component. The supraorbital canals, as is also mentioned below (p. 83), have certainly been situated far more dorso-medially. The variation in the postero-medial extension of the anterior antorbital has been treated of in the descriptions of the species *Ichthyostega stensiöi* (pp. 15—16), *I. watsoni* (p. 35) and *I. eigili* (p. 46).

6. Between each naso-postrostral and the orbit there is a rather large *posterior antorbital* (*Ant.* pls. I, II, III; pl. VI, fig. 1; pls. IX, X, XI; pl. XVI, fig. 1; pl. XVII, fig. 1; pls. XVIII, XX, XXI), suturally connected with the long straight postero-lateral margin of the naso-postrostral. The lateral margin of the posterior antorbital is more or less markedly concave. In *Ichthyostega stensiöi* and *I. eigili* the posterior antorbital has a narrow antero-lateral process, which in the former species meets the anterior antorbital in a short suture. The posterior antorbital has a greater backward extension in the genus *Ichthyostega* than in the genus *Ichthyostegopsis*, owing to the forward extension of the large orbits in the latter.

The growth-centre of the posterior antorbital is situated near the straight medial margin of the bone.

The determination of this bone as an antorbital is due to its position in relation to the orbit and especially to the probable course of the supra-

orbital sensory canal as described above and the below described, certain course of the suborbital part of the infraorbital sensory canal.

7. In the type-specimen of *Ichthyostega stensiöi* there is clearly shown to be an independent, triangular *anterior supraorbital* (So_1, pls. I, II) wedged in between the orbit, the posterior antorbital, and the frontal. In the other Ichthyostegids also this bone is probably independent, though this could not be determined with certainty on the available material.

So far there have been detected no traces of any sensory canal in the anterior supraorbital, and the course of the preserved parts of the supraorbital canals in *Ichthyostega? kochi* makes it certain that the greater part, at least, of the anterior supraorbital is not connected with the canal in question. It is, however, still possible that the most anterior end of the so-called anterior supraorbital is traversed by the supraorbital canal and thus presents a most posterior nasal element. In so far as this is not proved, it seems most natural to call the bone an anterior supraorbital, though it is not quite out of the question, that it may be a naso-supraorbital.

8. The posterior half of each frontal is excluded from the orbit by the anterior half of the long *posterior supraorbital* (So_2, pls. I, II, III). In *Ichthyostega stensiöi*, *Ichthyostega*? sp. b. and possibly in *Ichthyostega? kochi* this bone is thickened to form a swelling dorso-medial to the orbit, whereas in *Ichthyostegopsis* it shows a flatter orbital surface.

As the course of the posterior parts of the supraorbital sensory canal could not be determined with certainty in the present material there is, of course, a possibility that the bone called by me the posterior supraorbital contains also a frontal component traversed by the supraorbital canal. It seems, however, most probable on account of the shape of the bone in question that it is a homologue of the (posterior) supraorbital in *Osteolepis*, as will be readily seen by comparison of text-figs. 16 A and C, both given in the next chapter. *Ichthyostegopsis wimani* also furnishes facts that enable us to say that the supraorbital canal in that form probably ran near but medially to the medial margin of the posterior supraorbital (see p. 70).

9. Behind the frontals and medially to the posterior halves of the posterior supraorbitals, the dorsal side of the skull is covered by the anterior halves of the *fronto-parietals* (*Pa*, pls. I, II; pl. IV, figs. 2, 3; pl. XVI, fig. 2; pl. XVII, fig. 1; pls. XVIII, XX). Each of these bones has a narrower anterior and a broader posterior part. The posterior part has an approximately semicircular notch in its medial margin, to form with the notch in the corresponding bone of the other side a round, rather large pineal foramen. In the genus *Ichthyostegopsis* the two fronto-parietals are completely separated by a median suture, which in the genus

Ichthyostega seems to be developed only in front of the pineal foramen. This median suture is not continous with the median suture between the frontals. The growth-centre of each fronto-parietal is situated laterally to the pineal foramen.

As the bone, called by me the posterior supraorbital, seems from a comparison with the Crossopterygians most probably not to have been traversed by the supraorbital canal, the posterior parts of that canal must conceivably have traversed at least the anterior half of the fronto-parietal, which must then contain in its anterior half a frontal component. This theory is strongly supported by the similar position of the anterior parts of the bones in question and the frontals of the Crossopterygians in relation to the orbits and posterior supraorbitals and by the position of the pineal foramen, though, of course, the questions relating to the position and morphological importance of the pineal foramen cannot be discussed completely in so far as the endocranium of the forms has not been subjected to close investigation. That there is also a parietal component in the fronto-parietal is indicated by the relations of that bone to the anterior half of the supratemporo-intertemporal (cf. *Osteolepis* see below, text-fig. 16!)

10. Behind the orbit and posterior supraorbital, and laterally to the middle part of the fronto-parietal, there is on each side an irregularly formed *postorbito-dermosphenotic*, somewhat well preserved only in the material of *Ichthyostega stensiöi* (*Po. dsph*, pls. I, II), in *Ichthyostega*? sp. b. (*Po. dsph*, pl. XVI, fig. 2), and in *Ichthyostegopsis wimani* (*Po. dsph*, pl. XVI, fig. 1; pl. XVII, fig. 1; pl. XVIII). In the latter genus this bone is rather broad, but in the available material of *Ichthyostega* it is markedly longer than broad. The growth-centre of this bone is situated nearer its medial than its lateral margin.

In *Ichthyostega*? sp. b, *Ichthyostega*? *kochi*, and *Ichthyostegopsis wimani* the postorbito-dermosphenotic is clearly shown to be traversed by the suborbital part of the infraorbital canal (*ifc*, pl. XVI, fig. 2; pl. XVII, fig. 1; pl. XVIII; pl. XXI, fig. 2). This fact and the position of the bone in relation to the orbit and posterior supraorbital evidently justify the name postorbito-dermosphenotic (cf. *Osteolepis*, see below, text-fig. 16!).

11. The postero-medial margin of the postorbito-dermosphenotic and the postero-lateral margin of the fronto-parietal are suturally connected with the anterior part of the *supratemporo-intertemporal*. That bone is roughly square in *Ichthyostega eigili* (*St. it*, pl. IX) and possibly also in *Ichthyostega*? sp. b. (*St. it*, pl. XVI, fig. 2), whereas in *I. stensiöi* (*St. it*, pls. I, II) and *Ichthyostegopsis wimani* n. sp. (*St. it*, pl. XVIII) it has a narrow anterior process, or a markedly narrower anterior part, and a much broader posterior part. The growth-centre of the supratemporo-intertemporal is situated approximately in the mid-point of the bone.

No traces of the otic part of the infraorbital canal or of the postotic canal[1]) have as yet been found in an Ichthyostegid. The name supratemporo-intertemporal is due to the topographical relations of the bone under question as compared with the corresponding bones in Crossopterygians (cf. below p. 90).

12. The middle of the posterior marginal part of the dorsal side of the skull is covered by an unpaired median bone, the *parieto-extrascapular*. This bone is well preserved in *Ichthyostega eigili* (*Ext. m*, pl. IX) and especially in *Ichthyostegopsis wimani* (*Ext. m*, pl. XVII, fig. 1; pl. XVIII). It is broad in the latter form and apparently narrower in *Ichthyostega*. It has mainly convex lateral sides and a slightly convex anterior side, connected by suture with the posterior margins of the fronto-parietals. The anterior halves of its lateral sides are connected by sutures with the posterior halves of the medial sides of the supratemporo-intertemporals. The growth-centre of the parieto-extrascapular is situated in the median line of the skull and in the posterior half of the bone.

No lateral line canal has as yet been found in this bone. Its name is however justified by comparison with the corresponding bone in Crossopterygians as far as regards the extrascapular component, and if we are right in our naming of the supratemporo-intertemporal, its anterior part is homologous with the posterior parts of the parietals in the Crossopterygians, as anteriorly it lies medially to the posterior half of the bone, we have called the supratemporo-intertemporal. This question will be further discussed in the next chapter (pp. 90, 94).

13. Laterally to the posterior half of the parieto-extrascapular and posterior to the supratemporo-intertemporal the skull is covered by a *lateral extrascapular* (*Ext. l.*) of somewhat varying shape. There may always be distinguished three laminae of the lateral extrascapular, one dorsal horizontal lamina, one lateral vertical lamina, and one posterior (*Ichthyostegopsis*, *Ext. l, l. p*, pl. XVII, fig. 1) or postero-medial vertical lamina (*Ichthyostega watsoni*, *Ext. l, l. pm*, pl. VI, fig. 1; *I. eigili*, *Ext. l, l. pm*, pl. IX). In *Ichthyostega watsoni* and *I. eigili* there are traces of a posterior process (*Ext. l, pr. p;* pl. VI, fig. 1; pl. IX) projecting from the posterior end of the postero-medial lamina of the lateral extrascapular. This posterior process possibly served, as the similar "tabular horns" of the *Anthracosauroideae*, for the attachment of the shoulder girdle (cf. WATSON, 1926, a, p. 234; 1926 b, pp. 222, 226, fig. 4). A curious, gutter-shaped ventral process of the lateral extrascapular is seen in the Ichthyostegid sp. a (pl. V, fig. 2; *Ext. l, pr. v*, pl. VI, figs. 2, 3), in which it has been most completely exposed and described, in *Ichthyostega watsoni*, (*Ext. l, pr. v*, pl. VI, fig. 1; pl. VIII) and in *Ichthyostegopsis wimani* (*Ext. l, pr. v*,

[1]) The lateral line canal innervated by the dorsal branch of the n. glossopharyngeus; see SÄVE-SÖDERBERGH 1932 b.

pl. XVII, fig. 2). — The growth-centre of the lateral extrascapular is situated at the most dorso-postero-lateral point of the skull-roof, at the meeting-point of the three laminae of the bone.

Though no lateral line canal has been as yet detected with certainty (cf. p. 18, *Ichthyostega stensiöi*) in the lateral extrascapular, the topographical position of the bone makes it fairly certain that it is the homologue at least of a part of the bone with the same name in Crossopterygians. Whether it contains also other components (possibly a part homologous with the suprascapular of fishes) cannot yet be decided.

14. Posterior to each anterior antorbital, and laterally to each posterior antorbital, there is an elongate *lachrymal* (*La*, pls. I, II, III; pl. IV, fig. 1; pl. VI, fig. 1; pls. IX, X, XI; pl. XII, fig. 1; pl. XVI, fig. 1; pl. XVIII) with a more or less markedly convex medial margin, and in *Ichthyostega watsoni* (pl. VI, fig. 1), *I. eigili* (pl. IX) and also in *Ichthyostegopsis wimani* (pl. XVIII), extending forward to meet the naso-postrostral in a short suture. In *Ichthyostega stensiöi* the lachrymal has a straight anterior margin and does not meet the naso-postrostral. — The growth-centre of the lachrymal is situated nearest to the lateral margin of the bone.

The lachrymal is seen to be traversed by the suborbital part of the infraorbital canal in *Ichthyostega stensiöi* (*ifc*, pls. I, II), in *I. watsoni* (*ifp*, pl. VI, fig. 1) in *I. eigili* (*ifp*, pl. IX; *ifc*, pl. XII, fig. 2; pl. XIV), and in *Ichthyostegopsis wimani* (pl. XVIII). On account of this and its topographical relations to the external naris and the orbit, the bone in question must obviously be termed a lachrymal and be a homologue of the same bone in Crossopterygians (cf. below text-fig. 16!).

15. Behind the lachrymal, and laterally to the orbit and the post-orbito-dermosphenotic, there is a very long and large *jugal* (*Ju*, pls. I, II; pl. VI, fig. 1; pls. IX, X, XI, XIV; pl. XVI, fig. 1; pls. XVIII, XIX), narrower anteriorly and broadening behind the orbit. In the genus *Ichthyostega* the jugal meets the posterior antorbital, and the anterior suture of the jugal with the lachrymal, is situated in front of the orbit, whereas in *Ichthyostegopsis* the same suture is situated laterally to the orbit, a fact that has already been pointed out in the foregoing chapter (cf. p. 72) and that will be further mentioned below (p. 90).

The growth-centre of the jugal is situated near the mid-point of the lateral margin of the bone.

The jugal has been ascertained to be traversed by the suborbital part of the infraorbital canal in *Ichthyostega stensiöi* (*ifc*, pls. I, II), in *Ichthyostega watsoni* (*ifc*, pl. VI, fig. 1), in *Ichthyostega eigili* (p. 53) in *Ichthyostega?* sp. b. (*ifc*, pl. XVI, fig. 2), and in *Ichthyostegopsis wimani* (*ifp*, pl. XVI, fig. 1; *ift*, *ifp*, pl. XVII, fig. 1; *ifc*, *ifp*, pl. XVIII; *ifc*, *ifp*, *ift*, pl. XIX). The anterior part of the jugal canal has been found in the

jugal of the Ichthyostegid sp. a. (*juc*, pl. V, fig. 2), of *Ichthyostega eigili* (*juc*, pl. IX; *jut*, pls. X, XI), and of *Ichthyostegopsis wimani* (pl. XVIII; *juc*, pl. XIX). All this justifies the name given to the bone in question.

16. Behind the jugal and postorbito-dermosphenotic, and laterally to the supratemporo-intertemporal and lateral extrascapular, there is on each side an elongate, roughly oval or irregularly formed *squamosal* (*Sq*, pls. I, II; pl. V, fig. 2; pl. XVI, fig. 1; pl. XVII, fig. 1; pls. XVIII, XIX), which is rigidly connected by suture both with the supratemporo-intertemporal and with the lateral extrascapular (see especially the Ichthyostegid sp. a, pl. V, fig. 2 and VI, fig. 2, and *Ichthyostegopsis wimani*, pl. XVIII). The squamosal with its postero-medial margin forms the lateral margin and half of the anterior margin of the otic notch. The growth-centre of the squamosal is situated nearer to the medial than to the lateral margin of the bone.

In the Ichthyostegid sp. a, in *Ichthyostega eigili*, and in *Ichthyostegopsis wimani*, there has been found in the squamosal a posterior part of the jugal canal (*juc*, pl. V, fig. 1; *juc*, *jut*, pls. IX, X, XIV; *juc*, pls. XVIII, XIX), and traces, probably of the same canal, are to be seen in the squamosal of *Ichthyostega watsoni* (*juc*?, pl. VI, fig. 1). These facts and the above-described topographical relations of the bone in question wholly justify the name given to it.

17. In the Ichthyostegid sp. a, which shows an extremely well preserved posterior part of a cheek, there is, behind the squamosal and laterally to the most posterior part of the otic notch, an independent, small, elongate *preopercular* (*Pop*, pl. V, fig. 2) with rounded, broadened, antero-medial and postero-lateral ends and a narrower middle part. In the latter part is situated the growth-centre of the bone. — It could not be determined in the present material whether there is an independent preopercular also in the other Ichthyostegids. If not, this element fused in the other Ichthyostegids with either the squamosal or the quadrato-jugal or both these bones, or it may, at least partly, have failed to ossify.

The preopercular in the Ichthyostegid sp. a, is traversed by the preopercular sensory canal (*poc*, pl. V, fig. 2) and evidently occupies the same position as the similarly small preopercular in *Osteolepis* (cf. below, text-fig. 16; cf. also STENSIÖ 1932, text-fig. 17).

18. The postero-lateral part of the cheek, posteriorly to the jugal and laterally to the squamosal, is covered by the *quadratojugal*. This bone is most clearly shown in the Ichthyostegid sp. a, (*Quj*, pl. V, fig. 2) and approaches complete preservation only in that specimen and on the left side of the specimen of *Ichthyostega eigili* (*Quj*, pls. IX, X). The quadratojugal is an elongate bone with a long straight ventro-lateral and ventro-posterior free margin, a short anterior suture with the jugal,

and a long medial suture with the squamosal. At least in the Ichthyostegid sp. a, the quadratojugal has a posterior suture with the preopercular. The growth-centre of the quadratojugal is situated near the posterior half of the ventro-lateral margin of the bone.

In *Ichthyostegopsis wimani* there have been found in the quadratojugal portions of canal, probably belonging to a *quadratojugal sensory canal*, homologous with the vertical pit-line of the cheek found in fishes and, as is especially important, in connection with the quadratojugal of Crossopterygians (see below text-fig. 16 and SÄVE-SÖDERBERGH 1932 b). But even without the evidence furnished by this canal the position of the bone in question in the Ichthyostegids, in relation to the other already described and well-characterised bones of the cheek, excludes all doubt as to the correctness of the name given to it.

19. On each side of the skull there is a very long *maxillary* (*Mx*, pls. VII, VIII, IX, XI; pl. XII, fig. 1; pl. XIII; pl. XVI, fig. 1; pl. XVII, fig. 2, pl. XVIII), suturally connected with the ventral margins of the quadratojugal (pl. V, fig. 2), the jugal, and the posterior half of the lachrymal, and extending forward also below the anterior half of the lachrymal and below the anterior antorbital, to form with its most anterior part the lateral and anterior margin of the internal nostril (*n. i*, pl. VIII) and the posterior margin of the external nostril (*n. e*, pls. VIII, XIII). Except in the part that forms the posterior margin of the external nostril, the vertical lateral side of the maxillary has a sculpture like that of the same side of the tooth-bearing part of the rostro-premaxillary and of the external sides of the dermal bones of the dorsal side of the skull. Along its whole length the maxillary is armoured with long, pointed, conical or slightly compressed labyrinthine teeth, of various sizes, but markedly smaller in the most posterior part of the bone.

Dermal bones of the palate.

The palate of the Ichthyostegids is extensively ossified. Its openings are: a broad, short anterior palatal vacuity (*apv*, pl. IV, fig. 1; pls. VIII, XIV, XV), rather narrow, elongate, and widely separated internal nares (*n. i*, pl. IV, fig. 1; pls. VIII, XIV, XV; pl. XVII, fig. 2), medium-sized adductor fenestrae ("subtemporal fossae", fenestrae basitemporales), and very narrow interpterygoid vacuities. The dermal bones composing the palate are as follows:

1. The anterior and antero-lateral part of each side of the palate posterior to the anterior palatal vacuity, medially to the external naris and to the anterior half of the internal naris is ossified as a large elongate *vomer* (*Vo*, Pl. IV, fig. 1; pls. VIII, XV; pl. XVII, fig. 2), which meets its fellow of the other side in a median suture extending as far

back as the middle of the length of the bones. The lateral margin of the vomer has a suture with the rostro-premaxillary most anteriorly. Posterior to this suture the vomer has a vertical, lateral side divided into three portions. The anterior portion forms the medial boundary of the external naris (*n. e*, pl. VIII); the middle portion is produced into a spoon-like process for the attachment of the anterior end of the maxillary, and is most clearly shown on the left side in pl. VIII; finally the posterior, longer portion of the lateral side of the vomer forms the medial boundary of the internal naris (*n. i*, pl. VIII). — In *Ichthyostega watsoni* there has been found in the right vomer the base of a labyrinthine tooth (cf. p. 39), situated medially to the anterior portion of the vertical lateral side of the bone. Traces of at least one similar but more posteriorly situated tooth are found in the left vomer of *Ichthyostega eigili*, just medially to the internal naris (pl. XIV). — The growth-centre of each vomer is situated near the middle portion of the lateral margin of the bone.

2. Posteriorly to the vomer, and medially to the posterior part of the internal naris and to the middle part of the maxillary, there is on either side of the palate a rectangular *dermopalatine* (*Dpl*, pl. IV, fig. 1; pls. VIII, XV; pl. XVII, fig. 2), which is markedly smaller than the vomer. The anterior part of the lateral margin of the dermopalatine forms the posterior part of the medial boundary of the internal naris; the posterior part of the lateral margin of the bone is connected by suture with the middle part of the maxillary. In *Ichthyostegopsis wimani* there are seen two teeth in the dermopalatine (*dp*, pl. XVII, fig. 2), situated directly posterior to the internal naris. — The growth-centre of each dermopalatine is situated near the lateral margin of the bone.

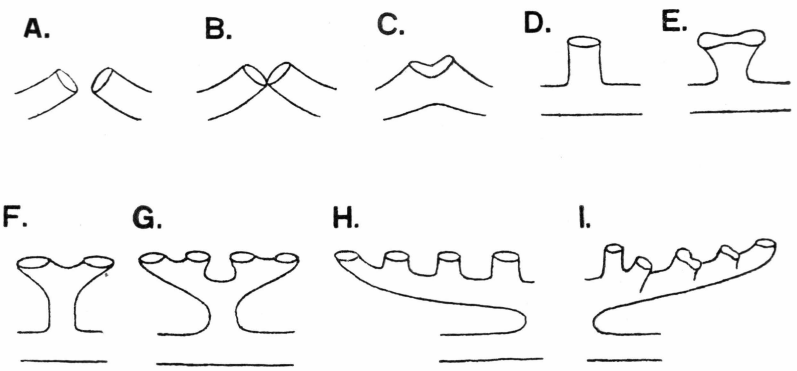
3. Between the posterior margin of the dermopalatine, the posterior part of the maxillary and the lateral part of the anterior margin of the adductor fenestra, there is on each side a long, rectangular *ectopterygoid* (*Ecpt*, pls. VIII, XV) connected by suture with the enumerated bones. Its growth-centre is situated, much as that of the dermopalatine, near the lateral margin of the bone.

4. The part of each half of the palate between the above-described three bones and the interpterygoid vacuities is ossified as the palatal ramus of the enormous *entopterygoid* (*Enpt*, pl. IV, fig. 1; pls. VIII, XV; pl. XVII, fig. 2; pl. XXII). Anteriorly this bone meets its fellow in a median suture, posteriorly it has a vertical quadrate ramus which is curved round laterally to form the medial and postero-medial wall of the adductor fossa and to meet the squamosal and preopercular or quadratojugal. — The growth-centre of each entopterygoid is situated near the medial margin of the bone, medially to or a little more anteriorly than the anterior margin of the adductor fenestra.

5. The narrow space between the posterior parts of the medial margins of the palatal rami of the entopterygoids is for the greater part filled by the long, gutter-shaped processus cultriformis of the *parasphenoid* (*Psph*, pl. IV, fig. 1; pl. XV). The posterior parts of this bone will be discussed in connection with the endocranium of the Ichthyostegids.

Lateral line system of the head.

