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UNDER LEDELSE AF LAUGE KOCH

SOME FEW PRELIMINARY
REMARKS ON TRIASSIC FISHES
FROM EAST GREENLAND

BY

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WITH 19 FIGURES IN THE TEXT

KØBENHAVN

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PREFACE

The fish material treated in this paper was collected on the Danish Three Year Expedition to East Greenland 1931—34, during the summers 1932 and 1933 and the winter 1932—33. The work of collecting was conducted by the author.

I am indebted to Dr. LAUGE KOCH, the leader of the great expedition, for allowing me to work up the unique material.

To Professor ERIK STENSIÖ I am indebted for working facilities in Stockholm and for much good advice and guidance during the work.

I take the opportunity to thank also in this place my assistants during parts of the field work, M. KØIE, A. JENSEN, and J. TROELSEN, for their help and for good companionship during the work.

I owe a special debt of gratitude to Dr. J. PIVETEAU, who with great readiness placed specimens of Madagascar *Palaeoniscidae* at my disposal.

INTRODUCTION

On the Danish Three-Year Expedition to East Greenland 1931—34 very large materials of fish remains comprising at least 2000 specimens was secured from the Eotriassic beds at Godthaab Gulf. These fishes have been briefly mentioned in a paper dealing with the stratigraphy of the area (E. NIELSEN 1935, pp. 99—108), to which the reader is referred for information about the localities.

The most recent years show an enormous development of our knowledge of the Triassic fish fauna, for since STENSIÖ's pioneer works came out in 1921 and 1925, papers on the Triassic fish fauna have appeared at short intervals from previously known as well as from newly discovered localities throughout a great part of the world (BROUGH 1931 and 1933, MOY THOMAS 1935, PIVETEAU 1929, 1931, and 1935, STENSIÖ 1932, WADE 1929, 1933, and 1935, WHITE 1932 and 1933).

As the final description of the Triassic fishes of Greenland will take several years, a preliminary account seems to be justified, considering the general interest taken in the matter, all the more so since a preliminary examination of the material has thrown light on several interesting features.

THE STATE OF PRESERVATION OF THE MATERIAL

The fishes occur in six well separated zones (E. NIELSEN 1935, p. 100), which are characterised by their different invertebrate faunas (see SPATH 1935).

Each fish zone seems to contain its special fish fauna, even though a number of forms are common to several zones.

In the lowermost fish zone (fish zone I) the fishes occur mainly in limestone bands, more rarely in concretions, and always as fragments. In the uppermost fish-bearing zone (the Stegocephalian horizon) the fishes occur in limestone bands, and are rarer than in any of the other zones.

In all the remaining zones (fish zones II, III, IV, and V) the fish remains are almost exclusively found in calcareous concretions and usually in an exceptionally good state of preservation. From these four zones the greater part of the large material is derived. The concretions mostly lie loose on the surface of the outcrops of the fish zones, and in many cases have become split on account of regelation. Not rarely parts of the same concretion are found at intervals of several metres, and it is often difficult to secure all the fragments of much destroyed concretions. If the concretions are undamaged, a slight blow with the hammer is often sufficient to expose the fish, but in cases in which the outer shape of the concretion indicates the presence of a fish fossil, it will be worth while to collect the concretion unopened for later preparation. Several hundreds of such unopened concretions have been brought home from the fish zones. By digging in the fish-bearing beds quite fresh and undisintegrated concretions may occasionally be met with which will hardly split even by severe blows of the hammer.

Many of the concretions contain entire fishes, others only heads or fragments of the body, more rarely isolated bones or scattered scales. The state of preservation of the fishes shows that formation of concretions has frequently taken place very soon after the death of the fishes, the various parts of a fish often occurring in their natural mutual

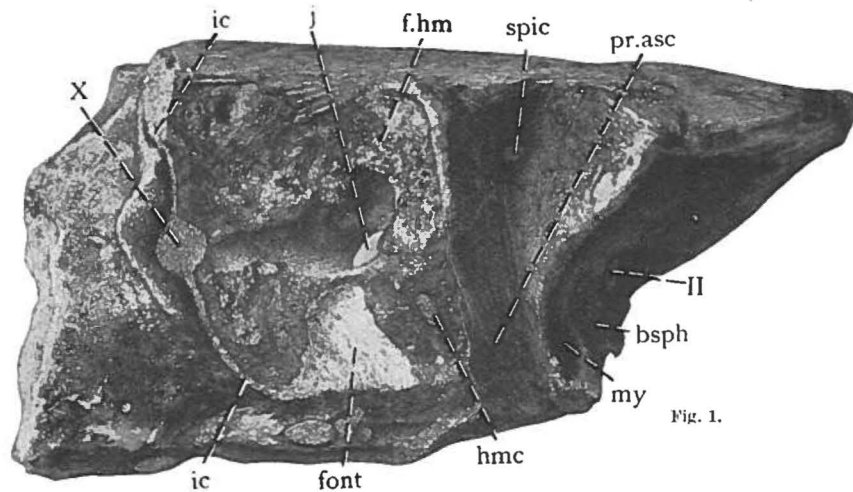


Fig. 1.

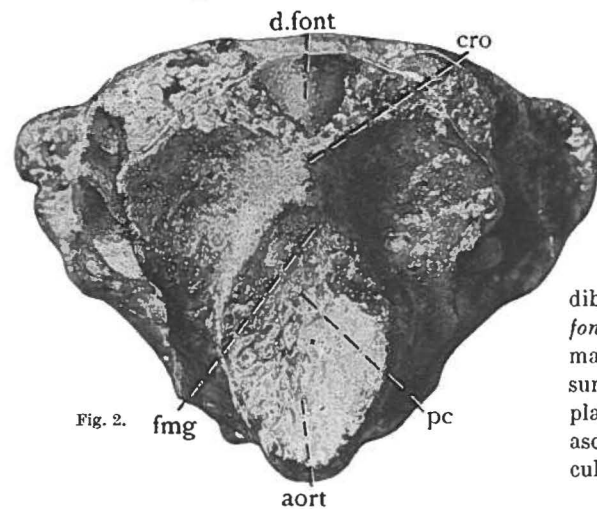


Fig. 2.

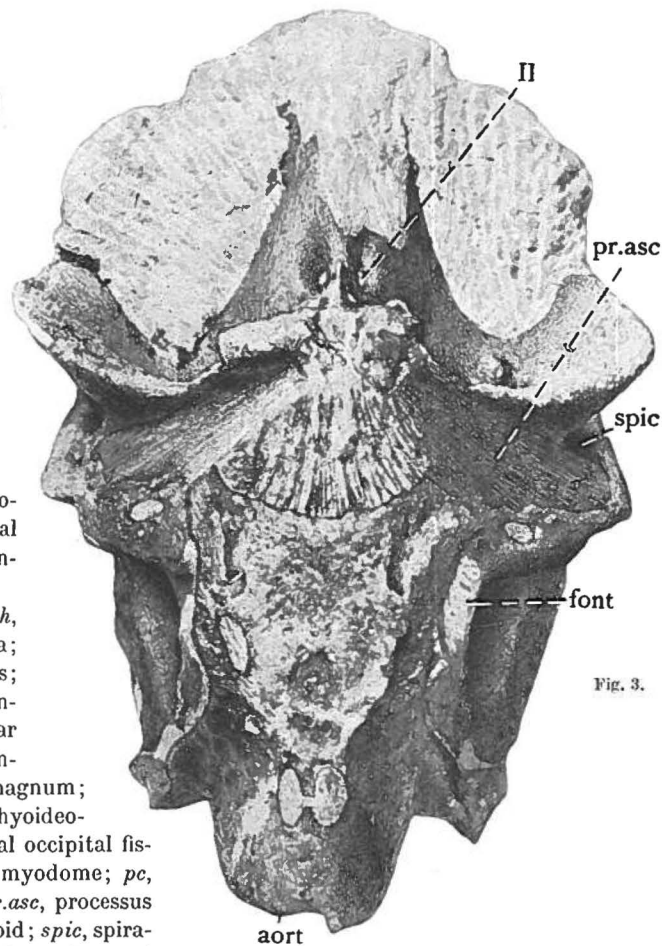


Fig. 3.

Figs. 1—3. An endocranium seen in lateral (1), caudal (2) and ventral (3) view. 3×.

aort, aorta canal; *bsph*, pars basisphenoidea; *cro*, crista occipitalis; *d.font*, dorsal fontanelle; *f.hm*, articular fossa for the hyomandibular; *fmg*, foramen magnum; *font*, lateral fontanelle; *hmc*, hyoideo-mandibular canal; *ic*, lateral occipital fissure; *j*, jugular canal; *my*, myodome; *pc*, place for the notochord; *pr.asc*, processus ascendens of the parasphenoid; *spic*, spiracular canal; *II*, foramen opticus; *X*, canal for the n. vagus.

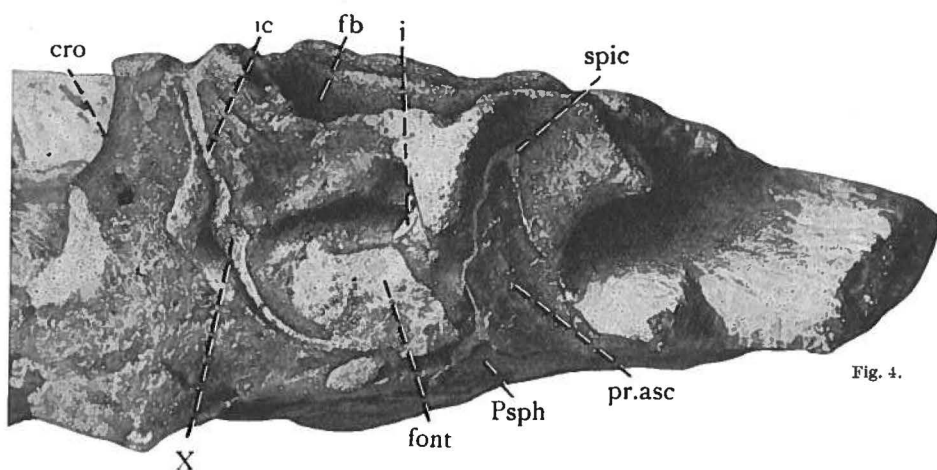


Fig. 4.

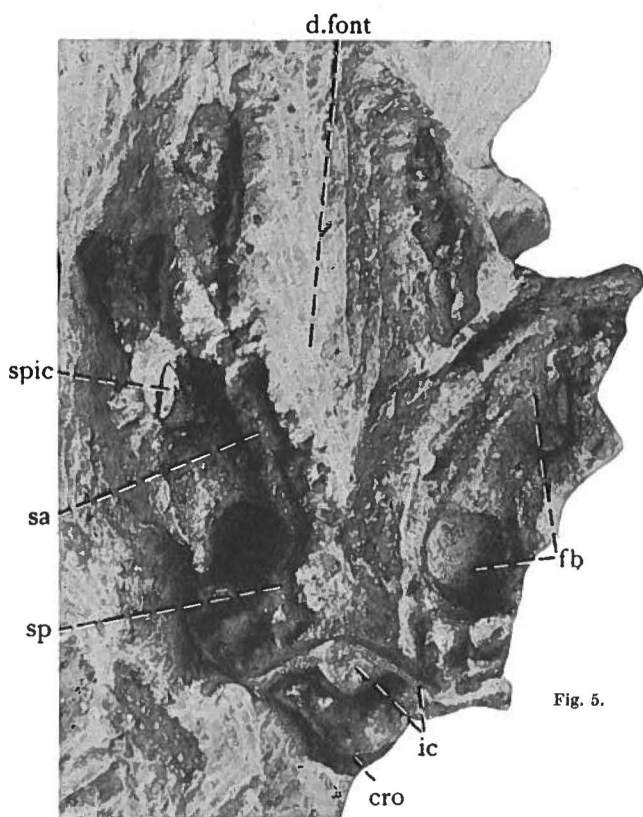


Fig. 5.

Fig. 4—5. An endocranium seen in lateral (4) and dorsal (5) view. 3 X.
Psph, parasphenoid; *cro*, crista occipitalis; *d.font*, dorsal fontanelle; *fb*, fossa bridgei; *font*, lateral fontanelle; *ic*, lateral occipital fissure; *j*, jugular canal; *pr.asc*, processus ascendens of the parasphenoid; *sa*, *sp*, ridge above the anterior and posterior semicircular canal; *spic*, spiracular canal; *X*, canal for the n. vagus.

Fig. 6.

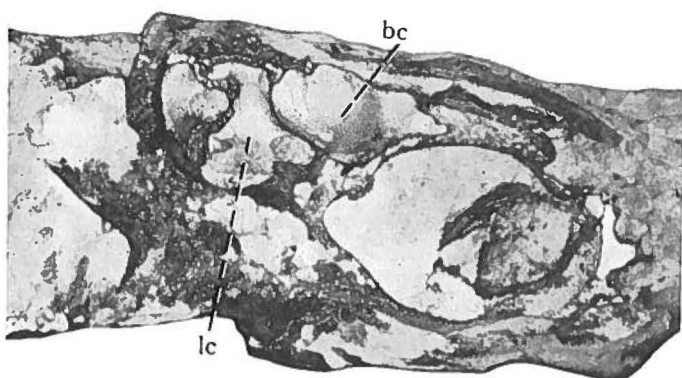


Fig. 7.

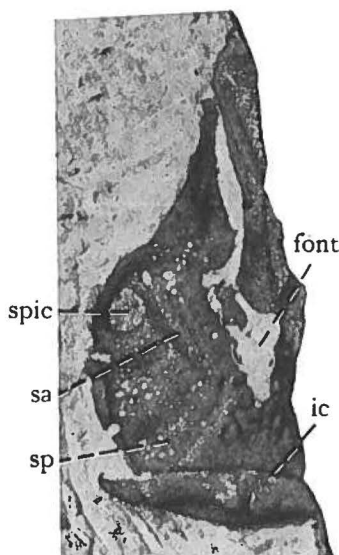


Fig. 6—7. A fish skull showing the brain cavity (6) and a part of the dorsal surface of the endocranium (7) 3 ×.

b.c., brain cavity; *font*, dorsal fontanelle; *ic*, lateral occipital fissure; *lc*, labyrinth cavity; *sa*, *sp*, ridge above the anterior and posterior semicircular canal; *spic*, spiracular canal.

position. In other cases the fishes have been in a more or less advanced stage of decomposition before the concretions were formed, with the result that the scales are in disorder and the individual bones of the head more or less separated from each other. In many cases the bodies of the fishes are lying straight while in other cases they are more or less curved. In *Australosomus* the well ossified vertebral column often exhibits a different curvature from that of the body of the fish, and sometimes it is even curved so much as to be situated in part above or below the very trunk. A large part of the vertebral column of *Australosomus* is

often found lying all alone in a concretion, quite isolated, but otherwise undamaged.

It is of great importance for the anatomical examination that the fishes in several cases are not or but slightly compressed. Thus we may find specimens in which the paired fins are situated in their natural position in relation to the body, and specimens in which the head has been but little damaged. In the latter cases the endocrania may be dissected out, and they show such an exceptionally beautiful state of preservation as is hardly known from any other fossil Ganoid material. In several cases the concretions contain quite isolated endocrania, which however, may as a rule be determined at least to their genus by comparison with the endocrania of more complete specimens. It is my plan to use the grinding method introduced in fish palaeontology by STENSIÖ to study the more interesting endocrania.

Many specimens of different forms exhibit the interesting feature that the pigment of the eye is preserved, and several specimens further show the distribution of the pigment of the body. Thus in the smaller Coelacanthids and in *Birgeria* it is easy to distinguish the dark dorsal side from the light-coloured ventral side of the fish.

