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ON THE DERMAL BONES OF THE HEAD IN LABYRINTHODONT STEGOCEPHALIANS AND PRIMITIVE REPTILIA

WITH SPECIAL REFERENCE TO EOTRIASSIC STEGOCEPHALIANS FROM EAST GREENLAND

BY

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WITH 68 FIGURES IN THE TEXT AND 15 PLATES

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PREFACE

The Danish Expeditions to East Greenland, under the leadership of Dr. LAUGE KOCH, Copenhagen, are already famous for their contributions to modern Vertebrate Palaeontology.

In 1932 I had the great pleasure of describing the very interesting material of Devonian Stegocephalians, collected during the expedition of 1931. In the summer of 1932, when my publication (SÄVE-SÖDERBERGH 1932) on these phylogenetically important primitive Tetrapods was still in the press, further important finds of Stegocephalians were made in East Greenland. During the summer expedition of 1932, very large collections of Devonian Fishes and Stegocephalians were brought together by a party under my leadership, and an extraordinary beautiful collection of Eotriassic vertebrates was made, at Cape Stosch, by another party, under the leadership of my friend and former assistant, Mr. E. NIELSEN. Mr. NIELSEN, as a member of the Second Wintering Party of the Danish Three-year East Greenland Expedition has now collected and brought home still more material of Triassic vertebrates.

The Eotriassic vertebrates, collected by the Danish expeditions up to 1931, have been exhaustively described by E. STENSIÖ (1932). They include Selachians (mainly teeth and fin-spines), Coelacanthids of the new genus *Laugia* STENSIÖ, and nine highly interesting and important species of Actinopterygians.

In the large collection of 1932 and 1933, from the Eotriassic of Cape Stosch, there are several new fish species. But there are also representatives of another group of vertebrates, the find of which was naturally to be expected because of the similarity of the fish-fauna with that of Spitsbergen. This group is the labyrinthodont Stegocephalians.

One of these Labyrinthodonts is so well preserved that it will have to be investigated by SOLLAS' grinding-method. Therefore I postpone the investigation of the endocranium of the new Triassic Stegocephalians, as well as of that of the Ichthyostegids, till the intended investigations by the grinding-method have been carried out.

In my above-mentioned paper on the Devonian Stegocephalians (1932), I attempted a detailed analysis of the dermal bones, and a homologisation with the dermal bones of the Crossopterygians. Then I had the occasion, in a later paper, on *Osteolepis* (1933), to put forward certain further facts, supporting the theoretical conceptions, at which I had arrived in my earlier paper. Finally I have now made an extensive study of the available literature on the dermal bones of the geologically younger Stegocephalians and primitive Reptiles. Thus I have reached a fairly definite opinion on the nature and homologies of the dermal bones of the Crossopterygians and earlier Tetrapods.

Now, in order to give a comprehensive account of the dermal bones of the new Eotriassic Stegocephalians from East Greenland, it is necessary to follow the phylogenetic development of the dermal bones of the skull, from the Crossopterygians and Ichthyostegids, over the Carboniferous and Permian Tetrapods to the Triassic Labyrinthodonts. For this purpose I have searched through all available more modern literature on the "*Embolomeri*", "*Rachitomi*", and "*Stereospondyli*", photographing, and making copies of all good figures of the dermal bones of the head.

I am indebted to Doctor LAUGE KOCH, Chief of the Geological Survey of Greenland (G. G. U., Copenhagen), and to my friend Mr. E. NIELSEN, Copenhagen, for the privilege of studying the interesting material of Eotriassic Stegocephalians from East Greenland.

The present publication was worked out in the Swedish Riksmuseum. I am highly indebted to the Keeper of the Palaeozoological Department of this museum, Professor E. STENSIÖ, not only for the privilege of working at his institute, with all its modern technical resources, but also for many interesting and instructive discussions, and for his great kindness and interest in my work.

The work of preparation was carried out with great patience and skill by Mrs. A. STENSIÖ and Miss A. BRASCH, who have also assisted in the preparation of the plates and text-figures. The drawing and retouch work was made by Mr. S. EKBLOM, and Miss I. EKBOM. I was assisted by Mrs. M. FERM in the photographic work, and the type-writing was done by Mrs. M. FERM and Miss B. ARNELL. Mr. J. W. ROCHE, English Lecturer at the University of Uppsala, made the necessary stylistic corrections of the manuscript. To all these collaborators I want to express my sincere thanks.

INTRODUCTION

Two different methods can be employed in examining the morphological importance of the dermal bones in the Vertebrate head.

In the study of these structures in a recent vertebrate, the most appropriate method is a thorough investigation of the ontogenetic development. By such an investigation one gains an idea of the ontogenetic origin of the dermal bones of the adult, each of which may arise from one or from several primordia; in other words the result of the investigation is a theory concerning the fate of the primordia forming the elements, by which the bones of the adult are built up. The results to be gained in this way will then be compared with the knowledge gained from studies of other animals, especially of related, but more primitive forms.

On the other hand, when dealing with fossil material, another method must naturally be used. This other method is the reverse of the first one: it begins with a comparative anatomical study, and may then be checked to a certain extent by embryological investigations of related recent animals. Here also the aim is, of course, to find out the number, importance and fate of the primordia. But this must here be done mainly by comparison with more primitive related forms.

As is now evident from the recent investigations on primitive Crossopterygians and Stegocephalians (SÄVE-SÖDERBERGH 1932, 1933), these two groups are very closely related, though (in spite of CASE's statement, 1933, p. 266) neither of them originates from the other. They had common fish ancestors, evidently with a greater number of dermal bones than that found in either of the two groups (see SÄVE-SÖDERBERGH 1932, pp. 87—98). More precisely, these ancestors must normally have had at least the following elements[1]):

[1]) Such bones as, for instance, the intratemporals (SÄVE-SÖDERBERGH 1933, pp. 39, 78—79, 113, and p. 185 of the present paper), or the double dermosphenotics (in *Osteolepis macrolepidotus*, SÄVE-SÖDERBERGH 1933, pp. 25—26; pl. 3), which are not normally independent in any of the two groups, may have been only exceptionally independent already in the ancestors of these two groups.

A. Bones developed in connection with the lateral line system:

1. connected with each supraorbital canal: a series of at least three *nasals*; an *anterior frontal*; a *dermosphenotic*;

2. connected with the anterior pit-lines: a *posterior frontal* on each side;

3. connected with the infraorbital canals:

a. connected with the ethmoidal commissure: at least one *median rostral*, and two *lateral rostrals* on each side;

b. connected with the postnasal connections[1]): a posterior antorbital on each side;

c. connected with the horizontal portion of each suborbital part: a *lachrymal* and a *jugal*, the latter also connected with the vertical portion, and with the most anterior part of the jugal canal;

d. connected with the vertical portion of each suborbital part: (a jugal, cf. above), a *postorbital*, and a *dermosphenotic*;

e. connected with each otic part: one, or possibly two, *intertemporals*;

4. connected with each jugal canal: (a jugal, cf. above),

a *squamosal*, also connected with the vertical pit-line;

5. connected with the preopercular canals: one or two *preopercular*s on each side;

6. connected with the vertical pit-lines of the cheeks: (a squamosal, cf. above, and) a *quadratojugal* on each side;

7. connected with each mandibular canal:

a *supraangular*, an *angular*, a *postsplenial* and a *splenial*;

8. connected with each postotic canal:

a *supratemporal*, also connected with the lateral part of the middle pit-line;

9. connected with the middle and posterior pit-lines: (a supratemporal, cf. above, and) a *posterior parietal* on each side;

10. connected with the cephalic divisions of the main lateral line canals and with the supratemporal commissural canal: a series of one *median extrascapular*, and two *lateral extrascapulars* on each side.

B. Bones developed in connection with the teeth of the jaws and the palate[2]):

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[1]) cf. SÄVE-SÖDERBERGH 1933, pp. 7—8.

[2]) This, of course, does not mean to be a statement concerning the correctness or incorrectness of HERTWIG's famous theory (cf. MOY-THOMAS 1934), nor does my mentioning of the theory in 1933 (p. 110) mean that I take a definite position concerning this difficult question. The connection actually existing is an empiric fact, not a theoretical conception.

1. in each upper jaw: a *premaxillary* and a *maxillary*;

2. in each side of the palate: a *vomer*, a *dermopalatine*, an *ectopterygoid*, and an *entopterygoid*;

3. in each half of the lower jaw: a (labial) *dentary* and a (lingual) series of three *coronoids*.

C. General membrane bones:

1. Between the rostrals, the nasals and the anterior frontals: a probably great number of *median* and *lateral postrostrals*;

2. Between the posterior antorbital, the nasals, and the lachrymal: an *anterior antorbital* on each side;

3. Between the frontals and the orbits: a series of at least two *supraorbitals* on each side;

4. Between the posterior frontal, the intertemporal, and the posterior parietal: an *anterior parietal* on each side;

5. Lateral to the supratemporal; an *extratemporal*[1]) on each side;

6. On the ventral surface of the neural endocranium: a median *parasphenoid*;

7. On the lingual surface of the lower jaw: a *prearticular* on each side.

Now, in investigating the fate of all these elements in the descendants of the discussed ancestors, one has to realise that there are for each element four possibilities in the evolution:

1. The element is kept unaltered throughout the series investigated;

2. It becomes fused with other elements to compound dermal bones;

3. It becomes secondarily subdivided;

4. It becomes reduced by continuous decrease in size, and finally fails to ossify.

Moreover, several of these modifications may occur subsequently in the evolution of one element.

It is one of STENSIÖ's most important contributions to the modern vertebrate palaeozoology, that he has recognised and analysed the frequent occurrence of fusions between different elements, as expressed in the compound bone-names he often uses (parieto-intertemporal, rostro-premaxillary, supratemporo-extrascapular, lachrymo-jugal, preoperculo-quadratojugal, etc.; see STENSIÖ 1921, 1922 a, b, 1925, 1931, 1932. Cf. also ALLIS, for instance 1899, p. 70)[2]).

[1]) See SÄVE-SÖDERBERGH 1933, p. 19.

[2]) STENSIÖ sometime uses longer terms of the type rostr*alo*-premaxillary, sometimes shorter terms of the type supratempor*o*-intertemporal. To my mind the shorter terms are the less ugly; and the most widely used terms are of that type.

WATSON, on the other hand, has been unwilling to accept these compound names and thinks that, as a rule, elements are more often reduced than fused with other elements (WATSON 1921 b). Modern embryological investigations (PEHRSON 1922 and others) have, however, confirmed the views of STENSIÖ, in regard to the dermal bones of Fishes. And, as I hope will be evident from my earlier works (1932, 1933), and from the present paper (for instance pp. 45—51), fusions do occur, and the analysis of them is important for the understanding of the dermal bones in Stegocephalians too.

I. THE PHYLOGENETIC EVOLUTION OF THE DERMAL BONES OF THE HEAD IN THE LABYRINTHODONT STEGOCEPHALIANS, AND IN PRIMITIVE REPTILIA

1. The Ichtyostegalia.

Concerning the dermal bones of the head in the *Ichthyostegalia*, the reader is referred in the main to my former work (1932). There are, however, a few additions to be made.

In all important points my earlier homologisations with the dermal bones of the Crossopterygians have been only confirmed by my further studies. Especially I want to call attention to the further support to my conception of the homologies of the frontals, parietals and extrascapulars, obtained by my study on *Osteolepis* and other Crossopterygians (SÄVE-SÖDERBERGH 1933, pp. 111—112, 115—116).

The supraorbital sensory canals could not be followed in their most anterior parts in the material available of the *Ichthyostegidae*. Nevertheless I am perfectly convinced of the correctness of the homologisations expressed in the names of the naso-postrostrals. But further considerations of the conditions in geologically younger Stegocephalians (*Baphetes*, *Orthosauriscus*, text-figs. 1, 2), and in *Dictyonosteus* (STENSIÖ 1922 a), has now led me to the conclusion that a nasal component also enters in the composition of the so-called rostro-premaxillary of the Ichthyostegids. This bone has, consequently, to be called the *naso-rostro-premaxillary*. The new interpretation is supported by the course of the anterior part of the supraorbital canal in *Baphetes* and in *Orthosauriscus* (cf. below, pp. 12, 14), and by the relations of the posterior part of the discussed bone to the interrostral, in Ichthyostegids, and in *Baphetes* and *Orthosauriscus* (cf. SÄVE-SÖDERBERGH 1932, text-figs. 16 A, 16 B, and text-figs. 1, 2 of the present paper).

As will be seen in the following, the structure of the parts at present known of the skull of the ancestors of the true *Labyrinthodontia* (*Loxommoideae*, "*Rhachitomi*", "*Stereospondyli*"; but not the *Anthracosauroideae*

see below, pp. 12, 97—105) has certainly not differed much from that of the corresponding parts in the *Ichthyostegidae*. Probably the ancestors of the true *Labyrinthodontia* may be included in the order *Ichthyostegalia*, which thus would comprise both the *Ichthyostegidae* and the "Ichthyostegid-like Stegocephalians" of the phylogenetic sketch in my former paper (1932 b, p. 104). — In the true *Labyrinthodontia*, as above defined, there is never found an independent intertemporal. All bones of the *Labyrinthodontia* called intertemporals will be proved below to be in reality dermosphenotics. Thus it may be supposed that the fusion of the intertemporal to the supratemporal took place as early as at the transition from the "Fish ancestors" to the "Ichthyostegid-like Stegocephalians" or primitive *Ichthyostegalia*. The same was very probably the case with the sutural attachment of the squamosal to the supratemporo-intertemporal which is found also in the *Loxommoideae*, though not in the *Anthracosauroideae* (cf. below, pp. 92—105).

2. The Loxommoidei.

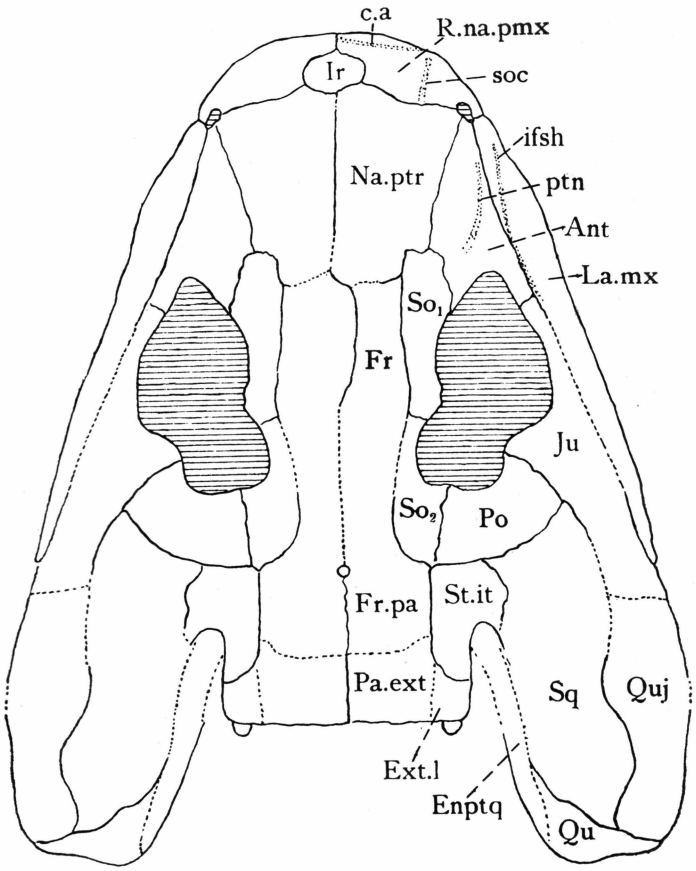
In the "*Embolomeri*" WATSON (1926 a, b) included two well distinguished superfamilies, the *Loxommoideae*, and the *Anthracosauroideae*.

The *Loxommoideae* are clearly and nearly related to the *Ichthyostegidae*; they may be considered the descendants of primitive representatives of the order *Ichthyostegalia*.

The *Anthracosauroideae*, on the other hand, differ in many, and in very important points from both the *Ichthyostegidae* and the *Loxommoideae* (see below, pp. 97—105). The differences are, indeed, so important that I think the two superfamilies of the "*Embolomeri*" have entirely different phylogenetic positions. The *Loxommoideae* form a very natural link between the *Ichthyostegalia* and the Permo-triassic *Labyrinthodontia* — whereas the *Anthracosauroideae* cannot possibly be derived from Ichthyostegid-like ancestors, and may even have arisen from the fish ancestors independently of the Ichthyostegids and the true *Labyrinthodontia*: the *Loxommoideae*, the "*Rhachitomi*", the "*Stereospondyli*".

In consequence of this view, I will here treat only the *Loxommoideae* with the other Labyrinthodonts. The *Anthracosauroideae* will be treated separately afterwards (pp. 92—105). As a further consequence of this I have to erect the new Labyrinthodont Suborder *Loxommoidei* (with the only family *Loxommidae*); and to the former superfamily *Anthracosauroideae* I must give a higher rank, calling it the Order *Anthracosauria*.

The *Loxommoidei* (text-figs. 1—3, 4 B; WATSON 1926 b; ROMER 1930,



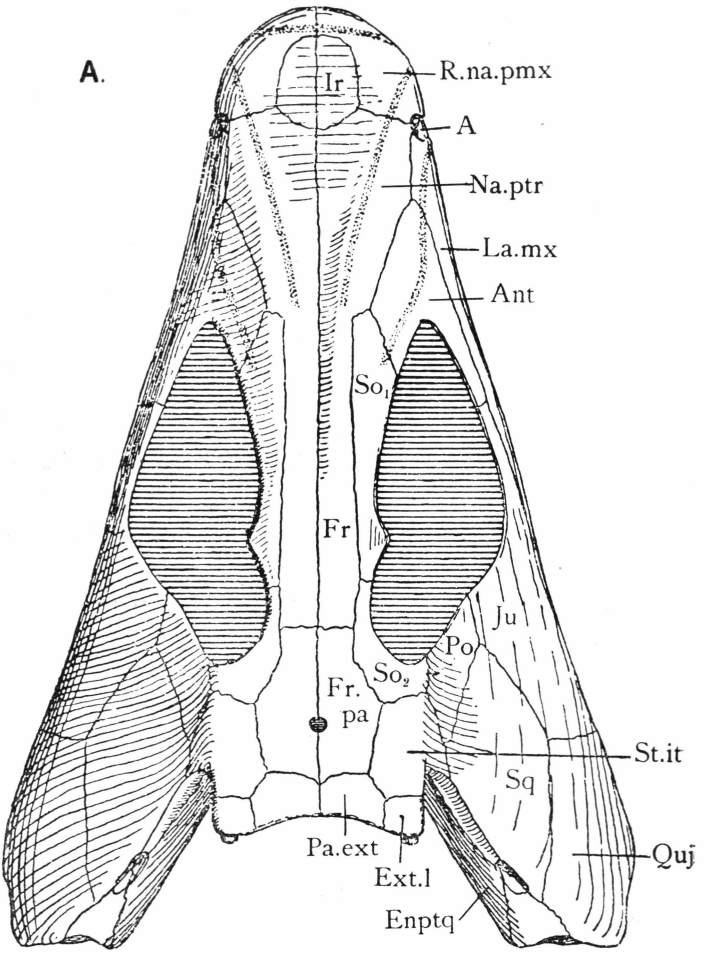
Text-fig. 1. *Baphetes kirkbyi* WATSON. Dorsal surface of the skull. After WATSON (1926 b, fig. 18).

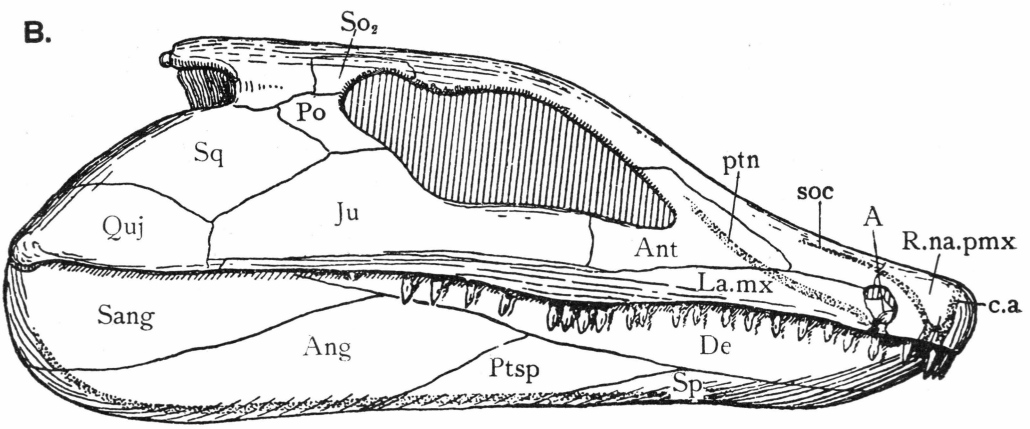
Ant, posterior antorbital; *Enptq*, quadrate ramus of the entopterygoid; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ir*, interrostral; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Qu*, quadrate; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; So_2, posterior supraorbital; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *c. a*, anterior commissure of the infraorbital canals; *ifsh*, horizontal portion of the suborbital part of the infraorbital canal; *ptn*, postnasal connection of the suborbital part of the infraorbital canal with the supraorbital canal; *soc*, supraorbital canal.

pp. 119—126) include the five genera *Loxomma*, *Orthosauriscus*[1]), *Baphetes*, *Macrerpeton*[2]) and *Spathicephalus*. Of these, *Spathicephalus* is rather in-

[1]) In a letter the late Baron NOPCSA kindly called my attention to the fact that the name *Orthosaurus* (BARKAS 1873) is preoccupied, and asked me to propose a new name. In the meantime, however, KUHN has proposed the new name *Orthosauriscus* (KUHN 1933, p. 37).

[2]) Incorrectly referred to the family *Eogyrinidæ* among the *Anthracosauroideae* by WATSON (1926 b, p. 225) and KUHN (1933, pp. 28—29). See ROMER 1930, pp. 119—126, figs. 19—21).





Text-fig. 2. *Orthosauriscus pachycephalus* (BARKAS). A. dorsal; B. lateral aspect of the skull. After WATSON (1926a, figs. 6, 7).
A, anterior antorbital or septomaxillary; *Ang*, angular; *Ant*, posterior antorbital; *De*, dentary; *Enptq*, quadrate ramus of the entopterygoid; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ir*, interrostral; *Ju*, jugal; *La.mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Ptsp*, postsplenial; *Quj*, quadrato-jugal; *R. na. pmx*, naso-rostro-premaxillary; *Sang*, supraangular; So_1, anterior supraorbital; So_2, posterior supraorbital; *Sp*, splenial; *Sq*, squamosal; *St. it*, supratemporo-intertemporal or supratemporo-intertempororo-dermosphenotic; *c. a*, anterior commissure of the infraorbital canals; *ptn*, postnasal connection of the suborbital part of the infraorbital canal with the supraorbital canal; *soc*, supraorbital canal.

completely known. According to WATSON (1926 b, p. 242, fig. 22) its skull represents "a most grotesque modification of the Loxommoid structure". The shape and relations of the fronto-parietals, frontals, supratemporo-intertemporals, and supraorbitals are unknown in *Spathicephalus*.

The other four genera are evidently nearly related to each other. The course of the sutures between their dermal bones is comparable in detail. Thus they afford a good opportunity for studying the fate of certain bone elements.

The dermal bones of the snout are known in *Baphetes* (text-fig. 1), and in *Orthosauriscus* (text-fig. 2 A). In both genera there is clearly an *interrostral* (*Ir*), single (*Baphetes*) or paired (*Orthosauriscus*), and situated, quite as in *Dictyonosteus* (STENSIÖ 1922 a; SÄVE-SÖDERBERGH 1932, text-fig. 16 A), just behind the median part of the ethmoidal commissure of the infraorbital canals. The single interrostral of *Baphetes* evidently represents a more primitive stage than the paired bone of *Orthosauriscus*.

From the course of the ethmoidal commissure, and of the most anterior part of the supraorbital canal, it is clear that the bone on each side, carrying the prenasal teeth (WATSON's premaxillary) is a *naso-rostro-premaxillary* (*R. na. pmx*, text-figs. 1, 2, 3 A), quite equivalent to that of the Ichthyostegids, except that it possibly includes also parts corresponding to the median rostral component, fused with the interrostral in the Ichthyostegids. It seems, however, not less probable that the median rostral has been totally reduced in the Loxommids.

The *naso-postrostrals* (*Na. ptr*, text-figs. 1, 2 A, 3 A), the *frontals* (*Fr*, text-figs. 1, 2 A, 3), and the *fronto-parietals* (*Fr. pa*, text-figs. 1, 2 A, 3) agree very closely in their shape and position with the bones of the same names in the Ichthyostegids, and so do the *supraorbitals* (So_1, So_2, text-figs. 1, 2, 3), except in their relative length. The anterior supraorbital is markedly longer in the *Loxommidae*, especially so in *Orthosauriscus*, owing to a general lengthening of an anterior part of the skull (cf. text-fig. 2).

The small *anterior antorbital* (*septomaxillary*; *A*, text-fig. 23) of *Baphetes* and *Orthosauriscus* has already been discussed in my earlier work (1932, pp. 101—102; cf. also below, pp. 33—38, text-figs. 13, 14, 60—64).

The *posterior antorbital* (*Ant*, text-figs. 1, 2, 3 A) is also identified without difficulty. Both in *Baphetes* and in *Orthosauriscus* it is clearly connected with the postnasal connection (*ptn*, text-figs. 1, 2) of the infraorbital canal with the supraorbital canal. Except for its very deep orbital notch, the posterior antorbital of the *Loxommidae* has the same general shape and extension as that of the *Ichthyostegidae* (cf. especially *Ichthyostega eigili*, SÄVE-SÖDERBERGH 1932, text-fig. 6). Thus it forms a large part of the orbital margin. It meets the jugal, laterally to the orbit, as in *Ichthyostega*. In *Loxomma* (text-fig. 3 A) and *Baphetes* (WATSON

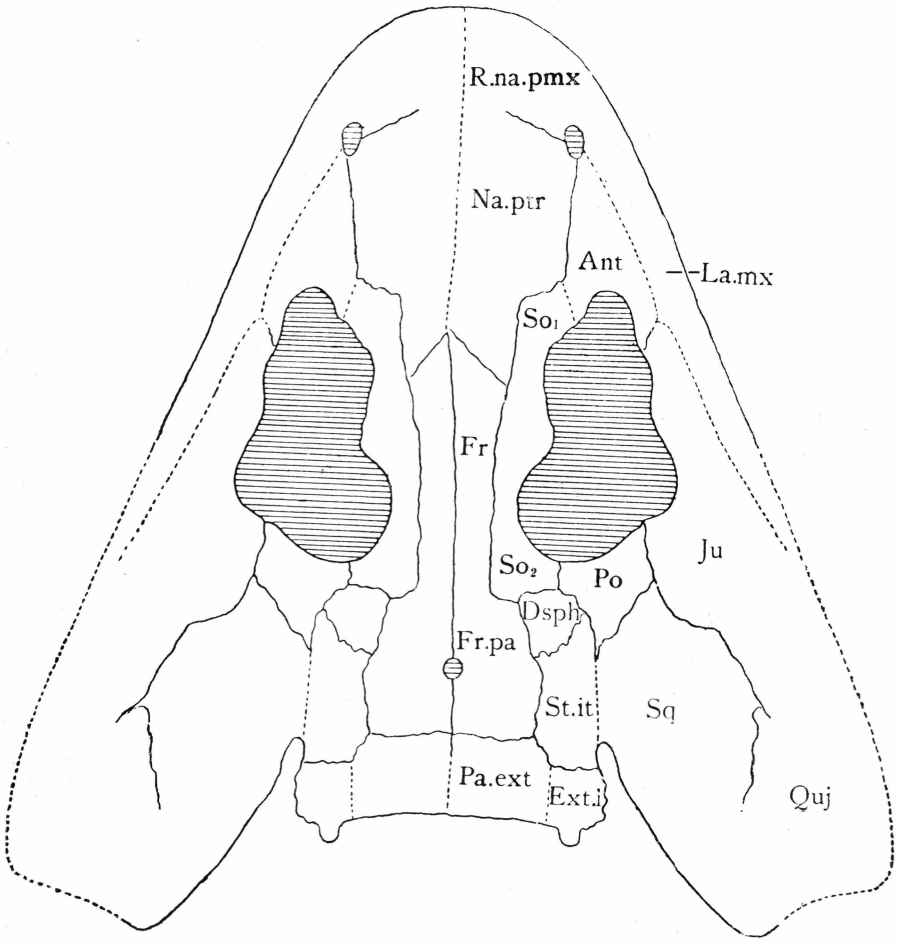


Fig. 3 A.

1926 b, fig. 20) it evidently is in contact with the anterior antorbital, as in *Ichthyostega stensiöi* (SÄVE-SÖDERBERGH 1932, text-fig. 2), whereas it fails to meet that bone in *Orthosauriscus*, as in *Ichthyostega watsoni*, *I. eigili*, and *Ichthyostegopsis wimani* (SÄVE-SÖDERBERGH, 1932, text-figs. 4, 6, 7, 11, 12).

From the above doubtless correct homologisations, as well as from the position of the horizontal portion of the suborbital part of each infraorbital canal in *Baphetes* (*ifsh*, text-fig. 1), the fate of the lachrymal is evident. It must have fused, in the *Loxommoidei*, with the maxillary, to form a compound *lachrymo-maxillary* (*La. mx*, text-figs. 1, 2, 3 A).

The *jugals*, *squamosals*, and *quadratojugals* are easily recognised in the Loxommids. They are very similar, even in details, to the corresponding bones of the Ichthyostegids. The only difficulty in the inter-

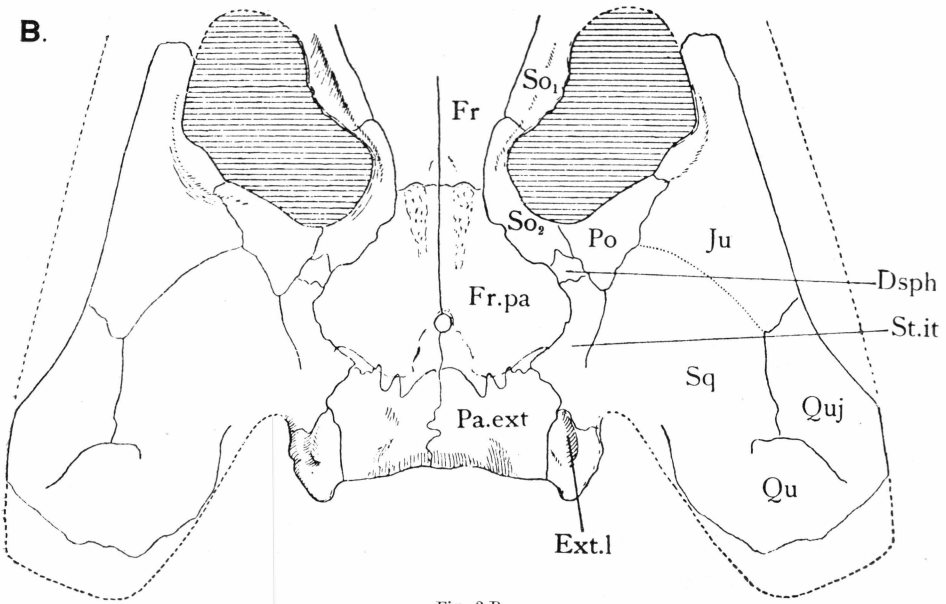


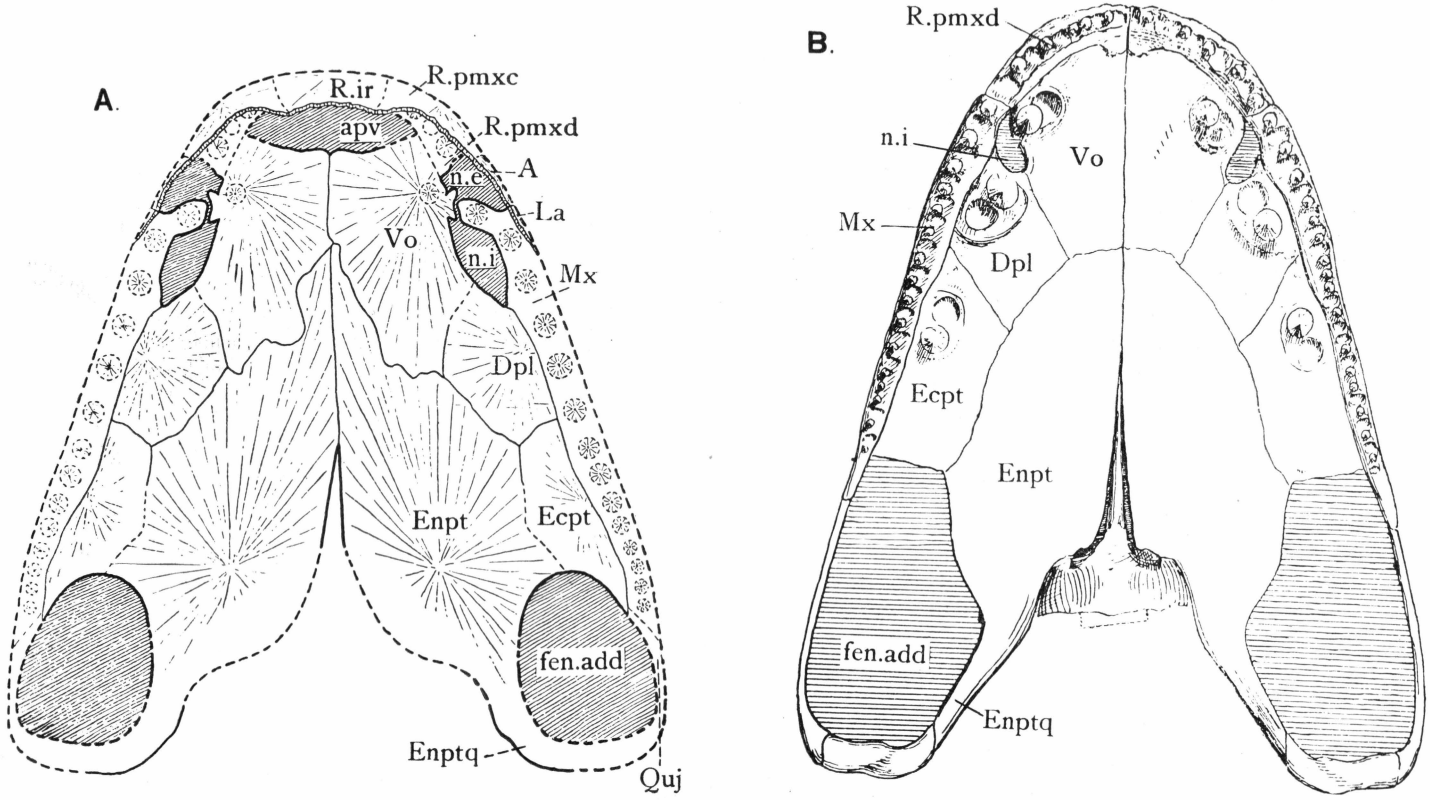
Fig. 3 B.

Text-fig. 3. *Loxomma.* Known parts of the dermal bones on the dorsal surface of the skull. From WATSON (1926 b, figs. 13, 14). A. *Loxomma acutirhinus* WATSON, dorsal surface; B. *Loxomma allmanni* HUXLEY, ventral surface of the bones.
Ant, posterior antorbital; *Dsph*, dermosphenotic; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Qu*, quadrate; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; So_2, posterior supraorbital; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

pretation of the dermal bones of the cheek lies in the explanation of the disappearance of the preopercular. This question is, indeed, too difficult to be solved without a personal close inspection of the *Loxommidae*. The discussed bone may conceivably have been reduced, or it may perhaps have fused with the quadratojugal, as in certain Coelacanthids (STENSIÖ 1932, pp. 36—38, text-fig. 16).

The *postorbitals* of *Loxomma*, *Orthosauriscus* and *Macrerpeton* (*Po*, text-figs. 2, 3; ROMER 1930, figs. 19—21) are clearly homologous with the postorbital components of the postorbito-dermosphenotics of the Ichthyostegids, and with the postorbitals of the Crossopterygians. As in the Crossopterygians, they meet the posterior supraorbitals, excluding all other bones from the postero-dorsal margins of the orbits.

The small bone (*Dsph*, text-fig. 3) in *Loxomma*, situated between the anterior half of the fronto-parietal and the middle third of the medial margin of the postorbital is clearly homologous with the *dermosphenotic*



Text-fig. 4. Palate, A. of *Ichthyostega watsoni* (SÄVE-SÖDERBERGH 1932, text-fig. 4), B. of *Baphetes kirkbyi* (after WATSON 1926 b, fig. 19).

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

of *Osteolepis*. Like this it does not take part in the formation of the orbital margin. It is very much smaller in *Loxomma allmanni* than in *L. acutirhinus*.

As is seen from a detailed comparison of the posterior margin of the posterior supraorbital, the medial margin of the postorbital and the lateral margin of the fronto-parietal in the three genera *Loxomma*, *Macrerpeton*, and *Orthosauriscus*, the dermosphenotic may possibly have fused with the supratemporo-intertemporal in *Orthosauriscus*, and with the posterior supraorbital in *Macrerpeton*. If this is the case, we have in *Orthosauriscus* a *supratemporo-intertemporo-dermosphenotic* (*St. it*, text-fig. 2 A) and in *Macrerpeton* a *supraorbito-dermosphenotic*. It should, however, be noticed, that a total reduction of the dermosphenotic in *Orthosauriscus* is not at all excluded, since a part of the area, covered by the dermosphenotic in *Loxomma*, may be covered by a posterior part of the posterior supraorbital in *Orthosauriscus*. In these circumstances I prefer provisionally calling the bone behind the posterior supraorbital only supratemporo-intertemporal. In *Baphetes* the bone, called by WATSON the postorbital (*Po*, text-fig. 1), has an unusually great medial extension, and is joined by suture with nearly the whole anterior margin of the supratemporo-intertemporal. From this fact it would seem that the dermosphenotic has here fused with the postorbital to a postorbito-dermosphenotic like that of the Ichthyostegids. But the discussed bone in *Baphetes* is not in contact with the fronto-parietal, and the posterior supraorbital has a short suture with the supratemporo-intertemporal. Thus in *Baphetes* each of the posterior supraorbital and the postorbital seem to cover a part of the area, covered in *Loxomma* by the dermosphenotic. And this makes it most probable that we have in *Baphetes* a total reduction of the dermosphenotic.

Except for the possible fusion with the dermosphenotic in *Orthosauriscus*, the *supratemporo-intertemporal* of the Loxommids (*St. it*, text-figs. 1, 2 A, 3) seems to correspond well to that of the Ichthyostegids. Unlike this, it forms a part of the medial margin of the very deep otic notch.

The *lateral extrascapular* of the Loxommids (*Ext. l*, text-figs. 1, 2 A, 3), unlike that of the Ichthyostegids, is not joined by suture with the squamosal.

The paired *parieto-extrascapular* (*Pa. ext*, text-figs. 1, 2 A, 3) of the Loxommids is evidently homologous with the single bone of the same name in the Ichthyostegids. Both bear the same relations to the supratemporo-intertemporals, which they meet, and to the lateral extrascapulars, which are thus excluded from contact with the fronto-parietals.

In the case of the parieto-extrascapular the median suture has evidently been earlier acquired than in the case of the interrostral, which is still single in *Baphetes*.

The Loxommid *palate* is most completely known in *Baphetes kirkbyi*, through the excellent account of WATSON (1926 b, p. 239, fig. 19). The palatal surface of *Baphetes* is extremely similar to that of, for instance, *Ichthyostega watsoni* (see text-fig. 4). There are only two differences of any importance: 1st, there is no anterior palatal vacuity in *Baphetes*; 2nd, the maxillary component of the lachrymo-maxillary meets the premaxillary component of the naso-rostro-premaxillary in *Baphetes*, as the external naris has here migrated to the dorsal surface. In the *Ichthyostegidae*, the external naris opens between the maxillary and the tooth-bearing component of the naso-rostro-premaxillary.

The palatal teeth are very incompletely known in the Ichthyostegids, but they seem to have been, at least in *Ichthyostegopsis*, more numerous than in the Loxommids.

A large anterior palatal vacuity, wholly similar to that of the Ichthyostegids, is found in *Orthosauriscus* (WATSON 1926 a, fig. 9). Otherwise the palate of this genus is quite similar to that of *Baphetes*, and to that of all other well known Loxommids.

3. The "Rhachitomi"-"Stereospondyli".

As will be further demonstrated below (pp. 83, 88—92), the division of the younger *Labyrinthodontia* into "*Rhachitomi*" and "*Stereospondyli*" is quite arbitrary and has no real systematic value. The fact seems to be that there is a general evolutionary trend towards a simplification of the vertebrae, so that in the Lower Triassic, various branches of the *Labyrinthodontia*, independently of each other, become "*Stereospondyli*".

Thus only for a practical reason have I sometimes made use, in the discussion of the dermal bones of the higher *Labyrinthodontia*, of the old terms "*Rhachitomi*" and "*Stereospondyli*". These terms, in the sense in which they are used by me, could in fact have been replaced by the words "older groups" and "younger groups of higher *Labyrinthodontia*".

The fundamental work on the "*Rhachitomi*"-"*Stereospondyli*" is now that of WATSON (1919 b). Though it mainly deals with the endocranium, the occiput, and the palate, it is important for the study of the phylogeny of the group, and also contains the results of a very extensive bibliographical work. It thus forms a very good introduction to the study of the higher *Labyrinthodontia*.

WATSON divided the "*Rhachitomi*" into twelve families and six *genera incertae sedis*, in the following way:

Rhachitomi.

1. Family *Eryopidae: Eryops*, *Parioxys*, *Onchiodon.*

2. Family *Actinodontidae: Actinodon*, *Sclerocephalus*, *Chelydosaurus*, *?Osteophorus*.
3. Family *Rhinesuchidae: Rhinesuchus*, *Uranocentrodon*[1]), *Laccocephalus*.
4. Family *Achelomidae: Acheloma*.
5. Family *Dissorophidae:* two subfamilies,
   A. *Aspidosaurinae: Aspidosaurus*, *Alegeinosaurus*, *Broiliellus;*
   B. *Dissorophinae: Cacops*, *Dissorophus*, *Zygosaurus*.
6. Family *Trematopsidae: Trematops*.
7. Family *Zatrachydidae: Zatrachys*, *Dasyceps*, *Platyhystrix*.
8. Family *Archegosauridae: Archegosaurus*.
9. Family *Trimerorhachidae: Trimerorhachis*.
10. Family *Lydekkerinidae: Lydekkerina*.
11. Family *Micropholidae: Micropholis*.
12. Family *Dvinosauridae: Dvinosaurus*.

Genera incertae sedis: Sparagmites, *Discosauriscus*[2]), *Cochleosaurus*, *Melosaurus*, *Chalcosaurus*, *Platyops*.

Later publications have added five new rhachitomous genera or generic names, viz.:

Benthosaurus EFREMOV 1929, from the Permo-Triassic of the N. Dvina Government, Russia,
Laccosaurus HAUGHTON 1925, from S. Africa,
Sclerothorax v. HUENE 1932, from Oberhessen,
Wetlugasaurus RIABININ 1930, from the Lower Triassic of NW. Russia,

finally

Acanthostoma CREDNER, formerly regarded as a Phyllospondyl (STEEN 1934; cf. WATSON 1919 b, p. 21).

In his important work already referred to, WATSON (1919 b, pp. 48, 49, 67, 68) gave the following classification of the "*Stereospondyli*":

1. Family *Capitosauridae: Capitosaurus*, *Cyclotosaurus*.
2. Family *Trematosauridae: Trematosaurus*, *Trematosuchus*, *Lyrocephalus*, *Lonchorhynchus*, *Aphaneramma*, *Platystega*, *Tertrema*.
3. Family *Metoposauridae: Metoposaurus*, *Anaschisma*.
4. Family *Mastodonsauridae: Mastodonsaurus*.

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[1]) "*Myriodon*" v. HOEPEN 1915, WATSON 1919b; see v. HOEPEN 1917; cf. HAUGHTON 1915, 1925; v. HUENE 1925.

[2]) "*Discosaurus*" CREDNER 1883 preoccupied; see KUHN 1933, p. 52.

5. Family *Brachyopidae: Brachyops*, *Bothriceps*, *Batrachosuchus*, *Plagiosternum*, *Plagiosaurus*.

Probable *Stereospondyli*, *incertae sedis: Diadetognathus*, *Dictyocephalus*, *Ekbainacanthus*, *Eupelor*, *Eurycervix*, *Glyptognathus*, *Gonioglyptus*, *Labyrinthodon*[1]), *Pachygonia*, *Pariostegus*, "*Petrophryne major*", *Platyceps*[2]), *Ptychosphenodon*, *Rhytidosteus*, *Xestorhytias*.

In later publications the following new stereospondylous genera, or, at least, generic names, have been introduced into literature:

Buettneria CASE 1922, from the Upper Triassic of Texas,
Plagiosuchus v. HUENE 1922, from the "Lettenkohle" of Wurtemberg and Thuringia,
Microposaurus HAUGHTON 1925, from S. Africa,
Kestrosaurus HAUGHTON 1925, from the Orange Free State,
Koskinodon BRANSON and MEHL 1929, from the Upper Triassic of Wyoming,
Borborophagus BRANSON and MEHL 1929, from the Upper Triassic of Wyoming,
Kalamoiketor BRANSON and MEHL 1929, from the Upper Triassic of Arizona,
Mentosaurus RÖPKE 1930, from the "Muschelkalk" near Halle,
Trigonosternum SCHMIDT 1931, from the "Lettenkohle" of Thuringia.

The systematic value and position of all these are discussed on pp. 74—92 of the present paper, where a discussion will also be found of most of the following genera[3]), established before 1919, but not mentioned by WATSON:

"*Rhachitomi*": *Anisodexis* COPE 1882,
Eryopsoides DOUTHITT 1917,
Gaudrya FRITSCH 1885,
Gondwanosaurus LYDEKKER 1885,
Nyřania FRITSCH 1885,
Phrynosuchus BROOM 1913,
Rhinosaurus FISCHER VON WALDHEIM 1847,
Tersomius CASE 1910,

"*Stereospondyli*": *Calamops* SINCLAIR 1917,
Hercynosaurus JAEKEL 1913,
Hyperokynodon PLIENINGER 1852,
Odontosaurus v. MEYER 1838,
Peltostega WIMAN 1916,
Syphonodon SEELEY 1908.

[1]) Cf. KUHN 1933, p. 79 (foot-note).
[2]) Cf. KUHN 1933, p. 108.
[3]) Those not discussed on pp. 74—92 are briefly mentioned in foot-note on p. 200.

Two new genera are introduced in the present paper:

Heptasaurus n. g. for "*Mastodonsaurus*" *cappelensis* WEPFER (see below pp. 77—80);

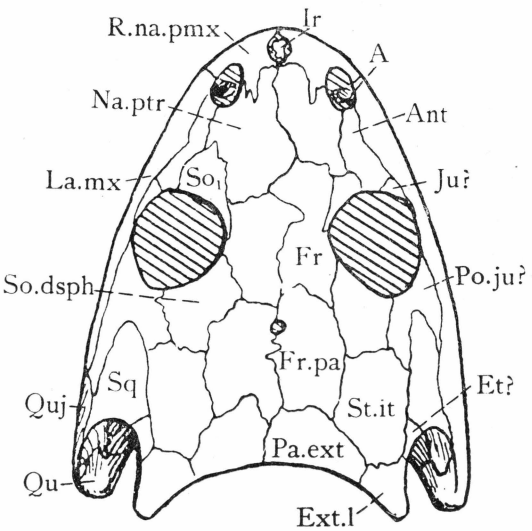
Stoschiosaurus n. g. (see pp. 131—150);

the last one from the Eotriassic of East Greenland.

The classification of the "*Rhachitomi-Stereospondyli*" is further discussed below on pp. 74—92.

A. Discussion of the dermal bones of the head in the higher Labyrinthodontia.

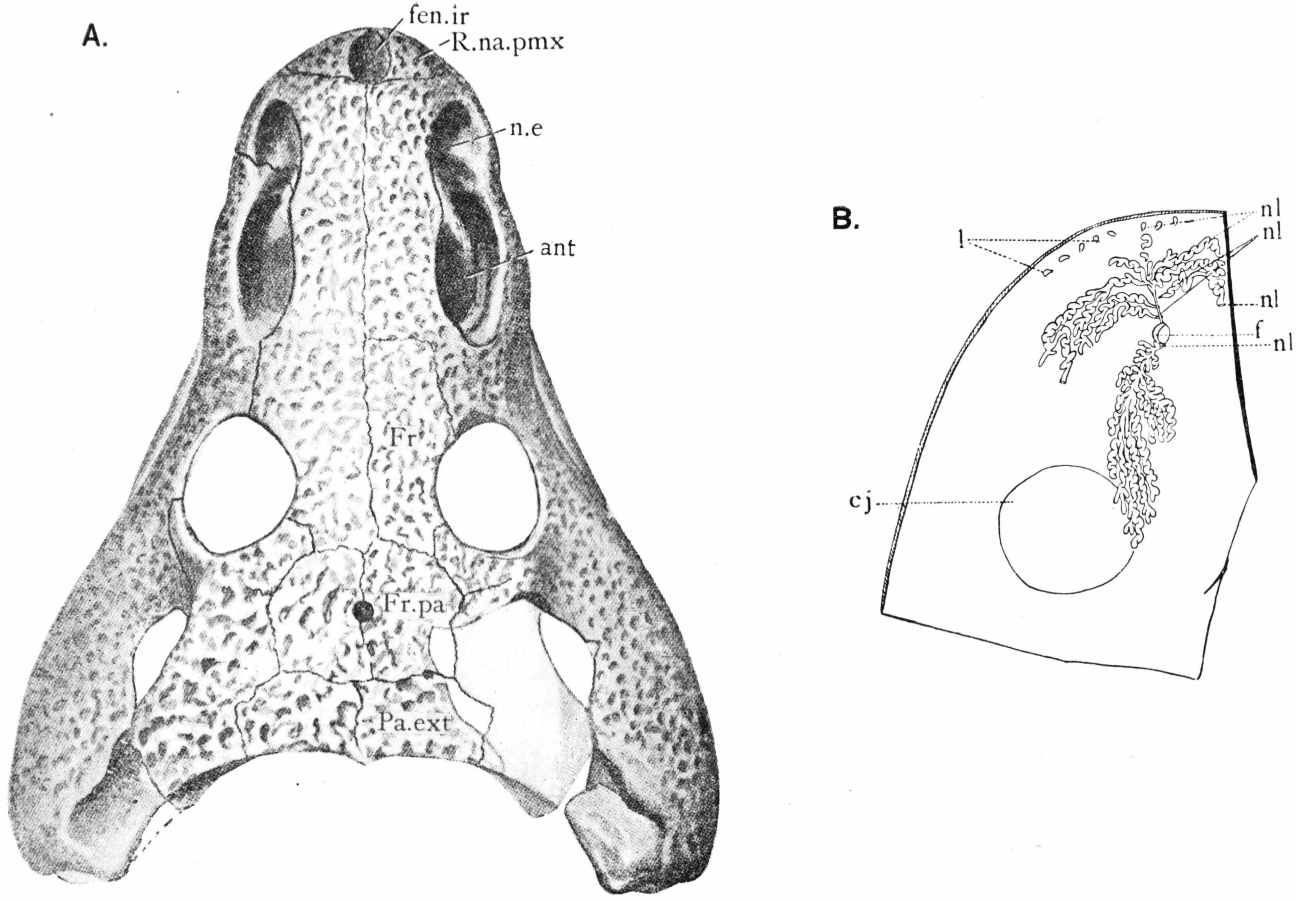
The *interrostral* (*Ir*, text-fig. 5) presents a rather curious evolution in certain higher *Labyrinthodontia*. Most often it is not found as an independent bone, but in *Micropholis stowi* (see text-fig. 5), WATSON (1913 a, pp. 340—341) described a small bone, "lying rather loosely



Text-fig. 5. *Micropholis stowi* HUXLEY. Dorsal aspect of the head. After WATSON (1913 a).

A, anterior antorbital or septomaxillary; *Ant*, posterior antorbital; *Et?*, extratemporal?; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ir*, interrostral; *Ju?*, jugal?; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po. ju?*, postorbital and jugal; *Qu*, quadrate; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

in a small fenestra", between the nasal parts of the two naso-rostro-premaxillaries (*R. na. pmx*, text-fig. 5). This small bone (WATSON's "internasal") has "the same ornament of tubercles as the other skull

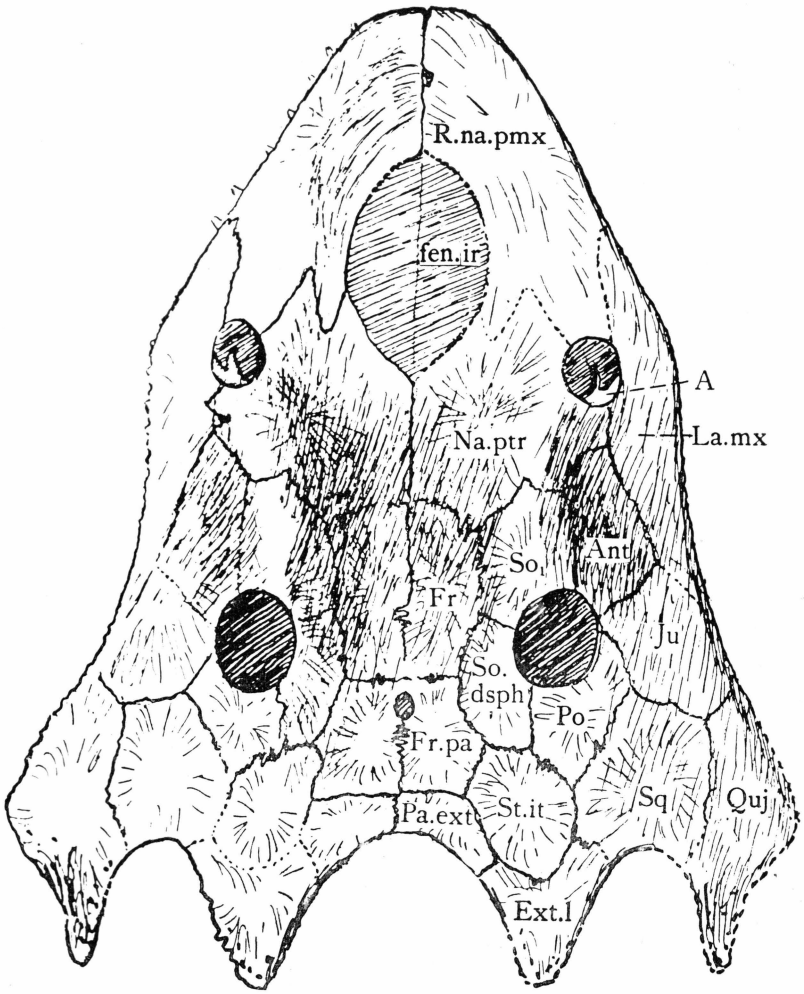


Text-fig. 6. A. *Trematops milleri* WILLISTON. Dorsal aspect of the skull. After WILLISTON (1909, fig. 1). B. *Desmognathus*. Skin of right side of the head with naso-labial glands (*nl*), and labial glands (*l*). After WHIPPLE (1906, fig. 5).

Fr, frontal; *Fr. pa*, fronto-parietal; *Pa. ext*, parieto-extrascapular; *R. na. pmx*, naso-rostro-premaxillary; *ant*, antorbital vacuity; *cj*, conjunctiva; *f*, crescentic fold in the external nostril; *fen. ir*, interrostral fenestra; *l*, labial glands; *n. e*, external nostril; *nl*, naso-labial glands.

bones". Thus it clearly belongs to the dermal cranial roof, and, according to its position, evidently represents an independent *interrostral* (*Ir*, text-fig. 5), homologous to that of the Crossopterygians and to that of the Loxommids. Accordingly the fenestra may be called the interrostral fenestra.

In a position quite corresponding to that of the interrostral fenestra



Text-fig. 7.

Zatrachys microphthalmus Cope. Dorsal aspect of the head. After Broom (1913 c). *A*, anterior antorbital or septomaxillary; *Ant*, posterior antorbital; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *fen. ir*, interrostral fenestra.

in *Micropholis*, there is in *Trematops* an exactly similar oval fenestra (*fen*, *ir*, text-fig. 6 A), called "rostral opening" by WILLISTON. Here no remain of the interrostral has been found; conceivably that bone failed to ossify.

In *Acanthostoma* (CREDNER 1883, pl. XI, fig. 1)[1]) there also seems to be a median interrostral fenestra. As in *Trematops*, there is in the palate of *Acanthostoma* (CREDNER, l. c., pl. XI, fig. 2) an anterior palatal vacuity, corresponding in position and shape to the interrostral fenestra in the cranial roof.

A large interrostral fenestra is found in the two closely allied and perhaps identical genera *Dasyceps* (HUXLEY 1859; HUENE 1910) and *Zatrachys* (text-fig. 7; BROOM 1913 c).

The importance of this reduction in the ossification of the interrostral region of the dermal cranial roof may seem difficult to explain. There are, however, not many possibilities. The only organ which can have been situated below the interrostral fenestra is the *glandula intermaxillaris*. This was already recognised by v. HUENE (1910 p. 41; also NOPCSA 1930, pp. 984, 985) who compared the vacuity ("die Facialgrube") with a similar vacuity, especially in the Urodeles, containing the intermaxillary gland.

Now this gland (see especially WIEDERSHEIM 1876) has a somewhat different position in the *Anura* and the *Urodela*. In the *Urodela* it lies in the internasal cavity, between the nasal capsules. In the *Anura* it is situated mainly in front of but also within the nasal capsules. In both groups it is immediately postero-medial to the ascending facial parts of the so-called premaxillaries. The *Anura* have a special muscular apparatus for the compression of the gland.

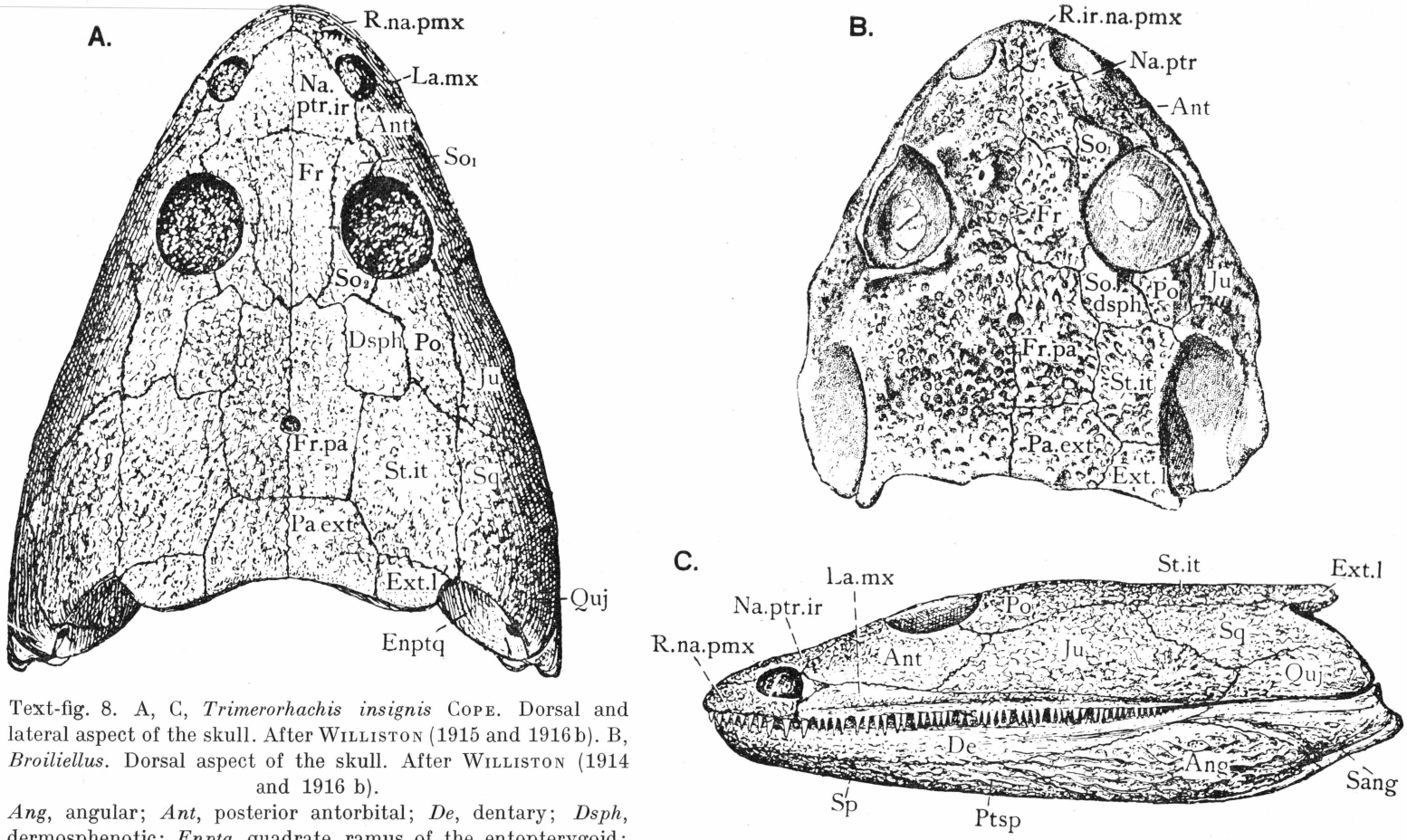
In spite of these differences the intermaxillary glands of the two groups are, at least usually, regarded as equivalent and homologous.

REICHELT (1882) clearly expressed such a view, when he wrote about the gland of the *Anura*: "Das Epithel der Drüse gleicht völlig dem der Intermaxillardrüse der Urodelen, und der Ort ihrer Ausmündung kennzeichnet sie deutlich als ein Homologon derselben" (REICHELT 1882, p.21).

To me, however, this homology does not seem quite so clearly established.

The gland of a Urodele like *Cryptobranchus*, *Desmognathus*, or *Triton* (see WIEDERSHEIM 1877, figs. 22, 103, 111) opens in a longitudinal slit-like fenestra between the vomeres, in the middle of the median length of those bones. On the other hand the intermaxillary gland of an Anure, like *Rana* (see WIEDERSHEIM 1876, Taf. III, figs. 14, 15, 16; cf. ECKER-WIEDERSHEIM-GAUPP 1896, fig. 14) has its openings in a transverse, bent row in front of the vomeres, between these bones and the "premaxillaries".

[1]) Placed by several earlier authors among the *Phyllospondyli*; cf. STEEN 1934.



Text-fig. 8. A, C, *Trimerorhachis insignis* COPE. Dorsal and lateral aspect of the skull. After WILLISTON (1915 and 1916 b). B, *Broiliellus*. Dorsal aspect of the skull. After WILLISTON (1914 and 1916 b).

Ang, angular; *Ant*, posterior antorbital; *De*, dentary; *Dsph*, dermosphenotic; *Enptq*, quadrate ramus of the entopterygoid; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Na. ptr. ir*, probably naso-postrostro-interrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Ptsp*, postsplenial; *Quj*, quadratojugal; *R. ir. na. pmx*, probably rostro-interrostro-naso-premaxillary; *R. na. pmx*, naso-rostro-premaxillary; *Sang*, supraangular; So_1, anterior supraorbital; So_2, posterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sp*, splenial; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

In the *Ichthyostegalia* and *Labyrinthodontia* the gland must conceivably have opened in the anterior palatal vacuity. Thus it is comparable with that of the *Anura*, but its homology to the gland of the *Urodela* seems at least very uncertain. Supposing it to be homologous with the gland of the Urodeles, one would be forced to postulate a considerable migration of the opening of the gland, either in the Urodeles, or in the *Anura* and *Ichthyostegalia-Labyrinthodontia*.

If by embryological investigation the two types of glands discussed should proove to be definitely genetically different, it would be most appropriate to use the term interrostral gland for that — more anteriorly situated — of the *Anura*, *Ichthyostegalia* and *Labyrinthodontia*, and to revive for that of the Urodeles the old term internasal gland, which so accurately expresses the position of the discussed organ in the Urodeles.

We are thus driven to homologise the interrostral fenestra of *Zatrachys*, *Dasyceps*, *Trematops*, *Acanthostoma* and *Micropholis* with the median one of the fenestrae, marked *a* in WIEDERSHEIM's figure 15 (1876). Its presence probably indicates an excessive development of an interrostral — or intermaxillary — gland, homologous with that of recent *Anura*.

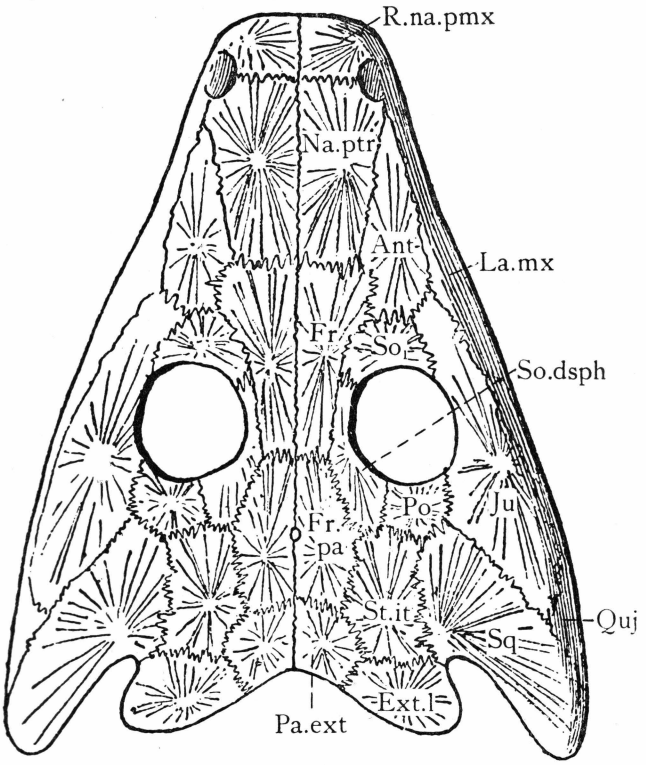
In the remaining "*Rhachitomi*" and in the "*Stereospondyli*" it is more difficult to trace the fate of the interrostral. In several cases (*Trimerorhachis*, text-fig. 8 A; *Eryops*, text-figs. 14, 21; *Osteophorus*, text-fig. 18; *Sclerocephalus*, text-fig. 15; *Nyřania*, FRITSCH 1885, fig. 138) the transverse suture, extending from one nostril to another, has a marked anteriorly directed median convexity. On the other hand, this suture is mainly quite straight in *Actinodon* (text-fig. 9) and *Chelydosaurus* (FRITSCH 1885, fig. 131); and in *Broiliellus* (text-fig. 8 B) it extends rather far back in its median parts. These facts may perhaps most naturally be thus interpreted, that each of the paired interrostrals has probably fused with the naso-postrostral in the genera first enumerated (*Trimerorhachis* etc.) but with the naso-rostro-premaxillary in *Broiliellus*, — whereas in *Actinodon* and *Chelydosaurus* it may have been totally reduced. This may conceivably also be the case in *Lydekkerina* (text-fig. 12).

Certain "*Stereospondyli*" — *Trematosuchus sobeyi* (text-fig. 10), *Tertrema acuta* (text-fig. 23) — have a course of the transverse suture between the external nostrils, conceivably indicating that the interrostral has, in those animals, fused with the bone posterior to it, to form a compound *naso-postrostro-interrostral* (*Na. ptr*, text-figs. 10, 23). But in all other, also in an evidently rather nearly allied genus, as *Trematosaurus* (text-fig. 11), there seems to be no evidence of such a fusion.

Except for the probable fusion with the interrostral in *Broiliellus*, the *naso-rostro-premaxillary* of the "*Rhachitomi*" (*R. na. pmx*, text-figs.

5, 6A, 7, 8, 9, 12, 14, 15, 18, 20, 21, 22, 32, 38) corresponds exactly to that of the Loxommids. In this connection *Lydekkerina* (text-fig. 12) is of interest, since in this genus the ethmoidal commissure and the most anterior part of each supraorbital canal are clearly connected with the naso-rostro-premaxillary.

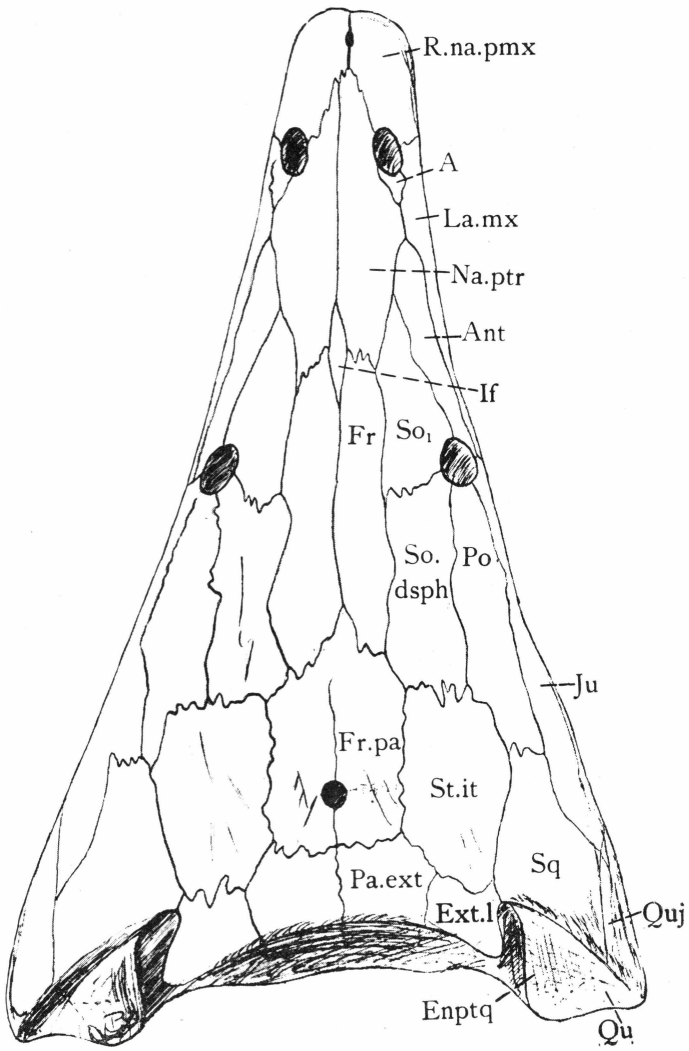
The narrow slit between the naso-rostro-premaxillaries in *Trematosuchus*, as figured by HAUGHTON (1915, my text-fig. 10) could perhaps



Text-fig. 9. *Actinodon latirostris* JOURDAN. Dorsal aspect of the skull. After LYDEKKER (1890, fig. 45).

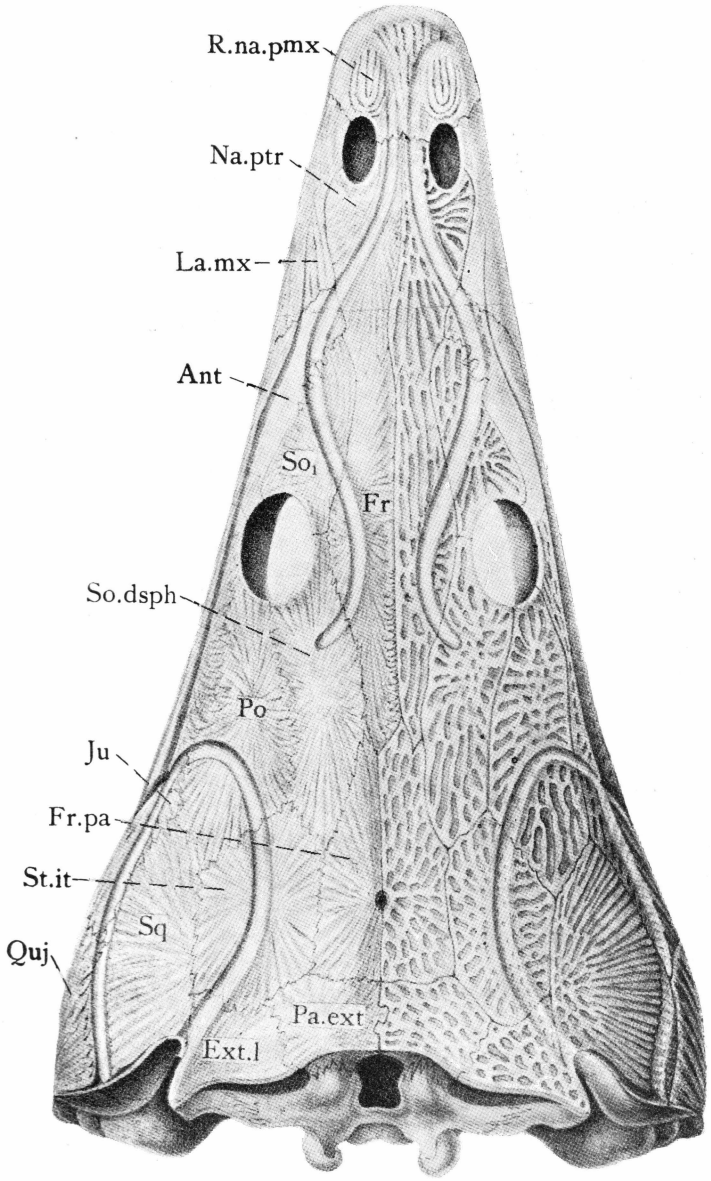
Ant, posterior antorbital; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

be interpreted as a homologon of the interrostral fenestra (see above, pp. 25—28), though it seems at first sight to have a position, remarkably much in front of the external nostrils. This position may, however, be due to a general lengthening of the snout so that morphologically the slit may be situated in about the same position as the mentioned fenestra in



Text-fig. 10. *Trematosuchus sobeyi* (HAUGHTON). Dorsal aspect of the skull. After HAUGHTON (1915, pl. VIII, fig. 2).

A, anterior antorbital or septomaxillary; *Ant*, posterior antorbital; *Enptq*, quadrate ramus of the entopterygoid (?); *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *If*, median postrostral (interfrontal); *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Qu*, quadrate; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

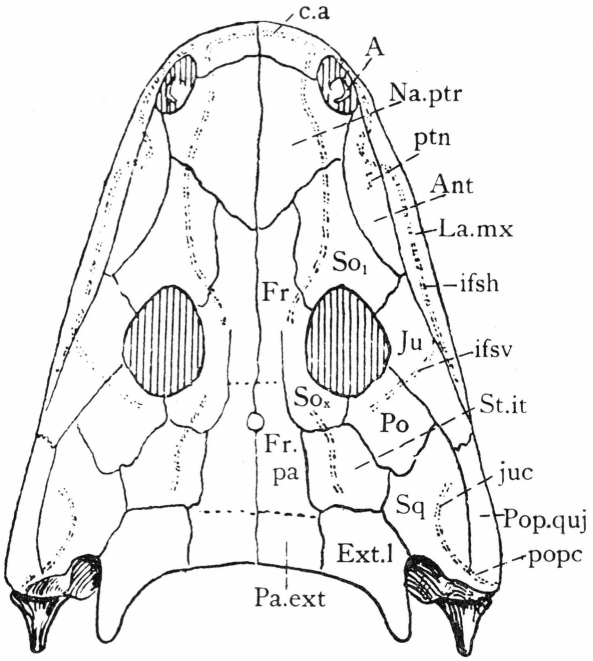


Text-fig. 11. *Trematosaurus braunii* Burmeister. Dorsal aspect of the skull. After Burmeister (1849).

Ant, posterior antorbital; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

Micropholis (text-fig. 5). Thus we must realize the two possibilities that the interrostral may have fused with the naso-rostro-premaxillary, or may have become totally reduced. Under these circumstances I think it is most practical, and also most correct, to speak — provisionally — only of naso-postrostrals and naso-rostro-premaxillaries in *Trematosuchus*.

Except with regard to the above discussed problem, the naso-rostro-premaxillaries of the "*Stereospondyli*" (*R. na. pmx*, text-figs. 10, 11, 13, 16, 17, 19, 23, 24, 25, 26, 27, 28, 29, 30, 31, 33, 37) are quite clearly homo-



Text-fig. 12. *Lydekkerina huxleyi* (LYDEKKER). Dorsal aspect of the skull. After WATSON (1919 b, fig. 9).

A, anterior antorbital or septomaxillary; *Ant*, posterior antorbital; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Pop. quj*, preoperculo-quadratojugal; So_1, anterior supraorbital; So_x, posterior supra-orbital or supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *c. a*, anterior commissure of the infraorbital canals; *ifsh*, horizontal portion of the suborbital part of the infraorbital canal; *ifsv*, vertical portion of the sub-orbital part of the infraorbital canal; *juc*, jugal canal; *popc*, preopercular canal; *ptn*, postnasal connection of the suborbital part of the infraorbital canal with the supraorbital canal.