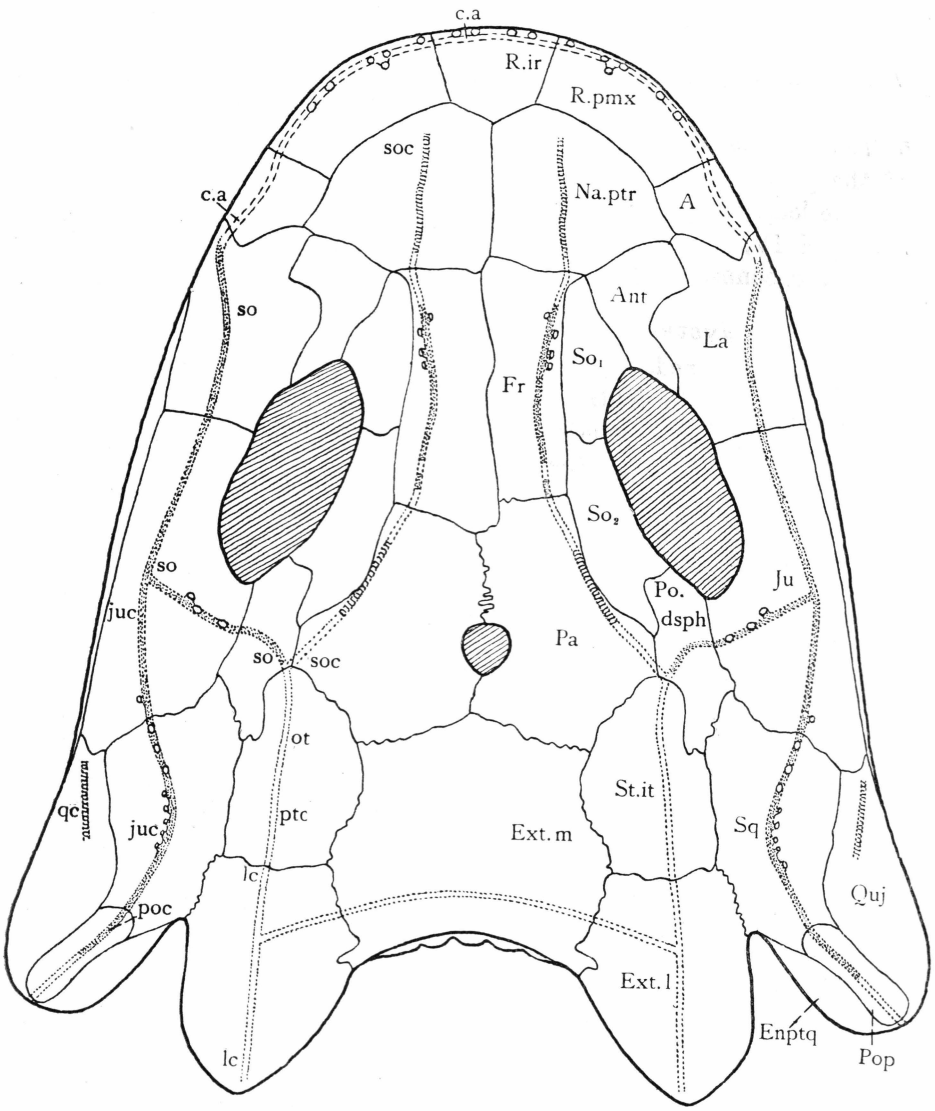
As already mentioned, at least the greater part of the lateral line system of the head in the Ichthyostegids was situated in closed canals in the dermal bones. These canals open outwards by short tubules into superficial pores, and the part of the canal between each two consecutive



Text-fig. 14. Scheme of development of lateral line canals. From Allis 1889. In A and B, the ends of two primordial canals approaching each other; in C, a primary pore formed at the junction between the two primordial canals; in D, a primary tube formed and the primordial canals straightened out to form a continuous compound canal. E—I, subdivision of the primary tube and pore into a system of tubes and a group of pores.

tubules is slightly curved (see especially pl. XIX and pl. XXI, fig. 1) in a way that suggests that the lateral line canals have had a similar ontogenetic development as that in *Amia* (Allis, 1889, p. 523): thus it is likely that one primordial canal developed around each primary organ by an invagination, beginning nearest to the primary organ and then extending in the directions of the two nearest developing primordial canals, with which it finally fused to form at each of its ends a primary pore and tube. But the original, slightly curved shape of the primordial canal developing around each primary organ is retained in the Ichthyostegids, whereas in *Amia* the primordial canals apparently lose their individuality by a straightening of the compound canal.

That is to say, the lateral line system of the Ichthyostegids does not reach the stage D in the scheme of development given above (text-fig. 14), whereas in *Amia* the system reaches the stages H and I (text-fig. 14). A shape of the canals similar to that in the head of the Ichthyostegids is,



Text-fig. 15. Attempted restoration of the lateral line system of the head in an Ichthyostegid.

A, anterior antorbital; *Ant*, posterior antorbital; *Enptq*, quadrate ramus of entopterygoid; *Ext. l*, lateral extrascapular; *Ext. m*, parieto-extrascapular; *Fr*, frontal; *Ju*, jugal; *La*, lachrymal; *Na. ptr*, naso-postrostral; *Pa*, fronto-parietal; *Po. dsph*, postorbito-dermosphenotic; *Pop*, preopercular; *Quj*, quadratojugal; *R. ir*, rostro-interrostral; *R. pmx*, rostro-premaxillary; So_1, anterior supraorbital; So_2, posterior supraorbital; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *c. a*, anterior commissure of the infraorbital canals; *juc*, jugal canal; *lc*, cephalic division of main lateral line canal; *ot*, otic part of the infraorbital canal; *poc*, preopercular canal; *ptc*, postotic canal; *qc*, quadratojugal canal; *so*, suborbital part of the infraorbital canal; *soc*, supraorbital canal.

The sensory canal parts actually observed in the present material are denoted by a dotted outline and dotted shading. The sensory canal parts which probably are present but which have not been observed with full certainty are denoted by dotted outline and cross-shading. The sensory canal parts of which no traces have been found as yet are denoted by dotted outlines; these parts have been reconstructed after the conditions in the Crossopterygians. The supposed course of the canals lying wholly ventrally to the dermal cranial roof is indicated by broken outlines.

however, evidently found in the main lateral line canal of *Amia*, as may be gathered from ALLIS, 1889, fig. 48, pl. 41, as compared with our pl. XXI, fig. 1.

The *supraorbital canal* has been observed with certainty only in the right frontal of *Ichthyostega? kochi* (p. 59, pl. XX, XXI, fig. 1) but its probable course in the naso-postrostral is indicated by a row of canals or openings to canals, found in *Ichthyostega stensiöi* (*c*, pls. I, II, III) and *Ichthyostega watsoni* (*c*, pl. VI, fig. 1) and stretching from near the point where the naso-postrostral meets the frontal and posterior antorbital towards the anterior margin of the naso-postrostral (cf. p. 22 and text-fig. 19). Posterior to the frontal the supraorbital canal probably pierced the fronto-parietal, near the suture between that bone and the posterior supraorbital (see above, *Ichthyostegopsis wimani*, p. 70).

Of the *infraorbital canal* only traces of the suborbital part and the anterior commissure have been found as yet in the Ichthyostegids, whereas the otic part of the infraorbital canal is still unknown.

For purposes of description the suborbital part of the infraorbital canal may be considered to consist of three portions: one vertical, most postero-medial portion from the otic part to the connection with the jugal canal, one horizontal portion from the said connection to the posterior end of the ethmoidal part, and a third portion constituted by the post-nasal connection between the infraorbital and supraorbital canals.

The most postero-dorsal parts found of the suborbital part of the infraorbital canal in the present material are the portions of canal shown in the postorbito-dermosphenotic of *Ichthyostega? kochi* (*ifc*, pl. XX; pl. XXI, fig. 2), and of *Ichthyostega?* sp. b, (pl. XVI, fig. 2), and further the pores in the same bone of *Ichthyostegopsis wimani* (pl. XVIII).

In the jugal of *Ichthyostega?* sp. b, there is preserved a short ventro-laterally directed piece of the vertical portion of the suborbital part of the infraorbital canal, but in *Ichthyostegopsis wimani* the corresponding part and its continuation towards the growth-centre of the jugal is much more clearly shown, with at least three primary tubes preserved (*ifc*, pl. XVIII; *ifc*, *ift*, pl. XIX). Around the growth-centre of the jugal in *Ichthyostegopsis wimani* there is a group of four pores (see pl. XIX), conceivably belonging to the part of the infraorbital canal connected with the anterior end of the jugal canal, or to the anterior part of that canal. Between this group and the portion of the infraorbital canal shown in pl. XIX there are two other pores belonging to the vertical portion of the suborbital part of the infraorbital canal.

The course of the horizontal portion of the suborbital part of the infraorbital canal is shown clearly in our material as far forward as the anterior part of the lateral margin of the lachrymal, and is indicated by the position of at least six pores in the jugal and nine pores in the

lachrymal of *Ichthyostegopsis wimani* (p. 70, pl. XVIII), by a portion of canal in *Ichthyostega stensiöi* (*ifc*, pls. I, II), by portions of canals and pores in *Ichthyostega watsoni* (*ifc*, *ifp*, pl. VI, fig. 1), and by a well-preserved portion of canal with tubules and pores in the lachrymal of *Ichthyostega eigili* (*ifp*, pl. IX; *ifp*, *ifc*, pls. X, XI; *ifc*, *ift*, *ifp*, pl. XII, fig. 2; *ifc*, pl. XIV), where there is shown to be a group of pores round the growth-centre of the lachrymal similar to that round the growth-centre of the jugal in *Ichthyostegopsis*.

No trace of the post-nasal connection between the infraorbital and the supraorbital canal has been found in the present material.

Owing to the position of the external naris, described above (p. 72), the anterior, ethmoidal part of the infraorbital canal must have left the skull-roof at the anterior end of the lachrymal, to curve down laterally to the anterior end of the maxillary (see text-fig. 8!). Then it certainly went ventrally to the external naris, and in front of this it conceivably rose dorsally along the lateral side of the tooth-bearing part of the rostro-premaxillary, to reach a groove between this and the laterally projecting margin of the rostral part of the rostro-premaxillary (see above pp. 53—54, text-fig. 8!). Imbedded in this groove the ethmoidal part of the infraorbital canal conceivably ran round the snout, lying laterally to the dorsal border of the vertical side of the tooth-bearing part of the rostro-premaxillary and ventral to the anterior and lateral borders of the rostro-interrostral and rostral part of the rostro-premaxillary, which are pierced by tubules conceivably belonging to the sensory canal in question (see especially pl. IX and pl. XIII).

The *jugal canal* is very clear in the Ichthyostegid sp. a (*juc*, pl. V, fig. 2), indicated by probable traces in *Ichthyostega watsoni* (*juc*?, pl. VI, fig. 1), and by traces of canals and two tubules in *Ichthyostega eigili* (*juc*, pls. IX, XIV; *jut*, pl. X, XI), but it is shown with exceptional clearness in *Ichthyostegopsis wimani* (*juc*, pls. XVIII, XIX!). As seen in *Ichthyostega eigili* and as may be also inferred from the position of the pores in *Ichthyostegopsis wimani*, the jugal canal is directly continuous anteriorly with the horizontal portion of the suborbital part of the infraorbital canal. Hence its most anterior part has a straight posterior or even slightly postero-lateral direction, but farther back the jugal canal is gently curved to a more postero-medial direction, which is retained when the canal passes from the jugal on to the squamosal. It is then directed towards the growth-centre of the squamosal; but a little before reaching this centre the jugal canal is again gently curved, this time in a more postero-lateral direction, to join the preopercular canal. — In the extremely well preserved portion of the jugal canal exposed in *Ichthyostegopsis wimani* (pl. XIX) there are at least nine primary tubes along the stretch from a little in front of the jugal-squamosal suture back

to the beginning of the postero-laterally directed part of the canal, and farther forward there must be at least two pores belonging with certainty to the jugal canal. Thus the jugal canal in *Ichthyostegopsis* had at least eleven primary tubes and pores and contained at least twelve primary sense-organs.

The *preopercular canal* is only shown as a groove in the preopercular of the *Ichthyostegid* sp. a (pl. V, fig. 2), and is probably enclosed in the postero-lateral half of that bone.

The possible traces of a *quadratojugal canal* found in the quadratojugal of *Ichthyostegopsis wimani* are as yet too uncertain to permit of any conclusion and the elucidation of the question as to the existence of this canal forms a point of extraordinary interest. It is also hoped that further collecting will secure specimens in which it will be possible to find traces of the as yet wholly unknown *postotic canals* and *supratemporal commissural canal*, and certain traces of the *main lateral line canals* (cf. pp. 18, 22) of the *Ichthyostegids*.

I would also point out here once more the many interesting questions that remain open for further investigation concerning the organisation of the dermal bones and lateral line system in the Ichthyostegids. The facts revealed by the relatively few parts of the lateral line system (shown on pl. XII, fig. 2; pl. XIX and pl. XXI, fig. 2) that are exposed in an approximately complete state render it probable that a larger material of Ichthyostegids will permit of a complete account of the organisation of the lateral line system of these forms, comprising the number of primary tubes and primary organs in each part of the system.

VI. Some points of comparison with certain primitive Crossopterygians and Dipnoans.

Already in the foregoing chapter I have been obliged to refer several times to the Crossopterygians, when discussing the most adequate mode of naming the different dermal bones of the Ichthyostegids. A study of some very fine material of *Osteolepis macrolepidotus* Agassiz (belonging to the Palaeontogical Institution of Uppsala), on which I am preparing a paper (1932 b), enables me to use for the comparison a Crossopterygian, with which I am personally acquainted. Certain points in the organisation of this species, not mentioned before in the literature or differently described by different authors (Pander 1860; Watson and Day 1916; Goodrich 1919; Watson 1926) are clearly displayed in the material at my disposal and in part greatly facilitate a comparison with the Ichthyostegids.

Text-figure 16 is intended to illustrate a comparison between the arrangement of the dermal bones of the dorsal side of the skull of the Ichthyostegids and that found in the Crossopterygians *Osteolepis* and

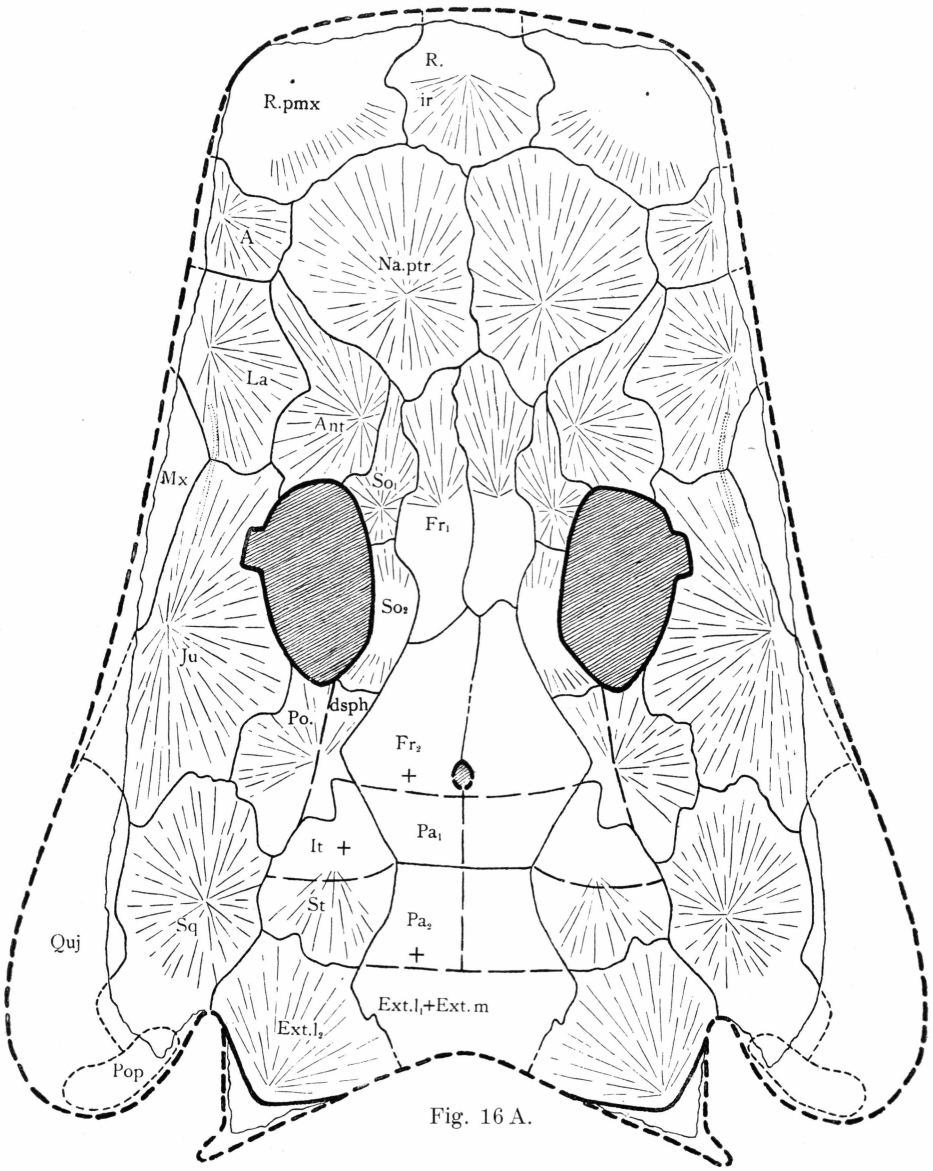


Fig. 16 A.

Text-fig. 16. *Ichthyostega stensiöi*, *A*, compared with the Crossopterygians *Dictyonosteus*, *B*, and *Osteolepis*, *C*.

A, Ant_1 anterior antorbital; *Ant*, Ant_2, posterior antorbital; *Dsph*, dermosphenotic; *E.s*, ethmoidal shield; *Ext. l*, (*Ext.* l_1, *Ext.* l_2) lateral extrascapular; *Ext. m*, median extrascapular; *Fr*, (Fr_1, Fr_2) frontal; *Ir*, interrostral; *It*, intertemporal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; Na_1, Na_2, Na_3, nasals; *Na. ptr*, naso-postrostral: *Op*, opercular; *Pa*, (Pa_1, Pa_2) parietal; *Pmx*, premaxillary; *Po*, postorbital; *Pop*, preopercular; *Ptr*, postrostral; *Quj*, quadratojugal; *R*, rostral; *R. ir* rostro-interrostral; *R. pmx*, rostro-premaxillary; *Scl*[1]), supracleithral; *Sclr*, sclerotic ring; *So*, So_1, So_2, So_3, supraorbitals; *Sop*, subopercular; *Sq*, squmosal; *Ssc*, suprascapular[1]); *St*, supratemporal; *al*, accessory lateral line of the trunk; *ap*, anterior pit-line; *dl*, dorsal lateral line of the trunk; *mp*, middle pit-line; na_1, anterior external naris; *pin*, pineal foramen; *pp*, posterior pit-line; *vp*, vertical pit-line of the cheek.

[1]) only partly shown in the figure.

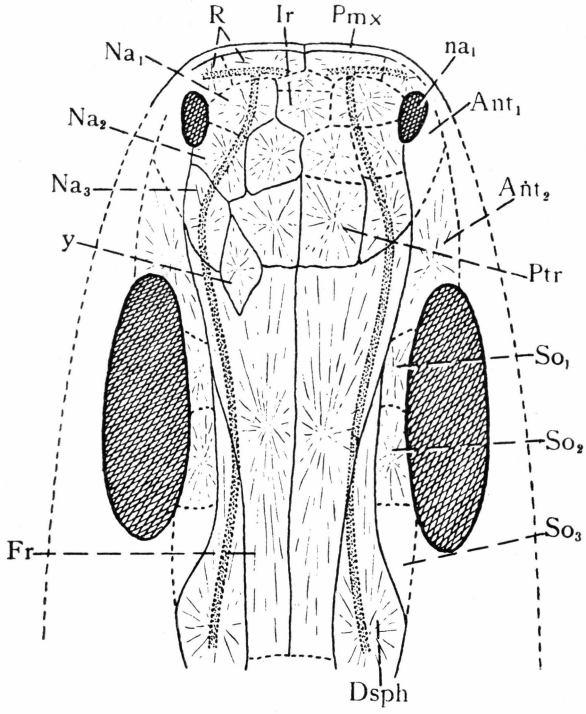


Fig. 16 B.

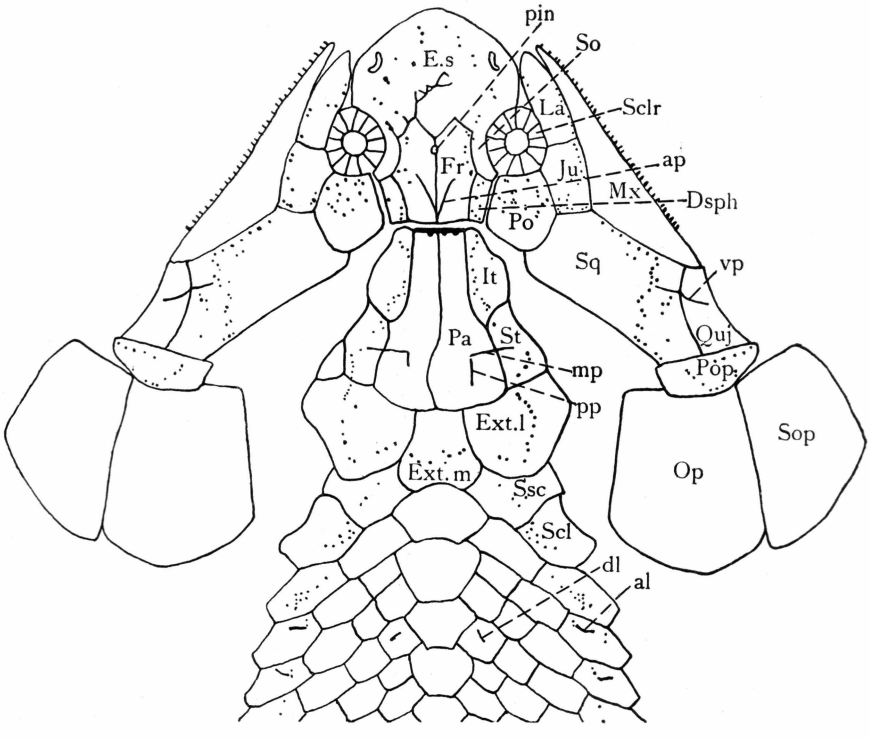


Fig. 16 C.

Dictyonosteus. The figure shows more clearly than any description the very great similarity in certain parts and the differences in others. It ought to be pointed out that the preopercular and quadratojugal of *Osteolepis* are clearly shown in several of the specimens I have examined, though most often the postero-lateral parts of the cheek are severely damaged. Thus the cheek of *Osteolepis* is rather similar to that of *Glyptopomus kinnairdi* (HUXLEY), as figured by WATSON and DAY (1916, text-fig. 2) and to that of *Holopthychius* sp. as figured by STENSIÖ (1932, text-fig. 87 on p. 37). The reader may also see the forthcoming paper on *Osteolepis* (SÄVE-SÖDERBERGH 1932 b).