THE FISH FAUNA

Elasmobranchii.

Remains of Elasmobranchs dominate in fish zone I (Koch 1931, STENSIÖ 1932, p. 14—16, E. NIELSEN 1935, p. 100), are extremely rare in fish zone II, and are absent from all the higher fish zones.

Only very few further finds of Elasmobranchs have been made since STENSIÖ in 1932 described the Elasmobranch fauna from the Eotriassic of East Greenland.

Polyacrodus.

Material: From fish zone II some few concretions are derived which contain heads of *Polyacrodus*. The heads are rather badly crushed but the arrangement of the teeth is only slightly disturbed. In a single case, in addition to teeth, the pigment of the eye, and parts of the calcified cartilage of the cranium, well preserved visceral arches are visible in the concretion. A few concretions contain fin-spines of *Polyacrodus* connected with fragments of the fin skeleton and together with remains of neural arches; no complete specimen of *Polyacrodus* has been found.

Remarks: The presence of this genus in East Greenland has been shown by STENSIÖ in 1932.

Fin-spines of the Nemacanthus type.

Material: Some new specimens from the lowermost fish zone are at hand. (STENSIÖ 1932, p. 9).

Remarks: Fin-spines of this type were recorded from East Greenland by STENSIÖ in 1932 (STENSIÖ 1932, p. 14).

Undetermined Edestid genus.

Material: A single symphysial row of teeth of a specialised Edestid collected from fish zone II in Neviatiakdalen.

Remarks: This interesting specimen is so far the youngest known representative of the family *Edestidae*.

Other fin-spines.

A number of still undetermined fin-spines have been secured from the lowermost fish zone.

Crossopterygii.

Coelacanthidae.

The *Coelacanthidae* constitute an important part of the newly collected fish material and represent a considerable number of genera. The state of preservation is often excellent, so that it is possible to dissect out the endocranium and all the dermal bones of the head. The fin skeleton is more completely preserved than in any other known Coelacanthid material (STENSIÖ 1932), and the pigment of the body as well as of the eye is preserved in many cases.

The composition of the Coelacanthid fauna varies from one fish zone to the other, for the present, however, no definitive information can be given as to the occurrence of the different genera within the zones.

In 1932 STENSIÖ gave a short review of all the Triassic Coelacanthid genera known up to that time, from which it appears that the greater number of these, even the Spitsbergen genera, are so incompletely known, that it will be very difficult or impossible to refer new Triassic Coelacanthid material to a definite genus. Regarding the whole group *Coelacanthidae*, STENSIÖ summarizes (STENSIÖ 1932, p. 46) as follows "From our present knowledge concerning them it is evident that the Coelacanthids, especially as regards the osteology of the head but also to some extent with regard to the trunk and fins, show a much larger range of variation than could have been anticipated. Our present knowledge also makes it clear that the Coelacanthids were specialized for different modes of living. In fact we can already distinguish among them several groups of genera for each of which it will perhaps eventually be necessary to erect a special sub-family. A monographic description of all the Coelacanthid material thus far discovered would certainly throw new light on this subject and is therefore greatly to be desired".

Undoubtedly the new Greenland material will greatly increase the sparse knowledge of the mutual relationship of at least the Triassic Coelacanthids. Furthermore an investigation of the endocranial ossifications will be of the utmost importance, as the Greenland material with regard to the reduction of the ossifications of the endocranium shows an intermediate position between the Devonian *Diplocercides* on one hand and the younger Triassic Spitsbergen forms and the other Mesozoic forms on the other.

Whiteia MOY-THOMAS.

Material: Several skulls; often connected with smaller or larger parts of the body. The skulls are not seldom in an excellent state of preservation, so that it is possible either to expose the ossifications of

the endocranium by preparation, or to investigate them more in detail after the grinding method of SOLLAS.

Remarks: The genus *Whiteia* was quite recently erected by MOY-THOMAS in his paper (MOY-THOMAS 1935) on the Coelacanthids of Madagascar, a paper which has been of considerable importance for the preliminary determination of the Greenland material.

Laugia STENSIÖ.

Material: A very large number of specimens, often well preserved. Endocrania, well suited for investigation by SOLLAS' grinding method, are at hand.

Remarks: The genus *Laugia* was erected 1932 by STENSIÖ on rather well preserved material from East Greenland (STENSIÖ 1932, p. 46). With the exception of the endocranium the skeleton of *Laugia* is more completely known than that of any other Coelacanthid.

In several of the Greenland genera the cheek is entirely covered by bones, and although some of the forms show reductions of the cheek-bones, in none of the genera is the reduction of these bones so far advanced as in the forms from Spitsbergen. Among the Greenland material *Laugia* seems to be the form in which the reduction is most advanced.

In the new material of *Laugia* we find in the space ascertained by STENSIÖ between the squamosal, the lacrymo-jugal and the opercular, a little bone, which judging from the course of the preopercular canal, represents the hindmost part of a preoperculo-quadratojugal of a similar type to that in *Whiteia*. The preoperculo-quadratojugal of *Laugia* is therefore not, as assumed by STENSIÖ, completely lacking, (STENSIÖ 1932, p. 55), but very much reduced, so that only the preopercular component of that bone is present.

The *Laugia* material seems to include more than one species.

Sassenia STENSIÖ.

Material: Some heads and parts of the body of rather big specimens. The preservation is rather good.

Remarks: This genus was described in 1921 from Spitsbergen by STENSIÖ (STENSIÖ 1921, p. 84), but from very incomplete material. The new Greenland material will add much to our knowledge of this form, especially regarding the dermal bones of the head.

There is hardly more than one species represented in the material.

Other genera.

Two or three other genera seem to be present in our large material. One of these genera bears some resemblance to the Spitsbergen genus *Wimania* STENSIÖ. Another resembles *Laugia* rather much, but lacks

the very characteristic specialisation of the lepidotrichia of the pelvic fins of *Laugia*. This *Laugia*-like genus is one of the most common Coelacanthids in East Greenland.

Anatomical remarks.

The material comprises among others the very complete head of a rather large Coelacanthid form from fish-zone 4 on Stensiö Plateau (figs. 8, 9, 10 and 14). The arrangement of the dermal bones of the fronto-ethmoidal and parietal shields is very easy to investigate in this specimen as the head has been compressed in a dorsi-ventral direction, while in most other cases the Coelacanthids from the East Greenland Triassic beds have been compressed from side to side. In this case the pressure has been so slight that the endocranial ossifications have not sustained any damage, and regarding the dermal and primordial bones both of the head and the visceral skeleton the specimen in question is among the most complete ones from the Triassic found as yet.

As an introduction to some few considerations regarding the dermal bones and the sensory canals in the cranial roof of the Coelacanthids in general I shall give below a description of the dermal bones in the fronto-ethmoidal shield of the specimen just referred to, as this specimen gives a more complete idea of that part of the head than any previously described Triassic form of the group. As I do not intend in this paper to describe the specimen in detail, I prefer at present not to determine it as to genus (it might belong to a previously described genus or it might represent a new one). I only want to point out, that the specimen shows rather close resemblance to *Whiteia* MOY-THOMAS.

The frontals are short and must be homologised with the posterior pair of frontals in *Whiteia* (MOY-THOMAS 1935, fig. 1). In front of these short frontals we find a pair of bones (*Fr.ptr*, fig. 8), the fronto-postrostrals, which represent the anterior frontals and the most posterior pair of postrostrals in *Whiteia*. That MOY-THOMAS is right in naming both the most posterior and the next following pair of bones in the frontal-postrostral series frontals in *Whiteia* is clearly shown by the course of the supraorbital canal and the position of the nasals (see below). Moreover these two pairs of frontals, which have been found in some Greenland *Whiteia* too (see fig. 11 and fig. 12), have the same rostro-caudal extent as the single pair of frontals found in for instance *Wimania* and *Axelia* and is, therefore, in all probability homologous with that pair. The anterior and posterior frontals in the fronto-ethmoidal shield of *Whiteia* are not homologous with the postulated two pairs of frontals in the common ancestor of Stegocephalians and Crossopterygians (SÄVE-SÖDERBERGH 1932, fig. 18), but probably only with the foremost pair in this theoretical ancestor (see below). Anterior to the frontals

in the Greenland specimen lie two pairs of postrostrals, the most anterior of which very likely contain rostral components and therefore should be termed rostro-postrostrals. The right rostro-postrostral is in a rather advanced process of fusion not only with the postrostral behind it but also with the adjoining lateral rostral. As seen in fig. 9 the suture between that rostro-postrostral and the adjoining more posteriorly lying postro-

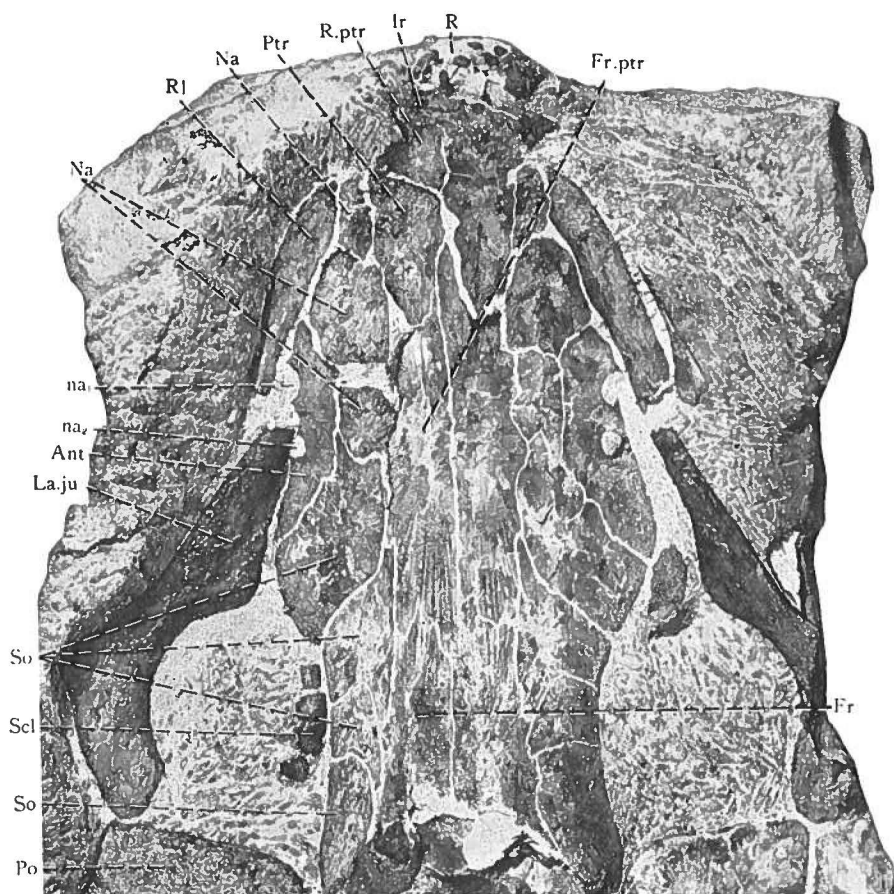


Fig. 8. Anterior part of the head of an undetermined Coelacanthid. $1\frac{1}{2} \times$.
Ant, antorbital; *Fr*, frontal; *Fr.pt*, fronto-postrostral; *Ir*, interrostral; *La.ju*, lacrimo-jugal; *Na*, nasal; *Po*, postorbital; *Ptr*, postrostral; *R*, rostral; *Rl*, lateral rostral; *R.pt*, rostro-postrostral; *Scl*, sclerotic plates; *So*, supraorbitals; *na₁*, *na₂*, anterior and posterior external nasal openings.

stral is incomplete, and only a thorough investigation reveals the line of fusion between the rostro-postrostral and the lateral rostral. On the other side of the head both these sutures are easily traced. It is of interest that the centres of radiation of the three partly fused bones on the right

side are still persistent and retain their original position, as seen from the conditions on the left side.

In the antero-lateral part of the right rostro-postrostral two irregular

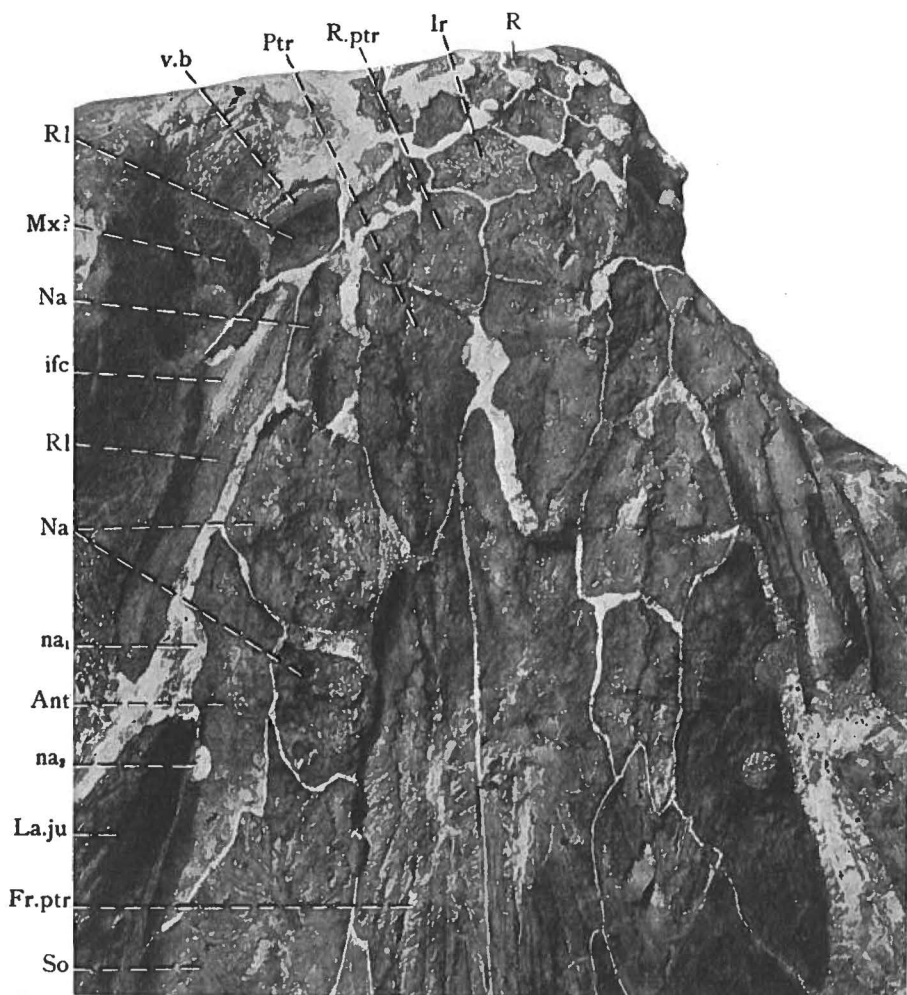


Fig. 9. Same specimen as shown in fig. 8 after further preparation. $2\frac{1}{2} \times$.
Ant, antorbital; *Fr.ptr*, fronto-postrostral; *Ir*, interrostral; *La.ju*, lacrimo-jugal;
Mx?, perhaps remains of maxillary; *Na*, nasal; *Ptr*, postrostral; *R*, rostral; *Rl*,
lateral rostral; *R.ptr*, rostro-postrostral; *So*, supraorbital; *ifc*, infraorbital canal;
na₁, *na₂*, anterior and posterior external nasal openings; *v.b*, ventrally directed small
branch from the ethmoidal commissure of the infraorbital canals.

sutures are seen, which run from the edge of the bone a short distance in a caudal direction. In the left rostro-postrostral no such blindly ending sutures are seen, but in front of that bone there is a short but broad independent plate, which, judging from its position and relations,

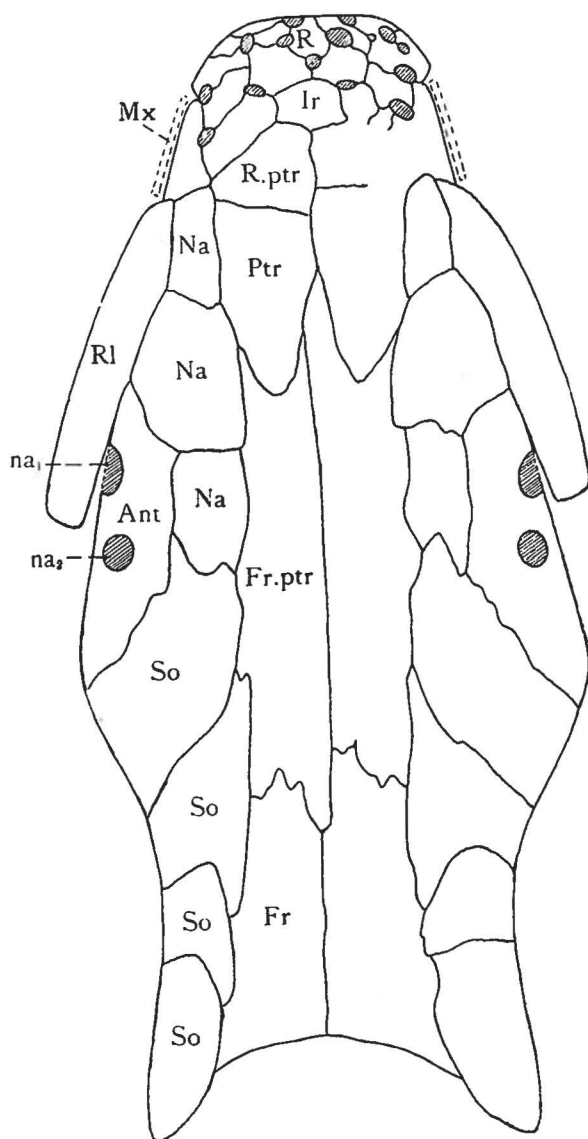


Fig. 10. $2\times$. Sketch of the fronto-ethmoidal shield of the specimen shown in fig. 8—9. The specimen is somewhat compressed in dorsi-ventral direction.