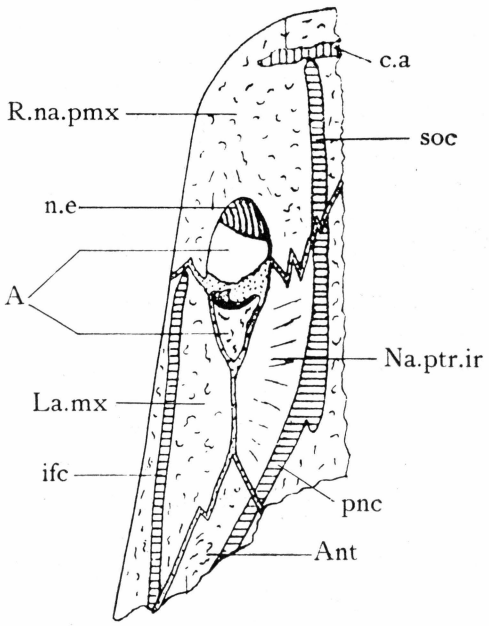
logous with those of most "*Rhachitomi*", and present no remarkable features. In certain forms, like *Trematosaurus* (text-fig. 33 A), they have rather large palatal laminae — quite as in "*Rhachitomi*" like *Eryops* and others (text-fig. 32 A).

In many rhachitomous genera the *naso-postrostral* or *naso-postrostro-*

interrostral (*Na. ptr*, text-figs. 5, 7, 8 B, 9, 10, 11, 12, 16, 17, 18, 19, 22, 24—29, 31, 37, 38, 60—64; *Na. ptr. ir*, text-figs. 8 A, 13, 14, 15, 20, 21, 23) has still mainly the same shape as in *Ichthyostegids*, except for the above discussed differences, which make it possible that it often also contains an interrostral component.

Though varying in their detailed shape the naso-postrostrals are clearly homologous with each other also in the different stereospondylous genera, except, perhaps, in the fusion or non-fusion with the interrostral.

The lateral part of each naso-postrostral is clearly connected with

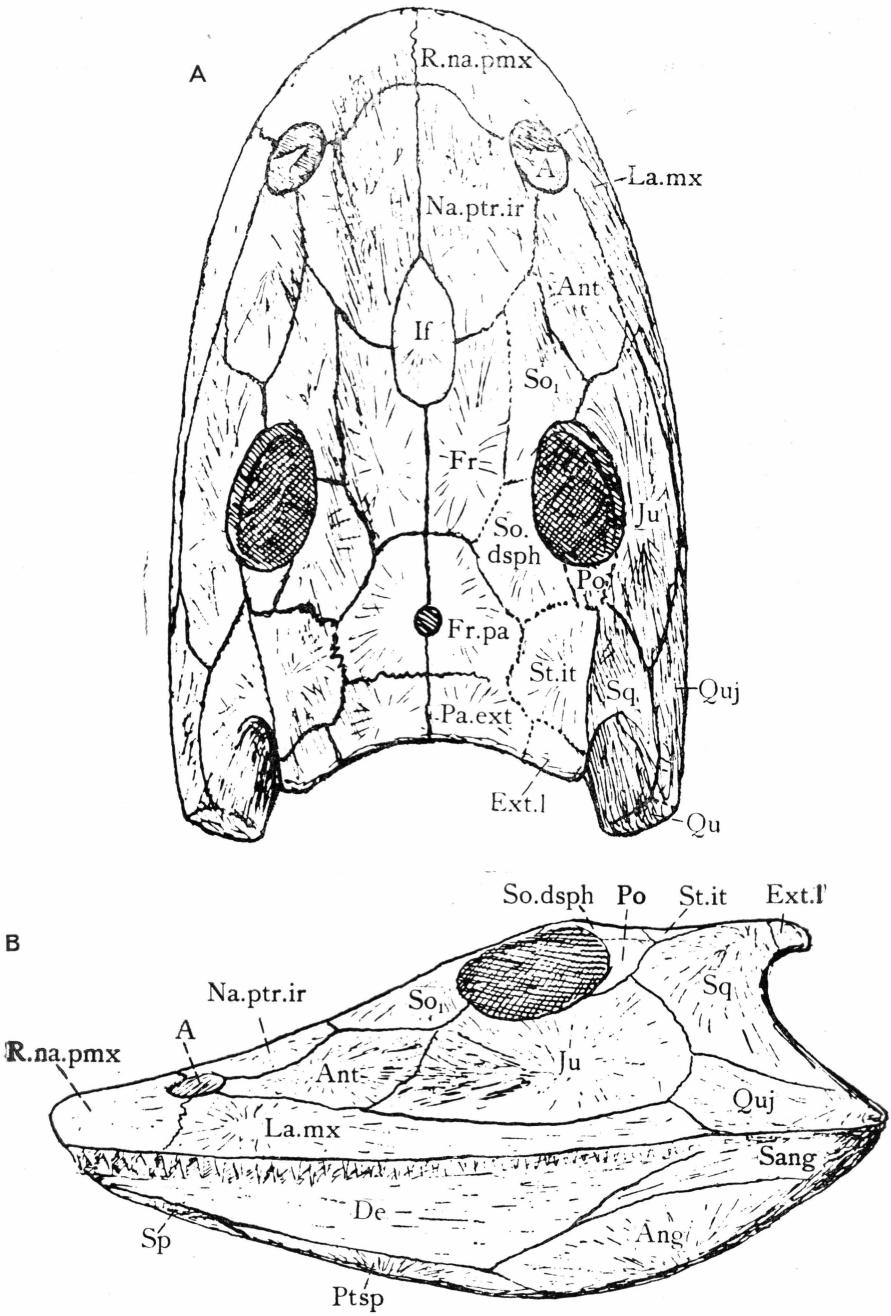


Text-fig. 13. *Trematosuchus? yakovlevi* RIABININ. Part of the skull in oblique antero-lateral view. After RIABININ (1927).

A, anterior antorbital or septomaxillary; *Ant*, posterior antorbital; *La. mx*, lachrymo-maxillary; *Na. ptr. ir*, probably naso-postrostro-interrostral; *R. na. pmx*, naso-rostro-premaxillary; *c. a*, anterior commissure of the infraorbital canals; *ifc*, horizontal portion of the suborbital part of the infraorbital canal; *n. e*, external naris; *pnc*, probably postnasal connection of the suborbital part of the infraorbital canal with the supraorbital canal; *soc*, supraorbital canal.

the supraorbital canal for instance in *Lydekkerina* (text-fig. 12), *Trematosuchus? yakovlevi* (text-fig. 13), *Anaschisma* (text-fig. 16), *Archegosaurus* (text-fig. 22), *Tertrema* (text-fig. 23), *Metoposaurus* (text-fig. 24), *Mastodonsaurus* (text-fig. 27), *Capitosaurus* (text-fig. 31), and *Lyrocephalus* (text-figs. 61, 63).

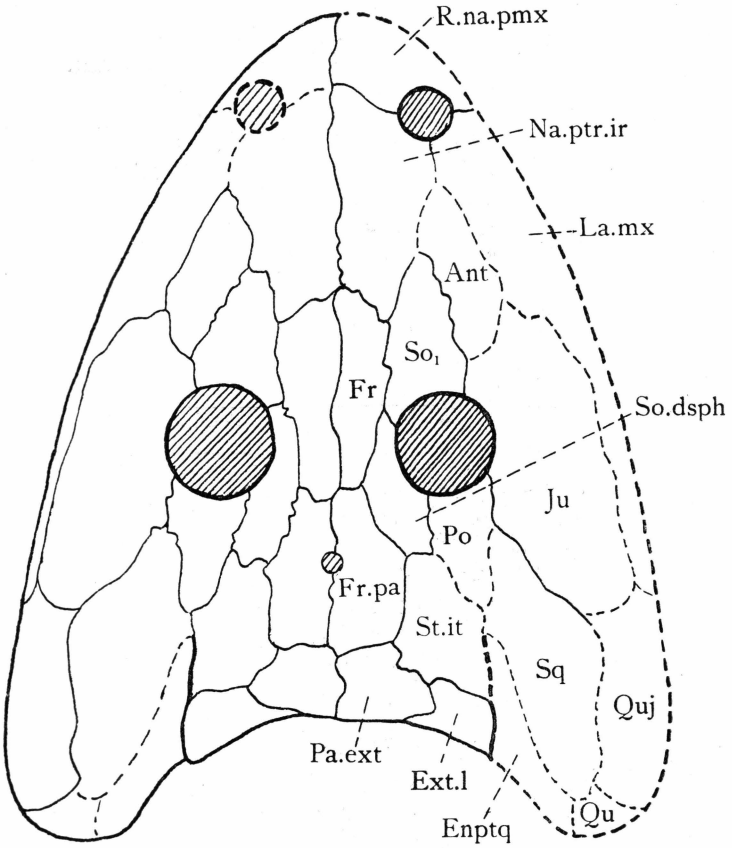
The *anterior antorbital* or *septomaxillary* (*A*, text-figs. 5, 7, 10, 12, 13, 14, 21, 60—64, 66), which still forms a part of the external surface



Text-fig. 14. *Eryops anatinus* Broom. A, dorsal; B, lateral aspect of the skull. After Broom (1913 c, figs. 19, 20).

A, anterior antorbital or septomaxillary; *Ang*, angular; *Ant*, posterior antorbital; *De*, dentary; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *If*, interfrontal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr. ir*, probably naso-postrostro-interrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Ptsp*, post-splenial; *Qu*, quadrate; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; *Sang*, supraangular; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sp*, splenial; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

of the dermal cranial roof in Ichthyostegids and Loxommids (cf. Säve-Söderbergh 1932, pp. 101, 102), is situated entirely below that surface in many "*Rhachitomi*" (*Eryops*, text-figs. 14, 21; v. Huene 1913, p. 318, fig. 1; Broom 1913 c, p. 579, fig. 11; p. 591, fig. 19; *Zatrachys*, text-fig. 7; Broom 1913 c; *Lydekkerina* text-fig. 12; Watson 1919, fig. 9; *Micropholis*, text-fig. 5; Watson 1913). Possibly also *Trimerorhachis* (text-fig. 8 A, C; Broom 1913 c, fig. 5) has the septomax-

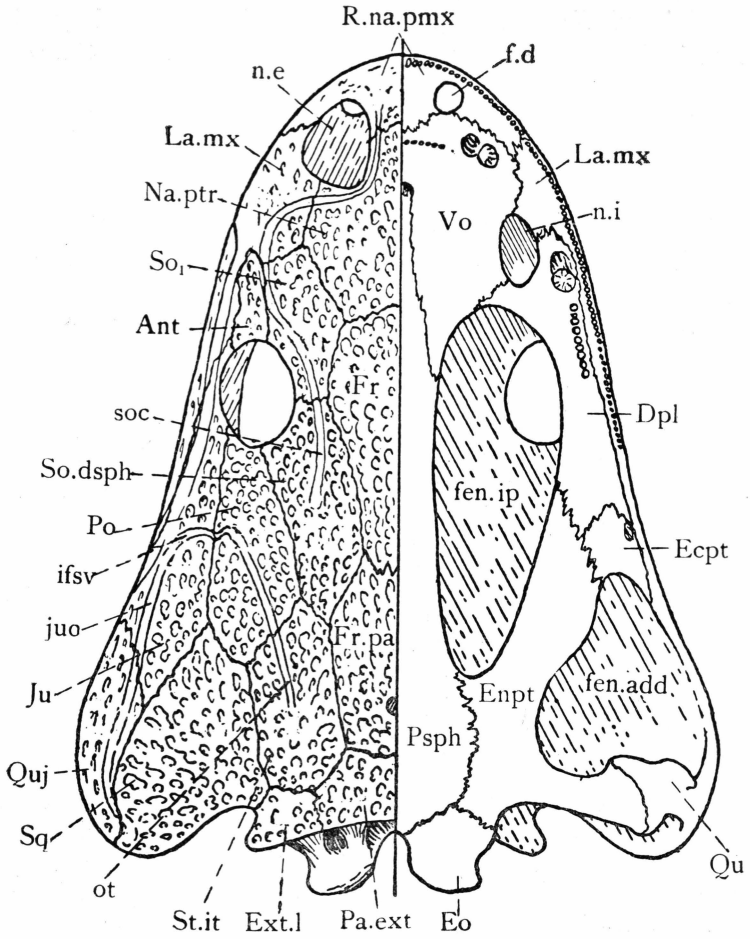


Text-fig. 15. *Sclerocephalus bavaricus* (Branco). Dorsal aspect of the head. After Branco (1885, Taf. I).

Ant, posterior antorbital; *Enptq*, quadrate ramus of the entopterygoid; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr. ir*, probably naso-postrostro-interrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Qu*, quadrate; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; *So*$_1$, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

illary entirely below the external surface, though Williston's figures, reproduced in my text-fig. 8 B, seem to indicate that the discussed bone has a small triangular sculptured facial part, exposed at the posterior

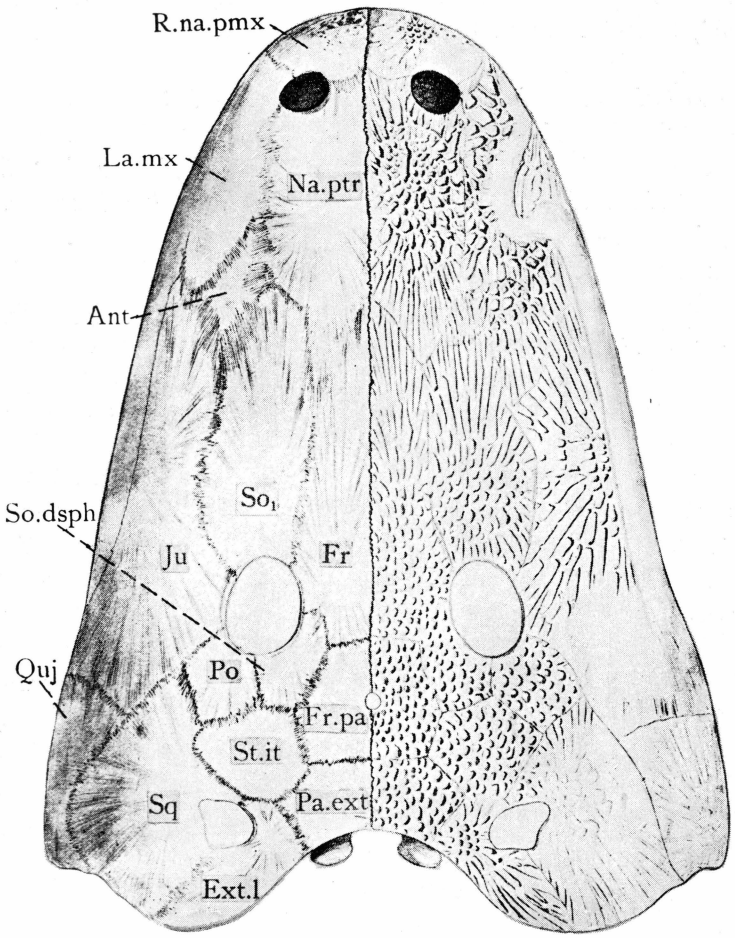
margin of the nostril. If this is true, the septomaxillary in *Trimerorhachis* presents an intermediate condition between that in the Loxommids and that in other "*Rhachitomi*"-"*Stereospondyli*" exactly as does the same bone in *Trematosuchus*, *Lyrocephalus*, and *Platystega*.



Text-fig. 16. *Anaschisma brachygnatha* BRANSON. Dorsal aspect of the skull. After BRANSON and MEHL (1929).

Ant, posterior antorbital; *Dpl*, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Eo*, exoccipital; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Psph*, parasphenoid; *Qu*, quadrate; *Quj*, quadrato-jugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *Vo*, vomer; *f. d*, vacuity for tooth of the lower jaw; *fen. add*, adductor fenestra; *fen. ip*, interpterygoid vacuity; *ifsv*, vertical portion of the suborbital part of the infraorbital canal; *juo*, jugal canal; *n. e*, external naris; *n. i*, internal naris; *ot*, otic part of the infraorbital canal; *soc*, supraorbital canal.

In *Trematosuchus sobeyi* (text-fig. 10; HAUGHTON 1915), in all species of *Lyrocephalus* (see below, text-figs. 60, 61, 63, 64), in *Platystega depressa* WIMAN (see below, text-fig. 62), and in the very partially known Stegocephalian, called by RIABININ *Trematosuchus? yakovlevi* (text-fig. 13; RIABININ 1927, text-fig. p. 523) the anterior antorbital (*A*) presents very



Text-fig. 17. *Cyclotosaurus robustus* v. MEYER. Dorsal aspect of the skull. After FRAAS (1889).

Ant, posterior antorbital; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

interesting conditions. Whereas in all other well known "Stereospondyls" the discussed bone, according to the existing figures, lies in the nostril, entirely below the surface, in the mentioned forms it consists of one

facial, pitted, superficial, triangular, posterior part and another smooth intranarial part. Thus we here find an intermediate stage between the primitive wholly superficial anterior antorbital of the Ichthyostegids and the wholly intranarial septomaxillary of most labyrinthodont Stegocephalians. An analogous condition is known with certainty for instance in *Theriodontia* (see for instance WATSON 1921 a, pp. 41—42, text-figs. 5,8; p. 59, text-fig. 17; p. 86, text-fig. 25), and is perhaps also found in *Trimerorhachis* (cf. above pp. 35—36).

The *posterior antorbital* (*Ant*, text-figs. 5, 7—27, 31, 37, 38, 60—64, 66) still retains its primitive extension, from the orbit to the anterior antorbital or posterior margin of the external nostril, in certain "*Rhachitomi*", as *Trimerorhachis* (text-fig. 8 A, B), *Broiliellus* (text-fig. 8 B), *Micropholis* (text-fig. 5), *Cochleosaurus* (BROILI 1905, fig. 1).

Though not reaching the orbital margin, it retains the primitive condition in the anterior parts, and reaches the nostril, in *Eryops anatinus* (text-fig. 14), *E. megacephalus* (text-fig. 21), *Lydekkerina* (text-fig. 12).

The reverse condition of the posterior antorbital, reaching the orbital margin but not the nostril, is found in the *Zatrachydidae* (*Zatrachys*, text-fig. 7; *Dasyceps* v. HUENE 1910, fig. 1).

A number of "*Rhachitomi*" show a still more specialized condition, with a posterior antorbital, excluded both from the orbit and from the nostril. This is the case in *Actinodon* (text-fig. 9), *Nyřania* (FRITSCH 1885, fig. 138), *Sclerocephalus* (text-fig. 15), *Osteophorus* (text-fig. 18), *Rhinesuchus* (BROOM 1912, pl. XIII, fig. 1).

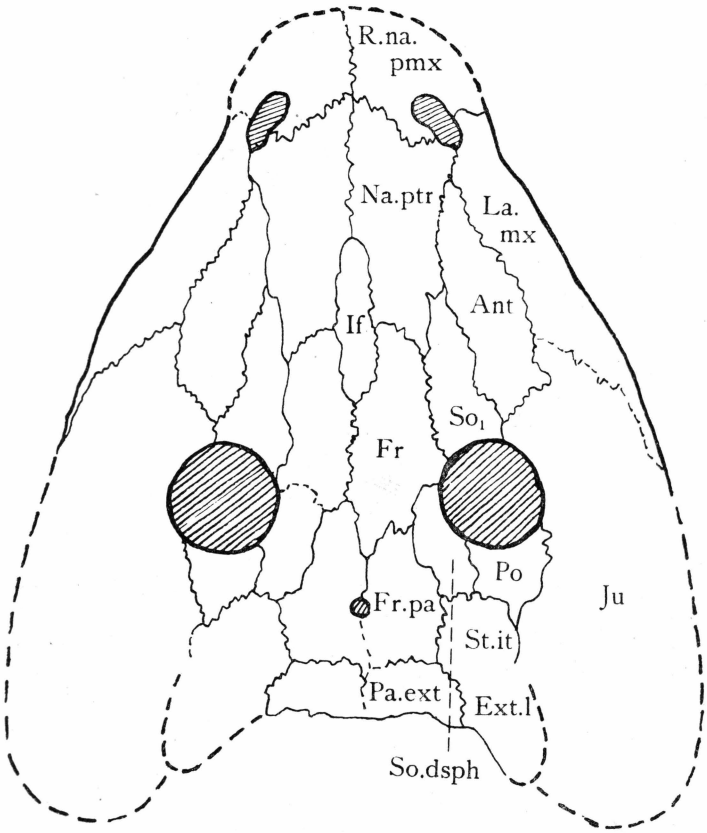
In the "*Stereospondyli*" the posterior antorbital is usually as much reduced as in the more advanced "*Rhachitomi*". In *Anaschisma*, according to the older figures (MOODIE 1908, BRANSON 1905), it extends quite from the nostril to the orbital margin, but according to the new restoration, given by BRANSON and MEHL (text-fig. 16; BRANSON and MEHL 1929, figs. 6, 7) it only reaches the orbital margin, but not the nostril. In *Trematosuchus*, and *Trematosaurus* (text-figs. 10, 11), *Buettneria*, *Koskinodon*, and *Borborophagus* (BRANSON and MEHL 1929, figs. 3, 8, 10), it also forms a part of the orbital margin and is excluded from the nostril.

In *Mastodonsaurus* (text-fig. 27), *Tertrema* (text-fig. 23), *Platystega* (text-fig. 62), *Metoposaurus* (text-fig. 24), *Peltostega* (text-fig. 26), and especially in *Cyclotosaurus* (text-fig. 17) the posterior antorbital is very much reduced, and far from contact with the nostril and the orbit, whereas in *Lyrocephalus* it is excluded from the orbit and seems to be separated from the anterior antorbital in certain species (*L. euri*, text-fig. 61; *L. kochi*, text-fig. 60), but to meet that bone in *L. rapax* (text-fig. 64) and *L. johanssoni* (text-fig. 63).

It may be noticed that the separation of the two antorbitals has

already begun in some of the Ichthyostegids (*Ichthyostega watsoni*, *I. eigili*, *Ichthyostegopsis wimani*; cf. SÄVE-SÖDERBERGH 1932, text-figs. 4, 6, 7, 11, 12).

The posterior antorbital of *Trimerorhachis* (text-fig. 8 A, C) is remarkable since it sends a large posterior process back along the lower margin of the orbit, to meet the postorbital, and thus excludes the jugal from the orbital margin.



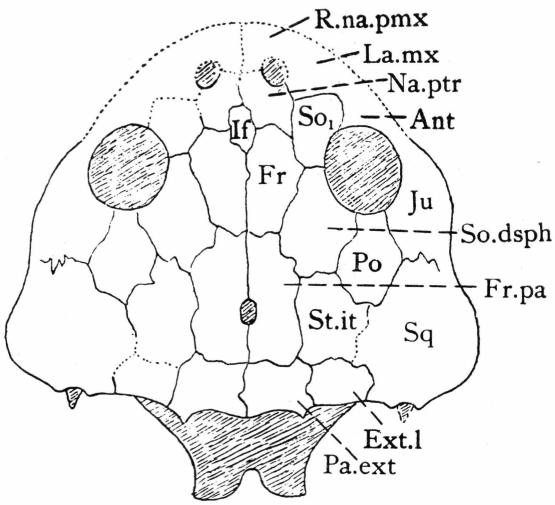
Text-fig. 18. *Osteophorus römeri* v. MEYER. Dorsal aspect of the skull. After v. MEYER (1860 b).

Ant, posterior antorbital; *Ext. l*, lateral extrascapular; *Fr.* frontal; *Fr, pa*, fronto-parietal; *If*, median postrostral (interfrontal); *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *St. it*, supratemporo-intertemporal.

In *Trematops* (text-fig. 6 A) there is in the region of the posterior antorbital a large oval, so called antorbital vacuity, confluent anteriorly with the external nostril. This vacuity conceivably may have lodged a strongly developed gland, comparable to the posterior of the naso-labial

glands in Plethodontid Salamanders (text-fig. 6 B), as figured by WHIPPLE (1906, fig. 5)[1]).

The *frontals* (*Fr*, text-figs. 5, 6 A, 7, 8 A, B, 9—12, 14—31, 37, 38, 53, 55, 56, 60—64, 66) in most "*Rhachitomi*" present no pecularities in shape and position, as compared with those of the Loxommids and Ichthyostegids, except that they generally have a somewhat greater posterior extension than in the earlier groups. The posterior margins of the frontals often lie as far back as the most posterior parts of the or-



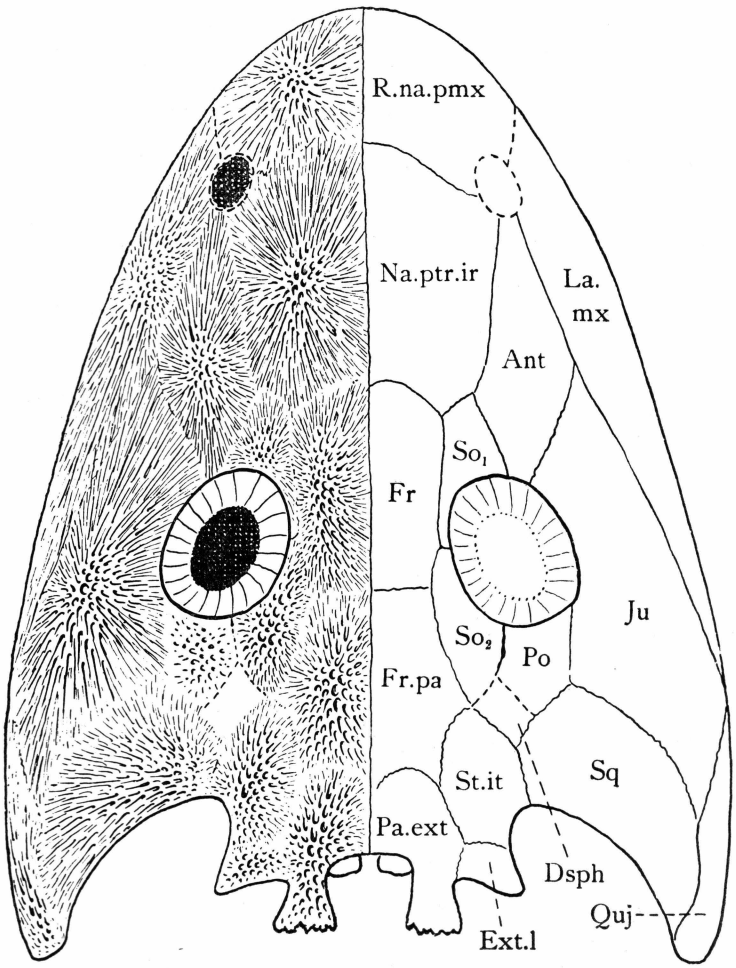
Text-fig. 19. *Batrachosuchus browni* BROOM. Dorsal aspect of the skull. After BROOM (1903). *Ant*, posterior antorbital; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *If*, median postrostral (interfrontal); *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

bits or even distinctly behind the orbits, as in *Trimerorhachis* (text-fig. 8 A; cf. text-fig. 2 A and SÄVE-SÖDERBERGH 1932, text-figs. 2, 11).

In the "*Stereospondyli*" the frontals differ considerably in their backward extension, in relation to the orbits. Whereas in the *Capitosauridae*

[1]) Cf. NOPCSA 1930, p. 986. The tentacular vacuities in the *Gymnophiona*, compared by NOPCSA to the antorbital vacuities of *Trematops* differ from these, since they may be confluent superficially with the orbits, but not with the nostrils with which they only communicate through the canal for Jacobson's organ (SARASIN and SARASIN 1890, p. 158). That tentacular vacuities may grow inward in the directions, in which the tentacles are retracted may be easily understood, not why they should expand in the directions towards the nostrils. See WERNER 1931; WIEDERSHEIM 1879, figs. 7, 21, 28; SARASIN and SARASIN 1890, Taf. XV, figs. 3, 4; PETER 1908, fig. 5; ENGELHARDT 1924, fig. 51.

(text-figs. 17, 31, 37), the *Mastodonsauridae* (text-fig. 27) and the *Brachyopidae* (text-figs. 19, 25, 28, 29, 30) — *Batrachosuchus* excepted (text-fig. 19) — they never extend behind the posterior margins of the orbits, in *Peltostega* (text-fig. 26), in *Lyrocephalus* (text-figs. 60, 61, 66), in *Batrachosuchus* (text-fig. 19), and probably also in *Platystega* (text-

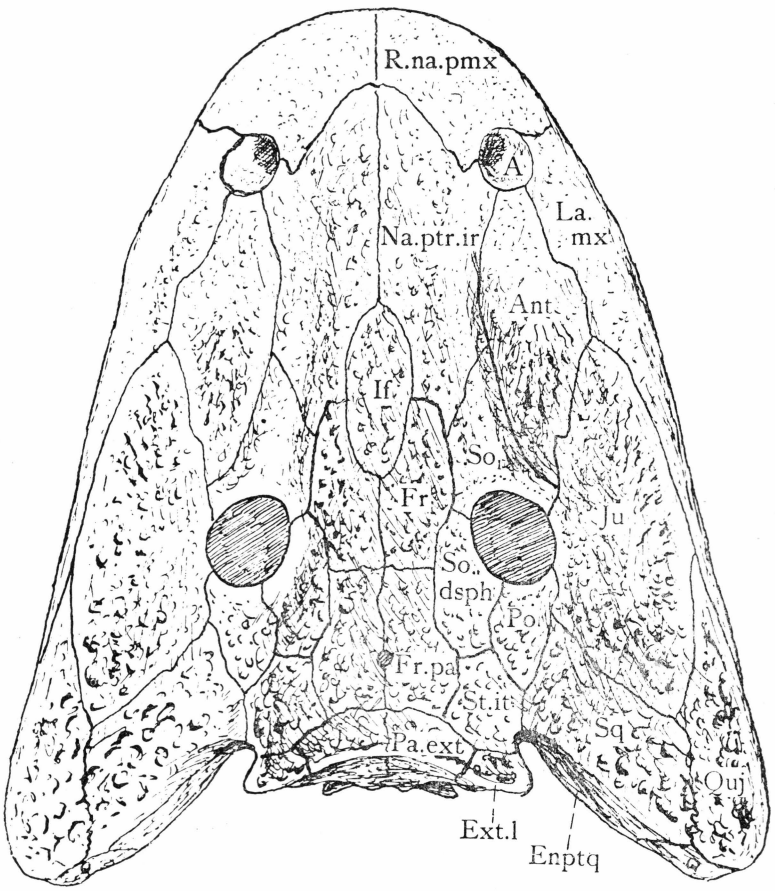


Text-fig. 20. *Cochleosaurus bohemicus* Fritsch. Dorsal aspect of the skull. After Broili (1905). *Ant*, posterior antorbital; *Dsph*, dermosphenotic; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr. ir*, probably naso-postrostro-interrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; So_2, posterior supraorbital; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

fig. 62), and *Stoschiosaurus* (text-fig. 55), they reach a little behind the orbits, and in all other Stereospondyls belonging to the families *Metopo-*

sauridae and *Trematosauridae* (text-figs. 10, 11, 16, 23, 24, 56) they extend far behind the posterior orbital margins.

Between the naso-postrostrals and the frontals, there occurs in certain "*Rhachitomi*" (*Eryops anatinus*, text-fig. 14; *E. megacephalus*, text-fig. 21; *Osteophorus*, text-fig. 18), and in *Kestrosaurus* (HAUGHTON 1925,



Text-fig. 21. *Eryops megacephalus* COPE. Dorsal aspect of the head. After BROOM (1913 c, fig. 11).

A, anterior antorbital or septomaxillary; *Ant*, posterior antorbital; *Enptq*, quadrate ramus of the entopterygoid; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, frontoparietal; *If*, median postrostral (interfrontal); *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr. ir*, probably naso-postrostro-interrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

text-fig. 11), *Trematosuchus* (text-fig. 10), and *Batrachosuchus* (text-fig. 19) a median so called interfrontal (*If*), which evidently is a *median postrostral*, well comparable to one or several of the large posterior median

postrostrals in *Osteolepis macrolepidotus* (SÄVE SÖDERBERGH 1933, text-figs. 6, 12, 19; *Ptr*, pls. 1, 4; pl. 5, figs. 1, 2; pl. 6; *Ptr. m*, pl. 9, fig. 2) and *Eusthenopteron* (SÄVE-SÖDERBERGH 1933, pl. 15, fig. 1; *Ptr*, pl. 16) and possibly also to the so called central frontal of *Dipterus* (SÄVE-SÖDERBERGH 1932, text-fig. 20, *Fr.c*).

The occurrence of this bone is rather remarkable, as it is not found in any of the known Loxommids or Ichthyostegids.

The *anterior supraorbital* (So_1, text-figs. 5, 7, 8 A, B, 9—12, 14—27, 31, 37, 38, 53, 55, 60—64, 66) presents a very interesting evolution in the higher *Labyrinthodontia*. Whilst in Ichthyostegids and Loxommids it is still mainly dorsal or medial to the orbit, in the "*Rhachitomi*" it gradually migrates to the anterior margin of the orbit. By this process it looses its contact with the posterior supraorbital or supraorbito-dermosphenotic in certain "*Rhachitomi*", and in others gets a new contact with the jugal, antero-laterally to the orbit, thus excluding the posterior antorbital from the orbital margin.

The most primitive condition, as far as I have found, is represented in *Trimerorhachis* (text-fig. 8 A, C). Here the long and rather narrow anterior supraorbital meets the supraorbito-dermosphenotic medially to the orbit, forms the anterior half of the medial margin of the orbit and does not exclude the posterior antorbital from the anterior margin of the orbit. This condition is very similar to that found in a Loxommid like *Baphetes* (text-fig. 1). The same primitive stage of evolution of the discussed region seems to be found also in *Chelydosaurus* (FRITSCH 1885, fig. 131).

In the *Zatrachydidae* (text-fig. 7; v. HUENE 1910, fig. 1) the anterior supraorbital has still similar relations as in *Trimerorhachis*. It meets the supraorbito-dermosphenotic at the middle of the medial margin of the orbit, and does not meet the jugal. But, especially in *Zatrachys*, it is distinctly larger anteriorly than in *Trimerorhachis*. Thus it consists of a large part in front of the orbit and a much narrower part above the orbit.

In *Cochleosaurus* (text-fig. 20), which represents an analogous stage, the anterior supraorbital has a very narrow posterior part, joined by suture, above the orbit, to the posterior supraorbital.

In certain "*Rhachitomi*" of small size, and with large orbits, like *Micropholis* (text-fig. 5) and *Broiliellus* (text-fig. 8 B) the narrow posterior part of the anterior supraorbital is totally reduced, so that the bone fails to meet the supraorbito-dermosphenotic. But it does not meet the jugal.

This, on the other hand, is the case in a number of other "*Rhachitomi*", which with regard to the discussed characters may be arranged in a series of stages ("Stufenserie"): (*Trimerorhachis*) — *Osteophorus* (text-

fig. 18) — *Eryops megacephalus* (text-fig. 21) and *Sclerocephalus* (text-fig. 15) — *Eryops anatinus* (text-fig. 14) — *Lydekkerina* (text-fig. 12).

In this series — which, of course, cannot pretend to represent a real phylogenetic succession of genera — the anterior supraorbital successively shifts its position until, in *Lydekkerina*, it gets much the same relation to the orbit as that, held by the posterior antorbital in Loxommids, Ichthyostegids, and Crossopterygians. In the whole series the anterior supraorbital retains its contact with the supraorbito-dermosphenotic.

In *Actinodon* (text-fig. 9) the anterior supraorbital has the same relation to the orbit as in *Lydekkerina*, and also meets the supraorbito-dermosphenotic. But it is unique in being so short that it fails to meet the naso-postrostral.

The anterior supraorbital shows a rather slightly specialized stage — approximately as in *Eryops megacephalus* among the "*Rhachitomi*" — in the "*Stereospondyli*", except the families *Capitosauridae* and *Mastodonsauridae*, and the most specialized genera of the *Brachyopidae*. In these families and genera the anterior supraorbital (So_1, text-figs. 17, 27, 28, 30, 31) has no contact with the posterior supraorbital or supraorbito-dermosphenotic, and in *Wetlugasaurus* (text-fig. 38), and the *Capitosauridae* (text-figs. 17, 31) it has an enormous extension in front of the orbit, owing to a very important lengthening of the part of the skull in front of the orbits, covered by the anterior parts of the frontals, by the anterior supraorbitals, by the anterior parts of the jugals (cf. below), and by the middle parts of the lachrymo-maxillaries.

In the Spitsbergen forms *Tertrema* (text-fig. 23) and *Peltostega* (text-fig. 26), WIMAN found no sutures between the anterior supraorbitals and the supraorbito-dermosphenotics.

On the whole *Cyclotosaurus* (text-fig. 17) represents the most specialized of all known Labyrinthodonts in regard to the region between the orbit and the nostril, with a very large anterior supraorbital, with a very long suture between that bone and the long preorbital part of the jugal, and with a very reduced posterior antorbital.

Trematosuchus (text-fig. 10), *Trematosaurus* (text-fig. 11), and the American genera of the *Metoposauridae* (text-fig. 16; BRANSON & MEHL 1929, figs. 3, 6, 7, 8, 10), on the other hand show a primitive condition in regard to the anterior supraorbital, which, in these Stereospondyls, does not meet the jugal, and has a relatively long suture with the supraorbito-dermosphenotic.

The *fronto-parietals* (*Fr. pa*, text-figs. 5, 6 A, 7, 8 A, B, 9—12, 14—31, 37, 38, 53, 55—57, 59—64, 66—68) of the higher *Labyrinthodontia* have a fairly uniform shape — being roughly rectangular with mainly straight anterior, median and posterior margins. The lateral margin is practically always markedly bipartite, most often with a con-

cave anterior and a straight or convex posterior part. Accordingly each fronto-parietal may be regarded as composed of an anterior part with a usually concave lateral margin and a posterior part with straight or convex lateral margin.

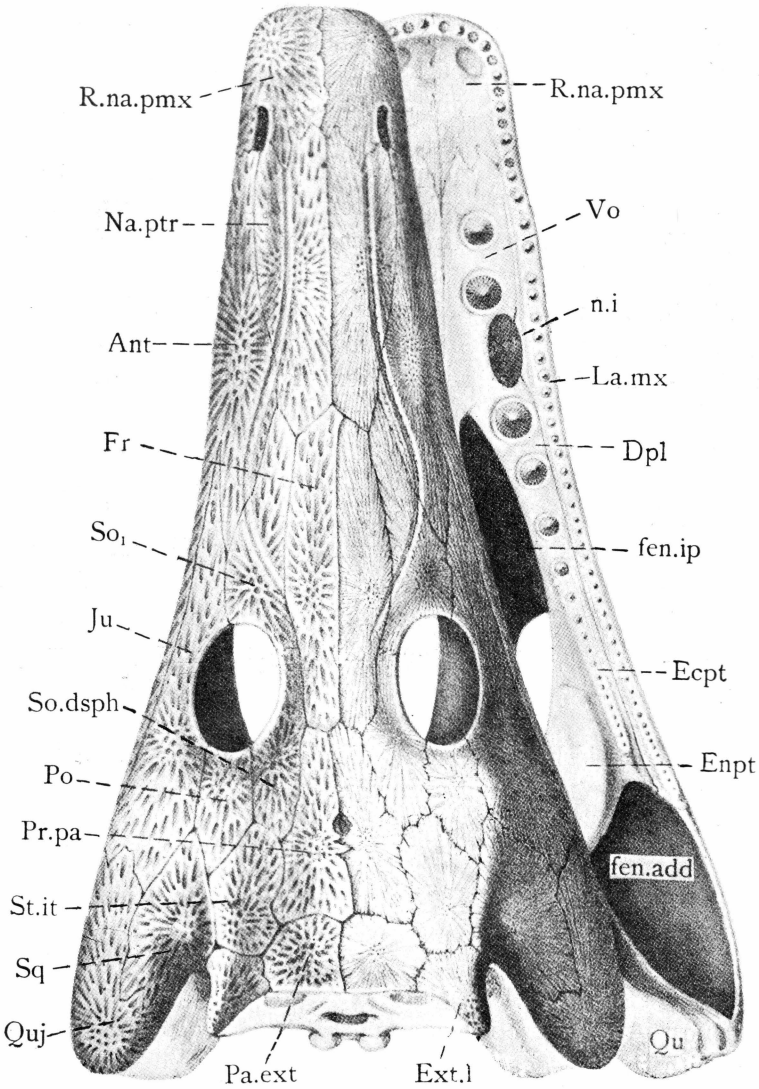
Very often the anterior and posterior parts of each fronto-parietal are about equally long (*Micropholis*, text-fig. 5; *Zatrachys*, text-fig. 7; *Trimerorhachis*, text-fig. 8 A; *Broiliellus*, text-fig. 8 B; *Actinodon*, text-fig. 9; *Onchiodon*, CREDNER 1893; *Sclerocephalus*, text-fig. 15; *Archegosaurus*, text-fig. 22; *Peltostega*, text-fig. 26; *Mastodonsaurus*, text-fig. 27; *Wetlugasaurus*, text-figs. 38, 53; *Stoschiosaurus*, text-fig. 55; *Aphaneramma*, text-fig. 56; *Lyrocephalus*, text-figs. 60, 61, 66; *Platystega*, text-fig. 62).

When this is not the case, the posterior part may be markedly shorter than the anterior one, as in *Eryops anatinus* (text-fig. 14), *E. megacephalus* (text-fig. 21), *Osteophorus* (text-fig. 18), the *Capitosauridae* (text-figs. 17, 31, 37), and *Cochleosaurus* (text-fig. 20). In the *Metoposauridae* (text-figs. 16, 24; BRANSON and MEHL 1929, figs. 3, 6, 7, 8, 10, 11), and the *Brachyopidae* (text-figs. 19, 25, 29), on the contrary, the posterior part of each fronto-parietal is markedly longer than the anterior part.

The pineal foramen is generally situated about at the boundary between the anterior and the posterior parts of the fronto-parietals. It lies markedly anteriorly to that boundary in *Zatrachys* and *Micropholis*, but clearly behind it in *Trimerorhachis*.

The fronto-parietals of the "*Stereospondyli*" (*Fr. pa*, text-figs. 10, 11, 16, 17, 19, 23—31, 37, 53, 55—57, 60—64, 66) vary as to their anterior extension, according to the above discussed variation in the posterior extension of the frontals. Otherwise there may be distinguished three types of fronto-parietals in the *Stereospondyli*: viz. 1. very long fronto-parietals with the pineal foramen markedly behind the middle of the bones — *Metoposauridae* and *Trematosauridae*; 2. short fronto-parietals with the pineal foramen just behind the middle of the bones — *Mastodonsauridae*; 3. very short fronto-parietals with the pineal foramen in front of the middle of the bones — *Peltostega*, *Capitosauridae*.

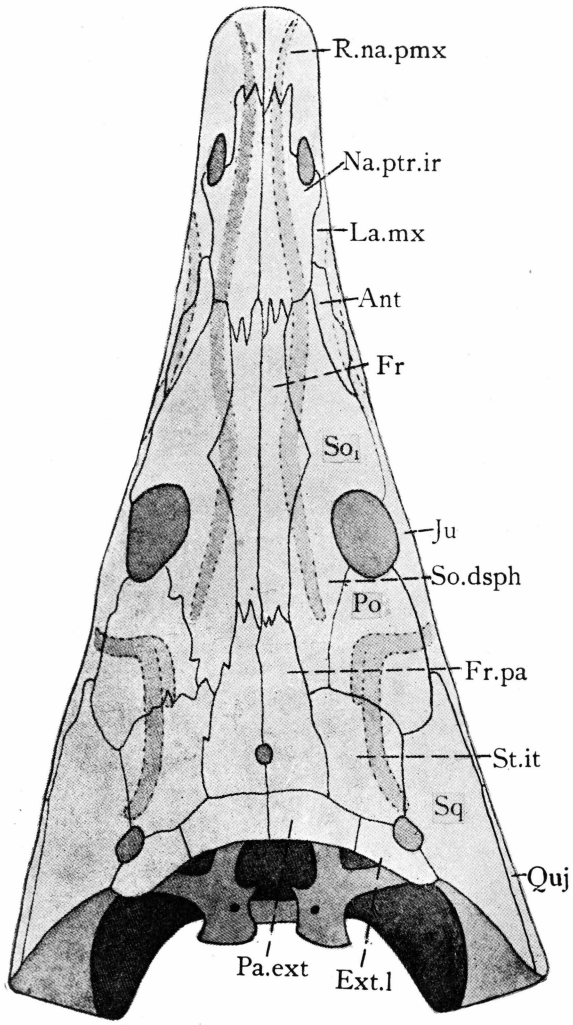
From a comparison with Ichthyostegids and Crossopterygians (cf. SÄVE-SÖDERBERGH 1932, pp. 87—98) it is evident that the anterior part, as defined above, of the fronto-parietal of the higher *Labyrinthodontia* must, at least in the main, represent the frontal component of the bone. Therefore, when in *Trimerorhachis* (see text-fig. 8 A) there is found a dermal bone situated laterally to the anterior part of the fronto-parietal, between that part and the postorbital (cf. below, pp. 62—63), it must quite clearly be a *dermosphenotic* (*Dsph*, text-fig. 8 A), and not an intertemporal as it is generally called. Now, on the other hand, the fact that this well developed dermosphenotic is connected with the fronto-



Text-fig. 22. *Archegosaurus decheni* GOLDFUSS. Dorsal aspect of the skull and partial palatal aspect. After BURMEISTER (1850).

Ant, posterior antorbital; *Dpl*, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Ju*, jugal; *La.mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Pr. pa*, fronto-parietal; *Qu*, quadrate; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *Vo*, vomer; *fen. add.*, adductor fenestra; *fen. ip*, interpterygoid vacuity; *n. i*, internal naris.

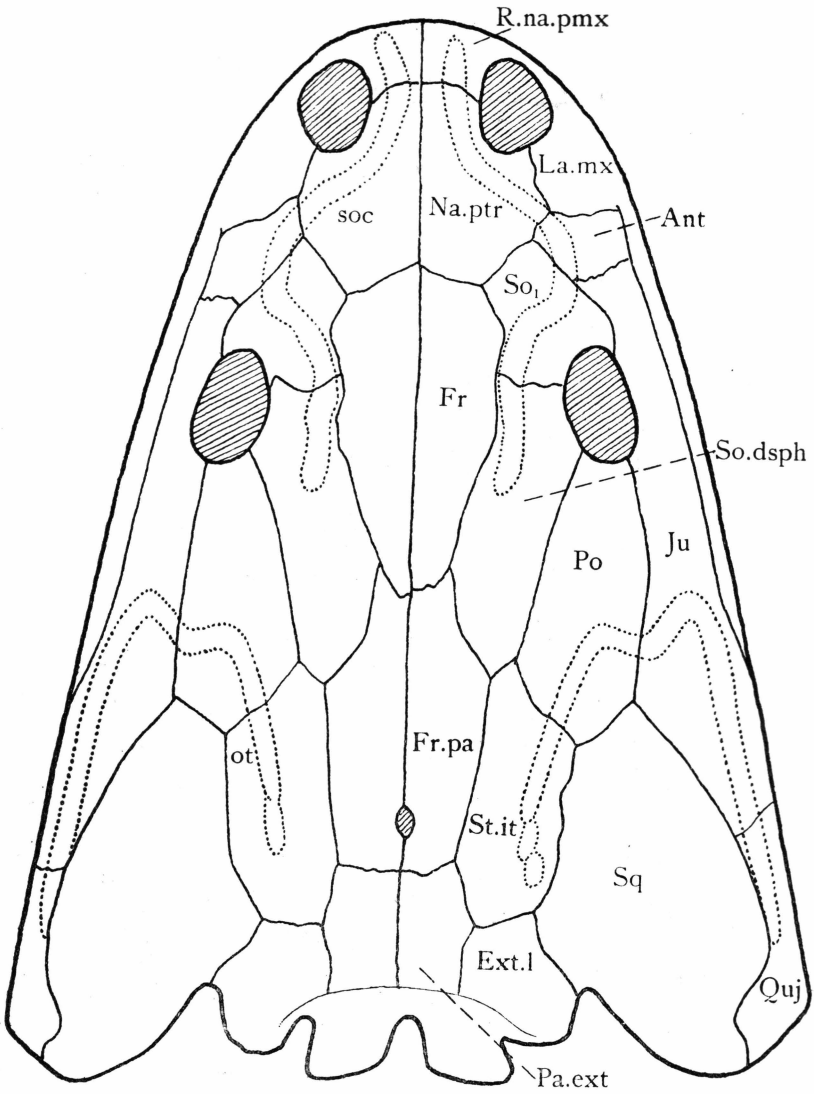
parietal by a suture which reaches exactly as far back as does that portion of the lateral margin of the fronto-parietal, above defined as the lateral margin of the anterior part of the bone, goes to prove that in



Text-fig. 23. *Tertrema acuta* WIMAN. Dorsal aspect of the skull. After WIMAN (1917). *Ant*, posterior antorbital; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr. ir*, naso-postrostro-inter-rostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; *R.na.pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermo-sphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

fact the so called anterior part of the fronto-parietal corresponds fairly closely to the frontal component of the bone. And this statement is of great importance for tracing the further fate of the dermosphenotic in the *Labyrinthodontia*.

A dermosphenotic, quite clearly with the same position and relations as that of *Trimerorhachis*, is figured by FRITSCH (1885, fig. 138) in *Nyřania*. The element, described by BROILI (1905) as possibly an inde-



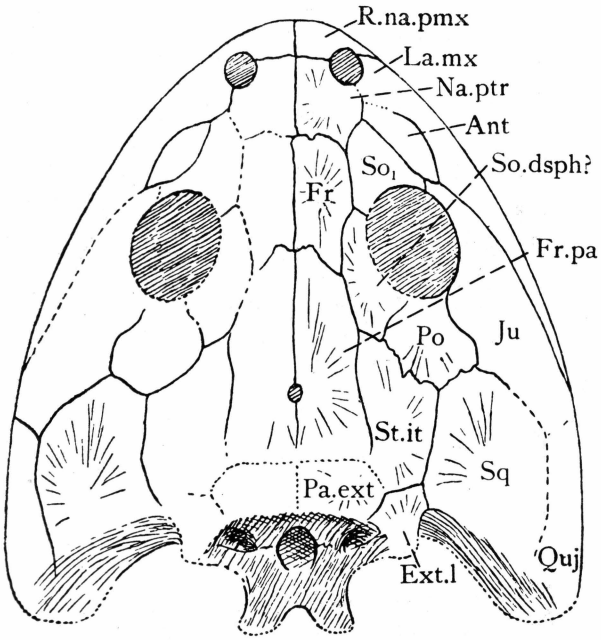
Text-fig. 24. *Metoposaurus diagnosticus* (v. MEYER). Dorsal aspect of the skull. After FRAAS (1889).

Ant, posterior antorbital; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *ot*, otic part of the infraorbital canal; *soc*, supraorbital canal.

pendent intertemporal in *Cochleosaurus* (*Dsph*, text-fig. 20), very probably also represents a dermosphenotic.

Before analysing the fate of the dermosphenotic in the other higher *Labyrinthodontia*, we must pay some attention to the bone

situated in front of it — the *posterior supraorbital* (So_2, text-figs. 8 A, 20). In *Trimerorhachis*, where it is best known, it is a long, bent, posteriorly expanded bone, forming the posterior half of the medial margin of the orbit. It meets the postorbital in a very short suture, thus excluding the dermosphenotic from the orbital margin — quite as in *Osteolepis* (see SÄVE-SÖDERBERGH 1933). Its most posterior part does not extend farther posteriorly than the anterior margin of the fronto-parietal, and has short sutures with that margin, and with the anterior margin of the dermosphenotic. It has medial sutures with the frontal and the fronto-parietal. The latter suture is more typically shown in *Trimerorhachis*



Text-fig. 25. *Bothriceps australis* HUXLEY. Dorsal aspect of the skull. After BROOM (1915).

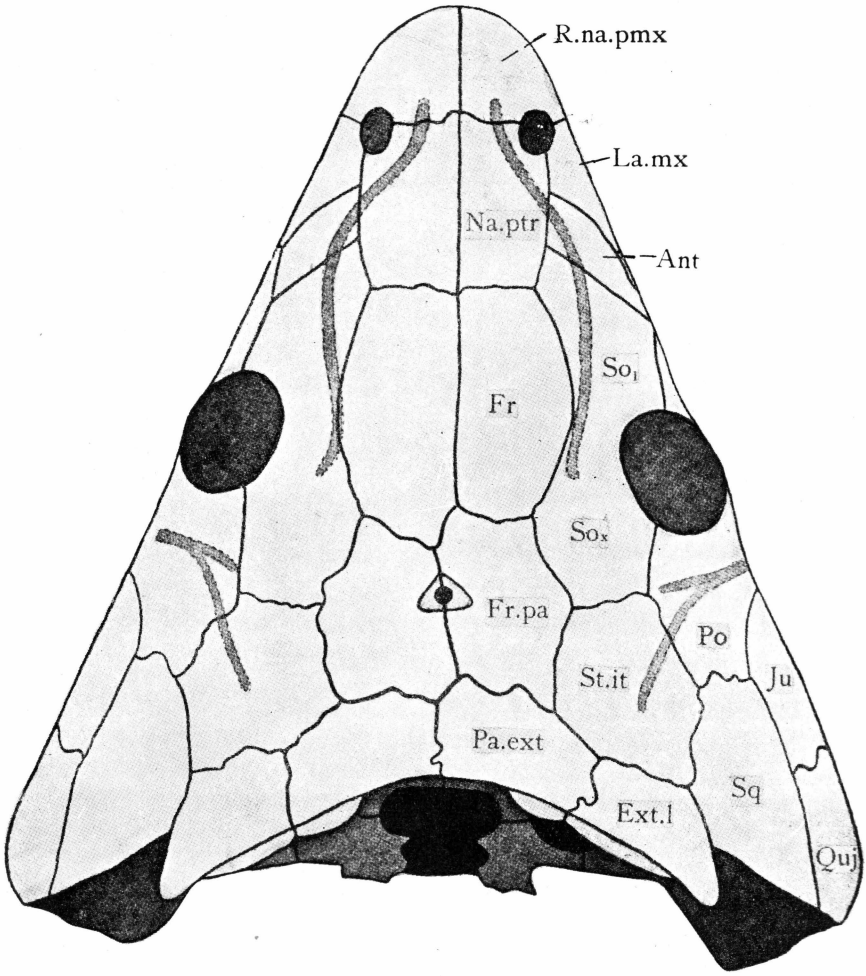
Ant, posterior antorbital; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

medius (BROOM 1913, fig. 10) and *Nyřania* (FRITSCH 1885, fig. 138) than in *Trimerorhachis insignis* (text-fig. 8 A).

In *Trimerorhachis* the lateral margin of the posterior supraorbital forms, together with the lateral margin of the dermosphenotic, a very characteristic line, running for a short stretch straight postero-medially from the orbital margin, then making a sharp bend and continuing in

a longer postero-laterally directed posterior part, with a convexity, turned antero-laterally (see text-fig. 8 A).

This characteristic line, which is the medial margin of the postorbital (cf. below, pp. 62—63), is easily recognised in *Broiliellus* (text-



Text-fig. 26. *Peltostega erici* WIMAN. Dorsal aspect of the skull. After WIMAN (1916). *Ant*, posterior antorbital; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; So_x, supraorbito-dermosphenotic or posterior supraorbital; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

fig. 8 B), but here it is formed by the suture of the postorbital with a single bone of the cranial roof. This single bone (*So. dsph*, text-fig. 8 B) also meets the whole lateral margin of the anterior part of the fronto-parietal, as above defined, and further has a short suture with the frontal

and forms a postero-medial part of the orbital margin. Thus this single bone evidently covers, except anteriorly, exactly the area covered in *Trimerorhachis* by the dermosphenotic and the posterior supraorbital. Evidently owing to the very large size of the orbit, it does not meet the anterior supraorbital.

The facts put forward above can, I think, hardly be explained in any more natural way than that in *Broiliellus* we have to do with a compound *supraorbito-dermosphenotic*, being the result of a fusion of the two elements, found as independent dermosphenotic and posterior supraorbital in *Trimerorhachis*.

As must of course be expected, the minute shape of the medial margin of the postorbital cannot be so successfully used for the analysis in all the other higher *Labyrinthodontia*. But the relations of the bones in question to the distinctly equivalent anterior parts of the lateral margins of the fronto-parietals, and the length of their sutures with the postorbitals, make it very probable that we have a compound supraorbito-dermosphenotic (*So. dsph*) also, at least in *Micropholis* (text-fig. 5), *Zatrachys* (text-fig. 7), and *Dasyceps* (v. HUENE 1910, fig. 1), *Actinodon* (text-fig. 9), *Eryops* (text-figs. 14, 21), *Sclerocephalus* (text-fig. 15), *Osteophorus* (text-fig. 18), *Archegosaurus* (text-fig. 22), *Melosaurus* (v. MEYER 1860 a, pl. X), *Chelydosaurus* (FRITSCH 1885, fig. 131), and *Acanthostoma* (CREDNER 1883, pl. XI, fig. 1).

Only in *Lydekkerina* (text-fig. 12), of the sufficiently well known "*Rhachitomi*", may there be a more grave doubt about the fate of the posterior supraorbital and dermosphenotic, owing to the rather short posterior extension of the single bone (So_x) at the postero-medial margin of the orbit. Possibly we have to do in this case with a reduction of the dermosphenotic, the bone So_x being a posterior supraorbital only.

An independent dermosphenotic has never been recorded in any stereospondylous genus. When discussing the difficult question as to the fate of that element in the "*Stereospondyli*", one may naturally divide these Labyrinthodonts into four groups:

1. In such a form as *Trematosaurus* (text-fig. 11) the conditions in the region in question seem to be very nearly the same as in *Archegosaurus* (text-fig. 22) — except for the very much greater length of the region in the stereospondylous form. On the other hand, the conditions in all members of the families *Trematosauridae* and *Metoposauridae* — as for instance *Trematosuchus* (text-fig. 10), *Tertrema* (text-fig. 23), *Aphaneramma* (text-fig. 56), the new genus *Stoschiosaurus* described below (text-figs. 55, 57, 59 A), *Lyrocephalus* (text-figs. 60, 61), *Platystega* (text-fig. 62), *Metoposaurus* (text-fig. 24), and *Anaschisma* (text-fig. 16) — are easily and naturally referred to the same type as *Trematosaurus*. Consequently in all these forms the dermosphenotic must be regarded as

fairly certainly fused with the posterior supraorbital to a compound *supraorbito-dermosphenotic* (*So. dsph*, text-figs. 10, 11, 16, 23, 24, 55, 56, 60—64). The chief arguments for this interpretation of the bone at the postero-dorsal corner of the orbit as a product of fusion of a posterior supraorbital and a dermosphenotic component are: (a) the length and posterior extension of the bone in question, as compared with the postorbital; (b) the very clear and most often not very short suture formed by the discussed bone with the supratemporo-intertemporal and with the anterior half of the lateral margin of the fronto-parietal; (c) the position of the developing centre of the discussed bone considerably behind the orbit in *Trematosaurus*.

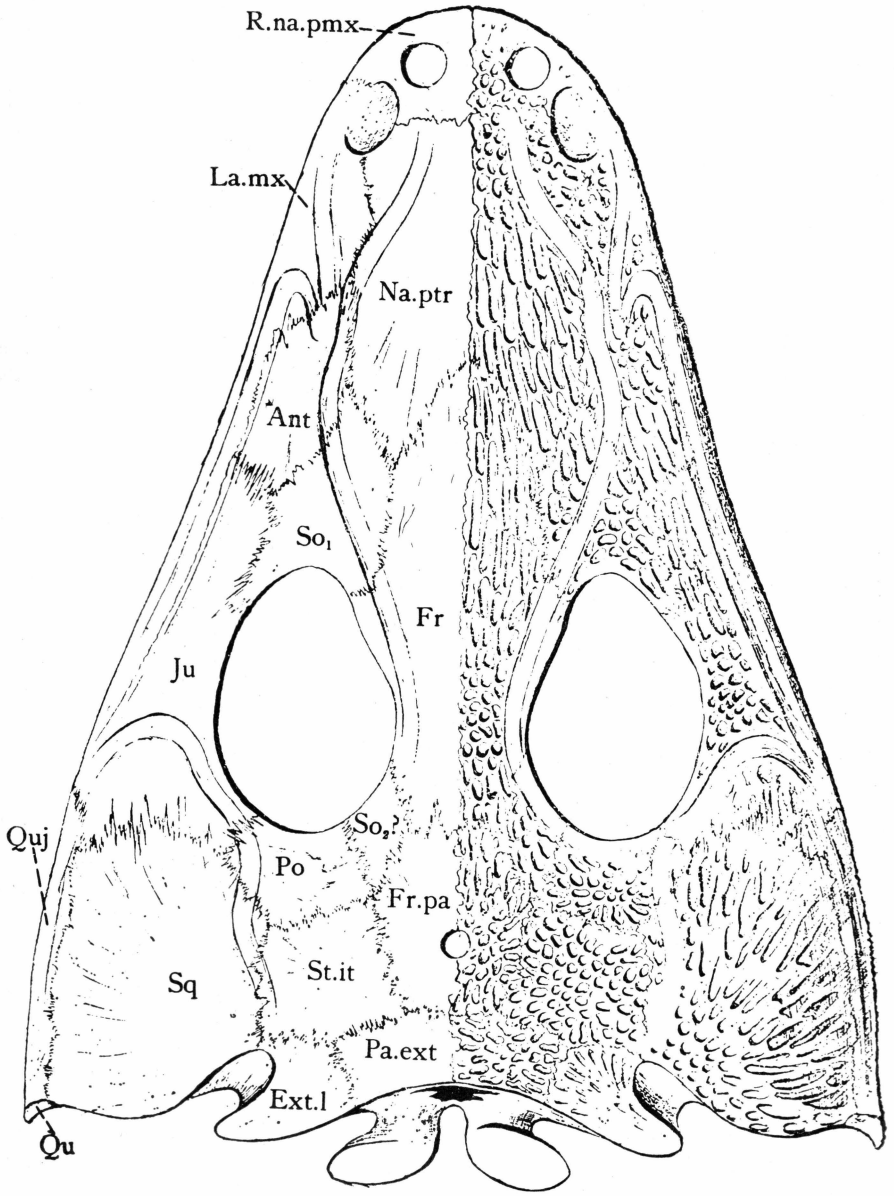
If it is true that, as WATSON supposes (1919 b, p. 48) the *Brachyopidae* are the descendants of rhachitomous forms similar to *Dvinosaurus* this family also most probably has — at least originally — a compound supraorbito-dermosphenotic. For as far as can be judged from AMALITZKI's figure (1924, pl. I) *Dvinosaurus* has a supraorbito-dermosphenotic like that of most "*Rhachitomi*". The much farther posterior extension of the postorbital than of the bone in question, especially in *Bothriceps* (text-fig. 25), would then be a secondary character. It may be of interest to notice the aspect of the large bone in question in *Batrachosuchus* (text-fig. 19), quite similar to the supraorbito-dermosphenotic of most "*Rhachitomi*".

2. In *Peltostega* (text-fig. 26) the discussed region as a whole is very much shorter than in the forms discussed under (1), and is therefore not so easily interpreted. On one hand the bone in question (So_x, text-fig. 26) seems to have much the same relation to the lateral margin of the fronto-parietal as a typical supraorbito-dermosphenotic. On the other hand, however, it is connected by suture with only $^2/_5$ of the medial or postero-medial margin of the postorbital. The discussed region as a whole shows in *Peltostega* fairly similar condition to those found in *Lydekkerina* (text-fig. 12).

3. Of the remaining two families of the "*Stereospondyli*" — the *Capitosauridae* and the *Mastodonsauridae* (text-figs. 17, 27, 31, 37), the members of the former show rather uniform conditions in the discussed region, which is there always very short.

The posterior margin of the postorbital here forms a roughly straight line, continuing without any marked bend in the posterior margin of the bone, medial to it. This bone has, in the *Capitosauridae*, a not very short suture with the supratemporo-intertemporal, and a rather long suture with the concave anterior half of the lateral margin of the fronto-parietal. All these facts seem to speak rather clearly in favour of an interpretation of the discussed bone as a *supraorbito-dermosphenotic* (*So. dsph*, text-figs. 17, 31, 37).

4. In *Mastodonsaurus* the bone (So_2?, text-fig. 27), medial to the postorbital is very small and just meets the supratemporo-intertemporal at



Text-fig. 27. *Mastodonsaurus giganteus* JAEGER. Dorsal aspect of the head. After FRAAS (1889).

Ant, posterior antorbital; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Qu*, quadrate; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; So_2?, posterior supraorbital or reduced supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

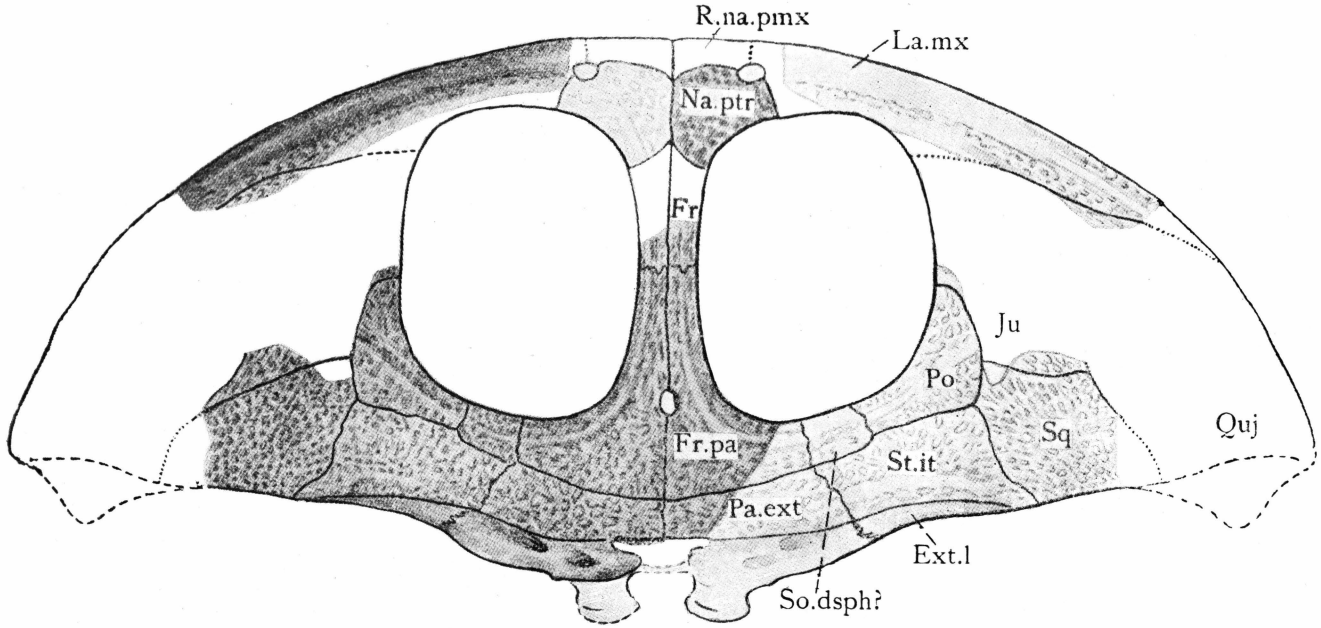
a point, where also the postorbital meets the fronto-parietal. This may be interpreted as a specialization of the condition in the *Capitosauridae* — by an important reduction of the *supraorbito-dermosphenotic* of this family. But it may also, and perhaps more naturally, be explained as the result of quite another process — a total reduction of a once independent dermosphenotic, just as in *Baphetes* (text-fig. 1).

In most "*Stereospondyli*" the supraorbito-dermosphenotic (or posterior supraorbital) forms the whole posterior half of the medial margin of the orbit, and meets the anterior supraorbital. Only in the *Capitosauridae* and in the *Mastodonsauridae* do we find a reduction of the anterior part of the supraorbito-dermosphenotic. In *Cyclotosaurus* (text-fig. 17) it reaches as far forward as half the medial orbital margin and does not seem to be more markedly narrower in its most anterior part, which, however, does not meet the very reduced part of the anterior supraorbital medial to the orbit. In *Capitosaurus* the supraorbito-dermosphenotic is most often figured approximately as in *Cyclotosaurus* or somewhat narrower in the most anterior part (ZITTEL 1890, fig. 337; JAEKEL 1903, Texttafel IX; ROEPKE 1923, Taf. I; SMITH WOODWARD 1932, fig. 313). But in *Capitosaurus helgolandiae* SCHROEDER (1914, see my text-fig. 31) figured a more short supraorbito-dermosphenotic,reputedly based upon material in the Berlin Museum für Naturkunde, and JAEKEL's figure.

The most specialized condition is, however, found in *Mastodonsaurus* (text-fig. 27). The very small size of the discussed bone in this genus may be due, at least to a certain extent, to the very large size of the orbits.

The dorsal lamina of the paired *parieto-extrascapular* (*Pa. ext*, text-figs. 5, 6A, 7, 8A, 9—12, 14—31, 37, 38, 53, 55—57, 59—62, 66—68) has very constant relations to the surrounding bones in the "*Rhachitomi*"-"*Stereospondyli*", meeting the posterior half of the medial margin of each supratemporo-intertemporal and thus separating from each other the two other bones which it meets on each side — the fronto-parietal and the lateral extrascapular. The only one of the "*Rhachitomi*" where this is not clearly the case, is *Lydekkerina* (text-fig. 12). In this form WATSON marked off a hypothetic anterior margin of the parieto-extrascapular, situated farther back than the sutures between each supratemporo-intertemporal and each lateral extrascapular. I am inclined to feel grave doubts about the correctness of WATSON's supposition as to the position of the said margin, not only because it would be unique amongst the true *Labyrinthodontia* (cf. below, pp. 97—104), but also on account of the details in the course of the medial margins of the supratemporo-intertemporals and lateral extrascapulars.

As compared with the corresponding bones of the *Ichthyostegidae*, the parieto-extrascapulars of the "*Rhachitomi*" are very short. In *Micropholis* (text-fig. 5), *Trematops* (text-fig. 6A), *Trimerorhachis* (text-fig. 8A),



Text-fig. 28. *Plagiosternum granulosum* Fraas. After Fraas (1913).
Ext. l, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

Broiliellus (text-fig. 8 B), *Actinodon* (text-fig. 9), *Sclerocephalus* (text-fig. 15), and *Dasyceps* (v. HUENE 1910, fig. 1), the said bones have about the same length as in *Loxomma* and *Baphetes*, but in other "*Rhachitomi*", like *Zatrachys* (text-fig. 7), and *Eryops* (text-figs. 14, 21) they are very much shorter.

Also in the "*Stereospondyli*" the parieto-extrascapulars are generally rather short, with a shape, varying from quadrate in, for instance, *Trematosuchus* (text-fig. 10), *Lyrocephalus* (text-figs. 60, 61), *Aphaneramma* (text-fig. 56), and the new genus *Stoschiosaurus* (text-figs. 55, 57, 59 A), to very short, as in *Mastodonsaurus* (text-fig. 27). Only in the *Metoposauridae* (text-figs. 16, 24) do we find parieto-extrascapulars with a length considerably greater than the breadth of the bones.

The rod-shaped ventral processes of the parieto-extrascapulars (*Pa. extv*, pl. 2, fig. 1; pl. 15, fig. 4) join these bones to the exoccipitals.

In one single genus of Labyrinthodonts, viz. *Aphaneramma* (text-fig. 56) is there found a median independent bone, a "*centroparietal*" (*Cp*, text-fig. 56; WIMAN 1914, p. 18), between the fronto-parietals and the parieto-extrascapulars.

The *supratemporo-intertemporal* (*St. it*, text-figs. 5, 7—12, 14—31, 37, 38, 53, 55—57, 59—62, 64, 66—68) has mainly the same relations in the higher *Labyrinthodontia* as in the Ichthyostegids and the Loxommids. Also its shape is in the main well comparable in the three groups. In all typical forms it constantly shows an elongated shape, with a straight posterior margin — in suture with the lateral extrascapular, a mainly convex lateral one — in suture with the postorbital and squamosal, and a bipartite, convex, medial margin, of which the anterior part is joined by suture with the posterior half of the fronto-parietal, and the posterior part has a suture towards the parieto-extrascapular (parietal component). Evidently the intertemporal component is represented by the part of the supratemporo-intertemporal, in suture with the fronto-parietal, whereas the part in suture with the parieto-extrascapular represents the supratemporal component.

In *Trimerorhachis* (text-fig. 8 A) the supratemporo-intertemporal seems to form a very short part of the margin of the otic notch. In *Cochleosaurus* it forms half the medial margin of the notch, and in *Broiliellus* (text-fig. 8 B) and *Trematops* (text-fig. 6 A) the otic notch apparently forms the greatest part of the lateral margin of the supratemporo-intertemporal. At least the condition in *Broiliellus* and *Trematops* must conceivably depend upon a secondary enlargement of the otic notch, and thus has nothing to do with the question of the more or less firm attachment of the cheek to the dermal cranial roof.

In the "*Stereospondyli*" each of the supratemporo-intertemporals is generally excluded from the otic notch by the meeting of the squamosal and lateral extrascapular. Only in *Tertrema* (text-fig. 23) — with a closed

otic notch — and in the most advanced of the *Brachyopidae* (*Plagiosternum*, text-fig. 31) does the supratemporo-intertemporal form part of the margin of the otic notch.

In *Archegosaurus* (text-fig. 22), in *Anaschisma* (text-fig. 16), and in certain of the *Trematosauridae* (*Trematosaurus*, text-fig. 11; *Trematosuchus*, text-fig. 10; *Aphaneramma*, text-fig. 56; *Stoschiosaurus*, text-figs. 55, 57, 59A) the supratemporo-intertemporal is generally about half as broad as it is long. It is, however, generally somewhat shorter in the "*Rhachitomi*" (see for instance text-figs. 15, 20, 21), and considerably shorter in *Lyrocephalus* (text-figs. 60, 61, 66), *Platystega* (text-fig. 62), *Peltostega* (text-fig. 26), *Batrachosuchus* (text-fig. 19), *Tertrema* (text-fig. 23) *Mastodonsaurus* (text-fig. 27), *Wetlugasaurus* (text-figs. 38, 53), and especially in *Plagiosaurus* (text-fig. 30), *Plagiosternum* (text-fig. 28), and the *Capitosauridae* (text-figs. 17, 31, 37).

In *Bothriceps* (text-fig. 25) there is an unusually long supratemporo-intertemporal, and a similar shape of the discussed bone is found in *Metoposaurus* (text-fig. 24).

The supratemporo-intertemporal is clearly connected with the otic part of the infraorbital canal in *Trematosaurus* (text-fig. 11), *Lydekkerina* (text-fig. 12), *Anaschisma* (text-fig. 16), *Tertrema* (text-fig. 23), *Capitosaurus* (text-fig. 31), *Aphaneramma* (text-fig. 56), *Lyrocephalus* (text-figs. 61, 66), *Metoposaurus* (text-fig. 24), *Wetlugasaurus* (text-figs. 38, 53), and with the postotic canal in *Lydekkerina* (text-fig. 12), *Tertrema* (text-fig. 23), *Capitosaurus* (text-fig. 31), *Aphaneramma* (text-fig. 56), and *Lyrocephalus* (text-figs. 61, 66).

The small element (*Et?*, text-fig. 5), figured by WATSON in *Micropholis* and called by him supratemporal, very clearly has not the relations held by all certainly identified supratemporals. If it is really an independent element[1]), it is most nearly comparable with the bone in *Osteolepis*, called by me the *extratemporal* (SÄVE-SÖDERBERGH 1933, p. 19; *Et*, pl. 1; text-fig. 19).

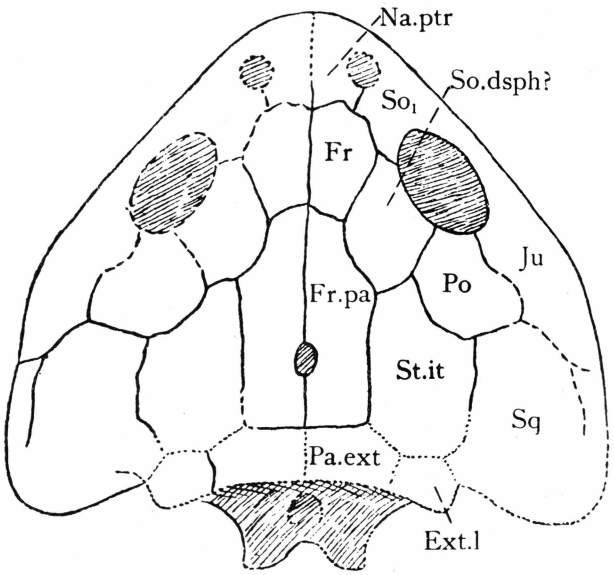
The *lateral extrascapulars* (*Ext. l*, text-figs. 5, 7—12, 14—31, 37, 38, 53, 55—62, 66—68) are very small in certain "*Rhachitomi*", as *Trimerorhachis* (text-fig. 8 A), *Eryops* (text-figs. 14, 21) and *Cochleosaurus* (text-fig. 20).

This small size of the lateral extrascapulars forms a common character of the Loxommids and the mentioned "*Rhachitomi*".

Also in the "*Stereospondyli*" each lateral extrascapular is usually rather small and most often has a triangular postero-lateral process, and a short suture towards the squamosal. The mentioned process is not well developed, since the postero-lateral corner of the bone is more

[1]) After an examination of the specimen (in the British Museum of Natural History) I am still uncertain as to wether the supposed suture between the areas denoted *Sq* and *Et?* in text-fig. 5 is a real suture or a fracture-line.

rounded, in *Metoposaurus* (text-fig. 24); and in the more advanced *Brachyopidae: Plagiosaurus* (text-fig. 30), *Plagiosternum* (text-fig. 28), *Batrachosuchus* (text-fig. 19) the posterior margin of the lateral extrascapular passes directly over into the posterior margin of the squamosal. The same is the case in one of the genera with a closed otic notch — *Cyclotosaurus* (text-fig. 17), whereas in *Tertrema* (text-fig. 23) there is still a shallow sinus as a remnant of the closed outer parts of the otic notch.