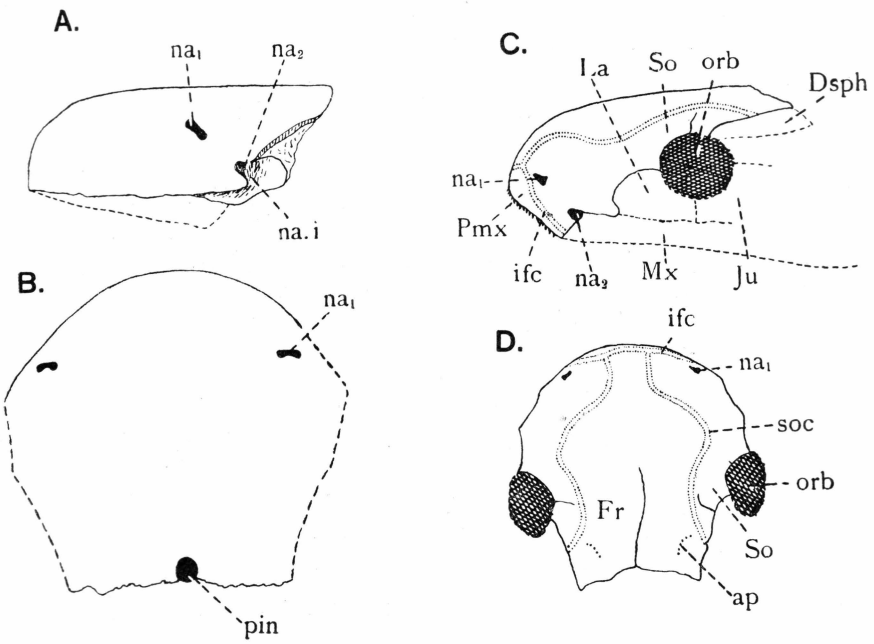
In text-fig. 16 A certain of the compound dermal bones are divided by broken lines into their components and it should be pointed out how little doubt is possible in regard to the position of these boundary lines. Thus the boundary between the postorbital and the dermosphenotic components of the postorbito-dermosphenotic is fixed anteriorly by comparison with the relation between the supraorbital, dermosphenotic, and postorbital in *Osteolepis*, and posteriorly this boundary must be continuous with the almost straight row of sutures formed between the cranial roof proper and the parts corresponding to the free cheek in *Osteolepis*. The hind margin of the frontal component of the fronto-parietal is fixed by the facts that it has to be continuous with the hind margin of the (postorbito-)dermosphenotic and to lie behind the pineal foramen. Likewise the boundary between the parietal and the extrascapular components of the parieto-extrascapular must be continuous with the hind margin of the supratemporo-intertemporal. The boundary between the supratemporal and intertemporal components of the supratemporo-intertemporal is fixed by the relation that these bones would bear to the cheek in *Osteolepis*, if the cheek were imagined to be turned up close to the lateral margin of the cranial roof proper, and by comparison with a specimen of *Eusthenopteron* that will be mentioned later on (p. 96, text-fig. 19).

As seen in the text-figs. 16, 2, and 11, the genus *Ichthyostega* seems to resemble the Crossopterygians less than does the genus *Ichthyostegopsis* in one respect: the relations of the jugals, lachrymals, and posterior antorbitals. In *Ichthyostegopsis* and in *Osteolepis* the suture between the lachrymal and the jugal is situated laterally to the orbit, and the jugal does not meet the posterior antorbital.

In regard to the postero-median parts of the dermal cranial roof of the Ichthyostegids, where no certain traces of the lateral line system have as yet been found, another interpretation of the bones could perhaps be thought possible, viz. that the portion denoted as the intertemporal (*It*) in text-fig. 16 A should be homologous with both the supratemporal and the intertemporal of *Osteolepis;* then the bone called by me the supratemporo-intertemporal would be an intertemporo-supratemporo-extra-

scapular, and the bone called by me parieto-extrascapular would be only an extrascapular. However, from a topographical point of view, the interpretation, given in the text-fig. 16 seems the only natural one, as will be readily seen by comparison with *Osteolepis*, if in that fish the cheek is thought to be turned up to lie close to the lateral margin of the cranial roof proper.

As is also seen in text-fig. 16, the parieto-extrascapular of the Ichthyostegids has a farther lateral extension than the median extrascapular of the Crossopterygians and accordingly it must include a



Text-fig. 17. Two indeterminable Crossopterygians from the Lower Devonian of Spitsbergen. Anterior part of the cranium, showing the ethmoid region, the position of the nasal capsules, and the nasal apertures. From STENSIÖ 1932.
A and B, lateral and dorsal view of one species, C and D another species in lateral and dorsal view.
Dsph, dermosphenotic; *Fr*, frontal, *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Pmx*, premaxillary; *So*, supraorbital; *ap*, anterior pit-line; *ifc*, infraorbital sensory canal; na_1, anterior external naris; na_2, posterior external naris; *na. i*, internal naris; *orb*, orbit; *pin*, pineal foramen; *soc*, supraorbital sensory canal.

part homologous with the most medial part of the large lateral extrascapular of the Crossopterygians.

The position of the external nares on the ventral side of the skull in the Ichthyostegids may seem at first very strange. But a similar arrangement is found at least in certain, very primitive Crossopterygians. The two indeterminable Crossopterygians from the Lower Devonian of Spitsbergen (text-fig. 17), figured and briefly described by STENSIÖ

(1932, text-fig. 30, description in the explanation of the figure), show two external nares and one internal naris. It is quite clear that it is the homologue of the posterior of the external nares that is found in the Ichthyostegids, whereas the more anterior external naris is not present in that group. If in the specimen shown in text-figure 17 A a maxillary is put in to separate the posterior external naris and the internal naris, the posterior external naris gets, in fact, exactly the same position in relation to the maxillary and premaxillary as the external naris of the Ichthyostegids. If we accept the homologies of the dermal bones put forward in text-fig. 16, the following would be the main differences between the dorsal side of the skull of the Ichthyostegids and that of the Crossopterygians *Dictyonosteus* and *Osteolepis*:

1. In the Ichthyostegids the lateral rostrals on each side have fused with the premaxillaries to rostro-premaxillaries and the interrostral with the median rostral (or with the postrostrals, cf. above p. 73).

2. The anterior nares have become closed in the Ichthyostegids.

3. In the Ichthyostegids the nasals on each side have fused with the postrostrals to naso-postrostrals.

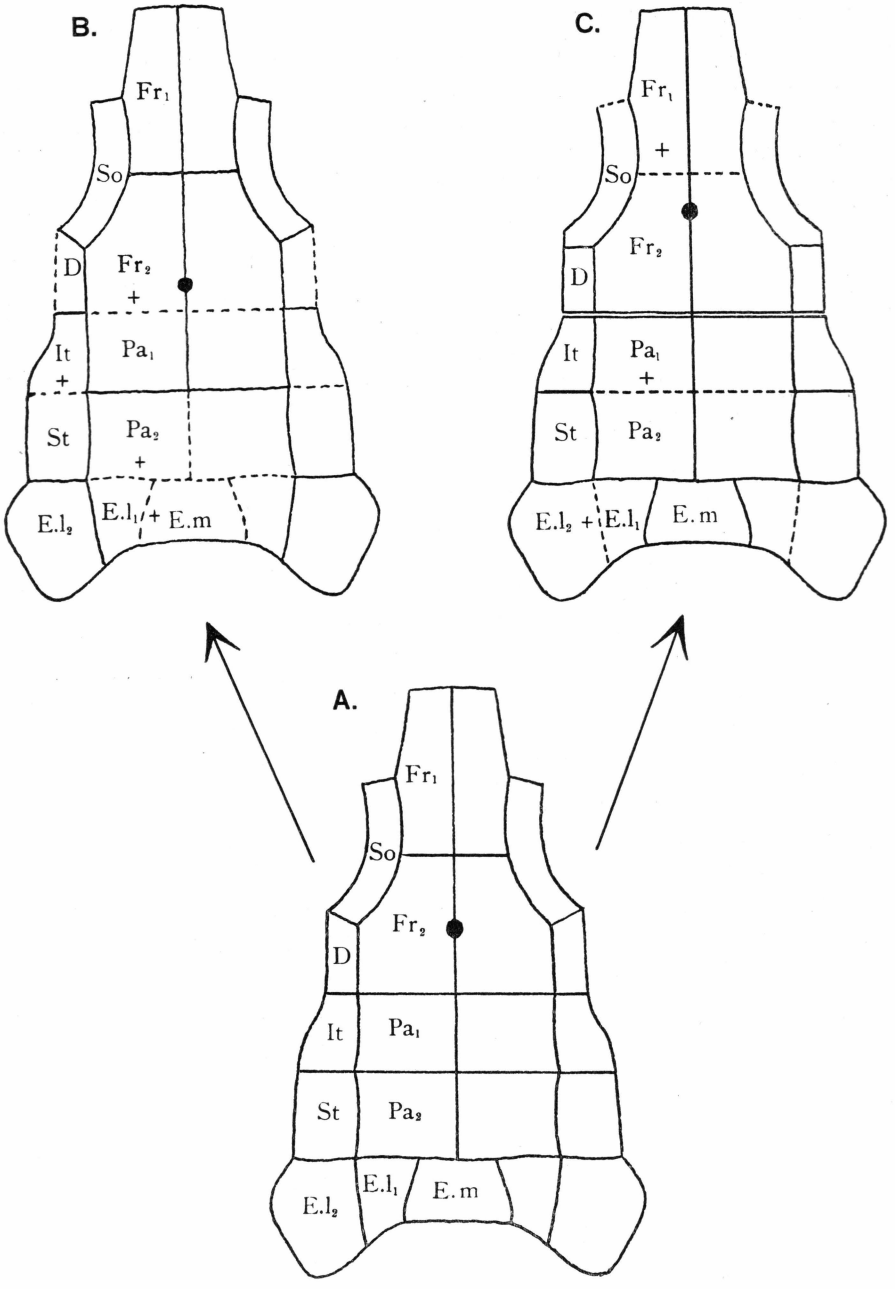
4. Each frontal and each parietal of the Crossopterygians must be regarded as divided into an anterior and a posterior portion, separated by a suture in the Ichthyostegids, and each lateral extrascapular as likewise divided into one more medial and one more lateral part, separated by suture in the Ichthyostegids. The anterior portion of the frontal is independent, the posterior portion of the frontal has fused with the anterior portion of the parietal to a fronto-parietal around the pineal foramen and the posterior portion of the parietal has fused with the median extrascapular and the medial portion of the lateral extrascapular to a parieto-extrascapular in the Ichthyostegids.

5. The intertemporal has fused with the supratemporal to a supratemporo-intertemporal in the Ichthyostegids.

6. In the Ichthyostegids the cheek has become rigidly attached to the cranial roof; the lachrymal has acquired a suture with the antorbitals, the postorbital has fused with the dermosphenotic, and the squamosal has acquired a suture with the supratemporo-intertemporal and with the lateral extrascapular.

7. In comparison with the relations in the Crossopterygians there is in the Ichthyostegids a considerable lengthening of the region in front of the pineal foramen and a very important shortening of the region covered in Crossopterygians by the parietals, intertemporals, supratemporals, and squamosals.

Owing to the many similar characters revealed by such a comparison as that illustrated in text-fig. 16 the supposition is inevitable that the



Text-fig. 18. Scheme of possible evolution of the arrangement of certain dermal bones in Ichthyostegids (B) and Crossopterygians (C) from a common ancestor (A). The changes in the relative length of the different regions are not shown in this figure. *D*, dermosphenotic; *E.l*$_1$, medial lateral extrascapular; *E.l*$_2$, the lateral of the lateral extrascapulars; *E.m*, median extrascapular; *Fr*$_1$, anterior frontal; *Fr*$_2$, posterior frontal; *It*, intertemporal; *Pa*$_1$, anterior parietal; *Pa*$_2$, posterior parietal; *So*, supraorbital; *St*, supratemporal.

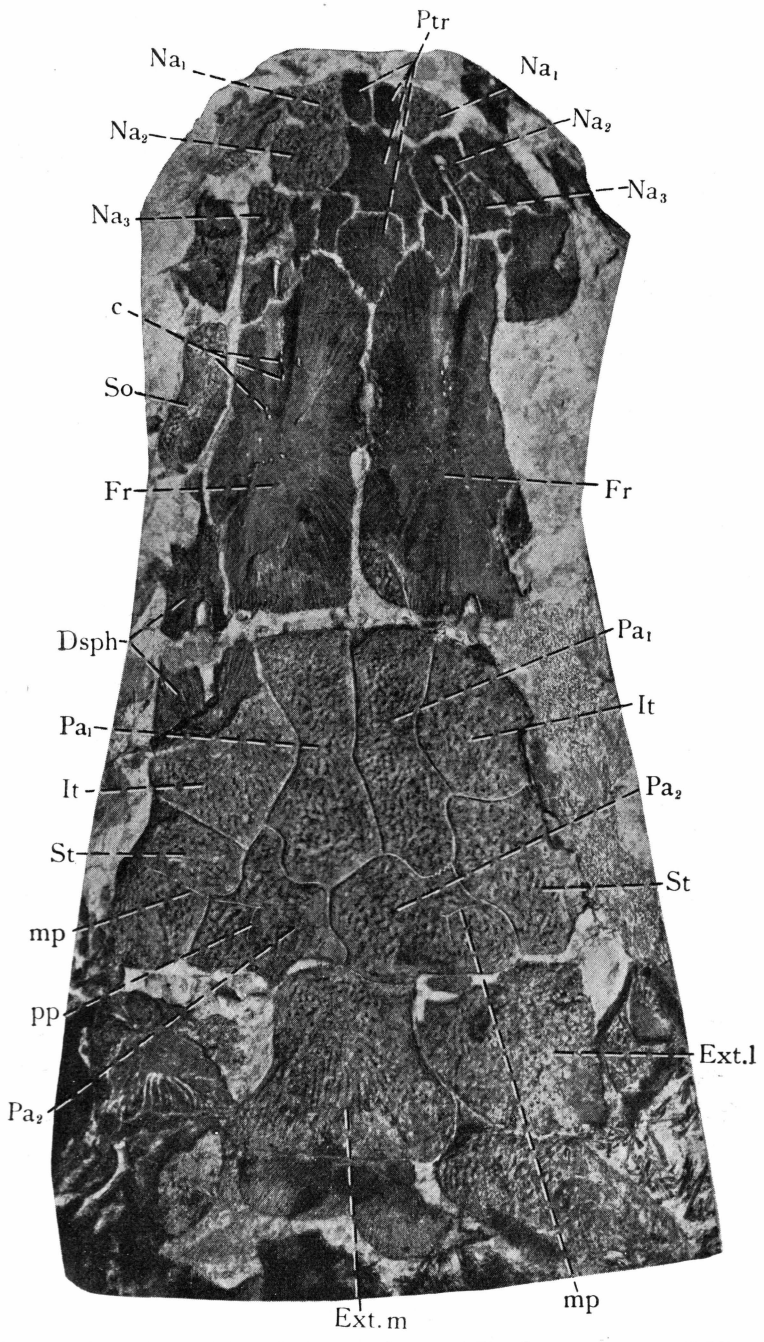
Ichthyostegids and the primitive Crossopterygians must have had a common ancestor from which neither of these groups has departed to any great extent.

Among the facts supporting this theory may be pointed out that the whole cheek has the same arrangement of its dermal bones in the two groups and that the anterior parts of the skull-roofs are also very easily comparable (text-fig. 16!).

The only difficulty lies in the interpretation of the fate of the *frontal*, *parietal*, and *extrascapular* elements and in the related question of the *bipartite primordial neurocranium* of the Crossopterygians. As pointed out by several authors (WATSON 1926 a, ALDINGER 1931; STENSIÖ 1932, pp. 23—27) the separation of the primordial neurocranium and dermal cranial roof in two parts, articulating with each other, is a fundamental character in Crossopterygians, whereas the Carboniferous Stegocephalians (WATSON 1926 a) have an uninterrupted ossification of their primordial neurocranium, and the arrangement of the bones in the dermal cranial roof of the Ichthyostegids excludes any articulation between an anterior and a posterior part of the skull in those forms.

A study of the evolution in other primitive vertebrate groups (see especially STENSIÖ 1921; 1922; 1932, pp. 17—30, 188—214, 228—249, 268—273) teaches us that the undivided primordial neurocranium of the Stegocephalians may with considerable probability be supposed to represent a more primitive stage of evolution than that of the Crossopterygians; and consequently the ancestor of the two groups most probably had an undivided primordial neurocranium. As to the critical dermal bones, there seem to be two possibilities of interpretation. Either the region in question was covered in the common ancestors by an undivided dermal bone, extending from the hind ends of the nasals and postrostrals to the hind margin of the skull-roof, or there were at least two pairs of frontals and two pairs of parietals in front of the extrascapulars. The first possibility seems rather improbable, as, owing to the similar arrangement of many dermal bones in the two groups under discussion, we are obliged to suppose a rather extensive subdivision of the dermal roof already in the ancestors. — The second possibility, on the other hand, seems very probable and is further illustrated by the scheme in text-fig. 18, showing the possible development of the scheme of dermal bones of the Crossopterygians and that of the Ichthyostegids from a common ancestor with two pairs of frontals and two pairs of parietals.

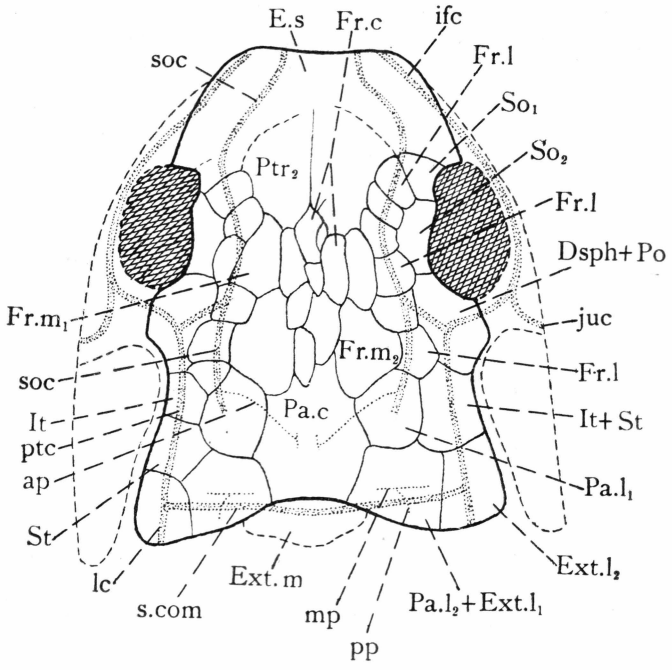
A wholly analogous problem arises when one tries to explain the difference as to the lateral extension of the most postero-medial bone of the dermal cranial roof in the two groups. Also in this case, the most probable solution is that there was in the common ancestor a greater number of bones than in any of the two groups, i. e. there were at least



Text-fig. 19. Dermal cranial roof of a specimen of *Eusthenopteron foordi* WHITEAVES from Scaumenac Bay, Canada. Magnification somewhat less than $^2/_1$ natural size. Photographed in alcohol. Specimen in the Royal State Museum, Stockholm. *Dsph*, dermosphenotic (by a mistake the most anterior part of the intertemporal also denoted as belonging to the dermosphenotic); *Ext. l*, lateral extrascapular; *Ext. m*, median extrascapular; *Fr*, frontal; *It*, intertemporal (the anterior part of this bone by mistake denoted as belonging to the dermosphenotic); Na_1, Na_2, Na_3, nasals; Pa_1, anterior parietal; Pa_2, posterior parietal; *Ptr*, postrostrals; *So*, supraorbital; *St*, supratemporal; *c*, canals for vessels and nerves to the supraorbital sensory canal; *mp*, middle pit-line; *pp*, posterior pit-line.

one median and four lateral extrascapulars, and the evolution in this case is also illustrated in text-fig. 18. (Cf. also STENSIÖ 1921, text-fig. 43; and 1932, text-fig. 15 B).

In connection with this theoretical analysis it is very interesting to find that my supposition as to the arrangement of the dermal bones in the common ancestor (text-fig. 18 A), put forward on theoretical grounds, is also strongly supported by concrete finds of a subdivision, at least of



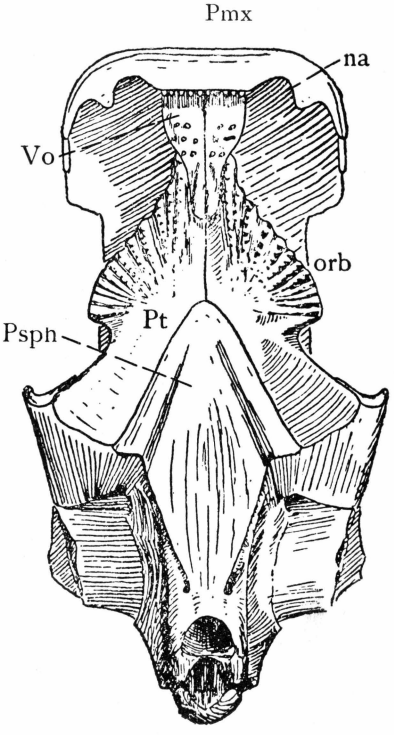
Text-fig. 20. Dermal cranial roof of *Dipterus platycephalus* (AG.) From a yet unpublished paper by E. STENSIÖ; sketch from a specimen in the Royal Scottish Museum of Nat. Hist., Edinburgh.

Dsph+Po, probably postorbito-dermosphenotic; *E. s*, ethmoidal shield; *Ext. m*, median extrascapular; *Ext. l_2*, the lateral of the lateral extrascapulars; *Fr. c*, central frontals; *Fr. l*, lateral frontal; *Fr. m_1*, *Fr. m_2*, medial frontals; *It*, intertemporal; *Pa. c*, central parietal; *Pa. l_1*, anterior lateral parietal; *Pa. l_2+Ext. l_1*, fused posterior lateral parietal and medial lateral extra-scapular; *Ptr_2*, postrostral; *So_1*, *So_2*, supraorbitals; *St*, supratemporal; *ap*, anterior pit-line; *ifc*, infraorbital canal; *juc*, jugal canal; *lc*, cephalic division of main lateral line canal; *mp*, middle pit-line; *pp*, posterior pit-line; *ptc*, otic part of the infraorbital canal; *s. com*, supratemporal commissure; *soc*, supraorbital canal.

the parietals, persisting in exceptional cases in Crossopterygians. In the extensive material of *Eusthenopteron foordi* WHITEAVES belonging to the Royal State Museum, Stockholm, Professor STENSIÖ has found a specimen showing quite clearly *two pairs of parietals*. Professor STENSIÖ has

most kindly allowed me to take and to publish here a photograph of this highly interesting specimen (text-fig. 19).

Now it is extremely interesting to compare the arrangement of the dermal bones postulated by me in a common ancestor of the Ichthyostegids and the Crossopterygians with that of a primitive Dipnoan. Professor STENSIÖ has most kindly allowed me to reproduce from one of his as yet unpublished papers a sketch of the dermal cranial roof in



Text-fig. 21. Palatal view of the skull of *Dipterus platycephalus* (AG.). — From WATSON and DAY 1916.
Pmx, premaxillary; *Pt*, (at least) entopterygoid; *Psph*, parasphenoid; *Vo*, vomer; *na*, notch for the external naris; *orb*, orbit.

Dipterus platycephalus (AG.) (text-fig. 20) which differs in several points from the latest previously published restoration, that of GOODRICH (1925, fig. 3). The arguments for the different interpretation of several dermal bones depend on the position of the lateral line canals and pit-lines and may be easily understood by comparing my text-fig. 20 with my text-fig. 1 B or 16 C (cf. also p. 7—10). I wholly agree with the view of GOODRICH (1925, p. 79, also 1919, p. 186, 187, and 1930, p. 285, 287) concerning the high importance of the lateral line system for homologising the dermal bones.

In the morphology of the dermal cranial roof of *Dipterus* we find still more support for my theory of the arrangement of the dermal bones in the

common ancestor, to which also the primitive Dipnoans must have been very nearly related. Thus there are in *Dipterus* five extrascapulars, and an ancestor of this fish must have had a subdivision at least of the lateral parietals, as there is in *Dipterus* one independent anterior lateral parietal (*Pa.* l_1, text-fig. 20) and the position of the middle pit-line of the head (*mp*, text-fig. 20) shows that a posterior lateral parietal has fused with the medial lateral extrascapular. Further there is found in *Dipterus* an extensive subdivision of the frontals.