Mx. maxillary; other letters as in fig. 8—9.

corresponds to that part of the right rostro-postrostral showing traces of longitudinal sutures. Anteriorly to the rostro-postrostrals lies a little unpaired interrostral, and anteriorly to that and to the rostro-postrostrals a complex of small rostral elements, between which the large pores of the ethmoidal commissure of the infraorbital sensory canals are situated. On account of the considerable size of these pores

the outlines of the rostrals are rather irregular. The rostral bones are of a very considerable thickness, and as they lack ornamentation, they probably have been situated somewhat below the epidermis. The premaxillary is not fused to the rostrals. It is a bone of a very considerable thickness, which like the rostrals has been situated rather deeply below the epidermis. The premaxillary shows indications of a paired origin, although its two halves are very intimately united. The teeth of the premaxillary are long and pointed, and slightly curved in a caudal direction. The other Greenland Coelacanthids seem to possess a similarly subdivided rostral complex as the form described, a fact which explains why this foremost part of the head is very seldom found in such a good state of preservation that its detailed structure can be made out.

Laterally to the frontals and to the hindmost part of the fronto-postrostrals lies a series of supraorbitals containing four elements. The hindmost of these supraorbitals constitutes the postero-lateral corner of the fronto-ethmoidal shield and is homologous to that postero-lateral part of the fronto-ethmoidal shield in forms like *Axelia* and *Wimania* which STENSIÖ considered as a dermosphenotic fused with the frontal (STENSIÖ 1921, p. 65 etc.), and also homologous to the independent "dermosphenotic" in forms like *Laugia* (STENSIÖ 1932, p. 53) and *Whiteia* (MOY-THOMAS 1935, p. 217). As will be shown below, the infraorbital canal does not pierce this bone, which cannot therefore be a dermosphenotic comparable to that of the Rhipidistids but is no doubt a bone of the supra-orbital series. The supraorbital series is continued anteriorly by the series of nasals, which comprises three bones. Laterally to the hindmost part of the nasal series and in front of the foremost supraorbital we find an antorbital of rather considerable dimensions. In this antorbital there are two foramina in approximately the same position as the two nasal openings described by STENSIÖ in the antorbital region of the naso-antorbital bone in *Axelia* (STENSIÖ 1921, p. 97, fig. 44). Like STENSIÖ in 1921 I consider these foramina to be external nares. (Regarding certain difficulties in that explanation see below p. 33). Laterally to the foremost part of the nasal series and to the foremost part of the antorbital there is a long lateral rostral. The outer surface of the hindmost greater part of that bone must have occupied a rather horizontal position in the living fish, whereas the foremost part, which joins the lateral edge of the rostro-postrostral, is curved in such a way as to be almost parallel with and close to the dorso-rostral part of the lateral wall of the ethmoidal region of the endocranium. Immediately behind the premaxillary the lateral rostral extends so far in a ventral direction (see fig. 14) between the foremost lateral corner of the ectethmoid and the premaxillary as to be visible in the roof of the mouth immediately anterior to the latero-rostral corner of the ventral face of the ectethmoid (fig. 15).

Of the Spitsbergen genera *Axelia* is that regarding which our knowledge of the elements building up the fronto-ethmoidal shield is most complete. Compared with *Axelia* the Greenland Coelacanthid here under description has a strikingly long rostral part of the head. The lateral rostral evidently corresponds exactly to the larger lateral rostral in *Axelia*, whereas the numerous small rostrals forming the very snout are represented in *Axelia* by the other more medially situated rostrals, which are in *Axelia* only 4—6 in number. The naso-antorbital of *Axelia* can be homologised with the antorbital + the three nasals in our form. Moreover the number of post-rostrals is greater in the Greenland form than in *Axelia*, but very likely *Axelia* possesses a small unpaired interrostral similar to that of the Greenland form.

The agreements between the large Greenland form and the Greenland specimens of *Whiteia* are so close, at least regarding the dermal bones of the fronto-ethmoidal shield, that with the guidance of the knowledge which we now possess of these we may be justified in completing and correcting to some extent the reconstruction of the *Whiteia* from Madagascar given by MOY-THOMAS (MOY-THOMAS 1935, fig. 1).

MOY-THOMAS's reconstruction of the cranial roof is rather incomplete in the foremost part, but shows very considerable similarities to the Greenland forms regarding the subdivided frontals and postrostrals. The antorbital, which in the Greenland form lies between the supraorbital-nasal series and the series containing the infraorbital canal is lacking in MOY-THOMAS's reconstruction, but it must certainly have been present in the Madagascar species as well as in the Greenland forms. It is possibly pictured in MOY-THOMAS's figure of the head of *Coelacanthus madagascariensis* SMITH WOODWARD, in which a small triangular bone is seen in front of the orbit (MOY-THOMAS 1935, fig. 9). According to the description this bone (MOY-THOMAS op. cit. p. 224) seems to be a dermal bone. But in the figure, however, no nasal openings are to be found in that bone.

In MOY-THOMAS's reconstruction the supraorbital canal lies in the dermosphenotic-supraorbital-antorbital series (representing the supraorbital-nasal series of my conception), and the supraorbital canal joins the infraorbital canal in the dermosphenotic (my posterior supra-orbital). MOY-THOMAS has restored the course of the sensory canals from the position of the pores (MOY-THOMAS 1935, p. 219) as the state of preservation of the material did not allow of a direct tracing of the canals in the bone. Undoubtedly the sensory canals in the Madagascar Coelacanthids had a similar course as in the Greenland forms, as their pores are placed in identical bones; but in a Greenland *Whiteia* (figs. 11, 12) it could be shown that the supraorbital canal does not pass as in MOY-THOMAS's fig. 1. And since especially the position of the supraorbital

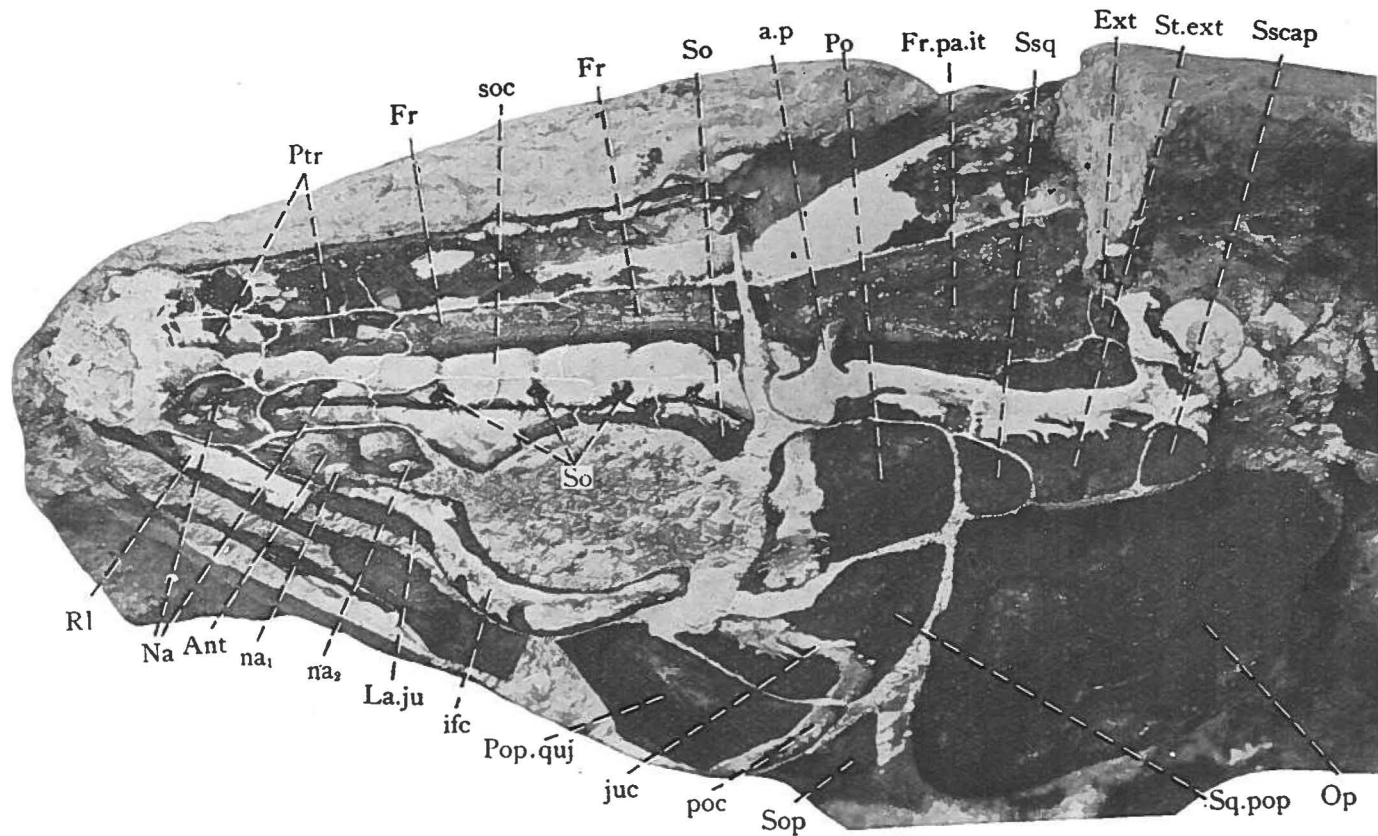


Fig. 11. *Whiteia* sp. Head in oblique dorsal view. 3 ×.

Ant, antorbital; *Ext*, extrascapular; *Fr*, frontal; *Fr.pa.it*, fronto-parieto-intertemporal; *La.ju*, lacrimo-jugal; *Na*, nasal; *Op*, opercular; *Po*, postorbital; *Pop.quj*, preoperculo-quadratojugal; *Ptr*, postrostral; *R.l*, lateral rostral; *So*, supraorbital; *Sop*, subopercular; *Sq.pop*, squamoso-preopercular; *Ssq*, suprasquamosal; *St.ext*, supratemporo-extrascapular; *a.p*, anterior pitline; *ifc*, infraorbital canal; *juc*, jugal canal; *na₁-na₂*, anterior and posterior external nasal openings; *poc*, preopercular canal; *soc*, supraorbital canal.

canal in Coelacanthids is of a great theoretical interest, it will be described in some detail here.

I have investigated the position of the canal in question in the beautiful specimen of *Whiteia* shown in figs. 11—12, and found that it has an identical position in the big Coelacanthid described above. It has also a quite similar position in all the other Triassic Greenland Coelacanthids which I have investigated, and in STENSIÖ's type-specimens from the Spitsbergen Triassic. Furthermore I have had an opportunity to see the type-specimen of *Dictyonosteus*, after a recent renewed preparation of that specimen by STENSIÖ, who most kindly has allowed me to mention some of his new results in this paper. STENSIÖ has moreover shown me the material and the manuscript to his description of some German Devonian Coelacanthids, and has given me important information regarding these forms.

As known, the sensory canals in the head of Coelacanthids are generally very well developed. In the Greenland specimens they are in many cases filled by white calcite, which makes the preparation of them very easy, although they are often situated very deeply below the outer surface of the dermal bones.

The position of the supraorbital canal is of extraordinary interest partly because this canal does not run through the centres of radiation in the frontals and nasals, and partly because it seems to lie in, or at least very near the suture between the frontal-postrostral series and the supraorbital-nasal series. The following description only deals with that part of the canal which is related to the nasal and frontal elements in the fronto-ethmoidal shield.

