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ON THE PLACODERMI OF THE UPPER DEVONIAN OF EAST GREENLAND II

BY

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WITH 308 FIGURES IN THE TEXT
AND 75 PLATES

Text

KØBENHAVN
C. A. REITZELS FORLAG
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FORORD

Det foreliggende bind af Palæozoologica Groenlandica er ligesom det foregående bekostet af billedhugger Viggo Jarl, der herigennem har ydet udforskningen af Grønlands forhistoriske dyreverden en uvurderlig støtte. For denne støtte udtrykker Zoologisk Museum i København herved sin allerbedste tak.

Det foreliggende bind indeholder udelukkende en enkelt afhandling af professor Erik Stensiö: On the Placodermi of the Upper Devonian of East Greenland. Den danner en fortsættelse af en i Meddelelser om Grønland (Vol. 97) i 1934 fremkommen afhandling. Manuskriptet til denne afhandling blev afleveret i 1943; dels på grund af arbejdets store omfang, dels på grund af de af krigsforholdene fremkaldte tilstande er det først nu lykkedes at tilendebringe trykningen.

PRÉFACE

Comme pour le volume précédent, c'est encore monsieur Viggo Jarl, sculpteur, qui a gracieusement fourni les fonds nécessaires à la publication du présent numéro de la série »Palaeozoologica Groenlandica«. Le Musée Zoologique de Copenhague tient à exprimer ici sa plus vive reconnaissance pour cette aide généreuse qui permet d'apporter des lumières nouvelles sur les animaux préhistoriques du Groenland.

Le volume présent n'est entièrement composé que d'un seul travail de monsieur le professeur Erik Stensiö intitulé: »On the Placodermi of the Upper Devonian of East Greenland« et fait suite à une étude parue en 1934 dans »Meddelelser om Grønland« (vol. 97). Le manuscrit a été donné pour publication en 1943, mais par suite des conditions difficiles causées par la guerre, ce n'est que cette année que l'impression d'un travail si considérable a pu être assurée.

Universitetets zoologiske Museum, København, i oktober 1948.

R. Spärck.

ERIK A:SON STENSIÖ

ON THE PLACODERMI OF THE UPPER DEVONIAN OF EAST GREENLAND

II

ANTIARCHI: SUBFAMILY BOTHRIOLEPINAE

WITH AN ATTEMPT AT A REVISION
OF THE PREVIOUSLY DESCRIBED SPECIES
OF THAT SUBFAMILY

Text

Det Hoffensbergske Etabl. Kbhvn.
5502

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INTRODUCTION

Part I of this monograph "On the *Placodermi* of the Upper Devonian of East Greenland", treating the *Phyllolepida* and *Euarthrodira,* appeared in the spring of 1934 (Stensiö 1934b). Two supplements to part I were published later on, the first one in 1936, the second one in 1939 (Stensiö 1936, 1939a).

Part II herewith brought out deals with all the *Bothriolepis*-material collected by the Danish East Greenland expeditions undertaken under Dr. Lauge Koch's leadership in the summers of 1929–34 and 1936 (cf. Stensiö 1934b, pp. 5–6; 1936, pp. 5–7; 1939a, p. 3; 1939b). In addition it contains also a general account of the organization of the *Bothriolepinae,* a fairly complete systematic description of *Bothriolepis canadensis,* and a first attempt at a revision of the other species of the subfamily *Bothriolepinae.*

According to the original plan for the publishing of this monograph drawn up in 1933 (Stensiö 1934b, p. 5) part II would have treated the whole Upper Devonian *Antiarchi*-material from East Greenland, i. e. both the *Bothriolepis*-material and the *Remigolepis*-material. This plan had to be abandoned, however, since in 1939 it appeared that a description of all that material would be much too large to be printed in one volume. Part II of the monograph had, therefore, to be devoted only to the *Bothriolepis*-material, whereas the description of the *Remigolepis*-material, that is now under preparation, will be published later on, as a third and last part of the monograph.

During my work on it I perceived pretty soon, that, because of its state of preservation and wide range of variation, the *Bothriolepis*-material from the Upper Devonian of East Greenland was difficult to determine, and that a satisfactory description of it could be worked out only after a thorough reexamination of, at least, the majority of the previously known *Bothriolepis*-species. Such a reexamination, above all of the Canadian and British species, was, therefore, begun in 1938. Though, owing to the present political conditions in Europe, this reexamination could not nearly be carried through to the extent originally planned the results gained from it are nevertheless of much importance. These results help considerably in throwing new light not only upon the characters of the various species representing the *Botriolepinae* and the range of variation of these characters, but also upon the

organization of the *Bothriolepinae* and the *Antiarchi* in general. It is therefore appropriate that they are published here together with the description of the Greenland material.

The *Bothriolepis*-material from East Greenland to be described here was entrusted to me by Dr. Lauge Koch, Copenhagen, for which I am deeply indebted to him. My indebtness is also due to Professor H. R. G. Spärck, director of the Zoological Museum of Copenhagen, for his kind interest in my work on the Greenland Placoderms and for much help and courtesy otherwise. I wish here further to thank Dr. W. Gross of Berlin most cordially both for his great kindness in making ready his paper on "Die *Bothriolepis*-Arten der *Cellulosa*-Mergel Lettlands" so that it could be taken into consideration here, and for a good and pleasant cooperation otherwise. The description by Gross on *Bothriolepis cellulosa* and *B. tuberculata,* as well as his general account of the *Antiarchi* in the paper by him just referred to, have been of fundamental importance for my work now before us. Moreover, I wish here to tender my most sincere thanks to Dr. E. I. White of the British Museum of Natural History in London, to Professor G. Hickling of the University of Durham, New Castle on Tyne, and to Dr. A. C. Stephen of the Royal Scottish Museum in Edinburgh for their courteous help and great kindness during a preliminary examination of the British *Bothriolepis*-species which I undertook in the summer of 1938.

It is also a pleasant duty for me to acknowledge my deepest gratitude to Wenner-Greenska Samfundet, Stockholm, and to captain H. Löfgreen of Norsholm, for supports which enabled the accomplishment of the technical work for part II of the monograph.

Finally, I wish here to express my deepest indebtedness to Sculptor V. Jarl of Copenhagen, who has donated the funds for the printing of this volume of the monograph.

GENERAL PART

Terminology.

Among the dermal bones of the head in *Antiarchi* there are several which beyond question are strictly homologous with certain bones in Arthrodires and others which may easily be derived from Arthrodire bones or components of Arthrodire bones. For all these bones of the *Antiarchi* Arthrodire terms have here now been introduced. Such terms are: rostral plate, postpineal plate, centro-nuchal plate, paranuchal-marginal plate, postmarginal plate, inferognathal, and the previously used term pineal plate. For certain other of the dermal head bones in the *Antiarchi* new terms, more adequate than the older ones, have been suggested. Such new terms are: infraprelateral plate, extramandibular plate, submandibular bone-series, subhyoideal bone or bone-series. The meanings of all these new terms may be easily understood from the accompanying table II (p. 10).

In some cases the postmarginal plate was found to be divided into two elements, anterior and posterior. These elements will be referred to as the anterior and posterior postmarginal plates respectively.

The terms applicated to the bones of the trunk-armour are the current ones used by Traquair and most subsequent writers. However, the complex plate formed by fusion of the posterior dorso-lateral and posterior lateral plates is termed the mixilateral plate (Stensiö 1931). A supernumerary plate, fortuitously developed at the corner between the anterior and posterior median dorsal plates and the mixilateral plate, will be described under the term of supramixilateral plate.

The older terminologies of the exoskeleton of the pectoral fin has in this work been dropped and replaced by the new one recently suggested by Gross (1941 a). This new terminology has great preferences to the previous ones in the following respects: it is established on a comparative-anatomical and morphological basis instead of a mainly functional one; it is applyable not only to the *Asterolepiformes*, but also to the *Remigolepiformes*; and, finally, it seems in all respects to be fully adequate. How it is in detail is elucidated by the accompanying table I (pp. 8–9), in which also the earlier terminologies used by Traquair, Hoffman, Gross and Stensiö are given for comparison.

Table 1

	The new terminology of the dermal bones of the pectoral fin suggested by Gross (1941) and adopted throughout this work.	Previous terminology of the Fam.	
		Traquair 1888-1906	Hoffmann 1911
Dorsal central series	Dorsal central plate 1 – – – 2 – – – 3*) – – – 4*) – – – 5*)	Dorsal articular plate – anconeal – – central – 1*) – – – 2*) – – – 3*)	Obere Gelenkplatte – Mittelplatte – Gelenkplatte*) ——— ———
Ventral central series	Ventral central plate 1 – – – 2 – – – 3*) – – – 4*) – – – 5*)	Ventral articular plate – anconeal – – central – 1*) – – – 2*) – – – 3*)	Untere Gelenkplatte – Mittelplatte – Gelenkplatte*) ——— ———
Lateral marginal series	Lateral marginal plate 1 (absent) – – – 2 – – – 3*) – – – 4*) – – – 5*)	——— External marginal plate – upper marginal plate*) – lover – – *) ———	——— Aussenplatte Aussengelenkplatte*) Aussenplatte*) ———
Medial marginal series	Medial marginal plate 1 – – – 2 – – – 3*) – – – 4*) – – – 5*)	Internal articular plate – marginal – – upper marginal plate*) – lower – – *) ———	Innengelenkplatte Innenplatte Innengelenkplatte*) Innenplatte*) ———
	Terminal plate*)	Terminal plate*)	Distal plate*)

*) This mark indicates that the plate belongs to the distal segment in the *Asterolepidae*.

For the detailed description of the exoskeletal bones a great many terms had to be introduced for margins, processes, notches, certain areas, certain depressions, certain ridges, and certain grooves etc. These new terms will all be explained in the chapters dealing with the exoskeleton.

Finally, it should also be pointed out in this connection that a new interpretation of the sensory canal system of the *Antiarchi* has been given here, a new interpretation which has necessitated considerable changes in the terminology of the sensory canals and pit-line grooves of the group (cf. Stensiö 1931; 1938).

dermal bones of the pectoral fin of the *Antiarchi*, all dropped here.

Asterolepidae.		Fam. *Remigolepidae.*
Gross 1931-1940	Stensiö 1931, 1938	Stensiö 1931
Articulare superius	Dorsal articular plate	Dorsal articular plate
Orbiculatum dorsale	– anconeal –	– central – 1
Articulare dorsale*)	– central – 1*)	– – – 2
———	– – – 2*)	– – – 3
———	– – – 3*)	———
Articulare inferius	Ventral articular plate	Ventral articular plate
Orbiculatum ventrale	– anconeal –	Ventro-medial marginal plate 1
Articulare ventrale*)	– central – 1*)	– – – – 2
———	– – – 2*)	– – – – 3
———	– – – 3*)	———
———	———	———
Marginale externum	Lateral marginal plate	Lateral marginal plate 1
Articulare – *)	– – – 1*)	– – – 2
Acutum – *)	– – – 2*)	– – – 3
———	– – – 3*)	– – – 4
Axillare	Axillary plate	Axillary plate
Marginale internum	Medial marginal plate	Dorso-medial marginal plate 1
Articulare internum*)	– – – 1*)	– – – – 2
Acutum internum*)	– – – 2*)	– – – – 3
———	– – – 3*)	– – – – 4
Distale*) (1931) Terminal platte*), in later publications	Terminal plate*)	Terminal plate

Table II.

Explanation of the new terms here applicated to the dermal bones of the head in the *Antiarchi*.

New terms here used	Previous terms	Arthrodiran equivalents
Rostral plate =	ethmoid (Patten 1904), = prepineal plate (Obrutschew 1927; Stensiö 1931; Gross 1941; 1942)	rostral plate.
Postpineal plate =	os medium posticum = (Pander 1857; Gross 1931), postmedian plate (Traquair 1888; 1893; 1894-1906; Woodward 1891; Stensiö 1931; Gross 1932; 1933; 1941; 1942), parietal (Jaekel 1903)	postpineal plate (cf. pp. 198-221 and text-figs. 69, 70, 71 and 73 below), plate *Y* (Watson 1938).
Centro–nuchal =	os occipitale medium = (Pander 1857; Gross 1931), median occipital (Traquair 1888; 1893; 1894-1904; Woodward 1891; etc.), superior occipital (Jaekel 1903), median nuchal (Stensiö 1931; 1938), median basal (Heintz 1931); nuchal (Gross 1932; 1940; 1941; 1942)	the central plates of both sides, the nuchal plate, and certain medial extrascapular elements.
Paranuchal-marginal =	os articulare capitis, = os occpitiale laterale (Pander 1857; Gross 1931), exoccipital (Traquair 1888; 1893; 1894–1906; Woodward 1891; etc.), epiotic (Jaekel 1903), lateral nuchal (Stensiö 1931; 1938), paranuchal (Gross 1932a; 1933a, b; 1940; 1941; 1942)	paranuchal plate, marginal plate, and perhaps also certain lateral extrascapular elements.
Postmarginal plate =	os angulare (Pander 1857; = Traquair 1894-1906; Jaekel 1903). Sufflaminal plate (Gross 1931; 1933; 1941; 1942; Stensiö 1931; 1938)	postmarginal plate.
Infraprelateral =	polygonal plate (Stensiö 1931)	———
Inferognathal =	maxilla (Patten 1904), = mandibular bone (Stensiö 1931), inferognathal (Gross 1941)	inferognathal
Extramandibular plate =	plate *Y* or possibly a postmandibular element (Stensiö 1931)	———
Submandibular bone-series =	postmandibular plate or plates (Stensiö 1931)	———
Subhyoideal bone-series =	ponticular plate or plates (Stensiö 1931)	———

Measurements.

The measurements necessary for the study of the proportions of the head-shield, trunk-armour, pectoral fin-armour and various bones composing these armours have been taken as follows.

Head-shield. – Length: along the median line. Breadth: across the postero-lateral (preobstantic) corners (*plc*, text-fig. 9).

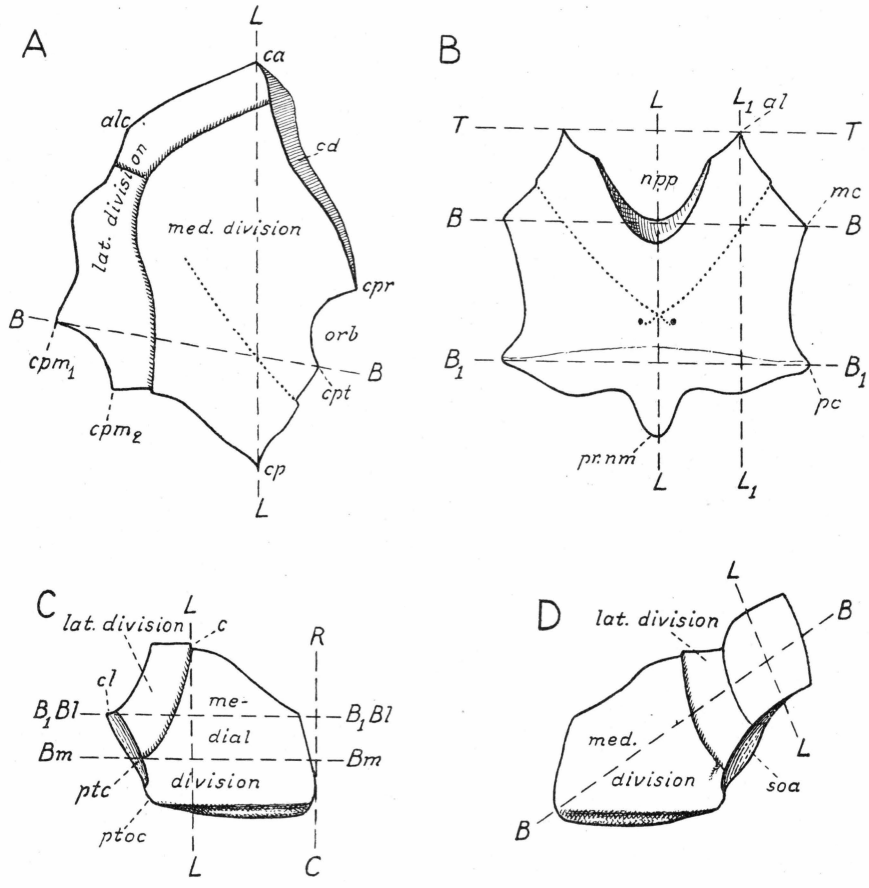
Trunk-armour. – Dorsal length: length of the dorsal wall along the median line. Dorsal breadth: breadth of the dorsal wall across the dorso-lateral ridges, at the suture between the anterior dorso-lateral and mixi-lateral plates (text-fig. 39). Ventral length: length of the ventral wall along the median line. Ventral breadth: breadth of the ventral wall across the ventro-lateral ridges, at the suture between the anterior and posterior ventro-lateral plates. Maximal ventral breadth: across the prepectoral corners (*prc*, text-figs. 2C, 41).

Pectoral fin-armour. – Length of proximal segment: from the proximal end of the dorsal or ventral central plate 1 to the beginning of the external articular area of the dorsal or ventral central plate 2 and thus exclusive of the external articular area of the latter plates. Breadth of proximal segment: across the widest part of the dorsal face of the segment, between the lateral and dorso-medial margins, exclusive of the lateral and medial rows of spines (or their equivalents). Length of distal segment: from the exposed proximal margin of the dorsal or ventral central plate 3 to the distal end of the terminal plate, and thus exclusive of the lateral and medial articular processes.

Premedian, rostral, pineal and postpineal plates. – Length: along the median line. Breadth: across the broadest parts of the plates.

Lateral plate (text-fig. 1A). – Length: from the antero-medial corner (*ca*) to the posterior corner (*cp*). Breadth: from the anterior postmarginal corner (cpm_1) to the postorbital corner (*cpt*).

Centro-nuchal plate (text-fig 1B) – Total length: along the median line (*L–L*), from a transverse line (*T–T*) through the antero-lateral (foremost) corners (*al*) backwards to the posterior margin of the plate (generally the posterior end of the posterior median process). Median length: along the median line (*L–L*), from the posterior end of the postpineal notch (*npp*) (exclusive of the overlapped area), to the posterior margin of the plate



Text-fig. 1. Four plates of the head-shield with the lines inlaid along which the measurings have been made. *A*, a left lateral plate of *Bothriolepis canadensis*. *B*, a centro-nuchal plate of *B. groenlandica*. *C*, left paranuchal-marginal plate of *B. canadensis*. *D*, right paranuchal-marginal plate of *B. canadensis* with postmarginal plate attached.
B–B, B_1–B_1, lines along which the breadth of the lateral, centronuchal and postmarginal plates have been measured; B_1, *Bl*–B_1, *Bl* line along which the total breadth of the paranuchal-marginal plate and the breadth of the lateral division of this plate have been measured; *Bm–Bm*, line along which the breadth of the medial division of the paranuchal-marginal plate has been measured; *L–L*, lines along which the length of the plates has been measured; L_1–L_1, line along which the paramedian length of the centro-nuchal plate has been measured; *R–C*, rostro-caudal line through the most medial corner of the exposed area of the paranuchal-marginal plate (parallel with the longitudinal axis of the head-shield); *T–T*, line connecting the antero-lateral corners (*al*) of the centro-nuchal plate. For explanation of other index letters see text-figs. 24, 25, 26, 27, 28 and 29 respectively.

(generally the posterior end of the posterior median process). Paramedian length: from the antero-lateral (formost) corner (*al*) to the posterior margin along a line (L_1–L_1) parallel with the median line (*L–L*) Breadth: across the middle lateral corners (*mc*), and across the postero-lateral corners (*pc*).

Paranuchal-marginal plate (text-fig. 1C). – Length: from the anterior corner (*c*) to the posterior margin of the plate along a line, *L–L*, drawn at right angles to the posterior margin (approximately parallel with the longitudinal axis of the head-shield). Total breadth: from the lateral corner (*cl*) to a line, *R–C*, drawn through the medial corner of the exposed area of the medial division of the plate, parallel with the line *L–L*, along the line *B*, *Bl–B*, *Bl*, at right angles to the lines *R–C* and *L–L*. Breadth of lateral division: from the lateral corner of the ornamented area of the division (thus exclusive of the subobstantic area which often is missing) to the infra-orbital sensory canal groove along the line *B*, *Bl–B*, *Bl*, at a right angle to the lines *R–C* and *L–L*. Breadth of medial division: from the lateral corner of the ornamented area of the division just at the posterior end of the postotic sensory canal groove (*ptc*) to the line *R–C*, along a line *Bm–Bm* parallel with the posterior margin of the plate and at right angle to the line *R–C* (thus exclusive of the subobstantic area which often is missing). As may be gathered, the measurements of the paranuchal-marginal plate have here been taken in a somewhat different way than what was done by Gross in one of his most recent publications on *Bothriolepis* (Gross 1941a, p. 9, text-fig. 2).

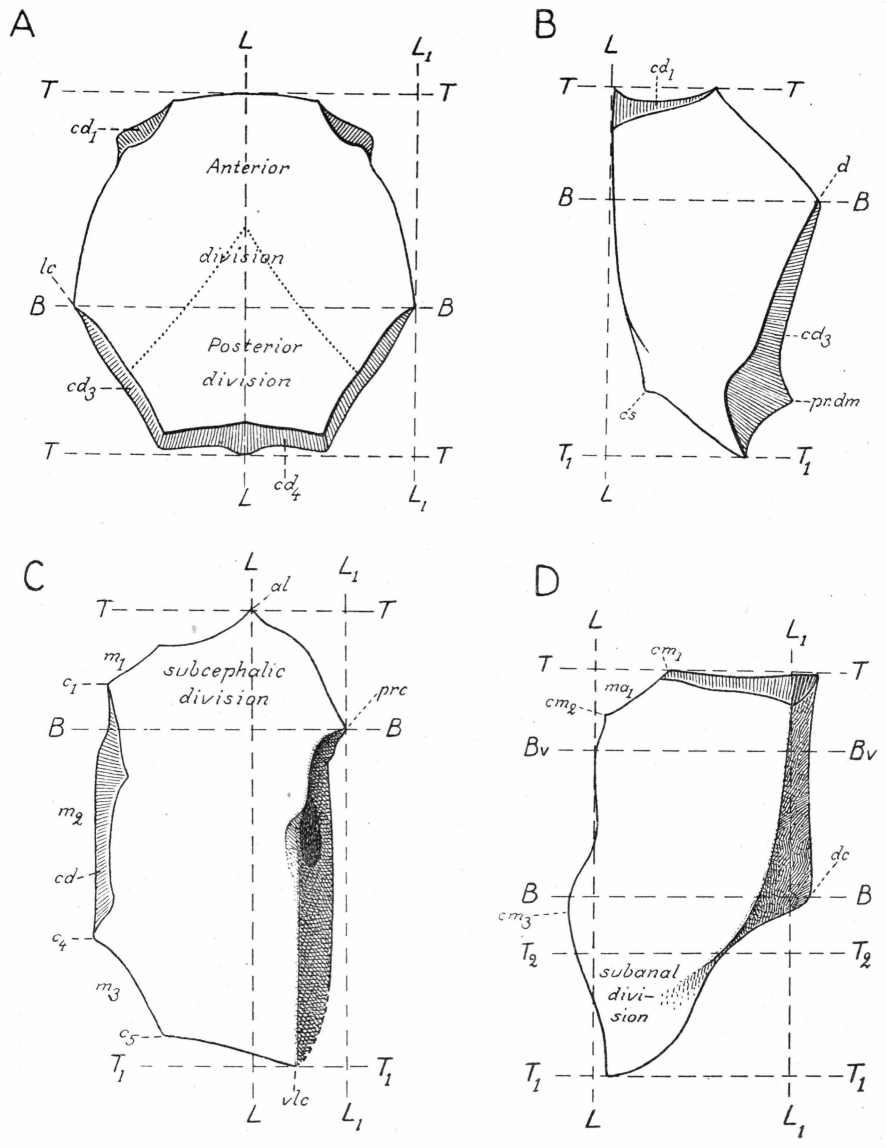
Postmarginal plate (text-fig. 1D). – Length: from the anterior to the posterior margin, along a line, *L–L*, through the middle of these margins. Breadth: from the middle of the medial margin to the middle of the lateral margin.

Anterior median dorsal plate (text-fig. 2A). – The measurings of this plate have all been taken in the same way as in the most recent papers published by Gross (1940b, pp. 33–34; 1941a).

Posterior median dorsal plate (text-fig. 45). – Length: from the anterior corner (*aa*) to the posterior median corner (*pa*) along the median line. Breadth: across the lateral corners (*l*) of the lateral processes(*prl*).

Anterior dorso-lateral plate (text-fig. 48). – Total length and length of dorsal and lateral laminae: from the foremost end of the processus obstans (*pro*) to the hindmost corner of the plate, at the level of the dorso-lateral ridge (*dlr*). Total breadth (maximum breadth): across the postero-dorsal corner of the dorsal lamina and the postero-ventral corner of the lateral lamina of the plate. Total breadth of dorsal lamina: across the internal postlevator process (*pr. pn*) and the dorso-lateral ridge (*dlr*), at right angles to the longitudinal axis of the trunk-armour. Height of lateral lamina: from the postero-ventral corner of the lamina to the dorso-lateral ridge (*dlr*), along a line at a right angles to the dorso-lateral ridge.

Mixilateral plate (text-fig. 2B). – Total length, length of dorsal lamina: from the foremost corner at the level of the dorso-lateral ridge (*dlr*) along a longitudinal line, *L–L*, parallel with the longitudinal axis of the dorsal wall of the trunk-armour backwards to a transverse line, T_1–T_1,



Text-fig. 2. Four plates of the trunk-armour with the lines inlaid along which the measurings have been made. *A*, an anterior median dorsal plate of *Bothriolepis cellulosa* in dorsal aspect. *B*, a left mixilateral plate of *B. canadensis* in dorsal aspect. *C*, a left anterior ventro-lateral plate of *B. canadensis* in ventral aspect. The brachial process removed. *D*, a left posterior ventro-lateral plate of *B. canadensis* in ventral aspect.

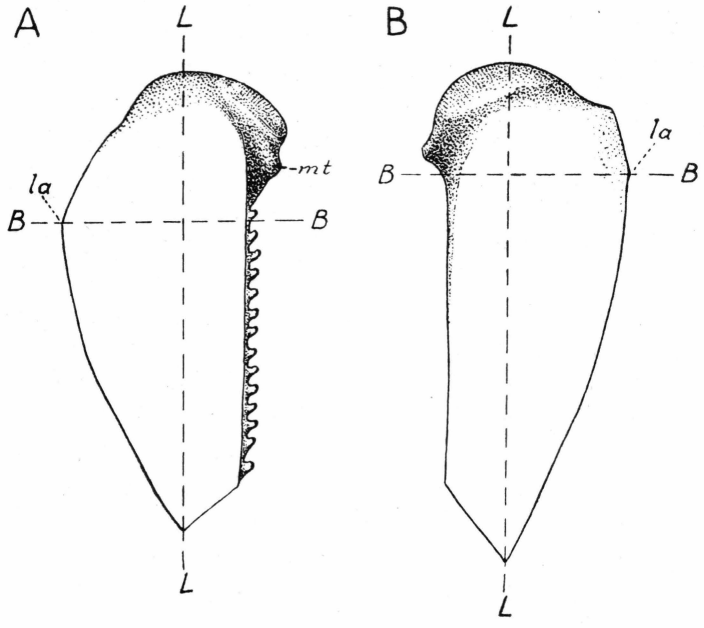
B–B, *Bv–Bv*, transverse lines along which the breadth-measurements have been taken; *L–L*, L_1–L_1, lines, parrallel with the longitudinal axis of the dorsal or ventral walls of the trunk-armour, along which the length-measurements have been taken; *T–T*, T_1–T_1, transverse lines through the foremost and hindmost corners of the plates; T_2–T_2, transverse line through the hindmost ventral part of the lateral lamina of the posterior ventro-lateral plate.

For explanation of other index letters see text-figs. 43, 44, 45, 47, 48, 50, 51, 52 and 53 respectively.

through the hindmost corner of the dorsal lamina and at right angle to the line *L–L*. Length of lateral lamina: along the dorso-lateral ridge (*dlr*) backwards to the corner *cs* (the postero-lateral corners of the dorsal wall of the trunk-armour as a whole). Total breadth: across the dorsal corner (*d*) and the ventral margin of the lateral lamina, along a line *B–B*, at a right angles to the line *L–L*. Breadth of dorsal lamina: across the dorsal corner (*d*) and the dorso-lateral ridge (*dlr*) along the line *B–B*. Height of lateral lamina: from the dorso-lateral ridge (*dlr*) straight down to the antero-ventral corner of the lamina and thus at or close behind the suture with the lateral lamina of the anterior dorso-lateral plate.

Anterior ventro-lateral plate (text-figs. 2C, 51). – Total length and length of the ventral lamina: from the antero-lateral corner (*al*) of the subcephalic division of the ventral lamina backwards to a transverse line, T_1–T_1, through the hindmost postero-ventro-lateral corner of the plate-along a line, *L–L*, parallel with the longitudinal axis of the ventral wall of the trunk-armour. Length of lateral lamina: from the prepectoral corner (*prc*) of the plate backwards along a line L_1–L_1, parallel with the longitudinal axis of the ventral wall of the trunk-armour, to the transverse line T_1–T_1 through the hindmost postero-ventro-lateral corner (*vlc*) of the plate. Height of lateral lamina (text-fig. 51A): the perpendicular distance from the exposed dorsal corner (*de*) of the lamina to the ventral margin of the articular fossa (*f. ap*) of the pectoral fin. Breadth of ventral lamina: across the prepectoral corner (*prc*) and the medial margin of the lamina, along a transverse line, *B–B*, at a right angles to the longitudinal axis of the ventral wall of the trunk-armour. Length of subcephalic division of ventral lamina: from the antero-lateral corner (*al*) of the lamina to a transverse line *B–B* through the prepectoral corner (*prc*) along the line *L–L*.

Posterior ventro-lateral plate (text-figs. 2D, 53). – Total length and length of ventral lamina: between the transverse lines *T–T* and T_1–T_1 thrcugh the foremost and hindmost ends of the ventral lamina, along the longitudinal axis, *L–L*, of the ventral wall of the trunk-armour. Total breadth: across the dorsal corner (*dc*) and the medial margin of the plate along a line, *B–B*, at right angles to the longitudinal axis of the ventral wall of the trunk-armour. Length of lateral lamina: from the antero-ventral corner of the lamina, at the transition to the ventral lamina, backwards to the transverse line T_2–T_2 through the postero-ventral end of the lateral lamina, along a line, L_1–L_1, parallel with the longitudinal axis of the ventral wall of the trunk-armour. Height of lateral lamina: across the dorsal corner (*dc*) of the lamina and the ventro-lateral ridge (*vlr*). Breadth of ventral lamina: across the ventro-lateral ridge and the medial margin, along a transverse line, *Bv–Bv*, a little behind the part (ma_1) of the medial margin of the lamina that is connected with the median ventral plate and



Text-fig. 3. *A*, a left dorsal central plate of *Bothriolepis canadensis*. Dorsal aspect. *B*, a left ventral central plate 1 of *B. canadensis*. Ventral aspect. From the same proximal segment as the plate in *A*. $^{6}/_{5}$.
B–B, *L–L*, lines along which the breadth and length respectively have been measured; *la*, lateral angle; *mt*, medial postarticular thickening.

at right angle to the longitudinal axis of the ventral wall of the trunk-armour (thus a little behind the corner marked cm_2). Length of subanal division of ventral lamina: from a transverse line T_2–T_2, passing through the hindmost ventral end of the lateral lamina transversally and at right angles to the longitudinal axis of the ventral wall of the trunk-armour, to a transverse line T_1–T_1, through the posterior end of the plate parallel to the line T_2–T_2.

Dorsal central plate 1 (text-fig. 3A). – Length: from the proximal end to the distal corner. Breadth: across the lateral angle (*la*) of the lateral margin and the dorso-medial margin, exclusive of both the dorso-medial row of spines and the medial lamina.

Ventral central plate 1 (text-fig. 3B). – Length: from the proximal end to the distal corner. Breadth: across the lateral angle (*la*) and the medial margin behind the medial postarticular thickening (*mt*) and including the medial lamina.

The other plates of the pectoral fin-armour. – Length: maximal length. Breadth: maximal breadth.

The angle between the dorsal and ventral walls of the trunk-armour has been measured on the outside of the anterior dorso-lateral and mixilateral plates.

Ratios between two different dimensions, as for instance between breadth and length, are given in the same way as by Gross (1940b, p. 23; breadth : length × 100) and are thus expressed in percents.

Historical remarks on the subfamily Bothriolepinae Stensiö 1931 and the present limitation of that subfamily.

The subfamily *Bothriolepinae* was erected by the present writer in 1931 (Stensiö 1931, pp. 156–158) and has later on been adopted by Gross (1932b, p. 23; 1933a, p. 36). At present it includes *Bothriolepis* and a new genus, *Grossilepis*, the latter of which will be defined below in this work.

The historical of the genus *Bothriolepis* Eichwald was exhaustively treated, first by Pander (1857, pp. 7–27), then by Traquair (1888b, pp. 495–501; 1894–1906, pp. 108–110), and finally, up to about 1931, by the present writer (Stensiö 1931, pp. 10–11). In 1931 and afterwards several new contributions to our knowledge of this genus have been given, which deserve to be briefly reviewed here.

In his paper "Les Poissons Famenniens de la Belgique" published in 1931 (pp. 15–19) Leriche for the first time gave a description of the *Bothriolepis*-remains recorded by Lohest in 1889 from Belgium (p. LVIII) and 1895 (p. XXXIX). The majority of these remains were referred to a new species, *B. lohesti* Leriche.

In 1932 Heintz (1932a, pp. 14–17) gave some supplementary contributions to our knowledge of *B. groenlandica* erected by him in 1930, material of which had also been described by the present writer in 1931 (Stensiö 1931, pp. 160–165).

