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KOMMISSIONEN FOR VIDENSKABELIGE UNDERSØGELSER I GRØNLAND
BD. 138

PALÆOZOOLOGICA GROENLANDICA
AFHANDLINGER OM ØSTGRØNLANDSKE VERTEBRATFOSSILER
INDSAMLEDE PAA DE AF DR. LAUGE KOCH I AARENE 1926-38 LEDEDE
EKSPEDITIONER UDGIVET AF UNIVERSITETETS ZOOLOGISKE MUSEUM

STUDIES ON TRIASSIC FISHES I.

BY

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WITH 78 FIGURES IN THE TEXT
AND 30 PLATES

KØBENHAVN
C. A. REITZELS FORLAG
DET HOFFENSBERGSKE ETABLISSEMENT
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Det Hoffensbergske Etabl. Kbhvn
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ERRATA

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I Efteraaret 1939 modtog Universitetets zoologiske Museum indtil videre de meget omfattende og videnskabeligt særdeles værdifulde Samlinger af Vertebratfossiler fra Østgrønland indsamlet i Aarene 1926–1938 paa de af Dr. *Lauge Koch* ledede Østgrønlandsekspeditioner. Hermed overtog Zoologisk Museum tillige Forpligtelsen til at drage Omsorg for dette Materiales fortsatte Bearbejdelse og for Offentliggørelsen af Resultaterne. Det paagældende Materiale er ikke alene enestaaende i Henseende til Eksemplarernes og Formernes Rigdom, idet det omfatter ikke mindre end ca. 500 Kasser Forsteninger, men det er tillige, som den allerede udførte Del af Bearbejdelsen har vist, af overordentlig stor videnskabelig Betydning. Man har gennem dette Materiale paa væsentlige Punkter faaet revideret Synspunkterne i Henseende til de fossile Fisks og Padders Morfologi og Systematik og derigennem tillige naaet vigtige Resultater med Hensyn til vor Opfattelse af hele Hvirveldyrklassens Nedstamnings- og Slægtskabsforhold.

Da Zoologisk Museum overtog Materialet, var Bearbejdelsen, der hidtil var foregaaet under Dr. *Kochs* Ledelse, allerede i fuld Gang, og der forelaa en Række Afhandlinger af *Stensiö*, *Säve-Söderbergh*, *Aldinger* og

En automne 1939 le Musée zoologique de l'Université de Copenhague a reçu les collections de fossiles de vertébrés de Groenland de l'Est, collections très étendues et extrêmement précieuses au point de vue scientifique, recueillies dans les années 1926–1938 au cours des expéditions en Groenland de l'Est dirigées par le Dr *Lauge Koch*. De ce fait le Musée zoologique s'est chargé également de l'obligation de prendre soin du traitement continué de ce matériel et de la publication des résultats. Le matériel en question n'est pas seulement unique quant à la richesse des exemplaires et des formes, étant donné qu'il ne comprend pas moins d'environ 500 caisses de fossiles, mais il est encore – comme il ressort de la partie déjà achevée du traitement – d'une importance scientifique primordiale. Grâce à ce matériel on a revisé, sur des points essentiels, les points de vue quant à la morphologie et la systématique des poissons et des batraciens fossiles et obtenu en outre par là des résultats importants au sujet de notre conception des rapports de descendance et de filiation de toute la classe des vertébrés.

Au moment où le Musée zoologique s'est chargé du matériel on était déjà en pleine activité avec le traitement exécuté jusqu'ici sous la direction du

E. Nielsen (Medd. om Grønland 83, 86, 94, 97, 98, 112). Materialet befandt sig paa det daværende Tidspunkt for langt den overvejende Dels Vedkommende i Stockholm og Uppsala, hvor Bearbejdelsen hidtil var udført. Da det var ønskeligt, at en Del af dette Arbejde nu skulde udføres paa Zoologisk Museum, overførtes Bearbejdelsen af Triasmaterialet, der var overdraget til mag. scient *Eigil Nielsen*, til Zoologisk Museum, hvor Mag. *Eigil Nielsen* genoptog Bearbejdelsen i Foraaret 1940. Det økonomiske Grundlag for dette skyldes i første Linie en Bevilling fra Carlsbergfondet, hvorved det dels blev muligt at anskaffe det vigtigste af den for Bearbejdelsen nødvendige Apparatur, dels at honorere Bearbejdelsesarbejdet i det første Aar. Til dette Formaal modtoges yderligere et Bidrag fra Kaptajn Alf Trolle og Hustrus Legat. Endelig har Carlsbergfondet ydet en Bevilling til Tegning og Fotografering. For disse Bevillinger udtaler jeg herved min allerbedste Tak. Fra April 1941 er Honoreringen af selve Bearbejdelsen overtaget af Staten gennem en Bevilling paa Finansloven. Som et Resultat af de første 2 Aars Arbejde fremlægges nu i nærværende Publikation det første Udbytte i Form af mag. scient. *Eigil Nielsens* Afhandling: Studies on Triassic Fishes I. Samtidig hermed er Bearbejdelsesarbejdet fortsat dels paa Naturhistoriska Riksmuseets palæontologiske Afdeling, Stockholm, under Ledelse af Prof. *E. Stensiö*, dels paa Uppsala Universitets palæontologiske Institution hos Prof. *G.Säve-Söderbergh*.

Dr *Koch*, et il avait été publié toute une série de travaux par *Stensiö*, *Säve-Söderbergh*, *Aldinger* et *E.Nielsen* (Medd. om Grønland 83, 86, 94, 97, 98, 112). A cette époque-là le matériel se trouvait, pour la plus grande partie de beaucoup, à Stockholm et à Uppsala où le traitement avait eu lieu jusqu'ici. Comme il était utile qu'une partie de ce travail fût faite maintenant au Musée zoologique, le traitement du matériel triasique, qui avait été confié à M. *Eigil Nielsen*, maître ès sciences, a été laissé au Musée zoologique où M. *Eigil Nielsen* a repris le traitement au printemps 1940. La possiblité économique de ces dispositions est due en premier lieu à une allocation de la Fondation Carlsberg ce qui nous a permis d'une part de procurer la partie principale des appareils nécessaires au traitement, d'autre part de payer le travail de traitement pendant la première année. A cet effet on a reçu ultérieurement une contribution de la fondation Capitaine Alf Trolle et son épouse. Enfin, la Fondation Carlsberg a accordé une allocation pour les dessins et les photographies. J'exprime ici mes meilleurs remerciements de ces allocations. A partir d'avril 1941 l'État s'est chargé directement du paiement du traitement par une allocation inscrite au budget. Comme un résultat du travail des 2 premières années nous donnons maintenant dans la présente publication le premier fruit sous forme de l'étude de M. *Eigil Nielsen:* Studies on Triassic Fishes. – En même temps le travail a été continué, d'une part au

Vi har under vort Arbejde modtaget overmaade megen Hjælp fra vore svenske Kolleger og ganske særlig har Prof. *E. Stensiö* paa mangfoldige Maader understøttet Bearbejdelsen derved, at en stor Del Præparationsarbejde, Fotografering, Tegning og Retouchering er blevet udført paa Naturhistoriska Riksmuseets palæozoologiske Afdeling, en Hjælp, for hvilken vi her udtrykker vor hjerteligste Tak.

I Betragtning af det østgrønlandske Fossilmateriales Værdi og Omfang har det været en nærliggende Tanke at søge Resultaterne af Bearbejdelsen offentliggjort i en særlig samlet Publikation paa lignende Maade som det i sin Tid gennem Værket »E Museo Lundii« er sket med det store Fossilmateriale, som *P. V. Lund* hjemsendte fra Sydamerika. Det er da ogsaa blevet besluttet, at dette skal ske i et Værk, *Palæozoologica groenlandica*, af hvilket 1ste Bind hermed fremkommer. Da imidlertid nogle Afhandlinger behandlende dette Materiale allerede er offentliggjort i »Meddelelser om Grønland«, vil det paa den anden Side være ønskeligt, at den fortsatte Bearbejdelse stadig kommer Læserne og Brugerne af »Meddelelser om Grønland« i Hænde. For at opnaa dette er der stillet det fornødne Antal Eksemplarer af Oplaget til Raadighed for Redaktionskommiteen for »Meddelelser om Grønland«, saaledes at hvert Bind af Palæozoologica Groenlandica tillige fremkommer som et Bind i »Meddelelser om Grønland«, det foreliggende Bd. 1 som Bind 138, medens Bd. 2, til hvilket Manuskript

service paléonthologique du Naturhistoriska Riksmuseet à Stockholm sous la direction du professeur *E. Stensiö*, d'autre part à l'institution paléonthologique de l'Université d'Uppsala chez le professeur *G. Säve-Söderbergh*. Au cours de notre travail nous avons reçu beaucoup d'assistance de la part de nos collègues suédois; le professeur *E. Stensiö* a tout particulièrement appuyé le travail de différentes manières, étant donné qu'une grande partie du travail de préparation, des photographies, des dessins et de la retouche a été faite au service paléozoologique du Naturhistoriska Riksmuseet, assistance de laquelle nous tenons à exprimer ici nos remerciements les plus sincères.

En considération de la valeur et de l'étendue du matériel de fossiles de Groenland de l'Est il était tout naturel de désirer la publication des résultats du traitement dans un ouvrage d'ensemble spécial de la même manière que celle à laquelle on a eu recours dans le temps, par l'ouvrage »E Museo Lundii«, pour le grand matériel de fossiles que *P. V. Lund* a envoyé de l'Amérique du Sud. En effet, il a été décidé que cela doit avoir lieu dans un ouvrage: *Palæozoologica groenlandica* dont le premier tome paraît maintenant. Étant donné, cependant, que quelques travaux traitant de ce matériel ont déjà été publiés dans les »Meddelelser om Grønland«, il serait utile d'autre part que le traitement continué parvienne toujours aux lecteurs et utilisateurs des »Meddelelser om Grønland«. A cette fin le nombre nécessaire d'ex-

tet foreligger (E. Stensiö: On the Placodermi of the Upper Devonian of East-Greenland II), vil blive Bd. 139.

Publikationen af et Værk som Palæozoologica groenlandica vil i Betragtning af den store Vægt, der maa lægges paa et righoldigt Illustrationsmateriale, nødvendigvis blive meget kostbar, og det vilde næppe have været muligt i nogenlunde nær Fremtid at tilvejebringe de til denne Publikation nødvendige Midler, hvis disse ikke var blevet stillet til Raadighed fra en interesseret Privatmands Side. Da Billedhugger *Viggo Jarl*, der i sin Egenskab af Kommanditist i Øresunds chemiske Fabrikker har indgaaende Kendskab til grønlandske Forhold, hørte, at et saadant Værk var under Forberedelse, og at der var Vanskeligheder ved at fremskaffe de fornødne Midler, stillede han beredvilligt det nødvendige Beløb til Trykning af de to første Bind af Palæozoologica groenlandica til Raadighed, hvorved det ikke alene blev muligt at skride til omgaaende Trykning, men ogsaa at offentliggøre Værket med et saadant Udstyr af Billedmateriale, som det ellers næppe vilde have været muligt at opnaa. For den store Hjælp, Billedhugger *Jarl* herved har ydet dansk Videnskab, udtrykker jeg herved vor allervarmeste Tak.

emplaires du tirage a été mis à la disposition du comité de rédaction des »Meddelelser om Grønland«, de sorte que chaque tome du Palæozoologica groenlandica paraît en outre comme un tome des »Meddelelser om Grønland«, le présent tome 1 comme tome 138, tandis que tome 2, pour lequel le manuscrit nous a été présenté (*E. Stensiö:* On the Placodermi of the Upper Devonian of East-Greenland II), sera tome 139.

La publication d'un ouvrage comme le Palæozoologica groenlandica doit en considération de la grande importance qu'il faut attacher à un matériel de figures varié – nécessairement devenir très coûteuse, et il n'aurait guère été possible, dans un avenir assez proche, de procurer les moyens nécessaires à cette publication à moins que ceux-ci n'eussent été fournis de la part d'un homme privé. Quand le sculpteur *Viggo Jarl* a appris qu'un tel ouvrage était en préparation, et qu'on éprouvait des difficultés à procurer les moyens y nécessaires, il a spontanément fourni le montant nécessaire à l'impression des deux premiers tomes du Palæozoologica groenlandica, fait par lequel il a été possible non seulement de procéder aussitôt à l'impression, mais encore de publier l'ouvrage avec un tel matériel d'images qu'on n'aurait guère pu obtenir autrement. J'exprime ici mes remerciements les plus chaleureux de l'aide grandiose qu'a fournie M. *Viggo Jarl* aux sciences danoises.

Universitetets zoologiske Museum, København, i Septbr. 1942.

R. SPÄRCK

EIGIL NIELSEN

STUDIES ON TRIASSIC FISHES FROM EAST GREENLAND

I.
GLAUCOLEPIS AND BOREOSOMUS

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PREFACE

In East Greenland Eotriassic deposits were first discovered in 1926 near Kap Stosch in the northwestern part of Hold with Hope by the Cambridge Expedition under the leadership of J. M. Wordie. From these deposits the expedition brought home a single fish besides a large number of invertebrates.

In the years 1928, 1929, and 1930 Norwegian trappers collected at Kap Stosch some few Triassic fishes, which now belong to the Palæontological Museum of Oslo.

On the Danish expeditions in 1929 and 1930 led by Dr. Lauge Koch, a small collection of fishes was brought home, derived partly from the Eotriassic area around Kap Stosch and partly from a newly discovered Eotriassic area on the south side of Clavering Ø; and in the first summer of the Danish Three-Year Expedition 1931–34 under the leadership of Dr. Lauge Koch some additional fish remains were found in the same regions.

The Triassic fishes collected by the Danish expeditions in 1929, 1930, and 1931 were described in 1932 by Professor E. Stensiö, and since at an early stage in the working up of the collections the material proved to be of very great interest, Dr. Lauge Koch in 1932 set me the task of making further investigations in the Eotriassic areas.

As early as 1931, as a member of the Danish Three-Year Expedition and serving as assistant to G. Säve-Söderbergh, now professor in the University of Uppsala, I visited the Eotriassic beds on Clavering Ø, and before leaving for East Greenland in 1932 as a member of the second wintering party of the Three-Year Expedition I was able, during nearly four months' stay in Stockholm, to become acquainted with modern vertebrate-palæontological working methods under the guidance of Professor E. Stensiö.

The investigation of the Eotriassic deposits from July, 1932, to August, 1933, resulted in the collection of about 2000 fishes and a considerable number of stegocephalians. A provisional sorting and preparation of the large fish material was carried out during my stay at the Riksmuseum, Stockholm, in the autumn of 1933, whereas the final working up of the material was not commenced till my stay in Stockholm from February, 1935, to June, 1936.

However, during the preparation it became evident that it would be of importance to make certain supplementary collections, so I passed the winter of 1936–37 at Eskimonæs as a member of the Danish East Greenland Expedition 1936–38 under the leadership of Dr. Lauge Koch. On this expedition I had several other tasks which required fairly long journeys; still I succeeded in securing about 1000 fishes and some stegocephalians from the Eotriassic beds. Moreover other members of the expedition, in the two years which the expedition lasted, discovered new areas of Eotriassic fish-bearing beds between Ella Ø and Scoresby Sund, from which, however, only a very few specimens were brought home.

In the summer of 1937 the ship, owing to unfavourable ice conditions, failed to call at Eskimonæs, and in the ensuing summer I became a member of another Greenland Expedition; hence I could not resume the working up of the Triassic fishes till the autumn of 1939. However, during my absence from 1936 to 1939 a fairly considerable amount of preparation and drawing work had been carried out in Stockholm under the supervision of Professor E. Stensiö.

Owing to various circumstances the collections had to be removed to Copenhagen in the spring of 1940, where the work has since then been continued at the Zoological Museum of the University.

For help during my work in Greenland, in Copenhagen, and in Stockholm I am indebted to a great number of persons. To Dr. Lauge Koch, the leader of the expeditions in which I partook in 1931, 1932, 1933, 1936, 1937, and 1938, who also procured the means for my stays in Stockholm in the years 1932, 1933, 1935, and 1936, I express special thanks for the tasks he set me and for his always ready help towards their solution. In this connection I wish to thank Messrs. Alexander Jensen, mag. sc. M. Køie, mag. sc. J. Troelsen, and O. Harder Jensen, who in different periods assisted me in collecting the material on which the present paper is based.

To Professor E. Stensiö I owe a great debt of gratitude for his indefatiguable guidance and encouragement, for countless valuable discussions, for a unique hospitality during my numerous and long sojourns at Stockholm, and for the readiness with which, time after time, at the sacrifice of his own work, he placed his personnel at my disposal, as also for taking care that the work on my series of sections and preparations was continued during my absence in Greenland.

At the Swedish Riksmuseum the photography, preparation, and other technical work for the present paper were carried out by Mrs. A. Stensiö, Miss A. Brasch, Mrs. B. Säve-Söderbergh, Mrs. M. Ferm, and Mr. G. Ahl, the retouching of the photographs and drawing of some of the text-figures by Mr. S. Ekblom, and of the greater part of the series of sections by Miss Ekbom. To all these persons I express my cordial thanks.

To Professor J. Piveteau, Écoles des Mines, Paris, I am indebted for valuable material from Madagascar.

To Professor G. Säve-Söderbergh, the head of the Palæontological Institution of the University of Uppsala, I tender thanks for his loan of Triassic fishes from Spitsbergen and for his always ready help.

To Dr. E. Jarvik, of the Swedish Riksmuseum, I owe thanks for checking the drawings of the sections during the last few years.

To Professor R. Spärck, the head of the Zoological Museum of the University, Copenhagen, I wish to express my grateful thanks for his efforts to procure me as good working conditions as possible and for the interest he has constantly taken in my work.

To Professor C. M. Steenberg I am indebted for the permission to use the instruments of the Laboratory for Comparative Anatomy for preparation of the wax-plates for the model of *Boreosomus*.

I wish, also, to express my thanks to Miss E. Gleerup, who has translated the present paper into English, and to Dr. C. Crossland for reading some of the first proofs.

Finally my thanks are due to Miss Ingeborg Frederiksen, who has drawn the greater number of the text-figures.

INTRODUCTION

In the Eotriassic deposits in East Greenland fishes have been found in many localities and are especially common around Kap Stosch and at Hird Bay. The bulk of the material has been collected around Kap Stosch where the fishes occur in six zones, viz. Fish-zones I–V and the so-called Stegocephalian-horizon (E. Nielsen 1935; 1936). The composition of the fish fauna changes from zone to zone, a change previously alluded to (E. Nielsen 1935, pp. 96–107; 1936, p. 7), but which cannot be explained in detail till the whole material has been worked up.

The subjoined table, based on my own stratigraphical, and on L. F. Spath's palæontological (Spath 1935, pp. 103–104) investigations, will suffice to convey a general idea of the occurrence of the forms treated in the present paper.

A total of about 3000 fishes have been brought home from the Eotriassic beds of East Greenland, comprising both Elasmobranchs, Crossopterygians, and Actinopterygians.

The Elasmobranch remains are few and rather unsatisfactorily preserved. Three or four genera are represented.

The Crossopterygian remains are fairly frequent and often exellently preserved. A preliminary examination shows that several genera of Coelacanthids are represented.

The Actinopterygian remains constitute by far the greater part of the material, and the state of preservation is in many cases excellent. According to a preliminary examination no less than eight families are represented, viz. *Palaeoniscidae* s. str., *Acrolepidae*, *Birgeriidae*, *Pholidopleuridae*, *Saurichthyidae*, *Bobasatraniidae*, *Perleididae*, and *Parasemionotidae*.

The present first part of the planned work on this Eotriassic fish material comprises the two genera *Glaucolepis* and *Boreosomus*. The remaining genera wil be treated in parts II–V.

The genera *Glaucolepis* and *Boreosomus* belong to the families *Palaeoniscidae* s. str. Aldinger and *Acrolepidae* Aldinger respectively, which are two of the many new families among which Aldinger in 1937 distributed a large number of the genera previously commonly comprised in the family *Palaeoniscidae* s. l. In the pages to follow I shall, like Aldinger, use the collective term *Palaeonisciformes* for all these new families

– ? –	*Anodontophora* beds	*A. fassaensis*		
		Myalina kochi	Stegocephalian-horizon	*Glaucolepis* sp. (one specimen)
		A. breviformis		
Gyronitan	*Proptychites* beds	*Proptychites rosenkrantzi*	Fish-zone V	*Glaucolepis magna* (common) *Glaucolepis stensiöi* (common) *Boreosomus piveteaui* (common)
	Vishnuites beds	*Ophiceras dubium*	Fish-zone IV	*Glaucolepis aldingeri* (one specimen) *Glaucolepis* sp. (five specimens) *Boreosomus piveteaui* (one specimen)
		Vishnuites decipiens and *Ophiceras ultimum*		
		Vishnuites decipiens and *Ophiceras kilenense*	Fish-zone III	*Glaucolepis gunnari* (common) *Glaucolepis* sp. (a few specimens) *Boreosomus piveteaui* (three specimens)
Otoceratan	*Ophiceras* beds	*Ophiceras commune* and *Ophiceras subsakuntala*	Fish-zone II	*Glaucolepis arctica* (common) *Glaucolepis aldingeri* (rare) *Glaucolepis gunnari* (three specimens, possibly slid down from Zone III) *Glaucolepis* sp. *Boreosomus piveteaui* (common)
		Ophiceras praecursor and *Glyptophiceras serpentinum*		
	Glyptophiceras beds	*Glyptophiceras minor*		
		Glyptophiceras triviale	Fish-zone I	

and for the genera within the family *Palaeoniscidae* s. l. which have not yet been grouped into new families.

To the *Palaeonisciformes* belong more than eighty genera, among others the earliest and most primitive Actinopterygians known; however, an exhaustive description of even one of all these genera is not available in the literature.

The neural endocranium of some few forms has been described in fair detail, while in others parts of the visceral skeleton have been described, and in others again observations have been made on the axial and fin skeletons. The exoskeleton of the head is fairly well known in some forms, and the same applies to the shape of the trunk and to the squamation, but the structure of the scales is the only character which can be regarded as really thoroughly investigated in more than a small number of genera (after Aldinger's large work (1937)).

In order to find out the relationship between the various families within the *Palaeonisciformes,* and between the *Palaeonisciformes* and the higher Actinopterygians, a thorough knowledge of at least one genus, preferably of all the genera, of each family within the *Palaeonisciformes* is required.

The present work is meant as a first step towards the fulfilment of this requirement. The anatomy of the genera *Glaucolepis* and *Boreosomus* is treated in great detail, and the structures investigated are compared as far as possible with the corresponding structures in other *Palaeonisciformes.* Comparisons are also made with other primitive *Chondrostei* and to a small extent with higher Actinopterygians, but of course no attempt can be made to clear up the relationships of the different Actinopterygian groups on the basis of a single Palaeoniscid and a single Acrolepid. Perhaps when the remaining part of the Eotriassic Actinopterygian material, which in addition to *Palaeonisciformes* contains other *Chondrostei* and some primitive *Holostei,* has been worked up, it will be possible to make such an attempt.

METHODS OF INVESTIGATION

The greater number of the fishes examined occurs in concretions of grey limestone; some few comparatively badly preserved specimens, however, are derived from thin limestone or sandstone beds. I have tried especially to bring home as many concretions as possible in an unopened state, for in the laboratory the preparation can, of course, always be carried out with greater care than in the field.

Only the roughest preparation in the laboratory was done by hammer and fine chisels, while the finer preparation was carried out by means of a special dental mallet or with thin needles. All the detailed preparation was done under a binocular microscope and with a Reichert pointolite lamp or a Leitz Monla lamp as the source of light.

In order to create a contrast between the bones and the rock during preparation or photographing, and to examine sutures and the position of sensory canals and radiation centres, it was necessary in many cases to immerse the object to be examined in alcohol, xylol, or oil of aniseed or at any rate to moisten it with one of these fluids. In such cases in which both the bones and the rocks were light-coloured, colouring of the bone with alizarin has been very helpful (cf. further pp. 15–16).

The grinding method applied in the examination of two specimens will be delt with in a later chapter (p. 15).

GLAUCOLEPIS Stensiö

The genus *Glaucolepis* was erected by Stensiö in 1921 on the basis of material derived from the Triassic beds of Spitsbergen (Stensiö 1921, p. 200), some specimens of which had been mentioned by Stensiö in a previous work under the name *Gyrolepis*? sp. (Stensiö 1918, p. 77).

Stensiö's material, which comprised only one species, *Glaucolepis gyrolepidoides*, was very incomplete; for instance it gave no information of the structure of the head.

In 1932 Stensiö described a species of *Glaucolepis*, *Glaucolepis arctica*, from the Eotriassic of East Greenland (Stensiö 1932, p. 119), and even though the material of this species, too, was very incomplete, it supplied facts which enabled Stensiö to make the generic diagnosis somewhat more complete.

In 1933 White, on the basis of material derived from the Eotriassic of Madagascar, erected the genus *Pteronisculus* with the species *Pteronisculus cicatrosus* and *Pteronisculus macropterus* (White 1933, p.118), and in 1934 Piveteau supplied further information about this genus (Piveteau 1934, p. 88).

After a provisional examination of my material in 1936 I arrived at the result that the genera *Pteronisculus* and *Glaucolepis* were identical (E. Nielsen 1936, p. 36), which was confirmed in a brief note by Piveteau in 1937.

In 1937, after an examination of the squamation, Aldinger gave an extended diagnosis of *Glaucolepis* (Aldinger 1937, p. 234) and in addition (his work having been sent to the press before my paper of 1936 was published) a diagnosis of *Pteronisculus* (Aldinger 1937, p. 237) worked out on the basis of White's and Piveteau's earlier works. It appears from Aldinger's two generic diagnoses that as early as 1937 *Glaucolepis* was one of the best known genera within the group *Palaeonisciformes*.

The East Greenland material of *Glaucolepis* comprises about 200 specimens belonging to five species. There are no significant anatomical differences between these five species. However, the state of preservation of the material available differs so much that certain parts of the anatomical examination could best be made on one, and other parts on other species. In the description I have therefore chosen to treat the five species on parallel lines, so that in each part of the anatomic description that species is first described which shows most distinctly the features treated in that part, and subsequently the corresponding features in the remaining species are dealt with. Not till the material has been dealt with in this way, are the observations gathered into diagnoses for each of the five species.

Description of the Material.

The neural endocranium.

a. Glaucolepis stensiöi.

General remarks. – A head of *Glaucolepis stensiöi* was examined by Sollas's grinding method. The specimen chosen for the grinding was collected in 1932 in Fish-zone V in the locality Pyramiden (E. Nielsen 1935, p. 104). The find consisted of one half of a concretion split by weathering and containing an essential part of the head and body of the fish. In spite of careful search the other half of the concretion was not found. I have chosen this specimen (No. 39) among the considerable *Glaucolepis* material found in the Greenland collections for two reasons. Firstly, the anterior part of the head was complete, which is very rarely the case in the Triassic fishes from Greenland, or in fossil fishes in general. Secondly, the dorsal part of the right half of the head was in such a highly weathered state that it was easily ascertained without preparation that the endocranium was well ossified and not deformed by pressure, and that its cavities and canals were filled with white, opaque calcite (not, as is the case with the greater number of specimens, with transparent calcite crystals), and I therefore assumed that it would be easy to distinguish the bone-laminæ from the rock on the grinding faces.

After being photographed, the head was cemented into hard plaster and ground in the usual way. The grinding was commenced in 1936 and was completed, after several interruptions of the work, in 1940, when the neural endocranium itself had been ground away.

The plane of grinding was placed fairly parallel with the dorsal side of the head so that the right and left halves of each section were made symmetrical as far as possible, and the grinding was carried out from the dorsal towards the ventral part of the endocranium.

Between each of the first 410 grinding faces drawn there is a distance of 25 μ, and between each of the last nineteen the distance is 50 μ. Each of the 429 grinding surfaces was drawn ten times magnified (linear) by means of an Edinger apparatus, and each fortieth face was photographed (Fig. 1).

During the work it soon proved that the delicate bone-laminæ were nevertheless very difficult to distinguish from the surrounding rock, and this rendered the actual drawing process, which (after the first sketching under the Edinger apparatus) was done with the specimen under a binocular microscope and with a pointolite lamp as illumination, a very time-consuming work. After trying several methods to make the bone appear more distinctly without satisfactory result, I attempted, on the advice of Professor Stensiö, to stain the bone with alizarin, and it turned out that this stain-

ing method was perfectly ideal for the purpose. After each grinding a solution of alizarin in alcohol was poured over the surface, which was then washed with pure alcohol when the colouring had exerted its influence. All the fine bone-laminae now stood out intensely red-coloured against the light-coloured rock. The intensity of the staining was proportional to the period during which the colour solution was allowed to act; as a rule half a minute's action was sufficient. It may be mentioned that this method of staining, after this first successful attempt, was tried on material of fishes from different periods, (from Devonian to Cretaceous), and that it was often very useful during preparation and photographing.

On the basis of the series of drawings two models were constructed of the neural endocranium and of the cavity of the endocranium respectively. The subjoined description is based on these two models, though supplemented to some extent from other, more or less well preserved specimens of the species.

The neural endocranium of Specimen No. 39 had a length of 24 mm, a maximum height of 11 mm, and a maximum breadth of 15 mm. As will appear from the figured sections (Fig. 2), the bone-tissue of the endocranium, has a similar macroscopic structure to the bone-tissue found in the genera *Saurichthys*, *Perleidus*, *Broughia*, *Ospia*, *Acropholis*, and others (Stensiö 1921, pp. 152–153; 1925, pp. 14 and 133–134; 1932, pp. 188 and 269; Aldinger 1937, p. 38), its endochondral mass being cancellate and the individual laminae being situated so that they form walls of small, more or less rounded chambers, the medullary spaces, in the fossil crania filled out by calcite. In case of fracture or weathering of such bone-tissue the fracture- or weathering surfaces acquire a characteristic granular appearance, since the bone will most frequently split along the walls of the rounded medullary spaces. The greater part of the surface of the cranial ossifications, both internally towards the cranial cavity and externally, as well as all the canals through the ossifications are lined with laminate perichondral bone. In certain canals for vessels or nerves this surrounding laminate perichondral bone-layer is not essentially thicker than the thin bone walls of the medullary spaces in the endochondral bone-tissue, though in most cases the perichondral bony layer is considerably thicker. Every trace of radiation is lacking. The microstructure of the bone-tissue has not been examined.

The model of the endocranium (Figs. 3–10) shows four ossifications, two of which (see below) are quite small, and in older, more strongly ossified specimens of the species have doubtless been fused with the foremost and the hindmost of the two large ossifications respectively. The anterior and largest of the large ossifications occupies the whole ethmoidal region and the orbito-temporal region as well as the dorsal and lateral parts of the otic region, while the posterior ossification occupies the occipital region and the ventral part of the otic region. Dorsally and laterally the two ossifications are separated by the fissura occipitalis lateralis (*f. occ. lat,* Figs 1, 2, 4, 6, 7, 9, 10, 11,

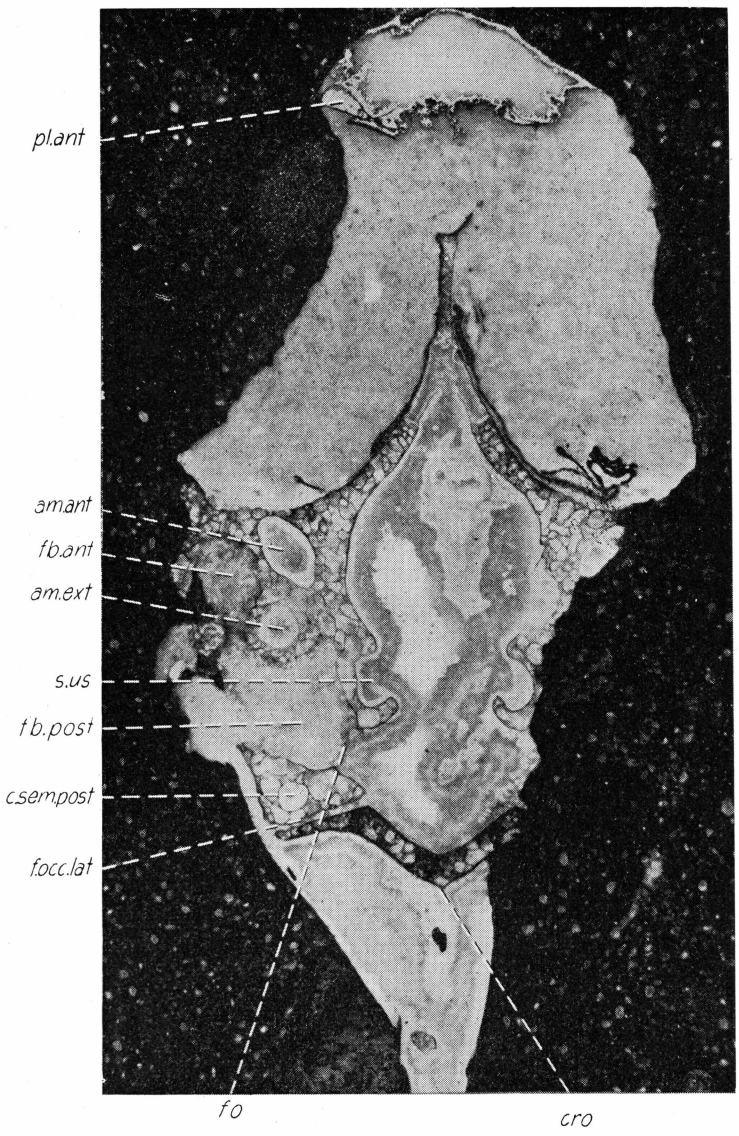


Fig. 1. *Glaucolepis stensiöi* n. sp. Photograph of section No. 120 of a complete grinding series (cf. p. 15). Specimen No. 39. 5 ×.
am. ant, division of the labyrinth cavity for the ampulla anterior; *am. ext*, division of the labyrinth cavity for the ampulla externa; *c. sem. post*, division of the labyrinth cavity for the canalis semicircularis posterior; *cro*, crista occipitalis; *fb. ant*, *fb. post*, anterior and posterior divisions of the fossa bridgei; *fo*, opening in the wall between the fossa bridgei and the cavum cerebrale cranii; *f. occ. lat*, fissura occipitalis lateralis; *pl. ant*, planum antorbitale; *s. us*, division of the labyrinth cavity for the sinus utriculi superior.

12, 47; Pls 1, 2) which farthest dorsally is widened to a posterior dorsal fontanelle (*font*$_2$, Figs 2, 7, 9, 12; Pls 1, 2) In the postero-ventral part of the lateral wall of the endocranium the fissure leaves the boundary line between the aforementioned cranial regions, and runs in a rostral direction to a large fontanelle (the so-called vestibular fontanelle) in the lateral wall of the saccular division of the labyrinth cavity. The walls of the lateral occipital fissure are lined with perichondral laminae nearly throughout, and the fissure was thus, to all appearance, not closed by cartilage in the living animal. As will be explained in more detail below, the ventral part of the vestibular fontanelle was occupied by cartilage in the living animal, while the dorsal part of the opening was probably closed merely by a membrane.

From the antero-ventral corner of the vestibular fontanelle a fissure extends across the basal part of the endocranium to the corresponding part of the vestibular fontanelle of the other side. This transverse fissure, the fissura oticalis ventralis (*f. ot. v,* Figs 4, 6, 7, 9, 10), was probably closed by cartilage in the living animal, for its walls are not lined with perichondral bone. Even in the most strongly ossified endocrania, both of this and of the other species of *Glaucolepis* this ventral fissure is always present. Owing to the above-mentioned fissures and fontanelles, tbe anterior and the posterior large ossification in the fossil endocranium have no contact with each other. Often the two ossifications do no longer occupy their natural mutual position and in a few specimens one of them is completely missing.

A lateral occipital fissure is known in various *Palaeonisciformes* from Kansas (Watson 1925, p. 825) also. According to Watson it extends in an antero-ventral direction from the vagus opening. No doubt this lateral fissure in the Kansas *Palaeonisciformes* is connected dorsally with the posterior dorsal fontanelle of the endocranium, even though this does not appear directly from Watson's figures.

A lateral occipital fissure has further been described in *Perleidus* (Stensiö 1932, p. 190), *Ospia* (Stensiö 1932, p. 231), *Broughia* (Stensiö 1932, p. 270), and *Australosomus* (Piveteau 1934, p.11), and has been observed in the Madagascan species of *Boreosomus* and *Glaucolepis* (Piveteau 1934, pp. 86, 88). In *Broughia*, *Australosomus*, and Watson's Kansas forms the lateral occipital fissure extends in an antero-ventral direction to a considerable vestibular fontanelle, as in *Glaucolepis*. In *Ospia* and *Perleidus*, however, the fissure is shorter and has no connection with the vestibular fontanelle.

Stensiö has pointed out that the lateral occipital fissure represents the broad incisure which occurs between the compound "occipital arch", pila occipitalis, and the otic region in embryonic stages of fishes (Stensiö 1932, p. 190; Goodrich 1930, pp. 244–245).

Occipital region. – The occipital region is comparatively short, but attains a greater height than any other part of the endocranium.

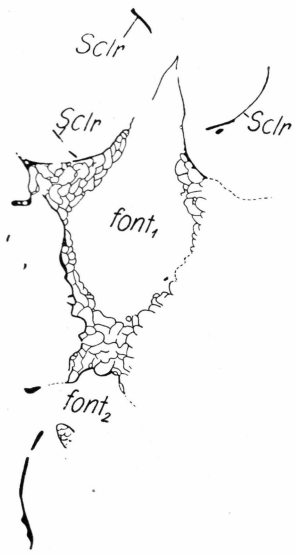
Dorsally, and to a great extent also laterally, this region, as stated above,



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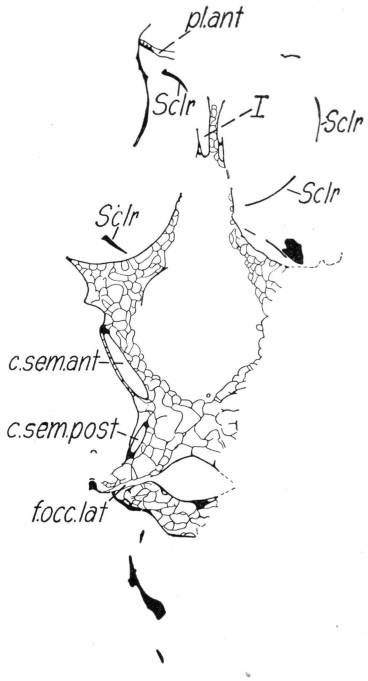
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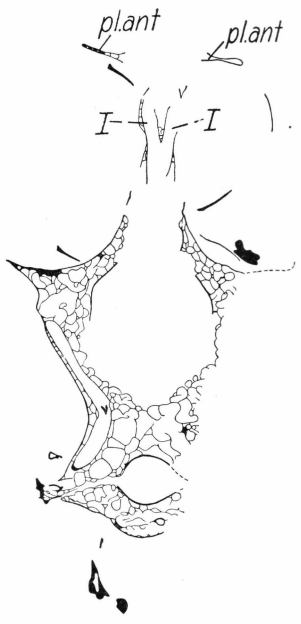
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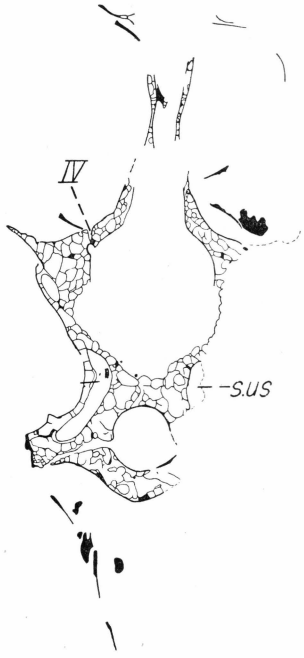
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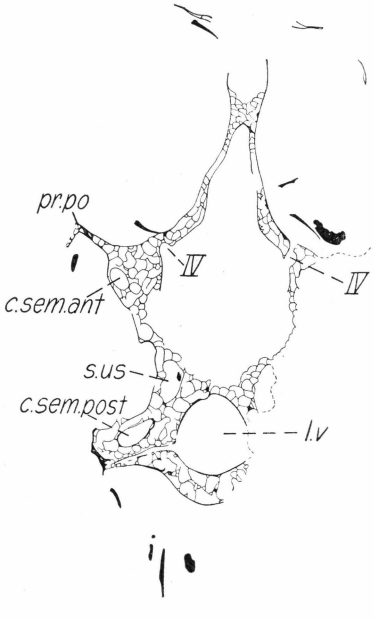
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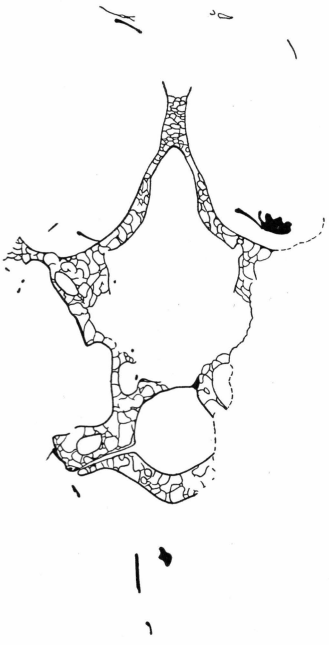
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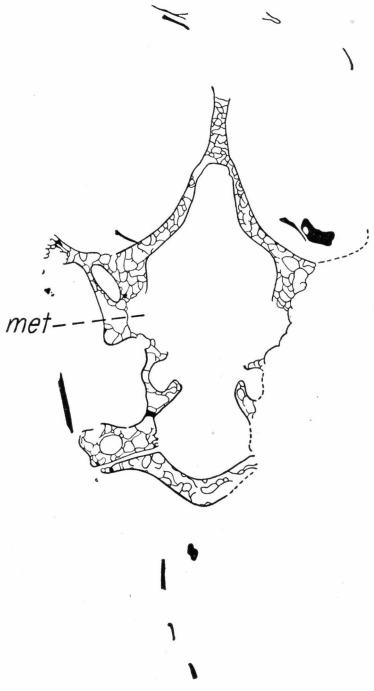
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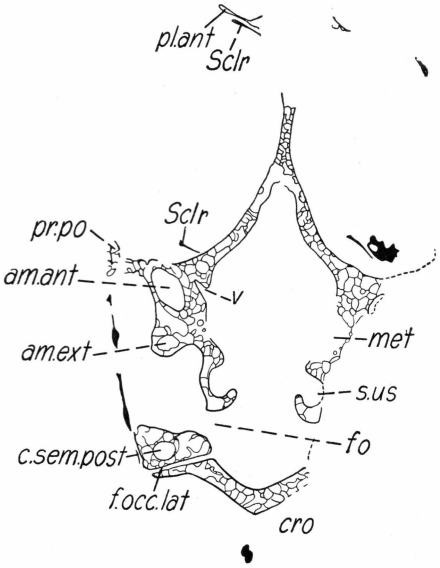
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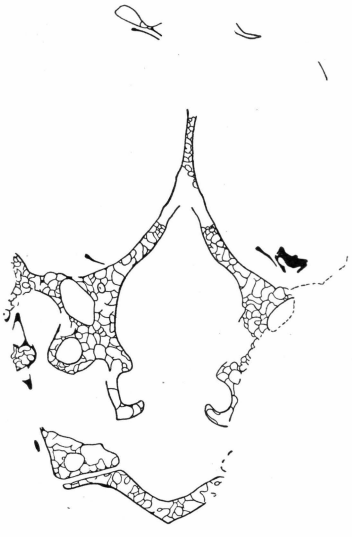
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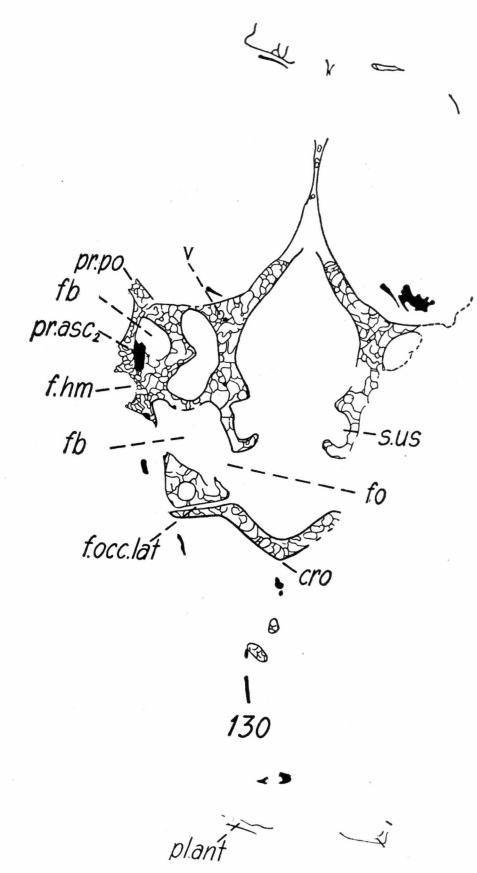
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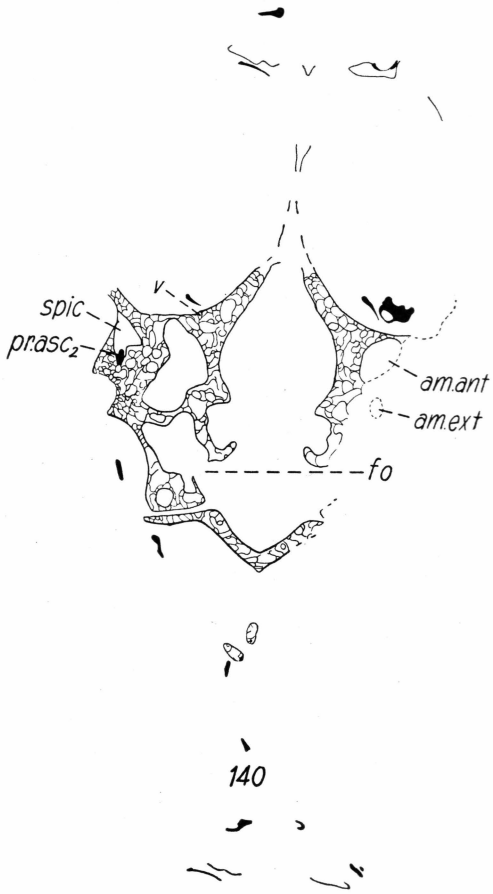
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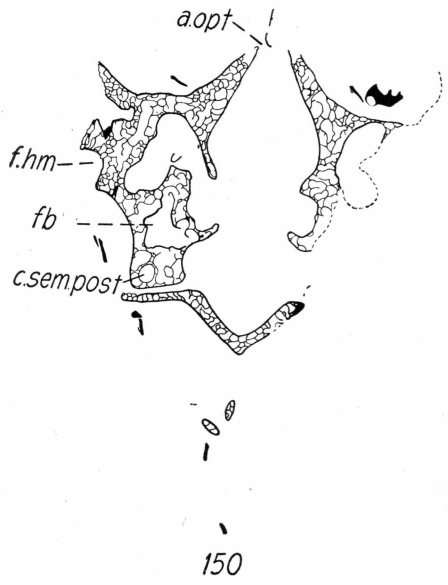


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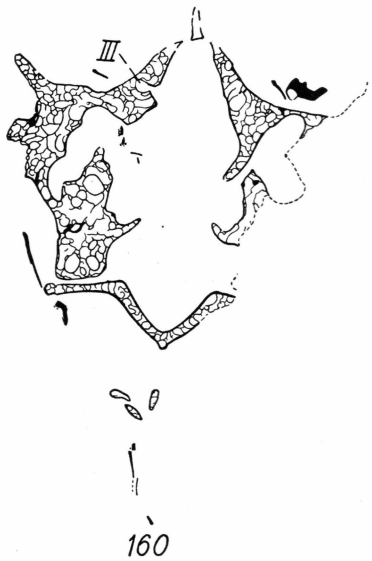


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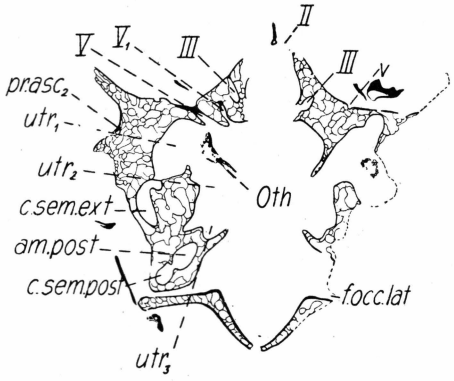
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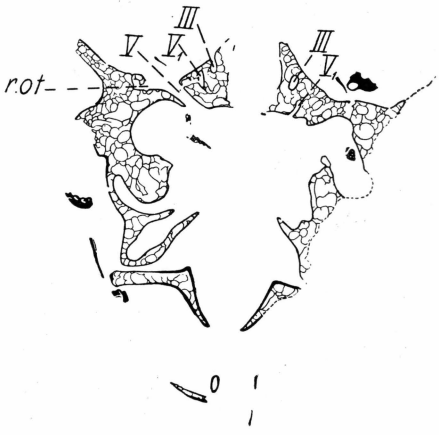
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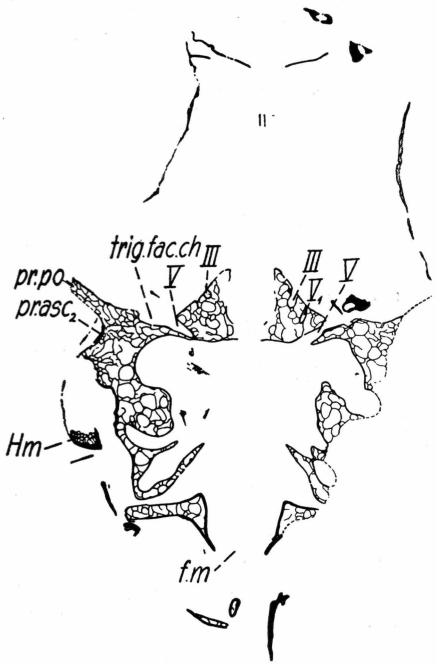
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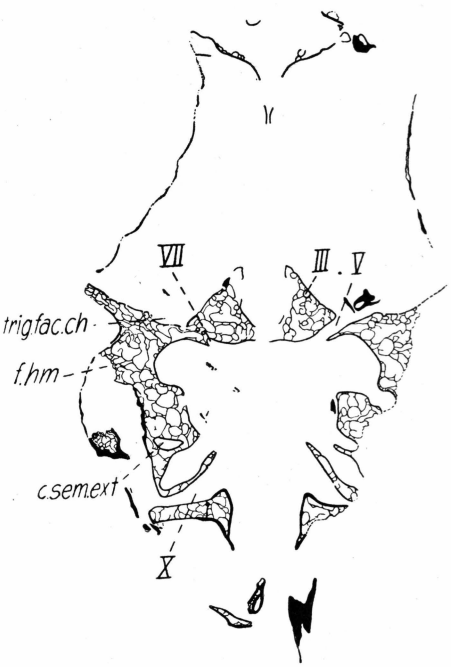
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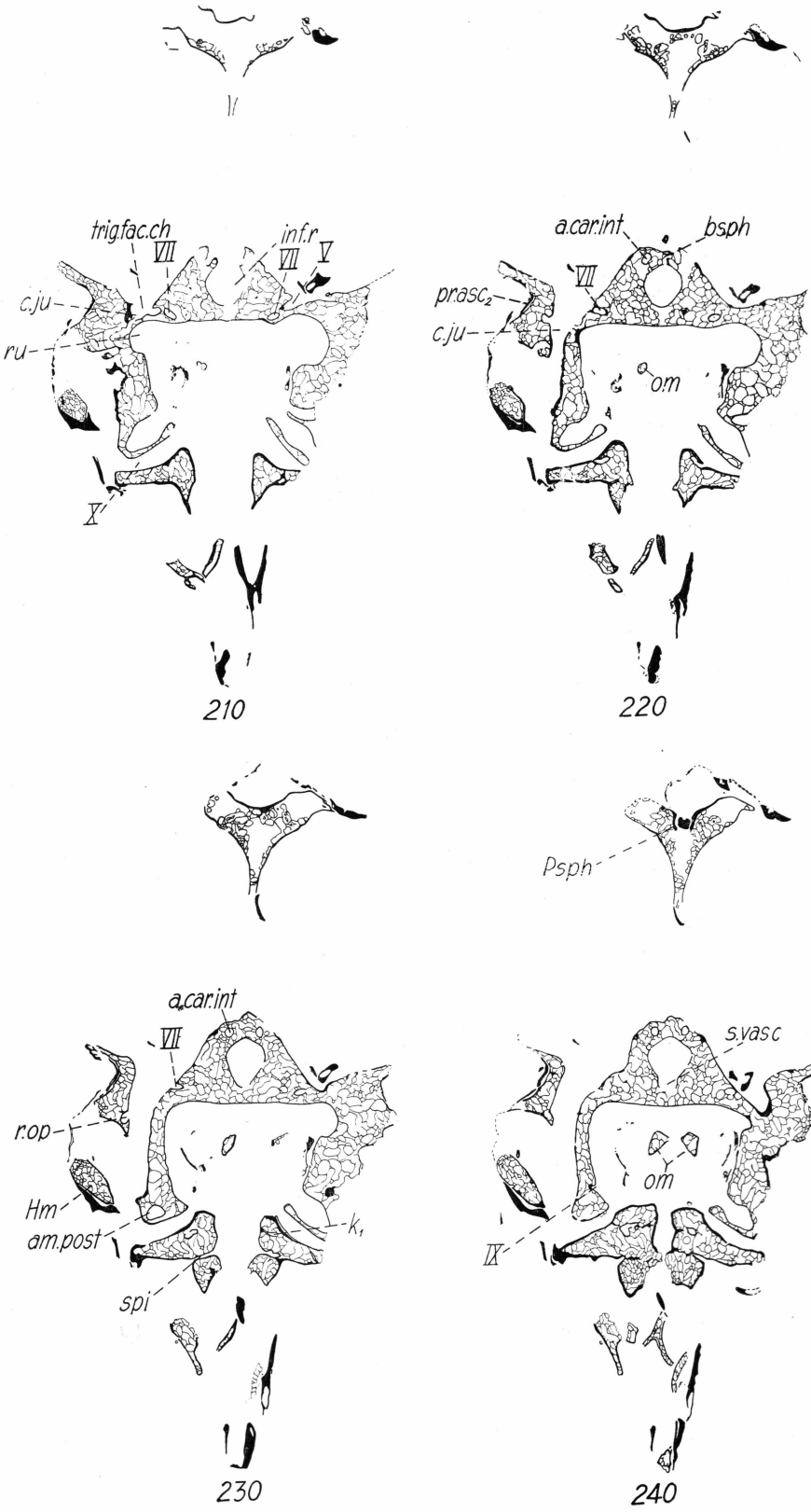
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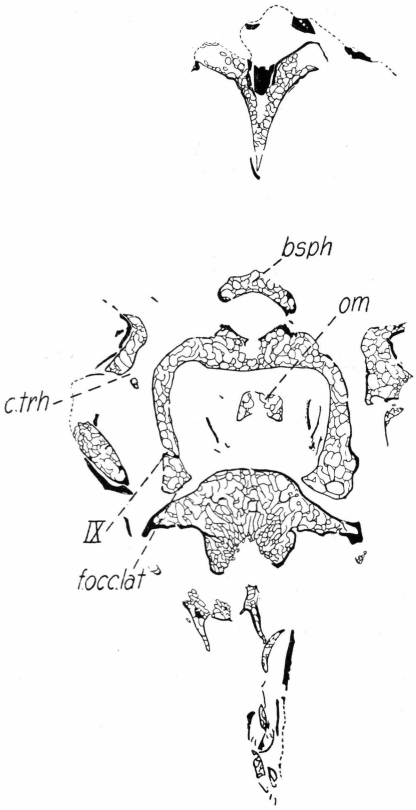


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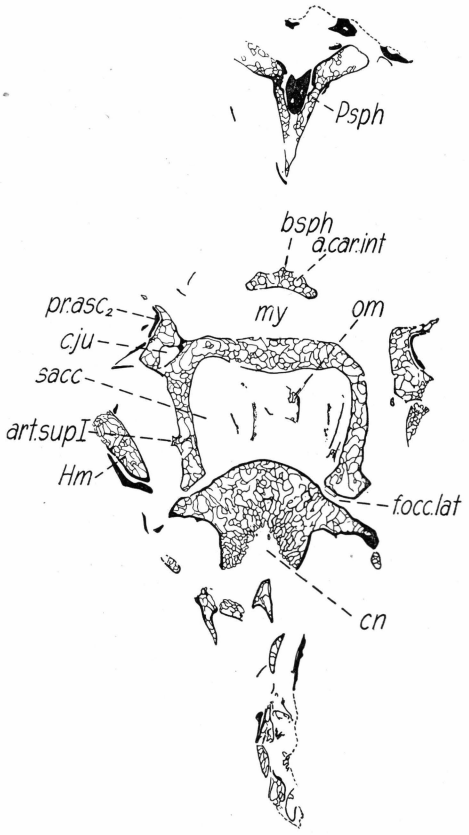


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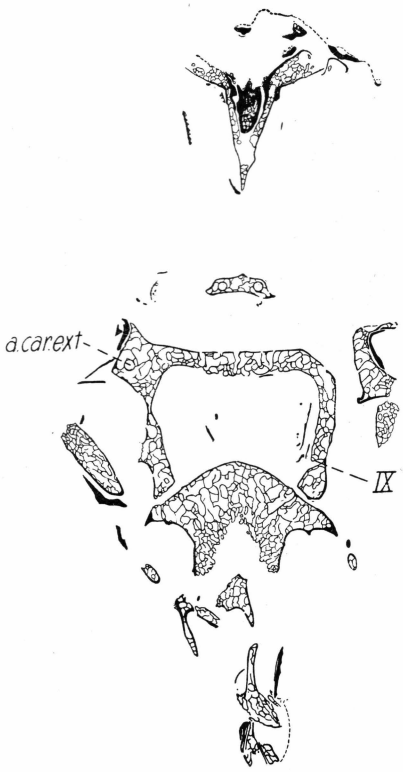

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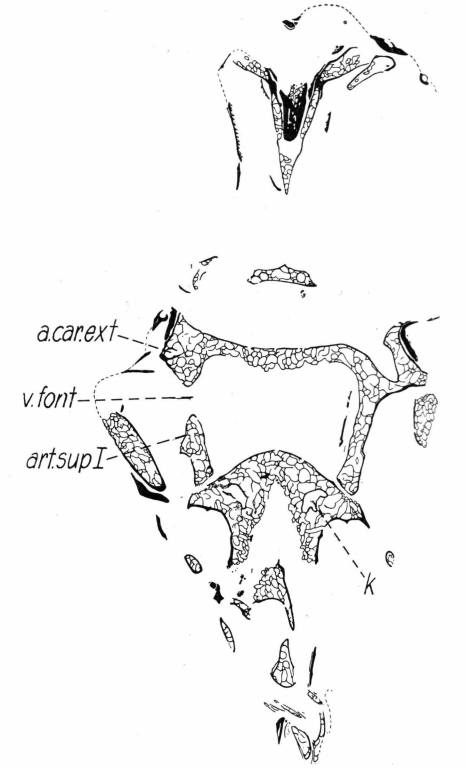
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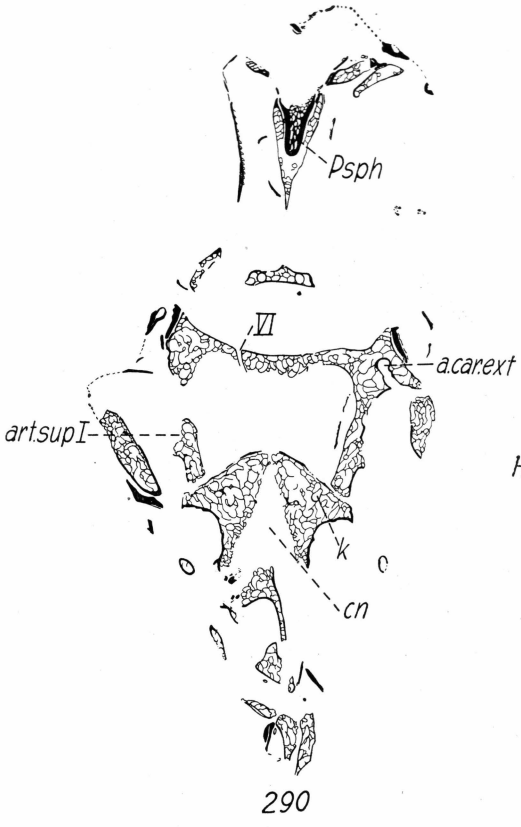
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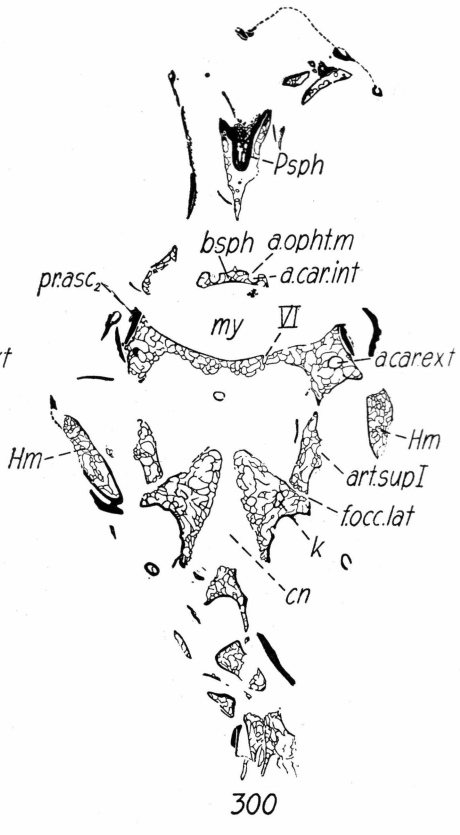
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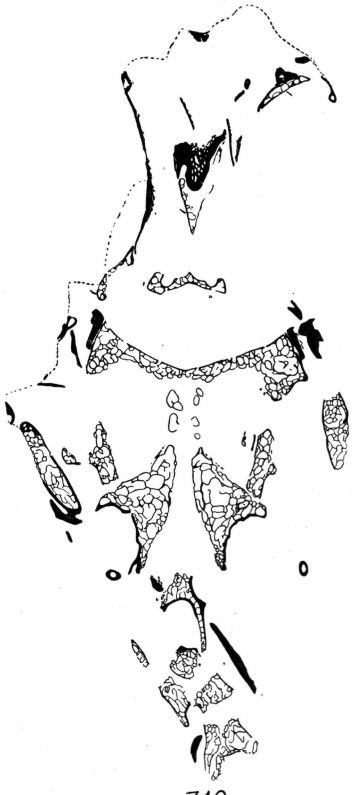
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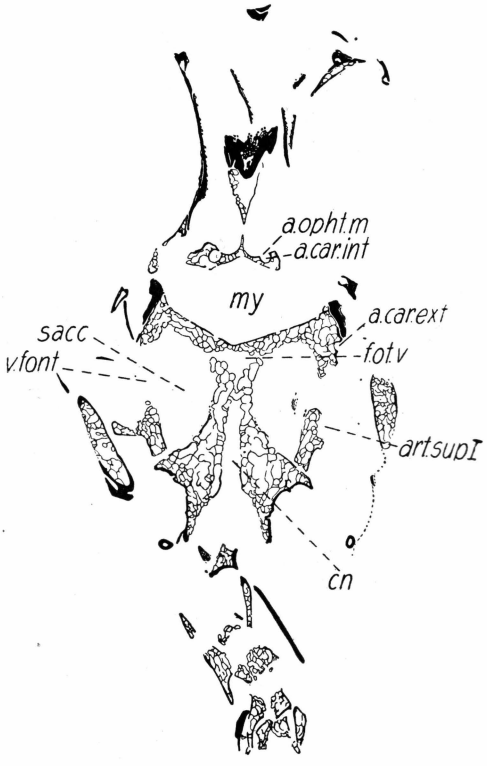
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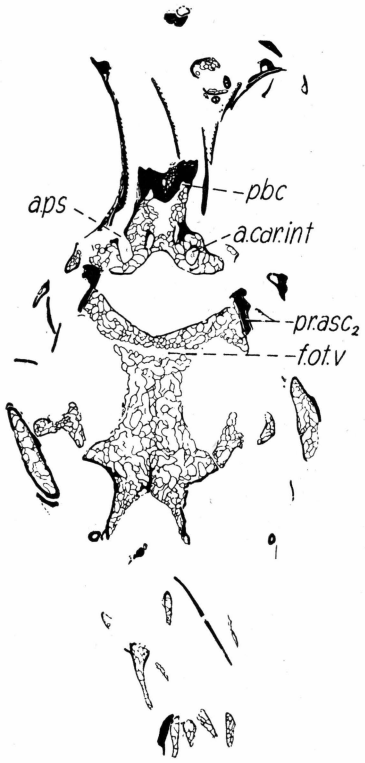
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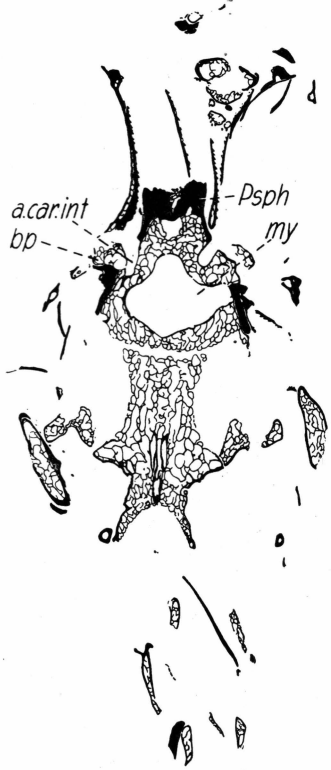
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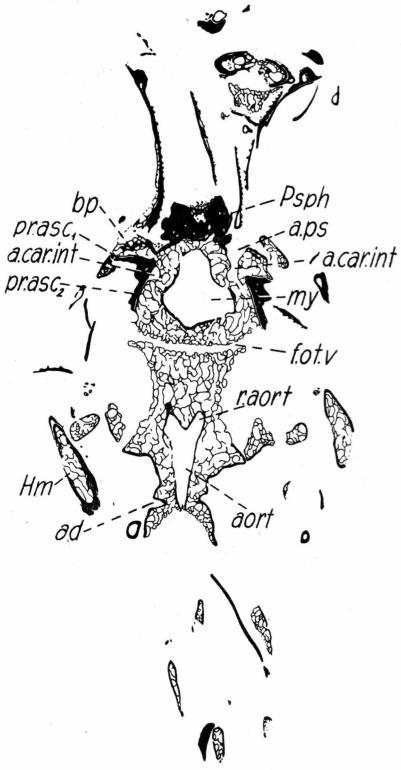
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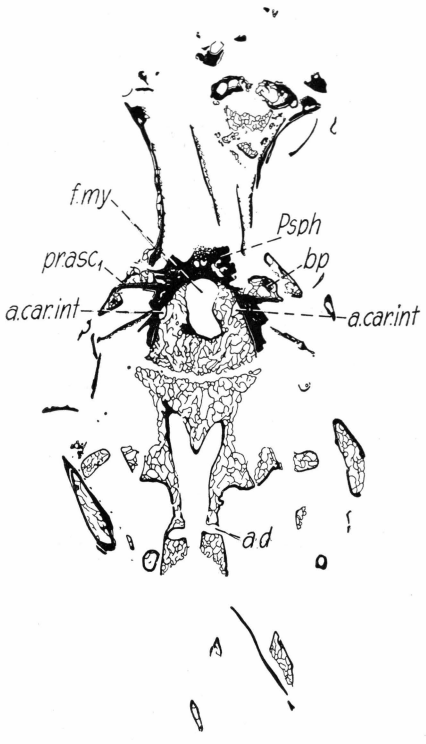
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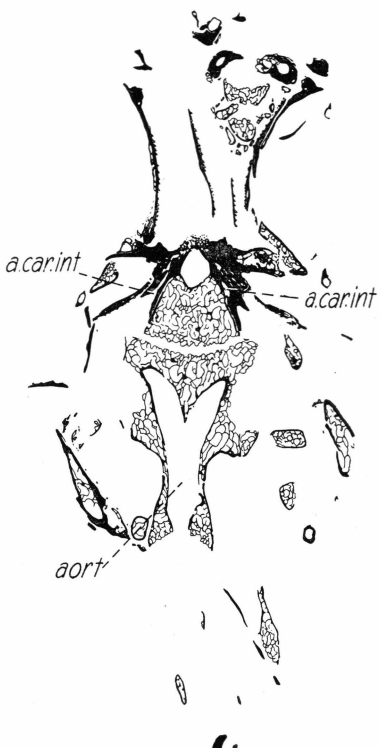
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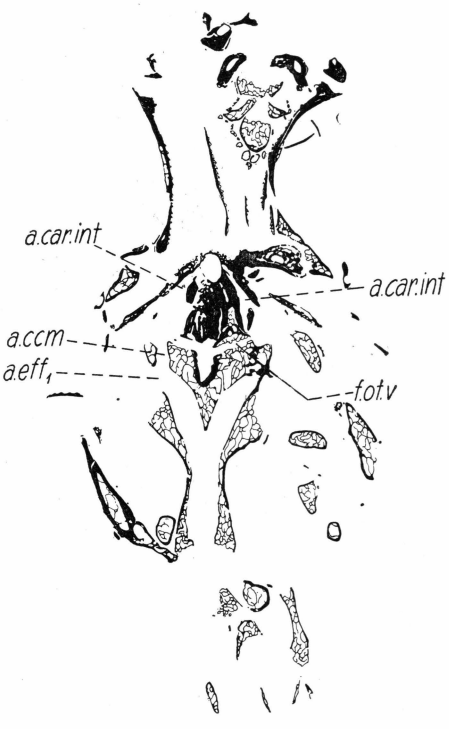
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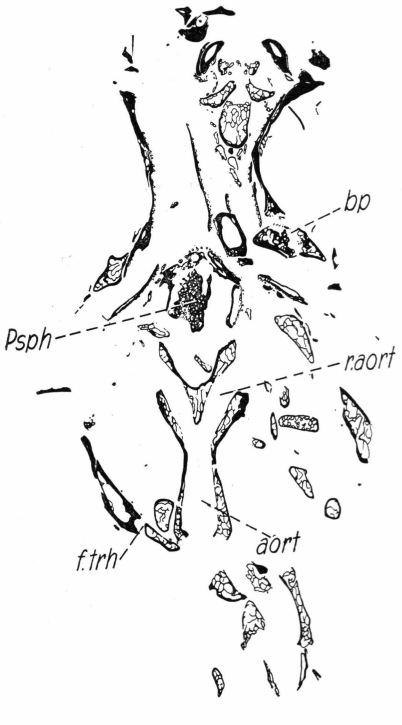
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Fig. 2. *Glaucolepis stensiöi* n. sp. Sections Nos. 10,20, etc. from a complete grinding series (cf. p. 15). Specimen No. 39. 3.3 ×.

a. car. ext, canal for the arteria carotis externa; *a. car. int*, canal for the arteria carotis interna; *a. ccm*, groove for the arteria carotis communis; *ad*, canal for an artery; *a. eff*$_1$, groove for the arteria branchialis efferens I; *am. ant*, *am. ext*, *am. post*, divisions of the labyrinth cavity for the ampulla anterior, the ampulla externa, and the ampulla posterior respectively; *a. opht. m*, opening for the arteria ophthalmica magna; *a. opt*, place of exit for the arteria optica; *aort*, aorta canal; *a. ps*, opening for the arteria pseudobranchialis efferens; *art. sup I*, place of articulation for the suprapharyngobranchial I; *bp*, processus basipterygius; *bsph*, pars basisphenoidea; *c. ju*, jugulo-hyoideomandibular canal; *cn*, space for the notochord; *cro*, crista occipitalis; *c. sem. ant*, *c. sem. ext*, *c. sem. post*, divisions of the labyrinth cavity for the canalis semicircularis anterior, the canalis semicircularis externus, and the canalis semicircularis posterior respectively; *c. trh*, place of exit for the truncus hyoideomandibularis; *fb*, deepest anterior and posterior divisions of the fossa bridgei; *f. hm*, articular fossa for the hyomandibula; *f. m*, foramen magnum; *f. my*, fenestra ventralis myodomus; *fo*, opening in the wall between the fossa bridgei and the cavum cerebrale cranii; *f. occ. lat*, fissura occipitalis lateralis; *font*$_1$, *font*$_2$, anterior and posterior dorsal fontanelles; *f. ot. v*, fissura oticalis ventralis; *f. trh*, canal for the truncus hyoideomandibularis; *inf. r*, infundibular recess; *k*, canal possibly for a vessel; *k*$_1$, canal from the cavum cerebrale cranii to the fissura occipitalis lateralis; *l. v*, division of the cavum cerebrale cranii for the "lobi vagi"; *met*, division of the cavum cerebrale cranii for the lateral part of the metencephalon; *my*, posterior myodome; *om*, separate ossification in the ventral wall of the otic region; *pbc*, canal for the ramus palatinus facialis and for a small branch of the arteria carotis interna; *pl. ant*, planum antorbitale; *pr. asc*$_1$, *pr. asc*$_2$, processus ascendens anterior and processus ascendens posterior of the parasphenoid; *pr. po*, processus postorbitalis; *r. aort*, groove for the aorta-root; *r. op*, place of exit for the ramus opercularis facialis; *r. ot*, canal for the ramus oticus lateralis; *ru*, division of the labyrinth cavity for the recessus utriculi; *sacc*, division of the labyrinth cavity for the sacculus; *spi*, canal for a spino-occipital nerve; *spic*, spiracular canal; *s. us*, division of the labyrinth cavity for the sinus utriculi superior; *s. vasc*, space for the saccus vasculosus; *trig. fac. ch*, trigemino-facialis chamber; *utr* $_1$, *utr* $_2$, *utr* $_3$, divisions of the labyrinth cavity for the prae-, supra-, and postsaccular parts of the utriculus respectively; *v*, canal for a (?) vessel; *v. font*, vestibular fontanelle; *Hm*, hyomandibula; *Oth*, remains of the otolith; *Psph*, parasphenoid; *Sclr*, sclerotic ring; *I*, groove for the nervus olfactorius; *III*, canal for the nervus oculomotorius; *IV*, canal for the nervus trochlearis; *V*, trigeminus canal; *V*$_1$, canal for the nervus ophthalmicus profundus; *VI*, canal for the nervus abducens; *VII*, facialis canal; *IX*, canal for the nervus glossopharyngeus; *X*, canal for the nervus vagus.

is distinctly separated from the otic region, partly by the posterior dorsal fontanelle, partly by the narrower part of the lateral occipital fissure. Ventrally and ventro-laterally the transition between the two regions is quite gradual.

Following Stensiö's description of *Perleidus* and *Ospia* (Stensiö 1932) the occipital region of *Glaucolepis* can be divided into an anterior and a posterior division, even though the boundary between these two divisions can in no way be said to be distinct.

The posterior division is a relatively narrow part of the endocranium, which attains only about two-thirds of the heigth of the anterior division.

On the posterior division we may for descriptive reasons distinguish between a caudal and a paired lateral face.

The caudal face is almost elliptical in outline, the long axis of the ellipse being vertical, and almost twice the length of the short axis. The shape of the caudal surface appears from Fig. 3. The surface is pierced by three large openings which together occupy nearly its whole area.

The more dorsal of these openings is the foramen magnum (*f. m*, Figs. 2, 3, 5, 9), whose width is somewhat greater than its height, and whose detailed shape will appear from Fig. 3.

Immediately ventrally to the foramen magnum lies the second and even larger opening (see Fig. 3), which leads to a large cavity (*cn*, Figs. 2, 3, 5, 7, 9), extending through the whole occipital region and, as will be seen later, through the greater part of the otic region. In the hindmost part of the occipital region the longitudinal axis of this cavity runs in an anterior and at the same time slightly dorsal direction; however, in front of the transition from the posterior to the anterior part of the occipital region the axis changes gradually to an antero-ventral direction. In the occipital region the transverse section of the cavity is elliptical, the long axis of the ellipse being vertical. In the posterior part of the occipital region the width of the cavity decreases rapidly in an anterior direction; while in front of the above-mentioned bend of the longitudinal axis of the cavity the width decreases much more slowly in an anterior direction. In the living animal the anterior part of the notochord was lodged in this cavity; but no doubt the diameter of the notochord was at any rate somewhat smaller than that of the cavity, since the walls of the cavity lack perichondral bone-layers and therefore were doubtless lined by cartilage. The bend of the notochordal space shows some agreement with the bend of the notochord known from the earliest embryonic stages of *Amia* and *Lepidosteus* (Hammarberg 1937, p. 212, Fig. 1).

The third and most ventral of the openings piercing the caudal face has a rounded elliptical outline, the long axis of the ellipse being horizontal. This opening leads inward to an unpaired aorta canal (*aort*, Figs. 2, 3, 9), which extends in an anterior direction through the most basal part of the occipital region, dividing closely behind the transition to the otic region into a right and a left branch. In the foremost and largest part of the unpaired

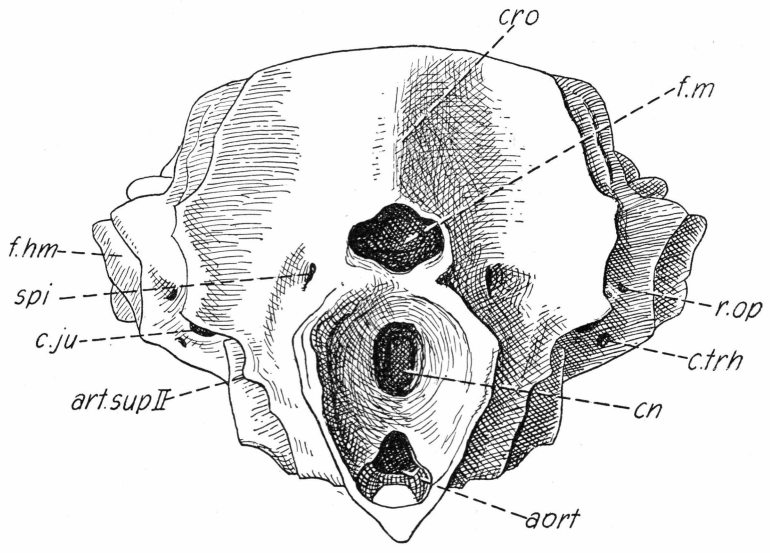


Fig. 3. *Glaucolepis stensiöi* n. sp. Neural endocranium in posterior view. On the basis of a wax model. 6–7 ×.

aort, posterior opening of the aorta canal; *art. sup II*, place of articulation for the suprapharyngobranchial II; *c. ju*, posterior opening of the jugulo-hyoideomandibular canal for the vena jugularis; *cn*, space for the notochord; *cro*, crista occipitalis; *c. trh*, posterior opening of the jugulo-hyoideomandibular canal for the truncus hyoideomandibularis; *f. hm*, articular fossa for the hyomandibula; f. m, foramen magnum; *r. op*, posterior opening of the jugulo-hyoideomandibular canal for the ramus opercularis facialis; *spi*, canal for a spino-occipital nerve.

aorta canal the vertical diameter is longer than the horizontal, while in the extreme hindmost part of the canal the horizontal diameter increases in length in relation to the vertical diameter, so that the posterior opening of the canal obtains the outline mentioned above.

As may be seen from Figs. 3 and 9, the three large openings on the caudal face are not so completely separated from each other as might perhaps be gathered from the above description. The fact is that that part of the hindmost division of the occipital ossification which forms the lower boundary of the foramen magnum, and at the same time the upper boundary of the opening of the notochordal space, has a deep notch in its posterior margin, so that in other words, the posterior margin of the partition wall between the two openings is very concave. The same applies, and to an even greater extent, to the posterior margin of the partition wall between the posterior openings of the notochordal space and the aorta canal.

To all appearance the notches in these partition walls were filled with cartilage in the living animal.

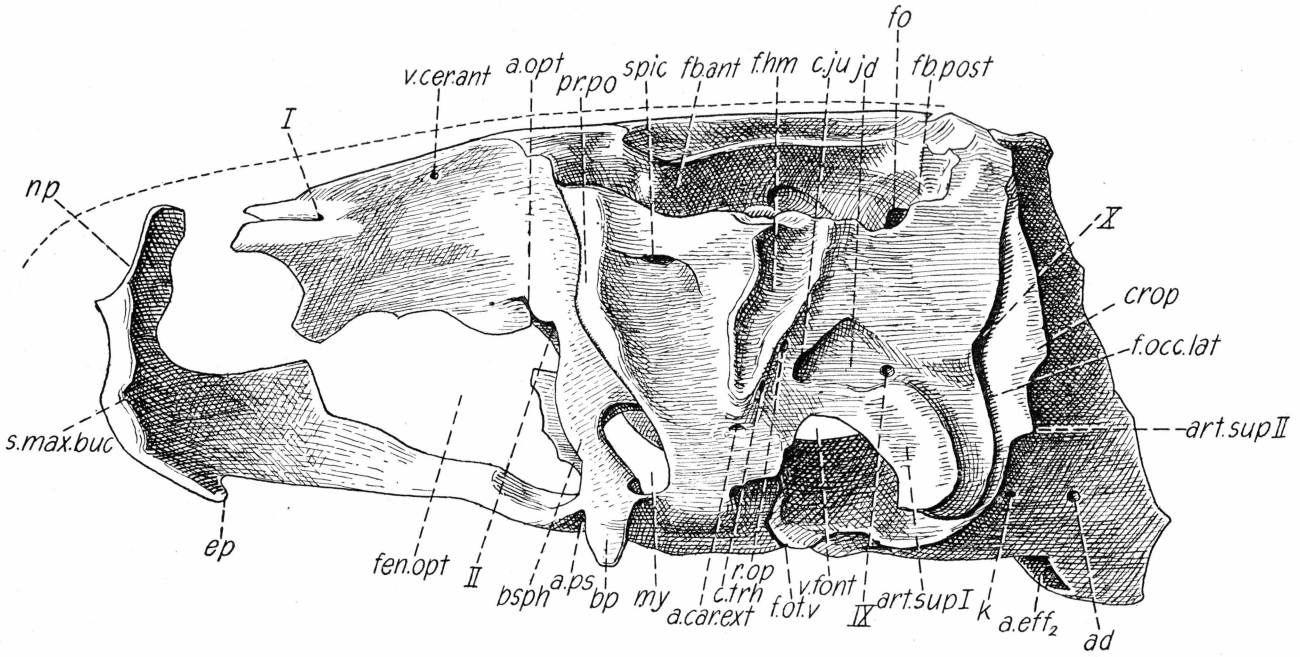


Fig. 4. *Glaucolepis stensiöi* n. sp. Neural endocranium in lateral view. On the basis of a wax model. 6–7 ×.
a. car. ext, canal for the arteria carotis externa; *ad*, canal for an artery; *a. eff*$_2$, canal for the arteria branchialis efferens II; *a. opt*, place of exit for the arteria optica; *a. ps*, opening for the arteria pseudobranchialis efferens; *art. sup I*, place of articulation for the suprapharyngobranchial I; *art. sup II*, place of articulation for the suprapharyngobranchial II; *bp*, processus basipterygius; *bsph*, pars basisphenoidea; *c. ju*, posterior opening of the jugulo-hyoideomandibular canal for the vena jugularis; *c. trh*, posterior opening of the jugulo-hyoideomandibular canal for the truncus hyoideomandibularis; *crop*, processus cranio-spinalis; *ep*, articular process for the pars autopalatina; *fb. ant*, *fb. post*, anterior and posterior divisions of the fossa bridgei; *fen. opt*, fenestra optica; *f. hm*, articular fossa for the hyomandibula; *fo*, opening in the wall between the fossa bridgei and the cavum cerebrale cranii; *f. occ. lat*, fissura occipitalis lateralis; *f. ot. v*, fissura oticalis ventralis; *jd*, jugular depression; *k*, canal possibly for a vessel; *my*, posterior myodome; *np*, nasal pit; *pr. po*, processus postorbitalis; *r. op*, posterior opening of the jugulo-hyoideomandibular canal for the ramus opercularis facialis; *s. max. buc*, notch for the ramus maxillaris trigemini, the nervus buccalis lateralis, and vessels; *spic*, spiracular canal; *v. cer. ant*, canal for the vena cerebralis anterior; *v. font*, vestibular fontanelle; *I*, opening for the nervus olfactorius; *II*, place of exit for the nervi optici; *IX*, canal for the nervus glossopharyngeus; *X*, canal for the nervus vagus.

The paired lateral face of the posterior division of the occipital region is roughly triangular in outline, being narrowest most dorsally, where it meets with the corresponding face of the opposite side immediately dorsally to the dorsal end of the caudal face, and broadest in its ventral part. The lateral face is convex in a dorso-ventral direction, while it is almost plane in a rostro-caudal direction.

Three small foramina are found on this face. The most dorsal one is situated almost at the boundary between the posterior and the anterior divisions of the occipital region and on a level with the floor of the cranial cavity of this region. This foramen (*spi*, Figs. 2, 3) is twice as high as broad, and is the opening of a canal which runs in a medial and very slightly anterior direction to the cavum cerebrale cranii; the internal opening (*spi*, Figs. 5, 9) is a little higher than broad. This canal can only have contained a spino-occipital nerve. Other canals for spino-occipital nerves are not found. The other two foramina on the lateral face of the posterior division of the occipital region are both situated on a level with the lowermost part of the wide caudal opening of the notochordal space.

The most posterior of these foramina (*ad*, Figs. 2, 4, 6, 10, 11, 47) is fairly large and has a rounded outline. It is the external opening of a short canal, which extends in an antero-medio-ventral direction to the aorta canal.

A similar foramen is described in the Kansas forms A and B (Watson 1925, p. 835, Figs. 10, 11, 14, 15, 20; 1928, Figs. 5 and 6; Case 1938, Pl.1) *Perleidus* (Stensiö 1932, p. 190, Figs. 59 A and C, and 60), *Broughia* (Stensiö 1932, p. 229, Fig. 73 A), and *Australosomus* (Piveteau 1934, p. 12, Figs. 6 and 7), and in all these forms it has been interpreted as the canal opening for an efferent branchial artery. (branchial artery No. 4, according to Watson, Stensiö (*Perleidus*), and Piveteau (*Australosomus*)).

It is obvious that we are here concerned with a canal for an artery; however, on account of its direction, its small diameter, and its position in relation to the dorsal elements of the fourth branchial arch (see below) I am inclined to assume that it contained no efferent branchial artery, but more probably a small artery which issued from that part of the aorta which lay between the places whence the second and the third efferent branchial arteries branched off.

The third foramen (k, Figs. 4, 6, 11, 47), which is quite small, is situated slightly anteriorly to the last-mentioned one, and is the opening of a short canal (*k*, Fig. 2) which runs in a dorsal direction into the wall of the occipital region. In the wax model this canal extends some way into the cancellate bone mass of the wall, but then ends blindly, or at any rate is indistinguishable in the drawings of the sections from the medullary spaces of the cancellate bone tissue.

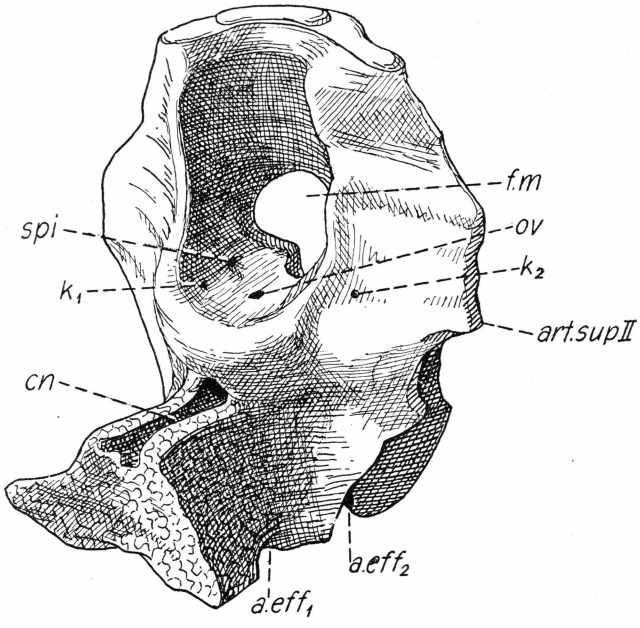


Fig. 5. *Glaucolepis stensiöi* n. sp. Posterior ossification of the neural endocranium in antero-dorso-lateral view. Faces devoid of perichondral bone reticulated. On the basis of a wax model. 6–7 ×.

a. eff$_1$, groove for the arteria branchialis efferens I; *a. eff*$_2$, canal for the arteria branchialis efferens II; *art. sup II*, place of articulation for the suprapharyngobranchial II; *cn*, space for the notochord; *f. m*, foramen magnum; k_1, k_2, openings of a canal from the cavum cerebrale cranii to the fissura occipitalis lateralis; *ov*, median depression in the floor of the cavum cerebrale cranii; *spi*, canal for a spino-occipital nerve.

More dorsally in the thick lateral wall of the occipital region there is a more or less distinct canal, which opens dorsally into a canal running from the cavum cerebrale cranii to the fissura occipitalis lateralis. From its dorsal opening the canal passes in a ventral direction, either to end blindly or to become indistinguishable from the medullary spaces of the cancellate bony tissue.

The direction of the two apparently blind canals mentioned above might suggest that they are the two ends of the same canal, and, if so, this canal has probably contained a vessel.

We cannot, or more correctly we need not, speak about an actual ventral face of the posterior division of the occipital region. For we may describe the ventral part of the external face of the region by saying that the most ventral part of the lateral face of the posterior division of the occipital region meets with the corresponding face of the opposite side at an acute angle, so that in this way a short median longitudinal keel is formed on the outer

side of that part of the endocranium which constitutes the ventral boundary of the aorta canal (Fig. 6).

Immediately anteriorly to this longitudinal keel there is a large unpaired opening (*a. eff*$_2$, Figs. 4, 6, 9, 10, 11), nearly rectangular in outline, the longitudinal axis of the opening being twice as long as the transverse axis. This opening leads to the aorta canal, and the arteria branchialis efferens II no doubt reached the aorta through it. (In *Glaucolepis magna* the corresponding opening (*a. eff*$_2$, Pl. 5, Figs. 1, 2; Pl. 6, Fig. 3) is divided by a quite narrow bone bridge into a right and a left half).

It is only anteriorly to this opening that the occipital region has an actual ventral face, the greater part of which, at any rate, according to our rather artificial subdivision of the region, must be referred to the anterior division of the occipital region and will therefore be described below.

As stated above, the anterior division of the occipital region is considerably higher than the posterior. If we consider the endocranium from behind, as in Fig. 3, the anterior division is broadly octagonal in outline, with a dorsal, a paired dorso-lateral, a paired lateral, a paired ventro-lateral, and a ventral margin.

This part of the endocranium attains its greatest width almost on a level with the foramen magnum. It presents the following external faces: a dorsal, a paired caudal, a paired lateral, and a ventral one.

The dorsal face lies on a level very slightly lower than that of the dorsal face of the otic region, and is slightly convex from side to side. The anterior margin of the dorsal face forms the posterior limit of the hindmost of the two unpaired dorsal fontanelles in the roof of the endocranium (*font*$_2$, Figs. 2, 7, 9, 12; Pls. 1, 2) and, laterally to this fontanelle, the hindmost limit of the narrow dorsal part of the lateral occipital fissure. The shape of the dorsal face is seen in Fig. 7.

Between the dorsal face and the dorsal margin of the foramen magnum there runs a prominent median crista occipitalis (*cro*, Figs. 1, 2, 3), which forms the boundary line between the dorsal parts of the right and the left caudal face of the anterior division of the occipital region. Farther ventrally these two faces are separated by the lower posterior division of the occipital region. Laterally to the crista occipitalis each of the two caudal faces shows a considerable concavity, which represents the area where the anterior part of the trunk musculature has been inserted on the cranium. No part of the trunk musculature has been inserted on any part of the endocranium, which lies anteriorly to the paired caudal face of the anterior division of the occipital region. For further details of the shape and extension of this caudal face, whose ventral part passes evenly into the lateral face of the posterior division of the occipital region, the reader is referred to Fig. 3.

The lateral face of the anterior division of the occipital region has a very

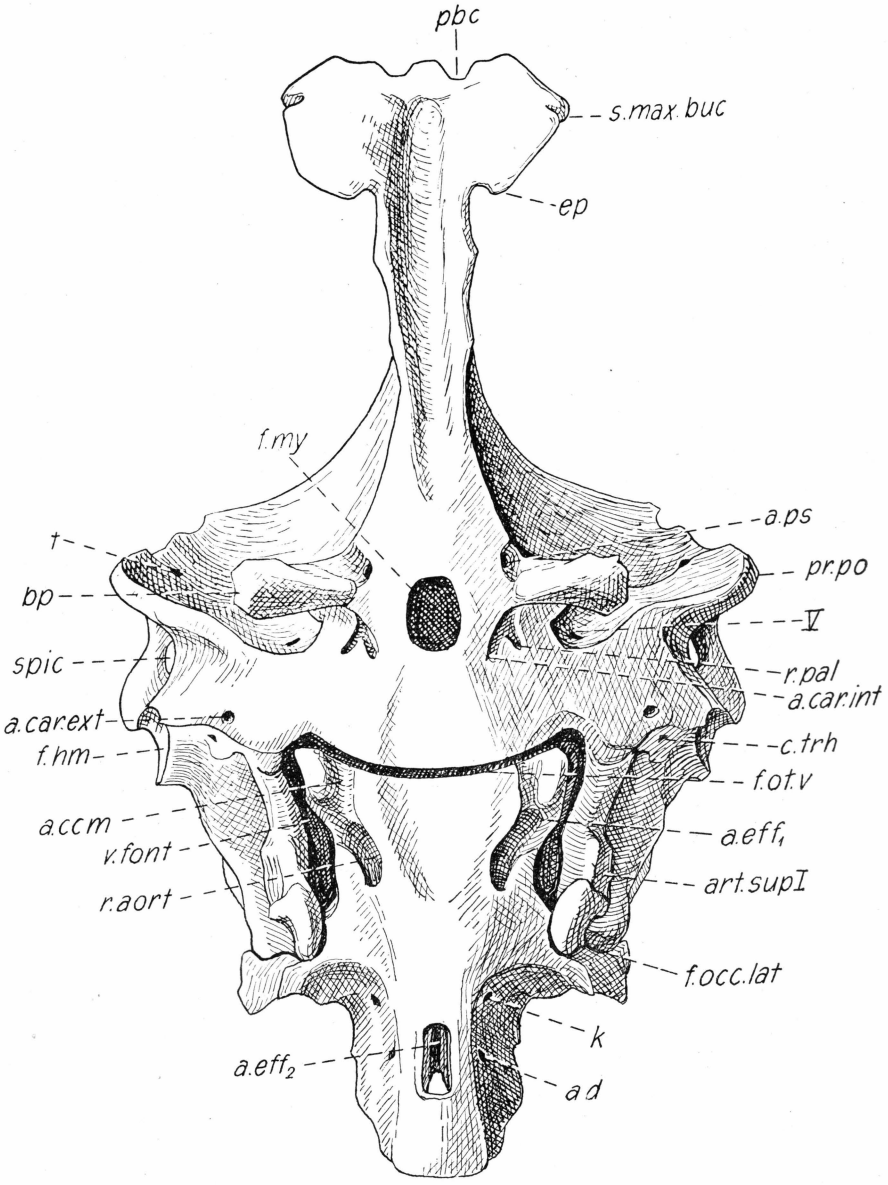


Fig. 6. *Glaucolepis stensiöi* n. sp. Neural endocranium in ventral view. On the basis of a wax model. 6–7 ×.

a. car. ext, canal for the arteria carotis externa; *a. car. int*, groove for the arteria carotis interna; *a. ccm*, groove for the arteria carotis communis; *ad*, canal for an artery; *a.eff*$_1$, groove for the arteria branchialis efferens I; *a. eff*$_2$, canal for the arteria branchialis efferens II; *a. ps*, opening for the arteria pseudobranchialis efferens; *art. sup I*, place of articulation for the suprapharyngobranchial I; *bp*, processus basipterygius; *c. trh*, posterior opening of the jugulo-hyoideomandibular canal for the truncus hyoideomandibularis; *ep*, articular process for the pars autopalatina; *f. hm*, articular fossa for the hyomandibula; *f. my*, fenestra ventralis myodomus; *f. occ. lat*, fissura occipitalis lateralis; *f. ot. v*, fissura oticalis ventralis; *k*, canal possibly for a vessel; *pbc*, groove for the ramus palatinus facialis and vessels; *pr. po*, processus postorbitalis; *r. aort*, groove for the aorta-root; *r. pal*, canal and groove for the ramus palatinus facialis; *s. max. buc*, notch for the ramus maxillaris trigemini, the nervus buccalis lateralis, and vessels; *spic*, spiracular canal; *t*, canal for a vessel, possibly a vein; *v. font*, vestibular fontanelle; *V*, trigeminus canal.

slight rostro-caudal extent, and is merely a narrow rim behind and parallel with the fissura occipitalis lateralis. This face attains its greatest width almost halfway between its dorsal and its ventral ends, that is to say, in the area that occurs directly posteriorly to the exit of the nervus vagus. Here the posterior margin of the face is produced in a posterior direction into a small process (*crop*, Fig. 4), which probably corresponds to the huge cranio-spinal process in *Saurichthys* and in the sturgeons. (*cf.* p. 87).

The ventral face, whose most caudal part, strictly speaking, belongs to the posterior division of the occipital region (*cf.* p. 36), passes anteriorly without any marked boundary into the ventral face of the otic region. It is slightly convex from side to side.

Viewing the occipital region from the front, which is possible because the posterior part of the fossil endocranium is completely separated from the anterior one, we shall see (Fig. 5), laterally to the cavum cerebrale cranii and to that part of the ossification which surrounds the notochordal space, that face of the hindmost ossification of the endocranium which forms the hind wall of the fissura occipitalis lateralis. This whole face is lined with perichondral bone except in two small areas almost on a level with the central part of the notochordal space. Possibly the lack of perichondral bone in these two areas indicates an incipient closing of that part of the fissure which is entirely closed in *Ospia* and *Perleidus*.

The cavum cerebrale cranii decreases considerably both in height and width in a caudal direction through the occipital region; its floor is concave from side to side, and lies throughout the region on a level with the ventral edge of the foramen magnum. In the floor of the cavum cerebrale cranii there is a median, fairly deep depression (*ov*, Figs. 5, 9), and antero-laterally to this depression a fine canal (k_1, Figs. 2, 5, 15) issues from the cavum cerebrale cranii in a dorso-lateral and at the same time slightly caudal direction through the antero-ventral part of the lateral wall of the cavum cerebrale cranii to that part (on one side of the head) of the fissura occipitalis lateralis which contained the nervus vagus. The place where this canal opens out into the vagus canal (k_2, Fig. 5) lies almost halfway between the internal and the external openings of the vagus canal.

As mentioned above (p. 35) a vertical canal opens out dorsally into the canal running from the cavum cerebrale cranii to the fissura occipitalis lateralis.

The aorta canal narrows somewhat immediately anteriorly to the opening for the arteria branchialis efferens II, and divides very closely behind the transition to the otic region into a right and a left canal (Figs. 6, 9, 14, 15) for the right and the left aorta-root respectively (X, Figs. 2, 4, 11).

The canal for the nervus vagus and the nervus lineae lateralis issues from the cavum cerebrale cranii immediately behind the labyrinth cavity.

As stated above, we are not here concerned with an independent canal, but merely with an extended part of the fissura occipitalis lateralis. The cerebral opening of the canal lies on a level with the most ventral part of the cavum cerebrale cranii in the occipital region. The external opening of the canal is situated postero-laterally to its cerebral opening, and immediately posteriorly to that part of the otic region which contained the ampulla of the canalis semicircularis posterior. However, the vagus canal is not straight, but curved in such a way that its posterior margin is convex and its anterior margin concave.

In transverse section the canal is elliptical, with the long axis of the ellipse pointing obliquely forwards and downwards. On p. 38 above mention has already been made of the narrow canal, whose cerebral opening occurs a short distance behind the cerebral opening of the vagus canal, and which on one side of the wax model leads to the dorsal part of the vagus canal about midway between its external and its internal ends. On the other (right) side of the wax model this narrow canal runs from the cavum cerebrale cranii to the fissura occipitalis lateralis immediately dorsally to the vagus canal.

Possibly this narrow canal, as is the case in *Saurichthys* (Stensiö 1925, pp. 20–21, Fig. 4), contained the vena encephalica posterior, even though in *Glaucolepis* the internal opening of the canal is situated much more ventrally in relation to the vagus canal than in *Saurichthys*.

In some cases in *Saurichthys* a special canal seems to exist for a dorsal branch of the nervus lineae lateralis to the cranial roof (Stensiö 1925, pp. 20–21). If in *Glaucolepis* a similar nerve branch issued from the vagus canal, it was probably situated in the dorsal part of the fissura occipitalis lateralis, without manifesting itself by a widening of this fissure.

Otic region. – The otic region is much longer than the occipital region, its extension in a rostro-caudal direction being about two-fifths the length of the whole neural endocranium; moreover it is the broadest part of the neural endocranium, and the width of the region is about one and a half times its length.

Posteriorly the region, as already stated, is well separated from the occipital region dorsally and laterally by the posterior dorsal cranial fontanelle and the narrower part of the fissura occipitalis lateralis, while ventrally the two regions pass into one another without any distinct boundary.

The otic region attains its greatest width between the well developed postorbital processes; farther backward the width decreases gradually to the posterior limit of the region, and in the most anterior part of the region the width decreases very suddenly towards the boundary to the narrower orbitotemporal region.

The external faces of the otic region are as follows: A dorsal, a paired lateral (mainly ventro-lateral), a paired orbital, and a ventral face.

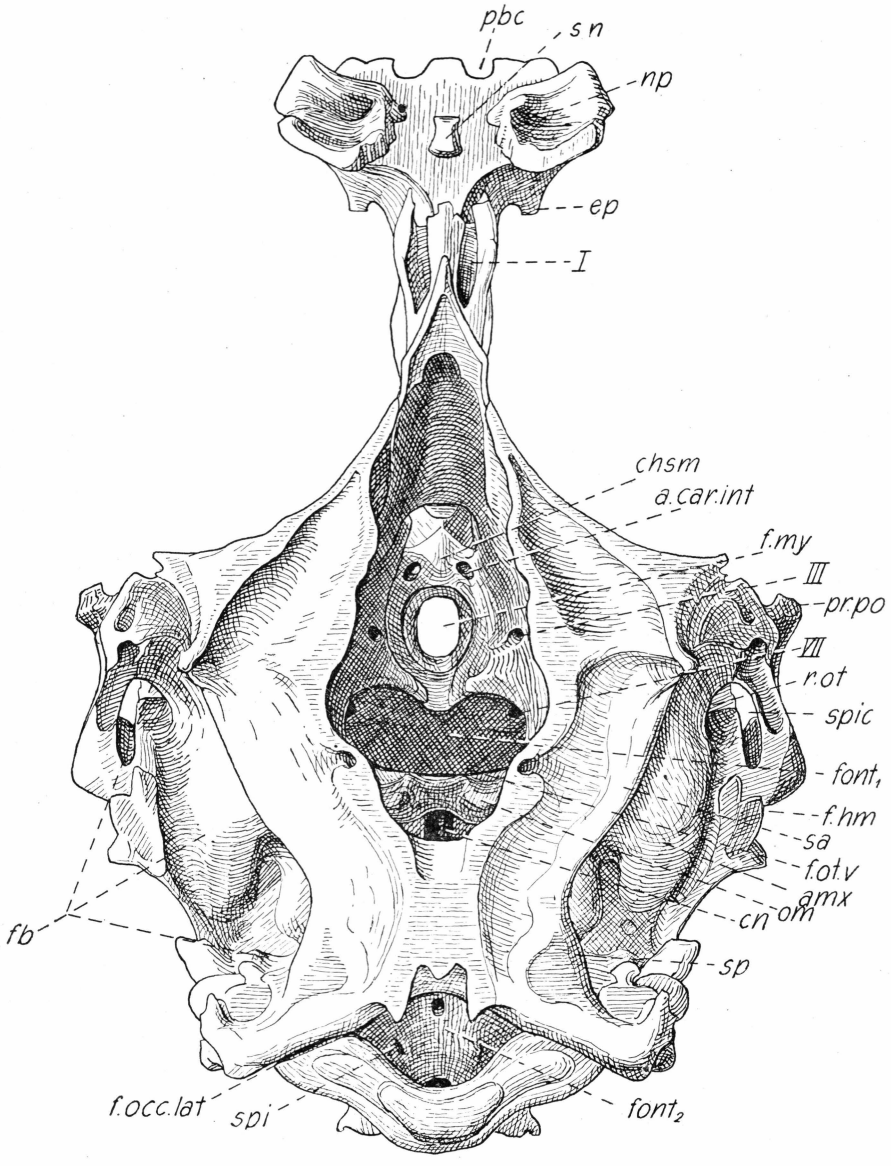


Fig. 7. *Glaucolepis stensiöi* n. sp. Neural endocranium in dorsal view. On the basis of a wax model. 6–7 ×.

a. car. int, canal for the arteria carotis interna; *amx*, bulge above the division of the labyrinth cavity for the ampulla externa; *chsm*, depression for the chiasma; *cn*, space for the notochord; *ep*, articular process for the pars autopalatina; *fb*, fossa bridgei; *f. hm*, articular fossa for the hyomandibula; *f. my*, fenestra ventralis myodomus seen through the pituitary fontanelle; *f. occ. lat*, fissura occipitalis lateralis; $font_1$, $font_2$, anterior and posterior dorsal fontanelles; *f. ot. v*, fissura oticalis ventralis; *np*, nasal pit; *om*, separate ossification in the ventral wall of the otic region; *pbc*, groove for the ramus palatinus facialis and vessels; *pr. po*, processus postorbitalis; *r. ot*, dorsal opening of the canal for the ramus oticus lateralis; *sa*, ridge above the canalis semicircularis anterior; *sn*, ossification in the posterior part of the septum nasi; *sp*, ridge above the canalis semicircularis posterior; *spi*, canal for a spino-occipital nerve; *spic*, spiracular canal; *I*, groove for the nervus olfactorius; *III*, canal for the nervus oculomotorius; *VII*, facialis canal.

The median part of the dorsal face is pierced by a very large fontanelle (*font*$_1$, Figs. 2, 7, 8), which extends from the hindmost third of the otic region to some distance into the orbitotemporal region. The fontanelle attains its greatest width at about one-third of its whole length from its caudal end. It narrows anteriorly and posteriorly, and its general shape will appear from Fig. 7. The part of the roof of the endocranium that surrounds the fontanelle lacks perichondral bone on its medial margin, and it is therefore probable that the fontanelle was surrounded by cartilage in the living animal and accordingly was at any rate somewhat narrower and shorter, too, than it appears now (cf. Fig. 12).

As mentioned repeatedly above, a small dorsal fontanelle is found at the boundary between the otic region and the occipital region. This fontanelle (*font*$_2$, Figs. 2, 7, 9, 12; Pls. 1, 2) is almost elliptical, with the short axis of the ellipse directed longitudinally and its long axis transversally. The greatest width of this posterior dorsal cranial fontanelle is somewhat smaller than the greatest width of the anterior dorsal cranial fontanelle. Laterally the posterior fontanelle is continued in the narrow fissura occipitalis lateralis, of which, as already mentioned, it may best be regarded as a widened division. There is nothing to indicate that the posterior fontanelle has been constricted by cartilage.

That part of the cranial roof which separates the anterior and posterior fontanelles, has on its caudal margin, which constitutes the anterior boundary of the posterior fontanelle, three small backward directed processes (Fig. 7), an unpaired median and a paired one. The presence of these processes makes the outline of the posterior fontanelle somewhat more complicated than would appear from the above description. The central and anterior parts of the cranial roof between the two cranial fontanelles lack the perichondral bone-layer on the dorsal side.

Both in fossil and in recent *Chondrostei* and *Holostei* fontanelles in the roof of the endocranium are fairly common occurrences.

In the Kansas *Palaeonisciformes* A and B, as in *Glaucolepis*, an anterior and a posterior dorsal fontanelle are found (see e. g. Watson 1925, pp. 837 and 846), of which the posterior one corresponds entirely to the posterior fontanelle in *Glaucolepis*. Watson points out that the posterior fontanelle in form B, in contrast to that of form A, is open posteriorly because the supraoccipital region is unossified. I am inclined to think that this is merely due to an injury to the specimen of form B figured. The anterior fontanelle of form A has a similar caudal extent as in *Glaucolepis*, while in form B it only pierces the roof of the anterior part of the otic region. Both in forms A and B the anterior fontanelle is much narrower than in *Glaucolepis*.

In *Saurichthys* (Stensiö 1925, pp. 22 etc.) a small fontanelle is found

in the cranial roof, which in the living animal has been further constricted, having been surrounded by cartilage. Stensiö (op. cit. p. 24) points out that this fontanelle corresponds to the posterior part of the fontanelle present in *Polypterus*, *Lepidosteus*, and the *Teleostei*, and to (Stensiö 1932, p. 193) the anterior fontanelle in the Kansas forms and *Perleidus*.

In *Ospia* (Stensiö 1932, p. 233) one fontanelle is found in the roof of the endocranium, almost corresponding to the anterior dorsal fontanelle in *Glaucolepis*, although it is somewhat broader in the fossil cranium. In *Perleidus* (Stensiö 1932, p. 193) the conditions are as in *Ospia*.

According to Piveteau (1934, p. 15) probably no dorsal fontanelles are found in *Australosomus*; however, after a preliminary examination of the Greenland material of *Australosomus* there is reason to assume the presence of at least a posterior dorsal fontanelle (E. Nielsen 1936, p. 45).

In the fragment of *Caturus groenlandicus* described by Aldinger (1932) the endocranium seems to lack dorsal fontanelles.

Only in early ontogenetic stages has *Amia* a fontanelle in the cranial roof (Pehrson 1922, pp. 21, 26, 29). The adult *Sinamia* (Stensiö 1935) lacks a dorsal fontanelle, too.

Acipenser has an extensive dorsal fontanelle (Bridge 1879, Parker 1882, etc.), which, judging from its position in relation both to the fossa bridgei and to the exit of the nervus vagus, seems to correspond most nearly to the posterior fontanelle of *Glaucolepis*. From a comparison between the Kansas *Palaeonisciformes* A and B, *Glaucolepis*, *Perleidus*, *Ospia*, *Australosomus*, and *Boreosomus* (*cf.* p. 287) it would seem probable that the posterior dorsal fontanelle, like the narrower part of the fissura occipitalis lateralis, closes more and more as we pass from the earliest to the more recent forms. This, however, seems not to be the case in the sturgeons, if the dorsal fontanelle present in *Acipenser* is actually homologous with the posterior dorsal fontanelle in *Glaucolepis*, etc., in which case it is remarkable that no posterior dorsal fontanelle exists in *Saurichthys*.

From our knowledge of the forms dealt with above we may conclude that the anterior dorsal fontanelle is probably a primitive structure within the group of Actinopterygians. On the basis of the conditions in the Kansas forms I have attempted (in Fig. 12) to give the most probable outline of this fontanelle in the living *Glaucolepis*, and in my description of *Boreosomus* (p. 319) I have put forward the assumption that the anterior part of the fontanelle in the living fish was the place of exit of the epiphysis.

If we disregard the detailed relief, the areas of the dorsal face of the otic region situated laterally to the anterior dorsal fontanelle may be said to slope downward laterally, in so far as the lateral edge of the dorsal face of the otic region lies on a somewhat lower level than the most medial part of the dorsal face of the region. However, as will appear from Fig. 7, the face

of these areas of the endocranium lying laterally to the anterior dorsal fontanelle are not plane, nor are they evenly rounded, but have quite a complicated relief. This is chiefly due to the presence of the well developed fossa bridgei (cf. Stensiö 1925, pp. 24–26).

We shall now proceed to a more detailed description of this part of the dorsal face of the otic region.

On the dorsal face a narrow, elevated zone is seen which extends from the postero-lateral corner of the face along the narrow part of the fissura occipitalis lateralis and the antero-lateral edge of the posterior dorsal fontanelle, to continue, then, in a rostral direction to the hindmost part of the edge of the anterior dorsal fontanelle. This elevated zone continues forward along the edge of the fontanelle to a short distance into the orbitotemporal region, where, as will appear from Fig. 7, it meets at a very acute angle with a similar elevated zone issuing from the antero-lateral part of the dorsal face of the otic region and extending in an antero-medial direction. The dermal cranial roof rested against these two elevated zones or ridges, and at the same time it was in contact with the somewhat lower-lying lateral margin of the dorsal face of the otic region and probably with the dorsal face of the cartilaginous zone, too, which must be supposed to have surrounded the anterior dorsal fontanelle. The whole considerable lateral area of the dorsal face of the otic region, however, which is enclosed by these contact zones, was without contact with the dermal cranial roof, and appears as a distinct depression. This depression on the dorsal face of the endocranium falls into a lateral and a medial portion, which are separated incompletely by two prominent ridges, which run on the dorsal face of the otic region above the cavities for the canalis semicircularis anterior and posterior.

The medial portion of the depression is shallow, of almost equal depth throughout. It is broadly speaking S-shaped in outline, extending in an antero-medial direction from the postero-lateral part of the dorsal side of the otic region, to continue further forward in an antero-lateral direction until anteriorly it again bends in an antero-medial direction, as will appear from the figure.

The lateral portion (*fb*, Figs. 2, 7, 12; *fb. ant, fb. post,* Figs. 1, 4, 11), which corresponds most nearly to Stensiö's fossa bridgei, is much deeper, and may be subdivided into an anterior and a posterior especially deep part separated by a threshold (*amx*, Fig. 7) on the bottom of the fossa, arising by the bottom bulging out over the space for the ampulla of the canalis semicircularis externus.

The anterior deep part of this actual fossa bridgei attains its greatest depth quite near the lateral margin of the dorsal face of the endocranium directly behind the postorbital process. The vertically extending spiracular canal (*spic*, Figs. 2, 4, 6, 7, 8, 10, 11, 12), through which the most dorsal end of the processus ascendens posterior of the parasphenoid reaches right into

the most anterior deep part of the fossa bridgei, has its dorsal opening on the floor of this deep part.

Slightly rostrally to and on a slightly higher level than the dorsal opening of the spiracular canal a short canal (*t*, Figs. 6, 10) which pierces the wall between the foremost part of the fossa bridgei and the orbit opens into the fossa bridgei.

Another canal (*r. ot*, Fig. 7) issues from the deepest part of the anterior section of the fossa bridgei just medially to the dorsal opening of the spiracular canal, extending from this point in a ventro-medial and at the same time a somewhat anterior direction through the lateral wall of the otic region laterally to the ampulla of the canalis semicircularis anterior, to open into the dorso-lateral part of the trigemino-facialis chamber.

The latter canal no doubt lodged the ramus oticus lateralis (cf. p. 82), and canal *t*, therefore, may be assumed to have contained a vessel, perhaps a vein which drained the deep fossa.

The posterior deep part of the actual fossa bridgei is considerably deeper than the anterior, and lies directly laterally to the angle between the canalis semicircularis posterior and the canalis semicircularis anterior. In the steep bone wall bounding the fossa bridgei behind, and accordingly forming the partition between the fossa bridgei on one side and the lateral occipital fissure and the cavum cerebrale cranii on the other side, lies the cavity for the canalis semicircularis posterior. Precisely in the centre of the arch formed by the cavity of the canalis semicircularis posterior (see Figs. 13 and 14) this posterior wall of the fossa bridgei is pierced by a wide round opening leading inward to the cavum cerebrale cranii (*fo*, Figs. 1, 2, 4, 9, 11; Pls. 1, 2). This wide opening between the fossa bridgei and the cavum cerebrale cranii was undoubtedly not closed by cartilage in the living fish.

In *Polyodon folium* Bridge (1878, pp. 694 and 696, Pl. 57) describes an opening between the fossa bridgei and the cavum cerebrale cranii, whose relation to the labyrinth cavity is precisely like that of the opening *fo* in *Glaucolepis*, and which no doubt is homologous with the latter. Whether nerves or vessels pass through this opening in *Polyodon*, does not appear from Bridge's description, which contains no satisfactory explanation of its origin either.

In *Acipenser* Bridge (1878, p. 697) describes a "depression in the roof of the otic cartilage external to the posterior vertical semicircular canal, and at the bottom of it there is a fat-infiltrated canal, which penetrates for a short distance into the substance of the cartilage, but does not communicate with the cranial cavity. The enormous growth of the cranial cartilage, which has effectually masked other embryonic features in the cranial structure of the Sturgeon has probably obliterated the primitive communication of these canals with the cranial cavity". Thus here, too, indications of the same com-

munication between the fossa bridgei and the cavum cerebrale cranii as found in *Glaucolepis* are preserved.

The communication between the cavum cerebrale cranii and the posterior deep part of the fossa bridgei was observed by me, besides in *Glaucolepis*, in *Boreosomus* (for the special conditions in this genus see p. 295) and in a specimen of *Rhadinichtys* (?) belonging to The State University of Iowa and found in Pennsylvanian deposits near Iowa City, Iowa.

It is moreover probable that such a communication exists in the Kansas forms A and B, too (judging from Watson's figures), and in *Perleidus* (judging from undescribed material). This shows that we are here concerned with a structural feature characteristic of several primitive Actinopterygian groups.

Aldinger (1932, pp. 16–17, Fig. 2) describes, in a cranial fragment of an Eugnathid in which the otic region is excellently preserved, a canal (*el. n*) issuing from the cavum cerebrale cranii in precisely the same way as the opening *fo* in *Glaucolepis*, and piercing the area of the cranial wall that is surrounded by the cavity for the canalis semicircularis posterior. Farther forwards the canal (*el. n*) traverses the area which corresponds topographically to the hindmost deep part of the fossa bridgei in *Glaucolepis*, but which is here filled with cancellate bony tissue. Aldinger assumes that this canal opens anteriorly into the cavum cerebrale cranii medially to the foremost part of the canalis semicircularis anterior and somewhat more dorsally than the foremost part of the utriculus.

A further preparation of Aldinger's original specimen has enabled me to confirm at all points Aldinger's assumption as to the foremost part of the canal.

Whether the canal, as suggested by Aldinger, lodged electric nerves or had some other function, will not be discussed here; but it seems beyond doubt that its hindmost part is homologous with a portion of the hindmost deep part of the fossa bridgei in *Glaucolepis*.

In *Glaucolepis stensiöi* I found no canal that could be supposed to have led the ramus supratemporalis dorsalis IX into the fossa bridgei. Probably this nerve branch reached the fossa bridgei either by passing medially to the vertical lamina of the supratemporo-intertemporal (cf. p. 119) between the lamina and that part of the lateral wall of the otic region which forms the lateral wall of the fossa bridgei, or by piercing the lateral wall of the fossa bridgei; in the latter case its canal must have been overlooked in the sectioned specimen.

Both in *Perleidus* and in *Ospia* the ramus supratemporalis dorsalis IX reached the fossa bridgei by a canal through the lateral wall of the fossa (Stensiö 1932, pp. 198–99, 233) similarly as is the case in *Amia* (Allis 1897, p. 684).

Besides in *Glaucolepis* the fossa bridgei has been described in the Kansas *Palaeonisciformes*, *Perleidus*, *Ospia*, *Australosomus*, *Saurichthys*, and (in the present paper) *Boreosomus*; in addition it is found in *Birgeria*, according to my as yet unpublished investigations. In other words, the fossa bridgei is found in nearly all the Palaeozoic and Triassic Actinopterygians whose endocrania have been examined in some detail.

Stensiö (1925, p. 25) points out that the fossa bridgei in *Saurichthys* corresponds to the F-shaped depression in the roof of the endocranium in *Polyodon* described by Bridge (1878, pp. 697–98) and to the similarly situated depression in *Acipenser*.

Furthermore, Stensiö regards it as probable that the fossa bridgei, as it appears in *Saurichthys*, *Polyodon*, and *Acipenser*, corresponds in all essentials to the temporal fossa of *Amia* and certain *Teleostei*. In the last-mentioned forms this fossa contains the anterior part of the trunk musculature, which is not the case in either *Polyodon* or *Acipenser*, in which the fossa bridgei is filled by a pigmented and somewhat fatty tissue.

In none of the fossil forms mentioned above can the foremost part of the trunk musculature have reached the fossa bridgei, for in these forms the fossa bridgei is completely closed by the dermal cranial roof. The foremost part of the trunk musculature can therefore only have been inserted partly on the paired caudal face of the anterior division of the occipital region, and partly on the posterior division of the occipital region.

In discussing the fossa bridgei in *Saurichthys*, Stensiö (1925, p. 26) deals with the question whether the fossa bridgei has developed from a temporal fossa from which the trunk musculature has withdrawn, or conversely, whether the temporal fossa has been formed by the trunk musculature having entered a fossa bridgei. Without expressing a final opinion, Stensiö is inclined to accept the first alternative on the ground that, according to our knowledge of the phylogenetic origin of the occipital region, it is probable that the trunk musculature of primitive fishes reached and in part was inserted on the posterior face of the labyrinth region and possibly to some extent on its dorsal surface, too. As, however, the trunk musculature in *Acipenser*, *Polyodon*, and *Saurichthys* (as well as in several fossil forms described after the publication of Stensiö's paper on *Saurichthys*) does not reach the otic region, Stensiö concludes that the area of insertion of the trunk musculature on the endocranium has moved farther backward. Stensiö goes on to say: "If this view is correct, it would obviously mean, that when in certain primitive Actinopterygians the dermal bones of the cranial roof in the whole posterior half of the labyrinth region rest directly against the dorsal surface of the primordial neurocranium, they came to occupy that position secondarily by the reduction of muscle fossae originally developed beneath them. Hitherto, as is well known, an opposite view with regard to this has generally been maintained in the literature (cf. Boas 1914)."

Even if the interpretation of the fossa bridgei as a primary place of insertion for the trunk musculature is accepted, this does not satisfactorily explain the fact that the fossa bridgei, in all the fossil forms in which the trunk musculature is only inserted on the occipital area, still appears as an extremely well developed fossa.

A comparison with *Ospia* (which in many respects has the character of an ancestor of *Amia* (cf. Stensiö 1935)) would seem to suggest that the temporal fossa of *Amia* has developed from a portion of the fossa bridgei by a shifting in an anterior direction of the area of insertion of the trunk musculature.

To sum up briefly, we are confronted with the fact that a number of primitive Actinopterygians on the dorsal side of the otic region have a deep, paired fossa, which is completely closed dorsally by the dermal cranial roof, its only openings being accordingly the wide communication with the cavum cerebrale cranii that probably existed in many different forms, the spiracular canal, and the fine canals for the ramus oticus lateralis and the ramus supratemporalis dorsalis IX and possibly one or several fine canals for vessels. The regular occurrence of the fossa bridgei and its peculiar communication with the cavum cerebrale cranii in my opinion strongly suggest that (at any rate in the Palaeozoic and the Triassic forms) it had some special function, as to which, however, it would be premature to form any conjecture (see further p. 101).

As stated above, the lateral face of the otic region is separated from the occipital region by the fissura occipitalis lateralis.

Only the most caudal part of the lateral face is fairly vertical, while the remaining and greater part faces somewhat ventro-laterally. Apart from minor details, the posterior part of the lateral face is fairly plane, while the anterior part is somewhat convex in a dorso-ventral direction. On this anterior part of the lateral face of the otic region is seen a broad groove running in a dorso-ventral direction; farthest dorsally the groove is continued in a short vertical canal, the spiracular canal, which, as already stated, opens dorsally on the floor of the deep anterior part of the fossa bridgei. The shape and position of the broad groove appear clearly from Fig. 4. Against the surface of this groove rests the large processus ascendens posterior of the parasphenoid, which process continues dorsally up through the spiracular canal to the fossa bridgei.

On the posterior half of the lateral face of the otic region, almost equally distant from the dorsal and ventral margins of the lateral face, there is a horizontal groove, which anteriorly reaches the posterior wide opening (*c. ju*, Figs. 3, 4, 8, 11) of the jugulo-hyoideomandibular canal; this groove was occupied by the vena jugularis in the same way as in the Kansas forms A and B (Watson 1925, p. 836, Figs. 10, 11, 14), *Cosmoptychius striatus* (Watson 1928, Fig. 1), *Perleidus* (Stensiö 1932, p. 193), *Ospia* (Stensiö 1932, p. 234), and *Australosomus* (Piveteau 1934, p. 16, Fig. 6), etc.

Ventrally this groove, termed the "jugular depression" by Stensiö, is bounded by a low saccular bulge, and dorsally by a prominent ridge, in which the cavity that lodged the canalis semicircularis externus and its ampulla is situated.

That part of the lateral face of the otic region which lies dorsally to this ridge, that is to say, the lateral face of the lateral wall of the posterior deep part of the fossa bridgei, is slightly concave both in a dorso-ventral and a rostro-caudal direction. This concavity has possibly been the place of insertion for the musculus retractor hyomandibulae.

Immediately in front of this concave face there extends from the dorsal margin of the lateral face of the otic region to a point almost lateral to the posterior part of the jugulo-hyoideomandibular canal an elevated area, whose shape will appear from Fig. 4. This elevated area bears the articular fossa for the hyomandibula (*f. hm*, Figs. 2, 3, 4, 6, 7, 8, 9, 11, 12, 47). The longitudinal axis of the articular fossa runs antero-ventrally to postero-dorsally, in such a way that it forms an angle of about 75° with the horizontal plane or, more precisely, with the plane of the ventral face of the otic region. The surface of the bone of the articular fossa is not lined with perichondral bone and the articular surface proper was therefore no doubt cartilaginous in the living animal.

In the jugular depression we find the external opening of the canal for the nervus glossopharyngeus (*IX*, Figs. 2, 4, 10, 11, 47); from this opening the glossopharyngeus canal extends in a caudo-medial direction through the cranial wall, to open in the posterior part of the saccular division of the labyrinth cavity, as is the case in *Perleidus* (Stensiö 1932, p. 198), *Ospia* (Stensiö 1932, p. 240), *Amia* (Allis 1897, p. 683), and probably in the Kansas forms A and B also (Holmgren and Stensiö 1936, p. 403) as well as in other forms.

Directly ventrally to the external opening of the glossopharyngeus canal lies an elevated area on the lateral face of the otic region (*art. sup I*, Figs. 2, 4, 6, 10, 11). This area is elliptical in outline, with its longitudinal axis pointing steeply downward and at the same time slightly backward. The surface of this area is very slightly concave and is not lined with perichondral bone, and it was therefore doubtless covered with cartilage in the living animal. Against this cartilaginous surface, the suprapharyngobranchial I articulated, as will be explained later (p. 190, Fig. 47).

Immediately in front of this elevated area we find a vestibular fontanelle of quite considerable dimensions (*v. font*, Figs. 2, 4, 6, 9, 10, 11). In lateral view this fontanelle is rounded triangular with a ventral margin, which coincides with the boundary line between the lateral and ventral faces of the otic region, an antero-dorsal, and a postero-dorsal margin. Along the margins of the most dorsal part of the fontanelle there is continuity between the perichondral bone-layers of the labyrinth cavity and of the external surface

of the otic region, whereas perichondral bone-layers are absent along the remaining part of the margins of the fontanelle.

It is probable, therefore, that while in the living animal the ventral and largest part of the fontanelle described here was more or less closed by cartilage, the most dorsal part of the fontanelle was open in the living animal (Fig. 11).

This dorsal, fairly small fontanelle may be supposed to have been nearly circular in outline.

In his account of the Kansas forms A and B, Watson (1925, p. 844) writes: "It is tempting to compare the large vestibular fontanelle, which occurs in this region in various Palaeoniscids with the membrane-covered vacuity, which in such Teleosts as the Herring has a direct contact with a pharyngeal projection from the air-bladder. But the bone surrounding this opening is so thick as to make it more probable that the space was occupied by cartilage or, at any rate, by a massive connective tissue."

Since the dorsal part of the vestibular fontanelle in *Glaucolepis*, as would seem to be the case, was not closed by cartilage, we cannot entirely disregard the possibility that a similar communication as in certain Teleosts may have existed between the labyrinth cavity and the air-bladder.