In a perfectly undamaged fronto-ethmoidal shield of a Greenland Triassic Coelacanthid one will observe that the tubuli of the supraorbital canal open towards the surface exclusively in the supraorbital and the nasal bones; by removing the bone concealing the canal it will be seen, however, that the canal is not completely enclosed in the bones pierced by the pores and the tubuli. That part of the supraorbital canal which has its pores in the supraorbital bones, lies in a groove in the lateral margin of the frontal, a groove which is bounded by a dorsal and a ventral lamella from the frontal. This groove is closed laterally by the supraorbital bones, which are equipped along their medial border with a little dorsal lamella, which joins the dorsal frontal lamella, and with a little ventral lamella, which joins the ventral frontal lamella. On account of the presence of this dorsal and this ventral lamella on the medial border of the supraorbitals the supraorbital canal lies to some extent in a furrow in the medial edge of the supraorbitals, but as the supraorbital lamella is much less developed than the frontal lamella the frontals constitute a much greater part of the bony walls of the

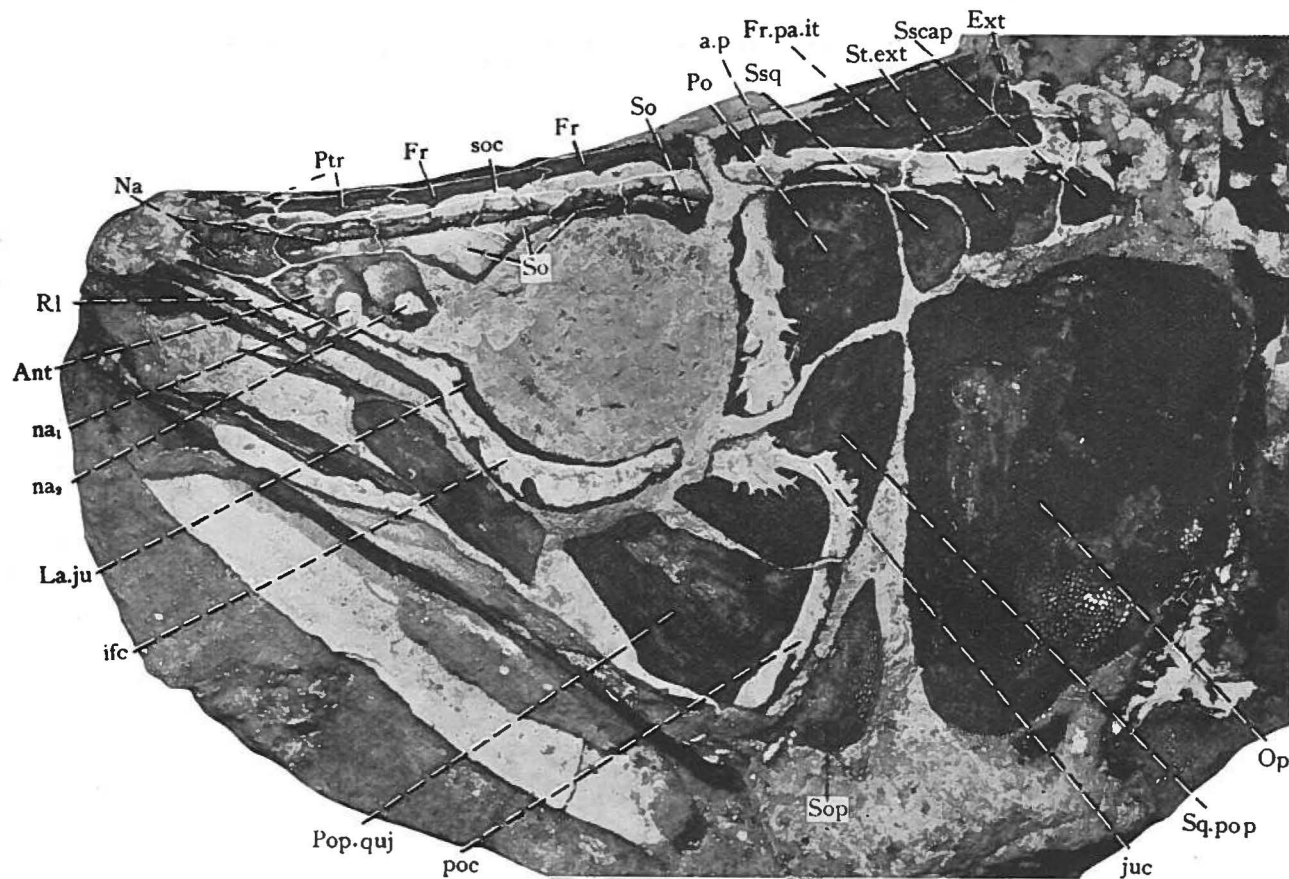


Fig. 12. *Whiteia* sp. Same specimen as shown in fig. 11, but in lateral view (lettering as fig. 11). ca. 3 ×.

canal than the supraorbitals. Only in the hindmost part of the most posterior supraorbital the supraorbital contributes just as much as the frontal to the formation of the canal walls. Farther forwards on the head the supraorbital canal continues between the postrostrals and the nasals lying in a similar way in a groove in the lateral edge of the postrostrals made by a dorsal and a ventral lateral postrostral lamella and closed laterally by the nasals, which bones are equipped with a dorsal and a ventral lamella on their medial edge. The dorsal nasal lamella is quite small, like the dorsal supraorbital lamella, but the ventral nasal lamella is better developed than the ventral supraorbital lamella and meets the ventral postrostral lamella in, or only a small distance laterally to, a vertical plane through the midline of the canal. While the dorsal postrostral lamella is of a similar size to the dorsal frontal lamella, the ventral postrostral lamella has a considerably shorter lateral extension than the ventral frontal lamella.

Although the canal is completely straight almost from the hindmost edge of the fronto-ethmoidal shield to the foremost nasal, the nasal bones form larger parts of its walls than the supraorbitals. In none of the bones of the fronto-ethmoidal shield does the supraorbital canal pierce the centre of radiation. There are reasons to believe that the thin nerves innervating its various sense organs pierced the ventral frontal lamella and the ventral nasal lamellae. SÄVE-SÖDERBERGH (1932, p. 111) does not ascribe great importance to the sutural course of the supraorbital canal in *Axelina*, but writes that an explanation of this condition might possibly be sought for in the excessive width of the canal. In this I cannot agree with SÄVE-SÖDERBERGH. An investigation of the Spitsbergen forms in general shows that the canal in question in these occupies an exactly corresponding position as in the Greenland form. It has also a similar position in *Laugia*, in STENSIÖ's reconstruction of which, however, it is too far laterally placed (STENSIÖ 1932, fig. 18). In the Devonian forms the supraorbital canal is not straight, but makes a curve in a similar way as in the *Rhipidistia* (STENSIÖ 1936). In spite of this, however, it occupies the same position in relation to the frontal and nasal bones as in *Whiteia*. Moreover STENSIÖ has demonstrated to me, that the canal in *Dictyonosteus* has a similar sutural course and does not, as previously assumed, pierce the centres of radiation of the nasals. More precisely it runs in that form in its foremost part in the sutures between the nasal and the postrostral bones, in its hindmost part in the suture between the frontals and the supraorbitals (among which the larger part if not the whole of the former dermosphenotic should probably be included).

That the supraorbital canal occupies a sutural position between a frontal-postrostral series and a supraorbital-nasal series thus seems to be a normal condition in all Coelacanthids and typical for that

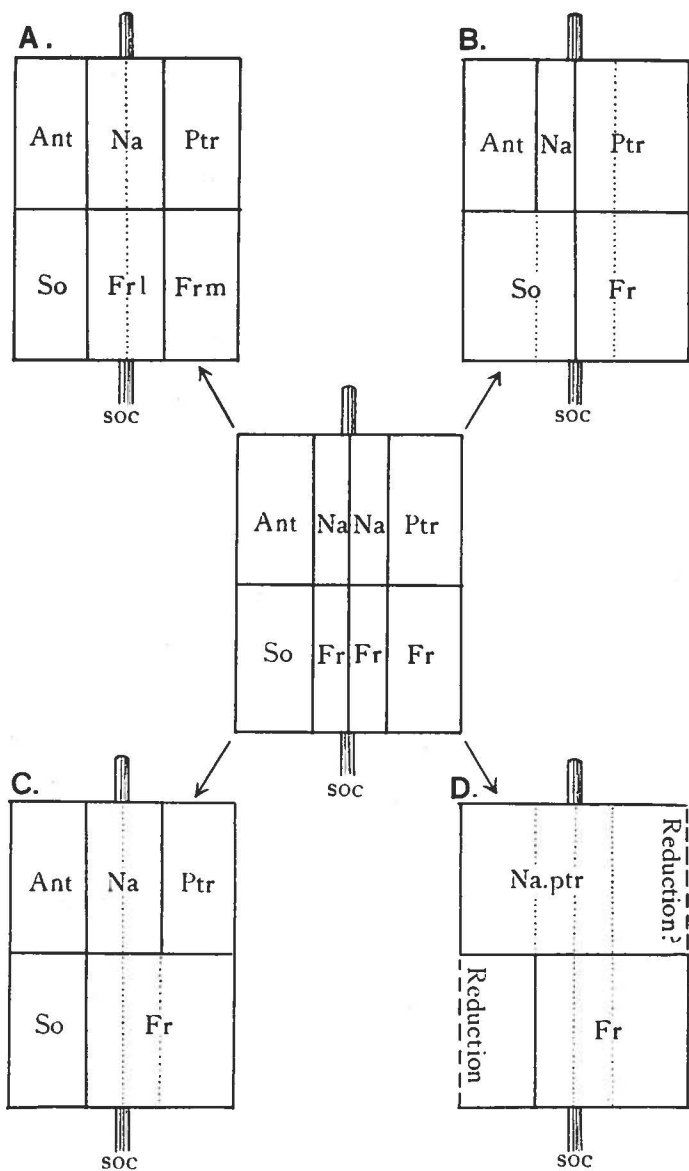


Fig. 13. Scheme of possible evolution of the arrangement of certain dermal bones and their relations to the supraorbital canal in Dipnoans (A), Coelacanth (B), *Rhipidistia* (C), and Amiids (D), from a common ancestor (in the middle). *Ant*, antorbital; *Fr*, frontal; *Fr.l*, lateral frontal; *Fr.m*, medial frontal; *Na*, nasal; *Na.ptr*, naso-postrostral; *Ptr*, postrostral; *So*, supraorbital; *soc*, supraorbital canal.

group.¹⁾ We never find that position of the canal in typical *Rhipidistia* or *Dipnoi*, the two primitive groups of *Choanata* most closely related to the Coelacanthids, but each of those two groups shows a particular position of the supraorbital canal in relation to the longitudinal rows of dermal bones in the fronto-ethmoidal shield.

Before dealing with the conditions in the *Rhipidistia* and the Dipnoans I wish to remark that regarding the frontals I only consider that foremost part of the bones which show relations to the supraorbital canal and not the hindmost part related to the anterior pit-line. Moreover I wish to point out, that the conditions are treated in a very schematic way only. I do not consider a possible subdivision of the longitudinal rows of postrostrals, a possible fusing of postrostral bones from the left and the right sides, or the presence of possible median frontals and postrostrals. Thus I shall consider only those bones which in some way or other are of interest for explaining the different positions of the supraorbital canal in the different groups.

The conditions in the *Rhipidistia* may be briefly summarized as follows: the supraorbital canal runs through the frontal, piercing its center of radiation, and continues forward through the nasal bones piercing their centres of radiations. Laterally to the frontal there is a series of supraorbitals; laterally to the nasals we find an antorbital series and medially to the nasals the postrostral series.

In the Dipnoans the supraorbital canal lies in a frontal-nasal series piercing its centres of radiation, laterally to this lies a supraorbital-antorbital series and medially to the frontal-nasal series a frontal-postrostral series.

Combining the conditions within the three above-mentioned primitive groups of *Choanata* with the results of PERSSON's embryological investigations on *Amia*, in which form he found that the canal components of the bones connected with the supraorbital canal have a paired origin, and assuming, that the same was the case within the primitive *Choanata*, we are able to construct a scheme of a hypothetical form from which it is possible to derive the different position of the supraorbital canal in the groups mentioned above (fig. 13). The conditions in this hypothetical ancestor would be as follows. The supraorbital canal runs in the suture between two longitudinal rows of sensory canal bones, the lateral and the medial frontal-nasal canal row respectively (fig. 13). One series of membrane bones is found on the lateral and one on the medial side of the two canal rows just described, a supraorbital-antorbital series and a frontal-postrostral series, respectively.

Within the Coelacanthids the lateral and the medial row of frontal-nasal canal bones do not fuse into a single series containing the canal,

¹⁾ And for *Dictyonosteus*, the systematic position of which is not quite settled.

but in the frontal part the lateral row fuses with the supraorbital series and the medial row with the frontal series. The canal retains its original position between two rows of bones. In the nasal region a similar fusion takes place between the medial canal row and the medial membrane (postrostral) series, while the lateral canal row gives origin to a row of independent bones not fusing with the more lateral series of membrane bones at least in some forms. Here too the canal retains its original position between two longitudinal rows of bones. In this way it is easy to explain why the canal does not pierce any centre of radiation in the bones to which it has relations (fig. 13 B.).

In the Dipnoans the medial and the lateral row of canal bones fuse with each other enclosing the canal, which therefore here necessarily runs through the centres of radiation of the compound bones formed. These canal bones do not fuse with the adjoining series of membrane bones, on account of which an independent canal bone series, running between two series of membrane bones, (fig. 13A) is met with here.

In the nasal part of the fronto-ethmoidal shield in *Rhipidistia* we find a similar general pattern as in the Dipnoans. On the other hand, in the frontal part the fused lateral and medial rows of canal bones also fuse with the more medial (frontal) series of membrane bones, while the more lateral series of membrane bones retain their original independence (fig. 13C.).

Within the *Actinopterygii* the supraorbital series of membrane bones seems to be independent, while the frontal canal bones fuse with the frontal membrane bones. In the nasal part, at least in some forms, all the four longitudinal series fuse, while in others the medial membrane bone series seems to be independent, moreover some of the different membrane bone series in different lines of development seem to be reduced more or less, but I do not wish to treat these conditions in this paper. (In fig. 13D. I therefore use the usual nomenclature for the elements of the figured region of the head).

The view given above is in a very schematic form. Quite recently ALLIS worked out (ALLIS 1935) a general pattern of the dermal bones of the cranial roof of fishes. (Mostly on the basis of the arrangement of the dermal bones in the specialised Actinopterygian *Polyodon*). According to his opinion these bones of fishes were originally arranged in seven longitudinal rows, a median, unpaired, and on either side of this three lateral, the midmost of which are canal bones. Regarding the foremost part of the head the scheme sketched by him agrees well with that given above, only I have not considered the median row. However, his canal

bone row should be compared to the two rows of canal bones in my hypothetical scheme in fig. 13. In the hindmost part of the cranial roof, which I do not intend to consider at present, we must necessarily assume two series of canal bones. The medial one of these is connected with the continuation of the supraorbital canal through the anterior and posterior pit-line to the dorsal lateral line of the body, and is probably of paired nature as in the foremost part of the head. The lateral one is connected with the infraorbital canal and the main lateral line of the body and is conceivably not of a paired origin.

Between these two series of canal bones there is a backward continuation of the supraorbital-antorbital series of membrane bones, and laterally to the lateral series of canal bones there are very likely one or more longitudinal rows of membrane bones.

After these general remarks we shall now return to our Greenland Coelacanthids.

As will be seen from fig. 11, the part of the supraorbital canal connected with the frontals and nasals contains seven canal organs, one exactly opposite each of the supraorbitals and one exactly opposite each of the nasals.

As already mentioned above in the description of the supraorbital bones of a Greenland Coelacanthid the postero-lateral corner of the fronto-ethmoidal shield is not pierced by any part of the infraorbital canal, and cannot, therefore, be homologised with the dermosphenotic as done by several authors. As shown in fig. 12 the supraorbital canal meets the infraorbital canal not within but behind the fronto-ethmoidal shield in the most anterior part of the parietal shield close behind the orbital border of the postorbital bone. On account of this we must look for the dermosphenotic in the antero-lateral corner of the parietal shield and not in the fronto-ethmoidal shield. A comparison with other Coelacanthids than the Greenland forms shows that the postorbital in all cases which I have had an opportunity of investigating, has a similar position in relation to the parietal shield as in the Greenland *Whiteia*, so that the dorsal edge of the postorbital in its whole length joins the parietal shield. And as the sensory canal in the postorbital in all cases leaves that bone at its dorsal edge, the dermosphenotic of the Coelacanthids seems normally to lie in the parietal shield and not in the fronto-ethmoidal shield. An investigation of the antero-lateral part of the parietal shield reveals that both the supraorbital and the infra-orbital sensory canals are situated beneath the bone in a slightly pronounced groove on its lower side and not, as in the greater part of the parietal shield, completely enclosed in the bone. STENSIÖ has called my attention to this peculiar position of the canals, which he discovered

himself in the Devonian Coelacanth *Diplocercides*. The communication between the infraorbital and the supraorbital canals takes place in these imperfectly enclosed parts of the canal system and Prof. STENSIÖ suggests that the peculiar conditions indicate that in *Diplocercides* the dermosphenotic has undergone a complete reduction and the foremost part of the parietal shield now occupies the previous place of the dermosphenotic, but of course without gaining any genetic relations to the sensory canals, which once belonged to the dermosphenotic.