In the same year Gross (1932b) published a catalogue on the *Antiarchi*. In this catalogue the classification of the group suggested by the present writer in 1931 (Stensiö 1931) was adopted. The catalogue under consideration critically treats all the species described at that time. As in addition it gives complete lists of the synonyms of the various genera and species and contains a practically complete list of the *Antiarchi*-literature until as late as almost up to its date of publication, it is very useful to all workers on the *Antiarchi*.

In 1933 there appeared a paper by Gross on the fishes of the Devonian of the Baltic States, a paper which filled a great gap in our knowledge of the *Bothriolepis*-species. In this paper Gross (1933a, pp. 36–43) gave a description of *B. cellulosa* (Pander) which, though known since 1846, had not before been properly described and defined. Moreover, in this paper

Gross also described a new *Bothriolepis*-species of very large size, *B. maxima*, and two plates of *B. ornata*, the genotype of *Bothriolepis*.

In 1932, 1935 and 1936 Hills (1932, p. 853; 1935, pp. 113–114; 1936, pp. 165–166) recorded new finds of *Bothriolepis*-remains from New South Wales and Victoria in Australia.

In 1938 Sohn (1938, pp. 111–113) introduced a new species name, *B. stensiöi*, for a head-shield from Scaumenac Bay, which was said in certain minor characters to differ from *B. canadensis*. As shown by Robertson (1938), however, this head-shield beyond question is of *B. canadensis*. Its supposed distinctive characters all fall within the normal range of variation of *B. canadensis*, on account of which the species name of *B. stensiöi* has to be dropped.

In 1939 Obrutschew (1939, pp. 115–116) described a mixilateral plate of a new species, *B. turanica*, from the upper Devonian near Tashkent in Turkestan. This new species is of special interest as the dorsal wall of its trunk-armour seems to have been of a high type.

In the same year the present writer (Stensiö 1939b, pp. 133–134) published a brief note on the fish-fauna of the Devonian of East Greenland in which inter alia the great variability of the Greenland species of *Bothriolepis* was pointed out.

A brief paper published by Obrutschewin in 1940 (pp. 890–892) inter alia contains several statements concerning new finds of *Bothriolepis* and the occurrence of representatives of that genus in Siberia and Central Asia. This paper is of particular interest from a stratigraphical point of view.

In 1940 *Bothriolepis*-remains were described for the first time from China (Chi 1940). These remains were referred to a new species, *B. sinensis* Chi.

Finally in a large paper published in 1941 Gross (1941a) treated the *Bothriolepis*-species of the *Cellulosa*-marl of Livonia. The first part of this paper contains very detailed and fully modern descriptions of *B. cellulosa* and of a new aberrant, highly interesting species, *B. tuberculata*, whereas the second and last part of the paper deals mainly with general problems concerning the pectoral fins of the *Antiarchi*. In the latter part a new terminology of the bones of the pectoral fin-armour is suggested, a new terminology which from all points of view is preferable to the current one, and which, as has been pointed out above (pp. 8–9), will be adopted in the present work[1]).

The second genus, *Grossilepis*, now included in the subfamily *Bothriolepinae* has been erected by the writer for the species *Bothriolepis tuberculata* Gross referred to just above (cf. Gross 1941a, pp. 32–57, 69–70). This genus will be discussed below and it is superfluous, therefore, to enter upon its characters here. In this connection it may be mentioned, however, that it is closely akin to *Bothriolepis*.

[1]) Concerning a more recent paper by Gross see under the Addenda at the end of thi work.

Diagnosis of the subfamily Bothriolepinae.

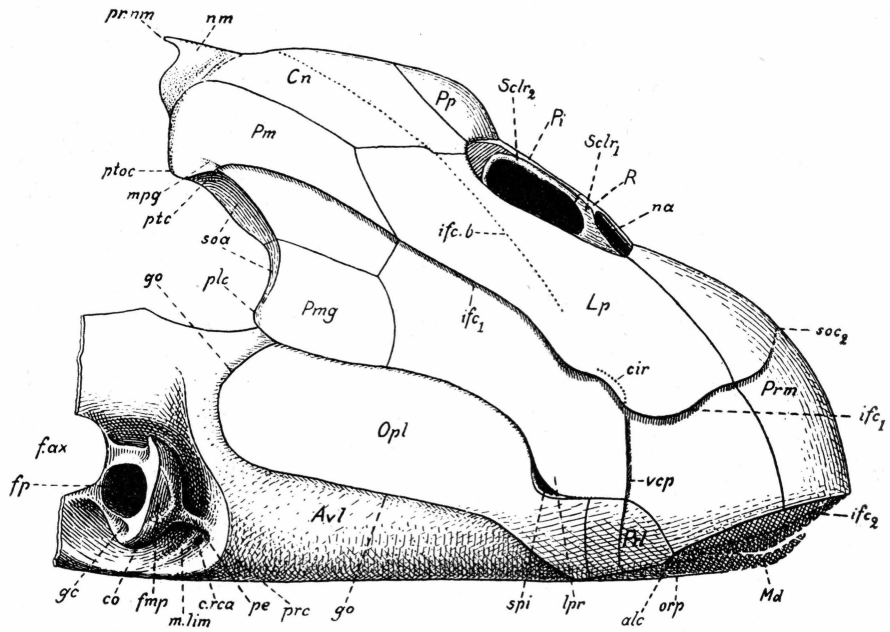
The diagnosis which at present can be given of the subfamily *Bothriolepinae* is as follows (cf. also Stensiö 1931, p. 158). Bothriolepid forms (cf. pp. 214–219) with the postero-lateral corners of the head-shield situated far in front of the posterior margin, at or somewhat behind a transverse plane through the orbital fenestra. Subobstantic area long, usually directed much laterally. Postpineal plate normally not in contact with the lateral plate of either side, but separated from that plate by the foremost part of the centro-nuchal plate participating into the formation of the posterior boundary of the orbital fenestra. Postmarginal plate fairly broad, clearly quadrilateral, and not overlapping any part of the outside of the anterior part of the anterior dorso-lateral plate. Extralateral (opercular) plate represented by two plates: a small anterior prelateral plate, and a long posterior extralateral plate proper. Infraprelateral, extramandibular, submandibular and subhyoideal plates present and fairly well developed. Trunk-armour in certain species with a high median dorsal crest. Lower side of dorsal wall of trunk-armour with a well developed levator fossa, a postlevator thickening, a post-levator crest, anterior and posterior ventral processes, and anterior and posterior ventral pits. In medium-sized and fully mature specimens this side of the dorsal wall also characterized by the presence of a median ventral ridge and a median ventral groove. Anterior median dorsal plate with a broad anterior margin and mostly relatively broad in proportion to its length; the anterior division of its lateral margin with a more or less pronounced postnuchal notch, and a laterally directed external postlevator process, causing the suture between the plate under consideration and the anterior dorso-lateral plate to be fairly undulating. Posterior median dorsal plate with a normally well developed lateral process on the posterior part of its lateral margin. Processus obstans broad (high) and strongly developed. Posterior dorso-lateral plate always completely fused with the posterior lateral plate forming with it a compound mixilateral plate. Semilunar plate unpaired and small. Posterior unarmoured division of trunk relatively long and slender with a highly vestigial squamation. Pectoral fin, when adducted to the body-wall, extending backwards to or mostly even somewhat behind a transverse plane through the posterior end of the ventral wall of the trunk-armour and

throughoust its extent equipped with a lateral and a medial series of spines. Dorsal central plate 2 always very short, not suturing with the dorsal central plate 1, but widely separated from it by the lateral and medial marginal plates 2. Medial marginal plate 1 long and slender. Dorsal central series and medial marginal series of bones of the distal segment of the pectoral fin often composed of 3 and sometimes even of 4 independent elements. Ornament in young individuals normally formed by continuous ridges with a regular reticular disposition; ornament in medium-sized and fully mature individuals more irregularly reticular, in many species more or less completely disolved into short ridges or tubercles, and in certain species even almost completely tubercular. Posterior oblique cephalic pit-line groove and vertical pit-line groove of the cheek generally present and well developed. Middle pit-line groove of skull-roof shallow and usually represented only by a lateral part connected with the upper infraorbital and postotic grooves at their transition into each other.

General organization.

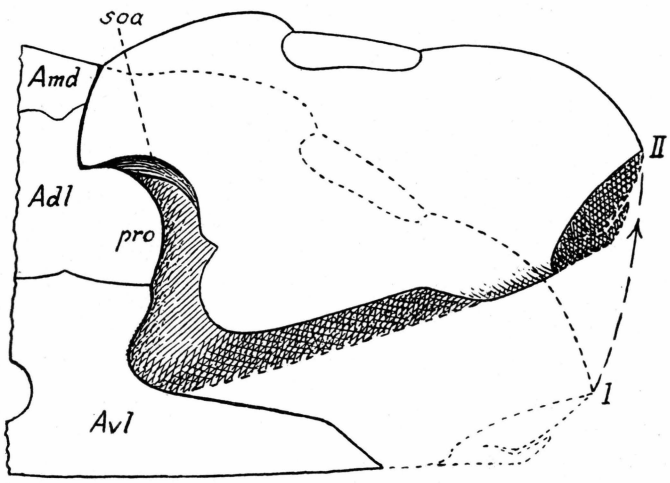
Head.

As is well known, the head in the *Bothriolepinae* in its general appearance is approximately as in the other *Antiarchi*-groups. As in those groups, it is broad and relatively low (text-figs. 4–14, 114). The eyes lay close to one another on its dorsal side and were completely bounded off from the cheek by a broad bridge of dermal bone which constitutes the lateral part of the head-shield (text-figs. 4, 9, 10, 114). The nasal apertures were situated close to one another between the foremost parts of the eyes, in the anterior part of the orbital fenestra, and were thus dorsal in position, as in Rhenanid Arthrodires (text-figs. 4, 6, 7, 21 C, 114). The cheek is low, short and developed principally only in the preorbital division of the skull (text-figs. 4, 38, 40 B, 114). The mouth opening lay postero-ventrally to the rostral end of the skull and was thus not terminal, but ventral, in position (text-figs. 4, 7, 8, 40 B, 114). The gill-arches did not extend backwards into the trunk, but were all situated underneath the cranium (text-fig. 7). They were covered from the outside by a long, but relatively low gill-cover continuous with and forming the posterior prologation of the cheek. The postspiracular gill-slits opened into a common gill-chamber, the external opening of which was behind and below the gill-cover (text-fig. 4). As will be made clear below, the primary rostral tip of the snout corresponding to that of the Brachythoracid Arthrodires is to be sought for approximately at the posterior part of the rostral plate, that is to say in the anterior part of the orbital fenestra, and thus far behind the anterior margin of the head-shield. The preorbital division of the head-shield as a whole, or at any event in its anterior longer portion, must, therefore, obviously represent those parts of the skull of the Brachythoracid Arthrodires and primitive Placoderms in general which lay antero-ventrally and latero-ventrally to the tip of the snout on the rostrally and laterally directed faces of the ethmoidal region of the endocranium. As we shall see, this division probably includes also certain parts primarily belonging to the cheek of the primitive Placoderms. Hence it is developed somewhat as the preorbital part of the skull-roof in Rhenanid Arthrodires (cf. pp. 31–32, 196–202 and text-figs. 68, 70 below; cf. also Stensiö 1931, pp. 30, 57). As to its proportions the division in question of the head-shield is broad and, as in *Pterichthyodes* (Traquair 1894–1906, text-figs.



Text-fig. 4. *Bothriolepis canadensis*. Restoration of the head in its most lowered position in relation to the foremost part of the anterior ventro-lateral plate of the trunk-armour. Lateral aspect. On account of the condition that the restoration is made mainly after a photograph the parts of it that were nearest to the objective have become somewhat too large in proportion to those situated more in the background. Approximately × $^{2}/_{1}$. *Avl*, anterior ventro-lateral plate (anterior part); *Cn*, centro-nuchal plate; *Lp*, lateral plate; *Md*, mandible; *Opl*, extralateral (opercular) plate; *Pi*, pineal plate; *Pm*, paranuchal-marginal plate; *Pmg*, postmarginal plate; *Pp*, postpineal plate; *Prl*, prelateral plate; *Prm*, premedian plate; *R*, rostral plate; $Sclr_1$, $Sclr_2$, anterior and postero-dorsal sclerotic plates respectively; *alc*, antero-lateral corner of the head-shield; *cir*, semicircular pit-line groove; *co*, pars condyloidea of the processus brachialis; *c.rca*, outer opening of a canal; *f.ax*, foramen axillare; *fmp*, area probably for the origin of the protractor muscles of the pectoral fin; *fp*, funnel pit of the processus brachialis; *gc*, groove dorsally and ventrally to the funnel pit; *go*, gill opening; ifc_1, upper infraorbital sensory canal groove; ifc_2,lower infraorbital sencory canal groove; *ifc.b*, posterior oblique cephalic pit-line groove; *lpr*, supraspiracular process; *m.lim*, margo limitans (inferior part) of the fossa articularis pectoralis; *mpg*, middle pit-line groove of the skull-roof; *na*, external nasal aperture; *nm*, obtected nuchal area; *orp*, oral pit-line groove; *pe*, pars pedalis of the processus brachialis; *plc*, postero-lateral (preobstantic) corner; *prc*, prepectoral corner; *pr.nm*, posterior median process of centro-nuchal plate; *ptc*, cephalic division of main lateral line groove; *ptoc*, postobstantic corner; *soa*, subobstantic area; soc_2, anterior median section of the supra-orbital sensory canal groove, the anterior median pit-line groove; *spi*, spiracle (external aperture); *vcp*, vertical pit-line groove of the cheek.

51, 52; Gross 1933a, text-fig. 14), nearly or approximately as long as the post-orbital division (text-figs. 4, 9–14, 82–84, 208, 224, 238, 258, 264, 265). It is thus longer relatively than in *Asterolepis* (Traquair 1894–1906, text-figs. 37–39; Gross 1931, pl. 12, fig. 7; Watson 1932, text-figs. 3, 4; Stensiö 1938, text-figs. 1, 7; Nilsson 1941, text-figs. 3, 4, 8) and *Remigolepis* (text-fig. 16; cf. also Stensiö 1931, text-fig. 80), but shorter than in *Microbrachius* (Watson 1935, text-fig. 28). The postorbital division of the head-shield, as normally in the *Antiarchi*, is much broader than long (text-figs.



Text-fig. 5. *Bothriolepis canadensis*. Sketch of the head in its natural position in relation to the foremost part of the trunk-armour. The sketch shows the head in its maximally lowered (*I*), and maximally raised (*II*) positions.
Adl, anterior dorso-lateral plate (anterior part only); *Amd*, anterior median dorsal plate (anterior part only); *Avl*, anterior ventro-lateral plate (anterior part only); *pro*, processus obstans; *soa*, subobstantic area.

4, 9–14, 82–84, 219, 233A, 249, 253A, 266, 273, 274). As in *Microbrachius* (Watson 1935, text-fig. 28), the paired obstantic margin (*om*, text-fig.s 9–12) of the head-shield is long, obliquely rostro-caudal in position, and usually directed much laterally. Owing to this the paired postero-lateral (preobstantic) corner (*plc*) of the head-shield is situated much further forward than in the *Asterolepidae* and *Remigolepidae*, but not quite as far forwards as in *Microbrachius*. More precisely, this corner lies at a transverse plane through or somewhat behind the posterior margin of the orbital fenestra, whereas in the *Asterolepidae* and *Remigolepidae* it is situated approximately opposite the middle of the orbital fenestra. Finally, a very characteristic feature of the head-shield is the shape of its paired lateral margin. Owing to the fact that the postero-lateral corner (*plc*) lies far forwards this margin is relatively short. It is not concave throughout its extent, but presents a more or less well pronounced supraspiracular process (*lpr*) which is bounded by a prelateral notch (*nprl*) in front and by a spiracular notch (*nsp*) behind (text-figs. 4, 9–14).

As is clearly seen from well preserved head-shields of various *Bothriolepis*-species, the head in the *Bothriolepinae* is shaped about as follows (text-figs. 4, 5, 38, 40B, 77A, 81A, 114). Its dorsal face is more or less strongly convex both in rostro-caudal and transverse directions. Each of its lateral faces in its foremost part, in front of the supraspiraculat process, is directed much laterally, whereas further backwards it faces more upwards, sometimes probably nearly as much upwards as the adjacent lateral parts of the

dorsal face. In *B. canadensis,* at any rate, the lateral face is lower than in *Asterolepis* and probably also than in *Remigolepis.* Finally, the ventral face was probably somewhat convex both from in front backwards and from one lateral side to the other. The foremost part of the ventral face, with the mouth-opening and the jaws, was directed somewhat forwards, whereas the longer posterior part of this face was directed mainly straight downwards.

The articular connection between the head and trunk, the occipital articulation, was fundamentally as in *Asterolepis* (cf. Gross 1931, pp. 46–48; 1933b, text-figs. 2, 3). The head articulated against the vertebral column by the posterior end of the occipital region, against the transversal laminae (the crista transversalis interna anterior) of the anterior dorso-lateral plates by the paranuchal trochleae, and against the precessus obstantes by the subobstantic areas (*soa,* text-figs. 4, 9, 10, 13, 14, 27, 28, 29, 82–84, 100, 273, 274, 279). These areas are much longer and reach much further forwards, however, than what is the case in the *Asterolepidae* (Gross 1933b, text-fig. 3), *Pterichthyodidae* and *Remigolepidae.* And hence in this respect the *Bothriolepinae* are very suggestive of *Microbrachius* in which the corresponding areas also have a considerable extent forwards and an obliquenly rostro-caudal position (Watson 1935, text-fig. 28).

As in the other *Antiarchi,* the mechanism of the occipital articulation was such that the head could be raised and lowered around a transverse axis through the paranuchal trochleae, whereas, on the other hand, it could not be bent laterally. When maximally lowered (text-figs. 4, 5, 38, 40B) it rested with the posterior parts of its lower side against the subcephalic divisions of the anterior ventro-lateral plates, thus against the subcephalic division of the ventral wall of the trunk-armour. In this position it was as follows. The dorsal side sloped rather steeply forwards. The tip of the snout was only slightly above the level of the ventral wall of the trunk-armour and the foremost part of its ventral side with the mouth-opening and the jaws was directed ventrally and somewhat anteriorly. The obtected nuchal area (*nm,* text-figs. 4, 9, 10) of the centro-nuchal plate rested firmly against the supranuchal area (*sna,* text-fig. 44) on the lower side of the anterior end of the anterior median dorsal plate. The posterior part of the centro-nuchal plate, by its obtected nuchal area, and the foremost part of the anterior median dorsal plate together with the subcephalic division of the ventral wall of the trunk-armour thus formed a complete stop for a further lowering.

The curvature of the articular areas of the paranuchal trochleae (*pcd,* text-fig. 19) seems to have enabled a rotation of about 25°–30° upwards of the head from the position which it occupied when maximally lowered, thus a rotation of about the same maximal amplitude as in *Asterolepis ornata* (Gross 1931, p. 48). This involves that the head could be raised at the maximum about as much (text-fig. 5, positoin II) that its rostral end was

about on a level with or somewhat higher than the transverse articular axis through the paranuchal trochleae. In this position the median part of its dorsal side as a whole was about horizontal in lateral aspect, and practically the whole of its lower side was elevated above the subcephalic division of the ventral wall of the trunk-armour.

The subobstantic area (*soa*, text-figs. 4, 5, 9, 11, 13, 14, 27, 28, 29, 82–84, 100, 273, 274, 279) is so developed and so placed that during the raising of the head generally it slid against the medial side of the processus obstans without obstructing the raising. In some cases, however, it is as broad and as horizontal in position that it seems to have stopped the raising already before the normal maximum, and in such cases the mobility of the head up and down may thus be suspected to have been more or less limited.

Endocranium.

With the exception possibly of a small Y-shaped bone, recorded by Patten (1912, e^1, text-fig. 253) and the writer (Stensiö 1931, p. 27), no remains of endocranial ossifications are to be found in the *Bothriolepinae*. The endocranium in the *Bothriolepinae* must, therefore, have consisted principally or entirely of cartilage without any impregnations or incrustations of lime. As no remains of ossified endocranial elements have been found in *Pterichthyodes, Gerdalepis, Asterolepis, Microbrachius, Grossilepis* and *Remigolepis* either, the conclusion readily suggests itself that the endocranium was entirely or practically entirely cartilaginous in all the *Antiarchi*-forms known from the Middle and Upper Devonian. The fact that it is more or less strongly ossified in representatives of different groups of Arthrodires and Acanthodians (Stensiö 1925, pp. 92–140, 150, 152–157, 160–164, 170, 182–184, 187; 1934a, pp. 4–23, 37–43, 48–64; Holmgren & Stensiö 1936, pp. 324–331; Hills 1936b; Gross 1937, pp. 22–23; 1940b, pp. 50–54; Watson 1937, pp. 84–85, 96–102, 117, 129–130) must involve, however, that the endocranium primarily was fairly well ossified in all primitive Placoderms and thus also in the primitive and geoloaically oldest *Antiarchi* still unknown to us. Its cartilaginous condition in the Middle and Upper Devonian *Antiarchi* is, therefore, certainly secondary and due to reduction.

The small Y-shaped bone referred to just above, besides in *B. canadensis*, has now been met with also in *B. groenlandica* (*E*, pl. 6, fig. 1; see that species) and in *Remigolepis* (Part III of the present monograph); and, as thus it occurs in representatives of the two families *Bothriolepidae* and *Remigolepidae*, which are widely separated from one another, it is likely that it was present in the *Antiarchi* in general. One may expect, therefore, that it will be found also in *Grossilepis, Microbrachius, Pterichthyodes, Gerdalepis*

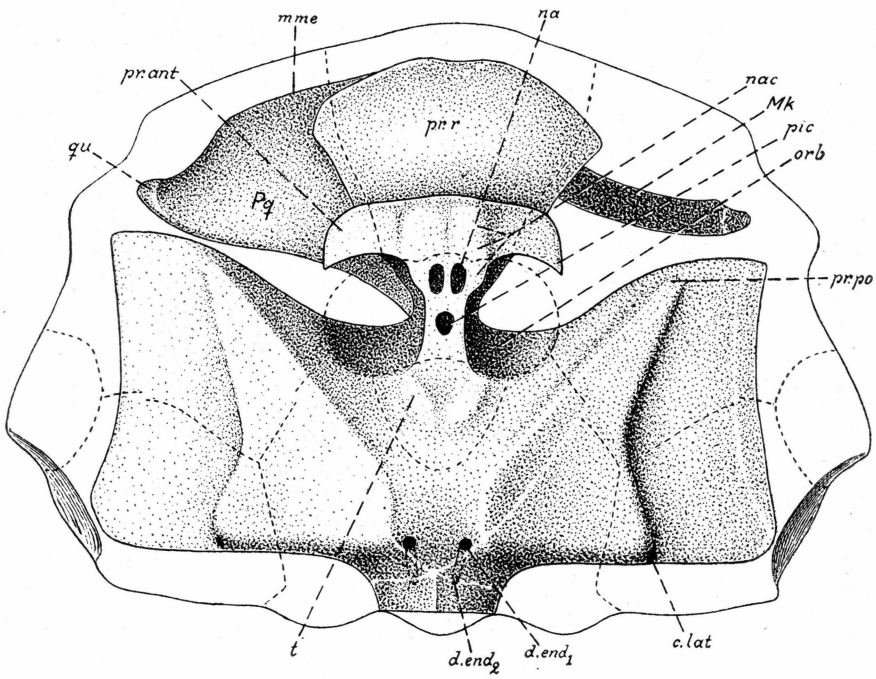
and *Asterolepis*. As in its structure the bone is mostly as a dermal element, its nature of a substitution bone can by no means be considered as certain. If actually a substitution bone it can only have been situated in the foremost part of the interorbital wall close behind the nasal capsules, and it would then correspond to the small *T*-shaped or *Y*-shaped bone found in *Coccosteus decipiens*, which probably had a similar position in the interorbital wall (Heintz 1931, pp. 299–300, text-fig. 6; 1938, p. 13, pl. 3, fig. 4; Watson 1934, pp. 442–443). In this case, of course, it would be an interorbital vestige of the large continuous ossification which in *Buchanosteus osseus* (Hills 1936b, pp. 216–225, text-figs. 2–4, Stensiö 1945, p. 24), the Dolichothoracid, Petalichthyid, and Rhenanid Arthrodires occupies the whole endocranium (Stensiö 1925, pp. 92–140, 150, 152–157, 160–164, 170, 182–184; 1934a, pp. 48–64, text-figs. 26–28; Stensiö 1944, pp. 2, 13, 1945 Holmgren & Stensiö 1936, pp. 324–331, text-figs. 250, 251, 254) and in *Pholidosteus* and *Leiosteus* is subdivided into several minor bones (Stensö 1934a, pp. 4–23, 37–43, text-figs. 1–3, 7, 20–22). If, on the other hand, it is a dermal bone it may either represent the anterior superognathals of the Euarthrodires, fused into one plate, or else it is a vestige of the parasphenoid of the *Dolichothoraci* and *Brachythoraci* (Stensiö 1945, p. 67).

Despitè the condition that the endocranium thus is not preserved at all, or perhaps is represented only by the small *Y*-shaped bone discussed just above several of its general characters may nevertheless be hypothetically deduced on the basis of the structure of the head-shield. A first attempt at a hypothetic deduction of its shape on such a basis was undertaken by the writer in 1931 (Stensiö 1931, pp. 27–30, 52–57), and a new one will now be made here with special reference to the *Bothriolepinae*. At this attempt the conditions in Arthrodires, which are now known to a certain extent, have also been taken into consideration. Through this a deeper insight could be gained into the special conditions in the *Antiarchi* than what was the case in 1931.

As shown by the writer already in 1931, the endocranium in the *Bothriolepinae* and *Antiarchi* in general must have been low and broad (text-figs. 6, 7). However, it cannot have been fully as low as was supposed on that occasion, for, as will be demonstrated below, it must be presumed, at least in the ethmoidal and orbitotemporal regions, to have extented basally below the level of the orbital margins of the premedian and lateral plates, that is to say below the orbital chamber and the suborbital fenestra (text-figs. 11, 12, 15C).

We shall now proceed to a discussion of the development of the various regions of the endocranium, beginning with the ethmoidal region, but before doing so it is necessary first to enter briefly upon the question concerning the position of the nasal apertures.

In 1931 the writer (Stensiö 1931, pp. 28–30, 54–56) was led to accept



Text-fig. 6. *Bothriolepis canadensis*. Sketch illustrating the writer's opinion of the shape of the endocranium. The endocranium shown in dorsal aspect in its position in relation to the head-shield. The palatoquadrate of the left side and Meckel's cartilage of the right side drawn somewhat in their probable position in relation to the endocranium and head-shield. The outlines of the orbital openings and the sutures of the head-shield denoted with broken blacks lines, the main sensory canal grooves with continuous red lines, and the pit-line grooves with dotted red lines. Approximately $\times$ $^4/_3$.
Mk, Meckel's cartilage; *Pq*, palatoquadrate; *c.lat*, canal probably for a lateralis nerve; $d.end_1$, ventral opening of the canal for the ductus endolymphaticus in the centro-nuchal plate; $d.end_2$, position of the dorsal opening of the canal for the ductus endolymphaticus in the centro-nuchal plate; *mme*, margin of the palatoquadrate attached to the inside of the mental plate; *na*, nasal aperture; *nac*, nasal capsule; *orb*, orbital cavity and the possible floor of the posterior part of this cavity; *pic*, pineal opening; *pr.ant*, antorbital process; *pr.po*, postorbital process; *pr.r*, rostral process; *qu*, pars quadrata of the palatoquadrate; *t*, possible elevation underneath the postmedian plate.

the opinion previously advanced by Patten (1904, p. 112; 1912, p. 375) that the external nasal apertures were situated close to one another in the foremost part of the orbital fenestra and that they were separated from one another by the middle, rostro-caudal, part of the rostral plate ("prepineal plate"). The correctness of this opinion is now borne out beyond question by the conditions in *Remigolepis*. In this *Antiarchi*-form (text-figs. 16, 22; cf. pp. 68 below; cf. also Part III of this monograph) the rostral plate is much broader than in *Bothriolepis* and besides of such a shape as fully clearly to prove that it was developed in relation to a paired, antero-dorsally facing opening in the foremost part of the orbital fenestra close behind the premedian plate, a paired opening which cannot be interpreted as anything

else but an external nasal aperture. Contrary to what is the case in *Bothriolepis* (text-figs. 4, 21 C, 114) the external nasal opening of either side in *Remigolepis* is not bounded laterally by the anterior sclerotic plate, but solely by a broad antero-lateral process of the rostral plate itself.

The fact that the external nasal apertures thus lay close to one another in the foremost part of the orbital fenestra far behind the tip of the snout and on the dorsal side of the cranium shows beyond question that the nasal capsules must have been situated in the foremost part of the orbital chamber, between the anterior parts of the eye-balls. It is obvious, therefore, that the nasal capsules formed the foremost dorsal part of the interorbital wall (*nac*, text-figs. 6, 7). Because of this position they must have been relatively small and situated close to one another, and hence they were certainly separated only by a thin wall or septum.

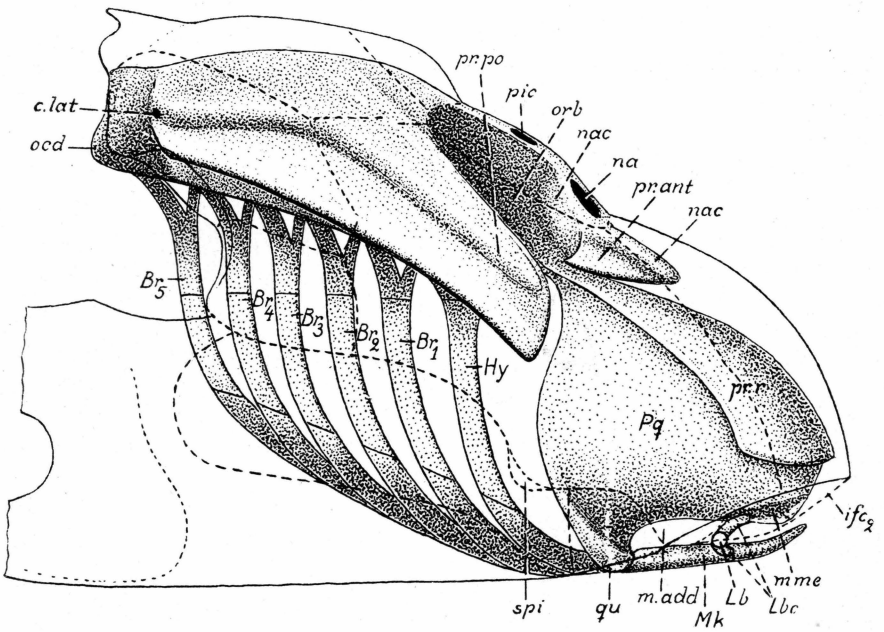
In *Bothriolepis*, in which a well developed preorbital recess (*prh*. prh_1, text-figs. 13–15; cf. pp. 48–52) is present in the head-shield, the nasal capsules seem to have extented forwards into the unpaired median division of this recess (*prh*) situated in the premedian plate, for this division of the recess (cf. pp. 48–52) is more or less bounded off from the paired lateral one (prh_1) and developed in such a manner that it must have housed a paired structure penetrating into it from behind, that is to say from the orbital chamber. Laterally to each nasal capsule the ethmoidal region in *Bothriolepis* was in all probability equipped with an antorbital process (*pr. ant*, text-figs. 6, 7) which lay mainly in the lateral paired division of the preorbital recess developed within the lateral plate of either side (prh_1, text-figs. 13–15, 233 A; cf. pp. below). Judging from the size and extent of the lateral division of the preorbital recess the antorbital process probably was considerably shorter in *Bothriolepis cellulosa* and *B. canadensis* than in *B. groenlandica* and *B. maxima*. As it could not have reached down to the very bottom of the ethmoidal region, the process in question seems to have been of a nature and embryonic origin similar to those in Selachians and fishes in general (Holmgren & Stensiö 1936, p. 298; text-figs. 238–241, 245, 246, 260, 262, 332, 334). In *Asterolepis* and *Remigolepis*, in which the preorbital recess is vestigial or absent, the nasal capsules throughout or practically throughout their extent probably lay in the foremost part of the orbital chamber, and hence it was probably smaller in these two genera than in *Bothriolepis*. The same applies also to the antorbital process in *Asterolepis* and *Remigolepis* which may perhaps even have been vestigial or absent. In *Bothriolepis* and other *Antiarchi* the ventral part of the ethmoidal region situated below the nasal capsules must be presumed to have been produced forwards into a solid, broad, but rather thin rostral process of cartilage (*pr.r*, text-figs. 6, 7) which lay underneath the preorbital division of the head-shield. This probable rostral process, which seems to have been suggestive of the rostrum or rostral process in Selachians, in *Bothriolepis* presumably ended

anteriorly at the oblique premedian ridges (*ri*, text-figs. 11, 12, 20B, 220E) on the lower side of the head-shield and thus somewhat behind the rostral margin of the premedian plate, whereas, on the other hand, in *Asterolepis* and *Remigolepis* it probably reached still further forwards. As far as may be judged it was needed both as a support for the preorbital division of the head-shield and, as will be made clear below in the account of the visceral endoskeleton (pp. 36–39), as an attachment for the larger anterior part of the palatoquadrate (text-figs. 6, 7).