Antero-laterally to its posterior and largest opening (*c. ju*, Figs. 3, 4, 8, 11) the jugulo-hyoideomandibular canal opens on the lateral face of the otic region with two smaller openings (*r. op*, *c. trh*, Figs. 2, 3, 4, 6, 8, 11, 47), both of which lie closely behind the ventral part of the articular fossa for the hyomandibula, one a little postero-dorsally to the other.

While the vena jugularis left the jugulo-hyoideomandibular canal through the large posterior opening, it must be assumed that the truncus hyoideomandibularis passed out through the most ventral of the two small openings, having first given off the ramus opercularis facialis, which left the canal by the more dorsal of the two small openings (cf. Stensiö 1932, pp. 197–198; Piveteau 1934, p. 16).

Immediately ventral to the articular fossa for the hyomandibula a small round foramen (*a. car. ext*, Figs. 2, 4, 6, 8, 11, 47,) is seen on the lateral face of the otic region; it is the ventral opening of a vertical canal whose dorsal opening is in the floor of the jugulo-hyoideomandibular canal a short distance behind the middle of the canal.

Through this vertical canal the arteria carotis externa passed on its way from the arteria carotis communis to the jugulo-hyoideomandibular canal (cf. Stensiö 1925, pp. 49–52; Watson 1925, Fig. 14; Holmgren and Stensiö 1936, p. 404, etc.). Eaton (1939, Figs. 1–3) takes the corresponding canal in an endocranium of a type similar to Watson's Kansas forms as a canal for the ramus palatinus facialis, which, of course, cannot be correct.

The ventral face of the otic region increases in breadth from its posterior part forward as far as the fissura oticalis ventralis (p. 18), which extends through the basal part of the endocranium, connecting the right and left vestibular fontanelles. In front of this transverse fissure the ventral face decreases in breadth in an anterior direction. Both anteriorly and posteriorly the ventral face of the otic region passes evenly into the ventral face of the occipital region and the orbitotemporal region respectively. With the exception of its most posterior part, the ventral face of the otic region is concave from side to side. The concavity is deepest behind the transverse fissure, though it is distinct, too, in front of this fissure (Fig. 6). The presence of this concavity makes the lateral margin of the ventral face project as a distinct edge, corresponding to the "sub-myodomic crest" described by Stensiö in *Perleidus* (Stensiö 1932, p. 195), though it is somewhat less prominent in *Glaucolepis* than in *Perleidus*.

Through the posterior half of the part of the ventral wall of the otic region lying behind the aforementioned transverse otic fissure, the canal for the lateral dorsal aorta continues from the occipital region on either side of the median line in an antero-lateral direction. The anterior opening of this canal lies on the ventral face of the otic region almost midway between the posterior part of the otic region and the transverse otic fissure. From this opening the lateral dorsal aorta continues in a rostral and at the same time slightly lateral direction in a deep groove (*r. aort.* Fig 6) on the ventral face of the otic region. Almost midway between the anterior opening of the aorta canal and the transverse fissure this groove divides into two, as will appear from Fig. 6. One of these (*a. eff*$_1$, Fig. 6) is quite short and runs in a lateral direction as far as the lateral margin of the ventral face of the region, while the other (*a. ccm*, Figs. 6, 10), which is somewhat longer, runs in a rostral direction as far as the ventral otic fissure. The lateral groove contained the arteria branchialis efferens I, and the groove running in a rostral direction accordingly lodged the arteria carotis communis.

Almost in the place where the arteria communis passed ventrally to the fissura oticalis ventralis, it must have divided into the arteria carotis externa, which ran in a dorso-lateral direction to the ventral opening (*a. car. ext*) of the small canal through which it reached the jugulo-hyoideomandibular canal, and into the arteria carotis interna, which entered a canal in the posterior part of the parasphenoid (p. 105).

The orbital paired face of the otic region is concave both in a horizontal and a vertical direction. As a whole this face is directed rostrally, but at the same time somewhat ventrally, too. Its transition to the orbital face of the orbitotemporal region is gradual.

The trigemino-facialis chamber and the myodome, which both are placed at the transition between the otic and the orbitotemporal region, will be

treated in a later chapter (p. 70) together with the jugulo-hyoideomandibular canal.

The division of the cavum cerebrale cranii which lies in the otic region is narrowest in the area between the suprasaccular utricular parts of the right and left labyrinth cavities. Both in front of and behind this area the cavum cerebrale cranii increases gradually in breadth (Fig. 13). We may regard this division of the cavum cerebrale cranii as bounded by four walls, viz. a dorsal partly cartilaginous, a paired lateral partly membranous, and a ventral partly cartilaginous wall.

The ossified part of the dorsal wall is made up of a transverse bridge that separates the anterior and the posterior dorsal fontanelle, and in addition of a narrow zone lateral to that part of the anterior dorsal fontanelle which lies in the otic region.

The transverse bridge between the anterior and the posterior dorsal fontanelle is exceedingly massive and, as will appear from Fig. 8, has a sharp transverse ridge on its cerebral face. That part of the dorsal wall which lies laterally to the anterior dorsal fontanelle is quite thin farthest medially, but increases in thickness in a lateral direction.

The cerebral face of this part of the dorsal wall, the dorsal part of the cerebral face of the lateral wall, and the part of the cerebral face of the transverse bridge lying in front of the sharp transverse ridge, gradually merge into one another, and all of them are devoid of perichondral bone. As a consequence of the last-mentioned fact not very much can be said about the accurate shape of the dorsal part of the cavum cerebrale cranii within the otic region; however, the presence of a considerable concavity (*met*, Fig. 9) on the cerebral face of the incompletely ossified dorsal part of the lateral wall indicates the presence of a well developed lateral cerebellar division. The exact position of this concavity will appear from Figs. 13 and 14.

It may be added that the lateral wall of the cavum cerebrale cranii within the otic region is incomplete in so far as it is pierced partly by the very wide opening between the cavum cerebrale cranii and the labyrinth cavity, as will be seen from Figs. 8 and 9, and partly by the aforementioned opening between the cavum cerebrale cranii and the posterior deep part of the fossa bridgei.

The following applies to the ventral boundary of the cavum cerebrale cranii in the otic region: The ventral wall consists of a thick bony mass, which forms a direct forward continuation of that part of the ossification of the occipital region which lies ventrally, and in part laterally, to the notochordal space, and which constitutes the anterior part of the posterior large ossification of the endocranium. On the dorsal face of this bony mass there is, as a continuation of the notochordal space of the occipital region, a groove for the most anterior part of the notochord (*cn*, Figs. 5, 7, 9). As will be

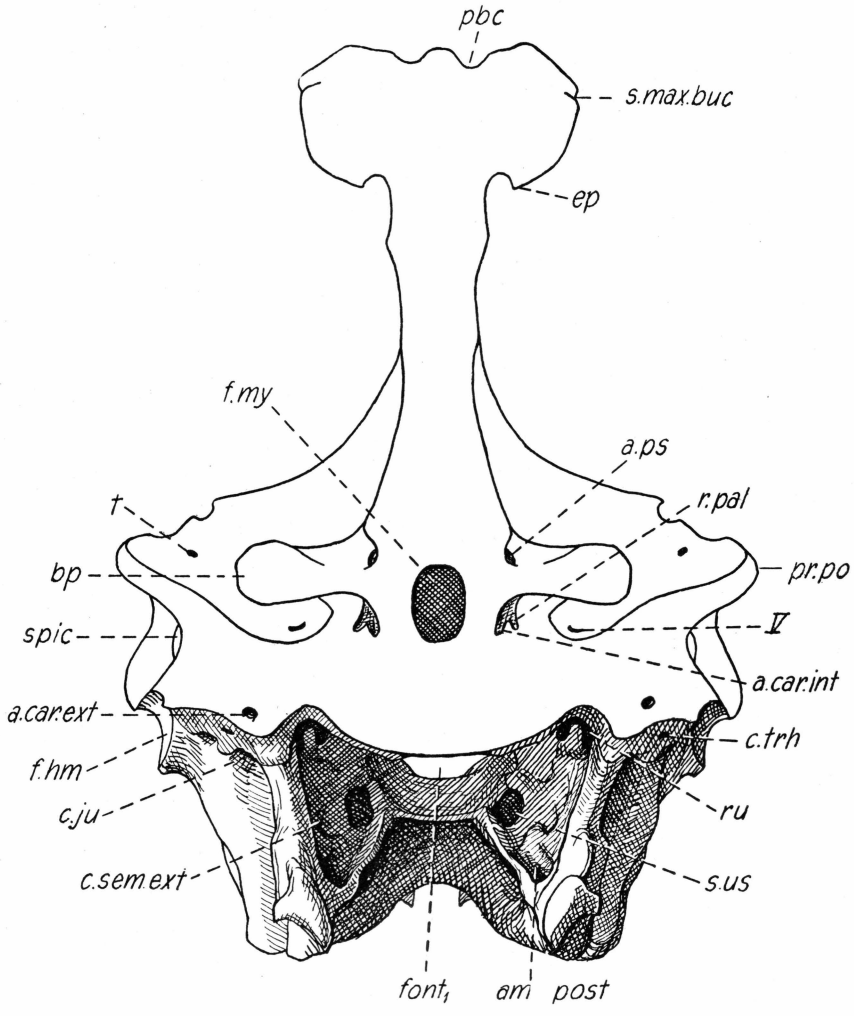


Fig. 8. *Glaucolepis stensiöi* n. sp. Anterior ossification of neural endocranium in ventral view. On the basis of a wax model. 6–7 ×.
am. post, division of the labyrinth cavity for the ampulla posterior; *c. ju*, posterior opening of the jugulo-hyoideomandibular canal for the vena jugularis; *c. sem. ext*, division of the labyrinth cavity for the canalis semicircularis externus; *ru*, division of the labyrinth cavity for the recessus utriculi; *s. us*, division of the labyrinth cavity for the sinus utriculi superior. Other letters as in Fig. 6.

seen from Fig. 5, this groove is fairly narrow, and in a rostral direction reaches the fissura oticalis ventralis; it must therefore be assumed that the anterior thin end of the notochord extended through a considerable part of the otic region.

The otic part of the posterior ossification of the endocranium consists of endochondral cancellate bone-tissue and is only provided with perichondral bone-layers on its ventral side, that is to say, on the above described

ventral face of the otic region. Its other four faces, viz. in addition to the dorsal face towards the cavum cerebrale cranii, a vertical anterior face, concave from side to side, towards the fissura oticalis ventralis, and a paired dorso-laterally directed face towards the labyrinth cavity, were covered by cartilage, and it is therefore impossible to ascertain the exact shape of this part of the endocranium in the living animal. It is probable, however, that the cartilaginous part of the ventral wall of the cavum cerebrale cranii was so thick that it entirely enclosed at any rate the anterior part of the notochord.

However, another circumstance enables us to conclude with some certainty that the cartilaginous part of the ventral wall had an even greater dorsal extent. For, as will appear very distinctly from a median sagittal section through the endocranium, a small bilaterally symmetrical ossification (*om*, Figs. 2, 7, 9), which has no contact with any other part of the ossifications of the endocranium, is found in the otic division of the cavum cerebrale cranii. It may best be described as a small horizontal plate of bone which is produced laterally into a strong process. The proximal and largest part of this process is directed antero-dorso-laterally, whereas the pointed distal end of the process points rather in an antero-lateral direction. Apart from the distal end of its paired process, the dorsal face of the ossification is saddle-shaped, being concave from side to side and convex in a rostro-caudal direction. The ventral face of the horizontal part of the ossification is fairly plane, and is the only face of the ossification which is devoid of a perichondral bone-layer. The largest rostro-caudal extent of the ossification is about one-third of the distance between the tips of its right and left lateral processes.

This small ossification was found in the endocranium investigated by the grinding method, but has not been observed in any other specimen of *Glaucolepis*. It it astonishing that an ossification like this can remain *in situ* during the fossilisation process, and it can only be explained by assuming that the endocranium was filled with clay even before its cartilaginous portions decayed. Against the objection which may possibly be raised that the small ossification was not found in the same place in the living animal which it occupied in the fossil cranium, it may be urged that at the time when the fish in question was embedded in the mud, it was lying on its side as can be seen from the shape as well as from the structure of the concretion in which it was found. If the ossification had changed its place in the endocranium after the death of the fish, it would probably have moved downward, that is to say, towards the lateral wall of the endocranium and hardly towards its dorsal or ventral walls. As will appear from the figures, the ossification has not been displaced in a lateral direction, and it is therefore fairly certain that it has not moved in other directions either in relation to the walls of the endocranium.

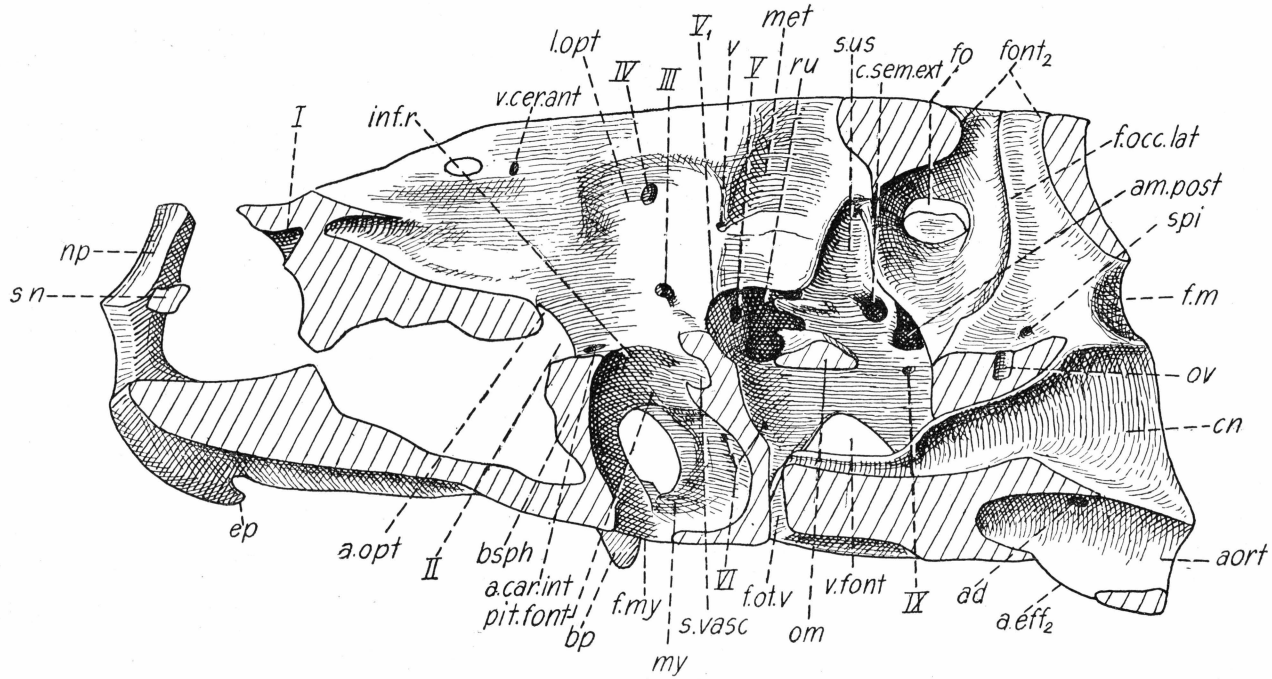


Fig. 9. *Glaucolepis stensiöi* n. sp. Right half of neural endocranium in medial view. Sectional faces ruled. On the basis of a wax model. 6–7 ×. *a. car. int*, canal for the arteria carotis interna; *ad*, canal for an artery; *a. eff*$_2$, opening for the arteria branchialis efferens II; *a. opt*, place of exit for the arteria optica; *aort*, aorta canal; *am. post*, division of the labyrinth cavity for the ampulla posterior; *bp*, processus basipterygius; *bsph*, pars basisphenoidea; *cn*, space for the notochord; *c. sem. ext*, division of the labyrinth cavity for the canalis semicircularis externus; *ep*, articular process for the pars autopalatina; *f. m*, foramen magnum; *f. my*, fenestra ventralis myodomus; *fo*, opening in the wall between the fossa bridgei and the cavum cerebrale cranii; *f. occ. lat*, fissura occipitalis lateralis; *font*$_2$, posterior dorsal fontanelle; *f. ot. v*, fissura oticalis ventralis; *inf. r*, infundibular recess; *l. opt*, division of the cavum cerebrale cranii for the lobus opticus; *met*, division of the cavum cerebrale cranii for the lateral part of the metencephalon; *my*, posterior myodome; *np*, nasal pit; *om*, separate ossification in the ventral wall of the otic region; *ov*, depression in the floor of the cavum cerebrale cranii; *pit. font*, pituitary fontanelle; *ru*, division of the labyrinth cavity for the recessus utriculi; *sn*, ossification in the posterior part of the septum nasi; *spi*, canal for a spino-occipital nerve; *s. us*, division of the labyrinth cavity for the sinus utriculi superior; *s. vasc*, space for the saccus vasculosus; *v*, canal for a (?) vessel; *v. font*, vestibular fontanelle; *v. cer. ant*, canal for the vena cerebralis anterior; *I*, groove for the nervus olfactorius; *II*, opening for the nervi optici; *III*, canal for the nervus oculomotorius; *IV*, canal for the nervus trochlearis; *V*, trigeminus canal; V_1, canal for the nervus ophthalmicus profundus; *VI*, canal for the nervus abducens; *IX*, canal for the nervus glossopharyngeus.

As stated above, the small ossification is devoid of perichondral bone on its ventral face. It is therefore a natural assumption that the whole interspace between the ventral face of the small ossification and the anterior half of the dorsal face of the bone mass which in part surrounds the anterior part of the notochord was occupied by cartilage. If so, the small ossification formed the ventral wall of the cavum cerebrale cranii in that part of the otic region in which it is placed. At the same time it was probably connected laterally with the membranous wall which separates the cavum cerebrale cranii from the labyrinth cavity.

Both in front of and behind the small ossification the floor of the cavum cerebrale cranii no doubt lay on a lower level.

Labyrinth cavity. – The subjoined description of the labyrinth cavity is a description of the massive body constituting the cast of the cavity itself in the model shown in Figs. 13, 14, and 15, so that for instance the term "convex" used for a part of the surface of the model of course means a concavity on the bony face surrounding the labyrinth cavity.

Both that part of the large labyrinth cavity which contained the sacculus and the part that contained the utriculus communicated in the fossil cranium with the cavum cerebrale cranii in the same way as in the Kansas Palaeonisciform A (Watson 1925, p. 844), *Perleidus* (Stensiö 1932, p. 200), and *Ospia* (Stensiö 1932, p. 238), and to a far greater extent than in *Saurichthys* (Stensiö 1925, p. 30). As pointed out i. a. by Stensiö, this wide communication between the cavum cerebrale cranii and the labyrinth cavity presents a point of resemblance with recent Actinopterygians and shows particularly good agreement with the conditions in *Acipenser*, *Amia*, and *Lepidosteus* (Stensiö 1932, p. 200).

In lateral view the saccular division (*sacc*, Fig. 13) is almost square in outline with a nearly vertical anterior and posterior and a nearly horizontal ventral margin. The lateral face of the saccular division is somewhat convex both in a vertical and a horizontal direction in so far as its accurate shape can be ascertained, which is difficult on account of the presence of the aforementioned large vestibular fontanelle in its lateral wall. In the model the lower part of the saccular division extends much farther in a ventral direction than the cavum cerebrale cranii, and is even situated far more ventrally than the part of the notochord lying in the otic region. Medially the ventral surface of the saccular division is bounded by the dorso-lateral face of that part of the posterior ossification of the endocranium which belongs to the otic region; as stated above, this face is devoid of perichondral bone and was, no doubt, lined with cartilage, which has thus formed the medial wall proper of the saccular division. There is no possibility of determining the thickness of this cartilage, so the exact shape of the ventral part of the saccular division cannot be ascertained. We can only say that this division was at any rate somewhat more latero-medially compressed than appears

from the model, and that it did not extend quite as far in a ventral direction as in the model.

No indication of a specially delimited lagena area is found, so it is reasonable to assume that similarly as in *Ospia* (Stensiö 1932, pp. 238–239), *Perleidus* (Stensiö 1932, p. 200), *Saurichthys* (Stensiö 1925, pp. 30–31), *Acipenser*, *Amia*, and *Lepidosteus* (Retzius 1881), a lagena was not differentiated.

Ventrally the utricular division passes directly into the saccular division, but extends beyond it both anteriorly and posteriorly. Following Stensiö in his description of the labyrinth cavity in *Perleidus* (Stensiö 1932, pp. 200–202), which agrees very well with that of *Glaucolepis*, we may therefore distinguish between a pre-saccular, a supra-saccular, and a post-saccular part of the utricular division.

As in *Perleidus* (and in *Ospia* and *Saurichthys* also) the pre-saccular and the post-saccular parts are not on a line with the supra-saccular part, but are curved somewhat laterally in proportion to the latter.

The ventro-lateral portion of the pre-saccular part has an irregularly rounded expansion, whose shape in detail will appear most distinctly from Figs. 14 and 15. This expanded part contained the recessus utriculi. The pre-saccular part is in wide open communication with the cavum cerebrale cranii, so that, unlike what is the case in *Saurichthys* (Stensiö 1925, p. 43), no special canal for the ramus vestibularis acustici is present.

As will be evident from the subjoined description (p. 79), it is difficult to decide whether the roots of the facialis nerve traversed the pre-saccular part of the utricular division, as in *Perleidus* (Stensiö 1932, pp. 195–198, 201) and *Ospia* (Stensiö 1932, p. 240), or ran entirely in front of it.

The division for the sinus utriculi superior (*s. us,* Figs 1, 2, 8, 9, 13, 14; Pls 1, 2) issues almost in a dorsal direction from the supra-saccular part of the utricular division. This division, which attains a considerable height in proportion to its breadth, is in open communication with the cavum cerebrale cranii along its whole medial side.

The divisions of the labyrinth cavity that contained the semicircular canals are fairly slender.

The division for the canalis semicircularis anterior (*c. sem. ant.*, Figs. 2, 13, 14) issues from the antero-dorsal portion of the pre-saccular part of the utricular division, and, just after its issue, has a large expansion (*am. ant*) which lodged the ampulla anterior; posteriorly the division for the canalis semicircularis anterior communicates with the most dorsal part of the division for the sinus utriculi superior. The canalis semicircularis anterior was considerably longer than the other two semicircular canals.

The division for the canalis semicircularis posterior (*c. sem. post*, Figs. 1, 2, 13, 14) issues from the post-saccular part of the utricular division. Just after its issue it has a large and well defined bulge (*am. post*) for the ampulla

posterior. This division, too, is connected with the most dorsal part of the division for the sinus utriculi superior.

The division for the canalis semicircularis externus (*c. sem. ext*, Figs. 2, 8, 9, 13, 14, 15; Pls 1, 2) issues from the pre-saccular part of the utricular division postero-dorsally to the expansion that lodged the recessus utriculi. Its front part shows an expansion (*am. ext*), which lodged the ampulla externa. The boundary between this expansion and the portion of the pre-saccular part whence it issues is not distinctly marked, as for instance in *Perleidus* (Stensiö 1932, Fig. 62 A). Behind the ampullary swelling the division for this semicircular canal runs in a plane (cf. Fig. 14) which slopes downward in a postero-ventral direction. In its course the division for the canalis semicircularis externus describes so large a part of a circular arch that its posterior end has an antero-medial direction immediately before it communicates with the supra-saccular part of the utricular division directly ventrally to the division for the sinus utriculi superior.

This means a distinct difference from both *Perleidus* (Stensiö 1932, Fig. 61), *Ospia* (Stensiö 1932, Fig. 74), and *Saurichthys* (Stensiö 1925, Fig. 9), in which the division for the canalis semicircularis externus communicates with a more posterior part of the utricular division, viz. the post-saccular part immediately in front of the division for the ampulla posterior.

In the drawings of the sections of *Glaucolepis stensiöi* remains of otoliths (*oth*, Fig. 2) are seen both in the right and the left labyrinth cavity. They do not seem, however, to be particularly well preserved. They lie in the saccular division of the labyrinth cavity as small irregularly shaped bodies, consisting of a fairly loose or porous tissue, whose nature could not be more closely examined.

Solid otoliths have been demonstrated (cf. Stensiö 1925, p. 32) in several *Chondrostei*; but for instance in the genus *Saurichthys*, which in an anatomical respect is one of the best examined fossil genera of *Chondrostei*, Stensiö sought in vain for otoliths. Stensiö puts forward as a possible explanation that in *Saurichthys* conditions may have been as in the Selachians, where a number of small, mutually free crystals are found instead of solid otoliths, and in the same connection refers to the otolith in *Acipenser*, described by Retzius (1881, pp. 33–34) as more brittle and less compact than in the *Teleostei*.

As the membranous labyrinth is of much smaller dimensions than the labyrinth cavity, the latter does not, of course, reflect the shape of the membranous labyrinth in all its details; still it gives a good general idea of it. The labyrinth cavity has been fairly well examined in several forms of fossil Ganoids, among others, as will appear from the above, in *Saurichthys* (Stensiö 1925, pp. 30–33), *Perleidus* (Stensiö 1932, pp. 200–202), and *Ospia* (Stensiö 1932, pp. 238–241). From the condition of the labyrinth cavity in these three genera Stensiö concludes that their mem-

branous labyrinth was typically Actinopterygian-like, and that it showed special agreement with the membranous labyrinth of *Acipenser*, *Amia*, and *Lepidosteus* (Stensiö 1925, pp. 30–33; 1932, pp. 200–202, 241).

Of all these genera *Glaucolepis* shows the greatest agreement as regards the labyrinth cavity with *Perleidus*, differing from this genus in a few details only, of which it may especially be noted that in *Perleidus* the division for the canalis semicircularis externus communicates with the post-saccular part of the utricular division, and that the division for the canalis semicircularis posterior has a smaller and less distinctly marked ampullary region.

Orbitotemporal region. – The orbitotemporal region is inconsiderably longer than the otic region, and posteriorly passes gradually into the latter. Its anterior boundary is more conspicuous, for, at the transition from the orbitotemporal region to the ethmoidal region, the endocranium suddenly increases very considerably in breadth. As is usual within the *Palaeonisciformes*, the eyes of *Glaucolepis* were very large, and the interorbital part of the region is accordingly narrow and pierced by a large fenestra optica. The cavum cerebrale cranii extends only a short distance into the interorbital part of the region.

If, for the present, we disregard the pars basisphenoidea, the orbitotemporal region has four external faces, viz. an unpaired dorsal, a paired lateral, and an unpaired ventral face.

Posteriorly the dorsal face passes evenly into the dorsal face of the otic region, and decreases in breadth forwards from this transitional zone, as will appear from Fig. 7. A very essential part of the area of the dorsal face is occupied by the anterior part of the anterior dorsal fontanelle described on p. 41. The breadth of the dorsal fontanelle decreases anteriorly, the fontanelle terminating in a point after traversing the posterior two-thirds of the orbitotemporal region.

On the posterior, broadest ,part of the dorsal face of the orbitotemporal region lies, laterally to the dorsal fontanelle, the anterior shallow part of the fossa bridgei, this term being used in its widest sense (cf. p. 43). The extent of this part of the fossa bridgei will further be evident from Fig. 7.

The degree of ossification of the antero-dorsal part of the orbitotemporal region and of the ethmoidal region in the sectioned specimen of *Glaucolepis stensiöi* is much smaller than that of several examined endocrania of *Glaucolepis magna* (p. 93, Figs. 16, 17A–B; Pl. 6, Figs. 1, 2). The nervus olfactorius ran, as it were, in a paired groove (I, Fig. 7), open towards the dorsal side, in the part of the region that lies in front of the cavum cerebrale cranii. In the living animal this groove was in all probability closed by cartilage dorsally; accordingly the nervus olfactorius ran in a closed canal. Immediately behind the ethmoidal region the nervus olfactorius apparently ran through the orbit proper (Figs. 4, 7), which, however, is due to the incomplete ossification of this foremost part of the region.

The posterior part of the lateral face of the orbitotemporal region is directed laterally, and at the same time somewhat antero-ventrally. The interorbital part of the lateral face is concave in a dorso-ventral direction, so that farthest dorsally it faces in a lateral and somewhat ventral, and farthest ventrally in a dorso-lateral direction. At the same time the lateral face is slightly concave in a horizontal direction. As will appear from Figs. 2, 4, 9, 10, and 11, the interorbital part of the lateral face is pierced by the large fenestra optica (*fen. opt*) and by an opening found in the fossil cranium anteriorly to and confluent with the fenestra optica; the presence of this opening is due to the fact that the most anterior part of the interorbital wall to a large extent consisted of cartilage.

Near the dorsal margin of the lateral face of the orbitotemporal region, dorsally to the anterior part of the fenestra optica, a very narrow canal leads through the cranial wall from the cavum cerebrale cranii to the orbit (*v. cer. ant*, Figs. 4, 9, 10); this canal was traversed by the vena cerebralis anterior. Some distance caudally and slightly ventrally to the orbital opening of this canal there is, on the lateral face, a fine opening (*IV*, Figs. 2, 10) of a canal which runs in a postero-medial direction through the cranial wall to the cavum cerebrale cranii. The cerebral opening (*IV*, Fig 9) of this canal is much wider than the orbital opening, and, as will be seen from Figs. 13, 14, and 15, the proximal and largest part of the canal has a width corresponding to the cerebral opening, while only its most distal part is narrow.

According to its position the canal must be assumed to have lodged the nervus trochlearis .

The nervi optici passed from the cavum cerebrale cranii to the orbit through a large unpaired (see, however, p. 61) opening placed on a level with, and immediately behind, the dorsal part of the fenestra optica (*II*, Figs. 4, 9, 10, 11). The outline of this opening appears most distinctly from Fig. 10, which shows that in the dorsal margin of the right and left halves of the opening an emargination (*a. opt*, Figs. 4, 9, 10, 11,) is present which as we shall see below (p. 89), corresponds to an independent canal in *Glaucolepis magna* which leads from the cavum cerebrale cranii to the orbit immediately dorsally to the paired foramen opticum of this species. This emargination (in *Glaucolepis stensiöi*) or canal (in *Glaucolepis magna*) contained the arteria optica.

On the part of the orbital face of the orbitotemporal region which lies behind a vertical transverse plane through the pars basisphenoidea, there are several other foramina, which will be described in more detail later (p. 70). In this place I will only mention that the orbital opening of the trigemino-facialis chamber and the myodome are found on the postero-ventral part of the orbital face of the region.

The ventral face of that part of the orbitotemporal region which lies in front of a vertical transverse plane through the pars basisphenoidea is entire-

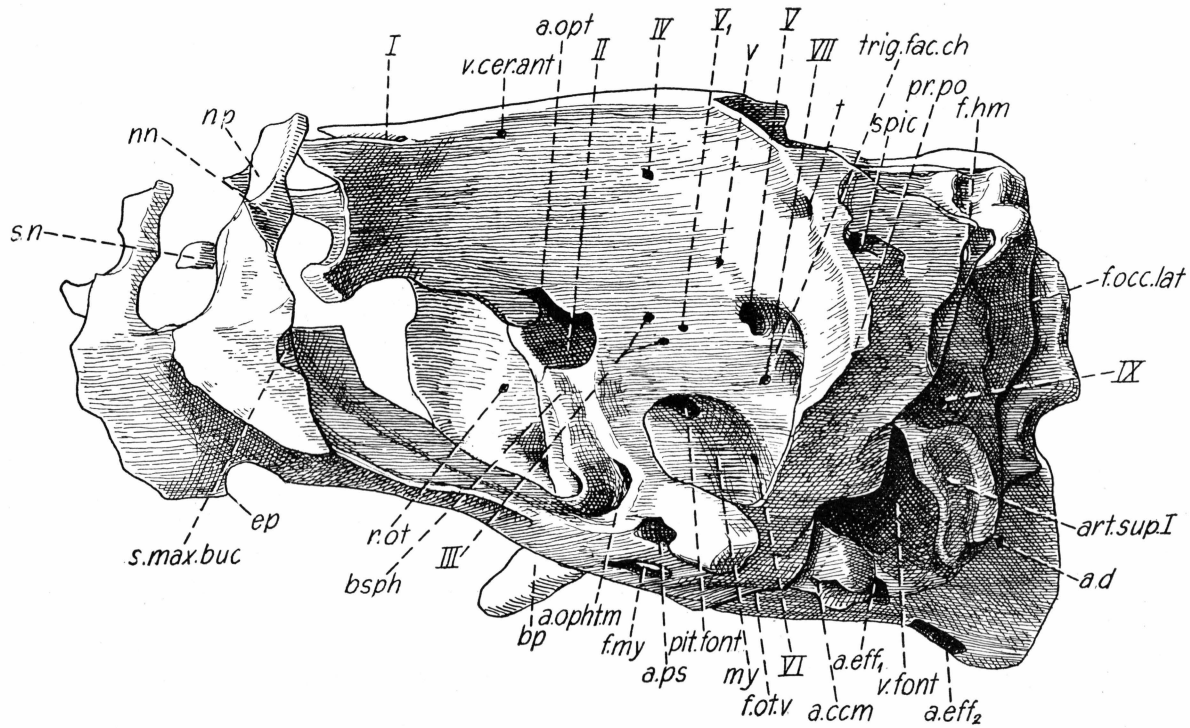


Fig. 10. *Glaucolepis stensiöi* n. sp. Neural endocranium in antero-ventro-lateral view. On the basis of a wax model. 6–7 ×.
a. ccm, groove for the arteria carotis communis; *ad*, canal for an artery; *a. eff*$_1$, groove for the arteria branchialis efferens I; *a. eff*$_2$, canal for the arteria branchialis efferens II; *a. opht. m*, opening for the arteria ophthalmica magna; *a. opt*, place of exit for the arteria optica; *a. ps*, opening for the arteria pseudobranchialis efferens; *art. sup I*, place of articulation for the suprapharyngobranchial I; *bp*, processus basipterygius; *bsph*, pars basisphenoidea; *ep*, articular process for the pars autopalatina; *f. hm*, articular fossa for the hyomandibula; *f. my*, fenestra ventralis myodomus; *f. occ. lat*, fissura occipitalis lateralis; *f. ot. v*, fissura oticalis ventralis; *my*, posterior myodome; *nn*, notch in the margin of the planum antorbitale; *np*, nasal pit; *pit. font*, pituitary fontanelle; *pr. po*, processus postorbitalis; *r. ot*, canal for the ramus oticus lateralis; *s. max. buc*, notch for the ramus maxillaris trigemini, the nervus buccalis lateralis, and vessels; *sn*, ossification in the posterior part of the septum nasi; *spic*, spiracular canal; *t*, canal for a vessel (vein?); *trig. fac. ch*, trigemino-facialis chamber; *v*, canal for a (?) vessel; *v. cer. ant*, canal for the vena cerebralis anterior; *v. font*, vestibular fontanelle; *I*, groove for the nervus olfactorius; *II*, opening for the nervi optici; *III*, the two orbital openings of the canal for the nervus oculomotorius; *IV*, canal for the nervus trochlearis; *V*, trigeminus canal; *V*$_1$, canal for the nervus ophthalmicus profundus; *VI*, canal for the nervus abducens; *VII*, facialis canal; *IX*, canal for the nervus glossopharyngeus.

ly covered by the pars anterior parasphenoidei. The width of the ventral face increases slowly towards the ethmoidal region. The ventral face is not plane as in *Glaucolepis magna* (p. 91), but concave from side to side, and the depth of the concavity increases from the posterior towards the anterior part of the face. This concavity (cf. Figs. 6, 9, 10), which thus appears as a broad longitudinal groove on the ventral face, is occupied by a longitudinal ridge from the dorsal side of the pars anterior parasphenoidei, however, in such a way, that between the endocranium and the parasphenoid a paired longitudinal canal for the ramus palatinus facialis and a forward directed branch of the arteria carotis interna is formed (cf. p. 103).

The large fenestra optica, which pierces the interorbital wall and whose outline appears from Figs. 4 and 9, is bounded caudally by a median vertical ridge on the anterior face of the pars basisphenoidea (cf. p. 63) except most dorsally, where the fenestra optica and the large unpaired opening for the nervi optici are confluent in the fossil cranium. There is good reason to assume, however, that the foramen opticum was divided into a right and a left half by a cartilaginous pillar, which at the same time formed the caudal boundary of the dorsal part of the fenestra optica. This cartilaginous pillar connected the dorsal part of the ossified pars basisphenoidea with the part of the ossification of the orbitotemporal region that forms the ventral wall of the anterior part of the cavum cerebrale cranii. At any rate such a small pillar is ossified in *Glaucolepis magna*, and on its anterior side it has a sharp vertical median ridge which forms a direct continuation of the median ridge on the anterior side of the pars basisphenoidea (see Fig. 16). Owing to this circumstance we must assume that in *Glaucolepis stensiöi* the nervus opticus did not enter the orbit through the posterior part of the fenestra optica, as is the case, according to Stensiö, e. g. in *Perleidus* (Stensiö 1932, p. 202) and *Broughia* (Stensiö 1932, p. 242).

Dorsally the fenestra optica is bounded by the fairly sharp median keel which terminates ventrally the dorsal interorbital part of the ossification of the orbitotemporal region.

Ventrally the fenestra optica is bounded by a sharp median keel on the dorsal side of that part of the ossification of the orbitotemporal region which directly overlies the pars anterior parasphenoidei. In the foremost part of the orbitotemporal region the median keels of both the ventral and the dorsal parts of the ossification increase so considerably in height that they are fused to a continuous interorbital wall whose caudal margin forms the anterior edge of the fenestra optica. In the sectioned specimen (Figs. 4, 9, 10, 11), this part of the interorbital wall is unossified to a considerable extent, especially in its dorsal part, the anterior margin of the fenestra optica being thus incomplete. However, a comparison with the conditions in *Glaucolepis magna* (Pl. 6, Fig. 2) shows beyond doubt that the anterior dorsal part of the interorbital wall in *Glaucolepis stensiöi* consisted of cartilage and that it

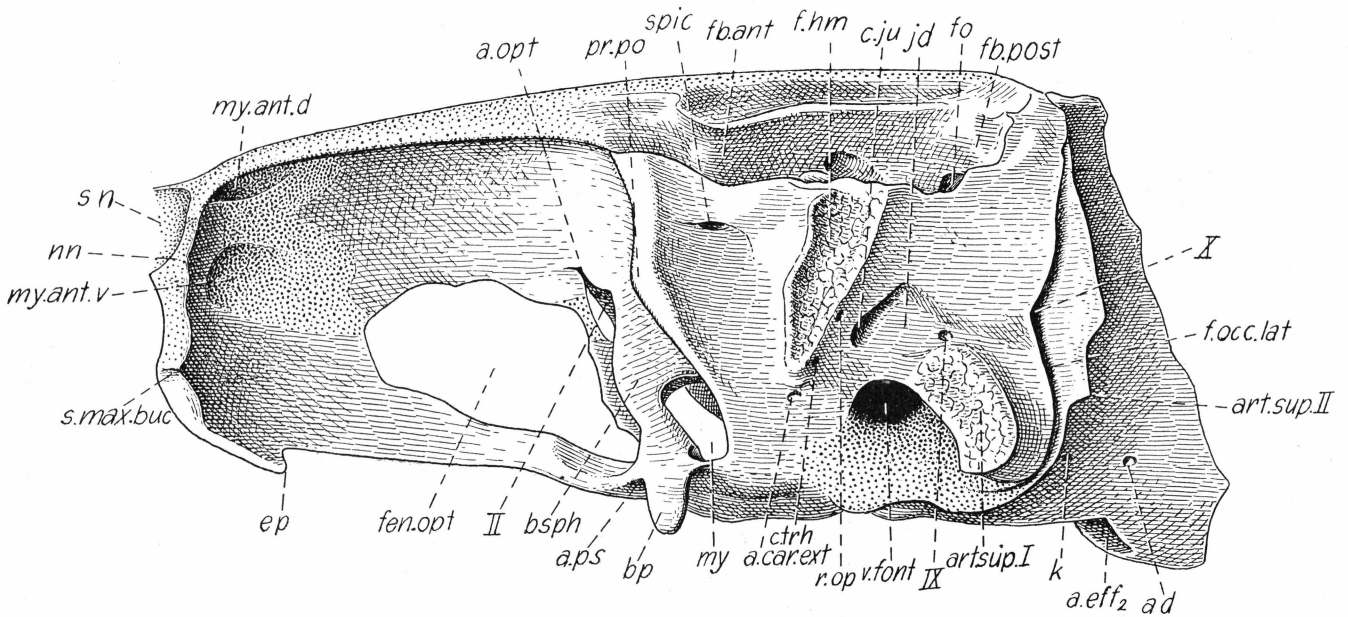


Fig. 11. *Glaucolepis stensiöi* n. sp. Attempted restoration of the complete neural endocranium in lateral view. Cartilaginous areas dotted, faces without perichondral bone reticulated. Fig. 4 has been used as a basis for the restoration. The ethmoidal region and the anterior part of the orbito-temporal region restored partly after well ossified specimens of *Glaucolepis magna*. 6–7 X.
my. ant. d, anterior dorsal myodome; *my. ant. v*, anterior ventral myodome; *sn*, septum nasi. Other letters as in Fig. 4.

was not, as is the case in *Saurichthys* (Stensiö 1925, pp. 35–36, etc.), pierced by any fenestra.

The continuity of the sharp median keel which entirely surrounded the fenestra optica, and to which the membrane must have been attached which closed the large fenestra in the living animal, shows that the fenestra optica was unpaired throughout its extent.

Stensiö (1932, pp. 202—03, 242) points out that the fenestra optica is not always directly comparable in the different primitive fossil Actinopterygians in which its size and place are known. In *Birgeria* it lies more ventrally than in *Ospia* and *Perleidus*, and in the two last-mentioned genera it extends farther backward than in *Saurichthys* and the Kansas forms A and B. According to Stensiö this difference in the backward extension of the fenestra optica is due to the fact that in *Perleidus* and *Ospia*, in contrast to what is the case in *Saurichthys* and the Kansas *Palaeonisciformes*, the fenestra optica extends posteriorly some way into the lateral wall of the cavum cerebrale cranii and is accordingly paired in its hindmost part.

If this is actually the case, which cannot be seen from Stensiö's figures, it is only in its postero-dorsal part that the fenestra optica in *Perleidus* and *Ospia* has a somewhat greater posterior extension, for in all the forms discussed above the fenestra optica is limited postero-ventrally by the anterior part of the pars basisphenoidea, whose relation to the arteria carotis interna, etc., shows that this anterior part is no doubt homologous in *Saurichthys*, the Kansas forms, *Ospia*, and *Perleidus*.

As the fenestra optica is developed in *Glaucolepis*, it is directly comparable to that of *Saurichthys* and those of the Kansas forms, and probably to the greater part of the fenestra optica in *Perleidus*, too.

The pars basisphenoidea reaches from the basal face of the endocranium so far dorsally that its most dorsal part forms the floor of the opticus canal. Anteriorly the most ventral part of the pars basisphenoidea passes gradually into that part of the ossification of the orbitotemporal region which lies ventrally to the fenestra optica, and it is continued posteriorly by the ventral wall of the myodome.

Above its most basal part, the pars basisphenoidea stands, broadly speaking, as a dorsally and at the same time somewhat forwardly directed, broad bone pillar (*bsph*, Figs. 2, 4, 9, 10, 11) which is compressed in a rostro-caudal direction. The anterior face of this pillar is roughly convex, and its posterior face roughly concave.

The anterior face is divided by the aforementioned vertical median keel into a right and a left half. Laterally to the median keel another vertical keel is found on the right and the left half of the anterior face, so that the anterior face of the pars basisphenoidea is divided by the unpaired median and the paired lateral keel into four smaller fields, viz. a medial and a lateral field on either side of the median keel.

The medial field is very slightly concave from side to side, and on its ventro-lateral part has an opening (*a. opht. m*, Fig. 10) leading to the canal which runs through the pars basisphenoidea in a dorso-ventral direction and which has contained the arteria carotis interna (*a. car. int,* Fig. 2) (cf. Watson 1925, p. 842; Stensiö 1921, p.177; 1925, pp. 39–41; 1932, p. 244; Allis 1897, pp. 497–498, etc.). Through this opening the arteria ophthalmica magna passed into the orbit.

Ventrally to this foramen (which is oblong in a dorso-ventral direction) for the arteria ophthalmica magna the concavity of the medial field is deeper, so that slightly medially to the ventral part of the canal for the arteria carotis interna the pars basisphenoidea is very thin (Fig. 2, section 330). This deep part of the concavity of the medial field was no doubt the place of insertion for one of the recti muscles of the eye.

In the Kansas form A (Watson 1925, p. 838; Fig. 16) and in *Perleidus* (Stensiö 1932, p. 203) the pars basisphenoidea is entirely perforated precisely in the place where this depression occurs in *Glaucolepis*, and accordingly the myodome, in addition to its large paired opening, has a smaller, likewise paired, more medially placed opening towards the orbit. The conditions in *Glaucolepis* must be regarded as more primitive than in the Kansas form A and in *Perleidus*.

The lateral field of the anterior face of the pars basisphenoidea is directed antero-laterally (cf. Fig. 10), and like the medial field is slightly concave from side to side. Probably the lateral field, too, has, to a greater or smaller extent, been the place of insertion for eye muscles.

The ventral face of the posterior part of the orbitotemporal region, that is to say, the ventral face of the pars basisphenoidea and of the anterior part of the ventral wall of the myodome, is entirely covered by the parasphenoid (cf. Pl. 5, Figs. 1, 2). This ventral face (for the time being we disregard the well developed basipterygoid processes) increases in breadth from its anterior part towards its gradual transition into the ventral face of the otic region. Below the pars basisphenoidea the ventral face is slightly convex from side to side, as it is below the myodome, too, except that its regular arch is here broken by the slight indications of the anterior part of the sub-myodomic crest (p. 50), which extends from the otic region some way forward into the orbitotemporal region.

From the basal part of the pars basisphenoidea there issues on either side a very well developed processus basipterygius (*bp*, Figs. 2, 4, 6, 8, 9, 10, 11) pointing in a lateral and at the same time slightly ventral direction. This process, which is rather triangular in transverse section, has, broadly speaking a dorsal, an antero-ventral, and a postero-ventral face. Against the postero-ventral face rests the processus ascendens anterior of the parasphenoid, which also covers the greater part of the antero-ventral face. Viewing the endocranium with the attached parasphenoid from the ventral side, we can only

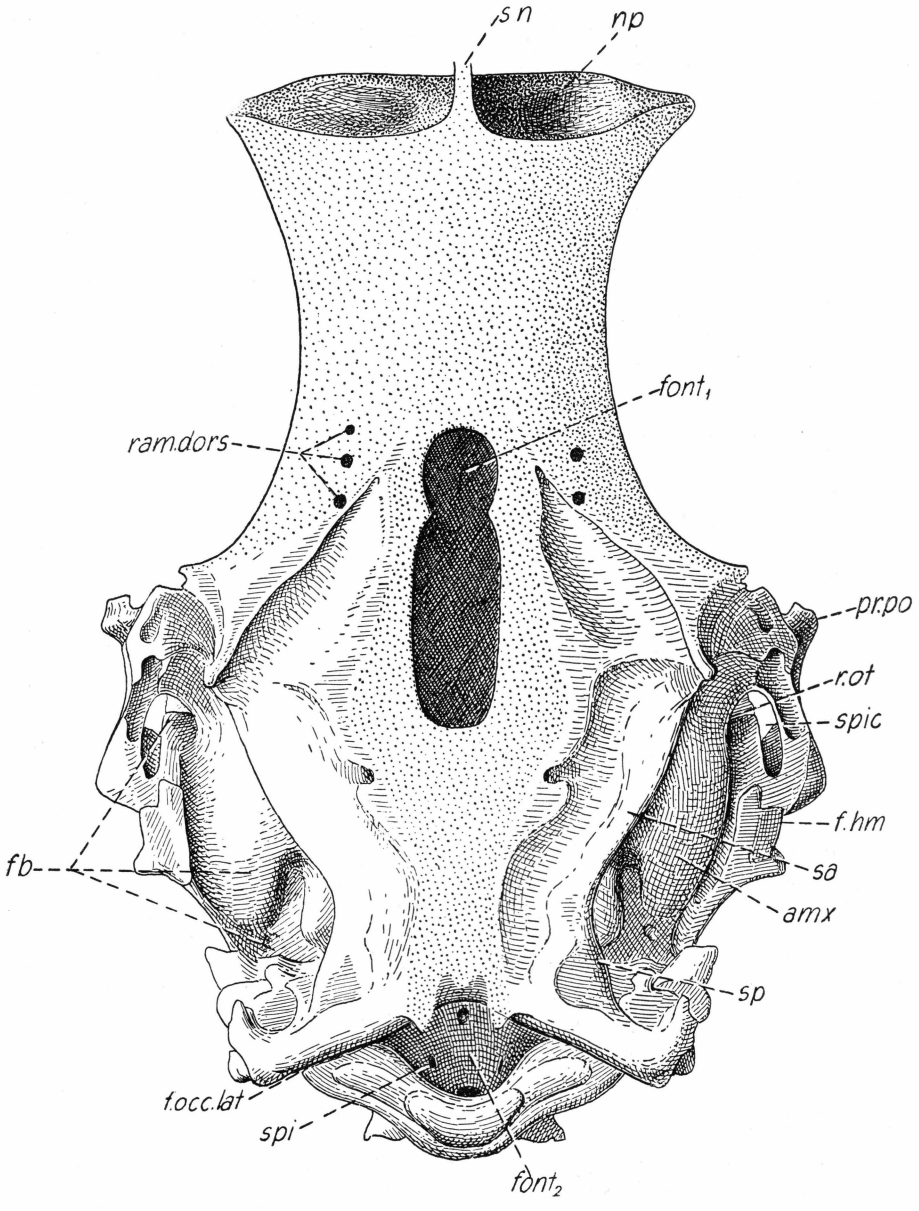


Fig. 12. *Glaucolepis stensiöi* n. sp. Attempted restoration of the complete neural endocranium in dorsal view. Cartilaginous areas dotted. Fig. 7 has been used as a basis for the restoration. Anterior part of the endocranium restored in part on the basis of well ossified specimens of *Glaucolepis magna*. Outline of the anterior dorsal fontanelle hypothetic. 6–7 ×. *ram. dors*, canals for branches of the ramus ophthalmicus superficialis trigemini, the nervus ophthalmicus lateralis, and vessels. Other letters as in Fig. 7.

see the most distal end of the processus basipterygius, this process being but slightly longer than the processus ascendens anterior.

The dorsal (and slightly anteriorly directed) face of the processus basi-

pterygius is nearly plane, except that its foremost part curves slightly downward to pass gradually into the anterior face of the process.

The details of the palato-basal articulation, the articulation between the processus basipterygius and the palatoquadrate, are very difficult to ascertain. The ossification of the palatoquadrate has not, as for instance in *Boreosomus* (Fig. 70), a well developed articular fossa for the processus basipterygius, but, as far as I can make out, it was in contact with the processus basipterygius by means of a fairly slender process, which probably rested against the distal end or the dorsal face of the processus basipterygius (see further p. 144).

On the ventral face of the endocranium, caudally to the base of the processus basipterygius and laterally to the fenestra ventralis myodomus, two short grooves (*r. pal*, *a. car. int*, Figs. 6, 8) are seen, which join to form a V, the apex of which points in a rostral direction. The caudal end of the most lateral of the two grooves continues in a short canal, which pierces the most lateral part of the floor of the myodome. Through this canal the ramus palatinus facialis passed from the myodome to the groove on the ventral face of the endocranium (cf. Watson 1925, pp. 839–40, Fig. 20; Stensiö 1932, pp. 210, 248, Figs. 65B and 73A), which is closed by the parasphenoid to form a canal. After having passed this canal, the ramus palatinus facialis continued in a rostral direction between the parasphenoid and the endocranium through the canal mentioned above on p. 61, the posterior end of which lies immediately in front of the apex of the V formed by the two short grooves.

In addition a canal issues in an antero-dorso-medial direction from the apex of the V groove, passing through the basal part of the processus basipterygius, in which it gradually changes its direction to continue as the aforementioned vertical canal for the arteria carotis interna, which pierces the pars basisphenoidea throughout its entire height.

Immediately before the arteria carotis interna curved into the pars basisphenoidea, it passed ventrally to the endocranium in the medial of the two aforementioned short grooves which together form a V, and behind this groove it passed through a canal (cf. p. 105) in the pars posterior of the parasphenoid to unite with the arteria carotis externa immediately behind the posterior margin of the parasphenoid.

Immediately in front of the base of the processus basipterygius opens on the ventral face of the endocranium a wide, short canal (*a. ps*, Figs. 2, 4, 6, 8, 10, 11), which leads to the canal for the arteria carotis interna in the basal part of the pars basisphenoidea.

This canal must have contained the arteria pseudobranchialis efferens, which in the pars basisphenoidea accompanied the arteria carotis interna on a short stretch and possibly communicated with the latter before it again left the pars basisphenoidea as the arteria ophthalmica magna through the aforementioned opening (*a. opht. m*) on the anterior side of the pars basi-

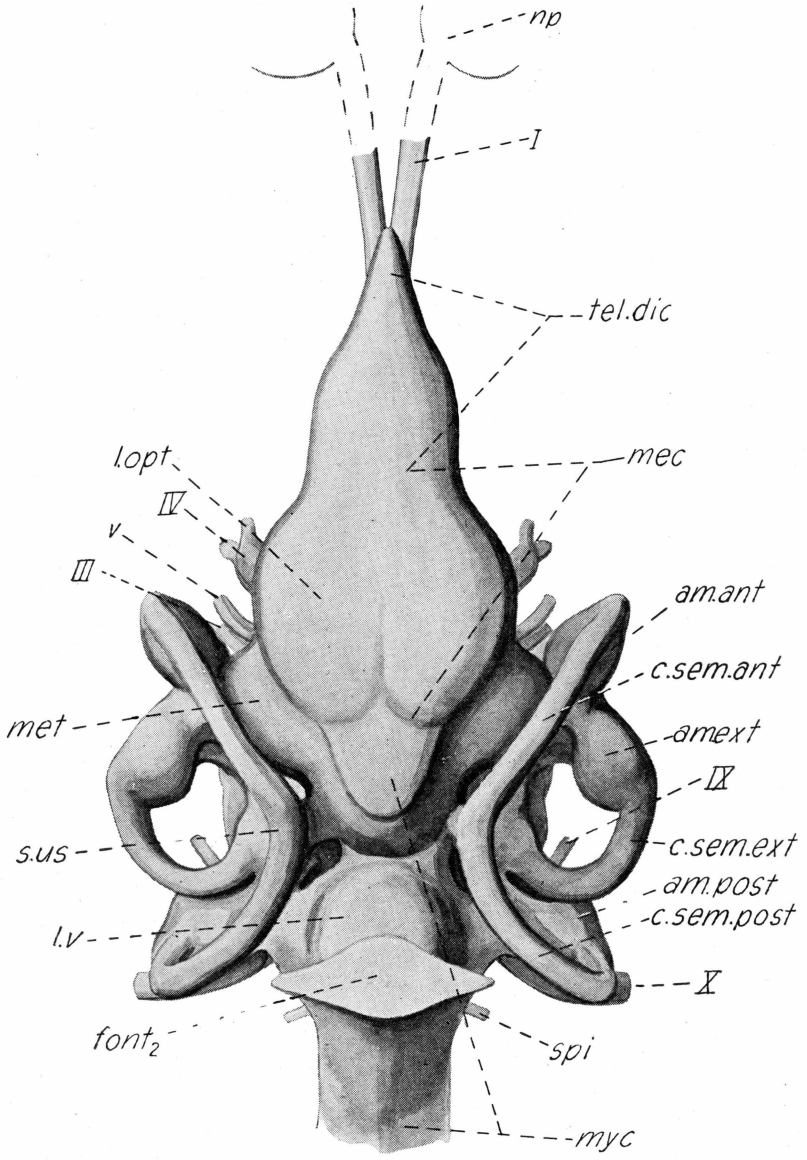


Fig. 13. *Glaucolepis stensiöi* n. sp. Cast of the cavities of the neural endocranium in dorsal view. On the basis of a wax model. 6–7 ×.

l. v, division of the cavum cerebrale crani for the "lobi vagi"; *mec*, division of the cavum cerebrale cranii for the mesencephalon; *myc*, division of the cavum cerebrale cranii for the myelencephalon; *tel. dic*, division of the cavum cerebrale cranii for the telencephalon and diencephalon. Other letters as in Fig. 14.

sphenoidea (cf. Watson 1925, p. 840; Stensiö 1925, pp. 39-40, 53; 1932, p. 244; etc.).

In the place where the arteria carotis interna from the ventral face of the endocranium curved into the pars basisphenoidea, it probably gave off a small branch, which together with the ramus palatinus facialis continued in a rostral direction in the canal between the parasphenoid and the endocranium, as was probably the case in *Broughia*, too (Stensiö 1932, pp. 271-272).

That part of the cavum cerebrale cranii which lies in the orbitotemporal region has its greatest width nearest the transition to the otic region, tapering anteriorly, as appears distinctly from the figures showing the model of the cranial cavity (Figs. 13, 14, 15).

This part of the cavum cerebrale cranii is bounded by a paired lateral, an unpaired ventral, and an unpaired dorsal wall; the last-mentioned wall is very incomplete, for it consisted chiefly of cartilage and was moreover pierced by the anterior part of the large anterior dorsal fontanelle.

The paired lateral wall, which is penetrated by several canals, is rather thin and is devoid of perichondral bone-layers farthest dorsally on its cerebral face. A considerable concavity (*l. opt*, Fig. 9) on the posterior half of the cerebral face of the lateral wall suggests the presence of well developed lobi optici (see further p. 100). The preserved part of the dorsal wall may most adequately be described as a narrow medially projecting ridge along the dorsal margin of the posterior half of the lateral wall; but the absence of perichondral bone on the dorsal part of its cerebral face indicates that an essential part of the dorsal boundary of the cavum cerebrale cranii was cartilaginous.

The floor of the cavum cerebrale cranii is divided by the large foramen opticum into an anterior and a posterior part.

The anterior part of the floor slopes upward from the dorsal edge of the foramen opticum to the anterior end of the cavum cerebrale cranii. As will be seen from Fig. 7, this part of the floor is quite narrow and may just as well be described as the most ventral part of the right and left lateral walls, which curve inwards and meet below the anterior part of the cavum cerebrale cranii.

The hindmost part of the floor lies on a level with the ventral margin of the foramen opticum and is formed chiefly by the dorsal face of the pars basisphenoidea and the dorsal margin of the prootic bridge (Figs. 2, 7). Between the prootic bridge and the dorsal part of the pars basisphenoidea the cavum cerebrale cranii narrows into an infundibular recess (*inf. r*, Figs. 2, 9), which ventrally communicates with the myodome by a pituitary fontanelle (*pit. font*, Figs. 9, 10). In the hind wall of the infundibular recess there is a fairly wide, round opening, which leads into a small rounded cavity (*s. vasc*, Figs. 2, 9), the significance of which will be dealt with below.

On that part of the floor of the cavum cerebrale cranii which is formed of the dorsal face of the pars basisphenoidea, lie the dorsal openings of the right and left canals for the arteria carotis interna, and on the dorsal face of the

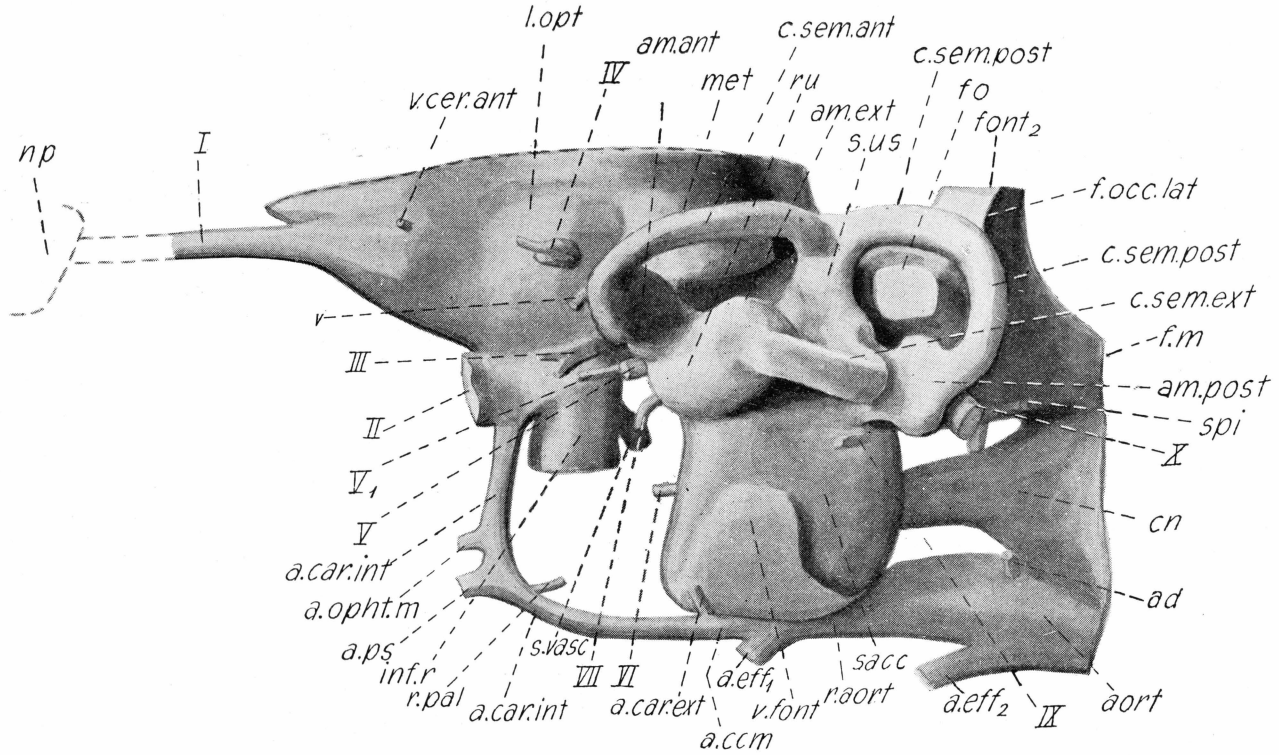


Fig. 14. *Glaucolepis stensiöi* n. sp. Cast of the cavities of the neural endocranium in lateral view. On the basis of a wax model. 6–7 ×. *a. car. ext*, canal for the arteria carotis externa; *a. car. int*, canal for the arteria carotis interna; *ad*, canal for an artery; *a. ccm*, canal for the arteria carotis communis; *a.eff*$_1$, *a.eff*$_2$, canals for the arteriae branchiales efferentes I and II respectively; *am. ant*, *am. ext*, *am. post*, divisions of the labyrinth cavity for the ampulla anterior, the ampulla externa, and the ampulla posterior respectively; *a. opht. m*, canal for the arteria ophthalmica magna; *aort*, aorta canal; *a. ps*, canal for the arteria pseudobranchialis efferens; *cn*, space for the notochord; *c. sem. ant*, *c. sem. ext*, *c. sem. post*, divisions of the labyrinth cavity for the canalis semicircularis anterior, the canalis semicircularis externus, and the canalis semicircularis posterior respectively; *f. m*, foramen magnum; *fo*, opening in the wall between the fossa bridgei and the cavum cerebrale cranii; *f. occ. lat*, fissura occipitalis lateralis; *font*$_2$. posterior dorsal fontanelle; *inf. r*, infundibular recess; *l. opt*, division of the cavum cerebrale cranii for the lobus opticus; *met*, division of the cavum cerebrale cranii for the lateral part of the metencephalon; *np*, place for the nasal sac; *r. aort*, canal for the aorta root; *r. pal*, canal for the ramus palatinus facialis; *ru*, division of the labyrinth cavity for the recessus utriculi; *sacc*, division of the labyrinth cavity for the sacculus; *spi*, canal for a spino-occipital nerve; *s. us*, division of the labyrinth cavity for the sinus utriculi superior; *s. vasc*, division of the cavum cerebrale cranii for the saccus vasculosus; *v*, canal for a (?) vessel; *v. cer. ant*, canal for the vena cerebralis anterior; *v. font*, vestibular fontanelle; *I*, canal for the nervus olfactorius; *II*, opening for the nervi optici; *III*, canal for the nervus oculomotorius; *IV*, canal for the nervus trochlearis; *V*, trigeminus canal; *V*$_1$, canal for the nervus ophthalmicus profundus; *VI*, canal for the nervus abducens; *VII*, facialis canal; *IX*, canal for the nervus glossopharyngeus; *X*, canal for the nervus vagus.

pars basisphenoidea, in front of a vertical transverse plane through these openings, runs a broad but shallow transverse groove (*chsm*, Figs. 7, 15), which on account of its position corresponds to the depression on the dorsal face of the pars basisphenoidea in *Saurichthys*, which is stated by Stensiö (1925, p. 80, Fig. 11) to indicate the position of the chiasma.

Myodome, trigemino-facialis chamber, jugulo-hyoideomandibular canal, and canals for nerves and vessels in the posterior part of the orbitotemporal region and the anterior part of the otic region. – In *Glaucolepis stensiöi* a well developed posterior myodome situated partly in the posterior part of the orbitotemporal region and partly in the anterior part of the otic region is developed (*my*, Figs. 2, 4, 9, 10, 11). In its relations to the surrounding endocranial structures it shows good agreement with the myodome of the Kansas forms and differs in no essential respect from that of *Perleidus*, which has been described in detail by Stensiö (1932, pp. 207–212).

The posterior myodome of *Glaucolepis stensiöi* is an intramural space, to which a very inconsiderable extracranial part is added, at least in some speimens. (NB. If, with Allis and others, we would regard the trabeculae as being of visceral origin, a much larger part of the myodome must, of course, be termed extracranial).

The myodome opens into each orbit with a very large opening, which dorso-laterally is confluent with the orbital opening of another intramural space, the so-called trigemino-facialis chamber. The right and left orbital myodome openings are separated from each other by the broad pars basisphenoidea, in which, as stated above, no opening is found corresponding to the paired medial orbital myodome opening in *Perleidus* (Stensiö 1932, Figs. 59A and 64A) and in the Kansas form A (Watson 1925, Fig. 16).

In sagittal section the myodome is irregularly elliptic in outline, the long diameter of the ellipse pointing forward and somewhat upward (Fig. 9). A horizontal section through the myodome (Fig. 2, section 300) shows that both its anterior and posterior sides are convex, the posterior side being, however, more curved than the anterior one. In *Perleidus* (Stensiö 1932, pp. 207–208) the anterior side of the myodome is concave, the posterior face of the pars basisphenoidea being convex in a transversal direction.

The dorsal and posterior boundary of the myodome is formed by a transversally placed bone wall, which is uniformly curved, its foremost part forming the nearly horizontal roof and its hindmost part the nearly vertical posterior wall of the myodome. The roof of the myodome passes anteriorly into the dorsal part of the pars basisphenoidea; it is a thick bony mass, which at the same time forms the floor of that part of the cavum cerebrale cranii which directly overlies the myodome.

The ventral face of the roof of the myodome, that is to say, the face directed towards the myodome, meets laterally with the orbital face of the

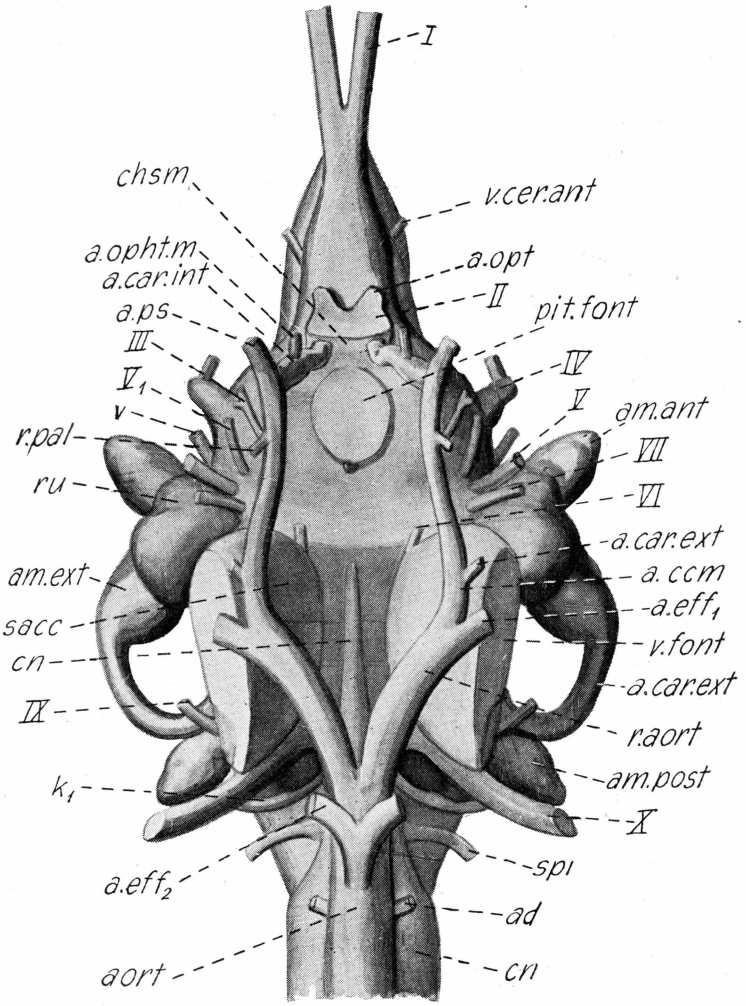


Fig. 15. *Glaucolepis stensiöi* n. sp. Cast of the cavities of the neural endocranium in ventral view. On the basis of a wax model. 6–7 ×.
a. opt, canal for the arteria optica; *chsm*, division of the cavum cerebrale cranii for the chiasma; k_1, canal from the cavum cerebrale cranii to the fossa bridgei; *pit. font*, pituitary fontanelle. Other letters as in Fig. 14.

orbitotemporal region in such a way that a rather conspicuous edge or ridge is formed. This edge or ridge runs from the dorsal part of the lateral margin of the pars basisphenoidea in a caudal direction, being continued farther posteriorly by a rather indistinct ridge (Fig. 10), which constitutes the very incomplete separation between the myodome and the trigemino-facialis chamber.

Immediately behind the pars basisphenoidea the roof of the myodome is perforated by a large median pituitary fontanelle (*pit. font*, Figs. 9, 10, 15), which is elliptic in outline, with its long diameter running in a rostro-caudal direction.

The part of the myodome wall which lies immediately behind the pituitary fontanelle forms at the same time the floor of that part of the cavum cerebrale cranii which lies in the anterior part of the otic region, and is equivalent to the prootic bridge in recent Actinopterygians. Posteriorly this part of the myodome wall curves gradually downward, to continue as the nearly vertical hind wall of the posterior part of the myodome. This hind wall is rather thin and bounds anteriorly the fissura oticalis ventralis. As stated above, this fissure was closed by cartilage, and the dorsal part of the floor of the otic region consisted largely of cartilage, too.

The nervus abducens must have passed through the dorsal unossified part of the floor of the otic region to continue forward through the ossified hind wall of the myodome, where its fine canal opens somewhat laterally to the median plane of the myodome (*VI*, Figs. 2, 9, 10). In the position of the myodomic opening of the abducens canal *Glaucolepis* agrees entirely with *Perleidus* (Stensiö 1932, p. 210) and the Kansas form B (Watson 1925, p. 842).

The floor of the myodome is quite thin in its most median part, but increases gradually in thickness both towards the pars basisphenoidea and towards the lateral and posterior walls of the myodome. The ventral face of the floor of the myodome is covered by the pars posterior parasphenoidei.

Immediately behind the basal part of the pars basisphenoidea the floor of the myodome is perforated by a large median fenestra ventralis myodomus (*f. my*, Figs. 2, 6, 7, 8, 9, 10). This fenestra is elliptic in outline, the long diameter of the ellipse running in a rostro-caudal direction.

The parasphenoid is not perforated by any opening corresponding to the fenestra ventralis myodomus, but the part of the parasphenoid which closes the fenestra ventralis myodomus ventrally has a depression on its dorsal side, so that in this place the parasphenoid is very thin. (cf. p. 104).

Through the most lateral part of the floor of the myodome, immediately caudally to the base of the processus basipterygius, there issues from the myodome, in an antero-medio-ventral direction, the aforementioned canal through which the ramus palatinus facialis reached the ventral side of the endocranium.

The anterior wall of the myodome is made up of the pars basisphenoidea, whose posterior face is slightly concave both vertically and transversally. The transverse concavity is especially marked in the most ventral part of the posterior face, where the curvature of the face coincides with the curvature of the anterior margin of the fenestra ventralis myodomus.

No groove or depression which might indicate the position of the pituitary vein is found on either the floor or the anterior wall of the myodome.

The lateral wall of the myodome is developed almost as in *Perleidus* (Stensiö 1932, p. 210, Figs. 64 B and 65 B) and the Kansas form A (Watson 1925, Fig. 20). Dorsally to the myodome the lateral wall continues as

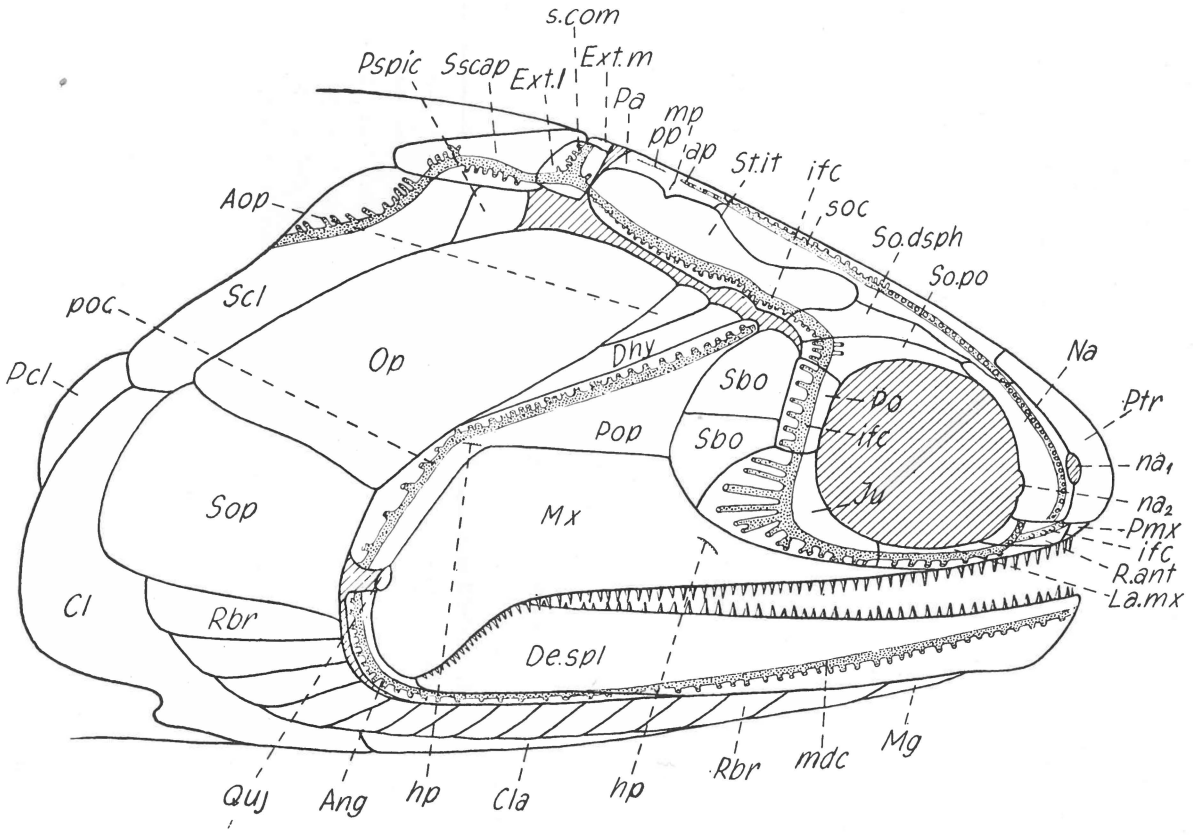


Fig. 27. *Glaucolepis stensiöi* n. sp. Head and dermal shoulder girdle in lateral view. Smallest teeth on the mandible, the lacrimo-maxillary, and the dentalo-splenial omitted. Mainly on the basis of specimen No. 39. 3–4 ×.

Ang, angular; *Aop*, antoperculum; *Cl*, cleithrum; *Cla*, clavicle; *De. spl*, dentalo-splenial; *Dhy*, dermohyal; *Ext. l*, lateral extrascapular; *Ext. m*, medial extrascapular; *Fr*, frontal; *Ju*, jugal; *La. mx*, lacrimo-maxillary; *Mg*, median gular plate; *Mx*, maxillary; *Na*, nasal; *Op*, operculum; *Pa*, parietal; *Pcl*, postcleithral; *Pmx*, premaxillary (not observed with certainty); *Po*, postorbital; *Pop*, preoperculum; *P. spic*, postspiracular bone; *Ptr*, postrostral; *Quj*, quadratojugal; *R. ant*, rostro-antorbital; *Rbr*, branchiostegal ray; *Sbo*, suborbital; *Scl*, supracleithral; *So. dsph*, supraorbito-dermosphenotic; *So. po*, supraorbito-postorbital; *Sop*, suboperculum; *Sscap*, suprascapular; *St. it*, supratemporo-intertemporal; *ap*, anterior pit-line; *hp*, horizontal pit-line of the cheek; *ifc*, infraorbital canal; *mdc*, mandibular canal; *mp*, middle pit-line; na_1, na_2, anterior and posterior nostrils; *poc*, preopercular canal; *pp*, posterior pit-line; *s. com*, supratemporal commissure; *soc*, supraorbital canal.

and the postrostral, but the connection between the rostro-antorbital and these two bones must have been very loose.

The shape of the exposed part of the bone will appear from Figs. 27 and 28. This part is bounded by a postero-dorsal, a dorsal, an antero-ventral, and a ventral and slightly posteriorly facing margin. The postero-dorsal, slightly concave margin constitutes part of the boundary of the orbital opening, while the nearly ventral margin suturates with the lacrimo-maxillary. In front of the antero-ventral margin there probably lies a small paired premaxillary (*Pmx*, Figs. 27, 28; Pl. 8, Fig. 3); however, the snout region is in no case so well preserved, that the presence of this bone can be regarded as quite certain. The dorsal part of the rostro-antorbital is covered by the nasal and the postrostral, and cannot be descried in detail in this species; to all appearance, however, the anterior part of the bone, similarly as in the case of *Glaucolepis gunnari*, is produced into an antero-dorsally pointing process (the rostral process), the greater part of which is concealed by the most ventral part of the postrostral (cf. Fig. 32). The distal end of the process is not in contact with the distal end of the corresponding process of the opposite side, but the distance between the two processes is only inconsiderable.

The radiation centre of the bone lies equally distant from its dorsal and its ventral margins, but much nearer the orbital margin than the middle of the bone.

The rostro-antorbital contains a three-branched part of the infraorbital canal. As will be seen from Fig. 27, the infraorbital canal passes from the lacrimo-jugal into the rostro-antorbital through the posterior part of the ventrally and slightly posteriorly facing margin of the rostro-antorbital. From its place of entrance the canal continues to the radiation centre, to divide there into two branches, one of which runs almost parallel with the postero-dorsal margin of the bone till it reaches the dorsal margin at a point situated far caudally to the place where the supraorbital canal reaches the ventral margin of the nasal (see further p. 206). The other of the two branches into which the infraorbital canal divides after reaching the radiation centre of the rostro-antorbital extends forward towards the rostral process, which it pierces to its distal end. (This is in part based on observations of the aforementioned specimen of *Glaucolepis gunnari*). That branch of the infraorbital canal which pierces the rostral process represents all of the ethmoidal commissure that is preserved in *Glaucolepis*. The most median part of the commissure must have run through the small interspace between the rostral processes of the right and the left rostro-antorbitals without being surrounded by bone.

As mentioned above (p. 122), a short groove is found on the internal face of the postrostral, which groove issues from the ventro-lateral corner of the bone towards a point slightly ventrally to the radiation centre. This

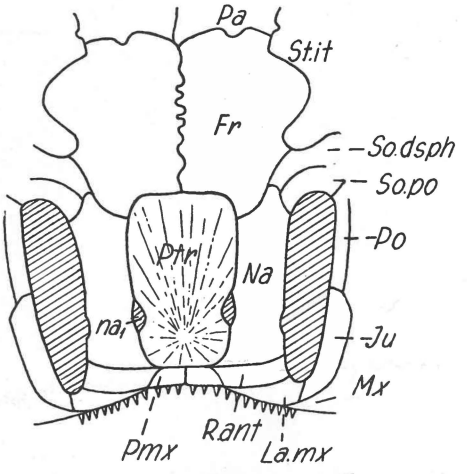


Fig. 28. *Glaucolepis stensiöi* n. sp. Dermal cranial roof, infraorbital series, and premaxillary in front view. Smallest teeth on the lacrimo-maxillary omitted. Mainly on the basis of specimen No. 39. 3–4 ×. Lettering as in Fig. 27.

groove is so situated that the thickening of that division of the rostral process which lies against the internal face of the postrostral and which is due to the presence of the ethmoidal commissure, must be supposed to lie in the groove. Thus the groove indicates the course of the ethmoidal commissure along a short stretch, even though this commissure does not pierce the postrostral itself. I regard it as probable that Moy Thomas's and Bradley Dyne's observation of the course of the commissure in the postrostral in *Canobius elegantulus* and *Canobius ramsayi* (Moy Thomas and Bradley Dyne 1938, Figs. 5 and 40) may be interpreted in a similar way.

In recent years our knowledge of the snout region in the *Palaeonisciformes* has been considerably increased, so that at present we have a fairly good knowledge of the dermal bones of that region and of their relations to the anterior part of the infraorbital canal in the following forms:

Cheirolepis trailli (Watson 1925, Figs. 1, 2, and 3),
Birgeria groenlandica (Stensiö 1932, Fig. 41),
Canobius elegantulus (Moy Thomas and Bradley Dyne, 1938, Fig. 5),
Canobius ramsayi (Moy Thomas and Bradley Dyne, 1938, Fig. 40),
Rhadinichthys fusiformis (Moy Thomas and Bradley Dyne 1938, Fig. 17),
Cornuboniscus budensis (White 1939, Fig. 1),

and the species of *Glaucolepis* and *Boreosomus* described in the present paper.

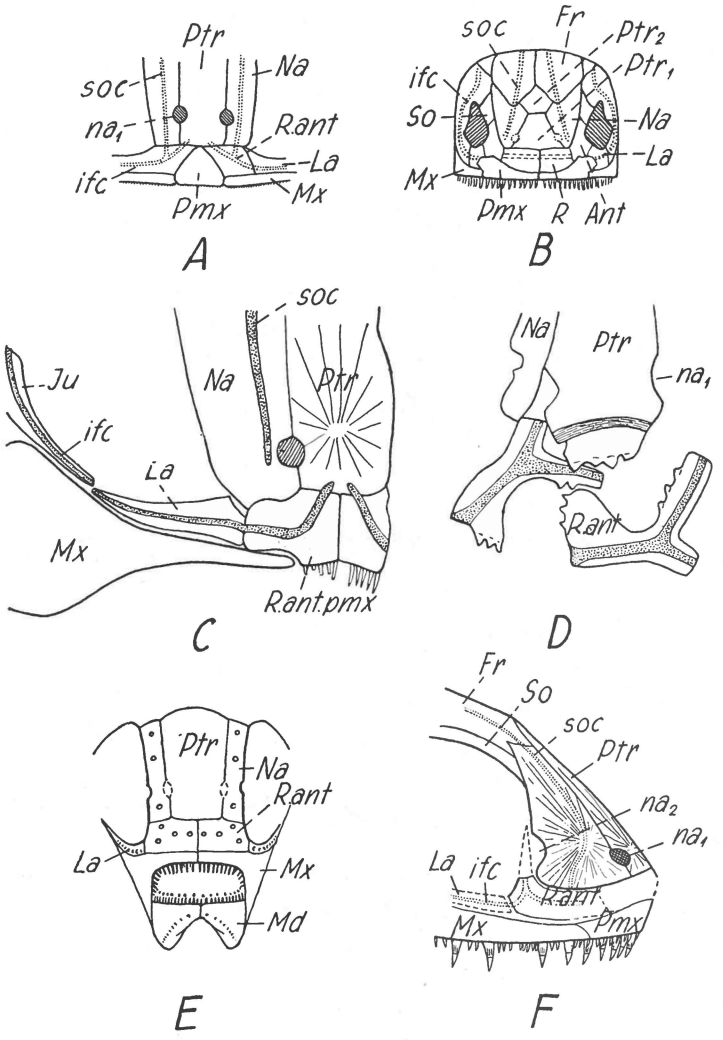


Fig. 29. Snout region of various *Palaeonisciformes*. A, *Canobius ramsayi* (diagrammatic). After Moy Thomas and Bradley Dyne 1938, Fig. 40. B, *Cheirolepis trailli*. After Watson 1925, Fig. 2. C, *Canobius elegantulus*. After Moy Thomas and Bradley Dyne 1938, Fig. 5. D, *Rhadinichthys fusiformis*. After Moy Thomas and Bradley Dyne 1938, Fig. 17. E, *Cornuboniscus budensis*. After White 1939, Fig. 1B. F, *Birgeria groenlandica*. After Stensiö 1932, Fig. 41.

Ant, antorbital; *Fr*, frontal; *Ju*, jugal; *La*, lacrimal; *Md*, mandible; *Mx*, maxillary; *Na*, nasal; *Pmx*, premaxillary; *Ptr*, postrostral; Ptr_1, Ptr_2, anterior and posterior postrostrals; *R*, rostral; *R. ant*, rostro-antorbital; *R. ant. pmx*, rostro-antorbito-premaxillary; *So*, supraorbital; *ifc*, infraorbital canal; na_1, na_2, anterior and posterior nostrils; *soc*, supraorbital canal.

In the earliest of these forms, *Cheirolepis trailli*, we find, according to Watson's figure (the present paper Fig. 29B), a paired nasal (Watson's antorbital), two median postrostrals, which together correspond to the single postrostral in the other forms mentioned above, a paired antorbital (Watson terms this bone the lacrymal, probably because he follows Stensiö (1921) in designating the bone in front of it the antorbital; he adds, however, that the bone most likely corresponds to the antorbital in *Amia*), which contains a three-branched part of the infraorbital canal, a paired rostral traversed by the ethmoidal commissure, and a paired premaxillary.

Westoll discusses the formation of the premaxillary in the Actinopterygians, and arrives at the result that a premaxillary such as that known from the higher Actinopterygians is either a new formation in these forms or does not, at any rate, correspond to independent elements in the *Palaeonisciformes*. He writes (Westoll 1937b, pp. 569–70): "... the writer has been able to study this point in a few Palaeoniscids of "normal" type (*Palaeoniscus*, *Nematoptychius* etc.) and in some of these the maxillaries probably met, or nearly met in the mid-line. In these fishes the bone usually called premaxillary is associated with the ethmoid commissure and may or may not bear teeth." Westoll regards this bone as a rostral.

About the premaxillary in *Cheirolepis* Westoll says (Westoll 1937b, p. 570): "Often however, in Mesozoic fossils, it has been figured as a bone distinct from rostral elements, bearing the ethmoid commissure; this is the case also in Watson's figure of Cheirolepis (1925), but the writer thinks that the evidence in this fish can be read in other ways". This remark, however, is of little value to us, for Westoll fails to inform us what these other ways are.

To Westoll's point of view it may be objected that an independent premaxillary, apparently without connection with the ethmoidal commissure, besides in *Cheirolepis*, occurs in *Canobius ramsayi* (Fig. 29A), in *Birgeria groenlandica* (Fig. 29F), and probably in *Glaucolepis* (Figs. 27, 28). Possibly no premaxillary is found in *Cornuboniscus* (Fig. 29E), if it has not become fused with the maxillary. In the rest of the aforementioned forms in which an independent premaxillary is absent, the bone which contains the ethmoidal commissure bears teeth and is so extensive that quite probably it contains a premaxillary component.

Among the forms discussed here an independent rostral is known in *Cheirolepis* only. (Stensiö (1932, p. 116) assumes, it is true, that a rostral was present in *Birgeria*; however, this is not the case). The paired bone in the other forms which contains the ethmoidal commissure or an essential part of it and, as we have just seen, in some cases a premaxillary component, contains in addition a component representing the independent antorbital in *Cheirolepis* and probably (though hardly in *Birgeria*) a rostral component. For in all cases except in *Canobius elegantulus* (Fig. 29C) the infraorbital

canal, after entering the bone from the element of the infraorbital series lying behind it, divides into two branches, one of which continues in a forward direction to form the ethmoidal commissure, while the other extends more steeply towards the dorsal margin of the bone. Compared with the bones in *Cheirolepis* and in recent Actinopterygians, that part of the bone which contains the place of division of the infraorbital canal, should be regarded as the antorbital part of the bone, while the canal-bearing part of the bone situated ventrally to or behind the ventral part of the postrostral must be regarded as the rostral part of the bone.

Thus in the forms dealt with above, in addition to the postrostral and the paired nasal, which are always independent, we find the following dermal bones in the anterior part of the head:

In *Birgeria groenlandica:* a paired antorbital, an unpaired premaxillary. In *Canobius elegantulus:* a paired rostro-antorbito-premaxillary. In *Canobius ramsayi:* a paired rostro-antorbital, an unpaired premaxillary. In *Rhadinichthys fusiformis:* a paired rostro-antorbito-premaxillary. In *Cornuboniscus budensis:* a paired rostro-antorbital. In *Glaucolepis:* a paired rostro-antorbital, possibly a paired or unpaired premaxillary. In *Boreosomus:* a paired rostro-antorbito-premaxillary.

As will be seen from Fig. 27, two suborbitals (*Sbo*, Fig. 27; Pls. 1, 3, 4, 13, 14), a dorsal and a ventral one, lie behind the vertical part of the infraorbital series. Their mutual connection and the connection between them and the surrounding bones were very loose.

The anterior margin of the dorsal suborbital is overlapped by the posterior part of the postorbital, while the ventral margin is overlapped by the ventral suborbital. The posterior margin overlaps the anterior margin of the preoperculum, and finally, the dorsal margin is without contact with any bone.

As to the ventral suborbital, its anterior margin is overlapped by the posterior part of the postorbital, and its antero-ventral margin by the postero-dorsal margin of the jugal; its posterior margin overlaps a portion of the anterior margin of the preoperculum and of the antero-dorsal margin of the maxillary, and its dorsal margin overlaps the ventral margin of the dorsal suborbital.

In both suborbitals the radiation centre is situated slightly in front of their mid-point. The two suborbitals seem to correspond to the two most dorsal of the three suborbitals in *Palaeoniscus freieslebeni* (Westoll's reconstruction).

The sclerotic ring (*Sclr*, Pls. 1, 2) most frequently consists of four segments; in some cases, however, it probably comprises three segments only.

b. Glaucolepis magna.

The elements of the infraorbital series (Fig. 30) differ in no essential respects from the corresponding ones in *Glaucolepis stensiöi*, and a detailed

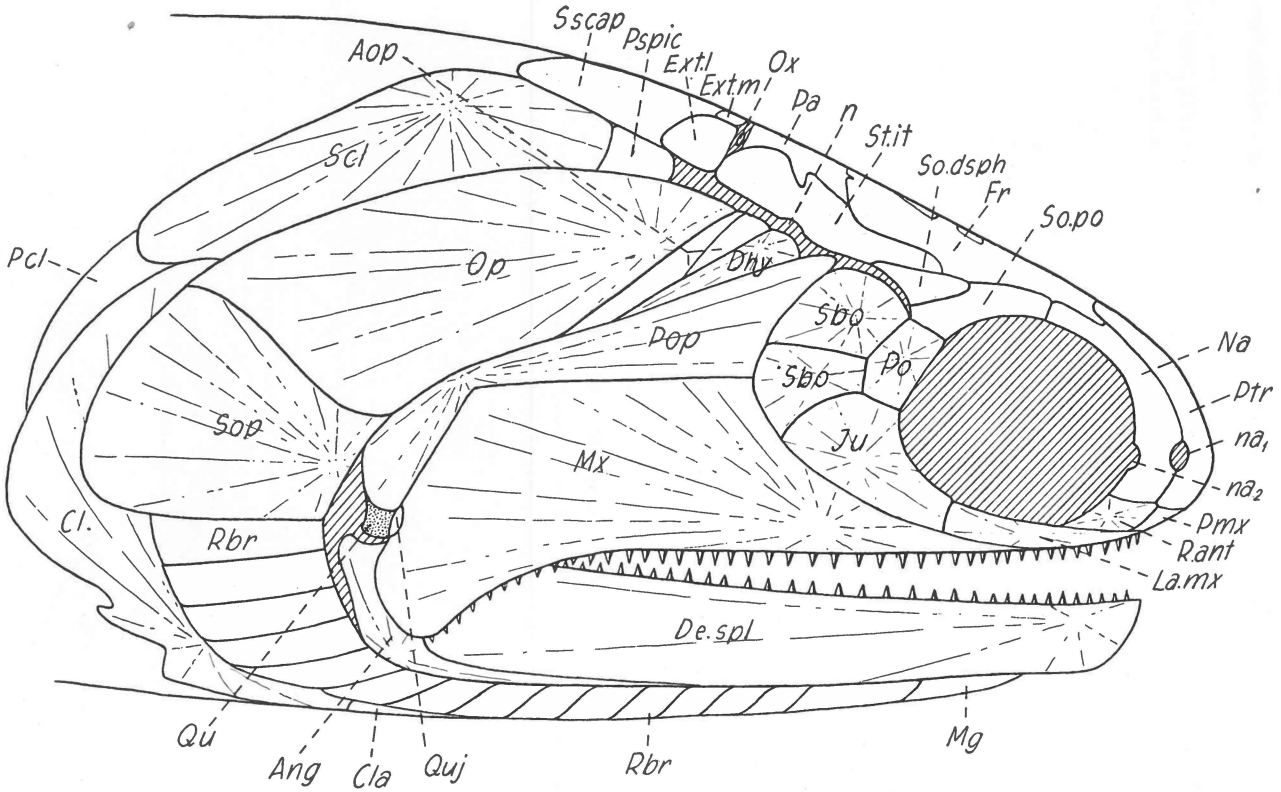


Fig. 30. *Glaucolepis magna* n. sp. Head and dermal shoulder girdle in lateral view. Smallest teeth on the maxillary, the lacrimo-maxillary, and the dentalo-splenial omitted Chiefly on the basis of specimen No. 51. 2 ×.
Ox, small dermal bone in front of extrascapular series; *Qu*, quadrate. Other letters as in Fig. 27.

description is accordingly superfluous. The lacrimo-maxillary is exceptionally well preserved in specimen No. 51, and is reproduced in Fig. 31. The row of large teeth on the internal horizontal lamina of this bone is concealed in the rock, so only the quite small teeth on the ventral margin of the bone are shown in the figure.

As a rule two suborbitals are present, namely, as in *Glaucolepis stensiöi*, a dorsal and a ventral one; but in some cases a third, rather narrow subor-

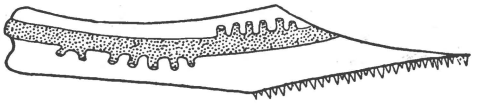


Fig. 31. *Glaucolepis magna* n. sp. Lacrimo-maxillary. Large teeth of the bone omitted. Based on specimen No. 51. 4.6 ×.

bital intervenes between the dorsal suborbital and the postorbital; the anterior margin of this third suborbital is overlapped by the postorbital, while its posterior margin overlaps the anterior margin of the normal dorsal suborbital.

The sclerotic ring in most cases consists of four segments (*Sclr*, Pl. 9, Fig. 1)

c. Gaucolepis aldingeri, arctica, and gunnari.

The infraorbital series in these species, in so far as it has been investigated (the lacrimo-maxillary and the rostro-antorbital are not preserved in *Glaucolepis aldingeri*), agree well with the infraorbital series in *Glaucolepis stensiöi*.

Fig. 32, which shows the exact shape of the rostro-antorbital and its position in relation to the postrostral, has been constructed on the basis of

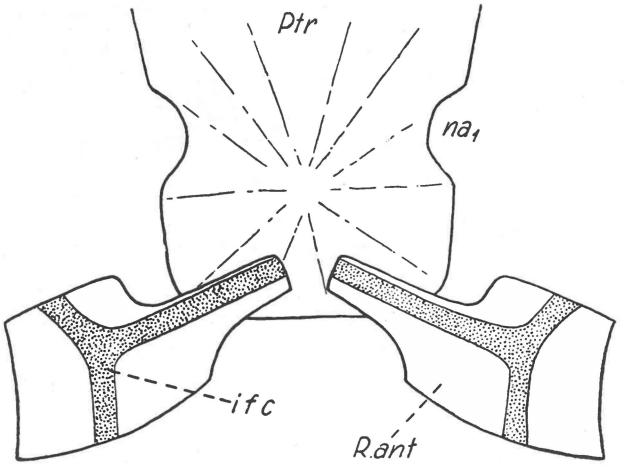


Fig. 32. *Glaucolepis gunnari* n. sp. Postrostral and right and left rostro-antorbitals in posterior view. Diagram showing the relations between these bones. On the basis of specimen No. 9. 5 ×.
Ptr, postrostral; *R. ant*, rostro-antorbital; *ifc*, infraorbital canal; na_1, anterior nostril.

a specimen of *Glaucolepis gunnari* (No. 9), which possesses an undamaged lacrimo-maxillary.

All three species have two suborbitals, whose relative size and position in relation to the surrounding bones agree with the two suborbitals in *Glaucolepis stensiöi*.

The sclerotic ring contains three or four segments.

The palatoquadrate and its dermal bones, and the dermal bones of the cheek which together with the palatoquadrate form the complex palatoquadrate-maxillary apparatus.

a. Glaucolepis magna.

On material of *Glaucolepis magna* it was especially easy, on account of the size of the species, to make the preparations required for an examination of the palatoquadrate, so I shall begin with this species.

The palatoquadrate has a very considerable length, its anterior part being in contact with the postero-ventral part of the ethmoidal region and its posterior part lying at any rate just as far caudally as the posterior part of the occipital region.

In most large specimens of *Glaucolepis magna* the palatoquadrate is ossified throughout as one bone. The macroscopic structure of the bone of the palatoquadrate is like that of the endocranium. Some few larger and several smaller specimens show a less degree of ossification. In these specimens as well as in a number of specimens of *Glaucolepis gunnari*, *arctica*, and *stensiöi* the palatoquadrate contains several ossifications, viz. one in the quadrate region, one in the metapterygoid region, and one in the autopalatine region. Where these ossifications occur independently, they are always separated by large unossified portions of the palatoquadrate and never join by suture. The process of ossification in the palatoquadrate advances with the increasing age of the animal, and it is possible to observe, from one specimen to the other, how the individual ossifications increase in extent, to fuse finally into the aforementioned complete palatoquadrate ossification. The course of this fusion is always that first the quadrate ossification fuses with the metapterygoid ossification, and only later does the autopalatine ossification fuse with the quadrato-metapterygoid. In the specimens in which the ossification of the palatoquadrate is complete, it is impossible to detect anything indicating that the palatoquadrate bone originated from three centres.

We shall now consider the completely ossified palatoquadrate of the adult *Glaucolepis magna*. (The subjoined description is chiefly based on specimens Nos. 2, 6, 8, and 164.)

Viewed from the medial side, the palatoquadrate ossification (Fig. 36) is roughly speaking, triangular in outline, with a postero-dorsal, an antero-dorsal, and a ventral margin, of which the ventral margin is the longest and the postero-dorsal one the shortest.

From about the middle of the antero-dorsal margin a small tongue-like process (*pr.pq*, Figs. 35, 36) issues in a dorsal and at the same time slightly lateral direction. In the living animal this process was in contact with the processus basipterygius. In no specimen, either of this or of the other species of *Glaucolepis*, could the basipterygoid process and the palatoquadrate process be observed to lie in the same relation to each other as they did in the living animal, and since no specially developed articular fossa is found on the palatoquadrate process, we can only form conjectures as to the details of the articulation between the palatoquadrate and the basipterygoid process (the palato-basal articulation). As far as I can make out, the palatoquadrate process rested against the distal end or the dorsal face of the basipterygoid process, and during the abduction of the palatoquadrate the two contact faces slid against each other.

Two processes (pr_1, pr_2), whose accurate place and shape appear from Figs. 35 and 36, issue from the midmost part of the posterior half of the antero-dorsal margin of the palatoquadrate ossification.

That part of the palatoquadrate ossification which lies behind a vertical transverse plane through the place of junction between the palatoquadrate and the basipterygoid process consists mainly of a rather thin, nearly vertical plate, which is curved in such a way that its lateral face is concave in a dorso-ventral direction and its medial face correspondingly convex.

This part of the ossification attains its greatest height about midway between its anterior and its posterior end. Since it bends in a lateral direction dorsally, its postero-dorsal margin is situated so far laterally that right from the postero-ventral end of the ossification to its most dorsal part it is in contact with the medial face of the preoperculum. The posterior part of the antero-dorsal margin of this portion of the palatoquadrate ossification is in contact with the medial face of the anterior part of the preoperculum, while the anterior part of the margin, that is to say, the part that lies nearest behind the place of connection with the basipterygoid process, does not extend so far in a lateral direction that it attains contact with the medial face of any of the dermal bones of the cheek

The most ventral part of the thin bone plate, like the dorsal part, is curved in a lateral direction except farthest posteriorly, where it forms the medial boundary of the opening for the musculus adductor mandibulae. Anteriorly to this opening the arching of the ventral half of the bone plate is so considerable that the most ventral part is almost horizontal, its lateral margin almost following the suture between the lateral horizontal lamina of the ectopterygoid and the medial horizontal lamina of the maxillary.

While in the metapterygoid region there is a very gradual transition between the dorsal laterally bent part and the vertical part of the palatoquadrate ossification, farthest caudally, that is to say, in the quadrate region, there is a distinct angle between the dorsal laterally bent part and the remaining vertical portion of the ossification. Within the posterior area of the quadrate region the laterally bent part of the ossification is curved, also in an anterior direction, so that the most caudal part of the space for the musculus adductor mandibulae is bounded not only caudally and medially, but laterally, too, by the palatoquadrate ossification; and accordingly the part of the quadrate region that lies behind the opening for the musculus adductor mandibulae has a considerable ventral surface (*cf.* Figs. 33 and 34), which is provided with a well developed double condyle for articulation with the lower jaw.

A broad, very conspicuous groove (*s.pq*, Figs. 35B, 36; Pl. 19, Fig. 3), whose position will appear from the figures, and to which we shall revert later, is always seen on the medial side of the palatoquadrate ossification.

The postero-dorsally facing margin of the palatoquadrate ossification is pierced a short distance antero-dorsally to its caudal end by a short transverse canal (*f.m.int*, Figs. 35A, 36). In some cases the thin postero-dorsal wall of the canal is lacking, so that, instead of a canal, only a short groove is present on the postero-dorsal margin of the quadrate region. A similar canal or groove is described by Aldinger in *Pygopterus nielseni* (Aldinger 1937, pp. 145–46, Fig. 40). Its interpretation will be dealt with below (pp. 179–80).

The part of the palatoquadrate ossification that lies in front of the point of junction with the basipterygoid process, is a thin bone plate which is a direct rostral continuation of the lowermost portion of the high part of the palatoquadrate lying behind it. Consequently this bone plate is so situated that its concave face is directed dorso-laterally and its convex face ventro-medially.

In ventral view (Fig. 33) this part of the palatoquadrate exhibits three free margins, viz. a lateral, a medial, and an anterior margin. When the palatoquadrate is not abducted, the medial margin lies close against the lateral margin of the pars anterior of the parasphenoid, as will be seen in Fig. 33. The short anterior margin contains a small notch indicating the place where the articulation between a small process issuing from the ventral margin of the ethmoidal region and the autopalatine region of the palatoquadrate took place.

As usual the oral side of the palatoquadrate is to a large extent covered by dermal bones, of which there are five, viz. a dermometapterygoid, an ectopterygoid, an entopterygoid, and an anterior and a posterior dermopalatine.

The *entopterygoid* (*Enpt*, Figs. 34A, 35C and D; Pl. 19, Figs. 2, 3) is

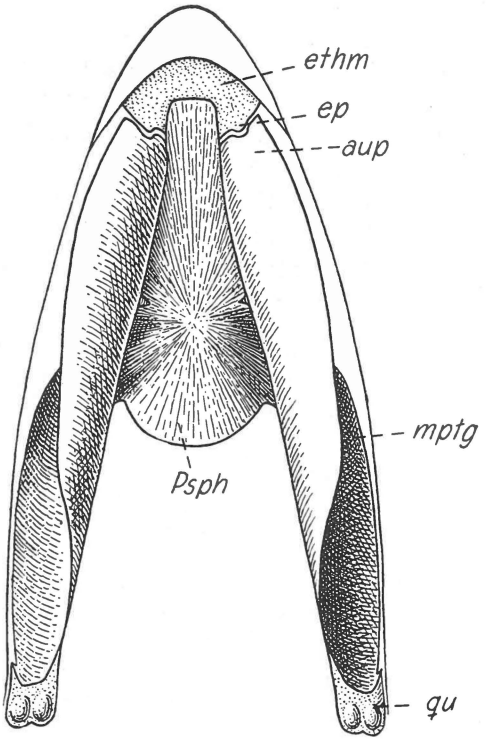


Fig. 33. *Glaucolepis magna* n. sp. Right and left palatoquadrate ossifications, parasphenoid, and part of ethmoidal region in ventral view. Oral margin and outline of snout indicated. On the basis of specimen No. 7. 1.5 ×.
Psph, parasphenoid; *aup*, pars autopalatina; *ep*, articular process for the pars autopalatina; *ethm*, ventral face of the ethmoidal region of the neural endocranium; *mptg*, pars metapterygoidea; *qu*, pars quadrata with its double condyle.

the largest of the five dermal bones on the oral face of the palatoquadrate; its anterior end rests against the anterior part of the palatoquadrate ossification and its pointed posterior end is situated just as far caudally as the most dorsal point of the palatoquadrate ossification.

The entopterygoid is bounded by a medial, a lateral, and a very short anterior margin. As will be seen from Fig. 35, its curvature is not entirely coincident with the dorso-ventral curvature of the palatoquadrate.

About midway between the anterior and posterior ends of the entopterygoid a small process is found on its medial margin, which process, as far as I can make out, is situated either directly medially to the aforementioned process by the aid of which the palatoquadrate articulated with the basipterygoid process, or perhaps slightly antero-medially to it. However, there is no contact between the process of the entopterygoid and the process of the palatoquadrate, for the latter points in a dorso-lateral direction, while the process of the entopterygoid points in a dorsal and slightly medial direction.

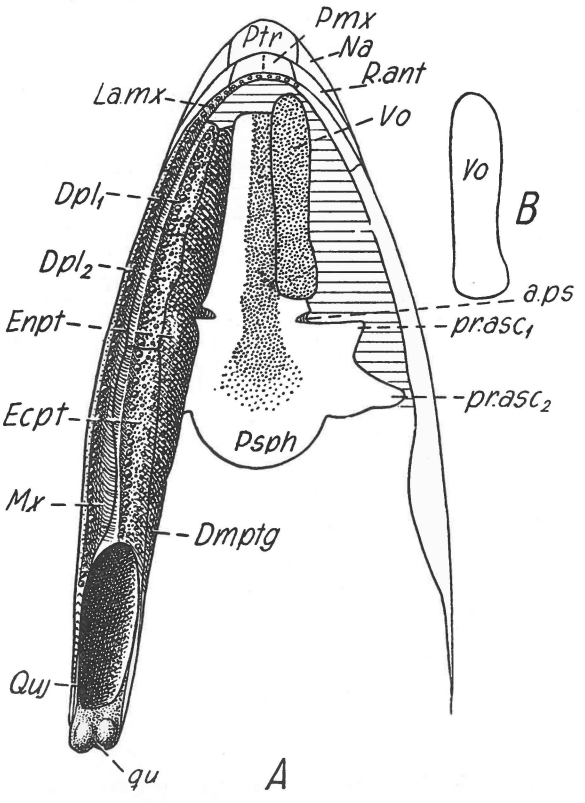


Fig. 34. *Glaucolepis magna* n. sp. A, head in palatal view. On right side the vomer, on left side the palatoquadrate and its dermal bones removed. Smallest teeth on the parasphenoid, the vomer, and the dermal bones of the visceral skeleton indicated by dots. Based on specimen No. 7. 1.5 ×. B, left vomer in ventro-medial view. Based on specimen No. 7. 1.5 ×. *Dmptg*, dermometapterygoid; Dpl_1, Dpl_2, anterior and posterior dermopalatines; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *La. mx*, lacrimo-maxillary; *Mx*, maxillary; *Na*, nasal; *Pmx*, premaxillary (not observed with certainty); *Psph*, parasphenoid; *Ptr*, postrostral; *Quj*, quadratojugal; *R. ant*, rostro-antorbital; *Vo*, vomer; *a. ps*, notch for the arteria pseudobranchialis efferens; *pr.* asc_1, processus ascendens anterior; *pr.* asc_2, processus ascendens posterior; *qu*, pars quadrata with its double condyle.

The process of the entopterygoid has a slightly convex anterior and a straight posterior margin, which meet at an acute angle. The process is so situated in relation to the parasphenoid that its straight posterior margin adjoins to that part of the processus ascendens anterior of the parasphenoid which rests against the anterior face of the processus basipterygius (p. 105). When the palatoquadrate complex is moved in relation to the endocranium, this movement is controlled to some extent by the process of the entopterygoid, which slides against the above-mentioned part of the processus ascendens anterior (cf. also Aldinger 1937, p. 336). Behind the process a small notch is found in the dorso-medial margin of the entopterygoid.

The anterior part of the dorso-medial margin of the entopterygoid lies against the lateral margin of the pars anterior of the parasphenoid, while

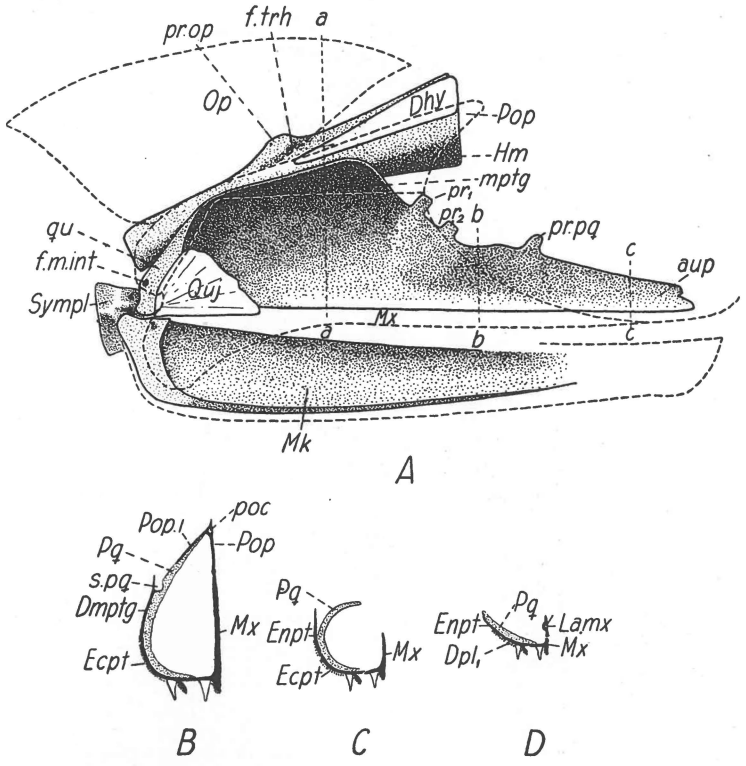


Fig. 35. *Glaucolepis magna* n. sp. A, part of the visceral skeleton in lateral view. Outlines of the maxillary, the preoperculum, the operculum, and the partial outline of the mandible indicated by broken lines. B, C and D, transverse sections through the palatoquadrate-maxillary apparatus along the lines *a-a*, *b-b*, and *c-c* respectively in Fig. A. Chiefly on the basis of specimen No. 2. 1.4×.

Dhy, dermohyal; *Dmptg*, dermometapterygoid; Dpl_1, anterior dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Hm*, hyomandibula; *La. mx*, lacrimo-maxillary; *Mk*, posterior ossification in the Meckelian cartilage; *Mx*, maxillary; *Op*, operculum; *Pop*, preoperculum; *Pop. i*, internal lamina of the preoperculum; *Pq*, palatoquadrate; *Quj*, quadratojugal; *Sympl*, symplectic; *aup*, pars autopalatina; *f. m. int*, canal probably for the ramus mandibularis internus facialis; *f. trh*, groove and canal for the truncus hyoideomandibularis; *mptg*, pars metapterygoidea; *poc*, preopercular canal; pr_1, pr_2, processes from the margin of the palatoquadrate; *pr. op*, processus opercularis; *pr. pq*, process which articulated against the processus basipterygius; *qu*, pars quadrata; *s. pq*, groove on the medial face of the palatoquadrate.

the posterior part of the dorso-medial (or dorsal) margin of the entopterygoid adjoins the dermometapterygoid behind the entopterygoid, covering a very narrow zone of the oral face of that bone. The ventro-lateral (farthest caudally rather the ventral) margin of the entopterygoid is connected by suture with the ectopterygoid, the posterior, and the anterior dermopalatine respectively (Figs. 34A, 35C and D) in such a way that the entopterygoid covers a narrow marginal zone of the oral face of these bones.

The radiation centre of the entopterygoid lies much nearer the dorso-medial than the ventro-lateral margin of the bone and directly ventrally to the posterior margin of its above-mentioned small process.

With the exception of a fairly broad zone immediately adjacent to that

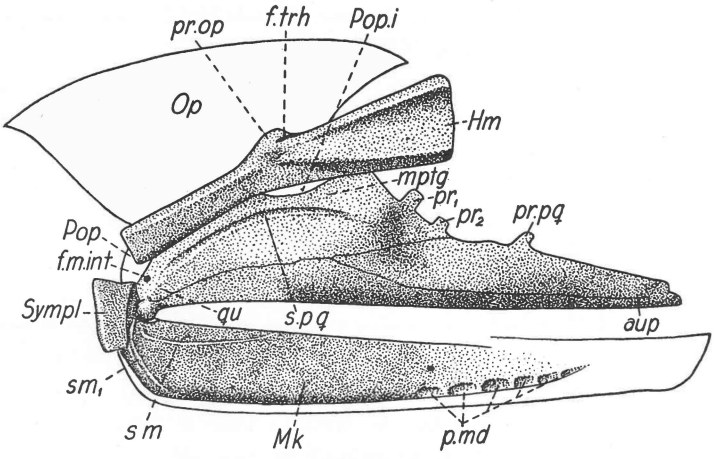


Fig. 36. *Glaucolepis magna* n. sp. Part of the visceral skeleton in medial view. Outline of those parts of the ectopterygoid, the anterior and posterior dermopalatines, and the entopterygoid which have contact with the palatoquadrate indicated by thin lines. Mainly on the basis of specimen No. 2. 1.4×.
p.md, shallow depressions on the surface of the posterior ossification in the Meckelian cartilage; *sm*, sm_1, grooves for nerves and (?) vessels. Other letters as in Fig. 35.

part of its dorso-medial margin which is not in contact with the dermometapterygoid, the oral face of the entopterygoid is covered by closely set small teeth of the same type as the teeth of the parasphenoid and the vomer.

The dermometapterygoid (*Dmptg*, Figs. 34A, 35B; Pl. 19, Figs. 2, 3) rests against the medial face of the posterior high part of the palatoquadrate and is bounded by a postero-dorsal convex and an antero-ventral nearly straight margin.

From its pointed anterior end the bone increases in height in a posterior direction throughout its anterior half, after which it again decreases in height, so that posteriorly, also, it terminates in a point. As stated above, the anterior part of the antero-ventral margin of the dermometapterygoid joins the entopterygoid by suture, while the remaining part of the margin is connected with the ectopterygoid in such a way that the dermometapterygoid covers a very narrow marginal zone of the oral face of the ectopterygoid.

Quite close to and parallel with the postero-dorsal margin of the dermometapterygoid a lamina issues from the aboral face of the bone; this lamina overlaps the ventral margin of the aforementioned (p. 145) broad groove on the oral face of the palatoquadrate, covering the ventral wall of the groove, as shown in Fig. 35B.

While the part of the dermometapterygoid that lies ventrally to the lamina just mentioned rests close against the medial face of the palatoquadrate, this is not the case with the rather low part of the bone situated dorsally to the line of issue of the lamina. For dorsally to the ventral margin of the palatoquadrate groove the palatoquadrate plate has a mainly dorso-lateral direction, while the part of the dermometapterygoid that lies dorsally to

the aboral lamina is nearly vertical and is accordingly separated from the palatoquadrate by a considerable interspace.

As probably always in dermal bones provided with an internal lamina (*e.g.* the preoperculum, the suboperculum, the supratemporo-intertemporal, the maxillary, and the lacrimo-maxillary), the radiation centre lies on the line along which this internal lamina meets the external lamina of the bone, which in this case means rather near the postero-dorsal margin of the dermometapterygoid, more precisely about midway between the mid-point of this margin and its caudal end.

I have called this bone the dermometapterygoid, because it mainly lies against the metapterygoid region of the palatoquadrate in a similar way as the dermopalatine lies against the autopalatine region.

Among recent fishes, only in *Polypterus* a bone is found which is directly comparable to the dermometapterygoid in *Glaucolepis*, viz. the so-called metapterygoid. The name metapterygoid is usually employed to designate a primary ossification in the palatoquadrate, whereas the metapterygoid in *Polypterus* is interpreted differently by several authors. Thus Allis, who further refers to van Wijhe and Pollard, regards the metapterygoid in *Polypterus* as a dermal bone (Allis 1922, p. 242), and de Beer is of the same opinion (De Beer 1937, p. 86). Other authors, however, regard the bone as a primary ossification in the postero-dorsal part of the palatoquadrate (Holmgren and Stensiö 1936, p. 392). The good agreement existing between the dermometapterygoid in *Glaucolepis* and the tooth-bearing "metapterygoid" in *Polypterus* as regards the position in relation both to the entopterygoid and to the ectopterygoid in connection with the fact that several authors have come to the result that the "metapterygoid" in *Polypterus* is no primary bone, tend to show that the dermometapterygoid in *Glaucolepis* corresponds more or less completely to the "metapterygoid" in *Polypterus*. I therefore think it more correct to use the name dermometapterygoid instead of metapterygoid for the bone in question in *Polypterus*.

To all appearance, as we shall see later, a dermometapterygoid is normally present in primitive Actinopterygians (pp. 162–63).

The ectopterygoid (*Ecpt*, Figs. 34A, 35B and C; Pl. 19, Figs. 2, 3) covers the postero-ventral part of the oral face of the palatoquadrate to an extent that will appear most distinctly from Fig. 36. In a caudal direction the bone extends almost as far as the dermometapterygoid, while in a rostral direction it has a much greater extent than the latter.

For descriptive reasons the ectopterygoid may be divided into a posterior and an anterior part by a vertical transverse section on a level with the anterior margin of the adductor opening. The posterior part lies on the oral vertical face of that part of the palatoquadrate which bounds the adductor opening and the posterior part of the adductor space medially. Broadly speaking this part of the ectopterygoid is accordingly nearly vertical.

The anterior part of the ectopterygoid is an anterior continuation of the posterior vertical part of the bone, and lies on the oral face of that part of the palatoquadrate which is situated just anteriorly to the adductor opening. As stated above, this part of the palatoquadrate is bent, so that its ventral part is almost horizontal. Roughly speaking, the anterior part of the ectopterygoid accordingly consists of a ventral, nearly horizontal, and a dorsal, nearly vertical, part, which pass evenly into one another by a gradual curvature of the bone.

That part of the ectopterygoid which is overlapped by the most ventral, nearly horizontal part of the portion of the palatoquadrate that lies in front of the adductor opening, is divided into an internal (dorsal) and an external (ventral) lamina.

The internal lamina is horizontal and lies on the ventral face of the most lateral part of the horizontal portion of the palatoquadrate. It joins the maxillary by suture, overlapping a narrow marginal zone of the dorsal face of the internal horizontal lamina of that bone. The external lamina points in a ventro-lateral direction and has a free ventro-lateral margin, whose course will be seen from Fig. 34A. The transverse section through the ectopterygoid, etc., represented in Figs. 35B and C, will better than a detailed explanation show the relations of the two laminae.

Immediately medially to the base of the external free lamina the ectopterygoid bears a series of large pointed teeth, and in addition the oral face of that part of the ectopterygoid which lies between the dorsal margin of the bone and the row of large teeth is covered by small, closely set, pointed teeth. Similar teeth are found on the ventro-medial face of the free external lamina, whereas the dorso-lateral face of this lamina as well as the internal lamina are devoid of teeth.

The dorsal margin of the ectopterygoid is joined by suture with the dermometapterygoid and with the entopterygoid, as described above. The short, straight anterior margin of the ectopterygoid is joined by suture with the posterior dermopalatine. The caudal concave margin of the horizontal part of the ectopterygoid bounds the adductor opening anteriorly, as shown in Fig. 34, and the ventral margin of the posterior vertical part of the ectopterygoid forms the medial margin of the adductor opening.

The radiation centre lies precisely at the boundary defined above between the anterior and posterior parts of the ectopterygoid and much nearer the ventral than the dorsal margin of the bone, as shown in Fig. 37, which, it is true, shows the conditions in *Glaucolepis aldingeri*, but in which the radiation centres of the five dermal bones of the palatoquadrate are situated in precisely the same way as in *Glaucolepis magna*.

The posterior dermopalatine (Dpl_2, Figs. 34A; Pl. 19, Figs. 2, 3) lies on the ventrally directed face of the ventral horizontal part of the palatoquadrate so that it forms a direct continuation in a rostral direction of the ventral, nearly horizontal part of the ectopterygoid.

A transverse section through the dermopalatine shows that it agrees entirely with the part of the ectopterygoid lying behind it both as regards the subdivision of its most lateral part into an internal and an external lamina and as regards its dentition.

Seen from the ventral side, as in Fig. 34A, the bone is rectangular in outline with a posterior, an anterior, a lateral, and a medial margin, the two last-mentioned of which are about three times as long as the other two.

The lateral margin of the bone, that is to say, the margin of the internal lamina of the bone, overlaps a narrow marginal zone of the dorsal face of the internal horizontal lamina of the maxillary. The anterior margin of the ectopterygoid is connected by suture with the anterior dermopalatine. The medial margin of the bone is overlapped orally by the entopterygoid, as stated above.

The radiation centre of the rectangular bone lies slightly caudally to the point of intersection of its two diagonals.

The anterior dermopalatine (*Dpl*$_1$, Figs. 34A, 35C; Pl. 19, Figs. 2, 3) lies on the ventrally directed face of the ventral horizontal part of the palato-quadrate in front of the posterior dermopalatine. As will be seen from Fig. 34A, it decreases gradually in breadth from the posterior to the anterior end, but otherwise agrees entirely in structure with the posterior dermo-palatine. A transverse section through the anterior dermopalatine is shown in Fig. 35C. The lateral margin of the bone, that is to say, the margin of its internal lamina, joins by suture with the maxillary and the lacrimo-maxillary, so that it overlaps a narrow marginal zone of the dorsal face of the internal horizontal lamina, which issues from these two bones. The medial margin of the anterior dermopalatine is overlapped orally by the entopterygoid.

The radiation centre of the bone lies midway between its lateral and its medial margin, somewhat nearer its posterior than its anterior margin.

The maxillary (*Mx*, Figs. 30, 34A, 35A, B, and C; Pl. 9, Fig. 1; Pl. 12, Fig. 1; Pl. 19, Figs. 1, 2, 3; Pl. 20, Fig. 3) is of the usual type with a low suborbital and a high postorbital part; as regards the outline of its exposed part it will suffice to refer the reader to Fig. 30. The suborbital part of the maxillary is relatively shorter than in *Palaeoniscus*, its anterior end lying ventrally to the middle part of the lacrimo-maxillary. In *Glaucolepis magna* the postorbital part of the maxillary is longer in relation to its height than in the other Greenland species of *Glaucolepis*.

As will be seen from the figures, we may regard the maxillary as bounded by the following margins: a dorsal, an antero-dorsal, a largely posterior, and a largely ventral margin. The dorsal margin and the dorsal part of the posterior margin overlap a narrow marginal zone of the preoperculum; and moreover, as seen clearly from Fig. 35A, the posterior part of the maxillary together with the preoperculum overlap the quadratojugal, so that only a very small part of the lateral face of the quadratojugal is visible when the head is seen in lateral view. This visible part of the quadratojugal lies

in a small indentation in the posterior margin of the maxillary, as described by me in a previous paper (E. Nielsen 1936, p. 38). As already stated, the antero-dorsal margin of the maxillary is overlapped by the ventral suborbital, the jugal, and the lacrimo-maxillary.

From the medial face of the maxillary and at a rather short distance from the ventral margin of the bone issues a horizontal longitudinal lamina. From its posterior end, which, as will be seen from Fig. 34A, lies laterally to the anterior part of the adductor opening, the lamina at first increases in breadth, attaining its greatest breadth laterally to the posterior half of the horizontal part of the ectopterygoid; farther anteriorly it decreases somewhat in breadth. At the anterior end of the maxillary the lamina adjoins the lamina which issues from the medial face of the lacrimo-maxillary (p. 142; cf. also p. 134).

The maxillary is connected by its horizontal lamina with the ectopterygoid and the two dermopalatines, as stated above, and as will appear from the transverse sections shown in Fig. 35.

On the free ventral margin of the maxillary and on the medial side of that part of the bone which lies ventrally to the plane of its horizontal lamina numerous small teeth are found (Fig. 35B and C). The teeth on the downward curved posterior part of the ventral margin are somewhat larger then the remaining ones (cf. Fig. 30). In addition a single row of very large teeth is found on the horizontal lamina of the maxillary immediately medially to the ventral part of the vertical plate of the bone.

The radiation centre of the maxillary lies on a level with the horizontal lamina of the bone in that part of the maxillary which lies ventrally to the posterior half of the jugal.

As stated in a previous paper, in *Glaucolepis* the anterior part of the horizontal pit-line of the cheek is situated on the maxillary (E. Nielsen 1936, pp. 39–40, Fig. 19). In *Glaucolepis magna* the anterior end of this pit-line (*hp*, Pl. 9, Fig. 1) lies on the surface of that part of the bone which contains the radiation centre, whence it extends for a short distance in a postero-dorsal direction.

As usual in the *Palaonisciformes*, the preoperculum (*Pop*, Figs. 30, 35A and B, 36; Pl. 9, Fig. 1, Pl. 12, Fig. 1; Pl. 20, Fig. 3) is a long, angularly bent bone, which falls naturally into an antero-dorsal and a postero-ventral part.

The outline of the exposed face of the preoperculum, when the cheek is seen in lateral view, is seen in Fig. 30; however, it does not correspond entirely to the actual outline of the bone, for, as has been mentioned above, a narrow marginal zone of the preoperculum is overlapped by the suborbital elements and the maxillary. The postero-dorsal margin of the preoperculum overlaps the antero-ventral margin of the dermohyal and the margin of the operculum and the subopercular, but evidently the preoperculum was not firmly connected with these bones. Furthermore the ventral

half of the antero-ventral margin of the postero-ventral part of the preoperculum overlaps the quadratojugal to some extent, as will appear from Fig. 35 A.

The preoperculum is pierced throughout its whole length by the preopercular canal, which in the antero-dorsal part of the bone runs parallel to and fairly near the postero-dorsal margin of the bone, and at the boundary between the antero-dorsal and the postero-ventral part of the bone, after a distinct bend, continues downward about midway between the postero-dorsal and antero-ventral margins of the postero-ventral part of the bone.

The preopercular canal changes its direction precisely at the point where it pierces the radiation centre of the preoperculum, and from this point the posterior part of the horizontal pit-line of the cheek (*hp*, Pl. 9, Fig. 1) runs in an anterior and at the same time slightly ventral direction across the external face of the bone, as previously described (E. Nielsen 1936, p. 39, Fig. 19). On the medial side of the preoperculum a prominent longitudinal ridge is found, which is a thickening of the zone of the bone that lodges the preopercular canal. In the posterior half of the antero-dorsal part of the preoperculum a lamina (*Pop.i*, Fig. 35A and B) issues in a ventro-medial direction from this ridge; the breadth of this lamina increases forwards from its posterior end for about two-thirds of the length of the lamina, then decreasing again towards the anterior end of the lamina.