In certain characters *Dipterus* seems to be more nearly related to the Ichthyostegids than are the Crossopterygians. Thus its dermosphenotic seems to have fused with the postorbital; on the right side of the specimen figured the supratemporal has fused with the intertemporal; and finally there is an unpaired central parietal, whereas in Crossopterygians there are only paired parietal elements. But there are also many differences between the morphology of the dermal bones in *Dipterus* on the one hand and that in Crossopterygians and Ichthyostegids on the other hand. The most apparent of these differences lies in the morphology of the maxillary and palate, which in the Ichthyostegids, as in the Carboniferous Embolomerous Stegocephalians, is very closely comparable to that of the Crossopterygians (cf. my text-fig. 5, 9 and pls. VIII, XIV, XV, pl. XVII, fig. 2 and pl. XXII with WATSON 1926 a, fig. 4), but in the Dipnoans, as is well known, is of a very different type (text-fig. 21, WATSON and DAY, 1916) generally regarded as an "adaptation to a durophagous habit" (WATSON, 1926 a, p. 198), which has also caused a reduction of the premaxillaries and maxillaries (WATSON and GILL, 1923, fig. 32, p. 210) and a modification of the lower jaw (WATSON and GILL, 1923, fig. 34, p. 210). There is, however, also in the palate one feature common to the Dipnoans and the Ichthyostegids, but not found in the Crossopterygians, viz. the median suture between the anterior parts of the entopterygoids.

A very interesting point in the organisation of the primitive Dipnoans here discussed is the position of the external nares on the ventral side of the snout. Now that the discoveries by STENSIÖ in the primitive Crossopterygians from the Lower Devonian of Spitsbergen (cf. pp. 91, 92) and my own discoveries in the Ichthyostegids have thrown new light upon this question, it seems impossible to regard the position of the external nares in the primitive Dipnoans as a consequence of a reduction of the maxillaries (WATSON and GILL, 1923, p. 210; WATSON, 1926 a; p. 198) and the only acceptable interpretation seems to be that the external nares of the Dipnoans, like those of the Ichthyostegids, are homologous with the posterior external nares in the most primitive Crossopterygians, and are primarily situated on the ventral side of the snout.

VII. Comparison with certain younger groups of Stegocephalians. The systematic position of the family Ichthyostegidae. Order Ichthyostegalia.

As may be easily gathered from the foregoing chapters, the Ichthyostegid skull is of a clearly Tetrapod type and the Ichthyostegids obviously appertain to the same large group as the most primitive previously known Tetrapods, the Stegocephalians, since they have a completely ossified skull-roof and, as will be shown below, many other important features in common with primitive representatives of that group.

There is, however, one very important difference between all previously known Stegocephalians and the Ichthyostegids: the position of the external nares. The external nares of the Ichthyostegids open on the ventral surface of the snout but in other Stegocephalians on the dorsal surface. As already shown (pp. 91—92, 98), the external nares of the Ichthyostegids are clearly homologous with the posterior external nares in the primitive Crossopterygians and with the external nares of the Dipnoans. But what are the dorsally opening nares of the later Stegocephalians? To my mind they must most naturally be regarded as the displaced homologues of the external nares of the Ichthyostegids and Dipnoans. This is supported by the position of the external nares in primitive Carboniferous Stegocephalians like *Orthosaurus pachycephalus* BARKAS (text-fig. 22, WATSON, 1926 a) and *Baphetes latirostris* WATSON (WATSON 1926 b, p. 240, fig. 20; cf. pp. 101, 102 of the present paper). In *Orthosaurus* the external nostrils lie very near the ventro-lateral margin of the snout, and only in the geologically younger Labyrinthodontia do the nostrils aquire a really dorsal position, as for instance in *Eryops* (v. HUENE 1913, fig. 1; BROOM 1913, figs. 11, 19), *Lonchorhynchus*, *Lyrocephalus*, *Tertrema* (WIMAN, 1914; 1917), *Metoposaurus* (FRAAS 1889, pl. XII), *Mastodonsaurus* (FRAAS 1889, fig. 1, pl. VIII, fig. 1), *Cyclotosaurus* (FRAAS 1889, pl. IX).

The migration of the external nares to the dorsal side of the snout is a rather important change in the organisation of the Stegocephalians. Though this process has of course gone on gradually there is clearly a great and important difference between the Ichthyostegids, where the external nares have not even caused any notch in the roofing bones of the skull, and all the other Stegocephalians, in which the nostrils are closed laterally by the marginal parts of the skull-roof.

Another important difference between the Ichthyostegids and the other Stegocephalians is the existence in the cranial roof of the former group of an unpaired parieto-extrascapular, an unpaired rostro-interrostral, a normal anterior antorbital dorso-medially to each external naris (cf. pp. 101, 102!) and, at least in certain forms, an independent

preopercular. Further the enclosed lateral line canals have not hitherto been recorded with certainty from later Stegocephalians (cf. WATSON, 1926 a, p. 220; ANDREWS, 1895; MOODIE, 1908).

The above important differences between the Ichthyostegids on the one hand and all previously known Stegocephalians on the other hand justify and necessitate the erection of a new Order, for which I propose the name *Ichthyostegalia*. The diagnosis of the Order Ichthyostegalia must of course still be very incomplete. It would run as follows:

Stegocephalians with external nares on the ventral side of the skull. Dermal cranial roof with an unpaired rostro-interrostral and an unpaired parieto-extrascapular, a small anterior antorbital dorsally to each external naris, joined by suture with the bones anterior, medial and posterior to it; at least in certain forms an independent preopercular. Lateral line system of the head in greater part enclosed in the dermal bones; with a true jugal canal, possibly also with a quadratojugal canal. Palate extensively ossified, with very narrow interpterygoid vacuities, and with entopterygoids meeting in a median suture.

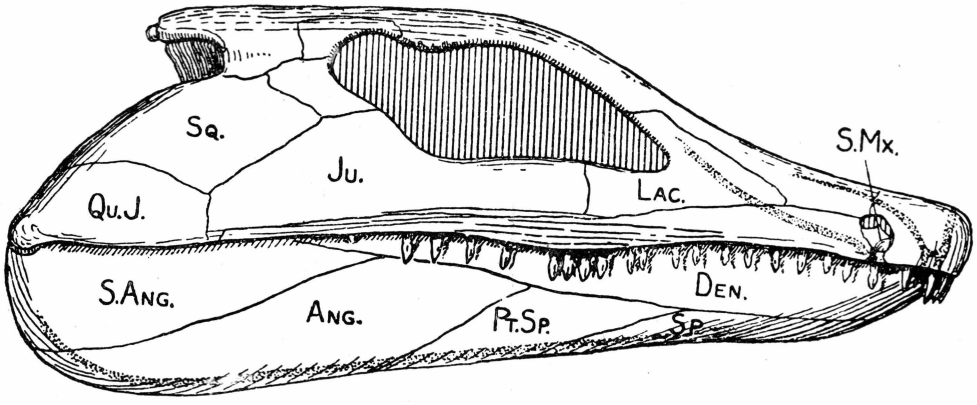
The organisation of the dermal bones of the head of the Ichthyostegids in many points resembles that of the Carboniferous *Embolomeri*. Above all may be pointed out the extreme similarity of the palate in the two groups. Like the palate of all *Embolomeri* that of the Ichthyostegids is characterised by the enormous extension of the palatal rami of the entopterygoids, which meet anteriorly in a median suture and posteriorly leave very narrow interpterygoid vacuities. Another common feature is the existence of independent tooth-bearing ectopterygoids behind the likewise tooth-bearing dermopalatines. The vomeres of the Ichthyostegids are large and tooth-bearing, as may be those of the Loxommoid *Embolomeri* (WATSON 1926 b, p. 235), and the size and shape of the internal nares and anterior palatal vacuity of the Ichthyostegids are very similar to those in certain *Loxommoideae* (cf. my text-fig. 5 to WATSON, 1926 a, fig. 9).

The very long maxillaries, the anteriorly broadening naso-postrostrals ("nasals"), the narrow frontals, the shorter and broader fronto-parietals ("parietals"), and the shape and extension of the jugals, squamosals, and quadratojugals are other common features of the Ichthyostegids and the *Embolomeri* (see especially WATSON 1926 a, figs. 6, 7, 8).

But there are also many differences between the Ichthyostegids and the *Embolomeri*, of which the more important have already been treated above. Further may be mentioned the difference in the dentition: in the Ichthyostegids there are two rows of teeth in each mandible and the teeth of the upper jaw are of the same size as those of the palate, relatively

larger than the teeth of the maxillary in the *Embolomeri* and smaller than the palatal tusks in that group. There are also several apparent differences in the dermal cranial roof but these are not easy to discuss properly before we obtain a more complete knowledge of the lateral line system both of the *Embolomeri* and of the Ichthyostegids.

The homologue of the small anterior antorbital of the Ichthyostegids may seem difficult to find in the younger Stegocephalians. There is, however, only one possible interpretation, viz. that the bone in question is homologous, at least for its greater part, with the septomaxillary. This dermal bone is described and figured in the Permian Stegocephalians as



Text-fig. 22. *Orthosaurus pachycephalus* Barkas. Right lateral aspect of the skull and lower jaw. From Watson 1926 a (fig. 7).
Lac, posterior antorbital; *S. Mx*, septomaxillary or anterior antorbital.

forming part of the "floor of the anterior nasal opening" (*Eryops*, Broom, 1913, p. 581, figs; 11, 19, v. Huene, 1913, fig. 1; Zatrachys, Broom, 1913, fig. 21; *Trimerorhachis* v. Huene, 1913, p. 372, fig. 56); and in *Rana* it is found as a small "hufeisenförmig gekrümmter Knochen, der die Decke für das Cavum medium der Nasenhöhle ergänzen hilft" (Ecker, Wiedersheim, Gaupp, 1896, p. 52). In Amniota it "tends to grow inwards so as to roof over and protect the organ of Jacobson" (Goodrich, 1930, p. 316).

As far as can be judged from the figures cited above the septomaxillary in the Permian Stegocephalians has no external sculpture such as that of the other dermal bones, and conceivably had really sunk into the naris. But in the Carboniferous Embolomerous Stegocephalian *Orthosaurus pachycephalus* Barkas, Watson (1926 a, p. 210, figs. 6, 7) described and figured septomaxillaries, which are "small, entirely superficial bones with the usual pitted and grooved external surface" and in *Baphetes latirostris* Watson there are, according to Watson (1926 b,

p. 240, fig. 20) septomaxillaries with "the ornament found on all the dermal skull bones", "rigidly attached by suture to the premaxilla, maxilla, lacrimal and very slightly to the nasal" and lying "behind rather than below the nostril". And these septomaxillaries (see text-fig. 22) have really the same position as the anterior antorbitals in the Ichthyostegids, above the anterior end of the maxillary or tooth-bearing part of the lachrymo-maxillary and the posterior end of the tooth-bearing part of the rostro-premaxillary, posterior to the rostral part of the rostro-premaxillary and anterior to the bone connected with the most anterior part of the suborbital division of the infraorbital canal (lachrymal of the Ichthyostegids, "maxillary" = lachrymo-maxillary of *Orthosaurus*). As the septomaxillary of *Baphetes*, *Orthosaurus* and other geologically younger Stegocephalians is attached to the bone posterior to it, the external nostril when shifting dorsally must have passed in front of the anterior antorbital or septomaxillary, where it lies in *Baphetes*, to acquire its actual position in *Orthosaurus* which is mainly dorsally to the septomaxillary.

Thus the septomaxillary can now be followed back to its origin from a part of the dermal cranial roof, situated dorsally to each external naris in primitive Tetrapods, and from the course of the supraorbital and infraorbital sensory canals in *Orthosaurus* (text-fig. 22!) it is clear that the bones in the Ichthyostegids called by me the anterior antorbital really appertains to the antorbital series (cf. p. 16 and pp. 7, 8, text-fig. 1 A) and that consequently the septomaxillary is homologous with at least the greater part of the anterior antorbital of primitive Crossopterygians (Ant_1, text-fig. 1 A).

It is important to note that some *Embolomeri* also display certain features, regarded by WATSON as primitive characters, directly inherited from the Fish ancestors — features, however, that are not found in the Ichthyostegids. Such features are the loose (ligamental) mesial attachment of the squamosal to the supratemporal and intertemporal (WATSON, 1926 a, p. 218; 1926 b, p. 229; cf. 1926 b, p. 237, fig. 18)[1]), the deep otic notch, wholly separating the small lateral extrascapular (tabular) from the squamosal, and the existence of free intertemporals or dermosphenotics (*Loxomma!*). From the preceding descriptions of the Ichthyostegids it is evident that in these forms the squamosal was firmly attached by an interlocked suture, not only to the compound supratemporo-intertemporal, but also to the lateral extrascapular.

The facts brought forward above may be interpreted in two ways. Either we have here an instance of "Spezialisationskreuzung", the *Embolomeri* being really, as supposed by WATSON, primitive in regard

[1]) Recently discussed also by PFANNENSTIEL (1932).

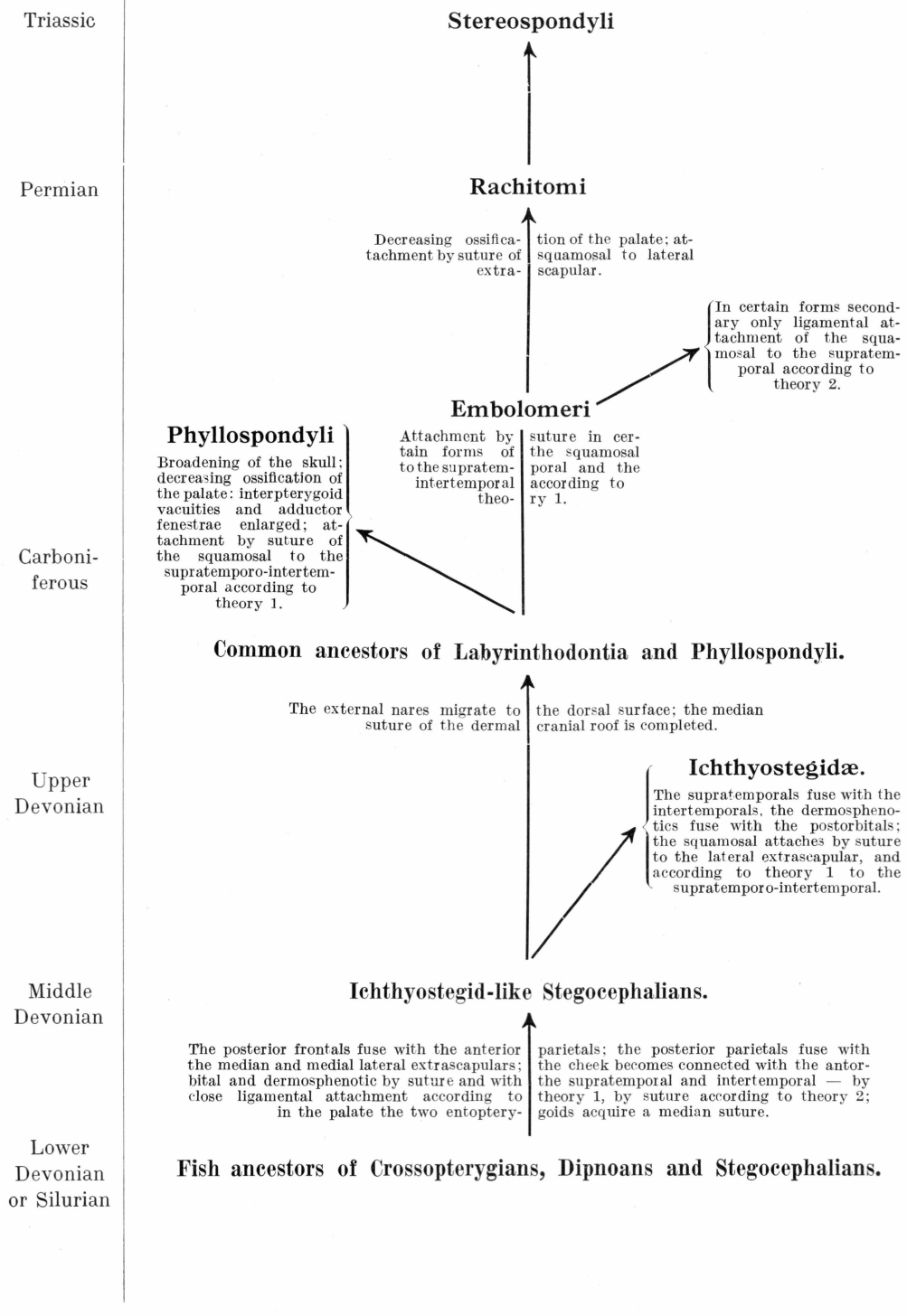
to the attachment of the squamosal and the development of the supratemporal and intertemporal, and in this case they must have developed parallel to the Ichthyostegids, or else they have developed from forms of the type of the Ichthyostegids and the features in question have been secondarily acquired. In regard to the free dermosphenotic or intertemporal it seems most probable that this is really a primitive feature, and thus we arrive at the conclusion that the *Embolomeri* and the Ichthyostegids are parallel groups, originating from a common ancestor, from which, however, the Ichthyostegids with their many primitive features have departed very little.

The question of the attachment of the cheek is more complicated, and for the solution of this problem we must take into consideration also the organisation and phylogeny of the *Rachitomi*, *Stereospondyli* and *Phyllospondyli*.

In the *Rachitomi* we find, for instance in *Lydekkerina* (Watson, 1919, fig. 9), a pattern of dermal bones of the skull-roof similar in many respects to that of the Ichthyostegids. The squamosal here is joined by suture with a large lateral extrascapular and with a compound supratemporo-intertemporal and in most *Rachitomi* (*Eryops*, Broom, 1913, p. 591, fig. 20; *Zatrachys*, ib., p. 593, fig. 21; Case, 1911, p. 86; *Dasyceps*, v. Huene, 1910; *Osteophorus*, Broili 1917, p. 571, fig. 15) and *Stereospondyli* (*Lyrocephalus*, Wiman, 1914, pl. I, 1; *Lonchorhynchus*, ib., pl. IV, 6; *Aphaneramma*, ib., pl. V, 1, 2; *Platystega*, ib., pl. VI, 5; *Peltostega*, Wiman 1916, pl. XV, 1; *Mastodonsaurus*, Fraas, 1889, fig. 1, pl. VIII, fig. 1; *Cyclotosaurus*, ib., pl. IX; *Metoposaurus*, ib., pl. XII) the squamosal likewise connects by suture both with the lateral extrascapular (tabular) and with the supratemporo-intertemporal.

The Phyllospondyls, according to more recent investigations (Watson, 1921; Bulman and Whittard, 1925; Steen, 1931), may be referred to a primitive type, represented by *Eugyrinus wildii* Watson from the Lower Coal Measures of Lancashire and *Pelion lyelli* Wyman, and *Erpetosaurus radiatus* Moodie from the Middle Coal Measures of Linton, Ohio. These primitive Phyllospondyls "share certain features in common with the skulls of Carboniferous and early Permian Labyrinthodonts" (Steen, 1931, p. 888). They represent a stage corresponding to that represented by an Upper Permian Labyrinthodont (Watson 1921, p. 73), and according to Steen" it is evident that the intervening morphological stages", between the *Phyllospondyli* and *Labyrinthodontia*, "must be sought at a much earlier period".

Now in the Carboniferous *Phyllospondyli* the squamosal does not meet the small lateral extrascapular, but is firmly attached by suture to the supratemporo-intertemporal (Steen, 1931, text-fig. 2). And if the *Phyllospondyli* originated from the ancestors of the early *Labyrintho-*


Triassic
Permian
Carboni-
ferous
Upper
Devonian
Middle
Devonian
Lower
Devonian
or Silurian
Stereospondyli
Rachitomi
Decreasing ossification of the palate; attachment by suture of squamosal to lateral extrascapular.
In certain forms secondary only ligamental attachment of the squamosal to the supratemporal according to theory 2.
Embolomeri
Phyllospondyli
Broadening of the skull; decreasing ossification of the palate: interpterygoid vacuities and adductor fenestrae enlarged; attachment by suture of the squamosal to the supratemporo-intertemporal according to theory 1.
Attachment by suture in certain forms of the squamosal to the supratemporal and the intertemporal according to theory 1.
Common ancestors of Labyrinthodontia and Phyllospondyli.
The external nares migrate to the dorsal surface; the median suture of the dermal cranial roof is completed.
Ichthyostegidæ.
The supratemporals fuse with the intertemporals, the dermosphenotics fuse with the postorbitals; the squamosal attaches by suture to the lateral extrascapular, and according to theory 1 to the supratemporo-intertemporal.
Ichthyostegid-like Stegocephalians.
The posterior frontals fuse with the anterior parietals; the posterior parietals fuse with the median and medial lateral extrascapulars; the cheek becomes connected with the antorbital and dermosphenotic by suture and with the supratemporal and intertemporal — by close ligamental attachment according to theory 1, by suture according to theory 2; in the palate the two entopterygoids acquire a median suture.
Fish ancestors of Crossopterygians, Dipnoans and Stegocephalians.

dontia it is clear that either 1) they have afterwards acquired the firm attachment of their squamosal as a parallel to a similar process in the *Labyrinthodontia*, or 2) that this feature was developed already in the common ancestor of the two groups and the ligamental attachment of the squamosal in certain *Embolomeri* is a secondary aquisition.

If we accept the first of the above theories, the ligamental attachment of the squamosal in certain *Embolomeri* would be a primitive character, directly inherited from the Fish ancestor, and then the sutural attachment of the squamosal in the Ichthyostegids would be the first instance of a thrice occurring parallel process of rigid attachment of the cheek in Stegocephalians.

If theory no. 2 is the right one, the sutural attachment of the squamosal to the supratemporal and intertemporal was without doubt acquired already in the common ancestors of the Ichthyostegids and the other Stegocephalians. Then the only necessary difference between these ancestors and the Ichthyostegids would be the fusion of the supratemporal with the intertemporal and of the dermosphenotic with the postorbital and the sutural attachment of the squamosal to the lateral extrascapular in the latter group.

In both cases it seems most probable that the sutural attachment of the squamosal to the lateral extrascapular is a specialised, parallel development in the *Rhachitomi-Stereospondyli* and in the Ichthyostegids, as it is found neither in any of the typical *Embolomeri* nor in the *Phyllospondyli*.

The conception of the phylogeny of the groups of Stegocephalians, here discussed, as a corollary of the above statements and deductions may be expressed in the form of a table, as given on the preceeding page.

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EXPLANATION OF PLATES

The photographs reproduced in the plates have been taken with Zeiss Tessar objectives 1 : 6,3, F. 36 cm, 1 : 6,3 F. 25 cm, 1 : 4,5, F. 16.5 cm. Ilford special rapid panchromatic plates have alone been used in connection with the Ilford Gamma filter.

All the specimens figured are in the possession of the Geol. Survey of Greenland (G. G. U.), Copenhagen.

Plate I.

Ichthyostega stensiöi n. sp. Imperfect cranial roof exposed from the ventral side. Specimen A. l. a. Natural size.

A, anterior antorbital; *Ant*, posterior antorbital; *Ext. l*, lateral extrascapular; *Ext. m*, parieto-extrascapular; *Fr*, frontal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na. ptr*, naso-postrostral; *Pa*, fronto-parietal; *Po. dsph*, postorbito-dermosphenotic; *Quj*, quadratojugal; *R. ir*, rostro-interrostral; *R. pmx*, rostro-premaxillary; So_1, anterior supraorbital; So_2, posterior supraorbital; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *c*, canals, probably for vessels and nerves to the supraorbital sensory canal; *ifc*, infraorbital sensory canal; *pin*, pineal foramen.