Under the presumption that what has just been set forth is true in the main the ethmoidal region in the *Bothriolepinae* was somewhat as follows (text-figs. 6, 7). Taken as a whole it was in all probability very long. It consisted of a relatively short and broad postero-dorsal part, comprising the nasal capsules (*nac*) and the antorbital processes (*pr.ant*), and of an antero-ventral long part developed as a large rostral process (*pr.r*). The nasal capsules lay close to one another in the foremost part of the orbital chamber between the anterior parts of the orbits and between the foremost parts of the eye-balls, whence they extended forwards into the median part of the preorbital recess. Because of this forward extent into the preorbital recess they were probably larger than in *Asterolepis* and *Remigolepis*. The lateral part of the nasal capsule of either side which must have bulged out somewhat into the orbit, as we shall see (pp. 83–84), was covered from above by the large nasal division (*nd*, text-fig. 30A–C) of the anterior sclerotic plate of its side. In *Remigolepis* the corresponding part of the nasal capsule instead was covered dorsally by an antero-lateral process of the rostral plate (text-figs. 16, 22). The external nasal apertures (*na*) lay approximately above the posterior halves of the nasal capsules and were bounded (text-figs. 4, 21C, 114) medially and posteriorly by the rostral plate, laterally by the nasal division of the anterior sclerotic plates. (In *Remigolepis*, on the other hand, they were bounded also laterally by the rostral plate.) Their anterior boundary was formed, as normally in the group, by the median part of the premedian plate which, owing to this, often is produced backwards into a short nasal process (*p*, text-figs. 9–11, 13, 20), sometimes slightly notched at its posterior end (cf. pp. 65–67). The antorbital process (*pr.ant*) was well developed and quite long in certain species. The rostral process (*pr.r*) which was formed by the ventral parts of the ethmoidal region, was long and broad, and extended forwards far beyond the nasal capsules.

As may readily be seen from the statements given here concerning its development, the ethmoidal region in the *Bothriolepinae* and *Antiarchi* in general was clearly of a somewhat modified Euarthrodiran type (cf. text-figs. 66, 67; cf. Stensiö 1934a, pp. 5–13, 50–51, text-figs. 1–4, 14, 15, 26; 1945, pp. 8–11, 60–61). It agrees fundamentally with that in Euarthrodires in the following characters: 1) the position of its postero-dorsal part in relation to the orbitotemporal region and the orbits; 2) the relatively small

breadth of its posterc-dorsal part in proportion to the breadth of the otic region; 3) the position of the nasal capsules within the region itself and in relation to the orbits; 4) the position of the nasal capsules close to one another; 5) the position of the external nasal apertures in relation to the region as a whole, to the nasal capsules, and to one another. These apertures, however, are secondarily directed more dorsally than in Euarthrodires; 6) the position of the external nasal apertures in relation to the rostral plate; and finally, as will be shown below (pp. 171–189), 7) the position of the external nasal apertures in relation to the sensory canal canal grooves. – These characters indicate that the region must have arisen from an Euarthrodire-like one which in most respects was suggestive of that in *Pholidosteus,* though with well developed antorbital processes. Its development from one of a *Pholidosteus*-like shape may be assumed to have taken place somewhat as follows. The dorsal part of the region including inter alia the nasal capsules was much shortened as compared to that of the Euarthrodires; the nasal capsules were pushed backwards so that they became situated as in Rhenanid Arthrodires. From being primarily directed anteriorly the external nasal apertures were turned almost straight upwards, but retained their position close to one another. The ventral part of the region was produced forwards into a large rostral process. In consequence of these processes of transformation the dorsal part of the internasal wall corresponding to the rostral tip of the endocranium of the Euarthrodires and several other non-Rhenanid Arthrodirens (text-fig. 67; cf. Stensiö 1934a, text-figs. 1–4, 14, 15) from a primarily forward pointing, rostral position was pushed upwards and backwards to a dorsal position far behind the rostral end of the skull. This dorsal part of the internasal wall in fact shifted as far backwards as to underneath the rostral plate, more precisely to a point just in front of or underneath the postnasal transverse part of the rostral plate, and thus to a point between the foremost parts of the orbits. In these circumstances it follows, of course, that the preorbital division of the head-shield in the Antiarchi must have been formed in the main by an outgrowth and upward swinging of a mass of tissue whose homologue in primitive Placoderms in general, in Euarthrodires and other non-Rhenanid Arthrodires lay on the rostral and lateral faces of the ethmoidal region ventrally, and latero-ventrally to the anteriorly directed nasal apertures, between them and the mouth-opening. However, it was chiefly only the upper part of that mass of tissue situated dorsally to the ethmoidal parts of the infraorbital sensory canal grooves that was modified into the preorbital division of the head-shield. The ventral part of the mass of tissue in question, on the other hand, retained its position ventrally to the tip of the snout. The outgrowth leading to the formation of the preorbi-



Text-fig. 7. *Bothriolepis canadensis*. Sketch illustrating the writer's opinion of the development of the endocranium and visceral endoskeleton in lateral view and in relation to the exoskeleton. The gill-arches drawn only to show their approximate position in relation to the endocranium and exoskeleton of the head. Their number, shape and segmentation are arbitrary. The extent of the exoskeleton (the head-shield, the cheek-plates and the anterior part of the anterior ventro-lateral plate) indicated with broken black lines. The course of the main sensory canal grooves with continuous red lines, the pit-line grooves with dotted red lines. × $^2/_1$ approximately.

Br_1–Br_5, branchial arches 1–5; *Hy*, hyoid arch; *Lb*, small bone behind the angle of the mouth-opening; this bone either a substitution bone in a labial cartilage or a dermal bone developed in relation to a labial cartilage; *Lbc*, labial cartilage; *Mk*, Meckel's cartilage; *Pq*, palatoquadrate; *c.lat*, canal probably for a lateralis nerve; ifc_2, lower infraorbital sensory groove; *m.add*, notch in the lower margin of the palatoquadrate for the m. adductor mandibulae; *mme*, margin of the palatoquadrate attached to the inside of the mental plate; *na*, external nasal aperture; *nac*, nasal capsule; *ocd*, occipital condyle; *orb*, orbital cavity; *pic*, pineal opening; *pr.ant*, antorbital process; *pr.po*, postorbital process; *pr.r*, rostral process; *qu*, pars quadrata of the palatoquadrate; *spi*, spiracular opening.

tal division of the head-shield also affected the lower part of the ethmoidal region itself, causing it to be produced into a rostral process.

Both at an earlier occasion (Stensiö 1931, pp. 30, 57) and above in this work (p. 21) it has been mentioned that in regard to certain characters in their ethmoidal region the Rhenanid Arthrodires are developed in a manner similar to that in the *Antiarchi*. For the sake of comparison we shall now dwell a little upon the ethmoidal region in Rhenanid Arthrodires.

The ethmoidal region of the Rhenanid Arthrodires is now rather well known in *Jagorina* (text-fig. 70; cf. also Holmgren & Stensiö 1936, text-

fig. 254), whereas the anterior part of the head-shield covering it is found more or less well preserved in *Gemündina* (Broili 1930a, text-figs. 2, 3; 1933a, text-figs. 1, 3, 4), *Asterosteus* (text-fig. 68) and *Jagorina* (text-fig. 70). In these three forms the preorbital division of the skull including both the ethmoidal region itself and its exoskeleton is fairly uniformily developed as to its outlines and general features. The nasal capsules are situated very close to one another between the anterior halves of the orbits, just as in the *Antiarchi*, and, as in then, they do not extend forward to the anterior end of the ethmoidal region. The external nasal apertures (*na*), as in the *Antiarchi*, are also situated close to one another on the dorsal side of the region. More precisely, they lie on the middle part of the dorsal side of the interorbital wall, far behind the rostral tip of the snout. The skull-roof has, therefore, an anterior preorbital and prenasal division, which is suggestive of the preorbital division of the head-shield in the *Antiarchi*. As will be demonstrated below (pp. 190–202), this preorbital and prenasal division of the skullroof in the Rhenanids differs from that of the *Antiarchi* chiefly in the following two respects: 1) anteriorly it includes bone components whose homologues in the *Antiarchi* lie on the ventral side of the rostral part of the head and form part of the mental plates; 2) laterally it is clearly devoid of bony cheek-components, whereas in the *Antiarchi* it seems also to comprise such components. – The median prenasal part of the ethmoidal region seems to correspond pretty well to the rostral process of the *Antiarchi*. The strongly developed lateral process on either side of the anterior part of the ethmoidal region, at any rate in its proximal dorsal part (*pr.ant*, text-fig. 70), is clearly an antorbital process. Its distal part however, is highly specialized and developed in a manner quite a different from that in the *Antiarchi*. This part is very large, occupied by an ossification of its own (*Anb*, text-fig. 70), and probably completely segmented off from the proximal part. It corresponds in all respects to the antorbital cartilage of the *Rajiformes* among the recent Selachians, and, as that cartilage, it forms a support for the excessively developed pectoral fin (Holmgren 1941, figs. 44, 45, 47, 50–55, 57).

From what is thus known concerning its development it is obvious that the preorbital division of the skull in the Rhenanid Arthrodires primarily was of the ordinary Arthrodiran type, in the main as represented in the Euarthrodires, and that from such a type it must have evolved much in the same way as the corresponding division in the *Antiarchi*. In contrast to what is the case in the *Antiarchi*, however, the homologue of the mass of tissue which in primitive Arthrodires in general and in Euarthrodires was situated on the rostral and lateral faces of the ethmoidal region has been practically entirely included in the head-shield. Because of this fact the mouth-opening has not retained its primary position ventrally to the tip of the snout, as in the non-Rhenanid Arthrodires and *Antiarchi*, but has been directed terminally or somewhat dorsally.

The *Antiarchi*-like development of the ethmoidal region and of the preorbital division of the head-shield in the Rhenanid Arthrodires here demonstrated cannot possibly mean that the Antiarchi and Rhenanid Arthrodires are directly or genetically more nearly related to each other. These two groups in most other respects differ so widely from one another that they must be assumed to represent two lineages, arisen independently from primitive Arthrodires. The agreements between them as to the ethmoidal region and the preorbital division of the head-shield are, therefore, in all probability parallelisms. Be this as it may, it is nevertheless of much interest that the same fundamental type of development both of the ethmoidal region itself and of the preorbital division of the head-shield is met with in two groups of Placoderms so widely different from one another as Rhenanid Arthrodires and *Antiarchi*.

The orbitotemporal region in the *Bothriolepinae* (text-figs. 6, 7) and *Antiarchi* in general was shorter than the ethmoidal and otic regions, but not quite as short as the occipital region. From a little behind the external nasal apertures it reached backwards only to a transverse plane somewhat behind the posterior margin of the orbital fenestra. Characteristic of it as a whole was also that it was narrower than the other regions. Across its dorsal wall it was about as broad as the pineal and postpineal plates (text-fig. 21 C), whereas further ventrally, below the cranial cavity, it was in all probability still narrower. If near its transition into the ethmoidal region it was occupied by the small *Y*-shaped bone already dealt with above (pp. 25–26) it was even as narrow towards its bottom that it formed there only a thin lamina between the orbits. In its posterior part it was presumably provided with an orbital floor (subocular shelf), which corresponded to the posterior parts of the orbital floor in *Macropetalichthys* (Stensiö 1925, pp. 104–119, text-figs. 3, 8) and other Euarthrodires with a platybasic endocranium, e. g. *Buchanosteus osseus* (Hills 1936b, pp. 216–217, 223, text-figs. 2, 6; Stensiö 1945, p. 24) and the Holichothoracids (Stensiö 1934a, p. 51, text-figs. 27, 28; Stensiö 1944, p. 2; 1945, p. 15). The dorsal wall of the region was pierced by a conceivably large pineal foramen (*pic*) situated underneath the pineal plate. The cranial cavity reached as far forward in the region as to somewhat in front of the pineal foramen.

The otic region in the *Bothriolepinae* (text-figs. 6, 7) and *Antiarchi* in general with regard to its proportions in relation to the endocranium as a whole and to the other regions must have been of a type fundamentally similar to that in the Arthrodires (Stensiö 1925, text-figs. 1, 3, 5, 8; 1934a, text-figs. 15, 26, 28; 1945, figs. 1, 3–5; Hills 1936b, text-fig. 6; Holmgren & Stensiö 1936, text-fig. 254; Gross 1940b, text-figs. 11, 12A, 13; cf. also text-figs. 69–71 below in this work). From a transverse plane somewhat behind the posterior margin of the orbital fenestra it must have extended as far backwards as almost to the transverse nuchal crista (*cr.tv*, text-figs. 11,

12) on the lower side of the head-shield and thus almost to the posterior end of the otico-occipital depression (*ood*, text-figs. 11, 12). Accordingly it was long, longer than the orbitotemporal and occipital regions, but about equally long as (*Bothriolepis, Pterichthyodes, Asterolepis* and *Remigolepis*), or somewhat shorter than (*Grossilepis, Microbrachius*), the ethmoidal region, including the presumed rostral process. Since, as will be made clear below (pp. 52–56), its dorsal wall must have been housed in the otico-occipital depression (cf. Stensiö 1931, p. 52) the region was much broader than long, and broader also than any one of the other regions. Its anterior dorso-lateral corner formed a post-orbital process (*pr.po*, text-figs. 6, 7). This process was strikingly short in *Remigolepis* (*pr.po*, text-fig. 16), somewhat longer in *Asterolepis* (text-fig. 17), but very long in the *Bothriolepinae* in which it was produced antero-laterally as far as to or beyond a transverse plane through the anterior margin of the orbital fenestra. Owing to this different development of the postorbital process the maximum breadth of the region is found at different places in different forms. In *Remigolepis* it was thus situated across the hindmost part of the region, near the transition to the occipital region, whereas in the *Bothriolepinae* it was across the anterior ends of the postorbital processes. Each lateral wall of the region descended from the dorsal wall along, and just medially to, the paramarginal crista (*cr.pm*, text-figs. 11, 12, 16), which forms the lateral boundary of the otico-occipital depression. In *Asterolepis* and *Remigolepis* this crista on the lower side of the head-shield lies almost straight underneath the upper infraorbital sensory canal groove (ifc_1) of its side, and the dorsal wall of the region in these forms had, therefore, much the same lateral extent as in Arthrodires and fishes in general. In the *Bothriolepinae*, on the other hand, the paramarginal crista is situated fairly far medially to the upper division of the infraorbital sensory canal groove of its side (text-figs. 6, 7, 9–12). A broad lateral part of the head-shield in the *Bothriolepinae*, therefore, probably extended laterally beyond the lateral wall of the otic region. As it is very unlikely that this broad lateral part of the head-shield projected freely laterally to the otic region, we are forced to the conclusion that it was supported by a lateral lamina of the dorsal wall of the otic region, a lateral lamina which with its proximal part lay ventrally to the paramarginal crest, protruding far laterally beyond the lateral wall of the otic region (text-figs. 6, 7). This probable lamina, which reached at least as far laterally as to underneath the upper infraorbital groove (ifc_1) in its position and extent seems to have been comparable nearest to an excessively developed spheno-pterotic ridge (Holmgren & Stensiö 1936, p. 313, text-figs. 238–241). Posteriorly the otic region probably passed over into the foremost part of the occipital region without any definite boundary. The median part of its dorsal face was probably somewhat depressed underneath the supraotic thickening (*sot*, text-figs. 11 12, 25B) of the centro-nuchal plate. The canal for the ductus endolymphati-

cus reached the dorsal side of the endocranium far posteriorly in this supposed median depression (*d.end*$_1$, text-fig. 6). It did not, however, end there, but continued in a postero-mediodorsal direction to the dorsal side of the head-shield through the centro-nuchal plate (*d.end*$_2$, text-figs. 6, 9, 10, 25).

The occipital region in the *Antiarchi* was exhaustively dealt with by the writer already in 1931 (Stensiö 1931, pp. 27, 28, 52) and nothing new of importance is, therefore, now to be added concerning its development. As demonstrated on that occasion it was short and composed of two divisions, an anterior broad one and a posterior narrow one. The anterior division, which lay underneath the hindmost part of the otico-occipital depression, was very short, but probably as broad as the adjacent hindmost part of the otic region. The posterior division, which lay underneath, and behind, the transverse nuchal crista (*cr.tv*, figs. 11, 12, 19), was longer than the anterior division, but except most anteriorly, only approximately as broad as the anterior end of the vertebral column. It articulated against the vertebral column by a condyle which presumably was paired (*ocd*, text-fig. 7).

As may be gathered from the above statements, the endocranium in the *Bothriolepinae* and other *Antiarchi*, though much modified, was nevertheless fundamentally of an Arthrodiran type (cf. Stensiö 1931, p. 30). In regard to the ethmoidal region it was modified in a manner somewhat similar to that in Rhenanid Arthrodires.

Visceral endoskeleton.

Only a small paired bone has been met with that perhaps may belong to the visceral endoskeleton. This bone, which will be described below in this chapter, may possibly be an ossification in a labial cartilage. Leaving this bone out of the question the visceral endoskeleton in the *Bothriolepinae* and other *Antiarchi*-forms known as yet must have consisted only of cartilage. As in the case of the endocranium, however, this condition cannot possibly be a primary one, but must be regarded as secondary and due to a regressive development. Since it is now known that it was more or less completely ossified both in various groups of Arthrodires (Broili 1929, p. 152, pl. 2; 1930a, pp. 10–13, text-figs. 4, 5; 1933b, pp. 420–426, text-figs. 3, 4, 6; Gross 1933b, pp. 61–62, pl. 7, fig. 3; Stensiö 1934a, pp. 23–29, 43–48, text-figs. 1 B, 3, 12, 14, 23–25; Watson 1934, pp. 457; 1938, pp. 400, 401, text-fig. 1) and in Acanthodians (Watson 1937), the visceral endoskeleton must be assumed to have been ossified primarily to some extent in all primitive Placoderms and accordingly also in the ancestors of the *Antiarchi*.

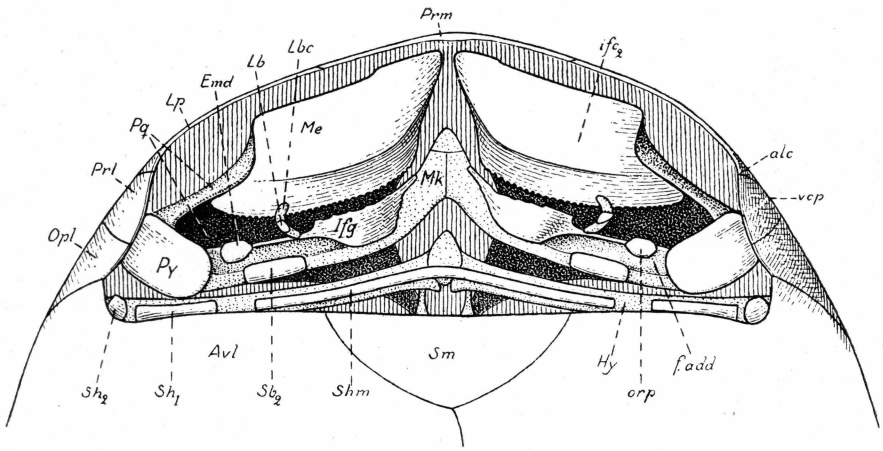
As has already been pointed out, the mouth opening in the *Antiarchi* (text-figs. 4, 5, 7, 8, 34, 38, 40B, 114) is situated on the foremost somewhat anteriorly facing part of the ventral side of the head. The mouth opening in the *Antiarchi* thus is not directed straight ventrally, but ventrally and somewhat anteriorly. Regarding its shape it is ray-like, that is to say it is short broad slit, which is mainly transversally placed. It lies entirely under-

neath the preorbital division of the head-shield, in front of both the orbits and nasal apertures, and thus is situated unusually far forwards. In this respect it is nearest as that of the Rhenanid Arthrodires, which also has a preorbital and prenasal position (Broili 1930a, text-figs. 2–5; 1933a, text-figs. 1, 3, 4), but it reminds also of that of the Ptyctodontid Arthrodires, which, though more rostro-caudally extended, seems also to have lain entirely in front of the orbits (text-fig. 71B; cf. Watson 1938, text-fig. 1). It was bounded dorsally by the palatoquadrates and the mental plates, whereas its ventral boundary was formed by Meckel's cartilages and the inferognathals. In *Bothriolepis* the symphysial parts of Meckel's cartilages and the foremost parts of the inferognathals were produced forwards and upwards into a hook-shaped process, which fitted into an angular notch between the medial (anterior) margins of the mental plates (text-figs. 8, 114). In *Pterichthyodes*, *Remigolepis*, and probably also in *Asterolepis*, on the other hand, the hook-shaped process of the lower jaws and the notch between the mental plates are not developed. The mouth opening of these forms was therefore straighter and more slit-like than that of the *Bothriolepinae*.

The possible substitution bone of the visceral endoskeleton referred to above has thus far been noticed only in a single unusually large specimen of *B. canadensis* (*Lb*, text-figs. 7, 8, 34, 111; cf. also Stensiö 1931, text-fig. 27). The bone is paired, very small, completely devoid of ornament and solid in structure. It lies at the angle of the mouth between the mental plate (*Me*) and the posterior, non-biting division of the inferognathal (*Ifg*) and approximately on a level with these two bones. As on both the right and left sides it occupies much the same position in relation to the two said dermal bones, it can hardly be much displaced. Judging from its position, it is most likely that it is either an ossification in a labial cartilage or else a dermal bone developed on the outside of such a cartilage in much the same way as the submandibular (*Sbm*$_1$, *Sbm*$_2$) and subhyoideal (*Sbm*, *Sh*$_1$, *Sh*$_2$) plates are developed in relation to Meckel's cartilage and the lower part of the hyoid arch respectively (cf. the account of the visceral exoskeleton, pp. 97–98). However, it is also not quite impossible that it may be a coronoid ossification or an ossification in a tendon of the m. adductor mandibulae. Whether the bone is only a fortuitous formation, or whether it is somewhat regularly present in very old individuals of *B. canadensis*, cannot be decided at present.

The position and development of the mouth opening indicates that the mandibular arch as a whole must have lain far anteriorly and that the conditions in this respect must have been somewhat as in Ptyctodontid and Rhenanid Arthrodires (fig. 71).

The palatoquadrate (*Pq*, text-figs. 6–8) must be assumed to have been a rather high, somewhat triangular element and was thus conceivably developed in a manner somewhat similar to that of the corresponding element in Ptyctodontid Arthrodires (text-fig. 71B; Gross 1933b, pl. 7, fig. 3; Watson



Text-fig. 8. *Bothriolepis canadensis*. Sketch showing the probable position of the palato-quadrates, Meckel's cartilages, and the lower parts of the hyoid arches etc. in relation to the exoskeletal bones of the lower side of the head. Pit-line grooves indicated with dotted red lines. Approximately × $^4/_3$.

Avl, anterior ventro-lateral plate; *Emd*, extramandibular plate; *Hy*, hyoid arch (arbitrarily restored); *Ifg*, inferognathal; *Lb*, labial bone (either a substitution bone in a labial cartilage or a dermal bone developed in relation to such a cartilage); *Lbc*, labial cartilage; *Lp*, lateral plate; *Me*, mental plate; *Mk*, Meckel's cartilage; *Opl*, extralateral (opercular) plate; *Pq*, palatoquadrate (shape arbitrarily); *Prl*, prelateral plate; *Prm*, premedian plate; *Py*, infraprelateral plate; Sb_2, plate of the submandibular series; *Shm*, Sh_1, Sh_2, plates of the subhyoideal series; *Sm*, semilunar plate; *alc*, antero-lateral corner of the head-shield; *f.add*, adductor fossa on the outside of Meckel's cartilage (for the insertion of the m. adductor mandibulae); ifc_2, lower infraorbital sensory groove, developed as a pit-line; *orp*, oral pit-line; *vcp*, pit-line probably corresponding to the vertical pit-line of the cheek in fishes in general.

1938, text-fig. 1). With its larger anterior part it lay underneath the preorbital division of the head-shield, that is to say underneath the ethmoidal region, the rostral process of which formed its main support. Whether it extended backwards as far as to the base of the postorbital process cannot be decided. Its posterior margin must have had such a position that from somewhere below the postorbital process, or from somewhere below the posterior parts of the orbital cavity, it passed downwards and somewhat forwards to the ventral end of the pars quadrata (*qu*, text-figs. 6, 7), which, as normally in Gnathostomes, formed a condyle for the articulation with the lower jaw. In *B. canadensis* the condyle of the pars quadrata and the jaw-articulation were in all probability situated about straight dorsally (internally) to the infraprelateral plate (*Py*, text-figs. 7, 8, 34) and medially to the hind part of the prelateral plate (*Prl*) and the foremost part of the extralateral plate (*Opl*). Anteriorly the palatoquadrate must certainly have been attached to, and have formed a support for, the mental plate of its side (*mme*, text-figs. 6, 7). The anterior parts of its oral margin must thus have been situated underneath the premedian plate and the foremost part of the lateral plate.

Meckel's cartilage (*Mk*, text-figs. 6–8) was almost transversal in position.

In consequence of this it did not extend backwards beyond the preorbital division of the cranium, but throughout its extent was situated below it. In *Bothriolepis* its posterior (articular) end lay just above (internally to) the infraprelateral plate and opposite, or a little behind, the suture between the prelateral and extralateral plates. In *Pterichthyodes, Asterolepis* and *Remigolepis* this part had a quite corresponding position, but as these forms have no prelateral plate, it lay in them opposite the postero-ventral part of the anterior division of the extralateral plate. As is evident from the shape of the inferognathal (text-figs. 8, 34, 36; pp. 96, 208 below; cf. also Stensiö 1931, pp. 63–68, 154; Gross 1941a, pp. 39–41), Meckel's cartilage must have been developed essentially in the same way as in the Brachythoracids (Stensiö 1934b, pp. 26–29, 45–47). It was thus fairly long and slender. With its posterior portion, including the pars articularis, it lay on the lateral side of the non-biting division of the inferognathal, whereas with its anterior portion it was situated on the medial face of the biting division of the said bone. Hence it crossed the inferognathal on the lower side at the transition between the non-biting and biting divisions. Its symphysial part was relatively long, and in the *Bothriolepinae*, as has already been pointed out, conceivably bent upwards like a hook. Whether Meckel's cartilages of both sides met directly into a symphysis anteriorly or whether, as in Brachythoracids (Stensiö 1934a, pp. 46–47), they were connected anteriorly by means of an independent symphysial element, is a question which must be left unanswered.

The palatoquadrate had such a position and extent that its posterior margin, which, as has already been pointed out, presumably was directed somewhat ventrally, must have lain approximately medio-ventrally to the middle part of the lateral plate of the head-shield, and medially to the hindmost part of the cheek. More precisely, the posterior margin of the palatoquadrate presumably had about the following position in relation to the exoskeleton. In the *Bothriolepinae* it lay ventro-medially and anteriorly to the supraspiracular process (*lpr*, text-figs. 4, 6, 7, 9–13; cf. pp. 44–46 below) and spiracular groove (*spg*, text-figs. 11, 12; cf. pp. 58–61 below) of the head-shield, medially to the foremost part of the extralateral plate and the hindmost part of the prelateral plate, and dorsally to the antero-lateral part of the infraprelateral plate. In the *Pterichthyodidae, Asterolepidae* and *Remigolepidae* it was situated ventro-medially and anteriorly to the deepest concavity of the lateral margin of the lateral plate and the spiracular groove (*spg*, text-figs. 16–18; cf. pp. 58–61 below) and medially to the anterior part of the large extralateral plate. As normally in Gnathostome vertebrates, the dorsal part of the hyoid arch (*Hy*, text-figs. 7, 8) must have been situated somewhat behind, and have been somewhat parallel with, the posterior margin of the palatoquadrate, whereas the vertral part of this arch extended forwards between the rami of the lower jaw. Hence, as far as may be judged, the dorsal part of the hyoid arch in the *Bothriolepinae* lay morphologically medio-ventrally and post-

eriorly to the supraspiracular process and the spiracular groove of the head shield and approximately opposite the foremost part of the high posterior division of the extralateral plate, and in the *Asterolepinae* and *Remigolepidae* medioventrally and posteriorly to the deepest concavity of the lateral plate of the head-shield and the spiracular groove and almost opposite, or in front of, the middle of the extralateral plate. On account of this the gill slit between the mandibular and hyoid arches, the spiracle, in its dorsal part must be assumed to have had the following position. In the *Bothriolepinae*: medioventrally to the supraspiracular process and spiracular groove of the head-shield and medially to the foremost part of the extralateral plate; in the *Pterichthyodidae, Asterolepidae* and *Remigolepidae*: medio-ventrally to the deepest concavity of the lateral margin of the lateral plate of the head-shield and the spiracular groove and medially to the middle or anterior part of the extralateral plate. The correctness of this opinion concerning the position of the spiracle is born out, as we shall see (pp. 58–61, 88–89) by the presence of a small external spiracular aperture. This spiracular aperture in the *Bothriolepinae* lies below the posterior part of the supraspiracular process, between that process and the upper margin of the extralateral plate (*spi*, text-figs. 4, 7, 40B), whereas in the *Asterolepidae, Remigolepidae,* and probably also the *Pterichthyoidae,* it is found between the upper margin of the extralateral plate and the deepest concavity of the lateral margin of the lateral plate. An external spiracular aperture situated in a similar way in relation to the gill-cover as the one in the *Antiarchi* is met with in the Acanthodians (Watson 1937, text-figs. 1, 2A, 3, 5–7, 9) and, besides, also at least in some Brachythoracid Arthroidires (cf. p. 207 below and text-fig. 74, *spi*). At the jaw articulation the hyoid arch seems to have lain close behind the palatoquadrate and Meckel's cartilage, and hence it is possible that it participated in the suspension of the jaw apparatus. Its ventral division was probably fairly transversal in position.

The branchial arches proper were all situated underneath the cranium (text-fig.7) where, owing to the far forward position of the jaw apparatus there was enough space for them. They had thus a position similar to that in Arthrodires, Holocephalians, *Choanichthyes* and Actinopterygians (Broili 1929, p. 152, pl. 2; 1930a, pp. 11–13, text-figs. 4, 5; 1933b, pp. 425–426, text-figs. 3, 6; Heintz 1932b, pp. 199–202, text-figs. 87–89; Stensiö 1934a, p. 29; Holmgren & Stensiö 1936, pp. 334, 342).

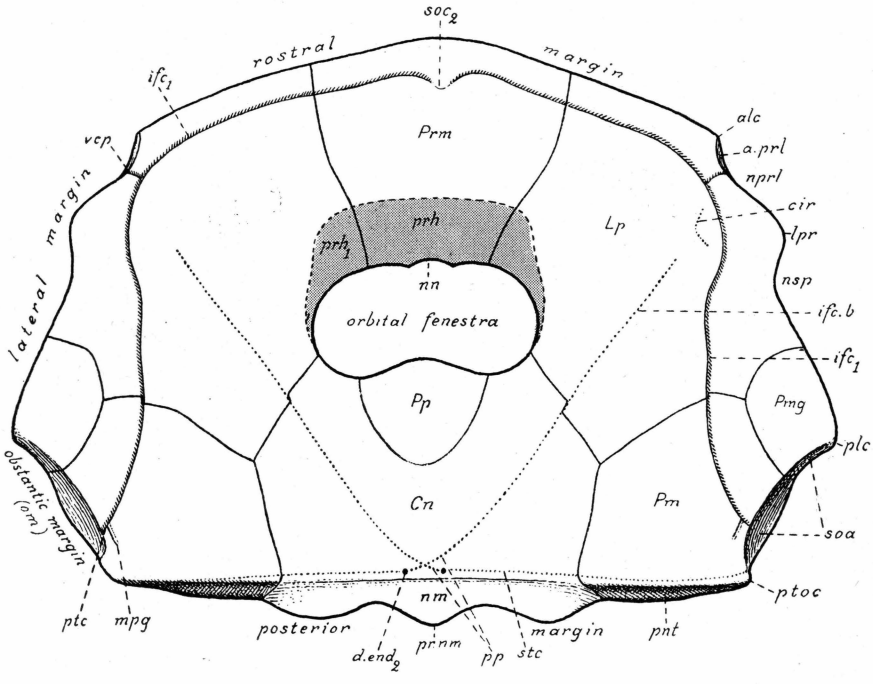
As is already known (Stensiö 1931, p. 58) and as has also been mentioned above (p. 21), the postspiracular gill-slits opened into a gill-chamber, bounded on the outside by a well developed gill-cover. The part of this gill-cover situated dorsally to the subcephalic division of the anterior ventro-lateral plate was strengthened by a dermal bone, the extralateral plate. Owing to the circumstance that it passed over into the cheek far forwards and as in addition it lay entirely outside, and was not connected with, the hyoid arch,

the gill-cover must have been a mandibular gill-cover, as that of the Acanthodians (Watson 1937, pp. 56, 63, 67–68, 86, 103–108, 118–119, 131–132) and Arthrodires (Broili 1933b, p. 425 and text-fig. 3; Stensiö 1934a, pp. 32–33; Holmgren & Stensiö 1936, p. 334), but not a hyoidean gill-cover, as that of other fishes.

Head-shield or exoskeletal skull-roof.

The head-shield or exoskeletal skull-roof in the *Antiarchi* covers the whole dorsal face of the endocranium and in addition certain dorsal parts of the cheeks. On the other hand, it does not extend downwards anteriorly below the tip of the snout so as to cover any parts of the lower face of the head antero-dorsally to the mouth opening. As we have already seen from the account of the endocranium (pp. 25–35) and as will be further explained below (pp. 189–196), its preorbital division as a whole or, at any rate to a large extent, is a special formation developed in a mass of tissue the homologue of which in non-Rhenanid Arthrodires, and probably in primitive Placoderms in general, lay entirely on the rostral and lateral sides of the ethmoidal region of the endocranium and on the dorsal parts of the cheeks. Thiss mass of tissue has become excessively developed and has swung upwards so as to form a secondary tip of the snout in front of the primary one. As regards the development of the preorbital division of the head-shield the *Antiarchi* are thus considerably more specialized than the non-Rhenanid Arthrodires.