The dorsal or postero-dorsal margin of the posterior high part of the palatoquadrate ossification is in contact with the medial ridge of the preoperculum throughout the whole postero-ventral part of the preoperculum and through that part of the antero-dorsal part of the preoperculum in which the medial ridge is continued by the ventro-medial lamina. The lamina itself is by its whole lateral or ventro-lateral face in contact with the most dorsal part of the medial face of the palatoquadrate ossification, as will be seen from Fig. 35A and B, and corresponding to the conditions in *Glaucolepis aldingeri* shown in Fig. 37. As regards the anterior half of the antero-dorsal part of the preoperculum, the contact zone with the antero-dorsal margin of the palatoquadrate extends obliquely forwards and downwards across the antero-ventral part of the antero-dorsal part of the preoperculum; in front of the preoperculum the antero-dorsal margin of the palatoquadrate has no contact with any of the dermal bones of the cheek.

To the postero-ventral part of the preoperculum it applies that not only the medial ridge is in contact with the palatoquadrate, but a very large area of the medial face of the part of the postero-ventral part of the preoperculum lying in front of the medial ridge is intimately connected with the laterally directed face of the quadrate region of the palatoquadrate (Fig. 35 A).

Laterally to the postero-ventral part of the palatoquadrate ossification, and nearly entirely covered laterally by the maxillary and the preoperculum, lies a triangular bone, the quadratojugal (*Quj*, Figs. 30, 34A, 35A; Pl. 12,

Fig. 1; Pl. 20, Fig. 3), as briefly mentioned in a previous paper (E. Nielsen 1936, p. 38, Figs. 17 and 19). The outline of the quadratojugal is shown in Fig. 35. The posterior part of the medial face of the bone rests against the anterior part of the lateral face of the laterally thickened part of the quadrate region of the palatoquadrate and is firmly connected with this face. The ventral margin of the quadratojugal together with the maxillary forms the lateral boundary of the adductor opening.

If the cheek is seen in lateral view, only a small postero-ventral part of the quadratojugal will be visible and that only because a small notch is found in the hind margin of the maxillary. A similar notch in the hind margin of the maxillary is found in *Acropholis stensiöi* and in *Plegmolepis kochi* (Aldinger 1937, Figs. 6 and 17), in which forms, however, no quadratojugal has been observed.

The whole remaining part of the lateral face of the quadratojugal is covered by the maxillary with the exception of a narrow zone along the hind margin of the bone which is overlapped by the preoperculum. The portion of the quadratojugal which is covered by the maxillary decreases in thickness with increasing distance from the uncovered part of the bone, the antero-dorsal marginal zone of the bone being accordingly very thin. As mentioned before (E. Nielsen 1936, p. 38), this may indicate that the quadratojugal, owing to the overlapping by the maxillary, has been reduced in the direction from its anterior towards its posterior part.

In other *Palaeonisciformes* the quadratojugal has disappeared entirely, and the conditions in *Glaucolepis* indicate that its disappearance may be due to its complete reduction rather than to its fusion with other dermal bones (cf. p. 341).

The radiation centre of the quadratojugal lies in the exposed part of the bone. As stated in a previous work (E. Nielsen 1936, p. 38, Fig. 19), in some few particularly well preserved specimens of *Glaucolepis* the exposed face of the bone shows traces of the vertical pit-line of the cheek. However, the presence of this pit-line could not be definitely ascertained in *Glaucolepis magna*.

The lacrimo-maxillary, too, belongs to the complex of dermal bones which form part of the palatoquadrate-maxillary apparatus, and has been described above (p. 142).

A small paired premaxillary is shown in Figs. 30 and 34 A. In this species, however, the premaxillary has not been observed in any specimen, whereas, as mentioned on p. 136, in *Glaucolepis stensiöi* fragmentary remains of a bone are found which may with a fair degree of probability be interpreted as a premaxillary.

The bone is indicated here because a measuring of the dermal bones of the snout present in *Glaucolepis magna* shows that the right and left lacrimo-maxillaries do not meet in the mid-line, and that the rostro-antorbital leaves

a space for an independent bone of the extent which has been given to the premaxillary in the figures.

b. Glaucolepis aldingeri.

Of this species only a single head is known, and I have split this head in such a way that the palatoquadrate-maxillary apparatus of the left side could be examined in detail (Fig. 37, Pl. 20, Fig. 1). The palatoquadrate contains two ossifications, viz. a quadrato-metapterygoid and an autopalatine. As will be seen from the figure, the postorbital part of the palatoquadrate

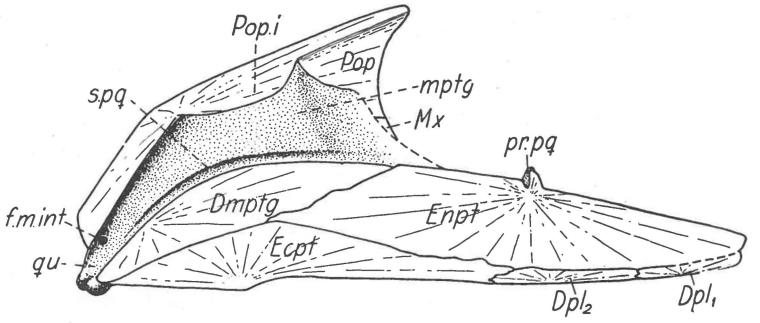


Fig. 37. *Glaucolepis aldingeri* n. sp. Palatoquadrate-maxillary apparatus in medial view. The free dorsal lamina of the dermometapterygoid, the free ventral lamina of the ectopterygoid, and of the anterior and posterior dermopalatines, and the teeth omitted. Mainly on the basis of specimen No. 43. 1.5 ×.
Lettering as in Fig. 35.

is relatively higher than in *Glaucolepis magna*, the distance between the medial palatoquadrate groove (*s.pq*, Figs. 37, Pl. 20, Fig. 1) and the postero-dorsal margin of the quadrato-metapterygoid being accordingly much greater than in that species. Apart from the difference in height, the palatoquadrate in *Glaucolepis aldingeri* agrees in all essentials with that of *Glaucolepis magna*.

The same applies to the dermal bones on the oral side of the palatoquadrate, as will appear from Fig. 37, in which the entopterygoid and the greater part of the dermometapterygoid, the ectopterygoid, and the two dermopalatines are seen. Only that part of the dermometapterygoid which had contact with the palatoquadrate is shown in the figure, while the free dorsal part (cf. *Glaucolepis magna* p. 149) has been omitted in order to show the palatoquadrate groove. The ectopterygoid and the two dermopalatines are shown as impressions of their aboral faces, and their free ventro-laterally directed laminae (cf. *Glaucolepis magna* Fig. 35, B, C) are therefore not seen in the figure. The position of the radiation centres of the five dermal bones of the palatoquadrate are all shown.

The postorbital part of the maxillary is shorter and higher than in *Glaucolepis magna*, and the same applies to the antero-dorsal part of the preoperculum. Otherwise these two bones agree in their mutual relations and in their relations to the palatoquadrate and its dermal bones with the corresponding bones in *Glaucolepis magna*.

As regards shape and position the quadratojugal agrees entirely with the quadratojugal in *Glaucolepis magna*.

A lacrimo-maxillary is present, but it is too badly preserved to allow of an examination. The snout part of the head is so incompletely preserved that nothing can be said as to whether or not a premaxillary is present.

c. Glaucolepis stensiöi.

It could be observed that the ossification of the palatoquadrate proceeded in a way similar to that in *Glaucolepis magna* (p. 143). The postorbital part of the palatoquadrate is even relatively higher than in *Glaucolepis aldingeri*, corresponding to the postorbital part of the maxillary and the antero-dorsal part of the preoperculum being comparatively higher and shorter in this species than in any of the other species of *Glaucolepis* (Fig. 27). Otherwise the details of the palatoquadrate agree with those found in *Glaucolepis magna*. The same applies to the dermal bones of the palatoquadrate. The sectioned specimen shows on the right side of the head a cast of part of the oral side of the dermometapterygoid, the entopterygoid, and the ectopterygoid (*Dmptg*, *Enpt*, *Ecpt*, Pl. 1). On the cast of the oral side of the ectopterygoid five small dorso-ventrally directed ridges are found indicating the presence of five small grooves on the oral side of the ectopterygoid; their position appears clearly from the figure. Nothing can be said about the significance of these grooves, which I have observed in no other specimen.

The proportions of the maxillary and the preoperculum will appear from Fig. 27. Their mutual relations and their relation to the palatoquadrate and its dermal bones are as in *Glaucolepis magna*. A lacrimo-maxillary (p. 134) like that in *Glaucolepis magna* is present. The sectioned specimen shows fragmentary remnants of a small paired dermal bone on the lower side of the snout (*Pmx*, Figs. 27, 28; Pl. 8, Fig. 3). The shape of this bone could not be determined. Probably it is a premaxillary (cf. pp. 136–40).

As regards shape and position the quadratojugal (*Quj*, Fig. 27; Pl. 12, Fig. 2) agrees with the quadratojugal in *Glaucolepis magna*. On the preoperculum and the maxillary the posterior and the anterior part respectively of the horizontal pit-line of the cheek (*hp*, Fig. 27) are found in the same position as in *Glaucolepis magna*.

d. Glaucolepis gunnari.

The ossification of the palatoquadrate proceeded as in *Glaucolepis magna*. The postorbital part of the palatoquadrate is but very slightly lower in proportion to its length than in *Glaucolepis magna*, corresponding to the postorbital part of the maxillary and the antero-dorsal part of the preoperculum being relatively lower in proportion to their lengths than in *Glaucolepis magna*.

The whole palatoquadrate-maxillary apparatus agrees so well with that of *Glaucolepis magna* that a more detailed description is superfluous. The horizontal pit-line is situated as in *Glaucolepis magna*. The vertical pit-line

of the cheek may in a few cases be seen on the exposed part of the quadratojugal (*vp*, Pl. 9, Fig. 2).

e. Glaucolepis arctica.

The ossification of the palatoquadrate proceeded as in *Glaucolepis magna* (p. 143). The postorbital part of the palatoquadrate, the postorbital part of the maxillary, and the antero-dorsal part of the preoperculum agree in their proportions with those of *Glaucolepis aldingeri*, and the whole palatoquadrate-maxillary apparatus agrees so completely with that of *Glaucolepis aldingeri* that a detailed description is superfluous. The horizontal pit-line lies as in the other species of *Glaucolepis* in which it has been ascertained. The vertical pit-line of the cheek has not been observed. The premaxillary has not been observed with certainty.

f. Discussion.

As has been shown above, the palatoquadrate ossification, the dermo-metapterygoid, the ectopterygoid, the entopterygoid, the two dermo-palatines, the maxillary, the quadratojugal, the preoperculum, and the lacrimo-maxillary are firmly connected with each other, forming the walls of a high, rather narrow space, in which the dorsal part of the musculus adductor mandibulae was situated.

This space opens anteriorly into the orbit, and has in addition an opening, the adductor opening, in the posterior part of its floor, through which the musculus adductor mandibulae passed to reach down into the muscular fossa of the mandible.

Such a space for the dorsal adductor musculature surrounded by firmly connected bones seems to be a normal feature in early *Palaeonisciformes* (Watson 1925, pp. 851–60; Aldinger 1937, pp. 331–32), but has not till now been described in detail in any form belonging to this group. Notably the important part which the quadratojugal and especially the preoperculum play in the delimitation of the muscular space has not been recognised. (Watson, for instance, seems to assume (1925, p. 853) that the maxillary alone constitutes the lateral wall of the muscular space).

In *Saurichthys*, however, Stensiö has made a very thorough investigation of the palatoquadrate-maxillary apparatus (Stensiö 1925, pp. 97–107, 142, 149, 162–64, and 199–200), which has on the whole a similar structure as in *Glaucolepis*.

According to Stensiö's description a dorsal part of the preoperculum is bent medially and so curved that it covers the dorsal margin and part of the medial side of the quadrato-metapterygoid (Stensiö 1925, pp. 101–02, Fig. 23). In my opinion it is not probable that the dorsal part of an originally plane preoperculum in *Saurichthys* should have been bent in a medial direction around the dorsal margin of the quadrato-metapterygoid; the conditions are more probably as in *Glaucolepis*, where a ventro-medially

directed lamina issues from the medial face of the preoperculum, while the original dorsal margin still lies in plane with the vertical face of the bone.

According to Stensiö the palatoquadrate in *Saurichthys* on its oral face has the following dermal bones: an ectopterygoid, a dermopalatine, and a very large entopterygoid. I have dissected out the dermal bones of the palate in a *Saurichthys* head from Greenland, and found that the area which in the *Saurichthys* species from Spitsbergen is occupied by the entopterygoid, is occupied in the Greenland form by two dermal bones, a posterior dermometapterygoid and an anterior entopterygoid. The conditions in Stensiö's species of *Saurichthys* may be explained by a fusion of the dermometapterygoid and the entopterygoid, even though in that case it is strange that the radiation centre of the large "entopterygoid" is situated just as far posteriorly as the radiation centre of the dermometapterygoid in the Greenland *Saurichthys*.

On the medial face of the entopterygoid *Saurichthys wimani* (Stensiö 1925, p. 142) has a longitudinal crista which according to Stensiö served as the place of insertion for muscles which at any rate corresponded partially to the adductor arcus palatini in the *Teleostei*.

Probably this crista corresponds to the vertical, dorsal, free part of the dermometapterygoid in *Glaucolepis* (p. 149), while that part of the "entopterygoid" in *Saurichthys* which lies dorsally to this crista corresponds to the lateral lamina issuing from the dermometapterygoid in *Glaucolepis* and covering the ventral wall of the palatoquadrate groove.

About the firm connection between the palatoquadrate and certain bones of the cheek in *Saurichthys* Stensiö writes as follows (Stensiö 1925, pp. 105–06): "A rigid connection between the palatoquadrate and the maxillary is not only characteristic of *Saurichthys* but is found also in several other fishes. Thus it occurs in Acipenserids (Parker 1873, Pl. XX, figs. 1, 2, 5; 1882, Pl. 18, figs. 4, 5), Polyodontids (Traquair 1877a, Pl. VII, figs. 1, 2; Bridge 1878, pp. 701–707), *Chondrosteus* (Traquair 1887, pp. 253–256), Palaeoniscids (Traquair 1877a, p. 18; Stensiö 1921, pp. 183, 243), and *Polypterus* (Stensiö 1921, p. 183); and it is possible that a connection of this sort also existed in other forms, e.g. the Catopterids. With regard to the connection between the palatoquadrate and other dermal bones on the postorbital part of the cheek, it is noteworthy that the posterior portion of the palatoquadrate, whether it is occupied by an independent quadrate or not, is in all fishes more or less bent laterally, so that it is situated transversally in relation to the portions in front of it, whereby it naturally comes into more or less close contact with the preoperculum, quadratojugal and possibly with homologues of certain squamosal elements as well. As we know, there occurs in fact in Teleosts, *Amia*, *Lepidosteus* and probably at least in certain *Protospondyli* (Seminotids, cf. Woodward 1916, Pl. VIII, fig. 1), a fixed connection between the posterior edge of the palatoquadrate and the preoperculum; and in Acipenserids the quadrato-

jugal lies firmly against the orbital process of the pars quadrata. In *Polypterus* the lower part of the preoperculum is joined by ligament to the quadrate and the posterior end of the metapterygoid, but on the other hand certain of the cheek-plates situated in front of the preoperculum are also contiguous to some extent with the same bones of the palatoquadrate. In Palaeoniscids both the preoperculum and the posterior end of the maxillary (the maxilloquadratojugal?) have of course been more or less closely connected with the pars quadrata of the quadrato-metapterygoid. That, under these circumstances, a fixed connection could arise in *Saurichthys ornatus* between the palatoquadrate on the one hand and the preoperculum, quadratojugal and maxillary on the other, is thus not very remarkable; nor is it a feature so foreign to the Actinopterygians as it might easily seem at first sight to be."

I quote this passage in extenso, because, as we have seen above, the connection between the palatoquadrate and the dermal bones of the cheek in *Glaucolepis* shows so good agreement with that in *Saurichthys* that the comparison drawn here by Stensiö between *Saurichthys* and other Actinopterygians may just as well be applied to the relations between *Glaucolepis* and these other forms.

The primary ossifications of the palatoquadrate is satisfactorily known in a small number only of the early Ganoids. Traquair made certain observations regarding the palatoquadrate in *Nematoptychius* and *Elonichthys*, and found that in these species it contains several ossifications (Traquair 1877, p. 18; 1901, p. 84; 1909, p. 118). However, the first fairly detailed description of the palatoquadrate in a member of the group *Palaeonisciformes* was given by Stensiö in 1921 in his treatment of *Boreosomus arcticus* (Stensiö 1921, pp. 211–12). In this species Stensiö found two primary ossifications, the autopalatine and the quadrato-metapterygoid, in the palatoquadrate.

In 1925 Watson (1925, pp. 851–60; cf. also Watson 1928, pp. 55–56) described the palatal region of a number of *Palaeonisciformes*, stating i.a. that the palatoquadrate contains a number of ossifications among which are homologues to the autopalatine, the metapterygoid, and the quadrate.

Below (p. 161) I shall deal in more detail with the palatoquadrate and its dermal bones in the forms treated by Watson.

In *Saurichthys* the palatoquadrate according to Stensiö (1925, pp. 97–99, etc.) contains a quadrato-metapterygoid and an autopalatine. Brough has described a metapterygoid in *Helichthys* (Brough 1931, p. 286).

In 1932 Stensiö described, in *Ospia*, a palatoquadrate, which is ossified in one piece from the front end of the pars palatina to the posterior part of the pars quadrata (Stensiö 1932, pp. 252–56).

In 1937 Aldinger supplied various particulars about the palatoquadrate in a number of Permian forms of the group *Palaeonisciformes*. In *Acropholis stensiöi* (Aldinger 1937, p. 43) the palatoquadrate comprises a quadrate, a metapterygoid, and possibly, in its anterior part, one more primary ossi-

fication. In *Plegmolepis kochi* (Aldinger 1937, p. 79) a quadrate is found. In *Boreolepis jenseni* (Aldinger 1937, pp. 126–27) the palatoquadrate is ossified throughout its extent as one bone. In *Pygopterus nielseni* (Aldinger 1937, pp. 145–46) the palatoquadrate contains a quadrato-metapterygoid and possibly in addition ossifications in its rostral part. In 1939 Brough (1939, pp. 63, 102–03) described a quadrato-metapterygoid in *Ptycholepis*.

Apart from *Saurichthys* it applies to all the above-mentioned forms that the observations concerning the palatoquadrate are based on an extremely small number of individuals. Considering that our large material of *Glaucolepis* includes individuals with the palatoquadrate entirely ossified into one piece, others with two or three smaller ossifications in the palatoquadrate, and others again with entirely unossified palatoquadrates, it is obvious that no great importance should be attached to the question whether a form of which only a small number of individuals are known, has one, two, or three ossifications in the palatoquadrate. Quite probably the degree of ossification of the palatoquadrate in many forms, as in *Glaucolepis*, depends on the age of the fishes, and it serves no purpose whatever to insert in the generic diagnoses, as done by Stensiö, Aldinger, and others, whether the palatoquadrate contains several small or one large ossification.

The dermal bones of the palatoquadrate are known fairly well in *Boreosomus* (Stensiö 1921, p. 212 (but see the present paper p. 339)), *Acrorhabdus* (Stensiö 1921, p. 225), *Saurichthys* (Stensiö 1925, pp. 94–101, etc.), *Helichthys* (Brough 1931, pp. 285–86), and in the *Palaeonisciformes* described by Watson in 1925 and 1928.

I may mention here that judging from Greenland material, *Boreosomus*, in contrast to *Glaucolepis* and *Saurichthys* (p. 159), has no dermometapterygoid (see further p. 338), but that a dermometapterygoid is found in Greenland specimens of *Birgeria*. I shall proceed, then, to a description of the forms whose palatal region was figured by Watson in 1925 and 1928.

Watsonichthys (*Elonichthys*) *pectinatus* (Traquair), (Watson 1925, pp. 851–53): In the palatoquadrate several ossifications are found whose number and shape are not indicated. On the posterior part of the foremost of these ossifications is a facet against which the basipterygoid process is stated to have articulated. If this is the case, the articulation is situated exceptionally far rostrally. The medial side of the hyomandibula is stated to be in contact with a ridge on the most dorsal part of the two hindmost ossifications of the palatoquadrate. The greater part of the oral face of the palatoquadrate is covered by a very large pterygoid which possibly corresponds to the entopterygoid plus the dermometapterygoid in *Glaucolepis*. In addition an ectopterygoid and a series of small dermopalatines (altogether five) are found.

Elonichthys binneyi Traquair (Watson 1925, pp. 853–54, Fig. 22): The palatoquadrate is stated to contain several small ossifications; the largest of these is termed by Watson the suprapterygoid 6 or the metapterygoid.

In my opinion this ossification is no primary ossification, but a dermal bone which as regards shape and position seems to agree well with the dermometapterygoid in *Glaucolepis*. Of other dermal bones an ectopterygoid and two dermopalatines are found. The tooth arrangement on these bones and on the maxillary is very similar to that in *Glaucolepis*.

Elonichthys aitkeni Traquair (Watson 1925, p. 855, Fig. 23) (according to Aldinger (1937, p. 207) *Elonichthys aitkeni* is not an *Elonichthys*): Several ossifications are found in the palatoquadrate, but the figure is very difficult to understand, and I dare not, therefore, express a definite opinion as to the bone termed by Watson "a deep and very large metapterygoid"; possibly it is a quadrato-metapterygoid. An entopterygoid, an ectopterygoid, and three dermopalatines are present.

Elonichthys semistriatus Traquair (Watson 1925, p. 856, Fig. 24) (according to Aldinger (1937, p. 207) *Elonichthys semistriatus* may possibly belong to another genus): Of the primary ossifications of the palatoquadrate only the quadrate and an element interpreted by Watson as an autopalatine are seen in the figure. The description of the relations of the latter, as also several other sections of Watson's description of the elements of the palatal region, shows some obscurity in the conception of the general relations between the dermal and the cartilage bones within this region. Thus Watson writes about this form: "...an anterior autopalatine which has acquired a direct contact with the anterior end of the palatine series" – and, "The palatine has been largely destroyed by breakage of the specimen. Anteriorly it has a direct contact with the autopalatine, so as to exclude the pterygoid from the anterior part of the palate." Watson's metapterygoid is undoubtedly a dermometapterygoid. Of dermal bones, an entopterygoid, an ectopterygoid, and indications of one or several dermopalatines are found.

Elonichthys caudalis Traquair (Watson 1925, pp. 856–58, Fig. 25): Watson's description and figure are very difficult to understand. It would seem that the palatoquadrate is unossified. An entopterygoid, an ectopterygoid, and a dermometapterygoid can be seen in the figure.

Nematoptychius greenocki (Watson 1925, p. 858, Fig. 26; 1928, pp. 55–56, Fig. 7): The foremost of Watson's suprapterygoids in this form is probably a part of the ossified palatoquadrate. Watson's metapterygoid, to which, according to the figure of 1928, belongs that part which in 1925 Watson termed the posterior suprapterygoid, is no doubt a dermometapterygoid. In addition an entopterygoid, an ectopterygoid, and two dermopalatines are present.

Gonatodus sp. (Watson 1925, p. 859, Fig. 27): In the figure part of the palatoquadrate ossification (*S Pt.*) is seen, as also a typical dermometapterygoid, an ectopterygoid, an entopterygoid, and a dermopalatine.

This treatment of the forms described by Watson in connection with what has been stated above as regards other forms, shows that the presence of an independent dermometapterygoid is a character which is common to

numerous early Ganoids, and the presence of the dermometapterygoid in *Polypterus* should therefore probably be regarded as a primitive character.

Mandible.

a. Glaucolepis magna.

Very few somewhat detailed investigations of the structure of the mandible within the suborder *Palaeonisciformes* are available (Watson 1925 and 1928; Stensiö 1921, 1925, and 1932; Aldinger 1937), and accordingly only

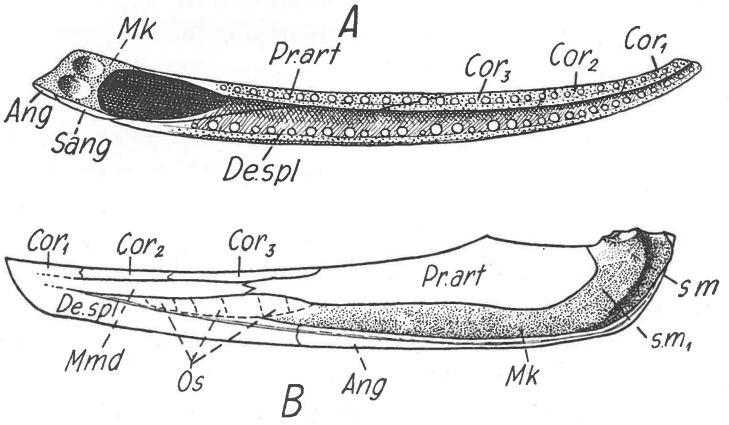


Fig. 38. *Glaucolepis magna* n. sp. Mandible. Based on specimen No. 7. 1.5 ×. A, dorsal view. Smallest teeth indicated by dots. B, medial view. Teeth and tooth-bearing dorsal laminae of the various dermal bones omitted.
Ang, angular; Cor_1, Cor_2, Cor_3, coronoids; *De. spl*, dentalo-splenial; *Mk*, posterior ossification in the Meckelian cartilage; *Mmd*, bone in the anterior part of the mandible containing an endochondral and probably a dermal component; *Os*, outlines of a series of small, tooth-bearing bones, whose presence is very doubtfull; *Pr. art*, prearticular; *Sang*, supraangular; *sm*, sm_1, grooves for nerves and (?) vessels on the medial face of the posterior ossification in the Meckelian cartilage.

few comparisons can be drawn in the subjoined description between the mandible in *Glaucolepis* and in other primitive *Chondrostei*.

Partly on account of its size and partly on account of the state of preservation of the material the mandible in *Glaucolepis magna* was especially well suited for a detailed investigation.

The Meckelian cartilage is ossified to a considerable extent, though not so completely as is the case in forms as for instance *Boreosomus* (Stensiö 1921, pp. 212–13; the present paper p. 342), *Saurichthys* (Stensiö 1925, pp. 107, 164, etc.), *Ospia* (Stensiö 1932, pp. 257–58), and *Pygopterus* (Aldinger 1937, p. 147), in which the cartilage is ossified as a single piece throughout its length.

In the most completely ossified specimens of *Glaucolepis magna* the Meckelian cartilage is ossified as one piece from the posterior part of the pars articularis forward through more than three-fourths of the whole length of the mandible.

This large ossification (*Mk*, Figs. 38A and B, 39C and D, 40A, 41; Pl. 10, Fig. 1; Pl. 19, Fig. 1; Pl. 20, Figs. 2, 3), whose extent does not justify the name "Meckelian bone" in Stensiö's application of the term (1925, p. 107; 1932, p. 258), consists of a similar endochondral mass surrounded by perichondral bone as is known to us from the ossifications of the neural endocranium. In the most anterior part of this bone the degree of ossification is slight; only very small remnants of endochondral bone can be observed here when the thin perichondral bone-layers are removed. Evidently the ossification was continued anteriorly by cartilage, and in less ossified (younger) specimens the boundary between the ossified and the unossified part of the Meckelian cartilage lies farther backwards than in the more completely ossified (older) specimens.

In the distal fourth of the lower jaw lies an ossification as to whose nature I have been in great doubt; it should probably, at any rate partially, be regarded as an ossification in the Meckelian cartilage, a mento-Meckelian ossification (*Mmd*, Figs. 38B, 39D and E, 40A and B, 41; Pl. 10, Fig. 1; Pl. 19, Fig. 1; Pl. 20, Fig. 2).

The middle part of this ossification is almost semicircular in transverse section, with a convex medial and a fairly straight lateral margin. The transverse sections show that this part of the bone consists of massive bone tissue, whose macroscopic structure is apparently lamellar.

The posterior part of the bone is much flattened from side to side, and lies medially to the anterior part of the large posterior ossification in the Meckelian cartilage, its posterior end meeting the rostral end of the prearticular in a deeply interlocked zig-zag suture. (Figs. 38B, 40A and B; Pl. 10, Fig. 1). The anterior half of the bone is flattened somewhat in a dorso-ventral direction, so that its anterior part, which adjoins the corresponding bone in the opposite jaw, has an elliptic transverse section, the long diameter of the ellipse being horizontal.

In *Glaucolepis magna* the bone seems to be entirely massive, whereas in the smaller species, *Glaucolepis gunnari*, the anterior half of the bone may sometimes be found to contain a cancellate bony substance. It is probable, therefore, that the bone includes a primary component corresponding to the mento-Meckelian ossification, even though the structure of the bone differs decidedly from that of the posterior ossification in the Meckelian cartilage.

The posterior part of the bone, which is flattened from side to side and lies medially to the anterior part of the posterior ossification in the Meckelian cartilage, and which is sutured with the prearticular, is so unlike a cartilage bone that I am most inclined to take it for a dermal bone which has fused by its anterior or lateral face with the mento-Meckelian ossification.

After this introduction I shall pass to a detailed description of the large posterior ossification in the Meckelian cartilage. This ossification consists in its anterior and largest part of a fairly thin bone plate, which bounds

the muscular fossa of the mandible medially and ventrally, and farthest caudally of a thicker mass of bone, the pars articularis, which forms the posterior or postero-ventral boundary of the muscular fossa.

Let us consider, first, that part of the ossification which lies in front of the pars articularis.

The internal face of this thin bone plate, that is to say, the face towards the muscular fossa, is concave in a dorso-ventral direction, while its external or medial face is correspondingly convex. A transverse section (Fig. 39C) through the bone plate shows that its thickness decreases from the most dorsal part almost as far as the middle, to increase again through its ventral part. That part of the ossification which forms the ventral wall of the muscular fossa of the jaw has on its ventral side, except in its most anterior part, a more or less distinct longitudinal keel. Laterally to this keel the external surface of the ossification is directed ventro-laterally, while medially to the keel it is directed ventro-medially.

The ventro-laterally directed face is in contact with a ridge on the medial side of the prearticular and the dentalo-splenial. This ridge is due to a thickening of those zones of the bones which lodge the mandibular canal.

On the dorsal part of the medial face of the ossification the prearticular always leaves a distinct impression. It will be seen from Figs. 38B and 40A that a considerable part of the medial surface of the ossification in the Meckelian cartilage is not covered by the prearticular, since this bone does not reach so far in either a caudal or a ventral direction as this cartilage bone. The greater part of this uncovered slightly convex surface is quite smooth, but, as will be seen from Figs. 40A and 41, a series of five or six depressions (*p.md*, Figs. 36, 40, 41; Pl. 10, Fig. 1; Pl. 19, Fig. 1) are found on its antero-ventral, medio-ventrally directed portion. These impressions or very shallow depressions, whose size and shape appear clearly from the figures, are bounded by slightly elevated margins. Without being able to supply a final explanation of the significance of these depressions, I shall put forward two possible interpretations.

One of these interpretations, and, I should think, the most probable one, is that the depressions are places of insertion for the musculus geniohyoideus inferius. For in *Polypterus* this muscle issues precisely from the medial face of the Meckelian cartilage ventrally to the ventral margin of the prearticular (Allis 1922, pp. 255–56).

The other interpretation is that we are dealing with impressions of small dermal bones. For in some specimens of *Glaucolepis magna* (Nos. 1 and 7) a series of small dermal bones is found (*Os*, Fig. 38B; Pl. 20, Fig. 2) in such a position that the elements of this series might very well be supposed to have produced the aforementioned impressions. There are two reasons why I cannot without hesitation accept this latter interpretation. In the first place the few specimens which present this series of dermal bones are not so well preserved that I feel entirely convinced that we are not concerned with de-

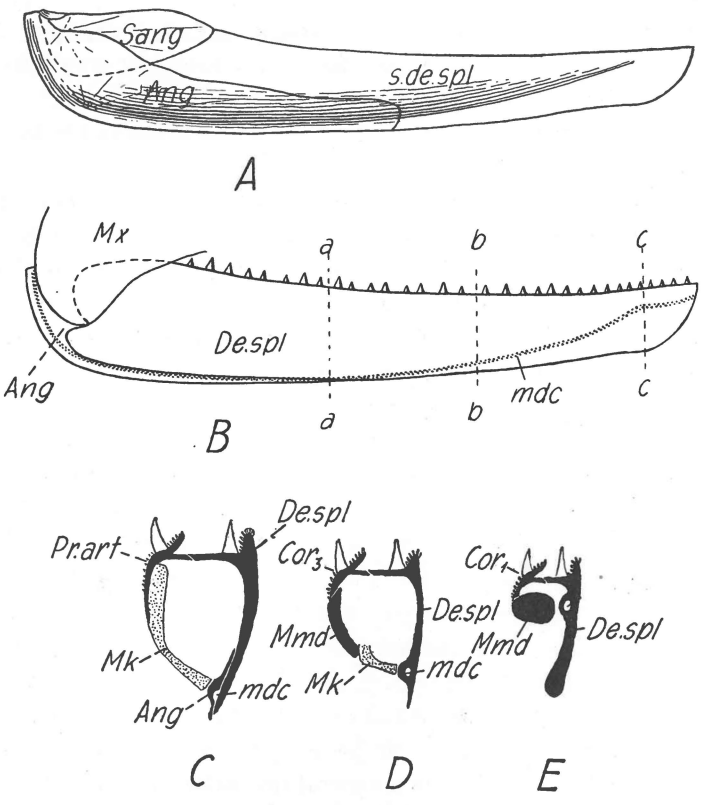


Fig. 39. *Glaucolepis magna* n. sp. Mandible. Based on specimen No. 7. A and B 1.5 ×, C, D and E 2.2 ×. A, lateral view. Dentalo-splenial removed; the part of the bone lying ventrally to its horizontal lamina represented by an impression of its medial face. B, lateral view. The small teeth on the dentalo-splenial omitted. C, D and E, transverse sections through the mandible along the lines *a-a*, *b-b*, and *c-c* respectively in Fig. A.
Mx, postero-ventral part of maxillary; *mdc*, mandibular canal; *s. de. spl*, impression of medial face of dentalo-splenial. Other letters as in Fig. 38.

tached fragments of another part of the dermal cranial skeleton, and secondly I have carefully dissected out the corresponding part of the jaw in other specimens of *Glaucolepis magna* without finding any trace of such bones. Nothing comparable to such a series of bones is known in other Actinopterygians. In Fig. 38B, which is based on specimen No. 7, the position of the dermal bones observed are indicated by dotted lines.

The most posterior part of the large ossification in the Meckelian cartilage may be described as a thickened posterior continuation of the above-described thin plate. The whole increase in thickness has taken place on the lateral side of the plate.

This thickened part, the pars articularis, forms the caudal and, as will be seen from the figures, to a slight extent the lateral boundary, too, of the muscular fossa of the jaw, extending so far in a lateral direction that its lateral face throughout its extent is in contact with the posterior part of the

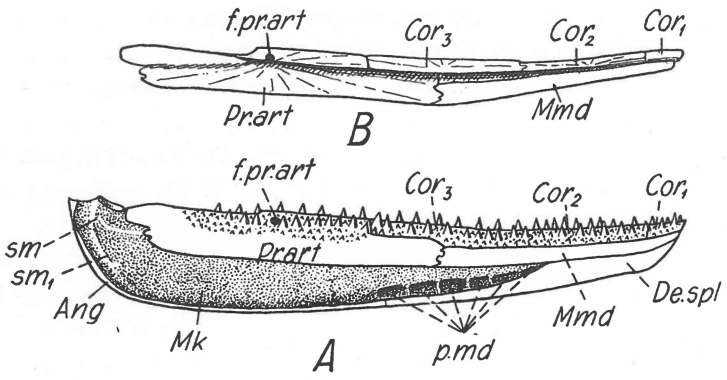


Fig. 40. *Glaucolepis magna* n. sp. A, mandible in medial view. B, prearticular, coronoids, and the bone *Mmd* in lateral view. Based on specimen No. 1. 1.4 ×.
f. pr. art, foramen through the dorsal lamina of the prearticular; *p.md*, shallow depressions on the surface of the posterior ossification in the Meckelian cartilage. Other letters as in Fig. 38.

medial faces of the angular and the supraangular. The face of the pars articularis directed towards the muscular fossa is concave both in a vertical and a horizontal direction. Of external faces the pars articularis has four, viz. a dorsal, a medial, a lateral, and a caudal (or more correctly caudo-medio-ventral) face.

The most dorsal part of the caudal face of the pars articularis is directed caudo-medially; but as a whole the face is so curved that farther ventrally it assumes a more and more ventral direction until it is continued by the most ventral part of the medial face of the thin bone plate lying in front of the pars articularis. The dorsal part of the caudal face of the pars articularis is slightly concave from side to side, and against this part lies the antero-ventral face of the symplectic (p. 180).

The aforementioned ventral keel on the thin bone plate which lies in front of the pars articularis, continues in a posterior direction, as will be seen from Fig. 41, on the pars articularis, to form the boundary between the lateral and caudal faces of this part. The most postero-dorsal part of this keel is situated between the dorsal part of the caudal and the dorsal part of the lateral face of the pars articularis immediately behind the very place of articulation with the pars quadrata and is produced into a very small processus retroarticularis.

The boundary between the caudal and medial faces of the pars articularis is formed by a small prominent ridge, which does not continue on that part of the ossification which lies in front of the pars articularis.

The dorsal face of the pars articularis has an obliquely rectangular outline, whose details will appear from Fig. 38A. On this face two distinct depres-

sions, elliptical in outline, for the articulation with the double condyle of the pars quadrata are found. This double articular fossa on the dorsal face of the pars articularis bears some resemblance to the hour-glass-shaped articular fossa of the articular in *Polypterus* (Allis 1922, Pl. 12, Figs. 35, 36, 37, 38).

Similarly as the lateral face of the quadrate region is covered by and intimately connected with the preoperculum and the quadratojugal, the lateral face of the pars articularis is covered by and firmly connected with the angular and the supraangular (pp. 169–70).

The caudal face of the pars articularis, unlike what is the case in *Saurichthys* (Stensiö 1925, pp. 165–66, Fig. 55B and D), is not covered by the angular, and since neither in a caudal nor in a ventral direction the prearticular (p. 171) extends as far as the Meckelian cartilage, the greater part of the medial face of the pars articularis is not covered by dermal bones either.

On the uncovered medial face of the pars articularis a faint groove is seen, which extends from the postero-dorsal corner of the medial face in a ventral and gradually more and more rostral direction towards the hind margin of the prearticular (*sm*, Figs 36, 38B, 40A; Pl. 20, Fig. 2).

In some few cases indications of another groove are found which issues from the posterior part of the above-mentioned groove, whence it extends forwards ventrally to that groove across the medial face of the pars articularis (sm_1, Figs. 36, 38B, 40A).

On removal of the prearticular the first-mentioned groove, or, at least in one specimen, both grooves, will be seen to continue in an antero-dorsal direction on that part of the medial face of the ossification against which the prearticular rested, to the posterior end of the groove whose walls are formed by the tooth-bearing parts of the dentalo-splenial and of the prearticular, and whose floor is for the greater part formed by the horizontal lamina of the dentalo-splenial (p. 172).

A comparison with the mandible in *Polypterus* (Allis 1922, Pl. 13, Fig. 42) and *Saurichthys* (Stensiö 1925, p. 166) shows that one of the small grooves on the medial face of the ossification in the Meckelian cartilage must have contained the ramus mandibularis internus facialis on its way to the longitudinal groove on the upper side of the mandible. The other groove may have contained a branch of the same nerve or perhaps a vessel.

In *Glaucolepis* the ramus mandibularis externus hardly, as in *Saurichthys* (Stensiö 1925, p. 166), accompanied the ramus mandibularis internus till the latter reached the canal between the prearticular and the ossification in the Meckelian cartilage, but no doubt ran immediately medially to the postero-dorsal corner of the angular in a ventral and then anterior direction in close relation to the ventral keel on the ossification in the Meckelian cartilage.

On the outer side of the mandible lie three dermal bones, which together form the lateral boundary of the muscular fossa of the mandible. These three bones are the dentalo-splenial, the supraangular, and the angular.

In lateral view the angular (*Ang*, Figs. 30, 38A and B, 39A, B, and C, 40A; Pl. 12, Fig. 1; Pl. 19 Figs. 1, 3; Pl. 20, Fig. 3) is roughly triangular in outline, with a posterior, a ventral, and an antero-dorsal margin. However, the obtuse angle between the posterior and ventral margins of the bone is much rounded. The posterior margin is much shorter than the other two, of which the antero-dorsal one is the longest. Both the posterior and the ventral margin are slightly convex, while the anterior margin, as shown by Fig. 39, has an irregularly winding course.

The radiation centre lies in the postero-ventral part of the bone at a small distance from its postero-ventral corner. The mandibular canal pierces the bone, running from its postero-dorsal end through the radiation centre towards its anterior part at a slight distance from and parallel with the caudal and ventral margins respectively of the bone.

If the complete mandible is viewed from the medial side, only the narrow rim of the angular will be visible, which in front of the radiation centre lies ventrally to and behind the radiation centre posteriorly to the mandibular canal.

If the complete mandible is viewed from the lateral side, the whole angular with the exception of its most posterior part and a narrow zone along its ventral margin will be seen to be covered by the dentalo-splenial.

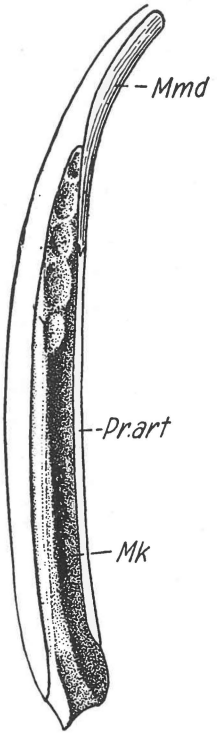


Fig. 41. *Glaucolepis magna* n. sp. Mandible in ventral view. Lateral extent of the dermal bones on the external side of the mandible indicated by a single line; otherwise these bones are omitted. Based on specimen No. 8. 1.5×.

Lettering as in Fig. 38.

The mandibular canal is seen to lie in a thickened part of the otherwise thin bone, and this thickening appears as a distinct ridge on the medial face of the bone. Against this ridge lies, as stated above (p. 165), that part of the face of the posterior ossification in the Meckelian cartilage which lies laterally to the ventral keel. Where, farthest posteriorly, this face attains a considerable extent as the lateral face of the pars articularis, it is in contact partly with the medial face of the angular and partly with the supraangular, as shown in Fig. 38A.

In lateral view the supraangular (*Sang*, Figs. 38A, 39A; Pl. 20, Fig. 3) is rounded triangular in outline, with a short posterior and somewhat longer dorsal and ventral margins. The supraangular is so situated in relation to the posterior ossification in the Meckelian cartilage that the posterior

part of its medial face covers and is firmly connected with the anterior part of the lateral face of the pars articularis. The remaining part of the medial face of the supraangular forms part of the lateral boundary of the muscular fossa of the mandible.

As will be seen from Fig. 39 A, the radiation centre of the bone lies near its postero-dorsal corner.

Viewing the complete mandible from the lateral side, we shall see only the most postero-dorsal part of the lateral face of the supraangular, the postero-ventral part of this face being concealed below the angular and the antero-dorsal part below the dentalo-splenial. The dentalo-splenial even overlaps a considerable area of that part of the angular which covers the lateral face of the supraangular, as will appear from a comparison of Fig. 39 A and B.

The dentalo-splenial (*De. spl*, Figs. 30, 38 A and B, 39 B, C, D and E, 40 A; Pl. 9, Fig. 1; Pl. 12, Fig. 1; Pl. 19, Figs. 1, 3; Pl. 20, Fig. 3) is, as usual, the largest of the three dermal bones on the outer side of the mandible.

In its posterior half the lateral face of the dentalo-splenial is fairly vertical, but in the anterior half of the bone, gradually as we approach the symphysial region, it grows increasingly oblique. Since moreover the mandible is, as a whole somewhat curved in the way shown in the figures, the anterior part of the external face of the dentalo-splenial is directed antero-laterally and somewhat ventrally. For the outline of the dentalo-splenial in lateral view, the reader is referred to Fig. 39.

As already stated, the dentalo-splenial overlaps considerable parts of the angular and supraangular.

After piercing the angular, the mandibular canal continues through the dentalo-splenial forwards to the anterior end of the mandible. It has not been possible to accurately determine the place where the mandibular canal passes from the angular into the dentalo-splenial. On account of the considerable overlapping of the angular by the dentalo-splenial, the location of this place would not be without interest.

Through the greater part of the dentalo-splenial the mandibular canal runs in an antero-dorsal direction, but a short distance behind the anterior end of the mandible it changes its direction, so that the most anterior part of the canal, as will be seen from Fig. 39 B, runs parallel with the dorsal margin of the dentalo-splenial. The radiation centre of the bone is pierced by the mandibular canal, and is situated precisely in the place where the canal changes its direction.

The mandibular canal lies in a thickened zone of the dentalo-splenial, and the thickening appears as a ridge on the medial face of the bone.

The area of the dentalo-splenial which lies ventrally to the mandibular canal is the only part of the bone which is visible when the entire mandible is viewed from the medial side. This area is roughly triangular in outline, with a posterior, an antero-dorsal, and an antero-ventral angle, the latter of which is obtuse.

As will be seen from Fig. 39B, a small concavity is found on the otherwise convex ventral margin of the dentalo-splenial, so that the height of the dentalo-splenial, after decreasing gradually forwards from the posterior part of the bone, increases along a very short stretch, to decrease again very rapidly through the anterior part of the bone. That part of the dentalo-splenial which lies anteriorly to the concavity just mentioned, is thicker than the more posterior part of the bone and is particularly thick in its most ventral part, as will be seen from Fig. 39E.

From the medial side of the dentalo-splenial issues a well developed horizontal lamina parallel with, but on a somewhat lower level than, the dorsal margin of the dentalo-splenial. As will be seen from Fig. 38A, the lamina begins laterally to the anterior part of the adductor opening, whence it extends to the anterior end of the jaw.

Medially the horizontal lamina is in contact with and overlaps a narrow marginal zone of a horizontal lamina, which issues from the lateral face of the tooth-bearing bones on the medial side of the mandible (cf. Fig. 39C, D, and E).

On the dorsal face of the horizontal lamina of the dentalo-splenial, and very close to the free dorsal margin of the bone, a row of about 25–35 large teeth are found, while the free margin itself is covered by diminutive acute teeth to an extent that will appear from the transverse sections shown in Fig. 39. Viewing the jaw from the lateral side, only the distal parts of the large teeth on the horizontal lamina are seen above the dorsal tooth-bearing margin of the dentalo-splenial.

Mandibles whose dermal bones are only represented by casts of their internal faces are of common occurrence in the material. Viewing such a mandible from the lateral side, we shall see that it is often lower than the complete mandible, because its dorsal margin is determined by the horizontal lamina mentioned above. Moreover its lateral face is strongly convex from the dorsal margin to the groove which indicates the course of that ridge on the medial face of the dentalo-splenial which lodges the mandibular canal.

The largest dermal bone on the medial side of the mandible is the prearticular (*Pr. art*, Figs. 38A and B, 39C, 40A and B, 41; Pl. 10, Fig. 1; Pl. 19, Fig. 1; Pl. 20, Fig. 2), which lies on the dorsal part of the medial face of the Meckelian cartilage, and which has such an extent that its posterior margin lies medially to the posterior margin of the adductor opening and its anterior margin lies a short distance behind the anterior end of the large posterior ossification in the Meckelian cartilage.

The outline of the exposed part of the medial face of the prearticular will best appear from Fig. 40A.

As will be seen from the transverse sections, the prearticular consists partly of a fairly vertical part, which lies on the medial face of the posterior ossification in the Meckelian cartilage, partly by a more dorsal part, which curves laterally over the dorsal margin of the ossification in the Mecke-

lian cartilage, to divide subsequently into two laminae. The most ventral one of these laminae is the aforementioned horizontal lamina of the prearticular, which laterally is in contact with the horizontal lamina of the dentalo-splenial. The more dorsal lamina has a dorso-lateral direction and forms the free medial wall of a longitudinal groove on the dorsal side of the mandible, whose lateral wall is formed by the dorsal tooth-bearing margin of the dentalo-splenial and whose bottom is formed by the horizontal laminae mentioned above.

Immediately medially to the place where it divides into two laminae, the prearticular bears a row of acute teeth, whose size and number correspond to the size and number of the teeth on the adjoining part of the horizontal lamina of the dentalo-splenial. Furthermore, the dorsal half of the medial face of the vertical part of the prearticular, except farthest caudally, is covered by numerous small, acute teeth, and this tooth-covering continues on the dorso-medially directed face of the dorsal part of the prearticular to the dorsal margin of its dorso-lateral lamina (Fig. 40A).

The radiation centre of the bones lies on the line along which the horizontal and dorso-lateral laminae of the bone meet and, as will appear from Fig. 40B, somewhat nearer the caudal than the rostral end of the bone.

Immediately dorsally to the radiation centre the dorso-lateral lamina of the prearticular is pierced by a large round opening (*f. pr. art*, Fig. 40A and B), through which possibly a nerve branch passed from the dorsal longitudinal groove of the mandible to the medial side of the prearticular.

Anteriorly the prearticular is joined by a deeply interlocked zig-zag suture with the posterior part of the aforementioned partially cartilage bone (p. 164) in the anterior part of the mandible. Farther rostrally the latter bone, which lies in front of the prearticular and whose lateral face by its posterior part is in contact with the medial face of the anterior, slightly ossified, part of the posterior ossification in the Meckelian cartilage, attains such a breadth that its most anterior part is in contact with, or at any rate lies very close to, the medial face of the dentalo-splenial, as will be seen from the transverse section shown in Fig. 39E.

On the antero-dorsal part of the medial face of the prearticular lies the posterior element of a coronoid series, which altogether contains three bones the anterior of which is the smallest (*Cor*$_{1-3}$, Figs. 38A and B, 39C, D and E 40A and B; Pl. 10, Fig. 1; Pl. 20, Fig. 2). A transverse section through any of the three coronoids shows that like the prearticular they consists partly of a dorsal dorso-laterally directed and a more ventral laterally directed lamina and partly by a more ventral part which extends in a ventral direction only as far as the tooth-bearing part of the prearticular.

The most dorsal lamina of that part of the posterior free coronoid which overlaps the prearticular, seems to replace the anterior part of the most dorsal lamina of the prearticular, whereas the more ventral lamina in the area in

which the coronoid partially overlaps the prearticular, belongs to the prearticular itself.

In front of the anterior part of the prearticular the lateral faces of the ventral parts of the coronoid elements lie against the dorso-medial part of the large bone *Mmd*, that is situated in front of the prearticular (Fig. 39E).

The radiation centres of the posterior two coronoids lie on the line of junction between their dorso-lateral and their horizontal laminae and about midway between their anterior and posterior ends. In the anterior coronoid it was impossible to localise the radiation centre.

As will be seen from Fig. 40A and from the transverse sections shown in Fig. 39, the coronoid elements are equipped with a series of large acute teeth, which form an anterior continuation of the row of large teeth on the prearticular, and in addition their whole medially or dorso-medially directed face is covered with closely set, small, acute teeth.

A comparison between *Glaucolepis magna* on the one hand and *Glaucolepis aldingeri* and *Glaucolepis stensiöi* on the other (cf. further p. 174) seems to show that the tooth-bearing part of the prearticular in *Glaucolepis magna* represents a posterior coronoid which has fused with the actual prearticular.

A groove comparable to the broad and deep longitudinal groove on the dorsal side of the mandible, whose medial wall is formed by the dorso-lateral laminae of the prearticular and the coronoid series and whose lateral wall is formed by the free dorsal margin of the dentalo-splenial, is found in *Polypterus* between the dorsal part of the dentalo-splenial and the dorsal margin of the prearticular plus the two small coronoid elements which lie in front of the prearticular (Allis 1922, p. 245, Pls. 11 and 12).

In *Polypterus* this longitudinal groove contains the ramus mandibularis internus facialis and a branch of the ramus mandibularis trigemini(Allis 1922, p. 245). In *Glaucolepis magna* the ramus mandibularis internus facialis, as has been stated above (p. 168), reached forwards to the posterior end of the longitudinal groove of the mandible through a canal extending between the prearticular and the posterior ossification in the Meckelian cartilage. It is probable, therefore, that, as in *Polypterus*, this nerve continued forwards in the longitudinal groove of the mandible. The ramus mandibularis trigemini may quite well have accompanied the ramus mandibularis internus facialis in the longitudinal groove itself; but there is no possibility of ascertaining this.

b. Glaucolepis aldingeri, arctica, gunnari, and stensiöi.

The mandible in all these four species shows all the elements which have been definitely ascertained in the mandible of *Glaucolepis magna*, but in none of the four species could it be so thoroughly investigated as in that species.

In the smallest specimens of *Glaucolepis stensiöi, gunnari,* and *arctica* and in the only specimen of *Glaucolepis aldingeri* in which the mandible could be investigated, the Meckelian cartilage is ossified to nearly the same extent as in *Glaucolepis magna.*

In shape and in mutual relations the dermal bones agree well with those in *Glaucolepis magna.* Only as regards the coronoid series and the prearticular will it be necessary to make a few remarks. As far as I could observe, these bones, in all the specimens in which they could be investigated with the exception of two, agree in number and shape with the corresponding bones in *Glaucolepis magna.* The specimens showing deviations are one specimen of *Glaucolepis stensiöi* (No. 49) and the only specimen present of *Glaucolepis aldingeri* (No. 66), in which the head is fairly well preserved.

These two specimens differ by containing, instead of the three free coronoids and the tooth-bearing part of the prearticular found in *Glaucolepis magna,* a continuous series of independent coronoids right from the symphysial region to the anterior part of the adductor opening, directly comparable to that described by Watson in *Elonichthys caudalis* (Watson 1925, p. 862) and *Nematoptychius greenocki* (Watson 1928, pp. 59–60).

Of the ten to twelve individual coronoids within this series, the five or six anterior ones seem to correspond to the three free coronoids in *Glaucolepis magna* and the five or six posterior ones to the tooth-bearing part of the prearticular in that species. The state of preservation of the two specimens does not enable us to decide whether the horizontal lamina which in *Glaucolepis magna* issues in a lateral direction from the prearticular, in these two specimens issues from the small free coronoids or from the actual prearticular.

Hyoid arch, dermohyal, antoperculum, operculum, suboperculum, branchiostegal rays, and gular plate.

a. Glaucolepis aldingeri.

I shall deal, first, with this species because certain elements of the hyoid arch are especially well preserved in the only fairly well preserved head at my disposal (specimen No. 66).

The following elements of the hyoid arch are preserved in this specimen: the hyomandibula, the symplectic, a posterior and an anterior ceratohyal ossification, and the hypohyal.

All the elements of the hyoid arch in this and the other species of *Glaucolepis* consist of endochondral cancellate bone more or less completely surrounded by perichondral bone-layers.

The hyomandibula (*Hm*, Pl. 20, Fig. 1) is somewhat damaged, especially in its dorsal part, and will not be described in this species since it corresponds in all details to the better preserved hyomandibula in *Glaucolepis magna.*

The symplectic (*Sympl*, Fig. 42A, B, and C; Pl. 20, Fig. 1), which articulated with both the palatoquadrate and the Meckelian cartilage, is a vertically placed, short and strong bone, bounded, broadly speaking, by a dorsal, a ventral, a posterior, an anterior, a lateral, and a medial face. The dorsal and ventral faces of the bone are devoid of perichondral bone-layers and were capped by cartilage.

The diameter of the dorsal part of the bone corresponds fairly well with the diameter of the ventral end of the hyomandibula. Throughout the ventral part of the bone the diameter decreases in a ventral direction.

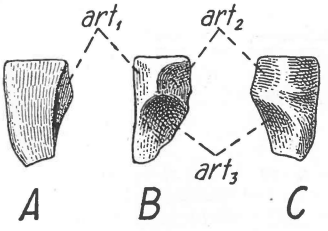


Fig. 42. *Glaucolepis aldingeri* n. sp. Symplectic. Based on specimen No. 43. 1.8 ×. A, medial view. B, front view. C, lateral view.
art_1, art_2, articular faces for the pars quadrata; art_3, articular face for the pars articularis.

The lateral, the posterior, and the medial faces of the bone are fairly smooth, as will partially appear from Fig. 42; the anterior face, however, has a more complicated relief. This face falls into three divisions (art_{1-3}, Fig. 42), viz. a dorso-lateral, a dorso-medial, and a ventral division, whose mutual relations will appear from the figures.

The dorso-lateral division is directed antero-laterally, and articulated with the posterior part of the lateral condyle of the pars quadrata. The dorso-medial division is directed antero-medially, and articulated with the posterior part of the medial condyle of the pars quadrata. The vertical ridge, which separates the dorso-lateral and the dorso-medial division, fits into the groove which separates the two condyles of the pars quadrata. The ventral one of the three divisions of the anterior face is directed antero-ventro-medially, and articulated with the posterior part of the posterior ossification in the Meckelian cartilage.

The large dorsal and the small ventral face of the symplectic are plane.

In the ceratohyal two ossifications (Chy_1, Chy_2, Fig. 43) are found, an anterior and a posterior one, whose position in relation to one another will appear from the figure.

The anterior ossification of the ceratohyal, ceratohyal I, is a vertically placed bone plate about half as long as the mandible, and its greatest height is about one-third its length. Its medial face is concealed in the rock. This bone, whose outline appears clearly from Fig. 43, attains its greatest height in its posterior part. The height decreases from this part forwards, to increase again towards the anterior end of the bone.

Like the other elements of the hyoid arch, the ceratohyal I consists of cancellate bone, and is on its outer faces lined with perichondral bone, except on its anterior and posterior narrow terminal faces. The endochondral mass of the bone in so far corresponds in outline to the external outline of the bone as its height decreases both from the anterior and the posterior end towards the lowest part of the bone, but the decrease in height of the endochondral mass is so considerable that in the lowest part of the bone the endochondral mass is only a very thin strand, as will be seen from the figure.

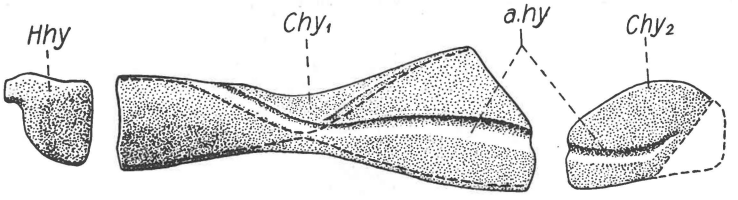


Fig. 43. *Glaucolepis aldingeri* n. sp. Ossifications in the ventral part of the hyoid arch in lateral view. The broken lines in the middle ossification show the upper and lower boundaries of the cancellate tissue of the bone. Based on specimen No. 43. 1.8 ×.
Chy_1, Chy_2, anterior and posterior ossifications in the ceratohyal; *Hhy*, hypohyal; *a. hy*, groove for the afferent hyoid artery.

This thin strand lies nearer the ventral than the dorsal margin of the bone, and an essential part of the bone dorsally and ventrally to this strand consists of a very thin vertical lamina, so that both the dorsal and ventral margins of the middle part of the ceratohyal I are very sharp.

On the lateral face of the ceratohyal I a broad longitudinal groove (*a.hy*, Fig. 43) for the afferent hyoid artery is found. Within the *Palaeonisciformes* a corresponding groove has been observed in *Plegmolepis* (Aldinger 1937, Fig. 19) and *Pygopterus* (Aldinger 1937, pp. 149-50, Fig. 41B); as is generally known, a similar groove is found in numerous higher Actinopterygians.

In the relief of its external surface the ceratohyal I shows distinct traces of radiation from a centre situated in that part of the bone in which the endochondral mass is most constricted.

The posterior ossification of the ceratohyal, the ceratohyal II, is not half as long as the ceratohyal I, and is a vertical plate consisting of cancellate bone, which laterally, medially, and ventrally is lined with perichondral bone-layers.

The outline of the ceratohyal II is seen from Fig. 43, which moreover shows that a posterior continuation of the longitudinal groove on the lateral face of the ceratohyal I is found on its lateral face. From the anterior margin of the bone the groove at first runs in a caudal and at the same time slightly ventral direction, to turn into a caudal and slightly dorsal direction a short distance behind the middle of the bone. The groove cannot be traced right to the posterior margin of the bone, the postero-ventral part of the bone being damaged.

Within the *Palaeonisciformes* the ceratohyal II has previously been ob-

served in a single specimen of *Acrorhabdus bertili* (Stensiö 1921, pp. 226–27, Fig. 72), and in this specimen only as an impression of a thin bone lamina situated behind and adjoining the ceratohyal I.

On account of a considerable curvature the hypohyal (*Hhy*, Fig. 43) falls naturally into two divisions, a proximal and a distal. (The terms proximal and distal are here preferable to the terms anterior and posterior, used in the description of the ceratohyal).

The proximal part of the hypohyal is a vertical, nearly transversely placed fairly thin bone plate, whose anterior face is slightly convex. Nearest its proximal margin the height of this plate is the same as the height of the distal (anterior) end of the ceratohyal I, but, as will be seen from Fig. 43, it decreases towards the distal part of the bone.

The distal part of the hypohyal is much lower and at the same time much thicker than the proximal part. This part of the bone may be described as a caudally pointing process issuing from the dorsal part of the medially facing margin of the higher part of the bone.

In the examined specimen of *Glaucolepis aldingeri* the position of the hypohyal in relation to the anterior part of the ceratohyal I is as shown in Fig. 43; however, this position is due to the compression of the head from side to side. The hypohyal was placed in the same way as the hypohyal in the restoration of *Glaucolepis stensiöi* shown in Fig. 45. It will be seen from this figure that the hypohyals of the right and left sides are only separated by a small interspace, which possibly lodged a small basihyal, at any rate in *Glaucolepis stensiöi* (p. 184). The distal end of the hypohyal articulated with the anterior part of the anterior large ossification in the basibranchial series and with the distal part of the hypobranchial I.

The hypohyal has previously been ascertained in two *Palaeonisciformes*, viz. in *Pygopterus nielseni* (Aldinger 1937, p. 150) and *Elonichthys aitkeni* (Watson 1925, p. 862, Fig. 29); but it is not particularly well preserved in these species.

About the dermohyal, the antoperculum, the operculum, the subopercu-lum, the branchiostegal series, and the gular plate in *Glaucolepis aldingeri* only little information can be given. A dermohyal is found in a normal position in relation to the hyomandibula, and the presence of an antoperculum could likewise be ascertained; but both these bones are in too bad a state of preservation to justify a detailed description.

The operculum is fairly well preserved, and agrees in all respects with that of *Glaucolepis stensiöi*, so it will suffice to refer the reader to the description and figure of that species. Likewise the not particularly well preserved subo-perculum seems to agree with that of *Glaucolepis stensiöi*.

Only very inconsiderable remains of the branchiostegal series are at hand,

and nothing can be stated about this series or the small unpaired gular plate, which probably occurred in this species as in the other species of *Glaucolepis*.

b. Glaucolepis magna.

In this species the following elements of the hyoid arch have been observed: the hyomandibula, the symplectic, the ceratohyal I, and the hypohyal.

The hyomandibula (*Hm*, Figs. 35A, 36; Pl. 9, Fig. 1; Pl. 12, Fig. 1; Pl. 19, Figs. 2, 3) articulated by its dorsal (proximal) end with the otic region of the neural endocranium; the position of the large articular fossa on the lateral face of the otic region is described above (p. 48). From the place of articulation the hyomandibula extends in a postero-ventral direction along the dorsal part of the medial face of the palatoquadrate, from which it is partly separated by the internal lamina of the preoperculum. Unlike the conditions in *Saurichthys hamiltoni* (Stensiö 1925, p. 168) the hyomandibula leaves no impression on that part of the medial face of the palatoquadrate with which it has contact. The ventral end of the hyomandibula lies a short distance dorsally to the posterior part of the quadrate region, as will be seen from Figs. 35 and 36.

As in several other *Palaeonisciformes*, the hyomandibula is angularly bent, consisting of two shanks of about equal length, a dorsal (antero-dorsal) and a ventral (postero-ventral), which meet at an obtuse angle, as shown in Figs. 35 and 36.

The dorsal shank is compressed from side to side, especially in its dorsal part, and the posterior margin of this part of the bone is fairly sharp. The ventral shank is rounded triangular in section and has a postero-lateral, an antero-lateral, and a medial face.

In its most dorsal part the hyomandibula attains a considerable breadth, which decreases gradually towards the middle part of the bone, where the posterior margin is produced into a rounded, not particularly prominent processus opercularis (*pr.op*, Figs. 35A, 36). The diameter of the hyomandibula increases through the ventral division of the bone in the direction towards its ventral end.

The broad, dorsal, transversely compressed shank of the hyomandibula is curved in the direction from its posterior to its anterior margin, its lateral face being convex, and its medial face concave.

As will be seen from Fig. 35, on the lateral, convex, face of the dorsal shank of the hyomandibula lies the triangular dermal bone which was called by me the dermohyal in a previous paper (E. Nielsen 1936, p. 42) and which will be described below.

Farthest ventrally, near the transition to the processus opercularis, the posterior margin of the dorsal shank of the hyomandibula is pierced by a short canal (*f.trh*, Figs. 35, 36), which, from the medial side of the hyomandi-

bula, runs in a ventro-lateral direction to the lateral side. From the medial opening of this canal a short groove extends in an antero-dorsal direction along the posterior margin of the hyomandibula, and from the lateral opening of the canal another short groove runs in a postero-ventral direction along the base of the processus opercularis. These two grooves and the canal connecting them lodged the truncus hyoideomandibularis facialis or at any rate the ramus hyoideus facialis.

As is generally known, *Polypterus* is unique among recent fishes as regards the relations between the truncus hyoideomandibularis and the hyomandibula, the ramus mandibularis facialis running rostrally and the ramus hyoideus facialis caudally to the hyomandibula (van Wijhe 1882, pp. 263–64; etc.). Stensiö (1925, p. 169) puts forward reasons in favour of a similar course of the two branches of the truncus hyoideomandibularis in *Saurichthys* and at the same time suggests that similar conditions existed in a number of *Palaeonisciformes*, while in others (*Gyrolepis*) the undivided truncus hyoideomandibularis pierced a similar canal in the hyomandibula as that in *Glaucolepis* described here.

In his summary of the information about the hyomandibula in the *Palaeonisciformes* supplied up to 1937 Aldinger writes as follows (1937, p. 333):

"Das Foramen für den Truncus hyoideomandibularis ist in allen Stadien der Ausbildung vorhanden: es fehlt ganz bei *Boreosomus*, *Acrorhabdus* und vielen palaeozoischen Formen. Bei *Pygopterus* und *Acropholis* ist im caudalen Rand des Hyomandibulare ein seichte Rinne für den Nerven entwickelt, bei *Boreolepis* und *Glaucolepis* ist diese Rinne von einer dünnen Knochenlamellen zu einem Foramen geschlossen, ein Foramen besitzt ausserdem *Gyrolepis* (Stensiö 1921, p. 244)."

In his description of *Pygopterus nielseni* Aldinger (1937, pp. 145–46), discussing a foramen or a groove in the posterior margin of the quadratometapterygoid, deals more closely with the relations between the hyomandibula and the truncus hyoideomandibularis.

In very cautious terms he mentions the possibility that this foramen (or groove) may be compared with the short canal in the posterior part of the metapterygoid in *Polypterus* through which the ramus mandibularis internus facialis passed on its way to the mandible (van Wijhe 1882, pp. 263–64; Allis 1922, p. 243). Aldinger regards it as possible that if this comparison holds good, the two branches of the truncus hyoideomandibularis facialis had similar relations to the hyomandibula as in *Polypterus*.

As described above, in *Glaucolepis* a groove or short canal is found in the posterior margin of the pars quadrata of the palatoquadrate ossification (p. 145) which doubtless corresponds to the canal or groove in *Pygopterus*. It seems to me quite probable that the ramus mandibularis internus facialis actually passed through this canal; however this needs in no way

imply that the ramus mandibularis facialis passed rostrally instead of caudally to the hyomandibula. In my opinion the position of the hyomandibula in relation to the palatoquadrate more probably indicates that from the opening through which it left the jugulo-hyoideomandibular canal the truncus hyoideomandibularis facialis passed undivided through the small canal in the hyomandibula, to divide, then, into a ramus hyoideus facialis and a ramus mandibularis facialis; the latter, again, divided into a ramus mandibularis internus facialis and a ramus mandibularis externus facialis, of which the former passed through the opening in the hind margin of the pars quadrata.

Both from the dorsal and from the ventral end of the hyomandibula the dimensions of its interior endochondral, cancellate mass decreases towards the midmost part of the bone, in which part only a very thin strand of cancellate bone can be observed. Both the dorsal and the ventral end of the hyomandibula were capped by cartilage.

Judging from the position of the hyomandibula it might be supposed that the spiraculum has been situated in the area between the dorsal margin of the dorsal suborbital and the lateral margin of the dermal cranial roof.

The symplectic (*Sympl*, Figs. 35A, 36; Pl. 19, Fig. 3) has been observed in several specimens of *Glaucolepis magna*, but in most cases it is rather poorly preserved, probably because it is less completely ossified than in *Glaucolepis aldingeri*. In its relations to the hyomandibula, the quadrate region, and the articular region it agrees perfectly with the symplectic in *Glaucolepis aldingeri*.

Only the ceratohyal I (Chy_1, Pl. 20, Fig. 2) has been found in this species, and it agrees well with the ceratohyal I in *Glaucolepis aldingeri*.

As in *Glaucolepis aldingeri*, the hypohyal is so curved that its proximal and distal parts meet at a fairly right angle. The distal part of the bone is but slightly lower than the proximal part, and the bone as a whole seems to be somewhat thicker than in *Glaucolepis aldingeri*. Its anteriorly directed face is uneven and provided with some irregular rounded ridges, which extend from the dorsal to the ventral margin of the bone.

On the lateral face of the dorsal shank of the hyomandibula lies a triangular dermal bone (*Dhy*, Figs. 30, 35A; Pl. 12, Fig. 1) which in lateral view has the outline shown in Fig. 35. The bone is curved in the same way as that part of the surface of the hyomandibula against which it rests, and accordingly has a lateral face convex in a postero-dorsal to antero-ventral direction and a correspondingly concave medial face.

The bone here described is so situated in relation to the adjacent dermal bones that its anterior (antero-ventral) margin is covered by the preoperculum, and its posterior (postero-dorsal) margin is covered partly by the anterior margin of one or two antopercular bones and partly by the operculum. The overlapping of the bone may in some cases be so considerable that the

bone is entirely concealed below the neighbouring bones. The radiation centre lies fairly near the postero-dorsal margin of the bone and much nearer its dorsal (antero-dorsal) than its ventral (postero-ventral) end.

Already in a previous paper (E. Nielsen 1936, p. 42) I discussed this dermal bone, the dermohyal, which I took to be homologous with the "accessory" hyomandibula in *Polypterus*, and on account of its relations to the hyomandibula I put forward the assumption that the bone had originated by fusion of small tooth plates on the hyomandibula.

A single dermohyal is found in numerous *Palaeonisciformes*, but in *Cheirolepis* (and possibly in other forms too) a dermohyal seems to be present on the ventral shank of the hyomandibula (Watson 1925, Fig. 3, *X*) in addition to the dermohyal found on the lateral face of the dorsal shank (Watson 1925, Fig. 3, *Y*).

Pehrson (1940, p. 22) puts forward the assumption that the preoperculum in *Cheirolepis* were formed by the rostral, and the dorsal and ventral dermohyals by the caudal elements of the double row of primordia arisen in relation to the preopercular canal. However, further investigations on primitive *Palaeonisciformes* must be made before a standpoint can be taken for or against Pehrson's hypothesis.

In the area behind the dermohyal and, as stated above, partially overlapping this bone, one or two small triangular antoperculars (*Aop*, Fig. 30; Pl. 9, Fig. 1) occur.

In the specimens in which only one antoperculum is found, this is a triangular bone with a dorsal (antero-dorsal), an antero-ventral, and a postero-dorsal margin, of which the dorsal margin is much shorter than the other two. The dorsal margin is free, the postero-dorsal margin overlaps a narrow marginal zone of the operculum, and the antero-ventral margin, as stated above, overlaps the dermohyal to a greater or smaller extent.

The same area which in some specimens is occupied by one antoperculum, in others is occupied by two smaller antoperculars, whose mutual size will be seen from Fig. 30. The hind margin of the anterior of these small antoperculars overlaps a very narrow zone of the posterior one.

Where one antoperculum is found, its radiation centre lies in the dorsal (antero-dorsal) half of the bone. Where two antoperculars are present, I failed to observe the radiation centres.

In a previous paper (E. Nielsen 1936, p. 42) I have compared the antoperculum in *Glaucolepis* with an element of the postspiracular series in *Polypterus*. However, there can be no question of a direct homologising between the antopercular elements in *Glaucolepis* and the postspiracular elements in *Polypterus*, for everything indicates that the antopercular elements in the family *Palaeoniscidae* have arisen within this family itself. Antopercular elements are present in varying numbers in many *Palaeonisciformes*, and have to all appearance arisen independently within several families,

probably by a subdivision of the antero-dorsal part of the operculum. Aldinger (1937, p. 336) points out that the presence of small independently movable dermal bones in this area is of importance for the movements of the hyomandibula and accordingly of the palatoquadrate-maxillary apparatus.

I shall mention here a dermal bone which owing to its position renders it tempting to make a direct comparison with an element in the postspiracular series in *Polypterus*, and which has not previously been found in any form within the *Palaeonisciformes*.

This bone (*Pspic*, Fig. 30) occupies the posterior part of the area which is bounded laterally by the dorsal suborbital, the preoperculum, the dermohyal, the antoperculum, and the operculum, and medially by the dermal cranial roof and the suprascapular. The bone is four-sided in outline, and its accurate position in relation to the surrounding bones is seen from Fig. 30.

With its posterior margin this bone overlaps the anterior margin of the supracleithral, without, however, being firmly connected with this or with any of the other dermal bones surrounding it. In its relations to the lateral extrascapular, the suprascapular, the supracleithral, and the operculum the bone shows so good agreement with the posterior element of the spiracular series in *Polypterus* that I consider it justifiable to rubricate it under the designation postspiracular bone.

The operculum (*Op*, Figs. 30, 35A, 36; Pl. 9, Fig. 1) may be regarded as a roughly triangular bone bounded by a postero-dorsal, an antero-ventral, and a postero-ventral margin. The postero-dorsal margin forms an evenly convex arch, the postero-ventral margin is *S*-curved, and the antero-ventral margin is angularly bent, its two halves forming an obtuse angle. The postero-ventral margin overlaps a fairly considerable antero-dorsal marginal zone of the suboperculum, and the antero-ventral margin is overlapped partly by the preoperculum and partly by the antoperculum, as stated above.

The operculum as a whole is very slightly curved in a dorso-ventral direction, so that its lateral face is slightly convex and its medial face correspondingly concave.

The radiation centre lies in the antero-dorsal part of the bone a short distance postero-dorsally to the middle of that part of the antero-ventral margin of the bone which is overlapped by the antoperculum.

In lateral view the suboperculum (*Sop*, Figs. 30, 44; Pl. 9, Fig. 1) has a four-sided outline with a posterior (postero-dorsal), a dorsal (antero-dorsal), an anterior (antero-ventral), and a ventral margin. The details in outline of the exposed, very slightly arched part of the suboperculum is seen from Fig. 30; the dorsal marginal zone of the bone is covered by the operculum, so it is not seen from the figure that the antero-dorsal corner of the bone is produced into a long antero-dorsally pointing process.

From the dorsal half of the medial face of the suboperculum a well devel-

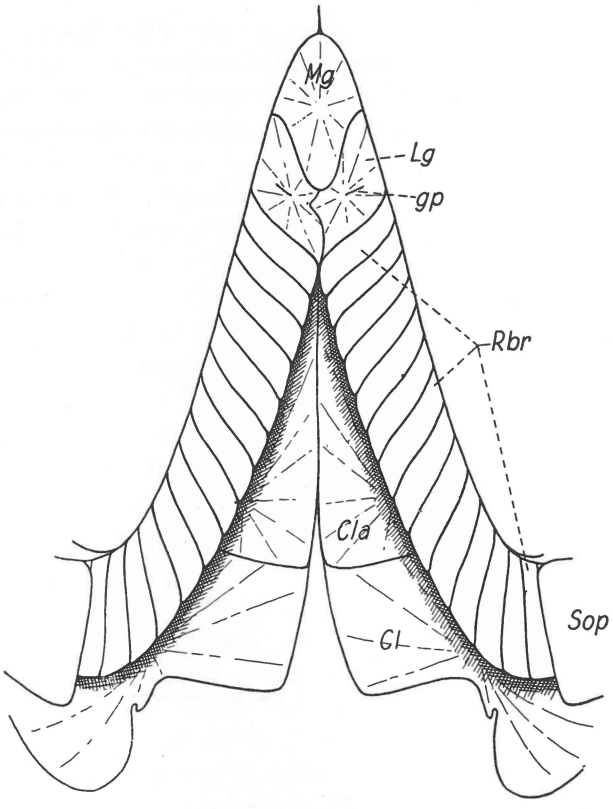


Fig. 44. *Glaucolepis magna* n. sp. Ventral part of the dermal visceral skeleton and of the series of dermal bones of the shoulder girdle in ventral view. Based mainly on specimen No. 7. 1.4 ×.
Cl, cleithrum; *Cla*, clavicle; *Lg*, anterior branchiostegal ray (lateral gular plate); *Mg*, median gular plate; *Rbr*, branchiostegal rays; *Sop*, suboperculum; *gp*, gular pit-line.

oped medially directed lamina issues at a short distance from and parallel with the anterior margin of the bone. This lamina is in intimate contact with the postero-ventral corner of the ossified part of the hyomandibula and must also have been in contact with the cartilage which formed the ventral termination of the hyomandibula.

The radiation centre of the suboperculum lies very close behind the middle of the anterior margin of the exposed face of the bone and precisely where the superficial lamina of the bone meets with the most ventral part of its internal lamina.

In the restorations shown in Figs. 30 and 44 the branchiostegal series between the suboperculum and the median gular plate comprises fifteen branchiostegal rays, but the number may possibly vary somewhat from specimen to specimen. Four of the about fifteen branchiostegal rays lie caudally to the mandible, but, as will be seen from the figures, the posterior margins of these four rays do not continue the uniformly curved line formed

by the posterior margins of the operculum and the suboperculum, because the branchiostegal rays are much shorter than the ventral margin of the suboperculum. The branchiostegal rays overlap each other to a greater or smaller extent, according to the position of the opercular fold. The position of the branchiosteal rays and the outline of their exposed faces when the gill-cavity is closed, is seen from the figures. The branchiostegal ray (*Lg*, Fig. 44) lying nearest behind the median gular plate is much larger than the remaining ones and either overlapped or underlay the medial margin of the corresponding branchiostegal ray belonging to the other side of the head. The anterior marginal zone of the exposed face of this branchiostegal ray is overlapped by the posterior part of the median gular plate.

The radiation centres of the branchiostegal rays lie much nearer their margins facing the mandible than their opposite margins, apart from the radiation centre of the anterior large ray, which has a fairly central position. On the exposed face of this branchiostegal ray a short pit-line (*gp*, Fig. 44) is found. This pit-line runs in a lateral direction from a point immediately below the radiation centre.

Between the anterior parts of the right and left mandibles lies a small median gular plate (*Mg*, Figs. 30, 44), roughly rhombic in outline, whose further details will appear from the figures. The paired postero-lateral margin of the gular plate overlaps a narrow marginal zone of the ventral face of the anterior large branchiostegal ray of the right and the left side.

The radiation centre lies at the point of intersection between the transverse and the longitudinal diagonals of the bone.

c. Glaucolepis stensiöi.

The following ossifications have been observed in the hyoid arch: the hyomandibula, the symplectic, the ceratohyal I, and the hypohyal. Furthermore, possibly a basihyal is present.

Corresponding to the relatively short and high postorbital parts of the maxillary and the palatoquadrate in this species, the hyomandibula has a steeper position than in *Glaucolepis magna*, and the angle between its antero-dorsal and postero-ventral shanks is less obtuse.

Apart from these differences the hyomandibula, as well as the symplectic, the ceratohyal I, and the hypohyal agree well with the corresponding ossifications in *Glaucolepis magna* and need no detailed description.

Several of the specimens are in such excellent state of preservation that it can be definitely stated that they had no posterior ossification in the ceratohyal.

In specimen No. 38, between the distal parts of the right and left hypohyals, traces of a very small unpaired ossification (*Bhy*, Fig. 45) are found, whose exact shape cannot be stated. Possibly this ossification is a basihyal,

which, as is well known, within the Actinopterygians has so far been ascertained in the *Teleostei* only. (For the basihyal in *Elonichthys aitkeni* recorded by Watson (1925, p. 863, Fig. 29) cf. p. 196).

The dermohyal agrees in shape and position with the dermohyal in *Glaucolepis magna*. Only one antoperculum is present; its dimensions is seen from Fig. 27. A spiracular bone like that found in *Glaucolepis magna* can be observed. The dorsal part of the operculum is relatively much broader than in *Glaucolepis magna*, as will be seen from Fig. 27. In the sectioned specimen the operculum of the right side is preserved as an impression of its medial face, and this impression shows that the operculum on its medial face had a series of small depressions (*p.Op*, Pl. 1). This series, consisting of seven or eight depressions, extends from the middle of the ventral margin of the operculum in an antero-dorsal direction through the ventral third of the operculum, and on the dorsal half of the medial face of the subopercular it has a continuation in a postero-ventral direction consisting of four or five similar depressions. I can give no satisfactory interpretation of these small depressions, which, besides in the sectioned specimen, have been observed in some few other specimens of *Glaucolepis stensiöi* and in a few specimens of *Glaucolepis gunnari* and *arctica*; for it is hardly conceivable that a musculus adductor operculi was inserted so far ventrally on the opercular bones.

The outline of the subopercular is seen from Fig. 27. As in *Glaucolepis magna*, this bone has a medially directed vertical internal lamina, which lies immediately behind the most ventral part of the hyomandibula. The shape and position of the branchiostegal rays agree with those observed in *Glaucolepis magna*, and their number ranges between twelve and fifteen. The median gular plate, too, is of the same shape as in *Glaucolepis magna*.

d. Glaucolepis arctica and gunnari.

As regards the position and shape of the hyomandibula *Glaucolepis gunnari* agrees most closely with *Glaucolepis magna*, and *Glaucolepis arctica* most closely with *Glaucolepis stensiöi*. The remaining elements of the hyoid arch observed in *Glaucolepis gunnari* and *Glaucolepis arctica*, viz. the symplectic, the ceratohyal I, and the hypohyal, do not differ from the corresponding elements in *Glaucolepis aldingeri* and *Glaucolepis magna*. The dermohyal, the single antoperculum, the postspiracular bone, the subopercular, the branchiostegal rays, and the median gular plate agree in shape and position with the corresponding dermal bones in *Glaucolepis magna* and *Glaucolepis stensiöi*.

e. Discussion.

In 1937 Aldinger gave a general account of the palatoquadrate-maxillary apparatus, the hyoid arch, and the opercular apparatus in the *Palaeo*

nisciformes, and drew various conclusions as to the arrangement of the visceral musculature in this group (Aldinger 1937, pp. 332–37). To Aldinger's very instructive summary it may perhaps be objected that he has generalised too much from the scanty and scattered data which were available up to that time concerning the visceral endoskeleton of the group.

In fact, up to 1937 no actually exhaustive account was available of the palatoquadrate-maxillary apparatus and its relations to the hyoid arch in any form belonging to the *Palaeonisciformes*, and it is therefore not surprising that Aldinger's conclusions as to certain points do not agree entirely with the conditions observed in *Glaucolepis*.

Thus Aldinger says that the hyomandibula has no direct connection with the palatoquadrate and the preoperculum; but in *Glaucolepis* the direct connection between the palatoquadrate, the preoperculum, and the hyomandibula is so intimate that the hyomandibula had no possibility for independent movements.

As regards the preoperculum Aldinger writes that it consists only of a superficial lamina and that it has no intimate connection with the palatoquadrate; however, in *Glaucolepis*, as has been shown above, the preoperculum has an internal lamina which is intimately connected with the palatoquadrate and which constitutes an important part of the wall of the chamber in which the musculus adductor mandibulae was enclosed.

However, the following description of the possibilities for movement of the palatoquadrate-maxillary apparatus, the hyomandibula, and the dermal bones of the visceral skeleton will confirm most of Aldinger's conclusions.

From the shape of the dorsal end of the hyomandibula in *Glaucolepis* and of its articular fossa on the lateral face of the otic region it appears that the hyomandibula can only have moved in a plane perpendicular to the long diameter of the articular fossa. In other words, the ventral end of the hyomandibula must have moved along part of a circular arch which is roughly transverse to the longitudinal axis of the body.

The hyomandibula is firmly connected with the medial lamina of the preoperculum and with the postero-dorsal part of the medial face of the palatoquadrate and in addition with the symplectic, which latter is so situated that it must have articulated both with the quadrate region of the palatoquadrate and with the articular region of the ossified Meckelian cartilage. Consequently the stiff palatoquadrate-maxillary complex must have followed the hyomandibula in its movements. However, the anterior end of the palatoquadrate was linked to the ethmoidal region by means of the ethmo-palatine articulation. When the ventral end of the hyomandibula moved, the palatoquadrate-maxillary complex therefore turned on the small articular process of the ethmoidal region.

As we have seen, the palatoquadrate had one more direct articulation

with the endocranium, the palato-basal articulation, and with Aldinger we must assume that this articulation was of such a nature that the processus basipterygius and the processus ascendens anterior acted as a slide for the articular process of the palatoquadrate, so that the palatoquadrate could move in different planes in relation to the processus basipterygius.

As regards the abduction of the operculum Aldinger points out that in the earlier forms within the *Palaeonisciformes* group it can have taken place to a small extent only by the aid of a musculus dilatator operculi, as the processus opercularis lies far from the antero-dorsal corner of the operculum. In *Glaucolepis* too the abduction of the operculum by the aid of a musculus dilatator operculi must have been somewhat smaller than in recent *Holostei* and *Teleostei*, as will appear from Figs. 35A and 36, which show the accurate position of the processus opercularis in relation to the operculum.

Aldinger assumes that the hyomandibula has in a different way contributed essentially to the opening of the gill-cavity, namely by the processus opercularis having pressed against the operculum, and the ventral end of the hyomandibula against the suboperculum, and this agrees well with the position of the hyomandibula in relation to the operculum and the suboperculum in *Glaucolepis*. As we have seen above, the connection between the hyomandibula and the suboperculum is especially firm owing to the presence of the internal lamina on the latter bone.

Branchial arches and basibranchial series.

In all the fairly complete skulls of the different species of *Glaucolepis*, remnants of the branchial arches are found; but in nearly all cases, as is usual in fossil fishes, they are in such a state of preservation that it is difficult to dissect out the individual ossifications and impossible to gain a general idea of their position in relation to one another and of their relation to the endocranium. However, some few specimens are so beautifully preserved that it is possible to obtain information about several details in the structure of the branchial arches, and one specimen shows the complete visceral skeleton *in situ*.

a. Glaucolepis stensiöi.

One specimen of *Glaucolepis stensiöi* (No. 38, Pls. 13–17) is preserved in a way which is probably unique among fossil Actinopterygians, for it exhibits all the branchial arches in their natural position without a single of their ossifications having shifted from the place it occupied in the living animal. Specimen No. 38 consists of the anterior half of a fish whose

head is nearly complete, only part of the snout region and some of the dermal bones of the right side of the head being absent.

The fish is preserved with the mouth wide open, and when it was found, the whole mouth cavity was filled with matrix. By a carefull preparation it was possible to remove this matrix, so that the visceral skeleton was exposed to the extent that appears from the photographs reproduced in the plates. After these photographs had been taken, the preparation was continued, and the individual branchial arches now appear much clearer than shown in the figures; unfortunately, however, during this part of the work I felt the want of the photographic equipment which was at my disposal at Stockholm, and I am therefore unable to publish any photographs of the completely prepared specimen.

Five branchial arches are present. The individual ossifications in these arches always consist of cancellate bone-tissue lined with perichondral bone. The ossifications were in contact with each other by cartilaginous epiphyses.

Before describing the individual elements of the branchial arches I shall mention that the greater number of these elements could not, naturally, be exposed so completely in specimen No. 38 that they could be examined from all sides. Besides on this specimen, the following description is therefore based on a number of less complete specimens of *Glaucolepis stensiöi*, not least on the sectioned specimen; still there are several details in regard to the shape of the individual ossifications of which our knowledge is as yet incomplete.

The first branchial arch comprises the following elements: the hypobranchial, the ceratobranchial, the epibranchial, the infrapharyngobranchial, and the suprapharyngobranchial.

The hypobranchial I (*Hbr I*, Fig. 45; Pl. 17) is a comparatively long, slender bone, which in specimen No. 38 is only exposed from the dorsal side. Its distal end is somewhat expanded and articulated partly with the distal end of the hypohyal and partly with the anterior part of the anterior ossification of the basibranchial series, as will be seen from Fig. 45.

The ceratobranchial I (*Cbr I*, Fig. 45; Pls. 13, 15, 16, 17) is a very long, slender, bone which is slightly curved, as will be seen from Fig. 45. The cancellate mass of this bone, as well as those of the ceratobranchials II, III, and IV, is thickest farthest distally and narrows in a proximal direction through the first one-fifth of the bone, to increase again very gradually towards the proximal end of the bone. A deep longitudinal groove is found on its posterior (morphologically lateral) side.

The epibranchial I (*Ebr I*, Figs. 45, 46, 47; Pls. 15, 16, 17) is a little more than half as long as the ceratobranchial I and is curved in the way shown in Figs. 45 and 47. The distal end of the epibranchial I has the same thickness as the proximal end of the ceratobranchial I, but towards the proximal end of the bone it grows somewhat thicker, as may

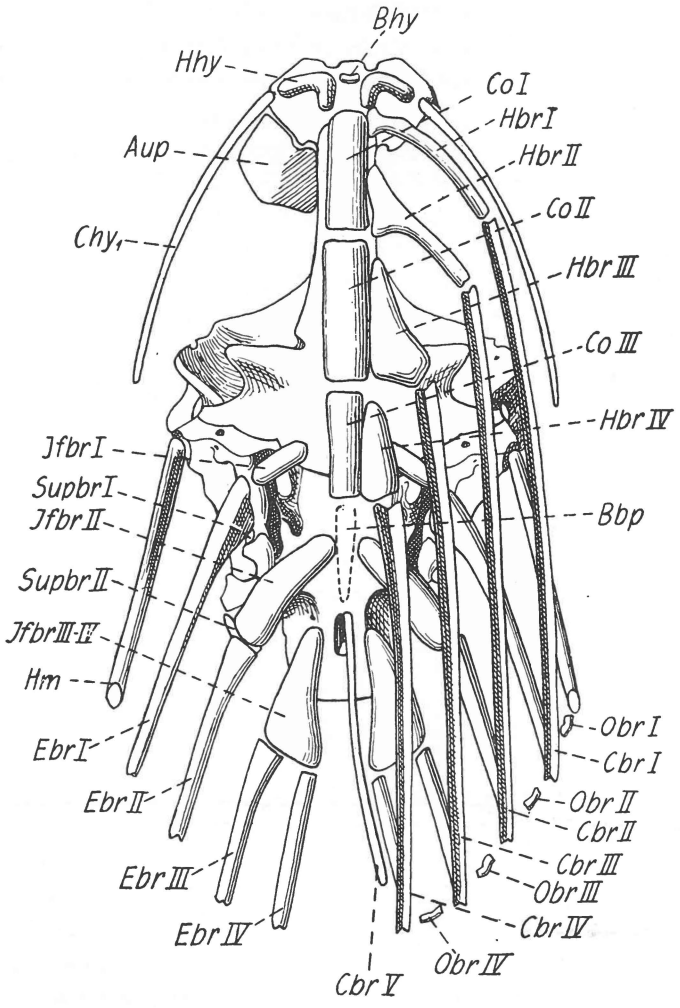


Fig. 45. *Glaucolepis stensiöi* n. sp. Neural endocranium, autopalatine, hyoid arch (except symplectic), branchial arches, and basibranchial series in ventral view. Left autopalatine and ventral ossifications in the right branchial arches omitted. Exact relief of the ventral surface of the ossifications in the basibranchial series and of the ventral surface of the hypobranchial elements unknown. Based partly on a wax model, partly on specimen No. 38. 3–4 ×.

Aup, autopalatine; *Bbp*, presumed outline of the posterior, cartilaginous part of the basibranchial series; *Bhy*, basihyal; *Cbr I–IV*, ceratobranchials I–IV; *Cbr V*, cerato- or hypoceratobranchial V; Chy_1, anterior ossification in the ceratohyal; *Co I–III*, ossifications in the basibranchial series; *Ebr I–IV*, epibranchials I–IV; *Hbr I–IV*, hypobranchials I–IV; *Hhy*, hypohyal; *Hm*, hyomandibula; *Jfbr I–II*, infrapharyngobranchials I–II; *Jfbr III–IV*, pharyngobranchial common for the third and fourth branchial arches; *Obr I–IV*, ossifications situated between the visceral arches; *Supbr I–II*, suprapharyngobranchials I–II.

be seen from Fig. 47. Its cancellate mass, like those of the epibranchials II, III, and IV, is thickest in the proximal end of the bone, narrowing in a distal direction through its proximal third or fourth, to increase in thickness again towards the distal end of the bone. On its posterior side a deep longitudinal groove is found. That part of the bone which forms the medial (morphologically caudal) wall for the most proximal part of the longitudinal groove is especially well developed, and forms a process issuing in a dorsal direction; farthest dorsally this process is continued by the independent suprapharyngobranchial element.

The infrapharyngobranchial I (*Ifbr I*, Figs. 45, 46, 47; Pl. 16), the actual pharyngobranchial element of the first branchial arch, is a small horizontal, rounded ossification, whose length is a little more than twice its breadth. By its distal end it articulated with the proximal end of the epibranchial I, and by its proximal end with the postero-lateral part of the corpus of the parasphenoid, as will be seen from Fig. 45.

The suprapharyngobranchial I (*Supbr I*, Figs. 45, 46, 47) is a slightly compressed vertical bone, whose outline is seen from the figures. As already stated, it articulates distally with the epibranchial I, and by its dorsal end, and possibly by a larger or smaller part of its medial face, it articulated with the prominent articular facet situated on the lateral face of the otic region posteriorly to the large vestibular fontanelle (p. 48).

The second branchial arch, like the first one, contains the following ossifications: the hypobranchial, the ceratobranchial, the epibranchial, the infrapharyngobranchial, and the suprapharyngobranchial.

The hypobranchial II (*Hbr II*, Fig. 45; Pls. 15, 17) is a little shorter than the hypobranchial I. As will be seen from Fig. 45, its proximal part is slender, while its distal part is expanded so that the distal end of the bone attains a considerable thickness. By its broad distal end the hypobranchial II articulated partly with the posterior half of the lateral face of the anterior ossification of the basibranchial series, partly, as far as I can decide, with the most anterior part of the lateral face of the second ossification of the basibranchial series. The ventral face of the hypobranchial II could not be exposed.

The ceratobranchial II (*Cbr. II*, Fig. 45; Pls. 15, 17) agrees in size and shape with the ceratobranchial I.

The epibranchial II (*Ebr II*, Figs. 45, 46, 47; Pls. 15, 16, 17) is about two-thirds the length of the epibranchial I, and like the latter has a deep longitudinal groove on its posterior side. Its proximal end is a little thicker than its distal end, and articulated with a large infrapharyngobranchial. That part of the bone which forms the medial wall of the most proximal part of the longitudinal groove articulated with a small suprapharyngobranchial.

The infrapharyngobranchial II (*Ifbr. II*, Figs. 45, 46, 47; Pls. 15, 16) may be described as a rather thin horizontal bone plate, whose whole antero-

lateral (morphologically anterior) margin and the postero-medial margin of its distal half is inflected upwards. In this way the dorsal face of the bone, which is not known in details, exhibits a longitudinal groove, which is indicated in the sketch shown in Fig. 46, and which lodged the arteria branchialis efferens II. The outline of the bone in ventral view is seen from Fig. 45. The proximal end of the infrapharyngobranchial II lies ventrally to the ventral face of the otic region, at a short distance from the corresponding part of the infrapharyngobranchial II of the opposite side, as will be seen from Fig. 45. It is uncertain whether the infrapharyngobranchial II articulated with the endocranium, no articular facet having been observed on the ventral face of the otic region.

The suprapharyngobranchial II (*Supbr II*, Figs. 45, 46, 47) is a small, nearly vertical bone, shaped almost like a slender cone with the point upwards. The dorsal pointed part of the bone was either in direct contact with, or connected by a ligament with, the posterior margin of the lateral face of the anterior division of the occipital region of the endocranium.

The third and fourth branchial arches contain each a hypobranchial, a ceratobranchial, and an epibranchial, but has a common pharyngobranchial.

The hypobranchial III (*Hbr III*, Fig. 45, Pl. 15) is a little shorter than the hypobranchial II. As will be seen from Fig. 45, it increases rapidly in width from its proximal towards its distal end, so that farthest distally it is about three times as broad as farthest proximally. Its distal end articulated with the lateral face of the midmost ossification of the basibranchial series. The dorsal face of the bone is convex in a transverse direction. Whether this convexity corresponds to a concavity on the ventral face of the bone is unknown, as this face could not be investigated.

The hypobranchial IV (*Hbr IV*, Fig. 45, Pl. 15) is a little shorter than the hypobranchial III and may be described as a dorso-ventrally somewhat flattened bone plate whose dorsal face is somewhat convex in a transverse direction. The outline of the bone will appear from Fig. 45. However, the ventral face of the bone could not be examined in detail. Distally the hypobranchial IV articulated with the lateral side of the posterior ossification of the basibranchial series.

The ceratobranchial III (*Cbr III*, Fig. 45; Pls. 15, 17) is of about the same length as the ceratobranchials I and II, and differs from them only in being somewhat broader in its most distal part.

The ceratobranchial IV (*Cbr IV*, Fig. 45, Pls. 15, 17) differs from the ceratobranchial III only in being somewhat shorter than that bone.

The epibranchial III (*Ebr III*, Figs. 45, 46, 47; Pls. 15, 16, 17) has about two-thirds the length of the epibranchial II and about the same breadth from its proximal to its distal end. Its posterior side has a deep longitudinal groove.

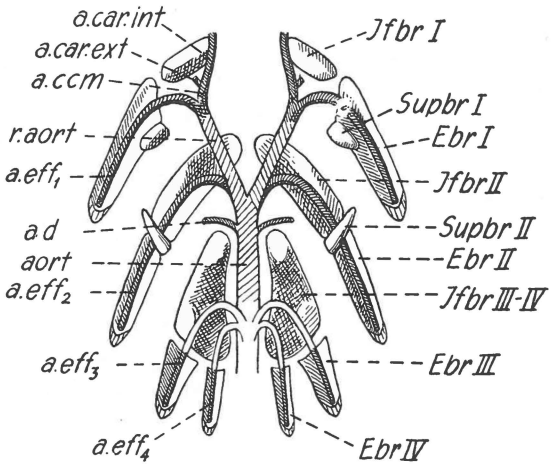


Fig. 46. *Glaucolepis stensiöi* n. sp. Dorsal view of the most dorsal part of the branchial arches with attempted restoration of a part of the arterial system. The course of ruled parts of the arteries definitely established; the course of white parts of the arteries entirely hypothetical. That part of the arterial system lodged in the basal part of the endocranium more finely ruled than the part lying outside the neural endocranium. Based partly on a wax model, partly on specimen No. 38. 3–4 ×.

Ebr I–IV, epibranchials I–IV; *Jfbr I–II*, infrapharyngobranchials I–II; *Jfbr III–IV*, pharyngobranchial common for the third and fourth branchial arches; *Supbr I–II*, suprapharyngobranchials I–II; *a. ccm*, arteria carotis communis; *a. car. ext*, arteria carotis externa; *a. car. int*, arteria carotis interna; *ad*, artery issuing in a dorso-lateral direction from the aorta; *a. eff*$_{1-4}$, arteriae branchiales efferentes I–IV; *aort*, aorta; *r. aort*, aorta root.

The epibranchial IV (*Ebr IV*, Figs. 45, 46, 47; Pls. 15, 16) resembles the epibranchial III in all details.

In specimen No. 38 the pharyngobranchial III–IV (*Ifbr III-IV*, Figs. 45, 46, 47; Pls. 15, 16) is only visible from the ventral side, and in ventral view (Fig. 45) it is triangular in outline with a long antero-lateral, a long medial, and a short postero-lateral margin. Its ventral face is somewhat convex in a transverse direction. From the sectioned specimen it seems to appear that the pharyngobranchial III-IV is a rather thin ossification, which is flattened in a dorso-ventral direction; its antero-lateral margin is bent upwards, and is highest and thickest in its anterior and posterior parts, as sketched in Figs. 46 and 47. The pharyngobranchial III–IV is so situated in relation to the endocranium that its proximal end lies ventro-laterally to the opening for the arteria branchialis efferens II on the ventral face of the occipital region. A ligamental connection possibly existed between the pharyngobranchial element and the endocranium.

The epibranchial III articulated with the postero-lateral corner of the pharyngobranchial III–IV, and the epibranchial IV with its postero-medial corner.

The fifth branchial arch presents only one ossification, which is either to be regarded as a ceratobranchial or a hypo-ceratobranchial. It is a very

slender ossification (*Cbr V*, Fig. 45; Pl. 15), whose length is about two-thirds the length of the ceratobranchial IV. Apparently the bone has no longitudinal groove. Its distal end lies rather far behind the posterior end of the posterior ossification of the basibranchial series, and must be supposed to have articulated with a posterior unossified part of this series.

Before concluding the description of the ossifications of the branchial arches, I shall mention some interesting very small bones which can be observed in specimen No. 38. These bones have not been found in any other specimens of *Glaucolepis stensiöi*, perhaps because owing to their small size they have no reasonable chance of being identified when the elements of the branchial arches are compressed and displaced from their natural position.

I am referring to four small, fairly horizontal tube-shaped ossifications (*Obr I-IV*, Fig. 45, Pls. 15, 17), which, as will be seen from the figures, show an abrupt bend at the middle so that each of them consists of an anterior and a posterior shank which meet at an obtuse angle. Their interior is filled by white calcite, and they should no doubt be regarded as perichondral diapophyses.

The foremost of these four ossifications lies in the interval between the distal end of the hyomandibula and the place of articulation between the epibranchial I and the ceratobranchial I. Ossification No. 2 lies between the place of articulation between the epibranchial I and the ceratobranchial I and the place of articulation between the epibranchial II and the ceratobranchial II. Ossifications Nos. 3 and 4 lie in a corresponding way between the second and third and the third and fourth branchial arches respectively. As will be seen from Fig. 45, the small ossifications have no direct contact with the ossifications in the visceral arches between which they are situated.

It is rather difficult to interpret these small bones which, as far as I can make out, hardly are simply modified gill-rays. In my opinion the only probable interpretation seems to be that the individual visceral arches articulated with each other by a partially ossified process, which issued in either an anterior or a posterior direction from the cartilage that capped the distal end of their epal, or the proximal end of their ceratal ossifications, and by means of which the visceral arches had become consolidated in their position in relation to each other. If this process issued in an anterior direction from the cartilage that capped the distal end of the epal element, it may be regarded as serially homologous with the symplectic, which, as is well known, connects the hyoid arch with the mandibular arch, and thus each half of the visceral skeleton would contain five symplectica instead of one.

In *Polypterus* the proximal ends of the ceratobranchials III and IV articulate with each other by a process which issues in an anterior direction from the cartilage that caps the proximal end of the ceratobranchial IV (Allis 1922, p. 233, Pl. 8, Figs. 16–17).

The basibranchial series contains three ossifications (*Co I-III*, Fig. 45,

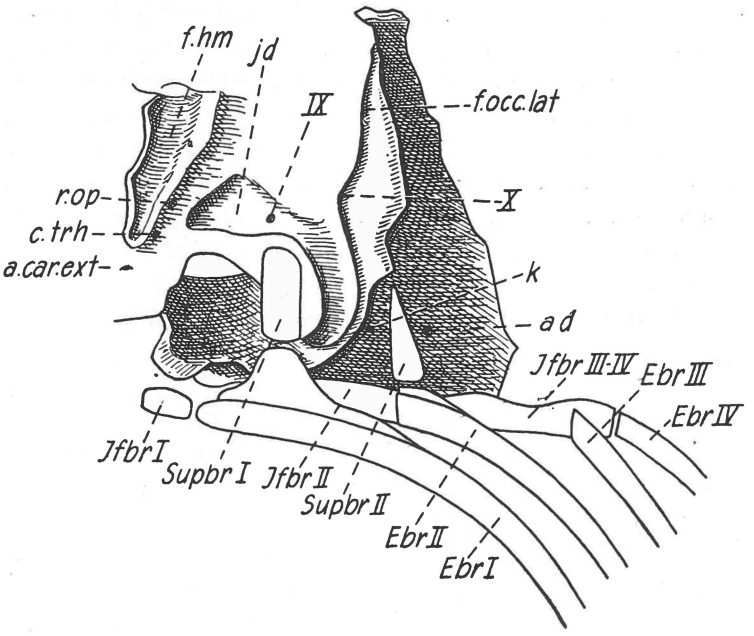


Fig. 47. Posterior part of the neural endocranium and dorsal part of the brancnial skeleton in lateral view. Based partly on a wax model, partly on specimen No. 38. C. 6 ×. *Ebr I–IV*, epibranchials I–IV; *Jfbr I–II*, infrapharyngobranchials I–II; *Jfbr III–IV*, pharyngobranchial common to the third and fourth branchial arches; *Supbr I–II*, suprapharyngobranchials I–II; *a. car. ext*, canal for the arteria carotis externa; *ad*, canal for an artery; *c. trh*, posterior opening of the jugulo-hyoideomandibular canal for the truncus hyoideomandibularis; *f. hm*, articular fossa for the hyomandibula; *f. occ. lat*, fissura occipitalis lateralis; *jd*, jugular depression; *k*, canal, possibly for a vessel; *r. op*, posterior opening of the jugulo-hyoideomandibular canal for the ramus opercularis facialis; *IX*, canal for the nervus glossopharyngeus; *X*, place of exit for the nervus vagus.

Pl. 15), whose exact shape cannot be stated, as the series could not be examined from the ventral side. The three ossifications seem most nearly to be shaped like cylinders flattened somewhat dorso-ventrally. The ossifications, whose relative size will appear from Fig. 45, consist of cancellate bone lined externally by perichondral bone-layers except on their anterior and posterior terminal faces. From the ossifications in the basibranchial series it is impossible to draw any conclusion as to the actual segmentation of the series (Gaupp 1904, pp. 909–910; Stensiö 1921, p. 185; 1925, p. 112).

To all the ossifications of the branchial arches and the basibranchial series it applies that their faces towards the mouth cavity were covered by numerous small dermal ossifications provided with close-set acute teeth. In the sections 410–25 (Fig. 2) the size of these thin, irregularly shaped tooth plates are seen, and likewise, that they lay in the skin without being firmly connected with the primary ossifications of the branchial skeleton.

In specimen No. 38 the tooth plates were very beautifully exposed during

preparation (Pls. 15, 16, 17), but it proved necessary to remove them to a considerable extent in order to examine structures which they concealed.

Between the right and left epibranchials IV, in the roof of the pharynx, occur the remnants of two very extensive, thin tooth plates (*Tp*, Pls. 15, 16), whose outline and accurate position could not be ascertained.

No traces of gill-rays, like those known from several *Palaeonisciformes* (*Acrorhabdus* (Stensiö 1921, p. 227), *Boreosomus* (cf. p. 351) and others), are found in *Glaucolepis stensiöi*.

b. Glaucolepis aldingeri, arctica, gunnari, and magna.

Apart from the four small ossifications between the visceral arches and apart from the suprapharyngobranchials I and II, these four species show more or less well preserved remnants of all the ossifications that have been ascertained in the branchial skeleton of *Glaucolepis stensiöi*. *Glaucolepis aldingeri* (specimen No. 66) further shows remnants of gill-rays (Pl. 20, Fig. 1).

As far as could be examined, the ossifications of the branchial skeleton in these four species agree in shape with the corresponding ones in *Glaucolepis stensiöi*. As to their position in relation to each other it can only be stated that in the few cases in which a specimen of one of the four species shows a larger og smaller number of the ossifications of the branchial skeleton in their original position, full agreement with the conditions in *Glaucolepis stensiöi* has been observed. There is therefore no reason to give a more detailed description.

c. Discussion.

Only few possibilities are available for comparing the branchial skeleton in *Glaucolepis* with that of other *Palaeonisciformes*, for the literature contains very few and no exhaustive descriptions of the branchial skeleton in any member of this group. Earlier authors (Traquair, Fritsch, etc.) supplied no other information of importance than that the branchial skeleton is well ossified in various *Palaeonisciformes*. In more recent works (Stensiö, Watson, and Aldinger), however, we find somewhat more complete particulars.

According to Stensiö (1921, pp. 184–186, Figs. 65–66), *Birgeria* has the following ossifications in its branchial arches: the hypobranchials I, II, and III, the ceratobranchials I, II, III, and IV, the epibranchials I, II, and III, and the infrapharyngobranchial II. From the shape of the proximal end of the epibranchials I and II Stensiö concludes that the first two branchial arches have both supra- and infrapharyngobranchials. In addition, the basibranchial series contains three ossifications.

According to Stensiö, the recent fishes to which *Birgeria* shows greatest resemblance as regards the ossifications in the basibranchial series and the branchial arches are *Amia* and the Teleosts.

Birgeria and *Glaucolepis* show good agreement as regards the very slightly specialised shape of the individual ossifications, whereas the two genera seem to differ considerably as regards the position of the basibranchial ossifications in relation to the branchial arches.

Stensiö (1921, p. 227) has further supplied a good deal of information about the branchial arches in *Acrorhabdus*, however, it is not exhaustive enough to allow of a comparison with *Glaucolepis*.

Watson (1925, p. 863, Fig. 29) describes and figures the ventral part of the branchial skeleton in *Elonichthys aitkeni* (as mentioned above p. 162, this species does not probably belong to the genus *Elonichthys*). He found the following ossifications: the hypobranchials I and II, and the ceratobranchials I, II, III, and IV. Furthermore he observed a basibranchial series with two ossifications, and in front of the most anterior of these a large basihyal.

If Watson's interpretation is correct, there is a considerable disagreement between *Elonichthys aitkeni* and *Glaucolepis* as regards the arrangement of the ventral ossifications of the branchial skeleton. If, however, the branchial arches in Watson's figure are interpreted as Nos. 2–5 instead of Nos. 1–4, and his basihyal is interpreted as an anterior ossification in the basibranchial series, this form agrees surprisingly well with *Glaucolepis*. I am therefore inclined to think that the first branchial arch in Watson's specimen was either concealed in the rock or had been lost. The simple shape of the ossifications in Watson's specimen agrees well with the conditions in *Glaucolepis*.

Aldinger (1937) supplies scattered information about the ossifications in the branchial skeleton in several *Palaeonisciformes*. It should merely be mentioned here that judging from the shape of the proximal end of the epibranchials I and II, in *Pygopterus nielseni*, as in *Birgeria* and *Glaucolepis*, supra- and infrapharyngobranchials were present in the first and second branchial arches.

In no other *Palaeonisciformes* than *Glaucolepis* are the exact relations between the branchial arches and the neural endocranium known. (Eaton (1939) indicates what he thinks to be the places of articulation of the first and second branchial arches on the neural endocranium of a Kansas Palaeonisciform, however, since these places of articulation have an entirely different position from those in *Glaucolepis*, their identification must be regarded with some doubt until more complete material has been examined).

Compared with the branchial skeleton in recent Actinopterygians, the branchial skeleton in *Glaucolepis* shows its primitive nature by its greater number of elements, and to some extent by the unspecialised type of these

elements. (However, in *Lepidosteus* and several *Teleostei* the elements of the branchial skeleton have a very simple shape too). The reduction of the number of segments within the branchial skeleton which has taken place during the development from the primitive branchial skeleton of the *Glaucolepis* type to the types in the recent Actinopterygians has affected partly the posterior branchial arches and partly the suprapharyngobranchials of the two anterior branchial arches.

We have seen above that the two anterior branchial arches, in so far as they are known in the *Palaeonisciformes*, contain both a suprapharyngobranchial and an infrapharyngobranchial. As regards *Glaucolepis* an account has been given of the relations of these pharyngobranchial elements to the neural endocranium (Fig. 47). According to Allis (1918 b) the infrapharyngobranchial element is the actual pharyngobranchial element of the branchial arch, while the suprapharyngobranchial element is a part of the epibranchial of the arch, which in certain forms has become independent. However, the circumstance that an independent suprapharyngobranchial occurs as early as in the *Palaeonisciformes*, does not speak in favour of the assumption that originally it was merely a dorsal process issuing from the epibranchial, but seems rather to suggest that originally this bone was an independent ossification which in certain more recent forms has fused with the epibranchial ossification.

In *Acipenser* both supra- and infrapharyngobranchials are found in the two anterior branchial arches. The infrapharyngobranchial I joins the corpus of the parasphenoid nearly at the base of the processus ascendens, while, a little more caudally, the infrapharyngobranchial II is attached by a ligament to the lateral margin of the parasphenoid. The suprapharyngobranchial I articulates with the neural endocranium behind the glossopharyngeus opening, and the suprapharyngobranchial II articulates with the occipital region of the neural endocranium (van Wijhe 1882, p. 226; Holmgren and Stensiö 1936, pp. 440–441; de Beer 1937, Pl. 31, Figs. 1 and 3). Thus in *Acipenser* the first branchial arch has precisely the same articulation with the neural endocranium as in *Glaucolepis*. As regards the second branchial arch, the infrapharyngobranchial element in *Glaucolepis* is not, of course, as in *Acipenser*, connected with the parasphenoid, this being very short in *Glaucolepis*. Even though the suprapharyngobranchial II in *Acipenser* is reported to articulate with the neural endocranium dorsally to the vagus opening, in a ten days old *Acipenser*, according to de Beer's figure, it has the same position in relation to the vagus opening as in *Glaucolepis*.

According to van Wijhe (1882, p. 245) the suprapharyngobranchial elements are absent in the specialised *Spatularia*, while the infrapharyngobranchials I and II have contact with the neural endocranium.

In *Polypterus*, according to van Wijhe (1882, pp. 257–258), a fairly large separate suprapharyngobranchial I is found, which has contact with the

neural endocranium; but according to Allis (1922, pp. 234–235) the suprapharyngobranchial I is not separated from the epibranchial, and the infrapharyngobranchial is in contact with the parasphenoid between the lateral and the horizontal plate of the processus ascendens, and is attached to this part of the parasphenoid by fibrous tissue.

According to Allis (1897) the first branchial arch in *Amia* has no suprapharyngobranchial, and, as already stated by van Wijhe (1882, pp. 284–285), the infrapharyngobranchial I is attached to the lateral margin of the parasphenoid.

In *Lepidosteus* the infrapharyngobranchial I rests against that part of the lateral margin of the parasphenoid which lies nearest behind the processus ascendens, and the infrapharyngobranchial II is attached to the parasphenoid closely behind the infrapharyngobranchial I (van Wijhe 1882, p. 272). Van Wijhe further records some very small suprapharyngobranchials in the two anterior branchial arches.

Finally, a much reduced suprapharyngobranchial I is found in various *Teleostei* (Ridgewood 1904, p. 89; etc.), its dorsal end articulating with the lateral face of the otic region; the infrapharyngobranchial I is connected with the parasphenoid.

According to the above it would seem that the double articulation of the first two branchial arches is a primitive character within the group of Actinopterygians, independent suprapharyngobranchials being well developed in the *Palaeonisciformes* and in *Acipenser*, while in the higher Actinopterygians they are either reduced or united with the epibranchial elements.

Säve-Söderbergh (1936, pp. 141–144) i.a. in the conditions in *Rhizodopsis* found support for the view that the double articulation of the visceral arches with the neural endocranium is a very primitive feature within the vertebrates. Säve-Söderbergh finds a strong argument speaking in favour of this point of view in the conditions in the Cephalaspids, about which he writes: "Here the visceral skeleton is extensively joined to the lateral surface of the neural endocranium, so that the endoskeleton of the head actually forms one single mass of bone, which can be only theoretically subdivided into visceral and neurocranial components (cf. Stensiö 1927, 1932 b; Holmgren and Stensiö 1936, pp. 247–269). This entensive junction takes place both dorsally and ventrally to the jugular vein (v. capitis lateralis), which is thus enclosed in a long canal (Stensiö 1927, text-figs. 23A, 27A, *v. cl*) marking the theoretical boundary, at least behind the labyrinth, between the neurocranium and the visceral skeleton."

According to this it might be expected that the visceral arches in the most primitive Actinopterygians as well as in the most primitive Choanates and Elasmobranchs articulated with the neural endocranium both dorsally and ventrally to the jugular vein; but curiously enough, in the Actinopterygians in which the suprapharyngobranchial I is best developed (*Glaucolepis*,

Acipenser (Sewertzoff 1928, p. 242, Pl. 7, Fig. 29), etc.) both articulations between the first branchial arch and the neural endocranium (or the parasphenoid), lie ventrally to the jugular vein. This means that even if the hypothesis as to the primitive articulation of the visceral arches with the neural endocranium dorsally and ventrally to the jugular vein is possibly correct, the conditions known within the Actinopterygians cannot, at any rate, be taken to support this hypothesis, as done by Säve-Söderbergh.

Ornament of the dermal bones of the head.

a. Glaucolepis stensiöi.

The external dermal bones of the head are ornamented with ganoine striae and more or less oblong ganoine tubercles.

On the dermal cranial roof these striae and tubercles are fairly well developed and extend in a mainly rostro-caudal direction. On the postrostral the direction of the striae is chiefly transverse.

The ornament of the elements of the infraorbital series and the suborbital complex is of the same type as that of the cranial roof, but the individual striae and tubercles are lower. The ornament of the preoperculum consists of striae and tubercles, largely so disposed that the direction of the striation in the antero-dorsal division of the bone is parallel with the longitudinal axis of this division, and in the postero ventral division parallel with the longitudinal axis of that division.

On the posterior or at any rate the postero-ventral portion of the postorbital part of the maxillary the ornament consists mainly of striae, which run parallel with the hind margin of the maxillary. Otherwise tubercles form the chief ornamental element on the maxillary, however, striae are often found near and parallel with the dorsal margin of the bone.

The ornament on the outer side of the mandible consists chiefly of striae, whose main direction is postero-dorsal to antero-ventral. Near the dorsal and ventral margins of the external face of the mandible the individual striae are subdivided into minor tubercles.

The antoperculum has a well developed ornament consisting of oblong tubercles or short striae, which are chiefly parallel with the longitudinal axis of the bone. The operculum and the subopercultum are ornamented with some few ganoine tubercles only, which are situated near the anterior margin of these two bones. The untuberculated areas of these bones are not quite smooth, exhibiting some very distinct concentric growth lines. Similar lines, which are often present in a number of twenty or more, are seen, though less distinctly, on several other dermal bones of the head.

At great magnification a fine ornament, formed by very close-set, extremely low, oblong elevations, may be seen on the outer faces of the oper-

culum and the suboperculum. As I have not examined the microstructure of the dermal bones, I can say nothing about the nature of these fine elevations.

A comparatively smooth operculum and suboperculum are known from several *Palaeonisciformes*, so these bones have evidently often been covered by a thick layer of connective tissue beneath the epidermis (Aldinger 1937, p. 182).

The ornament of the branchiostegal rays consists chiefly of oblong ganoine tubercles, whereas the small median gular plate is mainly striated.

b. Glaucolepis arctica.

Glaucolepis arctica agrees in all essentials with *Glaucolepis stensiö* as regards the ornament of the dermal bones of the head. The only difference is that in *Glaucolepis stensiöi* a larger part of the operculum and of the suboperculum is equipped with ganoine tubercles than in *Glaucolepis arctica*, and these tubercles are often so long that they should perhaps most correctly be termed striae.

c. Glaucolepis magna.

The ornament of the dermal bones of the head in this species is very characteristic, since in all the large specimens it consists chiefly of very small, round or oblong, close-set ganoine tubercles, while ganoine striae are predominant within small areas only of the individual dermal bones.

The operculum and the suboperculum which, similarly as in the preceding species, present very distinct concentric growth lines, are on their whole outer side provided with close-set ganoine tubercles. In some few specimens, however, the ganoine tubercles are few in number or entirely absent in a minor area of the postero-ventral part of the operculum and the posterior part of the suboperculum.

On the posterior portion of the postorbital part of the maxillary several tubercles are often united so as to form short striae of a very irregular course. The ornament of the mandible consists chiefly of rather short striae, extending mainly in a postero-dorsal to antero-ventral direction. Farthest anteriorly and farthest ventrally on the external face of the mandible, however, these striae are replaced by tubercles.

d. Glaucolepis gunnari.

As regards the ornament of the dermal bones of the head this species is highly reminiscent of *Glaucolepis magna*, the ornamental elements being chiefly small ganoine tubercles. However, on the dermal cranial roof these tubercles are relatively larger than in *Glaucolepis magna*, so that in *Glau-*

colepis gunnari the number of ornamental elements on the dermal cranial roof is smaller than in *Glaucolepis magna*.

The operculum and the suboperculum are less strongly ornamented than in *Glaucolepis magna*; the ornamental elements found on these two bones are in most cases short striae.

e. Glaucolepis aldingeri.

As will be evident from the above, our knowledge of the dermal bones of the head in this species is rather imperfect. The dermal bones preserved, which chiefly belong to the cheek, the mandible, and the opercular apparatus, exhibit an ornament consisting of coarse, rounded or oblong ganoine tubercles and occasionally of short ganoine striae.

The coarse ganoine tubercles are chiefly found on the maxillary, the preoperculum, the suborbitals, and the infraorbital series, while on the mandible a system of broad, short ganoine striae is found, whose direction is postero-dorsal to antero-ventral.

The antoperculum is provided with well developed irregular ganoine tubercles; apart from the usual concentric growth lines, the operculum and the suboperculum are only ornamented near their anterior margins, where the ornament consists of ganoine tubercles.

Dentition.

The five species agree so well in the arrangement and shape of their teeth that they will be dealt with *en bloc*. The position of the teeth has already been mentioned in the description of the individual tooth-bearing bones and will therefore only be briefly mentioned in this chapter. The largest teeth are arranged in four rows, viz. one row on the horizontal lamina of the maxillary (and on the premaxillary?), one on the ectopterygoid and the two dermopalatines, one on the horizontal lamina of the dentalo-splenial and one on the prearticular and the small coronoids.

It is difficult to determine the number of teeth in these rows, for as a rule it is only possible to expose small portions of the rows in the individual specimens, and moreover the number is hardly constant within the various species. In most cases the number of teeth in each row seems to range about 24–32. The large teeth are rather slender and are terminated distally in the usual way by a small acute enamel cap; they are either straight or slightly curved, as will be seen from Figs. 35B, C, D, and 39C, D, E. The enamel cap, whose length is equal to about one-eigth or one-tenth the entire length

of the tooth, has sharp anterior and posterior edges, and evenly rounded smooth lateral and medial faces. Proximally to the enamel cap the enamel-like surface layer of the teeth is sculptured by a very fine vertical striation. I can say nothing about the nature of this striated surface layer, as I have not examined the microstructure of the teeth. (Aldinger (1931, pp. 174–177) has investigated the corresponding surface layer on teeth of *Birgeria*, and found that its structure differs from that of the enamel cap). The pulp-cavity is very spacious, and extends right up into the basal part of the enamel cap.

Apart from the aforementioned rows of large teeth, the dentition consists of a very large number of very small acute teeth. These teeth are found in an area of the oral faces of the parasphenoid, the vomer, the ectopterygoid, the two dermopalatines, the dermometapterygoid, the entopterygoid, the prearticular, and the coronoids, and are moreover found on the ventral margin of the maxillary and the dorsal margin of the dentalo-splenial.

Similar small teeth are present on the mosaic of small, thin dermal bones of irregular outline which cover the oral faces of the ossifications of the basibranchial series and the branchial arches (p. 194) and on the two large, thin dermal bones situated in the roof of the pharynx behind or between the right and left epibranchials IV (p. 195).

It was possible to observe that in some cases, at any rate, these small teeth are equipped with a small, acute, enamel cap, and that altogether they agree fairly well in shape with the large teeth; but on account of their small size it was impossible to decide whether their surface is ornamented or smooth.

Sensory canal system of the head.

a. Glaucolepis stensiöi.

The various sensory canals of the head are enclosed in the dermal bones and open by numerous tubuli into small pores on the external faces of the dermal bones.

The sensory canals are generally wide and comparatively widest in the smallest specimens. On account of the width of the canals, the zone of the individual canal bones directly enclosing the canal space is thicker than the remaining part of the canal bone. The thickening appears as a distinct ridge on the internal face of the bone, but is not visible on its external face.

Owing to the presence of this ridge is it possible to trace the course of the sensory canals even in the many specimens in which the dermal bones are only represented by casts of their internal faces. Similar ridges on the ventral face of the parietal indicate the position of the pit-lines of this bone.

The number of the primary tubuli cannot be ascertained, for they are always subdivided into a large number of secondary tubuli, and this subdivision is so complete that the secondary tubuli are entirely separated right from their external opening to the place where they are united with the sensory canal proper. Moreover the secondary tubuli, as will appear from Figs. 19 and 27, are not arranged in groups, and we have thus no possibility, from the number or arrangement of the secondary tubuli, to draw conclusions as to the number of sensory organs within the different parts of the sensory canal system.

In a few cases some of the foramina through which nerve branches entered the sensory canals may be observed. However, in no case is it possible to ascertain the accurate number of these foramina even for a single canal bone, so in this way, also, it is impossible to form a judgment as to the number of sensory organs.

In each canal bone the sensory canal has such a course that it passes the radiation centre of the bone.

As usual there is no variation in the course of the sensory canals in relation to the dermal bones, whereas the number of secondary tubuli within the individual divisions of the sensory canals may vary somewhat, not only from one specimen to the other, but also from one side of the head to the other.

In addition to the deep-lying actual sensory canals, in some specimens, at any rate, grooves representing the so-called pit-lines are found on the surfaces of certain dermal bones. I express myself so cautiously, because the majority of the parts of the sensory canal system represented in some specimens as grooves in other specimens occur as very narrow canals. Probably very short tubuli issue from these canals, even though I have not succeeded in localising them. For practical reasons I shall apply the term pit-lines to these very narrow canals, too, because they doubtless correspond to the typical pit-lines in other specimens of the same species; but of course the term is not quite correct.

Not only in *Glaucolepis*, but in many other Triassic Ganoids, too, have I observed pit-lines occurring to a greater or smaller extent as narrow canals in the dermal bones; this, for instance, is the case in Parasemionotids, in *Bobasatrania*, *Boreosomus*, and *Perleidus*, and on the whole it must be pointed out that even where the pit-lines are typically developed in primitive Actinopterygians, they have in most cases a much less superficial position than in recent Actinopterygians. This is just what could be expected when it is taken into consideration that pit-lines represent parts of the sensory canal system which were primarily developed as typical sensory canals.

While the value of the actual sensory canals for the homologising of dermal bones (or, at any rate, series of dermal bones) in the Actinopterygians may be said to be generally acknowledged, Westoll (1937 a and b) among others has raised doubt as to whether pit-lines are of any value whatever

for a homologising of the dermal bones on whose surface they leave impressions. Westoll (1937b, p. 572) says as follows:

"Current research on dermal bones seems to show clearly that certain elements have a constant relationship to sensory canals; it is probable that this invariable relationship is connected with the comparatively deeply infolded organs of the sensory canals proper. When the sensory organs remain superficial it is the writer's experience that the resulting "pit-lines" have very variable courses with respect to the underlying bones. The first bone to involve the nerve-supply of the pit-line will "anchor" that line to it, and this idea adequately explains the conditions in "*A*" *blainvillei* and in many other fishes."

