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STUDIES ON TRIASSIC FISHES II.

BY
EIGIL NIELSEN

WITH 82 FIGURES IN THE TEXT
AND 20 PLATES

KØBENHAVN
C. A. REITZELS FORLAG
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FORORD

Det foreliggende bind, der danner en fortsættelse af dr. *Eigil Nielsens* bearbejdelse af triasfisk fra Østgrønland (Palæozoologica Groenlandica bd. I, Meddelelser om Grønland bd. 138), har ligeledes modtaget værdifuld støtte fra billedhugger *Viggo Jarl,* der har bekostet tavlernes fremstilling og fremstilling af clichéer, hvorfor jeg herved udtaler vor bedste tak.

PRÉFACE

Le présent volume, qui est la suite de l'étude de M. le Dr. *Eigil Nielsen* sur les poissons triasiques du Groenland oriental (Palæozoologica Groenlandica, vol. I, Meddelelser om Grønland, vol. 138), a également reçu un appui d'une grande valeur de la part de M. *Viggo Jarl,* sculpteur, qui a fait les frais de l'exécution des tableaux et des clichés; je tiens à profiter de cette occasion pour lui en exprimer nos vifs remerciements.

Universitetets zoologiske Museum, København, i december 1949.

R. SPÄRCK

EIGIL NIELSEN

STUDIES ON TRIASSIC FISHES FROM EAST GREENLAND

II.
AUSTRALOSOMUS AND BIRGERIA

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PREFACE

The present Part II of my monograph »Studies on Triassic Fishes from East Greenland« deals with the material of the genera *Australosomus* and *Birgeria* collected on the Danish East Greenland expeditions, mainly between 1932 and 1938. For the opportunity to describe this unique material I am highly indebted to the leader of the expeditions, Dr. Lauge Koch, who has always taken a very great interest in my work.

By far the greater part of the material treated in the present paper was collected by myself in the area around Kap Stosch and in the Hird Bay area, a few specimens, however, were collected in the region between Ella Ø and Gurreholm by Dr. W. Bierther and Dr. H. Stauber, to both of whom I owe sincere thanks for their readiness to place this material at my disposal. Further I thank Dr. Stauber for valuable information about the fish-bearing localities discovered by him in the southern Eotriassic area, which information proved to be of considerable help to me during my visit to the area in the summer of 1946.

The investigation of *Australosomus* and *Birgeria* was carried out in the Palaeozoological Department of the Swedish Riksmuseum and in the Zoological Museum of the University of Copenhagen. To the chiefs of these institutions, Professor E. Stensiö and Professor R. Spärck, respectively, I wish to express my gratitude for much valuable help in various ways.

The material was largely worked up in Copenhagen; but the grinding process of the head of *Australosomus*, the whole photographic work, and part of the preparation and drawing were carried out in Sweden.

The photographic work was undertaken by Mr. G. Ahl (Stockholm), the most difficult work of preparation by Miss A. Brasch (Stockholm), and the drawing and retouching by Mr. S. Ekblom (Stockholm) and by Miss I. Frederiksen (Copenhagen). To all these I express my most cordial thanks. I also wish here to thank my wife Mrs. Birgitta Nielsen for valuable help during the preparation of the serial drawings of the head of *Australosomus*.

The wax-plates for the models of *Australosomus* were made in the Institute for Comparative Anatomy of the University of Copenhagen, to the late

chief of which, Professor C. M. Steenberg, my first teacher in comparative anatomy, I owe a great debt of gratitude.

To the late Professor G. Säve-Söderbergh, then head of the Palaeontological Institution of the University of Uppsala, I am indebted for his loan of specimens of *Birgeria mougeoti* from Spitsbergen.

Finally I thank Miss E. Gleerup for correcting and revising the English manuscript.

INTRODUCTION

Both *Australosomus* and *Birgeria* are of common occurrence in the northern Eotriassic areas at Godthaabs Golf (the Kap Stosch area and the Hird Bay area (cf. E. Nielsen 1935)), and both are represented in the small collections of fishes brought home from the southern Eotriassic areas between Ella Ø and Gurreholm (Traill Ø, Scoresby Land, and Jameson Land (cf. H. Stauber 1942)).

Australosomus is represented in East Greenland by at least three, and *Birgeria* probably by only one species. All four species are found in the Kap Stosch area, where their occurrence within the various fish-bearing horizons is shown in the subjoined table. *Australosomus kochi*, *Birgeria groenlandica*, and *Australosomus simplex* have in addition been collected in the Hird Bay area in a fish-bearing horizon which seems to correspond to at least the lower part of Fish-zone II at Kap Stosch, and the same three species have been identified, though *Australosomus simplex* with doubt, from the southern Eotriassic areas, here probably likewise, judging from my own stratigraphical observations in the summer of 1946, derived from beds of upper Otoceras age.

In the present paper, as in the first part of the monograph, I have laid special stress upon elucidating as far as possible the anatomy of the genera concerned, while I have only to a slight degree gone into the phylogenetic problems of the Actinopterygian group, our knowledge regarding the greater number of the families of primitive Ganoids being still much too scanty for far-reaching conclusions.

The manuscript of the paper was finished already in 1947.

– ? –	*Anodontophora* beds	*A. fassaensis*		
		Myalina kochi	Stegocephalian horizon	
		A. breviformis		
Gyronitan	*Proptychites* beds	*Proptychites rosenkrantzi*	Fish-zone V	*Australosomus kochi* (seven specimens) *A. aff. simplex* (four specimens) *Birgeria groenlandica* (one specimen)
	Vishnuites beds	*Ophiceras dubium*	Fish-zone IV	*Australosomus kochi* (five specimens)
		Vishnuites decipiens and *Ophiceras ultimum*		
		Vishnuites decipiens and *Ophiceras kilenense*	Fish-zone III	*Australosomus kochi* (common)
Otoceratan	*Ophiceras* beds	*Ophiceras commune* and *Ophiceras subsakuntala*	Fish-zone II	*Australosomus kochi* (common) *A. simplex* (common) *A. pholidopleuroides* (one specimen) *Birgeria groenlandica* (common)
		Ophiceras praecursor and *Glyptophiceras serpentinum*		
	Glyptophiceras beds	*Glyptophiceras minor*		
		Glyptophiceras triviale	Fish-zone I	

AUSTRALOSOMUS PIVETEAU

Syn. 1924. *Pristiosomus* (in part), Priem, pp. 11–12.
1930. *Australosomus*, Piveteau, pp. 456–458.
1932. *Pholidopleurus* (in part), Stensiö in Koch, pp. 88–89.
1932. *Australosomus*, Stensiö, pp. 167–183.
1934. *Australosomus*, Piveteau, pp. 9–40.
1936. *Australosomus*, E. Nielsen, pp. 44–45.
1936. *Australosomus*, Haughton, pp. 58–60.

In 1930 Piveteau erected the genus *Australosomus* for a fish from the Eotriassic of Madagascar which in 1924 had been described by Priem as *Pristiosomus merlei*. A few years later Stensiö (1932), on the basis of material derived from the Eotriassic of East Greenland, described another species of the same genus which, in a preliminary list of the fishes from these beds (Stensiö in Koch 1932), he had referred to the genus *Pholidopleurus*. In 1934 Piveteau published a fairly detailed description of *Australosomus merlei*, in 1936 Haughton gave a brief description of a species of *Australosomus* from the Karroo of Tanganyika, and in the same year, after a provisional examination of the large number of Eotriassic fishes brought home from East Greenland in 1933, I published a brief note on the material of *Australosomus*.

Stensiö's material enabled him to make a close study of a large part of the axial skeleton as well as of the squamation and parts of the fins, but it was insufficient for an exhaustive description of the head region. Piveteau, owing to his much larger and in some respects better preserved material, was able to describe the outer aspect of the neural endocranium and to reconstruct the greater part of the dermal cranial roof. Thus, though *Australosomus* as compared with most fossil Actinopterygians must be regarded as fairly well known, many questions relative to its anatomy still remained unsettled, and I therefore deemed it necessary to make a very thorough investigation of the large new material from East Greenland, the bulk of which was collected by myself in the years 1932–33 and 1936–37.

The East Greenland collections comprise 235 specimens of *Australosomus* belonging to at least three species, two of which, as already suspected by Stensiö (1932, p. 182), were represented in the small collections treated by

him. The commonest, as also the best preserved, of the three species is *Australosomus kochi* Stensiö, and I therefore decided to subject the best preserved specimens of this species to the most detailed anatomical study while the other species, which differ in no very essential respects from *A. kochi*, have been dealt with in a more summary way.

The Greenland species of Australosomus.

Australosomus kochi (Stensiö).

(Figs. 1–46, 49–55; pls. 1–4; pl. 5, fig. 1; pls. 6, 7).

Syn. 1932. *Pholidopleurus kochi* (in part) Stensiö in Koch, p. 88.
1932. *Australosomus kochi* (in part) Stensiö, pp. 167–183.
(figs. 53–56; pls. 27–28; pl. 29, figs. 2,3; pl. 30, fig. 4; pl. 34, figs. 1–3).
1936. *Australosomus*, E. Nielsen, pp. 44–45.

MATERIAL AND LOCALITIES.

Specimens nos. 36 (holotype), 37, and 38 (Stensiö's numbers) of the material treated by Stensiö and collected prior to 1932. Of these specimens no. 37 is derived from the Hird Bay area and the other two from Fish-zone II in the Kap Stosch area. The following specimens of the material collected between 1932 and 1937: From Fish-zone II in the Kap Stosch area: specimens nos. 440–442, 444, 446–508, 511, 512, 514–517, 519, and 521; from Fish-zone III in the Kap Stosch area: specimens nos. 401–439 and 443; from Fish-zone IV in the Kap Stosch area: specimens nos. 560–563 and 565; from Fish-zone V in the Kap Stosch area: specimens nos. 548, 549, 551, 554, and 558. Moreover specimens 509, 510, 513, 520, 522–527 from Fish-zone II in the Kap Stosch area and specimens nos. 550, 552, and 559 from Fish-zone III in the Kap Stosch area probably belong to *A. kochi*. From Gurreholm Bjærg in N.W. Jameson Land specimen no. 636 (collected by H. Stauber).

HOLOTYPE.

Stensiö (1932, p. 167) has chosen the best preserved and most complete of his three specimens as holotype, viz. specimen no. 36, a fairly complete fish lacking only the most posterior part of the caudal region.

MEASUREMENTS.

According to Stensiö (1932, pp. 167–168) the holotype in its present state of preservation measures about 13 cm in length, while its estimated

total length is about 15 cm. The other dimensions of the holotype are given as follows (Op. cit. p. 168):

Length of head with opercular apparatus about 3 cm.

Maximum depth of trunk (situated in posterior part of anterior half of abdominal region) about 3.7 cm.

Distance between occiput and anterior margin of dorsal fin about 8 cm.

Distance between base of pectoral fin and base of pelvic fin about 5.3 cm.

Distance from base of anterior margin of pelvic fin to base of anterior margin of anal fin about 2.3 cm.

Stensiö's estimate of the total length of the holotype is confirmed by measurements made on more complete specimens within the large new material, and on the basis of the most complete specimens it is moreover easy to estimate with a fair degree of certainty the total length of a great many, even very fragmentary, specimens. The result of this estimation is given in the subjoined table, which shows that the specimens from Fish-zone II vary in length from about 9 to 19 cm, while those from the higher fish-zones show a much less variation in length, thus in Fish-zone III from about 10 to 15 cm, in Fish-zone IV from about 12 to 14 cm, and in Fish-zone V from about 11 to 15 cm.

	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	Estimated length in cm
Fish-zone V							×		×	×	×							
Fish-zone IV								×	×	×								
								×	×									
							×	×	×									
						×	×	×	×	×								
						×	×	×	×	×								
						×	×	×	×	×								
Fish-zone III						×	×	×	×	×	×							
											×							
											×							
											×							
											×							
									×	×	×	×						
									×	×	×	×						
									×	×	×	×	×					
							×		×	×	×	×	×					
							×		×	×	×	×	×					
							×	×	×	×	×	×	×					
						×	×	×	×	×	×	×	×					
						×	×	×	×	×	×	×	×					
Fish-zone II					×	×	×	×	×	×	×	×	×		×			

The table further shows that the average length of the specimens from Fish-zone II is larger than the average length of those from the higher fish-zones, a feature which is likewise conspicuous in the majority of the other forms represented in the Eotriassic fish faunas of East Greenland.

DESCRIPTION.

Neural endocranium.

General remarks. – An uncrushed head was examined by Sollas's grinding method. The specimen chosen was found in 1936 in Fish-zone III in the valley of River 13 in the Kap Stosch area (E. Nielsen 1935) and consisted of an almost complete fish, the caudal region of which, however, was rather poorly preserved.

The grinding was made, as far as possible, at right angles to the longitudinal axis of the endocranium and from the anterior towards the posterior part of the head. Staining with alizarin was used (E. Nielsen 1942, pp. 15–16). A number of 210 sections were drawn, nos. 1–172 through that part of the head which contained the neural endocranium, nos. 173–210 through the most posterior part of the head region and the anterior part of the abdominal region. The first 172 sections were drawn with an interspace of 100 μ except in a few cases in which the drawings were made with interspaces of only 50 μ in order to trace very fine canals or other delicate structures. The following sections were situated only 50 μ behind the preceding ones: nos. 2, 7, 8, 9, 10, 11, 15, 16, 17, 19, 37, 38, 40, 91, 92, 107, 108, 109, 110. Behind the neural endocranium the sections were drawn with an interspace of 200 or, in some cases, even 400 μ. The sections were drawn at a magnification of 17. On the basis of the drawings wax models were made of the neural endocranium, of some ossifications of the visceral endoskeleton, of the most anterior part of the axial skeleton, and of the cavities of the neural endocranium. On account of the fine state of preservation of the head these models proved very helpful for the study of the cranial structure.

The neural endocranium of specimen no. 407 had a length of 16.5 mm, a maximum height of 6.5 mm, and a maximum breadth of c. 7 mm. It proved to be almost completely ossified.

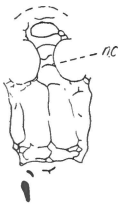
The macroscopic structure of the bone-tissue was like that of most other fossil lower Ganoids (Stensiö 1921, pp. 152–153; 1935, pp. 14, 133–134; 1932, pp. 188, 269; Aldinger 1937, p. 38; Nielsen 1942, p. 16; etc.), the endochondral mass being cancellate, and on the outside as well as on the surfaces of canals and cavities to a great extent lined with laminate perichondral bone-layers. No traces of radiation could be detected.

The model of the neural endocranium (figs. 2, 3, 4, 5, 6, 7, 8, 9, 11, 12, 13, 14) shows two large unpaired ossifications, one of which occupies the ethmoidal region, the orbitotemporal region, and the dorsal and lateral parts of the otic region, while the other occupies the occipital region and the ventral part of the otic region. As in *Pteronisculus* (*Glaucolepis*)[1]) (E. Nielsen 1942, pp. 17–18) the two ossifications are separated by a so-called fissura

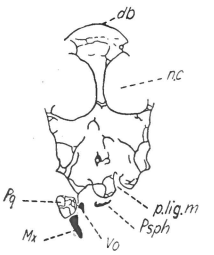
[1]) As pointed out by White and Moy Thomas (1940, p. 100), the name *Glaucolepis* Stensiö is preoccupied and must be replaced by the name *Pteronisculus* White.



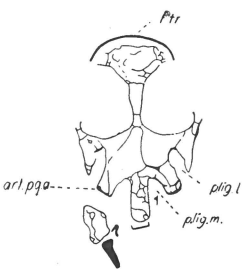
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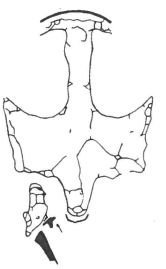
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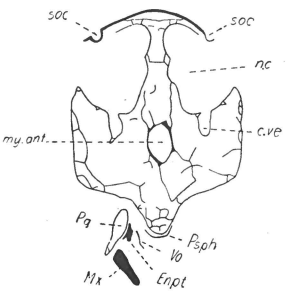
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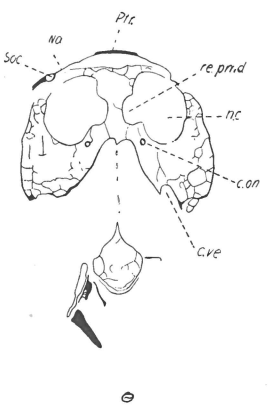
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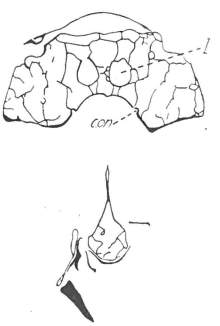
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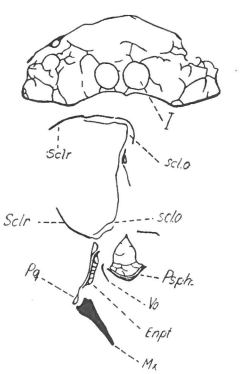
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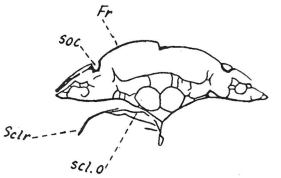


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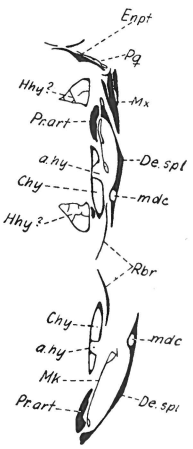
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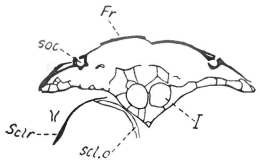

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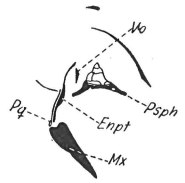




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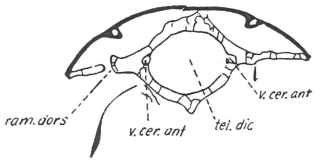



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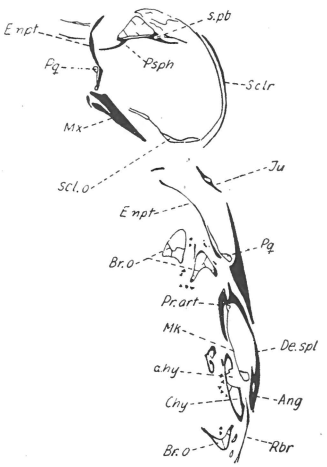


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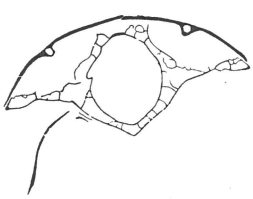

ram. dors
v. cer. ant
v. cer. ant
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tel. dic

75

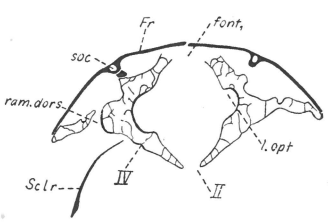

E npt
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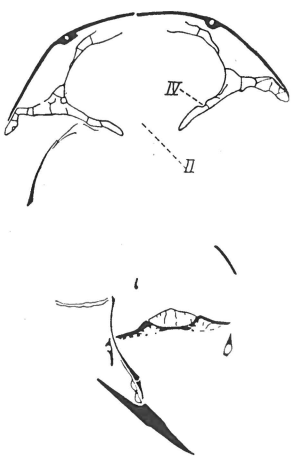

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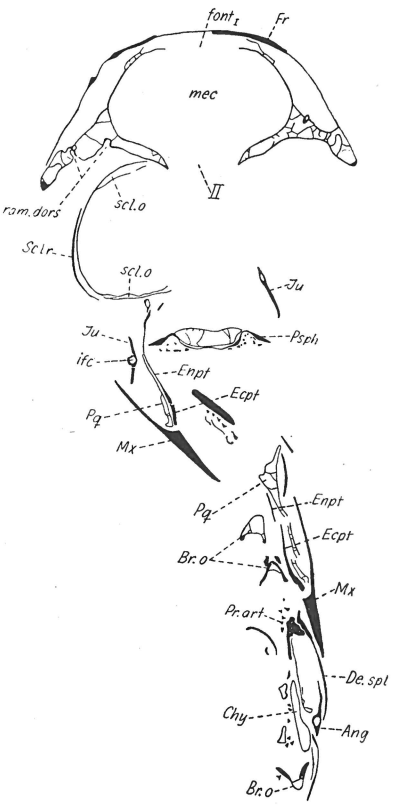

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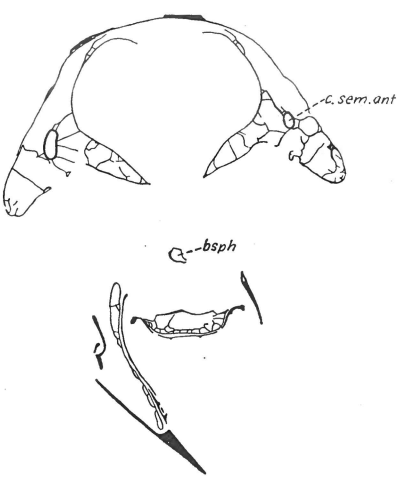
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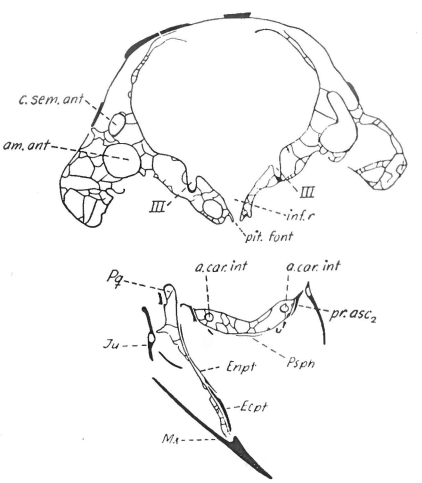
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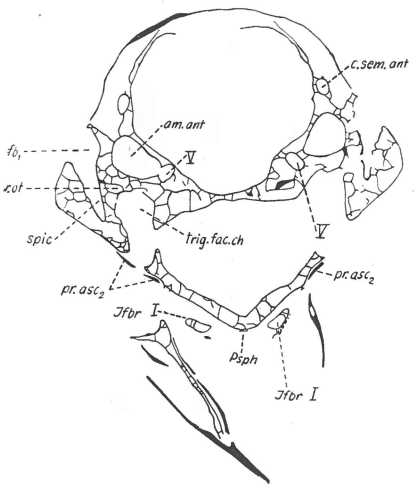
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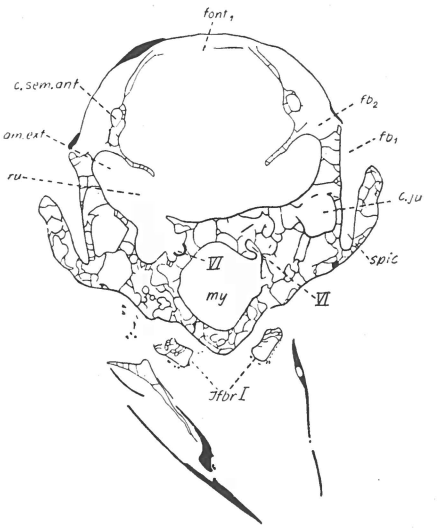
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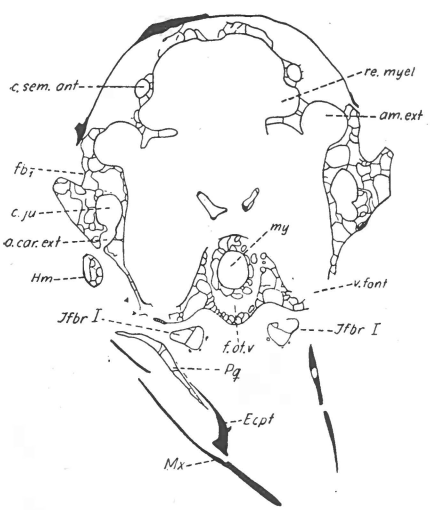
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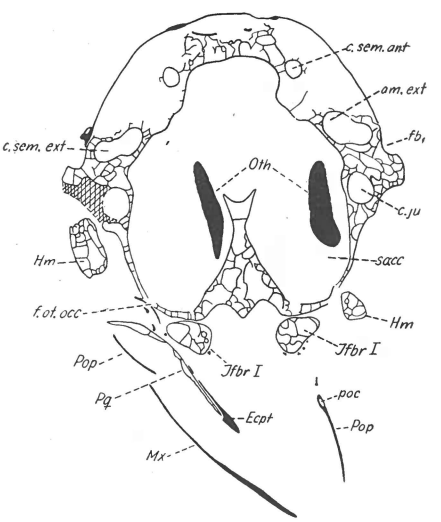
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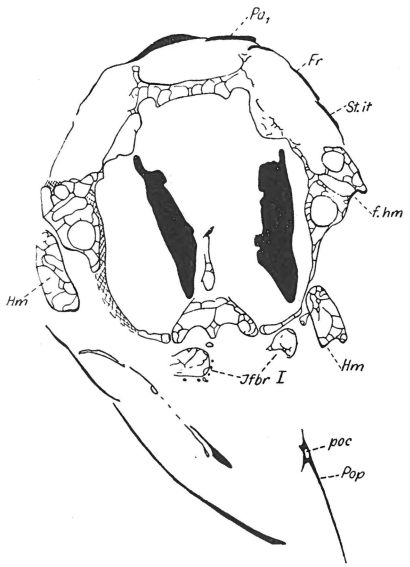
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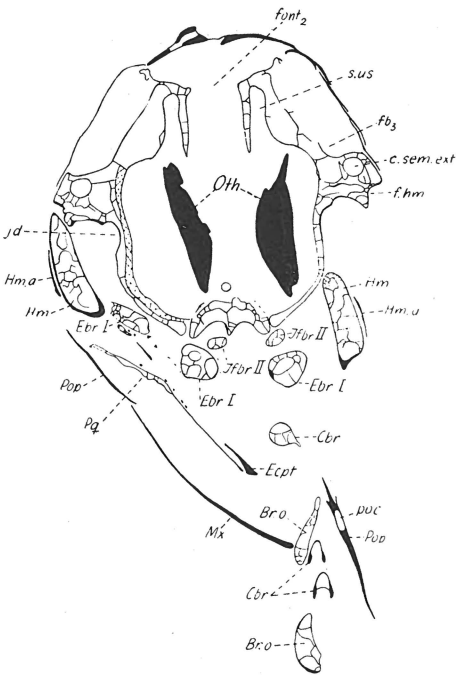
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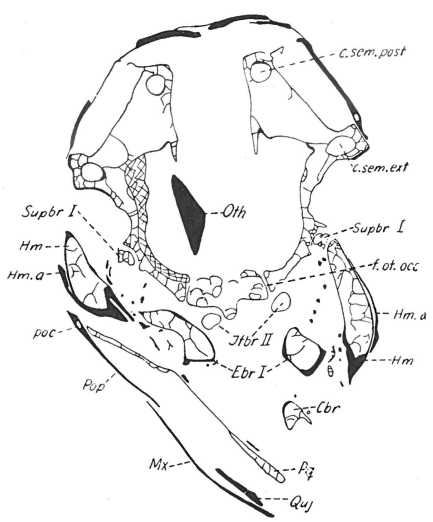
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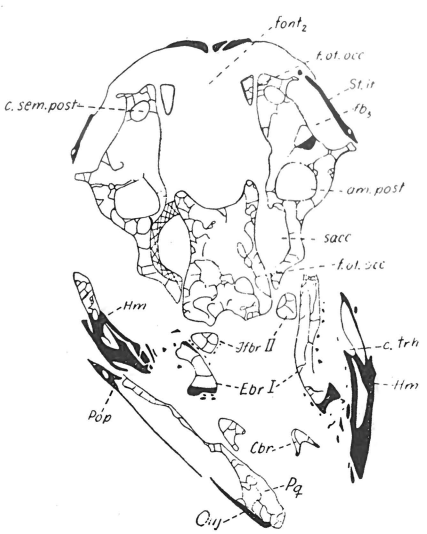
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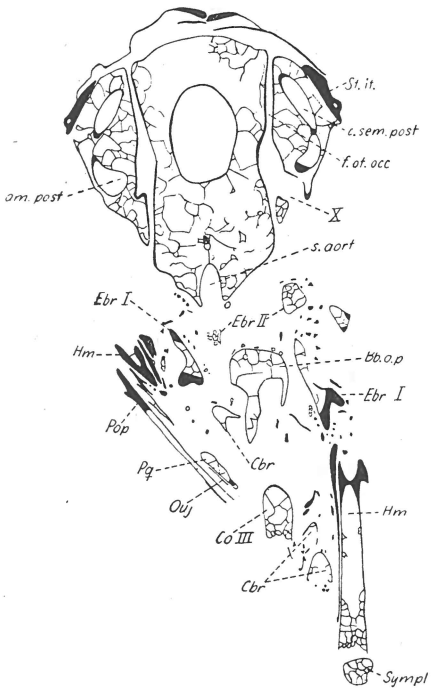
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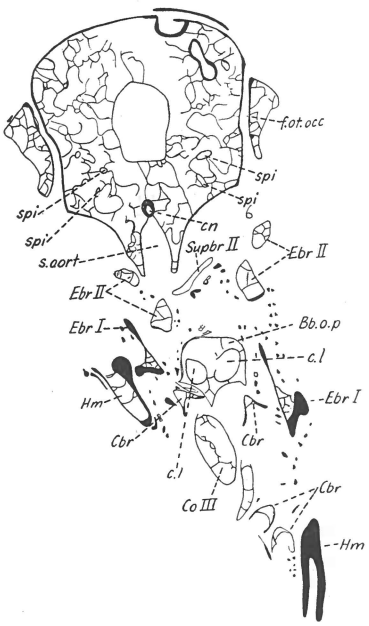
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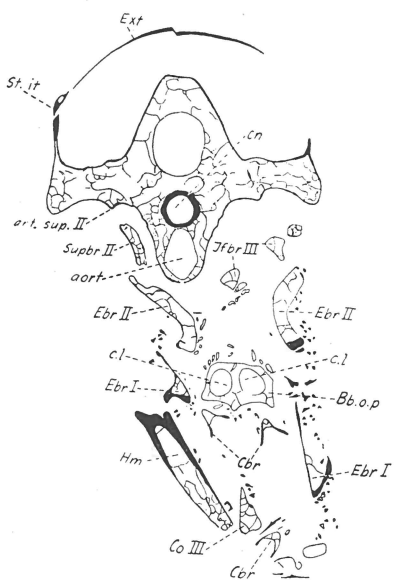
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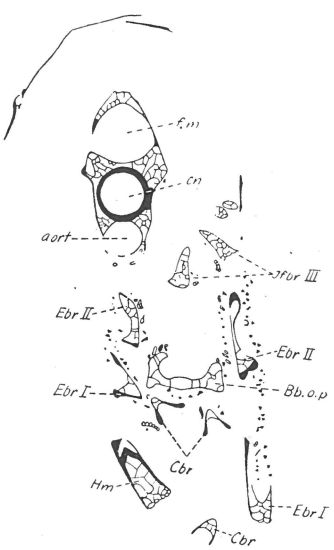
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Fig. 1. *Australosomus kochi* (Stensiö). Sections nos. 5, 10, 15 etc. from the complete grinding series (cf. p. 18). Specimen no. 407. 6–7×.

Ang, angular; *Bb. o. p*, posterior basibranchial ossification; *Br. o*, ossificatiom in the branchial arches; *Cbr*, ceratobranchial; *Chy*, ceratohyal ossification; *Co* III, third basibranchial ossification; *De. spl*, dentalo-splenial; *Ebr I–II*, epibranchial I–II; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Ext*, extrascapular; *Fr*, frontal; *Hhy*?, hypohyal?; *Hm*, hyomandibula; *Hm. a*, dermohyal (accessory hyomandibula); *Ifbr I–III*, infrapharyngobranchials I–III; *Ju*, jugal; *Mk*, Meckelian bone; *Mx*, maxillary; *Na*, nasal; *Oth*, otolith; Pa_1, anterior parietal; *Pop*, preoperculum; *Pq*, palatoquadrate; *Pr. art*, prearticular; *Psph*, parasphenoid; *Ptr*, posttemporal; *Quj*, quadratojugal; *Rbr*, branchiostegal ray; *Sclr*, sclerotic ring; *St. it*, supratemporo-intertemporal; *Supbr I–II*, suprapharyngobranchials I–II; *Sympl*, symplectic; *Vo*, vomer; *a. car. ext*, canal for the arteria carotis externa; *a. car. int*, canal for the arteria carotis interna; *a. hy*, groove for the afferent hyoid artery; *am. ant*, *am. ext*, *am. post*, divisions of the labyrinth cavity for the ampulla anterior, the ampulla externa, and the ampulla posterior respectively; *aort*, aorta canal; *art. pq.* a, articular facet for the pars autopalatina palatoquadrati; *art. sup. II*, presumed place of articulation for the suprapharyngobranchial II; *bsph*, pars basisphenoidea; *c. ju*, jugulohyoideomandibular canal; *c. l*, longitudinal canal in the posterior basibranchial ossification; *cn*, space for the notochord; *c. on*, canal probably for a vein; *c. sem. ant*, *c. sem. ext*, *o. sem. post*, divisions of the labyrinth cavity for the canalis semicircularis anterior, the canalis semicircularis externus, and the canalis semicircularis posterior respectively; *c. trh*, canal for the truncus hyoideomandibularis; *c. ve*, canal possibly for the ramus maxillaris trigemini and the ramus buccalis lateralis; *db*, dermal cranial roof; fb_1, fb_2, fb_3, divisions of the fossa bridgei; *f. hm*, articular fossa for the hyomandibula; *f. m*, foramen magnum; $font_1$, $font_2$, anterior and posterior dorsal fontanelles; *f. ot. occ*, fissura otico-occipitalis; *f. ot. v*, fissura oticalis ventralis; *ifc*, infraorbital sensory canal; *inf. r*, infundibular recess; *jd*, jugular depression; *l. opt*, division of the cavum cerebrale cranii for the lobus opticus; *mdc*, mandibular sensory canal; *mec*, division of the cavum cerebrale cranii for the mesencephalon; *my*, posterior myodome; *my. ant*, anterior myodome; *n. c*, nasal cavity; *pit. font*, pituitary fontanell e; *p. lig. l*, *p. lig. m*, pits for ligaments connecting the palatoquadrate and the neural endocranium; *poc*, preopercular sensory canal; $pr.\ asc_2$, processus ascendens posterior; *ram. dors*, canals for branches of the ramus ophthalmicus superficialis trigemini, the ramus ophthalmicus lateralis, and vessels; *re. myel*, division of the cavum cerebrale cranii for the antero-lateral part of the myelencephalon; *re. pmd*, postero-dorso-medial recess of the nasal cavity; *r. ot*, canal for the ramus oticus lateralis; *ru*, division of the labyrinth cavity for the sacculus; *s. aort*, groove for the dorsal aorta; *scl. o*, ossification in the sclera; *soc*, supraorbital sensory canal; *s. pb*, groove for the ramus palatinus facialis and for a small branch of the arteria carotis interna; *spi*, canal for a spino-occipital nerve; *spic*, spiracular canal; *s. us*, division of the labyrinth cavity for the sinus utriculi superior; *tel. dic*, division of the cavum cerebrale cranii for the telencephalon and diencephalon; *trig. fac. ch*, trigemino-facialis chamber; *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; *VI*, canal for the nervus abducens; *VII*, facialis canal; *X*, canal for the nervus vagus.

occipitalis lateralis (*f. ot. occ*, figs. 1–5, 8, 9, 16–18, 26; pl. 3, fig. 2), a paired lateral vestibular fontanelle (*v. font*, figs. 1, 2, 4–6, 9, 15, 16, 18, 26), and a fissura oticalis ventralis (*f. ot. v*, figs. 1, 4, 16, 19, 26; pl. 3, fig. 2).

In *Australosomus* as in several other forms (the Kansas *Palaeonisciformes* A and B (Watson 1925), *Pteronisculus*, *Boreosomus* (E. Nielsen 1942), etc.) the fissura occipitalis lateralis extends not only through the lateral wall of the endocranium but continues as a transverse fissure across the endocranial roof. Moreover the fissure in these forms extends in a mainly rostral direction throughout the ventro-lateral part of the otic region. Thus the term fissura occipitalis lateralis is not quite correct, and I therefore propose to substitute for it the term fissura otico-occipitalis.

The fissura otico-occipitalis, the dorsal part of which, as in many other forms, shows a marked expansion, the posterior dorsal fontanelle (*font*$_2$, figs. 1, 3, 8, 17, 21; pl. 2, fig. 1), was not closed by cartilage in the living animal, its walls being lined throughout with perichondral bone-layers. Perichondral bone, however, is lacking in some areas of the walls of the fissura oticalis ventralis (p. 45), so this fissure was probably partially closed by cartilage in the living animal. The dorsal part of the vestibular fontanelle seems likewise to have been occupied by cartilage (p. 41).

In *Australosomus merlei* the fi ssura otico-occipitalis is described by Piveteau (1934, p. 12) as separating the occipital and the otic regions dorsally and laterally, and it appears from his figures (Piveteau 1934, figs. 6, 7) that this fissure agrees well in extension with that of *Australosomus kochi*. A dorsal expansion of the fissure (the posterior dorsal fontanelle), however, was not observed by Piveteau, and moreover, in his figure of the endocranium in lateral view (fig. 6) the fissure seems to be closed along a short stretch just dorsally to the place of exit of the nervus vagus. These differences from the conditions in *Australosomus kochi* are probably due to the relatively unsatisfactory state of preservation of the Madagascan material.

In the smallest specimens of *Australosomus kochi* the endocranium is seemingly unossified or almost unossified, however, most of the smallest heads are in such a poor state of preservation that small ossified areas may quite possibly have been overlooked. In somewhat bigger specimens (with an estimated length of the complete neural endocranium of about 10 mm) at any rate the greater part of the endocranium, viz. the occipital, otic, and orbitotemporal regions, is rather extensively ossified, but whether the process of ossification is initiated by the formation of a large number of minor ossifications, as in *Pteronisculus* (E. Nielsen 1942, pp. 91–93), I am unable to decide. The bigger heads (with length of neural endocranium ranging between 12 and 18 mm) have almost completely ossified endocrania.

Occipital region. – The occipital region is short and high, though not quite as high as the highest part of the otic region. Dorsally and laterally it is well marked off from the otic region by the fissura otico-occipitalis, ven-

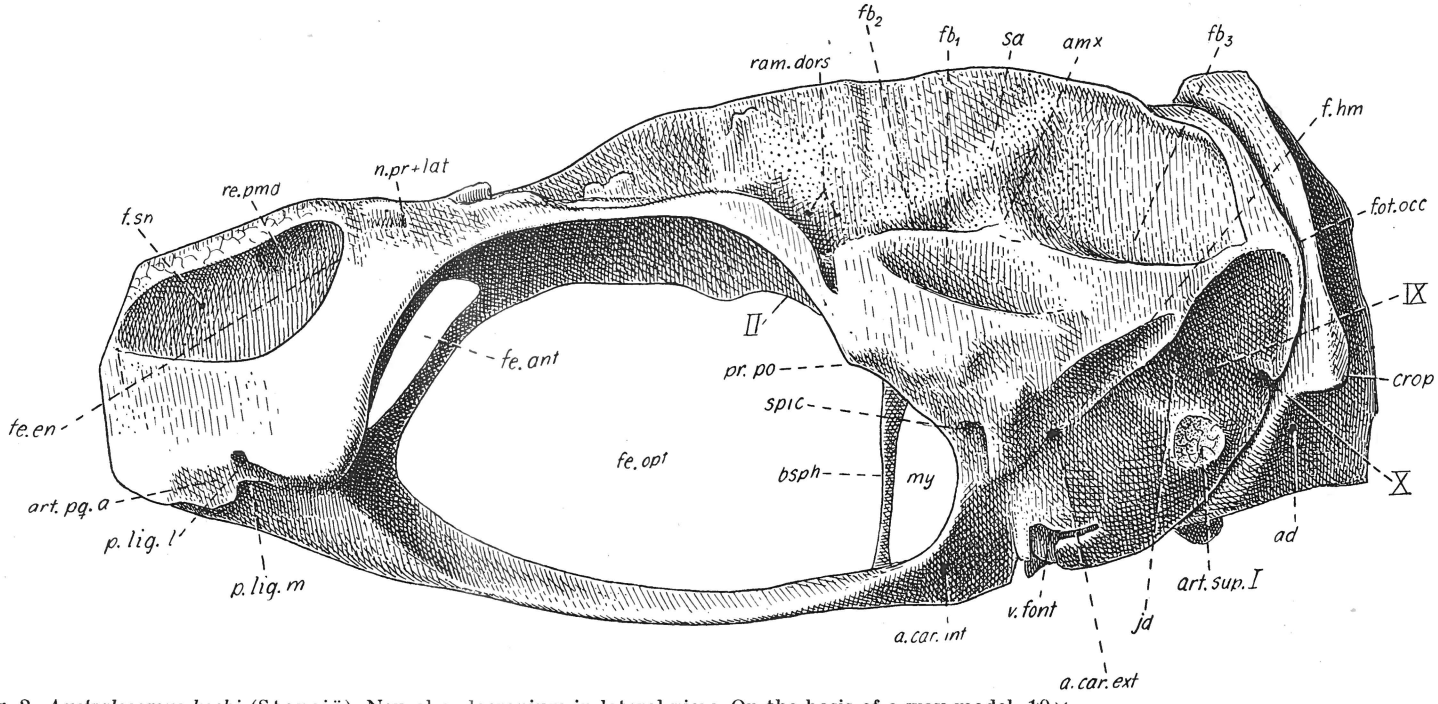


Fig. 2. *Australosomus kochi* (Stensiö). Neural endocranium in lateral view. On the basis of a wax model. 10×.
a. car. ext, canal for the arteria carotis externa; *a. car. int*, canal for the arteria carotis interna; *ad*, canal for an artery; *amx*, bulge above the division of the labyrinth cavity for the ampulla externa; *art. pq. a*, articular facet for the pars autopalatina palatoquadrati; *art. sup. I*, articular facet for the suprapharyngobranchial I; *bsph*, pars basisphenoidea; *crop*, processus cranio-spinalis; fb_1, fb_2, fb_3, divisions of the fossa bridgei; *fe. ant*, anterior fenestra inthe interorbital wall; *fe. en*, fenestra endonarina communis; *fe. opt*, fenestra optica; *f. hm*, articular fossa for the hyomandibula; *f. ot. occ*, tfissura otico-occipitalis; *f. sn*, foramen in the nasal septum; *jd*, jugular depression; *my*, posterior myodome; *n. pr. + lat*, canal for the ramus ophthalmicus lateralis, the nervus profundus, and the ramus ophthalmicus superficialis trigemini; *p. lig. l*, *p. lig. m.*, pits for ligaments connecting the palatoquadrate and the neural endocranium; *pr. po*, processus postorbitalis; *ram. dors*, canals for branches of the ramus ophthalmicus superficialis trigemini, the ramus ophthalmicus lateralis, and vessels; *re. pmd*, postero-dorso-medial recess of nasal cavity; *sa*, ridge above the canalis semicircularis anterior; *spic*, spiracular canal; *v. font*, vestibular fontanelle; *II*, opening for the nervi optici; *IX*, canal for the nervus glossopharyngeus; *X*, canal for the nervus vagus.

trally, however, there is no distinct boundary between the two regions. The largest breadth of the occipital region is found between the rather well developed postero-ventro-laterally directed cranio-spinal processes (*crop*, figs. 2, 4, 5, 7, 8). A horizontal plane through these processes divides the region into a ventral narrow and a dorsal broad part, and accordingly the caudal face of the region consists of a dorsal broad and a ventral narrow division, the outlines of which are shown in fig. 5. The ventral part of the dorsal division is pierced by the large foramen magnum (*f. m*, figs. 5, 8, 18; pl. 2, fig. 1), while the ventral division has two other large openings, viz. dorsally the posterior opening of the notochordal space (*cn*, figs. 1, 5, 15. 16,. 18, 42; pl. 2, figs. 1, 2) and ventrally the posterior opening of the aorta canal (*aort*, figs. 1, 4, 5, 15, 17–19, 26, 42; pl. 2, figs. 1, 2). The somewhat elevated narrow median area of the caudal face of the occipital region, which shows these three big, almost circular openings, is continued towards the dorsal margin of the face by a broad low median ridge, the height of which decreases in a dorsal direction. The ridge corresponds to the more pronounced crista occipitalis in forms such as *Pteronisculus* (E. Nielsen 1942, p. 36), *Saurichthys* (Stensiö 1925, p. 17), and *Perleidus* (Stensiö 1932, pp. 231–232). On either side of the crista occipitalis the broad dorsal division of the caudal face shows a pronounced concavity, which served as the place of insertion of the anterior part of the trunk musculature. Ventrally to this paired concavity and about midway between the cranio-spinal process and the margin of the foramen magnum a very small process or elevation is seen (fig. 5), just dorsally to which lies the external opening of a fine canal (*spi*, figs. 1, 4, 5, 8, 15–18, 26; pl. 2, figs. 1, 2) leading to the cranial cavity. As far as can be seen, the slender suprapharyngobranchial element of the second branchial arch articulated with this small process. The interpretation of the fine canal will be discussed below (p. 33).

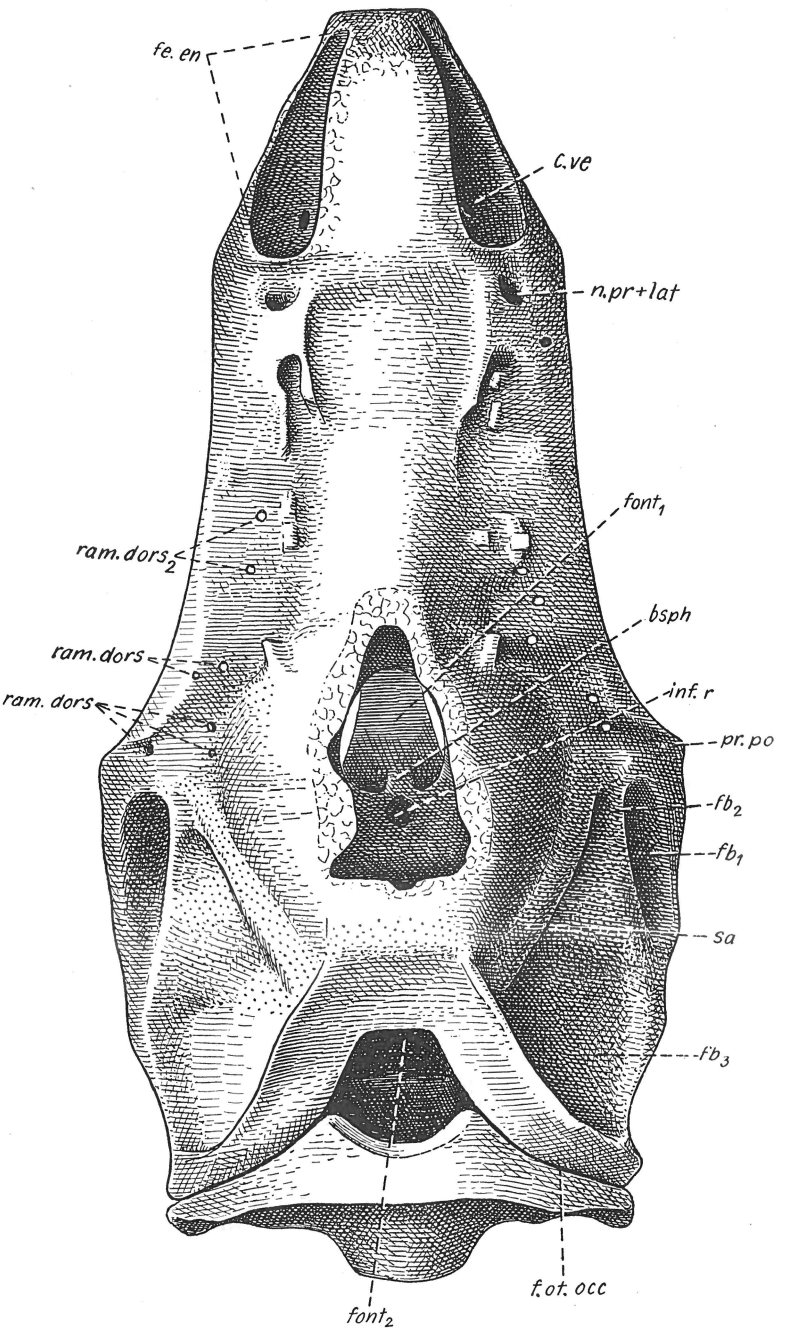
Apart from the caudal face described above, the occipital region is bounded by an unpaired dorsal, a paired lateral, and an unpaired ventral face.

The outline of the dorsal face, which is slightly convex from side to side, is shown in fig. 3 and needs no further description.

The lateral face might, for descriptive reasons, be divided into a dorsal division which forms the lateral face of the broad dorsal part of the occipital region, and a ventral division forming the lateral face of the narrow ventral part of the region.

The dorsal division is merely a narrow brim situated just behind that part of the fissura otico-occipitalis which traverses the lateral wall of the endocranium dorsally to the vagus exit (X, figs. 1, 2, 4, 8, 15–18, 26; pl. 2, fig. 2; pl. 3, fig. 2). The brim has its largest breadth farthest ventrally, where it constitutes the antero-laterally divided face of the cranio-spinal process. Dorsally the narrow brim passes gradually into the dorsal face of the region.

The ventral division consists of a narrow, mainly antero-laterally facing


fe. en
c.ve
n.pr+lat
font$_1$
ram. dors$_2$
bsph
ram. dors
inf. r
ram. dors
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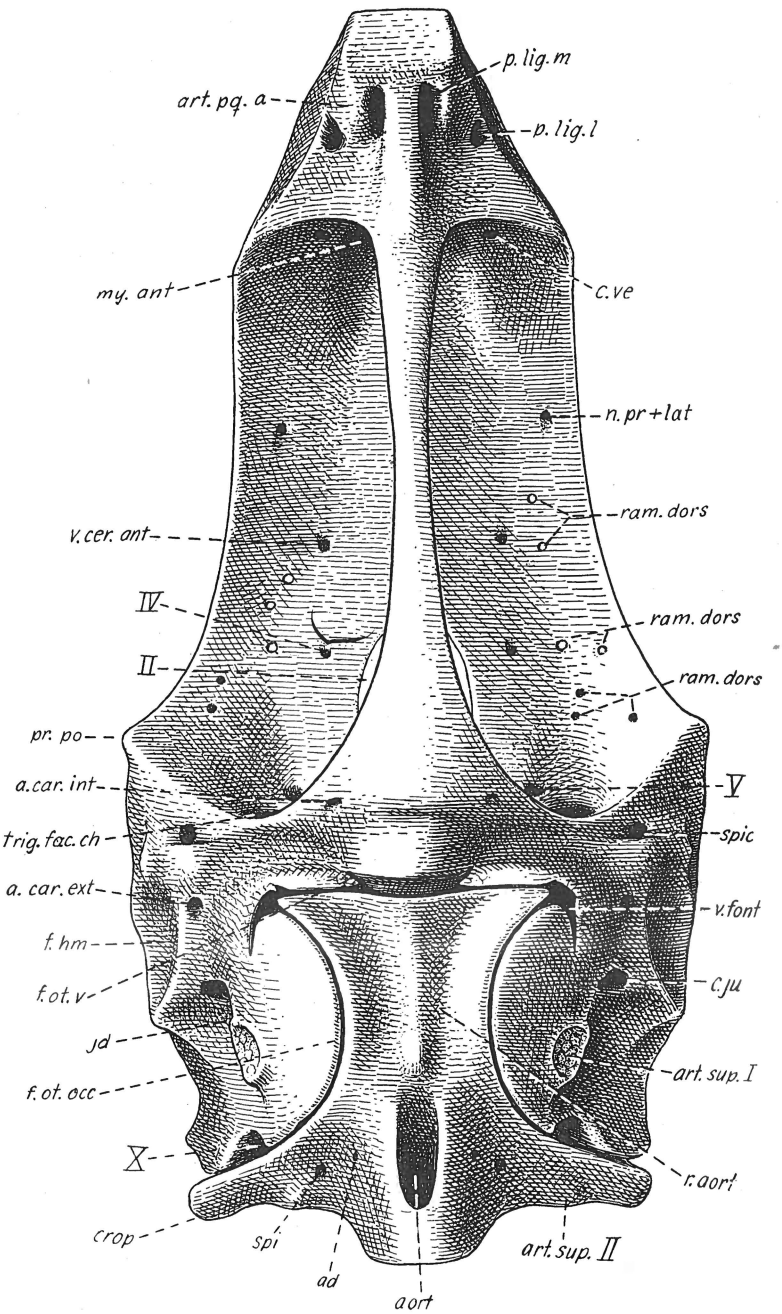
brim, lying immediately posteriorly to the fissura otico-occipitalis as a direct ventral continuation of the just described lateral face of the dorsal part of the region, and of a more posterior concave, roughly triangular area, which faces postero-ventro-laterally. On this latter area two small foramina are present, one of which is situated almost just dorsally to the other. The dorsal foramen (*spi*, figs. 1, 4, 5, 8, 15–18, 26; pl. 2, figs. 1, 2), which lies a short distance behind the most dorsal part of the anterior margin of the concave area, is another external opening of the fine canal leading from the cavum cerebrale cranii, which, as mentioned above (p. 29), has one external opening on the caudal face of the region. The ventral foramen (*ad*, figs. 2, 4, 5, 6, 15, 16, 18, 26; pl. 2, figs. 1, 2) is the outer opening of a very short canal, which leads in a postero-ventro-medial direction to the short aorta canal. Piveteau interprets the corresponding canal in *Australosomus merlei* as the canal for the arteria branchialis efferens IV (Piveteau 1934, p. 12, figs. 6, 7), while in the first part of this work I put forward the assumption that the canal, which is present in many lower Ganoids (the Kansas forms A and B, *Pteronisculus*, *Perleidus*, *Broughia*, etc.), lodged a minor artery issuing from the dorsal aorta between the points in which the second and the third efferent branchial arteries branched off (E. Nielsen 1942, p. 34).

The narrow ventral face of the occipital region (fig. 4) is convex from side to side in such a way that it passes quite gradually into the lateral faces of the region. In an anterior direction the ventral face is continued without any marked boundary in the ventral face of the otic region. On the ventral face there is a large oval unpaired foramen, the longitudinal axis of which is almost thrice as long as the transverse one.

This foramen is the anterior opening of the very short canal for the dorsal aorta (*aort*, figs. 1, 4, 5, 15, 17–19, 26, 42; pl. 2, figs. 1, 2). Anteriorly to the opening, at the transition towards the otic region, the short aorta canal is continued forward by a very short unpaired groove, which soon bifurcates into a right and a left branch.

Towards the fissura otico-occipitalis the posterior ossification of the neural endocranium has an anterior face, which is divided by two vertical ridges into a median unpaired and a lateral paired field (fig. 8). The median field, which bounds the posterior dorsal fontanelle posteriorly, is concave in a transverse and slightly convex in a vertical direction and faces mainly anteri-

Fig. 3. *Australosomus kochi* (Stensiö). Neural endocranium in dorsal view. On the basis of a wax model. Faces without perichondral bone either reticulated or (when the cartilaginous areas have been restored) dotted. 10×.
bsph, pars basisphenoidea; *c. ve*, canal possibly for the ramus maxillaris trigemini and the ramus buccalis lateralis; fb_1, fb_2, fb_3, divisions of the fossa bridgei; *fe. en*, fenestra endonarina communis; $font_1$, $font_2$, anterior and posterior dorsal fontanelles; *f. ot. occ*, fissura otico-occipitalis; *inf. r*, infundibular recess; *n. pr.* + *lat*, canal for the ramus ophthalmicus lateralis, the nervus profundus, and the ramus ophthalmicus superficialis trigemini; *pr. po*, processus postorbitalis; *ram. dors*, canals for branches of the ramus ophthalmicus superficialis trigemini, the ramus ophthalmicus lateralis, and vessels; *sa*, ridge above the canalis semicircularis anterior.


p. lig. m
art. pq. a
p. lig. l
my. ant
c. ve
n. pr+lat
ram. dors
v. cer. ant
IV
ram. dors
II
ram. dors
pr. po
a. car. int
V
trig. fac. ch
spic
a. car. ext
v. font
f. hm
f. ot. v
c. ju
jd
art. sup. I
f. ot. occ
X
r. aort
crop
spi
art. sup. II
ad
aort

orly. The very large paired lateral field, which bounds the narrow lateral part of the occipital division of the fissura otico-occipitalis, is concave from side to side and faces anteriorly and somewhat laterally. Both the median and the lateral fields are completely lined with perichondral bone.

The cavum cerebrale cranii decreases in width and even more in height towards the foramen magnum, the height of which is only slightly larger than the breadth. The walls of the occipital part of the cavum cerebrale cranii are all very thick. The floor, which is almost plane in a rostro-caudal direction and very slightly concave from side to side, lies roughly on a level with the ventral margin of the foramen magnum and, as shown in fig. 7, on a much higher level than the floor in the posterior part of the otic region. About halfway between the anterior and the posterior end of the occipital part of the cranial cavity, at the transition between its floor and its lateral wall, a small foramen (*spi*, fig. 8) is found, viz. the cerebral opening of a narrow canal, which issues in a lateral and slightly postero-ventral direction from the cranial cavity. In the cranial wall this canal bifurcates into a dorsal and a ventral branch. The dorsal branch runs in a postero-lateral direction, to open on the caudal face of the occipital region, while the ventral branch takes a more ventral course and has its external opening on the lateral face of the region. The exact position of the two external openings of the canal has been described above (pp. 29 and 31). The bifurcating canal must have lodged a spino-occipital nerve, and the fact that the canal bifurcates in the cranial wall may perhaps be explained by assuming that the dorsal and ventral nerve roots unite in the unpaired part of the canal, after which the dorsal and ventral nerves issue from the endocranium through the dorsal and the ventral of the two external openings of the canal respectively.

From its posterior opening, which is somewhat smaller than the foramen magnum, the notochordal space extends forwards below the brain cavity to a point a short distance behind the transition to the otic region. Thus the notochordal space has a much smaller forward extension than in *Pteronis-*

Fig. 4. *Australosomus kochi* (Stensiö). Neural endocranium in ventral view. On the basis of a wax model. Faces without perichondral bone reticulated. 10 ×.

a. car. ext, canal for the arteria carotis externa; *a. car. int*, canal for the arteria carotis interna; *ad*, canal for an artery; *aort*, groove for the dorsal aorta; *art. pq. a*, articular facet for the pars autopalatina palatoquadrati; *art. sup. I*, articular facet for the suprapharyngobranchial I; *art. sup. II*, presumed place of articulation for the suprapharyngobranchial II; *c. ju*, jugulo-hyoideomandibular canal; *crop*, processus cranio-spinalis; *c. va*, canal possibly for the ramus maxillaris trigemini, and the ramus buccalis lateralis; *f. hm*, articular fossa for the hyomandibula; *f. ot. occ*, fissura otico-occipitalis; *f. ot. v*, fissura oticalis ventralis; *jd*, jugular depression; *my. ant*, anterior myodome; *n. pr + lat*, canal for the ramus ophthalmicus lateralis, the nervus profundus, and the ramus ophthalmicus superficialis trigemini; *p. lig.* l, *p. lig. m*, pits for ligaments connecting the palatoquadrate and the neural endocranium; *pr. po*, processus postorbitalis; *ram. dors*, canals for branches of the ramus ophthalmicus superficialis trigemini, the ramus ophthalmicus lateralis, and vessels; *r. aort*, groove for the radix aortae; *spi*, canal for a spino-occipital nerve; *spic*, spiracular canal; *trig. fac. ch.*, trigemino-facialis chamber; *v. cer. ant*, canal for the vena cerebralis anterior; *v. font*, vestibular fontanelle; *II*, opening for the nervi optici; *IV*, canal for the nervus trochlearis; *V*, trigeminus canal; *X*, canal for the nervus vagus.

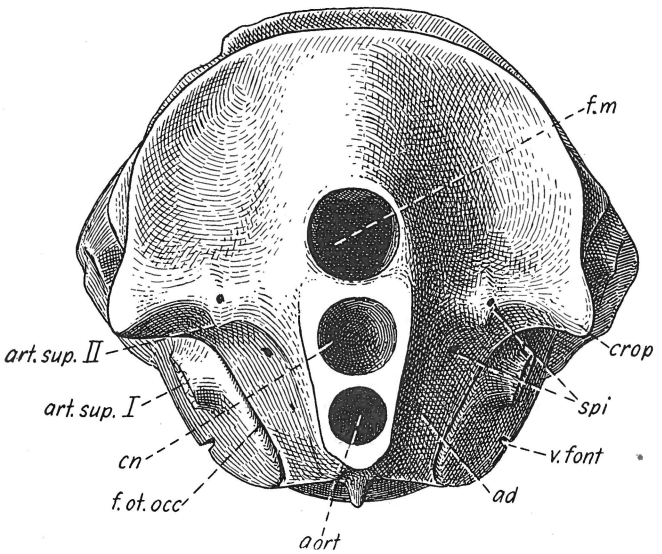


Fig. 5. *Australosomus kochi* (Stensiö). Neural endocranium in posterior view. On the basis of a wax model. 10×.

ad, canal for an artery; *aort*, aorta canal; *art. sup. I*, articular facet for the suprapharyngobranchial I; *art. sup. II*, presumed place of articulation for the suprapharyngobranchial II; *cn*, space for the notochord; *crop*, processus cranio-spinalis; *f. m*, foramen magnum; *f. ot. occ*, fissura otico-occipitalis; *spi*, canals for spino-occipital nerves; *v. font*, vestibular fontanelle.

culus (E. Nielsen 1942, pp. 51–52) and *Boreosomus* (according to the still unpublished part of the grinding series), in both of which the space reaches the fissura oticalis ventralis.

The most posterior part of the notochordal space (cn, pl. 2, fig. 1) is cylindrical in shape with the axis of the cylinder pointing in an anterior direction. Anterior to the cylindrical part the diameter of the space decreases rapidly to a point about halfway between the anterior and the posterior end of the space, this part of the space having a somewhat obliquely conical shape with the axis of the cone pointing antero-ventrally. The anterior half of the notochordal space extends in a antero-ventral direction from the foremost end of the conical part as a rather narrow canal.

The walls of the notochordal space are lined with bone tissue of quite the same type as that of the ring-like centra of the axial skeleton in the body region (cf. Stensiö 1932, pp. 174–176), and this dense bone tissue continues for a short distance forward from the anterior end of the notochordal space as a thin solid strand, which ends at the transition to the otic region. There can be no doubt that the bone layer which lines the endocranial notochordal space has a similar origin to that in the ring-like centra, which according to Stensiö developed within the fibrous sheat of the notochord (cf. Stensiö 1932, p. 176; the present paper pp. 134–141).

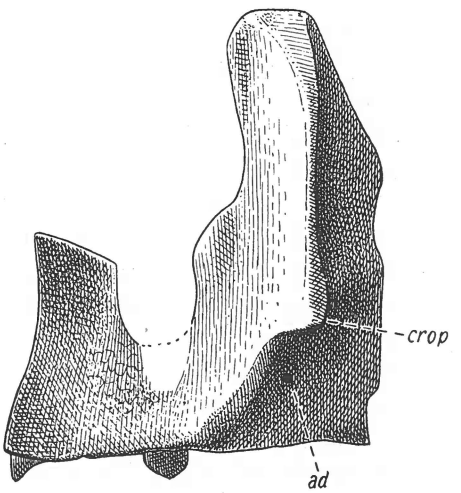


Fig. 6. *Australosomus kochi* (Stensiö). Posterior ossification of neural endocranium in lateral view. On the basis of a wax model. Faces without perichondral bone reticulated. Presumed dorsal boundary of completely unossified area indicated by a broken line. 10×. *ad*, canal for an artery; *crop*, processus cranio-spinalis.

The circular posterior opening of the very short aorta canal is somewhat smaller than that of the notochordal space, as shown in fig. 5. From this opening the vertical diameter of the aorta canal increases, while the horizontal diameter decreases in an anterior direction, cross-sections of the canal being elliptic in outline. As shown in fig. 15, the most posterior part of the canal has a rostro-caudal course, while the anterior part, after a sharp bend, extends in an antero-ventral direction.

The exit for the nervus vagus and the nervus lineae lateralis is merely an expanded part of the fissura otico-occipitalis, as in *Pteronisculus* (E. Nielsen 1942, p. 39), *Boreosomus* (ibid. p. 291), the Kansas forms A and B (Watson 1925, p. 833), *Perleidus* (Stensiö 1932, p. 191), *Ospia* (ibid. p. 232), *Broughia* (ibid. p. 270), etc. This expansion appears as a deep furrow on that face of the anterior ossification of the endocranium which bounds the fissura otico-occipitalis anteriorly, and as a very shallow groove on that face of the posterior endocranial ossification which bounds the fissure posteriorly. The cerebral opening of the vagus expansion lies medially and a little dorsally to the ampulla of the canalis semicircularis posterior, and its external opening, which faces antero-ventro-laterally, lies anteriorly to the small cranio-spinal process. The »canal«, which is curved in such a way that its posterior margin is convex and its anterior margin concave, is elliptical in transverse sections, as in *Pteronisculus* (E. Nielsen 1942, p. 39), with the long axis of the ellipse nearly vertical.

Otic region. – The greatest height and breadth of the endocranium are found in the otic region, viz. the largest breadth between the postorbital processes and the largest height a short distance farther back, as seen in

fig. 2. The length of the region is nearly one-third the total length of the endocranium. The breadth decreases gradually posteriorly, the most posterior part of the region having the same breadth as the adjoining part of the occipital region. For further details regarding the dimensions of the region the reader is referred to the figures.

Dorsally and laterally the otic region, as already stated, is separated from the occipital region by the fissura otico-occipitalis, while ventrally the two regions pass into one another without any distinct boundary. As usual the boundary towards the orbitotemporal region is difficult to define except dorsally, where it is marked by the sudden decrease in breadth in front of the postorbital processes.

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

If we disregard the details of its very complicated relief, the dorsal face might be described as strongly convex from side to side, as seen in the transverse sections nos. 105–155 (fig. 1) and in the reconstructed thick sections (figs. 8, 9, 11, 12). On the anterior part of the dorsal face and on the adjacent part of the dorsal face of the orbitotemporal region opens a large anterior dorsal fontanelle (*font*$_1$, figs. 1, 3, 11, 17), the outline of which is shown in fig. 3. On the margins bounding the fontanelle the neurocranial roof is devoid of perichondral bone, so the fontanelle must have been somewhat constricted by cartilage, its extension in the living animal being probably much the same as in *Boreosomus* (E. Nielsen 1942, pp. 293–294, 302, fig. 59) and in the Kansas *Palaeonisciformes* described by Moodie (1915, pp. 146–155, figs. 5, 6, 15, 16, 17) and Watson (1925, pp. 833–837, figs. 12, 13). As in these forms, the fontanelle in *Australosomus* most likely served as an epiphysial opening.

As already stated, a posterior dorsal fontanelle (*font*$_2$, figs. 1, 3, 8, 17, 21; pl. 2, fig. 1) is also present in *Australosomus*, the dorsal division of the fissura otico-occipitalis having a marked expansion, the outline of which is shown in fig. 3. The posterior dorsal fontanelle was not constricted by cartilage in the living animal.

The lateral part of the posterior marginal zone of the dorsal face of the otic region is developed as a rounded ridge, which extends from the postero-lateral angle of the face along the fissura otico-occipitalis to a point about midway between the anterior and the posterior end of the antero-lateral margin of the posterior dorsal fontanelle, becoming gradually less pronounced in an antero-medial direction. Postero-laterally to the broadest part of the posterior dorsal fontanelle the marginal ridge meets with a very high crest, the oblique otic crest, which from the point of junction extends in an antero-medial direction to a point a short distance behind the postero-lateral angle of the anterior dorsal fontanelle. Against this crest, the shape of which is best understood by studying the serial drawings (fig. 1, nos. 130–150), and

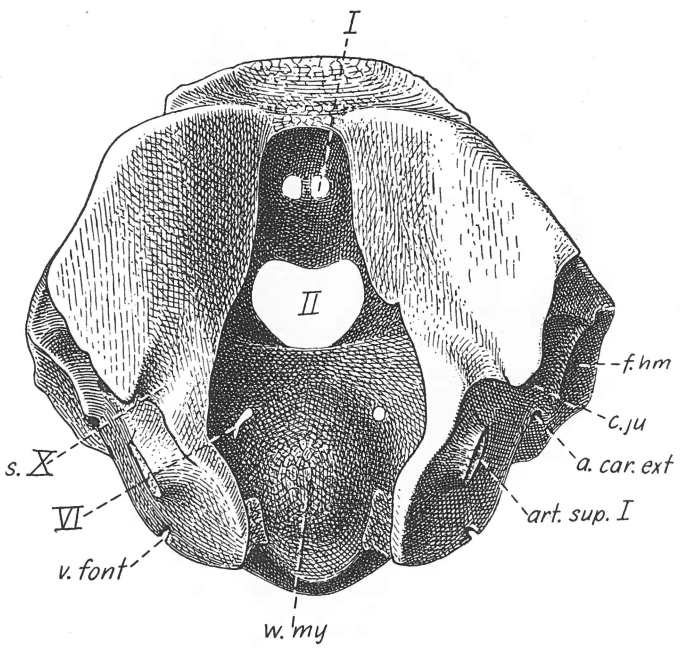


Fig. 7. *Australosomus kochi* (Stensiö). Anterior ossification of neural endocranium in posterior view. On the basis of a wax model. Faces without perichondral bone reticulated. 10 ×.

a. car. ext, canal for the arteria carotis externa; *art. sup. I*, articular facet for the suprapharyngobranchial I; *s. ju*, jugulo-hyoideomandibular canal; *f. hm*, articular fossa for the hyomandibula; *s. X*, groove for the nervus vagus; *v. font*, vestibular fontanelle; *w. my*, posterior wall of posterior myodome; *I*, canal for the nervus olfactorius; *II*, opening for the nervi optici; *VI*, canal for the nervus abducens.

against the lateral part of the marginal ridge rests the dermal cranial roof, as described in more detail in a later chapter (p. 85).

The postero-medial part of the dorsal face is well marked off laterally by the paired crest just mentioned and appears as a large, but rather shallow, concavity, the deepest part of which is occupied by the posterior dorsal fontanelle. The antero-medial part of this concave area as well as the medial part of the area which lies between the concavity and the anterior dorsal fontanelle is devoid of perichondral bone and must have been covered with cartilage in the living animal.

The antero-medial part of the dorsal face of the otic region and the adjoining part of the orbitotemporal region is strongly convex in a transverse as well as in a longitudinal direction, corresponding to the strong development of the lobi optici (p. 77). Postero-laterally this convex area, the central part of which is occupied by the anterior dorsal fontanelle, is bounded by a rounded ridge (*sa*, figs. 2, 3) developed above the space for the canalis semicircularis anterior.

On the more lateral part of the dorsal face two well defined depressions

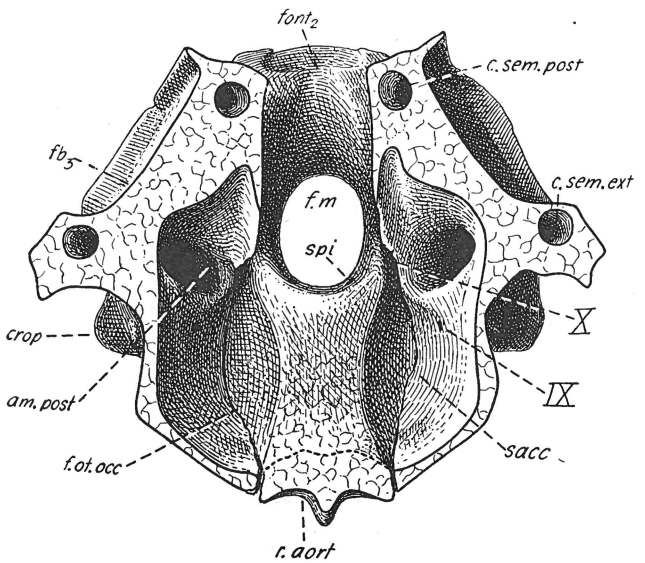


Fig. 8. *Australosomus kochi* (Stensiö). Posterior part of neural endocranium in anterior view. On the basis of a wax model (sections nos. 142–172 of the complete grinding series). Faces without perichondral bone reticulated, sectional faces unshaded. 10×.

am. post, division of the labyrinth cavity for the ampulla posterior; *crop*, processus craniospinalis; *c. sem. ext*, *c. sem. post*, divisions of the labyrinth cavity for the canalis semicircularis externus and the canalis semicircularis posterior respectively; fb_3, posterior division of the fossa bridgei; *f. m*, foramen magnum; $font_2$, posterior dorsal fontanelle; *f. ot. occ*, fissura otico-occipitalis; *r. aort*, groove for the radix aortae; *sacc*, division of the labyrinth cavity for the sacculus; *spi*, canal for a spino-occipital nerve; *IX*, canal for the nervus glossopharyngeus; *X*, canal for the nervus vagus.

are seen, one of which is rather large and shallow, while the other is much smaller but very deep.

The large and shallow depression is bounded antero-medially by the ridge above the space for the canalis semicircularis anterior, postero-medially by the oblique otic crest, posteriorly by the posterior marginal ridge, and laterally by a narrow elevated area situated along the lateral margin of the face. A rounded bulge (*amx*, fig. 2) at its bottom subdivides the depression into two divisions, viz. a small anterior (fb_2, figs. 1–3, 11) and a large posterior one (fb_3, figs. 1–3, 8).

The small and deep depression (fb_1, figs. 1–3, 9, 11, 21; pl. 1, figs. 1, 2) is situated on the broad anterior part of the elevated lateral marginal area of the dorsal face laterally to the anterior division of the large and shallow depression. The small depression is much longer than broad and fairly elliptic in outline. From its bottom extends the spiracular canal (*spic*, figs. 1, 2, 4, 11, 12, 14) in a ventral and slightly medial direction, to open ventrally on the ventro-laterally directed lateral face of the otic region. As shown in fig. 11, the transition between the depression and the spiracular canal is very gradual, in fact, the whole depression might be considered as the dorsal

division of a very long spiracular canal which narrows gradually in a ventral direction throughout its length. However, since the spiracular canal in *Pteronisculus* and *Boreosomus* evidently only corresponds to the ventral part of the very long canal in *Australosomus*, I prefer to use the term spiracular canal for that part alone. A short distance dorsally to the dorsal end of the spiracular canal the medial wall of the depression is pierced by a small canal (*r. ot*, figs. 1, 11), which extends from the depression in an antero-ventro-medial direction to the dorsal part of the trigemino-facialis chamber, and which lodged the ramus oticus lateralis (cf. E. Nielsen 1942, pp. 44, 75, 82).

The small depression just described as well as the marginal zone of the dorsal face of the otic region laterally to the depression is not covered by the dermal cranial roof, the lateral margin of which, as already pointed out by Stensiö (1932, pp. 169, 171, fig. 53), is deeply notched just above the depression. The relations between the depression and the dermal cranial roof are shown in fig. 21.

The small deep and the large shallow depression must be regarded as divisions of a large fossa bridgei, and may be homologised with divisions of the still larger fossa bridgei in *Boreosomus piveteaui* (E. Nielsen 1942, pp. 294–295, fig. 59). In this last-mentioned form the fossa bridgei consists of an anterior and a posterior part. The anterior part is subdivided by the most anterior part of the ridge above the space for the canalis semicircularis anterior into a rather shallow antero-medial and a very deep postero-lateral division, and the posterior part is more or less completely subdivided by a bony wall into a dorsal and a ventral division, the latter of which has a wide connection with the cranial cavity. The small deep depression in *Australosomus* corresponds to the lateral and deepest section of the deep postero-lateral division of the anterior part of the fossa bridgei in *Boreosomus*, while the anterior division of the large shallow depression in *Australosomus* must be compared to that section of the deep postero-lateral division of the anterior part of the fossa bridgei in *Boreosomus* which lies immediately laterally to the anterior part of the ridge above the space for the canalis semicircularis anterior. The posterior division of the large shallow depression in *Australosomus* corresponds to the dorsal division of the posterior part of the fossa bridgei in *Boreosomus*, while no part of the fossa bridgei in *Australosomus* can be compared with the ventral division of the posterior part of the fossa bridgei in *Boreosomus*, and accordingly the fossa bridgei in *Australosomus* has no connection with the myelencephalic division of the cranial cavity.

Anterior to the ridge above the space for the canalis semicircularis anterior in *Australosomus* we find a very shallow concavity, which must be homologous to what has been described as the antero-medial division of the anterior part of the fossa bridgei in *Boreosomus*. In *Australosomus*, however, this concavity has only a very indistinct anterior margin, appear-

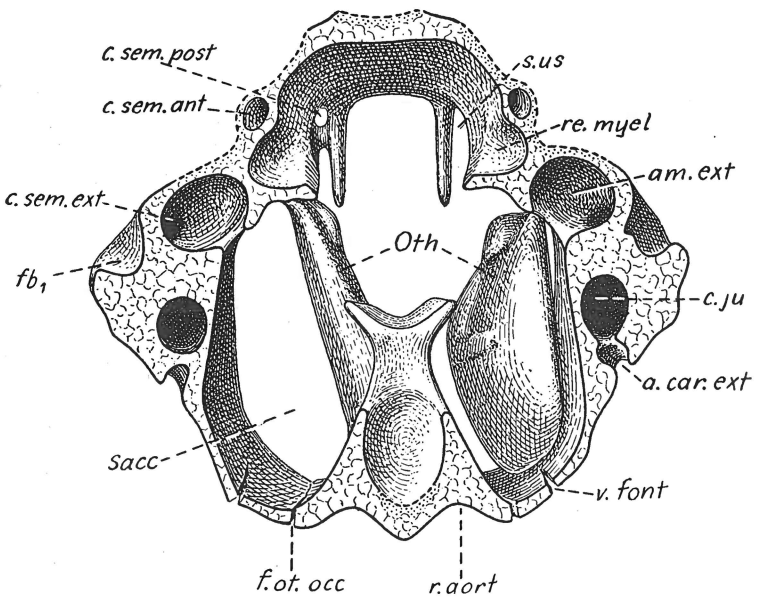


Fig. 9. *Australosomus kochi* (Stensiö). Thick transverse section through the neural endocranium, showing the middle part of the otic region in anterior view. On the basis of a wax model (sections nos 126–140 of the complete grinding series). Faces without perichondral bone reticulated, restored cartilaginous areas dotted, sectional faces unshaded. 10×.

Oth, otolith; *a. car. ext.* canal for the arteria carotis externa; *am. ext*, division of the labyrinth cavity for the ampulla externus; *c. ju*, jugulo-hyoideomandibular canal; *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, fb_1, spiracular division of the fossa bridgei; *f. ot. occ.*, fissura otico-occipitalis; *r. aort*, groove for the radix aortae; *re. myel*, divisions of the cavum cerebrale cranii for the antero-lateral part of the myelencephalon; *sacc*, divisions of the labyrinth cavity for the sacculus; *s. us*, division of the labyrinth cavity for the sinus utriculi superior; *v. font*, vestibular fontanelle.

ing rather as the most posterior part of a poorly defined, mainly longitudinal groove, which continues forward on the dorsal face of the orbitotemporal region, as shown in fig. 3, and I therefore hesitate to describe this concavity as part of the fossa bridgei, from which it is extremely well separated. In *Pteronisculus* the postero-ventral part of the fossa bridgei has a wide connection with the myelencephalic division of the cranial cavity (E. Nielsen 1942, pp. 43–47), however, this part of the fossa is not, as in *Boreosomus*, separated from the postero-dorsal part. In other details, also, the fossa bridgei in *Pteronisculus* differs from that in *Boreosomus*, and thus the fossa bridgei in all the three genera here discussed represents a type of its own. Summarising what has been said above, the three types can be characterised as follows:

The Australosomus type has the spiracular division completely separated from the rest of the fossa and has a shallow posterior part without communication with the myelencephalic division of the cranial cavity.

The Pteronisculus type, which has no separate spiracular division, has a deep posterior part communicating with the myelencephalic division of the cranial cavity.

The Boreosomus type has no separate spiracular division. Its posterior part is more or less completely subdivided into a dorsal and a ventral division, the latter of which communicates with the myelencephalic part of the cranial cavity.

Broadly speaking, the lateral face of the otic region is directed antero-laterally in so far as the otic region decreases in breadth in a ventral direction (figs. 1, 8, 9, 11); however, the face is not plane but shows a very complicated relief. Dorsally and anteriorly the face is marked off from the adjoining ones by fairly distinct edges, posteriorly it is separated from the lateral face of the occipital region by the fissura otico-occipitalis, and this fissure also forms the posterior part of its ventral boundary, while more anteriorly the lateral and the ventral faces of the otic region pass gradually into one another.

The postero-ventral division of the lateral face is dominated by a very large saccular bulge, on the posterior part of which is a small elevated area with a convex surface devoid of perichondral bone. This area (*art. sup. I*, figs. 2, 4, 5, 7, 26) is the place of articulation for the small suprapharyngobranchial ossification of the first branchial arch (p. 121) and thus it corresponds to the somewhat larger area of articulation found on the saccular bulge of *Pteronisculus* (E. Nielsen 1942, p. 48). In *Boreosomus*, also, as shown by the now completed investigation by the grinding method, the first suprapharyngobranchial articulated with the lateral wall of the neural endocranium in principally the same way. The antero-ventral part of the saccular wall is pierced by a small vestibular fontanelle (*v. font*, figs. 1, 2, 4, 5, 7, 9, 15, 16, 18, 26), which in the living animal was somewhat constricted, if not completely closed, by cartilage, the surrounding margins of the cranial wall being devoid of perichondral bone. As already mentioned, the vestibular fontanelle, the shape of which varies somewhat within the specimens investigated, is connected both with the fissura otico-occipitalis and the fissura oticalis ventralis.

Dorsally to the saccular bulge, on the lateral face of the otic region, there is a conspicuous groove, the jugular depression (*jd*, figs. 1, 2, 4, 26), which from the posterior opening of a long jugulo-hyoideomandibular canal extends in a posterior and slightly ventral direction to the otico-occipital fissure. In the jugular depression, and somewhat nearer its dorsal than its ventral margin, lies the external opening of the glossopharyngeus canal (*IX*, figs. 1, 2, 8, 15, 16), which extends from this point in a dorso-medial direction through the cranial wall to the posterior part of the saccular division of the labyrinth cavity, as in *Pteronisculus* and in several other forms (E. Nielsen 1942, p. 48). The postero-dorsal part of the lateral face of the otic region

is concave both in a dorso-ventral and a rostro-caudal direction and has probably served as the place of insertion for the musculus retractor hyomandibularis. In front of this concavity the otic region suddenly increases in breadth, a small field of its lateral face dorsally to the saccular bulge being directed mainly caudally. On the ventral part of this field we find the large posterior opening of the jugulo-hyoideomandibular canal (*c. ju*, figs. 1, 4, 7, 9, 11, 26), anteriorly to the field lies the articular fossa for the hyomandibula (*f. hm*, figs. 1, 2, 4, 7). The longitudinal axis of the hyomandibular fossa runs antero-ventrally to postero-dorsally, but it is much less steep than in *Pteronisculus* (E. Nielsen 1942, p. 48), forming an angle of only about 35° with the ventral mid-line of the postorbital part of the endocranium. The greater part of the articular fossa is situated on the lateral commissure which forms the lateral wall of the jugulo-hyoideomandibular canal, and the antero-ventral end of the fossa lies even more ventrally than the floor of the jugulo-hyoideomandibular canal. Thus *Australosomus* lends new support to the theory that the hyomandibula in the Actinopterygians has shifted its place of attachment on the endocranium from a ventral to a dorsal position in relation to the jugular vein by way of the lateral commissure (cf. Holmgren 1943, pp. 103–104). The serial drawings show that the enchondral bone of that part of the cranial wall with which the hyomandibula articulates has very small medullary spaces with very thick walls; however, it is not possible to decide whether this dense enchondral bone alone constitutes the surface layer of the fossa or whether a perichondral bone-layer is present.

Just ventrally to the anterior part of the hyomandibular fossa between the fossa and the saccular bulge lies the ventral opening of the short canal for the arteria carotis externa (*a. car. ext*, figs. 1, 2, 4, 7, 9, 14); the canal extends from its ventral opening in an antero-dorso-medial direction, to open through the floor of the jugulo-hyoideomandibular canal close behind the trigemino-facialis chamber. Piveteau wrongly interprets the corresponding canal in *Australosomus merlei* as the canal for the ramus hyoideomandibularis facialis (Piveteau 1934, p. 16; figs. 6, 7). From the outer (ventral) opening of the canal a transverse groove extends downwards anteriorly to the saccular bulge, to join, on the ventral face of the otic region, with the anterior end of the groove lodging the aorta root and the arteria carotis communis. The formation of this transverse groove is mainly due to the vigorous outward bulging of the saccular part of the lateral otic wall. The groove must have lodged the arteria carotis externa on its way from the arteria carotis communis to the canal which leads to the jugulo-hyoideomandibular canal. Piveteau, without further explanation, calls the corresponding groove in *Australosomus merlei* the »canal carotidien« (Piveteau 1934, fig. 6).

The most antero-dorsal part of the lateral face is directed mainly antero-

ventro-laterally and is partially separated from that part of the face on which the articular fossa for the hyomandibula is situated by a small vertical ridge, immediately anterior to which the aforementioned small ventral opening of the spiracular canal is found. Ventrally to this opening the narrow marginal zone of the lateral face anteriorly to the transverse groove for the arteria carotis externa is covered by the likewise narrow posterior processus ascendens of the parasphenoid, as shown in figs. 25, 29, 31, 37 and 38.

The posterior and greater part of the ventral face of the otic region, as already mentioned, is separated from the lateral face by the fissura oticooccipitalis, while the most anterior part of the face has no distinct lateral boundary. Anteriorly and posteriorly the ventral face passes gradually into the ventral face of the orbitotemporal and the occipital region respectively. The ventral face is rather broad in its foremost part, but narrows considerably in its intersaccular part, as shown in fig. 4. The face is divided into an anterior and a posterior division by the fissura oticalis ventralis, which, as in *Pteronisculus* (E. Nielsen 1942, p. 50), extends between the right and left vestibular fontanelles.

On the ventral face we find the broad and deep paired groove for the aorta roots. This groove (*r. aort*, figs. 4, 8, 9, 26), which extends forward from the boundary towards the occipital region, at the same time curving slightly outward, reaches the area just anteriorly to the fissura oticalis ventralis, whence it continues on to the lateral face of the region as the already described groove for the arteria carotis externa. The right and left aorta grooves are separated by a median longitudinal ridge, the breadth of which increases in an anterior direction, as shown in fig. 4. The height of the ridge increases both in an anterior and a posterior direction from a point about midway between the posterior end of the ridge and the fissura oticalis ventralis.

Piveteau gives a schematic reconstruction (Piveteau 1934, fig. 13) of that part of the arterial system of *Australosomus merlei* which has left its marks on the postorbital part of the ventral face of the endocranium. At the point where the unpaired aortic groove bifurcates, its lateral wall shows a small notch, which according to Piveteau marks the place where the coalesced arteriae branchiales efferentes II and III joined the aorta, while the arteria branchialis efferens I branched off at the anterior end of the paired groove and the arteria branchialis efferens IV reached the aorta through a small canal which pierces the lateral wall of the unpaired deep aorta groove.

The knowledge now gained of the relations between the neural endocranium and the branchial arches in *Australosomus kochi* (pp. 29, 41) as well as comparisons with the conditions in *Pteronisculus* (E. Nielsen 1942, pp. 187–199) enables us to reconstruct with a fair degree of certainty the relations between the efferent branchial arteries and the dorsal aorta in the

Greenland species. This reconstruction differs considerably from that given by Piveteau of the conditions in *Australosomus merlei*; however, since it is evident owing to the close agreement on many points between *A. kochi* and *A. merlei* that the arterial system in its main features was developed alike in both species, Piveteau's reconstruction, as far as I can see, should be altered in several respects.

The position of the first branchial arch shows that the arteria branchialis efferens I branched off at the anterior end of the groove for the aorta root, as is also assumed by Piveteau. According to the position of the second branchial arch it is probable that the notch in the lateral wall of the aorta groove at the point where this canal bifurcates (this notch is also developed, though very indistinctly, in *Australosomus kochi*) lodged only the arteria branchialis efferens II. The small canal through the lateral wall of the groove or canal for the unpaired aorta was not developed for an efferent branchial artery (see p. 31), and accordingly both the third and the fourth efferent branchial arteries must have joined the dorsal aorta behind the neural endocranium, as is also the case in *Pteronisculus* (E. Nielsen 1942, fig. 46).

The most anterior part of the ventral face of the otic region is convex from side to side, as is also the case with the adjoining part of the ventral face of the orbitotemporal region. Against this convex area rested the infrapharyngobranchial of the first branchial arch, as described in more detail below (p. 121).

The orbital face of the otic region is concave both in a horizontal and a vertical direction and is directed mainly antero-ventrally. The face has no distinct boundaries towards the orbital face of the orbitotemporal region and will be described together with that region. The myodome and the trigemino-facialis chamber, both of which are situated at the transition between the otic and the orbitotemporal region, will be treated in a special chapter (p. 55).

The otic division of the cavum cerebrale cranii is very narrow in the posterior part of the area between the suprasaccular utricular regions of the right and left labyrinth cavities, whence it increases considerably in breadth both in an anterior and a posterior direction. The height of the division varies throughout its length, the roof rising rather steeply from the posterior to the anterior dorsal fontanelle and the floor showing two marked depressions, the posterior of which is especially deep (fig. 6). As already stated (p. 36), the roof of the otic part of the cavum cerebrale cranii was partly cartilaginous, the otic part of the anterior dorsal fontanelle having been more or less completely closed by cartilage in the living animal. The ossified part of the roof consists, in addition to the transverse bridge separating the anterior and the posterior dorsal fontanelles, of a paired, rather narrow, brim laterally to the otic part of the anterior fontanelle. The transverse bridge is far less massive than the corresponding one in *Pteronisculus* (E. Nielsen 1942,

p. 51). The paired brim, which is very thin, curves downward laterally in such a way that it passes quite gradually into the lateral otic wall. This lateral wall is pierced by the very large opening towards the labyrinth cavity. Posteriorly to this opening the cavum cerebrale cranii, as stated above, increases in breadth in a posterior direction, and accordingly the cerebral face of the lateral wall of the most posterior part of the otic division of the cavum cerebrale cranii is mainly directed postero-medially. Anterior to the opening the lateral wall of the otic division of the cavum cerebrale cranii is very thin and its outer face (which forms part of the dorsal face of the otic region), as shown in fig. 3, is in part unossified. The cerebral face of this part of the lateral wall is strongly concave, corresponding to the strong development of the lobi optici (p. 77). A small recess (*re. myel*, figs. 1, 9, 11, 15, 18; pl. 1, fig. 3; pl. 2, fig. 2; pl. 3, fig. 2; pl. 5, fig. 1) on the postero-ventral part of this concave face no doubt corresponds to that part of the brain cavity in *Pteronisculus* which I interpreted as the lateral cerebellar division (E. Nielsen 1942, pp. 51, 101; fig. 14).

The ventral wall of the otic part of the cavum cerebrale cranii is divided by the fissura oticalis ventralis into an anterior and a posterior part. The posterior part of the wall is formed by the otic division of the posterior unpaired ossification of the endocranium (figs. 6, 8), which also constitutes the medio-ventral wall for the saccular division of the labyrinth cavity. The anterior part of the wall is formed by that part of the anterior ossification of the endocranium which lies postero-dorsally to the posterior myodome.

The otic division of the posterior ossification of the endocranium is a massive structure, the posterior part of which is very low, while the anterior part extends in a dorsal direction as a high pillar, which rises almost to the level of the floor of the cranial cavity in the posterior part of the occipital region. The low posterior part is devoid of perichondral bone on its dorsal face and perichondral bone is also lacking on the adjacent part of the anterior pillar and on the almost vertical anterior part of the floor in the occipital region, so obviously the posterior part of the otic floor must have been covered by a probably fairly thick layer of cartilage, as indicated in fig. 6. The high anterior pillar, which is very broad farthest ventrally, narrows in a dorsal direction throughout the greater part of its height, to widen again in its most dorsal part, as shown in figs. 6 and 9. The pillar has an anterior, a paired postero-lateral, and a dorsal face. The anterior face shows an oval concavity, the long axis of which is vertical (fig. 9). This concavity is opposite to a convexity on the posterior face of the wall separating the myodome from the fissura oticalis ventralis. A paired ventro-lateral area of the anterior face of the pillar is devoid of perichondral bone, as is also the case with the opposite areas of the posterior part of the wall between the myodome and the fissura oticalis ventralis, and it is therefore quite possible that the fissura oticalis ventralis was partly closed by cartilage in the living animal.

The postero-lateral face, which joins with its fellow on the opposite side in a sharp median crest, is concave both in a vertical and a horizontal direction and constitutes part of the medial delimitation of the saccular division of the labyrinth cavity.

The dorsal face of the pillar is triangular in outline and rather strongly concave from side to side.

A comparison with *Pteronisculus* shows that the most dorsal part of the pillar here described corresponds so well in shape and position to the small unpaired ossification present in the otic division of the cranial cavity in *Pteronisculus* (E. Nielsen 1942, pp. 53–54) that there can be no doubt of their homology, and thus my assumption as to a cartilaginous connection between the small ossification and the anterior part of the posterior large neurocranial ossification in *Pteronisculus* seems fully justified.

The dorsal part of the pillar is separated from the dorsal part of the transverse hind wall of the posterior myodome by the most dorsal part of the fissura oticalis ventralis. Farthest dorsally the width of the fissura is fairly great, but it decreases rapidly in a ventral direction. The posterior vertical face of the myodome wall, which bounds the fissura oticalis ventralis and the saccular division of the labyrinth cavity anteriorly, as already mentioned shows a median convexity corresponding to the concavity in the anterior face of the posterior endocranial ossification. This convex area lacks perichondral bone, as is also the case with the area situated ventro-laterally to the convexity. Laterally to the dorsal part of the convexity we observe the cerebral opening of the canal for the nervus abducens (*VI*, figs. 1, 7, 11, 12, 15, 16, 19).

That part of the floor of the otic division of the cavum cerebrale cranii which is situated anterior to the fissura oticalis ventralis lies on a slightly higher level than the dorsal face of the high pillar constituting the foremost part of the posterior ossification of the neural endocranium.

Labyrinth cavity. – The labyrinth cavity, and especially its saccular division, has a very considerable size and strongly influences the outer shape of the otic part of the neural endocranium.

The saccular division has a much greater latero-medial extension (breadth) than in *Pteronisculus*, and the membranous labyrinths must have met, or almost met, immediately behind the high anterior part of the posterior ossification of the neural endocranium (cf. figs. 1, 7–9, 16). In lateral view the saccular division is almost triangular in outline, with two free convex margins, viz. an anterior and a postero-ventral one (fig. 15). The nervus glossopharyngeus traverses the postero-dorsal part of the saccular division in the usual way. There is no indication of an especially well developed lagena.

The utricular division has a somewhat greater rostro-caudal extension than the dorsal part of the utricular division. As in *Perleidus* (Stensiö 1932, p. 200), *Ospia* (ibid. p. 239), *Saurichthys* (Stensiö 1925, fig. 9), *Pteronisculus*

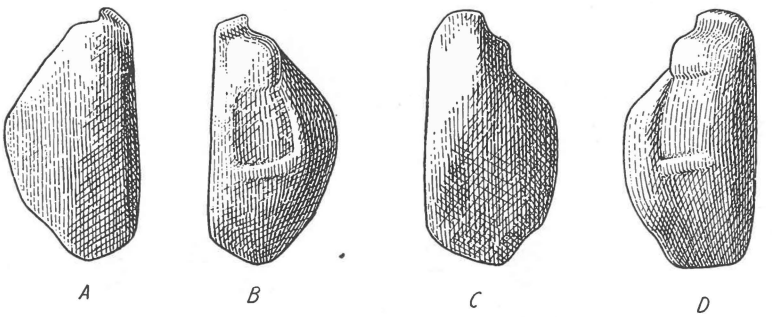


Fig. 10. *Australosomus kochi* (Stensiö). Otoliths. Based on wax models. 10 ×.
A and B. Right otolith in lateral and medial view.
C and D. Left otolith in lateral and medial view.

(E. Nielsen 1942, p. 56), and *Boreosomus* (ibid. p. 301), the presaccular and the post-saccular parts of the utricular division are curved somewhat laterally in relation to the supra-saccular part, but in *Australosomus* the curvature is rather slight (fig. 17).

If we look at the model of the labyrinth cavity from the side (fig. 15) or from above (fig. 17), the supra-saccular part will appear as a very conspicuous swelling medially to the canalis semicircularis externus. The pre-saccular part shows a very small expansion for the recessus utriculi (*ru*, figs. 1, 11, 15, 16). The division for the sinus utriculi superior (*s. us*, figs. 1, 9, 11, 15; pl. 2, figs. 1, 2; pl. 5, fig. 1), which issues in a dorsal direction from the supra-saccular part, is very broad farthest ventrally, but its breadth (rostro-caudal extension) decreases rapidly towards its dorsal end.

The courses of the semicircular canals are clearly shown in the figures and need only little description. The division for the canalis semicircularis anterior (*c. sem. ant*, figs. 1, 9, 11, 15, 17–19; pl. 2, figs. 1, 2) issues from the pre-saccular part of the utricular division anteriorly and very little dorsally to the small expansion for the recessus utriculi and ascends in the usual way to communicate with the most dorsal part of the division for the sinus utriculi superior. Just behind its point of issue from the pre-saccular part of the utricular division lies its well-developed ampullary swelling (*am. ant*, figs. 1, 15–17, 19). In transverse section the canal is oval with the longest diameter fairly vertical. The canalis semicircularis posterior (*c. sem. post*, figs. 1, 8, 9, 11, 15–18) extends from the dorsal part of the division for the sinus utriculi superior to the post-saccular part of the utricular division, into which the ampullary swelling (*am. post*, figs. 1, 8, 15–18) merges without any distinct boundaries.

The ampullary swelling of the canalis semicircularis externus (*am. ext*, figs. 1, 9, 15, 16, 18) is small and not clearly delimited. Posteriorly the external semicircular canal (*c. sem. ext*, figs. 1, 8, 9, 15–19; pl. 2, figs. 1, 2)

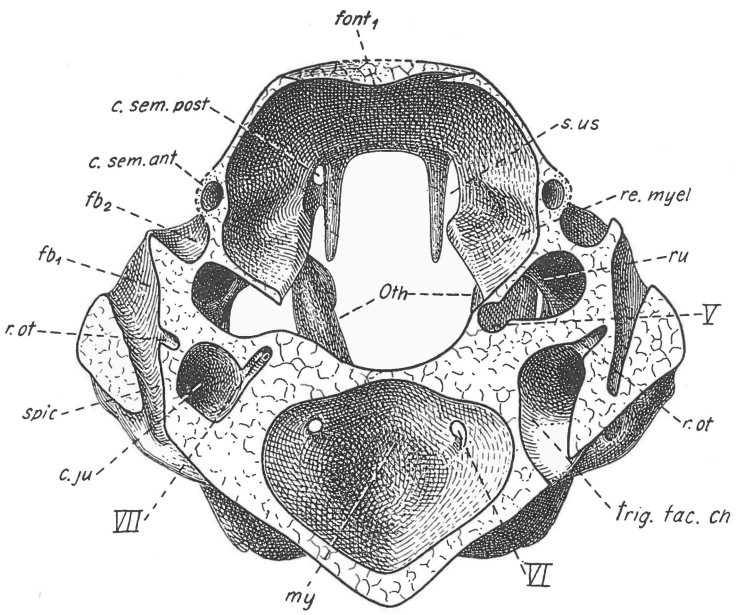


Fig. 11. *Australosomus kochi* (Stensiö). Thick transverse section through the neural endocranium, showing the anterior and middle part of the otic region in anterior view. On the basis of a wax model (sections nos 116–140 of the complete grinding series). Faces without perichondral bone reticulated, restored cartilaginous areas dotted, sectional faces unshaded. 10×.

Oth, otolith; *c. ju*, jugulo-hyoideomandibular canal; *c. sem. ant*, *c. sem. post*, divisions of the labyrinth cavity for the canalis semicircularis anterior and the canalis semicircularis posterior, respectively; fb_1, fb_2, the two anterior divisions of the fossa bridgei; $font_1$, anterior dorsal fontanelle; *my*, posterior myodome; *re. myel*, division of the cavum cerebrale cranii for the antero-lateral part of the myelencephalon; *r. ot*, canal for the ramus oticus lateralis; *ru*, division of the labyrinth cavity for the recessus utriculi; *spic*, spiracular canal; *s. us*, division of the labyrinth cavity for the sinus utriculi superior; *trig. fac. ch*, trigemino-facialis chamber; *V*, trigeminus canal; *VI*, canal for the nervus abducens; *VII* facialis canal.

communicates with the post-saccular part of the utricular division immediately in front of the swelling for the ampulla posterior. In this regard *Australosomus* agrees with *Perleidus* (Stensiö 1932, fig. 61), *Ospia* (ibid., fig. 74), and *Saurichthys* (Stensiö 1925, fig. 9) and differs from *Pteronisculus* (E. Nielsen 1942, p. 57) and *Boreosomus* (ibid., p. 301).

As observed by Stensiö (1932, p. 169; pl. XXIX, fig. 2), well developed saccular otoliths are present in *Australosomus*. The shape of the otoliths in the specimen investigated by grinding is shown in figs. 9 and 10, from which it appears that the right and the left otolith are not quite alike. The otoliths consist of a dense mass which could not be stained by alizarin.

The pre-saccular part of the utricular division was traversed by the roots of the facialis nerve and perhaps also by the trigeminus roots.

The abducens nerve passed through the most anterior part of the saccular division of the labyrinth cavity.

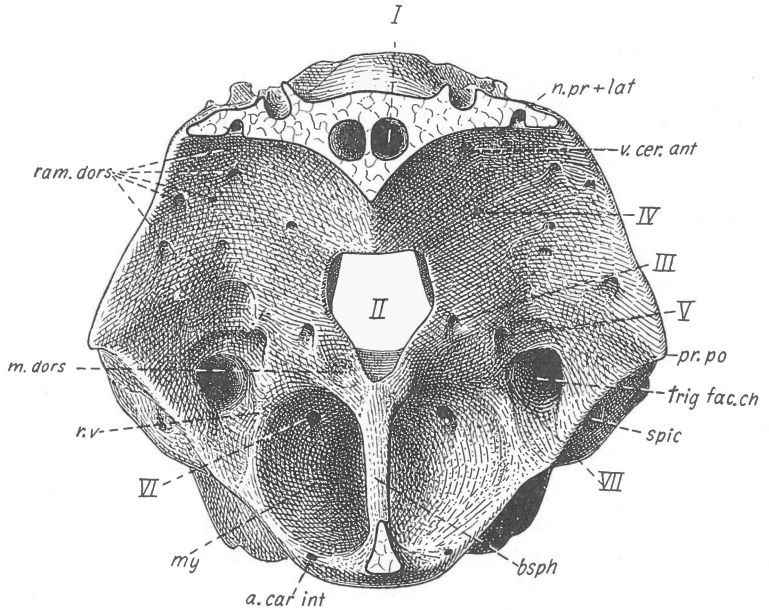


Fig. 12. *Australosomus kochi* (Stensiö). Posterior part of anterior ossification of neural endocranium in anterior view. Based on a wax model (sections nos 59–160 of the complete grinding series). Sectional faces reticulated and unshaded. 10×.

a. car. int, canal for the arteria carotis interna; *bsph*, pars basisphenoidea; *m. dors*, concavity probably for the insertion of eye-muscles; *my*, posterior myodome; *n. pr + lat*, canal for the ramus ophthalmicus lateralis, the nervus profundus, and the ramus ophthalmicus superficialis trigemini; *pr. po*, processus postorbitalis; *ram. dors*, canals for branches of the ramus ophthalmicus superficialis trigemini, the ramus ophthalmicus lateralis, and vessels; *r. v*, ridge between the trigemino-facialis chamber and the myodome; *spic*, spiracular canal; *trig. fac. ch.*, trigemino-facialis chamber; *v. cer. ant*, canal for the vena cerebralis anterior; *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; *VI*, canal for the nervus abducens; *VII*, facialis canal.

Orbitotemporal region. – The orbitotemporal region is the longest of all the endocranial regions, although differing only little in length from the otic region, into which it passes without any marked boundary. For the greater part of its height it is well marked off from the ethmoidal region, this region having well developed and completely ossified postnasal walls (Jarvik's term »postnasal wall« (Jarvik 1942, pp. 242–243) is adopted here instead of the term »planum antorbitale« used in the first part of this work (1942), only farthest dorsally is the transition between the two regions more gradual. The interorbital part of the region is very long and pierced by a fenestra optica (*fe. opt*, fig. 2; pl. 3, fig. 2), the size of which is so considerable that only very little of the interorbital wall is left. Ventrally to the fenestra optica the region is very narrow, while dorsally to the fenestra it has a considerable width and forms a rather extensive roof above the orbit. The broad dorsal part of the region consists of a rather thick median division,

containing the anterior part of the cavum cerebrale cranii and, more anteriorly, the canal for the nervi olfactorii, and flanked on either side by a much thinner lamina supraorbitalis.

The region has an unpaired dorsal, a paired lateral, and an unpaired ventral face.

The dorsal face is broadest farthest posteriorly and narrows in an anterior direction in such a way that its lateral margins are slightly concave (fig. 3). The median area of the face is very strongly convex from side to side and forms a direct forward continuation of the convex external face of the roof of the otic division of the cavum cerebrale cranii. The height of the convexity decreases in an anterior direction, as shown in fig. 2. As already described, the foremost part of the anterior dorsal fontanelle extends forward into the roof of the orbitotemporal region, and around this part of the fontanelle perichondral bone is lacking on the convex median area of the dorsal face to the extent shown in fig. 3.

The paired lateral area of the dorsal face is only slightly convex in a transverse as well as in a longitudinal direction. On this part of the face we find a number of small foramina, viz. the dorsal openings of short canals, which pierce the lamina supraorbitalis in a vertical direction (*ram. dors*, figs. 1, 2, 3, 4, 12, 14). The specimen investigated by grinding shows, on the left side, seven of these canals, the posterior three of which are situated in the transitional area between the otic and the orbitotemporal regions, while on the right side only five such canals are present, two of which lie near the posterior boundary of the orbitotemporal region. Five of the canals on the left side lie in an almost straight line; these canals must have lodged branches of the nervus ophthalmicus lateralis and probably also branches of the ramus ophthalmicus superficialis trigemini together with small vessels (e. g. *Saurichthys*, (cf. Stensiö 1925, p. 48), *Pteronisculus* and *Boreosomus* (E. Nielsen 1942, pp. 88, 303)). The same possibly holds good of the two more laterally placed canals on the left side, however, the most posterior of these canals may also be interpreted as the canal for the buccalis branch which innervated the uppermost sensory organ of the postorbital part of the infraorbital sensory canal. Of the canals on the right side the most posterior one probably corresponds to the posterior canal on the left side, while the other ones must be compared to the more anterior canals on the left side.

On the foremost part of the lateral area of the dorsal face of the orbitotemporal region or (in so far as an exact boundary between the dorsal faces of the two regions does not exist) on the hindmost part of the dorsal part of the ethmoidal region we find the large anterior opening of a long canal (*n. pr + lat*, figs. 2, 3, 4, 12, 13), which extends from this point in an almost caudal direction through the lamina supraorbitalis, to open in the orbit about one-third of the total length of the orbitotemporal region from its anterior end. This canal lodged the nervus ophthalmicus lateralis, the ramus

ophthalmicus superficialis trigemini, and the nervus profundus, all three of which, as in *Amia*, were probably closely connected (cf. Jarvik 1942, pp. 266, 269).

The dorsal face is provided with a number of small elevations of very varying shape (fig. 3). The most posterior one is situated on the postero-lateral part of the rather broad posterior division of the convex median area of the face, while the other ones are situated on the lateral area of the face near its medial boundary. On the left side we find four of these last-mentioned elevations, viz. two short and rather high longitudinal ridges situated a short distance behind the anterior opening of the canal for the ramus ophthalmicus lateralis, the ramus ophthalmicus superficialis trigemini, and the nervus profundus, and, more posteriorly, two smaller elevations placed one behind the other and separated by a very small interval. The two anterior ridges merge anteriorly into a larger elevated area on the antero-lateral part of the dorsal face, as shown in fig. 3. On the right side the most lateral one of the two anterior ridges is divided into two smaller processes, while the two more posterior elevations on the lateral area of the dorsal face are placed one laterally to the other.

Most of the elevations mentioned here serve as supports for the dermal cranial roof, being firmly connected with small processes issuing from the ridge on the ventral face of each frontal developed below the supraorbital sensory canal (p. 92, figs. 22, 23).

On the left side of the specimen investigated by grinding the lateral one of the two anterior ridges, a small part of the antero-lateral elevated area just anteriorly to the lateral ridges, the elevation nearest behind the lateral ridge, and the most posterior elevation had contact with the cranial roof, while on the right side the dermal cranial roof rested against the anterior of the two processes into which the anterior lateral ridge is subdivided, the lateral one of the two more posterior elevations on the lateral area, and the elevation on the strongly convex median area. Apart from these small elevations we find, on the dorsal face of the orbitotemporal region, three other areas, against which the dermal cranial roof rested, viz. a paired narrow area, which partly follows or (farthest posteriorly) runs rather close to the orbital margin of the face and partly extends from the antero-lateral part of the face in an antero-medial direction to continue on the ethmoidal region along the dorsal margin of the fenestra endonarina communis, and an unpaired, mainly cartilaginous area bordering the anterior part of the anterior dorsal fontanelle.

The paired orbital face of the orbitotemporal region is strongly concave, so that its most dorsal part faces more ventrally and its posterior part more anteriorly than laterally. The posterior part of the face, together with the orbital face of the otic region, constitutes the posterior boundary of the orbit, and here we find the orbital openings of the trigemino-facialis chamber

and the myodome, which structures will be treated in detail in a later chapter (p. 55).

In the interorbital wall we find two fenestrations, viz., in addition to the large fenestra optica already mentioned, a more anteriorly placed smaller fenestra (*fe. ant*, fig. 2) separated from the fenestra optica by a narrow bony bridge.

The fenestra optica is unpaired except in its most postero-dorsal part, which, as in *Boreosomus* (E. Nielsen 1942, p. 306), extends some way into the lateral wall of the mesencephalic division of the cavum cerebrale cranii. Through this postero-dorsal part of the fenestra the optic nerves reached the orbit, and thus the paired part of the fenestra (*II*, figs. 1, 2, 4, 6, 12, 15, 16) corresponds to the paired foramen, e. g. in *Pteronisculus* (E. Nielsen 1942, pp. 61, 89). No separate canal for the arteria optica is developed, and accordingly this vessel must have left the cavum cerebrale cranii together with the nervus opticus.

Dorsally and ventrally the unpaired part of the fenestra optica is bounded by a sharp median edge on the surrounding part of the endocranial ossification. Anteriorly it is delimited by the narrow bony bridge which separates it from the more anterior fenestration, while its posterior boundary is formed by the slender vertical pillar of the pars basisphenoidea.

The anterior fenestration in the interorbital wall forms, in the fossil endocranium, a communication between the foremost parts of the right and the left orbit. The fenestration, the vertical diameter of which is about twice as long as the horizontal one, is bounded posteriorly by the bony bridge already mentioned and anteriorly by the most anterior part of the interorbital wall, which appears as a rather inconspicuous median crest on the posterior face of the ethmoidal region.