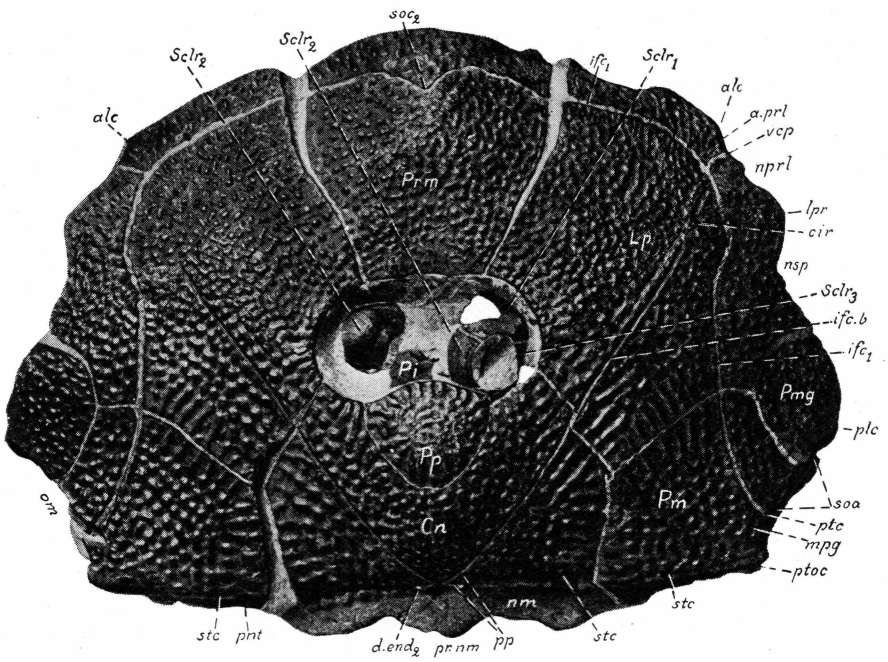
The head-shield in the *Bothriolepinae* (text-figs. 4, 9–15, 76–84, 114, 219, 229, 233A, 253A, 261, 266, 273, 274) is fundamentally as that in the other *Antiarchi*-forms. Regarding its details, however, it presents many differences several of which are of interest from both anatomic and taxonomic points the view. As normally in the group, it is always broader than long and broadest across its postero-lateral (preobstantic) corners (*plc*). Owing to the condition that these corners, as in *Microbrachius* (Watson 1935, text-fig. 28), are situated at a transverse plane through, or only a little behind, the orbital fenestra (*orb.fen*) its broadest place is much further forwards than in the *Pterichthyodidae, Asterolepidae* and *Remigolepidae,* in which the said corners (*plc*) lie as far caudally as at a transverse plane through the hindmost part of the centro-nuchal plate, or through the very posterior margin of this plate. As normally in the group, the shield as a whole is arched in such a manner that in both rostro-caudal and transverse directions it is more or less convex on its dorsal side and concave to a somewhat corresponding degree on its ventral side (text-figs. 4–7, 10–12, 15, 38, 40B, 76, 77A, 78C, 80B, 81A 114). The preorbital division, however, differs much as to its degree of arching in the various species. In certain species, e.g. *B. canadensis* (text-fig. 4) and *B. alvesiensis,* this division is thus strongly arched, whereas in several other species, such as *B. cellulosa, B. maxima, B. gigantea* and *B. groenlandica,* it



Text-fig. 9. *Bothriolepis canadensis*. Outline-restoration of a large head-shield. Dorsa aspect. The rostral, pineal and sclerotic plates omitted. Owing to the condition that the specimen after which this restoration has been made is somewhat flattened in a dorsi-ventral direction (text-fig. 10) the breadth has probably become somewhat too large in proportion to the length. The extent of the preorbital recess (*prh*, prh_1) indicated by an interrupted line and shading. Approximately × $^4/_3$.

Cn, centro-nuchal plate; *Lp*, lateral plate; *Pm*, paranuchal-marginal plate; *Pmg*, post-marginal plate; *Pp*, postpineal plate; *Prm*, premedian plate; *alc*, antero-lateral corner of head-shield; *a.prl*, prelateral area (for attachment of prelateral plate); *cir*, semicircular pit-line groove; $d.end_2$, external opening of canal for ductus endolymphaticus; ifc_1, upper infraorbital sensory groove; *ifc.b*, posterior oblique cephalic pit-line groove; *lpr*, supra-spiracular process; *mpg*, middle pit-line groove of the skull-roof; *nm*, obtected nuchal area; *nn*, nasal notch; *nprl*, prelateral notch; *nsp*, supraspiracular notch; *om*, obstantic margin; *plc*, postero-lateral (preobstantic) corner of head-shield; *pnt*, paranuchal trochlea; *pp*, posterior pit-line groove of skull-roof; *prh*, median unpaired division of preorbital recess; prh_1, lateral, paired division of preorbital recess; *pr.nm*, posterior median process of centro-nuchal plate; *ptc*, cephalic division of main lateral line groove; *ptoc*, postobstantic corner; *soa*, subobstantic area; soc_2, anterior median section of the supraorbital sensory canal groove, the anterior median pit-line; *stc*, supratemporal (cross-commissural) pit-line groove; *vcp*, vertical pit-line groove of cheek.

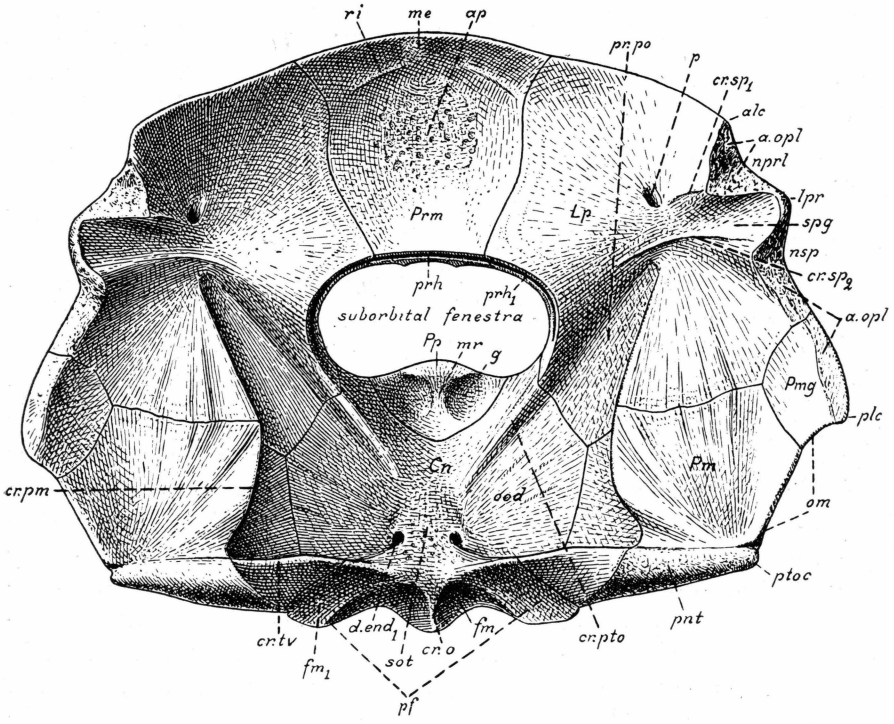
seems to have been fairly flat, about as flat as in *Asterolepis* (Gross 1931, text-fig. 11; Nilsson 1941, text-figs. 4, 8) and *Remigolepis*. The orbital fenestra varies somewhat both in shape and proportions, but is normally larger in immature individuals than in mature ones (text-figs. 9, 82–84, 273, 274). Those parts of the shield that are situated in front of, and laterally to, the main deep sensory canal grooves, the upper infraorbital groove, ifc_1, and the cephalic division of the main lateral line groove, *ptc*, are usually broad and for the most part broader relatively than in *Pterichthyodes*, *Asterolepis*



Text-fig. 10. *Bothriolepis canadensis.* A complete somewhat crushed head-shield of a large individual. Dorsal aspect. The restorations reproduced in text-figs. 9 and 11 based mainly on this head-shield. Specimen No. 2124 in the Swedish Museum of Natural History in Stockholm. This head-shield reproduced also in text-fig. 12. Previously reproduced by Stensiö in text-figs. 3 and 4 in 1931. Approximately × $^4/_3$.
Cn, centro-nuchal plate; *Lp*, lateral plate; *Pi*, pineal plate; *Pm*, paranuchal-marginal plate; *Pmg*, postmarginal plate; *Pp*, postpineal plate; *Prm*, premedian plate; $Sclr_1$, $Sclr_2$, $Sclr_3$, anterior, postero-dorsal, and postero-ventral sclerotic plates respectively; *alc*, anterolateral corner of head-shield; *a.prl*, prelateral area (for the attachment of the prelateral plate); *cir*, semicircular pit-line groove; $d.end_2$, external opening of the canal for the ductus endolymphaticus; ifc_1, upper infraorbital sensory groove; *ifc.b*, posterior oblique cephalicpitline groove; *lpr*, supraspiracular process; *mpg*, middle pit-line groove of skull-roof; *nm*, obtected nuchal area; *nprl*, prelateral notch; *nsp*, supraspiracular notch; *om*, obstantic margin; *plc*, postero-lateral (preobstantic) corner of head-shield; *pnt*, paranuchal trochlea (very fragmentarily preserved); *pp*, posterior pit-line groove of the skull-roof; *pr.nm*, posterior median process of centro-nuchal plate; *ptc*, cephalic division of main lateral line groove; *ptoc*, postobstantic corner; *soa*, subobstantic area; soc_2, anterior median section of supraorbital sensory canal grooves, the anterior median pit-line; *stc*, supratemporal (cross-commissural) pit-line groove; *vcp*, vertical pit-line groove of the cheek.

and *Remigolepis*. The obtected nuchal area (*nm*, text-figs. 4, 9, 10, 13, 14, 25A, 26) is well developed and generally broader than in *Asterolepis* and *Remigolepis*. In many cases it is not directed straight dorsally, but dorsally and somewhat anteriorly, and in these cases it meets the ornamented area of the centro-nuchal plate at an obtuse angle.

Regarding its general outlines in dorsal and ventral aspects (text-figs. 9–15, 76–84, 208, 209, 218, 219, 229, 233A, 249, 253, 261, 266, 273, 274) the head-shield is not pretty nearly four-sided, as in *Pterichthyodes* (Traquair 1894–1906, text-figs. 34, 51; Gross 1933a, text-fig. 14), *Gerdalepis* (Gross



Text-fig. 11. *Bothriolepis canadensis*. Restoration of a large head-shield in ventral aspect, but with the rostral pineal and sclerotic plates omitted. The restoration made after the specimen reproduced in text-figs. 10 and 12. As that specimen is somewhat flattened by pressure the breadth is probably a little too large in proportion to the length. Approximately × 4/3.

Cn, centro-nuchal plate; *Lp*, lateral plate; *Pm*, paranuchal-marginal plate; *Pmg*, post-marginal plate; *Prm*, premedian plate; *Pp*, postpineal plate; *alc*, antero-lateral corner of head-shield; *a.opl*, area of attachment for extralateral (opercular) plate; *ap*, poriferous area; *cr.o*, median occipital crista; *cr.pm*, paramarginal crista; *cr.pto*, postorbital crista; $cr.sp_1$, prespiracular crista; $cr.sp_2$, postspiracular crista; *cr.tv*, transverse nuchal crista; $d.end_1$, ventral opening of the canal for the ductus endolymphaticus in centro-nuchal plate; *fm*, fm_1, insertion fossae for levator muscles of the head; *g*, shallow pit on postpineal plate; *lpr*, supraspiracular process; *me*, median rostral elevation of premedian plate; *mr*, median-elevation of postpineal plate; *nprl*, prelateral notch; *nsp*, supraspiracular notch; *om*, obstantic margin; *ood*, otico-occipital depression; *p*, prespiracular pit; *pf*, posterior (nuchal) face of shield; *plc*, postero-lateral (preobstantic) corner of shield; *pnt*, paranuchal trochlea; *prh*, median unpaired division of preorbital recess (posterior opening); prh_1, lateral paired division of preorbital recess (posterior opening); *pr.po*, antero-lateral corner of otico-occipital depression developed for postorbital process of endocranium; *ptoc*, postobstantic corner of shield; *ri*, oblique premedian ridge; *sot*, supraotic thickening; *spg*, spiracular groove.

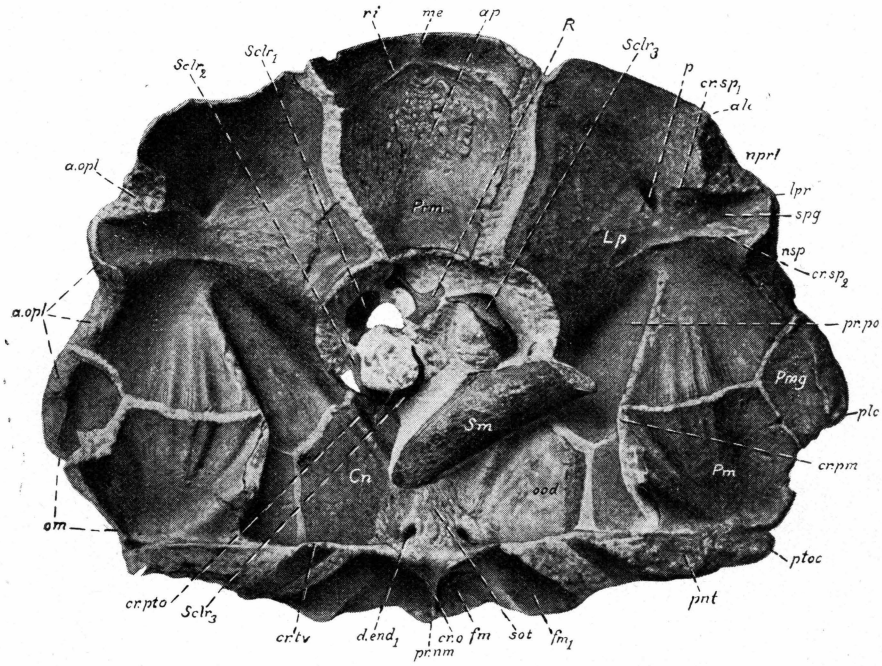
1941b, text-fig. 1A, 7), *Asterolepis* (Traquair 1894–1906, text-fig. 37; Gross 1931, text-fig. 12 and pl. 12, fig. 7; 1933a, text-fig. 16; Watson 1932, text-figs. 3, 4; Stensiö 1938, text-figs. 1, 7; Nilsson 1941, text-fig. 3) and *Remigolepis* (text-fig. 16; cf. also Stensiö 1931, text-fig. 80), but clearly six-sided, as in *Microbrachius* (Watson 1935, text-fig. 28). Its six margins are as follows (text-figs. 9–14): an unpaired rostral margin, bounded on either side by a usually well developed antero-lateral corner (*alc*); a paired lateral margin extending, backwards from the antero-lateral corner (*alc*) to

the postero-lateral (preobstantic) corner (*plc*); a paired obstantic margin (*om*), marked off anteriorly by the posterc-lateral (preobstantic) corner (*plc*) and posteriorly by the postobstantic corner (*ptoc*); and finally, an unpaired posterior margin, situated between the postobstantic corners (*ptoc*) of both sides. As it is in contact with the trunk-armour and besides participates into the articulation with this armour the obstantic margin is in fact only a specially developed lateral part of the posterior margin.

The rostral margin (text-figs. 4, 6, 7, 9–15, 38, 40B, 65, 76–84, 114, 219, 229, 233A, 249, 253, 266, 273, 274) is always long. In the majority of the species it is shorter than the posterior margin, but in some species it equals this margin in length. Taken as a whole it is convex and devoid of both a median notch and forward projecting unornamented parts. In its shape it is thus as in *Pterichthyodes* (Traquair 1894–1906, text-figs. 34, 51; Gross 1933a, p. 31, text-fig. 14) and *Microbrachius* (Watson 1935, text-fig. 28), whereas, on the other hand, it differs clearly from the corresponding margin in *Asterolepis* (Traquair 1894–1906, text-fig. 37; Gross 1931, p. 26, text-fig. 12 and pl. 12, fig. 7; 1933a, text-fig. 16; Stensiö 1931, pp. 31–34, text-fig. 7A; 1938, text-figs. 1, 7; Nilsson 1941, text-figs. 3, 4, 5a) and *Remigolepis* (Stensiö 1931, pp. 31–34, 166–168; text-fig. 80 and pl. 4, fig. 6). In *B. cellulosa* (text-figs. 218, 219, 220; cf. also Gross 1941a, p. 12, text-figs. 5, 7) it presents usually a median well marked rostral angle, but more or less distinct traces of such an angle may also be met with in *Bothriolepis canadensis*[1]) (text-figs. 82–86), *B. maxima* (*ra*, text-fig. 233E), *B. groenlandica* (text-fig. 273A), and *Grossilepis tuberculata* (text-fig. 267D). Throughout its extent the margin is only a thin edge, and both from this and from its development otherwise it is fully obvious that it cannot have served either as an area of attachment of, or as a support for, visceral skeletal elements. The mental plates, cannot, therefore, have been directly attached to it, but must have been firmly connected only with the palatoquadrates.

The lateral margin (text-figs. 4, 8, 9–15, 24, 28, 34, 40 B, 65, 76–84, 114, 219, 221, 233A, 249, 253, 266, 267 F–J, 273, 274, 277, 303B) is fairly short in proportion to the length and breadth of the shield, considerably shorter than in *Pterichthyodes, Asterolepis* and *Remigolepis,* but of somewhat the same relative length as in *Microbrachius*. Contrary to what is the case, at any rate in *Pterichthyodes* (Gross 1933a, text-fig. 14), *Asterolepis* (Gross 1931, pl. 12, fig. 7; Watson 1932, text-figs. 3, 4, Stensiö 1938, text-fig. 1; Nilsson 1941, text-fig. 3) and *Remigolepis* (Stensiö 1931, text-fig. 80), the margin is not in the main simply concave throughout its extent, but invariably has a more complicated configuration (text-figs. 9–14). Most anteriorly behind the anterior lateral corner (*alc*) of the shield it normally shows a well

[1]) In *B. canadensis* and *B. groenlandica* the rostral angle is normally well developed in very small individuals, but slightly pronounced or absent in larger individuals (cf. the descriptions of these species). In both these species its presence in a well developed condition is a character of immaturity.



Text-fig. 12. *Bothriolepis canadensis*. A complete somewhat crushed head-shield of a large individual. Ventral aspect. The restorations reproduced in text-figs. 9 and 11 based mainly on this head-shield. Specimen No. 2124 in the possession of the Swedish Museum of Natural, History in Stockholm. This head-shield is reproduced also in text-fig. 10 and previously, in 1931, by Stensiö in text-figs. 3 and 4. Approximately × $^4/_3$

Cn, centro-nuchal plate; *Lp*, lateral plate; *Pm*, paranuchal-marginal plate; *Pmg*, post-marginal plate; *Prm*, premedian plate; *R*, rostral plate; $Sclr_1$, $Sclr_2$, $Sclr_3$, anterior, postero-dorsal, and postero-ventral sclerotic plates respectively; *Sm*, semilunar plate (detached); *alc*, antero-lateral corner of head-shield; *ap*, poriferous area; *a.opl*, area for attachment of extralateral plate; *cr.o*, median occipital crista; *cr.pm*, paramarginal crista; *cr.pto*, post-orbital crista; $cr.sp_1$, prespiracular crista; $cr.sp_2$, postspiracular crista; *cr.tv*, transverse nuchal crista; $d.end_1$, ventral opening of canal for ductus endolymphaticus in centro-nuchal plate; *fm*, fm_1, insertion fossae for levator muscles of the head; *lpr*, supraspiracular process; *me*, median rostral elevation of premedian plate; *nprl*, prelateral notch; *nsp*, supra-spiracular notch; *om*, obstantic margin; *ood*, otico-occipital depression; *p*, prespiracular pit; *plc*, postero-lateral (preobstantic) corner of shield; *pnt*, paranuchal trochlea (deficient); *pr.nm*, posterior median process of centro-nuchal plates; *pr.po*, antero-lateral corner of otico-occipital depression developed for postorbital process; *ptoc*, postobstantic corner of shield; *ri*, oblique premedian ridge; *sol*, supraotic thickening; *spg*, spiracular groove.

marked notch, the prelateral notch (*nprl*), occupied by the prelateral plate. Behind this notch the margin is always provided with a more or less well developed, mostly rounded, process, the supraspiracular process (*lpr*) situated above the spiracular opening (*spi*) and the foremost low division of the extralateral plate. This process is bounded behind by a supraspiracular notch (*nsp*), also developed in relation to the spiracular opening. Behind the last-mentioned notch the whole remaining posterior part of the margin may be rather straight, a little concave, or a little convex. Except most anteriorly, nearest behind the antero-lateral corner (*alc*), where it often may be thin

and edge-like, the margin, as normally in the group, is rather thick, with a well developed area, the extralateral area (*a.opl*, text-figs. 11, 12, 15A, B, 221B, 277F), for the attachment of the extralateral plate. This area is broad at the middle of the prelateral notch and behind the spiracular groove, narrower on the very supraspiracular process and in its hindmost part. Except on the very spiracular process, it is directed much ventrally throughout its extent and as a whole, therefore, has a position different from that of the corresponding area in *Asterolepis* and *Remigolepis* (cf. text-figs. 16–18 and pp. 59–61 below), which faces almost straight laterally. It is strikingly rough in its anterior half or thereabouts, whereas it is almost smooth in the remaining posterior parts, on account of which it is obvious that it was quite rigidly attached only to the anterior parts of the extralateral plate. Along the anterior half of the prelateral notch there is normally a small overlapped area, the prelateral area (*a.prl*, text-figs. 9, 24A), on the outside of the lateral plate, behind the antero-lateral corner (*alc*), an area which served as an attachment for the prelateral plate. This overlapped area has such a position that usually it is not discernible when the head-shield is looked at from above.

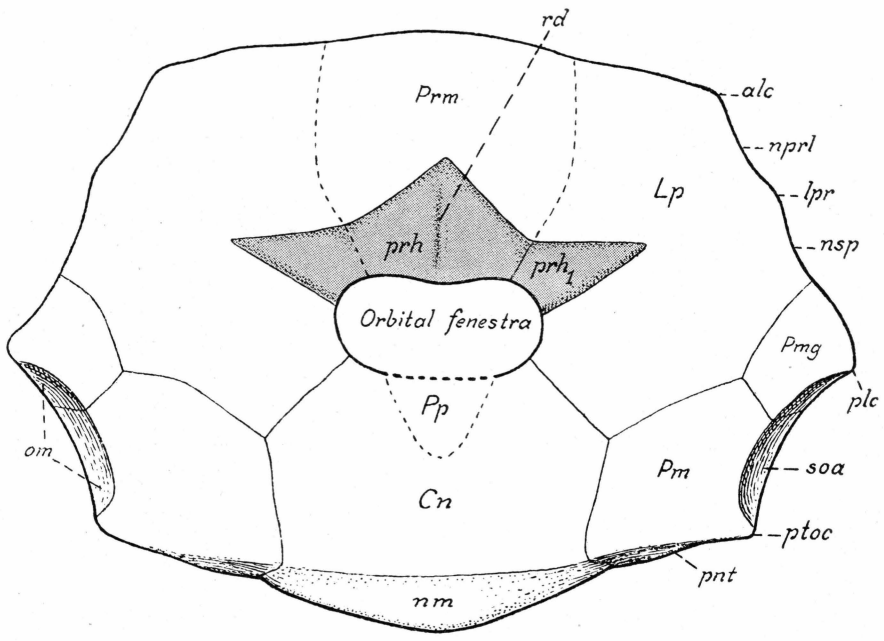
The obstantic margin (*om*, text-figs. 4, 6, 7, 9–15, 27–29, 65, 76–84, 219, 223, 229, 233A, 249, 253A, 266, 273, 274, 279) is strikingly long, approximately as long as in *Microbrachius* (Watson 1935, text-fig. 28), and considerably longer than in *Pterichthyodes, Gerdalepis, Asterolepis* and *Remigolepis* (Traquair 1894–1906, text-figs. 34, 37, 51; Gross 1931, pl. 12, fig. 7; 1933a, text-figs. 14, 16A; 1933b, text-fig. 3; 1941b, text-figs. 1A, 7; Stensiö 1931, text-fig. 80; Stensiö 1938, text-figs. 1, 7; Watson 1932, text-figs. 3, 4; Nilsson 1941, text-figs. 3, 4). Otherwise this margin differs from the one in the last-mentioned three genera in the following respects. 1) Its morphologically lateral end is not situated at or close in front of a transverse plane through the posterior margin, but considerably further anteriorly, at a transverse plane through, or fairly closely behind, the orbital fenestra. 2) Owing to the condition that it thus extends far forwards the margin as a whole is not directed posteriorly or chiefly posteriorly, but postero-laterally. 3) Finally, the margin is also as a rule only slightly concave, sometimes even fairly straight.

The area devoid of ornament that is present on the upper side of the shield along the obstantic margin and that is developed for the articulation of the shield with the processus obstans (*pro*) of the trunk-armour will throughout this work be termed the subobstantic area. The subobstantic area (*soa*, text-figs. 4, 9, 13, 14, 27–29) as thus defined extends forwards from the postobstantic corner of the shield not only along the whole lateral margin of the paranuchal-marginal plate, but also along the entire posterior margin of the postmarginal plate or nearly so. This area has, therefore, a considerably larger extent than in *Asterolepis*, in which from the paranuchal-marginal plate it continues only a short distance on to the postmarginal plate (Gross

1933b, text-fig. 3), and than in *Remigolepis*, in which, as we shall see, it is confined only to the paranuchal-marginal plate (cf. Part III of this monograph). It slopes towards the obstantic margin, and is normally broadest and best developed on the paranuchal-marginal plate. On the last-mentioned plate it is invariably lined by »Siebknochen« (Gross 1931, pp. 16–19), whereas further antero-laterally it is devoid of a lining of such bony tissue, a condition which clearly shows that a real articulation was developed only between approximately its posterior half on the one hand and the dorso-medial part of the lower (internal) side of the processus obstans one the other (cf. pp. 128–129 below). When the head is in a maximally lowered position the area is completely concealed by the processus obstans. No traces of articular or overlapping areas are to be found on the lower side of the shield near or along the obstantic margin. In contradistinction to what is the case in *Asterolepis* (Gross 1933b, text-fig. 3), therefore, the head-shield did not articulate against an area on the outside of the anterior dorso-lateral plate. As may thus be gathered, the conditions as to the obstantic margin and its articular connection with the trunk-armour are clearly different from those in *Pterichthyodes, Asterolepis* and *Remigolepis,* whereas, on the other hand, they seem to be much as the ones in *Microbrachius.*

Finally, the posterior margin of the shield (text-figs. 4, 6, 9–14, 25–29, 65, 76–84, 218, 219, 222, 229, 233A, 253, 266, 273, 274, 278, 279, 303 C–E) is mostly somewhat convex, but may also sometimes be almost straight. The median part formed by the centro-nuchal plate generally projects more backwards than what is the case in *Pterichthyodes* (Gross 1933a, text-fig. 14), *Gerdalepis* (Gross 1941b, text-fig. 1A, 7), *Asterolepis* (Gross 1933a, text-fig. 16A; Stensiö 1938, text-fig. 1) and *Remigolepis* (Stensiö 1931, pl. 3, figs. 1, 2; pl. 4, figs. 2, 3). In many cases this part bears a posterior median process (*pr.nm*) formed by the centro-nuchal plate and bounded on either side by a shallow notch; in several cases, however, it may, be entirely, or almost entirely, devoid of the process just mentioned, and in these cases its median part may be either convex or concave throughout. On the whole the margin in question seems to be much more variable with regard to its shape than in *Asterolepis* and *Remigolepis*. The obtected nuchal area (*nm*), which is situated on the upper side of the shield, along the median part of the posterior margin, and which lay underneath the anterior end of the anterior median dorsal plate, has a larger rostro-caudal extent than in *Asterolepis* and *Remigolepis*.

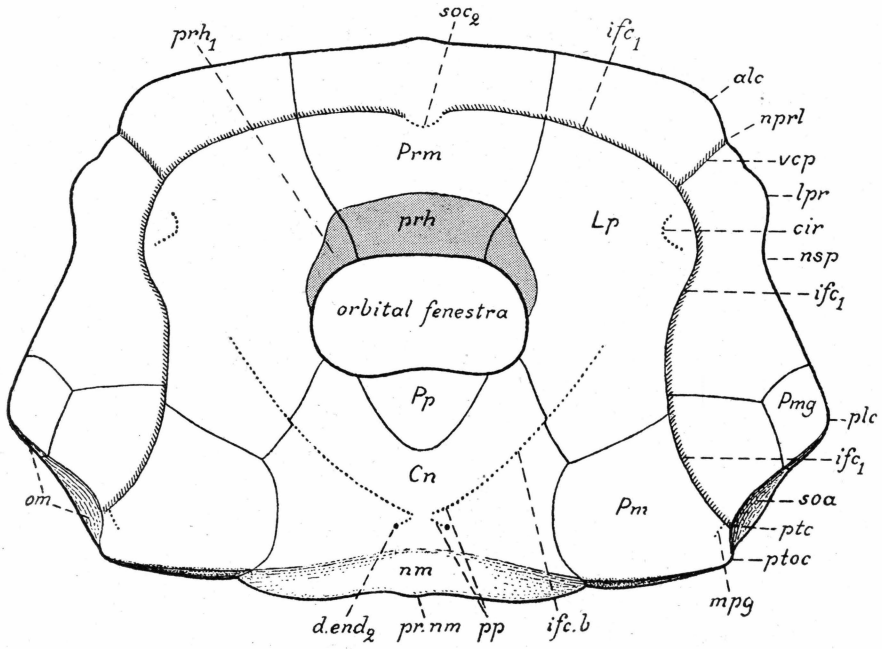
We shall now proceed to an examination of the lower (internal) side of the shield. This side is most completely known in *Bothriolepis canadensis* (text-figs. 11, 12, 15A, B), but it has also been found preserved in *B. cellulosa* (Gross 1941a, pl. 1; pl. 2, fig. 2), *B. groenlandica* (pl. 1; pl. 8, figs. 3–5; pl. 10; pl. 11, figs. 4, 5) and *Grossilepis tuberculata* (Gross 1941a, pl. 18). As is well known, it presents a large median opening, the fenestra suborbi-



Text-fig. 13. *Bothriolepis groenlandica.* Restoration of a large head-shield in dorsal aspect. The extent of the preorbital recess indicated by shading. The rostral, pineal and sclerotic plates omitted. About × $^4/_3$ of the natural size.
Cn, centro-nuchal plate; *Lp*, lateral plate; *Pm*, paranuchal-marginal plate; *Pmg*, post-marginal plate; *Pp*, postpineal plate; *Prm*, premedian plate; *alc*, antero-lateral corner of shield; *lpr*, supraspiracular process; *nm*, obtected nuchal area; *nprl*, prelateral notch; *nsp*, spiracular notch; *om*, obstantic margin; *plc*, postero-lateral (preobstantic) corner of shield; *pnt*, paranuchal trochlea; *prh*, median, unpaired division of preorbital recess; prh_1, lateral, paired division of preorbital recess; *ptoc*, postobstantic corner; *rd*, median ridge on dorsal side of median division of preorbital recess; *soa*, subobstantic area.

talis, which is situated opposite the orbital fenestra of the dorsal side, forming the ventral opening of the orbital chamber (cf. Stensiö 1931, p. 53). In *B. canadensis* and *B. maxima*, at any rate, this fenestra suborbitalis is both longer and broader than the fenestra orbitalis, a condition which is due to the fact that the orbital chamber is more capacious in its ventral than in its dorsal parts. On the other hand, both in *Asterolepis* (Gross 1931, pl. 12, fig. 7; 1933a, text-fig. 16; Obrutschew 1933b, pl. 1, fig. 3) and in *Remigolepis* the orbital chamber is developed in the reverse way, so that it is more capacious in its dorsal than in its ventral part and accordingly in such a manner that the fenestra orbitalis is larger than the fenestra suborbitalis.

In its anterior half or somewhat more the orbital chamber is in its fossil condition in open communication anteriorly and antero-laterally with a large cavity, the preorbital recess (*prh*, prh_1, text-figs. 9, 11, 13–15, 233A) already repeatedly referred to above (pp. 28–29), which is situated chiefly in the preorbital division of the shield, more precisely in the posterior half of the premedian plate and the adjacent medial parts of the lateral plates.