Stensiö and Jarvik (1937–38, p. 286) comment on the passage just quoted in the following words:

"Es ist sicher richtig, dass die Pitlinien etwas variieren, aber andererseits ist es klar, dass ihre Innervierung konstant bleibt, und dass sie bei der grossen Mehrzahl rezenter und fossiler Formen, wo sie bekannt sind, bezüglich ihrer Lage so beständig bleiben, dass sie schon dadurch leicht zu identifizieren sind." And further: "Unserer Meinung nach geht Westoll (1937 a; 1937 b) etwas zu weit, wenn er den Pitlinien, wenigstens bei den Actinopterygii, beinahe jede Bedeutung für die Homologisierung der Deckknochen abzusprechen versucht."

Pehrsson (1940, pp. 15–18 and 47) points out that the parietal and the gular plate in *Amia* have developed independently of the pit-organs in the very superficial pit-lines overlying these bones, while the canal bones in *Amia* always develop in association with canal organs.

It is obvious, however, that in *Glaucolepis* and numerous other primitive Actinopterygians the bones on which typical pit-lines may be found, are the same bones which were primarily pierced by the typical sensory canals from which these pit-lines have developed. This appears clearly from the fact that the pit-lines in these forms often occur as narrow canals in the dermal bones. These bones therefore no doubt originally developed in association with the canal organs in the typical sensory canals, and there is every probability that the bones which in *Glaucolepis* contain the aforementioned transitional stages between sensory canals and pit-lines, still develop in association with the sensory organs, no matter whether the latter are situated in a deep groove or in a canal. A circumstance speaking strongly for this point of view is that in *Glaucolepis*, as in numerous other primitive Actinopterygians, pit-lines issue from, or pierce, or pass across, the radiation centres of the bones with which they are associated.

Thus there is good reason to assume that pit-lines, at any rate in numerous primitive Actinopterygians, are of the same importance for the homologising of the dermal bones associated with them as the typical sensory canals.

In certain more modern Actinopterygians the pit organs, gradually as

they obtained a more superficial position, seem to have lost their importance for the development of bones, as pointed out by Pehrsson for *Amia*, and at the same time they probably to some extent lost their applicability for an exact homologising of bones.

The supraorbital canal (*soc*, Figs. 19, 20, 27; Pl. 2) extends from that margin of the nasal which overlaps the rostro-antorbital, as it is shown in Fig. 27, in a dorsal and postero-dorsal direction to the postero-medial part of the nasal and onwards to the frontal, as will be seen from Fig. 19. Through the frontal the canal runs chiefly in a posterior direction except along a short stretch in the middle part of the bone, where it runs in a postero-lateral direction. From the frontal it continues in a posterior direction through the anterior part of the parietal, so that the pointed posterior end of the canal just reaches the radiation centre of the parietal. This posterior part of the supraorbital canal in the parietal is in some cases no actual canal, but an open groove; in other words, this part of the canal is at a stage which has been described above as a transitional stage between a sensory canal and a pit-line, and corresponds to the anterior pit-line in *Palaeonisciformes*, as for instance *Boreosomus* (Piveteau 1935, Fig. 56, the present paper Fig. 68), *Palaeoniscus* (Aldinger 1937, Fig. 25A (after Westoll 1934)), *Boreolepis* (Aldinger 1937, Fig. 33), *Cornuboniscus* (White 1939, Fig. 1), etc.

The width of the supraorbital canal varies along its course, as is seen from Fig. 19.

Tventy to twenty-two tubuli issue from that part of the supraorbital canal which lies in the nasal. The anterior ten to twelve of these tubuli open with pores lying above the supraorbital canal, while the pores of the posterior ten to twelve tubuli lie laterally to the canal.

From the frontal division of the supraorbital canal issue about thirty-five tubuli (the number of the tubuli of the sensory canals vary somewhat from specimen to specimen). Apart from minor deviations in a few specimens, the pores by which the anterior sixteen to eighteen tubuli open lie laterally to the canal, while the pits for the sixteen or eighteen posterior tubuli lie medially to the canal.

From the parietal division of the supraorbital canal issue about four tubuli, the anterior of which has its external opening directly above the canal, while the pores of the remaining ones lie laterally to the canal.

The most anterior part which can be observed of the infraorbital canal (*ifc*, Figs. 19, 20, 27; Pls. 1, 2, 3, 4, 8) pierces the rostral process of the rostro-antorbital. We have seen above (p. 136) that the anterior ends of the rostral processes of the right and left rostro-antorbitals are only separated by a very small interspace, and it must be assumed that the infraorbital canals of the right and left sides meet in this interspace, forming an ethmoidal commissure. From the rostral process the canal continues in a

roughly posterior direction to the radiation centre of the rostro-antorbital, where it anastomoses with a part of the infraorbital canal, which runs from the ventral margin of the rostro-antorbital through the radiation centre to the dorsal margin of the bone, as will be seen from Fig. 27.

If we consider the antorbital component in other primitive Actinopterygians, we shall see that in many forms, as in *Glaucolepis*, it contains a three-branched part of the sensory canal system. One of these branches points ventrally or postero-ventrally, and continues in a posterior direction through the part of the infraorbital series lying ventrally to the orbit, another points in a roughly anterior direction, and the third, finally, points roughly dorsally. In the majority of the primitive Actinopterygians in which the courses of the sensory canals are known, for instance in *Palaeoniscus freieslebeni* (Aldinger 1937, Fig. 25 (after Westoll 1934)), *Canobius ramsayi* and *Rhadinichthys fusiformis* (the present paper Fig. 29A and D), *Paramesolepis tuberculata*, *Cycloptychius concentricus*, and *Rhadinichthys canobiensis* (Moy-Thomas and Bradley Dyne 1938, Figs. 31, 20, and 14), *Cornuboniscus budensis* (White 1939, Fig. 1), *Saurichthys* (Stensiö 1925, Figs. 21, 42, and 46), *Perleidus* (Stensiö 1921, Fig. 81; 1932, Fig. 68; Piveteau 1935, Fig. 30), etc., the dorsally directed of the three canal branches in the antorbital component anastomoses with the anterior end of the supraorbital canal. In certain other forms, as for instance *Coccocephalus wildi* (Watson 1925, Fig. 11) and *Birgeria groenlandica* (Stensiö 1932, Fig. 41), the dorsally directed of the three canal branches lies far behind the anterior end of the supraorbital canal, and cannot have anastomosed with the latter.

In *Lepidosteus* (Allis 1905, Pl. 8, Fig. 2a; Pl. 9, Fig. 3a) and in *Sinamia* (Stensiö 1935, Fig. 19) the antorbital component contains a four-branched part of the sensory canal system, the infraorbital canal having two connections with the supraorbital canal, viz. one in front of and one behind the posterior nostril.

The dorsally directed canal branch in the antorbital component in *Coccocephalus* and consequently in the related form *Birgeria*, too, corresponds to the posterior (postnasal) connection between the infraorbital canal and the supraorbital canal in *Lepidosteus* and *Sinamia* (Hammarberg 1937, pp. 291–292). The dorsally directed canal branch in the antorbital component in *Canobius*, *Paramesolepis*, *Palaeoniscus*, *Cycloptychius*, *Rhadinichthys*, *Cornuboniscus*, *Saurichthys*, *Perleidus*, etc., however, must correspond to the anterior communication between the infraorbital canal and the supraorbital canal in *Lepidosteus* and *Sinamia*.

According to its position in relation to the anterior end of the supraorbital canal it might be assumed that the dorsally directed canal branch in the antorbital component in *Glaucolepis* corresponded to the posterior communication between the infraorbital canal and the supraorbital canal in *Lepidosteus* and *Sinamia*; but in view of the fact that *Glaucolepis* is very

closely related to *Palaeoniscus*, this assumption seems improbable. In spite of its position the dorsally directed canal branch in *Glaucolepis* must correspond to the dorsally directed canal branch in *Palaeoniscus*. It must therefore be supposed that in *Glaucolepis* a communication existed between this canal branch and the anterior end of the supraorbital canal, and this communication may have extended as a horizontal canal in the soft tissue between the dorsal part of the rostro-antorbital and the internal face of the overlapping nasal.

From the ventral margin of the rostro-antorbital the infraorbital canal continues in the usual way through the lacrimo-maxillary, the jugal, the postorbital, the supraorbito-postorbital, and the supraorbito-dermosphenotic to the supratemporo-intertemporal (Fig. 27). In the supratemporo-intertemporal the infraorbital canal is continued in a posterior direction by the postotic canal (Säve-Söderbergh 1933, p. 7); but the accurate boundary between the posterior part of the infraorbital canal innervated by the ramus oticus lateralis and the postotic canal innervated by the nervus glossopharyngeus cannot be localised.

In that part of the rostro-antorbital which is not overlapped by other dermal bones, eight tubuli whose pores all lie directly above the canal issue from the infraorbital canal. Four of these tubuli issue from that part of the canal which runs from the ventral to the dorsal margin of the bone, and the other four issue from the forward-directed branch of the canal, which continues through the rostral process (the ethmoidal commissure).

From the canal lodged in the lacrimal division of the lacrimo-maxillary there issue about seven tubuli, whose pores lie ventrally to the canal.

In the jugal twelve to sixteen tubuli are found; their pores lie partly very near the postero-ventral and partly near the postero-dorsal margin of the bone; notably those tubuli which issue from the vertical division of the canal have a very considerable length (Fig. 27).

In the postorbital about six tubuli are found; their pores lie fairly near the posterior margin of the bone.

In the supraorbito-postorbital about four to six tubuli issue from the canal; they open partly in front of and partly behind the canal, as will be seen from Fig. 19.

In the supraorbito-dermosphenotic four or five tubuli issue from the canal; all of them lie laterally to the canal.

From the canal in the supratemporo-intertemporal, which, as stated above, comprises the posterior part of the infraorbital canal and the postotic canal, about twenty-five tubuli issue, which, as will be seen from Fig. 19, are of rather different length. All their pores lie laterally to the canal. The preopercular canal does not seem to have anastomosed with the longitudinal canal in the supratemporo-intertemporal.

The cephalic division of the main lateral line (*lc*, Figs 19; Pl. 2)

runs through the lateral part of the lateral extrascapular in a longitudinal direction as a direct posterior continuation of the postotic canal in the supratemporo-intertemporal.

From the longitudinal part of the canal issues a transverse branch (*s.com*, Figs. 19, 20, 27), which continues from the lateral into the medial extrascapular, in which bone it terminates, as will be seen from Fig. 19. This transverse canal branch corresponds to a part of the supratemporal commissure in other Actinopterygians. As is shown in the figures, some few tubuli, whose pores lie partly medially partly laterally to the canal, issue from the longitudinally directed part of the canal in the lateral extrascapular. About six tubuli, whose pores lie posteriorly to the canal, issue from the transverse part of the canal in the lateral extrascapular, and four tubuli, whose pores likewise lie posteriorly to the canal, issue from the canal in the medial extrascapular.

The preopercular canal (*poc*, Fig. 27) extends in the normal way through the preoperculum and apparently has no connection with the longitudinal canal in the supratemporo-intertemporal. Twenty to thirty tubuli issue from that part of the preopercular canal which lies in the antero-dorsal part of the preoperculum; the pores of these tubuli lie close to the postero-dorsal margin of this division of the bone. About five tubuli issue from that division of the preopercular canal which pierces the postero-ventral division of the preoperculum, and their pores lie posteriorly to the canal.

The mandibular canal (*mdc*, Fig. 27, Pl. 4) runs in the normal way through the angular and onwards through the dentalo-splenial. As stated above, the dentalo-splenial overlaps a considerable part of the angular, and I did not succeed in accurately localising the place where the canal passes from one into the other of these two bones The number of tubuli issuing from the canal may be estimated at about fifty to sixty, even though the canal is never so well preserved that all its tubuli can be observed in a single specimen.

In the angular the tubuli open with pores which lie posteriorly to the vertical and ventrally to the horizontal part of the mandibular canal and in the dentalo-splenial the pores lie ventrally to the canal.

In addition to the anterior pit-line already mentioned, we find on the parietal a middle pit-line (*mp*, Figs. 19, 27) and a posterior pit-line (*pp*, Figs. 19, 27), which both occur, now as deep narrow grooves, and now as narrow canals. The middle pit-line issues from the radiation centre of the parietal in a lateral or an antero-lateral direction, pointing towards the well defined protuberance on the lateral margin of the exposed part of the parietal, as will be seen from Fig. 19. In several cases this pit-line continues beyond the lateral margin of the parietal to the radiation centre of the supratemporo-intertemporal.

The posterior pit-line issues from the radiation centre of the parietal in a posterior or postero-lateral direction, as shown in Fig. 19.

The arrangement of the three pit-lines on the parietal agrees entirely with that known from *Palaeonisciformes* as for instance *Boreosomus* (Piveteau 1934, Fig. 56; the present paper Fig. 68), *Palaeoniscus* (Aldinger 1937, Fig. 25A (after Westoll 1934)), *Boreolepis* (Aldinger 1937, Fig. 33), *Cornuboniscus* (White 1939, Fig. 1), *Carboveles* and *Aetheretmon* (Moy-Thomas 1938, Figs. 5 and 7), *Gyrolepidotus* (Berg 1939, Fig. 1), etc. It is rather peculiar that the arrangement of the pit-lines on the parietal in a considerable number of *Palaeonisciformes* from Glencartholm examined by Moy-Thomas and Bradley Dyne (1938) differs essentially from that in *Glaucolepis* and the forms just mentioned.

From the radiation centre of the preoperculum there issues in an anterior and at the same time slightly ventral direction a pit-line (*hp*, Fig. 19), which now appears as a groove, now as a narrow canal. In addition a pit-line (*hp*, Fig. 19) is often found on the maxillary, which from the radiation centre of the bone (or from a point on the surface of the bone directly laterally to the radiation centre) runs in a postero-dorsal direction. This pit-line seems always to occur as a deep groove, not as a canal. In a previous paper (E. Nielsen 1936, pp. 38–39, Figs. 18–19) I interpreted the pit-lines on the preoperculum and the maxillary in *Glaucolepis* as the posterior and the anterior part respectively of the horizontal pit-line of the cheek, and set forth the assumption that the middle part of this pit-line must have been situated so superficially that it failed to leave any trace on the dermal bones. In the same paper I demonstrated the presence of the vertical pit-line of the cheek in *Glaucolepis* (*op. cit.* p. 38, Figs. 17 and 19). This pit-line can only be observed in some well preserved specimens of *Glaucolepis gunnari* and appears as a small groove running in an antero-dorsal direction from the point on the exposed face of the quadratojugal which lies directly laterally to the centre of radiation.

After the vertical and the horizontal pit-line of the cheek were discovered in *Glaucolepis* in 1936, they have been observed in several other genera, too, within the *Palaeonisciformes*. Thus the horizontal pit-line of the cheek has been observed in *Pygopterus humboldti* (Westoll 1937a, p. 370), *Carboveles ovensi* (Moy-Thomas 1938, Fig. 7), *Holurus parki* (Moy-Thomas and Bradley Dyne 1938, Figs. 26–27), *Canobius* and *Eurylepis* (Westoll 1937 a, p. 370), and *Brachydegma caelatum* (Dunkle 1939, Fig. 1), in the last-named two forms, however, only on the preoperculum, as in *Boreosomus* (Westoll 1937 a, p. 370; the present work p. 356, Fig. 69). The vertical pit-line on the quadrato-jugal has been observed in *Brachydegma caelatum* (Dunkle 1939, Fig. 1), and on the preoperculum in *Canobius* and *Boreosomus* (Westoll 1937 a, p. 370, Fig. 4E; the present work p. 356, Fig. 69). The vertical pit-line on the maxillary which Westoll (1937 a, p. 370) states that

he has observed on my Greenland material and which he has inserted on a drawing of a hypothetical Palaeonisciform (*op.cit.* Fig. 4B), is actually the pit-line which I have interpreted above as the anterior part of the horizontal pit-line of the cheek in *Glaucolepis*.

A pit-line on the dentalo-splenial like that found in *Brachydegma caelatum* (Dunkle 1939) has not been observed in *Glaucolepis*.

From the centre of radiation of the anterior branchiostegal ray or from a point on the outer side of this bone directly ventrally to the centre of radiation issues in a lateral direction a short pit-line, which probably always occurs as a groove on the surface of the bone. This pit-line, which corresponds to the transverse gular line in *Amia* (Säve-Söderbergh 1933, p. 8), has been observed in *Gyrolepidotus schmidti*, too (Berg 1939, Fig. 1).

b. Glaucolepis aldingeri, arctica, gunnari, and magna.

As regards the position of the sensory canals and pit-lines preserved these four species agree entirely with *Glaucolepis stensiöi*, so a detailed description will be superfluous.

The sensory canal system of the head may be investigated in all details in *Glaucolepis gunnari* and *Glaucolepis magna*, whereas it has been impossible to trace the courses of all the individual tubuli in *Glaucolepis arctica* and *Glaucolepis aldingeri*. Besides, the material of *Glaucolepis aldingeri* is so incomplete that neither the anterior part of the infraorbital canal or the part of the sensory canal system that is associated with the dermal cranial roof could be observed.

In Fig. 26A and C, which show portions of the dermal cranial roof of specimens of *Glaucolepis gunnari*, the sensory canals have been inserted in so far as they could be observed. As will be seen, the directions of the tubuli of the canals agree in their main features with those observed in *Glaucolepis stensiöi*, except that tubuli issue both in a medial and a lateral direction from the canal in the supraorbito-dermosphenotic. As is seen from the figures, the tubuli in *Glaucolepis gunnari*, at any rate in the supratemporo-intertemporal, the supraorbito-dermosphenotic, and the frontal, are mostly longer than in *Glaucolepis stensiöi*. The vertical pit-line of the cheek of *Glaucolepis gunnari* is found in a few cases (*vp,* Pl. 9, Fig 2).

In Figs. 23 and 24 the preserved parts of the sensory canals of the dermal cranial roof of two specimens of *Glaucolepis magna* are shown. In one of these specimens, as in the figured specimens of *Glaucolepis gunnari*, tubuli issue from the canal through the supraorbito-dermosphenotic both in a lateral and a medial direction, and in the lacrimo-maxillary tubuli issue both in a dorsal and a ventral direction (Fig. 31), but apart from this, the courses of the tubuli agree well with those in *Glaucolepis stensiöi*.

Axial skeleton.

a. Glaucolepis magna.

In specimens Nos. 46, 47, 175, 177, and 178 the ossifications of the axial skeleton are well preserved in the abdominal region, while the axial ossifications in the caudal region could not be investigated in detail in any specimen of this species.

The axial skeleton in the abdominal region is represented partly by dorsal and ventral arcuals and partly by supraneurals and ribs. All the ossifications of the axial skeleton in this as in the other species of *Glaucolepis* consist of cancellate endochondral bone surrounded by perichondral bone-layers. From the position of the dorsal and ventral arcual elements in relation to each other it appears with certainty that the dorsal elements are basidorsals and the ventral basiventrals plus interventrals (each basiventral having fused with the interventral of the metamere nearest behind its own).

The notochord was persistent in the abdominal region and was in no way constricted by the arcual elements.

The axial skeleton is not complete throughout the abdominal region in any specimen; but the different specimens supplement each other so well that only the arcual elements immediately behind the head are as yet unknown. The number of metameres in the abdominal region may be estimated at about sixteen.

In the middle part of the abdominal region the individual basidorsals (*Bd*, Fig. 48A, B and C; Pl. 21, Fig. 4; Pl. 23, Fig. 1) consist of a four-sided proximal plate and a long distal process.

The detailed outline of the four-sided plate is seen from the figures; the antero-dorsal part of the lateral face of the plate is slightly concave, while the remaining part of the face is slightly convex. On the medial face of the plate, a short distance ventrally to its dorsal margin, a sharp ridge (*r.m*, Fig. 48B and C) is found, which runs parallel with the dorsal margin. Both dorsally and ventrally to this ridge the medial face is concave in a dorso-ventral direction, but could not be examined in detail. The distal process, which issues from the postero-dorsal part of the proximal plate, is rather narrow in its proximal part, but increases considerably in breadth towards its distal end, as will be seen from the figures. The right and left basidorsals in each metamere are so situated in relation to each other that their distal processes are parallel, while their proximal plates diverge in a ventral direction (Fig. 48B). The medulla spinalis was situated between the divergent proximal plates of the opposed basidorsals, while the dorsal longitudinal ligament must have been situated in some place or other between the opposed distal processes.

The considerable distance between the ventral and the dorsal arcuals

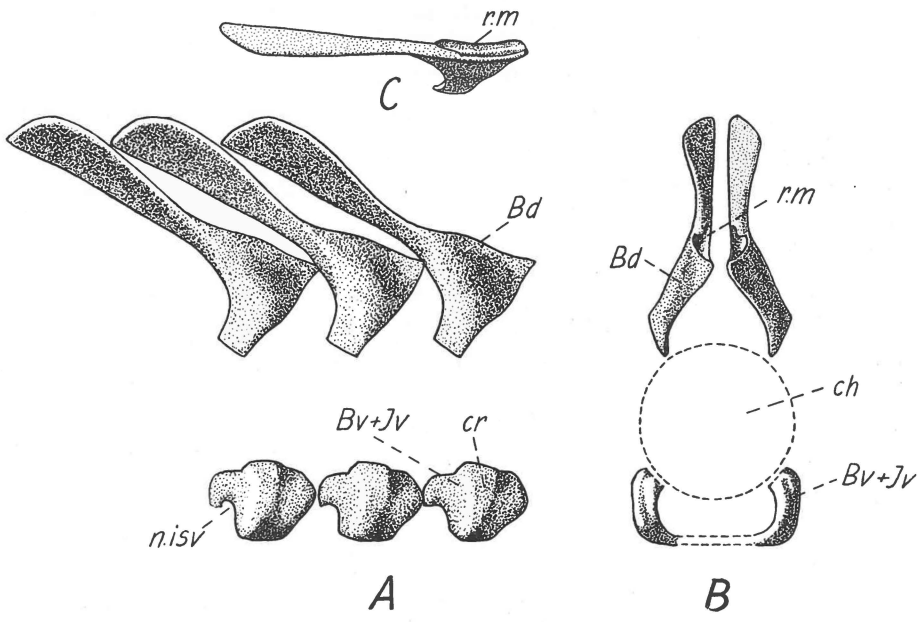


Fig. 48. *Glaucolepis magna* n. sp. Part of the vertebral column from the middle part of the abdominal region. Based on specimen No. 46. 3.3 ×. A, lateral view. B, posterior view. C, a single basidorsal ossification in dorsal view.
ch, presumed outline of the notochord; *r. m*, longitudinal ridge on the medial side of the basidorsal ossification. Lettering otherwise as in Fig. 49.

shows that the notochord had a large diameter, and in Fig. 48B an attempt is made to show how it may have been placed in relation to the basidorsal ossifications. However, the relations between the notochord and the basidorsal elements cannot be determined exactly, for possibly the most ventral parts of the basidorsal elements were cartilaginous.

The shape of the basidorsal ossifications changes gradually through the whole abdominal region, as shown in Fig. 50. From the middle part of the abdominal region the proximal plates of these ossifications increase in breadth in an anterior direction, assuming a more and more square outline, while their distal processes show an increasing backward inclination, so that farthest anteriorly, in the known part of the basidorsal series, they are almost horizontal. From the middle towards the posterior part of the abdominal region the proximal plates of the basidorsal ossifications narrow gradually, while their distal processes probably become somewhat shorter.

Distally to the basidorsals of the abdominal region a series of unpaired supraneurals is found (*Sn*, Pl. 23, Fig. 1). Each supraneural lies in the continuation of the distal processes of the right and left basidorsals of a metamere and is a bone rod which is broadest in its most proximal part and so curved that its anterior margin is concave. Its proximal terminal face was capped by cartilage.

The length of the individual supraneurals is almost equal to the length of the basidorsals in continuation of which they lie.

Fig. 48 A shows three successive ventral arcual elements of the middle part of the abdominal region. Each of these elements is a small, fairly thick bone plate (*Bv* + *Iv*, Fig. 48; Pl. 21, Fig. 4), on whose lateral face a broad rounded ridge is found (*cr*, Fig. 48; Pl. 21, Fig. 4), which from the dorsal margin of the face runs downward and slightly backward. Posteriorly to this ridge a distinct notch (*n.isv*, Fig. 48, Pl. 21, Fig. 1) is found in the postero-ventral margin of the ossification; no doubt intersegmental vessels passed through this notch (cf. Stensiö 1932, Fig. 85). Consequently that part of each of the ventral arcual ossifications which lies in front of this notch must represent a basiventral, and the smaller part lying above and behind the notch an interventra[1]. The most ventral part of the basiventral division of the ventral arcuals curves in a medial direction in the way seen in Fig. 48B. From the conditions in *Glaucolepis gunnari* (cf. p. 214) it would seem that the medially curved part of each of the ventral arcuals were connected by a cartilaginous bridge with the same part of the ventral arcual of the opposite side, and that accordingly in this species, as in *Glaucolepis gunnari*, a broad, low aorta canal is developed in the abdominal region.

From Fig. 48B, which shows the ventral arcuals seen from behind, it is seen that while the external or lateral (ventro-lateral) faces of these ossifications exhibit a fairly gradual smooth curvature in a dorso-ventral direction, their internal faces are divided by a rather sharp longitudinal ridge into a dorsal and a ventral division.

The dorsal division is a rather narrow, dorso-medially directed face, which no doubt had contact with the notochord, as shown in the figure, while the ventral and larger division is very concave in a dorso-ventral direction and forms the lateral boundary of the aorta canal. The mutual position of the successive ventral arcuals will be seen from Fig. 48.

In some few specimens traces of ossified ribs may be observed, which lie in a distal continuation of the well developed ridge on the lateral face of the basiventral division of each of the ventral arcuals. The exact length of the ribs cannot be stated.

The remnants of ossifications belonging to the axial skeleton in the caudal region which can be observed in this species agree, as far as they could be investigated, with the corresponding ossifications in *Glaucolepis aldingeri* (p. 219).

b. Glaucolepis gunnari.

In several specimens remnants of ossifications are seen in the axial skeleton, but only in specimen No. 3 portions of the axial skeleton are so well

preserved that a detailed investigation could be made. Specimen No. 3 is a much distorted fish which lacks nearly the whole head and the greater part of the caudal fin, and the majority of the ossifications of the axial skeleton no more occupy their original position in relation to each other. When the concretion enclosing the fish was split, essential parts of the axial skeleton were lost. The axial skeleton in the anterior part of the abdominal region is especially well preserved, and here it was possible to dissect out the individual ossifications in an area situated very closely behind the head (Fig. 49 A and B; Pl. 21, Figs. 1, 2, 3). As is seen from the figures, the dorsal and ventral arcuals lie much nearer each other than in *Glaucolepis magna*, which is no doubt due to a compression of the animal after its death. As in *Glaucolepis magna*, the dorsal arcual ossifications represent basidorsals, and each of the ventral ones a basiventral plus the interventral nearest behind it.

The basidorsal ossifications (*Bd*, Fig. 49A; Pl. 21, Fig. 2) entirely resemble the anterior basidorsal ossifications known in *Glaucolepis magna*, consisting of a proximal, nearly square plate and a distal, directly backward-pointing process. The relations between the successive basidorsals appear from Fig. 49; the relations between the right and left basidorsals in the same metamere are as in *Glaucolepis magna*.

The ventral arcual ossifications (*Bv* + *Iv*, Fig. 49A and B; Pl. 21, Figs. 1, 2, 3) are unpaired and consist of a right and a left lateral, nearly vertical division, and a median, roughly horizontal division, which latter connects the ventral parts of the two lateral divisions. Each of the lateral, vertical divisions corresponds to the vertical and largest part of a ventral arcual ossification in *Glaucolepis magna*, while the most lateral part of the median horizontal division corresponds to the small medially curved division of the ventral arcuals in *Glaucolepis magna*.

The paired lateral vertical division is a little broader in relation to its height than the vertical division of the ventral arcuals in that part of the axial skeleton of *Glaucolepis magna* which is shown in Fig. 48A. It is not impossible, however, that the ventral arcuals in *Glaucolepis magna* are broader nearer the head.

As will be seen from Fig. 49A, the outline of the paired lateral vertical division varies considerably, i.a. the intersegmental vessels have in some cases passed through a canal (*f. isv*, Fig. 49A; Pl. 21, Fig. 2) in the postero-ventral part of the division, in other cases through a notch (*n. isv*, Fig. 49A; Pl. 21, Fig. 2) in the postero-ventral margin of the division.

On the external (lateral) face of the vertical division a similar ridge is found as in *Glaucolepis magna*, and as in that species, the internal face is divided into two smaller faces, viz. a dorso-medially directed face, which was in contact with the notochord, and, ventrally to this face, a broader face concave in a dorso-ventral direction, which forms the lateral boundary of a broad and low aorta canal.

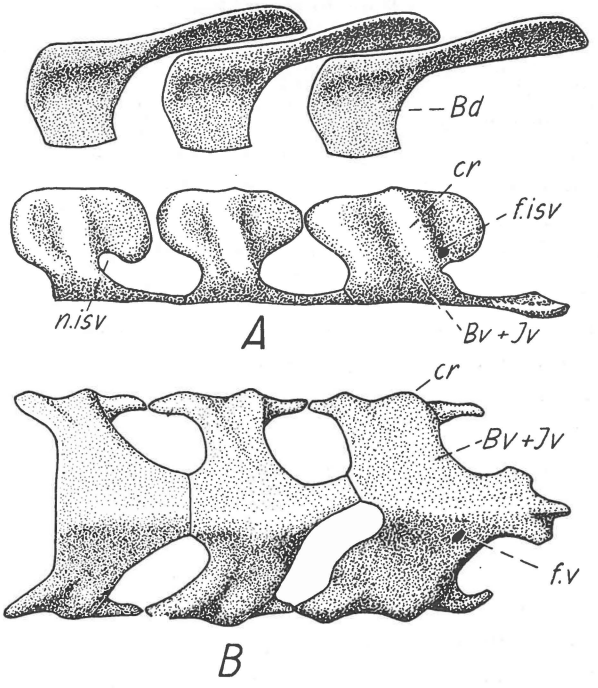


Fig. 49. *Glaucolepis gunnari* n. sp. Part of the vertebral column from the anterior division of the abdominal region. The distance between the dorsal and the ventral arcual series was no doubt greater in the living fish. Based on specimen No. 3. 4.5 ×. A, lateral view. B, ventral view.
Bd, basidorsal, *Bv* + *Iv*, fused basi- and interventral; *cr*, crista on lateral face of the ventral arcual ossification; *f. isv*, foramen for intersegmental vessels; *f. v*, foramen for a vessel; *n. isv*, notch for intersegmental vessels.

The median division of the unpaired ventral arcual ossifications is a fairly thin bone plate, which is slightly curved from side to side so that its dorsal face is concave and its ventral face convex. On the ventral face of the bone plate a longitudinal median keel is found, which in most cases is merely indicated, but which now and then is rather prominent. The outline of the bone plate is rather irregular and varies fairly much in the different arcual ossifications, as is seen from Fig. 49 B, which likewise shows the contact between the median parts of the successive bone plates.

No ribs have been observed, and the supraneurals belonging to the described part of the axial skeleton, if present, lie at any rate not *in situ*.

The most anterior basidorsals can be observed in their natural position in relation to the foramen magnum, but unfortunately they are so highly crushed that their shape cannot be ascertained.

The ossifications in the axial skeleton which can be observed in the caudal region in specimen No. 3 and in other specimens of *Glaucolepis gunnari*, show good agreement with those in *Glaucolepis aldingeri*.

c. Glaucolepis aldingeri.

In the greater part of the caudal region in a single specimen, No. 66, of *Glaucolepis aldingeri* (Pl. 24) the ossifications of the axial skeleton could be investigated in fairly great detail.

In other specimens of this species remnants of ossifications belonging to the axial skeleton are seen, but these remnants are so incomplete that they can supply no information of importance. The subjoined description of the axial skeleton of the caudal region is therefore almost exclusively based on specimen No. 66.

In the anterior part of the caudal region some basidorsals (*Bd*, Pl. 24) are found, and in addition, at any rate in the area below the posterior half of the dorsal fin, some small independent interdorsals (*Id*, Pl. 24). Whether supraneurals occur in this area, either separate or fused with the basidorsals, cannot be ascertained. In the middle part of the caudal region the dorsal arcuals are so poorly preserved that nothing can be stated as to their number or shape. In the axis of the caudal fin some small dorsal arcual elements (*Da*, Pl. 24) are found.

In the anterior part of the caudal region some ventral arcuals occur about whose structure very little can be stated. The greater number of these arcuals represent basiventrals (*Bv*, Pl. 24), but the most anterior of them possibly, as in the abdominal region, in addition includes a rather small interventral component. In the area dorsally to the anterior part of the anal fin some small independent interventral ossifications (*Iv*, Pl. 24) occur. Distally to the basiventral ossifications in the anterior part of the caudal region some unpaired infrahaemals (*Ih*, Pl. 24) are found.

In the middle part of the caudal region the basiventral ossifications have become fused with the unpaired infrahaemals, and these compound ossifications (*Bv* + *Ih*, Pl. 24), which in the sequel will be termed haemal arches, alternate with small interventrals. In the posterior part of the caudal region the unpaired distal parts of the haemal arches are widened so as to form so-called hypurals (*pr.hy*, Pl. 24), which probably include radial components, while the proximal part of each of the haemal arches consists of a solid unpaired mass of bone (*Va*, Pl. 24).

The following description of all these ossifications cannot be very detailed since many of the ossifications are rather poorly preserved in specimen No. 66 and not observed at all in other specimens of either *Glaucolepis aldingeri* or other species of *Glaucolepis*. The outline of the individual basidorsals in the anterior part of the caudal region is seen from Fig. 50, but it should be pointed out that as to several of these ossifications the outline shown in the figure has been partially constructed on the basis of the outlines of those lying immediately in front of or behind. As in the ab-

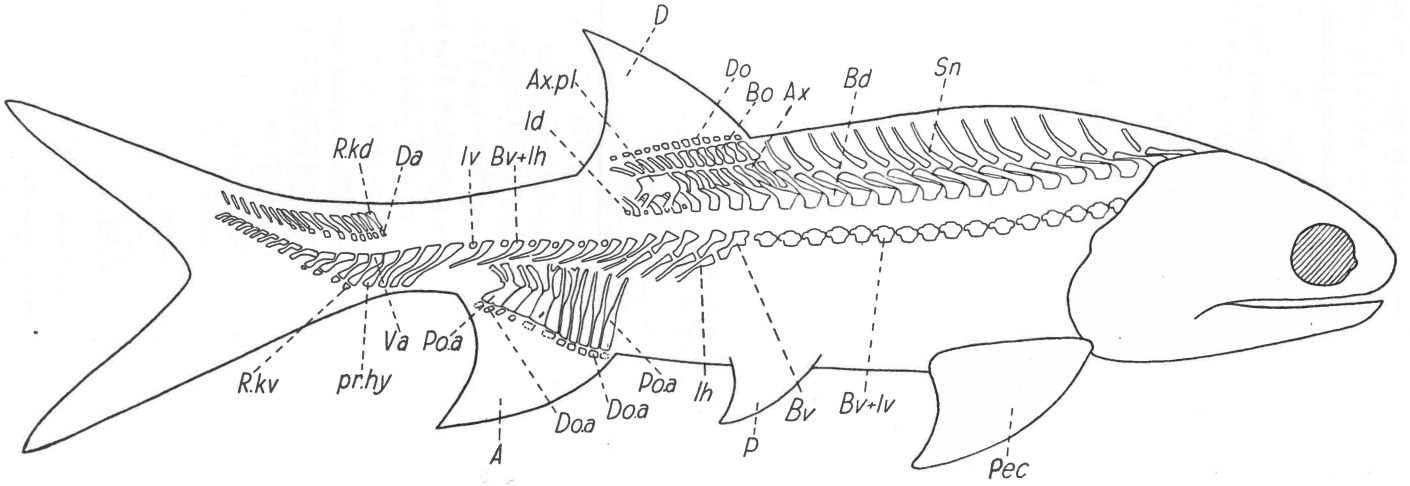


Fig. 50. *Glaucolepis*. Attempted restoration of the axial skeleton and the endoskeleton of the unpaired fins. Axial skeleton in the abdominal region chiefly after *Glaucolepis gunnari* and *Glaucolepis magna*. Axial skeleton in the caudal region and endoskeleton of the unpaired fins after *Glaucolepis aldingeri*. Outline of trunk after *Glaucolepis aldingeri*. Relations between the axial skeleton and the endoskeleton of the dorsal and anal fins unknown. *A*, anal fin; *Ax*, axonost; *Ax. pl*, compound axonost (axonost plate); *Bd*, basidorsal; *Bo*, baseost; *Bv*, basiventral; *Bv* + *Ih*, basiventral + infrahaemal; *Bv* + *Iv*, basiventral + interventral; *D*, dorsal fin; *Da*, dorsal arcual ossification in the caudal region; *Do*, distal radial ossification in the endoskeleton of the dorsal fin; *Do. a*, distal radial ossification in the endoskeleton of the anal fin; *Id*, interdorsal; *Ih*, infrahaemal; *Iv*, interventral; *P*, pelvic fin; *Pec*, pectoral fin; *Po. a*, proximal radial ossification in the endoskeleton of the anal fin; *R. kd*, epichordal radial ossification in the the endoskeleton of the caudal fin; *R. kv*, hypochordal radial ossification in the endoskeleton of the caudal fin; *Sn*, supraneural; *Va*, arcual division of a hypochordal ossification in the body axis of the caudal fin; *pr. hy*, hypural process.

dominal region the individual basidorsals consist of a proximal plate and a distal process, but the proximal plate narrows gradually from the anterior to the posterior end of that part of the basidorsal series which lies ventrally to the dorsal fin, so that the proximal plate and the distal process in the most posterior element of the series pass very gradually into each other. The distal processes are shorter than in the abdominal region; their exact length, however, cannot be ascertained, even though it is a fact that the distal ends of the processes lie more distally than the proximal ends of the axonosts. Independent supraneurals have not been observed, but it is not impossible that the distal ends of the distal processes, as for instance in *Pygopterus nielseni* (Aldinger 1937, Fig. 42), are fused with short unpaired supraneurals, and that the right and left basidorsals in each metamere are thus united into an unpaired ossification. As to the small interdorsals below the posterior half of the dorsal fin it can only be stated that in lateral view they have a four-sided outline.

The small dorsal paired arcuals in the posterior part of the caudal region (the axis of the caudal fin) are not particularly well preserved in specimen No. 66; and at least half the number of these elements have been lost. In Fig. 50 I have attempted to reconstruct this row of dorsal arcuals, even though it was impossible to definitely ascertain the number of ossifications in the row. About the shape of the individual ossifications no information can be given except what appears from the figure.

Distally to the row of dorsal arcuals in the preserved part of the caudal fin lies a series of unpaired ossifications which represent the epichordal radials (*R. kd*, Pl. 24) of the caudal fin. As far as I am able to decide, the number of dorsal arcuals (arcual pairs) corresponds to the number of radial ossifications, as shown in Fig. 50. The radial ossifications are bone rods, flattened slightly from side to side. They are broadest farthest distally and narrow gradually in a proximal direction through their distal two-thirds, to increase again a little in breadth in their proximal third. The length of the radial ossifications alters from the anterior to the posterior part of the series, as will be seen from Fig. 50. The distal cartilage-capped terminal faces of the radial ossifications were in contact with the ventral faces of the dorsal ridge scales of the caudal fin, while the proximal terminal faces, likewise capped by cartilage, were in contact with the small dorsal arcual pairs.

The ventral arcuals in the anterior part of the caudal region cannot be exposed so completely that their structural details can be observed. In lateral view they fall naturally into two divisions, viz. a broad proximal and a narrow distal division.

The broad proximal division is serially homologous with at any rate the basiventral component of the lateral division of the unpaired ventral arcual ossifications in the abdominal region in *Glaucolepis gunnari*; but it is quite possible that in addition it includes an interventral component. There is

every probability that this proximal division forms the lateral wall of an aorta canal, and that it is connected with its antimere by a median horizontal division which forms the floor of the aorta canal; however, the state of preservation of the material does not allow a closer investigation of these conditions. The narrow distal division issues as a postero-ventrally directed process, the haemal process, from the postero-ventral part of the broad proximal division. The distal terminal face of this process, which increases in breadth in a distal direction, was capped by cartilage.

The caudal vein was situated in the space between the right and left haemal processes.

As a direct prolongation of each pair of haemal processes lies an unpaired infrahaemal, a rod-shaped ossification which is thinnest at the middle and especially thick in its most proximal part. The proximal terminal faces of the infrahaemals were capped by cartilage. The length of the elements of the infrahaemal series and their position in relation to the ossifications of the endoskeleton of the anal fin have been tentatively represented in Fig. 50.

In the middle part of the caudal region diminutive independent interventrals alternate either with basiventrals (farthest anteriorly) or with haemal arches. As stated above, I apply the term haemal arches to the basiventral pairs whose haemal processes are fused with the unpaired infrahaemal lying distally to them. These haemal arches are pierced by two longitudinal canals, a dorsal which, as in the abdominal region in *Glaucolepis gunnari*, lodged the aorta, and a ventral which lodged the caudal vein. However, none of the haemal arches could be dissected out so completely that their exact shape could be ascertained. In lateral view the outline of the haemal arches changes through the series, as will be seen from Fig. 50.

In the posterior part of the caudal region immediately in front of the caudal fin and in the preserved part of the body axis of the caudal fin the hypochordal part of the axial skeleton is represented by unpaired ossifications which fall more or less distinctly into a proximal and a distal division.

The proximal division is a massive mass of bone which in the ossifications lying in the axis of the fin is shaped like a half-cylinder, whose axis is parallel with the axis of the fin and whose plane dorsal or antero-dorsal face is devoid of perichondral bone.

In the region immediately anterior to the caudal fin the shape of the proximal divisions of the ossifications is so altered that there is a gradual transition between the half-cylinder-shaped bodies in the axis of the fin to the proximal parts of the posterior typical haemal arches. Thus there can be no doubt that the proximal divisions of the unpaired ossifications in the posterior part of the caudal region include a basiventral component, and since no independent interventrals occur in this part of the caudal region, it is quite possible that they comprise an interventral component, too.

In *Pygopterus de geeri* and *Pygopterus nielseni* the proximal division of

the hypochordal ossifications of the axial skeleton in the axis of the caudal fin is half-cylindrical or even perfectly cylindrical in shape (Stensiö 1921, Pl. 25, Fig. 3; Aldinger 1937, pp. 157–158, Fig. 42). In a specimen of *Glaucolepis de geeri* figured by Stensiö the proximal end of some epichordal radial ossifications (which possibly include axial components) seems to be connected with one of the cylinder-shaped bodies, and from this Aldinger concludes that the cylinder-shaped bodies are vertebral centres which have replaced the notochord more or less completely. However, Stensiö's specimen of *Pygopterus de geeri* seems to me to be preserved in such a way that no conclusions at all can be drawn from the position of the epichordal radials, and in *Glaucolepis* the aforementioned thickened portions lie clearly ventrally to the notochord.

The distal division of each of the unpaired hypochordal ossifications is a long process flattened from side to side, the hypural process, which increases in breadth in a distal direction, as is seen from Fig. 50. The length of the hypural processes decreases in a posterior direction corresponding to the decreasing height of the axis of the fin. The distal terminal face of the individual hypurals was covered with cartilage. In Fig. 50 small ossifications (*R. kv*) are seen distally to some of the most well developed hypurals; traces of these ossifications have been found in a few detached caudal fins which may with some doubt be referred partly to *Glaucolepis arctica*, partly to *Glaucolepis magna*. These ossifications represent independent elements of the hypochordal radial skeleton of the caudal fin, which must otherwise for the greater part be regarded as fused with the hypural processes (cf. Schmalhausen 1912, pp. 525–528; 1913 a, p. 65; 1913 b, pp. 753–756).

d. Glaucolepis arctica and stensiöi.

In both these species remnants of ossifications in the axial skeleton may be observed, but the state of preservation is poor. As far as investigations could be made, the two species agree as regards the axial skeleton with the other three Greenland species of *Glaucolepis*.

e. Discussion.

Ossifications in the axial skeleton have been observed in numerous *Palaeonisciformes*, but only as regards *Birgeria* (Stensiö 1921, pp. 187–190; 1932, p. 290) and *Pygopterus* (most recently examined by Stensiö 1921, pp. 206–207, and Aldinger 1937, pp. 254–261) is a fairly detailed account of the axial skeleton available. Aldinger has investigated the conditions in *Gyrolepis holmi*, and after a brief report of his results he refers to a paper on this species just in press (Aldinger 1937, pp. 240 and 242). However, this paper has not yet been published, and at present it is therefore

impossible to make comparisons between the axial skeletons of *Glaucolepis* and *Gyrolepis*.

As far as can be judged from the position and shape of the ossifications present, the axial skeletons of *Glaucolepis* and *Pygopterus* are of the same primitive type. This type is characterised by its persistent and not constricted notochord and by the primitively arranged and very slightly specialised dorsal and ventral arcual elements, which enclose the notochord to a small extent only.

In *Pygopterus* indications of small independent interdorsal ossifications are found in the abdominal region (Stensiö 1921, p. 206; Aldinger 1937, p. 154), but not in the caudal region; in *Glaucolepis*, however, such ossifications are found in the caudal region, but not in the abdominal region. In *Pygopterus* no interventrals have been found, whereas in *Glaucolepis* small interventral ossifications occur, separate in part of the caudal region and fused with basiventral ossifications in the abdominal region and perhaps in the anterior part of the caudal region.

When it is taken into consideration how the process of ossification takes place in other parts of the skeleton in *Glaucolepis*, as for instance in the neural endocranium (cf. p. 92) and the palatoquadrate (cf. p. 143), it is obvious that no great importance should be attached to the above-mentioned differences between *Glaucolepis* and *Pygopterus*. The absence of ossifications in one of the genera hardly means anything but that the specimens investigated are so young individuals that the process of ossification has not yet set in in all the arcual elements, and there is good reason to assume that the ossifications which are lacking would be found on an examination of older and better preserved individuals. It is likewise probable that the interventral ossifications which in *Glaucolepis* have become fused with the basiventral ossifications, will prove to be independent in very young individuals.

As far as the larger arcual ossifications are known, they agree well within the two genera, which is obvious from a comparison between Aldinger's figures of *Pygopterus* (Aldinger 1937, Figs. 42–43) and Figs. 48, 49, and 50 of the present work. A difference between the two genera, to which, however, no great importance should be attached, is that independent supraneurals and infrahaemals occur in a greater part of the caudal region in *Pygopterus* than in *Glaucolepis*.

Stensiö (1932, pp. 262–263, Fig. 85) describes a part of the axial skeleton of the abdominal region in the primitive Holosteid *Ospia whitei*, and points out the considerable resemblance it bears to the axial skeleton in different *Palaeonisciformes* (*Birgeria*, *Coccolepis*, *Phanerosteon*, and *Pygopterus*). The agreement between *Ospia* and *Glaucolepis* is even more conspicuous than between *Ospia* and *Pygopterus* because we have a more detailed knowledge of this particular part of the axial skeleton in *Glaucolepis* than in *Pygopterus*. In lateral view the ventral arcual ossifications in the

abdominal region in *Ospia* have about the same appearance as in *Glaucolepis*, and the basidorsals in the two genera, too, show good agreement.

The ossifications in the axial skeleton of *Birgeria* is known in detail only within part of the caudal region, and the shape and mutual position of these ossifications differ considerably from those observed in the corresponding region in *Glaucolepis*. Each of the ventral arcual ossifications in *Birgeria*, which according to Stensiö represent a basiventral plus an interventral, and according to Aldinger (1937, p. 154) probably only an interventral, extends so far in a dorsal direction that together with its antimere it enclosed the ventral half of the notochord; thus we are here confronted with the incipient formation of a vertebral centre, a hypocentrum (Stensiö 1921, pp. 189–190). The unpaired ossifications interpreted by Stensiö (*op.cit.* pp. 189–190) as distal basiventral divisions, but in the present paper regarded as infrahaemals in agreement with Aldinger (1937, p. 161), are separate in an area of the caudal region where they have become fused with the basiventral ossifications both in *Glaucolepis* and in *Pygopterus*.

Stensiö (1921, p. 190) points out the peculiar fact that the axial skeleton in *Birgeria* in several respects, i.a. as regards the incipient formation of centres, is more specialised than that of the sturgeons and approaches the axial skeleton in *Amia* and certain higher fossil Ganoids. The axial skeleton in *Glaucolepis*, however, (and consequently in *Pygopterus* also) agrees in all essential respects with that in *Acipenser*, as far as can be judged from its ossifications. The presence in *Glaucolepis* of a similar aorta canal in the abdominal region as in *Acipenser* (Goodrich 1930, Fig. 34) should especially be pointed out, as well as the close agreement existing between the axial and radial endoskeletons of the caudal fin in the two genera. In the axis of the caudal fin in both genera a series of well developed independent epichordal radials are found distally to a series of small epichordal arcuals (cf. Schmalhausen 1912, pp. 527–28, Pl. 15, Fig. 13; 1913 a, pp. 4–5, Fig. 7; Goodrich 1930, Fig. 132 a, etc.), and ventrally to the notochord there occur haemal arches and hypurals as also a few small independent radial elements (cf. Schmalhausen 1912, pp. 526–27; 1913 a, p. 65; 1913 b, pp. 752–56; Goodrich 1930, Fig. 132; Aldinger 1937, p. 158). The only difference between the axial skeletons of the caudal fin in the two genera is that the massive half-cylindrical divisions of the unpaired hypochordal ossifications from which, in *Glaucolepis*, the unpaired hypurals issue, and which correspond to the most proximal parts of the haemal arches situated farther anteriorly in the caudal region, are apparently entirely, or almost entirely, reduced in *Acipenser* (cf. Schmalhausen 1912, pp. 526–27; 1913 a, pp. 27–28; 1913 b, pp. 752–53).

Endoskeleton of the shoulder girdle.

a. Glaucolepis magna.

The material of *Glaucolepis magna* was especially well suited for studies on the endoskeleton of the shoulder girdle, and I shall therefore commence with a description of the conditions in this species.

I have dissected out the endoskeleton of the shoulder girdle in specimens Nos. 1, 6, 7, and 60, of which No. 60, is especially well preserved, exhibiting the endoskeleton of both the right and the left side entirely uncompressed. In these specimens the two halves of the endoskeleton of the shoulder girdle have been ossified each in one piece and without indications of sutures. The two ossifications consist of cancellate endochondral bone-tissue, whose surface is covered by thin perichondral bone-layers, and which in all details show the same macroscopic structure as the bones of the endocranium.

In other (smaller) specimens of *Glaucolepis magna* as well as in numerous specimens of the smaller species of *Glaucolepis*, the endoskeletal shoulder girdle is in most cases poorly preserved, which seems to be due to the less advanced process of ossification. Whether this process in the endoskeleton of the shoulder girdle, in young individuals, similarly as the process of ossification in the neural endocranium and the palatoquadrate (pp. 92, 143), begins in several areas in the cartilage of the shoulder girdle, could not be ascertained. If this be the case, we might expect to find young specimens with two or more smaller ossifications in each half of the shoulder girdle; however, the state of preservation of the young individuals did not allow a closer investigation of this point.

The completely ossified endoskeletal shoulder girdle has a very complicated shape, as is seen from Figs. 51, 52, 53, Pl. 22, Fig. 1, and Pl. 23, Figs. 1, 2.

The ossification may be described as a plate with two abrupt bends, its most dorsal part being almost vertical, while its middle part is almost horizontal, and its most ventral part is bent downwards in such a way that it has a dorso-medial convex and a ventro-lateral concave face. The figure of the ossification seen from behind (Fig. 53A) shows better than a detailed explanation the relations between the dorsal, middle, and ventral parts of the bone plate.

From the medial face of the dorsal part to the transition between the medial faces of the middle and ventral parts extends a well developed mesocoracoid arch (*msc*, Figs. 51, 53A; Pl. 23, Figs. 1, 2), which is strongly curved so, that its convexity is dorso-medially directed and its anterior margin is slightly convex and its posterior margin correspondingly concave (Fig. 53).

If the ossification is viewed from its dorso-medial side, precisely as in Fig. 51, its outline is roughly triangular, so that for descriptive purposes,

disregarding the mesocoracoid arch, we may distinguish between a posterior margin equipped with two processes, a nearly straight antero-dorsal margin, and an antero-ventral margin with two bends.

Of the two processes on the posterior margin the most dorsal one, the processus glenoidalis (*pr.gl*, Figs. 51, 52, 53A; Pl. 23, Figs. 1, 2), is the most well developed. It issues from the dorsal part of the ossification extending in a postero-ventral and slightly medial direction; its shape is seen from the figures. The other process, the processus radialis (*pr.r*, Figs. 51, 52, 53A; Pl. 23, Figs. 1, 2), issues at the boundary between the ventral and middle parts of the ossification and points in a caudal direction. Between the processus radialis and the processus glenoidalis, the posterior margin of the ossification, the margo radialis (*m.r*, Figs. 51, 52, 53; Pl. 23, Fig. 2), is so much thickened that on this part of the ossification we may speak about a caudal face, the glenoid face. On this glenoid face a number of small depressions are found which indicate the places of articulation for the radials of the pectoral fin. In several cases these radials may be observed in their original position in relation to the glenoid face.

Seen dorso-medially the antero-dorsal margin of the ossification has a fairly straight course from the most dorsal to the most anterior part of the ossification (Fig. 51).

The ossification increases considerably in breadth from its most dorsal narrow part to the boundary between its midmost and its ventral parts. The ventral part of the ossification is only half as broad as the broadest portion of the midmost part, so the antero-medial area of the midmost part forms, as it were, a very well developed process issuing in an anterior direction, as seen from Fig. 51. The shape of the ventral part of the ossification is seen clearly from the figures.

The dorsal, very concave face of the midmost part of the ossification together with the mesocoracoid arch bound a space open both anteriorly and posteriorly, which space lodged the dorsal (or dorso-medial) musculature of the pectoral fin.

Fig. 52 shows the endoskeletal ossification of the shoulder girdle in ventro-lateral view, that is to say, precisely the opposite view to that shown in Fig. 51; the outlines of the two figures are therefore almost alike. In the living animal the dorsal part of the ossification was so situated that its lateral face was in contact with the medial face of the ascending part of the cleithrum. As the anterior marginal zone of this part of the cleithrum is curved inwards (cf. p. 231) to form the posterior boundary of the branchial space, the contact face of the endoskeletal shoulder girdle ossification with the cleithrum is not plane, but curved so as to correspond to the curvature of that part of the cleithrum with which it is in contact.

Almost at the boundary between the dorsal and the middle part of the ossification a distinct rostro-caudally directed keel (k_1, Figs. 52, 53A) is

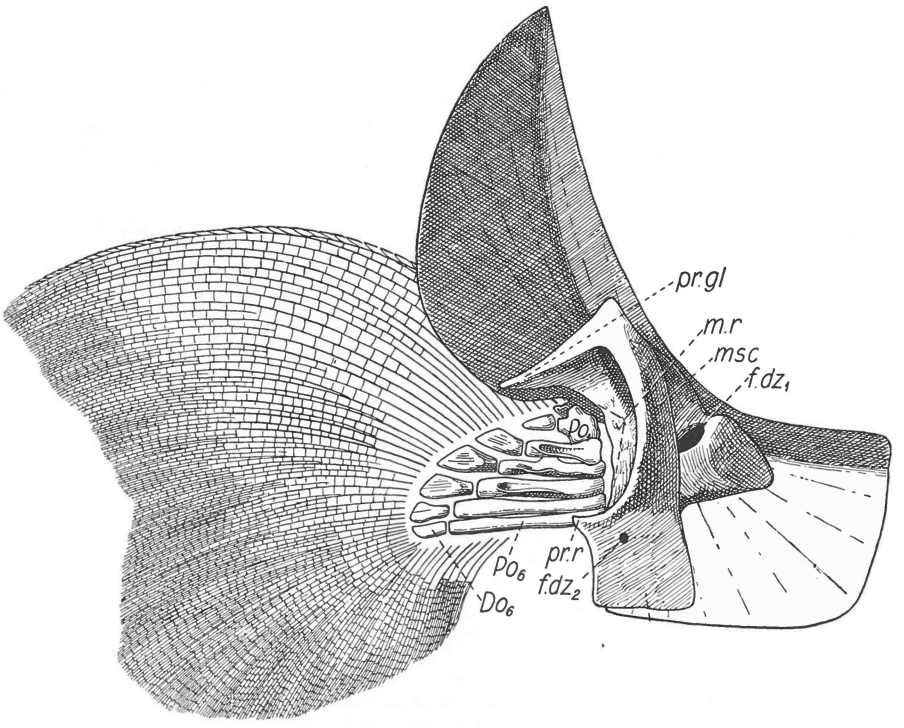


Fig. 51. *Glaucolepis magna* n. sp. Cleithrum, endoskeletal shoulder girdle ossification, and pectoral fin in dorso-medial view. The most proximal parts of the lepidotrichia omitted. Based mainly on specimen No. 60. C. 2 ×.
Do_6, most posterior distal radial ossification; Po_1, Po_6, most anterior and most posterior proximal radial ossifications; *f.* dz_1, *f.* dz_2, canals for diazonal nerves; *m. r*, margo radialis; *msc*, mesocoracoid arch; *pr. gl*, processus glenoidalis; *pr. r*, processus radialis.

found on its lateral or ventro-lateral face. The part of the surface of the ossification which lies medially or ventro-medially to this keel, in other words the ventral face of the middle part of the ossification and the ventro-lateral face of its ventral part, is not in contact with the internal surface of the cleithrum, as is seen from Fig. 53A. Only the ventral margin of the ventral part of the endoskeletal shoulder girdle ossification joins the most postero-medial part of the horizontal plate of the cleithrum. Thus between the cleithrum and the endoskeleton of the shoulder girdle a fairly large space, open anteriorly and posteriorly, is found, in which the ventral musculature of the pectoral fin was situated.

The anterior opening of this space (*f. cor. cl*, Fig. 53A) corresponds to the anterior opening of the muscle space described by Aldinger in *Pygopterus nielseni* and about which he says (1937, p. 164): "Die vordere Öffnung dieses Raums entspricht der Fenestra coraco-cleithralis der Teleostier (vgl. Ren-

dahl 1930, p. 5) und von *Lepidosteus* (vgl. Gegenbauer 1865, p. 103, Taf. VI, Fig. 5A, Starks 1930, p. 8, Goodrich 1930, Text-fig. 167), sie war wohl wie bei höheren Fischen durch eine Membran verschlossen."

The face of the endoskeletal ossification directed towards the muscle space is divided by a prominent rostro-caudally running keel (k_2, Figs. 52, 53A) into two smaller faces, both of which are concave. As is seen from Fig. 52, the most lateral one of these concave faces is bounded by the two prominent keels on the lateral or ventro-lateral face of the endoskeletal

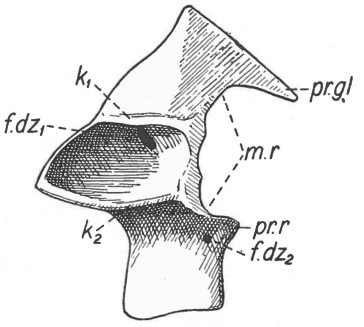


Fig. 52. *Glaucolepis magna* n. sp. Endoskeletal shoulder girdle ossification in ventro-lateral view. Based on specimen No. 60. 2 ×.
k_1, k_2, ridges on the cleithral side of the ossification. Other letters as in Fig. 51.

ossification not only laterally and medially, but also rostrally, where the two keels bend towards each other and meet at the anterior margin of the middle part of the ossification.

The presence of the keel k_2 on the roof of the muscle space seems to indicate a subdivision of the ventral fin musculature (cf. *Acrorhabdus*, Aldinger 1937, p. 285).

The ossification is pierced by two canals for diazonal nerves. The largest of these ($f.dz_1$, Figs. 51, 52, 53A; Pl. 23, Fig. 1) is elliptic in transverse section and pierces the horizontal middle part of the ossification from its dorsal to its ventral face. The other and smaller canal ($f.dz_2$, Figs. 51, 52; Pl. 23, Figs. 1, 2) pierces the ventral part of the ossification from its dorso-medial to its ventro-lateral face. The accurate position of the two canals is seen in the figures.

b. Glaucolepis arctica, gunnari, and stensiöi.

In each half of the shoulder girdle in the best ossified specimens of these species an endoskeletal ossification has been observed which, in so far the state of preservation of the material allowed an investigation, seems to be of the same shape and extent as in *Glaucolepis magna*. However, in many, notably smaller, individuals it seems beyond doubt that the endoskeleton of

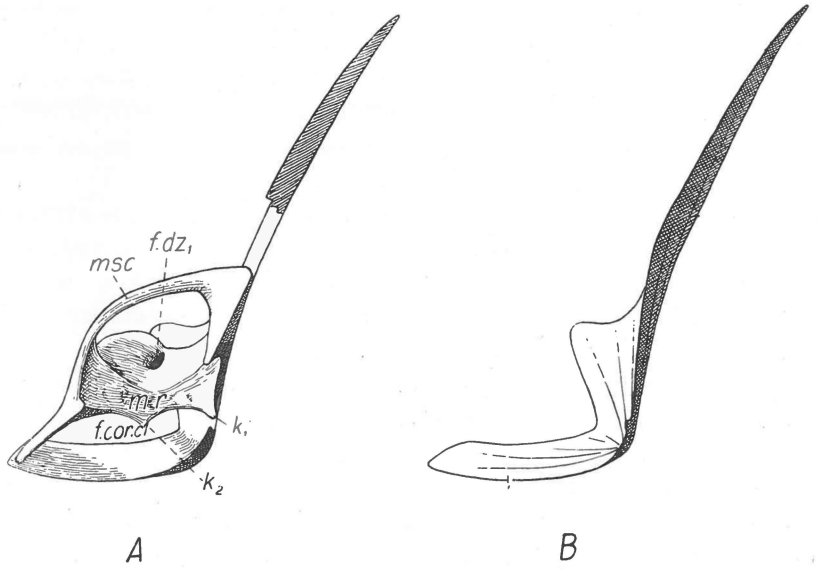


Fig. 53. *Glaucolepis magna* n. sp. Based on specimen No. 60.2 ×. A, Cleithrum and endoskeletal shoulder girdle ossification in dorsal view. Part of the vertical division of the cleithrum removed. B, Cleithrum seen from behind.
f. cor. cl, fenestra coraco-cleithralis; k_1, k_2, ridges on the cleithral side of the endoskeletal shoulder girdle ossification. Other letters as in Fig. 51.

the shoulder girdle is unossified or slightly ossified, a feature mentioned already in the description of *Glaucolepis magna*.

c. Glaucolepis aldingeri.

The shoulder region is so poorly preserved that nothing can be stated about the shape of its endoskeleton.

d. Discussion.

The endoskeleton of the shoulder girdle has been described in some detail in only a small number of genera belonging to the suborder *Palaeonisciformes*, viz. in *Acrorhabdus* (Stensiö 1921, pp. 228–230; Aldinger 1937, pp. 283–286), *Palaeoniscus* (Aldinger 1937, pp. 108–110), and *Pygopterus* (Aldinger 1937, pp. 161–164). Some interesting observations have further been made by Watson on the endoskeleton of the shoulder girdle in *Amblypterus* (Watson 1925, pp. 824–826) even though his material did not allow him to make a complete description.

Watson was able to demonstrate that in *Amblypterus* the face of the endoskeleton of the shoulder girdle against which the radials of the pectoral fin articulated, the glenoid face (margo radialis), is so situated that its longest diameter is horizontal and forms an angle of c. 45° with the longitudinal axis of the trunk.

In all the three forms described and figured by Aldinger the longest diameter of the oblong glenoid face forms an angle with the horizontal plane, in *Acrorhabdus* so "dass die Ebene der Pectoralflosse etwa im Winkel von 60° von aussen oben nach unten innen verläuft" (Aldinger 1937, p. 286). In *Pygopterus* and *Palaeoniscus* the margo radialis is even steeper, almost vertical.

In his paper on the interesting genus *Cornuboniscus*, White (1939) discusses the phylogenetic development of the pectoral fin in the Actinopterygians, and despite the fact that only very little is known about the anatomy of the pectoral fin of the fossil forms, he arranges the different fin-types known upon certain lines of development.

Similarly as *Tarassius* (Moy-Thomas 1934) and the *Polypterus* group, *Cornuboniscus* has vertical "paddle-like" pectoral fins and a vertical margo radialis. White contrasts the fin-type in these forms with the normal Palaeoniscoid fin-type, where the fin is employed as a "horizontal balancer" and the margo radialis is horizontal, as in *Lepidosteus*, *Acipenser*, and *Amblypterus*. He then writes (1939, p. 59): "– but Stensiö (1921, fig. 71), and more recently Aldinger (1937, figs. 27, 44, 84), have figured three primary girdles of Permian and Triassic Palaeoniscids, which are in the form of vertical plates: it is difficult in these cases to see how the fins functioned, unless they were held vertically, which was certainly not the case in *Palaeoniscus*, for this has the most typical of Palaeoniscoid fins, while the fin of *Pygopterus* is figured by Aldinger (fig. 37) with the base sloping downwards and forwards, which does not in any case seem likely, for this position is unknown among Actinopterygians so far as I am aware, and would tend always to depress the head of the fish instead of countering gravity by raising it, which is the effect desired."

In his criticism of Aldinger's restoration of *Pygopterus*, White is undoubtedly right; the position of the pectoral fin must have been different from that figured by Aldinger. (As Aldinger (1937, p. 163) assumed that the anterior lepidotrich of the pectoral fin in *Pygopterus* was placed in a round groove (cf. Aldinger op. cit. Fig. 44) situated dorsally to the margo radialis, his figure, which shows the position of the fin, does not agree very well with his own text.)

It has been seen above that the margo radialis in *Glaucolepis* is horizontal, and it will be evident from the below that the plane of the pectoral fin is likewise horizontal. If the close relationship between *Glaucolepis* and *Palaeoniscus* is taken into consideration, there can be no doubt that the endoskeletons of their shoulder girdles must be of roughly the same type. I assume, therefore, that Aldinger's material was insufficient for an accurate reconstruction of the endoskeleton of the shoulder girdle in *Palaeoniscus*.

If this is borne in mind, a comparison between the endoskeletons of the shoulder girdles in *Glaucolepis* and *Palaeoniscus* (Aldinger 1937, Fig. 27 A, and

B) shows that they agree in several details. Thus both genera have a well developed mesocoracoid arch, and the size and shape of both the processus glenoidalis and the processus radialis agree in the two genera.

Corresponding to the most ventral of the two longitudinal keels on the lateral face of the ossification in *Glaucolepis*, in *Palaeoniscus* a keel is found which according to Aldinger was in contact with the cleithrum. As stated above, this is not the case in *Glaucolepis*, and if the assumption mentioned above, that *Palaeoniscus* has a horizontal margo radialis, is correct, this keel must have been situated at a considerable distance from the cleithrum. However, a closer comparison of the two forms will be useless until a complete restoration of the endoskeleton of the shoulder girdle in *Palaeoniscus* is available.

A comparison with *Acrorhabdus* and *Boreosomus* will be made after the description of the latter (p. 360).

As regards the endoskeleton of the shoulder girdle, *Pygopterus* differs from *Glaucolepis* by lacking every trace of a mesocoracoid arch. Moreover, as mentioned above, the margo radialis, according to Aldinger, is nearly vertical in *Pygopterus*, while in *Glaucolepis* it is fairly horizontal. Aldinger's restoration (1937, Fig. 44A, B and C) is so detailed that there can hardly be any doubt as to the correctness of this feature, and it must therefore be assumed that the position of the pectoral fin in *Pygopterus* (as also in *Boreosomus* and *Acrorhabdus* (cf. p. 364)) was more nearly as in *Cornuboniscus*, *Tarassius*, and *Polypterus* than as in *Glaucolepis*, *Palaeoniscus*, and *Amblypterus*.

Apart from this there is a surprisingly good agreement in the details of the endoskeleton of the shoulder girdle between *Pygopterus* and *Glaucolepis*. The processus glenoidalis as well as the processus radialis are similarly developed in the two genera. In both, the ventral boundary of the dorsal part of the ossification is marked by a longitudinal keel on the cleithral side of the ossification, and immediately ventrally to this keel the ossification is pierced by a canal for diazonal nerves. *Pygopterus*, too, has a more ventral diazonal nerve canal, whose position corresponds closely to that of the smallest of the two diazonal nerve canals in *Glaucolepis*.

The two diazonal nerve canals in *Pygopterus* and *Glaucolepis* correspond, according to their position, entirely to the two diazonal nerve canals in the endoskeleton of the shoulder girdle of *Lepidosteus* (cf. Goodrich 1930, Fig. 173).

In *Lepidosteus* and *Amia* the anterior diazonal nerves pass through a canal piercing the mesocoracoid arch, and the ventral nerve branches then continue through the most dorsal of the two aforementioned diazonal nerve canals. In *Glaucolepis* as in the recent *Chondrostei* and *Teleostei* (Goodrich 1930, pp. 167–168), however, the anterior diazonal nerves entered the space between the mesocoracoid arch and the remaining part of the ossification through the anterior opening of this space.

Dermal bones of the shoulder girdle.

a. Glaucolepis magna.

The series of dermal bones of the shoulder girdle consists, as normally, of a suprascapular, a supracleithral, a cleithrum, a clavicle, and, behind the ventral part of the supracleithral and the dorsal part of the cleithrum, a postcleithral.

The suprascapular (*Sscap*, Figs. 22, 30; Pl. 9, Fig. 1) is a rounded triangular bone with a lateral, a postero-medial, and an anterior margin. The lateral and postero-medial margins are convex, the anterior margin nearly straight. The bone is slightly curved in a transverse direction, its external face being accordingly slightly convex and its internal face correspondingly concave. The shape of the bone is shown in the figures. The elements of the extrascapular series overlap by their posterior parts the anterior part of the suprascapular, as will be seen from Fig. 22. The connection between the extrascapular series and the suprascapular was rather loose.

The suprascapular is pierced by the main lateral line, which passes through the centre of radiation of the bone; the position of this centre corresponds entirely to that of *Glaucolepis stensiöi* (Fig. 20).

The supracleithral (*Scl*, Fig. 30; Pl. 9, Fig. 1) is a long and narrow bone with the following margins: a long postero-dorsal margin, whose middle part is slightly concave, while its dorsal and ventral parts are slightly convex; a short ventral or postero-ventral convex margin; a long antero-ventral straight margin, in Fig. 30 largely concealed below the posterior part of the operculum; a very short, straight, anterior margin; and a somewhat longer dorsal margin. Further details in the outline of the bone are seen from Fig. 30. The rather short dorsal margin adjoins the posterior half of the lateral margin of the suprascapular, while the short anterior margin joins the small postspiracular bone.

The centre of radiation of the supracleithral lies in the postero-dorsal part of the bone, and is pierced by the main lateral line, which traverses this bone in the usual way.

The ventral part of the cleithrum (*Cl*, Figs. 30, 44, 51, 53A and B, 54A and B; Pl. 9, Fig. 1; Pl. 22, Fig. 1; Pl. 23, Fig. 1) is curved in a medial direction in relation to the remaining part of the bone, so that in broad features the bone falls into two divisions, viz. a dorsal division, which is almost vertical, and a ventral division, which is almost horizontal.

The dorsal division has a strongly convex posterior margin (Fig. 54A); the regularity of its arch is broken by a small deep notch in the ventral part of the margin. Through this notch the anterior lepidotrichia of the pectoral fin passed. Furthermore the dorsal division has a concave antero-dorsal margin, which farthest dorsally meets the posterior margin at a very acute angle, and finally a short anterior margin. The most ventral part of

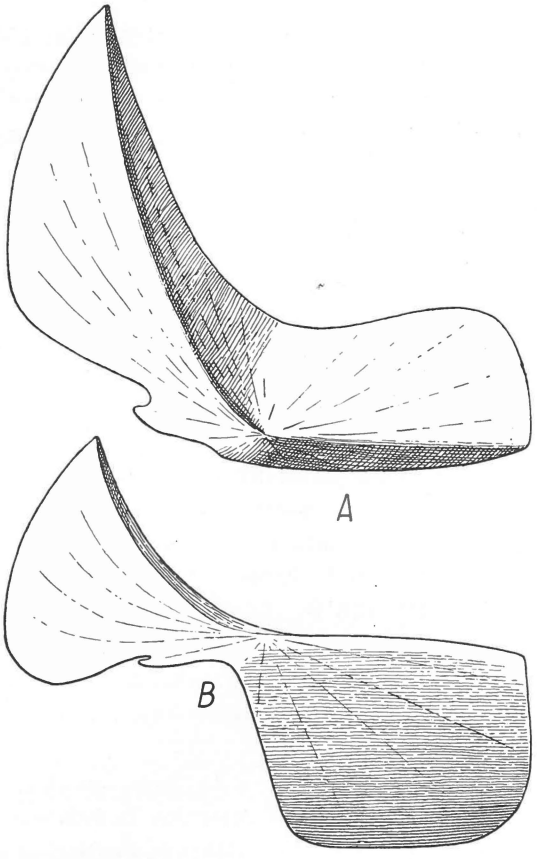


Fig. 54. *Glaucolepis magna* n. sp. Cleithrum. Based on specimen No. 60. 2 ×. A, lateral view. B, ventral view.

the dorsal division of the cleithrum bends in a medial direction, forming the transition to the ventral division.

Only a part of the lateral face of the dorsal division is ornamented and exposed in the living fish, viz. roughly speaking that part which lies behind a line running from the dorsal point of the cleithrum in an antero-ventral direction to the posterior part of the transitional area between the ventral and dorsal divisions. The ornamented face of the dorsal division of the cleithrum lying behind this line is slightly convex in a rostro-caudal, and slightly concave in a dorso-ventral direction, and as a whole directed laterally and slightly postero-ventrally. The unornamented, or nearly unornamented, anterior part of the dorsal division of the cleithrum curves inward, as seen from Figs. 53A and B and 54A, to form the posterior boundary of the branchial cavity.

The ventral division of the cleithrum is nearly rectangular in outline, as will be seen from Fig. 54B. This roughly horizontal part of the cleithrum is

so arched that its ventral face is convex and its dorsal face partially concave. That its dorsal face must be termed partially concave, is due to the presence of a broad and very low ridge, which runs from the postero-lateral towards the antero-medial point of the face, breaking its concavity. The ridge is highest and broadest in its postero-lateral part and decreases forwards in both these dimensions so that it fails to reach the antero-medial corner of the horizontal part of the bone.

The position of the centre of radiation of the cleithrum is seen from Fig. 54A and B.

As mentioned above, the endoskeletal ossification of the shoulder girdle has contact with the internal face of both the dorsal and the ventral division of the cleithrum. The lateral face of the dorsal part and the antero-dorsal marginal zone of the lateral face of the middle part of the endoskeletal ossification are in contact with the dorsal division, and the ventral margin of the endoskeletal ossification with the ventral division of the cleithrum. As will be seen from Fig. 51, this area of contact is situated on the postero-medial part of the dorsal face of the ventral division of the cleithrum at a very short distance from and parallel with the medial margin of this face. Since the right and the left cleithrum do not touch each other, there is no contact between the right and left endoskeletal shoulder girdle ossifications; but the distance between them has been inconsiderable, and probably they were connected by a ligament.

The ventral part of the clavicle (*Cla*, Figs. 30, 44; Pl. 22, Fig. 1; Pl. 23, Fig. 1) is curved in a medial direction in relation to the remaining part, so that the clavicle, like the cleithrum, consists of a dorsal, nearly vertical, and a ventral, fairly horizontal division.

The horizontal ventral division of the clavicle is bounded by a long medial, a short postero-lateral, and an even shorter anterior margin. Laterally it passes into the dorsal ascending division of the bone. Fig. 44 shows the ventral divison of the clavicle in ventral view. In the figure this division is triangular in outline, however, this is because a small anterior part of the division is concealed by the branchiostegal rays so that the very short anterior margin of the division is not visible. The ventral division of the clavicle is slightly curved, so that its ventral face is convex from side to side.

The right and left clavicles meet medially, as will be seen from Fig. 44, but were hardly very intimately connected, for they are rarely found in their natural mutual position. In *Acrorhabdus bertili* the connection between the right and left clavicles seems to have been more intimate, for Stensiö's figure (1921, Fig. 74B) shows an irregular suture between their ventral divisions. In *Hyllingia* the two clavicles are stated to be firmly fused (Aldinger 1937, pp. 271–72, Fig. 80).

In lateral view the vertical dorsal division of the clavicle is triangular in outline, with a long dorsal or antero-dorsal and a short posterior margin,

while the third side of the triangle is the boundary line between the vertical and the horizontal division of the bone. The dorsal angle of the vertical triangular part of the clavicle is produced into a very long postero-dorsally pointing process, whose outline is seen from Pl. 23, Fig. 1.

The relations of the clavicle to the cleithrum were as follows: the posterior part of the horizontal division of the clavicle covered ventrally the anterior part of the horizontal division of the cleithrum, and the posterior part of the vertical division of the clavicle covered laterally the anterior part of the vertical division of the cleithrum.

The centre of radiation of the clavicle lies on the boundary line between its dorsal and ventral divisions and much nearer the posterior end of this line than its midpoint.

In *Acrorhabdus bertili* (Stensiö 1921, p. 229, Fig. 74) a process, *prc* is found on the anterior part of the dorsal margin of the clavicle, and in front of and behind this process a distinct emargination is seen in the dorsal margin. The dorsal margins of the right and left clavicles are in contact by means of this process. According to Stensiö (1921, p. 230, Fig. 75) a corresponding process is found on the dorsal margin of the clavicle in *Acipenser ruthenus*, and as in *Acrorhabdus* this process is in contact with the corresponding process on the other side. From the presence of this process in *Acrorhabdus* Stensiö concludes that the musculus coraco-arcualis was divided into two parts, as in *Acipenser*.

No trace of such a process is found in *Glaucolepis magna*.

The postcleithral (*Pcl*, Fig. 30) is a small dermal bone situated directly behind the dorsal part of the cleithrum and the ventral part of the supracleithral so that its anterior margin is overlapped by these two bones. The postcleithral is but slightly larger than the flank scales of the trunk lying nearest behind it; the outline of its exposed part is seen from the figures. Its connection with the supracleithral and the cleithrum was not particularly intimate.

The dermal bones of the shoulder girdle are ornamented in a way similar to those of the head.

b. Glaucolepis aldingeri, arctica, gunnari, and stensiöi.

The dermal bones of the shoulder girdle differ neither in shape nor number from the corresponding bones in *Glaucolepis magna*. In each of the four species the ornament of the shoulder girdle is of the same type as the ornament of the head.

Pectoral Fin.

a. Glaucolepis magna.

Within the material of *Glaucolepis magna* the endoskeleton of the pectoral fin was accessible for investigation notably in specimens Nos. 1, 6, 7, and 60, but remnants of the endoskeleton could be observed in several other specimens, too.

The radial endoskeleton of the fin presents a proximal and a distal series of ossifications. The elements of each of the two series consist of cancellate endochondral bone surrounded by thin perichondral bone-layers.

The proximal series consists of six ossifications (Po_{1-6}, Fig. 51; Pl. 22, Figs. 1, 2), which by their proximal cartilage-lined ends articulate with the horizontal margo radialis of the endoskeletal shoulder girdle ossification. (In the restoration shown in Fig. 51 the proximal radial series has been placed at a too great distance from the margo radialis in order not to conceal the details in the outline of that margin).

The various elements of the proximal series of radial ossifications lie so close to each other that an exhaustive examination of the details of their shape can only be made by destroying parts of the series. The well preserved pectoral fins are so few in number that I would not employ that procedure, so the shape of the individual proximal radial ossifications shown in the restoration should perhaps to some extent be regarded as sketchy. The following description of the proximal radial ossifications records the details it has been possible to observe.

The first (anterior) proximal radial ossification is a short, thick bone of a rather irregular shape, which seems to be subject to some variation from specimen to specimen. The greatest length of the bone is almost equal to its breadth, and as far as I can judge, its thickness is considerable. On its distal end a process is found with a flattened articular face, with which the first radial ossification of the distal series articulated. Between the base and the distal articular face, on the anterior margin of the bone, another process is found against which the anterior lepidotrich of the fin articulated.

The second proximal radial ossification is about one and a half times as long as the first one, and more slender. Proximally this bone has a considerable breadth, but it narrows in a distal direction through its proximal half, to grow broader again farther distally, as is seen from Fig. 51. This one, like the other proximal radial ossifications, is terminated distally by a fairly plane terminal face, against which the proximal end of a distal radial ossification articulated. On the dorsal face of the bone a vertical longitudinal ridge of considerable height is found. This ridge served as place of insertion for some muscles. The ventral face of the second proximal radial ossification is evenly convex from side to side.

The third proximal radial ossification is somewhat longer than the second one, but in the main of the same shape. Its proximal end is narrower than the proximal end of the second radial ossification, and its dorsal longitudinal ridge is even higher than that found on the second radial ossification. Besides, a fairly well developed process, which ends ventrally to the second radial ossification, issues from the side turned towards the second radial ossification, at right angles to the longitudinal axis of the bone. This process possibly served as a place of insertion for some muscles, but at the same time counteracted any very great movements of the second radial ossification in relation to the third one.

The fourth proximal radial ossification is somewhat longer than the third one, and has in the main the same shape; however, it has no transverse process. The dorsal longitudinal ridge is a little lower than in the third proximal radial ossification.

The fifth proximal radial ossification is a little longer than the fourth one, from which it differs in that its dorsal longitudinal ridge is very low.

The sixth proximal radial ossification is a little longer than the fifth one, and it is the most slender element within the proximal series. It has no dorsal longitudinal ridge.

The number of radial ossifications in the distal series corresponds to the number of ossifications in the proximal series, a distal radial ossification corresponding to each proximal radial ossification (Do_{1-6}, Fig. 51; Pl. 22, Figs. 1, 2).

The first and second distal radial ossifications are about two-thirds the length of the first and second proximal radial ossifications respectively. The succeeding distal radial ossifications decrease in length in relation to the corresponding proximal ones from the third to the sixth ossification. The length of the sixth distal radial ossification is only about one-fifth of that of the sixth proximal one. The most proximal part of each of the distal radial ossifications is almost circular in transverse section, while the distal part is flattened dorso-ventrally so that each distal radial ossification ends distally in a sharp edge running obliquely in relation to the longitudinal axis of the bone, as shown in Fig. 51.

In the undisturbed pectoral fin the proximal ends of the lepidotrichia entirely conceal the distal radial ossifications; these proximal ends of the lepidotrichia are not shown in Fig. 51.

The two series of radial ossifications together acted nearly as a stiff plate, as the possibilities of the individual elements for moving in relation to each other must have been extremely slight. This plate was almost horizontally placed, and only its most proximal part lay in the very trunk of the fish, while its distal and larger part supported a well developed scaly fin lobe.

The number of lepidotrichia is mostly difficult to ascertain, as the pectoral fin is rarely expanded because the fishes are most frequently compressed

from the side. According to observations made on several specimens, the fin seems to have contained some 45 to 50 closely set lepidotrichia in fan-shaped arrangement, as shown in the restoration represented in Fig. 51. In the complete fin the proximal ends of the lepidotrichia cover, both dorsally and ventrally, partly the distal radial ossifications and partly the distal half of the sixth proximal radial ossification. The segmentation of the individual lepidotrichia and the subdivision of their distal parts are seen clearly from the restoration.

The most anterior lepidotrich articulated with the aforementioned process on the anterior proximal radial ossification, and is rather short. The succeeding lepidotrichia increase rapidly in length, so that already the fourth or fifth is the longest of the fin and of about the same length as the mandible of the fish. The following lepidotrichia decrease gradually in length to about the 25th lepidotrich, and from here they increase in length to about the 35th one, after which they decrease again in length towards the most posterior one. On account of the varying length of the lepidotrichia the distal margin of the fin has a peculiar course, as will be seen from Fig. 51. The anterior margin of the fin is equipped with from 50 to 60 small fulcra.

The exposed part of the individual lepidotrichia is equipped with a continuous layer of ganoine raised in striae. The striae are occasionally divided into rows of small tubercles. The direction of striation when the fin is expanded as shown in Fig. 51, is fairly parallel with the longitudinal axis of the trunk. In some specimens this system of striae is very indistinct or entirely lacking on the three to five anterior lepidotrichia, which are then provided with some few short striae, largely parallel with the longitudinal axis of the lepidotrichia in question.

b. Glaucolepis gunnari.

The endoskeleton of the pectoral fin is well ossified and agrees in all essentials with that of *Glaucolepis magna*. In specimen No. 170 (Pl. 11) the proximal parts of the fifth and sixth proximal radial ossifications are fused.

The pectoral fin contains 35 to 40 close-set lepidotrichia, which agree in all essentials (ornament, segmentation, and subdivision) with those of the pectoral fin in *Glaucolepis magna*. The course of the distal fin margin cannot be observed in this species.

c. Glaucolepis stensiöi.

The endoskeleton of the pectoral fin is well ossified, but could not be exposed so that it could be examined in detail.

The fin contains about 35 to 40 close-set lepidotrichia, and agrees in all respects with the pectoral fin in *Glaucolepis magna* except that the ganoine-layer of the lepidotrichia is apparently smooth.

d. Glaucolepis arctica.

The endoskeleton of the pectoral fin is well ossified, but could not be investigated in detail.

The pectoral fin contains about 35 to 40 close-set lepidotrichia. It agrees in size, outline, and other details with that of *Glaucolepis magna*, except for the ganoine-layer of the lepidotrichia, which is apparently smooth. The number of fulcra on the anterior margin of the fin ranges between 40 and 50.

e. Glaucolepis aldingeri.

The pectoral fin is too poorly preserved to allow an investigation of the details of its exo- or endoskeleton.

f. Discussion.

Extremely few and very incomplete descriptions of the endoskeleton of the pectoral fin in the *Palaeonisciformes* are found in the earlier literature. The conditions are best known in *Tarassius* (Moy-Thomas 1934, p. 372, Fig. 4), *Cornuboniscus* (White 1939, pp. 48–49, Fig. 4), *Cheirolepis* (White 1939, p. 55, Fig. 10), and *Amblypterus* (White 1939, p. 55, Fig. 11). These forms have a series of proximal radial ossifications, which in *Tarassius*, *Cornuboniscus*, and *Cheirolepis* lie nearly parallel, while the conditions in *Amblypterus* are more specialised owing to the presence of a metapterygial axis. In none of these forms have distal radial ossifications like those found in *Glaucolepis* been ascertained, but White assumes (1939, p. 49) that cartilaginous distal radial segments existed in *Cornuboniscus*, and Aldinger (1937, pp. 166 and 286) assumes the existence of a distal radial series in *Pygopterus nielseni* and in *Acrorhabdus bertili*.

In 1939 White, as already stated, discussed the evolution of the pectoral fin within the Actinopterygian group. On considering the pectoral fins of the most primitive Actinopterygians, White arrives at the result that their endoskeleton shows not the faintest trace of the axis which we might expect to find according to the common conceptions of the fin of Actinopterygians (Goodrich 1930, pp. 149–58). According to White the most primitive pectoral fin of the *Palaeonisciformes* had a large basal lobe supported by numerous parallel radials but without any basal elements comparable to the basipterygia of the Selachians. From this primitive fin, which was expanded in a horizontal plane, White supposes that the evolution proceeded upon several lines.

One line leads to the *Cheirolepis* fin by reduction in number of radials and by an increase in breadth of the remaining radials. Another line leads

to a vertical fin with a well developed lobe (*Cornuboniscus*, *Tarassius*, *Polypterus*). A third line leads over the *Stegotrachelus* and *Lepidosteus* fin towards the Teleost fin by a reduction of the number of radials and by an irregular development of the remaining ones, but with retention of the parallelism of the radial elements. Within the fourth line (*Amblypterus*, *Acipenser*, *Amia*) there arises what is termed by White a false "metapterygial" axis by "the elimination of the hinder radials by the forward movement of the hindmost, or more likely by the fusion of the hinder radials, as certainly happens in the pelvic fins of Sturgeons" (White 1939, p. 57). That White terms this axis false, only means that the axis originated within the Actinopterygian group and cannot, therefore, be homologised with the fin axis in Elasmobranchs and Choanates. In principle it is formed in the Actinopterygians, as in other groups, by fusion of radial elements, but naturally it hardly comprises entirely the same area of the radial skeleton in the different groups.

The horizontal pectoral fin just described, whose well developed scaly lobe is supported by parallel, irregularly developed radial elements, must be situated in the line which White draws from the primitive *Palaeonisciformes* fin over the *Lepidosteus* fin to the Teleost fin. The close agreement with *Lepidosteus* is conspicuous as regards the endoskeletons of both the fin and the shoulder girdle (cf. Goodrich 1930, Fig. 173).

Pelvic plate and pelvic fin.

In only some few of the Greenland specimens of *Glaucolepis* the pelvic plate and the radial skeleton of the pelvic fin are found in such a state of preservation that it is possible to make a detailed investigation of these elements. This probably means that the endoskeleton of the pelvic fin is rarely ossified, which is perhaps to some extent due to the small size of the pelvic fin. When the endoskeleton is ossified, the individual ossifications consist of cancellate endochondral bone lined with perichondral bone-layers.

a. Glaucolepis gunnari.

The endoskeleton of the pelvic fin is well ossified in specimen No. 3, which is otherwise remarkable in that the elements of the axial skeleton are more completely ossified than in any other specimen of *Glaucolepis gunnari*.

The endoskeleton of each pelvic fin consists of a pelvic plate, a small metapterygial ossification, and a series of proximal radial ossifications (Fig. 55A; Pl. 21, Figs. 1, 3).

The pelvic plate (*Pv*, Fig. 55A; Pl. 21, Figs. 1, 3) is an oblong, rather thin plate, whose antero-medial corner is produced into a long and slender process (*pr*) pointing in an antero-medial direction. The distal and greater

part of the process was lost during the preparation. Apart from the process, the pelvic plate, whose exact outline will be seen from Fig. 55 A, has a lateral, an anterior, a medial, and a posterior margin. The dorsal and the ventral face of the plate are convex from side to side in such a way that the greatest thickness of the plate lies nearer its medial than its lateral margin. On the ventral face of the pelvic plate five or six groove-like depressions are found, which extend, parallel with each other, in an antero-medial direction from the lateral to the medial margin of the plate (E. Nielsen 1936, p. 43). According to Aldinger (1937, p. 168), similar low depressions are found on the ventral face of the pelvic plate in *Birgeria* (cf. Stensiö 1921, Pl. 23, Fig. 3) as also in the recent sturgeons, where their presence is due to the pelvic plate being formed by fusion of several elements. Corresponding to the depressions on the ventral face of the pelvic plate in *Glaucolepis*, small emarginations occur in the lateral and medial margins of this plate, as will be seen from Fig. 55 A.

Immediately behind the posterior margin of the pelvic plate lies a very small four-sided separate metapterygial ossification (*Mt*, Fig. 55 A; Pl. 21, Fig. 1), which is somewhat longer than broad.

Eight proximal radial ossifications are present (*Po*, Fig. 55 A; Po_1, Po_6, Po_8, Pl. 21, Figs. 1, 3), which were probably capped by cartilage both proximally and distally. The six anterior ones articulated with the lateral margin of the pelvic plate, and the foremost of these articulations took place rather far behind the antero-lateral corner of the pelvic plate.

The seventh proximal radial ossification articulated either with the posterior part of the lateral margin of the pelvic plate or with the lateral margin of the independent metapterygial ossification. The eighth proximal radial ossification articulated with the posterior part of the metapterygial ossification. The anterior three radial ossifications are rather short, but after the third one the ossifications increase in length till the eighth, which is about three times as long as the three anterior ones; the third and the fourth are broader than the remaining ones, and distally have two terminal surfaces each. The three posterior ones are curved so that their anterior margins are convex and their posterior margins concave.

No ossified distal radial ossifications, as in *Birgeria* (Stensiö 1921, p. 193), *Saurichthys* (Stensiö 1925, pp. 122–23), *Boreosomus* (p. 367), are present, but probably unossified distal radial elements were attached to the proximal radial ossifications.

In specimen No. 18 the pelvic fin contains c. 18-20 lepidotrichia. It can be observed that these lepidotrichia are segmented to their base, that the anterior margin of the fin is equipped with a number of small fulcra, and that the exposed faces of the lepidotrichia are covered by ganoine and strongly ornamented. The ornamental elements are mainly close-set striae, whose direction in relation to the longitudinal axes of the lepidotrichia

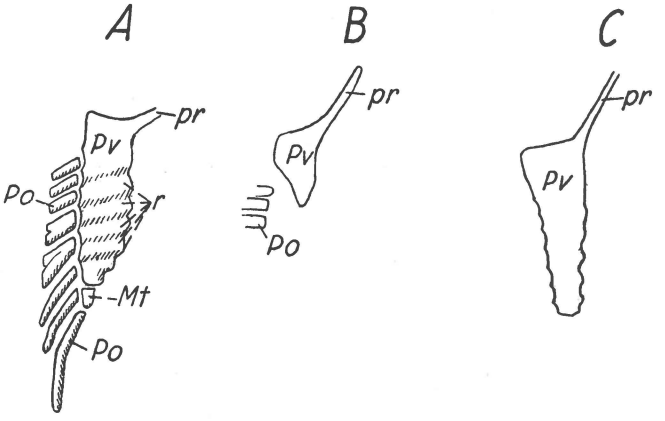


Fig. 55 A, *Glaucolepis gunnari* n. sp. Pelvic plate and endoskeleton of pelvic fin in ventral view. Based on specimen No. 3. 2 ×. B, *Glaucolepis arctica* Stensiö. Pelvic plate and remnants of endoskeleton of pelvic fin in ventral view. Based on specimen No. 64. 2 ×. C, *Glaucolepis aldingeri* n. sp. Pelvic plate in dorsal view. Based on specimen No. 66. 2 ×. *Mt*, metapterygial element; *Po*, proximal radial ossification; *Pv*, pelvic plate; *pr*, antero-medially directed process of the pelvic plate; *r*, low ridges on the ventral face of the pelvic plate.

corresponds to the direction of the striation of the exposed faces of the lepidotrichia of the dorsal and the anal fin.

It is impossible to observe the shape of the fin and the precise number of scale-rows between its anterior margin and the posterior margin of the supracleithral. All that could be ascertained concerning these conditions is that the fin is very small, and that it is situated about midway between the anal fin and the pelvic fin.

b. Glaucolepis arctica.

In specimen No. 64 the endoskeleton of the pelvic fin could be exposed. The pelvic plate is a four-sided plate, whose antero-medial corner is produced into a long, slender, antero-medially directed process, as will be seen from Fig. 55B. A comparison between Figs. 55B and 55A shows that the pelvic plate in *Glaucolepis arctica* corresponds to the anterior part of the pelvic plate in *Glaucolepis gunnari*. Of the proximal radial series, only the proximal part of the anterior three radial ossifications are preserved in specimen No. 64. Judging from the position of these ossifications in relation to the pelvic plate, they articulated either with an unossified posterior division of the pelvic plate or with independent metapterygial elements, which continued the ossified pelvic plate in a caudal direction.

Judging from specimens Nos. 69, 71, and 154, there are about 14 transverse rows of scales between the anterior margin of the pelvic fin and the posterior margin of the supracleithral. In specimen No. 154 the fin con-

tains 17 closely set lepidotrichia, which are segmented right to their base. The most anterior lepidotrich is very short, the succeeding ones increase in length till Nos. 5 or 6, which is the longest in the fin. The number of segments of the longest lepidotrich is about ten. After Nos. 5 or 6 the remaining lepidotrichia decrease gradually in length in such a way that the outline of the fin is almost like that of the much larger dorsal fin. With the exception of the four or five anterior ones, all the lepidotrichia of the fin are covered with ganoine, whose surface is probably smooth. Stensiö (1932. p. 122) states about the posterior lepidotrichia that they are ornamented with two longitudinal striae of ganoine.

The anterior margin of the fin is provided with about fifteen small fulcra.

c. Glaucolepis stensiöi.

Remnants of proximal radial ossifications can be observed, but otherwise nothing can be stated about the endoskeleton of the pelvic fin.

Number of transverse scale-rows between the anterior margin of the pelvic fin and the posterior margin of the supracleithral (in this and in the following lists the most reliable figures are in italics):

Specimen	No.	38	Number	of	scale-rows	21
–	–	48	–	–	–	18
–	–	49	–	–	–	*20*
–	–	95	–	–	–	*14*
–	–	97	–	–	–	18–19
–	–	98	–	–	–	16
–	–	103	–	–	–	*20*
–	–	108	–	–	–	14
–	–	113	–	–	–	22

Number of lepidotrichia in the pelvic fin:

Specimen	No.	48	Number	of	lepidotrichia	*22–24*
–	–	49	–	–	–	*21*
–	–	97	–	–	–	19
–	–	106	–	–	–	23
–	–	108	–	–	–	21
–	–	109	–	–	–	20

As regards the length, segmentation, and division of the lepidotrichia and the shape of the fin *Glaucolepis stensiöi* agrees with *Glaucolepis arctica.*

The exposed faces of the lepidotrichia are covered with ganoine, whose surface is probably smooth.

d. Glaucolepis aldingeri.

The pelvic plate and the radial skeleton of the pelvic fin can be observed in specimen No. 66. The pelvic plate (*Pv*, Fig. 55C; Pl. 24) on the whole corresponds in extent to that of *Glaucolepis gunnari*, from which, as will be seen from the figure, it differs only by being broader in its anterior part. Probably an independent metapterygial element has been situated behind the pelvic plate, but this element is not preserved. The proximal radial series includes eight ossifications (*Po*, Pl. 24), the posterior two of which are incompletely preserved. These radial ossifications are relatively longer than in *Glaucolepis gunnari,* and apparently all of them are more or less curved, their anterior margins being convex and their posterior margins accordingly concave. No trace of distal radial ossifications is found.

In specimen No. 148 16 to 18, and in specimen No. 66 at least 16, transverse rows of scales are found between the posterior margin of the supracleithral and the anterior margin of the pelvic fin.

In specimen No. 66 the number of lepidotrichia is about 18, the longest of which has twelve or thirteen segments. As far as I can make out, the anterior lepidotrich of the fin articulated with the anterior part of the lateral margin of the pelvic plate, while the remaining lepidotrichia covered the distal third of the proximal radial ossifications.

The exposed faces of the lepidotrichia, at any rate in the greater part of the fin, are covered by a smooth layer of ganoine.

e. Glaucolepis magna.

No information can be given about the pelvic fin or its endoskeleton.

f. Discussion.

Within the fossil *Chondrostei* the endoskeleton of the pelvic fin is fairly completely known only in *Birgeria mougeoti* (Stensiö 1921, pp. 192–99, Fig. 68), *Saurichthys ornatus* (Stensiö 1925, pp. 122–31, Fig. 28), and *Pygopterus nielseni* (Aldinger 1937, pp. 166–74, Fig. 45). With these forms as a point of departure, Stensiö (1921 and 1925) and Aldinger (1937) discuss at great length the endoskeleton of the pelvic fin in the Actinopterygians, and draw comparisons with the conditions in the Elasmobranchs.

Glaucolepis agrees in all essentials with *Pygopterus* as regards the endoskeleton of the pelvic fin, and thus supplies no fresh contributions to the elucidation of the development of that structure in the Actinopterygians. Hence it is fully sufficient to draw a comparison here between the endoskeletons of the pelvic fin in *Glaucolepis* and in *Pygopterus*.

In *Glaucolepis gunnari* and *Glaucolepis aldingeri* a very long pelvic plate is present which shows indications of having been formed by fusion of a series of smaller elements, and in *Glaucolepis gunnari* a small metapterygial element has been observed behind this plate. In *Pygopterus nielseni* the pelvic

plate is much shorter and corresponds fairly well in shape with the anterior part of the pelvic plate in these two species of *Glaucolepis;* behind the pelvic plate in *Pygopterus nielseni* lies a long series of independent metapterygial elements (Aldinger 1937, Fig.45). It is quite evident that the difference between this part of the endoskeleton of the pelvic fin in the two above-mentioned species of *Glaucolepis* and *Pygopterus* is that in *Glaucolepis* all the metapterygial elements which are free in *Pygopterus,* have fused with the pelvic plate.

In *Glaucolepis arctica* the pelvic plate is much shorter than in *Pygopterus,* and can only correspond to the anterior part of the plate in the latter genus. It must be assumed that in *Glaucolepis* the bony pelvic plate was continued in a caudal direction by cartilage, or that an even longer series of independent, probably unossified, metapterygial elements than in *Pygopterus* was situated behind it.

Both in *Pygopterus* and *Glaucolepis* a series of proximal radial ossifications is found, whose relations to the pelvic plate plus the metapterygial series are alike in the two genera.

Thus, as regards the conditions of the pelvic plate and the metapterygial elements *Pygopterus* is more primitive than *Glaucolepis,* if we may conclude from the few specimens in which these ossifications are known. But it should be pointed out that further finds of *Pygopterus nielseni* will possibly bring to light a pelvic plate of the same extent as that described here from *Glaucolepis gunnari,* and that further finds of younger specimens of the *Glaucolepis* species may possibly show a relatively short pelvic plate, continued caudally by a series of independent ossified metapterygial elements. Furthermore it should be pointed out that the differences in the shape of the pelvic plate observed in *Glaucolepis arctica, gunnari,* and *aldingeri* cannot claim to be specific differences as long as the pelvic plate of only a single specimen of each of these three species is known.

Unpaired fins.

a. Glaucolepis aldingeri.

Among the few specimens known of this species, No.66 (Pl.24) shows especially plainly the structural details of the dorsal and the caudal fin. Besides on specimen No.66 the following description of the anal fin is based on specimen No.179.

The exact number of transverse rows of scales present between the hind margin of the supracleithral and the anterior margin of the dorsal fin cannot be stated, but judging from specimen No.148 it exceeds 40.

The endoskeleton of the dorsal fin is excellently preserved and consists of numerous radials each including three ossifications, viz. an axonost, a baseost, and a small distal ossification. As is well known, a similar segmentation

of the radial skeleton is found within the greater number of the Actinopterygians, even though the distal segment has not previously been observed in the *Palaeonisciformes* (The endoskeleton of the dorsal fin shown in Fig. 50 has been drawn after specimen No. 66).

The individual ossifications are made up of endochondral cancellate bone lined with perichondral bone-layers.

The axonost series consists of nine elements (*Ax, Ax. pl,* Fig. 50; Pl. 24), the most caudal of which is formed by fusion of a fairly large number of axonosts. The foremost three axonosts are relatively long and slender and very slightly S-shaped, as shown in Fig. 50. They are not vertically placed, but are inclined backward, forming an angle of only about 30° with the horizontal plane. Farther posteriorly in the axonost series the axonosts to and including No. 8 grow steeper and steeper and at the same time shorter and shorter. These first eight axonosts are narrowest in the middle, increasing in breadth downward and, in an even higher degree, upwards. Notably the dorsal part of the seventh and the eighth attains a considerable breadth, as seen from Fig. 50.

The hindmost ossification in the axonost series is a large plate, which is broader than high. The irregular outline of this bone plate will appear from Fig. 50. Its ventral margin is equipped with three well developed long processes pointing in a postero-ventral direction, and between the foremost two of these, a fourth, very short, process is found. The four processes must represent the ventral free ends of four axonosts, whose dorsal parts are contained in the large plate-shaped ossification.

Since each of the anterior free axonosts is continued distally by a baseost, and five baseosts are situated distally to the compound axonost plate, it is probable that besides the four axonosts whose ventral parts can still be observed, the plate includes a fifth, which has entirely fused with the axonost plate. Apart from the ventral processes just mentioned the axonost plate shows no trace, either in shape or structure, of having originated by fusion of several elements.

Fusion of the hindmost axonosts of the dorsal fin has been described by Aldinger (1937, p. 175, Figs. 42, 47) in *Pygopterus nielseni,* though the boundaries between the individual axonosts of which the axonost plate is made up in this form, are still indicated in the structure of the plate. Judging from material not yet described, *Birgeria groenlandica* has likewise an axonost plate formed by the caudal elements of the axonost series, and within the group *Pholidopleuridae* the hindmost elements of the axonost series of the dorsal fin are united into a large plate in *Australosomus kochi* (Stensiö 1932, p. 177, Fig. 56). Within the Rhipidistids and the Coelacanthids even more extensive fusions of elements in the radial skeleton of the unpaired fins are known (cf. e.g. Stensiö 1932, pp. 65–70).

Judging from the preserved parts of the axial skeleton, in *Glaucolepis*

aldingeri two axonosts correspond to each metamere in that part of the trunk upon which the dorsal fin is situated. The same is the case in *Pygopterus nielseni,* and in his description of this form Aldinger (1937, pp.177–78) deals with the question whether the polymery ascertained in the radial skeleton of the dorsal fin (and the anal fin, too) is original or is due to concentration of this fin. Aldinger is inclined to assume that the polymery is due to concentration; he finds support for this view in the structure of the endoskeleton of the anal fin, in which the foremost radial elements point in an antero-dorsal, and the hindmost one, in a postero-dorsal direction. In *Glaucolepis,* as we shall see below, a similar change of direction of the radial elements takes place from the anterior towards the posterior part of the endoskeleton of the anal fin, and similar conditions as regards the axonost series of the dorsal fin have been described above.

The baseost series consist of thirteen baseosts (*Bo,* Fig.50; Pl.24), the anterior eight of which each lies distally to one of the eight free axonosts, while the posterior five lie distally to the axonost plate. As in *Birgeria mougeoti* (Stensiö 1921, p.191), the axonosts and the baseosts are of the same order of magnitude.

The anterior eight elements of the baseost series are narrowest in the middle, and broaden upwards and downwards so that in lateral view they present an hour-glass-shaped outline. In anterior or posterior view these baseosts are likewise narrowest in their middle part, but increase much more in thickness upward than downward. The baseosts, therefore, have a dorsal terminal face of fairly large dimensions. This face is concave from side to side.

While the foremost six baseosts are of about the same shape, the seventh and eighth are somewhat thicker and exhibit a less marked constriction of their middle part.

The hindmost five baseosts are less completely preserved, but it seems beyond doubt that they were altogether more slender than the foremost eight. While the foremost eight baseosts are vertical or but slightly inclined backward, the backward inclination increases considerably in the posterior five, the hindmost of which forms an angle of only about 30° with the horizontal plane. The position and direction of the elements of the baseost series is clearly seen from Fig. 50.

The rounded, slightly thickened proximal ends of the right and left lepidotrich-halves articulated with the right and left lateral margins respectively of the distal terminal faces of the baseosts. One might therefore get the impression that the radial endoskeleton consists only of axonosts and baseosts; however, by cautiously removing parts of the lepidotrichia, a small distal radial ossification was found distally to each element of the baseost series. These distal ossifications (*Do,* Fig.50; Pl.24), which articulated with the distal ends of the baseosts, are situated wholly in the fin itself, so that the base-line of the fin corresponds to the boundary line between the baseost series and the distal series.

Of the ossifications in the distal series, the fifth, sixth, and seventh are the largest, and they are slightly longer than broad. Farther posteriorly the ossifications decrease gradually in size and at the same time they decrease in length in proportion to their breadth. The length of the largest ossifications of the series ranges between one-half and one-third the length of the baseosts with which they articulated.

Three lepidotrichia, on an average, occur on each distal radial ossification.

The dorsal fin contains about 40 lepidotrichia jointed throughout their whole length. In the anterior part of the fin the hind part of each of the lepidotrichia covers nearly the foremost third of the lateral face of the lepidotrich following immediately behind. The overlapped zone of the individual lepidotrichia narrows gradually towards the posterior part of the fin.

Throughout nearly the whole fin the individual segments of the lepidotrichia have about the same length, and the boundaries of the segments are so situated in relation to each other in successive lepidotrichia that they form roughly continuous lines across the fin. These lines are slightly curved, with the concavity upward, but run on the whole parallel with the base of the fin. In the proximal part of the fin the exposed faces of the individual segments are twice as long as broad, and on their exposed ganoine-covered face all the segments have a sharp longitudinal keel. In the foremost lepidotrichia this longitudinal keel divides the exposed face of the segments into two equally large parts, while farther backwards in the fin it gradually approaches the anterior margin of the face. Apart from this longitudinal keel the segments are either smooth or exhibit merely very slight indications of a striation in an antero-ventral to postero-dorsal direction.

The outline of the fin can be seen fairly well in specimen No. 66, though the most distal tip of the fin is lacking. The fin is nearly triangular in outline; its posterior margin is concave, so that the hindmost part of the fin is very low (Fig. 50). The foremost lepidotrich is very short, but the succeeding ones increase rapidly in length to and including the eighth, which is the longest in the fin, and which may be estimated to have contained about twenty segments. The lepidotrichia following after the eighth decrease gradually in length.

All the lepidotrichia which reach the posterior margin of the fin are branched dichotomically in their distal part.

The posterior margin of the fin is provided with a number of small fulcra.

In specimen No. 148 about 37 tranverse scale-rows lie between the posterior margin of the supracleithral and the anterior margin of the anal fin.

The endoskeleton of the anal fin is less satisfactorily preserved in specimen No. 66 than that of the dorsal fin, and the following description is therefore essentially based on specimen No. 179.

The endoskeleton consists of a series of radials, each containing two ossifications, viz. a large proximal and a smaller distal one. The individual ossi-

fications consist of endochondral cancellate bone-tissue surrounded by perichondral bone-layers. In the sequel the proximal and the distal ossifications in the endoskeleton of the anal fin will be termed the proximal and the distal series respectively.

The proximal series contains ten ossifications (*Po. a*, Fig. 57; Pl. 24), which decrease gradually in length from the foremost to the hindmost. In specimen No. 179 only the most distal part of the two foremost of these ossifications is preserved, while of the succeeding three only the midmost part is lacking (Fig. 57). In the foremost five ossifications the distal part is fairly thick, while the proximal part, in so far as it is preserved, is very slender. The proximal end of the fifth ossification is forked, as will be seen from Fig. 57.

The next four ossifications consist of a broad distal plate and a narrow proximal rod, which issues as a dorsally or postero-dorsally directed process from the distal plate. The proximal end of the foremost but one of these five ossifications is split.

The hindmost ossification within the proximal series consists of a broad distal plate, from whose dorsal margin the proximal part of the ossification issues as two postero-dorsally directed processes. On the lateral face of the distal plate of the hindmost ossification two ridges are found which run parallel with the anterior margin of the plate, while the distal plate of the hindmost ossification but one and the hindmost but two have one similar ridge each. Moreover the hindmost ossification corresponded to two ossifications of the distal series, while only one distal ossification corresponded to each of the remaining ossifications in the proximal series. Thus there is every indication that the hindmost ossification within the proximal series has arisen by fusion of two proximal elements.

The distal plates of the five posterior proximal ossifications are firmly connected with each other, forming together one larger plate. However, in specimen No. 179 it is easy to distinguish the boundaries between the five ossifications.

In specimen No. 66 (Pl. 24), in which only very little of the proximal series and none of the ossifications of the distal series are found, the distal parts of the posterior elements of the proximal series, as far as I can make out, are so intimately connected that the plate thus formed shows no other traces of its compound nature than that processes representing the free proximal parts of the ossifications issue from the dorsal margin of the plate.

The distal series contains eleven small ossifications (*Do. a*, Fig. 57), viz. one distally to each of the anterior nine, and two distally to the tenth of the ossifications of the proximal series. In specimen No. 179, Nos. 2, 3, 4, 5, 9, and 10 of the distal ossifications are completely preserved, while Nos. 1, 6, 7, 8, and 11 are fragmentary.

The anterior five distal ossifications are just as broad as the distal ends of the corresponding proximal ossifications, and their breadth far exceeds their

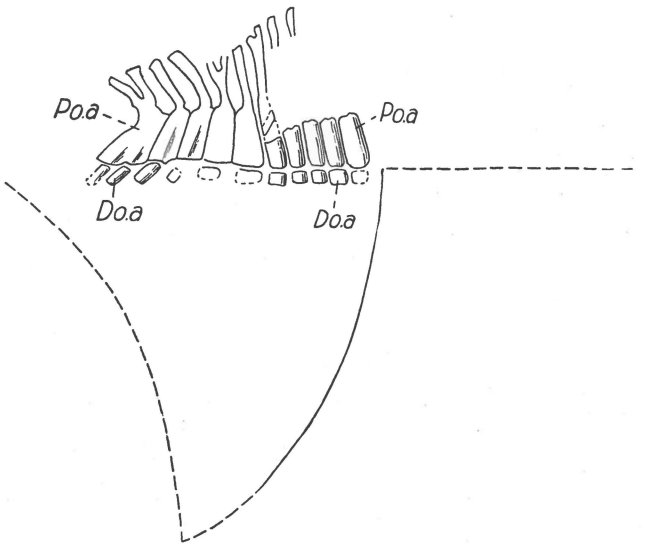


Fig. 56. *Glaucolepis aldingeri* n. sp. Endoskeleton of the anal fin. Based on specimen No. 179. 2 ×.
Do. a, distal radial ossifications; *Po. a*, proximal radial ossifications.

length. The distal ossifications Nos. 6 and 7 seem to be a little narrower than the corresponding proximal ossifications; they probably agree in length with the foremost five distal ossifications. The hindmost four distal ossifications are narrower than those anterior to them and much narrower than the distal ends of the proximal ossifications with which they were connected. These relatively slender posterior distal ossifications point in a postero-ventral direction.

The distal series lies in the proximal part of the fin itself, the boundary between the fin and the trunk almost coinciding with the boundary line between the distal and the proximal series.

The number of radials in the endoskeleton of the anal fin exceeds the number of associated infrahaemals, but the accurate proportion between the number of radial and axial elements cannot be stated. From the direction of the radial elements we may conclude with the same degree of probability as for the dorsal fin that the polymery of the fin skeleton is due to concentration (cf. p. 245).

Generally the endoskeletal radials of the anal fin (as of the dorsal fin) in the Actinopterygians are divided into three segments. In the *Palaeonisciformes* previously described the proximal and middle radial segments are in some cases ossified, but never the distal ones. Thus in *Elpisopholis* (Woodward 1908, p. 20; Stensiö 1921, p. 248; Aldinger 1937, p. 178) and probably in *Hyllingia* (Aldinger 1937, p. 340) ossified axonosts and baseosts occur throughout the radial series. In *Birgeria* (Stensiö 1921, pp. 190–191, 1932, pp. 291–292) independent ossified baseosts are only found in the posterior radial elements, while in the other radial elements the baseosts, accord-

ing to Stensiö, are either fused with the axonosts or have been reduced. Aldinger (1937, p.178) regards the latter alternative as the most probable on the ground that the independent baseosts in the posterior part of the fin skeleton decrease in size forwards in the series. In *Pygopterus* only one series of ossifications is found in the endoskeleton of the anal fin, and Aldinger (1937, p.178) thinks it probable, judging from the conditions in *Birgeria,* that these ossifications represent an axonost series and that the baseost series has been completely reduced. In *Tarassius* (Moy-Thomas 1934, p.372) and several other *Palaonisciformes* likewise only a single series of ossifications in the radial skeleton of the anal fin is known; but, as will be understood from the above, Moy-Thomas's statement, that the anal fin in the *Palaeonisciformes* is always supported by only one series of ossifications, is incorrect.

If we compare *Pygopterus nielseni* (Aldinger 1937) with *Glaucolepis,* we shall detect at once that the series of ossifications found in the endoskeleton of the anal fin in *Pygopterus* corresponds to the proximal series in *Glaucolepis*. The agreement in the shape of the ossifications is simply striking.

Hesitating, like Aldinger, about drawing conclusions on the basis of a comparison with so remote a form as *Birgeria,* I shall confine myself to saying that in *Glaucolepis* the proximal series is either an axonost series or a series of fused axonosts and baseosts. In the first case, the distal series of ossifications in the endoskeleton of the anal fin in *Glaucolepis* may be either the baseost series or, if this series has been reduced, ossifications in the distal radial segments. In the second case the distal series must be ossifications in the distal radial segments.

Without being able to definitely settle the question as to how the distal series of ossifications in the endoskeleton of the anal fin in *Glaucolepis* should be interpreted, I would regard it as probable, judging from its place in the proximal part of the fin itself, that it represents the distal and not the middle radial segments.

Like the dorsal fin, the anal fin contains about 40 lepidotrichia; the arrangement and segmentation of these as also the shape of the fin agree with the conditions in the dorsal fin, so a more detailed account will be superfluous. The accurate relation between the lepidotrichia and the endoskeleton of the fin, which has been described above for the dorsal fin, cannot be observed.

As far as can be seen from the few specimens available of *Glaucolepis aldingeri,* the ornament of the lepidotrichia is somewhat more distinct in the anal fin than in the dorsal fin.

The anterior margin of the fin is provided with a large number of small fulcra.

The caudal fin is best preserved in specimen No. 66, but is not complete, the distal part of both its ventral and its dorsal lobe lacking.

The endoskeleton of the fin has been described in the chapter on the axial skeleton (pp. 218–20).

The fin is deeply cleft, and as far as could be observed, it is equilobate or nearly so. The body axis extends through the dorsal lobe to its extreme distal end. Dorsally the body axis is covered by a series of long, pointed, unpaired fulcral scales, whose precise number cannot be given. Laterally the body axis is covered by long, narrow scales, arranged in the way typical of the *Palaeonisciformes*. As in the other Greenland species of *Glaucolepis* the scales which lie nearest the ventral margin of the lateral face of the body axis of the fin are probably pierced by the main lateral line, which probably continued to the distal end of the axis.

The lepidotrichia of the fin are close-set and jointed throughout their whole length. The proximal segment of each of the lepidotrichia is much longer than the remaining ones, and tapers proximally to a point. Nearly the whole of this segment is covered by the scales of the trunk. The proximal ends of the proximal segments are situated just distally to the distal ends of the hypural processes, but do not seem to have been in contact with the latter.

In the ventral lobe the length of the lepidotrichia increases from the foremost one, which is quite short, to the tenth, which is the longest of the whole fin. The anterior nine of these lepidotrichia reach the ventral margin of the ventral lobe, and are unbranched. The segments of these lepidotrichia are only a little longer than broad. The next sixteen or seventeen lepidotrichia, which decrease gradually in length from the foremost to the hindmost, extend to the postero-dorsal margin of the ventral lobe. The segments of the proximal part of most of these lepidotrichia (apart from the most proximal segment) are nearly twice as long as broad. Distally these lepidotrichia are dichotomously branched.

The number of lepidotrichia in the dorsal lobe cannot be stated, its distal part not being preserved. The length of the lepidotrichia of the dorsal lobe decreases from the anterior towards the posterior one and at the same time the unbranched proximal part of the individual lepidotrichia grows gradually shorter in relation to the branched distal part. Most of the segments of these lepidotrichia are a little longer than broad.

All the lepidotrichia of the fin are covered by ganoine, which is probably smooth.

The ventral margin of the ventral lobe is covered by a series of small fulcral scales.

b. Glaucolepis stensiöi.

In several specimens of this species the exoskeletons of the unpaired fins are more or less completely preserved, while in no case the endoskeleton is so

well preserved that a detailed investigation can be made. The remnants of the endoskeleton which can be observed in the different specimens show close agreement with what has been observed in *Glaucolepis aldingeri.*

Number of transverse scale-rows between the anterior margin of the dorsal fin and the posterior margin of the supracleithral:

Specimen No.	41	Number of scale-rows				*41*
–	–	49	–	–	–	*42*
–	–	86	–	–	–	36
–	–	88	–	–	–	30–32
–	–	90	–	–	–	34
–	–	97	–	–	–	*37*
–	–	98	–	–	–	*43*
–	–	103	–	–	–	*41*
–	–	109	–	–	–	36
–	–	114	–	–	–	34

Number of lepidotrichia in the dorsal fin:

Specimen No.	48	Number of lepidotrichia				13
–	–	89	–	–	–	26
–	–	90	–	–	–	30–32
–	–	91	–	–	–	*31*
–	–	94	–	–	–	25
–	–	97	–	–	–	40–42
–	–	98	–	–	–	*32*
–	–	109	–	–	–	37
–	–	114	–	–	–	32

The number of lepidotrichia ranges between 31 and c. 40; the most reliable countings arrived at the numbers 31 and 32, but a single specimen seemed to have at least 40 lepidotrichia.

The outline of the fin as well as the position, jointing, and branching of the individual lepidotrichia are entirely as in *Glaucolepis aldingeri.* The exposed face of the lepidotrichia seems to be entirely covered with a continuous layer of ganoine; however, the segments of the hindmost lepidotrichia seem to be provided with only one longitudinal stria of ganoine, which is much narrower than the exposed faces of the segments.

The ganoine is smooth except on the foremost lepidotrichia, where in some cases, at any rate, a very fine longitudinal striation can be observed.

The anal fin begins almost at the 35th transverse scale-row (reckoned from the posterior margin of the supracleithral), the fin thus beginning about six scale-rows in front of the anterior margin of the dorsal fin. Since, however,

the transverse scale-rows are oblique, the anal fin in this as in the other species of *Glaucolepis* is actually situated farther backward than the dorsal fin.

Number of lepidotrichia in the anal fin:

Specimen No.	48	Number of lepidotrichia				*23*
– –	49	–	–	–		22
– –	88	–	–	–		28
– –	91	–	–	–		20
– –	97	–	–	–		*21*
– –	98	–	–	–		*25*
– –	109	–	–	–		28
– –	114	–	–	–		19

The most reliable countings gave 21, 23, and 25 lepidotrichia respectively; but, as will be seen, the number seems to be greater in other specimens.

At any rate the anal fin contains a much smaller number of lepidotrichia than the dorsal fin, but in its proportions agrees well with the latter.

The ganoine covering of the individual lepidotrichia segments agrees entirely with that of the dorsal fin in extent and ornament.

The distal and largest part of both the ventral and the dorsal lobe of the caudal fin is either entirely absent or extremely poorly preserved. The proximal part of the caudal fin does not differ essentially from the corresponding part of the caudal fin in *Glaucolepis aldingeri*. In specimen No. 109 the long acute proximal segments of the lepidotrichia are very distinctly seen. The lepidotrichia are covered by a smooth layer of ganoine.

c. Glaucolepis arctica.

The endoskeleton of the dorsal fin is never well preserved, but in specimens in which parts of it could be investigated (e. g. No. 64) it showed good agreement with the conditions in *Glaucolepis aldingeri*.

Number of transverse scale-rows between the anterior margin of the dorsal fin and the posterior margin of the supracleithral:

Specimen No.	63	Number of scale-rows				*35*
– –	64	–	–	–		35 ?
– –	65	–	–	–		*34*
– –	67	–	–	–		36–37
– –	71	–	–	–		*33*
– –	74	–	–	–		*33*
– –	154	–	–	–		36

Number of lepidotrichia in the dorsal fin:

Specimen	No.	63	Number	of	lepidotrichia	*29–30*
–	–	64	–	–	–	35–36
–	–	65	–	–	–	35
–	–	67	–	–	–	*28*
–	–	71	–	–	–	31 ?
–	–	74	–	–	–	28–30
–	–	154	–	–	–	*35–36*

Thus the number of lepidotrichia ranges between 28 and 35, which is somewhat lower than in the preceding two species. As regards the position, segmentation, and branching of the lepidotrichia and the shape of the fin *Glaucolepis arctica* resembles in all essentials *Glaucolepis aldingeri* and *Glaucolepis stensiöi*. The anterior margin of the fin bears a number of small fulcra (c. 35–40).

According to Stensiö's description (1932, p. 122), the exposed part of the foremost lepidotrichia of the dorsal fin is covered by a continuous layer of ganoine, while the hindmost lepidotrichia are ornamented with two longitudinal striae of ganoine. As far as I can make out, however, the exposed faces of all the lepidotrichia are entirely covered with ganoine. In some cases, at any rate, the apparently smooth surface of the ganoine-layer shows traces of very fine striae running in a postero-dorsal direction from the anterior margin of the exposed part of the segments.

The endoskeleton of the anal fin in specimen No. 64 exhibits a number of fairly slender ossifications, which correspond to the proximal ossifications of the anterior radials in *Glaucolepis aldingeri* (and *Pygopterus nielseni*). The distal end of these ossifications is somewhat thickened. The number of lepidotrichia in that part of the anal fin which lies distally to these ossifications may be estimated at about three times the number of the radial elements.

The anal fin begins at the 30th transverse scale-row.

Number of lepidotrichia in the anal fin:

Specimen	No.	63	Number	of	lepidotrichia	*30*
–	–	64	–	–	–	33
–	–	65	–	–	–	28–29
–	–	67	–	–	–	28
–	–	154	–	–	–	*35–36*

According to the most reliable countings the numbers of lepidotrichia are 30 and 35–36 respectively, or about the same figures as those found in the dorsal fin. In all other features the anal fin agrees so closely with the dorsal fin that a more detailed description will be superfluous.

In specimen No. 63 the caudal fin is completely preserved, though only as an impression, but otherwise the most distal part of both the dorsal and the ventral fin lobe is always lacking.

The fin is equilobate and deeply cleft. The body axis continues through the dorsal lobe to its extreme distal end. The dorsal margin of the axis is provided with a series of well developed acute unpaired fulcral scales, and the lateral side of the axis is covered with long narrow scales. The main lateral line continues to the distal end of the axis ot the fin, running very close to the ventral margin of the lateral face of the axis.

The close-set lepidotrichia agree in segmentation and branching with the corresponding ones in *Glaucolepis aldingeri*.

The exposed face of the lepidotrich segments is covered by a continuous and smooth layer of ganoine.

The ventral margin of the ventral lobe carries c. 35–40 small fulcra.

d. Glaucolepis gunnari.

The material contains many specimens of *Glaucolepis gunnari*; but since the main part of these are derived from Fish-zone III, in which the concretions are particularly small as compared with the fishes they contain, fragments of the unpaired fins are only rarely preserved. Only two specimens supply information of importance about the unpaired fins, viz. specimen No. 16, which shows the proximal parts of the dorsal and anal fins, and specimen No. 18, which shows the proximal parts of all the unpaired fins. Nothing can be stated about the endoskeleton of the unpaired fins.

Nothing is known about the number of transverse scale-rows between the posterior margin of the supracleithral and the anterior margin of the dorsal fin. The number of lepidotrichia in the dorsal fin in specimen No. 18 is 43 or 44, as to specimen No. 16 I can only say that it exceeds 33. Since only the proximal parts of the lepidotrichia are preserved, the shape of the fin cannot be ascertained, but judging from specimen No. 18 it had a longer base than in any other species. As usual the lepidotrichia are close-set and segmented. The length of the segments is two or three times the breadth of their exposed parts. As far as I could observe, the exposed part of the segments is covered by ganoine. On the foremost 10–12 lepidotrichia the ornament consists of one distinct longitudinal keel only, which divides the exposed face of the individual segments into two; in front of and behind this keel the ganoine-layer is smooth. In the succeeding lepidotrichia the gradual transition to the very strongly ornamented segments typical of the middle and posterior parts of the dorsal fin may be seen. The transition is effected by the longitudinal keel approaching more and more the anterior margin of the exposed face of the segments the farther backwards we go in the fin, and at the same time the surface of the ganoine-layer laying behind the longitudinal keel exhibits an increasingly prominent ornament. Within each segment the ornament consists of six or seven striae extending in an antero-ventral to postero-dorsal direction. Often these striae are, to a smaller or greater extent, divided into small tubercles.

The anterior margin of the fin is provided with small fulcra.

The number of transverse scale-rows between the posterior margin of the supracleithral and the anterior margin of the anal fin cannot be stated; but the position of the anal fin in relation to the dorsal fin agrees fairly well with the conditions in *Glaucolepis aldingeri, stensiöi,* and *arctica.* In specimen No. 16 the number of lepidotrichia is about 35, in specimen No. 18 about 38. As regards the position, segmentation, and ornament of the lepidotrichia, the preserved part of the anal fin agrees entirely with the dorsal fin.

The caudal fin is partially preserved in specimen No. 18; as far as it could be investigated, it shows agreement with the fin in *Glaucolepis arctica.* Its lepidotrichia are covered by a thin layer of ganoine, whose ornament consists of obliquely running striae.

e. Glaucolepis magna.

No information can be given about the unpaired fins.

Squamation.

a. General remarks.