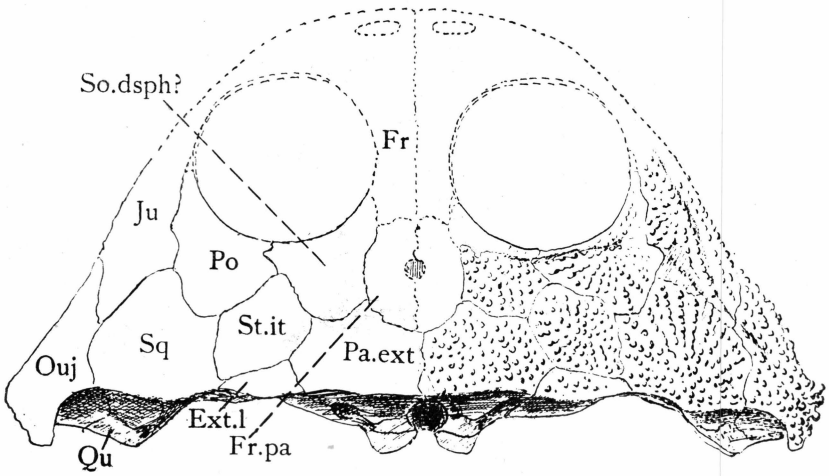
Text-fig. 29. *Brachyops laticeps* OWEN. Dorsal aspect of the skull. After BROOM (1915). *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

In the higher Labyrinthodonts, as shown by WATSON (1919b), ventral processes from the lateral extrascapulars (*Ext. lv*, text-fig. 58; pl. 1; fig. 2; pl. 2, fig. 1; pl. 4, figs. 1, 3, 4; pl. 5; pl. 6, fig. 2; pl. 15, fig. 4) gradually developed to meet the exoccipital and hide the opisthotics in posterior view.

The lateral extrascapulars are connected with the supratemporal commissural canal in *Lyrocephalus* (text-figs. 60, 61).

The *lachrymo-maxillary* (*La. mx*, text-figs. 5, 7, 8 A, C, 9—28, 32, 33, 37, 38, 54, 56, 58—66) of the higher *Labyrinthodontia* is clearly homologous with the bone so named in the Loxommids. Its relations to the surrounding bones are constant, and the same as in the Loxommids, except in one point: the relation of the posterior end of the bone to the quadratojugal. In both groups the lachrymo-maxillary is very long and reaches far behind the orbits. But whereas no case has

been recorded of its meeting the quadratojugal in the Loxommids, it clearly does so in many higher *Labyrinthodontia*, as *Eryops* (text-figs. 14, 21), *Sclerocephalus* (text-fig. 15), *Actinodon* (text-fig. 9), *Onchiodon* (CREDNER 1893, Taf. XXX, fig. 1), and *Lyrocephalus rapax* (text-fig. 64). The lachrymo-maxillary is clearly connected with the horizontal portion of the suborbital part of the infraorbital canal in *Lydekkerina* (text-fig. 12). The lachrymo-maxillaries are also clearly connected at least with parts of the horizontal portions of the suborbital parts of the infraorbital canals in *Trematosuchus? yakovlevi* (text-fig. 13), *Anaschisma* (text-fig. 16), *Tertrema* (text-fig. 23), *Cyclotosaurus* (text-fig. 17),

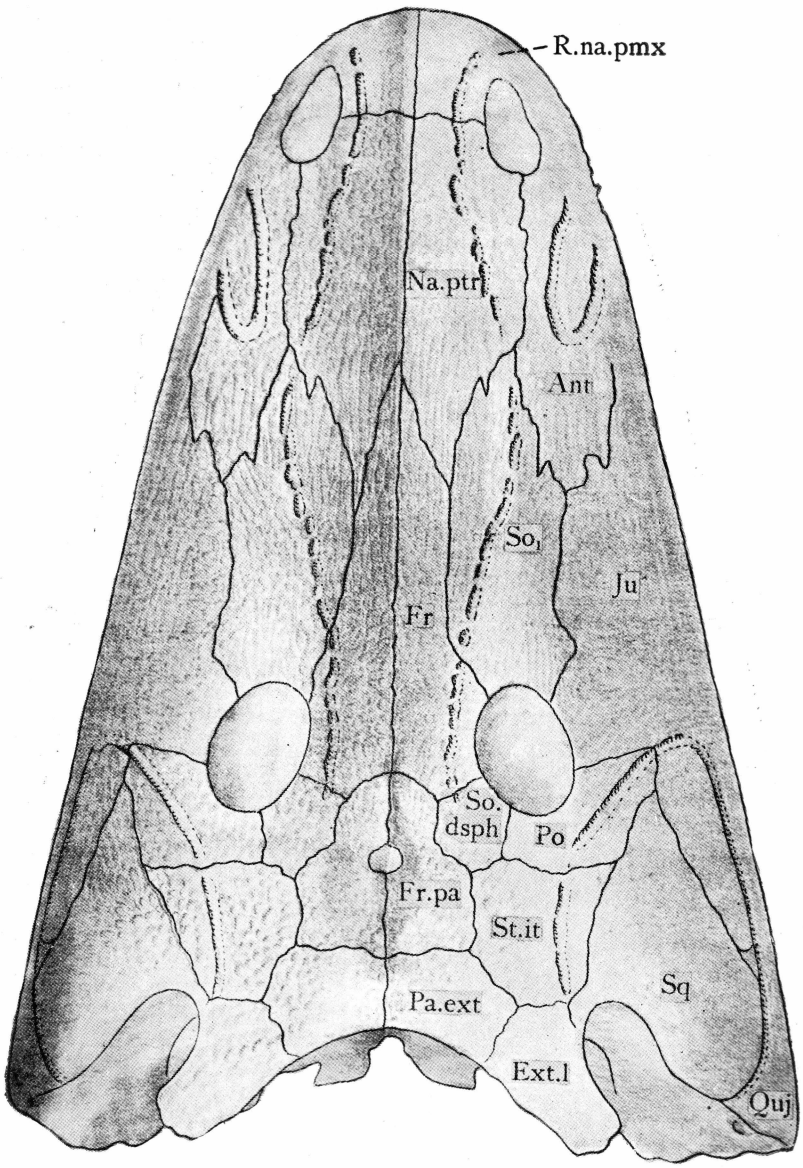


Text-fig. 30. *Plagiosaurus depressus* JAEKEL. Dorsal aspect of the skull. After JAEKEL (1914).

Ext. l, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Qu*, quadrate; *Quj*, quadratojugal; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

Mastodonsaurus (text-fig. 27), *Wetlugasaurus* (text-fig. 38), and *Lyrocephalus* (text-figs. 60, 61, 63, 64 A). They are especially interesting in *Cyclotosaurus*, as figured by FRAAS (1889, see my text-fig. 17). In that genus FRAAS figures a short but distinct part of an incomplete suture evidently separating the lachrymal from the tooth-bearing component of the lachrymo-maxillary.

The *jugal* (*Ju*, text-figs. 5, 7—12, 14—31, 37, 38, 53, 55—57, 59—64, 66—68) is generally a large bone in the higher *Labyrinthodontia*, with about the same relation to the orbit as in *Ichthyostega stensiöi* (SÄVE-SÖDERBERGH 1932, pl. II; text-fig. 2). (The special, very great, anterior extension of the orbit in the Loxommids makes this relation a little different in that group.) In all the above mentioned and discussed "*Rha-*



Text-fig. 31. *Capitosaurus nasutus* v. MEYER. Dorsal aspect of the skull. After SCHROEDER (1914).

Ant, posterior antorbital; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supra-temporo-intertemporal.

chitomi", where the anterior supraorbital meets the jugal (cf. pp. 43—44), the two bones have the same relations as those between the jugal and posterior antorbital in *Ichthyostega stensiöi*. The evolution of this curious analogy has already been traced when discussing the anterior supraorbital (pp. 43—44).

The jugals of *Trematosaurus* (text-fig. 11), *Lydekkerina* (text-fig. 12), *Anaschisma* (text-fig. 16), *Tertrema* (text-fig. 23), *Metoposaurus* (text-fig. 24), *Mastodonsaurus* (text-fig. 27), *Wetlugasaurus* (text-figs. 38, 53), *Aphaneramma* (text-fig. 56), and *Lyrocephalus* (text-figs. 60, 61) are seen to be connected with the vertical, those of *Trematosaurus* (text-fig. 11), *Anaschisma* (text-fig. 16) and *Lyrocephalus* (text-figs. 60, 61, 63, 66) also with the horizontal portion of the suborbital part of the infraorbital canal. The jugals of *Trematosaurus* (text-fig. 11), *Anaschisma* (text-fig. 16), *Metoposaurus* (text-fig. 24), *Capitosaurus* (text-fig. 31), *Wetlugasaurus* (text-fig. 38), *Aphaneramma* (text-fig. 56), and *Lyrocephalus* (text-figs. 60, 61, 66) are also clearly connected with the anterior parts of the jugal canals.

In certain "*Rhachitomi*" exceptional relations of the jugal are found. Thus in *Trimerorhachis* (text-fig. 8 A, C) (and possibly also in *Chelydosaurus*; FRITSCH 1885, fig. 131), by the meeting of the posterior antorbital and the postorbital, the jugal is excluded from the orbital margin. In *Zatrachys* there is an exceptionally short jugal with a very short orbital margin. Quite unique conditions are found in *Micropholis* (text-fig. 5), if WATSON is right in his conception of the course of the sutures in that animal. In any case it is quite impossible that the area (*Po. ju*, text-fig. 5) denoted by WATSON as the postorbital, should represent only that element. A closer examination of the type specimen (in the British Museum of Natural History) reveals the fact that each of them is clearly composed of one dorsal or medial and one ventral or lateral bone, separated from each other by a clear suture as well on the left as on the right side of the skull. The dorsal bone corresponds quite well to the postorbital of other Labyrinthodonts, the ventral one bears the relations, generally held by the jugal, except that it possibly does not meet the posterior antorbital. This exceptional condition if really existing, is conceivably due to the excessively large size of the orbit; it is apparently also found in *Broiliellus* (text-fig. 8 B).

The small element in *Micropholis* (*Ju*?, text-fig. 5), figured by WATSON as an independent bone at the antero-ventral corner of the orbit, seems very mysterious, and after seeing the material I am inclined to think that it may possibly be a most anterior part of the jugal, connected with the posterior main part either by a very thin part, or by a part, hidden by the matrix filling the orbit. I have unfortunately had no time to undertake a complete cleaning of the specimen.

In the "*Stereospondyli*" the jugals have a very varying anterior extension. Except in the more specialized of the *Brachyopidae* (and perhaps in certain of the *Trematosauridae*) it always extends in front of the orbits, though usually only a short way. In *Cyclotosaurus* (text-fig. 17), however, it extends more than half the distance from the orbits to the anterior margin of the snout.

The *postorbital* (*Po*, text-figs. 7, 8 A, B, 9—12, 14—31, 37, 38, 53, 55—57, 59—62, 64—68) seems to be very similar in the "*Rhachitomi*" to that of the *Loxommids* and Ichthyostegids. Only one more remarkable exception is found, in that *Zatrachys* (text-fig. 7) shows a postorbital with a large part, extending below the orbit so as to nearly meet the posterior antorbital and occupy a large part of the orbital margin, usually occupied by the jugal.

In the "*Stereospondyli*" the shape of the postorbital is subject to strong variation, but it is always more or less distinctly pentagonal. In the *Trematosauridae* and the *Metoposauridae* (text-figs. 10, 11, 23, 55, 56, and 16, 24) it is most often very long (it is broader in *Lyrocephalus*, text-figs. 60, 61, 64, and in *Platystega*, text-fig. 62, than in the other Trematosaurids) and generally has a very distinct pentagonal form, each of its five margins forming either part of the orbital margin or a suture with one of the surrounding bones — the supraorbito-dermosphenotic (posterior supraorbital), the supratemporo-intertemporal, the squamosal, or the jugal. The same regular shape is found in the very short postorbital of *Cyclotosaurus* (text-fig. 17) or *Mastodonsaurus* (text-fig. 27), and also, more or less pronounced, in the postorbital of *Peltostega* (text-fig. 26) and the more primitive *Brachyopidae* (text-figs. 19, 25, 29). In *Capitosaurus* (text-fig. 31) and *Wetlugasaurus* (text-figs. 38, 53; pl. 1, fig. 1; pl. 2, fig. 1) the postorbital has a curious shape, similar to that found in *Zatrachys* (text-fig. 7), since it extends laterally to the orbit, generally as far as the middle of the lateral orbital margin — in *Capitosaurus semiclausus* (SWINTON 1927, pp. 178, 181) it even meets the anterior supraorbital and thus excludes the jugal from the orbital margin. In these two genera also, it has five margins, but two of these — the straight short anterior one, and the long convex postero-lateral one — take part in the formation of the suture with the jugal. This suture thus becomes angular in a very characteristic way. Indeed, as Professor WIMAN informs me, the same characteristic aspect of the discussed suture is his chief argument for referring to the genus *Capitosaurus* the fragment, called by him *Capitosaurus polaris*.

In the more specialized members of the *Brachyopidae* (text-figs. 28, 30) the postorbital is unusually broad and somewhat irregular in shape.

Curiously enough the postorbital of the "*Stereospondyli*" seems to be fairly constantly connected with the bend in the vertical portion of

the suborbital part of the infraorbital canal — *i. e.* with the part of the said canal primarily connected with the dermosphenotic. This connection seems, however, to be rather clearly a secondary character, acquired through the migration, in a lateral direction, of the postotic canal and posterior parts of the infraorbital canal. For only by such a migration is it possible to explain the position of the mentioned canals in the highly specialized *Mastodonsaurus* (text-fig. 27).

The *squamosal* (*Sq*, text-figs. 5, 7, 8 A, C, 9—12, 14—17, 19—31, 37, 38, 53, 55—57, 59, 61, 62, 64, 66—68) has in the main the same relations in the higher *Labyrinthodontia* as in the Ichthyostegids, except: (1) that it has no definite part of its ventral margin to suturate with the preopercular (cf. below), (2) that it does not always meet the lateral extrascapular, since in certain forms (*Trimerorhachis*, *Cochleosaurus*, *Broiliellus*, *Trematops*, cf. above, p. 56) the otic notch extends so far forward as to separate the two mentioned bones.

In the higher *Labyrinthodontia* the squamosal tends as shown by WATSON (1919 b), to develop a posterior lamina (*Sqp*, text-figs. 53, 55, 57—59, 61, 62, 66), covering the posterior side of the cheek. Except for this specialization, it does not generally differ very much from the same bone in the lower Labyrinthodonts. When, as in *Tertrema* and *Cyclotosaurus* (text-figs. 17, 23) the otic notch is closed behind, the squamosal has a postero-dorsal margin consisting of an anterior concave part, forming the antero-lateral margin of the closed notch, and a straight posterior part, in suture with the lateral extrascapular.

In *Trematosaurus* (text-fig. 11), *Lydekkerina* (text-fig. 12), *Wetlugasaurus angustifrons* (text-fig. 38), *Aphaneramma* (text-fig. 56), and the new species *Lyrocephalus kochi*, (text-fig. 60), described below, the squamosal is clearly connected with an undoubted, typical jugal canal (*juc*, text-fig. 12; pls. 8, 9; text-figs. 56, 60).

Owing to the incomplete knowledge of the lateral line system of the *Labyrinthodontia* it is in most cases hardly possible to find out the fate of the preopercular. Only in *Lydekkerina* is there apparently found a somewhat clear preopercular canal (*popc*, text-fig. 12). The position of this canal indicates that, at least in *Lydekkerina*, we have a *preoperculo-quadratojugal* (*Pop. quj*, text-fig. 12) like that of certain Coelacanthids (STENSIÖ 1932, pp. 36—38).

The position of the centre of development of the so called quadratojugal for instance in *Eryops anatinus* (text-fig. 14 B), very far back and more dorsally than in an Ichthyostegid, may indicate a fusion of the quadratojugal and the preopercular also in this genus.

In the other "*Rhachitomi*" and "*Stereospondyli*" the preopercular may have likewise fused with the quadratojugal, but I prefer to wait for further evidence before changing the name of the bone, which possibly

is the result of such a fusion. Therefore, in all higher *Labyrinthodontia* except *Lydekkerina* I will provisionally call the most postero-ventral bone of the cheek the quadratojugal (*Quj*, text-figs. 5, 7, 8 A, C, 9—11, 14—17, 20—28, 30, 31, 32 A, 33 A, C, D, 38, 53—55, 57—62, 64—68.

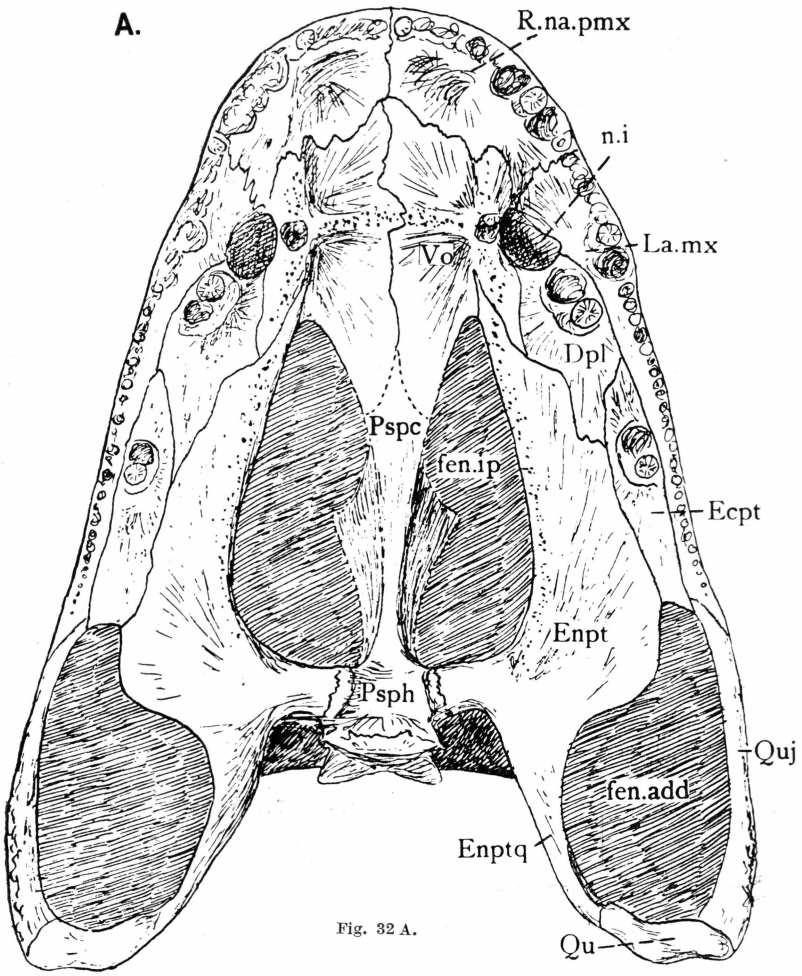


Fig. 32 A.

Text-fig. 32. Palatal aspect, A. of *Eryops megacephalus*, after BROOM (1913, fig. 12), B. of *Rhinesuchus*, after WATSON (1919 b, fig. 3), C. of *Micropholis*, after WATSON (1913, fig. 3).

Dpl, dermopalatine; *Ecpt*, ectopterygoid; *Ecpt?*, probably ectopterygoid; *Enpt*, entopterygoid; *Enptq*, quadrate ramus of the entopterygoid; *La. mx*, lachrymo-maxillary; *Psph*, parasphenoid; *Pspc*, processus cultriformis of the parasphenoid; *Qu*, quadrate; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; *Vo*, vomer; *fen. add*, adductor fenestra; *fen. ip*, interpterygoid vacuity; *n. i*, internal naris.

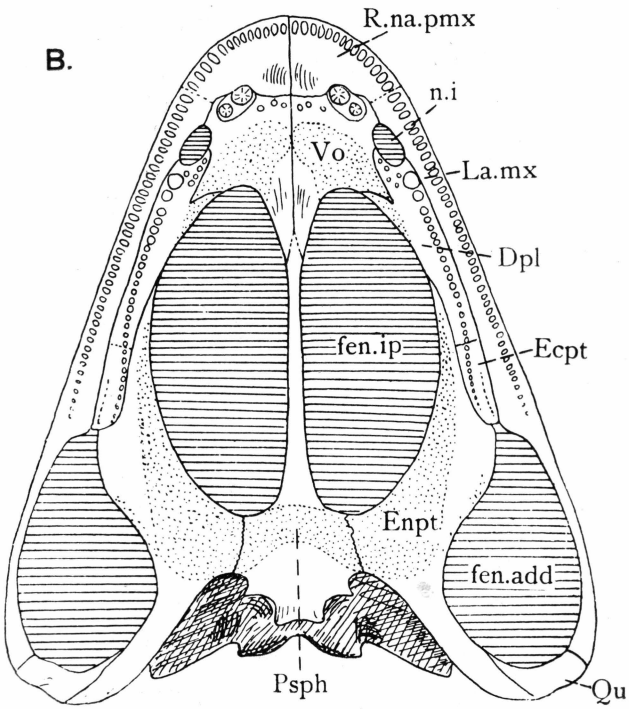


Fig. 32 B.

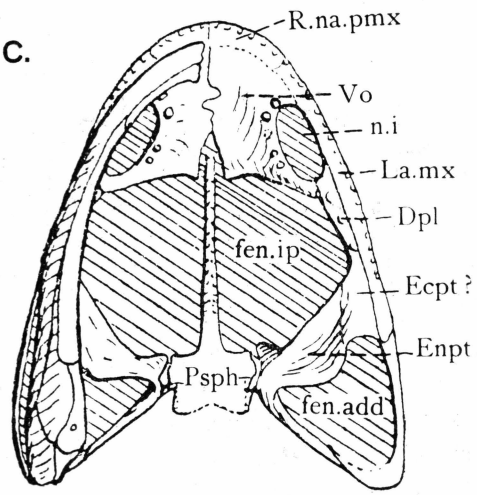


Fig. 32 C.

In the new species *Lyrocephalus kochi*, described below, there is possibly no groove for a preopercular canal on the ossified parts of the cheek, and the jugal canal clearly ran posteriorly over the posterior margin of the ornamentated surface of the cheek. Accordingly the preopercular was possibly not developed as an ossified dermal bone in that genus and thus there may in *Lyrocephalus kochi* be an un-

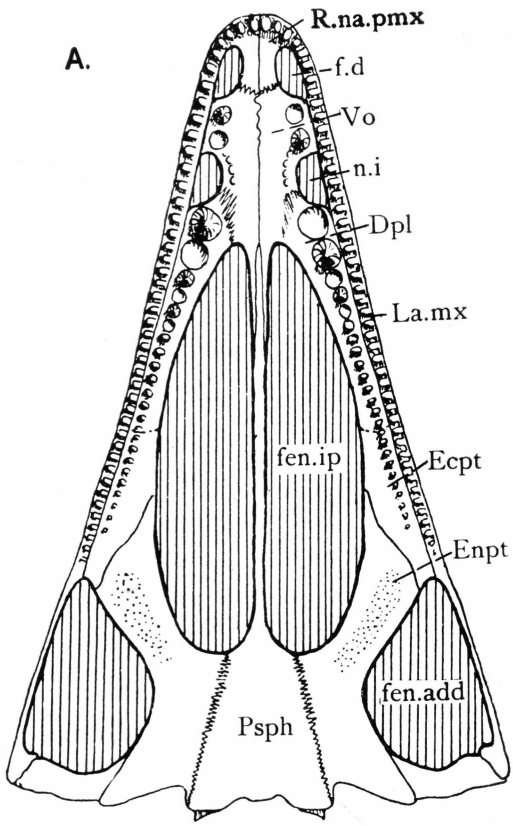


Fig. 33 A.

Text-fig. 33. Palate of "*Stereospondyli*". A. *Trematosaurus brauni*, B. *Metoposaurus diagnosticus*, C. *Capitosaurus*, D. *Batrachosuchus* sp. A—D after WATSON (1919 b). *Dpl*, dermopalatine; *Dpl* + *Ecpt*, dermopalatine and ectopterygoid; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Eo*, exoccipital; *La. mx*, lachrymo-maxillary; *Psph*, parasphenoid; *Qu*, quadrate; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; *Vo*, vomer; *f. d*, foramen for tooth of the lower jaw; *fen. add*, adductor fenestra; *fen. ip*, interpterygoid vacuity; *n. i*, internal naris.

mixed quadratojugal (*Quj*, pl. 8; pl. 9, figs. 1, 2; text-fig. 60). This may possibly be the case also in other higher *Labyrinthodontia*.

In several of the previously published figures of the skulls of "*Stereospondyli*" showing the lateral line system (see, for instance, text-figs. 16, 24, 27), the quadratojugal is connected with a canal, running backwards from the junction between the vertical and the horizontal portions of the suborbital part of the infraorbital canal. This canal will be further discussed below (p. 74).

In *Zatrachys* (text-fig. 7) the quadratojugal has a marked posterior process and, at least in certain Trematosaurids it has a narrow posterior lamina (*Qujp*, pl. 4, fig. 1; pl 7; pl. 15, fig. 4), covering part of the quadrate.

The *palate* of the higher Labyrinthodonts has been discussed in a

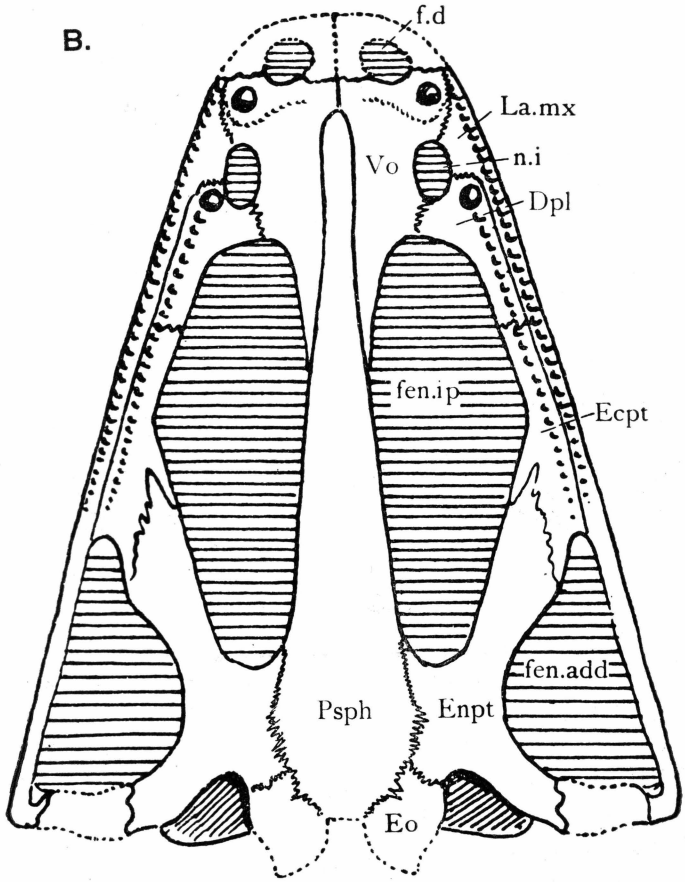


Fig. 33 B.

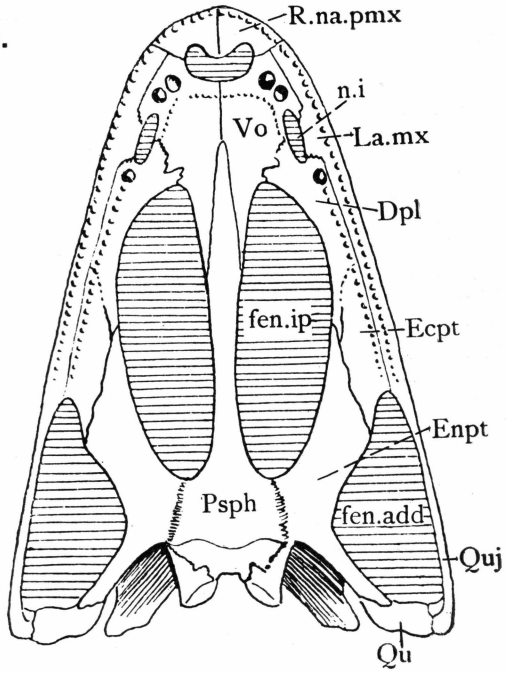


Fig. 33 C.

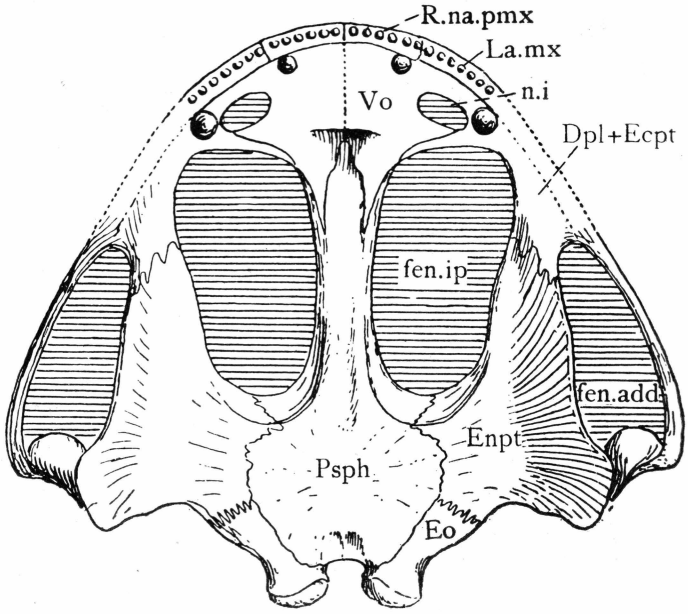


Fig. 33 D.

very instructive way by WATSON (1919 b, pp. 5—20, figs. 2, 3, 5, 6, 10, pp. 51, 55, 62, 63, fig. 29 A, B; cf. also WATSON 1926 a, pp. 190—194). However, the palate seems to be really well known only in four of the "*Rhachitomi*", viz. *Eryops* (BROOM 1913, fig. 12), *Rhinesuchus* (WATSON 1919 b, fig. 3), *Archegosaurus* (WHITTARD 1928, fig. 1), and *Wetlugasaurus* (text-fig. 54; RIABININ 1930). In *Micropholis* (WATSON 1913, fig. 3) the structure of the palate is tolerably well, though not completely known. All the other figures I have been able to find are so incomplete that the shape and extension of the various bones of the palate remain largely unknown.

The chief differences between the palate of the "*Rhachitomi*", and that of the Loxommids and the Ichthyostegids, depend upon a successive enlargment of the interpterygoid vacuities, as shown by WATSON (*l. c.*). The granular teeth, largely distributed on the bones of the palate in many "*Rhachitomi*" (for instance *Rhinesuchus*, text-fig. 32 B; *Cochleosaurus*, BROILI 1905, fig. 2), do not seem to have been recorded in any Loxommid.

The palate of *Eryops* (text-fig. 32 A) shows a type still rather similar in many respects to that of a Loxommid (text-fig. 4 B) but the palatal rami of the entopterygoids are already considerably reduced in their antero-medial parts, and the vomeres are reduced in their postero-lateral parts. As a consequence of these reductions, the parasphenoid is exposed along its whole length, from its hindermost end, overlapping the basioccipital — in ventral view — to its anterior extremity, wedged in between the vomeres.

The palatal parts of the naso-rostro-premaxillaries, as well as the anterior parts of the palatal surface of the lachrymo-maxillaries are distinctly larger than in the Loxommids. There are granular teeth on the vomeres and entopterygoids.

Otherwise the palate of *Eryops* agrees perfectly with that of *Baphetes* (text-fig. 4 B), even in such details as the distribution of the teeth.

In *Rhinesuchus* (text-fig. 32 B) the interpterygoid vacuities are still much larger, so that the entopterygoids here fail to meet the vomeres, and are connected by sutures only with the posterior halves of the dermopalatines. The normal teeth are here numerous on the vomeres, dermopalatines, and ectopterygoids, and the granular teeth are distributed on larger areas of the entopterygoids and vomeres, and also on the dermopalatines and the parasphenoid.

Micropholis (text-fig. 32 C) shows similar advanced conditions, with very large interpterygoid vacuities, each bounded by the transverse posterior margin of the strongly reduced vomer, the medial margin of the very narrow dermopalatine (and ectopterygoid?), the straight anteromedial margin of the palatal ramus of the entopterygoid, the anterior margin of the expanded posterior plate (corpus) of the parasphenoid, and the lateral margin of the narrow processus cultriformis of the same bone.

The palate of the "*Stereospondyli*" seems to be a little better known than that of the "*Rhachitomi*". Its main characters and general evolutionary trend have been elucidated by WATSON's brilliant paper (1919 b), already referred to several times.

At least in several forms, as *Trematosaurus* (text-fig. 33 A), *Metoposaurus* (text-fig. 33 B), and *Capitosaurus* (text-fig. 33 C) all the bones of the primitive Choanate palate are still preserved, though partially very reduced in size by the important enlargement of the interpterygoid vacuities. In *Mastodonsaurus* and *Cyclotosaurus* FRAAS (1889, pls. II, VII, X) figured no independent dermopalatine and ectopterygoid, but a comparison with WATSON's figures of other "*Stereospondyli*" (my text-figs. 33 A, B, C) suggests that there may be an inaccuracy in the figures given by FRAAS. WATSON also stated that FRAAS' figure is "inaccurate . . ., in the position of the pterygotransverse suture, . . ." (WATSON 1919 b, p. 30).

Likewise the absence of any suture between the dermopalatines and ectopterygoids in WATSON's figure of the palate of *Batrachosuchus* sp. (text-fig. 33 D) may be due merely to the incomplete knowledge of the matter, since there is uncertainty in the said figure concerning the region normally covered by the two mentioned bones (WATSON 1919 b, p. 45).

So far as the conditions are completely known, the entopterygoid of the "*Stereospondyli*" is connected by suture laterally only with the ectopterygoid (*Trematosaurus*, text-fig. 33 A, *Metoposaurus*, text-fig.

33 B), except in *Capitosaurus* (text-fig. 33 C; WATSON 1919b, p. 27; — cf. *Wetlugasaurus*, text-fig. 54).

The processus cultriformis of the parasphenoid presents variations, which seem to have a systematic value. Thus the said process, according to BROILI, has a characteristic widening in the middle part in *Actinodon* and *Sclerocephalus* (BROILI 1926, p. 220, text-fig. 1; THEVENIN 1910, pp. 18—19, fig. 4). In the *Trematosauridae* it is very narrow, but in the *Metoposauridae* and *Peltostegidae* it is very broad. — The corpus of the parasphenoid is traversed by canals for the internal carotids (*c. i*, text-fig. 58).

The bones of the *lower jaw* in the higher *Labyrinthodontia*, as shown for instance in *Eryops* (text-figs. 35C, D; 14B), *Trimerorhachis* (text-fig. 35 A, B) and *Archegosaurus* (WHITTARD 1928, figs. 2, 3) are most nearly comparable to those found in *Orthosauriscus* (text-fig. 34 A, B). The important changes are as follows:

1. The *splenial* (*Sp*, text-figs. 8C, 14B, 34, 35) and *postsplenial* (*Ptsp*, text-figs. 8C, 14B, 34, 35) are reduced on the external surface of the jaw and the dentary (*De*, text-figs. 8C, 14B, 34, 35 B, C, D) thus comes to form nearly the whole of the anterior half of that surface.

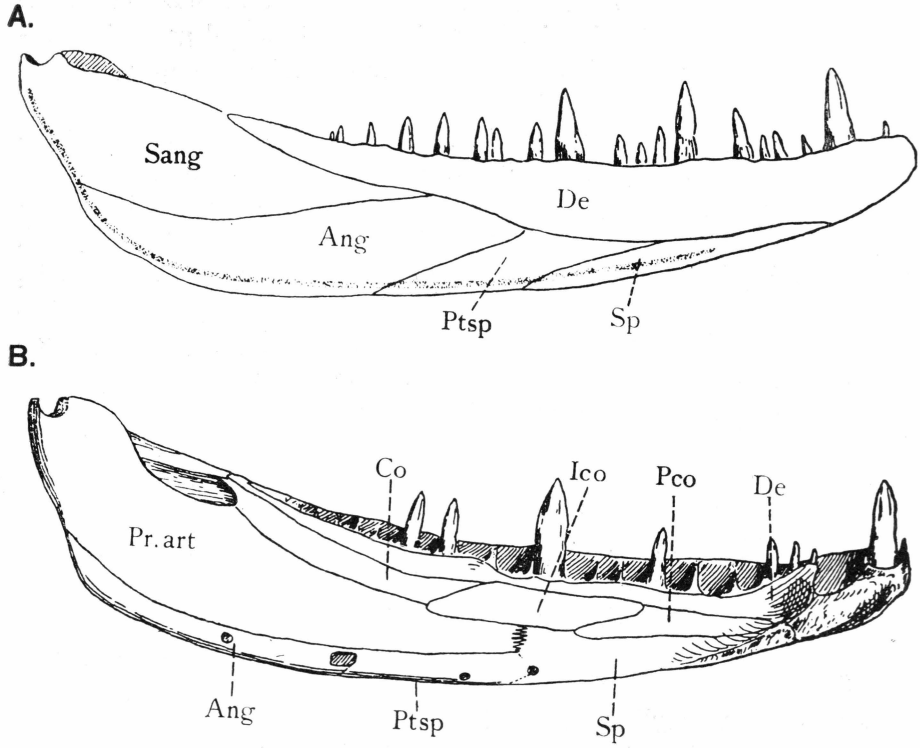


Fig. 34 A and B (see page 71).

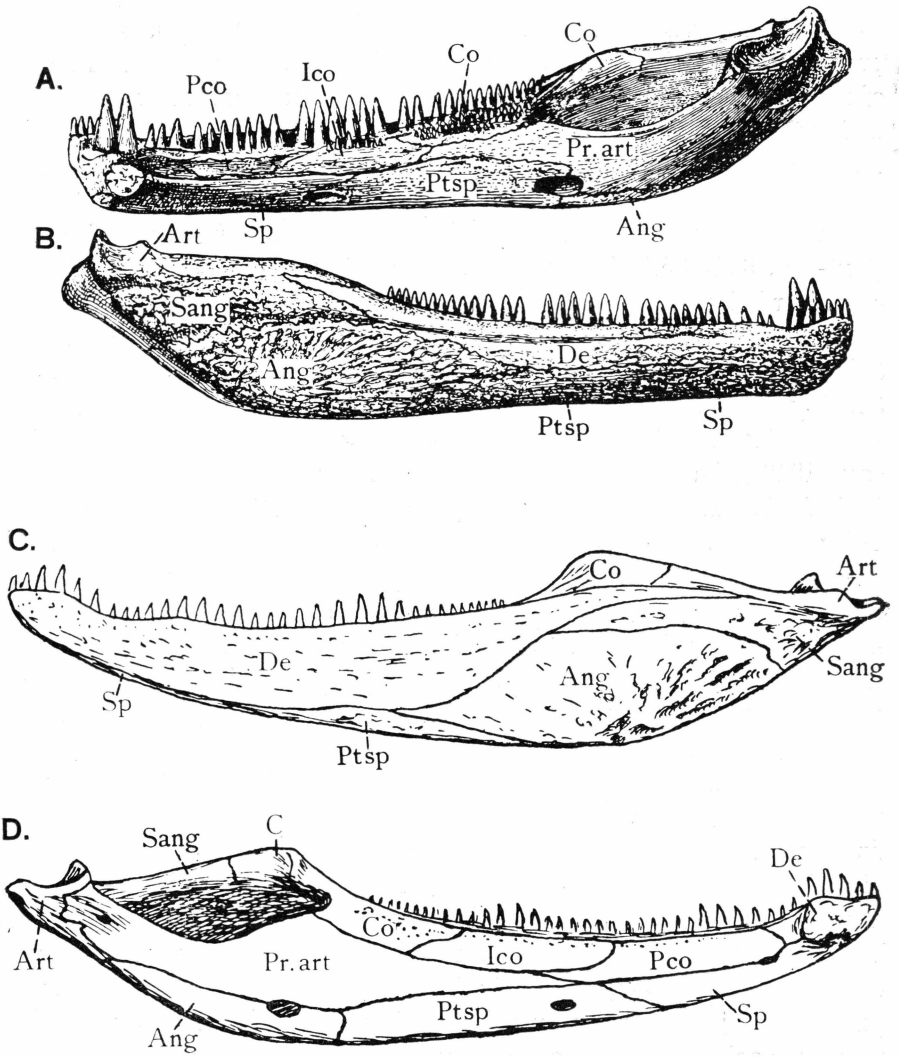


Fig. 35.

Text-figs. 34 and 35. Lower jaws of *Orthosauriscus*, text-fig. 34 A, B — *Trimerorhachis*, text-fig. 35 A, B — and *Eryops*, text-fig. 35 C, D. 34 A, 35 B, C, in external (labial), 34 B, 35 A, D, in internal (lingual) view. 34 A, B, after Watson (1926a); 35 A, B, after Williston (1914); 35 C, D, after Broom (1913 c).
Ang, angular; *Art*, articular; *C*, *Co*, coronoid; *De*, dentary; *Ico*, intercoronoid; *Pco*, precoronoid; *Pr. art*, prearticular; *Ptsp*, postsplenial; *Sang*, supraangular; *Sp*, splenial.

2. The *angular* (*Ang*, text-figs. 8C, 14B, 34, 35) becomes higher and covers a large part of the area, originally covered by the *supraangular* (*Sang*, text-figs. 8C, 14B, 34A, 35B, C, D) which is very reduced in in height.

3. The *coronoid* (*Co*, text-figs. 34B, 35A, C, D) sends a posterior process (*Co*, text-fig. 35C; *C*, text-fig. 35D) back along the dorsal margin of the lower jaw and thus becomes visible on the external surface of the jaw, in front of the supraangular. The adductor fossa also increases in length, reducing the length of the anterior, tooth-bearing part of the coronoid.

In the higher *Labyrinthodontia* the coronoids, *intercoronoids* (*Ico*, (text-figs. 34B, 35A, D), and *precoronoids* (*Pco*, text-figs. 34B, 35A, D) are recorded as bearing teeth, at least in *Eryops*.

The *lateral line system* is very incompletely known in the "*Rhachitomi*". According to a commonly accepted opinion (MOODIE 1915, pp. 317, 318) several "*Rhachitomi*" lacked this system, because they were not aquatic. MOODIE (1908, fig. 11) figured the system only in *Eryops*. WATSON (1919b) has given a good figure of at least parts of the system in *Lydekkerina* and finally it is well known in *Wetlugasaurus* (RIABININ 1930; and pp. 122—131, with text-fig. 53, of the present paper).

The parts figured in *Lydekkerina* show rather normal positions, only the supraorbital canal has become related to the largely expanded anterior supraorbital, and the horizontal portion of the suborbital part of the infraorbital canal runs over part of the posterior antorbital. Also, the anterior end of the jugal canal lies in a furrow in the lachrymomaxillary, whereas the posterior part of the canal has its usual course.

If MOODIE's representation of the lateral line grooves in *Eryops* is really correct, there are already in that genus many important specializations. The supraorbital canal would be very much displaced in lateral direction to run over the supraorbital component of the supraorbitodermosphenotic, the anterior supraorbital, and the posterior antorbital. The postnasal connection would run between the posterior antorbital and the jugal, partly even on the latter bone alone. The whole anterior part of the jugal canal would be lacking, or represented by a groove, running back over the jugal and quadratojugal, only then turning dorsally and antero-dorsally, on to the squamosal. As we will see later on, a similar specialized type of lateral line system is also found in several "*Stereospondyli*".

The supratemporal commissural canal seems more normal, in *Eryops* traversing the lateral extrascapulars and the parieto-extrascapulars. (These bones are obviously very incorrectly figured by MOODIE).

In the "*Stereospondyli*" the lateral line canals are evidently capable of migrations in relation to the dermal bones. In this way the supraorbital canal becomes connected with the supraorbital, in all "*Stereospondyli*", where its course is known, and not seldom also with the posterior antorbital.

The *supraorbital canal* is fairly completely known in *Trematosaurus*

(text-fig. 11; JAEKEL 1903, Text-tafel VIII), *Lydekkerina* (text-fig. 12), *Anaschisma* (*soc*, text-fig. 16), *Archegosaurus* (text-fig. 22), *Tertrema* (text-fig. 23), *Metoposaurus* (*soc*, text-fig. 24), *Peltostega* (text-fig. 26), *Mastodonsaurus* (text-fig. 27), *Capitosaurus* (text-fig. 31), *Wetlugasaurus* (text-fig. 38), and *Lyrocephalus* (text-figs. 61, 63, 66).

The *ethmoidal commissure* of the *infraorbital canal* has been found in *Lydekkerina* (*c. a*, text-fig. 12), *Trematosuchus? yakovlevi* (*c. a*, text-fig. 13), in *Tertrema* (WIMAN 1914, pl. VII; STENSIÖ 1921, p. 145), in *Rhytidosteus* (observed by the present writer in the type specimen, *R.* 455, in the British Museum of Natural History), and in *Lyrocephalus* (see below, text-figs. 60, 63, 66).

In *Wetlugasaurus*, the *Capitosauridae*, and the *Mastodonsauridae* the horizontal portion of the *suborbital part* develops a postero-medially directed loop at the posterior end of its anterior $^1/_4$ or $^1/_3$ (see *Cyclotosaurus*, text-fig. 17; *Mastodonsaurus*, text-fig. 27; *Capitosaurus*, text-fig. 31; and, for a more primitive stage, *Wetlugasaurus*, text-fig. 38). This loop is sometimes distinctly connected with the posterior antorbital and possibly represents the postnasal connection with the supraorbital canal. Parts of this connection also seem to be preserved in *Lydekkerina* (*ptn*, text-fig. 12), and possibly in *Trematosuchus? yakovlevi* (*pnc*, text-fig. 13).

The vertical portion of the suborbital part, where preserved and described (see for instance text-fig. 11; *ifsv*, text-figs. 12, 16; text-figs. 23, 24, 31, 38; *ifsv*, text-figs. 53, 56, 60, 61, 66), shows its normal connections with the jugal and postorbital, but its most medial parts have evidently migrated laterally so that they are far from connection with the supraorbito-dermosphenotic. Likewise the *otic part* of the infraorbital canal and the *postotic canal* are sometimes, especially in the *Capitosauridae* and *Mastodonsauridae*, unusually lateral in their position on the supratemporo-intertemporal, and may even run partly on the squamosal. The vertical portion has a special postero-medial branch in the Spitsbergen forms *Tertrema* (text-fig. 23), *Peltostega* (text-fig. 26), *Aphaneramma* (text-fig. 56) and *Lyrocephalus euri* (text-fig. 61). This branch is connected with the supraorbital canal in an East Greenland species (text-fig. 66).

In *Trematosaurus* (text-fig. 11; JAEKEL 1903, Text-tafel VIII) the infraorbital canal is continuous throughout and with the postotic canal, which is directly continuous with the cephalic division of the main lateral line canal. Other genera present a more or less distinct subdivision of this continuous groove into shorter grooves, representing the different morphological elements. Thus, in *Lydekkerina* (text-fig. 12), *Capitosaurus* (text-fig. 34) and *Anaschisma* (text-fig. 23), there is an interruption between the suborbital and the otic parts of the infraorbital canal. The otic part is more or less clearly separated from the postotic canal in *Metopo-*

saurus (text-fig. 24; MOODIE 1908, fig. 15), but the two form a straight continuous, clearly compound canal in *Trematosaurus* (text-fig. 11), *Tertrema* (text-fig. 23), *Capitosaurus* (text-fig. 31), *Aphaneramma* (text-fig. 56) and *Lyrocephalus* (text-figs. 61, 66). There seems to be a short groove in the supratemporo-intratemporal only for the otic part, — the postotic canal apparently lacking — in *Anaschisma* (text-fig. 16). In other cases the groove discussed is more difficult to interpret (for instance in *Wetlugasaurus*, text-figs. 38, 56).

The *jugal canal* (*juc*, text-figs. 12, 56, 60, 66; text-figs. 11, 16, 24, 27, 31, 38) is rather normally developed in *Lydekkerina* (text-fig. 12) and in the new species *Lyrocephalus kochi*, described below, which possibly has no groove on any dermal bone for the preopercular canal. In other forms (*Trematosaurus*, text-fig. 11; *Wetlugasaurus*, text-fig. 38; *Aphaneramma*, text-fig. 56; *Lyrocephalus euri*, text-fig. 61), the jugal canal seems to have been situated much more laterally than in the primitive condition; in *Capitosaurus* (text-fig. 31) it runs over a part of the quadratojugal; and in *Mastodonsaurus* (text-fig. 27) and the *Metoposauridae* (text-figs. 16, 24; BRANSON and MEHL 1929, figs. 3, 6, 7, 8, 10) it is situated almost always completely in the jugal and quadratojugal. In certain cases one may even be doubtful wether there is a true jugal canal, or a *quadratojugal canal*, comparable to that of *Palaeogyrinus* (cf. below, p. 102).

The *cephalic division of the main lateral line canal* has often left no groove in the lateral extrascapular. This may possibly be due to a migration lateralwards of the canal, analogous to that of the postotic canal — see for instance *Trematosaurus* (text-fig. 11), *Tertrema* (text-fig. 23), *Mastodonsaurus* (text-fig. 27) and *Capitosaurus* (text-fig. 31).

Grooves for parts of the *supratemporal commissural canal* have been stated by the present writer in *Lyrocephalus* (text-figs. 60, 61), *Lonchorhynchus* (cf. WIMAN 1914, pl. IV, fig. 6), and *Batrachosuchus* (specimen *R.* 3589 in the British Museum of Natural History, figured by WATSON, 1919b, pl. 1).

B. Classification of the higher Labyrinthodontia.

In earlier classifications one often encounters statements as to the position of the orbits "far forward" or "far back". Now the position of the orbits, in relation to the length of the skull, is, of course, to be explained by the relative length of the different parts of the skull, in front of or behind the orbits. And, as will be evident by comparing, for instance, *Capitosaurus* (text-fig. 36 A) with *Metoposaurus* (text-fig. 36 B), the relatively greater length of the postorbital parts in *Metoposaurus* is not brought about by all the bones behind the orbits being lengthened at the same rate, but for the greatest part by the lengthening of the

bones, covering a definite transverse belt, in this case by a lengthening of the supraorbito-dermosphenotics, the postorbitals, the most posterior parts of the frontals, and the middle parts of the jugals.

To analyse the relative length of the different parts of the dermal cranial roof it is convenient to introduce terms for these parts. Thus I will call prenarial division the region of the dermal cranial roof in front of a transverse line through the points where the naso-rostro-premaxillaries and the naso-postrostrals meet each other at the medial margins of the external nares; the parts between this division and a transverse line through the median point of the sutures between the frontals and the naso-postrostrals will be called the postnarial division; behind this follows the preorbital division extending back to the anterior margins of the orbits. The postorbital division extends from the orbits to a transverse line through the anterior ends of the supratemporo-intertemporals; behind this line is the prenuchal division, in front of the anterior margin of the parieto-extrascapulars at the median line, and behind this the nuchal division of the dermal cranial roof (see text-fig. 36).

As may of course be expected even from the relative age of the "*Rhachitomi*" and "*Stereospondyli*", the latter show much clearer than the former the differentiation into several lines of evolution. Therefore the most appropriate method of tracing the phylogeny of the higher *Labyrinthodontia* is to begin with the "*Stereospondyli*", and then to try to find out in the older group "*Rhachitomi*" the origin of the different lines of evolution recognised in the younger group.

When trying a systematic classification of the "*Stereospondyli*", one will soon recognise that in many respects the grouping into families found in WATSON's paper (1919 b), often cited above, really forms a good basis for further discussion. Also it is significant that somewhat later v. HUENE (1920 a, b) arrived independently at a fairly similar classification. Therefore the first part of my discussion of the matter will be a critical review of WATSON's stereospondylous families, together with an attempt to insert the new genera, described after the publication of WATSON's paper.

To begin with the *Capitosauridae*, I find it quite evident that *Capitosaurus* and *Cyclotosaurus* are really very closely related to each other — if not as "parent and child" (WATSON 1919 b, p. 22, note; SWINTON 1927, p. 185), at least as uncle and nephew. The close relationship is now further illustrated by the condition of the otic notch in the new species *Capitosaurus semiclausus*, described by SWINTON (1927).

There is, however, at least one character in which *Capitosaurus* is more specialized than *Cyclotosaurus*, *viz.* the unique condition of the postorbitals, already found in *C. nasutus* and *C. helgolandiae* (see

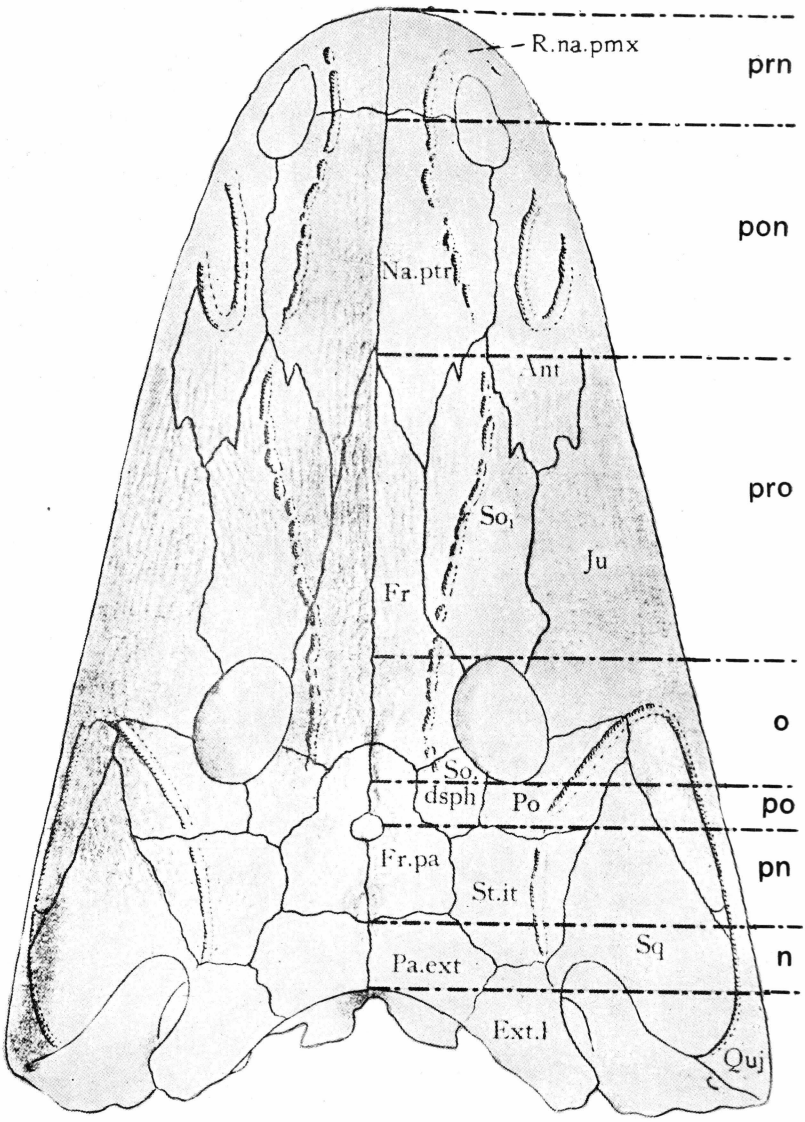


Fig. 36 A.

Text-fig. 36. Examples showing the different divisions of the dermal cranial roof. A. *Capitosaurus*, B. *Metoposaurus*.

Ant, posterior antorbital; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *ot*, otic part of the infraorbital canal; *soc*, supraorbital canal; **n**, nuchal division of the dermal cranial roof; **o**, orbital division; **pn**, prenuchal division; **po**, postorbital division; **pon**, postnarial division; **prn**, prenarial division; **pro**, preorbital division.

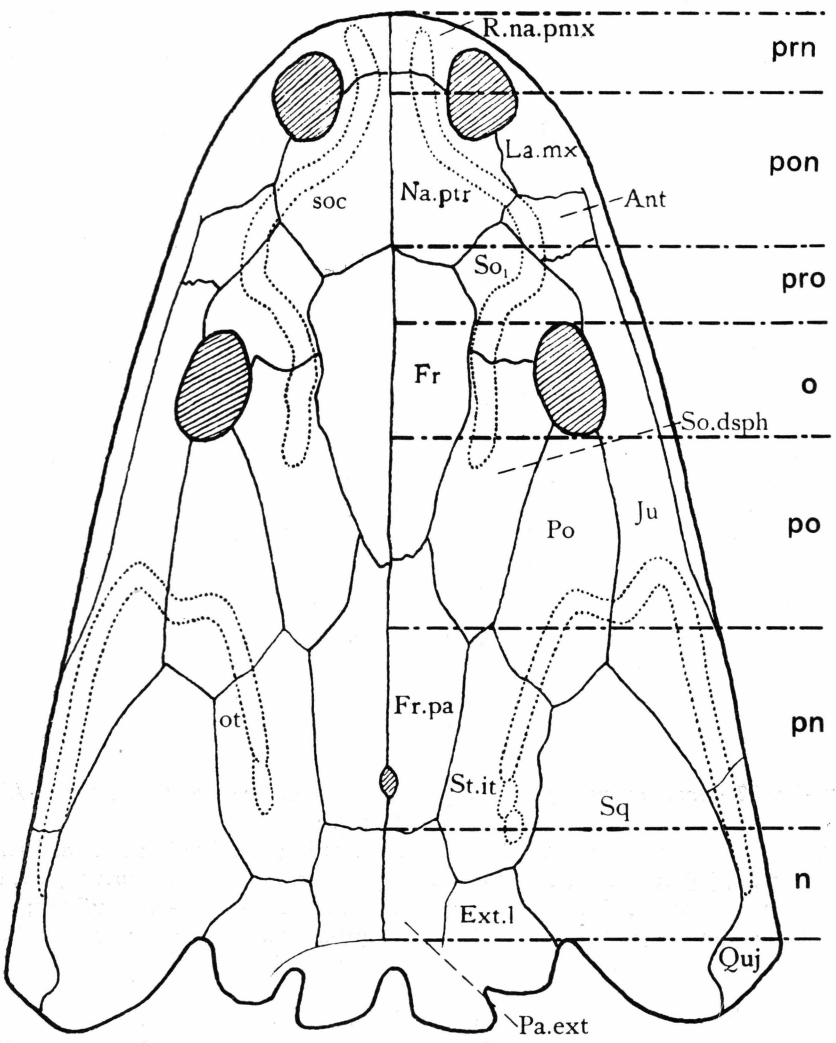
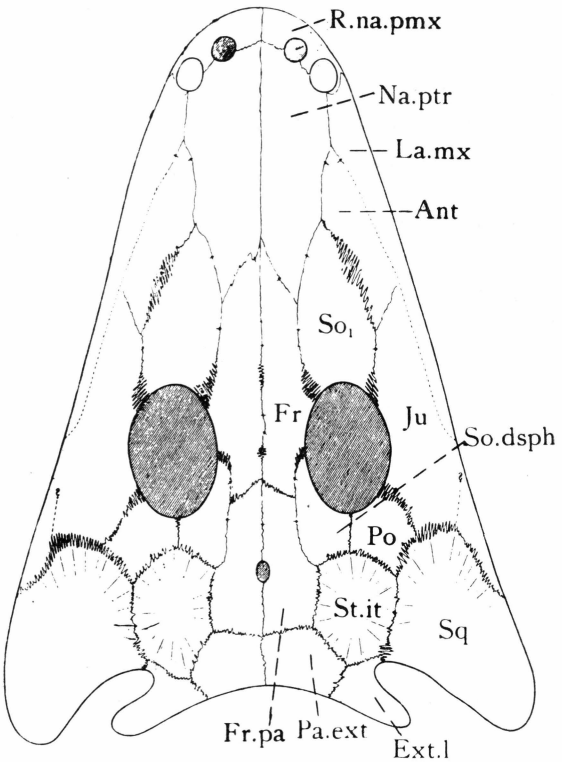


Fig. 36 B.

above, p. 62, text-fig. 36 A; SCHROEDER 1912, Taf. 16), and leading to the meeting with the anterior supraorbitals and the exclusion of the jugals from the orbital margins in *C. semiclausus* (SWINTON 1927, pp. 178, 181).

Thus it seems evident that *Capitosaurus* and *Cyclotosaurus* have — though probably for a comparatively short time — evolved independently of each other, from a common ancestor, which must be supposed to have been in most features more similar to *Capitosaurus* than to *Cyclotosaurus*.

"*Mastodonsaurus cappelensis*" WEPFER (1923; my text-fig. 37) differs



Text-fig. 37. *Heptasaurus cappelensis* (WEPFER). Dorsal aspect of the skull. After WEPFER (1923).

Ant, posterior antorbital; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

very markedly from the true *Mastodonsaurus* (text-fig. 27), since it presents a very clear supraorbito-dermosphenotic (*So. dsph*, text-fig. 37), still more typical even than that of *Capitosaurus* and *Cyclotosaurus*, with a rather long suture towards the supratemporo-intertemporal. In fact "*Mastodonsaurus cappelensis*" seems to me fairly obviously more related to the Capitosaurids, differing from both *Capitosaurus* and *Cyclotosaurus* only by the occasional presence of foramina for the mandibular teeth in the naso-rostro-premaxillaries and by the larger size of the orbits. However, in the size of the orbits it also differs from the true *Mastodonsaurus*, which has still considerably larger orbits. This character is of course not of a very high systematic value, and the same can certainly be said about the presence or absence of foramina in the naso-rostro-premaxillaries. It might be noticed that these foramina are not a constant character in "*Mastodonsaurus cappelensis*" (WEPFER 1923, p. 51).

From *Capitosaurus nasutus* and *C. helgolandiae* the discussed species differs by the normal, straight course of the suture between the postorbital and the jugal, and by the apparently somewhat narrower otic notch. The angular course of the mentioned suture is however, as emphasized above, a special character of the two mentioned species of *Capitosaurus*. The otic notches are also more comparable to those of *Capitosaurus nasutus* than to those of the true *Mastodonsaurus*, which are quite different, very shallow in transverse direction, whereas those of "*M. cappelensis*" are deep in transverse direction (cf. text-figs. 27, 31, 37).

The supraorbito-dermosphenotic of "*M. cappelensis*" is quite similar to that of *Capitosaurus nasutus*, as figured by ZITTEL (1890), JAEKEL (1903), and ROEPKE (1923).

From *Cyclotosaurus* the discussed species differs mainly by its open otic notches, and the narrower form of the snout, agreeing in both these characters with *Capitosaurus*.

The main differences between the true *Mastodonsaurus* and "*M. cappelensis*" are:

1. the above mentioned clear supraorbito-dermosphenotic in "*M. cappelensis*" — cf. text-figs. 27, 37,
2. the larger size and irregular shape of the orbits in the true *Mastodonsaurus*,
3. the markedly longer preorbital division of the cranial roof in "*M. cappelensis*",
4. the shape of the anterior supraorbital,
5. the long suture of the postorbital with the jugal in "*M. cappelensis*",
6. the much longer parieto-extrascapulars in "*M. cappelensis*" (quite similar to those of *Capitosaurus nasutus*),
7. the very broad lateral extrascapulars in "*M. cappelensis*", and the thus deeper otic notches.

In all of these points the discussed species clearly agrees with the Capitosaurids.

Thus it is clear that the form, described by WEPFER, is no *Mastodonsaurus*, nor even a Mastodonsaurid, but a Capitosaurid, closely related both to *Capitosaurus* and to *Cyclotosaurus*. The differences existing only justify a generic separation from the previously known Capitosaurids. Hence I must introduce a new name for the Capitosaurid genus represented by "*Mastodonsaurus*" *cappelensis*, and I propose to call it *Heptasaurus*, after the seven fenestrae in the cranial roof.

The species "*Mastodonsaurus acuminatus*" (FRAAS 1889, Taf. VIII, fig. 1) is very incompletely known; yet it is clear from the figure cited

that in several respects it markedly differs from the true *Mastodonsaurus* (*M. giganteus* JAEGER), and it does not seem impossible that it really belongs to the same genus as *Heptasaurus cappelensis*.

Kestrosaurus HAUGHTON was placed by SMITH WOODWARD (1932) among the Capitosaurids. It differs in having an independent median postrostal ("interfrontal") quite as has *Trematosuchus* (text-fig. 10). Anyhow the structure of its palate shows that it can probably be included within the homogenous unity, formed by the true Capitosaurids, though for the present it is too incompletely known to be more closely discussed, and no diagnosis is therefore given for it here.

The family *Capitosauridae* would thus comprise at present three closely allied well-defined genera:

1. *Capitosaurus* MÜNSTER,

diagnosis: Capitosaurids with open otic notches; very small orbits (length about $^1/_8$—$^1/_7$ of the median length of the skull); postorbitals with angular sutures towards the jugals, or with sutures both towards the jugals and towards the anterior supraorbitals;

2. *Cyclotosaurus* FRAAS,

diagnosis: Capitosaurids with closed otic notches; very small orbits (length about $^1/_9$—$^1/_8$ of the median length of the skull); postorbitals with interlocked, but mainly straight, not angular sutures towards the jugals;

3. *Heptasaurus* n. g.,

diagnosis: Capitosaurids with open otic notches; medium-sized orbits (length about $^1/_5$ of the median length of the skull); postorbitals with interlocked, but mainly straight, not angular sutures towards the jugals; each naso-rostro-premaxillary generally with a fenestra at the suture towards the naso-postrostral, for a mandibular tooth.

The most important characters, connecting the three genera may be summarized in the following *diagnosis of the family Capitosauridae* WATSON:

Stereospondyli with elongated skulls, with broad prenarial, very long postnarial and preorbital, very short postorbital, short or medium-sized prenuchal, and medium-sized nuchal divisions of the dermal cranial roof. With small to medium-sized orbits. Posterior antorbitals elongated, far from contact with the orbits. With typical supraorbito-dermosphenotics, not meeting the anterior supraorbitals. Posterior margins of the supraorbito-dermosphenotics

forming a nearly straight line with the posterior margins of the short postorbitals. The parts of the lateral extrascapulars, situated behind the otic notches, roughly rectangular.

The type species of *Mastodonsaurus*, *M. giganteus* JAEGER, seems to be in reality the only well known species of the family *Mastodonsauridae*.

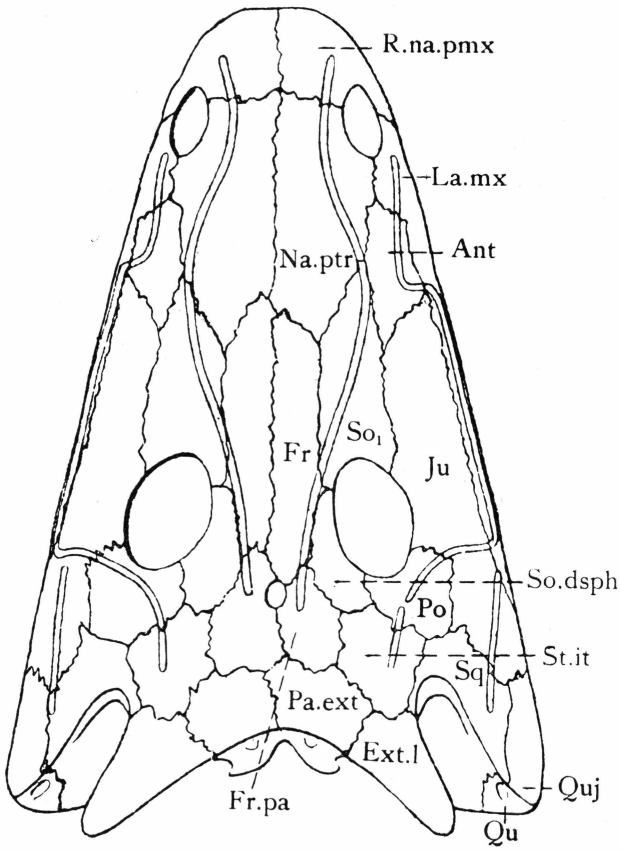
The new genus "*Mentosaurus*" ("*M. waltheri*" RÖPKE 1930) is founded on the rather slight evidence furnished by a fragmentary lower jaw, an episternum, and a quite indeterminable small fragment of a cranial roof, the whole illustrated by very bad photographs, and a schematic drawing of the lower jaw. The large size of the lower jaw, together with positive differences from *Mastodonsaurus*, seem to be the only arguments for the erection of a new genus. Anyhow it seems at present quite impossible to state anything about the systematic relations of "*Mentosaurus*" and, on the whole, it seems to me preferable not to make any new systematic unit out of a material, so poor and fragmentary as that described by RÖPKE. The same applies to the "genera" "*Ptychosphenodon*" (SEELEY 1907), "*Odontosaurus*" (v. MEYER 1838), "*Syphonodon*" (SEELEY 1908), "*Hercynosaurus*" (JAEKEL 1913), "*Diadetognathus*" (MIALL 1874), and "*Pachygonia*" (HUXLEY 1865), all included by KUHN (1933) with or without hesitation in the family *Mastodonsauridae*.

The main characters distinguishing the genus *Mastodonsaurus* JAEGER and the family *Mastodonsauridae* WATSON may be summarized in the following *diagnosis:*

Stereospondylous *Labyrinthodontia* with roughly triangular skulls, with medium-sized prenarial, very long postnarial, long preorbital, very short postorbital, medium-sized prenuchal and short nuchal divisions of the dermal cranial roof. Very large orbits. Pineal foramen in the posterior halves of the fronto-parietals. Posterior antorbitals elongate, far from contact with the orbits. With small posterior supraorbitals or reduced supraorbito-dermosphenotics, just touching the anterior ends of the supratemporo-intertemporals, and not meeting the anterior supraorbitals. The parts of the lateral extrascapulars, situated behind the otic notches, roughly triangular.

Though after the above revision the two families *Capitosauridae* and *Mastodonsauridae* are distinct enough from each other, they also present several common characters, separating them from all other "*Stereospondyli*". Thus the relative size of the different divisions of the dermal cranial roof, though not identical, is evidently of nearly related types

in the two families. Several other characters, as the advanced condition of the supraorbito-dermosphenotics or posterior supraorbitals, not meeting the anterior supraorbitals; the posterior antorbitals, far from contact with the orbits, etc., further strengthen the impression of a closer relationship between the *Capitosauridae* and the *Mastodonsauridae* than between each of them and any other "*Stereospondyli*". According to this,



Text-fig. 38. *Wetlugasaurus angustifrons* RIABININ. Dorsal aspect of the skull. After RIABININ (1930).

Ant, posterior antorbital; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Qu*, quadrate; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

and also because other analogous cases of families, evidently nearly allied to each other, are found in the "*Stereospondyli*" (see below p. 88), I find it convenient to group the "*Stereospondyli*" into superfamilies, the first of which will be the superfamily *Capitosauroideae.*

An extraordinarily interesting new genus, *Wetlugasaurus*, from NW. Russia, has been described by RIABININ (1930). Its skull is very clearly of a Capitosauroid type. Though it retains certain primitive features — such as the meeting of the anterior supraorbital with the supraorbito-dermosphenotic — it must be said to have advanced very far in the direction of *Capitosaurus* and *Cyclotosaurus* — so far, indeed, that it should perhaps hardly be excluded from the family *Capitosauridae*. However, it may for the present be placed in a new family of its own, the *Wetlugasauridae* — but then this family must be placed in the superfamily *Capitosauroideae*. In the structure of the skull *Wetlugasaurus* is clearly not so nearly related to any "*Rhachitomi*" as to the *Capitosauridae*. And it seems hardly necessary to point out that it cannot be more closely related to, or belong to a group ancestral to, the other "*Stereospondyli*". However, it shows a rachitomous type of vertebrae.

To me this seems a most conclusive evidence of the truth of the view that the "*Rhachitomi*" and "*Stereospondyli*" are no real systematic units, but that the stereospondylous type of vertebrae is acquired independently in several parallel series of evolution. Thus the systematic importance ascribed to the structure of the vertebrae by v. HUENE (1926; 1931), and others, seems rather exaggerated. One may also recall here the fact that the "*Embolomeri*" represent two very distinct and not nearly related series of evolution (cf. above pp. 12—20, and below pp. 92—105).

The *Wetlugasauridae* are distinguished from the other Capitosauroids by the following characters: anterior supraorbitals meeting the supraorbito-dermosphenotics; postorbitals about as long as they are broad; supratemporo-intertemporals markedly longer than they are broad; parieto-extrascapulars about as long as they are broad.

In the angular shape of the suture between the jugal and the postorbital and the characteristic course of the vertical portion of the suborbital part of the infraorbital canal *Wetlugasaurus* is strikingly similar to *Capitosaurus*.

Thus the new superfamily *Capitosauroideae* includes the families *Capitosauridae*, *Mastodonsauridae*, and *Wetlugasauridae*, and it may be defined by the following *diagnosis:*

Rhachitomous or stereospondylous *Labyrinthodontia* with elongate or triangular skulls, always markedly longer than broad, with medium-sized prenarial, very long postnarial, long or very long preorbital, very short postorbital, and short to medium-sized prenuchal and nuchal divisions of the dermal cranial roof. Orbits of varying size, but larger than the external nares; pineal foramen, at least for the greatest

part, in the middle or anterior third of the fronto-parietals. Posterior antorbitals far from contact with the orbits; anterior supraorbitals meeting the jugals, but most often not the posterior supraorbitals or supraorbito-dermosphenotics; each frontal thus most often forming a part of the medial orbital margin. Postorbitals short. Horizontal portion of the suborbital part of the infraorbital canal tending to develop a postero-medially directed loop in its anterior half.

A very natural unit is formed by WATSON's family *Metoposauridae*, including *Metoposaurus* and *Anaschisma* (text-figs. 16, 24).

The new American genus *Buettneria*, described by CASE (1922, 1925, 1931, 1932; also BRANSON and MEHL 1929, fig. 3) forms, with the new genera *Koskinodon* (BRANSON and MEHL 1929, fig. 8), *Borborophagus* (BRANSON and MEHL 1929, fig. 10), and probably also *Kalamoiketor* (BRANSON and MEHL 1929, fig. 11), an assemblage of "*Stereospondyli*", very closely related *inter se* and to *Anaschisma*, and evidently appertaining to the family *Metoposauridae*, where they were also placed by BRANSON and MEHL (1929, pp. 77—81), as well as by SMITH WOODWARD (1932, pp. 215, 216).

KUHN (1933, pp. 99—100) referred to the *Metoposauridae* also the "genera" *Dictyocephalus*, *Trigonosternum*, and *Calamops*. However, the skull fragment, described as *Dictyocephalus* (LEIDY 1856; EMMONS 1860, figs. 158, 159, 162) is far too incomplete to be placed with reasonable certainty in any higher systematic unit, and the same applies, only in a still more evident way, to the interclavicle, described by M. SCHMIDT (1931) as the type of the new genus "*Trigonosternum*", and to the mandibular fragment upon which SINCLAIR (1917, pp. 319—321, fig. 1) founded the new genus "*Calamops*".

SMITH WOODWARD also placed, though with hesitation, the Spitsbergen genus *Peltostega* among the *Metoposauridae*. However, by many not to say most, characters, *Peltostega* differs so markedly from the true Metoposaurids, that it does not seem to be more nearly related to them than are the *Trematosauridae* (cf. below pp. 85—88).

The widely-spread, but remarkably uniform genera of the true *Metoposauridae* show the following common characters, forming the *diagnosis of the family Metoposauridae* WATSON:

Stereospondylous *Labyrinthodontia*, with elongated skulls, most often more markedly broadening posteriorly from some distance behind the orbits. With short or medium-sized prenarial, medium-sized or long postnarial, short or very short

preorbital, long to very long postorbital, and long prenuchal and nuchal divisions of the dermal cranial roof. With small to medium-sized orbits, and very large external nares, sometimes even larger than the orbits; pineal foramen in the posterior halves, most often[1]) in the posterior thirds of the fronto-parietals. Posterior antorbitals excluded from the external nares by the meeting of the lachrymo-maxillaries and the naso-postrostrals. With long and large supraorbito-dermosphenotics, joined by rather long sutures with the anterior supraorbitals anteriorly, and with the supratemporo-intertemporals posteriorly. Frontals extending far behind the orbits. Lateral extrascapulars square, with almost no part behind the otic notches. With long postorbitals. Processus cultriformis of the parasphenoid very broad. Jugal(?) canals situated in the jugals and quadratojugals.

The *Metoposauridae* may naturally be subdivided into two subfamilies, one including the European, the other the American genera:

1. Subfamily *Metoposaurinae:* Posterior antorbital large, short and broad, not forming any part of the orbital margin. — *Metoposaurus* Lydekker[2]);

2. Subfamily *Buettneriinae:* Posterior antorbital elongated, most often very narrow[3]), always forming a distinct part of the orbital margin. — *Buettneria*, *Anaschisma* (see Branson and Mehl 1929, figs. 6, 7; incorrectly figured by Branson 1905, fig. 1, and Moodie 1908), *Koskinodon*, *Borborophagus*, probably also *Kalamoiketor*.