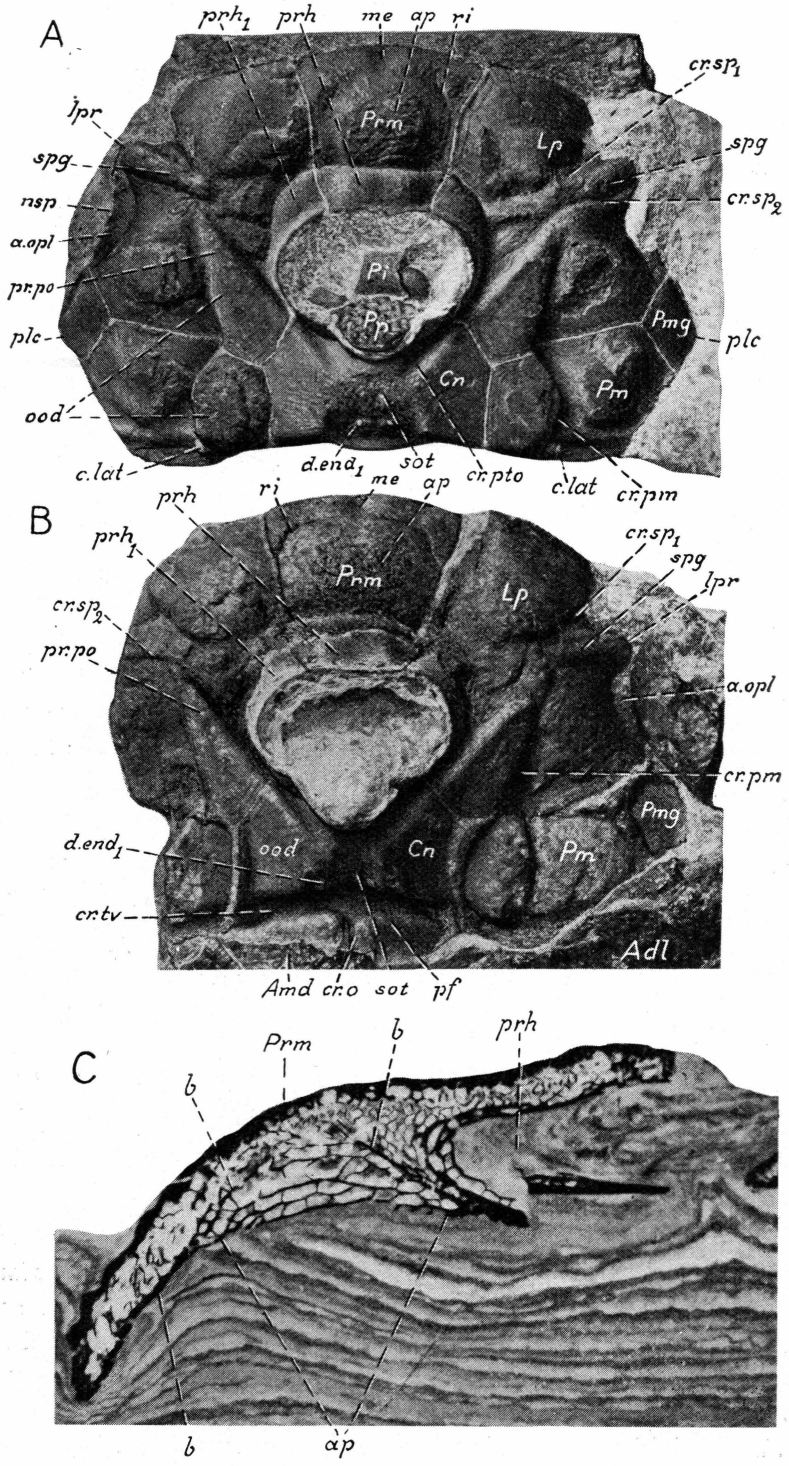


Text-fig. 14. *Bothriolepis cellulosa.* Restored nead-shield in dorsal view. The rostral, pineal and sclerotic plates omitted. The extent of the preorbital recess indicated by shading. Approximately × $^{8}/_{5}$.

Cn, centro-nuchal plate; *Lp*, lateral plate; *Pm*, paranuchal-marginal plate; *Pmg*, post-marginal plate; *Pp*, postpineal plate; *Prm*, premedian plate; *alc*, antero-lateral corner of head-shield; *cir*, semicircular pit-line groove; *d.end*$_2$, dorsal opening of canal for ductus endolymphaticus; *ifc*$_1$, upper infraorbital sensory canal groove; *ifc.b*, anterior oblique cephalic pit-line groove; *lpr*, supraspiracular process; *mpg*, middle pit-line groove of skull-roof; *nm*, obtected nuchal area; *nprl*, prelateral notch; *nsp*, supraspiracular notch; *om*, obstantic margin; *plc*, postero-lateral (preobstantic) corner of head-shield; *pp*, posterior pit-line groove of skull-roof; *prh*, *prh*$_1$, median unpaired and lateral paired divisions respectively of the preorbital recess; *pr.nm*, posterior median process of centro-nuchal plate; *ptc*, cephalic division of main lateral line; *ptoc*, postobstantic corner; *soa*, subobstantic area; *soc*$_2$, anterior median division of supraorbital sensory groove (the anterior median pit-line groove); *vcp*, vertical pit-line groove of the cheek.

This recess was well figured by Patten in 1912 (text-figs. 252A, 253:2) and was termed by him the olfactory recess. Later on it has been figured also by the present writer (Stensiö 1931, text-figs. 5, 21) and by Gross (1941a, pl. 2, fig. 2; pl. 18, fig. 1). As it has not been described by previous writers it will now be briefly dealt with here.

Among the *Bothriolepis*-species in which it is known as yet the preorbital recess is largest and best developed in *B. groenlandica* and *B. maxima.* In these two species (*prh*, *prh*$_1$, text-figs. 13, 233A, C, J, 234B, 235E; pl. 1; pl. 8, fig. 4) it is as a whole three-indented and clearly subdivided into a median unpaired division (*prh*), situated in the premedian plate, and a paired lateral division (*prh*$_1$) lying in the adjoining part of the lateral plate of either side. These divisions are continuous posteriorly nearest in front of the orbital


A
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prh
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chamber, whereas further anteriorly they are completely separated from each other. They are produced into marked points and are almost triangular in outline when exposed from the dorsal or ventral sides. The median division stretches forwards to about the middle of the premedian plate, whereas the lateral division reaches as far laterally as to a point close in front of the antero-lateral corner (*pr.po*) of the otico-occipital depression (*ood*) on the lower side of the shield, being separated from this corner of the otico-occipital depression by a thin wall of bone only. By means of a more or less distinct rostro-caudal ridge (*rd*) on the inside of its dorsal wall the median division in *B. groenlandica* (text-fig. 13) in its uppermost part is imperfectly subdivided into right and left halves, a condition which shows that a paired formation must had extended into it from behind, that is to say from the orbital chamber.

In *Bothriolepis canadensis* and *B. cellulosa* the preorbital recess (*prh*, prh_1, text-figs. 9, 11, 14, 15, 20A, 218, 221B) is of type a somewhat different from that in *B. groenlandica* and *B. maxima* in that it is smaller relatively and as a whole almost semilunar in outline when exposed from above or from below. Its median (*prh*) and lateral (prh_1) divisions are continuous with each other throughout their extent forwards, and owing to this they are not nearly as well marked off from each other as in *B. groenlandica* and *B. maxima*. The median unpaired division, at any rate in *B. canadensis*, however, is a little higher than the lateral paired one. Usually it ends anteriorly already at the transition between the posterior and middle thirds of the premedian plate and in no case stretches as far forwards as to the middle of this plate.

Text-fig. 15. *Bothriolepis canadensis*. *A*, *B*, impressions of the lower side of the head-shield of two medium-sized individuals with the preorbital recess preserved as a cast. Specimens Nos. P. 2143 and P. 2343 respectively in the Swedish Museum of Natural History, Stockholm. In the specimen reproduced in *B* the median part of the preorbital recess is imperfect anteriorly. In this specimen the impression of the otico-occipital depression is affected by pressure in the rock so that its shape does not stand out quite clearly. For the understanding of figs. *A* and *B* compare text-figs. 11 and 12. *C*, rostro-caudal section through the median part of the premedian plate, showing the position and forward extent of the median, unpaired division of the preorbital recess and the structure of the bone above the poriferous area (*ap*). The posterior part of the floor of the preorbital recess broken off and dislocated somewhat upwards from its original position. Specimen No. P. 2213 in the Swedish Museum of Natural History, Stockholm. *A*, *B*, × 4/3, *C*, × 3.6.

Adl, anterior dorso-lateral plate; *Amd*, anterior median dorsal plate; *Cn*, centro-nuchal plate; *Lp*, lateral plate; *Pi*, pineal plate; *Pm*, paranuchal-marginal plate; *Pmg*, post-marginal plate; *Pp*, postpineal plate; *Prm*, premedian plate; *a.opl*, area for attachment of extralateral plate; *ap*, poriferous area; *b*, ventral bone-layer of premedian plate; *c.lat*, canal probably for a lateralis nerve; *cr.o*, median occipital crista (impression); *cr.pm*, paramarginal christa (impression); *cr.pto*, postorbital crista (impression); $cr.sp_1$, prespiracular crista (impression); $cr.sp_2$, postspiracular crista (impression); *cr.tv*, transverse nuchal crista (impression); $d.end_1$, ventral opening of canal for ductus endolymphaticus in centro-nuchal plate; *lpr*, supraspiracular process; *me*, median elevation between anterior ends of oblique premedian ridges; *nsp*, supraspiracular notch; *ood*, otico-occipital depression (impression); *pf*, posterior (nuchal) face of head-shield (impression); *plc*, postero-lateral corner of head-shield; *prh*, prh_1, median unpaired and lateral paired divisions respectively of preorbital recess (casts); *pr.po*, antero-lateral corner of otico-occipital depression developed for postorbital process; *ri*, oblique premedian ridge (impression); *sol*, supraotic thickening (impression); *spg*, spiracular groove (impression).

Its anterior margin is fairly straight or slightly convex and as a rule not produced into any distinct angle or point. The lateral paired division is short, ending already a short distance laterally to the orbital chamber and thus very far proximally to the antero-lateral corner (*pr.po*) of the otico-occipital depression. The lateral margin of this division as a whole is normally convex with a concavity anteriorly, but in certain cases in *B. canadensis* it may be extended into a fairly pronounced angle (Patten 1912, text-fig. 252A). In *B. canadensis* the median division in its dorsal parts is imperfectly subdivided into right and left halves. This imperfect subdivision is effected by a broad, low rostro-caudal thickening, which is the homologue of the similarly situated rostro-caudal ridge in *B. groenlandica*. No corresponding subdivision of the median division seems to occur in *B. cellulosa* (text-fig. 218).

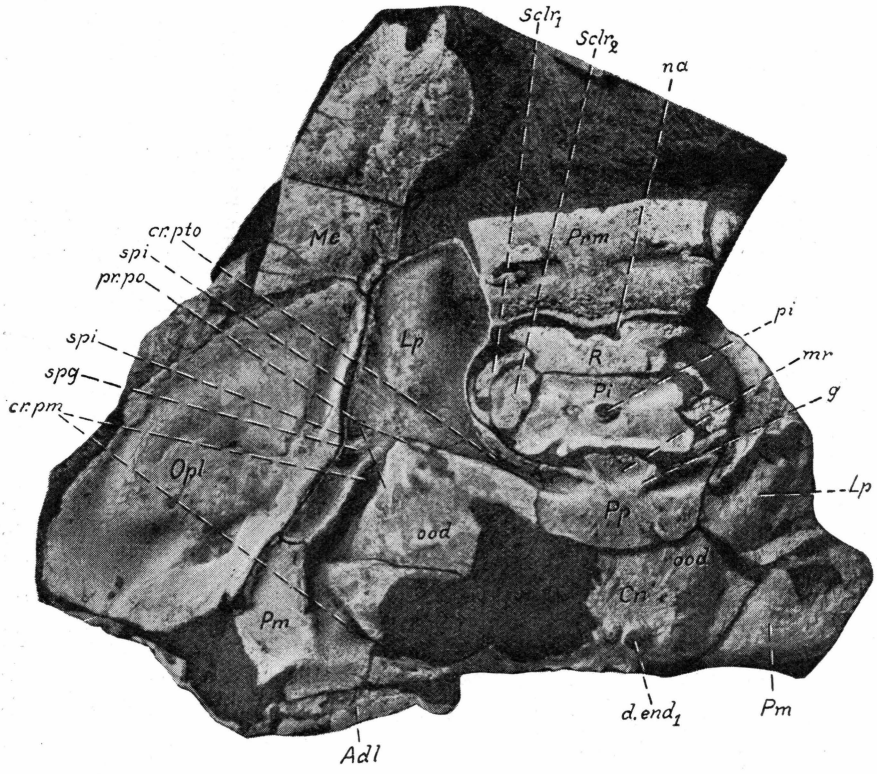
In *Grossilepis* there is also a well developed preorbital recess (Gross 1941a, pl. 18, fig. 1), the median unpaired division of which seems to be approximately as the corresponding division in *B. cellulosa*. The lateral paired division of the recess in this form is still unknown.

Among the *Asterolepidae* the preorbital recess is known only in *Asterolepis ornata* where it is slightly developed and represented only by a more or less vestigial part of its median, unpaired division. In the *Remigolepidae* the recess is practically absent. In *Pterichthyodes*, *Gerdalepis* and *Microbrachius* nothing at all is known so far concerning the development of the recess in question.

As has already been pointed out above in the chapter on the endocranium (pp. 28–29), the median unpaired division of the preorbital recess must have housed the anterior parts of the nasal capsules, whereas the lateral paired division of the recess in all probability was developed for the antorbital process of the ethmoidal region.

Laterally and posteriorly to the suborbital fenestra the lower side of the head-shield in the *Antiarchi* presents a large depression known already since long ago (Patten 1912, text-fig. 252A; Obrutschew 1933b, pl. 1, fig. 2) and described by me in 1931 (Stensiö 1931, pp. 39, 52, text-figs. 4–6) as the otico-occipital depression. This depression in the *Bothriolepinae* (*ood*, text-figs. 11, 12, 15A, B) is considerably narrower in proportion to the breadth of the head-shield than the corresponding one in *Asterolepis* and *Remigolepis* and in addition is shallower than it. In *Grossilepis* (cf. Gross 1941, pl. 18, fig. 2) it is even strikingly narrow not only in proportion to the breadth of the head-shield, but also in proportion to its own length. It is situated chiefly behind the suborbital fenestra, but its paired antero-lateral corner (*pr.po*) stretches far forwards laterally to that fenestra. With its main posterior part it lies underneath the centro-nuchal plate and an adjoining medial part of the paranuchal-marginal plate of both sides, while with its antero-lateral corner (*pr.po*) it extends underneath the posterior medial part of the lateral plate of either side. It is bounded antero-medially, from the orbital chamber,

by a paired obliquely running postorbital crista (*cr.pto*). This crest is lower than in *Asterolepis* (*cr.pto*, text-figs. 17, 18) and *Remigolepis* (*cr.pto*, text-fig. 16), and contrary to what is the case in these two forms it does not pass on backwards to the postpineal plate, but to the centro-nuchal plate. It is more rostro-caudal throughout its extent, therefore, than in *Asterolepis* and *Remigolepis*. The lateral boundary of the depression is formed by a paired, mainly rostro-caudal paramarginal crista (*cr.pm*), which is lower than the corresponding crest in *Asterolepis* (*cr.pm*, text-figs. 17, 18) and *Remigolepis* (*cr.pm*, text-fig. 16) and, besides, differs from the one in the said two genera also in the following conditions: 1) it is not situated approximately underneath the upper infraorbital sensory canal groove and the cephalic division of the main lateral line, but considerably medially to these two grooves; 2) it does not descend mainly vertically from the skull-roof, but issues from it in a ventro-medial direction (Stensiö 1931, text-fig. 6); 3) as a whole it rises only fairly slightly above the level of the lower face of the shield situated laterally to the otico-occipital depression; and 4) it is not straight or curved so as to be a little convex on its lateral side and concave on its medial side, but is concave on its lateral side and correspondingly convex on its medial side with the deepest concavity, respectively the most pronounced convexity, approximately at the suture between the lateral and paranuchal-marginal plates. Finally, the posterior boundary of the depression is constituted by the strongly developed transverse nuchal crista (*cr.tv*, text-figs. 11, 12, 15A, B, 19), which, as normally in the group, is fairly straight or bent so that it is slightly convex anteriorly and correspondingly concave posteriorly, and which also, as in the other *Antiarchi*-forms known, is lowest and least pronounced in its median part situated above the foremost part of the low posterior division of the occipital region of the endocranium. The antero-medial, or, more correctly, morphologically anterior margin of the antero-lateral corner (*pr.po*) of the depression is somewhat more rostro-caudal in extent than in *Asterolepis* and much more so than in *Remigolepis* (text-fig. 16), in which it is almost transverse. The depression is always clearly broadest across the anterior ends of its antero-lateral corners (*pr.po*), narrowest approximately at the suture between the lateral and paranuchal-marginal plates, whereas the corresponding depression in *Asterolepis* is of fairly uniform breadth throughout its length (Stensiö 1938, pl. 1, fig. 1) and the one in *Remigolepis* is broadest somewhat in front of its posterior end and narrowest across its antero-lateral corners (text-fig. 16). The antero-lateral corner (*pr.po*) extends as far forwards as to, or beyond, a transverse plane through the anterior margin of the orbital fenestra and thus is much longer than that in *Asterolepis* and that in *Remigolepis*, which end anteriorly opposite the middle of the orbital fenestra and at transverse plane through the posterior margin of the orbital fenestra respectively (text-fig. 16; cf. Gross 1931, pl. 4, fig. 14;



Text-fig. 16. *Remigolepis* sp. An imperfect head-shield with the left extralateral plate attached to it and the mental plates detached and somewhat displaced. With the exception of the premedian plate, the head-shield is preserved as an impression of its lower side. The extralateral and mental plates also in the main preserved as impressions of their inner sides. The otico-occipital depression well shown. Dorsal view. Approximately × 5/4. *Adl*, fragment of anterior dorso-lateral plate (a part of the transverse lamina, crista transversalis interna anterior, with the articular fossa for the paranuchal trochlea; *Cn*, centro-nuchal plate; *Lp*, lateral plate; *Me*, mental plate; *Opl*, extralateral plate; *Pi*, pineal plate; *Pm*, paranuchal-marginal plate; *Pp*, postpineal plate; *Prm*, premedian plate; *R*, rostral plate; $Sclr_1$, $Sclr_2$, anterior and postero-dorsal sclerotic plate respectively; *cr.pm*, paramarginal crista (preserved as impression); *cr.pto*, postotic crista (preserved as impression); $d.end_1$, internal opening of canal for ductus endolymphaticus through centro-nuchal plate; *g*, groove or pit on lower side of postpineal plate (impression); *mr*, median thickening on lower side of the postpineal plate (impression); *na*, external nasal aperture; *ood*, otico-occipital depression (impression); *pi*, pineal opening; *pr.po*, antero-lateral corner of otico-occipital depression developed for postorbital process; *spg*, spiracular groove; *spi*, spiracular opening.

Stensiö 1931, text-fig. 8; 1938, pl. 1, fig. 1; Obrutschew 1933b, pl. 1, fig. 2). They are also narrower and shallower than those in the two genera just referred to. On the posterior median part of the depression, as normally in the group, there is a rostro-caudal broad elevation, the supraotic thickening (*sot*, text-figs. 11, 12, 15A, B, 25 B, 233 K, 236 B), which is situated on the lower face of the centro-nuchal plate in front of the median low part of the transverse nuchal crista (*cr.tv*) and which gradually diminishes in height forwards from the said crista, finally disappearing at or somewhat behind the

posterior ends of the postorbital crests (*cr.pto*). This thickening, which probably varies rather much in shape and development, generally is fairly rough in appearance (text-figs. 11, 12, 237B; cf. also Gross 1940b, pl. 4, fig. 13) and may also be poriferous. As to its minute structure it seems to be mainly as the poriferous area described below on the ventral face of the premedian plate (cf. pp. 57–58 below; cf. also Stensiö 1931, text-figs. 6, 7, 14).

Close laterally to, or in the lateral part of, the supraotic thickening just described we find in the *Bothriolepinae*, as in *Asterolepis* and *Remigolepis* (cf. text-fig. 20; cf. also Stensiö 1931, text-fig. 14; Gross 1931, pl. 4, fig. 6; 1940b, text-fig. 8A), the ventral opening (*d.end*$_1$, text-figs. 11, 12, 15A, B, 25B, 236B) of the paired canal trough which the ductus endolymphaticus ascended to the upper side of the skull-roof. This canal pierces the centro-nuchal plate in a postero-medio-dorsal direction, so that upwards it approaches its fellow of the opposite side (Stensiö 1931, pp. 44–49, text-figs. 17, 18). Besides this canal, only one more canal, also paired, issues from the otico-occipital depression. This last-mentioned canal (*c.lat*, text-fig. 15A, B; text-fig. 235L), which was noticed by the writer already in 1931 (Stensiö 1931, p. 51, text-figs. 5, 16B), passes off from the hindmost ventro-lateral corner of the depression and runs laterally and upwards in the paranuchal-marginal plate in a direction towards the cephalic division of the main lateral line groove (*ptc*). Though it could not be traced fully as far as to the said sensory canal groove, it is highly probable that it transmitted a lateralis nerve to this sensory canal groove. Judging from its position, this lateralis nerve may very well have been given off from the lateralis fibres which had their exit from the endocranium with the n. vagus.

Its position and extent show clearly that the otico-occipital depression of the *Antiarchi* housed certain dorsal parts of the endocranium, more precisely certain dorsal parts of the otic region and certain parts of the anterior broad division of the occipital region. The circumstance that, as we have seen, only the canal for the ductus endolymphaticus, piercing the centro-nuchal plate, and another canal, conceivably for a postotic lateralis nerve, pass off from it indicates that it was occupied only by certain upper parts of the said regions of the endocranium which were situated far dorsally to the exits of the n. facialis, n. glossopharyngeus, and n. vagus (cf. Stensiö 1925, text-figs. 1, 5, 6–8; 1934a, text-figs. 27, 38; 1945, figs. 3–5).

The otico-occipital depression in *Remigolepis* (*ood*, text-fig. 16) is deeper and better developed not only than that in the *Bothriolepinae*, but also than that in *Asterolepis*. As that in *Asterolepis*, it reaches as far laterally as almost to underneath the upper infraorbital sensory canal groove and the cephalic division of the main lateral line groove. The paramarginal crista in *Remigolepis* (*cr.pm*) is very thick and high and is situated exactly underneath the upper infraorbital sensory canal groove and the cephalic division of the main lateral line groove, strikingly close to the lateral margin of the head-shield.

This crista by its position thus marks the lateral extent of the dorsal wall of the endocranium both in the otic region and in the anterior broad division of the occipital region. On account of its height it must also have extended as far downwards that it covered the outside of the uppermost part of the lateral wall of the whole broad postorbital division of the endocranium. It is thus fully obvious that the otico-occipital depression must have housed the dorsal walls both of the otic region and of the anterior broad division of the occipital region. Its antero-lateral corner (*pr.po*) in *Remigolepis* is only very slightly produced antero-laterally and, therefore, is short and broad. This corner in *Remigolepis* is very well bounded by the bone-tissue of the lateral plate not only laterally and antero-medially, but, in its distal part, also ventrally. As is fully evident from its position and development, it was occupied in *Remigolepis* by the anterior and dorsal parts of a fairly normally developed postorbital process.

Summing what has just been set forth we thus find that the otico-occipital depression in the *Bothriolepinae* must have had the following relations to the endocranium (cf. Stensiö 1931, p. 52; cf. also pp. 33–35 above in this work). It housed the dorsal wall of the entire otic region and the dorsal wall of the anterior broad division of the occipital region. Its antero-lateral corner is the impression of the dorsal side of an excessively developed postorbital process. The paramarginal crista was developed only along the uppermost parts of the otic region and the anterior broad division of the occipital region. Hence, it did not extend as far downwards as to cover the principal part of the outside of the lateral wall of the broad postorbital division of the endocranium. The dorsal wall of the broad postorbital division of the endocranium was conceivably produced laterally into a thin solid lamina of cartilage which lay ventrally to the paramarginal crest, forming a support for the broad lateral part of the head-shield which is situated laterally to the said crest, the upper infraorbital sensory canal groove (*ifc*$_1$), and the cephalic division of the main lateral line groove (*ptc*).

After the description of the otico-occipital depression we shall proceed to the other parts of the lower face of the head-shield. In so doing we shall first turn to the part that is formed by the premedian plate, that is to say the lower face of the premedian plate.

This face is differently developed in the individual *Antiarchi*-forms. In the *Bothriolepinae* (text-figs. 11, 12, 15, 20B, 86; pl. 1; pl. 3, fig. 1; pl. 8, figs. 3, 5), and conceivably also in *Microbrachius* and the *Pterichthyoidae*, it is concave both in rostro-caudal and transverse directions and deepest concave approximately in its central part. In *Asterolepis* and *Remigolepis* (Stensiö 1931, pp. 34, 167–168; cf. also part III of this work), on the other hand, it

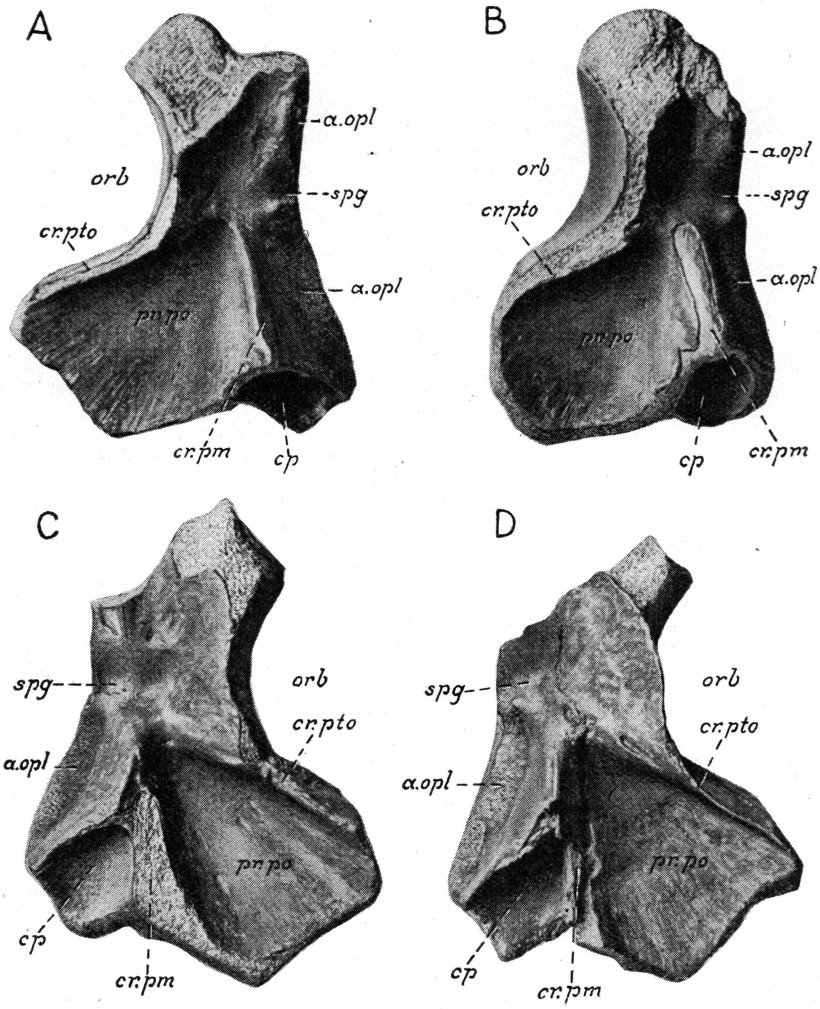
is relatively short and developed as a broad rostro-caudal groove, leading forwards to the anterior margin. Its different development in the *Bothriolepinae*, *Pterichthyodes* and *Microbrachius* on the one hand, and in *Asterolepis* and the *Remigolepidae* on the other, is certainly due to a different development of the jaw apparatus (Stensiö 1931, p. 34). At least in *B. canadensis*, *B. cellulosa* and *B. maxima* the face under consideration at the rostral margin presents a more or less long, unpaired median thickening or elevation (*me*, text-figs. 11, 12, 15A, B, 20B, 86, 218, 220E, 233C, F; cf. Stensiö 1931, pp. 34–36, text-figs. 4, 5, 23A, B; Gross 1941a, text-fig. 5E; cf. also below) from which a paired oblique ridge, the premedian oblique ridge (*ri*), passes off in a direction backwards and more or less laterally. In *B. canadensis* and *B. cellulosa* this ridge (*ri*), extends to the lateral notch (*nl*) in the ventral margin of the premedian plate; in *B. maxima* it seems to vary considerably in position (text-fig. 233C, F). Besides the formations mentioned, we find on the face in question in the three *Bothriolepis*-species referred to also an unpaired median tubercle (*t*, text-fig. 233C, F) or a median ridge (*rv*, pl. 1) which is situated on the middle or posterior part of the premedian plate. In *B. groenlandica* (pl. 1; pl. 3, fig. 1; pl. 8, figs. 3–5) both the median elevation (*me*) and the premedian oblique ridge (*ri*) are entirely absent. What functions the elevations and ridges just described may have had is difficult to make sure. In 1931. (Stensiö 1931, pp. 35–36) I was of the opinion that the oblique premedian ridge (*ri*) served as the place of origin of certain visceral muscles, but from what is now known concerning the jaw-apparatus it is evident that this cannot be true. For the time being I am mostly inclined to believe that it was developed at the anterior end of the presumed rostral process of the ethmoidal region of the endocranium and that it thus simply marks the forward extent of this presumed process (cf. pp. 28–29 above).

Except probably in very small individuals, the central parts of the concave lower face of the premedian plate in the *Bothriolepinae* form a characteristic rough and porous area, which will here be termed the poriferous area (*ap*, text-figs. 11, 12, 15, 20B, 86). Sections through the premedian plate in the *Bothriolepinae* show (text-fig. 15C) that this plate consists of a cancellate bone, lined above and below by more solid layers. At the poriferous area, below the ventral layer (*b*), there are a few layers made up of large cancellae. Several of the cancellae of the most basal one of these layers are more or less open ventrally, their ventral walls being imperfectly developed or absent. In addition, below these cancellae, there are thin ventrally descending bone-trabecles which indicate that a new layer of large cancellae is in an initial stage of development below the basalmost complete one. The part of the ventral bone layer (*b*) of the plate, situated above the cancellous layers forming the poriferous area, may be more or less resorbed. As far as I can see, an apposition of cancellous bone was thus in progress at the poriferous area in the *Bothriolepinae*. This apposition took place ventrally to the primary

ventral layer of the premedian plate and seems to have been going on fairly independently of the growth of the plate otherwise. In this connection it should also be pointed out that the supraotic thickening (*sot*, text-figs. 11, 12, 15A, B; 25B; cf. pp. 54-55), which lies on the median posterior part of the centro-nuchal plate, is of a rough porous appearance similar to that of the poriferous area already described. It is therefore likely that the supraotic thickening has the same structure and is of the same nature as the poriferous area.

The part of the lower face of the head-shield in the *Bothriolepinae* that is situated on the preorbital division of the lateral plate (text-figs. 11, 12, 15A, B, 218, 221B, 233J, 234B, 277 F) is very broad and concave both in rostro-caudal and transverse directions. It differs, therefore, clearly from the corresponding part of the lower face of the head-shield in *Asterolepis* (text-fig. 17; cf. also Gross 1931, pl. 4, fig. 14; Stensiö 1931, text-fig. 8 B, E) and *Remigolepis* (text-fig. 16) which is fairly narrow and more or less clearly grooved in a rostro-caudal direction. Whether it is also developed in a manner different from that of the corresponding part of the lower face in *Pterichthyodes* and *Microbrachius* cannot be decided.

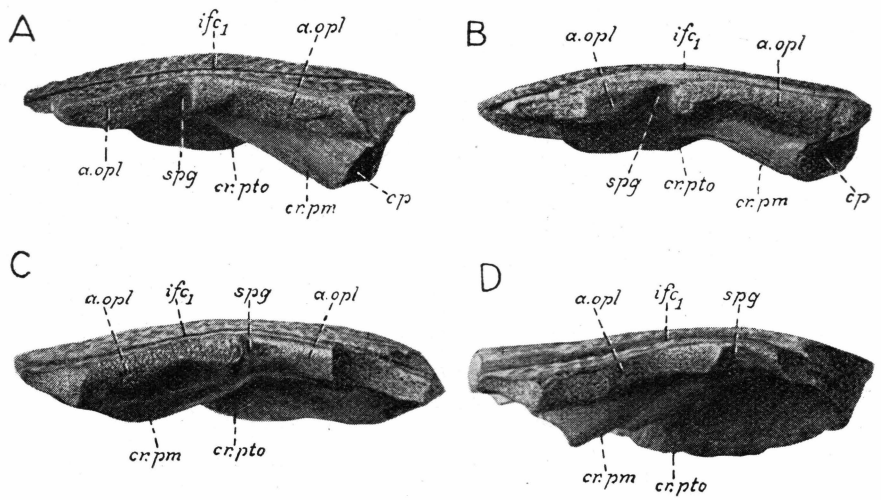
A particularly interesting formation on this part of the lower face of the head-shield in the *Bothriolepinae* is a transverse fairly broad groove which is situated close in front of the antero-lateral corner (*pr.po*) of the otico-occipital depression. This groove, which will be referred to as the spiracular groove (*spg*, text-figs. 11, 12, 15A, B, 218, 233J, 234B, 277F; pl. 1; pl. 8, fig. 4; pl. 10), passes off from the distal end of the supraspiracular process (*lpr*) in a direction medially and somewhat posteriorly. When completely developed it extends almost across the entire lower face of the lateral plate and thus almost to the antero-lateral part of the suborbital fenestra (text-figs. 15A, B, 233J, 234B; pl. 10, fig. 1), but in many cases it is traceable only to about midway between the lateral and orbital margins of the plate to a point close in front of the anterior end of the antero-lateral corner (*pr.po*) of the otico-occipital depression. It is bounded anteriorly and posteriorly by low transverse crests, termed here respectively the prespiracular (*cr.sp*$_{L}$) and post-spiracular (*cr.sp*) crests. It is narrowest in its middle part, in front of the antero-lateral corner of the otico-occipital depression, broadest towards the lateral and medial ends. Its lateral half is always broader and deeper than its medial one. With at least its lateral half the groove in question lay close above the interspaace between the palatoquadrate and the hyoid arch (cf. pp. 38-39 above), and laterally it leads outwards to the spiracular aperture (*spi*, text-figs. 4, 7) which is situated between the supraspiracular process dorsally and the hindmost part of the upper margin of the anterior low division of the extralateral plate venstrally (cf. also pp. 88 90 below, and text-fig. 32). Its topographical position and other conditions show clearly, therefore, that it must have been developed in relation to the upper parts



Text-fig. 17. *Asterolepis ornata*. Four somewhat deficient lateral plates in ventral aspect. *A*, *B*, two left plates and *C*, *D*, two right plates. All the plates in the possession of the Swedish Museum of Natural History in Stockholm. Approximately × $^3/_2$.
a.opl, area for attachment of extralateral (opercular) plate; *cp*, deep posteriorly opening pit in paramarginal crista; *cr.pm*, paramarginal crista; *cr.pto*, postorbital crista; *orb*, orbital notch; *pr.po*, antero-lateral corner of otico-occipital depression developed for postorbital process; *spg*, spiracular groove.

of the spiracular gill-slit and to the external opening of this gill-slit. The term spiracular groove here suggested for it is thus fully appropriate.