Before describing the squamation in the individual species, I shall make the following remarks concerning the arrangement and shape of the scales; they apply to all five species of *Glaucolepis,* but I point out that the caudal region in *Glaucolepis magna* is very incompletely known.

The abdominal region and the caudal region are entirely covered with scales arranged in the usual way in rows which anteriorly to the inversion line of the caudal region have a roughly tranverse course.

In several early *Palaeonisciformes* (cf. Aldinger 1937, pp. 342–343) the ventral face of the abdominal region is sharply marked off from the sides of the region, a transverse section through the region being an isosceles triangle. In *Glaucolepis* the ventral face is not sharply marked off, and a transverse section through the abdominal region is oval. The approximate boundary line between the flank scales and the scales on the ventrum runs from the pectoral fin through the base of the pelvic fin to the anus. Ventrally to the cleithrum lie 6–8 short transverse scale-rows in front of the transverse scale-row which lies immediately behind the dermal shoulder girdle. According to Stensiö's terminology (1932, p. 158) these short scale-rows is termed subcleithral rows.

On the sides of the abdominal region the transverse rows are, as usual, slightly curved, the posterior margin of the rows being convex dorsally to the lateral line, and concave ventrally to the lateral line. In the caudal region the curvature gradually becomes less marked.

As is the case in several other *Palaeonisciformes* (*Acropholis, Pygopterus, Palaeoniscus* (Aldinger 1937, partly after Westoll 1934)), the transverse scale-rows in *Glaucolepis* have a polymeric arrangement, and there seems to be about three transverse scale-rows per myotome.

The lobe of the pectoral fin is scaly, but the precise arrangement of the scales could not be made out.

In the foremost transverse scale-rows of the abdominal region the lateral line scale and some scales situated just dorsally and ventrally to the lateral line scale are higher than broad. In the remaining transverse rows anteriorly to the inversion line the lateral line scale is either a little higher than broad or of the same height and breadth. In all the transverse rows within the abdominal region the height of the scales decreases gradually in relation to their breadth with increasing distance from the lateral line, the dorsal and ventral flank scales being accordingly very low. The scales on the ventrum are likewise very low.

Similar variations in the dimensions of the scales take place in the anterior part of the caudal region, while in the middle and posterior parts of this region the height of the scales varies only very little. On the body axis of the caudal fin the scales are very narrow.

The flank scales articulate with each other by a peg-and-socket articulation, which in most cases is better developed in the abdominal region than in the caudal region. The foremost part of each scale is overlapped by the hindmost part of the scale lying immediately in front of it. The ornament of the scales is most strongly developed in the antero-dorsal part of the abdominal region, as in so many other *Palaeonisciformes*.

The microstructure of the scales has not been investigated (cf. however, Aldinger 1937, pp. 235–37).

b. Glaucolepis stensiöi.

As will be seen from the subjoined table, only very few specimens of this species are so well preserved that the number of transverse scale-rows and the number of scales in the rows can be counted. This is because the concretions derived from Fish-zone V in many cases are, so to speak, too small for the fishes they enclose, and moreover the fishes often lie in a contorted position.

Number of transverse scale-rows between the posterior margin of the supracleithral and the line of inversion in the caudal region:

Specimen	No.	49	Number	of	scale-rows	60
–	–	88	–	–	–	55
–	·	89	–	–	–	64
–	–	91	–	–	–	57
–	–	97	–	–	–	63
–	–	98	–	–	–	62
–	–	103	–	–	–	*64*
–	–	109	–	–	–	59

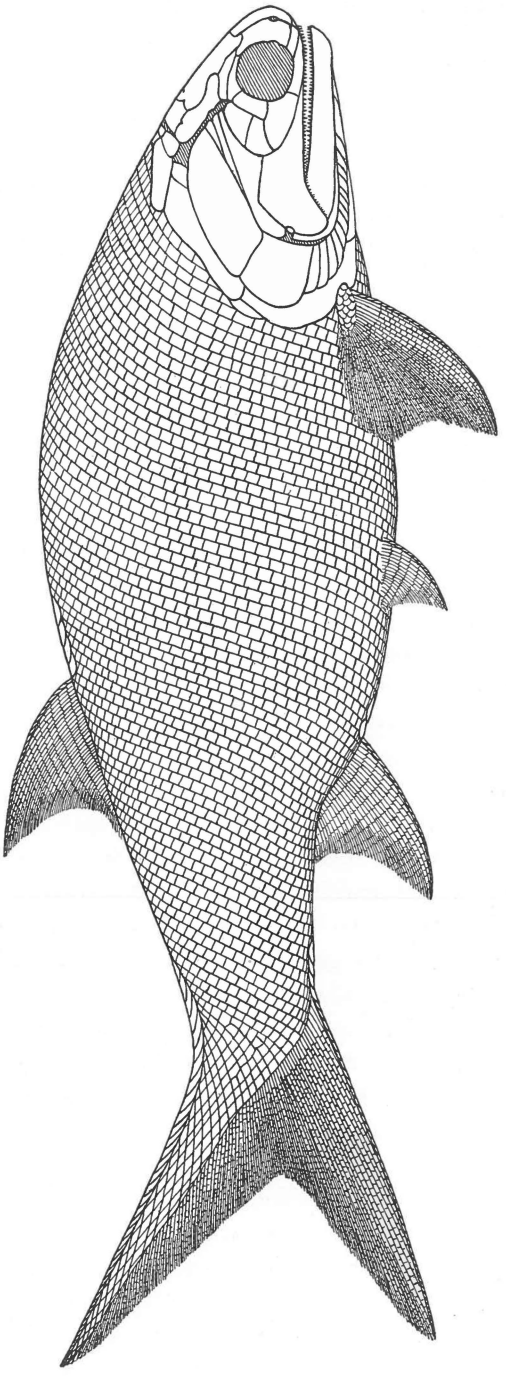


Fig. 57. *Glaucolepis stensiöi* n. sp. Attempted restoration. Arrangement of scales on the lobe of the pectoral fin unknown. Based on several specimens. About nat. size.

Number of scales in a transverse row above the pelvic fin reckoned from the base of the pelvic fin in a dorsal direction:

Specimen No.	90	Number of scales			40
–	- 97	–	-	–	36
–	- 98	–	-	–	34
–	- 103	–	-	–	33

In each of the foremost abdominal transverse rows one or two scales dorsally to the lateral line scale, the lateral line scale itself, and five or six scales ventrally to it are higher than broad. In the rows following immediately behind, the high scales decrease gradually in number, the last high scales being found in the 10th, 11th, or 12th transverse row. All the remaining flank scales are rhombic and almost as high as broad. Farthest dorsally and ventrally in the transverse rows the relative height of the scales decreases, as mentioned in the introduction to this chapter.

Anteriorly to the dorsal fin three or four, and anteriorly to the ventral lobe of the caudal fin four enlarged ridge scales are found. The aforementioned row of ridge scales on the dorsal side of the body axis of the caudal fin continues some distance in an anterior direction on the dorsal side of the caudal pedicle, but does not reach the posterior part of the dorsal fin.

In front of the anus lies a large preanal scale, and on each side of the anus likewise a large scale.

The peg-and-socket articulation is well developed, and in connection with this the scales have a vertical ridge on their medial side. The antero-dorsal corner of the flank scales of the abdominal region is produced in an antero-dorsal direction.The overlapped zone of the scales narrows gradually with increasing distance from the shoulder girdle, and in the caudal region it is very narrow. The posterior margin of the scales is serrated.

The exposed face of the scales is covered by a continuous layer of ganoine.

In the anterior relatively high flank scales in the abdominal region the ornament consists partly of broad, flat, and low striae, and partly of very fine striae. The broad, flat, and low striae constitute the ornament of the whole exposed face of the scale except its antero-ventral part. They extend nearly parallel with the long diagonal of the scale, and continue in the serrations of the posterior margin of the scale. The antero-ventral part of the high flank scales is ornamented with the above-mentioned very fine striae, which are so situated on the individual scales that their anterior part is fairly parallel with the anterior margin, and their hindmost part with the ventral margin of the scale. The more dorsal and ventral scales in the anterior part of the abdominal region exhibit the same type of ornament as the high abdominal scales; but the number of ornamental elements decreases simultaneously with the height of the scales. The fine striae on the antero-ventral part of the scales are entirely absent from the lowest scales.

Through the posterior part of the abdominal region and the caudal region the ornamental elements of the scales can be observed to fuse more and more with increasing distance from the head, so that in the posterior part of the caudal region the scales are entirely smooth.

The lateral scales on the body axis of the caudal fin seem to be smooth.

The large ridge scales present an ornament of fairly well developed striae running in an almost longitudinal direction.

c. Glaucolepis aldingeri.

None of the few specimens at hand of this species is completely preserved, so it is difficult to give even fairly precise figures as regards the squamation.

Number of transverse scale-rows between the posterior margin of the supracleithral and the line of inversion in the caudal region:

Specimen No.	66	Number of scale-rows			65
–	- 148	–	-	–	66

Thus the number of scale-rows seems to be greater than in *Glaucolepis stensiöi.*

Number of scales in a transverse row above the pelvic fin reckoned from the base of the pelvic fin in a dorsal direction:

Specimen No.	66	Number of scales			42
–	- 75	–	-	–	45
–	- 147	–	-	–	52

Although the precise number cannot be given, it is undoubtedly greater than in any other species of *Glaucolepis.*

In the anterior 15–20 transverse rows in the abdominal region some flank scales are found which are higher than broad. More precisely, the foremost, or one of the foremost, of these transverse rows contains of high scales: one scale dorsally to the lateral line scale, the lateral line scale itself, and two or three scales ventrally to it. In the hindmost of the 15–20 transverse rows the only high scale is the lateral line scale itself. With increasing distance from the lateral line the height of the scales decreases rapidly in dorsal and ventral directions, by far the greater number of the scales in the abdominal and caudal regions being remarkably low.

Anteriorly to the dorsal fin three, and in front of the ventral lobe of the caudal fin three or four, enlarged ridge scales are found. On the dorsal side of the caudal pedicle, in continuation of the dorsal row of ridge scales on the body axis of the caudal fin, four to six? enlarged ridge scales are found.

Around the anus, remnants of three anal scales are found, which seem to have been placed as the anal scales in *Glaucolepis stensiöi.*

In this species the scales are remarkably thick. The peg-and-socket articulation is well developed both in the abdominal region and the caudal region, and in connection with this the flank scales have on their medial face a broad and well developed vertical ridge. The overlapped area of the scales is rather narrow. The hind margin of the scales is serrated.

The exposed face of the scales is covered with a layer of ganoine of varying thickness, so the surface of the layer presents a marked ornament consisting of striae which from the dorsal and anterior margin of the individual scales run in a postero-lateral direction towards the posterior margin of the scales, in whose serrations they continue precisely as in *Glaucolepis stensiöi*.

On the relatively high flank scales in the abdominal region the number of striae is six to nine. The individual striae are very narrow in their anterior part, but increase in breadth in a postero-lateral direction throughout the greater part of their length, to taper again in their hindmost part. The striae often fuse in that area of the scale in which they attain their greatest width. The anterior end of the two most ventral striae is often bent somewhat upward, but not so much that it becomes parallel with the anterior margin of the scale. Occasionally short, rather fine striae are inserted between the foremost narrow ends of the long striae on the anterior part of the scales.

The ornament of the lower scales in the anterior part of the abdominal region is of the same type as that described here for the high scales, but the number of ornamental elements decreases with the decreasing height of the scales.

In the posterior part of the abdominal region and the caudal region the long striae in the postero-ventral part of the scales can be seen to fuse more and more into a smooth mass of ganoine with increasing distance from the head, while the individual striae can still be observed on the remaining and greatest part of the surface of these scales.

The narrow rhombic scales which cover the body axis of the caudal fin, in so far as they could be investigated (the distal part of the caudal fin is unknown), are covered by a continuous layer of ganoine and are ornamented with two or three striae which run parallel with the long diagonal of the scales.

The enlarged ridge scales lying in front of the median fins have a continuous covering of ganoine and are ornamented with a number of mainly longitudinal striae. Thus the ornament of ridge scale No. 2 in front of the dorsal fin consists of 18–20 long striae, which in the posterior part of the scale run nearly parallel with the median axis of the scale, and in the anterior part of the scale converge in an anterior direction with this axis. Shorter striae are inserted between the foremost parts of the long striae.

d. Glaucolepis magna.

No specimens of this species are so complete that the number of transverse rows or the number of scales in these rows can be ascertained.

The squamation is best preserved in the anterior part of the abdominal region in the large specimens Nos. 51, 56, 175, 176, and 177. In some few specimens parts of the squamation of the caudal region are found, but the state of preservation of these specimens is poor.

In the foremost 20–30 transverse rows behind the supracleithral a number of scales are found which are much higher than broad. In one of the foremost transverse rows behind the supracleithral this applies to five scales situated dorsally to the lateral line scale, to this scale itself, and to about seven scales situated ventrally to it, altogether about thirteen scales. In this row of about thirteen scales the midmost ones are the highest, and the ratio between their height and breadth is nearly three to one. In the succeeding transverse rows the number of high scales decreases with increasing distance from the head, and in the hindmost of the 20–30 rows only the lateral line scale is higher than broad.

Apart from the high scales mentioned here, most of the flank scales of the abdominal region are of about the same height and breadth and rhombic in outline. Farthest dorsally and farthest ventrally in the transverse rows the scales grow relatively low, as normally.

The number of enlarged ridge scales cannot be stated, even though remnants of dorsal ridge scales are seen in front of the dorsal fin in a single case.

In this species the scales are surprisingly thin, and the peg-and-socket articulation, which can be distinctly observed in the anterior part of the abdominal region, is faintly developed. A vertical ridge on the medial face of the scales is either entirely absent or much reduced.

The breadth of the anterior overlapped zone of the flank scales of the abdominal region is between one-third and one-fourth the breadth of the exposed face of the scales. The posterior margin of the flank scales was probably serrated, as in the other species of *Glaucolepis*, but is so poorly preserved that this question cannot be definitely settled.

The exposed face of the high flank scales in the anterior part of the abdominal region is ornamented with a large number of low and rather narrow ganoine striae, which are often to a greater or smaller extent subdivided into oblong ganoine tubercles. Whether the ganoine-layer of the scales is continuous, or the ganoine is entirely absent at the bottom of the narrow grooves which separate the individual striae and tubercles, I am unable to decide.

From the dorsal margin and from the dorsal and greater part of the anterior margin of the exposed face of a flank scale whose height is almost twice its breadth, about sixteen narrow striae run in a postero-ventral di-

rection to the posterior margin of the scale. The greater number of these striae are as a rule divided into small tubercles, especially in their foremost and hindmost parts. The striae are straight or slightly curved.

The antero-ventral part of the same scale is provided with about eight or nine narrow striae, which run from the ventral part of the anterior margin of the exposed face of the scale in a postero-ventral direction to the ventral margin of the scale. These striae point more steeply downward than the system of striae on the dorsal part of the scale. The interspace between the two systems of striae diverging in a posterior direction is occupied by striae which do not reach the anterior margin of the scale.

On the lower more dorsal or more ventral abdominal scales the number of striae is, of course, smaller than on the high flank scales. However, the type of ornament is on the whole the same, though the difference in the direction of the striae in the antero-ventral part and in the remaining part of these scales is less marked, and the subdivision of the individual striae less developed.

The material of *Glaucolepis magna* comprises specimens whose ornament of the scales does not agree entirely with the above description. Thus in some specimens all the striae on the high flank scales run in the same direction, and some specimens show all degrees of subdivision of the individual striae into small tubercles. In the most extreme case (specimen No. 51) all the striae of the high lateral scales are subdivided throughout their extent into small oblong tubercles.

e. Glaucolepis gunnari.

As far as I can make out, the arrangement of the scales is typical, but since the scales are very thin and the peg-and-socket articulation slightly developed, the scales often lie fairly disturbed in relation to each other, so it is impossible to precisely ascertain the number of transverse scale-rows of the trunk or the number of scales in these rows.

In some of the foremost transverse rows behind the supracleithral the lateral line scale and some few scales above and below this scale are higher than broad, though never as high in relation to their breadth as in *Glaucolepis magna*. In one of the foremost transverse rows behind the supracleithral the following high scales are found: two or three scales dorsally to the lateral line scale, that scale itself, and four or five scales ventrally to it.

The number of high scales decreases in the succeeding transverse rows to about the tenth row, in which the lateral line scale is the only high scale.

Several specimens show a good deal of variation in regard to these high abdominal scales; thus, in some specimens the highest of these scales are only a little higher than broad, while in other specimens the ratio between height and length of the highest scales is two to one.

Most of the remaining flank scales in the abdominal and caudal regions have about the same height and breadth, and the exposed face of these scales is rhombic. The number of ridge scales in front of the unpaired fins cannot be given.

As regards the flank scales the slightly developed peg-and-socket articulation has been observed both in the abdominal and in the caudal region. A vertical ridge on the medial side of the scales is either very slightly developed or absent.

As regards the shape of the flank scales it can be mentioned that their antero-dorsal corner is produced somewhat in an antero-dorsal direction and that their posterior margin is probably serrated.

In the foremost transverse rows behind the dermal shoulder girdle the breadth of the anterior overlapped zone of the scales ranges between one-fourth and one-eighth the breadth of the exposed face of the same scales.

The scales are covered with a continuous layer of ganoine.

The ornament of the flank scales in the anterior part of the abdominal region consists of rather narrow, low striae, which run from the dorsal and anterior margins of the exposed face of the scales in a postero-ventral direction towards the posterior and ventral margins of the scales.

The main direction of the striae in that part of one of the high scales which lies dorsally to the long diagonal of the scale, is antero-dorsal to postero-ventral, but a little less steep than the direction of the diagonal.

On the highest scales the number of striae dorsally to the long diagonal is about ten; in rare cases some of these striae are subdivided into smaller pieces.

Ventrally to the long diagonal, that is to say, on the antero-ventral part of the exposed face of a high scale, the most ventral striae are slightly curved so that their direction approaches the direction of the anterior and the ventral margin respectively of the exposed face of the scale. The other striae on this part of the scale have about the same direction as the striae lying dorsally to the long diagonal of the scale.

On the highest scales the number of striae lying ventrally to the long diagonal is eight to nine and these striae are often subdivided into two or three oblong tubercles.

The number of striae on the exposed face of the scales decreases with decreasing height of the scales.

The ornament of the scales grows less marked in the posterior part of the abdominal region and in the caudal region, but even in the posterior part of the caudal region the scales are never entirely smooth as in *Glaucolepis stensiöi* and *Glaucolepis arctica*.

The narrow scales on the body axis of the caudal fin exhibit an ornament which consists of some few striae running parallel with the long diagonal of the scales.

f. Glaucolepis arctica.

Number of transverse scale-rows between the posterior margin of the supracleithral and the line of inversion in the caudal region:

Specimen No.	63	Number of scale-rows			55
– -	64	–	-	–	52
– -	65	–	-	–	55
– -	67	–	-	–	59
– -	68	–	-	–	57–58
– -	121	–	-	–	58–59

Thus the number of transverse scale-rows ranges about 55–59, which is somewhat lower than in *Glaucolepis stensiöi.*

Number of scales in a transverse row above the pelvic fin reckoned from the base of the pelvic fin in a dorsal direction:

Specimen No.	63	Number of scales			30
– -	65	–	-	-	35
– -	67	–	-	-	35–36
– -	68	–	-	-	35
– -	71	–	-	-	32
– -	121	–	-	-	35

As usual the anterior 10–12 transverse scale-rows behind the dermal shoulder girdle include some scales which are higher than broad. In one of the foremost transverse rows the following high scales are found: the scale lying dorsally to the lateral line scale, this scale itself, and four to six scales lying just ventrally to the lateral line scale. Of these scales the midmost are the highest, and their height is up to twice their breadth. The number of high scales in the transverse rows and their height decrease gradually with increasing distance from the head; the last high scale, the lateral line scale, lies in the 10th, 11th, or 12th transverse row.

Apart from the high scales mentioned above, the greater number of flank scales in the transverse rows of the abdominal and caudal regions are of nearly the same height and breadth, and their exposed face is rhombic in outline.

As usual the scales farthest ventrally and farthest dorsally in the transverse rows grow gradually lower in a ventral and a dorsal direction respectively. The ratio between height and breadth of the most ventral flank scales in the abdominal region is almost 1 to 3. On the ventral side of the trunk the scales are even lower in relation to their breadth.

In front of the dorsal fin three or four, and in front of the ventral lobe of the caudal fin four enlarged ridge scales are found. On the dorsal side of

the caudal pedicle three to five enlarged ridge scales are found as an anterior continuation of the dorsal row of fulcral ridge scales on the trunk axis of the caudal fin.

As usual three anal scales are situated around the anus.

The scales are relatively thick and have well developed peg-and-socket articulation. The anterior overlapped zone of the scales is rather narrow. The posterior margin of the scales is serrated.

The ornament of the scales has been described in some detail by Stensiö (1932, pp. 123–24). Stensiö mentions that the main direction of the striation is diagonal, the striae running backward and downward. Moreover one or two of the most ventral striae on the flank scales in the anterior part of the abdominal region are often so curved that their foremost part is nearly parallel with the anterior, and their hindmost part nearly parallel with the ventral margin of the exposed face of the scales. Similar conditions have been described by Stensiö in *Glaucolepis gyrolepidoides* (1921, p. 202).

As pointed out by Stensiö, the individual striae on the scales fuse more and more, gradually as we move away from the head, and in the posterior part of the caudal region the fusion is so complete that the surface of the scales is entirely smooth.

In so far as they can be investigated, the ridge scales show a marked ornament of mainly longitudinal striae. The scales on the body axis of the caudal fin are smooth.

Sensory canal system of the trunk.

Only the main lateral line of the trunk has been observed. After piercing the suprascapular and the supracleithral, it runs through the trunk scales to the base of the body axis of the caudal fin. On the axis of the caudal fin traces of the lateral line are only visible in a few cases; the lateral line seems to run here through the most ventral scales on the lateral face of the axis to, or nearly to, its extreme distal end.

The lateral line runs through the scales as a rather narrow canal. How this canal opens externally, could not be observed.

Generic Diagnosis.

(Partly after Stensiö 1921, pp. 201–03; 1932, pp. 121–25; White 1933, 118–20; Piveteau 1934, p. 88; Aldinger 1937, pp. 234–37).

Small to medium-sized, more or less deeply fusiform Palaeoniscids, transverse section of trunk oval, head fairly broad and low with small rostrum, eyes large and situated far anteriorly. Neural endocranium in youngest individuals unossified, in somewhat older specimens with a larger

number of independent ossifications, and in the oldest with two large unpaired ossifications, viz. an anterior, comprising the ethmoidal region, the orbitotemporal region, and part of the otic region, and a posterior, comprising the remaining part of the otic region and the whole occipital region. The two ossifications separated laterally and dorsally by a vestibular fontanelle and a fissura occipitalis lateralis, the latter widened farthest dorsally to form a posterior dorsal fontanelle. Ventrally the two ossifications separated by an unossified zone, the fissura oticalis ventralis, in the ventral part of the endocranium between the right and left vestibular fontanelles. A cranio-spinal process indicated. Roof of orbitotemporal region and otic region largely cartilaginous and pierced by an anterior dorsal fontanelle. Fossa bridgei well developed, its posterior deep part in wide communication with the cavum cerebrale cranii. From lateral face of otic region to anterior part of fossa bridgei a short vertical spiracular canal. Aorta canal unpaired in occipitalregion and paired in otic region. Notochordal space extending through whole occipital region and greater part of otic region. Articular fossa for hyomandibula very steep. Jugulo-hyoideomandibular canal long with three posterior openings. Trigemino-facialis chamber well developed. Large unpaired posterior myodome with a spinal and a prespinal part. In roof of myodome a large pituitary fontanelle, in floor of myodome a large oblong fenestra ventralis myodomus closed ventrally by the parasphenoid. No openings through pars basisphenoidea for communication between myodome and orbit. Processus basipterygius very well developed. Owing to strong development of the eyes, interorbital part of endocranium compressed into a thin interorbital wall with a large unpaired fenestra optica. Nervus olfactorius intracranial throughout its extent. A dorsal and a ventral paired anterior myodome developed for the musculus obliquus superior and the musculus obliquus inferior respectively. Very short ethmoidal region with a process for articulation with the palatoquadrate. Cavum cerebrale cranii in the living animal almost entirely occupied by the brain. Parasphenoid with well developed processus ascendens anterior fused with long processus ascendens posterior. Posterior part of parasphenoid situated ventrally to the posterior myodome and containing a paired canal for the arteria carotis interna. Vomer paired, very large, without firm connection with other bones. Paired medial and lateral extrascapulars, the medial one small and mostly without contact with that on the other half of the head. In front of extrascapular series often one to several pairs of small rounded dermal bones. Parietals, frontals, supratemporo-intertemporals, nasals, and postrostrals arranged according to the usual Elonichthyid-Palaeoniscid pattern. Parietals long, but partly concealed below the frontals. Suture between right and left frontals strongly sinuous. Postrostral large and highly arched. Anterior nostril between postrostral and nasal, posterior nostril in posterior margin of nasal. Supratemporo-intertemporal with well developed ventral lamina, its anterior part joined by

suture with processus ascendens posterior of the parasphenoid. Medial supraorbital series fused with dermosphenotic, and lateral supraorbital series with a postorbital. In the infraorbital series: postorbital, jugal, lacrimo-maxillary, and rostro-antorbital. No independent rostrals, possibly a paired or unpaired premaxillary. Two or three suborbitals. Palatoquadrate in young individuals unossified, in older with three ossifications (autopalatine, metapterygoid, and quadrate), in old individuals ossified in one piece. Between palatoquadrate and neural endocranium an ethmo-palatine and a palato-basal articulation. On oral face of palatoquadrate: ectopterygoid, anterior and posterior dermopalatines, dermometapterygoid, and entopterygoid. Maxillary of normal Palaeonisciform type. Preoperculum very oblique, on its medial side a well developed internal lamina. Large triangular quadratojugal almost entirely covered by maxillary. Palatoquadrate and its dermal bones, maxillary, lacrimo-maxillary, preoperculum, and quadratojugal, firmly connected with each other and forming the walls of a chamber for the musculus adductor mandibulae. Mandible long and low. Posterior two-thirds of Meckelian cartilage ossified in one piece in old individuals; in anterior third of mandible a thick ossification including a mento-Meckelian component. On external side of mandible: supraangular, angular, and dentalo-splenial; on internal side: prearticular and coronoids. In hyoid arch: hyomandibula, symplectic, two ceratohyal ossifications, and hypohyal. Hyomandibula well developed, angularly bent, with a small processus opercularis and a groove or short canal for the truncus hyoideomandibularis, much forward inclined and firmly connected with preoperculum, palatoquadrate, and suboperculum. Symplectic very well developed, articulating with quadrate and articular regions of mandibular arch. Ceratohyal ossifications high and compressed. Hypohyal angularly bent, and probably connected with the corresponding one on the other side by a very small basihyal. Triangular dermohyal in intimate contact with dorsal part of hyomandibula. One or two antoperculars. Operculum much higher, but a little narrower than suboperculum. Suboperculum with an internal lamina. About twelve to fourteen branchiostegal rays, the foremost (the lateral gular plate) largest. A small, median, unpaired gular plate. Basibranchial series with three ossifications. In each of the foremost two branchial arches: suprapharyngobranchial, infrapharyngobranchial, epibranchial, ceratobranchial, and hypobranchial. In each of the next two branchial arches: epibranchial, ceratobranchial, and hypobranchial; common to the two arches: a pharyngobranchial. In fifth branchial arch a slender ceratobranchial or hypo-ceratobranchial. In front of the place of articulation between epibranchial and ceratobranchial in each of the first four branchial arches a small ossification. Gill-rays as a rule not preserved. Articulation between foremost two branchial arches and endocranium (with parasphenoid) as in *Acipenser*. External dermal bones of head ornamented with striae and tubercles. Oral face of parasphenoid,

vomer, dermal bones of palatoquadrate, prearticular, and coronoids provided to a large extent with small acute teeth. Similar teeth on ventral margin of maxillary and dorsal margin of dentalo-splenial and on a mosaic of small tooth plates covering the oral face of the branchial arches and the ossifications of the basibranchial series. In roof of pharynx, behind right and left epibranchials IV, a pair of large tooth plates with small acute teeth. Four rows of large acute teeth, viz. a labial row on maxillary, lacrimo-maxillary, and ? premaxillary, a lingual row on ectopterygoid and the two dermopalatines, a labial row on dentalosplenial, and a lingual row on prearticular and coronoids. Teeth of normal Palaeonisciform type, enamel cap very small. Sensory canal system of head of normal Palaeonisciform type. Sensory canals fairly wide, canal bones with prominent ridge on internal face for each canal. Primary tubuli entirely subdivided into secondary tubuli. Anterior, middle, and posterior pit-lines on parietal, middle one often continuing on supratemporo-intertemporal. Vertical pit-line of cheek on quadratojugal, horizontal pit-line partly on preoperculum partly on maxillary. Pit-line on anterior branchiostegal ray (lateral gular plate). Pit-lines very deep, often closed to small canals. Notochord persistent and not constricted. In axial skeleton ossified basidorsals, interdorsals (in part of caudal region), supraneurals (independent in abdominal region), basiventrals (in abdominal region fused with interventrals), interventrals (independent in part of caudal region), infrahaemals (independent in anterior part of caudal region), and ribs. Ventral arcual elements in abdominal region and probably in greater part of caudal region laterally and ventrally bounding an aorta canal, in middle part of caudal region moreover a canal for the caudal vein. Ventral arcual elements in posterior part of caudal region with well developed hypural processes. Endoskeleton of shoulder girdle unossified in young individuals and ossified into one piece in older individuals, with processus glenoidalis and processus radialis, well developed mesocoracoid arch, two openings for diazonal nerves, and nearly horizontal margo radialis. Fenestra coraco-cleithralis well developed. Series of dermal bones of shoulder girdle comprising suprascapular, supracleithral, cleithrum, clavicle, and postcleithral. Dorsal part of cleithrum steep, ventral part nearly horizontal. Clavicle very large. In endoskeleton of pectoral fin a proximal and a distal series of radial ossifications. In the proximal series six well developed, and in the distal series six small, ossifications. Radials of fin parallel, supporting a scaly fin lobe. Pectoral fin large and expanded in a horizontal plane. Proximal part of anterior lepidotrichia of fin unsegmented. Pelvic plate ossified in old individuals, with long antero-medially directed slender process; behind pelvic plate in some cases independent metapterygial elements. In endoskeleton of pelvic fin eight proximal, but no distal radial ossifications. Pelvic fin small, situated nearly midway between base of pectoral fin and anal fin. Lepidotrichia segmented throughout. In endoskeleton of dorsal fin three series of ossi-

fications: an axonost series, a baseost series, and a distal series. In axonost series nine ossifications, the hindmost one compound. In baseost series and in distal series thirteen ossifications. Posterior part of dorsal fin low. Lepidotrichia close-set and segmented throughout. Posterior part of dorsal fin situated dorsally to anterior part of anal fin. In endoskeleton of anal fin a proximal and a distal series of ossifications. In proximal series ten ossifications, the hindmost one compound; the five posterior ossifications fairly intimately connected. In distal series eleven ossifications. Shape of anal fin like that of dorsal fin; lepidotrichia closely set and segmented throughout. Endoskeleton of caudal fin represented by a long series of epichordal and (in some cases) a few hypochordal radial ossifications. Greater part of hypochordal radial skeleton probably fused with hypurals. Caudal fin well developed, deeply cleft, equilobate or nearly so. Lepidotrichia closely set and segmented throughout Body axis of caudal fin with a dorsal series of large ridge scales. Anterior margin of all fins with small fulcra. Trunk covered with scales. A number of flank scales behind shoulder girdle higher than broad, remaining trunk scales rhombic or lower than broad. From 55 to 72 transverse, polymerically arranged scale-rows between posterior margin of supracleithral and line of inversion in caudal region. In front of dorsal fin (except in *Glaucolepis gyrolepidoides*) and on dorsal and ventral margins of caudal pedicle a number of enlarged ridge scales. Around anus three large anal scales. Peg-and-socket articulation best developed in abdominal region. Posterior margin of scales serrated. Ornament of scales consisting of fine striae, mostly running nearly diagonally; in some cases a greater or smaller number subdivided into tubercles. Ornament of scales most strongly developed on anterior part of trunk, decreasing in intensity with increasing distance from head. Scales consisting of a bone-layer, a cosmine-layer, and, in most cases at any rate, a continuous ganoine-layer. Bone-layer pierced by ascending canals only in posterior part of individual scales. Radial canals in cosmine-layer arranged as in *Palaeoniscus* but less frequently than in that species connected by fine anastomoses. Ascending canals through ganoine-layer very fine, few, or lacking. Ganoine lamellae slightly undulated.

The Greenland Species of Glaucolepis.

a. **Glaucolepis arctica** Stensiö.

(Fig. 55 B)

Syn: *Glaucolepis arctica*, Stensiö 1932, p. 121.

Diagnosis. – Rather small, somewhat deeply fusiform species, largest specimens a little more than 20 cm in length. Postorbital plate of maxillary rather high in relation to its length. Ornament of external dermal bones of head consisting of striae and tubercles, striae being the dominating orna-

mental elements. Operculum but slightly ornamented. 55–59 transverse scale-rows between posterior margin of supracleithral and inversion line of caudal region. From posterior margin of supracleithral to anterior margin in pelvic fin about 14, to anterior margin of dorsal fin 33–35, and to anterior margin of anal fin about 30 transverse scale-rows. Number of lepidotrichia in pelvic fin about 17, in dorsal fin 28–35, and in anal fin 30–35. Exposed surface of lepidotrichia smooth or with slight striation. In each of the anterior 10–12 transverse scale-rows one or more flank scales higher than broad. Majority of remaining flank scales rhombic. Scales fairly thick. Abdominal flank scales with vertical ridge on medial side and with well developed peg-and-socket articulation. Ornament of scales chiefly consisting of nearly diagonally disposed striae. Scales in posterior half of caudal region smooth.

Holotype. – Stensiö's holotype is designated No. 17 in the material collected prior to 1932. Stensiö gives the dimensions of the holotype as follows: total length of the preserved part of the specimen about 18 cm, estimated length of the complete fish 20 cm. Maximum height of the trunk (a short distance behind the shoulder girdle) somewhat more than 5 cm, but probably somewhat less in the living fish. Distance from the anterior margin of the base of the pectoral fin to the anterior margin of the base of the pelvic fin about 4.9 cm. Distance from the anterior margin of the base of the pelvic fin to the anterior margin of the base of the anal fin probably about 3.5 cm. Distance from the anterior margin of the base of the anal fin to the anterior margin of the base of the ventral lobe of the caudal fin about 3.4 cm.

Material. — Specimens Nos. 17 (holotype), 18, and 42 (Stensiö's numbers) of the material treated by Stensiö and collected prior to 1932. Specimens Nos. 5, 14, 15, 63, 64, 65, 67, 68, 69, 71, 74, 76, 121, 123, 124, 125, 131, 132, 135, 140, 141, 145, 146, 149, and 154 of the material collected in the years 1932 to 1937. All these specimens are derived from Fish-zone II, from which the following specimens of *Glaucolepis*, the great majority probably belonging to *Glaucolepis arctica*, were likewise collected: Nos. 62, 70, 84, 122, 126, 127, 130, 133, 136, 137, 138, 142, 143, 150, 151, 152, 157, and 180–190.

Localities. — The Kap Stosch area and the Hird Bay area.

Remarks. — According to Stensiö (1932, p. 124), *Glaucolepis arctica* differs from *Glaucolepis gyrolepidoides* by its larger size, by the presence of enlarged dorsal ridge scales in front of the dorsal fin, and by the smoothness of the scales in the posterior part of the caudal region.

From *Glaucolepis cicatrosus* it differs i.a. in its much smaller number of transverse scale-rows between the supracleithral and the inversion line of the caudal region, and from *Glaucolepis macropterus* it differs in its smaller number of lepidotrichia in the pelvic fin.

b. Glaucolepis stensiöi n. sp.

(Figs. 1–15, 19–21, 25, 27, 28, 45–47, 57; Pls. 1–4; Pl. 8, Fig. 3; Pl. 9, Fig. 1; Pl. 12, Fig. 2; Pls. 13–17).

Diagnosis. — Rather small, fusiform species, largest specimens measuring about 19 cm in length. Postorbital plate of maxillary even higher in relation to its length than in *Glaucolepis arctica*. Ornament of external dermal bones of head consisting of striae and tubercles, striae being the predominant ornamental element. Operculum nearly smooth. About 63 transverse scale-rows between posterior margin of supracleithral and inversion line in caudal region. From posterior margin of supracleithral to anterior margin of pelvic fin about 20, to anterior margin of dorsal fin 41–43, and to anterior margin of anal fin 35 transverse scale-rows. Number of lepidotrichia in pelvic fin 21–24, in dorsal fin 31–?40, and in anal fin 21–25. Exposed surface of lepidotrichia smooth. In anterior 10–12 transverse scale-rows one or more flank scales higher than broad. Majority of remaining flank scales rhombic. Scales fairly thick. Abdominal flank scales with vertical ridge on medial side and well developed peg-and-socket articulation. Ornament of scales consisting mainly of nearly diagonal striae. Scales entirely smooth in posterior part of caudal region.

Holotype. — As holotype I have choosen specimen No. 38, which is a fairly complete fish, only the distal parts of the pectoral fin, the anal fin, the caudal fin, and the dorsal fin lacking. Distance from tip of snout to base of concavity in margin of caudal fin about 154 mm, estimated length of complete fish about 190 mm. Height of trunk at anterior margin of anal fin 32 mm, at anterior margin of pelvic fin 43 mm. Distance from anterior margin of base of pectoral fin to anterior margin of base of pelvic fin 23 mm. Distance from anterior margin of base of pelvic fin to anterior margin of base of anal fin 31 mm. Distance from anterior margin of base of anal fin to anterior margin of base of ventral lobe of caudal fin 41 mm. Distance from posterior margin of medial extrascapular to anterior margin of base of dorsal fin 75 mm.

Material. — The material of *Glaucolepis stensiöi*, which is exclusively derived from Fish-zone V, comprises the following specimens: Nos. 38 (type specimen), 39 (sectioned specimen), 40, 41, 42, 48, 49, 50, 72, 73, 86–100, 103–114, 116, 117, and 118. Specimens Nos. 115 and 119, likewise derived from Fish-zone V, have been referred with some doubt to the same species.

Localities. — The Kap Stosch area.

Remarks. — *Glaucolepis stensiöi* is very closely related to *Glaucolepis arctica*, but can be easily distinguished from the latter by its greater number of transverse scale-rows (which, however, is much smaller than in *Glaucolepis cicatrosus*), by its smaller number of lepidotrichia in the anal fin, and by the shape of the postorbital plate of the maxillary.

c. *Glaucolepis magna* n. sp.

(Figs. 16–18, 22–25, 30, 31, 33–36, 38–41, 44, 48, 51–54; Pls. 5–7; Pl. 8, Figs. 1, 2; Pl. 10, Fig. 1; Pl. 12, Fig 1; Pl. 19; Pl. 20, Figs. 2, 3; Pl. 21, Fig. 4; Pls. 22, 23).

Diagnosis. — Large, slender species, estimated length of largest specimens about 40 cm. Postorbital plate of maxillary very low in relation to its length. Ornament of external dermal bones of head consisting of striae and tubercles, on several of the dermal bones tubercles are the predominant ornamental elements. Operculum strongly ornamented. In anterior 20–30 transverse scale-rows one or several flank scales higher than broad. Majority of other flank scales rhombic. Exposed surface of lepidotrichia with marked ornament of parallel striae, running obliquely in relation to the longitudinal axis of the lepidotrichia. Scales very thin. Abdominal scales without or with a slightly developed vertical ridge on medial side, and with slightly developed peg-and-socket articulation. Ornament of flank scales in abdominal region consisting of nearly diagonal striae, often subdivided to a considerable extent into tubercles. None of the trunk scales entirely smooth.

Holotype. — Since no specimen of this species is even fairly complete, I have chosen as holotype specimen No. 1, which shows large parts of the exo- and endoskeletons of the head and parts of the exo- and endoskeletons of the shoulder girdle, the pectoral fin, and scales of the anterior part of the abdominal region. The length of the head measured from the anterior end of the mandible to the postero-ventral corner of the suboperculum 78 mm, in the largest specimens of the species about 90 mm.

Material. — The material of this species is derived exclusively from Fish-zone V, and comprises the following specimens: Nos. 1 (type specimen), 2, 4, 6, 7, 8, 10, 11, 13, 46, 47, 51–61, 77, 80, 81, 85, 164, 165, 166, and 175–178.

Localities. — The Kap Stosch area.

Remarks. — *Glaucolepis magna* differs from *Glaucolepis arctica* and *Glaucolepis stensiöi* in size, shape of the postorbital plate of the maxillary, ornament of the dermal bones and of the lepidotrichia, and in the shape and ornament of the scales. It is rather difficult to mention definite points of differences between *Glaucolepis magna* and the Madagascan species of *Glaucolepis* because White's (1933, Figs. 1 and 2) and Piveteau's (1934, Fig. 57) figures of the dermal bones of the head in the Madagascan forms are incomplete and (White's figures) partly incorrect, and because the number of scale-rows and the size and position of the fins are nearly unknown in *Glaucolepis magna*. The only points of difference that can be mentioned at present are that larger portions of the lepidotrichia of the pectoral fin are unsegmented in the Madagascan forms than in *Glaucolepis magna*, and that the operculum is nearly smooth in the Madagascan forms, while it is strongly ornamented in *Glaucolepis magna*. *Glaucolepis magna* differs from *Glaucolepis gyrolepidoides* i.a. in the ornament of its scales and in size.

d. Glaucolepis gunnari n. sp.

(Figs. 26, 32, 49, 55 A; Pl. 9, Fig. 2; Pl. 10, Fig. 2; Pls. 11, 18; Pl. 27, Figs. 1–3).

Diagnosis. – Medium-sized slender species, estimated length of largest specimens ranging between 25 and 30 cm. Postorbital plate of maxillary a little higher and shorter than in *Glaucolepis magna*, but not as high and short as in *Glaucolepis arctica*. Ornament of external dermal bones of head consisting of striae and tubercles, striae being the predominant ornamental elements. Operculum less markedly ornamented than in *Glaucolepis magna*. Number of lepidotrichia in pelvic fin about 19, in dorsal fin 43–44, and in anal fin 35–38. Exposed surface of most lepidotrichia with marked ornament of striae running obliquely to the longitudinal axis of the lepidotrichia. In anterior 10–12 transverse scale-rows one or more flank scales higher than broad, majority of other flank scales rhombic. Scales very thin; flank scales without a vertical ridge or with a very faint vertical ridge on the medial side and with a slightly developed peg-and-socket articulation. Ornament of flank scales in abdominal region consisting predominantly of nearly diagonally disposed striae, most ventral striae on highest scales in abdominal region often subdivided into tubercles. Scales of caudal region never unornamented.

Holotype. – As holotype I have chosen specimen No. 18, which consists of a fairly complete fish, only the distal part of all the fins lacking. Total length of preserved part of the specimen 226 mm, estimated length of the complete fish about 250 mm. Height of trunk at anterior margin of anal fin 33 mm, at anterior margin of pelvic fin 44 mm. Length of head measured from tip of snout to postero-ventral corner 60 mm. Distance from anterior margin of base of pectoral fin to anterior margin of base of pelvic fin 27 mm. Distance from anterior margin of base of pelvic fin to anterior margin of base of anal fin 42 mm. Distance from anterior margin of base of anal fin to anterior margin of base of ventral lobe of caudal fin 37 mm. Distance from posterior margin of medial extrascapular to anterior margin of base of dorsal fin 83 mm.

Material. – Specimens Nos. 3, 9, 16, 18 (holotype), 19–23, 25, 26, 27, 34, 37, 44, 101, 102, 158, 160, 169, and 170 are derived from Fish-zone III, while specimens Nos. 128, 134, and 144 were found in Fish-zone II but have possibly slid down from Fish zone III. In addition a number of *Glaucolepis* specimens derived from Fish-zone III probably belong to *Glaucolepis gunnari*. These specimens are as follows: Nos. 17, 24, 28, 29, 30, 31, 32, 35, 45, 159, 161, and 171–173.

Localities. – The Kap Stosch area.

Remarks. – *Glaucolepis gunnari* is very closely related to *Glaucolepis magna*, but differs from it in that tubercles play a less part in the ornament of the scales and of the dermal bones of the head, in the slighter ornament of the operculum, and in the smaller number of high abdominal flank scales. *Glaucolepis gunnari* has been named after Professor Gunnar Säve-Söderbergh, University of Uppsala.

e. Glaucolepis aldingeri n. sp.

(Figs. 37, 42, 43, 55 C, 56; Pl. 20, Fig. 1; Pl. 24).

Diagnosis. – Large, slender species, largest specimens about 30 cm in length. Ratio between height and breadth of postorbital plate of maxillary as in *Glaucolepis arctica*. Ornament of greater number of external dermal bones of the head very coarse, consisting of striae and tubercles. Tubercles the predominant ornamental elements on many of the dermal bones. Operculum slightly ornamented. More than 65 transverse scale-rows between posterior margin of supracleithral and inversion line in caudal region. From posterior margin of supracleithral to anterior margin of pelvic fin 16–18, to anterior margin of dorsal fin more than 40, and to anterior margin of anal fin c. 37 transverse scale-rows. Number of lepidotrichia in pelvic fin c. 18, in dorsal fin c. 40, and in anal fin c. 40. Exposed surface of lepidotrichia in some cases with a system of very faint parallel striae running obliquely to the longitudinal axis of the lepidotrichia. In other cases no trace of this system of striae. In the anterior c. 20 transverse scale-rows one or more flank scales higher than broad. Majority of other flank scales of the trunk much broader than high. Scales thick, flank scales with vertical ridge on medial side and well developed peg-and-socket articulation. Ornament of abdominal flank scales consisting predominantly of nearly diagonal striae. Scales of caudal region never entirely smooth.

Holotype. – As holotype I have chosen specimen No. 66, a fish lacking head, shoulder girdle, pectoral fin, and the posterior part of the caudal fin. Total length of the preserved part of the specimen 185 mm, estimated length of the complete fish 240–260 mm. Height of trunk at anterior margin of anal fin 37 mm, at anterior margin of pelvic fin 40 mm. Distance from anterior margin of base of pelvic fin to anterior margin of base of anal fin 47 mm. Distance from anterior margin of base of anal fin to anterior margin of base of ventral lobe of caudal fin 59 mm.

Material. – The following specimens of *Glaucolepis aldingeri* are at hand: Nos. 43, 66 (holotype), 75, 147, 148, and 179. All these specimens are derived from Fish-zone II except the last-mentioned, which was found in Fish-zone IV.

Localities. – The Kap Stosch area.

Remarks. – *Glaucolepis aldingeri* is easily distinguishable from all other species of *Glaucolepis* by the majority of its flank scales being very low.

In addition to that part of the material which could be referred with a greater and smaller degree of certainty to the five species mentioned above, some specimens are found which owing to their incomplete state of preservation could not be specifically identified. These specimens are Nos. 36, 79, 82, 83, 168, and 174. All of them are derived from Fish-zone IV except No. 36, which was found in Fish-zone VI (the Stegocephalian-horizon) as the only specimen of *Glaucolepis* from this zone.

Remarks on other Species of Glaucolepis.

a. Glaucolepis gyrolepidoides Stensiö.

This species, erected by Stensiö (1921, pp. 200–203) on the basis of material derived from the Triassic of Spitsbergen, is easily distinguishable from the other species of *Glaucolepis* because it lacks dorsal enlarged ridge scales in front of the dorsal fin. Head, shoulder girdle, and pectoral fin are unknown.

b. Glaucolepis cicatrosus (White) and Glaucolepis macropterus (White).

The characters in which these two Madagascan Eotriassic species erected by White (1933, pp. 118–128) differ from the other species of *Glaucolepis* have been mentioned on the preceding pages. I shall therefore here merely correct some conspicuous errors in White's restoration of the head of *Glaucolepis* (White 1933, Figs. 1 and 2), supporting my corrections on a single well preserved specimen of a Madagascan *Glaucolepis* which is at my disposal.

In White's restoration the postrostral is shown as a small oval bone. which does not extend as far in a ventral direction as the much larger nasal, (Curiously enough White (1933, p. 122) mentions in his text the postrostral as a relatively large bone). Later Brough (1939, p. 94) interpreted the small size of the postrostral in White's restoration as a character pointing towards the Parasemionotids. Actually, however, the postrostral in the Madagascan *Glaucolepis* has the same great extent and the same shape as in the Greenland species. The supraorbito-postorbital (White's postfrontal) is in contact with the posterior margin of the nasal, as in the Greenland *Glaucolepis*, which does not appear from White's restoration. Laterally to the dorsal part of the nasal White indicates the presence of a prefrontal. Actually no bone is found in this place. Between the ventral part of the nasal and the orbit, an antorbital (White's lacrimal) is seen in White's restoration. In my only specimen of *Glaucolepis* from Madagascar the antorbital cannot be investigated; but it is hardly too bold to assume that it must have been placed in the same way in relation to the nasal as in the Greenland species. It is likewise probable that the lacrimal (White's jugal) is fused with the maxillary component, as in the Greenland species. However, the proof of this can only be obtained by a reinvestigation of well preserved material. A dermohyal is not indicated in White's restoration, but is distinctly seen on my Madagascan specimen.

Aldinger (1937, p. 96) points out that *Palaeoniscus crassus* Woodward (Woodward 1908, pp. 9–11; Pl. 2, Figs. 3, 4) derived from the Hawkesbury formation, New South Wales, in several respects (shape of trunk, position of pelvic fin, and number of enlarged ridge scales in front of dorsal fin) bears greater resemblance to *Glaucolepis* than to *Palaeoniscus*.

REMARKS ON THE FAMILY PALAEONISCIDAE

S. STR. ALDINGER

Aldinger (1937, pp. 229-230) erected the family *Palaeoniscidae* s. str., which includes the genera *Palaeoniscus, Glaucolepis, Gyrolepis,* and *Oxygnathus.* As Aldinger points out himself, his diagnosis of this family is not particularly precise, since nearly all the structures that could be investigated changed more or less from the first appearance of the family in the Permian to its disappearance in the Lias. Of course the family diagnosis can be supplemented to some extent on the basis of the present investigation of *Glaucolepis;* but until a detailed investigation of the other three genera of Palaeoniscids has been made, such a supplementation will be without any particular value, for on the whole it will be merely a repetition of the diagnosis of the genus *Glaucolepis.*

Aldinger (1937, p. 249) writes as follows about the relations between the four genera of the *Palaeoniscidae:* "Ein befriedigendes Bild von der Entwicklung der *Palaeoniscidae* zu geben ist noch nicht möglich, denn alle Genera sind nur oberflächlich bekannt, die äusseren Merkmale ändern zwar mehr oder weniger stark, aber wenn wirklich bedeutsame Veränderungen im Lauf der Entwicklung vor sich gegangen sein sollten, so müssen sie sich im Innenskelett abgespielt haben. Die wichtigste Frage, die sich in diesem Zusammenhang erhebt, ist die, ob die Genera der Familie eine geschlossene Entwicklungsreihe bilden, oder ob Glieder der Reihe fehlen bezw. ein Teil der Genera nur Seitenzweigen vorstellt. Die geologische Überlieferung ist insofern sehr vollständig, als zu allen Zeiten vom Mittleren Perm bis Unteren Lias, aus welchen marine Fischfaunen bekannt sind, auch *Palaeoniscidae* s. str. vorliegen, die einzelnen Genera schliessen lückenlos aneinander. Da auch keine tiefgehenden Spezialisationskreuzungen nachzuweisen sind, so steht einstweilen nichts im Wege, die verschiedenen Genera als eine genetische Reihe aufzufassen."

The present detailed investigation of *Glaucolepis* does not essentially elucidate the picture of the development of the *Palaeoniscidae,* for most of the structures investigated in *Glaucolepis,* principally the endoskeletal ones, are so far entirely unknown in the other three Palaeoniscid genera.

Common to the four genera are the following characters: I) the *Elonichthys*-like shape of the frontal and the supratemporo-intertemporal; II) the

two pairs of extrascapulars; III) the presence of two series of supraorbitals, a lateral and a medial, which are either separate or present as components in compound bones; IV) the very oblique suspensorium; V) the large operculum; VI) the rather faint ornament on the dermal bones of the head; VII) the horizontal pectoral fin; VIII) the small scales.

The most important structural changes that can be observed from one form to the other are as follows: 1) In *Palaeoniscus* the anterior margin of the extrascapular series is in contact throughout its length with the posterior margin of the mutually connected parietals and supratemporo-intertemporals. In *Glaucolepis* and *Oxygnathus,* however, one or more pairs of small rounded dermal bones are situated between the extrascapular series and the supratemporo-intertemporal-parietal series. 2) In *Palaeoniscus* and *Oxygnathus* the majority of the elements of the supraorbital series are separate; in *Glaucolepis* the two series are completely fused with the dermosphenotic and a postorbital element respectively. 3) The bases of the dorsal and anal fins increase in length from the older to the younger forms. 4) In *Palaeoniscus* the pelvic fin lies nearer the anal fin than the pectoral fin, while in the younger genera it lies either at equal distances from the anal and pectoral fins or nearest the latter fin. 5) In *Palaeoniscus* the ventral lobe of the caudal fin is decidedly shorter than the dorsal lobe, while in the younger forms the two lobes are practically of the same length. 6) In *Palaeoniscus* the lepidotrichia of the pectoral fin are segmented right down to the base, while through the series *Glaucolepis-Gyrolepis-Oxygnathus* an increasing number of lepidotrich segments of the pectoral fin are united into an unsegmented proximal lepidotrich division. 7) The scale structure, which in *Palaeoniscus* is of entirely the same type as in certain species of *Elonichthys*, changes gradually through *Glaucolepis* and *Gyrolepis* to *Oxygnathus* by a gradual reduction of the cosmine-layer and (to a less extent) of the ganoine-layer and by an increase of the number of canals in the bone-layer. 8) The number of ridge scales in front of the dorsal fin and on the dorsal and ventral margins of the caudal pedicle decreases from the older towards the younger forms. 9) Only in *Glaucolepis* have a postspiracular bone and an antoperculum been observed; likewise in this genus alone has a fusion of the lacrimal and a maxillary component been observed.

In all the characters mentioned here the earliest genus, *Palaeoniscus*, is no doubt primitive, and within the series of Palaeoniscid genera the changes designated 1, 3, 4, 5, 6, 7 and 8 take place in such a way that they are not inconsistent with the conception of the series as a single continuous developmental series. As regards the change numbered 2 the case is different. In *Palaeoniscus* and *Oxygnathus* two rows of independent supraorbitals are found, but in *Glaucolepis*, which is intermediate as to time between *Palaeoniscus* and *Oxygnathus*, none of the elements of the supraorbital series is independent. This seems to indicate that *Glaucolepis* does not lie in the

line of evolution leading from *Palaeoniscus* to *Oxygnathus*. The change designated 9, viz. that *Glaucolepis* has an antoperculum, while such a bone is absent both in *Palaeoniscus* and in the younger genera points in the same direction. (Aldinger's (1937, pp. 249–50) arguments for assuming that the isolated occurrence of an antoperculum in *Glaucolepis* is not inconsistent with a genetic association between *Glaucolepis* and the younger forms do not sound very convincing). From the presence in *Glaucolepis* of a postspiracular bone, a lacrimo- maxillary, a dermohyal, and a quadratojugal, however, we can hardly at present draw any conclusions as to the interrelationship of the Palaeoniscid genera, for neither *Palaeoniscus*, *Gyrolepis*, nor *Oxygnathus* have been so thoroughly investigated that the absence of the bones in these forms can be taken for granted.

According to Aldinger's (1937, p. 234) investigations, *Palaeoniscus* shows so complete agreement with *Elonichthys* in the scale structure that in all probability the family *Palaeoniscidae* is derived from *Elonichthys* or at any rate from an Elonichthyid. However, the present investigation of *Glaucolepis* throws no new light on the interrelationship of the families *Palaeoniscidae* and *Elonichthyidae*, as we have only a superficial knowledge of the genera belonging to the family *Elonichthyidae* and are accordingly unable to draw even a fairly detailed comparison between these genera and *Glaucolepis*.

In my description of the material of *Glaucolepis*, I have dealt with the considerable agreement that exists between *Glaucolepis* and *Pygopterus* in regard to the axial skeleton, the endoskeletal shoulder girdle, and the endoskeletons of the pelvic plate and the unpaired fins (pp. 221, 229, 242–43). Aldinger (1937, pp. 309–10) groups *Pygopterus* with *Nematoptychius* and (with some doubt) *Cosmoptychius* in a special family, the *Pygopteridae*, but points out that our knowledge of these three genera is so unsatisfactory that this grouping is perhaps a little premature. Aldinger (1937, p. 314) writes as follows about the relationship of the family *Pygopteridae* to the other *Palaeonisciformes:* "Im äusseren Habitus, in der Anordnung der Deckknochen des Schädeldachs, der Wangen und des Visceralskeletts, sind die *Pygopteridae* nur wenig verschieden von den älteren Vertretern der *Elonichthyidae*, *Palaeoniscidae* s. str. und *Acrolepidae*. Im Bau des Parasphenoids, des primären Schultergürtels, des Innenskelettes der unpaaren Flossen und vielleicht auch im Aussenskelett und Endocranium weichen die *Pygopteridae*, oder zumindest *Pygopterus* und *Cosmoptychius*, dagegen erheblich von den genannten Familien ab.

Am Parasphenoid von *Pygopterus* und *Cosmoptychius* sind, wie schon oben gesagt wurde, vorderer und hinterer Processus ascendens vollständig von einander getrennt wie bei *Rhadinichthys* (Day 1915), bei den *Palaeoniscidae* dagegen (*Palaeoniscus*), bei *Acrolepidae* (*Hyllingea*) und wahrscheinlich auch den *Elonichthyidae* (vgl. Watson 1925) sind sie miteinander verbunden oder der vordere Fortsatz fehlt. Am primären Schultergürtel von *Pygopterus* ist

kein Fortsatz vorhanden, der dem Mesocoracoid der Holostei verglichen werden könnte, wie bei *Acrolepidae* (*Acrorhabdus*) und wohl auch *Palaeoniscidae* (*Palaeoniscus*). Die Analflosse hat eine Serie von Flossenträgern, die am distalen Ende verdickt sind und mit einander gelenken, ebenso sind die Baseoste der Dorsalflosse zum Teil verbreitert und mit einander verbunden. Im Achsenskelett innerhalb der Caudalflosse sind knöcherne Wirbelzentren vorhanden.

Alle diese Merkmale machen es wahrscheinlich, dass die *Pygopteridae* eine Familie sind, die mit den *Acrolepidae* und *Palaeoniscidae* (und damit auch *Elonichthyidae*) nicht sehr nahe verwandt ist. Möglicherweise bestehen Beziehungen zu *Rhadinichthys*."

To the points of difference between *Pygopteridae* and *Palaeoniscidae* mentioned by Aldinger in the passage quoted above, I wish to add a few comments. Our knowledge of the Pygopterid endocranium is based exclusively on Watson's brief description of a part of an endocranium of a young individual of *Cosmoptychius striatus* (Watson 1928, pp. 48–55, Figs. 1–3). This incomplete endocranium agrees in all essentials with the endocranium in *Glaucolepis*, to which it is much more closely related as regards the course of the aorta canal and the size of the processus basipterygius than to the Kansas forms.

It has been pointed out above (p. 109) that probably no sharp limit can be drawn between a type of parasphenoid in which the processus ascendens anterior is separated from the processus ascendens posterior, and a type in which these two processes are entirely fused. The difference between the parasphenoids in the *Elonichthyidae* and the *Palaeoniscidae* need not, accordingly, mean that the two families are only remotely related to each other.

As I have explained above (p. 278), the axial skeleton and the skeletons of the unpaired fins in *Glaucolepis* and *Pygopterus* present great points of resemblance, and the same applies to the pelvic plate and the endoskeletal shoulder girdle (p. 278), except that a mesocoracoid arch seems to be entirely absent in the *Pygopteridae* (*Pygopterus*). The absence of the mesocoracoid arch, which is perhaps merely due to an incomplete ossification of the endoskeletal shoulder girdle (cf. p. 359), and the very considerable length of the bases of the dorsal and anal fins are at present the only characters known by which the *Pygopteridae* may be distinguished from the *Palaeoniscidae*. It is probable, therefore, that the two families are even very closely related, and that accordingly the ancestor of the *Pygopteridae* should be looked for among the *Elonichthyidae*.

BOREOSOMUS Stensiö

The genus *Boreosomus* was erected by Stensiö (1921, p.210) on the basis of material derived from the Triassic of Spitsbergen; previously Woodward (1912, pp.292–93) had referred some specimens of the same material to the genus *Acrolepis*.

Stensiö's material, which comprised the species *Boreosomus arcticus*, *Boreosomus reuterskiöldi*, and *Boreosomus ? scaber* in addition to indeterminable *Boreosomus* remains, was very incomplete and for instance supplied only little information about the structure of the head.

In 1928 Corroy (1928, p.20) described a scale derived from the Triassic of Lorraine as *Boreosomus cf. reuterskiöldi*. Stensiö (1932, p.117) and later Aldinger (1937, p.277) have expressed doubts as to the correctness of this identification.

In 1932 Stensiö (1932, p.117) provisionally referred a fragment of a fish from the Eotriassic of East Greenland to *Boreosomus*.

In 1933 Brough (1933, pp.78–87) on the basis of material from the Eotriassic of Madagascar erected the genus *Diaphorognathus* with the species *Diaphorognathus gillioti* (Priem) (Priem's *Gyrolepis ? gillioti* (Priem 1924, p.107)), and in 1934 Piveteau (1934, pp.86–88) described further material of this species.

In 1936, after a preliminary examination of part of the material treated in the present paper, I arrived at the result that *Boreosomus* (and possibly the closely related genus *Acrorhabdus*, too) occurs in the Eotriassic of East Greenland, and that the genera *Diaphorognathus* and *Boreosomus* are identical (E. Nielsen 1936, pp. 35 and 44), and this was confirmed in a brief note by Piveteau in 1937.

In 1937 Aldinger (1937, p.282), without knowing my paper of 1936, discussed the relations between *Boreosomus* and *Diaphorognathus*, and came to the result that the two genera are very closely related or perhaps even identical. In the same work Aldinger (1937, p.298) pointed out the close relationship that exists between *Boreosomus* and *Ptycholepis*, a fact which was later, but independently of Aldinger, recognised by Brough (1939, pp.99–104).

The East Greenland material of *Boreosomus* comprises about 140 specimens, which all seem to belong to the same species, though they exhibit considerable variations. This species also includes the specimens which, after a first examination of the material, I was inclined to refer to *Acrorhabdus*.

Description of the Material.

The neural endocranium.

General remarks. – A head of *Boreosomus piveteaui* was chosen for investigation by the aid of Sollas's grinding method.

The specimen (No. 310) was collected in 1932 in Fish-zone V on the Stensiö Plateau. It consisted of a fragment of a concretion which by preparation in the laboratory proved to contain a head of *Boreosomus*. By the preparation the dermal cranial roof was exposed, and an attempt was made to expose the right cheek. It turned out, however, that the cheek was very unsatisfactorily preserved, nearly all its dermal bones being absent.

The mutual position of the various exposed parts of the exoskeleton of the head indicated that the head had not been compressed; but since the neural endocranium itself was not visible, it was in some degree at random that I chose that specimen for investigation.

The specimen was photographed (Pl. 29, Figs. 1, 2) and cemented into plaster, after which the grinding was commenced. As in *Glaucolepis stensiöi* the grinding plane was placed fairly parallel with the dorsal side of the head, the right and the left half of each section thus being symmetrical as far as possible, and the grinding was made from the dorsal towards the ventral part of the endocranium.

The grinding was commenced in 1936, but was stopped after a few weeks and was not continued till 1940-41.

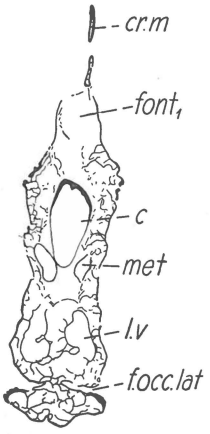
Between each of the grinding faces drawn there is a distance of 50 μ, and so far 93 drawings have been completed, which means that between one-half and one-third of the neural endocranium has been investigated by grinding (after the manuscript was finished, sixty more drawings have been made).

One of the reasons why the grinding has proceeded so slowly is that both the matrix and the bone exhibit nearly the same dark hue, and even staining with alizarin produces no particularly good contrast between bone and rock.

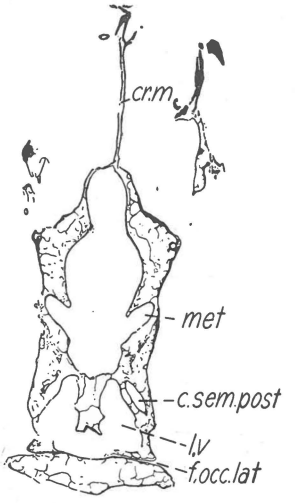
On the basis of the drawings, which, as in the case of *Glaucolepis stensiöi*, were drawn ten times magnified, two models were constructed, one of the dorsal part of the neural endocranium and one of the dorsal part of the cavity of the endocranium.

The subjoined description is based partly on these models and partly on a number of fairly complete endocrania dissected by means of the dental mallet (viz. the specimens Nos. 278, 295, 296, 298, 300, 301, 306, 307, and 309).

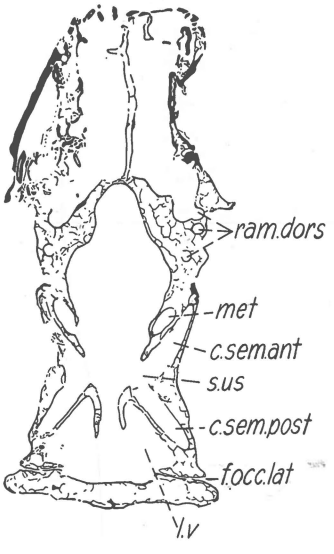
It should be pointed out at once that the investigation of the part of the neural endocranium not prepared by grinding is not by far so detailed as the investigation of the ground part, since several details, notably regarding the course of the canals for nerves and vessels, could not be accurately examined in the very small endocrania. The description of the neural endocrani-


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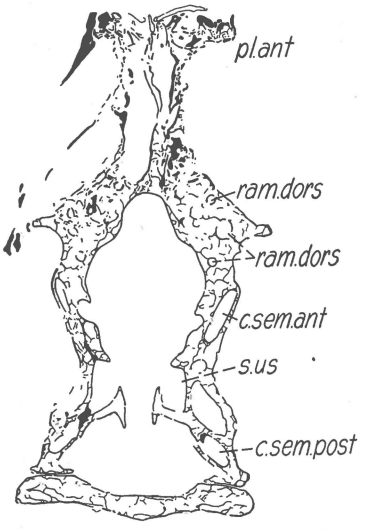
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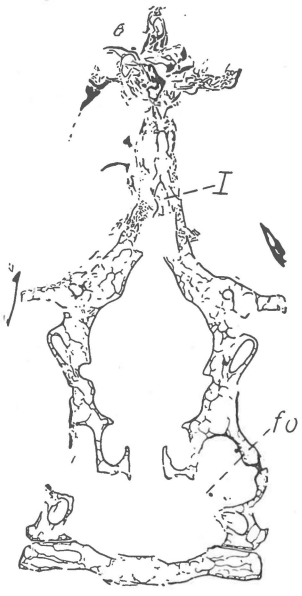
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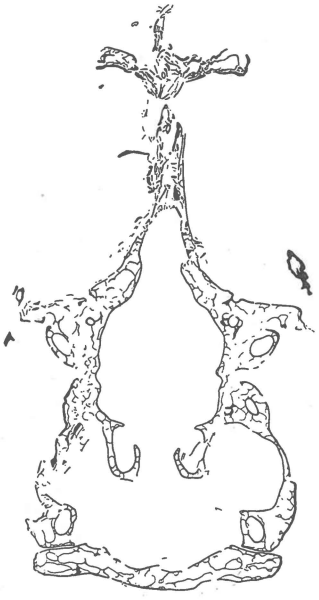
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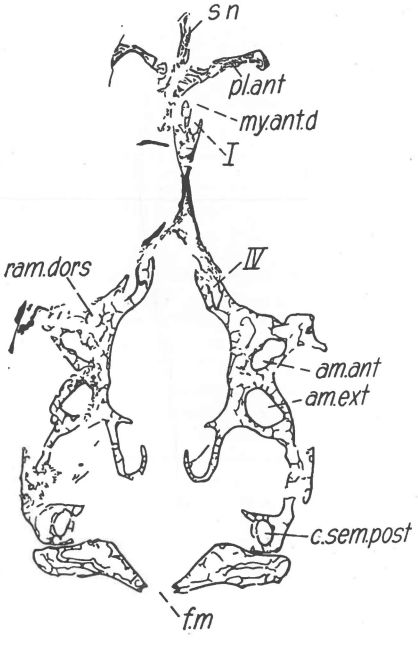
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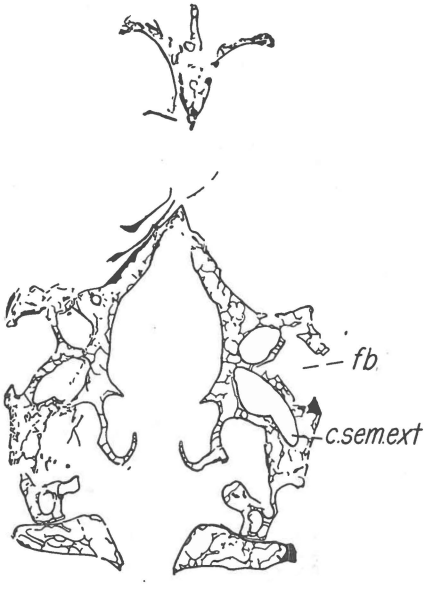
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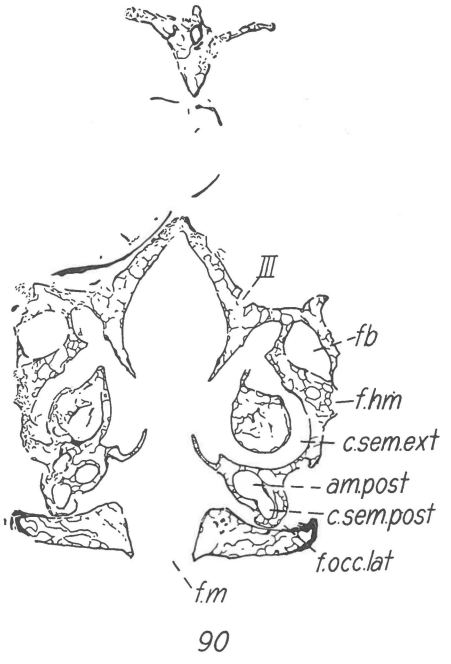


Fig. 58. *Boreosomus piveteaui*, n. sp. Sections Nos. 10, 20 etc. from an unfinished grinding series (cf. p. 281). Specimen No. 310. 3.2 ×.

am. ant, *am. ext*, *am. post*, divisions of the labyrinth cavity for the ampulla anterior, the ampulla externa, and the ampulla posterior respectively; *c*, cavum cerebrale cranii; *c. sem. ant*, *c. sem. ext*, *c. sem. post*, divisions of the labyrinth cavity for the canalis semicircularis anterior, the canalis semicircularis externus, and the canalis semicircularis posterior respectively; *cr. m*, median crista on the dorsal face of the orbitotemporal region; *fb*, anterior part of the fossa bridgei; *f. hm*, articular fossa for the hyomandibula; *f. m*, foramen magnum; *fo*, opening in the wall between an intramural space in the dorsal wall of the otic region and the cavum cerebrale cranii; *f. occ. lat*, fissura occipitalis lateralis; *font*$_1$, anterior dorsal fontanelle; *l. v*, division of the cavum cerebrale cranii for the "lobi vagi"; *met*, division of the cavum cerebrale cranii for the lateral part of the metencephalon; *my. ant. d*, anterior dorsal myodome; *pl. ant*, planum antorbitale; *ram. dors*, canals for branches of the nervus ophthalmicus lateralis, the ramus ophthalmicus superficialis trigemini and vessels; *sn*, septum nasi; *s. us*, division of the labyrinth cavity for the sinus utriculi superior; *I*, canal for the nervus olfactorius; *III*, canal for the nervus oculomotorius; *IV*, canal for the nervus trochlearis.

um must therefore to some extent be regarded as preliminary, all the more so since I hope to be able later to publish the complete series of sections of this form. In spite of the preliminary character of the investigation I considered it of importance to publish it here, for it gives a sufficiently clear picture of the neural endocranium to enable us to draw fairly detailed comparisons with the neural endocranium in *Glaucolepis*.

The partially sectioned endocranium had a length of about 26 mm and a maximum breadth (the distance between the right and left postorbital processes) of about 14–15 mm. The dimensions of some of the other endocrania are as follows:

Specimen No. 296. Length c. 27 mm, greatest breadth 15 mm, greatest height 11–12 mm.

Specimen No. 278. Length c. 22 mm, greatest breadth 13–14 mm, greatest height at least 9 mm.

Specimen No. 307. Length 23–24 mm, greatest breadth c. 15 mm, greatest height 11 mm.

As is seen from the sections shown in Fig. 58, the bone-tissue of the endocranium has a macroscopic structure which differs somewhat from that of *Glaucolepis*. The individual laminae of the endochondral bone have, indeed, formed the walls of small, more or less rounded chambers, medullary spaces, as in *Glaucolepis;* but, as a comparison of the drawings will show, these walls are far more incomplete in *Boreosomus* than in *Glaucolepis*.

The endochondral mass of bone is lined with perichondral bone-layers both on its external faces and on its faces towards the cavities and canals of the endocranium. In many, but not in all the specimens this perichondral bone-layer is perforated by numerous minute round openings which are easily mistaken for the openings of the smallest canals for nerves and vessels leading from the cavum cerebrale cranii to the external faces of the endocranium. In several of the figures the first-mentioned small openings are distinctly seen (Pl. 25, Fig. 1; Pl. 26, Fig. 1; Pl. 27, Fig. 1; Pl. 28). The bone shows no trace of radiation. The bone-tissue of the other endoskeletal ossifications in *Boreosomus* are of the same type as that of the neural endocranium.

In many cases the neural endocranium is completely ossified, and constitutes one large ossification extending from the posterior part of the occipital region to the anterior part of the ethmoidal region. In other cases the endocranial ossification has a more limited forward extension, the ethmoidal region being unossified. Finally, in the smallest specimens the endocranium is completely unossified.

As stated above, the neural endocranium in the most strongly ossified specimens of *Glaucolepis* has a large anterior and a large posterior unpaired ossification, while the smallest specimens lack any trace of ossifica-

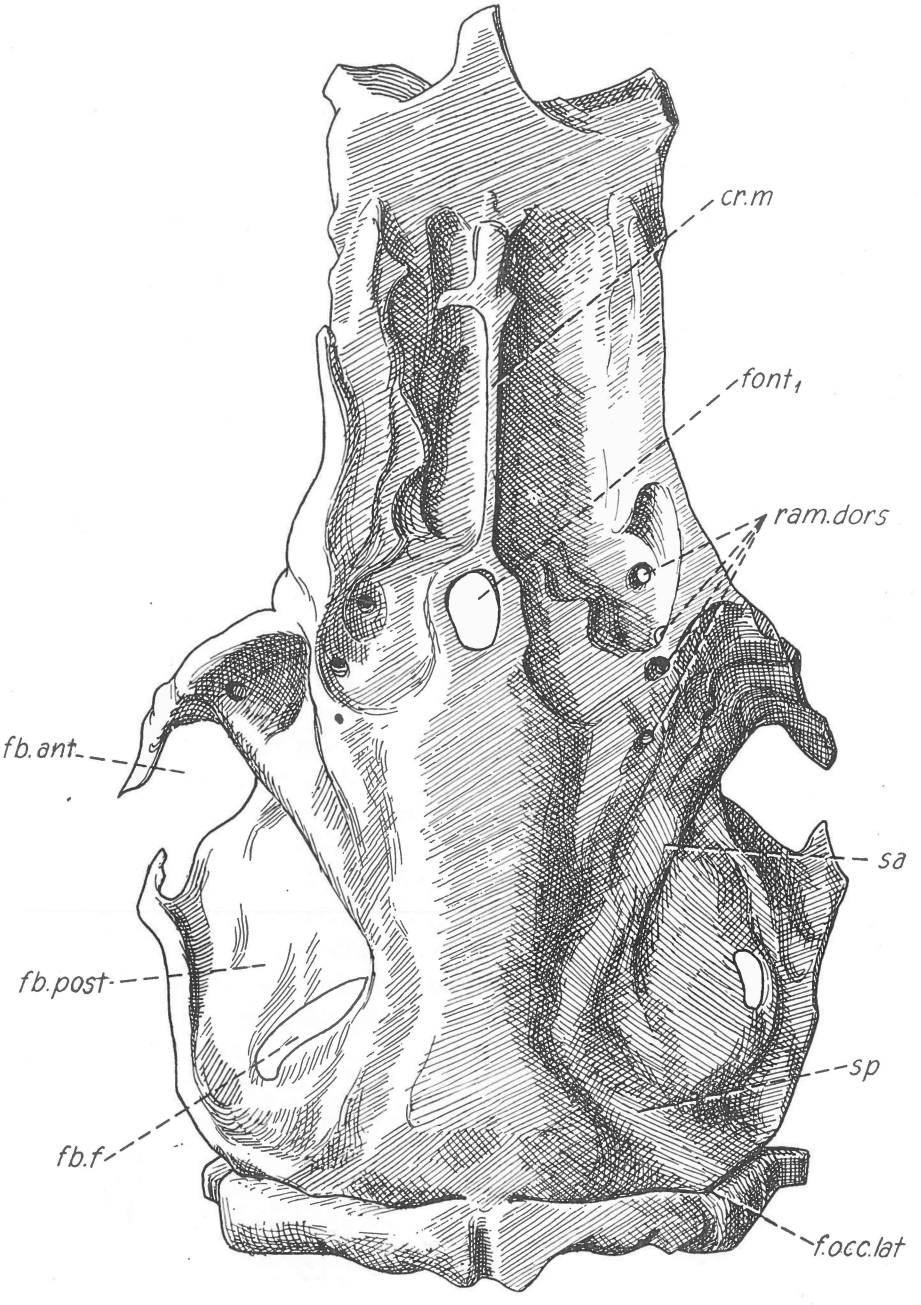


Fig. 59. *Boreosomus piveteaui* n. sp. Dorsal part of the neural endocranium in dorsal view. Based on a wax model. 6–7 ×.

fb. ant, fb. post, anterior and posterior parts of the fossa bridgei; *fb. f,* opening in the wall between the posterior part of the fossa bridgei and an intramural space in the dorsal wall of the otic region; *sa,* ridge above the canalis semicircularis anterior; *sp,* ridge above the canalis semicircularis posterior. Other letters as in Fig. 58.

tions. Between these extremes, specimens with a greater number of small paired and unpaired ossifications in the endocranium are found, and thus it can be ascertained that the process of ossification begins in several areas of the cartilaginous endocranium.

Corresponding intermediate stages are unknown in *Boreosomus*, so it is impossible to decide whether the process of ossification takes place from more than one area.

In the occipito-otic division of the endocranial ossification the cranial wall is pierced by a fissure (*f. occ. lat*, Figs. 58, 59, 60, 62, 63, 66; Pl. 25, Figs. 1, 2, 3; Pl. 26, Figs. 1, 2; Pl. 27, Figs. 1, 2; Pl. 28), whose walls are lined with perichondral bone and which accordingly was not only a cartilaginous zone of the cranial wall. Through the dorsal wall of the endocranium the fissure has a transverse course, and often separates the roof of the occipital region from that of the otic region. This part of the fissure is often very narrow, but in some cases its median part is expanded, so that a median fontanelle is formed in the roof of the endocranium (*font*$_2$, Pl. 28); this fontanelle corresponds to the posterior dorsal fontanelle in *Glaucolepis*. In other cases the transverse fissure in the roof of the endocranium effects no complete separation of the roof of the occipital from that of the otic region, the fissure being completely closed in its middle part, that is to say, curiously enough precisely in that part which in certain other specimens is expanded to form the posterior dorsal fontanelle. This applies i. a. to the sectioned specimen. The fissure continues from the roof of the endocranium down through its lateral wall, where farthest dorsally it separates the dorsal part of the lateral wall of the occipital region from the dorsal part of the lateral wall of the otic region. The passage of the vagus nerve is indicated by an expansion of the otherwise very narrow fissure (X, Figs. 62, 63; Pl. 26, Fig. 1; Pl. 27, Figs. 1, 2; Pl. 30, Fig. 1). Ventrally to the exit of the vagus the fissure runs in an antero-ventral direction to a diminutive vestibular fontanelle in the lateral wall of the otic region (*v. font*, Figs. 62, 63; Pl. 26, Fig. 1; Pl. 27, Fig. 1).

The above-mentioned fissure agrees in its course with the fissura occipitalis lateralis in *Glaucolepis*, and is undoubtedly homologous with that structure.

As stated above, the basal part of the otic region in *Glaucolepis* is pierced by a transverse fissure, the fissura oticalis ventralis, which connects the right and left vestibular fontanelles. In contrast to the lateral occipital fissure, this fissure was filled with cartilage. The cartilage is not preserved in the fossil cranium, so that on account of the connection between the lateral occipital fissure (which is expanded dorsally into the posterior dorsal fontanelle), the vestibular fontanelle, and the ventral otic fissure, the posterior part of the endocranial ossification is completely separated from the anterior part.

In *Boreosomus* a transverse unossified zone, (*f. ot. v*, Figs. 62, 63; Pl. 26, Fig. 1; Pl. 27, Fig. 1) situated as far forward as the anterior opening of the

aorta canal, is sometimes found in the basal part of the otic region. As will be seen from the figures, this zone is very short and does not reach the small vestibular fontanelle on the lateral face of the otic region. Consequently the continuity of the endocranial ossification in *Boreosomus* is not interrupted as in *Glaucolepis*.

In the majority of specimens of *Boresomus* in which the median part of the dorsal division of the lateral occipital fissure is open, the lateral occipital fissure has precisely the same extent as in the Kansas forms A and B (Watson 1925, Figs. 10–13).

In *Perleidus* (Stensiö 1932, Fig. 59) that part of the occipital fissure which in the Kansas forms is widened to form the posterior dorsal fontanelle, is entirely closed, as is the case in a few specimens of *Boreosomus* also. In *Perleidus* the vestibular fontanelle and nearly the whole fissure between this fontanelle and the vagus opening are likewise closed. In *Ospia* (Stensiö 1932, Figs. 72–73) the occipital fissure is even shorter than in *Perleidus*.

Occipital region. – The occipital region is very short in relation to the whole endocranium (Fig. 62, Pl. 26, Fig. 1). It is of about the same height as the otic region, and its maximum breadth is a little greater than its height.

A subdivision of the occipital region into an anterior and a posterior part corresponding to the subdivision of the occipital region in *Glaucolepis* (p. 31) is, of course, possible, but would appear so artificial that I prefer to treat the region as a whole.

Dorsally, and to some extent laterally also, the occipital region is separated from the otic region by the occipital fissure. Farther ventrally there is no marked boundary between the two regions.

Broadly speaking the occipital region has the following external faces: an unpaired dorsal, an unpaired posterior, a paired lateral, and an unpaired ventral face.

The outline of the unpaired posterior face is seen from the sketch shown in Fig. 61. It will be seen from the sketch that the posterior face is very broad farthest dorsally while it grows narrower in a ventral direction. A fairly large, oblong, rounded median opening is found in this face, which opening is nearly thrice as long as broad; it corresponds to the foramen magnum plus the posterior opening of the notochordal space plus the posterior opening of the aorta canal in *Glaucolepis*. In the complete specimens of *Boreosomus* I was unable to remove the matrix from this opening without damaging the specimens more than desirable, and the posterior margin of the wall between the cavum cerebrale cranii and the notochordal space and of the wall between the notochordal space and the aorta canal could not, therefore, be exposed. In specimen No. 232 (Pl. 26, Fig. 2; Pl. 27, Fig. 2) the wall between the notochordal space and the cavum cerebrale cranii will be seen to have a much indented posterior margin, so probably it was cartilaginous in its pos-

terior part, as in *Glaucolepis* (p. 32). The same probably applies to the wall between the notochordal space and the aorta canal, though it could not be directly observed. The foramen magnum was almost as high as broad, and was of a rounded four-sided outline. As to the notochordal opening it can only be stated that it was higher than broad. As in *Glaucolepis* (p. 31), the walls of the notochordal space are devoid of perichondral bone-layers. The anterior extension of the notochordal space is unknown. The broad dorsal part of the posterior face of the occipital region was the area of insertion of the foremost

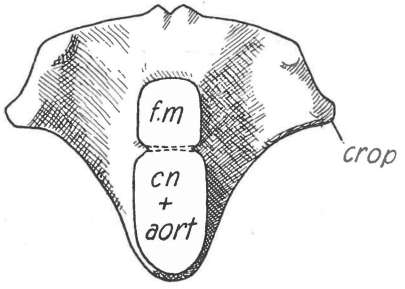


Fig. 61. *Boreosomus piveteaui* n. sp. Sketch of the occipital region of the neural endocranium in posterior view. Based mainly on specimen No. 296. 3-4 ×.
cn + *aort*, posterior opening of the aorta canal and the notochordal space; *crop*, craniospinal process; *f. m*, foramen magnum.

part of the trunk musculature and, as will be seen from Fig. 61, presents some low depressions and elevations. From the slightly convex dorsal margin of the face, very near the mid-line of the endocranium, a small paired process issues in a postero-dorsal direction.

The dorsal face of the occipital region is short, but very broad. Anteriorly it is, as a rule, entirely separated from the dorsal face of the otic region by the occipital fissure, and in the few cases in which the median part of the occipital fissure is closed, the boundary line between the median part of the dorsal face of the occipital region and the otic region is indicated by a transverse groove, which connects the right and left open parts of the occipital fissure (Fig. 59). The dorsal face is slightly convex from side to side; its precise outline is seen from Fig. 59; Pl. 25, Fig. 1; and Pl. 28.

The paired lateral face of the occipital region may for descriptive reasons be divided into a dorsal and a ventral part. The dorsal part of the face corresponds on the whole to the narrow lateral face of the anterior part of the occipital region in *Glaucolepis*. This part of the lateral face lies as a rather narrow zone immediately behind the occipital fissure. Farthest dorsally, that is to say, behind that part of the occipital fissure which lies dorsally to the vagus opening, the face is directed almost dorso-laterally, and postero-dor-

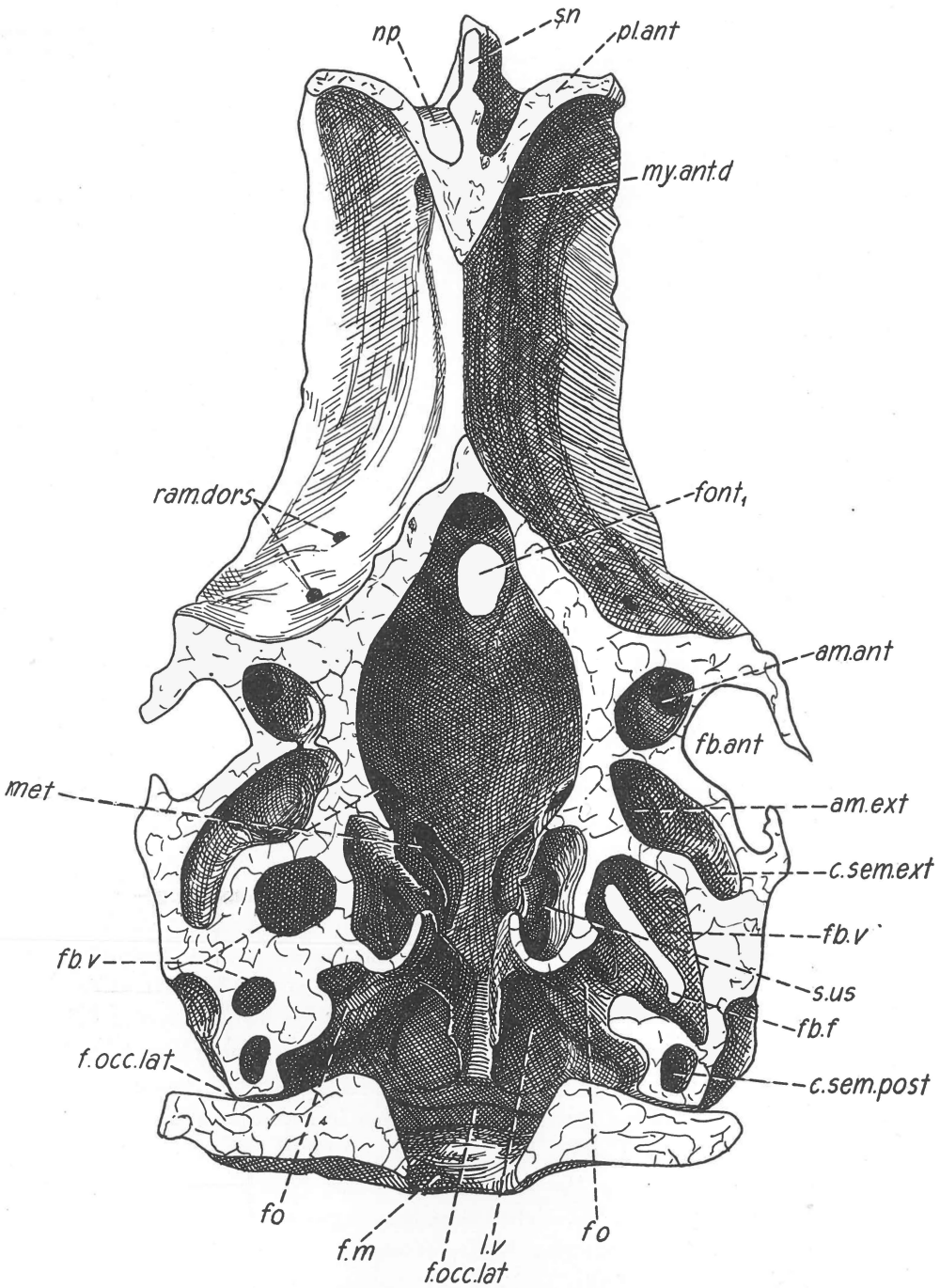


Fig. 60. *Boreosomus piveteaui* n. sp. Dorsal part of the neural endocranium in ventral view. Sectional faces reticulated. Based on a wax model. 6-7 ×.
fb. ant, anterior part of the fossa bridgei; *fb. f*, opening in the wall between the posterior part of the fossa bridgei and an intramural space in the dorsal wall of the otic region; *fb. v*, intramural space in the dorsal wall of the otic region; *np*, nasal pit. Other letters as in Fig. 58.

sally to the vagus opening it is provided with a small process pointing in a lateral direction (*crop*, Figs. 61, 62; Pl. 26, Fig. 1) which may no doubt be homologised with the slighthy developed cranio-spinal process in *Glaucolepis* (pp. 86-87). Behind that part of the occipital fissure which lies antero-ventrally to the vagus opening, the dorsal part of the lateral face of the occipital region is continued in an antero-ventral direction as a very narrow rim, as will be seen from Fig. 62. Behind this narrow rim lies what has been called by me the ventral part of the lateral face of the occipital region. As will appear particularly clearly from Fig. 62, this part of the lateral face is roughly triangular in outline. It faces mainly ventro-laterally and is slightly concave in a rostro-caudal direction, its anterior part accordingly facing somewhat posteriorly, too.

Farthest dorsally a small opening is found on the ventral part of the lateral face; it is the external opening of a narrow canal which issues in a lateral and at the same time slightly posterior direction from the ventro-lateral part of the cavum cerebrale cranii and no doubt contained a spino-occipital nerve. The course of the canal may be seen plainly in specimen No. 232 (*spi*, Pl. 26, Fig. 2; Pl. 27, Fig. 2). I have observed no other canal opening on the lateral face of the occipital region; quite possibly, however, I may have overlooked such an opening, for, as already stated (p. 285), it is very difficult to distinguish small canal openings from the round openings which often, in large numbers, perforate the perichondral bone-layers in *Boreosomus*. Thus it cannot be taken for granted that the short canal extending from the aorta canal to the lateral face of the occipital region which has been ascertained in the Kansas forms A and B, as also in *Glaucolepis, Perleidus, Broughia*, and *Australosomus* (cf. p. 34), is not present in *Boreosomus*.

The ventral face of the occipital region is highly convex from side to side, and laterally passes gradually into the lateral face of the region. It may be described as the surface of a narrow, rounded, ventral longitudinal ridge which forms the most ventral part of the occipital region and which is pierced longitudinally by the unpaired aorta canal. In an anterior direction this longitudinal ridge continues as the most ventral part of the otic region (Fig. 63; Pl. 27, Fig. 1).

In *Glaucolepis* a large, unpaired or paired, opening is found on the ventral face of the occipital region, through which opening the arteria branchialis efferens II passed (p. 36). In *Boreosomus* no similar opening is found in the occipital region.

The cavum cerebrale cranii decreases considerably in height and breadth in a caudal direction through the occipital region. The floor of this division of the cavum cerebrale cranii lies on a level with the ventral margin of the foramen magnum and is slightly concave from side to side.

As in *Glaucolepis*, the canal for the nervus vagus and the nervus lineae lateralis is a widened part of the occipital fissure. This canal *(X)* opens into

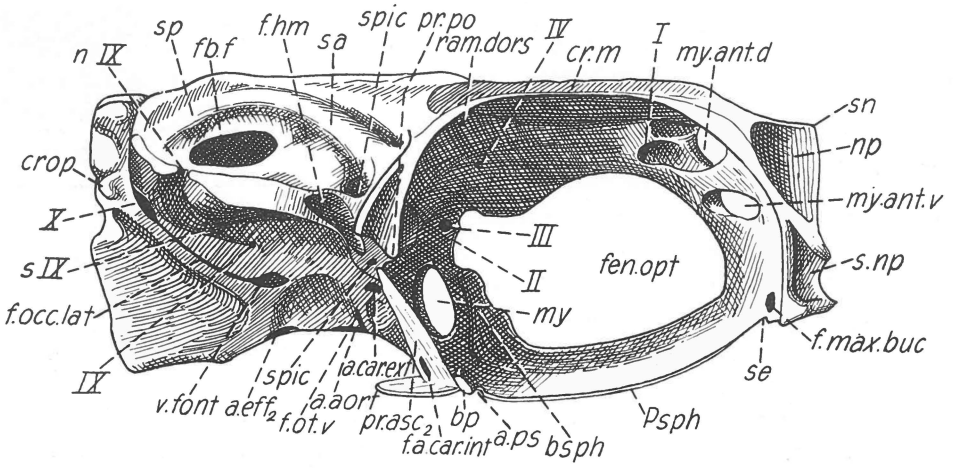


Fig. 62. *Boreosomus piveteaui* n. sp. Neural endocranium with parasphenoid and vomer in lateral view. Mainly based on specimen No. 296. 3-4 ×.

Psph, parasphenoid; *a. aort*, anterior opening of the aorta canal; *a. car. ext*, canal for the arteria carotis externa; *a. eff*$_2$, opening for the arteria branchialis efferens II; *a. ps*, notch for the arteria pseudobranchialis efferens; *bp*, processus basipterygius; *bsph*, pars basisphenoidea; *cr. m*, median crista on the dorsal face of the orbitotemporal region; *crop*, cranio-spinal process; *f. a. car. int*, foramen for the arteria carotis interna; *fb. f*, opening in the wall between the posterior part of the fossa bridgei and an intramural space in the dorsal wall of the otic region; *fen. opt*, fenestra optica; *f. hm*, articular fossa for the hyomandibula; *f. max. buc*, canal for the ramus maxillaris trigemini, the nervus buccalis lateralis, and vessels; *f. occ. lat*, fissura occipitalis lateralis; *f. ot. v*, fissura oticalis ventralis; *my*, posterior myodome; *my. ant. d*, anterior dorsal myodome; *my. ant. v*, anterior ventral myodome; *np*, nasal pit; *n IX*, notcn in the dorso-lateral margin of the otic region for the supratemporal branch of the nervus glossopharyngeus; *pr. asc*$_2$, processus ascendens posterior; *pr. po*, processus postorbitalis; *ram. dors*, canal for branches of the nervus ophthalmicus lateralis, the ramus ophthalmicus superficialis trigemini, and for vessels; *sa*, ridge above the canalis semicircularis anterior; *se*, groove on the ventral face of the ethmoidal region; *sn*, septum nasi; *s. np*, depression on the anterior face of the ethmoidal region ventrally to the nasal pit; *sp*, ridge above the canalis semicircularis posterior; *spic*, spiracular canal; *s IX*, groove for the supratemporal branch of the nervus glossopharyngeus; *v. font*, vestibular fontanelle; *I*, foramen for the nervus olfactorius; *II*, opening for the nervi optici; *III*, canal for the nervus oculomotorius; *IV*, canal for the nervus trochlearis; *IX*, canal for the nervus glossopharyngeus; *X*, place of exit for the nervus vagus.

the cavum cerebrale cranii immediately behind the large opening between the cavum cerebrale cranii and the labyrinth cavity, and in front of and rather on a level with the most ventral part of the cavum cerebrale cranii in the occipital region. From its cerebral opening the vagus canal extends in a posterolateral direction to its external opening, and, as in *Glaucolepis*, it is so curved that its anterior side is concave and its posterior side convex. In transverse section the canal is elliptical with the long diameter ot the ellipse pointing obliquely forward and downward. There is no separate canal for the vena encephalica posterior.

Otic region. – The length of the otic region is about two-fifths the total length of the endocranium. In its posterior part the region has about the same

breadth as the occipital region; but it increases in breadth towards its anterior part, where the endocranium attains its greatest breadth between the well developed postorbital processes.

Posteriorly the otic region, as stated above, is well separated dorsally from the occipital region, while ventrally no marked boundary is found between the two regions. It is difficult to draw an exact boundary line between the otic region and the orbitotemporal region, though the latter as a whole is much narrower than the former.

The external faces of the region are as follows: an unpaired dorsal, a paired lateral, a paired orbital, and an unpaired ventral face.

The outline of the dorsal face of the region is seen from Fig. 59. As will be seen from this figure, the face is well bounded posteriorly and laterally, while anteriorly it passes gradually into the dorsal face of the orbitotemporal region.

That part of the dermal cranial roof which covers the otic region dorsally is curved in the usual way, its ventral face being concave from side to side. In accordance with this, the dorsal face of the otic region may be said to be roughly convex from side to side, in so far as its medial part lies on a much higher level than its lateral margins. However, the detailed relief of the dorsal face is exceedingly complicated, and the face is only in contact with the dermal cranial roof by its high median part and by its narrow lateral and orbital raised margins.

As in *Glaucolepis,* a paired angular ridge (*sa*, *sp*, Figs. 59, 62; Pl. 25, Fig. 1; Pl. 26, Fig. 1; Pl. 28) is seen on the dorsal face of the otic region running above the spaces in the cranial wall for the canalis semicircularis anterior and the canalis semicircularis posterior. The dorsal face is divided by this ridge into three divisions, viz. an unpaired median and a paired lateral division. The median division of the face is fairly evenly arched, so that it is convex from side to side, but on close inspection its relief indicates the most important details in the shape of the dorsal face of that part of the cavum cerebrale cranii above which it lies. Thus, medially to the posterior half of the ridge above the canalis semicircularis anterior and parallel with that ridge a low ridge is seen, corresponding to the underlying space for the lateral division of the cerebellum (p. 300). On the posterior part of the median division we further find indications of a paired elevation corresponding to the paired "lobus vagus" of the myelencephalon (p. 299). In some cases the median division is pierced by the posterior part of an anterior dorsal fontanelle (*font*$_1$, Pl. 25, Fig. 1; Pl. 28), in other cases the roof of the otic region is entirely ossified.

When largest, the anterior dorsal fontanelle reaches from the posterior third of the otic region to some distance into the orbitotemporal region, that is to say, its longitudinal extent in the otic region corresponds to that of the

anterior dorsal fontanelle in *Glaucolepis*. In *Boreosomus,* however, the fontanelle is always much narrower than in *Glaucolepis*.

In the living animal that part of the fontanelle which lies in the otic region was no doubt entirely closed by cartilage, and the material of *Boreosomus* shows clearly the transition from specimens in which a large area of the roof of the otic region is unossified to specimens, as for instance the sectioned specimen, in which every trace of a fontanelle in the roof of the otic region has disappeared.

On the most anterior part of the median division of the dorsal face of the otic region, two concavities occur on either side of the mid-line, as will be seen from Fig. 59; they are separated by a small longitudinal ridge, which is situated rather precisely as a posterior continuation of the lateral margin of the dorsal face of the orbitotemporal region.

The medial of these concavities is the posterior part of a deep and broad longitudinal groove, the greater part of which is situated in the roof of the orbitotemporal region. The lateral of the two concavities is the anterior part of the fossa bridgei, which otherwise lies laterally to the ridge above the canalis semicircularis anterior. (*fb,* Fig. 58; Pl. 25, Fig. 1; Pl. 28; *fb. ant, fb. post,* Figs. 59, 60).

Laterally to the anterior part of the ridge overlying the canalis semicircularis anterior the lateral division of the dorsal face of the otic region has a deep concavity corresponding to the anterior deep part of the fossa bridgei in *Glaucolepis*. In the deepest portion of this part of the fossa bridgei the spiracular canal has its dorsal opening (*spic,* Fig. 62; Pl. 25, Fig. 1; Pl. 28). Behind this deep part of the fossa bridgei the dorsal face of the otic region is nearly plane. Only along the lateral margin of the face occurs a small ridge, as will be seen in Fig. 59. Thus, apparently no marked depression is found on the dorsal face of the otic region, corresponding to the deepest posterior division of the fossa bridgei in *Glaucolepis*.

However, in many, but not in all, cases a larger or smaller opening (*fb. f,* Figs. 59, 60, 62; Pl. 26, Fig. 1; Pl. 28) is present on the posterior half of the lateral division of the dorsal face of the otic region. A closer examination shows that this opening leads into a intramural space (*fb. v,* Fig. 60,) all the walls of which are lined with perichondral bone. In shape and in its relation to the labyrinth cavity this intramural space corresponds entirely to the deep division of the fossa bridgei in *Glaucolepis* lying behind the bulge above the space for the ampulla of the canalis semicircularis externus.

We may now ask the question whether this intramural space in *Boreosomus* is formed by a roof having developed above the postero-ventral part of a fossa bridgei, or, conversely, whether the large fossa bridgei in *Glaucolepis* has arisen by a smaller fossa bridgei having fused with an earlier independent space of the cranial roof by reduction of the wall that separated them. At

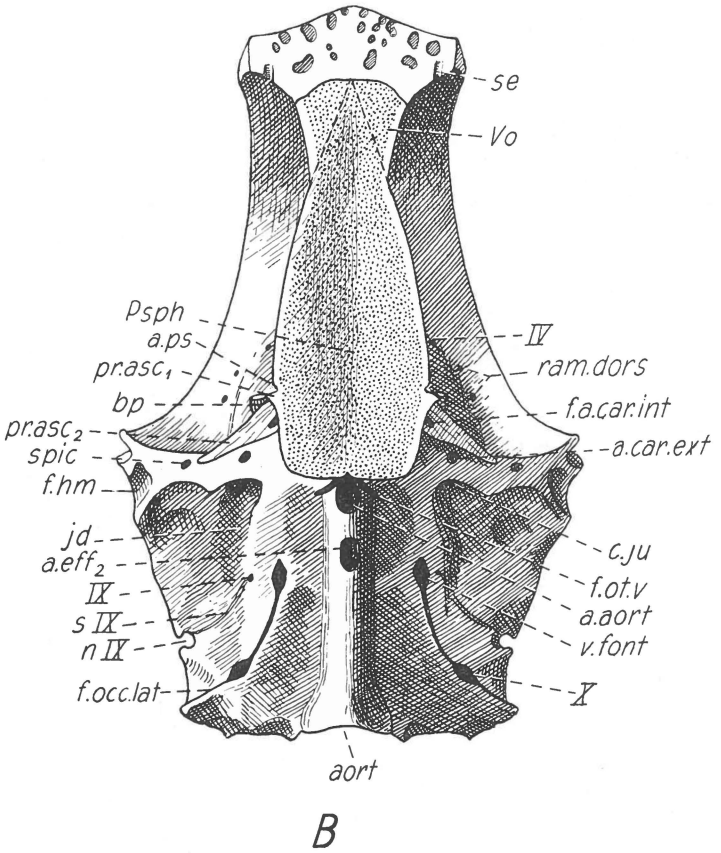


Fig. 63. *Boreosomus piveteaui* n. sp. Neural endocranium with parasphenoid and vomer in ventral view. Based on specimen No. 296. 3.5 ×.
Vo, vomer; *aort*, posterior opening of the aorta canal; *c. ju*, posterior opening of the jugulohyoideomandibular canal; *jd*, jugular depression; *pr. asc*$_1$, processus ascendens anterior. Other letters as in Fig. 62.

present no definite answer can be given to this question, our knowledge of the earlier *Palaeonisciformes* being much too sparse.

In Watson's Kansas forms the fossa bridgei consists, as far as I can see, of an anterior part connected with the spiracular canal, and a posterior part, which must correspond to the posterior part of the fossa bridgei in *Glaucolepis*. The posterior part which probably had a connection with the cavum cerebrale cranii similar to that in *Glaucolepis*, has no roof. Thus this might be the primitive feature; however, an investigation of a greater number of primitive *Palaeonisciformes* will be required before final conclusions can be drawn.

The canalis semicircularis posterior was situated in the cranial wall between the intramural space and the posterior part of the cavum cerebrale cranii in the otic region Just at the centre of the nearly entire circular arch described by the cavity for the canalis semicircularis posterior, this cranial wall is pierced by a wide round opening (*fo*, Figs. 58, 60; Pl. 25, Figs. 2,3),

which connects the intramural space and the cavum cerebrale cranii. This connection corresponds entirely to the connection between the posterior deep part of the fossa bridgei and the cavum cerebrale cranii in *Glaucolepis*.

If we compare Fig. 64, which, among other things, shows the otic region in front view, with Fig. 62, which shows the neural endocranium in lateral view, we shall gain an impression of the shape and direction of the postorbital process (*pr.po*). It will be seen from the figures that the dorsal face of the remaining part of the otic region passes gradually into the largely dorso-lateral face of the postorbital process, and that a groove increasing in breadth and depth in a ventro-lateral direction is present on the dorso-lateral face of the postorbital process.

The paired lateral face of the otic region is well delimited from the dorsal and orbital faces of the region, while its boundary towards the ventral face is less distinct. Farthest dorsally the lateral face of the occipital region is separated from the otic region by the occipital fissure; ventrally, however, the lateral faces of the two regions pass gradually into one another.

The postero-ventral part of the otic region increases gradually in breadth in a dorsal direction, the lateral face of this part of the region being accordingly directed ventro-laterally. Dorsally and anteriorly to this ventro-lateral face the otic region increases suddenly very rapidly in breadth, the postero-ventral narrow part of the otic region being thus rather sharply delimited from the dorsal and anterior broader parts. Just dorsally to the postero-ventral and narrow part of the otic region, its lateral face, therefore, is almost directly ventral, but curves upward a short distance before reaching the boundary towards the lateral part of the dorsal face of the otic region, so that its most dorsal part, as will be seen from the figures, faces direct laterally. Anteriorly to the narrow postero-ventral part of the otic region, the lateral face is directed chiefly postero-ventro-laterally. On the whole the relief of the lateral face of the otic region agrees with that of the Kansas form A (Watson 1925, Fig. 10).

Just ventrally to the prominent dorsal part of the otic region a longitudinal groove, the jugular depression (*jd*, Fig. 63; Pl. 26, Fig. 1; Pl. 27, Figs. 1, 2; Pl. 30, Fig. 1), is seen on the lateral face of the region; this groove extends forwards to the posterior wide opening of the jugulo-hyoideomandibular canal; The jugular depression, which lodged the vena jugularis, is deepest immediately behind the posterior opening of the jugulo-hyoideomandibular canal, but decreases gradually in depth in a posterior direction and is indistinguishable on the posterior part of the lateral face of the otic region.

Ventrally to the jugular depression occurs a very faint saccular bulge, whose postero-ventral part is pierced by a small oblong vestibular fontanelle (*v.font*, Figs. 62, 63; Pl. 26, Fig. 1; Pl. 27, Fig. 1), which is continued in a postero-dorsal direction by the occipital fissure. The margins of the vestibular fontanelle are lined with perichondral bone, so the fontanelle was not

closed by cartilage. In extent and shape it agrees most nearly with the vestibular fontanelle in the Kansas form A (Watson 1925, Fig. 10).

In the posterior very shallow part of the jugular depression lies, posterodorsally to the vestibular fontanelle, the external opening of the canal for the nervus glossopharyngeus (*IX*, Figs. 62, 63; Pl. 26, Fig. 1). I was unable to trace the course of this canal through the cranial wall, and could not, therefore, decide whether the nervus glossopharyngeus passed through the saccular division of the labyrinth cavity, as is the case in *Glaucolepis* and in several other forms (cf. p. 48). From the external opening of the glossopharyngeus canal a delicate groove (*s IX*, Figs. 62, 63), which is only distinguishable on particularly well preserved specimens, extends in a postero-dorso-lateral direction to a notch (*n IX*, Figs. 62, 63; Pl. 25, Fig. 1; Pl. 26, Fig. 1; Pl. 27, Fig. 2) in the margin between the dorsal and the lateral face of the otic region. Through this groove and this notch the ramus supratemporalis dorsalis IX passed to the space between the dermal cranial roof and the dorsal side of the otic region.

In *Boreosomus*, in contrast to *Glaucolepis*, no place of articulation for the suprapharyngobranchial I is visible on the lateral face of the otic region.

The postero-ventro-laterally directed anterior part of the lateral face of the otic region is partially covered by the rather short processus ascendens posterior of the parasphenoid, as will be seen from Fig. 62. Just posteriorly to the dorsal part of the processus ascendens posterior this face has a fairly wide opening (*a. car. ext*, Figs. 62, 63), which is the ventral opening of a vertical canal that opens dorsally into the rather short jugulo-hyoideomandibular canal. A comparison with *Glaucolepis* shows that this canal must have lodged the arteria carotis externa on its way to the anterior part of the jugulo-hyoideomandibular canal.

One more opening is found on the postero-ventro-laterally directed part of the lateral face of the otic region (*spic*, Figs. 62, 63). It lies just dorsally to the processus ascendens posterior of the parasphenoid and on closer examination proves to be the ventral opening of the spiracular canal, which, as we have seen above, opens dorsally into the anterior deep part of the fossa bridgei. The ventral opening of the spiracular canal is relatively narrow and is situated more ventrally than in *Glaucolepis*, the canal having a fairly considerable length. The dorsal end of the processus ascendens posterior of the parasphenoid does not extend into the canal itself.

On the most dorsal part of the lateral face of the otic region, immediately behind the postorbital process, lies the articular fossa for the hyomandibula (*f. hm*, Figs. 58, 62, 63; Pl. 26, Fig. 1). The fossa is oblong and its longitudinal axis runs antero-ventrally to postero-dorsally, forming a fairly considerable angle with the horizontal plane, as will be seen from the figures. The surface

of the bone in the articular fossa is devoid of perichondral bone-layers, and was no doubt covered with cartilage in the living animal.

The most ventral part of the posterior and largest part of the otic region may be said to be a direct anterior continuation of the rounded ventral longitudinal ridge which constitutes the most ventral part of the occipital region and lodged the unpaired dorsal aorta. The ventral face of this part of the otic region is consequently convex from side to side, as is seen from Fig. 63.

On this face an anterior and a posterior large unpaired opening are found, whose accurate positions will be seen from Fig. 63. Both these openings lead to the aorta canal. The anterior opening (*a. aort*, Figs. 62, 63; Pl. 26, Fig. 1; Pl. 27, Fig. 1) is the largest, and is the anterior opening of the aorta canal proper. On a comparison with *Glaucolepis* it seems probable that the dorsal aorta immediately before or after leaving this opening divided into a right and a left branch, which just outside the aorta canal received the arteria branchialis efferens I and immediately after divided into the arteria carotis externa and the arteria carotis interna. The arteria branchialis efferens II no doubt passed through the posterior opening (*a. eff*$_2$, Figs. 62, 63; Pl. 26, Fig. 1; Pl. 27, Fig. 1; Pl. 30, Fig. 1) to reach the aorta canal.

In the Kansas form A (Stensiö 1932, Fig. 62C), as in *Boreosomus*, the aorta canal extends undivided through the occipital region and the greater part of the otic region. Its paired opening *a. eff*$_3$ according to its position corresponds to the posterior unpaired opening in *Boreosomus*, and its paired opening *a. eff*$_2$ corresponds to the anterior unpaired opening in *Boreosomus*.

In front of the anterior opening of the aorta canal the ventral face of the otic region is flattened at the same time as it increases somewhat in width. Furthermore the anterior part of the ventral face of the otic region bends downward, thus being mainly postero-ventrally directed (cf. Fig. 62).

Dorsally or antero-dorsally to this part of the ventral face of the region lies the myodome; accordingly this face corresponds to that division of the ventral face of the otic region in *Glaucolepis* with which the posterior part of the corpus of the parasphenoid is in contact. Strangely enough, in *Boreosomus* that part of the corpus of the parasphenoid which lies below the anterior part of the otic region has no contact with the ventral face of this anterior part, as will be seen from Fig. 62.

The orbital paired face of the otic region (Fig. 64) is concave both in a horizontal and a vertical direction and is as a whole antero-ventrally directed. No definite boundary between this face and the orbital face of the orbito-temporal region can be drawn.

The trigemino-facialis chamber and the myodome, which lie at the transition between otic and the orbitotemporal regions, like the jugulo-

hyoideomandibular canal will be treated in a later chapter of the present paper.

That division of the cavum cerebrale cranii which lies in the otic region has its smallest width immediately behind the point where the cavum cerebrale cranii is in open communication with that part of the labyrinth cavity which lodged the sinus utriculi superior (Fig. 60).

From this point the cavum cerebrale cranii increases in width in a posterior direction through the posterior part of the otic region, and in an anterior direction through the whole anterior part of the otic region with the exception of its foremost part, where it again decreases somewhat in width.

For descriptive reasons we may regard the otic division of the cavum cerebrale cranii as bounded by an unpaired dorsal, a paired lateral, and an unpaired ventral wall, though the cerebral faces of these walls are on the whole so curved that they pass gradually into one another. The cerebral faces of all four walls are lined with perichondral bone, as is also the case with the cerebral faces of the walls of the other cranial divisions. The shape of the cavum cerebrale cranii may therefore be determined with the greatest accuracy, while in *Glaucolepis*, as stated above, the cavum cerebrale cranii was surrounded by cartilage to a considerable extent.

The dorsal cranial wall roofing the posterior broad division of the cavum cerebrale cranii in the otic region, on its cerebral face has a median narrow and thickened longitudinal zone and on either side of this a kidney-shaped concavity (*l.v*, Figs. 58), in whose deepest part the cranial wall is very thin. The exact shape of this paired kidney-shaped concavity is seen most distinctly from Fig. 66.

The dorsal cranial wall roofing the anterior broad division of the cavum cerebrale cranii in the otic region is very thin, especially in its median part, and, as we have seen above, in some specimens partially unossified. Its cerebral face is evenly concave both in a transverse and a longitudinal direction.

In the otic region the lateral cranial wall attains a considerable thickness (Fig. 58). The labyrinth cavity, which is situated in this thick wall, is in open communication medially with the cavum cerebrale cranii to the same extent as in *Glaucolepis* and other primitive *Chondrostei* (cf. p. 300). On that part of the cerebral face of the lateral wall of the otic region which lies behind the wide communication with the labyrinth cavity, we find the fairly wide rounded opening (*fo*, Figs. 58, 60; Pl. 25, Figs. 2, 3) which connects the posterior broad part of the otic division of the cavum cerebrale cranii with the above-described (p. 294) intramural space that corresponds to the posterior deep part of the fossa bridgei in forms such as *Glaucolepis*, etc.

That part of the cerebral face of the lateral wall of the otic region which lies in front of the opening towards the labyrinth cavity is roughly concave both in a vertical and a horizontal direction, but in its relief presents certain details which deserve a detailed description. Thus immediately in front of

the dorsal part of the opening leading to the labyrinth cavity the cerebral face has a fairly deep concavity, which is elliptic in outline, as will be seen from the figures, and in front of this concavity a groove-like depression is found (*met*, Figs. 58, 60). This groove-like depression begins on the cerebral face of the dorsal cranial wall dorso-medially to the most dorsal part of the sinus utriculi superior. It continues in an antero-ventral direction on the cerebral face of the lateral wall of the otic region, where it ends a short distance behind the place where the cavum cerebrale cranii attains its greatest width. Thus the full length of the groove-like depression is a little smaller than the length of the space for the canalis semicircularis anterior from the sinus utriculi superior to the ampulla anterior. The groove-like depression is deepest at its middle part, where, at any rate in some cases, it is closed along a very short stretch to a canal, as will be seen from Fig. 60. The ventral cranial wall of the otic region is fairly thick, and in this wall lies both the space that lodged the anterior part of the notochord and the aorta canal. For the present I can give no information about the extent or shape of the anterior part of the notochordal space. The cerebral face of the ventral cranial wall in the otic region has not been investigated in such great detail as the other cerebral faces of the region. Between the right and left saccular divisions of the labyrinth cavity the floor of the cavum cerebrale cranii is fairly horizontal. Posteriorly to this, that is to say, at the transition to the occipital region, the floor rises very abruptly to the level at which the floor of the cavum cerebrale cranii lies in the short occipital region. Anteriorly to its intersaccular part the floor of the cavum cerebrale cranii rises in an anterior direction, but not quite as steeply as at the transition from the otic to the occipital region.

Labyrinth cavity. — As in *Glaucolepis*, the labyrinth cavity (Figs. 58, 60, 66; Pl. 25, Figs. 2, 3; Pl. 27, Fig. 2) extends throughout the whole otic region. As mentioned above the labyrinth cavity has a single but very wide communication with the cavum cerebrale cranii, as in the case of *Glaucolepis* and several other forms (cf. p. 55). The dorsal part of the labyrinth cavity has been investigated by grinding, the ventral part, however, by direct preparation of suitable specimens, notably specimens Nos. 232 and 307. Altogether we have a very good knowledge of the labyrinth cavity in *Boreosomus*, and it agrees so well with that of *Glaucolepis* that the subjoined description can be very short.

The ventral part of the saccular division, which in *Glaucolepis* was bounded by cartilage, in *Boreosomus* has completely ossified walls, so in this species, in contrast to *Glaucolepis*, the shape of the saccular division of the labyrinth cavity can be exactly indicated.

In lateral view the saccular division (*sacc*, Pl. 25, Fig. 3) is rectangular with almost vertical anterior and posterior margins, and a nearly horizontal ventral margin and with rounded antero-ventral and postero-ventral corners.

As will be seen from Pl. 25, Figs. 2, 3, the dorso-ventral extension of the saccular division is much smaller than the rostro-caudal one, and the ventral margin of the saccular division lies rather on a level with the ventral margin of the small vestibular fontanelle. In the model of *Glaucolepis* (Fig. 14) the margin of the saccular division is situated far more ventrally (which is due, at any rate partially, to the less complete ossification of the endocranium). There is nothing to indicate that a lagena was developed.

The relations between the utricular division and the saccular division are entirely as in *Glaucolepis*, a pre-saccular, a supra-saccular, and a post-saccular part being distinguishable. These three parts agree in all details with the corresponding parts in *Glaucolepis*. From the supra-saccular part of the utricular division issues in a dorsal and somewhat posterior direction the division for the sinus utriculi superior (*s.us*, Figs. 58, 60; Pl. 25, Figs. 2, 3), and, as will be seen from Fig. 60, this division is somewhat broader than the corresponding division in *Glaucolepis*. The divisions for the semicircular canals extend on the whole as in *Glaucolepis*, and their ampullary swellings agree in shape with the corresponding ones in *Glaucolepis*.

As in *Glaucolepis*, but unlike the conditions in forms such as *Ospia*, *Perleidus*, and *Saurichthys* (cf. p. 57), the canalis semicircularis posterior opens posteriorly into the supra-saccular, and not in the post-saccular part of the utricular division. The canalis semicircularis anterior is comparatively longer than in *Glaucolepis*. The roots of the facialis nerve traversed the presaccular part of the utricular division, as in *Perleidus* and *Ospia* (Stensiö 1932, pp. 195–98, 201, 240), while the roots of the trigeminus nerve traversed the wall of the endocranium immediately in front of the utricular division (Pl. 26, Fig. 2; Pl. 27, Fig. 2). Whether the glossopharyngeus nerve traversed the posterior part of the saccular division, cannot yet be definitely decided, but probably this was the case.

Remnants of otoliths have not yet been observed; but it is quite possible that such will be found during the continued grinding.

On account of the good agreement existing between the shape of the labyrinth cavities in *Glaucolepis* and *Boreosomus* it would seem probable that the membranous labyrinths were fairly alike in the two genera.

Orbitotemporal region. — This region has about the same length as the otic region, and even though there is no marked boundary between the two regions, the orbitotemporal region is in all essentials narrower and higher than the otic region (cf. Figs. 62, 63). Throughout the greater part of its height the orbitotemporal region is well separated from the ethmoidal region, owing to the greater breadth of the latter. Only farthest dorsally has the anterior part of the orbitotemporal the same breadth as the ethmoidal region, so it is difficult to draw a boundary between the most dorsal parts of the two regions.

The orbitotemporal region attains its greatest breadth in its most dorsal

part, which is equipped with a well ossified crista supraorbitalis. On account of the relatively large size of the eyes, the interorbital part of the region is highly compressed and pierced by a large fenestra optica (*fen.opt*, Fig. 62; Pl. 25, Figs. 2, 3; Pl. 26, Fig. 1; Pl. 30, Figs. 1, 2).

The cavum cerebrale cranii extends only through the posterior half of that part of the orbitotemporal region which lies dorsally to the fenestra optica, but is continued forward in the interorbital wall by an unpaired canal for the nervus olfactorius. A short distance in front of the anterior end of the cavum cerebrale cranii this canal divides into a right and a left canal, which will be dealt with in more detail below, and which open into the right and the left orbit respectively at some distance behind the anterior boundary of the orbitotemporal region.

If for the present we disregard details in the shape of the pars basisphenoidea, the orbitotemporal region may be regarded as having four external faces, an unpaired dorsal, a paired lateral, and an unpaired ventral face.

The outline of the dorsal face is seen from Fig. 59, which likewise shows the gradual transition between this face and the dorsal face of the otic region.

On the posterior part of the dorsal face of the orbitotemporal region an unpaired oval fontanelle is found (*font*$_1$, Figs. 58, 59, 60; Pl. 25, Fig. 1; Pl. 28), whose margins in the most completely ossified endocrania are lined with perichondrial bone, so that the fontanelle in these specimens has not been constricted by cartilage. In less completely ossified endocrania the fontanelle extends in a posterior direction through the anterior two-thirds of the otic region; however, this posterior continuation of the fontanelle was no doubt closed by cartilage in the living animal (p. 294).

The small anterior dorsal fontanelle in *Boreosomus* dealt with here corresponds in extent and position closely to the anterior dorsal fontanelle in the *Palaeonisciformes* from the Coal Measures of Kansas which have been described and figured i.a. by Moodie (1915, pp. 146–155, Figs. 5, 6, 15, 16 and 17). In Watson's Kansas forms, which are probably identical with Moodie's forms (Case 1937), the anterior dorsal fontanelle is larger than in any of the specimens figured by Moodie. A comparison between Watson's and Woodie's figures shows that the small fontanelle in the orbitotemporal region in Moodie's specimens corresponds closely to the anterior part of the large fontanelle in Watson's specimens. The posterior boundary of the foremost part of the fontanelle in Watson's specimens is indicated by a constriction of the fontanelle (Watson 1925, Figs. 12 and 13), and I regard it as probable that that part of the fontanelle which lies posteriorly to this constriction was closed by cartilage in the living animal. Thus it would seem that the anterior dorsal fontanelle both in the Kansas forms and in *Boreosomus* had a comparatively slight extent and was situated entirely in the roof of the orbitotemporal region. Judging from its position in relation to the

diencephalon (cf. p. 319), it seems possible that the anterior dorsal fontanelle is an epiphysial opening.

That part of the dorsal face of the orbitotemporal region on which the anterior dorsal fontanelle is found, lies almost on a level with the median part of the dorsal face of the otic region and higher than any other part of the dorsal face of the orbitotemporal region. In front of this highest part of the dorsal face a median longitudinal crista is found (*cr.m*, Figs. 58, 59, 62, 64, 65 A and B; Pl. 26, Fig. 2; Pl. 27, Fig. 2; Pl. 28), which together with the area around the anterior dorsal fontanelle forms the boundary between a right and a left largely longitudinally placed groove on the dorsal face of the endocranium. This paired groove, whose posterior part is situated in the otic region (p. 294), extends in an anterior direction, as will be seen from Fig. 59, to the boundary between the orbitotemporal region and the ethmoidal region.

On the posterior part of the floor of the paired groove a number of small foramina are seen (*ram.dors*, Figs. 58, 59, 60, 63, 64; Pl. 26, Fig. 2; Pl. 27, Fig. 2; Pl. 28), the hindmost of which in many cases lies behind the rather ill defined boundary between the orbitotemporal region and the otic region. The number of the small foramina varies somewhat not only from one specimen to the other, but also from the right to the left side of the individual endocrania. Thus in specimen No. 232 four foramina are found on the right and three on the left side, and on the sectioned specimen three foramina are found on the right and two on the left side. These foramina are the dorsal openings of small canals which from the dorsal side of the endocranium extend in a ventral or antero-ventral direction through the posterior part of the crista supraorbitalis (as regards the hindmost canal in many cases partially through the roof of the otic region), and whose ventral openings lie on the postero-dorsal part of the orbital face of the orbitotemporal region. On its right side the sectioned specimen has three dorsal, but only two orbital foramina, because the hindmost of the small canals issuing from the orbital face of the endocranium has two openings on the dorsal face of the endocranium. Probably these small canals, similarly as in *Glaucolepis magna* (p. 88), lodged branches of the nervus ophthalmicus lateralis, which innervated part of the supraorbital canal, and moreover some minor vessels and branches of the ramus ophthalmicus superficialis trigemini passed through these canals to the dorsal side of the endocranium

The lateral face of the orbitotemporal region is roughly concave both in a vertical and a horizontal direction. The posterior part of the lateral face is directed laterally and at the same time antero-ventrally, and together with the orbital face of the otic region constitutes the posterior boundary of the orbit. The remaining part of the lateral face may in broad features be divided into a supraorbital, an interorbital, and a suborbital division. The supraorbital division, which is the orbital face of the crista supraorbitalis, faces ventrally

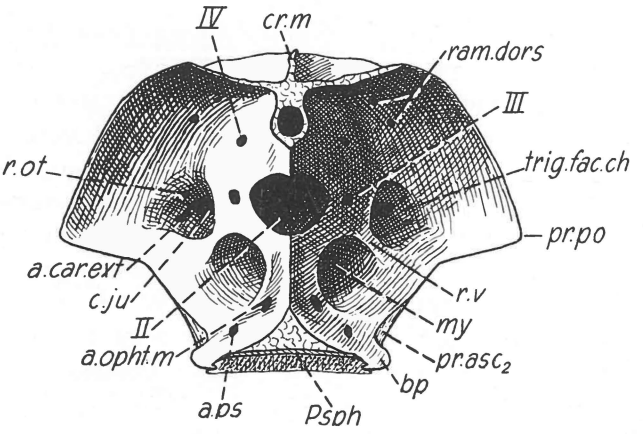


Fig. 64. *Boreosomus piveteaui* n. sp. Posterior part of the orbitotemporal region and anterior part of the otic region in anterior view. Anterior part of the neural endocranium removed. Sectional face reticulated. Based mainly on specimen No. 296. 3–4 ×. *Psph*, parasphenoid; *a. car. ext*, canal for the arteria carotis externa; *a. opht. m*, opening for the arteria ophthalmica magna; *a. ps*, opening for the arteria pseudobranchialis efferens; *bp*, processus basipterygius; *c. ju*, jugulo-hyoideomandibular canal; *cr. m*, median crista on the dorsal face of the orbitotemporal region; *my*, posterior myodome; *pr. asc*$_1$, processus ascendens posterior; *pr. po*, processus postorbitalis; *ram. dors*, canals for branches of the nervus ophthalmicus lateralis, the ramus ophthalmicus superficialis trigemini and for vessels; *r. ot*, canal for the ramus oticus lateralis; *r. v*, ridge between the myodome and the trigemino-facialis chamber; *trig. fac. ch*, trigemino-facialis chamber; *II*, opening for the nervi optici; *III*, canal for the nervus oculomotorius; *IV*, canal for the nervus trochlearis.

and slightly laterally. The interorbital division faces mainly laterally and, as stated above, is pierced by a large fenestra optica. From Fig. 64 it will be seen that that part of the interorbital division which lies dorsally to the fenestra optica is convex in a vertical direction, the supraorbital and interorbital divisions of the lateral face of the region meeting at a right angle. The orbital openings of the small canals through the posterior part of the crista supraorbitalis lie laterally to the boundary line between the supraorbital and the interorbital division of the lateral face; probably, however, the ramus ophthalmicus lateralis ran along this boundary line. Whether the ramus ophthalmicus superficialis trigemini accompanied the ramus ophthalmicus lateralis through the orbit, cannot be ascertained.