On that part of the lateral face which lies dorsally to the fenestrated part of the interorbital wall we find the ventral openings of the above-described canals through which nerves and vessels passed from the orbit to the dorsal face of the region. On the corresponding part of the lateral face in *Australosomus merlei* Piveteau found a pronounced groove leading backward from the orbital opening of the canal for the nervus ophthalmicus lateralis, the ramus ophthalmicus superficialis trigemini, and the nervus profundus (Piveteau 1934, p. 19; fig. 19). No similar groove has been observed with certainty in *Australosomus kochi*, and if developed at all, it must, at any rate, be much less distinct than in *A. merlei*.

In addition to the canals from the dorsal face of the endocranium two canals from the cavum cerebrale cranii open on the dorsal part of the lateral face of the orbitotemporal region. The posterior one of these (*IV*, figs. 1, 4, 12, 15, 16) extends from the orbit in a postero-dorsal direction through the cranial wall, to open in the antero-ventral part of the division of the cavum cerebrale cranii, which lodged the mesencephalon and was, no doubt, tra-

versed by the nervus trochlearis. The other canal (*v. cer. ant*, figs. 1, 4, 12, 15–17, 19), the orbital opening of which lies antero-dorsally to that of the trochlearis canal, leads in a postero-medial direction to the diencephalic division of the cavum cerebrale cranii and, as shown by a comparison with *Pteronisculus* (E. Nielsen, 1942, p. 59), must have lodged the vena cerebralis anterior.

The pars basisphenoidea (*bsph*, figs. 1, 2, 3, 12; pl. 3, fig. 2), as in *Boreosomus* (E. Nielsen, 1942, p. 306), may be regarded as consisting of a ventral broad and a dorsal slender division. The ventral division lies roughly between the floor of the myodome and that part of the orbitotemporal region which is situated beneath the fenestra optica, but has no marked anterior or posterior boundaries. Its ventral face, which is convex from side to side, is almost completely covered by the parasphenoid (fig. 26). A basipterygoid process is not developed. Quite near its lateral margin we find, on the dorsal face of the ventral division of the pars basisphenoidea, the round anterior opening of a rather narrow longitudinal canal which opens posteriorly on the ventral face of the most lateral part of the floor of the myodome. This canal (*a. car. int*, figs. 1, 2, 4, 12, 26) lies as an anterior continuation of the groove on the ventral face of the otic region developed for the aorta root and must have lodged the arteria carotis interna.

The narrow dorsal division of the pars basisphenoidea appears as a high, almost vertical pillar, which forms the posterior boundary of the postero-ventral part of the fenestra optica and divides the anterior opening of the posterior myodome inte a right and a left half. The pillar extends so far in a dorsal direction that its most dorsal part, which forms a deeply concave transverse edge, bounds the foramen opticum (the paired posterior part of the fenestra optica) ventrally. The concavity of the dorsal edge of the pillar is possibly due to the development of the chiasma. In transverse sections the basisphenoid pillar is elliptical throughout the greater part of its height, with a short longitudinal and a long transverse axis; only in its most dorsal part, which increases in breadth in a dorsal direction, as shown in fig. 12, the transverse sections assume another shape, the posterior face of the pillar showing a small median groove, which lodged the most anterior part of the hypophysis (p. 77). At the transition between the anterior face of the dorsal broadest part of the pillar and the adjoining part of the orbital face of the orbitotemporal region we find, laterally to the ventral part of the optic foramen on the right side of the head, a rounded shallow concavity (*m. dors*, fig. 12). As shown in fig. 12, the corresponding area on the left side is developed in a rather different way, the left half of the most dorsal part of the basisphenoid pillar being less than half as broad as the right one, yet a faint depression on the left side evidently corresponds to the dorso-medial part of the right concavity just described. The small concavity probably served as a place of insertion for some of the recti eye-muscles.

The arteria carotis interna must have reached the cavum cerebrale cranii through the ventral division of the foramen opticum without traversing any part of the vertical basisphenoid pillar, which is evidently homologous with a very small part, only, of the basisphenoid pillar, in, for instance, *Pteronisculus* (E. Nielsen 1942, p. 63) and *Boreosomus* (ibid. p. 306). The basisphenoid pillar may also be compared to the median unpaired root of the pars basisphenoidea in Kansasform A (Watson 1925, p. 838) and *Perleidus* (Stensiö 1932, pp. 203–204), in which forms, as suggested in the first part of the present work (E. Nielsen 1942, p. 64), the paired lateral basisphenoid root must correspond more or less completely to the lateral part of the broad basisphenoid pillar in *Pteronisculus*. Holmgren (1943, p. 169) puts forward the assumption that the paired lateral basisphenoid root in *Perleidus* and Kansas form A is a homologue to the alisphenoid pedicle or pila lateralis in *Amia;* however, the relation between the alisphenoid pedicle and the jugular vein in *Amia* in my opinion speaks very strongly against this homologisation, as does also the fact that a small alisphenoid pedicle is present in *Pteronisculus magna* just anterior to the orbital opening of the trigemino-facialis chamber (E. Nielsen 1942, p. 90).

The arteria pseudobranchialis efferens and the arteria ophthalmica magna were situated entirely outside the neural endocranium; accordingly nothing can be said regarding the exact course of these vessels.

The ventral face of the orbitotemporal region is broadest farthest posteriorly and narrows in an anterior direction throughout the two-thirds of its length, to widen somewhat in its anterior third. The face, which is convex from side to side, is completely covered by the much broader parasphenoid. No parabasal canal is developed between the narrow ventral face of the orbitotemporal region and the parasphenoid, the ramus palatinus evidently having had a more lateral course (p. 81).

The orbitotemporal division of the cavum cerebrale cranii attains its greatest width and height farthest posteriorly, and the breadth as well as the height decreases in an anterior direction to the rostral end of the cavity, which lies somewhat nearer to the anterior than to the posterior end of the region. As is evident from the figures of the model of the neurocranial cavities (figs. 15–17), the decrease in breadth and height is not quite gradual, the height descreasing fairly much just anterior to a vertical transverse plane through the anterior end of the anterior dorsal fontanelle, and the breadth decreasing very suddenly a short distance farther posteriorly.

The orbitotemporal division of the cavum cerebrale cranii is bounded by an unpaired dorsal, a paired lateral, and an unpaired ventral wall, but there is no distinct boundaries between these walls, all of which are rather thin. As already described (p. 53) the lateral wall is pierced by the trochlearis canal and the canal for the vena cerebralis anterior, while the ventral wall is pierced by the large foramen opticum, a short distance posterior to which

we observe a very small infundibular recess (*inf. r*, figs. 1, 3, 15, 19), which communicates with the myodome by a pituitary fontanelle (*pit. font*, figs. 1, 16) situated just posteriorly to the dorsal end of the pars basisphenoidea.

Myodome, trigemino-facialis chamber, jugulo-hyoideomandibular canal, and canals for nerves and vessels in the posterior part of the orbito-temporal region and the anterior part of the otic region. – The posterior myodome (*my*, figs. 1, 2, 11, 12, 14; pl. 2, figs, 1, 2; pl. 3, fig. 2) appears as an unpaired cavity situated partly in the posterior part of the orbitotemporal region and partly in the anterior part of the otic region, as in *Pteronisculus*, *Boreosomus*, the Kansas forms, *Perleidus*, etc., and consists of a large intramural and a very small extracranial part. It opens into each orbit with a large opening, which, as in *Pteronisculus* (E. Nielsen 1942, p. 70), is confluent with the somewhat smaller orbital opening of the more dorso-laterally situated trigemino-facialis chamber. Between the orbital myodome openings stands the vertical basisphenoid pillar, and as that pillar only corresponds to the median rod of the pars basisphenoidea in *Perleidus* and Kansas form B (cf. p. 54), the myodome openings in *Australosomus* contain equivalents not only to the lateral but also to the medial orbital myodome openings in these forms.

In its general shape the posterior myodome agrees more closely with that in *Boreosomus* (E. Nielsen 1942, pp. 309–311) than with that in *Pteronisculus* (ibid., pp. 70–74), the height of the space much exceeding the length (i. e. its rostro-caudal extension).

For descriptive reasons we may consider the myodome as bounded by six walls, viz. a dorsal, a ventral, a paired lateral, a posterior, and an anterior one; however, with the exception of the latter, which is very well defined, all these walls pass very gradually into one another, so that it is impossible to draw fairly satisfactory boundary lines between them. Owing to this and to the very large size of the orbital myodome openings, the myodome may perhaps best be characterised as a rather deep median concavity in the ventral part of the anterior face of the postorbital division of the endocranium bridged by the narrow basisphenoid pillar.

The roof of the myodome is formed by the rather thin bony wall which forms the floor of the cavum cerebrale cranii immediately behind the dorsa end of the pars basisphenoidea. The anterior part of this wall is pierced by the small pituitary fontanelle, which is about twice as broad as long, and the posterior part corresponds rather well to the prootic bridge, e. g. in *Pteronisculus* (E. Nielsen 1942, p. 72). The posterior wall of the myodome forms the anterior boundary of the fissura oticalis ventralis. In its midmost part this wall is very thin, but its thickness increases somewhat towards the periphery. The dorso-lateral part of the wall is pierced by the canal for the nervus abducens (VI, figs. 1, 6, 11, 12, 15, 16, 19), which, as in many other Actino-

pterygians, opens into the posterior myodome. The floor of the myodome is rather thin in its median part a short distance behind the pars basisphenoidea, whence it increases in thickness both in an anterior, a posterior, and a lateral direction. There is no fenestra ventralis myodomus. The anterior part of the ventral face of the floor is covered by the parasphenoid to the extent shown in fig. 26. Just behind the posterior edge of the parasphenoid we find, on the most lateral part of the ventral face, the posterior opening of the above-mentioned canal for the arteria carotis interna, the anterior opening of which is situated on the dorsal face of the ventral broad division of the pars basisphenoidea (p. 53). The ramus palatinus facialis left the myodome through its orbital opening, not, as in *Pteronisculus* (E. Nielsen 1942, p. 72), through a special canal in its floor.

The anterior wall is formed by the basisphenoid pillar, which, as already stated, must be compared to the medial rod of the pars basisphenoidea in *Perleidus* and Kansas form A. The posterior face of the pillar is very slightly convex from side to side except in its most dorsal part, where it shows a short median groove, the width of which increases in a dorsal direction.

The lateral wall is formed partly by the endocranium and partly by the ascending process of the parasphenoid. The endocranial part of the wall is less strongly developed than in the Kansas forms (Watson 1925, figs. 16–18), *Perleidus* (Stensiö 1932, p. 210, figs. 64, 65), *Amia* (ibid., p. 248; fig. 73 A), and *Pteronisculus* (E. Nielsen 1942, pp. 72–73, figs. 4, 6, 10, 11, 16); thus the continuity between this wall and the lateral wall of the trigemino-facialis chamber, if actually existing, is much less pronounced than in these forms. That part of the wall which is formed by the ascending process of the parasphenoid is very narrow and only antero-ventrally bounds a small anterior part of the myodome. The ascending process moreover covers the antero-ventro-laterally directed marginal zone of the external face of the endocranial part of the lateral myodomic wall.

The size and position of the pituitary fontanelle and the absence of a fenestra ventralis myodomus render it probable that the hypophysis only occupied a small antero-dorsal part of the myodome and did not communicate with the oral cavity. As in *Amia* (Allis 1897, p. 494), the saccus vasculosus was probably situated below that part of the roof of the myodome which corresponds to the prootic bridge, and the front end of the hypophysis was most likely placed in the groove on the dorsal part of the posterior face of the basisphenoid pillar.

The myodome thus comprises a spinal and a prespinal part, as in the Kansas forms, *Pteronisculus*, *Boreosomus*, and *Perleidus* (cf. E. Nielsen 1942, pp. 73, 311). It agrees most closely in shape with that of *Boreosomus;* however, on account of the great reduction of the basisphenoid pillar most of these recti muscles, which in *Boreosomus* are inserted on the anterior face of the basisphenoid pillar, presumably entered the myodome.

The trigemino-facialis chamber (*trig. fac. ch*, figs. 1, 4, 11, 12, 14) forms a depression on the orbital face of the endocranium dorso-laterally to and not completely separated from the myodome. The chamber consists of an anterior rather wide and a posterior much narrower division. The boundaries between the chamber and the adjoining parts of the orbital face are not very distinct, however, the orbital opening of the chamber may be roughly described as irregularly oval in outline with its vertical diameter almost $1\frac{1}{2}$ times as long as its horizontal one. The posterior narrow division of the trigemino-facialis chamber, which is somewhat better defined, is continued in a caudal direction by the long jugulo-hyoideomandibular canal, and may, in fact, be regarded as the foremost widened part of the canal. In its most anterior part the posterior division is rounded triangular in transverse section, more posteriorly, however, the space gradually narrows, its transverse sections growing more elliptical, with the long axis of the ellipse nearly vertical. The lateral wall of the chamber is fairly thick and contains the above-described (p. 39) almost vertical spiracular canal. On the most dorsal part of the medial face of the lateral wall of the posterior narrow division of the chamber we find the opening of the rather fine canal through which the ramus oticus lateralis reached the spiracular canal (cf. p. 39). The corresponding opening in *Pteronisculus* (E. Nielsen 1942, p. 75) has a more anterior position, while in *Boreosomus* (ibid. p. 312) it is situated almost as in *Australosomus*. *Australosomus* and *Boreosomus* likewise agree as regards the course of the oticus canal, the canal in both species connecting the trigemino-facialis chamber with the most dorsal part of the spiracular canal.

The roof of the trigemino-facialis chamber, which separates the chamber from the most anterior part of the utricular division of the labyrinth cavity, is rather thin. A floor is only developed in the posterior division of the chamber, and the ramus palatinus facialis evidently left the chamber through its orbital opening, not by piercing its floor.

The medial wall separates the chamber from the cavum cerebrale cranii, and as in many other primitive Actinopterygians, it is pierced by two canals one for the roots of the nervus trigeminus (*V*, figs. 1, 4, 11, 12, 15, 16, 19; pl. 2, figs. 1, 2; pl. 5, fig. 1) and one for those of the nervus facialis (*VII*, figs. 1, 11, 12, 15, 16, 19; pl. 5, fig. 1). Both canals issue from the antero-medial part of the utricular division of the labyrinth cavity, the latter postero-ventrally to the former. Both canals pierce the cranial wall in antero-ventro-lateral directions, the canals, however, are not parallel, the facialis canal having a more ventral direction than the trigeminus canal. The latter canal opens in the anterior division of the trigemino-facialis chamber on the dorsal part of the lateral face of the medial wall, while the facialis canal opens in the posterior division of the chamber, where its external opening is found on the most dorsal part of the lateral face of the medial wall postero-ventro-laterally to the external opening of the trigeminus canal.

The two canals show good agreement with the corresponding ones in *Pteronisculus* (E. Nielsen 1942, pp. 79–81), the trigeminus canal being wider than the facialis canal and more elliptical in transverse section. A trigemino-facialis recess is not developed and everything seems to indicate that the trigemino-facialis ganglionic complex, as in *Pteronisculus* (E. Nielsen 1942, pp. 81–84), was situated mainly or exclusively in the trigemino-facialis chamber.

Between the external opening of the trigeminus canal and the foramen opticus lies the external opening of a short wide canal (*III*, figs. 1, 12, 15, 16), which extends in a postero-medial direction through the cranial wall, to open in the cavum cerebrale cranii immediately dorsally to the infundibular recess. A comparison with *Pteronisculus* (E. Nielsen 1942, p. 72), *Boreosomus* (ibid. pp. 312–313), *Saurichthys* (Stensiö 1925, pp. 38, 48–49), and the Kansas forms (cf. E. Nielsen 1942, p. 78) shows that this canal must have lodged the nervus oculomotorius.

As in *Saurichthys* (Stensiö 1925, pp. 48–49) and *Boreosomus* (E. Nielsen 1942, p. 313), in *Australosomus* there is no separate canal for the nervus profundus. As regards *Saurichthys*, Stensiö thinks it probable that the nervus profundus left the cranial cavity through the same canal as the nervus oculomotorius, basing this view mainly on the course of the profundus nerve in *Polypterus;* I have argued in the same way regarding the probable course of the nervus profundus in *Boreosomus*. However, judging from Jarvik's investigations on the snout of the lower Gnathostomes (Jarvik 1942) *Polypterus* seems to be more distantly related to the Actinopterygians than previously assumed, and hence it is perhaps a little far-fetched to draw conclusions regarding such anatomical details as the course of the profundus nerve in the Actinopterygians on the basis of the conditions in *Polypterus*, all the more so since in *Polypterus* the nervus profundus, as emphasised by Jarvik (1942, p. 268), is probably developed in quite a different way from that in the Actinopterygians. The lack of a separate profundus canal in *Saurichthys*, *Boreosomus*, and *Australosomus* might therefore perhaps better be explained by assuming that the profundus nerve accompanied the trigeminus through the trigeminus canal, the profundus nerve having fused completely with the ramus ophthalmicus superficialis trigemini, as is the case in most Teleosts (H. Stannius 1849, p. 39; Allis 1897, pp. 538–539).

The long jugulo-hyoideomandibular canal, which extends in a mainly posterior direction from the trigemino-facialis chamber, curves around the most dorsal part of the saccular division of the labyrinth region in such a way that its medial side is concave and its lateral side correspondingly convex in a rostro-caudal direction. The floor of the canal just behind the trigemino-facialis chamber is pierced by the rather wide vertical canal for the arteria carotis externa, the ventral opening of which, as already described (p. 42), is situated on the lateral face of the otic region. The jugulo-hyoideo-

mandibular canal has only one posterior opening. As mentioned above, the articular fossa for the hyomandibula extends across the external face of the lateral wall of the jugulo-hyomandibular canal, the anterior end of the fossa being situated more ventrally and the posterior end more dorsally than the canal (p. 42).

Ethmoidal region. – In the specimen investigated by serial sectioning the ethmoidal region is ossified almost throughout its extent, only the most anterior part and a small paired superficial area situated on the postero-dorsal part of the region having consisted of cartilage. The anterior cartilaginous part of the region cannot be reconstructed with certainty; however, it seems probable that it was developed as a short and blunt rostrum.

The region attains its maximum height and width in its most posterior part and decreases gradually both in height and width in an anterior direction, as shown in the figures. The maximum breadth is almost equal to the maximum height, however, as the breadth decreases more rapidly than the height, the region is higher than broad throughout the greater part of its length. The length of the ossified part of the region is about three-fifths the maximum breadth or height. The nasal sacs are enclosed in real nasal cavities, not situated in mere pits as in most Actinopterygians. The lateral wall of each nasal cavity is pierced by a very large fenestra endonarina communis (cf. Jarvik 1942, p. 246).

The region presents six external faces, viz. a posterior, a dorsal, a ventral, an anterior, and a paired lateral face.

The posterior face (fig. 13), which, broadly speaking, is almost square in outline with a dorsal, a ventral and a paired lateral margin, curves backward dorsally in such a way that it passes into the orbital face of the orbitotemporal region without any marked boundary, while laterally and in part also ventrally it meets respectively the lateral and the ventral face of the ethmoidal region in pronounced edges. On the posterior face we observe a very inconspicuous median crest, which extends from the dorsal margin of the face to a point situated at about one-third of the whole height of the face from its ventral margin, to continue, after an interruption on the transitional area, towards the orbital face of the antero-ventral part of the orbitotemporal region.

This crest may best be compared to the most anterior part of the interorbital wall in forms in which this wall is better developed and in which it completely divides the posterior face of the ethmoidal region into a right and a left half. If we disregard the median crest just mentioned, the posterior face of the ethmoidal region presents a large unpaired concavity (*my. ant*, figs. 1, 4, 13), the breadth of which is somewhat less than half the breadth of the face, and which extends from the ventral to the dorsal margin of the face.

This concavity, which has its greatest depth in its ventral half, must be regarded as an anterior myodome, the ventral deep part of which was

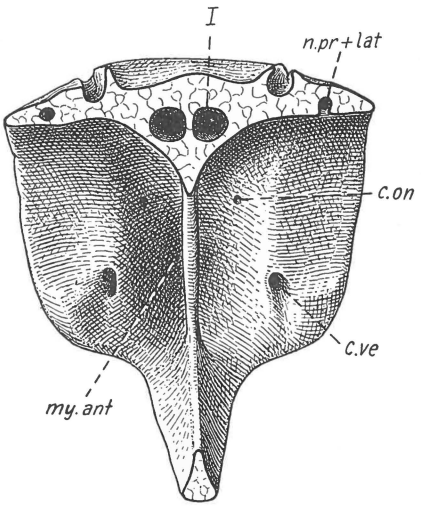


Fig. 13. *Australosomus kochi* (Stensiö). Anterior part of anterior ossification of neural endocranium in posterior view. On the basis of a wax model (sections nos. 1–58 of the complete grinding series). Sectional faces reticulated and unshaded. 10 ×.

c. on, canal probably for a vein; *c. ve*, canal possibly for the ramus maxillaris trigemini and the ramus buccalis lateralis; *my. ant*, anterior myodome; *n. pr + lat*, canal for the ramus ophthalmicus lateralis, the nervus profundus, and the ramus ophthalmicus superficialis trigemini; *I*, canal for the nervus olfactorius.

developed for the musculi obliqui inferiores, while its dorsal, more shallow part was the place of insertion for the musculi obliqui superiores. Judging from the position of the anterior myodome, the anterior fenestration in the interorbital wall has arisen in connection with the musculi obliqui.

As is evident from the above description, the large anterior myodomic depression in *Australosomus* contains homologues to the paired dorsal as well as to the paired ventral anterior myodomes in *Pteronisculus* (E. Nielsen 1942, pp. 94–96; fig. 17 A) and *Boreosomus* (ibid. pp. 304–305; figs. 62, 64).

That part of the posterior face of the ethmoidal region which is situated laterally to the myodomic depression is slightly concave in a dorso-ventral direction, apart from a small convexity on its ventro-lateral part, and almost plane from side to side.

On the posterior face we find two paired foramina, the smaller of which is situated in the myodomic depression a little nearer the dorsal than the ventral margin of the face, while the other is placed on the lateral area of the face just laterally to the deepest part of the myodomic depression. The smaller foramen is the posterior opening of a canal, which extends in an anterior direction through the postnasal wall, to open in the posterior part of the nasal cavity (*c. on*, figs. 1, 13–17).

The other and larger foramen, from which a shallow groove leads in a ventral direction to the ventral margin of the lateral area of the posterior face, is the orbital opening of a wide canal, leading in a dorsal and somewhat

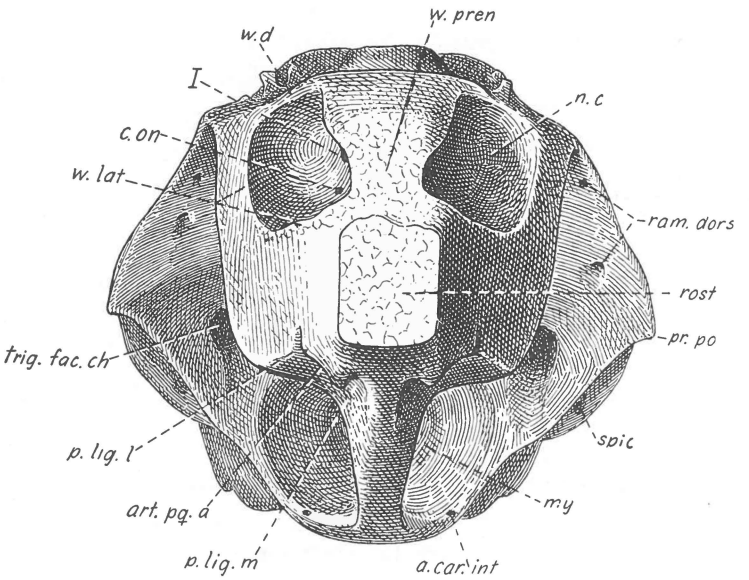


Fig. 14. *Australosomus kochi* (Stensiö). Neural endocranium in anterior view. On the basis of a wax model. Faces without perichondral bone reticulated. 10×.

a. car. int, canal for the arteria carotis interna; *art. pq. a*, articular facet for the pars autopalatina palatoquadrati; *c. on*, canal probably for a vein; *my*, posterior myodome. *n. c*, nasal cavity; *p. lig. l*, *p. lig. m*, pits for ligaments connecting the palatoquadrate and the neural endocranium; *pr. po*, processus postorbitalis; *ram. dors*, canals for branches of the ramus ophthalmicus superficialis trigemini, the ramus ophthalmicus lateralis, and vessels; *rost*, rostral face of ethmoidal region; *spic*, spiracular canal; *trig. fac. ch*, trigemino-facialis chamber; *w. d*, tectum nasi; *w. lat*, lateral nasal wall; *w. pren*, prenasal wall; *I*, canal for the nervus olfactorius.

anterior direction to the postero-ventral part of the nasal cavity (*c. ve*, figs. 1, 3, 4, 13, 15–17, 19). On the left side of the head the canal opens in the nasal cavity with a single opening, on the right side, however, it bifurcates quite near its antero-dorsal end and has accordingly two openings towards the nasal cavity, one of which lies a very short distance postero-laterally to the other.

Of the two canals described here, the dorsal and narrower one probably lodged a vessel and might perhaps best be compared with the canal through the postnasal wall in sturgeons described by De Beer (1937, p. 93) as the orbito-nasal canal and lodging a vein. As regards the ventral and wider canal one might be tempted to compare it with the canal for the posterior external nasal tube, which in *Eustenopteron* perforates the ventro-lateral part of the postnasal wall (Jarvik 1942, pp. 436, 446). Two facts, however, speak against such a comparison, viz. the bifurcation of the antero-dorsal part of the canal on the one side of the head and the presence of the groove which from the orbital opening of the canal leads in a ventral direction to the ventral margin of the posterior face of the ethmoidal region. Another possibil-

ity is that the canal lodged the ramus maxillaris trigemini and the nervus buccalis lateralis. Both in *Pteronisculus* (E. Nielsen 1942, pp. 85, 93, fig. 17) and in *Saurichthys* (E. Stensiö 1925, pp. 74, 78, 90; figs. 1, 6, 14, 16) these nerves together with vessels were lodged in a distinct groove on the lateral face of the ethmoidal region, and such a groove is certainly not developed in *Australosomus*. It might therefore be assumed that in *Australosomus* the canal arose owing to the closing of a similar nature to that found in *Saurichthys* or *Pteronisculus*. In *Polypterus* (cf. Jarvik 1942, pp. 263–265) the ramus maxillaris trigemini and the nerves buccalis lateralis together with vessels reach the nasal cavity through a closed canal, and in *Boreosomus*, also, (E. Nielsen 1942, pp. 316–317; fig. 65) a canal for the nerves in question seems to be developed. The only objection that may be raised against comparing the canal in *Australosomus* with the canal or groove for the ramus maxillaris trigemini and the nerves buccalis lateralis in the forms mentioned above is the almost vertical course of the canal in *Australosomus*. However, this course may find its explanation in the extraordinary enlargement of the orbits which has taken place in *Australosomus* at the expense of the surrounding part of the neural endocranium.

The dorsal face of the ethmoidal region consists of a very short broad part situated behind the external openings of the large nasal cavities and of a much longer, relatively narrow part placed between these openings.

The posterior broad part of the face is curved much in the same way as the most anterior part of the dorsal face of the orbitotemporal region, into which it passes without any marked boundary. As mentioned above, the anterior opening of the paired canal for the nervus ophthalmicus lateralis, the nervus profundus, and the ramus ophthalmicus superficialis trigemini is situated on the dorsal face of the neural endocranium at the transition between the orbitotemporal and the ethmoidal regions. From this opening a groove extends forward to the posterior margin of the external opening of the nasal cavity (the fenestra endonarina communis). In its posterior half this groove is very deep, while more anteriorly it is rather shallow. The floor of the posterior deep part of the groove lacks perichondral bone and was probably covered by cartilage in the living animal.

The anterior narrow part of the dorsal face falls into an anterior and a posterior division, which meet in a rather distinct angle, the anterior division, which comprises about two-thirds of the whole narrow part of the face, being somewhat more anteriorly directed than the posterior one. From side to side the anterior part of the face is slightly convex except farthest posteriorly, where it presents a small and very shallow median concavity. Along its lateral margins the face is devoid of perichondral bone to the extent shown in fig. 3, and thus the bony roof of the nasal cavity was prolonged in a lateral direction by a cartilaginous marginal zone, the breadth of which, however, cannot be determined. The anterior part of the dermal

cranial roof (postrostrals and nasals) probably rested upon this cartilaginous zone and had no contact with the ossified part of the anterior narrow part of the dorsal face (cf. figs. 3, 23).

The ventral face of the ethmoidal region is well marked off from the adjoining faces except posteriorly, where it passes quite gradually into the ventral face of the orbitotemporal region. The breadth of the face decreases uniformly in an anterior direction. The most anterior area of the ventral face is fairly plane and is directed somewhat more anteriorly than the rest of the face. Between the plane anterior area, the length of which is about one-third the whole length of the ventral face, and the posterior boundary of the region extends a strong median keel, which forms a direct anterior continuation of the narrow ventral part of the orbitotemporal region. The breadth of the keel increases in a posterior direction, as shown in fig. 4. Against this keel as well as against a narrow median zone of the anterior plane area rests the foremost part of the parasphenoid.

That part of the ventral face which lies laterally to the median keel appears, if we disregard the finer details of its rather complicated relief, as a mainly ventro-laterally directed field. Against the triangular antero-lateral part of this field (*art. pq. a*, figs. 1, 2, 4, 14) articulates the pars autopalatina of the palatoquadrate. The articular area, which is slightly concave from side to side, is completely covered with perichondral bone. Between the posterior part of the articular area and the foremost part of the median keel lies a deep and narrow pit, the oblong opening of which faces postero-ventrally (*p. lig. m*, figs. 1, 2, 4, 14, 26, 29, 31; pl. 2, fig. 2; pl. 3, fig. 2).

A still deeper pit (*p. lig. l*, figs. 1, 2, 4, 14, 29, 31; pl. 1, fig. 2) is found postero-laterally to the articular area on the edge between the ventral and the lateral face of the ethmoidal region. From its outer opening, which is almost circular on the one side of the head and somewhat longer than broad on the other, the pit extends in a dorso-medial direction, to end immediately below the bottom of the nasal cavity of its side.

The two pits described here most probably served as places of insertion for the strong ligaments which connected the anterior part of the palatoquadrate with the ethmoidal region of the endocranium.

The anterior face, which is well marked off from the adjoining faces by pronounced edges, is roughly rectangular in outline and more than twice as high as broad. That part of its paired lateral margin which bounds the fenestra endonarina communis anteriorly shows a small concavity, the shape of which is shown in fig. 14. On the wax-model the ventral part of the face presents a forward-directed entirely plane area of a fairly considerable extent. This, however, is due to the circumstance that a very thin slice of the rostral end of the endocranium was removed by grinding before the first section was drawn; no doubt, the whole anterior face of the ethmoidal region of the specimen investigated by grinding was faintly convex in a dorso-ventral

direction as well as from side to side. The whole face is devoid of perichondral bone, a fact from which we may conclude that the foremost part of the endocranium in the living fish consisted of cartilage.

Anteriorly, ventrally, and posteriorly the lateral face meets the adjoining faces at distinct angles. The antero-dorsal part of the face is occupied by the very large fenestra endonarina communis (*fe. en*, figs. 2, 3, 15, 17, 19, 21, 25; pl. 1, fig. 2), behind which the face passes quite gradually into the posterior part of the dorsal face of the region. The fenestra endonarina communis, which, as shown in the figures, has an oblong irregularly rounded outline, faces antero-dorso-laterally, its longest diameter pointing forwards and downwards. Ventrally and postero-ventrally to the fenestra the lateral face is mainly directed antero-laterally and slightly ventrally. This part of the face presents a very shallow dorso-ventral concavity. Posterior to the fenestra the lateral face is slightly convex in a dorso-ventral direction and faces laterally and slightly antero-dorsally.

The whole lateral face is covered by perichondral bone, which, however, is not continuous with the perichondral lining of the foremost half of the nasal cavity, the dorsal edge of the anterior part of the lateral wall of the nasal cavity having been cartilaginous in the living fish.

The paired nasal cavity (*n. c*, figs. 1, 14–17, 19; pl. 1, fig. 4; pl. 2, figs. 1, 2; pl. 3, figs. 1, 2) has well developed walls, the nasal capsules, as already stated, being much more complete than in most Actinopterygians. Using the terms introduced by Jarvik (1942, p. 245), we may distinguish between an internasal wall, a prenasal wall, a postnasal wall, a lateral nasal wall, a tectum nasi, and a solum nasi.

The internasal wall forms a nasal septum, which is rather thin, though of varying thickness in its different parts. Farthest anteriorly it passes into the diviso prenasalis communis. Two areas of the nasal septum are especially thin, viz. a rather large central area of the anterior half of the septum and a much smaller area of its postero-dorsal part. A very fine canal (*f. sn*, fig. 2) through the dorsal part of the anterior thin area connects the right and the left nasal cavities. The anterior thin area owes its presence to the general concavity of the lateral faces of the septum, while the small postero-dorsal thin area is due to the existence of a well defined postero-dorso-medial recess in the nasal cavity (*re. pmd*, figs. 1, 2, 15, 17, 19). Ventrally to this recess a broad and shallow longitudinal groove on the lateral face of the nasal septum leads to the anterior end of the olfactory canal.

The postnasal wall[1]) is very thin in its central part, but increases fairly much in thickness towards its margins. On the concave anterior face of the wall we find two foramina, the larger of which is situated just below the

[1]) N. B. As the nasal cavities occupy a relatively dorsal position in the ethmoidal region, I only use the term postnasal wall for that part of the ethmoidal region which is situated behind each nasal cavity and the term solum nasi for that part of the region which lies ventrally and postero-ventrally to each nasal cavity.

most posterior part of the postero-dorso-medial recess of the nasal cavity, while the other lies somewhat more ventro-laterally. The larger foramen is the anterior opening of the wide olfactory canal (*I*, figs. 1, 7, 12–19; pl. 2, fig. 1; pl. 5, fig. 1), which extends backward from this point to the cavum cerebrale cranii, and the smaller foramen is the anterior opening of the canal already described, which is possibly comparable to De Beer's orbito-nasal canal (cf. p. 61).

In the fossil endocranium the lateral nasal wall is only present ventrally and posteriorly to the large fenestra endonarina communis; since, however, in the living fish, as mentioned above, this fenestra was to some extent constricted by cartilage in its anterior part, it is quite possible that a lateral nasal wall was also developed anteriorly and dorsally to the fenestra.

Ventrally to the fenestra the lateral nasal wall decreases in thickness in a dorsal direction, and except anteriorly, where it was continued by cartilage, its free edge is rather sharp. The medial face of the wall is concave in a rostro-caudal as well as in a dorso-ventral direction, while the lateral face, as already described, is almost plane.

The ossified part of the prenasal wall (the dorso-lateral part of the divisio prenasalis communis) is very thin farthest dorso-laterally, but increases in thickness in a medial as well as in a ventral direction. The posterior face of the wall is concave.

The tectum nasi extends from the most dorsal part of the nasal septum in a mainly lateral direction and comprises a posterior very thin division above the postero-medial part of the nasal cavity, including the postero-medio-dorsal recess and an anterior thicker division, which roofs the antero-medial part of the nasal cavity. The lateral free edge of the posterior division is very sharp, while the lateral free edge, of the anterior division is more blunt and, judging from its lack of perichondral bone, was probably continued by cartilage in a lateral or ventro-lateral direction.

The solum nasi is by far the thickest of the walls of the nasal capsule, the nasal cavity having a relatively dorsal position within the ethmoidal region. On its dorsal face, which is concave both in a longitudinal and a transverse direction, we find the single or double opening of the above-described ascending canal which connects the nasal cavity with the antero-ventral part of the orbit.

Each nasal cavity is a long, high, and rather narrow space, which might perhaps best be described as kidney-shaped. The ratio between its greatest length, height, and width is about 6:5:3. The space attains its greatest height in its posterior half, the most dorsal part of which, as already mentioned, is developed as a well defined postero-medial recess. As shown in fig. 1, each transverse section through the cavity attains its greatest width on a level with the ventral margin of the fenestra endonarina communis, whence it narrows both in a dorsal and a ventral direction. The maximum width of

the whole space is found in the area inside the most postero-ventral part of the margin of the fenestra endonarina communis, i. e. in the highest part of the space.

The narrow canal between the two nasal cavities, and the canals leading from the nasal cavities to the orbits have been described above (pp. 60-64). The only other canals opening in the nasal cavities are the olfactory canals (*I*, figs. 1, 7, 12–17, 19; pl. 2, fig. 1; pl. 5, fig. 1), which are separate throghout their length and have a wholly intracranial course. Each olfactory canal issues from the foremost part of the cavum cerebrale cranii, whence it extends in an anterior and slightly ventral direction, to open in the postero-medial part of the nasal cavity just ventrally to the most posterior part of the recessus postero-medialis. Throughout its length the olfactory canal is curved in such a way that its dorsal face is slightly convex and its ventral face correspondingly concave in a longitudinal direction, and moreover the most anterior part of the canal, as shown in figs. 16 and 17, is bent somewhat laterally. In transverse sections the canal, which has about the same dimensions throughout its length, is circular or slightly oval, the height being a little greater than the width.

Discussion. – As pointed out by Piveteau (1935, pp. 23–24), the endocranium of *Australosomus merlei* shows considerable agreement with the famous Palaeonisciform endocrania from the Carboniferous of Kansas (in the present work termed Kansas forms A and B), as well as with that of *Perleidus*. In several other characters, however, as stated by different anthors (Piveteau 1935, pp. 32, 37; Wade 1935, p. 65; E. Nielsen 1936, pp. 44–46), *Australosomus* bears a striking resemblance to *Saurichthys*, which according to Stensiö (1925, pp. 207–224), though closely related to the *Palaeonisciformes*, cannot have evolved from these.

The problem with which we are confronted here is accordingly whether *Australosomus* should be regarded as a Palaeonisciform derivative, or whether it is more closely related to the Saurichthyids. This problem will be treated here on the basis of the present detailed investigation of the neural endocranium of *Australosomus kochi*.

If we briefly consider the apparent structural differences between the neural endocrania of the two best known species of *Australosomus*, viz. *Australosomus kochi* and *Australosomus merlei* (as far as is known, the other species of *Australosomus*, which are described below (pp. 163–173), as regards their neurocranial structures differ in no important respects from *Australosomus kochi*). Judging from Piveteau's description and figures, the neural endocranium of *Australosomus merlei* differs from that of *Australosomus kochi* mainly in the following respects:

1) Both the anterior and the posterior dorsal fontanelle are lacking.
2) The otico-occipital fissure is closed just dorsally to the vagus exit.

3) The aorta was lodged in a groove on the ventral face of the endocranium, not in a canal.
4) A separate canal is developed for the arteria optica.
5) The fenestra endonarina communis is circular in outline.

Considering the rather poor state of preservation of Piveteau's material, none of the differences listed above are very significant, and probably all, or most, of them will turn out to be non-existent when better preserved material of *Australosomus merlei* becomes available. As a basis for the following comparison I have therefore chosen to use only the characters of the neural endocranium of *Australosomus kochi*).

The *Palaeonisciformes* comprise a very large number of genera belonging to several families (cf. Aldinger 1937), however, only in a few forms has the neural endocranium been studied in detail, viz. in the Kansas forms A and B, *Pteronisculus*, *Boreosomus*, and *Birgeria*. As demonstrated in the first part of the present work, the neural endocrania of the Kansas forms, *Pteronisculus*, and *Boreosomus* show fairly close agreement in most respects, and as these four forms represent at least three different families within the *Palaeonisciformes*, it is hardly too bold a guess that also in other families within the *Palaeonisciformes* the neural endocranium will prove to possess a similar structure, all the more so since this is the case with several higher Ganoids the ancestors of which must be sought for among the *Palaeonisciformes*, for instance *Perleidus* (Stensiö 1932, pp. 188–214), *Ospia* (ibid., pp. 228–249), *Broughia* (ibid., pp. 268–273), *Leptolepis* (D. H. Rayners 1937, pp. 57–65), and *Amia* (Allis 1897).

This uniformity in the structure of the neural endocranium of four of the best investigated *Palaeonisciformes* renders it convenient for comparative purposes to define a generalised type of neural endocranium based on all the important characters common to all four forms and on decidedly primitive characters even though they may be lacking in one or more of the forms in question. This generalised type, which in the following pages will be termed the central Palaeonisciform type, may be characterised as follows:

1) The occipital and the ethmoidal regions are very short, comprising together not more than one-fifth of the whole length of the endocranium.
2) The posterior third of the endocranium is excavated laterally in such a way that its broad dorsal part appears as a more or less well marked horizontal ledge overhanging the much narrower ventral part.
3) The endocranium possesses a long fissura otico-occipitalis, which ends anteriorly in a vestibular fontanelle, and a fissura oticalis ventralis, which connects the right and the left vestibular fontanelle.
4) The cranio-spinal processes are very small.
5) The dorsal aorta was lodged in a canal in the posterior part of the base of the endocranium.

6) The roof of the endocranium is pierced by two median fontanelles, the posterior of which is an expansion of the dorsal part of the fissura otico-occipitalis, while the other served as the endocranial epiphysial opening.
7) A large paired fossa bridgei is developed. This fossa consists of a deep anterior portion, into which opens the spiracular canal, a shallow middle and a deep posterior portion, which latter communicated with the cavum cerebrale cranii through a wide opening.
8) The lateral face of the otic region shows two articular areas, viz. a dorsal one for the hyomandibula and a ventral one for the suprapharyngobranchial I.
9) A jugulo-hyoideomandibular canal is present, the anterior part of which is widened so as to form a trigemino-facialis chamber of a primitive type.
10) A posterior unpaired myodome comprising spinal and prespinal divisions is developed for the musculus rectus externus. The roof of the myodome is pierced by a pituitary fontanelle and the floor by a fenestra ventralis myodomus.
11) The dorsal part of the pars basisphenoidea is developed as an ascending pillar pierced by a paired canal for the arteria carotis interna and dividing the orbital opening of the myodome into a right and a left half.
12) Strong basipterygoid processes are developed.
13) The orbits are very large and are separated by a thin interorbital septum, the greater part of which is occupied by an large interorbital fenestra.
14) The main element in the short ethmoidal region is a vertical transversely placed postnasal wall.
15) The adult endocranium is almost completely ossified and is occupied either by a single large ossification or by two smaller ones, viz. an anterior one extending throughout the ethmoidal and the orbitotemporal region, and the antero-dorsal part of the otic region, and a posterior one comprising the postero-ventral part of the otic and the entire occipital region.

Most of the structural details summarised above probably also existed in the hypothetic ancestor of the typical *Palaeonisciformes*, and hence it is very interesting that many of these details, according to the reconstructions made by Watson (1937, figs. 17–18), are also found in the neural endocranium of the Acanthodians, all the more so since the scales of the Devonian *Cheirolepis* are of a decidedly Acanthodian type.

According to Watson (1937), the Acanthodians are very primitive Gnathostomians characterised i. a. by a complete gill-slit between the mandibular and the hyoid arches. The Acanthodians are less closely related to the Selachians than generally assumed.

The essential differences pointed out by Watson between the neural endocranium of the Acanthodians and the earliest Selachians have been summarised by Holmgren (1942, p. 131) as follows:

1) The Acanthodian skull contains perichondral bone-lamellae, that of the Selachians is calcified with lime prisms.
2) The neural cranium in the Acanthodians is tropibasic, that of the Selachians is platybasic.
3) The occipital region in the Acanthodians is long and passes directly into the otic region; in the Selachians it is short and ends abruptly at the transversely placed posterior surface of the otic capsules.
4) The otic region in the Acanthodians has a »horizontal crest, below which it is excavated, passing smoothly into the ventral surface«. In the Selachians the otic capsules are square-cut masses forming the transversely placed hinder wall of the orbit. Their lateral surface is nearly at right angles to their ventral surface.
5) In the Acanthodians »the postorbital process is independent of the otic capsule and is connected with the basis cranii by powerful sloping columns of cartilage, perforated by the jugular canal«. In the Selachians the postorbital process is fused on to the otic capsules.
6) In the Acanthodians no hyomandibular facet occurs on the otic capsule. In the Selachians such a facet is present.
7) In the Acanthodians there are no articular facet for the orbital process and no basal angle; in the Selachians both may be present.
8) No definite suborbital shelf occurs in the Acanthodians, whereas such a shelf exists in the Selachians.
9) An interorbital septum is present in the Acanthodians, but not in the Selachians.
10) In the Acanthodians the olfactory capsules must have been small, in contact with each other with anteriorly directed nostrils. In the Selachians the olfactory capsules are large, »separated, often very widely, by the extension forward of the brain cavity as the precerebral cavity, the walls of which support the rostrum«. The nasal openings are never directed forward.

The individual characters in the above list are critically treated by Holmgren, who points out that the evidence brought forward by Watson regarding the phylogenetic relations of the Acanthodians might also be interpreted so that most of the apparent differences between the Acanthodians and the Selachians lose their value as arguments for a wide separation between the two groups (Holmgren 1937, pp. 131–141).

The point which is of interest in Holmgren's discussion in this connection is that many of his arguments for a closer relationship between the Acanthodians and the Selachians may just as well be regarded as arguments for a relationship between the Acanthodians and the Actinopterygians, as will be evident from a study of his paper. To me, therefore, it does not seem quite unlikely that the ancestors of at least the greater part of the Actino-

pterygians should be sought for, if not among the Acanthodians themselves, so at any rate among forms which were ancestral or in some other way closely related to the Acanthodians (see further pp. 70, 92, 109).

The neural endocranium of *Australosomus* agrees in so many particulars with the central Palaeonisciform type that all doubt as to a close relationship between the *Pholidopleuridae* and the typical *Palaeonisciformes* must be out of the question. The only essential points on which the neural endocranium of *Australosomus* differs from that of the central Palaeonisciform type are the following:

1) The shape of the fossa bridgei.
2) The absence of basipterygoid processes.
3) The structure of the ethmoidal region.

As to 1) In *Australosomus* the fossa bridgei, which is completely subdivided into minor fossae, the antero-lateral and deepest of which is not roofed over by the dermal cranial roof, while the posterior one is very shallow and does not communicate with the cavum cerebrale cranii, may quite possibly have arisen from an undivided fossa bridgei with a deep posterior part, as in the central Palaeonisciform type. In fact, the fossa bridgei in *Boreosomus* might in some degree be regarded as intermediate between the fossa in *Pteronisculus* and that in *Australosomus*.

As to 2) An initial reduction of the vertical basisphenoid pillar as well as of the basipterygoid processes is observed in *Boreosomus*, and the complete reduction of the basipterygoid processes in *Australosomus* must be regarded as one of the many points in which the development of *Australosomus* has approached that of the higher Ganoids.

As to 3) At present it is difficult to decide whether the long and massive ethmoidal region with its complete nasal cavities in *Australosomus* should be regarded as specialised or primitive compared with the short and simply built one in the central Palaeonisciform type. On the one hand the ethmoidal region in the Crossopterygians, which were probably rather closely related to the ancestral Actinopterygians, is large and shows complete nasal cavities (cf. Jarvik 1942), as is also the case with the ethmoidal region in the Sturgeons and the Saurichthyids; on the other hand, however, the Acanthodians, which seem to agree in many respects with the primitive Actinopterygians (cf. pp. 69), probably had a very short ethmoidal region (Watson 1937), while the ethmoidal region in most higher Actinopterygians is, if anything, longer than in the central Palaeonisciform type. The question might perhaps be answered by an investigation of the most primitive Pholidopleurids. I wish, however, to premise that from a morphological point of view it does not seem impossible that the ethmoidal region of *Australosomus* should have developed from the simple one of the central Palaeonisciform type.

The endocranium of *Saurichthys*, which has been investigated in very

great detail by Stensiö (1925), differs from that of the central Palaeonisciform type in many respects; it will suffice here to mention the following points:

1) The occipital and the ethmoidal regions are both very long and together comprise about four-fifths of the total length of the endocranium.
2) The otic region is not excavated laterally.
3) There is no otico-occipital fissures and no vestibular fontanelles. The ventral otic fissure is likewise lacking.
4) The cranio-spinal processes are very large.
5) The dorsal aorta was not enclosed in a canal in the base of the endocranium.
6) Only one median fontanelle pierces the endocranial roof. This fontanelle may best be compared to the anterior dorsal fontanelle in the central Palaeonisciform type, although it did not serve as a place of exit for the epiphysial stalk.
7) The paired fossa bridgei seems entirely to lack homologues to the posterior part of the fossa bridgei in the central Palaeonisciform type, and has no connection with the spiracular canal.
8) There is no distinct articular facet for the suprapharyngobranchial I.
9) The posterior myodome is spinal in its position.
10) The basisphenoid pillar is a very massive structure, the caudal extension of which is much larger than in the central Palaeonisciform type.
11) There are no basipterygoid processes.
12) The ethmoidal region has a very long rostrum and complete nasal capsules separated by a thick internasal wall.
13) The whole neural endocranium is very extensively ossified and with the exception of the posterior end of the occipital region forms a single large ossification.

In 1925 Stensiö made a comparison between the neural endocranium of *Saurichthys* and that of the *Palaeonisciformes*, and arrived at the conclusion that »most of the characters so far known by which the primordial neurocranium of the Saurichthyids differs from that of the Palaeoniscids are of such a nature that the primordial neurocranium of the Saurichthyids can be thought to have developed from that of a Palaeoniscid or from a Palaeoniscid-like one.« (Stensiö 1925, pp. 207–208). It must be borne in mind, however, that at that time very little was known of the neural endocranium of the *Palaeonisciformes*, only the otic and the orbitotemporal regions of the Triassic genera *Birgeria* and *Acrorhabdus* having been investigated in some detail (Stensiö 1921, pp. 152–175, 177–180, 224, 240–241), and accordingly Stensiö's comparison rested on a very uncertain basis.

In 1932, i. e. at a time when our knowledge of the structure of the neural endocranium of the primitive Actinopterygians was much greater than in

1925, Stensiö, after a critical treatment of certain views held by Sewertzoff regarding the relationships of the Chondrosteans, again discussed the relationships of *Saurichthys* and again arrived at the result that the Saurichthyids »are closely allied to the Palaeoniscids« (Stensiö 1932, pp. 74–96).

All the differences enumerated here are of such a nature that the neural endocranium of *Saurichthys* might theoretically be assumed to have developed from the central Palaeonisciform type. However, it is by no means certain that such an evolution has actually taken place, for as regards some points in the list it is impossible from our present sparse knowledge to decide whether the conditions in *Saurichthys* are specialised or primitive as compared with those in the central type.

As undoubted specialisations in *Saurichthys*, I regard the extreme length of the occipital and the ethmoidal regions, the lack of otico-occipital fissures and vestibular fontanelles, the large size of the cranio-spinal processes, the lack of the posterior dorsal fontanelle, the course of the spiracular canal, and the lack of basipterygoid processes.

As discussed above (p. 70), it is not quite certain, though quite probable, that the extreme shortness of the ethmoidal region in the central Palaeonisciform type is an ancestral character. The evolution within the Actinopterygians may therefore have proceeded along two lines from an ancestral ethmoidal region shorter than that in *Saurichthys* but longer than that in the central Palaeonisciform type. It is also doubtfull whether *Saurichthys* is specialised as compared with the central Palaeonisciform type in its lack of a ventral otic fissure and an aorta canal and in its development of the median dorsal fontanelle, the fossa bridgei, the posterior myodome, and the pars basisphenoidea.

As to the ethmoidal region we may in a way regard the neural endocranium of *Australosomus* as intermediate between that of *Saurichthys* and that of the central Palaeonisciform type. The basisphenoid pillar in *Australosomus*, however, shows i. a. that *Australosomus* cannot form a connecting link between the Saurichthyids and the typical *Palaeonisciformes*, this part of the endocranium being reduced as compared with that of the central Palaeonisciform type, while the basisphenoid pillar in *Saurichthys* is still more massive than in the central type.

Summarising what has been said above, the known neural endocrania of typical *Palaeonisciformes* are modifications of the same general type – the central Palaeonisciform type – which probably had most of its essential characters in common with the neural endocranium of the ancestor of the *Palaeonisciformes*, and which moreover resembles the Acanthodian neural endocranium in many respects. The neural endocranium of many later Actinopterygians can also be regarded as modifications of the central Palaeonisciform type.

The endocranium in *Australosomus* has most probably developed from

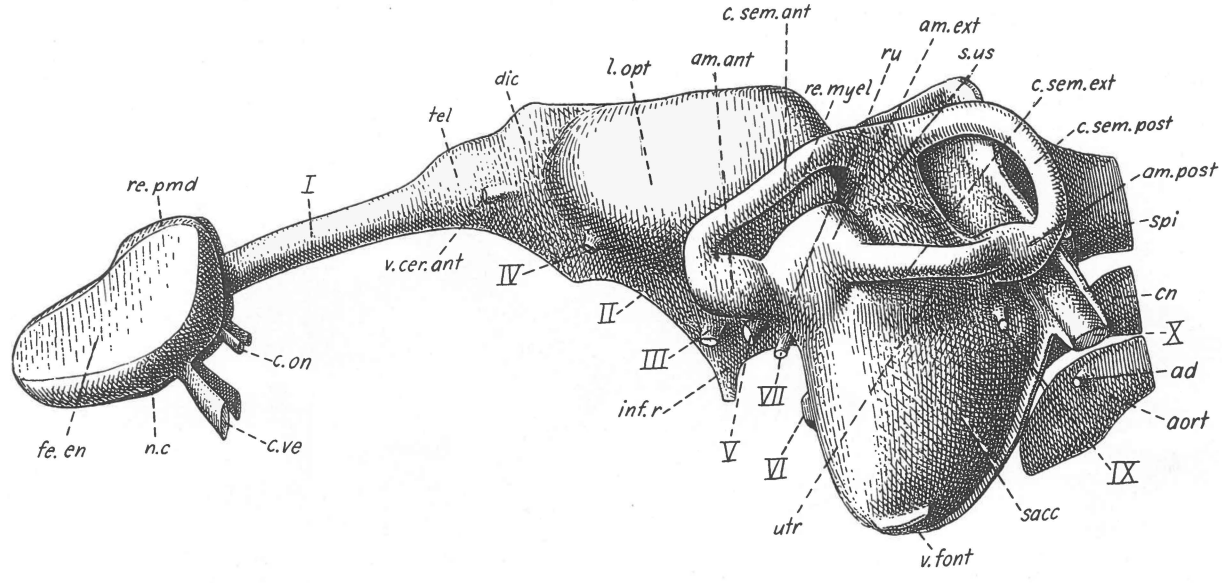
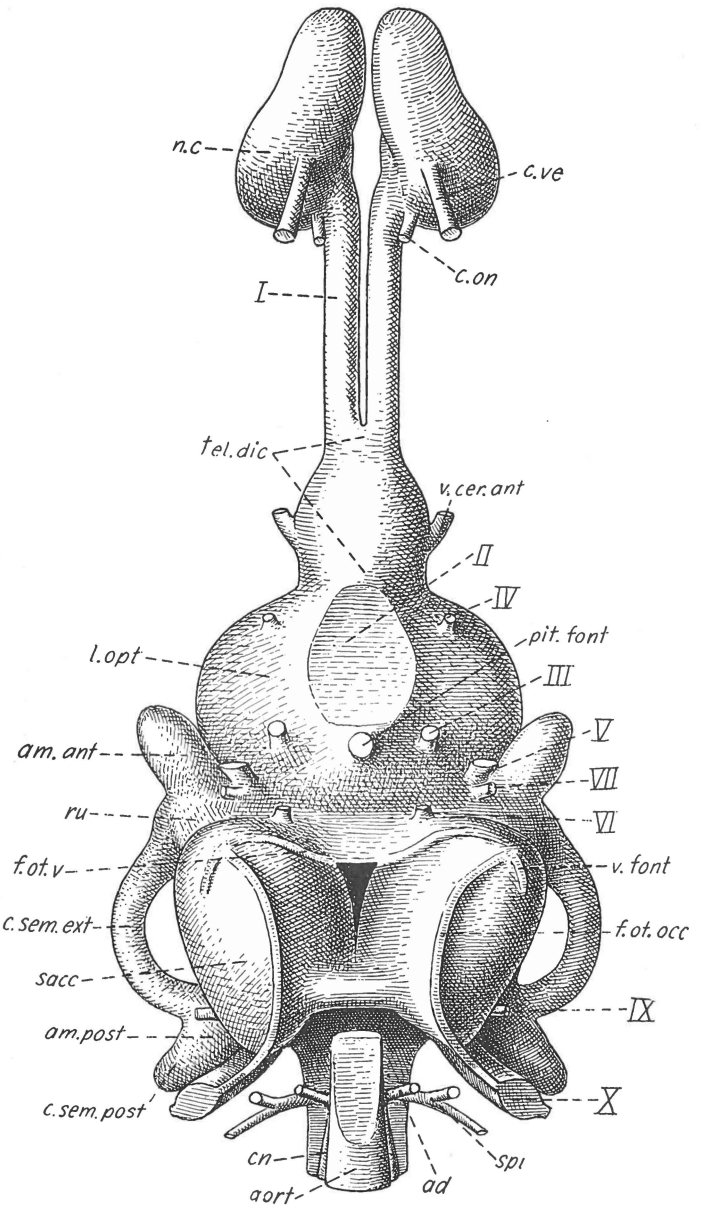


Fig. 15. *Australosomus kochi* (Stensiö). Cast of the cavities of the neural endocranium in lateral view. On the basis of a wax model. 10×.

ad, canal for an artery; *am. ant*, *am. ext*, *am. post*, divisions of the labyrinth cavity for the ampulla anterior, the ampulla externa, and the ampulla posterior, respectively; *aort*, aorta canal; *cn*, space for the notochord; *c. on*, canal probably for a vein; *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. ve*, canal possibly for the ramus maxillaris trigemini and the ramus buccalis lateralis; *dic*, divisions of the cavum cerebrale cranii for the diencephalon; *fe. en*, fenestra endonarina communis; *inf. r*, infundibular recess; *l. opt*, division of the cavum cerebrale cranii for the lobus opticus; *n. c*, nasal cavity; *re. myel*, division of the cavum cerebrale cranii for the antero-lateral part of the myelencephalon; *re. pmd*, postero-dorso-medial recess of the nasal cavity; *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; *tel*, division of the cavum cerebrale cranii for the telencephalon; *utr*, division of the labyrinth cavity for the utriculus; *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; *VI*, canal for the nervus abducens; *VII*, facialis canal; *IX*, canal for the nervus glossopharyngeus; *X*, canal for the nervus vagus.


n.c
c.ve
c.on
I
tel.dic
v.cer.ant
II
IV
pit. font
l.opt
III
V
am. ant
VII
ru
VI
f.ot.v
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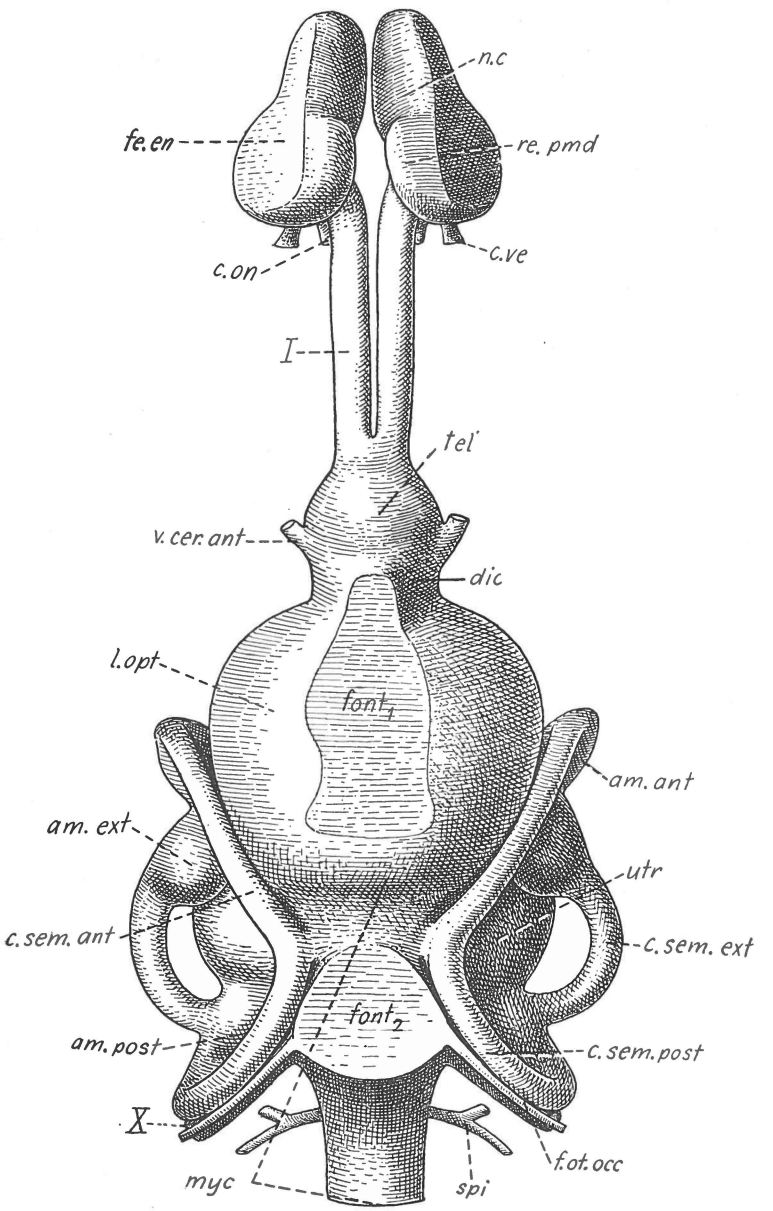
the central Palaeonisciform type and is specialised in a holostean direction. The neural endocranium in *Saurichthys* might perhaps also be supposed to have been derived from the central Palaeonisciform type. *Australosomus* and *Saurichthys* show a somewhat similar development of the ethmoidal region of the neural endocranium, but in other respects the neural endocrania of the two genera have developed in different ways, and hence *Australosomus* cannot be regarded as ancestral to *Saurichthys*.

Remarks on the brain.

Since in the specimen investigated by grinding the cavum cerebrale cranii was almost completely lined with perichondral bone, its shape could be determined with still greater accuracy than was the case in *Pteronisculus* (E. Nielsen 1942, p. 100). Probably the cavum cerebrale cranii was nearly or completely filled by the brain and it is therefore possible from the shape of the cavum cerebrale cranii to obtain some information about the structure of the brain.

The telencephalon and the diencephalon (*dic*, figs. 15, 17; pl. 5, fig. 1. – *tel*, figs. 15, 17; pl. 5, fig. 1. – *tel. dic*, figs. 1, 16, 19; pl. 1, fig. 3) must have been of a type not very different from that known from the Kansas forms (Moodie, 1915, figs. 15–17), *Pteronisculus* (E. Nielsen, 1942, p. 100; figs. 13, 14, 15), and *Boreosomus* (ibid. p. 319, fig. 66), and as in these forms and in *Saurichthys* (Stensiö 1925, p. 159, fig. 52), the posterior part of the diencephalon was to some extent covered by the antero-lateral part of the mesencephalon. The telencephalon was probably somewhat broader than the diencephalon. As in the Kansas forms, *Pteronisculus*, and *Boreosomus* (cf. E. Nielsen 1942, pp. 100, 319), it is probable, judging from the relations between the anterior dorsal fontanelle and the brain, that the epiphysial stalk left the brain cavity through the anterior part of the fontanelle. The hypothalamus region was smaller than in *Pteronisculus* (E. Nielsen 1942,

Fig. 16. *Australosomus kochi* (Stensiö). Cast of the cavities of the neural endocranium in ventral view. On the basis of a wax model. 10×.
ad, canal for an artery; *am. ant*, *am. post*, divisions of the labyrinth cavity for the ampulla anterior and the ampulla posterior, respectively; *aort*, aorta canal; *cn*, space for the notochord; *c. on*, canal probably for a vein; *c. sem. ext*, *c. sem. post*, divisions of the labyrinth cavity for the canalis semicircularis externus and the canalis semicircularis posterior, respectively; *c. ve*, canal possibly for the ramus maxillaris trigemini and the ramus buccalis lateralis; *f. ot. occ*, fissura otico-occipitalis; *f. ot. v*, fissura oticalis ventralis; *l. opt*, division of the cavum cerebrale cranii for the lobus opticus; *n. c*, nasal cavity; *pit. font*, pituitary fontanelle; *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; *tel. dic*, division of the cavum cerebrale cranii for the tel- and diencephalon; *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; *VI*, canal for the nervus abducens; *VII*, facialis canal; *IX*, canal for the nervus glossopharyngeus; *X*, canal for the nervus vagus.


n.c
fe.en
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I
tel
v. cer. ant
dic
l.opt
font1
am. ant
am. ext
utr
c. sem. ant
c. sem. ext
font2
am. post
c. sem. post
X
f. ot. occ
myc
spi

p. 74), the infundibular recess being relatively narrow and short and the pituitary fontanelle very small. As mentioned above (p. 56), the most ventral part of the hypophysis, as well as the saccus vasculosus, was situated in the dorsal part of the myodome, and there was no connection between the hypophysis and the mouth cavity. The nervi optici issued from the ventral part of the diencephalon immediately in front of the indundibulum. A chiasma was probably developed.

The mesencephalon (*mec*, fig. 1) was very large, and the lobi optici were probably still more prominent than in *Pteronisculus* (E. Nielsen 1942, p. 100, figs. 13–15). As in the Kansas forms (Moodie 1915, figs. 15–17), *Saurichthys* (Stensiö 1925, pp. 38, 159, figs. 12, 17, 52), *Pteronisculus* (E. Nielsen 1942, p. 100, figs. 13–15), and *Boreosomus* (ibid. p. 321, fig. 66), the nervus oculomotorius and the nervus trochlearis left the cranial cavity laterally to the mesencephalon, the latter of these nerves, however, considerably more antero-ventrally than in *Pteronisculus* and *Boreosomus*.

In *Boreosomus* a paired, very prominent bulge is seen on the model of the cranial cavity just behind the division for the mesencephalon, and postero-ventrally to the anterior half of this bulge lies another bulge, which, however, is shorter and less prominent (E. Nielsen 1942, p. 321, fig. 66). The longer of these bulges I interpreted as the division of the cavum cerebrale cranii for the lateral part of the metencephalon and compared it to the metencephalon bulge present in the Kansas forms. As to the shorter bulge, which is not found in the Kansas forms, I put forward the assumption that it represented the division of the cranial cavity for the antero-lateral corner of the myelencephalon (tuberculum acusticum). In *Pteronisculus* (ibid. pp. 100–101) the mesencephalic and the metencephalic divisions of the cavum cerebrale cranii are not lined with perichondral bone in their dorsal parts, and hence their exact shape cannot be determined. It seems certain, however, that a fairly large recess was developed a short distance anterior to the most dorsal part of the opening between the cavum cerebrale cranii and the division of the labyrinth cavity for the sinus utriculi superior. This recess I compared to the metencephalic bulge on the models of the endocrania of

Fig. 17. *Austrolosomus kochi* (Stensiö). Cast of the cavities of the neural endocranium in dorsal view. On the basis of a wax model. 10×.

am. ant, *am. ext*, *am. post*, divisions of the labyrinth cavity for the ampulla anterior, the ampulla externa, and the ampulla posterior, respectively; *c. on*, canal probably for a vein; *c. ve*, canal possibly for the ramus maxillaris trigemini and the ramus buccalis lateralis; *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; *dic*, division of the cavum cerebrale cranii for the diencephalon; *fe. en*, fenestra endonarina communis; $font_1$, $font_2$, anterior and posterior dorsal fontanelles; *f. ot. occ*, fissura otico-occipitalis; *l. opt*, division of the cavum cerebrale cranii for the lobus opticus; *myc*, division of the cavum cerebrale cranii for the myelencephalon; *n. c*, nasal cavity; *re. pmd*, postero-dorso-medial recess of the nasal cavity; *spi*, canal for a spino-occipital nerve; *tel*, division of the cavum cerebrale cranii for the telencephalon; *utr*, division of the labyrinth cavity for the utriculus; *v. cer. ant*, canal for the vena cerebralis anterior; *I*, canal for the nervus olfactorius; *X*, canal for the nervus vagus.

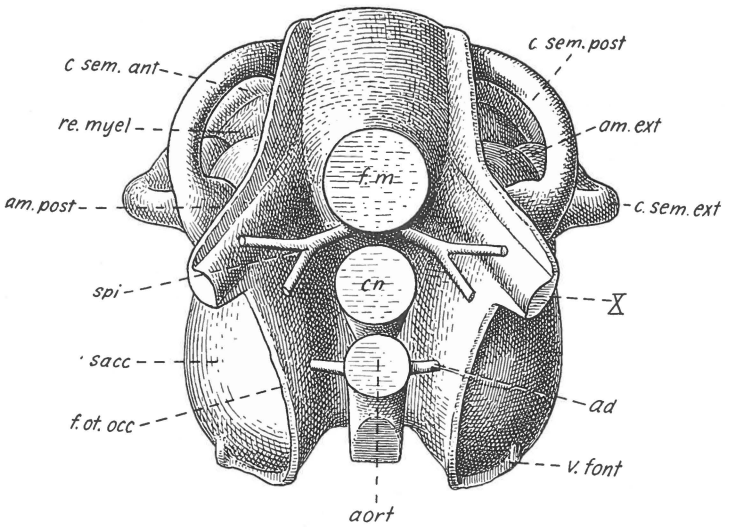


Fig. 18. *Australosomus kochi* (Stensiö). Cast of the cavities of the neural endocranium in posterior view. On the basis of a wax model. 10×.

ad, canal for an artery; *am. ext*, *am. post*, divisions of the labyrinth cavity for the ampulla externa and the ampulla posterior, respectively; *aort*, aorta canal; *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; *f. ot. occ*, fissura otico-occipitalis; *re. myel*, division of the cavum cerebrale cranii for the antero-lateral part of the myelencephalon; *sacc*, division of the labyrinth cavity for the sacculus; *spi*, canal for a spino-occipital nerve; *v. font*, vestibular fontanelle; *X*, canal for the nervus vagus.

the Kansas forms and *Boreosomus*. On the model of the cranial cavities of *Australosomus* we find a well defined bulge (*re, myel*, figs. 1, 9, 11, 15, 18; pl. 1, fig. 3; pl. 2, fig. 2; pl. 3, fig. 2; pl. 5, fig. 1), which in position and probably in size, also, corresponds very well to the above-mentioned recess in *Pteronisculus*. A comparison with the now completed model of the cranial cavities in *Boreosomus* shows, however, that the bulge in *Australosomus* corresponds to the ventral one of the two bulges in *Boreosomus* and thus most probably represents a recess developed for the antero-lateral corner of the myelencephalon. From this it follows that in both *Australosomus* and *Pteronisculus* the division for the lateral part of the metencephalon must be sought for in the region dorsally to the myelencephalic recess, and in this region, at any rate in *Australosomus*, there is no trace of a recess corresponding to the pronounced metencephalic bulge in the model of *Boreosomus*.

The myelencephalon (*myc*, fig. 17) seems to have been very long, as in the Kansas forms (Moodie 1915, figs. 15–17), *Pteronisculus* (E. Nielsen 1942, p. 101, figs. 13–15), and *Boreosomus* (ibid. p. 321, fig. 66), but it was rather low and narrow. The greatest breadth and height of the myelencephalic division of the cavum cerebrale cranii are found in the region just below the posterior dorsal fontanelle; however, both the height and the breadth of

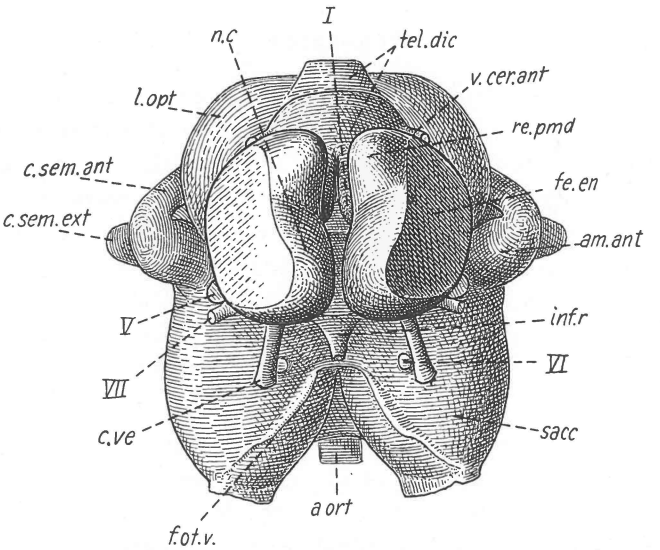


Fig. 19. *Australosomus kochi* (Stensiö). Cast of the cavities of the neural endocranium in anterior view. On the basis of a wax model. 10×.

am. ant, division of the labyrinth cavity for the ampulla anterior; *aort*, aorta canal; *c. sem. ant*, *c. sem. post*, divisions of the labyrinth cavity for the canalis semicircularis anterior and the canalis semicircularis posterior, respectively; *c. ve*, canal possibly for the ramus maxillaris trigemini and the ramus buccalis lateralis; *fe. en*, fenestra endonarina communis; *f. ot. v*, fissura oticalis ventralis; *inf. r*, infundibular recess; *l. opt*, division of the cavum cerebrale cranii for the lobus opticus; *n. c*, nasal cavity; *re. pmd*, postero-dorso-medial recess of the nasal cavity; *sacc*, division of the labyrinth cavity for the sacculus; *tel. dic*, division of the cavum cerebrale cranii for the tel- and diencephalon; *v. cer. ant*, canal for the vena cerebralis anterior; *I*, canal for the nervus olfactorius; *V*, trigeminus canal; *VI*, canal for the nervus abducens; *VII*, facialis canal.

this part of the cranial cavity are relatively much smaller than in the Kansas forms, *Pteronisculus*, and *Boreosomus*, in which forms the myelencephalon in the most posterior part of the otic region must have had a huge swelling.

In *Pteronisculus* and *Boreosomus*, and probably also in the Kansas forms, the expanded part of the myelencephalic division of the cranial cavity communicated with the posterior part of the fossa bridgei (or with an intramural space just below this part of the fossa), and in part I of the present work (E. Nielsen 1942, pp. 101–102, 321) it is stated that some relation existed between the swelling of the myelencephalon and the presence of a communication between the myelencephalic part of the cavum cerebrale cranii and the fossa bridgei. The conditions described here for *Australosomus* seem to support this assumption in so far as *Australosomus* lacks the excessive swelling of the myelencephalon as well as the communication between the myelencephalic part of the cavum cerebrale cranii and the fossa bridgei.

Parasphenoid.

The parasphenoid (*Psph*, figs. 1, 25, 26, 29, 31) consists of a corpus the most posterior part of which is resolved into a number of small, thin plates (*Psph. o*, fig. 26), and from which issues a single pair of ascending processes (*pr. asc*$_2$, figs. 1, 20, 26). For comparative reasons it would be desirable to treat the corpus as consisting of a pars anterior and a pars posterior, in accordance with the terminology introduced by Stensiö (1932) and employed by me in the descriptions of *Pteronisculus* and *Boreosomus* (E. Nielsen 1942). It appeared impossible, however, to make such a subdivision of the corpus, as the center of radiation of the parasphenoid could not be localised with certainty.

The undivided part of the corpus of the parasphenoid extends from the anterior end of the ventral face of the ossified part of the ethmoidal region in a posterior direction to a point below the central part of the floor of the posterior myodome. From its anterior pointed end this part of the corpus increases gradually in breadth in a posterior direction almost throughout its whole length, as shown in the figures, and the ventral aspect of the corpus may accordingly be described as roughly triangular in outline. The posterior margin of the corpus shows a deep paired concavity, which is partly filled by the above-mentioned small plates representing a posterior subdivided part of the parasphenoid.

The corpus is very thin in its foremost part below the ethmoidal region and the anterior part of the orbitotemporal region, as well as in its hindmost part below the pars basisphenoidea and the floor of the posterior myodome, but it is quite massive below the middle part of the orbitotemporal region, where it serves as a support for the narrow endocranial bar which forms the ventral boundary of the interorbital fenestra. Below the ethmoidal region and the anterior part of the orbitotemporal region the whole dorsal face of the corpus is in contact with the ventral face of the endocranium, and the same holds good for the short hindmost part of the corpus, which lies below the floor of the posterior myodome. The long midmost part of the corpus, however, is broader than the overlying ventral face of the orbitotemporal region, and accordingly only a median zone of the dorsal face of this part of the corpus is in contact with the endocranium, while a paired lateral zone forms part of the ventral boundary of the orbit.

From the transverse sections shown in fig. 20 we obtain a fairly good idea of the detailed shape of the corpus. Farthest anteriorly the otherwise almost plane ventral face of the corpus is provided with a short and narrow median longitudinal crest. Below the more posterior part of the ethmoidal region the ventral face grows convex from side to side, and still further back the convexity again flattens out and a median concavity appears (sections 60 and 70). In its most posterior part the ventral face shows two deep

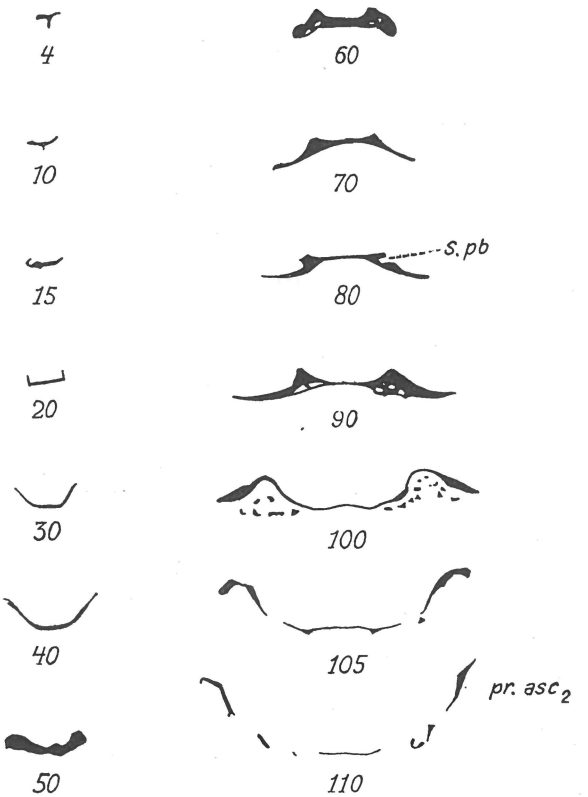


Fig. 20. *Australosomus kochi* (Stensiö). Transverse sections through the parasphenoid. From the complete grinding series. C. 12×.

pr. asc$_2$, processus ascendens posterior; *s. pb*, groove for the ramus palatinus facialis and for a small branch of the arteria carotis interna.

lateral furrows separated by a rather plane median area (section 100). In the furrows we find a number of quite small ossicles, which seem to represent a much reduced superficial part of the corpus rather than small detached teeth. That part of the dorsal face of the corpus which is in contact with the endocranium is curved in accordance with the endocranial face upon which it rests, that is, it is mainly concave both in a transverse and a longitudinal direction. The lateral free zone of the dorsal face of the orbitotemporal division is also concave in the transverse and longitudinal directions, but since this lateral zone as a whole faces dorso-laterally instead of dorsally, it is separated from the median contact area by a distinct longitudinally running ridge. Just laterally to this longitudinal ridge we find, on the dorsal face of the corpus, a narrow longitudinal furrow (*s. pb*, fig. 20), which in places seems to be closed so as to form a fine canal. As no canal for the ramus palatinus facialis is developed between the corpus and the ventral face of the endocranium, this nerve must have been situated laterally to the narrow

ventral face of the orbitotemporal region, and probably it extended forward through the narrow furrow just described.

The paired ascending process issues from the postero-lateral corner of the corpus, extending in a mainly dorso-lateral direction along the postero-ventral part of the orbital margin of the endocranium, to end in the most ventral part of the spiracular canal. The process, which according to its relations to the endocranium must be regarded as a processus ascendens posterior (cf. E. Nielsen 1942, pp. 106–113), is very narrow in its most distal part, but grows broader towards its base, as shown in figs. 37–38. The transition between the process and the corpus is quite gradual.

No teeth have been observed on any part of the parasphenoid.

Discussion. – As is well known, in most *Palaeonisciformes* the parasphenoid only extends in a caudal direction as far as the area just behind the boundary between the orbitotemporal and the otic regions, while that of most higher Actinopterygians extends much farther backward. Probably, therefore, a short parasphenoid should be regarded as a primitive feature within the Actinopterygians. Similar conditions are known within the Choanates, the parasphenoid in the Crossopterygians extending backwards approximately to the boundary between the orbitotemporal and the otic region, whereas in most higher Choanates it reaches much farther backwards (Jarvik 1942, p. 500, footnote 1). Thus it must be assumed that the parasphenoid in the hypothetic common ancestor of the Choanates and the Actinopterygians was short; in this connection it is of interest that the anterior big basal ossification in the neural endocranium of *Acanthodes* (Watson 1937, p. 97, fig. 17), which, as commented upon by Holmgren (1942, p. 132), has an »extreme parasphenoid-like aspect«, has about the same backward extension as the parasphenoid of the primitive Actinopterygians and Choanates.

In *Eustenopteron*, according to Jarvik, an unpaired dental plate is situated on the lower side of the parasphenoid, and in a posterior continuation of the unpaired parasphenoid dental plate, but separated from it by an interspace, lies, below the otic region, a large paired paraotic dental plate (Jarvik 1942, p. 500, footnote 1; 1944, pp. 26–30, fig. 13). Jarvik puts forward the supposition that the paraotic dental plates are homologous to the posterior part of the parasphenoid in forms in which this bone extends below the otic region of the neural endocranium. He finds support for this supposition in the fact that in certain reptiles and birds, and possibly in some amphibians, also, the parasphenoid has developed from an unpaired anterior and a paired posterior primordium, and that, according to Pehrson's investigations (Pehrson 1940, p. 38, fig. 39), the parasphenoid of *Amia* has probably arisen in a similar way. Jarvik concludes his argumentation by the following foot-note (Jarvik 1944, p. 30):

»The so-called parasphenoid in those fishes and Amphibians in which it

extends caudally below the otic region is thus probably a compound bone, including homologues of both the paraotic dental plates and the parasphenoid in *Eustenopteron*. For this compound bone the term parabasal, introduced by Gaupp, may be used.«

According to the above, in typical *Palaeonisciformes* we might expect to find paraotic dental plates behind the short parasphenoid, but such plates have not been observed in any Palaeonisciform and are, undoubtedly, not developed in the best known species, *Pteronisculus stensiöi*. At present, therefore, the only evidence of a compound nature of the long corpus parasphenoidei in the higher Actinopterygians is that of its ontogenetic development in *Amia*, and I hesitate to acknowledge the value of such isolated evidence, all the more so since direct observations on members of different phylogenetic lines within the Actinopterygians – as for instance the *Palaeonisciformes-Ospia-Amia* line – seem to show that the long parasphenoid in the higher forms develops from the short one in the lower forms by a quite gradual growth in a caudal direction. Hence I am inclined to believe that the long parasphenoid in the higher Actinopterygians cannot be compared to the compound parabasal in the higher Choanates.

In *Australosomus* the development of the parasphenoid has evidently proceeded differently, the bone in this form having a still less caudal extension than in typical *Palaeonisciformes*, and farthest posteriorly it is extremely thin and partially resolved into small plates. There can be no doubt that the posterior part of the parasphenoid is in full reduction, and hence it seems very likely that in the ancestors of *Australosomus* the bone had a similar caudal extension to that found in the typical *Palaeonisciformes*.

In *Pteronisculus* (E. Nielsen 1942, p. 72) the centre of radiation of the parasphenoid lies just below the fenestra ventralis myodomus. In other primitive Actinopterygians the centre of radiation lies in the corresponding area, viz. beneath the hypophysial region of the neural endocranium (E. Nielsen 1942, pp. 106–113). In *Australosomus*, however, the caudal margin of the corpus parasphenoidea is situated so far forward that the centre of radiation, the exact position of which is unknown, cannot have been situated beneath the posterior myodome. If, therefore, as is most probable, the parasphenoid has developed from a normal Palaeonisciform parasphenoid, a forward shifting of the centre of radiation must have taken place simultaneously with the gradual reduction of the hindmost part of the bone.

In the first part of the present work I made a comparison of the processus ascendentes in different Actinopterygians, pointing out that the processus ascendens posterior is present both in higher and in lower forms, while the processus ascendens anterior probably always occurs in association with a basipterygoid process, and accordingly it is only found, at any rate as a separate process, in forms exhibiting this primitive structure (E. Nielsen 1942, pp. 106–113). The conditions in *Australosomus* are in good accordance

with this view, the basipterygoid process in this genus having disappeared and the only existing ascending process being the processus ascendens posterior.

According to Pehrson (1940, p. 38, figs. 38–41), the processus ascendens in *Amia* – which he, following Stensiö (1925, pp. 85–86; 1935, p. 15), regards as an anterior ascending process, while in my opinion it is either a posterior process or possibly contains homologues to both an anterior and a posterior process (E. Nielsen 1942, p. 112) – developed as a separate bone which became fused with the corpus. From this observation he draws the conclusion that there once existed fishes, so far unknown, in which the ascending processes persisted as separate bones throughout their life. In a later paper Holmgren (1943, p. 39) proposes the name lateral parasphenoids for these bones.

Here, again, we are confronted with a case in which the fossils fail to answer the demands of embryologists, and here, again, I regard the isolated ontogenetic evidence as too slight a basis for such far-reaching conclusions. In *Lepidosteus* the processus ascendens develops continuously with the corpus and is never independent (Hammarberg 1937, pp. 319–321), and even in *Arthrodira* the short parasphenoid has a processus ascendens (Stensiö 1945, p. 67, Addendum).

I take the opportunity here to comment upon the statement of Holmgreen (1943, p. 39), that the ascending process in *Amia* is not comparable to that in *Acipenser*, which latter process (his medial ascending process) is a part of the parasphenoid which lies medially to the lateral aorta in close contact with the lateral free face of the endocranium, while the former (his lateral ascending process) is situated laterally to the lateral aorta. As previously pointed out both by Aldinger (1938, pp. 324–327) and myself (1942, pp. 108, 112), even in closely related forms in which there can be no reasonable doubt as to their homology, the processes ascendentes posteriores may possess highly different relations to the lateral aorta. Hence, in my opinion Holmgreen's statement affords no proof of a difference in principle of the ascending parasphenoid processes in the two forms in question, even if they are perhaps not necessarily strictly homologous (cf. E. Nielsen 1942, p. 112).

Vomer.

In *Australosomus kochi* we find a homologue to the paired tooth-bearing bone in *Pteronisculus* interpreted by me, though with some doubt, as a vomer (E. Nielsen 1942, pp. 113–114, figs. 34 A, B). In *Australosomus kochi* this paired bone (*Vo*, figs. 1, 26, 27, 30; pl. 7), which has only been observed in the sectioned specimen, is a thin, long, and narrow plate with

a ratio between length and breadth of about 13:1. Its lateral and medial margins are straight or very slightly convex, and its anterior and posterior ends are rounded, as shown in fig. 26. The bone is a little less than half as long as the parasphenoid and seems to have been situated in the roof of the mouth in a similar way to the vomer in *Pteronisculus*, from which it differs in being completely devoid of teeth. More precisely, the bone was placed loosely in the mucous membrane of the mouth below the posterior part of the ethmoidal region and the anterior part of the orbitotemporal region, covering ventrally a narrow lateral zone of the parasphenoid and an adjoining, likewise narrow, medial zone of the entopterygoid.

Discussion. – The bone described above, as well as the corresponding one in *Pteronisculus*, differs from the vomer in *Saurichthys* (Stensiö 1925, p. 88, figs. 18, 19), *Amia* (Allis 1898, pl. XXXIII, figs. 5, 6; Holmgreen and Stensiö 1936, p. 478, fig. 360; Hammarberg 1937, pp. 321–322, fig. 45), and other higher Ganoids by lacking any firm connection with other dermal bones or with the neural endocranium. Quite probably the vomer in *Elonichthys binneyi* described by Watson (1925, p. 835, fig. 22) had similar loose connections to its neighbouring bones, and if so, this feature seems to be of fairly common occurrence within the more primitive Actinopterygians.

One might ask whether the bone discussed here is at all comparable to the vomer in the higher Ganoids. The only answer to this question which can be given on the basis of our present knowledge is that as regards *Pteronisculus* and *Australosomus* it is quite certain, and as regards *Elonichthys binneyi* it is at any rate very probable, that no other bone exists which can be compared to the vomer in the higher Ganoids. If, therefore, the firmly attached vomer in the higher forms is not an entirely new formation, there is every reason to believe that it is identical with the loosely attached bone described above in the more ancestral forms.

Dermal bones on the dorsal side of the neural endocranium.

General remarks. – The width of the gap which separates the Crossopterygians from the Actinopterygians has been estimated very differently by different authors (Watson 1925; Säve-Söderbergh 1934; E. Nielsen 1936; Westoll 1937 a, b; Stensiö and Jarvik 1937–38; Moy Thomas 1939; Robertson 1942; etc.), and it remains an open question whether it is possible, by the aid of the knowledge we are able to gain by studying the fossil forms of the two groups known at present, to bridge the gap in a safe way.

Quite recently Jarvik (1942, pp. 615–619) on the basis of Stensiö's previous investigations (1921–32) tackled the problem, making an interesting attempt to compare the dermal bones of the snout in the Crossoptery-

gians with those of the Actinopterygians. His arguments may be briefly summarised as follows:

1) On the dorsal side of the snout of the Crossopterygians we find a rostral series pierced by the infraorbital sensory canal, a nasal series pierced by the supraorbital sensory canal, and – between the nasal and the rostral series – a tectal series forming a more or less direct anterior continuation of the series of supraorbitals.

   The supraorbital sensory canal joins the infraorbital one a short distance behind the tip of the snout antero-medially to the anterior external nostril, and in some cases (some Coelacanthids, *Polypterus*) moreover one or two transverse commissural sensory canals connect the supraorbital and the infraorbital sensory canals, passing between the anterior and the posterior external nostrils.
2) The sensory canal system of the snout in *Sinamia* shows close resemblance to that of the Coelacanths if we homologise the two transverse commissural canals between the anterior and posterior external nostrils with the transverse commissural canals in the Coelacanths. In *Amia* the anterior commissure is vestigial, being represented by the foremost laterally bent part of the supraorbital sensory canal.
3) If these homologisations are correct, in *Amia*, also, we may distinguish between a rostral series pierced by the infraorbital sensory canal, a nasal series pierced by the supraorbital sensory canal, and a tectal series between the rostral and the nasal series. The rostral series comprises a lateral rostral (part of the so-called antorbital) and two medial rostrals (parts of the median rostral), the nasal series consists of two elements (parts of the so-called nasal), and the tectal series is composed of a posterior tectal (the so-called dermectetmoid), a middle tectal (part of the so-called antorbital), and an anterior tectal (that part of the so-called nasal which is pierced by the anterior transverse commissural canal). Thus the so-called antorbital is a rostro-tectal and the so-called nasal a tecto-nasal.
4) In the *Palaeonisciformes* and other lower Ganoids the most anterior part of the supraorbital sensory canal is in all essentials like the anterior transverse commissure between the infraorbital and the supraorbital sensory canals in *Amia*, *Sinamia*, *Polypterus*, and the Coelacanths. Accordingly the so-called nasal is probably a tecto-nasal. A posterior transverse commissure seems to exist in some *Palaeonisciformes*, as for instance *Cheirolepis* and *Birgeria*, and the course of this commissure in a form like *Birgeria* seems to suggest that in this form the so-called antorbital is a rostro-tectal.

It is difficult, not to say impossible, on the basis of our scanty knowledge of the primitive Actinopterygians to adopt a definite attitude to Jarvik's

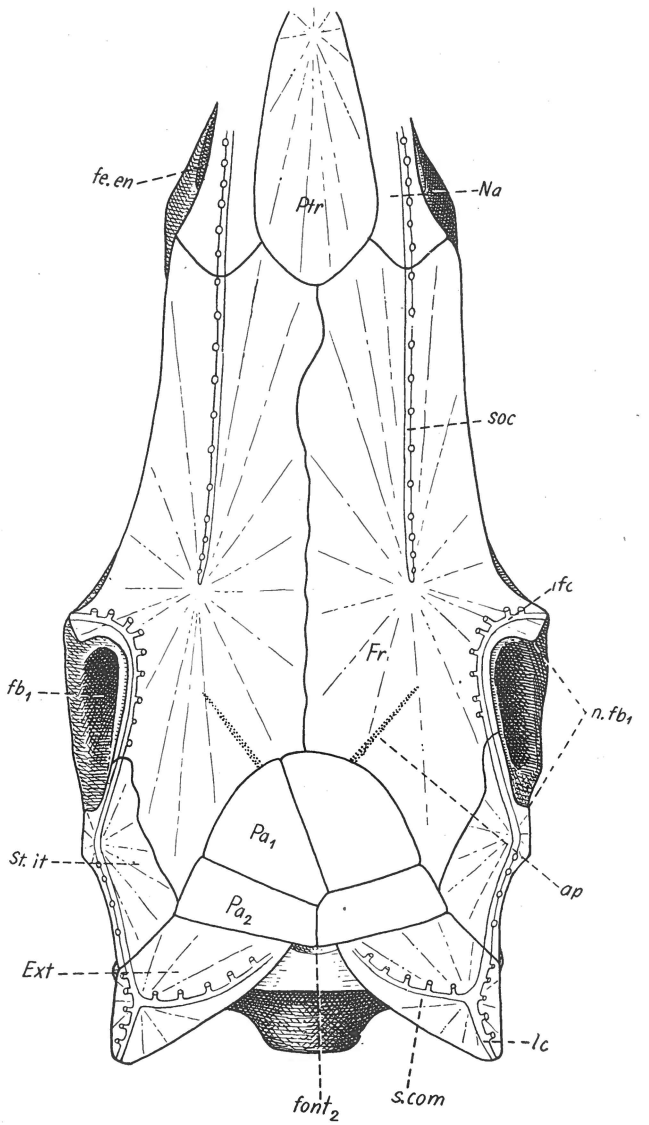


Fig. 21. *Australosomus kochi* (Stensiö). Neural endocranium with dermal cranial roof in dorsal view. Neural endocranium and outlines of dermal bones on the basis of the complete grinding series. Sensory canal system based on several specimens. C. 8×. *Ext*, extrascapular; *Fr*, frontal; *Na*, nasal; Pa_1, Pa_2, anterior and posterior parietal; *Ptr*, postrostral; *St. it*, supratemporo-intertemporal; *ap*, anterior pit-line; fb_1, spiracular division of the fossa bridgei; *fe. en*, fenestra endonarina communis; $font_2$, posterior dorsal fontanelle; *ifc*, infraorbital sensory canal; *l. c*, cephalic division of main lateral line; $n.fb_1$, notch in the margin of the dermal cranial roof above the spiracular division of the fossa bridgei; *s. com*, supratemporal commisure; *soe*, supraorbital sensory canal.

attempt at an interpretation as reported here; if it proves to be correct, it will necessitate quite a different terminology for the dermal bones of the snout of the Actinopterygians than that generally employed. I take the opportun-

ity, however, to point out a few features which in my opinion invalidate Jarvik's arguments to some extent.

The fact that the transverse commissures between the supraorbital and the infraorbital sensory canals in the Coelacanths are only completely developed in more modern forms, while the anterior commissure is lacking and the posterior one either lacking or feebly developed in the Devonian genera (Jarvik 1942, pp. 336–338) seems to me to be a serious argument against homologising these commissures with those in *Sinamia* and *Amia* in so far as it indicates that these commissures have arisen independently within the Coelacanths and the Actinopterygians. Apart from the course of the sensory canals the only reasons speaking in favour of the presence of a tectal series in *Amia* are, according to Jarvik (1942, p. 618), the independent development of the antero-lateral part of the nasal and the existence of the independent dermectethmoid. As regards the dermectethmoid described by Pehrson as »a very questionable dermal component of the ectethmoid« (Pehrson 1944, p. 150), it seems peculiar to me, if in a rather recent form like *Amia* this bone is actually homologous with a tectal bone in the Crossopterygians, that it should not be developed in the more primitive Ganoids also.

Further criticism of Jarvik's hypothesis has been put forward by Pehrson (1944, pp. 149–151), but neither his nor my objections carry such weight that Jarvik's attempt at an interpretation may not quite well prove to be correct. It should, however, be borne in mind that it is always theoretically possible to compare even the most different patterns of dermal bones if we use the fusion of bones and the reduction of sensory canals as the only explanatory factors, so until more convincing evidence of the existence of a tectal series within the Actinopterygian group has been obtained, I prefer to use the same terminology for the dermal bones of the head as in the first part of this work (1942).

Extrascapular. – As in *Australosomus merlei* (Piveteau 1934, pp. 30–31, fig. 23), only a single extrascapular (*Ext*, figs. 1, 21, 22, 23, 25; pl. 1, fig. 1, 2; pl. 4, figs. 1, 2) is present on either side of the mid-line. The bone is irregularly four-sided, with a lateral, an antero-lateral, an antero-medial, and a postero-medial margin. The antero-lateral margin is overlapped by the supratemporo-intertemporal, the antero-medial margin by the posterior parietal, and the bone itself overlaps the uppermost element in the dermal shoulder-girdle, the posttemporal (see p. 148). All these overlappings are very small. The centre of radiation lies at about the same distances from the antero-lateral and the postero-medial margins of the bone and not far from its lateral margin. As usual, the longitudinally disposed cephalic division of the main lateral line and the transversely placed supratemporal commissure join in the centre of radiation.

Parietals. – Four parietals are present, viz. an anterior (Pa_1, figs. 1,

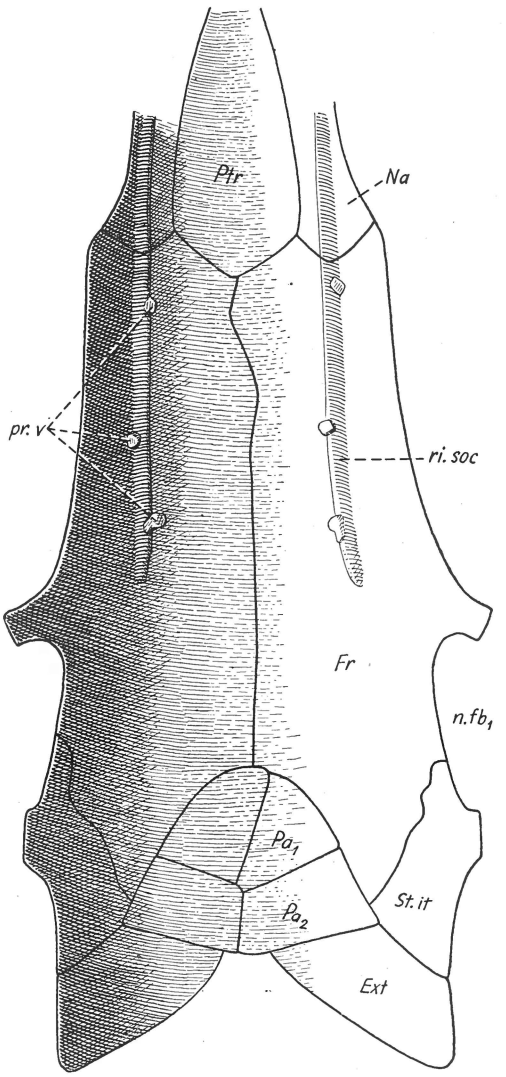


Fig. 22. *Australosomus kochi* (Stensiö). Dermal cranial roof in ventral view. Mainly on the basis of the complete grinding series. C. 8×.
pr. v, ventral processes from the frontal; *ri, soc*, ridge below the supraorbital sensory canal. Other letters as in fig. 21.

21, 23, 25; pl. 1, figs. 1, 2; pl. 4, figs. 1, 2) and a posterior pair (Pa_2, figs. 21, 22, 23, 25; pl. 1, figs. 1, 2; pl. 4, figs. 1, 2), as in *Australosomus merlei* (Piveteau 1934, pp. 29–30, figs. 19, 23). The parietal complex as a whole is bounded anteriorly and laterally by a strongly convex margin, the shape of which corresponds very closely to the anterior and antero-lateral boundaries of the big median concavity on the posterior part of the dorsal face of the otic region of the neural endocranium (p. 36, fig. 3). In fact, the shape of the parietal complex seems to be determined by the development of the underlying part of the neural endocranium.

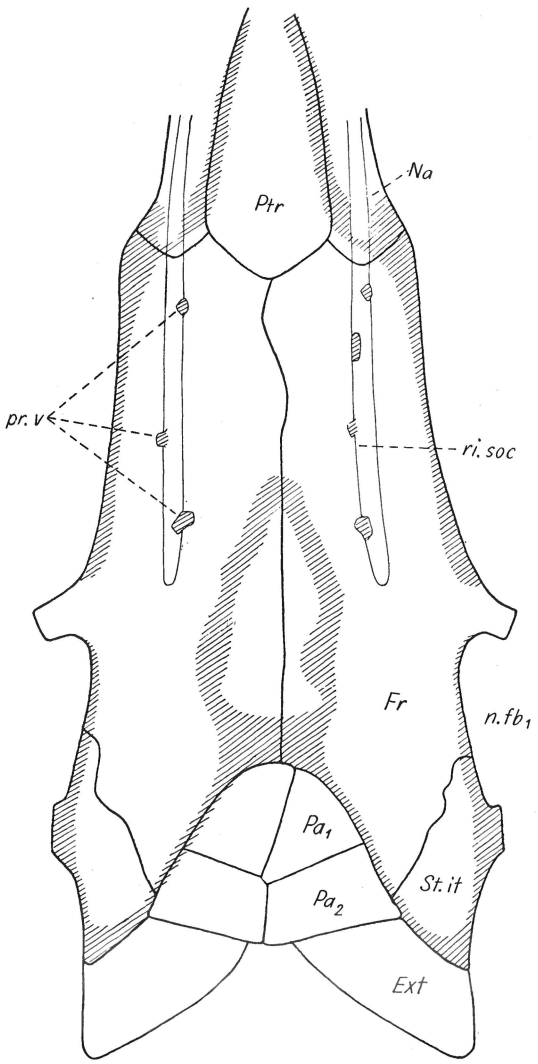


Fig. 23. *Australosomus kochi* (Stensiö). Dermal cranial roof in ventral view. Mainly on the basis of the complete grinding series. Those parts of the roof which rested directly on the neural endocranium indicated by cross-ruling. C. 8×.
Lettering as in figs. 21 and 22.

Although the outline of the parietal complex is fairly constant, the shape of the individual bones within the complex varies considerably from one specimen to the other. Generally speaking, however, the posterior parietals are four-sided in outline and much broader than long, while the anterior parietals are longer than broad and three-sided in outline. The complex as a whole overlaps all the adjoining bones, viz. the frontals, the supratemporo-intertemporals, and the extrascapulars; probably it is only loosely connected with these bones, the whole complex being often absent in specimens which

show both frontals and supratemporo-intertemporals in undisturbed positions. Within the complex the anterior parietals overlap a fairly broad zone of the posterior ones, as appears from a comparison between figs. 21 and 22. The centres of radiation have not been localised with certainty.

No pit-lines have been observed on any element in the parietal complex; however, as pit-lines are present on the parietals of the closely related species *Australosomus merlei* (Piveteau 1934, pp. 30, 33; fig. 23), their apparent absence in *A. kochi* is probably due either to their more superficial position or to the fact that very few specimens are so well preserved that the dorsal face of the parietal complex can be examined in detail.

Supratemporo-intertemporal and frontal. – Anteriorly to the extrascapular the anterior continuation of the main lateral line pierces two bones of the dermal cranial roof; in the following description these bones are termed the supratemporo-intertemporal and the frontal respectively, though probably neither of these terms are quite correct, as will discussed below (p. 94).

The supratemporo-intertemporal (*St. it*, figs. 1, 21, 22, 23, 25; pl. 1, figs. 1, 2; pl. 4, figs. 1, 2) is a four-sided bone more than twice as long as broad and bounded by an antero-medial, an antero-lateral, a postero-lateral, and a postero-medial margin. In dorsal view the bone is, broadly speaking, trapezoid in outline. The relations between the supratemporo-intertemporal and the neural endocranium are very clearly seen from the serial drawings. The bone roofs over the posterior part of the fossa bridgei, resting against the dorsal face of the otic region laterally and posteriorly to this part of the fossa (cf. figs. 21, 23). The bone is not connected with the neural endocranium by a descending lamina, as is the case in many Actinopterygians and Crossopterygians (cf. E. Nielsen 1942, pp. 119–120). The antero-medial margin of the supratemporo-intertemporal is slightly overlapped by the frontal, while the postero-medial margin of the bone, as already mentioned, overlaps the extrascapular. The centre of radiation is situated somewhat nearer the anterior than the posterior end of the bone and much nearer its lateral than its medial margin. The radiation centre is pierced by the longitudinal sensory canal, which is lodged in the bone, and which according to the usual terminology (Säve-Söderbergh 1933, pp. 5–8) is either the postotic sensory canal alone or this sensory canal plus the otic part of the infraorbital sensory canal.

The frontal (*Fr*, figs. 1, 21, 22, 23, 24, 25; pl. 1, figs. 1, 2; pl. 4, figs. 1, 2) is by far the largest bone in the dermal cranial roof. Roughly speaking, it is five-sided, with an antero-lateral, an anterior, a medial, a postero-medial and a postero-lateral margin. The shape of the bone is seen from figs. 21–22, which were drawn on the basis of the serial drawings, so the following remarks will be sufficient. The anterior margin has a somewhat varying course in the different specimens; the postero-lateral margin shows a very

marked concavity, which, together with a smaller concavity in the antero-lateral margin of the supratemporo-intertemporal, forms the very large notch in the lateral margin of the dermal cranial roof (*n.* fb_1, figs. 21, 22, 23, 24, 25; pl. 1, fig. 1; pl. 4, figs. 1, 2), as was already observed by Stensiö (1932, pp. 169, 171, fig. 53); the postero-lateral margin is concave in such a way that it rests against, and is firmly connected with, the curved ridge which forms the antero-lateral boundary of the deep concavity on the dorsal face of the otic region. The centre of radiation is almost equally distant from the anterior and the posterior end of the bone and lies a little nearer its lateral than its medial margin. On the internal face of the frontal we find a well marked longitudinal ridge, extending from the centre of radiation of the anterior margin of the bone, and developed beneath the short supraorbital sensory canal. As shown in fig. 22, three small blunt processes extend in a ventral direction from this ridge, and, as already stated (p. 51), these processes are in contact with some of the elevations developed on the dorsal face of the neural endocranium. In the specimen investigated by grinding another neurocranial elevation on one side of the head is in contact with an area of the internal frontal ridge, which is not developed as a process. The internal face of the frontal is moreover in contact with the lateral marginal zone of the dorsal face of the orbitotemporal region and with a narrow area of the ridge which forms the medial boundary of the spiracular part of the fossa bridgei. Furthermore, the frontal probably rested against the partly cartilaginous area of the neurocranial roof which surrounded the anterior fontanelle, and against the ridge which forms the antero-lateral boundary of the posterior deep concavity on the dorsal face of the otic region. Thus the margins of the frontal largely follow the course of certain structures of the neural endocranium.

Apart from the supraorbital sensory canal, which extends in a forward direction from the centre of radiation, the frontal is pierced by a posterior part of the infraorbital sensory canal, which from the anterior end of the supratemporo-intertemporal continues forward fairly parallel to and quite near the margin of the big notch above the spiracular part of the fossa bridgei. Thus we are here confronted with the very curious case that the frontal lodges two completely separated sensory canals, one of which has nothing at all to do with the centre of radiation. Probably, as discussed later (p. 96), this condition is caused by the development of the notch in the lateral margin of the dermal cranial roof.

On the posterior part of the frontal we find a well developed anterior pit-line (*ap*, figs. 21, 24, 25), which, as shown in the figures, extends in an antero-lateral direction from a point on the postero-medial margin, and which must be regarded as the last remnant of the posterior degenerated part of the supraorbital sensory canal.

Postrostral. – The postrostral (*Ptr*, figs. 1, 21, 22, 23, 25; pl. 1, figs.

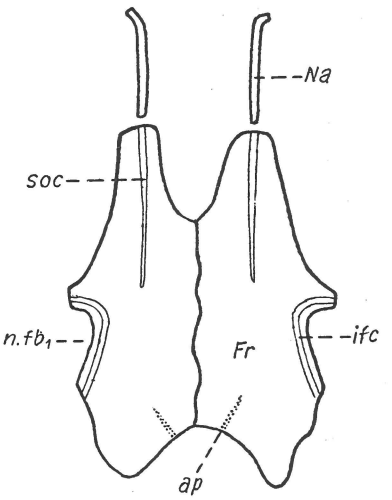


Fig. 24. *Australosomus kochi* (Stensiö). Attempted restoration of the frontals and nasals in specimen no. 447. 4×.
Lettering as in fig. 21.

1, 2; pl. 4, figs. 1, 2), which is about half as long as the frontal, is relatively narrow, its greatest breadth, which is found at a distance of about one-fifth its total length from its posterior end, being less than half its length. The outline of the postrostral (apart from its extreme anterior end, which is lacking in all the specimens investigated) is shown in fig. 21, and need no further description. The dorsal face of the bone is convex in a rostro-caudal direction as well as from side to side. The longitudinal curvation of the bone is most pronounced in its anterior part. Posteriorly the bone slightly overlaps the frontals, whereas no overlapping takes place between the postrostral and the nasal when these bones join (see below). As shown in fig. 23, only a narrow lateral marginal area of the internal face of the postrostral is in contact with the neural endocranium. As is also the case in typical *Palaeonisciformes* the radiation centre lies very far forward.

Nasal. – The nasal (*Na*, figs. 1, 21, 22, 23, 24, 25; pl 1, figs. 1, 2) presents two different shapes; thus, in most specimens it is fairly broad, while in a few cases it is only developed as a tube for the supraorbital sensory canal. Of the relatively broad nasal, only the posterior part is preserved in the specimens investigated, a faci which can be best explained by assuming that the anterior and larger part was very fragile, and was probably deeply buried in the skin of the snout. The greatest breadth of the preserved part of the bone is found quite near its posterior end, and from here the bone narrows in an anterior direction in such a way that both its lateral and its medial margins are somewhat concave. Posteriorly the bone slightly overlaps the frontal, while medially it adjoins the postrostral without overlapping it. As

the anterior part of the bone is unknown, neither the centre of radiation nor the external nostrils could be localised; however, judging from the relations between the bone and the fenestra endonaria communis, the nostrils were situated as in most *Palaeonisciformes*, viz. one on each side of the nasal. The supraorbital sensory canal continues from the frontal in a rostral direction through the preserved part of the nasal and somewhat nearer its medial than its lateral margin. Like the frontal, the nasal is thickened around the sensory canal, the thickening appearing as a marked ridge on the ventral face of the bone. As already mentioned, the narrow nasal, which is found in a few specimens, is only a bony tube enclosing the sensory canal. Curiously enough, this narrow bone tube is better preserved than the broader nasal, in so far as its anterior part shows no sign of reduction. This anterior part, which probably separated the two external nostrils, is distinctly laterally bent, as shown in fig. 24. As far as can be seen, the narrow nasal has no contact with the lateral margin of the postrostral.

Discussion. – The dermal cranial roof of *Australosomus kochi* shows good agreement in its main characters with that of *Australosomus merlei* Piveteau 1934, fig. 23). In the details of their shape, however, the elements of the dermal cranial roof of the two species differ a good deal, and it is especially interesting that the paired anterior parietal in *Australosomus kochi* is replaced by an unpaired bone in *Australosomus merlei*. As described below (p. 170), the parietal complex in *Australosomus pholidopleuroides*, the dermal cranial roof of which in most respects agrees closely with that of *Australosomus kochi*, differs from that of the other species of *Australosomus* in being subdivided into a large number of smaller parietal elements and thus shows similar conditions to those found in *Pholidopleurus* (Wade 1935, fig. 32).