Relatively much shorter parts of the sensory canals are lying freely on the lower side of the parietal shield in the Greenland specimens investigated by me than in *Diplocercides*. In fact only the very part of the system where the supraorbital canal meets the infraorbital canal and the latter curves towards the postorbital has that free position; a condition which may indicate that in the Greenland forms perhaps only a part of the dermosphenotic has been reduced, and the remaining part of the dermosphenotic has fused with the antero-lateral part of the parietal shield.

In STENSIÖ's reconstruction of the head of *Laugia* a single strikingly wide long "tubulus" extends medially into the parietal shield from the longitudinal running sensory canal in that shield (STENSIÖ 1932, fig. 52).

Judging from the connection between the supraorbital canal and the infraorbital canal this "tubulus" might very well be regarded as belonging to the hindmost part of the supraorbital canal. An investigation of the new material shows that this "tubulus" in fact must be regarded as a small, medio-caudally directed branch from the hindmost part of the supraorbital canal, and according to its position probably represents the anterior pit-line for instance in *Rhipidistia*. In *Diplocercides* the anterior pit-line has a similar position on the parietal shield (STENSIÖ 1936), though it is not developed as a canal. In some of the Greenland specimens these canal homologues of the anterior pit-line have such a considerable length that they nearly meet in the mid-line of the parietal shield.

The whole or the greater part of the anterior pit-line of the cranial roof in *Rhipidistia* lies on the hindmost half of the frontals. This hindmost part of the frontals in *Rhipidistia* is not pierced by the supraorbital canal but very likely comprises components developed in relation to this anterior pit-line, and represents the posterior pair of frontals in the hypothetic ancestor of Crossopterygians and Ichthyostegids (SÄVE-SÖDERBERGH 1932, fig. 18). In *Rhipidistia* the theoretical line of separation between the postulated anterior and posterior pair of frontals would therefore be on the fronto-ethmoidal shield, and probably very near a connecting line between the anterior ends of the right and left dermo-

sphenotic; a continuation of this line downwards onto the cheeks follows the orbital border of the postorbital.

If we look for the same line of separation between the postulated anterior and posterior frontals of SÄVE-SÖDERBERGH's in the Coelacanthids it is easy to understand, from the statements made above, that it is most probably represented by the line of separation between the fronto-ethmoidal shield and the parietal shield. Thus the posterior pair of frontals of SÄVE-SÖDERBERGH's is included in the parietal shield of the Coelacanthids.

The course of the supraorbital canal, the position of the anterior pit-line, the position of the dermosphenotic and the postorbital, are in accordance with that theory. The bones of Coelacanthids previously termed parieto-intertemporals should therefore correctly be termed fronto-parieto-intertemporals (or, at least in some Coelacanthids, perhaps even (see above) fronto-parieto-intertemporo-dermosphenotics). Accordingly we have in Coelacanthids traces of no less than three pairs of frontals, one pair of which is included in the parietal shield, the two others in the fronto-ethmoidal shield.

Not only the anterior but also the posterior pit-line of the cranial roof is present in some of the Greenlandic Celacanthids developed as a canal running in a rostral direction from the supratemporal commissure through the posterior part of each fronto-parieto-intertemporal rather near the mid-line of the parietal shield. The pit-line so developed is a vestige of the connection between the dorsal lateral line of the body and the supraorbital canal in the ancestors of Coelacanthids. No traces have been found of the middle pit-line of the cranial roof of the Greenland forms, but in *Diplocercides* this pit-line too has been discovered on the parietal shield (STENSIÖ 1936).

A suprasquamosal (MOY-THOMAS 1935) is present at least in the larger of the Greenland species (fig. 11, 12). It seems not to be homologous with the extratemporal (SÄVE-SÖDERBERGH 1934) of the Rhipidistids. According to my opinion it represents a spiracular bone and will probably be found in the majority of the Coelacanthids.

MOY-THOMAS describes (MOY-THOMAS 1935) an independent preopercular bone in *Whiteia* and points out the presence of a corresponding bone in *Coelacanthus elegans* Newb. and *Coelacanthus madagascariensis* SMITH WOODWARD. Concerning the relationships of that bone to the sensory canal system he writes as follows (MOY-THOMAS 1935, p. 218): "The sensory canal is continued backward from the lacrymojugal into the squamosal in which it passes postero-ventrally presumably into the preopercular, but no trace of it has been identified in this bone".

To settle the question of the course of the preopercular canal in

relation to the "preopercular" of MOY-THOMAS, which is also present in the Greenland *Whiteia* (see fig. 12) and in other Greenland forms, I dissected out the jugal and the preopercular canals in the Greenland specimen of *Whiteia* shown in fig. 12. Judging from the course of the sensory canals across the cheek the bone called squamosal by MOY-THOMAS also includes a preopercular component, since the jugal and the preopercular canals seem to meet in this bone. Further the preopercular canal does not run, as assumed by MOY-THOMAS, through the bone he terms preopercular, but through the hindmost part of what he calls quadratojugal. Consequently the bone called by MOY-THOMAS quadratojugal must be considered a preoperculo-quadratojugal. The bone called preopercular by MOY-THOMAS, judging from its position, seems to be a subopercular or at least a bone belonging to the opercular series. As mentioned above (p. 14) a separate preopercular, however, is present in *Laugia*. WATSON mentions (1922, p. 331) a little bone in *Macropoma* lying immediately anterior to the lowermost part of the opercular; this bone seems to be homologous to the bone interpreted here as subopercular.

The nasal openings in Coelacanthids. As early as 1921 STENSIÖ ascertained the position of the nasal openings in the naso-antorbital of a Spitsbergen Coelacanthid, *Axelia* (STENSIÖ 1921, p. 93—94, fig. 43—44), but in 1932 he omitted these openings in an altered reconstruction of this fish (STENSIÖ 1932, fig. 15B). STENSIÖ's altered view is due to his mostly unpublished investigations of the endocranium of *Diplocercides*, from which it seemed probable (STENSIÖ 1932, p. 25) that the nasal cavity of the Coelacanthids was not situated as previously assumed by himself (STENSIÖ 1921, pp. 93—94, 1932a, p. 185), but more anteriorly.

In the new Greenland Coelacanthid material (see for instance figs. 9—10) a considerable part of the foremost region of the head is often preserved, and in all the specimens in which the above (p. 19) described antorbital bone could be seen and studied, it shows two openings in almost exactly the same position as the two openings found in the naso-antorbital of *Axelia*. Nothing indicates that the two openings can be explained as two especially well developed pores from the sensory canal system, and it seems to me quite evident that STENSIÖ's opinion in 1921 about the position of the outer nasal openings of the Triassic Coelacanthids was correct. As pointed out above, the foremost part of the head of the Greenland forms is much prolonged compared with the corresponding part of the head in *Axelia*, and therefore the difficulty which made STENSIÖ alter his opinion regarding the openings in question, meet us in much greater degree in our material. In order to determine the position of the nasal cavity I have prepared the foremost part of the head

of the above described large Coelacanthid specimen from the side and from below and succeeded in discovering the place of the internal nostril of that form (figs. 14—15). Below I shall give a short description of the foremost part of the endocranium and the skeletal roof of the mouth in order to facilitate an orientation on the figures. As usual in Mesozoic Coelacanthids the ethmoidal region of the endocranium contains a paired ossification, the ectethmoid, the hindmost part of which is underlain by the antero-lateral border of the parasphenoid. This ectethmoid extends through a considerable part of the vertical lateral and the horizontal ventral wall of the endocranium, but is separated from that of the other side by a longitudinal unossified part of the ventral wall of the region. Dorsally the foremost and larger part of the ectethmoid is rather firmly connected with the foremost vertically placed part of

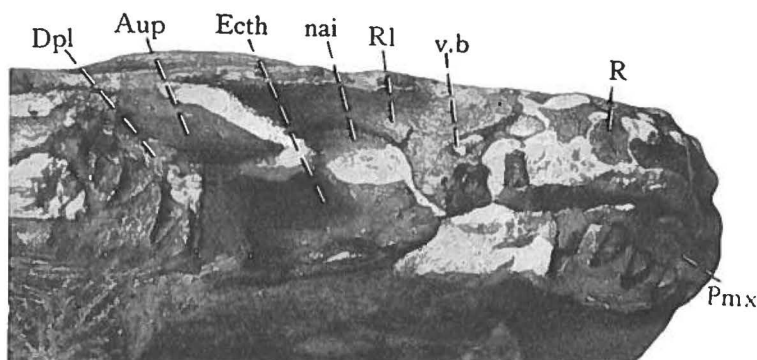


Fig. 14. Side view of the foremost part of the head shown in fig. 8—9. $3\times$. *Aup*, autopalatinum; *Dpl*, dermopalatinum; *Ecth*, ectethmoid; *Pmx*, premaxillary; *R*, rostral; *Rl*, lateral rostral; *nai*, opening from the nasal cavity to the internal nostril; *v.b*, ventrally directed small branch from the ethmoidal commissure of the infraorbital canals.

the lateral rostral. The suture between these two bones is seen on the side of the ethmoidal region running in a direction from above downwards and forwards, in such a way that the antero-ventral corner of the lateral rostral is seen from the palatal side lying immediately anterior to the antero-lateral corner of the ventral face of the ectethmoid (fig. 15), between that bone and the premaxillary. The opening leading from the nasal cavity to the internal nostril in the roof of the mouth is situated in the suture between the lateral rostral and the ectethmoid (*nai*, fig. 14). As shown in the diagram, a vomerine bone similar to that described by WATSON in *Macropoma* (WATSON 1921) lies on the ventral surface of the ectethmoid. Laterally or latero-caudally to that bone the internal nostril must lie in the form in question. Moreover in several of the Greenland specimens remains of a little tooth-bearing dermal bone is found

immediately lateral to the foremost vertical surface of the lateral rostral. As it lies in continuation of the row of teeth of the premaxillary, and its teeth together with the premaxillary teeth are opposed to the teeth in the dental region of the lower jaw, this bone is presumably the strongly reduced maxillary. Of course the internal nostril has been situated medially to that bone. The maxillary bone described in Spitsbergen Coelacanths by STENSIÖ (1921) has been shown by WATSON (1922) to be an ectopterygoid. From what has now been set forth it is easy to understand the difficulties in explaining the foramina in the antorbital as external nasal openings. I think, however, that an explanation must be sought for

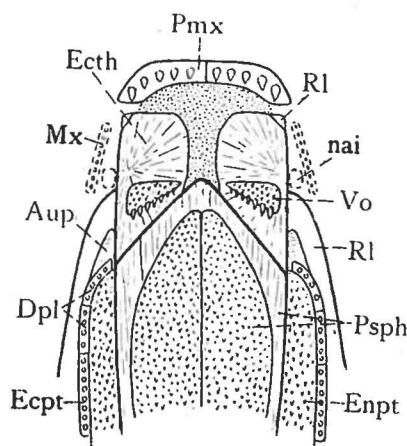


Fig. 15. Schematic figure of the lower side of the foremost part of the head in a Greenland Coelacanthid.

Aup, autopalatinum; *Dpl*, dermopalatinum; *Ecpt*, ectopterygoid; *Ecth*, ectethmoid; *Enpt*, entopterygoid; *Mx*, maxillary; *Pmx*, premaxillary; *Psph*, parasphenoid; *Rl*, lateral rostrals; *Vo*, vomer; *nai*, internal nasal opening.

in a secondary lengthening of the foremost part of the head, a lengthening which, as shown above, is very pronounced in the Greenland specimens. This lengthening is met with also in the Spitsbergen forms, though in them it is much less pronounced.

During the preparation of the ventral side of the large Greenland Coelacanthid skull several arches of the visceral skeleton, together with the so-called urohyal and a big unpaired ossification in the basibranchial series were exposed. The last-mentioned ossification has a convex dorsal face, curved somewhat more from side to side than in a rostro-caudal direction. The accompanying fig. 16 shows its ventral face. The bone seems to be pierced by a wide longitudinal canal, which might have lodged nerves and vessels. No other ossifications are present in the basibranchial series, but both the ossified part and the cartilaginous parts

of the series have been covered by a paired row of tooth-bearing dermal bones, the teeth of which were opposed to the teeth of the parasphenoid. The first pair is found immediately anterior to the basi-branchial ossification, the two next pairs cover the dorsal side of the very ossification and at least two pairs are lying behind it. Professor



Fig. 16. The ventral face of the ossification in the basibranchial series of the large Coelacanth shown in fig. 8—9. 3 ×.

Uhy, urohyal (rostral end).

STENSIÖ has informed me that a similar big ossification as in our form is present in the basibranchial series of *Eusthenopteron*, and that ossification is also covered by a paired series of tooth-bearing bones.

As shown in the diagram the tooth-bearing part of the parasphenoid shows indications of a subdivision into a right and a left half.

Actinopterygii.

Palaeoniscidae.

During the last few years it has gradually become evident that the family *Palaeoniscidae* includes forms differing from each other in characters of much more than generic value. (See for instance STENSIÖ 1932, p. 97—98 etc.). On account of our still very sparse knowledge of the internal anatomy of the different genera included in the group it is at present

impossible to undertake a rational subdivision of the *Palaeoniscidae*, and we shall therefore in the present paper use that term in its old wide sense, as also done by STENSIÖ in 1932.

Palaeoniscids referable to several genera constitute a considerable, and a most important part of the new material. The family *Palaeoniscidae* I intend to describe in the first volume of the monograph of the Eotriassic fish fauna from East Greenland.

Boreosomus STENSIÖ.

(Synonym: *Diaphorognathus* BROUGH 1932).

Material: A great number of specimens is present, many of which are in an excellent state of preservation. In several of the best preserved specimens the endocranium is quite undamaged, so that it can be investigated in every detail by SOLLAS' grinding method.

Remarks: The genus *Boreosomus* was erected by STENSIÖ in 1921 (STENSIÖ 1921, p. 210) on rather incomplete material from Spitsbergen. From the Eotriassic of East Greenland *Boreosomus* was recorded by STENSIÖ, though with some hesitation, in 1932 (*Boreosomus?* sp. STENSIÖ 1932, p. 117).

The large fresh material confirms STENSIÖ's determination of his very fragmentary specimens and further shows that the Palaeoniscid genus *Diaphorognathus* from Madagascar erected by BROUGH (BROUGH 1932) is undoubtedly identical with *Boreosomus* STENSIÖ, on account of which the younger name *Diaphorognathus* must be dropped. Fresh material of *Boreosomus* from Spitsbergen (collected 1929 by THORSLUND's expedition) has been very helpful in the identification. In this connection it should be mentioned that in his paper on *Diaphorognathus* BROUGH states that during a visit to Stockholm he has seen Palaeoniscid remains from Greenland, which greatly recalled *Diaphorognathus* from Madagascar. According to verbal information from STENSIÖ these remains are the very same which in 1932 were referred by him with some hesitation to *Boreosomus*.

As regards the relations of *Boreosomus* (*Diaphorognathus*) to the other Palaeoniscid genera BROUGH arrived at the result that it is more closely related to *Palaeoniscus* than to any other form known. I cannot agree with BROUGH in this; *Boreosomus* undoubtedly belongs to quite another group of Palaeoniscids than *Palaeoniscus*, and is rather related to such forms as for instance *Acrorhabdus* and *Acrolepis*.

As a difference between *Boreosomus* and *Diaphorognathus* PIVETEAU in his great work on the Madagascar Triassic fish-fauna states (PIVETEAU 1935, p. 30) that according to STENSIÖ *Boreosomus* has only one pit-line on each parietal, while *Diaphorognathus* has three, an anterior, a middle and a posterior. PIVETEAU here bases his account on STENSIÖ's descrip-

tion of *Boreosomus Reuterskiöldi* (STENSIÖ 1921, p. 218), but there is no doubt that the reason why in this specimen of *Boreosomus* from Spitsbergen only one pit-line has been found on the parietal is the less good state of preservation of the fossil.