Both Watson (1919 b) and v. Huene (1920 a, b) placed *Trematosaurus* in the family *Trematosauridae*, together with all the new genera from Spitsbergen, described by Wiman, excepting only *Peltostega*, which was later placed by Smith Woodward, though with hesitation, among the *Metoposauridae* (Smith Woodward 1932, p. 216). Watson further included in the *Trematosauridae* the genus *Trematosuchus*.

All of the Spitsbergen forms differ considerably more from *Trematosaurus* than does *Trematosuchus*. On the other hand, such forms as *Lonchorhynchus*, *Aphaneramma*, and *Tertrema*, seem much more nearly related to *Trematosaurus* than do forms like *Peltostega*, *Lyrocephalus*, and *Platystega*.

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[1]) Exception only *Koskinodon* (Branson and Mehl 1929, fig. 8).

[2]) *Metopias* (v. Meyer 1842) preoccupied; see Lydekker 1890, p. 152.

[3]) Except in *Borborophagus* (Branson and Mehl 1929, fig. 10).

Peltostega has a remarkably broad processus cultriformis of the parasphenoid, whereas the other Spitsbergen forms here discussed present a type of palate similar to that of *Trematosaurus*. *Peltostega* also differs from the latter by the position of the pineal foramen in a triangular depressed area in the anterior half of the suture between the fronto-parietals.

Accordingly *Peltostega* seems to represent a separate family, whereas the skulls of *Lyrocephalus* and *Platystega* seem to represent mainly a broader modification of the same essential structure as those of the typical *Trematosauridae*, and may be worth only a distinction as the subfamily *Lyrocephalinae*, in contrast to the subfamily *Trematosaurinae*, including the other Trematosaurids, except *Lonchorhynchus*, which owing to the very large size of its orbits and the quite extraordinary length of its snout seems to be so specialized that it has to form a subfamily of its own: the *Lonchorhynchinae*. Of course the classification must remain provisional as far as so little is known about the endocranium of the discussed forms, as is at present the case with the Trematosaurids. So far the main characters distinguishing the *Lyrocephalinae* would be (1) the markedly triangular skulls, with broad posterior parts; (2) the relatively large size of the orbits (maximum length of the orbits generally greater than or nearly as great as the distance, along the median line of the skull, from the posterior margin of the orbital division to the anterior margin of the pineal foramen), which are situated relatively far from the lateral margin of the skull, on its dorsal surface; whereas the *Lonchorhynchinae* are characterised (1) by the enormous length of the snout; (2) by the very lateral position and, at least in the type specimen, the remarkably large size of the orbits (they are very much smaller in the other specimen figured by WIMAN 1914, pl. IV); and the *Trematosaurinae* have (1) long narrow skulls, with (2) small orbits (maximum length of the orbits markedly shorter than the distance from the posterior margin of the orbital division to the anterior margin of the pineal foramen), situated near the lateral margin of the skull.

Microposaurus (HAUGHTON 1925, pp. 253—256, text-figs. 17, 18), from the *Cynognathus* Zone of South Africa, was referred by HAUGHTON, and by KUHN (1933, p. 78) to the *Trematosauridae*. It is however really too incompletely known to be referred with certainty to any family at all; i. a. no sutures have been found on the dorsal surface of the skull. In its general shape the skull of *Microposaurus* shows a type more similar to that of *Trimerorhachis* and the Metoposaurids than to that of the Trematosaurids. The part of the skull in front of the orbits is much shorter than that behind the orbits, and the orbits are not much larger than the external nostrils. The pineal foramen is situated far behind the orbits. — Equally difficult is a discussion of the systematic position of the incompletely known genera *Hyperokynodon* (impression of a palate,

PLIENINGER 1852, pp. 465—470, no figure; cf. KUHN 1933, p. 77), *Benthosaurus* (EFREMOW 1929: skull, probably of a Trematosaurid, allied to *Lyrocephalus*; cf. below, p. 196), *Gonioglyptus* (HUXLEY 1865, pp. 3—5, pl. VI, fig. 1; v. HUENE 1920 b: probably nearly allied to *Aphaneramma* and *Lonchorhynchus*), and "*Glyptognathus*" (LYDEKKER 1882, fig. 1: a quite indeterminable fragment of a lower jaw). These genera are therefore not included in the present discussion.

The diagnosis of the family *Trematosauridae* WATSON must at present include the following characters:

Stereospondylous *Labyrinthodontia* with elongated or triangular, not extremely depressed skulls, narrow in their most anterior parts. With medium-sized, long, or very long prenarial, long or medium-sized postnarial, long, medium-sized or short preorbital, short to very long postorbital, long or medium-sized prenuchal and short or medium-sized nuchal divisions of the dermal cranial roof. With large, medium-sized or small orbits, and small external nares; pineal foramen in the posterior halves of the fronto-parietals. Posterior antorbitals excluded from the external nares by the meeting of the lachrymo-maxillaries and the naso-postrostrals or naso-postrostro-interrostrals, most often also excluded from the orbits by the meeting of the jugals and anterior supraorbitals. With long and large supraorbito-dermosphenotics, joined by rather long sutures with the anterior supraorbitals anteriorly, and with the supratemporo-intertemporals posteriorly. Frontals extending markedly behind the orbits. With long postorbitals. Processus cultriformis of the parasphenoid very high and narrow.

Diagnoses are given below, in the special part, of the genera *Trematosaurus*, *Trematosuchus*, *Tertrema*, *Aphaneramma* (pp. 138—140), *Stoschiosaurus* (p. 131), *Lyrocephalus*, and *Platystega* (p. 163).

The family *Peltostegidae* n. fam. would be provisionally characterised as follows:

Stereospondylous *Labyrinthodontia* with triangular skulls, very markedly broadening in their posterior parts. With long prenarial and postnarial, medium-sized preorbital, postorbital and prenuchal, and long nuchal divisions of the dermal cranial roof. With medium-sized, very much laterally placed orbits, and small external nares. Pineal foramen situated in a triangular depressed area in the anterior halves of the fronto-parietals. Posterior antorbitals excluded from the external nares by the meeting of the lachrymo-maxillaries and the naso-postrostrals, and from the orbital

margins by the meeting of the jugals and anterior supraorbitals. With large supraorbito-dermosphenotics or posterior supraorbitals, joined by rather long sutures to (or fused with) the anterior supraorbitals and the supratemporo-intertemporals. Frontals extending somewhat behind the posterior margins of the orbits. With broad postorbitals. Processus cultriformis of the parasphenoid very broad.

As will be easily seen by comparing the diagnosis of the *Trematosauridae* with those of the *Metoposauridae* and the *Peltostegidae*, these three families seem to form a fairly natural unit, characterised by several important common features. To this provisional systematic unit I propose to give the rank of a suborder, calling it the *Trematosauroidei*. Its diagnosis will be given below (p. 91).

The *Brachyopidae*, according to WATSON (1919 b, p. 56) form a very distinct and obviously natural group. For the sake of conformity in the classification they may be included into a superfamily, *Brachyopoideae*. Certain of the members, as well as their ancestor according to WATSON, the important genus *Dvinosaurus*, are not very completely known from published evidence. Therefore I do not want to discuss the Brachyopids more closely on this occasion, but only to point out that if, as I think, WATSON is correct in putting the rhachitomous *Dvinosaurus* and the Brachyopids on the same line of evolution (cf. SUSHKIN 1923; EFREMOW, 1932, p. 66), this forms one more argument in favour of the view that the "*Stereospondyli*" are a polyphyletic assemblage and no natural group. The *Brachyopoideae* and the *Dvinosauridae* (being the only family in a superfamily *Dvinosauroideae*) may be put together in a suborder *Brachyopoidei*.

After this inspection of the relationships of the geologically youngest *Labyrinthodontia* we may try to find out the origin of the groups recognised.

The case of the rhachitomous Capitosauroid, *Wetlugasaurus* and also that of the rhachitomous Brachyopoid *Dvinosaurus*, seem to me to prove the correctness of the view that the development from a rhachitomous to a stereospondylous type of vertebrae has taken place independently in several lines of evolution (cf. v. HUENE 1932). Thus we may not expect to find among the "*Rhachitomi*" a "central type" from which may have evolved all the highest "*Labyrinthodontia*", but possibly we may find several types belonging to earlier parts of the evolutionary lines recognised among the "*Stereospondyli*".

Thus there are among the "*Rhachitomi*" a number of types, which may, I think, most naturally be interpreted as the fore-runners of the

Capitosauroids. To these types belong the genera of the family *Eryopidae* — *Eryops*, *Parioxys*[1]), *Onchiodon*, probably also *Eryopsoides* DOUTHITT (1917), whilst *Anisodexis* (see CASE 1911, pp. 33, 104), and *Chalcosaurus* (v. MEYER 1866, pl. XXI, fig. 1), also included in this family by KUHN (1933, pp. 39—45), are too incompletely known to be discussed at all —; the *Rhinesuchidae* — *Rhinesuchus*, *Laccocephalus*, *Uranocentrodon*, and *Laccosaurus* (HAUGHTON 1925, pp. 234—236; text-figs. 5—7), but not certainly *Gondwanosaurus* (LYDEKKER 1885; KUHN 1933, p. 56) —; the *Zatrachydidae* — *Zatrachys*, *Dasyceps*, *Platyhystrix* —; conceivably also the rather incompletely known *Trematopsidae*, *Acanthostoma*[2]), the *Achelomidae* (cf. CASE 1911, pl. 11; v. HUENE 1913, fig. 55), and *Melosaurus* (v. MEYER 1860 a, pl. 10; RIABININ 1916); and without doubt the genus *Osteophorus*, referred by WATSON (1919b, p. 64) with hesitation to the family *Actinodontidae*. In fact the differences between *Osteophorus* on the one hand and *Eryops* on the other, hardly seem to justify a wider separation than into two subfamilies: the American *Eryopinae* with broader snout, and posterior antorbital forming part of the margins of the external nares; the European *Osteophorinae* (conceivably including *Onchiodon*) with somewhat narrower snout, and posterior antorbitals excluded from the external nares by the meeting of the lachrymo-maxillaries and naso-postrostrals.

Together with the *Zatrachydidae*, the *Rhinesuchidae*, and probably also the *Trematopsidae*, *Acanthostoma*, the *Achelomidae*, and *Melosaurus*, the *Eryopidae* may be included in a provisional superfamily, *Eryopoideae*, characterised by the following diagnosis:

Rhachitomous *Labyrinthodontia* with elongated skulls, with muzzles very broad, or broad with lateral convavities (as in *Zatrachys* and *Osteophorus*). With long or very long postnarial, medium-sized or short preorbital, short or very short postorbital and prenuchal, and very short to medium-sized nuchal divisions of the dermal cranial roof. With medium-sized to small orbits, and small external nares.

The superfamilies *Capitosauroideae* and *Eryopoideae* together form the suborder *Capitosauroidei*, with i. a. the following common characters: skulls elongated or triangular; with broad muzzles; with medium-sized to long prenarial, long to very long postnarial, short to very long preorbital, short to very short postorbital, and medium-sized to very short prenuchal and nuchal divisions of the dermal cranial roof.

The less specialized of the *Eryopoideae*, the *Eryopidae* and the

[1]) Cf. KUHN 1933, p. 45; CASE 1911, pp. 32—33, fig. 4.
[2]) Cf. STEEN 1934.

Rhinesuchidae, are those which most clearly foreshadow the structure of the Capitosauroids, though differing, of course, from the latter by many, mostly primitive features. Thus the supraorbito-dermosphenotics most often meet the anterior supraorbitals in the Eryopids; it may, however, be noticed that in respect of these bones *Osteophorus* is quite similar to a typical Capitosauroid.

Another quite remarkable instance of a rhachitomous type, apparently nearly related to a stereospondylous family is furnished by *Trimerorhachis* (text-fig. 8 A, C). Together with the two genera *Micropholis* (text-fig. 5) and *Broiliellus* (text-fig. 8 B), certainly nearly related to each other, — possibly also with the other *Dissorophidae*, which are very incompletely known, — *Trimerorhachis* forms a group, which seems rather clearly to belong to the line, represented, among the "*Stereospondyli*", by the *Metoposauridae*. There is, in fact, an astonishing degree of similarity even in the shape of individual bones (frontals, fronto-parietals, parieto-extrascapulars, anterior supraorbitals) between *Trimerorhachis* (text-fig. 8 A) and a Metoposaurid like *Anaschisma brachygnatha* (text-fig. 16; BRANSON and MEHL 1929, fig. 7).

In fact the relationship between the "*Rhachitomi*" mentioned and the family *Metoposauridae* being closer than that of the Metoposaurids to the Trematosaurids necessitates a widening of the suborder *Trematosauroidei* to comprise also the *Trimerorhachidae*, *Broiliellus* (with the other *Dissorophidae*?), and *Micropholis*. The two last-mentioned genera may at present hardly be put into separate families.

Together with the *Metoposauridae* the mentioned rhachitomous *Labyrinthodontia* (*Trimerorhachidae*, *Broiliellus*, *Micropholis*, *Dissorophidae*?) may be included in a superfamily *Metoposauroideae*, with the following common characters: skulls triangular or elongated, markedly broadening in their posterior parts, with short, medium-sized, or long prenarial, medium-sized or long postnarial, short or very short preorbital, long to very long postorbital, long prenuchal, and long or medium-sized nuchal divisions of the dermal cranial roof; with large external nares; orbits in the anterior half of the skull; pineal foramen markedly behind, most often far behind the orbits, and in the middle or posterior third of the fronto-parietals.

The origin of the family *Trematosauridae*, which may be regarded as the type family of a superfamily *Trematosauroideae*, seems more uncertain. At first sight it may be tempting to look upon the two apparently closely related genera *Archegosaurus* and *Platyops* (see EFREMOV 1933, figs. 1, 2, 13) as belonging to a group ancestral to certain *Trematosauridae* (cf. EFREMOV 1933, pp. 144—146). And there certainly are

several important resemblances between the latter and the two genera mentioned. But on the other hand *Archegosaurus* and *Platyops* seem in certain characters to be far more specialized than the *Trematosauridae*: they have a relatively much more elongated snout, and much shorter postorbital and prenuchal divisions of the dermal cranial roof. Thus in any case they are not quite close to the line leading to the *Trematosauridae*. In fact it may be subject to grave doubt wether the very elongated shape of the skull found in *Archegosaurus* and in Trematosaurids may not have been acquired independently in two evolutionary lines. The presence in the Lower Triassic of the *Lyrocephalinae*, with their broader skulls, suggests the possibility of several phylogenetic branches of the *Labyrinthodontia* with strongly elongated snout originating from a persistent stock of more normally shaped forms. — Not improbably however, a more complete knowledge of the structure of the forms discussed may, none the less, justify a further widening of the superfamily *Trematosauroideae* to comprise also the rhachitomous family *Archegosauridae* (with the two subfamilies *Archegosaurinae* and *Platyopinae*; cf. EFREMOV 1933). But this question must at present be left without solution, and the *Archegosauridae* will provisionally only be included in the same suborder as the *Trematosauridae*.

Accordingly the suborder *Trematosauroidei* would, at present, have to include the rhachitomous families *Archegosauridae*, *Trimerorhachidae*, the genera *Broiliellus* and *Micropholis* (the family *Dissorophidae*?), and the stereospondylous families *Metoposauridae*, *Peltostegidae*, and *Trematosauridae*. Its diagnosis would run as follows:

Rhachitomous or stereospondylous *Labyrinthodontia* with elongated or triangular skulls. With short to very long prenarial, medium-sized or long, rarely very long, postnarial, very short to long, rarely very long, preorbital, very long to short postorbital, long or medium-sized prenuchal, and long to short nuchal divisions of the dermal cranial roof. Orbits of varying size. With independent posterior supraorbitals and dermosphenotics or, most often, with elongated large supraorbito-dermosphenotics, joined by rather long sutures with the supratemporo-intertemporals.

Finally it is necessary to point out here that the attempt at classification given above and summarised below, on pp. 199—200 must, of course, not be regarded as pretending to be a final solution of the problem discussed. Since at present very little is known about the endocranium, there is a great uncertainty in the phylogenetic discussion, still increased by the incompleteness of our knowledge even of the dermal bones in many cases. None the less I have thought it suitable

to give as exact an account as possible of the present state of the problem, and the classification introduced for this purpose may, I hope, be of value as a basis for further discussion of the matter.

4. The Anthracosauria, Seymouria and the Reptilia.

A. The Anthracosauria.

All typical members of the *Anthracosauroideae* — one of the two superfamilies of WATSON's "Grade Embolomeri" — present, as far as they are known, a strikingly uniform pattern of the dermal cranial bones, especially of those of the cranial roof.

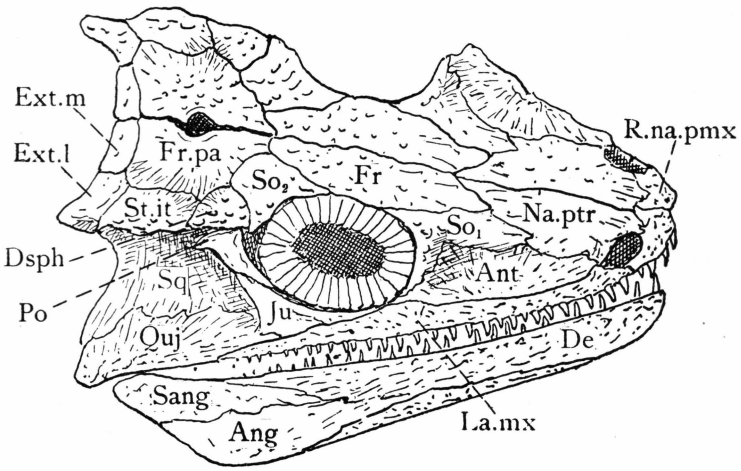
The dermal bones of the head are most completely known in "*Gephyrostegus*" (or *Diplovertebron*), as figured by JAEKEL (1902), and in *Palaeogyrinus decorus*, described by WATSON (1926 a). In most genera the bones of the cheek and those of the snout are as yet unknown. The loose, at least partly only ligamental attachment of the cheek seems to be a characteristic primitive feature of several members of the discussed group, and may explain why the dermal bones of the cheek are so far well known only in *Palaeogyrinus* (text-fig. 46) and in "*Gephyrostegus*" (text-fig. 39). According to PFANNENSTIEL (1932) the fact that the dermal bones of the snout are lost in most specimens — and in fact, well known only in "*Gephyrostegus*" (text-fig. 39) — may be explained in an analogous way.

As far as known the external nares of the Anthracosaurids are situated low down, near the ventral margin of the snout (see "*Gephyrostegus*", text-fig. 39; *Palaeogyrinus*, text-figs. 41, 46).

To judge from the condition in "*Gephyrostegus*" (text-fig. 39) each of the premaxillaries of the Anthracosauroids has fused, like that of all the Stegocephalians treated above, and those of certain Coelacanthids (STENSIÖ 1932, p. 33, text-figs. 16, 18, 19), with the rostrals of its side. And the backward extension, in relation to the external nares, of the two bones (*R. na. pmx*, text-figs. 39, 46), forming the anterior margin of the snout, as compared with the condition in, for instance, *Baphetes* (text-fig. 1), makes it probable that each of those bones also includes the homologon of the most anterior nasal element of the Crossopterygians. It is possible too, that an interrostral component enters into the formation of each of the discussed bones, but this is very uncertain, and can only be decided when we know somewhat more about the structure of the snout in a greater number of Anthracosauroids. Accordingly the bones discussed will for the present have to be termed *naso-rostro-premaxillaries* (*R. na. pmx*, text-figs. 39, 46), and considered to be most probably homologous with the bones of the same name in the Loxommids, and the higher *Labyrinthodontia*.

The *naso-postrostrals* (*Na. ptr*, text-figs. 39, 41, 43) are clearly homologous with those of the Ichthyostegids (cf. text-fig. 39 and SÄVE-SÖDERBERGH 1932, text-fig. 2) and all the groups of Stegocephalians here discussed. In *Palaeogyrinus* (text-fig. 41) they are clearly connected with the anterior parts of the supraorbital canals.

Likewise the *frontals* (*Fr*, text-figs. 39, 40, 41, 43, 44) correspond quite clearly to those of the Ichthyostegids, and accordingly have to be regarded as homologous with the anterior halves of the frontals of the Crossopterygians. They are still connected with the supraorbital canals, at least in *Palaeogyrinus* (text-fig. 41) and in *Pteroplax* (text-fig. 40).

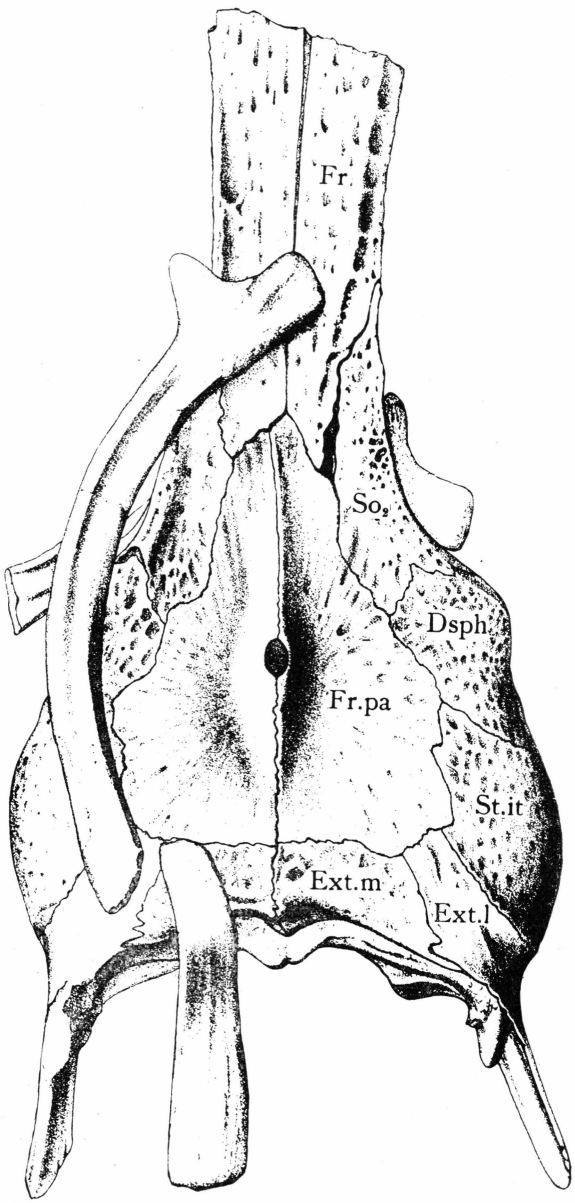


Text-fig. 39. "*Gephyrostegus bohemicus* JAEKEL.". Dorso-lateral aspect of the skull. After JAEKEL (1902).

Ang, angular; *Ant*, posterior antorbital; *De*, dentary; *Dsph*, dermosphenotic; *Ext. l*, lateral extrascapular; *Ext. m*, median extrascapular; *Fr*, frontal; *Fr. pa*, frontoparietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Po*, postorbital; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; *Sang*, supraangular; So_1, anterior supraorbital; So_2, posterior supraorbital; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

The *anterior antorbitals* have as yet been described in none of the Anthracosauroids.

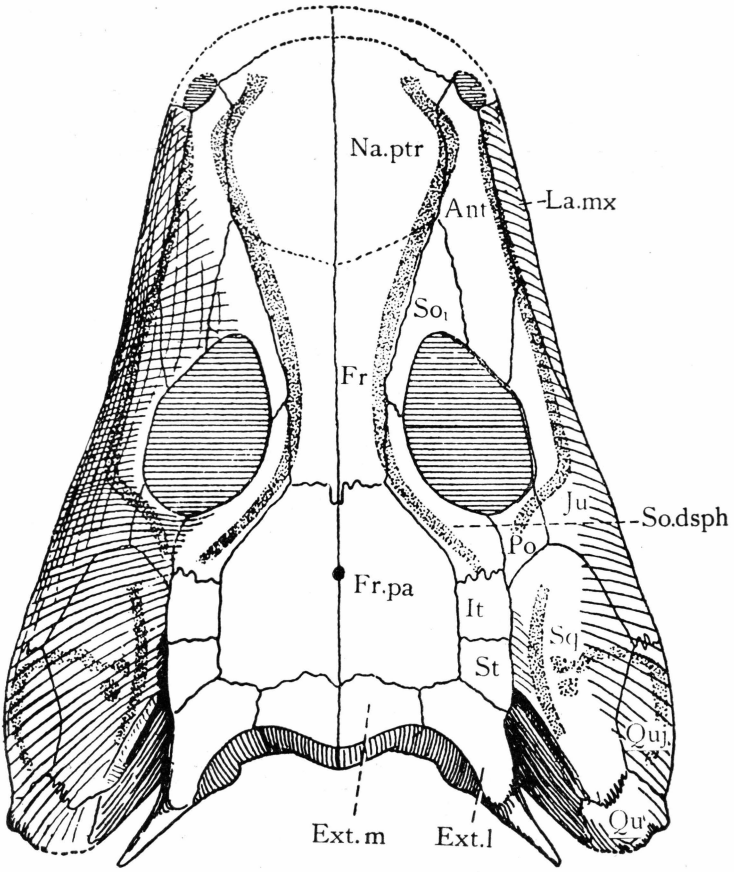
The *posterior antorbitals* (*Ant*, text-figs. 39, 41, 43, 46) present a successive reduction, quite parallel to that found in the "*Rhachitomi*" (pp. 38, 39). In *Palaeogyrinus* (text-figs. 41, 46) they still form considerable parts both of the orbital margins and of the margins of the external nostrils. In "*Gephyrostegus*" (text-fig. 39) they just reach the nostrils and have very short orbital margins, and in *Cricotus* (text-fig. 43) they are considerably reduced and their hindermost ends are rather far from the orbital margins.



Text-fig. 40. *Pteroplax cornuta* HANCOCK and ATTHEY. Dorsal aspect of an anteriorly damaged dermal cranial roof. After ATTHEY (1878).
Dsph, dermosphenotic; *Ext. l*, lateral extrascapular; *Ext. m*, median extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; So_2, posterior supraorbital; *St. it*, supratemporo-intertemporal.

During the process of reduction of the posterior antorbitals, the *anterior supraorbitals* (So_1, text-figs. 39, 41, 43, 46), just as in the "*Rhachitomi*", come to form successively greater parts of the anterior margins

of the orbits. In *Palaeogyrinus*, which shows the most primitive condition, the anterior supraorbitals have just the same position and very much the same shape as the anterior supraorbitals of the Ichthyostegids (cf. text-figs. 41, 46, and SÄVE-SÖDERBERGH 1932, text-figs. 2, 11, 12). It should be pointed out that the characteristic shape of these bones gives a very



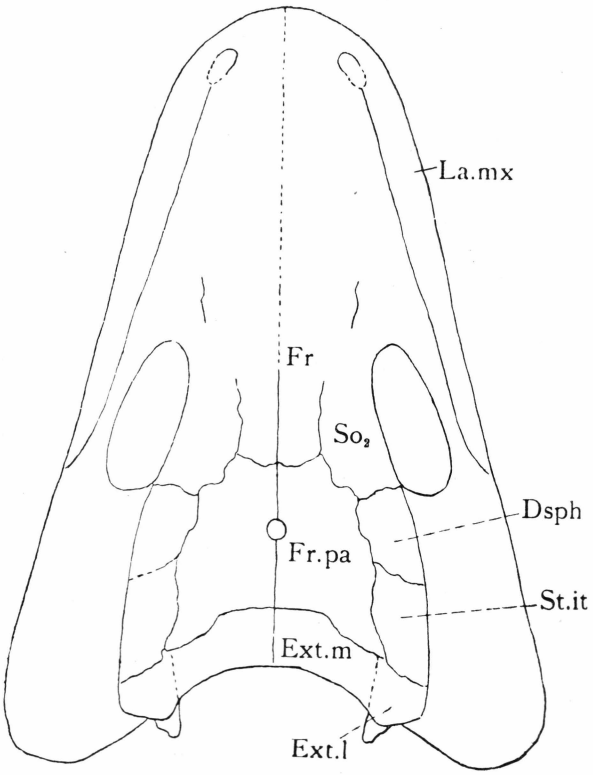
Text-fig. 41. *Palaeogyrinus decorus* WATSON. Dorsal aspect of the skull. After WATSON (1926 a).

Ant, posterior antorbital; *Ext. l*, lateral extrascapular; *Ext. m*, median extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *It*, intertemporal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Po*, postorbital; *Qu*, quadrate; *Quj*, quadrato-jugal; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St*, supratemporal.

strong support to the interpretation of the frontals and the naso-postrostrals.

Posterior supraorbitals (So_2) doubtless homologous to those of the Crossopterygians and Ichthyostegids are found in *Cricotus* (text-fig. 43), *Pholidogaster* (text-fig. 42), *Pteroplax* (text-fig. 40), and *Eogyrinus* (text-

fig. 44), most probably also in "*Gephyrostegus*" (text-fig. 39). Only in *Palaeogyrinus* (text-fig. 41) may there arise a well-founded doubt as to whether each posterior supraorbital has not here fused with a dermosphenotic, as the bone in question (*So. dsph*, text-fig. 41) in *Palaeogyrinus* is joined by sutures with the greatest part of the medial margin of the



Text-fig. 42. *Pholidogaster pisciformis* HUXLEY. Dorsal aspect of a skull. After WATSON (1926 b).

Dsph, dermosphenotic; *Ext. l*, lateral extrascapular; *Ext. m*, median extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *La. mx*, lachrymo-maxillary; So_2, posterior supraorbital; *St. it*, supratemporo-intertemporal.

postorbital and with the whole antero-lateral margin of the fronto-parietal (cf. *Pteroplax*, text-fig. 40).

The differences in the relations of the bone in *Palaeogyrinus* denoted *So. dsph*, and those of the other Anthracosauroids, denoted So_2, can only be explained by two alternative assumptions: either that the bone *So. dsph* is the product of a fusion of a posterior supraorbital and a dermosphenotic, or that the dermosphenotic has been totally reduced in *Palaeogyrinus*, and the area originally covered by it has become

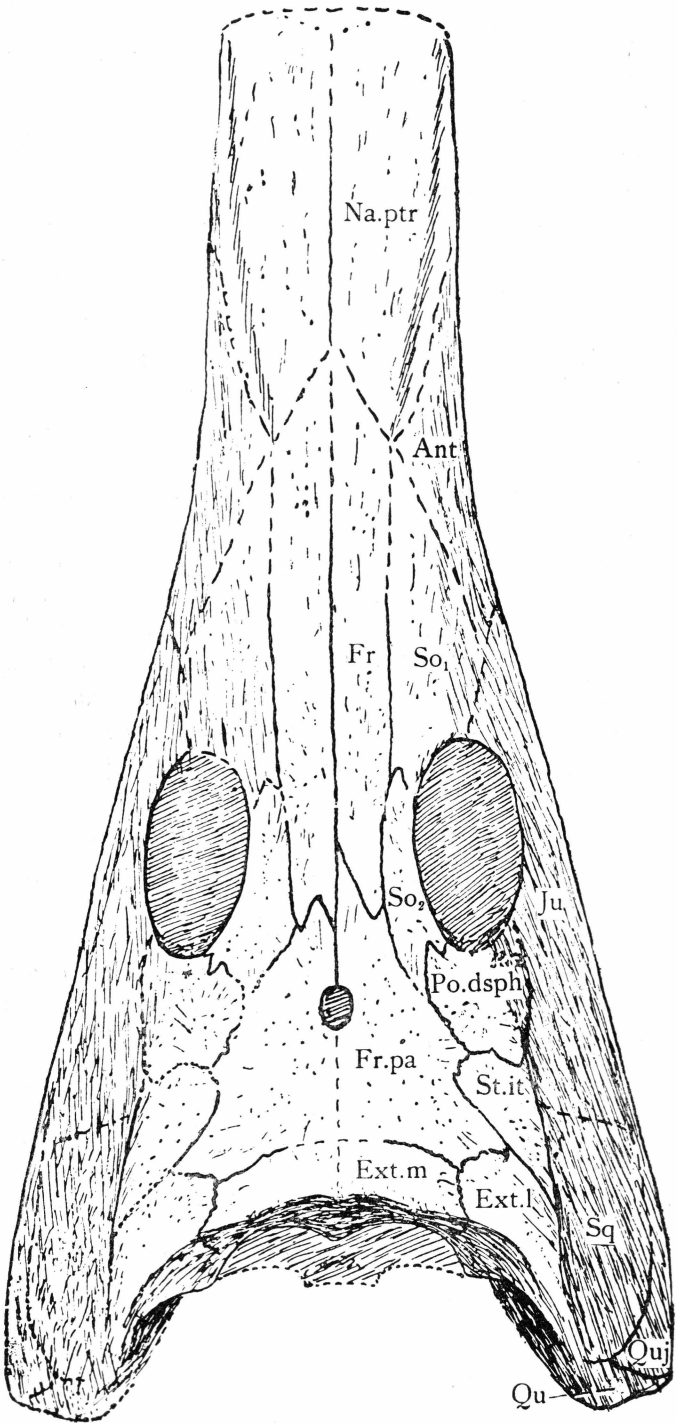
covered by a secondary expansion of the posterior supraorbital. Now, as the dermosphenotics show no tendencies to reduction in the other *Anthracosauroids* (see below), it seems almost inevitable to assume that the bone *So. dsph* in *Palaeogyrinus* really is a *supraorbito-dermosphenotic.*

As may readily be seen by comparison with the Crossopterygians and Ichthyostegids (see SÄVE-SÖDERBERGH 1932, text-fig. 16), the dermosphenotics of the other Anthracosauroids present two different types. In *Pteroplax* (text-fig. 40), *Eogyrinus* (text-fig. 44), *Pholidogaster* (text-fig. 42) and "*Gephyrostegus*" (text-fig. 39) each dermosphenotic is represented by an independent, more or less rectangular bone (*Dsph*) just postero-medially to the orbit, posterior to the posterior supraorbital, lateral to the part of the fronto-parietal pierced by the pineal foramen, and medial to the postorbital.

In *Cricotus*, on the other hand, each dermosphenotic has evidently fused with the postorbital of its side to a compound *postorbito-dermosphenotic* (*Po. dsph*, text-fig. 43), quite as in the Ichthyostegids. The two small square bones posterior to each supraorbito-dermosphenotic and medially to the anterior two thirds of the squamosal in *Palaeogyrinus* (*It*, *St*, text-figs. 41, 46) have very clearly the same position and relations as the *intertemporal* and *supratemporal* of a Crossopterygian, as *Osteolepis* (see for instance SÄVE-SÖDERBERGH 1932, text-fig. 16 C; 1933, text-fig. 19). Evidently these two bones correspond in the other Anthracosauroids (text-figs. 39, 40, 42, 43, 44) to the single, rectangular bone, denoted *St. it*, which accordingly is a *supratemporo-intertemporal* like that of the Ichthyostegids, Loxommids, and higher *Labyrinthodontia*, and that of several Crossopterygians (*Thursius*, *Osteolepis microlepidotus*; see SÄVE-SÖDERBERGH 1933), that of *Dipterus* (SÄVE-SÖDERBERGH 1932, text-fig. 20) and that of *Amia* and other Actinopterygians (see, for instance, PEHRSSON 1922).

The *fronto-parietals* (*Fr. pa*, text-figs. 39, 40, 41, 42, 43, 44) have the same extension anteriorly as the fronto-parietals of the Ichthyostegids and other Stegocephalians. None the less they are of a quite different nature, as, unlike the fronto-parietals of the mentioned groups, they extend as far back as the posterior margins of the supratemporals or supratemporo-intertemporals, thus meeting the bones of the extrascapular series situated posterior to the supratemporals or supratemporo-intertemporals. Hence it is clear that each fronto-parietal of an Anthracosauroid contains not only the homologons of a posterior frontal and an anterior parietal of a Crossopterygian but also the homologon of a posterior parietal of the Crossopterygian.

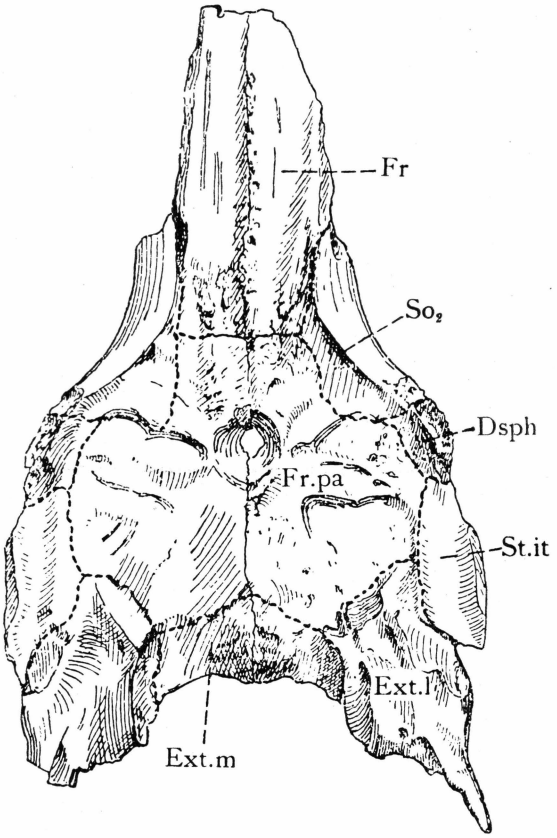
From the above deductions it follows that the two most posterior bones (*Ext. m*, text-figs. 39, 40, 41, 42, 43, 44) in the middle of the dermal cranial roof of an Anthracosauroid are by no means homologous with



Text-fig. 43.

Cricotus crassidiscus Cope. Dorsal aspect of the skull. After Broom (1913 c). *Ant*, posterior antorbital; *Ext. l*, lateral extrascapular; *Ext. m*, median extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *Na. ptr*, naso-postrostral; *Po. dsph*, postorbito-dermosphenotic; *Qu*, quadrate; *Quj*, quadratojugal; So_1, anterior supraorbital; So_2, posterior supraorbital; *Sq*, squamosal; *St.it*, supratemporo-intertemporal.

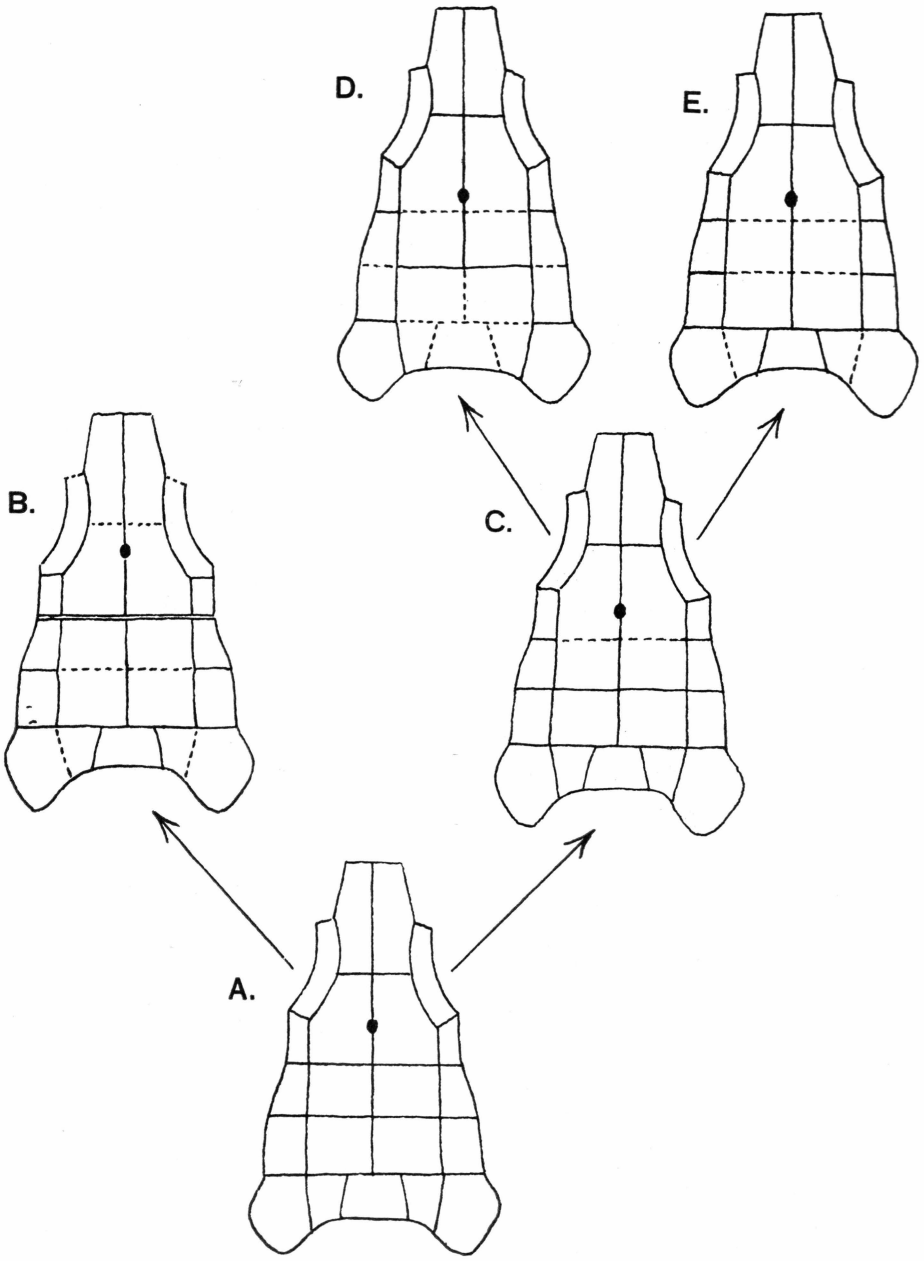
the similarly situated bones in other Stegocephalians. For, as may be easily seen by comparing, for instance, *Palaeogyrinus* (text-fig. 41) or *Eogyrinus* (text-fig. 44) with *Osteolepis* (SÄVE-SÖDERBERGH 1933, text-fig. 19 A), the discussed bones (*Ext. m*) of the Anthracosauroids are nothing else than the paired homologon of the median extrascapular of the Crossopterygians. Like the latter they are joined by suture only with the me-



Text-fig. 44. *Eogyrinus attheyi* WATSON. Ventral aspect of imperfect dermal cranial roof. After WATSON (1926 a).

Dsph, dermosphenotic; *Ext. l*, lateral extrascapular; *Ext. m*, median extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *So*$_2$, posterior supraorbital; *St. it*, supratemporo-intertemporal.

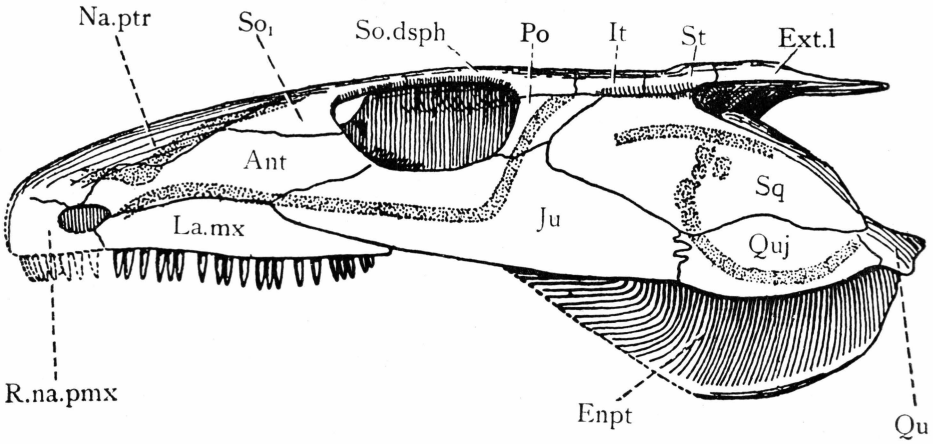
dial parts of the posterior margins of the (fronto-)parietals. Eo ipso it follows that the *lateral extrascapulars* of the Anthracosauroids (*Ext. l*, text-figs. 39, 40, 41, 42, 43, 44) are not homologous with the bones of the same name in the other Stegocephalians, but with the lateral extrascapulars of the Crossopterygians and the four lateral extrascapular components in the common ancestor of the Crossopterygians, the



Text-fig. 45. Scheme of possible evolution of certain dermal bones in Anthracosauroids (E) and *Ichthyostegalia-Labyrinthodontia* (D) from a common ancestor (C), itself originating from a common ancestor (A) with the Crossopterygians (B). The bones figured are two pairs of frontals and two pairs of parietals along the median line; a pair of posterior supraorbitals, laterally to the posterior halves of the anterior frontals and the anterior halves of the posterior frontals; a pair of dermosphenotics, laterally to the posterior halves of the posterior frontals; a pair of intertemporals, laterally to the anterior parietals; and a pair of supratemporals, laterally to the posterior parietals; finally a row of five extrascapulars along the posterior margin of the skull-roof, behind the parietals and the supratemporals. Cf. also SÄVE-SÖDERBERGH 1932, text-fig. 18. For the sake of clearness the paired median extrascapular of the Anthracosauroids is denoted as an unpaired bone.

Dipnoans, and the Tetrapods (SÄVE-SÖDERBERGH 1932, pp. 94—98, text-fig. 18).

Thus in regard to the arrangement of the bones of the posterior parts of the dermal cranial roof the Anthracosauroids are more nearly related to the Crossopterygians than to the other labyrinthodont Stegocephalians. Moreover none of the three patterns, found in the Crossopterygians, the Anthracosauroids, and the other Stegocephalians here discussed, can be derived from any of the other two, but all the three are to be derived from a pat-



Text-fig. 46. *Palaeogyrinus decorus*. Lateral aspect of the skull. After WATSON (1926 a).

Ant, posterior antorbital; *Enpt*, entopterygoid; *Ext.l*, lateral extrascapular; *It*, intertemporal; *Ju*, jugal; *La.mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Po*, postorbital; *Qu*, quadrate; *Quj*, quadratojugal; *R.na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So.dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St*, supratemporal.

tern like that postulated by me in the common ancestor of the Crossopterygians and the Tetrapods. Thus, either the labyrinthodont Stegocephalians arose polyphyletically, or there was once a most primitive labyrinthodont Stegocephalian with at least two pairs of parietals and five extrascapulars. The anterior of these pairs of parietals may have been fused with the posterior frontals, but the posterior parietals must have been totally independent. This hypothetical ancestral form would have to be placed between the "Fish ancestors" and the "Ichthyostegid-like Stegocephalians" or primitive *Ichthyostegalia* (see text-fig. 45).

The dermal bones of the cheek are fairly completely known only in *Palaeogyrinus* (text-fig. 46) and in "*Gephyrostegus*" (text-fig. 39). In *Palaeogyrinus*, in spite of the more dorsal course of the horizontal portion of the suborbital part of the infraorbital canal, the bone ventral to the

posterior antorbital must evidently be a *lachrymo-maxillary* (*La. mx*, text-fig. 46) like that of the other Stegocephalians. The same may also probably be the case in "*Gephyrostegus*", but in this, partly rather specialised form, another interpretation may also be possible. The bone, called by me the anterior supraorbital (cf. above) may possibly, though not probably, be the posterior antorbital — the bone ventral to it then being an independent lachrymal. The shape of the bone in "*Gephyrostegus*", denoted So_1 (text-fig. 36) is rather like that of the posterior antorbital in *Ichthyostega stensiöi* (SÄVE-SÖDERBERGH 1932, text-fig. 2). However, it seems more probable that this is a convergence and that the two bones in front of the orbit are the same in "*Gephyrostegus*" as in *Palaeogyrinus*, *viz.* the anterior supraorbital and the posterior antorbital.

The lachrymo-maxillary of *Palaeogyrinus* is strikingly short, as compared with the corresponding bone in the Ichthyostegids and Loxommids.

The *jugal* of *Palaeogyrinus* (*Ju*, text-fig. 46) is quite similar in its main shape and relations to that of an Ichthyostegid as *Ichthyostega stensiöi* (SÄVE-SÖDERBERGH 1932, text-fig. 2). It is clearly connected with the vertical and horizontal portions of the suborbital part of the infraorbital canal.

In "*Gephyrostegus*" the jugal (*Ju*, text-fig. 39) seems to be very reduced in size. According to JAEKEL's figure (my text-fig. 39) it is a narrow crescent-shaped bone along the postero-ventral margin of the orbit.

The *postorbital* (*Po*, text-figs. 39, 46) seems to be strikingly short both in *Palaeogyrinus* and in "*Gephyrostegus*". In the former it is connected with the vertical portion of the suborbital part of the infraorbital canal.

It seems impossible to make out with certainty the fate of the preopercular on the available evidence. However, the course of the jugal canal towards the posterior margin of the squamosal (cf. below), and the fact that the squamosal seems to extend a little farther back than the quadratojugal at the suture between the two bones and the quadrate, at least in *Palaeogyrinus*, make it most probable that the preopercular is not represented by any ossified part in the Anthracosauroids. Therefore the two bones, covering the posterior third of the cheek, are here termed simply the *squamosal* (*Sq*, text-figs. 39, 46) and the *quadratojugal* (*Quj*, text-figs. 39, 46). Both these bones are connected in *Palaeogyrinus* (text-fig. 46) with a groove for a lateral line canal, a *quadratojugal canal*, which is evidently the homologon of the vertical pit-line of the cheek in Crossopterygians and other Fishes (cf. SÄVE-SÖDERBERGH 1933, pp. 7—8, 92; text-fig. 19 B; *vp*, pls 1, 15). The squamosal is also connected with a horizontal groove, evidently homologous with the

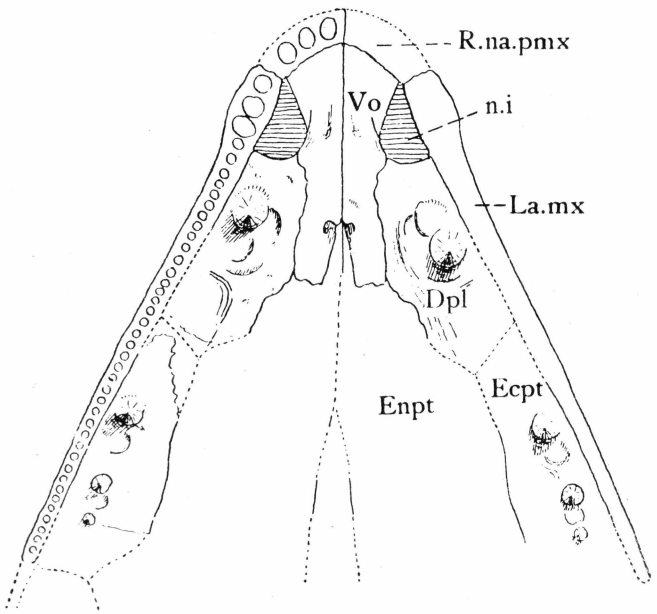
jugal canal of other *Choanata* and with the horizontal pit-line of the cheek in the Actinopterygians.

The *palate* of the Anthracosauroids (text-fig. 47), as already pointed out by WATSON (1926 b), differs markedly in several respects from that of the Loxommids. The main characters of the Anthracosauroid palate, distinguishing it from the Loxommid one, are:

1. The long and narrow, toothless vomeres (*Vo*, text-fig. 47);

2. The large internal nares (*n. i*, text-fig. 47), situated near the anterior end of the snout, and near each other.

As will be evident from the account given above (pp. 19—20, text-fig. 4 B), the palate of the Loxommids has very large, tooth-bearing vomeres, widely separating the two very small internal nares.



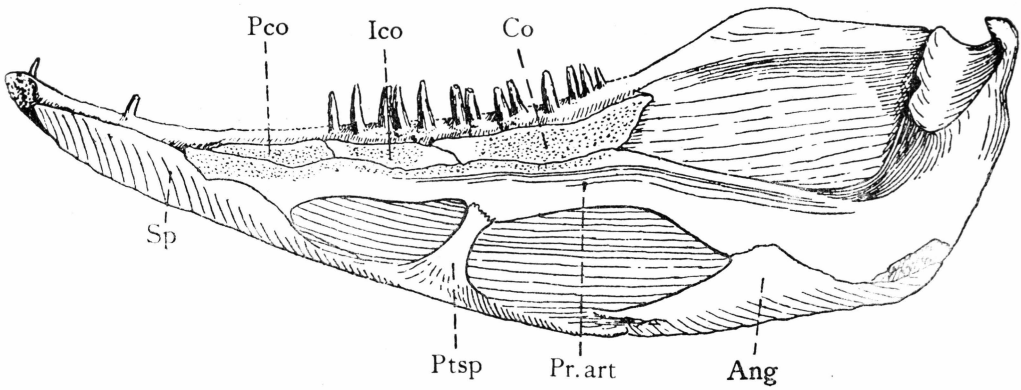
Text-fig. 47. *Pholiderpeton scutigerum* HUXLEY. Ventral aspect of the anterior parts of the palate. After WATSON (1926 b).

Dpl, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *La. mx*, lachrymo-maxillary; *R. na. pmx*, naso-rostro-premaxillary; *Vo*, vomer; *n. i*, internal naris.

Now it is important to note that in regard to both of the characters mentioned, the Loxommid palate agrees perfectly with that of the Ichthyostegids (cf. text-figs. 4 A, B, 47).

On the other hand the Anthracosauroid palate agrees in the characters discussed with that of *Seymouria*, and, as is especially important, with that of the Reptiles, except only that the reptilian vomeres may be tooth-bearing. In fact WATSON, when discussing the systematical

position of *Seymouria* (WATSON 1919 a, pp. 289, 292, 293) cited as a reptilian character of that genus, the choanae lying near to the middle line. This, however, can only be realized by a relative narrowing of the vomeres.



Text-fig. 48. *Eogyrinus attheyi* WATSON. Lingual aspect of the lower jaw. After WATSON (1926 a).
Ang, angular; *Co*, coronoid; *Ico*, intercoronoid; *Pco*, precoronoid; *Pr.art*, prearticular; *Ptsp*, postsplenial; *Sp*, splenial.

The *lower jaw* is rather well known in *Eogyrinus* (text-fig. 48) thanks to WATSON's excellent description (1926 a). It differs from the lower jaw of a Loxommid like *Orthosauriscus* chiefly by the presence of large interior mandibular vacuities, separated by a narrow process of the postsplenial.

To summarise, the pattern of dermal bones on the posterior parts of the cranial roof, the structure of the anterior parts of the palate, and the looser attachment of the cheek, clearly indicate that the Anthracosauroids are much less related to the Loxommids and Ichthyostegids than are these two groups to each other. In several characters the Anthracosauroids are more primitive and fish-like than the Ichthyostegids. They have evidently separated very early from the common line of descent of the Ichthyostegids and Loxommids. Expressed in systematics, this means that WATSON's group "*Embolomeri*" can no longer be retained as a systematic unit, and that, as already mentioned above (p. 12) we are forced to place the Anthracosauroids as an independent order: the *Anthracosauria*, probably belonging, as will be shown below, to the line of evolution leading from the fish ancestors of the Tetrapods to the Reptilians.

The *Loxommidae*, which are thus the only Carboniferous Stegocephalians on the same line of evolution as the later *Labyrinthodontia*, accordingly represent a systematic group, co-ordinated with the largest

groups of the higher *Labyrinthodontia*. For this group, which forms a suborder, the name *Loxommoidei* is here introduced.

The curious genus *Otocratia*, described by WATSON (1926 b, pp. 227-229, figs. 5, 6) is probably not nearly related to the *Anthracosauria*. From WATSON's figure it seems most probable that this genus has the Loxommoid type of dermal cranial roof, with a parieto-extrascapular and small lateral extrascapulars. It differs from all Scotch *Anthracosauria*, and agrees with *Cricotus*, and with the Ichthyostegids, by having a rather clear postorbito-dermosphenotic, meeting the fronto-parietal. However, in the anterior part of the palate, *Otocratia* presents, according to WATSON's description, a pronounced similarity to *Pholiderpeton*. And finally it differs both from the *Anthracosauria* and from all Carboniferous Labyrinthodonts, and agrees with the Ichthyostegids, in the very close attachment of the cheeks to the dermal cranial roof. For the present the systematic position of *Otocratia* must be regarded as entirely unknown.

B. Seymouria, and the Reptilia.

In his above-mentioned paper, WATSON (1919 a) argued the opinion, previously expressed also by BROILI (1904, 1913 a, pp. 74—76; cf. also 1927) and WILLISTON (1911 a, b), that *Seymouria* is a primitive Reptile, forming, according to WATSON, a link between the "*Embolomeri*" and the more advanced *Reptilia*. Later on SUSHKIN, in several papers (1925, 1926, 1927, 1928), and PIVETEAU (1926, p. 99) maintained the view that *Seymouria* is, in reality a Stegocephalian, a view that had been already expressed by BROOM (1922, p. 458), and has lately been accepted by SMITH WOODWARD (1932) in ZITTEL's text-book.

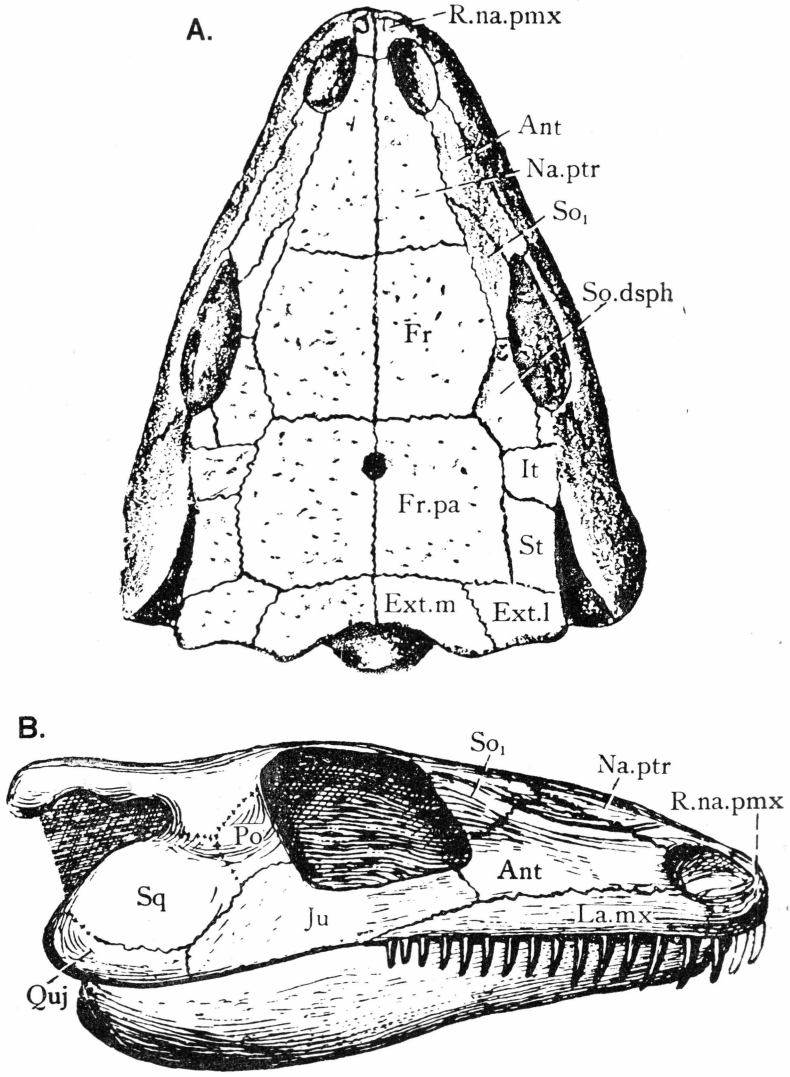
I do not intend to discuss here in detail the structure of *Seymouria*, but a glance at its dermal bones (text-fig. 49 A, B) is sufficient to show the close relationship with a member of the *Anthracosauria*, like *Palaeogyrinus* (text-figs. 41, 46). Each of the dermal bones in *Seymouria* has its undoubted homologon in one bone in *Palaeogyrinus*, and most of the bones have fairly exactly the same shape in the two genera. The discussion of the bone, denoted *So. dsph* (see above, pp. 96—97), applies to *Seymouria* as well as to *Palaeogyrinus*. *Median* and *lateral extrascapulars* (*Ext. m*, *Ext. l*, text-fig. 49 A), beyond doubt homologous to those of the Crossopterygians are also found in *Seymouria*.

The only somewhat important differences from *Palaeogyrinus* in the dorsal side of the skull are the more triangular shape of the snout, with large external nostrils, placed rather close together, and the shorter shape of the posterior parts of the cheeks, and of the region covered by the supraorbito-dermosphenotics, the intertemporals, and the anterior parts of the fronto-parietals, in *Seymouria*.

The very great similarity of the palate of *Seymouria* with that of

the Anthracosauroids will be evident from WATSON's account (1919 a, p. 289) and from pp. 103—104 of the present paper.

In his list of characters in which *Seymouria* has advanced above the "*Embolomeri*", WATSON also enumerates the fact (point 10) that the posterior antorbital ("lachrymal" of WATSON) extends from the orbit



Text-fig. 49. *Seymouria baylorensis* BROILI. A, dorsal; B, lateral aspect of the skull. A, after WILLISTON (1916); B, after WILLISTON (1911 a).

Ant, posterior antorbital; *Ext. l*, lateral extrascapular; *Ext. m*, median extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *It*, intertemporal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Po*, postorbital; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermo-sphenotic; *Sq*, squamosal; *St*, supratemporal.

to the nostril. This condition is said to be "known in scarcely any Temnospondyl". As is now evident, however, this is, on the contrary, a general primitive Tetrapod character, obtained everywhere, when the bone discussed is not excluded from the nostril by a facial part of the anterior antorbital (septomaxillary), or by a secondary meeting of the lachrymo-maxillary and the naso-postrostral, or excluded from the orbit by a likewise secondary meeting of the jugal and the anterior supraorbital.

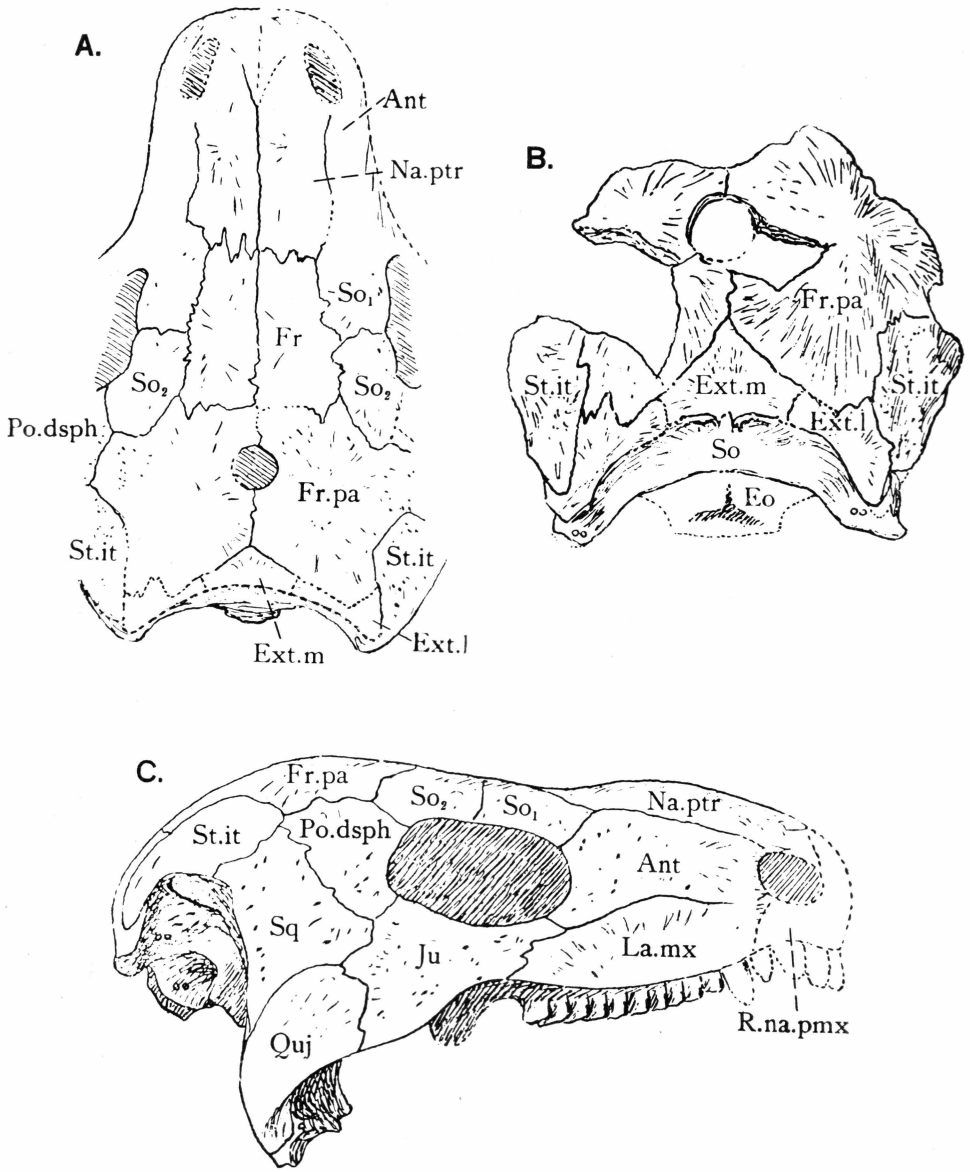
According to SUSHKIN (1925 etc.), the *Seymouriamorpha* cannot be considered as ancestral forms of the Reptiles, owing to the higher degree of specialisation of their stapes. This view of SUSHKIN has as yet not been proved to be false. Therefore, though I am not personally convinced of the correctness of his arguments (cf. also ROMER 1928) the problem of the phylogenetic relations of the *Reptilia* to primitive Stegocephalians cannot for the present be regarded as definitely solved by showing, as I have tried above, that *Seymouria* clearly belongs to the same line of evolution as the *Anthracosauria*.

One of the most important characters, separating the two main lines of evolution of the Tetrapods here discussed — represented by the *Ichthyostegalia-Labyrinthodontia*, and the *Anthracosauria-Seymouriamorpha* respectively — is the different development of the dermal bones in the posterior parts of the cranial roof. Thus the question arises, whether we can find, in any undoubted Reptile, a pattern of dermal bones in the posterior parts of the cranial roof, clearly belonging to any of the two types, represented in the mentioned two lines of evolution.

This is possible in very few cases. In most of those Reptiles, which are at all sufficiently well known, there is no independent supratemporo-intertemporal present at the same time as there are any dermal bones posterior to them and to the fronto-parietals.

In *Diadectes huenei*, however, as figured by BROOM (1914 a, figs. 2, 4; see my text-fig. 50), the most posterior parts of the cranial roof retain a very primitive condition, and a glance at the figure will be enough to recognise at once the anthracosauroid pattern, with a small, even unpaired *median extrascapular* (*Ext. m*, text-fig. 50 A, B) not meeting the *supratemporo-intertemporals* (*St. it*, text-fig. 50), and with broad *lateral extrascapulars* (*Ext. l*, text-fig. 50 A, B), in suture with the posterior margins of the *fronto-parietals* (*Fr. pa*, text-fig. 50).

On the whole, the scheme of the dermal bones, found in *Diadectes*, is very easily comparable to that found in *Cricotus* (text-fig. 43) among the *Anthracosauria*. Like *Cricotus*, the Reptile discussed shows an independent *posterior supraorbital* (*So_2*, text-fig. 50 A, C.) and a *postorbito-dermosphenotic* (*Po, dsph*, text-fig. 50 C). In regard to the other dermal bones of the cheek, which are not well known in *Cricotus*, *Diadectes* is quite similar to, and very easily comparable with both *Seymouria* (text-



Text-fig. 50. The dermal cranial bones of *Diadectes*. A, B, *D. huenei* BROOM, dorsal aspect of imperfect cranial roofs. A. partly restored after B. C, *D. molaris* COPE. Lateral aspect of the skull. After BROOM (1914a).

Ant, posterior antorbital; *Eo*, exoccipital; *Ext. l*, lateral extrascapular; *Ext. m*, median extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Po. dsph*, postorbito-dermosphenotic; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; *So*, supraoccipital; So_1, anterior supraorbital; So_2, posterior supraorbital; *Sq*, squamosal; *St. it*, supra-temporo-intertemporal.

fig. 49 B) and *Palaeogyrinus* (text-fig. 46). The *lachrymo-maxillary* (*La.mx*, text-fig. 50 C) is high and thus clearly shows its lachrymal component; the *posterior antorbital* (*Ant*, text-fig. 50 C) extends from the orbit to the nostril, and meets the *jugal* (*Ju*, text-fig. 50 C) which by its expanded postorbital part is suturated to the postorbito-dermosphenotic, the high *squamosal* (*Sq*, text-fig. 50 C) and the lower *quadratojugal* (*Quj*, text-fig. 50 C).

The development of the palato-quadrate complex (SUSHKIN 1927, pp. 290, 291, fig. 119), the unpaired median extrascapular ("interparietal"), the differentiated dentition, and several other characters clearly show the reptilian or at least not Stegocephalian character of *Diadectes*.

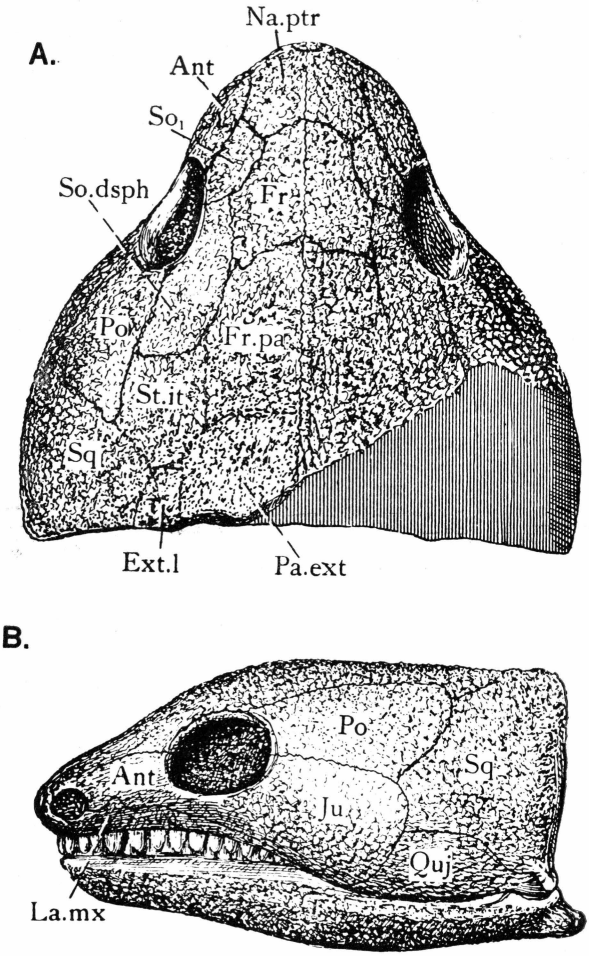
On the assumption that the *Reptilia* really form a monophyletic assemblage, and even if they may only be considered as the descendants of nearly related immediate ancestors, the above considerations are sufficient to prove that all true *Reptilia* have followed the anthracosauroid line of evolution, though, of course, they are not the direct descendants of the *Anthracosauria*. That they are not so, is made probable even by the fact that they show, probably as a primitive character[1]), the original unpaired condition of the median extrascapular, which has become paired in the *Anthracosauria*.

Now, for the present I do not want to discuss more closely the correctness of the commonly accepted view that the *Cotylosauria*, as a whole, stand at the base of the *Reptilia*, connecting the different orders of this large and varied Tetrapod "Class". Anyhow, according to WATSON (1914, p. 170), *Diadectes* "is the typical form" of the group *Cotylosauria*.

However, it has to be pointed out that one form, described as a member of the *Cotylosauria*, *Pantylus*, seems to show a pattern of dermal bones, not referable to the anthracosauroid type. As figured by BROOM (1913 b, fig. 1) and WILLISTON (1916 a, fig. 120; text-fig. 51 of the present paper) *Pantylus* has a dermal cranial roof quite similar to that of an unspecialized Labyrinthodont, such as would be, for instance, an *Archegosaurus* or a Trematosaurid with a short skull, or a *Broiliellus* with the supraorbito-dermosphenotic still meeting the anterior supraorbital. Indeed, if the figures cited are correct (cf. below) the similarity with the Labyrinthodonts is so great that it really seems quite impossible to interpret the dermal bones of *Pantylus* in another way than those of the mentioned Stegocephalians. Thus we find, that according to the mentioned figures *Pantylus* has clear *supraorbito-dermosphenotics* (*So.dsph*, text-fig. 51 A), *supratemporo-intertemporals* (*St. it*, text-fig. 51 A), and, as is especially important, two large *parieto-extrascapulars* (*Pa. ext*, text-fig. 51 A), and two *lateral extrascapulars* (*Ext. l*, text-fig. 51 A), quite

[1]) In other Reptiles, and, most clearly, in the *Mammalia*, the unpaired condition of the "interparietal" would seem to be a secondary character, as it is said to arise from paired primordia (see WATSON 1913 b, p. 70; v. HUENE 1912, fig. 1).

certainly homologous to those of the *Loxommoidei*, and the higher *Labyrinthodontia*. *Pantylus* thus seems to belong to the same line of evolution as the true *Labyrinthodontia* in regard to the structure of its dermal cranial roof. Under such circumstances it seems utterly im-



Text-fig. 51. *Pantylus*. A. dorsal, B. lateral aspect of the skull. After WILLISTON (1916 a).

Ant, posterior antorbital; *Ext.l*, lateral extrascapular; *Fr*, frontal; *Fr.pa*, fronto-parietal; *Ju*, jugal; *La.mx*, lachrymo-maxillary; *Na.ptr*, naso-postrostral; *Pa.ext*, parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; So_1, anterior supra-orbital; *So.dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St.it*, upratemporo-intertemporal.

probable that *Pantylus* should be more nearly related to *Diadectes* and the true *Cotylosauria*. And in fact, there are not many characters which argue in favour of the old view, according to which the Pantyloids are ranged as a suborder of the *Cotylosauria* (as, for instance, in ZITTEL's

text-book 1932). The obliteration of the otic notches, and the vertical position of the quadrate are also found in certain higher *Labyrinthodontia* (cf. the Brachyopids, cf. above p. 58; *Acheloma* CASE 1911, p. 38; BROILI 1913 b, pl. IX, figs. 1, 2). The palate (WILLISTON 1916 a, fig. 22), as far as known, differs in no essential point, except the large size of the internal nares, from that of a primitive Labyrinthodont. The posterior aspect of the cheek, with the high quadrate ramus of the entopterygoid meeting the squamosal, is also quite similar to that in a Labyrinthodont. In the lower jaw there are "two splenial bones", "here for the first time recognized in a reptile" (WILLISTON 1916 a). Concerning the vertebrae it is to be observed that, as WILLISTON wrote (1916 a, p. 174), "the arches are in no way thickened and expanded, as is characteristic of other known Cotylosaur vertebrae. Indeed, so aberrant are the vertebrae of *Ostodolepis*[1]) for a Cotylosaur that I referred them unhesitatingly to the Theromorpha" (cf. below).

SUSHKIN (1928), when discussing the relations of *Captorhinus*, also states of *Pantylus* (p. 277), inter alia, that "unfortunately the condition of the paroccipital bar and its relation to the tabular or squamosal are unknown". The only characters, connecting *Pantylus* with *Captorhinus* and other *Cotylosauria*, except the large internal nares, seem to be the "relations of the stapes and the quadrate" and the "relief" of "the articular end of the mandible". However, until we have any clear figures showing the mentioned characters, it seems impossible to undertake a closer discussion of their significance. — It also ought to be pointed out, however, that the sutures of the critical region of the dermal cranial roof of *Pantylus* are apparently not quite certainly determined. The figure of WILLISTON (my text-fig. 51) does not agree well with that given by BROOM, and in both the discussed sutures are marked with dotted lines only.

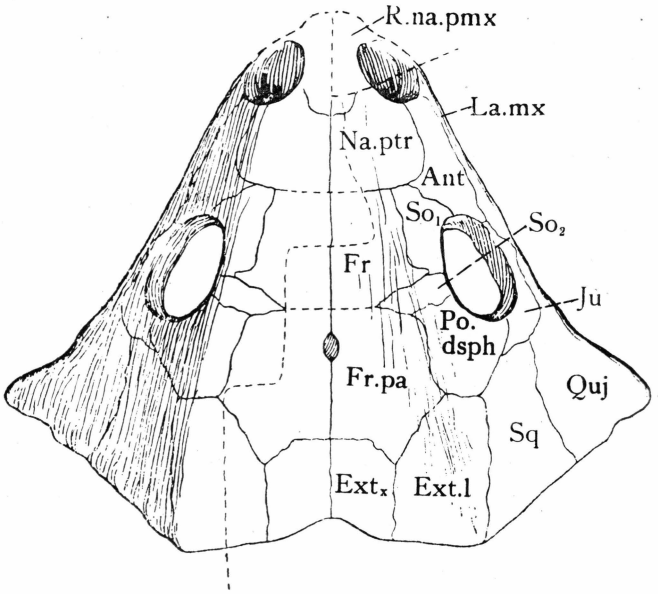
Now the question arises, whether perhaps still other so called *Reptilia* may be interpreted as belonging to the same line of evolution as the *Labyrinthodontia*.