Whether this variability in the number of parietal elements within the genus *Australosomus* should be regarded as a kind of degeneration due to the shortening of the supraorbital sensory canal (cf. Westoll 1944, pp. 68–69), it is difficult to decide. It is perhaps more probable that the increasing subdivision of the parietal complex served as a means to create a certain mobility of this part of the cranial roof necessitated by unkown functions of some structure situated in the underlying posterior median dorsal fontanelle. Apart from the conditions of the parietal complex, the most remarkable character of the dermal cranial roof of *Australosomus* is the development of the two bones pierced by the infraorbital sensory canal and its posterior continuation, viz. the bones described as the supratemporo-intertemporal and the frontal respectively. In typical *Palaeonisciformes* the supratemporo-intertemporal covers the whole fossa bridgei and thus overlies the dorsal opening of the spiracular canal (cf. E. Nielsen 1942, pp. 119–120, 327–328; figs. 21, 72). Anterior to the supratemporo-intertemporal the infraorbital sensory canal passes through a dermosphenotic which often contains supraorbital components. The small supratemporo-intertemporal in *Australosomus*

covers only the posterior part of the fossa bridgei, and probably, therefore, this bone is only homologous to a posterior part of the supratemporo-intertemporal in typical *Palaeonisciformes*. In *Amia* the supratemporo-intertemporal contains one supratemporal and two intertemporal components (Pehrson 1940, pp. 14–15), and if the same is the case in typical *Palaeonisciformes*, the supratemporo-intertemporal in *Australosomus* may perhaps lack one, if not both, of the intertemporal components; in the latter case the bone should, of course, be termed a supratemporal. Anterior to the supratemporo-intertemporal the infraorbital canal enters the so-called frontal, in which bone, as already described, it passes forward quite near the deep notch in the lateral margin, to leave it at the tip of the stout process which bounds the notch anteriorly. This course of the infraorbital sensory canal may be explained by assuming that the so-called frontal comprises both intertemporal and dermosphenotic components, in fact, Stensiö (1932, p. 171) identifies the area of the cranial roof bounding the notch above the spiracular part of the fossa bridgei anteriorly and antero-medially with the dermosphenotic. However, if a fusion has taken place between the frontal, a part of or the whole intertemporal, and the dermosphenotic, it is peculiar that the infraorbital sensory canal does not pierce the common centre of radiation as is normally the case when a fusion between dermal bones takes place (cf. E. Nielsen 1936, pp. 39–41). Another possibility is that the development of the notch above the spiracular part of the fossa bridgei may have forced the infraorbital sensory canal to invade the area of the frontal, while the intertemporal or its anterior part and the dermosphenotic have been completely reduced.

In this connection it is of interest to recall the remarkable changes in the course of the sensory canals of the dermal cranial roof of *Pyritocephalus* caused by the development of a very deep notch in the lateral margin of the roof (Westoll 1944, pp. 69–71, figs. 40, 41). In *Pyritocephalus* the infraorbital sensory canal has been interrupted behind the dermosphenotic, and its posterior part has been forced inward so as to anastomose with the supraorbital sensory canal. Indepent supraorbitals are lacking in *Australosomus* and are thus either included in the frontal or completely reduced. In *Macroaethes*, however, an anterior supraorbital is present, and in addition the postorbital undoubtedly contains a posterior supraorbital component (Wade 1935, fig. 33), and judging from the somewhat lateral position of the supraorbital series in this form, I think it most likely that the lack of supraorbitals in *Australosomus* is due to reduction. As described above (p. 93), the nasals and the postrostral in *Australosomus kochi* show signs of reduction, and judging from the figure given by Piveteau (1935, fig. 23), the same bones are also reduced anteriorly in *Australosomus merlei*. In neither of the two species have any remnants of lacrimals, antorbitals, rostrals, and premaxillaries been observed, and thus it would seem that the snout region was only very slightly protected by dermal bones. The most probable explanation

of this peculiar feature is that the protruding snout region of *Australosomus* was covered by very thick skin, in which the foremost part of the supraorbital and the infraorbital sensory canals were lodged without being protected by bone.

Similar conditions probably existed in *Pholidopleurus*, in which the only known dermal bones in the snout region are the postrostral and the nasals, which latter bones are markedly short and narrow (Wade 1935, fig. 32). In neither *Macroaethes* (Wade 1935, fig. 33) nor in *Arctosomus* (Berg 1941, fig. 22) is the snout region known in detail. However, in both these genera at least a well developed lacrimal is present, and thus the reduction of the dermal bones of the anterior part of the head seems to be less advanced than in *Australosomus* and *Pholidopleurus*. The large notch in the lateral margin of the dermal cranial roof above the spiracular part of the fossa bridgei in *Australosomus kochi* is also developed in *Australosomus merlei* (Piveteau 1935, fig. 23), *A. simplex* (p. 165), and *A. pholidopleuroides* (p. 170) as well as in the other Pholidopleurid genera in which this part of the dermal cranial roof is known, viz. *Arctosomus* (Berg 1941, fig. 23) and *Pholidopleurus* (Wade 1935, fig. 32); thus it seems to be a characteristic feature within the *Pholidopleuridae*.

As already mentioned, a somewhat similar, but much larger, notch is present in *Pyritocephalus* (Fritsch 1893, pp. 86–87, fig. 280; pl. 115; Westoll 1944, pp. 42–60, 69–71; figs. 23–25, 28–31, 35, 40, 41), where its significance has been discussed by Westoll as follows:

»The probable position of the fenestration in primitive *Pyritocephalus* was somewhere near the front of the fossa bridgei, which is a depression on the dorsal aspect of the endocranium receiving extensions of the body musculature. The original fenestration may, therefore, have been caused by the further encroachment of muscles, but in the well-known species the fenestrae extend so far forward that they overlie the orbits. It is thus possible that the whole fenestration may be due to structures associated with a proportionately large eye-ball, or that such structures increased the importance of fenestration primarily due to other causes.«

According to Westoll it is more unlikely that the fenestration (the notch) in *Pyritocephalus* should be comparable to the supraorbital fontanelle of *Polypterus*, which structure has some connection with the origin of the »temporal« division of musculus adductor mandibulae (Allis 1922, p. 191).

There can be no doubt that the notch in *Australosomus* is only related to the spiracular part of the fossa bridgei, for its margin closely follows the edge of this part of the fossa. In *Australosomus*, therefore, the size of the eye-ball has nothing to do with the development of the notch. In *Pyritocephalus*, however, it is not impossible, as suggested by Westoll, that the eye played a role in the development of the very large notch; it should, however, be borne in mind that the neural endocranium in *Pyritocephalus* is unknown,

so it is impossible to state the exact relations between the fossa bridgei and the notch in the dermal cranial roof. Westoll's view, that the fossa bridgei contains extensions of the body musculature, certainly does not hold good for such fossil Chondrosteans in which the head is known in detail, as for instance *Pteronisculus* (E. Nielsen 1942, pp. 46–47), *Boreosomus* (ibid. p. 294), *Saurichthys* (Stensiö 1925, pp. 25–26), *Australosomus* (present paper p. 38), and *Birgeria* (present paper p. 195), and it is therefore highly improbable that the body musculature had any connection with the development of the notch in *Pyritocephalus*. It is, at any rate, more probable that the posterior part of the notch in *Pyritocephalus* and the whole notch in *Australosomus* were developed by a simple reduction of part of the dermal cranial roof in order to allow the spiracular canal to open on the dorsal face of the head. The dermal cranial roof of the *Pholidopleuridae* might very well be regarded as a specialised derivative of the type of dermal cranial roof found in typical *Palaeonisciformes*, the most important changes being a shortening of the supraorbital sensory canal, a subdivision of the parietal, a reduction of the roof above the spiracular part of the fossa bridgei, and a more or less pronounced reduction of the foremost part of the roof. The dermal cranial roof of the Pholidopleurids seems to agree less closely with that of *Saurichthys* than previously assumed by Aldinger (1938, p. 379) and myself (E. Nielsen 1936, pp. 45–46), the only points of resemblance being the shortening of the supraorbital sensory canal and the development of the parietal complex, which latter, at least in *Saurichthys ornatus* (Stensiö 1925, fig. 20), contains four elements arranged in much the same way as in some species of *Australosomus*, while in other respects the differences are so considerable that it is entirely out of the question that the dermal cranial roof of *Saurichthys* may have been derived from the Pholidopleurid one, or *vice versa*.

Infraorbitals and sclerotic ring.

The infraorbital series comprises only two bones, which are undoubtedly comparable to the postorbital and the jugal, respectively, in a typical Palaeonisciform such as *Pteronisculus* (E. Nielsen 1942, pp. 132–134, fig. 27). The lack of lacrimal and antorbital elements in the series can hardly be explained by the bad state of preservation of the specimens investigated, but rather, as mentioned above, by the complete reduction of these elements.

Postorbital. – The postorbital (*Po*, fig. 25) is a rectangular bone which is more than twice as high as broad. The bone is separated by an interval from the dermal cranial roof above, and from the jugal below, and as the suborbitals seem to be completely reduced, the bone must have been situated loosely in the skin without contact with other bones. The infraorbital sensory canal traverses the bone in a dorso-ventral direction. The centre of radiation has not been localised.

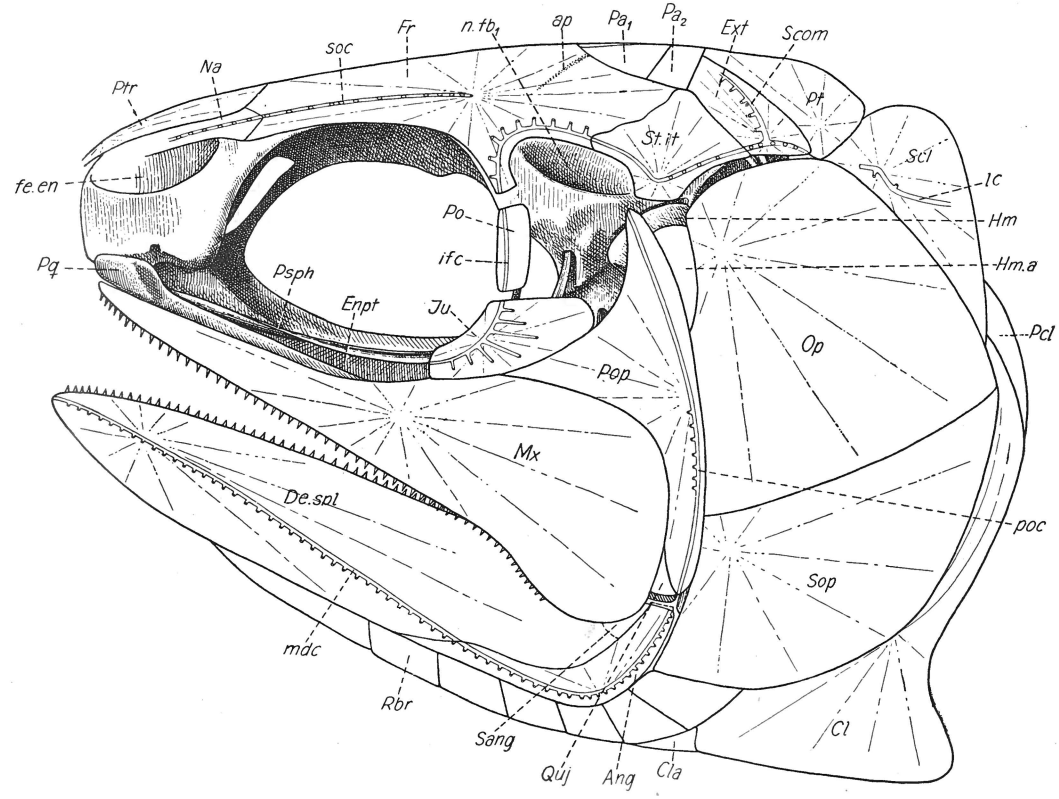


Fig. 25. *Australosomus kochi* (Stensiö). Head and dermal shoulder-girdle in lateral view. Based on several specimens. 5.6×.

Ang, angular; *Cl*, cleithrum; *Cla*, clavicle; *De. spl*, dentalo-splenial; *Enpt*, entopterygoid; *Ext*, extrascapular; *Fr*, frontal; *Hm*, hyomandibula; *Hm. a*, dermohyal (accessory hyomandibula); *Ju*, jugal; *Mx*, maxillary; *Na*, nasal; *Op*, operculum; Pa_1, Pa_2, anterior and posterior parietal; *Pcl*, anocleithrum; *Po*, postorbital; *Pop*, preoperculum; *Pq*, palatoquadrate; *Psph*, parasphenoid; *Pt*, posttemporal; *Ptr*, postrostral; *Quj*, quadratojugal; *Rbr*, branchiostegal ray; *Sang*, supraangular; *Scl*, supracleithrum; *Sop*, suboperculum; *St. it*, supratemporo-intertemporal; *ap*, anterior pit-line; *fe. en*, fenestra endonarina communis; *ifc*, infraorbital sensory canal; *lc*, main lateral line; *mdc*, mandibular sensory canal; *n.* $^tb_1$, notch in the dermal cranial roof above the spiracular division of the fossa bridgei; *poc*, preopercular sensory canal; *s. com*, supratemporal commisure; *soc*, supraorbital sensory canal.

Jugal. – The jugal (*Ju*, figs. 1, 25, 17; pl. 4, fig. 2; pl. 5, fig. 1) is a fairly large five-sided bone with an anterior, an antero-dorsal, a dorsal, a posterior, and a postero-ventral margin. The postero-ventral margin overlaps a narrow marginal zone of the maxillary and the preoperculum. The infraorbital sensory canal passes through the bone from a point on the dorsal to a point on the anterior margin, changing gradually from a dorso-ventral to a rostro-caudal direction and piercing the centre of radiation, which is situated ventrally to the antero-dorsal angle of the bone and somewhat nearer the dorsal than the postero-ventral margin. As usual, the backward-directed tubuli issuing from the jugal part of the infraorbital sensory canal have a considerable length.

Sclerotic ring. – The sclerotic ring (*Sclr*, fig. 1; pl. 1, fig. 4; pl. 5, fig. 1) consists of two or three segments. Connected with the sclerotic ring we observe, in the specimen investigated by grinding, fairly extensive perichondral scleral ossifications (*scl. o*, fig. 1).

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

Palatoquadrate. – In the large specimens the palatoquadrate (*Pq*, figs. 1, 25; pl. 1, fig. 4) is completely or almost completely ossified and appears as a single large bone extending from beneath the ethmoidal region to beneath the posterior part of the otic region. In the smaller specimens it is difficult to examine the palatoquadrate in detail; however, as far as can be seen, the process of ossification set in very early and probably, as in *Pteronisculus* (E. Nielsen 1942, p. 143) and *Boreosomus* (ibid. pp. 336–337), in more than one place, a few smaller specimens showing remnants of at least two independent bones, viz. one in the autopalatine region and one in the quadrate region.

The structural details of the palatoquadrate ossification could best be studied in the serial drawings of the specimen investigated by grinding, and the subjoined description is based exclusively on these drawings.

The palatoquadrate ossification consists of cancellar endochondral bone lined with a thin perichondral bone layer. However, the perichondral lining is not complete, and in one fairly large area the bone is not ossified endochondrally; but although the palatoquadrate in the investigated specimen is thus not fully ossified, its shape can be made out fairly exactly, the relations of the palatoquadrate to the preoperculum and the maxillary giving sufficient evidence of the extension of its cartilaginous parts.

For descriptive reasons we will distinguish between a posterior and an anterior division of the palatoquadrate.

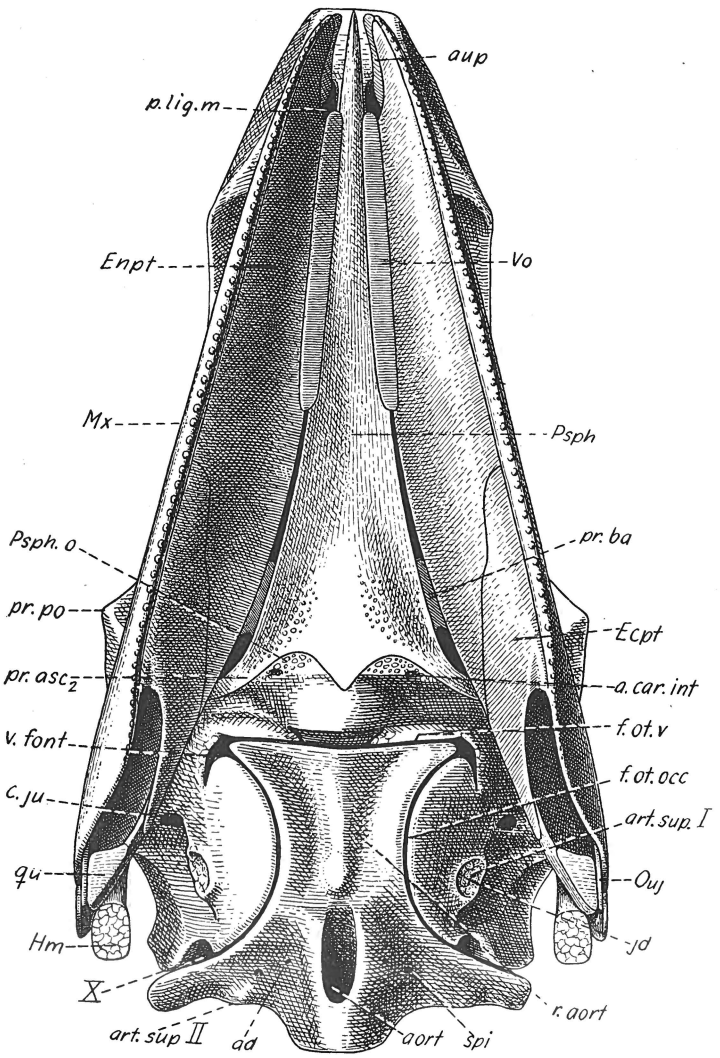


Fig. 26. *Australosomus kochi* (Stensiö). Ventral aspect of neural endocranium with its ventral dermal bones and of right and left palatoquadrate-maxillary apparatus and hyomandibula. Mainly on the basis of the grinding series. 8.5×.

Ecpt, ectopterygoid; *Enpt*, entopterygoid; *Hm*, hyomandibula; *Mx*, maxillary; *Psph*, parasphenoid; *Psph. o*, posterior parasphenoid ossicles; *Quj*, quadratojugal; *Vo*, vomer; *a. car. int*, canal for the arteria carotis interna; *ad*, canal for an artery; *aort*, groove for the dorsal aorta; *art. sup. I*, articular facet for the suprapharyngobranchial I; *art. sup. II*, presumed place of articulation for the suprapharyngobranchial II; *aup*, pars autopalatina; *c. ju*, jugulo-hyoideomandibular canal; *f. ot. occ*, fissura otico-occipitalis; *f. ot. v*, fissura oticalis ventralis; *jd*, jugular depression; *p. lig. m*, medial pit for ligaments connecting the palatoquadrate and the neural endocranium; *pr. asc*$_2$, processus ascendens posterior; *pr. ba*, basal process; *pr. po*, processus postorbitalis; *qu*, pars quadrata; *r. aort*, groove for the radix aortae; *spi*, canal for a spino-occipital nerve; *v. font*, vestibular fontanelle; *X*, canal for the nervus vagus.

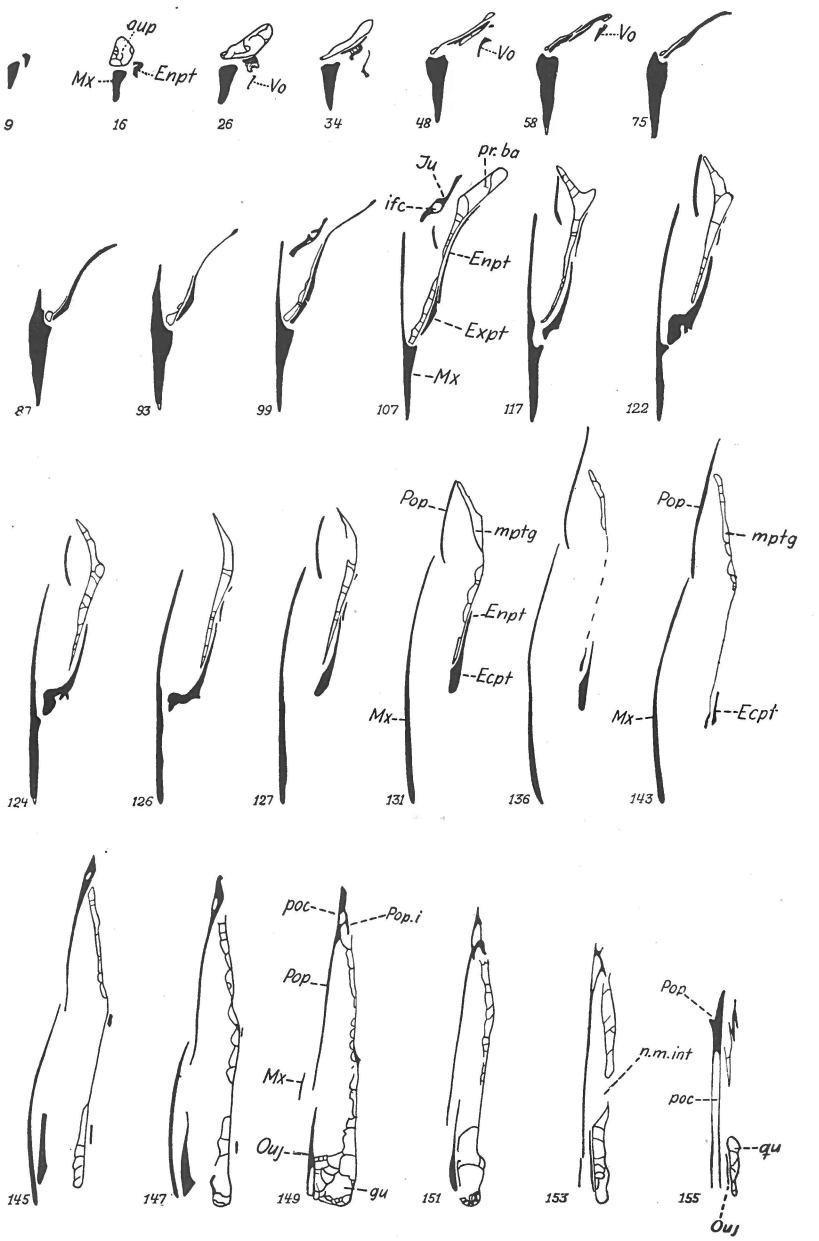


Fig. 27. *Australosomus kochi* (Stensiö). Transverse sections through the palatoquadrate-maxillary apparatus. From the complete grinding series. C. 7×.

Ecpt, ectopterygoid; *Enpt*, entopterygoid; *Ju*, jugal; *Mx*, maxillary; *Pop*, preoperculum; *Pop. i*, internal lamina of the preoperculum; *Quj*, quadratojugal; *Vo*, vomer; *aup*, pars autopalatina; *ifc*, infraorbital sensory canal; *mptg*, pars metapterygoidea; *n. m. int*, notch in the posterior margin of the palatoquadrate; *poc*, preopercular sensory canal; *pr. ba*, basal process; *qu*, pars quadrata.

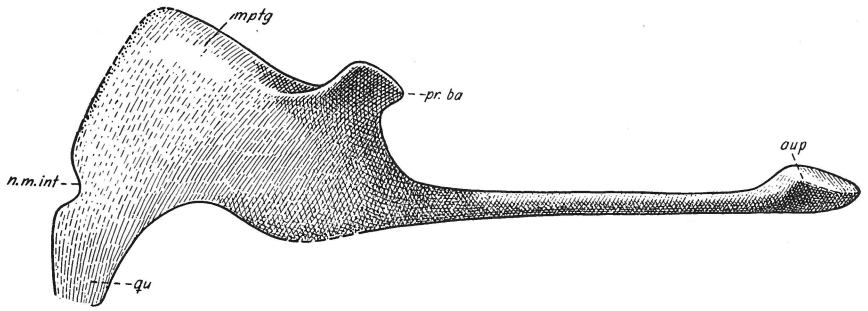


Fig. 28. *Australosomus kochi* (Stensiö). Palatoquadrate in medial view. Mainly on the basis of the complete grinding series. Restored cartilaginous areas dotted. C. 7×. Lettering as in fig. 27.

The posterior division is a fairly high, mainly vertically placed plate, which is bent in such a way that the greater part of its lateral face is concave both in a dorso-ventral and a rostro-caudal direction, and its medial face is correspondingly convex. The plate is very thin except in the quadrate region, which is fairly massive, as shown in the figures. From the antero-dorsal part of the medial face of the plate issues a very prominent process, the basal process (*pr. ba,* figs. 26–30), in an antero-dorso-medial direction. The process has a very broad base and is flattened in such a way that its medial face is directed somewhat posteriorly and ventrally and its lateral face correspondingly anteriorly and dorsally.

The outline of the posterior division is rather complicated, broadly speaking, however, the bent plate may be described as four-sided, with a posterior, a dorsal, an anterior, and a ventral margin.

In the posterior margin we find a fairly deep notch (*n. m. int,* figs. 27–30), which should probably be compared to the groove or canal in the posterior margin of the pars quadrata in *Pteronisculus* (E. Nielsen 1942, pp. 145, 179–180) and *Pygopterus* (Aldinger 1937, pp. 145–146), and which thus probably lodged the ramus mandibularis internus facialis. Dorsally to this notch the posterior margin was cartilaginous, and this unossified part of the margin was enclosed between and in contact with the external and the internal lamina of the preoperculum (see p. 107). Except farthest anteriorly the dorsal margin of the posterior division of the palatoquadrate was also in contact with the preoperculum, as shown in fig. 27.

The ventral margin comprises an anterior, almost straight, cartilaginous part, which was in contact with the maxillary anteriorly to the opening for the musculus adductor mandibulae, a middle deeply concave part medially to the postero-ventral part of the space for the adductor muscle, and a posterior part, which forms the triangular, mainly ventrally directed articular face of the pars quadrata. The postero-ventral part of the lateral face of the pars quadrata was intimately connected with the small quadratojugal (p. 108).

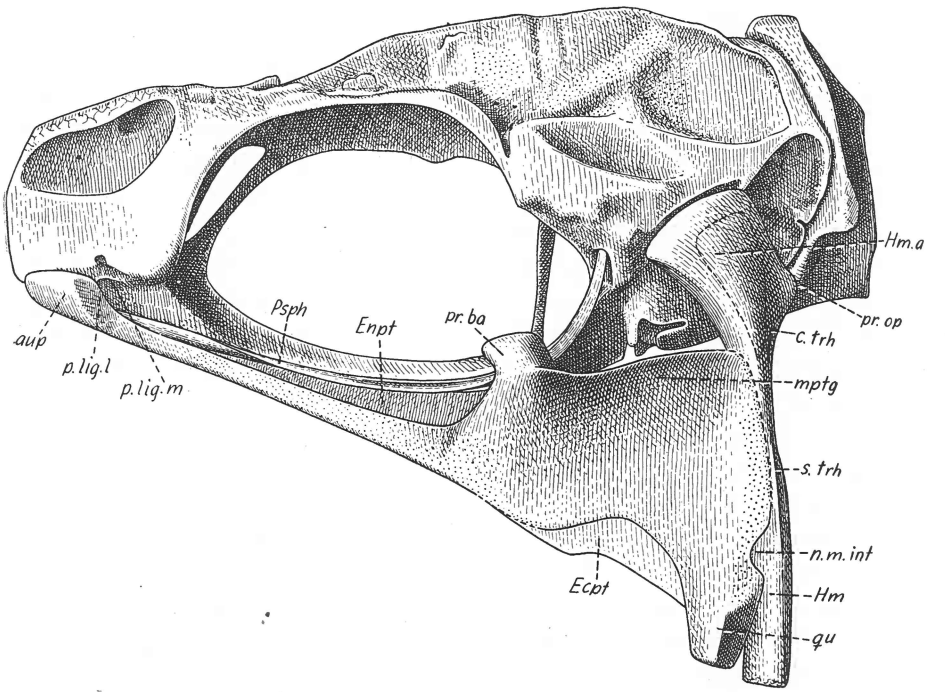


Fig. 29. *Australosomus kochi* (Stensiö). Lateral aspect of neural endocranium with parasphenoid, palatoquadrate with ecto- and entopterygoid, and hyomandibula with outlines of dermohyal. Mainly on the basis of the complete grinding series. Restored cartilaginous areas dotted. C. 7×.

Ecpt, ectopterygoid; *Enpt*, entopterygoid; *Hm*, hyomandibula; *Hm. a*, dermohyal (accessory hyomandibula); *Psph*, parasphenoid; *aup*, pars autopalatina; *c. trh*, canal for the truncus hyoideomandibularis; *mptg*, pars metapterygoidea; *n. m. int*, notch in the posterior margin of the palatoquadrate; *p. lig. l*, *p. lig. m*, pits for ligaments connecting the palatoquadrate and the neural endocranium; *pr. ba*, basal process; *pr. op*, processus opercularis; *qu*, pars quadrata; *s. trh*, groove for the truncus hyoideomandibularis.

The anterior division of the palatoquadrate may be described as a long and narrow plate, the most anterior part of which is very massive and fully ossified, while the posterior and larger part is very thin and less completely ossified, its lateral face being devoid of perichondral bone to the extent shown in fig. 29, and its interior being only partially occupied by endochondral bone, as appears from the serial drawings nos. 48, 58, 75, 87, 93 and 99 (fig. 27).

The plate is so situated that its oral face is directed mainly ventro-medially and its aboral face mainly dorso-laterally. Its ventro-lateral margin is in contact with the maxillary (see further p. 106), and the most anterior part of its dorso-medial margin is widened so as to form a dorso-medially directed articular facet (figs. 27–30), which rested against the above described articular facet on the ventral face of the ethmoidal region of the neural endocranium.

On the oral face of the palatoquadrate we find only two dermal bones, one of which is an ectopterygoid, while the other is probably an entopterygoid. No independent dermopalatines have been observed, but it is not quite impossible that this is due to the difficulty in tracing the sutures between thin and firmly joined dermal bones by the aid of serial grinding, and if this is actually the case, the entopterygoid in the figures should be divided into a ventral or ventro-lateral dermopalatine series and a dorsal or dorso-medial true entopterygoid. More probably, however, the absence of independent dermopalatines is due either to their complete reduction or to their fusion with the entopterygoid; in the latter case the entopterygoid must be regarded as a complex bone. The lack of a dermometapterygoid is probably due to reduction.

Entopterygoid. – The entopterygoid (*Enpt*, figs. 1, 21, 22, 23, 25; pl. 2, fig. 2) is a very long bone extending from the anterior end of the palatoquadrate to a point dorsally to the anterior end of the adductor opening. Corresponding to the curvature of the palatoquadrate, the posterior part of the entopterygoid is mainly vertical, while the anterior part is placed obliquely in such a way that its oral face is directed mainly ventro-medially and its aboral face mainly dorso-laterally. Except farthest anteriorly the obliquely placed part of the entopterygoid is much broader than that part of the palatoquadrate against which it rests, so that a broad medial zone of the aboral face of this part of the bone has no contact with the palatoquadrate. The details of the shape of the bone are shown in the figures, from which it will also be seen that the bone joins by suture with the ectopterygoid and the maxillary. Between the entopterygoid and the ectopterygoid there is a slight overlapping, the entopterygoid covering a narrow marginal area of the oral face of the ectopterygoid. The centre of radiation of the bone could not be localised.

Ectopterygoid. – The ectopterygoid (*Ecpt*, figs. 1, 26, 27, 29, 30) is situated postero-ventrally to the posterior part of the entopterygoid, resting in part on the oral face of the palatoquadrate and in part as shown in fig. 26, forming the medial wall of the adductor space ventrally to the deeply concave part of the ventral margin of the palatoquadrate.

Corresponding to the curvature of the palatoquadrate, the posterior part of the ectopterygoid is mainly vertical, while the anterior part is rather strongly curved in a transverse direction, its oral face being convex and directed mainly ventro-medially.

As seen in fig. 30, which together with fig. 26 gives a good idea of its detailed shape, the bone may be said to be bounded by a dorsal and a ventral margin. The dorsal margin is irregularly curved, but mainly convex, while the ventral margin consists of an anterior fairly straight part, which joins by suture with the maxillary, and a posterior part, which forms the anterior and larger part of the medial edge of the adductor opening. Just anteriorly to the adductor opening the ectopterygoid is much thickened and shows a

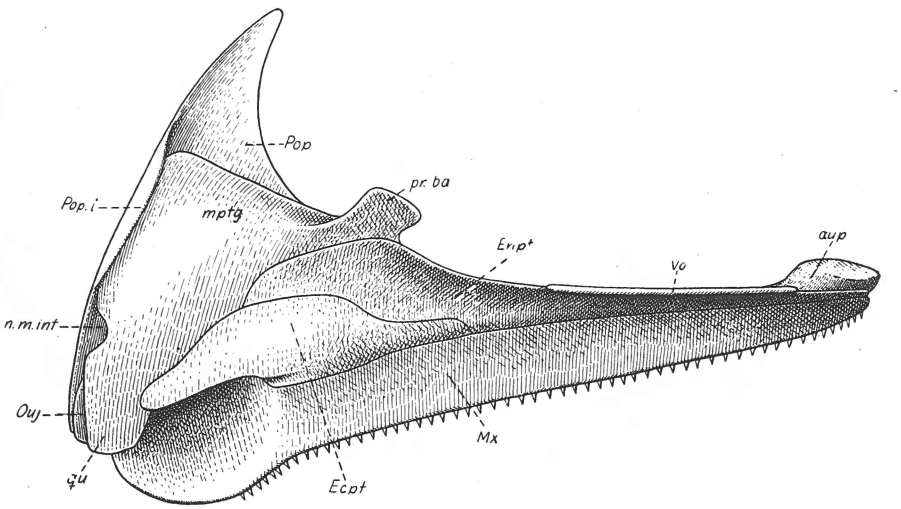


Fig. 30. *Australosomus kochi* (Stensiö). Palatoquadrate-maxillary apparatus and vomer in medial view. Mainly on the basis of the complete grinding series. C. 7×.

Ecpt, ectopterygoid; *Enpt*, entopterygoid; *Mx*, maxillary; *Pop*, preoperculum; *Pop. i*, internal lamina of the preoperculum; *Quj*, quadratojugal; *Vo*, vomer; *aup*, pars autopalatina; *mptg*, pars metapterygoidea; *n. m. int*, notch in the posterior margin of the palatoquadrate; *pr. ba*, basal process; *qu*, pars quadrata.

very short longitudinal groove on its oral face. The radiation centre is found a short distance antero-medially to the posterior end of the straight anterior part of the ventral margin of the bone.

Maxillary. – The maxillary (*Mx*, figs. 1, 25, 26, 27, 30, 31, 32; pl. 1, fig. 4; pl. 2, figs. 1, 2; pl. 4, figs. 1, 2; pl. 5, fig. 1) comprises a high postorbital and a low suborbital division and in its general shape agrees very well with the typical Palaeonisciform maxillary. The detailed outline of the bone varies somewhat in the different specimens; this also appears from a comparison between fig. 25, which is mainly based on the serial drawings, and fig. 32, which is drawn after the specimen shown in pl. 4.

In transverse sections the anterior division of the maxillary is triangular, this part of the bone, in addition to its external and internal faces, having a well defined dorsal face (fig. 27). In the foremost part of the posterior division of the maxillary the transverse sections change gradually in a posterior direction, as shown in fig. 27, that is to say, the external face of the bone increases much more in height than the internal face, so that the dorsal face becomes more and more medially directed at the same time as it increases in width (height). Thus the posterior continuation of the dorsal face of the anterior division of the maxillary forms the internal face of the dorsal part of the high posterior division of the bone, but anterior to the adductor opening it is still separated from the internal face of the more ventral part of the bone by a distinct edge, which is the posterior continuation of the dorso-medial edge of the anterior division of the bone.

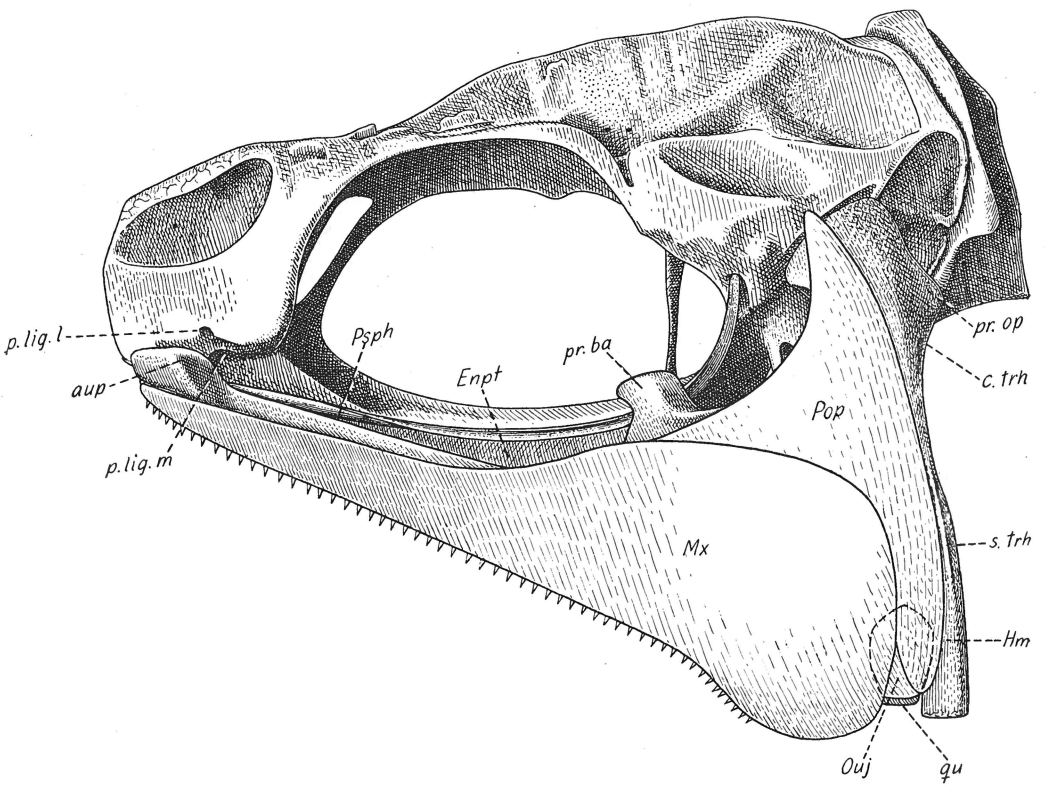


Fig. 31. *Australosomus kochi* (Stensiö). Lateral aspect of neural endocranium with parasphenoid, palatoquadrate-maxillary apparatus and hyomandibula. Mainly on the basis of the complete grinding series. C. 7 ×.

Enpt. entopterygoid; *Hm*, hyomandibula; *Mx*, maxillary; *Pop*, preoperculum; *Psph*, parasphenoid; *Quj*, quadratojugal; *aup*, pars autopalatina; *c. trh*, canal for the truncus hyoideomandibularis; *p. lig. l*, *p. lig. m*, pits for the ligaments connecting the palatoquadrate and the neural endocranium; *pr. ba*, basal process; *pr. op*, processus opercularis; *qu*, pars quadrata; *s. trh*, groove for the truncus hyoideomandibularis.

Thus an internal edge extends in a posterior direction from the anterior end of the maxillary to the adductor opening, and against this edge, which obviously corresponds to the internal lamina of the maxillary in *Pteronisculus* (E. Nielsen 1942, p. 153), lie the ventral (lateral) margins of the ectopterygoid and the entopterygoid, while the palatoquadrate itself is in contact with the maxillary just dorsally or, in the anterior division of the bone, just laterally to the internal edge.

As already described, a narrow marginal zone of the maxillary is overlapped by the jugal, while the maxillary itself overlaps a narrow anteroventral marginal area of the preoperculum and a relatively broad anterior part of the small quadratojugal.

The sharp ventral margin bears a single row of rather small pointed teeth, arranged as shown in fig. 25.

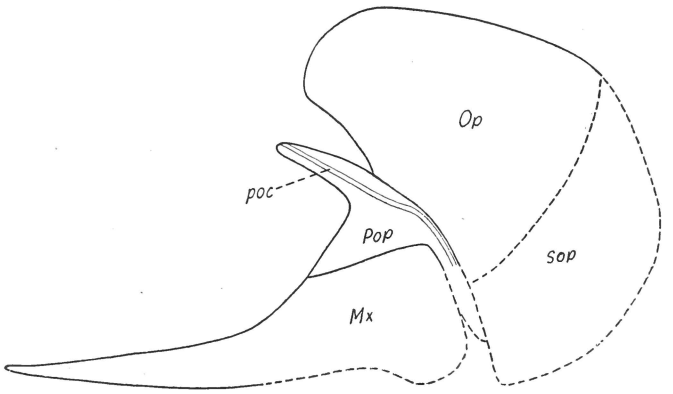


Fig. 32. *Australosomus kochi* (Stensiö). Sketch of the maxillary, the preoperculum, the operculum, and the suboperculum in specimen no. 403. 4×.
Mx, maxillary; *Op*, operculum; *Pop*, preoperculum; *Sop*, suboperculum; *poc*, preopercular sensory canal.

The centre of radiation lies, as shown in fig. 25, in the anterior part of the posterior division of the bone on a level with the internal edge.

The horizontal pit-line of the cheek has left no traces on the maxillary.

Preoperculum. – The preoperculum (*Pop*, figs. 1, 25, 27, 30, 39; pl. 4, figs. 1, 2) has a very steep position and consists of a broad antero-dorsal and a narrow postero-ventral part, which pass very gradually into one another. Fig. 25 shows the outline of the exposed part of the bone, which, however, does not correspond entirely to the outline of the whole bone, for, as already mentioned, a narrow marginal area of the bone is concealed below the maxillary. The preoperculum itself slightly overlaps the anterior margin of the lateral face of the dermohyal (accessory hyomandibula), the anterior margin of the operculum, and a dorsal part of the anterior margin of the suboperculum, and moreover it covers a large postero-dorsal area of the lateral face of the quadratojugal. Thus, in its relations to the adjoining bones the preoperculum shows good agreement with that in *Pteronisculus*. (E. Nielsen 1942, pp. 153–154).

The preopercular sensory canal, as shown in fig. 25, passes through the bone fairly near its posterior margin, as usual piercing the centre of radiation, which is situated about midway between the dorsal and the ventral end of the bone. Around the sensory canal the bone is thickened somewhat, so that a rather indistinct ridge is developed on its internal face. From the middle third of this ridge issues, in an antero-ventro-medial direction, a small lamina (*pop. i*, figs. 27, 30), which corresponds to the internal preopercular lamina in *Pteronisculus* (E. Nielsen 1942, p. 154, figs. 35–37) and *Saurichthys* (Stensiö 1925, pp. 97–107, 142, 149, 162–164, 199–200; E. Nielsen 1942, pp. 158–159). As mentioned above (p. 102) the dorsal half of the

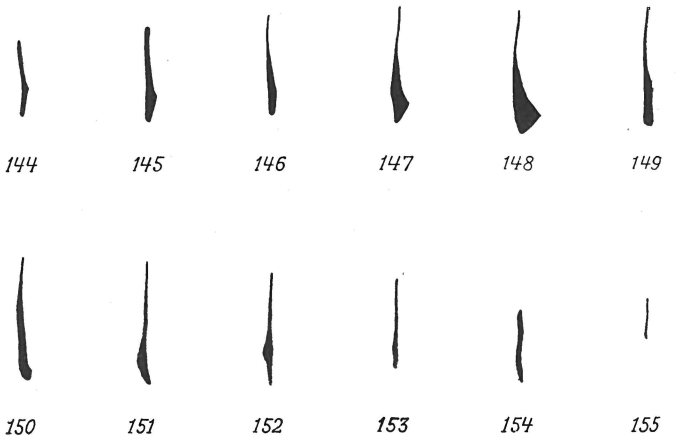


Fig. 33. *Australosomus kochi* (Stensiö). Transverse sections through the quadratojugal. Medial face of the bone to the right. From the complete grinding series. 9×.

posterior marginal zone of the palatoquadrate is enclosed between the external plate and the internal lamina of the preoperculum, the cartilaginous edge of the palatoquadrate reaching the sensory canal ridge itself, while the narrow postero-dorsal marginal zone of the medial face of the palatoquadrate is in close contact with the antero-ventro-laterally directed face of the internal preopercular lamina. Moreover, as already mentioned, the antero-dorsal edge of the palatoquadrate rests against the medial face of the broad antero-dorsal part of the preoperculum.

The external face of the preoperculum shows no traces of any of the pit-lines of the cheek.

Quadratojugal. – The quadratojugal (*Quj*, figs. 1, 25, 26, 27, 30, 31) is a small bone which is somewhat higher than broad and roughly elliptic in outline. As already mentioned, it is overlapped externally to a considerable extent by the preopercular and the maxillary, and the postero-ventral part of its medial face is in close contact with the lateral face of the pars quadrata. The bone varies in thickness in a way which will best be understood from fig. 33.

The centre of radiation could not be localised on the material at my disposal, nor could any traces of the vertical pit-line be observed.

Premaxillary. – An independent premaxillary is not developed, and it does not seem very probable that a premaxillary element is included in the maxillary, for this bone is separated by a fairly large interval from its fellow on the other side of the head. The lack of a premaxillary is therefore probably due to reduction.

Discussion. – As may be gathered from the above, the palatoquadrate and its dermal bones are firmly connected with the preoperculum, the maxillary, and the quadratojugal in much the same way as the corresponding

bones in *Pteronisculus* (E. Nielsen 1942, pp. 143–158), *Saurichthys* (Stensiö 1925, pp. 97–107, 142, 149, 162–164, 199–200; E Nielsen 1942, pp. 158 160), and in many other primitive Actinopterygians (Watson 1925, pp. 851 –860; Aldinger 1938, pp. 331–332; etc.) so as to form a high and narrow chamber for the dorsal part of the musculus adductor mandibulae.

The palatoquadrate in *Australosomus* might without difficulty be derived from the type known in typical *Palaeonisciformes* and their allies, a type which may be briefly characterised as follows:

The palatoquadrate is a rather thin plate, consisting of a high posterior and a low anterior division. The plate is bent in such a way that its posterior division is mainly vertical, with laterally bent posterior, dorsal, and ventral margins, while its anterior division has a mainly dorso-laterally directed aboral, and a mainly ventro-medially directed oral face. The plate has two articulations with the neural endocranium, viz. an ethmoidal and a palatobasal one; for the latter of these articulations a strong basal process is developed. Moreover the ventral face of the postero-ventral part of the plate forms a facet or a condyle for the articulation with the lower jaw. The most dorsal part of the high posterior division of the plate is developed as an otic process, which, however, is not in contact with the neural endocranium. The plate ossifies from two or three separate areas, but when fully ossified, it consists of only one bone, the smaller ossifications having fused without leaving any trace of their separate origion.

A palatoquadrate of a somewhat similar type is found in the Acanthodians, which group has lately been the subject of a very close study by Watson (1938). The similarity is of special interest if we bear in mind the resemblance between the neural endocranium of the primitive Actinopterygiand and that of the Acanthodians discussed above (pp. 68–70). The Acanthodian palatoquadrate agrees with that of the typical *Palaeonisciformes* in the following respects:

1) In consisting of a thin plate comprising a high posterior and a low anterior division.
2) In its general curvation.
3) In possessing a palatobasal articulation and an otic process.
4) In ossifying from three centra.

As to 3). Holmgren (1941, pp. 138–141) regards the palato-basal articulation of Watson as an ethmoidal articulation; however, as far as I can see, the place of articulation is exactly the same as the place of the palatobasal articulation in the *Palaeonisciformes*. The ethmoidal region is poorly known in the Acanthodians, and at present it is not known whether the anterior end of the palatoquadrate articulated with the neural endocranium. If such an articulation existed, the relations between the neural endocranium and the palatoquadrate would be almost similar to those in primitive

Actinopterygians, the only difference being that in some Acanthodians the otic process, also, articulates with the neural endocranium, which articulation has not been observed so far in any primitive Actinopterygian.

In its general shape the palatoquadrate of *Australosomus* presents fairly good agreement with that of *Boreosomus* (E. Nielsen 1942, figs. 70–72), however, in regard to the development and the mutual position of its basal and otic processes it is clearly specialised in a Holostean direction, as will be evident from a comparison with the palatoquadrate in forms such as *Ospia*, *Sinamia*, and *Amia* (Stensiö 1935, pp. 22–23; figs. 10–13), and accordingly it is out of the question to regard the palatoquadrate of *Australosomus* as ancestral to that of *Saurichthys*, which presents no Holostean features at all.

The development and arrangement of the dermal bones of the complex palatoquadrate-maxillary apparatus of *Australosomus* also clearly points to a Palaeonisciform ancestry of the genus. The complete reduction of the dermometapterygoid and the considerable diminution of the internal lamina of the maxillary might both be regarded as specialisations in a Holostean direction. The narrowness and relative shortness of the muscle chamber formed by the palatoquadrate-maxillary apparatus indicate that the adductor musculature was less strongly developed than in the typical *Palaeonisciformes*.

Mandible.

The following description of the mandible is based on the serial drawings and on a rather considerable number of more or less well preserved specimens.

Meckelian bone. – The Meckelian cartilage is ossified to some extent in the specimen investigated by grinding, in which it is represented by a single large ossification (*Mk*, figs. 1, 34, 35; pl. 3, figs. 1, 2) extending almost from the posterior end of the mandible to a point a short distance behind its anterior end. Throughout the greater part of its length, however, the Meckelian bone lacks perichondral bone on its lateral face, and it is also very sparsely ossified endochondrally; accordingly the lateral face was to a considerable extent covered with cartilage in the living animal, and also the interior of the structure must have been mainly cartilaginous. Thus it is impossible to state the actual thickness of the Meckelian element, but it can hardly have been very great.

The Meckelian bone may be described as a thin vertically placed plate with one laterally and one medially directed face. The plate, the length of which is about six times its greatest height, grows gradually lower from its posterior to its anterior end, as shown in fig. 35.

The medial face is slightly convex in a dorso-ventral direction, while the

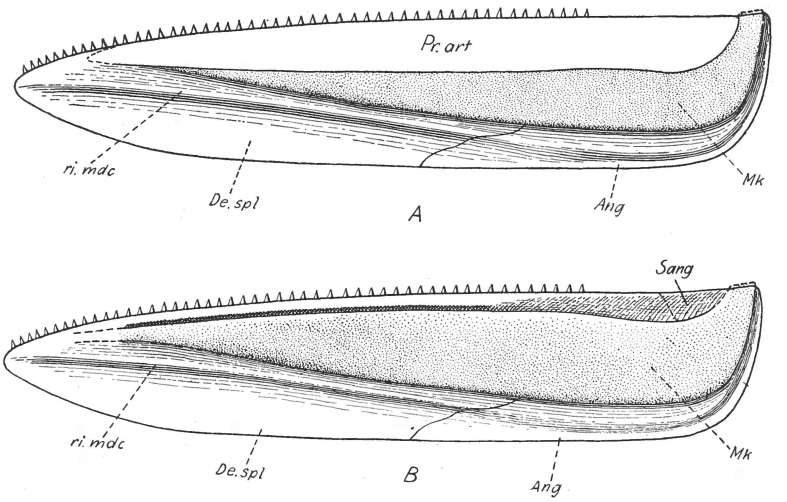


Fig. 34. *Australosomus kochi* (Stensiö). A. Mandible in medial view. B. Same as in A with prearticular removed. Mainly based on the complete grinding series. C. 7×.
Ang, angular; *De. spl*, dentalo-splenial; *Mk*, Meckelian bone; *Pr. art*, prearticular; *Sang.* supraangular; *ri, mdc*, ridge medially to the mandibular sensory canal.

lateral face is correspondingly concave. The posterior end of the plate, the pars articularis, is somewhat thickened and bent in a lateral direction so as to form the posterior wall of the muscular fossa, which is bounded medially by the thinner part of the plate. The dorsal edge and the dorsal part of the medial face rest against the lateral face of the prearticular, and more anteriorly the dorsal edge is in contact with a medial longitudinal ridge on the dentalo-splenial. The posterior part of the ventral edge is in contact with the medial face of the angular just dorsally to the ridge which encloses the mandibular sensory canal. The posterior thickened part of the plate adjoins the medial faces of the angular and the supraangular.

Angular. – As shown in the figures, the angular (*Ang*, figs. 1, 25, 34, 35; pl. 3, fig. 1), has the traditional shape, being roughly triangular, with a posterior, a ventral, and an antero-dorsal margin, the latter of which is completely hidden below the dentalo-splenial. The angular itself, as far as I can make out, overlaps a rather narrow posterior marginal area of the small supraangular.

The angular is traversed by the mandibular sensory canal, which extends through the bone rather near and fairly parallel with its posterior and ventral margins. On its way it pierces the radiation centre, which is situated in the postero-ventral part of the bone. As shown in fig. 36, the bone is thickened around the canal, the thickening appearing as a fairly distinct rounded ridge on its medial face.

Supraangular. – It is very difficult to study the supraangular (*Sang*, figs. 34, 35) in detail; as far I can make out, it is triangular in outline and

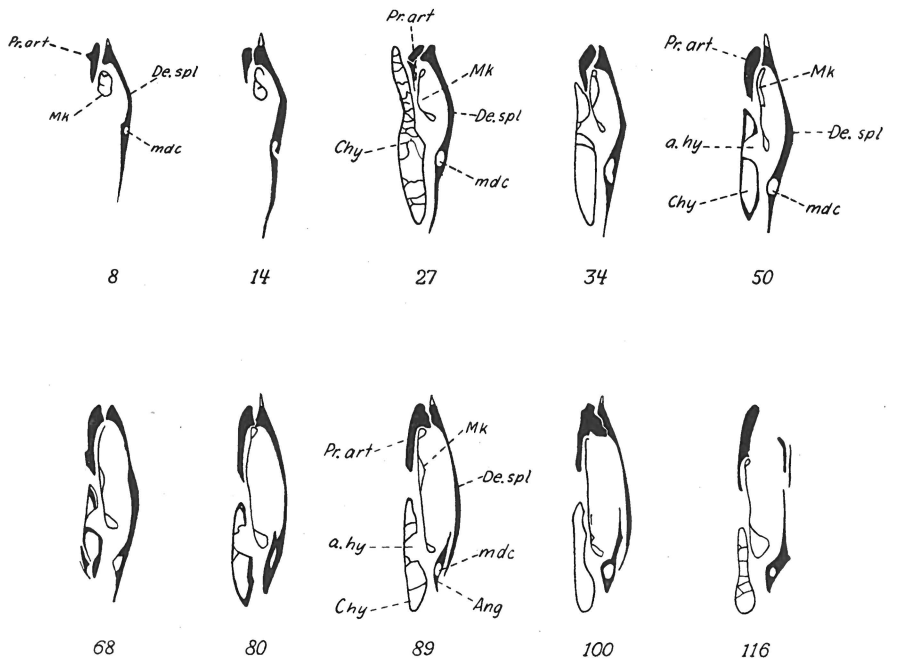


Fig. 35. *Australosomus kochi* (Stensiö). Transverse sections througt the mandible and the ceratohyal ossification. From the complete grinding series. 9×.
Ang, angular; Chy_1, ceratohyal ossification; *De. spl*, dentalo-splenial; *Mk*, Meckelian bone; *Pr. arl*, prearticular; *a. hy*, groove for the afferent hyoid artery; *mdc*, mandibular sensory canal.

overlapped in part by the angular and in part by the dentalo-splenial. Its centre of radiation could not be localised.

Dentalo-splenial. – The dentalo-splenial (*De, spl*, figs. 1, 25, 34, 35; pl. 1, fig. 4; pl. 2, figs. 1, 2; pl. 3, fig. 1; pl. 5, fig. 1) is by far the largest of the dermal bones of the mandible. Figs. 34 and 35 together give a clear idea of its shape, so it will suffice here to comment only on its more important structural details. Broadly speaking, the bone is bent in such a way that its lateral face is convex and its medial face concave both in a rostro-caudal and a dorso-ventral direction. The dorso-ventral curvature is very gradual in the posterior part of the bone, but appears as a sharp bend more anteriorly, where a distinct edge separates the dorsal and the ventral part of its lateral face. Quite possibly this edge indicates the line of fusion between the dental and the splenial elements of the complex bone. The most dorsal part of the bone is thickened, and this thickening is visible on the medial face as an elevated area, which adjoins a, likewise thickened, dorsal part of the prearticular so as to form the roof of the muscular fossa of the jaw.

The mandibular sensory canal traverses the bone in a mainly longitudinal direction, being lodged in a slightly thickened zone, which, as is normally

the case, is only apparent on the medial face of the bone. On its way the sensory canal pierces the radiation centre, which is situated far forwards in the bone.

The convex dorsal edge of the dentalo-splenial bears a single row of small conical sharply pointed teeth.

Prearticular. – The prearticular (*Pr. art*, figs. 1, 34, 35; pl. 3, fig. 1) is the only dermal bone on the inner side of the mandible. Except for its most anterior part, which is still unknown, the details of the bone could best be studied in the serial drawings.

The prearticular is very long and not very high, as seen in fig. 34 A, which shows the bone in medial view. It is not impossible that the foremost part of the bone includes coronoid elements. The bone is very massive, and, as already mentioned, it has a dorsal thickening which together with the thickening of the dentalo-splenial forms the roof above the muscular fossa of the jaw. Ventrally to the thickening the medial face of the prearticular is in contact with the dorsal part of the Meckelian bone. The centre of radiation has not been observed.

Discussion. – According to the reconstruction given by Piveteau (1934, fig. 21), the oral margin of the mandible in *Australosomus merlei* differs from that of *Australosomus kochi* by being more strongly convex. I do not feel convinced, however, that this convexity was not somewhat exaggerated by Piveteau, in any case it appears to me to be far less marked, if existing at all, in some of the specimens figured by Piveteau on pls. I-IV. Piveteau also mentions the presence, in *Australosomus merlei*, of a well developed processus coronoideus; however, after studying his plates, I feel convinced that such a process does not exist, and that Piveteau has been misled by the overlapping of the mandible by the postero-ventral part of the maxillary. Only little is known of the structure of the mandible in other Pholidopleurid genera. Wade figures the mandible of *Pholidopleurus typus* (Wade 1935, fig. 32) and that of *Macroaethes brookvalei* (ibid. fig. 33), both in lateral view and with the most posterior part hidden below the maxillary, while Berg figures the mandible of *Arctosomus sibiricus* in the same way (Berg 1941, fig. 470). All the three figures are somewhat sketchy and can hardly be used for closer comparative purposes; it would seem, however. that the mandible of *Arctosomus* is narrower than that of *Australosomus*, from which it also differs in the peculiar course of its sensory canal, if this canal is not wrongly represented in the reconstruction, as seems most likely.

The mandible of *Australosomus* agrees in its main features with the typical Palaeonisciform mandible, from which it may without difficulty be regarded as a derivative. The lack of independent coronoid elements may either be explained as due to their complete reduction or to their fusion with the prearticular, and the narrowness of the muscle space of the mandible, which agrees with the narrowness of the chamber for the dorsal part of the

musculus adductor mandibulae, shows that the jaw muscles were somewhat reduced as compared with those of typical *Palaeonisciformes* with their wider gapes and stronger dentition. On the other hand, *Saurichthys* with its very long jaws had still stronger jaw muscles than the typical *Palaeonisciformes*, judging from the size of the spaces for both the dorsal and the ventral part of the musculus adductor mandibulae.

Hyoid arch, dermohyal (accessory hyomandibula), operculum, suboperculum, branchiostegal rays, and gular plate.

The hyoid arch with the dermohyal has been studied by the aid of the serial drawings as well as by the aid of direct preparation; the other bones enumerated above have all been investigated without the help of the grinding method.

Hyomandibula. – From its dorsal articulation with the lateral face of the otic region of the neural endocranium the hyomandibula (*Hm*, figs. 1, 25, 29, 31, 36; pl. 1, fig. 4; pl. 3, figs. 1, 2; pl. 5, fig. 1) extends in a ventral and slightly posterior direction, to end ventrally a short distance posteromedially to the most ventral part of the quadrate region. The hyomandibula passes just medially to the posterior marginal zone of the medial face of the palatoquadrate, from which it is separated, except farthest ventrally, by the internal lamina of the preoperculum. Thus in its relations to the palatoquadrate the hyomandibula of *Australosomus kochi* closely resembles that of *Pteronisculus* (E. Nielsen 1942, p. 178, figs. 35, 36).

The hyomandibula might for descriptive reasons be considered to consist of a dorsal and a ventral division, which, however, pass quite gradually into one another. The dorsal division is compressed from side to side in such a way that it appears as a fairly massive plate, the breadth of which decreases in a ventral direction, while the ventral division is formed as a slender rod, the diameter of which decreases in a dorsal direction. The transitional area between the two divisions is situated somewhat nearer the dorsal than the ventral end of the bone.

As shown in the figures, the hyomandibula is slightly bent, with the convexity facing backward and the dorsal articular face of the bone directed mainly antero-dorsally. This long and narrow articular face is convex in a longitudinal as well as in a transverse direction, and it is lined throughout with perichondral bone. In addition to the articular face we find, on the dorsal division of the hyomandibula, a medial, a lateral, and an antero-ventro-lateral face, which meet each other along fairly distinct edges. The medial face is slightly concave apart from a small antero-dorsal area, which, at least in some cases, as seen in fig. 36, shows a slight convexity. The lateral face is convex both in a dorso-ventral and a rostro-caudal direction, while

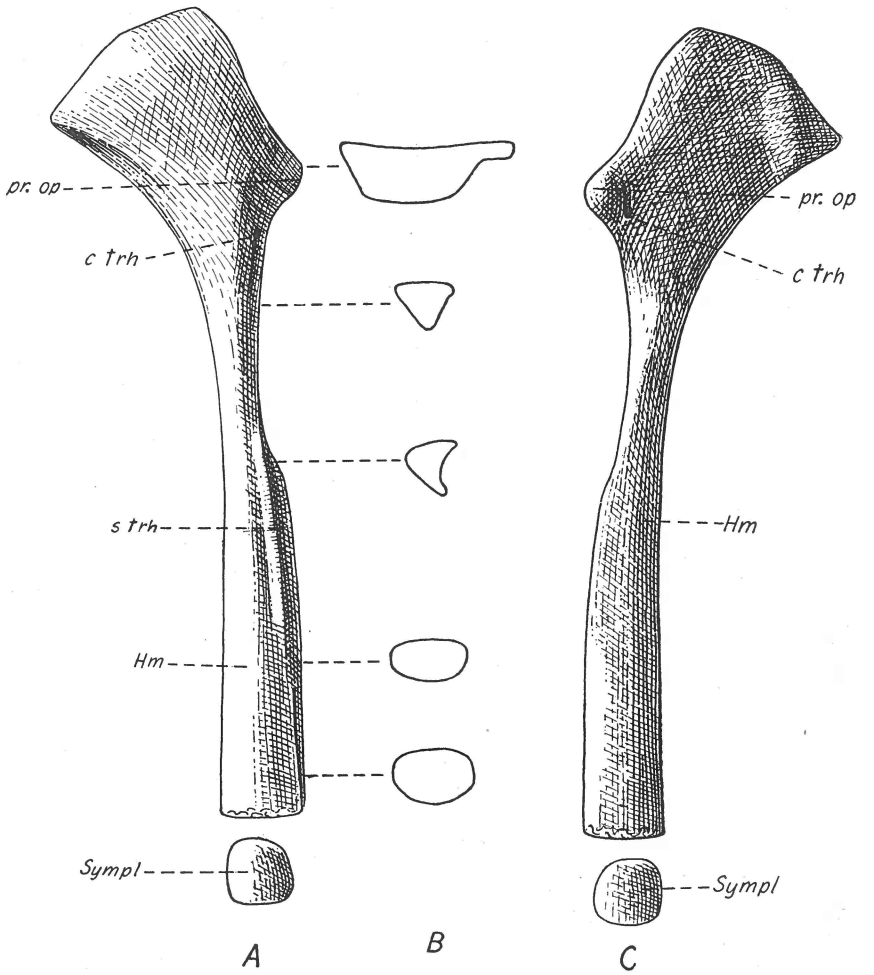


Fig. 36. *Australosomus kochi* (Stensiö). A and C. Hyomandibula and symplectic in lateral and medial view respectively. B. Transverse sections through hyomandibula, medial face of bone upwards. On the basis of the complete grinding series. C. 11 ×.
Hm, hyomandibula; *Sympl*, symplectic; *c. trh*, canal for the truncus hyoideomandibularis; *pr. op*, processus opercularis; *s. trh*, groove for the truncus hyoideomandibularis.

the rather narrow antero-ventro-lateral face is convex in a dorso-ventral direction.

On the edge between the medial and the lateral face we find a small rounded processus opercularis (*pr. op*, figs. 29, 31, 36), and just antero-ventrally to the base of this process the bone is pierced by an almost vertical and very narrow canal for the ramus hyoideomandibularis (*c. trh*, figs. 1, 24, 31, 36). The dorsal opening of this canal is situated on the medial face of the bone just anteriorly to the ventral part of the base of the processus opercularis; the ventral opening lies on the lateral face of the bone a short distance further ventrally. Dorsally as well as ventrally the canal continues

on the external faces of the hyomandibula as a short groove. The most ventral part of the dorsal division is triangular in transverse sections, and the same is the case with the dorsal part of the ventral division, while the transverse sections of the ventral part of the ventral division are elliptical with the long axis extending in a rostro-caudal direction. The dorsal part of the ventral division has a medial, an antero-lateral, and a postero-lateral face. The antero-lateral face is a ventral continuation of the antero-ventro-lateral face of the dorsal division, and the postero-lateral face is the ventral continuation of the lateral face of the dorsal division. The postero-lateral face is concave from side to side, being developed as a broad groove, which probably lodged the ramus hyoideomandibularis.

The ventral terminal face of the hyomandibula is devoid of perichondral bone and was accordingly covered by cartilage in the living animal.

As in *Pteronisculus* (E. Nielsen 1942, p. 180) and *Boreosomus* (ibid. p. 346) the endochondral cancellar mass of the hyomandibula has a considerable breadth farthest dorsally, whence it narrow towards the transitional area between the dorsal and the ventral division so as to form a mere stalk, to widen again in a ventral direction throughout the ventral division.

It appears from the oblong shape of the dorsal end of the hyomandibula and of its articular fossa on the endocranium that the possibilities for movement of the hyomandibula were much the same as in *Pteronisculus* (E. Nielsen 1942, pp. 186–187) and *Boreosomus* (E. Nielsen 1942, pp. 349–350), that is, the ventral end of the bone could only be moved in a mainly transverse plane, not backward or forward. The hyomandibula was probably firmly connected with the stiff palatoquadrate-maxillary apparatus, being in contact, in the fossil heads, with the internal lamina of the preoperculum as well as with the palatoquadrate itself, and by way of the symplectic it was possibly also connected with the pars articularis of the Meckelian cartilage. Consequently the movements of the hyomandibula were also determined by the possibilities for movement of the palatoquadrate-maxillary apparatus; but since the palatoquadrate, as described above, has only one direct articulation – the ethmopalatine articulation – with the neural endocranium, the connection between the palatoquadrate and the hyomandibula presented no obstacles for transverse movements of the latter bone.

By the abduction of the hyomandibula the bone was pressed against the operculum and the suboperculum in much the same way as in *Pteronisculus* (E. Nielsen 1942, p. 187), and thus it contributed essentially to the opening of the gill-cavity.

Dermohyal. – On the lateral face of the dorsal division of the hyomandibula lies a small triangular dermohyal (*Hm. a*, figs. 1, 25, 29), the outlines of which are indicated in fig. 29. The anterior margin of the dermohyal is overlapped by the preoperculum and the posterior margin by the operculum. Curiously enough, judging from the serial drawings it seems

that another dermohyal bone is situated on the medial face of the ventral division of the hyomandibula; however, this bone has not been observed in any other specimen.

Symplectic. – The symplectic (*Sympl*, figs. 1, 36; pl. 3, fig. 2) is represented by a diminutive ossification situated a short distance ventrally to the ventral end of the hyomandibula. In transverse section this ossification is elliptical, the dimensions of the ellipse being somewhat less than the likewise elliptical ventral terminal face of the hyomandibula. Both dorsally and ventrally the ossification was capped by cartilage in the living animal.

The exact relations of the symplectic to the mandibular arch could not be established on the specimen investigated by grinding. As far as I can see, however, its position must have been somewhat more ventral in relation to the place of articulation between the palatoquadrate and the Meckelian bone than in *Pteronisculus* (E. Nielsen 1942, p. 175, figs. 35, 36), *Boreosomus* (ibid. p. 346, fig. 70), or *Acrorhabdus* (Stensiö 1921, p. 226; fig. 72).

Ceratohyal. – In the ceratohyal (*Chy*$_1$, figs. 1, 36, 37; pl. 2, fig. 2; pl. 3, figs. 1, 2) there is only a single ossification, which evidently corresponds to the anterior ceratohyal ossification in *Pteronisculus* (E. Nielsen 1942, pp. 175–176; fig. 43). This ossification appears as a laterally compressed, very thin plate, the length of which is somewhat more than half the length of the mandible, and the greatest height of which is between one-third and one-fourth its length. The outline of the ossification in lateral view is seen in fig. 37 and needs no further description. The same figure also shows the course on its lateral face of a broad longitudinal groove (*a. hy*, figs. 1, 36, 37) for the afferent hyoid artery. Except farthest anteriorly the groove is so deep that its bottom is formed by the perichondral bone layer which lines the medial face of the bone.

The ceratohyal ossification consists, like the other primary ossifications, of a cancellar endochondral mass, which is lined with perichondral bone except on its posterior and at least the dorsal part of its anterior narrow terminal face.

The lack of perichondral bone on the terminal faces shows that the ceratohyal ossification was continued by cartilage both anteriorly and posteriorly, and owing to the fact that the bottom of the afferent hyoid artery groove is formed by the medial perichondral bone layers, it is probable that the artery groove was also lined with cartilage to a great extent.

Hypohyal. – Anteriorly to the dorsal part of the anterior terminal face of the ceratohyal ossification lies a small hypohyal ossification (*Hhy*, figs. 1, 37; pl. 3, fig. 2). This ossification is a thin vertically placed plate, which has a mainly transverse position and is curved in such a way that its anterior (morphologically lateral) face is convex and its posterior (morphologically medial) face concave in a transverse direction. The hypohyal attains its greatest height at its posterior (proximal) end, whence the height decreases

slowly throughout the proximal two-thirds of the bone, to increase again towards the anterior (distal) terminal face, the height of which is about half the height of the posterior terminal face. The length of the bone is between twice and thrice its greatest height. Proximally and distally the bone was probably capped by cartilage.

Operculum. – The operculum (*Op*, figs. 25, 32; pl. 1, figs. 3, 4; pl. 3, figs. 1, 2; pl. 4, figs. 1, 2) is a roughly four-sided bone with an anterior, a ventral, a posterior (postero-dorsal), and a dorsal margin. The breadth of the bone increases in a ventral direction, and the height is about equal to the greatest breadth. The bone is slightly curved dorso-ventrally in such a way that its lateral face is convex and its medial face correspondingly concave. The dorsal part of the anterior margin overlaps a posterior marginal area of the dermohyal, while the ventral part of the same margin is overlapped by the preoperculum.

The radiation centre, as shown in fig. 25, lies a short distance behind the dorsal part of the anterior margin.

Subopercul um. – The subopercul um (*Sop*, figs. 25, 32; pl. 1, figs. 3, 4; pl. 2, figs. 1, 2; pl. 3, figs. 1, 2; pl. 4, fig. 2) may be described as a four-sided bone with an anterior, a dorsal, a posterior, and a ventral margin, however, the two last-mentioned margins, both of which are convex, are so curved that they pass quite gradually into one another. The anterior and the dorsal margin are both slightly concave. The height of the bone is a little more than half the height of the operculum; the breadth increases gradually in a dorsal direction, to attain its maximum farthest dorsally, where it is equal to the breadth of the most ventral part of the operculum.

The centre of radiation lies in the antero-dorsal part of the bone, as shown in fig. 25.

Branchiostegal rays. – The branchiostegal series in most cases comprises seven branchiostegal rays (*Rbr*, figs. 1, 25; pl. 2, fig. 2; pl. 3, fig. 1); possibly, however, the number varies from six to eight. The rays are very short, and accordingly the free margin of the series does not form an even continuation of the curved line formed by the posterior margins of the operculum and the subopercul um (cf. fig. 25). The posterior ray is long and narrow, the following ones grow gradually somewhat shorter and broader. The foremost one (the lateral gular) is much larger than any of the other and triangular in outline.

The branchiostegal rays overlap each other in the normal way, the degree of overlapping varying in accordance with the different positions of the opercular fold.

Gular plate. – Between, as well as anterior to, the lateral gulars we observe, in some specimens, remnants of a small median gular plate, the exact shape of which, however, it was impossible to make out. Neither on the median nor on the lateral gulars could any trace of pit-lines be detected.

Discussion. – Very little is known of the elements of the hyoid arch in other Pholidopleurids. Piveteau (1934, fig. 22) gives a sketch of the hyomandibula in *Australosomus merlei*, and Wade (1935, pp. 68, 73) briefly describes the hyomandibula and the ceratohyal in *Pholidopleurus typus* and *Macroaethes brookvalei* and gives rough outline drawings (ibid. figs. 35, 36) of these bones and the symplectic in the latter species. There seems to be fairly good agreement between the hyomandibulae of *Australosomus kochi* and *Australosomus merlei*, while the hyomandibula of *Macroaethes* differs from that of *Australosomus* by having an extraordinarily expanded dorsal end. In *Australosomus merlei* (Piveteau 1934, fig. 21) as well as in *Pholidopleurus typus* (Wade 1935, fig. 32) a dorsal dermohyal is present similar to that in *Australosomus kochi*. In 1936 (p. 42) I homologised the dermohyal, which is common to a large number of primitive Ganoids, with the accessory hyomandibula in *Polypterus* (see also E. Nielsen 1942, pp. 180–181), which bone was regarded by most authors, i. a. Stensiö and Holmgren (1936, p. 392), as a dermal structure. In a more recent work Holmgren alters his opinion regarding the accessory hyomandibula, which he now takes to be of perichondral origin; he bases his conjecture on the statement by Allis, that the bone in question contains a bit of cartilage (Holmgren 1943, p. 96), and in accordance with his new point of view Holmgren rejects my supposition, that the accessory hyomandibula should have originated by fusion of small tooth plates, and he likewise rejects the term »dermohyal«. To this I can only observe that the dermohyal in *Pteronisculus* (E. Nielsen 1942) as well as in *Australosomus* has been carefully investigated by serial grinding, and as far as I can see, it does not differ in structure from the other dermal bones of the head in these forms. However, as is evident from the different interpretations of the accessory hyomandibula in *Polypterus*, it will be difficult to decide without any ontogenetic studies whether a bone is of dermal or of perichondral origin, and hence it is not impossible that the view held by Holmgren may turn out to be correct. On the other hand, there is a possibility that the dermohyal in the Actinopterygians is of dermal origin and has nothing to do with the accessory hyomandibula in *Polypterus*. I therefore prefer to retain the term »dermohyal« for the bone in the Actinopterygians until undoubted proofs of its non-dermal origin have been supplied.

In so far as they are known, the operculum and the suboperculum have developed in much the same way within the different Pholidopleurid genera. The branchiostegal rays, however, vary considerably in number and size. Apart from the foremost large one, there are, in *Macroaethes*, about 14 long and slender rays (Wade 1935, p. 74, fig. 33), in *Pholidopleurus* only a few (4?) likewise long and slender rays (ibid. p. 68, fig. 32), and in *Australosomus* between 5 and 7, all of which are rather short (Piveteau 1934, fig. 21, and above). In *Arctosomus* there are, according to Berg, numerous rays (Berg 1941, p. 471), and judging from his figure 22, the branchiostegal series con-

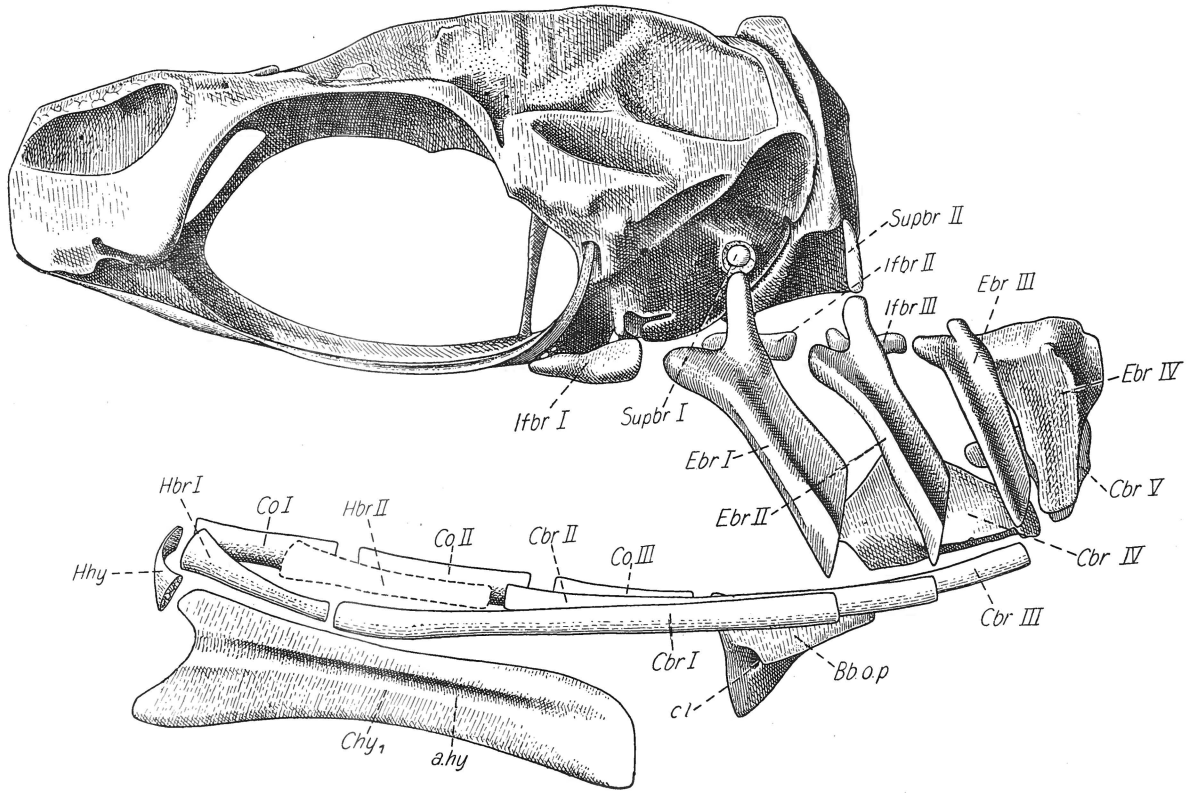


Fig. 37. *Australosomus kochi* (Stensiö). Neural endocranium, branchial arches, ventral part of hyoid arch, and basibranchial series in lateral view. Partly based on the complete grinding series and partly on specimens nos 405 and 548. C. 7×.

Bb. o. p, posterior basibranchial ossification; *Cbr I–V*, ceratobranchials I–V; *Chy*$_1$, ceratohyal ossification; *Co I–III*, three foremost basibranchial ossifications; *Ebr I–IV*, *epibranchials I–IV; Hbr I–II*, hypobranchials I–II; *Hhy*, hypohyal; *Ifbr I–III*, infrapharyngobranchials I–III; *Supbr I–II*, suprapharyngobranchials I–II; *a. hy*, groove the afferent hyoid artery; *c. l*, longitudinal canal in the posterior basibranchial ossification.

tains at least 12 short rays, which diminish in size from the hindmost to the foremost one. Thus, if the figure is correct, the branchiostegal series in *Arctosomus* differs from that in the other Pholidopleurids by lacking the large anterior element.

There seem to be no important structural differences between the Pholidopleurids and the *Palaeonisciformes* in regard to the ossifications of the hyoid arch and the bones of the opercular fold. On the other hand, these elements are fairly uniformly developed in many groups of primitive Actinopterygians, and their agreement within the Pholidopleurids and the *Palaeonisciformes* does not, therefore, necessarily imply any particularly close relationship between these two groups.

Branchial arches and basibranchial series.

In many specimens remnants of the ossifications of the branchial arches and the basibranchial series are present, but only in a few cases are these small ossifications found in their original position in relation to each other, and even when this is the case, as for instance in specimen no. 405 (pl. 3, fig. 2), it was impossible to expose certain of the ossifications without destroying others.

On the basis of the serial drawings, however, it was possible to reconstruct a considerable part of the branchial skeleton of the specimen investigated by grinding, viz. the dorsal ossifications of the anterior branchial arches, all the ossifications of the posterior arches, and the posterior ossifications of the basibranchial series. The ventral ossifications of the anterior branchial arches were also present in the sectioned specimen, but are not shown on the serial drawings. The following description is therefore based in part on the specimen investigated by grinding and in part on direct observations of especially well preserved specimens.

All the ossifications of the branchial arches as well as the basibranchial series consist of a cancellate endochondral mass lined more or less completely with perichondral bone. In most cases, at any rate, the ossifications articulated with each other by cartilaginous epiphyses. In the serial drawings a large number of very small loose-lying pointed teeth were observed which were undoubtedly situated in the skin above the oral faces of the branchial and basibranchial elements, without being firmly attached to the primary ossifications.

First branchial arch. – The first branchial arch comprises the followins ossifications: the hypobranchial, the ceratobranchial, the epibranchial, the infrapharyngobranchial, and the suprapharyngobranchial.

Hypobranchial I (*Hbr. I*, fig. 37; pl. 3, fig. 2) is a fairly slender bone, the distal end of which is expanded as shown in fig. 37, and probably articulated

both with the foremost part of the basibranchial series and with the distal end of the hypohyal.

Ceratobranchial I (*Cbr I*, fig. 37; pl. 3, fig. 2) is a very long rod, which narrows slightly from both ends towards a point situated at a distance of about one-third of its total length behind its anterior end. In transverse sections the bone is V-shaped, a deep longitudinal groove being present on its ventral (morphologically lateral) face.

Epibranchial I (*Ebr I*, figs. 1, 37, 38; pl. 3, fig. 2) is a rather short, quite massive, and slightly curved bone, with the convexity facing backward and a little outward. The posterior or postero-lateral (morphologically lateral) face of the bone has a deep longitudinal groove for the branchial vessels. As in *Pteronisculus* (E. Nielsen 1942, p. 190), the medial wall of the most proximal part of the groove is developed as a dorsally directed process, against the tip of which suprapharyngobranchial I articulated; the process in *Australosomus*, however, is better defined and much higher than that in *Pteronisculus*.

Infrapharyngobranchial I (*Ifbr I*, figs. 1, 37, 38) is a fairly large, somewhat flattened bone, the length of which is about twice its greatest breadth, and which is situated in the anterior continuation of the mainly anteriorly directed most proximal part of epibranchial I. The two main faces of the bone are directed ventro-laterally and dorso-medially respectively. The ventro-lateral face is entirely plane, and its lateral margin has a rather deep notch. The dorso-medial face lies fairly close against the external face of that part of the neural endocranium which, anteriorly to the fissura oticalis ventralis, forms the ventral or ventro-lateral wall of the posterior myodome and, posteriorly to the fissure, the foremost part of the ventral wall of the saccular space; the relief of the face corresponds roughly to that part of the neural endocranium against which it rests. Thus the face is divided into an anterior and a posterior part by a transverse ridge, which fits into the deep transverse groove extending from the anterior end of the groove for the radix aortae towards the ventral opening of the canal for the arteria carotis externa (p. 43). Moreover the anterior part of the face shows a slight concavity corresponding to the slight convexity of the external face of the myodomic wall, while the posterior part of the face exhibits a much deeper concavity, corresponding to some extent to the rather strongly convex external face of the antero-ventral part of the saccular wall. The contact between the neural endocranium and the posterior part of the dorsal face of infrapharyngobranchial I was not quite close, as the arteria carotis communis or possibly the arteria carotis externa and the arteria carotis interna extended forward between the endocranium and the branchial ossification.

Suprapharyngobranchial I (*Supbr I*, figs. 1, 37), which, as already mentioned, is situated directly above the dorsal end of the dorsal process of epibranchial I, is a very small rounded ossification lined laterally with

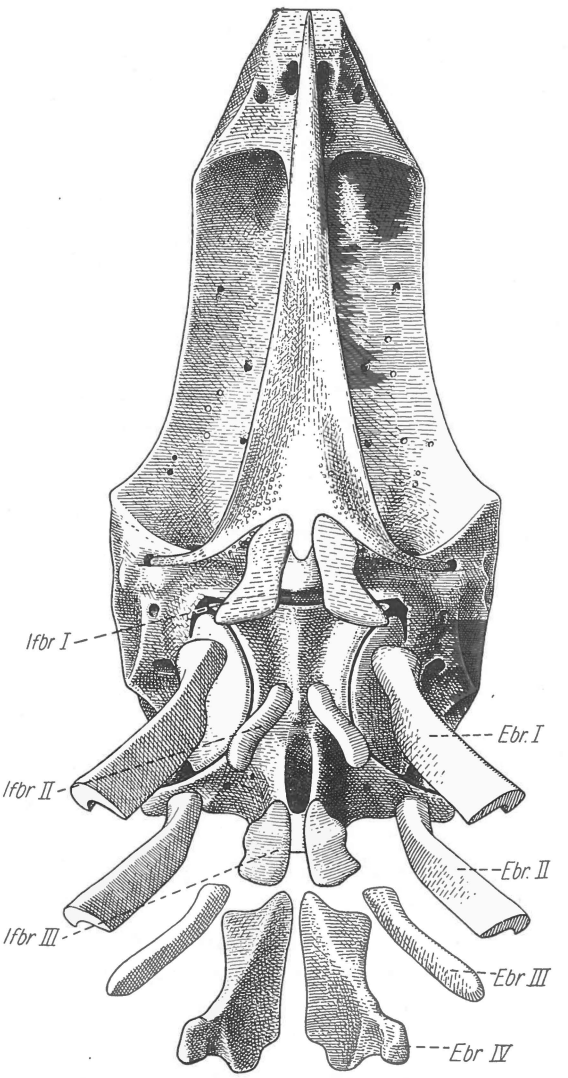


Fig. 38. *Australosomus kochi* (Stensiö). Neural endocranium with parasphenoid and dorsal parts of the branchial arches in ventral view. Mainly on the basis of the complete grinding series. C. 7×.
Lettering as in fig. 37.

perichondral bone. The small ossification lies just laterally to, and undoubtedly articulated with, the very prominent articular facet found on the lateral face of the otic region of the neural endocranium just anteriorly to the jugular groove and antero-laterally to the external opening of the canal for the nervus glossopharyngeus.

Second branchial arch. – The second branchial arch contains the following elements: The hypobranchial, the ceratobranchial, the epibranchial, the infrapharyngobranchial, and the suprapharyngobranchial.

Hypobranchial II (*Hbr II*, fig. 37; pl. 3, fig. 2) has only been identified in specimen no. 405, and in this specimen it was so badly damaged during preparation that only little can be made out regarding the details of its shape. As far as can be seen, hypobranchial II is somewhat longer than hypobranchial I; its slightly expanded distal end articulated with the lateral face of the foremost ossification of the basibranchial series.

Ceratobranchial II (*Cbr II*, fig. 37; pl. 3, fig. 2), though a little shorter, agrees well in its general shape with ceratobranchial I.

Epibranchial II (*Ebr II*, figs. 1, 37, 38; pl. 3, fig. 2) likewise agrees in its general shape with epibranchial I, though it is more slender and has a shorter dorsal process. Its proximal end articulated with infrapharyngobranchial II, and its dorsal process with suprapharyngobranchial II.

Infrapharyngobranchial II (*Ifbr II*, figs. 1, 37, 38) is a slightly S-curved slender rod, situated a short distance ventrally to the ventral face of the posterior ossification of the neural endocranium at the transition between the otic and the occipital regions. Infrapharyngobranchial II is shorter and much less massive than infrapharyngobranchial I, in marked contrast to the conditions in *Pteronisculus* (E. Nielsen 1942, pp. 190–191, fig. 45), in which infrapharyngobranchial II is a much larger structure than infrapharyngobranchial I.

Suprapharyngobranchial II (*Supbr. II*, figs. 1, 37) is a very slender, vertically placed rod of bone, which narrows slightly in a dorsal direction. The dorsal end of the structure probably articulated with, or was connected by a ligament with, the lateral face of the occipital region of the neural endocranium; however, the exact place of articulation or connection could not be determined.

Third branchial arch. – The third branchial arch probably contained a hypobranchial, a ceratobranchial, an epibranchial, and a pharyngobranchial. The hypobranchial, however, has not been identified with certainty in any specimen, and as far as I can make out, the pharyngobranchial, as in *Pteronisculus* (E. Nielsen 1942, pp. 191–192), is common to the third and the fourth branchial arches.

Ceratobranchial III (*Cbr III*, fig. 37) is somewhat shorter, but of principally the same shape as ceratobranchial II.

Epibranchial III (*Ebr III*, figs. 37, 38; pl. 3, fig. 2) is also shorter than the corresponding element in the second arch, and moreover it is much less massive. It differs in shape from epibranchial II by its much shorter dorsal process and by its more shallow longitudinal groove.

Infrapharyngobranchial III (*Ifbr III*, figs. 1, 37, 38) is a dorso-ventrally flattened plate, the breadth of which is a little more than half its length. In lateral view the plate, as shown in fig. 37, is slightly S-shaped, and seen from below or from above its outline may be described as roughly triangular, with a medial, a posterior, and an antero-lateral margin. The

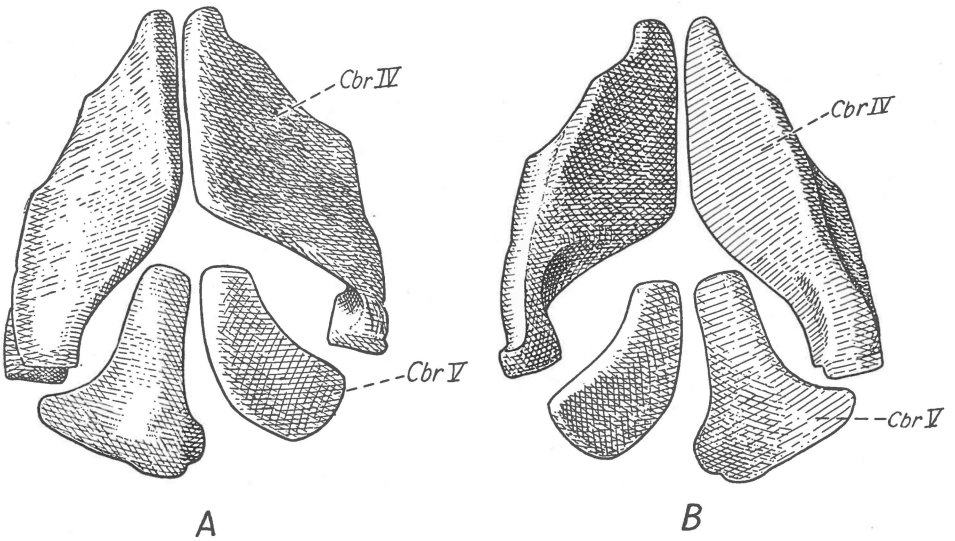


Fig. 39. *Australosomus kochi* (Stensiö). A and B. Ceratobranchials IV and V in dorsal and in ventral view respectively. On the basis of the complete grinding series. 11–12×. Lettering as in fig. 37.

medial and the posterior margins are both slightly convex, while the antero-lateral margin is sinuous, this latter margin showing a middle convexity separating an anterior and a posterior concavity. In relation to the neural endocranium the plate is so situated that its anterior half underlies, but is separated by a rather large interval from, the most posterior part of the occipital region.

Fourth branchial arch. – The fourth branchial arch comprises only two ossifications, both of which have a very specialised shape and should probably be interpreted as a ceratobranchial and an epibranchial respectively.

Ceratobranchial IV (*Cbr IV*, figs. 37, 39; pl. 2, fig. 2) is a fairly large plate, which, as far as could be made out, occupied the position shown in the figures, i. e. with one face directed dorso-laterally, the other ventro-medially, and with an antero-dorso-medial, a postero-dorso-medial, a mainly ventral, and an antero-ventral-lateral edge, the latter of which is rather short and somewhat concave, while the others are longer and almost straight when seen in lateral view. The ventral edge is fairly broad and equipped with a rather distinct longitudinal groove, which evidently lodged the branchial vessels. The postero-ventral corner of the plate is bent somewhat inward, and the antero-dorso-medial edge probably joined with the corresponding edge on the other half of the visceral skeleton. As shown in the figures, the right and the left ceratobranchial IV differ slightly in shape.

Epibranchial IV (*Ebr IV*, figs. 37, 38; pl. 2, figs. 1, 2), which articulated by its most ventral part with ceratobranchial IV, is a roughly triangular,

fairly massive plate with a dorsal (dorso-medial), an antero-ventral, and a posterior edge. On the aboral face of the plate is a small process, which should probably be compared to the better developed dorsal process present on each of the three preceding epibranchials. From this process a distinct edge extends in an anterior direction, while another edge extends from the posterior part of the process in a downward direction. The plate is rather strongly curved in such a way that its dorsal and broadest part forms a roof above the most posterior part of the gill cavity, while the more ventral and narrower part is just as steep as the more anterior epibranchials. In its most ventral part the plate is somewhat thickened, and just dorsally to this thickening a small groove is found on its oral face.

Fifth branchial arch. – The fifth branchial arch contains only a single ossification, probably a ceratobranchial.

Ceratobranchial V (*Cbr V*, figs. 37, 39) is a small plate situated close behind ceratobranchial IV, with one face directed dorso-laterally and the other ventro-medially. The shape of the plate appears clearly from the figures, which also show that the right and the left ceratobranchial V are rather differently developed.

Gill-rays. – Many specimens contain remnants of gill-rays, which, as shown distinctly in pl. 3, fig. 2, are arranged in double rows on the posterior faces of the branchial arches. The rays are filiform, and their length is about one-fifth the length of the ventral margin of the operculum. In some specimens we further observe a number of much longer gill-rays, which are situated just beneath the opercular fold in such a way that they probably supported an opercular gill. These gill-rays, likewise filiform, are of about the same length as the ventral margin of the operculum.

Basibranchial series. – The basibranchial series includes four ossifications, the three anterior of which seem to correspond to the three basibranchial ossifications in *Pteronisculus* (E. Nielsen 1942, pp. 193–194; fig. 45). These three anterior ossifications (*Co I–III*, figs. 1, 37; pl. 3, fig. 2), the middle one of which is somewhat longer than the others, have the shape of slightly dorso-ventrally flattened cylinders, and were probably capped by cartilaginous epiphyses both anteriorly and posteriorly. The fourth ossification (*Bb. o. p*, figs. 1, 37, 40; pl. 2, figs. 1, 2), however, has a very peculiar shape, which needs a more detailed description. The structure in question is a very solid ossification, which may be roughly described as a horizontally placed thick rectangular plate, the length of which is greater than its breadth, and which increases very much in thickness in an anterior direction. The plate is pierced in a longitudinal direction by a paired canal (*c. l*, figs. 1, 37, 40) and on the anterior part of its ventral face provided with a longitudinal crista, which increases rapidly in height in an anterior direction.

For a more detailed description we may regard the ossification as bounded by six faces, viz. a postero-dorsal, a paired lateral, a ventral, an anterior, and a posterior one.

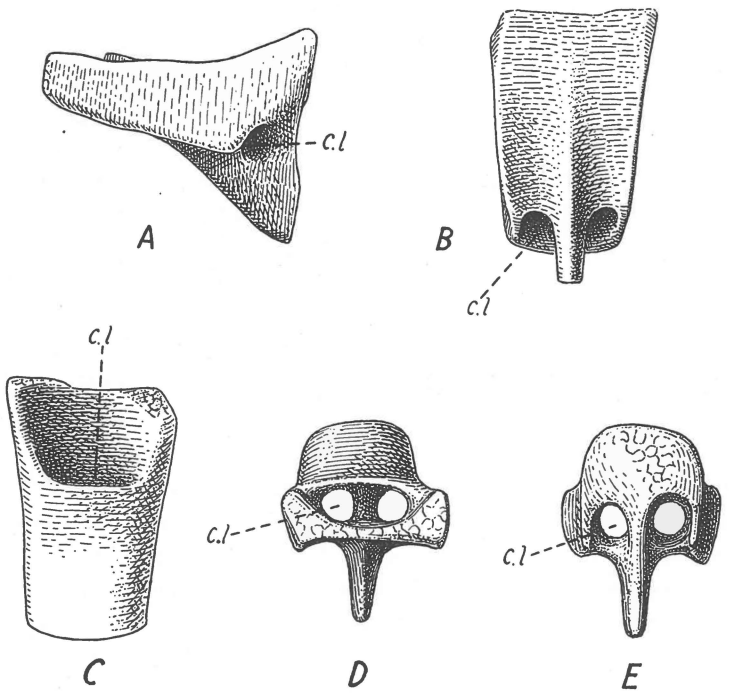


Fig. 40. *Australosomus kochi* (Stensiö). Posterior basibranchial ossification. Mainly on the basis of the complete grinding series. Faces without perichondral bone reticulated. C. 11×.

A, lateral view. B, ventral view. C, dorsal view. D, posterior view. E, anterior view. *c. l*, longitudinal canal.

The postero-dorsal face, which is concave in a longitudinal direction, increases in breadth backwards, the breadth of its foremost part being about half, and that of its hindmost part about two-thirds its length. The greater part of the posterior two-thirds of the face is occupied by a very broad unpaired longitudinal groove; this groove is the posterior continuation of the paired canal which pierces the anterior and greater part of the structure.

The paired lateral face is almost plane and decreases in height in a posterior direction. This face is bounded by a dorsal (or postero-dorsal), an antero-ventral, a ventral, and a posterior margin. The dorsal margin is concave, the others are fairly straight.

The ventral face has about the same length as the dorsal one, and is equipped with the above-mentioned longitudinal crista, which is very high in its anterior part and becomes gradually lower in a posterior direction, to end a short distance behind the middle of the face. On each side of the crista the face is occupied by a broad shallow groove, while behind the posterior end of the crista the face is fairly plane.

The anterior face, which, as shown in fig. 40 E, is to some extent devoid of perichondral bone, is almost plane in a dorso-ventral as well as in a trans-

verse direction. On this face we find the two anterior openings of the wide paired canal which pierces the element in a longitudinal direction. The right one of these openings is much smaller than the left one, as clearly shown in fig. 40 E.

The posterior face, which is very low in its midmost part but increases considerably in heigth laterally, is completely devoid of perichondral bone, and thus it was probably covered by cartilage in the living animal.

The paired longitudinal canal is elliptical in transverse section, the long diameter of the ellipse being vertical. The right and the left canal are only separated by a very thin wall. The height of the left canal in the sectioned specimen is much greater than that of the right one, especially in the foremost part of the bone.

The postero-dorsal and to some extent also the paired lateral face of the posterior basibranchial structure here described are equipped with scattered, quite small, pointed denticles, and accordingly the peculiar structure must have been situated in the floor of the gill cavity and cannot have been placed below the basibranchial series, as is the urohyal in the Teleosts. The structure is accordingly either a specialised posterior basibranchial ossification or possibly such an ossification which has become fused with the hypobranchials of the fourth branchial arch. The dorsal unpaired longitudinal groove and the paired canal which forms the anterior continuation of the groove may have lodged the bifurcating ventral aorta, while the high ventral ridge probably served as a place of attachment of strong muscles.

Discussion. – Extremely little is known regarding the branchial skeleton in the other Pholdiopleurid genera, viz. only the few details of the branchial arches and the basibranchial series in *Macroaethes* given by Wade (1935, p. 74, fig. 37). However, neither Wade's figure nor his description are of any very great use for comparative purposes, the only thing which can be stated with some certainty is that *Macroaethes* and *Australosomus* agree in the development of a double row of supporting gill-rays on the branchial arches, in possessing other gill-rays, which supported an opercular gill, and in having three fairly long ossifications in the anterior part of the basibranchial series.

The foremost three branchial arches as well as the anterior and greater part of the basibranchial series in *Australosomus*, as far as they are known, agree fairly well in their general development with the corresponding parts of the branchial skeleton of *Pteronisculus* (E. Nielsen 1942, pp. 187–195; figs. 45–47). It is especially interesting that the relations between the two foremost branchial arches and the neural endocranium are of the same primitive type in both genera. The two posterior branchial arches in *Australosomus* are much more specialised than in *Pteronisculus*, and the same is probably the case with the peculiar posterior basibranchial ossification in *Australosomus*, though it bears a certain resemblance to the large unpaired basibranchial structure known in the Coelacanthids (E. Nielsen 1936, p. 33, fig. 16; Smith 1939, pp. 66–68, figs. 8, 9; pls. 23, 24).

Ornament of the dermal bones of the head.

As stated by Stensiö (1932, pp. 171–173), the external dermal bones of the head are entirely devoid of ganoine, still, however, their exposed external faces are not quite smooth, but exhibit some very delicate ornamental elements, among which we may distinguish between three types. The first type is best developed on the operculum, the suboperculum, the branchiostegal rays, and the median gular plate, and consists of very fine elevated growth lines arranged in a similar way to the growth lines found on the corresponding dermal bones in *Pteronisculus* (E. Nielsen 1942, p. 199) and several other *Palaeonisciformes*. The second type is mostly found on the operculum and the suboperculum and consists of very fine short ridges arranged in such a way that their long axes point towards the centre of radiation of the bone to which they belong. There are only some few of these ridges, scattered all over the exposed faces of the bones. The third type of ornamental elements are fine ramifying grooves, which issue from the external openings of the vascular canals, forming a more or less extensive network, and which must be compared to the vascular grooves extending from the vertical canals in the scales (Stensiö 1932, p. 181). In most cases these grooves are both shallow and very delicate, now and then, however, we find a single very deep and broad one extending across a considerable part of the bone.

A few especially well preserved specimens exhibit, on the external face of the anterior low division, and of the ventral part of the posterior high division of the maxillary, a system of mainly vertical, fine, whitish striae the nature of which it is difficult to explain. Probably these striae should be compared to the striae present along the anterior margin of the body scales and described by Stensiö (1932, p. 182). It is not quite excluded that such striae are formed by a rudimentary ganoine layer; however, a microscopic examination could not be made on account of the scarcity of sufficiently well preserved material.

Dentition.

A single row of teeth is found on the oral margins of the maxillary and the dentalo-splenial, consisting, on each bone, of about fifty small acutely conical teeth. The structural details of the teeth could not be observed owing to their small size.

Teeth are also present on the oral faces of the ossifications of the branchial arches and the basibranchial series. In some cases these very small conical teeth are single, but in other cases they are attached several together to small dermal ossicles of irregular outline. Both the single teeth and the tooth plates were situated loosely in the skin.

Stensiö (1932, p. 173) mentions the existence of teeth on the ectopterygoid also, but as far as I can make out, this bone as well as the other dermal bones of the palatoquadrate, the prearticular and the parasphenoid, are toothless.

Discussion. – As far as is known, the dentition of *Australosomus merlei* agrees fairly well with that of *Australosomus kochi* (Piveteau 1934, p. 31, fig. 21). Small pointed teeth are also present on the oral margins of the maxillary and the dentalo-splenial in *Pholidopleurus* (Wade 1935, p. 68), and somewhat larger, but likewise pointed, teeth in *Arctomus* are described by Berg (1941, pp. 470–471, fig. 22). *Macroaethes*, however, according to the description given by Wade (1935, pp. 69, 73), differs from the other Pholidopleurid genera in lacking teeth on its jaws. Instead of teeth the oral border of its maxillary bears »numerous, sinuous, transverse rugae, some of which are branched« (ibid., p. 73). A more detailed description of this peculiar feature is highly desirable.

Sensory canal system of the head.

As is normally the case, the sensory canals of the head are enclosed in the dermal bones and open by tubuli into pores on the external faces of the bones.

The canals are fairly easy to follow in the series of drawings as well as in specimens immersed in alcohol or xylol, while the tubuli have only been localised with certainty in some parts of the system. As in *Pteronisculus* and *Boreosomus*, it is impossible to state the exact number of primary tubuli, for these are always divided throughout their whole length into a number of secondary ones. Nor could the exact number of the small foramina through which the nerve branches reach the sensory canals be made out.

As in *Pteronisculus* (E. Nielsen 1942, p. 203) and *Boreosomus* (ibid. p. 353), the number of secondary tubuli varies somewhat not only from specimen to specimen, but also from one side of the head to the other.

The only pit-line localised in *Australosomus kochi* is, as far as I can see, always represented by a shallow groove, but never, as may be the case for some pit-lines in *Pteronisculus* and *Boreosomus* (E. Nielsen 1942, pp. 203, 353), by a narrow canal.

Supraorbital sensory canal. – The supraorbital sensory canal (*soc*, figs. 1, 21, 24, 25; pl. 1, fig. 1; pl. 4, figs. 1, 2) extends from the most anterior part of the nasal backward on to the frontal, to end posteriorly in the centre of radiation of this latter bone. The foremost part of the nasal division of the supraorbital sensory canal is only known from the few specimens in which the nasal is developed as a slender tube surrounding the canal (p. 94, fig. 24), while the posterior and longer part of the nasal division and the

whole frontal division of the canal are easy to study in a large number of specimens. Apart from the most anterior part of its nasal division, which is bent fairly much laterally, the supraorbital sensory canal has a somewhat longitudinal course, showing only a very slight S-shaped bend. The posterior pointed end of the canal does not open on the outer face of the frontal and thus has no connection with the pit-line found on the posterior part of this bone.

From the posterior part of the nasal division of the canal issue 6–7 short tubuli, the pores of which lie dorso-laterally to the canal. Tubuli probably also issue from the most anterior part of the canal, though such tubuli could not be localised on the specimens investigated by me. From the frontal division of the sensory canal issue about 12 short tubuli, all of which open dorso-laterally to the canal.

Infraorbital sensory canal. – As the anterior elements of the infraorbital series are completely reduced (cf. p. 95), both the ethmoidal commissure and the greater part of the suborbital section of the infraorbital sensory canal are quite unknown. The sensory canal (*ifc*, figs. 1, 21, 24, 25, 27; pl. 1, figs. 1, 2; pl. 4, figs. 1, 2), however, could be followed through the jugal, the postorbital, and the frontal, and it ends posteriorly somewhere in the supratemporo-intertemporal (if we assume that this latter bone actually contains intertemporal components (cf. p. 95)). As usual the jugal section of the canal is strongly bent, forming the transition between the vertical postorbital and the horizontal suborbital sections of the canal. From the jugal section of the infraorbital sensory canal issue about seven tubuli, which all open below or behind the canal. The length and direction of the tubuli are shown in fig. 25. In the postorbital the canal is almost straight and extends in a vertical direction from the ventral to the dorsal edge of the bone, much nearer its anterior than its posterior margin. No tubuli were observed, a fact which is probably due to the unsatisfactory state of preservation of this small bone. In the frontal the infraorbital canal extends quite near and fairly parallel to the strongly concave part of the lateral margin which forms the deep notch above the spiracular division of the fossa bridgei. Accordingly the sensory canal in the frontal changes its direction from almost vertical (dorso-medial) to longitudinal.

As already mentioned (p. 92), the canal, curiously enough, does not traverse the radiation centre of the frontal, a fact which in my opinion speaks clearly against the assumption that dermophenotic elements are included in the frontal. From the frontal section of the canal issue about nine short tubuli, the directions of which are shown in fig. 21. From the frontal the infraorbital sensory canal is continued backward through the so-called supratemporo-intertemporal by a sensory canal section, the most anterior part of which, as mentioned above, possibly still belongs to the infraorbital sensory canal, while at least the posterior part represents the postotic sens-

ory canal. The tubuli of the possibly infraorbital part of the sensory canal in the supratemporo-intertemporal could not be localised owing to the rather bad state of preservation of this part of the bone.

Postotic sensory canal. – From the longitudinal sensory canal section in the posterior part of the supratemporo-intertemporal issue at least four short tubuli, which all open dorso-laterally to the canal.

Cephalic division of the main lateral line. – The postotic canal is continued backward by the main lateral line (*lc*, figs. 21, 25; pl. 4, fig. 1, pl. 7) which pierces the extrascapular in a mainly longitudinal direction, running rather near the lateral margin of the bone and piercing the centre of radiation on its way. From the extrascapular section of the main lateral line issue about six short tubuli, whose pores are situated dorso-laterally to the canal.

Supratemporal commissure. – On passing the centre of radiation of the extrascapular the main lateral line gives off a transverse branch in a medial and slightly anterior direction. This transverse sensory canal branch (*s. com*, figs. 21, 25; pl. 4, fig. 2), which extends to the medial corner of the extrascapular but does not communicate with that on the other side of the head, corresponds to the supratemporal commissure in other Actinopterygians. From the transverse canal branch in each extrascapular issue about five tubuli, all of which open anteriorly to the canal.

Preopercular sensory canal. – The preopercular sensory canal (*poc*, figs. 1, 25, 27, 32; pl. 4, figs. 1, 2) extends through the preoperculum from its dorsal to its ventral end, fairly near and almost parallel to its posterior margin, piercing the centre of radiation on its way. A fairly considerable number of tubuli probably issued from the preopercular sensory canal, however, tubuli have only been localised with certainty on a rather small section of the canal just ventrally to the centre of radiation.

As shown in fig. 25, seven short tubuli issue from this section, and their pores are all situated anteriorly to the canal. Stensiö's restoration of the dermal cranial roof (Stensiö 1932, fig. 53) shows a connection between the preopercular sensory canal and the longitudinally running sensory canal lodged in the supratemporo-intertemporal; however, judging from the specimens at my disposal such a connection does not exist.

Mandibular sensory canal. – The mandibular sensory canal (*mdc*, figs. 1, 25, 36; pl. 1, fig. 4; pl. 3, fig. 1) extends through the angular and the dentalo-splenial in the same way as in most primitive Actinopterygians. From the canal issue between 60 and 70 short tubuli, the outer openings of which are situated ventrally or posteriorly to the canal, as shown in fig. 25. The diameter of the short tubuli decreases very much towards their distal ends.

Pit-lines. – The only pit-line localised in *Australosomus kochi* (*ap*, figs. 21, 24, 25) extends in an antero-lateral direction from the convex antero-lateral margin of the anterior parietal to a point some distance behind the

centre of radiation of the frontal. Piveteau observed two pit-lines on the dermal cranial roof of *Australosomus merlei* (Piveteau 1934, p. 33, fig. 23), and it is obvious that the foremost of these, his anterior pit-line, corresponds most closely to that present in *Australosomus kochi*, although it differs by extending backwards on to the anterior parietal. It does not seem quite certain to me, however, that Piveteau's interpretation of this pit-line is correct, for the following reasons: In primitive Ganoids the anterior pit-line normally forms a direct posterior continuation of the supraorbital sensory canal, or in any case it is directed towards the centre of radiation of the frontal. Moreover the anterior parietals in *Saurichthys*, the parietal complex of which bears a great resemblance to that in *Australosomus*, exhibit the middle, but not the anterior, pit-line (Stensiö 1925, fig. 20). As the foremost pit-line in *Australosomus merlei* and the only pit-line in *Australosomus kochi* differ from a normal anterior pit-line both in having a more lateral direction and in lacking connection with the supraorbital sensory canal, I think it possible, though I prefer to leave the question open, that it should be compared rather to a middle than to an anterior pit-line.

Discussion. – In its main features the sensory canal system of *Australosomus kochi* shows good agreement with that of *Australosomus merlei* as far as this latter has been investigated (Piveteau 1934, pp. 32–33, figs. 22, 23), and judging from our scanty knowledge of the sensory canal system in the other Pholidopleurid genera, the characteristic features of the sensory canal system of *Australosomus* seem likewise to be present in these genera (Wade 1935, figs. 32–34; Berg 1941, p. 471, figs. 22, 23).