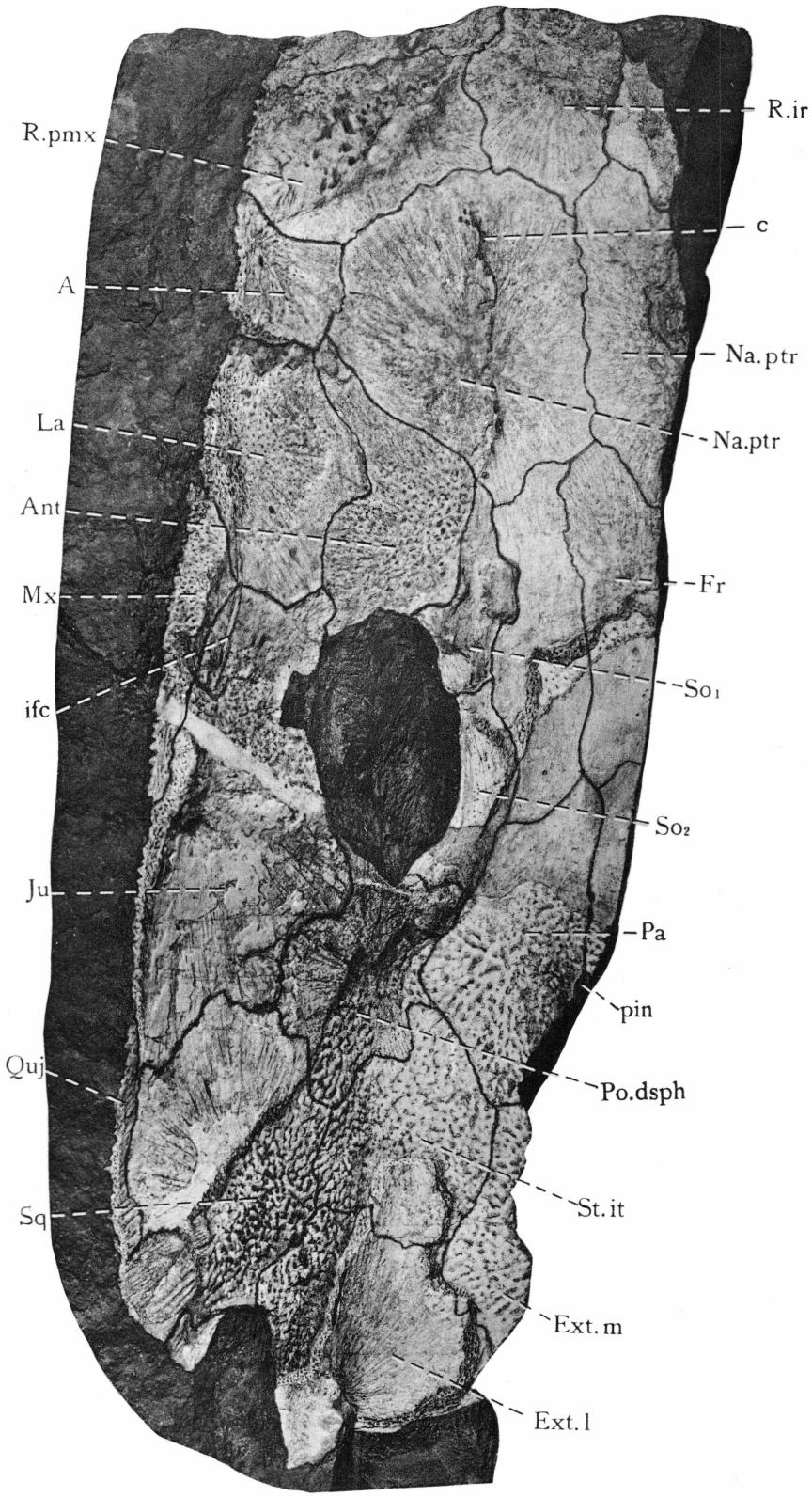

R.pmx
R.ir
c
A
Na.ptr
La
Na.ptr
Ant
Mx
Fr
ifc
So1
So2
Ju
Pa
pin
Quj
Po.dsph
Sq
St.it
Ext.m
Ext.l

Plate II.

Ichthyostega stensiöi n. sp. Same specimen as in pl. I, in ventro-lateral view. Natural size.

A, anterior antorbital; *Ant*, posterior antorbital; *Ext. l*, lateral extrascapular; *Ext. m*, parieto-extrascapular; *Fr*, frontal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na. ptr*, naso-postrostral; *Pa*, fronto-parietal; *Po. dsph*, postorbito-dermosphenotic; *Quj*, quadratojugal; *R. ir*, rostro-interrostral; *R. pmx*, rostro-premaxillary; So_1, anterior supraorbital; So_2, posterior supraorbital; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *ifc*, infraorbital sensory canal.

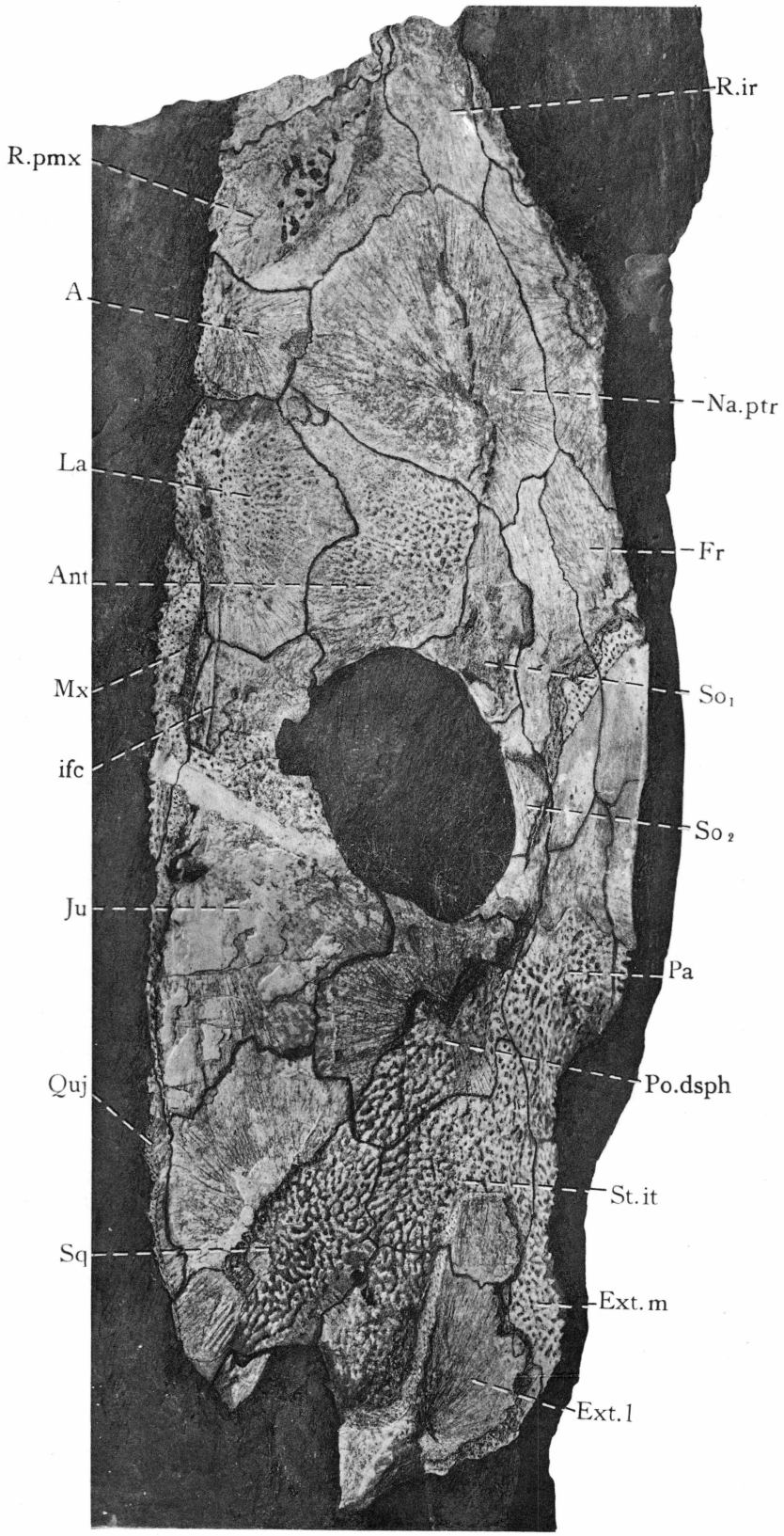

R.ir
R.pmx
A
Na.ptr
La
Fr
Ant
Mx
So1
ifc
So2
Ju
Pa
Quj
Po.dsph
St.it
Sq
Ext.m
Ext.l

Plate III.

Ichthyostega stensiöi n. sp. Antero-lateral part of the cranial roof in dorsal view. Specimen A. l. b. × $^3/_2$.

A, anterior antorbital; *Ant*, posterior antorbital; *Fr*, frontal; *Ju*, jugal; *La*, lachrymal; *Na. ptr*, naso-postrostral; *R. ir*, rostro-interrostral; *R. pmx*, rostro-premaxillary; So_1, anterior supraorbital; So_2, posterior supraorbital.

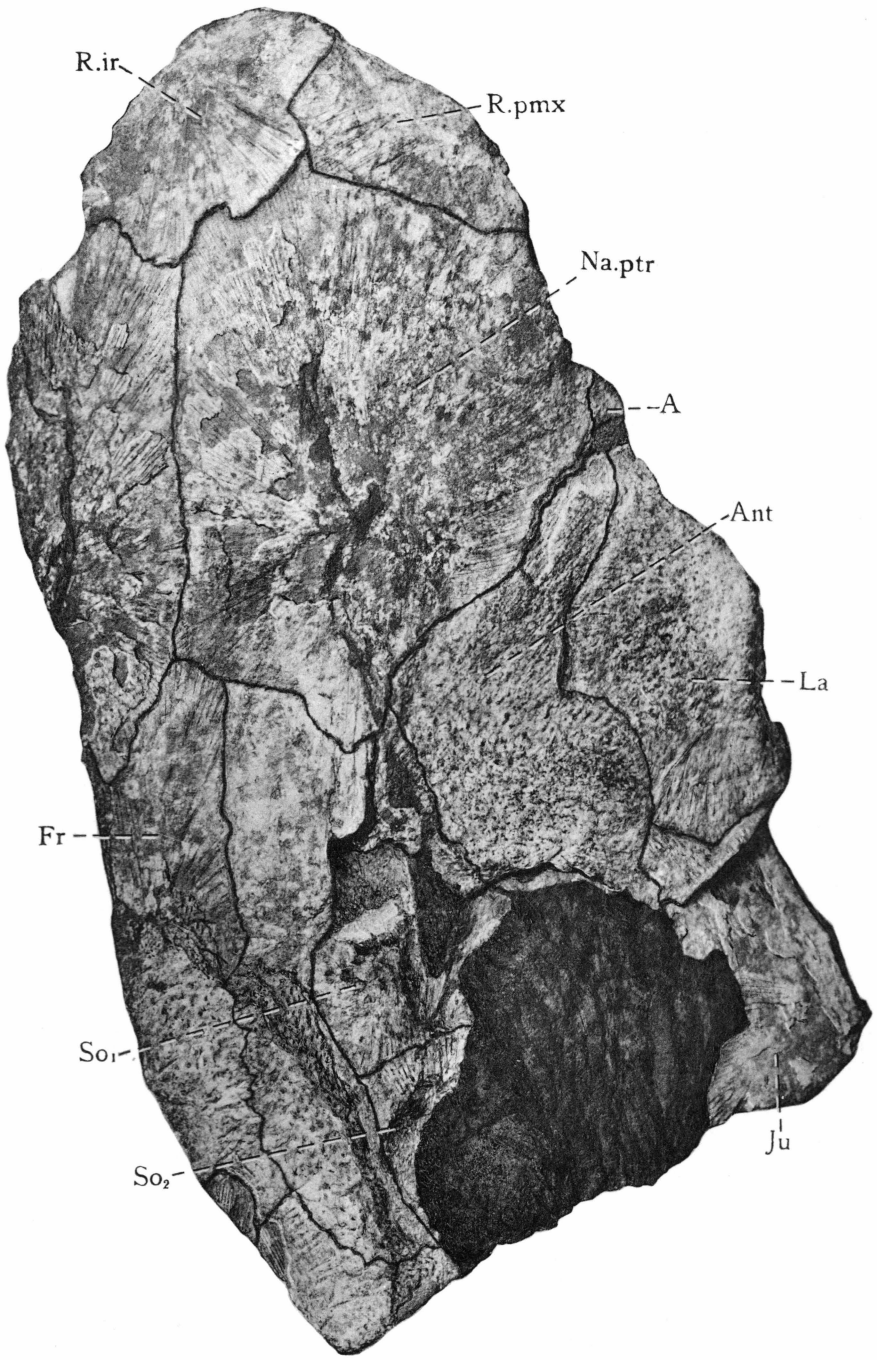

R.ir
R.pmx
Na.ptr
A
Ant
La
Fr
So1
So2
Ju

Plate IV.

Fig. 1. *Ichthyostega stensiöi* n. sp. Antero-lateral part of a skull in ventral view. Specimens A. l. a. and A. l. b., put together. $\times {}^{3}/_{2}$.

Fig. 2. *Ichthyostega stensiöi* n. sp. Positive cast of the sculpture of the part of the dermal cranial roof nearest to the pineal foramen. From specimen A. l. a. $\times {}^{4}/_{3}$.

Fig. 3. *Ichthyostega?* sp. b. Positive cast of the sculpture of the part of the dermal cranial roof surrounding the pineal foramen. From specimen A. 2. $\times {}^{4}/_{3}$.

A, anterior antorbital; *Dpl*, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *La*, lachrymal; *Mx*, maxillary; *Psph*, parasphenoid; *R. ir*, rostro-interrostral; *R. pmx*, rostro-premaxillary; *Vo*, vomer; *apv*, anterior palatal vacuity; *n. i*, internal naris; *pin*, pineal foramen; *s*, suture between the fronto-parietals.

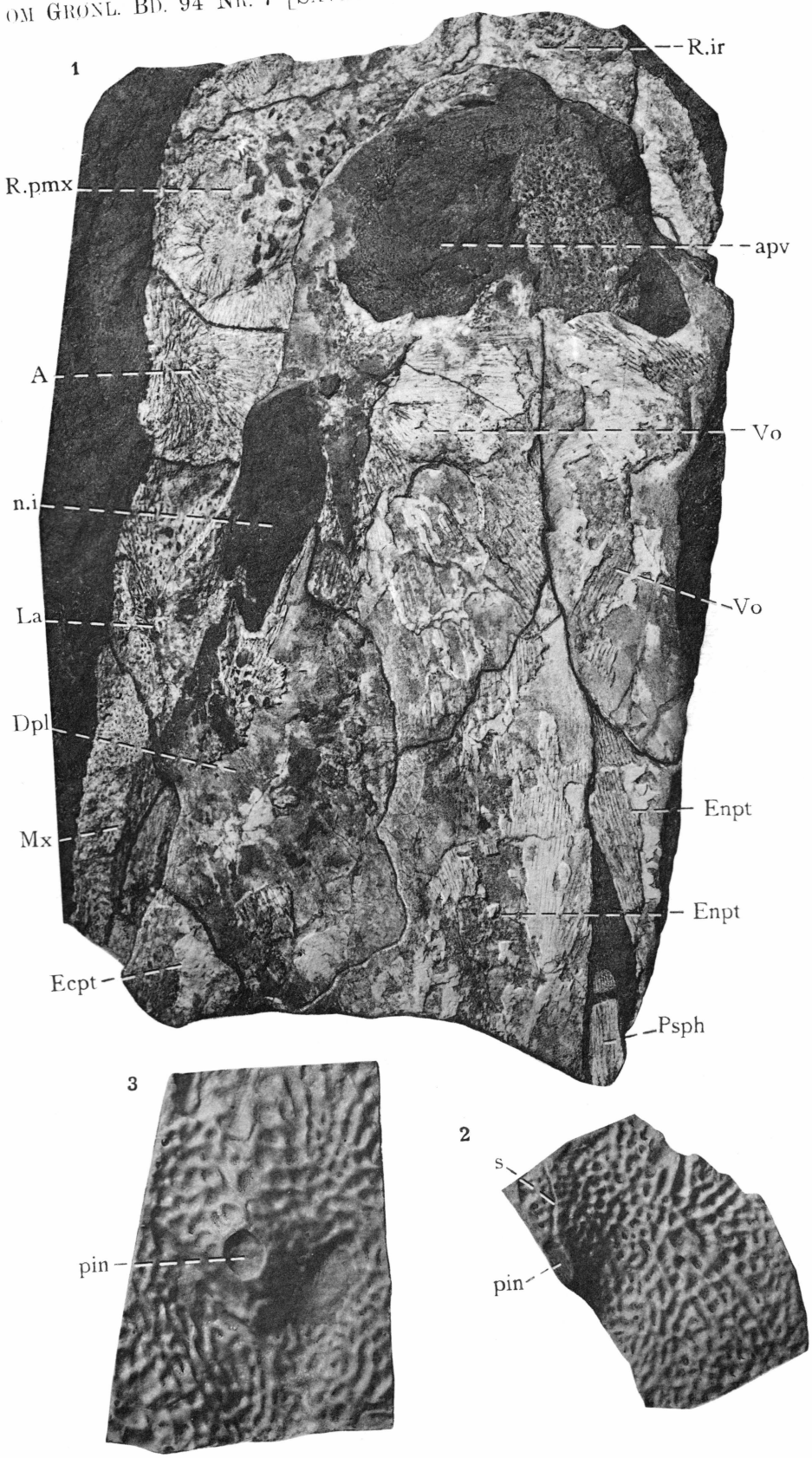
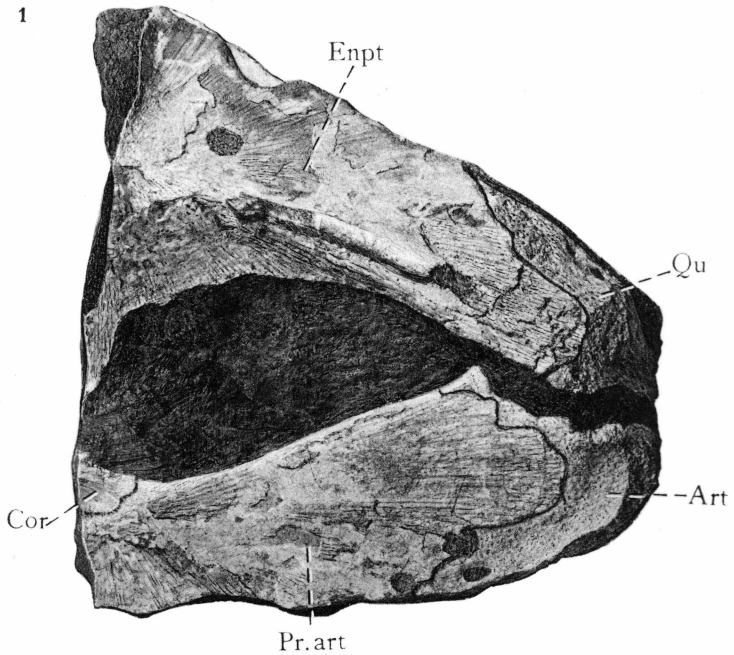

1
R.ir
R.pmx
apv
A
Vo
n.i
Vo
La
Dpl
Enpt
Mx
Enpt
Ecpt
Psph
3
pin
2
s
pin

Plate V.

Ichthyostegid sp. a. Postero-lateral part of the cheek. Specimen A. 6. $\times {}^{3}/_{2}$.
Fig. 1. In palatal view.
Fig. 2. In lateral view.
Ang, supraangulo-angular; *Art*, articular; *Cor*, coronoid; *De*, dentary; *Enpt*, entopterygoid; *Ext. l*, lateral extrascapular; *Ju*, jugal; *Mx*, maxillary; *Po. dsph*, postorbito-dermosphenotic: *Pop*, preopercular; *Pr. art*, prearticular; *Qu*, quadrate; *Quj*, quadratojugal; *Sq*, squamosal; *juc*, jugal sensory canal; *mc*, mandibular sensory canal; *poc*, preopercular sensory canal.


1
Enpt
Qu
Art
Cor
Pr.art

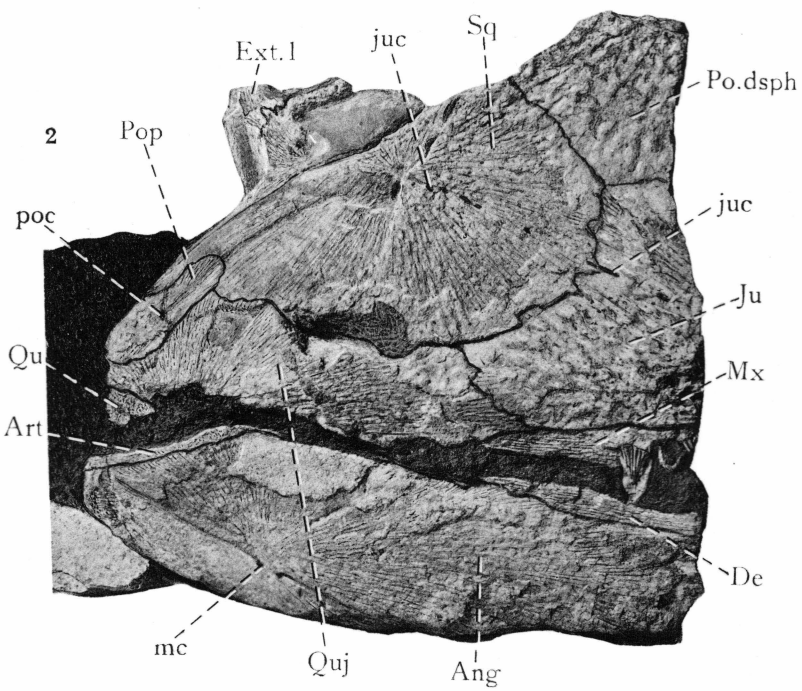

2
Ext.l
juc
Sq
Po.dsph
Pop
poc
juc
Ju
Qu
Mx
Art
De
mc
Quj
Ang

Plate VI.

Fig. 1. *Ichthyostega watsoni* n. sp. Imperfect skull in dorsal view. Specimen A. 3. Natural size.

Fig. 2. Ichthyostegid sp. a. The parts surrounding the otic notch.

Fig. 3. Ichthyostegid sp. a. Palatal view of the ventral process of the lateral extrascapular. Figs. 2 and 3 slightly magnified ($\times$ $^{6}/_{5}$).

A, anterior antorbital; *Ant*, posterior antorbital; *Dpl*, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Ext. l*, *l. d*, dorsal lamina of lateral extrascapular; *Ext. l*, *l. pm*, postero-medial lamina of lateral extrascapular; *Ext. l*, *pr. p*, posterior process of lateral extrascapular; *Ext. l*, *pr. v*, ventral process of lateral extrascapular; *Ext. m*, parieto-extrascapular; *Fr*, frontal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na. ptr*, naso-postrostral; *Pop*, preopercular; *Quj*, quadratojugal; *R. ir*, rostro-interrostral; *R. pmxc*, rostro-premaxillary, sensory canal component; *R. pmxd*, rostro-premaxillary, tooth-bearing component; So_1*?*, probably anterior supraorbital; *Sq*, squamosal; *c*, canal probably for vessels and nerves to the supraorbital sensory canal; *ifc*, infraorbital sensory canal; *ifp*, pore of the infraorbital sensory canal; *juc*, jugal sensory canal.