For all those groups, in which there occurs a more or less triangular, unpaired, and usually small "interparietal" (which probably always represents a median extrascapular) a descent from the same type as *Diadectes* seems more probable. Such groups are, for instance, the Theromorphs (WATSON 1931, text-fig. 1; BROOM 1913 a, figs. 8, 17; HAUGHTON 1929, figs. 13, 20; PARRINGTON 1934, text-fig. 1), the *Eosuchia* (*Youngina*, BROOM 1914 b, text-fig. 1; 1925, text-fig. 2), the *Parasuchia* (*Machaeroprosopus*, CAMP 1930, fig. 29), the *Pseudosuchia* (*Euparkeria*, BROOM 1913 d, pl. LXXVI, fig. 6), the *Crocodilia* (young *Alligator*, MOOK 1921), also the *Mammalia* (v. HUENE 1912, pp. 522—524), and probably the

[1]) The isolated vertebrae of *Pantylus* had been earlier described by WILLISTON as "*Ostodolepis*" (WILLISTON 1913 a).

Captorhinidae (*Captorhinus isolomus*, SUSHKIN 1928, fig. 1; cf. however *Captorhinus aguti*, SUSHKIN 1928, figs. 2, 3).

In the Pareiasaurids there are according to WATSON's description and figure (1914 a, p. 163, text-fig. 4; my text-fig. 52) two large "postparietals" (Ext_x, text-fig. 52) between the "tabulars", or lateral extrascapulars (*Ext. l*, text-fig. 52). These "postparietals" may be interpreted as parieto-extrascapulars, but the uncertainty as to the fate of the supratemporo-intertemporals makes any interpretation quite hypothetical.



Text-fig. 52. Pareiasaurid skull. Dorsal aspect. After WATSON (1914 a). *Ant*, posterior antorbital; Ext_x, median extrascapular or parieto-extrascapular; *Ext. l*, lateral extrascapular (possibly with supratemporal and intertemporal components); *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Po. dsph*, probably postorbito-dermosphenotic; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; So_2, posterior supraorbital; *Sq*, squamosal.

Moreover the excellent recent work by BOONSTRA (1933) shows that at least most of the *Pareiasauria* have skulls with unpaired, often rather small "postparietals" (see BOONSTRA 1933, pl. II). Thus the bones in question may equally well be only occasionally enlarged median extrascapulars, homologous to those of the *Anthracosauria*. This latter interpretation seems to be the more acceptable one for the likewise paired"postparietals" of *Captorhinus aguti* (SUSHKIN 1928; cf. also above, pp. 111—112).

On the whole much work remains to be done on the groups, included in the "*Cotylosauria*" before we can get even a very general idea of

their interrelationships. However, I regard it as a more established fact that at least the *Diadectids* belong to the Anthracosauroid line of evolution. *Pantylus* probably belongs to the other line, the one also represented by the *Labyrinthodontia*. For the present it seems at least most probable that most of the *Reptilia* followed the same line as the Diadectids, and that, consequently, *Pantylus* must be regarded, not as a true Reptile, but as a specialized descendant of very primitive forms, belonging to the line of evolution of the *Ichthyostegalia-Labyrinthodontia*.

Thus the class "*Reptilia*" in the old sense is probably a polyphyletic group, and it has to be pointed out that even if *Pantylus* is excluded it is quite possible that the remaining "*Reptilia*" do not represent a monophyletic assemblage.

5. Conclusions.

In the preceding parts of the present paper I have tried to trace the fates of the dermal bones of the primitive *Choanata* in the two series of evolution, represented, one by the *Ichthyostegalia-Labyrinthodontia*, the other by the *Anthracosauria-Seymouriamorpha* and most probably also the majority of the *Reptilia*.

All the more closely examined members of these two lines of evolution present the primitive condition of the dermal skull-bones, expressed in the old term "*Stegocephalia*": the dermal bones of the cranial roof and cheeks have a superficial position, and form a continuous bony coating of the skull, with openings only for the orbits, the nostrils, and the pineal foramen (sometimes also with an interrostral fenestra, cf. above, pp. 23—32). In such a continuous bony coating the different elements can, of course, not easily change their positions and relations to each other; and owing to this fact the pattern of dermal bones is more uniform and easy to analyse in the discussed groups than in the higher Tetrapods.

None the less changes do occur also in the groups, here dealt with, and these changes are chiefly of two cathegories:

1. changes in the number and position of the dermal bones;
2. changes in the proportions of whole regions.

The changes in the number of dermal bones are most often reductions, but in two cases an increased number arises in the evolution by a division of a median, originally unpaired bone. Thus the unpaired median interrostral becomes divided into a pair of bones in the *Loxommoidei*, and the originally unpaired parieto-extrascapular of the *Ichthyostegalia* becomes paired at the transition to the *Loxommoidei*.

When analysing the cases of reductions of the number of dermal bones, we find that they can be referred to three types:

1. Often the space covered by two independent dermal bones in one form, is covered by one dermal bone only in a closely related form. Such is, for instance, the case with the posterior supraorbital and dermosphenotic in *Trimerorhachis*, and the supraorbito-dermosphenotic in *Broiliellus* (cf. above pp. 45—51, text-fig. 8). Here a fusion has evidently taken place between two originally independent elements.

2. In other cases the space occupied by an independent dermal bone in one form is occupied in a related form by parts of several of the neighbouring bones. This is the case, for instance, with the dermosphenotic in *Loxomma* and *Baphetes* (cf. above pp. 17—19); and this may most naturally be interpreted as a reduction finally leading to a total disappearance of the bone in question.

3. Finally there occur forms with reduced number of dermal bones, not so nearly related to any known forms with a fuller number, that it is possible to state whether we have to do with a fusion or with a reduction. This is, for instance, the case with the dermosphenotic in *Lydekkerina* (text-fig. 12).

In the changes of position of certain dermal bones orthogenetic "evolutionary trends"[1]) seem to be recognisable, apparently occurring independently in parallel phyletic series. Thus there is a general tendency towards a reduction of the posterior antorbital, which loses its contact with the orbit and the external naris, and gradually becomes more and more distant from these openings. This process is recognisable in the *Labyrinthodontia*, the *Anthracosauria*, the recent *Lacertilia* (GAUPP 1910, p. 540) and is completed in the *Aves* and the *Mammalia*, where the posterior antorbital seems to be totally lost (cf. below and GAUPP 1910, p. 541). It is followed by an expansion and migration of the anterior supraorbital, which sends down a process to meet the jugal in front of the orbit, and finally shifts its position from the dorsal to the anterior margin of the orbit.

Certain changes in the relative length of the different parts of the dermal cranial roof, and in the general proportions of the skull, also present distinct evolutionary trends in the series *Ichthyostegalia-Labyrinthodontia*. The two most prominent of these evolutionary trends are:

1. A general shortening of the nuchal division of the dermal cranial roof (cf. SÄVE-SÖDERBERGH 1932, text-figs. 2 or 11, and text-figs. 3, 8 and 16 of the present paper);

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[1]) Cf. WATSON 1919 b; 1926 ; 1931, p. 1202.

2. A general flattening of the skull, which is high in the *Ichthyostegalia* but becomes flatter in the different lines of evolution of the higher *Labyrinthodontia*.

The general tendency towards a flattening of the skull has already been emphasized and discussed by WATSON (1919 b, pp. 50—51) who also pointed out the trends leading to an increase in size of the interpterygoid vacuities and a reduction in length of the quadrate ramus of the entopterygoid.

In all my homologisations, in this as in my earlier papers (1932, 1933), I have employed the terminology for the dermal bones of the head, introduced for Crossopterygians and Actinopterygians by STENSIÖ (1921, 1922 etc.). For this I have two reasons, 1st the homologisations with the dermal bones of the Fishes could be made only on the basis, furnished by the above-mentioned papers of STENSIÖ, 2nd apart from STENSIÖ's nomenclature there is at present only one other, based upon distinct definitions, viz. the nomenclature of the human anatomy. And this latter could, of course, not be employed, i. a. because there are as yet too many questions unsolved in the phyletic development of the dermal bones, from the early Tetrapods, discussed by me, up to Man. However, the fixed human terminology has a clear priority over that of STENSIÖ, and it is not likely to be abandoned in favour of a more phyletic nomenclature, expressing the derivation of the products forming the dermal bones of Man. On the other hand, for several reasons, the human nomenclature is not suitable for use in comparative anatomy, which must try to express the phyletic morphological importance of the organs described.

Thus we will have to admit the use of two nomenclatures: the old nomenclature of human anatomy, and a new nomenclature of comparative anatomy. And the latter evidently has to follow the evolution, beginning with primitive Choanate Fishes, and then expressing, in the Tetrapods, what corresponds to the primordia inherited from the Fish ancestors. For this purpose STENSIÖ's nomenclature is provisionally used, but must in future be at least partly replaced by another, 1st, because it uses terms from human anatomy, and, as I will show below, for quite other bones than those homologous to the bones of the same names in Man, 2nd, because the greater knowledge we now possess of the primitive *Choanata* shows that there were originally more bones than those distinguished by STENSIÖ's nomenclature in the Crossopterygians (e. g. there were originally at least two pairs of parietals; and the products of fusion should of course be differently termed if there enters in these an anterior or a posterior parietal component). However, before fixing a definite nomenclature for the dermal bones of the *Choanata*, we must, as I have already before pointed out (1933, p. 9), get a still

fuller knowledge of the original number of dermal bones in the group. We especially need an investigation of the great group of the *Choanata* represented by the *Dipnoi.*

In what following I will try to compare the nomenclature used by STENSIÖ and myself with the bone names, commonly used in the earlier literature on Tetrapods, partly also with the nomenclature of the human anatomy.

Such a comparison has never before been carried out except for a few of the dermal bones. In STENSIÖ's work of 1921 (pp. 143—146) one finds remarks on the homologies in Stegocephalians of the intertemporals, the median extrascapular, the dermosphenotics, the posterior supraorbitals, the premaxillaries, the rostrals, the nasals, the interrostrals, the squamosals, the preoperculars, the quadratojugals, the jugals, the lachrymals, and the postorbitals. However, the rather scanty knowledge of the earlier Stegocephalians in 1921 — when the *Ichthyostegalia* were unknown, the *Loxommoidei* and *Anthracosauria* very fragmentarily known — made it quite impossible to find the correct homologies in several cases. The important correct homologisations made by STENSIÖ are, the parallelisation (at least for certain forms) of the so-called postfrontal with a dermosphenotic + a posterior supraorbital, of the so-called premaxillary with a premaxillary + rostrals + a nasal component, of the so-called nasal with nasals + postrostrals, and finally the mainly correct homologisation of the squamosals and quadratojugals, in opposition to the more phantastic theories, advanced by BAUR (1896, p. 662), and GREGORY (1915), and partly accepted by MOODIE (1908, pp. 536—538) and ALLIS (1898, pp. 442—444; 1919 b).

The earlier attempts at homologisations, referred to by STENSIÖ in 1921 (ALLIS 1898, 1899, 1919 a, b; BAUR 1896; GOODRICH 1919; GREGORY 1915; MOODIE 1908; POLLARD 1892; WATSON and DAY 1916; WOODWARD 1898) are all either very incomplete, or very incorrect or both incomplete and incorrect. The positive correct results are only the identifications of the supratemporo-intertemporals (so-called "squamosals") by three and of the postorbitals by most of the mentioned authors (BAUR 1896, MOODIE 1908, ALLIS 1919 b — POLLARD 1892, WOODWARD 1898, MOODIE 1908, WATSON and DAY 1916), and especially an, at least mainly, correct homologisation of the jugals, postorbitals, squamosals, and quadratojugals by WOODWARD (1898), and the recognition of rostral ("ethmoid") components in the Tetrapod "premaxillaries" (ALLIS 1898).

Of later publications dealing with the problems here discussed, the three most important are those by WATSON (1926 a), GOODRICH (1930), and SALOMON (1930).

SALOMON only discusses the homologies of the so-called "lachrymal"

and "prefrontal" of *Amniota*, but his paper is important since he seems to have correctly identified the "lachrymal" with the posterior antorbital ("l'os qui se trouve au bord antérieur de l'orbite chez les Poissons nommés" — i. e. the *Osteolepidae*), and the "prefrontal" with an anterior supraorbital ("quant au préfrontal, c'est — bien probablement — l'homologue de l'os qui est situé au bord antéro-supérieur de l'orbite chez les mêmes Poissons" SALOMON 1930, p. 153).

WATSON's paper (1926 a) is important as confirming WOODWARD's homologisation (1898, cf. above) of the dermal bones of the cheek, except the lachrymal of *Osteolepis*, which he erroneously identified with the so-called "lachrymal" (posterior antorbital) of the lower Tetrapods. However, the chief importance of WATSON's paper lies, not in the very fragmentary discussion of the dermal bones of the cranial roof and cheeks, but in the elaborate study and comparison of the palate and lower jaw in Crossopterygians and Tetrapods. In this respect it is of fundamental importance.

Finally GOODRICH, in 1925, and in his otherwise excellent book of 1930, made a rather unfortunate attempt at a "diagram of fundamental plan of roofing-bones of skull in *Pisces*", by which he was misled in certain of his homologisations. He repeated WATSON's error concerning the lachrymal, confirmed WOODWARD's and WATSON's homologisations of the other cheek-bones, and, as is most important, took a step in the direction towards a correct analysis of the posterior bones of the dermal cranial roof by recognising the original *five* bones in the extrascapular series (1930, p. 312, fig. 290, "tabulars", "postparietals", "dermal supraoccipital").

The most important of the new points brought forward in my earlier paper (1932), and in the present paper, are the homologisations: (1) of the Tetrapod "frontals" with an anterior pair of frontals of a primitive Choanate, and, accordingly, with the anterior halves only of the Crossopterygian frontals, (2) of the "parietals" of the *Labyrinthodontia* with the posterior pair of frontals + the anterior pair of parietals of a primitive Choanate, *i. e.* with the posterior halves of the Crossopterygian frontals + the anterior (halves of the) Crossopterygian parietals, (3) of the "parietals" of the groups, belonging to the line *Anthracosauria-Seymouriamorpha* with the posterior pair of frontals + both pairs of parietals of a primitive Choanate — and with the posterior halves of the Crossopterygian frontals and the whole of the Crossopterygian parietals, (4) of the "postparietals" of the *Labyrinthodontia* with the posterior pair of parietals + the median extrascapular + the medial pair of lateral extrascapulars of a primitive Choanate = the posterior (halves of the) parietals + the median extrascapular + the medial halves of the lateral extrascapulars of a Crossopterygian, (5) of the "postparietals" of the groups on the line *Anthracosauria-Seymouriamorpha* with the median extrasca-

My terminology	Commonly used terms in the earlier literature on Tetrapods
Naso-rostro-premaxillary Naso-rostro-interrostro-premaxillary	Premaxillary
Interrostral	Internasal
Naso-postrostral Naso-postrostro-interrostral	Nasal
Median postrostral	Interfrontal
Frontal	Frontal
Anterior antorbital	Septomaxillary
Posterior antorbital	Lachrymal, or Adlachrymal, or Postnasal
Anterior supraorbital	Prefrontal, or Lachrymal
Posterior supraorbital Supraorbito-dermosphenotic	Postfrontal
Dermosphenotic	Intertemporal
Fronto-parietal	Parietal
Parieto-extrascapular Median extrascapular	Postparietal, Dermosupraoccipital
Supratemporo-intertemporal	Supratemporal, Squamosal, Suprasquamosal
Lateral extrascapular	Tabular
Lachrymo-maxillary	Maxillary
Jugal	Jugal
Postorbital Postorbito-dermosphenotic	Postorbital
Squamosal	Squamosal, Prosquamosal, Paraquadrate (Supratemporal)
Quadratojugal	Quadratojugal
Vomer	Prevomer, Vomer
Dermopalatine	Palatine
Ectopterygoid	Transverse, Ectopterygoid
Entopterygoid	Pterygoid
Parasphenoid	Parasphenoid

pular of a primitive Choanate and of the Crossopterygians, (6) of the "tabulars" of the *Labyrinthodontia* with the lateral pair of lateral extrascapulars of a primitive Choanate = the lateral halves of the Crossopterygian lateral extrascapulars, (7) of the "tabulars" of the groups on the line *Anthracosauria-Seymouriamorpha* with both pairs of lateral extrascapulars of a primitive Choanate and with the lateral extrascapulars of

the Crossopterygians, (8) of the Tetrapod "postfrontals", partly with posterior supraorbitals, partly with dermosphenotics + posterior supraorbitals of Fishes, (9) of the so-called "intertemporal" of *Labyrinthodontia* with the dermosphenotic of Fishes, (10) of the Tetrapod "maxillary" with the Crossopterygian lachrymal + the Crossopterygian maxillary, (11) of the Tetrapod septomaxillary with the anterior antorbital of Crossopterygians.

The table given on p. 118 will illustrate the result of a comparison of the earlier most commonly used terms for the Tetrapod dermal bones with the terminology used by me.

The bones of the lower jaw have been denoted according to the common nomenclature already used both for Fishes and for Tetrapods.

As is evident from the table given above, several of the older Tetrapod terms were used in different forms for bones of different morphological importance. Thus the term postfrontal was used for a bone at the postero-dorsal corner of the orbit, irrespective of its fusion or nonfusion with the dermosphenotic (cf., for instance, *Trimerorhachis* and *Broiliellus*, text-fig. 8).

Certain of the dermal bones deserve a few additional remarks. Some of them are — more or less easily — recognisable throughout the series of *Tetrapoda* up to the *Mammalia*.

That the so-called "nasals" of most *Tetrapoda* include both nasal and postrostral components seems quite clear since this is the case in all primitive *Tetrapoda*, and the bones in question meet in the median line also in all typical younger *Tetrapoda*, that is, when there is not a secondary opening for glands, as in *Molge* (Parker, Reynolds 1913, fig. 36), or a general reduction in the degree of ossification, as in *Rana* (Ecker-Wiedersheim-Gaupp 1896, figs. 13, 15).

The anterior supraorbital is the bone, called "prefrontal" in the *Tetrapoda* by the majority of more modern students of vertebrate paleontology (*i. a.* Watson 1926 a; Goodrich 1930; Smith Woodward 1932; Branson and Mehl 1929; also Reynolds 1913), but "lachrymal" by several, mainly German authors (see Gaupp 1898, p. 14; 1906, p. 850; 1910; Jaekel 1905; Abel 1919, Wiman 1917, fig. 1) and "supralachrymal" by Salomon (1930, p. 182). According to the most recent investigation, that of Salomon (1930), the discussed bone — the anterior supraorbital — is clearly homologous with the "lachrymal" of the *Mammalia*, as first suggested by Gaupp (*l. c.*). Thus there are not less than three different and not homologous bones, termed lachrymal by different authors: 1. the Mammalian "lachrymal", which by the right of priority has to be called so, and is the homologon of the Reptilian "prefrontal", according to the usual English terminology, and of the anterior supraorbital of the Crossopterygians; 2. the "lachrymal" of the

Crossopterygians, which has the advantage of being well defined by its relation to the anterior half of the horizontal portion of the suborbital part of the infraorbital canal — and enters into the composition of the so-called "maxillary" of the Tetrapods; 3. the "lachrymal" of the usual terminology for Reptilians, — which bone is the homologon of the posterior antorbital of the Crossopterygians, and seems to be lacking in Mammalians. This third sort of "lachrymal", though perhaps the one for which this name is most widely used, lacks any terminological right of being so-called. It has also been termed adlachrymal (GAUPP 1910, p. 555) or postnasal (JAEKEL 1905).

The existence of a lachrymal component (in the sense of the nomenclature used by me) in the so-called maxillary of *Amniota* is further illustrated by the presence of the characteristic high facial part of this bone, as especially typically seen for instance in certain *Cotylosauria* (WATSON 1914 c, text-fig. 2 B; also in the *Pareiasauria*, BOONSTRA 1933, pl. I), in the Theromorphs (WATSON 1914 b, text-fig. 1; 1920, figs. 2, 11; 1921, text-figs. 5, 8, 15, 17, 21 A, C, 25, 28 A; 1931, text-fig. 2), in *Grippia* (WIMAN 1928, 1933), in *Lacertilia* (*Varanus*, REYNOLDS 1913, fig. 50; *Lacerta*, GAUPP 1910, fig. 1), in *Crocodilia* (*Caiman*, REYNOLDS 1913, fig. 70), in *Rhynchocephalia* (*Sphenodon*, REYNOLDS 1913, fig. 80; v. ZITTEL 1890, fig. 525), in *Mammalia* (*Canis*, REYNOLDS 1913, fig. 102; *Thylacinus*, ibid., fig. 119; *Moeritherium*, ibid., fig. 125; *Gorilla*, ibid., fig. 131; *Homo*, RAUBER-KOPSCH 1911, figs. 160, 161; cf. LE DOUBLE 1906, pp. 166—306).

II. THE EOTRIASSIC STEGOCEPHALIANS OF EAST GREENLAND

1. Material and methods.

The material of *Labyrinthodontia* described in the present publication was collected by Mr. E. NIELSEN and his assistants during the summer expeditions of 1932 and 1933, and the wintering of 1932—1933. It consists of one practically complete skull No. *At.* 1, and fragments of skulls and other parts, numbered *At.* 2—*At.* 38. Most of the skulls are preserved as natural internal casts of the dermal cranium, with the endocranium, at least sometimes, in situ. When the internal casts are not eroded to any important extent, it is a very easy task to trace the sutures of the dermal bones. When, on the contrary, such a cast is eroded, it may be quite impossible to follow the course of the sutures. The same rules apply to a few fragments, representing parts of external casts of the dermal bones (Nos. *At.* 17, *At.* 23).

When (as is especially the case in No. *At.* 1) the bony substance is left, the use of alcohol, and especially of xylol — with illumination from a Pointolite Lamp, or a Monla Lamp (Reichert) — is very suitable for showing the radiate structure of the dermal bones, and the sutures between them. In these cases one may, of course, always be fairly certain of not committing any major errors in tracing the boundaries of the dermal bones — though it may sometimes be rather difficult to find out the minute course of the often very deeply interlocked sutures.

For the purpose of getting clear photographs, one is forced to trace out the sutures in black, and sometimes for the sake of clearness it is necessary to give a more uniform colour to the bony substance or the matrix, both of which may present a very irregularly coloured surface, owing to weathering etc. Generally the preserved parts of bony substance are more or less pure white in colour, at least after exposure to the air, but when just cleaned of the matrix they may be dark brown; and in specimen No. *At.* 1 they are light brown.

Generally the skulls are not much affected by pressure or crushing; this good state of preservation probably depends upon the fact that the

fossils were embedded in nodules, harder than the surrounding clayey matrix.

As usual, for clearing away the matrix the special dental mallet of Doctor H. ARNELL has been used. It hardly needs to be especially pointed out that all work on the present material was carried out with binocular microscopes.

2. Description of the material.

Suborder Capitosauroidei.

Superfamily Capitosauroideae.

Family Wetlugasauridae.

Wetlugasaurus RIABININ.

Wetlugasaurus groenlandicus n. sp.

(Pls. 1, 2; text-fig. 53).

Diagnosis: Posterior parts of dermal cranial roof mainly as in *Wetlugasaurus angustifrons* RIABININ; but length of orbits shorter than median length of the fronto-parietals and shorter than the distance from the pineal foramen to the posterior margin of the skull-roof. Postorbitals with long sutures towards the squamosals. The parts of the entopterygoids and parasphenoid, joined by suture to each other, forming bars with parallel sides between the interpterygoid fenestrae and the otic notches.

Holotype. Specimen *At.* 2: A natural internal cast of the posterior parts mainly of the right half of a skull, preserved as far forward as just in front of the orbit.

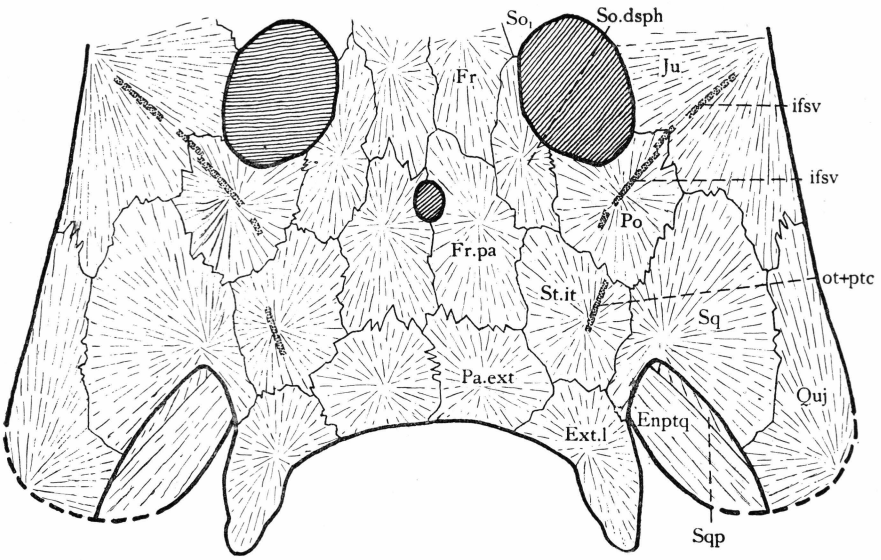
Cotype. Specimen *At* 17: The impression of the imperfect posterior parts of a dermal cranial roof, preserved just as far forward as the type specimen.

The dermal bones at present exposed, or the moulds or impressions of which are preserved in these specimens include: in the type specimen, the most posterior parts of both frontals and of the right anterior supraorbital; the right supraorbito-dermosphenotic; the most medial parts of the left, and the whole right fronto-parietal and parieto-extrascapular; the right supratemporo-intertemporal; most of the right lateral extrascapular; the posterior half of the right jugal; the right squamosal and quadratojugal; the right entopterygoid; and the posterior parts of the parasphenoid; — in the cotype, the most posterior parts of the frontals and of the anterior supraorbitals; the supraorbito-dermosphenotics; the fronto-parietals; the parieto-extrascapulars; the whole left and most

of the right supratemporo-intertemporal; the left lateral extrascapular and the most medial part of the right one; the postorbitals; most of the posterior two thirds of the left and a small part of the right jugal; the whole left squamosal and an antero-medial fragment of the right one; and most of the left quadratojugal.

Description.

General shape. As will be evident from the figures, the preserved fragments must have belonged to depressed skulls with very short and



Text-fig. 53. *Wetlugasaurus groenlandicus* n. sp. Posterior part of the skull in dorsal view. About $\frac{2}{3}$ natural size.

Enptq, quadrate ramus of the entopterygoid; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *Sqp*, posterior lamina of the squamosal; *St. it*, supratemporo-intertemporal; *ifsv*, vertical portion of the suborbital part of the infraorbital canal; *ot+ptc*, otic part of the infraorbital canal and probably also postotic canal.

broad posterior parts; with small, somewhat elongated orbits, situated near the median line of the skull; with extremely short postorbital, short prenuchal, and medium-sized nuchal divisions of the dermal cranial roof. More exactly, the dimensions are as shown in the following table (measurements mostly from the cotype):

Median length of the part, preserved in the type specimen . .	52 mm
Median length of the part, preserved in the cotype	50 mm
Restored maximum breadth of the skull (type specimen)	55 mm
Restored maximum height of the skull (type specimen)	18 mm
Length of the orbit	20 mm

Breadth of the orbit	14 mm
Length of postorbital division	about 6 mm
Length of prenuchal division	11 mm
Length of nuchal division	12 mm

Dermal bones of the cranial roof and cheeks. The preserved most posterior parts of the impressions of the *frontals* (*Fr*, pl. 1, fig. 1; pl. 2, fig. 2; text-fig. 53) show that these bones reached as far back as the posterior halves of the orbits. In the type specimen (internal side of the skull-roof) the left frontal was evidently a little farther back than the right one, and its sharply sigmoid posterior margin was joined by suture with, and overlapped both fronto-parietals. The right frontal overlapped the left one along a very gently sigmoid median suture, and also had a sharply sigmoid posterior margin, joined by suture with and partly overlapping the right fronto-parietal. Laterally the posterior parts of the right frontal met the anterior half of the supraorbito-dermosphenotic in a nearly straight suture, and the anterior supraorbital in a gently curved suture. In the cotype (external side of the skull-roof) the posterior margins of the frontals are less strongly curved than in the type specimen.

The impressions of the *anterior supraorbitals* (*So*$_1$, pl. 1, fig. 1; pl. 2, fig. 2; text-fig. 53) show that each of these bones had a gently concave postero-lateral margin, towards the orbit, and an irregularly curved medial suture towards the frontal and the supraorbito-dermosphenotic.

The long *supraorbito-dermosphenotic* (*So. dsph*, pl. 1, fig. 1; pl. 2, fig. 2; text-fig. 53) formed by far the greatest part of the medial margin of the orbit. It met the anterior supraorbital in a short, more or less strongly curved suture, and had a long, gently convex medial margin, joined by suture to the frontal and the fronto-parietal. It also had a short posterior margin with an interlocked suture towards the supratemporo-intertemporal; and a considerable part of its lateral margin was joined by suture to, and overlapped by the postorbital.

Each of the *fronto-parietals* (*Fr. pa*, pl. 1, fig. 1; pl. 2, fig. 2; text-fig. 53) evidently had a roughly quadrangular shape, with a narrower anterior, and a broader posterior half. Its irregularly bent anterior margin was joined by suture to the frontal, and overlapped by the frontal; the left fronto-parietal was overlapped by the left frontal, whereas the right fronto-parietal was overlapped both by the left and the right frontal. In the middle or anterior third of the nearly straight median suture between the fronto-parietals is the pineal foramen, mainly circular in shape, but with an angular anterior margin in the type specimen. At its strongly sigmoid posterior margin

the right fronto-parietal of the type specimen was overlapped for a short stretch by the left parieto-extrascapular, met the median half of the anterior margin of the right parieto-extrascapular, and finally overlapped the lateral half of the same margin. In specimen *At.* 17 the posterior margins of both fronto-parietals were evidently joined to the anterior margins of the parieto-extrascapulars by interlocked zig-zag sutures, and here the left fronto-parietal was joined to both parieto-extrascapulars, but the right one only to the right parieto-extrascapular. The lateral margin of each fronto-parietal consisted of an anterior, slightly concave part, and a posterior slightly sigmoid or mainly convex one; the anterior part of this margin met the medial margin of the supraorbito-dermosphenotic in a finely crenulated suture, the posterior part was overlapped by the supratemporo-intertemporal. Evidently the centre of development of the fronto-parietal was close to the mid-point of the bone, and a little farther back than the pineal foramen.

The impressions of the right *supratemporo-intertemporals* (*St. it*, pl. 1, fig. 1; pl. 2, fig. 2; text-fig. 53) have a fairly characteristic shape forming a very elongated hexagone with four long concave or slightly sigmoid sides, the medial, the antero-lateral, the postero-lateral, and the postero-medial, whereas the fifth, posterior, side is very short, and the sixth, anterior, is still shorter especially on the ventral side of the bone (spec. *At.* 2). When the bone was still in situ it accordingly had six margins; one medial, overlapping the fronto-parietal; one anterior, meeting the supraorbito-dermosphenotic; one antero-lateral, overlapped by the postorbital; one postero-lateral, overlapping the squamosal; one posterior, overlapping the lateral extrascapular; and one postero-medial, overlapping the parieto-extrascapular. The centre of development was just in front of the posterior third of the bone. On the whole, the ventral surface of the bone (spec. *At.* 2, pl. 1, fig. 1) is markedly narrower than the dorsal one (spec. *At.* 17, pl. 2, fig. 2). The latter is shown in the cotype to have a groove (*ot* + *ptc*; pl. 2, fig. 2; text-fig. 53) for the otic part of the infraorbital canal, and probably also for the postotic canal.

The roughly hexagonal dorsal lamina of the right *parieto-extrascapular* of the type specimen (*Pa. ext*, pl. 1, fig. 1; cf. pl. 2, fig. 2; text-fig. 53) had a median margin, partly overlapped by that of the left parieto-extrascapular, a short antero-medial margin meeting the right fronto-parietal, which bone also overlapped the medial half of the antero-lateral margin of the parieto-extrascapular. The other half of this margin, as well as the main part of the short lateral margin was overlapped by the supratemporo-intertemporal, whereas the most posterior part of the lateral margin was overlapped by the lateral extrascapular, and the postero-lateral margin met that bone in a finely inter-

locked suture. Finally the parieto-extrascapular had a gently concave posterior margin, and a ventral process (*Pa. extv*, pl. 2, fig. 1), originating from the postero-lateral quarter of the bone, just behind and very slightly laterally to the centre of development of the bone.

The impression of the dorsal surface of the left parieto-extrascapular of spec. *At.* 17 (*Pa. ext*, pl. 2, fig. 2) agrees well in shape with the ventral impression of the right one in the type specimen. On the whole the sutures of the bone discussed are evidently more interlocked on the dorsal surface.

In most facts the impression of the right parieto-extrascapular of spec. *At.* 17 agrees with that of the other side, but evidently the right bone differed from the left one by having a very short antero-medial margin, in suture with the fronto-parietal of the other side of the skull. An analogous difference is found between the two parieto-extrascapulars of the type specimen, though in this case it was the left bone that met the fronto-parietal of the opposite side.

The impression of the dorsal lamina of the right *lateral extrascapular* of the type specimen (*Ext. l*, pl. 1, fig. 1, text-fig. 53) is incompletely preserved in the most lateral and posterior parts, and there is a matrix-filled fissure, a few millimetres broad across the posterior part. None the less it is evident that the bone was of the type generally met with in the Capitosauroids, with a considerable part postero-medially to the otic notch. The anterior part of the bone had a nearly straight antero-medial margin, meeting the parieto-extrascapular in its main part, but overlapped by that bone most anteriorly, and also overlapped by the supratemporo-intertemporal; and a roughly straight antero-lateral margin, joined by suture to the supratemporo-intertemporal and the squamosal.

Viewed ventrally (pl. 1, fig. 2) and posteriorly (pl. 2, fig. 1) the type specimen shows the well preserved ventral or ventro-medial process of the right lateral extrascapular (*Ext. lv*, pl. 1, fig. 2; pl. 2, fig. 1). This process meets the exoccipital in a deeply interlocked suture. As already suggested by STENSIÖ (1921, p. 141), the "opisthotic" of WIMAN'S descriptions of the Spitsbergen Stegocephalians (WIMAN 1914, 1916, 1917) is clearly identical with the ventral process of the lateral extrascapular (tabular).

In specimen *At.* 17 much more is exposed of the smooth ventral surface of the left lateral extrascapular (*Ext. l*, pl. 2, fig. 2), including the most dorsal part of the ventral or ventro-medial process (*Ext. lv*, pl. 2, fig. 2). In front of this process there is a cup-shaped depression in the ventral surface, bounded postero-laterally by a vertical lamina, continuous with the ventral process. The postero-lateral side of the process mentioned has a marked vertical groove, leading to a shallow

depression in the ventral surface of the lateral extrascapular, postero-laterally to the process. Otherwise the thick posterior part of the lateral extrascapular, posterior and laterally to the otic notch, shows a gently sigmoid, mainly convex lateral margin, a rounded posterior end, and a gently convex postero-medial margin.

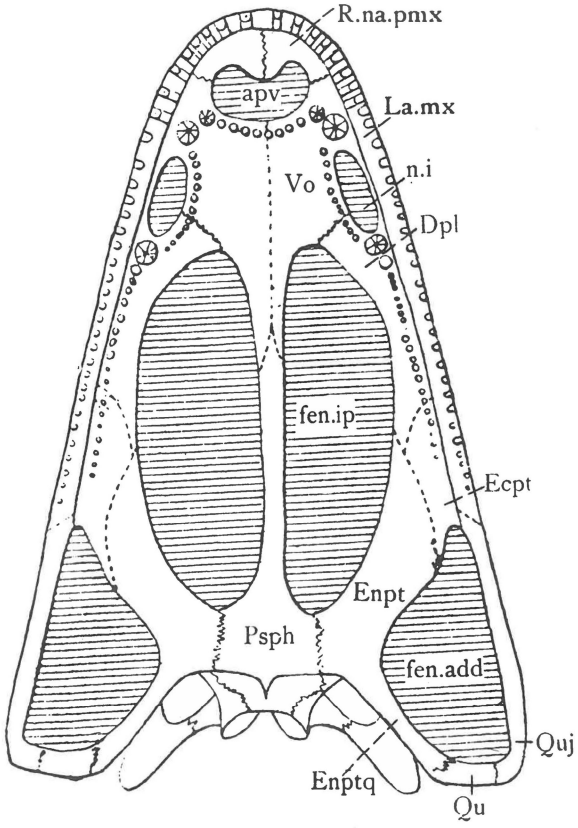
The posterior part of the *jugal* (*Ju*, pl. 1, fig. 1; pl. 2, fig. 2; text-fig. 53) formed the main part of the lateral margin of the orbit, and was further bounded by a probably slightly curved ventral margin, a postero-lateral margin with a deeply interlocked suture towards the quadratojugal, and an irregularly curved postero-medial margin, consisting of a deeply interlocked, mainly angular suture towards the postorbital, and a roughly sigmoid or mainly convex suture towards the squamosal. The centre of development of the jugal was situated laterally to the most anterior parts of the orbit, near the antero-lateral end of the preserved parts of the skulls.

A groove (*ifsv*, pl. 2, fig. 2; text-fig. 53) for the vertical portion of the suborbital part of the infraorbital canal runs over the jugal and the *postorbital* (*Po*, pl. 1, fig. 1; pl. 2, fig. 2; text-fig. 53), which has quite the same shape as in *Wetlugasaurus angustifrons* (cf. above, text-fig. 38). Its centre of development is very near the mid-point of the bone.

The elongated dorso-lateral lamina of the *squamosal* (*Sq*, pl. 1, fig. 1; pl. 2, figs. 1, 2, 3; text-fig. 53) may be described as having had four margins; one long slightly convex antero-medial margin, joined by suture to the supratemporo-intertemporal and the postorbital; another likewise long and slightly convex postero-ventral margin, with a suture towards the quadratojugal; a short antero-lateral margin with a more or less interlocked suture towards the jugal; and finally a short postero-medial margin, consisting of a very short extreme antero-medial part, joined by suture with the lateral extrascapular, and a longer postero-lateral part joined to a low posterior lamina of the bone (*Sqp*, pl. 2, fig. 2; text-fig. 53) forming the anterior margin and most of the lateral margin of the otic notch. As is especially well shown in the cotype, the two above mentioned parts of the postero-medial margin of the squamosal are separated by a short but distinct postero-lateral margin, forming the most anterior part of the medial margin of the otic notch. The centre of development of the squamosal was situated just in front of the otic notch, nearer to the antero-medial margin of the bone than to the antero-lateral and postero-lateral margins of the bone. On the ventral surface of the bone, behind the centre of development, there was a V-shaped ridge. The limbs of the V were united just at the centre of development, and from this point diverged in postero-medial and postero-lateral directions, one of the limbs leading to the suture with the lateral extrascapular, and continuing to the vertical lamina and the ventral process

of that bone, the other limb forming the mentioned low posterior lamina of the bone, and resting upon the dorsal surface of the quadrate.

The elongated *quadratojugal* (*Quj*, pl. 1, fig. 1; pl. 2, figs. 1, 2, 3; text-fig. 53) evidently had a long ventro-lateral and postero-ventral free margin, forming the lateral and postero-lateral margins of the



Text-fig. 54. *Wetlugasaurus angustifrons* RIABININ. Palatal view.
Dpl, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Enptq*, quadrate ramus of the entopterygoid; *La. mx*, lachrymo-maxillary; *Psph*, parasphenoid; *Qu*, quadrate; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; *Vo*, vomer; *apv*, anterior palatal vacuity; *fen. add*, adductor fenestra; *fen. ip*, interpterygoid vacuity; *n. i*, internal nostril.

adductor fenestra. Its long convex antero-medial margin had a partly deeply interlocked suture with the jugal and a suture with the squamosal, by which bone it was overlapped. It was also partly overlapped by the jugal — at the most dorsal part of the suture with that bone. In its posterior parts the quadratojugal seemingly overlapped a considerable part of the dorsal side of the quadrate. The centre of development of

the quadratojugal was situated in the most postero-lateral parts of the bone, just above a shallow ridge, extending on the inner side, and along the ventro-lateral margin of the bone.

The external ornamentation of the dermal bones was of a rather fine type. It consisted partly of small tubercles, separated by reticulating grooves, partly of ridges and grooves, radiating from the centres of development of the bones.

Dermal bones of the palate. In the palate the bony substance of the *entopterygoid* (*Enpt*, pl. 1, fig. 2) is partly preserved. The entopterygoid, as usual in higher *Labyrinthodontia*, shows a slender palatal ramus and a quadrate ramus (*Enptq*, pl. 1, fig. 2; pl. 2, figs. 1, 3), both diverging from a broad central bar, joined by an interlocked suture to the parasphenoid. The palatal ramus, forming a relatively narrow bony bar between the interpterygoid vacuity and the adductor fenestra, has its anterior end joined by suture, conceivably both to the ectopterygoid and the dermopalatine. Of these two latter bones too little is preserved to allow any description.

The quadrate ramus of the entopterygoid (*Enptq*, pl. 1, fig. 2; pl. 2, figs. 1, 3) is triangular in transverse section, and consequently has three longitudinal sides, one medial, one dorsal, and one ventro-lateral. The medial side is almost flat, but the two other sides are concave in transverse sections. The ventro-lateral side is fairly low and attached to the quadrate; the higher medial side reaches nearly up to the squamosal. With its ventro-lateral side the quadrate ramus also forms (at least part of) the postero-medial wall of the adductor fossa.

The *parasphenoid* (*Psph*, pl. 1, fig. 2) is rather poorly preserved. It has a not very broad, but evidently horizontally expanded processus cultriformis (*Pspc*, pl. 1, fig. 2), and an expanded posterior part (corpus), with a broad lateral process, meeting the entopterygoid in an interlocked suture.

Parts still bearing shagreen-like teeth are seen both on the palatal ramus of the entopterygoid and on the broader posterior part of the parasphenoid.

Though this paper deals mainly with the dermal bones, it may be suitable in the description of the present specimen to give a few notes, also of certain endocranial features. Thus to understand the structure of the palate in *Wetlugasaurus groenlandicus* it is necessary to add here a few words on the *quadrate* (*Qu*, pl. 1, figs. 1, 2; pl. 2, figs. 1, 3). This bone may be described as consisting of a roughly triangular, thick, nearly vertical plate, attached to the lateral side of the most posterior part of the quadrate ramus of the entopterygoid, and provided with a powerful long, horizontal, lateral crista along its postero-dorsal margin.

Thus the quadrate has large medial, postero-dorsal, and ventro-lateral sides. The medial side, attached to the quadrate ramus of the entopterygoid, is convex in transverse but concave in longitudinal sections, since the quadrate is slightly expanded at its posterior end, where it is uncovered by dermal bones. The posteriorly sloping postero-dorsal side is nearly flat, and a little broader in its posterior than in its anterior parts. It also forms the dorsal side of the crista; the ventro-lateral and ventral side of which is formed by the dorsal half of the ventro-lateral side of the quadrate. This ventro-lateral side is strongly concave in transverse sections, and about as high as it is long, and has long straight anterior, postero-dorsal, and ventral margins, and a convex posterior margin. A number of foramina which once transmitted vessels to the quadrate are to be seen on the ventro-lateral side of the bone. The anterior side of the quadrate is not exposed in the present state of the specimen but a section through the bone near that side has a triangular shape with a short, straight dorsal margin, a much longer straight medial margin and a still longer, strongly concave ventro-lateral margin.

Lateral line system of the head. A straight, discontinuous groove for the vertical portion of the suborbital part of the infraorbital canal (*ifsv*, pl. 2, fig. 2; text-fig. 53) runs over the jugal and postorbital, crossing the suture between these just at its typical sharp bend. In the supratemporo-intertemporal there is another straight groove (*ot+ptc*, pl. 2, fig. 2; text-fig. 53) for the otic part of the infraorbital canal, probably also for the postotic canal.

Horizon. *Myalina kochi* horizon, at the bottom of the *Anodontophora fassaensis* Beds (see below, pp. 194—196; and KOCH 1931, NIELSEN 1934).

Locality. Cape Stosch, Stensiö Plateau, Ridge VIII—IX, between 538 and 543 m altitude (KOCH 1931, NIELSEN 1934).

Remarks. The skull fragments here discussed present in several characters a clearly Capitosauroid type. Among such characters may be mentioned: the shape of the orbits, and their position far from the lateral margin of the skull; the very short postorbital division, and the not very long prenuchal and nuchal divisions of the dermal cranial roof; the shape of the fronto-parietals, parieto-extrascapulars, and lateral extrascapulars; the relatively broad processus cultriformis of the parasphenoid. In one character, the angular suture between the jugal and the postorbital, the specimen discussed shows a rather remarkable similarity to *Wetlugasaurus angustifrons* RIABININ, and to *Capitosaurus*. — There is in the specimen discussed one primitive character, not recorded in any stereospondylous Capitosauroid: the anterior supraorbitals meeting the supraorbito-dermosphenotics. This character is

typical of the *Wetlugasauridae*, as defined above (p. 83). Moreover many other characters seem to justify a reference of the specimen discussed to that family, and even to the genus *Wetlugasaurus*. I need only mention the similarities in the shape of the supraorbito-dermosphenotics, the parieto-extrascapulars, the postorbitals, the posterior parts of the palate, and the striking similarity in the oblique course of the vertical portion of the suborbital part of the infraorbital canal. None the less there are certain differences between the specimen discussed and *Wetlugasaurus angustifrons*, as will be evident from the diagnosis given above. These facts justify a determination of the East Greenland form as *Wetlugasaurus groenlandicus* n. sp.

Suborder Trematosauroidei.

Superfamily Trematosauroideae.

Family Trematosauridae.

Subfamily Trematosaurinae.

Stoschiosaurus n. g.

Diagnosis: *Trematosaurinae* with relatively broad skulls (at least in the posterior parts); with medium-sized orbits, situated on the dorso-lateral sides of the skull, far from the median line. Frontals not extending further back than just behind the orbits. The parts of the anterior supraorbitals and supraorbito-dermosphenotics, situated between the orbits, broad. Fronto-parietals and supratemporo-intertemporals very elongated. Parieto-extrascapulars about as long as they are broad, or longer. Adductor fenestrae relatively large: their length about $^3/_2$ of their maximum breadth.

Stoschiosaurus nielseni n. sp.

(Pl. 3; text-fig. 55).

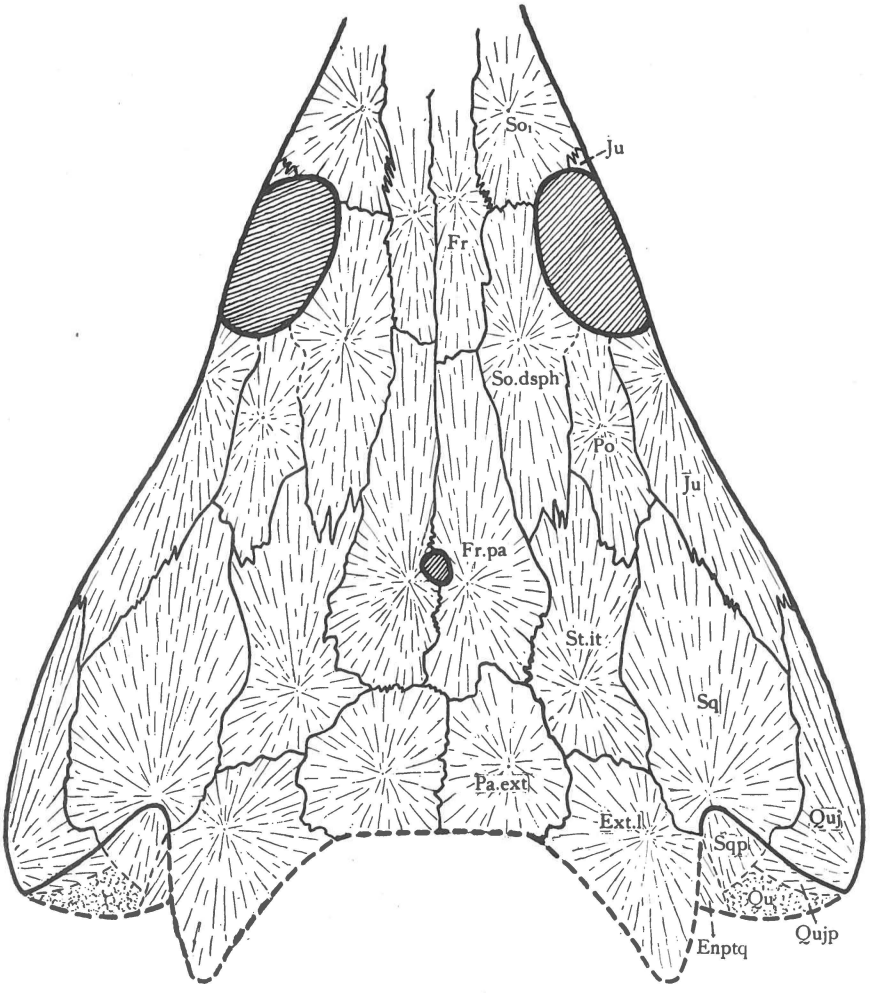
Holotype. *At.* 6: An internal cast of a skull, lacking the most anterior parts of the snout, and most of the left half of the posterior parts of the skull. The bony substance of the dermal bones is only preserved in relatively small patches antero-medially to the orbits, and in front of the right otic notch.

Description.

General shape. This specimen has its palate crushed and conceivably the whole skull has suffered from pressure in dorso-ventral

direction, so that it now appears more flat than it was in life. A comparison with apparently very nearly related specimens (cf. below) also tends to show that the present one is abnormally flattened.

The following measurements are taken from the holotype without correction, so that the height is certainly too little, and the breadth somewhat exaggerated.



Text-fig. 55. *Stoschiosaurus nielseni* n. sp. Dorsal view of the preserved parts of the skull. About $\frac{8}{7}$ natural size.

Enptq, quadrate ramus of the entopterygoid; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Qu*, quadrate; *Quj*, quadratojugal; *Qujp*, posterior lamina of the quadratojugal; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *Sqp*, posterior lamina of the squamosal; *St. it*, supratemporo-intertemporal.

Median length of the fragment	70 mm
Restored maximum breadth	about 72 mm
Maximum height	about 11 mm
Restored breadth over the middle of the orbits	about 32 mm
Distance from the posterior margin of the orbit to the postero-lateral end of the cheek	51 mm
Restored distance *a*: from the pineal foramen to the posterior margins of the parieto-extrascapulars	about 23 mm
Distance *b*: from the postero-median corner of the parieto-extrascapular to the postero-lateral end of the quadrato-jugal	38 mm
$\frac{\text{Distance } a}{\text{Distance } b}$	0.61
Distance from the pineal foramen to the posterior margin of the orbital division	18 mm
Length of the orbit	15 mm
Breadth of the orbit	9 mm
Distance *c*: from the posterior margin of the pineal foramen to the meeting-point of the postorbital, the supraorbito-dermosphenotic, and the orbit	27 mm
$\frac{\text{Distance } a}{\text{Distance } c}$	0.85

Dermal bones of the cranial roof and cheeks. As already mentioned we lack any indication of the shape of the most anterior parts of the skull discussed, the most anterior bone impressions preserved in the specimen being those of the frontals and the anterior supraorbitals. Even these bones are not completely known. However, it is clear that the *frontals* (*Fr*, pl. 3; text-fig. 55) have been very long and narrow bones, with long, irregularly curved lateral margins, joined by sutures to the anterior supraorbitals and the supraorbito-dermosphenotics, and with short, likewise irregularly curved posterior margins. The right frontal extended a little farther posteriorly than the left one; both bones extended a little more posteriorly than a transverse line through the posterior margins of the orbits.

The *anterior supraorbitals* (*So*$_1$, pl. 3; text-fig. 55) are in great part preserved, though damaged on the surface and broken off anteriorly. Certain anterior and antero-lateral parts of them can be restored after impressions of their ventral surface. Each anterior supraorbital evidently was an elongated bone with a finely crenulated but mainly straight, long medial margin, meeting the anterior half of the lateral margin of the frontal; a short, finely zig-zag posterior margin, joined by suture

to the supraorbito-dermosphenotic; a concave, short postero-lateral orbital margin; and a long irregularly sigmoid lateral margin. The centre of development is situated in the anterior half of the preserved part of each anterior supraorbital.

The very long *supraorbito-dermosphenotics* (*So. dsph*, pl. 3; text-fig. 55) are only preserved most anteriorly, near their short, finely zig-zag sutures with the anterior supraorbitals. However, their other parts can be easily restored from the impressions of their ventral surfaces. Thus it is clear that each supraorbito-dermosphenotic also had a very long, in the main slightly convex medial margin, joined by sutures to the posterior half of the lateral margin of the frontal, and the anterior half of the lateral margin of the fronto-parietal. The posterior margin of the supraorbito-dermosphenotic met the anterior margin of the supratemporo-intertemporal in a deeply interlocked suture, whereas its lateral margin consisted of two parts, a concave anterior part, forming the dorsal (medial) margin of the orbit, and a nearly straight posterior part, in suture with the postorbital.

Of the *fronto-parietals* (*Fr. pa*, pl. 3; text-fig. 55) only small patches of the bony substance are preserved, but the complete impression of the ventral surface of the parts lacking show the bones mentioned to have been very elongated, and roughly quadrangular in shape, narrower anteriorly and broader posteriorly. Each fronto-parietal had a long, mainly straight, median margin, with a bend in its most posterior fifth, and a notch, situated just in the anterior margin of the posterior third of the bone, and forming half of the pineal foramen. Thus the pineal foramen was situated very far back on the skull-roof, its distance from a transverse line through the posterior margins of the orbits being markedly longer than the maximum length of the orbits. The median margin of the left fronto-parietal had a short part in suture with the right frontal. The long lateral margin of each fronto-parietal consisted of a mainly straight anterior part joined by suture with the supraorbito-dermosphenotic, and a sigmoid posterior part, in suture with the supratemporo-intertemporal. The short, irregularly curved, anterior margins of the fronto-parietals were joined by sutures to the frontals; and their posterior margins were joined by sutures to the parieto-extrascapulars, that of the right one by a sigmoid suture with both parieto-extrascapulars, that of the left by a finely interlocked but mainly straight suture with the left parieto-extrascapular only. The centre of development of each fronto-parietal was evidently situated in the posterior half of the bone.

The ventral surfaces of the fronto-parietals showed ridges and depressions. Thus there was a marked bent ridge (*r*, pl. 3) extending in a bow from the postero-lateral corner of the bone to near the

pineal foramen. Hence it continued along the median margin of the bone, forming with the ridge of the other fronto-parietal, a median crista (*c.m*, pl. 3). Laterally and antero-laterally to the above-described ridge the ventral surface of the fronto-parietal sloped gently down to the surface of the neighbouring bones, whereas postero-medially to the ridge there was a flat triangular part of the surface in question.

Of the *parieto-extrascapulars* only an antero-lateral part of the right one is actually preserved, and even the impressions of these bones (*Pa. ext*, pl. 3; text-fig. 55) are not quite completely preserved in the most posterior parts. None the less it is evident that the dorsal lamina of each parieto-extrascapular was about as long as, or a little longer, than its maximum breadth, and had a roughly pentagonal shape. It had irregular curved margins, except 1) the median one, which was mainly straight, and joined by an only slightly zig-zag suture to the parieto-extrascapular of the other side, and 2) the mainly straight or slightly convex anterior margin of the left parieto-extrascapular, joined by suture with both fronto-parietals. The strongly sigmoid anterior margin of the right parieto-extrascapular, in suture with the right fronto-parietal, looks very different from the corresponding suture of the left side.

The gently undulating antero-lateral margins of the parieto-extrascapulars are joined by sutures with the supratemporo-intertemporals, whereas the more irregularly curved postero-lateral margins (the right one incompletely shown in the present specimen) have sutures with the lateral extrascapulars. The centre of development of each parieto-extrascapular has been situated approximately at the mid-point of the bone. On its ventral surface each parieto-extrascapular had a semilunar ridge (*c.s*, pl. 3), beginning near the antero-lateral corner of the bone, then turning medially, postero-medially, and posteriorly, growing more and more pronounced, and finally ending at the posterior margin of the bone, just at the point where the bone has a ventral process, connected with the exoccipital.

Almost nothing is shown of the left *supratemporo-intertemporal*, but the right one (*St. it*, pl. 3; text-fig. 55) is well preserved in its postero-lateral and most posterior parts; and the other parts of it have left a complete impression of their ventral surface. Evidently the bone discussed was very elongated, and had a roughly pentagonal shape with a short, mainly straight posterior margin, joined by a finely interlocked suture with the lateral extrascapular; long parallel, slightly sigmoid, medial and lateral margins; a short antero-medial margin with a very deeply interlocked suture towards the supraorbito-dermosphenotic; and finally a mainly sigmoid but partly irregularly crenulated antero-lateral margin, meeting the postorbital in an interlocked suture. The medial margin

consisted of a mainly concave anterior part, joined by suture with, and partly overlapping, the fronto-parietal, and a more straight posterior part, in suture with the parieto-extrascapular. Along its whole lateral margin the supratemporo-intertemporal overlapped the greater part of the medial margin of the squamosal. The centre of development of the supratemporo-intertemporal is situated remarkably far back, in the preserved parts of the bony substance, in the most anterior part of the posterior fourth of the supratemporo-intertemporal, about as far forward as the anterior margins of the parieto-extrascapulars.

Of the *lateral extrascapulars* (*Ext. l*, pl. 3; text-fig. 55) the left one is represented only by an impression of the most medial parts of its dorsal lamina, whereas the right one is a little better, though still very incompletely preserved. Combining the evidence from the two sides one will find that each lateral extrascapular conceivably had a dorsal lamina with an irregularly curved medial or antero-medial margin, in suture with the parieto-extrascapular; a mainly straight, though irregularly crenulated, anterior margin, joined by suture to the supratemporo-intertemporal; and a likewise mainly straight lateral margin, with a finely interlocked suture towards the squamosal.

In the present state of the specimen nothing can be said about the *lachrymo-maxillaries*; moreover the *jugals* are only very incompletely known from the imperfect impression of the internal surface of the discussed bone of the right side (*Ju*, pl. 3; text-fig. 55). However, this much can be said, that the jugal was a very long bone, with a narrow anterior part, ventrally and antero-ventrally to the orbit, and a broader posterior part. Of the anterior part a small fragment is preserved, with a curved medial suture towards the anterior supraorbital. For the rest the very long medial margin of the jugal consisted of a concave part, forming the ventral margin of the orbit; and a long posterior part, with a slightly bent suture towards the postorbital, and a long irregularly shaped, though mainly straight suture, along which it was overlapped by the antero-lateral margin of the squamosal. Evidently the jugal also had an irregularly curved postero-lateral margin, with an interlocked suture towards the quadratojugal; and its centre of development was situated in the most anterior portion of the postorbital part of the bone.

The impression of the roughly pentagonal right *postorbital* (*Po*, pl. 3; text-fig. 55) shows that bone to have been long, and narrower than the supraorbito-dermosphenotic. The postorbital had a long, nearly straight medial margin, in suture with the supraorbito-dermosphenotic; a likewise long, slightly bent lateral margin, in suture with the jugal; a short, concave antero-lateral orbital margin; a shorter postero-medial margin, joined by a finely interlocked suture with the

supratemporo-intertemporal; and finally a gently undulating postero-lateral margin, overlapping the most anterior part of the medial margin of the squamosal. Evidently the centre of development of the post-orbital was situated in the anterior half of the bone.

The *squamosal* (*Sq*, text-fig. 55), of which only a very small medial fragment is actually preserved, is shown — by the shape of its impression (*Sq*, pl. 3) — to have had an elongated, roughly quadrangular dorso-lateral lamina, with a very long convex medial margin, joined by suture to, and mostly overlapped by, the postorbital, the supratemporo-intertemporal and the lateral extrascapular. The said lamina also had a long, mainly straight or slightly concave antero-lateral margin, overlapping the jugal; a mainly convex ventral margin, overlapping the quadratojugal; and a postero-medial margin of unknown shape. The centre of development was close to the dorsal half of the last-mentioned margin.

The *quadratojugal* (*Quj*, text-fig. 55), as far as its shape can be found from that of the impression (*Quj*, pl. 3), preserved in the specimen, was an elongated, roughly triangular bone, with long dorsal — or antero-dorsal — and ventral margins and a shorter posterior margin. The dorsal margin had a long suture with the squamosal, and a somewhat shorter suture towards the jugal; the ventral margin formed the lateral boundary of the adductor fenestra; and the posterior margin probably covered a part of the quadrate. The centre of development of the quadratojugal seems to have been close to the postero-lateral corner of the bone.

The ornamentation of the dermal bones, as far as preserved seems to be of a rather coarse type. Else it seems to have agreed in the main with that found in *Wetlugasaurus groenlandicus*, consisting like that, of tubercles, and of ridges, radiating from the centres of development of the dermal bones.

Dermal bones of the palate. The palate of the present specimen is too damaged to allow any closer description. It can only be stated that the *parasphenoid* had a narrow processus cultriformis, forming a vertical lamina posteriorly and growing a little broader anteriorly.

Horizon. The *Myalina kochi* horizon, at the bottom of the *Anodontophora fassaensis* Beds (see below, pp. 194—196; and KOCH 1931, NIELSEN 1934).

Locality. C. Stosch, Stensiö Plateau, Ridge VIII—IX, between 538 and 543 m altitude (KOCH 1931, NIELSEN 1934).

Remarks. This new species — named in honour of its collector, Mr. E. NIELSEN — is a very typical *Trematosaurid*, and shows a very advanced stage of specialization towards an extreme Trematosaurine type, in certain characters: the very lateral position of the orbits and

the great length of the postorbital and prenuchal divisions of the dermal cranial roof. It is more primitive in such a feature as the relatively large size of the orbits; and the great breadth of the parts of the supraorbito-dermosphenotics, situated between the frontals and the orbits, is a character which it shares with certain Trematosaurids from Spitsbergen (for instance *Tertrema*, text-fig. 23, *Aphaneramma*, text-fig. 56; WIMAN 1914, pl. V, figs. 1, 3; *Platystega*, text-fig. 12; WIMAN 1914, pl. VI, fig. 5), and also with *Trematosuchus* (text-fig. 10). In the last-mentioned genus, however, this is due at least mainly, to the extremely small size of the orbits.

With a reservation, due to the present lack of knowledge concerning the endocranial characters, I ascribe a generic value to the differences found between the present species and the previously known *Trematosaurinae*.

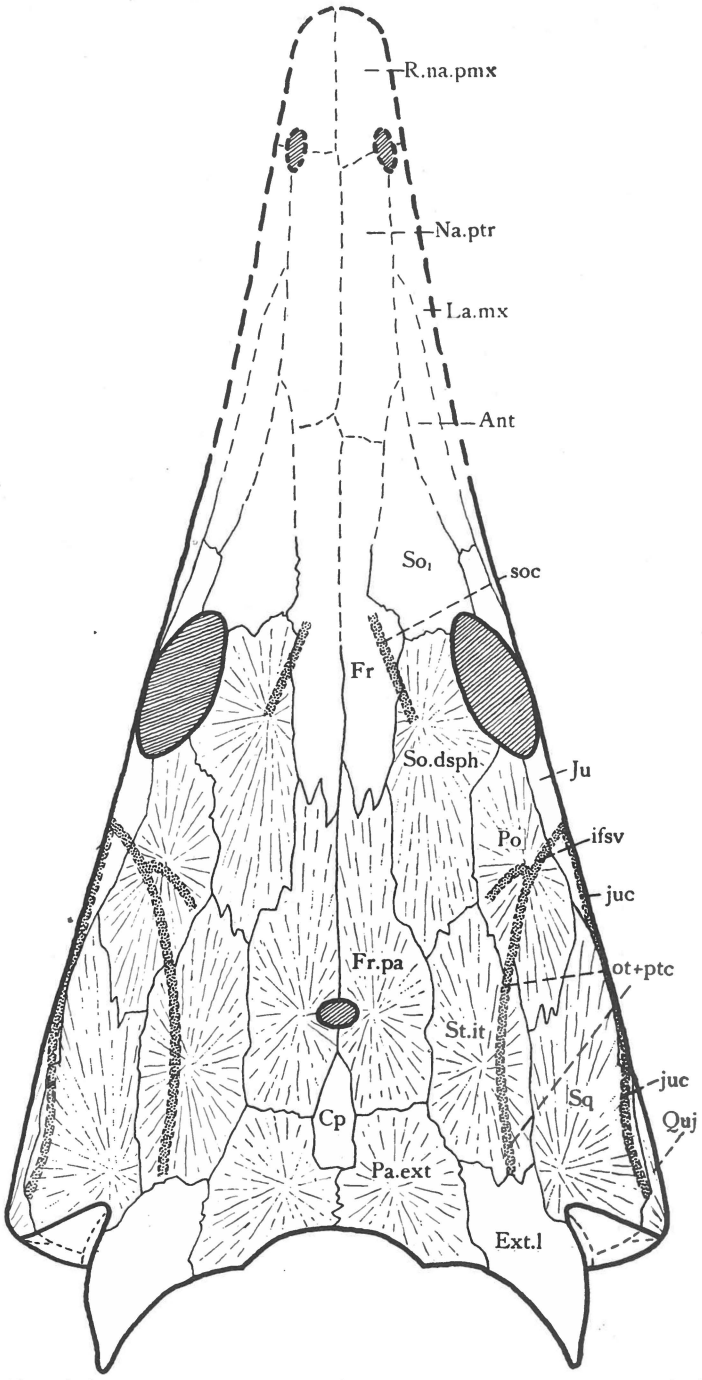
To emphasize the characters separating the new genus *Stoschiosaurus* from the previously fairly well known genera of the *Trematosaurinae* I will here give a short (of necessity incomplete) diagnosis of each of the latter — to be compared with the diagnosis of *Stoschiosaurus*, given above (p. 131). The new genus seems more closely related to *Aphaneramma* than to any other genus at present known.

Diagnoses of the other genera of the *Trematosaurinae:*

Trematosaurus: Trematosaurinae with narrow skulls; with small orbits, situated near the lateral margins of the skull, though not so laterally as to prevent, when viewed dorsally, a narrow bar of dermal bones from being visible laterally to each orbit. Frontals extending far behind the orbital division of the dermal cranial roof. Anterior supraorbitals and supraorbito-dermosphenotics with narrow parts between the frontals and the orbits. Breadth of the supratemporo-intertemporals about half the length of these bones. Parieto-extrascapulars short and broad: their breadth more than $1^1/_2$ times their median length.

Trematosuchus: Trematosaurinae with narrow skulls; with extremely small orbits, situated as in *Trematosaurus*. Frontals extending very far behind the orbital division of the dermal cranial roof. Anterior supraorbitals and supraorbito-dermosphenotics with broad parts between the frontals and the orbits. Breadth of the supratemporo-intertemporals about half the length of the bones. Breadth of the parieto-extrascapulars a little greater than the median length of the bone.

With an interfrontal; septomaxillaries with exposed facial parts.



Text-fig. 56. *Aphaneramma rostratum* Sm. Woodw. Dorsal aspect of the skull, restored after Smith Woodward 1904, and Wiman 1914 [1]). Nearly $\frac{8}{5}$ natural size. *Ant*, posterior antorbital; *Cp*, centroparietal (interparietal); *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *ifsv*, vertical portion of the suborbital part of the infraorbital canal; *juc*, jugal canal; *ot+ptc*, otic part of the infraorbital canal and postotic canal; *soc*, supraorbital canal.

[1]) The specimen, figured by Wiman (1914, pl. IX, fig. 2, text-figs. 9, 10) as an indeterminable snout, it so seems to belong to *Aphaneramma* (cf. Smith Woodward 1904).

Tertrema: Trematosaurinae with narrow skulls; with small orbits, situated as in *Trematosaurus*. Frontals extending only a short distance behind the orbital division of the dermal cranial roof. Supraorbito-dermosphenotics with broad parts between the frontals and the orbits. Breadth of the supratemporo-intertemporals about half the length of the bones. Parieto-extrascapulars very short and broad, their median length being about half their breadth.

With closed otic notches.

Aphaneramma: Trematosaurinae with narrow skulls; with medium-sized orbits, situated as in *Stoschiosaurus*, on the dorso-lateral sides of the skull. Frontals extending only as far back as just behind the orbits. Supraorbito-dermosphenotics with broad parts between the orbits and the frontals. Fronto-parietals and supratemporo-intertemporals very elongated: length of the latter about $2^1/_2$ times their breadth. Parieto-extrascapulars about as long as they are broad.

With acentroparietal (interparietal).

Stoschiosaurus nielseni? n. sp.

(Pls. 4, 5; pl. 15, fig. 2; text-figs. 57, 58).

Material. *At.* 7 and *At.* 8: The imperfect internal casts of the posterior parts of two skulls.

In *At.* 7 (pl. 4, figs. 3, 4; pl. 15, fig. 2; text-fig. 57 A), the parts in front of the centre of development of the jugal, and most of the left half of the skull are broken off, the latter along an angular fracture line through the impressions of the left fronto-parietal, supratemporo-intertemporal, lateral extrascapular, and parieto-extrascapular. Moreover the most posterior marginal parts are also partly broken off. The palate is preserved to a corresponding extent.

The dermal bones of the cranial roof and cheeks preserved, or the impressions of which are at present exposed in specimen *At.* 7, include: the posterior parts of the right supraorbito-dermosphenotic; most of the right, and small parts of the left, fronto-parietal; most of both parieto-extrascapulars; the complete right supratemporo-intertemporal, and a very small part of the left one; most of the right lateral extrascapular, and the antero-medial corner of the left one; the posterior half of the right jugal; the posterior parts of the right postorbital; the complete right squamosal; and most of the right quadratojugal. In the palate there are seen the greater parts of the parasphenoid, and of the right entopterygoid, probably also a small part of the right ectopterygoid.

Specimen *At.* 8 (pl. 4, figs. 1, 2; pl. 5; text-figs. 57 B, 58) is

preserved posteriorly, and to the left of, two straight fractures; one transverse fracture situated about as far forward as the centre of development of the jugal, and one longitudinal fracture through the right fronto-parietal and parieto-extrascapular, and the parasphenoid.

The dermal bones of the cranial roof and cheeks, the shape of which is shown in specimen *At.* 8 include: the most posterior parts of the left supraorbito-dermosphenotic; most of the left and a little less than half the right fronto-parietal; the whole left parieto-extrascapular and a small part of the right one; the left supratemporo-intertemporal; most of the left lateral extrascapular; the posterior half of the left jugal; a posterior part of the left postorbital; and the whole left squamosal and quadratojugal.

In the palate there are impressions of the dorsal surfaces of a great part of the parasphenoid, of most of the left entopterygoid, and of a posterior part of the left ectopterygoid.

The interest of the two specimens in question depends upon the fact that they show the posterior parts of the skull in an uncrushed condition, whereas in the type specimen of *Stoschiosaurus nielseni*, described above, this part is badly crushed. The impressions of the lateral extrascapulars are also better preserved in specimens *At.* 7 and *At.* 8 than in specimen *At.* 6.

Description.

General shape. The present specimens must have belonged to skulls with relatively high occipital surfaces. The exact dimensions are as follows:—

	At. 7	*At.* 8
Median dorsal length of the fragment	32 mm	32 mm
Restored maximum breadth of the skull about	57 mm	70 mm
Restored breadth between the lateral margins of the lateral extrascapulars	28 mm	36 mm
Maximum height of the skull	15 mm	20 mm
Distance *a*: from the posterior end of the pineal foramen to the posterior margin of the parieto-extrascapulars	19 mm	23 mm
Distance *b*: from the postero-median corner of the parieto-extrascapular to the postero-lateral end of the quadratojugal	30 mm	38 mm
$\frac{\text{Distance } a}{\text{Distance } b}$	0.63	0.61

Dermal bones of the cranial roof and cheeks. In most characters the dermal bones of the present specimens agree with specimen

At. 6, the type specimen of *Stoschiosaurus nielseni*. Thus it is not necessary to give a detailed description of specimens *At.* 7 and *At.* 8, and I shall confine myself to an enumeration of the chief differences between the specimens mentioned and the type specimen of *Stoschiosaurus nielseni*.

The most important features found in specimen *At.* 7, and not in the type specimen (*At.* 6) are as follows:

1. Of the *fronto-parietals* (*Fr. pa*, pl. 4, fig. 3; text-fig. 57 A) the left had a short extreme posterior part of its median margin joined by suture with the right parieto-extrascapular — whereas the right fronto-parietal did not meet the left parieto-extrascapular.

2. On the ventral surface of each *parieto-extrascapular* (*Pa. ext*, pl. 4, fig. 3; text-fig. 57 A), antero-medially to the curved ridge (*c*, pl. 4, fig. 3) also described above in specimen *At.* 6, there was a small tubercle (*t*, pl. 4, fig. 3), of unknown importance.

3. The *supratemporo-intertemporal* (*St. it*, pl. 4, fig. 3; text-fig. 57 A) was much broader in its anterior than in its posterior part; and its lateral margin was much more strongly sigmoid than the medial one.

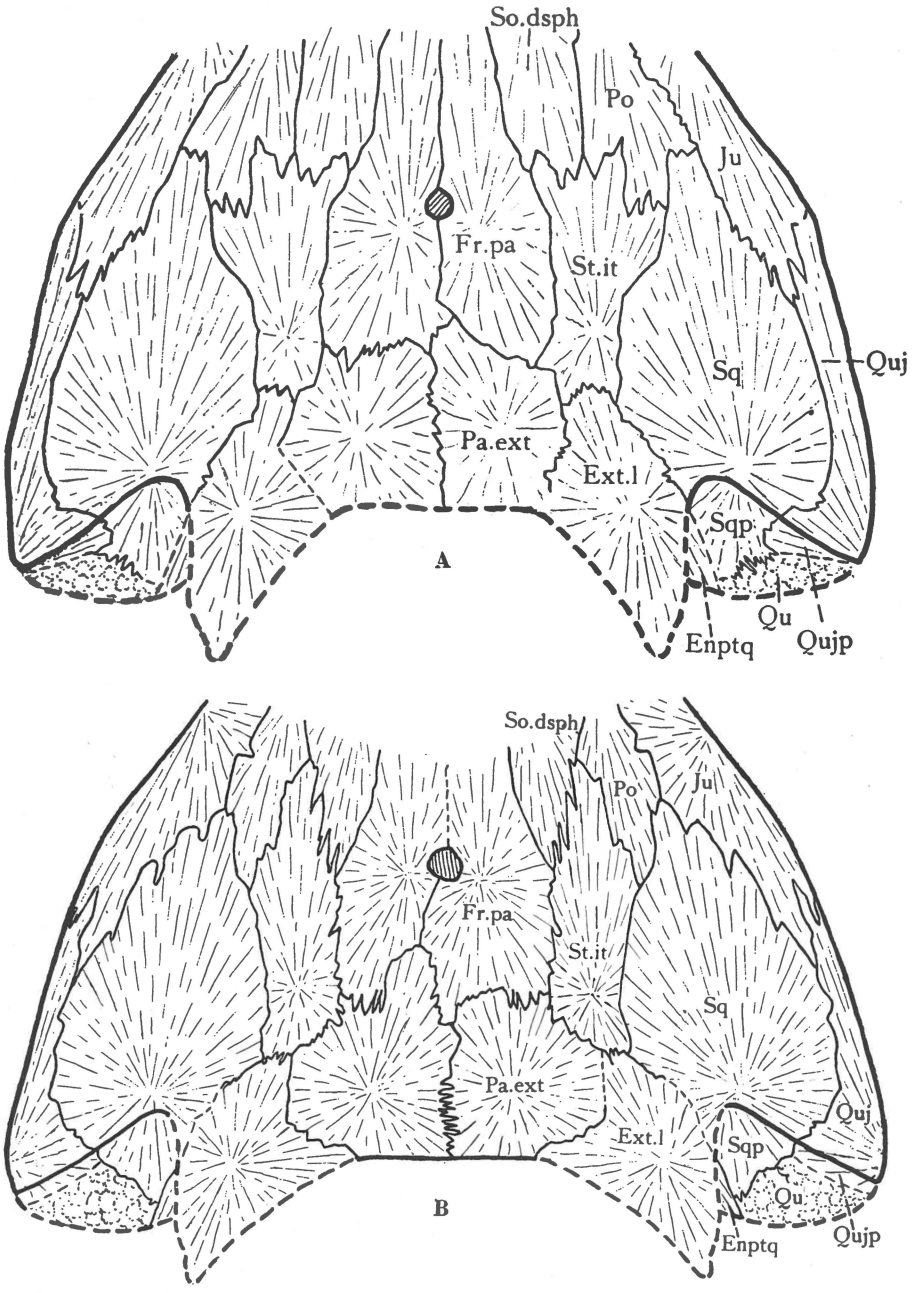
4. The internal impression of the anterior parts of the horizontal lamina of the *lateral extrascapular* (*Ext. l*, pl. 4, fig. 3; text-fig. 57 A) is well preserved on the right side. It is roughly quadrangular in shape, with a straight broken posterior margin, and irregularly curved medial, anterior, and lateral margins, joined by sutures respectively with the parieto-extrascapular, the supratemporo-intertemporal and the squamosal. The centre of development of the lateral extrascapular was at the postero-lateral corner of the preserved part of the horizontal lamina of the bone. From the same corner arises a ventro-medially directed process (*Ext. lv*, pl. 4, figs. 3, 4), joined by a strongly interlocked suture to the dorso-lateral branch of the exoccipital (*Eo*, pl. 4, figs. 3, 4).