Common to all the four genera are the short supraorbital sensory canal and, at least to *Australosomus*, *Pholidopleurus*, and *Arctosomus*, the peculiar course of the infraorbital sensory canal through a marginal area of the frontal. The *Pholidopleuridae* differ from the normal *Palaeonisciformes* in both these characters, while regarding the first-mentioned character they resemble *Saurichthys*, as previously pointed out by Wade (1935, p. 65), Piveteau (1934, p. 32), and the present author (1936, p. 45). As stated by Westoll (1944, pp. 68–69), however, a shortening of the supraorbital sensory canal takes place within numerous groups of fishes, and accordingly this character is of no great value for phylogenetic conclusions. As already discussed, the abnormal course of the infraorbital sensory canal is probably a specialisation within the *Pholidopleuridae* caused by the development of the large notch in the dermal cranial roof above the spiracular part of the fossa bridgei, and to a certain degree comparable to the likewise specialised course of the infraorbital sensory canal in the Haplolepid genus *Pyritocephalus* (Westoll 1944), although, probably, no close phylogenetic relations existed between the *Pholidopleuridae* and the *Haplolepidae*. In other respects the sensory canal system of the *Pholidopleuridae* agrees well with the typical Palaeonisciform pattern, from which it might without difficulty be thought to have been derived.

Axial skeleton.

The axial skeleton, which is well ossified even in small specimens, and which accordingly is often well preserved, has already been described in fairly great detail by Stensiö (1932, pp. 174–177) on the basis of the few specimens at his disposal. However, the much larger material now available permits a still more thorough elucidation of the many interesting points in the anatomy of this structure.

Stensiö has pointed out that the vertebral column is equipped with ring-like centra, which he regards as chordal and thus differing in principle from those of other Teleostomians.

In the abdominal region as well as in the greater part of the caudal region these centra ($Cn_2 + Cn_1$, figs. 41–46; pl. 2, figs. 1, 2; pls. 6, 7) are intermetameric in position, each consisting of the caudal centrum of one metamere and the cranial centrum of the metamere following immediately behind. However, in the middle part of the caudal region below the midmost third of the long base of the dorsal fin there is a number of independent fairly long caudal (Cn_2, fig. 46; pl. 6) and very short cranial (Cn_1, fig. 46) centra alternating with each other. In most cases we find six of these independent centra, viz. three cranial and three caudal ones, but in a few cases there are probably only four. In a single specimen (no. 466) each of the short independent cranial centra is represented by a dorsal (Cn_1d, pl. 6) and a ventral (Cn_1v, pl. 6) half-ring or crescent-shaped structure.

Apart from the centra the vertebral column contains dorsal and ventral arcual ossifications throughout its length and, in addition, in its most anterior part a number of small supradorsal ossifications. Supraneurals or infrahaemals have not been observed.

In the abdominal region, dorsally to each centrum, we find independent paired basidorsal and interdorsal ossifications and, ventrally, a single large paired or unpaired ossification, the interventral of each metamere having coalesced with the basiventral of the metamere in front, and this compound ossification having moreover coalesced, at least in the anterior part of the region, with its fellow on the other side.

In the midmost part of the caudal region, where the cranial and the caudal centra have not coalesced, the dorsal and the ventral arcual ossifications are also independent. Elsewhere in the caudal region the basiventrals have fused with the interventrals in the same way as is the case in the abdominal region, and farthest anteriorly, where the conditions are as in the abdominal region, the dorsal arcual ossifications are likewise compound structures, the basidorsal of each metamere having fused with the interdorsal of the metamere next behind. In the posterior part of the caudal region both the dorsal and the ventral arcual ossifications are unpaired, and in the midmost part the independent interdorsal and interventral ossifications are

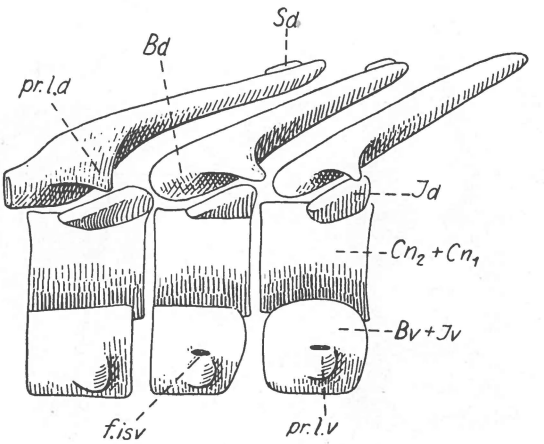


Fig. 41. *Australosomus kochi* (Stensiö). Foremost part of vertebral column in lateral view. Mainly on the basis of the grinding series. C. 11×.

Bd, basidorsal; *Bv* + *Iv*, fused basi- and interventral; Cn_2 + Cn_1, fused caudal and cranial centrum; *Id*, interdorsal; *Sd*, supradorsal; *f. isv*, foramen for intersegmental vessels; *pr. l. d*, lateral basidorsal process; *pr. l. v*, lateral process from the fused basi- and interventral.

paired, while the basiventral and possibly also the basidorsal ossifications are unpaired. In the anterior part of the region the dorsal and probably also the ventral arcualia are paired.

According to Stensiö (1932, p. 176) the proximal parts of the arcual elements consist of cancellar bone tissue lined with thin perichondral bone layers, while the distal arcual processes (Stensiö's neural and haemal spines) were cartilaginous in their interior and surrounded by a thick layer of perichondral bone. However, in all the specimens investigated by me the distal basidorsal processes in the area just behind the head as well as the hypural processes are ossified in their interior in the same way as the proximal parts of the arcual elements, while their perichondral bone layer is not particularly thick.

We shall now proceed to a more detailed description of the arcual ossifications mentioned above.

In the midmost part of the abdominal region each basidorsal ossification (*Bd*, fig. 43; pl. 7) consists of a proximal fairly large plate and a distal long and slender postero-dorsally pointing process or spine (Stensiö's neural spine). The proximal plate is situated partially above the foremost part of the interdorsal ossification attached to the same centrum, but has no contact with any of these structures. On the lateral face of the plate we find a small laterally directed process (*pr. l. d*, fig. 43), the base of which has its greatest extension in a dorso-ventral direction.

If we pass backwards or forwards from the midmost part of the abdominal region, the shape of the basidorsal ossifications gradually changes in the way shown in fig. 46. Thus the distal basidorsal processes attain their great-

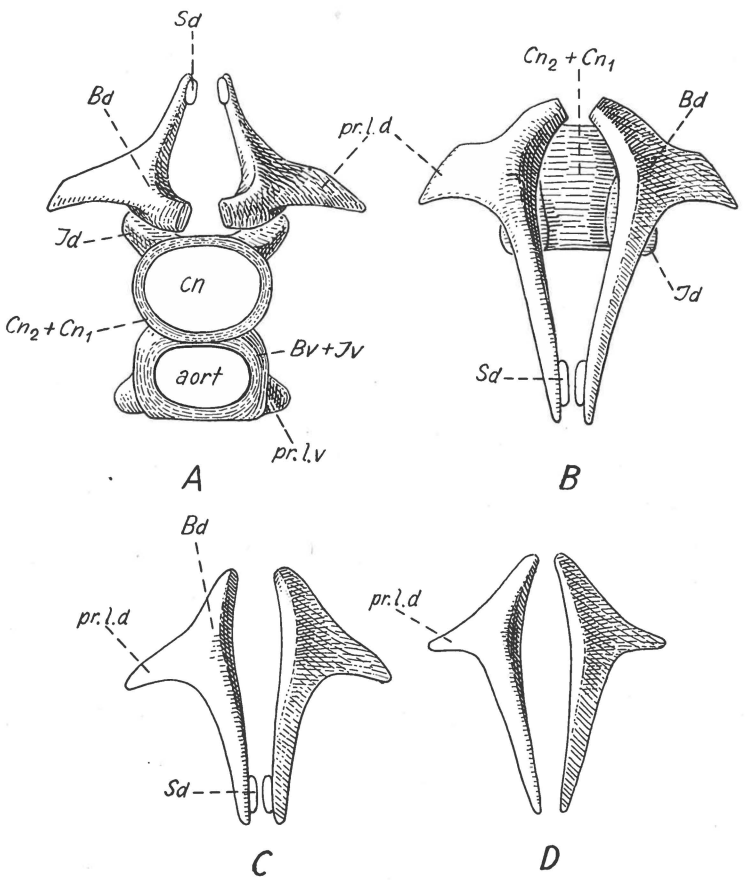


Fig. 42. *Australosomus kochi* (Stensiö). Certain ossifications of the foremost part of the vertebral column. Mainly based on the complete grinding series. C. 11×.

A and B, foremost ossifications of the vertebral column in anterior and dorsal view respectively. C, basidorsals and supradorsals of second metamere behind the head in dorsal view. D, basidorsals of third metamere behind the head in dorsal view.
aort, aorta canal; *cn*, notochordal space. Other letters as in fig. 41.

est length in the area a little behind the middle of the region and decrease slowly in length with increasing distance from this area. In the most anterior part of the abdominal region the gradual shortening of the basidorsal processes towards the head is accompanied by a gradual increase in thickness, and at the same time the lateral processes on the proximal plates become gradually more prominent, to attain a most remarkable size in the foremost three or four metameres of the region (*pr. l. d*, figs. 41, 42, 46). An interpretation of these processes will be attempted below (p. 143).

Each of the small paired interdorsal ossifications in the abdominal region (*Id*, figs. 41–43, 46; pl. 7) rests upon, and is firmly connected with, their centrum. As already mentioned, they are separated by a narrow interspace from the proximal plate of the basidorsal ossification in front; however, as

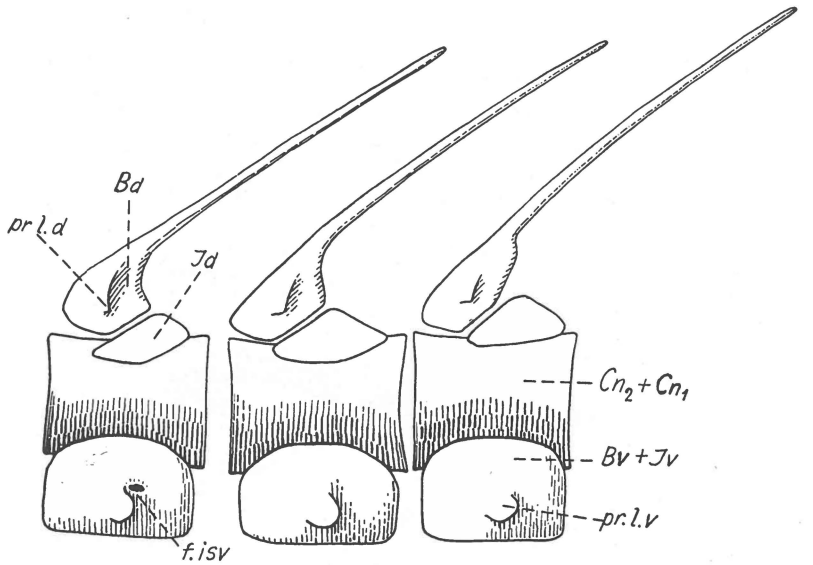


Fig. 43. *Australosomus kochi* (Stensiö). Part of the vertebral column from the posterior part of the abdominal region. Mainly based upon specimen no 404. C. 11×. Lettering as in fig. 41.

the opposite faces of the inter- and basidorsal ossifications of each vertebral segment are devoid of perichondral bone, it is not quite impossible that the interspace was filled up with cartilage in the living animal, and very probably this cartilage was pierced by canals for the roots of the spinal nerve.

Medially to the distal end of the distal processes of each of the basidorsal ossifications of the two foremost metameres we find a quite small supradorsal ossification (*Sd*, figs. 41–42), which is ellipsoid in shape with its long axis directed almost longitudinally.

The ventral arcual ossifications in the abdominal region (*Bv* + *Iv*, figs. 41, 42, 43, 46; pl. 7) are fairly large unpaired elements, each of which is situated ventrally to, and is firmly connected with, the centrum to which it belongs. The most anterior of the ventral arcual ossifications forms the roof, the lateral walls, and the floor of a wide longitudinal canal (*aort*, fig. 42 A), which lodged the dorsal aorta and may best be described as a somewhat dorso-ventrally flattened ring. The lateral mainly vertically placed walls are fairly massive, while the floor is somewhat thinnèr and the roof extremely thin, especially in its median part. Each of the lateral walls has, on its lateral face, a fairly prominent process (*pr. l. v*, fig. 42 A), with which the ventral (pleural) rib articulated, and which accordingly corresponds to the similarly situated ridge in *Pteronisculus* (E. Nielsen 1942, pp. 213–214, figs. 48, 49) and *Ospia* (Stensiö 1932, p. 262, fig. 85). The other ventral arcual ossifications in the abdominal region differ from the foremost one mainly in lacking the floor of the aorta canal, and thus throughout the greater part of the abdominal region the dorsal aorta was not situated in a closed canal but in

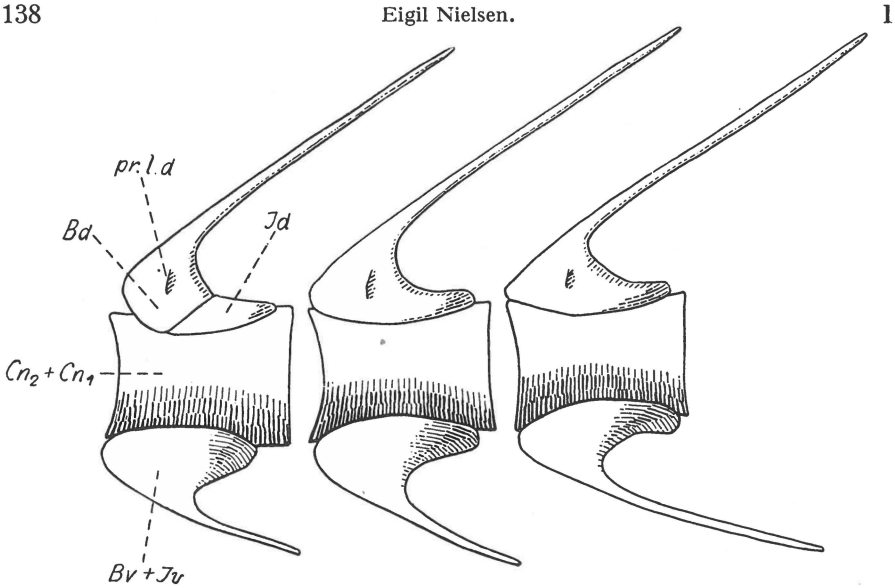


Fig. 44. *Australosomus kochi* (Stensiö). Part of vertebral column from the anterior part of the caudal region. Mainly based upon specimen no. 404. C. 11. ×
Lettering as in fig. 41.

a ventrally open groove. It can be stated with certainty that this groove was not closed by cartilage ventrally, the perichondral lining of its ossified walls being complete. *Australosomus kochi* differs in this respect from *Pteronisculus* (E. Nielsen 1942, pp. 211–220), in which the ventral arcuals probably form a complete aorta canal extending through the whole, or almost the whole, length of the abdominal region. The lateral wall of most, if not all, of the ventral arcual ossifications is pierced by a narrow transversely running canal (*f. isv*, figs. 41, 43) situated just dorsally or posteriorly to the process with which the rib articulated. The canal undoubtedly lodged intersegmental vessels, and thus bears evidence of the compound nature of the ventral arcuals.

As already mentioned, the basidorsal and interdorsal ossifications in the caudal region are independent farthest anteriorly as well as in the area below the middle third of the base of the dorsal fin, while elsewhere in the region these ossifications appear as compound structures, each basidorsal having fused with the interdorsal following next behind. Anteriorly to the body axis of the caudal fin the independent basidorsal ossifications (*Bd*, figs. 44, 46; pl. 6) as well as the basidorsal components of the compound dorsal arcual ossifications (*Bd* + *Id*, figs. 44, 45; pls. 6, 7) are shaped rather much as in the abdominal region, each consisting of a proximal plate and a distal postero-dorsally pointing slender process or spine. As shown in fig. 46, the distal spines decrease in length in a caudal direction, as is also the case in the posterior part of the abdominal region. On the lateral face of the foremost caudal basidorsal ossifications we find a small process corresponding

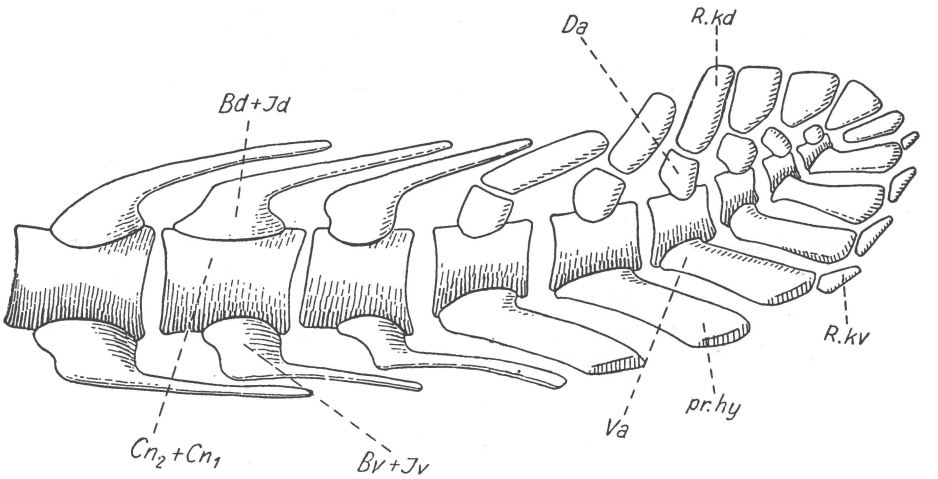


Fig. 45. *Australosomus kochi* (Stensiö). Hindmost part of vertebral column and radial ossifications of caudal fin. Mainly based upon specimen no. 404. C. 11×.

Bd + *Id*, fused basi- and interdorsal; *Bv* + *Iv*, fused basi- and interventral; Cn_2 + Cn_1, fused caudal and cranial centrum; *Da*, dorsal arcual ossification; *R. kd*, epichordal radial ossification; *R. kv*, hypochordal radial ossification; *Va*, arcual division of hypochordal ossification in body axis of caudal fin; *pr. hy*, hypural process.

to the lateral basidorsal processes in the abdominal region. In the anterior part of the caudal region the dorsal arcual elements are paired, however, posterior to a point somewhere beneath the posterior third of the base of the dorsal fin the dorsal arcuals are unpaired, the distal spines of each pair of arcuals having fused. The compound dorsal arcuals (*Da*, figs. 45, 46) in the body axis of the caudal fin are represented by some very small unpaired ossifications, distally to each of which we find a solid rod-like radial ossification (*R. kd*, figs. 45, 46; pl. 6).

The independent interdorsal ossifications (*Id*, fig. 44) in the most anterior part of the caudal region are shaped like the interdorsal ossifications in the abdominal region, while the independent interdorsal ossifications below the dorsal fin (*Id*, fig. 46, pl. 6) are smaller and more square in lateral aspect. In the compound dorsal arcuals in the caudal region the interdorsal component comprises the postero-ventral part and, as far as can be seen, decreases gradually in size towards the posterior end of the vertebral column (fig. 46).

As pointed out by Stensiö (1932, p. 176, fig. 55), the ventral, if not both the roots of the spinal nerve, passed outward through a marked notch in the posterior margin of the compound dorsal arcuals.

In that part of the caudal region in which the cranial and the caudal centra have not fused the basiventral (*Bv*, fig. 46, pl. 6) and interventral (*Iv*, fig. 46, pl. 6) ossifications are independent, as already described by Stensiö (1932, p. 175, fig. 55). Elsewhere the ventral arcual ossifications in the caudal region (*Bv* + *Iv*, fig. 45) are compound, each consisting of a basiventral fused with the interventral of the metamere nearest behind.

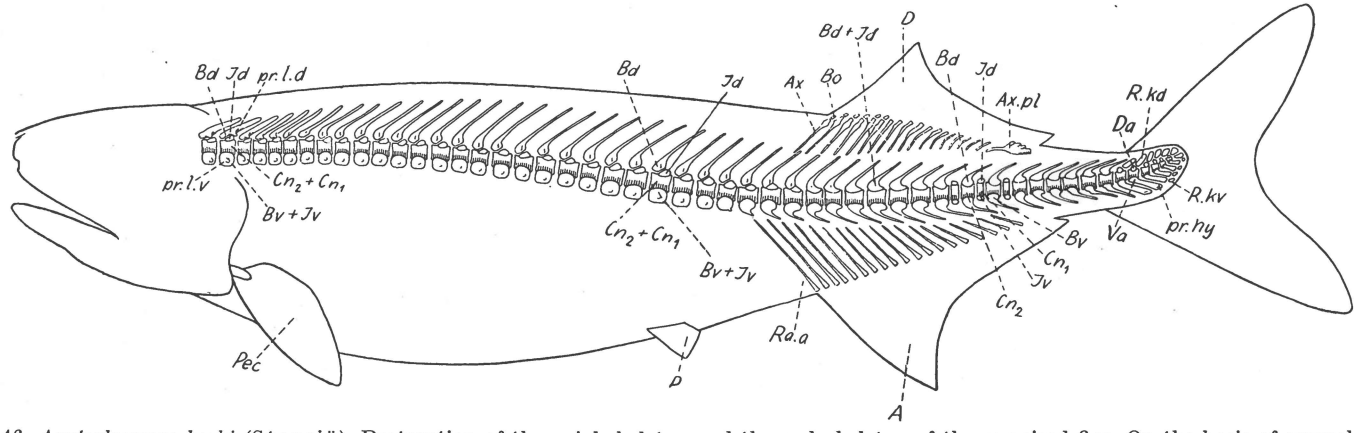


Fig. 46. *Australosomus kochi* (Stensiö). Restoration of the axial skeleton and the endoskeleton of the unpaired fins. On the basis of several specimens.

A, anal fin; *Ax*, element in the proximal series of ossifications in endoskeleton of dorsal fin; *Ax. pl*, compound posterior element in the proximal series of ossifications in endoskeleton of dorsal fin; *Bd*, basidorsal; *Bd+Id*, fused basi- and interdorsal; *Bo*, element in the distal series of ossifications in endoskeleton of dorsal fin; *Bv*, basiventral; *Bv + Iv*, fused basi- and interventral; Cn_1, cranial centrum; Cn_2, caudal centrum; $Cn_2 + Cn_1$, fused caudal and cranial centrum; *D*, dorsal fin; *Da*, dorsal arcual ossification; *Id*, interdorsal; *Iv*, interventral; *P*, pelvic fin; *Pec*, pectoral fin; *Ra. a*, element in the single series of ossifications in endoskeleton of anal fin; *R. kd*, epichordal radial ossification in endoskeleton of caudal fin; *R. kv*, hypochordal radial ossification in endoskeleton of caudal fin; *Va*, arcual division of hypochordal ossification in body axis of caudal fin; *pr. hy*, hypural process; *pr. l. d.*, lateral basidorsal process; *pr. l. v*, lateral process from the fused basi- and interventral.

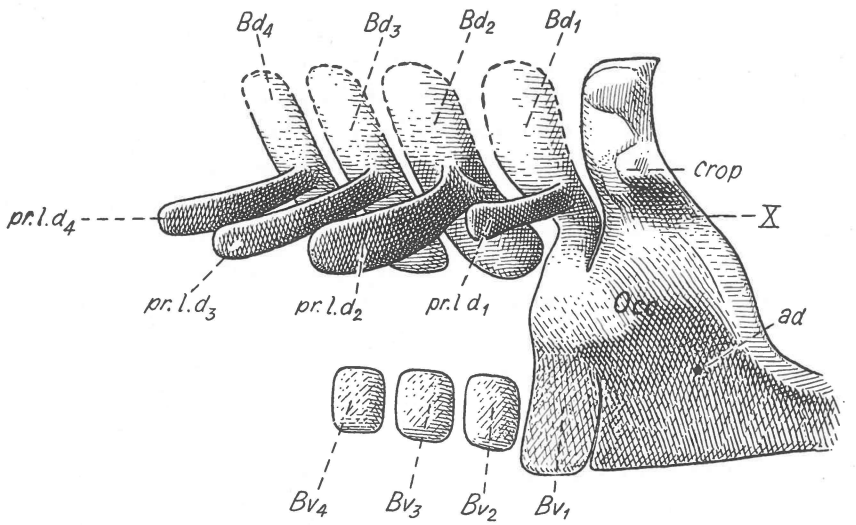


Fig. 47. *Boreosomus piveteaui* Nielsen. Posterior part of neural endocranium and anterior part of vertebral column in lateral view. Based on a grinding series (cf. p. 142). 7–8×. Bd_{1-4}, basidorsals; Bv_{1-4}, basiventrals; *Occ*, occipital region of neural endocranium; *ad*, canal for an artery; *crop*, processus cranio-spinalis; *pr. l.* d_{1-4}, lateral basidorsal processes; *X*, place of exit for the nervus vagus.

Each of the compound ventral arcual ossifications anterior to the body axis of the caudal fin consists, in the caudal region, of a proximal expanded division and a distal postero-ventrally pointing slender process or spine. In the foremost part of the region the distal spine is very short, but it increases rapidly in length backward through the region, as shown in fig. 46.

In the anterior part of the caudal region the ventral arcual ossifications form the lateral walls and probably also the roof of a ventrally open aorta groove. More posteriorly the distal spines of each ventral pair of arcual ossifications fuse, so that here the ossifications are pierced by a longitudinal canal, the dorsal part of which lodged the dorsal aorta and the ventral part probably the caudal vein.

In the body axis of the caudal fin the ventral arcuals are unpaired, each consisting of a quite small proximal division (*Va*, figs. 45, 46; pls. 6, 7) corresponding to the proximal parts of the compound arcual pairs in the anterior part of the caudal region, and a distal very thick hypural process (*pr. hy*, figs. 45, 46; pls. 6, 7), the shape of which changes gradually along the body axis of the fin, as shown in the figures. Distally to the posterior hypural processes we find some very small ossifications (*R. kv*, figs. 45, 46), which represent the hypochordal radial skeleton of the caudal fin.

In the type-specimen of *Australosomus kochi*, Stensiö (1932, pp. 176–177) found remnants of ossified ribs, and similar remnants can be observed in several specimens in the fresh collections; however, in all the specimens they are too poorly preserved to permit a closer investigation.

Discussion. – One of the most peculiar features in the now well-known axial skeleton of *Australosomus kochi* is the presence of well ossified centra, according to Stensiö of chordal origin. Similar centra are also found in the other Greenlandic species of *Australosomus* (pp. 166, 170), in *Australosomus merlei* (Piveteau 1934, pp. 33–35), and in *Arctosomus* (Berg 1941, p. 471), *Pholidopleurus* and *Macroaethes* (Wade 1935, pp. 70, 74–75, figs. 39–40). Wade's brief description of the axial skeleton in the latter genus is accompanied by two figures of parts of the vertebral column, but like many of his other figures, these, also, are so sketchy that they are absolutely of no value for comparative or other purposes.

The presence of chordal centra gives the *Pholidopleuridae* a most isolated position within the Teleostomian fishes, although the fibrous sheath of the notochord in the Acipenserids is invaded by mesoblast cells (cf. Goodrich 1930, p. 13; Stensiö 1932, p. 176). Hence one might ask whether the chordal origin of the centra in *Australosomus* is proved beyond doubt, and we shall therefore here briefly consider Stensiö's arguments regarding this question (Stensiö 1932, pp. 174–177).

According to Stensiö the arcual elements differ decidedly from the centra in the structure of their bone tissue, moreover they are fairly well bounded off from their centra, they do not cover them laterally, and they are not, or only along short stretches, in contact with each other dorsally and ventrally to the centra.

There can be no doubt that of these points the first-mentioned one is by far the most important, but the difference in structure does not necessarily imply that the formation of the centra took place within the chordal sheath. Regarding the other points, it seems to me that the perichordal centra and their arcuals in many recent Teleosts are also fairly well separated and quite often the arcuals in recent Teleostomes leave free a large part of the centra (Goodrich 1930, figs. 36–40, 49–50). I prefer, therefore, to take a somewhat more cautious view than Stensiö and, until further investigations of the development of the structure of the vertebral centra in the Mesozoic Ganoids have been carried out, to regard the centra of *Australosomus* merely as probably of chordal origin.

Another peculiar feature in the structure of the axial skeleton of *Australosomus kochi* is the appearance of strong lateral processes on the dorsal arcual ossification just behind the head. Such processes have not been described in other Pholidopleurids, however, future investigations will most probably prove their existence also in other genera of this family as well as in many other fossil Ganoids, which supposition is based on the fact that similar processes also exist in another of the few primitive Ganoids which I have had the opportunity to investigate, viz. *Boreosomus*.

In *Boreosomus* the now completed grinding series (cf. E. Nielsen 1942, p. 281) shows, in addition to the cranial structures, the ossifications of the

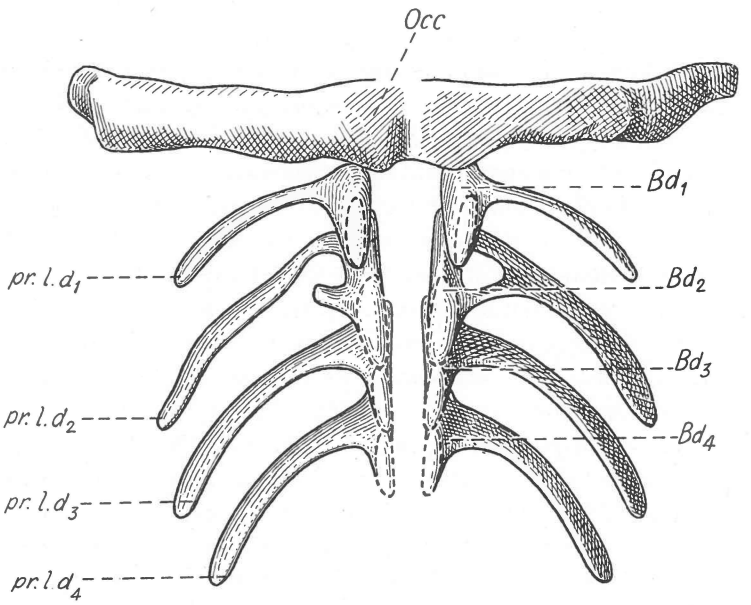


Fig. 48. *Boreosomus piveteaui* Nielsen. Posterior part of neural endocranium and anterior part of vertebral column in dorsal view. Based on a grinding series (cf.p. 142). 7–8×. Lettering as in fig. 47.

foremost part of the vertebral column, viz. the dorsal and ventral arcual ossifications of the foremost four metameres. The dorsal arcual ossifications (Bd_{1-4}, figs. 46–47) are probably basidorsals, and the ventral ones (Bv_{1-4}, figs. 47–48) either basiventrals or basiventrals plus interventrals. The shape and position of the arcual ossifications are shown in figs. 47 and 48, and, as is seen from the former of these figures, the foremost dorsal and ventral paired arcual ossifications are to some extent fused with the most posterior part of the neural endocranium. Each of the dorsal arcual ossifications is equipped with a very long and slender, backward-curving lateral spine (*pr. l. d*, figs. 47, 48), which is, no doubt, comparable to the lateral process found in *Australosomus*.

A comparison with recent Teleostomians shows that the lateral basidorsal processes cannot be homologous with any of the different types of ribs found in this group. At the outset the ventral (pleural) ribs present in the Teleostomians are, of course, out of the question, *Australosomus* possessing ventral ribs attached to the ventral arcual ossifications in the normal way. (As mentioned by Goodrich (1930, p. 73, foot-note) it is quite possible that the pleural ribs of the Teleostomians are homologous with the dorsal ribs of the Selachians, in which case the dorsal ribs in the Teleostomians must represent a new set of extensions in the horizontal septum. Since, however, this question has not yet been settled, I employ the terms ventral and dorsal ribs in the usual way). The dorsal ribs present in most *Teleostei*

are attached by ligaments either to the sides of the centra or to the ventral ribs (Goodrich 1930, p. 73) and are thus situated far more ventrally than the lateral basidorsal processes in *Australosomus* and *Boreosomus*. In many Teleosts, however, we find slender rib-like ossifications embedded in the muscles dorsally to the horizontal septum. These ossifications extend either from the centra (epicentrals) or from the neural arches (epineurals) and are, at any rate in the *Salmonidae*, preformed in cartilage (Goodrich 1930, p. 75). Personally I think it most likely that the lateral basidorsal processes should be regarded as homologous with the epineural ossifications in the *Teleostei*, though the epineurals are not continuous with the neural arches.

The arcual elements in *Australosomus kochi* show a development fairly similar to that of the arcual elements in *Pteronisculus* (E. Nielsen 1942, pp. 211–220) and *Pygopterus* (Aldinger 1937, pp. 254–261), the most significant differences being the absence, in *Australosomus*, of supradorsalia and infrahaemalia, and in any case, as regards the arcual elements *Australosomus* shows much better agreement with typical *Palaeonisciformes* than with *Saurichthys*, the very peculiar axial skeleton of which has been described by Stensiö (1925, pp. 116–120, fig. 27; pl. 3, fig. 3; pl. 14, figs. 4, 5).

Endoskeleton of the shoulder-girdle.

Many specimens contain remnants of ossifications belonging to the endoskeleton of the shoulder-girdle, but these remnants are in most cases so badly crushed that they are quite unidentifiable. In a few specimens, however, they are better preserved, and on the basis of these it is possible to make a restoration which, though probably not accurate in all details, still gives the main features of the structures in question.

In the investigated specimens each of the two halves of the endoskeleton of the shoulder-girdle (figs. 49–51) is thoroughly ossified in one piece, and consists of cancellate endochondral bone, which is completely, or almost completely, lined with perichondral bone-layers. It is an open question whether the process of ossification started from one centrum or more centra, the smallest specimens being always too badly preserved for a closer investigation.

The endoskeletal ossification may be roughly described as a very steeply placed plate, which is slightly S-bent in a dorso-ventral direction, and from the medial face of which a laterally flattened high and blunt process (*msc*, figs. 49–50) issues in a dorsal direction.

For descriptive reasons we may regard the plate as consisting of a broad ventral division below and a narrow dorsal division above the almost horizontal line of issue of the flattened vertical process.

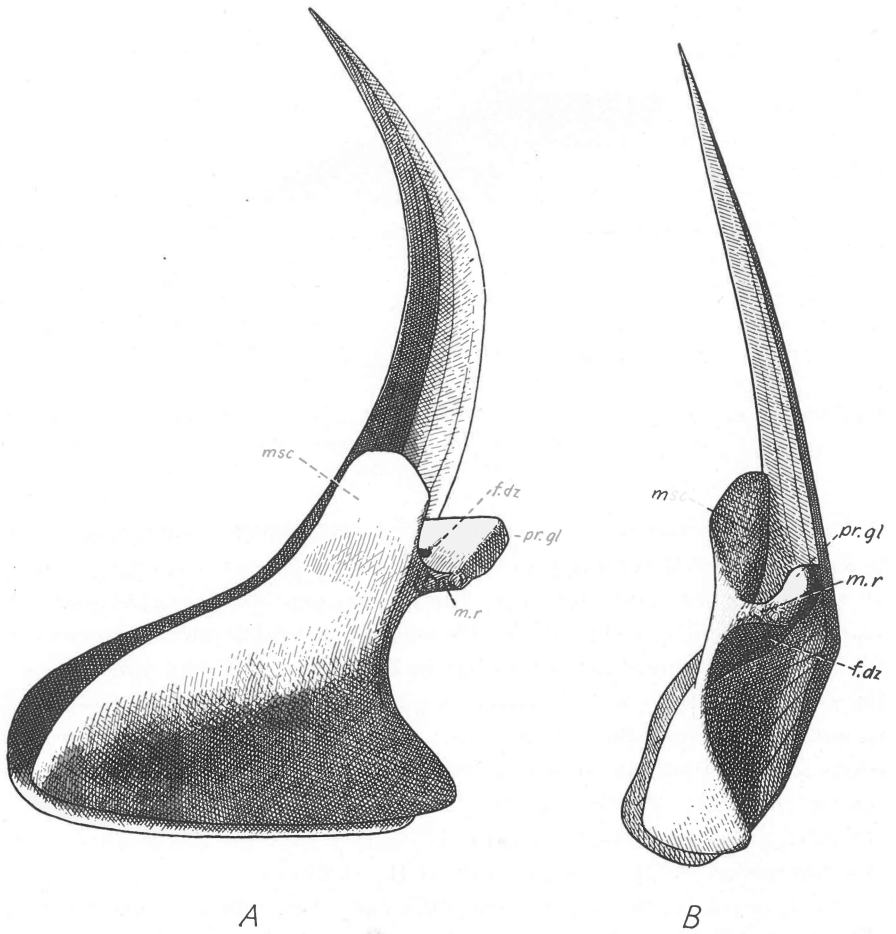


Fig. 49. *Australosomus kochi* (Stensiö). Right cleithrum and endoskeletal shoulder-girdle ossification in (A) medial and (B) posterior view. Based mainly on specimen no. 407. 8-9 ×. *f. dz*, canal for diazonal nerves; *m. r*, margo radialis; *pr. gl*, processus glenoidalis; *msc*, incomplete mesocoracoid arch.

The ventral division is a very thin, mainly vertical, plate, which is slightly bent in such a way that its lateral face is concave in a dorso-ventral direction and its medial face correspondingly convex. The plate, which is broadest in its most ventral part and narrows gradually in a dorsal direction, as seen in fig. 50, has three free margins, viz. a ventral, slightly convex, an antero-dorsal, somewhat more strongly convex, and a posterior or postero-dorsal concave one. Except farthest posteriorly the ventral margin is in contact with the most ventral part of the inner face of the cleithrum, while the antero-dorsal margin is in contact with the postero-medially directed face of the internal cleithral lamina.

The dorsal division of the endoskeletal ossification is much thicker than

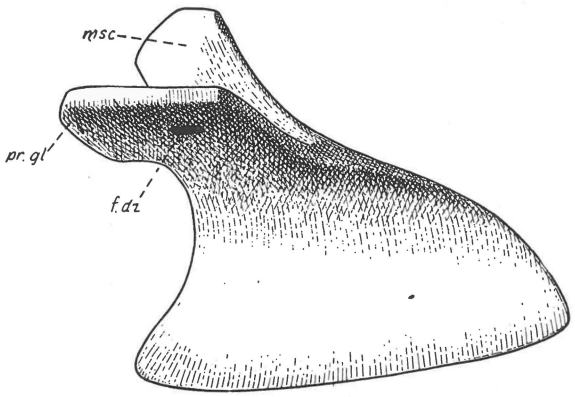


Fig. 50. *Australosomus kochi* (Stensiö). Right endoskeletal shoulder-girdle ossification in lateral view. Based mainly on specimen no. 407. 8-9×.
Lettering as in fig. 49.

the ventral one and may be described as a plate which is obliquely placed in such a way that its inner face is directed mainly dorso-medially and its outer face mainly ventro-laterally. The plate is bent dorso-ventrally in such a way that its dorso-medial face is concave and its ventro-lateral face convex. The plate, which increases somewhat in breadth in a dorsal direction, has three free margins, viz. a posterior or postero-ventro-medial, a dorsal, and an anterior or antero-dorso-lateral one. Of these margins the first-mentioned one is convex, while the others are fairly straight. The anterior margin rests against the postero-medial face of the internal cleithral lamina, while the anterior part of the dorsal margin is in contact with the medial face of the external lamina of the ascending part of the cleithrum.

On the most ventral, fairly horizontal, part of the posterior margin there are some small depressions which indicate the places of articulation for the radials of the pectoral fin. Thus this part of the posterior margin (*m. r*, fig. 49) is the glenoid face or the margo radialis, while the postero-dorsal corner of the dorsal division (*pr. gl*, figs. 49–51) must be regarded as a strong, blunt processus glenoidalis. Just anteriorly to the margo radialis the plate is pierced by a wide vertical canal (*f. dz*, figs. 49–50) for diazonal nerves. In transverse sections the canal is oval with its long axis extending rostro-caudally. Possibly, also, the ventral division of the plate was pierced by a canal for diazonal nerves, as in *Pteronisculus* (E. Nielsen 1942, p. 226, figs. 51, 52); however, this could not be determined with certainty.

The laterally compressed vertical process, which issues from the internal face of the S-bent plate just described, is somewhat higher than broad and may best be described as a vertically placed, rather thin plate which is bounded by almost straight anterior and posterior margins and a somewhat convex dorsal margin. The anterior margin rests against the postero-medially directed face of the internal cleithral lamina. The process should without

doubt be regarded as a mesocoracoid process corresponding to the ventral part of the complete mesocoracoid arch present for instance in *Pteronisculus* (E. Nielsen 1942, p. 223, figs. 51, 53 A). It can be stated with certainty that the perichondral lining of the process is complete, and accordingly the process was not prolonged by cartilage in the living animal so as to form a complete arch.

The space between the mesocoracoid process and the dorsal division of the main plate of the endoskeletal structure lodged the dorsal musculature of the pectoral fin, while the ventral fin-muscles were evidently situated in the anteriorly closed space between the ventral division of the main plate and the cleithrum.

Discussion. – In *Australosomus simplex* the endoskeletal shoulder-girdle, as far as can be seen, was developed in the same way as in *Australosomus kochi*. In other Pholidopleurids nothing at all is known of this structure. The endoskeletal shoulder-girdle in *Australosomus* agrees with that in typical *Palaeonisciformes* such as *Pteronisculus*, *Palaeoniscus*, and *Amblypterus* (cf. E. Nielsen 1942, pp. 227–229) in possessing a fairly horizontal margo radialis, which implies that the pectoral fin was held horizontally or nearly so. Broadly speaking, there is also a certain similarity in general shape between the well-known shoulder-girdle ossification in *Pteronisculus* and the more superficially investigated shoulder-girdle in *Australosomus*. In both these genera the scapulo-coracoid plate is S-bent, the processus glenoidalis is stout, and anteriorly to the margo radialis the plate is pierced by a wide canal for diazonal nerves. Moreover the mesocoracoid process in *Australosomus* corresponds to the ventral part of the mesocoracoid arch in *Pteronisculus*, and might well be regarded as the result of a reduction of an arch of this type. Altogether it seems quite possible that the endoskeleton of the shoulder-girdle in *Australosomus* has developed from that in typical *Palaeonisciformes*. At present it is impossible to make comparisons between *Australosomus* and *Saurichthys* as regards the endoskeleton of their shoulder-girdles, since almost nothing is known of that structure in the latter genus (cf. Stensiö 1925, p. 121).

Dermal bones of the shoulder-girdle.

In 1944 Jarvik published an instructive review of the dermal shoulder-girdle in the Teleostomians, pointing out, among other things, that the dorsal postcleithrum in the Actinopterygians is probably homologous with the anocleithrum in the Crossopterygians, a bone situated between and separating the supracleithrum and the cleithrum. Accepting this homologisation, I think it most consistent to use the term anocleithrum in the following description, and for the reasons given by Jarvik (1944, p. 4, foot-note) I

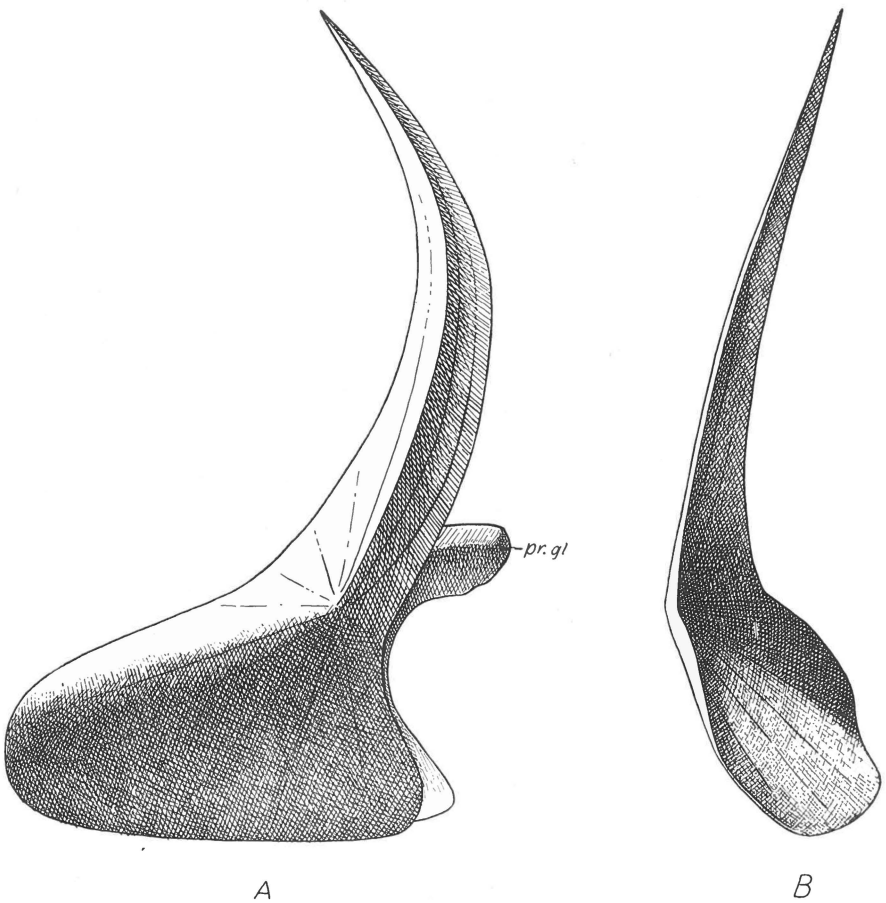


Fig. 51. *Australosomus kochi* (Stensiö). Cleithrum and endoskeletal shoulder-girdle ossification. Based mainly on specimen no. 407. 8-9×.

A, left cleithrum and endoskeletal shoulder-girdle ossification in lateral view. *B*, left cleithrum in posterior view.

Lettering as in fig. 49.

also adopt the term posttemporal instead of the term suprascapular used in the first part (1942) of the present work.

The series of dermal bones of the shoulder-girdle in *Australosomus kochi* contains a posttemporal, a supracleithrum, an anocleithrum, a cleithrum, and a clavicle.

Posttemporal. – The posttemporal (*Pt*, fig. 25; pl. 7, fig. 2) is a four-sided bone with an antero-lateral, a medial, a posterior, and a lateral margin. The antero-lateral margin, which is overlapped by the extrascapular, is slightly convex, the median and the posterior margins are slightly concave, and the short lateral margin is straight. As far as I can see, the bone is not pierced by the main lateral line, thus in this respect it agrees with the post-

temporal in *Lepidosteus* (Hammarberg 1937, p. 319; Jarvik 1944, p. 5). The centre of radiation is situated very laterally, as shown in fig. 25.

Supracleithrum. – The supracleithrum (*Scl*, fig. 25; pl. 1, fig. 3; pl. 4, figs. 1, 2) is a roughly triangular bone with a short antero-dorsal, a long postero-dorsal, and a long antero-ventral margin. The dorsal angle of the triangle is much rounded, the antero-dorsal as well as the dorsal part of the postero-dorsal margin being rather strongly convex. The foremost part of the bone is overlapped by the posttemporal, and the antero-ventral margin is covered by the posterior or postero-dorsal margin of the operculum. The centre of radiation lies rather near the anterior corner of the bone and is pierced by the main lateral line, which passes through the bone, as described later (p. 162).

Anocleithrum. – The anocleithrum (*Pcl*, fig. 25) is a small narrow bone bounded by an anterior and a posterior convex margin and pointed dorsally and ventrally. The bone is situated behind, and is slightly overlapped by, the most ventral part of the supracleithrum and the most dorsal part of the cleithrum, but does not, as in the Crossopterygians, completely separate these two bones. The centre of radiation has not been localised.

Cleithrum. – The cleithrum (figs. 49, 51; *Cl*, fig. 25; pl. 1, fig. 3; pl. 2, figs. 1, 2; pl. 3, fig. 1; pl. 4, fig. 2; pl. 5, fig. 1) is a very high bone, which may for descriptive reasons be regarded as consisting of three divisions, viz. an anterior high and narrow, almost crescent-shaped division, which forms the posterior boundary of the branchial cavity, a postero-dorsal, fairly vertical high and narrow division lying on a level with the lateral surface of the trunk, and a broad ventral obliquely placed division, the external face of which is directed ventro-laterally.

The anterior inwardly curved cleithral division, the internal cleithral lamina, meets with the postero-dorsal division in a sharp edge, while its transition to the ventral division has the shape of a rounded ridge. The shape of the different cleithral divisions is seen in the figures, which also show the position of the centre of radiation at the point where the three divisions meet.

The endoskeletal ossification of the shoulder-girdle is in contact with the inner face of the cleithrum in the following way. Against the ventral cleithral division rests the ventral margin of the ventral division of the scapulo-coracoid plate, against the internal cleithral lamina rests the antero-dorsal margin of the same division of the scapulo-coracoid plate, the anterior (antero-dorsal) margin of the mesocoracoid process, and the anterior (antero-dorsal) margin of the dorsal division of the scapulo-coracoid plate, and against the postero-dorsal division of the cleithrum rests the anterior part of the dorsal margin of the dorsal division of the scapulo-coracoid plate.

The right and the left cleithrum do not join in the ventral mid-line, but are separated by a rather small interspace.

Clavicle. – According to the diagnosis given by Stensiö (1932, pp. 165–166), the clavicle is absent in the *Pholidopleuridae*. The present investigation shows, however, that this bone is found in *Australosomus kochi* (– as well as in *Australosomus simplex* (p. 166)).

In *Australosomus kochi* the clavicle (*Cla*, fig. 25) is never well preserved, but as far as could be made out, it is a rather short and narrow element, consisting of an internal lamina, which forms an anterior continuation of the internal cleithral lamina, and an external plate, which forms the anterior continuation of the ventral cleithral division. Probably the right and left clavicles met in the ventral mid-line, however, without being very firmly connected. The centre of radiation could not be localised with certainty, but was probably situated on the line of junction between the internal lamina and the external plate of the bone.

Discussion. – The dermal shoulder-girdle described here and, in so far they are known, the dermal shoulder-girdles in other Pholidopleurids (Piveteau 1934, p. 35, fig. 23; Wade 1935, pp. 68–69, 76, figs. 32, 32, 38) do not differ from the dermal shoulder-girdle of the typical *Palaeonisciformes* in any very important respects. The small size or the complete absence of the clavicle in the Pholidopleurids is another of the many features in which this family shows a development towards the higher Ganoids, and the peculiar course of the main lateral line laterally to the posttemporal observed in *Australosomus kochi* and *Australosomus simplex* is probably likewise a specialisation in the same direction.

In *Saurichthys*, according to the investigations of Stensiö (1925, pp. 121–122, figs. 20–21), the dermal shoulder-girdle contains only three bones, viz. the posttemporal, the supracleithrum, and the cleithrum. The ventral division of the cleithrum extends very far forward between the mandibles, and probably its foremost part corresponds to the clavicle in the *Palaeonisciformes* and Acipenserids. This fusing between the cleithrum and the clavicle must be a very late specialisation within the genus *Saurichthys*, for in a probably new species of *Saurichthys* from East Greenland I have observed an independent clavicle situated anterior to the ventral division of the cleithrum. This independent clavicle, however, is not reduced as compared with that in typical *Palaeonisciformes*, as is the clavicle in the Pholidopleurids, so here, again, we are confronted with a structure in *Saurichthys* which is less specialised than, or specialised in quite a different way from, the corresponding one in *Australosomus*.

Pectoral fin.

The endoskeleton of the pectoral fin is ossified in a great many specimens, but the very small radial ossifications are almost always poorly preserved, at any rate they could not be satisfactorily exposed by direct preparation. The following remarks are almost exclusively based on specimen no. 407,

the pectoral radial ossifications of which were investigated by preparing a few transverse sections by means of grinding. Only a single series of radial ossifications was observed, and as far as I could make out, this series contains four or five elements. The foremost ossification is very short and relatively massive, while the other ones are somewhat longer and rather strongly compressed from side to side. The radial elements, which, no doubt, correspond to the proximal radial elements in *Pteronisculus* (E. Nielsen 1942, pp. 234–235) and *Boreosomus* (ibid., pp. 362–364), together form a very small and comparatively thick horizontally placed plate, and probably the possibilities for independent movements of the individual elements in the plate were extremely small, as in *Pteronisculus* (ibid., p. 235). The radials are parallel, and there is no trace of any »metapterygial« axis, as is the case for instance in *Boreosomus*, *Amia*, *Amblypterus*, and *Acipenser* (cf. E. Nielsen 1942, p. 365).

The radials supported a very small fin-lobe, the squamation of which is unknown.

The pectoral fin (*Pec*, fig. 46; pl. 2, figs. 1, 2; pl. 5, fig. 1), which was held horizontally, contains about 18 lepidotrichia in fan-shaped arrangement. The lepidotrichia decrease gradually in length from the foremost to the hindmost one in the way shown in fig. 46. The foremost lepidotrich is unjointed and unbranched, while the others are jointed farthest distally, where they also bifurcate once or twice. The unjointed part of each of the foremost five lepidotrichia is very broad and overlaps to a considerable extent the lateral face of the lepidotrich following nearest behind. The more posterior lepidotrichia grow gradually more slender, and furthermore the breadth of the unjointed part of each of these lepidotrichia decreases markedly from the distal towards the proximal end. In this part of the fin overlapping between successive lepidotrichia takes only place farthest proximally, while the more distal and by far the longer part of each lepidotrich is separated from its neighbours by an interspace, the breadth of which in the living fish depends, of course, on the mutual movements of the lepidotrichia within the fin. All the lepidotrichia lack ganoine and are quite smooth. There are no fulcra on the anterior margin of the fin.

Discussion. – Except for the Greenlandic species of *Australosomus*, the endoskeleton of the pectoral fin has only been observed in one other Pholidopleurid, viz. *Macroaethes brookvalei* (Wade 1935, p. 77, fig. 41). However, no comparison can be made on the basis of Wade's brief description and his quite unintelligible figure. The exoskeleton of the pectoral fin is better known, though the descriptions hitherto published are far from exhaustive. In *Macroaethes brookvalei* (Wade 1935, p. 76) and *Australosomus merlei* (Piveteau 1934, p. 35) the number of lepidotrichia is stated to be small, and in *Arctosomus* (Berg 1941, p. 470) it is reported to be no less than nine. In other structural details the lepidotrichia seem to agree very well with *Australosomus kochi*.

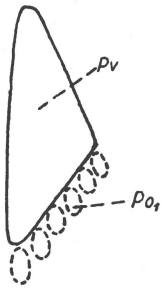


Fig. 52. *Australosomus kochi* (Stensiö). Attempted sketch of pelvic plate and endoskeleton of pelvic fin. Based partly on the type specimen and partly on specimen no. 569. C. 3×. Po_1, radial ossification; *Pv*, pelvic plate.

Pelvic plate and pelvic fin.

In some specimens we find remnants of the ossified pelvic plate and in a very few cases also of small ossified elements belonging to the radial skeleton of the pelvic fin. The ossifications, however, which consist of a cancellate endochondral mass partly lined with perichondral bone, are always poorly preserved, and accordingly the following description, which is based mainly on specimen no. 569 and the type specimen, is by no means exhaustive.

The paired pelvic plate (*Pv*, fig. 52) is a thin triangular plate with an antero-lateral, a medial (postero-medial), and a postero-lateral margin. Of these margins, which are all fairly straight, the postero-medial one is the longest and the postero-lateral one the shortest. As far as I could make out, the plate, the approximate outline of which is shown in fig. 52, had no antero-medial process comparable to the long antero-medial process in *Pteronisculus* (E. Nielsen 1942, pp. 238–240, 242, fig. 55) and was not pierced by foramina for diazonal nerves. The relief of the ventral face of the plate is unknown. Along the postero-lateral margin of the pelvic plate remnants of five or six radial ossifications have been observed. These ossifications (Po_1, fig. 52), which were probably capped by cartilage proximally and distally, are very short. The small pelvic fin, which was stretched out from the body as a »keel«, commences at about the 19th or 20th transverse scale-row reckoned from the posterior margin of the supracleithrum. The fin contains about thirteen lepidotrichia, of which the foremost one is very short, while the one next behind is the longest in the fin, the following ones decreasing gradually in length, as shown in fig. 46. The two foremost lepidotrichia are unjointed and unbranched, while each of the remaining ones bifurcates once in its distal third or fourth, which is also crossed by one or two articulations. There are no fulcra.

Discussion. – In *Pholidopleurus* (Wade 1935, p. 69) and *Arctosomus* (Berg 1941, p. 470) the pelvic fin seems to be completely reduced. In *Australosomus merlei* (Piveteau 1934, p. 35) and *Macroaethes* (Wade 1935, p. 76),

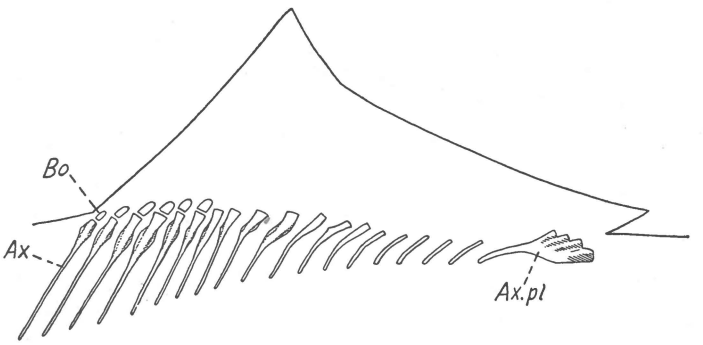


Fig. 53. *Australosomus kochi* (Stensiö). Endoskeleton of dorsal fin. Based on several specimens. C. 3×.

Ax, element in the proximal series of radial ossifications; *Ax. pl*, compound posterior element in the proximal series of radial ossifications; *Bo*, element in the distal series of radial ossifications.

however, the pelvic fin is present, and developed much as in *Australosomus kochi*. The radial endoskeleton of the pelvic fin is, if anything, better developed in *Macroaethes* than in *Australosomus kochi*, judging from the very sketchy figure given by Wade (1935, fig. 42).

Unpaired fins.

Dorsal fin. – The dorsal fin (fig. 53; *D*, fig. 46) is situated rather far back, the number of transverse scale-rows between its anterior margin and the posterior margin of the supracleithrum being about 31–34. The endoskeleton of the fin has been investigated in fairly great detail by Stensiö (1932, p. 177, fig. 56; pl. 27, fig. 2; pl. 28; pl. 34, fig. 3) and only little can be added to his description.

As pointed out by Stensiö, the radial skeleton is represented by two series of ossifications, a proximal and a distal one. The proximal series contains about 19–21 ossifications (*Ax*, *Ax. pl*, figs. 46, 53; pl. 1, fig. 3; pl. 6), the most posterior of which is compound, representing at least four radial elements. The independent proximal elements decrease gradually in length from the foremost to the hindmost one, as shown in the figures. The foremost eight ossifications are fairly straight, while the following ones are more or less sharply bent, their dorsal halves pointing more backward than their ventral ones. The distal series, in the type specimen, contains six ossifications (*Bo*, figs. 46, 53), one distally to each of the foremost six ossifications in the proximal series. The number of distal radial ossifications varies in other specimens from none to at least eight. All the distal ossifications are very short, their height being about equal to or only slightly greater than their breadth.

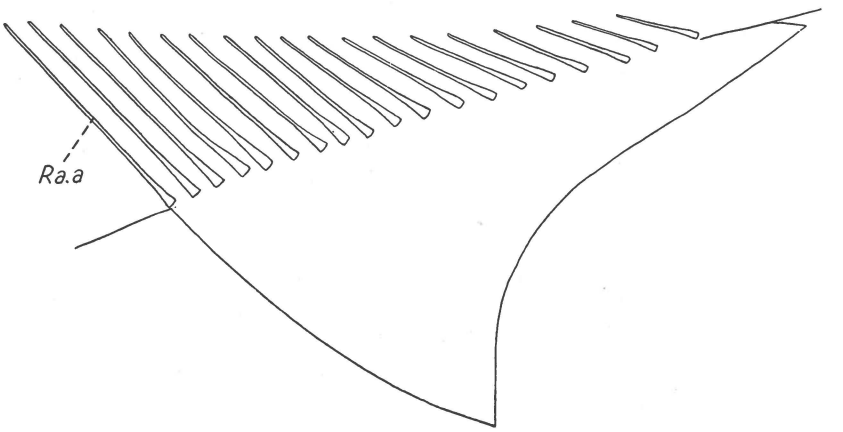


Fig. 54. *Australosomus kochi* (Stensiö). Endoskeleton of anal fin. Based on several specimens. C. 3×.
Ra. a, radial ossification.

Stensiö interprets the proximal series as an axonost series and the distal one as a baseost series; if this interpretation is correct, *Australosomus* agrees with *Pteronisculus* (E. Nielsen 1942, p. 244, fig. 50), *Pygopterus* (Aldinger 1937, p. 175, figs. 42, 47), and *Birgeria* (E. Nielsen 1942, p. 244; the present paper p. 274, fig. 53) in possessing an axonost plate formed by fusion of the most posterior elements in the axonost series. A comparison with *Pteronisculus*, however, seems to show that the two series in *Australosomus* do not necessarily correspond to an axonost and a baseost series, *Pteronisculus* having, in addition to the axonost and the baseost series, a third more distal series, which may possibly be compared to the distal one of the two series in *Australosomus*. If this latter view is correct, the proximal series in *Australosomus* is either an axonost or a baseost series or possibly a series of fused axonosts and baseosts. At present it is hardly possible to decide the question with certainty, though I am most inclined to adopt the interpretation given by Stensiö. Judging from the axial skeleton, the number of radials in *Australosomus kochi* is more than twice the number of metameres in that part of the trunk on which the dorsal fin is situated.

The dorsal fin contains about 38–42 lepidotrichia, which, as described by Stensiö (1932, p. 178), are closely set in the anterior third of the fin, where their number is about thrice the number of their endoskeletal supports, but are situated somewhat more apart in the posterior part of the fin, where their number, however, is always greater than that of their supporting radials.

For further details regarding the dorsal fin the reader is referred to the description given by Stensiö and to the figures in the present paper.

Anal fin. – The anal fin (fig. 46 *A*, fig. 54; pl. 1, fig. 3; pl. 6) commences at about the 27th transverse scale-row counted from the posterior margin of the supracleithrum. The endoskeleton of the fin is represented by a single

series of about 19 long and slender ossifications (*Ra. a*, figs. 46, 54; pl. 1. fig. 3; pl. 6), the length of which decreases gradually in a posterior direction, The ossifications, which are somewhat expanded in their most distal parts, change gradually their direction from the foremost to the hindmost one, as shown in the figures. The ossifications, described by Stensiö (1932, p. 178) as axonosts, are probably homologous to the proximal series of ossifications in the endoskeleton of the anal fin of *Pteronisculus* (E. Nielsen 1942, pp. 246–247, fig. 56) and *Pygopterus* (Aldinger 1937, p. 178) and must accordingly be regarded either as axonosts alone or as axonosts fused with baseosts (cf. E. Nielsen 1942, p. 249). The anal fin has much the same shape, but is somewhat larger than the dorsal fin. It contains about 50 lepidotrichia, which show general agreement in arrangement, segmentation, and bifurcation with the lepidotrichia of the dorsal fin, as already pointed out by Stensiö (1932, p. 178).

Caudal fin. – The deeply cleft caudal fin is symmetrical or almost symmetrical and, as pointed out by Stensiö (1932, p. 178), of much the same type as that of the Saurichthyids and the Gadids. Its endoskeleton is described in the chapter on the axial skeleton (p. 141, fig. 45). The fin contains about 56 close-set lepidotrichia, half of which belong to the dorsal and the other half to the ventral lobe of the fin. In the ventral lobe the length of the lepidotrichia increases from the foremost, which is very short, to about the fifteenth one, whence it decreases again as far as the hindmost (uppermost) one. In the dorsal lobe the lepidotrichia likewise at first increase and subsequently decrease in length, the maximum length being attained at about the seventeenth lepidotrich reckoned from the boundary towards the ventral lobe. The 9–10 foremost lepidotrichia in the ventral lobe and the 5–6 foremost ones in the dorsal lobe are unbranched, while almost all the other lepidotrichia in the fin branch distally in the way shown in fig. 55. In the midmost part of the fin the lepidotrichia are comparatively broad. The proximal segment of each lepidotrich is especially long, and its pointed proximal end is deeply embedded in the short body axis of the fin, overlapping not only its endoskeletal support but also the most distal parts of the axial ossifications. There are no fulcra or ridge scales either on the dorsal or on the ventral lobe of the caudal fin.

Discussion. – All the Pholidopleurids so far known agree closely with each other in the structure and shape of their unpaired fins as well as in the far backward position of their dorsal and anal fins (Piveteau 1934, Wade 1935, Berg 1941). As pointed out by Stensiö (1932, p. 179), the dorsal and the anal fin are »in the main of the Palaeoniscid type, but show in their posterior parts a distinct development in the same direction as do the dorsal and anal fins of the Bobasatraniids, Perleidids, Ospiids, and *Holostei*«, while the caudal fin is of a far more specialised type, characterised by its complete, or almost complete, external symmetry, and bearing a close resemblance to

the caudal fin of the Saurichthyids and Gadids. In his chapter on the unpaired fins of *Australosomus merlei*, Piveteau, after summing up the results of Stensiö's investigations on *Australosomus kochi*, puts forward some considerations on the development of the endoskeleton of the unpaired fins of the *Palaeonisciformes*, saying as follows (Piveteau 1934, p. 37): »Dans les Paléoniscides primitifs (*Elpisopholis*), chaque rayon endosquelettique comprend deux segments: un proximal court et un distal allongé. Dans le genre triasique *Birgeria*, seuls les rayons postérieurs présentent deux ossifications, les autres n'en ont plus qu'une seule. Enfin, chez *Coccolepis*, qui est le derniere Paléoniscide connu, on n'observe, tout le long de la nageoir impaire, qu'une seule ossification. Ainsi, dans cette famille des Paléoniscidés, il y a, semble-t-il, tendance à la réduction à un seul article de chaque support endosquelettique«.

The same conclusion based on the same grounds was put forward by Stensiö already in 1921 (p. 191). However, Stensiö only refers to the conditions of the endoskeleton of the anal fin, while Piveteau evidently discusses both the endoskeleton of the dorsal and the anal fin, going on as follows (Piveteau 1934, p. 37):

»Australosomus nous parait être, à ce point de vue, au même stade que *Birgeria;* mais, dans le premier genre, la réduction se fait de l'arrière a l'avant, et de l'avant a l'arrière dans le deuxième. Dans les deux cas, nous sommes en présence d'un véritable phénomène d'orthogenèse«.

Here Piveteau's argumentation is wrong, for in both *Birgeria* (according to what was known at the time Piveteau published his paper) and *Australosomus* it is posterior elements which are lacking in the endoskeleton of the dorsal fin, while only one series of elements is known in the endoskeleton of the anal fin of *Australosomus*. Furthermore, the possible reduction in the endoskeleton of the dorsal fin of *Birgeria* took place in the proximal and in *Australosomus* in the distal series of radial elements.

Westoll in his work on the *Haplolepidae* (1944, pp. 86–88) discusses the mechanical significance of the size, shape, and position of the fins in the lower Ganoids, and maintains that the alteration of the caudal fin from heterocercal to abbreviate heterocercal or symmetrical, which took place within different phylogenetic lines issuing from the *Palaeonisciformes*, is due to changes in the milieu in which the fishes lived. The highly heterocercal caudal fin necessitated horizontal pectoral fins, and with the shortening of the body axis of the caudal fin the position of the pectoral fins changed from horizontal to vertical. In *Australosomus*, however, the pectoral fins are still held horizontally, though the caudal fin is symmetrical or nearly so.

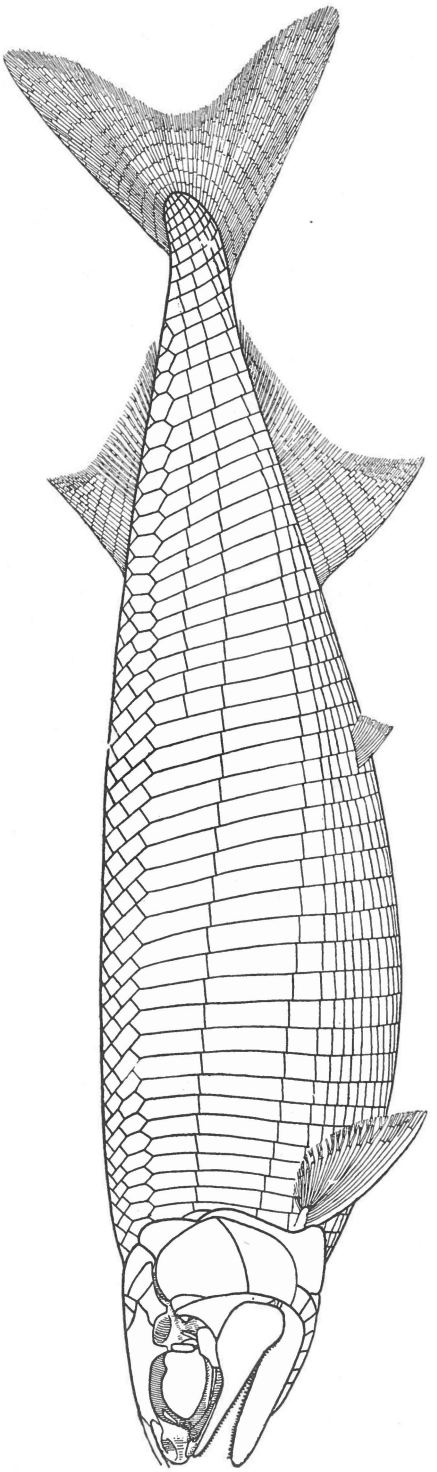


Fig. 55. *Australosomus kochi* (Stensiö). Attempted restoration. Based on several specimens.

Body shape and squamation.

Stensiö (1932, pp. 167, 179–182) based his description of the squamation of *Australosomus kochi* on five specimens, however, it was only with great hesitation that he referred two of these to the species in question. He expressed his doubt in the following words (Stensiö 1932, p. 182):

»As already mentioned in the description of the squamation, it is not impossible that two of the specimens described here, those shown in pl. 29, fig. 1 (no. 39) and pl. 38, fig. 1 (no. 40) may differ from the holotype in regard to the number of scales in the dorsal forwardly-inclined part of the transverse rows and to the proportions of the three high scales of the transverse rows. If this, as is very likely, proves to be the case a new independent species must of course be erected for them«.

The investigation of the present large material of *Australosomus* has fully justified Stensiö's suspicion. There is now not the slightest doubt that Stensiö's specimens nos. 39 and 40 do not belong to *Australosomus kochi*, but to a new species, *Australosomus simplex*, which will be described later in the present work. Stensiö's description of the squamation was to a great extent based on his specimens nos. 39 and 40, and it is therefore necessary to redescribe the squamation of *Australosomus kochi* in fairly great detail.

The trunk is entirely covered with scales, which are arranged in transverse rows. The number of rows behind the posterior margin of the supracleithrum is about 50–52, and thus, judging from the number of vertebral elements (see fig. 46), the scale-rows are metamerically arranged. Anteriorly to the ventral part of the foremost complete row we find three or four short subcleithral ones, and furthermore it is likely that the very small pectoral fin-lobe was covered by scales, although no such scales have been observed with certainty.

In the anterior part of the abdominal region the transverse rows are fairly vertical in lateral view except for their most dorsal part, which is forwardly inclined, as shown in fig. 55. Backwards through the posterior part of the region and the caudal region the transverse rows exhibit an increasing forward inclination.

As far as can be judged from the shape of the cleithrum and from the arrangement of the scales, the ventrum was not flattened as in many *Palaeonisciformes* (Watson 1925, p. 825; Aldinger 1937, pp. 32, 37, 342–343; Westoll 1944, pp. 61, 77–78), and probably the abdominal region was fairly oval in transverse section.

In the abdominal region and in the caudal region anterior to the dorsal fin each transverse row can be traced from a small median dorsal scale, which is rhombic in outline and curved from side to side, its external face being convex. The dorsal oblique part of each of these scale rows consists of

two scales, the shape of which varies somewhat in the different rows. In most cases the dorsal one of these scales is only a little higher than broad and almost rhombic in outline, but in a few rows a short distance behind the head the scale is somewhat higher in proportion to its breadth and almost rectangular in outline. The ventral one of the two scales is always considerably higher than broad, and in the foremost transverse rows and in the rows just anteriorly to the dorsal fin it is irregularly hexagonal, while in the other rows it is rectangular or nearly rectangular.

Ventrally to these scales we find, in each of the foremost 20–22 transverse rows, two very high scales, of which the dorsal one is the lateral line scale. Backward from the head region the high scales first increase and then decrease in height in the way shown in fig. 55. In the longitudinal row formed by the lateral line scales the highest scales, which are situated in about the 15th to the 19th transverse row, are 3–3½ times as high as broad, and in the longitudinal row formed by the scales just ventrally to the lateral line scales the highest scales, belonging to about the 11th to 15th transverse rows, are 3½–3¾ times as high as broad. In the foremost part of this longitudinal row the scales are even between four and five times as high as broad, but this is due to the circumstance that the vertical parts of the foremost transverse scale rows are especially narrow.

In each of the more posterior transverse scale-rows in the abdominal region we find, ventrally to the small dorsal scales already described, three high scales, of which the dorsal and the middle one together occupy an area corresponding to that occupied by the high lateral line scale in the more anterior rows, while the ventral one occupies an area corresponding to that occupied by the ventral high scale in the anterior rows. The middle one of the three dominating scales in each of the posterior abdominal transverse rows is the lateral line scale. The dorsal high scales are 1⅓–1½, the middle ones 1½–2, and the ventral ones 2½–2¾ times as high as broad.

The fact that the row of very high lateral line scales found on the anterior part of the trunk is continued in the most posterior part of the abdominal region by two scale-rows, seems to show that each of the high lateral line scales on the anterior part of the trunk has arisen by fusion of a smaller lateral line scale and the scale immediately above, and thus it gives an interesting contribution to the question, touched on by Westoll, of the origin of especially high scales (Westoll 1944, p. 81).

The ventral part of each of the transverse scale-rows in the abdominal region consists of fairly small scales, the number of which gradually increases from about 9 in the foremost row to a maximum of about 11 in the 7th, 8th, and 10th rows, to decrease gradually again to about 4–6 in the hindmost abdominal row. In the foremost transverse rows the most dorsal one of these scales is almost twice as high as broad, but in the following rows it decreases gradually in height, being, in the hindmost abdominal rows, about 1½ times

as broad as high. The more ventral scales in each abdominal transverse row are always broader than high, and decrease in height towards the ventral mid-line of the body, the most ventral ones being about four times as broad as high.

Passing backward through the anterior and middle parts of the caudal region, we observe that the number of scales in the transverse rows decreases gradually in a posterior direction, and if we follow backward the longitudinal scale rows of the abdominal region, we shall find that it is the most dorsal and the most ventral longitudinal rows which disappear in the anterior and middle part of the caudal region, while the midmost abdominal longitudinal rows can be traced backward to the posterior tip of the trunk.

The most dorsal longitudinal row in the abdominal region ends posteriorly just anterior to the dorsal fin. The longitudinal row nearest below ends posteriorly below the hindmost part of the dorsal fin. In the caudal region and in the posterior part of the abdominal region this row is composed of fairly large irregularly hexagonal scales, and dorsally to this row we observe, below the base of the dorsal fin, a longitudinal row consisting of very small triangular scales, which together with the corresponding ones on the other side of the trunk should probably be regarded as serially homologous with the row of dorsal median scales anterior to the dorsal fin. Below the row of hexagonal scales we find three longitudinal rows of fairly high scales, which form the posterior continuation of the three middle rows of high scales in the posterior part of the abdominal region. These three rows can be traced backward as far as the posterior tip of the trunk, the scales in each row diminishing gradually in height in a posterior direction. The lateral line can be followed in the middle one of the three rows to the area below the posterior end of the dorsal fin. Farther back it probably traversed scales belonging to more ventral longitudinal rows, but its most posterior part could not be observed in any of the specimens at my disposal.

The longitudinal abdominal scale-row ventrally to the three rows of very high scales can also be traced backward through the whole caudal region, but of the more ventral abdominal rows only the two most dorsal ones can be followed a short distance into the caudal region. In the most posterior part of the caudal region, however, we find, ventrally to the longitudinal rows described here, a few short longitudinal rows of low scales, which rows have no connection with the ventral abdominal rows.

By far the greater number of the specimens examined show the above-described arrangement of the scales, however, some specimens, most of which are derived from Fish-zone III, differ in having only one scale instead of two in the dorsal oblique part of each abdominal transverse row. As, however, these specimens agree with *A. kochi* in all other characters, I hesitate to erect a new species for them, though it is not improbable that future investigations will justify their separation from *Australosomus kochi*.

The flank scales are all provided with a fairly strong peg-and-socket articulation and have a relatively narrow anterior overlapped area.

Stensiö's description of the microstructure of the scales (Stensiö 1932, pp. 181–182; pl. 34, fig. 4; pl. 35, fig. 3; pl. 36, fig. 1; pl. 37, fig. 30) seems chiefly to be based on specimen no. 40, which, as mentioned above, belongs to another species. As might be expected, however, the scales in the two species of the same genus are built in much the same way, and hence a very summary description of the conditions in *Australosomus* will suffice here.

The scales consist only of a thick isopedine layer, the ganoine and cosmine layers being completely, or almost completely, reduced. The isopedine layer in the central part of the scales is pierced by a small number of narrow ascending vascular canals, each of which opens on the external face of the scales with a small rounded opening. From the external openings extend, in some cases, a few fine, ramifying grooves, while in other cases no traces of such grooves can be detected. In Stensiö's specimen (which, as already mentioned, belongs to another species) these grooves are much more numerous (cf. p. 168), and Stensiö (1932, p. 181) compares them with »the system of horizontal canals described by Goodrich (1907, pp. 757–758) in the Palaeoniscid scale immediately basally to the cosmine layer« and refers to them as the horizontal plexus of vascular grooves. In addition to these fine grooves the external surfaces of the scales in some specimens show a very fine vertical striation, while in other cases it is quite smooth. The system of fine rostro-caudally running striae observed by Stensiö (1932, p. 182) on the anterior marginal zone of the outer face of the scales is seen in many specimens. On impressions of the scales they appear, as described by Stensiö, as very fine whitish rods, and on the scales themselves they are represented by very fine grooves. As far as I can make out, the fine rods must be explained as a system of extremely fine ridges, which do not belong to the isopedine layer, and which accordingly might perhaps be interpreted as a last remnant of a ganoine layer.

Discussion. – Much the same arrangement of the high flank scales as described above seems to exist in some of the specimens of *Australosomus merlei* figured by Piveteau (1934, pl. 1, fig. 4; pl. 2, fig. 3; pl. 4, fig. 3; pl. 5, fig. 5); in other of his specimens figured as *Australosomus merlei* on his plates 1–5, however, the high flank scales are arranged in three longitudinal rows not only on the posterior but also on the anterior half of the trunk. It is therefore most likely that also the material of *Australosomus* investigated by Piveteau includes more than one species.

High flank scales are developed not only in *Australosomus* but also in the other Pholidopleurid genera so far known, viz. *Macroaethes*, *Pholidopleurus* and *Arctosomus*. However, our knowledge of the arrangement of these high scales in *Macroaethes* (Wade 1935, pp. 65–78, fig. 43; pl. 9, fig. 3) and *Arctosomus* is still too scanty for detailed comparisons, and as regards *Pholi-*

dopleurus (Bronn 1858, pl. 1, figs. 14, 15; Kner 1866, pl. 4, fig. 2; Abel 1919, fig. 165; Stensiö 1932, p. 180; Wade 1935, pp. 65–66,) the conditions are not much better known. According to Stensiö the dorsal and the middle of the three high flank scales in his specimens nos. 39 and 40 (*A. simplex* n. sp.) are represented in *Pholidopleurus* by a single very high scale. If this is really so, which does not appear from the figure of *Pholidopleurus typus* given by Abel (1919, fig. 165), the dorsal and the middle rows of high flank scales have fused throughout their whole length in *Pholidopleurus*, while they are still separated on the posterior half of the trunk in *Australosomus kochi*.

The scales of *Pholidopleurus* and *Arctosomus* (Stensiö 1932, p. 166; Berg 1941, p. 470) differ from those of *Australosomus* in being covered by ganoine. The scales of *Macroaethes*, especially on the posterior part of its body, are thinner than those of the other Pholidopleurids (Wade 1935, pp. 77, 79; 1940, p. 392).

It will be understood from the above that only little can be made out regarding the relationships between the different Pholidopleurid genera on the basis of our present knowledge of the squamation, viz. 1) The development of the high flank scales are probably more advanced in *Pholidopleurus* than in *Australosomus kochi*, 2) *Australosomus* is more specialised than *Pholidopleurus* and *Arctosomus*, completely, or almost completely, lacking ganoine on its scales, and 3) *Macroaethes* is more specialised than the other Pholidopleurids in the extreme thinness of its scales.

Sensory canal system of the trunk.

As far as can be seen, the main lateral line passes directly from the extrascapular into the supracleithrum (p. 149), the central part of which it traverses, as shown in fig. 25. In the supracleithrum the sensory canal gives off only two tubuli, one of which opens ventrally and the other dorsally to the canal.

Behind the supracleithrum the main lateral line continues backward to the area below the most posterior part of the dorsal fin, traversing, in the anterior and middle part of the abdominal region, the dorsal and, farther backward, the middle row of high flank scales.

Each lateral line scale shows a fine longitudinal canal, which opens both anteriorly and posteriorly on the external face of the scale, the anterior opening lying some distance behind the anterior, and the posterior opening some distance before the posterior margin of the scale. The canals, which in some specimens are very easy to follow, as they are filled up with white calcite, show no traces of tubuli.

DIAGNOSIS.

Our increased knowledge of *Australosomus kochi* renders it necessary to replace the diagnosis given by Stensiö (1932, p. 182) by the subjoined one, which gives more exact information about some of the specific characters used by Stensiö and in addition mentions some new features found, which are necessary for the definition of the species. The new diagnosis runs as follows:

Fairly large species, estimated length of largest specimen c. 19 cm. Parietal complex comprising two anterior and two posterior parietals. Number of branchiostegal rays c. 7. Pelvic fin commencing at about 19th–20th transverse scale-row. Dorsal fin commencing at about 31th–34th transverse scale-row. Anal fin commencing at about 27th transverse scale-row. Total number of transverse scale-rows behind dermal shoulder-girdle about 50–52. On anterior and middle parts of abdominal region two longitudinal rows of high flank scales, the dorsal one traversed by the main lateral line. On posterior part of abdominal region and on caudal region three longitudinal rows of high flank scales in continuation of the two dominant rows more anteriorly, the anterior half of the middle of the three rows traversed by the main lateral line. Number of low scales in ventral part of transverse rows in middle part of abdominal region about 10–11. Horizontal plexus of vascular grooves on exposed faces of dermal bones and scales weakly developed or lacking.

REMARKS.

Australosomus kochi differs from *Australosomus merlei* in having a paired anterior parietal and, as already pointed out by Stensiö (1932, p. 182), a larger number of low ventral scales in each transverse row as well as a somewhat larger number of transverse scale-rows between the pelvic and anal fins. To these differences might probably be added some other, perhaps more significant ones, if a closer investigation of the structure of *Australosomus merlei* was made. *Australosomus kochi* differs from *Australosomus stockleyi*, which has been very briefly treated by Haughton (1936, pp. 58–60; pl. 6, figs. 1, 2), in having a smaller (not greater, as stated by Haughton (op. cit. p. 58)) number of branchiostegal rays, and perhaps, as emphasised by Haughton, in having a less elongate shape.

Australosomus simplex n. sp.

(Fig. 56; pls. 8–9).

Syn. 1932. *Pholidopleurus kochi* (in part) Stensiö in Koch, p. 88.
1932. *Australosomus kochi* (in part) Stensiö, pp. 161–183, fig. 57; pl. 34, figs. 4–5.
1932. *Australosomus kochi*? Stensiö, pls. 35–36; pl. 37, figs. 3–4; pl. 38, fig. 1; pl. 39, fig. 1.
1936. *Australosomus*. E. Nielsen, pp. 44–45.

MATERIAL AND LOCALITIES.

Specimens nos. 39 and 40 (Stensiö's numbers) of the material treated by Stensiö and collected prior to 1932. Both these specimens are derived from Fish-zone II in the Kap Stosch area. The following specimens of the material collected in the years between 1932 and 1937: From Fish-zone II in the Kap Stosch area: specimens nos. 479, 518, 566–592, 600, 603, and 614; from Fish-zone II in the Hird Bay area: specimen no. 638. Moreover, specimens nos. 593–598 and 601–613 from Fish-zone II in the Kap Stosch area, probably belong to *A. simplex*. Specimen no. 637 from Mesters Vig, camp 8, profile 7 (collected by W. Bierther) probably likewise belongs to *A. simplex*.

HOLOTYPE.

As holotype I have chosen specimen no. 568 (pl. 8), a fish which lacks the posterior part of the caudal region and the greater part of the fins, but in which the squamation and most of the dermal bones of the head are in a fairly good state of preservation.

MEASUREMENTS.

The holotype (specimen no. 568) in its present condition measures 11.5 cm in length; its total length may be estimated at about 17 cm. The length of the head measured from the tip of the snout to the posterior corner of the operculum is 3.0 cm. The maximum height of the trunk, measured at a distance behind the shoulder-girdle of about one-fourth of the whole length of the trunk, is c. 4.3 cm. The distance from the posterior margin of the extrascapular series to the base of the anterior margin of the dorsal fin is about 7.9 cm, the distance between the base of the pectoral fin lobe and the base of the anterior margin of the pelvic fin is about 6.2 cm, and the distance between the base of the anterior margin of the pelvic fin and the base of the anterior margin of the anal fin is about 2.2 cm.

	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	Estimated length in cm
Fish-zone V		× ×	× ×																		
Fish-zone IV																					
Fish-zone III																					
Fish-zone II						×	×	× ×	×	×	× ×	× ×	×	×	× ×	×	×		×		

The above table shows the estimated lengths of the most complete specimens of *Australosomus simplex* and of four small specimens of *Australosomus* from Fish-zone V, which latter are discussed later as *Australosomus aff. simplex*.

As will be seen from the table, *Australosomus simplex* attains a larger size than *Australosomus kochi*, the examined specimens varying in length from about 10 to about 23 cm, most of them belonging to columns 15–19. One of the specimens (no. 594), which is probably referable to the species in question though this is not certain, even attains an estimated length of 26 cm. As far as can be seen, the specimens from Fish-zone V only differ from the typical *Australosomus simplex* by being much smaller than the smallest specimens from Fish-zone II, and this difference in size, together with the fact that *Australosomus simplex* does not occur in Fish-zones III and IV, makes me doubt whether the small specimens really belong to *Australosomus simplex*.

DESCRIPTION.

Head.

The neural endocranium is ossified to about the same extent as in *Australosomus kochi* and in some specimens it is very well preserved. As far as could be made out by direct preparation, it agrees with that of *Australosomus kochi*, and I have therefore considered it superfluous to employ the grinding method for a close investigation of its structure, though without grinding it proved impossible to study the following features in detail: The shape of the cranial cavities, the course of the finest canals for nerves and vessels, and the relief of the dorsal faces of the otic and the orbitotemporal region.

The posterior branchial arches and the posterior ossifications of the basibranchial series, also, could not be studied in detail by direct preparation. The more anterior parts of the visceral endoskeleton agrees closely with the corresponding parts of the visceral endoskeleton in *Australosomus kochi*.

The dermal bones of the head resemble those of *Australosomus kochi* in most respects. The operculum is perhaps a little broader in proportion to its height, and it is not impossible that there are also other minor differences in the proportions of the dermal bones between the two species; however, the material of *Australosomus simplex* at my disposal is not sufficient to enable me to decide whether such differences are of specific value or whether they should only be regarded as individual variations.

The external faces of the external dermal bones of the head are in some cases less smooth than in *Australosomus kochi*, the network of fine ramifying grooves, comparable to the horizontal plexus of vascular grooves on the scales, being denser and deeper. In other specimens, however, the dermal bones of the head are just as smooth as in *Australosomus kochi*.

Axial skeleton, shoulder– girdle, pelvic plate, paired and unpaired fins.

All these structures agree entirely with the corresponding ones in *Australosomus kochi*, with the exception of the unpaired fins, which seem to be a little smaller in *Australosomus simplex*.

Squamation.

As already mentioned, the squamation of *Australosomus simplex* differs rather much from that of *Australosomus kochi*. The number of transverse scale-rows behind the posterior margin of the dermal shoulder-girdle is about 55–57, of which about 28–30 belong to the abdominal region. Anterior to the ventral part of the foremost complete transverse row we find 3–4 short subcleithral scale-rows, and further the very small pectoral fin-lobe was probably scaly. The first complete scale-row behind the dermal shoulder-girdle is curved throughout its length in such a way that its anterior margin is concave and its posterior margin correspondingly convex. Backward from this point the middle and ventral parts of the transverse abdominal rows are gradually straightened out, so that in the middle part of the abdominal region the rows grow almost vertical except for their most dorsal part, which is still forwardly inclined. In the posterior part of the abdominal region and the caudal region the scale-rows become gradually more forwardly inclined throughout their height, as shown in fig. 56.

Judging from the appearance of the abdominal transverse scale-rows the ventrum was not flattened, and probably the abdominal region was fairly oval in transverse sections, as in *Australosomus kochi*.

Each of the abdominal transverse scale-rows can be traced from a small rhombic median dorsal scale and may for descriptive reasons be regarded as consisting of a dorsal, a middle, and a ventral part. The dorsal, forwardly inclined, part of each row consists of small scales, the breadth and height of which increase gradually downward so that the ratio between the height and the breadth increases with increasing distance from the dorsal mid-line of the trunk. The lowermost one of these scales is higher than broad, while all the others are broader than high. In the foremost row there are four small dorsal scales, but the number increases in the following rows to attain a maximum of 9–10 in the most posterior abdominal rows. The middle part of each transverse row consists of three high rectangular or almost rectangular scales the dorsal one of which is the lateral line scale. In the foremost transverse row the lateral line scale is about 1½ times as high as broad. If we pass backward through the abdominal region, the scale first increases and then decreases in height, attaining its maximum height (about twice the breadth) in about the 6th–8th row. The midmost one of the three high scales varies in height throughout the region in a somewhat similar way. In the

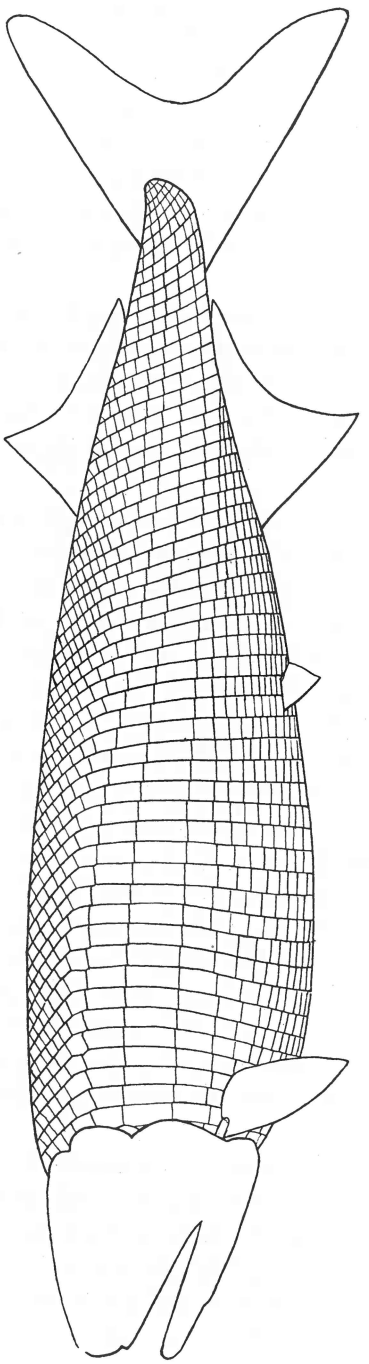


Fig. 56. *Australosomus simplex* n. sp. Attempted restoration of the squamation. Based on several specimens.

foremost row it is about 2–2¼ times as high as broad, in the 2nd–15th rows it is still a little higher, and in the more posterior rows it decreases slowly in height in a caudal direction. In the foremost c. 10 rows the ventral one of the three scales is about twice as high as broad, but further backward it decreases slowly in height in a caudal direction.

In a few specimens the scales forming the middle part of the transverse abdominal rows are somewhat broader and lower than described above; however, the available material is not sufficient to enable us to decide whether this is a character of specific value or it is only due to individual variations.

The ventral part of the transverse rows is made up of fairly small rectangular scales, which decrease gradually in height downwards. The uppermost one or two of these scales in the foremost 11–14 transverse rows are higher than broad or of about the same height as breadth, while all the others are broader than high. The most ventral scales are about twice as broad as high.

The three longitudinal rows formed by the high scales situated in the middle part of the abdominal transverse scale-rows continue backward through the whole caudal region. The main lateral line can be traced backward through the anterior half of the caudal region in the dorsal one of the three longitudinal rows, while its course in the posterior half of the caudal region is unknown. That part of each of the caudal transverse scale-rows which lies dorsally to the three longitudinal rows just mentioned consists of rather small scales, the height of which decreases in a dorsal direction. In each of the anterior caudal transverse rows there are about 9 such small scales; their number decrease gradually in a posterior direction, the hindmost caudal rows containing only a single small scale in their dorsal part. Ventrally to the three longitudinal rows of high scales we find, in the foremost 9–10 caudal transverse rows, some low scales corresponding to those comprising the ventral part of the abdominal transverse rows. Of these scales there are about 6–7 in the foremost caudal row; the number decreases in the succeeding rows, as shown in fig. 56. In the middle part of the caudal region low ventral scales are lacking, but in the most posterior part of the region they appear again, as is also the case in *Australosomus kochi* (p. 160, fig. 55).

The microstructure of the scales of *Australosomus simplex* has been described in detail by Stensiö (1932, pp. 181–182), so I shall only mention here that in many specimens the horizontal plexus of vascular grooves described by Stensiö is extremely well developed.

Discussion. – As is evident from the above description, the squamation of *Australosomus simplex* differs from that of *Australosomus kochi* in the following respects: 1) the number of transverse scale-rows, 2) the number and size of the scales in the individual rows, and 3) the ornamentation of the scales.

As to 1). A comparison between figs. 55 and 56 shows that the larger number of transverse scale-rows in *Australosomus simplex* is solely due to a different number of caudal transverse rows in the two species, while the number of abdominal transverse rows is about the same. The difference may therefore be explained by assuming that the caudal region of *Australosomus kochi* has undergone a shortening as compared with that of *Australosomus simplex*.

As to 2). The larger number and the smaller size of the scales in *Australosomus simplex* must be regarded as primitive features, since, as previously described, certain conditions in the arrangement of the scales in *Australosomus kochi* seem to indicate that high scales are formed by fusion of smaller scales within the individual transverse rows. If from this point of view we compare the squamations of *Australosomus kochi* and *Australosomus simplex*, it will be evident from the position of the main lateral line that each of the very high abdominal lateral line scales in *Australosomus kochi* corresponds to an abdominal lateral line scale plus one or more of the smaller scales dorsally to the lateral line scale in *Australosomus simplex*, while the ventral longitudinal row of high abdominal flank scales in *Australosomus kochi* corresponds to the middle longitudinal row of high abdominal flank scales in *Australosomus simplex*.

As to 3). The stronger development of the horizontal plexus of vascular grooves in *Australosomus simplex* than in *Australosomus kochi* may also be regarded as a relatively primitive feature in the former species.

DIAGNOSIS.

Large species, estimated length of largest specimen about 23 (26?) cm. Parietal complex comprising two anterior and two posterior parietals. Number of branchiostegal rays c. 7. Pelvic fin commencing at about 20th transverse scale-row. Dorsal fin commencing at about 33th–35th transverse scale-row. Total number of transverse scale-rows behind the dermal shoulder-girdle about 55–57. On anterior part of trunk high flank scales, arranged in three longitudinal rows, which continue on to the posterior part of the trunk, though here they are less predominant. The dorsal one of these rows lodges the main lateral line. Number of low scales in ventral part of transverse rows in middle part of abdominal region 9–10. Horizontal plexus of vascular grooves on exposed faces of dermal bones and scales mostly well developed.

REMARKS.

Australosomus simplex may easily be distinguished from *Australosomus kochi* by its larger number of transverse scale-rows and by the larger number and smaller size of the scales in the individual rows. As far as can be seen

from Piveteau's figures, which, as already mentioned, very likely represent more than one species, it also differs from *Australosomus merlei* in having a larger number of scales in the transverse rows, and judging from our very sparse knowledge of *Australosomus stockleyi*, it may be distinguished from this species by its smaller number of branchiostegal rays.

Australosomus aff. simplex.

As already mentioned (p. 165), four specimens (nos. 553, 555–557) of *Australosomus* from Fish-zone V in the Kap Stosch area show close resemblance to *Australosomus simplex*, since, as far as could be seen, they only differ from that species in their total length not being more than about 6–7 cm.

Taking into consideration, however, that no large specimens of *Australosomus simplex* have been collected from Fish-zone V, and that the species does not occur in either Fish-zones IV or III, I hesitate to regard the four small specimens, whose state of preservation is far from satisfactory, as sufficient evidence of the existence of *Australosomus simplex* in the *Proptychites* beds, but prefer to leave the question open and to provisionally designate the four small specimens *Australosomus aff. simplex*.

Australosomus pholidopleuroides n. sp.

(Fig. 57; pl. 5, fig. 2).

MATERIAL AND LOCALITIES.

Specimen no. 445, derived from Fish-zone II in the Kap Stosch area.

MEASUREMENTS.

The specimen, which is mainly preserved as an impression, shows most of the dermal cranial roof, some other dermal bones of the head, and a considerable part of the trunk. In its present state of preservation it measures about 14 cm in length. Its total length may be estimated at about 17 cm. The distance from the posterior margin of the extrascapular series to the base of the anterior margin of the dorsal fin is about 7.5 cm.

DESCRIPTION.

The preserved part of the dermal cranial roof comprises the extrascapulars, the parietal complex, the supratemporo-intertemporals, and the frontals. As in *Australosomus merlei* and *A. kochi* (p. 88), there is only one extrascapular on either side of the mid-line. This bone (*Ext*, fig. 57; pl. 5, fig. 2) is irregularly four-sided, with a lateral, an antero-lateral, an antero-medial, and a postero-medial margin, and it differs from the extrascapular of *Australo-*

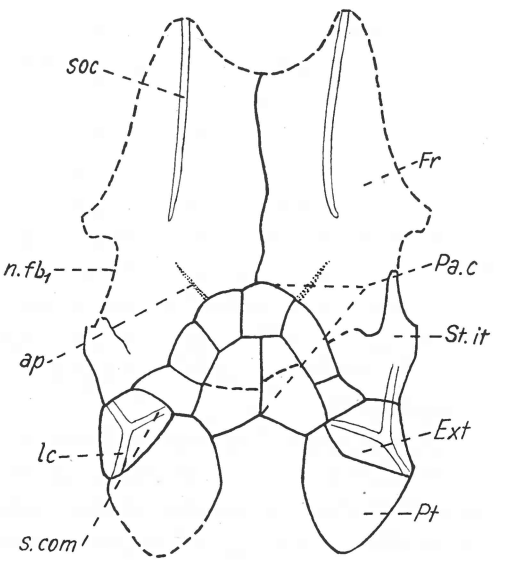


Fig. 57. *Australosomus pholidopleuroides* n. sp. Greater part of dermal cranial roof and posttemporals. On the basis of specimen no. 445 (holotype). C. 4 ×.

Ext, extrascapular; *Fr*, frontal; *Pa. c*, parietal complex; *Pt*, posttemporal; *St. it*, supratemporo- intertemporal; *ap*, anterior pit-line, *l. c*, cephalic division of main lateral line; *n. fb_1*, notch in the margin of the dermal cranial roof above the spiracular division of the fossa bridgei; *s. com*, supratemporal commissure; *soc*, supraorbital sensory canal.

somus kochi mainly in having a smaller extension in a medial direction. The longitudinally running cephalic division of the main lateral line (*lc*, fig. 57) and the transversely running supratemporal commissure (*s. com*, fig. 57) meet in the centre of radiation of the bone in the usual way. The parietal complex (*Pa. c*, fig. 57; pl. 5, fig. 2) comprises no less than five pairs of small parietals, viz. three anterior pairs, corresponding to the anterior pair of parietals in *Australosomus kochi*, and two posterior pairs, corresponding to the posterior pair of parietals in *Australosomus kochi* (cf. fig. 21). The outline and size of the individual parietal elements are shown in fig. 57. The supratemporo-intertemporal (*St. it*, fig. 57; pl. 5, sig. 2) has about the same shape as that of *Australosomus kochi*, while the frontal (*Fr*, fig. 57; pl. 5, fig. 2) seems to be somewhat broader and shorter than the frontal of *Australosomus kochi*, with which it otherwise shows good agreement, thus, for instance, in possessing a well marked pit-line (*ap*, fig. 57; pl. 5, fig. 2) extending in an antero-lateral direction from its postero-medial margin. As far as can be seen, the operculum (*Op*, pl. 5, fig. 2) and the suboperculum (*Sop*, pl. 5, fig. 2) are also developed much as in *Australosomus kochi*, and the same holds good regarding the little that can be studied of the outlines of the dermal bones of the shoulder-girdle, viz. the posttemporal (*Pt*, fig. 57; pl. 5, fig. 2), the supracleithrum (*Scl*, pl. 5, fig. 2), and the cleithrum (*Cl*, pl. 5, fig. 2). The exposed faces of the dermal bones seem to be fairly smooth.

Both the paired and the unpaired fins are poorly preserved. Of the pectoral fins only a few lepidotrichia are found, and nothing is left of the pelvic fins. Of the unpaired fins remnants can be observed of the basal segments of a number of lepidotrichia, so it can be stated that the dorsal fin commences at about the 25th and the anal fin at about the 30th transverse scale-row. The number of transverse scale-rows seems to exceed 50, and the scales in the individual rows are arranged as in *Australosomus simplex* rather than as in *Australosomus kochi*, in so far as the dorsal forwardly inclined part of each abdominal transverse row contains several smaller scales. The arrangement of the high scales forming the middle part of the abdominal scale-rows cannot be made out with certainty, and the ventral part of the abdominal rows is lacking on the specimen.

Discussion. – The most interesting feature in the structure of *Australosomus pholidopleuroides* known so far is the large number of independent elements in the parietal complex. Somewhat similar conditions are known in *Pholidopleurus typus* (Wade 1934, fig. 32), in which, however, the number of parietal elements is even larger than in *Australosomus pholidopleuroides*. As already discussed (p. 94), this subdivision of the parietal complex should probably be regarded as a specialisation with a definite purpose rather than as a degeneration caused by the shortening of the supraorbital sensory canal. One might ask whether on account of the development of its parietal complex the species here treated should not be referred to *Pholidopleurus* rather than to *Australosomus*, and, of course, this question is not easy to answer on the basis of our present sparse knowledge of the species. According to Stensiö (1932, p. 166) *Australosomus* differs from *Pholidopleurus* especially in the following characters: 1) the presence of pelvic fins; 2) the almost equal length of the dorsal and anal fins; 3) the commencement of the dorsal fin opposite or only a little further backward than the anal fin; 4) the presence of three moderately deepened scales in the midmost part of each vertical scale-row instead of the single very high scale in *Pholidopleurus*; 5) the greater number of scales in each vertical scale-row; and 6) the absence of ganoine on all the dermal bones and on the scales.

As to characters 1, 2, and 6 nothing is known from the Greenland species. As to characters 3, 4, and 5, however, the species agrees better with *Australosomus* than with *Pholidopleurus*; thus (3) the relative positions of the dorsal and anal fins are the same as in *Australosomus kochi*, (4) the midmost part of the abdominal transverse scale-rows does not contain a single very high scale, but either two or three moderately high scales, and (5) the dorsal part of the transverse scale-row contains several smaller scales.

On account of the said agreement I think it most correct at present to refer the species to *Australosomus*, though it can hardly be regarded as quite impossible that future investigations of more complete specimens will show that the species belongs to a genus which differs from both *Australosomus* and *Pholidopleurus*.

DIAGNOSIS.

Medium-sized species, estimated length of only specimen about 17 cm. Parietal complex comprising 5 pairs of small parietal elements. Dorsal fin commencing at about the 25th transverse scale-row. Anal fin commencing at about the 30th transverse scale-row. Total number of transverse scale-rows > 50. Two or three longitudinal rows of high flank scales in abdominal region. Several smaller scales in forwardly inclined dorsal part of each abdominal scale-row.

REMARKS.

Australosomus pholidopleuroides is easily distinguishable from all the other species of *Australosomus* so far known by the large number of independent parietal elements.

Indeterminable specimens of Australosomus.

In addition to the specimens already treated the material of *Australosomus* from East Greenland includes the following specimens, which cannot be referred to a species owing to their poor state of preservation:

Specimens nos. 614–621 and 623–635 from Fish-zone II in the Kap Stosch area, specimens nos. 622 and 639 from Fish-zone II in the Hird Bay area.

Generic diagnosis.

(Partly after Stensiö 1932, pp. 166–167, and Piveteau 1934, p. 38).

Small to medium-sized slender fishes, transverse section of trunk oval, head small, with short blunt rostrum and very large eyes. Neural endocranium in youngest specimens unossified or almost unossified, in older specimens highly ossified with one ossification occupying the ethmoidal region, the orbitotemporal region, and part of the otic region, and another occupying the remaining part of the otic region and the occipital region. The two ossifications are separated by a fissura oticalis ventralis, a vestibular fontanelle, and a fissura otico-occipitalis, the latter widened dorsally to a posterior dorsal fontanelle. The fissura oticalis ventralis and the vestibular fontanelle partly closed by cartilage in the living animal.

Cranio-spinal process small. Roof of orbitotemporal region and otic region pierced by an anterior dorsal fontanelle, somewhat restricted by cartilage in the living animal. Fossa bridgei subdivided into a lateral (antero-lateral) and a medial division. Lateral division, into which opens the long nearly vertical spiracular canal, uncovered by the dermal cranial roof. Medial division without communication with the cavum cerebrale cranii. Short un-

paired aorta canal in basal part of occipital region. Notochordal space situated wholly in occipital region. Articular fossa for hyomandibula very oblique. Jugulo-hyoideomandibular canal long with only one posterior opening. Trigemino-facialis chamber well developed. Large unpaired posterior myodome with a spinal and a prespinal division. Roof of posterior myodome pierced by a small pituitary fontanelle. Pars basisphenoidea comprising a ventral broad and low and a dorsal high and slender division. Dorsal division of pars basisphenoidea not pierced by any canals. Processus basipterygoideus completely reduced. Interorbital part of orbitotemporal region compressed so as to form a thin interorbital wall pierced by two large fenestrae. Nervus olfactorius intracranial throughout its extent. Unpaired anterior myodome developed for the oblique eye-muscles. Ethmoidal region fairly long, with very complete nasal cavities and a well marked facet for articulation with the palatoquadrate. On either side of articular facet deep pits developed for ligaments connecting palatoquadrate and neural endocranium. Parasphenoid with only one (the posterior) processus ascendens. Posterior part of parasphenoid subdivided into smaller independent ossicles. Vomer paired, long and narrow without firm connection with other bones. Dermal cranial roof thin with an emargination on each lateral margin corresponding to the spiracular part of the fossa bridgei. Extrascapular series consisting of two plates. Parietal complex forming a lid above the posterior dorsal fontanelle and consisting of a varying number of smaller plates not firmly connected with each other or with the surrounding bones of the cranial roof. Supratemporo-intertemporals (possibly supratemporals) rather small. Frontals very large and reaching far back between the parietal complex and the supratemporo-intertemporals. Postrostral long and somewhat reduced posteriorly. Nasals narrow and more or less reduced.

Supraorbitals and dermosphenotic probably completely reduced. Posterior part of infraorbital series comprising a small postorbital and a large jugal. Anterior part of infraorbital series completely reduced. No suborbitals. Palatoquadrate in young individuals partly cartilaginous with at least two small separate ossifications, in older specimens almost completely ossified so as to form a single large bone. Between palatoquadrate and neural endocranium an ethmo-palatine, but no palato-basal, articulation. On oral face of palatoquadrate only two dermal bones, viz. an ectopterygoid and an entopterygoid, the latter perhaps including dermopalatine components. Maxillary with a low suborbital and a high postorbital part. Preoperculum consisting of a narrow ventral and a broad antero-dorsal part. Quadratojugal small and partly covered by maxillary and preoperculum. Palatoquadrate and its dermal bones, maxillary, preoperculum, and quadratojugal, firmly connected with each other and forming the walls of a narrow chamber for the musculus adductor mandibulae. Mandible long and fairly high, with somewhat convex oral border. Meckelian cartilage containing a single large

ossification extending from its posterior almost to its anterior end. Supra-angular small and completely covered by dentalo-splenial and angular. Prearticular long and low, possibly including coronoid components. In hyoid arch hyomandibula, symplectic, one ceratohyal ossification, and hypohyal. Hyomandibula stout, slightly bent, with short canal for truncus hyoideo-mandibularis and small processus opercularis. Symplectic small and feebly ossified. Ceratohyal ossification compressed from side to side and with distinct groove for afferent hyoid artery. Hypohyal angularly bent. Small dermohyal resting on dorsal part of lateral face of hyomandibula. No ant-opercula. Operculum and suboperculum well developed. Operculum somewhat higher than suboperculum. About 6–10 short paired branchiostegal rays, the foremost (the lateral gular plate) largest. One small median unpaired gular plate. Basibranchial series with four ossifications, hindmost one pierced by wide paired longitudinal canal. In each of foremost two branchial arches: suprapharyngobranchial, infrapharyngobranchial, epibranchial, ceratobranchial, and hypobranchial. In third branchial arch: epibranchial, ceratobranchial, and hypobranchial, and in fourth: epibranchial and ceratobranchial; common to the two arches is a pharyngobranchial. In fifth branchial arch only a single ossification, probably a ceratobranchial. Ceratobranchials of fourth and fifth branchial arches and epibranchial of fourth branchial arch highly specialised, being developed as large plate-like structures of complicated shape. Fairly short filiform gill-rays arranged in double rows on branchial arches, moreover longer gill-rays supporting an opercular gill. Articulation between foremost two branchial arches and endocranium as in *Pteronisculus* and *Acipenser*. External dermal bones of head rather thin and devoid of both ganoine and more pronounced ornament. Small acute teeth arranged in a single row on oral border of maxillary and mandible. Still smaller, likewise acute teeth either isolated or attached to small dermal ossicles of irregular outline occurring in the skin covering oral faces of ossifications of basibranchial series and branchial arches. Sensory canal system of head specialised in certain respects, viz. supraorbital sensory canal extending backward only to centre of radiation of frontal, infraorbital sensory canal traversing lateral marginal area of frontal medially and anteriorly to emargination on lateral margin of dermal cranial roof, supratemporal commissure not continuous, only one or two pit-lines on dermal cranial roof. Sensory canals narrow, primary tubuli entirely sub-divided into secondary tubuli. Notochord persistent and somewhat constricted by ring-like or crescent-shaped centra. Ossified basidorsals, interdorsals, basiventrals, interventrals, supradorsals (in foremost part of abdominal region), and ribs. In greater part of caudal region basidorsals fused with interdorsals, in abdominal and greater part of caudal region basiventrals fused with interventrals. Foremost basidorsals provided with stout lateral process. Ventral arcual elements of foremost abdominal vertebra forming the walls of a canal for the dorsal aorta. Ventral arcual

elements in posterior part of caudal region showing well developed hypural processes. Endoskeleton of shoulder-girdle, at least in older specimens, ossified in one piece, with incomplete mesocoracoid arch and short, nearly horizontal margo radialis. Series of dermal bones of shoulder-girdle comprising posttemporal, supracleithrum, cleithrum, and, at any rate in some species, a small clavicle. Endoskeleton of pectoral fin with a few radial ossifications arranged in a single series and supporting a very small fin-lobe. Pectoral fin rather small, foremost lepidotrich unbranched and unsegmented, more posterior lepidotrichia segmented and branched farthest distally. Pelvic plate small, triangular. Endoskeleton of pelvic fin with at least five small radial ossifications arranged in a single series. Pelvic fin very small, foremost lepidotrichia unbranched and unsegmented, more posterior lepidotrichia segmented and branched in their most distal part. Dorsal and anal fins situated far back. Endoskeleton of dorsal fin with two series of ossifications, posterior element in proximal series compound. Posterior part of dorsal fin low. Lepidotrichia close-set in anterior and more apart in posterior part of fin, segmented throughout and, except for the foremost ones, branched farthest distally. Endoskeleton of anal fin with a single series of long and slender radial ossifications. Anal fin commencing slightly further forward and extending slightly further backward than the somewhat smaller dorsal fin. Lepidotrichia of anal fin agreeing in arrangement and structure with those of dorsal fin. Endoskeleton of caudal fin with independent epichordal and hypochordal radial ossifications. Other hypochordal radial elements probably fused with hypurals. Caudal fin deeply cleft and almost symmetric. Lepidotrichia close-set and thoroughly segmented. Fulcra lacking both on paired and unpaired fins. Trunk covered with scales situated in about 50–58 transverse metamerically arranged rows. Middle part of each row except farthest caudally containing two or three especially high scales. Scales rather thin, with a narrow anterior overlapped area and with peg-and-socket articulation. Scales consisting of an isopedine layer, part of the external face of which shows a system of diminutive ridges, possibly representing a rudimentary ganoine layer. Isopedine layer pierced in the central part of the scales by a number of ascending canals opening on its external face into a network of more or less pronounced grooves.