The specimens from East Greenland possibly belong to two different species.

Glaucolepis STENSIÖ.

(Synonym: *Pteronisculus* WHITE 1933).

Material: A still greater number of specimens than of the preceding genus is now at hand from East Greenland. The state of preservation is marvellous, indeed I think that the material of this form is better preserved and more complete than is the case with any other Palaeoniscid material known as yet. A considerable number of endocrania is present, in many case still in situ in the head region of the fish, more seldom lying isolated in smaller concretions.

They are ideal objects for the grinding method.

Remarks: The genus *Glaucolepis* was erected by STENSIÖ in 1921 on the basis of a fish specimen from Spitsbergen lacking the head (STENSIÖ 1921, p. 200). The presence of this genus in Greenland was ascertained by STENSIÖ in 1932 (STENSIÖ 1932, p. 119) but on very poorly preserved material, so that our knowledge of the head of *Glaucolepis* was still very slight, as it was only possible to make out a few and insignificant characters on the head of the Greenland specimen. Now *Glaucolepis* has turned out to be a very commonly occurring Palaeoniscid in most of the fish zones in East Greenland.

A preliminary examination of the material seems to show that *Glaucolepis* STENSIÖ is identical with the Palaeoniscid genus *Pteronisculus* erected by WHITE on material from Madagascar (WHITE 1933, p. 118). PIVETEAU has kindly placed material both of this genus and of *Boreosomus* from Madagascar at my disposal for comparison.

The new material of *Glaucolepis* seems to belong to three or perhaps even more species.

Anatomical remarks.

Comparison between the cheek of Crossopterygians and that of Palaeoniscids. The homologisation of the dermal bones of the head of the *Actinopterygii* with those of the lower *Choanata* rests on an uncertain basis. Without sufficient reason the same nomenclature is used for the dermal bones within both these groups, which are well separated already at their first appearance in the Palaeozoic. One may ask if it would not be most logical to introduce a special nomenclature for the dermal bones in the Actinopterygians, as it has been necessary to do for the third of the large Gnathostome branches, the *Elasmobranchii*. The reason why such a step is not taken here is that during my preliminary investi-

gations of primitive Actinopterygians I have been led to the opinion, that the gap between the Actinopterygians and the *Choanata* is probably not broader, than it might be bridged by closer investigations and that we will probably be able to make out rather exactly which bones or parts of bones in one group are strictly comparable to the bones in the other. Some facts, which throw new light on the relationships between the *Actinopterygii* and the *Choanata* shall be mentioned in the

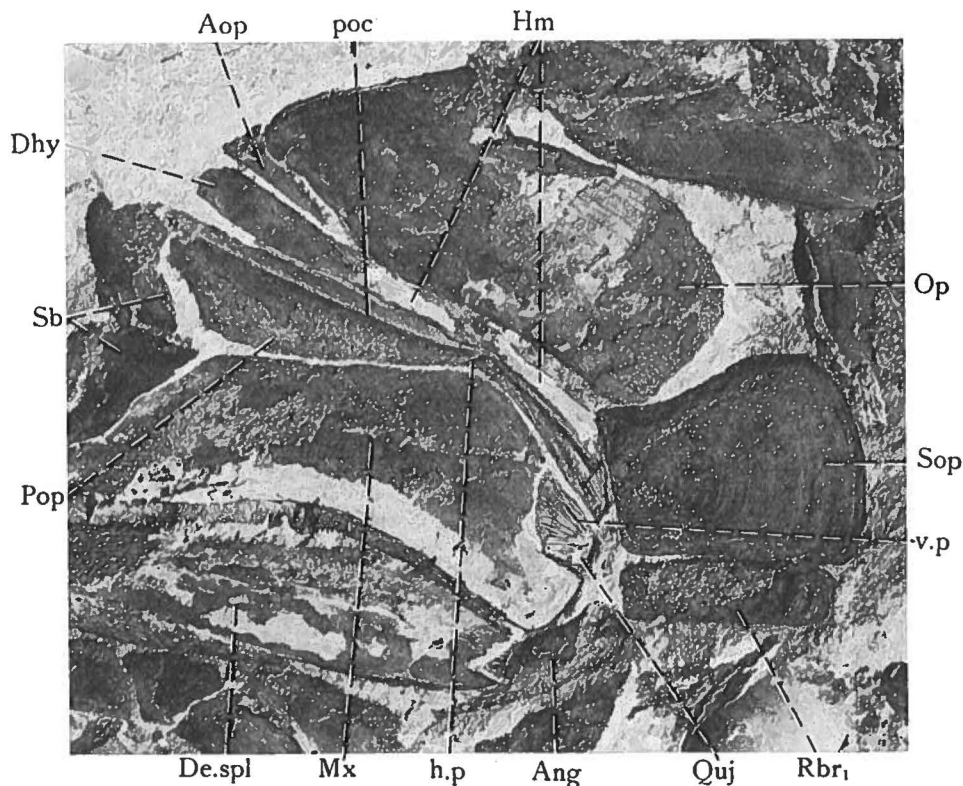


Fig. 17. *Glaucolepis* sp. The bones of the cheek seen from the medial side. $3\times$. *Ang*, angular; *Aop*, antopercular; *De.spl*, dento-splénial; *Dhy*, dermohyal; *Hm*, hyomandibular; *Mx*, maxillary; *Op*, opercular; *Pop*, preopercular; *Quj*, quadrato-jugal; *Rbr*, the most dorsal branchiostegal ray; *Sb*, suborbitals; *Sop*, subopercular; *h.p*, horizontal pit-line of the cheek; *poc*, preopercular canal; *v.p*, vertical pit-line of the cheek.

following, but first I wish to point out, that even if the same terms for bones within the two groups are employed here, this does not necessarily mean that such bones really are strictly homologous, but that, if not the whole, at least a part of the element in question in one group is homologous to either the whole or a part of the similarly named bone in the other group.

My studies on *Glaucolepis* have shown that an independent quadratojugal is present in that genus. This bone has not previously been described in any *Palaeoniscid*, although WATSON in 1925 suggested its possible presence in a single specimen of *Cheirolepis*. (WATSON 1925, p. 821). Its discovery in *Glaucolepis* shows that the quadratojugal has not fused with the postorbital expanded part of the maxillary but lies as an independent bone immediately anterior to the anterior edge of the lower part of the preopercular, and is covered by the maxillary in such a way that only a very small part of it is visible from the outside of the cheek in undamaged specimens (fig. 17 and 19). Only this small part discernible from the outside is ornamented with ganoine and lies in or in some cases even extends a little behind a very distinct notch in the posterior border of the maxillary.

The centre of radiation of the quadratojugal lies in the small exposed part, i. e. near the postero-ventral corner of the bone. The form of the bone is triangular, as seen in fig. 19. The postero-dorsal straight margin joins the preopercular; the anterior and the ventral margin are entirely overlapped by the maxillary.

The quadratojugal in *Saurichthys* (STENSIÖ 1925) must have occupied a very similar position medially to and covered by the maxillary, as it is only visible in specimens showing the impression of the inside of the maxillary.

The hindmost freely exposed part of the quadratojugal in *Glaucolepis* attains the same thickness as the other dermal bones of the cheek, but the overlapped part of the bone decreases in thickness towards its anterior margin, so that its most anterior part consists only of a very thin lamella. I am inclined to suppose that this condition indicates a beginning reduction of the bone, a reduction caused by backward growth of the maxillary.

In the specimen of *Glaucolepis* shown in fig. 17 and in some few other specimens I have found a pit-line lying in an antero-dorsal postero-ventral direction on the uncovered part of the bone. No doubt this pit-line, which is connected with the centre of the bone, is homologous with the vertical pit-line of the cheek in other forms.

In some specimens of *Palaeoniscus freieslebeni*, which I have had at my disposal, a similar independent quadratojugal as in *Glaucolepis* is present; and I find it most probable that a quadratojugal will be found in a considerable number of previously described Palaeoniscids. It is still present in some recent Ganoids (*Polypterus*, *Acipenser*)¹).

Several of the Greenland specimens of *Glaucolepis* show a very interesting feature, viz. traces of a pit-line on the maxillary. (According

¹) Regarding the conditions in Teleosts see HOLMGREN & STENSIÖ 1936 p. 497.

to verbal information from Dr. T. S. WESTOLL a pit-line the exact position of which is unknown to me, is also found on the maxillary in an English Permian Palaeoniscid. This pit-line in *Glaucolepis* extends from near the centre of radiation of the maxillary a short distance in a dorso-caudal direction (se fig. 11). In all probability it represents a part of the horizontal pit-line of the cheek, since in a few specimens (one of which is possibly generically different from *Glaucolepis*) it extends with a single interruption across the postorbital expanded part of the maxillary to the radiation centre of the preopercular. In a rather great number of specimens the part of the horizontal pit-line situated on the preopercular is visible (fig. 17 and 18).

As early as 1921 STENSÖ set forth the supposition that squamosal elements homologous to those in the Crossopterygians formed part of the maxillary and preopercular and possibly also of the postorbital of the *Palaeoniscidae* (STENSÖ 1921, pp. 139, and 293).

On account of the presence of an independent quadratojugal in *Saurichthys*, STENSÖ was inclined to assume that the quadratojugal was included in the maxillary of Palaeoniscids (STENSÖ 1925, pp. 103, 105, 211). As mentioned above after the latest investigations there is no reason to believe that quadratojugal components are included in the maxillary of Palaeoniscids; but on the other hand the presence of the horizontal pit-line on the cheek shows that squamosal elements are probably present in the maxillary (and perhaps in the preopercular?).

There are reasons to believe that the different pit-lines occurring on the head of fishes have similar constant relations to the dermal bones as have the sensory canals proper. In primitive Actinopterygians, such as the *Palaeoniscidae*, the pit-lines show so distinct relations to a number of the dermal bones, that it might be assumed that their sensory organs influenced the development of these dermal bones. These bones therefore probably contain sensory canal components. It seems to be a rule within the *Palaeoniscidae* that the pit-lines cross their bones through the centre of radiation, or at least (if very short), have such directions that they point straight towards the centre. In this latter case we must assume that the pit-lines once continued in the skin over the centre without leaving impressions on the surface of the bone.

The normal sensory canals in *Palaeoniscidae* always pierce the centres of ossifications of the bones to which they are related.

The foremost end of the horizontal pit-line of the cheek in *Glaucolepis*, obviously, reaches or very nearly reaches (and in this latter case has a direction towards) the centre of radiation of the maxillary. As is well known the maxillary in *Crossopterygii* has no connection with the sensory canal system. If now the ancestor of the *Palaeoniscidae* possessed an independent squamosal of a type like that in

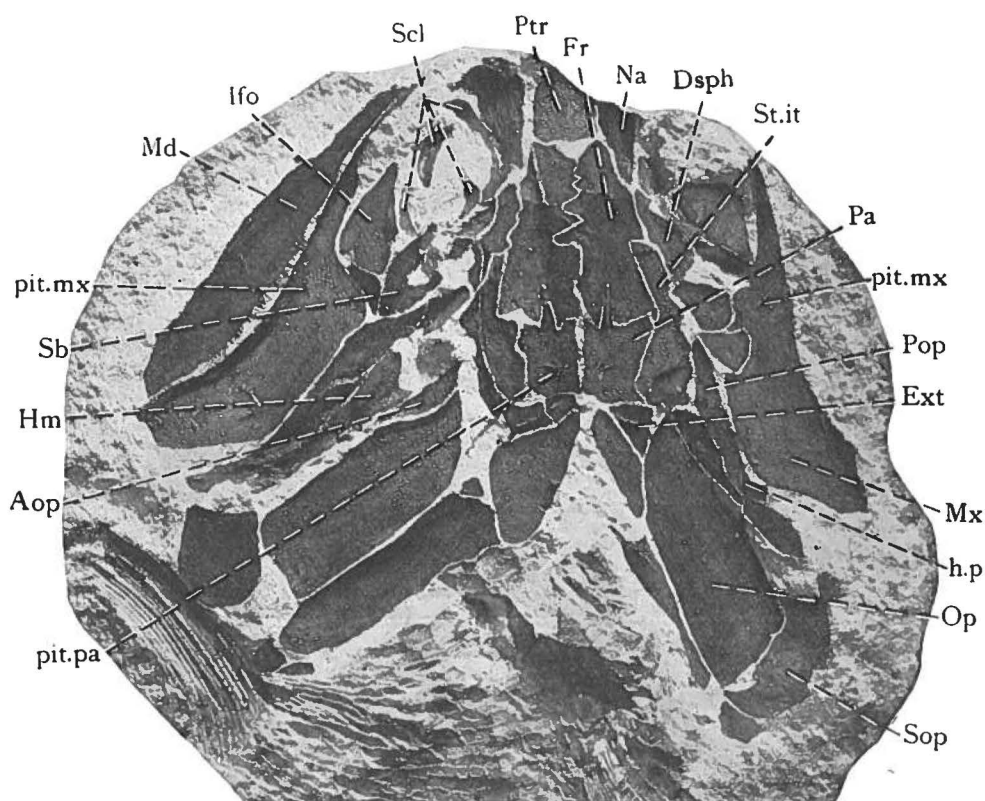


Fig. 18. Impression of the dermal bones of the head of *Glaucolepis*. 2 ×.

Aop, antopercular; *Dsph*, dermosphenotic; *Ext*, extrascapular; *Fr*, frontal; *Ifo*, infraorbital; *Ma*, mandibula; *Mx*, maxillary; *Na*, nasal; *Op*, opercular; *Pa*, parietal; *Pop*, preopercular; *Ptr*, postrostral; *Sb*, suborbital; *Sop*, subopercular; *Scl*, sclerotic-bones; *St.it*, supratemporo-intertemporal; *hm*, hyomandibular; *h.p*, horizontal pit-line of the cheek (posterior end); *pit.mx*, horizontal pit-line of the cheek (anterior end); *pit.a*, the three pit-lines on the parietal.

Crossopterygii, and the absence of the element in Palaeoniscids was due to its complete reduction, the pit-line belonging to the squamosal very probably would be found lying over the expanded postorbital part of the maxillary. But as in that case it would have nothing to do with the development of the maxillary, it would seem very improbable, that it should show so close connection to the centre of radiation of that bone as it seems to do in *Glaucolepis*. It is, therefore, much more probable that the squamosal was fused with the maxillary and formed a large part of the postorbital expanded division of this. It seems to be a rule among Palaeoniscids, that when two bones fuse, they obtain a common centre, which lies on the connection line between the two original centres. As the horizontal pit-line passed over the squamosal centre, it must in the case of a fusion of the maxillary and

the squamosal centre necessarily be connected with the common centre. According to what has just been set forth we must assume that the centre of the original ancestral Palaeoniscid maxillary lay antero-ventrally to the centre of the bone which we now call maxillary.

Both the horizontal and the vertical pit-line and the bones connected with them, the squamosal and the quadratojugal, can thus be traced in the cheek of Palaeoniscids.