5. There is a very clearly shown triangular posterior lamina of the *squamosal* (*Sqp*, pl. 4, fig. 3; text-fig. 57 A).

The most important characters found in the shape of the dermal bones of the cranial roof and cheeks of specimen *At.* 8 are as follows:

1. On the ventral surface of each *fronto-parietal* (*Fr.pa*, pl. 5, fig. 1; text-fig. 57 B) there was a paramedian ridge (c_1, pl. 5, fig. 1) in front of the pineal foramen, and situated on the slope from this median ridge down to the lateral parts of the surface. The impression of this paramedian ridge is especially clear on the left side of the specimen.

2. The left *parieto-extrascapular* (*Pa. ext*, pl. 5, fig. 1; text-fig. 57B) stretched very far forward: its suture towards the left fronto-parietal had an oblique course, so that the parieto-extrascapular had an antero-lateral



Text-fig. 57. *Stoschiosaurus nielseni?* n. sp. Dorsal aspect, A, of specimen *At.* 7, $\frac{6}{5}$ natural size; B, of specimen *At.* 8, $\frac{4}{5}$ natural size.

Enptq, quadrate ramus of the entopterygoid; *Ext. l*, lateral extrascapular; *Fr. pa*, fronto-parietal; *Ju*, jugal; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Qu*, quadrate; *Quj*, quadratojugal; *Qujp*, posterior lamina of the quadratojugal; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *Sqp*, posterior lamina of the squamosal; *St. it*, supratemporo-intertemporal.

rather than an anterior margin. It had a long part of its median margin joined by suture with the right fronto-parietal. Otherwise the bone discussed agreed with the corresponding bone in specimen *At.* 6; like the latter it lacks the tubercle (*t*, pl. 4, fig. 3), found in specimen *At.* 7.

3. The left *supratemporo-intertemporal* (*St. it*, pl. 5, fig. 1; text-fig. 57B) is intermediate in shape between that of specimen *At.* 6 and that of *At.* 7, but agrees more clearly with that of specimen *At.* 6.

4. The left *lateral extrascapular* (*Ext. l*, pl. 4, figs. 1,2; pl. 5, fig. 1; text-fig. 57B), with its ventro-medial process (*Ext. lv*, pl. 4, fig. 1; pl. 5, figs. 1,2; text-fig. 58), had a shape quite corresponding to that above described, of the right lateral extrascapular in specimen *At.* 7.

5. The *postorbital* (*Po*, pl. 4, fig. 2; pl. 5, fig. 1; text-fig. 57B) was much narrower, at least in its posterior parts, than in specimens *At.* 6 and *At.* 7.

6. The impression of the internal surface of the left *squamosal* (*Sq*, pl. 4, fig. 2; pl. 5, fig. 1; text-fig. 57B; *Sqp*, pl. 5, fig. 1; pl. 4, fig. 1; text-figs. 57B, 58) is more completely shown in the present specimen. Thus there is shown to have existed a narrow, very marked groove extending antero-medially from below the centre of development of the bone.

7. The impression of the internal surface of the left *quadratojugal* (*Quj*, pl. 4, fig. 2; pl. 5, fig. 1; text-figs. 57B, 58; *Qujp*, pl. 4, fig. 1, text-fig. 57B) is also very well shown. Evidently there was on the internal surface a marked rounded ridge (*c*, pl. 4, fig. 2), stretching anteriorly along the ventral margin from near the postero-lateral corner of the bone. This ridge became gradually flatter and less prominent anteriorly and disappeared on the anterior parts of the internal surface of the bone.

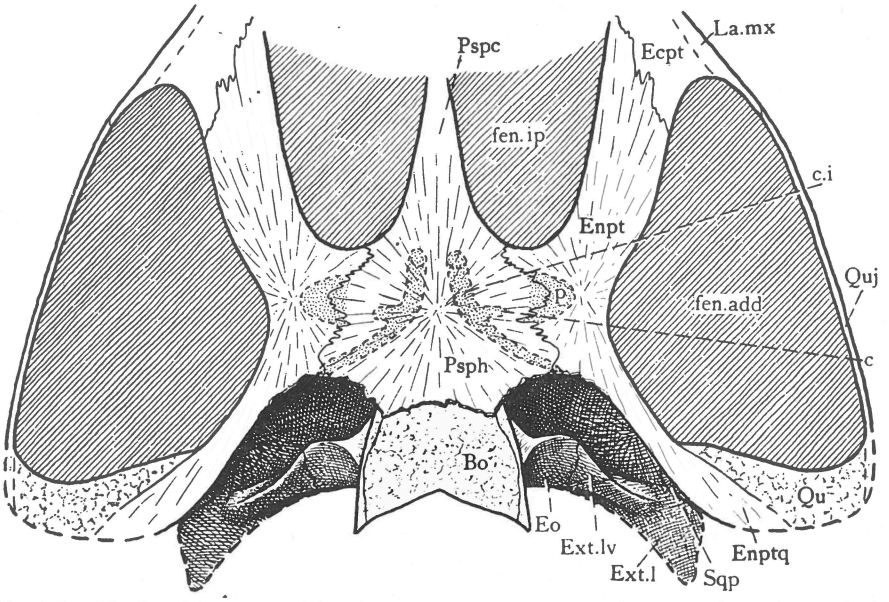
Dermal bones of the palate. The dermal bones of the posterior parts of the palate are well preserved in both of the specimens here discussed, either as bony substance or as impressions of the dorsal surfaces.

The position of the sutures between the *entopterygoids* (*Enpt*, pl. 4, fig. 4; pl. 5, fig. 2; text-fig. 58) and the *ectopterygoids* (*Ecpt*, pl. 4, fig. 4; pl. 5, fig. 2, text-fig. 58) shows that the latter bones formed the anterior margins of the adductor fenestrae (*fen. add*, pl. 4, fig. 4; pl. 5, fig. 2; text-fig. 58). The concave antero-medial or medial margins of these fenestrae were formed by the palatal rami of the entopterygoids (*Enpt*, pl. 4, fig. 4), which stretched as narrow bony bars, with parallel antero-medial (medial) and postero-lateral (lateral) margins, between the adductor fenestrae and the interpterygoid vacuities (*fen. ip*, pl. 4, fig. 5; pl. 5, fig. 2; text-fig. 58).

The centre of development of each entopterygoid is situated at

the junction of the palatal ramus and the quadrate ramus of the bone, medially to a bend between the antero-medial and the postero-medial margins of the adductor fenestra, laterally to the middle of the strongly interlocked suture between the entopterygoid and the corpus of the parasphenoid (*Psph*, pl. 4, fig. 4; pl. 5, fig. 2; text-fig. 58). As shown in specimen *At.* 8 there is a triangular pouch, or recess (*p*, pl. 4, fig. 4; text-fig. 58) in the most medial parts of the dorsal surface of the entopterygoid, just medially to the centre of development of the bone.

The quadrate ramus of each entopterygoid (*Enptq*, pl. 4, fig. 4; pl. 5, fig. 2; text-fig. 58) is a high and thick vertical bony plate. It is



Text-fig. 58. *Stoschiosaurus nielseni?* n. sp. Restored palatal aspect of specimen *At.* 8. $\frac{4}{5}$ natural size. *Bo*, basioccipital; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Enptq*, quadrate ramus of the entopterygoid; *Eo*, exoccipital; *Ext. l*, dorsal lamina of the lateral extrascapular; *Ext. lv*, ventral process of the lateral extrascapular; *La. mx*, lachrymo-maxillary; *Pspc*, processus cultriformis of the parasphenoid; *Psph*, corpus of the parasphenoid (partly broken away to show underlying parts); *Qu*, quadrate; *Quj*, quadratojugal; *Sqp*, posterior lamina of the squamosal; *c*, canal branching off from the canal for the internal carotid; *c. i*, canal for the internal carotid; *fen. add*, adductor fenestra; *fen. ip*, interpterygoid vacuity; *p*, recess, or pouch in the dorsal surface of the palate.

not completely shown in the present state of the specimens discussed. It forms the postero-medial margin of the adductor fenestra and its posterior parts lie close to the medial surface of the quadrate (*Qu*, pl. 4, fig. 4; pl. 5, fig. 2; text-fig. 58). Postero-dorsally it is joined by suture to the posterior lamina of the squamosal.

Of the *parasphenoids* (*Psph*, pl. 4, fig. 4; pl. 5, fig. 2; text-fig. 58)

the anterior and greatest parts of the processus cultriformes (*Pspc*, pl. 4, fig. 4; pl. 5, fig. 2; text-fig. 58) are lacking, but the morphology of the bony plate, forming the corpus of the parasphenoid is very well shown both in specimen *At.* 7 and *At.* 8. It is roughly heptangular in shape with a free posterior margin; free postero-lateral margins; lateral margins, joined by interlocked sutures to the entopterygoids; and slightly concave antero-lateral margins, forming the postero-medial margins of the interpterygoid vacuities. The anterior part of the corpus parasphenoidei is thus triangular; it merges into the gradually narrower and higher processus cultriformis (*Pspc*, pl. 4, fig. 4; pl. 5, fig. 2; text-fig. 58). The most posterior parts of each parasphenoid overlap the exoccipitals (*Eo*, pl. 4, fig. 4; pl. 5, fig. 2; text-fig. 58) in ventral view.

The middle part of each half of the corpus parasphenoidei is traversed by a curved canal (*c. i*, pl. 4, fig. 4; pl. 5, fig. 2; text-fig. 58), leading from the space between the quadrate ramus of the entopterygoid and the exoccipital, to the anterior third of the dorsal surface of the corpus. This canal evidently transmitted the internal carotid artery, and is probably homologous with the parabasal canal in recent forms (cf. GOODRICH 1930, p. 298, fig. 308). It is probably also found in the *Phyllospondyli*, judging from the descriptions by STEEN (1931) and BULMAN and WHITTARD (1926).

From the middle of the concave antero-lateral side of the curved canal *c. i* a narrower canal (*c*, pl. 5, fig. 2; text-fig. 58) leads anterodorsally to the dorsal surface of the parasphenoid.

Horizon. *Myalina kochi* horizon, at the bottom of the *Anodontophora fassaensis* Beds (see below, pp. 194—196; and KOCH 1931; NIELSEN 1934).

Locality. Cape Stosch, Stensiö Plateau, Ridge VIII—IX, 538—543 m altitude (cf. KOCH 1931, NIELSEN 1934).

Remarks. The present two specimens agree in most of the important points with *Stoschiosaurus nielseni*, described above, and are here described in order to give a more complete account of the morphology of the genus *Stoschiosaurus*, to which they certainly seem to belong. However, the present incomplete knowledge of the skulls, of which the fragments described once formed parts, does not allow a specific determination of specimens *At.* 7 and *At.* 8, which are therefore provisionally described as *Stoschiosaurus nielseni*? n. sp.

Stoschiosaurus n. sp.?

(Pl. 6; pl. 15, figs. 3, 4; text-fig. 59).

Material. Specimen *At.* 9: The complete cast of the internal surface of the posterior parts of the dermal bones of the cranial roof, cheeks and palate of a small skull. The specimen is bounded anteriorly by a

transverse fracture, passing through the most anterior parts of the fronto-parietals, the supraorbito-dermosphenotics, the postorbitals, the middle of the jugals, and the ectopterygoids.

The shape of the following dermal bones of the cranial roof and cheeks can be described from this specimen: the posterior halves of the supraorbito-dermosphenotics; the greatest parts of the fronto-parietals; the parieto-extrascapulars; the supratemporo-intertemporals; the ventral processes and parts of the dorsal laminae of the lateral extrascapulars; the posterior parts of the jugals and postorbitals; the squamosals; and the quadratojugals. In the palate there are seen the impressions of the dorsal surfaces of the posterior parts of the ectopterygoids, and of the palatal rami of the entopterygoids; the ventral surfaces of the quadrate rami of the entopterygoids; and the impressions or the bony substance of the greatest part of the parasphenoid (lacking the anterior parts of the processus cultriformis).

Description.

General shape. The dimensions of the present specimen are as follows:

Median length of the fragment	29 mm
Maximum breadth of the skull	53 mm
Breadth between the lateral margins of the lateral extrascapulars	26 mm
Maximum height of the skull	14 mm
Distance *a*: from the posterior margin of the pineal foramen to the posterior margin of the parieto-extrascapulars	16 mm
Distance *b*: from the postero-median corner of the parieto-extrascapular to the postero-lateral end of the quadratojugal	28 mm
$\frac{\text{Distance } a}{\text{Distance } b}$	0.57
Distance *c*: from the posterior margin of the pineal foramen to the meeting-point of the postorbital, the supraorbito-dermosphenotic, and the orbit	19.5 mm
$\frac{\text{Distance } a}{\text{Distance } c}$	0.82

Thus it is evident that in certain features of its general shape, the present specimen is slightly, but distinctly, different from the specimens, above described, of *Stoschiosaurus nielseni* and *S. nielseni?* The importance of these differences will be further discussed below (p. 150).

Dermal bones of the cranial roof and cheeks. Though dif-

fering in certain features from the specimens of *Stoschiosaurus* already described, the present specimen agrees with them in most of the main points concerning the shape of the dermal bones. Therefore a detailed description of the dermal bones of the present specimen is superfluous; I will only enumerate the points of difference, certain of which may be of interest in judging the relationship between the present specimen and *Stoschiosaurus nielseni*.

1. In the present specimen the slightly concave posterior margins of the *parieto-extrascapulars* (*Pa. ext*, pl. 6, fig. 1; text-fig. 59 A) are well preserved.

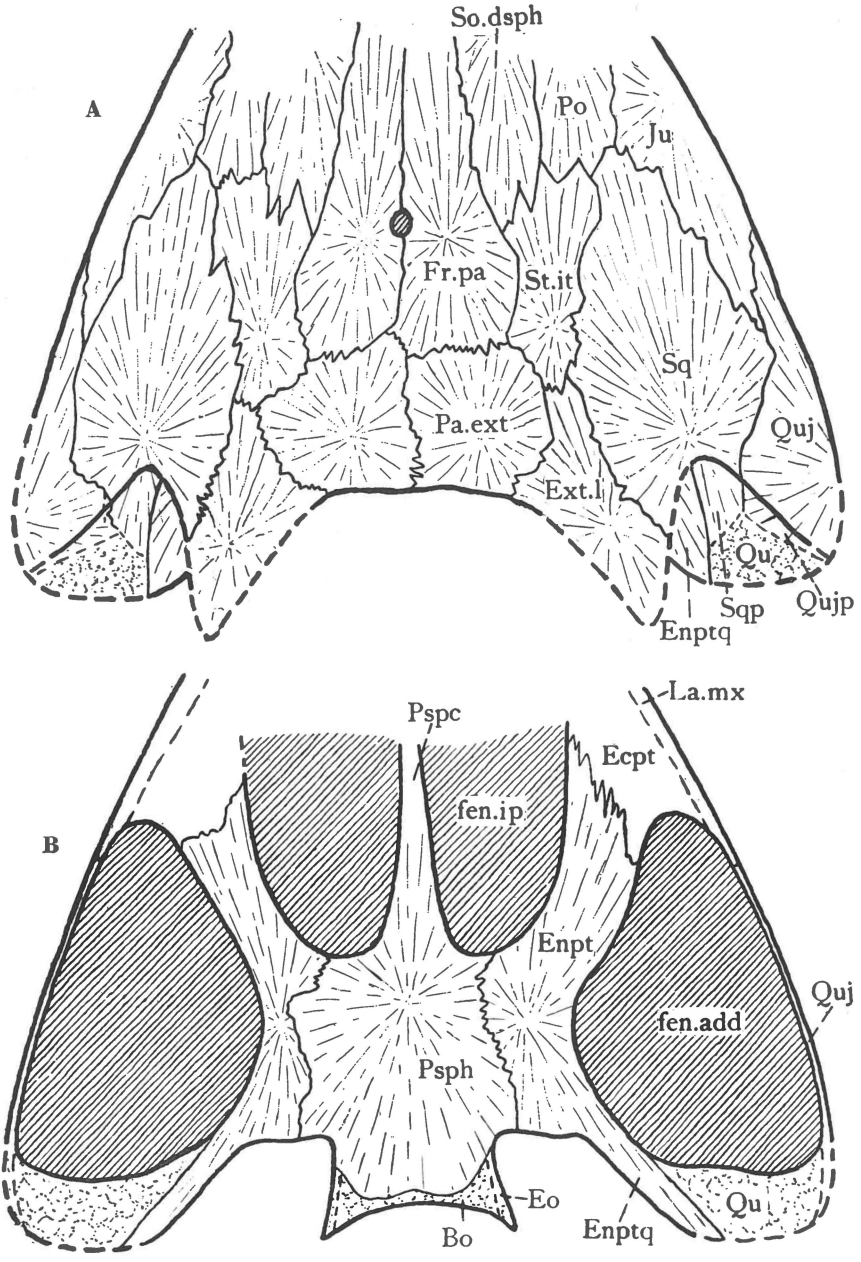
2. Just as in specimen *At.* 7 the *supratemporo-intertemporals* (*St. it*, pl. 6, fig. 1; text-fig. 59 A) were much broader in their anterior than in their posterior halves. They differed, however, from the corresponding bones of specimen *At.* 7 in that they had mainly transverse, zigzag sutures towards the postorbitals (*Po*, pl. 6, fig. 1; text-fig. 59 A; cf. below), and very short posterior margins, in suture with the lateral extrascapulars (*Ext. l*, pl. 6, fig. 1; text-fig. 59 A).

3. The impressions of the *lateral extrascapulars* (*Ext. l*, pl. 6, fig. 1; text-fig. 59 A; *Ext. lv*, pl. 6, fig. 2; pl. 15, fig. 4) are better preserved in the present specimen, especially in their posterior marginal parts. The ventral surface of each of these bones evidently had a rounded swelling along the postero-medial margin, and a shallow triangular depression in front of this swelling.

4. The *postorbitals* (*Po*, pl. 6, fig. 1; pl. 15, fig. 3; text-fig. 59 A) were relatively shorter in the present specimen. In the specimens above described as *Stoschiosaurus nielseni* and *S. nielseni?* the postorbitals were always distinctly longer than the supraorbito-dermosphenotics, and had oblique, postero-medial margins, in suture with the supratemporo-intertemporals, and oblique, postero-lateral margins, in suture with the squamosals. In the present specimen, on the contrary, the postorbitals were markedly shorter than the *supraorbito-dermosphenotics* (*So. dsph*, pl. 6, fig. 1; text-fig. 59 A), and had transverse, posterior margins with zig-zag sutures towards the supratemporo-intertemporals (*St. it*, pl. 6, fig. 1, text-fig. 59 A) and slightly curved sutures towards the squamosals (*Sq*, pl. 6, fig. 1; pl. 15, fig. 3; text-fig. 59 A; *Sqp*, pl. 6, fig. 1; pl. 15, fig. 4; text-fig. 59 A).

In the shape of the dermal bones of the palate (pl. 6, fig. 2; text-fig. 59 B), the present specimen agrees most perfectly with those, described above as *Stoschiosaurus nielseni?*

Horizon. *Myalina kochi* horizon, at the bottom of the *Anodontophora fassaensis* Beds (see below, pp. 194—196; KOCH 1931, and NIELSEN 1934).



Text-fig. 59. *Stoschiosaurus* n. sp.? A, dorsal, B, palatal aspect of the skull. $\frac{3}{2}$ natural size.

Bo, basioccipital; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Enptq*, quadrate ramus of the entopterygoid; *Eo*, exoccipital; *Ext. l*, lateral extrascapular; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Pspc*, processus cultriformis of the parasphenoid; *Psph*, corpus of the parasphenoid; *Qu*, quadrate; *Quj*, quadratojugal; *Qujp*, posterior lamina of the quadratojugal; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *Sqp*, posterior lamina of the squamosal; *St. it*, supratemporo-intertemporal; *fen. add*, adductor fenestra; *fen. ip*, interpterygoid vacuity.

Locality. Cape Stosch, Stensiö Plateau, Ridge VIII—IX, between 538 and 543 m altitude (see KOCH 1931, NIELSEN 1934).

Remarks. The facts enumerated above concerning the general shape of the skull discussed, tend to show that the differences between the present specimen on the one hand and the type specimen of *Stoschiosaurus nielseni* and the two specimens, above described as *S. nielseni?* on the other are more important than those between the three last mentioned specimens. This is confirmed by the study of the shape of the dermal bones: the relatively short postorbitals with transverse posterior sutures towards the supratemporo-intertemporals and the squamosals are typical of the specimen discussed, which in this respect contrasts with the three other specimens mentioned. All these three, on the other hand, show a quite uniform shape of the postorbitals, and thus seem to belong to a group of animals more closely related to each other than to that represented by specimen *At.* 9.

However, the evidence brought forward above is far from sufficient as a basis for the erection of a new species. Large parts — indeed the greater part — of this animal remain totally unknown and thus for the present the specimen here discussed — *At.* 9 — has to be determined as *Stoschiosaurus* n. sp.?

Subfamily **Lyrocephalinae.**

Lyrocephalus WIMAN.

Lyrocephalus kochi n. sp.

(Pl. 7; pl. 8, figs. 1, 2; text-fig. 60).

Diagnosis: Skull triangular, comparatively low and narrow (maximum breadth about 0.85 of the median length of the skull; maximum height about 0.25 of the median length of the skull), with small orbits. With medium-sized prenarial, long postnarial, medium-sized preorbital, short postorbital, and medium-sized prenuchal and nuchal divisions of the dermal cranial roof. Distance between the orbits about 0.65, or less, of the distance from the anterior margin of the orbit to the posterior margin of the external naris, and about 0.35 of the distance from the anterior margin of the orbit to the anterior margin of the skull. Distance from the pineal foramen to the posterior margin of the orbital division of the dermal cranial roof considerably shorter than the maximum length of the orbits. Distance from the posterior margin of the orbit to the posterior end of the cheek longer than the distance from the posterior margin of the orbit to the posterior margin of the external naris. Naso-rostro-premaxillaries

short and broad (median length shorter than the breadth of the bones). Anterior supraorbitals very long, much longer than the maximum length of the orbits. Frontals extending as far back as the posterior margin of the orbital division. Pineal foramen equally distant from the anterior and the posterior margins of the fronto-parietals. Length of each parieto-extrascapular about $1^1/_4$, or less, of the breadth of the bone. Grooves for the jugal canal situated for a great part in the squamosal, and consisting of a straight part in the jugal, and a sharply angular part in the squamosal, with a sharp bend near the centre of development of the squamosal.

Holotype. Specimen *At.* 1: A complete skull, preserved in part and counter-part, at present not cleaned from the matrix on its ventral surface but showing all the dermal bones of the dorsal and lateral sides of the skull.

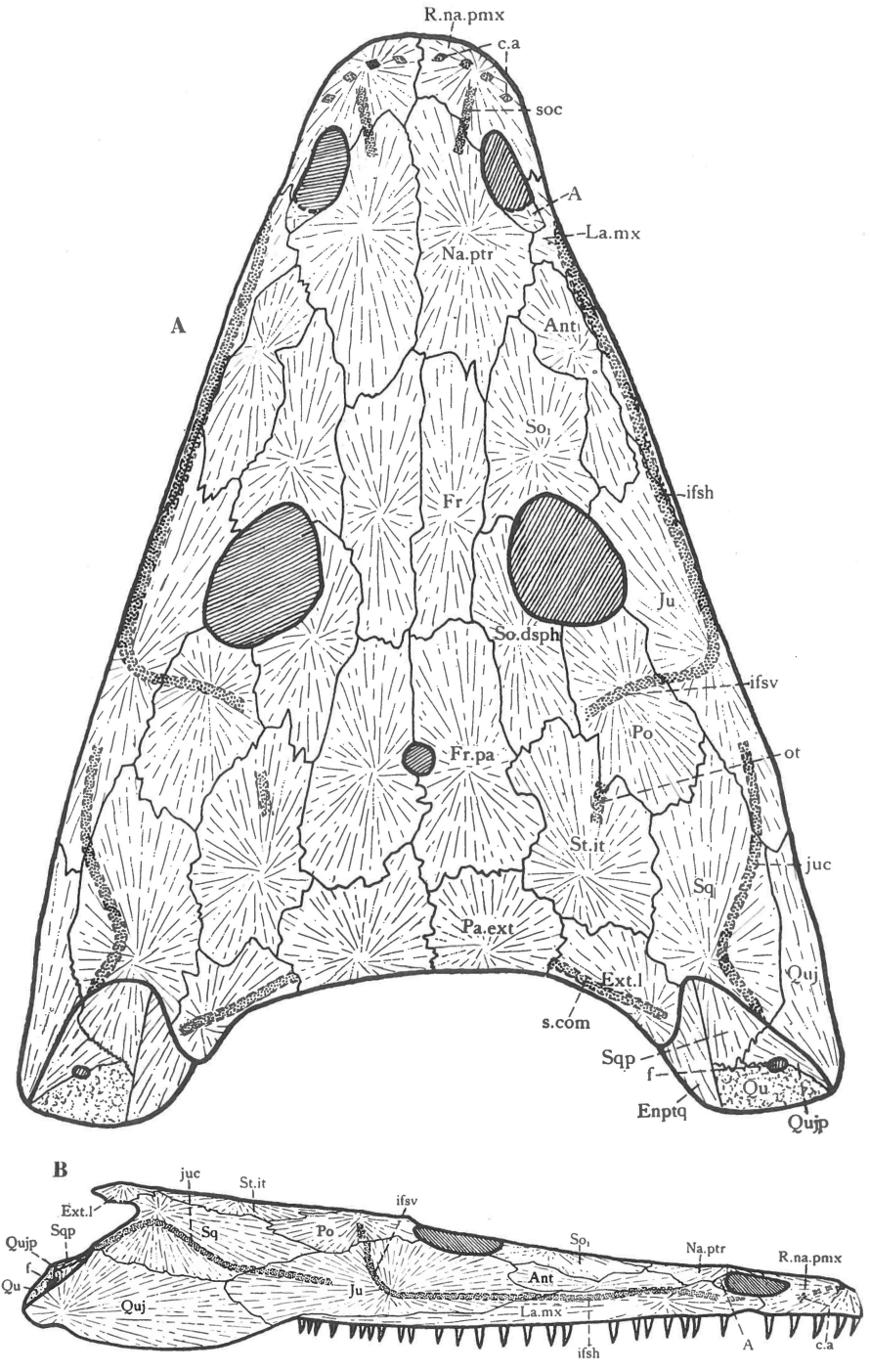
Description.

General shape. The well preserved type specimen shows that the present species had a triangular skull with a similar general shape as that found in *Lyrocephalus euri* WIMAN, from Spitsbergen. The skull is, however, markedly lower and narrower in the present species, and it also seems to be less pronouncedly triangular than that of *L. euri*, owing to the more obtuse form of the snout. The nostrils are possibly larger and more elongated, and the pineal foramen is situated nearer the orbital division of the dermal cranial roof in *L. kochi*.

The proportions of the skull in *L. kochi* will be evident from the following measurements taken from the type specimen:

Median length of the skull	118 mm
Breadth of the skull at the middle of the external nares	33 mm
Breadth of the skull at the middle of the orbits	70 mm
Breadth of the skull at the posterior ends of the quadratojugals	100 mm
Height of the skull	about 23 mm
Length of the prenarial division	16 mm
Length of the postnarial division	27 mm
Length of the preorbital division	19 mm
Length of the postorbital division	11 mm
Length of the prenuchal division	17 mm
Length of the nuchal division	12 mm
Length of the orbit	17 mm
Breadth of the orbit	15 mm

Dermal bones of the cranial roof and cheeks. The most



Text-fig. 60. *Lyrocephalus kochi* n. sp. A, dorsal, B, lateral aspect of the skull. *A*, slightly more than natural size; *B*, about $\frac{5}{6}$ natural size.

A, anterior antorbital or septomaxillary; *Ant*, posterior antorbital; *Enptq*, quadrate ramus of the entopterygoid; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-

anterior parts of each side of the skull are covered by the relatively long *naso-rostro-premaxillary* (*R.na.pmx*, pls. 7, 8; text-fig. 60). Each naso-rostro-premaxillary has a mainly straight median margin, with an interlocked suture towards the corresponding bone of the other side; the left one also has a short, straight suture towards the right naso-postrostral. Further the naso-rostro-premaxillaries have mainly concave posterior margins, joined by irregularly curved sutures with the naso-postrostrals, and with the lachrymo-maxillaries. Between these two sutures, there is a rather deep notch in the margin described, for the anterior part of the external naris. The anterior and antero-lateral margins of each naso-rostro-premaxillary form together a gently curved line, and along both of them there is a smooth ventral rim, just above the bases of the teeth. There are seven teeth in the left naso-rostro-premaxillary, and six in the right one. The teeth are all small, sharply pointed, and furrowed at the base, whereas the distal parts have a smooth surface.

On each naso-rostro-premaxillary there are seen traces of the ethmoidal commissure of the infraorbital canals (cf. below, p. 158).

The *naso-postrostrals* (*Na. ptr*, pl. 7; pl. 8, fig. 1; text-fig. 60) are elongated, and roughly pentagonal in shape. Each naso-postrostral has a long, mainly straight median margin, in suture with the naso-postrostral of the other side — that of the right one also with short sutures towards the left naso-rostro-premaxillary and the left frontal —; a short postero-medial margin, with an irregularly curved suture towards the frontal (the right one towards both frontals, the left one towards the left frontal only); a long mainly straight postero-lateral margin with sutures towards the anterior supraorbital, the posterior antorbital, the lachrymo-maxillary; a concave antero-lateral margin, forming the greatest part of the medial margin of the external naris, and certainly once meeting the anterior antorbital; and finally a mainly convex anterior margin, with an irregularly curved suture towards the naso-rostro-premaxillary (left side) or both naso-rostro-premaxillaries (right side).

The centre of development of each naso-postrostral is situated a little in front of the mid-point of the bone.

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parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Qu*, quadrate; *Quj*, quadratojugal; *Qujp*, posterior lamina of the quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *Sqp*, posterior lamina of the squamosal; *St. it*, supratemporo-intertemporal; *c. a*, anterior commissure of the infraorbital canals; *f*, foramen between the quadratojugal and the quadrate; *ifsh*, horizontal portion of the suborbital part of the infraorbital canal; *ifsv*, vertical portion of the suborbital part of the infraorbital canal; *juc*, jugal canal; *ot*, otic part of the infraorbital canal; *s. com*, supratemporal commissural canal; *soc*, supraorbital canal.

Traces of the supraorbital canal (*soc*, text-fig. 60 A; cf. below, p. 158) are seen on each naso-postrostral.

The *anterior antorbitals* (*A*, text-fig. 60) have fallen away in the present specimen, and are restored in text-fig. 60 after the other species of *Lyrocephalus* (cf. below, pp. 166—167, 173; text-figs. 61, 63, 64).

The roughly hexangular *posterior antorbitals* (*Ant*, pls. 7, 8; text-fig. 60) are excluded both from the orbits and from the external nares and the anterior antorbitals. They are long, and in the present state of the specimen they have a rather peculiar shape, owing to the very irregular course of the sutures of their long medial margins towards the anterior supraorbitals. This fact is, however, probably at least in part due to the circumstance that the bony substance is incompletely preserved, so that the mentioned suture is now shown partly on the surface of the bones, partly in deeper layers of them. — The long lateral margin of each posterior antorbital has a mainly straight suture towards the lachrymo-maxillary, which is also joined by a straight suture with the short antero-lateral margin of the posterior antorbital. The likewise short antero-medial margin of the posterior antorbital has an interlocked suture with the naso-postrostral; and the short postero-lateral and postero-medial margins are both in suture with the jugal.

The centre of development of the posterior antorbital is a little in front of the mid-point of the bone.

The *frontals* (*Fr*, pl. 7; text-fig. 60 A) are long and narrow, roughly quadrangular in shape. Each of them has long median and lateral, and short anterior and posterior margins, all meeting the surrounding bones in irregularly crenulated, but mostly mainly straight sutures. The lateral margin of each frontal meets the anterior supraorbital and the supra-orbito-dermosphenotic; the median margin of the right frontal meets the same margin of the left one and a very short part of the median margin of the left fronto-parietal, whereas the median margin of the left frontal meets that of the right one and a short part of the median margin of the right naso-postrostral. The anterior margin of each frontal meets the naso-postrostral in an irregularly curved suture; and the posterior margin has a mainly straight suture with the fronto-parietal.

The centre of development of each frontal is situated a little behind the mid-point of the bone.

The *anterior supraorbitals* (*So*$_1$, pls. 7, 8; text-fig. 60) are very long, and roughly triangular in shape, each with a posterior, a medial, and an antero-lateral side. The posterior side is formed by a short, gently curved suture towards the supraorbito-dermosphenotic, and a slightly concave orbital margin; the antero-lateral side is irregularly curved, and has a short posterior part in suture with the jugal, and a much longer anterior part, in suture with the posterior antorbital;

finally the long and gently convex medial margin is joined by sutures with the naso-postrostral and the frontal.

The centre of development of the anterior supraorbital is situated a little behind, and medially to, the mid-point of the bone.

Each of the long *supraorbito-dermosphenotics* (*So. dsph*, pl. 7; pl. 8, fig. 2; text-fig. 60 A) consists of a narrower anterior part, medially to the orbit, and a broader posterior part. It has a very short anterior margin, in suture with the anterior supraorbital; a long, slightly sigmoid medial margin, joined by sutures with the frontal, and with the fronto-parietal; a short postero-lateral margin with an interlocked suture towards the supratemporo-intertemporal; and a long lateral margin, consisting of a posterior part, in suture with the postorbital, and an anterior, concave part, forming the medial margin of the orbit.

The centre of development of each supraorbito-dermosphenotic lies near the mid-point of the bone.

The *fronto-parietals* (*Fr. pa*, pl. 7; text-fig. 60 A) are markedly shorter and broader than the frontals, and their posterior parts are broader than their anterior parts. Each fronto-parietal has four mainly straight margins: an anterior margin, with a suture towards the frontal; a lateral margin, joined by sutures with the supraorbito-dermosphenotic and the supratemporo-intertemporal; a posterior margin, in suture with the parieto-extrascapular; finally a median margin, with a notch, forming half of the pineal foramen, and sutures in front of and behind this foramen towards the fronto-parietal of the other side. The median margin of the left fronto-parietal also has a very short suture towards the right frontal, whereas the same margin of the right fronto-parietal has a short suture towards the left parieto-extrascapular.

The pineal foramen is situated at about the same distance from the anterior as from the posterior margins of the fronto-parietals.

The centre of development of each parieto-extrascapular is to be found laterally to the pineal foramen, near the mid-point of the bone.

The dorsal laminae of the *parieto-extrascapulars* (*Pa. ext*, pl. 7; text-fig. 60 A) are roughly pentagonal in shape, and the left one is somewhat longer than the right one. Each parieto-extrascapular has an anterior margin, joined by an irregularly curved suture with the fronto-parietal; a mainly straight, though finely zig-zag median margin, in suture with the corresponding bone of the other side of the skull, that of the left parieto-extrascapular also with a shorter part in suture with the right fronto-parietal; further an antero-lateral margin joined by suture with the supratemporo-intertemporal; a lateral margin, in suture with the lateral extrascapular; and a mainly straight or very slightly concave posterior margin.

The centre of development of each parieto-extrascapular lies rather far back, near the mid-point of the posterior margin of the bone.

The elongated *supratemporo-intertemporals* (*St. it*, pls. 7, 8; text-fig. 60) are also roughly pentagonal. Each of them has a short antero-medial margin, in suture with the supraorbito-dermosphenotic; a somewhat longer, slightly concave medial margin, in suture with the posterior half of the fronto-parietal; a short postero-medial margin with an irregularly curved suture towards the parieto-extrascapular; a mainly straight or zig-zag posterior margin, joined by suture with the lateral extrascapular; and finally a very long, convex lateral margin, joined by sutures with the postorbital and the squamosal.

The small *lateral extrascapulars* (*Ext. l*, pls. 7, 8; text-fig. 60) are only exposed from the dorsal side. Each of them shows a dorsal surface with a short medial margin, in suture with the parieto-extrascapular; a longer anterior margin, with an irregularly curved suture towards the supratemporo-intertemporal; an antero-lateral margin, in suture with the squamosal; a short free lateral margin forming part of the medial margin of the otic notch; and finally a very gently concave free posterior margin.

Each of the very long and low *lachrymo-maxillaries* (*La. mx*, pls. 7, 8; text-fig. 60) has a lower posterior and a higher anterior part. The posterior part has a long straight dorsal suture with the jugal, and a free ventral margin with 14 small pointed conical teeth. The anterior broader part of the lachrymo-maxillary has a short anterior suture with the naso-rostro-premaxillary below the external naris; a concave antero-medial margin towards the nostril; a short medial suture towards the naso-postrostral; a long, very gently concave medial suture towards the posterior antorbital; a shorter, slightly convex postero-medial suture towards the jugal; and finally a straight ventral margin with 10 small pointed conical teeth. The whole posterior part, and the ventral portion of the anterior part of the bone are not exposed in dorsal view (pl. 7; text-fig. 60 A), but the dorsal portion of the anterior part of the bone covers a lateral marginal part of the dorsal surface of the skull. This portion is connected with the anterior half of the horizontal portion of the suborbital part of the infraorbital canal (*ifsh*, pl. 8, fig. 1; text-fig. 60 B; cf. below), and is evidently homologous with the lachrymal of the Ichthyostegids and the Crossopterygians (cf. above p. 16, and SÄVE-SÖDERBERGH 1932, pp. 79, 101—102).

The positions of the centres of development of the lachrymo-maxillaries are not easy to find out in the present specimen. They seem, however, to have been situated near the dorsal margin of each lachrymo-maxillary, in the posterior parts of the high, anterior portion of the bone.

The large *jugals* (*Ju*, pls. 7, 8; text-fig. 60) are elongated bones, each with five margins. The long ventral margin of each jugal is joined by suture with the lachrymo-maxillary, and consists of a straight posterior and a gently concave anterior part. Its strongly sigmoid anterior margin has a short straight medial part, in suture with the anterior supraorbital, and a mainly concave lateral part, in suture with the posterior antorbital. The short, concave medial margin of each jugal forms the lateral margin of the orbit; and the long very slightly undulating postero-medial margin of the same bone is joined by suture with the postorbital and the squamosal. Finally the jugal has a short postero-lateral margin, with a suture towards the quadratojugal. The centre of development of the jugal is situated in the mid-length of the bone, but very near its ventral margin.

Each *squamosal* consists of two parts, one sculptured dorso-lateral lamina (*Sq*, pls. 7, 8; text-fig. 60) forming part of the external surface of the skull, and another smooth lamina, facing posteriorly (*Sqp*, pl. 7; text-fig. 60). The sculptured lamina of the squamosal is roughly quadrangular in shape. It has a very long convex ventral (lateral) margin, joined by sutures with the jugal and the quadratojugal; a short concave antero-medial margin, with a suture towards the postorbital; an irregularly curved medial margin with a short sharply zig-zag suture towards the lateral extrascapular and a much longer suture towards the supratemporo-intertemporal; and a concave free postero-medial and posterior margin, joined to the smooth part of the squamosal, and forming the antero-lateral, anterior, and part of the antero-medial margin of the otic notch.

The posteriorly facing smooth lamina of the squamosal (*Sqp*, pl. 7; text-fig. 60) has an external surface with a marked triangular depression (housing the m. depressor mandibulae according to WATSON's interpretation in *Lydekkerina*, 1919 b, p. 14), bounded by gentle ridges dorso-laterally and medially, but ventrally continuing on the quadratojugal. This part of the squamosal is joined by sutures with the quadratojugal (ventrally) and meets the dorsal margin of the quadrate ramus of the entopterygoid.

The centre of development of the squamosal is situated near the posterior margin of the dorso-lateral lamina, and in the dorsal half of the bone.

The sculptured external surface of the squamosal shows a discontinuous groove for a typical jugal canal (cf. below, p. 159).

The *quadratojugal* of each side has a smooth posterior, and a sculptured lateral lamina. The latter (*Quj*, pls. 7, 8, text-fig. 60) is quadrangular in shape and has a long, markedly convex, free ventral

margin; a short antero-medial margin, in suture with the jugal; a longer dorsal (medial) margin, in suture with the squamosal; and a short, straight, postero-medial margin, joined to the smooth posterior lamina of the quadratojugal. The external surface of this latter lamina (*Qujp*, pl. 7; text-fig. 60) is divided by a small ridge (parallel to the postero-medial margin of the sculptured surface). Laterally to the ridge there is a long groove; whereas medially to the ridge there is a more irregularly shaped, but mainly concave part of the surface. In this part, near the ridge, and just at the boundary towards the quadrate (*Qu*, pl. 7; text-fig. 60), there is a circular foramen (*f*, pl. 7; text-fig. 60), with its opening directed posteriorly and slightly postero-dorsally.

The smooth posterior lamina of the quadratojugal has a dorsal suture towards the squamosal, and a ventral boundary towards the quadrate (*Qu*, pl. 7; text-fig. 60).

The centre of development of the quadratojugal is situated near the posterior end of the bone.

The ornamentation of the dermal bones is in part well preserved. As a general rule on each dermal bone there may be distinguished a central field, around the centre of development, and a peripheral field. In the central field the ornamentation consists of small rounded pits, separated by reticulating ridges. In the peripheral field the pits are elongated and arranged in distinct rows, radiating from the centre of the bone, and the ornamentation may also be described as consisting of radiating, discontinuous grooves, separated by a system of long radiating and short transverse ridges.

The ornamentation, though not very coarse, is of a coarser type than that found in *Wetlugasaurus groenlandicus* (cf. above p. 129).

Dermal bones of the palate. The *palate* is not exposed at all in the present state of the specimen and will not be prepared because the specimen is to be investigated by SOLLAS' grinding-method.

Lateral line system of the head. Only very short most anterior parts are preserved of the grooves for the *supraorbital canals* (see pl. 7; *soc*, text-fig. 60 A).

The position of the *ethmoidal commissure of the infraorbital canals* (*c. a*, pl. 7; text-fig. 60 A) is indicated by a series of short grooves across the naso-rostro-premaxillaries. There are at least four short grooves on the right side, and four on the left.

The course of the horizontal portion of the *suborbital part of the right infraorbital canal* (*ifsh*, pl. 7; pl. 8, fig. 1; text fig. 60) is clearly shown by a groove, extending from a point below the middle of the nostril over the dorsal half of the anterior part of the lachrymo-maxillary and the anterior half of the jugal to near the centre of development of

the latter bone. In the jugal the groove runs near, and parallel to, the ventral margin of the bone.

The posterior end of the groove for the horizontal portion is directly continuous with the groove for the vertical portion of the suborbital part of the infraorbital canal; the former bends from a posterior to a dorsal direction and merges into the latter.

The vertical portion of the suborbital part was situated in a straight, partly discontinuous groove (*ifsv*, pl. 7; pl. 8, fig. 1; text-fig. 60), running from the posterior end of the horizontal portion dorsally over the jugal and the anterior half of the postorbital.

A short groove for the *otic part of the infraorbital canal* (*ot*, pl. 7; text-fig. 60 A) is shown in the right supratemporo-intertemporal.

The discontinuous groove for the *jugal canal* (*juc*, pl. 7; pl. 8, fig. 1; text-fig. 60) has a course which is rather interesting. After a straight course in the posterior part of the jugal the canal merges into the squamosal. Here it soon bends in a postero-dorsal direction and runs back to near the centre of development of the squamosal. Then it bends sharply in a postero-ventral direction and continues to the extreme posterior end of the sculptured part of the squamosal.

The *preopercular canal* may possibly have been situated in the groove described above in the smooth posteriorly facing part of the quadratojugal (this bone then probably representing a preoperculo-quadratojugal), but it seems at least equally probable that it was either absent or situated in soft parts only.

A groove for part of the *supratemporal commissural canal* (*s. com*, pl. 7; text-fig. 60 A) is clearly shown in the right lateral extrascapular.

Horizon. Uppermost part of the fish-horizon in the uppermost zone of the *Otoceras* Beds (cf. pp. 194—196; Koch 1931; and Nielsen 1934).

Locality. Cape Stosch, Spath Plateau, Stegocephalian Ridge (between the two branches of River 7; cf. Koch 1931, Nielsen 1934).

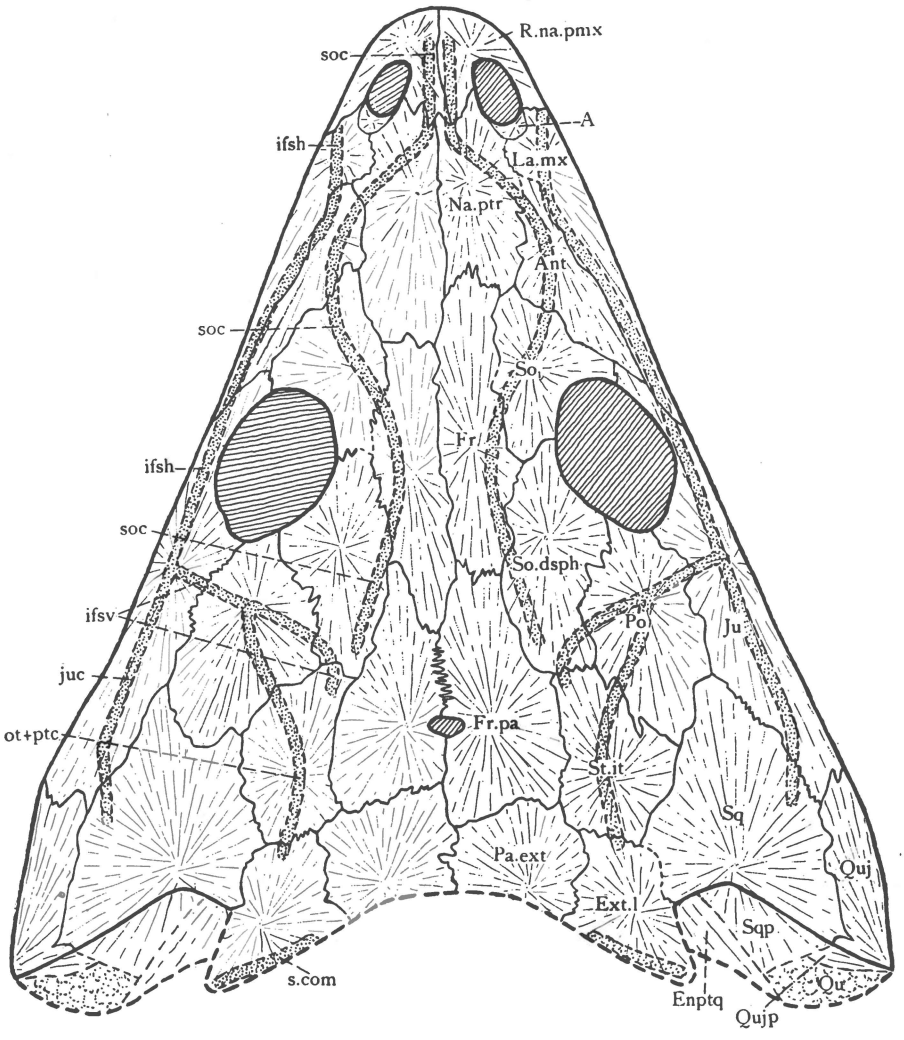
Remarks. In the parts known at present the specimen here discussed does not differ so decidedly from the Spitsbergen species *Lyrocephalus euri* Wiman as to justify the erection of a new genus. The differences are just important enough to justify a specific separation of the two forms discussed. Thus for the time being we have to include (with reservation) the specimen here described in the genus *Lyrocephalus* Wiman, and for the new species it represents I propose the name *L. kochi*, after the leader of the Danish East Greenland Expeditions and the Chief of the Geological Survey of Greenland, Dr. Lauge Koch.

To show more clearly the differences between the new species and that from Spitsbergen I give below a diagnosis also of *L. euri*, and a figure of the skull in dorsal view (text-fig. 61), mainly after a specimen which belongs to the Palaeontological Institute of Uppsala, and is at present being investigated by SOLLAS' grinding-method.

Diagnosis of *Lyrocephalus euri* WIMAN:

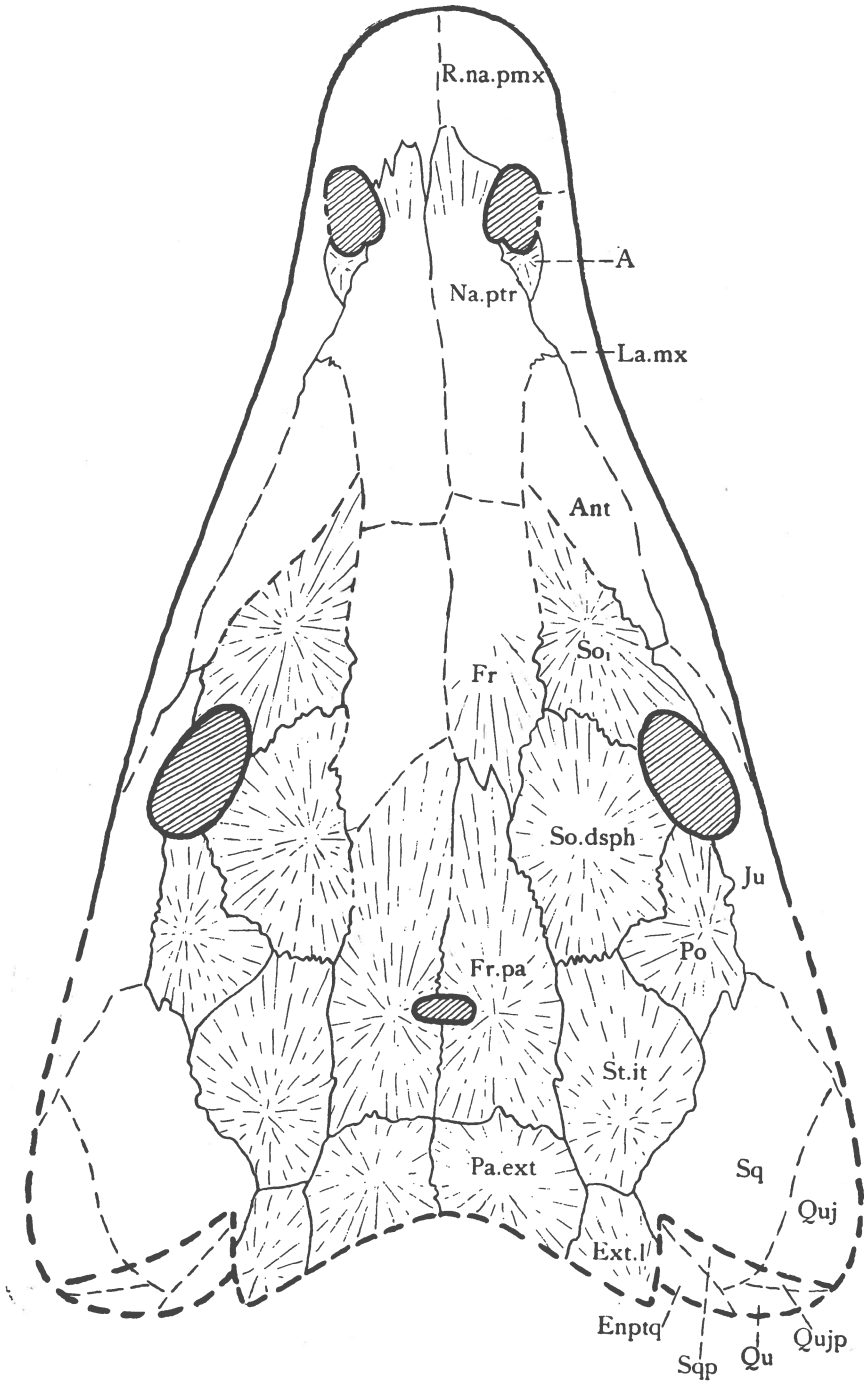
Skull triangular, higher and broader than that of *L. kochi* in its posterior parts (maximum breadth about 0.95—1.00 of the median length of the skull), with short external nares and medium-sized orbits. With medium-sized prenarial, long postnarial, short preorbital and medium-sized postorbital, prenuchal, and nuchal divisions of the dermal cranial roof. Distance between the orbits about 0.81 of the distance from the anterior margin of the orbit to the posterior margin of the external naris, and about 0.55 of the distance from the anterior margin of the orbit to the anterior margin of the skull. Distance from the pineal foramen to the posterior margin of the orbital division of the dermal cranial roof as long as, or longer than the maximum length of the orbits. Distance from the posterior margin of the orbit to the posterior end of the cheek longer than the distance from the posterior margin of the orbit to the posterior margin of the external naris. Naso-rostro-premaxillaries long (median length about as great as the breadth of each bone). Anterior supraorbitals not very long, much shorter than the maximum length of the orbits. Frontals extending markedly behind the posterior margin of the orbital division of the dermal cranial roof. Pineal foramen markedly nearer the posterior than the anterior margins of the fronto-parietals. Length of each parieto-extrascapular about $1^1/_3$ or more of the breadth of the bone. Grooves for the supraorbital canals situated very close together on the most anterior parts of the naso-postrostrals, between the external nares (distance between the grooves less than the distance from each of the grooves to the external naris). Groove for the jugal canal only with a very short, straight part in the squamosal.

The greater difference between the two species ascribed to the genus *Lyrocephalus*, on the one hand, and the other genus of the *Lyrocephalinae*, *Platystega*, on the other hand will be evident from the following diagnoses of the two genera, and the accompanying figures (text-figs. 60, 61, 62).



Text-fig. 61. *Lyrocephalus euri* WIMAN. Dorsal aspect of the skull. After specimens belonging to the Palaeontological Institute of Uppsala. $\frac{3}{4}$ natural size.

A, anterior antorbital or septomaxillary; *Ant*, posterior antorbital; *Enptq*, quadrate ramus of the entopterygoid; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Qu*, quadrate; *Quj*, qudratojugal; *Qujp*, posterior lamina of the quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *Sqp*, posterior lamina of the squamosal; *St. it*, supratemporo-intertemporal; *ifsh*, horizontal portion of the suborbital part of the infraorbital canal; *ifsv*, vertical portion of the suborbital part of the infraorbital canal; *juc*, jugal canal; *ot + ptc*, otic part of the infraorbital canal and postotic canal; *s. com*, supratemporal commissural canal; *soc*, supraorbital canal.


R.na.pmx
A
Na.ptr
La.mx
Ant
So
Fr
So.dsph
Ju
Po
Fr.pa
St.it
Pa.ext
Sq
Quj
Ext.l
Enptq
Sqp
Qu
Qujp

Text-fig. 62.

Diagnosis of the genus *Lyrocephalus* WIMAN:

Lyrocephalinae with low triangular skulls, with nearly straight, very slightly convex lateral margins. With small or medium-sized orbits. With medium-sized prenarial, long or medium-sized postnarial, short or medium-sized preorbital (medium-sized or long postnarial+preorbital), short or medium-sized postorbital, and medium-sized prenuchal and nuchal divisions of the dermal cranial roof. Anterior antorbitals (septomaxillaries) with comparatively broad and short facial parts, not markedly longer than broad. Anterior supraorbitals with normally long sutures towards the supraorbito-dermosphenotics. Supraorbito-dermosphenotics with narrow anterior parts medially to the orbits.

Diagnosis of the genus *Platystega* WIMAN:

Lyrocephalinae with very low, long skulls, with lateral margins, concave in their anterior halves, so that the skull has a comparatively narrow snout. External nostrils with markedly bipartite posterior margins consisting of two concave parts. With very small orbits. With long prenarial, long postnarial+preorbital, short postorbital, medium-sized prenuchal, and probably short nuchal divisions of the dermal cranial roof. Anterior antorbitals (septomaxillaries) with elongated facial parts, markedly longer than broad, each with a sigmoid anterior margin, the lateral part of which forms the lateral one of the concave parts of the bipartite posterior margin of the external nostril. Anterior supraorbitals with very long sutures towards the supraorbito-dermosphenotics. Supraorbito-dermosphenotics broad in their anterior parts, even broader than in the posterior parts, situated behind the orbital division of the dermal cranial roof.

Text-fig. 62. *Platystega depressa* WIMAN. Attempted restoration of the dorsal side of the skull, after WIMAN 1914, and the type specimen. $\frac{1}{2}$ natural size. *A*, anterior antorbital or septomaxillary; *Ant*, posterior antorbital; *Enptq*, quadrate ramus of the entopterygoid; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, frontoparietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Qu*, quadrate; *Quj*, quadratojugal; *Qujp*, posterior lamina of the quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *Sqp*, posterior lamina of the squamosal; *St. it*, supratemporo-intertemporal.

Lyrocephalus johanssoni n. sp.

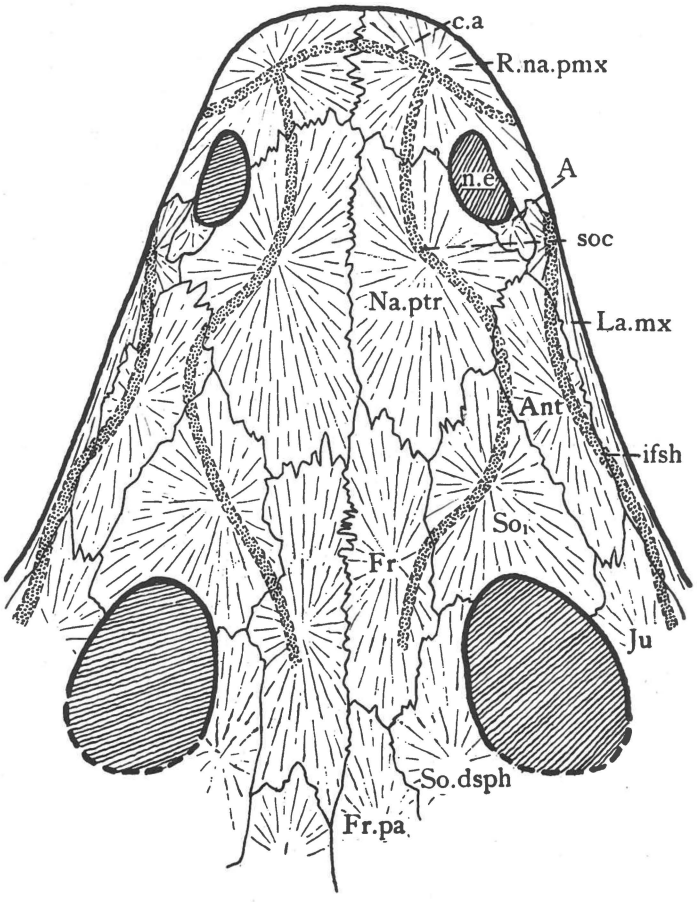
(Pl. 9, figs. 1, 2; pl. 10, figs. 1, 2, 3; text-fig. 63).

Diagnosis: Anterior parts of the skull similar to the corresponding parts in *Lyrocephalus kochi*, but shorter and broader than in that species. Distance between the orbits about 0.40—0.42 of the distance from the anterior margin of the orbit to the anterior margin of the skull, and about 0.70 of the distance from the anterior margin of the orbit to the posterior margin of the external naris. Naso-rostro-premaxillaries short and broad (median length shorter than the breadth of the bones). Anterior supra-orbitals not very long, probably not markedly longer than the maximum length of the orbits. Frontals probably extending as far back as the posterior margin of the orbital division of the dermal cranial roof. Supraorbital canals widely separated also in the most anterior parts of the naso-postrostrals, between the external nares: each supra-orbital canal running nearer to the external naris than to the median margin of the naso-postrostral.

Holotype. Specimen *At.* 28: The anterior parts of a skull, preserved as far back as the middle of the right orbit, the most anterior parts of the fronto-parietals, the antero-medial third of the left orbit, and the posterior parts of the left posterior antorbital. The dermal bones of the cranial roof and cheeks preserved in this specimen include: both naso-rostro-premaxillaries, naso-postrostrals, and frontals; the right posterior antorbital and anterior supraorbital, and most of the left posterior antorbital and anterior supraorbital; the anterior parts of the supraorbito-dermosphenotics, the fronto-parietals, and the lachrymo-maxillaries; and the most anterior part of the right jugal. In the palate, part of the processus cultriformis of the parasphenoid is exposed. Very fragmentary parts of the lower jaw are also shown in this specimen.

Description.

General shape. Though only the anterior parts of the skull are known in the present species, it is clear that in the general shape *L. johanssoni* was very similar to *L. kochi*. However, as shown by the comparison of the distance between the orbits and that between the orbit and the nostril, the anterior parts of the skull are evidently comparatively shorter and broader in *L. johanssoni*. The snout is still more obtuse than in *L. kochi*, and even shows a straight anterior margin. The external nares are elongated, though probably broader than in *L. kochi*. The imperfectly shown orbits may have had approximately the same shape as in *L. kochi*.



Text-fig. 63. *Lyrocephalus johanssoni* n. sp. Restored dorsal aspect of the anterior part of the skull. $\frac{3}{2}$ natural size.

A, anterior antorbital or septomaxillary; *Ant*, posterior antorbital; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *c. a*, anterior commissure of the infraorbital canals; *ifsh*, horizontal portion of the suborbital part of the infraorbital canal; *n. e*, external nostril; *soc*, supraorbital canal.

The parts preserved of the skull of *L. johanssoni* have the following dimensions:

Median length of the fragment	81 mm
Breadth over the middle of the external nares	35 mm
Restored breadth over the middle of the orbits ..... about	61 mm
Distance between the orbits	23 mm
Distance from the anterior margin of the orbit to the anterior margin of the skull	55 mm

Dermal bones of the cranial roof and cheeks. The *naso-rostro-premaxillaries* (*R. na. pmx*, pl. 9, figs. 1, 2; pl. 10, figs. 1, 3; text-fig. 63) are large and roughly quandrangular in shape, with nearly straight anterior and lateral free margins; a median margin with a finely zig-zag suture towards the corresponding bone of the other side, that of the right one also with a suture towards the left naso-postrostral; finally a tripartite posterior, or postero-medial margin, consisting of a medial part, joined by a zig-zag suture to the naso-postrostral, a concave middle part, forming the margin of the anterior part of the external nostril, and a short lateral part with an irregularly curved suture towards the lachrymo-maxillary.

On the ventral side, along the anterior and lateral margins, each naso-rostro-premaxillary is armed by a number of small, pointed, labyrinthic teeth (*dpmx*, pl. 10, fig. 2), 15 on the left bone, and at least 9 on the right one.

The centre of development of each naso-rostro-premaxillary is situated in the middle of the antero-lateral half of the bone.

In the naso-rostro-premaxillaries of the present specimen there are beautifully clear grooves for the ethmoidal commissure of the infra-orbital canals, and for the most anterior parts of the supraorbital canals (cf. below, p. 169).

In their general shape the *naso-postrostrals* (*Na. ptr*, pl. 9, figs. 1, 2; pl. 10, figs. 1, 3; text-fig. 63) of the present species are very similar to those of *L. kochi*, but they are a little shorter and broader than in that species. Further they differ from the same bones of *L. kochi* in the minute shape of the margins, and by the fact that the left naso-postrostral has a very short suture towards the right naso-rostro-premaxillary, and a longer suture towards the right frontal.

The centre of development of each naso-postrostral is situated, as in *L. kochi*, postero-medially to the external nostril, in the antero-lateral half of the bone.

Both naso-postrostrals are connected with parts of the grooves for the supraorbital canals (cf. below, p. 169).

The facial, exposed part of the *anterior antorbital* or septomaxillary (*A*, pl. 9, fig. 2; pl. 10, figs. 1, 3; text-fig. 63) is preserved on the left side, but is lost on the right. It is a small, triangular bony lamina with a concave anterior margin towards the external nostril, mainly straight or convex, postero-medial and antero-lateral margins and a rounded posterior end. Its antero-lateral margin is joined by suture to the lachrymo-maxillary, whereas its postero-medial margin is in suture with the naso-postrostral. Its posterior end seems to meet the posterior antorbital (the figures are probably a little incorrect in this detail). The centre of development of the anterior antorbital is near the anterior margin

of the exposed part of the bone, where the facial part is joined to the smooth intranarial part of the bone. The intranarial part forms a horizontal floor in the posterior part of the naris.

The elongated *posterior antorbitals* (*Ant*, pl. 9, figs. 1, 2; pl. 10, figs. 1, 3; text-fig. 63) have a more normal shape than in *L. kochi*, since their medial margins, joined by sutures with the anterior supraorbitals, are mainly straight, only slightly crenulated. Otherwise they agree with the same bones of *L. kochi* in all important points, and like these they are cut off from both the external nostrils and the orbits, by the presence of the anterior antorbitals and the meeting of the anterior supraorbitals with the jugals. Each posterior antorbital has its centre of development slightly laterally (ventrally) to the mid-point of the bone, and its ventral half has a curved groove for part of the horizontal portion of the suborbital part of the infraorbital canal, and another very short groove for a part of the supraorbital canal just laterally to the meeting-point of the posterior antorbital, the naso-postrostral and the anterior supraorbital (cf. below, p. 169).

The *frontals* (*Fr*, pl. 9, fig. 2; pl. 10, fig. 3; text-fig. 63) of the present specimen are actually preserved in their anterior parts, whereas the shape of their posterior parts is shown by sharp impressions. The bones discussed are relatively shorter than in *L. kochi*. The right frontal is situated very far forward, its posterior margin extending about as far back as the middle of the orbits only, whereas the left frontal probably reached farther back than the posterior margins of the orbits. Accordingly the right frontal has a part of its median margin joined by suture with the left naso-postrostral; and the left frontal has a remarkably long part of its median margin in suture with the right fronto-parietal. The posterior margin of the left frontal, in suture with the left fronto-parietal, has a strongly irregular shape. Otherwise there are only unimportant differences in the minute shape of the margins of the frontals between the present specimen and the type specimen of *L. kochi* already described.

The centre of development of each frontal is near, or in front of, the mid-point of the bone.

In the most postero-lateral part of the preserved portion of each frontal (i. e. once in the middle of the lateral half of each frontal), there is a longitudinal groove for a part of the supraorbital canal (cf. below, p. 169).

The triangular *anterior supraorbitals* (*So*$_1$, pl. 9, figs. 1, 2; pl. 10, fig. 3; text-fig. 13) are markedly shorter and broader in the present specimen than in *L. kochi*. Otherwise each of them agrees in most characters with the corresponding bone of the last-mentioned species, and has a long convex medial margin, with sutures towards the frontal and the

naso-postrostral; a similarly long lateral margin with a nearly straight suture towards the posterior antorbital, and a sigmoid suture towards the jugal (at least on the right side); and a bipartite posterior margin, consisting of a small medial part, with an irregularly curved suture towards the supraorbito-dermosphenotic, and a large, strongly concave lateral part, forming the anterior margin of the orbit.

The centre of development of each anterior supraorbital is situated about the mid-length of the bone, but nearer the medial than the lateral margin of the bone. A groove for part of the supraorbital canal runs over the antero-medial half of the anterior supraorbital. Though, as will be evident from above (pp. 15, 72; text-fig. 2), this canal is probably not phylogenetically or embryologically connected with the bone mentioned, it is interesting to find that the groove runs over the centre of development of the anterior supraorbital.

Of the *supraorbito-dermosphenotics* (*So. dsph*, pl. 9, fig. 2; text-fig. 63) only the narrow anterior parts, situated medially to the orbits, are preserved. In general shape and in their relations to the surrounding bones these parts agree in the main with the corresponding parts in *L. kochi*, except that the medial margin of the right supraorbito-dermosphenotic seems to have had a very irregularly curved suture towards the right frontal.

The very fragmentary impressions of the most anterior parts of the *fronto-parietals* (*Fr. pa*, pl. 9, fig. 2; text-fig. 63) only show that these bones were narrower in their anterior parts and had more irregular anterior margins than in the specimen of *L. kochi* described above.

Of the *lachrymo-maxillaries* (*La. mx*, pl. 9, figs. 1, 2; pl. 10, figs. 1, 3; text-fig. 63) the present specimen shows only the anterior parts, including the whole high part (with the lachrymal component) on the right side, and a little less than half of this part on the left. The parts preserved agree in shape with the corresponding parts in *L. kochi*. They are clearly connected with the most anterior parts of the horizontal portions of the suborbital parts of the infraorbital canals (cf. below, p. 169). Twelve small pointed teeth are preserved on the right lachrymo-maxillary, and 9 on the left.

The preserved most anterior part of the right *jugal* (*Ju*, pl. 9, figs. 1, 2; text-fig. 63) does not differ in any important respect from the corresponding part in *L. kochi*.

The ornamentation of the external surfaces of the dermal bones seems to be of a type, very similar to that found in *L. kochi* (cf. above, p. 158).

Dermal bones of the palate. In the oblique section through the skull, shown in pl. 10, fig. 1, there is seen a large fragmentary tooth (*dp*, pl. 10, fig. 1), probably situated in the left *dermopalatine*

(cf. below, p. 176; pl. 12, fig. 1). Another fragmentary tooth is found further back on the right side, and probably belongs to the *ectopterygoid*.

Otherwise the only part exposed in the palate of the present specimen is the processus cultriformis of the *parasphenoid* (*Pspc*, pl. 10, fig. 2), narrower posteriorly, broader anteriorly, and armed with small granular teeth in its posterior parts.

The lower jaw (*Md*, pl. 9, fig. 1; pl. 10, figs. 1, 2, 3) is too imperfectly preserved to be closely described.

Lateral line system of the head. The grooves for the lateral line canals are unusually well preserved in the present specimen.

The grooves for the *supraorbital canals* (*soc*, pl. 9, figs. 1, 2; text-fig. 63) are very clearly shown. Each of them begins at the centre of development of the naso-rostro-premaxillary, where it is directly continuous with the groove for the ethmoidal commissure of the infraorbital canals. Then the groove for the supraorbital canal runs in a slightly curved line, with its convexity directed medially back to the centre of development of the naso-postrostral. Here it bends markedly postero-laterally and continues in a more strongly curved line, with the convexity directed laterally, runs over the lateral part of the naso-postrostral, the most medial part of the posterior antorbital, the antero-medial half of the anterior supraorbital, and the lateral half of the middle third of the frontal. It is not preserved farther back in the present specimen.

The *ethmoidal commissure of the infraorbital canals* was evidently situated in a slightly curved groove (*c. a*, pl. 9, fig. 2) extending across the naso-rostro-premaxillaries.

The groove for the horizontal portion of the *suborbital part of the infraorbital canal* (*ifsh*, pl. 9, figs. 1, 2; pl. 10, fig. 1; text-fig. 63) is best preserved on the right side. Beginning in the dorsal half of the most anterior part of the lachrymo-maxillary, it runs first straight posteriorly, then it turns slightly dorso-posteriorly and merges into the posterior antorbital. In the middle of this bone it again makes a gentle bend and turns slightly postero-ventrally, passing once more over a dorsal marginal part of the lachrymo-maxillary, finally continuing straight posteriorly in the anterior part of the jugal. Its more posterior parts are not preserved.

Horizon. Uppermost part of the Middle *Vishnuites* Zone (cf. below, pp. 194—196; Koch 1931; Nielsen 1934).

Locality. Cape Stosch, Stensiö Plateau, Ridge IX (cf. Nielsen 1934).

Remarks. The characters enumerated in the diagnosis clearly

justify the erection of a new species for the specimen discussed. However, in many important characters it closely agrees with *Lyrocephalus kochi* and thus for the time being it is included in the same genus, *Lyrocephalus*, though with reservation for the possibility that the investigation of the endocranium, and of other as yet unknown parts, may show differences important enough to necessitate the erection of a new genus.

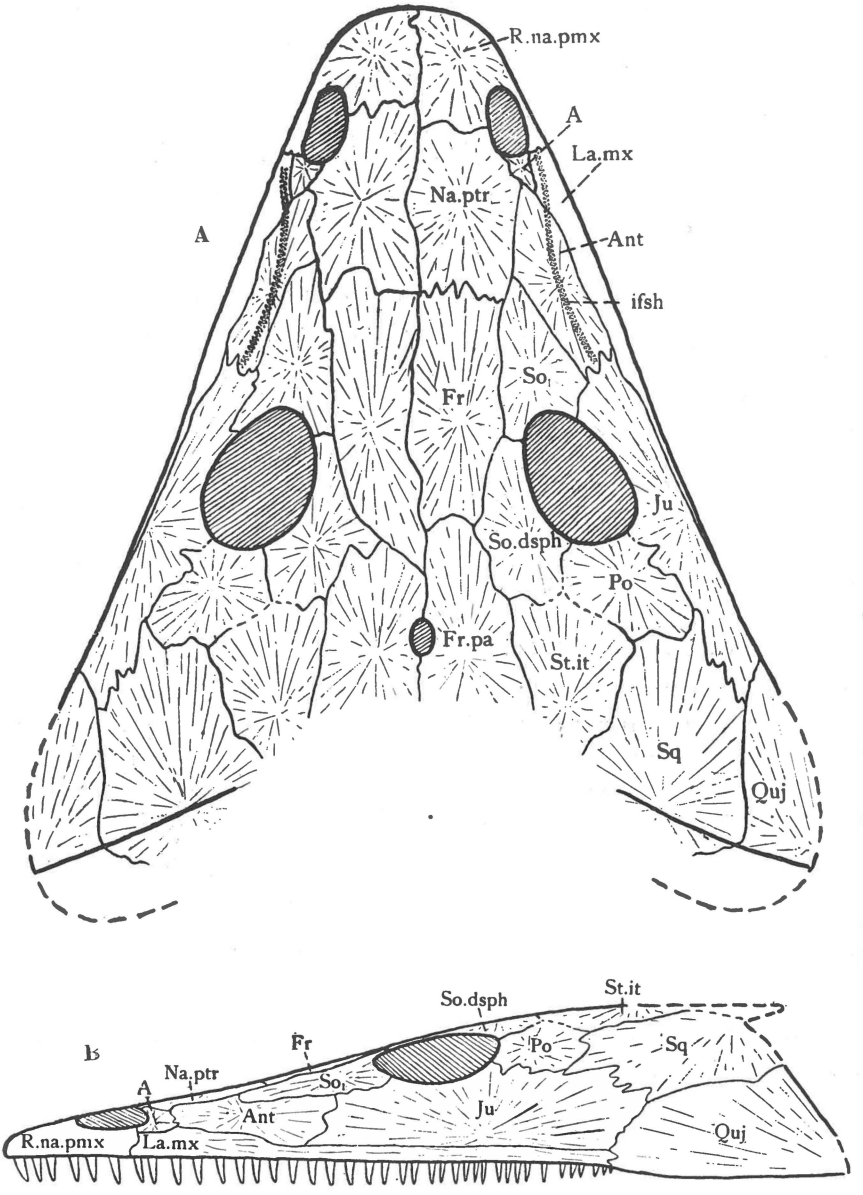
Lyrocephalus johanssoni is named in honour of Mr. E. JOHANSSON, who assisted Mr. NIELSEN in collecting Triassic Vertebrates during part of the summer expedition 1932.

Lyrocephalus rapax n. sp.

(Pl. 11, figs. 1, 2; pl. 12, figs. 1, 2; text-figs. 64, 65).

Diagnosis: Skull triangular, comparatively low and narrow (maximum breadth probably about 0.85 of the median length of the skull; maximum height about 0.20—0.25 of the median length of the skull). With elongated external nares, and medium-sized orbits, situated relatively near the lateral margins of the skull. With medium-sized prenarial, postnarial, and preorbital, short post-orbital, and medium-sized prenuchal divisions of the dermal cranial roof. Distance between the orbits about 0.45—0.47 of the distance from the anterior margin of the orbit to the anterior margin of the skull, and about 0.82 of the distance from the anterior margin of the orbit to the posterior margin of the external naris. Distance from the pineal foramen to the posterior margin of the orbital division of the dermal cranial roof about half the maximum length of the orbits. Distance from the posterior margin of the orbit to the posterior end of the cheek much shorter than the distance from the posterior margin of the orbit to the posterior margin of the external naris. Naso-rostro-premaxillaries long (median length about as great as the breadth of the bones). Anterior supraorbitals not very long, only very slightly longer than the maximum length of the orbits. Frontals extending as far back as the posterior margin of the orbital division.

Holotype. Specimen *At.* 29: The internal cast of an imperfect skull, lacking its right postero-lateral parts, — with fragmentary remains of certain dermal bones of the cranial roof and cheeks, and with large



Text-fig. 64. *Lyrocephalus rapax* n. sp. A, restored dorsal aspect of the greater part of the skull; B, restored lateral aspect of the skull. A, $\frac{6}{5}$ natural size; B, nearly natural size.

A, anterior antorbital or septomaxillary; *Ant*, posterior antorbital; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Po*, postorbital; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *ifsh*, horizontal portion of the suborbital part of the infraorbital canal.

parts of the dermal bones of the palate (lacking the most posterior and right postero-lateral parts).

Description.

General shape. As will be evident from pl. 11, figs. 1, 2, and pl. 12, figs. 1, 2, the present skull is of the same general type as those of the other members of the genus *Lyrocephalus*. In the shape of the anterior parts of the skull, with narrow prenarial division of the dermal cranial roof, and in the position of the orbits near the lateral margins of the skull, it is most similar to *L. euri*, but differs very markedly from that species by the relative shortness of the distance from the orbit to the posterior end of the cheek. The shortness of the distance from the pineal foramen to the posterior margin of the orbital division indicates that possibly the whole posterior part of the skull was shorter in the present species than in the other members of the genus *Lyrocephalus*.