Remarks on the genus Australosomus.

The genus *Australosomus* comprises at least five species, all of which are of Triassic age, viz. *Australosomus merlei* (Priem) and possibly one more *Australosomus* species (cf. p. 161) from Madagascar, *Australosomus kochi* (Stensiö), *Australosomus simplex* n. sp., and *Australosomus pholidopleuroides*, n. sp., all from East Greenland, and *Australosomus stockleyi* Haughton from Tanganyika.

At present it is impossible to make out the exact phylogenetic relations between these species, some of which (especially *Australosomus pholidopleuroides* and *Australosomus stockleyi*) are very incompletely known; still, however, a consideration of certain important characters has given some hints as to the evolutionary tendencies within the genus.

Thus it is most likely that the specialised squamation of *Australosomus kochi* has developed from a squamation more like that of *Australosomus simplex* by fusion of scales within the individual transverse rows. It is also very likely that the original number of elements in the parietal complex was four and that a larger or smaller number was obtained by subdivision or fusion respectively. Accordingly there cannot be much doubt that *Australosomus simplex* with its large number of relatively small scales on the transverse rows and with a parietal complex comprising four independent elements is the least specialised of the Greenlandic species, and that it is also more primitive than *Australosomus merlei*. In fact, as far as is known at present, there would seem to be no objection for regarding *Australosomus simplex* as ancestral both to *Australosomus kochi*, *Australosomus pholidopleuroides*, and *Australosomus merlei*, all three of which are specialised in different directions so that none of them may be regarded as ancestral to any of the others.

In *Australosomus stockleyi* neither the squamation nor the parietal complex is known in detail, however, the relatively large number of branchiostegal rays in this species must be regarded as a primitive character.

REMARKS ON THE FAMILY PHOLIDOPLEURIDAE WADE.

According to Stensiö (1932, p. 165) the family *Pholidopleuridae* was erected by Wade (1932, pp. 473–475) for the genera *Pholidopleurus* Bronn and *Macroaethes* Wade. Already in 1919, however, Abel (p. 211) grouped the genera *Pholidopleurus* Bronn, *Hydropessum* Brown, and *Pleuropholis* Traquair in a family under the name of *Pholidopleuridae*, claiming, solely on the basis of certain similarities in the shape and position of their unpaired fins, that a close relationship existed between these three genera. Abel gives no diagnosis of the family, and from his figures (designated »Orig-Rekonstr« or »Nach---, ergänzt«) it appears clearly that his knowledge of the structure of the forms he is dealing with is extremely sparse. In my opinion, therefore, he cannot claim the authorship of the family *Pholidopleuridae*, the less so because his assumption regarding a close relationship between *Hydropessum* and *Pleuropholis* on the one hand and *Pholidopleurus* on the other hand is undoubtedly wrong. Following Stensiö, I therefore consider the family *Pholidopleuridae* to be erected by Wade.

In 1932 Stensiö (p. 165) added *Australosomus* Piveteau to the family and suggested that perhaps *Peltopleurus* Kner would also turn out to be a

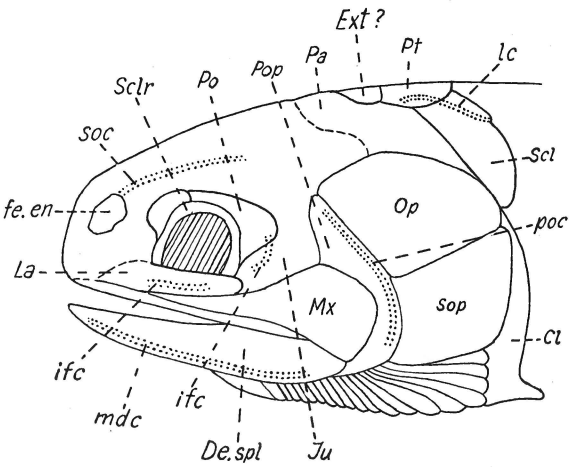


Fig. 58. *Macroaethes brookvalei* Wade. Head and dermal shoulder-girdle in lateral view. After Wade 1935, fig. 33. 1.5×.
Cl, cleithrum; *De. spl*, dentalo-splenial; *Ext?*, extrascapular?; *Ju*, jugal; *La*, lacrimal; *Mx*, maxillary; *Op*, operculum; *Pa*, parietal; *Po*, postorbital; *Pop*, preoperculum; *Pt*, posttemporal; *Scl*, supracleithrum; *Sclr*, sclerotic ring; *Sop*, suboperculum; *fe. en*, fenestra endonaria communis; *ifc*, infraorbital sensory canal; *lc*, main lateral line; *mdc*, mandibular sensory canal; *poc*, preopercular sensory canal; *soc*, supraorbital sensory canal.

Pholidopleurid. In 1939, however, Brough in his work on the Triassic fishes of Besano (pp. 23–37) erected the family *Peltopleuridae* Brough, and judging from his description of *Peltopleurus*, this genus does not even bear a remote resemblance to any of the typical Pholidopleurid genera.

In 1941 Berg (pp. 468–471) described one more Pholidopleurid genus, viz. *Arctosomus*, and thus at present the family comprises four genera, all of which are derived from beds of Triassic age.

Both Stensiö (1932, pp. 165–166) and Wade (1935, pp. 64–65) have given a diagnosis of the *Pholidopleuridae*, that of Stensiö is based mainly on the genera *Australosomus* and *Pholidopleurus*, that of Wade exclusively on the genera *Macroaethes* and *Pholidopleurus*.

On the basis of the present investigation it is, of course, possible to some extent to supplement and verify the previous diagnoses; however, as many of the structural details in *Australosomus* now elucidated are still unknown in *Macroaethes*, *Arctosomus*, and *Pholidopleurus*, I shall confine myself to giving the following list of important characters common to all the four genera:

1) Body slender, head small, with orbital openings situated rather far forward and with blunt snout. Gape wide.
2) Frontal large, with supraorbital sensory canal extending backwards only to the centre of radiation.
3) Maxillary rather small, consisting of a high postorbital and a low suborbital division. Preoperculum consisting of a narrow postero-ventral and a wider antero-dorsal shank.

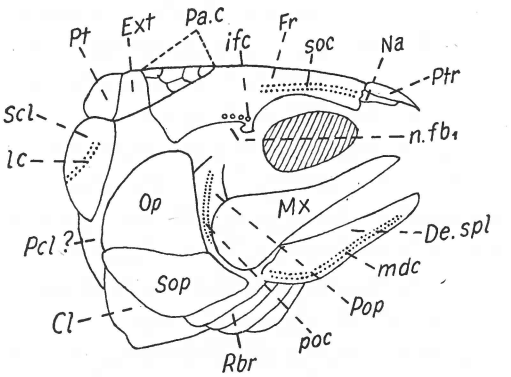


Fig. 59. *Pholidopleurus typus* Bronn. Head and dermal shoulder-girdle in lateral view. After Wade 1935, fig. 32. 2.4×.

Cl, cleithrum; *De. spl*, dentalo-splenial; *Ext*, estrascapular; *Fr*, frontal; *Mx*, maxillary; *Na*, nasal; *Op*, operculum; *Pa. c*, parietal complex; *Pcl*?, anocleithrum?; *Pop*, preoperculum; *Pt*, posttemporal; *Ptr*, postrostral; *Rbr*, branchiostegal ray; *Scl*, supracleithrum; *Sop*, suboperculum; *ifc*, infraorbital sensory canal; *lc*, main lateral line; *mdc*, mandibular sensory canal; *n.* fb_1, notch in the lateral margin of the dermal cranial roof above the fossa bridgei; *poc*, preopercular sensory canal; *soc*, supraorbital sensory canal.

4) Mandible long, without coronoid process.
5) Vertebral column with ring-like centra and with ossified arcuals.
6) Pectoral fins with rather few lepidotrichia. Pelvic fins very small or absent.
7) Dorsal and anal fins long-based and placed far backward. Caudal fin symmetrical or almost symmetrical, with extremely short body axis.
8) Fulcra absent on all fins.
9) Scales thin, arranged in transverse rows. Middle part of each row except most posteriorly consisting of a few very high scales.

The above list might probably be considerably increased if the neural endocranium of *Macroaethes*, *Pholidopleurus*, and *Arctosomus*, the dermal cranial roof of *Macroaethes* and *Arctosomus*, the endoskeleton of the trunk of *Macroaethes*, *Pholidopleurus*, and *Arctosomus*, and the arrangement and structure of the scales in *Macroaethes* and *Arctosomus* were better known. Of important features which will probably turn out to be common to all the four genera the following may be mentioned as especially characteristic:

1) A well ossified neural endocranium differing from that of the typical *Palaeonisciformes* especially in having a longer ethmoidal region with fairly complete nasal cavities and a short blunt rostrum.
2) A parietal complex of three, four, or more elements and fitting like a lid on the posterior dorsal fontanelle.
3) A large emargination in the lateral margin of the dermal cranial roof above the spiracular part of the fossa bridgei.
4) The course of the infraorbital sensory canal through a lateral marginal area of the large frontal.

Judging from Wade's very summary description and most unsatisfactory figures, *Macroaethes* differs from the other Pholidopleurid genera in having a much larger number of branchiostegal rays (NB. In his generic diagnosis Wade (1935, p. 69) writes that branchiostegal rays are absent in *Macroaethes*, and on the same page he mentions that numerous branchiostegal rays are present in *Macroaethes*, while such rays are absent in *Pholidopleurus*. In his description of *Pholidopleurus* he says (p. 68) that a few branchiostegal rays are present in this genus, and judging from his figures, both *Pholidopleurus* (fig. 32) and *Macroaethes* (fig. 33) possess branchiostegal rays. In this case I take it for granted that Wade's figures are more correct than his text) – in lacking teeth, and in the scales on the posterior part of its body being in a much reduced state. From *Australosomus* and *Pholidopleurus* it moreover differs in possessing better developed circumorbital bones, viz. a supraorbito-postorbital, a jugal, a lacrimal, and an anterior supraorbital.

Australosomus differs from *Pholidopleurus* in having shorter and broader branchiostegal rays, a less subdivided parietal complex, small clavicles, pelvic fins, less high abdominal flank scales, and in lacking ganoine at any rate on the greater part of the exposed faces of its scales. From *Arctosomus* it may be distinguished by its smaller number of branchiostegal rays and by the absense of ganoine at least on the greater part of the exposed faces of the dermal bones of the head and on the scales.

Pholidopleurus differs from *Arctosomus* in the greater length of its branchiostegal rays and in the smaller height of its mandible.

As appears from the above, primitive and specialised characters are mixed in such a way in the four Pholidopleurid genera that these genera cannot be ranged into a single phylogenetic line. *Arctosomus* is primitive in having both the dermal bones of the head and the scales covered with ganoine, in having relatively large teeth, and in having a fairly large number of branchiostegal rays; but in regard to its squamation (Berg 1941, fig. 19) it seems to be more specialised than *Australosomus simplex* (fig. 56). *Macroaethes* is primitive as regards the development of its circumorbital bones, as well as in having a very large number of branchiostegal rays and in possessing a pelvic fin, but it is specialised in lacking teeth and in having extremely thin scales at least on the posterior part of its body. *Australosomus* is primitive in possessing clavicles and pelvic fins, but specialised in lacking ganoine at least on the greater part of the exposed faces of the dermal bones of the head and on the scales. *Pholidopleurus* is primitive in having its scales covered with ganoine, but specialised in possessing a very large number of independent parietals and in lacking clavicles and ventral fins.

Thus, in opposition to the view put forward by Wade (1940, pp. 392–393), neither *Pholidopleurus* nor *Macroaethes* can be regarded as descendants from *Australosomus*, but all the four Pholidopleurid genera known must have evolved from some primitive, still unknown Pholidopleurids, probably of Permian age.

Stensiö (1932, p. 164) regards the *Pholidopleuridae* as representing a line of evolution leading from certain primitive *Palaeonisciformes* and pointing »to a certain extent« towards the Pholidophorids and certain other Holostei. Both Wade (1935, p. 66) and Piveteau (1934, p. 40) likewise consider the *Pholidopleuridae* as related to the *Palaeonisciformes*, however, while Wade assumes a Palaeoniscid ancestry for the *Pholidopleuridae*, Piveteau expresses himself with more reservation, saying that the *Pholidopleuridae* »peut être rattachée d'une façon assez lointaine et purement théorique au groupe central des Paléoniscidés«.

The present detailed investigation of *Australosomus* would seem to confirm Stensiö's view regarding the relationships of the *Pholidopleuridae*, in so far as the structure of *Australosomus* offers no serious objection to considering the genus as a derivative of primitive *Palaeonisciformes*, and *Australosomus* is without doubt in many respects specialised in a Holostean direction.

As pointed out by Stensiö (1932) and further discussed by Brough, White, and others, within a considerable number of evolutionary lines issuing from the *Palaeonisciformes* we find this tendency to a development towards the Holostean stage of organisation, a stage, however, which, as far as is known at present, was only reached in a very few cases.

For the many forms belonging to the evolutionary lines which extend into or in some cases even bridges the gap between the *Palaeonisciformes* and the *Holostei*, Brough (1936, 1939) has erected the new order *Sub-Holostei*, classifying the *Actinopterygii* in the following way (Brough 1939, p. 109):

»Order I. *Palaeoniscoidea.*

Diagnosis. – Maxilla and preoperculum large and firmly fixed together on cheek; tail fully heterocercal; dermal fin-rays more numerous than endoskeletal supports.

Order II. *Sub-Holostei.*

Diagnosis. – Maxilla and preoperculum, with few exceptions, preserve Palaeoniscid relationships. Preoperculum rarely in two distinct limbs, as commonly in *Palaeoniscidae*, but usually in form of large, vertical plate, expanded dorsally (it always preserves its broad, plate-like character). Tail hemiheterocercal, or more rarely, homocercal. Dermal fin-rays resemble those of Palaeoniscids, but in many groups they take on full Holostean character, and equal endoskeletal supports in number.

Order III. *Holostei.*

Diagnosis. – Maxilla and preoperculum reduced and completely separated, and preoperculum narrow dorsally. The tail is hemiheterocercal, or rarely, homocercal. Dermal fin-rays few and equal endoskeletal supports in number.

Order IV. Teleosts. As usually defined.«

Westoll (1944, p. 96) criticises Brough's use of the term »order« to indicate progressive grades of evolution without paying sufficient regard to phylogeny, and continues:

»– – – it is an object of this discussion to show that the »Orders« Sub-Holostei and Holostei not only cut across phyletic lines, but are based on characters which are of adaptational nature. It seems far better to regard *all* Actinopterygii which notably differ from palaeoniscids in structure as forming a fringe of evolutionary twigs and branches around a central compact bush in which we may hope some day to distinguish the origin of each derivative group. Within this fringe it is legitimate to recognize close and similar groups, to which handy names such as Teleostei may be given but of group names now in use neither Holostei nor Sub-Holostei can be considered satisfactory. The former certainly covers polyphyletic forms, and the fishes grouped in the latter are not only polyphyletic, in all probability, but are arbitrarily marked off from pre-Triassic fishes which have at least a very remarkably similar degree of specialization«.

Westoll's criticism appears to me to be fully justified, so I cannot accept the orders *Sub-Holostei* and *Holostei*, but until the individual lines of evolution within the Actinopterygians can be more sharply defined, I prefer, like Stensiö and Westoll, for practical reasons to use the terms Subholostean and Holostean as indicating a lower and a higher stage of organisation, respectively, within the non-Palaeonisciform Ganoids.

The *Pholidopleuridae* belong to the Subholostean stage, and as far as is known, the evolutionary line which they represent became extinct before reaching the Holostean stage. About the direction of this line Stensiö (1932, p. 164), as already mentioned, writes that it »to a certain extent seems to point towards the Pholidophorids and certain other *Holostei*«. Now, the *Pholidophoridae*, which, as demonstrated by Brough (1939, p. 111 et seq.) »has served as a reservoir for little-known forms«, are badly in need of a revision, but as far as I can see, Stensiö's assumption is based mainly on the resemblance between the two families in the squamation and the position and shape of the unpaired fins, a resemblance which finds sufficient explantion in parallel development. According to Abel (1919, p. 208), high flank scales, a posterior position and backward lengthening of the dorsal and anal fins, together with reduction of the pelvic fin, are features which only develop in forms in which the shape of the body has changed from fusiform to deep and laterally compressed, and accordingly the ancestors of the fusiform *Pholidopleuridae* should be deep-bodied forms. However, this point of view can hardly be maintained if it is taken into consideration that the characteristics discussed by Abel are not only found in the groups mentioned above, but also in several other primitive Ganoids, as for instance in *Saurichthys*, a form which can hardly be imagined to have been derived from deep-bodied ancestors.

The close resemblance in other respects, also, between the *Saurichthyidae* and the *Pholidopleuridae* has been pointed out by Stensiö (1932, pp. 166, 178), Wade (1935, pp. 65–66), Piveteau (1934, pp. 30, 32, 37–40), E. Niel-

sen (1936, pp. 44–46), and Aldinger (1938, pp. 377, 379) and commented upon especially by Wade and E. Nielsen.

Wade briefly summarises the similarities and dissimilarities between the two families, and draws the conclusion »that the most important particulars in which there is agreement between the two families are also those in which they respectively approach the *Palaeoniscidae* and for which a common Palaeoniscid ancestry would account. The features in which they differ are due to divergent specialization, since the Saurichthyids are well adapted for life in surface waters, and the Pholidopleurids with their extensive gill developments, for bottom-feeding.«

Wade's list of similarities between the two families is as follows:

»(I) The neuro-crania are essential Palaeoniscid in character.
(II) The maxilla has a large post-orbital expansion.
(III) The palates, as far as they are known, are very similar in the extent of the separate bones and the attachment of the pre-operculum to the palate.
(IV) The hyomandibula have no opercular processes.
(V) The supra-orbital sensory canals end posteriorly in the frontals.
(VI) The trunks are long.
(VII) The anal and dorsal fins are very long, with low posterior fringes.
(VIII) The paired fins are very small.
(IX) The shoulder-girdles lack clavicles as separate elements.
(X) The pelvics are supported by rows of radials.
(XI) The dermal rays of the anal and dorsal fins are far more numerous than the radials.
(XII) There are ossified vertebral elements in each with long neural spines.«

To this list I added, in 1936, another point of resemblance, viz.

The agreement in the arrangement of the dermal bones of the cranial roof.

Points (IV) and (IX) must now be struck off the list, the present investigation having shown that both a processus opercularis and a clavicle are present in *Australosomus* and that moreover a clavicle is also developed in a Greenland species of *Saurichthys*. As to point (VI), the slight lengthening of the trunk of *Australosomus* can hardly be compared to the extreme lengthening of the trunk of *Saurichthys*, but as to the other points of the list Wade is probably right in regarding them as sufficiently explained by assuming a Palaeonisciform ancestry of the two families. To most of these points, however, it must be remarked that they deal with features which are common to most of or all the primitive Ganoids.

Wade's list of dissimilarities between the two families runs as follows:

»(I) The snout in the *Pholidopleuridae*, though prominent, is blunt and rounded.

(II) The maxilla in the *Saurichthyidae* is excavated by a quadrato-jugal at the angle of the mouth.

(III) The pre-opercula differ in shape and extent.

(IV) The operculum, sub-operculum and branchiostegal rays are very well developed in the *Pholidopleuridae.*

(V) The dentition of *Saurichthys* was powerful; no teeth have been found in *Macroaethes,* and those of *Pholidopleurus* are small.

(VI) The tail of the *Pholidopleuridae* is slightly asymmetrical; that of the *Saurichthyidae* is symmetrical.

(VII) The vertebral columns differ greatly in structure.

(VIII) The neural spines of the *Saurichthyidae* are paired and there are ribs; in the *Pholidopleuridae* the neural spines are single and there are no ribs.

(IX) The *Pholidopleuridae* have a complete covering of scales, but the *Saurichthyidae* merely four longitudinal lines of scales.«

As pointed out by the present author already in 1936, point (IX) in the above list must be dropped, and as is evident from Stensiö's investigations in 1932 as well as from the present study, the same is the case with points (II) and (VIII). Of the remaining points in the list the greater number are of little significance, the only puzzling one being point (VII), which deals with the vertebral column. Regarding this point it is at present impossible to form an opinion of the mutual position of the *Pholidopleuridae* and the *Saurichthyidae,* for the structures of the axial skeleton in these two groups differ so much that a direct comparison cannot be made, and our knowledge of the vertebral column in the *Palaeonisciformes* is so scarse that it is impossible to judge whether the specialised vertebral structures in the *Pholidopleuridae* and the *Saurichthyidae* have possibly developed from the primitive structure in a common Palaeonisciform ancestor.

Wade's lists of similarities and dissimilarities as revised above offer little support for the assumption put forward by Aldinger and myself regarding a close relationship between the *Pholidopleuridae* and the *Saurichthyidae* (E. Nielsen 1936, pp. 44, 45; Aldinger 1938, p. 379), and the present study of the structures of *Australosomus* has supplied no other proofs of the existence of anything like a closer relationship between the two groups. Wade may be right in explaining the resemblances between the two groups as solely due to their Palaeonisciform origin, although sufficient grounds for the Palaeonisciform origin of *Saurichthys* have not yet been given.

BIRGERIA STENSIÖ.

Syn. 1844. *Saurichthys* (in part), Agassiz, Poissons fossiles, vol. II, part 2, p. 85.
1907. *Xenestes*, Jordan, pp. 120–121.
1919. *Birgeria*, Stensiö, pp. 177–181.
1921. *Birgeria*, Stensiö, pp. 150–200.
1928. *Birgeria*, Corroy, pp. 19–20.
1931. *Birgeria*, Aldinger, pp. 167–180.
1932. *Birgeria*, Stensiö, pp. 98–117.
1936. *Birgeria*, E. Nielsen, p. 43–44.
1938. *Birgeria*, Aldinger, pp. 324–348, 376–379.

For the history of *Birgeria* prior to 1932 the reader is referred to Stensiö 1932 (pp. 98–99). Its later history is brief. In 1936 I published a few remarks on the genus, and in 1938 Aldinger briefly discussed its relationships.

Parts of the skeleton of *Birgeria* have been described in fairly great detail by the previous investigators (chiefly by Stensiö and Aldinger), while other parts have remained almost or entirely unknown. On the basis of the large fresh material from East Greenland, the bulk of which was collected by myself in the years 1932–33 and 1936–37, it is now possible to investigate in detail almost the whole skeleton of *Birgeria* and thus to considerably increase our knowledge of this highly interesting form.

The East Greenland collections comprise 109 specimens of *Birgeria*, all of which probably belong to the same species.

The Greenland species of Birgeria.

Birgeria groenlandica Stensiö.

(Figs. 60–66, 69–81; pls. 11–20).

Syn. 1932. *Birgeria groenlandica*, Stensiö, pp. 109–117, 290–292. Figs. 40–41; pl. 10, fig. 3; pl. 12, fig. 4; pl. 26, fig. 1; pl. 30, figs. 2, 3.
1936. *Birgeria*. E. Nielsen, pp. 43–44.

MATERIAL AND LOCALITIES.

Specimens nos. 15 (holotype) and 48 (Stensiö's numbers) of the material treated by Stensiö and collected prior to 1932. Specimens nos. 650–756 of the material collected in the years 1932–1937. Specimen no. 705 was collected in Fish-zone V in the Kap Stosch area, specimen no. 756 was found by H. Stauber on Gurreholms Bjærge, N.W. Jameson Land, in 1938, specimen no. 664 and Stensiö's specimen no. 48 are derived from the only fish-zone (Fish-zone II) in the Hird Bay area, while all the others have been collected in Fish-zone II in the Kap Stosch area.

HOLOTYPE.

As holotype Stensiö (1932, p. 109) has chosen specimen no. 15, consisting of a head which lacks the occipital parts of the cranium, the posterior part of the maxillary, and the opercular apparatus.

MEASUREMENTS.

In its present state of preservation the head chosen as holotype measures about 12 cm in length, and Stensiö estimates its total length at at least 15 cm. (Stensiö 1932, p. 109). Stensiö's other specimen, which consists of the posterior part of the abdominal region and the greater part of the caudal region, measures only 7 cm in length (ibid., p. 290)) and its total length must thus have been very much smaller than that of the holotype.

The large fresh collections comprise 107 specimens belonging to two well separated size groups without any intermediary forms. The largest group comprises 95 specimens, the estimated total length of which varies from 9 to 21 cm, while the other comprises only 12 species, the estimated total length of which varies from 53 to 84 cm. This curious fact, which is illustrated in the accompanying diagram, might make us suspect that the material comprises two different species (a possibility which has already been touched upon by Stensiö (1932, p. 292)), but a comparison between the large and the small specimens has revealed nothing at all to support this suspicion, and accordingly I must at present refer the whole material to the species *Birgeria groenlandica*. I wish to point out, however, that the comparison between the large and the small specimens has been less detailed than desirable, since the greater part of the structure of the endo- and exoskeleton of the head could not be studied in detail in the small specimens, the heads of these being always badly crushed, while the skeletons of the dorsal, anal, and pelvic fins, as well as considerable parts of the axial skeleton, are not preserved in any of the big specimens.

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of *Birgeria* was collected, was the spawning area of *Birgeria*, which the young individuals left after attaining a certain age, and to which they returned later in order to spawn.

Most of the large specimens consist of more or less complete heads, and some of them further present remnants of the shoulder-girdle, the pectoral fin, and the most anterior part of the axial skeleton of the abdominal region. A single specimen (no. 655) consists of a portion of the axial skeleton of the anterior part of the caudal region.

The dimensions of the largest specimen (no. 650), which consists of the head with the shoulder-girdle, the most anterior part of the axial skeleton, and remnants of the endoskeleton of the pectoral fin, are as follows:

Length of head from tip of snout to posterior margin of suboperculum about 20 cm. Maximum height of head about 13 cm.

Breadth of the slightly flattened dermal cranial roof just behind orbit 7.2 cm. Length of frontal 5.2 cm. Estimated length of lower jaw about 16.5 cm. Estimated total length of fish about 84 cm.

The small specimens in most cases consist of the more or less crushed head together with the shoulder girdle, the pectoral fin, and a smaller or greater part of the axial skeleton of the abdominal region. Some specimens, however, are almost complete, and of these specimen no. 661 (pl. 10) is especially beautifully preserved.

The dimensions of specimen no. 661 are as follows:

Total length about 15 cm. Length of head 3.5 cm.

Estimated maximum depth of trunk (a short distance behind the shoulder girdle) 2 cm.

Distance from posterior margin of extrascapular series to base of anterior margin of dorsal fin 8.3 cm.

Distance from base of anterior margin of pectoral fin to base of anterior margin of pelvic fin 2.3 cm.

Distance from base of anterior margin of pelvic fin to base of anterior margin of anal fin 2.7 cm.

Distance from base of anterior margin of anal fin to base of anterior margin of ventral lobe of caudal fin 2.6 cm.

It is on the basis of the dimensions of specimen no. 661 given here that the total lengths of a number of incomplete specimens included in the diagram on p. 186 have been estimated. The method is probably fairly reliable as regards the small specimens, but less so as regards the large ones.

DESCRIPTION.

Neural endocranium.

General remarks. – The neural endocranium contains a number of ossifications, which in the small specimens, however, are always too much

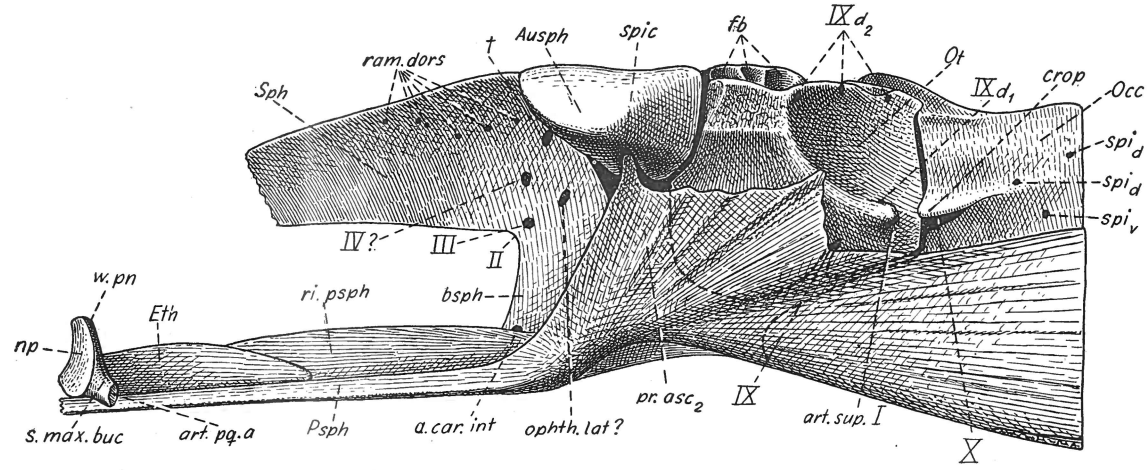


Fig. 60. *Birgeria groenlandica* Stensiö. Attempted restoration of neural endocranium with parasphenoid in lateral view. Mainly based on specimens nos. 651 and 652. Faces without perichondral bone reticulated. Outlines of those parts of the occipital ossification and the prootico-opistotic, which are covered by the parasphenoid indicated by broken lines. C. 1.5×.

Ausph, autosphenotic; *Eth*, ethmoidal ossification; *Occ*, occipital ossification; *Ot*, prootico-opistotic; *Psph*, parasphenoid; *Sph*, sphenoid; *a. car. int*, canal for the arteria carotis interna; *art. pq. a*, articular process for the pars autopalatina palatoquadrati; *art. sup. I*, articular process for suprapharyngobranchial I; *bsph*, pars basisphenoidea; *crop*, processus cranio-spinalis; *fb*, fossa bridgei; *np*, nasal pit; *ophth. lat*?, canal possibly lodging the ramus ophthalmicus lateralis; *pr. asc*$_2$, processus ascendens posterior; *ram. dors*, canals for branches of the ramus ophthalmicus lateralis; the ramus ophthalmicus superficialis trigemini and vessels; *ri. psph*, parasphenoid rigde; *s. max. buc*, groove for the ramus maxillaris trigemini, the ramus buccalis lateralis, and vessels; *spic*, spiracular canal; *spi*$_d$, *spi*$_v$, canals for roots of spino-occipital nerves; *t*, canal perhaps for a vessel; *w. pn*, postnasal wall; *II*, opening for the nervi optici; *III*, canal for the nervus oculomotorius; *IV*?, canal perhaps for the nervus trochlearis; *IX*, notch for the nervus glossopharyngeus; *IXd*$_1$, *IXd*$_2$, canals for supratemporal branches of the nervus glossopharyngeus; *X*, notch for the nervus vagus.

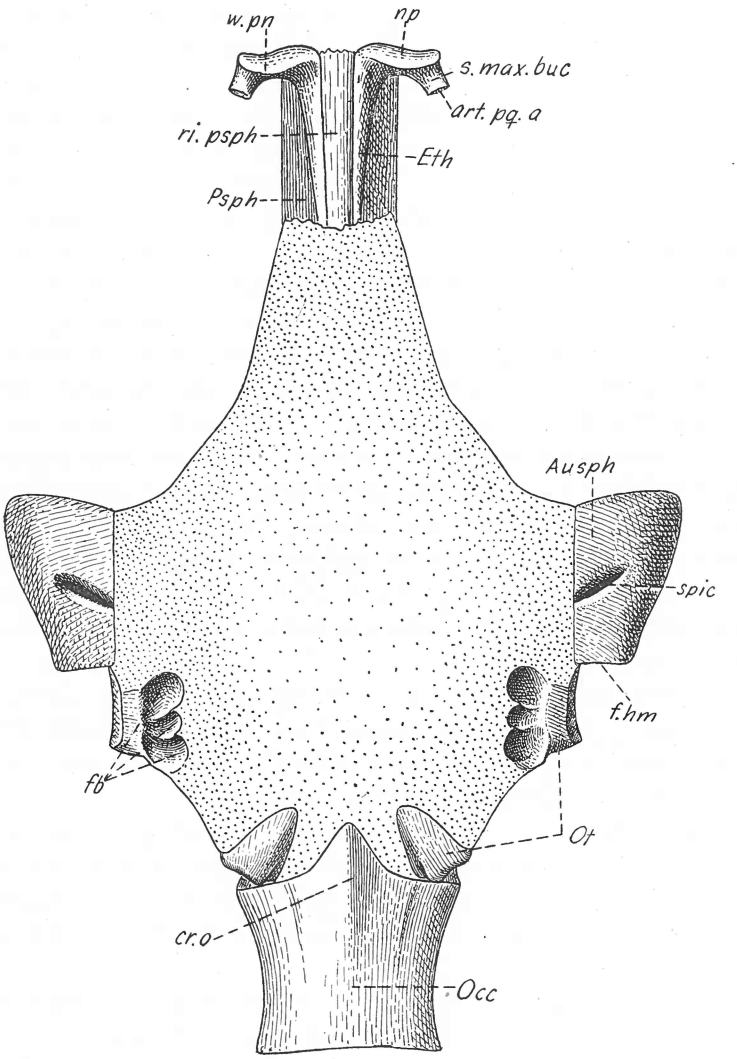


Fig. 61. *Birgeria groenlandica* Stensiö. Attempted restoration of neural endocranium in dorsal view. Mainly based on specimens nos. 651 and 652. Restored cartilaginous areas dotted. C. 1.5×.

cr. o, crista occipitalis; *f. hm*, articular facet for the hyomandibula. Other letters as in fig. 60.

crushed to allow a close examination of them; hence the following description is based exclusively on the large heads, especially on specimens nos. 651 and 652, in which the neurocranial ossifications are better preserved.

The following ossifications have been observed: An unpaired occipital ossification, a paired prootico-opistotic, a paired autosphenotic, an unpaired sphenoid, and a paired ethmoidal ossification. The ossifications, which consist

of cancellar endochondral bone lined, on the greater part of their external and on some internal faces, by a fairly thick layer of perichondral bone, are separated by more or less broad interspaces, which in the living animal were probably completely, or almost completely, occupied by cartilage.

The unpaired occipital ossification (*Occ*, figs. 60–62, 65; pl. 11, figs. 1, 3; pl. 12, figs. 1, 2; pl. 13, fig. 1) is situated partly in the occipital region and partly in the postero-ventral part of the otic region. The paired prooticoopistotic (*Ot*, figs. 60–62, 65; pl. 11, figs. 1, 3; pl. 13, fig. 1) and the paired autosphenotic (*Ausph*, figs. 60–62, 65; pl. 11, figs. 1, 3; pl. 12, fig. 1; pl. 13, fig. 1) are situated in the otic region. The unpaired sphenoid (*Sph*, figs. 60, 62; pl. 11, fig. 3; pl. 12, fig. 1; pl. 13, fig. 1) is mainly situated in the posterior and middle part of the orbitotemporal region, and the paired ethmoidal ossification (*Eth*, figs. 60–62; pl. 12, fig. 1) is situated partly in the anterior part of the orbitotemporal region and partly in the ethmoidal region.

On the basis of its ossifications we are able to form a general idea of the external shape of the neural endocranium, but as a considerable part of the structure is unossified, and as, moreover, most of its ossifications are to some extent damaged, it is not possible to reconstruct the neural endocranium with anything like the same exactness as in the case of *Australosomus* or *Pteronisculus*.

The endocranium of specimen no. 652 measures about 8.5 cm in length, 5.5 cm in greatest breadth, and about 3 cm in greatest height. The endocranium of specimen no. 651 measures about 6 cm in total length and probably about 2.5 cm in greatest height.

Occipital region. – The length of the occipital region (figs. 60–62) is about two-ninths of the total length of the neural endocranium, and the ratio between its breadth, length, and height is about 2:2:3. Compared with that of typical *Palaeonisciformes*, the occipital region is thus relatively long and narrow.

For descriptive reasons the occipital region may be divided into two divisions situated above, respectively below, a level determined by the lateral margins of the occipital part of the parasphenoid. The dorsal division is fully occupied by the dorsal part of the occipital ossification and, as shown in the figures, it is well marked off from the otic region. The ventral division, which is only partially ossified, contains the postero-ventral part of the occipital ossification, while, as already mentioned, the antero-ventral part of the occipital ossification extends forwards into the likewise only partially ossified postero-ventral part of the otic region. The transition between the ventral part of the occipital region and the adjoining part of the otic region is quite gradual.

Taken as a whole, the occipital region is bounded by an unpaired posterior, an unpaired dorsal, and a paired lateral face.

The posterior face is well defined, while the lateral and the dorsal faces

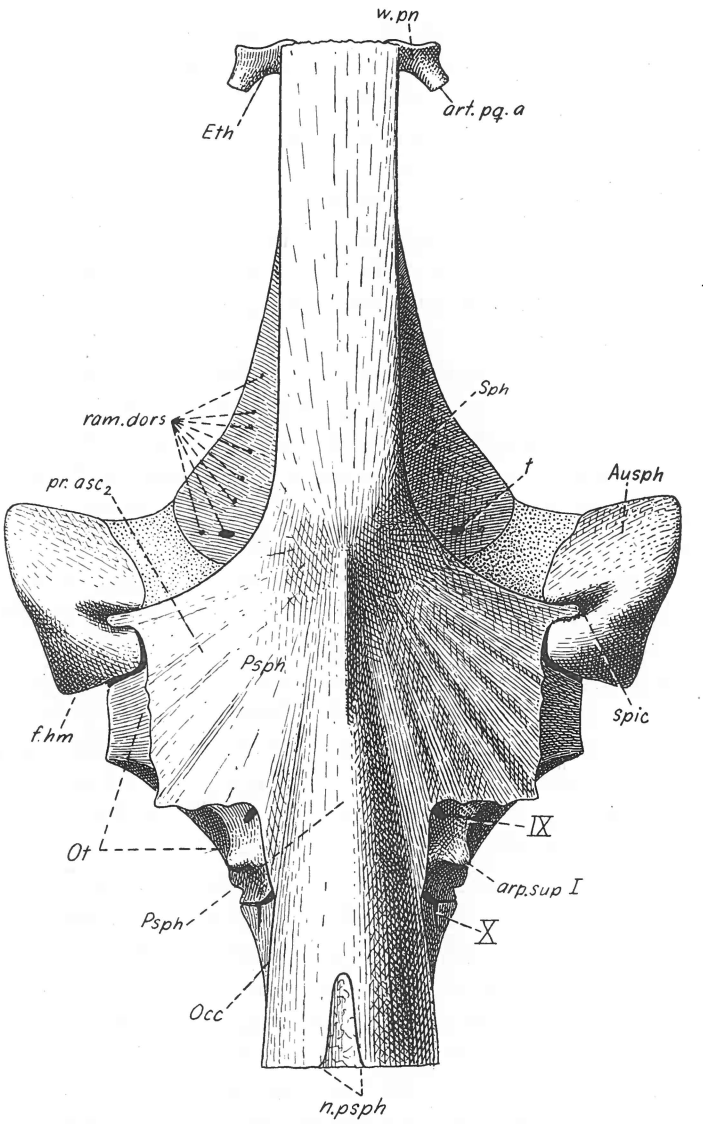


Fig. 62. *Birgeria groenlandica* (Stensiö). Attempted restoration of neural endocranium with parasphenoid in ventral view. Mainly based on specimens nos. 651 and 652. Faces without perichondral bone reticulated. Restored cartilaginous areas dotted. C. 1.5×. *n. psph*, notch in the posterior margin of the parasphenoid. Other letters as in figs. 60 and 61.

pass quite gradually into one another except farthest anteriorly, where they are separated by a small ridge. Ventrally the lateral face meets its fellow of the other side in a median longitudinal keel, which fits into the deepest part of the deep longitudinal groove formed by the posterior part of the parasphenoid.

The posterior face is poorly exposed in the two specimens investigated,

but as far as can be seen, it is about twice as high as broad and has a rounded outline, which differs from an ellipse by being somewhat compressed from side to side in its ventral part. On the posterior face we find two large openings, one above the other, viz. dorsally the foramen magnum, and ventrally the posterior opening of the notochordal space (*cn*, pl. 11, fig. 1). In one of my specimens (no. 652) the wall separating the two foramina seems to have been cartilaginous in its median part. The foramen magnum is almost circular in outline except for a slight ventral flattening, on account of which the opening is somewhat broader than high. The rounded opening of the notochordal space is, in the fossil state, considerably higher than broad; however, since the notochordal space is not lined with perichondral bone, and since, moreover, the most ventral part of the occipital region in both specimens is almost completely unossified, the opening must have been constricted by cartilage to some extent in the living animal and may very well have been circular or almost circular. In fact, as the most ventral part of the occipital region in both the specimens investigated consisted mainly of cartilage, it is not even possible from the preserved part of the occipital region to decide whether an aorta canal was developed ventrally to the notochordal space, as is the case in typical *Palaeonisciformes*.

The posterior half of the dorsal face, which is mainly convex from side to side, as already mentioned passes gradually into the lateral face, from which the anterior half of the dorsal face is separated by a short longitudinal ridge, the height of which increases slowly in an anterior direction. On the dorsal face, the outline of which is shown in fig. 61, we find a short median crest (*cr. o*, figs. 61, 65; pl. 11, fig. 1), which extends from the anterior margin to the central part of the face and decreases in height in a posterior direction throughout its whole length. The median crest undoubtedly corresponds to the crista occipitalis in typical *Palaeonisciformes*.

Posteriorly the lateral face is about twice as high as broad, and from here decreases slowly in height in an anterior direction. That part of the face which belongs to the dorsal division of the occipital region, i. e. that part which is not covered by the parasphenoid, is somewhat longer than high and in lateral view presents a roughly rectangular outline. On this face, which is convex in a dorso-ventral and slightly concave in a rostro-caudal direction, we find, just behind the anterior and a short distance above the ventral margin, a strong process (*crop*, fig. 60), which extends in a lateral and slightly ventral direction. As the process is somewhat flattened in a dorso-ventral direction, it might also be described as a short ridge extending from the anterior margin to a point situated midway between the anterior and the posterior margin and decreasing in height from its anterior to its posterior end. Just ventrally to this process or ridge, which may best be interpreted as a cranio-spinal process, we find, in the anterior margin of the occipital ossification, a very deep fissure-like notch (X, figs. 60, 62;

pl. 11, fig. 3; pl. 12, fig. 1), which should undoubtedly be interpreted as the place of exist for the nervus vagus and the nervus lineae lateralis. More posteriorly on the dorsal part of the lateral face we observe the external openings of three narrow canals, which issue from the occipital division of the cavum cerebrale cranii and which probably lodged the roots of spino-occipital nerves. As shown in fig. 60, two of these canals (spi_d) have a fairly dorsal position and accordingly probably lodged dorsal nerve-roots, while the third one (spi_v) was most likely passed by ventral roots. That part of the lateral face which belongs to the ventral division of the occipital region, i. e. that part of the lateral face which is covered laterally by the parasphenoid, in lateral view has a trapezoidal outline, its anterior and its posterior margins being both vertical, and the former being shorter than the latter. The ossified area of this part of the lateral face is slightly convex in a dorso-ventral direction and is not pierced by any foramina.

The occipital division of the cavum cerebrale cranii is rounded in transverse sections, with its floor much less concave than its roof, and with its breadth somewhat greater than its height. Both its floor and its lateral walls are fairly massive, while its roof is relatively thin. The cerebral faces of the lateral walls and the roof are completely lined with perichondral bone, and the same is the case with the floor in specimen no. 651, while the floor in specimen no. 652, as already mentioned, is partially unossified.

The notochordal space, which extends forward through the whole occipital region and the greater part of the otic region, was probably constricted by cartilage to some extent in the living animal, its walls not being lined with perichondral bone. Accordingly its exact shape cannot be stated. Ventrally to the notochordal space the occipital region is at any rate partially unossified, and in both the specimens investigated it is so badly crushed that no details regarding its structure can be given.

Otic region. – The otic region is almost twice as long as the occipital region, its rostro-caudal extent being slightly less than two-fifths of the total length of the neural endocranium. Farthest posteriorly the breadth of the region is almost equal to that of the most anterior part of the occipital region. The breadth increases in an anterior direction to reach its maximum, not only for the otic region but for the whole neural endocranium, between the stout postorbital processes. The maximum breadth is about 1.7 times the length of the region. Throughout the region the breadth decreases rapidly in a ventral direction. The most posterior part of the otic region is slightly lower than the adjoining part of the occipital region, and from here the height decreases slowly towards the foremost part of the region, as shown in fig. 60. As already mentioned, the boundary towards the occipital region is well defined dorsally, while ventrally the transition between the two regions is very gradual. Owing to its much greater breadth, the otic region is well separated dorsally from the orbitotemporal region, but more ventrally

no exact boundary between the two regions can be drawn, for here the neurocranial wall is partially unossified. Strictly speaking, a small posterior part of the unpaired sphenoid is situated in the otic region; however, for practical reasons the whole sphenoid will be dealt with in the description of the orbitotemporal region.

In addition to the antero-ventral part of the occipital ossification the otic region contains two paired ossifications, viz. an autosphenotic and a prootico-opistotic. The otic part of the occipital ossification is situated in the postero-ventral part of the otic region, while the prootico-opistotic forms the greater part of the lateral neurocranial wall dorsally and antero-dorsally to the otic part of the occipital ossification and furthermore it extends into the roof of the region, and, finally, the autosphenotic occupies the strong postorbital process.

To all the ossifications in the otic region it applies that only their external faces have been investigated in detail, while their internal faces, which were probably devoid of perichondral bone, could not be exposed without the specimens being too much damaged.

On the basis of its ossifications it is possible to obtain a fairly satisfactory picture of the otic region as a whole, although, of course, the details of its unossified parts cannot be made out.

As the region is roughly triangular in transverse section, with one corner of the triangle pointing downwards, we may distinguish between an unpaired dorsal and a paired mainly ventro-lateral face.

The dorsal face presents three small paired ossified areas, all of which are situated along its lateral margin. The foremost of these areas is the dorsal face of the autosphenotic, the midmost one is the dorsal face of the anterior part of the prootico-opistotic, and the hindmost one is the dorsal face of the most posterior part of the prootico-opistotic. Apart from these small marginal areas the roof of the otic region was entirely cartilaginous, and accordingly it is impossible to decide whether the central part of the roof was pierced by a median dorsal fontanelle, as in some typical *Palaeonisciformes*.

The hindmost ossified marginal area of the dorsal face is situated just anteriorly to the boundary between the otic and the occipital regions. It is triangular in outline, with a straight postero-lateral, a convex antero-lateral, and a convex postero-medial margin. The two latter margins are of about the same length and much longer than the former. The area is slightly convex from side to side and on its posterior part shows a short blunt postero-dorsally pointing process.

The midmost ossified marginal area is somewhat longer than broad and shows, on its medial part, a very deep depression (*fb*, figs. 60, 61; pl. 11, fig. 1) which is incompletely subdivided by two sharp transverse crests into an anterior, a middle, and a posterior division, of which the middle one, as

shown in fig. 61, is the smallest and the posterior one, which is much deeper than the others, is the largest. In the living animal the depression probably extended much farther forward, for in the fossils its anterior margin lies on a lower level than its lateral, medial, and posterior margins.

The depression described here must undoubtedly be homologised with the posterior deep portion of the fossa bridgei in *Acipenser* (Stensiö 1925, pp. 25–26; 1932, p. 89, fig. 92) and *Polyodon* (Bridge 1878, pp. 694-698, pl. 56, fig. 5; Stensiö 1925, p. 25), and probably also with the posterior deep part of the fossa bridgei in a typical Palaeonisciform such as *Pteronisculus* (E. Nielsen 1942, pp. 43–44). In *Polyodon* and *Pteronisculus* this posterior deep part of the fossa bridgei communicates with the cavum cerebrale cranii by way of a very wide canal, which passes beneath the dorsal part of the canalis semicircularis posterior (Bridge 1878, p. 696; E. Nielsen 1942, p. 44), and rudiments of a similar canal has also been observed in *Acipenser* (Bridge 1878, p. 697). In *Birgeria* there are no traces of such a canal, the only canal opening in the depression here described being a very narrow one (*IX* d_2, fig. 60; pl. 11, fig. 3), which pierces the lateral wall of the posterior division of the depression and which evidently lodged a branch of the ramus supratemporalis dorsalis IX.

The anterior ossified marginal area of the dorsal face is formed by the dorsal or dorso-lateral face of the autosphenotic. This face has a four-sided outline, with an anterior, a medial, a posterior, and a lateral or postero-lateral margin, all of which are fairly straight. The face is somewhat convex from side to side, its most lateral part being mainly dorso-laterally directed. On this face we find a narrow oblong depression, the longest diameter of which is directed laterally and somewhat anteriorly, and which probably extends on to the dorsal face of the cartilaginous roof of the region. At the bottom of this depression we find the dorsal opening (*spic*, fig. 61; pl. 11, fig. 1) of a canal, which pierces the autosphenotic in a vertical direction, to open ventrally (*spic*, figs. 61, 62; pl. 11, fig. 3; pl. 13, fig. 1) on the ventro-lateral face of the otic region, as described below. The dorsal opening of this canal, which should, no doubt, be interpreted as a spiracular canal, is long and narrow, almost fissure-like, with its longest diameter pointing laterally and somewhat anteriorly. The depression in which the spiracular canal opens dorsally must be homologised with the most anterior part of the fossa bridgei in *Acipenser* (Stensiö 1932, fig. 35), *Polyodon* (Bridge 1878, pp. 694–698; pl. 56, fig. 50), *Pteronisculus* (E. Nielsen 1942, pp. 43–44, fig. 7), *Boreosomus* (ibid., p. 294, fig. 59), *Perleidus* (Stensiö 1932, p. 193, fig. 59), *Ospia* (ibid., p. 233, fig. 73), etc., and in the living animal this depression was probably connected with the depression on the midmost ossified area of the otic region so as to form a long fossa bridgei of a type similar to that of *Polyodon* and *Acipenser*.

As the lateral wall of the otic region except for an antero-ventral com-

pletely unossified area is occupied by extensive ossifications separated by very narrow unossified zones, the shape of the greater part of the ventro-lateral face of the region can be studied in detail on the fossil material.

On this face we may distinguish between three ossified areas, viz. an antero-dorsal one formed by the mainly ventro-laterally directed face of the autosphenotic, a central or postero-dorsal one formed by the lateral or ventro-lateral face of the prootico-opistotic, and a postero-ventral one formed by the lateral or ventro-lateral face of the otic part of the occipital ossification.

On the antero-dorsal area of the ventro-lateral face, i. e. on that part of the face which is formed by the autosphenotic, we may distinguish between two well separated minor faces, viz. a small posterior backward-directed face and a more anterior, somewhat larger, and mainly ventro-laterally directed face, which is angularly bent in such a way that its most posterior part is also directed somewhat posteriorly and its most anterior part somewhat anteriorly. The small posteriorly directed face, which is almost twice as high as broad and roughly rectangular in outline, is entirely devoid of perichondral bone and in the living animal was probably covered by cartilage, which formed part of the articular area for the hyomandibula. On the mainly ventro-laterally directed face, which in ventral view (fig. 62) is roughly triangular in outline, we find the ventral opening of the spiracular canal. This opening (*spic*, figs. 60, 62; pl. 11, fig. 3; pl. 13, fig. 1), the most medial part of which was situated on the ventro-lateral face of the cartilaginous part of the lateral wall of the otic region medially or ventro-medially to the ventro-lateral face of the autosphenotic, is long and narrow, like the dorsal opening of the spiracular canal, with its longest diameter pointing laterally and somewhat anteriorly. As in several other *Palaeonisciformes*, the most dorsal part of the processus ascendens posterior of the parasphenoid enters the spiracular canal through its ventral opening, to end dorsally after traversing the canal in its whole length.

In lateral view (fig. 60) the lateral face of the prootico-opistotic is almost rectangular in outline, with a dorsal, a ventral, an anterior, and a posterior margin. Its breadth is somewhat greater than its height. The face is divided into a postero-dorsal and an antero-ventral division by a strong oblique ridge, which extends from the antero-dorsal angle of the face in a postero-ventral direction, to end a short distance before reaching the postero-ventral angle of the face. Farthest antero-dorsally the ridge is much widened and appears as an almost rectangular, highly elevated area, which is completely devoid of perichondral bone, and which was probably covered by cartilage in the living animal. As shown in the figures, the elevated area is situated just behind the posterior face of the autosphenotic, and its cartilaginous lining probably formed part of the articular area for the hyomandibula. Backwards from its widened antero-dorsal part the oblique ridge at first

grows lower and then increases in height in such a way that its most postero-ventral part appears as a rather slender, mainly laterally directed process (*art. sup, I*, figs. 60, 62; pl. 12, fig. 1), against which suprapharyngobranchial I articulated, and which must accordingly be compared to the elevated articular area developed on the postero-ventral part of the lateral face of the otic region in *Pteronisculus* (E. Nielsen 1942, p. 48), *Australosomus* (the present paper p. 41), and other primitive Actinopterygians.

The oblique ridge divides the lateral face of the prootico-opistotic into a postero-dorsal and an antero-ventral division. The postero-dorsal division is directed mainly laterally and posteriorly and is markedly concave, while the antero-ventral division is rather plane and mainly ventro-laterally directed. The latter division, except for its most dorsal and most posterior parts, is covered by the parasphenoid. In the ventral margin we find, somewhat nearer the posterior than the anterior end, a very deep fissure-like notch (*IX*, figs. 60, 62; pl. 11, figs. 1, 3; pl. 12, fig. 1; pl. 13, fig. 1), which should evidently be interpreted as the place of exit for the greater part of the nervus glossopharyngeus. Just dorsally or antero-dorsally to the process against which suprapharyngobranchial I articulated we observe the small opening of a very narrow canal (*IX* d_1, fig. 60), which probably lodged the ramus supratemporalis dorsalis IX, and quite near the dorsal margin of the postero-dorsal division of the lateral face of the prootico-opistotic we find the fairly large openings of three canals (*IX* d_2, fig. 60; pl. 11, fig. 3), which pierce the sharp crest separating the dorsal and the lateral faces of the otic region, and through which branches of the ramus supratemporalis dorsalis IX probably reached the dorsal face of the endocranium. The foremost of these canals opens, as already mentioned, in the posterior deep division of the fossa bridgei, while the other two open on the cartilaginous area of the dorsal face behind the fossa bridgei.

The lateral face of the otic part of the occipital ossification is completely covered by the parasphenoid, so it is difficult to investigate it in detail. The face, which is triangular in outline, with an antero-dorsal, a posterior, and an antero-ventral margin, is slightly convex in a dorso-ventral direction, as is also the case with the adjoining part of the lateral face of the occipital region, into which it passes without any marked boundary.

The internal faces of the autosphenotic and the prootico-opistotic are poorly exposed in my two specimens. As far as could be seen, they are devoid of perichondral bone, and hence the otic division of the cavum cerebrale cranii was probably completely surrounded by cartilage.

The labyrinth cavity, which is mainly enclosed in the prootico-opistotic, has not been investigated in order not to destroy important parts of the endocrania.

Orbitotemporal region. — The orbitotemporal region is almost as long as the otic and the occipital region together. Farthest anteriorly its

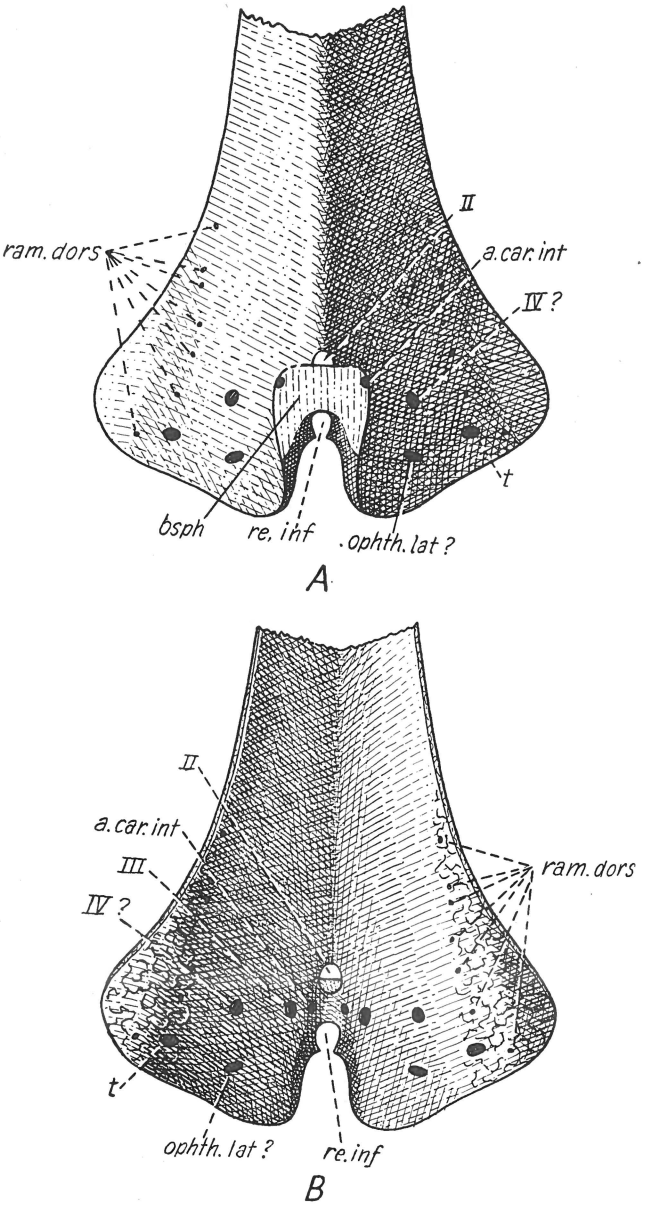


Fig. 63. *Birgeria groenlandica* Stensiö. Attempted sketch of the sphenoid in (A) ventral and (B) dorsal view. Mainly based on specimens nos. 651 and 652. Faces without perichondral bone reticulated. C. 2×

re. inf, infundibular recess. Other letters as in fig. 60.

breadth, which decreases throughout the region in an anterior direction, is, in the fossil state, much less than that of the ethmoidal region. Posteriorly the height of the region, in the fossil state, is equal to that of the foremost part of the otic region, but decreases gradually in an anterior direction.

Since, however, the region is largely unossified, it is probable that both its breadth and its height were at least somewhat greater in the living animal.

The orbitotemporal region contains three ossifications, viz. a large unpaired sphenoid situated in the posterior and postero-dorsal part of the region, and a rather small paired ossification situated in the antero-ventral part of the region and forming the posterior part of the paired ethmoidal ossification. The antero-dorsal part as well as the whole roof of the region is unossified and it is therefore impossible to obtain an exact picture of the shape of the region. It appears, however, that the eyes were large, and on account of their strong development, a large interorbital fenestra has arisen in the interorbital wall, while the interorbital division of the cavum cerebrale cranii has been confined to the dorsal part of the wall.

The sphenoid is rather poorly preserved in the specimens investigated, and especially its ventral and posterior parts are much damaged. The following description is therefore far from complete, and as far as this structure is concerned, the accompanying drawings (figs. 60, 62, 63) must be regarded as mere sketches.

On the sphenoid of *Birgeria mougeoti*, Stensiö (1921, p. 162) distinguishes an unpaired ventral pars basalis and a paired dorsal (dorso-lateral) pars lateralis, and similarly we may distinguish, on the sphenoid of *Birgeria groenlandica*, a dorsal division situated partly in the lateral wall of the cranial cavity and partly in the lamina supraorbitalis, and a ventral division situated below the cranial cavity. The ventral division, however, only corresponds to the pars basisphenoidea of the pars basalis in *Birgeria mougeoti*, while the dorsal division differs from the pars lateralis in *Birgeria mougeoti* in having a less backward extent and in being unpaired, the right and the left half of the foremost and larger part of the dorsal division having fused below the cranial cavity.

Each half of the dorsal division may be described as a fairly thin, somewhat curved plate, one face of which is mainly ventro-laterally, and the other mainly dorso-medially directed. In a longitudinal direction the plate is slightly curved in such a way that its orbital face is slightly concave and its dorso-medial face correspondingly convex. More precisely, a rather small postero-dorsal part of the plate is bent fairly much outward occupying a nearly horizontal position, while the greater part of the plate is more evenly curved, with the concavity facing ventro-laterally and slightly anteriorly. The plate is roughly four-sided in outline, with an anterior, a dorsal (dorso-lateral), and a posterior free edge, while ventrally it passes gradually into the pars basisphenoidea farthest posteriorly and meets with that of the other side more anteriorly.

The dorsal, the anterior, and perhaps also the posterior edge are devoid of perichondral bone and were thus joined to cartilage in the living animal. Perichondral bone is further lacking on the dorsal face of the almost

horizontal postero-dorsal part of the plate and it is therefore likely that the lamina supraorbitalis, in which this part of the plate was evidently situated, had a greater thickness in the living animal, though probably not by far as great as in *Birgeria mougeoti* (Stensiö 1921,fig. 63). As in *Birgeria mougeoti*, the dorsal division of the sphenoid is pierced by a number of canals for nerves and vessels, however, it is no easy task to give an interpretation of these canals, for they are not arranged in the same way in *Birgeria groenlandica* and in *Birgeria mougeoti*. On account of the rather poor state of preservation of the specimens investigated by me it is moreover possible that one or more canals may have been overlooked.

Just anteriorly to the most dorsal part of the pars basisphenoidea the dorsal division of the sphenoid is pierced by a large unpaired opening (*II*, figs. 60, 63; pl. 12, fig. 1; pl. 13, fig. 1), which is, no doubt, the foramen opticum. In *Birgeria mougeoti* the foramen opticum is paired, and immediately in front of it there is another smaller foramen, which according to Stensiö (1921, p. 168) most probably lodged the arteria optica.

The postero-ventral part of the dorsal division of the sphenoid is pierced by three fairly wide canals extending from the cavum cerebrale cranii to the posterior part of the orbit. One of these canals (*III*, figs. 60, 63; pl. 12, fig. 1; pl. 13, fig. 1) pierces the cranial wall a short distance postero-dorso-laterally to the foramen opticum and probably lodged the nervus oculomotorius. Of the other two canals, one (*IV*?, figs. 60, 63; pl. 11, fig. 3; pl. 13, fig. 1) is situated some distance dorso-laterally, and the other (*ophth. lat*, figs. 60, 63; pl. 11, fig. 3; pl. 13, fig. 1) a similar distance postero-dorso-laterally to the foramen for the nervus oculomotorius. A comparison with *Birgeria mougeoti* does not contribute very much to facilitate the interpretation of these two canals. It is possible that the dorsalmost one is the trochlearis canal, but it is situated somewhat more antero-dorsally than the external opening of the trochlearis canal in *Birgeria mougeoti* (Stensiö 1921, pp. 168–169, figs. 62, 63), and moreover it differs from the trochlearis canal in *Birgeria mougeoti* by its larger diameter, which, however, may be explained on the assumption that it also lodged the vena cerebralis anterior, which in *Birgeria mougeoti* has a canal of its own situated just antero-ventrally to the trochlearis canal. The external opening of the hindmost of the three canals dealt with here is situated almost like the hindmost opening of the canal which, in *Birgeria mougeoti*, lodged the nervus ophthalmicus lateralis and the ramus ophthalmicus superficialis trigemini (Holmgren and Stensiö 1936, p. 407, fig. 303), but in *Birgeria mougeoti* this canal does not communicate with the cavum cerebrale cranii. The canal should therefore perhaps rather be compared to the notch in the hinder margin of the sphenoid in *Birgeria mougeoti*, through which the truncus maxillomandibularis and perhaps also the ramus ophthalmicus superficialis trigemini passed.

The postero-dorsal part of the dorsal division of the sphenoid is pierced by about seven very narrow vertical canals (*ram. dors*, figs. 60, 62, 63; pl. 11, fig. 3; pl. 13, fig. 1), which probably continued in a dorsal direction through the cartilaginous dorsal part of the lamina supraorbitalis, and which probably should be compared to the short vertical canals piercing the posterior part of the lamina supraorbitalis in *Pteronisculus* (E. Nielsen 1942, p. 88), *Boreosomus* (ibid., p. 303), etc., and through which branches of the nervus ophthalmicus lateralis and perhaps also branches of the ramus ophthalmicus superficialis trigemini and vessels reached the dorsal face of the neural endocranium. A short distance medially to the hindmost of the narrow canals described here we find a much wider canal (*t*, figs. 60, 62, 63; pl. 11, fig. 3; pl. 13, fig. 1), which also pierces the ossified part of the supraorbital lamina in a vertical direction. Judging from its position this canal, like the narrow ones just mentioned, may very well have served as a passage for nerves and vessels on their way to the dorsal face of the neural endocranium; however, the possibility also exists that the canal never reaches the dorsal face, but after piercing the ossified part of the supraorbital lamina opened in the cavum cerebrale cranii, in which case it probably contained minor vessels only.

The ventral division of the sphenoid, which, as already mentioned, corresponds to the pars basisphenoidea in *Birgeria mougeoti*, is rather badly damaged in both the specimens investigated and accordingly cannot be described in detail. As far as could be made out, it is a fairly massive bone-pillar (*bsph*, figs. 60, 63; pl. 11, fig. 1; pl. 12, fig. 1) reaching from the cavum cerebrale cranii in a ventral direction to the level of the ventral part of the orbitotemporal region. On this pillar we may distinguish six faces separated by distinct edges, viz. a dorsal, a ventral, an anterior, a posterior, and a right and a left lateral face.

The dorsal face, which forms the bottom of the cranial cavity behind the foramen opticum, laterally passes gradually into the cerebral face of the lateral cranial wall, while posteriorly it has a free, deeply concave margin. As shown in fig. 63, the anterior part of the concavity (*re. inf*, fig. 63; pl. 13, fig. 1) is partially separated from the posterior one by two small medially pointing processes issuing from the right and the left half, respectively, of the posterior margin. A comparison with *Birgeria mougeoti* (Stensiö 1921, pp. 164–165) shows that this foremost part of the concavity must be interpreted as the dorsal opening of the fossa hypophyseus and the small processes as that part of the basal parachordal plate which corresponds to the anterior part of the prootic bridge in *Amia* and the Teleosts. It is not impossible that the two processes were connected by cartilage. The posterior face is deeply concave from side to side throughout its height and probably the anterior part of this concavity lodged the infundibulum and the hypophysis. The ventral face, which rests against the most posterior part of the pars anterior parasphenoidea, is plane and, as shown in fig. 63 A, is bounded

by an anterior, a paired lateral, and a posterior margin, the last-mentioned of which is deeply concave, while the others are straight or slightly convex. The lateral face, which is slightly convex in a rostro-caudal direction, increases in breadth upwards, its anterior margin being vertical, or almost vertical, while its posterior margin is somewhat backwardly inclined. The anterior face, which is fairly rectangular in outline, with a somewhat greater height than breadth, is only partially lined with perichondral bone, so it is impossible to decide whether a canal for the arteria ophthalmica magna opened on this face, as is the case in *Pteronisculus* and in several other primitive Ganoids.

The pars basisphenoidea is pierced in a vertical direction by a paired canal (*a. car. int*, figs. 60, 63; pl. 12, fig. 1; pl. 13, fig. 1), the ventral opening of which is situated just behind the anterior end of the edge between the ventral and the lateral face of the pillar, and which opens on its dorsal face postero-laterally to the foramen opticum. A comparison with *Birgeria mougeoti* (Stensiö 19 p. 171) shows that this canal must have lodged the arteria carotis interna, which artery in *Birgeria* has thus similar relations to the pars basisphenoidea as in *Pteronisculus* (E. Nielsen 1942, p. 64), *Boreosomus* (ibid., p. 307), Watson's Kansas forms (Watson 1925), *Perleidus* (Stensiö 1932, p. 244), *Saurichthys* (Stensiö 1925, pp. 39–41), and many recent forms (cf. Stensiö 1921, p. 171).

Between the ventral division of the sphenoid and the anterior part of the stout ascending process of the parasphenoid there is a large cavity, which roughly corresponds to the large postorbital cavity in *Birgeria mougeoti* interpreted by Stensiö (1921, pp. 166, 177–180) both as a trigemino-facialis chamber and as a posterior myodome. This cavity cannot be studied in detail in the Greenlandic species; it is evident, however, that its myodomic part differs considerably in shape from that of *Birgeria mougeoti*, for there can be no doubt that *Birgeria groenlandica* lacks homologues both with the stout basipterygoid process and with the posterior and greater part of the basal parachordal plate of *Birgeria mougeoti*. Regarding that part of the cavity which corresponds to a trigemino-facialis chamber, it is probable that it was continued backwards between the posterior part of the processus ascendens parasphenoidea and the prootico-opistotic by a long jugulo-hyoideomandibular canal; however, no such canal could be localised with certainty in the specimens investigated by me.

The orbitotemporal part of the paired ethmoidal ossification is a vertically placed triangular plate-like structure extending in a backward direction from the postnasal wall, and decreasing both in thickness and height towards its posterior end, as shown in the figures. The plate is intimately connected with the parasphenoid, its ventral margin resting against the horizontal lamina of the pars anterior parasphenoidea and its medial face being in close contact with the strong median vertical lamina (*ri. psph*, figs. 60, 61;

pl. 12, fig. 1) present on the dorsal face of the pars anterior parasphenoidea. All the free faces of the plate are lined with perichondral bone.

The exact extent of the fenestra optica cannot be determined, as the antero-dorsal part of the orbitotemporal region is completely unossified; however, there can be no doubt that the fenestra was considerably larger than in *Birgeria mougeoti* (Stensiö 1921, fig. 63). The posterior part of the fenestra is bounded dorsally and posteriorly by the sphenoid and ventrally by the strong median vertical lamina on the pars anterior parasphenoidea.

Ethmoidal region. – The ethmoidal region, as already mentioned, contains the anterior part of a paired ossification, the posterior part of which is situated in the orbitotemporal region. That part of the ossification which belongs to the ethmoidal region is developed as a transversely placed plate, which, judging from its extension and shape, represents the whole or at least the ventro-medial and greater part of the postnasal wall. The height of the plate is about equal to its breadth. The plate has a considerable thickness in its ventro-medial part and grows gradually thinner both in a dorsal and a lateral direction, so that, apart from its relatively large anterior and posterior faces, it presents only a ventral and a medial face, while dorsally and laterally it ends in a sharp crest.

The medial half of the ventral face is covered by the foremost part of the horizontal lamina of the pars anterior parasphenoidea, while the ventral half of the medial face lies close against the foremost part of the prominent vertical median lamina on the dorsal face of the parasphenoid. The lateral and the dorsal margins of the plate are separated from the roofing dermal bones of the snout by wide interspaces, and one might therefore believe that the plate was continued laterally and dorsally by cartilage so as to form a more complete postnasal wall. Curiously enough, however, both these margins are completely lined with perichondral bone and thus show no sign of having been joined to cartilage.

The anterior face is developed as a slight concavity (*np*, fig. 61), which must evidently be regarded either as the whole or the ventro-medial part of the nasal pit. The posterior face is mainly convex both in a dorso-ventral and a transverse direction except farthest medially, where it is curved in such a way that it passes quite gradually into the lateral face of the orbitotemporal division of the ossification. From the ventro-lateral part of the posterior face issues a stout process in a postero-ventro-lateral direction. This process is almost circular in transverse section and has a flattened distal face (*art. pq. a*, figs. 60, 61, 62), which served as an articular facet for the anterior end of the palatoquadrate. Quite near the base of the process its dorsal face is crossed by a distinct groove (*s. max. buc*, figs. 60, 61), by way of which the ramus maxillaris trigemini, the nervus buccalis lateralis, and various vessels probably reached the foremost part of the snout, and which thus corresponds to the groove on the lateral face of the ethmoidal region in *Saurichthys*

(Stensiö 1925, pp. 74, 78, 79, figs. 1, 6, 14, 16) and *Pteronisculus* (E. Nielsen 1942, p. 85, figs. 4, 6, 8, 10, 11, 17) as well as to the canal which pierces the ventro-lateral part of the postnasal wall in *Boreosomus* (ibid., pp. 310–318, figs. 62, 65 A, B).

As all the faces of the plate described here, except for the small distal articular area on the postero-ventro-lateral process, are completely lined with perichondral bone, it can be stated with certainty that the plate is not pierced by any canals. The nervus olfactorius must accordingly have reached the nasal pit by passing above the dorsal edge of the plate, while the posterior nasal lobe must have reached the fenestra exonarina posterior by passing laterally to the dorsal part of the lateral margin of the plate in much the same way as in *Pteronisculus* (E. Nielsen 1942, pp. 86, 96; figs. 10, 11, 17 A, B; pl. 6, figs. 1, 2), though not, as in that genus, leaving any traces of its passage.

Discussion. – The above description gives a more complete picture of the neural endocranium of *Birgeria* than that gained by Stensiö's studies of *Birgeria mougeoti* (Stensiö 1921, pp. 152–182), for although the sphenoid in Stensiö's specimen is in a more complete condition than in the Greenland specimens treated here, both the ethmoidal and the occipital region are lacking and the ossifications of the otic region are in a rather unsatisfactory state of preservation. To carry out anything like an exhaustive comparison between the neural endocrania on the basis of our present knowledge is, therefore, out of the question, and I shall confine myself to discussing a few important points of agreement or disagreement between the two species, which will give me an opportunity to correct some obvious errors in Stensiö's reconstruction of the Spitsbergen forms.

According to Stensiö (1921, pp. 152–175, figs. 59–64; pl. 20, fig. 6; pl. 21, figs. 1–3; pl. 22, figs. 1, 3; pl. 24, fig. 2) the known part of the neural endocranium of *Birgeria mougeoti* contains the same ossifications as the corresponding part of the neural endocranium of *Birgeria groenlandica*, viz., in the otic region, a paired autosphenotic, a paired prootico-opistotic, and the foremost part of an unpaired occipital ossification, and in the orbito-temporal region, a large unpaired sphenoid. In both species the ossified areas of the endocranium are separated by larger or smaller interspaces; however, judging from the description given by Stensiö, the individual ossifications in *Birgeria mougeoti* have a relatively greater thickness and the sphenoid moreover a greater rostro-caudal extent than in *Birgeria groenlandica*. The differences in the relative thickness of the endocranial ossification of the two species can easily be explained as due to the greater size, and accordingly probably the greater age, of Stensiö's specimen; however, it seems to me doubtful whether the same explanation also holds good for the differences in the rostro-caudal extent of the sphenoid, in so far as this explanation would imply that the sphenoid in *Birgeria groenlandica* was continued both back-

wards and forwards by cartilage, and although perichondral bone is lacking on the anterior margins of the dorsal division of the sphenoid, this seems not to be the case neither on that part of the ossification which bounds the large fenestra optica, nor on any part of its posterior margin. Thus we are here probably concerned with structural differences of a more serious nature than those which are only due to their different age.

According to Stensiö's reconstructions (Stensiö 1921, figs. 59–62, 64), the relations between the individual ossifications in the known part of the neural endocranium of *Birgeria mougeoti* differ fairly much from those of *Birgeria groenlandica;* thus the otic part of the occipital ossification is situated medially to the postero-ventral part of the prootico-opistotic, from which it is separated by a strong ascending lamina of the pars posterior parasphenoidea, while the autosphenotic is situated laterally to the middle part of the sphenoid and does not reach so far back as to the processus ascendens.

A reinvestigation of Stensiö's specimen, however, has convinced me that these apparent differences do not exist. The peculiar relations between the occipital ossification, the parasphenoid, and the prootico-opistotic find their explanation in the strong dorso-ventral compression to which the specimen, as also mentioned by Stensiö (1921, p. 152), has been subjected. By this compression the occipital ossification and the median part of the parasphenoid have been wedged in between the prootico-opistotics, while the lateral parts of the parasphenoid have remained in place on the lateral faces of the prootico-opistotics.

Thus actually the otic region had about the same relative height as in *Birgeria groenlandica*, and the profound lamina of the parasphenoid described by Stensiö does not exist. The forward position of the autosphenotic may also be explained as a post-mortem deformation of the specimen in question. Stensiö's figure of the neural endocranium in ventral view (Stensiö 1921, fig. 61) shows, on the ventral face of the autosphenotic and quite near its medial margin, the ventral opening of a canal (t), which according to Stensiö lodged either a nerve or a vessel. Judging from the conditions in *Birgeria groenlandica* this opening must be the ventral opening of the spiracular canal, and there can be no doubt that the autosphenotic was originally placed so far back that the processus ascendens parasphenoidea was directed towards, or possibly penetrated some distance into, the spiracular canal in the usual way (cf. E. Nielsen 1942, pp. 106–113).

Thus the only important structural differences between the neural endocrania of *Birgeria mougeoti* and *Birgeria groenlandica* hitherto discussed are the differences in the rostro-caudal extent of the sphenoid. To these must be added that the basipterygoid process is developed in *Birgeria mougeoti*, but entirely absent in *Birgeria groenlandica*, and that canals for nerves and vessels through the dorsal division of the sphenoid are apparently arranged in a somewhat different way in the two species.

These differences together might perhaps raise some doubt as to whether the two species may arctually be grouped in the same genus; however, a closer study of the structure of the sphenoid within both species will be necessary if we are to decide whether or not such a doubt is justified. At present it will suffice to state that *Birgeria mougeoti* as regards its sphenoidal structures is decidedly more primitive than *Birgeria groenlandica.*

The endocranium of *Birgeria* differs from the central Palaeonisciform type (defined above (pp. 67–68) as a generalised type uniting the important common characters of the best known endocrania of typical *Palaeonisciformes*) in many respects, the most important of which, judging from our present knowledge, are as follows:

1) The occipital region is high and narrow throughout its whole length, the otic region is narrow posteriorly but extremely wide in its foremost part, and the posterior part of the endocranium is not excavated laterally.
2) The postorbital processes are very stout.
3) The posterior part of the fossa bridgei is situated a considerable distance anteriorly to the boundary between the occipital and the otic regions and medially to the articular area for the hyomandibula.
4) An aorta canal is not developed.
5) The ventral parts of the otic and the occipital region are covered externally by the pars posterior parasphenoidea.
6) The adult endocranium contains a greater number of relatively small ossifications separated by unossified areas.

The significance of the differences enumerated as 1, 2, and 3 is difficult to estimate. We are here dealing with differences in shape, and such differences may, of course, always be explained by assuming a gradual change from one to the other of the two objects we are comparing, but according to our present sparse knowledge, the trend of evolution of the most primitive Actinopterygians is very difficult to decide; thus, for instance, it is impossible to decide whether the large postorbital process of *Birgeria* has developed from a smaller one, as in the central Palaeonisciform type, or whether the evolution has taken the opposite course.

As to point 4) in the above list we know that the aorta canal decreases in length, to disappear, finally, in certain phyletic lines issuing from typical *Palaeonisciformes,* and it is therefore not unreasonable to assume that a similar development may have taken place in a phyletic line leading from the typical *Palaeonisciformes* to *Birgeria.* On the other hand, the absence of an aorta canal may, of course, also be regarded as an original feature.

In the typical *Palaeonisciformes* the parasphenoid is short, and within the phyletic lines leading towards the *Holostei* and the *Teleostei* there is a tendency to a lengthening of the parasphenoid in a posterior direction. It is difficult to consider the long parasphenoid in *Birgeria* as an original structure,

for the parasphenoid is short in the *Crossopterygii* and hence probably also in the hypothetic common ancestors of the *Crossopterygii* and the *Actinopterygii*.

As to point 6) it is obvious from what is now known of the process of ossification in typical *Palaeonisciformes* (cf. E. Nielsen 1942, pp. 91–93) that it offers no basis for conclusions as to the relationship between *Birgeria* and the typical *Palaeonisciformes*. At a certain stage of its ontogenetic development the neural endocranium of a typical Palaeonisciform contains several small ossifications and thus shows somewhat similar conditions to those of the adult neural endocranium of *Birgeria;* but in many phyletic lines we also find a development from an endocranium which is fully ossified in one or a few pieces to an endocranium containing a large number of smaller ossifications (Stensiö 1932, p. 297).

The points discussed above thus offer no very serious objection to considering *Birgeria* as a descendant of some typical *Palaeonisciformes*, but also no direct proofs of such a relationship. It seems quite possible that the *Birgeria* line branched off from the line to which the typical *Palaeonisciformes* belongs at a very early stage, so that the endocranium of the common ancestor of *Birgeria* and the typical *Palaeonisciformes* was much less specialised than the central Palaeonisciform type.

Most of the above-mentioned characters in which the neural endocranium of *Birgeria* differs from the central Palaeonisciform type are also found in the endocranium of the recent sturgeons (*Acipenseridae*, *Polyodontidae*), as will be evident from the following:

1) In the sturgeons the occipital region, apart from its strong craniospinal processes, is high and narrow, the otic region is narrow posteriorly, but increases very much in height towards its anterior end, and the posterior part of the endocranium is not excavated laterally (Bridge 1878, pl. 56, figs. 4, 5; Stensiö 1932, fig. 35).

2) The postorbital processes are strong in the sturgeons, though somewhat less prominent than in *Birgeria* (Bridge 1878, pl. 56, figs. 4, 5; Stensiö 1932, figs. 31, 35).

3) In the sturgeons the fossa bridgei is situated a considerable distance anterior to the posterior boundary of the otic region. In *Acipenser* (Parker 1882, pl. 15, fig. 13; Stensiö 1932, fig. 35) its hindmost part lies medially to the place of articulation of the hyomandibula, while in *Polydon* (Bridge, 1878, pl. 56, fig. 5) it lies somewhat farther back. As pointed out in the first part of this work (E. Nielsen 1942, pp. 44–45), the relations of the fossa bridgei to the labyrinth cavity are similar to those in *Pteronisculus*, and accordingly the increased distance between the fossa bridgei and the hind margin of the otic region in the sturgeons compared with that in typical *Palaeonisciformes* is not due to a reduction of the hindmost part of the fossa bridgei, but rather to changes in the shape of the otic region; the same

probably holds good for the fossa bridgei of *Birgeria*, the shape and position of which show close agreement with that in the sturgeons.

4) The neural endocranium of the sturgeons has no aorta canal.

5) The parasphenoid of the sturgeons extends backwards below the whole otic and occipital regions (Bridge 1878, pl. 55, figs. 2, 3; pl. 56, fig. 4; Parker 1882, pl. 16, fig. 3; Stensiö 1932, fig. 34).

6) The endocranium of the sturgeons, though mainly cartilaginous, in very large specimens contains a number of small ossifications (Bridge 1878, p. 698, pl. 57, fig. 7; Parker 1882, pp. 175–176; pl. 18, figs. 1, 2; Holmgren and Stensiö 1936, pp. 437–438, 445, fig. 336). According to Holmgren and Stensiö the following ossifications have been observed in the neural endocranium of *Acipenser*: an »ectethmoid«, an »orbitosphenoid«, an »alisphenoid«, a »prootic«, an »opistotic«, and a lateral occipital ossification, while neither an autosphenotic nor a basioccipital has been found.

The »ectethmoid« agrees in shape and position very well with the ethmoidal ossification in *Birgeria*. The »orbitosphenoid«, the »alisphenoid«, and probably also the »prootic« correspond to different parts of the large unpaired sphenoid in *Birgeria*. The opistotic seems to be homologous with the posteroventral part of the prootico-opistotic in *Birgeria*, and the lateral occipital must be regarded as the last remnant of the large occipital ossification in *Birgeria*.

On the other hand the neural endocranium of the sturgeons differs from that of *Birgeria* in several respects, of which the following may be mentioned as the most important:

1) The endocranium of the sturgeons shows a strongly developed rostrum.
2) Actual nasal cavities are enclosed in the ethmoidal region of the sturgeons.
3) The interorbital wall in the sturgeons is very thick.
4) The sturgeons have very large cranio-spinal processes.
5) A posterior myodome is not developed in the sturgeons.

As to 1), the rostrum of the sturgeons is probably »no primitive structure, but arose rather late in phyletic development« (Stensiö 1932, p. 85).

As to 2). The complete nasal cavities are probably due to the development of the rostrum, and thus these cavities, also, cannot be regarded as a primitive character.

Points 3) and 5) may both be regarded as primitive characters, but on the other hand they may also be regarded as a result of a gradual decrease in the size of the eye during the phyletic development of the sturgeons.

As to point 4), the large cranio-spinal processes probably arose within the sturgeon line, and quite probably they developed from cranio-spinal processes of the type found in *Birgeria* and in typical *Palaeonisciformes*.

Thus the differences considered here are of such a nature that they present no obstacle to the assumption that the neural endocranium of the sturgeons may have developed from a type very similar to, if not identical with, that of *Birgeria*.

We arrive, thus, at the conclusion that the neural endocranium of *Birgeria*, though probably related to the central Palaeonisciform type, shows certain specialisations pointing towards the recent sturgeons. Hence it might be of interest to compare the endocranium of *Birgeria* with that of *Saurichthys*, the Saurichthyids, according to Stensiö (1932, p. 96), being in a certain sense intermediate between the sturgeons and the *Palaeonisciformes*.

From Stensiö's discussions of the relationships of *Saurichthys* (Stensiö 1925, pp. 207–223; 1932, pp. 78–97) it is evident that the neural endocranium of this form as regards some characters agrees better with the sturgeons than with *Birgeria*. Of such characters we may mention:

1) The long rostrum.
2) The very complete nasal cavities.
3) The strong cranio-spinal processes.

On the other hand *Saurichthys* agrees better with *Birgeria* than with the sturgeons in the following important respects:

4) The thin interorbital wall.
5) The presence of a posterior myodome.

Both the latter characters are also found in the central Palaeonisciform type, and thus they should probably be regarded as primitive, while, as already mentioned, the characters numbered 1, 2, and 3 should probably be regarded as specialisations.

Regarding the peculiar course of its spiracular canal (Stensiö 1925, pp. 28, 73), *Saurichthys* seems to be more specialised than *Birgeria* and the recent sturgeons.

According to the above *Saurichthys* thus seems to be somewhat more specialised in a direction pointing towards the sturgeons than *Birgeria*, but it must be regarded as representing a side-branch, not one of the lines leading to the recent forms. Judging from our present incomplete knowledge of the endocranium of *Birgeria*, there seems to be no serious objection to considering *Birgeria* as directly ancestral to *Saurichthys*.

Parasphenoid.

The parasphenoid (*Psph*, figs. 60, 61, 62; pl. 10; pl. 12, fig. 1) consists of a corpus, which, as usual, may be regarded as composed of a pars anterior in front of, and a pars posterior behind, the centre of radiation, and from which issues a single pair of processes. Anteriorly the parasphenoid terminates

below the ossified part of the ethmoidal region, and posteriorly it reaches to the posterior end of the occipital region; in other words, its rostro-caudal extent is about equal to that of the neural endocranium.

The centre of radiation lies about midway between the anterior and the posterior ends of the bone, that is, ventrally to the fossa hypophyseos.

The pars anterior may be described as a horizontal plate, which on its dorsal face is provided with a high median longitudinal crista (*ri. psph*, figs. 60, 61; pl. 12, fig. 1). The horizontal plate, which, as shown in fig. 62, is bounded by straight anterior and lateral margins, increases slightly in breadth and decreases slightly in thickness in an anterior direction. The transverse anterior margin, which, as shown in the figures, is slightly serrated, was separated from the likewise serrated posterior margin of the palatal lamina of the rostro-premaxillary (cf. p. 236, fig. 70) by a very narrow interspace.

The dorsal face of the plate, as already described (p. 203), is in contact with the ventral face of the ethmoidal ossification. On this face we find the median longitudinal crest, which attains its greatest height about midway between its two ends and from here decreases gradually in height both backwards and forwards. The crest is quite massive, and its thickness remains the same throughout its anterior and middle parts, to decrease very rapidly farthest posteriorly, so that the hindmost part of the crest forms a foundation for, and is of the same breadth as, the strong basisphenoid pillar.

The pars posterior has a more complicated shape, this part of the bone being strongly curved both in a longitudinal and a transverse direction. From its anterior end the median longitudinal axis of the external face of the pars posterior first extends in a postero-dorsal direction, but a little farther back it curves downwards, continuing to its posterior end in a postero-ventral direction, while the median longitudinal axis of the internal face of the pars posterior farthest forward has the same direction as the dorsal margin of the longitudinal crest on the pars anterior and then curves downwards, to continue to its posterior end parallel with the median longitudinal axis of the external face of the pars posterior. This difference in the direction of the two axes in the foremost part of the pars posterior is due to the fact that the median area of the foremost part of the pars posterior decreases rapidly in thickness backward, while more posteriorly the thickness remains constant. The pars posterior is strongly bent from side to side in such a way that laterally it encloses the ventral parts of both the otic and the occipital region, as shown in the figures. The transition between the pars posterior and the paired processus ascendens (*pr. asc*$_2$, figs. 60, 62; pl. 11, fig. 3; pl. 12, fig. 1; pl. 13, fig. 1) is quite gradual, so it is difficult to determine the exact breadth of the anterior part of the pars posterior. As far as can be seen, however, the pars posterior increases gradually in breadth in a posterior direction, as will be understood on considering the parasphenoid in ventral view, as shown in fig. 62.

In the posterior margin we find a deep median notch (*n. psph*, fig. 62), probably developed for the dorsal aorta, and if so, corresponding to a similar, though still deeper notch in the hind margin of the parasphenoid of *Acipenser* (see e. g. Parker 1882, pl. 16, fig. 3). Of other details we may mention a short median longitudinal crista developed on the ventral face of the anterior part of the pars posterior and shown in figs. 60 and 62.

The processus ascendens issues in a dorso-lateral direction from the anterior half of the lateral margin of the pars posterior, its base having thus a very considerable length. In a distal direction the processus ascendens decreases only very slightly in breadth, and accordingly it presents, in addition to its anterior and posterior margins, a fairly long distal margin. This latter margin, which, as shown in fig. 60, has a somewhat undulating course, is provided with two small processes, one issuing from its foremost and one from its hindmost part. The foremost of the small processes enters the spiracular canal through its ventral opening and ends dorsally after traversing the canal in its whole length in the spiracular part of the fossa bridgei without, as previously assumed by me (E. Nielsen 1942, p. 111), attaining contact with the dermal cranial roof. On the lateral face of the processus ascendens we find a number of poorly defined ridges converging towards the centre of radiation of the parasphenoid.

As already mentioned, the jugulo-hyoideomandibular canal must be assumed to have extended backwards between the ascending process and the prootico-opistotic. Dorsally and ventrally to this canal the ascending process rested close against the lateral face of the prootico-opistotic, and moreover the process was probably in contact with the unossified part of the neural endocranium between the prootico-opistotic and the sphenoid, thus strengthening the lateral wall of the trigemino-facialis chamber and the posterior myodome.

According to its relations to the hypophysial region and to the spiracular canal (cf. E. Nielsen 1942, pp. 106–113), the process described here must contain homologues to the processus ascendens posterior in other *Actinopterygii*; however, as will be evident from the above description, it has a much greater backward extent than is usually the case.

Discussion. – Stensiö has investigated the parasphenoid in *Birgeria mougeoti*, and judging from his description, which is based on insufficient material, this bone differs markedly from that of *Birgeria groenlandica*, a point which has already been commented upon in the chapter dealing with the neural endocranium (p. 205). According to Stensiö (1921, pp. 154, 175–177; figs. 59–64) the parasphenoid of *Birgeria mougeoti* possesses a paired longitudinal lamina, which issues from the dorsal face of its pars posterior in a dorsal or dorso-lateral direction, penetrating into the wall of the neural endocranium medially to the prootico-opistotic and laterally to the foremost part of the occipital ossification. However, a reinvestigation of

Stensiö's specimen has convinced me that this »profound« lamina is nothing but the dislodged median part of the pars posterior, which together with the occipital ossification has been pressed upwards between the prootico-opistotics.

Judging from Stensiö's description, the parasphenoid of *Birgeria mougeoti* furthermore differs from that of *Birgeria groenlandica* in having a relatively narrow processus ascendens, the dorsal end of which is situated posteriorly or postero-laterally to the autosphenotic, and in lacking both the median longitudinal crista on the dorsal face of its pars anterior and the median longitudinal crista on the anterior part of the ventral face of its pars posterior. However, these differences, also, are probably due to the unsatisfactory state of preservation of the specimen investigated by Stensiö, and, in fact, as far as I can see, two of the photographs in Stensiö's paper (1921, pl. 22, figs. 1, 3) might indicate the existence of the median longitudinal crista on the dorsal face of the pars anterior.

Stensiö first arrived at the conclusion (Stensiö 1921, p. 176) that apart from its »profound« lamina the parasphenoid of *Birgeria* was of a similar type to that of the recent sturgeons, but later on (1925, p. 87) he altered this view; thus after a study of the different types of parasphenoids in the Actinopterygians he became of the opinion that the ascending process of the parasphenoid of *Birgeria* should be regarded as a processus ascendens anterior and that of recent sturgeons as a processus ascendens posterior.

Stensiö's former view is the more correct, for, as already pointed out in the first part of the present work (1942, pp. 111–112), the processus ascendens of both *Birgeria* and the sturgeons must be regarded as a processus ascendens posterior, and when moreover Stensiö's »profound« lamina has turned out to be non-existent, the similarity between the parasphenoids of *Birgeria* and the recent sturgeons will be even closer than originally assumed by Stensiö.

As pointed out by Stensiö, the parasphenoid of *Saurichthys* also belongs to the sturgeon type (Stensiö 1925, pp. 82–88, 218) characterised by its long pars posterior, its single pair of ascending processes, and its deeply notched posterior margin. As in *Birgeria*, we find, on the ventral face of the pars posterior parasphenoidea in *Saurichthys*, a median longitudinal crest; the processus ascendens of *Saurichthys* is intermediate in breadth between that of *Birgeria* and that of the recent sturgeons.

It might now be asked whether the type of parasphenoid found in *Birgeria*, *Saurichthys*, and the sturgeons may be supposed to have developed from the type found in typical *Palaeonisciformes* and characterised by its very short pars posterior and by possessing two pairs of ascending processes.

The answer to this question is that such a development seems to be possible and perhaps even likely. For, as will be generally known, within several of the phyletic lines leading from the Palaeonisciform group towards

the higher Ganoids and Teleosts, we may trace a gradual reduction of the processus ascendens anterior as well as a gradual prolongation of the pars posterior, so it is quite possible that a similar tendency of development has prevailed within a phyletic line which may have led from typical *Palaeonisciformes* towards *Birgeria*, *Saurichthys*, and the sturgeons. Even if *Birgeria*, *Saurichthys*, and the sturgeons are not derived from typical *Palaeonisciformes*, it seems probable that their ancestors possessed a short parasphenoid, for such a parasphenoid is also known from the groups within the fishes which must be assumed to be most closely related to the Actinopterygian group, viz. the different Crossopterygian groups and perhaps also the Acanthodians. Neither *Birgeria* nor *Saurichthys* afford any evidence in support of the hypothesis put forward by Jarvik regarding the lengthening of the parasphenoid within the Actinopterygians, and already discussed in the present work (cf. pp. 82–83).

Vomer.

No vomer could be demonstrated in *Birgeria*; in this respect the genus thus differs from *Saurichthys*, in which this bone attains a considerable size (Stensiö 1925, p. 88). As regards the development of the vomer in the sturgeons opinions differ. Several authors claim the existence of a vomer, however, according to Holmgren and Stensiö (1936, pp. 443–445) this bone is actually a basirostral plus a subrostral, while a true vomer is lacking.

Dermal bones on the dorsal side of the neural endocranium.

The dermal cranial roof has a very considerable thickness, but most of its elements are so firmly joined to each other that the boundaries between them are very difficult to trace except on impressions.

Extrascapular series. – The extrascapular series contains only a single large bone (*Ext*, figs. 64, 69; pl. 14; pl. 15, fig. 1) on either side. This bone is angularly bent in such a way that it may best be described as consisting of a medial (antero-medial) and a lateral (postero-lateral) shank, the former of which has a fairly transverse and the latter an almost longitudinal direction. As a whole the extrascapular, the shape of which is shown in detail in fig. 64, is bounded by an anterior, a lateral, a medial, and a postero-medial margin, of which the first-mentioned three are slightly convex, while the last-mentioned one is strongly concave.

The extrascapular is only in contact with the most anterior part of the medial margin of its fellow on the other side of the mid-line of the cranial roof, but apart from this the bone, as far as could be made out, overlaps all the neighbouring bones, viz. the frontal, the parietal (*Pa*), the supratemporal, and the posttemporal. The extent of the overlapped areas of the

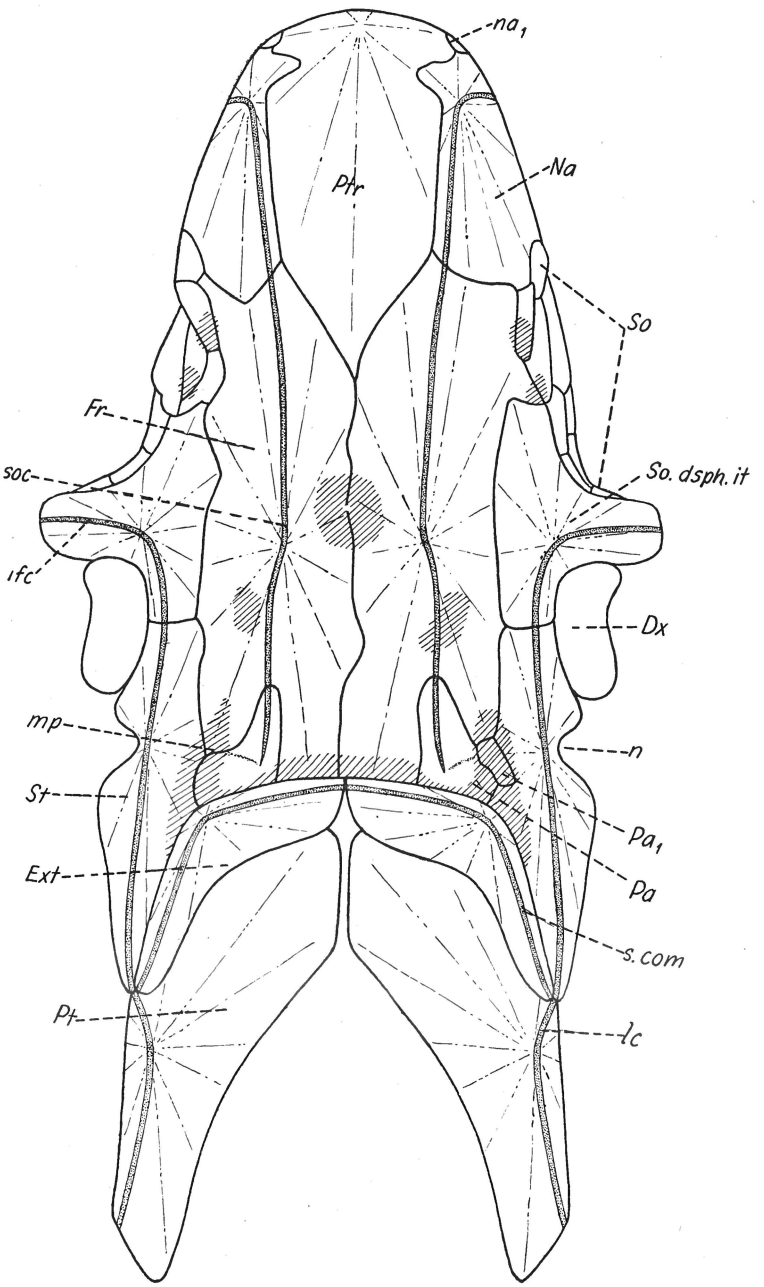


Fig. 64. *Birgeria groenlandica* Stensiö. Dermal cranial roof and posttemporals in dorsal view. Mainly based on specimen no. 650, but with additions from other large specimens. Presumed nerve-sack areas indicated by cross-ruling. 1.3×.

Dx, supraspiracular plate; *Ext*, extrascapular; *Fr*, frontal; *Na*, nasal; *Pa*, Pa_1, parietal elements; *Pt*, posttemporal; *Ptr*, postrostral; *So*, supraorbitals; *So. dsph. it*, supraorbito-dermosphenotico-intertemporal; *St*, supratemporal; *ifc*, infraorbital sensory canal; *n*, notch in the lateral margin of the dermal cranial roof; na_1, fenestra exonarina anterior; na_2, fenestra exonarina posterior; *lc*, main lateral line; *s. com*, supratemporal commisure; *soc*, supraorbital sensory canal.

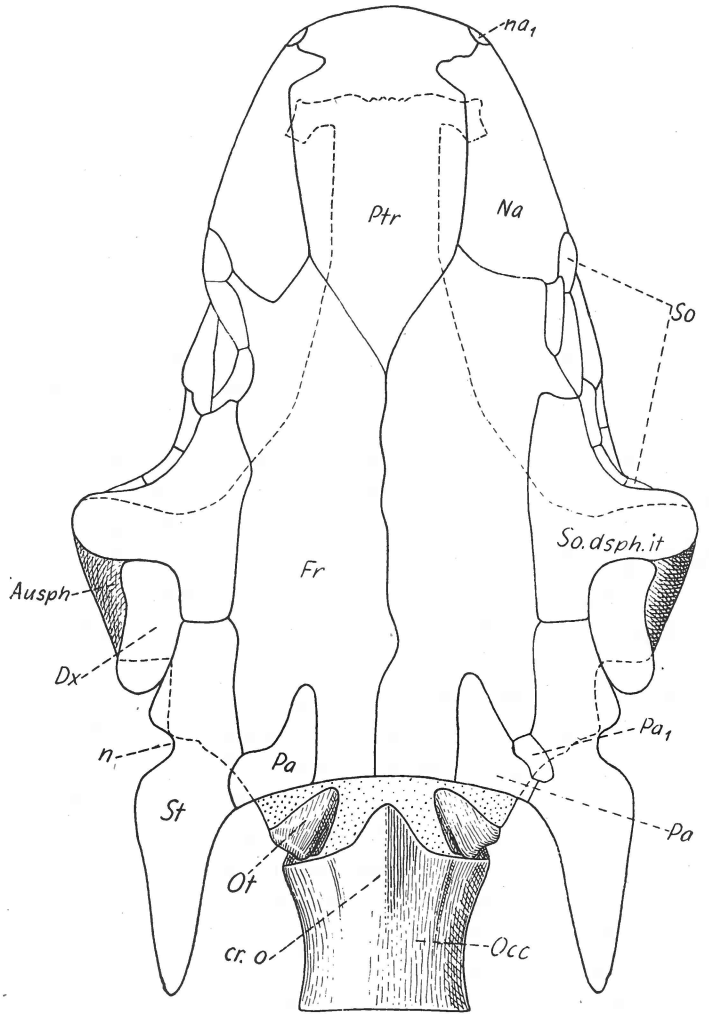


Fig. 65. *Birgeria groenlandica* Stensiö. Neural endocranium and dermal cranial roof in dorsal view. Mainly based on specimens nos 650–652. 1.3×.
Ausph, autosphenotic; *Occ*, occipital ossification; *Ot*, prootico-opistotic; *cr. o*, crista occipitalis. Other letters as in fig. 64.

frontal and the parietal cannot be stated with certainty, but they are probably not very large; the overlapped area of the supratemporal is very narrow, while that of the posttemporal has a considerable breadth.

The radiation centre of the bone is situated a short distance posteromedially to its antero-lateral corner, and as usual it is pierced by the supratemporal commissure, which traverses the two shanks of the bone parallel with and rather near the lateral and the anterior margins, respectively, as shown in fig. 64.

Parietal elements. – On either side of the mid-line we find one or two independent parietal elements (*Pa*, Pa_1, figs. 64–66, 69, pl. 14; pl. 15, figs. 1–3) situated laterally to the most posterior part of the long frontal. In the cases in which there are two such elements the smaller one (Pa_1) is always situated laterally to the other. As shown in the figures, the parietals vary fairly much in shape, not only from specimen to specimen, but also from one side of the head to the other.

The parietal or, if two are present, the parietal complex joins by sutures with the frontal, the supratemporal, and the extrascapular, which latter bone, as already mentioned, overlaps its most posterior part. The larger parietal lodges the hindmost part of the supraorbital sensory canal, which extends in a rostral direction from a point (the centre of radiation?) situated postero-medially to the central part of the bone, to continue through the frontal in the normal way. In some cases we find, on the external face of the larger parietal, a shallow groove extending from the area above the posterior end of the supraorbital sensory canal in a lateral and slightly anterior direction to the margin of the bone. As far as could be seen, the groove (*mp*, figs. 64, 69), which without doubt represents the middle pit-line of the dermal cranial roof, did not continue on to other elements of the dermal cranial roof.

Supratemporal. – The postero-lateral part of the dermal cranial roof is occupied by the large bone (*St*, figs. 64–66, 69, pl. 14; pl. 15, figs. 1–3), which was regarded by Stensiö (1932, p. 109, figs. 40, 41) as a supratemporo-intertemporal, but which, as will be explained in more detail below (pp. 222–223), as far as I can see should rather be interpreted as a supratemporal. It is a roughly triangular bone, bounded by a long lateral, a long medial, and a short anterior margin. In its anterior margin we find, somewhat nearer the anterior than the posterior end, a deep notch (*n*, figs. 64–66, 69; pl. 14), which, judging from its position above the dorsal end of the hyomandibula, must be compared to the marked notch in the lateral margin of the supratemporo-intertemporal in *Pteronisculus* (E. Nielsen 1942, p. 119), *Boreosomus* (ibid., p. 327), *Cheirolepis* (Watson 1925, fig. 1), and several other *Palaeonisciformes*.

As already mentioned, the posterior part of the medial marginal zone of the bone is overlapped by the extrascapular. Furthermore the bone adjoins the parietal(s), the frontal, and the supraspiracular plate, however, its detailed relations to these bones are difficult to make out, and the only thing that can be determined with certainty is that the connection with the supraspiracular plate is less intimate than with the other dermal bones. The centre of radiation is situated a short distance medially to the notch in the lateral margin and is pierced by a sensory canal, which traverses the bone in a longitudinal direction, and which, if my interpretation of the bone is correct, must be regarded as the postotic canal.

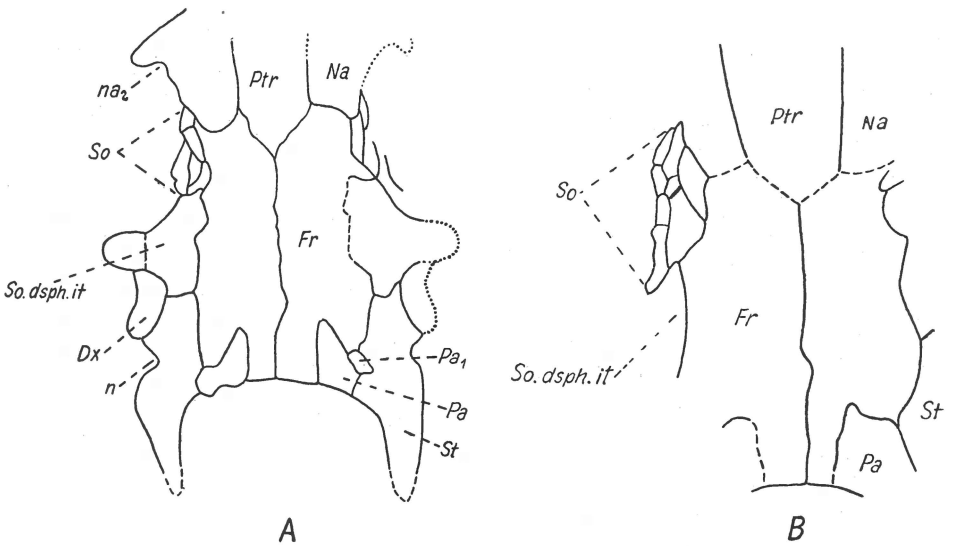


Fig. 66. *Birgeria groenlandica* Stensiö. A, incomplete dermal cranial roof. Based on specimen no. 650. C. 0.7×. B, incomplete dermal cranial roof. Based on specimen no. 660. C. 0.9×.
Lettering as in fig. 64.

According to Stensiö (1921, p. 181), a long, mainly ventrally directed process and a ventral lamina issue from the ventral face of the supratemporal (his supratemporo-intertemporal) in *Birgeria mougeoti*. The process, the shape of which is unknown in detail, lies close against the lateral face of the otic region and marks the posterior opening of the jugulo-hyoideomandibular canal laterally. The lamina, the details of which are also unknown, is, at any rate posteriorly, in contact with the lateral face of the otic region. In *Birgeria groenlandica* it is difficult to investigate the whole ventral face of the supratemporal, but in some specimens the state of preservation is so good that we might expect to find remnants of a stout process such as that of *Birgeria mougeoti* just described. However, no such remnants are found, nor have I discovered any trace of the ventral lamina. I have therefore examined the specimen of *Birgeria mougeoti* described by Stensiö, and the result of my examination is that the long process in this form is probably only a casual bone fragment which has been pressed towards the lateral face of the otic region, while the ventral lamina actually seems to exist. As is well known, a longitudinal ventral lamina issuing from the supratemporo-intertemporal is found in many Actinopterygians as well as in some Crossopterygians (Sagemehl 1884, pp. 188–189; Stensiö 1921, pp. 63, 81, 96, 181–182; 1925, p. 92; 1935, p. 19; Aldinger 1937, p. 41; E. Nielsen 1942, pp. 119–120, etc.), and it is most likely that its apparent absence in *Birgeria groenlandica* is due to the poor state of preservation of the material rather than to its complete reduction.

Frontal. – The frontal (*Fr*, figs. 64–66, 69; pl. 10; pl. 11, figs. 1, 2; pl. 12, fig. 2; pl. 14; pl. 15, figs. 1–3; pl. 19; pl. 20, fig. 2), as already mentioned, extends backward between the parietals to the extrascapular series, and thus it has a relatively greater length than in typical *Palaeonisciformes*. The posterior (interparietal) part of the bone is much narrower than the more anterior part, the breadth of which is fairly constant throughout the greater part of its length. As a whole the bone may be described as roughly four-sided, with an anterior, a medial, a lateral, and a posterior margin. The detailed shape varies somewhat in the different specimens and from one side of the head to the other, as is evident from the figures. The bone is joined by sutures, medially with the frontal of the other side, anteriorly with the postrostral and the nasal, laterally with the supraorbitals, the supraorbito-dermosphenotico-intertemporal, and the supratemporal, and posteriorly with the parietal(s) and the extrascapular. As already mentioned, the extrascapular overlaps the hind margin of the interparietal part of the frontal; whether other overlappings took place between the frontal and the adjacent bones, could not be ascertained. The centre of radiation is situated at about equal distances from the lateral and the medial margin of the bone, and somewhat nearer its posterior than its anterior end. The centre is pierced by the supraorbital sensory canal, which traverses the bone in a longitudinal direction.