The suborbital division of the lateral face (the orbital face of the most ventral part of the orbitotemporal) is roughly dorso-laterally directed.

On the posterior part of the interorbital division of the lateral face lies the orbital opening (*IV*, Figs. 62, 63, 64) of a canal, which from the orbit runs in a posterior direction through the cranial wall to the cavum cerebrale cranii, and through which the nervus trochlearis passed. No independent canal for the vena cerebralis anterior has been observed.

On the antero-dorsal part of the interorbital division of the lateral face of the orbitotemporal region two depressions are seen (*my. ant. d, my. ant. v*, Figs. 58, 60, 62, 65 A; Pl. 25, Fig. 3; Pl. 26, Fig. 1; Pl. 30, Figs. 1,2), whose anterior parts

lie at the very transition to the ethmoidal region. These two depressions, one of which lies postero-dorsally to the other, may be compared to the dorsal and ventral anterior myodomes in *Glaucolepis magna*.

The dorsal depression, whose accurate position will be seen most distinctly from Figs. 62 and 65 A, is so deep in its anterior part that the interorbital wall in that area is completely reduced, the depression in the fossil cranium being thus in open communication with the corresponding depression on the opposite side. The canal for the nervus olfactorius opens into the postero-ventral part of the depression; accordingly the nervus olfactorius passed through the depression, which it left through the posterior opening of a short canal piercing that part of the ethmoidal region which forms the anterior boundary of the depression.

This dorsal depression may be conceived to have arisen by an expansion of an anterior dorsal myodome of the *Glaucolepis* type. This expansion has taken place partly at the expense of that part of the interorbital wall which separated the anterior dorsal myodomes of the right and the left side from each other, partly at the expense of that part of the interorbital wall which bounded the anterior part of the olfactorius canal dorsally and laterally. By incorporating part of the olfactorius canal, the anterior dorsal myodome acquired an open communication with the nasal cavity. It is probable that not only the nervus olfactorius, but also the ramus ophthalmicus lateralis passed through this opening, and it is quite possible that the ramus ophthalmicus superficialis trigemini and the nervus profundus, too, as well as some smaller vessels reached the snout region by the same opening.

The ventral of the two depressions in *Boreosomus* has no doubt arisen in the area of insertion for the musculus obliquus inferior, and corresponds entirely to the anterior ventral myodome in *Glaucolepis magna*, only the depression in *Boreosomus* is so deep that it is in open communication with the corresponding depression on the opposite side.

The position of the two small open communications between the antero-dorsal parts of the right and the left orbit in *Boreosomus* which have arisen in connection with the musculus obliquus superior and the musculus obliquus inferior respectively, corresponds well with the position of the two small anterior fenestrations of the interorbital wall in *Saurichthys ornatus* (Stensiö 1925, pp. 35–36); thus the conditions in *Boreosomus* indicate to an even greater extent than those in *Glaucolepis* (p. 96) that the two fenestrations in *Saurichthys* must have arisen in association with the musculi obliqui.

The greater part of the fenestra optica lies ventrally and antero-ventrally to that part of the interorbital wall which houses the anterior part of the cavum cerebrale cranii and the partially paired olfactorius canal. This part of the fenestra optica is unpaired, which is evident from the fact that its dorsal, anterior, ventral, and postero-ventral boundaries are constituted by a continuous sharp median keel on the surrounding parts of the endocranial ossification,

as will be seen from Figs. 64 and 65 A. Only the most postero-dorsal part of the fenestra optica extends some way into that part of the cranial wall which lies laterally to the cavum cerebrale cranii, and is accordingly paired. Through this small postero-dorsal paired part of the fenestra optica the optic nerve reached the orbit. Consequently the fenestra optica extends a little farther in a postero-dorsal direction than in *Glaucolepis* and seems to agree most nearly with the fenestra optica in a form as *Perleidus* (cf. further the discussion on p. 63).

On the posterior part of the orbital face of the orbitotemporal region various openings are found, among which are the orbital openings of the trigeminofacialis chamber and the myodome, which will be dealt with in more detail below (p. 309).

The ventral face of that part of the orbitotemporal region which lies in front of the pars basisphenoidea is entirely covered by and intimately connected with the pars anterior of the parasphenoid and with the vomer, if this latter bone is present (cf. p. 322). The connection is so intimate that it was impossible to expose this part of the ventral face of the endocranium so completely that it could be examined in detail. Still it was possible to observe, however, that the ventral face is slightly concave from side to side, and that it decreases in breadth in an anterior direction through its posterior two-thirds, to increase in breadth again in its anterior third. Between the pars anterior of the parasphenoid and the ventral face of the orbitotemporal region runs a paired longitudinal canal for the ramus palatinus facialis and a forward directed branch of the arteria carotis interna (*pbc*, Fig. 67).

The pars basisphenoidea (*bsph*, Figs. 62; Pl. 25) lies ventrally to the cavum cerebrale cranii between the myodome and the fenestra optica; farthest ventrally it is in contact with the corpus of the parasphenoid.

Anteriorly the most ventral part of the pars basisphenoidea passes gradually into that part of the orbitotemporal region which lies ventrally to the fenestra optica, and posteriorly, ventrally to the myodome, it passes gradually into the antero-ventral part of the otic region.

For descriptive reasons we will distinguish, in the sequel, between this ventral part and the more dorsal part of the pars basisphenoidea, drawing the boundary line between the two parts on a level with the most ventral part of the floor of the myodome.

The ventral part of the pars basisphenoidea is very broad, while the dorsal part is rather narrow; the ratio between the breadths of the two parts may best be seen from Fig. 64. The dorsal, rather narrow part of the pars basisphenoidea may be described as a transversely placed vertical wall, which forms the anterior boundary of the median part of the myodome. The posterior face of this vertical wall is slightly concave in a dorso-ventral direction, but could not be investigated in detail. The anterior face of the vertical wall is halved by its aforementioned median keel. Each half of the anterior face is strongly concave from side to side. A little dorsally to the

deepest part of the concavity on each half of the anterior face of the pars basisphenoidea lies a foramen (*a. opht. m*, Fig. 64), and ventro-laterally to this, nearly at the boundary between the dorsal and ventral parts of the pars basisphenoidea, lies a second foramen (*a. ps*, Fig. 64). The mutual position of the two foramina will be seen from the figures.

Owing to the small size of the endocranium of *Boreosomus*, and since its ventral part has not yet been investigated by grinding, it is not very easy to gain a general idea of the course of the very fine canals in the pars basisphenoidea. As far as I can see, the pars basisphenoidea is pierced, as in *Glaucolepis*, in a roughly dorso-ventral direction by a paired canal for an ascending branch of the arteria carotis interna (cf. p. 64), and this canal is in open communication with the orbit by the two foramina mentioned above. If this is the case, the arteria pseudobranchialis efferens probably passed the ventro-lateral foramen to enter the ascending canal in the pars basisphenoidea. In that canal it accompanied, and possibly communicated with, the arteria carotis interna, after which it left the ascending canal as the arteria ophthalmica magna through the other of the two small foramina.

From either side of the ventral part of the pars basisphenoidea a short, slender processus basipterygius (*bp*, Figs. 62, 63, 64) issues in a roughly lateral direction. As will be seen from the figures, this process is flattened in such a way that it has an antero-dorsal and a postero-ventral face, and a postero-dorsal, an antero-ventral, and a lateral margin. The very short processus ascendens anterior of the parasphenoid lies against the most proximal part of the antero-lateral margin of the process, as will be seen from Fig. 63. The anterior margin of the most proximal part of the processus ascendens posterior is probably in contact with the postero-ventral part of the processus basipterygius; however, the precise relations between the proximal part of the processus ascendens posterior of the parasphenoid and the postero-ventral part of the orbitotemporal region cannot be stated until the region in question has been investigated by the grinding method. As will be dealt with below (p. 334) the palatoquadrate ossification has a surprisingly large fossa for articulation with the small processus basipterygius.

While the ventral face of that part of the orbitotemporal region which lies in front of the myodome is directed ventrally or, farthest anteriorly, even antero-ventrally, the ventral face of that part of the orbitotemporal region which lies ventrally to the myodome as well as the foremost part of the ventral face of the otic region are chiefly postero-ventrally directed. Since the posterior part of the parasphenoid does not curve upwards like the posterior part of the ventral face of the orbitotemporal region, the parasphenoid has no contact with the endocranium behind a transverse line running through its radiation centre, but extends there freely backwards somc distance below the endocranium (Fig. 2).

In front of the anterior opening of the aorta canal the arteria carotis communis divided into an anteria carotis externa and an arteria carotis in-

terna, and the latter extended in an anterior direction in the wide space between the endocranium and the pars posterior of the parasphenoid to a foramen in the proximal part of the processus ascendens posterior (*f. a. car. int*, Figs. 62, 63, 67). I could not trace the course of the artery from this foramen to the supposed ascending canal in the dorsal part of the pars basisphenoidea, so in this case, too, we must await the results of the investigation by the grinding method.

As will be seen from the figures (Fig. 66; Pl. 25, Figs. 2, 3), that part of the cavum cerebrale cranii which lies in the orbitotemporal region falls into a posterior, chiefly high and broad, and an anterior, low and narrow, division. The boundary between the two divisions is a vertical transverse plane situated immediately in front of the small anterior dorsal fontanelle. The anterior division of the cavum cerebrale cranii lies in the interorbital part of the orbitotemporal region dorsally to the posterior part of the unpaired division of the fenestra optica, and is continued in an anterior direction by the aforementioned olfactorius canal.

That part of the cavum cerebrale cranii which lies in the orbitotemporal region may be regarded as bounded by four walls, viz. an unpaired dorsal, a paired lateral, and an unpaired ventral wall. The cerebral faces of these walls pass into one another with a perfectly even curvature, and posteriorly they pass gradually into the cerebral faces of the walls of the otic region. The cerebral faces of the walls of the orbitotemporal region are lined with perichondral bone.

The dorsal wall is comparatively thin. Above the posterior high part of the cavum cerebrale cranii in the orbitotemporal region the dorsal wall is almost horizontal and lies on a level with the dorsal wall of the otic region. This part of the dorsal wall is pierced by the aforementioned anterior dorsal fontanelle. In front of the dorsal fontanelle the dorsal wall curves downward, forming an anterior, nearly vertical, transverse wall for the dorsal part of the high posterior division of the cavum cerebrale cranii in the orbitotemporal region. The cerebral face of the nearly vertical division of the dorsal wall is concave from side to side. At the transition to the anterior low division of the cavum cerebrale cranii the dorsal wall curves forward again, thus being roughly horizontal above the anterior division of the cavum cerebrale cranii. On the cerebral face of the anterior horizontal part of the dorsal wall there is an unpaired longitudinally directed ridge.

On a level with the posterior division of the cavum cerebrale cranii in the orbitotemporal region the paired lateral wall attains a considerable thickness (Figs. 58, 60), but on a level with the anterior part of the cavum cerebrale cranii it is much thinner, since immediately in front of the transition between its posterior and anterior divisions the cavum cerebrale cranii expands rather suddenly in a lateral direction at the expense of the cranial wall. The details in the shape of the cerebral face of the lateral wall will be seen from Fig. 66.

The ventral wall of that part of the cavum cerebrale cranii which lies in the orbitotemporal region is not known in details so far. On the whole, however, this wall seems to resemble the corresponding wall in *Glaucolepis*. Thus the posterior part of the cerebral face of the wall forms a transverse ridge which corresponds closely to the ridge in *Glaucolepis* compared by me to the prootic bridge (p. 68). In front of this ridge, and behind the most dorsal part of the pars basisphenoidea, the cerebral face of the ventral wall of the cavum cerebrale cranii shows a deep concavity corresponding to the infundibular recess in *Glaucolepis*. Ventrally this infundibular recess communicates with the myodome by means of a pituitary fontanelle, about whose size and shape, however, nothing can be stated. In front of the infundibular recess the cavum cerebrale cranii is bounded ventrally along a short stretch by the dorsal face of the pars basisphenoidea. On this face we find the dorsal openings of the paired canal for the arteria carotis interna, which pierces the pars basisphenoidea, but probably not, as in *Glaucolepis* (p. 70), a depression indicating the position of the chiasma.

In front of the pars basisphenoidea the ventral wall of the cavum cerebrale cranii slopes upward, the anterior part of the cavum cerebrale cranii decreasing rapidly in height.

Myodome, trigemino-facialis chamber, jugulo-hyoideomandibular canal, and canals for nerves and vessels in the posterior part of the orbitotemporal region and the anterior part of the otic region. – In the transitional area between the otic region and the orbitotemporal region lies the well developed posterior myodome, which, though of different shape, in its relationship to the surrounding endocranial structures corresponds well to the posterior myodome in *Glaucolepis*. The myodome in *Boreosomus* could not be investigated in just as great detail as that of *Glaucolepis,* and the subjoined description must therefore in so far be regarded as preliminary as the investigation by the grinding method now in progress will supply a more complete knowledge of the details of the myodome.

The myodome, which comprises an intramural and an extracranial division, opens into each of the orbits with a large, rounded, antero-laterally directed opening (*my*, Figs. 62, 64; Pl. 25, Fig. 3; Pl. 26, Fig. 1) which unlike that in *Glaucolepis* (p. 70) is well separated from the orbital opening of the trigemino-facialis chamber.

The right and left orbital myodome openings are separated from each other by the ascending part of the pars basisphenoidea, which is not, as in *Perleidus* and the Kansas form A (cf. p. 70), pierced by a medial orbital myodome opening.

In sagittal section, as far as I can make out, the myodome is rather irregularly oval in outline, its vertical extent being greater than its horizontal. A horizontal section through the myodome shows that the posterior

side of the space is convex in a transverse direction, while its anterior side is hardly curved transversely.

The dorsal wall of the myodome is constituted medially by the fairly thick part of the ventral wall of the cavum cerebrale cranii, which contains the infundibular recess, and laterally by the ventral wall of the trigemino-facialis chamber. The dorsal wall is pierced by a median pituitary fontanelle, whose shape and size are so far unknown.

Laterally the ventral face of the dorsal wall of the myodome meets the orbital face of the orbitotemporal region almost at a right angle, so that the boundary between the two faces is marked by a rather sharp edge, which, as will be seen from Fig. 64, is so curved that it is convex in a dorsal direction.

The posterior wall of the myodome is constituted by the antero-ventral part of the otic region. The dorsal part of this wall is that part of the thick basal plate of the otic region which contains the aorta canal and the ventral part of the saccular division of the labyrinth cavity and further, between the right and left saccular divisions, probably also the anterior part of the notochordal space. On the anterior part of the cerebral face of the ventral wall of that part of the cavum cerebrale cranii which lies in the otic region, there is a small paired foramen (*VI*, Pl. 26, Fig. 2; Pl. 27, Fig. 2), which is the cerebral opening of the abducens canal. From the cavum cerebrale cranii the abducens canal extends in an antero-ventral direction towards the postero-dorsal part of the myodome; but its opening towards the myodome has not been observed owing to the difficulties in exposing the walls of the myodome by preparation. The ventral part of the posterior wall of the myodome is formed by the most antero-ventral, downward curved part of the otic region; this wall is rather thin.

The ventral wall of the myodome is a direct continuation in an antero-ventral direction of the last-mentioned thin wall, and is constituted by that part of the most ventral portion of the orbitotemporal region which lies dorsally to, but without contact with, the pars posterior of the parasphenoid.

It was impossible to decide whether the ventral wall of the myodome is pierced by a fenestra ventralis myodomus, as is the case in *Glaucolepis* (p. 72). At any rate it is certain that that part of the corpus of the parasphenoid which lies ventrally to the ventral wall of the myodome, is not pierced by any opening.

In *Glaucolepis* the most lateral part of the ventral wall of the myodome is pierced by a small canal, which lodged the ramus palatinus facialis (p. 66). No corresponding canal has been observed in *Boreosomus*, but it is quite possible that it may be found during the investigation by the grinding method.

The anterior wall of the myodome is formed by the ascending part of the pars basisphenoidea, whose posterior face, as stated above, is concave in a dorso-ventral direction and probably not curved in a transverse direction.

The lateral boundary of the myodome is formed partly by the antero-medi-

ally directed face of that part of the antero-lateral portion of the otic region with which the processus ascendens posterior of the parasphenoid is in contact, and partly, as will be seen from Fig. 64, by the anterior marginal zone of the proximal half of the processus ascendens posterior itself.

The face of that part of the lateral wall of the myodome which is directed towards the myodome, and which is made up of endochondral bone, is curved in such a way that it forms an even continuation of the concavity of the anterior face of the posterior wall of the myodome. Dorsally to the myodome the lateral wall continues as the lateral wall of the trigemino-facialis chamber.

It will be evident from what has been stated above that, as in *Glaucolepis*, the myodome in *Boreosomus* comprises a spinal and a prespinal part (cf. p. 73), and that the myodome in *Boreosomus* differs from that of *Glaucolepis* in shape only, its dorso-ventral extent being greater in relation to its rostro-caudal extent than in *Glaucolepis*. The difference in the shape of the myodome in the two genera has evidently some relation to the fact that the strong development of the eyes in *Boreosomus* has resulted in an increase in height of the orbitotemporal region, and by this increase in height that part of the endocranium in which the myodome is situated was, as it were, expanded or drawn out in a dorso-ventral direction.

Dorso-laterally to the orbital opening of the myodome lies the orbital opening of the trigemino-facialis chamber (*trig. fac. ch*, Fig. 64; Pl. 26, Figs. 1, 2), which chamber may be described as a depression of a part of the anteriorly directed face of the endocranium which forms the posterior boundary of the orbit. As is seen from Fig. 64, the orbital opening of the chamber is rounded triangular in outline, with a medial, a ventro-lateral, and a dorso-lateral margin. The rostro-caudal extent of the chamber is somewhat smaller than the height of its orbital opening and is accordingly relatively larger than in *Glaucolepis*.

Caudally the actual trigemino-facialis chamber is continued by a fairly wide, but very short canal, the jugulo-hyoideomandibular canal, whose posterior opening, as stated above, lies on the lateral face of the otic region. The diameter of the jugulo-hyoideomandibular canal is equal to about one-third the height of the orbital opening of the trigemino-facialis chamber, and the length of the jugulo-hyoideomandibular canal is much smaller than that of the actual trigemino-facialis chamber.

The trigemino-facialis chamber is bounded by the following walls: a dorsal or postero-dorsal, a medial, a posterior, a lateral, and a ventral wall.

The lateral wall is the dorsal continuation of the lateral wall of the myodome, but, as will be seen from Fig. 64, it is much thicker than the latter, comprising both the well developed postorbital process, which is situated rather far ventrally, and that part of the otic region which is situated just behind the postorbital process and pierced by the vertical spiracular canal.

The ventral wall is fairly thick and extends farther in an anterior direc-

tion than in *Glaucolepis*, the trigemino-facialis chamber and the myodome in *Boreosomus* being entirely separated. Laterally the ventral wall of the trigemino-facialis chamber passes so evenly into the lateral wall that it is impossible to draw an exact boundary between these walls. Almost at the transition between the faces of the lateral and ventral walls directed towards the chamber occurs a fairly large, round foramen (*a. car. ext*, Fig. 64); it is the dorsal opening of the vertical canal the ventral opening of which on the lateral face of the otic region has been mentioned above (p. 297) and which lodged the arteria carotis externa.

As in *Glaucolepis*, the dorsal wall separates the trigemino-facialis chamber from that part of the labyrinth cavity which contained the recessus utriculi. The face of the dorsal wall towards the chamber is directed antero-ventrally, and its boundary towards the predominantly dorso-medially directed face of the lateral wall of the chamber is rather well marked. At the very boundary between these two faces lies a small foramen (*r. ot*, Fig. 64; Pl. 26, Fig. 2; Pl. 27, Fig. 2), which is the medial opening of a canal, which extends in a lateral direction and connects the trigemino-facialis chamber with the spiracular canal. The only possible interpretation of this canal is that it is the canal for the ramus oticus lateralis, which thus has a different course from that in *Glaucolepis*, where, as we have seen above, it extends from the trigemino-facialis chamber in a dorso-lateral direction to the anterior deep part of the fossa bridgei (cf. pp. 44, 75 and 82).

The medial wall which separates the chamber from the cavum cerebrale cranii, attains a fairly considerable thickness. On the face of this wall towards the chamber two foramina occur, which are the external openings of two canals issuing from the cavum cerebrale cranii. One of these canals (*V*, Pl. 26, Figs. 2; Pl. 27, Fig. 2) opens into the dorso-medial part of the trigemino-facialis chamber and is very wide, while the other (*VII*, Pl. 26, Fig. 2; Pl. 27, Fig. 2) opens more ventrally or postero-ventrally in the trigemino-facialis chamber and is rather narrow.

In contrast to the conditions in *Glaucolepis*, the posterior wall is very thin and, as already stated, pierced by the jugulo-hyoideomandibular canal, which owing to the inconsiderable thickness of the wall is necessarily extremely short.

In order to interpret the two canals that pierce the medial wall of the trigemino-facialis chamber, we will consider first that part of the wall of the orbitotemporal region which lies between the trigemino-facialis chamber and the place of exit of the nervus opticus.

On the orbital face of this part of the cranial wall in *Boreosomus* lies a single foramen (*III*, Figs. 62, 64; Pl. 25, Fig. 3; Pl. 26, Figs. 1, 2), while on the corresponding face in *Glaucolepis* there are three foramina, viz. two for the nervus oculomotorius and one for the nervus ophthalmicus profundus (p. 76). As this part of the orbital face of the orbitotemporal region is well preserved in

several specimens of *Boreosomus*, a foramen cannot possibly have been overlooked. The foramen present, which lies a little nearer the posterior margin of the paired part of the fenestra optica than the orbital opening of the trigemino-facialis chamber, and which is comparatively large, is the orbital opening of a canal issuing, no doubt, from the cavum cerebrale cranii, though the cerebral opening of the canal has not been observed in any specimen.

A comparison with *Glaucolepis* (p. 79), *Saurichthys* (Stensiö 1925, pp. 38 and 48–49), and the Kansas forms (p. 78) shows that the nervus oculomotorius must have passed through this canal on its way from the cavum cerebrale cranii to the orbit. Probably the nervus ophthalmicus profundus accompanied the nervus oculomotorius through the cranial wall, since in contrast to what is the case in *Glaucolepis* it had no canal of its own. In *Polypterus* (Traquair 1871, p.170; Van Wijhe 1882, pp.259–60; Lehn 1918, p. 380; Allis 1922, pp.270–71) and probably in *Saurichthys*, too (Stensiö 1925, pp.48–49) the nervus oculomotorius and the nervus ophthalmicus profundus passed through a common canal from the cavum cerebrale cranii to the orbit.

According to this interpretation of the only canal that pierces the cranial wall between the posterior margin of the fenestra optica and the trigemino-facialis chamber, the two canals piercing the medial wall of the trigemino-facialis chamber are the only canals through which the nervus trigeminus and the nervus facialis, or the roots of these nerves, can have left the cavum cerebrale cranii.

The dorsal and widest of the two canals has its cerebral opening (*V*, Pl.26, Fig.2; Pl.27, Fig.2) just in front of the opening between the cavum cerebrale cranii and the labyrinth cavity and on a level with that division of the labyrinth cavity which lodged the anterior part of the utriculus including the recessus utriculi. From this point the canal runs in an antero-ventro-lateral direction through the cranial wall to the trigemino-facialis chamber.

The ventral and narrowest of the two canals issues from the ventral part of that division of the labyrinth cavity which contained the anterior part of the utriculus (*VII*, Pl.26, Fig.2; Pl.27, Fig.2), that is to say that the internal opening of this canal lies postero-ventrally to the cerebral opening of the wide dorsal canal. From the labyrinth cavity the canal runs in an antero-ventro-lateral direction through the cranial wall to the trigemino-facialis chamber.

According to its position the dorsal canal corresponds to the trigeminus canal in *Glaucolepis*, and the ventral canal in regard to its position differs from the facialis canal in *Glaucolepis* only by opening into the anterior part of the labyrinth cavity instead of in the part of the cavum cerebrale cranii that lies just in front of the labyrinth cavity. On the whole there is such a great agreement between *Boreosomus* and *Glaucolepis* as regards the position of these canals that the dorsal canal in *Boreosomus* must be regarded as a trigeminus canal, and the ventral as a facialis canal.

No trigemino-facialis recess is developed in *Boreosomus,* and this in connection with the fact that neither the trigeminus canal nor the facialis canal are wider than the corresponding canals in *Glaucolepis,* tend to show that the trigemino-facialis ganglionic complex lay on the whole laterally to the medial wall of the trigemino-facialis chamber (cf. p. 81). Thus to all appearance the trigeminus canal contained the actual trigeminus roots and the accompanying lateralis roots, while the facialis canal contained the facialis roots and the accompanying lateralis roots.

There is no indication that the trigeminus canal was subdivided as in *Saurichthys*; but since the transverse section of at any rate its distal part is elliptic with the long axis of the ellipse running antero-ventrally to postero-dorsally, there is reason to assume that, as in *Glaucolepis,* the lateralis roots lay in the postero-dorsal, and the actual trigeminus roots in the antero-ventral part of the canal.

The trigeminus canal opens more posteriorly to the orbital opening of the trigemino-facialis chamber than in *Glaucolepis,* and it is quite probable, therefore, that no part of the ganglion gasseri lay in front of the trigemino-facialis chamber. Whether part of the ganglion gasseri lay in the most distal part of the trigeminus canal, as in *Saurichthys* (cf. p. 81), cannot be decided. The ganglion whence the nervus ophthalmicus lateralis and the nervus buccalis lateralis issued, probably lay in the trigemino-facialis chamber dorsally or postero-dorsally to the ganglion gasseri, as in *Glaucolepis.* The circumstance that no special canal for the ramus palatinus facialis is found, likewise seems to show that the ganglion geniculi lay in the trigemino-facialis chamber.

Thus, according to the above, the trigemino-facialis chamber in *Boreosomus* agrees well with that in *Glaucolepis* and *Saurichthys* (pp. 74–84), only has its ventral and possibly its lateral wall, too, a slightly greater anterior extent. As a consequence of this greater extent of the chamber in an anterior direction the chamber is more clearly separated from the myodome than in *Glaucolepis* and *Saurichthys,* and probably no part of the trigemino-facialis ganglionic complex lay in front of the orbital opening of the chamber. The ventral wall of the chamber is not pierced by any canal for the ramus palatinus facialis, consequently this nerve branch must have left the chamber through its orbital opening.

In conclusion I shall sum up what has been ascertained as regards the relations of the different vessels and nerves to the myodome and the trigemino-facialis chamber.

The nervus oculomotorius passed through the cranial wall in front of the trigemino-facialis chamber, and was possibly accompanied by the nervus ophthalmicus profundus, since, in contrast to *Glaucolepis,* no separate canal for this nerve is found. The canal for the nervus abducens opens into the myodome, as in *Glaucolepis,* but the accurate position of the opening of the canal in the myodome is unknown. The trigemino-facialis ganglionic complex

lay in the trigemino-facialis chamber. The ramus oticus lateralis passed from the trigemino-facialis chamber in a lateral direction through the wall of the chamber to the spiracular canal and not, as in *Glaucolepis,* to the fossa bridgei. The ramus palatinus facialis must have left the trigemino-facialis chamber through its orbital opening; but its further course towards the ventral face of the endocranium through the orbit and possibly through the lateral part of the myodome is unknown. The truncus hyoideomandibularis left the trigemino-facialis chamber through the extremely short jugulo-hyoideomandibular canal, which, in contrast to the conditions in *Glaucolepis,* has only one posterior opening. The vena jugularis ran through the jugulo-hyoideomandibular canal and the trigemino-facialis chamber, as in *Glaucolepis.* After entering the orbit through the orbital opening of the trigemino-facialis chamber, it must have continued in an antero-ventral direction, passing immediately in front of the orbital opening of the myodome, where it received the pituitary vein, whose precise course through the myodome is unknown. The arteria carotis externa passed from the lateral face of the otic region through a vertical canal which dorsally opens into the trigemino-facialis chamber, and not, as in *Glaucolepis,* in the jugulo-hyoideomandibular canal.

Ethmoidal region. – The ethmoidal region is well ossified in several cases, thus, in the first place, in specimens Nos. 295, 296, 300, 305, and 307, but on account of its delicate structure it was exceedingly difficult to investigate, and only in a single specimen (No. 296) did I succeed in exposing the whole ossified part of the region. The subjoined description is chiefly based on this specimen, for the part of the investigation by the grinding method so far completed supplies no very exact information about the ethmoidal region, the bone-tissue in the dorsal part of the region in the ground specimen being, as it were, crushed, as will be seen from the drawings (Fig. 58).

The ethmoidal region is much broader and a little lower than the anterior part of the orbitotemporal region and has a very small rostro-caudal extent, as will be seen from Fig. 62.

Broadly speaking the ethmoidal region consists of a medial wall, the septum nasi (*sn*, Figs. 60, 62, 65 B), from which issues on either side a transversally placed, fairly vertical wall, the planum antorbitale (*pl. ant*, Figs. 58, 60; Pl. 29, Figs. 1, 2), which forms the anterior boundary of the orbit and the posterior boundary of the nasal cavity.

If we disregard the details, the ethmoidal region may be said to be bounded by a paired posterior, an unpaired anterior, a dorsal, and a ventral face and by a paired lateral margin (viz. the thin lateral margin of the planum antorbitale).

The paired posterior face, whose outline is seen from Fig. 65 A, is concave both in a vertical and a horizontal direction, and posteriorly, as will be seen from Fig. 62, it passes gradually into the lateral face of the orbitotemporal region. The two depressions interpreted above as the dorsal and the

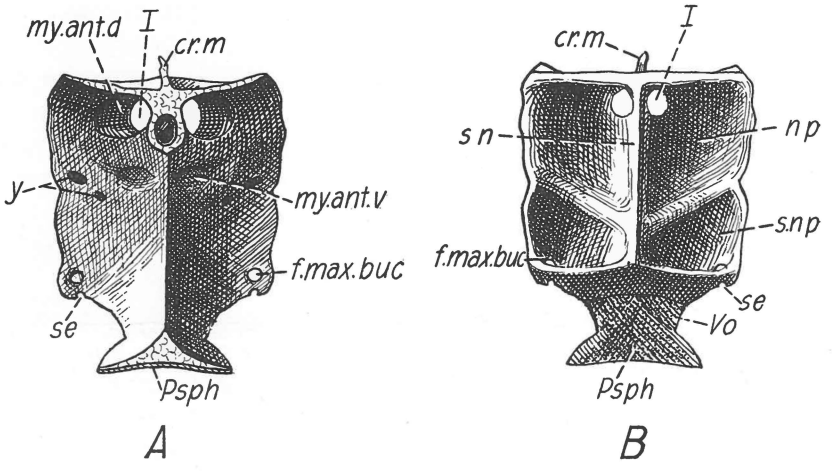


Fig. 65. *Boreosomus piveteaui* n. sp. Anterior part of the neural endocranium. Sketch based on several specimens. 3–4 ×. A, Ethmoidal region and anterior part of the orbitotemporal region in posterior view; the remaining part of the endocranium removed. Sectional faces reticulated. B, same part of endocranium as in Fig. A in anterior view.
Psph, parasphenoid; *Vo*, vomer; *cr. m*, median crista on the dorsal face of the orbitotemporal region; *f. max. buc*, canal for the ramus maxillaris trigemini, the nervus buccalis lateralis, and vessels; *my. ant. d*, anterior dorsal myodome; *my. ant. v*, anterior ventral myodome; *np*, nasal pit; *se*, groove on the ventral face of the ethmoidal region; *sn*, septum nasi; *s. np*, depression on the anterior face of the ethmoidal region ventrally to the nasal pit; *y*, probably small depressions on the orbital face of the planum antorbitale; *I*, foramen for the nervus olfactorius.

ventral anterior myodome extend, as already stated, some distance onto the dorso-medial part of the posterior face of the ethmoidal region. It has likewise been stated above that the nervus olfactorius passed through the anterior dorsal myodome, continuing in a canal through that part of the ethmoidal region which forms the anterior boundary of this myodome. Accordingly the posterior opening of this canal, the canalis olfactorius ethmoidalis, as will be seen from Fig. 65 A, lies on the most dorso-medial part of the posterior face of the ethmoidal region. Laterally to that part of the anterior ventral myodome which extends into the ethmoidal region, two small foramina (*y*) are indicated in Fig. 65 A. Probably these foramina are the orbital openings of two small depressions in, not two canals through, the planum antorbitale, for corresponding foramina have not been observed on the anterior face of the ethmoidal region in the only specimen in which this face could be examined.

On the most ventro-lateral part of the posterior face a fairly large foramen is found, which is the posterior opening of a canal (*f. max. buc*, Figs. 62, 65 A and B) extending in an anterior direction through the planum antorbitale. This canal probably corresponds to the notch in the lateral margin of the

ethmoidal region in *Glaucolepis* through which the ramus maxillaris trigemini, the nervus buccalis lateralis, and various vessels passed (cf. p. 85). Ventrally to the orbital opening of this canal a very small notch is seen in the ventral margin of the posterior face; it indicates the position of a short, longitudinal groove on the ventral face of the ethmoidal region (*se*, Figs. 62, 63, 65 A–B). Whether a vessel or a nerve passed in this groove, I am unable to decide.

The anterior face of the ethmoidal region is divided into a right and a left half by a vertical median ridge, which constitutes the anterior and largest part of the aforementioned median bone wall, the septum nasi (cf. Fig. 65B). As is seen from Figs. 62 and 65A, two deep depressions are found on each of these halves.

The dorsal and largest of these depressions (*np*, Figs. 60, 62, 65B), whose outline is seen from Fig. 65B, may be described as an anteriorly open space with a medial, a dorsal, a ventral, and a postero-lateral wall.

The medial wall consists of the dorsal part of the vertical median ridge, which, as will be seen from Fig. 62, has a considerable height (rostro-caudal extent). The postero-lateral wall is concave both in a vertical and a horizontal direction in such a way that the greatest depth of the space occurs in its dorso-medial part, and in this deepest part of the space opens the aforementioned canalis olfactorius ethmoidalis. The ventral wall is formed by a conspicuous ridge running in a dorso-lateral direction on the anterior face of the ethmoidal region, and the dorsal wall is formed by a transverse ridge on the most dorsal part of the anterior face of the region. The anterior margin of the last-mentioned ridge is concave from side to side.

The above-described depression on the anterior face of the ethmoidal region lodged the nasal sac; thus *Boreosomus* has a much better delimited nasal pit than *Glaucolepis* (cf. p. 96), though the walls of the pit are not by far so complete as in *Australosomus*, *Saurichthys*, and the sturgeons.

Antero-laterally to the wide anterior opening of the nasal pit lies the anterior nostril, as will be seen from Fig. 72. As in *Glaucolepis*, the posterior nostril lies laterally to the anterior part of the orbit; but in the margin of the postero-lateral wall of the nasal cavity there is not, as in *Glaucolepis* (pp. 86, 96), an emargination for the communication between the nasal sac and the posterior nostril.

The ventral and smaller of the two depressions on the anterior face of the ethmoidal region (*s.np*, Figs. 62, 65B) may, like the dorsal depression, be described as an anteriorly open space. This space, which is less deep than the nasal pit, may be regarded as bounded by a dorsal, a medial, a posterior, a lateral, and a ventral wall.

The dorsal wall is the ridge on the anterior face of the ethmoidal region which forms the ventral wall of the nasal pit, and the medial wall is

constituted by the most ventral and thickest part of the vertical median ridge of the anterior face of the ethmoidal region. The posterior wall is concave both in vertical and horizontal directions in such a way that the greatest depth of the space occurs nearer its lateral than its medial wall. The lateral wall is rather thin, and its face towards the space passes gradually into the concave anteriorly directed face of the posterior wall of the space. The ventral wall forms a horizontal plate, which, as will be seen from Fig. 63, showing the ethmoidal region in ventral view, is pierced by a large number of irregular openings.

In the ventro-lateral corner of the space just described opens the aforementioned canal which contained the ramus buccalis lateralis, the ramus maxillaris trigemini, and various vessels.

The dorsal face of the ethmoidal region, whose outline will be seen from Fig. 59, passes posteriorly into the dorsal face of the orbito-temporal region. The dorsal face is directed dorsally and at the same time very slightly anteriorly, and is fairly plane both in a longitudinal and a transverse direction.

The ventral face, whose outline will be seen from Fig. 63, is directed ventrally and slightly anteriorly. Posteriorly it passes gradually into the much narrower ventral face of the orbitotemporal region. The most posterior part of the ventral face is covered by the anterior part of the parasphenoid (and the paired vomer, if any such bone is present (cf. p. 322)).

On the ventral face a number of irregular openings are found, which, as stated above, lead to the paired depression on the ventral part of the anterior face of the ethmoidal region. In addition, as has likewise been stated above, a short longitudinal groove is found on the most lateral part of the ventral face. The anterior part of the palatoquadrate ossification articulated with the postero-ventral margin of the ethmoidal region, that is to say, with the edge between the ventral and posterior faces of the region. However, no articular fossa or articular process is found on this margin which might indicate the exact place of this articulation, and in spite of preparation of several specimens I failed to find the palatoquadrate and the ethmoidal region in their natural position in relation to each other. However, by carefully measuring the specimens in which both the neural endocranium and the palatoquadrate are well preserved it could be established with a fair degree of certainty that the place of articulation was situated as shown in Fig. 72.

As will be seen from Fig. 62, the paired lateral margin of the ethmoidal region is rather narrow except in its most ventral part, where it increases in breadth in a ventral direction.

A comparison between the ethmoidal regions in *Boreosomus* and in *Glaucolepis* reveals fairly considerable differences. Among these it should especially be pointed out that the walls of the nasal pit in *Boreosomus* are more well developed than in *Glaucolepis* and that ventrally to the nasal pits in *Boreosomus* a paired depression is found on the anterior face of

the ethmoidal region, while any trace of such a depression is lacking in *Glaucolepis*. A comparison with recent Ganoids supplies no explanation of the significance of this paired depression.

Remarks on the brain.

As will be evident from the above, the walls of the cranial cavity, in contrast to those of *Glaucolepis*, are entirely ossified, and from this it follows that the cranial cavity in the fossil cranium is identical with that of the living fish. The size and shape of the cavity suggest that it has been almost entirely occupied by the brain. Thus Fig. 66, which has been executed chiefly on the basis of the model of the cavities in the dorsal part of the endocranium which was constructed on the basis of the incomplete grinding series, gives a fairly accurate picture of the brain in dorsal view. The ventral part of the cranial cavity has not yet been investigated by grinding, and its shape could not, therefore, be ascertained in detail.

That part of the cranial cavity which lodged the telencephalon and the diencephalon (*tel, dic*, Fig. 66; Pl. 25, Figs. 2, 3; Pl. 26, Fig. 2; Pl. 27. Fig. 2) has about the same shape as in the Kansas forms (Moodie 1915, Figs. 15–16), and hence the telencephalon and the diencephalon were probably of the same type as in Moodie's forms. As will be seen from Fig. 66, the model of the anterior part of the cranial cavity shows a dorsal median groove, which indicates the position of the hemispheres. As in the Kansas forms, and in *Saurichthys* and *Glaucolepis*, the posterior part of the diencephalon was covered by the antero-lateral part of the mesencephalon. Dorsally to that division of the cranial cavity which contained the diencephalon the roof of the endocranium is pierced by the small well defined anterior dorsal fontanelle. As it can be established with certainty that the epiphysis did not leave any impression on the cerebral face of that part of the roof of the endocranium which lies in front of the anterior dorsal fontanelle, as for instance in *Saurichthys* (Stensiö 1925, p. 159, Fig. 82), there is every probability that the epiphysial stalk extended up through the fontanelle itself and actually caused the formation of the fontanelle. In the most completely ossified specimens of the Kansas forms (cf. *e.g.* Moodie 1915, Fig. 15) the anterior dorsal fontanelle has almost the same shape and position in relation to the diencephalon as in *Boreosomus*, and may also be interpreted as an epiphysial opening in the roof of the endocranium. In *Glaucolepis*, in which the large anterior dorsal fontanelle must be supposed to have been closed by cartilage, the epiphysial stalk probably passed through that part of the fontanelle which was open in the living animal, too. In this connection it may be mentioned that within the *Palaeonisciformes* a pineal foramen between the frontals has been observed in *Gyrolepidotus schmidti* (Berg 1939). (A pineal foramen has likewise been observed in young specimens of *Aci-*

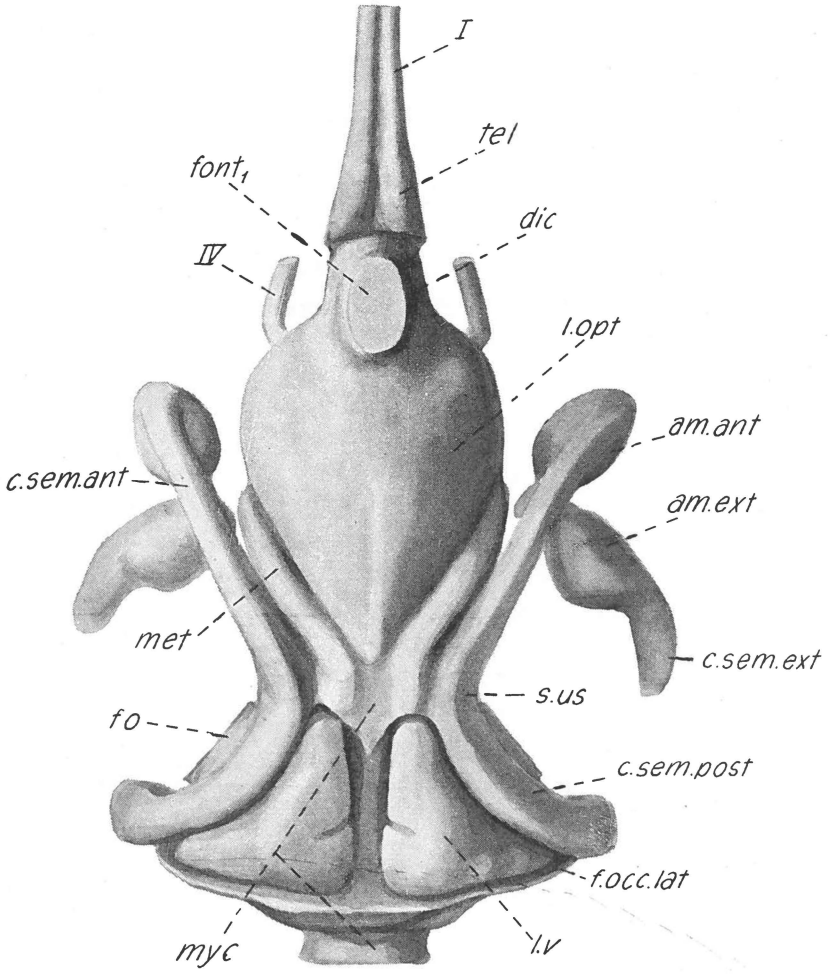


Fig. 66. *Boreosomus piveteaui* n. sp. Cast of the cavities in the dorsal part of the neural endocranium in dorsal view. Based on a wax model. 6–7 ×.
am. ant, *am. ext*, divisions of the labyrinth cavity for the ampulla anterior and the ampulla externa respectively; *c. sem. ant*, *c. sem. ext*, *c. sem. post*, divisions of the labyrinth cavity for the canalis semicircularis anterior, the canalis semicircularis externus, and the canalis semicircularis posterior; *dic*, division of the cavum cerebrale cranii for the diencephalon; *f. occ. lat*, fissura occipitalis lateralis; *fo*, opening in the wall between the cavum cerebrale cranii and an intramural space in the dorsal wall of the otic region; $font_1$, anterior dorsal fontanelle; *l. opt*, division of the cavum cerebrale cranii for the lobus opticus; *l. v*, division of the cavum cerebrale cranii for the "lobus vagus"; *met*, division of the cavum cerebrale cranii for the lateral part of the metencephalon; *myc*, division of the cavum cerebrale cranii for the myelencephalon; *s. us*, division of the labyrinth cavity for the sinus utriculi superior; *tel*, division of the cavum cerebrale cranii for the telencephalon; *I*, canal for the nervus olfactorius; *IV*, canal for the nervus trochlearis.

penser (Luther 1913). The hypothalamus region is not yet known in detail. The nervi optici issued from the ventral part of the diencephalon just in front of the infundibulum. In the mesencephalon the lobi optici (*l. opt*, Fig. 66; Pl. 25, Figs. 2, 3) were, as usual, well developed. The boundary between the posterior part of the right and the left lobus is indicated by an inconsiderable median groove on the dorsal side of the model of the cranial cavity. As in *Glaucolepis*, the nervus trochlearis and the nervus oculomotorius left the cranial cavity laterally to the mesencephalon.

In the model of the dorsal part of the cranial cavity a paired, very prominent bulge (*met*, Fig. 66) is seen immediately behind the mesencephalic division. From the area between the right and left divisions of the labyrinth cavity for the sinus utriculi superior this bulge first extends some distance in an anterior direction, continuing then, after an abrupt bend, in an anterolateral direction till it terminates anteriorly, dorso-medially to the foremost part of the division of the labyrinth cavity for the ampulla of the canalis semicircularis externus. The contact face between the anterior long division of the bulge and the remaining portion of the model is exceedingly narrow, and along a short stretch the middle part of this division of the bulge is even separated by an interspace from that part of the model which it overlaps, as may be seen most distinctly from Fig. 60. The long anterior division of the bulge corresponds to the bulge which in the Kansas forms and in *Glaucolepis* (cf. p. 101) represents that division of the cranial cavity which lodged the lateral part of the metencephalon. Nothing can be inferred from the shape of the cavity as to the median part of the metencephalon, and it is, of course, impossible to decide whether the valvula cerebelli was concealed below the lobi optici.

The posterior, longitudinally directed, short division of the bulge just mentioned must be referred to the myelencephalic division of the cranial cavity and seems to correspond to the structures in the Kansas forms which were interpreted by Moodie (1915, Figs. 4, 6, 8, 15 and 16) as indicating the presence of the tubercula acustica (lobi acustici laterales). From the shape of the myelencephalic division (*myc*) of the cranial cavity, which is of the same relative length as in the Kansas forms and *Glaucolepis*, it appears that farthest anteriorly and farthest posteriorly the myelencephalon was narrow, and that its middle part had a very large paired bulge (*l. v*, Fig. 66), which is no doubt comparable to the less well developed bulge of the myelencephalon in *Glaucolepis*. The connection between the development of this bulge, whose size and shape, in so far as they are known, will be seen from Fig. 66, and a space in the wall of the endocranium lying laterally to the bulge has been dealt with in the account of *Glaucolepis* (pp. 101-02).

On the lateral face of the model of the myelencephalic division of the cranial cavity, just postero-ventrally to the anterior half of the metencephalic bulge, lies another bulge parallel with the latter, but shorter and less pro-

minent (in Fig. 66 it is concealed by that division of the labyrinth cavity which contained the canalis semicircularis anterior); this bulge probably represents that division of the cranial cavity which contained the anterior part of the tuberculum acusticum, that is to say, the antero-lateral corner of the myelencephalon. A corresponding structure has not been observed in either the Kansas forms or in *Glaucolepis*.

In the main features the brain in *Boreosomus* agrees well with that of the Kansas forms and of *Glaucolepis*, thus principally in the relative proportions of its individual divisions.

Dermal bones on the ventral side of the neural endocranium.

As in most of the *Palaeonisciformes* the parasphenoid (*Psph*, Figs. 62, 63, 64, 65 A and B, 67, 71; Pl. 26, Fig. 1; Pl. 27, Fig. 1; Pl. 30, Fig. 1) consists of a corpus from which issue two pairs of processes. In the following description, as in that of *Glaucolepis*, I shall regard the corpus of the parasphenoid as consisting of a pars anterior in front of, and a pars posterior behind the centre of radiation.

The parasphenoid extends so far in an anterior direction that its most anterior part rests on the ventral face of the ethmoidal region, and so far in a posterior direction that its posterior part lies ventrally to that part of the otic region which lies anteriorly to the aorta canal.

The ratio between the lengths of the pars posterior and the pars anterior is almost one to four, which means that the centre of radiation lies relatively nearer the posterior margin of the parasphenoid than in *Glaucolepis*. However, the relations of the centre of radiation both to the neural endocranium and to the processus ascendentes are the same as in *Glaucolepis* (p. 102).

Before commencing a more detailed description of the parasphenoid, I shall say some words about the relation between the parasphenoid and the paired vomer, whose position is indicated in Figs. 63, 65 B, 67, and 71. In the few specimens of *Boreosomus* in which it was possible to investigate the dermal bones on the ventral side of the neural endocranium it was very difficult to decide whether the paired vomer actually exists, or whether it is merely a part of the parasphenoid. Without venturing to make a final decision, I am most inclined to think that a vomer is present, and that the anterior part of the parasphenoid is pointed, as shown in the figures, and as taken for granted in the below description. However, the broken line marking the boundary between the parasphenoid and the vomer in the figures is meant to indicate that quite possibly the supposed vomer is merely the antero-lateral part of the parasphenoid, whose anterior part in that case is relatively broad.

The pars anterior attains its greatest breadth in its posterior part, narrowing in a forward direction so that the bone, as stated above, tapers an-

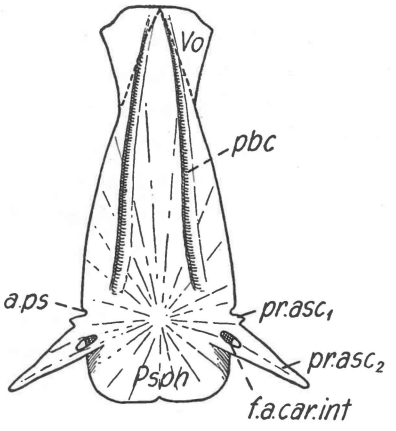


Fig. 67. *Boreosomus piveteaui* n. sp. Parasphenoid and vomer (or parasphenoid only, in case the sutures indicated by the broken lines do not exist) in dorsal view. Based mainly on specimen No. 296. C. 3 ×.
Psph, parasphenoid; *Vo*, vomer; *a. ps*, notch for the arteria pseudobranchialis efferens; *f. a. car. int*, foramen for the arteria carotis interna; *pbc*, groove for the ramus palatinus facialis and a branch of the arteria carotis interna; *pr. asc*$_1$, processus ascendens anterior; *pr. asc*$_2$, processus ascendens posterior.

teriorly to a point. The paired lateral margin of the pars anterior is convex, and the small triangular vomer is sutured with the anterior part of this margin. As in *Glaucolepis* (p. 103), a small notch (*a. ps*, Figs. 63, 67, 71) is found in the posterior part of the lateral margin of the pars anterior; this notch indicates the place where the arteria pseudobranchialis efferens and probably the ramus palatinus posterior facialis passed the margin of the bone.

The ventral face of the pars anterior is slightly concave in a transverse, and slightly convex in a longitudinal direction. With the exception of a very narrow zone along that part of the lateral margin which is not in contact with the vomer, the ventral face of the pars anterior is covered with close-set small blunt teeth. The free part of the lateral margin of the pars anterior and the lateral margin of the vomer follow closely the lateral margin of that part of the ventral face of the endocranium on which the pars anterior and the vomer lie. On the dorsal face of the pars anterior occurs a fairly broad paired longitudinal groove, which farthest anteriorly has a short continuation on the antero-medial part of the dorsal face of the vomer (*pbc*, Fig. 67). This paired groove, whose accurate course is seen from the figure, is closed dorsally by the ventral face of the endocranium so as to form a paired longitudinal canal, which, as already mentioned (p. 306), must be supposed to have lodged the ramus palatinus facialis and a minor branch of the arteria carotis interna. How the ramus palatinus facialis and the anteriorly directed branch of the arteria carotis interna reached the posterior end of this longitudinal canal is a question that cannot be answered

till the investigation by the grinding method now in progress has been completed.

The pars posterior, whose length is only one-fifth the full length of the parasphenoid, is a little narrower than the broadest part of the pars anterior and has a straight posterior margin, as will be seen from Figs. 63, 67, and 71. This part of the corpus of the parasphenoid lies ventrally to the posterior part of the orbitotemporal region and the anterior part of the otic region, but, as stated above (pp. 298, 307), it has no contact with the endocranium.

The ventral face of the pars posterior, which is slightly concave in a transverse direction, apart from a very narrow zone along its lateral margin is covered by close-set teeth of the same type as those on the ventral face of the pars anterior.

From the anterior part of the lateral margin of the pars posterior issues in a lateral direction a very small processus ascendens anterior (*pr. asc*$_1$, Figs.63, 67, 71; Pl. 30, Figs. 1, 2), which lies against the proximal part of the ventral margin of the processus basipterygius.

Immediately behind the processus ascendens anterior the somewhat larger processus ascendens posterior (*pr.asc*$_2$, Figs. 62, 63, 64, 67, 71; Pl. 30, Figs. 1, 2) issues in a postero-dorso-lateral direction from the pars posterior. This process does not issue from the lateral margin of the pars posterior, as is normal in the *Palaeonisciformes*, but from its dorsal face, the line of issue of the process running from that part of the lateral margin of the pars posterior which lies immediately behind the processus ascendens anterior, in a postero-medial direction on the dorsal face of the pars posterior, as shown in Fig. 67.

With its plane antero-dorso-medially directed face the processus ascendens posterior is in contact with that part of the otic region which forms the lateral wall of the myodome, and, as stated above, the anterior part of the proximal half of the process forms the anterior part of the lateral boundary of the myodome. The process is broadest in its proximal part, decreasing gradually in breadth towards its pointed distal end, which lies slightly ventrally or ventro-medially to the ventral opening of the spiracular canal.

The proximal broad part of the processus ascendens posterior is pierced by an oblong opening (*f.a.car.int*, Figs. 62, 63, 67, 71) for the arteria carotis interna. This opening lies nearer the posterior than the anterior margin of the process.

Thus, in *Boreosomus*, the parasphenoid has a very small processus ascendens anterior and a fairly well developed processus ascendens posterior, and accordingly, as stated above (p. 111), it belongs to the Parasphenoid-type 3, according to Aldinger's classification. In the relation of the processus ascendens anterior to the processus basipterygius and the relation of the processus ascendens posterior to the spiracular canal and the hypophysial

region *Boreosomus* agrees well with the Kansas form A (cf. p. 111), which is the best known of the forms with a parasphenoid of Type 3 mentioned by Aldinger.

As explained above (p. 322), *Boreosomus* possibly has a small paired vomer (*vo*, Figs. 63, 65B, 67, 71). This vomer lies mainly on the antero-lateral part of the ventral face of the orbitotemporal region, but in addition covers a small part of the ventral face of the ethmoidal region. As will be seen from Figs. 63, 67, and 71, the vomer is roughly triangular in outline and ventrally it is joined by suture with the anterior part of the lateral margin of the parasphenoid. With the exception of a narrow zone along its lateral (or postero-lateral) margin, the ventral face of the bone is covered by close-set small teeth of the same type as the teeth found on the parasphenoid. On the antero-medial part of the dorsal face of the vomer a continuation is seen of the longitudinal groove on the dorsal face of the pars anterior of the parasphenoid.

The radiation centre of the bone could not be localised.

According to the above, the vomer in *Boreosomus* is of a different type from that in *Glaucolepis* (pp. 113-114); owing to its firm connection with the parasphenoid and with the ventral face of the endocranium it is more like the vomer found in *Saurichthys* and in recent *Holostei*.

Dermal bones on the dorsal side of the neural endocranium.

On each side of the mid-line two extrascapulars are found, of which the medial is much larger than the lateral (*Ext.m*, *Ext. l.*, Figs. 68A, 69, 72; Pl. 29, Figs. 1, 2).

The shape of the extrascapulars varies somwhat as shown in the figures. In specimen No. 310 (Pl. 29) the medial extrascapular is very broad and perhaps includes the lateral extrascapular.

A narrow antero-lateral marginal zone of the lateral extrascapular is overlain by the posterior part of the supratemporo-intertemporal, and both the lateral and medial extrascapulars overlap a fairly large anterior part of the small suprascapulars. The elements of the extrascapular series join each other by suture without any or with an inconsiderable overlapping. A very narrow marginal zone of the medial extrascapular is overlapped by the posterior part of the parietal, at any rate in several specimens, while the lateral extrascapular is probably not overlapped by the part of the parietal with which it is in contact.

The lateral extrascapular is pierced in the usual way by the cephalic division of the main lateral line, and both the lateral and the medial extrascapulars are pierced by the supratemporal commissure. These sensory canals pierce the radiation centres of the bones which they traverse.

In *Glaucolepis* a considerable part of the parietal is overlapped partly by

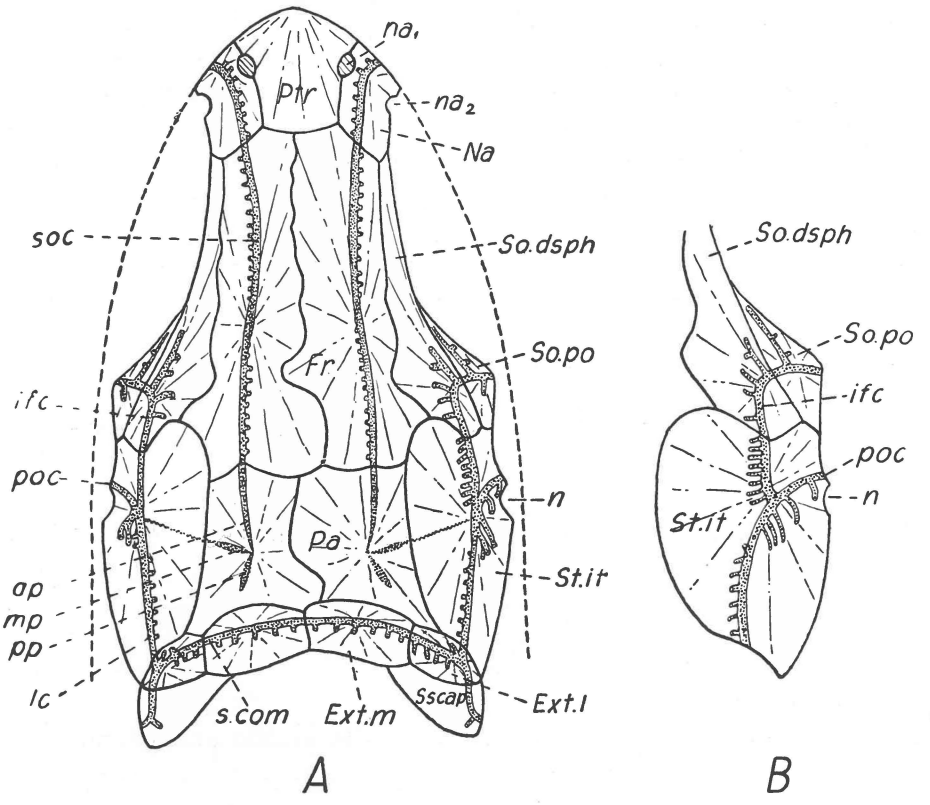


Fig. 68. *Boreosomus piveteaui* n. sp. Based mainly on specimen No. 305. C. 2 ×. A, dermal cranial roof in dorsal view. B, detail of the dermal cranial roof in dorso-lateral view. *Ext. l*, lateral extrascapular; *Ext. m*, medial extrascapular; *Fr*, frontal; *Na*, nasal; *Pa*, parietal; *Ptr*, postrostral; *So. dsph*, supraorbito-dermosphenotic; *So. po*, supraorbito-postorbital; *Sscap*, suprascapular; *St. it*, supratemporo-intertemporal; *ap*, anterior pit-line; *ifc*, infraorbital canal; *lc*, postotic canal; *mp*, middle pit-line; *n*, notch in the margin of the supratemporo-intertemporal dorsally to the dorsal end of the hyomandibula; na_1, na_2, anterior and posterior nostrils; *poc*, preopercular canal; *pp*, posterior pit-line; *s. com*, supratemporal commissure; *soc*, supraorbital canal.

the frontal and partly by the supratemporo-intertemporal. Thus, as stated above (pp. 117, 124), there is a rather considerable difference between the shape of the uncovered part of the parietal and the complete parietal. The other elements, too, of the dermal cranial roof in *Glaucolepis* exhibit so large overlapped areas that in ventral view the dermal cranial roof presents quite a different sutural pattern than in dorsal view. In the dermal cranial roof in *Boreosomus*, however, the overlapped areas are rather inconsiderable, and the differences between the sutural pattern of the dorsal and the ventral side of the dermal cranial roof are accordingly small.

The parietal (*Pa*, Figs. 68A, 69, 72; Pl. 29, Figs. 1, 2) is somewhat longer than broad and is roughly rectangular in outline. As the difference between

the outlines of the exposed part of the parietal and of the whole bone is inconsiderable, the further details is seen fairly well from Fig. 68A. It should merely be pointed out here that, as in *Glaucolepis*, the postero-lateral corner of the parietal is somewhat produced in a postero-lateral direction.

A lateral narrow marginal zone of the parietal is overlapped by the supratemporo-intertemporal, and an anterior, possibly a little broader, marginal zone of the bone is overlapped by the posterior part of the frontal.

As will be seen from Fig. 68A, the suture between the right and left parietals has a somewhat irregularly undulating course, and either parietal overlaps part of the margin of the other parietal.

The radiation centre of the parietal lies a little nearer the lateral than the medial margin of the bone and somewhat nearer its posterior than its anterior margin. The posterior, the middle, and the anterior pit-line issue from the radiation centre; the anterior pit-line is continued through the anterior part of the parietal by the supraorbital canal, as will be explained below.

The external face of the supratemporo-intertemporal (*St. it*, Figs. 68A and B, 69, 72; Pl. 29, Figs. 1, 2), which is both longer and broader than the parietal, is convex from side to side and is mainly dorso-laterally directed. To give an idea of the outline of the supratemporo-intertemporal Fig. 68, therefore, besides the dermal cranial roof in dorsal view, shows the supratemporo-intertemporal in dorso-lateral view. Broadly speaking, the outline of the supratemporo-intertemporal is four-sided, as we may distinguish between a postero-medial, a medial, an anterior, and a lateral margin of the bone.

The postero-medial margin, which is slightly concave, overlaps a narrow antero-lateral marginal zone of the lateral extrascapular, while the medial concave margin overlaps the lateral margin of the parietal and the postero-lateral margin of the frontal. The anterior irregular margin probably, without overlapping, joins by suture with the margins of the supraorbito-dermosphenotic and the supraorbito-postorbital. The predominantly convex lateral margin as usual forms the posterior part of the free lateral margin of the dermal cranial roof.

As in *Glaucolepis* and in various other *Palaeonisciformes*, for instance *Cheirolepis* (Watson 1925, Fig. 1), the lateral margin of the supratemporo-intertemporal has a small distinct notch (*n*, Fig. 68; Pl. 29, Fig. 2) directly dorsally to the most dorsal part of the hyomandibula. Medially to this small notch and nearer the lateral than the medial margin of the bone lies the centre of radiation.

The supratemporo-intertemporal is pierced by a longitudinal sensory canal, whose anterior part is constituted by the posterior part of the infraorbital canal, and whose posterior part is the postotic canal. Where this sensory canal pierces the centre of radiation, it gives off an antero-laterally directed branch, which anastomosed with the sensory canal in the preoper-

culum. In several cases a groove or narrow canal, which represents the middle pit-line of the cranial roof (cf. p. 356), further issues from the centre of radiation towards the radiation centre of the parietal.

Like all other canal bones, the supratemporo-intertemporal on its internal face has a ridge which follows the course of the sensory canals through the bone, but unlike the conditions in *Glaucolepis*, etc., (pp. 110-20) no internal lamina issues from this ridge for the consolidation of the connection between the dermal cranial roof and the neural endocranium.

The frontal (*Fr*, Figs. 68 A, 69, 72; Pl. 26, Fig. 2; Pl. 27, Fig. 2; Pl. 29, Figs. 1, 2) is a comparatively long and slender bone, which is bounded by a medial, a posterior, a postero-lateral, a lateral, and an anterior margin.

The medial margin is irregularly undulating, though not nearly so much as in *Glaucolepis*. Each of the convex divisions of the medial margin of the frontal very slightly overlaps the medial margin of the opposite frontal. The posterior margin of the frontal overlaps the anterior margin of the parietal, while the short concave postero-lateral margin of the bone is overlapped by the anterior part of the medial margin of the supratemporo-intertemporal. The long, slightly irregular lateral margin of the frontal adjoins the supraorbito-dermosphenotic, and probably the two bones meet without overlapping. The angular anterior margin of the frontal is overlapped by a posterior very narrow part of the nasal and the postrostral.

The radiation centre of the frontal lies a little nearer the posterior and lateral, than the anterior and medial margins of the bone.

As usual the frontal is pierced longitudinally by the supraorbital canal, which on its way passes the radiation centre of the bone.

The supraorbito-dermosphenotic (*So. dsph*, Figs. 68 A and B, 69, 72; Pl. 26, Fig. 2; Pl. 27, Fig. 2; Pl. 29, Figs. 1, 2) is a long, narrow bone with a lateral, an anterior, a medial, and a posterior margin.

The posterior half of the slightly concave lateral margin of the bone has contact with the relatively short supraorbito-postorbital, while the anterior half of the lateral margin forms part of the margin of the orbital opening. The anterior margin is very short and has contact with the nasal, which probably overlaps an inconsiderable anterior zone of the supraorbito-dermosphenotic. The relations of the supraorbito-dermosphenotic to the frontal and the supratemporo-intertemporal have been dealt with above.

As is seen from Fig. 68 A and B, the radiation centre of the bone lies very far behind the middle of the bone and nearer the lateral than the medial margin.

The posterior part of the bone is pierced by the infraorbital canal, which passes through the radiation centre in the normal way.

The supraorbito-postorbital (*So. po*, Figs. 68 A and B, 69, 72) which lies laterally to the posterior half of the supraorbito-dermosphenotic is roughly triangular in outline, as will be seen from the figures.

The posterior margin, which is angular, as will be seen from Figs. 68A and 69, adjoins and possibly overlaps the anterior margin of the supraorbito-dermosphenotic and the lateral part of the anterior margin of the frontal. Medially the nasal, as stated above, joins by suture with the postrostral. In the lateral margin of the nasal, which constitutes part of the anterior boundary of the orbital opening, an emargination is found, as in numerous other *Palaeonisciformes* (cf. p. 123), which emargination indicates the position of the posterior nostril (na_2, Figs. 68A, 69). The anterior or ventral margin of the nasal overlaps the posterior part of the antero-dorsal margin of the rostro-antorbito-premaxillary.

The radiation centre of the nasal, which lies between the anterior and posterior nostrils, as will be seen from Fig. 68A, is pierced by the supraorbital canal, which passes the nasal longitudinally.

Infraorbitals, suborbitals, and sclerotic ring.

According to Brough's reconstruction of *Boreosomus* (*Diaphorognathus*) *gillioti* (Brough 1933, Figs. 1 and 2), no infraorbitals are found between the suborbital series and the orbit. Aldinger (1937, p. 280) puts forward the assumption that this is merely due to the unsatisfactory state of preservation of the Madagascan material, and this assumption is confirmed by an investigation of the Greenland material. For in *Boreosomus piveteaui* the infraorbital series bounds the orbital opening both ventrally and caudally and comprises four bones, namely (in accordance with the terminology applied in the description of *Glaucolepis*) a postorbital, a jugal, a lacrimal, and a rostro-antorbito-premaxillary.

The postorbital (*Po*, Fig. 69), which has not been observed in *Boreosomus gillioti*, attains a considerable height and is so narrow that it may most adequately be termed a tube surrounding the infraorbital canal. This tube, which is slightly curved, with the convexity directed backward, forms part of the posterior boundary of the orbital opening and by its posterior side it is in contact with the anterior margin of the three or four most dorsal suborbitals. The connection between the postorbital and the suborbital series was no doubt rather loose, for in a few cases only the postorbital has retained its original position in relation to the suborbital series. Dorsally the suborbital has contact with the supraorbito-postorbital and ventrally with the jugal.

It has been impossible to localise the radiation centre of the bone.

The jugal (*Ju*, Figs. 69, 73) may for descriptive reasons be regarded as consisting of a very narrow dorsal and a broader ventral division.

The ventral division is bounded by a dorsal, a postero-ventral, an anterior, and an antero-dorsal margin. From the anterior part of the straight dorsal (or in some cases postero-dorsal) margin issues the dorsal division of

In this bone the radiation centre has a fairly central position and is pierced by the infraorbital canal, which passes through the bone in a transverse direction.

In 1937 Aldinger gave a review of the family *Acrolepidae*, from which it appears that a long supraorbito-dermosphenotic, extending from the supratemporo-intertemporal to the nasal, is of normal occurrence in this family (Aldinger 1937, pp. 263, 280, 289, Figs. 74, 83). In *Acrolepis sedgwicki* (Aldinger 1937, Fig. 74 (after Westoll 1934)) an independent supraorbital is seen laterally to the anterior and largest part of the long supraorbito-dermosphenotic, and Aldinger (1937, p. 263) therefore assumes that the supraorbital components of the supraorbito-dermosphenotic in this form represent a medial supraorbital series; thus the bone seems to correspond entirely to the supraorbito-dermosphenotic in *Glaucolepis*.

Whether the supraorbital in *Acrolepis sedgwicki* only represents a lateral supraorbital series or it is pierced by the infraorbital canal, too, and thus contains a canal component also, is unknown. If it is pierced by the infraorbital canal, it seems to correspond entirely to the supraorbito-postorbital in *Glaucolepis*.

The supraorbito-dermosphenotic in *Boreosomus* corresponds entirely to that of *Acrolepis sedgwicki*, and should accordingly be regarded as a dermosphenotic which has become fused with the medial supraorbital series. The supraorbito-postorbital in *Boreosomus* has no contact with the nasal, and its supraorbital component, therefore, probably corresponds only to the posterior part of the lateral supraorbital series, which is represented in the supraorbital (or perhaps the supraorbito-postorbital) in *Acrolepis sedgwicki*.

The postrostral (*Ptr*, Figs. 68A, 69, 72; Pl. 26, Figs. 1, 2; Pl. 27, Fig. 1; Pl. 28; Pl. 29, Figs. 1, 2) is bounded by a posterior, a paired lateral, and an anterior (or, according to the position of the postrostral, rather a ventral) margin.

The postrostral is very strongly curved both in a transverse and a longitudinal direction, the bone forming in the normal way a short, blunt rostrum, as seen from the figures. The radiation centre of the bone lies in the most prominent part of this rostrum. The slightly convex posterior margin of the postrostral adjoins, and possibly slightly overlaps, the anterior parts of the frontals. Laterally the postrostral adjoins the nasal, probably without overlapping. In the middle part of the lateral margin of the postrostral an emargination is found, which together with an emargination in the medial margin of the nasal forms the boundary of the anterior nostril (na_1, Figs. 68A, 69). The anterior or ventral margin of the postrostral overlaps the dorso-medial part of the rostro-antorbito-premaxillary.

The nasal (*Na*, Figs. 68A, 69, 72; Pl. 26, Figs. 1, 2; Pl. 27, Fig. 1; Pl. 29, Figs. 1, 2), which compared with the nasal in *Glaucolepis* is rather short, is limited by a posterior, a medial (antero-medial), a lateral (postero-lateral), and an anterior or rather a ventral margin.

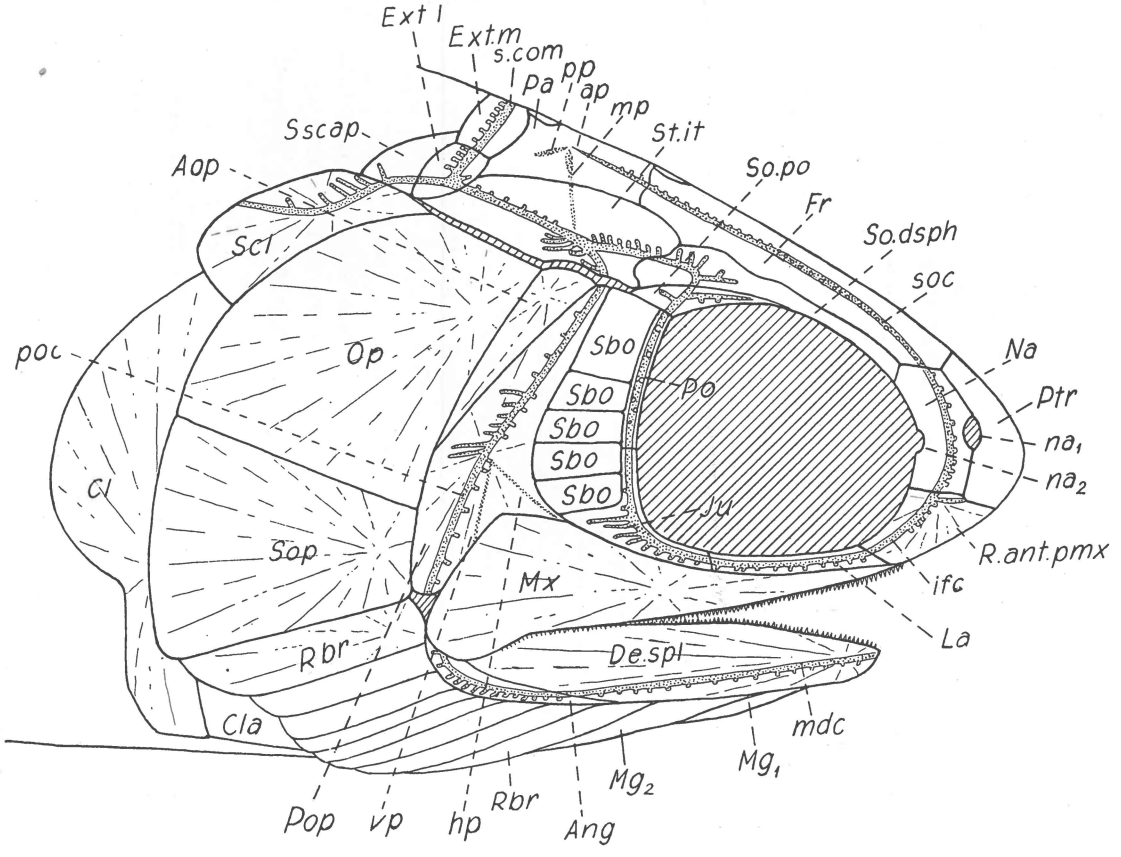


Fig. 69. *Boreosomus piveteaui* n. sp. Head and dermal shoulder girdle in lateral view. Based mainly on specimen No. 305. C. 2 ×.
Ang, angular; *Aop*, antoperculum; *Cl*, cleithrum; *Cla*, clavicle; *De. spl*, dentalo-splenial; *Ext. l*, lateral extrascapular; *Ext. m*, medial extrascapular; *Fr*, frontal; *Ju*, jugal; *La*, lacrimal; Mg_1, Mg_2, anterior and posterior median gular plates; *Mx*, maxillary; *Na*, nasal; *Op*, operculum; *Pa*, parietal; *Po*, postorbital; *Pop*, preoperculum; *Ptr*, postrostral; *R. ant. pmx*, rostro-antorbito-premaxillary; *Rbr*, branchiostegal ray; *Sbo*, suborbital; *Scl*, supracleithral; *So. dsph*, supraorbito-dermosphenotic; *So. po*, supraorbito-postorbital; *Sop*, suboperculum; *Sscap*, suprascapular; *St. it*, supratemporo-intertemporal; *ap*, anterior pit-line; *hp*, horizontal pit-line of the cheek; *ifc*, infraorbital canal; *mdc*, mandibular canal; *mp*, middle pit-line; na_1, na_2, anterior and posterior nostrils; *poc*, preopercular canal; *pp*, posterior pit-line; *s. com*, supratemporal commissure; *soc*, supraorbital canal; *vp*, vertical pit-line of the cheek.

the bone as a process pointing in a dorsal direction. The remaining part of the dorsal margin adjoins and possibly overlaps the most ventral part of the ventral suborbital. The postero-ventral margin is convex and overlaps the antero-dorsal margin of the maxillary. The anterior margin is very short and joined by suture with the posterior margin of the lacrimal. The antero-dorsal margin is concave and constitutes part of the boundary of the orbital opening.

The dorsal division of the jugal has the same breadth as the postorbital, and like this bone may best be described as a tube surrounding a part of the infraorbital canal. This division of the jugal, which lies in the direct ventral continuation of the postorbital, forms part of the posterior boundary of the orbital opening and by its posterior side it is in contact with the anterior margin of the two most ventral suborbitals.

The radiation centre of the jugal could not be definitely localised, but probably it is situated in that part of the bone in which the infraorbital canal changes its direction from vertical to horizontal.

If we compare the jugal and the postorbital in *Boreosomus* with the corresponding bones in a relatively primitive Acrolepid such as *Acrolepis sedgwicki* (Aldinger 1937, Fig. 74 (after Westoll 1934)), it will be evident that the two bones in *Boreosomus* have been the subject of a considerable reduction (NB. the postorbital is not indicated on Westoll's restoration, but it appears from the shape of the jugal that it had a rather considerable breadth).

The reduction of the jugal and the postorbital as well as of the anterior part of the supraorbito-postorbital in *Boreosomus* is no doubt due to the strong development of the eye, which, as we have seen above, has also set its mark upon the shape of the neural endocranium.

The shape of the lacrimal (*La*, Figs. 69, 73) agrees fairly well with that of the lacrimal component of the lacrimo-maxillary in *Glaucolepis*, being a low long bone with a dorsal, an antero-dorsal, a ventral, and a posterior margin.

The dorsal margin is slightly concave and forms part of the ventral boundary of the orbital opening. The antero-dorsal margin is in contact with the postero-ventral margin of the rostro-antorbito-premaxillary, but I am unable to decide whether an overlapping takes place. The ventral slightly convex margin overlaps the anterior part of the antero-dorsal margin of the maxillary. As already stated, the short posterior margin is in contact with the anterior margin of the jugal.

The infraorbital canal is so broad, compared with the lacrimal, that it has been impossible to localise the radiation centre.

The anterior element of the infraorbital series (*R. ant. pmx*, Figs. 69, 73) is a four-sided bone of fairly considerable dimensions. The somewhat convex external face of this bone, whose shape is seen from the figures, faces

mainly antero-ventro-laterally. Its four margins may roughly be designated as a dorsal, a postero-lateral, a postero-ventral, and a medial margin.

As stated above, the dorsal margin is overlapped by the anterior or ventral margins of the nasal and postrostral. The postero-lateral (actually postero-dorso-lateral) margin is concave and forms part of the boundary of the orbital opening. The postero-lateral part of the postero-ventral (actually postero-ventro-lateral) margin has contact with the antero-dorsal margin of the lacrimal, as stated above. The antero-medial part of the postero-lateral margin, however, forms the anterior part of the oral margin, as will be seen from Fig. 73. Whether this part of the margin bears teeth, I have been unable to ascertain. The medial margin has no contact with the medial margin of the corresponding bone on the other side of the head, but is separated from that bone by a narrow interspace.

The bone contains a three-branched division of the infraorbital canal (cf. further p. 354), and the three canal branches meet in the centre of radiation.

The three-branched division of the infraorbital canal shows that the bone described here includes an antorbital component corresponding to the antorbital in *Cheirolepis* (cf. p. 139), and since, as we shall see later (p. 354), one of the three branches represents the ethmoidal commissure, it must be assumed that the bone includes also a component corresponding to the rostral in *Cheirolepis*. Moreover the bone forms part of the oral margin, and it is therefore probable that it further comprises a component corresponding to the premaxillary in *Cheirolepis*.

Accordingly the bone must be regarded as a rostro-antorbito-premaxillary, a bone which, as stated above (p. 140), occurs in *Canobius elegantulus* and *Rhadinichthys fusiformis*, too.

Behind the postorbital part of the infraorbital series lies a vertical series of suborbitals (*Sbo*, Fig. 69). This series in some cases consist of five, in other cases six or seven bones. As is seen from Fig. 69, the most dorsal suborbital in the specimens whose suborbital series comprises only five bones, is much higher than the others. If more than five suborbitals are present, this high dorsal suborbital may be divided by a horizontal suture into two smaller ones, and in addition that area which in Fig. 69 is occupied by the four low suborbitals may be occupied by five still lower bones. Thus the elements of the suborbital series show a rather considerable variation, as is also the case in several other *Palaeonisciformes*.

The posterior margin of the suborbital series overlaps the anterior margin of the preoperculum, but the connection between the preoperculum and the suborbital series was hardly very firm. The individual suborbital elements join each other without overlapping and they were probably rather firmly connected, for not rarely the bones in a detached suborbital series are found in their natural mutual position.

The centres of radiation of the suborbitals lie nearer their anterior than

their posterior margins, but are not indicated in Fig. 69, as it is difficult to localise them exactly.

The sclerotic ring contains three or four elements.

The palatoquadrate and its dermal bones, the maxillary, and the preoperculum.

In the smallest specimens the palatoquadrate is probably unossified like the neural endocranium (p. 258); but in all the larger specimens, in which the neural endocranium is well ossified, the palatoquadrate is ossified in one piece from the autopalatine region to the quadrate region.

The Greenland material contains no specimens of *Boreosomus* in which, as in several specimens of *Glaucolepis,* various separate ossifications occur in the palatoquadrate; however, as we shall see later, judging from material of *Boreosomus* from Spitsbergen, there is reason to assume that the process of ossification in the palatoquadrate took place in practically the same way as in *Glaucolepis.*

The palatoquadrate articulated by its anterior part with the postero-ventral part of the ethmoidal region (cf. p. 318), while posteriorly it did not extend as far as the posterior part of the neural endocranium, as will be seen from Fig. 72. Thus the palatoquadrate is relatively shorter than in *Glaucolepis.*

In lateral or medial view the complete palatoquadrate ossification (Fig. 70; *Pq*, Figs. 71, 72; Pl. 30, Fig. 1) is roughly triangular in outline, with a postero-dorsal, an antero-dorsal, and a ventral margin. From the middle of the posterior half of the antero-dorsal margin issues a large process, on whose medial face a deep concavity is found (*f. art*, Fig. 70B and C; Pl. 30, Fig. 1) corresponding to a convexity on the lateral face of the process. The deep concavity is the articular fossa for the processus basipterygius of the neural endocranium. Since in *Boreosomus* the processus basipterygius is very small (p. 307), it is peculiar that this articular fossa on the palatoquadrate is so large.

Judging from the shape of the processus basipterygius and of the articular fossa on the palatoquadrate corresponding to it, in *Boreosomus,* in contrast to *Glaucolepis,* the palatoquadrate cannot possibly have moved in relation to the neural endocranium by sliding along a face of the processus basipterygius (cf. pp. 144 and 187).

The palatoquadrate ossification is a thin bone plate, which in broad features shows a similar curvature as the palatoquadrate in *Glaucolepis,* and as in the description of that bone in *Glaucolepis* we will for descriptive reasons regard the palatoquadrate ossification as consisting of an anterior and a posterior part. The boundary between these two parts is deter-

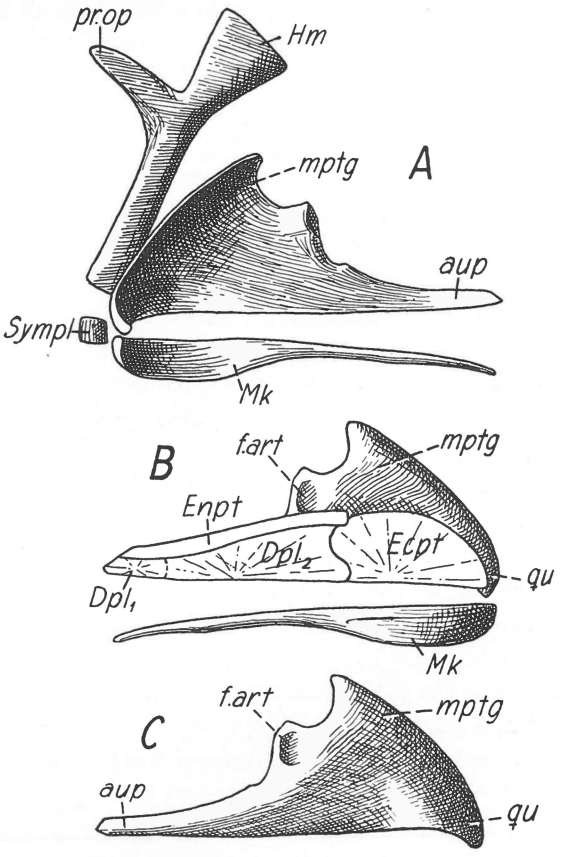


Fig. 70. *Boreosomus piveteaui* n. sp. Attempted sketches based mainly on specimen No. 278. C. 3 ×. A, part of the visceral endoskeleton in lateral view. B, palatoquadrate and its dermal bones and the Meckelian bone in medial view. C, palatoquadrate in medial view. Dpl_1, Dpl_2, anterior and posterior dermopalatines; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Hm*, hyomandibula; *Mk*, Meckelian bone; *Sympl*, symplectic; *aup*, pars autopalatina; *f. art*, articular fossa for the processus basipterygius; *mptg*, pars metapterygoidea; *pr. op*, processus opercularis; *qu*, pars quadrata.

mined by a vertical transverse plane through the area of articulation between the palatoquadrate and the processus basipterygius.

The posterior part of the palatoquadrate ossification is a rather thin, mainly vertical plate, which is so curved that its lateral face is chiefly concave and its medial face is correspondingly convex in a dorso-ventral direction. The shape of this part of the palatoquadrate ossification is seen from Figs. 70 A and C, and 71, and it is likewise seen from the figures that this part of the ossification attains its greatest height much nearer its anterior than its posterior end.

On account of the curvature of the palatoquadrate the postero-dorsal margin of the posterior part of the palatoquadrate ossification lies very near

the external dermal bones of the cheek (Fig. 71), but as far as I can see, only that part of this margin which lies nearest the area of articulation for the mandible had contact with one of the dermal bones of the cheek (the maxillary). Thus, as in *Glaucolepis,* the posterior division of the posterior part of the palatoquadrate ossification forms a posterior boundary of the space lying medially to the maxillary and occupied by the musculus adductor mandibulae in the living animal. The pars articularis of the Meckelian bone articulated with the lowermost margin of this hind wall of the dorsally open muscular space. The articular face of this part of the palatoquadrate is very difficult to investigate, but it can be ascertained that it was not, as in *Glaucolepis,* developed as a double condyle.

The antero-dorsal margin of the posterior part of the palatoquadrate ossification had no contact with the external dermal bones of the cheek lying laterally to this margin.

The most ventral division of the posterior part of the palatoquadrate ossification is likewise curved in a lateral direction except farthest posteriorly, where it forms the medial boundary of the opening for the musculus adductor mandibulae. A groove or a canal through the posterior part of the palatoquadrate ossification, as present in *Glaucolepis* and *Pygopterus* (p. 145), never occurs in *Boreosomus.*

The anterior part of the palatoquadrate ossification is a thin plate, which forms an anterior continuation of the most ventral, laterally curved part of that division of the palatoquadrate ossification which lies immediately behind it. Thus, broadly speaking, the anterior part of the palatoquadrate ossification is so situated that its slightly concave face is directed dorso-laterally and its corresponding convex face ventro-medially.

In ventral view (Fig. 71) this anterior part of the palatoquadrate ossification has three free margins, a lateral, a medial, and an antero-medial. The medial margin is so strongly concave that, as will be seen from the figure, it is separated by a large interspace from the lateral margin of the most ventral part of the orbitotemporal region and from the dermal bones associated with this part of the neural endocranium. The very short antero-medial margin, however, is in contact with the neural endocranium, as stated above. The lateral margin is convex.

In his description of the material of *Boreosomus arcticus* from Spitsbergen Stensiö (1921, pp. 211–12, Fig. 70) states that in the palatoquadrate he found two ossifications separated by a large unossified area. The anterior of these ossifications is an autopalatine, the posterior much larger ossification a quadrato-metapterygoid. In the shape of the palatoquadrate *Boreosomus arcticus* seems to agree well with *Boreosomus piveteaui,* and judging from the conditions in *Glaucolepis,* the circumstance that in the Spitsbergen form the degree of ossification is less than in the Greenland form, merely means that the Spitsbergen material described by Stensiö is derived from

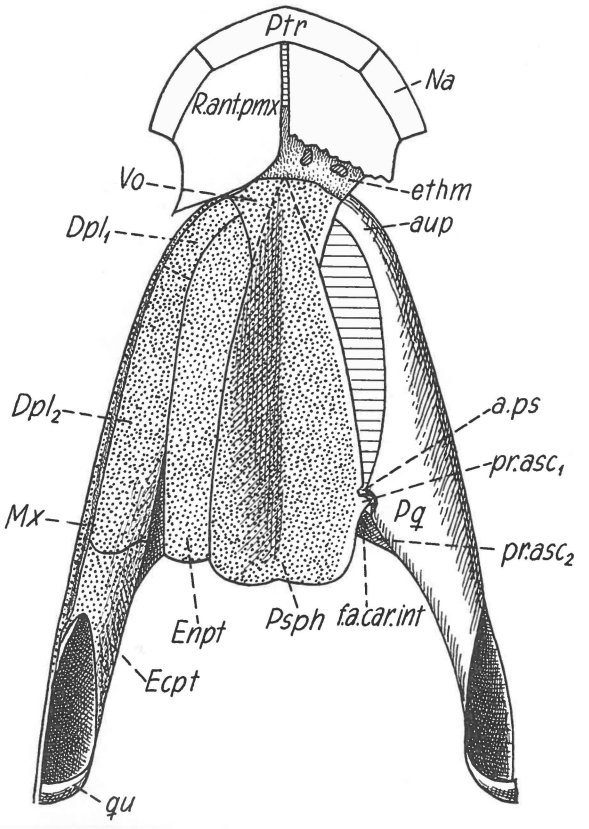


Fig. 71. *Boreosomus piveteaui* n. sp. Attempted sketch of snout and palate in ventral view. Dermal bones of palatoquadrate, the maxillary, and part of the rostro-antorbito-premaxillary removed on left side. Relations between the pars autopalatina and the neural endocranium uncertain. Based mainly on specimens Nos. 295 and 296. C. 4 ×.
Dpl_1, Dpl_2, anterior and posterior dermopalatines; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid, *Mx*, maxillary; *Na*, nasal; *Pq*, palatoquadrate; *Psph*, parasphenoid; *Ptr*, postrostral; *R. ant. pmx*, rostro-antorbito-premaxillary; *Vo*, vomer; *a. ps*, notch for the arteria pseudobranchialis efferens; *aup*, pars autopalatina; *ethm*, ventral face of the ethmoidal region; *f. a. car. int*, foramen for the arteria carotis interna; *pr.* asc_1, processus ascendens anterior; *pr. asc* , processus ascendens posterior; *qu*, pars quadrata.

a young individual. I found a confirmation of this on investigating a specimen of *Boreosomus reuterskiöldi* collected in Spitsbergen in 1929 and belonging to the Paleontological Museum, Upsala. For in this exceptionally well preserved specimen the palatoquadrate is ossified in one piece from the autopalatine region to the quadrate region, and agrees entirely in shape with that of *Boreosomus piveteaui*.

Although, as stated above, the Greenland material does not supply any information about the course of the process of ossification in the palatoquadrate, the Spitsbergen material suggests that this process has taken place in a way which corresponds to that observed in *Glaucolepis*.

Judging from the few specimens in which the roof of the mouth could be investigated, it would seem that four dermal bones are situated on the oral side of the palatoquadrate, viz. an entopterygoid, an ectopterygoid (possibly with a dermometapterygoid component), a posterior and an anterior dermopalatine.

The entopterygoid (*Enpt*, Figs. 70B, 71) is a long, narrow bone, whose shape is seen most distinctly from Fig. 71. Roughly speaking it is bounded by a medial, a lateral, and a posterior margin. Medially the entopterygoid covers a narrow lateral marginal zone of the oral face of the parasphenoid and the vomer, but it was hardly firmly connected with these two bones. The anterior two-thirds of the lateral margin of the entopterygoid overlap a narrow medial marginal zone of the two dermopalatines. How firm the connection was between the entopterygoid and these two bones, cannot be ascertained. The radiation centre of the entopterygoid could not be localised.

The oral face of the entopterygoid is covered by close-set, very small teeth of the same type as those found on the parasphenoid.

The ectopterygoid (*Ecpt*, Figs. 70B, 71) lies partly on the medially directed part of the oral face of the palatoquadrate, and partly on the ventral, laterally curved part of the palatoquadrate lying in front of the adductor opening; this means that it almost covers that area of the palatoquadrate which in *Glaucolepis* is covered partly by the dermometapterygoid and partly by the ectopterygoid. Since moreover no independent dermometapterygoid is found in *Boreosomus*, it is quite possible that the ectopterygoid contains a dermometapterygoid component; but on the other hand it is very conceivable, too, that the dermometapterygoid has been entirely reduced, so until investigations on other *Acrolepidae* are available, I will prefer to avoid using the term ectopterygoideo-dermometapterygoid.

The curvature of the ectopterygoid corresponds to the curvature of that division of the oral face of the palatoquadrate against which it lies, its dorsal part being mainly vertical, and its ventral (antero-ventral) part mainly horizontal.

The lateral margin of the horizontal part of the ectopterygoid is in contact with the posterior part of a longitudinal ridge on the medial side of the maxillary. Anteriorly the ectopterygoid joins by suture with the posterior dermopalatine, probably without overlapping. As will be seen from Fig. 70B, the suture is S-shaped.

The centre of radiation of the ectopterygoid, whose surface is covered by teeth of the same type as those found on the parasphenoid, or perhaps slightly more pointed, lies a little medially to the anterior end of the adductor opening and accordingly almost as the radiation centre of the ectopterygoid in *Glaucolepis*. This position of the radiation centre would seem to indicate that the ectopterygoid is not fused with a dermometapterygoid.

Stensiö (1921, pp. 211–12, Fig. 70) has described an entopterygoid and

an ectopterygoid in *Boreosomus arcticus* from Spitsbergen; however, these two bones differ so considerably in shape and position from those found in *Boreosomus piveteaui* that I am not capable of drawing comparisons between the two species as regards these bones.

The posterior dermopalatine (Dpl_2, Figs. 70B, 71) covers the oral face of the palatoquadrate to the extent shown in Fig. 70. The bone follows the curvature of the palatoquadrate in a normal way. It is bounded by an anterior, a dorsal, a posterior, and a ventral (or, owing to the curvature of the bone, rather lateral) margin. The lateral margin is in contact with the above-mentioned longitudinal ridge on the medial side of the maxillary. Anteriorly the posterior dermopalatine joins by suture with the anterior dermopalatine; but the exact course of the suture is unknown. Dorsally (medially) and posteriorly the bone is in contact with the entopterygoid and the ectopterygoid respectively, as described above. The radiation centre of the bone lies a little in front of the middle of the bone and somewhat nearer its lateral than its dorsal margin. Its oral face is covered by teeth of the same type as those of the ectopterygoid.

The posterior dermopalatine has precisely the same position in relation to the place of articulation between the palatoquadrate and the processus basipterygius as in *Glaucolepis* (cf. e.g. Fig. 37).

The anterior dermopalatine (Dpl_1, Figs. 70B, 71) covers the oral face of the anterior part of the palatoquadrate, following the curvature of this face. Its shape is seen from Figs. 70B and 71; it should be pointed out, however, that its posterior boundary has not been definitely ascertained. Laterally or antero-laterally it is probably in contact with the foremost part of the aforementioned longitudinal ridge on the medial side of the maxillary. Antero-medially it overlaps a very narrow zone of the oral face of the vomer. Medially or postero-medially it is in contact with the entopterygoid, as described above. The radiation centre of the bone lies fairly centrally, and the oral face is covered by teeth of the same type as those of the ectopterygoid.

The maxillary (*Mx*, Figs. 69, 71, 72, 73; Pl. 30, Fig. 2) may most adequately be described as a triangular bone with a postero-dorsal, an antero-dorsal, and a ventral margin. The details of its outline are seen most distinctly from Fig. 69. The anterior narrow part of the bone curves somewhat in a medial direction, as will be seen in Fig. 73, and is in contact with the well developed rostro-antorbito-premaxillary.

A large part of the postero-dorsal margin of the maxillary and the posterior part of its antero-dorsal margin overlap the antero-ventral margin of the preoperculum, while the greater part of the antero-dorsal margin of the maxillary is covered by the lacrimal and the jugal.

On the medial side of that part of the maxillary which lies in front of the adductor opening, at an inconsiderable distance from and parallel with the ventral margin of the bone, runs the low, rounded, longitudinal ridge mentioned repeatedly above. As stated above, the ectopterygoid and the

posterior or perhaps both dermopalatines are in contact with this ridge, but the connection was hardly very firm, for in the compressed heads the maxillary is often separated from the dermal bones of the palate. The low longitudinal ridge corresponds to the horizontal longitudinal lamina found on the medial side of the maxillary in *Glaucolepis*. On the ventral margin of the maxillary a series of acutely conical teeth are found which are about three times as long as the small teeth on the dermal bones of the palatoquadrate. The precise number of these teeth could not be ascertained. In addition to these comparatively large teeth there occur on the ventral margin of the maxillary and possibly on the oral face of the longitudinal medial ridge of the maxillary also, a large number of acutely conical teeth of the same size as, or but slightly larger than, the teeth found on the dermal bones of the palatoquadrate.

The radiation centre of the maxillary lies nearly midway between the anterior and posterior ends of the bone and very slightly nearer its ventral than its antero-dorsal margin.

No trace of any pit-line is found on the maxillary.

The preoperculum (*Pop*, Figs. 69, 72, 73; Pl. 30, Fig. 2) in this species has a very steep position and shows only a slight indication of the curvature which characterises it in *Glaucolepis* and in numerous other *Palaeonisciformes*.

On the whole the outline of the preoperculum is seen from Fig. 69; it should, however, be borne in mind that the suborbital series and the maxillary each overlaps a narrow marginal zone of the bone. The outline of the preoperculum is roughly triangular, with a convex posterior (or postero-dorsal), a concave anterior, and a concave antero-ventral margin. The concave anterior and the concave antero-ventral margin meet at an acute angle in such a way that the preoperculum has a fairly prominent antero-ventral pointed process.

The preoperculum has not, as in *Glaucolepis* (p. 154), an internal lamina and has no connection with the palatoquadrate.

As will be seen from Fig. 69, the centre of radiation has a fairly central position in the bone and is pierced by the preopercular canal, which has a rather straight course through the bone. From the centre of radiation, or from a point on the external face of the bone just above the radiation centre, issue two pit-lines. One of these, the horizontal pit-line of the cheek, extends from the radiation centre in an antero-ventral direction to the anterior tip of the antero-ventrally directed large process of the preoperculum. The other of the two pit-lines, the vertical pit-line of the cheek, runs from the radiation centre in a ventral direction across the ventral part of the preoperculum. (p. 356).

The only trace of the vertical pit-line of the cheek found in *Glaucolepis* is a short groove situated on the small exposed face of the fairly large quadrato-

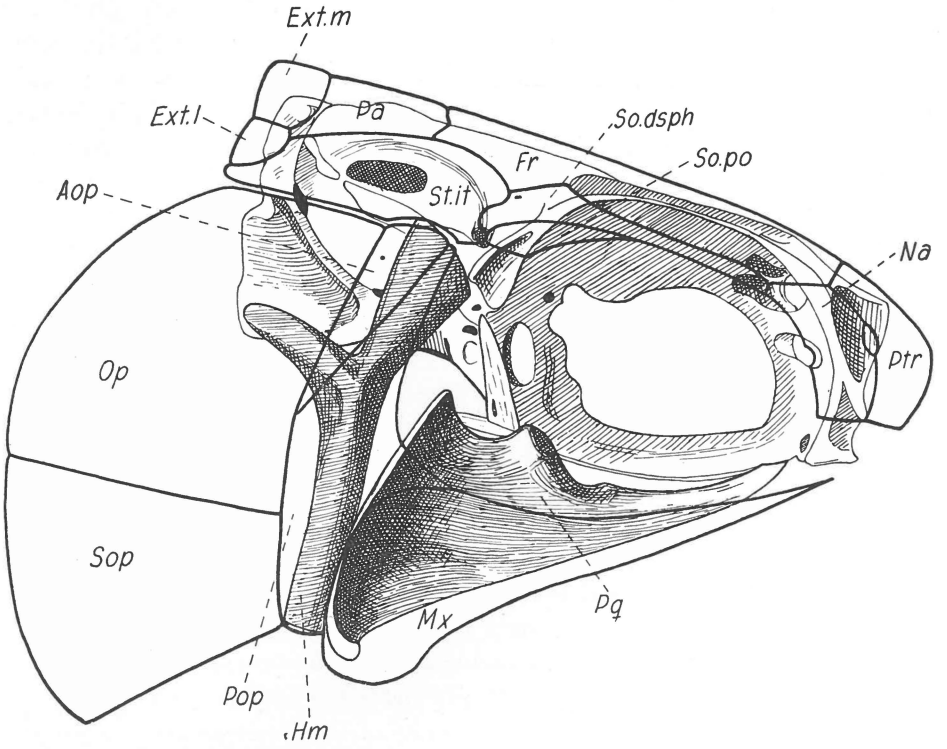


Fig. 72. *Boreosomus piveteaui* n. sp. Attempted sketch of the neural endocranium, the palatoquadrate, the hyomandibula, and some of the external dermal bones of the head. Relations between the pars autopalatina and the ethmoidal region uncertain. Based mainly on specimens Nos. 278, 295 and 296.
Aop, antoperculum; *Ext. l*, lateral extrascapular; *Ext. m*, medial extrascapular; *Fr*, frontal; *Hm*, hyomandibula; *Na*, nasal; *Op*, operculum; *Pa*, parietal; *Pop*, preopercular; *Pq*, palatoquadrate; *Ptr*, postrostral; *So. dsph*, supraorbito-dermosphenotic; *Sop*, subopercular; *So. po*, supraorbito-postorbital; *St. it*, supratemporo-intertemporal.

jugal (cf. p. 209). It can be definitely established that no quadratojugal is found in *Boreosomus*. In *Glaucolepis* it was possible to demonstrate that that part of the quadratojugal which is covered by the maxillary shows signs of reduction (p. 155), and it is quite possible that a corresponding but more extensive reduction has taken place within the *Acrolepidae*, so that the absence of the quadratojugal in *Boreosomus* is due to its complete reduction and not to its fusion with the maxillary or the preoperculum.

In *Glaucolepis* and other forms the palatoquadrate and its dermal bones together with the maxillary and the preoperculum form the walls of a high and narrow chamber for the dorsal part of the musculus adductor mandibulae, as stated above (pp. 144–55). Although the corresponding cranial elements have not, so far, been investigated in detail in the younger Acrolepid species,

Aldinger (1937, p. 332) has put forward the following assumption regarding these: "Es ist anzunehmen, dass bei den jüngeren *Palaeonisciformes*, bei welchen die postorbitale Platte des Maxillare zurückgebildet wird, (*Boreosomus-Ptycolepis* Gruppe), kein solcher geschlossener Hohlraum für die Adductormuskulatur mehr vorhanden war, ob der Adductor mandibulae in Zusammenhang damit seine Ursprünge vom Palatoquadratum auch auf andere Knochen (?Hyomandibulare) ausgedehnt hat, ist einstweilen noch fraglich, sicher ist jedoch, dass am Praeoperculum kein Ursprung des Adductors lag."

Aldinger bases these remarks on the assumption, which he shares with Watson, (p. 158), that in the earlier *Palaeonisciformes* the postorbital face of the maxillary alone forms the lateral wall of the chamber for the adductor musculature. In these forms, however, the preoperculum, in spite of the considerable size of the postorbital plate of the maxillary, actually plays an important part in the palatoquadrate-maxillary apparatus. There is therefore nothing to prevent that a similar muscular chamber may have persisted in forms in which the postorbital plate of the maxillary is so much reduced as in *Boreosomus*. The absence of such a closed chamber in *Boreosomus* may be explained by the fact that owing to a shortening of its postorbital part and owing to the nearly vertical position of the preoperculum the palatoquadrate is no more situated medially to that part of the preoperculum which is pierced by the preopercular canal. For from this part of the preoperculum issues in the less specialised forms the internal lamina which plays such an important part for the connection between the preoperculum and the palatoquadrate.

In *Boreosomus* the postero-dorsal margin of the palatoquadrate is still so much curved in a lateral direction that in spite of the absence of the internal preopercular lamina, it is improbable that the musculus adductor mandibulae may have extended its area of insertion so as to comprise part of the hyomandibula. More probably part of the musculus adductor mandibulae has been inserted on the processus postorbitalis of the neural endocranium.

Mandible.

On the basis of the available material it is possible to supply various particulars about the structure of the mandible, even though the material is insufficient for so detailed a description as that given above of the mandible in *Glaucolepis* (pp. 162–74).

The Meckelian cartilage is ossified in one piece from the hindmost to the foremost end of the mandible; this agrees well with the observations made by Stensiö (1921, pp. 212–13) in *Boreosomus arcticus*. The Meckelian bone (*Mk*, Figs. 70A, B, 72; Pl. 30, Fig. 1) may for descriptive reasons be regarded as consisting of a posterior and an anterior division.

The posterior division of the bone is a plate nearly half as high as the mandible and somewhat less than half as long as the Meckelian bone.

This plate, which is rather thin, is so curved that its lateral face is concave and its medial face correspondingly convex in a rostro-caudal direction. The posterior part of the plate, the pars articularis, is bent laterally similarly as the posterior part of the palatoquadrate ossification. This laterally bent posterior part is somewhat thicker than the more anterior part of the posterior division of the Meckelian bone, and on its small dorsal face bears the articular fossa for the palatoquadrate.

The lateral margin of the laterally bent posterior part of the Meckelian bone has contact with the medial face of the angular and probably with the medial face of the supraangular, too, and thus forms a posterior boundary for the muscular fossa of the mandible. Anteriorly the comparatively high posterior division of the Meckelian bone decreases gradually in height, the transition to the anterior division being very even, as will be seen from Fig. 70.

The anterior division of the Meckelian bone is a slender rod, whose anterior end points somewhat downward, corresponding to the course of the anterior part of the oral margin of the mandible. The few specimens of the Meckelian bone which have been dissected out show no grooves or canals for nerves or vessels.

On the external face of the mandible, as in *Glaucolepis*, three dermal bones are found, viz. an angular, a supraangular, and a dentalo-splenial.

The angular (*Ang*, Figs. 69, 73; Pl. 30, Fig. 2) is roughly triangular in outline, with a posterior, a ventral, and an antero-dorsal margin. However, the angle between the posterior and the ventral margin of the bone is much rounded. The posterior margin is shortest, and both this margin and the much longer ventral margin are somewhat convex. The course of the antero-dorsal and longest margin is not known in details, but probably it was fairly straight, as in *Glaucolepis*. The angular is about half as long as the mandible.

The radiation centre of the angular could not be localised, but probably it lay near the postero-ventral corner of the bone, for the course of the mandibular canal agrees fairly well with that of *Glaucolepis*.

If the complete mandible is seen in lateral wiev, only the posterior and the most ventral part of the angular are visible, a very large antero-dorsal part of the bone being overlapped by the dentalo-splenial. If the complete mandible is seen in medial view, a much greater area of the angular is visible than in *Glaucolepis*, for in *Boreosomus* the Meckelian bone does not extend so far in a ventral direction as the posterior ossification of the Meckelian cartilage in *Glaucolepis* (cf. Figs. 38 and 40).

A supraangular can be observed in several specimens, but it is not so well preserved that its exact shape can be determined. As far as I can see, it corresponds in its relations to the dentalo-splenial and the angular, and in the position of its radiation centre to the supraangular in *Glaucolepis*.

The dentalo-splenial (*De. spl*, Figs. 69, 73) is, as usual, the largest dermal bone of the mandible. The external face of this bone is convex in a dorso-ventral and a rostro-caudal direction, and moreover it is so curved that its

posterior part is almost vertical, while farther forwards it faces more ventrally.

In lateral wiev (Fig. 69) the dentalo-splenial is bounded by a dorsal and a ventral margin. The dorsal margin is not straight, but its anterior part forms an obtuse angle with the posterior part, as shown in Fig. 69. The ventral margin is convex in such a way that it is most strongly curved farthest anteriorly and farthest posteriorly.

The centre of radiation lies very far anteriorly in the bone, and is pierced by the mandibular canal, which extends through the greater part of the bone in a longitudinal direction. The posterior part of the dentalo-splenial overlaps a large part of the angular and the supraangular.

On the medial side of the dentalo-splenial, parallel with and a short distance ventrally to the dorsal margin of the bone, issues a well developed ridge, which extends from the anterior part of the adductor opening to the symphysial region. This ridge corresponds to the well defined horizontal lamina found on the medial side of the dentalo-splenial in *Glaucolepis* (p. 171). In *Boreosomus* the ridge is in contact with a longitudinally directed ridge issuing from the lateral face of the prearticular, and, in front of the prearticular, probably with a similar ridge issuing from the lateral face of the coronoid elements.

The dorsal margin of the dentalo-splenial and its longitudinal medial ridge are equipped with teeth, which in size and arrangement correspond to those on the ventral margin and the longitudinal medial ridge of the maxillary.

On the medial side of the mandible a prearticular and probably two coronoids are found; however, very little can be stated about these bones.

The prearticular lies on the medial side of the Meckelian bone in such a way that its posterior end is situated a short distance in front of the posterior end of the Meckelian bone, while anteriorly it ends nearly at the boundary between the anterior and the middle third of the Meckelian bone. The prearticular is broadly speaking a vertically placed bone, which is slightly lower than the posterior plate-shaped division of the Meckelian bone.

From the lateral face of the prearticular, parallel with and a short distance ventrally to its dorsal margin, issues a longitudinal ridge, which, as already stated, has contact with the longitudinal ridge on the medial side of the dentalo-splenial.

Nothing can be stated about the position of the radiation centre.

In front of the prearticular the remnants of (?) two small coronoids are seen, which are probably built up almost as the prearticular, in so far as they are fairly vertical and provided on their lateral faces with a ridge which continues the longitudinal ridge of the prearticular in an anterior direction. No further particulars can be given as to the structure of these small dermal bones.

As stated above, the longitudinal ridge on the prearticular and coronoids and the longitudinal ridge on the dentalo-splenial meet, forming the

roof above the muscular fossa of the mandiblė, and at the same time the floor of a longitudinal groove, whose side walls are formed by the most dorsal parts of the dentalo-splenial, the prearticular, and the coronoids. The height of the two ridges is however so inconsiderable that the muscular fossa of the mandible in *Boreosomus* is relatively much narrower than in *Glaucolepis;* this must mean that the jaw musculature was relatively weak in *Boreosomus.*

Both the prearticular and the coronoids are provided, at any rate on the dorsal halves of their medial faces, with numerous teeth of the same type as those of the ectopterygoid and the two dermopalatines.

Hyoid arch, antoperculum, operculum, subopercul um, branchiostegal rays, and median gular plates.

The hyoid arch comprises four ossifications, a hyomandibula, a symplectic, an ossification in the ceratohyal, and a hypohyal.

By its dorsal (proximal) end the hyomandibula articulated with the otic region of the neural endocranium, as will be evident from the above (p. 297). From the place of articulation the hyomandibula extends in a posteroventral direction, and the bone is so steeply placed that its ventral (distal) end lies immediately behind the quadrate region, as will be seen from Fig. 72.

The hyomandibula (*Hm*, Figs. 70 A, 72; Pl. 30, Fig. 1) in *Boreosomus piveteaui* is on the whole of the same type as that of *Boreosomus arcticus* (Stensiö 1921, Fig. 70); thus it is provided with a very long processus opercularis (*pr. op*, Fig. 70 A) which issues from the posterior margin of the bone and whose distal end was capped by cartilage.

In the subjoined description the hyomandibula is regarded as composed of a dorsal and a ventral division; the boundary between the two divisions has been drawn through that part of the bone from which the processus opercularis issues.

The dorsal division of the hyomandibula is compressed from side to side and increases in breadth from its most ventral to its most dorsal end, the latter of which is extremely broad, as will be seen from Fig. 70 A. The dorsal terminal face of the hyomandibula was capped by cartilage.

The ventral division of the hyomandibula, which is not compressed from side to side like the dorsal division, increases slightly in diameter from its dorsal towards its ventral end. Its ventral terminal face was also capped by cartilage.

In the angle between the dorsal division of the hyomandibula and the processus opercularis and in the angle between the ventral division of the hyomandibula and the processus opercularis the bone is so much compressed from side to side that, as in *Boreosomus arcticus* (Stensiö 1921, Fig. 70), it is only a thin lamina. In the area in which the dorsal and ventral divisions of

the bone meet, the most anterior part of the hyomandibula is likewise compressed so as to form a thin lamina; but this lamina is much narrower than in *Boreosomus arcticus* (Stensiö 1921, Fig. 70). The interiors of both the processus opercularis and the dorsal and ventral divisions of the hyomandibula are cancellate, but the cancellate mass does not extend into the thin laminae. The cancellate mass attains a considerable breadth in the distal end of the processus opercularis and in the most distal and most proximal ends of the hyomandibula; but its dimensions decrease gradually from these three ends towards that part of the bone from which the processus opercularis issues, being very thin in this boundary area between the dorsal and ventral divisions of the bone.

No canal for the truncus hyoideomandibularis pierces the hyomandibula; most probably this nerve passed caudally to the bone.

Judging from the position of the hyomandibula in relation to the endocranium it must be assumed that the spiraculum, if present, was situated between the dorsal margin of the dorsal suborbital element and the lateral margin of the dermal cranial roof.

The symplectic (*Sympl*, Fig. 70 A), which is not by far as well ossified as in *Glaucolepis*, is represented by a very short cylindrical ossification situated just posteriorly to the place of articulation between the palatoquadrate and the Meckelian bone. This ossification is made up of cancellate bone-tissue lined with perichondral bone-layers except on its two terminal faces, which were capped by cartilage. The diameter of the ossification is a little smaller than that of the most ventral part of the hyomandibula.

In the ceratohyal only a single ossification is found, which nearly always corresponds to the anterior of the two ceratohyal ossifications in *Glaucolepis* (p. 43). In a few cases, however, the ceratohyal ossification seems to correspond to both the anterior and the posterior ceratohyal ossification in *Glaucolepis*. In a very few cases only could the ceratohyal ossification be dissected out.

In most cases (except when it corresponds to both the ceratohyals I and II in *Glaucolepis*) the ceratohyal ossification is almost half as long as the mandible and resembles in shape the ceratohyal ossification in *Acrorhabdus bertili* (Stensiö 1921, Fig. 72). It is a bone plate compressed from side to side and consisting of a cancellate mass of bone lined with perichondral bone except on its narrow terminal faces. The ossification is lowest in its middle part and highest at its proximal and distal ends, so in lateral view the bone has an hour-glass-shaped outline.

The hypohyal is a short and thick somewhat compressed bone of about the same shape as the hypohyal in *Glaucolepis*, being so bent that the angle between its proximal and distal parts is nearly 90°. The proximal and distal terminal end-faces of the bone were covered by cartilage. The position of the hypohyal in relation to its fellow on the other side of the head could not be ascertained.

Between the dorsal part of the preoperculum and the anterior margin of the operculum lies a narrow dermal bone, which is triangular in outline (*Aop*, Figs. 69, 72). Of the three margins of the bone, the dorsal and shortest is convex, while the postero-dorsal and antero-ventral margins are fairly straight. The antero-ventral margin is overlapped by the dorsal part of the posterior margin of the preoperculum, while the postero-dorsal margin of the narrow bone very slightly overlaps the anterior (antero-ventral) margin of the operculum. As is seen from Fig. 69, the centre of radiation lies in the dorsal part of the bone.

This bone varies somewhat in length in the different specimens, the ventral end of the bone often lying more dorsally than shown in the restoration. However, the length of the bone always exceeds half the length of the antero-ventral margin of the operculum.

From Fig. 72 it will be seen that the bone lies partly laterally to the dorsal part of the hyomandibula and thus to a certain extent reminds one of the dermohyal in *Glaucolepis* (p. 180). A closer examination shows, however, that in *Boreosomus* the bone is not so intimately connected with the hyomandibula as in *Glaucolepis*. When moreover, as stated above, the postero-dorsal margin of the bone overlaps the anterior margin of the operculum, it is obvious that the bone must be regarded as an antoperculum.

In conclusion it may be mentioned that in a few cases the antoperculum is subdivided into two smaller bones, the postero-dorsal corner of the triangular antoperculum being separated from the remaining and larger part of the bone by a distinct suture.

The operculum (*Op*, Figs. 69, 72) is a four-sided bone, which is strongly curved in a dorso-ventral direction, so that its external side is convex. It is seen clearly from Fig. 69 how the four margins of the bone are orientated, so it will hardly give rise to any misunderstanding when in the sequel, for the sake of brevity, I refer to them as the dorsal, the posterior, the ventral, and the anterior margin respectively.

The dorsal margin, which is the shortest, is straight. The posterior margin is convex, and the anterior slightly concave. Finally, the ventral margin is either straight, as shown in Fig. 69, or slightly S-shaped. The most ventral part of the operculum overlaps the dorsal margin of the suboperculum.

The centre of radiation lies in the antero-dorsal part of the bone, as will be seen from Fig. 69. The ratio between the breadth and height of the operculum shows some variation from one specimen to the other. The operculum figured here is relatively broad.

The suboperculum (*Sop*, Figs. 69, 72, 73) is a four-sided bone with a dorsal, a posterior, a ventral, and an anterior margin. The details of its shape are seen from Fig. 69. The radiation centre of the bone lies very near the anterior margin of the bone. The relative breadth of the suboperculum varies in accordance with the variation of the relative breadth of the operculum.

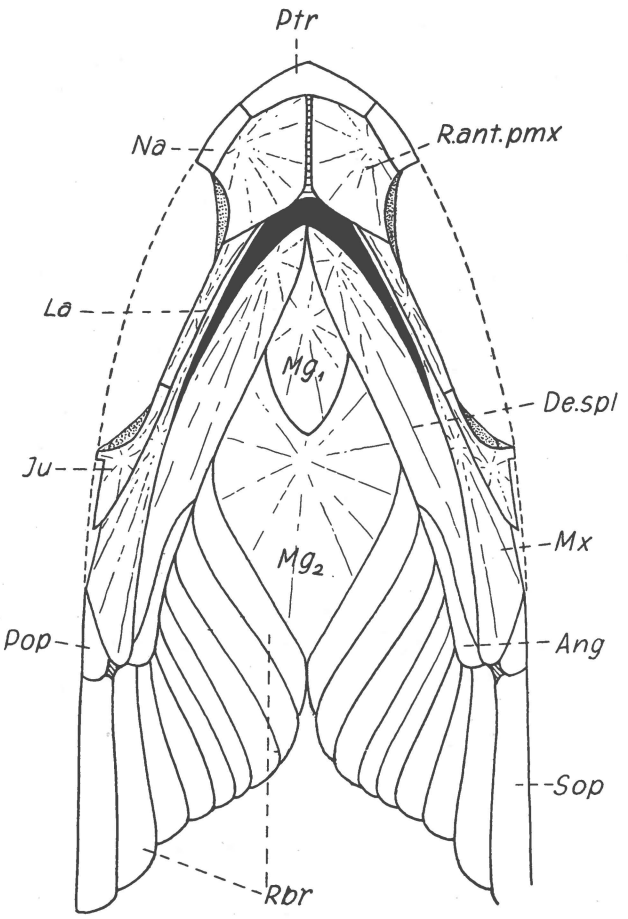


Fig. 73. *Boreosomus piveteaui* n. sp. Head in ventral view. Based mainly on specimen No. 305. C. 2 ×.
Ang, angular; *De. spl*, dentalo-splenial; *Ju*, jugal; *La*, lacrimal; Mg_1, Mg_2, anterior and posterior median gular plates; *Mx*, maxillary; *Na*, nasal; *Pop*, preoperculum; *Ptr*, post-rostral; *R. ant. pmx*, rostro-antorbito-premaxillary; *Rbr*, branchiostegal rays; *Sop*, sub-operculum.

Between the ventral margin of the suboperculum and the posterior of the two median gular plates lies a series of branchiostegal rays (*Rbr*, Figs. 69, 73). In the best preserved specimens the series comprises eight rays; but judging from several of the less completely preserved specimens, the number varies, at any rate from seven to nine. The shape of the exposed part of the individual branchiostegal-rays is seen in the figures. Each of the rays covers a narrow zone of the external side of the ray lying just in front of it. However, the rays were not immovably connected with each other.

The radiation centre of the individual branchiostegal rays seems to have been shifted towards the anterior part of the bone, as shown in Fig. 69 for one of the rays.

The large posterior median gular plate (Mg_2, Figs. 69, 73) is rhombic and nearly twice as long as broad. The centre of radiation lies at the point of intersection between its short and its long diagonal. The anterior part of the posterior gular plate is overlapped by the much smaller anterior median gular plate (Mg_1, Figs. 69, 73), whose outline, too, as will be seen from Fig. 73, is roughly rhombic. The radiation centre of the anterior median gular plate lies a short distance in front of the point of intersection between its short and its long diagonal. The anterior and posterior median gular plates cannot have been very firmly connected, for specimens in which only the posterior gular plate has remained in its position between the jaws are of common occurrence.

In *Boreosomus reuterskiöldi* from Spitsbergen Stensiö (1921, Fig. 71) has found only one median gular plate, and this no doubt corresponds to the large posterior gular plate in *Boreosomus piveteaui* and *Boreosomus gillioti* (Brough 1933, Fig. 1). If better preserved specimens of the species of *Boreosomus* from Spitsbergen are found, it will no doubt be possible to demonstrate the presence of a dermal bone corresponding to the small anterior gular plate in the species from Greenland and Madagascar.

No traces of pit-lines have been found on either the anterior or the posterior median gular plate in *Boreosomus piveteaui*.

Judging from the shape and the position of the articular fossa on the endocranium for the hyomandibula, the latter could only move in a plane at right angles to the long diameter of the articular fossa. Thus the ventral end of the hyomandibula could only move in a direction which is roughly transverse to the longitudinal axis of the fish.

In order to make out how great were the possibilities for the hyomandibula to move in the way mentioned above, it is necessary to examine with which bones, besides the endocranium, the hyomandibula was connected.

The preoperculum has not, as in *Glaucolepis*, an internal lamina and accordingly was not firmly connected with either the hyomandibula or the palatoquadrate. The suboperculum, too, lacks an internal lamina, and the firm connection between the suboperculum and the hyomandibula that can be ascertained in *Glaucolepis*, did not, therefore, exist in *Boreosomus*. On the other hand it is quite possible that the ventral part of the hyomandibula was connected with the posterior part of the palatoquadrate; but since it has left no impression on that part of the palatoquadrate ossification with which it may have had contact, the connection between the hyoid arch and the mandibular arch was hardly very intimate. It is difficult to decide how the connection between the hyoid arch and the mandibular arch via the symplectic was; but on the small symplectic ossification, at any rate, no special articular faces have developed for the articulation between this bone and the palatoquadrate and the Meckelian bone respectively, as in the case of *Glaucolepis*. (p. 175).

Thus it would seem that in *Boreosomus* the hyomandibula and the palatoquadrate were less firmly connected than in *Glaucolepis*.

The possibilities of movement for the palatoquadrate itself cannot be fully elucidated, as it is impossible to say how the ethmo-palatine articulation acted. It is obvius, however, that the palato-basal articulation was of a different type from that of *Glaucolepis*, for the palatoquadrate could very well rotate around the processus basipterygius, but could hardly be shifted in a lateral direction in relation to this process.

From this it appears that the possibilities of the palatoquadrate for moving in relation to the endocranium were at any rate smaller than in *Glaucolepis*, even if one would assume that no connection whatever existed between the palatoquadrate and the hyoid arch. Since, however, it is probable that such a connection, though not very firm, existed, the possibilities of the hyomandibula and the palatoquadrate for moving must have been rather small.

The abduction of the hyomandibula cannot, therefore, as in *Glaucolepis*, have played the main part in the opening of the gill cavity, and already Stensiö (1921, p.213) interpreted the presence of the well developed processus opercularis as an evidence showing that the movements of the operculum, as in the higher *Holostei* and *Teleostei,* were effected by a musculus dilatator operculi. It will appear from Fig.72 that the processus opercularis, even though it did not articulate with the operculum as near the antero-dorsal corner of this bone as in recent *Holostei* and *Teleostei,* was situated so much antero-dorsally to the mid-point of the operculum that Stensiö's interpretation must be regarded as probable. However, in this connection it should be mentioned that the medial face of the operculum is entirely smooth and shows no traces of having articulated with the distal end of the processus opercularis.

Branchial arches and basibranchial series.

In the material of *Boreosomus*, in contrast to the material of *Glaucolepis*, no specimen is found which shows the ossifications of the branchial skeleton in their natural position, and the information that can be supplied as to the branchial skeleton is accordingly very sparse.

Specimen No.309 shows the epibranchials I to IV in their original mutual position; in other specimens ceratobranchial ossifications can also be identified, and it can be ascertained that ossifications occur in the basibranchial series. An infrapharyngobranchial has been observed in specimen No.295 (*Ifbr*, Pl.30, Fig.1). Hypobranchials and suprapharyngobranchials, however, have not been observed with certainty.

In *Acrorhabdus bertili* from Spitsbergen, which is very closely related to *Boreosomus*, Stensiö (1921, p.227) has observed hypobranchials, ceratobranchials, and epibranchials.

The epibranchials I, II, and III (*Ebr I-III*, Pl. 30, Figs. 1, 2) are rather thick ossifications, about half as long as the mandible. On their posterior (morphologically lateral) side there is a broad, deep longitudinal groove. Both on their lateral (morphologically anterior) and medial (morphologically posterior) side seven to nine small processes at regular intervals are seen. The epibranchial IV (*Ebr IV*, Pl. 30, Fig. 1) is poorly preserved, and the only thing that can be stated about this bone is that it is more slender than the three epibranchials lying in front of it. The ossifications interpreted as ceratobranchials have a similar structure to that of the three anterior epibranchials, but are somewhat longer than these bones.

All the ossifications belonging to the branchial skeleton are made up of cancellate endochondral bone-tissue lined with perichondral bone.

Along their posterior faces the branchial arches were equipped with two rows of comb-shaped supporting gill rays, precisely as in *Acrorhabdus* (Stensiö 1921, p. 227). These gill rays are curved, and the processes which form the teeth of the combs issue from their concave sides. The longest gill rays are almost of the same length as the ventral margin of the operculum. As in *Acrorhabdus*, a single row of gill rays seems to be placed in such a way that *Boreosomus* must be assumed to have had a large hyoid gill.

Ornament of the dermal bones of the head.