The spiracular groove in *Asterolepis* (*spg*, text-figs. 17, 18) is narrow and shallow and not bounded by any ridges, on account of which it is so slightly pronounced that it may easily be overlooked. It is represented only by its lateral half, which is traceable as far medially as to just in front of the antero-lateral corner (*pr.po*) of the otico-occipital depression. With its lateral



Text-fig. 18. *Asterolepis ornata*. Four somewhat defective lateral plates in lateral aspect. *B*, *B*, two left, and *C*, *D*, two right plates. The same plates as in text-fig. 17. Approximately × 4/5.
a.opl, area for attachment of extralateral plate; *cp*, deep posteriorly opening pit in paramarginal crista; *cr.pm*, paramarginal crista; *cr.pto*, postorbital crista; *ifc*$_1$, upper infraorbital sensory groove; *spg*, spiracular groove.

part it crosses the laterally facing area (*a.opl*) of attachment for the extralateral plate so that it divides this area into an anterior and a posterior part. Its very lateral end is situated at the deepest concavity of the lateral margin of the lateral plate, just opposite the marked spiracular notch in the upper margin of the extralateral plate described by Gross and shown in several of the reproductions and restorations published by him (Gross 1931, pl. 4, figs. 14, 15; pl. 12, fig. 7; 1933, text-fig. 16; cf. also Nilsson 1941, p. 52). As we thus find, the groove also here leads outwards to a spiracular opening.

A spiracular groove has now been detected also in *Remigolepis*. The spiracular groove in this form (*spg*, text-fig. 16) is developed in a manner somewhat similar to that in *Asterolepis*. It is thus shallow, little conspicuous and represented only by a lateral part, which divides the laterally facing area of attachment for the extralateral plate in two divisions, anterior and posterior. As that in *Asterolepis*, it leads laterally to the deepest concavity of the lateral margin of the lateral plate. Its most important differences from the corresponding groove in *Asterolepis* may be summarized as follows. 1) It does not extend quite as far medially as to just in front of the anterior end of the antero-lateral corner (*pr. po*) of the otico-occipital depression, but ends somewhat laterally to it. It is thus somewhat shorter relatively than that in *Asterolepis*. 2) As in the *Bothriolepinae*, it is bounded by a prespiracular and a postspiracular crest, but these crests are low and obscure. 3) Finally, it leads outwards to a special pit in the uppermost part of the extralateral plate, a pit which in its turn leads forewards to the interspace between

the lateral and extralateral plate. The spiracular opening (*spi*) in *Remigolepis* is therefore situated in front of the spiracular groove and is developed as a slit between the lateral and extralateral plates.

The conditions as to the spiracular groove are unknown so far in *Pterichthyodes, Gerdalepis, Microbrachius* and other *Antiarchi* forms. However, in *Gerdalepis* Gross (1941b, p. 196, figs. 1A, 7, 11) has found a large opening between the lateral plate and the extralateral plate, an opening which is clearly a large spiracular opening.

Everything seems thus to show that in the *Antiarchi* in general there was an external spiracle opening between the lateral and extralateral plates.

Close in front of the spiracular groove the lower face of the lateral plate in the *Bothriolepinae,* or, at any rate in *Bothriolepis,* exhibits a marked pit, the prespiracular pit (*p,* text-figs. 11, 12, 218, 221B, 233J, 277F; pl. 10, figs. 1–4). More precisely, this pit is situated fairly straight in front of the antero-lateral corner of the otico-occipital depression, and thus just in front of the narrowest part of the spiracular groove. In many cases it may be entirely absent (text-figs. 15A, B; pl. 10, fig. 6). Its function is still unknown.

The part of the lower face of the shield that is situated behind the orbital fenestra and between the posterior parts of the postotic crests (*cr.pto*) in the *Bothriolepinae* (text-figs. 11, 87C, 236B) extends backwards on to the foremost parts of the centro-nuchal plate, whereas this is not the case in *Asterolepis* and *Remigolepis.* In the latter two forms (text-figs. 16, 17) the part here in question of the lower face of the head-shield is confined only to a more or less large anterior portion of the postpineal plate, and consequently is much smaller in them than in the *Bothriolepinae.* That this is so is due to the fact that the postotic crests in both *Asterolepis* and *Remigolepis,* as has already been pointed out, do not pass on backwards to the centro-nuchal plate, but curve medially so as to end posteriorly on the postpineal plate. The foremost portion of the part of the lower face of the shield here under description that lies on the postpineal plate in the *Bothriolepinae* (text-figs. 11, 87C, 236B) is somewhat depressed as compared to the posterior portion of the same face. As in *Asterolepis* (Gross 1931, p. 25; pl. 4, fig. 1; Stensiö 1931, p. 42, text-fig. 12) and *Remigolepis* (text-fig. 16), it presents a median rostro-caudal thickening or ridge (*mr*) and to either side of this a groove or pit (*g*), which leads forwards and somewhat laterally to the uppermost postero-lateral part of the orbital chamber. No interpretation of these formations can be given here.

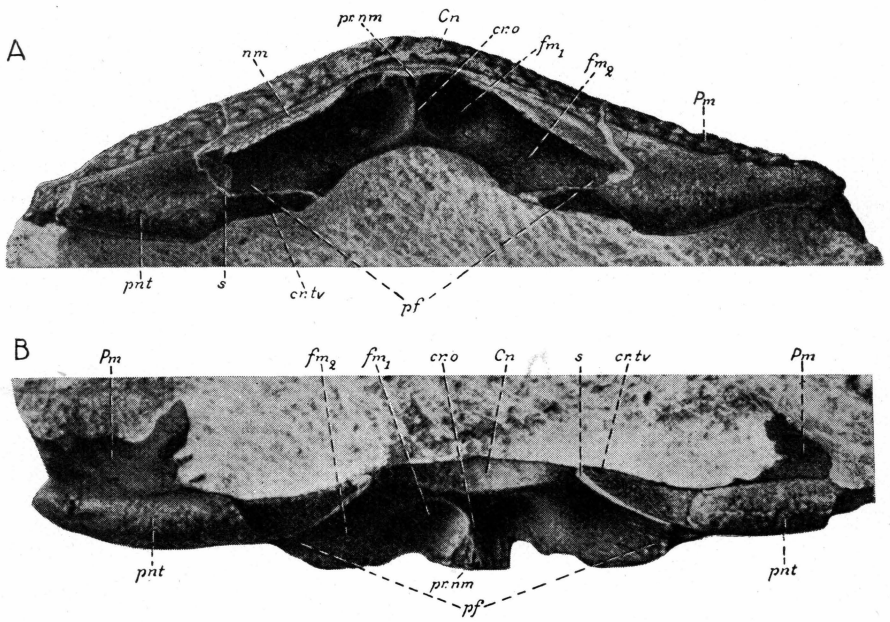
Finally, the postero-lateral part of the lower face of the head-shield that lies behind the spiracular groove and laterally to the paramarginal crista (text-figs. 11, 12; cf. also Gross 1941a, pl. 18, fig. 2) is strikingly broad in the *Bothriolepinae,* much broader than in the *Asterolepidae* and *Remigolepidae* (text-fig. 16). In the *Bothriolepinae* it is curved in such a manner that throughout its length it is somewhat concave in transverse directions,

while in the *Asterolepidae* and *Remigolepidae* it is practically plain in its posterior portion. Both in the *Bothriolepinae* and *Remigolepidae* it is completely devoid of all vestiges of the large posteriorly opening pit (*cp*, text-figs. 17, 18; Obrutschew 1933b, pl. 1, fig. 2) that is found in *Asterolepis* in the paramarginal crest, laterally to the antero-lateral corner (*pr.po*) of the otico-occipital depression.

In this connection the transverse nuchal crista in the *Bothriolepinae* has to be dealt with more in detail than what has been done above (p. 53). This crista (*cr.tv*, text-figs. 11, 12, 15B, 19, 25B, 27, 237B) in its position is exactly as the corresponding one in other *Antiarchi* (text-fig. 16). It is formed by the centro-nuchal plate and the medial parts of the paranuchal-marginal plates of both sides and extends across the parts of these plates which enter into the formation of the otico-occipital depression. Laterally it is continuous with the paranuchal trochlea (*pnt*) of either side. In dorsal or ventral aspects (text-figs. 11, 12, 15B) it may be either practically straight or curved in such a way that it is a little convex anteriorly and correspondingly concave posteriorly. When looked at from in front or from behind (text-fig. 19) its lower margin is strongly concave. It is highest in its lateral parts, lowest in its median part, where it presents a pronounced notch, a notch which was caused by the foremost part of the posterior narrow, low division of the occipital region of the endocranium.

Besides the upper and lower faces already described, a posterior face may also be distinguished on the head-shield of the *Antiarchi*. This face is formed by the posterior face of the transverse nuchal crista and by the posterior face of the lateral parts of the paranuchal-marginal plates.

The posterior face of the head-shield in the *Bothriolepinae* is completely kown only in *B. canadensis*, where it is as follows (text-figs. 9 12, 15B, 19, 25B, 27; cf. also Stensiö 1931, text-fig. 16). Its median unpaired division (*pf*) formed by the transverse nuchal crista (*cr.tv*) is fairly well bounded off laterally from either lateral division and is smooth in appearance. Taken as a whole it is curved in such a way that it is more or less concave both in dorso-ventral and transverse directions. It is normally provided with a distinct median occipital crista (*cr.o*) which runs downwards from the lower side of the posterior median process (*pr.nm*) of the centro-nuchal plate. On either side of this crista there are two depressions or fossae, a sometimes rather deep medial one (*fm*) and a shallow lateral one (fm_1). These two depressions or fossae probably served as areas of insertion for the levator muscles of the head (Stensiö 1945, pp. 5-7. The lateral paired division of the face, formed by the paranuchal-marginal plate, as a whole seems to be a little more rough in its appearance than the median division. At any rate it is not as smooth as it. Its upper part is vertical and practically transversally placed; its lower part forms the paranuchal trochlea. This trochlea (*pnt*), which is developed for the articulation with the trunk-armour, how-

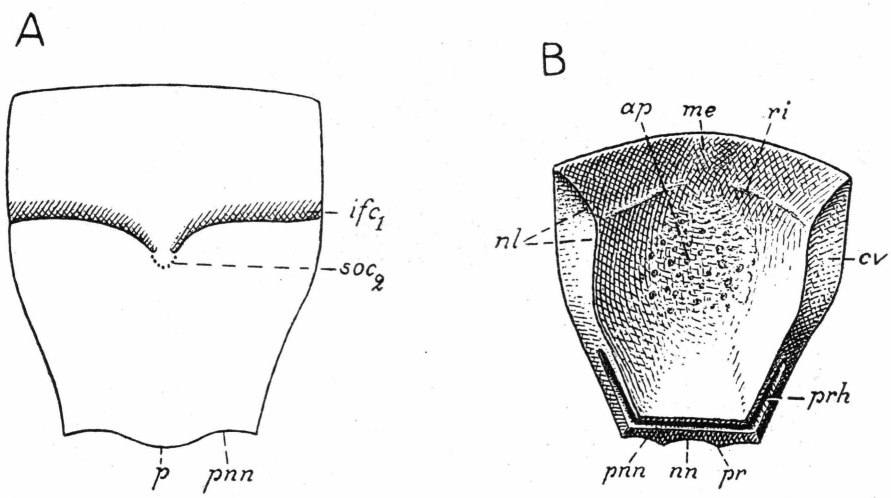


Text-fig. 19. *Bothriolepis canadensis*. Posterior part of the head-shield reproduced in text-fig. 79 A, B. The posterior face with the paranuchal trochlea well shown. *A*, in posterior aspect. *B*, in ventral aspect. In front of the paranuchal trochlea of either side certain postero-lateral parts of the lower face of the shield are exposed. Specimen No. P. 2107 in the possession of the Swedish Museum of Natural History in Stockholm. About × 2.6. *Cn*, centro-nuchal plate; *Pm*, paranuchal-marginal plate; *cr.o*, median occipital crista; *cr.tv*, transverse nuchal crista; fm_1, fm_2, depressions or fossae probably for insertion of levator muscles of the head; *nm*, obtected nuchal area; *pf*, posterior face of head-shield (formed by the transverse nuchal crista); *pnt*, paranuchal trochlea; *pr.nm*, posterior median process of centro-nuchal plate; *s*, suture between centro-nuchal and paranuchal-marginal plates.

ever, extends also somewhat downwards on to the lower side of the paranuchal-marginal plate, and thus a little on to the lower face of the shield (text-figs. 11, 12, 19B). Contrary to that in *Asterolepis ornata* (cf. Gross 1931, pl. 5, fig. 4; pl. 11, fig. 1; 1933b, text-fig. 2; Stensiö 1931, text-fig. 19) and *Remigolepis* (Stensiö 1931, pl. 3, fig. 1), which is highest laterally, the paranuchal trochlea in the *Bothriolepinae* decreases in height laterally so that it is very low at its lateral end. It differs also considerably from the corresponding one in *Asterolepis*, in that it is not subdivided into a number of secondary trochleae.

In *B. groenlandica* the posterior face of the head-shield seems normally to be as *B. canadensis*, whereas in *B. maxima* the median occipital crest (*cr.o*, text-fig. 237) at least sometimes is broader, and the lateral one (fm_1) of the two paired depressions or fossae smaller, than in *B. canadensis*.

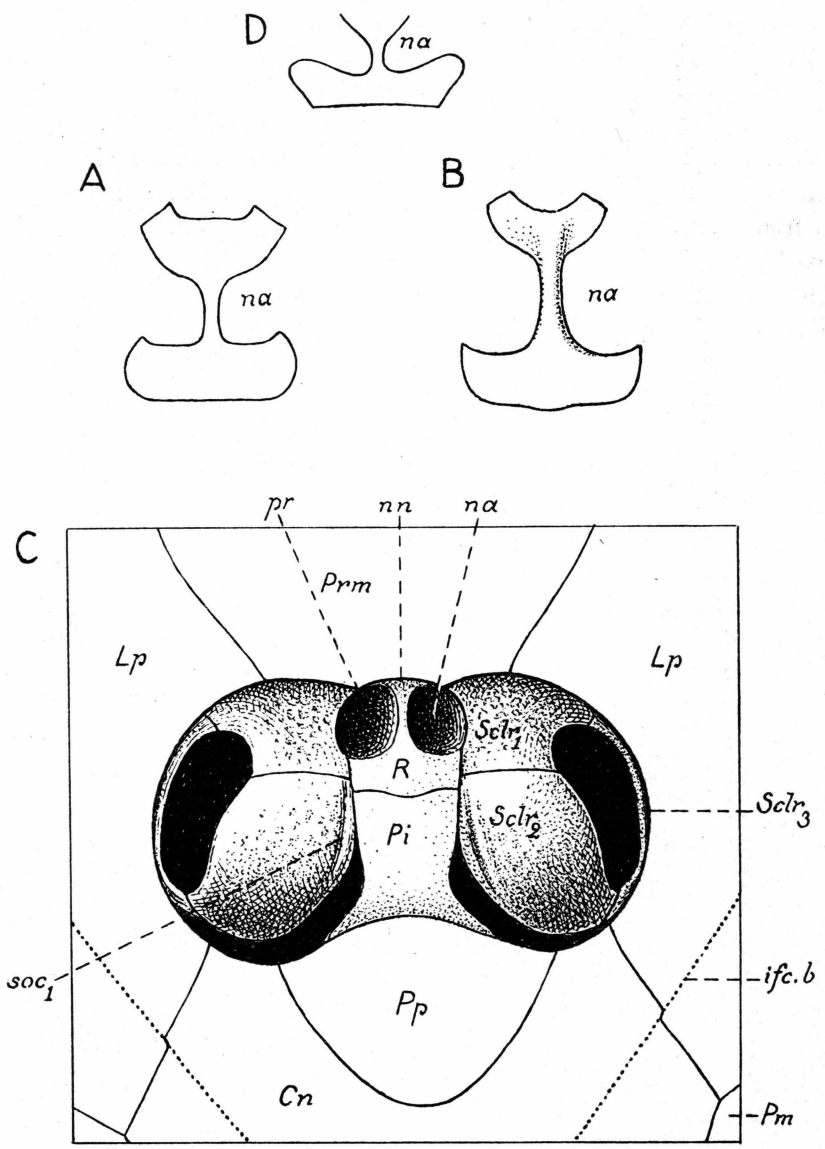
After the above general remarks we shall now proceed to an account of the various bones composing the head-shield in the *Bothriolepinae*. Since they are already well known from previous works (Stensiö 1931, pp. 31–57;



Text-fig. 20. *A*, a premedian plate of a large individual of *Bothriolepis groenlandica* in dorsal aspect. × $^1/_1$. *B*, a premedian plate of a large individual of *B. canadensis* in ventral view. × $^3/_2$.
ap, poriferous area; *cv*, area overlapping lateral plate; *me*, median elevation between the ridges *ri*; *nl*, ventral lateral notch; *nn*, nasal notch; *p*, nasal process; *pnn*, paranasal notch; *pr*, paranasal process; *prh*, preorbital recess, median unpaired division; *ri*, oblique premedian ridge; soc_2, anterior median section of supraorbital sensory canal groove (the anterior median pit-line);

Gross 1933a, pp. 36–43; 1941) and since in addition several of their features have been dealt with above in this chapter these bones will not be exhaustively treated here.

According to our present knowledge of the preorbital division of the head-shield (cf. pp. 29-31, above and pp. 189-196 below) the premedian plate of the *Antiarchi* in all probability as a whole, or at any rate in the main, was formed by a mass of tissue the homologue of which in the primitive ancestors of the *Antiarchi*, and in the non-Rhenanid Arthrodires, was situated ventrally to the rostral tip of the endocranium, but somewhat above the mouth opening. The plate in question in the *Bothriolepinae* (text-figs. 4, 6–15, 20, 21C, 40B, 65, 7–686, 114, 220, 229, 233A–J, 235A, 247, 249, 252, 253A, B, 267A–E, 273, 274, 275) is very variable in shape and proportions, but, judging from the conditions in *B. canadensis* (text-figs. 85–86) and certain other *Bothriolepis*-species (text-figs. 220, 273, 274, 275), it is normally broader in proportion to its length in young individuals than in older ones. During the growth of the individuals it must thus normally have increased proportionally more in length than in breadth. It is broader in its anterior than in its posterior half, and hence it is also broader at its rostral than at its posterior end. The rostral margin is convex and thin. However, the plate increases in thickness backwards so that most posteriorly it is fairly thick (text-fig. 15C). On account of the circumstance that the plate overlaps the lateral plate of either side its dorsal face is always broader than its ventral



Text-fig. 21. *Bothriolepis canadensis*. *A*, *B*, two rostral plates in dorsal and ventral aspects respectively. *C*, reconstruction, showing the rostral plate, the pineal plate and the three sclerotic plates in their position in relation to each other and to the adjacent bones of the head-shield. × $^{4}/_{1}$. *D*, *B. panderi*. A rostral plate in dorsal aspect. After Obrutschew 1927 (cf. text-fig. 230). × $^{3}/_{1}$.

Cn, centro-nuchal plate; *Lp*, lateral plate; *Pi*, pineal plate; *Pm*, paranuchal-marginal plate; *Pp*, postpineal plate; *Prm*, premedian plate; *R*, rostral plate; $Sclr_1$, anterior sclerotic plate; $Sclr_2$, postero-dorsal sclerotic plate; $Sclr_3$, postero-ventral sclerotic plate; *ifc.b*, posterior oblique cephalic pit-line groove; *na*, nasal notch or (in *C*) nasal apertures; *nn*, nasal notch (in the premedian plate); *pnn*, paranasal notch; *pr*, paranasal process; soc_1, posterior, paired division of the supraorbital sensory canal groove, developed as a very shallow pit-line.

face. The overlapping area (*cv*) along either of the lateral margins of the plate anteriorly is situated so that it faces much downwards, whereas, posteriorly it is directed laterally and only slightly downwards. The posterior face, which participates into the anterior boundary of the orbital chamber, is directed fairly straight backwards. On this face we find the wide posterior opening of the median division (*prh*) of the preorbital recess. As is clearly seen from text-fig. 15C, the ventral wall of this division of the preorbital recess is considerably thinner than the dorsal one. The more detailed description necessitates the distinguishing on the plate of a dorsal and a ventral lateral margin, both paired, and a dorsal and a ventral posterior margin, both unpaired (fig. 20B). The dorsal lateral margin is very variable in its configuration. The ventral lateral margin in some *Bothriolepis*-species, e.g. *B. canadensis* (text-figs. 11, 12, 20B, 86) and *B. cellulosa* (text-fig. 220E; cf. also Gross 1941a, text-fig. 5B, E; pl. 1, fig. 2; pl. 2, fig. 2), and in *Grossilepis* (text-fig. 267E; cf. also Gross 1941a, text-fig. 28E, H; pl. 18, figs. 1, 2) normally presents a more or less marked notch, the ventral lateral notch (*nl*), at or in front of its middle, while in other *Bothriolepis* species such as *B. maxima* (text-fig. 233C, F), and *B. groenlandica* (text-fig. 275D; pl. 1; pl. 3, fig. 1; pl. 8, figs. 3–5), it is almost or entirely devoid of such a notch. The dorsal posterior margin, which forms the main part of the anterior boundary of the orbital fenestra, in some of the *Bothriolepis*-species (*B. cellulosa, B. panderi, B. alvesinsis*), and in *Grossilepis*, normally or at least in most cases, is rather straight or somewhat concave, without any features of special interest (text-figs. 14, 219, 220, 229, 230, 247, 249; cf. also Gross 1941a, text-figs. 5, 28; pl. 1; pl. 2, fig. 1; pl. 4, fig. 2; pl. 6, figs. 1, 2; pl. 19, figs. 4–8), whereas in several other *Bothriolepis*-species its shape is normally clearly influenced by the nasal apertures. In the latter species it may be developed in two somewhat different ways. In *B. maxima* and *B. groenlandica* (text-figs. 13, 20A, 233A–E, 235A, 273–275; cf. also Gross 1940b, text-fig. 14E) in its median part it is thus generally produced backwards into a more or less marked nasal process (*p*), sometimes clearly notched posteriorly (*nn*), while in *B. canadensis* (text-figs. 9–11, 20B, 21C, 65, 76–85, 87D–F, 108, 129, 208, 209; cf. also Stensiö 1931, text-fig. 7D, E) it often presents a median nasal notch (*nn*), bounded on either side by a small paranasal process (*pr*). The part of the margin situated on either side of the nasal process itself, or laterally to either paranasal process, in *B. maxima, B. groenlandica* and *B. canadensis* is often more or less clearly concave, because of which it will be referred to as the paranasal notch (*pnn*). For comparison it may be mentioned here that a nasal process, a nasal process with a nasal notch and paranasal processes, or a nasal notch with paranasal processes are met with also in *Asterolepis* and *Remigolepis* (text-fig. 16; cf. also Gross 1931, pl. 4, figs. 8, 9; pl. 12, fig. 7; 1933a, text-figs. 14, 16A; Stensiö 1931, text-figs. 7A–C; pl. 4, fig. 6; 1938, text-figs. 1, 7; Nilsson 1941, text-

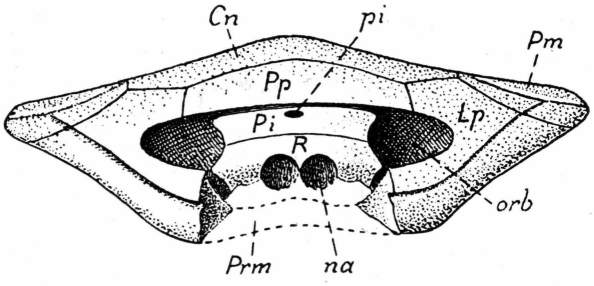
figs. 3, 5A). Finally, the ventral posterior margin of the plate in question in *Bothriolepis* is straight or somewhat concave, while at least sometimes in *Grossilepis* (text-fig. 267E; cf. also Gross 1941a, text-fig. 28E, H; pl. 18) it may be produced backwards into a short median subnasal process (*prsn*).

The rostral plate (= "prepineal plate"; *R*, text-figs. 4, 12, 21, 65, 87A, D, E, 114, 230, 262A) among the *Bothriolepinae* is known thus far in *B. canadensis* (cf. Stensiö 1931, pp. 40–41 and text-figs. 4, 10), *B. panderi* (Obrutschew 1927, pl. 9, fig. 9) and *B. hydrophila*. In these three species it is of a fairly uniform shape, but in *B. canadensis* it is longer and narrower relatively than in the other two species. At either lateral side it exhibits a deep nasal notch (*na*) for the external nasal aperture. For the description it may be considered as composed of three divisions, prenasal, internasal, and postnasal, situated respectively in front, between, and behind the nasal notch. The prenasal division lies close postero-ventrally to the median part of the posterior dorsal margin of the premedian plate, or to the nasal process or nasal notch of the premedian plate, and is thus situated in the anterior uppermost part of the orbital chamber. Probably it reached also a little forwards into the postero-dorsal part of the median division (*prh*) of the preorbital recess. It is always a little expanded towards the sides and, at least in *B. canadensis*, has often a clearly concave anterior margin. In consequence of its position it must have covered a small median part of the nasal capsules in front of the external nasal apertures. The internasal division is very narrow and must have covered the part of the internasal wall situated between the externasal nasal apertures. Finally, the postnasal division of the plate is much broader than the other two, being of approximately the same breadth as the anterior margin of the pineal plate, which it overlapped with a narrow area along its posterior margin. Its antero-lateral corner may often be a little produced forwards, so that it participates somewhat in the lateral boundary of the external nasal aperture, but the main part of the lateral boundary of the external nasal aperture, however, is always formed by the medial margin of the nasal division of the anterior sclerotic plate. The postnasal division of the plate just under description no doubt covered the hindmost part of the nasal capsules and an adjoining foremost part of the roof of the orbitotemporal region.

Besides in *Bothriolepis* among the *Bothriolepinae* the rostral plate is now known also in *Pterichthyodes, Gerdalepis* and *Remigolepis*.

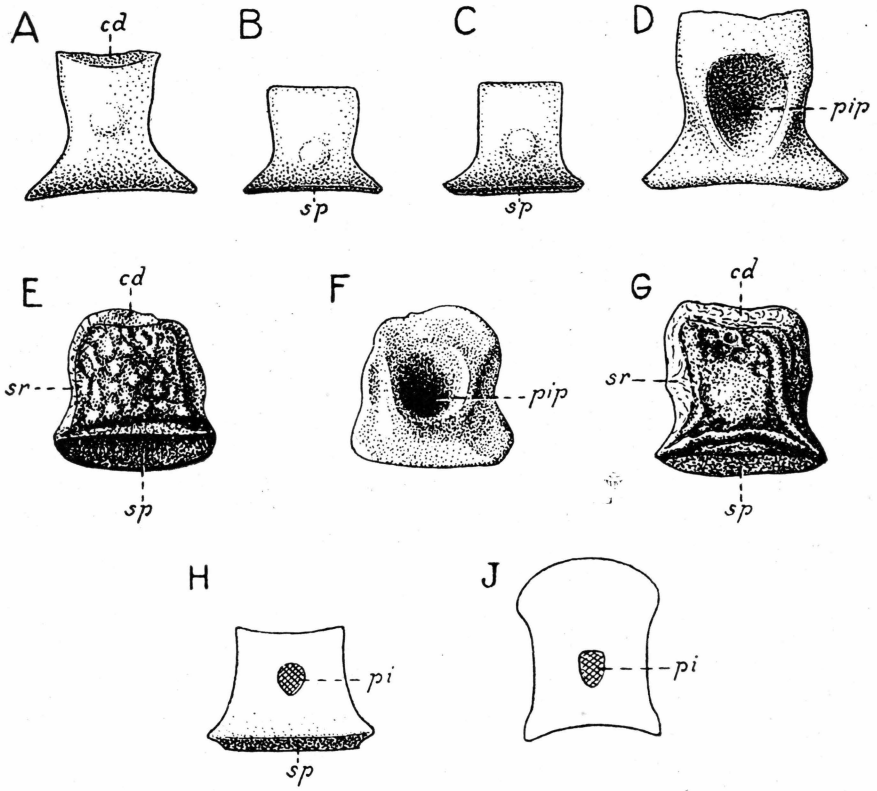
In *Pterichthyodes* it was found completely preserved in a specimen from Lethen Bar in the possession of the Swedish Museum of Natural History in Stockholm, where it is clearly seen that it is narrow and of much the same shape as in *Bothriolepis*[1]). As shown by Gross (1941b, p. 195, fig. 1A, B, E, *C*), it is of fundamentally the same shape in *Gerdalepis* too. In *Remigo-*

[1]) The rostral plate (»prepineal plate«) of *Pterichthyodes milleri* described and figured by Gross in 1941 (1941b, p. 195, fig. 1G) is probably imperfect anteriorly.



Text-fig. 22. *Remigolepis* sp. Sketch of a head-shield in rostral view. The premedian plate removed so as to show the rostral plate from in front. × $^2/_1$.
Cn, centro-nuchal plate; *Lp*, lateral plate; *Pi*, pineal plate; *Pm*, paranuchal-marginal plate; *Pp*, postpineal plate; *Prm*, gap for the premedian plate; *R*, rostral plate; *na*, external nasal aperture; *orb*, orbit; *pi*, pineal opening.

lepis, on the other hand, it is of a different type. In this genus (*R*, text-figs. 16, 22) it is broad and short and represented only by its postnasal division and a small posterior part of its internasal division, whereas the larger anterior part of its internasal division and its entire prenasal division are absent, and hence in this genus it is not nearly as complete as in *Bothriolepis*, *Pterichthyodes* and *Gerdalepis*. The persisting part of the internasal division forms only a short anterior process between the nasal notches (*na*). The postnasal division is not only broader, but as a whole also larger, relatively than in *Bothriolepis*. This division differs also from the corresponding one in *Bothriolepis* in the condition that its paired antero-lateral corner is strikingly broad and projects so far anteriorly that to a large extent it forms a lateral boundary of the nasal notch of its side. Because of this development of the antero-lateral corner of the division it is much more obvious here than what is the case in *Bothriolepis* that the rostral plate was developed in relation to a paired anteriorly and dorsally directed opening. This opening (*na*) in its position, and in other respects as well, was very much as the paired external nasal aperture in the Brachythoracid Arthrodires (*Pholidosteus*, text-fig. 67B; cf. also Stensiö 1934a, text-figs. 14, 15), and it cannot be doubted any longer, therefore, that it actually must have been the external nasal aperture. Hence it must be considered as fully proved now that the external nasal aperture of the *Antiarchi* in general was situated exactly as maintained by Patten (1904, p. 112; 1912, p. 375) and the present writer (cf. pp. 27–30 above; cf. also Stensiö 1931, pp. 28–30, 54–56), and not on the lower side of the head, as previously assumed by Woodward (1898, p. 14, fig. 14). The lateral boundary of the external nasal aperture in front of the antero-lateral corner of the postnasal division of the rostral plate in *Remigolepis* was formed only by soft tissue. Contrary to what is the case in *Bothriolepis* the anterior sclerotic plate in *Remigolepis* thus did not participate into the lateral boundary of the external nasal aperture, but was completely



Text-fig. 23. *A–C*, three pineal plates of *Bothriolepis canadensis* in dorsal view. × $^{4}/_{1}$. *D*, a pineal plate of *B. canadensis* in ventral aspect. × $^{6}/_{1}$. *E*, *F*, a pineal plate of *B. cellulosa* in dorsal and ventral aspects respectively. × $^{6}/_{1}$. *G*, a pineal plate of *B. cellulosa* in dorsal aspect. × $^{6}/_{1}$. *E–G*, from Gross 1941a. *H*, a pineal plate of *B. panderi* in dorsal aspect. × $^{3}/_{1}$. After Obrutschew 1927 (cf. text-fig.219). *J*, a pineal plate of *B. groenlandica* in dorsal aspect. × $^{2}/_{1}$.
cd, area overlapped by rostral plate; *pi*, pineal opening; *pip*, pineal pit; *sp*, unornamented area along posterior margin; *sr*, unornamented area along lateral margin.