Supraorbito-dermosphenotico-intertemporal. – Anteriorly to the supratemporal and laterally to the middle part of the frontal lies a fairly large bone, which is termed by Stensiö (Stensiö 1932, pp. 101, 111) the main dermosphenotic plate. In shape this bone agrees more closely with the main dermosphenotic plate of *Birgeria mougeoti* than appears from Stensiö's figures (Stensiö 1932, p. 101, figs. 37, 38), being a long, rather narrow bone provided with a very strong, obtuse lateral process. The centre of radiation lies a little posteriorly or postero-laterally to the central part of the bone and is pierced by the infraorbital sensory canal, which traverses the most posterior part of the bone in a longitudinal direction and then curves laterally to continue through the strong lateral process in a mainly transverse direction. The relation between the bone and the neural endocranium were as follows: the posterior part of the bone probably rested on the cartilaginous roof of the otic region in such a way that it covered an anterior part of the fossa bridgei, the greater part of the lateral process rested on the dorsal face of the postorbital process, and the anterior part of the bone was situated mainly dorsally to the cartilaginous supraorbital crest, but perhaps also formed part of the roof of the orbit laterally to the lateral margin of the supraorbital crest. As discussed below (p. 222), it is probable that the posterior part of the bone described here corresponds to the intertemporal part of the supratemporo-intertemporal in typical *Palaeonisciformes*, and from its position above the eye it seems also probable that the

anterior part of the bone contains supraorbital components. Accordingly the bone is a supraorbito-dermosphenotico-intertemporal.

Supraorbitals. – Along the lateral or antero-lateral margin of the supraorbito-dermosphenotico-intertemporal we find a varying number of small bones (*So*, figs. 64–66, 69; pl. 14; pl. 15, fig. 2), which were described by Stensiö (1932, p. 111) as anterior dermosphenotic plates and were considered by him to be formed by subdivision of his dermosphenotic. However, as these small bones are situated laterally to the supraorbital part of the supraorbito-dermosphenotico-intertemporal, they must be interpreted as supraorbitals. Anteriorly to these small bones and to the supraorbito-dermosphenotico-intertemporal and laterally to the foremost part of the frontal and the hindmost part of the nasal we find a complex of somewhat larger supraorbitals arranged as shown in the figures. According to Stensiö (1932, fig. 40), the posterior supraorbitals (his anterior dermosphenotic plates) lie at some distance from each other, and from the supraorbito-dermosphenotico-intertemporal; in the new material investigated by me, however, both the posterior and the anterior supraorbitals are firmly connected with each other and with the adjacent bones of the dermal cranial roof.

Supraspiracular plate. – Laterally to, but probably only loosely connected with, the anterior part of the supratemporal and the posterior part of the supraorbito-dermosphenotico-intertemporal lies a fairly large oblong plate, described by Stensiö as the spiracular (Stensiö 1932, p. 101) or the supraspiracular (ibid. p. 110, figs. 37, 38, 40, 41) plate. This plate, which is about twice as long as broad, is rounded anteriorly and posteriorly and has a convex medial and an S-shaped lateral margin. The concave part of its lateral margin is interpreted by Stensiö as the dorsal boundary of the spiracular foramen, and this interpretation is probably correct, though the autosphenotic, as shown in fig. 65, extends in a lateral direction rather far beyond the concavity. The centre of radiation of the supraspiracular plate could not be localised in any of the specimens investigated by me.

Postrostral. – The postrostral (*Ptr*, figs. 64–66, 69, 73; pl. 10; pl. 11, fig. 2; pl. 14; pl. 15, fig. 2) is a very large bone bounded by an unpaired anterior, a paired lateral, and a paired postero-lateral margin. The bone attains its greatest breadth (about half its total length) in its most anterior part and tapers posteriorly to a point in the way shown in the figures. As in typical *Palaeonisciformes* the postrostral is curved both in a transverse and a longitudinal direction in such a way that its external face is convex, with the maximum of convexity, which, however, is far less than in typical *Palaeonisciformes*, far anteriorly. The centre of radiation lies in this anterior and most strongly curved part of the bone. Anteriorly the bone joins by suture with the rostro-premaxillary, laterally with the nasal, and postero-laterally with the frontal. Probably no great overlappings took place along these sutures.

In typical *Palaeonisciformes* the fenestra exonarina anterior is situated between the postrostral and the nasal, and some distance behind the anterior end of the suture between these two bones (cf. Stensiö 1932, p. 111); in *Birgeria groenlandica*, however, this fenestra has a more anterior (antero-ventral) position and is bounded anteriorly (ventrally) by the rostro-premaxillary. As regards the position of the fenestra exonarina anterior, *Haplolepis* and *Pyritocephalus*, according to Westoll (1944) differ still more from the typical *Palaeonisciformes* than *Birgeria*, the fenestra in these two genera being bounded exclusively by the nasal and the rostro-premaxillary (Westoll's dentigerous rostral). Westoll (1944, p. 75) regards the deviating position of the fenestra exonarina anterior in the *Haplolepidae* as a result of the reduction of the underlying portion of the snout and the upward movement of the premaxillary region, a reduction which has most likely caused the loss of the projecting rostrum. Since *Birgeria*, also, lacks the prominent rostrum typical of most *Palaeonisciformes*, it is tempting to explain the forward position of its anterior external nostril in a similar way; however, as shown in the figures, the lateral margin of the postrostral has a very deep notch, which is situated on a level with the centre of radiation of the bone, i. e. precisely in the place where one would look for the anterior nostril in a typical Palaeonisciform, and to me it does not seem quite inconceivable that this notch should represent the original fenestra exonarina anterior, which has been completely closed by a process from the nasal.

Nasal. – The nasal (*Na*, figs. 64–66, 73; pl. 10; pl. 11, fig. 2; pl. 14; pl. 15, fig. 2; pl. 20, fig. 2) is a fairly large, roughly four-sided bone with a medial (antero-medial), a posterior (postero-dorsal), a lateral (postero-lateral), and a ventral margin. The detailed outline of the bone is shown in the figures. As usual, the nasal is somewhat curved in such a way that its external face is convex and its internal face correspondingly concave. Posteriorly the bone joins by suture with the frontal and one or more supraorbitals, medially with the postrostral, and ventrally with the rostro-premaxillary and the antorbital. The ventral part of the lateral (postero-lateral) margin is in contact with, but was probably not firmly connected with, the anterior margin of the dorsal processes of the antorbital. As pointed out by Stensiö (1932, pp. 103, 111, figs. 37, 38, 40, 41), the fenestra exonarina posterior is situated between the nasal and the dorsal antorbital process, that is, in much the same way as in *Coccocephalus* (Watson 1925, fig. 6). Dorsally to the antorbital process the lateral (postero-lateral) margin forms part of the anterior boundary of the orbital opening. From the ventral margin of the nasal issues a small rounded process, the greater part of which is overlapped by the rostro-premaxillary. No other overlappings between the nasal and the adjacent bones have been observed with certainty. The centre of radiation is situated in the anterior broad part of the nasal and much nearer its medial than its lateral margin. The centre is pierced by the supraorbital sensory

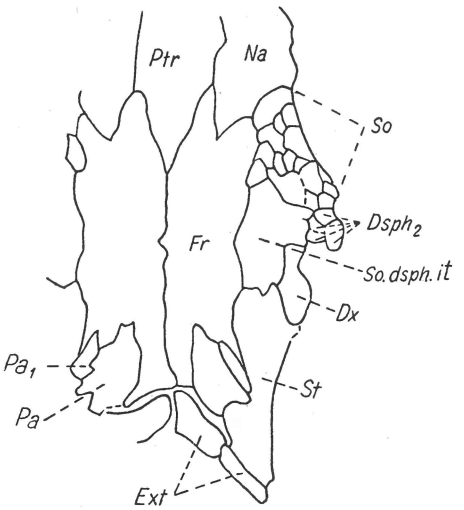


Fig. 67. *Birgeria mougeoti* (Agassiz). Part of the dermal cranial roof. Drawn after Stensiö 1932, fig. 37. C. 0.6×.
$Dsph_2$, independent dermosphenotic elements. Other letters as in fig. 64.

canal, which traverses the posterior part of the bone rather near and parallel with its medial margin, while more anteriorly it bends outwards, to reach the process on the ventral margin of the bone, as shown in the figures.

Discussion. – As might be expected, the dermal cranial roof agrees in most important respects with that of *Birgeria mougeoti*, from which it differs mainly in having a smaller number of independent supraorbitals, a difference which Stensiö (1932, p. 106) explains by assuming that a progressive subdivision of the dermal bones overlying the orbit took place in the period from the Lower to the Upper Eotrias. As far as I can see, Stensiö's explanation, supported as it is by the relative age of the two species in question, is more probable than the assumption that the number of supraorbitals decreased (by fusion or reduction) within the *Birgeria* line.

The dermal cranial roof of *Birgeria* differs from that of the typical *Palaeonisciformes* i. a. in the frontals extending backwards between the parietals and joining by suture with the extrascapulars. Somewhat similar conditions in the *Palaeonisciformes* are otherwise only met with in *Coccocephalus wildi* (Watson 1925, pp. 826–830, fig. 5; the present paper fig. 82), as already pointed out by Stensiö (1932, p. 99). In other important respects, also, the dermal cranial roof of *Coccocephalus* shows relatively close agreement with that of *Birgeria*, thus the extrascapular series is strongly curved in such a way that its middle part has a much more anterior position than its lateral ends, and anteriorly to the lateral extrascapular the main lateral line and the infraorbital sensory canal traverse only two bones of the dermal cranial roof. Moreover the dermal cranial roof of the two genera shows

agreement as to some commoner Palaeonisciform characters, for instance in the position of the fenestra exonarina posterior and in the large size of the postrostral, while it differs mainly in the number of the supraorbitals and the elements of the extrascapular series, i. e. in characters of no very great phylogenetic value.

The comparison between the two genera made here seems to afford fairly strong evidence of the correctness of the assumption put forward by previous investigators (Stensiö 1932, pp. 103, 109; E. Nielsen 1936, p. 46; Aldinger 1937, pp. 330, 377), viz. that *Birgeria* is fairly closely related to *Coccocephalus*. It must, however, be borne in mind that our knowledge of *Coccocephalus* is extremely sparse, and that renewed investigations of that highly interesting form is absolutely necessary before its relationship to *Birgeria* can be regarded as established with anything like certainty.

As pointed out in a previous chapter, the neural endocranium of *Birgeria* exhibits remarkable similarities to that of the recent sturgeons, and hence a certain agreement between *Birgeria* and the sturgeons in the structure of the dermal cranial roof might be expected. This question will now be considered.

In *Acipenser* (Pehrson 1944, pp. 27–40) the elements of the dermal cranial roof, apart from the specialised snout region, are developed much as in typical *Palaeonisciformes*, and present none of the features especially characteristic of *Birgeria*.

In *Polyodon*, however, conditions are different. As is well known, the peculiar structure of the dermal cranial roof in this genus has been the subject of much speculation, which has resulted in very different interpretations of the individual dermal bones. Of these interpretations those given by Pehrson (1944, pp. 27–40) appear to me to be the most reliable, based, as they are, on studies of the innervation of the organs of the sensory canals, a method which has not been systematically employed by any of the previous investigators of *Polyodon*.

The most remarkable result of Pehrsson's studies is that the intertemporal in *Polyodon* is fused with the dermosphenotic to form a large bone, posteriorly to which lies a number of supratemporals arranged in a longitudinal row. (fig. 68). Thus in this respect *Polyodon* differs markedly from most *Palaeonisciformes*, for in these the supratemporal and the intertemporal elements always form a compound supratemporo-intertemporal. In typical *Palaeonisciformes* and in most other primitive Actinopterygians the supratemporo-intertemporal forms the roof above the whole fossa bridgei. In *Birgeria*, however, the bone termed supratemporo-intertemporal by Stensiö only forms the roof above the posterior part of the fossa bridgei, an anterior part of which is roofed over by Stensiö's »dermosphenotic«. Thus there is reason to doubt whether the »supratemporo-intertemporal« of *Birgeria* is homologous with the whole supratemporo-intertemporal of typical *Palaeonisciformes*, and if we compare this with the conditions in *Polyodon* just men-

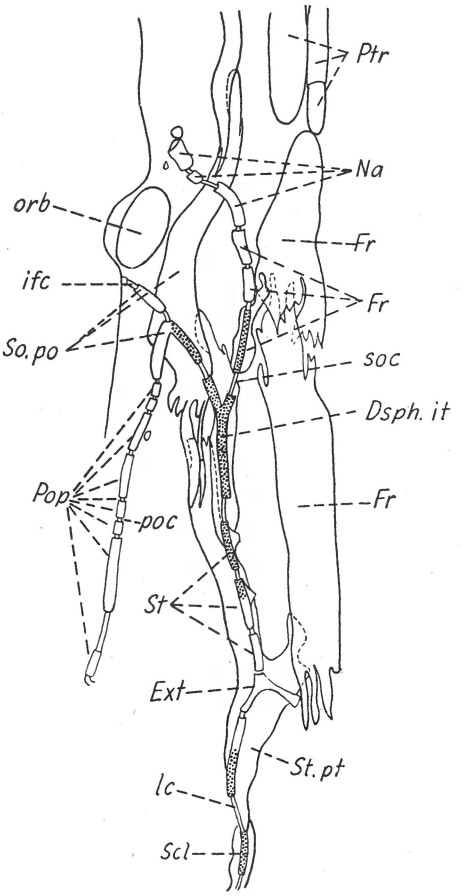


Fig. 68. *Polydon folium* (Lac). 120 mm. Dorsal view of left side of the head showing dermal bones and sensory canals. Drawn after Pehrson 1944, fig. 11. Dotted parts of the canals bones are fused with underlying membraneous portions. 4–5×.

Dsph. it, dermosphenotico-intertemporal; *Ext*, extrascapular; *Fr*, frontal elements; *Na*, nasal elements; *Pop*, preopercular elements; *Ptr*, postrostral elements; *Scl*, supracleithrum; *So. po*, supraorbital and postorbital elements; *St*, supratemporal elements; *St. pt*, supratemporo-posttemporal; *ifc*, infraorbital sensory canal; *lc*, main lateral line; *orb*, eye; *poc*, preopercular sensory canal; *soc*, supraorbital sensory canal.

tioned, it seems reasonably safe to conclude that Stensiö's »supratemporo-intertemporal« is, in fact, a supratemporal, while his »dermosphenotic« includes homologues to the intertemporal part of the supratemporo-intertemporal of typical *Palaeoniscif ormes*. As already mentioned, Stensiö's »dermosphenotic«, judging from its considerable forward extension (cf. p. 219), also includes supraorbital components, and accordingly it must be regarded as a supraorbito-dermosphenotico-intertemporal.

In *Polyodon* the infraorbital sensory canal from the dermosphenotico-intertemporal continues forward through a large bone of a rather complicated shape. According to Holmgren and Stensiö (1936, pp. 445–446), this bone

is a postorbito-supraorbito-dermosphenotic, while Pehrson (1944, pp. 42–43) interprets it as a »dorsal postorbital fused with a jugal ossicle«. Pehrson (p. 42) describes the bone as »a very long membraneous bone provided with a canal bone in the shape of an inverted V«. The medial arm of the V plus the large membrane bone he interprets as the postorbital component, and the lateral arm as the foremost element of a row of small jugals. Pehrson's identification of the jugal elements of *Polyodon* will be dealt with in a later chapter (p. 258); here we shall only consider that part of the bone which he interprets as a dorsal postorbital component. The investigation carried out by Pehrson leaves no doubt that at least the medial branch of the V-shaped portion of the bone is a postorbital; however, the considerable forward extension of the membranous portion seems decidedly to suggest that the bone also contains components which are comparable to the independent supraorbitals and to the supraorbital part of the supraorbito-dermosphenotico-intertemporal of *Birgeria*, I am therefore inclined to regard the bone as a supraorbito-postorbital, which together with the dermosphenotico-intertemporal corresponds to the greater part of the supraorbito-dermosphenotico-intertemporal of *Birgeria*.

The frontals of *Polyodon* (Holmgren and Stensiö 1936, p. 416; Pehrson 1944, pp. 41–42) are represented on each side by three small cylindrical (lateral frontals) and a single larger (medial frontal) bone; posteriorly this latter adjoins a large parietal.

Thus we are here concerned with a point on which *Birgeria* and *Polyodon* seem to differ so much from each other that it serves no purpose at all to speak of a close relationship between these two genera. However, the difficulties may be overcome if we adopt a new interpretation of the particular bones in *Polyodon*, namely that the so-called parietal represents the posterior part of the very long frontal in *Birgeria*, while the actual parietal, which would be situated more laterally, has been completely reduced (cf. pp. 259–260).

Hence the conditions in *Polyodon* may be supposed to have developed from those in *Birgeria* in the following way: On the prolongation of the head, which is a consequence of the development of a strong rostrum, the long frontal of *Birgeria* has become further prolonged and in addition divided by a transverse suture into an anterior and a posterior part. The posterior part of the supraorbital sensory canal has been reduced, and either as a consequence of this (cf. Westoll 1944, p. 68) or of the extreme development of the nerve-sacks (cf. p. 260) the parietals have entirely disappeared. The fenestration between the posterior frontal and the more lateral bones of the dermal cranial roof occupy precisely the area in which the parietals were formerly situated. The anterior frontal has been subdivided into tube-shaped elements around the sensory canal, and a large plate not directly connected with the sensory canal.

Thus it would seem that the very peculiar structure of the dermal cranial roof of *Polyodon* may be explained in a plausible way if we assume that *Polyodon* has been derived from *Birgeria* or a *Birgeria*-like form. *Birgeria* may possibly have evolved from a type such as *Coccocephalus*, which according to our present knowledge in certain respects seems to form a kind of connecting link between *Birgeria* and the typical *Palaeonisciformes*.

Infraorbitals, suborbitals, and sclerotic ring.

The infraorbital series comprises about eight bones, viz. four or five postorbitals, a jugal, a lacrimal, and an antorbital.

Postorbitals. – The postorbitals (*Po. s*, fig. 69), which are always poorly preserved, are small rectangular bones arranged in a nearly vertical row extending from the lateral process of the supraorbito-dermosphenotico-intertemporal to the dorsal edge of the jugal. These bones, the centres of radiation of which could not be localised, are pierced in the normal way by the postorbital part of the infraorbital sensory canal.

Jugal. – The jugal (*Ju*, fig. 69; pl. 19), which occupies its normal position postero-ventrally to the orbital opening, is bounded by a dorsal, a posterior, a ventral, an anterior, and an antero-dorsal margin. The dorsal margin, which is slightly convex, adjoins the ventral margin of the most ventral postorbital and overlaps the anterior ends of the two largest suborbitals. The almost straight posterior margin adjoins the anterior margin of the triangular ventral suborbital. The ventral and the anterior, likewise almost straight, margins respectively overlaps the dorsal margin of the maxillary and adjoins without overlapping the posterior margin of the lacrimal. The concave antero-dorsal margin forms part of the boundary of the orbital opening. The infraorbital sensory canal traverses the bone from its dorsal to its anterior margin, gradually changing its course from nearly vertical to horizontal and piercing the centre of radiation, which is situated a little nearer the posterior than the anterior end of the canal.

Lacrimal. – The lacrimal (*La*, figs. 69, 73) is a long low bone with an antero-dorsal, a ventral, a posterior, and a dorsal margin. The dorsal margin, which forms part of the ventral boundary of the orbital opening, is slightly concave, while the other three margins are straight. The antero-dorsal margin is overlapped by the antorbital, and the ventral margin overlaps the dorsal margin of the maxillary. Both overlappings are very small. The posterior margin, as already mentioned, is in contact with the jugal. The bone, the radiation centre of which could not be localised, is pierced in a longitudinal direction by the infraorbital sensory canal.

Antorbital. – The antorbital (*Ant*, figs. 69, 73; pl. 11, fig. 2) may be described as a four-sided bone with an anterior, a dorsal, a posterior, and a

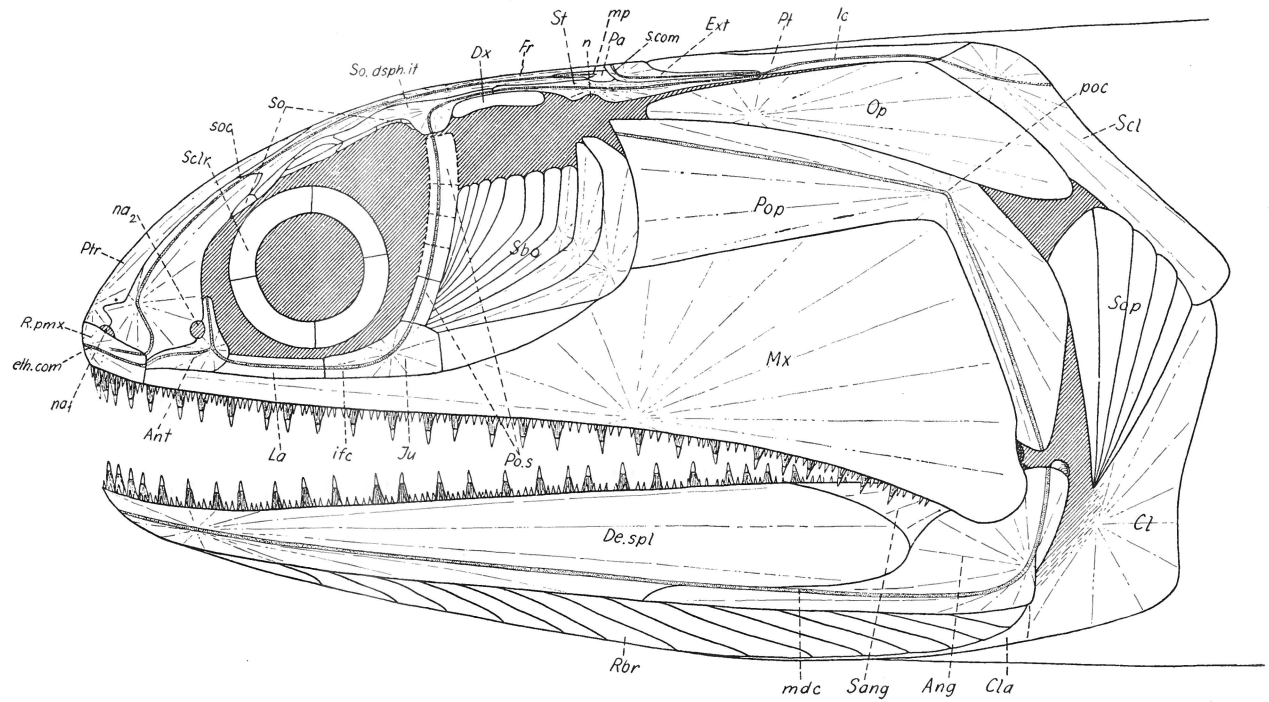


Fig. 69. *Birgeria groenlandica* Stensiö. Head and dermal shoulder-girdle in lateral view. Based on several large specimens. About nat. size. *Ang*, angular; *Ant*, antorbital; *Cl*, cleithrum; *Cla*, clavicle; *De. spl*, dentalo-splenial; *Dx*, supraspiracular plate; *Ext*, extrascapular; *Fr*, frontal; *Ju*, jugal; *La*, lacrimal; *Mx*, maxillary; *Op*, operculum; *Pa*, parietal; *Pop*, preoperculum; *Po. s*, postorbital series; *Pt*, posttemporal; *Ptr*, postrostral; *Rbr*, branchiostegal ray; *R. pmx*, rostro-premaxillary; *Sang*, supraangular; *Sbo*, suborbitals; *Scl*, supracleithrum; *Sclr*, sclerotic ring; *So*, supraorbitals; *So.* dsph. *it*, supraorbito-dermosphenotico-intertemporal; *St*, supratemporal; *eth. com*, ethmoidal commisure; *ifc*, infraorbital sensory canal; *lc*, main lateral line; *mdc*, mandibular sensory canal; *n*, notch in the lateral margin of the dermal cranial roof; na_1, na_2, fenestra exonarina anterior and posterior, respectively; *s. com*, supratemporal commissure; *soc.* supraorbital sensory canal.

ventral margin. The bone, which is somewhat shorter than the lacrimal, is very low at its foremost end and increases slowly in height backward. From the posterior part of its dorsal margin issues a very stout process in a dorsal direction. This process, as shown in fig. 69, forms the posterior boundary of the fenestra exonarina posterior and adjoins the posterior (postero-lateral) margin of the nasal both dorsally and ventrally to the fenestra, which is thus completely separated from the orbital opening.

Anterior to the dorsal process the slightly convex dorsal margin adjoins the posterior part of the ventral margin of the nasal. The short anterior margin overlaps a small postero-laterally directed process of the premaxillary (cf. p. 237), the straight ventral margin slightly overlaps the foremost part of the dorsal margin of the maxillary, and the convex posterior margin, as already mentioned, meets with the concave anterior margin of the lacrimal without any overlapping. The centre of radiation is situated a short distance below the base of the dorsal process, that is, much nearer the posterior than the anterior margin of the bone. The antorbital contains a three-branched part of the sensory canal system. In more detail, the infraorbital sensory canal passes from the lacrimal into the antorbital, from the posterior margin of which it extends in an antero-dorsal direction to the centre of radiation where it divides into two branches, one of which extends forwards to the anterior margin, whence it continues into the rostro-premaxillary, while the other traverses the dorsal process of the bone in its whole length. For the interpretation of these sensory canal branches the reader is referred to the chapter on the sensory canal system (p. 256).

Suborbitals. – Behind the vertical part of the infraorbital series we find about eleven suborbitals (*Sbo*, fig. 69; pl. 10; pl. 12, figs. 1, 2; pl. 13, fig. 1; pl. 14; pl. 15, fig. 3; pl. 19; pl. 20, fig. 1), arranged in a very different way from that met with in typical *Palaeonisciformes* (cf. fig. 69).

The lowermost suborbital is situated behind the jugal and is a fairly large triangular bone with a short and straight anterior, a long, likewise straight, dorsal, and a long convex ventral (postero-ventral) margin. The anterior margin adjoins the posterior margin of the jugal, the ventral margin overlaps the dorsal margin of the maxillary, and the dorsal margin adjoins the ventral margin of the most posterior of the more dorsal suborbitals. The bone is always rather poorly preserved, and hence its centre of radiation could not be localised with certainty.

The other, more dorsal, suborbitals are long and narrow, and are arranged in a mainly longitudinal series, within which they increase in size from the foremost to the hindmost one. In the anterior part of the series the suborbitals are fairly straight, but in the middle and the posterior part of the series they gradually become more and more distinctly bent, their dorsal part forming an increasing angle with their ventral part, as shown in fig. 69. The blunt dorsal ends of the foremost eight dorsal suborbitals in the series are

situated at about the same level, while the more pointed ends of the two hindmost elements of the series are situated somewhat more dorsally. Ventrally all the dorsal suborbitals are pointed, and these pointed ends are overlapped by the infraorbital series. The anterior margin of the foremost dorsal suborbital is overlapped by the midmost part of the postorbital series, while the hindmost suborbital slightly overlaps the anterior margin of the preoperculum as also a short stretch of the dorsal margin of the maxillary. Within the series each suborbital element is overlapped to some extent by that following nearest behind. As far as can be made out, the dorsal suborbitals were only loosely connected with each other, so this part of the cheek skeleton was probably of a certain elasticity.

The centre of radiation could only be localised in the hindmost elements of the dorsal suborbital series, where it is situated in the most strongly bent part of the individual bones, at about equal distances from the anterior and the posterior margin.

In Stensiö's attempted restoration of the cheek of *Birgeria groenlandica* (Stensiö 1932, fig. 41) the suborbitals adjoin the supraspiracular plate; however, as shown in fig. 69, there is a very large interspace between the dorsal ends of the dorsal suborbitals and the lateral margin of the supraspiracular plate; probably only a relatively small part of this interspace was occupied by the spiraculum, the place of which, as already mentioned, is indicated by the fairly well marked concavity in the lateral margin of the supraspiracular plate.

Sclerotic ring. – The sclerotic ring (*sclr*, fig. 69; pl. 11, fig. 2; pl. 12, fig. 2; pls. 14, 19) consists, as described by Stensiö (1932, p. 113), of four pieces and, as shown in fig. 69, it has a considerable size.

Discussion. – According to Stensiö (1932, p. 103) in *Birgeria mougeoti* that part of the infraorbital series which bounds the orbital opening posterodorsally and posteriorly is represented by numerous small polygonal plates, while that part of the series which bounds the orbital opening ventrally and antero-ventrally consists of three or four somewhat larger plates, the foremost of which, by the aid of a dorsal process, separates the fenestra exonarina posterior from the orbital opening. This foremost element of the infraorbital series of *Birgeria mougeoti* is evidently homologous with the antorbital of *Birgeria groenlandica*, and the greater number of the more posterior infraorbital elements of *Birgeria mougeoti* may possibly be explained as due to subdivisions of elements homologous with the lacrimal, the jugal, and the postorbitals, respectively, of *Birgeria groenlandica*, if, as seems to me more probable, it is not due to post-mortem disturbances of the specimen investigated by Stensiö. Stensiö gives the number of suborbitals in *Birgeria mougeoti* as eight or nine, and according to his figures these bones are arranged in principally the same way as in *Birgeria groenlandica*. Regarding their mutual relations Stensiö states (1932, p. 105) that »each of the suborbitals

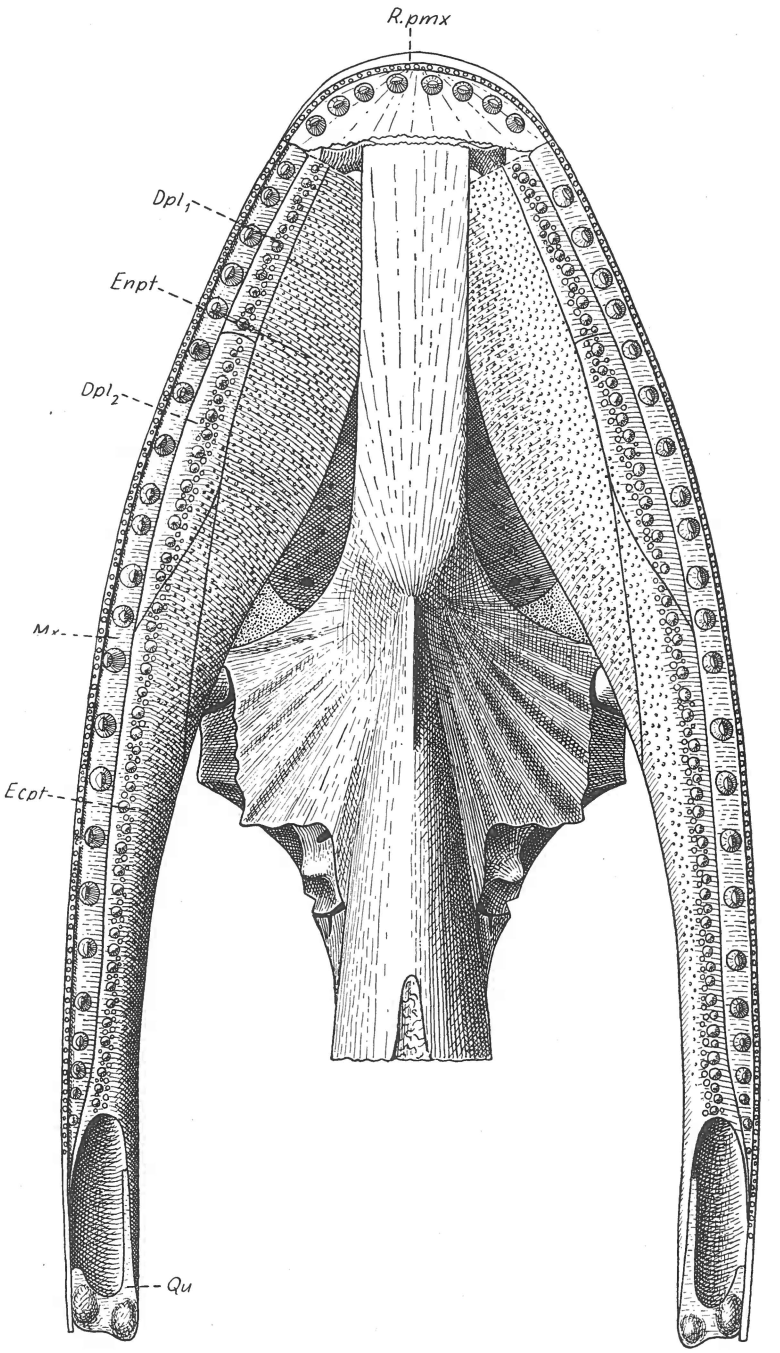


Fig. 70. *Birgeria groenlandica* Stensiö. Neural endocranium with parasphenoid, right and left palatoquadrate-maxillary apparatus, and rostro-premaxillary in ventral view. Based on several large specimens. C. 1.4×.

Dpl_1, Dpl_2, anterior and posterior dermopalatines; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Mx*, maxillary; *R. pmx*, rostro-premaxillary.

in its posterior half overlaps the suborbital next below it, but in its anterior half is overlapped by that plate«. In this respect *Birgeria mougeoti* thus seems to differ from Birgeria groenlandica, in which species each suborbital is overlapped throughout its length by the suborbital next behind (p. 228).

The infraorbitals of *Birgeria* are of much the same type as those of typical *Palaeonisciformes* except for the antorbital, which differs from the usual type by possessing a high dorsal process. As pointed out by Stensiö (1932, p. 111), a similar antorbital as in *Birgeria* is found in *Coccocephalus*, a genus which, as discussed above (p. 221), shows marked affinities to *Birgeria* also in the structure of the dermal cranial roof.

Suborbitals are not developed in the recent sturgeons, and the infraorbital series presents no characters which speak decidedly for or against a close relationship between the sturgeons and *Birgeria*.

The palatoquadrate and its dermal bones, the maxillary, the preoperculum, and the rostro-premaxillary.

The palatoquadrate had, without doubt, a very considerable length, its anterior end, as already described, having articulated with the ventro-lateral part of the ethmoidal region, and its most posterior part being situated far behind a transverse section through the posterior end of the occipital region. This very extensive palatoquadrate is only ossified farthest posteriorly, where a small quadrate has been observed both in small and in larger specimens.

On the oral face of the palatoquadrate we find five dermal bones, viz. an ectopterygoid, an entopterygoid, a dermometapterygoid, and two dermopalatines.

Quadrate. – The quadrate (*Qu*, figs. 70–72; pls. 14,16; pl. 18, fig. 1) is a strongly bent plate which bounds the most posterior part of the musculus adductor mandibulae medially, posteriorly, and, to a smaller extent, laterally, and which is provided with a strong double condyle for articulation with the lower jaw.

Ectopterygoid. – The ectopterygoid (*Ecpt*, figs. 70–72; pl. 12, fig. 2; pl. 16; pl. 17, fig. 1) extends from the most posterior part of the palatoquadrate to a point situated antero-ventrally to the radiation centre of the entopterygoid and thus has a very considerable length. The maximum breadth (height) of the bone is found at about equal distances from its anterior and its posterior end, whence the height decreases both in an anterior and a posterior direction, as shown in fig. 70. The bone is bent in such a way that it may be regarded as consisting of a broad, roughly vertical division medially to, and a narrow, almost horizontal division ventrally to the space which contained the dorsal part of the musculus adductor mandibulae. The ventral division, as shown in the figures, has a less backward extension than the dorsal one owing to the presence of the oval adductor

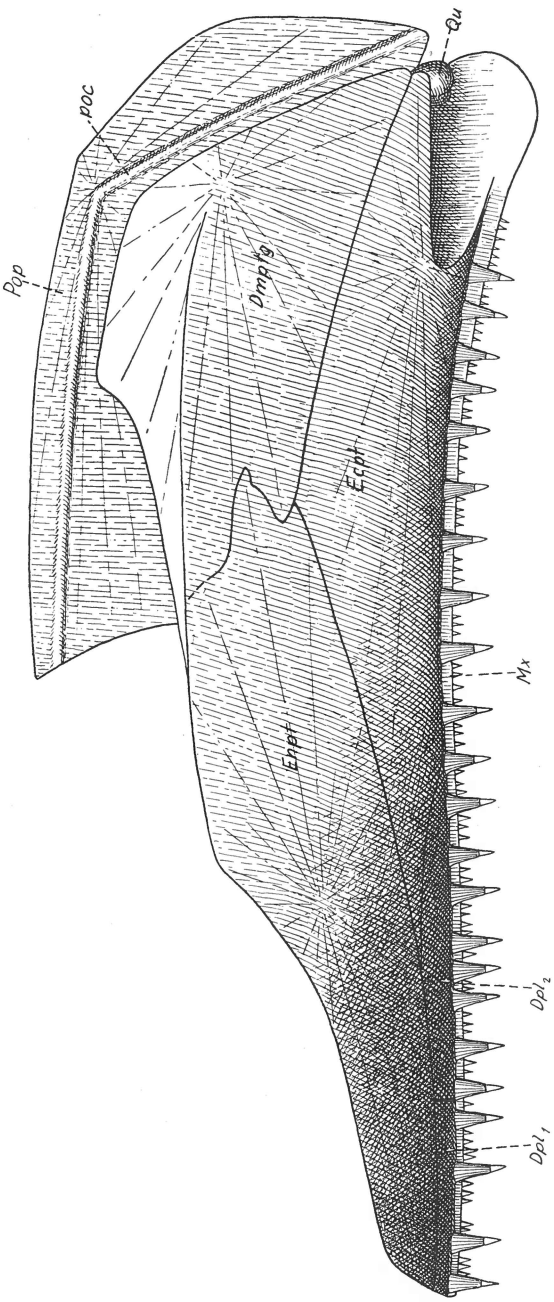


Fig. 71. *Birgeria groenlandica* Stensiö. Palatoquadrate-maxillary apparatus in medial view. Mainly based on specimen no. 756. C. 1.3 ×. *Dmplg*, dermometapterygoid; Dpl_1, Dpl_2, anterior and posterior dermopalatines; *Ectpt*, ectopterygoid; *Enpt*, entopterygoid; *Mx*, maxillary; *Pop*, preoperculum; *Qu*, quadrate; *poc*, preopercular sensory canal.

opening, laterally to the middle part of which it ends as a sharply pointed process. As already stated, antero-dorsally the ectopterygoid adjoins the entopterygoid and postero-dorsally the dermometapterygoid. Anteriorly it joins by suture with the posterior dermopalatine, probably without overlappings, and ventrally it adjoins the maxillary, overlapping a narrow marginal zone of the dorsal face of the internal lamina of that bone. The centre of radiation is situated in the ventral part of the dorsal division of the bone on a level with the most anterior part of the adductor opening. The ventral horizontal part of the bone is equipped with a longitudinal series of fairly large pointed teeth, between which a greater number of much smaller teeth are found. The antero-ventral part of the oral face of the dorsal division is covered by very small teeth similar to those found on the oral face of the dermometapterygoid.

Entopterygoid. – The entopterygoid (*Enpt*, figs. 70–72, pl. 10; pl. 12, figs. 1, 2; pl. 16; pl. 20, figs. 1, 2) is a large bone, which is bent in such a way that its oral face is convex in a transverse direction, and moreover so that its hindmost part is more vertical than its anterior one. The bone, which extends from the anterior end of the palatoquadrate to a point somewhat nearer the posterior than the anterior end, attains its greatest breadth in its middle part whence it narrows both in an anterior and a posterior direction, as shown in the figures. The bone is bounded by a medial (dorso-medial), a lateral (ventro-lateral), an anterior, and a posterior margin; the two last-mentioned margins are much shorter than the other two. The anterior third of the medial margin adjoins the lateral margin of the pars anterior parasphenoidea, the posterior irregularly toothed margin is joined by suture with the dermometapterygoid, the lateral margin is connected by suture with the ectopterygoid and the dermopalatines, overlapping a narrow medial marginal zone of the oral face of these bones, while the anterior margin, the exact course of which could not be ascertained, has probably no contact with any other bones.

The radiation centre of the entopterygoid lies at about equal distances from its anterior and posterior ends and somewhat nearer its medial than its lateral margin. The oral face of the bone is equipped with a dense covering of small teeth.

Dermometapterygoid. – The dermometapterygoid (*Dmptg*, figs. 71, 72; pl. 12; pl. 16, fig. 2; pl. 17, fig. 1) is a fairly large bone, reaching from the posterior margin of the entopterygoid to the hind margin of the palatoquadrate. The bone, on which we may distinguish a dorsal, a postero-dorsal, a ventral, and an antero-ventral margin, is pointed both anteriorly and posteriorly and attains its greatest breadth in its middle third. It is bent in such a way that its oral face is convex and its aboral face correspondingly concave in a transverse direction, and it is so situated that its ventral part is mainly vertical, while its dorsal part is bent outward towards the medial face of the preoperculum. The postero-ventral part of the bone rests against the medial

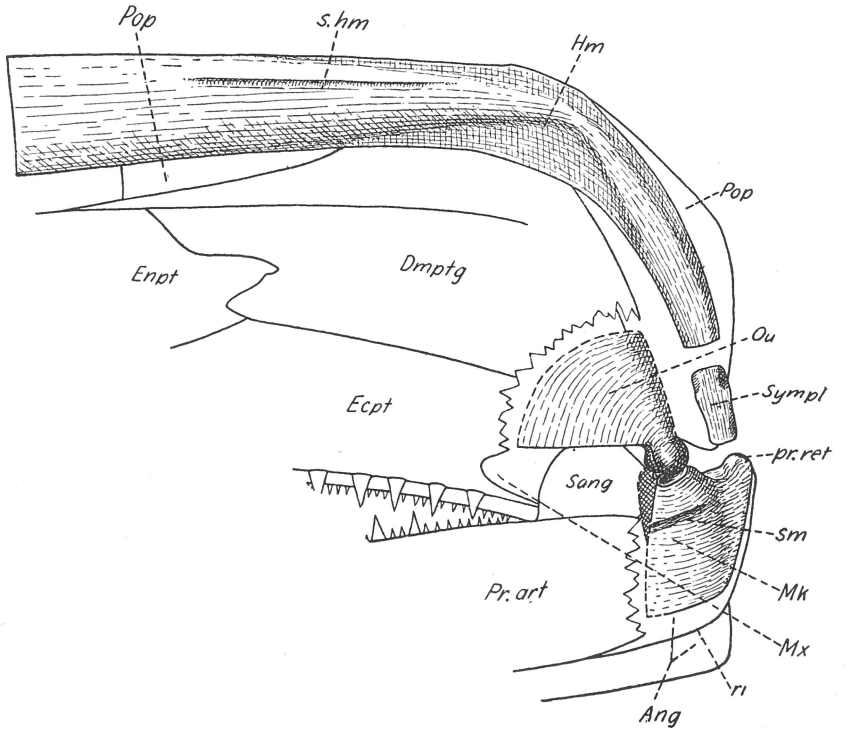


Fig. 72. *Birgeria groenlandica* Stensiö. Attempted sketch showing the ossifications of the mandibular arch and of the dorsal part of the hyoid arch, and their relations to the dermal bones of the palatoquadrate-maxillary apparatus and the lower jaw. Based on several larger specimens. Posterior part of ectopterygoid, dermometapterygoid, and prearticular removed. C. 1. 3×.

Ang, angular; *Dmptg*, dermometapterygoid; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Hm* hyomandibula; *Mk*, articular ossification; *Mx*, maxillary; *Pop*, preoperculum; *Pr. art*, prearticular; *Qu*, quadrate ossification; *Sang*, supraangular; *Sympl*, symplectic; *pr. ret*, retroarticular process; *ri*, internal angular ridge or lamina; *s. hm*, groove for the truncus hyoideomandibularis; *sm*, groove probably for the ramus mandibularis internus facialis.

face of the quadrate ossification, and probably the whole or the greater part of the remaining part of the bone had similar relations to the unossified pars metapterygoidea. The antero-ventral margin adjoins the entopterygoid, probably without overlapping, while the ventral margin is connected by suture with the ectopterygoid in such a way that the dermometapterygoid covers a narrow marginal zone of the oral face of the ectopterygoid. Possibly the posterior half of the dorsal margin was in contact with the medial face of the dorsal shank of the preoperculum; however, if so, the connection was, without doubt, fairly loose. From the oral face of the dermometapterygoid issues a vertical lamina, the base of which extends in a caudal direction as an almost straight line from the foremost end of the bone to a point just ventrally to the postero-dorsal angle of the bone. The height of the lamina decreases from its midmost part both in an anterior and a posterior direction in such a way that the dorsal margin of the lamina is slightly convex and forms, when the palate is seen in medial view, a direct posterior continuation

of the posterior part of the dorsal margin of the entopterygoid (cf. figs. 71–72). A comparison with the dermometapterygoid of *Pteronisculus* (E. Nielsen 1942, pp. 149–150) shows that the vertical lamina described here corresponds to the most dorsal part of the dermometapterygoid of *Pteronisculus*, while the most dorsal part of the dermometapterygoid of *Birgeria* corresponds to the small lamina which, in *Pteronisculus*, issues from the aboral face of the dermometapterygoid. The centre of radiation of the dermometapterygoid is situated a short distance postero-ventrally to the posterior end of the line of issue of the vertical lamina. As far as could be seen, at least the antero-ventral part of the oral face of the dermometapterygoid was covered with small pointed teeth.

Dermopalatines. – The two dermopalatines (Dpl_1, Dpl_2, figs. 70, 71; pl. 12, fig. 1; pl. 16) form an anterior continuation of the ventral division of the ectopterygoid, being developed as mainly horizontal plates which cover the antero-lateral part of the oral face of the palatoquadrate. Their shape will appear from fig. 70.

Laterally they adjoin the maxillary, overlapping a narrow marginal zone of the dorsal face of the internal lamina of that bone, and medially they adjoin the entopterygoid, which slightly overlaps their medial margin. Furthermore they are joined to each other by sutures, but, as far as I can see, without overlapping. The anterior margin of the anterior dermopalatine could not be exposed on the specimens at my disposal, nor could the centres of radiation of any of the two bones be localised. The longitudinal row of large teeth present on the ectopterygoid continues forward throughout the whole length of the oral faces of the two dermopalatines, which moreover, as far as could be seen, medially to the row of large teeth were covered with close-set very small teeth.

Maxillary. – The maxillary (*Mx*, figs. 69–73; pl. 10; pl. 12, fig. 2; pl. 14; pl. 15, fig. 3; pl. 16; pl. 17; figs. 1, 2; pl. 18, fig. 1; pl. 19; pl. 20, figs. 1, 2) is of the normal Palaeonisciform type, consisting of a low suborbital and a high postorbital division, both of which are very long. The outline of its exposed part is shown in fig. 69. The bone may be regarded as bounded by a dorsal, a posterior (postero-dorsal), a ventral, and an anterior margin. The dorsal margin consists of an anterior concave part overlapped by the adjoining suborbitals and infraorbitals, and a posterior straight part, which overlaps a narrow marginal zone of the antero-dorsal shank of the preoperculum. The two parts of the dorsal margin meet in a distinct angle. The posterior margin, which is somewhat forwardly inclined, is straight except for a shallow concavity near its ventral end. Dorsally to the concavity the margin overlaps a narrow marginal zone of the postero-ventral shank of the preoperculum. The concavity itself is so situated in relation to the pars quadrata that it must be compared to the distinct concavity in the hind margin of the maxillary in such forms as *Acropholis stensiöi*, *Plegmolepis kochi*, and *Pteronisculus*

(Aldinger 1937, figs. 6, 17; E. Nielsen 1942, p. 155). In *Pteronisculus* the concavity is occupied by the posterior part of a small quadratojugal. In *Acropholis* and *Plegmolepis* the quadratojugal has not been observed, and in *Birgeria* its presence is doubtful, but there can be no doubt that even in these forms the concavity in the hind margin of the maxillary originally developed in relation to a quadratojugal, even if this bone has later been completely reduced. The long ventral margin, which meets the posterior one in a gently rounded angle, is slightly S-bent, its anterior half being convex and its posterior half concave. This margin bears a row of small acutely pointed teeth. The anterior margin is extremely short and adjoins the likewise short posterior margin of the rostro-premaxillary, as shown in the figures.

As in *Pteronisculus* (E. Nielsen 1942, p. 153), the maxillary is equipped with a strong internal horizontal lamina, which issues from the medial face of the bone a short distance above its ventral margin, and which, as already stated, adjoins the ectopterygoid and the two dermopalatines. This internal lamina attains its greatest height laterally to the midmost part of the ectopterygoid, whence it decreases rapidly in height backwards and more slowly forwards. Posteriorly the lamina ends laterally to the adductor opening, and anteriorly it adjoins the palatal lamina of the rostro-premaxillary, as shown in fig. 70. The ventral face of the lamina is equipped with a single row of very large teeth.

The radiation centre of the maxillary is situated on a level with the internal lamina in the area ventrally to the distinct angle between the anterior concave and the posterior straight part of the dorsal margin of the bone.

Preoperculum. – The preoperculum (*Pop*, figs. 69, 71, 72; pl. 14; pl. 15, fig. 3; pl. 19), as in typical *Palaeonisciformes*, consists of an antero-dorsal and a postero-ventral shank meeting each other in a distinct angle. From its anterior end the antero-dorsal shank decreases gradually in breadth (dorso-ventral extent) backwards, so that the breadth of its hindmost part is only about one-third of the breadth of its foremost one.

On the antero-dorsal shank we may distinguish three free margins, viz. an anterior, a dorsal, and a ventral margin. The anterior, slightly concave margin is overlapped, except farthest dorsally, by the most posterior suborbital, the ventral straight margin is overlapped by the maxillary, and the dorsal, slightly convex margin overlaps the ventral (antero-ventral) margin of the operculum. The postero-ventral shank is broadest in its middle part, narrowing towards both ends, as shown in fig. 69. On this shank we may distinguish an anterior (antero-ventral), a posterior, and a ventral (antero-ventral) margin. The straight anterior margin is overlapped by the maxillary. The posterior margin, the middle part of which is strongly bent so that its dorsal half faces somewhat dorsally and its ventral half slightly ventrally,

overlaps the most dorsal part of the anterior margin of the preoperculum. The short straight ventral margin has no contact with other dermal bones.

The medial face of the antero-dorsal shank, as already stated, is possibly connected with the midmost part of the dorsal margin of the dermometapterygoid and was possibly also connected with the dorsal margin of the unossified pars metapterygoidea. The latter connection, however, if it existed at all, was not, as in *Pteronisculus* (E. Nielsen 1942, p. 154), strengthened by an internal lamina from the preoperculum. Whether the medial face of the ventral preopercular shank was in contact with a posterior part of the palatoquadrate, as is the case for instance in *Pteronisculus* (E. Nielsen 1942, pp. 144, 154), could not be ascertained.

The centre of radiation of the preoperculum lies at the transition between its two shanks, and somewhat nearer the posterior (dorsal) than the anterior (ventral) margin of the bone.

The preoperculum is pierced throughout its length by the preopercular sensory canal, which passes from the postero-ventral angle of the postero-ventral shank of the bone in an almost straight line to the centre of radiation, and from here, after abruptly changing its direction, in a likewise straight line through the antero-dorsal shank of the bone to a point just below the dorsal end of its anterior margin.

Quadratojugal. – In a few specimens remnants of an apparently dermal bone (*Quj*?, pl. 16) are seen between the posterior part of the maxillary and the palatoquadrate. However, on the basis of the available material it is impossible to decide whether we are here concerned with a quadratojugal or with remnants of bones of another origin which obtained their present position as a result of a post-mortem compression of the heads.

Rostro-premaxillary. – Stensiö (1932, pp. 113, 116, fig. 41) describes, in *Birgeria groenlandica*, an unpaired premaxillary separated from the postrostral and the nasals by independent nasals; however, as pointed out already in the first part of the present work (E. Nielsen 1942, p. 139), separate rostrals do not exist in *Birgeria groenlandica*, and a close investigation of Stensiö's premaxillary leaves no doubt that this bone includes rostral components and thus must be termed a rostro-premaxillary. This rostro-premaxillary (*R. pmx*, figs. 69, 70, 73; pl. 11, fig. 2; pl. 20, fig. 2) is a fairly large bone consisting of an external (facial) vertical plate, from which issues an internal (palatal) horizontal lamina. The vertical plate is arched in such a way that its external face is convex and its internal face concave from side to side. The plate is bounded by a convex dorsal, a concave ventral, and a paired straight lateral or postero-lateral margin, and each half of the plate increases strongly in height from its lateral margin to the mid-line of the snout. As already stated, the dorsal margin of the plate is joined by suture with the postrostral and the nasals, while the postero-lateral margin adjoins the antorbital and the maxillary. The only overlapped part of the

plate is a small tongue-shaped process formed by the dorsal part of its posterior margin and overlapped by the antero-ventral part of the antorbital. The plate itself, as already mentioned, overlaps a small tongue-shaped process issuing from the ventral margin of the nasal. Apart from these small overlappings the external plate of the rostro-premaxillary meets edge to edge with the adjacent bones. The ventral free margin is provided with a series of pointed teeth of similar size to those found on the ventral margin of the maxillary. The horizontal lamina issues from the internal face of the vertical plate a short distance above its ventral margin. As shown in fig. 70, the height (rostro-caudal extent) of the lamina decreases in a lateral direction in such a way that the posterior margin of the lamina has a roughly transverse course. The most lateral part of the posterior margin adjoins the internal lamina of the maxillary, while its middle part is situated just anteriorly to the anterior margin of the parasphenoid. As shown in fig. 73 B, the lamina is very massive at its base, but decreases rapidly in thickness in a posterior direction. From side to side the lamina is arched in such a way that its dorsal face is somewhat convex and its ventral face correspondingly concave. On the oral face of the lamina we find, just inside the dentigorous ventral margin of the external plate of the rostro-premaxillary, a series of about eight strong teeth of the same type as the teeth on the internal lamina of the maxillary. The centre of radiation of the bone lies somewhat nearer its ventral than its dorsal margin.

The infraorbital sensory canal enters the rostro-premaxillary through its posterior or postero-lateral margin, and extends from here to the radiation centre, thus forming, together with that of the other side of the head, a complete ethmoidal commissure. As shown in fig. 73 B, the commissure is lodged in a well defined ridge developed on the internal face of the vertical plate of the bone and situated just above the place of issue of the horizontal lamina. Laterally or postero-laterally the ridge is continued by the above-described small tongue-shaped process issuing from the posterior (lateral) margin of the bone and overlapped by the antero-ventral part of the antorbital.

The supraorbital sensory canal, curiously enough, also enters the rostro-premaxillary, for this canal continues from the ventral part of the nasal through the postero-dorso-lateral part of the rostro-premaxillary towards, but without reaching, the centre of radiation.

Discussion. – As is evident from the above, in *Birgeria groenlandica* the ossified part of the palatoquadrate, the dermometapterygoid, the ectopterygoid, the entopterygoid, the two dermopalatines, the maxillary, and the preoperculum are more or less firmly connected with each other (and probably also with the unossified part of the palatoquadrate), forming the walls of a high and rather narrow chamber for the dorsal part of the musculus adductor mandibulae.

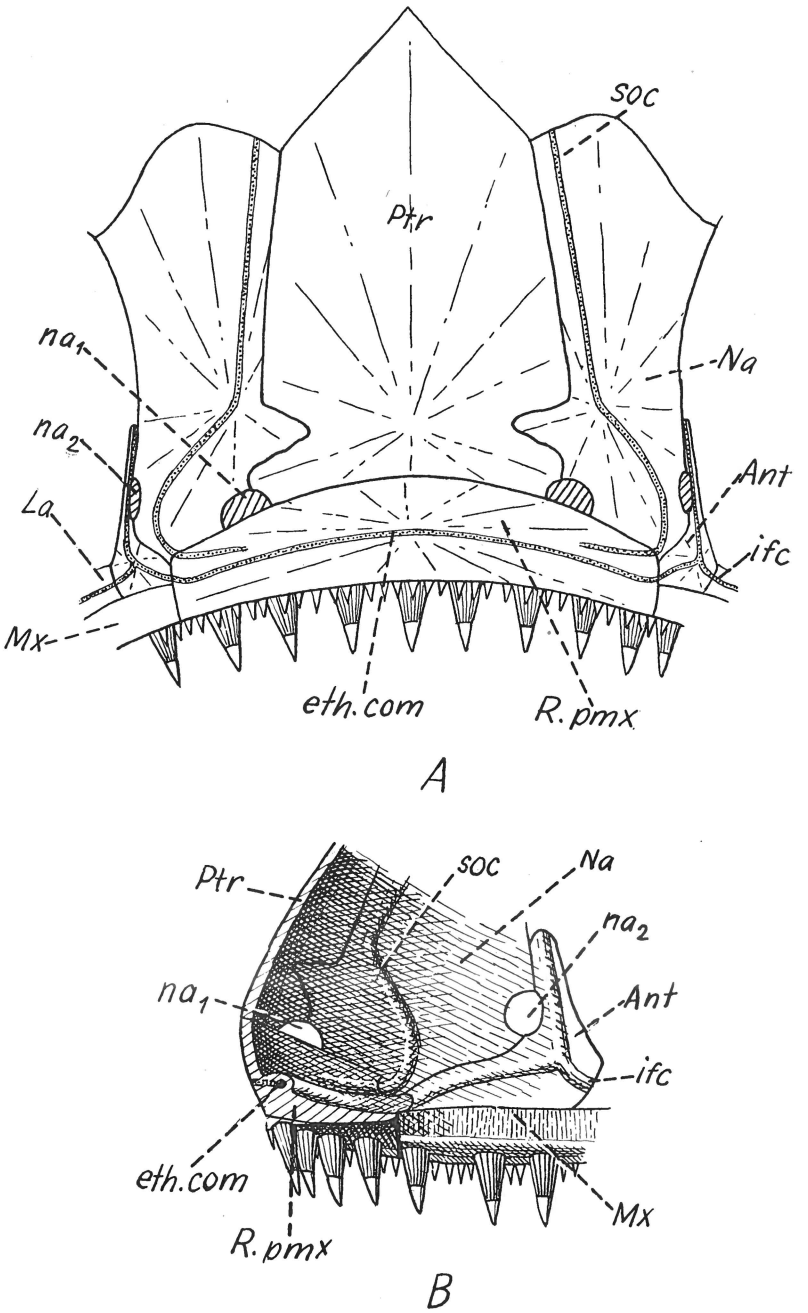


Fig. 73. *Birgeria groenlandica* Stensiö. A, dermal bones of snout region in anterior view. B, dermal bones of right half of snout region in medial view. Based on several large specimens. C. 2.5×.

Ant, antorbital; *La*, lacrimal; *Mx*, maxillary; *Na*, nasal; *Ptr*, postrostral; *R. pmx*, rostropremaxillary; *eth. com*, ethmoidal commisure; *ifc*, infraorbital sensory canal; na_1, na_2, fenestra exonarina anterior and posterior, respectively; *soc*, supraorbital sensory canal.

A similar structure is probably also developed in the other species of *Birgeria*, however, our present knowledge of these forms is much too sparse to permit more detailed comparisons. In *Birgeria mougeoti* parts of the following elements of the palatoquadrate-maxillary apparatus are known: The ecto- and entopterygoid (Stensiö 1921, p. 183, fig. 65), the maxillary (Stensiö 1919; 1921, p. 183; 1932, p. 105), and the preoperculum (Stensiö 1932, p. 105). In general shape and in mutual relations these bones apparently agree very well with the corresponding ones in *Birgeria groenlandica*, thus for instance the ectopterygoid is firmly connected with the maxillary. Aldinger has described the ectopterygoid, the entopterygoid, one dermopalatine, and the maxillary in *Birgeria stensiöi* (Aldinger 1931, pp. 167–171). The ectopterygoid is a long and narrow bone, which is probably firmly connected with the maxillary, and thus it shows good agreement in its main features with the ectopterygoid in *Birgeria groenlandica*. The entopterygoid has a greater backward extension than in *Birgeria groenlandica*, and accordingly the dermometapterygoid must have been relatively short. As far as can be seen, the maxillary agrees fairly well in shape with that of *Birgeria groenlandica*, the most conspicuous difference being the smaller number of teeth in the lingual row.

As is well known, a complex palatoquadrate-maxillary apparatus is developed also in normal *Palaeonisciformes*, *Saurichthys*, and *Australosomus* (Watson 1925, pp. 851–860; Stensiö 1925, pp. 97–107, 142, 149, 162–164, 199–200; Aldinger 1937, pp. 331–332; E. Nielsen 1942, pp. 143–163; present work pp. 99–101; etc.), and as pointed out by Stensiö (1925, pp. 105–106 (cf. E. Nielsen 1942, pp. 158–160)), a firm connection between the palatoquadrate, its dermal bones, and certain dermal bones of the cheek moreover exists in many other Actinopterygians, of which especially the sturgeons (Acipenserids, Polyodontids, and Chondrosteids) present features comparable to those in primitive *Palaeonisciformes*.

The palatoquadrate-maxillary apparatus of *Birgeria* agrees in most respects with that of the comparatively primitive Palaeonisciform *Pteronisculus*, from which it differs mainly in lacking an internal preopercular lamina for consolidation of the connection between the palatoquadrate and the preoperculum, and moreover in having a relatively longer and less high postorbital division. *Boreosomus* (E. Nielsen 1942, pp. 334–342) likewise lacks an internal preopercular lamina, but in this form the postorbital division of the palatoquadrate is much shorter than in *Pteronisculus*, a condition which is evidently due to the specialisation within the *Boreosomus*-line in a Subholostean direction, and the absence of an internal preopercular lamina may accordingly hardly be considered to support an assumption of a close relationship between *Birgeria* and *Boreosomus*.

Among the sturgeons, *Polyodon*, as already pointed out by Aldinger (1937, pp. 330–331), as regards the development of the palatoquadrate agrees

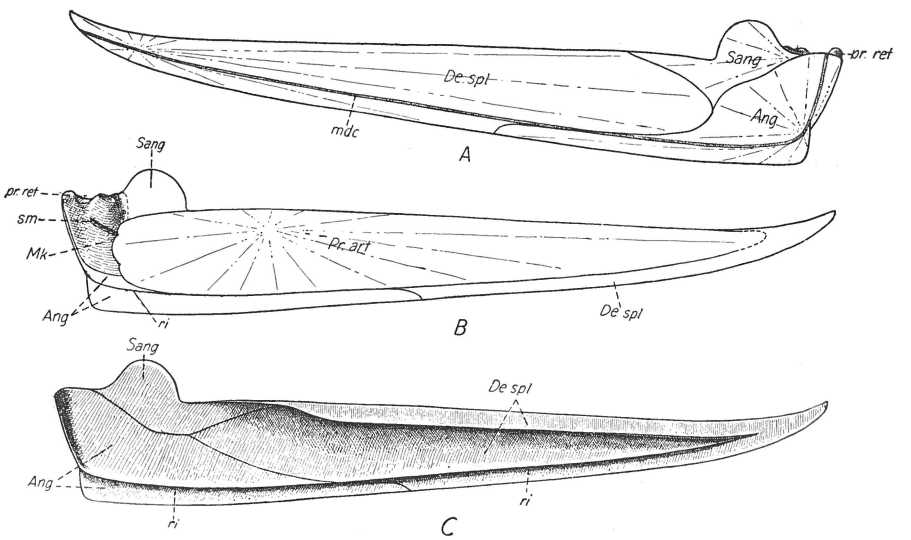


Fig. 74. *Birgeria groenlandica* Stensiö. Mandible. Mainly based on specimens nos. 651, 656, and 662. Teeth omitted. C. 0.8×. A, lateral view. B, medial view. C, medial view of external dermal bones.

Ang, angular; *De. spl*, dentalo-splenial; *Mk*, articular ossification; *Pr. art*, prearticular; *Sang*, supraangular; *mdc*, mandibular sensory canal; *pr. ret*, retroarticular process; *ri*, internal lamina of the angular and the dentalo-splenial; *sm*, groove probably for the ramus mandibularis internus facialis.

more closely with *Birgeria*, and as far as I can see, the palatoquadrate-maxillary apparatus of *Birgeria* may without difficulty be considered as ancestral to the corresponding structure in *Polyodon*.

Mandible.

Meckelian cartilage. – The Meckelian cartilage is only ossified is its hindmost part (pars articularis), where a single large osssification (Mk. figs. 72, 74; pl. 12, fig. 2; pl. 14; pl. 17, fig. 1) is found both in large and in smaller specimens. The ossification, which is mainly situated behind the muscle space of the lower jaw, but which also bounds the most posterior part of the muscle space laterally and medially, is relatively high and narrow, the ratio between its maximum height, lenght, and breadth being about 3:2:2. Both the height and the breadth decrease in a posterior direction. On the ossification we may distinguish a dorsal, a medial, a lateral, an anterior, and a ventral face. The dorsal face, which is roughly triangular in outline, shows three marked elevations or processes separated by fairly narrow grooves, and occupying the antero-lateral, the antero-medial, and the posterior part, respectively, of the face.

Distally the two anterior processes, both of which are elliptical in transverse section, with the long diameter directed rostro-caudally, carry a well

defined depression for articulation with the lateral and the median condyle, respectively, on the pars quadrata. The posterior process, which is likewise elliptical in transverse section, with the long diameter directed rostro-caudally, is bluntly rounded distally and must be interpreted as a well developed processus retroarticularis. The medial face, which, as shown in fig. 72, is four-sided in outline, may for descriptive reasons be considered as consisting of an anterior and a posterior division separated by a line running from a point on the dorsal margin of the face, on a level with the posterior end of the medial articular fossa on the dorsal face, to the postero-ventral angle of the face. The posterior division of the face is slightly concave in a longitudinal direction and faces postero-medially, while the anterior division is slightly convex in a longitudinal direction and faces direct medially. On the anterior division, the anterior part of which is covered by the hindmost part of the prearticular, we observe a distinct longitudinal groove (sm, fig. 5 72, 74), which must be compared to the dorsal one of the two grooves found on the medial face of the pars articularis of *Pteronisculus* (E. Nielsen 1942, p. 168, figs. 36, 38B, 40A), and which must thus be assumed to have lodged either a branch of the ramus mandibularis internus facialis or a vessel. The lateral face is completely covered by the posterior and highest part of the angular. The face is divided by a distinct bend into an anterior large, mainly laterally directed division covered by that part of the angular which is situated anteriorly to the posterior ascending part of the mandibular sensory canal, and a posterior, much smaller, postero-ventro-laterally directed division covered by that part of the angular which lies behind the ascending part of the mandibular sensory canal. The lateral and the medial faces meet posteriorly in a very sharp angle.

The anterior face is mainly occupied by a deep and extensive concavity, which represents the hindmost part of the muscular fossa in the jaw. Laterally, ventrally, and medially to the concavity the anterior face is devoid of perichondral bone and was accordingly joined to cartilage. The small ventral face could not be investigated in detail, but as far as could be seen, it was probably only developed as a narrow rounded longitudinal ridge which separated the lateral and the medial faces.

Angular. – The hindmost one of the three dermal bones on the lateral side of the mandible is the fairly large angular. This bone (*Ang*, figs. 69, 72, 74; pl. 12, fig. 2; pl. 14; pl. 17; fig. 2; pl. 18, fig. 1; pl. 20, fig. 1) consists of an external plate and an internal lamina. The external plate is roughly triangular in outline, with a short posterior, a much longer ventral, and a still longer antero-dorsal margin. The posterior and the ventral margins are almost straight, while the anterior margin is irregularly S-bent. Antero-dorsally the angular adjoins the supraangular and the dentalo-splenial, overlapping the postero-ventral margin of the former and being overlapped by the postero-ventral margin of the latter of these two bones. The centre of

radiation lies in the postero-ventral part of the plate, somewhat nearer the posterior than the ventral margin.

The mandibular sensory canal traverses the plate from its postero-dorsal angle, running via the centre of radiation to a point on the antero-dorsal margin a short distance behind its anterior end, gradually changing its course in the postero-ventral part of the plate, i. e., in the area in which it passes the radiation centre, from nearly vertical to nearly horizontal. The sensory canal lies in a thickened part of the bone, and this thickening appears, as usual, as a well marked ridge (*ri*, figs. 72, 74) on its internal (medial) face.

The ridge may also be described as the basal part of the strong internal lamina, which, as already mentioned, forms part of the angular. Corresponding to the bent course of the sensory canal the ridge may, broadly speaking, be regarded as consisting of two parts which pass gradually into one another, viz. an anterior almost horizontal, and a posterior almost vertical one. From the horizontal part the internal lamina extends in a medial direction, while from the posterior part it extends in a postero-medial direction. The sharp medial edge of the horizontal part of the internal lamina abuts against, and is probably connected with, the most ventral part of the large prearticular, while its more posterior part, which issues mainly from the posterior margin of the external plate of the angular, lies close against the posterior part of the lateral face of the ossified part of the palatoquadrate.

Supraangular. – The supraangular (*Sang*, figs. 69, 72, 74; pl. 12, fig. 2; pl. 16; pl. 17, fig. 2; pl. 18, fig. 1) may be described as a roughly triangular, mainly vertically placed bone, bounded by a dorsal, an antero-ventral, and a postero-ventral margin. The posterior part of the long dorsal margin is produced upward into a very strong dorsal process, the shape of which is shown in fig. 74, and from the anterior two-fifths of the dorsal margin issues, in a medial direction, a lamina, the height of which increases gradually in an anterior direction, and the distal edge of which forms part of the boundary of the adductor opening of the jaw. The postero-dorsal, slightly convex margin is overlapped by the angular, while the antero-ventral, slightly concave margin is overlapped by the dentalo-splenial. Both these overlappings are fairly considerable. The centre of radiation is situated very near the posterior end of the exposed part of the bone. The hindmost part of the medial face covers, and is firmly connected with, the antero-dorsal part of the lateral face of the Meckelian ossification, while the remaining part of the medial face forms part of the boundary of the muscular fossa of the jaw.

Dentalo-splenial. – The dentalo-splenial (*De. spl*, figs. 69, 74; pl. 10; pl. 12, fig. 2; pls. 14, 16; pl. 17, fig. 2; pl. 18, fig. 1; pl. 19; pl. 20, fig. 2) is long and low, though not quite as low as in the reconstruction given by Stensiö (1932, fig. 41). The bone consists of an external plate, from which issue two internal laminae, viz. a ventral one extending in a medial direction from the medial face of the plate and forming an anterior continutation of

the internal lamina of the angular, and a dorsal one, which, as far as can be seen, extends in a medial direction from the dorsal margin of the plate as an anterior continuation of the internal lamina of the supraangular.

The external plate, the outline of which is shown in figs. 69 and 74, attains its greatest height on a level with the anterior end of the exposed part of the angular, whence it decreases gradually in height in a forward, and somewhat more irregularly in a backward direction. Posteriorly the external face of the plate is fairly vertical, while anteriorly it grows increasingly oblique, being directed more and more ventrally towards its anterior end. Moreover, as the anterior part of the mandible curves inward in the usual way, the anterior part of the external face of the dentalo-splenial is also somewhat anteriorly directed. Posteriorly the external plate of the dentalo-splenial, as already mentioned, adjoins and overlaps the angular and the supraangular to a fairly considerable extent. The mandibular sensory canal continues in the usual way from the angular forward through the external plate of the dentalo-splenial, piercing the radiation centre, which, as shown in fig. 74, is situated very far anteriorly. The sensory canal, which has an almost straight course, lies in a thickened zone of the plate, visible as a distinct ridge on its medial face. The ridge forms the base of the above-mentioned ventral internal lamina, the distal edge of which reaches, and is probably connected with, the most ventral part of the medial face of the long prearticular, thus forming the whole floor of that part of the muscular fossa of the jaw which is situated anteriorly to the angular. The dorsal internal lamina, which, as mentioned above, probably issues from the dorsal margin of the external plate, is somewhat higher than the ventral lamina and consists of a proximal horizontal part, which forms the roof of the muscular fossa anteriorly to the anterior end of the supraangular, and a distal part, which is bent downward and forms the most dorsal part of the fairly vertical medial wall of the same part of the muscular fossa. The medial face of this vertical part of the dorsal lamina is covered by and firmly connected with the lateral face of the prearticular, while its ventral margin in the extreme foremost part of the jaw is fused with the medial margin of the ventral internal lamina, so that the dentalo-splenial completely surrounds the most anterior end of the muscular fossa.

The teeth attached to the dentalo-splenial are arranged in a labial row containing about 100 small teeth, and a lingual row containing about 25 large teeth. The labial row is situated on the dorsal edge of the external plate of the bone, while the lingual row is situated on the horisontal part of the dorsal internal lamina. Both rows continue backward on to the anterior part of the supraangular, where the labial one is represented by 5–7 small teeth situated on the dorsal edge of the external plate of the bone, while the lingual row is represented by one or two larger teeth situated on the foremost part of the dorsal face of its internal lamina.

Prearticular. – On the medial side of the mandible only a single dermal bone, the prearticular (*Pr. art*, figs. 72, 74; pl. 17, fig. 1; pl. 18, fig. 1; pl. 20, fig. 1) has been observed. This bone, the foremost end of which could not be investigated in detail, is a mainly vertically placed plate, roughly triangular in outline, and bounded by a short posterior, a long dorsal, and a long ventral margin. The bone has a very considerable length, its posterior margin lying medially to the posterior end of the adductor opening and its foremost end being situated only a short distance behind the symphysial region. The radiation centre is situated much nearer the posterior than the anterior end of the bone and only a short distance beneath its dorsal margin.

The most posterior part of the lateral face of the prearticular covers and is firmly connected with the anterior part of the medial face of the ossified part of the Meckelian cartilage. Further, as mentioned above, the prearticular is in contact with the dorsal and the ventral internal lamina of the dentalo-splenial as well as with the ventral internal lamina of the angular, and thus it forms the greater part of the medial wall of the muscle space of the jaw in the fossil specimens. In the living animal, however, the lateral face of the prearticular and perhaps also the dorsal face of the ventral horizontal lamina of the dentalo-splenial rested against the Meckelian cartilage, which probably bounded the muscular fossa medially and ventrally to a very considerable extent.

Discussion. – As is evident from the above, the restoration of the lower jaw of *Birgeria groenlandica* given by Stensiö (1932, fig. 41) is not quite correct. On the specimen investigated by Stensiö the supraangular with its strong dorsal process is not exposed, and Stensiö therefore obtained the impression that the postero-dorsal corner of the angular was »produced upward into a truncated, well-pronounced dorsal process (*pr. ang*, pl. XII, fig. 4)« (Stensiö 1932, p. 113).

Stensiö also described a dorsally or postero-dorsally directed angular process in *Birgeria mougeoti* (Stensiö 1932, p. 105, fig. 39). In this case, however, the process observed by Stensiö, as far as I can see, represents the postero-dorsal part of a supraangular developed in much the same way as in *Birgeria groenlandica*.

The presence of the strong supraangular process, which most likely supported a well developed processus coronoideus, and the lack of independent coronoids are the most important characters in which the lower jaw of *Birgeria* differs from that of normal *Palaeonisciformes* (cf. Watson 1925, 1928; E. Nielsen 1942). A strong dorsal process, formed, at least partially, by the supraangular, is found in several higher Ganoids, as for instance in *Ospia* (Stensiö 1932, p. 228), *Amia*, and *Lepidosteus*, but not in the sturgeons.

In *Birgeria* the process serves partly as a place of insertion for adductor muscles and partly as a support for the joint of the jaw, its lateral face hav-

ing slid against the medial face of the lateral wall of the muscle space in the palatoquadrate-maxillary apparatus, and there can be no doubt that the strong development of the supraangular process in this case is due to the immense lengthening of the lower jaw, as is also the fairly strong development of the processus retroarticularis.

The lack of the supraangular process in *Polyodon*, in which genus the jaws also have a very considerable length, probably finds its explanation in the altered mode of living, since *Polyodon* with its peaceful habits need not use its jaws with the same force as the carnivorous fish *Birgeria*.

In other respects the lower jaw of *Polyodon* shows a fairly close resemblance to that of *Birgeria*; thus its large external dermal bone, which contains homologues to the dentalo-splenial, is equipped with very strong dorsal and ventral internal laminae, which form the dorsal and the ventral wall, respectively, of the muscle chamber of the jaw, and there can be no serious objections to the assumption that the lower jaw of *Polyodon* may have developed from a jaw of the type found in *Birgeria*.

It is quite probable that future investigations will show that a strong supraangular process is found in several normal *Palaeonisciformes*, for many of these have been carnivorous and accordingly needed vigorous jaws. Possibly, also, such a process has developed within several Palaeonisciform lines independently of each other; thus, for instance, it is hardly probable that the *Ospia-Amia* line and the *Birgeria* line have a common starting point within the Palaeonisciform group.

Hyoid arch, operculum, subopercuIum, branchiostegal rays, and gular plate.

In the hyoid arch four ossifications have been observed with certainty, viz. the hyomandibula, the symplectic, a ceratohyal, and a hypohyal ossification. They are all four rather difficult to study, for in most cases they are rather poorly preserved.

Hyomandibula. – The hyomandibula (*Hm*, fig. 72; pl. 12, fig. 2; pl. 16; pl. 18, fig. 1; pl. 19; pl. 20, figs. 1, 2) articulated by its dorsal (proximal) end with the above-described articular fossa on the lateral face of the otic region of the neural endocranium, and extended from here backward and downward, as shown in fig. 72, its ventral (distal) end being situated posteriorly to the pars quadrata. As in normal *Palaeonisciformes*, the hyomandibula consists of two shanks, a dorsal (antero-dorsal) fairly horizontal and a ventral (postero-ventral) somewhat more oblique one, which meet each other at an obtuse angle. The transition between the two shanks is fairly gradual.

The dorsal shank, which is more than twice as long as the ventral one, is strongly compressed from side to side, so that in addition to its proximal

terminal face it presents a lateral and a medial face separated by sharp dorsal and ventral edges. The breadth (dorso-ventral extension) of the dermal shank decreases slowly in a backward direction.

The ventral shank is less compressed than the dorsal one and decreases gradually in breadth towards its distal end.

The interior of both shanks are cancellate except in the ventral or antero-ventral part of the distal division of the dorsal and the antero-dorsal part of the proximal division of the ventral shank, where the bone is compressed to a very thin lamina, the extent of which is indicated in fig. 72, and which consists of compact bone. Both terminal faces of the hyomandibula are devoid of perichondral lining, and were probably capped by cartilage in the living animal.

A processus opercularis is not developed, and the truncus hyoideomandibularis did not pierce the bone, as in many normal *Palaeonisciformes*. The only indication of the course of the truncus hyoideomandibularis is a distinct longitudinal groove (*s. hm*, fig. 72) on the medial face of the dorsal shank. Judging from the position of this groove the relations between the truncus hyoideomandibularis and the hyomandibula must have been much the same as in *Acipenser* and *Polyodon*, in which forms the truncus hyoideomandibularis from its place of exit through the cranial wall passes backward and crosses the posterior margin of the hyomandibula (von Wijhe 1882, pp. 236–237, 250–251; pl. XV, figs. 1, 4; Allis 1915, pp. 605–610; 1918 b).

Symplectic. – The symplectic (*Sympl*, fig. 72; pl. 14; pl. 18, fig. 1; pl. 19), which has only been observed in a few specimens, is a small bone capped by cartilage both dorsally and ventrally and situated between the ventral end of the hyomandibula and the processus retroarticularis. In fig. 72 the bone is drawn in the same position as in specimen no. 656; however, as the dimensions of the cartilaginous epiphyses of both the symplectic and the hyomandibula are unknown, it is quite probable that the position of the symplectic was actually the same as in *Acipenser* and *Polyodon*. The exact shape of the bone cannot be made out on the basis of the material at hand, but it can be stated that the antero-dorso-medial and the postero-dorso-medial corners of the bone were both developed as distinct facettes, the former of which probably served as the place of insertion for a ligamentous connection between the symplectic and the pars quadrata.

Ceratohyal. – Remnants of a ceratohyal ossification (*Chy*$_1$, pl. 18, fig. 1; pl. 20, fig. 2) have been found in a number of small specimens, and a fairly complete ceratohyal ossification is present in the large specimen no. 656 (pl. 18, fig. 1). The ceratohyal ossification, which, without doubt, corresponds to ceratohyal I in *Pteronisculus* (E. Nielsen 1942, pp. 175–176), is a vertically placed plate, the length of which is about one-third of the length of the mandible. The ossification, which was capped by cartilage in the living animal both anteriorly and posteriorly, attains its greatest height farthest

posteriorly, whence the height decreases forward through its posterior three-fourths, to increase somewhat again in its foremost fourth, as shown in pl. 18, fig. 1. Neither the medial nor the lateral face of the ossification could be studied in detail, and it was impossible to ascertain whether, as in *Pteronisculus* (E. Nielsen 1942, p. 176, fig. 43), a groove was developed for the afferent hyoid artery.

Hypohyal. – Anteriorly to the ceratohyal ossification we find, in specimen no. 656, a small ossification (*Hhy*, pl. 18, fig. 1), which should undoubtedly be interpreted as a hypohyal. This ossification, which was capped by cartilage in the living animal, at least posteriorly, is only seen in sagittal section, and hence its exact shape could not be made out. The length of the ossification is about one-fourth of the length of the ceratohyal ossification just described, and as far as can be seen, its height decreases from its posterior end to a point a short distance behind its anterior end, to increase again forward through its most anterior part, as shown in the figure. Whether the hypohyal ossification articulated anteriorly with a basihyal ossification, could not be ascertained.

Operculum. – The operculum (*Op*, fig. 69; pls. 10, 14, 19; pl. 20, fig. 2), which is well preserved in both small and large specimens, is a long and narrow triangular bone, bounded by a dorsal, a postero-dorsal, and an antero-ventral margin. All the three margins, of which the antero-ventral one is the longest and the postero-dorsal one the shortest, are slightly convex. The antero-ventral margin, except farthest posteriorly, is overlapped by the antero-dorsal shank of the preoperculum, the dorsal margin is separated by a small interspace from the lateral margin of the supratemporal and the posttemporal, and the postero-dorsal margin overlaps the antero-ventral margin of the dorsal half of the supracleithrum. The operculum is curved in a dorso-ventral direction, so that its lateral face is slightly convex and its medial face correspondingly concave. The centre of radiation lies far anteriorly in the bone and nearer its antero-ventral than its dorsal margin.

Suboperculum. – The suboperculum (*Sop*, fig. 69; pls. 10, 19; pl. 20, fig. 1) is situated in the area just behind the postero-ventral shank of the preoperculum. It is a fairly large bone, the structure of which is quite unique among primitive Ganoids. The bone consists of four, five, or six long and narrow, roughly vertical rays, which are fused with each other only farthest ventrally. Each of the rays is triangular in outline, with a long anterior and posterior and a very short dorsal margin. In the foremost ray the dorsal margin faces antero-dorsally, while in the more posterior rays it faces postero-dorsally. As shown in fig. 69, the length of the rays changes from the foremost to the hindmost one in such a way that the whole suboperculum may be described as a four-sided bone bounded by an anterior, an antero-dorsal, a postero-dorsal, and a postero-ventral margin. The anterior margin is formed by the anterior margin of the foremost ray, the antero-dorsal margin by the

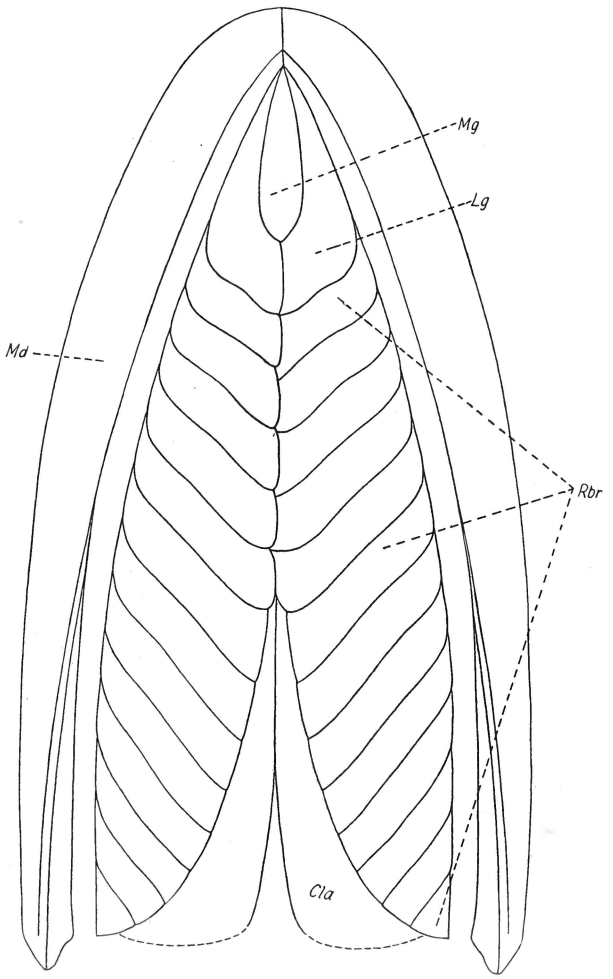


Fig. 75. *Birgeria groenlandica* Stensiö. Attempted sketch of head with clavicles in ventral view. Based on several large and small specimens.
Cla, clavicle; *Lg*, lateral gular plate; *Md*, mandible; *Mg*, median gular plate; *Rbr*, branchiostegal ray.

upper margin of the following rays, and the postero-ventral margin by the posterior margin of the hindmost ray. Each ray slightly overlaps that following next behind. The centre of radiation is situated in the extreme ventral end of the bone.

Branchiostegal rays. – In the reconstructions given here (figs. 69, 75) the branchiostegal series comprises fourteen rays (*Rbr*, figs. 69, 75; pl. 16; pl. 20, figs. 1, 2; *Lg*, fig. 75), but the number probably varies somewhat from specimen to specimen. The whole series is situated medially to the ventral margin of the lower jaw, and is thus separated from the suboperculum by a considerable gap. The foremost and the hindmost of the rays are triangular

in outline, while the others are four-sided. The shape and relative size of the exposed parts of the individual rays are shown in fig. 75, so it will suffice here to call attention to the fact that, as already pointed out by Stensiö (1932, p. 113), the antero-lateral corner of the four-sided rays is produced in a characteristic way, though less so than in *Birgeria mougeoti*. Each ray overlaps the antero-medial margin of that following next behind in the series, and probably the size of the overlapped areas varied in breadth according to the position of the opercular fold. The foremost five to seven rays in the series on the one side of the head moreover overlap to some extent the corresponding rays of the series on the other side. The centre of radiation could only be localised in some of the rays in which it was situated much nearer the lateral than the medial margin. No pit-lines have been observed.

Gular plate. – Between the foremost parts of the right and the left branchiostegal series we find a small median gular plate (*Mg*, fig. 75), bounded by convex right and left margins and pointed at both ends. The length of the plate is between three and four times its maximum breadth, which it attains much nearer its posterior than its anterior end. The plate overlaps a narrow marginal zone of the foremost branchiostegal ray. Its centre of radiation could not be localised.

Discussion. – Very little is known about the hyoid arch in *Birgeria mougeoti*, the only information given by Stensiö regarding this structure being that the hyomandibula, as far as could be seen, »was a long, slender bar of bone strongly inclined forwards and without an opercular process« (Stensiö 1932, p. 105).

The specimen of *Birgeria mougeoti* described and figured by Stensiö in 1932 shows the fragmentary impression of a dermal bone, which we are now able to identify as the operculum. This bone, which is situated dorsally to the preserved part of the preoperculum, corresponds very well in shape to the anterior part of the operculum of *Birgeria groenlandica*.

The suboperculum has not been observed in *Birgeria mougeoti*, but in Stensiö's specimen from 1932 the greater part of the branchiostegal series is preserved. The branchiostegal rays are developed much as those in *Birgeria groenlandica*, from which they mainly differ, as pointed out by Stensiö (1932, p. 113), in their antero-lateral corners being still more produced.

As regards the structures treated here *Birgeria* differs from the normal *Palaeonisciformes* in its extremely oblique suspensorium as well as in its comparatively small operculum and its peculiarly shaped suboperculum. In *Coccocephalus*, which, as mentioned above, in certain other respects show some agreement with *Birgeria*, the operculum and the suboperculum are of the normal Palaeonisciform type, but the operculum is relatively smaller than in most normal *Palaeonisciformes*, and it may therefore be regarded as representing an intermediate stage between the normal Palaeonisciform operculum and that of *Birgeria*.

In a recent work Westoll, after demonstrating the existence of a gap between the suboperculum and the branchiostegal series in *Pyritocephalus* (Westoll 1944, pp. 42–60, 77; figs. 23–26, 28–31, 33) mentions a number of other cases in which there is a gap between the dorsal and the ventral division of the series of bones in the opercular fold (*Holoptychius*, the Coelacanths, the Saurichthyids, *Polypterus*, and perhaps also the *Catopteridae*), and writes (p. 77): »It is not clear whether or not all these cases can be ascribed to similar causes operating in each group. The *Holoptychius* cheek is distinctly longer, with a more oblique suspensorium, than the cheek in the more »normal« osteolepids, while in each of the other groups it is much shorter than in the presumed »normal« ancestors. Although a single mechanical basis for this condition of the opercular system seems to be made unlikely by these facts, one functional aspect seems to be of interest. Certain groups of these fishes may have lived generally in comparatively poorly oxygenated waters. It is possible that modification of the opercular apparatus may be due to the presence of accessory respiratory structures in the pharyngeal or branchial region, either external gills or respiratory diverticula in which bubbles of air could be used. Many recent fishes living in poorly oxygenated waters have such structures (see Carter and Beadle, 1931).«

In *Birgeria*, which is clearly distinct from the groups discussed by Westoll, the break in the series of bones in the opercular fold is probably due solely to the extreme lengthening of the cheek, and in any case considering the well oxygenated waters of the open sea in which *Birgeria* lived, it is highly improbable that it was in need of accessory respiratory structures.

In the recent sturgeons (*Acipenser* and *Polyodon*) the operculum is completely reduced (Hennig 1925, p. 128; Aldinger 1937, p. 366), a condition which may be regarded as the final result of the development commenced by *Birgeria* (and possibly also by *Coccocephalus*), viz. the lengthening of the cheek which resulted in a very oblique position of the hyomandibula. In this connection it is of very great interest that the suboperculum of *Polyodon* is developed in much the same way as in *Birgeria*, consisting of a number of rays which are only fused at one end. In *Polyodon*, however, we find a single branchiostegal ray situated distinctly posteriorly to the lower jaw, and thus not comparable to any of the branchiostegal rays in *Birgeria*. The presence of this ray, which is split up in much the same way as the suboperculum, speaks decidedly against the hypothesis that *Birgeria* should be directly ancestral to *Polyodon*, but, of course, it does not exclude the possibility that *Birgeria* and *Polyodon* have a common ancestor with a continuous series of bones in the opercular fold.

Of differences between *Polyodon* and *Birgeria* regarding the hyoid arch we may mention that the dorsal part of the hyomandibula in *Polyodon* is compressed in a direction which is almost vertical to that of its ventral part

(Bridge 1878, p. 707; pl. 57, fig. 1), while in *Birgeria* both shanks of the bone are laterally compressed. Moreover the symplectic of *Polyodon* is entirely unossified. The two genera agree in having only a single ceratohyal ossification.

Branchial arches and basibranchial series.

Ossifications belonging to the branchial skeleton are found in many small as well as larger specimens; however, they are mostly in a poor state of preservation, and since, moreover, owing to the post-mortem compression of the fragile head, they are always more or less displaced, it is impossible to decide whether four or five branchial arches were present.

Remnants of the following elements have been identified: Infrapharyngobranchials, epibranchials I, II, III, and IV, ceratobranchials I, II, III, hypobranchials I, II, III, and basibranchials.

Discussion. – On the basis of our present knowledge of the branchial skeleton of *Birgeria groenlandica* it is, of course, impossible to make comparisons with *Birgeria mougeoti* and *Birgeria stensiöi*, in which two species parts of the branchial skeleton have been investigated in fairly great detail (Stensiö 1921, pp. 184–186; Aldinger 1931, pp. 170–174). In *Birgeria mougeoti* remnants of four branchial arches are known. Each of the two foremost branchial arches contains a hypobranchial, a ceratobranchial, an epibranchial, and probably both a supra- and an infrapharyngobranchial. In the third branchial arch a hypobranchial, a ceratobranchial, and an epibranchial have been observed, and of the ossifications belonging to the fourth arch the ceratobranchial has been identified. The basibranchial series of *Birgeria mougeoti* contains at least three ossifications.

Ornament of the dermal bones of the head.

The ornament of the external dermal bones of the head consists of tubercles and striae, the arrangement of which has been treated in fairly great detail by Stensiö (1932, pp. 105–106, 114, 295), who i. a. pointed out that the striated areas are of a relatively greater extent than in the somewhat younger *Birgeria mougeoti*, a fact which he explains by assuming a progressive breaking up of the striae into tubercles.

The fresh materal permits a still more detailed study of the ornament of the dermal bones than that carried out by Stensiö on his one incomplete specimen, and, as will be evident from the below, this renewed study reveals problems of no little interest.

Except for certain minor unornamented areas, the dermal cranial roof is ornamented with fairly close-set rounded tubercles of varying size. On

the most anterior part of the roof the tubercles are very small, but they increase considerably in size in the posterior part of the postrostral and the nasal. On the large frontal conditions are more complicated. Anteriorly to the centre of radiation we find, above the supraorbital sensory canal, a fairly narrow longitudinal zone with tubercles of about the same size as on the posterior part of the postrostral and the nasal. Laterally and medially to this zone the tubercles are much smaller. Posteriorly to the centre of radiation the tubercles are of rather varying size, but except most postero-laterally they are fairly large. On the supraorbital complex the tubercles are very small, while on the supraorbito-dermosphenotico-intertemporal, the supratemporal, the parietal(s), and the extrascapular they are rather large, though smaller than the largest ones on the frontal.

In fig. 64 the distribution of the above-mentioned unornamented areas of the dermal cranial roof is indicated by hatching. As shown in the figure, there are five such areas on each half of the cranial roof, viz. two small supraorbital ones, two somewhat larger frontal ones, situated antero-medially and postero-laterally, respectively, to the centre of radiation, and a single extensive posterior one comprising parts of the external faces of both the frontal, the parietal(s), and the supratemporal. Two of the unornamented areas, viz. the area antero-medially to the radiation centre of the frontal and the large posterior area, reach the mid-line of the cranial roof and thus join with the corresponding ones of the other half of the roof.

The lack of ornament on the hindmost part of the frontal of *Birgeria mougeoti* was already observed by Aldinger (1938, p. 330), who put forward the supposition that this condition was due to this part of the frontal being overlapped by small dermal bones situated anteriorly to the extrascapular series. However, such small bones have never been observed in any species of *Birgeria*, and even if they do exist, they would neither explain the development of the more lateral parts of the large posterior unornamented area nor that of the more anterior, smaller, and smooth areas. In a following chapter I shall advance another hypothesis as to the nature of these interesting structures (cf. p. 259).

The known elements of the infraorbital series as well as the suborbitals are ornamented with round or oblong medium-sized tubercles. On the anterior and greater part of the antero-dorsal shank of the preoperculum the predominant ornamental elements are shorter or longer, mainly vertically disposed striae, except in a narrow zone along the margins, where tubercles are fairly common. More posteriorly the preoperculum seems principally to be ornamented with rather coarse tubercles; however, a considerable part of the external face of the most postero-ventral part of the bone could not be exposed in the specimens at my disposal.

According to Stensiö the ornament of the maxillary consists both of striae and tubercles, the striae occurring on the main dorsal part of the

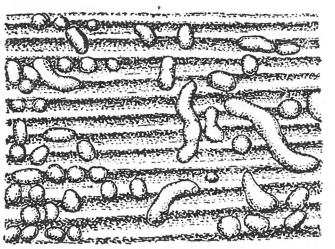


Fig. 76. *Birgeria groenlandica* Stensiö. Ornament of posterior part of lower jaw (dentalo-splenial) of specimen no. 652. C. 8×.

postorbital division and the tubercles on the whole suborbital and on the oral margin of the postorbital division of the bone. Most posteriorly the striae have a general rostro-caudal direction, while more anteriorly they curve downward and forward. (Stensiö 1932, p. 114). In Stensiö's specimen, however, the maxillary on either side of the head lacks a very considerable postero-dorsal part of its postorbital division, and accordingly that part of the bone on which Stensiö observed striae with a general rostro-caudal direction lies rather far anterior to the posterior margin. In more complete specimens the striae on the posterior part of the postorbital division of the maxillary can be seen to be mainly parallel with the posterior margin, while on the dorsal part of the postorbital division they are mainly parallel with the dorsal margin, and on the anterior part with the anterior margin, or, in other words, the system of striae on the peripheral part of the postorbital division shows a roughly concentric arrangement. With increasing distance from the margins the direction of the striae is gradually altered, becoming mainly rostro-caudal in the central part of the posterior division.

Tubercles occur not only on the suborbital and the oral margin of the postorbital division of the maxillary, but also, though more scattered, on the striated area of the postorbital division, where they are attached to and cover parts of the striae in a way the significance of which will be discussed below.

On the lower jaw the ornament also consists of both striae and tubercles. The striae are predominant on the posterior half of the dentalo-splenial, while the anterior half of this bone as well as the angular and the ventral part of the supraangular are densely tuberculated. As on the maxillary, however, scattered tubercles also occur on the striated area.

According to Stensiö (1932, p. 106), the tubercles arose by a breaking up of the longer striae. If this view is correct, the tubercles must be expected to be arranged, at least to a certain degree, in rows, which at the transition from a tuberculated to a striated area should pass continuously into striae. However, this is not the case either on the maxillary or on the mandible, and on studying the relations between the tubercles and the striae in the mainly striated areas of the dentalo-splenial and the maxillary, there can

be no doubt that the tubercles cannot be regarded as derivatives of the striae. In fig. 76 a part of the striated area of the dentalo-splenial is seen which shows the conditions very clearly. As will be seen, the striae form a very regular system of parallel ridges, while the rounded or more or less prolonged tubercles are disposed in a very casual way, but evidently as more superficial structures. Some tubercles are only connected with a single ridge, others extend across two, three, or even more ridges, in some cases a tubercle rests on the top of a ridge, in others in the depression between two ridges. By means of a fine needle the tubercles may easily be detached from their substratum, and it then turns out that the ridges beneath the tubercles are by no means deformed. If we extend the investigation to comprise the densely tuberculated areas of the mandible, we shall find that here, also, the tubercles often overlie normally developed striae, and the same seems to be the case on the maxillary. In view of the above statements and the fact that the tubercles contain a distinct pulp, the tubercles should probably rather be regarded as structures of the same general nature as the denticles which have for long been known to occur on the external faces of the scales and the dermal bones in *Polypterus*, *Lepidosteus*, and some *Siluridae* even though they differ from these by being more firmly connected with their substratum. In a recent paper Goodrich (1942, pp. 459–464) has demonstrated the existence of typical denticles in a Carboniferous Palaeonisciform, *Whiteichthys greenlandicus*, from East Greenland, and has put forward the assumption that similar structures may also turn out to exist in other fossil Actinopterygians.

As far as could be seen, the branchiostegal rays are ornamented with rounded tubercles, and the same is the case with the suboperculum. The operculum is also tuberculated, but here the tubercles are mostly oblong, with their main axes fairly parallel with the longitudinal axis of the bone. It is doubtful whether the tubercles on the last-mentioned bones as well as on the other dermal bones of the head apart from the maxillary and the external bone of the lower jaw, should be regarded as denticles which have secondarily become attached to the dermal bones, for as far as could be made out, these tubercles do not seem to overlie a system of striae, and at any rate as far as the preoperculum is concerned, there seems to be indications of subdivision of striae into tubercles. Thus there is a possibility that the tubercles on the dermal bones of the head of *Birgeria* belong to two different types, viz. true denticles on the maxillary and the external dermal bones of the mandible, and subdivided striae on the remaining dermal bones of the head.

Dentition.

The arrangement of the teeth has been described in its main features in the preceding chapters, so a brief summary will suffice here.

On the maxillary, the rostro-premaxillary, the supraangular, and the dentalo-splenial we find two rows of teeth, viz. a labial row containing a large number of fairly small teeth, and a lingual row containing a comparatively small number of very large teeth. On the ectopterygoid and the dermopalatine we find a single row of medium-sized teeth, between and in part medially to which there occur a considerable number of rather small teeth. The row of medium-sized teeth runs parallel with, and is only separated by a fairly small interspace from, the lateral margins of the bones to which it belongs, and thus it is parallel with the two rows of teeth on the maxillary. Medially to the series of medium-sized and fairly small teeth the greater part of the oral faces of the dermal bones of the palate is covered with fairly close-set very small teeth. The approximate number of the latter teeth mentioned above may be seen from figs. 69 and 70, which were drawn on the basis of some of the larger specimens. Probably the number of these teeth varies to some extent from specimen to specimen; however, the material is not sufficient to enable me to give any information of value about this variation.

Small teeth seem also to have been present both on the prearticular and on the ossifications of the branchial series; however, on the basis of the present material I am unable to give any information either of the number or of the arrangement of these teeth.

As described by Stensiö (1932, p. 114), the large teeth are provided with a two-edged enamel cap, which, except on the largest teeth of the premaxillary where a delicate vertical striation is observed, is quite smooth, while basally to the enamel cap the teeth are coated with a shining layer, which extends almost down to the base, and which is provided with a fine vertical striation. According to Aldinger, the structure of this layer in *Birgeria stensiöi* differs markedly from that of the enamel cap (Aldinger 1931, pp. 174–177).

The small teeth are probably built in principally the same way as the larger ones; however, owing to their small size even their external features are very difficult to investigate in detail.

Discussion. – As regards the arrangement of the teeth *Birgeria groenlandica* agrees, as far as is known, fairly well with *Birgeria mougeoti* (Stensiö 1921, pp. 186–187; 1932, p. 106). But, as pointed out by Stensiö (1932, p. 106), the striation of the enamel caps of the teeth is much more marked in the Spitsbergen than in the Greenland form. Our knowledge of the arrangement of the teeth in *Birgeria stensiöi* is very incomplete; it seems, however, as if the lingual row on the maxillary of this species contained a smaller number of teeth than in the other two species.

The teeth in *Birgeria* are arranged in much the same way as in a normal Palaeonisciform such as *Pteronisculus*, as will be evident on a comparison with figs. 34 and 38 in the first part of the present work (1942), and even in

the structure of the teeth *Birgeria*, as far as is known, shows fairly close agreement with the normal *Palaeonisciformes* (cf. E. Nielsen 1942, pp. 201–202). Probably, therefore, the teeth of *Birgeria* both in their structure and their arrangement present fairly primitive Palaeonisciform characters.

Sensory canal system of the head.

The sensory canals are deeply embedded in the thick dermal bones of the head, and since, moreover, the tubuli by which they open outwards are extremely fine, it is very difficult to follow the course of the canals in specimens in which only the external faces of the dermal bones are exposed. On the inside of the dermal bones, however, the sensory canals have left more distinct traces, since here the canal zone in the individual bones appear as a distinct ridge, in the same way as is the case in typical *Palaeonisciformes*. Owing to the presence of such canal ridges, the course of the canals can also be traced in specimens in which the dermal bones are only represented as casts of their internal faces. The only pit-line observed is developed as an open groove; if other pit-lines existed, they have probably left no marks on the dermal bones, which, however, as discussed below, bear evidence of the existence, in *Birgeria*, of another type of sensory organs not previously known in fossil Ganoids.

The description given below is chiefly based on the large specimens, on account of their better state of preservation. However, parts of the sensory canal system have also been studied in the small specimens, and as far as can be seen, the only difference between the large and the small specimens regarding this structure is that the sensory canals in the small specimens are relatively broader than in the large ones.

Supraorbital sensory canal. – The supraorbital sensory canal (*soc*, figs. 64, 69, 73; pl. 11, fig. 2; pl. 12, fig. 2; pl. 20, fig. 2) ends blindly both anteriorly and posteriorly and has no connection with other parts of the sensory canal system. The anterior end of the canal is situated in the rostro-premaxillary between the fenestra exonarina anterior and the ethmoidal commissure of the infraorbital sensory canals, and from here the supraorbital sensory canal passes in a straight line to the dorso-lateral (postero-dorso-lateral) corner of the bone, to enter the large nasal. In the nasal the canal shows a distinct S-bend, curving first upward and then, after piercing the centre of radiation, backward again, to continue through the posterior part of the bone parallel with and fairly close to its medial margin. From the nasal the canal passes into the frontal, which it traverses in a mainly longitudinal direction, showing only a slight S-shaped curve in the central part of the bone, i. e. just before and after piercing the radiation centre. From the frontal the canal continues backward through the greater part of the

parietal (if two parietals, the medial one) to end posteriorly at its centre of radiation. The posterior end of the sensory canal is pointed, but in no case has the hindmost part of the canal been transformed into a pit-line, as in many normal *Palaeonisciformes*.

Nothing can be stated regarding the number or the distribution of the probably extremely narrow tubuli of the supraorbital sensory canal.

Infraorbital sensory canal. – In the rostro-premaxillary the infraorbital sensory canal (*ifc*, figs. 64, 73; pl. 11, fig. 2) forms, with that of the other side of the head, a complete ethmoidal commissure (*eth. com*, figs. 69, 73; pl. 20, fig. 2) and extends from here backward through the antorbital, the lacrimal, the jugal, the postorbital, and the supraorbito-dermosphenotico-intertemporal, behind which it is continued by the postotic canal. On its way the infraorbital sensory canal, which, as usual, pierces the centres of radiation of the bones in which it is lodged, exhibits two fairly marked bends, one in the jugal and one in the supraorbito-dermosphenotico-intertemporal, the middle (postorbital) stretch of the canal being almost vertical, while both its posterior and its anterior part are mainly horizontal. On passing the centre of radiation of the antorbital, the canal gives off a branch, which passes upward to the dorsal tip of the strong process which separates the fenestra exonarina posterior from the orbital opening. As already mentioned in the first part of this work (1942), this dorsal branch corresponds to the posterior connection between the infraorbital and the supraorbital sensory canals in *Lepidosteus* and *Sinamia* (Hammarberg 1937, pp. 291–292; E. Nielsen 1942, p. 206). Several long and very fine tubuli issue from the ethmoidal commissure in a mainly anterior direction, to open through very small pores on the external face of the rostro-premaxillary. No tubuli issuing from the more posterior part of the infraorbital sensory canal have been observed.

Postotic sensory canal. – The infraorbital sensory canal is continued backward through the supratemporal by a longitudinal sensory canal, which corresponds, at any rate fairly closely, to Säve-Söderbergh's postotic canal (Säve-Söderbergh 1933, p. 7). No tubuli are known to issue from this canal.

Supratemporal commissure. – The postotic sensory canal is continued backward by the main lateral line, the foremost part of which is lodged in the posttemporal, not, as is usually the case, in the extrascapular (cf. fig. 64). From the junction between the postotic canal and the main lateral line issues a medial sensory canal branch, which pierces the large extrascapular to join its fellow on the opposite side of the head, thus forming a complete supratemporal commissure (*s. com*, figs. 64, 69). More precisely, this medial branch passes from the posterior end of the extrascapular in an anteromedial direction to the centre of radiation of the bone, to continue from here in an almost directly transverse direction towards the mid-line of the cranial

roof. In this part of the sensory canal system, also, no tubuli could be traced.

Preopercular sensory canal. – The preopercular sensory canal (*poc*, figs. 69, 71; pl. 14; pl. 15, fig. 3) traverses the preoperculum in the usual way, passing in a straight line from a point on the anterior margin of the bone to its centre of radiation and from here in a likewise straight line to the ventral end of the bone. Accordingly the canal, as shown in fig. 69, in the antero-dorsal shank of the bone runs fairly near the dorsal and in the postero-ventral shank fairly near the anterior or antero-ventral margin. A few fine tubuli have been observed issuing from the canal; however, several others have probably been overlooked.

The preopercular sensory canal has no connection with the lateral sensory canal of the dermal cranial roof, and its dorsal part is much more forward directed than in normal *Palaeonisciformes*. In this connection it is of interest to notice that the preopercular sensory canal in both *Saurichthys* (Stensiö 1925, figs. 20, 21; Holmgren and Stensiö 1936, p. 443) and *Acipenser* (Holmgren and Stensiö 1936, p. 443) in the dorsal shank of the preoperculum has a very marked forward direction and in *Polyodon* (Holmgren and Stensiö 1936, pp. 443, 445) even communicates with the postorbital division of the infraorbital sensory canal. From this unusual direction of the canal Pehrson (1944, pp. 34, 43) draws the conclusion that in *Acipenser* and *Polyodon* we are not dealing with a preopercular, but with a jugal sensory canal. However, the direction of the undoubtedly preopercular sensory canal in *Birgeria* in my opinion forms a satisfactory intermediate stage between a preopercular canal joining the postorbital part of the infraorbital sensory canal and one which, as in the normal *Palaeonisciformes*, joins the infraorbital sensory canal or its posterior continuation in the dermal cranial roof. The forward direction of the preopercular sensory canal in *Birgeria*, *Saurichthys*, and the recent sturgeons is more probably solely due to the extreme lengthening of the postorbital part of the cheek region.

Mandibular sensory canal. – The mandibular sensory canal (*mdc*, fig. 74) passes in the normal way through the angular and the dentalosplenial, piercing the centres of radiation of both these bones and on its way changing its direction from nearly vertical in the posterior part of the angular to nearly horizontal in the anterior part of the angular and in the dentalosplenial. In a few small specimens a number of tubuli are seen to issue from the dentalo-splenial division of the canal; however, the exact number of tubuli in that bone could not be ascertained, and no tubuli have been observed in the angular.

Pit-lines. – The only pit-line observed extends from a point on the dorsal face of the only, or the medial, parietal above the centre of radiation in a lateral and slightly anterior direction to the lateral margin of this parietal element, and is developed as a fairly distinct, though shallow groove (*mp*, figs. 64, 69), which is undoubtedly homologous with the parietal pit-line

observed by Stensiö in *Birgeria mougeoti* (Stensiö 1932, p. 99, figs. 37, 38). According to its direction towards the centre of radiation of the supratemporal, this pit-line should more probably be identified as a middle than as a posterior pit-line. If other pit-lines were present in *Birgeria groenlandica* they have probably left no traces on the dermal bones.

Nerve-sack areas. – As previously described, the dermal cranial roof of *Birgeria groenlandica* presents a number of well defined unornamented areas (pp. 251–252, fig. 64), and judging from Stensiö's figures (Stensiö 1932, figs. 37, 38) at least two such areas are also developed in *Birgeria mougeoti*, viz. one corresponding to the central area of the frontals in *Birgeria groenlandica* and another corresponding to the still larger hindmost area situated just anteriorly to the extrascapular series in *Birgeria groenlandica*. The regular occurrence of such areas in *Birgeria groenlandica* and their existence in *Birgeria mougeoti* also have convinced me that these areas have arisen in relation to certain superficial structures in *Birgeria* and should not only be regarded as the result of more casual variations in the distribution of the sculptural elements. As already discussed above, Aldinger's interpretation of the medial part of the posterior unornamented area as a part of the cranial roof which is overlain by minor dermal bones can hardly be maintained (cf. pp. 215, 252), and a corresponding interpretation can, at any rate, not be applied at all to the more lateral parts of this area or to any of the remaining unornamented areas.

It seems to me more probable that the absence of ornament in certain areas of the dermal cranial roof in *Birgeria* is due to the development in that genus of similar nerve-sack groups to those known in recent sturgeons. Thus, if this view holds good, we have, in the size and distribution of the unornamented areas, a direct means for determining the size and distribution of the nerve-sack groups.

Luther has given a detailed account of the distribution of the nerve-sacks in *Acipenser*, *Scaphirhynchus*, and *Polyodon* (Luther 1913, pp. 14–17). In *Polyodon*, where the nerve-sack groups have a very considerable extent, he distinguished, on each half of the cranial roof, between a rostral, a supranasal, a supraorbital, and a parietal group, and moreover a group situated posterior to the supratemporal commissure. Each of the groups, with the exception of the hindmost one, is situated above, and agrees in general shape with, one of the fenestrations in the dermal cranial roof, and it seems probable, therefore, that the fenestrations were caused by the nerve-sacks.

In *Acipenser* and *Scaphirhynchus* the nerve-sacks are distributed in much the same way as in *Polyodon*, although the individual groups have a much smaller extent. Below each group the external face of the dermal cranial roof shows a concavity the bottom of which is pierced by a small fenestra or foramen.