As regards the ornament of the dermal bones of the head *Boreosomus piveteaui* presents a very rich variation. In a number of specimens the ornament is very coarse, and the ornamental elements consist chiefly of long, broad, and high ganoine striae separated by very narrow intervals. In other specimens the ornamental elements are narrow and very low ganoine striae, which are often to a great extent subdivided into short pieces; the intervals between these narrow striae are very broad. Transitional types between the most coarsely and the most finely ornamented types are represented, so it is impossible to use the variation in ornament as a basis for a division of the Greenland material of *Boreosomus* into several species. The individual striae are straight, evenly curved, or irregularly undulating. On most of the dermal bones the predominant direction of striation is fairly parallel with the longitudinal axis of the fish; but the direction often varies within smaller areas of the individual bones. On the postrostral and the nasal the striae are much broader and higher than on the other bones of the dermal cranial roof, and on the anterior part of the postrostral, in particular, extensive fusions between the individual striae can often be observed, this part of the bone in the most strongly ornamented specimens being covered by a thick, nearly continuous layer of ganoine. On the operculum the most dorsal long striae or series of short striae extend from the anterior margin of the bone in a posterior direction, while with increasing distance from the dorsal margin of the bone they run more and more steeply in a postero-ventral direction. In the broad intervals between the predominant striae in the posterior and

largest part of the operculum (and the suboperculum) in a number of the comparatively slightly ornamented specimens, a larger or smaller number of very fine striae occur which run parallel with the predominant ones. On the maxillary and the dermal bones on the lateral side of the mandible the ornament is in most cases rather coarse. The direction of the striation on the postorbital face of the maxillary and on the mandible is predominantly longitudinal, while on the suborbital part of the maxillary the individual striae are directed obliquely backward and downward. Nearest the tooth-bearing margin a narrow zone with a very fine ornamentation often occurs even in coarsely ornamented specimens; the ornamental elements within this zone may most nearly be characterised as oblong tubercles. In some cases the median gular plates are extremely slightly ornamented, while in other cases their ornament is fairly conspicuous.

Dentition.

As mentioned above in the description of the individual dermal bones, both obtusely and acutely conical small teeth are found in this species. The obtusely conical teeth are found on the oral face of the parasphenoid, the vomer, the entopterygoid, and probably also on part of the oral face of the ectopterygoid, the anterior and the posterior dermopalatine, the prearticular, and the coronoids. In addition obtusely conical teeth are found on small detached dermal bones of irregular outline, which probably covered the oral face of the branchial arches and the elements of the basibranchial series. The obtusely conical teeth are very short. Acutely conical teeth are found on the maxillary and the dentalo-splenial, probably also on that part of the oral face of the ectopterygoid which lies nearest these two bones, and further on the anterior and posterior dermopalatines, the prearticular, and the coronoids. The greater number of the acutely conical teeth are just as short or but a little longer than the obtusely conical teeth; but a small number of acutely conical teeth on the ventral margin of the maxillary and on the dorsal margin of the dentalo-splenial are distinguished by their relatively large size, being three times as long and correspondingly thicker than the other teeth.

On account of the small size of the teeth it is difficult to observe their structural details, but still it is possible to see that the largest acutely conical teeth are provided with an enamel cap, whose height is about one-fourth the whole height of the teeth. Whether, as in *Acrorhabdus*, (Stensiö 1921, p. 220), the obtusely conical teeth, also, are provided with an enamel cap, could not be ascertained on the basis of the available material.

The microstructure of the teeth has not been investigated.

Sensory canal system of the head.

As usual the sensory canals are enclosed in the dermal bones and open through numerous tubuli in small pores on the external side of the canal bones.

The diameter of the sensory canals is relatively smaller than in *Glaucolepis*, but, as in *Glaucolepis*, a distinct ridge indicating the course of the canals through the individual bones is found on the internal side of all the canal-bearing bones. In addition short ridges corresponding to the pit-lines of the parietal are present on the internal side of that bone.

As in *Glaucolepis*, it is impossible to ascertain the number of primary tubuli, these being always subdivided throughout their extent into a large number of secondary tubuli. Thus it is impossible in this way to determine the number of sensory organs, nor can it be determined by investigating the number of nerve branches entering the individual sensory canals, for the openings for these nerve branches at the bottom of the sensory canals are so small that they can only be observed in a few cases.

As usual the relations of the sensory canals to the dermal bones of the head are entirely constant, and the canals always pierce the radiation centres of the bones in which they are enclosed.

The number and position of the secondary tubuli, as in the species of *Glaucolepis*, show some variation not only from one specimen to the other, but also from one side of the same head to the other.

In addition to the actual sensory canals, a number of pit-lines occur which are represented either by deep grooves on the external side of some of the dermal bones or by very narrow canals in these bones, Thus, as in *Glaucolepis*, we are here concerned with a kind of intermediate stage between typical pit-lines and typical sensory canals.

The supraorbital canal (*soc*, Figs. 68 A, 69; Pl. 26, Fig. 2) extends from the anterior (ventral) margin of the nasal backward through the nasal, the frontal, and the anterior part of the parietal, as is seen from Figs. 68 A and 69. In the frontal the canal is not entirely straight, but is so curved that its anterior half is convex in a medial, and its posterior half is convex in a lateral direction, a course which on the whole corresponds to that of the supraorbital canal in *Glaucolepis*. The canal narrows gradually in its posterior part, and its posterior pointed part just reaches the radiation centre of the parietal. In some cases the posterior narrow part of the canal is no actual canal, but an open groove, and thus corresponds entirely to that part of the supraorbital canal in *Glaucolepis* which has been termed the anterior pit-line (p.205).

From that part of the supraorbital canal which lies in the nasal about ten tubuli issue, whose pores all lie medially to the canal. In the frontal 25–30 tubuli issue from the canal, the anterior of which open laterally to, and the posterior medially to the canal, while four or five tubuli issuing from the middle part of the canal open directly above it. Thus the pores of the frontal division of the slightly S-curved supraorbital canal lie almost on a straight line.

From that part of the supraorbital canal in the parietal which is developed as a typical sensory canal, two or three small tubuli issue, whose pores lie immediately above the canal.

The anterior division of the infraorbital canal (*ifc*, Figs. 68 A, 69) lies in the rostro-antorbito-premaxillary, and as usual in the *Palaeonisciformes* (cf. p. 206), it is three-branched in such a way that a short antero-dorsal, a long postero-ventral, and a long antero-medial canal branch issue from the radiation centre of the bone.

The antero-medially directed canal branch extends from the radiation centre through the most dorsal part of the bone to the most dorsal part of its antero-medial margin.

As stated above, the dorsal part of the rostro-antorbito-premaxillary is overlapped by the nasal and the postrostral, and in that part of the rostro-antorbito-premaxillary which is concealed below the most ventral part of the postrostral runs the anterior part of the antero-medially directed canal branch just mentioned. Thus, as seen clearly from Fig. 69, this canal branch has entirely the same position in relation to the postrostral as that part of the ethmoidal commissure in *Glaucolepis* which pierces the rostral process (p. 136). However, in contrast to the conditions in *Glaucolepis*, no groove is found on the internal side of the postrostral corresponding to the groove which can be observed in *Glaucolepis* on that part of the internal side of the postrostral with which the proximal part of the rostral process has contact.

As the right and left rostro-antorbito-premaxillaries are only separated by a very small space, there is every probability that the antero-medially directed canal branches from the right and left sides of the head were united into a normal ethmoidal commissure.

The short antero-dorsally directed canal branch issuing from the radiation centre of the rostro-antorbito-premaxillary anastomoses with the anterior end of the supraorbital canal, as in the greater number of *Palaeonisciformes* (cf. p. 206).

The canal branch issuing from the centre of radiation in a postero-ventral direction continues in the normal way through the lacrimal, the jugal, the postorbital, the supraorbito-postorbital, the supraorbito-dermosphenotic, and the anterior part of the supratemporo-intertemporal. As in *Glaucolepis*, the infraorbital canal in the supratemporo-intertemporal is continued in a posterior direction by the postotic canal, but the exact boundary between the two canals cannot be localised.

At the point where the longitudinal sensory canal passes the centre of radiation of the supratemporo-intertemporal, it gives off a short antero-laterally directed branch, which, as will be seen from Fig. 68 A and B, continues as far as the lateral margin of the supratemporo-intertemporal, where it was in connection with the dorsal end of the preopercular canal.

In the rostro-antorbito-premaxillary, which is very rarely satisfactorily preserved, it has only been possible to observe tubuli from that part of the infraorbital canal which extends in a postero-ventral direction from the centre of radiation. From this part of the canal issue five tubuli, whose pores lie antero-medially to the canal.

From the lacrimal division of the infraorbital canal issue ten to twelve short tubuli, whose pores lie near the ventral margin of the bone.

In the jugal likewise ten or twelve tubuli issue from the canal. The pores of the anterior nine are situated very near the postero-ventral margin of the bone, so the hindmost of these nine tubuli have a fairly considerable length. The two or three posterior tubuli open very near the posterior margin of the narrow dorsal part of the bone.

In the long, very narrow postorbital, which forms merely a tube around the infraorbital canal, I have observed six tubuli; but it is quite possible that more are present. These six tubuli open with pores situated immediately outside the canal.

In the supraorbito-postorbital a fairly long backward-directed and a very long forward-directed tubulus issue from the canal. As will be seen from Figs. 68 A and B and 69, the forward-directed tubulus has two small lateral branches, which both open with a pore, while it is uncertain whether the long tubulus opens distally with a pore or whether it ends blindly.

In the supraorbito-dermosphenotic three or four tubuli, whose pores lie medially or antero-medially to the canal, issue from the canal. The foremost and longest of these tubuli issues in an antero-medial direction and has one or two small medial branches, each of which, like the long tubulus itself, terminates in a pore on the external side of the bone, as will be seen from Fig. 68 A and B.

From the longitudinal canal of the supratemporo-intertemporal, whose anterior part belongs to the infraorbital canal and whose posterior part is the postotic canal, issue at any rate about eighteen tubuli, whose pores are situated partly laterally partly medially to the canal, as is seen from Fig. 68 A and B. From the aforementioned antero-laterally directed branch of the longitudinal canal in the supratemporo-intertemporal issue in some cases a couple of tubuli in a posterior direction.

The cephalic division of the main lateral line (*lc*, Pl. 29, Fig. 2) pierces the lateral part of the lateral extrascapular as a posterior continuation of the postotic canal in the posterior part of the supratemporo-intertemporal.

As will be seen from Fig. 68 A, the extrascapular series, unlike the conditions in *Glaucolepis* (Fig. 19), is pierced transversally by a typical supratemporal commissure (*s. com*, Figs. 68 A, 69; Pl. 29, Fig. 1). In the lateral extrascapular five tubuli, whose pores lie partly anteriorly partly posteriorly to the commissure, issue from the supratemporal commissure. In the medial extrascapular five or six tubuli, whose pores lie posteriorly to the commissure, issue from the supratemporal commissure.

The preopercular canal (*poc*, Fig. 69; Pl. 29, Fig. 2) pierces the preoperculum in the normal way, but it was very difficult to localise its tubuli. From that part of the canal which lies dorsally to the centre of radiation issue ten or eleven (or more?) tubuli which open posteriorly to the canal, and at least

four whose pores lie anteriorly to the canal. From that part of the preopercular canal which lies ventrally to the centre of radiation, at least six tubuli issue, whose pores lie anteriorly to the canal.

The mandibular canal (*mdc*, Fig. 69; Pl. 30, Fig 1) pierces the angular and, in front of it, the dentalo-splenial in the normal way. In the angular about fifteen tubuli issue from the canal; all the pores of these tubuli are situated posteriorly or ventrally to the canal. In the dentalo-splenial at least sixteen tubuli issue from the canal; all their pores are situated ventrally to the canal.

In addition to the above-mentioned anterior pit-line there occur on the parietal, as usual in the *Palaeonisciformes*, a middle and a posterior pit-line, both of which may be either deep grooves or narrow canals.

The middle pit-line (*mp*, Figs. 68 A, 69) runs from the radiation centre of the parietal in a lateral and at the same time slightly anterior direction; in some cases it is so long that it continues across the supratemporo-intertemporal to the radiation centre of this bone, while in other cases it does not extend beyond the lateral margin of the parietal.

In a large number of Actinopterygians, as in *Boreosomus*, the middle pit-line continues onto the supratemporo-intertemporal, and in material of *Parasemionotidae* and *Perleididae* from Greenland I could ascertain that the middle pit-line, as in *Boreosomus*, extends as a straight line from the parietal to the radiation centre of the supratemporo-intertemporal.

In his excellent restoration of the head of *Brachydegma caelatum*, Dunkle (1939, Fig. 1 A and B) indicates a suture which from the medial margin of the supratemporo-intertemporal extends in a lateral and slightly posterior direction without reaching the lateral margin of the bone. Dunkle interprets (op. cit. p. 267) this suture as an incomplete suture between the supratemporal and intertemporal divisions of the supratemporo-intertemporal. I am inclined to assume that we are not here dealing with a suture, but with the lateral part of the middle pit-line.

The posterior pit-line (*pp*, Figs. 68 A, 69) issues from the centre of radiation of the parietal in a postero-lateral direction, but does not reach the posterior margin of the bone.

On the external side of the preoperculum two grooves are found (probably never closed so as to form canals); they both issue from a point lying just laterally to the centre of radiation. One of these grooves (*hp*, Fig. 69) extends in an antero-ventral direction through that part of the preoperculum which lies immediately dorsally to the highest part of the maxillary. The other groove (*vp*, Fig. 69) extends in a ventral and possibly slightly posterior direction as far as the antero-ventral margin of the exposed face of the preoperculum.

These two grooves represent the horizontal and the vertical pit-line respectively of the cheek, and *Boreosomus* accordingly agrees with *Palaeonisciformes* such as *Brachydegma* (Dunkle 1939, Fig. 1), *Canobius*, and *Eurylepis*

(Westoll 1937 a, p.370) in that the pit-lines of the cheek have left their impressions on the preoperculum only.

No other pit-lines than those mentioned above have been observed in *Boreosomus*.

Axial Skeleton.

In several specimens ossifications can be observed in the axial skeleton, but in all the specimens they are so poorly preserved both in the abdominal region and in the greater part of the caudal region that they do not allow of a detailed investigation, probably because the degree of ossification is slight within the greater part of the axial skeleton. Only in the posterior part of the caudal region are the ossifications of the axial skeleton so well preserved that they can be investigated in detail.

Both the axial and the radial ossifications within this area agree so completely with those of *Glaucolepis* (pp. 216–19) that the description of them can be very brief.

Dorsally to the notochord a series of small arcual ossifications is found, and distally to this series occurs a series of well developed independent radials. The relations between the epichordal arcuals and the radial ossifications seem to be entirely as in *Glaucolepis*.

As in *Glaucolepis*, a series of unpaired well developed ossifications are seen ventrally to the notochord; each ossification consists of a massive half-cylindric proximal division, from which issues a typical hypural as an unpaired distal process. As in *Glaucolepis*, a small independent radial ossification lies distally to the distal end of each of the two or three longest hypurals.

Endoskeleton of the shoulder girdle.

The endoskeleton of the shoulder girdle could be investigated in detail in specimens Nos. 233 and 309, in which each of the two halves of the endoskeleton is represented by a single ossification without indication of sutures. The ossification consists of cancellate endochondral bone-tissue surrounded by perichondral laminate bone and has entirely the same macroscopic structure as the bones of the neural endocranium.

The large specimens Nos. 233 and 309 are the only ones in which the endoskeletal shoulder girdle ossification is well preserved. In several other specimens, however, there are indications showing that the endoskeleton of the shoulder girdle is ossified; but the ossification was hardly very much advanced in these specimens, the endoskeleton having been too delicate to retain its original shape; it is therefore only preserved as a compressed mass, which affords no possibility of a detailed investigation. In many other cases there is no trace at all of an ossification of the endoskeletal shoulder girdle. From these facts it may be concluded that, as in *Glaucolepis*, the process of ossification set in at a relatively late stage.

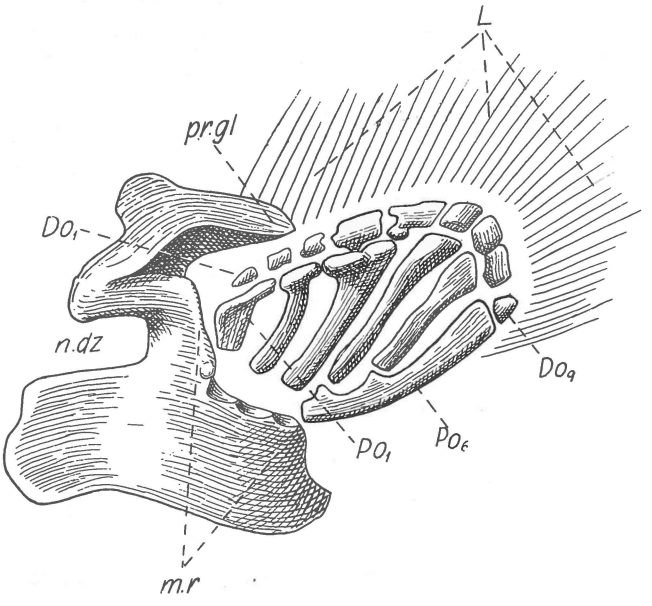


Fig. 74. *Boreosomus piveteaui* n. sp. Endoskeletal shoulder girdle ossification and ossifications in the endoskeleton of the pectoral fin in lateral view. Direction of the lepidotrichia of the pectoral fin indicated by short lines (*L*). Based mainly on specimen No. 233. C. 4 ×. Do_1, Do_9, foremost and hindmost distal radial ossifications; Po_1, Po_6, foremost and hindmost proximal radial ossifications; *m. r*, margo radialis; *n. dz*, notch for diazonal nerves; *pr. gl*, processus glenoidalis.

The complete endoskeletal shoulder girdle ossification (Figs. 74, 75 A and B) shows many points of resemblance to the endoskeletal shoulder girdle ossification in *Acrorhabdus bertili* (Aldinger 1937, pp. 283–86, Fig. 84) and is thus of a different type from that found in *Glaucolepis*.

In *Boreosomus* the ossification may be described as a plate which, as will be seen from Fig. 75 B, is very slightly bent and almost vertical. This plate falls naturally into two divisions, viz. a dorsal relatively narrow division with a rather complicated outline, and a ventral broad division, which is roughly rectangular in outline.

In lateral view the dorsal division of the ossification has the outline shown in Fig. 74. From the most dorsal part of the posterior margin of this division of the ossification issues a caudally directed very well developed processus glenoidalis (*pr. gl*, Figs. 74, 75 A and B). As will be seen from Fig. 75 B, the antero-dorsal part of the lateral face of the dorsal division of the ossification has contact with the medial face of the vertical part of the cleithrum. From the medial face of the dorsal division there issues in a medial direction a well developed rostro-caudally flattened process (*msc*, Fig. 75 B), which corre-

sponds to the process *pr. m* in *Acrorhabdus* (Aldinger 1937, Fig. 84). Aldinger regards this process as a very primitive mesocoracoid and writes as follows (1937, pp. 285–86): "Das Mesocoracoid bildet zwar bei *Amia*, *Lepidosteus*, *Cypriniformes* und *Clupeiformes* meist einen geschlossenen korpeligen oder knöcheren Bogen (Gegenbaur 1865, Taf. VI, VII, Derjugin 1910, p. 604 ff., Goodrich 1930, p. 167, Textfig. 171, 173, Starks 1930, p. 91), aber es entsteht bei *Clupea* aus knorpeligen Fortsätzen am dorsalen Ende der Scapula und an der Grenze von Scapula und Coracoid, die sich zu einem Bogen vereinigen und die Grundlage für die spätere Verknöcherung bilden (Derjugin 1910, p. 605, Taf. XXVIII, Fig. 30). Der Fortsatz pr. m bei *Arorhabdus* ist vergleichbar einem dieser Fortsätze, wahrscheinlich dem ventralen, auf der Grenze zwischen Scapula und Coracoid gelegenen bei *Clupea*."

In the well preserved specimen of *Boreosomus reuterskiöldi* mentioned on p. 337, I dissected out the endoskeletal shoulder girdle ossification and found that it agrees in all essentials with the corresponding ossification in *Acrorhabdus* and *Boreosomus piveteaui*, except that it has a mesocoracoid arch which is just as complete and well developed as in *Glaucolepis*. The most dorsal part of this arch corresponds entirely to the medial process in *Acrorhabdus* and *Boreosomus piveteaui*, which means that Aldinger's interpretation quoted above does not hold good. There can be no doubt that *Acrorhabdus* (as also *Boreosomus piveteaui*) had a complete mesocoracoid arch, it was only less completely ossified than in *Boreosomus reuterskiöldi*. It is quite probable that the absence of a mesocoracoid arch in *Pygopterus nielseni* (Aldinger 1937, p. 163) can be explained in a similar way, and that the presence of a well developed mesocoracoid arch is a character which is common to all the most primitive Actinopterygians.

The radials of the pectoral fin articulated against that part of the dorsal margin which lies posteriorly to the transitional area between the dorsal and ventral divisions of the ossification. This appears from the fact that this part of the margin (the glenoid face or margo radialis) (*m. r*, Figs. 74, 75 A) is provided with three or four small depressions, whose surface is devoid of perichondral bone. No processus radialis is developed.

The anterior margin of the ventral division of the ossification had contact with the anterior medially bent part of the cleithrum and the anterior part of the ventral margin had contact with the dorso-medially directed face of the ventral part of the cleithrum. The lateral faces of the ventral division and of the most ventral part of the dorsal division of the ossification have no contact with the cleithrum, as will be seen from Fig. 75 B. Thus in *Boreosomus*, as in *Acrorhabdus*, a high narrow space is found between the cleithrum and the endoskeletal shoulder girdle ossification, which space lodged the ventro-lateral fin musculature. In *Boreosomus*, as in *Acrorhabdus*, the space was probably closed anteriorly, a fenestra coraco-cleithralis hardly being developed.

If we consider the endoskeletal shoulder girdle as a whole, we shall see

that the distinct separation between the narrow dorsal and the broad ventral division of the ossification is due to the presence of a very deep emargination (*n. dz*, Fig. 74) in the anterior margin of the ossification. A comparison with *Acrorhabdus* shows that this emargination in *Boreosomus* corresponds to the large opening for diazonal nerves termed *c* in Aldinger's figure (1937, Fig. 84) of *Acrorhabdus;* the diazonal nerves in *Boreosomus* accordingly passed this notch on their way to the muscular fossa between the cleithrum and the endoskeletal ossification. Anteriorly this notch was possibly bordered by cartilage.

The lateral face of the ventral division of the ossification in *Boreosomus* is slightly concave anteriorly and slightly convex posteriorly, and nothing is found on this face corresponding to the ridges (*r* and r_1) in *Acrorhabdus* which were supposed by Aldinger to indicate a subdivision of the ventro-lateral fin musculature.

If we compare the figures of the endoskeletal shoulder girdle of *Boreosomus* (Fig. 75B) and of *Acrorhabdus* (Aldinger 1937, Fig. 84C), we shall see that in both forms the margo radialis is so steep that the plane of the pectoral fin must have been almost vertical. Thus the pectoral fin has acted in a different way from that in the family *Palaeoniscidae*. Apart from the different course of the margo radialis, the following essential points of difference between the endoskeletal shoulder girdles in *Boreosomus* and *Acrorhabdus* on the one hand and in *Glaucolepis* and *Palaeoniscus* on the other hand should especially be pointed out: In contrast to *Boreosomus* and *Acrorhabdus*, *Glaucolepis* and *Palaeoniscus* have a well developed processus radialis and a fenestra coraco-cleithralis.

According to Aldinger (1937, Fig. 44) the margo radialis in *Pygopterus nielseni* is almost vertical, and a mesocoracoid arch is lacking. In spite of this, *Pygopterus* seems to agree much better with *Glaucolepis* than with *Boreosomus* as regards the structural details of the endoskeletal shoulder girdle ossification. A comparison between the endoskeletons of the shoulder girdle in *Glaucolepis* and in *Pygopterus* has been made above (p. 229).

Dermal bones of the shoulder girdle.

The dermal bones of the shoulder girdle comprise a suprascapular, a supracleithral, a cleithrum, and a clavicle. In his restoration of *Boreosomus gillioti* Brough (1933, Fig. 2) indicates three postcleithrals, which no doubt corresponds to the relatively high trunk scales occurring in *Boreosomus piveteaui* in the first complete transverse scale-row behind the shoulder girdle. Judging from their development in the Greenland form I can se no reason to term them postcleithrals.

The suprascapular (*Sscap*, Figs. 68, 69; Pl. 29, Fig. 2) is a small bone with a lateral, a postero-medial, and an anterior margin. The lateral and postero-

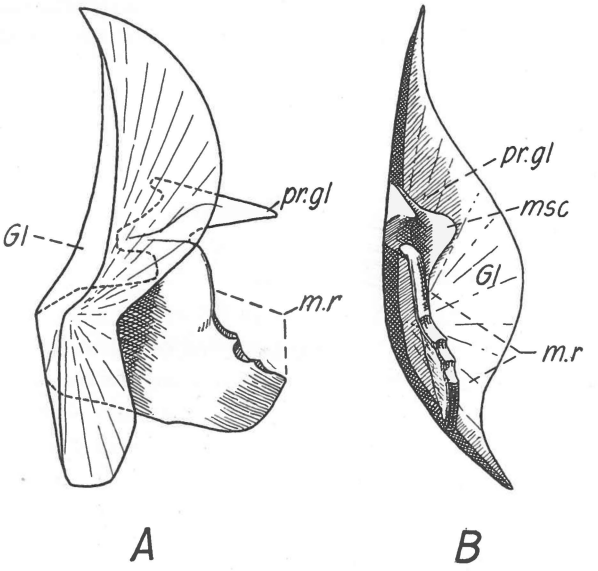


Fig. 75. *Boreosomus piveteaui* n. sp. Based on specimens Nos. 233 and 309. C.2 ×. A, cleithrum and endoskeletal shoulder girdle ossification in lateral view. B, cleithrum and endoskeletal shoulder girdle ossification seen from behind. *Gl*, medially directed lamina of the cleithrum; *m. r*, margo radialis; *msc*, ossified part of the mesocoracoid arch; *pr. gl*, processus glenoidalis.

medial margins are convex, while the anterior margin is fairly straight. The bone, whose transverse extent far exceeds its longitudinal extent, is curved in such a way that its external face is convex and its internal face correspondingly concave in a transverse direction. A rather considerable anterior part of the suprascapular is overlapped by the posterior parts of the lateral and the medial extrascapular.

The suprascapular is pierced by the main lateral line, which passes the radiation centre of the bone, whose position will be seen from Fig. 68.

The supracleithral (*Scl*, Fig. 69) is a four-sided bone with an antero-dorsal, a postero-dorsal, a postero-ventral, and an antero-ventral margin. The antero-ventral margin, which is concealed beneath the operculum, is convex, while the other three margins are slightly concave. The bone, which is almost twice as long as broad, is slightly curved from its antero-dorsal to its postero-ventral margin, its external face being accordingly convex. The outline of the exposed part of the bone is seen from Fig. 69, which likewise shows the position of the centre of radiation.

The supracleithral is pierced by the main lateral line, which as usual pierces the centre of radiation.

In *Boreosomus* the cleithrum (*Cl*, Figs. 69, 75 A and B) has an entirely different shape from that of *Glaucolepis*. The bone falls naturally into an anterior and a posterior division, which meet at a nearly right angle.

The posterior division lies in plane with the lateral surface of the trunk, while the anterior division is placed as a vertical transverse wall, which forms the posterior boundary of the branchial cavity.

The posterior division of the cleithrum consists of a dorsal vertical, and a ventral oblique part. The relation between these two parts is seen from Fig. 75 A and B. The dorsal part of the posterior division of the bone is bounded by an anterior concave and a posterior convex margin, which meet farthest dorsally at a very acute angle. This part of the bone decreases in breadth from its middle part both in a dorsal and a ventral direction, as may be seen from Fig. 75 A. The ventral part of the posterior division of the bone is so situated that its external face is directed ventro-laterally and its internal face dorso-medially. The largest breadth of this part of the bone occurs somewhat nearer its ventral than its dorsal end; the details of its outline are seen from Fig. 75 A. The ventral part of the posterior division of the cleithrum corresponds to the ventral horizontal division of the cleithrum in *Glaucolepis*.

In contrast to the posterior division, the anterior transversally placed division of the cleithrum has no ornamentation and consists of a thin bone lamina, which decreases in breadth from its middle part both in a dorsal and a ventral direction, as will be seen from Fig. 75 B and C.

The radiation centre of the cleithrum lies at the point where the horizontal boundary line between the dorsal and the ventral part of the posterior division of the cleithrum meets the vertical boundary line between the anterior and the posterior division of the bone. The areas of contact between the cleithrum and the endoskeletal shoulder girdle ossification have been dealt with above.

It appears from the position of the cleithrum that the distance between the right and the left half of the endoskeletal shoulder girdle was much greater than in *Glaucolepis*.

In a few cases remnants of a very small clavicle may be seen in front of the cleithrum; however, the clavicle is always in a poor state of preservation, so nothing can be stated as to its shape or its relation to the cleithrum. Probably it was of the same type as in *Acrorhabdus* (Stensiö 1921, Fig. 74), considering the great resemblance which this genus bears to *Boreosomus*.

Pectoral fin.

The endoskeleton of the pectoral fin is especially accessible for investigation in the specimens in which the endoskeletal shoulder girdle is best ossified, that is to say, in the specimens Nos. 233 and 309.

As in *Glaucolepis* (p. 234), the radial endoskeleton of the fin has a proximal and a distal series of ossifications, which, like the other primary ossifications, consist of cancellate endochondral bone-tissue surrounded by perichondral bone, which, however, is lacking on the articular faces.

The proximal series comprises six ossifications (Po_1, Po_6, Fig. 74), of which Nos. 1, 2, 3, and 6 articulated with the endoskeletal shoulder girdle ossifica-

tion, while Nos. 4 and 5 articulated with the proximal half of No. 6, as will be seen from Fig. 74.

The first (anterior) proximal radial ossification is short and somewhat flattened from side to side; its proximal terminal face is devoid of perichondral bone and has been covered by cartilage. The distal end of the ossification is much broader and also somewhat thicker than the remaining part of the bone. Distally to the distal end lie the foremost two distal radial ossifications.

The second proximal radial ossification, which is somewhat longer than the first one, is a somewhat curved bone rod, whose distal end, which is broader and thicker than the remaining parts of the bone, had contact with the distal ends of the first and third proximal radial ossifications. The proximal terminal face of the ossification was capped by cartilage. Distally to the distal end of the ossification lies the third distal radial ossification.

The third proximal radial ossification is somewhat longer than the second one, and is a slightly curved bone rod, whose proximal terminal face was capped by cartilage, and whose distal end is much broader and thicker than the remaining part of the bone. As seen from Fig. 74, this thick distal end is divided by a small groove into an anterior and a posterior division. Distally to each of these divisions lies an ossification of the distal series (the fourth and fifth respectively).

The fourth proximal radial ossification is of the same length as the third one, and is a rather slender bone rod, whose distal end is only a little broader than the remaining part of the bone. The ossification, whose proximal terminal face was probably capped by cartilage, had contact with a small distinct facet on the anterior side of the sixth proximal radial ossification. Distally to the fourth proximal radial ossification lies the sixth ossification of the distal series.

The fifth proximal radial ossification is shorter than the third and fourth ones, and is a rather slender bone rod, whose distal end is broader than the remaining part of the bone. Probably the proximal end of the bone was capped by cartilage. The ossification had contact with the sixth proximal radial ossification similarly as the fourth proximal radial ossification. Distally to the fifth ossification lie the seventh and eighth ossifications of the distal series.

The sixth proximal radial ossification is the longest of the whole series. It is a somewhat curved bone rod, whose proximal half is fairly slender and on its anterior side is provided with the two small protuberances, to which the fourth and fifth proximal radial ossifications were attached. The ossification increases gradually in breadth towards its distal end, distally to which lies the ninth ossification of the distal series.

The proximal terminal face of the ossification and the faces to which the fourth and fifth proximal radial ossifications were attached, were probably capped by cartilage.

It will appear from the above description that the number of distal radial ossifications far exceeds the number of proximal ones.

Of the distal radial ossifications (Do_1, Do_9, Fig. 74), the foremost three and the hindmost one are very small, while the five intermediate ones are somewhat larger. As these small ossifications could not be entirely exposed, nothing can be stated as to their shape except what is shown in Fig. 74. As in *Glaucolepis*, the distal radial ossifications are concealed by the proximal ends of the lepidotrichia in the complete pectoral fin.

The radial skeleton of the pectoral fin supported a well developed scaly fin lobe, which, in contrast to the lobe of the pectoral fin in *Glaucolepis*, was almost vertical.

In surprisingly few cases the lepidotrichia of the pectoral fin are so well preserved that their number can be determined, and in no case are they in so good a state of preservation that the exact outline of the fin can be made out. In this connection it may be mentioned that the pelvic fin, the anal fin, and the dorsal fin, too, are nearly always poorly preserved, even in specimens in which the trunk scales are undisturbed.

The subjoined description of the lepidotrichia of the pectoral fin is based in all essentials on specimen No. 233.

The number of lepidotrichia may be estimated at c. 32–40. As indicated in Fig. 74, the greater number of these issue from the dorsal and the posterior margin of the fin lobe, covering the distal series of radial ossifications, while the posterior three or four issue from the ventral (postero-ventral) margin of the fin lobe, covering the most distal part of the sixth proximal radial ossification.

The anterior lepidotrich is very short, but the succeeding ones increase rapidly in length, the fifth and the sixth being the longest of the fin and of about the same length as the mandible. The following lepidotrichia decrease in length to and including the hindmost one, which is of about the same length as the second proximal radial ossification.

As regards the segmentation of the lepidotrichia, specimen No. 233, the only specimen in which the segmentation can be examined in detail, presents rather interesting facts. In lateral view the lepidotrichia will be seen to be segmented throughout their extent, and so closely that the longest lepidotrich contains about twenty-five segments. The length of the individual segments increases somewhat towards the distal end of all the lepidotrichia except the posterior ones, in which all the segments, which are very short, are of about the same length.

In medial view the proximal parts of at least the 20–25 anterior lepidotrichia seem to be unsegmented, while the distal parts of these and of the posterior lepidotrichia are segmented in the same way as when they are viewed from the lateral side. A closer examination of the apparently unsegmented divisions of the anterior 20–25 lepidotrichia shows that these divisions

have arisen by fusion of segments whose boundaries are still distinguishable in the structure of the ossifications. This means that as regards the segmentation of at least the 20–25 foremost lepidotrichia, some specimens of *Boreosomus piveteaui*, at any rate show the peculiar feature that the segments in the proximal parts of the medial lepidotrich halves are fused, while in the lateral halves they are separate.

This fact is of interest, because one of the few characters used by Stensiö (1921, p. 223) as a basis for distinction between the two closely related genera *Boreosomus* and *Acrorhabdus* is the segmentation of the lepidotrichia of the pectoral fin.

According to Stensiö all the lepidotrichia of the pectoral fin in *Acrorhabdus* are segmented to the base (apart from the anterior two or three), while in *Boreosomus* they are unsegmented, at any rate in their proximal halves. The intermediate conditions in *Boreosomus piveteaui* depicted here show that hardly too much import should be attached to the segmentation of the lepidotrichia of the pectoral fin as a distinguishing character between *Boreosomus* and *Acrorhabdus*.

With the exception of the four or five anterior ones, the lepidotrichia dichotomise in their distal parts. The anterior margin of the fin is provided with a series of small fulcra.

The exposed parts of the individual lepidotrichia are covered by a continuous and probably smooth layer of ganoine.

As in *Amblypterus*, *Acipenser*, and *Amia*, the endoskeleton of the pectoral fin described above is so developed that it contains what is termed by White (1939, p. 57) a false "metapterygial" axis, which in this case has evidently arisen by a shortening of the base of the radial skeleton. The closer mutual position of the radial elements which is a consequence of such a shortening, besides the formation of the axis, may explain the greater number of distal than of proximal radial ossifications (a feature which is fairly common in higher Actinopterygians), for it may be conceived to be due to a fusion or a reduction of the elements of the proximal part of the radial skeleton. The shape of the distal end of the third proximal radial ossification might indicate that this ossification has arisen by fusion of two elements.

However, the pectoral fin in *Boreosomus* differs in an essential degree from those of *Amblypterus*, *Acipenser*, and *Amia* by being almost vertical, in which respect it agrees more closely with forms such as *Cornuboniscus*, *Tarassius*, and *Polypterus* (White 1939).

Thus it is difficult to place this fin type in White's table (cf. p. 237–38); it should be pointed out, however, that if a reduction of the proximal parts of the middle radial elements took place, the endoskeleton of the vertical fin in *Boreosomus* would be of the same type as that of the vertical fin in *Polypterus*.

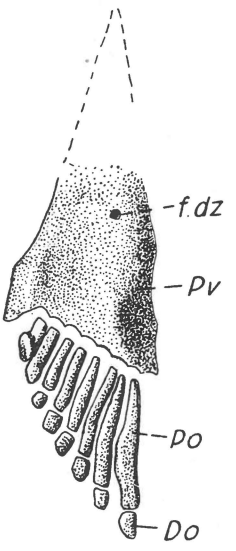


Fig. 76. *Boreosomus piveteaui* n. sp. Pelvic plate and ossifications in the endoskeleton of the pelvic fin in ventral view. Based on specimen No. 218. 3.5 ×.
Do, distal radial ossification; *Po*, proximal radial ossification; *Pv*, pelvic plate; *f. dz*, foramen for diazonal nerves.

Pelvic plate and pelvic fin.

The pelvic plate and the radial skeleton of the pelvic fin are ossified, at any rate in some of the largest specimens, but in all cases except one the ossifications are so much crushed and compressed that it is impossible to investigate their structure. The only exception forms specimen No. 218, in which a large part of the right pelvic plate and all the ossifications in the endoskeleton of the right pelvic fin are intact (Fig. 77), and this specimen alone forms the basis of the subjoined description.

The individual ossifications consist of cancellate endochondral bone-tissue, whose external faces, apart from the terminal faces, which were capped by cartilage, are lined with perichondral bone.

Of the pelvic plate (*Pv*, Fig. 77) the posterior and largest part is well preserved, while the anterior part is so much destroyed that its external outline can only be determined with a great amount of doubt. The pelvic plate, which is so situated in the rock that it can only be observed from the ventral side, is a rather thin, roughly triangular plate with an antero-lateral, a postero-lateral, and a postero-medial margin. The antero-lateral and postero-medial margins are very long and nearly straight, the lateral part of the short postero-lateral margin is produced into a small postero-laterally pointing process, while the remaining part of this margin is provided with a number of small concavities, each indicating an articular fossa for one of the radials of the pelvic fin.

The ventral face of the pelvic plate is slightly irregularly undulated, as will be seen from the figure, but has no system of parallel grooves like that

found on the corresponding face in *Glaucolepis* (p. 239) and in *Birgeria* (Aldinger 1937, p. 160). On the anterior part of the ventral face of the well preserved part of the pelvic plate is a small foramen for diazonal nerves (*f. dz*, Fig. 77).

Eight proximal radial ossifications (*Po*, Fig. 77) are present, all of which lie outside the postero-lateral margin of the pelvic plate. The proximal terminal faces of these eight ossifications were capped by cartilage.

The posterior six proximal radial ossifications are rather slender bone rods, which increase regularly in length from the foremost to the hindmost one. The distal terminal face of each of these ossifications was covered by cartilage, and distally to each terminal face lies a small distal radial ossification (*Do*, Fig. 77), whose proximal terminal face, too, was probably covered by cartilage.

The anterior two of the so-called proximal radial ossifications are of such a length and shape that each must be supposed to have been formed by fusion of a proximal and a distal radial ossification. For, as will be seen from Fig. 77, the most distal parts of these two ossifications lie as a natural anterior continuation of the series of independent distal radial ossifications and differ from the proximal parts of the two ossifications by being both broader and thicker.

Distal radial ossifications in the endoskeleton of the pelvic fin are unknown in *Glaucolepis*, but have been ascertained in *Birgeria* (Stensiö 1921, p. 193) and in *Saurichthys* (Stensiö 1925, pp. 122–23).

The exoskeleton of the pelvic fin is, as a rule, poorly preserved and in many cases the pelvic fin cannot be localised even though the squamation of the trunk is almost intact.

The number of transverse scale-rows between the posterior margin of the supracleithral and the anterior margin of the pelvic fin ranges about thirteen.

The number of lepidotrichia in the pelvic fin probably ranges between sixteen and twenty, but the lepidotrichia are never so well preserved that it is possible to determine the exact outline of the fin; it is a fact, however, that the fin was very small.

The foremost lepidotrich is short, but the succeeding ones increase in length to and including the fourth or fifth, after which they decrease in length to and including the hindmost one.

The lepidotrichia are close-set and, with the exception of the anterior three or four, segmented to their base, and enclose the distal radial ossifications with their most proximal parts. As far as I am able to decide, the exposed faces of the lepidotrichia are covered by a smooth layer of ganoine.

The anterior margin of the fin is provided with a series of small fulcra.

The pelvic plate and the endoskeleton of the pelvic fin agree in their main features with those of other *Chondrostei*. It is true that the antero-medial part of the pelvic plate is thicker than in *Birgeria* (Stensiö 1931, Fig. 68), *Pygopterus* (Aldinger 1937, Fig. 45), and *Glaucolepis* (Fig. 55), in which it is produced into a very slender antero-medially directed process, but it is hardly thicker than in forms as for instance *Acipenser* (Rautenfeld 1882, Taf. 1, Fig. 4) and *Saurichthys* (Stensiö 1925, Fig. 28).

Judging from the position of the radial skeleton, it seems beyond doubt that no ossified or unossified metapterygial elements were situated behind the pelvic plate in *Boreosomus*. Besides in recent *Chondrostei*, such elements are found both in *Birgeria*, *Saurichthys*, *Pygopterus*, and *Glaucolepis*, and quite probably their absence in *Boreosomus* is due to their fusion with the pelvic plate by a similar, but more far-reaching, fusion than that pointed out above for *Glaucolepis* (p. 243).

Unpaired fins.

The endoskeleton of the dorsal fin can only be investigated in some few specimens, and is best preserved in specimens Nos. 232 and 290. In No. 290 the radial skeleton is represented by an axonost series, a baseost series, and a distal series of small ossifications. The individual ossifications are made up of endochondral cancellate bone-tissue surrounded by perichondral bone.

The elements of the axonost series (*Ax*, Fig. 76, Pl. 28) are exceedingly poorly preserved, and neither their shape nor their number can be determined.

The baseost series consists of eleven elements (*Ba*, Fig. 76; Pl. 28), of which the foremost is a fairly well developed rectangular plate about three times as long as broad, while the others are more slender ossifications, whose proximal parts are rather tiny, while their distal parts increase in breadth and thickness in a distal direction, their distal terminal faces, which were probably capped by cartilage, being accordingly of fairly large dimensions.

The baseosts are parallel with each other and point in a dorsal and at the same time slightly posterior direction. They decrease gradually in length from the foremost to the hindmost one, the length of the hindmost baseost being less than one-third the length of the foremost one.

The distal radial series comprises thirteen ossifications (*Do*, Fig. 76; Pl. 28), three of which lie distally to the foremost baseost and one distally to each of the succeding ones. The proximal, probably cartilage-lined, terminal faces of the distal ossifications articulated with the probably cartilage-covered distal terminal faces of the elements of the baseost series. In lateral view the distal radial ossifications present the outlines shown in Fig. 77, which likewise shows their relations to each other and to the baseost series. The anterior very small distal radial ossification is rounded, while those following behind it are nearly cuboid, with an anterior, a posterior, a dorsal, a ventral, and a paired lateral face. Towards the posterior end of the series the distal radial ossifications gradually change in shape, their postero-dorsal part being prolonged in a posterior direction, protruding across the ossifications following next behind them, at the same time as the antero-dorsal parts grow lower. In this way the ossifications gradually assume the shape of plates, whose two largest faces are directed antero-dorsally and postero-ventrally respectively. The antero-dorsal face corresponds to the anterior and the dorsal face, while the pos-

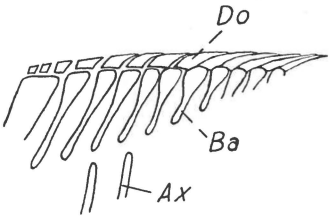


Fig. 77. *Boreosomus piveteaui* n. sp. Endoskeleton of the dorsal fin. Based on specimen No. 290. 2 ×.
Ax, dorsal part of an axonost; *Ba*, baseost; *Do*, distal radial ossification.

tero-ventral face corresponds to the posterior face of the cube-shaped ossifications.

By the ventral part of its postero-ventral face each of the flattened distal radial ossifications is in contact with the antero-dorsal part of the baseost ossification in the radial lying immediately behind that to which it belongs itself, and by the dorsal part of its postero-ventral face it is in contact with the antero-dorsal face of the distal radial element lying immediately posteriorly to it.

The fact that three distal radial ossifications are situated distally to the foremost baseost, may be explained by the assumption that this exceptionally broad radial ossification has arisen by fusion of three normal baseosts; thus in *Boreosomus* a fusion has taken place between quite different radial ossifications from those in *Glaucolepis*. (p. 244).

As in *Glaucolepis* (p. 245), the distal series of radial ossifications is enclosed by the most proximal part of the lepidotrichia, and possibly the slightly thickened proximal ends of the lepidotrichia articulated with the distal parts of the middle radial segments.

The number of transverse scale-rows between the posterior margin of the supracleithral and the anterior margin of the dorsal fin ranges about 19–21.

The dorsal fin contains about 24–27 close-set lepidotrichia, or nearly two for each distal radial element. All the lepidotrichia are segmented to their bases, and the segments increase in length from the proximal to the distal parts of the lepidotrichia. The longest lepidotrich consists of about ten segments. All the lepidotrichia that reach the posterior margin of the fin are dichotomously branched in their distal parts.

The foremost lepidotrich is very short, but the succeeding ones increase in length to and including the sixth, seventh, or eigth, one of these three being the longest lepidotrich of the fin. From the longest one the lepidotrichia decrease gradually in length to and including the hindmost one. The outline of the fin and its size is seen from Fig. 78.

The exposed faces of the lepidotrichia are ornamented with ganoine striae, which extend fairly parallel with the longitudinal axes of the lepidotrichia.

The anterior margin of the fin is provided with small fulcra.

Not the slightest trace of the endoskeleton of the anal fin has been observed, which must mean that it has been ossified to a very slight extent only or not at all, or that it has been extremely delicate.

The number of transverse scale-rows between the posterior margin of the supracleithral and the anterior margin of the anal fin ranges about 25–29. The anal fin contains 17 or 18 close-set lepidotrichia, which agree with those of the dorsal fin in segmentation and subdivision. The fourth or fifth is the longest lepidotrich of the fin. The anal fin has the same shape as the somewhat longer dorsal fin, as will be seen from Fig. 78.

The exposed faces of the lepidotrichia are ornamented with ganoine striae, which extend fairly parallel with the longitudinal axes of the lepidotrichia.

The anterior margin of the fin is provided with small fulcra.

The caudal fin, which is excellently preserved in several specimens, is deeply cleft, equilobate, and abbreviate heterocercal. The endoskeleton of the fin has been dealt with in the chapter on the axial skeleton. As is seen from Fig. 78, the body axis of the caudal fin is fairly slender and does not reach the distal end of the dorsal lobe. Dorsally the body axis is covered by a number of well developed fulcral scales, and laterally by long, narrow scales, which are longest and narrowest in the posterior and narrowest part of the axis.

The lepidotrichia of the fin are close-set and segmented to the base. The proximal segment of each lepidotrich is relatively long, and its proximal pointed end is concealed beneath the scales of the fin axis and the caudal pedicle. The succeeding segments are very short, being shortest in the lepidotrichia belonging to the ventral fin lobe, while the more distal segments increase somewhat in length. Distally all the lepidotrichia reaching the posterior margin of the fin are subdivided, as will be seen from Fig. 78. The anterior ten to fifteen lepidotrichia are the broadest of the fin. The foremost one is very short, but the succeeding ones increase in length as far as the seventh, eighth, ninth, or tenth, one of these being the longest of the fin, and containing more than fifty segments. The following lepidotrichia decrease rather rapidly in length as far as c. the 20th, which is the hindmost (the most dorsal) lepidotrich in the ventral lobe. The number of lepidotrichia in the dorsal lobe ranges between 30 and 35, but it is difficult to determine accurately. The length and breadth of the lepidotrichia of the dorsal lobe decrease in the usual way from the anterior to the posterior one.

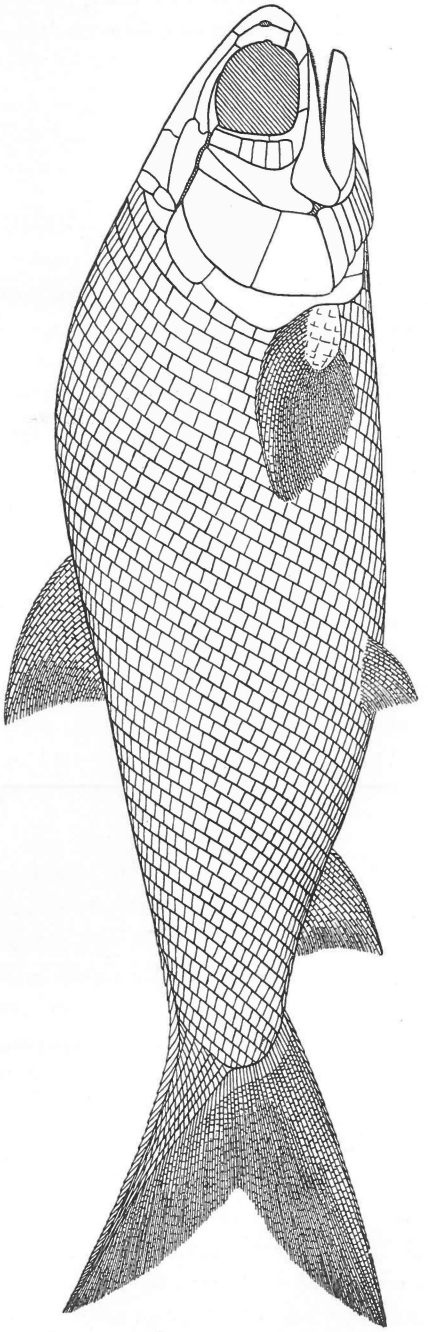


Fig. 78. *Boreosomus piveteaui* n. sp. Attempted restoration. Exact outline of the pectoral fin and the scale arrangement on its lobe unknown. Based on several specimens. About nat. size.

The exposed faces of the lepidotrichia of the caudal fin are ornamented with one or several ganoine striae, which run parallel with the longitudinal axes of the lepidotrichia. The anterior margin of the ventral fin lobe is provided with a number of small fulcra.

Squamation.

The abdominal and caudal regions are entirely covered by scales, which are arranged in 42–43 transverse rows between the posterior margin of the supracleithral and the distinct line of inversion in the posterior part of the caudal region. It is difficult to state the number of scales in the abdominal transverse rows, for the very low scales on the ventrum rarely lie in their original position. The foremost transverse scale-row, which is intersected by the base of the pelvic fin, contains about 29 scales dorsally to the base of the fin; about fourteen of these scales lie ventrally to the lateral line.

In front of the ventral part of the first transverse scale-row behind the supracleithral six to ten short subcleithral scale-rows are found.

On the sides of the abdominal and caudal regions the transverse scale-rows run, broadly speaking, from above downwards and at the same time slightly backwards. In the anterior part of the abdominal region the transverse scale-rows are slightly S-curved, so that dorsally to the lateral line the posterior margin of the individual scale-rows is convex, while ventrally to the lateral line it is concave. The S-curvature decreases with increasing distance from the head, so in the caudal region the transverse scale-rows are fairly straight.

In the anterior transverse scale-rows behind the supracleithral the lateral line scale and the scales nearest dorsally and ventrally to the lateral line scale are higher than broad. More precisely, in the first and second transverse rows this applies to one or two scales situated dorsally to the lateral line scale, the lateral line scale itself, and four or five scales situated ventrally to the lateral line scale. The highest of the high scales in the first transverse scale-row is the scale immediately ventrally to the lateral line scale, and this scale is often between two or three times as high as broad. In the succeeding rows the number of high scales and the height of the individual scales decrease, the 12th, 13th, or 14th row containing only a single high scale, viz. the lateral line scale, and this is only slightly higher than broad. The scales situated just dorsally and ventrally to the high scales in the anterior transverse rows as also the lateral line scale and the scales situated nearest dorsally and ventrally to that scale in the other transverse rows are nearly as broad as high.

Farther dorsally and ventrally in the transverse rows the height of the scales decreases with increasing distance from the lateral line, the most dorsal

and the most ventral scales being accordingly very low. The lowest scales of the trunk are found on the ventral side of the abdominal region.

Since the axial skeleton is so poorly preserved that it is impossible to ascertain the number of dorsal or ventral arcual elements, it cannot be decided whether the transverse scale-rows are polymerically or metamerically arranged; however, the first alternative must be regarded as the most probable.

Behind the inversion line of the caudal region the flank scales are predominantly narrow and rhombic, and as usual in *Palaeonisciformes*, these scales are arranged in rows which are considerably less steep than the rows in front of the inversion line.

The lobe of the pectoral fin is scaly, but the precise arrangement of the scales cannot be ascertained.

Enlarged scales are not found either in front of the dorsal fin or around the anus. In front of the ventral lobe of the caudal fin three to five somewhat enlarged ridge scales are found, and on the dorsal side of the caudal pedicle lies a series of eight or nine enlarged ridge scales as an anterior continuation of the aforementioned series of fulcral ridge scales on the dorsal side of the body axis of the caudal fin.

In many specimens the flank scales are thick and have a well developed peg-and-socket articulation and, in connection with this, a well developed ridge on the medial face. In other specimens the flank scales are comparatively thin, and the peg-and-socket articulation and the medial ridge are slightly developed. Other specimens, again, show transitions between these two scale types.

The antero-dorsal corner of the flank scales is produced somewhat in an antero-dorsal direction and together with the peg-and-socket articulation contributes to consolidating the connection between the individual scales. The posterior margin of the flank scales is finely serrated. The foremost overlapped area of the scales lying nearest behind the head is rather narrow; farther posteriorly the overlapped area of the scales grows gradually narrower.

The exposed faces of the scales are ornamented with ganoine striae and ganoine tubercles. The ornament of the scales shows a surprisingly great variation from one specimen to the other. This is rather interesting, for Stensiö (1921) used the ornament of the scales as the most important distinguishing character between the species of *Boreosomus* from Spitsbergen. In *Boreosomus piveteaui* the ornament of the scales varies just as much as in the Spitsbergen material of *Boreosomus*, but the large collections from Greenland contain so many intermediate forms between the most extreme types of ornament that it is impossible to subdivide the material into several species. And it is quite possible, also, I think, that on examination of a greater material of *Boreosomus* from Spitsbergen transitional types between the species erected by Stensiö may be found.

To illustrate the variation of the ornament of the scales I chose to describe the ornament of an abdominal rhombic flank scale of each of the specimens Nos. 218, 209, and 214. As regards all three specimens, the description is based on scales from the area situated immediately ventrally to the few high scales of the sixth, seventh, and eighth transverse scale-rows. For the sake of brevity the anterior and dorsal margins of the exposed face of the scale will be termed the anterior and the dorsal margin of the scale respectively.

The scale chosen from specimen No. 218 is ornamented with a system of about ten fairly broad flat striae, which continue posteriorly in the small serrations on the posterior margin of the scale. The main direction of the striation system is almost parallel with, though somewhat less steep, than the longitudinal diagonal of the scale. However, the individual striae are not entirely parallel, the foremost ends of the five or six most ventral striae being curved upward, so as to be nearly parallel with the anterior margin of the scale, while the posterior and longest parts of these striae run almost parallel with the ventral margin of the scale. The most ventral striae are most strongly curved, and the transition between them and the most dorsal, fairly straight striae is very gradual. In continuation of the upward curved anterior parts of the five or six most ventral striae lie some oblong tubercles, a fairly broad tuberculated zone thus occurring in front of the striated part of the face of the scale. Occasionally some of the striae are fused along a short stretch; fusion of a large number of striae may especially be observed immediately in front of the posterior margin of the scale.

The ornament of this scale is remarkably reminiscent of the ornament of the scales of *Boreosomus ? scaber* from Spitsbergen (Stensiö 1921, p. 222).

On that half of the exposed face of the scale chosen from specimen No. 209 which lies postero-dorsally to the long diagonal of the scale, five to seven striae occur, which run parallel with the long diagonal from the dorsal to the posterior margin of the scale. On the other half of the exposed face of the scale ten or twelve striae are found, whose anterior parts are almost parallel with the anterior margin of the scale while their posterior parts are parallel with the ventral margin of the scale. In front of the anterior end of most of these curved striae one, or occasionally two, oblong tubercles are found, a very narrow tuberculated zone thus occurring in front of the striated area. Especially characteristic of the type of ornament described here is the very different direction of the striation on the postero-dorsal and of that on the antero-ventral part of the scale.

The ornament of the corresponding scale of specimen No. 214 resembles most closely that of the last-described scale, but differs from it in that the individual striae on the postero-dorsal part of the scale are fused to a very large extent, and in that the intervals between the striae are constricted so as to form very narrow fissures with steep walls.

In other specimens, in contrast to the three specimens described above,

the surface of the scales is striated right to the anterior margin, and no tubercles are found among the elements of ornamentation.

On the whole the ornament of the scales in *Boreosomus piveteaui* is most marked in the anterior part of the abdominal region, and the number of ornamental elements decreases with the decreasing size of the scales, the low scales farthest dorsally and farthest ventrally in the transverse rows exhibiting a very small number of striae. With increasing distance from the head the striae of the scales become increasingly fused, the fusion being most complete near the posterior and ventral margins of the scales, while the postero-ventral part of the scales in the caudal region is often entirely smooth.

Sensory canal system of the trunk.

Only the main lateral line of the trunk is known. It pierces the suprascapular and the supracleithral in the usual way, and behind the supracleithral it can be traced through the scales to the base of the body axis of the caudal fin. The scales on the body axis of the caudal fin are rarely so well preserved that the course of the posterior part of the lateral line can be observed; apparently, however, the lateral line continues through the most ventral scales on the lateral face of the axis right to, or almost to, the posterior end of the axis.

In the abdominal region and the caudal region the main lateral line is a rather narrow canal in the scales. The external openings of this canal have not been observed.

Generic Diagnosis.

(In part after Stensiö 1921, pp. 210–22; Brough 1933, pp. 78–87; Piveteau 1934, pp. 86–88; Aldinger 1937, pp. 276–82).

Small to medium-sized fusiform *Acrolepidae*, transverse section of trunk oval, head comparatively high and short, with small rostrum and very large eyes. Neural endocranium unossified in young, and ossified in one piece in old individuals. Small vestibular fontanelle and long fissura occipitalis lateralis; dorsal part of the latter in some cases expanded to form a small posterior dorsal fontanelle, in other cases without expansion, and in others, again, entirely closed along a short stretch. Small cranio-spinal process indicated. Small well defined anterior dorsal fontanelle in orbitotemporal region. Fossa bridgei well developed. Ventrally to posterior part of fossa bridgei an intramural space, connected with the cavum cerebrale cranii. From lateral face of otic region to anterior part of fossa bridgei a long, ventrally very narrow spiracular canal. Long unpaired aorta canal. Notochordal space extending through whole occipital and greater part of otic region. Articular fossa for hyomandibula rather steep. Jugulo-hyoideomandibular canal very short and with undivided posterior opening. Trigemino-facialis chamber of fairly large

dimensions and with well developed lateral and ventral walls. Unpaired posterior myodome with a spinal and a prespinal part, in roof of myodome a pituitary fontanelle. No openings through pars basisphenoidea for communication between myodome and orbit. Processus basipterygius very short and slender. Owing to huge development of the eyes, dorso-ventral extent of orbitotemporal region greater than of any other divisions of endocranium. Interorbital part of orbitotemporal region compressed to a thin interorbital wall with a large unpaired fenestra optica. Antero-dorsal part of orbit traversed by nervus olfactorius. A dorsal and a ventral unpaired anterior myodome for musculus obliquus superior and musculus obliquus inferior respectively. Well developed septum nasi. Fairly deep paired nasal pit, ventrally to this, one more deep paired cavity. Cavum cerebrale cranii probably entirely occupied by the brain. Parasphenoid with diminutive processus ascendens anterior and more well developed processus ascendens posterior pierced by foramen for arteria carotis interna. Probably small paired vomer firmly connected with parasphenoid and neural endocranium. Paired lateral and medial extrascapulars, the lateral much smaller than the medial. Parietals, frontals, supratemporo-intertemporals, supraorbito-dermosphenotics, supraorbito-postorbitals, nasals, and postrostral arranged according to the normal Acrolepid pattern. Parietals and frontals long and narrow. Suture between right and left frontals and between right and left parietals somewhat undulating. Supratemporo-intertemporal without ventral lamina. Supraorbito-dermosphenotic of almost same length as frontal, anteriorly joined by suture with the nasal. Supraorbito-postorbital nearly half as long as supraorbito-dermosphenotic. Infraorbital series comprising postorbital, jugal, lacrimal, and rostro-antorbito-premaxillary. Postorbital and dorsal part of jugal consisting of thin bone tubes surrounding postorbital part of infraorbital canal. Rostro-antorbito-premaxillary of large size. Five to seven suborbitals. Palatoquadrate in young individuals with an autopalatine and a quadrato-metapterygoid ossification, in old individuals ossified in one piece throughout its extent. Between palatoquadrate and neural endocranium an ethmo-palatine and a palato-basal articulation. On oral face of palatoquadrate: ectopterygoid, anterior and posterior dermopalatines, and entopterygoid. Postorbital part of maxillary much shorter and lower than in older *Acrolepidae*. Preoperculum small, vertically placed, and slightly curved, without internal lamina. No quadratojugal. Maxillary connected with ectopterygoid and probably with both dermopalatines, accordingly unable to move in relation to the palatoquadrate. No connection between preoperculum and palatoquadrate, space for musculus adductor mandibulae consequently open dorsally. Mandible short, fairly high, anterior part of its dorsal margin pointing obliquely forward and downward. Meckelian cartilage ossified in one piece throughout its extent. On external side of mandible: supraangular, angular, and dentalo-splenial; on internal side: pre-

articular and two coronoids. In hyoid arch: hyomandibula, symplectic, one ceratohyal ossification, and hypohyal. Hyomandibula rather steep, with very long processus opercularis, without canal or groove for truncus hyoideomandibularis. Ventral part of hyomandibula connected with posterior part of palatoquadrate. Symplectic very small. Ceratohyal ossification corresponding mostly to ceratohyal I in *Glaucolepis*, but to ceratohyal I + ceratohyal II in especially well ossified specimens. Hypohyal small and angular. No dermohyal. One or two antoperculars. Operculum and suboperculum relatively broad. From four (or five) to eight branchiostegal rays, hindmost one broader than remaining ones. Small anterior and large posterior median gular plate. Ossifications of branchial arches and basibranchial series not known in detail, only epibranchials I-IV and ceratobranchials I-IV identified. Comb-shaped ossified gill-rays. Articulation of branchial arches with endocranium unknown. External dermal bones of head ornamented with more or less coarse ganoine striae. Oral face of parasphenoid, vomer, entopterygoid, ectopterygoid, anterior and posterior dermopalatines, prearticular, and coronoids equipped with small partly obtusely pointed and partly acutely pointed teeth. A series of comparatively large, and a large number of small acutely pointed teeth on ventral margin of maxillary and dorsal margin of dentalo-splenial. Oral faces of elements of branchial arches and basibranchial series probably covered by a mosaic of small tooth-bearing dermal bone plates. Sensory canal system of head of normal Palaeonisciform type. Sensory canals narrow and deep-lying, primary tubuli subdivided into secondary tubuli. Anterior, middle, and posterior pit-lines on parietal, middle one often continuing on supratemporo-intertemporal. On preoperculum traces of horizontal and vertical pit-lines of cheek. Individual pit-lines very deep and often closed to narrow canals. Axial skeleton very slightly ossified. Dorsal and ventral arcual ossifications in posterior part of caudal region, ventral ones with typical hypural processes. Endoskeleton of shoulder girdle most strongly ossified in old individuals and containing a single ossification. Well developed, but only partially ossified mesocoracoid arch, large processus glenoidalis, large opening for diazonal nerves only partially bounded by bone; margo radialis almost vertical; processus radialis and fenestra coraco-cleithralis absent. Series of dermal bones of shoulder girdle comprising suprascapular, supracleithral, cleithrum, and clavicle. Cleithrum very large, angle between its dorsal and ventral parts obtuse. Clavicle very small. Endoskeleton of pectoral fin comprising a proximal and a distal series of radial ossifications. In proximal series six well developed ossifications, the posterior one forming a metapterygial axis. In distal series nine small ossifications. Radial skeleton of fin supporting a scaly finlobe. Pectoral fin vertically placed, its lepidotrichia entirely or partially unsegmented in their proximal parts. Pelvic plate well ossified in old individuals, with a single opening for diazonal nerves. Endoskeleton of pelvic fin with eight proximal radial ossifications, each of anterior two fused with a distal

radial ossification, distally to each of six posterior ones a small independent distal radial ossification. Pelvic fin small, with close-set lepidotrichia, segmented throughout. Endoskeleton of dorsal fin including three series of ossifications: an axonost series, a baseost series, and a series of small distal ossifications. Baseost series comprising eleven ossifications, anterior one compound. Distal series comprising thirteen ossifications, anterior ones small and without mutual contact, succeeding ones increasing gradually in size in posterior direction and articulating with each other. Dorsal fin small and situated farther anteriorly than pelvic fin. Anal fin smaller than dorsal fin and situated very far backward. Lepidotrichia of dorsal fin and anal fin close-set and segmented throughout. Endoskeleton of caudal fin represented by a long series of epichordal and (in some cases) a few hypochordal radial ossifications. Greater part of hypochordal radial skeleton fused with hypurals. Caudal fin well developed, deeply cleft, equilobate or nearly so. Body axis of fin not always reaching extreme point of dorsal lobe. Lepidotrichia close-set and segmented throughout. Body axis of caudal fin with a dorsal series of large ridge scales. All fins with a series of small fulcra. Trunk entirely covered with scales. A number of flank scales nearest behind shoulder girdle higher than broad, other trunk scales rhombic or lower than broad, 42–50 transverse scale-rows between supracleithral and inversion line in caudal region. On dorsal and ventral margins of caudal pedicle and in some species in front of dorsal fin some enlarged ridge scales. Peg-and-socket articulation more or less well developed. Posterior margins of scales serrated. Ornament of scales consisting of more or less coarse ganoine striae, predominant direction of striation a little less steep than long diagonal of individual scales. Anterior end of most ventral striae often curved upward, in front of these striae often a narrow or broad zone ornamented with oblong ganoine tubercles. At increasing distance from head fusion of ornamental elements more or less common, especially in postero-ventral part of the individual scales. Scales consisting of a bone-layer, a cosmine-layer, and aforementioned ganoine striae and tubercles. Bone-layer not pierced, or only pierced in its posterior part by ascending canals.

The Greenland Species of Boreosomus.

Boreosomus piveteaui n. sp.

(Figs. 58–78; Pls. 25–30).

Syn: *Boreosomus?* sp. Stensiö 1932, p 117.

Diagnosis. – Rather small species, largest specimens measuring about 22–24 cm in length. Largest height of trunk (about one-fourth the total length of the fish) very closely behind the shoulder girdle. Antoperculum much shorter than anterior margin of operculum. Anterior thin lamina of hyomandibula rather narrow. Number of branchiostegal rays eight. Anterior and posterior median gular plates, the posterior one pointed posteriorly. Ornament of external dermal bones of head highly variable. Between posterior margin of

supracleithral and inversion line in caudal region 42–43 transverse scale-rows; from posterior margin of supracleithral to anterior margin of pelvic fin about 13, to anterior margin of dorsal fin 19–21, and to anterior margin of anal fin 25–29 rows. Number of lepidotrichia in pelvic fin from 16 to 20, in dorsal fin 24–27, in anal fin 17-18. Proximal segments of lepidotrichia of pectoral fin partially fused. Scales ornamented with coarser or finer, nearly diagonal striae, anterior ends of ventral striae often curved upward, moreover often a narrow or broad anterior zone of exposed face of scales ornamented with oblong ganoine tubercles.

Holotype. – As holotype I have chosen specimen No. 201, which is a fairly complete fish, lacking only the extreme distal parts of the dorsal and ventral lobes of the caudal fin. The head and the paired fins are rather poorly preserved. Length of preserved part of the specimen 215 mm, estimated length of the complete fish about 220 mm. Height of trunk at anterior margin of anal fin 31 mm, at anterior margin of pelvic fin 50 mm, largest height of trunk 55 mm. Distance from anterior margin of base of pectoral fin to anterior margin of base of pelvic fin about 53 mm. Distance from anterior margin of base of pelvic fin to anterior margin of base of anal fin about 42 mm, distance from anterior margin of base of anal fin to anterior margin of base of ventral lobe of caudal fin 33 mm, distance from posterior margin of medial extrascapular to anterior margin of base of dorsal fin about 52 mm.

Material. – In addition to Stensiö's specimen (Stensiö's No. 17) the material derived from Fish-zone II comprises specimens Nos. 201 (holotype), 202–255, 257–276, 311, 312, 315, 316, 319–322, 325, 326, 328–332, and 334–337; from Fish-zone III specimens Nos. 256, 290, and 324; from Fish-zone IV specimen No. 294; from Fish-zone V specimens Nos. 277–289, 291, 292, 293, 295–309, 310 (the sectioned specimen), 314, 317, 318, 323, 327, 333, and 338.

Localities. – The Kap Stosch area and the Hird Bay area.

Remarks. – *Boreosomus arcticus* and *Boreosomus reuterskiöldi* are so imperfectly known that only a very few comparisons can be drawn between these species and *Boreosomus piveteaui*. In *Boreosomus arcticus* the ectopterygoid and the entopterygoid have different shapes (cf. Stensiö 1921, Fig. 70) from those in *Boreosomus piveteaui*, and moreover the hyomandibula in *Boreosomus arcticus* has a very broad anterior lamina. *Boreosomus reuterskiöldi* seems only to differ from *Boreosomus piveteaui* by having four or five branchiostegal rays (Stensiö 1921, p. 216).

As distinguishing characters between *Boreosomus piveteaui* and *Boreosomus gillioti* I may mention that in the former the length of the antoperculum is more than half the length of the anterior margin of the operculum and the posterior gular plate is pointed posteriorly, while the latter has a shorter antoperculum and a posteriorly rounded posterior gular plate (cf. Brough 1933, Fig 1; 1939, Figs. 44 A and B).

Remarks on other Species of Boreosomus.

a. Boreosomus arcticus (A. S. Woodward) and Boreosomus reuterskiöldi Stensiö.

These two species from the Lower Triassic of Spitsbergen is described by Stensiö (1921, pp. 211–19) in as great detail as his very incomplete material allowed. In the same paper (pp. 219–22) Stensiö describes some fish fragments under the designations *Boreosomus ? scaber* and *Boreosomus* sp. From the Triassic of Lorraine Corroy (1928, p. 20, Pl. II, Fig. 9) describes and figures a scale under the designation *Boreosomus cf. reuterskiöldi* Stensiö. Both Stensiö (1932, p. 117) and Aldinger (1937, p. 277) express some doubt as to the reliability of this identification. The Spitsbergen species differ from each other principally in the ornament of their scales, a character as to whose applicability I have expressed some doubt above (p. 373). *Boreosomus reuterskiöldi* differs from *Boreosomus gillioti* by having four or five branchiostegal rays and in that its posterior medial gular plate is pointed posteriorly. On the basis of our present imperfect knowledge, however, it is impossible to mention other points of difference between *Boreosomus arcticus* and *Boreosomus piveteaui* than those found in the ornamentation of the dermal bones and of the scales.

b. Boreosomus gillioti (Priem).

The most complete description of this species, which occurs in the Eotriassic of Madagascar, has been given by Brough (1933, pp. 78–87, Figs. 1, 2; 1939, Fig. 44 A and B). On a specimen of *Boreosomus gillioti* at my disposal the preoperculum is not, as in Brough's restoration, divided into a small dorsal and a larger ventral bone. The postorbital part of the infraorbital series is not indicated in Brough's restoration, which, as already assumed by Aldinger (1937, p. 280), must be due to the unsatisfactory state of preservation of Brough's material. The jugal (denoted by Brough by the misleading term »supramaxillary«), the lacrimal, and the rostroantorbito-premaxillary, in contrast to what appears from Brough's restoration, no doubt had the same mutual relations as in *Glaucolepis piveteaui*.

Piveteau's restoration of the dermal cranial roof in *Boreosomus gillioti* (Piveteau 1934, Fig. 56) differs in several respects from that published by Brough. On the basis of my material I am unable to decide which of the two restorations is the more correct; however, as regards the relations of the suprascapular, the extrascapular series, and the supratemporo-intertemporal Brough's restoration agrees most closely with *Boreosomus piveteaui*. The conjecture put forward by Piveteau (1934, p. 87), that the antoperculum lodges a branch of the preopercular canal, was received by Aldinger (1937 p. 280) with justifiable doubt.

REMARKS ON THE RELATIONSHIP BETWEEN BOREOSOMUS AND THE OTHER GENERA OF THE FAMILY ACROLEPIDAE ALDINGER

Aldinger (1937, pp. 252–53) refers a large number of Palaeonisciform genera, whose interrelationship appears mainly from the structure of their scales, to the family *Acrolepidae*. According to Aldinger (1937, p. 302), this family is so closely related to the family *Elonichthyidae* Aldinger, judging from the structure of the scales, that quite probably the two families had common ancestors in the Middle or Upper Devonian.

According to Aldinger, several lines of evolution occur within the *Acrolepidae*, but of these we shall only consider that on which he places *Boreosomus*. Aldinger (1937, p. 300) writes as follows about this line: "Unter den triassischen Genera stellen *Boreosomus* (Ältere Trias) und *Ptycholepis* (Mittlere Trias bis Oberer Lias) eine Entwickelungsreihe vor, auf Grund der Schuppenskulptur ist man versucht folgende Artreihe aufzustellen: *Boreosomus reuterskiöldi* (oder *scaber*) – *Ptycholepis barboi* (Mitteltrias) – *Ptycholepis monilifer* (Unterer Lias) – *Ptycholepis bollensis* (Oberer Lias) – *Acrorhabdus* (Eotrias) ist wohl ein blind endigender Seitenzweig, wenn nicht *Urolepis* (Mittlere Trias) darauf beziehbar ist." According to Aldinger, the connecting links between the *Boreosomus-Ptycholepis* line and the earlier *Acrolepidae* must be supposed to be small Permian forms, so far unknown, resembling "*Elonichthys*" *aitkeni* (which species Aldinger is inclined to regard as an Acrolepid) in external habitus. For *Boreosomus* and *Acrorhabdus* are small forms with a specialised branchiostegal skeleton, while all the known Permian *Acrolepidae* are large forms with a normal branchiostegal skeleton.

At nearly the same time, and independently of Aldinger, Brough (1939, pp. 98–104) drew similar conclusions as to the relationship between *Boreosomus* and *Ptycholepis*, but instead of, like Aldinger, placing *Ptycholepis* in the same family as *Boreosomus*, Brough erected the family *Ptycholepidae*, which he placed in his order *Subholostei*. In his comparison between *Boreosomus* and *Ptycholepis* Aldinger (1937, p. 304) emphasised that within the *Boreosomus-Ptycholepis* line a development has taken place towards the *Holostei*, even though that line became extinct before reaching

the Holosteid stage. Thus Aldinger and Brough give the same picture of the *Boreosomus-Ptycholepis* line, even though Aldinger places the line entirely within the Acrolepid family, while Brough regards it as extending beyond the limits of this family. It must, of course, always be a matter of judgment where to let a family limit intersect a line of evolution; however, in my opinion the agreement between *Boreosomus* and *Ptycholepis* is so great that I do not think it necessary to place *Ptycholepis* outside the limits of the Acrolepid family.

The more intimate knowledge of *Boreosomus* acquired by the investigation of the Greenland material cannot be employed for the present in a more detailed comparison between this genus and *Ptycholepis*, our knowledge of *Ptycholepis* not having been correspondingly increased. It should be pointed out, however, that the neural endocranium in *Boreosomus* presents no typical Holosteid characters (perhaps apart from the slight development of the processus basipterygius), but is on the whole of the same primitive type as the Carboniferous endocrania of the *Palaeonisciformes* from Kansas, of which the most detailed descriptions have been given by Moodie (1915) and Watson (1925 and 1928). As regards for instance the aorta canal and the relations of the dorsal cranial fontanelles, the cranium of *Boreosomus* shows a closer agreement with these Carboniferous endocrania than the cranium of *Glaucolepis*, whose type seems on the whole to be more related to the primitive Holosteid type known from forms such as *Ospia* and *Broughia* (Stensiö 1932).

Very little can be stated about the relationship between *Acrorhabdus* and *Boreosomus*, *Acrorhabdus* being very unsatisfactorily known. According to Stensiö (1921, pp. 222–38), *Acrorhabdus* differs from *Boreosomus* in the ornament of its dermal bones and scales, in its more intensely segmented pectoral fin, and in the shape of various dermal bones of the head (the preoperculum and the dermal bones of the palatoquadrate).

As stated on p. 365, too much importance should not be attached to the segmentation of the pectoral fin as a distinguishing character between the two genera, for *Boreosomus piveteaui* presents intermediate conditions in this respect. Of other distinguishing characters, the ornament of the scales is no doubt the most important, the numerous fine short striae inserted between the posterior ends of the longer striae, which are characteristic of *Acrorhabdus*, not having been observed in any species of *Boreosomus*. Whether this character alone justifies the maintenance of the genus *Acrorhabdus*, is perhaps doubtful when it is borne in mind that several species of *Boreosomus* differ rather much in the ornamentation of their scales.

SUMMARY AND CONCLUSIONS

In the very large material of Eotriassic fishes collected in East Greenland in the years 1932–33 and 1936–37 *Glaucolepis* is represented by five species (*Glaucolepis arctica* Stensiö, *Gl. aldingeri* n.sp., *Gl. gunnari*, n.sp., *Gl. magna* n.sp., and *Gl. stensiöi* n.sp.) and *Boreosomus* by one species (*Boreosomus piveteaui* n.sp.). These species have been made the subject of detailed palaeoanatomical investigations, whose most important special and general results are as follows:

1) In the neural endocranium of *Glaucolepis* the process of ossification set in relatively late in the the life of the animal with the development of a large number of small ossifications, paired as well as unpaired. With increasing age the process of ossification advanced by a gradual increase in the extent of the areas first ossified, which areas finally fused in such a high degree that in the oldest individuals the neural endocranium consists of only two unpaired ossifications, an anterior one, occupying the ethmoidal region, the orbitotemporal region, and the greater part of the otic region, and a posterior one, occupying the remaining part of the otic region and the whole occipital region. These two ossifications show no trace of having been formed by the fusion of smaller ossifications.

In young individuals of *Boreosomus* the neural endocranium is unossified, while in older individuals it is completely ossified, consisting of one large unpaired ossification. How the process of ossification is initiated, is unknown, since the intermediate stages could not be investigated in detail.

There is reason to assume that in the majority of the primitive *Chondrostei* (*Palaeonisciformes*) the ossification proceeded in practically the same way as in *Glaucolepis*.

2) The ossification of the palatoquadrate in *Glaucolepis* proceeded like that of the neural endocranium, for at intermediate stages the palatoquadrate, which in young individuals is entirely unossified and in the oldest individuals is completely ossified and consists of one ossification, contains two or three small ossifications.

In *Boreosomus* the process of ossification of the palatoquadrate was as in *Glaucolepis*.

In the most primitive *Palaeonisciformes* and in other primitive *Chondrostei* the ossification of the palatoquadrate took place in the same way as in *Glaucolepis* and *Boreosomus*.

3) Both in *Glaucolepis* and in *Boreosomus* the Meckelian cartilage, the branchial arches, the basibranchial series, the axial skeleton, the endoskeleton of the shoulder girdle, the pelvic plate, and the endoskeletons of the fins are more completely ossified in older than in younger individuals.

4) A long fissura occipitalis lateralis and a vestibular fontanelle connected with this fissure separate the dorsal parts of the anterior and of the posterior

unpaired ossification in the wholly ossified neural endocranium of *Glaucolepis*. That part of the fissura occipitalis lateralis which extends through the dorsal wall of the endocranium expands so as to form the so-called posterior dorsal fontanelle. The fissura occipitalis lateralis and the dorsal part of the vestibular fontanelle were not completely closed by cartilage in the living animal.

A fissura occipitalis lateralis and a vestibular fontanelle are present in *Boreosomus*, too. That part of the fissure in this form which extends through the dorsal wall of the endocranium in some cases expands so as to form a small posterior dorsal fontanelle, but in other cases it is not broader than the lateral part of the fissure and may even be entirely closed for a short stretch.

A long open occipital fissure is found in all the *Palaeonisciformes* whose endocranial structure is known. Within the lines of development from the *Palaeonisciformes* towards the *Holostei*, the fissura occipitalis lateralis and the vestibular fontanelle gradually became more and more closed. In recent *Chondrostei* and higher Actinopterygians an open fissura occipitalis lateralis can only be observed in early embryonic stages.

5) In *Boreosomus* that part of the roof of the endocranium which lies dorsally to the division of the cavum cerebrale cranii that lodged the diencephalon, is pierced by a small anterior dorsal fontanelle. Through this fontanelle the epiphyseal stalk probably passed. In *Glaucolepis* a considerable part of the roofs of the otic and orbitotemporal regions is unossified, so the fossil endocrania have a very large anterior dorsal fontanelle. The size and exact position of the dorsal fontanelle in the living *Glaucolepis* cannot be determined, but it is possible that it was not very much larger than the dorsal fontanelle in *Boreosomus* and that it had a similar position in relation to the diencephalon.

Since an anterior dorsal fontanelle developed as in *Boreosomus* is found, also, in the Carboniferous *Palaeonisciformes* whose endocranial structure has been investigated, the presence of such a fontanelle must be regarded as a very primitive structural feature within the group of Actinopterygians.

6) *Glaucolepis* has a large fossa bridgei, consisting of deep anterior and posterior divisions and a shallow middle division. At the bottom of the anterior division opens the vertical spiracular canal, and the posterior deep division communicates with the cavum cerebrale cranii by a very large opening through that part of the cranial wall which contains the division of the labyrinth cavity that lodged the canalis semicircularis posterior.

Boreosomus, too, has a large fossa bridgei, but it corresponds only to the deep anterior division, the shallow middle division, and the dorsal part of the deep posterior division of the fossa bridgei in *Glaucolepis*. The part of the posterior deep division of the fossa bridgei in *Glaucolepis* is represented, in *Boreosomus*, by an intramural space, which is separated from the fossa

bridgei and which in a similar way as the corresponding part of the fossa bridgei in *Glaucolepis* is in communication with the cavum cerebrale cranii. Both in *Glaucolepis* and *Boreosomus* the fossa bridgei is entirely closed dorsally by the dermal cranial roof and cannot, therefore, have lodged the anterior part of the trunk musculature.

The fossa bridgei, which is always present in the *Chondrostei*, is largest in the most primitive forms. The wide communication between the fossa bridgei (or between an intramural space ventrally to the fossa bridgei) and the cavum cerebrale cranii seems to be a normal feature in the *Chondrostei* and is preserved in various higher Actinopterygians, too. In *Polyodon* this communication is developed wholly as in *Glaucolepis*, while in *Acipenser* it is much reduced.

7) *Glaucolepis* has a trigemino-facialis chamber of the same extent as in the Carboniferous *Palaeonisciformes* and in *Saurichthys*. From the orbital face of the orbitotemporal region immediately in front of the chamber issues in some cases a more or less well developed process, which may best be compared to the alisphenoid pedicle in *Amia*.

In *Boreosomus* a trigemino-facialis chamber of the same type as that in *Glaucolepis* is found, except that it has a slightly greater forward extent.

8) Both *Glaucolepis* and *Boreosomus* possess an unpaired posterior myodome, consisting of a spinal and a prespinal division for the musculus externus rectus, and a dorsal and a ventral paired (*Glaucolepis*) or unpaired (*Boreosomus*) anterior myodome for the musculus obliquus superior and the musculus obliquus inferior respectively. The roof of the posterior myodome is pierced by a pituitary fontanelle, and its floor, at any rate in *Glaucolepis*, by a fenestra ventralis myodomus. In *Glaucolepis* the hypophysis was quite probably situated in the anterior part of the posterior myodome. In *Boreosomus* the nervus olfactorius passed through the anterior dorsal myodome.

A posterior paired (*Birgeria*) or unpaired myodome is present in all the *Palaeonisciformes* whose endocranial structures are known, and the early occurrence of this structure must be associated with the relatively large size of the eyes in the primitive *Chondrostei*. Probably the anterior myodomes developed just as early within the Actinopterygians as the posterior one, though neither the ethmoidal region nor the anterior part of the orbitotemporal region have been investigated in such great detail in the Palaeozoic *Palaeonisciformes* that the presence of the anterior myodomes has been established.

9) Both *Glaucolepis* and *Boreosomus* have an aorta canal which extends through the occipital region and a large part of the otic region. In *Boreosomus* the aorta canal is unpaired throughout, or almost throughout, its whole length, while in *Glaucolepis* it is unpaired in its posterior and paired in its anterior part.

A long aorta canal of the same type as that of *Boreosomus* is found in Carboniferous *Palaeonisciformes*. Within the evolutionary lines leading towards the *Holostei* the aorta canal is gradually reduced from its anterior towards its posterior end. In primitive *Holostei* the aorta canal extends only through the occipital region, and the aorta divided immediately in front of the anterior opening of the canal, that is to say, in a place corresponding to the place of division of the aorta in *Glaucolepis*. It is probable, therefore, that forms such as *Ospia* and *Broughia* are derived from *Chondrostei* whose aorta canal was of the same type as that of *Glaucolepis*.

10) A very well developed processus basipterygius occurs in *Glaucolepis*, and a very poorly developed one in *Boreosomus*.

11) Both in *Glaucolepis* and in *Boreosomus* the ethmoidal region is very short and is chiefly made up of a transverse bone wall, the planum antorbitale, which forms the anterior boundary of the orbit. In *Glaucolepis* the septum nasi is only ossified in its most posterior part, and the nasal pits are very shallow depressions on the anterior face of the ethmoidal region. In *Boreosomus* the ossified septum nasi has a greater forward extent, and the nasal pits are fairly deep depressions on the anterior face of the region. In *Boreosomus* a large depression is found on the anterior face of the ethmoidal region ventrally to each of the nasal pits.

12) Both in *Glaucolepis* and in *Boreosomus*, as normally in primitive Actinopterygians, the cavum cerebrale cranii was entirely, or almost entirely, occupied by the brain. The shape and relative proportions of the individual divisions of the brain were almost as in the few Carboniferous *Palaeonisciformes* investigated. That part of the myelencephalon which lay medially to the wide opening in the cranial wall connecting the cavum cerebrale cranii with the posterior deep part of the fossa bridgei (*Glaucolepis*) or with the closed space in the cranial wall corresponding to this part of the fossa bridgei (*Boreosomus*) had an unpaired or paired swelling which must be supposed to have had some relation to the nerve, or nerves, which passed out through the opening.

As regards the course of the canals for the cranial nerves, *Boreosomus* and *Glaucolepis* agree in their main features with the few earlier *Palaeonisciformes* whose endocranial structures are known.

The labyrinth cavity differs only in a few details from that of the Carboniferous *Palaeonisciformes* and other primitive *Chondrostei*. Remains of otoliths have been observed in *Glaucolepis*.

13) The parasphenoid in *Glaucolepis* has two well developed, paired, mutually connected processes, the processus ascendens anterior and the processus ascendens posterior. The processus ascendens anterior rests against the processus basipterygius, while the processus ascendens posterior lies against the lateral face of the otic region and extends dorsally through the spiracular

canal up into the fossa bridgei, where it attains contact with a ventral lamina of the supratemporo-intertemporal.

In *Boreosomus*, too, the parasphenoid has paired processus ascendentes. The processus ascendens anterior, which rests against the processus basipterygius, is very much reduced. The processus ascendens posterior, which lies against the lateral face of the endocranium, dorsally reaches only the ventral opening of the spiracular canal.

In *Glaucolepis* the posterior part of the corpus of the parasphenoid rests against the ventral face of the endocranium and is pierced by a short paired longitudinal canal for the arteria carotis interna.

In *Boreosomus* a large space, through which the arteria carotis interna passed, lies between the posterior part of the corpus of the parasphenoid and the ventral face of the endocranium.

The processus ascendens of the parasphenoid in recent *Chondrostei*, *Holostei*, and *Teleostei* corresponds fairly well to the processus ascendens posterior in the *Palaeonisciformes* and other primitive Actinopterygians.

14) *Glaucolepis* has a large paired (?) vomer, which is not firmly connected either with the parasphenoid or with the neural endocranium. *Boreosomus* probably has a small paired vomer, which is firmly connected both with the parasphenoid and with the neural endocranium.

15) In *Glaucolepis* the dermal bones of the head overlap each other to a considerable extent, thus for instance the posterior part of the frontal overlaps the anterior third of the parietal, and the maxillary covers almost the whole quadratojugal. In *Boreosomus* the dermal bones of the head overlap each other to a less extent than in *Glaucolepis*. In several other *Palaeonisciformes* (as also in higher Actinopterygians) the dermal bones of the head overlap each other to a greater or smaller extent, a fact which should be pointed out i. a. for the reason that for instance the dermal cranial roof in such forms has quite a different sutural pattern when viewed from the ventral side than when it is viewed from the dorsal side, a point often not sufficiently considered when restorations are made. The overlapped parts of the dermal bones are very thin, and there are grounds for assuming that in the course of development they have been increasingly reduced, the overlapping bones having replaced the overlapped ones to a greater or smaller extent. Thus the absence of a separate quadratojugal, for instance in *Boreosomus*, can be explained by its complete reduction owing to the overlapping of the maxillary, and not necessarily by its fusion with the maxillary.

16) In *Glaucolepis* the elements of the dermal cranial roof are roughly arranged according to the usual Palaeoniscid pattern, and in *Boreosomus* in broad features according to the usual Acrolepid pattern. In both genera the dermosphenotic is fused with a medial supraorbital series, and laterally to this supraorbito-dermosphenotic lies a bone which must be regarded as a postorbital fused with a lateral supraorbital series. In *Glaucolepis* a well developed

lamina issues in a ventral direction from the ventral side of the supratemporo-intertemporal.

17) In *Glaucolepis* the infraorbital series comprises a postorbital, a jugal, a lacrimo-maxillary, and a rostro-antorbital. The last-mentioned bone is only loosely connected with the nasal and the postrostral. An independent premaxillary is probably present.

In *Boreosomus* the infraorbital series comprises a very slender tube-shaped postorbital, a small jugal, whose dorsal part is a slender tube-shaped process, a lacrimal, and a rostro-antorbito-premaxillary.

18) Both in *Glaucolepis* and in *Boreosomus* an entopterygoid, an ectopterygoid, and two dermopalatines are found on the oral face of the palatoquadrate, and in *Glaucolepis* one more dermal bone, viz. the dermometapterygoid, which seems to correspond to the so-called metapterygoid in *Polypterus*.

An examination of previously described *Palaeonisciformes* shows that a dermometapterygoid is present in many cases.

19) In *Glaucolepis* the preoperculum, from whose medial side issues a well developed internal lamina, the maxillary, the lacrimo-maxillary, the quadratojugal, the palatoquadrate, and the dermal bones of the latter are connected with each other so as to form the so-called palatoquadrate-maxillary apparatus, which enclosed the musculus adductor mandibulae.

In *Boreosomus* the maxillary, the palatoquadrate, and the dermal bones of the latter are connected to form a palatoquadrate-maxillary apparatus; but since the preoperculum has no connection with the palatoquadrate, the space for the musculus adductor mandibulae is not closed dorsally.

Both in *Glaucolepis* and in *Boreosomus* the palatoquadrate was connected with the endocranium by a palato-basal and an ethmo-palatine articulation.

20) In *Glaucolepis* the Meckelian cartilage contains a posterior and an anterior ossification, of which the latter seems to include a dermal component. In *Boreosomus* the whole Meckelian cartilage is ossified in one piece.

21) Both in *Glaucolepis* and in *Boreosomus* the hyoid arch includes a hyomandibula, a symplectic, one or two ceratohyal ossifications, and a hypohyal. The hyomandibula plays an important part in the suspension of the palatoquadrate. In *Glaucolepis* the symplectic is a robust ossification, which articulated both with the palatoquadrate and with the Meckelian cartilage. In *Boreosomus* the symplectic ossification is small and has no contact with the mandibular arch.

22) In *Glaucolepis* a dermohyal is found in intimate connection with the dorsal part of the hyomandibula. In *Boreosomus* no dermohyal is found. So far our knowledge of the occurrence of the dermohyal within the group *Palaeonisciformes* is very incomplete; it seems certain, however, that the dermohyal is most highly developed in the most primitive members of the group.

23) The ossifications of the branchial arches and the basibranchial series could be investigated fairly closely in *Glaucolepis*. Five branchial arches are present, of which the anterior two had a double articulation with the neural endocranium plus the parasphenoid, precisely as in *Acipenser*.

The suprapharyngobranchials I and II are most well developed in the most primitive Actinopterygians and show a more or less complete reduction within the lines of evolution that lead towards the higher forms.

24) Both in *Glaucolepis* and in *Boreosomus* the sensory canal system of the head is of the usual *Palaeonisciformes* type. On the cranial roof an anterior, a middle, and a posterior pit-line are found. In *Glaucolepis* traces of the horizontal pit-line of the cheek are found on the preoperculum and the maxillary, while vestiges of the vertical pit-line are present on the quadratojugal. In *Boreosomus* traces of both the vertical and the horizontal pit-line of the cheek occur on the preoperculum. In *Glaucolepis* a short pit-line is found on the anterior branchiostegal ray. Various pit-lines, both in *Glaucolepis* and in *Boreosomus*, may be more or less closed to form narrow canals.

In primitive Actinopterygians the sensory canal branches of the head always pass through the radiation centres of the canal-bearing bones, and if a canal-bearing bone is equipped with an internal lamina, the canal pierces precisely that part of the bone from which the lamina issues. The individual pit-lines issue either from a radiation centre or from a point on the outer face of a bone directly outside a radiation centre.

25) The axial skeleton in *Glaucolepis* shows a very considerable agreement with that in *Acipenser*. In a single case ossified ribs have been observed.

26) The endoskeletal shoulder girdle in *Glaucolepis* has a well developed mesocoracoid arch, two openings for diazonal nerves, a processus glenoidalis, and a processus radialis. Between the cleithrum and the endoskeletal shoulder girdle is a space for the ventral fin musculature, which space opens anteriorly with a fenestra coraco-cleithralis. The margo radialis is almost horizontal. In *Boreosomus* the endoskeletal shoulder girdle has a vigorous, but partially unossified mesocoracoid arch, one opening for diazonal nerves, and a processus glenoidalis. No fenestra coraco-cleithralis is present. The margo radialis is almost vertical.

It is probable that the endoskeletal shoulder girdle in the group *Palaeonisciformes* was always equipped with a well developed mesocoracoid arch, and that the absence of such an arch in various higher Actinopterygians is due to reduction.

27) In *Glaucolepis* and *Boreosomus* the endoskeleton of the pectoral fin contains a proximal and a distal series of radial ossifications. In *Glaucolepis* an equal number of ossifications is found in the proximal and in the distal series, and the radials of the fin were parallel. In *Boreosomus* the number of distal radial ossifications exceeds that of the proximal ones, and the posterior radial was developed as a metapterygial axis.

The pectoral fin is placed horizontally in *Glaucolepis* and vertically in *Boreosomus*.

28) A large pelvic plate occurs both in *Glaucolepis* and in *Boreosomus*. Remains of metapterygial elements are found in *Glaucolepis*.

29) In *Glaucolepis* the endoskeleton of the pelvic fin has a proximal series of radial ossifications, while in *Boreosomus* it has both a proximal and a distal series.

30) Both in *Glaucolepis* and in *Boreosomus* the endoskeleton of the dorsal fin contains an axonost series, a baseost series, and a series of distal radial ossifications. In *Glaucolepis* the posterior elements of the axonost series are fused so as to form an axonost plate, and in *Boreosomus* the anterior elements of the baseost series are fused so as to form a baseost plate.

In *Glaucolepis* the endoskeleton of the anal fin contains a proximal and a distal series of radial ossifications.

Both in *Glaucolepis* and in *Boreosomus* the endoskeleton of the caudal fin contains epichordal and occasionally in addition hypochordal radial ossifications.

Thus both *Glaucolepis* and *Boreosomus* show good agreement with recent *Chondrostei* in regard to the endoskeleton of the unpaired fins.

31) Nothing seems to prevent us from regarding *Glaucolepis* as a direct descendent of *Palaeoniscus*; but *Glaucolepis* lies on another line of evolution than that leading from *Palaeoniscus* to the youngest Palaeoniscid genera.

There is much to suggest that the families *Palaeoniscidae* and *Pygopteridae* are very closely related.

32) The investigation of *Boreosomus* throws no new light on the lines of evolution within the family *Acrolepidae*, for our knowledge of the other Acrolepid genera is so inconsiderable that any detailed comparison is excluded. It would seem that the difference between *Boreosomus* and *Acrorhabdus* is less than was previously assumed.

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Plate 1.

Glaucolepis stensiöi n. sp.

The head used for serial sectioning in lateral view. Most of the dermal bones, the palatoquadrate, and the posterior ossification in the Meckelian cartilage preserved as impressions of their internal faces. Specimen No. 39 (same specimen as shown in Pls. 2, 3, 4, and Pl. 8, Fig. 3). 5 ×.

De.spl, dentalo-splenial; *Dmptg*, dermometapterygoid; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Fr*, frontal; *Hm*, hyomandibula; *Ju*, jugal; *La.mx*, lacrimo-maxillary; *Mk*, posterior ossification in the Meckelian cartilage; *Mx*, maxillary; *Na*, nasal; *Op*, operculum; *Pa*, parietal; *Po*, postorbital; *Pop*, preoperculum; *Pq*, dorsal part of the palatoquadrate; *Pr.art*, preaiticular; *Pspic*, postspiracular bone; *Ptr*, postrostral; *R.ant*, rostroantorbital; *Sbo*, suborbitals; *Scl*, supracleithral; *Sclr*, segment of the sclerotic ring; *Sop*, suboperculum; *Sscap*, suprascapular; *am.ant*, *am.ext*, *am.post*, divisions of the labyrinth cavity for the ampulla anterior, the ampulla externa and the ampulla posterior respectively; *c.sem.ext*, division of the labyrinth cavity for the canalis semicircularis externus; *fo*, opening in the wall between the fossa bridgei and the cavum cerebrale cranii; *f.occ.lat*, fissura occipitalis lateralis; $font_2$, posterior dorsal fontanelle; *ifc*, infraorbital canal; na_1, na_2, anterior and posterior nostrils; *p.Op*, series of small depressions on the medial faces of the operculum and suboperculum; *s.pq*, groove on the medial face of the palatoquadrate; *s. us*, division of the labyrinth cavity for the sinus utriculi superior.



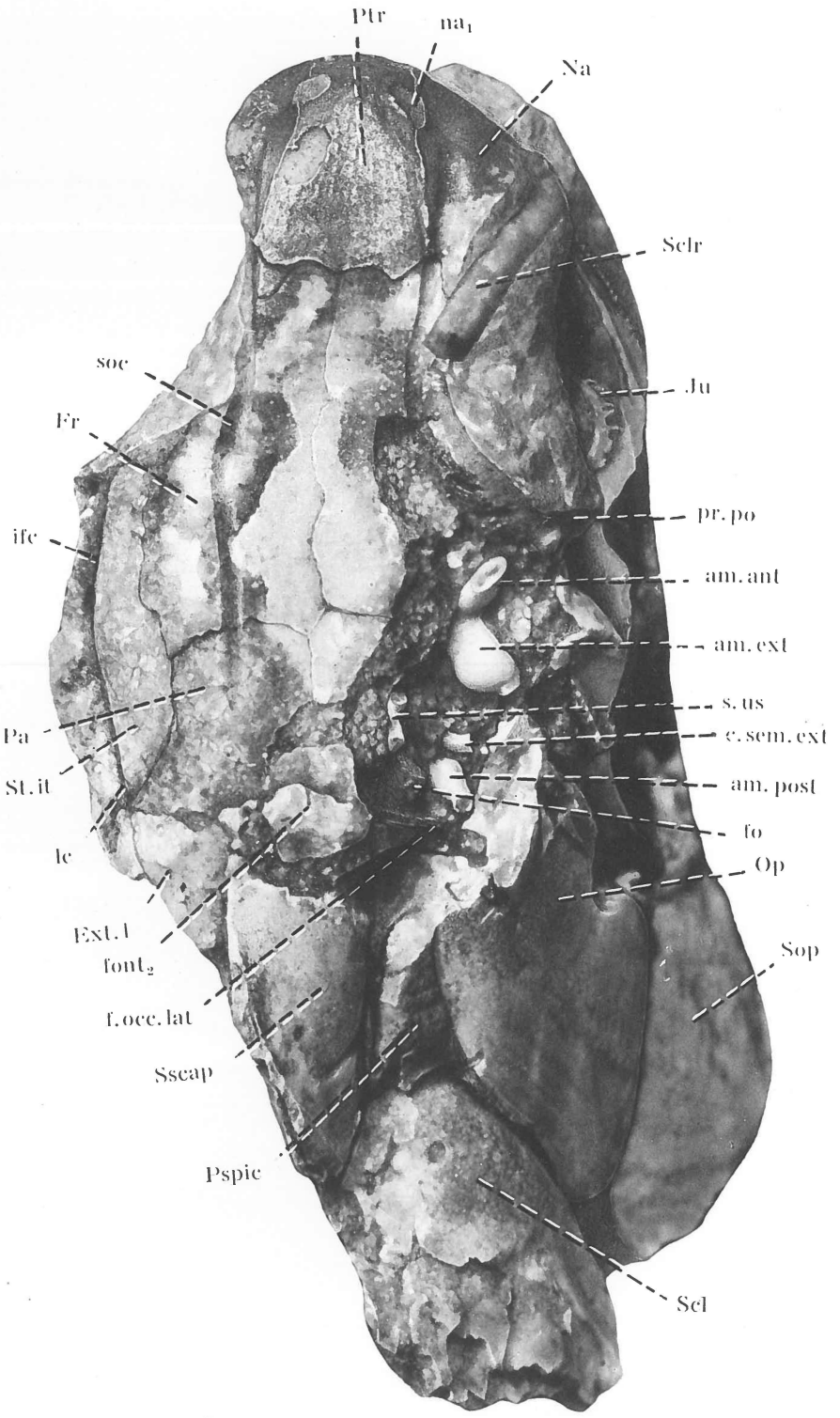
Nordisk Kunst- og Lystryk

Plate 2.

Glaucolepis stensiöi n. sp.

Head in dorsal view. The dermal bones preserved as impressions of their internal faces. Specimen No. 39 (same specimen as shown in Pls. 1, 3, 4, and Pl. 8, Fig. 3). 5 ×.

Ext. l, lateral extrascapular; *Fr*, frontal; *Ju*, jugal; *Na*, nasal; *Pa*, parietal; *Pspic*, postspiracular bone; *Ptr*, postrostral; *Op*, operculum; *Scl*, supracleithral; *Sclr*, segment of the sclerotic ring; *Sop*, suboperculum; *Sscap*, suprascapular; *St. it*, supratemporo-intertemporal; *am. ant*, *am. ext*, *am. post*, divisions of the labyrinth cavity for the ampulla anterior, the ampulla externa and the ampulla posterior respectively; *c. sem. ext*, division of the labyrinth cavity for the canalis semicircularis externus; *fo*, opening in the wall between the fossa bridgei and the cavum cerebrale cranii; *f. occ. lat*, fissura occipitalis lateralis; $font_2$, posterior dorsal fontanelle; *ifc*, infraorbital canal; *lc*, postotic canal; na_1, anterior nostril; *pr. po*, processus postorbitalis; *soc*, supraorbital canal; *s. us*, division of the labyrinth cavity for the sinus utriculi superior.



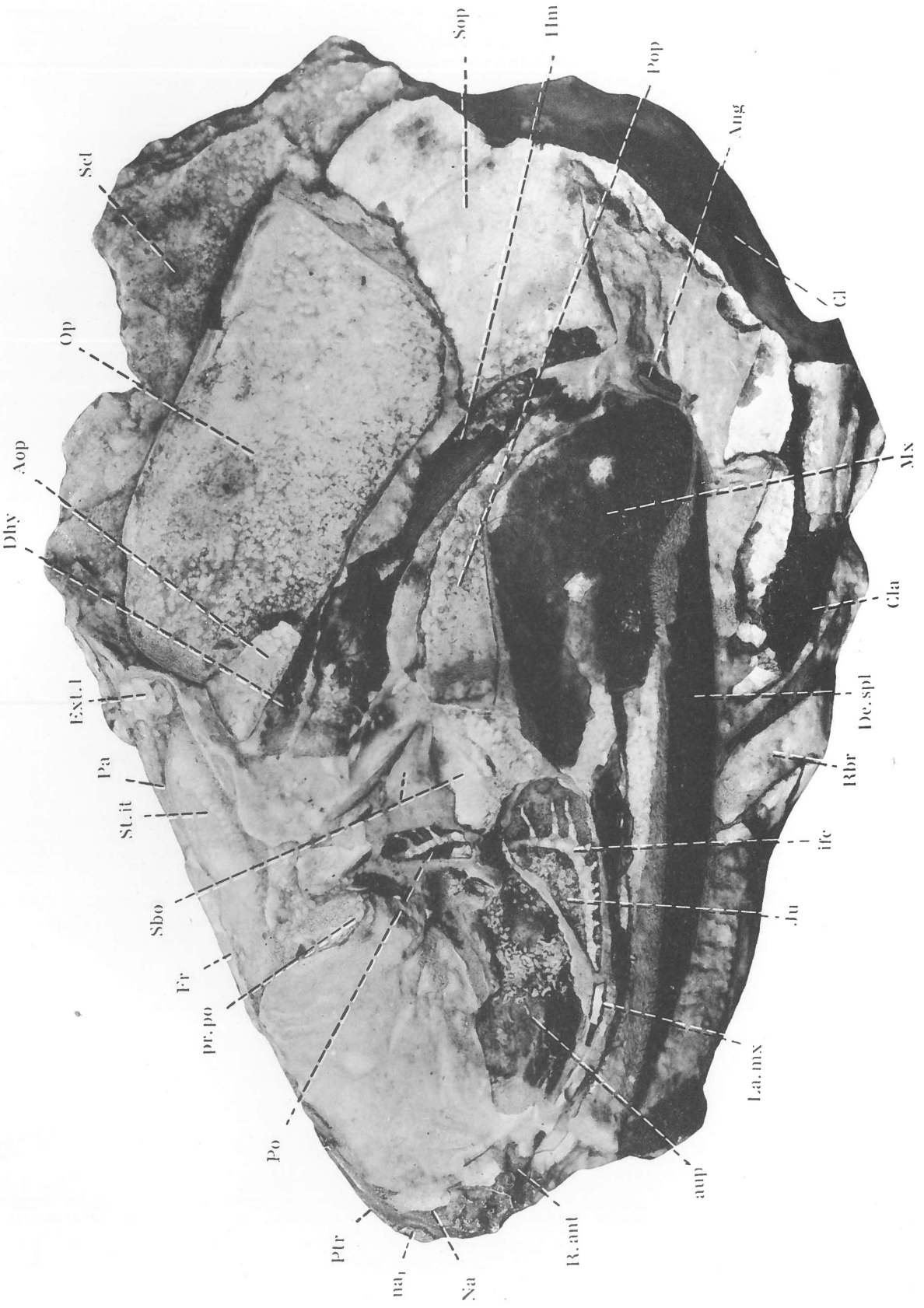
Nordisk Kunst- og Lystryk

Plate 3.

Glaucolepis stensiöi n. sp.

Head in lateral view. Many of the dermal bones preserved as impressions of their internal faces. Specimen No. 39 (same specimen as shown in Pls. 1, 2, 4, and Pl. 8, Fig. 3). 5 ×.

Ang, angular; *Aop*, antoperculum; *Cl*, cleithrum; *Cla*, clavicle; *De.spl*, dentalo-splenial; *Dhy*, dermohyal; *Ext.l*, lateral extrascapular; *Fr*, frontal; *Hm*, hyomandibula; *Ju*, jugal; *La.mx*, lacrimo-maxillary; *Mx*, maxillary; *Na*, nasal; *Op*, operculum; *Pa*, parietal; *Po*, postorbital; *Pop*, preoperculum; *Ptr*, postrostral; *R.ant*, rostro-antorbital; *Rbr*, branchiostegal ray; *Sbo*, suborbitals; *Scl*, supracleithral; *Sop*, suboperculum; *St.it*, supratemporo-intertemporal; *aup*, pars autopalatina; *ifc*, infraorbital canal; na_1, anterior nostril; *pr.po*, processus postorbitalis.



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Plate 4.

Glaucolepis stensiöi n. sp.

Head in ventro-lateral view. Specimen No. 39 (same specimen as shown in Pls. 1, 2, 3, and Pl. 8, Fig. 3). 5 ×.

mdc, antero-ventral part of the dentalo-splenial containing a series of tubuli from the mandibular canal. Other letters as in Pl. 3.

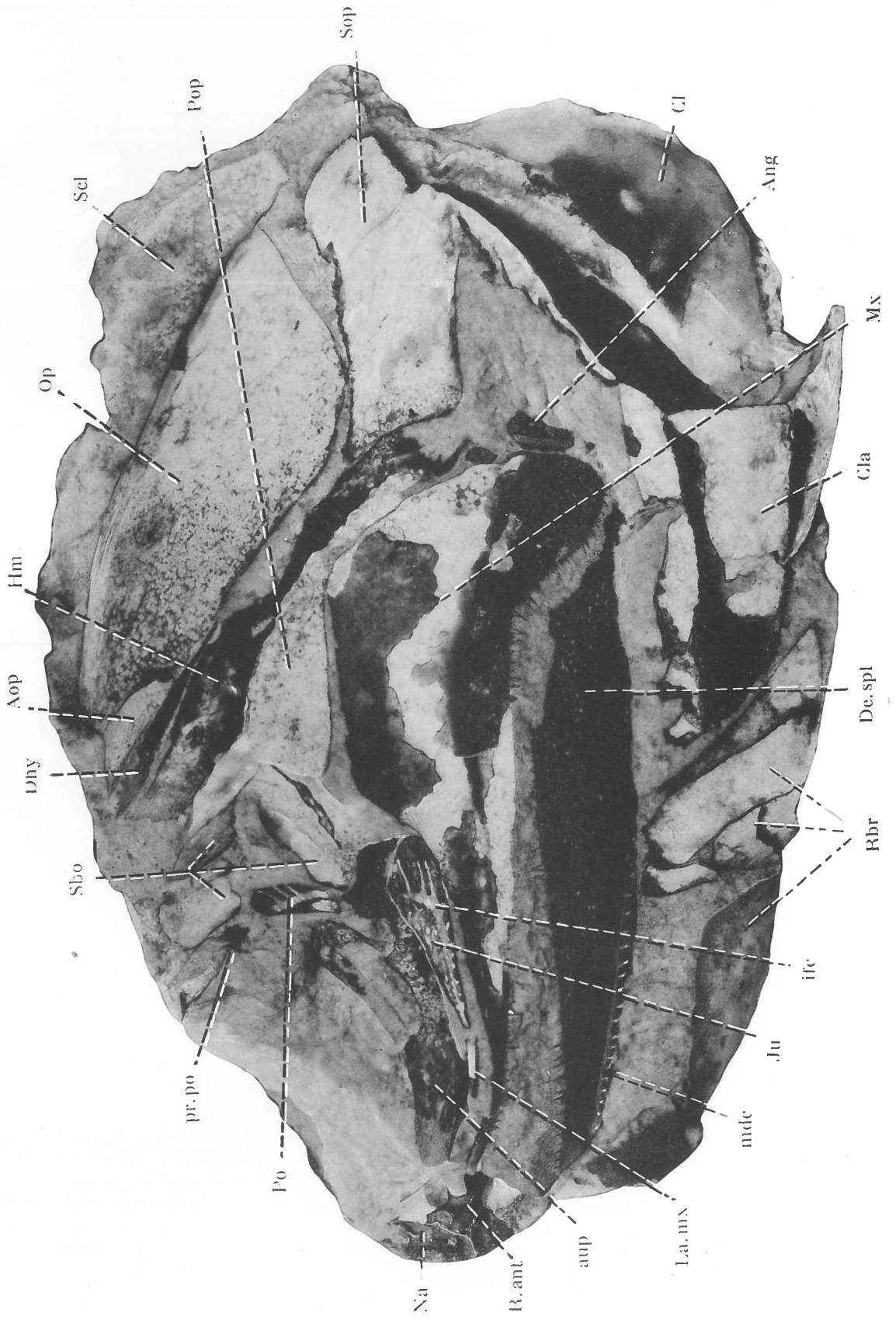

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Plate 5.

Glaucolepis magna n. sp. Specimen No. 11 (same specimen as shown in Pl. 7, Fig. 1). 3 ×. Figs. 1 and 2. Neural endocranium with various dermal bones in lateral and in ventral view respectively. The ethmoidal region and the anterior part of the orbitotemporal region are missing.

Fr, frontal; *Psph*, parasphenoid; *St. it*, supratemporo-intertemporal; *a. ccm*, groove for the arteria carotis communis; *a. car. ext*, canal for the arteria carotis externa; *ad*, canal for an artery; $a.eff_1$, $a.eff_2$, openings for the arteriae branchiales efferentes I and II respectively; *aort*, posterior opening of the aorta canal; *art. sup I*, dorsal and ventral parts of area of articulation for the suprapharyngobranchial I; *bsph*, pars basisphenoidea; *c. ju*, posterior opening of the jugulo-hyoideomandibular canal for the vena jugularis; *cnp*, posterior opening of the notochordal space; *crop*, processus cranio-spinalis; *f. hm*, articular fossa for the hyomandibula; *f. m*, foramen magnum; *f. occ. lat*, fissura occipitalis lateralis; $font_2$, posterior dorsal fontanelle; *f. ot. v*, fissura oticalis ventralis; *i. st. it*, ventral lamina of the supratemporo-intertemporal; *jd*, jugular depression; *my*, posterior myodome; *pd*, alisphenoid pedicle; $pr.asc_2$, processus ascendens posterior of the parasphenoid; *pr. po*, processus postorbitalis; *spic*, spiracular canal; *v. font*, vestibular fontanelle; *II*, opening for the nervus opticus; *IX*, canal for the nervus glossopharyngeus; *X*, canal for the nervus vagus.

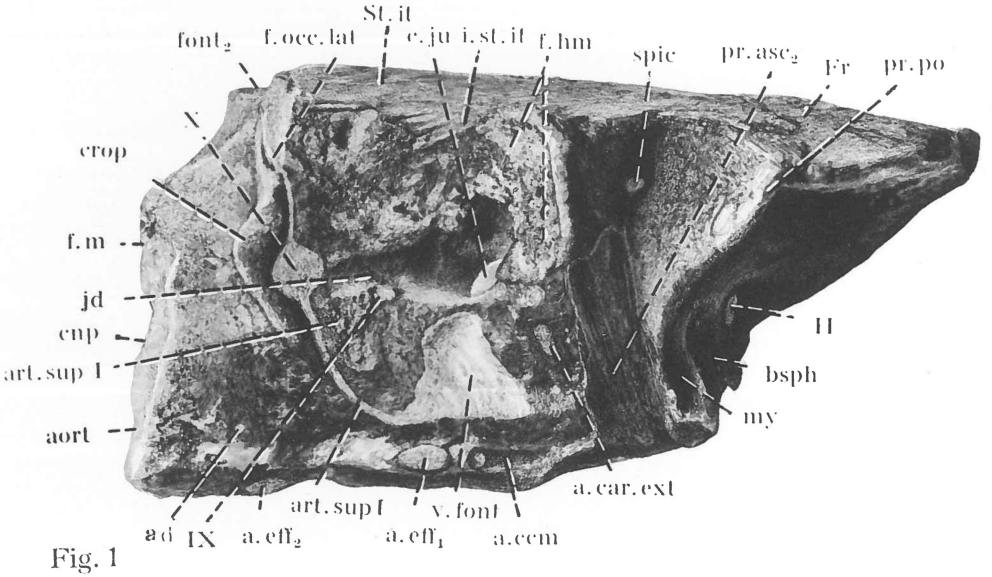


Fig. 1

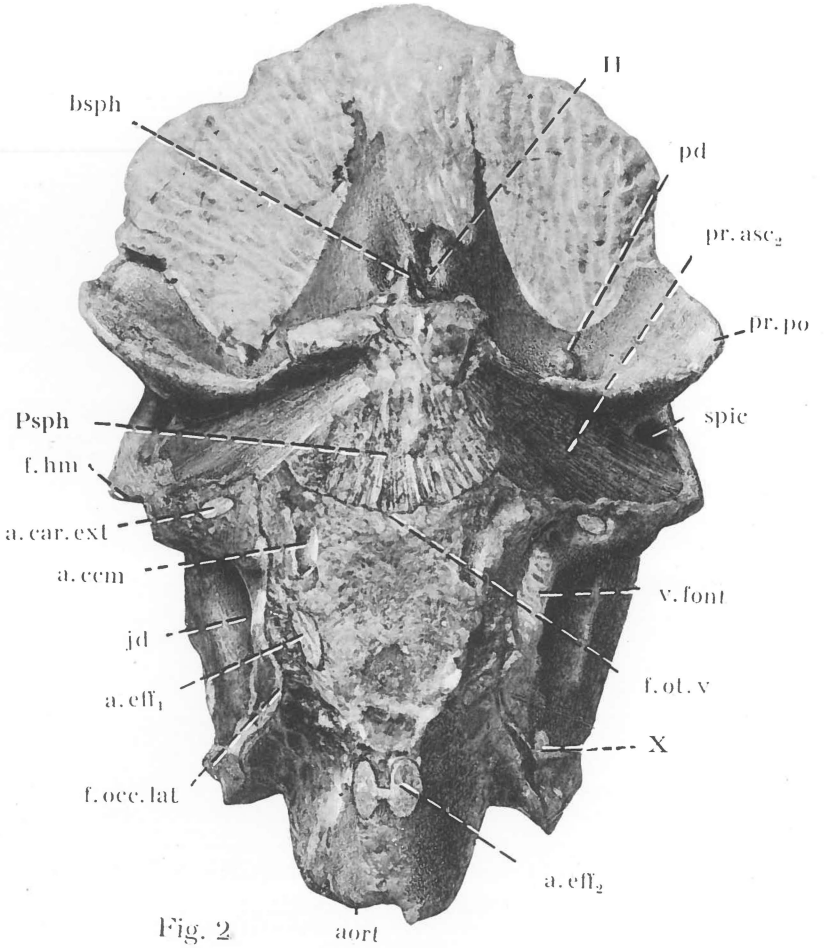


Fig. 2

Nordisk Kunst- og Lystryk

Plate 6.

Figs. 1 and 2. *Glaucolepis magna* n.sp. Neural endocranium with various dermal bones in front view and antero-ventro-lateral view respectively. Specimen No. 4 (same specimen as shown in Pl. 8, Fig. 2). 3 ×.

Fig. 3. *Glaucolepis magna* n.sp. Neural endocranium with the parasphenoid in lateral view. Anterior part of the endocranium incomplete. Specimen No. 1 (same specimen as shown in Pl. 8, Fig. 1, and Pl. 20, Figs. 2, 3). 3 ×.

Psph, parasphenoid; *a.car.ext*, canal for the arteria carotis externa; *a.eff*$_1$, *a.eff*$_2$, openings for the arteriae branchiales efferentes I and II respectively; *a.opht.m*, opening and groove for the arteria ophthalmica magna; *a.opt*, canal for the arteria optica; *aort*, posterior opening of the aorta canal; *a.ps*, opening for the arteria pseudobranchialis efferens; *art.sup.I*, place. of articulation for the suprapharyngobranchial I; *bp*, processus basipterygius (damaged); *bsph*, pars basisphenoidea; *c.ju*, posterior opening of the jugulohyoidemandibular canal for the vena jugularis; *c.trh*, posterior opening of the jugulohyoideomandibular canal for the truncus hyoideomandibularis; *cro*, crista occipitalis; *crop*, processus cranio-spinalis; *fb*, fossa bridgei; *fen.opt*, fenestra optica; *f.hm*, articular fossa for the hyomandibula; *f.m*, foramen magnum; *f.occ.lat*, fissura occipitalis lateralis; *font*$_2$, posterior dorsal fontanelle; *jd*, jugular depression; *my*, posterior myodome; *my.ant.d*, anterior dorsal myodome; *my.ant.v*, anterior ventral myodome; *nn*, notch in the margin of the planum antorbitale; *np*, nasal pit; *pd*, alisphenoid pedicle; *pr.asc*$_2$, processus ascendens posterior of the parasphenoid; *pr.po*, processus postorbitalis; *ram.dors*, one of the canals for branches of the ramus ophthalmicus superficialis trigemini, the nervus ophthalmicus lateralis and vessels; *sa*, ridge above the canalis semicircularis anterior; *s.max.buc*, notch for the ramus maxillaris trigemini, the nervus buccalis lateralis and vessels; *spic*, spiracular canal; *trig.fac.ch*, trigemino-facialis chamber; *v.font*, vestibular fontanelle; *I*, canal for the nervus olfactorius; *II*, opening for the nervus opticus; *III*, canal for the nervus oculomotorius; *IV*, canal for the nervus trochlearis; *V*, trigeminus canal; V_1, canal for the nervus ophthalmicus profundus; *IX*, canal for the nervus glossopharyngeus; *X*, canal for the nervus vagus.

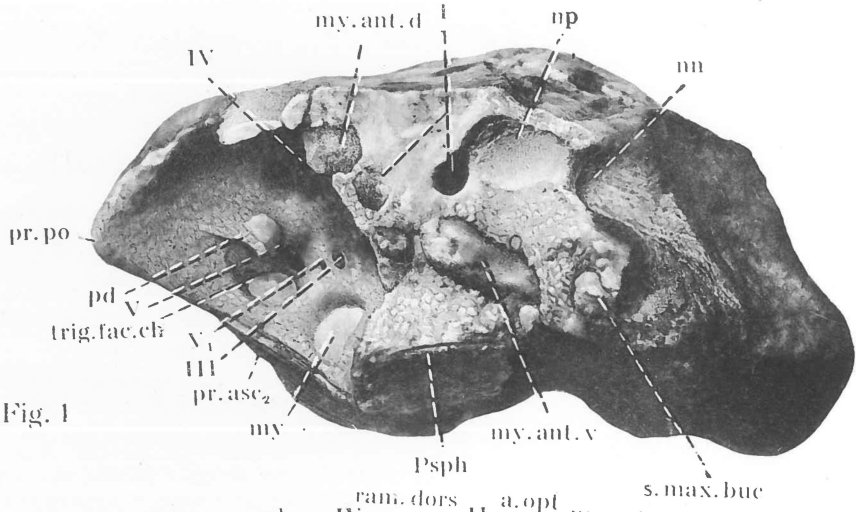


Fig. 1

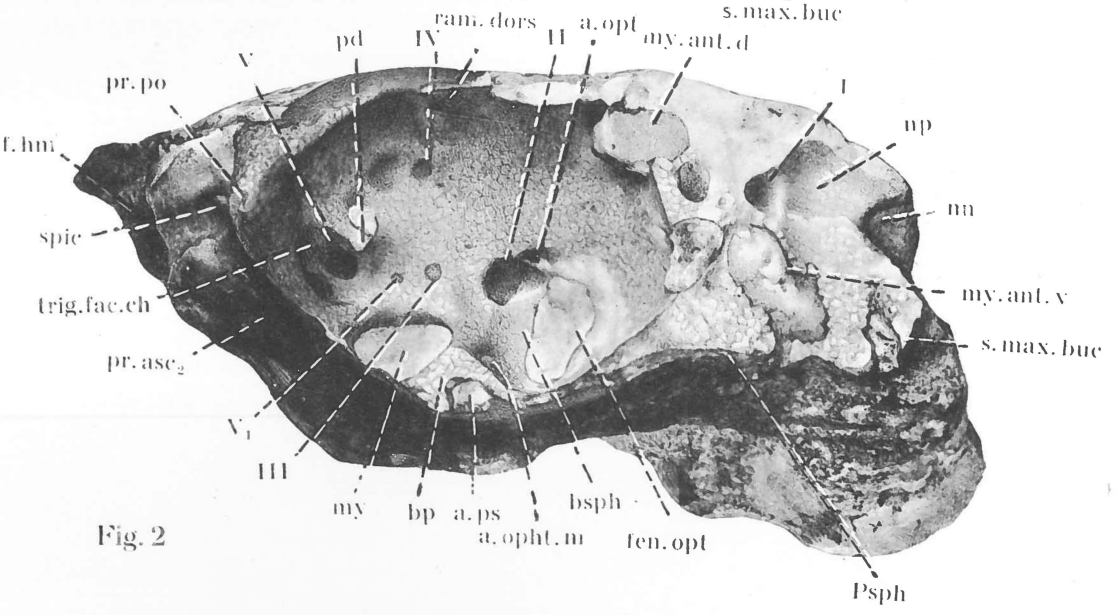


Fig. 2

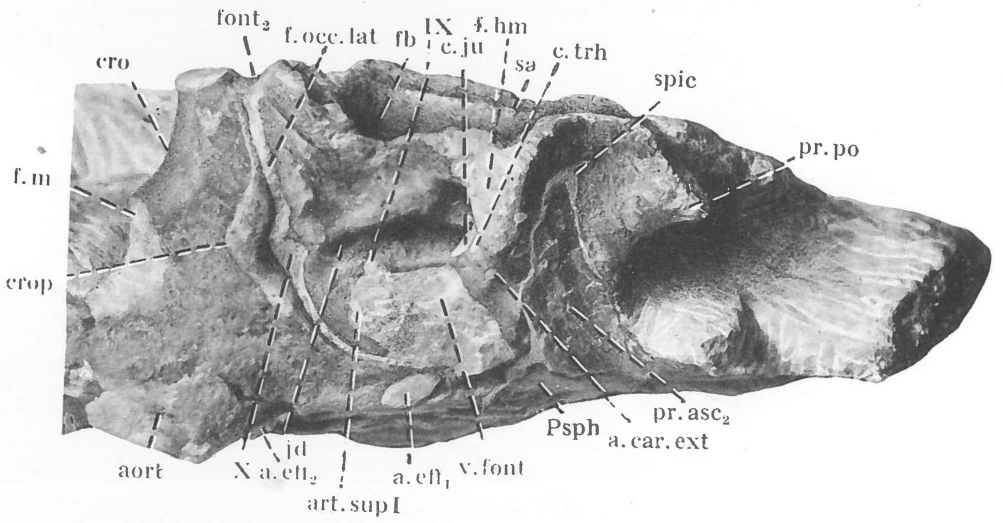


Fig. 3

Nordisk Kunst- og Lystryk

Plate 7.

Fig. 1. *Glaucolepis magna* n.sp. Neural endocranium in posterior view. Specimen No. 11 (same specimen as shown in Pl. 5). 3 ×.

Fig. 2. *Glaucolepis magna* n.sp. Neural endocranium with the parasphenoid in ventral view. Part of the parasphenoid and of the endocranium itself has been removed, so that the myodome, the trigemino-facialis chamber, and the anterior part of the jugulo-hyoideomandibular canal are visible on the right side of the endocranium. Specimen No. 13. 3 ×.