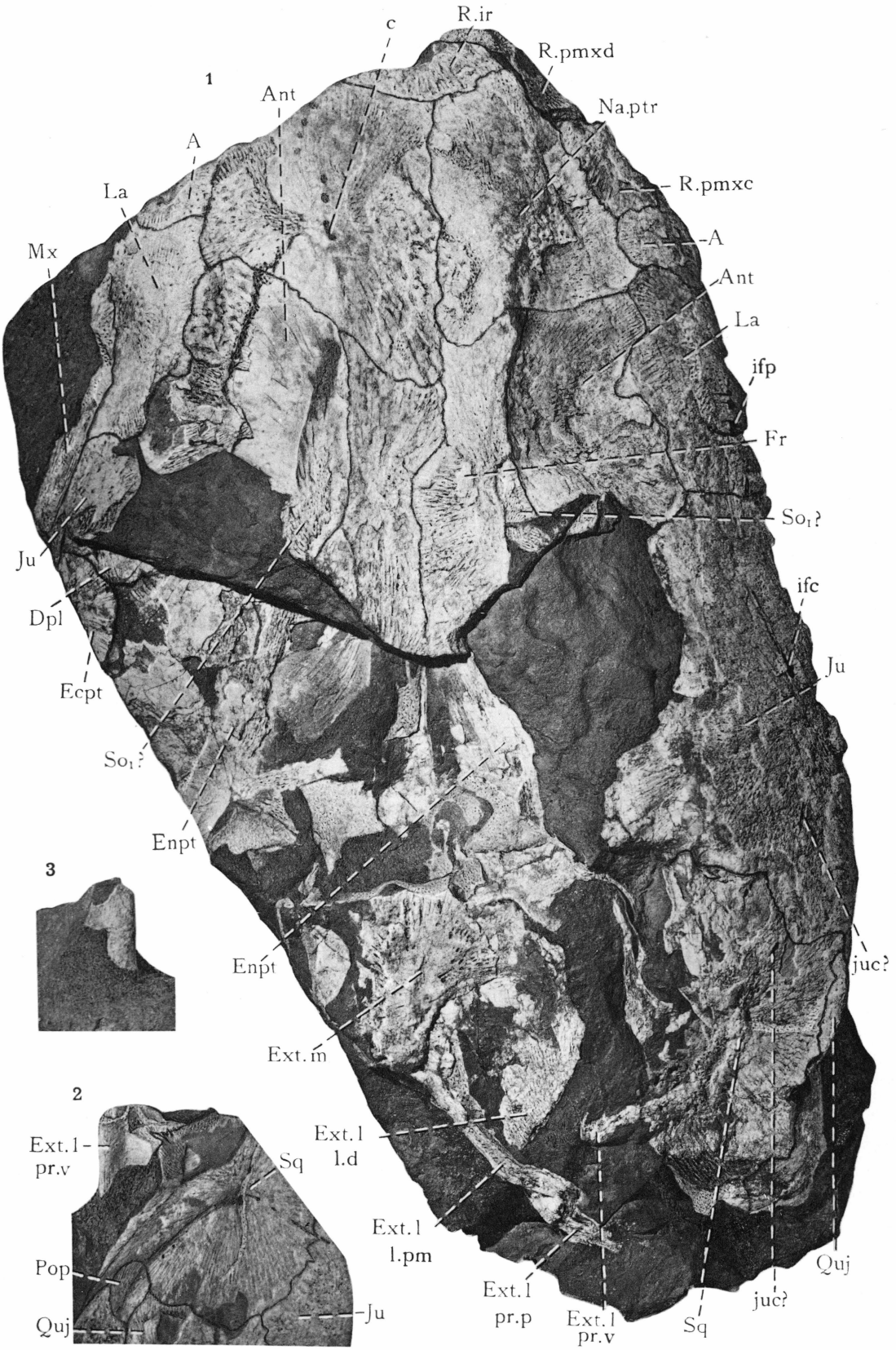

1
c
R.ir
R.pmxd
Ant
Na.ptr
A
R.pmxc
La
A
Mx
Ant
La
ifp
Fr
So1?
Ju
ifc
Dpl
Ju
Ecpt
So1?
Enpt
3
Enpt
juc?
Ext.m
2
Ext.l
pr.v
Sq
Ext.l
l.d
Ext.l
l.pm
Pop
Quj
Ju
Ext.l
pr.p
Ext.l
pr.v
Sq
juc?
Quj

Plate VII.

Ichthyostega watsoni n. sp. Same specimen as in pl. VI, fig. 1, in ventro-lateral view. Natural size.

Enptq, quadrate ramus of entopterygoid; *Ju*, jugal; *Mx*, maxillary; *Pmx*, rostro-premaxillary, tooth-bearing component; *Quj*, quadratojugal.

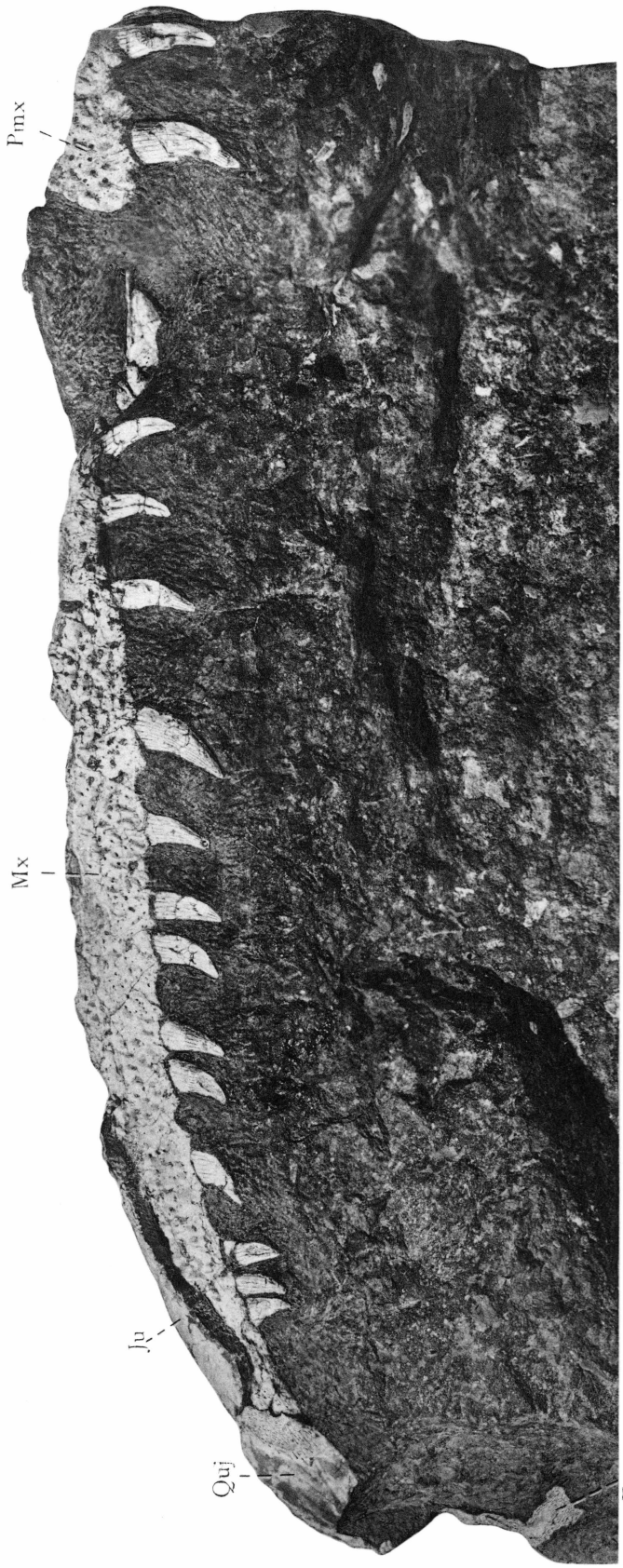

Pmx
Mx
Ju
Quj
Enptq

Plate VIII.

Ichthyostega watsoni n. sp. Same skull as in pl. VI, fig. 1 and pl. VII. Most of the cranial roof removed so as to show the palate in dorsal view. Natural size. *A*, anterior antorbital; *Dpl*, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Enptq*, quadrate ramus of entopterygoid; *Ext. l*, *l. pm*, postero-medial lamina of lateral extrascapular; *Ext. l*, *pr. v*, ventral process of lateral extrascapular; *Ju*, jugal; *Mx*, maxillary; *Quj*, quadratojugal; *R. ir*, rostro-interrostral; *R. pmx?*, probably part of the left rostro-premaxillary; *R. pmxc*, rostro-premaxillary, sensory canal component; *R. pmxd*, rostro-premaxillary, tooth-bearing component; *Sq*, squamosal; *Vo*, vomer; *apv*, anterior palatal vacuity; *n. e*, external naris; *n. i*, internal naris.

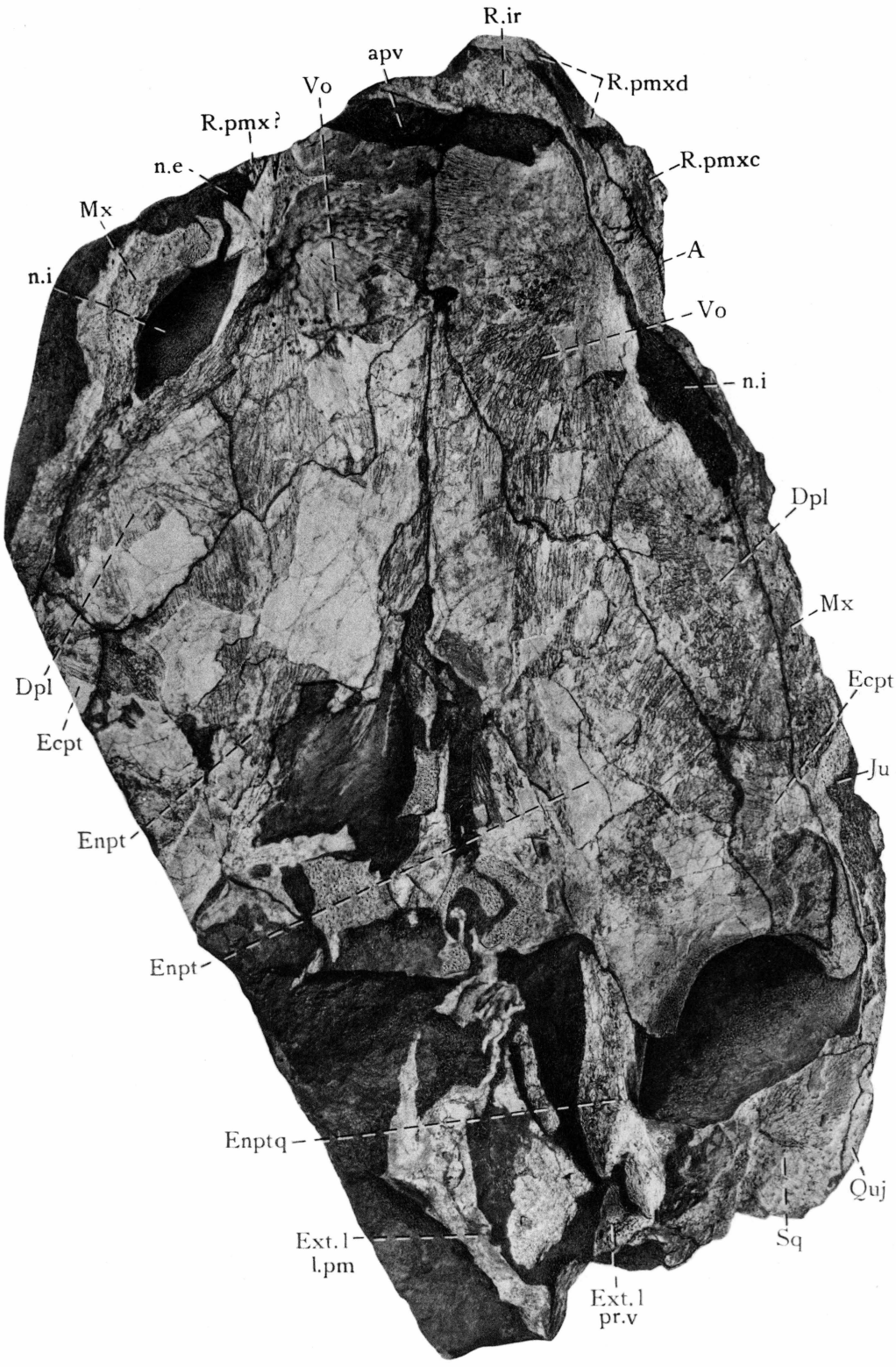

R.ir
apv
Vo
R.pmxd
R.pmx?
n.e
R.pmxc
Mx
A
n.i
Vo
n.i
Dpl
Mx
Dpl
Ecpt
Ecpt
Ju
Enpt
Enpt
Enptq
Quj
Sq
Ext.l
l.pm
Ext.l
pr.v

Plate IX.

Ichthyostega eigili n. sp. Imperfect skull in dorsal view. Specimen A. 4. Natural size.

A, anterior antorbital; *Ant*, posterior antorbital; *Ext. l, l. d*, dorsal lamina of lateral extrascapular; *Ext. l, l. l*, lateral lamina of lateral extrascapular; *Ext. l, l. pm*, postero-medial lamina of lateral extrascapular; *Ext. l, pr. p*, posterior process of lateral extrascapular; *Ext. m*, parieto-extrascapular; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na. ptr*, naso-postrostral; *Pa*, fronto-parietal; *Po. dsph*, postorbito-dermosphenotic; *Quj*, quadratojugal; *R. ir*, rostro-interrostral; *R. pmxc*, rostro-premaxillary, sensory canal component; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *ifp*, pores of the horizontal portion of the suborbital part of the infraorbital sensory canal; *juc*, jugal sensory canal; *pin*, pineal foramen.

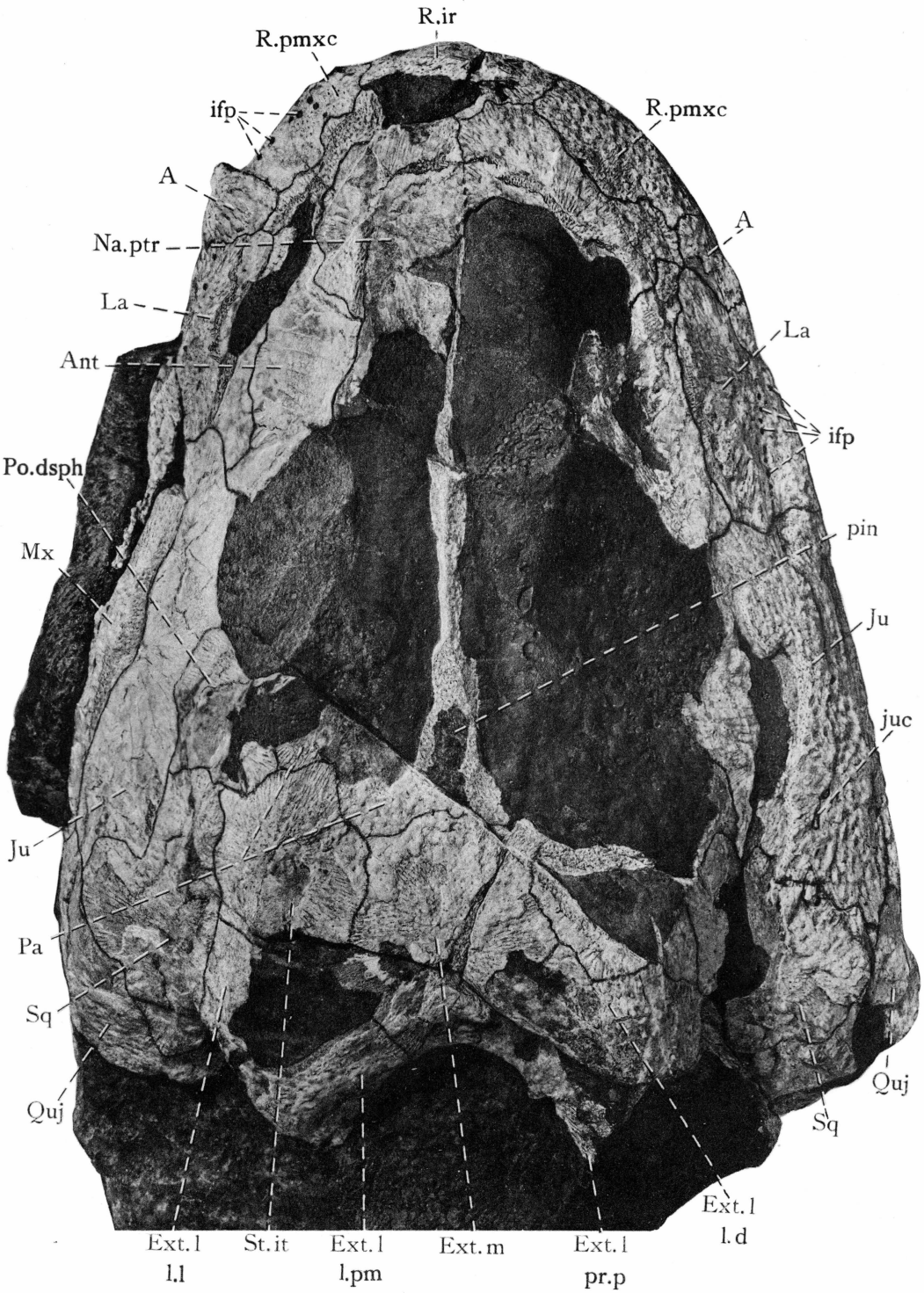

R.ir
R.pmxc
ifp
R.pmxc
A
A
Na.ptr
La
La
Ant
ifp
Po.dsph
pin
Mx
Ju
juc
Ju
Pa
Sq
Quj
Quj
Sq
Ext.l
l.d
Ext.l
l.l
St.it
Ext.l
l.pm
Ext.m
Ext.l
pr.p

Plate X.

Ichthyostega eigili n. sp. Dorsal view of the same specimen as in pl. IX. The most postero-dorso-lateral parts removed so as to show the left cheek. Natural size.
A, anterior antorbital; *Ant*, posterior antorbital; *Enpt*, entopterygoid; *Enptq*, quadrate ramus of entopterygoid; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na. ptr*, naso-postrostral; *Pop?*, possible position of preopercular; *Quj*, quadratojugal; *R. ir*, rostro-interrostral; *R. pmxc*, rostro-premaxillary, sensory canal component; *Sq*, squamosal; *ifc*, horizontal portion of the suborbital part of the infraorbital sensory canal; *ifp*, pore of the horizontal portion of the suborbital part of the infraorbital sensory canal; *jut*, primary tube of the jugal sensory canal; *pin*, pineal foramen.

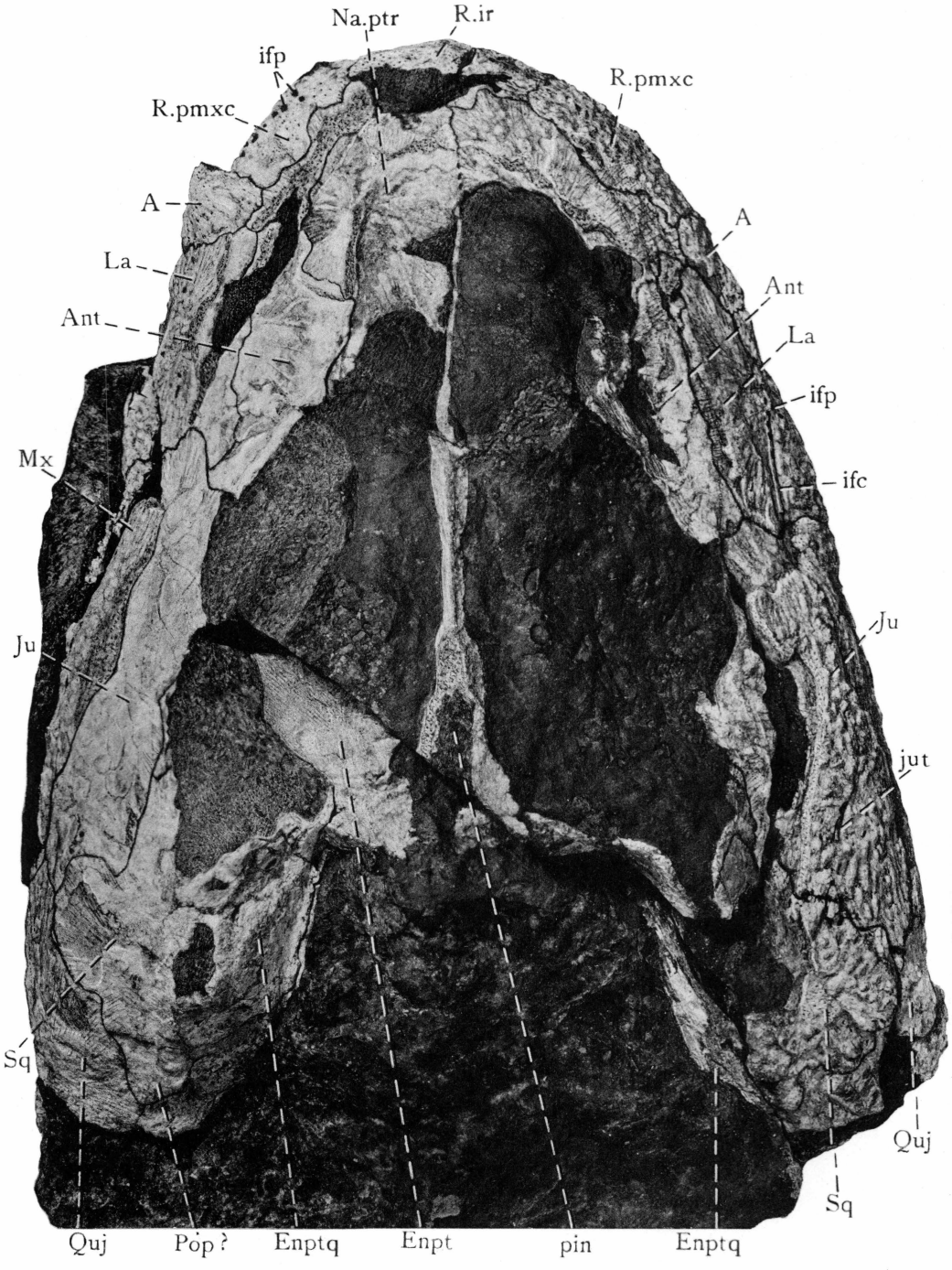

Na.ptr
R.ir
ifp
R.pmxc
R.pmxc
A
A
La
Ant
Ant
La
ifp
Mx
ifc
Ju
Ju
jut
Sq
Quj
Sq
Quj
Pop ?
Enptq
Enpt
pin
Enptq

Plate XI.

Ichthyostega eigili n. sp. Lateral view of the same specimen as in pls. IX, X. Natural size. *A*, anterior antorbital; *Ant*, posterior antorbital; *Ext. l*, *l. l*, lateral lamina of lateral extrascapular; *Ext. l*, *l. pm*, postero-medial lamina of lateral extrascapular; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na. ptr*, naso-postrostral; *Po. dsph*, postorbito-dermosphenotic; *Quj*, quadratojugal; *R. ir*, rostro-interrostral; *R. pmxc*, rostro-premaxillary, sensory canal component; *R. pmxd*, rostro-premaxillary, tooth-bearing component; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *ifc*, horizontal portion of the suborbital part of the infraorbital sensory canal; *ifp*, pore of the horizontal portion of the suborbital part of the infraorbital sensory canal; *jut*, primary tubes of the jugal sensory canal; *n. e*, external naris.