In *Birgeria groenlandica* the two small supraorbital areas agree fairly

well in position with the supraorbital group in the sturgeons, while the hindmost large area may best be compared with the posterior part of the parietal group in the sturgeons. Of the two areas on the middle part of the frontal of *Birgeria* the postero-lateral one perhaps corresponds to the anterior part of the parietal group in the sturgeons (in *Acipenser* and *Scaphirynchus* this anterior part is widely separated from the posterior part of the same group), while the antero-medial one has no homologues in the recent sturgeons.

In no case have foramina been observed on the unornamented areas in *Birgeria*, but if the unsatisfactory state of preservation of the material is taken into consideration, it is quite probable that fine canals through the dermal cranial roof may have been overlooked, in which connection I wish to point out that only in a very few places has it been possible to trace the fine tubuli which issue from the various branches of the sensory canal system of the head. However, as already discussed (p. 224), the parietal(s) in *Birgeria* occupies almost the same position as the large fenestration below the parietal nerve-sack group in *Polyodon*, and thus there is reason to believe (if we consider *Birgeria* as at any rate closely related to the ancestors of *Polyodon*) that the complete reduction of the parietals in *Polyodon* is caused by the parietal nerve-sack group.

Nerve-sack areas have not previously been recognised in any fossil Ganoid.

Axial skeleton.

The ossifications of the axial skeleton are well preserved in many of the small specimens, and they are especially beautifully exposed in the very complete specimen no. 661 (pl. 10). In the larger specimens remnants of the axial skeleton have only been found in a few cases, thus the most anterior part of the axial skeleton is exposed in specimen no. 650, the anterior part of the axial skeleton of the caudal region in specimen no. 655, and parts of the axial skeleton of the body axis of the caudal fin in a still unnumbered specimen brought home from East Greenland by Professor A. Rosenkrantz in 1945.

The axial elements were much more strongly ossified in the large than in the small specimens, but since the axial skeleton can be studied throughout its whole length in the small specimens and only in certain regions of the body in the large ones, I have chosen first to describe the axial structures of the small specimens, which I have also used as a basis for the reconstruction given in fig. 77.

In the small specimens the notochord was persistent throughout the whole abdominal and caudal regions and was by no means constricted by the arcual elements. In the abdominal region, which contained about 32 metameres, the axial skeleton is represented by paired dorsal and ventral arcual ossifications as well as by unpaired supraneurals. The series of arcual elements

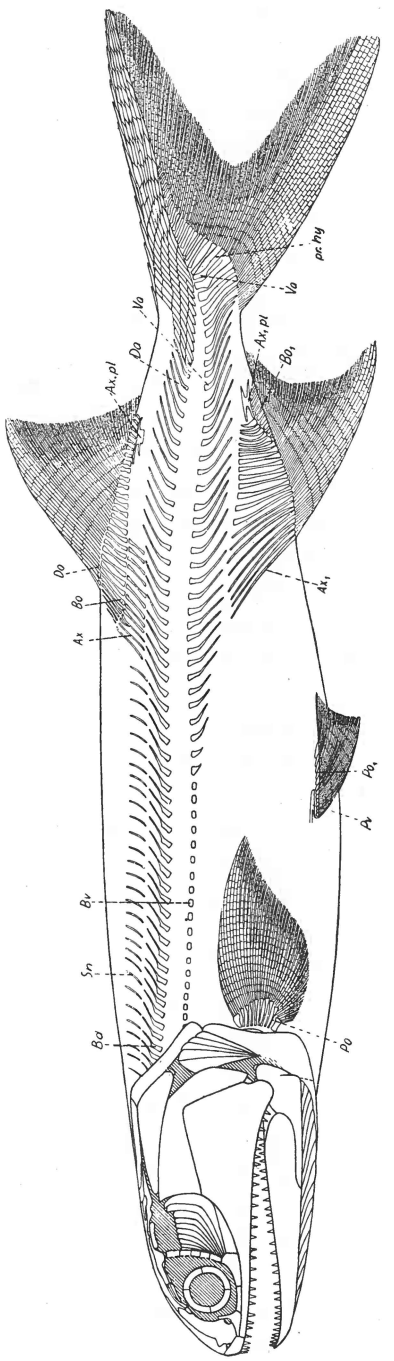


Fig. 77. *Birgeria groenlandica* Stensiö. Attempted restoration. Head region based mainly on large and trunk region mainly on small specimens. Small teeth of the jaws and small lateral-line scales of the trunk omitted.

Ax, axonost in endoskeleton of dorsal fin; *Ax. pl*, axonost plate in endoskeleton of dorsal fin; Ax_1. *pl*, axonost plate in endoskeleton of anal fin; *Bd*, basidorsal; *Bo*, baseost in endoskeleton of dorsal fin; Bo_1, baseost in endoskeleton of anal fin; *Bv*, basiventral; *Da*, dorsal arcual ossification in caudal region; *Do*, distal radial ossification in endoskeleton of dorsal fin; *Po*, radial ossification in endoskeleton of pectoral fin; Po_1, radial ossification in endoskeleton of pelvic fin; *Pv*, pelvic plate; *Sn*, supraneural; *Va*, ventral arcual ossification in caudal region; *pr. hy*, hypural process.

continue from the abdominal region backward through the caudal region, in the middle and posterior parts of which the right and left dorsal arcual ossifications of each metamere have fused with each other and perhaps also with a supraneural, while, as far as can be seen, the ventral arcual ossifications are unpaired throughout the whole region. If any infrahaemals are developed, they must form part of the ventral arcuals.

All the ossifications of the axial skeleton are lined with perichondral bone except on their proximal terminal faces and contain an anterior calcite-filled cavity, in which faint remnants of endochondral bone-laminae can be seen, at any rate in some cases.

In the abdominal region each of the paired dorsal arcual ossifications (*Bd*, fig. 77; pls. 10, 14, 19; pl. 20, figs. 1, 2) consists of a broad proximal four-sided plate and a slender distal spine. The shape of the proximal plate changes gradually throughout the region, as shown in fig. 77. The height of the plate is about or slightly less than twice its breadth. The distal spine is somewhat longer than the proximal plate to which it belongs, and, as shown in fig. 77, it is more backwardly inclined than the plate itself. Distally to the distal spines of each pair of basidorsals lies an unpaired supraneural ossification (*Sn*, fig. 77; pls. 10, 14, 19; pl. 20, figs. 1, 2), developed as a slender spine, which is slightly curved in such a way that its anterior face is concave and its posterior face correspondingly convex. The supraneurals, the length of which is about the same as that of the arcual spines to which they are related, are only slightly backwardly inclined.

The ventral arcual ossifications in the abdominal region (*Bv*, fig. 77; pls. 10, 14; pl. 20, fig. 1) lie opposite to the dorsal ones, and consist, except in the hindmost part of the region, of fairly massive vertically placed plates, which are roughly rectangular in lateral view. On the central part of the lateral face of each of these ossifications we observe a low, blunt, laterally directed process comparable to the similarly situated process or ridge for instance in *Pteronisculus* (E. Nielsen 1942, pp. 213–214; figs. 48, 49), Ospia (Stensiö 1932, p. 262; fig. 85), and *Australosomus* (present paper p. 137; figs. 41, 43, 46) and accordingly serving as the place of attachment for the ventral (pleural) rib. The ventral arcual ossifications increase in height backward through the hindmost part of the abdominal region, and each ossification is provided with a distal spine, the length of which likewise increases in a posterior direction through the series.

The exact number of metameres in the caudal region cannot be ascertained, the distal half of the body axis of the caudal fin being completely covered by scales, so the axial skeleton cannot be studied in this region. However, from the anterior end of the caudal region to about the middle of the body axis of the caudal fin the number of metameres can be stated to be about 48.

The foremost dorsal arcuals in the caudal region have about the same

shape and size as the hindmost ones in the abdominal region; more posteriorly, however, the distal spines of the arcual ossifications grow gradually longer and at the same time become more backwardly inclined, while their proximal plate diminishes in breadth. From below the middle part of the dorsal fin and backwards the distal spines of the right and the left arcual ossification of each metamere are fused, so that here each dorsal axial ossification consists of a right and a left proximal plate and a single distal spine (*Da*, fig. 77; pl. 10; pl. 13, fig. 2). The ventral arcual ossifications (*Va*, fig. 77; pl. 10; pl. 13, fig. 2) are unpaired throughout the whole caudal region. Anteriorly to the caudal pedicle each of these ossifications consists of a paired proximal plate, the breadth of which decreases in a distal direction, and a long unpaired distal spine, which is directed downward and backward, and the length and backward inclination of which increase slightly in a posterior direction. In the caudal pedicle and the body axis of the caudal fin the ventral arcual ossifications at first increase and then decrease in size, as shown in fig. 77. In the foremost part of the body axis of the caudal fin the distal spine of these elements is developed as a fairly strong hypural process (*pr. hy*, fig. 77; pl. 10; pl. 13, fig. 2), the breadth of which is greater at their distal ends. Probably these hypural processes include hypochordal components of the radial skeleton of the fin (cf. Schmalhausen 1912, pp. 525–528; 1913 a, p. 65; 1913 b, pp. 753–756). The axial elements supporting the fin decrease rapidly in length in a posterior direction through the middle part of the body axis of the caudal fin, as shown in fig. 77. As already mentioned, the axial elements of the hindmost part of the body axis of the caudal fin could not be studied on account of the scale-covering. Probably, however, they were numerous and of a very small size.

We shall now consider the ossifications of the axial skeleton in the large specimens.

Specimen no. 650 shows remnants of the foremost part of the axial skeleton of the abdominal region. Although the specimen is rather badly compressed, it is still possible to identify paired dorsal and ventral arcual ossifications. The dorsal elements differ from those in the small specimens by their relatively greater massiveness and by the distal part of their distal processes being strongly flattened from side to side. The details of the shape of the ventral elements could not be made out. No supraneurals have been observed in this specimen.

In specimen no. 655 (pl. 18, fig. 2) remnants of the axial ossifications of the foremost part of the caudal region are exposed. The specimen shows a dorsal and a ventral series of axial ossifications, which are somewhat crushed in their most proximal part, and the most distal part of which is lacking.

The dorsal series consists of alternating very long, strongly ossified, and very small, slightly ossified elements, while the ventral series is made up exclusively of long and strongly ossified elements. A comparison shows that

the long and massive dorsal and ventral elements correspond to the axial ossifications in the corresponding region of the small specimens, in which I have been unable to detect any remnants of the small dorsal elements present in the large specimen considered here.

In each of the long dorsal ossifications we may, as in the small specimens, distinguish a short, fairly broad, and somewhat backwardly inclined proximal and a long, comparatively slender and much backwardly inclined distal part; however, the difference in breadth between the two parts is relatively less than in the smaller specimens. At the transition between the proximal and the distal part the anterior margin in some of the dorsal elements shows a small, but fairly well marked emargination, which probably indicates the place of exit of a spinal nerve root. The smaller dorsal ossifications, which are situated in the interspaces between the proximal parts of the larger ones, are always badly crushed owing to their less extensive ossification, and the only thing that can be stated regarding their shape is that they are somewhat narrower than the proximal plates of the long ossifications and only slightly higher than broad.

In the ventral elements we may likewise distinguish a short proximal, fairly wide, and somewhat backwardly inclined part and a longer distal, more slender, and more oblique part. The proximal part is probably paired; however its state of preservation is too bad to permit a detailed description.

In the specimen collected by A. Rosenkrantz the hypochordal axial ossification of the caudal axis and the anterior part of the body axis of the caudal fin are seen, though in a highly weathered state. Apart from being more massive, these ossifications agree well in shape with the corresponding ones in the small specimens.

We shall now attempt to interpret the different axial ossifications described in the preceding pages. As to some of the axial structures such an attempt has already been made by Stensiö (1932, p. 290), who had at his disposal a single small incomplete specimen of *Birgeria groenlandica*. Stensiö's interpretations are based mainly on comparisons with *Birgeria mougeoti*, part of the axial skeleton of which was described by him in 1921 (pp. 187–190). According to this description the known part of the axial skeleton of *Birgeria mougeoti*, viz. the axial skeleton of the anterior and middle parts of the caudal region, contains in each body segment two paired dorsal and two paired or unpaired ventral ossifications. Stensiö interprets the dorsal ossifications according to their relations to the roots of the spinal nerves as interdorsals and basidorsals, respectively, and the ventral ones, mainly according to their position in relation to the inter- and basidorsals, as interventrals (probably with a proximal basiventral component) and basiventrals (or rather distal parts of basiventrals), respectively.

In his small specimen of *Birgeria groenlandica* Stensiö (1932, p. 290), in addition to the dorsal and ventral axial ossifications also observed by me,

found remnants of small ossifications (which I have been unable to rediscover in Stensiö's own specimens or to detect in any other specimens), which he considered as homologous to the interventrals (+basiventrals) in *Birgeria mougeoti*, while he homologised the larger, better ossified dorsal and ventral axial elements with the long dorsal and the long ventral axial elements, respectively, in *Birgeria mougeoti*.

Aldinger has later expressed the opinion (Aldinger 1938, p. 159) that the ventral ossifications interpreted by Stensiö as interventrals (+basiventrals) are only interventrals, while the hypochordal elements interpreted by Stensiö as distal parts of basiventrals (or haemal spines) are infrahaemals.

As far as I can see, no objection can be raised against Stensiö's interpretation of the dorsal arcuals in the small specimens as basidorsals and in the larger specimens as alternating basi- and interdorsals. As to the ventral axial elements, I am not convinced that either Stensiö's or Aldinger's interpretations are correct. In my opinion each of the large ventral axial ossifications in *Birgeria groenlandica* should be compared to two ossifications in the specimen of *Birgeria mougeoti* investigated by Stensiö, the broad proximal part representing Stensiö's interventral (+basiventral) and the more slender distal part his haemal spine. For in specimen no. 655 the ventral arcual ossifications lie ventrally to the basidorsals, not to the interdorsals, and in the small specimens of *Birgeria groenlandica* the ventral axial ossifications are always situated below the dorsal ones. Accordingly the ventral axial ossifications in *Birgeria groenlandica* must be regarded as basiventrals, possibly with infrahaemal components in their distal parts. According to Stensiö's description the proximal hypochordal ossifications in *Birgeria mougeoti* lie opposite to the interdorsals (Stensiö 1921, p. 190; fig. 67); however, from his photograph of the specimen (pl. 21, fig. 4) it appears to me that these ossifications might just as well be regarded as opposite to the basidorsals. I am therefore inclined to belive that these structures should be homologised with the proximal parts of the basiventrals in *Birgeria groenlandica*, while the distal hypochordal ossifications should be compared to the distal parts of the basiventrals.

If this is so, the main difference between the ventral arcual ossifications of *Birgeria groenlandica* and *Birgeria mougeoti* is that the basiventral of the latter form contains two rather small and, in the former, one large ossification. It is true that the proximal ventral ossifications in *Birgeria mougeoti* are broader than the proximal parts of the basiventral ossifications in *Birgeria groenlandica* and hence it is not impossible that these ossifications in *Birgeria mougeoti* include a small interventral component.

Another difference between the ventral arcual ossifications in the two species in question is that while in *Birgeria groenlandica* these elements are situated completely or almost completely ventrally to the notochord, the dorsal part of each proximal ossification in *Birgeria mougeoti*, according to

Stensiö (1921, pp. 189–190), extends upward along the notochord. This difference may, of course, be explained by assuming that the ventral arcual elements are more extensively ossified in *Birgeria mougeoti* than in *Birgeria groenlandica*; however, it seems to me more probable that the comparatively small distance between the dorsal and the ventral arcual series in *Birgeria mougeoti* is due to post-mortem disturbances of the specimen investigated by Stensiö, so that the presumed incipient formation of vertebral centres discussed by Stensiö has no foundation in fact.

Discussion. – If the above interpretations of the axial elements of *Birgeria* are correct, the axial skeleton of this genus does not differ in principle from those of the normal *Palaeonisciformes* in which this structure has been investigated in satisfactory detail, viz. in *Pygopterus* (Stensiö 1921, pp. 206–207; Aldinger 1937, pp. 254–261; E. Nielsen 1942, p. 221), *Pteronisculus* (E. Nielsen 1942, pp. 211–220), and *Gyrolepis* (Aldinger 1937, pp. 240–242).

Accordingly the axial skeleton of *Birgeria* also shows general agreement with the much less ossified axial skeleton in recent sturgeons (cf. E. Nielsen 1942, p. 222), but a closer comparison must be postponed until better preserved and more complete specimens of *Birgeria* have been secured.

Endoskeleton of the shoulder-girdle.

Both in fairly small and fairly large specimens ossifications belonging to the endoskeleton of the shoulder-girdle are found, but in no case is the endoskeleton, as is the case e. g. in *Pteronisculus* (E. Nielsen 1942, pp. 223–227) thoroughly ossified, and from its ossified parts alone it is not possible to reconstruct the whole structure.

In many of the small specimens only a single ossification is present, situated just anterior to the basal part of the radial skeleton of the pectoral fin. In a few small and in those of the large specimens in which the shoulder-girdle region can be studied we find, in addition to this ossification, another one which occupies a more ventral position.

Both ossifications consist of cancellate endochondral bone more or less completely lined with a thin perichondral layer.

The dorsal ossification (*Eg*, fig. 78; pls. 10, 19) is a fairly thin vertically or almost vertically placed plate, one face of which is directed laterally and the other medially. The plate, whose outline is shown in detail in fig. 78, is pierced in its central part by a single fairly large rounded foramen (*f. dz*, fig. 78) for diazonal nerves.

Both the lateral and the medial face of the plate is lined with perichondral bone, but as far as could be made out, this is not the case with its edges, which accordingly were probably all joined to cartilage. Judging from the

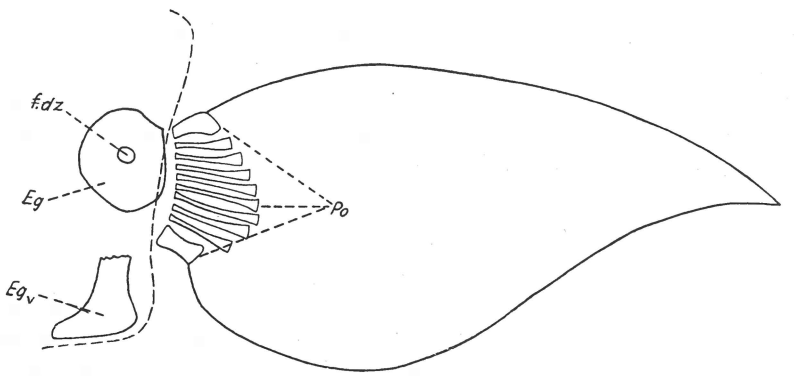


Fig. 78. *Birgeria groenlandica* Stensiö. Endoskeleton of pectoral fin with attempted sketch of the ossified parts of the endoskeletal shoulder-girdle. Based mainly on small specimens.

Eg, Eg_V, dorsal and ventral endoskeletal shoulder-girdle ossifications; *Po*, radial ossifications.

relations between the plate and the pectoral radials, the cartilage-clad posterior edge must be regarded as the margo radialis, and as the posterior edge of the ossification shows no articular grooves, we must assume that its cartilaginous lining had quite a considerable thickness.

The ventral ossification (Eg_v, fig. 78) is a plate of about the same thickness as the dorsal one, but, as shown in fig. 78, it is of a very different shape. The most dorsal part of the plate is fairly vertical, its middle part curves somewhat inward, and its most ventral part curves downward again towards the ventro-medial part of the internal face of the cleithrum. The plate is completely lined with perichondral bone except on its dorsal edge, which, as might be expected at the outset, must thus have been joined to cartilage in the living animal.

Discussion. – On the basis of the two ossifications just described it is, of course, impossible to make a close comparison between *Birgeria* and the normal *Palaeonisciformes* regarding the endoskeleton of the shoulder-girdle. However, there can be no doubt that the dorsal ossification corresponds to a middle, and the ventral one to a ventral part of the large endoskeletal shoulder-girdle plate in forms such as *Pteronisculus* (E. Nielsen 1942, pp. 223–227) and *Boreosomus* (ibid., pp. 357–360), and the shape and position of the two ossifications do not exclude the possibility that an endoskeletal shoulder-girdle structure in *Birgeria* has developed from that of a typical Palaeonisciform.

In *Acipenser* the endoskeleton of the shoulder-girdle is an extremely massive structure, while in *Polyodon* it shows a more normal development (Gegenbauer 1865, pl. 6; figs. 2 A–C, 3 A–C). In both these genera the margo radialis is horizontal or nearly so, and thus in this respect *Acipenser*

and *Polyodon* are probably less specialised than *Birgeria*. Moreover the ventral part of the endoskeletal structure in *Polyodon* narrows towards its ventral end, while the corresponding part of the endoskeletal structure in *Birgeria* increases very much in breadth in a ventral direction, as shown in fig. 78.

Dermal bones of the shoulder-girdle.

The series of dermal bones of the shoulder-girdle consists of a posttemporal, a supracleithrum, a cleithrum, and a clavicle. An anocleithrum has not been found and must therefore, if at all present, probably be very small.

The exposed faces of the dermal bones of the shoulder-girdle are ornamented with fairly small tubercles, which are probably of the same nature as those on the dermal cranial roof.

Posttemporal. – The posttemporal (*Pt*, figs. 64, 69; pls. 10, 14; pl. 15, fig. 1) is a large, roughly five-sided bone with an antero-lateral, a medial, a postero-medial, a postero-lateral, and a lateral margin. The bone is very broad in its anterior part, but narrows strongly in a posterior direction in the way shown in fig. 64. It is slightly bent from side to side, the external face being convex and the internal one correspondingly concave. The antero-lateral margin is convex and the postero-medial margin concave. The other three margins are fairly straight. The antero-lateral marginal zone of the bone is overlapped by the extrascapular, and just laterally or postero-laterally to the overlapped area the posttemporal adjoins the posterior end of the supratemporal. Postero-laterally the bone adjoins the supracleithrum, probably without overlapping it. Medially the anterior broad part of the bone almost reaches the mid-line, and thus it is here only separated by a very narrow interspace from its fellow on the opposite side of the head.

The posttemporal is pierced by the main lateral line, which enters the bone at the angle between its antero-lateral and its lateral margin, whence it continues, as shown in the figures, in a mainly posterior direction through the bone, which it leaves just posteriorly to the angle between the lateral and the postero-lateral margin, probably after piercing the centre of radiation, which, however, could not be localised with certainty.

Supracleithrum. – The supracleithrum (*Scl*, fig. 69; pl. 10 (*Pcl*); pls. 14, 19; pl. 20, fig. 2) is a very long, narrow bone bounded by an antero-dorsal, a postero-dorsal, a postero-ventral, and an antero-ventral margin. The bone attains its greatest breadth not far from its dorsal (antero-dorsal) end, whence it narrows towards its midmost part, to widen slightly again more ventrally. The antero-dorsal and the antero-ventral margins are fairly straight, the postero-dorsal margin is somewhat S-shaped, while the postero-ventral margin is convex. A considerable part of the antero-ventral margin is overlapped by the operculum and the suboperculum, while the postero-ventral margin overlaps the dorsal end of the cleithrum.

The centre of radiation is situated in the dorsal and broadest part of the bone and is pierced by the main lateral line, which traverses the bone in a mainly longitudinal direction, as shown in fig. 69.

Cleithrum. – The cleithrum (*Cl*, fig. 69; pls. 10, 14, 19; pl. 20, fig. 1) consists of an anterior smooth and a posterior ornamented division, which pass gradually into one another. The anterior division forms the posterior boundary of the branchial cavity, while the posterior division lies on a level with the lateral surface of the trunk, and accordingly it is curved in a dorso-ventral direction, with the convexity facing outward. The anterior smooth division may be described as a fairly thin bone lamina extending in a mainly antero-medial direction from the entire antero-dorsal margin of the posterior ornamental division. The lamina attains its greatest breadth in its middle part, whence it narrows gradually towards both ends. The posterior division is roughly triangular in outline, with an antero-dorsal, slightly concave, a posterior S-shaped, and a ventral almost straight margin. The antero-dorsal margin is the longest and the ventral one the shortest.

The centre of radiation of the cleithrum is situated at the boundary between the anterior and the posterior division of the bone and much nearer the ventral than the dorsal end of this boundary.

As is evident from fig. 69, the cleithra do not meet ventrally, but are separated by a rather considerable interspace.

Clavicle. – The clavicle (*Cla*, figs. 69, 75) can only be seen in a few specimens, as a long and narrow, fairly horizontal plate situated medially to the posterior part of the branchiostegal series and anteriorly to the ventral part of the cleithrum, overlapping, to some extent, the most ventral part of the posterior (external) division of the latter bone. It is probable that this horizontal plate, which, as far as can be seen, is roughly triangular in outline, forms only a part of the complete clavicle, which otherwise consisted of an internal lamina issuing from the lateral margin of the horizontal plate and forming an anterior continuation of the internal lamina of the cleithrum. Such a lamina, which is developed both in normal *Palaeonisciformes* (Stensiö 1921, pp. 229–230, fig. 74; E. Nielsen 1942, p. 232) and in the sturgeons (Stensiö 1921, pp. 229, 230, fig. 75), seems at any rate to exist in *Birgeria mougeoti* (cf. Stensiö 1932, fig. 39). The centre of radiation could not be localised.

Discussion. – Our knowledge of the dermal shoulder-girdle in the other species of *Birgeria* is extremely sparse. In *Birgeria mougeoti* Stensiö (1932, p. 105, figs. 37–39) has identified the posttemporal, the clavicle, and the cleithrum, the latter element, however, with doubt. Only rather small fragments of the posttemporal and the cleithrum are preserved in Stensiö's specimen; the clavicle, however, is somewhat more complete, and as far as can be seen, it is much broader than in *Birgeria groenlandica*. In *Birgeria stensiöi* Aldinger (1931, p. 169, pl. 18) interpreted a large fragmentary

dermal bone as the caudal part of the posttemporal, though with some doubt. This identification is probably wrong; I am more inclined to believe that the fragment is the caudal part of the parasphenoid, a possibility which was also considered by Aldinger, but which he rejected on account of the position of the centre of radiation.

The dermal shoulder-girdle of *Birgeria* differs from that of normal *Palaeonisciformes* especially in the relatively greater length of its two dorsal bones and in the absence of an anocleithrum. The first-mentioned difference is due to the extreme lengthening of the gape in *Birgeria*, while the absence of an anocleithrum, if not merely due to the poor state of preservation of the material at hand, must be explained by its complete reduction, which possibly took place simultaneously with the disappearance of the scales on the body.

In *Polyodon*, according to Pehrson (1944, p. 46), we find, as the most dorsal element in the dermal shoulder-girdle, a very long posttemporal (Allis (1935) and Holmgren and Stensiö (1936, pp. 445–446) have interpreted this bone differently), and posterior to this bone a likewise long and narrow supracleithrum. Of other bones, the shoulder-girdle contains a cleithrum, which is relatively smaller than in *Birgeria*, a clavicle, the internal lamina of which is very strong, and an anocleithrum (Gegenbaur 1865, p. 100; pl. 6, fig. 3 A, B; Traquair 1877, pl. 7, fig. 1).

The pectoral fin.

The endoskeleton of the pectoral fin is beautifully preserved in several small and some large specimens and is represented by a single vertical series of about ten mainly rod-like ossifications (*Po*, figs. 77, 78; pls. 10,19; pl. 20, fig. 1), each of which consists of endochondral bone lined with perichondral bone-layers except on its proximal and distal terminal faces, which were evidently capped by cartilage in the living fish. The radial ossifications increase gradually in length from the uppermost (morphologically foremost) to the seventh one, to decrease from here to the lowermost (morphologically hindmost) one, the length of which, as shown in fig. 78, is about equal to that of the foremost one. The uppermost and the lowermost radial ossification are compressed from side to side and are thus plate-shaped rather than rod-shaped. The intermediate radial ossifications are developed as slender rods, which are slightly expanded proximally and more strongly so distally. Judging from the position of the radial ossifications in relation to the endoskeletal shoulder-girdle (cf. fig. 78) the series must be regarded as a proximal radial series. No remnants of a distal series have been found, and probably, therefore, the distal radial elements were entirely unossified.

The fin contains about forty closely set and thoroughly segmented lepidotrichia in fan-shaped arrangement. The lepidotrichia increase rapidly

in length from the uppermost (foremost) to about the ninth, tenth, or eleventh lepidotrich, one of which is the longest in the fin, and from here they decrease in length towards the lowermost (hindmost) one. The lepidotrichia, which reach the upper (anterior) border of the fin, are undivided, while the more ventral (posterior) ones dichotomise distally, as shown in fig. 77. No fulcra are present on the fin.

Discussion. – The pectoral fin in *Birgeria*, judging from the Greenlandic species alone, its structure in the other species of *Birgeria* being unknown, was vertically held, and thus in this respect it agrees with the pectoral fin in forms as for instance *Tarassius* (Moy Thomas 1934, fig. 4) and *Boreosomus* (E. Nielsen 1942, pp. 362–365, fig. 78).

In a recent paper Westoll (1944), as already discussed in the present paper (p. 156), puts forward some interesting points of view regarding the mechanical significance of the position of the paired fins, and he maintains that the change from a horizontally to a vertically held pectoral fin goes hand in hand with a change of the caudal fin from heterocercal to more symmetric. However, as pointed out above, *Australosomus* with its horizontally held pectoral fin and its symmetrical caudal fin does not fit in very well with Westoll's hypothesis and no less so does *Birgeria*, which presents the following combination: a vertically held pectoral fin and a caudal fin with an unreduced body axis.

The pectoral fin in recent sturgeons is held horizontally and thus in this respect it is apparently less advanced than in *Birgeria*. This is rather amasing, if *Birgeria*, as there seem to be fairly good reasons to believe, is an early member of the sturgeon group. This matter can only be explained either by assuming that *Birgeria* represents a side-branch on the sturgeon line and accordingly is not directly ancestral to the recent forms, or by assuming that the horizontal pectoral fin in the later sturgeons evolved from a vertical fin. The latter assumption does not seem very probably, as we must take it for granted that the ancestral Actinopterygian pectoral fin was horizontal, and consequently a development from a horizontal to a vertical and subsequently from a vertical to a horizontal fin would have taken place within the sturgeon line. Hence, without taking up a definite standpoint in the matter, I am inclined to prefer the former assumption, viz. that *Birgeria* is not directly ancestral to any of the recent sturgeons.

Pelvic plate and pelvic fin.

The pelvic fin and its endoskeleton could only be studied in the small specimens, the pelvic region being not preserved in any of the large specimens at my disposal.

The endoskeleton of each pelvic fin consists of a pelvic plate and a series of proximal radial ossifications. The pelvic plate (*Pv*, fig. 79; pl. 10; pl. 20,

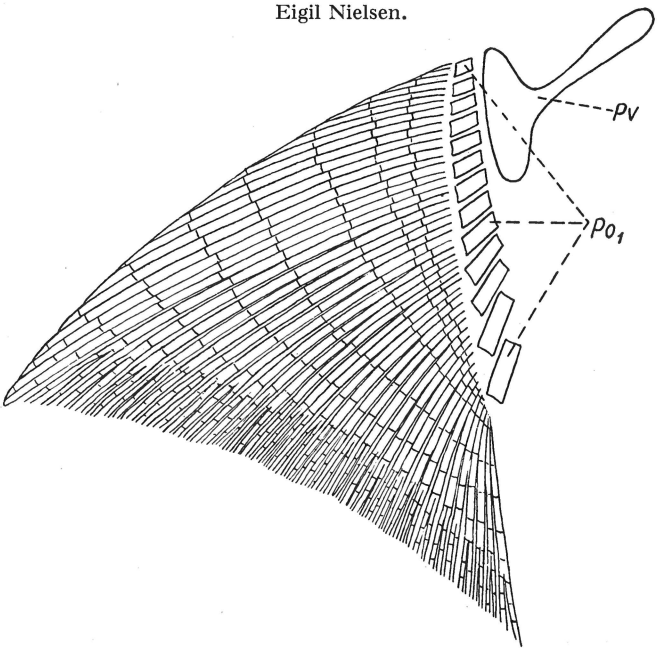


Fig. 79. *Birgeria groenlandica* Stensiö. Pelvic plate and endoskeleton of pelvic fin. Based on several small specimens.
Po_1, radial ossifications; *Pv*, pelvic plate.

fig. 1) is an oblong, rather thin plate, from the medial or antero-medial margin of which issues a long and slender process in an antero-medial direction. The outline of the plate with its process is shown in fig. 79. The distal end of the process is only separated by a small interspace from, and was probably connected by ligament with, that of the opposite side. The proximal radial series contains about thirteen ossifications (Po_1, figs. 77, 79; pl. 10), the foremost seven or eight of which articulated with the pelvic plate, while the more posterior ones probably, as in *Birgeria mougeoti* (Stensiö 1921, p. 193, fig. 68), articulated with unossified metapterygoid elements. The ossifications are developed as slender rods consisting of cancellar bone lined with a thin perichondral bone layer except on their proximal and distal terminal faces, which, as usual, were capped by cartilage in the living animal. The length of the radial ossifications increases gradually from the foremost to the hindmost one, and at the same time their direction gradually changes from nearly transverse to more and more oblique, as shown in fig. 79.

In *Birgeria mougeoti* (Stensiö 1921, p. 193) as well as in *Saurichthys* (Stensiö 1925, pp. 122–123) and *Boreosomus* (E. Nielsen 1942, p. 367) the endoskeleton of the pelvic fin shows, in addition to the proximal series, a distal series of ossifications. Very likely such a distal series will prove to exist also in the large specimens of *Birgeria groenlandica*; in the small specimens investigated by me, however, no distal radial ossifications were developed.

The pelvic fin is fairly large and contains about 50 close-set unornamented lepidotrichia, all of which are segmented throughout their whole length. The foremost lepidotrich is very short, the following ones increase rapidly in length to and including the 16–18th, whence they decrease in length again throughout the remaining part of the fin. All the lepidotrichia which reach the posterior margin of the fin dichotomise distally once or twice, as shown in fig. 79. Nu fulcra are developed.

Discussion. – As already pointed out by Stensiö (1932, pp. 290–291), the pelvic plate and the pelvic fin of *Birgeria groenlandica* agree very well with those of *Birgeria mougeoti*, which were described in fairly great detail by Stensiö in 1921 (pp. 192–194, fig. 68). The elements of the proximal radial series, however, are shorter and more massive in *Birgeria groenlandica* than in *Birgeria mougeoti*, and, as mentioned above, no distal radial ossifications have been found in the Greenlandic species.

As regards the structures treated here *Birgeria* does not differ in any fundamental respect from other primitive *Chondrostei* as for instance *Pteronisculus* (E. Nielsen 1942, pp. 238–243, fig. 55), *Boreosomus* (ibid., pp. 266–268, fig. 76), *Pygopterus nielseni* (Aldinger 1937, pp. 166–174, fig. 45), and *Saurichthys ornatus* (Stensiö 1925, pp. 22–131, fig. 28). It also agrees very well with the recent sturgeons (Rautenfeld 1882, pl. 1, figs. 1–8), thus especially with *Polyodon*, which has a larger number of pelvic radials than *Acipenser*, and the pelvic fin of which is almost identical in shape with that of *Birgeria*.

Unpaired fins.

The unpaired fins can be studied in detail in many of the small specimens, but are not preserved in the large ones, apart from that collected by A. Rosenkrantz in 1945, which shows the basal parts of the caudal fin, though in a rather bad state of preservation.

Although Stensiö has given some information about the unpaired fins in the young *Birgeria groenlandica* (Stensiö 1932, pp. 291–292), his description is by no means exhaustive, and a great many new details can be added on the basis of the large fresh material.

The dorsal and the anal fin are high, and both are situated far posteriorly on the body. According to Stensiö the dorsal fin commences a little behind the anal fin, but does not extend as far backward as that fin. However, in all the specimens investigated by me (including Stensiö's specimen) the dorsal fin, as shown in fig. 77, commences anteriorly to the anal fin. Stensiö also states that the lepidotrichia in both fins are unbranched throughout their height, but in well preserved specimens the lepidothrichia behind the highest part of the fins can be clearly seen to dichotomise distally in the same way as the paired fins.

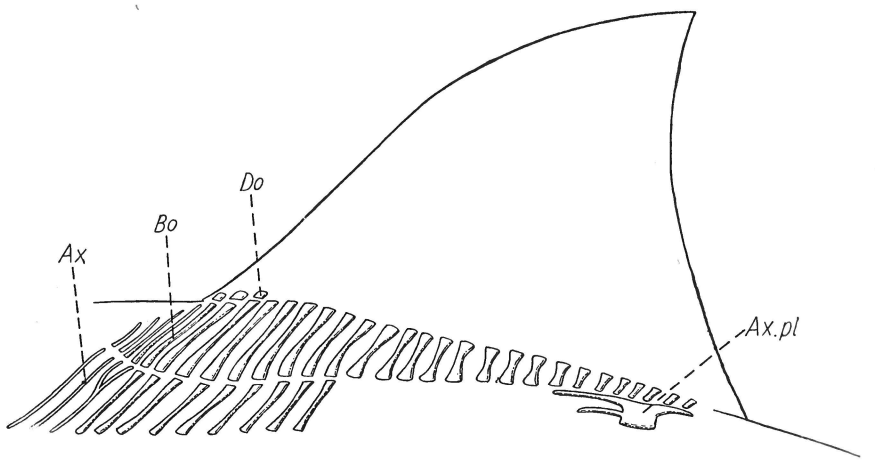


Fig. 80. *Birgeria groenlandica* Stensiö. Endoskeleton of dorsal fin. Based on several small specimens.
Ax, axonost; *Ax.pl*,axonost plate; *Bo*, baseost; *Do*, distal radial ossification.

Dorsal fin. – The dorsal fin is roughly triangular, with a slightly convex anterior and a slightly concave posterior margin. The anterior margin has about the same length as the base, while the posterior one is somewhat shorter.

The endoskeleton of the dorsal fin is represented by three series of ossifications, viz. an axonost series, a baseost series, and a series of small distal ossifications. The individual ossifications are made up of endochondral cancellate bone lined with thin perichondral bone-layers, except on the proximal and distal terminal faces of the baseost and axonost series, and on the proximal terminal faces of the distal series.

The axonost series consists of 13–15 slender rod-like ossifications (*Ax*, figs. 77, 80; pl. 10; pl. 13, fig. 2; pl. 20, fig. 2) situated below the anterior third of the fin, and a rather extensive plate (*Ax. pl*, figs. 77, 80; pl. 10; pl. 13, fig. 2) situated below the most posterior part of the fin. Below the middle part of the fin no axonost ossifications are found, and thus the proximal radial segments within this area were presumably entirely cartilaginous. The axonost rods, all of which are somewhat backwardly inclined, decrease gradually in length in a posterior direction, the hindmost being only about half as long as the foremost one. The foremost 3–5 rods are somewhat expanded both proximally and distally. In some specimens we observe more or less extensive fusion between the slender axonost ossifications, thus in fig. 80 the third and the fourth axonost ossifications are fused proximally, and in specimen no. 661 (pl. 10), for instance, the first axonost is fused with the second distally, the third with the fourth, likewise distally, and the fifth with the sixth proximally. In a specimen of *Polyodon* I have observed similar

fusions in the foremost part of the axonost series. The posterior large ossification in the axonost series may best be described as a roughly rectangular, vertically situated plate, the length of which is somewhat greater than the height, and from which issue a number of long and slender processes. In specimen no. 661 there are three such processes, viz. two issuing in an anterior direction from the anterior, and one in a posterior direction from the posterior margin of the plate. In other cases there seems to be only one anterior and one posterior process, in others, again, two posterior and one or two anterior processes. The length of the individual processes also shows considerable variation.

The strange posterior axonost element should probably be compared to the axonost plate formed by fusion of the caudal elements in the axonost series in other primitive Actinopterygians such as *Pygopterus nielseni* (Aldinger 1937, p. 175, figs. 42, 47), *Australosomus* (Stensiö 1932, p. 177, fig. 56; present paper pp. 153–154, figs. 53), and *Pteronisculus* (E. Nielsen 1942, p. 241, fig. 50); however, while in these forms the compound nature of the axonost plate is still evident from its shape, the shape of the axonost plate in *Birgeria* shows no indication of having originated from several independent axonost elements.

The baseost series contains about thirty ossifications (*Bo*, figs. 77, 80; pl. 10; pl. 13, fig. 2), the foremost 13–15 of which lie each in a distal continuation of one of the slender axonost ossifications, while the 7–8 hindmost ones are situated distally to the axonost plate. The foremost 3–4 baseost ossifications are very slender rod-like structures of about the same thickness throughout their length, and situated antero-ventrally to the base of the freely projecting part of the dorsal fin, while the more posterior baseost ossifications are developed as more massive rods, which, as shown in fig. 80, are somewhat expanded both proximally and distally. The baseost ossifications increase in length from the foremost to the 7–9th, to decrease from here to the posterior end of the series. All of them are somewhat backwardly inclined.

The distal radial series has only been observed in a few specimens, in which it is represented by 3–4 very small ossifications (*Do*, figs. 77, 80), each of which is situated distally to one of the foremost strong ossifications in the baseost series below the most anterior part of the dorsal fin. As in *Pteronisculus* (E. Nielsen 1942, p. 245), the distal radial ossifications are situated in the basal part of the free fin enclosed between the proximal ends of the right and the left halves of the lepidotrichia. The ossifications may be described as very short cylinders, the diameter of which are almost equal to that of the distal terminal faces of the baseost ossifications against which they articulated.

Judging from the number of elements in the axial skeleton, the number of radials in the endoskeleton of the dorsal fin is about twice the number

of metameres in that part of the trunk on which the dorsal fin is situated. According to Aldinger (1937, pp. 177–178) such a polymeric arrangement of the radials of the dorsal (and the anal) fin is of common occurrence within the *Palaeonisciformes* and is probably due to concentration of the fins. In this connection it is of interest that, as described above, the foremost elements both of the axonost and the baseost series seem to be in a state of reduction and are situated so far forward in relation to the fin base that they act no longer as actual fin-supports, a fact which speaks decidedly in favour of a backward movement of the anterior margin of the freely projecting part of the fin. Similar conditions are recorded by Stensiö from *Birgeria mougeoti* (Stensiö 1921, p. 191 foot-note; cf. also Traquair 1877 a, p. 24).

The dorsal fin contains about 53—57 close-set lepidotrichia, which are segmented as shown in fig. 77. The foremost lepidotrich is very short, the succeeding ones increase rapidly in length backwards to about the 13th or 14th lepidotrich, behind which they decrease more slowly in length throughout the remaining part of the fin. The lepidotrichia are unornamented, and no fulcra are developed.

Anal fin. – The anal fin has almost the same size as the dorsal fin and is roughly triangular, with a slightly convex anterior and a rather strongly concave posterior margin. The anterior margin is a little longer and the posterior margin somewhat shorter than the base of the fin.

The endoskeleton of the anal fin is represented by two series of ossifications, one of which extends basally to the whole length of the fin, while the other is wedged in between the posterior third of the former series and the fin-base.

The longer series contains about 22 rod-like elements (Ax_1, figs. 77, 81; pl. 10; pl. 13, fig. 2; pl. 20, fig. 1), behind which lies a single fairly large plate (Ax_1 *pl*, figs. 77, 80; pl. 10; pl. 13, fig. 2). The 17 foremost rods extend distally to the base of the freely projecting part of the fin, while the five hindmost ones as well as the large plate are separated from the fin-base by the shorter series of radial ossifications. In the anterior parts of the series the rods, which decrease in length in a posterior direction, are very slender, but grow more massive in its middle and posterior part. Throughout the series the rods are expanded distally and in its middle part also proximally. The large posterior element of the series probably represents a number of completely fused smaller radial ossifications, though every trace of its compound nature has disappeared. This peculiar structure, which varies a good deal in shape in the different specimens, may best be described as a vertically placed rectangular plate, from which issues four strong processes, two in an anterior direction from its anterior, and two in a posterior direction from its posterior margin.

The shorter series consists of about 10 short and fairly massive rods (Bo_1, figs. 77, 81; pl. 13, fig. 2), each of the foremost five of which lies distally

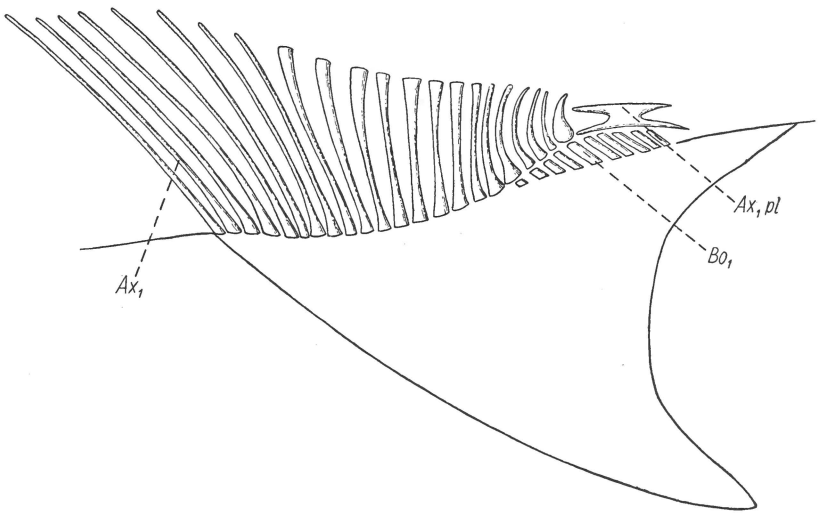


Fig. 81. *Birgeria groenlandica* Stensiö. Endoskeleton of anal fin. Based on several small specimens.
Ax_1, axonost; Ax_1pl, axonost plate; Bo_1, baseost.

to one of the hindmost five rod-like elements in the longer series, while the hindmost five lie distally to the large plate just described. In a posterior direction the rods at first increase and then decrease in length throughout the series, the sixth rod reckoned from the anterior end of the series being the longest.

In accordance with Stensiö (1932, pp. 291—292) and Aldinger (1937, p. 178) I regard the long series as an axonost series and the shorter one as a baseost series. A third, more distal, series has not been observed.

The anal fin contains about 60—62 close-set and unornamented lepidotrichia, the segmentation of which is demonstrated in fig. 77. The foremost lepidotrich is very short, the succeeding ones increase rapidly in length as far as about the 15—17th, whence they decrease in length posteriorly through the remaining part of the fin. Behind the highest portion of the fin the lepidotrichia are dichotomically branched in their distal part. No fulcra are developed.

Caudal fin. – The deeply cleft caudal fin is equilobate or nearly so. It possesses a strong body axis, which extends to the distal end of its dorsal lobe. Dorsally this body axis is covered with about 14 long and pointed unpaired fulcral scales, and laterally by long, very narrow scales arranged as shown in fig. 77. As in several other *Palaeonisciformes*, the scales along the ventral margin of the lateral face of the axis are probably pierced by the main lateral line; however, their state of preservation does not permit a close investigation on this point. No separate ossifications have been observed in the endoskeleton of the caudal fin, but it is quite probable that hypochordal radial elements are included in the ventral axial ossifications supporting the fin (cf. Schmalhausen 1912, pp. 525—528; 1913 a, p. 65; 1913 b, pp. 753—756; E. Nielsen 1942, p. 220).

The caudal fin contains about 65 lepidotrichia crossed by close-set articulations except in their most proximal part. The foremost 21 lepidotrichia are close-set and undivided, while the remaining ones are situated somewhat apart from each other and distally ramify dichotomically once, twice, or thrice. The length of the lepidotrichia increases from the foremost, which is very short, to about the eighteenth, which reaches the distal end of the ventral lobe, and from here decreases backward, at first rapidly, then (in the dorsal fin-lobe) more slowly throughout the remaining part of the fin. All the lepidotrichia are unornamented. Fulcra are entirely absent from the antero-ventral margin of the ventral lobe.

Discussion. – As already pointed out by Stensiö (1932, p. 292), the unpaired fins of *Birgeria groenlandica* agree very well with those of *Birgeria mougeoti* in so far as these latter are known.

In most normal *Palaeonisciformes* the endoskeleton of the dorsal fin contains only two series of ossifications, viz. an axonost and a baseost series, but both *Pteronisculus* and *Boreosomus* (E. Nielsen 1942, pp. 243–246, 368–369) in addition to the axonost and the baseost ossifications possess a series of smaller ossifications corresponding to the distal radial series in *Birgeria*. It seems most probable, therefore, that the radial supports of the dorsal fin in primitive Ganoids, as is the case in higher Actinopterygians, were divided into three segments. The apparent lack of distal segments in a number of *Palaeonisciformes* may be explained either by their failing ossification or simply by the fact that these forms have not been the subject of a sufficiently detailed examination.

Fusion of the hindmost axonosts of the dorsal fin to form an axonost plate comparable to that in *Birgeria* has hitherto only been observed in two normal Palaeonisciform genera, viz. *Pygopterus* (Aldinger 1937, p. 175, figs. 42, 47) and *Pteronisculus* (E. Nielsen 1942, p. 244), but it will probably be found to exist in several other *Palaeonisciformes* the internal fin skeleton of which is still unknown.

The reduction of the foremost radials observed in *Birgeria* is a feature which is unknown in normal *Palaeonisciformes*, whereas the polymeric arrangement of the radials is recorded from several *Palaeonisciformes* and many other Actinopterygians.

The dorsal fin itself is built much as in normal *Palaeonisciformes*, apart from its complete lack of fulcra, a character which on the basis of our present sparse knowledge of the ancestors of *Birgeria* might just as well be considered primitive as specialised.

The endoskeleton of the anal fin of *Birgeria* is especially interesting on account of its partially reduced baseost series, and, as pointed out by Aldinger, *Birgeria* may in this respect be regarded as intermediate between certain *Palaeonisciformes* with two and others with only one series of ossifications in the endoskeleton of the anal fin. In accordance with this view

Aldinger interprets the only series of ossifications in the endoskeleton of the anal fin in *Pygopterus nielseni* as an axonost series, maintaining that the baseosts are completely reduced (Aldinger 1937, p. 178). If this interpretation is correct, there can be only little doubt that in the endoskeleton of the anal fin of *Pteronisculus* the baseost series is also completely reduced, and that the distal series of small ossifications in the endoskeleton of the anal fin of *Pteronisculus* must be regarded as ossifications in distal radial segments, analogous to the distal segments in the endoskeleton of the dorsal fin (cf. E. Nielsen 1942, pp. 247–249, fig. 56). Thus, if Aldinger is right in his view, the forms discussed here give strong evidence for the assumption that the endoskeletal supports of the anal fin, like those of the dorsal fin, of the *Palaeonisciformes*, were originally divided into three segments. Moreover, if the radial ossifications in the endoskeleton of the anal fin of *Pygopterus* are axonosts, as emphasised by Aldinger, there is, both in *Pygopterus* and *Pteronisculus*, a tendency towards the development of an axonost plate comparable to that present in the endoskeleton of the anal fin of *Birgeria*.

Regarding the caudal fin and the freely projecting parts of the dorsal and anal fins *Birgeria* shows a striking resemblance to the recent *Polyodon*, from which it differs mainly in having a less forward position of the dorsal fin in relation to the anal fin. As regards the endoskeleton of the dorsal and the anal fin *Polyodon* differs from *Birgeria* in its smaller number of radials, its complete lack of compound axonost plates, and in having a complete row of baseosts in the endoskeleton of the anal fin. The two first-mentioned differences may easily be explained as the result of progressive reduction from both ends of the axonost and baseost series in a theoretic phylogenetic line leading from *Birgeria* to *Polyodon*; however, the fact that the baseost series in the endoskeleton of the anal fin is much more reduced in *Birgeria* than in *Polyodon* leaves it quite out of the question to consider the former as directly ancestral to the latter. There can be no doubt, however, that the close argeement between the unpaired fins in other respects speaks in favour of fairly close relations between these two genera.

Body shape and squamation.

As pointed out by Stensiö (1932, p. 292), the squamation is very much reduced, the only scales present anteriorly to the caudal pedicle being developed along the main lateral line, while a more extensive scale-covering only exists on the dorsal half of the caudal pedicle and on the greater part of the body axis of the caudal fin.

The lateral-line scales of the body, which are described by Stensiö as short bony tubes, are, in fact, very small irregularly rounded plates (*lc. s*,

pl. 18, fig. 2) pierced by the lateral line in a longitudinal direction. On account of their small size they are always poor preserved, so it could not be definitely settled whether or not they are ornamented; the latter alternative, however, is the more probable. As far as can be seen, there are about four lateral line scales per myotome.

The scales on the dorsal part of the caudal pedicle and on the body axis of the caudal fin are high and narrow and, as shown in fig. 77, have much the same arrangement as in most other *Palaeonisciformes*. They are entirely devoid of ganoine and are seemingly quite smooth. As already mentioned, those situated along the ventral margin of the lateral face of the body axis of the caudal fin were probably pierced by the main lateral line in the normal way.

From the much reduced squamation it is difficult to form an idea of the shape of the body, but some aid in this respect is obtained from the pigment of the naked skin, which is often preserved to a considerable extent. It can therefore be stated with a fair degree of certainty that the body, as shown in fig. 77, was slender and fusiform, and judging from the shape of the cleithrum, the venter was not flattened, but gently rounded from side to side. From the distribution of the pigment it can further be seen that the back of the fish was very dark, and that the same was the case with the lobe of the pectoral fin.

Discussion. – In *Birgeria mougeoti* the squamation probably had the same extent as in *Birgeria groenlandica*, although so far no lateral-line scales have been recorded from the abdominal region.

As pointed out by Moy-Thomas and Bradley Dyne (1938, p. 464), the scales in *Phanerosteon* are present in just the same regions in which the scales begin to develop in *Brookvalia* (Wade 1935, pp. 27–28). From this fact they draw the conclusion that the scales of *Phanerosteon* have been arrested in their development and thus offer an example of paedomorphosis. *Birgeria*, which in addition lacks the scales behind the pectoral girdle, possibly represents a more advanced stage of a similar development.

In the recent *Polyodon* the arrangement of the scales on the caudal pedicle and the body axis of the caudal fin is principally the same as in *Birgeria* (cf. Traquair 1877, pl. VII, fig. 3), and thus in this respect, also, these two genera show strikingly good agreement.

Sensory canal system of the trunk.

The main lateral line extends in the normal way from the posterior margin of the supracleithrum to the body axis of the caudal fin, on which, as already mentioned, it also occupies its normal position. Throughout its whole extent the main lateral line is protected by scales, which, however,

on account of their diminutive size are difficult to study in detail, and accordingly it has been impossible to ascertain how the rather fine canal opened outwards.

DIAGNOSIS.

Our now greatly extended knowledge of *Birgeria groenlandica* enables us to replace Stensiö's preliminary diagnosis of the species (Stensiö 1932, pp. 116–117) with the following more satisfactory one:

Fairly large species, estimated length of largest specimen about 84 cm. One or two parietals on each side of the median line. Large supraorbito-dermosphenotico-intertemporal, anterior to which lie a number of smaller independent supraorbitals. External dermal bones of the head ornamented mainly with tubercles of varying shape and size, certain areas of external faces of preoperculum, maxillary, and dentalo-splenial ornamented with striae, which, at least on the maxillary and the dentalo-splenial, partly underlie tubercles of varying shape. Upper and lower jaws with a lingual row of large and a labial row of smaller teeth. Number of teeth in lingual row about 25–27. Enamel cap of teeth of jaws constituting almost one-third of the total length of the teeth, on the large teeth of the rostro-premaxillary with fine vertical striae, on the other teeth smooth.

REMARKS.

Birgeria groenlandica differs from the other known species of *Birgeria* in lacking vertical striae on the enamel caps of almost all its teeth. From *Birgeria mougeoti* it further differs by its smaller number of independent elements in the supraorbital part of the dermal cranial roof, and from *Birgeria stensiöi* by its larger number of large teeth on its jaws.

Generic diagnosis.

(Partly after Stensiö 1932, pp. 107-108).

Large or fairly large fishes. Trunk long and slender, oval in transverse section. Head rather large, with big eyes and extremely long jaws. Neural endocranium narrow both anteriorly and posteriorly, but very broad in its middle part and especially between its strong postorbital processes. Neural endocranium in both small and large specimens partly occupied by a number of independent bones. In fairly large specimens such bones are: an unpaired occipital ossification, a paired prootico-opistotic, a paired autosphenotic, an unpaired sphenoid, and a paired ethmoidal ossification (occupying also an antero-ventral part of the orbitotemporal region). Cranio-spinal process small. Fossa bridgei comprising, in the fossil state, an incompletely

subdivided posterior division on the dorsal face of the prootico-opistotic and an anterior spiracular division on the dorsal face of the autosphenotic; in the living animal the two divisions were probably connected by a middle division on the cartilaginous part of the neurocranial roof. Posterior part of fossa bridgei not connected with the cavum cerebrale cranii. Jugulo-hyoideomandibular canal probably long, anteriorly widened to a trigemino-facialis chamber. Posterior myodome small, paired, in a very primitive stage of development. Pars basisphenoidea developed as a very massive vertical pillar pierced throughout its height by a paired canal for the arteria carotis interna. Interorbital part of orbitotemporal region ventrally compressed to a thin interorbital wall pierced by a larger or smaller fenestra optica. Ethmoidal region low and extremely short, with very shallow nasal pits, and with strong processes for articulation with the palatoquadrate. Sclerotic ring well developed, consisting of 3–4 pieces. Parasphenoid robust, extending beneath the whole endocranium and provided with a broad paired processus ascendens corresponding mainly to a posterior one. Extrascapular series consisting of two (or four?) elements. Parietals represented by one or two plates on each side of the median line and separated from those of the opposite side by the frontals. Frontals very large, extending with a paired process between the parietals to the extrascapular series. Laterally to the anterior part of the supratemporal and the posterior part of the supraorbito-dermosphenotico-intertemporal lies a supraspiracular plate with a more or less well marked spiracular notch. Several small independent supraorbitals. Postrostral and nasals large. Fenestra exonarina anterior situated at the foremost (lower) end of the suture between the nasal and the postrostral. Fenestra exonarina posterior, as usual in primitive Ganoids, situated at the postero-ventral margin of the nasal, its position being indicated by a well marked notch. Infraorbital series consisting of several small postorbitals, a large jugal, a long and slender lacrimal, and a fairly large antorbital. Antorbital provided with a strong dorsal process separating the fenestra exonarina posterior from the orbital opening and adjoining the nasal dorsally to the fenestra exonarina posterior. About 8–11 long and narrow suborbitals. Palatoquadrate very long, only ossified in the quadrate region. On oral face of palatoquadrate an ectopterygoid, a dermometapterygoid, an entopterygoid, and two dermopalatines. Maxillary very long, with a low suborbital and a high postorbital division. Preoperculum as a whole very oblique, consisting of an antero-dorsal and a postero-ventral shank. Palatoquadrate and its dermal bones, maxillary, and preoperculum connected with each other and forming the walls of a long and narrow chamber for the musculus adductor mandibulae. Unpaired rostro-premaxillary consisting of an external (facial) vertical plate, and a strong internal (palatal) lamina. Lower jaw long and slender. Meckelian cartilage only ossified farthest posteriorly. Well developed processus retroarticularis. Two grooves for articulation with the double condyle of the pars

quadrata. Supraangular with a strong dorsal process. Prearticular very long. In hyoid arch hyomandibula, symplectic, one ceratohyal, and hypohyal. Hyomandibula much inclined forward, consisting of two shanks forming an angle with each other. No processus opercularis and no canal for the truncus hyoideomandibularis. Symplectic relatively long. Ceratohyal compressed from side to side and somewhat expanded at both ends. No dermohyals or antopercular elements. Operculum long and narrow, pointed at both ends. Suboperculum consisting of a number of long and narrow triangular plates fused only at their extreme ventral ends. Radii branchiostegi numerous, with a more or less produced antero-lateral corner and separated from the suboperculum by a large interspace. Median gular plate small, lateral gulars somewhat larger. Basibranchial series with three ossifications. Branchial arches well ossified; the following ossifications hitherto observed: hypobranchial, ceratobranchial, and epibranchial of the three foremost arches, infrapharyngobranchial of the second arch, and ceratobranchial of the fourth arch. Suprapharyngobranchials of the foremost two arches and infrapharyngobranchial of the foremost one probably cartilaginous. Relations between the foremost two arches and the neural endocranium probably as in *Pteronisculus*, *Australosomus*, and *Acipenser*. External dermal bones of head relatively thick and mainly ornamented with tubercles, to a smaller extent, however, also with striae. Striae best developed on maxillary and dentalo-splenial, and on these bones to some extent covered by more superficially situated tubercles of varying shape. On the jaws a labial row of small, and a lingual row of large teeth. Parallel with these two rows, a third row consisting of small to medium-sized teeth on the ventral or ventro-lateral part of the oral faces of the ectopterygoid and the dermopalatines. Moreover large areas of oral faces of ectopterygoid, entopterygoid, dermopalatines, dermometapterygoid, and prearticular covered by very small teeth. Small teeth also present on ossifications of basibranchial series and branchial arches. Teeth of jaws and at least larger teeth on dermal bones of palate pointed and conical with a two-edged enamel cap, in the geologically older species on the whole smooth, in the geologically youngest species equipped with vertical, elevated, sharp striae; basally to enamel cap the teeth of all the species vertically striated, either with fine striae alone or with coarse striae which in their turn bear the fine striae; plicidentine not present. Teeth of branchial arches more slender than those of the jaws and with an enamel cap, which always seems to be smooth. Sensory canal system of head differing from the normal Palaeonisciform pattern in the following respects: supraorbital sensory canal ends blindly in the rostro-premaxillary without communicating with the infraorbital sensory canal, and the sensory canal piercing the dorsal shank of the preoperculum is directed towards the most dorsal part of the postorbital section of the infraorbital sensory canal. Sensory canals very narrow and deeply embedded in their dermal bones. Tubuli extremely fine. Nerve-sack

groups seemingly developed much as in recent sturgeons. Notochord persistent and unconstricted. Axial skeleton containing the following ossifications: In the abdominal region, basidorsals, basiventrals, and supraneurals; in the caudal region, basidorsals (possibly fused with supraneurals), interdorsals (only in fairly old specimens), basiventrals, infrahaemals (either free or fused with basiventrals). Ventral lobe of caudal fin supported by strong hypural processes, possibly containing radial components. About 32 metameres in abdominal region and about 48 from anterior end of caudal region to about middle of body axis of caudal fin. Endoskeleton of shoulder-girdle with two rather small ossifications. Margo radialis vertical. Series of dermal bones of shoulder-girdle comprising posttemporal, supracleithrum, cleithrum, and clavicle. Posttemporal and supracleithrum very long and narrow. Endoskeleton of pectoral fin with about 10 radial ossifications arranged in a single series and probably supporting a small fin-lobe. Pectoral fin large and vertically held. Lepidotrichia numerous, segmented throughout their length and apart from the foremost ones branched dichotomically at their distal end. Pelvic plate well ossified, with very long antero-medially directed slender process. Behind pelvic plate probably cartilaginous metapterygial elements. Endoskeleton of pelvic fin with a proximal and possibly also a distal series of ossifications. Pelvic fin long-based, with very numerous segmented lepidotrichia, those reaching hind margin of fin distally branched. Endoskeleton of dorsal fin with three series of ossifications: an axonost series, a baseost series, and a distal series. In axonost series about 11–13 slender rod-like ossifications situated antero-ventrally to foremost part of dorsal fin, and a single compound axonost plate situated below hindmost part of dorsal fin. In baseost series about 28–30 rod-like ossifications. In distal series a few very small ossifications. Endoskeleton of anal fin with two series of ossifications: a complete axonost series and a strongly reduced baseost series. In axonost series about 22 rod-like ossifications and a posterior compound axonost plate. In baseost series only about 10 small ossifications situated distally to hindmost part of axonost series. Dorsal and anal fins situated far backward, anal fin slightly farther back than dorsal fin. Lepidotrichia of both fins numerous, close-set, segmented throughout, and apart from the foremost ones branched farthest distally. Caudal fin deeply cleft and nearly equilobate. Dorsal lobe supported by a strong body axis. Lepidotrichia thoroughly segmented, those reaching posterior margin of fin branched distally. Lepidotrichia of all fins devoid of ganoine. Fulcral scales (ridge scales) well developed on dorsal margin of caudal fin, otherwise not known. Squamation absent, except on part of caudal pedicle, on body axis of caudal fin, and on flanks of trunk as a single row of lateral-line scales. Scales on posterior part of caudal region long, narrow, and without ganoine ornament. Lateral-line scales anterior to caudal pedicle very small and rounded in outline.

Remarks on the genus Birgeria.

According to the literature, the genus *Birgeria* comprises the following species, all of which are of Triassic age: *Birgeria mougeoti* (Agassiz) derived from Europe and Spitsbergen (cf. Stensiö 1919, pp. 177–181), *Birgeria* sp. Stensiö from Spitsbergen (Stensiö 1921, pp. 199–200), *Birgeria stensiöi* Aldinger from Europe (Aldinger 1931, pp. 167–180), *Birgeria groenlandica* Stensiö, from Greenland (Stensiö 1932, pp. 109–117, 289–292), and *Birgeria velox* (Jordan), from California (Jordan 1907, pp. 120–121; Stensiö 1932, p. 98). Two little known species of *Saurichthys*, both from Europe and previously described as *Saurichthys acuminatus* Agassiz and *Saurichthys annulatus* Winkler, respectively, have also, though with doubt, been referred to *Birgeria* (Stensiö 1921, p. 150; 1925, p. 174), and further, according to kind verbal information from Dr. J. P. Lehman, a species of *Birgeria* has recently been identified in a collection from the Triassic of Madagascar.

Thus the number of species referred to *Birgeria* is fairly considerable; however, most of these species are very imperfectly known, and it is by no means impossible that a more detailed investigation will reduce the number of species.

On the basis of the available descriptions the following species, only, can at present be referred with certainty to the genus *Birgeria*: *Birgeria mougeoti*, *Birgeria groenlandica*, and *Birgeria stensiöi*, and only the first-mentioned two species are fairly well known. However, to these three may be added as an undoubted species Lehman's species of *Birgeria* from Madagascar, which I had the opportunity to examine myself and of which a specimen in such a good state of preservation is available that every doubt as to the correctness of the identification can be excluded, and *Birgeria velox* from California, examined by Professor E. Stensiö. Since, however, no descriptions of the two last-mentioned species are available, only the other three, and of these especially *Birgeria mougeoti* and *Birgeria groenlandica*, are at our disposal for studies of the evolutionary trends within the genus *Birgeria*.

Such studies have already been carried out by Stensiö (1932, pp. 106, 295), who arrived at the following results:

1) The suborbitals and the dermal cranial roof just posteriorly to the supraorbitals (Stensiö's dermosphenotic) underwent a progressive subdivision into minor plates during the period from the Lower to the Upper Eotrias.

2) Those areas of the external faces of the maxillary and the dentalosplenial which were ornamented with striae decreased very much in extent in the period from the Lower to the Upper Eotrias, owing to the striae breaking up into tooth-like tubercles.

As to 1), Stensiö is probably right, although his description of the

conditions in *Birgeria groenlandica*, as already mentioned (p. 219), is not quite correct in so far as the supraorbitals in this species were already subdivided, though to a less extent than in *Birgeria mougeoti*.

As to 2), however, Stensiö is undoubtedly wrong, as likewise pointed out above (p. 254). The striae constituting the ornamentation of certain areas of the external faces of the maxillary and the dentalo-splenial do not break up into small tubercles, but in the course of development they have become more and more concealed below a more superficial layer of tooth-like tubercles, which attain a secondary attachment to the surfaces of the striated areas, and should most probably be compared to the small denticles occurring loosely in the skin of certain recent and fossil fishes.

Another interesting observation can be made on comparing the Lower Eotriassic *Birgeria groenlandica* with the Upper Eotriassic *Birgeria mougeoti*, viz. that the endocranium of the younger form is absolutely more strongly ossified than that of the older one. As pointed out above (p. 204), this difference can only in part be explained by the greater size, and accordingly probably the greater age, of the specimen of *Birgeria mougeoti* investigated by Stensiö, while, in part it must be regarded as a real structural difference, the significance of which, however, cannot be estimated at present. It must suffice here to point out that the fact that *Birgeria mougeoti* occurs in younger strata than *Birgeria groenlandica* does not necessarily imply that the former species is the most primitive in all respects, for we have no definite proof that the older form is ancestral to the younger one.

Thus at present we cannot state very much regarding the evolutionary trends within the genus *Birgeria*, but there is reason to assume that significant conclusions as to these may be drawn with a fair degree of certainty when more complete descriptions of all or the majority of the species so far referred to *Birgeria* have become available.

REMARKS ON THE SYSTEMATIK POSITION OF BIRGERIA.

In 1919 the genus *Birgeria* was referred by Stensiö to the family *Palaeoniscidae*, which at that time already comprised a large number of genera, and since a few years later (1921) *Birgeria* was described by Stensiö in much more detail than had been the case with any of the previously known members of the family, it was for some time in a certain respect regarded as a typical representative of the family. However, even before that time various authors (Woodward 1891, p. 425; Fritsch 1895, p. 126; Gregory 1907, p. 463) had expressed a suspicion that the *Palaeoniscidae* were a comprehensive family, and this suspicion was intensified when a few years after the appearance of Stensiö's pioneer work on the Triassic fishes from

Spitsbergen (1921) Watson published his investigations on some especially well preserved Palaeoniscid remnants (Watson 1925, 1928), for during these investigations it turned out that the structure of the neural endocranium of some Kansas forms differed in a very considerable degree from the neural endocranium of *Birgeria*. According to Watson (1925, p. 850) *Birgeria* is more closely related to the *Chondrosteidae*, the *Acipenseridae*, and the *Polyodontidae* that to the other members of the *Palaeoniscidae*. Similar opinions were expressed by Stensiö in 1932, when he pointed out partly (pp. 97–98) the comprehensive nature of the *Palaeoniscidae*, and partly (p. 109) that »*Birgeria* represents a type of its own among the Palaeoniscidae, a type which approaches somewhat the sturgeons, for instance in regard of the position of the nostrils, the presence of the spiraculum, and the tendency to reduction of the exoskeleton. It is also clear that *Birgeria* somewhat resembles *Coccocephalus*«. On account of the still insufficient knowledge of the internal anatomy of the greater number of the *Palaeoniscidae*, however, Stensiö made no subdivision of the group; but in a foot-note (p. 97) he wrote as follows: »It is very likely that such genera as for instance *Cheirolepis* (Watson 1925), *Coccocephalus* (Watson 1925), *Dicellopyge* (Brough 1931) and *Birgeria* (cf. the account of this genus below) represent families of their own«.

In 1937 Aldinger made a far-ranging attempt at a subdivision of the *Palaeoniscidae*, grouping, chiefly on the basis of his investigations of the structure of the scales, a large number of Palaeoniscid genera in minor families which, in the descriptive part of his work, he placed in the suborder of the *Palaeonisciformes*. As regards the remaining Palaeoniscid genera he made no corresponding re-grouping, on account of lack of material, apart from mentioning the following cases in which a close relationship between two or more of these genera was presumed (p. 337):

»*Carboveles*, *Phanerosteon* (White 1927, p. 267–268).
Coccocephalus, *Birgeria* (siehe oben Seite 329).
Cheirolepis, *Tarassius*, *Holurus* (Moy-Thomas 1934)«.

The suborder *Palaeonisciformes* was included by Aldinger, with the forms classed by Stensiö (1931, pp. 96–97) in his groups B–F, in the order *Chondrostei*. Aldinger points out, however, that the above classification is entirely artificial, as it gives no expression of the genetic relations of the groups, so he outlines the following scheme for an actual genetic classification of the Actinopterygians:

Actinopterygii.

Ord. *Cheirolepidomorpha*. *Cheirolepis*, *Tarassius*.
Ord. *Sturiomorpha*.
U.–O. *Chondrosteiformes*
- A. *Birgeriidae*.
  Polyodontidae.
- B. *Chondrosteidae*.
  Acipenseridae.

U.–O. *Saurichthyiformes*
- A. *Phanerorhynchidae.*
- *Saurichthyidae.*
- B. *Pholidopleuridae.*

Ord. *Elonichthyomorpha.*

U.–O. *Elonichthyiformes*
- A. *Elonichthyidae.*
- *Palaeoniscidae.*
- *Brachiopterygii.*
- B. *Acrolepidae.*

U.–O. *Platysomiformes*
- *Platysomidae.*
- *Dorypteridae.*
- *Bobasatraniidae.*
- ? *Cleithrolepidae.*
- ? *Pycnodontidae.*

U.–O. *Eugnathiformes*
- ? *Canobiidae.*
- *Perleididae.*
- *Semionotidae.*
- *Parasemionotidae.*
- und übrige *Holostei*, *Teleostei.*

Against the details of this classification, in which Aldinger has attempted to include the more or less hypothetical phylogenetic conclusions drawn by himself and a number of other workers in a clear and perspicuous way, many justifiable objections may, of course, be raised; as a whole, however, it gives a clearer view of the group of Actinopterygians than any of the earlier attempts at classifications.

What is here of special interest to us is that *Birgeria* is placed in a family of its own, viz. the *Birgeriidae*, which as the only one of the many Palaeonisciform families is included in the order *Sturiomorpha*, where, with the family *Polyodontidae*, it forms a special group within the suborder *Chondrosteiformes.*

Aldinger gives no diagnosis of the family *Birgeriidae*, nor does he state whether *Coccocephalus*, whose presumed close association with *Birgeria* is repeatedly touched upon in his paper (pp. 330, 367, 377–378), should also be regarded as a Birgeriid.

In 1940 Berg in his »Classification of fishes, both recent and fossil« (pp. 398–401) defined an order *Palaeonisciformes* with the two suborders *Palaeoniscoidei* and *Platysomoidei.* The suborder *Palaeoniscoidei*, which corresponds most closely to the family *Palaeoniscidae* in its old conception and thus to Aldinger's suborder *Palaeonisciformes*, he divided into the following families:

Cheirolepidae
Palaeoniscidae
Oxygnathidae

Coccolepidae
Birgeriidae
Holuridae
Urostenidae (incertae sedis).

Of all these families Berg gives more or less exhaustive diagnoses, and thus we here get the first diagnosis of the *Birgeriidae*, to which family he also refers, though with some doubt, in addition to the type genus, the genus *Psilichthys* Hall from the Triassic of Victoria (Hall 1900, pp. 147–151). His diagnosis runs as follows:

»Body, excepting the dorsal lobe of caudal fin and bone tubes around the lateral line, naked. Two nasal openings on each side, an anterior at the orbit and, as usually in *Palaeoniscidae*, a posterior between the nasal and postrostral. Sensory canal system on head as in *Palaeoniscidae*. Premaxillaries fused together. Parietals (a pair on each side) separated by frontals. Two tabulars (extrascapulars) on each side. Dermosphenotic subdivided into many small plates. Chondrocranium ossified not in a single piece but in separate bones (a basioccipital, two prootico-opistotics, two autosphenotics, a sphenoid). Myodome (paired) present but small. Parasphenoid strong, extending far back. Mouth large, preopercular oblique. Teeth strong. Opercular small, subopercular lobate as in *Polyodon*. Spiracle present. Branchiostegal rays numerous. Fin rays jointed, devoid of ganoine. Ventrals each with about 50 rays. Dorsal above the anal, each with more than 50 rays. Fulcra only on the caudal fin. Dorsal radials ossified, in two rows. Notochord persistent. Axial skeleton, at least in the caudal part, with ossified neural and haemal arches. Skeleton of ventral fin consisting of a paired ossified pelvic plate and 16–17 ossified radials on each side«.

Referring to Stensiö's researches (1932) Berg drops the groups *Chondrostei*, *Holostei*, and *Teleostei*, dividing, instead, the *Actinopterygii* into a series of orders, of which the following, together with the order *Palaeonisciformes*, comprise the genera previously included in the *Chondrostei*:

Tarrasiiformes
Gymnonisciformes
Phanerorhynchiformes
Dorypteriformes
Bobasatraniiformes
Redfieldiiformes
Perlediiformes
Ospiiformes
Pholidopleuriformes
Saurichthyiformes
Acipenseriformes.

Berg gives only little information regarding the genetic relations between these orders, and the relationship between *Birgeria* and the sturgeons pointed out *i. a.* by Aldinger is only treated very briefly in a foot-note (p. 410).

One of the most interesting features in Berg's classification of the Palaeoniscid group is that he groups the families *Styracopteridae* Moy-Thomas and *Trissolepidae* Fritsch with a large number of the new families erected by Aldinger, viz. the *Elonichthyidae*, the *Palaeoniscidae*, the *Scanilepidae*, the *Canobiidae*, the *Acrolepidae*, the *Boreolepidae*, and the *Pygopteridae*, in a single family, to which he applies the name *Palaeoniscidae*.

Whether this step is fully justified, cannot be decided until we have obtained a more comprehensive knowledge of the internal anatomy of the members of the said groups, but I am inclined to believe that Aldinger has at least gone somewhat too far in his attempt at a subdivision of the old Palaeoniscid group. In this connection I may refer the reader to Part I of the present work (1942), in which I pointed out (p. 279) that the families *Pygopteridae* Aldinger and *Palaeoniscidae* Aldinger in so far as they have been investigated, only differ very slightly from each other.

The family *Palaeoniscidae* Berg comprises all the least specialised or otherwise deviating members of the old Palaeoniscid group, that is, precisely the forms whose common characteristics form the basis of the concept repeatedly referred to in the present paper: typical or normal *Palaeoniscidae*. The family comprises a very large number of genera, and among the members of these genera we are in all probability to look for at any rate the large majority of the ancestral forms of the higher Ganoids and their derivatives, the *Teleostei*.

After the present investigation of *Birgeria groenlandica* there can be no doubt as to the justification of Berg's placing *Birgeria* in a separate family. According to our present knowledge, however, Berg's diagnosis of the family *Birgeriidae* should be altered as follows:

Body almost naked, scales only present on dorsal half of caudal pedicle, on body axis of caudal fin, and anteriorly to the caudal pedicle in a single row along the main lateral line. As in the *Palaeoniscidae*, two nasal openings on each side, one anterior and one posterior to the postrostral. Sensory canal system differing from that in *Palaeoniscidae* mainly in the following respects: Supraorbital sensory canal ending blindly in rostro-premaxillary without communicating with ethmoidal commissure of infraorbital sensory canals; dorsal part of preopercular sensory canal extending from radiation centre of preoperculum in an almost anterior direction towards most dorsal part of postorbital vertical section of infraorbital sensory canal. Very large, unpaired rostro-premaxillary. Parietals (one or two on each side) separated by frontals. One (or two?) extrascapulars on each side. Supratemporal independent. Intertemporal fused with dermosphenotic and with a number of posterior supraorbitals. A larger or smaller number of free supraorbitals.

Neural endocranium not ossified in a single piece but in separate bones (an unpaired occipital bone, a paired prootico-opistotic, a paired autosphenotic, an unpaired sphenoid, and a paired ethmoidal bone). Posterior myodome smaller than in *Palaeoniscidae*. Parasphenoid strong, extending backward below the whole neural endocranium, and with a strong paired processus ascendens. Mouth much larger than in *Palaeoniscidae*. Suspensorium very oblique. Teeth on jaws arranged in a labial and a lingual row. Labial teeth small, lingual teeth very large. Operculum small, subopercular lobate much as in *Polyodon*. Spiracle present. Branchiostegal rays numerous. Fin rays jointed, devoid of ganoine. Pelvic fin large, with about 50 lepidotrichia. Dorsal and anal fins both situated far back, dorsal fin slightly anteriorly to anal fin, both fins large and with more than 50 lepidotrichia. Fulcra present only on the body axis of the caudal fin. Endoskeleton of dorsal fin represented by three series of radial ossifications; an axonost, a baseost, and a distal series. Endoskeleton of anal fin represented by two series of radial ossifications, probably an axonost and a baseost series; baseost series very short, supporting only posterior third of fin. Posterior elements of axonost series of endoskeleton of both dorsal and anal fins fused to a fairly extensive axonost plate. Notochord persistent. Axial skeleton with ossified dorsal and ventral arcuals, in abdominal region moreover with supraneurals, in part of caudal region possibly also with independent infrahaemals. Skeleton of pelvic fin consisting of an ossified pelvic plate and one or two rows of radial ossifications.

As revised above, Berg's diagnosis gives a fairly good picture of the new family. The picture may perhaps become clearer if we include a larger number of the generic characters of *Birgeria*, but this seems to me little desirable at a time when it is not yet known on what principles the final division of the old Palaeoniscid group is to be based. The reader is therefore referred to the very detailed diagnosis of the genus *Birgeria* already given in the present paper (pp. 281–284). The genus *Psilichthys* Hall, which Berg referred with doubt to the family *Birgeriidae*, presents, as far as I can see, no special *Birgeria*-characters. It is true that the squamation in *Psilichthys* is reduced in the same way as in *Birgeria*, but this is the case in several normal *Palaeonisciformes* also, and as regards the position of the unpaired fins *Psilichthys* differs decidedly from *Birgeria* by its dorsal fin being placed a great distance in front of the anal fin.

The principal differences between the families *Birgeriidae* Berg and *Palaeoniscidae* Berg are found in the structure of the neural endocranium, in the development and arrangement of the bones of the dermal cranial roof and the opercular fold, and in the development of the parasphenoid, the rostrals, the premaxillaries, and the suborbitals. As regards the body skeleton *Birgeria* agrees well with the normal *Palaeonisciformes*, and certain dermal bones of the head of *Birgeria* likewise exhibit unmistakable Palae-

oniscid features, thus principally the maxillary, the preoperculum, the dermal bones of the palatoquadrate, and the dermal bones of the mandible. The Palaeoniscid features in *Birgeria* point decidedly to a not too remote relationship between the *Birgeriidae* and the *Palaeoniscidae*, and it seems quite likely that *Coccocephalus* might represent a sort of connecting link between the two groups. However, our knowledge of *Coccocephalus* is very incomplete, and it is therefore impossible at present to decide whether this form, which in its main features is a Palaeoniscid, is actually ancestral to *Birgeria*. If not, the Palaeoniscid features of *Birgeria* may possibly be explained by assuming a common, not very remote, ancestor, probably of Devonian age.

Whether we assume a Palaeoniscid ancestry of the *Birgeriidae* or a common, not very remote ancestor of the *Birgeriidae* and the *Palaeoniscidae*, it seems certain that *Birgeria* lies on a line, or on a short side-branch of a line, leading towards more recent sturgeons. As already mentioned (p. 287), this view has previously been maintained by other workers, e. g. Watson, Stensiö, and Aldinger, most clearly by the latter, who in his classification of the Actinopterygians groups the family *Birgeriidae* most closely with the *Polyodontidae*, writing as follows (1937, p. 378):

»Innerhalb der *Chondrosteiformes* bilden *Birgeria* (und *Coccocephalus*?) und die *Polyodontidae* eine Einheit, von der wahrscheinlich schon sehr früh (vor dem Lias) die *Chondrosteidae* und *Acipenseridae* abzweigen (Watson 1925).«

On the basis of the investigations now available the relations of *Birgeria* to *Polyodon* may be estimated more clearly than before, and the result of a comparison between the two genera may be summarised in the following points:

1) The endocranium of *Polyodon* may be supposed to have been derived from that of *Birgeria*, from which it differs i. a. by the extreme development of the cranio-spinal processes, by the complete absence of a posterior myodome, and by the possession of an exceedingly well developed rostrum.

2) The parasphenoids of the two genera agree principally in that they extend beneath the whole neural endocranium.

3) The peculiar pattern of the dermal cranial roof of *Polyodon* may without difficulty be conceived to have been derived from the pattern of the dermal cranial roof of *Birgeria*.

4) The palatoquadrate and its dermal bones in *Birgeria* are specialised in a direction which points decidedly towards the conditions in *Polyodon*.

5) The mandible is seemingly more specialised in *Birgeria* than in *Polyodon* in so far as the supraangular in *Birgeria* is equipped with a very strong dorsal process, which is absent in *Polyodon*.

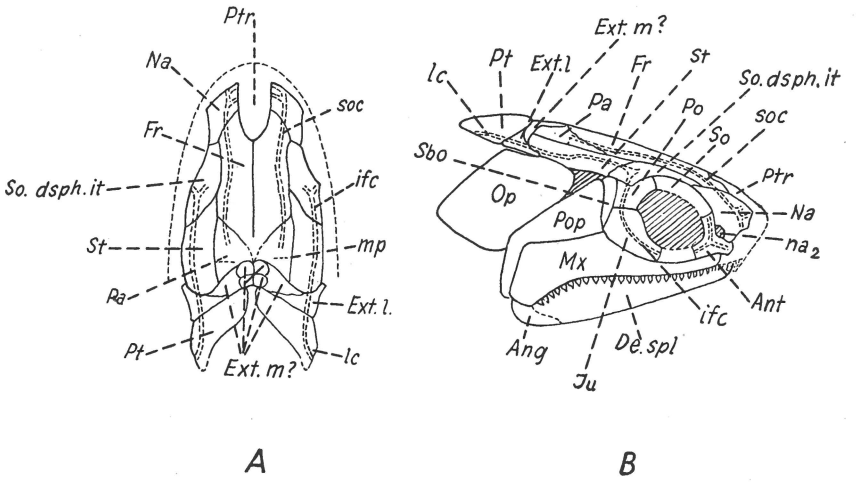


Fig. 82. *Coccocephalus wildi* Watson. A and B, head in dorsal and in lateral view respectively. After Watson 1925, figs. 5 and 6. Nat. size..

Ang, angular; *Ant*, antorbital; *De. spl*, dentalo-splenial; *Ext. l*, lateral extrascapular; *Ext. m?*, medial extrascapulars?; *Fr*, frontal; *Ju*, jugal; *Na*, nasal; *Op*, operculum; *Pa*, parietal; *Po*, postorbital; *Pop*, preoperculum; *Pt*, posttemporal; *Ptr*, postrostral; *Sbo*, suborbital; *So*, supraorbital; *So. dsph. it*, supraorbito-dermosphenotico-intertemporal; *Sop*; suboperculum; *St*, supratemporal; *ifc*, infraorbital sensory canal; *lc*, main lateral line; *mp*, middle pit-line; na_2, fenestra exonarina posterior; *soc*, supraorbital sensory canal.

6) The operculum is small in *Birgeria*, in *Polyodon* it is completely reduced.
7) The suboperculum is lobate in both genera.
8) In the opercular fold of *Polyodon* a well developed branchiostegal ray is found posteriorly to the mandible, while no branchiostegal rays are present in the corresponding part of the opercular fold of *Birgeria*. Thus in this respect *Birgeria* is more advanced than *Polyodon*.
9) An anocleithrum is present in *Polyodon*, but no such has been observed in *Birgeria*. If the absence of this bone in *Birgeria* is due to its complete reduction and not to the insufficient state of preservation of the material at hand, *Polyodon* is less advanced in this respect than *Birgeria*.
10) The margo radialis and the pectoral fin are vertical in *Birgeria* and horizontal in *Polyodon*. In this respect, therefore, *Polyodon* is more primitive than *Birgeria*.
11) The pelvic girdle is built in much the same way in both genera.
12) The baseost series of the anal fin in *Birgeria* is much reduced, while in *Polyodon* it is fairly complete.
13) The development and position of the fins are much the same in both genera.
14) The squamation is reduced to a considerable extent in both genera.

As appears from the above list, *Birgeria* has much in common with *Polyodon* but the characters enumerated as 5, 8, 9, 10, and 12 show that *Birgeria*, though rather primitive in other respects, cannot be regarded as a direct ancestor of *Polyodon*, but must be placed on a side-branch of the true *Polyodon* stem. However, there cannot be much doubt that the common ancestor of *Birgeria* and *Polyodon* should be looked for not very much earlier than the appearance of *Birgeria*, and judging from our present knowledge, this ancestral form may have been *Coccocephalus*.

SUMMARY AND CONCLUSIONS.

The present, second, part of my monograph on the Triassic fishes from East Greenland deals with the genera *Australosomus* and *Birgeria*. In the large collections brought home from East Greenland mainly in the years 1932–33 and 1936–37 *Australosomus* is represented by at least three species (*Australosomus kochi* (Stensiö), *A. simplex* n. sp., and *A. pholidopleuroides* n. sp.), while *Birgeria* is probably only represented a by single species (*Birgeria groenlandica* Stensiö). *Australosomus kochi* and *Birgeria groenlandica* have been subjected to a very detailed anatomical investigation; in the investigation of the head region of the former species Sollas's grinding method was used. The two new species of *Australosomus* have only been investigated in detail to such an extent as proved necessary for giving as correct a specific diagnosis as possible.

The most important special and general results of the studies of the above-mentioned forms are as follows:

A. *Australosomus*.

(Most of the special results are based on the detailed investigation of *Australosomus kochi*.)

1) The neural endocranium is unossified or very slightly ossified in the smallest specimens and almost completely ossified in the largest ones, in which it contains two unpaired ossifications, viz. 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. The palatoquadrate of the smallest specimens contains at least two independent ossifications, viz. one in the autopalatine region and the other in the quadrate region, while the palatoquadrate of the larger specimens is almost completely occupied by a single large ossification. How the process of ossification took place in other parts of the endoskeleton is entirely unknown.

2) The neural endocranium agrees in most respects with the central Palaeonisciform type, a type defined by the characters common to all and by certain decidedly primitive characters found in some of the best known typical Palaeonisciform endocrania, namely those of the Kansas forms A and B, *Pteronisculus* (*Glaucolepis*), and *Boreosomus*. It differs mainly from this type in completely lacking a basipterygoid process, in possessing a long and well ossified ethmoidal region with very complete nasal cavities, and in having the spiracular part of the fossa bridgei completely separated from the rest of the fossa. These differences, however, form no serious obstacles to considering the endocranium of *Australosomus* as a derivative from that of primitive, typical Palaeonisciformes.

   The central Palaeonisciform type of the neural endocranium agrees in many important respects with the Acanthodian neural endocranium, and it is suggested that the ancestors of at least the bulk of the Actinopterygians should be sought for, if not among the Acanthodians themselves, then at any rate among forms which are closely related to the Acanthodians.

3) The saccular division of the labyrinth cavity contains a large and solid otolith.

4) The parasphenoid is extremely short and evidently in full reduction in its hindmost part, which is subdivided into a large number of very small independent bones. Only a single (a posterior) pair of ascending processes is present.

   Neither in *Australosomus* nor in any other primitive Actinopterygians investigated in detail have independent paraotic dental plates been observed behind the short parasphenoid. I therefore hesitate to consider the long corpus parasphenoidea found in higher Actinopterygians as a compound bone (formed by fusion of an unpaired short corpus parasphenoidea with a paired paraotic plate); I am more inclined to believe that the long parasphenoid in the higher Actinopterygians has arisen from the short one found in more primitive forms by a gradual backward lengthening.

   The primitive *Palaeonisciformes* as well as other primitive Ganoids lend no support, so far, to the theory that the posterior ascending process of the parasphenoid originally existed in adult fishes as an independent bone.

5) In the anterior part of the roof of the mouth *Australosomus* has a paired long and narrow dermal bone, which is comparable to the paired vomer found in *Pteronisculus* (*Glaucolepis*).

6) The dermal cranial roof includes a single pair of extrascapulars, a varying number of parietals, paired supratemporo-intertemporals, frontals

and nasals, and an unpaired postrostral. The anterior part of the dermal cranial roof, viz. parts of the nasals and the postrostral, is more or less reduced.

The complex of small parietals has the same outline as, and fits like a lid on, the large unpaired depression in the dorsal face of the neural endocranium, at the bottom of which the posterior median fontanelle opens. The parietal elements are fairly loosely connected with the surrounding dermal bones, and thus the dermal roof of the posterior median fontanelle was evidently movable in some degree. As the supraorbital sensory canal ends posteriorly in the central part of the frontal, the variability in number of the parietals might possibly be regarded as a kind of degeneration, but it is perhaps more probable that the increasing subdivision and slight rigidity of the parietal area finds its explanation in an unknown function of some structure placed in the underlying large fontanelle.

Of other interesting details it may be mentioned that the dermal cranial roof possesses a deep notch in its lateral margin above that part of the fossa bridgei into which the spiracular canal opens, and, moreover, that both the dermosphenotic and the supraorbital elements seem to be completely reduced.

7) The infraorbital series contains only two elements, viz. the postorbital and the jugal, while both the lacrimal and the antorbital elements are completely reduced. Rostral and premaxillary elements are also lacking, and, as already mentioned, the anterior part of the dermal cranial roof is more or less reduced. From these facts we must conclude that the snout region was protected to a considerable extent by thick skin.

8) The palatoquadrate and its dermal bones, viz. the ectopterygoid and the entopterygoid, together with the maxillary, the preoperculum, and the quadratojugal form a complex palatoquadrate-maxillary apparatus of principally the same type as in typical *Palaeonisciformes*, although somewhat specialised in a Holostean direction. The dermometapterygoid is completely reduced, and either the same is the case with the dermopalatines or these bones are included in the large entopterygoid.

9) The Meckelian cartilage contains a single ossification, which, however, does not occupy the whole structure. On the external face of the jaw we find an angular, a supraangular, and a dentalo-splenial, and on the internal face a prearticular.

The muscle-spaces both of the palatoquadrate maxillary apparatus and of the lower jaw are relatively narrow, which shows that the adductor muscles were weak.

10) The ossifications of the hyoid arch and the dermal bones of the opercular fold differ in no essential respect from those of typical *Palaeo-*

nisciformes. On the lateral face of the dorsal division of the hyomandibula lies a small dermohyal, and perhaps a second dermohyal was situated on the medial face of the ventral division of the hyomandibula.

11) Most of the ossifications of the branchial arches have been identified. There are five arches, the foremost two of which articulated with the neural endocranium in a similar way as in *Pteronisculus* (*Glaucolepis*) and *Acipenser*. The ossifications belonging to the two hindmost arches are developed as fairly extensive plate-like structures.

The basibranchial series contains four ossifications, the hindmost of which is a solid structure of a very characteristic shape and pierced by a paired longitudinal canal. Possibly this hindmost basibranchial ossification, which bears a certain resemblance to the large basibranchial element in the Coelacanths, includes homologues to the hypobranchials of the fourth branchial arch.

12) The sensory canal system of the head differs from the normal Palaeonisciform pattern mainly in two respects, viz. the supraorbital sensory canal ends posteriorly in the centre of radiation of the frontal, and the infraorbital sensory canal traverses a marginal area of the frontal, a course which is most likely caused by the development of the large notch in the lateral margin of the dermal cranial roof above the spiracular division of the fossa bridgei, not by fusion of the frontal with dermosphenotic and intertemporal elements.

13) The well ossified axial skeleton, part of which have been described in fairly great detail by earlier investigators, has been studied in its whole extent. Of specially interesting new details may be mentioned: the presence of small paired supradorsal ossifications in the segments just behind the head; the subdivision, in a single specimen, of the independent ring-like caudal and cranial centra in the middle part of the caudal region into dorsal and ventral half-rings, and the presence of very strong lateral processes on the foremost basidorsal ossifications behind the head. Strong lateral basidorsal processes were also observed in the anterior part of the abdominal region in *Boreosomus*, and it is suggested that similar structures will turn out to exist in a great many other primitive Chondrosteans.

The basidorsal processes, which, of course, cannot be compared to true ribs, are probably homologous with the epineural ossifications which are embedded in the musculature dorsally to the horizontal septum in recent Teleosts.

The question as to whether the ring-like centra in *Australosomus* are of chordal origin, is left open for future research.

14) Each half of the endoskeleton of the shoulder-girdle is ossified into a single piece consisting of a slightly S-bent plate, from which issues a

fairly strong dorsally directed process, which represents a reduced mesocoracoid arch. The plate is pierced by at least one canal for diazonal nerves. The margo radialis is short and almost horizontal.

15) A small clavicle is present both in *Australosomus kochi* and *A. simplex*.

16) The endoskeleton of the pectoral fin contains a single series of radial ossifications which support a very small fin lobe. The fin itself was held horizontally.

17) The endoskeleton of the small pelvic fin consists of a pelvic plate and a series of short radials.

18) The endoskeleton of the dorsal fin contains two series of radial ossifications, that of the anal fin only a single series. The two radial series of the dorsal fin are probably an axonost and a baseost series, respectively, but the possibility also exists that the distal series corresponds to the distal one of the three radial series in *Pteronisculus* (*Glaucolepis*), in which case the proximal series is either an axonost or a baseost series, or possibly a series of fused axonosts and baseosts. The radial series of the anal fin is probably either an axonost series or a series of axonosts and baseosts fused together.

19) In most species within the family *Pholidopleuridae* the transverse scale-rows in the abdominal region and at least in the anterior part of the caudal region contain a few specially high flank scales. In *A. simplex*, however, none of the flank scales are particularly high, and a comparison between the squamations in *A. simplex* and *A. kochi* seems to show that the formation of high flank scales within the genus *Australosomus* is due to fusion of scales within the individual transverse rows.

20) A new diagnosis of the genus *Australosomus* is given.

21) Regarding the relationship between the different genera within the *Pholidopleuridae* only few conclusions can be drawn at present. Each genus seems to be specialised in some respects and primitive in others, so none of them can be ancestral to any of the others. It is probable, therefore, that the four Triassic genera have evolved from still unknown Pholidopleurids of Permian age.

22) The present investigation confirms Stensiö's view, that the *Pholidopleuridae* represent a line of evolution leading from certain primitive *Palaeonisciformes* in a Holostean direction, a line which, however, as far as known at present, became extinct already in the Sub-holostean stage.

23) Some authors have claimed that close relationship existed between the *Pholidopleuridae* and the *Saurichthyidae*; however, the present investigation does not support such claims, and I am more inclined to believe

that Wade was nearer the mark when he explained the existing resemblance between the two families as solely due to their Palaeonisciform origin, though I must add that the Palaeonisciform origin of the *Saurichthyidae* is at present rather a hypothesis than a certainty.

B. *Birgeria.*

1) The material of *Birgeria* brought home from East Greenland comprises a large number of rather small, and a much smaller number of very large individuals, while no medium-sized individuals are known at all. This fact might make us suspect that two species are represented in the material, but as far as can be made out, no structural differences exist between the small and the large specimens. The whole material is therefore referred to the same species, and it is suggested that the lack of medium-sized specimens is due to migratory habits of the form in question.

2) The neural endocranium, even in the large specimens, contains several ossifications, viz. an unpaired occipital ossification, a paired prooticoopistotic, a paired autosphenotic, an unpaired sphenoid, and a paired ethmoidal ossification, separated by more or less extensive unossified areas.

   The shape of the endocranium can be reconstructed in fairly great detail from its ossified areas, and seems to differ essentially from that of the central Palaeonisciform type, for in several respects it bears a much closer resemblance to that of recent sturgeons, thus for instance in the mutual dimensions of the occipital, the otic, and the orbitotemporal region, in the development of the fossa bridgei, and in the lack of an aorta canal. In this connection it is interesting that very large specimens of recent sturgeons show neurocranial ossifications arranged in the main in the same way as those found in *Birgeria.*

   The existing differences between the neural endocrania of *Birgeria* and the recent sturgeons are mainly of such a nature that they may without difficulty be explained as later specialisations within the sturgeon line or lines.

3) The neural endocranium of *Saurichthys*, which, as pointed out by Stensiö, also shows certain tendencies towards a specialisation in a sturgeon direction, seems in most respects to be more specialised than that of *Birgeria*, and judging from our present incomplete knowledge there seem to be no very serious hindrances to considering the neurocranial type represented by *Birgeria* as ancestral to that represented by *Saurichthys.*

4) The parasphenoid extends from beneath the ethmoidal region backward to the posterior end of the occipital region and has thus a much greater length than in normal *Palaeonisciformes*, in which respect it also shows close agreement with that in recent sturgeons. From the corpus issues a single pair of ascending processes, which must be interpreted as mainly posterior ones, though possibly they also include homologues to the anterior ascending processes found in primitive *Palaeonisciformes*. Moreover the parasphenoid is equipped with two median laminae, one issuing in a dorsal direction from the pars anterior, and the other in a ventral direction from the foremost part of the pars posterior.

5) No vomerine bones have been observed.

6) The dermal cranial roof includes one (or two?) pair of extrascapulars, one or two parietals on either side of the mid-line, a paired supratemporal, a paired frontal, a paired supraorbito-dermosphenotico-intertemporal, a paired complex of small supraorbital elements, a paired supraspiracular plate, an unpaired postrostral, and a paired nasal.

The frontals are very large and extend backwards to the extrascapular series separating the right and the left parietal(s). The independent supratemporals extend much farther back than either the parietals or the frontals. The postrostral and the nasals are relatively large. In all these respects *Birgeria* differs from the normal *Palaeonisciformes*, but a sort of connecting link is found in the little known Palaeonisciform genus *Coccocephalus*, the dermal cranial roof of which might be regarded in a certain sense as intermediate between that of *Birgeria* and the normal Palaeonisciform pattern.

On the other hand, the dermal cranial roof of *Birgeria* might be regarded as intermediate between that of *Coccocephalus* and the very peculiar dermal cranial roof of the recent *Polyodon* if we regard the so-called parietal in *Polyodon* as homologous with the posterior part of the long frontal in *Birgeria* and assume that the actual parietals in *Polyodon* are completely reduced.

7) The infraorbital series contains 4–5 postorbitals, a jugal, a lacrimal, and an antorbital. Behind the postorbital part of the series lies a large suborbital complex, the elements of which show an arrangement very different from that in normal *Palaeonisciformes*.

8) The palatoquadrate and its dermal bones, viz. an ectopterygoid, an entopterygoid, a dermometapterygoid, and two dermopalatines, together with the maxillary and the preoperculum form a complex palatoquadrate-maxillary apparatus, which differs mainly from that in normal *Palaeonisciformes* by its greater length. A quadratojugal is possibly included in this complex. The palatoquadrate is only ossified in the quadrate

region, and the quadrate ossification is equipped with a double condyle for the articulation with the lower jaw.

9) The premaxillary is fused with rostral elements to a large unpaired rostro-premaxillary, which is equipped with a strong internal (palatal) lamina.

10) The lower jaw is of normal Palaeonisciform type. The Meckelian cartilage in small as well as in large specimens is ossified only in the articular region, where it shows two facets for articulation with the quadrate and a fairly strong processus retroarticularis.

On the external face of the jaw we find an angular, a supraangular, and a dentalo-splenial, and on the internal face a prearticular. Coronoids were not observed. The angular process described by Stensiö does not exist, but the supraangular is produced into a strong dorsal process, which probably supported a fairly strong processus coronoideus.

11) In the hyoid arch a hyomandibula, a symplectic, a ceratohyal, and a hypohyal were observed. The hyomandibula has no processus opercularis and was not traversed by the truncus hyoideomandibularis, which probably, as in the recent sturgeons, from its place of exit through the cranial wall passed backward and crossed the posterior margin of the bone.

12) The operculum, which is situated above the almost horizontal shank of the preoperculum, is relatively smaller than in normal *Palaeonisciformes*, and a comparison between *Pteronisculus* (*Glaucolepis*), *Coccocephalus*, and *Birgeria* clearly illustrates how the gradual lengthening of the jaws, which results in a more and more oblique suspensorium, causes an increasing reduction in the size of the operculum. In recent sturgeons, as is well known, the operculum is completely reduced.

13) The suboperculum, which is situated behind the ventral shank of the preoperculum and separated from the operculum by an interspace, consists of 4–6 long and narrow rays fused with each other only at their extreme distal ends. Thus it shows a certain resemblance to the suboperculum of *Polyodon*.

14) The branchiostegal series contains about 14 rays, all of which are situated medially to the ventral margin of the lower jaw, and thus separated by an interspace from the suboperculum. The foremost part of the interspace between the right and the left lower jaw is occupiëd by a small unpaired gular plate.

In *Polyodon* the hindmost branchiostegal ray is situated posteriorly to the lower jaw, i. e. in an area corresponding to the gap in *Birgeria* between the branchiostegal series and the suboperculum. The presence of this ray speaks decidedly against considering *Birgeria* as directly ancestral to *Polyodon*.

15) No new observations have been made concerning the structure of the branchial arches.

16) A number of unornamented areas on the dermal cranial roof indicate the presence, in *Birgeria*, of similar nerve-sack areas to those in recent sturgeons. It is suggested that the assumed complete loss of parietals in *Polyodon* is due to the excessive development of the parietal nerve-sack groups in this genus.

17) Apart from the nerve-sack areas the external dermal bones of the head are ornamented with striae or tubercles or both. In certain areas, at any rate, the tubercles did not arise by subdivision of striae, as suggested by Stensiö, but seem rather to be comparable to the small superficial denticles found in the skin above the dermal bones in *Polypterus*, *Lepidosteus*, some *Siluridae*, and the Carboniferous Palaeonisciform *Whiteichthys*.

18) The whole ossified axial skeleton could be investigated in the small specimens, and part of this structure also in the large specimens. On the basis of these investigations new interpretations have been given of some of the axial elements.

In the small specimens the dorsal arcual ossifications are basidorsals, which are paired in the anterior and unpaired in the posterior part of the trunk. In the area between the dorsal fin and the head independent supraneurals are found; quite possibly the distal part of the posterior unpaired basidorsal elements include supraneural components. In the large specimens the basidorsal ossifications in the abdominal region and in at least the foremost part of the caudal region alternate with small interdorsal ossifications. The hypochordal axial ossifications in both small and large specimens are basiventrals, in the caudal region perhaps containing infrahaemal components. The incipient formation of vertebral centres described by Stensiö has most probably no foundation in fact.

Interpreted as above, the axial skeleton of *Birgeria* is developed much as in normal *Palaeonisciformes*, and thus it also agrees in a general respect with that of recent sturgeons.

19) The endoskeleton of the shoulder-girdle contains two smaller ossifications separated by an unossified area, viz. a dorsal, vertically placed, rounded, and a ventral, more oblong, and somewhat S-bent plate. The dorsal ossification, which is pierced by a large foramen for diazonal nerves, corresponds to a middle, and the ventral one to a ventral part of the large endoskeletal ossification in normal *Palaeonisciformes*. The detailed shape of the complete endoskeletal structure cannot be made out on the basis of the ossified areas, however, there can be no doubt that the margo radialis was vertical or nearly so.

20) Apart from the anocleithrum, which has not been observed, the dermal shoulder-girdle contains the same elements as in normal *Palaeonisciformes*. As regards details the series differs from that of normal *Palaeonisciformes* mainly in the relatively greater length of the posttemporal and the supracleithrum, a difference which is due to the extreme lengthening of the gape in *Birgeria*.

21) The endoskeleton of the pectoral fin contains about 10 mainly rod-like ossifications arranged in a single series. The pectoral fin itself was vertically held. In recent sturgeons the pectoral fin is horizontal, so in this respect *Birgeria* seems to be the more advanced; this is another point which speaks against regarding *Birgeria* as directly ancestral to the recent sturgeons.

22) The large pelvic fin is supported by one or two series of radial ossifications articulating with a fairly strong pelvic plate.

23) The endoskeleton of the dorsal fin contains three series of ossifications, viz. an axonost series, a baseost series, and a series of small distal ossifications. The hindmost elements in the axonost series are fused to a large axonost plate.

The endoskeleton of the anal fin contains two series of radial ossifications, viz. a long axonost series extending basally to the whole length of the fin, and a short baseost series wedged in between the posterior third of the axonost series and the fin-base. The hindmost elements in the axonost series are fused to a large axonost plate.

Both in *Pteronisculus* (*Glaucolepis*) and *Boreosomus* the endoskeleton of the dorsal fin in addition to the axonost and the baseost series possesses a series of smaller ossifications comparable to the distal series in *Birgeria*. Probably, therefore, the radial supports of the dorsal fin in primitive Ganoids, as is also the case in higher Actinopterygians, were divided into three segments, and the apparent lack of the distal series in a number of *Palaeonisciformes* may be explained either by their failing ossification or as due to a not sufficiently detailed examination of the forms in question.

An axonost plate comparable to that in the endoskeleton of the dorsal fin in *Birgeria* is known in two normal Palaeonisciform genera, viz. *Pygopterus* and *Pteronisculus* (*Glaucolepis*), and will probably turn out to exist in several other *Palaeonisciformes*, also.

The development of the endoskeleton of the anal fin in *Birgeria* with its partly reduced baseost series might, as pointed out by Aldinger, be regarded as intermediate between certain *Palaeonisciformes* with two and others with only one series of anal radial ossifications. In accordance with this view Aldinger maintains that the only series of radial ossifications in the endoskeleton of the anal fin in *Pygopterus* is an axonost

series. If this is correct, the baseost series is probably also completely reduced in *Pteronisculus* (*Glaucolepis*), and thus the series of small distal radial ossifications in the endoskeleton of the anal fin in this genus must be analogous to the distal series in the endoskeleton of the dorsal fin. Thus here we have evidence for the assumption that in the *Palaeonisciformes* the endoskeletal supports of the anal fin, like those of the dorsal fin, were originally divided into three segments.

If Aldinger is right in his interpretations, there is a tendency both in *Pygopterus* and *Pteronisculus* towards the formation of an anal axonost plate comparable to that of *Birgeria*.

The unpaired fins in *Birgeria* agree very closely in their shape and structure with those in the recent *Polyodon*. As regards the endoskeleton of the dorsal and anal fins *Polyodon* differs from *Birgeria* in its smaller number of radials, in lacking compound axonost plates, and in possessing a complete row of anal baseosts. In view of the last-mentioned point it is quite out of the question to consider *Birgeria* as directly ancestral to *Polyodon*.

24) The arrangement of the scales on the caudal pedicle and on the body axis of the caudal fin in *Birgeria* is principally the same as in *Polyodon*.

25) A new diagnosis of the genus *Birgeria* is given.

Of the only three species of *Birgeria* investigated in some detail no certain conclusions regarding the phylogenetic structure of the genus can be drawn, though it seems probable that *B. mougeoti* is in certain respects more specialised than *B. groenlandica*.

26) As already suggested by various authors, *Birgeria* undoubtedly represents a separate family. The existing diagnosis of this family has been altered in accordance with the results of the present investigation of *Birgeria groenlandica*.

A number of Palaeoniscid features in *Birgeria* decidedly point to a not too remote relationship between the *Birgeriidae* Berg and the *Palaeoniscidae* Berg. The genus *Coccocephalus* possibly represents a sort of connecting link between the two families.

In many respects *Birgeria* shows tendencies to a development towards the recent sturgeons, and among these especially towards *Polyodon*, but certain features in *Birgeria* make it evident that this genus cannot be regarded as a direct ancestor of *Polyodon*. However, according to our present inclompete knowledge it is not impossible that *Coccocephalus* was the common ancestor of *Birgeria* and *Polyodon*.

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Plate 1.

Australosomus kochi (Stensiö).

Figs 1 and 2. Neural endocranium with greater part of dermal cranial roof in dorsal and lateral view respectively. Specimen no. 407 (the specimen investigated by serial grinding). 4 ×. Alcohol.

Fig. 3. Fish lacking the posterior part of the caudal region. To a large extent preserved as impression only. Specimen no. 406. C. 1.5 ×. Dry.

Fig. 4. Incomplete head in lateral view. Specimen no. 401. 4 ×. Alcohol.

A, anal fin; *Ax*, element in the proximal series of ossifications in endoskeleton of dorsal fin; *Cl*, cleithrum; *D*, dorsal fin; *De. spl*, dentalo-splenial; *Ext*, extrascapular; *Fr*, frontal; *Hm*, hyomandibula; *Md*, mandible; *Mx*, maxillary; *Na*, nasal; *Op*, operculum; *P*, pelvic fin; Pa_1, Pa_2, anterior and posterior parietal; *Pq*, palatoquadrate; *Ra. a*, element in the single series of ossifications in endoskeleton of anal fin; *Scl*, supracleithrum; *Sclr*, sclerotic ring; *Sop*, suboperculum; *St. it*, supratemporo-intertemporal; *c. v*, brain cavity; *eth*, ethmoidal region of neural endocranium; fb_1, spiracular division of fossa bridgei; *fe. en*, fenestra endonarina communis; *ifc*, infraorbital sensory canal; *l. opt*, division of the cavum cerebrale cranii for the lobus opticus; *mdc*, mandibular sensory canal; *n. c*, nasal cavity; *n.* fb_1, notch in the lateral margin of the dermal cranial roof above the spiracular division of the fossa bridgei; *orb*, orbit; *ot*, otic region of neural endocranium; *p. lig. l*, lateral pit for ligaments connecting the palatoquadrate and the neural endocranium; *re. myel*, division of the cavum cerebrale cranii for the antero-lateral part of the myelencephalon; *sacc*, division of the labyrinth cavity for the sacculus; *soc*, supraorbital sensory canal; *tel. dic*, division of the cavum cerebrale cranii for the tel- and diencephalon; *I*, canal for the nervus olfactorius.