The exact proportions of the type specimen of *L. rapax* will be evident from the following measurements:

Median length of the fragment	80 mm
Restored maximum breadth of the skull	about 78 mm
Height of the skull	about 21 mm
Breadth over the middle of the external nares	29 mm
Breadth over the middle of the orbits	about 56 mm
Distance from the anterior end of the skull to the pineal foramen	70 mm
Distance from the anterior margin of the orbit to the anterior margin of the skull	49 mm
Maximum length of the orbits	18 mm
Breadth of the orbits	14 mm
Distance from the posterior margin of the orbit to the posterior end of the cheek	about 43 mm

Dermal bones of the cranial roof and cheeks. The *naso-rostro-premaxillaries* (*R. na. pmx*, pl. 11, figs. 1, 2; pl. 12, fig. 2; text-fig. 64) differ from the corresponding bones in *Lyrocephalus kochi* and *L. johanssoni* in that they are longer than they are broad and lack any definite anterior margins. In this respect they agree with the corresponding bones of *L. euri*. Otherwise they agree in all important points with the corresponding bones of the other two species from East Greenland. The bony substance is for the greatest part worn off, and it is impossible to state the position of the centres of development of the bones discussed. Several of the small teeth (*dpmx*, pl. 12, fig. 1) of the naso-rostro-premaxillaries are preserved in the present specimen.

The *naso-postrostrals* (*Na. ptr*, pl. 11, figs. 1, 2; text-fig. 64) were evidently very similar in shape to those of *L. johanssoni*, but owing

to the fact that the bony substance is almost totally worn off, it is sometimes difficult to state with certainty the course of the sutures towards the surrounding bones. It seems, however, that the naso-postrostrals (and especially the right one) of the present specimen have had shorter parts of their postero-lateral margins joined by sutures with the anterior supraorbitals.

The left naso-postrostral has a short extreme anterior part of its median margin in suture with the right naso-rostro-premaxillary, and the most posterior part of the same margin has a very short suture towards the right frontal.

The sharp impression of the facial part of the left *anterior antorbital* or septomaxillary and the preserved bone on the right (*A*, pl. 11, figs. 1, 2; pl. 12, fig. 2; text-fig. 64) show that this bone had quite the same shape as in *L. johanssoni*. Its posterior end clearly met the posterior antorbital in a distinct suture, forming part of the long postero-medial margin of the bone. Also the intranarial part of the anterior antorbital was quite similar to the corresponding part in *L. johanssoni*.

The *posterior antorbitals* (*Ant*, pl. 11, figs. 1, 2; pl. 12, fig. 2; text-fig. 64) are also essentially similar to those of *L. johanssoni*, though a little shorter and broader. The right one shows a groove for part of the horizontal portion of the suborbital part of the infraorbital canal (cf. below, p. 177).

The *frontals* (*Fr*, pl. 11, fig. 1; text-fig. 64), as usual, are quadrangular in shape, with short anterior and posterior, and long lateral and median margins, joined by irregularly curved sutures respectively to the naso-postrostrals, the fronto-parietals, the anterior supraorbitals and supraorbito-dermosphenotics, and the frontal of the other side. The median margin of the right frontal has a short extreme anterior part in suture with the left naso-postrostral; and the most posterior part of the median margin of the left frontal has a short suture with the right fronto-parietal.

The centre of development of each frontal is situated very markedly behind the mid-point of the bone.

The *anterior supraorbitals* (So_1, pl. 11, figs. 1, 2; pl. 12, fig. 2; text-fig. 64) are relatively small and narrow in the present specimen. In their triangular general shape, as well as in their relations to the surrounding bones, they agree with the anterior supraorbitals of the other species of *Lyrocephalus*, except that they have remarkably short sutures towards the naso-postrostrals.

The *supraorbito-dermosphenotics* (*So. dsph*, pl. 11, fig. 1; text-fig. 64) are almost totally worn off, and even the impressions of these bones are incompletely shown in the present specimen. Owing to this fact

it is impossible to give a close description of the shape and size of the posterior parts of the bones discussed. In the shape and relations of their anterior parts they agree in the main with those of *L. kochi* and *L. johanssoni*. Only the left supraorbito-dermosphenotic is very narrow in its most anterior parts, and has a very irregularly shaped medial margin.

The impressions of the *fronto-parietals* (*Fr. pa*, pl. 11, fig. 1; text-fig. 64 A) are broken off posteriorly. In their anterior parts, as far back as a little behind the pineal foramen, the fronto-parietals of the present specimen agree with those of *L. kochi*, except that the right one has the extreme anterior part of its median margin in suture with the left frontal, and that the part of the median suture between the two fronto-parietals, situated in front of the pineal foramen, is much shorter in the present specimen.

The centre of development of the left fronto-parietal is clearly shown to have been situated a little nearer the medial than the lateral margin of the bone, and a little farther back than the pineal foramen.

The very fragmentary impression of the left *supratemporo-intertemporal* (*St. it*, pl. 11, figs. 1, 2; text-fig. 64) shows that the part of the bone, situated laterally to the posterior part of the fronto-parietal, was narrower than in *L. kochi*. However, the bad state of preservation precludes a closer description of this bone.

The very long *lachrymo-maxillaries* (*La. mx*, pl. 11, figs. 1, 2; pl. 12, fig. 2; text-fig. 64) as far as they are preserved, agree in shape and relations to the surrounding bones with the corresponding bones in the species of *Lyrocephalus* previously described. In the more completely preserved left lachrymo-maxillary there are 24 small teeth, more or less well preserved.

The left *jugal* (*Ju*, pl. 11, figs. 1, 2; pl. 12, fig. 2; text-fig. 64), like the corresponding bone in *L. kochi*, is very long and low, with a long ventral margin, joined by a straight suture to the lachrymo-maxillary; a short anterior margin, with an irregularly zig-zag suture towards the posterior antorbital; and a very long medial (dorsal) margin with a short, finely zig-zag suture towards the anterior supraorbital, a longer concave part, forming the lateral margin of the orbit, and a long, mainly slightly sigmoid part, with interlocked sutures towards the postorbital and the squamosal. Finally the jugal has a short posterior or postero-ventral margin, joined by suture with the quadratojugal.

The centre of development of the jugal lies in the mid-length of the bone, but much nearer the lateral than any of the other margins of the bone.

The impression of the left *postorbital* (*Po*, pl. 11, figs. 1, 2; text-

fig. 64) is very imperfect but still shows that the bone mentioned was much shorter in the present species than in *L. kochi*. It had irregularly curved sutures towards the jugal and the squamosal.

The impression of the left *squamosal* (*Sq*, pl. 11, figs. 1, 2; text-fig. 64) is complete, except in the most postero-medial parts. The shape of the other parts, and the position of the centre of development must have been the same as in *L. kochi*.

The left *quadratojugal* (*Quj*, pl. 11, figs. 1, 2; text-fig. 64) was evidently also quite similar to the corresponding bone in *L. kochi*, and like this it had its centre of development situated in its most postero-lateral parts.

The ornamentation of the external surface of the skull is too imperfectly preserved to be here described.

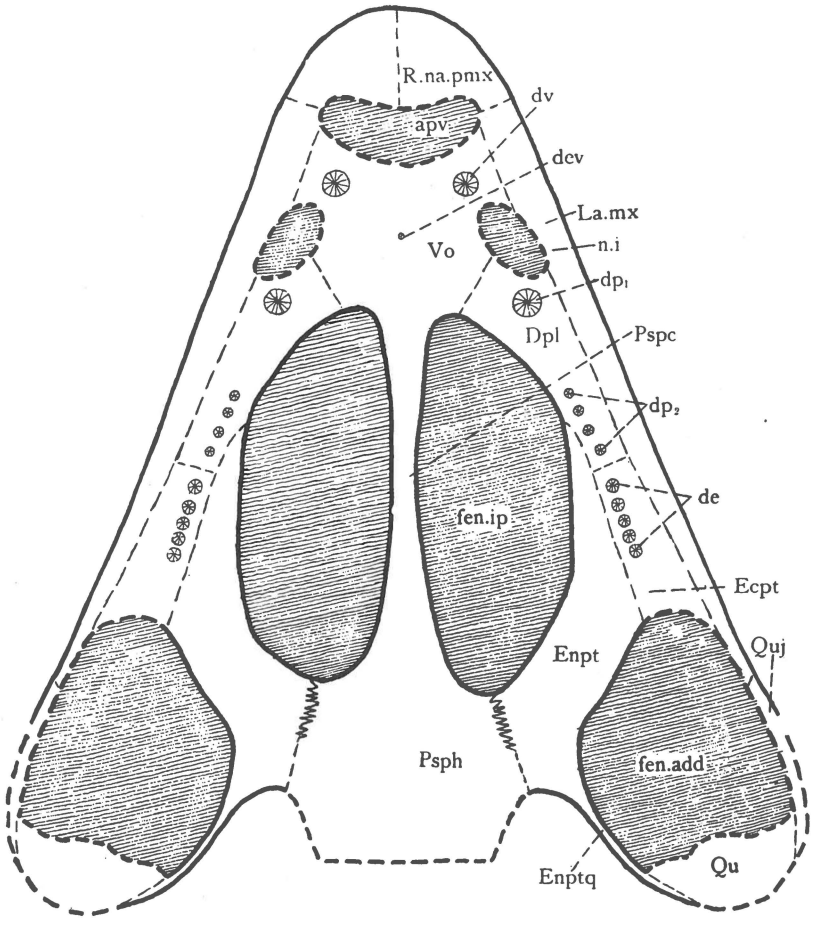
Dermal bones of the palate. The palate of the present specimen is interesting since it shows most of the palatal teeth, but the state of preservation is such that very little can be seen of the sutures between the different dermal bones. This is especially the case when the specimen is dry, but even after immersion into alcohol, xylol, or oil of aniseed, very little can be elucidated concerning the shape and extension of the individual bones.

In the extreme anterior part of the palate there is a small anterior palatal vacuity (*apv*, pl. 12, fig. 1; text-fig. 65). Postero-laterally to this vacuity there are two very long, narrow, pointed teeth (*dv*, pl. 12, fig. 1; text-fig. 65), one on each side. These teeth evidently belong to the vomeres; and the very small tooth (*dcv*, pl. 12, fig. 1; text-fig. 65) situated on the quadrangular plate of bone behind the anterior palatal vacuity probably belongs also to the same bones. There have originally been several such small, more or less "granular" teeth on the medial parts of the vomeres.

The median part of the quadrangular plate of bone mentioned above passes over posteriorly in the narrow processus cultriformis of the *parasphenoid* (*Pspc*, pl. 12, fig. 1; text-fig. 65), while its lateral parts are bounded posteriorly by the large, roughly oval interpterygoid vacuities (*fen. ip*, pl. 12, fig. 1; text-fig. 65). The processus cultriformis has a very elongated triangular shape; it becomes slightly broader in its posterior parts. Its posterior half is armed with numerous small granular teeth.

The suture between the parasphenoid and the entopterygoid is shown on the left side of the specimen.

Laterally each interpterygoid vacuity is bounded by a long narrow bony bar (preserved only on the left side), evidently consisting of a *dermopalatine* and an *ectopterygoid*. The suture between these two bones could not be found in the present specimen.



Text-fig. 65. *Lyrocephalus rapax* n. sp. Outlines of the palate. Slightly more than natural size (about $\frac{9}{8}$).

Dpl, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Enptq*, quadrate ramus of the entopterygoid; *La. mx*, lachrymo-maxillary; *Pspc*, processus cultriformis of the parasphenoid; *Psph*, parasphenoid; *Qu*, quadrate; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; *Vo*, vomer; *apv*, anterior palatal vacuity; *dcv*, very small tooth on the vomer; *de*, teeth probably on the ectopterygoid; dp_1, anterior, large tooth of the dermopalatine; dp_2, posterior, small teeth of the dermopalatine; *dv*, large tooth on the vomer; *fen. add*, adductor fenestra; *fen. ip*, interpterygoid vacuity; *n. i*, internal nostril.

On the bony bar laterally to the interpterygoid vacuity there are seen one very large, four very small, and five medium-sized, narrow, pointed teeth. The very large tooth (dp_1, pl. 12, fig. 1; text-fig. 65), which is the most anterior one of these now discussed, as well as the four very small ones (dp_2, pl. 12, fig. 1; text-fig. 65), which follow next behind, all belong without much doubt to the dermopalatine,

whereas the five medium-sized, most posterior teeth (*de*, pl. 12, fig. 1; text-fig. 65) probably belong to the ectopterygoid.

Postero-laterally the interpterygoid vacuity is bounded by the palatal ramus of the entopterygoid (*Enpt*, pl. 12, fig. 1; text-fig. 65). The suture between this bone and the ectopterygoid could not be found in the present state of the specimen, and thus the lateral margin of the palatal ramus of the entopterygoid cannot be described. Its antero-medial margin, forming the postero-lateral margin of the interpterygoid vacuity, is slightly concave; its postero-lateral margin is sigmoid, and forms the antero-medial margin of the relatively small adductor fenestra (*fen. add*, pl. 12, fig. 1; text-fig. 65).

The palatal ramus of the entopterygoid seems to be furnished with numerous small granular teeth.

The quadrate ramus of the entopterygoid (*Enptq*, pl. 12, fig. 1; text-fig. 65) is very imperfectly preserved in the present specimen. It is evidently remarkably short.

Lateral line system of the head. There is very little of the grooves for the lateral line canals to be seen in this specimen, owing to the fact that most of the dermal bones are almost completely worn off. The only part still shown is the anterior half of the horizontal portion of the *suborbital part of the left infraorbital canal* (*ifsh*, pl. 11, fig. 1; pl. 12, fig. 2; text-fig. 64 A), running over the left lachrymo-maxillary and posterior antorbital, just as in *L. johanssoni* (cf. above pp. 167—169).

Horizon. *Proptychites* Beds, probably from the lower part (cf. below, pp. 194—196; Koch 1931; Nielsen 1934).

Locality. Cape Stosch, Stensiö Plateau, Ridge IX (see Koch 1931; Nielsen 1934).

Remarks. The present species differs very markedly from the other members of the genus *Lyrocephalus*, especially by the very short shape of the cheeks. It is not impossible that it represents a genus of its own, nearly related, however, to *Lyrocephalus*. This question will have to be solved by the investigation of the endocranial remains, and perhaps also by investigation of fresh material more completely preserved than that at present available. For the time being I prefer to include this species provisionally in the genus *Lyrocephalus*.

Lyrocephalus sp.

(Pl. 13, fig. 2; text-fig. 66).

Material. *At.* 3: An imperfect dermal cranial roof with most of the left cheek, exposed from the internal side. Many of the dermal bones are worn off and have to be described from the impressions of their external sculptured surface. The specimen is chiefly interesting for the

very clearly shown impressions of the lateral line canals of the right side of the skull.

The shape of the following bones is more or less completely shown in the present specimen: the frontals, the anterior supraorbitals, the supraorbito-dermosphenotics, the fronto-parietals, the parieto-extrascapulars, the supratemporo-intertemporals, the lateral extrascapulars, the postorbitals, the left squamosal. Large parts of the left posterior antorbital, the left jugal, the right squamosal, and the left quadratojugal are shown, whereas only very small parts are shown of the naso-postrostrals.

Description.

General shape. In its present state of preservation the specimen is totally flattened out, so that nothing can be said about the original height of the skull. Also the breadth is difficult to calculate, owing to the flattened state of the skull roof, and the absence of large parts of the cheeks. In the proportions of the parts preserved the specimen differs more or less from all the other specimens above described. In the proportion between the distance from the pineal foramen to the posterior margin of the orbital division and the maximum length of the orbits, it is intermediate between *L. kochi* and *L. rapax:* this distance is a little more than half the maximum length of the orbit.

The exact dimensions of the specimen are as follows:

Median length of the specimen	75 mm
Distance from the anterior margin of the pineal foramen to the posterior margin of the orbital division of the dermal cranial roof	11 mm
Distance from the posterior margin of the pineal foramen to the posterior margin of the dermal cranial roof	25 mm
Distance between the orbits	26 mm
Distance between the otic notches	56 mm
Maximum length of the orbit	20 mm
Breadth of the orbit	14 mm

Dermal bones of the cranial roof and cheeks. The parts preserved of the impressions of the *naso-postrostrals* (*Na. ptr*, pl. 13, fig. 2; text-fig. 66) do not allow any closer description of these bones. The left naso-postrostral evidently met the right frontal in a short median suture, and had a groove for a part of the supraorbital canal (*soc*, pl. 13, fig. 2; text-fig. 66; cf. below p. 181).

The left *posterior antorbital* (*Ant*, pl. 13, fig. 2; text-fig. 66) had a long sigmoid postero-medial margin, in suture with the anterior supra-

orbital, and an antero-lateral margin, in suture with the naso-postrostral. Its centre of development was situated laterally to the anterior end of the anterior supraorbital, probably in the anterior half of the bone. The posterior antorbital had a very short groove in its most medial parts, for part of the supraorbital canal, and a longer, curved groove (*ifsh*, pl. 13, fig. 2), in its lateral parts, for a part of the horizontal portion of the suborbital part of the infraorbital canal (cf. below, p. 183).

The *frontals* (*Fr*, pl. 13, fig. 2; text-fig. 66) are in great part preserved. They have much the same shape as the corresponding bones in the specimens of *Lyrocephalus* previously described.

The median margin of the right frontal has a short anterior part, joined by suture to the left naso-postrostral, a long middle part, with a remarkably strongly interlocked suture towards the frontal of the other side, and a short posterior part in suture with the left fronto-parietal. In the right frontal there was a groove (*soc*, pl. 13, fig. 2) for a short part of the supraorbital canal (*soc*, text-fig. 66), running in a slightly curved line — with the convexity directed medially — over the middle third of the lateral half of the bone (cf. below, p. 183).

The *anterior supraorbitals* (So_1, pl. 13, fig. 2; text-fig. 66) were relatively short, and broad in their anterior parts. Thus they are fairly similar to the corresponding bones in *L. johanssoni* but differ from those of *L. rapax* and *L. euri* and still more from those of *L. kochi*. The centre of development of each anterior supraorbital was evidently situated nearer the posterior than the anterior end of the bone, and in the medial half of the bone. As in *L. johanssoni*, there are grooves for part of the supraorbital canals (*soc*, pl. 13, fig. 2; text-fig. 66; cf. below, p. 183) running over the centres of development of the anterior supraorbitals.

The *supraorbito-dermosphenotics* (*So. dsph*, pl. 13, fig. 2; text-fig. 66) agree very well in shape with those of *L. kochi* (cf. above, p. 155; pl. 7, text-fig. 60). The left supraorbito-dermosphenotic shows the centre of development, situated in the mid-point of the bone, at the boundary between the anterior, narrow, and the posterior, broader, part of the bone. On the right side of the skull there is an impression of the sculptured external surface of the supraorbito-dermosphenotic, with a very slightly sigmoid groove (*soc*, pl. 13, fig. 2) for a posterior part of the supraorbital canal (*soc*, text-fig. 66; cf. below, p. 183).

The *fronto-parietals* (*Fr. pa*, pl. 13, fig. 2; text-fig. 66) also agree in their general shape with the corresponding bones of *L. kochi*, but differ from them in several details.

The median margin of the left fronto-parietal has a short anterior part in suture with the right frontal; a long, partly strongly interlocked, middle part, with a semicircular notch forming half of the pineal foramen; and a very short posterior part, joined by suture to the right

parieto-extrascapular. The lateral margin of each fronto-parietal consists of a concave anterior part, in suture with the supraorbito-dermosphenotic, and a very slightly sigmoid posterior part, concave in its anterior half, convex in the posterior half, and joined by suture to the supratemporo-intertemporal.

The position of the centre of development is very clearly shown by the structure of the preserved parts of bony substance in the left fronto-parietal. It is situated near the mid-point of the bone, laterally to the pineal foramen.

The *parieto-extrascapulars* (*Pa. ext*, pl. 13, fig. 2; text-fig. 66) have a more regular shape than in *L. kochi*, owing to the straighter main course of their sutures towards the surrounding bones. Each parieto-extrascapular has the usual five margins: the free posterior margin; the lateral margin, in suture with the lateral extrascapular; the antero-lateral margin, with a suture towards the supratemporo-intertemporal; the anterior margin, joined by suture to the fronto-parietal; and the median margin, mainly meeting the parieto-extrascapular of the other side, that of the right one, however, also meeting the left fronto-parietal in a very short suture. Two of these margins — the posterior, and the antero-lateral, — are slightly concave, whereas the other three are mainly straight.

The centre of development of each parieto-extrascapular is in the centre of the posterior third of the bone.

The large *supratemporo-intertemporals* (*St. it*, pl. 13, fig. 2; text-fig. 66) are irregularly oval in shape, with long sutures towards the fronto-parietals, the postorbitals, and the squamosals; short sutures towards the parieto-extrascapulars, and the lateral extrascapulars; and very short strongly bent sutures towards the supraorbito-dermosphenotics. The centre of development of the well preserved left supratemporo-intertemporal is at the mid-point of the posterior half of the bone, laterally to the suture between the fronto-parietal and the parieto-extrascapular.

On the right side there is an impression of a straight groove (*ot* + *ptc*, pl. 13, fig. 2; text-fig. 66) in the supratemporo-intertemporal, evidently for the otic part of the infraorbital canal and the postotic canal (cf. below, p. 183).

The *lateral extrascapular* (*Ext. l*, pl. 13, fig. 2; text-fig. 66) had a dorsal surface with a shape quite similar to that of the corresponding surface in *L. kochi* (cf. above, p. 156; pl. 7; text-fig. 60).

The centre of development is shown to be situated below the postero-lateral quarter of the discussed surface.

The fragmentarily preserved left *jugal* (*Ju*, pl. 13, fig. 2; text-fig. 66) differs from the corresponding bone in *L. kochi* by having a more distinctly

convex postero-lateral margin (with very irregularly curved sutures towards the postorbital and the squamosal).

In the present state of preservation of the specimen no certain traces of lateral line canals can be seen in the jugal.

The *postorbitals* (*Po*, pl. 13, fig. 2; text-fig. 66) of the present specimen are long and relatively large, thus agreeing with those of *L. kochi* and differing from those of *L. rapax*. Their margins, and their sutures with the surrounding bones are the same as in *L. kochi*. On the left side of the skull the centre of development is very clearly shown, situated in the anterior third of the bone, laterally to the suture between the supraorbito-dermosphenotic and the supratemporo-intertemporal, and nearer to the medial than to the lateral margin of the bone. The right postorbital, on the other hand, is totally worn off, but the shape of its external surface is shown by a very sharp impression. In this surface there were evidently several grooves for lateral line canals: a short transverse groove in the medial half of the bone probably housed a part of the supraorbital canal; whereas parts of the vertical portion of the suborbital part of the infraorbital canal were evidently situated in one long and two very short transverse grooves in the more lateral parts of the bone, as well as in a longer longitudinal groove, continuous posteriorly with the groove for the otic part of the infraorbital canal, in the supratemporo-intertemporal (cf. below, p. 183).

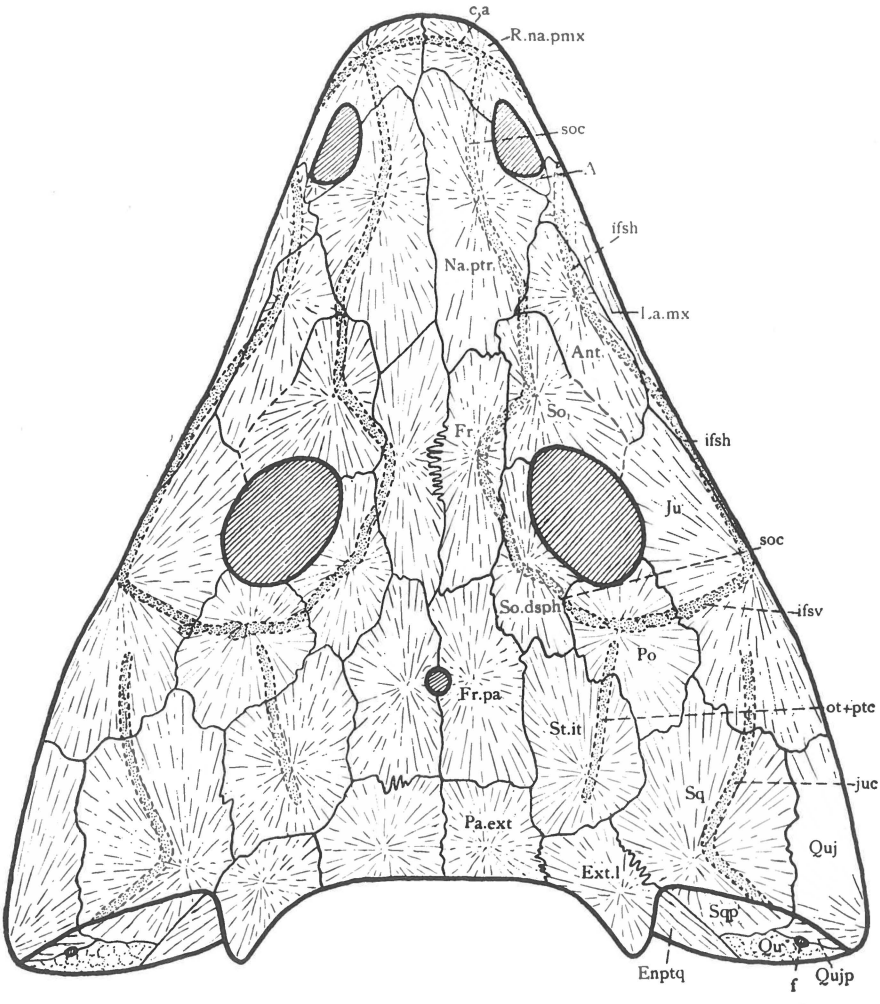
The dorso-lateral lamina of the *squamosal* (*Sq*, pl. 13, fig. 2; text-fig. 66) is well preserved on the left side. It seems to differ from the corresponding bone in *L. kochi* only by the more strongly concave shape of its antero-medial margin (in suture with the postorbital). The centre of development is situated near the medial and the postero-medial margins of the dorso-lateral, sculptured surface of the bone.

Of the left *quadratojugal* (*Quj*, pl. 13, fig. 2; text-fig. 66) too little is preserved to allow any description of this bone.

The ornamentation of the dermal bones must have been quite similar to that found in *L. kochi* (cf. above, p. 158), and *L. johanssoni* (p. 168).

Lateral line system of the head. The present specimen is especially interesting since it shows very clearly the impressions of grooves for great parts of the lateral line canals of the head.

Thus, there is on the right side of the specimen a long, sigmoid groove (*soc*, pl. 13, fig. 2) for the posterior two thirds of the *supraorbital canal* (*soc*, text-fig. 66). The anterior part of the groove is bent, with its convexity directed laterally, whereas the posterior part has its convexity directed medially. The most anterior part preserved is in the postero-lateral part of the left naso-postrostral. Hence the groove runs



Text-fig. 66. Attempted restoration of the skull of an East Greenland *Lyrocephalus*, dorsal view, with the parts at present known of the lateral line system except the supratemporal commissural canal. Based mainly upon *Lyrocephalus* sp. (specimen *At.* 3), supplemented with details from *L. kochi* (spec. *At.* 1: suborbital parts of the infraorbital canals, jugal canals) and *L. johanssoni* (spec. *At.* 28: most anterior parts of the supraorbital canals, ethmoidal commissure of the infraorbital canals). Nearly natural size.

A, anterior antorbital or septomaxillary; *Ant*, posterior antorbital; *Enptq*, quadrate ramus of the entopterygoid; *Ext. l*, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Qu*, quadrate; *Quj*, quadratojugal; *Qujp*, posterior lamina of the quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *Sqp*, posterior lamina of the squamosal; *St. it*, supratemporo-intertemporal; *c. a*, anterior commissure of the infraorbital canals; *f*, foramen between the quadratojugal and the quadrate; *ifsh*, horizontal portion of the suborbital part of the infraorbital canal; *ifsv*, vertical portion of the suborbital part of the infraorbital canal; *juc*, jugal canal; *ot + ptc*, otic part of the infraorbital canal and postotic canal; *soc*, supraorbital canal.

back over a very small, extreme medial part of the posterior antorbital, and then merges into the anterior supraorbital. In this bone it runs first posteriorly to a point over the centre of development of the bone, and then bends, continuing in a postero-medial direction, towards the posterior half of the suture between the frontal and the anterior supraorbital. From this suture it runs in a posterior direction over the middle third of the lateral half of the frontal, merges into the supraorbito-dermosphenotic, and runs with a slightly zig-zag course to near the suture between the supraorbito-dermosphenotic and the postorbital.

A short transverse groove in the medial part of the anterior third of the right postorbital probably housed the most posterior part of the supraorbital canal.

The parts of the *infraorbital canals* situated in grooves, now visible in the specimen, include a short part of the horizontal portion of the *suborbital part* of the left infraorbital canal (pl. 13, fig. 2; *ifsh*, text-fig. 66) in the left posterior antorbital; and a large part of the vertical portion of the suborbital part of the right infraorbital canal in the right postorbital (*ifsv*, pl. 13, fig. 2; text-fig. 66). This latter part was evidently situated in three transverse grooves and one longitudinal groove. The three transverse grooves include a long lateral one, and two very short, more medial, ones, situated close to the centre of development of the postorbital. The longitudinal groove is situated in the posterior, and in the medial half of the postorbital. It is directly continuous with a straight longitudinal groove (*ot* + *ptc*, pl. 13, fig. 2; text fig. 66) in the supratemporo-intertemporal evidently once housing the *otic part of the infraorbital canal* and the *postotic canal.* This groove does not quite reach the posterior margin of the supratemporo-intertemporal.

Horizon. Upper part of the *Proptychites* Beds (cf. below, pp. 194—196; Koch 1931; Nielsen 1934).

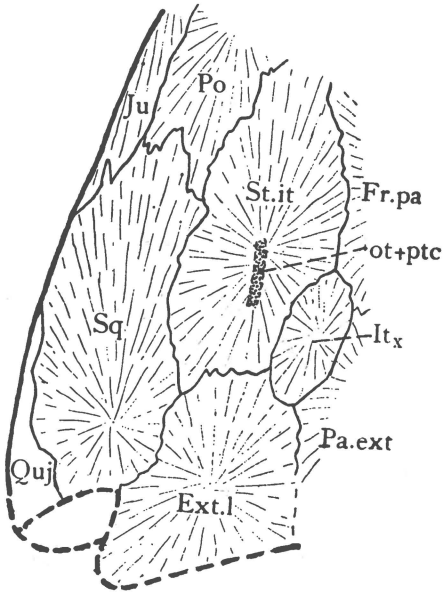
Locality. Cape Stosch, Stensiö Plateau, Ridge No. IX, about 280 m altitude (Nielsen 1934).

Remarks. This interesting specimen evidently belongs to a form closely related to *Lyrocephalus kochi.* As mentioned above (p. 178), it differs, however, in its general proportions from *L. kochi*, and differences — though probably of little importance — are also to be found in the minute shape of certain dermal bones. Anyhow, the fragmentary state of our present knowledge of the morphology of the animal, to which the specimen discussed belongs, excludes a reference to a definite species.

Two indeterminable, possibly Lyrocephaline skull fragments.

a. Specimen *At.* 4 (pl. 13, fig. 1; text-fig. 67).

Material. *At.* 4: The imperfect left postero-lateral part of a small skull, showing the following dermal bones of the cranial roof and cheeks: the posterior end of the left supraorbito-dermosphenotic; the lateral marginal parts of the left fronto-parietal and parieto-extrascapular; the partly damaged left supratemporo-intertemporal; most of the dorsal lamina of the left lateral extrascapular; the posterior parts of the left postorbital, and of the left jugal; the dorso-lateral lamina of the left squamosal; the impression of the internal surface of the left quadrato-



Text-fig. 67. Indeterminable, possibly Lyrocephaline skull fragment. Specimen *At.* 4. Dorsal view. $\frac{3}{2}$ natural size.
Ext. l, lateral extrascapular; *Fr. pa*, fronto-parietal; It_x, posterior intratemporal; *Ju*, jugal; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *ot + ptc*, otic part of the infra-orbital canal and postotic canal.

jugal; finally an independent bone (posterior intratemporal) of the left side, situated between the fronto-parietal, the parieto-extrascapular, the supratemporo-intertemporal, and the lateral extrascapular.

In the palate are seen the left lateral marginal parts of the corpus of the parasphenoid, the left entopterygoid, and the most posterior part of the left ectopterygoid.

Description.

Dermal bones of the cranial roof and cheeks. The *supraorbito-dermosphenotic* (*So. dsph*, pl. 13, fig. 1), the *fronto-parietal* (*Fr. pa*, pl. 13, fig. 1; text-fig. 13), and the *parieto-extrascapular* (*Pa. ext*, pl. 13, fig. 1; text-fig. 67) are too fragmentary to be closely described.

The long *supratemporo-intertemporal* (*St. it*, pl. 13, fig. 1; text-fig. 67) is fairly similar in general shape to that of *Lyrocephalus kochi* (*St. it*, pl. 7, text-fig. 60) and *Lyrocephalus* sp. (*St. it*, pl. 13, fig. 2; text-fig. 66). It may be described as roughly quadrangular, with a long convex lateral margin, joined by sutures to the postorbital and the squamosal; a short, concave posterior margin, in suture with the lateral extrascapular; and a long medial margin, consisting of an anterior, slightly convex part, with a suture towards the fronto-parietal, and a posterior, concave part, in suture with a bone (*St$_x$*, pl. 13, fig. 1; text-fig. 67), described below. The anterior margin of the supratemporo-intertemporal, in suture with the supraorbito-dermosphenotic, is very imperfectly preserved.

The centre of development of the supratemporo-intertemporal is situated in the posterior half of the bone. Just above the centre of development a part is preserved of a longitudinal groove (*ot+ptc*, pl. 13, fig. 1; text-fig. 67), probably for the otic part of the infraorbital canal and for the postotic canal.

Postero-laterally to the posterior parts of the fronto-parietal, laterally to the anterior half of the parieto-extrascapular, antero-medially to the lateral extrascapular, and medially to the posterior half of the supratemporo-intertemporal, there is a small, oval bone (*St$_x$*, pl. 13, fig. 1; text-fig. 67). It has short antero-medial and postero-lateral sutures towards the fronto-parietal and the lateral extrascapular, and long lateral and medial sutures towards the supratemporo-intertemporal and the parieto-extrascapular. Its centre of development is in the middle of the bone, as may be seen from the sculpture of its external surface.

This independent bone, which has never before been described in any Tetrapod or Crossopterygian, evidently represents a primordium, normally fusing with the supratemporal (or supratemporo-intertemporal). It is certainly a general membrane bone, not connected with any part of the lateral line system, and it is comparable to a so-called lateral parietal of a Dipnoan. I propose to call it the *posterior intratemporal*, — the anterior intratemporal being a bone, situated between the intertemporal (corresponding to the anterior half of the supratemporo-intertemporal) and the anterior parietal (corresponding to the posterior half of the fronto-parietal) in certain specimens of *Osteolepis* (see Säve-Söderbergh 1933, pp. 39, 78—79, 113).

The relatively large dorsal lamina of the *lateral extrascapular* (*Ext. l*,

pl. 13, fig. 1; text-fig. 67) is imperfectly preserved posteriorly and postero-laterally. It has slightly convex anterior and lateral margins, with finely undulating sutures towards the supratemporo-intertemporal and the squamosal; a short, concave, antero-medial margin, in suture with the posterior intratemporal; and a medial margin with a nearly straight suture towards the parieto-extrascapular. The centre of development is near the postero-lateral end of the preserved part of the dorsal lamina of the lateral extrascapular.

The parts preserved of the left *jugal* (*Ju*, pl. 13, fig. 1; text-fig. 67) show that this bone had a very long part behind the orbit, and was similar in shape to the corresponding bone in *Lyrocephalus kochi* (*Ju*, pl. 7; pl. 8, figs. 1, 2; text-fig. 60) or *Lyrocephalus* sp. (pl. 13, fig. 2; text-fig. 66). The centre of development is in the most anterior preserved parts of the bone.

Also the *postorbital* (*Po*, pl. 13, fig. 2; text-fig. 67) must in all probability have been long, not very high, and quite similar to the corresponding bone in *Lyrocephalus kochi* (*Po*, pl. 7; pl. 8, figs. 1, 2; text-fig. 60) and *L.* sp. (*Po*, pl. 13, fig. 2; text-fig. 66). It is preserved as far forward as near the centre of development.

The dorso-lateral lamina of the *squamosal* (*Sq*, pl. 13, fig. 1; text-fig. 67) is relatively long and low. It has a long medial margin, with a long concave anterior part, in suture with the supratemporo-intertemporal, and a shorter, angular, posterior part, in suture with the lateral extrascapular. It further has a short anterior margin, with an irregular suture towards the postorbital; and longer antero-lateral and ventral margins, in suture with the jugal and the quadratojugal respectively.

The centre of development is in the most postero-medial part of the bone.

The *quadratojugal* (*Quj*, pl. 13, fig. 1; text-fig. 67) is comparatively high and short. It had a long antero-dorsal margin with an irregularly curved suture towards the squamosal; a slightly shorter antero-ventral margin, joined by suture to the jugal, and a ventral margin, forming the postero-lateral margin of the adductor fenestra.

The ornamentation of the external surfaces of the dermal bones is of a finer type than in the species of *Lyrocephalinae* above described. The peripheral fields, with radiating discontinuous grooves, cover a much larger space than the central fields, with rounded pits.

Dermal bones of the palate. The dermal bones of the palate, shown in the present specimen, agree, as far as can now be seen, with those of *Stoschiosaurus nielseni?* (cf. above, pp. 144—146; pl. 4, fig. 4; pl. 5, fig. 2; text-fig. 58) or another Trematosaurid. However, the state of preservation is such that it seems difficult if not impossible to trace the

sutures between the different bones, and accordingly a closer description of the palate is hardly justified.

Lateral line system of the head. The only part of the grooves for the lateral line system shown in the present specimen is that (*ot+ptc*, pl. 13, fig. 1; text-fig. 67), above described, in the left supratemporo-intertemporal. It probably housed both the *otic part of the infraorbital canal* and the *postotic canal.*

Horizon. *Myalina kochi* horizon, at the bottom of the *Anodontophora fassaensis* Beds (see below, pp. 194—196; KOCH 1931; NIELSEN 1934).

Locality. Cape Stosch, Stensiö Plateau, Ridge VIII—IX, 538—543 m altitude (cf. KOCH 1931; NIELSEN 1934).

Remarks. The present fragment is described because it shows the posterior intratemporal bone, not previously found in any Tetrapod or Crossopterygian. It seems fairly certain that the specimen belongs to a Trematosaurid, but a reference to a definite genus is, of course, quite impossible.

b. Specimen *At.* 30 (pl. 14, fig. 2; text-fig. 68).

Material. *At.* 30: The imperfect left postero-lateral parts of a relatively small skull. It shows the following dermal bones of the cranial roof and cheeks: the posterior parts of the left supraorbito-dermosphenotic; lateral parts of the left fronto-parietal and parieto-extrascapular; the left supratemporo-intertemporal; the anterior parts of the left lateral extrascapular; the postero-medial marginal parts of the left jugal; the left postorbital; and the greater part of the left squamosal. In the palate fragments are preserved of the parasphenoid and of the left entopterygoid.

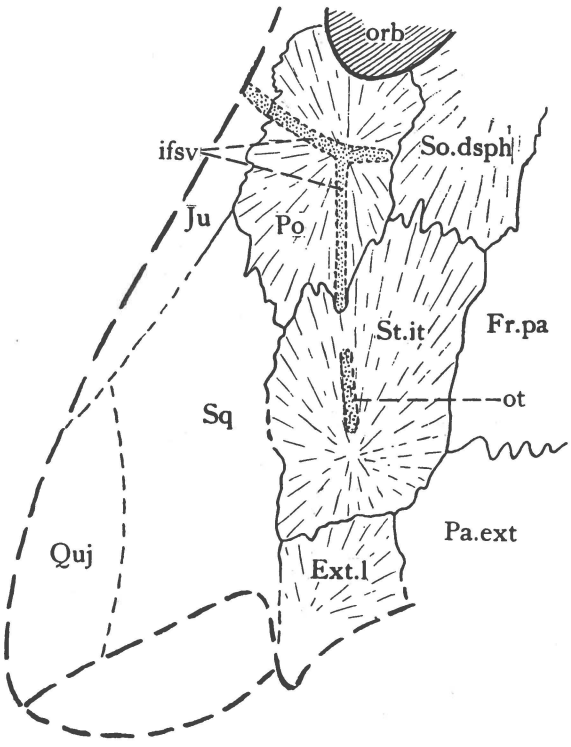
Description.

Dermal bones of the cranial roof and cheeks. The preserved posterior part of the *supraorbito-dermosphenotic* (*So. dsph*, pl. 14, fig. 2; text-fig. 68) has roughly straight posterior, medial and lateral margins, joined by irregular sutures respectively to the supratemporo-intertemporal, the fronto-parietal, and the postorbital. The centre of development is on a level with the posterior margin of the orbit, and is situated in the most anterior parts preserved.

The *fronto-parietal* (*Fr. pa*, pl. 14, fig. 2; text-fig. 68) and the *parieto-extrascapular* (*Pa. ext*, pl. 14, fig. 2; text-fig. 68) show no character of peculiar interest. Since, moreover, they are not well preserved, they will not be more closely described. It ought only to be mentioned that the parieto-extrascapular shows a well preserved ventral process joining the lateral occipital.

The *supratemporo-intertemporal* (*St. it*, pl. 14, fig. 2; text-fig. 68) is

well preserved, and may be described as roughly quadrangular, with short anterior and posterior margins, a long medial, and a very long lateral margin. It is clearly of the same type as the corresponding bone of the specimens of *Lyrocephalus*, described above (*St. it*, pl. 7; pl. 11, fig. 1; pl. 13, fig. 2; text-figs. 60, 61, 66; cf. also pl. 13, fig. 1; text-fig. 67). Its mainly straight anterior margin has a finely zig-zag suture towards the



Text-fig. 68. Indeterminable, possible Lyrocephaline skull fragment, specimen *At* 30. Dorsal aspect. $\frac{3}{2}$ natural size.

Ext. l, lateral extrascapular; *Fr. pa*, fronto-parietal; *Ju*, jugal; *Pa. ext*, parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; *Sq*, squamosal; *St. it*, supra-temporo-intertemporal; *ifsv*, vertical portion of the suborbital part of the infra-orbital canal; *orb*, orbit; *ot*, otic part of the infraorbital canal.

supraorbito-dermosphenotic; its posterior margin is joined by suture to the lateral extrascapular; its medial margin consists of a longer anterior part, in suture with the fronto-parietal, and a shorter, posterior part, in suture with the parieto-extrascapular; finally the convex lateral margin of the supratemporo-intertemporal has an irregularly curved suture towards the postorbital, and a more straight suture towards the squamosal.

The centre of development is in the posterior half of the bone, straight laterally to the suture between the fronto-parietal and the parieto-extrascapular. Just in front of the centre of development there is a short, longitudinal groove, probably for the otic part of the infraorbital canal (cf. below, p. 190). A short part of another lateral line groove is found at the middle of the suture towards the postorbital.

The *lateral extrascapular* (*Ext. l*, pl. 14, fig. 2; text-fig. 68), preserved with an impression of its ventral process, is too imperfectly preserved to be closely described.

The same is the case with the fragmentary remains of the left *jugal* (*Ju*, pl. 14, fig. 2; text-fig. 68).

The *postorbital* (*Po*, pl. 14, fig. 2; text-fig. 68) is remarkably broad, and roughly pentagonal in shape, with one sigmoid and three mainly straight margins. The fifth margin is the concave, anterior, orbital one. The medial margin has a very slightly sigmoid suture towards the supraorbito-dermosphenotic; the sigmoid postero-medial margin has an irregularly curved suture towards the supratemporo-intertemporal; the postero-lateral margin is joined by suture to the squamosal; and the ventral margin is in suture with the jugal.

The centre of development of the postorbital is situated in the anterior third, and in the medial half of the bone. Two grooves for the vertical portion of the suborbital part of the infraorbital canal are found in the postorbital, as described below (pp. 189—190).

The *squamosal* (*Sq*, pl. 14, fig. 2; text-fig. 68) is imperfectly preserved, but seems to agree in the main with that of, for instance, *Lyrocephalus kochi*.

Dermal bones of the palate. The fragmentary remains of the palate do not merit any special description.

The ornamentation of the dermal bones is of a rather coarse type, and similar to that of the skulls of *Lyrocephalus* above described.

Lateral line system. The chief interest of the present specimen is that it shows well preserved grooves for the vertical portion of the *suborbital part of the left infraorbital canal*, and for the *otic part* of the same canal. The vertical portion of the suborbital part was evidently situated in two grooves (*ifsv*, pl. 14, fig. 2; text-fig. 68), one transverse, the other longitudinal. The transverse one runs over the preserved part of the jugal, across the middle of the suture between the jugal and the postorbital, over the centre of development of the latter bone, to a point, just at the middle of the suture between the postorbital and the supraorbito-dermosphenotic. The horizontal groove is confluent with the transverse one at the centre of development of the postorbital, and from there it runs posteriorly over the suture between the postorbital and

the supratemporo-intertemporal, and ends a little behind the middle of this suture.

A short longitudinal groove (*ot*, pl. 14, fig. 2; text-fig. 68) in front of the centre of the supratemporo-intertemporal probably housed the *otic part of the infraorbital canal.*

Horizon. Fish Zone III (III b) in the Lower or Middle *Vishnuites* Beds (see below, pp. 194—196; KOCH 1931; NIELSEN 1934).

Locality. Cape Stosch, Spath Plateau, above the "Western Locality", in the Neviatiak Valley. About 396 m altitude (cf. KOCH 1931, NIELSEN 1934).

Remarks. The present specimen is, of course, too imperfect to be referred to a definite genus or species. Like specimen *At.* 4 just described, it agrees in the shape of the supratemporo-intertemporal with the specimens of *Lyrocephalus* from East Greenland. Specimen *At.* 30 — the present one — differs from *At.* 4, i. a. by the broad shape of its postorbital. It is here described mainly because is shows such well preserved grooves for parts of the lateral line system.

Indeterminable skull fragment of a large Stegocephalian.

(Pl. 14, fig. 1; pl. 15, fig. 1).

Material. *At.* 10: Internal cast of the right postero-lateral part of a large skull, with fragments of the parasphenoid and the right entopterygoid. The impressions of the following dermal bones of the cranial roof and cheeks are shown: the most posterior part of the right supraorbito-dermosphenotic; parts of both fronto-parietals; most of the right supratemporo-intertemporal; the posterior parts of the right jugal, and of the right postorbital; the right squamosal; and the dorsal parts of the right quadratojugal. In the palate the right entopterygoid is preserved, partly as bone, partly as an impression of the lateral and ventral surface; and a small fragment is preserved of the processus cultriformis of the parasphenoid.

Description.

Dermal bones of the cranial roof and cheeks. The preserved most posterior part of the impression of the *supraorbito-dermosphenotic* (*So. dsph*, pl. 14, fig. 1) is remarkably narrow. It has a rectangular shape with long lateral and medial margins and a short posterior margin. The medial margin of the bone was in suture with the fronto-parietal; the posterior and lateral margins were joined by sutures to the supratemporo-intertemporal.

The shape of the *fronto-parietals* (*Fr. pa*, pl. 14, fig. 1) can only be very incompletely made out from the present specimen. Evidently

they were joined by undulating lateral sutures to, and overlapped by, the supraorbito-dermosphenotics and the supratemporo-intertemporals. There was a median ventral ridge (*c. m*, pl. 14, fig. 1) in front of the pineal foramen (*pin*, pl. 14, fig. 1).

The impression of the right *supratemporo-intertemporal* (*St. it*, pl. 14, fig. 1) shows that this bone was very long, with a pointed anterior end. The shape of its most posterior parts is not clearly shown in the present specimen. The supratemporo-intertemporal had a very long medial margin, with a short angular suture towards the supraorbito-dermosphenotic, and a long, undulating suture towards the fronto-parietal, which it overlapped. It also had a very long convex lateral margin. The anterior half of the lateral margin had a suture towards the postorbital; the posterior half had an interlocked suture towards the squamosal, and overlapped the medial marginal parts of that bone.

The centre of development of the supratemporo-intertemporal was situated very far back, near the posterior end of the bone.

As is seen from the preserved posterior part of the impression of the *jugal* (*Ju*, pl. 14, fig. 1), this bone had a long postero-medial margin, with an anterior, mainly concave part, in suture with the postorbital, and a posterior, mainly convex part, joined by suture to the squamosal. The short posterior margin had a zig-zag suture towards the quadratojugal.

The *postorbital* (*Po*, pl. 14, fig. 1) had an irregular shape, with a long pointed posterior end, wedged in between the supratemporo-intertemporal and the squamosal. It had a long, slightly concave postero-medial margin, in suture with the supratemporo-intertemporal; a strongly concave postero-lateral margin with a suture towards the squamosal; and a slightly convex lateral margin, joined by suture to the jugal. The shape of the anterior parts of the postorbital, with the centre of development, is quite unknown.

The impression of the internal surface of the *squamosal* (*Sq*, pl. 14, fig. 1) is very completely shown in the present specimen. The bone may be regarded as composed of two laminae, one dorso-lateral, forming part of the external sculptured surface of the skull, the other posterior, and meeting the quadrate ramus of the entopterygoid.

The dorso-lateral lamina of the squamosal was convex in transverse section, and may be described as roughly triangular, with long antero-medial and antero-lateral margins, and a shorter posterior margin, passing over into the posterior lamina of the bone. At its posterior margin the dorso-lateral lamina of the bone was slightly angular in transverse section, and thus showed one more dorsal and another more lateral part of its surface. The centre of development was just at the boundary between the dorso-lateral and the posterior lamina of the bone. The antero-

medial margin of the dorso-lateral lamina had a long posterior part with a slightly undulating suture towards the supratemporo-intertemporal, by which it was overlapped, and a shorter, strongly convex anterior part in suture with the postorbital. The antero-lateral (antero-ventral) margin of the dorso-lateral lamina had an anterior, concave part, joined by suture to the jugal, and a posterior, slightly convex part, in suture with and overlapping the quadratojugal.

The posterior lamina of the squamosal was very high and narrow, and roughly quadrangular in shape. At the short dorsal and long dorso-lateral margins it passed over into the dorso-lateral lamina. Its short ventral margin had a straight suture towards the quadratojugal, which it overlapped; its long ventro-medial margin had a long concave ventro-lateral part in suture with the quadrate ramus of the entopterygoid, and a shorter dorso-medial part, joined by suture to the lateral extrascapular.

The imperfect impression of the right *quadratojugal* (*Quj*, pl. 14, fig. 1) shows that this bone had one lateral and another posterior lamina. It had a short anterior margin with a zig-zag suture towards the jugal, and a long dorsal suture, both towards the dorso-lateral and the posterior lamina of the squamosal, by which it was overlapped.

Dermal bones of the palate (pl. 15, fig. 1). The *entopterygoid* was a very strong bone, with a broad and strong palatal ramus (*Enpt*, pl. 15, fig. 1), joining the ectopterygoid, and a short and high quadrate ramus (*Enptq*, pl. 15, fig. 1). The palatal ramus has a broad ventral surface, probably once supplied with small, shagreen-like teeth, and a narrower, concave antero-ventro-medial surface, forming the postero-medial half of the antero-medial margin of the bone, and thus a part of the postero-lateral margin of the interpterygoid vacuity (*fen. ip*, pl. 15, fig. 1).

The quadrate ramus of the entopterygoid (*Enptq*, pl. 15, fig. 1) had an irregularly curved anterior margin; a strongly convex postero-dorsal margin, partly in suture with the posterior lamina of the squamosal; and a ventral margin, straight in lateral view, but slightly curved in ventral view, with the concavity directed antero-laterally towards the adductor fenestra (*fen. add*, pl. 15, fig. 1). The anterior margin of the quadrate ramus had an angular notch for the insertion of the epipterygoid (*Ept*, pl. 15, fig. 1), and another, more dorsal, rounded notch for the rr. maxillaris and mandibularis n. trigemini. The most antero-ventral part of the lateral surface of the quadrate ramus was more antero-laterally directed than the other parts, and was continuous with the antero-lateral surface of the epipterygoid. Posteriorly the quadrate ramus of the entopterygoid was attached to the medial surface of the quadrate (*Qu*, pl. 15, fig. 1).

The processus cultriformis of the *parasphenoid* (*Pspc*, pl. 15, fig. 1) is not very broad, but strongly built, and much broader than it is high. Its dorsal side is concave, its ventral side convex in transverse section.

Horizon. *Myalina kochi* horizon, at the base of the *Anodontophora fassaensis* Beds (see below, pp. 194—196; KOCH 1931; NIELSEN 1934).

Locality. Cape Stosch, Stensiö Plateau, Ridge VIII-IX, between 538 and 543 m altitude (see KOCH 1931; NIELSEN 1934).

Remarks. The present specimen differs in many characters from the other Eotriassic East Greenland Stegocephalians but its fragmentary state of preservation precludes any detailed systematic discussion. Further finds must be made before we can give a determination of this large form.

Indeterminable fragments of Stegocephalians.

Specimen *At.* 5: Fragment of the long snout of a small form with ornamentation of a fine type (Trematosaurine?).
Locality: Cape Stosch, Stensiö Plateau, Ridge VIII—IX. 538—543 m altitude.

At. 11: Fragment of a badly crushed, probably Trematosaurine skull, showing the region just in front of, and behind the orbits.
Locality: Cape Stosch, Stensiö Plateau, Ridge VIII—IX, 538—543 m altitude.

At. 12: Left postero-lateral parts of the internal cast of a small, probably Trematosaurid skull.
Locality: Cape Stosch, Stensiö Plateau, Ridge VIII—IX, 538—543 m altitude.

At. 13: Right postero-lateral parts of an indeterminable skull, preserved mostly as the internal cast of the dermal bones.
Locality: Cape Stosch, Stensiö Plateau, Ridge VIII—IX, 538—543 m altitude.

At. 14—16, 18—22, 33—38: Diverse fragments, including a large part of an endocranium (orbitosphenoid?), part of a lower jaw, etc.
Locality: Cape Stosch, Stensiö Plateau, Ridge VIII—IX, 538—543 m altitude.

At. 23: Impression of the external surface of a left lateral part of a probably Trematosaurine skull, with clearly shown grooves for several lateral line canals.

Locality: Cape Stosch, Stensiö Plateau, Ridge III, 480 m altitude.

At. 24—26: Fragments.
Locality: Cape Stosch, Stensiö Plateau, Ridge III, 480 m altitude.

Horizon for the above mentioned specimens: *Myalina kochi* horizon, at the bottom of the *Anodontophora fassaensis* Beds (see below, pp. 194—196; KOCH 1931; NIELSEN 1934).

Specimen *At.* 27: Part of a vertebral column, ribs, etc.
Locality: Cape Stosch, Spath Plateau, Smalleryg (between River 13 and River 14), ca. 351 m altitude.
Horizon: Lowermost *Vishnuites* Zone (cf. below, pp. 194—196; KOCH 1931; NIELSEN 1934).
At. 31: Part of a possibly Lyrocephaline skull, showing the orbital region of the dermal cranial roof, part of the lower jaw, and of the endocranium.
Locality: Cape Stosch, Stensiö Plateau.
At. 32: Right postero-lateral parts of a possibly Lyrocephaline skull.
Locality: Cape Stosch, Stensiö Plateau, Ridge VIII, 245 m.
Horizon for *At.* 31 and *At.* 32: Upper Zone of the Proptychites Beds (cf. below, pp. 194—196; KOCH 1931; NIELSEN 1934).

3. Stratigraphical and palaeogeographical remarks.

The stratigraphical inter-relations of the above-described Stegocephalians will be evident from the scheme given below. In this scheme the stratigraphy is partly from the work of KOCH (1931; cf. also SPATH 1930), but much improved according to verbal informations, kindly given by Dr. L. F. SPATH and Mr. E. NIELSEN. Mr. NIELSEN is going to publish, in the near future, an exhausting description of the stratigraphy of Cape Stosch (NIELSEN 1934).

As is evident from the scheme, most of the specimens described come from the lowermost part of the *Anodontophora fassaensis* Beds, the *Myalina kochi* horizon, which has yielded not less than 29 specimens. There are four specimens from the *Proptychites* Beds, three from the Upper, and one probably from the Lower zone; three specimens from the Vishnuites Beds, and only one from the *Otoceras* Beds.

It is quite interesting to notice that as far as the available material shows, different species are found in different horizons. Of course, the material is not sufficient to be used as a basis for more extensive strati-

Scheme showing
the stratigraphical distribution of the Stegocephalians in the Eotriassic of Cape Stosch.

	Formations and great divisions	Zones	Stegocephalians
	Cretaceous		
Eotriassic	*Anodontophora fassaensis* Beds	12. Layers with *Anodontophora fassaensis*	
		11. Sandy clay with bands of sandstone rich in *Myalina kochi**)	Spec. *At.* 2, *At.* 17: *Wetlugasaurus groenlandicus* n. sp.; Spec. *At.* 6: *Stoschiosaurus nielseni* n. g.; n. sp.; Spec. *At.* 7, *At.* 8: *Stoschiosaurus nielseni?* n. sp.; Spec. *At.* 9: *Stoschiosaurus* n. sp.?; Spec. *At.* 4: Lyrocephaline?; Spec. *At.* 5, *At.* 11, *At.* 24: *Trematosaurinae?*; Spec. *At.* 12: Trematosaurid?; Spec. *At.* 13, *At.* 14—16, *At.* 18—22, *At.* 24—26, *At.* 33—38.
	Anodontophora (breviform) Beds	10. Mostly grey sandstones	
	Proptychites Beds	9. Zone with *Proptychites rosenkrantzi**)	Spec. *At.* 3: *Lyrocephalus* sp.; Spec. *At.* 31, 32: *Lyrocephalinae?*
		8. ? Zone with *Koninckites*? n. sp. ?*)	? Spec. *At.* 29: *Lyrocephalus rapax* n. sp.
	Vishnuites Beds	7. Upper *Vishnuites* Zone*)	Spec. *At.* 28: *Lyrocephalus johanssoni* n. sp.
		6. Middle *Vishnuites* Zone	
		5. Lower *Vishnuites* Zone*)	Spec. *At.* 27; Spec. *At.* 30: Lyrocephaline?
	Otoceras Beds	4. *Ophiceras commune* (*sakuntala*) Zone	*) Spec. *At.* 1: *Lyrocephalus kochi* n. sp.
		3. Zone with *Ophiceras* n. sp.	
		2. Upper *Glyptophiceras* Zone	
		1. Lower *Glyptophiceras* Zone*)	
	Permo- carboniferous	*) Fish-horizon.	

graphical conclusions; none the less it is a striking fact that as yet all specimens of *Trematosaurinae* and of *Wetlugasaurus* have been found in the *Myalina kochi* horizon. Here also fragments of a small Lyrocephaline? have been found. The larger forms belonging to the last-mentioned subfamily, on the other hand, have as yet only been found in the lower zones of the Eotriassic, from the Otoceras Beds (spec. *At.* 1: *Lyrocephalus kochi* n. sp.) to and inclusive the *Proptychites* Beds (spec. *At.* 3, spec. *At.* 31, and spec. *At.* 32).

Also for the palaeogeography the material described in the special part of the present paper is of considerable interest. Thus the Eotriassic Stegocephalian fauna of East Greenland is clearly related to, but composed on the whole at least, of clearly more primitive forms than the Stegocephalian fauna of Spitsbergen (see WIMAN 1910, 1913, 1914, 1916, 1917). In both cases Trematosaurids are by far the most frequently found members of the fauna, and both the *Lyrocephalinae* and the *Trematosaurinae* are represented. Capitosauroids are of less frequent occurrence in both areas (Spitsbergen: *Capitosaurus polaris* WIMAN, East Greenland: *Wetlugasaurus groenlandicus* n. sp.). The Metoposaurids, the Mastodonsaurids and the Brachyopoids seem to be totally lacking in both areas.

It might be noticed that of related Spitsbergen and East Greenland forms, those from Spitsbergen are always much larger than those from East Greenland.

The Eotriassic Stegocephalians of East Greenland also show other still more interesting fauna relations, viz. with certain forms from N. Russia. The genus *Wetlugasaurus* and the family *Wetlugasauridae* are represented only in the Eotriassic of East Greenland and in the Lower Triassic at the river Vetluga in NW. Russia (RIABININ 1930). It also has to be pointed out that the Russian genus *Benthosaurus* (EFREMOV 1929) will not improbably prove to be closely related to the *Lyrocephalinae* of East Greenland. *Benthosaurus* is found in the "Permo-triassic, vari-coloured beds, at the River Scharschenga (a tributary of the Jug)" — (EFREMOV 1929). *Benthosaurus* is, however, at present very incompletely known: in EFREMOV's figure the two sides of the dermal skull roof have a very different aspect. Possibly this is the result of a violent deformation of the specimen described. In any case further investigations of the Triassic Stegocephalians of N. Russia are necessary before we can discuss more closely the fauna relations with the Eotriassic of East Greenland.

III. SUMMARY AND CONCLUSIONS.

A. The Eotriassic Stegocephalians of East Greenland.

The following forms, from different parts of the Eotriassic of Cape Stosch, East Greenland (74°4′ N., 21°42′ W.), are described:

1. *Wetlugasaurus groenlandicus* n. sp. (pp. 122—131), closely related to *W. angustifrons* RIABININ, from the Lower Triassic of NW. Russia.

2. *Stoschiosaurus* n. g. (pp. 131—150), a Trematosaurid genus, more nearly related to the Spitsbergen genus *Aphaneramma* than to any other genus at present known. This genus is represented by the type species: *S. nielseni* (pp. 131—140); by two specimens, provisionally determined as *S. nielseni*? (pp. 140—146); and finally by one specimen, described as *S.* n. sp.? (pp. 146—150).

3. Three new species, and one specimen, the species of which cannot be determined — all (provisionally) referred to the genus *Lyrocephalus* WIMAN, previously known from Spitsbergen. The three new species: *L. kochi* (pp. 150—159), *L. johanssoni* (pp. 164—170), and *L. rapax* (pp. 170—177), are probably nearly related to each other. The specimen, indeterminable as to species, described as *Lyrocephalus* sp. (pp. 177—183), is probably also nearly related to the other species of *Lyrocephalus* from East Greenland.

4. Three indeterminable specimens, two of which can possibly be referred to the subfamily *Lyrocephalinae* (see below, and above, pp. 85—86) and are interesting from a morphological point of view. One of them (pp. 187—190) shows well preserved grooves for certain parts of the lateral line system, the other (pp. 184—187) shows an independent dermal bone, the posterior intratemporal, — not previously recorded in any Tetrapod or Crossopterygian — situated between the parieto-extrascapular, the supratemporo-intertemporal, and the lateral extrascapular.

The third specimen (pp. 190—193) is of interest since it proves the occurrence, in the fauna discussed, of much larger Stegocephalians than those above enumerated.

Palaeogeographical and stratigraphical relations with the Lower Triassic of Spitsbergen and NW. Russia are demonstrated.

B. General conclusions.

The analysis of the dermal bones of the head in the *Ichthyostegalia*, the so-called "*Embolomeri*", "*Rhachitomi*", and "*Stereospondyli*", and certain primitive "*Reptilia*" gives the following important results:

1. A detailed homologisation with the dermal bones of the Crossopterygians is attempted, and found to be quite possible largely owing to the evidence furnished by the study of the Devonian Ichthyostegids from East Greenland. Only a few important questions have to be left completely unsolved, *viz.* (a) the fate of the interrostral and of the preopercular in most of the geologically younger Stegocephalians (b) the fate of the dermosphenotic in a few cases (see pp. 19, 51—54). All the other dermal bones of the head of the forms discussed can be homologized, with a high degree of certainty, with definite bones, or parts of bones, of the Crossopterygians. The new results thus gained are briefly enumerated above on pp. 117—119.

2. The groups studied are shown to belong to two main lines of evolution.

a. To the first of these lines of evolution belong the *Ichthyostegalia*, the *Loxommoidei* (one of the two superfamilies of the "*Embolomeri*"), and the groups, included in the so-called "*Rhachitomi*" and "*Stereospondyli*", possibly also the *Pantyloidei*, a group, earlier referred to the *Cotylosauria*.

All the forms belonging with certainty to this line of evolution have: (1) fronto-parietals, corresponding to the posterior halves of the frontals and the anterior halves of the parietals of the Crossopterygians (cf. SÄVE-SÖDERBERGH 1932, pp. 87—98; 1933, p. 116), (2) compound, median, paired or unpaired parieto-extrascapulars, — corresponding to the median extrascapulars, the medial halves of the lateral extrascapulars, and the posterior (halves of the) parietals of the Crossopterygians (cf. SÄVE-SÖDERBERGH 1932, pp. 87—98; 1933, p. 116); (3) lateral extrascapulars, corresponding to the lateral halves of the lateral extrascapulars of the Crossopterygians (cf. SÄVE-SÖDERBERGH 1932, pp. 87—98; 1933, p. 116).

Certain facts, which cannot be more closely discussed in this connection (cf. SÄVE-SÖDERBERGH 1934, pp. 9—13, 16—18) indicate that the *Phyllospondyli* (cf. WATSON 1921 c, fig. A; BULMAN and WHITTARD 1926, text-figs. 1, 7, 14; BULMAN 1928, text-figs. 2, 4; ROMER 1930, figs. 6, 7, 8, 11, 14, 15, 16; STEEN 1931, text-figs. 1 B, 2, 7, 11, 13), and probably the *Anura*, also belong to this line of evolution. Accordingly, since a name is now needed for the large group *Ichthyostegalia* — *Labyrinthodontia s. str.* (*Loxommoidei*, "*Rhachitomi*" — "*Stereospondyli*") —

Phyllospondyli — (?)*Anura*, I have proposed to call it the *Batrachomorpha* (SÄVE-SÖDERBERGH 1934).

b. To the second main line of evolution belong the *Anthracosauroideae* (the second superfamily of the "*Embolomeri*"), the *Seymouriamorpha*, the Diadectids, and probably also the majority of the "*Reptilia*" (except the *Pantyloidei*), the *Aves* and the *Mammalia*.

The groups belonging to this line of evolution have originally possessed: 1) fronto-parietals, corresponding to the posterior halves of the frontals and the whole parietals of the Crossopterygians (cf. above, pp. 97—101); 2) median extrascapulars, homologous to those of the Crossopterygians; 3) lateral extrascapulars, likewise homologous to those of the Crossopterygians.

The *Anthracosauroideae* represent an independent Order — the *Anthracosauria*.

The large systematic unit *Anthracosauria* — *Reptilia* (parte) — ?*Aves* — ?*Mammalia* may be called the *Reptiliomorpha* (SÄVE-SÖDERBERGH 1934).

3. The true *Labyrinthodontia* (*Loxommoidei*, "*Rhachitomi*", "*Stereospondyli*") branch into several lines of evolution. The *Loxommoidei* probably represent one such line; the other two "groups" merely represent stages in a polyphyletic evolution of the higher *Labyrinthodontia*. Each of them includes representatives of several lines of evolution; accordingly each such line may include both rhachitomous and stereospondylous members. It is too early as yet to give a settled classification of the *Labyrinthodontia* (for this purpose i. a. the endocranial structures have to be further investigated), but the present state of the problem may suitably be expressed in the following attempt at a classification:

Order **Labyrinthodontia.**

A. Suborder **Loxommoidei.**

B. Suborder **Capitosauroidei.**

1. *Eryopoideae*

Eryopidae a) *Eryopinae*
b) *Osteophorinae*

Zatrachydidae

Rhinesuchidae

? *Acanthostomatidae*

? *Achelomidae*

? *Melosauridae*

? *Trematopsidae*

2. *Capitosauroideae*
Wetlugasauridae
Capitosauridae
Mastodonsauridae

C. Suborder **Trematosauroidei.**
1. *Metoposauroideae*
Trimerorhachidae
Micropholis, *Broiliellus*, ?*Dissorophidae*
Metoposauridae a) *Metoposaurinae*
b) *Buettneriinae*
2. *Trematosauroideae*
Trematosauridae a) *Trematosaurinae*
b) *Lyrocephalinae*
c) *Lonchorhynchinae*
Peltostegidae
? *Archegosauridae* a) *Archegosaurinae*
b) *Platyopinae*

D. Suborder **Brachyopoidei**
1. *Dvinosauroideae*
Dvinosauridae
2. *Brachyopoideae*
Brachyopidae

Labyrinthodontia incertae sedis:[1])
Actinodontidae
Lydekkerinidae
Rhytidosteidae

Thus the study of the Devonian and Triassic Stegocephalians of East Greenland has thrown much new light upon the relationship and organisation of the labyrinthodont "*Stegocephali*". Indeed very little is now left of the old larger classification. The "*Embolomeri*" are shown to include two fundamentally different groups: 1) the *Loxommoidei*, forming part of a line of evolution leading from primitive *Choanata* (cf. SÄVE-SÖDERBERGH 1933, pp. 114—118) over the Devonian *Ichthyostegalia* to the Permian and Triassic *Labyrinthodontia*, and also to the *Phyllospondyli* and probably to the *Anura;* 2) the *Anthracosauria*, belonging to another line of evolution, also originating from primitive

[1]) *Phrynosuchus* BROOM and *Goniocara* HAY (1929, p. 835) included by KUHN (1933, pp. 70, 71—72) in the *Melosauridae*, or in the "*Rhachitomi* inc. sed." do not seem to be any undoubted Labyrinthodonts, as far as one can judge from the existing descriptions and figures (BROOM 1913 e; BROILI 1913, p, 98; pl. 9, figs. 3, 4). Also *Rhinosaurus* FISCHER v. WALDHEIM (1847, pl. V) and *Tersomius* CASE (CASE 1910, text-fig. 10; 1911, text-fig. 9; cf. STEEN 1931, p. 889) are too incompletely known to be referred with certainty to the *Labyrinthodontia.*

Choanata, but leading to *Seymouria*, the Diadectids, and probably also to the majority of the "*Reptilia*", the *Aves*, and the *Mammalia*.

The "*Rhachitomi*" and "*Stereospondyli*" are also polyphyletic groups and have to be abandoned as systematic units.

The group *Labyrinthodontia* in the old sense is, of course, also polyphyletic, since it includes the *Anthracosauria;* and I propose to use the name *Labyrinthodontia* in a new sense, including only the *Loxommoidei*, and the groups, formerly called "*Rhachitomi*" and "*Stereospondyli*".

But still greater changes in the classification of the Vertebrates are now necessary. As I have pointed out in two other works (SÄVE-SÖDERBERGH 1933, pp. 114—118; 1934, pp. 5—18) the relationship between the Tetrapods, the Crossopterygians and the *Dipnoi* is much closer than that between the "Fish" groups mentioned and the *Actinopterygii* and *Elasmobranchii*. Accordingly the three first-mentioned groups have to be put into one large group, which I have called the *Choanata*. Thus we are forced to abandon the use of the name *Pisces* as a systematic unit. The Gnathostome Vertebrates have to be divided into three large groups: 1) the *Elasmobranchii*, 2) the *Actinopterygii*, 3) the *Choanata*. The two latter groups are probably more nearly related to each other than to the *Elasmobranchii*.

As demonstrated, for instance, by WINTREBERT (1910, 1922 a, b) and, quite recently, by HOLMGREN (1934) the Urodeles are very nearly related to the *Dipnoi* and apparently not so much to the *Crossopterygii*. On the other hand, the investigations of the Devonian Ichthyostegids from East Greenland (SÄVE-SÖDERBERGH 1932) show that these primitive representatives of the line of evolution, leading to the *Labyrinthodontia*, the *Phyllospondyli*, and probably also to the *Anura*[1]), are more nearly related to the Crossopterygians than to the Dipnoans. The evidence brought together in the present paper shows that also the line of evolution, leading to the *Anthracosauria*, the Diadectids, — and probably to the majority of the "*Reptilia*", the *Aves*, and the *Mammalia*, — has its origin nearer the ancestors of the *Crossopterygii* than those of the *Dipnoi*.

Thus there seem to be two main lines of the *Choanata:* 1) the first leading to the Dipnoans and the Urodeles, 2) the second leading to the *Crossopterygii* and a Tetrapod stem branching into two lines, a) the *Batrachomorpha*, b) the *Reptiliomorpha*. — The *Reptiliomorpha* and the *Batrachomorpha* together form a group, which I have proposed to call the *Eutetrapoda* (SÄVE-SÖDERBERGH 1934).

Accordingly the old class *Amphibia* is a polyphyletic group and can not be regarded as a systematic unit.

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[1]) The origin of the third group of recent "*Amphibia*", the *Gymnophiona*, seems at present quite obscure.

Much work remains to solve the question to which lines of evolution belong the different groups, included in the old class "*Reptilia*". However, at least in its old extension, this class will certainly prove to be polyphyletic: the Diadectids, and probably the majority of the "*Reptilia*", belonging to the same line of evolution as the *Anthracosauria*, — the Pantyloids, on the other hand, probably belonging to the same line as the *Ichthyostegalia*, the *Labyrinthodontia*, and the *Phyllospondyli*.

Finally it has to be pointed out that the "classes" *Aves* and *Mammalia*, probably representing specialized branches of the Reptilian stem, have of course a much more subordinate systematic rank than that given to them in the older classifications. This will be evident if we try to express the results sketched out above in an attempted classification of the *Gnathostomata*. — Of course this classification is a provisional one, and can only claim to be a stage on the way from the old anthropomorphistic classification, to a new based on objective morphological and phylogenetic analysis.

VERTEBRATA GNATHOSTOMATA

I. **Elasmobranchii.**

II. **Actinopterygii.**

III. **Choanata.**

A. Class 1. **Dipnoi.**

Class 2. **Urodela.**

B. Class 3. **Crossopterygii.**

Class 4. **Eutetrapoda.**

a. Superorder *Batrachomorpha*

Orders: *Ichthyostegalia*
Labyrinthodontia
Phyllospondyli
? *Pantyloidei*
? *Anura*

b. Superorder *Reptiliomorpha*

Orders: *Anthracosauria*
Seymouriamorpha
"*Reptilia*" (several groups)
? *Aves*
? *Mammalia*

Thus the study of the Stegocephalians from East Greenland has caused not only a thorough revision of the morphology and classification of the *Labyrinthodontia*, but also a revision of larger groups, resulting into a totally changed classification of the Gnathostome Vertebrates.

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Færdig fra Trykkeriet den 22. Januar 1935.

PLATES

The photographs reproduced in the plates have been taken with a Zeiss Tessar objective 1 : 6,3, F. 36 cm, on Ilford Special Rapid Panchromatic plates. In certain cases an Ilford Gamma filter has been used. All the specimens have been photographed dry.

All specimens figured in the plates belong to the Geological Survey of Greenland (G. G. U.), Chief: Dr. LAUGE KOCH, Copenhagen.

Plate 1.

Wetlugasaurus groenlandicus n. sp.

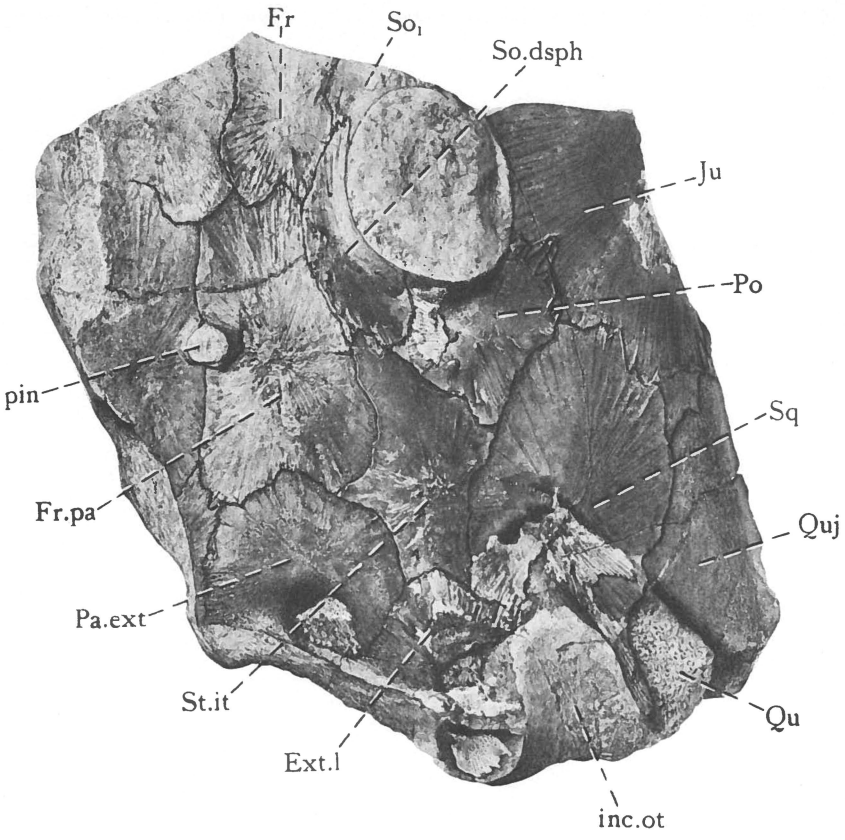
Fig. 1. Fragmentary internal cast of a skull in dorsal view. Spec. *At.* 2. $^3/_2$ natural size.

Ext. l, lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *Pa. ext*, dorsal lamina of the parieto-extrascapular; *Po*, postorbital; *Qu*, quadrate; *Quj*, quadratojugal; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *inc. ot*, otic notch; *pin*, pineal foramen.