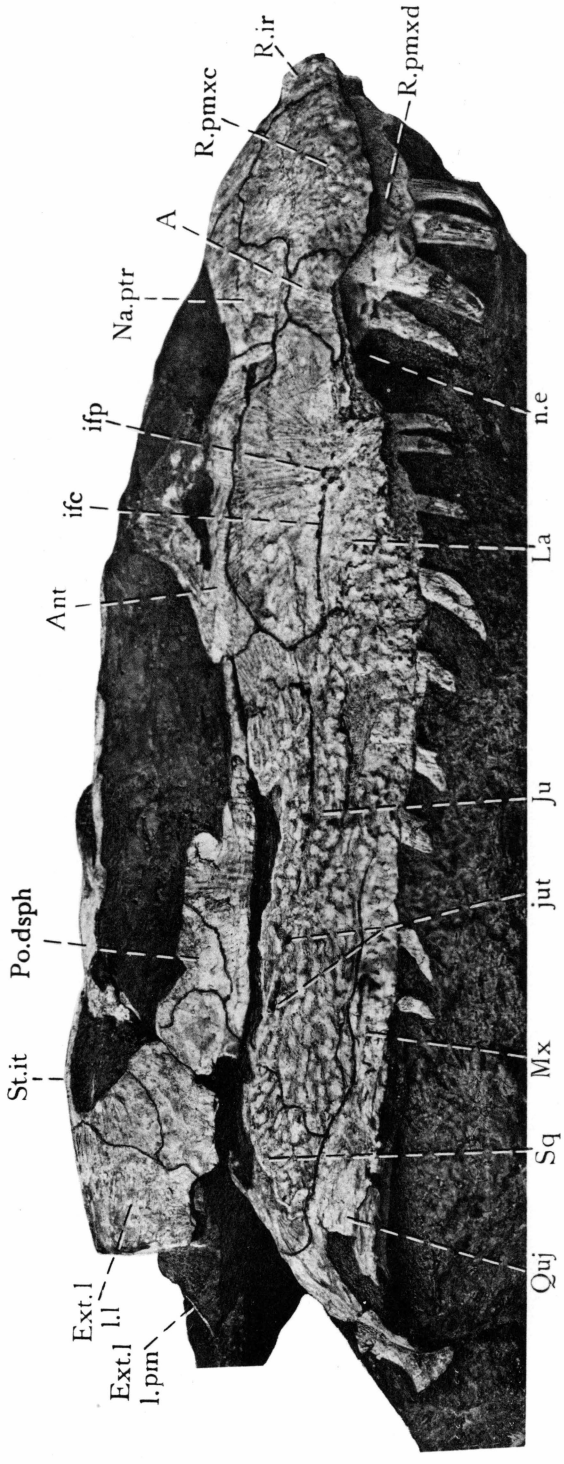

R.ir
R.pmxc
R.pmxd
A
Na.ptr
ifp
n.e
ifc
La
Ant
Ju
jut
Po.dsph
St.it
Mx
Sq
Quj
Ext.l
l.l
Ext.l
l.pm

Plate XII.

Ichthyostega eigili n. sp.

Fig. 1. Same specimen as in pls. IX, X, XI, in ventral and left lateral view. × $^3/_2$.

Fig. 2. Part of the lachrymal of the same specimen to show a part of the infraorbital sensory canal. × 7.

A, anterior antorbital; *La*, lachrymal; *Mx*, maxillary; *R. ir*, rostro-interrostral; *R. pmxc*, rostro-premaxillary, sensory canal component; *R. pmxd*, rostro-premaxillary, tooth-bearing component; *ifc*, horizontal portion of the suborbital part of the infraorbital sensory canal; *ifg?*, groove, probably for the ethmoidal commissure of the infraorbital sensory canal; *ifp*, pores of the horizontal portion of the suborbital part of the infraorbital sensory canal; *ift*, primary tubes of the horizontal portion of the suborbital part of the infraorbital sensory canal; *n. e*, external naris.

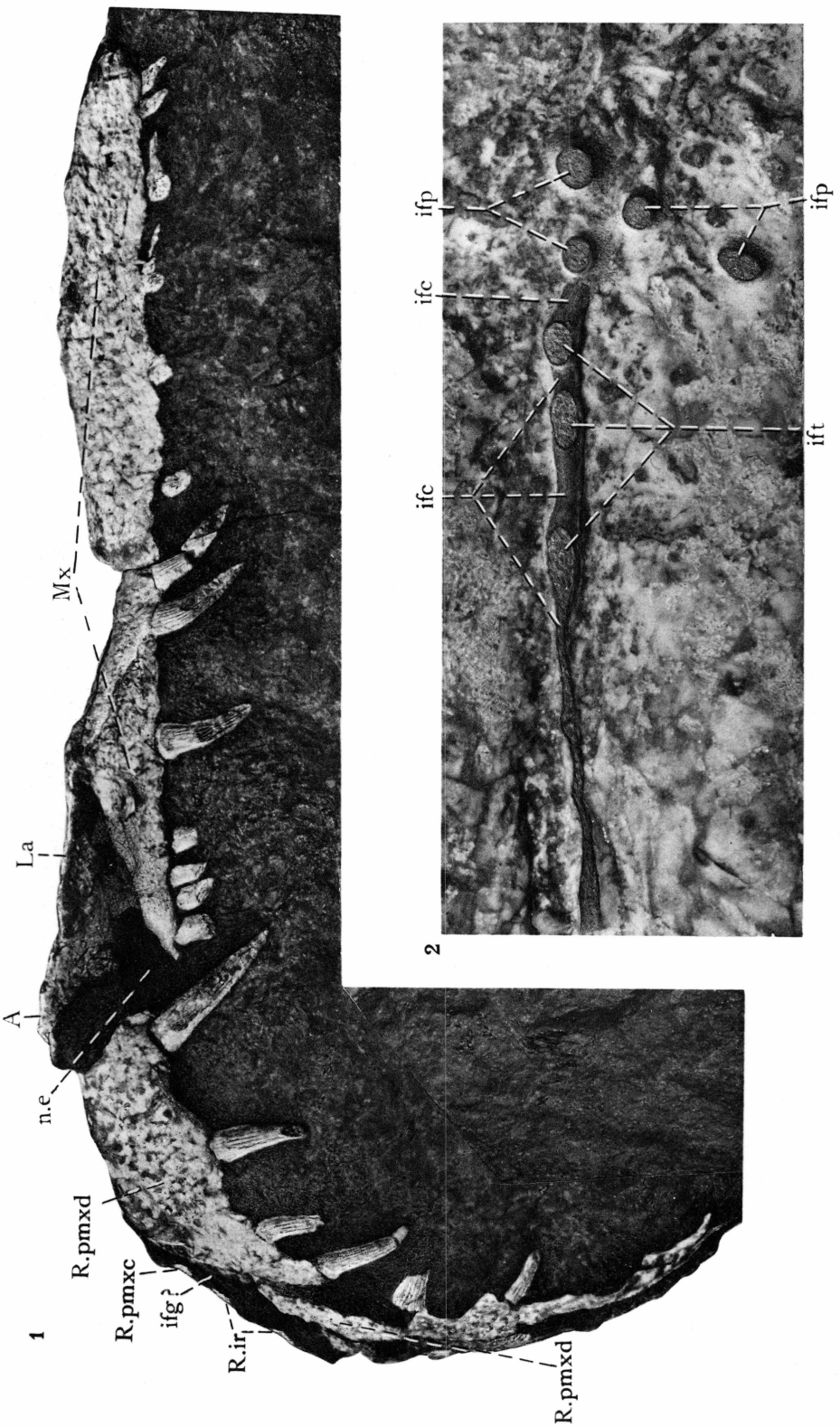

1
A
La
Mx
n.e
R.pmxd
R.pmxc
ifg?
R.ir
R.pmxd
2
ifp
ifc
ifc
ift
ifp

Plate XIII.

Ichthyostega eigili n. sp. Same specimen as in pls. IX, X, XI, XII. The snout seen from in front, below and somewhat from the left side. $\times$ $^3/_2$.

A. anterior antorbital; *Mx*, maxillary; *R. ir*, rostro-interrostral; *R. pmxc*, rostro-premaxillary, sensory canal component; *R. pmxd*, rostro-premaxillary, tooth-bearing component; *n. e*, external naris.

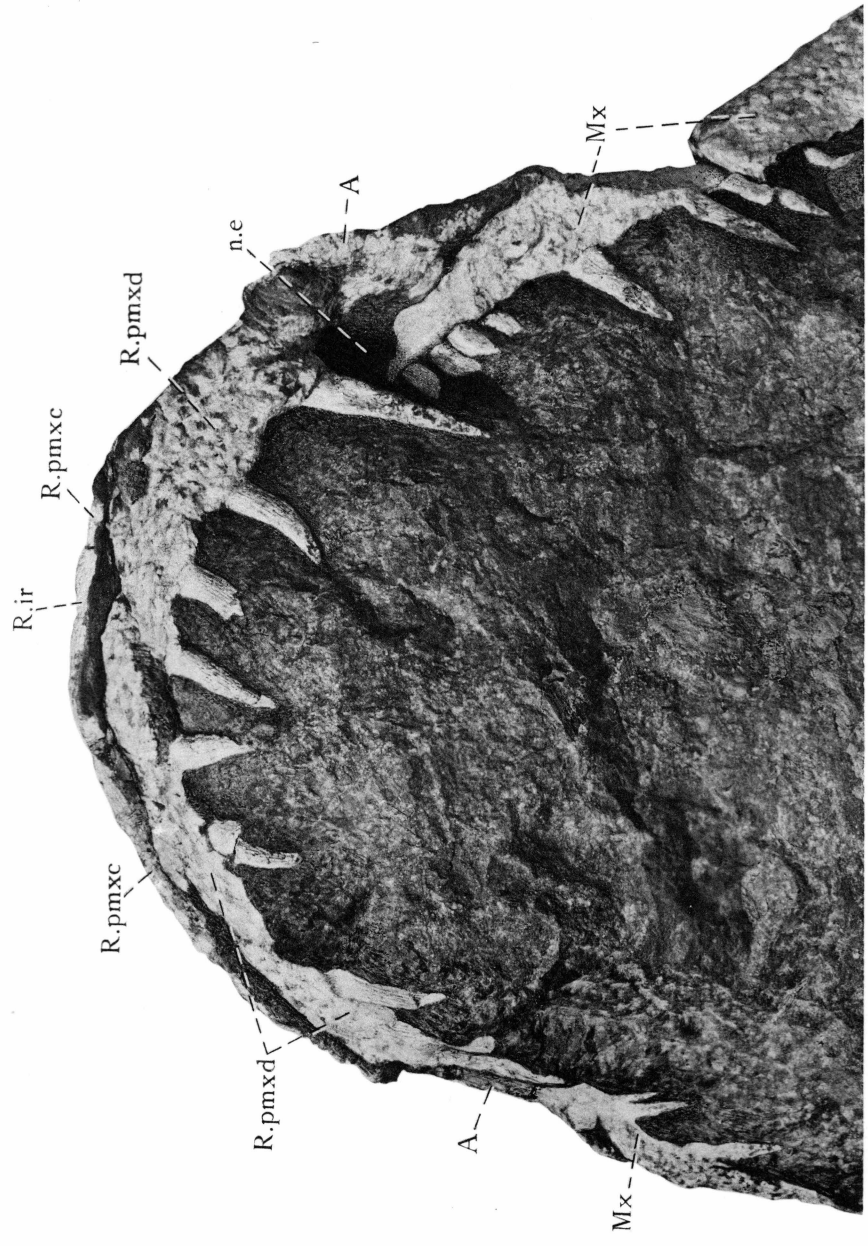

R.ir
R.pmxc
R.pmxd
n.e
A
Mx
R.pmxc
R.pmxd
A
Mx

Plate XIV.

Ichthyostega eigili n. sp. Same specimen as in pls. IX, X, XI, XII, XIII. Most of the cranial roof removed so as to show the palate in dorsal view. Natural size.

A, anterior antorbital; *Dpl*, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Enptq*, quadrate ramus of entopterygoid; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na. ptr*, naso-postrostral; *Quj*, quadratojugal; *R. ir*, rostro-interrostral; *R. pmx*, rostro-premaxillary; *R. pmxc*, rostro-premaxillary, sensory canal component; *Sq*, squamosal; *Vo*, vomer; *apv*, anterior palatal vacuity; *cp*, canals, probably for branches of the art. palatina, v. palatina medialis and n. palatinus; *fen. add*, adductor fenestra; *ifc*, horizontal portion of the suborbital part of the infraorbital sensory canal; *juc*, jugal sensory canal; *n. ec*, communication between the external and internal naris; *n. i*, internal naris.

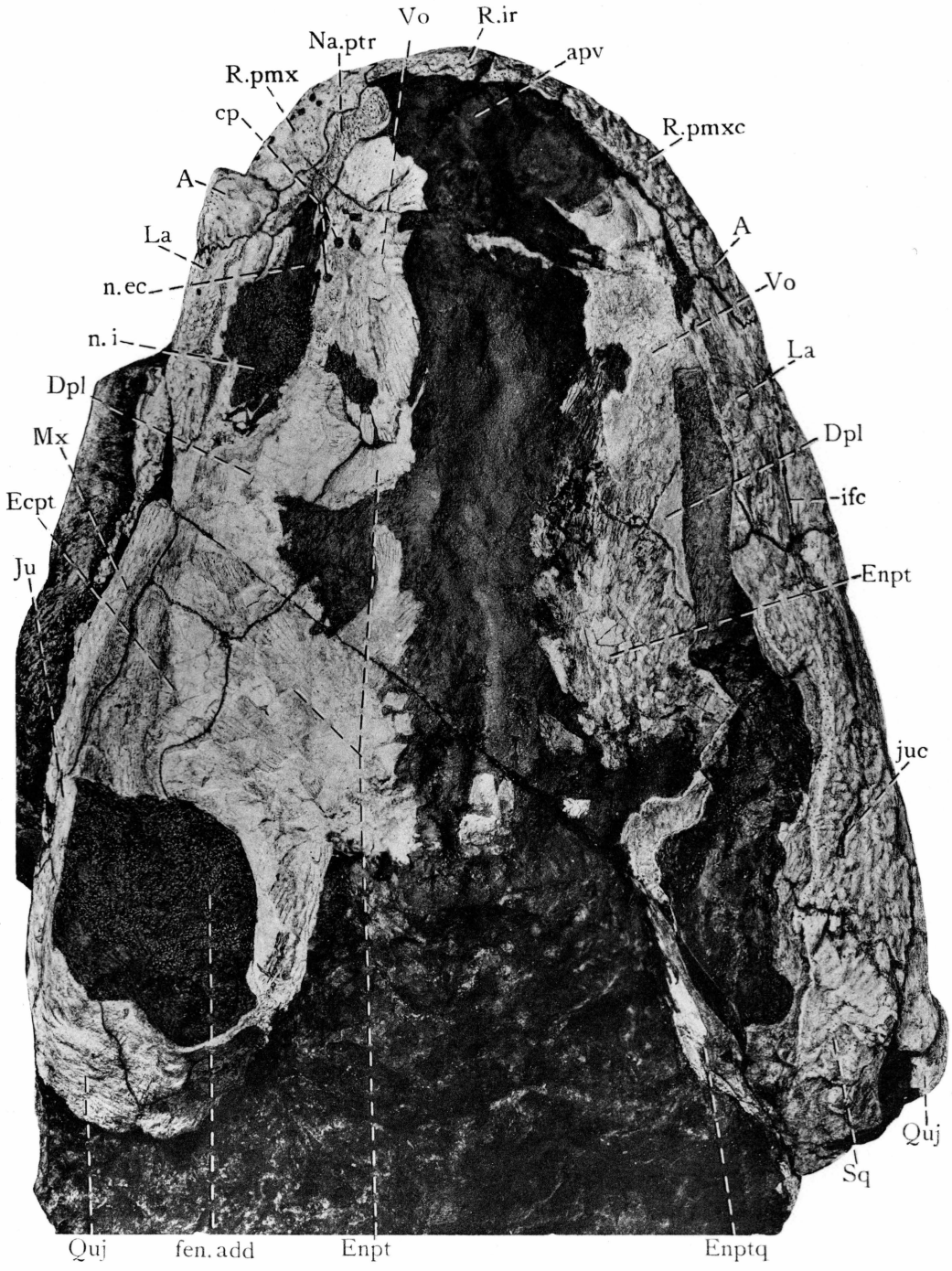

Vo
R.ir
Na.ptr
apv
R.pmx
cp
R.pmxc
A
A
La
n.ec
Vo
n.i
La
Dpl
Dpl
Mx
ifc
Ecpt
Enpt
Ju
juc
Quj
Sq
Quj
fen.add
Enpt
Enptq

Plate XV.

Ichthyostega eigili n. sp. Same specimen as in pls. IX, X, XI, XII, XIII, XIV. The parts removed in pl. XIV shown in ventral view. Natural size.

Dpl, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Enptq*, quadrate ramus of entopterygoid; *Psph*, parasphenoid; *Rpmxc*, rostro-premaxillary, sensory canal component; *Vo*, vomer; *apv*, anterior palatal vacuity; *fen. add*, adductor fenestra.

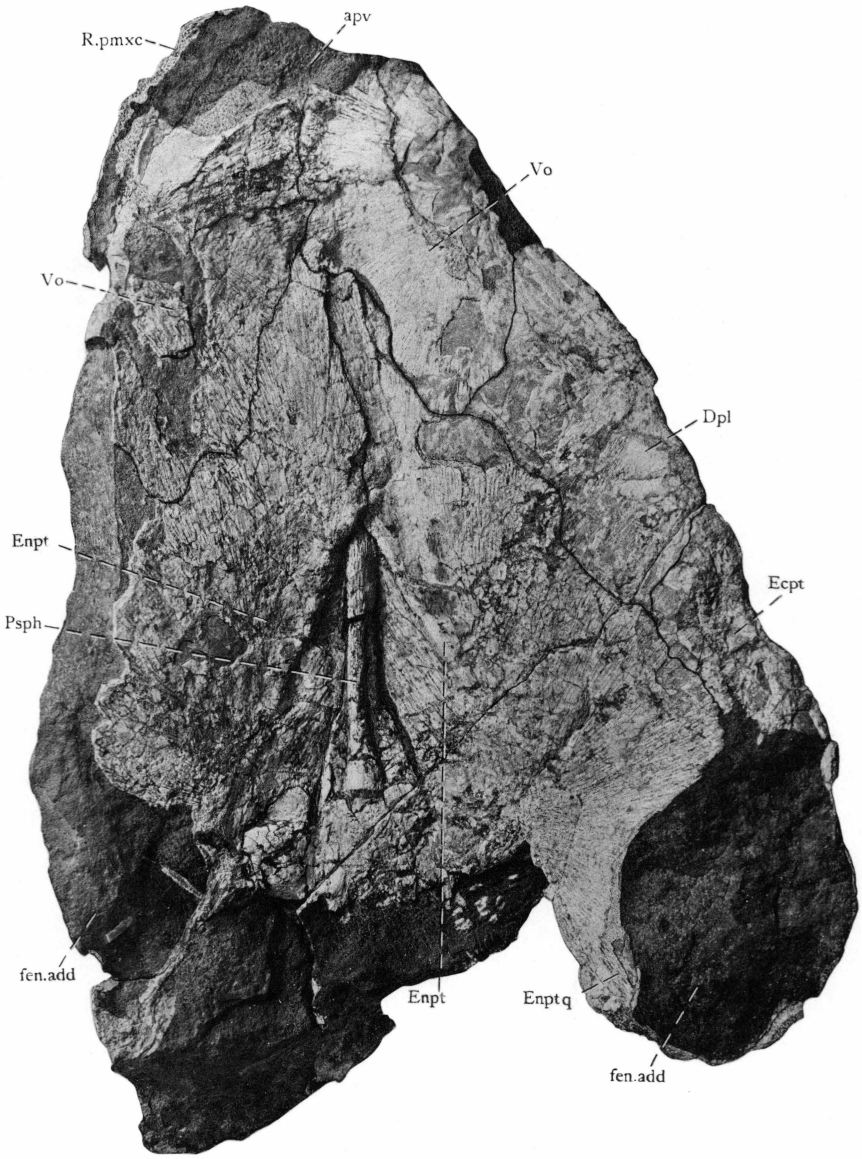
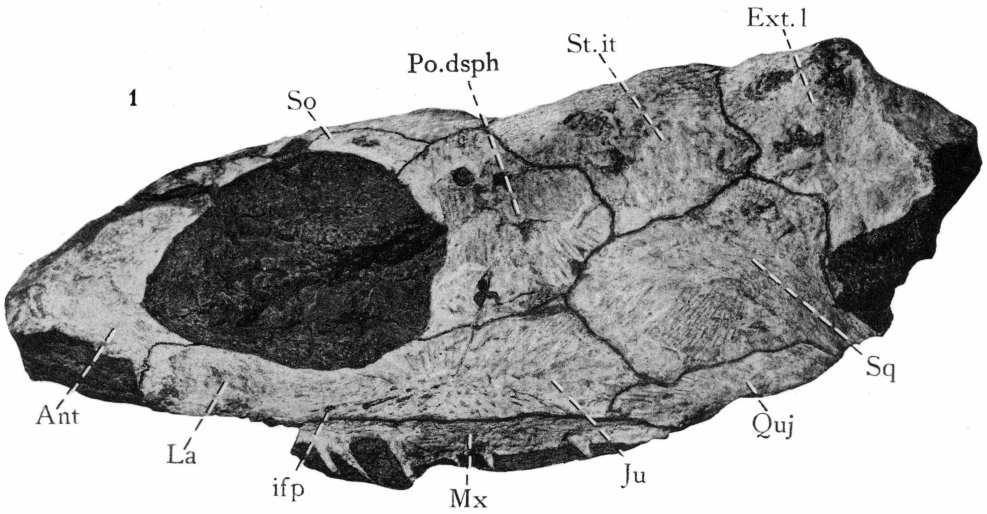

apv
R.pmxc
Vo
Vo
Dpl
Enpt
Ecpt
Psph
fen.add
Enpt
Enptq
fen.add

Plate XVI.

Fig. 1. *Ichthyostegopsis wimani* n. sp. Imperfect skull in lateral view. Specimen A. 5. a. × $^3/_2$.

Fig. 2. *Ichthyostega?* sp. b. Part of the cranial roof in ventral view. Specimen 2. × $^4/_3$.

Ant, posterior antorbital; *Ext. l*, lateral extrascapular; *Ext. m*, parieto-extrascapular; *Fr*, frontal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Pa*, fronto-parital; *Po. dsph*, postorbito-dermosphenotic; *Quj*, quadratojugal; *So*, posterior supraorbital; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *ifc*, vertical portion of the suborbital part of the infraorbital sensory canal; *ifp*, pore of the horizontal portion of the suborbital part of the infraorbital sensory canal.