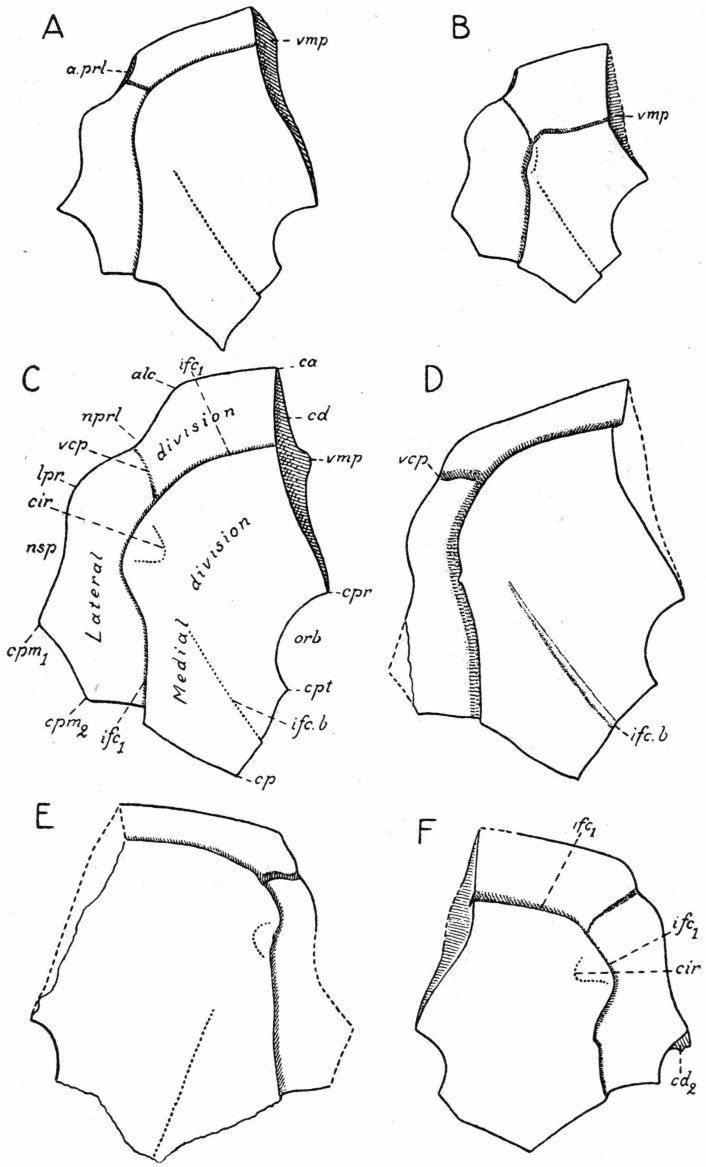
separated from this aperture by a broad lateral part of the postnasal division of the rostral plate.

The pineal plate in *Bothriolepis* (*Pi*, text-figs. 4, 10, 21C, 23, 65, 87B, D–F, 88, 101, 104, 114, 131, 230, 262A, 276; pl. 5, figs. 3–5; cf. also Stensiö 1931, text-figs. 5, 10, 11A–C; Gross 1941a, text-fig. 6D–H) is always quadrilateral in shape with the postero-lateral corner or process directed laterally or laterally and somewhat posteriorly. In the *Bothriolepis*-species in which it is known at present it is comparatively narrow, except in *B. panderi* (text-figs. 23H, 230), where it is comparatively short and broad and somewhat suggestive of the corresponding plate in *Asterolepis* (Gross 1931, pl. 4, fig. 12) and *Remigolepis* (text-figs. 16, 22; cf. also Stensiö 1931, pl. 4, fig. 4; pl. 24, fig. 6). In most species it is broadest across the postero-lateral processes, but in *B. groenlandica* (text-figs. 23J, 276; pl. 5, figs. 3–5)

it is about equally broad across its foremost part as across its postero-lateral processes. Its narrowest part is mostly in front of the postero-lateral processes, and thus behind the middle, but may also be approximately at, or in front of, the middle. In *B. canadensis*, *B. cellulosa*, *B. panderi* and *B. hydrophila* the maximum breadth of the plate is larger than, or approximately equal to, the length, whereas in *B. groenlandica*, on the other hand, the maximum breadth is normally smaller than the length. The anterior margin of the plate is mostly slightly concave and often more or less irregular or ragged, but may also, as in *B. groenlandica*, be rather strongly convex. Along this margin, at any rate in *B. canadensis* and *B. cellulosa* (text-fig. 23), there is an unornamented area (*cd*) overlapped by the postnasal division of the rostral plate. The lateral margin of the plate is mostly straight or somewhat convex in its anterior part and more or less concave in its posterior part, but may also, as in *B. panderi* and *B. groenlandica*, be concave throughout its length. The unornamented area (*sr*) which in *B. cellulosa* (text-fig. 23) is developed along this margin cannot possibly have been overlapped by the posterior sclerotic plate, as maintained by Gross (1941a, p. 12). Such an overlapping, of course, would have entirely prevented the movements of the eye. That this area is devoid of ornament is certainly due only to the condition that it lay fairly deep in the skin, along the medial margin of the postero-dorsal sclerotic plate. The posterior margin of the plate may be fairly straight, a little convex, or a little concave. Often or perhaps even normally there is a more or less broad unornamented area (*sp*) along this margin. When it is in its natural position in the skull-roof the plate reaches backwards a little underneath the postpineal plate, but is not directly overlapped by, or attached to, that plate. Because of this position in relation to the postpineal plate its posterior margin and the unornamented area in front of it are not visible when the head-shield is looked at from above (text-fig. 21C). On the lower side of the plate there is always a large deep pineal pit (*pip*, text-figs. 23D, F, 87B, E, F). This pit in *B. panderi* and *B. groenlandica* opens with an unpaired foramen (*pi*, text-fig. 23H, J) on the dorsal side of the plate in the same way as in *Asterolepis* and *Remigolepis*, whereas this is not the case in *B. canadensis* and *B. cellulosa*. In the last-mentioned two species, however, the bone-layer covering the deepest part of the pit is thin and often somewhat elevated into a more or less clearly marked pineal elevation on the dorsal side of the plate[1]).

The lateral plate in the *Antiarchi* is in all probability of a very complex nature (cf. pp. 29–31 above and pp. 200–201 below). Its main antero-

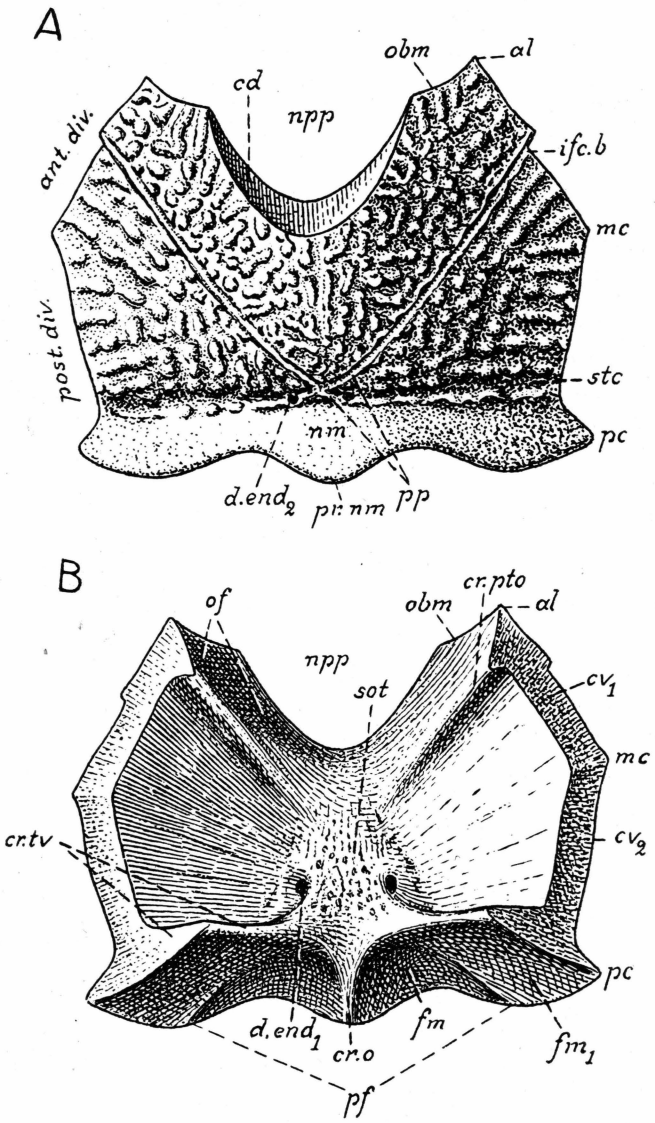
[1]) According to the restorations given by Traquair (1894–1906, text-fig. 51) the pineal plate in *Pterichthyodes milleri* is of a fairly broad type. In a few specimens of this pecies from Lethen Bar available to the writer, however, it is of a narrow type similar to that in *Bothriolepis*. In these specimens it seems also not to be perforated by a pineal foramen. The pineal plate in *Gerdalepis* is of a narrow shape and is pierced by a pineal opening (Gross 1941b, p. 194, fig. 1 A, B, D).



Text-fig. 24. Six lateral plates in dorsal aspect. *A*, *B*, of *Bothriolepis canadensis*. *A*, a plate with a relatively narrow lateral division. × $^{1}/_{1}$. *B*, a plate with a broad lateral division. Somewhat diminished. *C*, of *B. cellulosa*. × $^{6}/_{5}$. *D*, of *B. maxima*. Diminished. *E*, of *B. gigantea*. Diminished. *F*, of *B. groenlandica*. Diminished.

alc, antero-lateral corner; *a.prl*, prelateral area, for attachment of the prelateral plate; *ca*, antero-medial corner; *cd*, area overlapped by premedian plate; cd_2, area overlapped by postmarginal plate; *cir*, semicircular pit-line groove; *cp*, posterior corner; cpm_1, cpm_2, anterior and posterior postmarginal corners respectively; *cpr*, preorbital corner; *cpt*, postorbital corner; ifc_1, upper infraorbital sensory canal groove; *ifc.b*, posterior oblique cephalic pit-line groove; *lpr*, supraspiracular process; *nprl*, prelateral notch; *nsp*, supraspiracular notch; *orb*, orbital notch; *vcp*, vertical pit-line groove of cheek; *vmp*, ventral medial process.

medial preorbital part is presumably an ossification in a mass of tissue the homologue of which in the primitive ancestors of the *Antiarchi* and in the non-Rhenanid Arthrodires was situated on the anterior and lateral faces of the ethmoidal region of the endocranium, ventrally and postero-ventrally to the nasal aperture, but dorsally to the rostral section of the lower infra-orbital sensory canal groove (*ifc*$_2$). Its anterior lateral part seems to include a component primarily belonging to the cheek. And finally, its posterior largest part seems to correspond chiefly to the postorbital plate and an antero-lateral component of the central plate of the Euarthrodires. The lateral plate in the *Bothriolepinae* (*Lp*, text-figs. 1A, 4, 6–14, 15A, B, 24, 29, 31E, 34, 65, 76–84, 89–91, 95–99, 101–103, 109, 110–117, 127–134, 140, 154, 155, 157–162, 208, 209, 218, 219, 221, 229, 230, 233A, H, J, 234A, B, 247, 249, 253A, C, D, 267F–J, 273, 274, 277, 303B) is characteristically developed and will, therefore, be dealt with somewhat in detail. Its lateral and medial divisions (see text-fig. 24C) vary much in breadth, but the lateral division is normally much broader than the corresponding one in the *Asterolepidae* and *Remigolepidae*. The margins and corners of the plate which deserve to be specially termed are as follows (text-fig. 24C): a rostral margin, extending between the antero-medial corner (*ca*) and the antero-lateral corner (*alc*), the latter of which is also the antero-lateral corner of the head-shield as a whole; a lateral margin, extending from the antero-lateral corner backwards to the anterior postmarginal corner (*cpm*$_1$); a posterior margin, which is situated between the anterior postmarginal (*cpm*$_1$) and postorbital (*cpt*) corners and is divided by the posterior postmarginal (*cpm*$_2$) and posterior (*cp*) corners into a lateral division, attached to the postmarginal plate, a middle division, attached to the paranuchal-marginal plate, and a medial division, attached to the centro-nuchal plate; a very thick orbital margin, which forms the lateral boundary of the orbital and suborbital fenestrae and the orbital chamber and is bounded posteriorly by the postorbital corner (*cpt*) and anteriorly by the preorbital corner (*cpr*); and, finally, an antero-medial margin, which is bounded by the preorbital (*cpr*) and antero-medial (*ca*) corners and is attached to the premedian plate. Along the antero-medial margin there is always an overlapped area (*cd*), which in several *Bothriolepis*-species (*B. canadensis*, *B. cellulosa* and others) is provided with a more or less pronounced ventral medial process (*vmp*), which is received into the ventral lateral notch (*nl*, text-figs. 20A, 220E) of the premedian plate. Two other overlapped areas may fortuitously be found developed along the middle and lateral divisions of the posterior margin (*cd*$_1$, *cd*$_2$, text-figs. 24E, 277A, D, F; pl. 9, figs. 3, 4). Very characteristic of the plate under consideration in the *Bothriolepinae* is the fact that it is always broad in proportion to its length, much broader than in *Gerdalepis*, *Asterolepis* and *Remigolepis*. It differs also from the corresponding plate in the said genera in the following respects: the more complicated configuration of its lateral margin (cf. pp.



Text-fig. 25. *Bothriolepis canadensis*. Centro-nuchal plate of a large individual. *A*, in dorsal, *B*, in ventral aspect. × $^{2}/_{1}$.

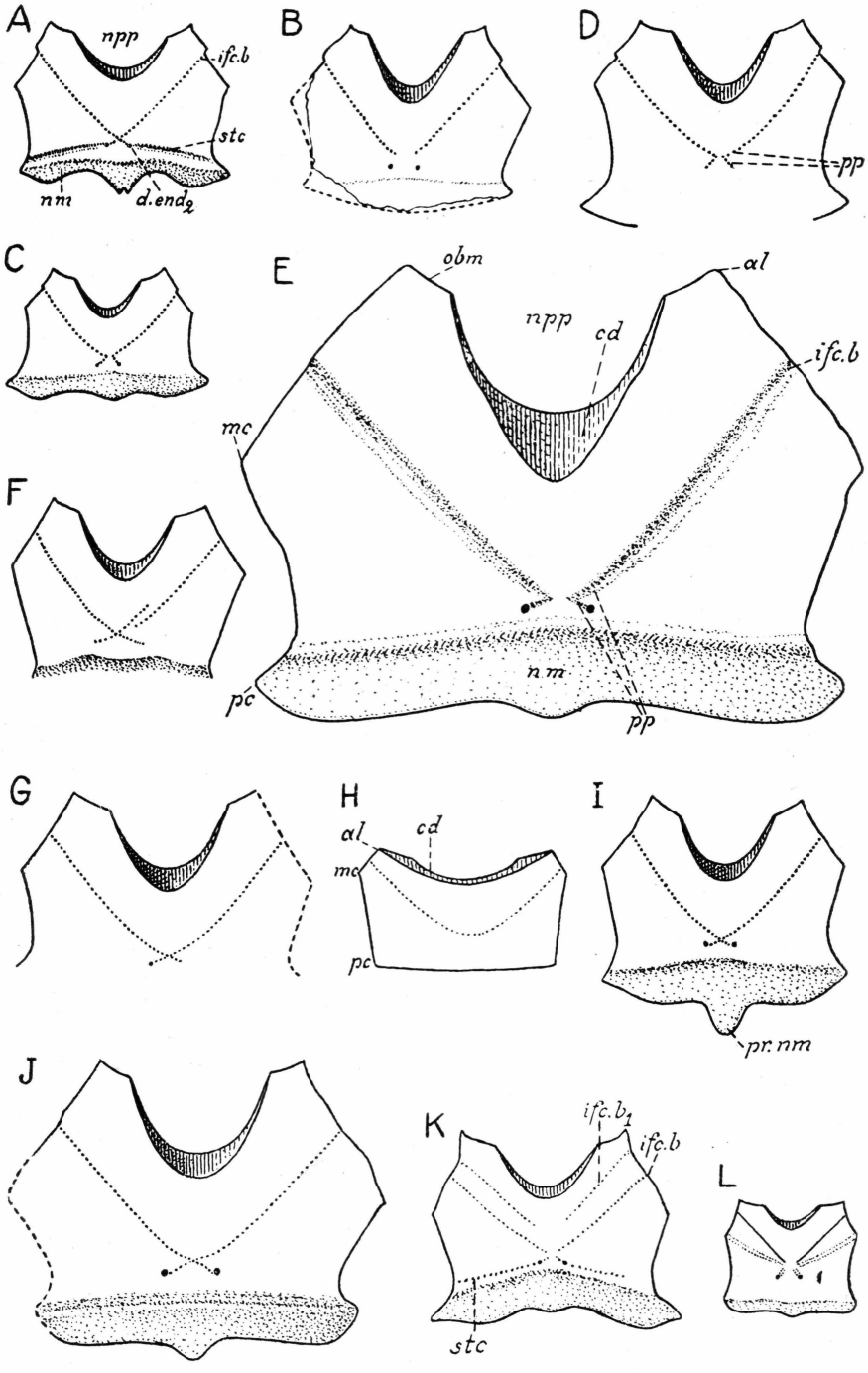
al, antero-lateral corner; *cd*, area overlapped by postpineal plate; *c.ro* median occipital crista; *cr.pto*, postorbital crista; *cr.tv*, transverse nuchal crista; cv_1, area overlapping lateral plate; cv_2, area overlapping paranuchal-marginal plate; $d.end_1$, $d.end_2$, dorsal and ventral openings respectively of canal for ductus endolymphaticus through the centro-nuchal plate *fm*, fm_1, fossae for insertion of levator muscles of head; *ifc.b*, posterior oblique cephalic pit-line groove; *mc*, lateral corner; *nm*, obtected nuchal area; *npp*, postpineal notch; *obm*, orbital facet of anterior margin; *of*, orbital area; *pc*, postero-lateral corner; *pf*, posterior face; *pp*, posterior pit-line groove; *pr.nm*, posterior median process; *sot*, supraotic thickening; *stoc*, supratemporal (cross-commissural) pit-line groove.

44–46 above); the presence of a supraspiracular process; the presence of two, and mostly even three, delicate pit-lines on its dorsal face (cf. pp. 176–178 below); the more complete development of the spiracular groove (cf. pp. 58–61 above); the ventral position of the area of attachment for the extralateral plate; and the fact that it has no direct sutural connection with the postpineal plate, but is separated from that plate by the foremost lateral part of the centro-nuchal plate.

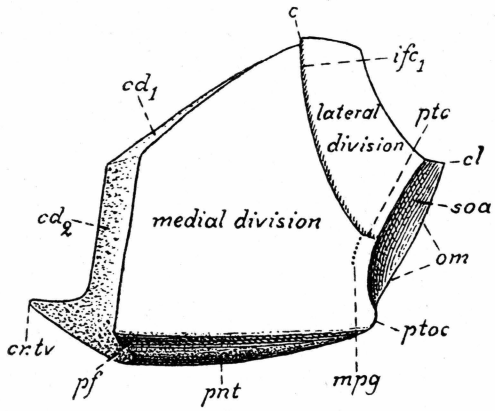
The postpineal plate in the *Bothriolepinae* (= "postmedian plate"; *Pp*, text-figs. 4, 6, 7, 9, 10, 12–14, 15A, 21C, 40B, 65, 76–84, 87C–F, 88, 90, 91, 93–98, 101, 102, 109, 114, 115–117, 127–129, 131–133, 148, 154, 155, 157–159, 203, 208, 209, 218, 219, 222, 233A, K, 235C–H, 236A, B, 237A, B, 247, 249, 252A, 253A, 266, 273, 274, 278A, C, F, K, 303D) has mostly the shape of an isoscelous triangle with the base forwards and the point backwards. The point is almost always much rounded off, however, and, therefore, is normally absent or very indistinct. The anterior margin is mostly more or less convex, but in certain species (*B. maxima*, *B. groenlandica*) it may also be straight, slightly convex, or slightly concave. In certain species, such as *B. canadensis* and *B. cellulosa*, the plate is clearly shorter and broader in proportion to its length in young individuals than in mature ones (cf. pp. 255–256 and text-figs. 82–84, 93, 222, 273, 274, 278; cf. also Gross 1941a, p. 8, text-fig. 1), whereas in other species, such as *B. maxima* (text-fig. 235C–H) its length: breadth ratio in young individuals seems to have been much the same as in old ones. The plate is narrower as a rule than the anterior margin of the centro-nuchal plate, and on account of this it is generally not in any contact with the lateral plate of either side. In one of the *Bothriolepis*-species, *B. gippslandiensis* (cf. text-fig. 26H), however, it is practically equally broad anteriorly as the anterior margin of the centro-nuchal and is said by Hills (1931, p. 218) to meet the lateral plates with the deeper situated parts of its antero-lateral corners. With regard to its lateral extent in this species it is thus almost as in *Pterichthyodes*, *Gerdalepis* (Gross 1941b, fig. 1A), *Asterolepis* and *Remigolepis*. In all the *Bothriolepinae* it is situated in a notch in the centro-nuchal plate, the postpineal notch (*npp*), where it overlaps a narrow area of the centro-nuchal plate.

The centro-nuchal plate (= "nuchal plate" or "median plate") of the *Antiarchi*, as will be shown below (pp. 205–206), is certainly a complex bone. In all probability it has been formed by fusions of components which represent certain of the central elements, the nuchal plate and the medial elements of the extrascapular bone series of the Arthrodires (cf. text-figs. 66, 67, 69, 70–73). The centro-nuchal plate in the *Bothriolepinae* (*Cn*, text-figs. 1B, 4, 9–14, 15A, B, 19, 21C, 25, 26, 65, 76–84, 87, 88, 90–99, 101, 102, 106, 109, 114–117, 127–134, 140, 146–148, 154, 155, 157–159, 203–206, 208, 209, 215, 218, 219, 222, 229, 230, 233K, 235J–L, 236A, B, 237A, B, 247–249, 252, 253A, E, 258, 261, 266, 267K–M, 273, 274, 278, 303C, D) increased

normally more in length than in breadth during the growth of the individuals, and hence it is usually somewhat narrower and longer in old individuals than in younger ones (cf. text-figs. 82–84, 93, 219, 222, 267K–M, 278). As to its general shape the plate is fundamentally as in *Pterichthyodes*, *Gerdalepis* (Gross 1941b, fig. 1), *Asterolepis* and *Remigolepis*. Roughly taken it is thus four-sided with an unpaired anterior margin, a paired lateral margin and an unpaired posterior margin. Contrary to what is the case in the said genera it is not completely bounded off from the orbital fenestra by the postpineal plate, but extends forwards to this fenestra at either side of the premedian plate, between that and the lateral plate. Its anterior margin is thus provided with a paired lateral division, the orbital facet (*obm*, text-figs. 25, 26), which participates into the posterior boundary of the orbital fenestra. However, in *B. gippslandiensis* (text-fig. 26H) where, as pointed out, the postpineal plate is very broad, it is in fact only the very antero-lateral corner (*al*) of the plate, on either side of the postpineal plate, that reaches forwards to the orbital fenestra. The postpineal notch (*npp*), which differs somewhat as to shape and depth in the various species, is mostly relatively broader and shallower in very small individnals than in medium-sized and large ones, and consequently it is obvious that with the growth of the individuals it increased in rostro-caudal extent to about the same degree as did the postmedian plate. The antero-lateral corner (*al*) of the plate is always well developed and so is also the lateral corner (*mc*). By means of the last-mentioned corner the lateral margins, in the normal way characteristic of the *Antiarchi*, is divided into an anterior and a posterior division, suturally connected with the lateral and paranuchal-marginal plates respectively. The anterior one of these divisions in several species is about as long as, or even longer than, the posterior one, but in the majority of the species, however, it is shorter than that division, in *B. gippslandiensis* even less than a third thereof (text-fig. 26H). Between the antero-lateral corner and the posterior oblique cephalic pit-line groove (*ifc.b*) this division in several species usually, or normally, is situated somewhat further antero-laterally than what it is behind the said pit-line groove, and in such species its anterior and posterior parts, therefore, at the posterior oblique cephalic pit-line groove are clearly marked off from each other by a nick. The posterior division of the margin just under consideration in *B. gippslandiensis* is practically straight, whereas in all *Bothriolepis*-species and in *Grossilepis* it is as a whole more or less concave with the deepest concavity somewhat behind the middle or near the posterior end. The posterior division as a whole may face straight laterally, laterally and slightly anteriorly, or laterally and slightly posteriorly. The postero-lateral corner (*pc*) is well pronounced and, except in *B. gippslandiensis*, it is always produced laterally into a more or less long lateral process. The posterior margin in small individuals is of a simple configuration, being more or less strongly convex with a median angle (text-figs. 84A, B, 93A–E,



Text-fig. 26. Centro-nuchal plates of several *Bothriolepis*-species and of *Grossilepis*. All the plates in dorsal aspect. *A*, of *B. canadensis*. *B*, of *B. ornata*; this restoration based on a figure given by Gross (1933a, pl. 4, fig. 7). *C*, of *B. cellulosa*. *D*, of *B. panderi*; restoration



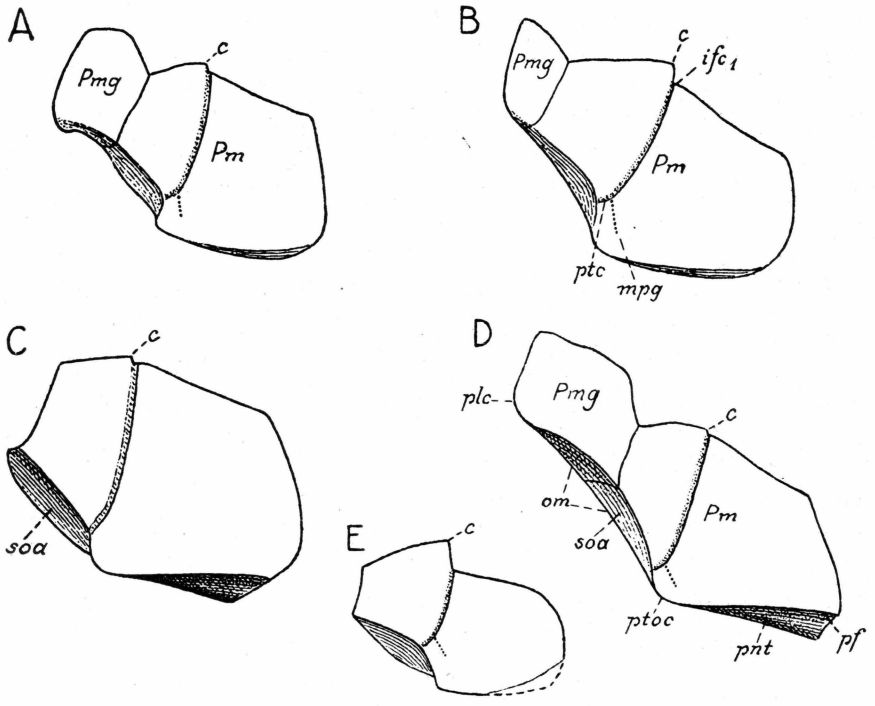
Text-fig. 27. *Bothriolepis canadensis*. A right paranuchal-marginal plate in dorsal aspect. × $^2/_1$.
c, anterior corner; cd_1, cd_2, areas overlapped by lateral and centro-nuchal plates respectively (the area cd_1, much varying in extent, often absent); *cl*, lateral corner; *cr.tv*, transverse nuchal crista; ifc_1, upper infraorbital sensory canal groove; *mpg*, middle pit-line groove of skull-roof; *om*, obstantic margin; *pf*, posterior face; *pnt*, paranuchal trochlea; *ptc*, cephalic division of main lateral line; *ptoc*, postobstantic corner; *soa*, subobstantic area.

219A, 273A, 278A). In medium-sized and large individuals it sometimes retained this simple configuration (text-figs. 13, 26H, 203), but generally in such individuals it is of a more complicate shape, mostly being provided with a median process (*pr.nm*, text-figs. 25, 26, 82, 83, 84C, 93F–O, 222A–D, F, G, J, K, 233A, 236A–B, 237A, B, 253E, 267K–M, 278B–K, 303C, D) usually flanked at either side first by a concavity and further laterally by a more or less pronounced convexity. In certain cases, however, the median process it not developed, and in these cases (text-fig. 222E, H) the median part of the margin is occupied by a more or less marked concavity, whereas each lateral part is convex. The obtected nuchal area (*nm*) is always well developed and both it and a transverse ornamented zone immediately in front of it are often somewhat depressed below the level of the outer face of the plate otherwise (text-fig. 94A, B). The area (*cd*) overlapped by the postpineal plate has almost always its greatest rostro-caudal extent in its median parts (text-fig. 26); but in *B. gippslandiensis* it is developed in the reverse way (text-fig. 26H; Hills 1931, p. 218). The areas (cv_1, cv_2) overlapping the

based on a reproduction given by Gross (1933a, pl. 4, fig. 16). *E*, of *B. maxima*. *F*, of *B. alvesiensis* n. sp. *G*, of a small specimen of *B. gigantea* Traquair. *H*, of *B. gippslandiensis* from Hills 1931 (probably somewhat incorrectly restored by Hills). *I*, *J*, of *B. groenlandica*. *K*, of *B. jarviki*. *L*, of *Grossilepis tuberculata* (from Gross 1941). *A–G*, *I–K*, *L*, slightly diminished; *H*, about $^7/_5$.
al, antero-lateral corner; *cd*, area overlapped by postpineal plate; $d.end_2$, canal for ductus endolymphaticus (external opening); *ifc.b.* posterior oblique cephalic pit-line groove; *ifc.* b_1, anterior obliques cephalic pit-line groove; *mc*, lateral corner; *nm*, obtected nuchal area; *npp*, postpineal notch; *obm*, orbital facet of anterior margin; *pc*, postero-lateral corner; *pp*, posterior pit-line groove of skull-roof; *pr.nm*, posterior median process; *stc*, supratemporal pit-line groove.

lateral and paranuchal-marginal plates are always present and are also well developed.

The paranuchal-marginal plate (= "paranuchal plate", "lateral nuchal plate") in the *Antiarchi* in general is certainly of a complex nature. As will be demonstrated below (p. 206), it is likely that it includes components which represent the paranuchal plate and the marginal elements of the Arthrodires (cf. text-figs. 66, 67A, 69–73). In addition it may perhaps also include certain of the lateral extrascapular elements, which presumably were present in primitive Arthrodires behind the paranuchal plate. The plate in question in the *Bothriolepinae* (*Pm*, text-figs. 1C, D, 4, 6, 7, 9–14, 15A, B, 27–29, 65, 76–84, 94–103, 106, 109, 114–117, 127–134, 140, 147, 148, 154, 155, 157–159, 203, 208, 209, 218, 219, 223, 229, 233A, 235K, L, 236C, 247–249, 252, 253A, 266, 267M, N, 273, 274, 279, 303E) in its general shape is fundamentally as the corresponding plate in other *Antiarchi*, but its obstantic margin (*om*, figs. 27–29) is longer and extends much further forwards than in *Pterichthyodes, Gerdalepis, Asterolepis* and *Remigolepis* (cf. Gross 1931, pl. 4, figs. 4, 5; 1933a, text-figs. 14A, 16; 1933b, text-fig. 3; 1941b, figs. 1A, 7; cf. also part III of this monograph). The lateral corner (*cl*, figs. 27–29) is therefore situated much further anteriorly than in the said four genera. Though variable in breadth the lateral division of the plate (text-fig. 27) is normally broader at least than in *Pterichthyodes, Gerdalepis, Asterolepis* and *Remigolepis*. Concerning this division it is also worthy of notis that in many cases, and probably even normally, it is in the various species broader relatively in small individuals than in medium-sized and large ones (text-figs. 99, 100, 223, 267M, N, 279). As in *Pterichthyodes, Gerdalepis* and *Asterolepis*, the plate presents five margins: an anterior margin, connected with the lateral plate; a medial margin, connected with the centro-nuchal plate; a posterior free margin; an obstantic free margin, already mentioned above, which forms the lateral margin of the posterior parts of the subobstantic area (*soa*); and, finally, a lateral margin, which is connected with the postmarginal plate. The anterior margin just laterally to the upper infraorbital sensory canal groove (ifc_1) shows a more or less clearly marked anterior corner (*c*) by which it is divided into a medial and a lateral part, corresponding to the medial and lateral divisions respectively of the outside of the plate. The lateral part of the margin is mostly situated somewhat in front of the medial part, and as a rule it is also separated from this part by a more or less pronounced nick. The posterior margin is very thick and forms, therefore, a fairly high posterior face (*pf*), which bears the paranuchal articular trochlea (*pnt*). The postobstantic corner (*ptoc*) may not rarely be fairly rounded off. The part of the subobstantic area (*soa*) which belongs to the plate is longer and stronger developed than in *Pterichthyodes, Gerdalepis* and *Asterolepis*. Finally, the lateral margin as a whole is more or less concave with the deepest concavity near its posterior end.



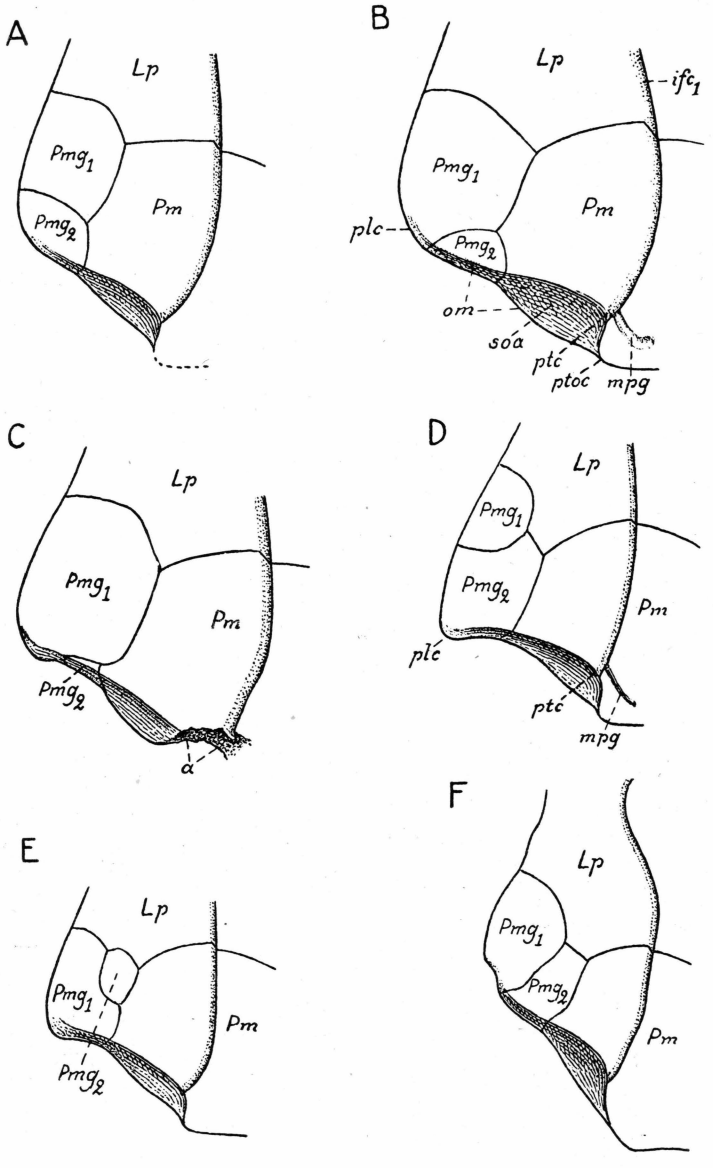
Text-fig. 28. Five paranuchal-marginal plates, three of them with the postmarginal plate attached. *A*, of *Bothriolepis canadensis*. × $^3/_2$. *B*, of *B. cellulosa*. × $^2/_1$. *C*, of *B. panderi*. From Gross 1941a. × $^3/_2$. *D*, of *B. groenlandica*. × $^1/_1$. *E*, of *Grossilepis tuberculata*. From Gross 1941a. × $^3/_2$.