Fig. 2. Ventral aspect of the same specimen as in figure 1. $^3/_2$ natural size.

Enptc, corpus of the entopterygoid; *Enptp*, palatal ramus of the entopterygoid; *Enptq*, quadrate ramus of the entopterygoid; *Ext. lv*, ventral process of the lateral extrascapular; *Pspc*, processus cultriformis of the parasphenoid; *Psph*, corpus of the parasphenoid; *Qu*, quadrate; *d. psph*, teeth of the parasphenoid; *fen. add*, adductor fenestra.

1


Fr
So1
So.dsph
Ju
Po
pin
Sq
Fr.pa
Quj
Pa.ext
St.it
Qu
Ext.l
inc.ot

2

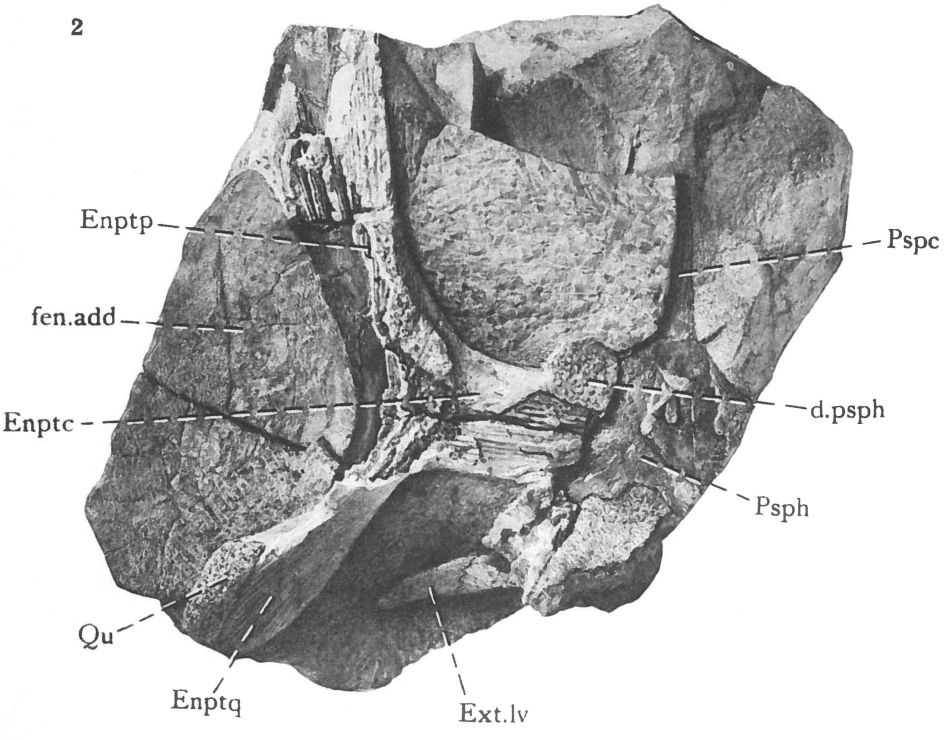

Enptp
Pspc
fen.add
Enptc
d.psph
Psph
Qu
Enptq
Ext.lv

Plate 2.

Wetlugasaurus groenlandicus n. sp.

Fig. 1. Posterior aspect of specimen *At.* 2. $^3/_2$ natural size.

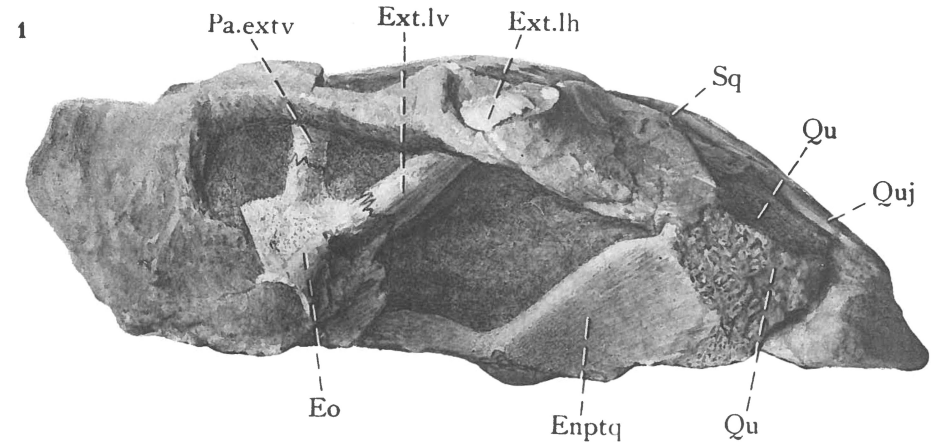
Enptq, quadrate ramus of the entopterygoid; *Eo*, exoccipital; *Ext. lh*, dorsal lamina of the lateral extrascapular; *Ext. lv*, ventral process of the lateral extrascapular; *Pa. extv*, ventral process of the parieto-extrascapular; *Qu*, quadrate; *Quj*, quadratojugal; *Sq*, squamosal.

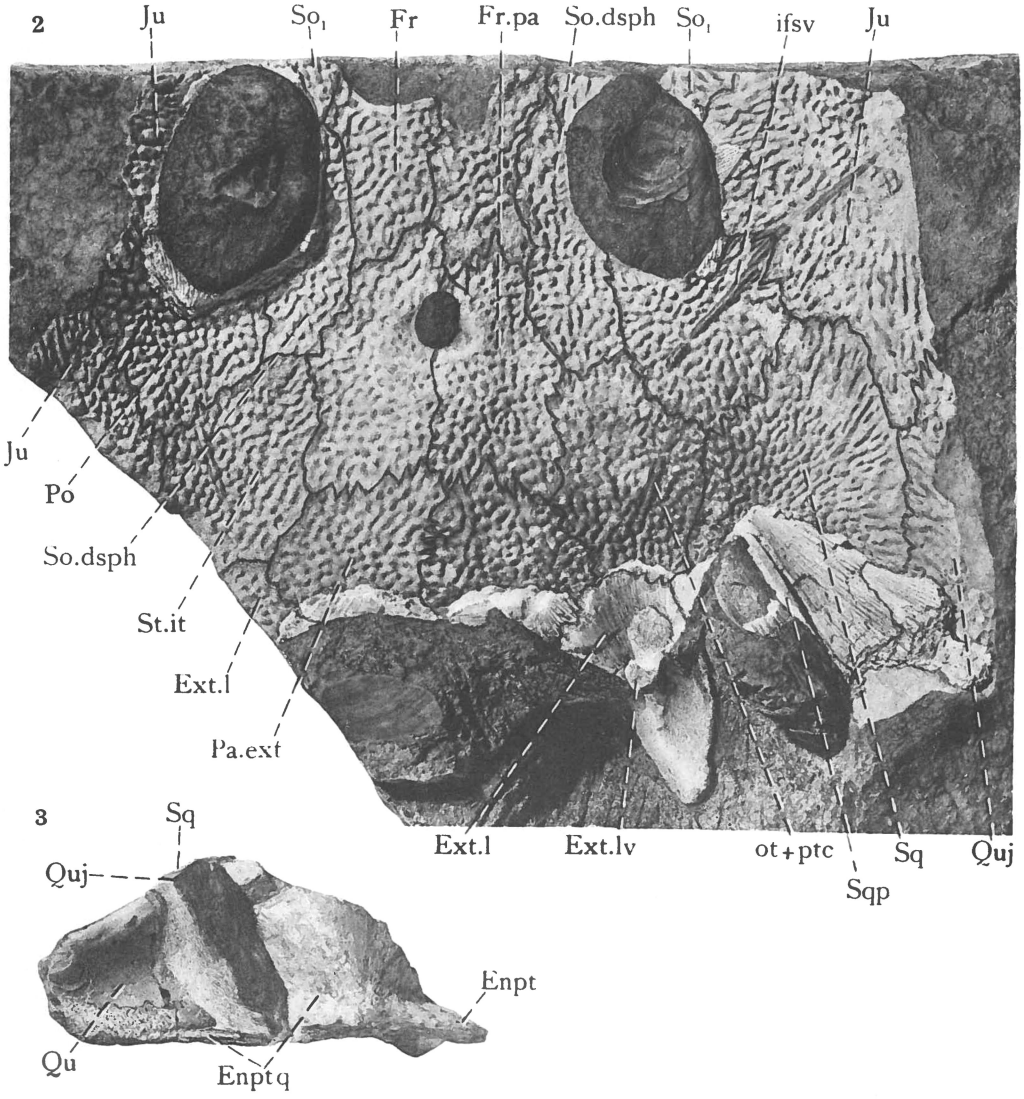
Fig. 2. Imperfect impression of the posterior parts of a skull. Spec. *At.* 17. $^3/_2$ natural size.

Ext. l, dorsal lamina of the lateral extrascapular; *Ext. lv*, ventral process of the lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *Pa. ext*, dorsal lamina of the parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, dorso-lateral lamina of the squamosal; *Sqp*, posterior lamina of the squamosal; *St. it*, supratemporo-intertemporal; *ifsv*, vertical portion of the suborbital part of the infraorbital canal; *ot+ptc*, otic part of the infraorbital canal, probably also postotic canal.

Fig. 3. Lateral aspect of the quadrate and part of the entopterygoid. Spec. *It.* 2. $^3/_2$ natural size.

Enpt, palatal ramus of the entopterygoid; *Enptq*, quadrate ramus of the entopterygoid; *Qu*, quadrate; *Quj*, quadratojugal; *Sq*, squamosal.


1
Pa.extv
Ext.lv
Ext.lh
Sq
Qu
Quj
Eo
Enptq
Qu


2
Ju
So1
Fr
Fr.pa
So.dsph
So1
ifsv
Ju
Ju
Po
So.dsph
St.it
Ext.l
Pa.ext
Ext.l
Ext.lv
ot+ptc
Sq
Quj
Sqp

3
Sq
Quj
Enpt
Qu
Enptq

Plate 3.

Stoschiosaurus nielseni n. g., n. sp.

Imperfect skull in dorsal view. Spec. *At.* 6. $^3/_2$ natural size.

Ext. l, dorsal lamina of the lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *Pa. ext*, dorsal lamina of the parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *c. m*, median crista of the fronto-parietals; *c. s*, semilunar ridge on the ventral surface of the parieto-extrascapular; *r*, ridge on the posterior part of the ventral surface of the fronto-parietal.

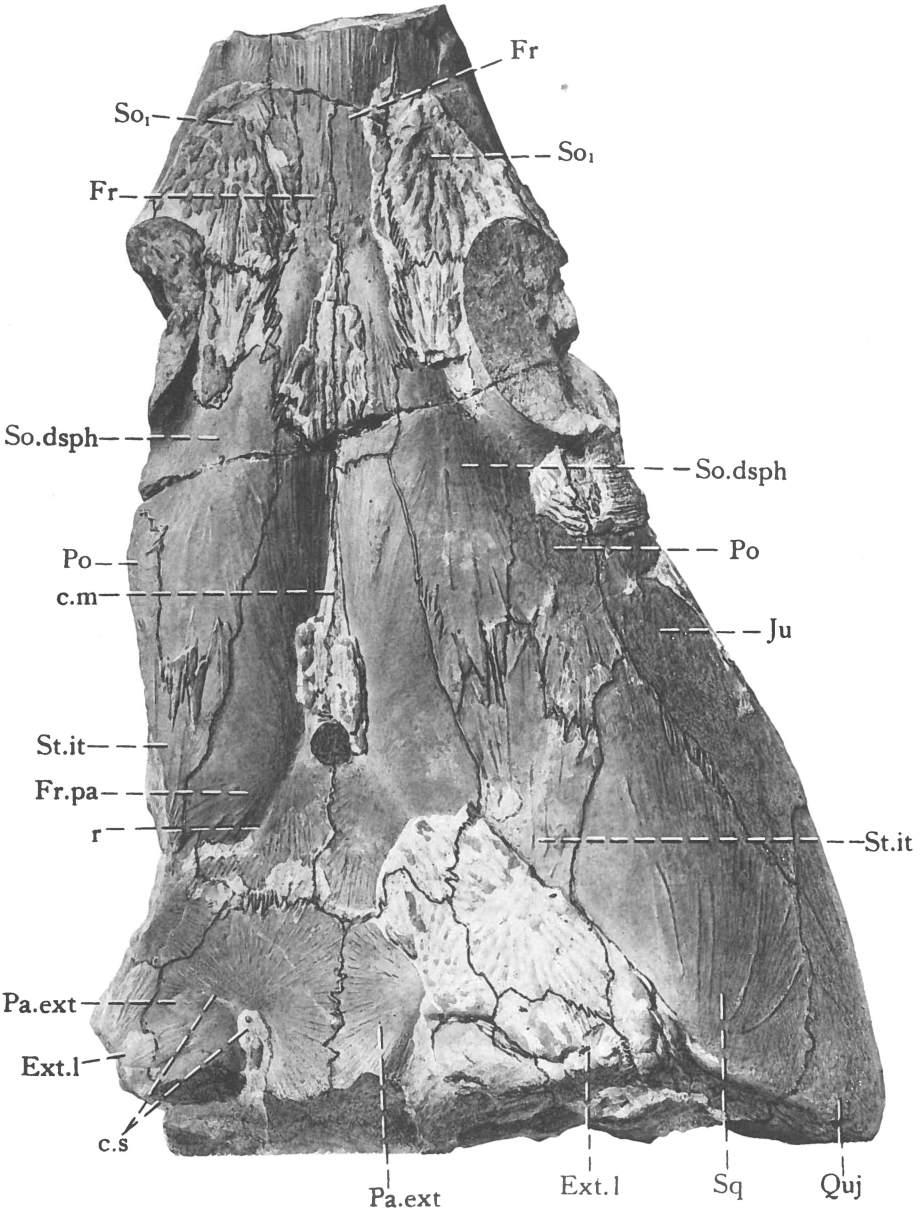

Fr
So1
So1
Fr
So.dsph
So.dsph
Po
Po
c.m
Ju
St.it
Fr.pa
r
St.it
Pa.ext
Ext.l
c.s
Pa.ext
Ext.l
Sq
Quj

Plate 4.

Stoschiosaurus nielseni? n. sp.

Fig. 1. Imperfect skull in posterior aspect. Spec. *At.* 8. $^3/_2$ natural size.

Enptq, quadrate ramus of the entopterygoid; *Eo*, exoccipital; *Ext. l*, dorsal lamina of the lateral extrascapular; *Ext. lv*, ventral process of the lateral extrascapular; *Pa. ext*, parieto-extrascapular; *Qu*, quadrate; *Qujp*, posterior lamina of the quadratojugal; *Sqp*, posterior lamina of the squamosal.

Fig. 2. Left lateral aspect of the same specimen as in figure 1. $^3/_2$ natural size.

Ext. l, dorsal lamina of the lateral extrascapular; *Ju*, jugal; *Po*, postorbital; *Quj*, quadratojugal; *Sq*, squamosal; *c*, ridge on the internal surface of the quadratojugal.

Fig. 3. Imperfect internal cast of a skull in dorsal view. Spec. *At.* 7. $^3/_2$ natural size.

Eo, exoccipital; *Ext. l*, dorsal lamina of the lateral extrascapular; *Ext. lv*, ventral process of the lateral extrascapular; *Fr. pa*, fronto-parietal; *Ju*, jugal; *Pa. ext*, dorsal lamina of the parieto-extrascapular; *Po*, postorbital; *Qu*, quadrate; *Quj*, quadratojugal; *So. dsph*, supraorbito-dermosphenotic; *Sq*, dorso-lateral lamina of the squamosal; *Sqp*, posterior lamina of the squamosal; *St. it*, supratemporo-intertemporal; *c*, semilunar ridge on the ventral surface of the parieto-extrascapular; *t*, tubercle on the ventral surface of the parieto-extrascapular.

Fig. 4. Ventral aspect of the same specimen as in figure 3. $^3/_2$ natural size.

Ecpt, ectopterygoid; *Enpt*, palatal ramus of the entopterygoid; *Enptq*, quadrate ramus of the entopterygoid; *Eo*, exoccipital; *Ext. lv*, ventral process of the lateral extrascapular; *Pspc*, processus cultriformis of the parasphenoid; *Psph*, corpus of the parasphenoid; *Qu*, quadrate; *c. i*, canal for the internal carotid artery; *fen. add*, adductor fenestra; *fen. ip*, interpterygoid vacuity.

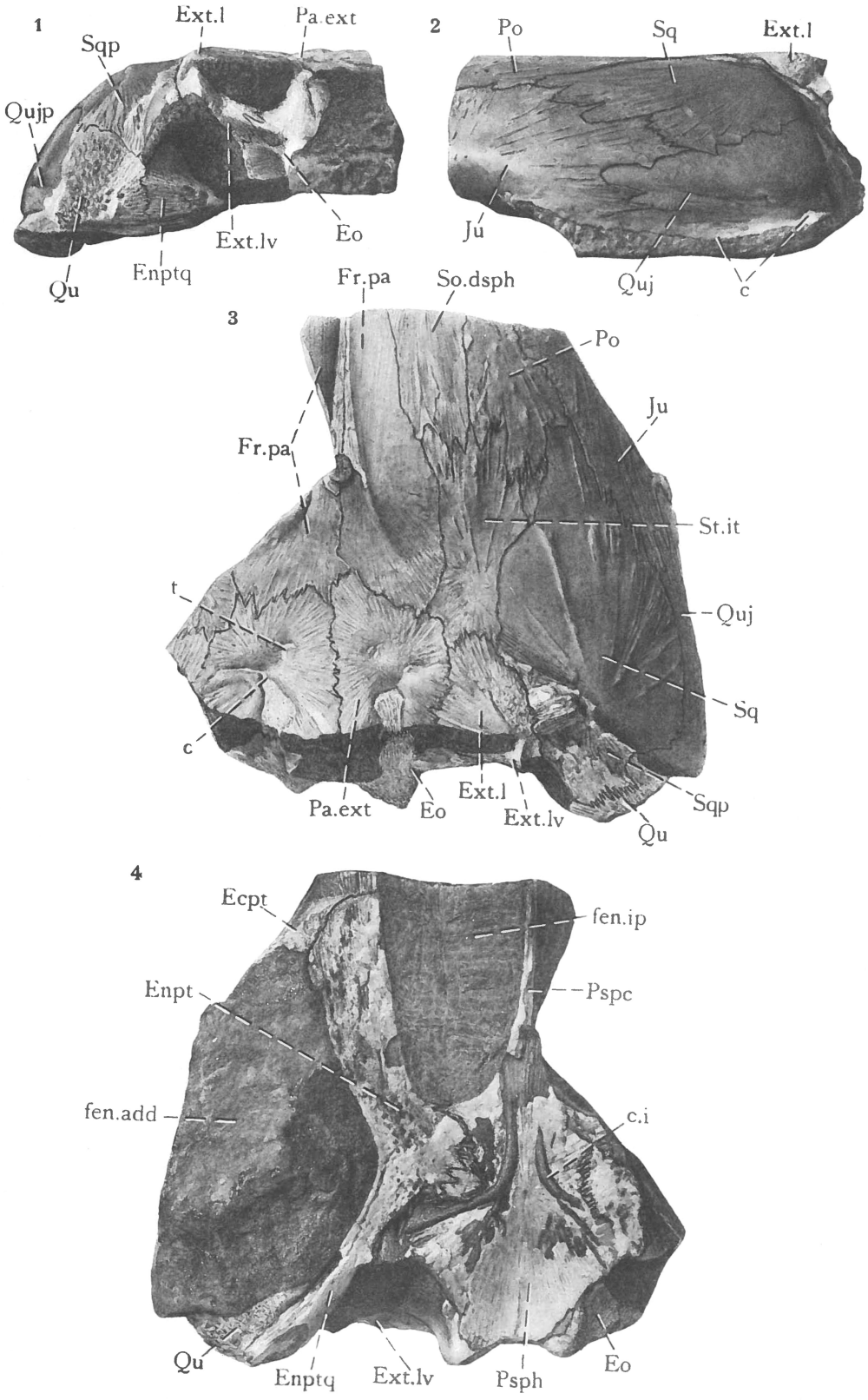

1
Ext.l
Pa.ext
Sqp
Qujp
Ext.lv
Eo
Enptq
Qu
2
Po
Sq
Ext.l
Ju
Quj
c
3
Fr.pa
So.dsph
Po
Ju
Fr.pa
St.it
t
Quj
Sq
c
Pa.ext
Eo
Ext.l
Ext.lv
Sqp
Qu
4
Ecpt
fen.ip
Enpt
Pspc
fen.add
c.i
Qu
Enptq
Ext.lv
Psph
Eo

Plate 5.

Stoschiosaurus nielseni? n. sp.

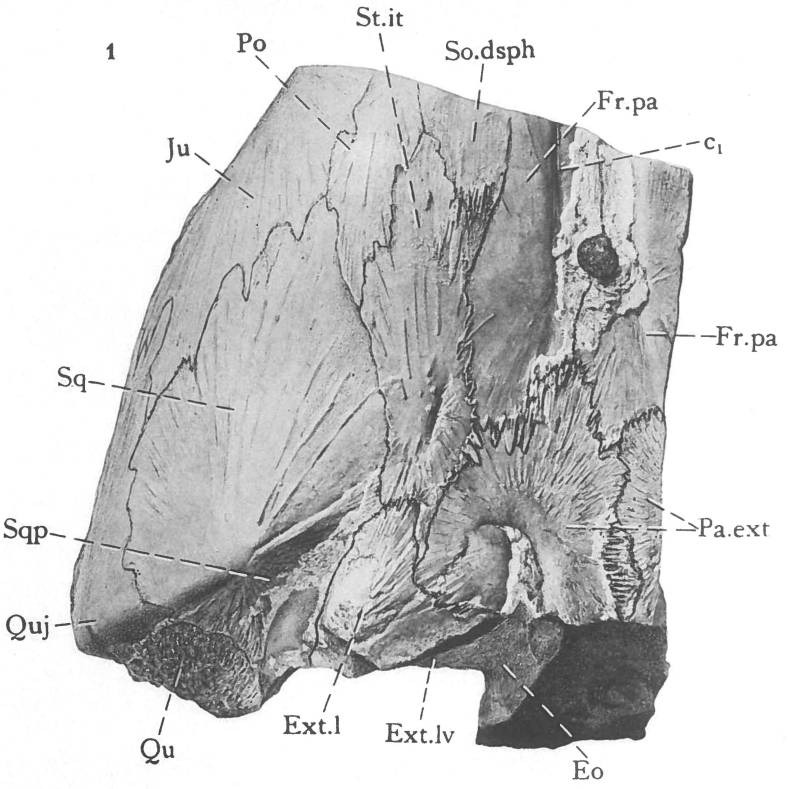
Imperfect internal cast of the left postero-lateral part of a skull. Spec. *At.* 8. $^3/_2$ natural size.

Fig. 1. Dorsal aspect.

Eo, exoccipital; *Ext. l*, dorsal lamina of the lateral extrascapular; *Ext. lv*, ventral process of the lateral extrascapular; *Fr. pa*, fronto-parietal; *Ju*, jugal; *Pa. ext*, dorsal lamina of the parieto-extrascapular; *Po*, postorbital; *Qu*, quadrate; *Quj*, quadratojugal; *So. dsph*, supraorbito-dermosphenotic; *Sq*, dorso-lateral lamina of the squamosal; *Sqp*, posterior lamina of the squamosal; *St. it*, supratemporo-intertemporal; c_1, ridge on the ventral surface of the fronto-parietal.

Fig. 2. Palatal aspect.

Bo, basioccipital; *Ecpt*, ectopterygoid; *Enpt*, palatal ramus of the entopterygoid; *Enptq*, quadrate ramus of the entopterygoid; *Eo*, exoccipital; *Ext. lv*, ventral process of the lateral extrascapular; *Pspc*, processus cultriformis of the parasphenoid; *Psph*, corpus of the parasphenoid; *Qu*, quadrate; *c*, canal, branching off from the canal for the internal carotid artery; *c. i*, canal for the internal carotid artery; *fen. add*, adductor fenestra; *fen. ip*, interpterygoid vacuity; *p*, pouch leading down into the corpus of the entopterygoid from the dorsal surface of the palate.


1
St.it
Po
So.dsph
Fr.pa
Ju
c_1
Fr.pa
Sq
Sqp
Pa.ext
Quj
Qu
Ext.l
Ext.lv
Eo

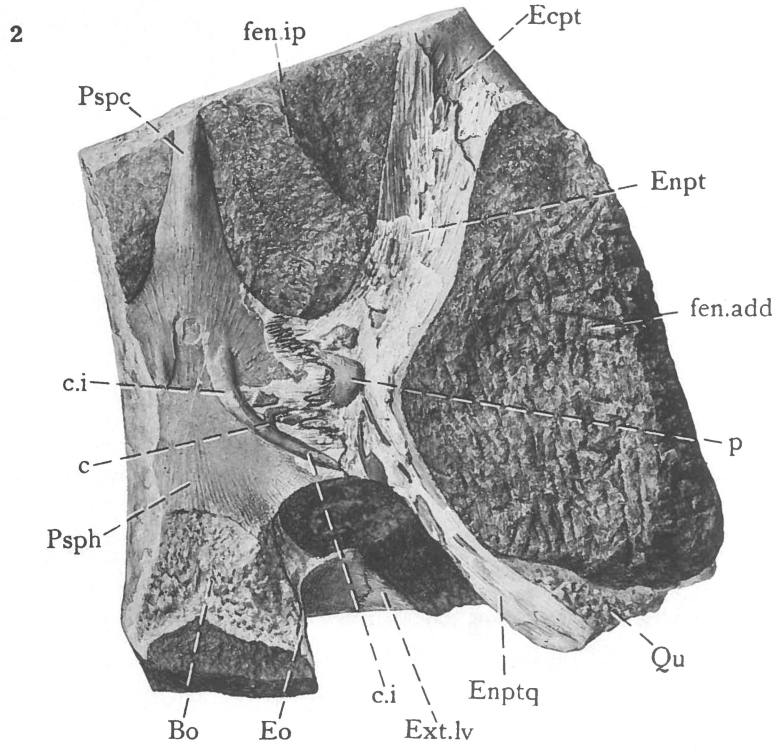

2
fen.ip
Ecpt
Pspc
Enpt
fen.add
c.i
p
c
Psph
Qu
Bo
Eo
c.i
Enptq
Ext.lv

Plate 6.

Stoschiosaurus n. sp.?

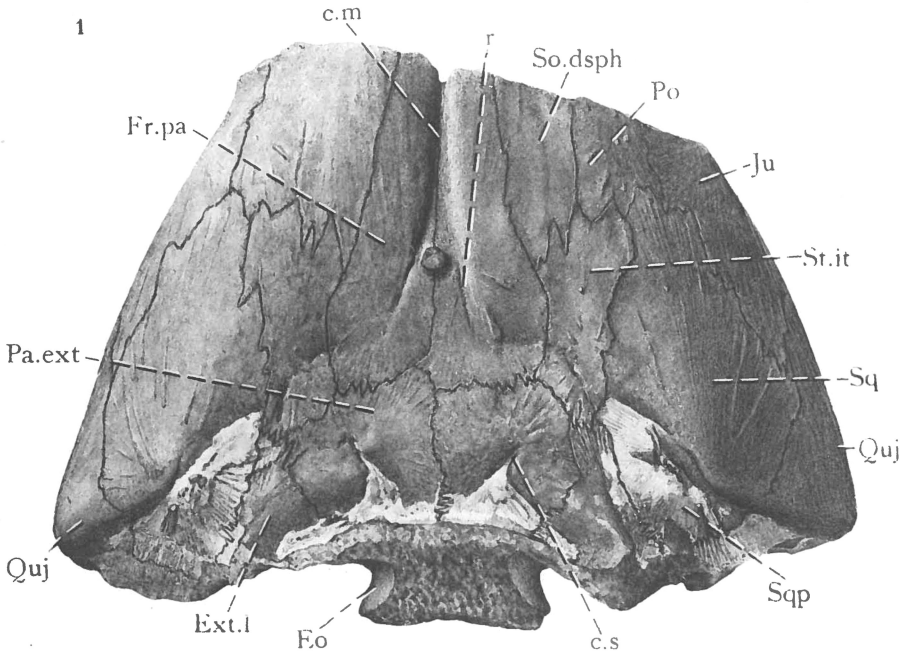
Internal cast of the posterior parts of a skull. Spec. *At.* 9. $^3/_2$ natural size.

Fig. 1. Dorsal aspect.

Eo, exoccipital; *Ext. l*, dorsal lamina of the lateral extrascapular; *Fr. pa*, fronto-parietal; *Ju*, jugal; *Pa. ext*, dorsal lamina of the parieto-extrascapular; *Po*, post-orbital; *Quj*, quadratojugal; *So. dsph*, supraorbito-dermosphenotic; *Sq*, dorso-lateral lamina of the squamosal; *Sqp*, posterior lamina of the squamosal; *St. it*, supra-temporo-intertemporal; *c. m*, median ridge on the ventral surface of the fronto-parietals; *c. s*, semilunar ridge on the ventral surface of the parieto-extrascapular; *r*, ridge on the ventral surface of the fronto-parietal.

Fig. 2. Palatal aspect.

Ecpt, ectopterygoid; *Enpt*, palatal ramus of the entopterygoid; *Enptq*, quadrate ramus of the entopterygoid; *Eo*, exoccipital; *Ext. lv*, ventral process of the lateral extrascapular; *Pspc*, processus cultriformis of the parasphenoid; *Psph*, corpus of the parasphenoid; *Qu*, quadrate; *c. i*, canal for the internal carotid artery; *fen. add*, adductor fenestra; *fen. ip*, interpterygoid vacuity.


1
c.m
r
So.dsph
Po
Fr.pa
Ju
St.it
Pa.ext
Sq
Quj
Quj
Ext.l
Eo
c.s
Sqp

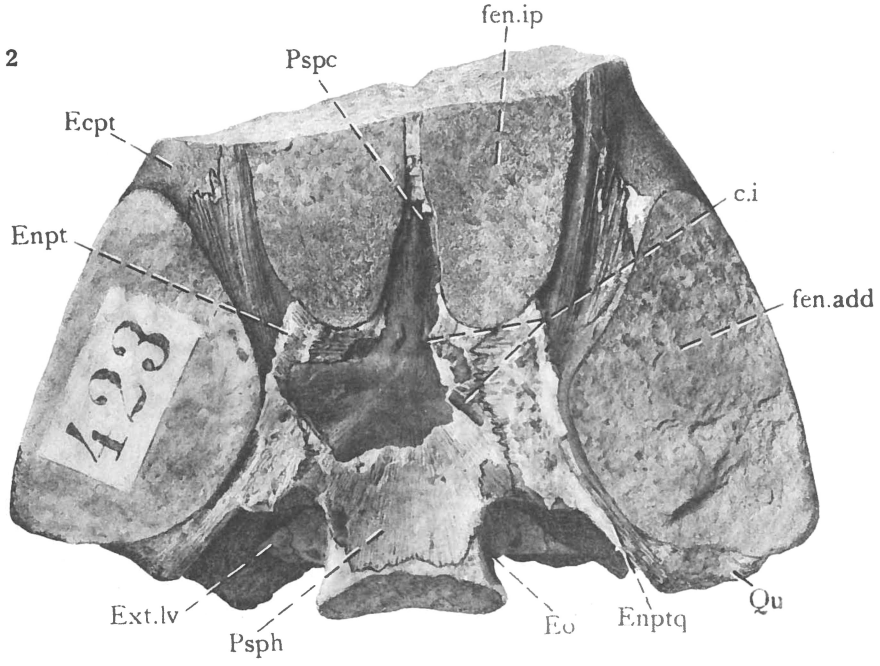

2
fen.ip
Pspc
Ecpt
c.i
Enpt
fen.add
123
Ext.lv
Psph
Eo
Enptq
Qu

Plate 7.

Lyrocephalus kochi n. sp.

Dorsal aspect of a skull. Spec. *At.* 1. $^{3}/_{2}$ natural size.

Ant, posterior antorbital; *Co*, stapes; *Enptq*, quadrate ramus of the entopterygoid; *Ext. l*, dorsal lamina of the lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Pa. ext*, dorsal lamina of the parieto-extrascapular; *Po*, postorbital; *Qu*, quadrate; *Quj*, quadrato-jugal; *Qujp*, posterior lamina of the quadratojugal; *R. na. pmx*, naso-rostro-pre-maxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, dorso-lateral lamina of the squamosal; *Sqp*, posterior lamina of the squamosal; *St. it*, supratemporo-intertemporal; *c. a*, ethmoidal commissure of the infraorbital canals; *f*, foramen between the quadrate and the quadratojugal; *ifsh*, horizontal portion of the suborbital part of the infraorbital canal; *ifsv*, vertical portion of the suborbital part of the infraorbital canal; *juc*, jugal canal; *ot*, otic part of the infraorbital canal; *s. com*, supratemporal commissural canal.

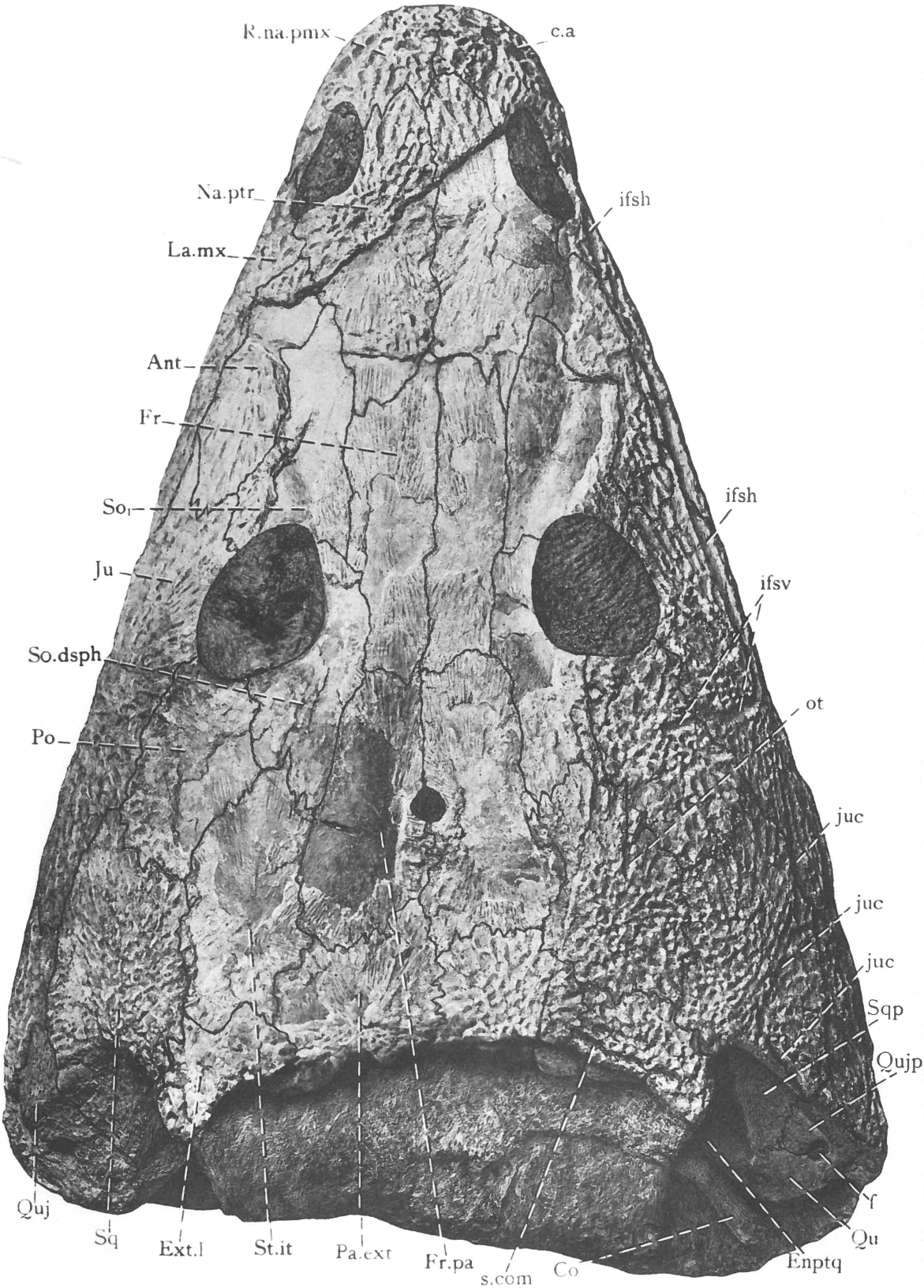

R.na.pmx
c.a
Na.ptr
ifsh
La.mx
Ant
Fr
So1
ifsh
Ju
ifsv
So.dsph
ot
Po
juc
juc
juc
Sqp
Qujp
Quj
Sq
Ext.l
St.it
Pa.ext
Fr.pa
s.com
Co
Enptq
Qu
f

Plate 8.

Lyrocephalus kochi n. sp.

Lateral aspects of the same skull as in plate 7, spec. *At.* 1. $^3/_2$ natural size.

Fig. 1. Right lateral aspect.

Fig. 2. Left lateral aspect.

Ant, posterior antorbital; *Ext. l*, dorsal lamina of the lateral extrascapular; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Quj*, quadratojugal; *Po*, postorbital; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, dorso-lateral lamina of the squamosal; *St. it*, supratemporo-intertemporal; *ifsh*, horizontal portion of the suborbital part of the infraorbital canal; *ifsv*, vertical portion of the suborbital part of the infraorbital canal; *inc. ot*, otic notch; *juc*, jugal canal.

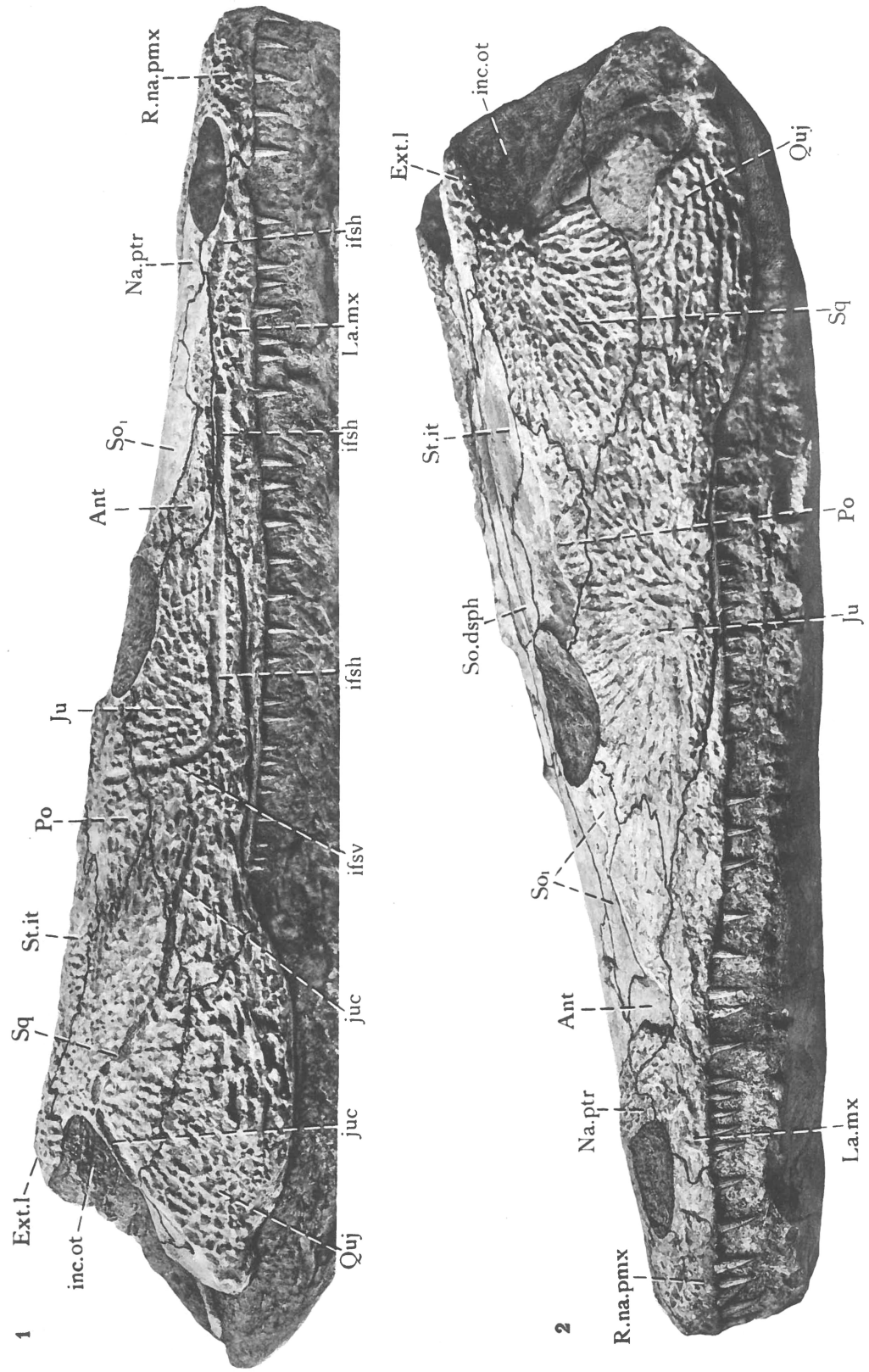

1
Ext.l
inc.ot
Sq
St.it
Po
Ju
Ant
So1
Na.ptr
R.na.pmx
ifsh
l.a.mx
ifsh
ifsh
ifsv
juc
juc
juc
Quj
2
Ext.l
inc.ot
Quj
Sq
St.it
Po
So.dsph
ju
So1
Ant
Na.ptr
La.mx
R.na.pmx

Plate 9.

Lyrocephalus johanssoni n. sp.

Anterior part of a skull. Spec. *At.* 28. $^3/_2$ natural size.

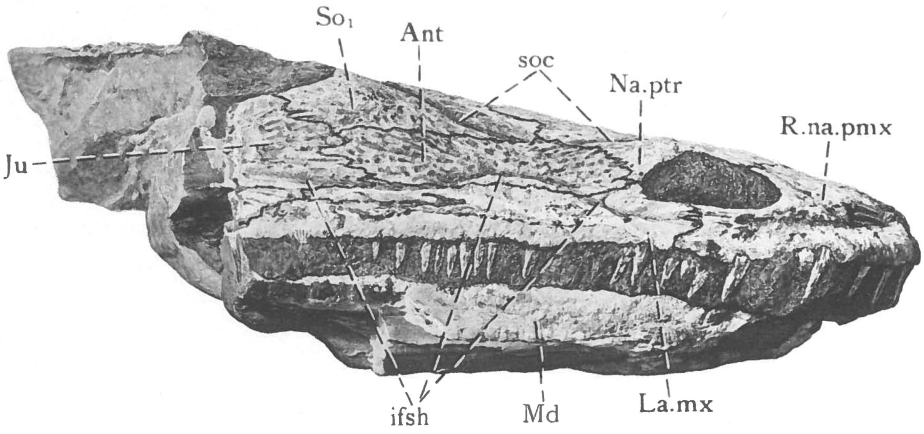
Fig. 1. Right lateral aspect.

Ant, posterior antorbital; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Md*, lower jaw; *Na. ptr*, naso-postrostral; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *ifsh*, horizontal portion of the suborbital part of the infraorbital canal; *soc*, supraorbital canal.

Fig. 2. Dorsal aspect.

A, anterior antorbital or septomaxillary; *Ant*, posterior antorbital; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *c. a*, ethmoidal commissure of the infraorbital canals; *ifsh*, horizontal portion of the suborbital part of the infraorbital canal; *n. e*, external nostril; *soc*, supraorbital canal.

1


So1
Ant
soc
Na.ptr
R.na.pmx
Ju
ifsh
Md
La.mx

2

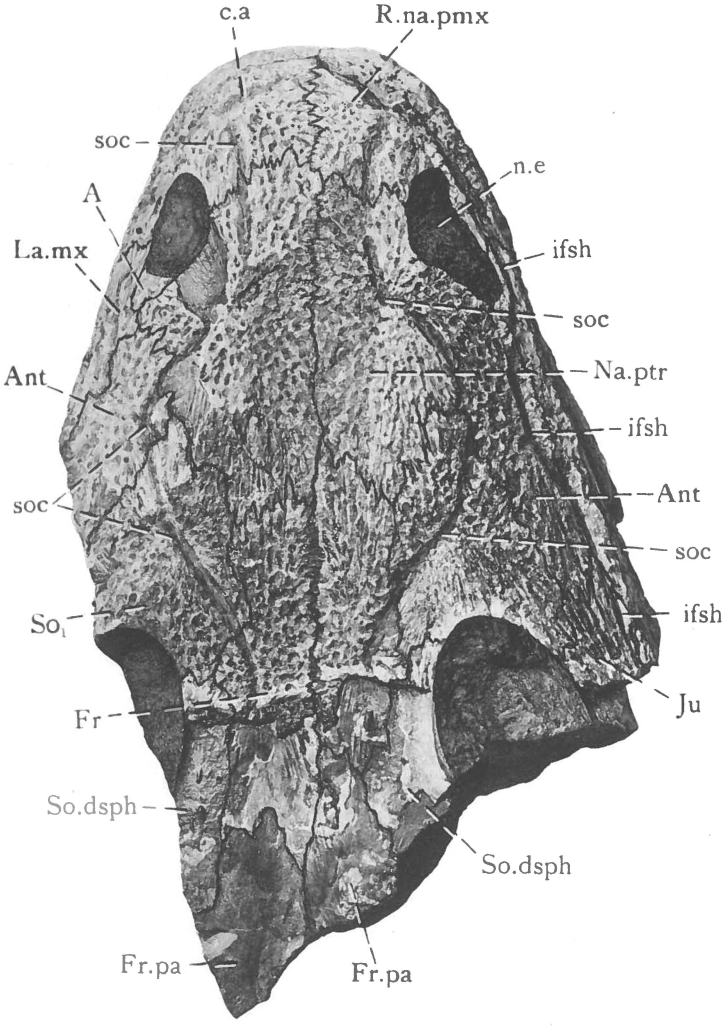

c.a
R.na.pmx
soc
n.e
A
La.mx
ifsh
soc
Ant
Na.ptr
ifsh
soc
Ant
soc
So1
ifsh
Ju
Fr
So.dsph
So.dsph
Fr.pa
Fr.pa

Plate 10.

Lyrocephalus johanssoni n. sp.

Anterior part of the skull. Spec. *At.* 28. $^3/_2$ natural size.

Fig. 1. Left lateral aspect.

A, anterior antorbital or septomaxillary; *Ant*, posterior antorbital; *La. mx*, lachrymo-maxillary; *Md*, lower jaw; *Na. ptr*, naso-postrostral; *R. na. pmx*, naso-rostro-premaxillary; *dp*, tooth of the dermopalatine; *ifsh*, horizontal portion of the sub-orbital part of the infraorbital canal; *n. e*, external nostril.

Fig. 2. Ventral aspect.

Md, lower jaw; *Pspc*, processus cultriformis of the parasphenoid; *dpmx*, teeth of the naso-rostro-premaxillaries.

Fig. 3. Anterior aspect.

A, anterior antorbital or septomaxillary; *Ant*, posterior antorbital; *Fr*, frontal; *La. mx*, lachrymo-maxillary; *Md*, lower jaw; *Na. ptr*, naso-postrostral; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *n. e*, external nostril.

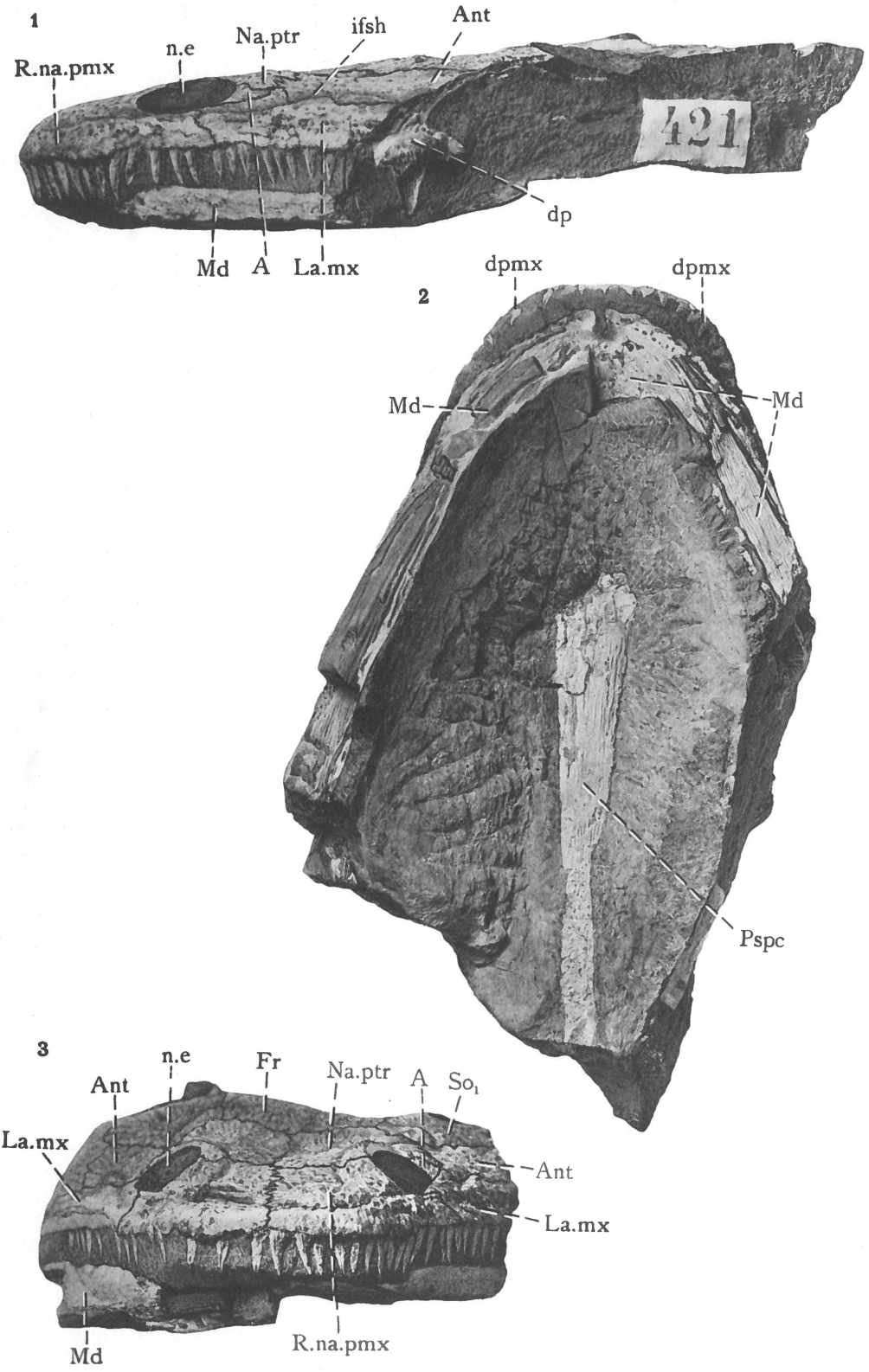

1
R.na.pmx
n.e
Na.ptr
ifsh
Ant
421
dp
Md
A
La.mx
2
dpmx
dpmx
Md
Md
Pspc
3
n.e
Fr
Na.ptr
A
So1
Ant
La.mx
Ant
La.mx
Md
R.na.pmx

Plate 11.

Lyrocephalus rapax n. sp.

Imperfect skull. Spec. *At.* 29. $^3/_2$ natural size.

Fig. 1. Dorsal aspect.

A, anterior antorbital or septomaxillary; *Ant*, posterior antorbital; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Po*, postorbital; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1 anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *ifsh*, horizontal portion of the suborbital part of the infraorbital canal.

Fig. 2. Left lateral aspect.

A, anterior antorbital or septomaxillary; *Ant*, posterior antorbital; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *Na. ptr*, naso-postrostral; *Po*, postorbital; *Quj*, quadratojugal; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *Sq*, squamosal; *St. it*, supratemporo-intertemporal.

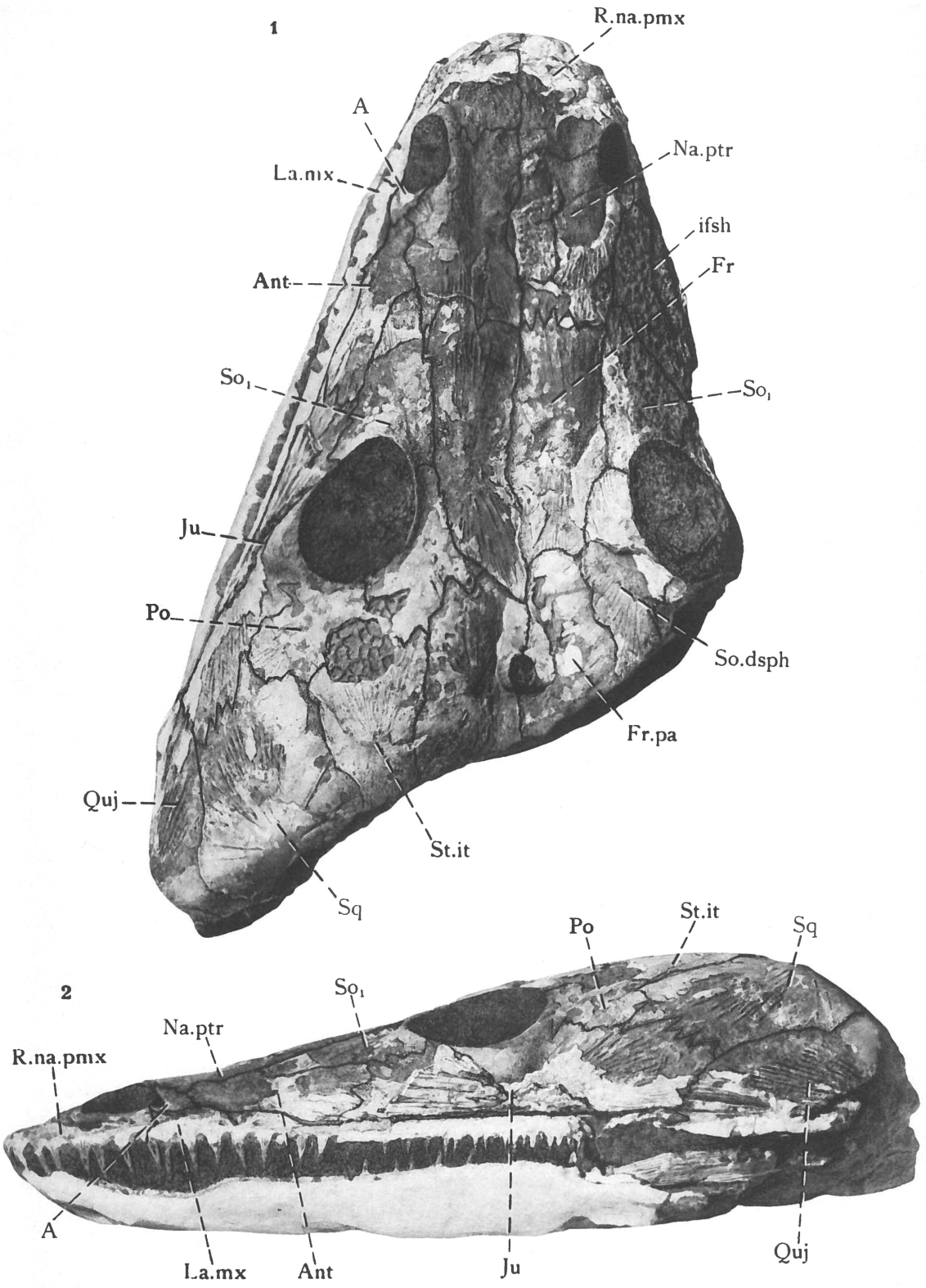

1
R.na.pmx
A
Na.ptr
La.mx
ifsh
Fr
Ant
So1
So1
Ju
Po
So.dsph
Fr.pa
Quj
St.it
Sq
2
Po
St.it
Sq
So1
Na.ptr
R.na.pmx
A
La.mx
Ant
Ju
Quj

Plate 12.

Lyrocephalus rapax n. sp.

Imperfect skull. Spec. *At.* 29. $^3/_2$ natural size.

Fig. 1. Ventral aspect.

Enpt, palatal ramus of the entopterygoid; *Enptq*, quadrate ramus of the entopterygoid; *Pspc*, processus cultriformis of the parasphenoid; *apv*, anterior palatal vacuity; *dcv*, very small tooth on the vomer; *de*, teeth probably on the ectopterygoid; dp_1, anterior, large tooth of the dermopalatine; dp_2, posterior small teeth of the dermopalatine; *dpmx*, tooth of the naso-rostro-premaxillary; *dv*, large teeth on the vomeres; *fen. add*, adductor fenestra; *fen. ip*, interpterygoid vacuity; *x*, plaster to support the palatal teeth.

Fig. 2. Right lateral aspect.

A, anterior antorbital or septomaxillary; *Ant*, posterior antorbital; *Ju*, jugal; *La. mx*, lachrymo-maxillary; *R. na. pmx*, naso-rostro-premaxillary; So_1, anterior supraorbital; *ifsh*, horizontal portion of the suborbital part of the infraorbital canal.

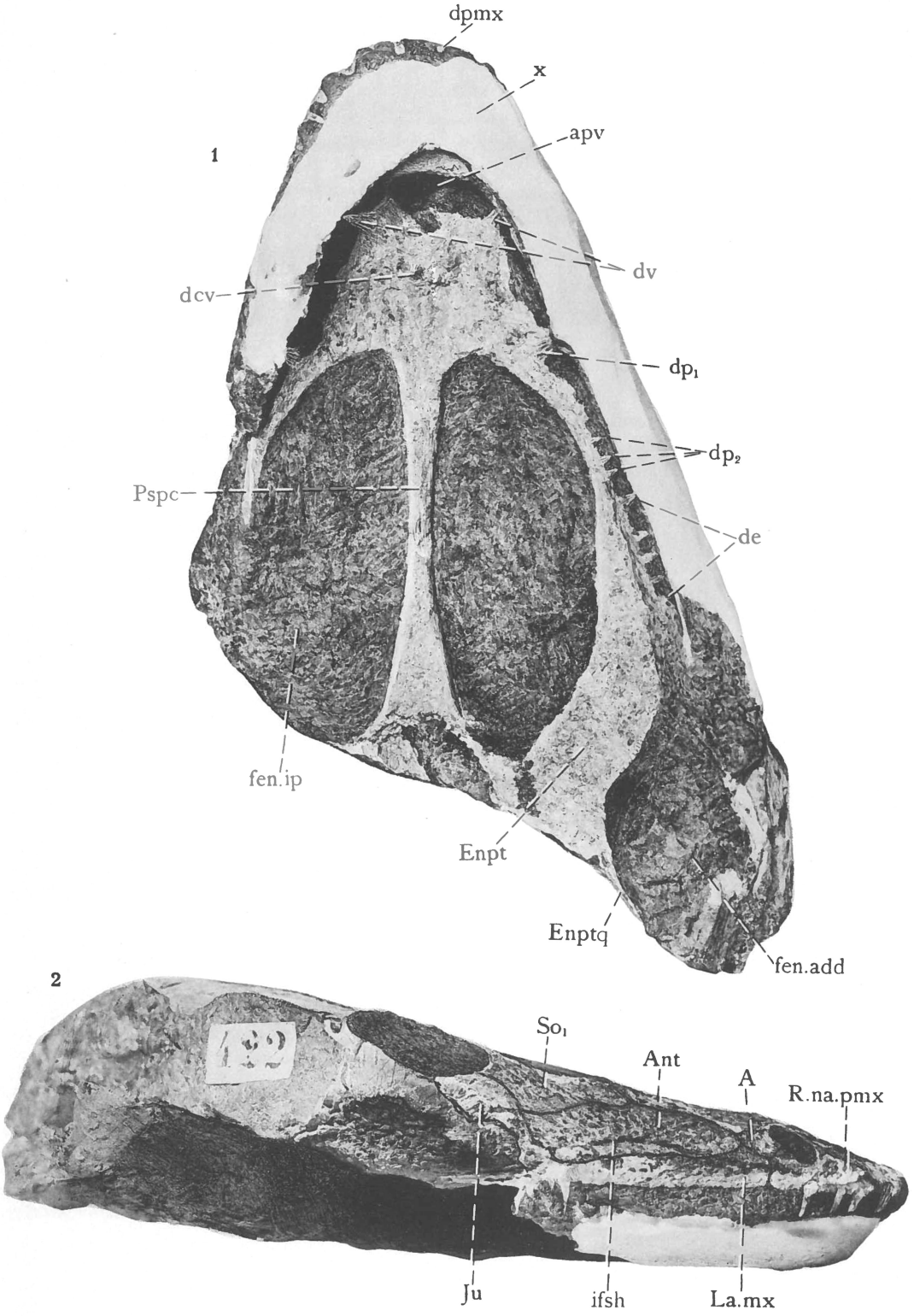

1
dpmx
x
apv
dv
dcv
dp1
dp2
Pspc
de
fen.ip
Enpt
Enptq
fen.add
2
So1
Ant
A
R.na.pmx
Ju
ifsh
La.mx

Plate 13.

Fig. 1. Indeterminable, possibly Lyrocephaline skull fragment in dorsal view. Spec. *At.* 4. $^{3}/_{2}$ natural size.

Ext. l, dorsal lamina of the lateral extrascapular; *Fr. pa*, fronto-parietal; *Ju*, jugal; *Pa. ext*, dorsal lamina of the parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; *So.dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; St_x, posterior intratemporal; *St. it*, supratemporo-intertemporal; *ot* + *ptc*, groove for the otic part of the infraorbital canal and the postotic canal.

Fig. 2. *Lyrocephalus* sp. Imperfect dermal cranial roof in ventral view. $^{3}/_{2}$ natural size. Spec. *At.* 3.

Ant, posterior antorbital; *Ext. l*, dorsal lamina of the lateral extrascapular; *Fr*, frontal; *Fr. pa*, fronto-parietal; *Ju*, jugal; *Na. ptr*, naso-postrostral; *Pa. ext*, dorsal lamina of the parieto-extrascapular; *Po*, postorbital; *Quj*, quadratojugal; So_1, anterior supraorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *ifsv*, vertical portion of the suborbital part of the infraorbital canal; *ot*, otic part of the infraorbital canal; *ptc*, probably postotic canal; *soc*, supraorbital canal.

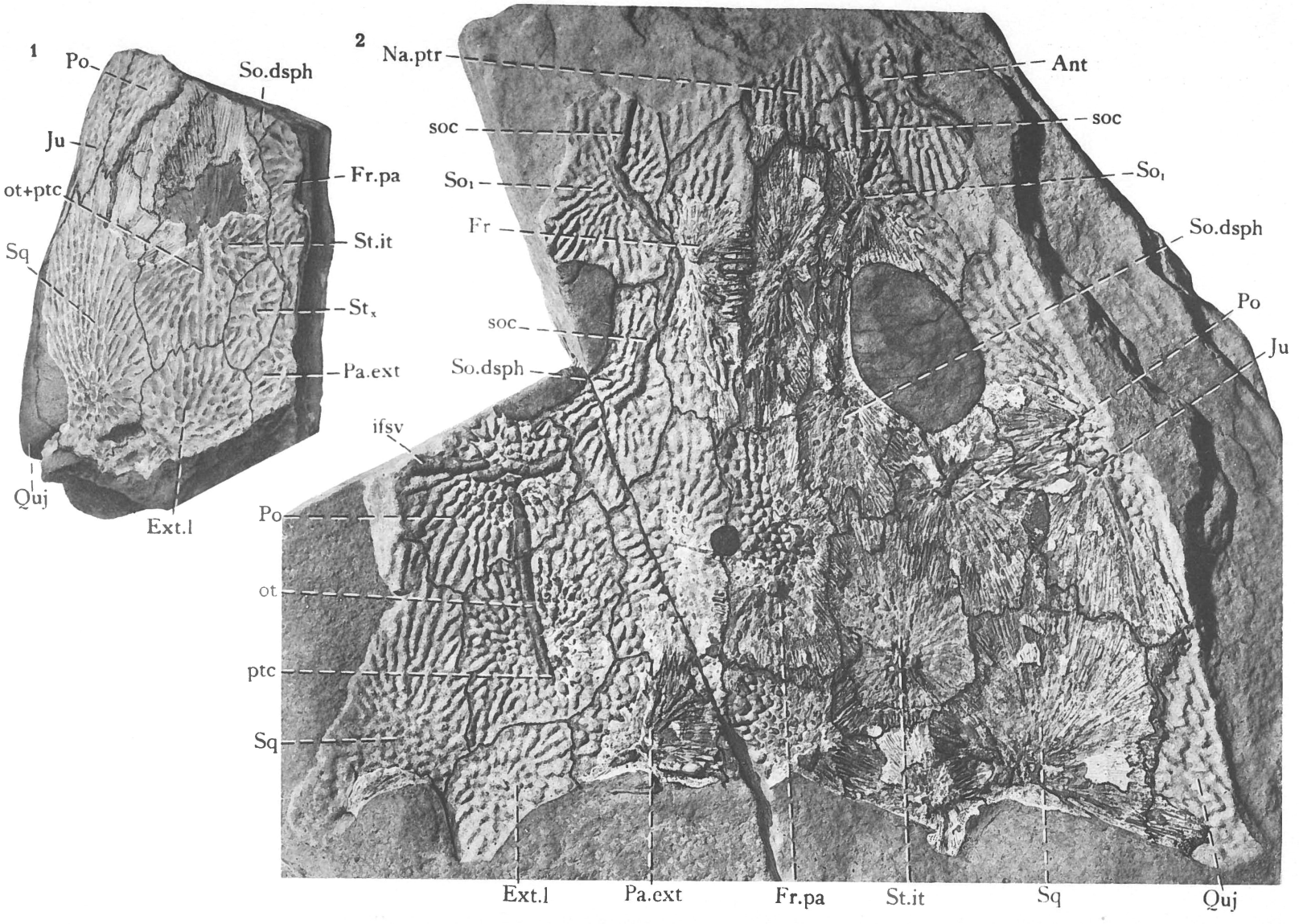

1
Po
So.dsph
Ju
Fr.pa
ot+ptc
St.it
Sq
St$_x$
Pa.ext
Quj
Ext.l
2
Na.ptr
Ant
soc
soc
So$_1$
So$_1$
Fr
So.dsph
Po
soc
Ju
So.dsph
ifsv
Po
ot
ptc
Sq
Ext.l
Pa.ext
Fr.pa
St.it
Sq
Quj

Plate 14.

Fig. 1. Indeterminable skull fragment of a large Stegocephalian, in dorsal view. Spec. *At.* 10. $^3/_2$ natural size.

Fr. pa, fronto-parietal; *Ju*, jugal; *Po*, postorbital; *Quj*, quadratojugal; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *c. m*, median crista on the ventral surface of the fronto-parietals; *pin*, pineal foramen.

Fig. 2. Indeterminable, possibly Lyrocephaline skull fragment in dorsal view. Spec. *At.* 30. $^3/_2$ natural size.

Ext. l, dorsal lamina of the lateral extrascapular; *Fr. pa*, fronto-parietal; *Ju*, jugal; *Pa. ext*, dorsal lamina of the parieto-extrascapular; *Po*, postorbital; *So. dsph*, supraorbito-dermosphenotic; *Sq*, squamosal; *St. it*, supratemporo-intertemporal; *ifsv*, vertical portion of the suborbital part of the infraorbital canal; *orb*, orbit; *ot*, otic part of the infraorbital canal.

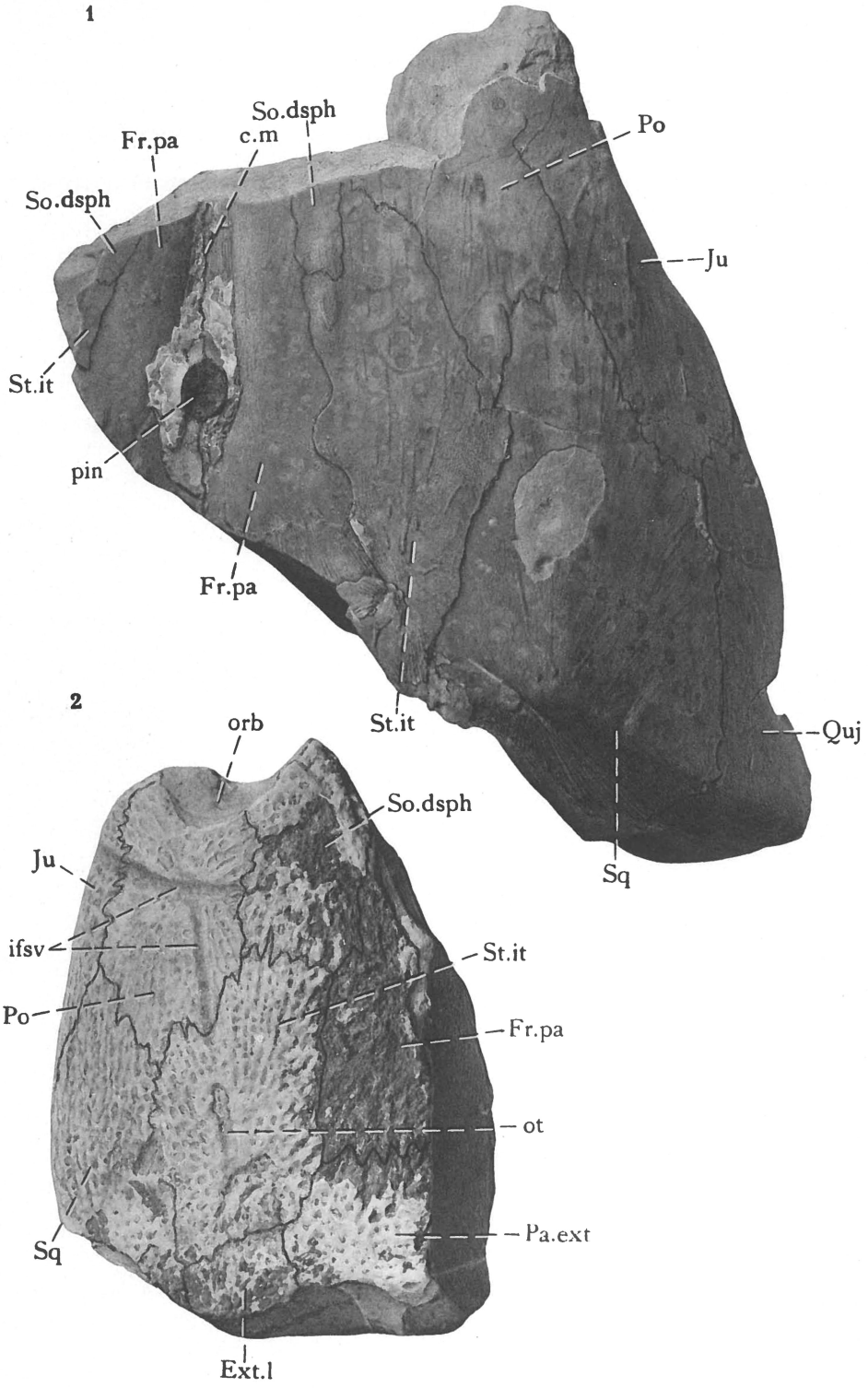

1
So.dsph
Fr.pa
c.m
Po
So.dsph
Ju
St.it
pin
Fr.pa
St.it
Quj
Sq
2
orb
So.dsph
Ju
ifsv
St.it
Po
Fr.pa
ot
Pa.ext
Sq
Ext.l

Plate 15.

Fig. 1. Indeterminable skull fragment of a large Stegocephalian in ventral view. Spec. *At.* 10. $^3/_2$ natural size.

Enpt, palatal ramus of the entopterygoid; *Enptq*, quadrate ramus of the entopterygoid; *Eppt*, epipterygoid; *Pspc*, processus cultriformis of the parasphenoid; *Qu*, quadrate; *fen. add*, adductor fenestra; *fen. ip*, interpterygoid vacuity.

Fig. 2. *Stoschiosaurus nielseni?* n. sp. Imperfect cast of posterior part of a skull in right lateral view. Spec. *At.* 7. Natural size.

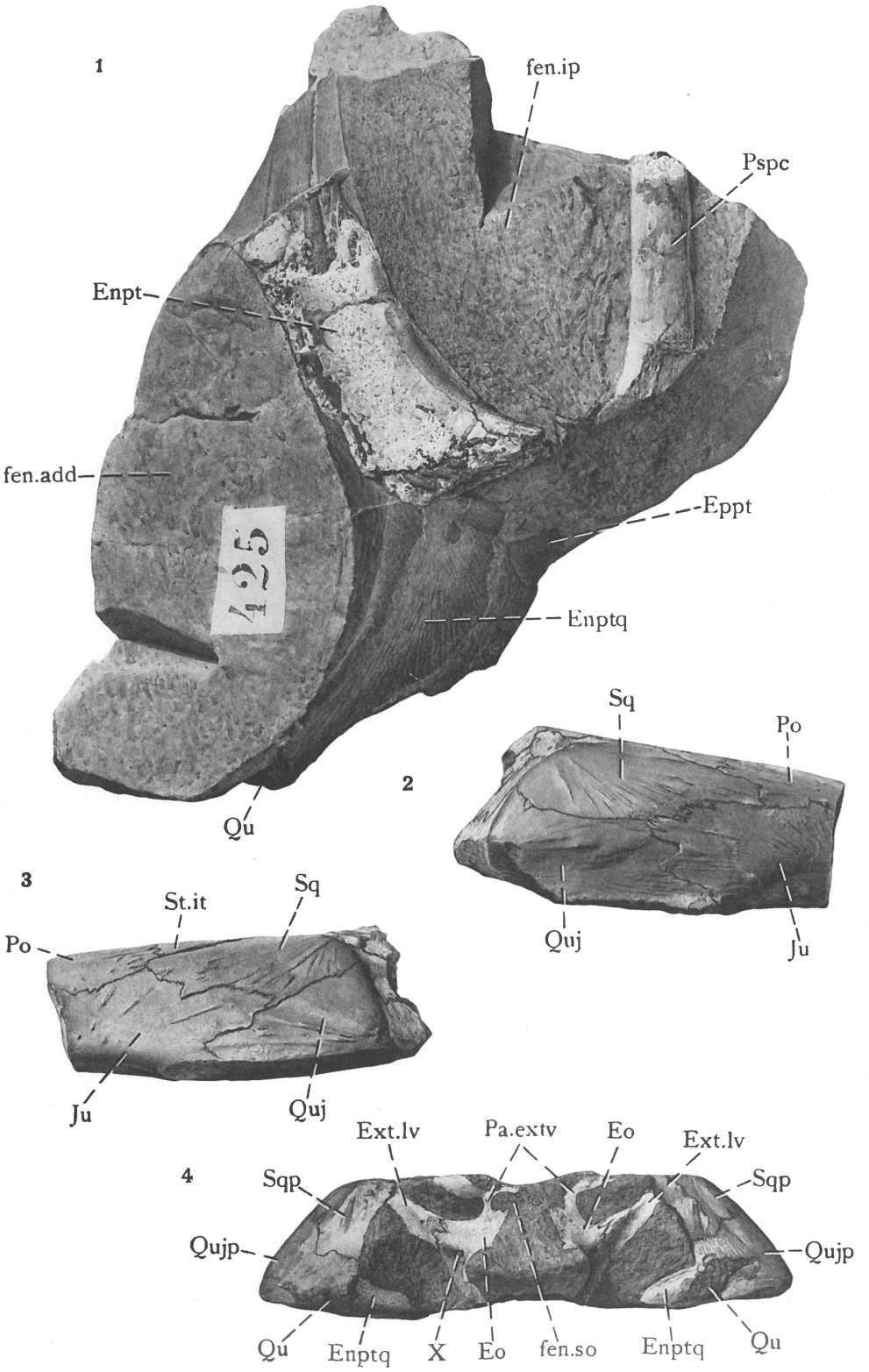
Ju, jugal; *Po*, postorbital; *Quj*, lateral lamina of the quadratojugal; *Sq*, dorsolateral lamina of the squamosal.

Fig. 3. *Stoschiosaurus* n. sp.? Internal cast of the posterior parts of a skull. Spec. *At.* 9. Left lateral aspect. Natural size.

Ju, jugal; *Po*, postorbital; *Quj*, lateral lamina of the quadratojugal; *Sq*, dorsolateral lamina of the squamosal; *St. it*, supratemporo-intertemporal.

Fig. 4. Same specimen, *At.* 9, as in figure 3, in posterior view. Natural size.

Enptq, quadrate ramus of the entopterygoid; *Eo*, exoccipital; *Ext. lv*, ventral process of the lateral extrascapular; *Pa. extv*, ventral processes of the parieto- extrascapulars; *Qu*, quadrate; *Qujp*, posterior lamina of the quadratojugal; *Sqp*, posterior lamina of the squamosal; *X*, vagus foramen; *fen. so*, space for the supraoccipital cartilage.


1
fen.ip
Pspc
Enpt
fen.add
425
Eppt
Enptq
Qu
2
Sq
Po
Quj
Ju
3
St.it
Sq
Po
Ju
Quj
4
Ext.lv
Pa.extv
Eo
Ext.lv
Sqp
Sqp
Qujp
Qujp
Qu
Enptq
X
Eo
fen.so
Enptq
Qu