Nordisk Kunst- og Lystryk

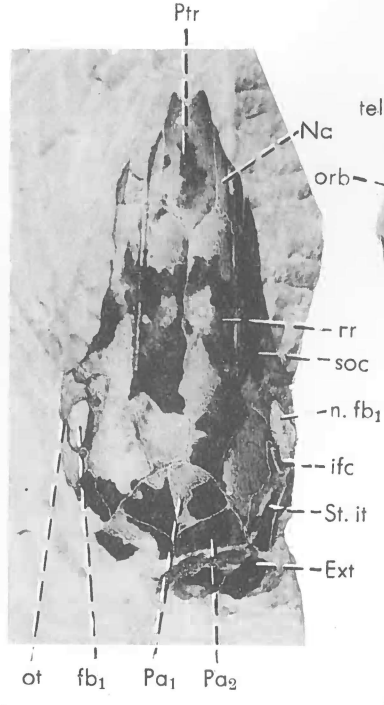


Fig. 1

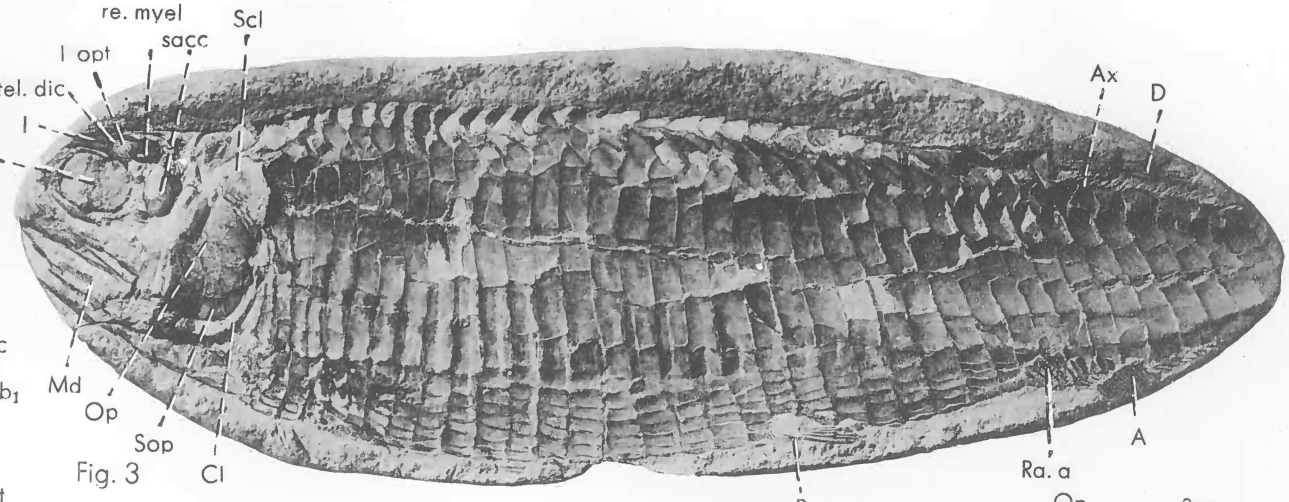


Fig. 3

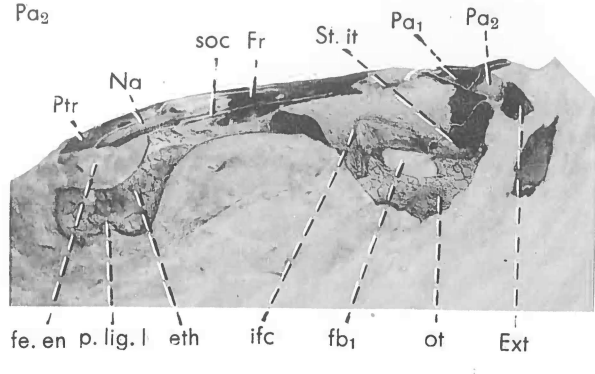


Fig. 2

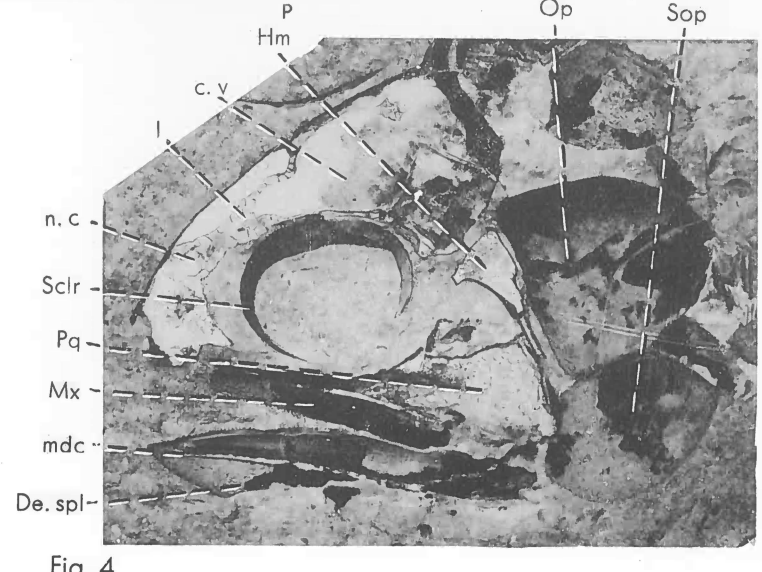


Fig. 4

Plate 2.

Australosomus kochi (Stensiö).

Figs 1 and 2. Head and foremost part of trunk (in counterpart). Showing parts of the neural endocranium, elements of the visceral endoskeleton, and foremost part of the axial skeleton. Specimen no. 548. 3 ×. Xylol.

Bb. o. p, posterior basibranchial ossification; *Br. o*, ossifications in the branchial arches; *Bv + Iv*, fused basi- and interventral; *Cbr*, ceratobranchial; *Cbr. IV*, ceratobranchial IV; *Chy*, ceratohyal ossification; *Cl*, cleithrum; $Cn_2 + Cn_1$, fused caudal and cranial centrum; *De. spl.* dentalo-splenial; *Ebr IV*, epibranchial IV; *Eg*, endoskeletal shoulder-girdle ossification; *Enpt*, entopterygoid; *Id*, interdorsal; *Mx*, maxillary; *Pec*, pectoral fin; *Rbr*, branchiostegal ray; *Sop*, suboperculum; *ad*, canal for an artery; *aort*, aorta canal; *cn*, space for the notochord; *c. sem. ant*, *c. sem. post*, divisions of the labyrinth cavity for the canalis semicircularis anterior and the canalis semicircularis posterior respectively; *f. m*, foramen magnum; $font_2$, posterior dorsal fontanelle; *f. ot. v*, fissura oticalis ventralis; *l. opt*, division of the cavum cerebrale cranii for the lobus opticus; *msc*, incomplete mesocoracoid arch; *my*, posterior myodome; *n. c*, nasal cavity; *orb*, orbit; *p. lig. m*, medial pit for ligaments connecting the palatoquadrate and the neural endocranium; *re. myel*, division of the cavum cerebrale cranii for the antero-lateral part of the myelencephalon; *re. pmd*, postero-dorso-medial recess of the nasal cavity; *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; *I*, canal for the nervus olfactorius; *V*, trigeminus canal; *X*, canal for the nervus vagus.

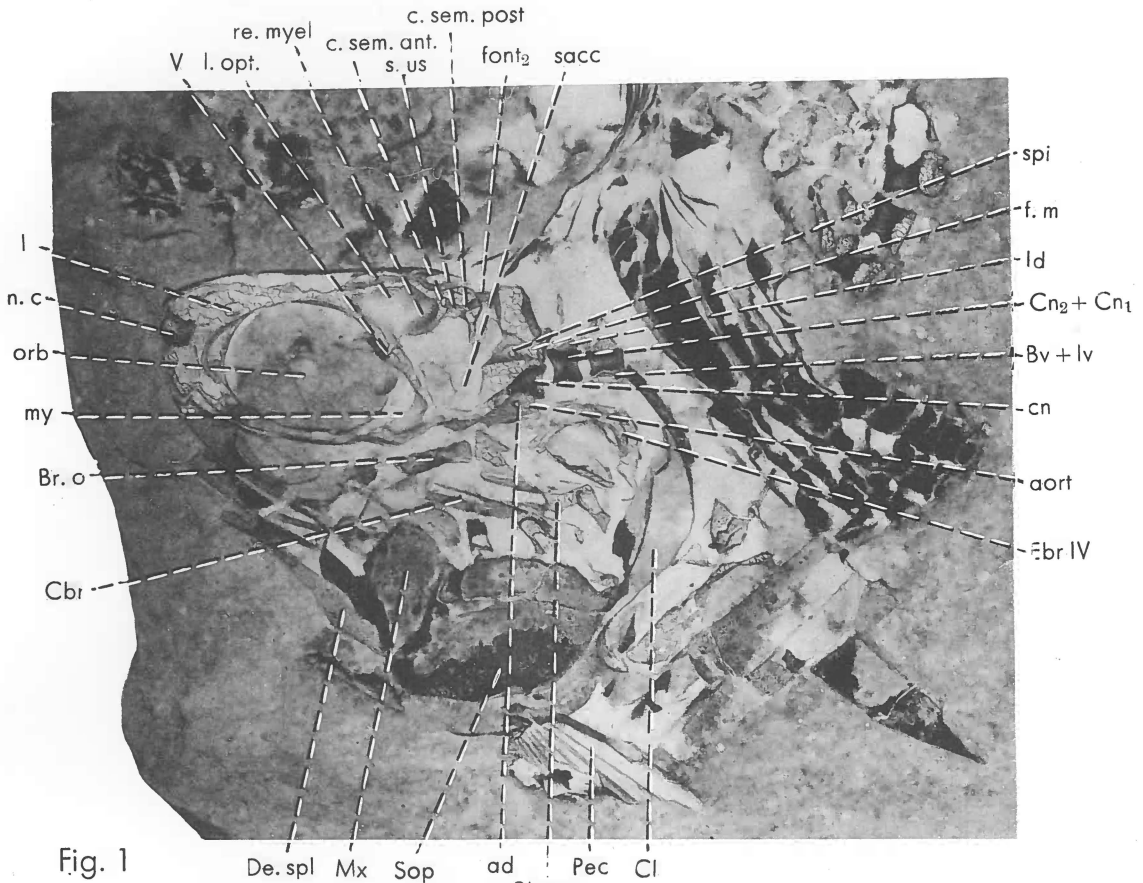


Fig. 1

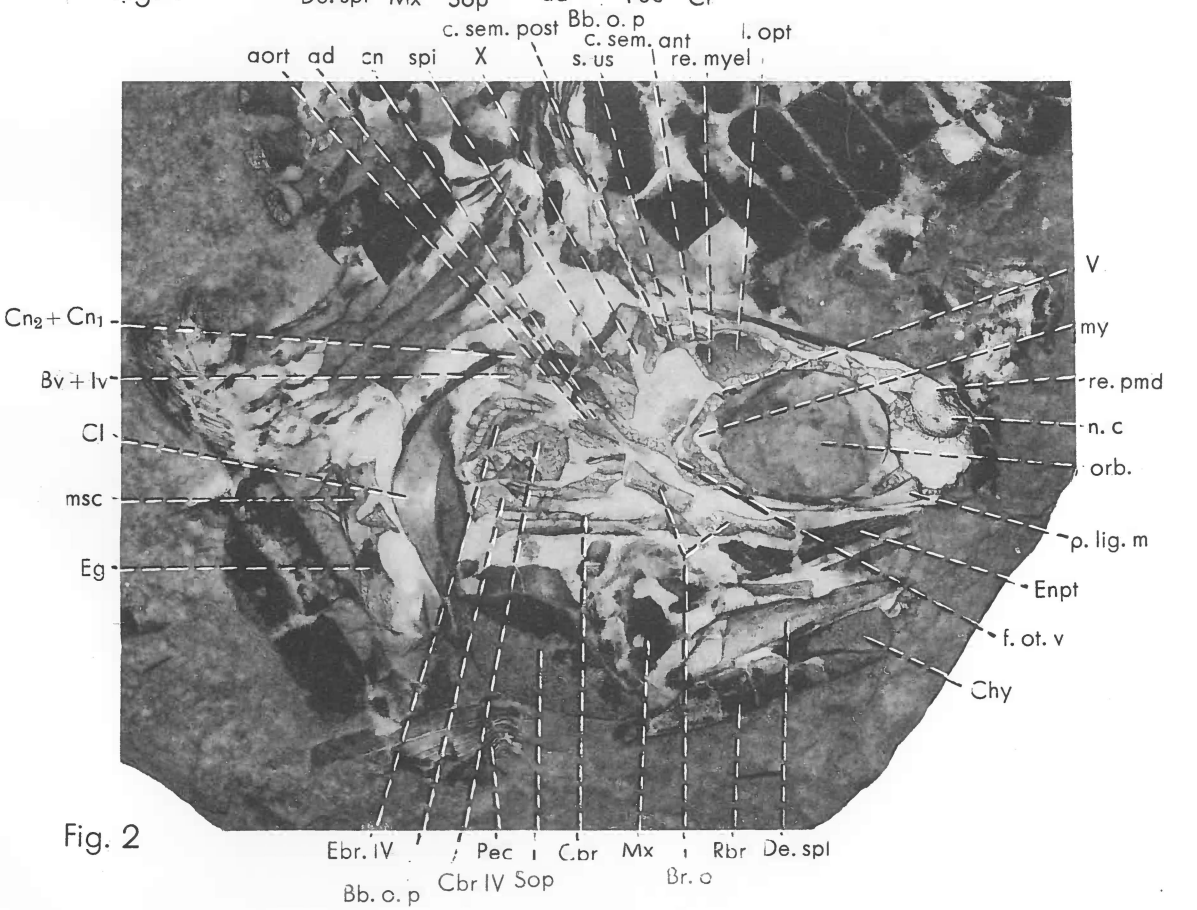


Fig. 2

Nordisk Kunst- og Lystryk

Plate 3.

Australosomus kochi (Stensiö).

Figs. 1 and 2. Head and foremost part of trunk (in counterpart). Showing much of the visceral endoskeleton. Specimen no. 405. 4 ×. Oil of aniseed.

Ang, angular; *Chy*$_1$, ceratohyal ossification; *Cbr I–II*, ceratobranchials I–II; *Cl*, cleithrum; *Co I*, foremost basibranchial ossification; *De. spl*, dentalo-splenial; *Ebr I–III*, epibranchials I–III; *Hbr I–II*, hypobranchials I–II; *Hhy*, hypohyal; *Hm*, hyomandibula; *Mk*-Meckelian bone; *Op*, operculum; *Pr. art*, prearticular; *Qu*, pars quadrati; *Rbr*, branchio, stegal ray; *Sop*, suboperculum; *Sympl*, symplectic; *bsph*, pars basisphenoidea; *fe. opt*, fenestra optica; *f. ot. occ*, fissura otico-occipitalis; *l. opt*, division of the cavum cerebrale cranii for the lobus opticus; *mdc*, mandibular sensory canal; *my*, posterior myodome; *n. c*, nasal cavity; *orb*, orbit; *p. lig. m*, medial pit for ligaments connecting the palato-quadrate and the neural endocranium; *re. myel*, division of the cavum cerebrale cranii for the antero-lateral part of the myelencephalon; *sacc*, division of the labyrinth cavity for the sacculus; *X*, canal for the nervus vagus.

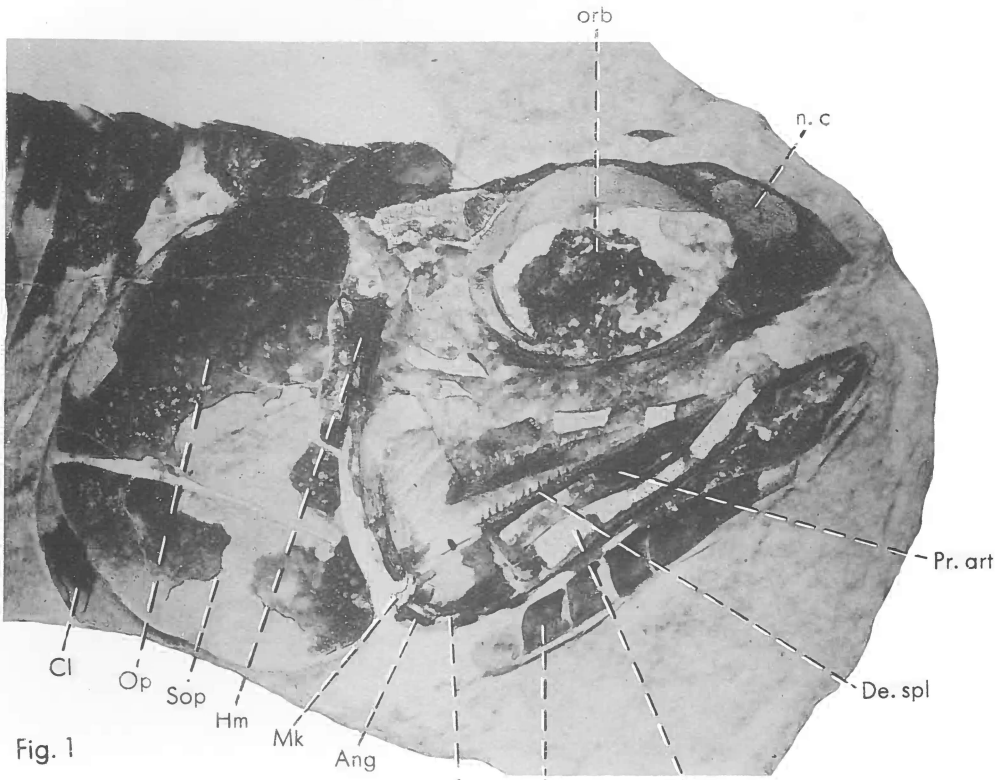


Fig. 1

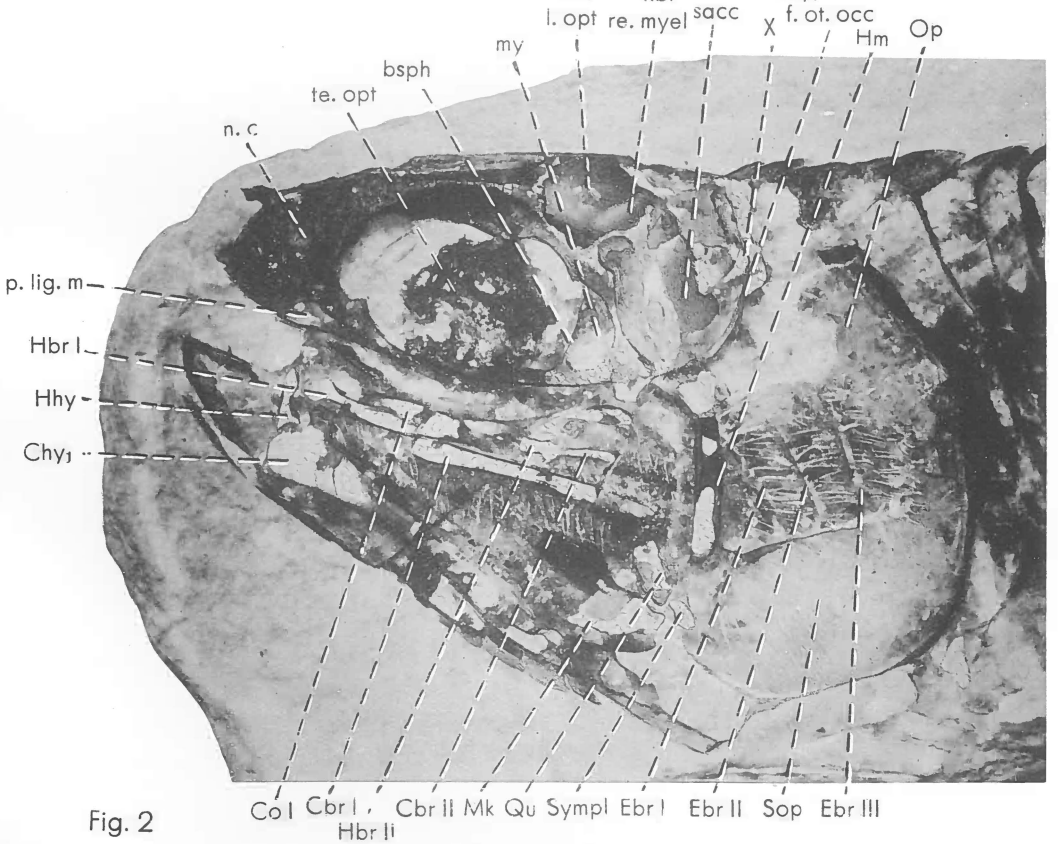


Fig. 2

Nordisk Kunst- og Lystryk

Plate 4.

Australosomus kochi (Stensiö).

Figs. 1 and 2. Head and foremost part of trunk in dorsal and in lateral view respectively Specimen no. 403. 4 ×. Oil of aniseed.

Cl, cleithrum; *Ext*, extrascapular; *Fr*, frontal; *Hm. a*, dermohyal (accessory hyomandibula); *Ju*, jugal; *Mx*, maxillary; *Op*, operculum; Pa_1, Pa_2, anterior and posterior parietal; *Pop*, preoperculum; *Pt*, posttemporal; *Ptr*, postrostral; *Scl*, supracleithrum; *Sop*, suboperculum; *St. it*, supratemporo-intertemporal; *eth*, ethmoidal region of neural endocranium; *ifc*, infraorbital sensory canal; *l c*, main lateral line; *n.* fb_1, notch in the lateral margin of the dermal cranial roof above the spiracular division of the fossa bridgei; *orb*, orbit; *ot*, otic region of neural endocranium; *poc*, preopercular sensory canal; *s. com*, supratemporal commissure; *soc*, supraorbital sensory canal.

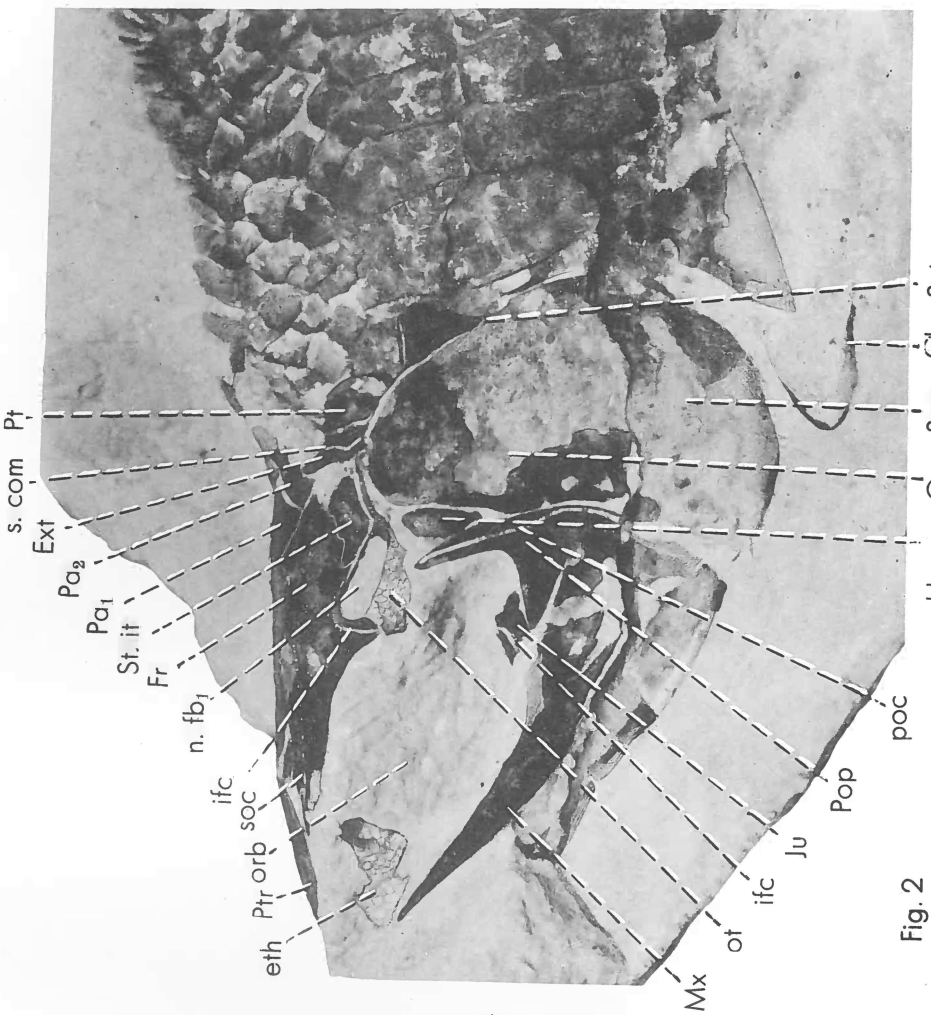

Pt
s. com
Ext
Pa2
Pa1
St. it
Fr
n. fb1
ifc
soc
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eth
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ifc
Ju
Pop
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Hm. a
Op
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Cl
Scl

Fig. 2

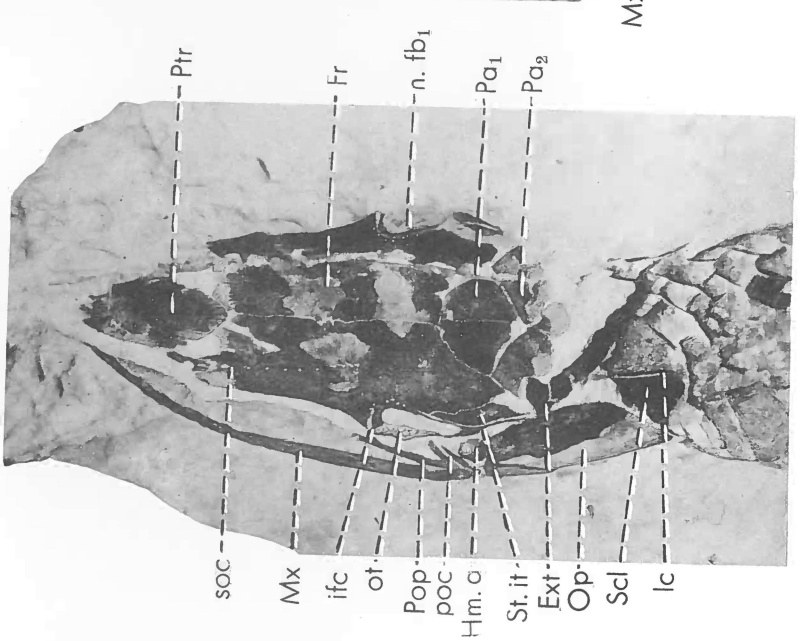

Ptr
Fr
n. fb1
Pa1
Pa2
soc
Mx
ifc
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Hm. a
St. it
Ext
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Scl
Ic

Fig. 1

Plate 5.

Fig. 1. *Australosomus kochi* (Stensiö). Head and anterior part of trunk in lateral view. Specimen no. 449. 4 ×. Dry.

Fig. 2. *Australosomus pholidopleuroides* n. sp. Impressions of head and anterior part of trunk. Specimen no. 445 (holotype). 2.5 ×. Dry.

Cl, cleithrum; *De spl*, dentalo-splenial; *Ext*, extrascapular; *Fr*, frontal; *Hm*, hyomandibula; *Ju*, jugal; *Mx*, maxillary; *Op*, operculum; *Pa. c*, parietal complex; *Pec*, pectoral fin; *Pt*, posttemporal; *Scl*, supracleithrum; *Sclr*, sclerotic ring; *Sop*, suboperculum; *St. it*, supratemporo-intertemporal; *ap*, anterior pit-line; *dic*, division of the cavum cerebrale cranii for the diencephalon; *l. opt*, division of the cavum cerebrale cranii for the lobus opticus; *re. myel*, division of the cavum cerebrale cranii for the antero-lateral part of the myelencephalon; *sacc*, division of the labyrinth cavity for the sacculus; *soc*, supraorbital sensory canal; *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; *V*, trigeminus canal; *VII*, facialis canal.

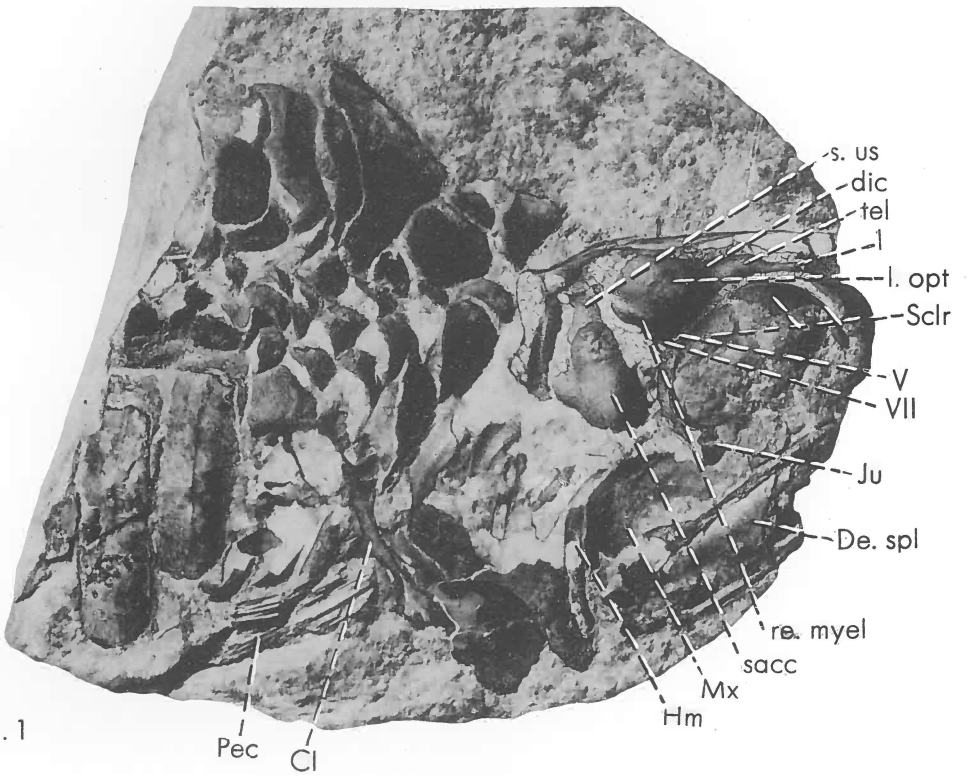


Fig. 1

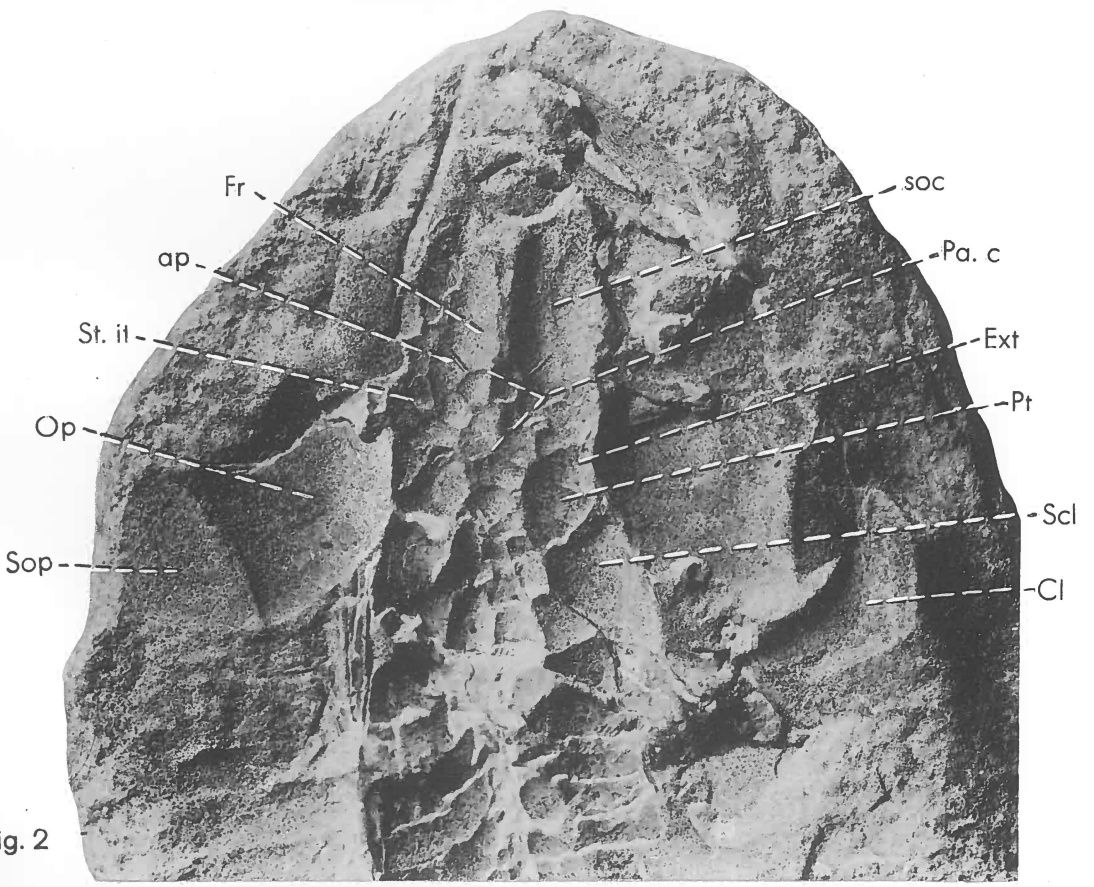


Fig. 2

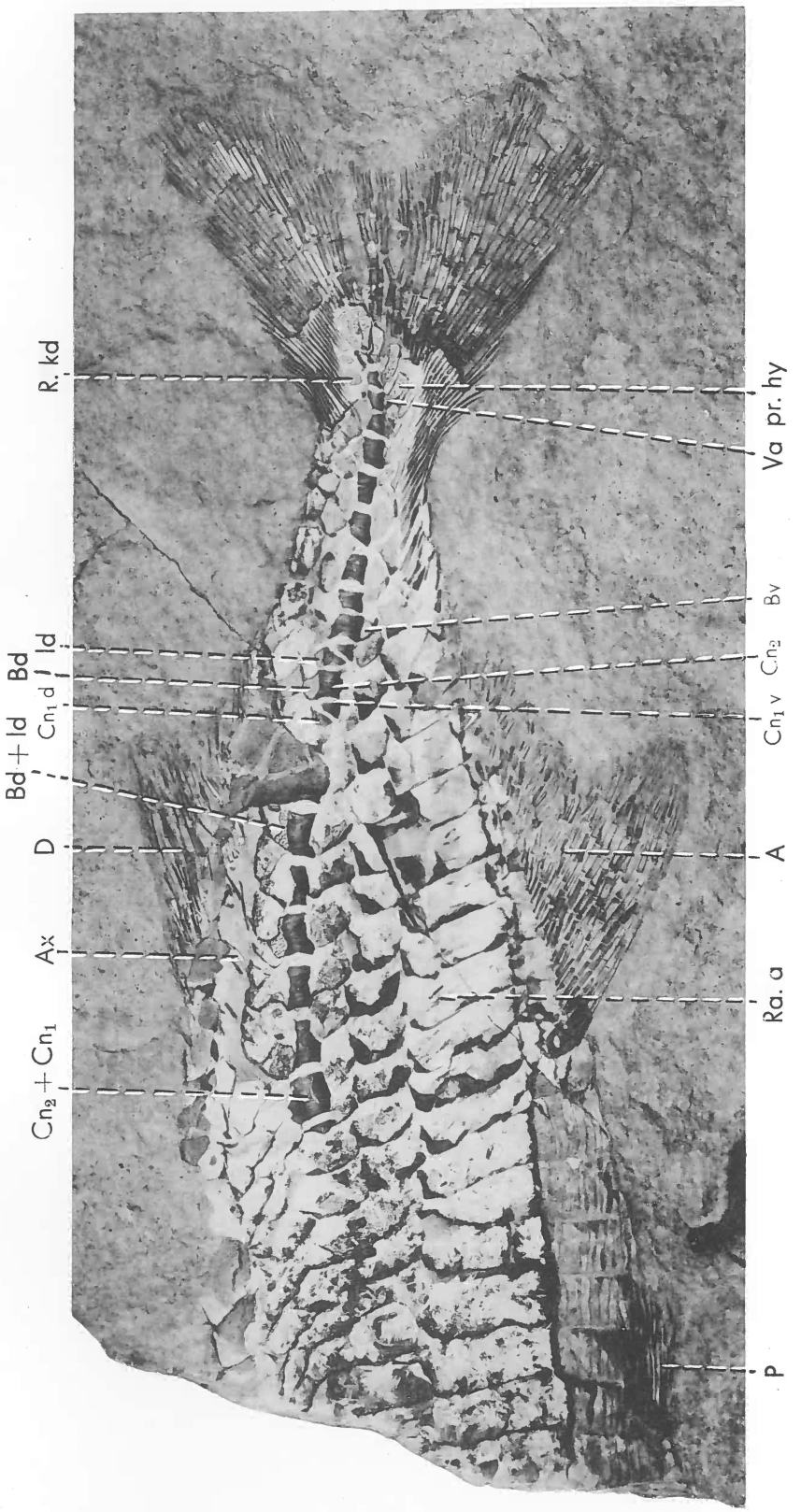
Nordisk Kunst- og Lystryk

Plate 6.

Australosomus kochi (Stensiö).

Posterior part of trunk. Showing much of the axial skeleton. Specimen no. 446. 3 ×. Alcohol.

A, anal fin; *Ax*, element in the proximal series of ossifications in endoskeleton of dorsal fin; *Bd*, basidorsal; *Bd* + *Id*, fused basi- and interdorsal; *Bv*, basiventral; Cn_1d, Cn_1v, dorsal and ventral half respectively of cranial centrum; Cn_2, caudal centrum; $Cn_2 + Cn_1$, fused caudal and cranial centrum; *D*, dorsal fin; *Id*, interdorsal; *P*, pelvic fin; *Ra. a*, element in the single series of ossifications in endoskeleton of anal fin; *R. kd*, epichordal radial ossification in endoskeleton of dorsal fin; *Va*, arcual division of hypochordal ossification in body axis of caudal fin; *pr. hy*, hypural process.



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Plate 7.

Australosomus kochi (Stensiö).

Greater part of trunk. Showing much of the axial skeleton. Specimen no. 404. 4 ×. Xylol.

Bd, basidorsal; *Bv* + *Iv*, fused basi- and interventral; Cn_2 + Cn_1, fused caudal and cranial centrum; *D*, dorsal fin; *Id*, interdorsal; *Va*; arcual division of hypochordal ossification in body axis of caudal fin; *lc*, main lateral line; *pr. hy*, hypural process.

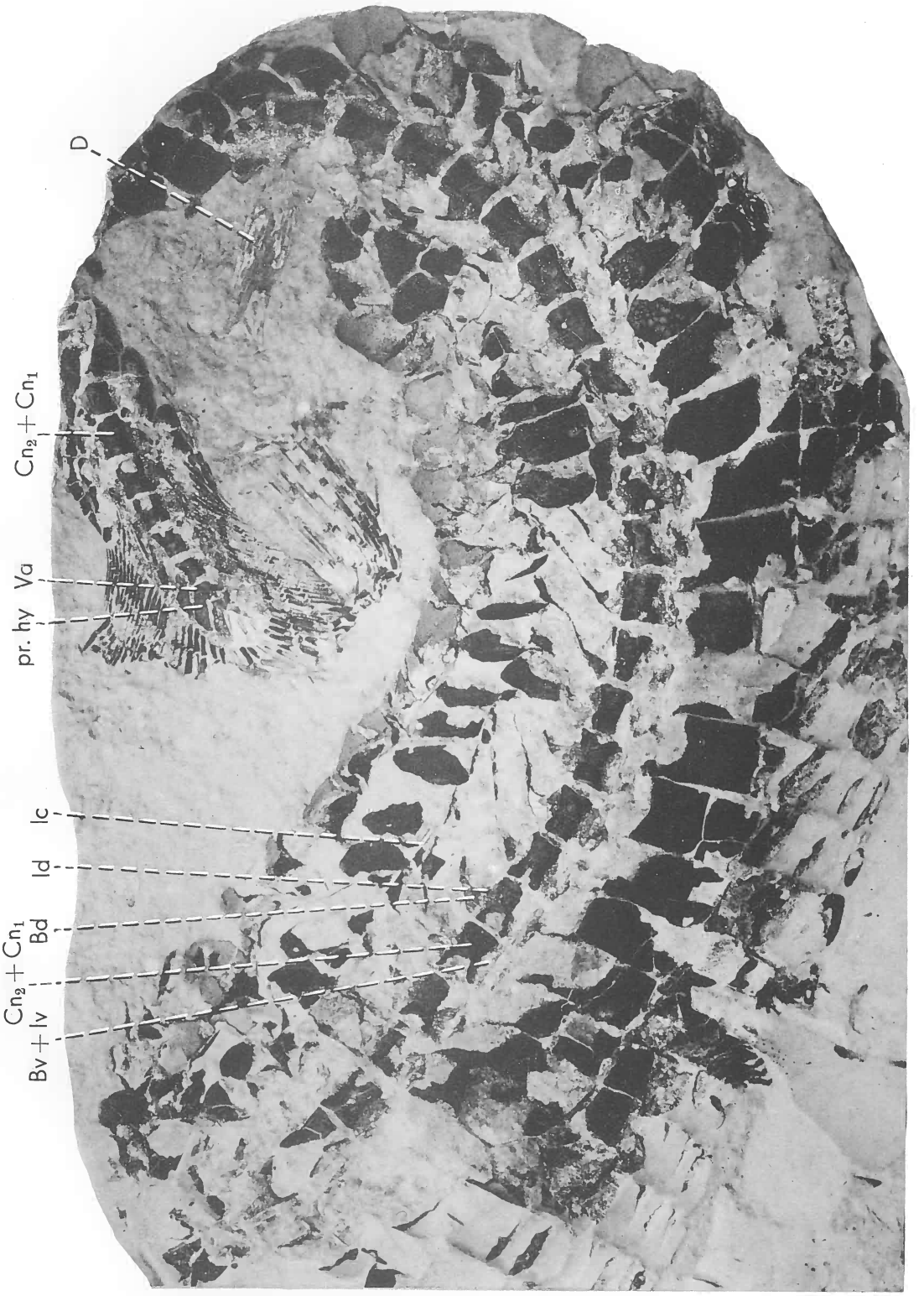
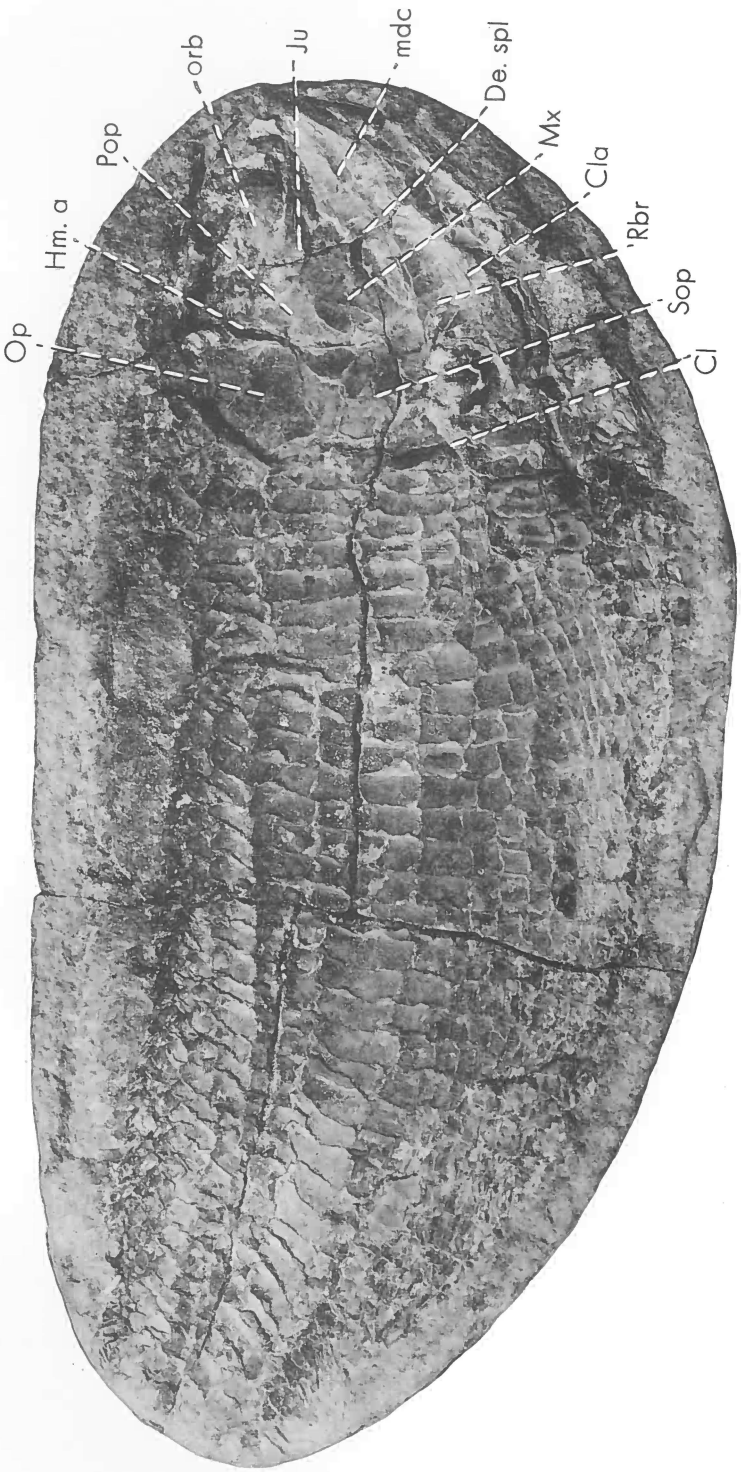

D
Cn2 + Cn1
pr. hy
Va
Ic
Id
Bd
Cn2 + Cn1
Iv
Bv

Plate 8.

Australosomus simplex n. sp.

Fish lacking the posterior part of the caudal region. Specimen no. 568 (holotype). 1.5 ×. Dry.

Cl, cleithrum; *Cla*, clavicle; *De. spl*, dentalo-splenial; *Hm. a*, dermohyal (accessory hyomandibula); *Ju*, jugal; *Mx*, maxillary; *Op*, operculum; *Pop*, preoperculum; *Rbr*, branchiostegal ray; *Sop*, suboperculum; *mdc*, mandibular sensory canal; *orb*, orbit.



Nordisk Kunst- og Lystryk

Plate 9.

Australosomus simplex n. sp.

Incomplete specimen. Showing squamation of dorsal part of trunk. Specimen no. 570
2 × Alcohol.

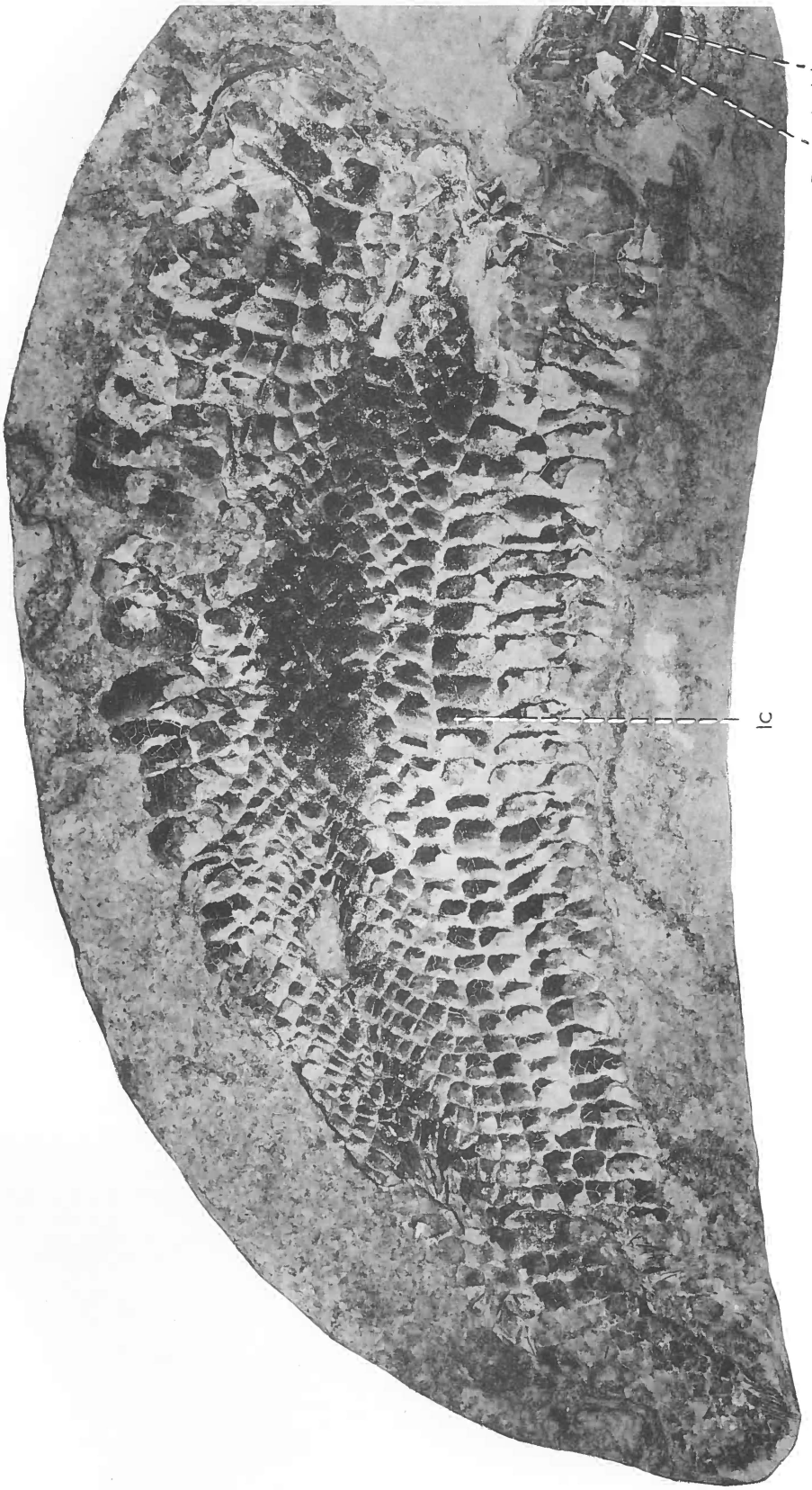
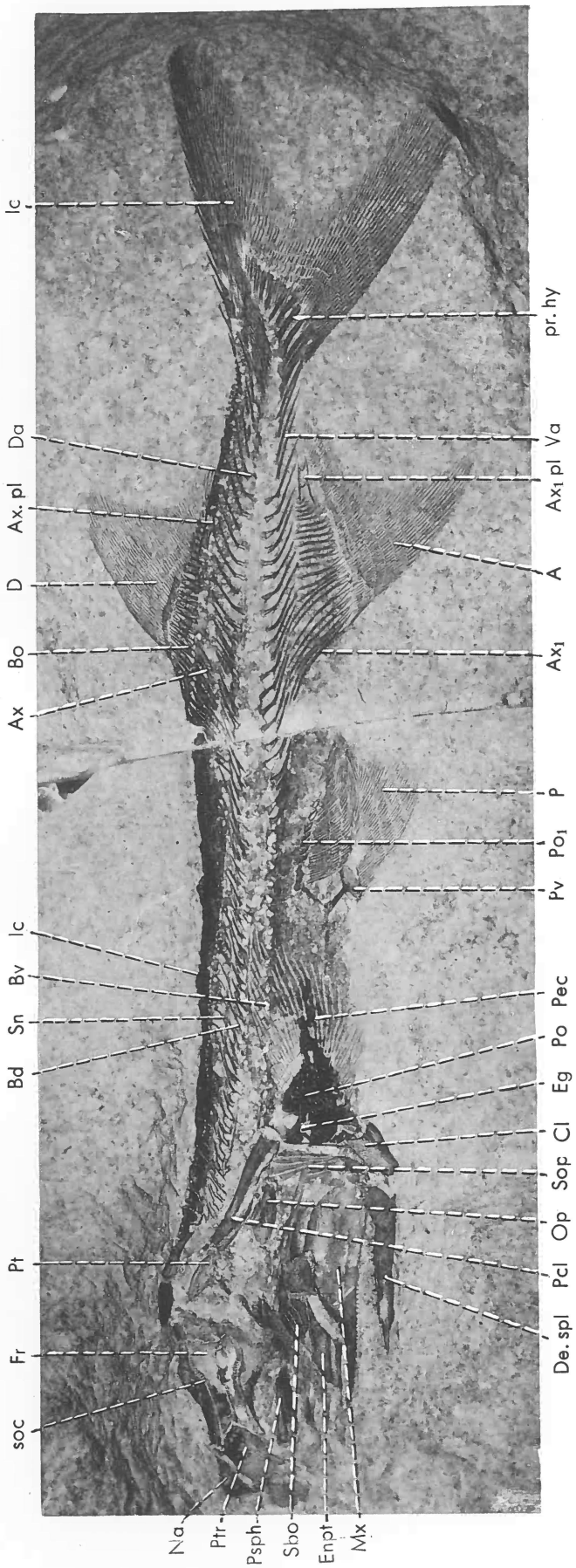

Mx
De. spl
Ic

Plate 10.

Birgeria groenlandica Stensiö.

Almost complete fish. Specimen no. 661. 1.5 ×. Xylol.

A, anal fin; *Ax*, axonost in endoskeleton of dorsal fin; Ax_1, axonost in endoskeleton of anal fin; *Ax. pl*, axonost plate in endoskeleton of dorsal fin; Ax_1pl, axonost plate in endoskeleton of anal fin; *Bd*, basidorsal; *Bv*, basiventral; *Cl*, cleithrum; *D*, dorsal fin; *Da*, dorsal arcual ossification in caudal region; *De. spl*, dentalo-splenial; *Eg*, ossification in endoskeleton of shoulder-girdle; *Enpt*, entopterygoid; *Fr*, frontal; *Mx*, maxillary; *Na*, nasal; *Op*, operculum; *P*, pelvic fin; *Pcl* (error for *Scl*), supracleithrum; *Pec*, pectoral fin; *Po*, radial ossification in endoskeleton of pectoral fin; Po_1, radial ossification in endoskeleton of pelvic fin; *Psph*, parasphenoid; *Pt*, posttemporal; *Ptr*, postrostral; *Pv*, pelvic plate; *Sbo*, suborbitals; *Sn*, supraneural; *Sop*, suboperculum; *Va*, ventral arcual ossification in caudal region; *lc*, main lateral line; *pr. hy*, hypural process.



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Plate 11.

Birgeria groenlandica Stensiö.

Neural endocranium with remnants of dermal bones of the head. Specimen no. 652 (same specimen as shown in pl. 12, fig. 1 and pl. 13, fig. 1). C. 1.1 ×. Dry.

Fig. 1. Posterior part of endocranium with remnants of dermal bones in dorsal view.

Fig. 2. Anterior part of endocranium with remnants of dermal bones in lateral view.

Fig. 3. Posterior part of endocranium in lateral view.

Ant, antorbital; *Ausph*, autosphenotic; *Fr*, frontal; *Na*, nasal; *Occ*, occipital ossification; *Ot*, prootico-opistotic; *Ptr*, postrostral; *R. pmx*, rostro-premaxillary; *Sclr*, sclerotic ring; *Sph*, sphenoid; *Supbr I*, suprapharyngobranchial I; *art. pq. a*, articular process for the pars autopalatina palatoquadrati; *art. sup. I*, articular process for suprapharyngobranchial I; *cn*, space for the notochord; *cr. o*, crista occipitalis; *fb*, fossa bridgei; *f. hm*, articular facet for the hyomandibula; *ifc*, infraorbital sensory canal; *ophth. lat*?, canal possibly lodging the ramus ophthalmicus lateralis; *pr.* asc_2, processus ascendens posterior; *ram. dors*, canals for branches of the ramus ophthalmicus lateralis, the ramus ophthalmicus superficialis trigemini, and vessels; *soc*, supraorbital sensory canal; *spic*, spiracular canal; *t*, canal perhaps for a vessel; *w. pn*, postnasal wall; *IV*?, canal perhaps for the nervus trochlearis; *IX*, notch for the nervus glossopharyngeus; IXd_2, canal for a supratemporal branch of the nervus glossopharyngeus; *X*, notch for the nervus vagus.

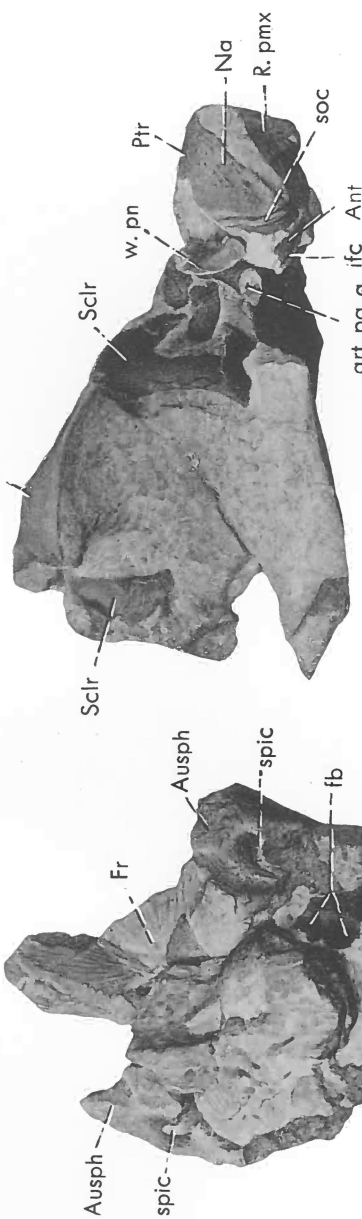


Fig. 2

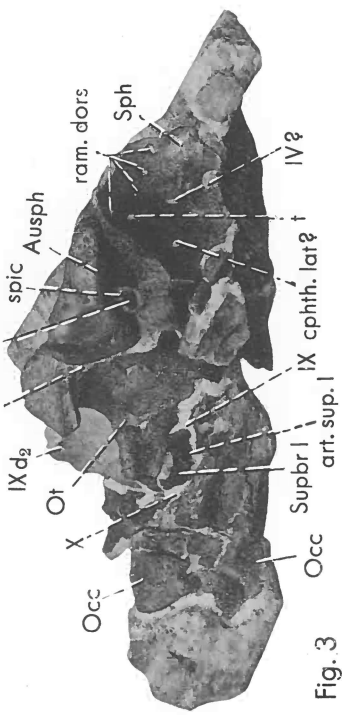


Fig. 3

Fig. 1

Plate 12.

Birgeria groenlandica Stensiö.

Fig. 1. Neural endocranium with remnants of dermal bones in ventro-lateral view. Specimen no. 652 (same specimen as shown in pl 11 and in pl 13, fig. 1). C. 1.1 ×. Dry.

Fig. 2. Incomplete and strongly compressed head. Specimen no. 663. C. 2.2 ×. Dry.

Ang, angular; *Ausph*, autosphenotic; *De. spl*, dentalo-splenial; *Dmptg*, dermometapterygoid; Dpl_2, posterior dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Eth*, ethmoidal ossification; *Fr*, frontal; *Hm*, hyomandibula; *Mk*, articular ossification; *Mx*, maxillary; *Occ*, occipital ossification; *Psph*, parasphenoid; *Sang*, supraangular; *Sbo*, suborbital; *Sclr*, sclerotic ring; *Sph*, sphenoid; *a. car. int*, canal for the arteria carotis interna; *art. sup. I*, articular process for suprapharyngobranchial I; *bsph*, pars basisphenoidea; *fe. opt*, fenestra optica; *pr.* asc_2, processus ascendens posterior; *ri. psph*, parasphenoid ridge; *s. dmptg*, groove on the medial face of the dermometapterygoid; *s. hm*, groove for the truncus hyoideomandibularis; *soc*, supraorbital sensory canal; *w. pn*, postnasal wall; *II*, opening for the nervi optici; *III*, canal for the nervus oculomotorius; *IX*, notch for the nervus glossopharyngeus; *X*, notch for the nervus vagus.

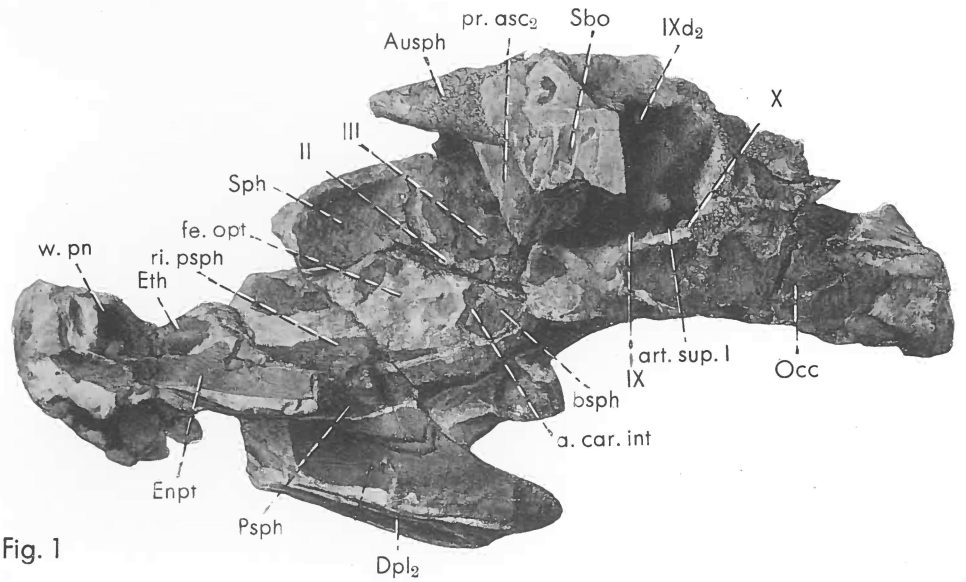

pr. asc2
Sbo
IXd2
Ausph
X
III
II
Sph
fe. opt
w. pn
ri. psph
Eth
art. sup. I
IX
Occ
bsph
a. car. int
Enpt
Psph
Dpl2

Fig. 1

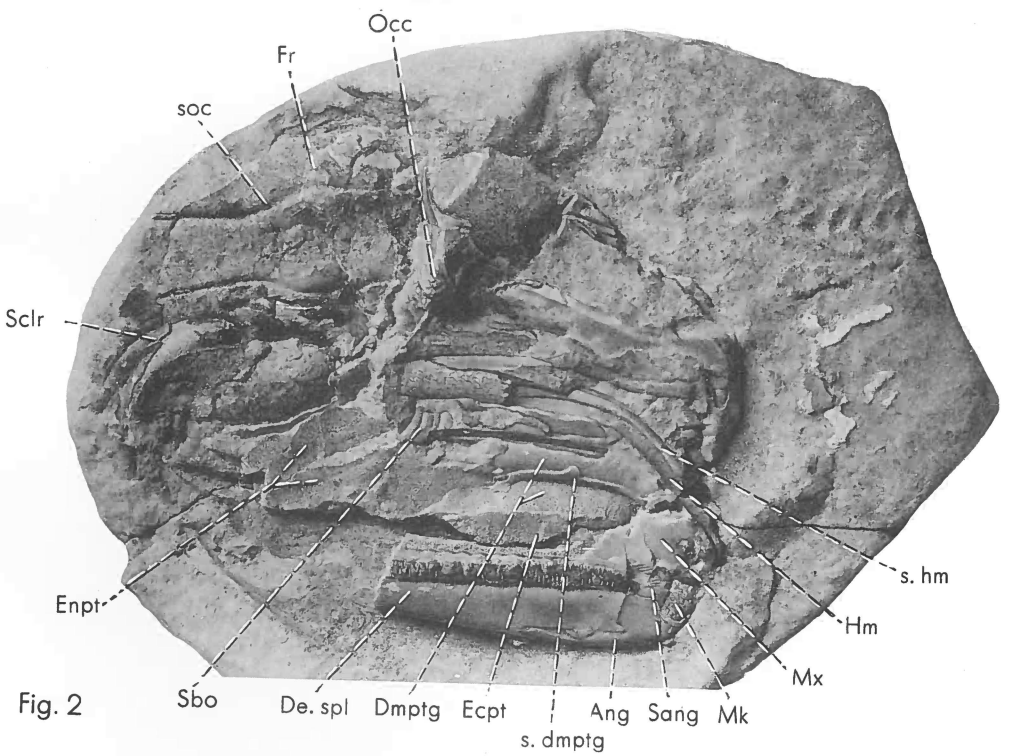

Occ
Fr
soc
Sclr
s. hm
Hm
Enpt
Mx
Sbo
De. spl
Dmptg
Ecpt
Ang
Sang
Mk
s. dmptg

Fig. 2

Plate 13.

Birgeria groenlandica Stensiö.

Fig. 1. Posterior part of neural endocranium in ventral view. Specimen no. 652, (same specimen as shown in pl. 11 and pl. 12, fig. 1). C. 1.1 ×. Dry.
Fig. 2. Posterior part of caudal region. Specimen no. 662. 1.5 ×. Xylol.

A, anal fin; *Ausph*, autosphenotic; *Ax*, axonost in endoskeleton of dorsal fin; Ax_1, axonost in endoskeleton of anal fin; *Ax. pl*, axonost plate in endoskeleton of dorsal fin; Ax_1pl, axonost plate in endoskeleton of anal fin; *Bo*, baseost in endoskeleton of dorsal fin; Bo_1, baseost in endoskeleton of anal fin; *D*, dorsal fin; *Da*, dorsal arcual ossification in caudal region; *Occ*, occipital ossification; *Ot*, prootico-opistotic; *Sbo*, suborbital; *Sph*, sphenoid; *Supbr. I*, suprapharyngobranchial I; *Va*, ventral arcual ossification in caudal region; *a. car. int*, canal for the arteria carotis interna; *f. hm*, articular facet for the hyomandibula; *ophth. lat*?, canal possibly lodging the ramus ophthalmicus lateralis; *pr.* asc_2, processus ascendens posterior; *pr. hy*, hypural process; *ram. dors*, canals for branches of the ramus ophthalmicus lateralis, the ramus ophthalmicus superficialis trigemini, and vessels; *re. inf.* infundibular recess; *spic*, spiracular canal; *t*, canal perhaps for a vessel; *II*, opening for the nervi optici; *III*, canal for the nervus oculomotorius; *IV*?, canal perhaps for the nervus trochlearis; *IX*, canal for the nervus glossopharyngeus.

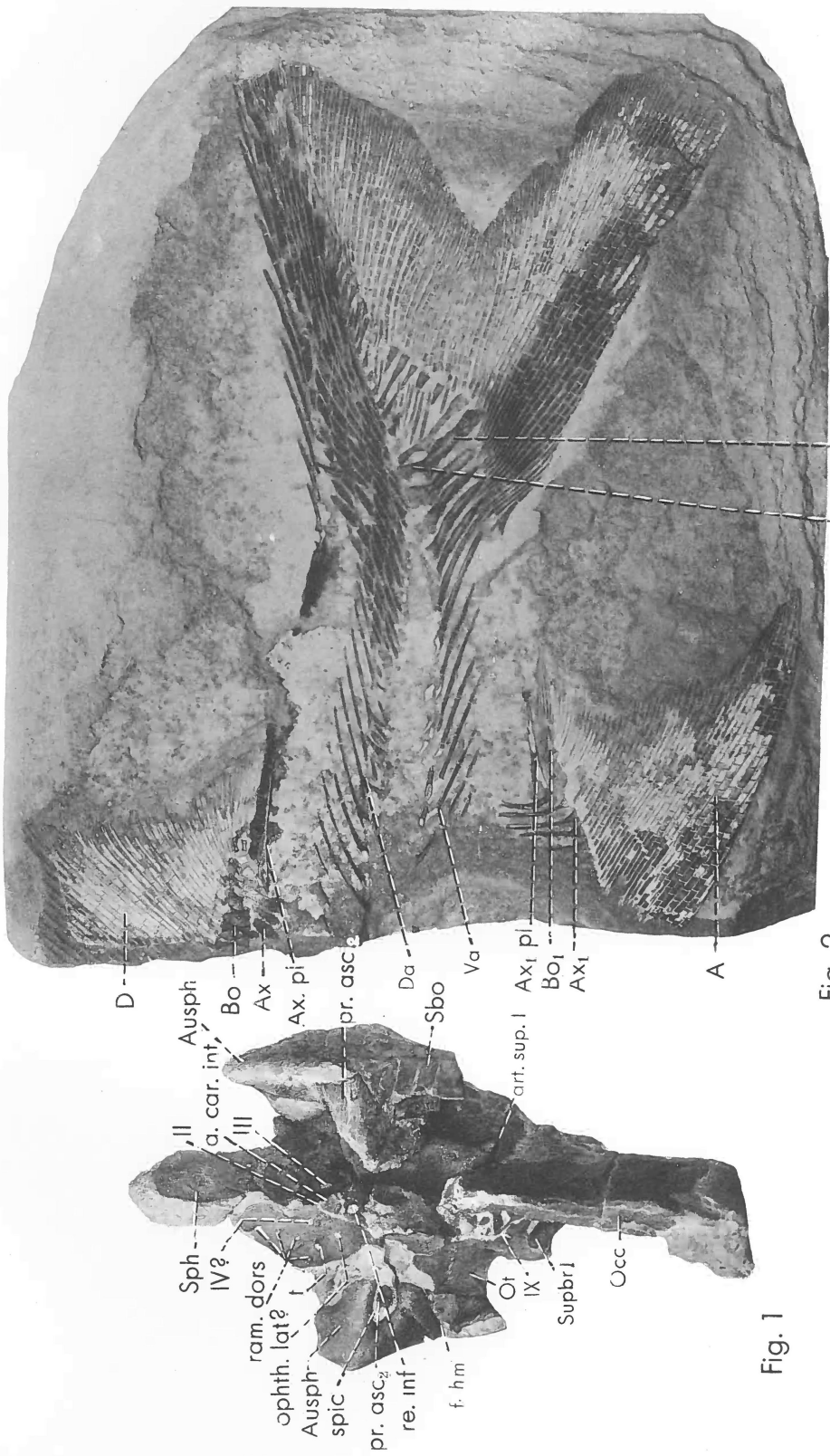

D
Ausph
Bo
Ax
Ax. pi
pr. asc
Da
Sbo
Va
Ax1 pl
Bo1
Ax1
A
Va
pr. hy
II
a. car. int.
III
art. sup. I
Sph
IV?
ram. dors
ophth. lat?
Ausph
spic
pr. asc.
re. inf
f. hm
Ot
IX
Supbr I
Occ

Fig. 2

Fig. 1

Plate 14.

Birgeria groenlandica Stensiö.

Head and foremost part of trunk. Specimen no. 650. 0.8 ×. Dry.

Ang, angular; *Bd*, basidorsal; *Bv*, basiventral; *Cl*, cleithrum; *De. spl*, dentalo-splenial; *Dx*, supraspiracular plate; *Ext*, extrascapular; *Fr*, frontal; *Mk*, articular ossification; *Mx*, maxillary; *Na*, nasal; *Op*, operculum; *Pa*, Pa_1, parietal elements; *Pop*, preoperculum; *Pt*, posttemporal; *Ptr*, postrostral; *Qu*, quadrate; *Sbo*, suborbital; *Scl*, supracleithrum; *Sclr*, sclerotic ring; *Sn*, supraneural; *So*, supraorbitals; *So. dsph. it*, supraorbito-dermo-sphenotico-intertemporal; *St*, supratemporal; *Sympl*, symplectic; *n*, notch in the lateral margin of the dermal cranial roof; *poc*, preopercular sensory canal.

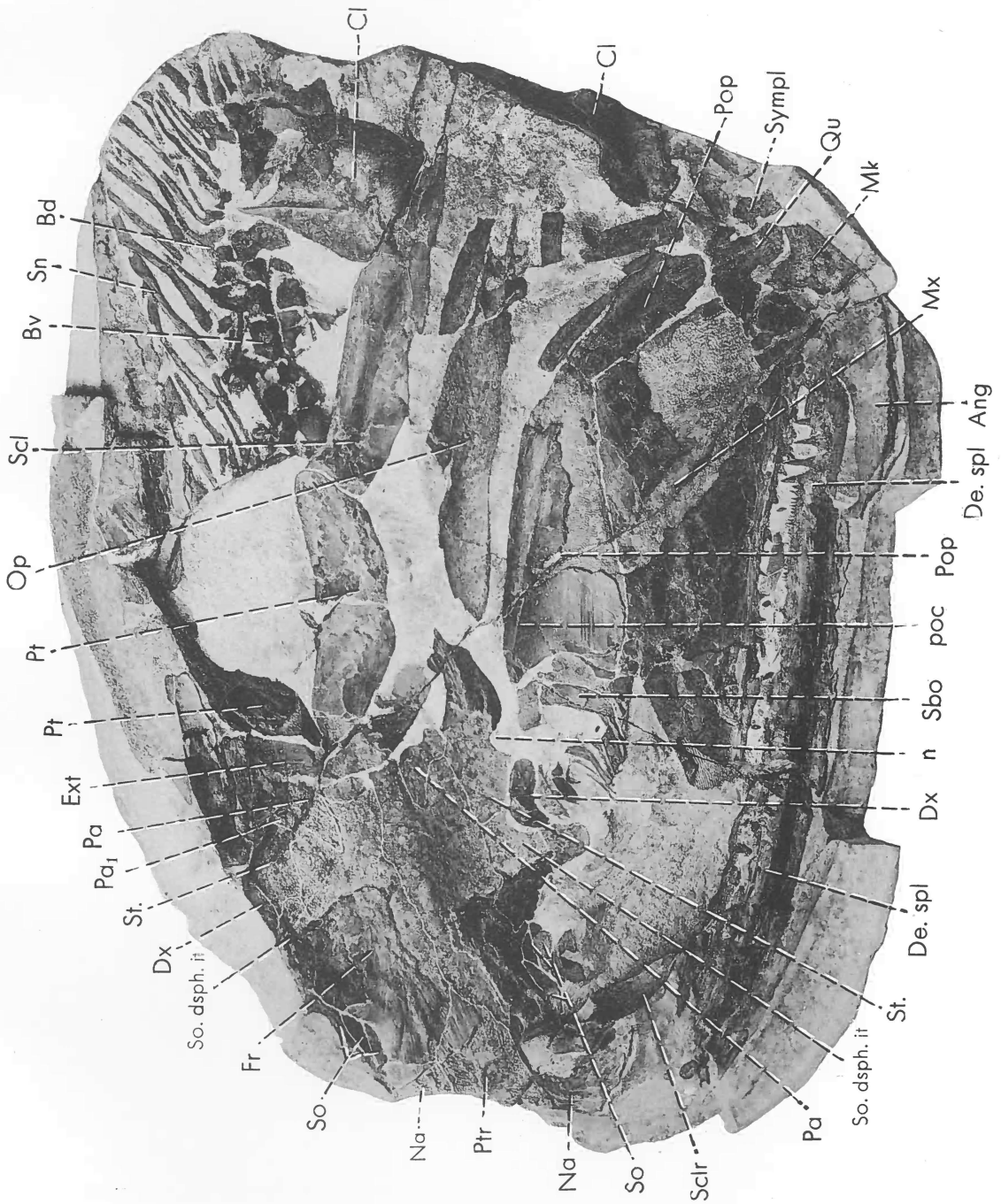

Cl
Cl
Pop
Sympl
Qu
Mk
Mx
Ang
De. spl
Pop
poc
Sbo
n
Dx
De. spl
St.
So. dsph. it
Pa
Sclr
So
Na
Ptr
Na
So
Fr
So. dsph. it
Dx
St.
Pa1
Pa
Ext
Pt
Pt
Op
Scl
Bv
Sn
Bd

Plate 15.

Birgeria groenlandica Stensiö.

Fig. 1. Posterior part of dermal cranial roof and dorsal part of dermal shoulder-girdle. Mainly preserved as impression. Specimen no. 651 (same specimen as shown in fig. 3 and in pl. 17). C. 1.4 ×. Dry.

Fig. 2. Greater part of dermal cranial roof. Mainly preserved as impression. Specimen no. 660. C. 1.4 ×. Dry.

Fig. 3. Parts of cheek and of dermal cranial roof. Mainly preserved as impression. Specimen no. 651 (same specimen as shown in fig. 1 and in pl. 17). C. 1.4 ×. Dry.

Ext, extrascapular; *Fr*, frontal; *Mx*, maxillary; *Na*, nasal; *Pa*, Pa_1, parietal elements; *Pop*, preoperculum; *Pt*, posttemporal; *Ptr*, postrostral; *Sbo*, suborbital complex; *So*, supraorbitals; *So. dsph. it*, supraorbito-dermosphenotico-intertemporal; *St*, supratemporal; *poc*, preopercular sensory canal.

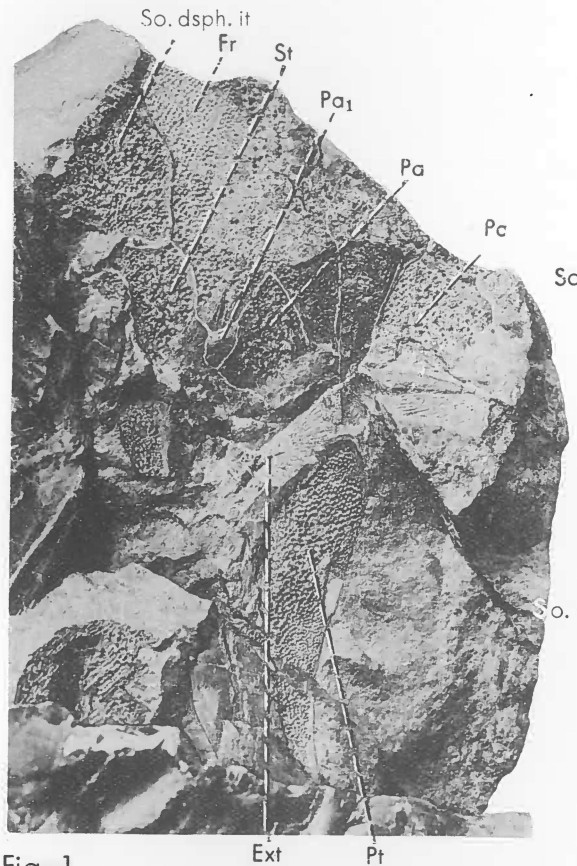


Fig. 1

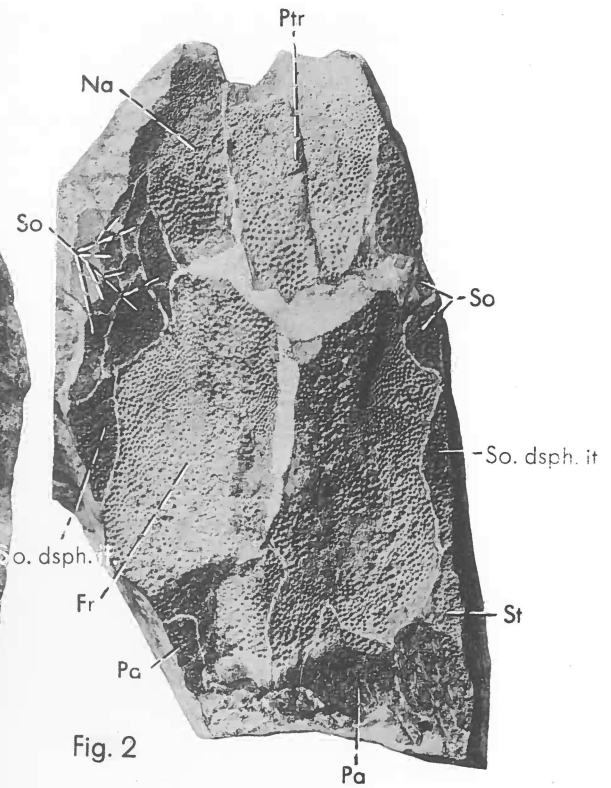


Fig. 2

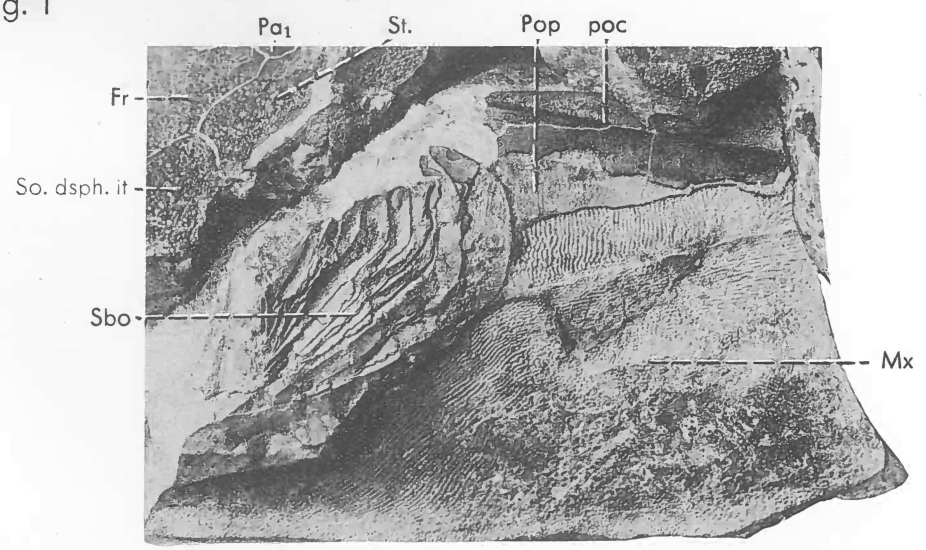


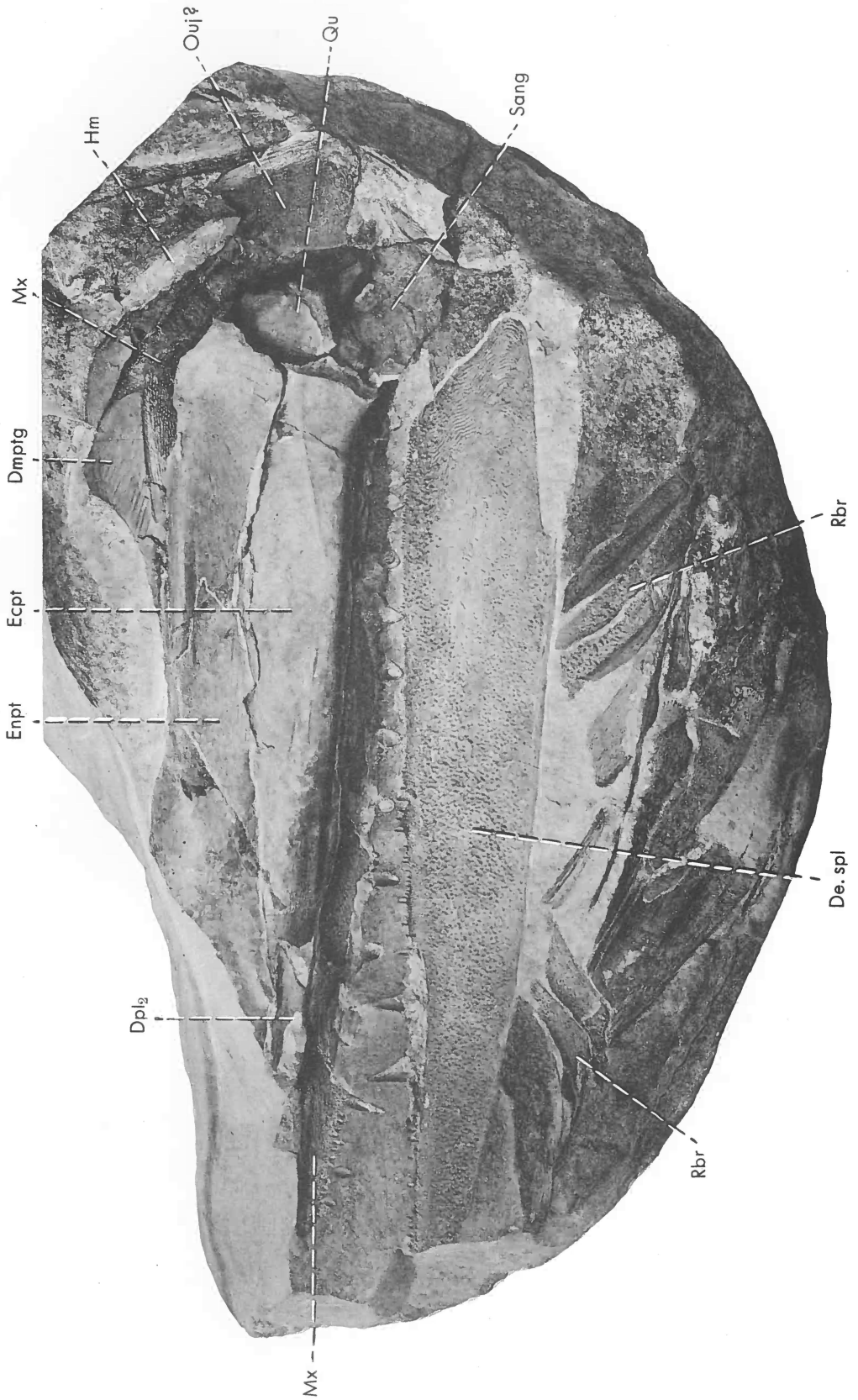
Fig. 3

Plate 16.

Birgeria groenlandica Stensiö.

Greater part of right palatoquadrate-maxillary apparatus in medial view together with external dermal bones of right mandible and scattered branchiostegal rays. Mainly preserved as impression. Specimen no. 756. 1.5 ×. Dry.

De. spl, dentalo-splenial; Dpl_2, posterior dermopalatine; *Dmptg*, dermometapterygoid; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Hm*, hyomandibula; *Mx*, maxillary; *Qu*, quadrate; *Quj*?, quadratojugal?; *Rbr*, branchiostegal rays; *Sang*, supraangular.



Nordisk Kunst- og Lystryk

Plate 17.

Birgeria groenlandica Stensiö.

Figs 1 and 2. Posterior parts of palatoquadrate-maxillary apparatus and mandible in medial and in lateral view respectively. Specimen no. 651 (same specimen as shown in pl. 15, figs. 1, 3). C. 2.3 ×. Dry.

Ang, angular; *De. spl*, dentalo-splenial; *Dmptg*, dermometapterygoid; *Ecpt*, ectopterygoid; *Mk*, articular ossification; *Mx*, maxillary; *Pr. art*, prearticular; *Sang*, supraangular; *sm* groove probably for the ramus mandibularis internus facialis.

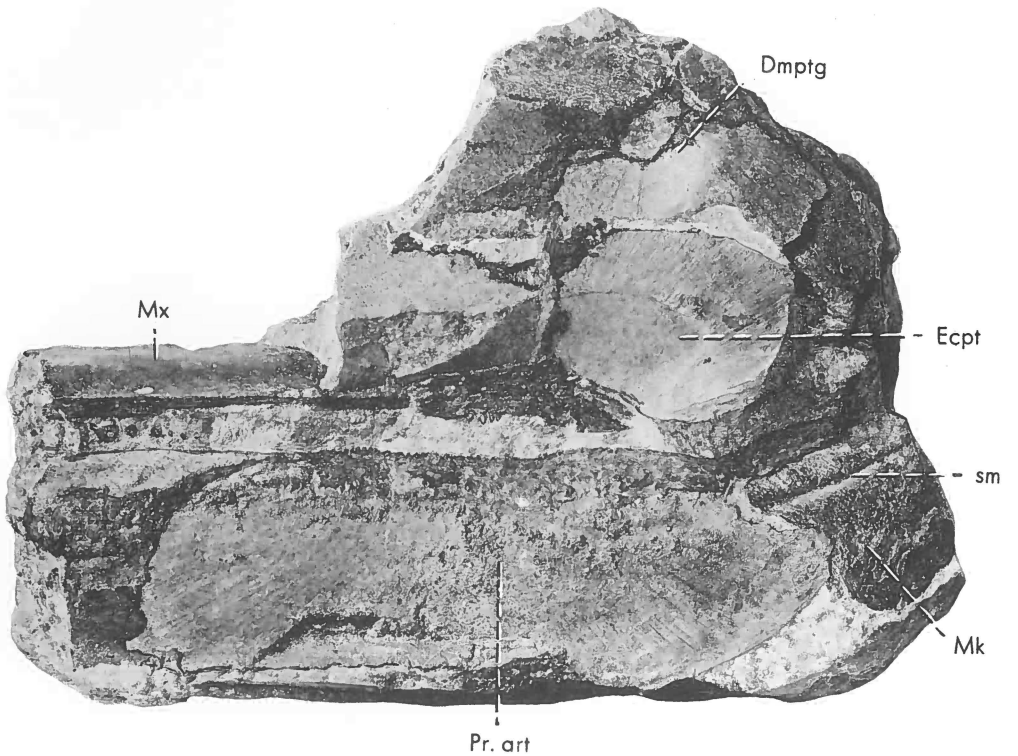


Fig. 1

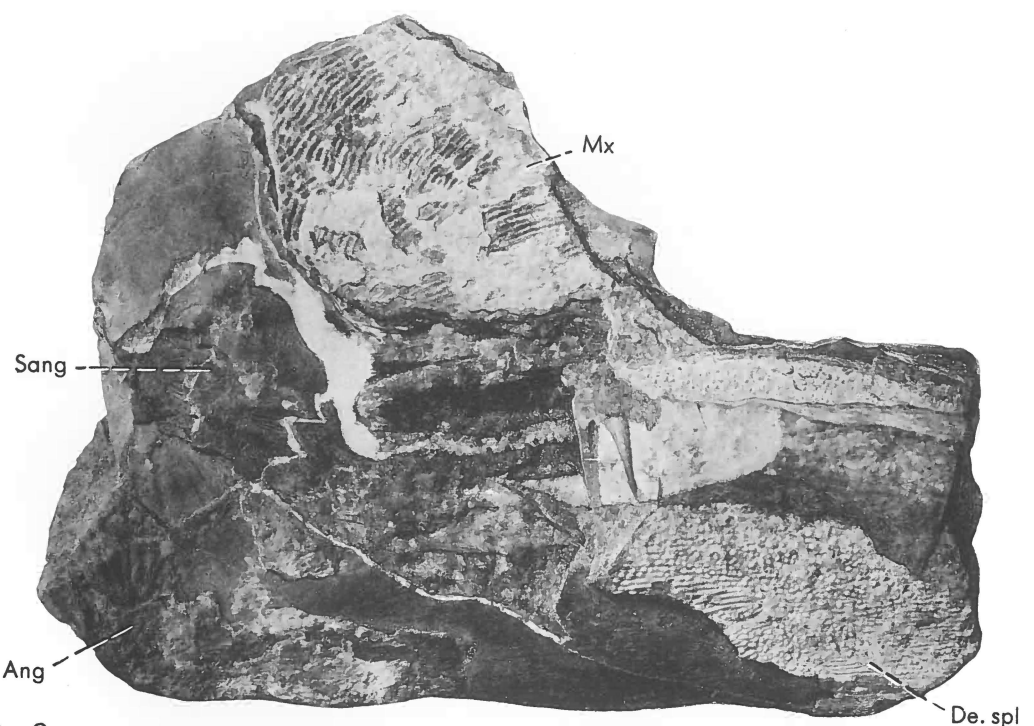


Fig. 2

Plate 18.

Birgeria groenlandica Stensiö.

Fig. 1. Scattered elements of visceral skeleton. Specimen no. 656. Nat. size. Xylol.
Fig. 2. Part of axial skeleton and series of lateral-line scales from anterior part of caudal region. Specimen no. 655. C. 1.3 ×. Xylol.

Ang, angular; *Br. o*, ossifications in the branchial arches; *Cbr*, ceratobranchial; Chy_1, ceratohyal ossification; *De. spl*, dentalo-splenial; *Ebr*, epibranchials; *H. hy*, hypohyal; *Hm*, hyomandibula; *Mx*, maxillary; *Pr. art*, prearticular; *Qu*, quadrate; *Sang*, supraangular; *Sympl*, symplectic; *lc*, main lateral line; *lc. s*, lateral-line scale.

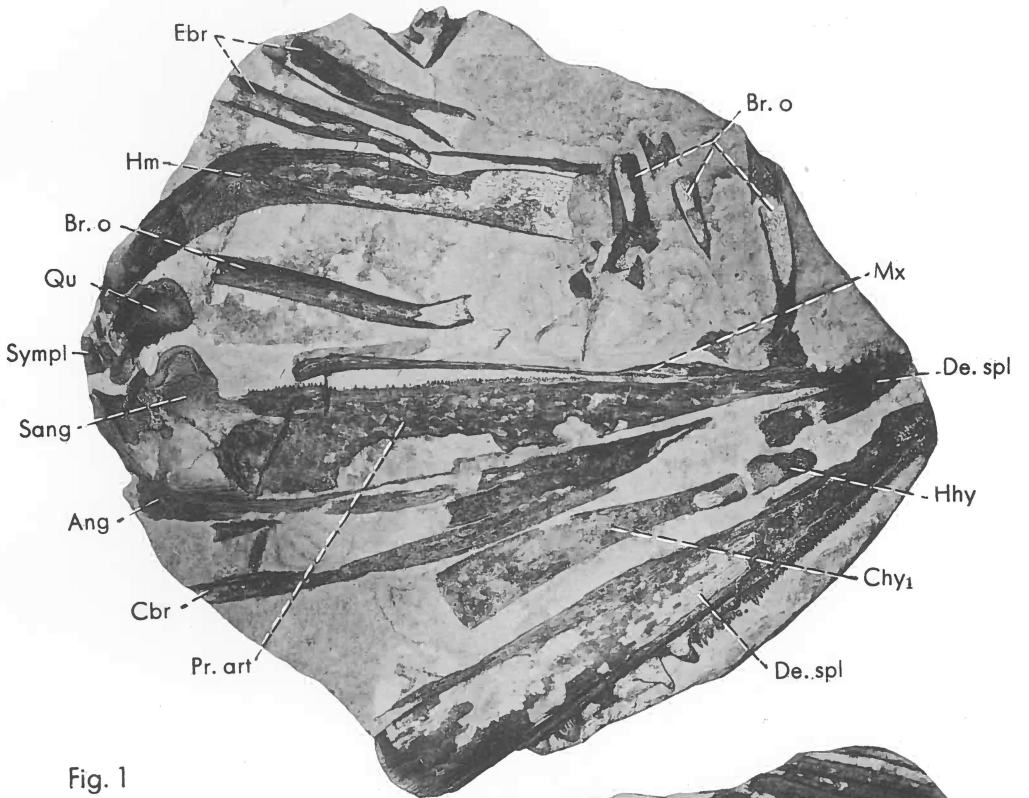


Fig. 1

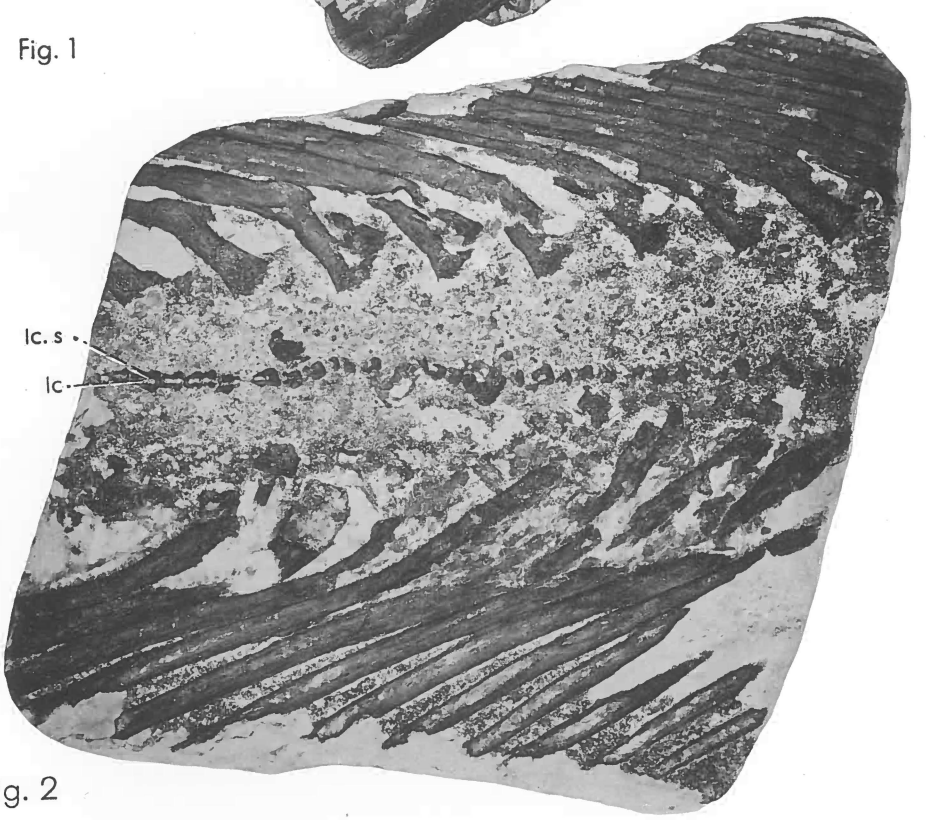
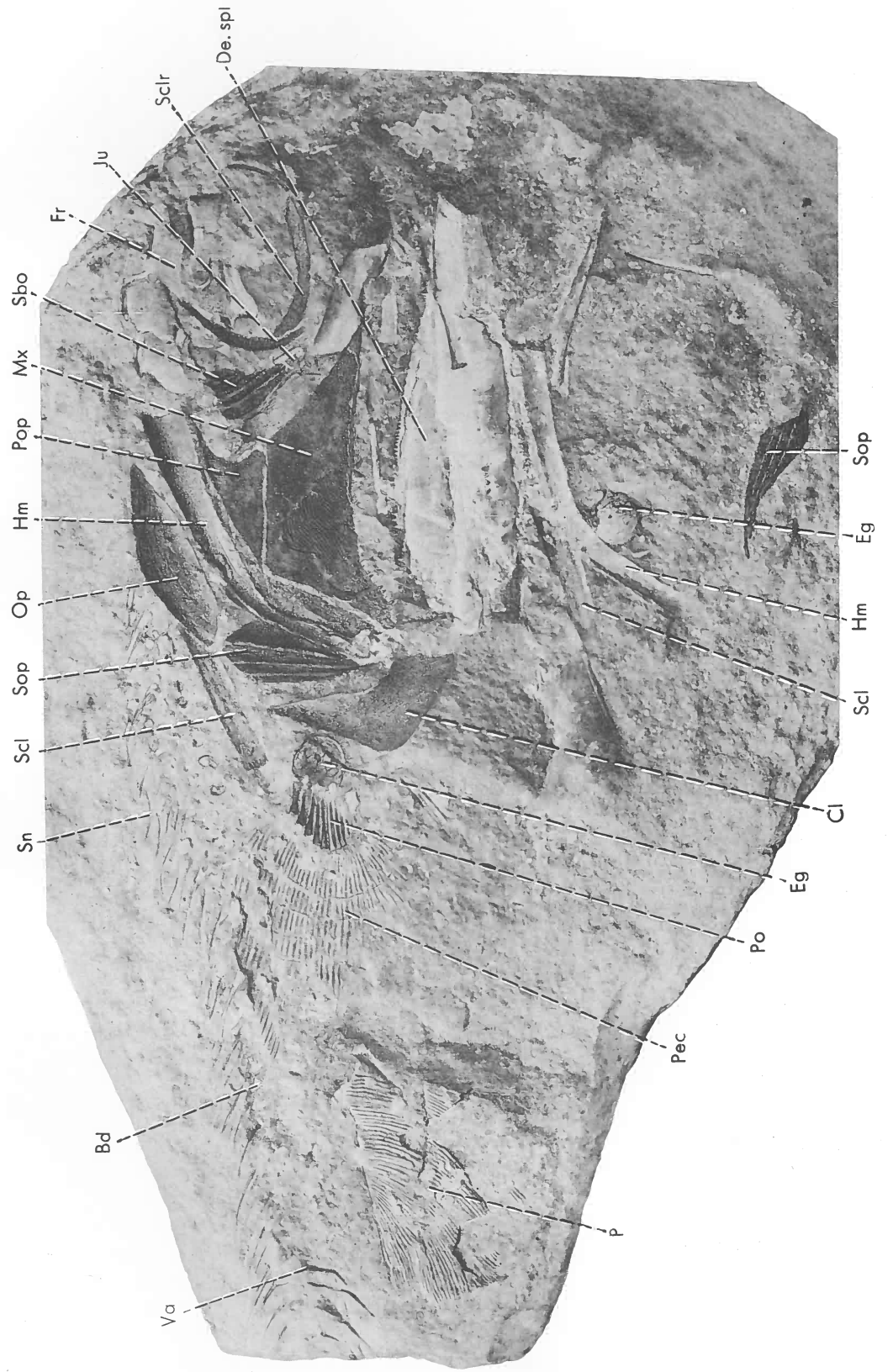


Fig. 2

Nordisk Kunst- og Lystryk


De. spl
Sclr
Ju
Fr
Sbo
Mx
Pop
Hm
Op
Sop
Scl
Sn
Bd
Va
P
Pec
Po
Eg
Cl
Scl
Hm
Eg
Sop

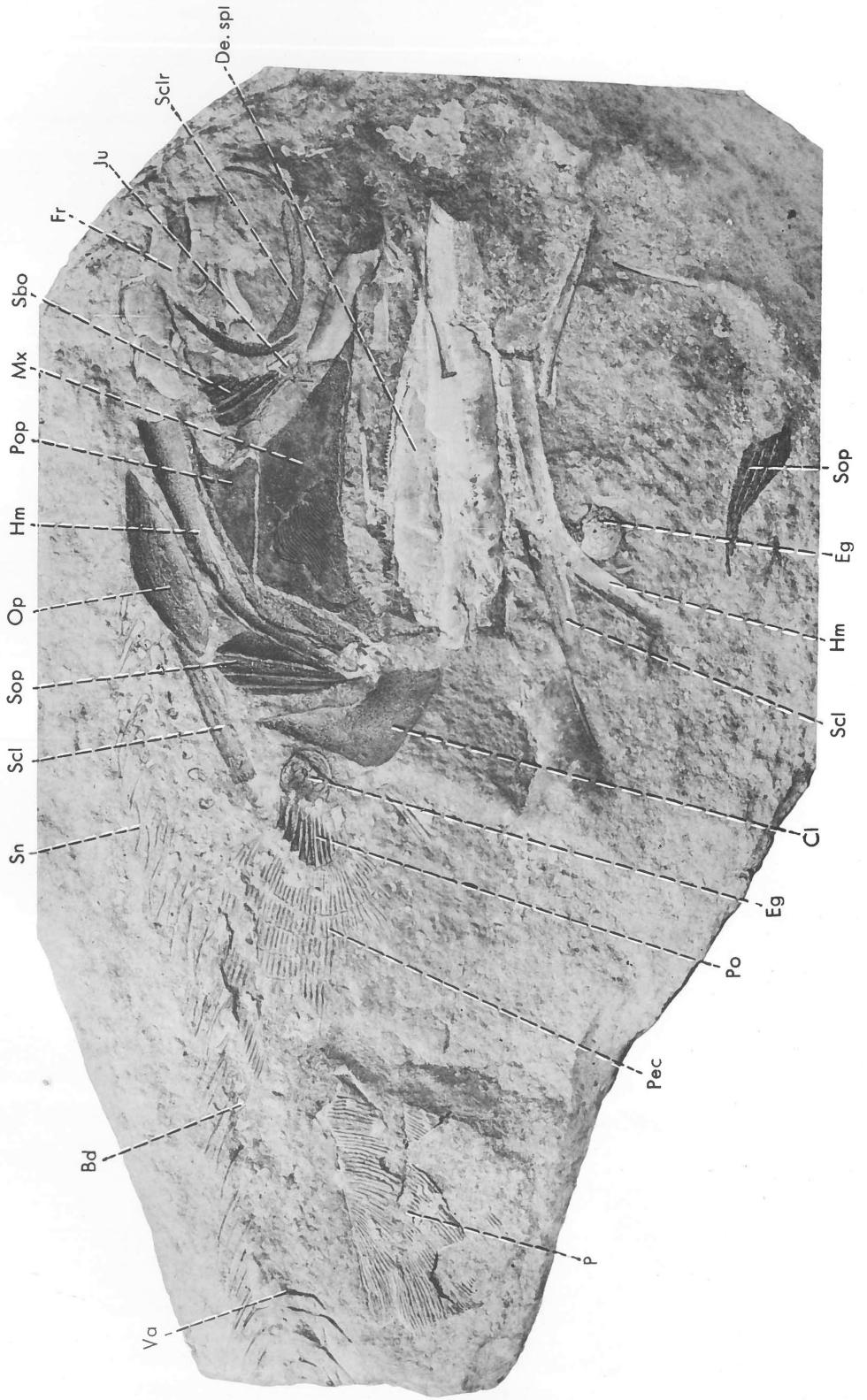

De. spl
Sclr
Ju
Fr
Sbo
Mx
Pop
Hm
Op
Sop
Scl
Sn
Bd
Va
P
Pec
Po
Eg
Cl
Scl
Hm
Eg
Sop

Plate 20.

Birgeria groenlandica Stensiö.

Fig. 1. Fish lacking the greater part of the caudal region. Head and anterior part of abdominal region dorso-ventrally compressed. Specimen no. 670. 1.5 ×. Xylol.

Fig. 2. Laterally compressed fish lacking the greater part of the caudal region. Specimen no. 772. C. 2 ×. Xylol.

A, anal fin; *Ang*, angular; *Ax*, axonost in endoskeleton of dorsal fin; Ax_1, axonost in endoskeleton of anal fin; *Bd*, basidorsal; *Bv*, basiventral; *Br. o*, ossification in the branchial arches; Chy_1, ceratohyal ossification; *Cl*, cleithrum; *De. spl*, dentalo-splenial; *Enpt*, entopterygoid; *Fr*, frontal; *Hm*, hyomandibula; *Mx*, maxillary; *Na*, nasal; *Op*, operculum; *P*, pelvic fin; *Pec*, pectoral fin; *Po*, postorbital; *Pr. art*, prearticular; *Pv*, pelvic plate; *Rbr*, branchiostegal ray; *R. pmx*, rostro-premaxillary; *Sbo*, suborbital; *Scl*, supracleithrum; *Sn*, supraneural; *Sop*, suboperculum; *eth. com*, ethmoidal commissure; *orb*, orbit; *soc*, supraorbital sensory canal.

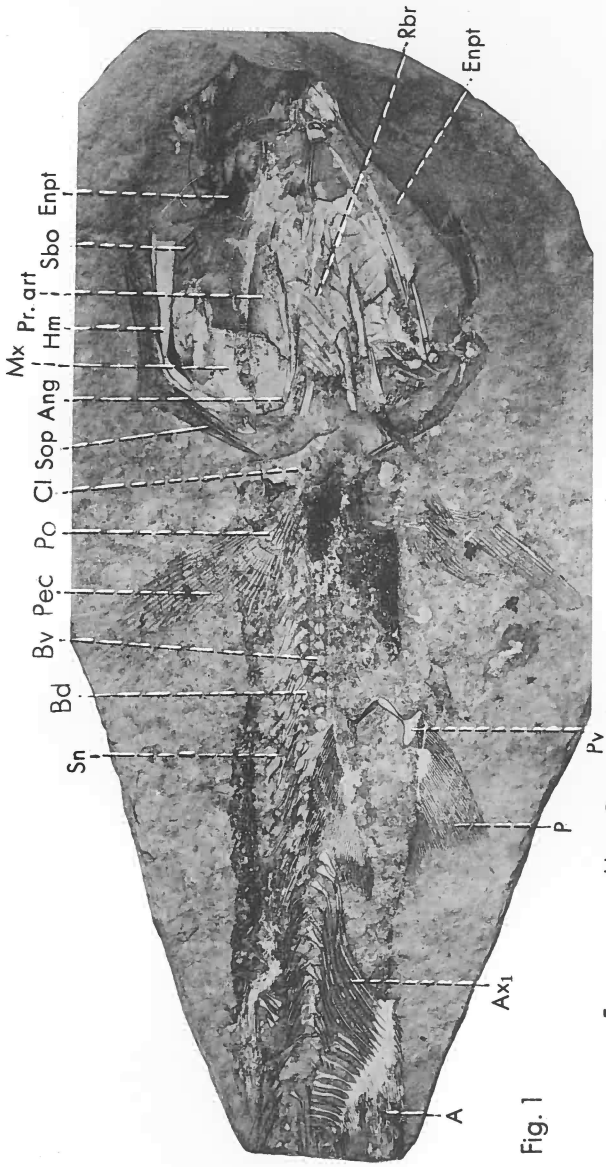

Rbr
Enpt
Mx
Pr. art
Sbo
Enpt
Hm
Ang
Sop
Cl
Po
Pec
Bv
Bd
Sn
P
Ax1
A

Fig. 1

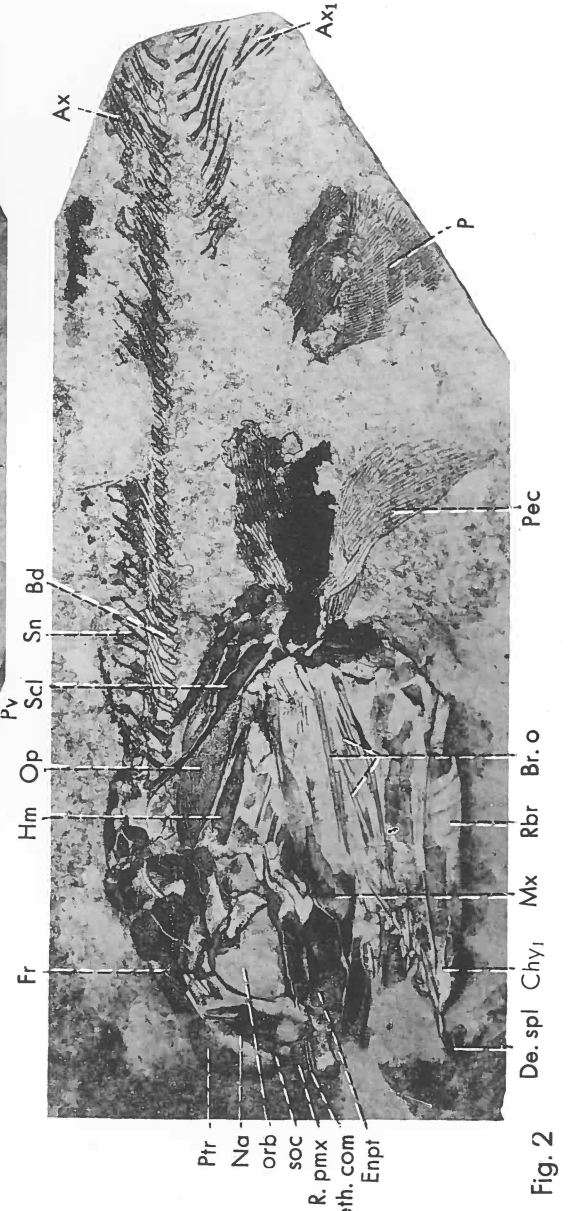

Ax1
Ax
P
Pec
Bd
Sn
Scl
Pv
Op
Br. o
Hm
Rbr
Mx
Fr
Chy1
De. spl
Ptr
Na
orb
soc
R. pmx
eth. com
Enpt

Fig. 2