Between the preopercular and the opercular of *Cheirolepis*, WATSON described two dermal bones, X and Y, homologues of which have not yet been found in *Crossopterygii*. The most dorsal of these bones,

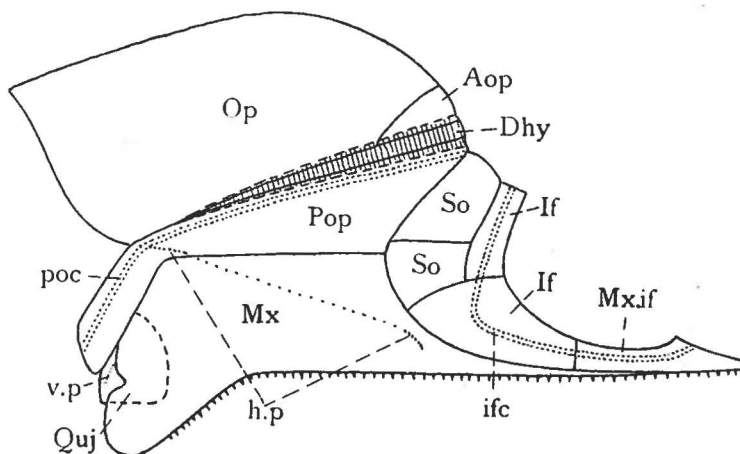


Fig. 19. Attempted sketch of some bones of the side of the head of a Greenland *Glaucolepis*.

Aop, antopercular; *Dhy*, dermohyal; *If*, infraorbital; *Mx*, maxillary; *Mx.if*, maxillo-infraorbital; *Op*, opercular; *Pop*, preopercular; *Quj*, quadratojugal; *Sb*, suborbital; *h.p*, horizontal pit-line of the cheek (midmost part partly hypothetical); *ifc*, infra-orbital canal; *poc*, preopercular canal; *v.p*, vertical pit-line of the cheek.

bone Y, has not, as suggested by WATSON (1925, p. 821), any connections with the preopercular canal (STENSJÖ and HOLMGREN 1936, p. 413). In *Glaucolepis* we find a bone corresponding to Y behind the upper part of the preopercular, and between this "Y bone" and the antero-dorsal part of the opercular lies another small bone (*Aop*, fig. 17, 18 and 19).

A number of *Palaeoniscids* have in this region a considerable number of smaller bones. ALDINGER in 1936 (p. 45) gives to these bones the name antopercular bones. After a study of *Glaucolepis* and comparison of that form with *Polypterus* I have got the impression that the antoperculars in ALDINGER's conception are of two different types in regard to their origin.

The hindmost of the two "antoperculars" in *Glaucolepis* lies rather

superficially as compared with the adjoining bones. Its posterior margin covers the adjoining part of the anterior margin of the opercular and its anterior part covers a smaller or greater part of the more deeply lying foremost "antopercular". This latter bone, on the other hand, lies so deeply that its anterior margin is covered by the neighbouring part of the dorso-posterior margin of the preopercular, and the more posterior part of the bone is to a great extent covered by the overlying hindmost "antopercular" and by the opercular. Some specimens do not show this deeper lying »antopercular" from the outside, a condition which is due to the fact that the opercular and the hindmost "antopercular" join the preopercular. In other specimens it can be observed between the preopercular on the one hand and the hindmost "antopercular" and opercular on the other.

By preparation it is possible to investigate the shape of the anterior "antopercular" (see fig. 19). It has almost the same length as the dorsal shank of the preopercular, and its lateral face is convex in a rostro-caudal direction. Moreover it always covers the dorsal half of the hyomandibular on the lateral side and lies very close to that bone. I therefore put forward the idea that it may be homologous to the "accessory hyomandibular" of *Polypterus*, which according to STENSIÖ and HOLMGREN (1936, p. 392) is a dermal bone (regarded by STENSIÖ and HOLMGREN as a specialised spiracular bone). In *Polypterus* only the uppermost end of this bone is visible from the outside of the head, immediately behind the spiraculum. In opposition to STENSIÖ's and HOLMGREN's explanation of the origin of the bone, I think it probable, on account of its close connection to the hyomandibular, that it originates from fused tooth plates on the hyomandibular in a similar way to what is generally the case with dermal bones related to the visceral skeleton. (STENSIÖ has called my attention to the presence of such tooth plates on the dorsal part of the hyomandibular in *Eusthenopteron* and pointed out their analogy to the foremost "antopercular" in *Glaucolepis*). As thus this foremost "antopercular" seems to differ principally from the posterior one I propose to restrict the name antopercular to the latter of the two bones in *Glaucolepis* and some other forms, and to the corresponding complex of superficial bones found in other forms. The deeper-lying bone homologous to the "accessory hyomandibular" I propose to name "dermohyal". *Cheirolepis* possesses in addition to the dorsal dermohyal, Y, a ventral dermohyal, X, which probably occupies a similar relation to the ventral part of the hyomandibular as the bone Y to the dorsal part. In a great many later Palaeoniscids at least the dorsal dermohyal seems to be present.

The antopercular of *Glaucolepis* should in my opinion be compared to an element in the post-spiracular series of *Polypterus*.

Among the material there is also an interesting *Glaucolepis*-specimen with uncrushed head and the mouth widely open. This specimen was prepared in such a way that the matrix filling the buccal cavity was removed. By this preparation the visceral skeleton could be completely exposed. The visceral arches are well ossified, and covered by dermal tooth-plates. There are five arches behind the hyoid arch.

In the anterior part of the mouth roof in *Glaucolepis* there is a well developed paired mesial dermopalatine. After all it seems to be homologous with the mesial dermopalatine in *Polypterus*, but has a relatively greater extension in the mouth roof.

The internal skeleton of the shoulder girdle and the pectoral fin is well ossified. The shoulder girdle possesses a strong mesocoracoid arch and the pectoral fin shows indications of an axis at least similarly well pronounced to that of *Tarassius* (Moy-THOMAS 1935).

The pelvic plate shows indications of having arisen by fusion of several basalia. The axial skeleton can be studied in a few specimens only and in these it is strongly ossified.

Birgeria STENSIÖ.

Material: Of *Birgeria* a considerable material is now at hand from East Greenland. This material contains a small number of heads of large specimens and a larger number of remains of very small individuals. These small specimens are in some cases rather perfect, in other cases they only represent the foremost or hindmost half of a fish. Only in one case a part of the body of a big *Birgeria* has been secured, but not in connection with a head. Specimens intermediate in size between the large and the small ones are very rare.

The head of the smaller as well as of the greater specimens often shows parts of the endocranium preserved. A preparation of one of the big heads has revealed an endocranium much more complete than that previously described from Spitsbergen (STENSIÖ 1921, p. 152). In many cases the pigment of the body is preserved, so that it is possible to ascertain that like a great many recent fishes *Birgeria* was dark on the back and light on the ventre.

Remarks: The genus *Birgeria* was erected by STENSIÖ in 1919 (STENSIÖ 1919, p. 177—178). In 1921 he gave a very comprehensive description of material of this genus from Spitsbergen, and in 1932 he also described fragmentary remains of *Birgeria* from East Greenland.

The new material from East Greenland allows of an investigation of every detail of the skeleton; thus, for instance, it shows the opercular and the subopercular bones, which have not been described before. The opercular is strikingly small, and lies, with a nearly horizontal longitudinal axis, above the foremost half of the preopercular. The suboper-

cular is lobed in a similar way to the opercular bone of *Polyodon*, a genus with which *Birgeria* shows considerable agreement in several characters. The endocranium of *Birgeria* has previously been described (STENSIÖ 1921, p. 152) on the basis of an incomplete specimen from Spitsbergen. The new material renders it possible to investigate those parts of the endocranium, which were lacking in the Spitsbergen specimen. The previously unknown occipital region appears to contain a strong, unpaired ossification, and is much less wide than the otic and orbito-temporal regions. In the otic and orbito-temporal region the various ossifications have a greater extension than in the form from Spitsbergen. In regard to the number and position of its endocranial ossifications *Birgeria* shows a fundamental agreement with the recent Acipenserids (cf. HOLMGREN and STENSIÖ 1935, p. 206, fig. 336). The parasphenoid extends backwards below the whole occipital region, where it is V-shaped in a transverse section.

It is very possible, though not finally settled, that the very small and very big specimens, which constitute our new material of *Birgeria* belong to the same species.

Other Palaeoniscids.

In addition to the above-mentioned Palaeoniscids there occur one or perhaps more not yet determined genera, and to all appearance also *Acrorhabdus* STENSIÖ, a genus which has been erected in 1921 on Spitsbergen material (STENSIÖ 1921, p. 222).

Pholidopleuridae and Saurichthyidae.

As will be discussed below there is a considerable resemblance between the forms belonging to these two families. It therefore lies near to conclude that the relationship between the *Pholidopleuridae* and the *Saurichthyidae* is closer than generally accepted. A definitive standpoint cannot, however, be chosen, before a detailed comparison has been made of the endocranial structures within the two groups in question.

Australosomus PIVETEAU.

Material: In two of the fish-zones (fish zones II and III) *Australosomus* is extremely common, and a very complete material of this form is therefore at my disposal. Of the small and rather fragile endocrania several complete ones have been secured, so that a very comprehensive investigation of the cranial anatomy can be undertaken by SOLLAS's grinding method.

Remarks: The Greenland species of *Australosomus* has been described by STENSIÖ (STENSIÖ 1932, p. 166) in as great detail as possible on the basis of the insufficient material he had at his disposal. On

more complete material PIVETEAU founded his beautiful description of the genotype of *Australosomus* from Madagascar (PIVETEAU 1935, p. 9). PIVETEAU succeeded in making out the interesting arrangement of the dermal bones of the cranial roof, an arrangement which differs only in smaller details from the most common arrangement of the dermal bones of the Greenland forms. In some Greenland specimens the subdivision of the elements of the dermal cranial roof caudally to the frontals has gone so far, that the cranial roof shows similar conditions as in WADE's reconstruction of *Pholidopleurus* (WADE 1935, fig. 36). Our well preserved endocrania show many details which PIVETEAU was unable to make out on the basis of his less well preserved material; thus, for instance, I have been able to find a posterior fontanelle in the dorsal wall of the endocranium.

At present it is impossible to decide whether or not the new material includes more than one species of *Australosomus*.

Saurichthys AGASSIZ.

Material: *Saurichthys* is one of the rarest fishes in the Eotriassic of East Greenland; only five or six finds have been made of this interesting form, among which are a couple of very well preserved specimens. One of these is the main part of a head with a nearly complete endocranium, the other a head and part of the body preserved in a big concretion.

Remarks: The Greenland *Saurichthys* is distinguished by being completely covered with scales in a manner strikingly resembling that of *Australosomus*.

It is very likely that the Greenland specimens of *Saurichthys* represent more than one species.

Australosomus $\rightleftharpoons$ *Saurichthys*.

It seems very likely that the *Saurichthyidae* and the *Pholidopleuridae* are closely related. PIVETEAU has pointed out several points of resemblance between them, as for instance the short supraorbital canal, ending posteriorly in the frontals (PIVETEAU 1935, p. 32), and the symmetrical caudal fin (PIVETEAU 1935, p. 37). The similarity between the two families has most recently been treated by WADE (WADE 1935, p. 65), who gives a list of 12 interesting points of resemblance and another list of 9 dissimilarities between them. In the list of dissimilarities Nos. 4, 5, 7 and 8 in my opinion appear to be the most fundamental. No. 9, the difference in the squamation, must be dropped now that we know the *Australosomus*-like scale arrangement of the Greenland *Saurichthys*. One of the most striking points of resemblance, which, however, has not been pointed out either by PIVETEAU or by WADE, is in my opinion to be found in the arrangement of the dermal bones of the cranial roof.

This arrangement contrasts strongly with the likewise peculiar arrangement in the two mutually related forms *Birgeria* and *Coccocephalus*.

Bobasatraniidae.

Bobasatrania WHITE.

Material: Several hundred specimens of this fish are now available. It dominates in fish zone II and has also been found in fish zones I and III. Only a small percentage of the specimens show well preserved endocrania, still a sufficient material is at hand to allow of a detailed description of it.

Remarks: The genus has been erected on Madagascar material in 1933 by WHITE (manuscript finished 1932), and is mentioned from East Greenland in 1932 by STENSIÖ, who described some beautiful specimens from Greenland together with some fragmentary remains from Spitsbergen.

The fresh material enables us to make a complete reconstruction of all the dermal bones of the skull and thus also to complete the figure given by STENSIÖ in 1932 of the head of *Bobasatrania* (STENSIÖ 1932, fig. 43).

The whole material seems to belong to the same species, which varies in length from a few to more than 40 cm.

Perleididae.

Perleidus DE ALESSANDRI.

Material: Considerable and excellently preserved materials are at hand, on the basis of which it is possible to make out every detail in the skeleton of *Perleidus*. Beautiful endocrania have been secured, one or two of which will be examined after SOLLAS' grinding method.

Remarks: None of the Greenland specimens shows traces of the horizontal pit-line of the cheek on the preopercular bone ascertained by PIVETEAU (PIVETEAU 1935, p. 47) in *Perleidus* from Madagascar.

The *Perleidus* material seems to comprise two or more species.

Helmolepis STENSIÖ.

Material: Only a single specimen has been found in the new collection from Greenland, but in a much better state of preservation than the one previously known.

Remarks: In 1932 STENSIÖ erected the genus *Helmolepis* on the basis of fragments of the body of a single specimen from East Greenland (STENSIÖ 1932, p. 283). As regards its systematical position STENSIÖ classed *Helmolepis* under the heading "Incertae sedis in group D", group D otherwise comprising the *Catopteridae*, *Perleididae* and *Parasemionotidae*.

The new specimen of *Helmolepis* has exactly the same dimensions as the type-specimen, but shows many details not previously known.

The head recalls in every respect that of *Perleidus*, so that the only characters separating *Helmolepis* from the bigger specimens of *Perleidus* occurring in East Greenland are the characters presented by the fins and previously described by STENSIÖ. Thus *Helmolepis* must no doubt be referred to the *Perleididae*.

Other genera.

A new Perleidid genus may possibly be represented in the material.

Parasemionotidae.

The families *Parasemionotidae* and *Ospiidae* were erected by STENSIÖ in 1932 (STENSIÖ 1932 pp. 183—84 and 225—283). These two interesting families were thought to form a long wanted link between the *Chondrostei* and the *Holostei*, even though both, according to STENSIÖ, must be referred to the *Chondrostei* (STENSIÖ 1932, p. 184). The family *Ospiidae* comprised the Greenland genera *Ospia* and *Broughia*, the family *Parasemionotidae* the Madagascar genus *Parasemionotus* erected by PIVETEAU 1921, pp. 1017—1019). The most important points of distinction between the two families were (STENSIÖ 1932, p. 226) the absence of an interopercular in the *Ospiidae* and their much more free maxillary, not connected with the preopercular.

In PIVETEAU's latest work on the Triassic fishes of Madagascar (PIVETEAU 1935) *Parasemionotus* and another closely related genus, *Watsonia*, are described in great detail, so that on the basis of that work it is possible to a much greater extent than when STENSIÖ wrote his paper on the Triassic fishes of East Greenland, to draw comparisons between the Madagascar and the East Greenland genera.

In a treatise just published (STENSIÖ 1935) STENSIÖ states (p. 23, foot-note) that at any rate some *Ospiidae* have a real interopercular. Since when writing that, STENSIÖ had at his disposal only the material of the genera *Ospia* and *Broughia*, which he described himself in 1932, he must by a renewed examination of it have discovered, either in *Ospia* or in *Broughia*, traces of an interopercular which he has previously overlooked.

Thus the most important distinction between the families *Ospiidae* and *Parasemionotidae* has disappeared, and from an inspection of the new large material from East Greenland it is quite evident that the families *Ospiidae* and *Parasemionotidae* should be included in one family under the name *Parasemionotidae*.