Psph, parasphenoid; *St.it*, supratemporo-intertemporal; *aort*, posterior opening of the aorta canal; *c.ju*, posterior opening of the jugulo-hyoidemandibular canal for the vena jugularis; *cnp*, posterior opening of the notochordal space; *cro*, crista occipitalis; *crop*, processus cranio-spinalis; *c.trh*, posterior opening of the jugulo-hyoideomandibular canal for the truncus hyoideomandibularis; *f.hm*, articular fossa for the hyomandibula; *f.m*, foramen magnum; *f.occ.lat*, fissura occipitalis lateralis; $font_1$, $font_2$, anterior and posterior dorsal fontanelles; *i.st.it*, ventral lamina of the supratemporo-intertemporal; *my*, posterior myodome; *pd*, alisphenoid pedicle; $pr.asc_1$, processus ascendens anterior of the parasphenoid; $pr.asc_2$, processus ascendens posterior of the parasphenoid; *pr.po*, processus postorbitalis; *r.ot*, canal for the ramus oticus lateralis; *ru*, division of the labyrinth cavity for the recessus utriculi; *s.lv*, depression on the cerebral face of the roof of the otic region; *s.us*, division of the labyrinth cavity for the sinus utriculi superior; *trig.fac.ch*, trigeminofacialis chamber; *v.font*, vestibular fontanelle; *III*, canal for the nervus oculomotorius; *IV*, canal for the nervus trochlearis; *V*, trigeminus canal; V_1, canal for the nervus ophthalmicus profundus; *VI*, canal for the nervus abducens.

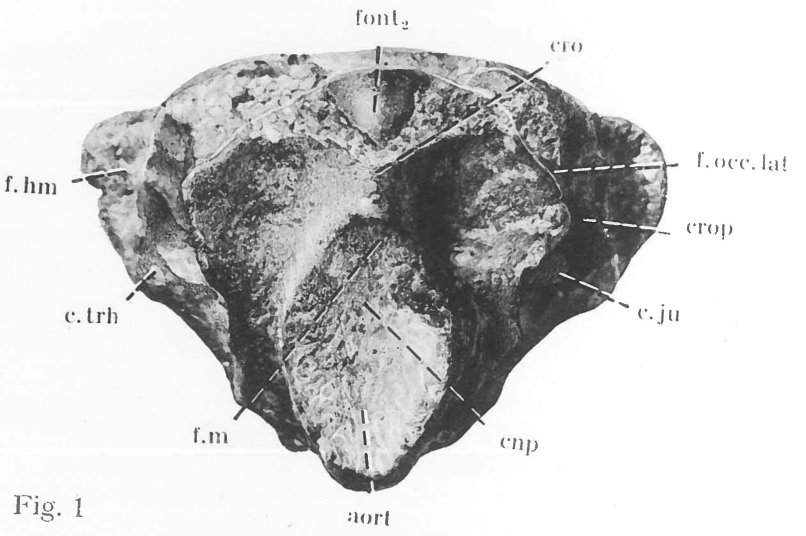


Fig. 1

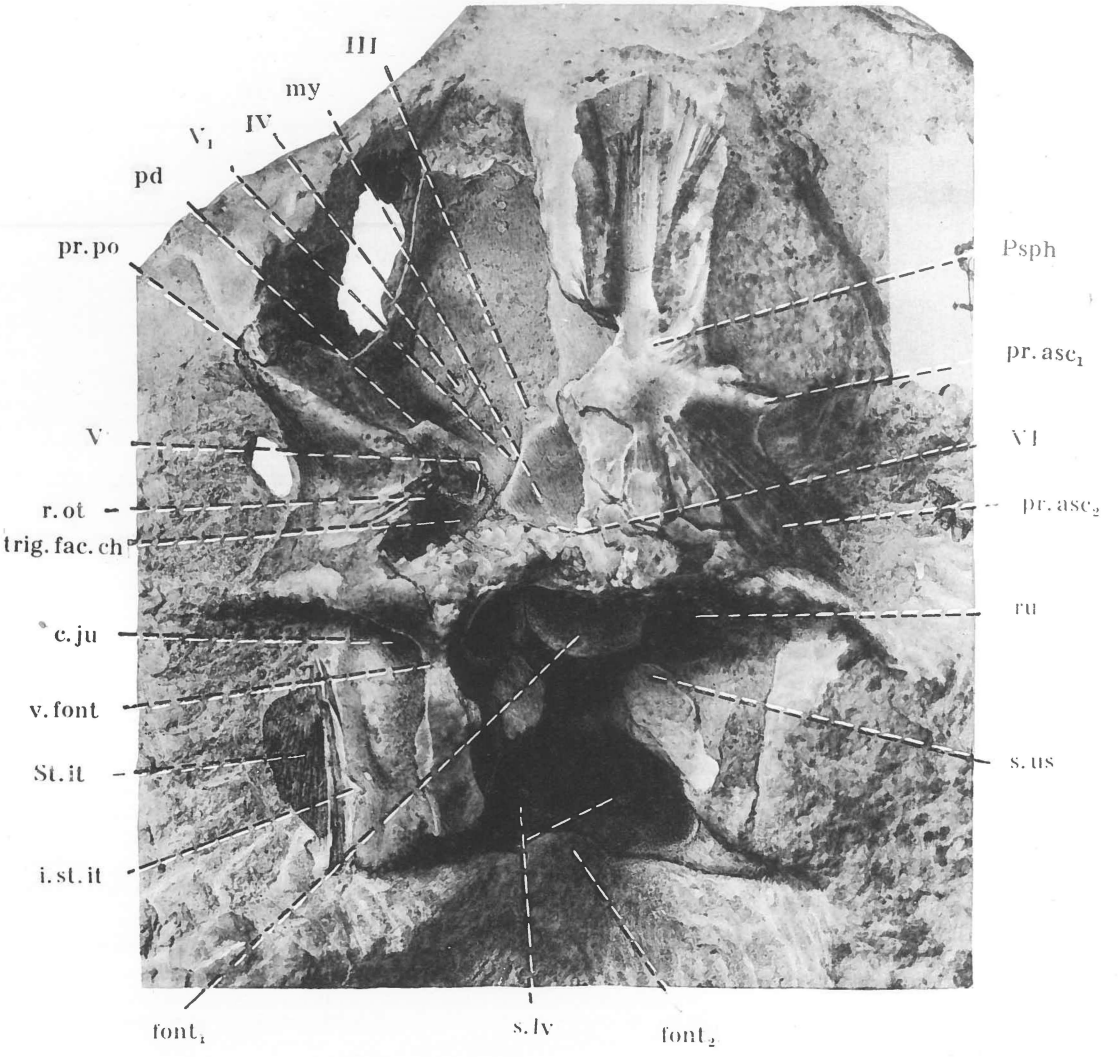


Fig. 2

Nordisk Kunst- og Lystryk

Plate 8.

Fig. 1. *Glaucolepis magna* n.sp. Neural endocranium in dorsal view. Specimen No. 1 (same specimen as shown in Pl. 6, Fig. 3, and Pl. 20, Figs. 2, 3). 3 ×.

Fig. 2. *Glaucolepis magna* n.sp. Incomplete head in dorsal view. The dermal bones are preserved as impressions of their internal faces. Specimen No. 4 (same specimen as shown in Pl. 6, Figs. 1, 2). 2 ×.

Fig. 3. *Glaucolepis stensiöi* n.sp. Head in anterior view. Specimen No. 39 (same specimen as shown in Pls. 1, 2, 3, and 4). 5 ×.

De.spl, dentalo-splenial; *Fr*, frontal; *Na*, nasal; *Pa*, parietal; *Pmx*, (?) premaxillaries; *Ptr*, postrostral; *So.dsph*, supraorbito-dermosphenotic; *So.po*, supraorbito-postorbital; *St.it*, supratemporo-intertemporal; *R.ant*, rostro-antorbital; *X*, two small dermal bones; *amx*, bulge above the division of the labyrinth cavity for the ampulla externa; *ausph*, ossification (separate?) of the pars autosphenotica; *cro*, crista occipitalis; fb, fossa bridgei; *f.occ.lat.* fissura occipitalis lateralis; $font_1$, $font_2$, anterior and posterior dorsal fontanelles; *ifc*, infraorbital canal; *mdc*, mandibular canal; na_1, anterior nostril; *pr.po*, processus postorbitalis; *sa*, ridge above the canalis semicircularis anterior; *soc*, supraorbital canal; *s.orb.cr*, ossification in the crista supraorbitalis; *sp*, ridge above the canalis semicircularis posterior; *spic*, spiracular canal.

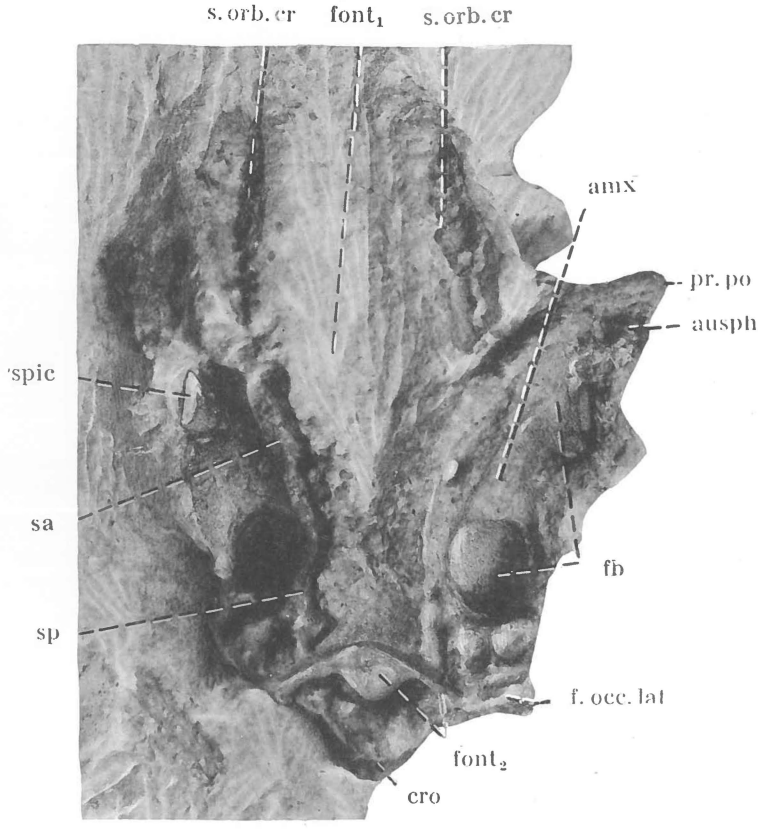


Fig. 1

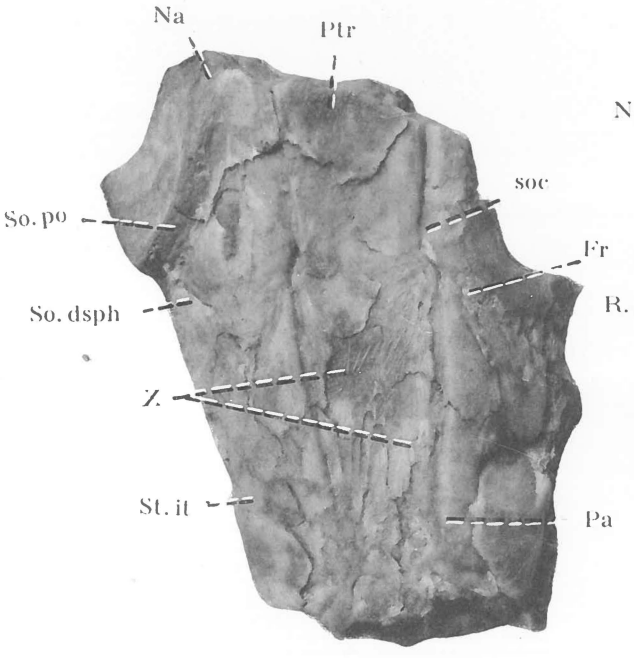


Fig. 2

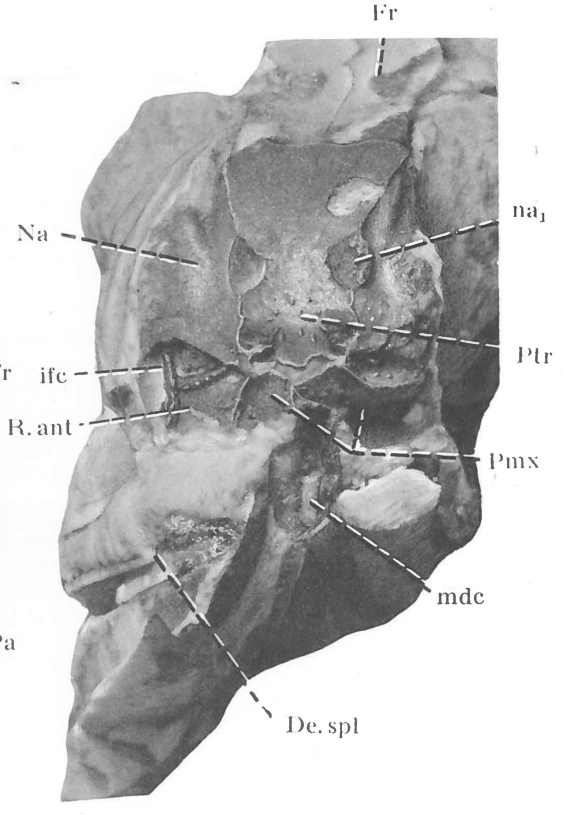


Fig. 3

Nordisk Kunst- og Lystryk

Plate 9.

Fig. 1. *Glaucolepis stensiöi* n.sp. Impressions of the head and the anterior part of the abdominal region. Specimen No. 50. 2 ×.

Fig. 2. *Glaucolepis gunnari* n.sp. Dermal bones of the cheek in medial view. Specimen No. 27. 3 ×.

Ang, angular; *Aop*, antoperculum; *De.spl*, dentalo-splenial; *Dhy*, dermohyal; *Ext.l*, *Ext.m*, lateral and medial extrascapulars; *Fr*, frontal; *Hm*, hyomandibula; *Ju*, jugal; *Mx*, maxillary; *Na*, nasal; *Op*, operculum; *Pa*, parietal; *Pec*, pectoral fin; *Pop*, preoperculum; *Pspic*, postspiracular bone; *Ptr*, postrostral; *Quj*, Quadratojugal; *Rbr*, branchiostegal ray; *Sbo*, suborbitals; *Scl*, supracleithral; *Sclr*, segments of the sclerotic ring; *So.dsph*, supraorbito-dermosphenotic; *Sop*, suboperculum; *Sscap*, suprascapular; *St.it*, supratemporo-intertemporal; *hp*, horizontal pit-line of the cheek; *pa.p*, the three pit-lines on the parietal; *poc*, preopercular canal; *soc*, supraorbital canal; *vp*, vertical pit-line of the cheek.

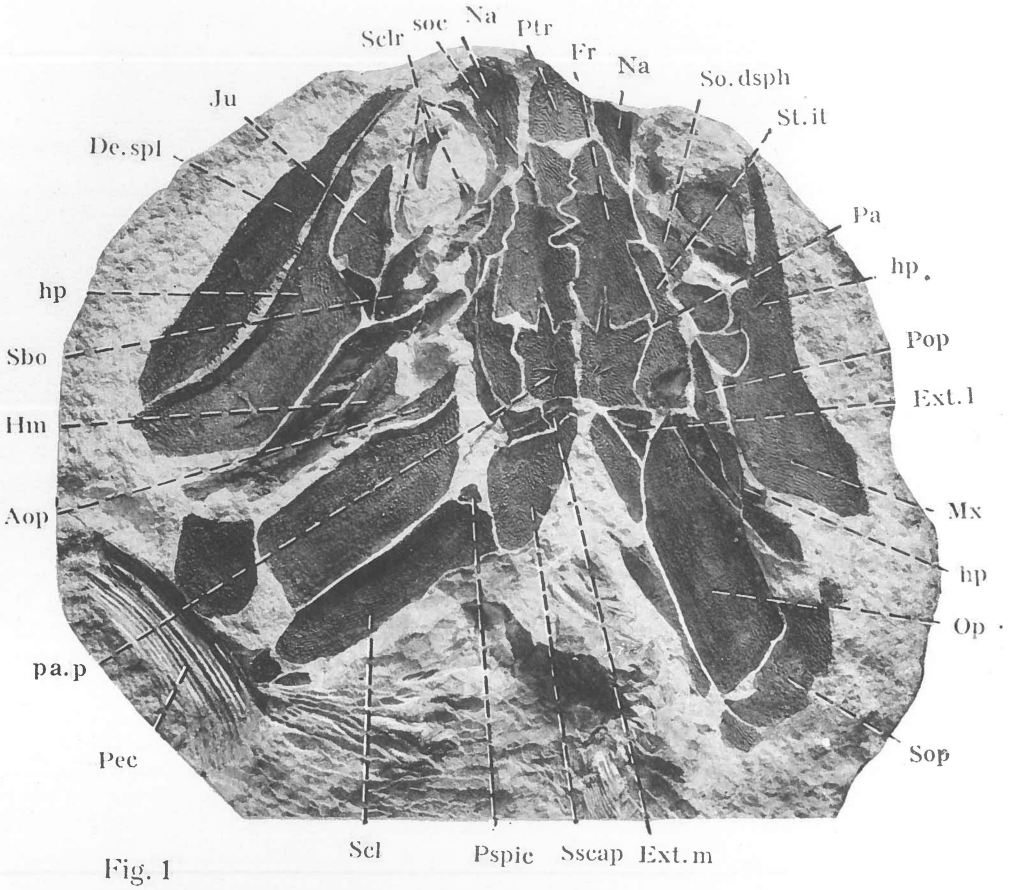

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Fig. 1

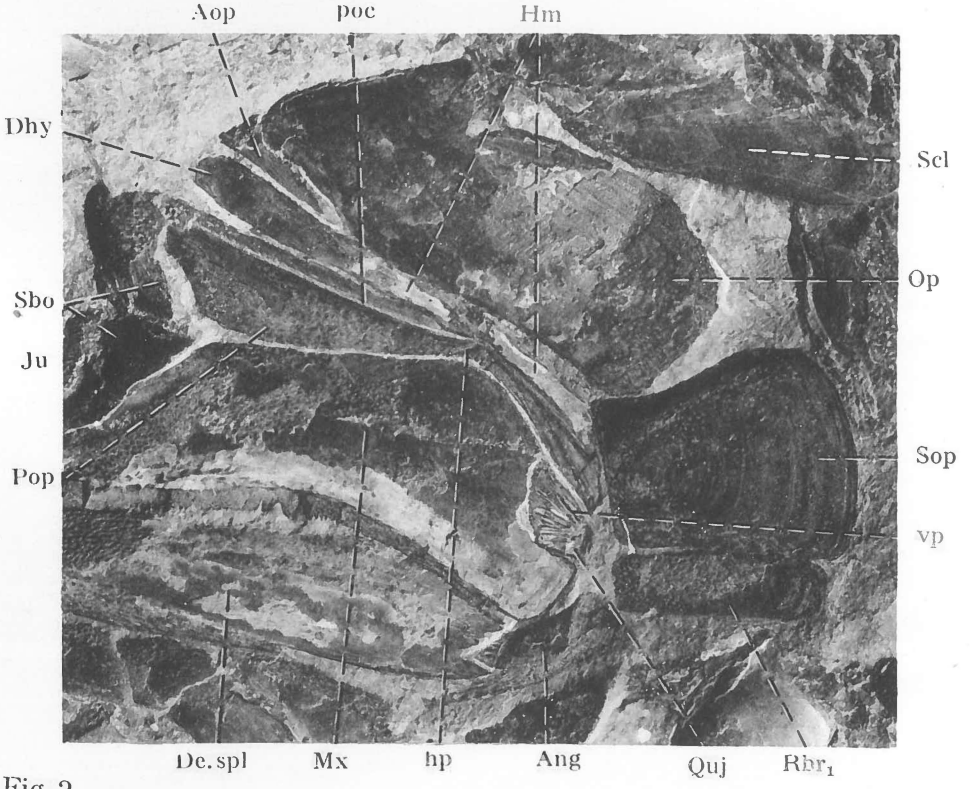

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Fig. 2

Plate 10.

Fig. 1. *Glaucolepis magna* n.sp. Incomplete mandible in medial view. Specimen No. 8 (same specimen as shown in Pl. 19). 2 ×.

Fig. 2. *Glaucolepis gunnari* n.sp. Incomplete head in dorsal view. Specimen No. 169. 3 ×.

Aop, antoperculum; Cor_3, posterior coronoid; *Ext.l*, *Ext.m*, lateral and medial extrascapulars; *Fr*, frontal; *Hm*, hyomandibula; *Mk*, posterior ossification in the Meckelian cartilage; *Mmd*, bone in the anterior part of the mandible containing an endochondral and probably a dermal component; *Mx*, maxillary; *Na*, nasal; *Op*, operculum; *Pa*, parietal; *Pop*, preoperculum; *Pr.art*, prearticular; *Ptr*, postrostral; *Sbo*, suborbitals; *Scl*, supracleithral; *So.dsph*, supraorbito-dermosphenotic; *Sop*, suboperculum; *So.po*, supraorbito-postorbital; *Sscap*, suprascapular; *St.it*, supratemporo-intertemporal; *p.md*, shallow depressions on the posterior ossification in the Meckelian cartilage; *soc*, supraorbital canal.

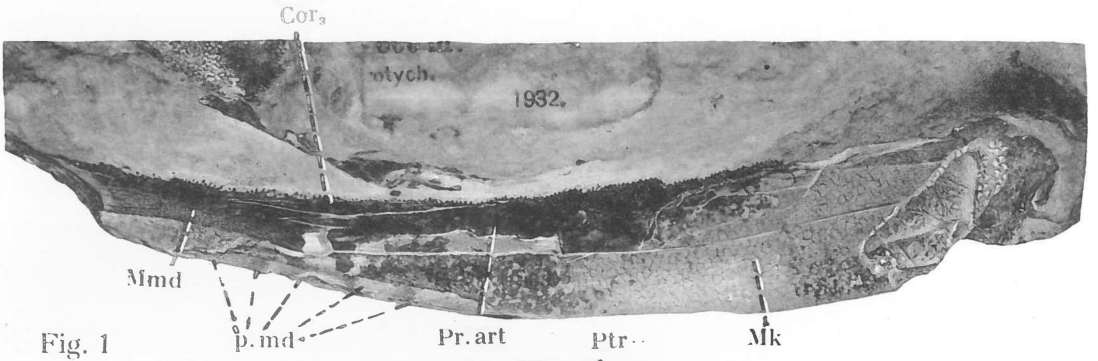


Fig. 1

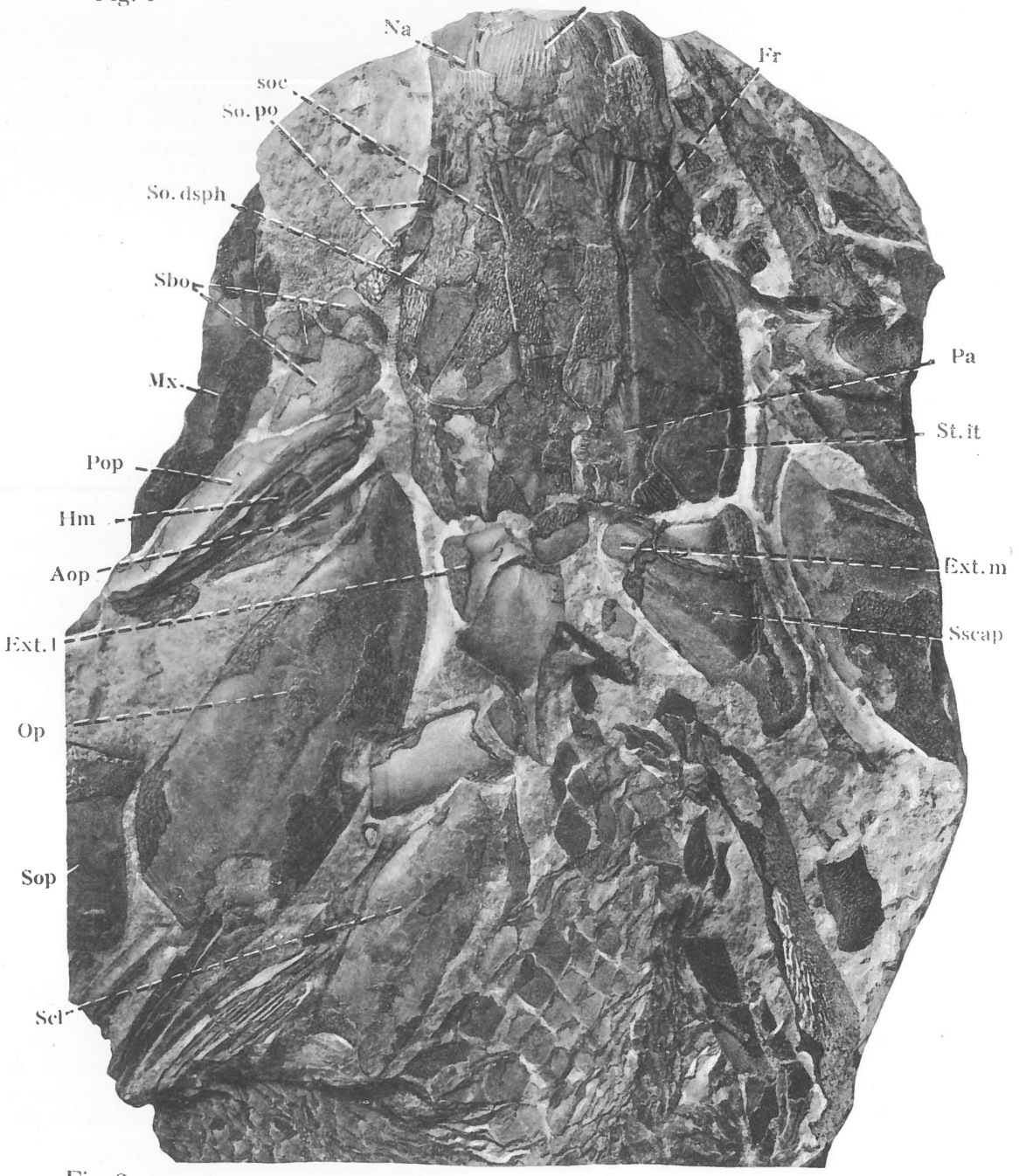


Fig. 2

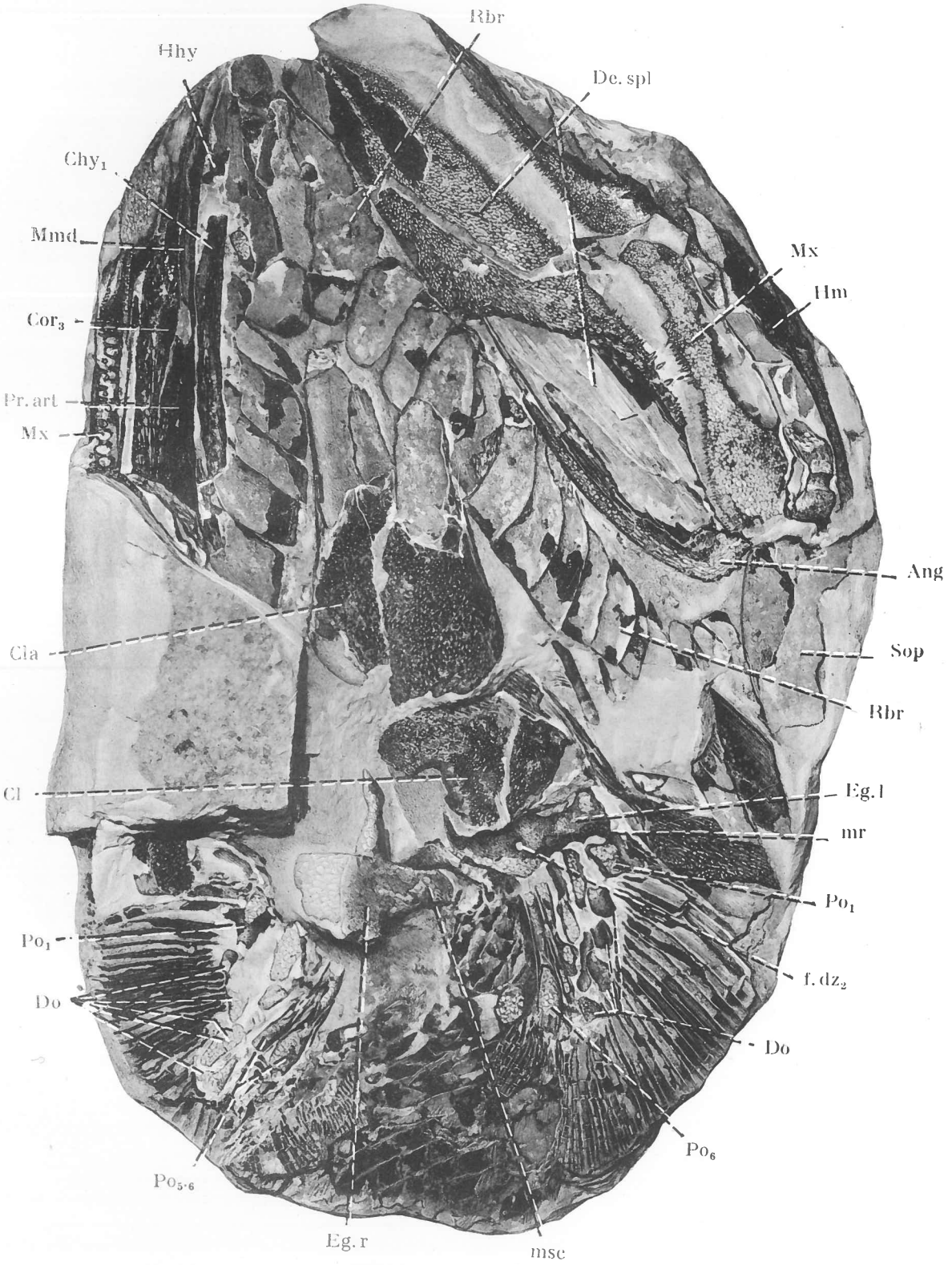
Nordisk Kunst- og Lystryk

Plate 11.

Glaucolepis gunnari n. sp.

Head and anterior part of the abdominal region of a dorso-ventrally flattened specimen in ventral view. Specimen No. 170. 3 ×.

Ang, angular; Chy_1, anterior ceratohyal ossification; *Cl*, cleithrum; *Cla*, clavicle; Cor_3, posterior coronoid; *De.spl*, dentalo-splenial; *Do*, distal ossification in the endoskeleton of the pectoral fin; *Eg.l*, *Eg.r*, left and right endoskeletal ossifications of the shoulder girdle; *Hhy*, hypohyal; *Hm*, hyomandibula; *Mmd*, bone in the anterior part of the mandible containing an endochondral and probably a dermal component; *Mx*, maxillary, Po_1, Po_6, first and sixth proximal ossifications in the endoskeleton of the pectoral fin; $Po_{5.6}$, partly fused fifth and sixth proximal ossifications in the endoskeleton of the pectoral fin; *Pr.art*, prearticular; *Rbr*, branchiostegal rays; *Sop*, suboperculum; $f.dz_2$, foramen for diazonal nerves; *mr*, lateral end of margo radialis; *msc*, mesocoracoid arch.



Nordisk Kunst- og Lystryk

Plate 12.

Fig. 1. *Glaucolepis magna* n.sp. Part of the head in lateral view. Most of the dermal bones preserved as impressions of their medial faces. Specimen No. 59. 2 ×.

Fig. 2. *Glaucolepis stensiöi* n.sp. Incomplete head and anterior part of the abdominal region in lateral view. Most of the dermal bones preserved as impressions of their internal faces. Specimen No. 95. 2 ×.

Ang, angular; *Aop*, antoperculum; *De.spl*, dentalo-splenial; *Dhy*, dermohyal; *Ext.l*, *Ext.m*, lateral and medial extrascapulars; *Hm*, hyomandibula; *Ju*, jugal; *La.mx*, lacrimo-maxillary; *Mx*, maxillary; *Pa*, parietal; *Pec*, pectoral fin; *Pop*, preoperculum; *Pspic*, postspiracular bone; *Op*, operculum; *Quj*, quadratojugal; *Rbr*, branchiostegal ray; *Sbo*, suborbitals; *Scl*, supracleithral; *Sclr*, segment of the sclerotic ring; *Sop*, suboperculum; *Sscap*, suprascapular; *St.it*, supratemporo-intertemporal; *n*, notch in the margin of the supratemporo-intertemporal dorsally to the dorsal end of the hyomandibula.

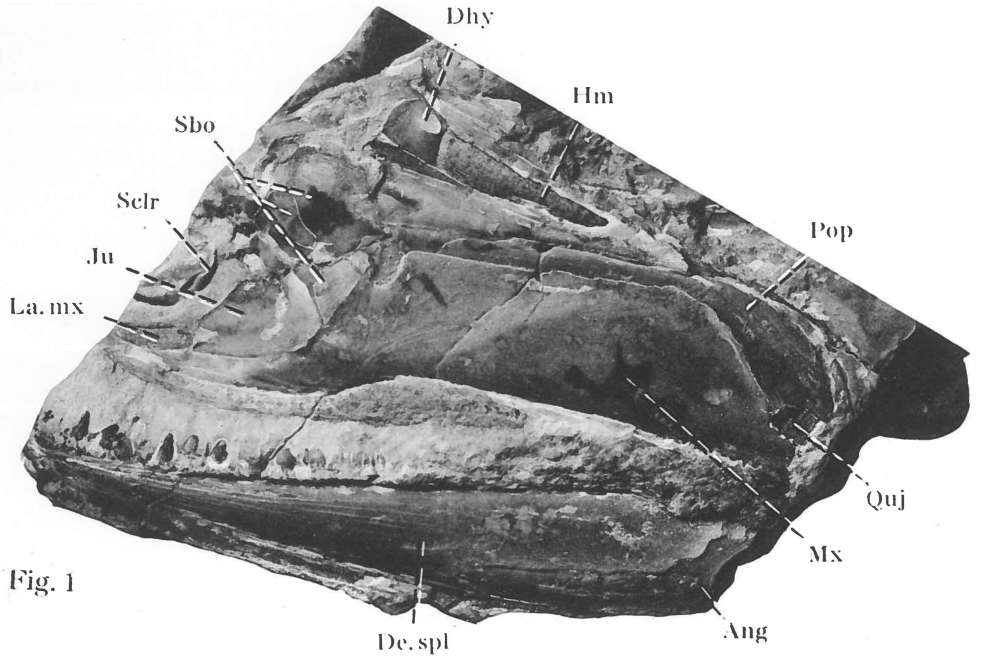


Fig. 1

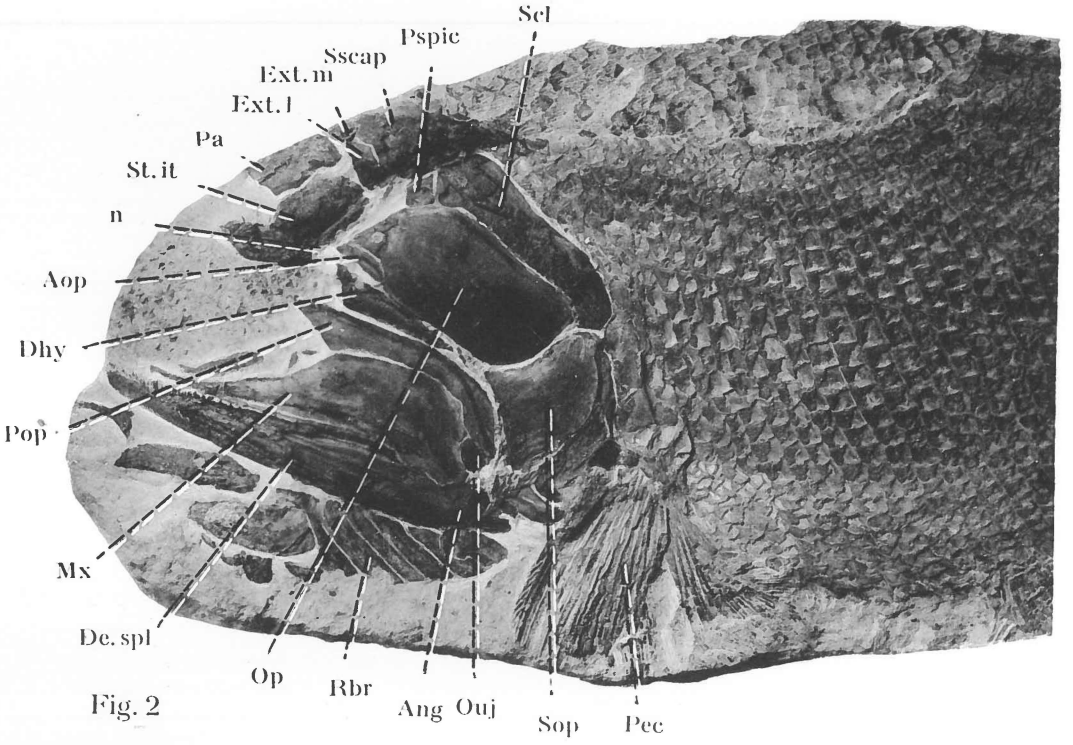


Fig. 2

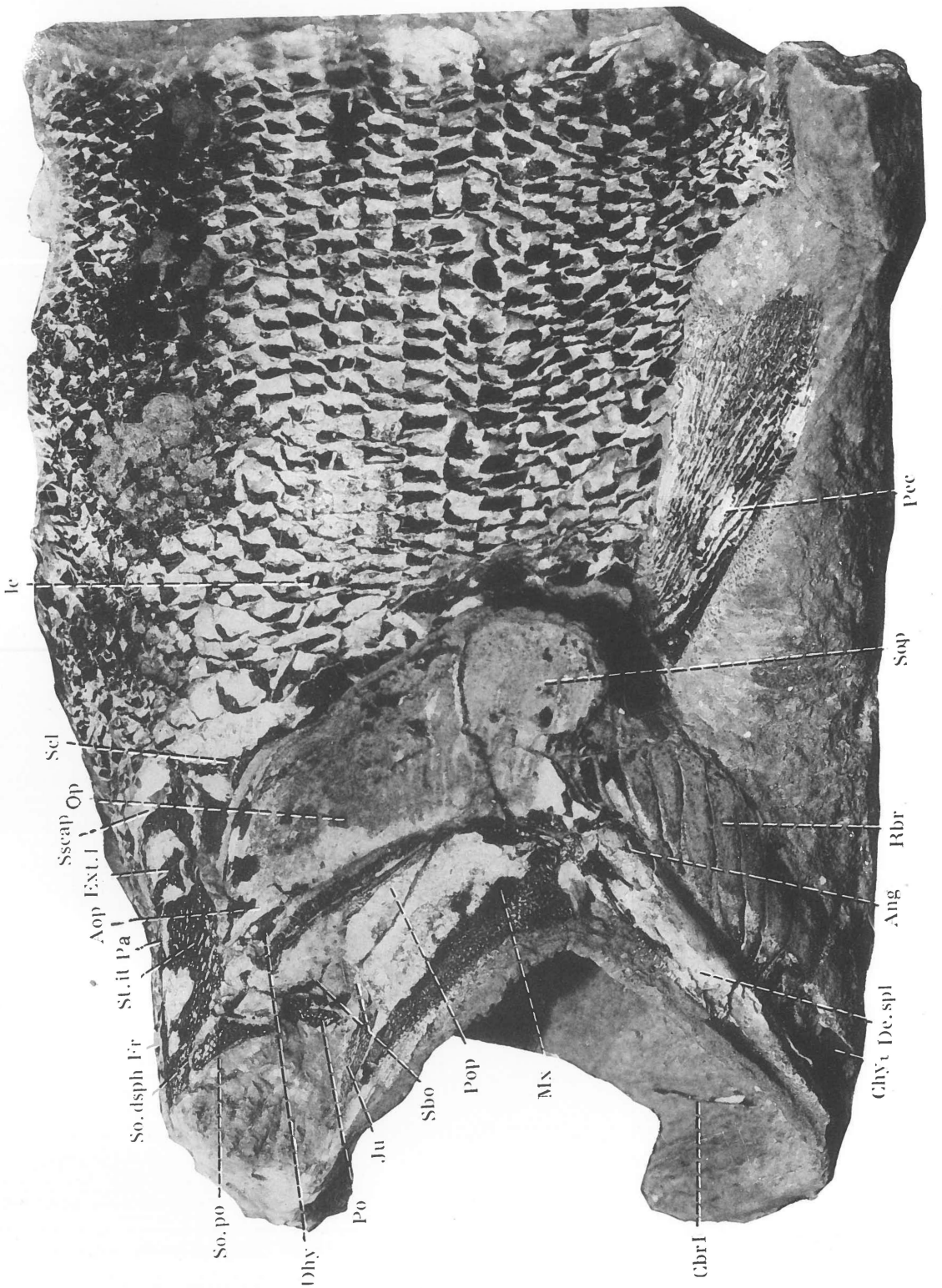
Nordisk Kunst- og Lystryk

Plate 13.

Glaucolepis stensiöi n. sp.

Head and anterior part of the abdominal region in lateral view. Snout incomplete. Specimen No. 38 (same specimen as shown in Pls. 14, 15, 16, and 17). 2.4 ×.

Ang, angular; *Aop*, antoperculum; *CbrI*, ceratobranchial I; Chy_1, anterior ceratohyal ossification; *De.spl*, dentalo-splenial; *Dhy*, dermohyal; *Ext.l*, lateral extrascapular; *Fr*, frontal; *Ju*, jugal; *Mx*, maxillary; *Op*, operculum; *Pa*, parietal; *Scl*, supracleithral; *Pec*, pectoral fin; *Po*, postorbital; *Pop*, preoperculum; *Rbr*, branchiostegal ray; *Sbo*, suborbifals; *So.dsph*, supraorbito-dermosphenotic; *Sop*, suboperculum; *So.po*, supraorbito-postorbital; *Sscap*, suprascapular; *St.it*, supratemporo-intertemporal; *lc*, main lateral line.



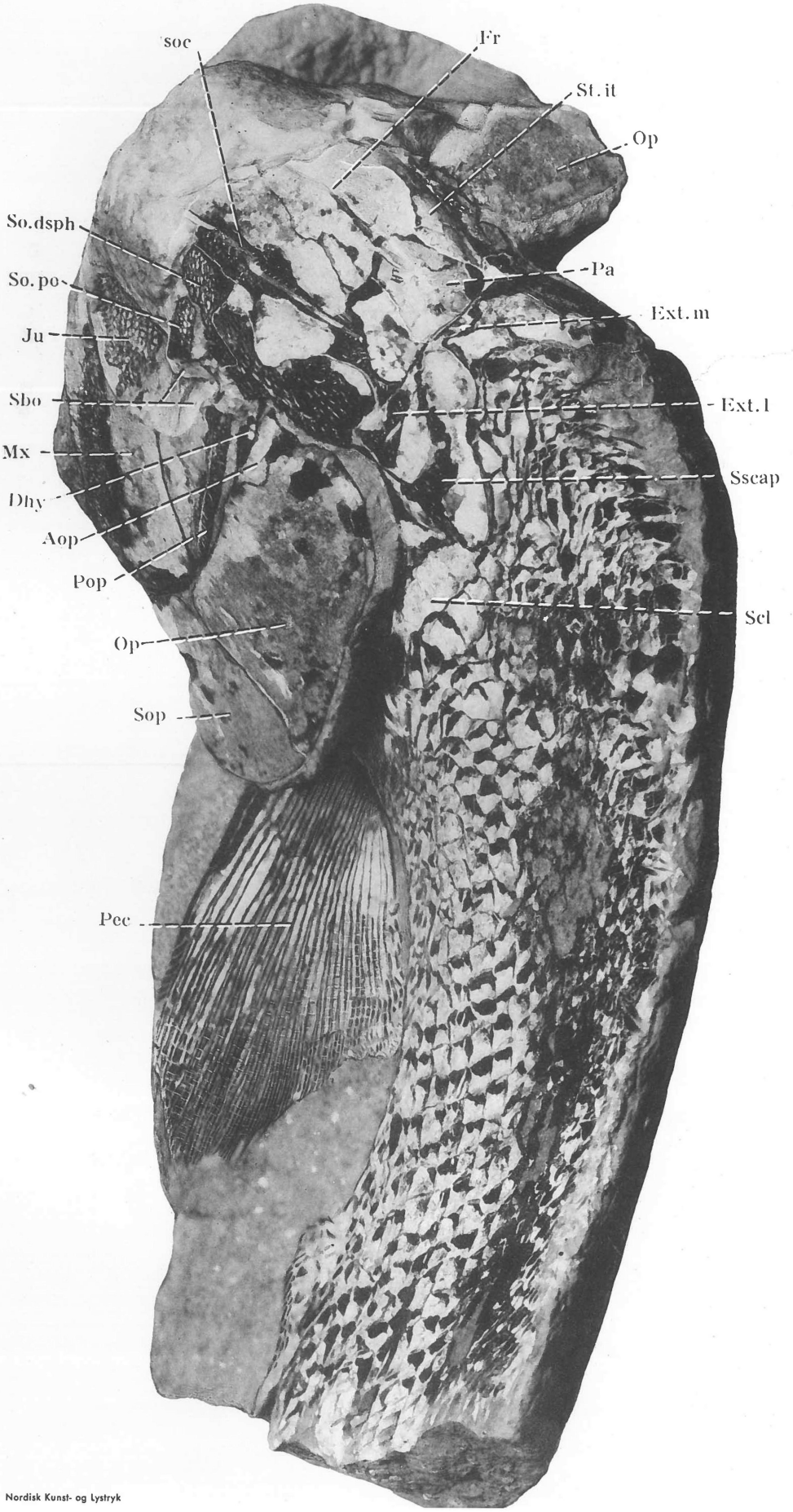
Nordisk Kunst- og Lystryk

Plate 14.

Glaucolepis stensiöi n. sp.

Head and anterior part of the abdominal region in dorsal view. Specimen No. 38 (same specimen as shown in Pls. 13, 15, 16, and 17). 3 ×.

Aop, antoperculum; *Dhy*, dermohyal; *Ext.l*, *Ext.m*, lateral and medial extrascapulars; *Fr*, frontal; *Ju*, jugal; *Mx*, maxillary; *Op*, operculum; *Pa*, parietal; *Pec*, pectoral fin; *Pop*, preoperculum; *Sbo*, suborbitals; *Scl*, supracleithral; *So.dsph*, supraorbito-dermosphenotic; *Sop*, suboperculum; *So.po*, supraorbito-postorbital; *Sscap*, suprascapular; *St.it*, supratemporo-intertemporal; *soc*, supraorbital canal.



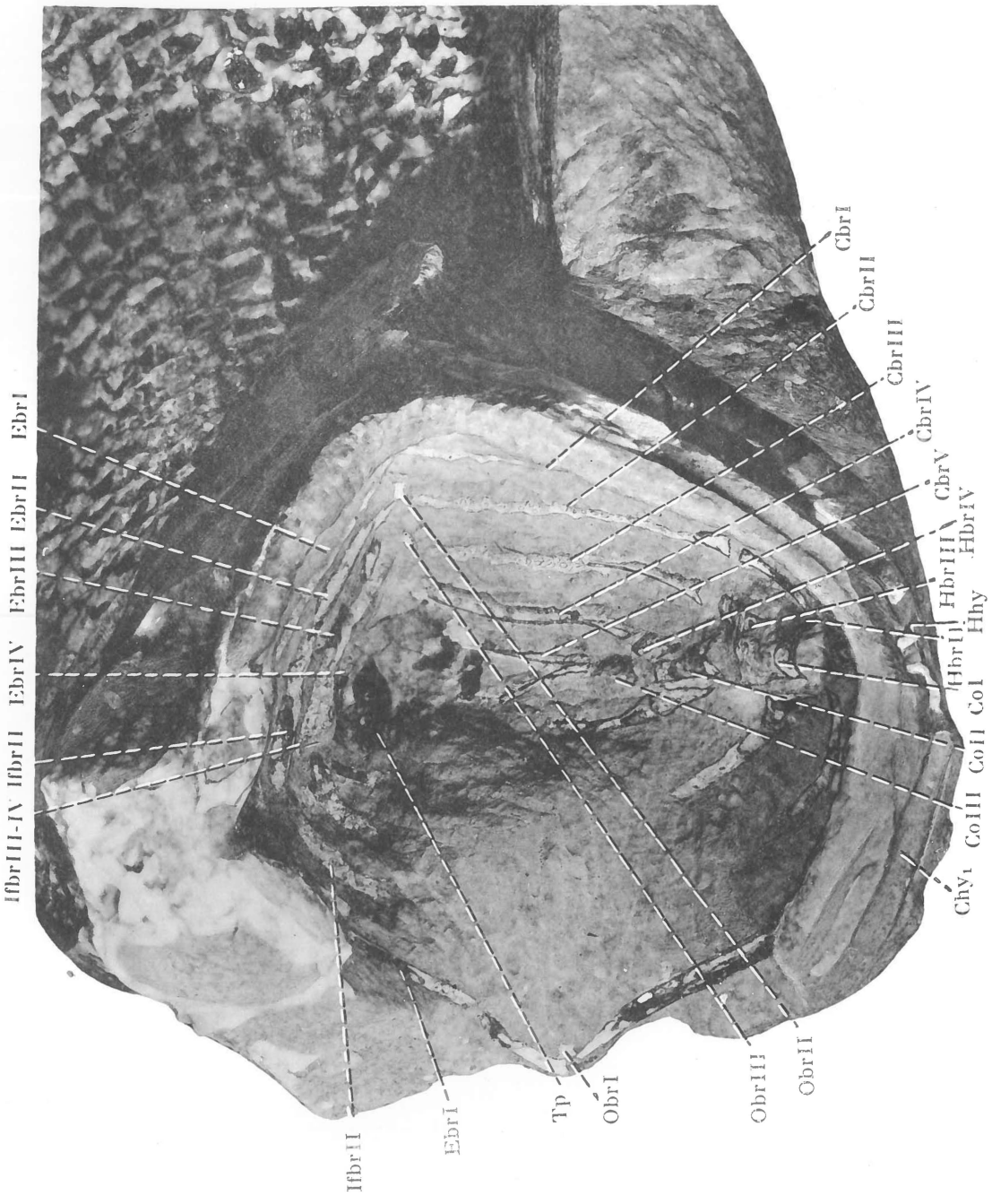
Nordisk Kunst- og Lystryk

Plate 15.

Glaucolepis stensiöi n. sp.

Head with open mouth in front view. The endoskeletal ossifications of the branchial arches to a great extent concealed beneath small tooth-bearing dermal bones. Specimen No. 38 (same specimen as shown in Pls. 13, 14, 16, and 17). 3 ×.

Cbr I-IV, ceratobranchials I-IV; *Cbr V*, cerato- or hypo-ceratobranchial V; Chy_1, anterior ceratohyal ossification; *Co I-III*, ossifications in the basibranchial series; *Ebr I-IV*, epibranchials I-IV; *Hbr II-IV*, hypobranchials II-IV; *Hhy*, hypohyal; *Ifbr II*, infrapharyngobranchial II; *Ifbr III-IV*, pharyngobranchial common for the third and fourth branchial arches; *Obr I-III*, ossifications situated between the visceral arches; *Tp*, remains of tooth-bearing dermal bones behind the epibranchial IV.



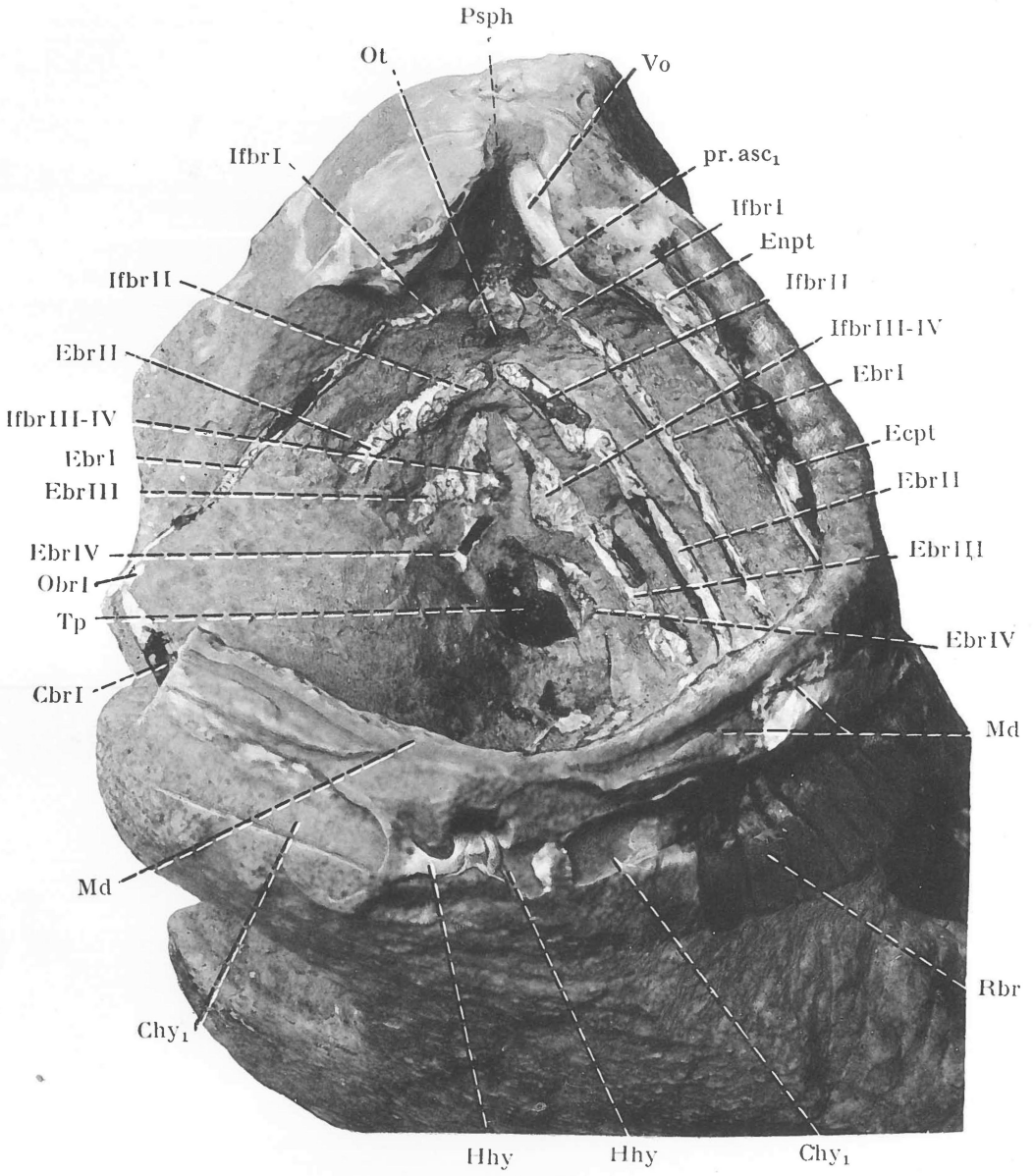
Nordisk Kunst- og Lystryk

Plate 16.

Glaucolepis stensiöi n. sp.

Head with open mouth in antero-ventral view. The endoskeletal ossifications of the branchial arches to a great extent concealed below small tooth-bearing dermal bones. Specimen No. 38 (same specimen as shown in Pls. 13, 14, 15, and 17). 3 ×.

Cbr I, ceratobranchial I; *Chy*$_1$, anterior ceratohyal ossification; *Ebr I-IV*, epibranchials I-IV; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Hhy*, hypohyal; *Ifbr I-II*, infrapharyngobranchials I-II; *Ifbr III-IV*; pharyngobranchial common for the third and fourth branchial arches; *Md*, mandible; *Obr I*, ossification situated between the hyoid arch and the first branchial arch; *Ot*, ventral face of the otic region of the neural endocranium; *Psph*, parasphenoid; *Rbr*, branchiostegal ray; *Tp*, remains of tooth-bearing dermal bones behind the epibranchial IV; *Vo*, vomer; *pr.asc*$_1$, processus ascendens anterior of the parasphenoid.



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Plate 17.

Glaucolepis stensiöi n. sp.

Head with open mouth in antero-lateral view. The endoskeletal ossifications of the branchial arches to a great extent concealed beneath small tooth-bearing dermal bones. Specimen No. 38 (same specimen as shown in Pls. 13, 14, 15, and 16). 3 ×.

Cbr I-IV, ceratobranchials I-IV; Chy_1, anterior ceratohyal ossification; *Cl*, cleithrum; *Dmptg*, dermometapterygoid; *Ebr I-III*, epibranchials I-III; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Hbr I-II*, hypobranchials I-II; *Hhy*, hypohyal; *Hm*, hyomandibula; *Md*, mandible; *Mk*, posterior ossification in the Meckelian cartilage; *Obr I-III*, ossifications situated between the visceral arches; *Op*, operculum; *Sscap*, suprascapular; *Sympl*, symplectic; *Vo*, vomer; *pr. po*, processus postorbitalis.

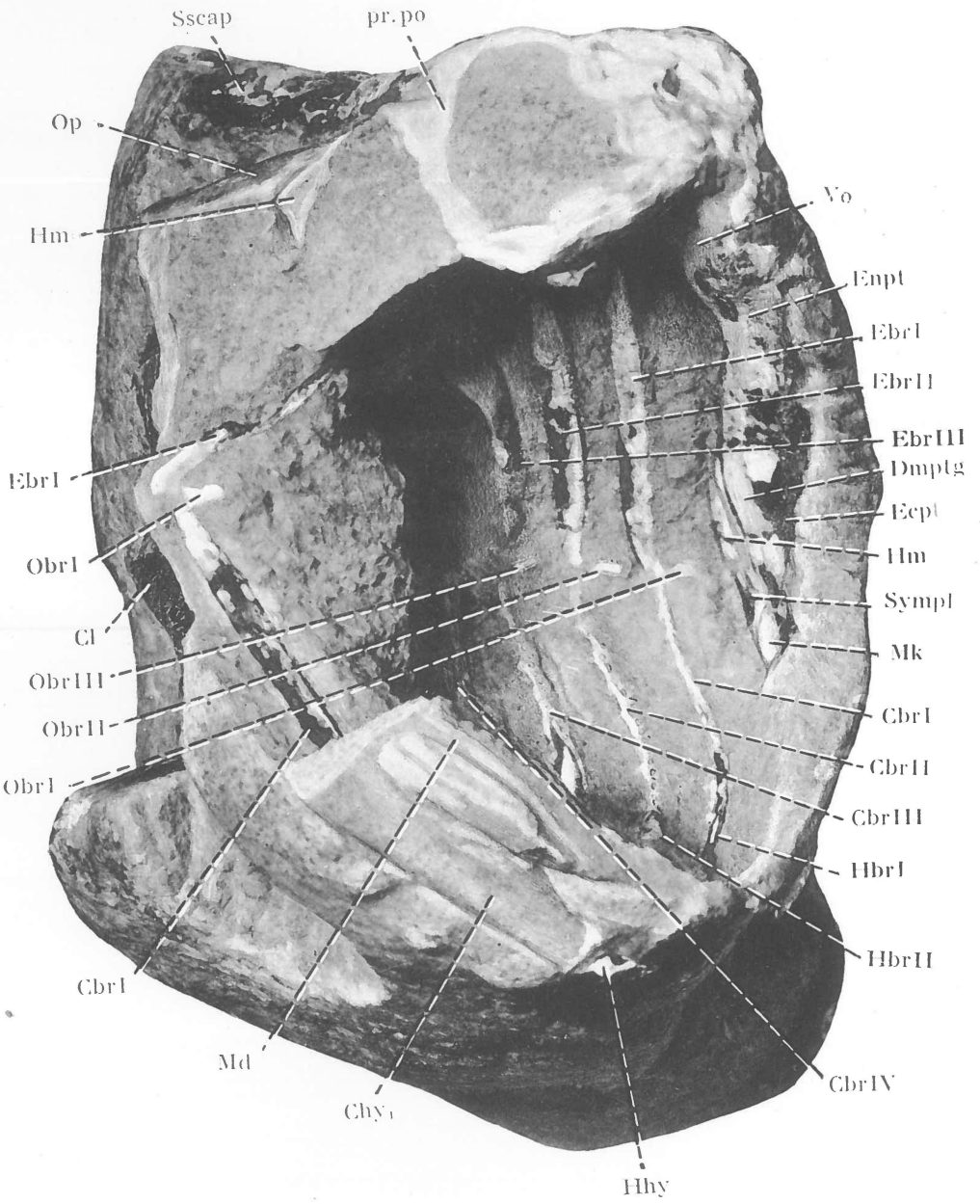
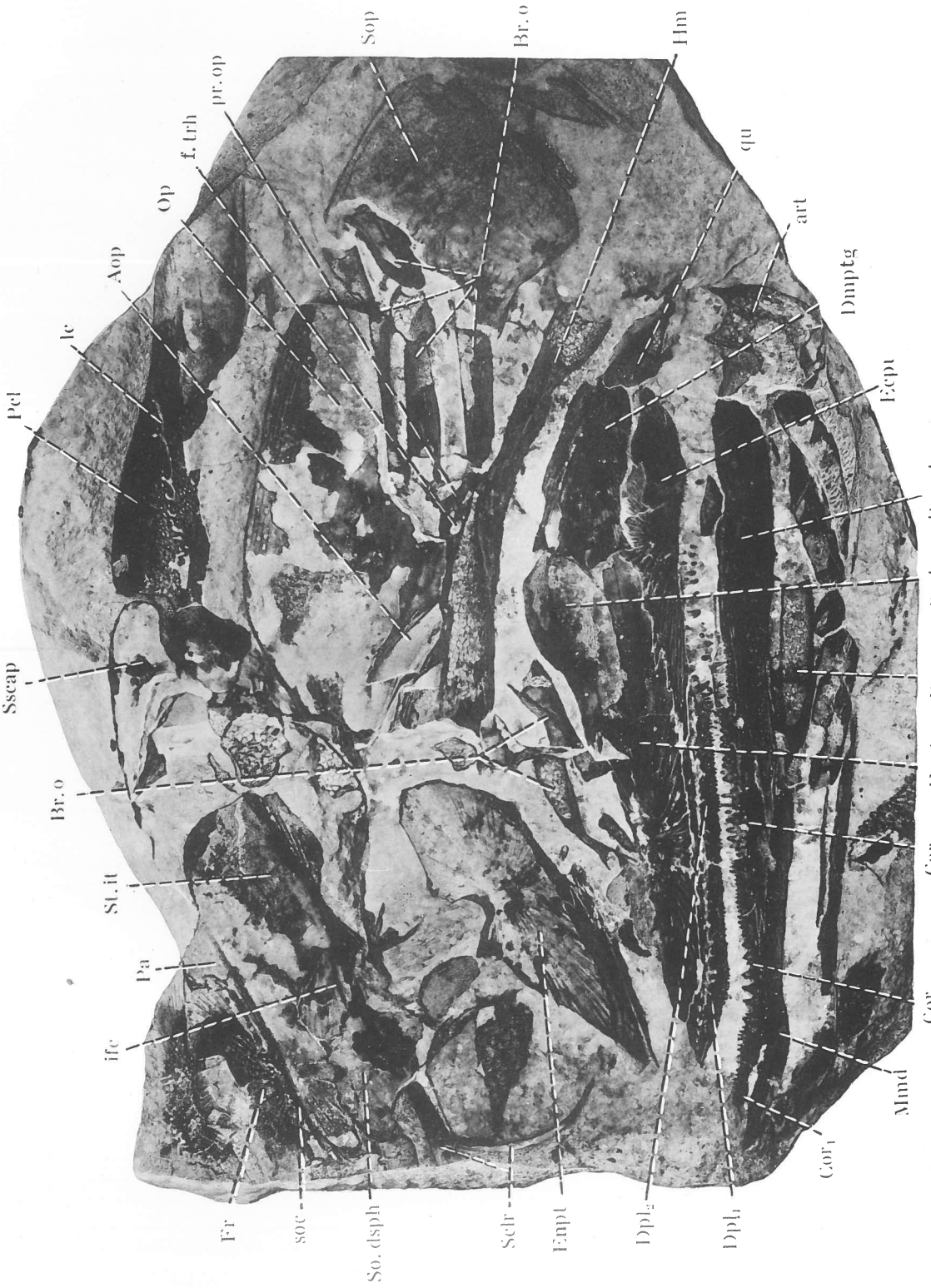

Sscap
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HbrI
HbrII
CbrIV
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Chy
Md
CbrI
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Cl
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ObrI
EbrI

Plate 18.

Glaucolepis gunnari n. sp.
Incomplete and compressed head in lateral view. Specimen No. 158. 3 ×.

Aop, antoperculum; *Br. o*, ossifications in the branchial arches; Cor_1, Cor_2, Cor_3, coronoids; *Dmptg*, dermometapterygoid; Dpl_1, Dpl_2, anterior and posterior dermopalatines; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Fr*, frontal; *Hm*, hyomandibula; *Mmd*, bone in the anterior part of the mandible containing an endochondral and probably a dermal component; *Op*, operculum; *Pa*, parietal; *Pcl*, postcleithral; *Pr. art*, prearticular; *Sclr*, segment of the sclerotic ring; *So. dsph*, supraorbito-dermosphenotic; *Sop*, suboperculum; *Sscap*, suprascapular; *St. it*, supratemporo-intertemporal; *art*, pars articularis; *f. trh*, canal for the truncus hyoideomandibularis; *ifc*, infraorbital canal; *lc*, main lateral line; *mptg*, pars metapterygoidea; *pr. op*, processus opercularis; *qu*, pars quadrata; *soc*, supraorbital canal.



Nordisk Kunst- og Lystryk

Plate 19.

Glaucolepis magna n. sp.

Specimen No. 8 (same specimen as shown in Pl. 10, Fig. 1). 1.7 ×.

Fig. 1. Mandible in ventral view.

Fig. 2. Part of the palatoquadrate-maxillary apparatus in dorsal view. The greater number of the bones of the palate preserved as impressions of their oral faces.

Fig. 3. Mandible and part of the palatoquadrate-maxillary apparatus in lateral view.

Ang, angular; *Cbr*, ceratobranchial; *De.spl*, dentalo-splenial; *Dmpty*, dermometapterygoid; Dpl_1, Dpl_2, anterior and posterior dermopalatines; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Hm*, hyomandibula; *Mk*, posterior ossification in the Meckelian cartilage; *Mmd*, ossification in the anterior part of the mandible containing an endochondral and probably a dermal component; *Mx*, maxillary; *Pr. art*, prearticular; *Sympl*, symplectic; *p.md*, shallow depressions on the posterior ossification in the Meckelian cartilage; *qu*, pars quadrata, *s.pq*, groove on the medial face of the palatoquadrate.

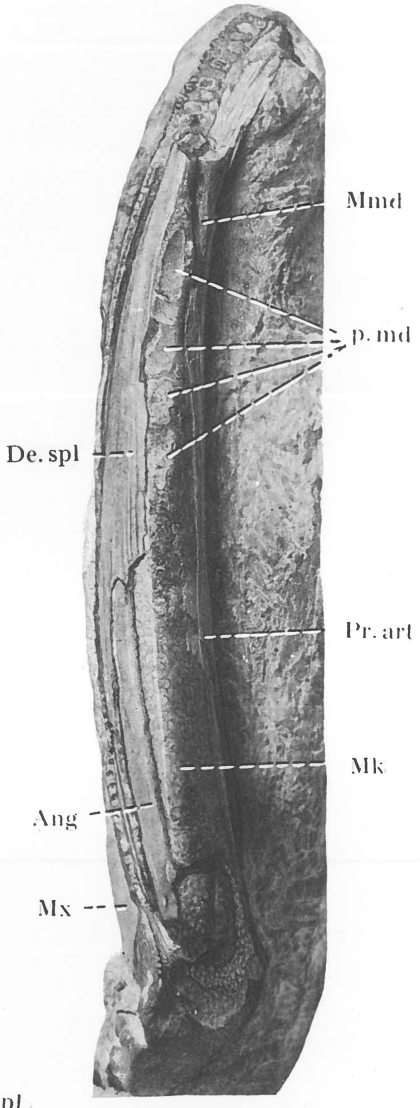


Fig. 1

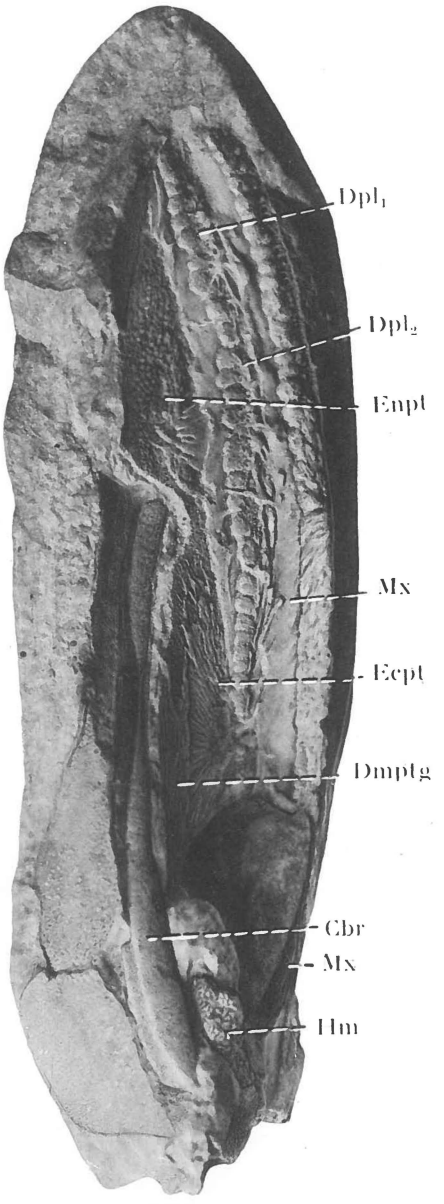


Fig. 2

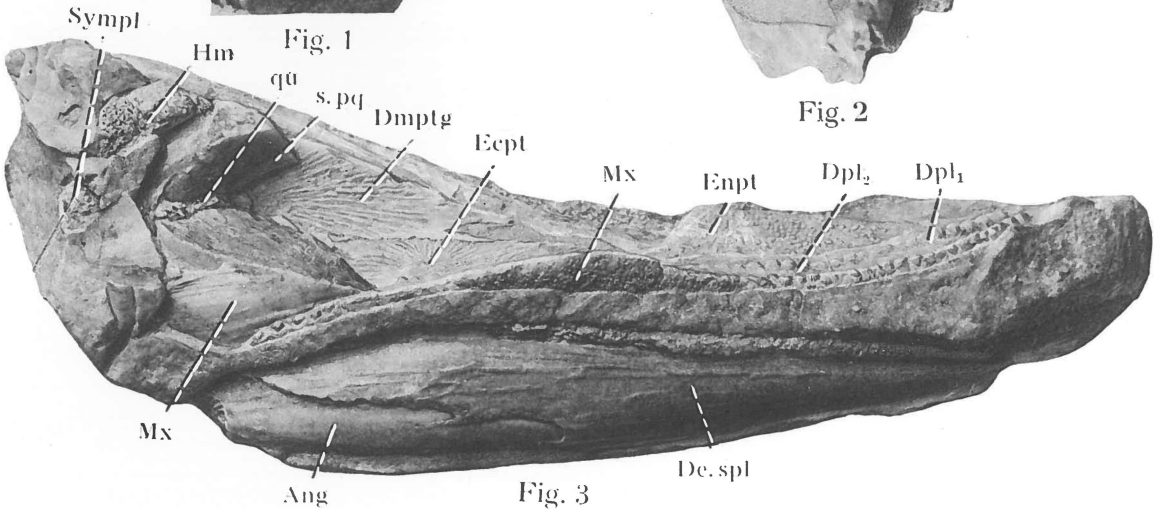


Fig. 3

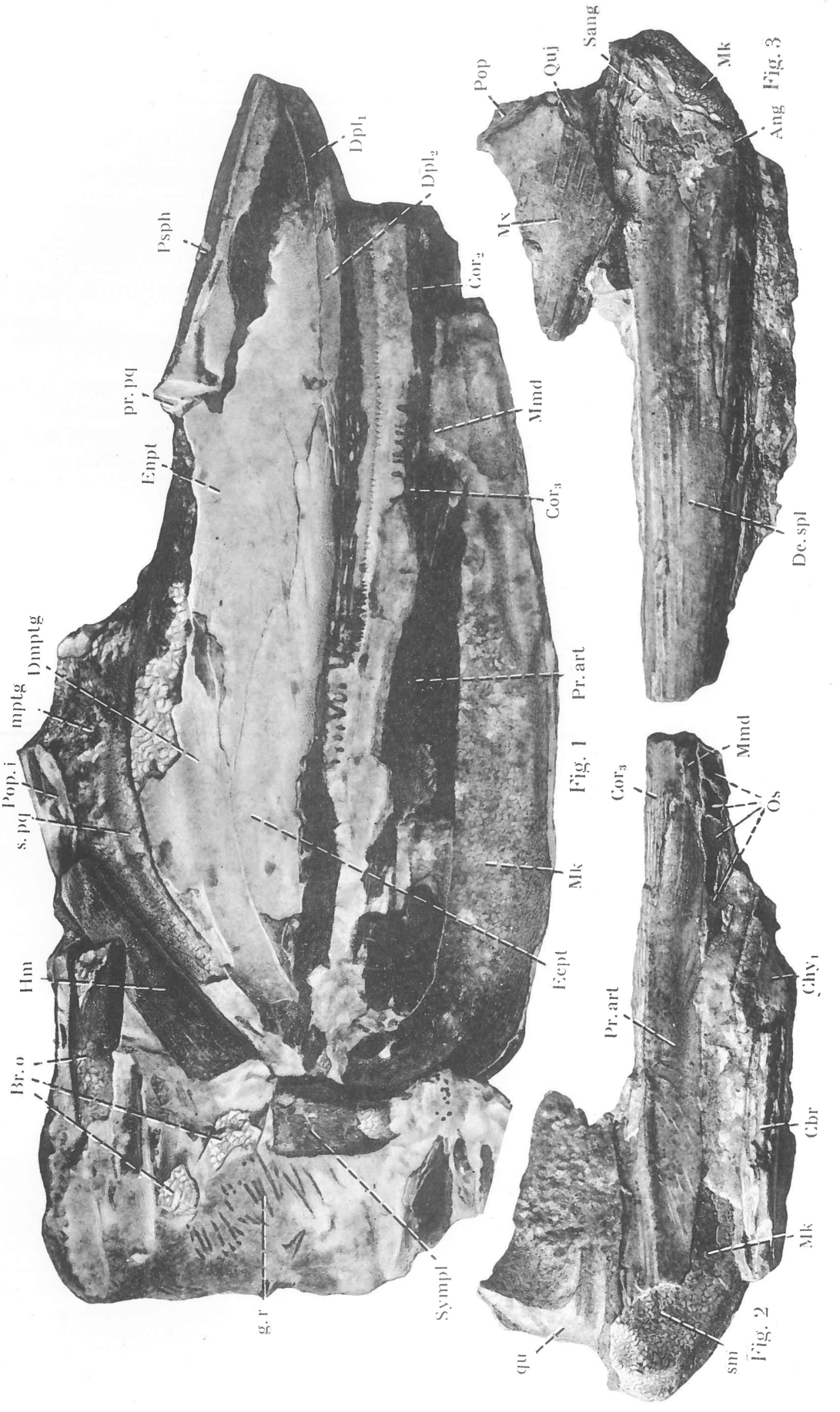
Nordisk Kunst- og Lystryk

Plate 20.

Fig. 1. *Glaucolepis aldingeri* n. sp. Palatoquadrate-maxillary apparatus, mandible, and other bones in medial view. Specimen No. 43. 3 ×.

Figs. 2 and 3. *Glaucolepis magna* n. sp. Incomplete mandible and postero-ventral part of the palatoquadrate-maxillary apparatus in medial and in lateral view respectively. Specimen No. 1 (same specimen as shown in Pl. 6, Fig. 3, and Pl. 8, Fig. 1). 3 ×.

Ang, angular; *Br. o*, ossifications in the branchial arches; *Cbr*, ceratobranchial; Chy_1, anterior ceratohyal ossification; Cor_2, Cor_3, middle and posterior coronoids; *De. spl*, dentalosplenial; *Dmptg*, dermometapterygoid; Dpl_1, Dpl_2, anterior and posterior dermopalatines; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Hm*, hyomandibula; *Mk*, posterior ossification in the Meckelian cartilage; *Mmd*, ossification in the anterior part of the mandible containing an endochondral and probably a dermal component; *Mx*, maxillary; *Os*, remains of small tooth-bearing dermal bones; *Pop*, preoperculum; *Pop. i*, internal lamina of the preoperculum; *Pr. art*, prearticular; *Psph*, parasphenoid; *Quj*, quadratojugal; *Sang*, supraangular; *Sympl*, symplectic; *g. r*, gill rays; *mptg*, pars metapterygoidea; *pr. pq*, process which articulated against the processus basipterygius; *qu*, pars quadrata; *sm*, groove for nerves and (?) vessels; *s. pq*, groove on the medial face of the palatoquadrate.



Nordisk Kunst- og Lystryk

Plate 21.

Fig. 1. *Glaucolepis gunnari* n. sp. Pelvic plate and endoskeleton of the pelvic fin in ventral view and part of the vertebral column of the anterior part of the abdominal region in ventro-lateral view. Specimen No. 3 (same specimen as shown in Figs. 2 and 3). 3 ×.

Fig. 2. *Glaucolepis gunnari* n. sp. Part of the vertebral column of the anterior part of the abdominal region in lateral view. Specimen No. 3 (same specimen as shown in Figs. 1 and 3). 3 ×.

Fig. 3. *Glaucolepis gunnari* n. sp. Pelvic plate and endoskeleton of the pelvic fin in ventro-lateral view and part of the vertebral column of the anterior part of the abdominal region in ventral view. Specimen No. 3 (same specimen as shown in Figs. 1 and 2). 3 ×.

Fig. 4. *Glaucolepis magna* n. sp. Fragment of the middle part of the abdominal region with part of the vertebral column. Specimen No. 46. 2 ×.

Bd basidorsal; *Bv* + *Iv*, basiventral + interventral; *Mt*, metapterygial element; Po_1, Po_6, Po_8, first, sixth and eight proximal ossifications in the endoskeleton of the pelvic fin; *Pv*, pelvic plate; *cr*, crista on lateral face of ventral arcual ossification; *f.isv*, foramen for intersegmental vessels; *f.v*, foramen for a vessel; *n.isv*, notch for intersegmental vessels.

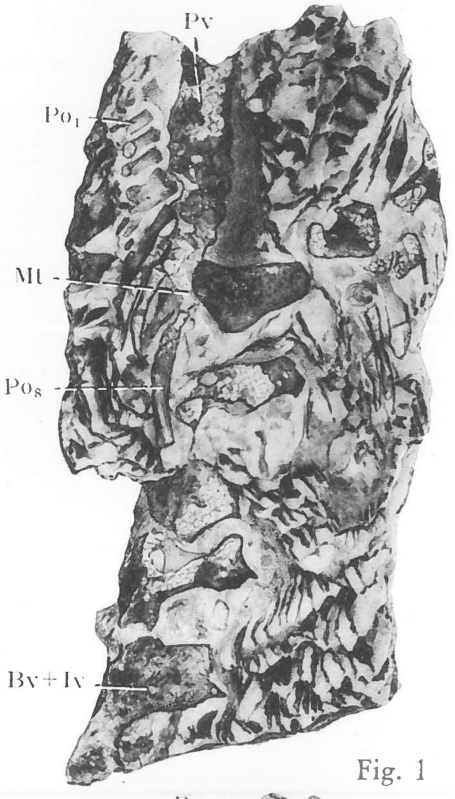


Fig. 1

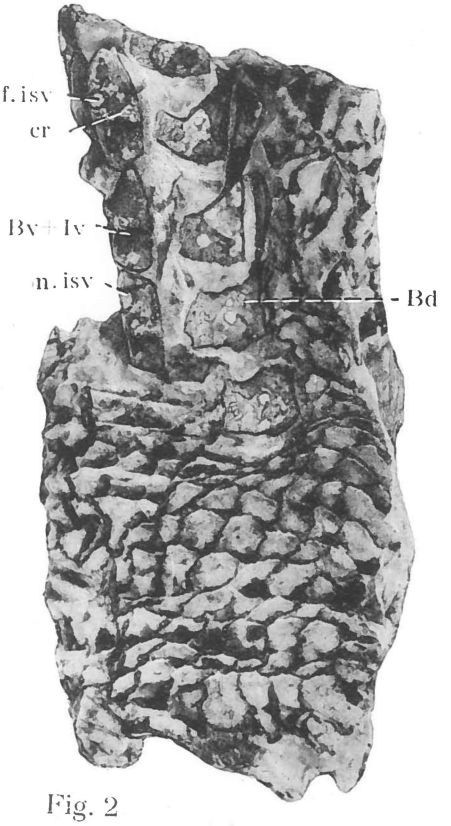


Fig. 2

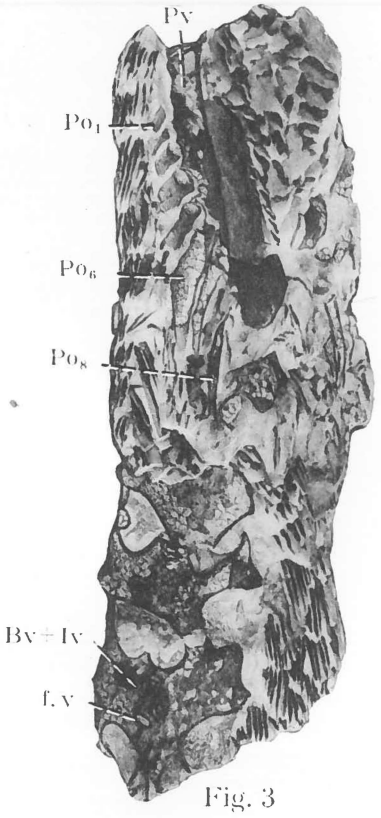


Fig. 3

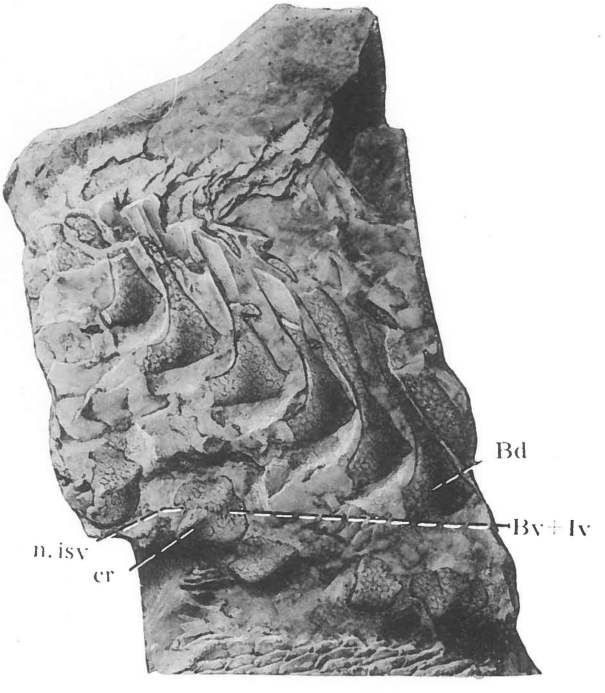


Fig. 4

Plate 22.

Fig. 1. *Glaucolepis magna* n. sp. Pectoral fins and ventral parts of shoulder girdle in ventral view. Specimen No. 60 (same specimen as shown i Fig. 2 and in Pl. 23). 2.7 ×.
Fig. 2. *Glaucolepis magna* n. sp. Counterpart to the right pectoral fin shown in Fig. 1. 2.7 ×.

Cl, cleithrum; *Cla*, clavicle; Do_{1-6}, first to sixth distal ossifications in the endoskeleton of the pectoral fin; *Eg*, endoskeletal ossification of the shoulder girdle; *Pec*, pectoral fin; Po_{1-6}, first to sixth proximal ossifications in the endoskeleton of the pectoral fin.

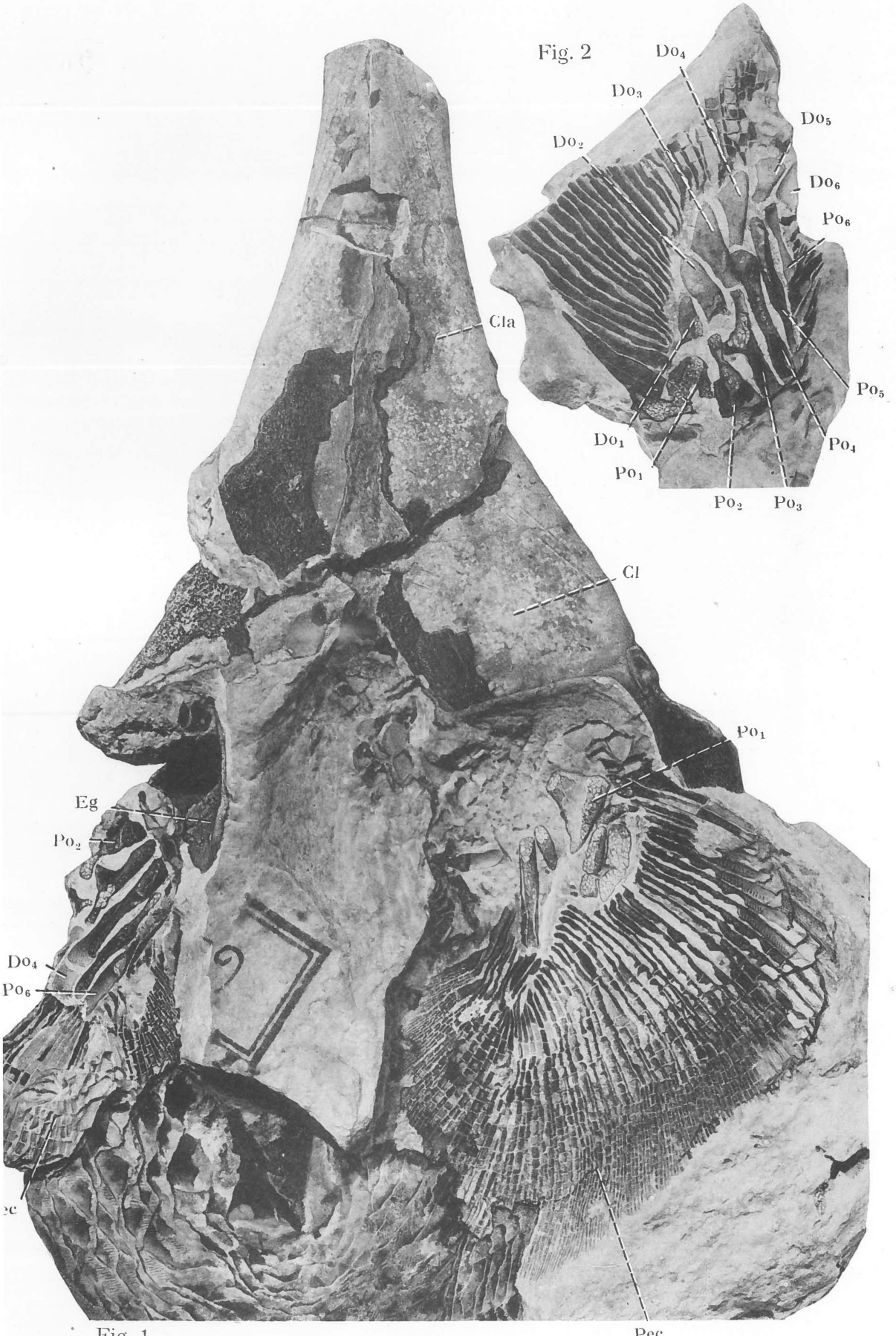


Fig. 1

Nordisk Kunst- og Lystryk

Plate 23.

Fig. 1. *Glaucolepis magna* n. sp. Dorsal view of the specimen shown in Pl. 22, Fig. 1. 2.7 ×.
Fig. 2. *Glaucolepis magna* n. sp. Left endoskeletal shoulder girdle ossification of the specimen shown in Fig. 1, in postero-dorso-medial view. 2.7 ×.

Bd, basidorsal; *Cl*, cleithrum; *Cla*, clavicle; *Eg*, endoskeletal ossification of the shoulder girdle; *Sn*, supraneurals; *f.dz*$_1$, *f.dz*$_2$, foramina for diazonal nerves; *m.r*, margo radialis; *msc*, mesocoracoid arch; *pr.cla*, postero-dorsally directed process of the clavicle; *pr.gl*, processus glenoidalis; *pr.r*, processus radialis.

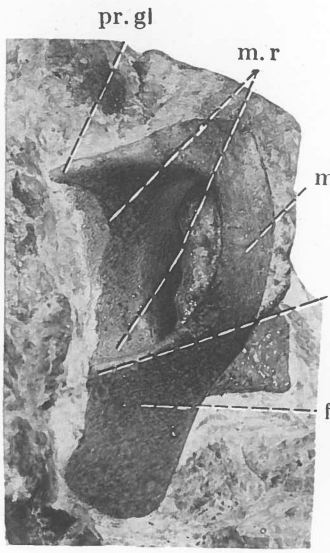


Fig. 2

Fig. 1

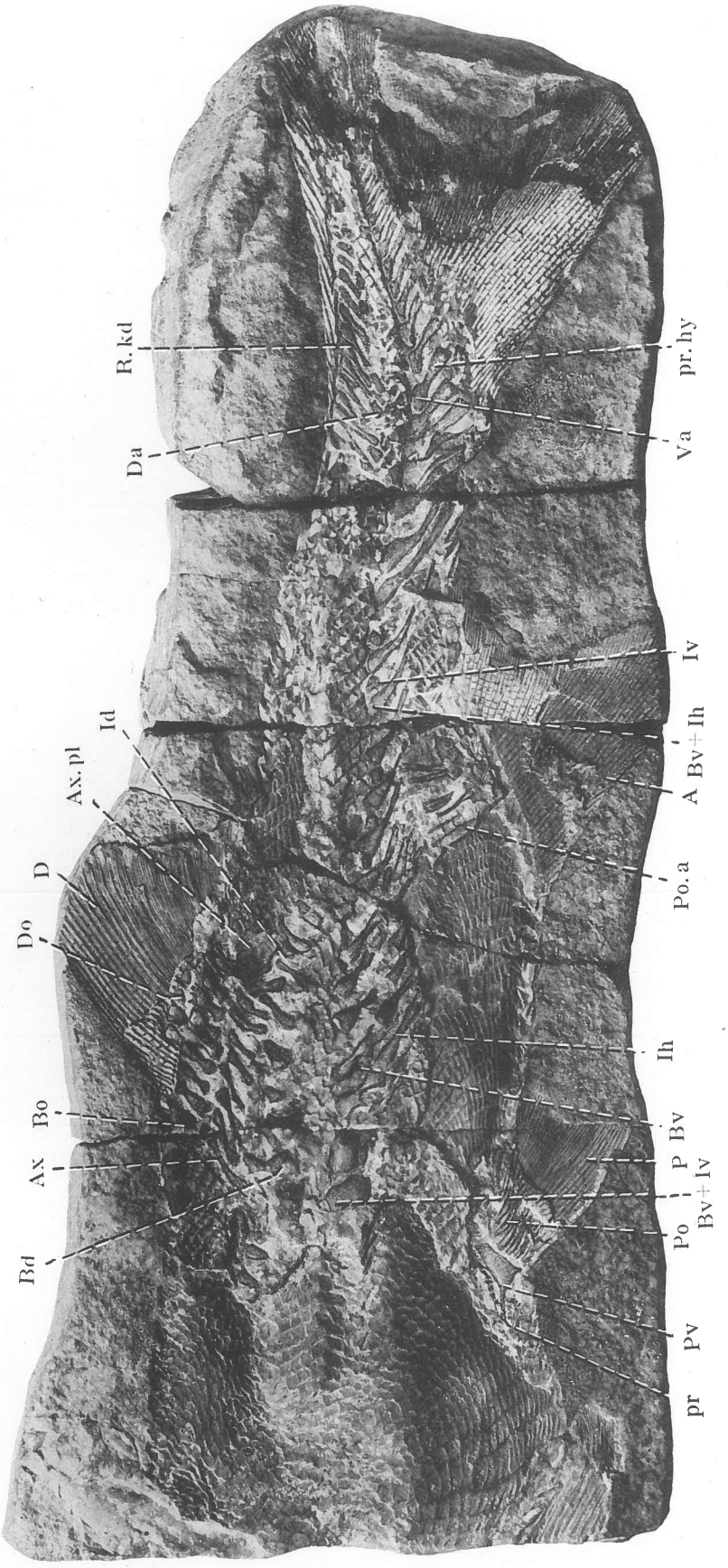
Nordisk Kunst- og Lystryk

Plate 24.

Glaucolepis aldingeri n. sp. Holotype.

The greater part of the abdominal region and the caudal region in lateral view. Specimen No. 66. Nat. size.

A, anal fin; *Ax*, axonost; *Ax.pl*, compound axonost (axonost plate); *Bd*, basidorsal; *Bo*, baseost; *Bv*, basiventral; *Bv* + *Ih*, basiventral + infrahaemal; *Bv* + *Iv*, basiventral + interventral; *D*, dorsal fin; *Da*, dorsal arcual ossification in the caudal region; *Do*, distal radial ossification in the endoskeleton of the dorsal fin; *Id*, interdorsal; *Ih*, infrahaemal; *Iv*, interventral; *P*, pelvic fin; *Po*, proximal ossification in the endoskeleton of the pelvic fin; *Po.a*, proximal radial ossification in the endoskeleton of the anal fin; *pr*, anteromedially directed process of the pelvic plate; *Pv*, pelvic plate; *R.kd*, epichordal radial ossification in the endoskeleton of the caudal fin; *Va*, arcual division of a hypochordal ossification in the body axis of the caudal fin; *pr.hy*, hypural process.



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Plate 25.

Boreosomus piveteaui n. sp.

Incomplete neural endocranium. Specimen No. 307. 3 ×.

Fig. 1. Dorsal view.
Fig. 2. Lateral view.
Fig. 3. Same view as in Fig. 2, but after further preparation.

aort, posterior opening of the aorta canal; *bsph*, pars basisphenoidea; *c.sem.ant*, *s.sem.ext*, *c.sem.post*, divisions of the labyrinth cavity for the canalis semicircularis anterior, the canalis semicircularis externus, and the canalis semicircularis posterior respectively; *dic*, division of the cavum cerebrale cranii for the diencephalon; *fb*, fossa bridgei; *fen.opt*, fenestra optica; *fo*, opening in the wall between the cavum cerebrale cranii and an intramural space in the wall of the otic region; $font_1$, anterior dorsal fontanelle; *f.occ.lat*, fissura occipitalis lateralis; *l.opt*, division of the cavum cerebrale cranii for the lobi optici; *met*, division of the cavum cerebrale cranii for the lateral part of the metencephalon; *my*, posterior myodome; *my.ant.d*, anterior dorsal myodome; *my.ant.v*, anterior ventral myodome; *n IX*, notch for the ramus supratemporalis dorsalis glossopharyngei; *np*, nasal pit; *ru*, division of the labyrinth cavity for the recessus utriculi; *sa*, ridge above the canalis semicircularis anterior; *sacc*, division of the labyrinth cavity for the sacculus; *sp*, ridge above the canalis semicircularis posterior; *spic*, spiracular canal; *s.us*, division of the labyrinth cavity for the sinus utriculi superior; *tel*, division of the cavum cerebrale cranii for the telencephalon; *II*, opening for the nervi optici; *III*, canal for the nervus oculomotorius; *IV*, canal for the nervus trochlearis.

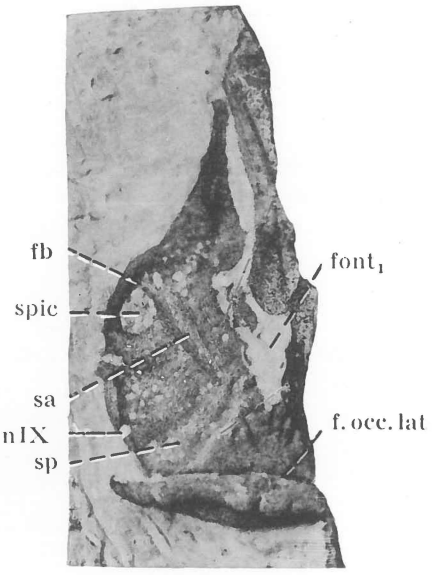


Fig. 1

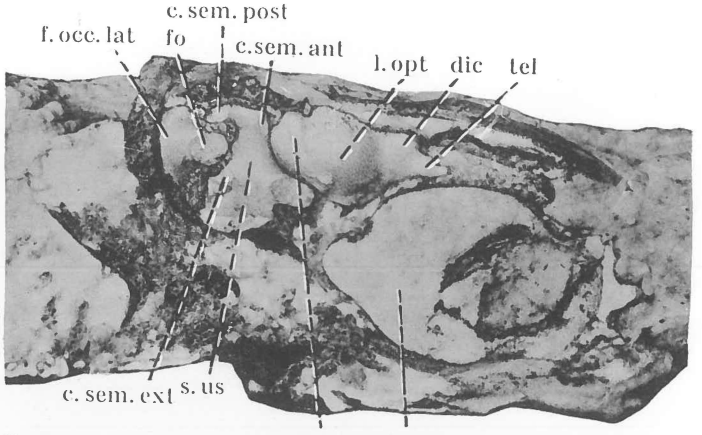


Fig. 2

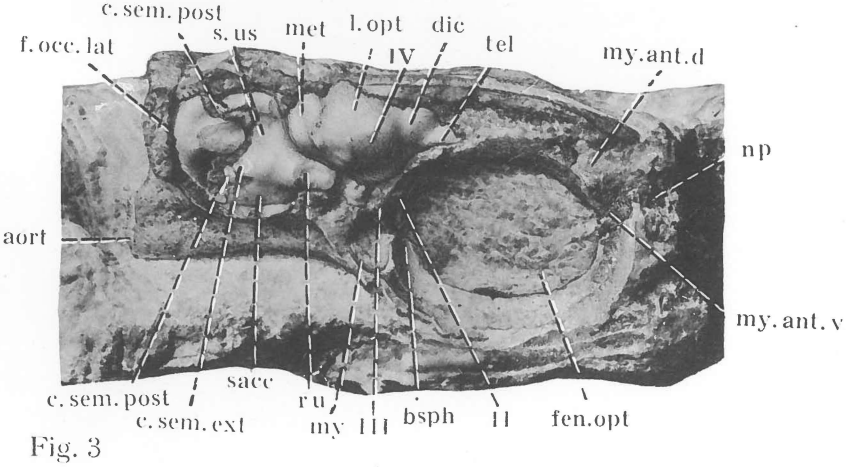


Fig. 3

Nordisk Kunst- og Lystryk

Plate 26.

Fig. 1. *Boreosomus piveteaui* n.sp. Neural endocranium with a few dermal bones in lateral view. Specimen No. 296 (same specimen as shown in Pl. 27, Fig. 1, and Pl. 28). 3 ×.

Fig. 2. *Boreosomus piveteaui* n.sp. Part of the neural endocranium in dorsal view. Specimen No. 232 (Counterpart to the specimen shown in Pl. 27, Fig. 2). 3 ×.

Fr, frontal; *Na*, nasal; *Psph*, parasphenoid; *Ptr*, postrostral; *So.dsph*, supraorbito-dermosphenotic; *a.aort*, anterior opening of the aorta canal; *aort*, posterior opening of the sorta canal; *a.eff*$_2$, opening for the arteria branchialis efferens II; *cn*, notochordal space; *cr.m*, median crista on the dorsal face of the orbitotemporal region; *crop*, processus cranio-spinalis; *fb.f*, opening in the wall between the fossa bridgei and an intramural space in the wall of the otic region; *fen.opt*, fenestra optica; *f. hm*, articular fossa for the hyomandibula; *f.occ.lat*, fissura occipitalis lateralis; *f.ot.v*, fissura oticalis ventralis; *inf*, division of the cavum cerebrale cranii for the ventral part of the diencephalon; *jd*, jugular depression; *my*, posterior myodome; *my.ant.d*, anterior dorsal myodome; *my.ant.v*, anterior ventral myodome; *n IX*, notch for the ramus supratemporalis dorsalis glossopharyngei; *pr.po*, processus postorbitalis; *ram.dors*, canals for branches of the ramus ophthalmicus superficialis trigemini, the nervus ophthalmicus lateralis, and vessels; *r.ot*, canal for the ramus oticus lateralis; *sa*, ridge above the canalis semicircularis anterior; *sacc*, division of the labyrinth cavity for the sacculus; *soc*, supraorbital canal; *sp*, ridge above the canalis semicircularis posterior; *spi*, canal for a spino-occipital nerve; *tel*, division of the cavum cerebrale cranii for the telencephalon; *trig.fac.ch*, trigemino-facialis chamber; *v.font*, vestibular fontanelle; *II*, opening for the nervi optici; *III*, canal for the nervus oculomotorius; *V*, trigeminus canal; *VI*, canal for the nervus abducens; *VII*, facialis canal; *IX*, canal for the nervus glossopharyngeus; *X*, canal for the nervus vagus.

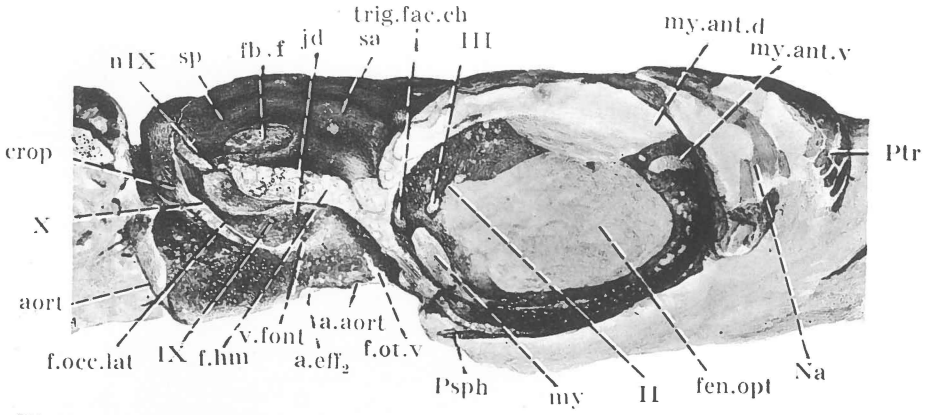


Fig. 1

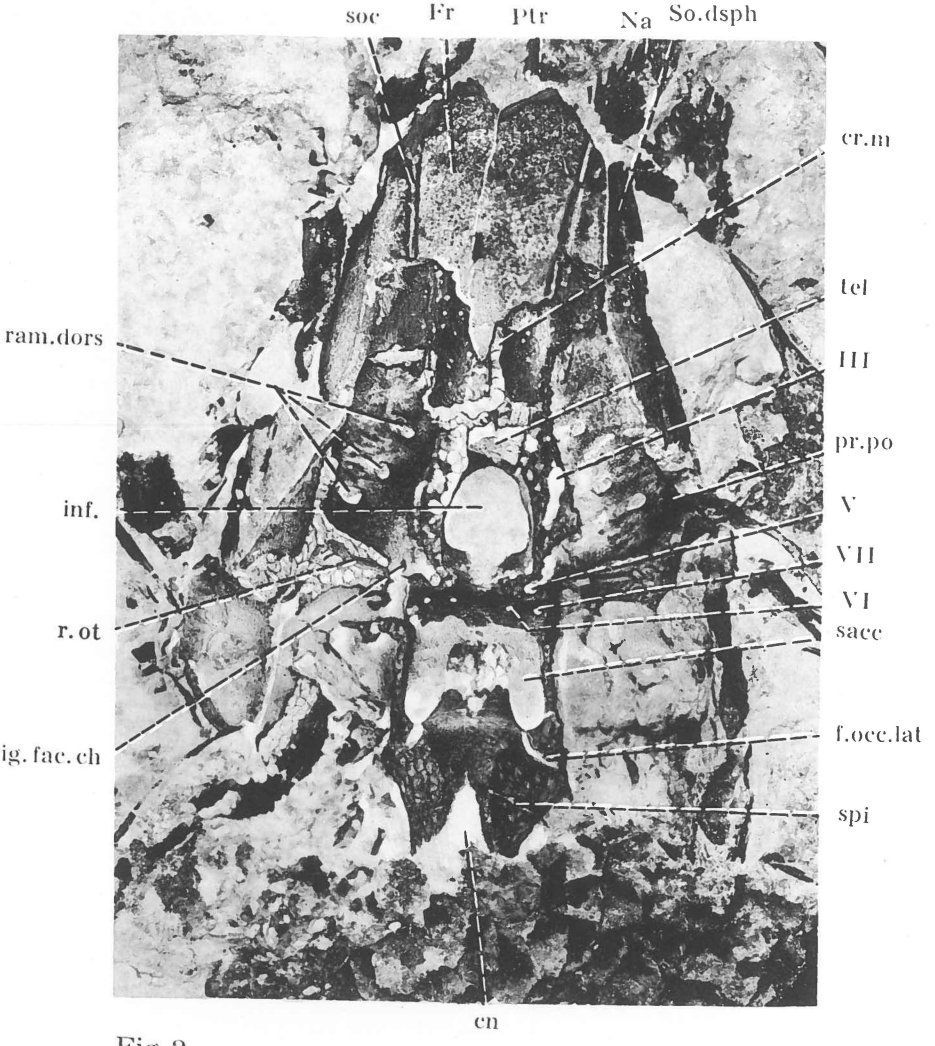


Fig. 2

Nordisk Kunst- og Lystryk

Plate 27.

Fig. 1. *Boreosomus piveteaui* n.sp. Neural endocranium with a few dermal bones in ventral view. Specimen No. 296 (same specimen as shown in Pl. 26, Fig. 1, and Pl. 28). 3 ×.

Fig. 2. *Boreosomus piveteaui* n.sp. Part of the neural endocranium in ventral view. Specimen No. 232 (counterpart to the specimen shown in Pl. 26, Fig. 2). 3 ×.

Fr, frontal; *Na*, nasal; *Psph*, parasphenoid; *Ptr*, postrostral; *So.dsph*, supraorbito-dermosphenotic; *a.aort*, anterior opening of the aorta canal; *aort*, posterior opening of the aorta canal; *a.eff*$_2$, opening for the arteria branchialis efferens II; *c.ju*, posterior opening of the jugulo-hyoideomandibular canal; *cr.m*, median crista on the dorsal face of the orbitotemporal region; *f.m*, foramen magnum; *f.occ.lat*, fissura occipitalis lateralis; *f.ot.v*, fissura oticalis ventralis; *jd*, jugular depression; *n IX*, notch for the ramus supratemporalis dorsalis glossopharyngei; *ram.dors*, canals for branches of the ramus ophthalmicus superficialis trigemini, the nervus ophthalmicus lateralis and vessels; *r.ot*, canal for the ramus oticus lateralis; *sacc*, division of the labyrinth cavity for the sacculus; *spi*, canal for a spino-occipital nerve; *spic*, spiracular canal; *tel*, division of the cavum cerebrale cranii for the telencephalon; *utr*, division of the labyrinth cavity for the anterior part of the utriculus; *v.font*, vestibular fontanelle; *IV*, canal for the nervus trochlearis; *V*, trigeminus canal; *VI*, canal for the nervus abducens; *VII*, facialis canal; *X*, canal for the nervus vagus.

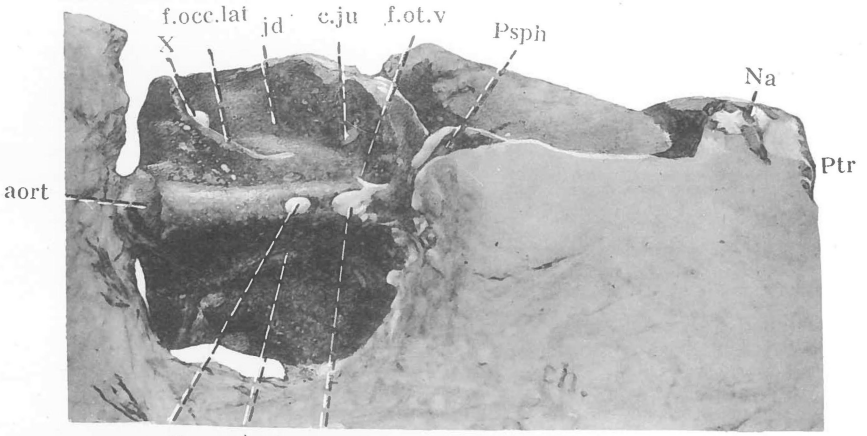


Fig. 1

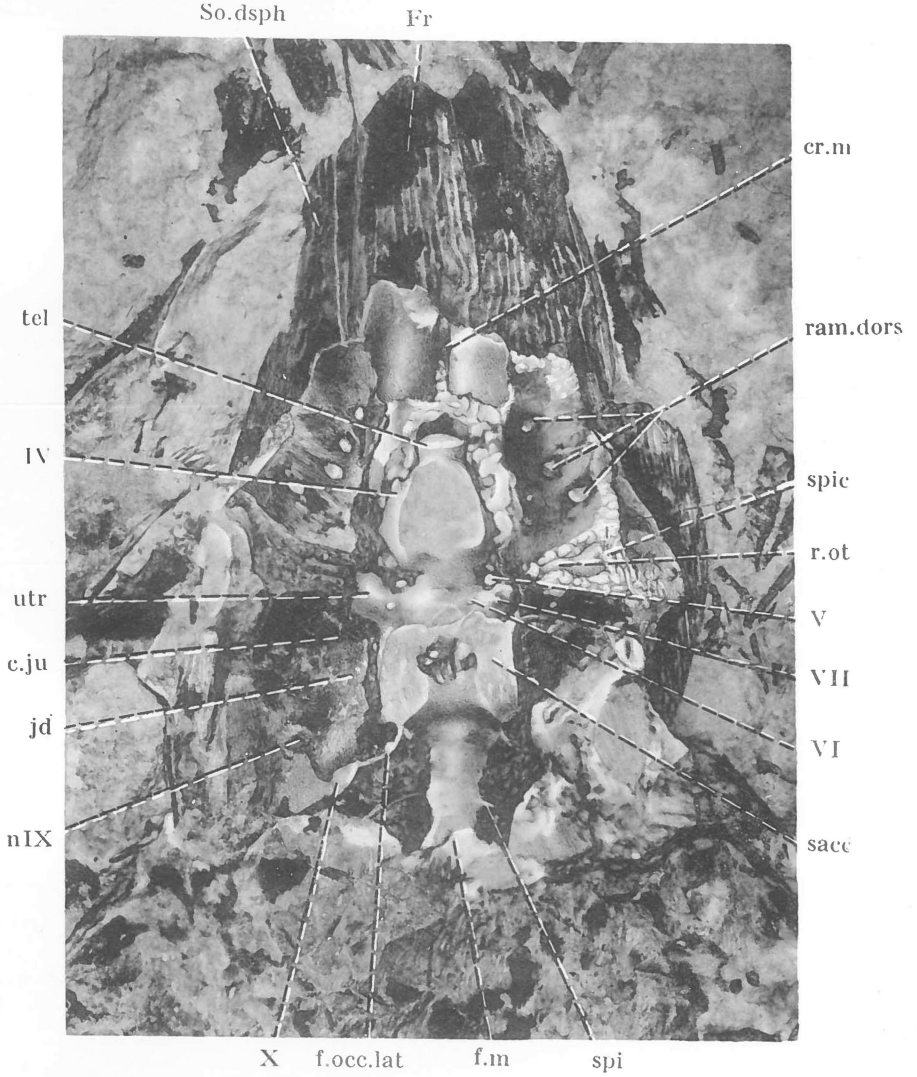


Fig. 2

Nordisk Kunst- og Lystryk

Plate 28.

Boreosomus piveteaui n. sp.

Incomplete fish in dorsal view. Specimen No. 296 (same specimen as shown in Pl. 26, Fig. 1, and Pl. 27, Fig. 1). 3 ×.

Ax, axonost; *Ba*, baseost; *D*, dorsal fin; *Do*, distal radial ossification in the endoskeleton of the dorsal fin; *Ptr*, postrostral; *cr.m*, median crista on the dorsal face of the orbito-temporal region; *fb*, fossa bridgei; *fb. f*, opening in the wall between the posterior part of the fossa bridgei and an intramural space in the wall of the otic region *f.occ.lat*, fissura occipitalis lateralis; $font_1$, $font_2$, anterior and posterior dorsal fontanelles; *ram.dors*, canals for branches of the ramus ophthalmicus superficialis trigemini, the nervus ophthalmicus lateralis, and vessels; *sa*, ridge above the canalis semicircularis anterior; *sp*, ridge above the canalis semicircularis posterior; *spic*, spiracular canal.

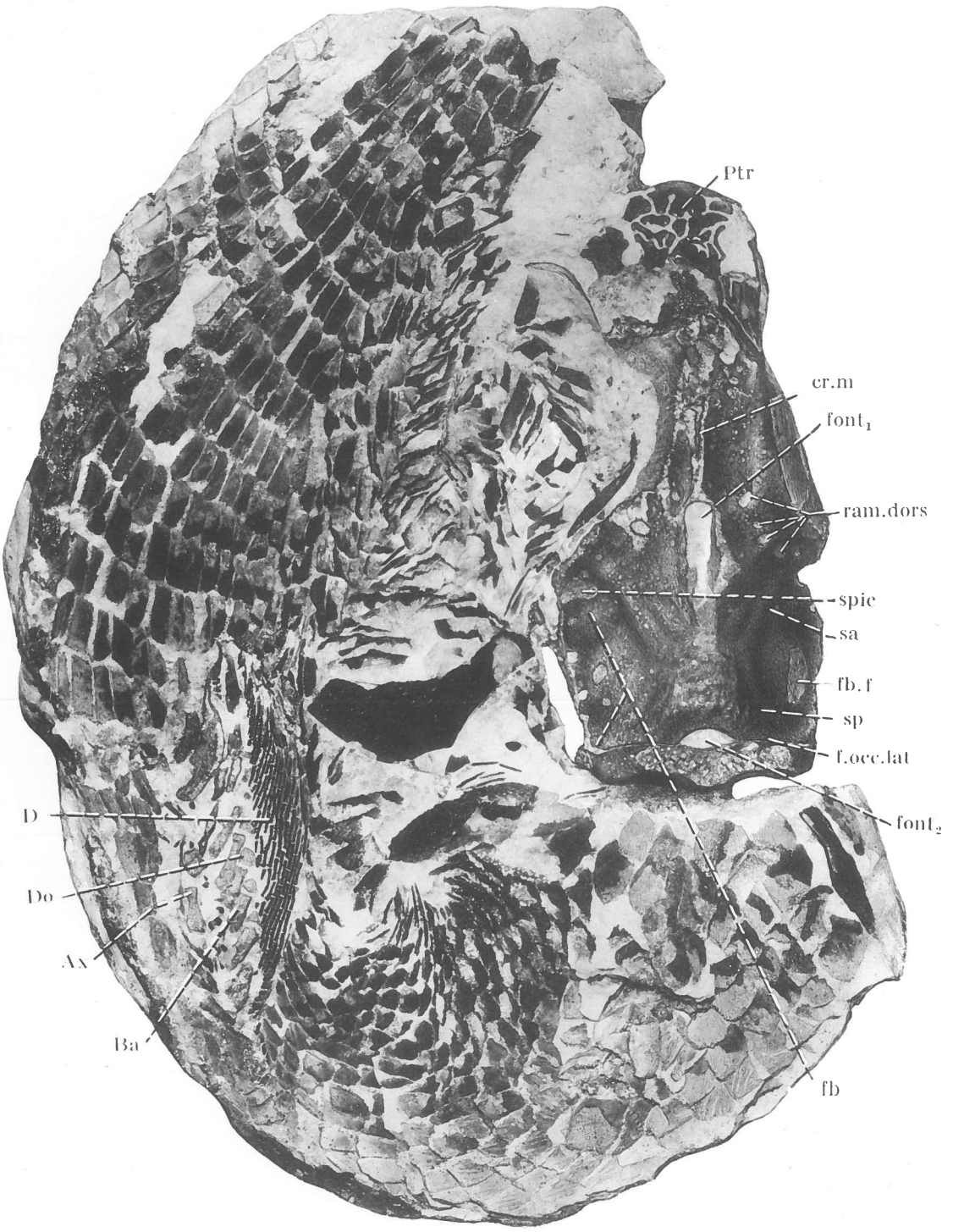

Ptr
cr.m
font$_1$
ram.dors
spic
sa
fb.f
sp
f.occ.lat
font$_2$
D
Do
Ax
Ba
fb

Plate 29.

Figs. 1 and 2. *Boreosomus piveteaui* n. sp. The head used for serial sectioning, in dorsal and in lateral view respectively. Specimen No. 310. 5 ×.

Cbr, ceratobranchial; *Ebr*, epibranchial; *Ext.m*, medial extrascapular; *Fr*, frontal; *Mx*, maxillary; *Na*, nasal; *Pa*, parietal; *Pcl*, postcleithral; *Pop*, preoperculum; *Pq*, palatoquadrate; *Ptr*, postrostral; *So.dsph*, supraorbito-dermosphenotic; *Sscap*, suprascapular; *St.it*, supratemporo-intertemporal; *ifc*, infraorbital canal; *lc*, main lateral line; *n*, notch in the margin of the supratemporo-intertemporal dorsally to the dorsal end of the hyomandibula; *poc*, preopercular canal; *s.com*, supratemporal commissure.

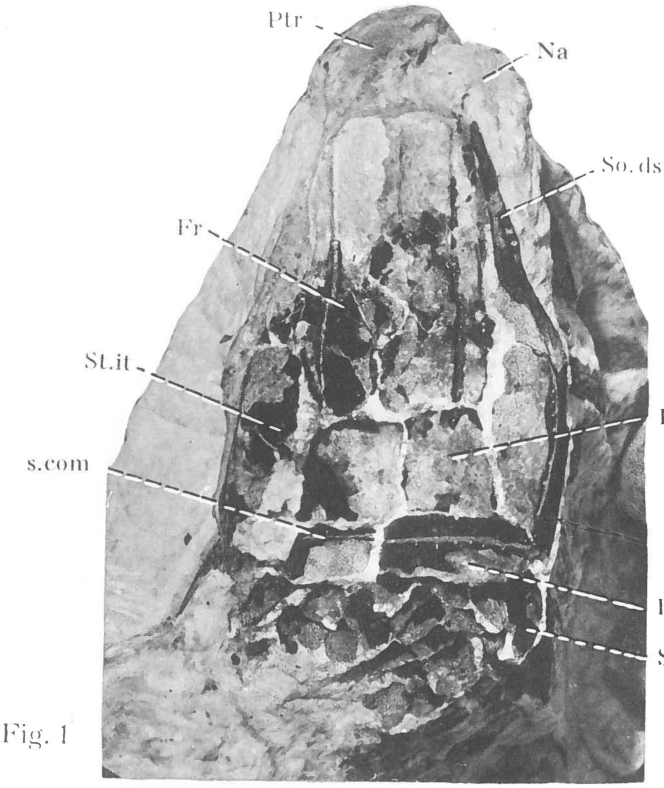


Fig. 1

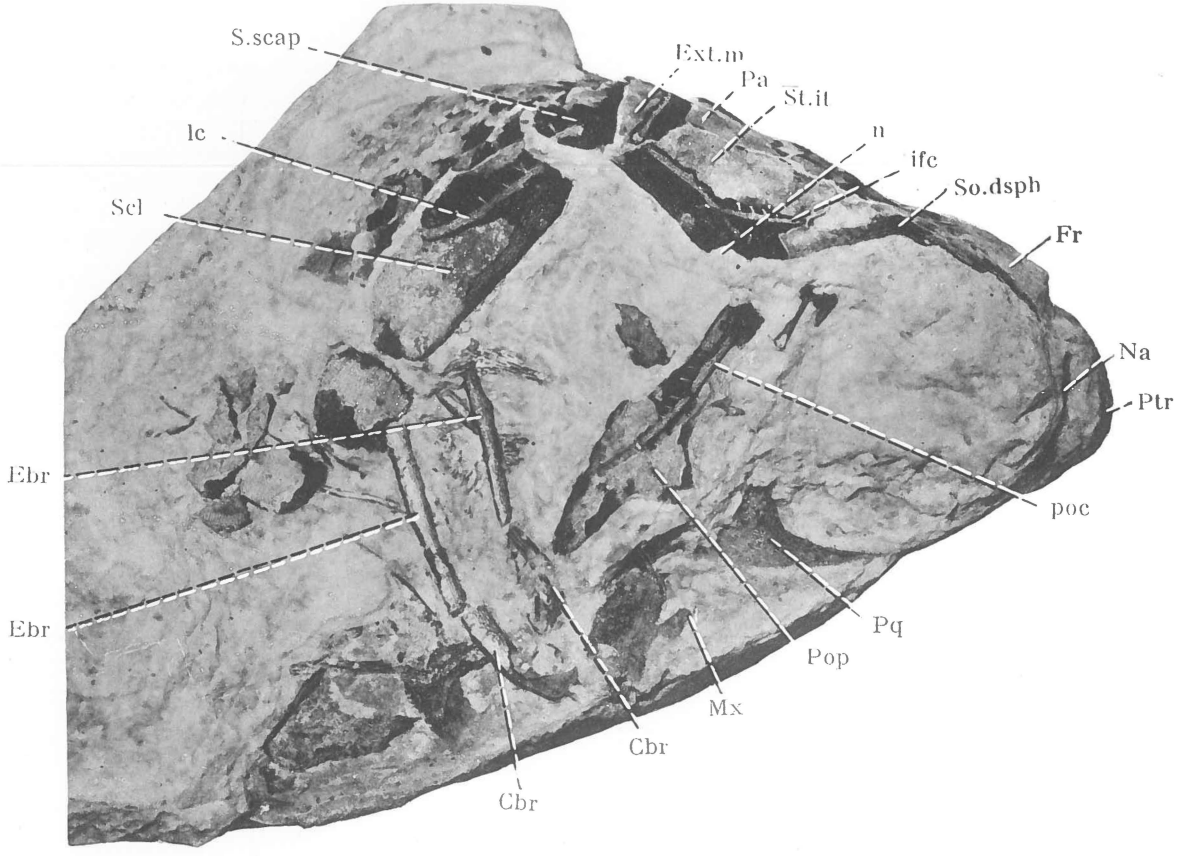


Fig. 2

Nordisk Kunst- og Lystryk

Plate 30.

Fig. 1. *Boreosomus piveteaui* n.sp. Neural endocranium and various ossifications of the visceral skeleton. Specimen No. 295. 3 ×.

Fig. 2. *Boreosomus piveteaui* n.sp. Anterior part of the endocranium shown in Fig. 1, in lateral view. 3 ×.

Ang, angular; *Ebr I-IV*, epibranchials I-IV; *Hm*, hyomandibula; *Ifbr*, infrapharyngobranchial; *Mk*, Meckelian bone; *Pq*, palatoquadrate; *Psph*, parasphenoid; *aort*, posterior opening of the aorta canal; $a.eff_2$, opening for the arteria branchialis efferens II; *aup*, pars autopalatina; *c.ju*, posterior opening of the jugulo-hyoideomandibular canal; *f.art*, articular fossa for the processus basipterygius; *fen.opt*, fenestra optica; *jd*, jugular depression; *mdc*, mandibular canal; *my.ant.d*, anterior dorsal myodome; *my.ant.v*, anterior ventral myodome; *pl.ant*, planum antorbitale; $pr.asc_1$, processus ascendens anterior of the parasphenoid; $pr.asc_2$, processus ascendens posterior of the parasphenoid; *pr.po*, processus postorbitalis; *qu*, pars quadrata.

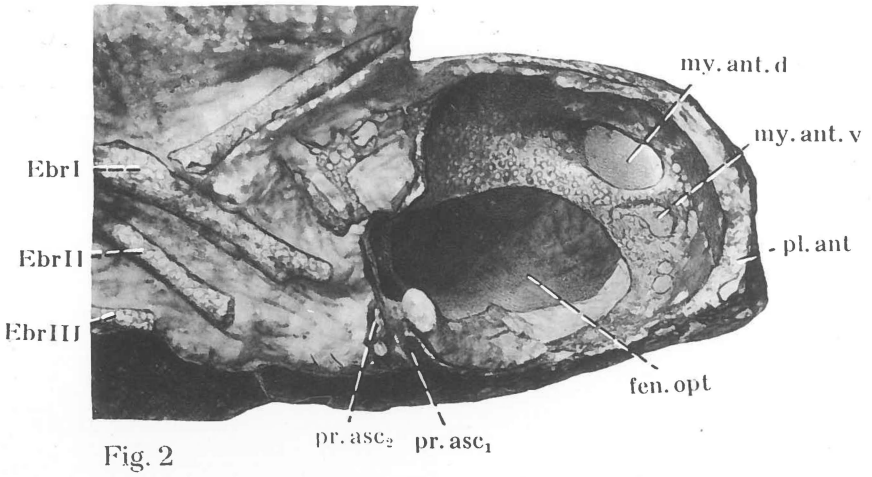


Fig. 2

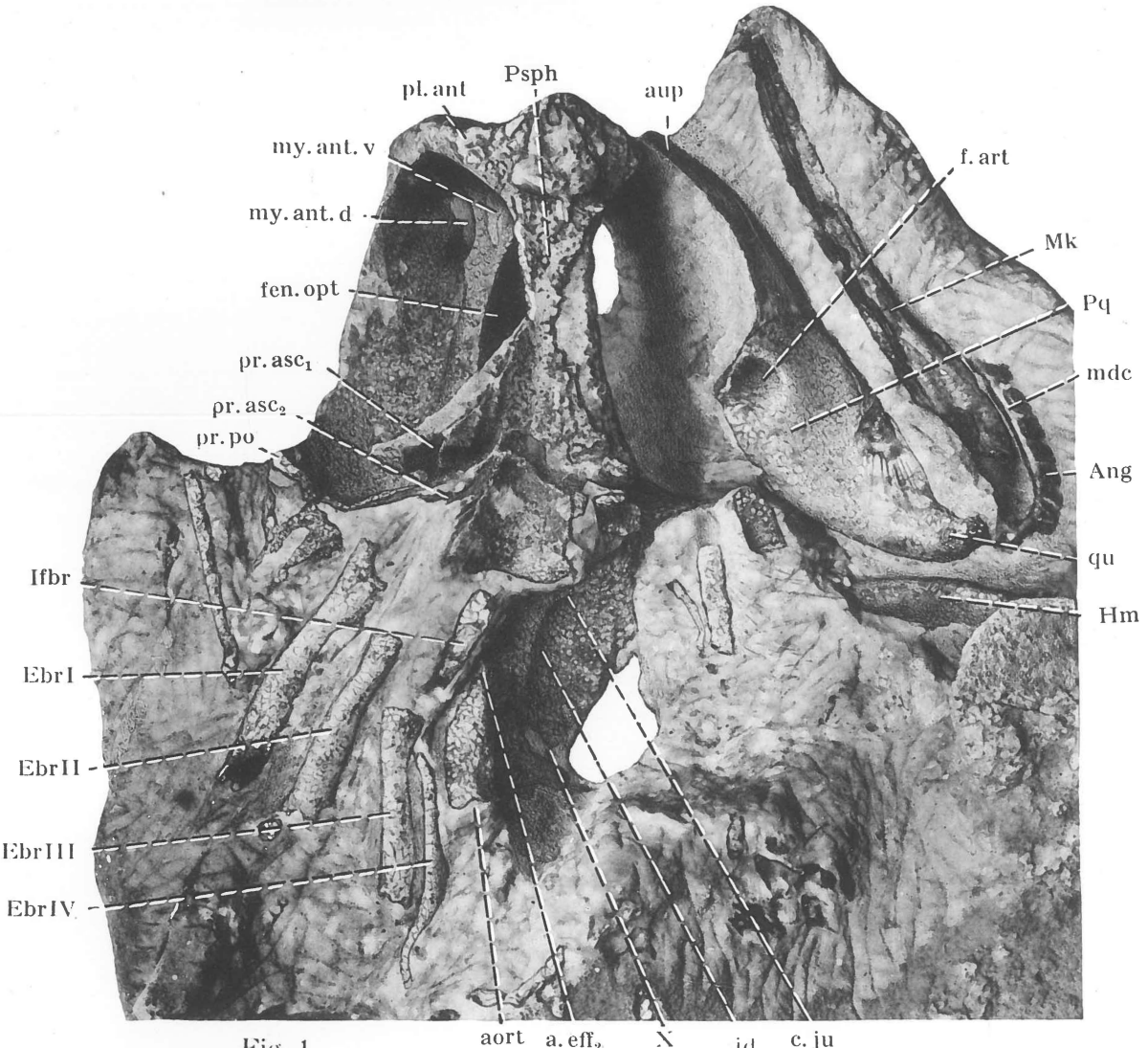


Fig. 1

Nordisk Kunst- og Lystryk