1
Ext.l
St.it
Po.dsph
So
Sq
Ant
La
ifp
Mx
Ju
Quj

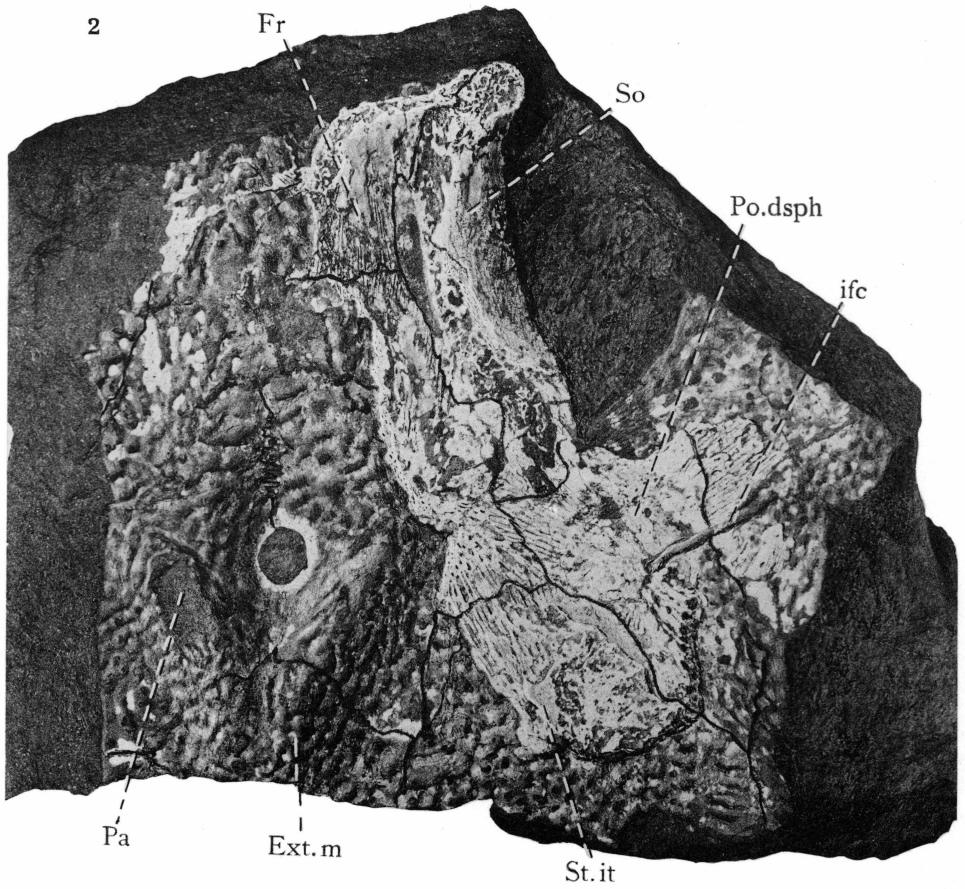

2
Fr
So
Po.dsph
ifc
Pa
Ext.m
St.it

Plate XVII.

Ichthyostegopsis wimani n. sp. Imperfect skull. Specimen A. 5. a. × $^3/_2$.
Fig. 1. In dorsal view.
Fig. 2. In palatal view.
Ant, posterior antorbital; *Dpl*, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Ext. l*, *l. d*, dorsal lamina of lateral extrascapular; *Ext. l*, *l. l*, lateral lamina of lateral extra-scapular; *Ext. l*, *l. p.* posterior lamina of lateral extrascapular; *Ext. l*, *pr. v*, ventral process of lateral extrascapular; *Ext. m*, parieto-extrascapular; *Fr*, frontal; *Ju*, jugal; *La*, lachrymal; *Pa*, fronto-parietal; *Po. dsph*, postorbito-dermosphenotic; *Psph*, parasphenoid; *Quj*, quadratojugal; *So*, posterior supraorbital; *Sq*, squamosal; *St. it.* supratemporo-intertemporal; *Vo*, vomer; *dm*, teeth of the maxillary; *dp*, palatal teeth; *ifp*, pore of the horizontal portion of the suborbital part of the infraorbital sensory canal; *ift*, primary tube of the horizontal portion of the suborbital part of the infraorbital sensory canal; *n. i*, internal naris.

1
Ant
Fr
La
ifp
Po.dsph
ift
Ju
So
Pa
St.it
Quj
Sq
Ext.l
l.l
Ext.l
l.p
Ext.l
l.d
Ext.m

2
Vo
n.i
Dpl
dp
dm
Ecpt
dm
dp
Enpt
Enpt
Psph
Ext.l
pr.v
Ext.l
pr.v

Plate XVIII.

Ichthyostegopsis wimani n. sp. Imperfect cranial roof, exposed from within. Specimen A. 5. b. × $^3/_2$.

Fig. 1. In ventro-lateral view.

Fig. 2. In ventral view.

Ant, posterior antorbital and anterior supraorbital or possibly antorbito-supraorbital; *Ext. l*, lateral extrascapular; *Ext. m*, parieto-extrascapular; *Fr*, frontal; *Ju*, jugal; *La* lachrymal; *Mx*, maxillary; *Pa*, fronto-parietal; *Po. dsph*, postorbito-dermo-sphenotic; *Quj*, quadratojugal; *So*, posterior supraorbital; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *ifc*, vertical portion of the suborbital part of the infraorbital sensory canal; *ifp*, pore of the horizontal portion of the suborbital part of the infraorbital sensory canal; *juc*, jugal sensory canal.

1
Ant
Fr
So
Pa
Ext.m
La
Mx
ifp
Ju
ifc
Po.dsph
juc
Quj
Sq
Ext.l
St.it
2

Plate XIX.

Ichthyostegopsis wimani n. sp. A lateral part of the cranial roof showing the lateral line system in the jugal and squamosal. Specimen A. 5. b. × $^{11}/_{2}$.

Ju, jugal; *Mx*, maxillary; *Po. dsph*, postorbito-dermosphenotic; *Quj*, quadrato-jugal; *Sq*, squamosal; *ifc*, vertical portion of the suborbital part of the infraorbital sensory canal; *ifp*, pore of the horizontal portion of the suborbital part of the infra-orbital sensory canal; *ift*, primary tubes of the suborbital part of the infraorbital sensory canal; *juc*, jugal sensory canal; *jut*, primary tube of the jugal sensory canal; *orb*, orbit.

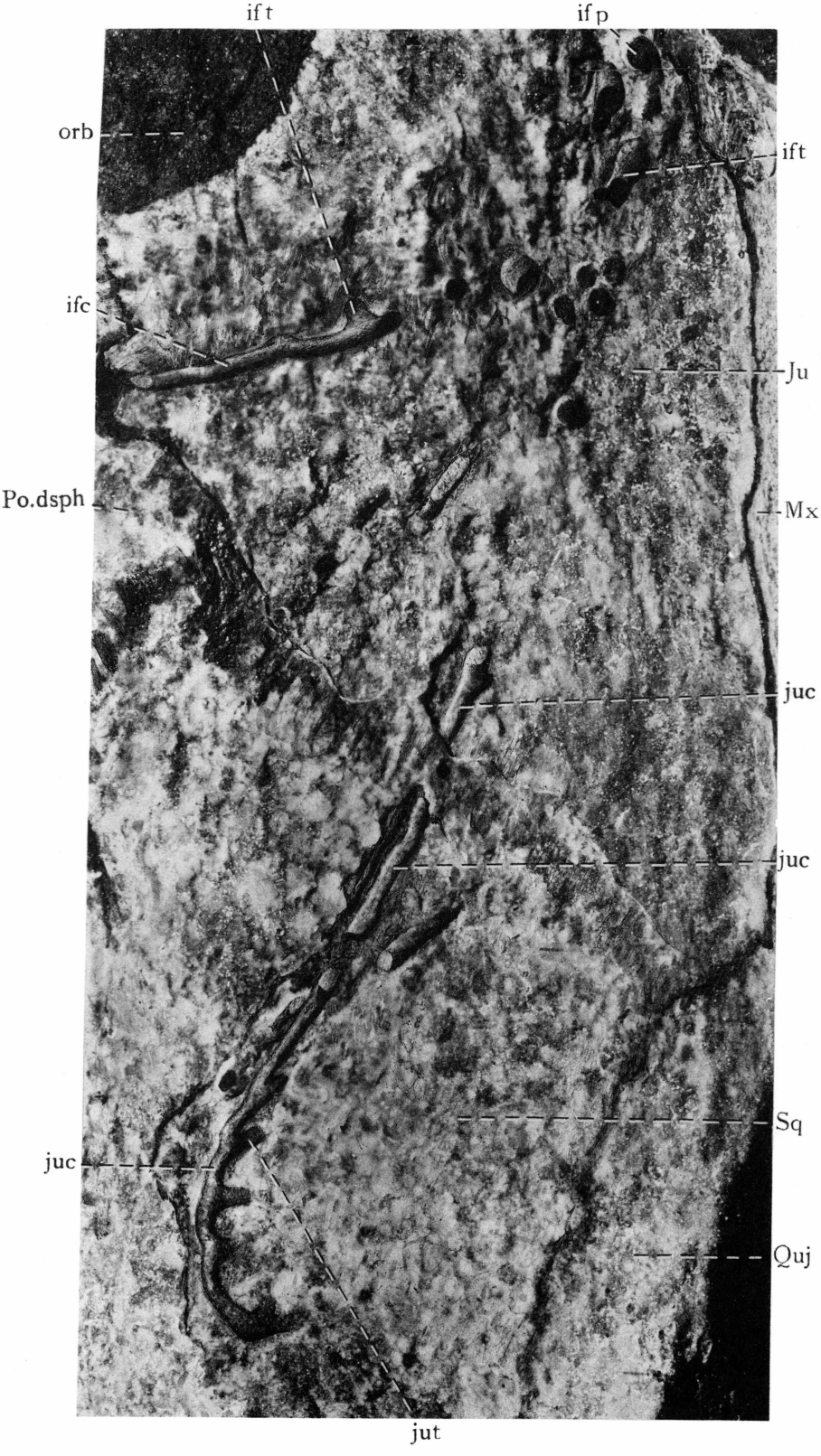

if t
if p
orb
ift
ifc
Ju
Po.dsph
Mx
juc
juc
Sq
juc
Quj
jut

Plate XX.

Ichthyostega? kochi n. sp. Imperfect right half of a skull. Specimen A. 7. $\times$ $^3/_2$. *Ant*, posterior antorbital; *Fr*, frontal; *Ju*, jugal; *Na. ptr*, naso-postrostral; *Pa*, fronto-parietal; *Po. dsph*, postorbito-dermosphenotic; *R. ir*, rostro-interrostral; So_1?, probably independent anterior supraorbital; So_2, posterior supraorbital; *Sq*, fragment of the squamosal; *St. it*, fragment of the supratemporo-intertemporal; *ifc*, vertical portion of the suborbital part of the infraorbital sensory canal; *ifp*, pore of the vertical portion of the suborbital part of the infraorbital sensory canal; *pin*, pineal foramen; *soc*, supraorbital sensory canal; *sop*, pores of the supraorbital sensory canal; *sot*, primary tubes of the supraorbital sensory canal.

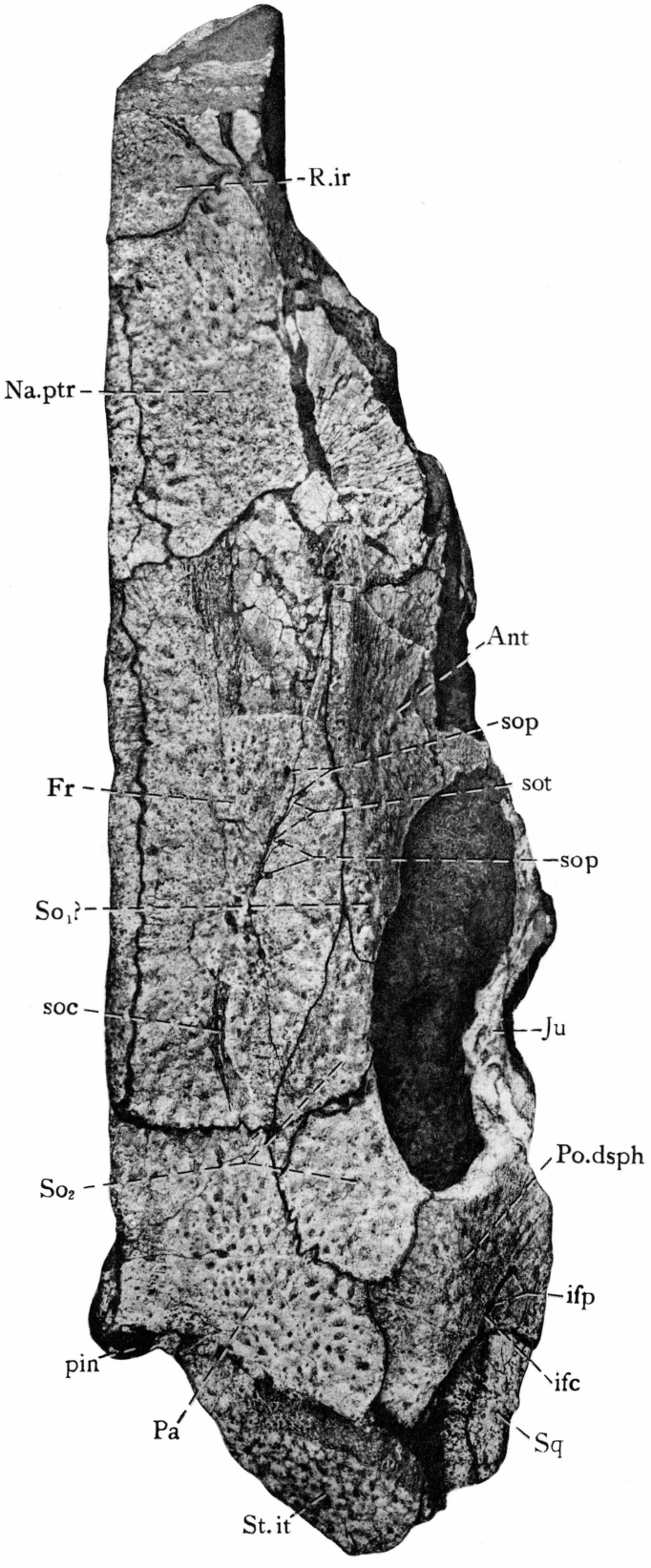

R.ir
Na.ptr
Ant
sop
Fr
sot
sop
So1?
soc
Ju
Po.dsph
So2
ifp
pin
ifc
Pa
Sq
St.it

Plate XXI.

Ichthyostega? kochi n. sp. Same specimen as in pl. XX.

Fig. 1. Fragment mainly of the right frontal with section to show supraorbital sensory canal. The matrix filling the canal consists of a peripheral, thin, dark layer and a central more bright mass. In the greater part of the exposed portion of the canal the preparation has cut through the peripheral dark layer, which appears as a thin dark line bounding the sections through the canal and its tubes; but in the midmost part of the middle curved portion of the canal (not denoted by any lettering) there are left parts of the peripheral dark layer round the whole canal. × 5.

Fig. 2. The skull in lateral view. × $^3/_2$.

Ant, posterior antorbital; *Fr*, frontal; *Ju*, jugal; *Na. ptr*, naso-postrostral; *Pa*, frontoparietal; *Po. dsph.* postorbito-dermosphenotic; So_1*?*, probably independent anterior supraorbital; So_2, posterior supraorbital; *Sq*, fragment of the squamosal; *St. it*, fragment of the supratemporo-intertemporal; *ifc*, vertical portion of the suborbital part of the infraorbital sensory canal; *ifp*, pore of the vertical portion of the suborbital part of the infraorbital sensory canal; *pin*, pineal foramen; *soc*, supraorbital sensory canal; *sop*, pore of the supraorbital sensory canal; *sot*, primary tube of the supraorbital sensory canal.

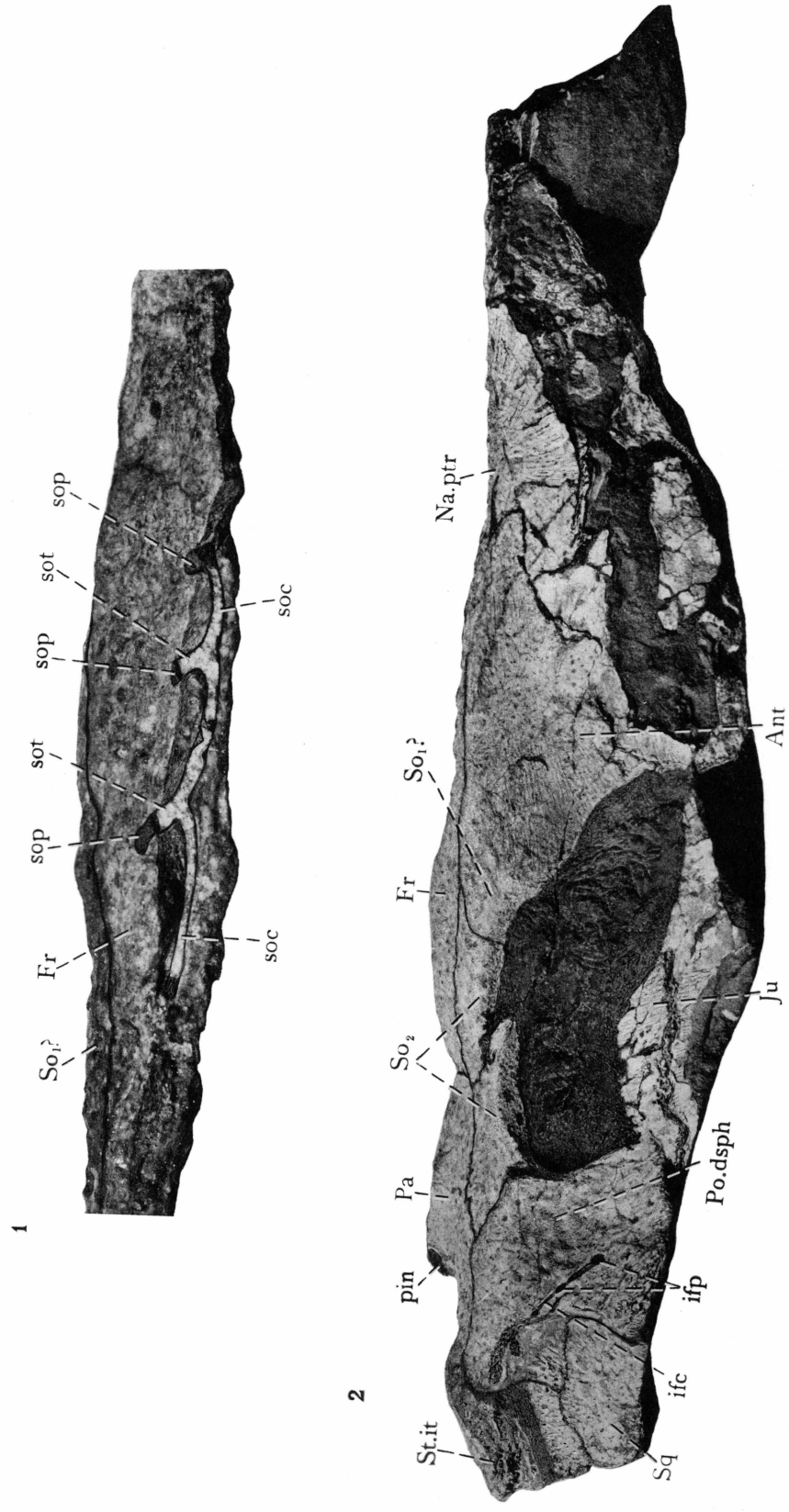
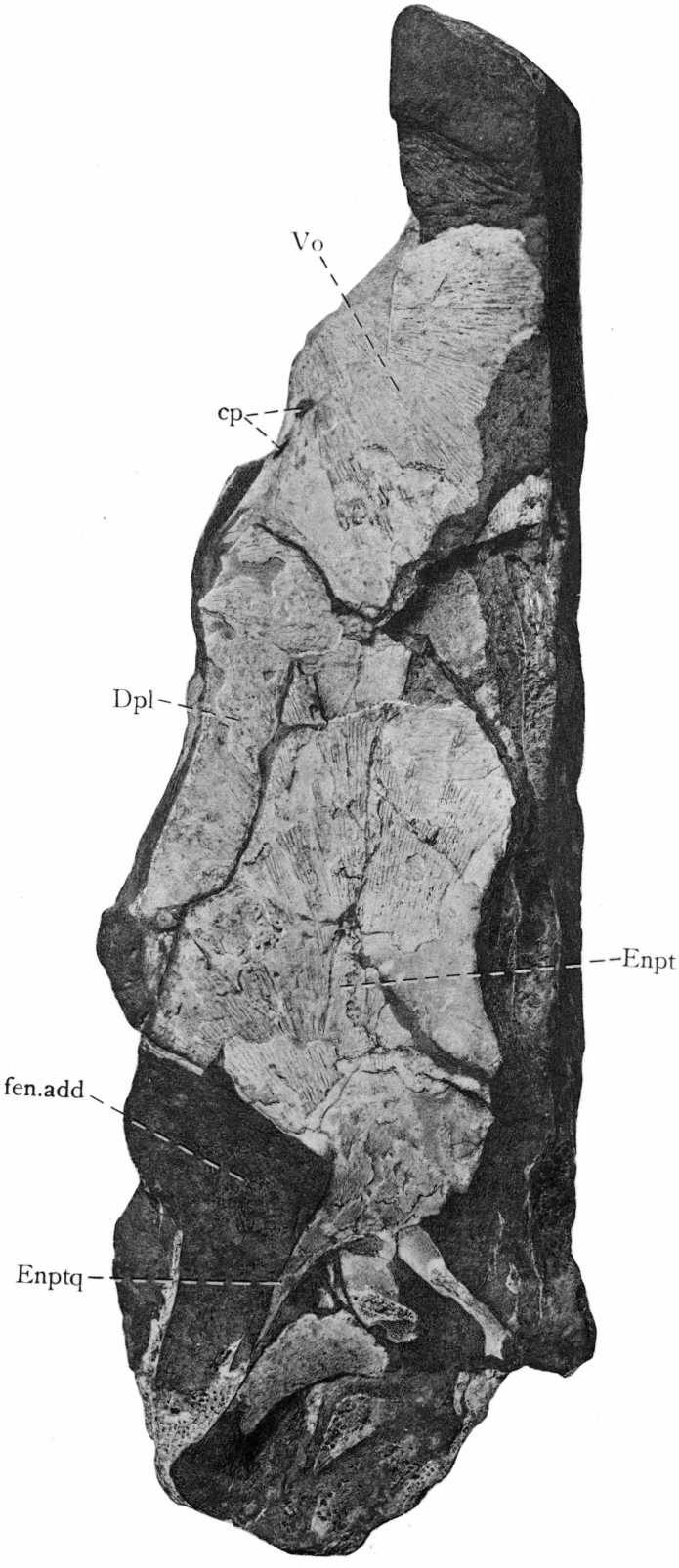

1
So1?
Fr
sop
sot
sop
soc
sop
sot
sop
soc
2
St.it
Sq
ifc
ifp
pin
Pa
So2
So1?
Fr
Na.ptr
Ant
Ju
Po.dsph

Plate XXII.

Ichthyostega? kochi n. sp. Same specimen as in pls. XX, XXI in palatal view. $\times {}^{3}/_{2}$
Dpl, dermopalatine; *Enpt*, entopterygoid; *Enptq*, quadrate ramus of entopterygoid; *Vo*, vomer; *cp*, canals, probably for branches of the arteria palatina, the vena palatina medialis and the nervus palatinus; *fen. add*, adductor fenestra.


Vo
cp
Dpl
Enpt
fen.add
Enptq