On account of the considerable similarity between the Madagascar and the East Greenland Eotriassic fish-fauna, I almost expected that

the two Madagascar genera should appear to be identical with the two Greenland genera. Already PIVETEAU recognised the great similarity that existed between *Ospia* and *Watsonia* (PIVETEAU, p. 65). However, after a preliminary inspection I have arrived at the result that *Parasemionotus* and *Watsonia* occur in East Greenland, but neither of them is identical with *Ospia* or *Broughia*. In fact all four genera and in addition one or perhaps several new genera of the family *Parasemionotidae* are present in the rich Eotriassic fauna of Greenland. The distribution of the individual *Parasemionotid* genera within the fish zones seems to present various points of interest; however, the determinations should be carefully checked before anything can be published about these observations. So much, however, can be stated that the genera *Ospia* and *Watsonia* seem to be much more common than the genera *Broughia* and *Parasemionotus*.

Of the greatest interest is PIVETEAU's discovery of the vertical pit-line of the cheek (in *Parasemionotus*) and the horizontal pit-line (in *Parasemionotus* and *Watsonia*), both situated on the well developed *Parasemionotid* preopercular. From this fact he infers (PIVETEAU 1935, p. 80) that even though no strict homology exists, a certain correspondence may be observed between the squamosal-quadratojugal-preopercular in *Osteolepis* on one hand and the preopercular in the *Parasemionotidae* on the other.

As regards the formation of the interopercular, PIVETEAU (1935, p. 80) considers the shape of the interopercular of *Parasemionotus* a decisive proof that the interopercular is a modified branchiostegal ray. It seems, however, more natural to regard the interopercular as a separated corner of the subopercular.

Both the interopercular and the pit-lines of the cheek appear very distinctly on the Greenland material. Well developed pit-lines on the parietals similar to those figured by PIVETEAU are very distinct, too. The middle pit-line extends as a perfectly straight line from the centre of ossification in the parietal to the centre of ossification in the supratemporo-intertemporal.

A comprehensive investigation of the anatomy of the *Parasemionotidae* will of course be of the greatest interest on account of the important place of this group near the base of the Holostei.

Ospia STENSIÖ.

Material: Several fine specimens, often with most excellently preserved endocrania.

Remarks: The genus was erected in 1932 by STENSIÖ on a single specimen from East Greenland. The new material very likely comprises more than one species.

Broughia STENSIÖ.

Material: The presence of *Broughia* in the new material has not yet been established with certainty.

Parasemionotus PIVETEAU.

Material: Only very sparse materials of this genus has been recognised in the new collections.

Watsonia PIVETEAU.

Material: Considerable and well preserved materials are at hand, comprising excellent specimens of endocrania well fitted for investigation after SOLLAS's grinding method.

Other genera.

One or more new genera are included in the Parasemionotid material; some of these are represented by very beautifully preserved specimens.

COMPARISON BETWEEN THE TRIASSIC FISH FAUNAS OF GREENLAND, SPITSBERGEN, AND MADAGASCAR

As previously pointed out (STENSIÖ 1932; p. 294, E. NIELSEN 1935, p. 107), a close agreement exists between the Triassic fish faunas of East Greenland, Spitsbergen, and Madagascar. This question has most recently been treated by PIVETEAU in his great work on the Triassic fishes of Madagascar (PIVETEAU 1935, pp. 90 et seq.). PIVETEAU found the Madagascar fauna to be more closely allied to the Greenland fauna than to the Spitsbergen fauna. Now that a much more comprehensive material from Greenland is at hand, similarities and dissimilarities between the faunas of the three areas are much more obvious. The East Greenland Triassic is the oldest of the three, then comes the Triassic of Madagascar, and finally the Triassic of Spitsbergen, which is considerably younger than that of Madagascar. (Spath 1935, p. 110 et seq.).

Our knowledge of the Elasmobranchs is still too slight to allow of a comparison. It should only be mentioned that the genus *Polyacrodus* is common to Greenland and Spitsbergen.

Table for comparison of the Lower Triassic fish faunas of
Madagascar, Greenland, and Spitsbergen.

I. Crossopterygii.

Madagascar	Greenland	Spitsbergen
—	— ?	Wimania
—	Sassenia	Sassenia
—	—	Axelia
—	—	Mylacanthus
—	—	Scleracanthus
Whiteia	Whiteia	—
—	Laugia	—
Coelacanthus?	—	—

As regards Greenland there is still a number of undetermined genera, among others ?*Wimania*, as indicated above.

At present it is impossible to make a satisfactory comparison of the Coelacanthids of the three areas, our knowledge of the *Coelacanthidae* being rather deficient. It will be evident from the table that at present one genus, viz. *Whiteia*, is common to Madagascar and Greenland, and at least one genus, *Sassenia*, is common to Greenland and Spitsbergen, while no genus common to Madagascar and Spitsbergen is known.

Considered as a whole the Greenland Coelacanthid fauna shows more primitive characters than that of Spitsbergen. The cheek is often completely covered with bones, and in those cases in which reductions of the dermal bones of the cheek can be observed, the reductions are nowhere so extensive as in the forms from Spitsbergen. The extrascapular series comprises a smaller number of bones in the Greenland forms than in the Spitsbergen forms. The endocranium, at any rate in *Laugia* (STENSTRÖM 1932, p. 51), is more extensively ossified than in the Spitsbergen forms. Moreover in Greenland such big forms as in Spitsbergen are apparently never met with. The Madagascar forms show a similar slight reduction of the bones of the cheek as the least reduced Greenland forms; in the number of extrascapulars they also agree with the Greenland forms; nothing is known about the extension of their endocranial ossifications.

Dipnoi are only known from a single find on Spitsbergen, but are not ascertained from Greenland or from Madagascar.

Table for comparison of the Lower Triassic fish faunas of Madagascar, Greenland, and Spitsbergen.

II. Actinopterygii.

Madagascar		Greenland		Spitsbergen
Boreosomus		Boreosomus	—>	Boreosomus
—		Acrorhabdus	—>	Acrorhabdus
Glaucolepis	<—	Glaucolepis		Glaucolepis
—		Birgeria	—>	Birgeria
—		—		Pygopterus
Australosomus		Australosomus		—
Saurichthys ¹⁾		Saurichthys	—>	Saurichthys
Bobasatrania		Bobasatrania	—>	Bobasatrania
Ecrinesomus		—		—
Perleidus		Perleidus		Perleidus
—		Helmolepis		—
Parasemionotus		Parasemionotus		—
Watsonia		Watsonia		—
—		Ospia		—
—		Broughia		—

¹⁾ According to kind information by Dr. PIVETEAU.

To the forms mentioned in the table must be added a number of still undetermined genera from Greenland, and an undetermined fish fragment from Spitsbergen which in 1925 was referred with doubt to the family *Semionotidae* (STENSIÖ 1925, p. 225), but later stated by STENSIÖ to have a certain superficial resemblance to *Helmolepis*.

The arrows in the table indicate the direction from more primitive to more specialised forms in those cases in which it is possible on a preliminary inspection to ascertain characters indicative thereof (see below).

A comparison of the faunas of Madagascar and Greenland will show that eight of the nine Actinopterygian genera known from Madagascar occur in Greenland too. The ninth genus is *Ecrinesomus*, whose relationship to *Bobasatrania* has not yet been finally settled. Five genera are represented in Greenland but not in Madagascar; two of these, *Birgeria* and *Acrorhabdus*, are common to Greenland and Spitsbergen.

As mentioned by PIVETEAU, there is less agreement between the faunas of Spitsbergen and Madagascar, only five of the nine genera of Madagascar occurring in Spitsbergen. Three Spitsbergen genera, two of which also occur in Greenland, are absent in Madagascar. All the Spitsbergen genera are found in Greenland with the exception of *Pygopterus*, but nevertheless the two faunas are very dissimilar, no less than six Greenland genera being absent from Spitsbergen, among others *Australosomus*, *Watsonia* and *Parasemionotus* which are common to Greenland and Madagascar.

It will be obvious from the table that while the faunas of Greenland and Madagascar are closely related, that of Spitsbergen differs relatively much from both of them, though it is much more like that of Greenland than that of Madagascar.

On account of the well preserved and well described Actinopterygian material from all three areas it is already now possible to draw some interesting comparisons between more or less specialised species within several of the genera common to two of the three or to all the three areas, which represent three different periods of the Lower Triassic.

As regards the Stegocephalians occurring together with the fishes in East Greenland and Spitsbergen, SÄVE-SÖDERBERGH has shown that, as might be expected, the Triassic Stegocephalian fauna of Greenland is decidedly more primitive than that of Spitsbergen (SÄVE-SÖDERBERGH 1935, p. 196, 1936). SÄVE-SÖDERBERGH also points out the conspicuous fact that related forms within the two areas exhibit a considerable difference in size, the Spitsbergen forms being of much larger dimensions than those of East Greenland.

Within the Stegocephalians there are thus indications of a develop-

ment from older, small, primitive Greenland forms to younger, bigger more specialised Spitsbergen forms.

A similar course of development can already now be distinguished within the Actinopterygians and (as already mentioned above) also within the Crossopterygians. Where it is possible to make a judgement, the Madagascar fishes as compared with those of Spitsbergen show a similar primitive stage of development as the fishes of Greenland, while a comparison between those from Greenland and those from Madagascar at the present time in a single case only indicated that the Madagascar forms are the youngest. As regards *Boreosomus*, *Birgeria* and *Bobasatrania* the Greenland forms are on the whole smaller than those of Spitsbergen.

The endocranium of the Greenland form of *Birgeria* is much more completely ossified than that of the Spitsbergen *Birgeria*. STENSIÖ has shown that *Birgeria groenlandica* in other respects also is more primitive than *B. mougeoti* from Spitsbergen, the subdivision of the supraorbitals and the dermosphenotic being much less advanced in the former than in the latter (STENSIÖ 1932, p. 106). With regard to a number of other characters too, for instance the ornamentation of the dermal bones of the head, STENSIÖ points out that *B. groenlandica* is more primitive than the geologically younger *B. mougeoti*.

As stated above, the scale covering of the Greenland *Saurichthys* is less reduced than that of the Spitsbergen *Saurichthys*.

During the planned thorough investigation of the Greenland material of Actinopterygians it will very probably turn out as regards several more genera common to Greenland and Spitsbergen that the Greenland forms are more primitive than those from Spitsbergen. A careful comparison of related forms with such a small difference of age as exists between the individual members of the Triassic fish faunas of Greenland and Spitsbergen, will no doubt enable us to draw important phylogenetic conclusions. A closer comparison of primitive and more specialised characters within the genera common to Greenland and Madagascar cannot be made at present. As regards *Glaucolepis* alone it would seem that a larger number of dermal bones may be found between the parietals and the extrascapular series in the Madagascar form than has even been observed in the Greenland forms, and in this respect the former must therefore be considered more specialised than the latter ones.

LIST OF LITERATURE

- ALDINGER, H. 1936. Permische Ganoidfische aus Ostgrönland. København. Medd. om Grønland. Vol. 102. No. 3.
- ALLIS, E. P. 1922. The cranial anatomy of *Polypterus*, with special reference to *Polypterus bichir*. J. Anat. London. Vol. LVI.
- 1935. On a general pattern of arrangement of the cranial roofing bones in fishes. J. Anat. London. Vol. LXIX, pl. II.
- BROUGH, J. 1931. On Fossil Fishes from the Karroo System, and some General Considerations on the Bony Fishes of the Triassic Period. London. Zool. Soc. Proc.
- 1933. On a new Palaeoniscid genus from Madagascar. Annals and Magaz. Nat. Hist. Vol. XI.
- Koch, L. 1932. Carboniferous and Triassic Stratigraphy of East Greenland. København. Medd. om Grønland. Vol. 83. No 2.
- MOY-THOMAS, J. A. 1934. The Structure and Affinities of *Tarrasius problematicus* Traquair. Proceed. of Zool. Soc. of London. 1934. pt. 2.
- 1935. The Coelacanth Fishes from Madagascar. Geol. Mag. Vol. LXXII. No. 851.
- NIELSEN, E. 1935. The Permian and Eotriassic Vertebrate-bearing beds at Godthaab Gulf. København. Medd. om Grønland. Vol. 98. No. 1.
- PEHRSSON, T. 1922. Some points in the cranial development of Teleostomian Fishes. Acta Zoologica. Bd. 3. 1922.
- PIVETEAU, M. J. 1929. Sur un type nouveau de poisson fossile provenant du nord de Madagascar. Paris Acad. Sci. R. C. Tome 189, No. 93.
- 1930a. Particularités structurales d'un type nouveau de poisson fossile des formations permo-triasiques du nord de Madagascar. Paris. Acad. Sci. C. R. Tome 191, No. 11.
- 1930b. Contribution à l'étude des poissons ganoides fossiles: la famille des Catopterides. Paris. Acad. Sci. C. R. Tome 191. No. 13.
- 1934. Les Poissons Du Trias Inférieur. Contribution A L'étude Des Actinoptérygiens. Annales de Paléont. Tome XXIII.
- SPATH, L. F. 1935. Additions to the Eo-triassic Invertebrate-fauna of East Greenland. København. Medd. om Grønland. Vol. 98. No. 2.
- STENSIÖ, E. A:son. 1921. Triassic Fishes from Spitsbergen. Part I. Vienna.
- 1922. Über zwei Coelacanthiden aus dem Oberdevon von Wildungen. Pal. Zeitschr. Vol. 4.
- 1925. Triassic Fishes from Spitsbergen. Part II. Stockholm. K. Vet. Akad. Handl. Ser. 3. Vol. 2.

- STENSIÖ, E. A:SON 1932. Triassic Fishes from East Greenland. København. Medd. om Grønland. Bd. 83. No. 3.
- 1935. *Sinamia zdanskyi*. Palaeontologia Sinica. Ser. C. Vol. III, Fasc. I. Peking.
- 1936. Devonian Coelacanthids of Germany with special reference to the dermal skeleton (in press).
- STENSIÖ, E. A:SON and HOLMGREN, N. 1936. Kraniaum und Visceralskelet der Acranier, Cyclostomen und Fische. (In Bolk, Göppert, Kallius, Lubosch. Anatomie. Bd. IV).
- SÄVE-SÖDERBERGH, G. 1932. Preliminary note on Devonian Stegocephalians from East Greenland. København. Medd. om Grønland. Bd. 94, No. 7.
- 1933. The dermal bones of the head and the lateral line system in *Osteolepis macrolepidotus*. Ag. Nov. Acta Reg. Soc. Sci. Upsaliensis. Ser. IV, Vol. 9. No. 2.
- 1935. On the dermal bones of the head in Labyrinthodont Stegocephalians and primitive Reptilia. København. Medd. om Grønland. Vol. 98, No. 3.
- 1936. On the morphology of Triassic Stegocephalians from Spitsbergen. Stockholm. K. Vet. Akad. Handl. (in press).
- WADE, R. T. 1932. Preliminary note on *Macroaethes brookvalei*, representing a new family of Chondrosteian Fishes, the Pholidopleuridae. Ann. & Mag. Nat. Hist. London. (10). IX.
- 1933. On a new Triassic Catopterid Fish from New South Wales. Ann. & Mag. Hist. London. (10). XII.
- 1935. The Triassic fishes of Brookvale. British Mus. (Nat. Hist.).
- 1936. On the morphology of Triassic Stegocephalians from Spitsbergen. Stockholm. K. Vet. Akad., Handl. (In press).
- WATSON, D. M. S. 1921. On the Coelacanth Fish. Ann. and Mag. of Nat. Hist. Ser. 9. Vol. VIII.
- 1925. The Structure of Certain Palaeoniscids and the Relationships of that Group with other Bony Fish. Proc. Zool. Soc. Bd. LIV.
- WHITE, E. I. 1932. On a new Triassic Fish from North East Madagascar. Ann. and Mag. Nat. Hist. Vol. X, 1932.
- 1933. New Triassic Palaeoniscids from Madagascar. Ann. and Mag. Nat. Hist. Vol. XI.