Pm, paranuchal-marginal plate; *Pmg*, postmarginal plate; *c*, anterior corner of paranuchal-marginal plate; *ifc*$_1$, upper infraorbital sensory canal groove; *mpg*, middle pit-line groove of skull-roof; *om*, obstantic margin; *pf*, posterior face of paranuchal-marginal plate; *plc*, postero-lateral corner of postmarginal plate and of head-shield; *pnt*, paranuchal trochlea; *ptc*, cephalic division of main lateral line; *ptoc*, postobstantic corner; *soa*, subobstantic area.

The postmarginal plate (= "sufflaminal plate") is present in *Pterichthyodes*, *Gerdalepis*, *Asterolepis*, *Microbrachius*, and the *Bothriolepinae*, but is absent in *Remigolepis*, where it is reduced. In the *Bothriolepinae* (*Pmg*, text-figs. 1D, 6, 7, 9–14, 15A, B, 28A, B, D, 29, 76–84, 98–103, 106, 109, 114, 128–134, 147, 154, 155, 157–159, 208, 219, 229, 233A, 234C, D, 235M, N, 247–249, 253A, 266, 273, 274, 279) it is normally broader and more decidedly quadrilateral in shape than in the other forms (Gross 1931, pl. 4, figs. 2, 3; pl. 12, fig. 7; 1933a, text-figs. 14, 16; 1933b, text-fig. 3; 1941b, fig. 7; Watson 1935, fig. 28; Nilsson 1941, text-figs. 3, 4). Its posterior margin in the *Bothriolepinae* (text-figs. 28A, B, D, 29) and in *Microbrachius* is directed more or less laterally, whereas in *Pterichthyodes*, *Gerdalepis* and *Asterolepis* (cf. Gross 1931, pl. 4, figs. 2, 3; 1933a, text-fig. 14A; 1933b, text-fig. 3; Nilsson 1941, text-figs. 3, 4) it faces postero-medially. The subobstantic area (*soa*) in the *Bothriolepinae* (text-figs. 4, 9, 13, 14, 28, 29) and probably also in *Microbrachius* (Watson 1935, fig. 28) extends practically along the

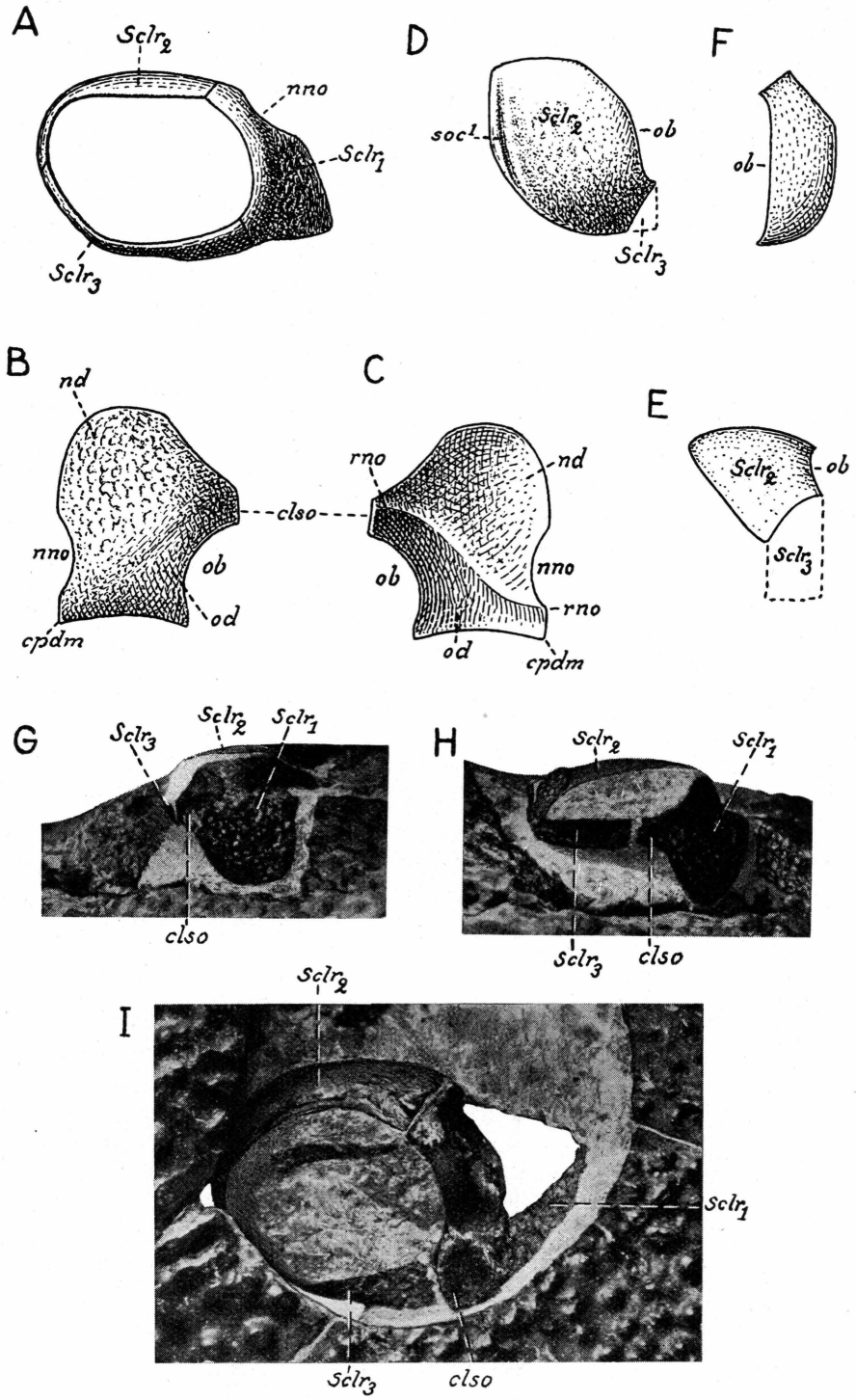
whole posterior face of the plate and thus to, or nearly to, the postero-lateral corner (*plc*) of the head-shield. In *Asterolepis*, and probably also in *Gerdalepis* and *Pterichthyodes*, on the other hand, this area is developed only nearest to the paranuchal-marginal plate (cf. Gross 1931, pl. 4, figs. 2, 3; 1933a, text-fig. 14A; 1933b, text-fig. 3; 1941b, fig. 7). However, the area in question in the *Bothriolepinae* throughout its extent on the postmarginal plate is completely devoid of "Siebknochen", and besides, it is often imperfectly defined from the ornamented area most antero-laterally. An articular facet corresponding to the one on the lower side of the plate in *Asterolepis ornata* (Gross 1931, pl. 4, fig. 3; 1933b, text-fig. 3) is not present in *Bothriolepis*. As is thus obvious, the plate did not actually articulate in the *Bothriolepinae* against the processus obstans, but was only slightly concealed by that process when the head was in a lowered position. Contrary to what is the case in *Asterolepis ornata* the plate in question in the *Bothriolepinae* did not either articulate against the outside of the anterior dorso-lateral plate ventrally to the processus obstans.

In seven specimens of *Bothriolepis canadensis* the postmarginal plate was represented by two plates, which according to their position will be referred to as the anterior and posterior postmarginal plates respectively (Pmg_1, Pmg_2, text-figs. 29, 103). These two plates present the following variations as to their development and position. 1) In three of the specimens the posterior postmarginal plate (Pmg_2) is a triangular bone wedged in into the hindmost part of the suture between the anterior postmarginal plate (Pmg_1) and the paranuchal-marginal plate in such a way that together with the said two plates it forms the subobstantic area and the obstantic margin of the shield (text-figs. 29B, C, 103B, C); and in one of these three specimens (text-figs. 29C, 103C) it is very small, hardly more than a splint of bone at the very obstantic area. 2) In one specimen the posterior postmarginal plate (Pmg_2) is wedged in into the anterior part of the suture between the anterior postmarginal plate (Pmg_1) and the paranuchal-marginal plate (text-figs. 29E, 103E) so that it does not reach backwards to the obstantic area and the obstantic margin, which in this case are formed solely by the anterior postmarginal and paranuchal-marginal plates. 3) In two specimens the posterior postmarginal plate (Pmg_2) from the lateral plate extends backwards to the obstantic margin, completely separating the anterior postmarginal (Pmg_1) from the paranuchal-marginal plate (text-figs. 29D, F, 103D, F); and in one of these two specimens it participates together with the anterior postmarginal and paranuchal-marginal plates into the formation of the subobstantic area and the obstantic margin (text-figs. 29F, 103F), whereas in the other specimen it is as broad posteriorly that alone it forms not only the whole lateral part of the subobstantic area and subobstantic margin situated laterally to the paranuchal-marginal plate, but also the postero-lateral corner (*plc*) and the hindmost part of the lateral margin of



Text-fig. 29. *Bothriolepis canadensis*. *A–F*, six cases in which the postmarginal plate is divided into two plates, an anterior and a posterior. Dorsal aspect. *A–C, F*, × 5/2. *D,E*, × 5/3. *Lp*, lateral plate; *Pm*, paranuchal-marginal plate; Pmg_1, Pmg_2, anterior and posterior postmarginal plate respectively; *a*, at this place a piece of the *pm*-plate is missing: ifc_1, upper infraorbital sensory canal grove; *mpg*, middle pit-line groove of the skull-roof; *om*, obstantic margin; *plc*, postero-lateral corner of the postmarginal plate and of the head-shield; *ptc*, cephalic division of main laterai line; *ptoc*, postobstantic corner; *soa*, subobstantic area.

the shield (text-figs. 29 D. 103 D). The anterior postmarginal plate (Pmg_1) in the last-mentioned case is fairly small and wedged in into the lateral parts of the sutura between the lateral plate and posterior postmarginal $(Pmg)_2$.



Text-fig. 30. *Bothriolepis canadensis*. *A*, restoration of a right sclerotic ring in lateral aspect. *B*, *C*, restorations of a flattened right anterior sclerotic plate in dorsal and ventral aspects

4) Finally, in one specimen the posterior postmarginal plate (Pmg_2) is so developed that it corresponds to about the posterior third of the undivided postmarginal plate (text-figs. 29A, 103A), and in this case it also forms alone the whole lateral part of the subobstantic area and subobstantic margin laterally to the paranuchal-marginal plate and, besides, also the postero-lateral corner (*plc*) and a hindmost part of the lateral margin of the shield. Subdivisions of the sufflaminal plate in a manner somewhat similar to that here described in *B. canadensis* will conceivably be met also in other *Bothriolepis*-species and in *Grossilepis* too.

Though not actually belonging to the head-shield the sclerotic ring may nevertheless be properly described in this chapter. Owing to its development as a whole and to the presence of ornament on its outside, it is fully obvious that this skeletal formation in the *Antiarchi* is of dermal origin.

At present the sclerotic ring is known in any detail only in *Bothriolepis canadensis* where it is as follows. Both in lateral and medial aspects (text-figs. 4, 10, 12, 21C, 30A, G, H, J, 65) it is not circular, but clearly longer than high. Its external opening (text-figs. 4, 10, 21C, 30A, J) is also longer than high and in addition not regularly oval, but somewhat four-sided. As is now well-known (Patten 1904, p. 122, text-fig. 6; 1912, p. 375, text-fig. 255; Obrutschew 1927, pl. 9, fig. 9; Stensiö 1931, p. 57; Gross 1941a, pp. 13–14), the ring is composed of three elements, which according to their position are termed the anterior, the postero-dorsal, and the postero-ventral sclerotic plates ($Sclr_1$, $Sclr_2$, $Sclr_3$) respectively.

The anterior sclerotic plate ($Sclr_1$, text-figs. 4, 10, 12, 21C, 30A–C, G–I, 65, 87D, E, 114, 230) is attached to the postero-dorsal sclerotic plate about opposite the suture between the rostral and pineal plates, from where it extends forwards and downwards to the antero-lateral corner of the orbital chamber. It includes two divisions (text-fig. 30B, C), a postero-lateral ocular division (*od*), which is developed in relation to the eye-ball, and an antero-medial nasal division (*nd*), which, situated entirely in front of the eye-ball, is developed in relation to the nasal capsule and the external nasal aperture of its side. On the lower face of the plate these two divisions are separated

respectively. *D*, *E*, restorations of a right postero-dorsal sclerotic plate in dorsal and posterior aspects respectively. *F*, restoration of a postero-ventral sclerotic plate in ventral aspect. *G*. a somewhat crushed sclerotic ring in anterior aspect, showing well the nasal division of the anterior sclerotic plate ($Sclr_1$). *H*, the same sclerotic ring as in fig. *G* in ventro-lateral and somewhat anterior aspect. Specimen No. P. 2109 in the Swedish Museum of Natural History in Stockholm. *I*, a complete sclerotic ring with the anterior sclerotic plate ($Sclr_1$) somewhat destroyed. Specimen No. P. 2124 in the Swedish Museum of Natural History Stockholm. All figures. Approximately × 4.5

$Sclr_1$, anterior sclerotic plate; $Sclr_2$, postero-dorsal sclerotic plate; $Sclr_3$, postero-ventral sclerotic plate; *clso*, lateral subocular corner of anterior sclerotic plate; *cpdm*, posterior dorso-medial corner of anterior sclerotic plate; *nd*, nasal division of anterior sclerotic plate; *nno*, nasal notch; *ob*, lateral margin; *od*, ocular division of anterior sclerotic plate; *rno*, naso-ocular ridge; soc_1, posterior division of supraorbital sensory canal groove, developed as a shallow pit-line.

from each other by a marked ridge, the naso-occular ridge (*rno*), which passes diagonally between the posterior dorso-medial corner (*cpdm*) and the lateral subocular corner (*clso*). The ocular division seems to vary much in breadth in various specimens. With its posterior dorso-medial corner (*cpdm*) it lies close laterally to the lateral margin of the postnasal division of the rostral plate, with its lateral subocular corner (*clso*), which is somewhat produced backwards, it is attached to the postero-ventral sclerotic plate ($Sclr_3$). Its posterior margin is straight or somewhat concave, its lateral margin (*ob*) deeply concave. The nasal division covered a postero-lateral part of the nasal capsule. The medial margin of this division shows posteriorly a more or less marked nasal notch (*nno*), anteriorly to which it is somewhat convex. It passes over without any boundary into the antero-lateral margin of the division. The last-mentioned margin is directed downwards and somewhat laterally and is straight, except most postero-laterally, where it is slightly concave.

The postero-dorsal sclerotic plate ($Sclr_2$, text-figs. 4, 10, 12, 21C, 30A, D, E, G, H, I, 65, 87D–F, 104, 114, 230) covered the posterior part of the dorsal side, and in addition a considerable dorsal part of the posterior side, of the eye-ball. Th eanterior margin of the plate may be straight or somewhat convex. The lateral margin (*ob*) is somewhat convex in its longer anterior part and concave in its posterior part. The posterior margin, which faces fairly much laterally and is attached to the postero-ventral sclerotic plate ($Sclr_3$), is generally fairly straight. Finally, the medial margin consists of an anterior and a posterior part, separated by a more or less well marked medial angle. The anterior one of these parts is always straight and lies along, and close to, the foremost part of the pineal plate. The posterior part is either straight or slightly concave. This part is always situated at some distance laterally to the pineal plate, so that there is an interspace between it and that plate, an interspace which was filled only by soft tissue. In several cases on the outside of the dorsal part of this plate, near the medial margin, we find a more or less pronounced rostro-caudal pit-line groove (soc_1, text-figs. 21C, 30D, 65, 104), which presumably represents a posterior vestigial section of the supraorbital sensory canal groove (cf. pp. 172–173 below).

Finally, the postero-ventral sclerotic plate ($Sclr_3$, text-figs. 4, 12, 21C, 30A, F–I, 65) covered the eye-ball ventrally and, besides, also posteriorly, below the postero-dorsal sclerotic plate. This plate throughout its extent is relatively narrow, narrower than the other two sclerotic plates. Its narrowest part is at the anterior end, at its connection with the lateral subocular corner (*clso*) of the anterior sclerotic plate. The margins of the plate are still imperfectly known, but this much seems to be clear that looked at from the lateral side the lateral margin (*ob*) was fairly straight anteriorly and concave posteriorly (text-fig. 30A, I).

As is obvious from the account just given, the sclerotic ring in *Bothrio-*

lepis is highly influenced by the position of the eye in relation to the external nasal aperture and nasal capsule of its side. A special nasal division has developed on the anterior sclerotic plate, a special nasal division which formed the main part of the lateral boundary of the external nasal aperture and, besides, also covered the dorsal side of a posterior part of the nasal capsule of its side. It must be assumed, of course, that this nasal division was not firmly attached to the nasal capsule, but that it could slide against the upper side of this capsule in rostro-caudal and latero-medial directions. In spite of that, however, the mobility of the eye-ball by this development of the anterior sclerotic plate must naturally have been relatively small.

Dermal bones of the cheek and visceral skeleton.

The division of the lateral side of the head usually referred to as the cheek in fishes in general is situated laterally to the palatoquadrate and the dorsal parts of the musculus adductor mandibulae. Normally this division of the lateral side of the head in fishes in general comprises both a suborbital part and a postorbital part, the former of which anteriorly passes over into the mass of tissue on the lateral side of the ethmoidal region, whereas the latter is continuous posteriorly with the gill-cover.

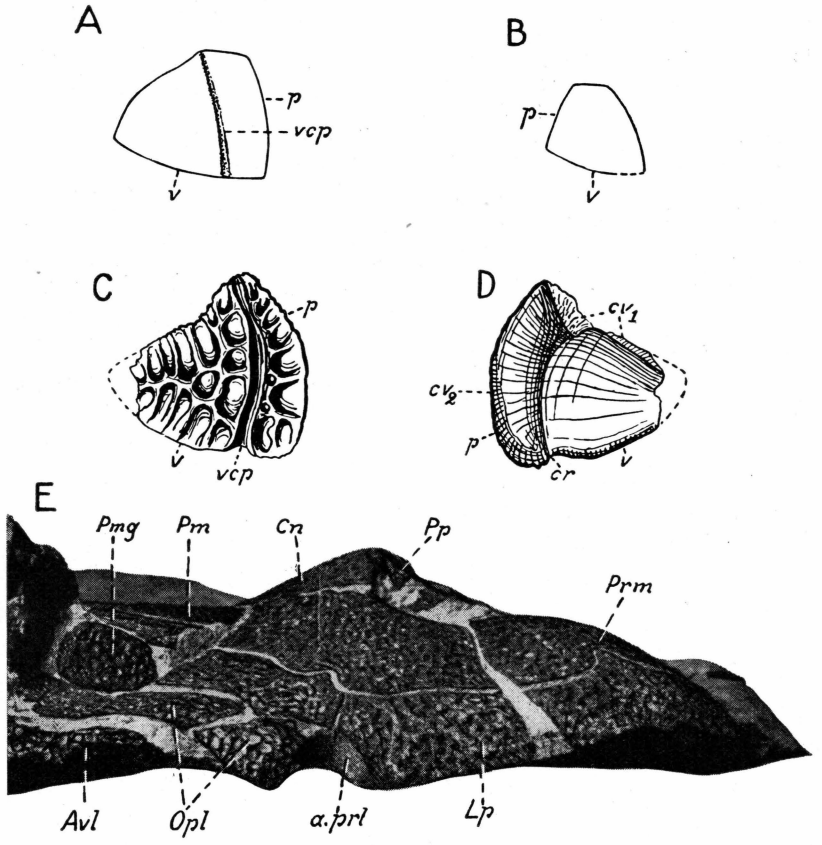
A cheek of this ordinary simple type is not found in the *Bothriolepinae* or the *Antiarchi* otherwise. The considerable transformations which have taken place in the anterior parts of the head in the *Antiarchi* (cf. pp. 29–31 above; cf. also pp. 189–190 below) have also highly influenced the development of the cheek. In consequence of these transformations the cheek in the *Antiarchi* has shifted much forwards and downwards and become much shortened, in addition to which it has undergone several other important changes. It is situated ventro-laterally and ventrally to the preorbital division of the endocranium (text-figs. 4, 6, 7, 8, 34, 114) and from a transverse plane through the antero-lateral corner of the head-shield reaches as far backwards as approximately to a transverse plane through the spiracular opening. Owing to the dorsal position of the eye it is suborbital in position throughout its extent. A mass of tissue primarily forming the dorsal parts of the cheek in all probability is included in the head shield, more precisely in the lateral part of the lateral plate, between the antero-lateral corner (*alc*) and the supraspiracular process (*lpr*). The other parts of the cheek not included in the head-shield consists of two divisions, upper and lower. The upper division (text-figs. 4, 6, 7, 8, 40B, 114) is situated chiefly on the lateral side of the head, whereas the lower division lies entirely on the ventral side of the head. Both these divisions are situated morphologically externally to the palatoquadrate and to the m. adductor mandibulae and both of them pass over anteriorly into a ventral mass of tissue which primarily belonged to the foremost infraorbital part of the cheek and the

lateral side of the ethmoidal region. The upper division is continuous posteriorly with the gill-cover. The ventral position of the lower division beyond question is due to the broad and comparatively flat shape of the head.

Three dermal bones are developed on the cheek in the *Bothriolepinae*, or at least in *Bothriolepis*. These three bones are the prelateral plate (*Prl*), the extralateral (opercular) plate (*Opl*), and the infraprelateral plate (*Py*; = "polygonal plate", Stensiö 1931, pp. 57–60, 69), of which, however, the extralateral plate extends forwards on to the cheek only with its anterior part, whereas with its larger posterior part it lies in the gill-cover (cf. pp. 39–40 above; cf. also Stensiö 1931, p. 58). The prelateral plate and the foremost part of the extralateral plate cover together completely the upper division of the cheek. The infraprelateral plate is developed on the posterior part of the lower division of the cheek whereas the anterior part of the last-mentioned division of the cheek was completely devoid of dermal bones. As is well known, the prelateral plate is absent in *Pterichthyodes*, *Asterolepis* and *Remigolepis*, the whole upper division of the cheek in them being covered only by the extralateral (cf. Traquair 1894–1906, text-figs. 34, 36, 37, 39, 51; Gross 1931, pl. 12, fig. 7; 1933a, text-figs. 14, 16; Watson 1935, text-figs. 26, 27; Nilsson 1941; Stensiö 1931, text-figs. 80, 81; cf. also text-fig. 16 in the present work). This seems also to apply to *Gerdalepis* (Gross 1941b, p. 196, figs. 7, 11). The lower part of the prelateral plate and the adjoining foremost part of the extralateral plate in *B. canadensis* are curved somewhat medially, on account of which the lower parts of their external faces are directed somewhat ventrally (text-figs. 8, 34). The extralateral plate in the *Bothriolepinae* extends forwards medially to the extralateral plate.

The prelateral plate (*Prl*, text-figs. 4, 6–8, 31A–D, 34, 40B, 65, 83D, 98, 110, 112C, 114, 131, 140, 180A, 181C, 182; cf. also Stensiö 1931, text-fig. 22C; Patten 1904, text-fig. 3; 1912, text-fig. 254E; 1932, text-fig. 5)[1]) is known at present only in *Bothriolepis canadensis* and *B. cellulosa*, but, as shown by the shape of the lateral margin of the lateral plate, it must have been present not only in *Bothriolepis* in general, but also in *Grossilepis*. It is a small bone, longer ventrally than dorsally. In *B. canadensis* it may vary considerably in length, but is usually fairly clearly four-sided with anterior, dorsal, posterior and ventral margins. The anterior, posterior, and ventral margins are all somewhat convex, whereas the dorsal margin, which is shorter than the other three, mostly seems to be comparatively straight. In some cases the last-mentioned margin may be indistinctly bounded off from the anterior one, and in these cases the plate is almost triangular in outline. In *B. cellulosa* (text-fig. 31C, D) the plate is probably larger relatively than in *B. canadensis* and, besides, more clearly triangular in shape, its dorsal margin being very short and not clearly bounded off from the anterior one. The

[1]) The small plate denoted by the writer in 1931 in text-fig. 26 with the letter *X* is in all probability simply a somewhat deficient prelateral plate (Stensiö 1931, p. 69).

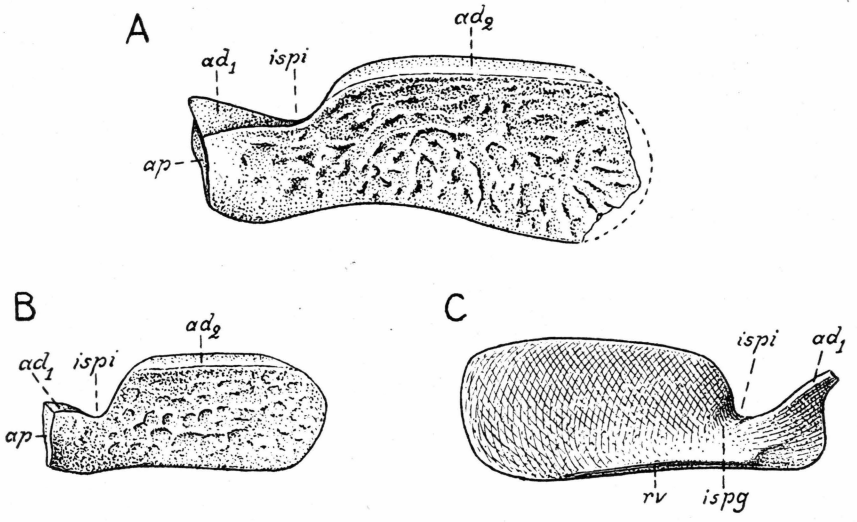


Text-fig. 31. *A*, *B*, outlines of a left and a right prelateral plate of *Bothriolepis canadensis*. Lateral aspect. × $^5/_2$. *C*, *D*, a left prelateral plate of *B. cellulosa* in lateral and medial aspects respectively. From Gross 1941a. × $^5/_2$. *E*, a crushed and flattened head-shield in lateral aspect. The prelateral area (*a.prl*) for the attachment of the prelateral plate clearly shown. Specimen No. P. 2129 in the Swedish Museum of Natural History, Stockholm. × $^3/_2$. *Avl*, anterior ventro-lateral plate (subcephalic division); *Cn*, centro-nuchal plate; *Lp*, lateral plate; *Opl*, extralateral (opercular) plate; *Pm*, paranuchal-marginal plate; *Pmg*, postmarginal plate; *Pp*, postpineal plate; *Prm*, premedian plate; *a.prl*, prelateral area, for attachment of prelateral plate; *cr* dorso-ventral crest on medial side of prelateral plate; *cr*, dorsi-ventral crest on medial side of prelateral plate; cv_1, area overlapping lateral plate; cv_2, area overlapping extralateral (opercular) plate; *p*, *v*, posterior and ventral margins respectively of prelateral plate; *vcp*, vertical pit-line groove of cheek.

outside of the plate is crossed in a dorso-ventral direction by a well developed pit-line groove (*vcp*) which is here interpreted as the vertical pit-line groove of the cheek (cf. pp. 178–179 below). At least in *B. cellulosa* the course of this pit-line groove on the medial face of the plate is marked by a distinct ridge (*cr*, text-fig. 31D). When in position the plate occupies the anterior parts of the prelateral notch (*nprl*, text-figs. 9–14, 24) of the lateral margin of the head-shield, where it overlaps a narrow area, the prelateral area (*a.prl*, text-figs. 9, 10, 31E), on the outside of the lateral plate. Posteriorly it overlaps an area (*ap*, text-fig. 32) on the outside of the anterior

end of the extralateral plate. Its two overlapping areas (cv_1, cv_2, text-fig. 31 D) are fairly clearly marked. Since it is only rarely found preserved among the great number of *Bothriolepis*-specimens examined by the writer the plate in question must obviously have been loosely attached to the lateral and extralateral plates.

The extralateral or opercular plate in the *Bothriolepinae* has thus far been found preserved in *B. canadensis* only (*Opl*, text-figs. 4, 7, 8, 32, 34, 40B, 65, 80B, 83D, 90, 91, 98, 105, 110, 111, 112, 114, 116, 128, 129, 132, 140, 148, 154, 155, 157, 209) where it is a somewhat large bone, considerably longer than high, more precisely normally from about 2½–2¾ times as long as high. In approximately its foremost fourth which is situated in front of, and ventrally to, the supraspiracular process (*lpr*) of the head-shield, the plate is fairly low, whereas in its other further posteriorly situated parts it is considerably higher (text-figs. 32, 105). Owing to this different shape in its foremost and in its posterior parts the plate may be considered as composed of two divisions, anterior and posterior, which will be referred to as the prespiracular and postspiracular divisions respectively. Anteriorly and dorsally the plate is fairly thick, whereas it is thin ventrally and posteriorly. The antero-dorsal corner (text-figs. 32, 105) is well marked and sometimes even somewhat produced into an antero-dorsal process. The antero-ventral corner may often be fairly rounded off, and so are generally also the postero-dorsal and postero-ventral corners. The anterior margin, which is much shorter than the other three, varies considerably in its configuration, but is normally as a whole mainly concave and directed fairly straight forwards. Along it we find a narrow but well pronounced area (*ap*) which was overlapped by the prelateral plate. The dorsal margin in its anterior parts slopes more or less strongly backwards, thence at the transition to the postspiracular division of the plate rapidly rising for a short distance. Further backwards, on the longer posterior part of the postspiracular division, it is practically horizontal. Along this margin (text-figs. 32, 105) we find a prespiracular (ad_1) and a postspiracular (ad_2) area for the attachment of the plate to the lateral margin of the head-shield, more precisely to the area *a.opl* (text-figs. 11, 12) on the lower side of the head-shield. Both these areas of attachment of the extralateral plate are fairly broad, above all the prespiracular one, and both of them are directed dorsally and much laterally. They are separated from one another by a more or less pronounced notch, the infraspiracular notch (*ispi*), just at the angle between the prespiracular and postspiracular divisions of the plate. This notch, which forms the ventral boundary of the spiracular opening (*spi*), is always lined by a smooth layer layer of bone, whereas the whole prespiracular area (ad_1) and the anterior part of the postspiracular area (ad_2) of attachment are rough in appearance. The posterior part of the postspiracular area of attachment, however, is also practically smooth. The posterior margin of the plate is thin and fairly



Text-fig. 32. *Bothriolepis canadensis*. Restorations of three extralateral (opercular) plates, all from the left side of the head; *A*, *B* , in lateral aspect. *C*, in medial aspect. Compare fig. 105. × $^2/_1$

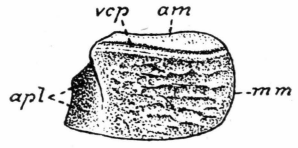
ad_1 prespiracular area of attachment (this area attached to those parts of the area *a.opl* of the head-shield which are situated along the prelateral notch and on the supraspiracular process); ad_2 postspiracular area of attachment (this area attached to those parts of the area *a.opl* of the head-shield which are situated behind the supraspiracular process); *ap.* area overlapped by prelateral plate; *ispg*, groove leading to infraspiracular notch; *ispi*, infraspiracular notch; *rv*, ventral longitudinal crista.

strongly convex. Finally, the ventral margin as a whole is more or less concave, often with a more or less marked convexity in the prespiracular division. The medial face of the plate near its dorsal margin shows a shallow groove (*g*, text-figs. 32C, 105C), which passes obliquely forwards and upwards to the infraspiracular notch. In addition on this face there is a ventral longitudinal ridge (*rv*), which runs along the very ventral margin of the face.

The extralateral plate was attached to the head-shield as follows. The prespiracular area of attachment (ad_1) was connected with the foremost part of the area *a.opl* of the head-shield, thus with that part of the area *a.opl* that is situated medially and nearest behind the prelateral plate, in front of the spiracular groove (*spg*) and the supraspiracular process (*lpr*, text-figs. 11, 12); the postspiracular area of attachment (ad_2) was connected with the posterior longer part of the area *a. opl* of the head-shield. Owing to the fact that both the posterior parts of the postspiracular area of attachment (ad_2) and the posterior parts of the area *a.opl* are quite smooth the connection between the posterior longer part of the plate and the head-shield must have been comparatively loose. It is obvious, therefore, that the extralateral plate in the *Bothriolepinae* was somewhat moveable posteriorly against the head-shield.

It may be mentioned for comparison that the area *a. opl* of the head-shield in *Asterolepis* (text-figs. 17, 18) and *Remigolepis* does not face chiefly

ventrally, as in *Bothriolepis*, but in the main is directed laterally, in consequence of which the prespiracular and postspiracular areas of attachment of the extralateral plate in *Asterolepis* and *Remigolepis* are placed so that they face dorsally, or dorsally and somewhat medially (text-fig. 16), and not dorsolaterally, as is the case in *Bothriolepis*.

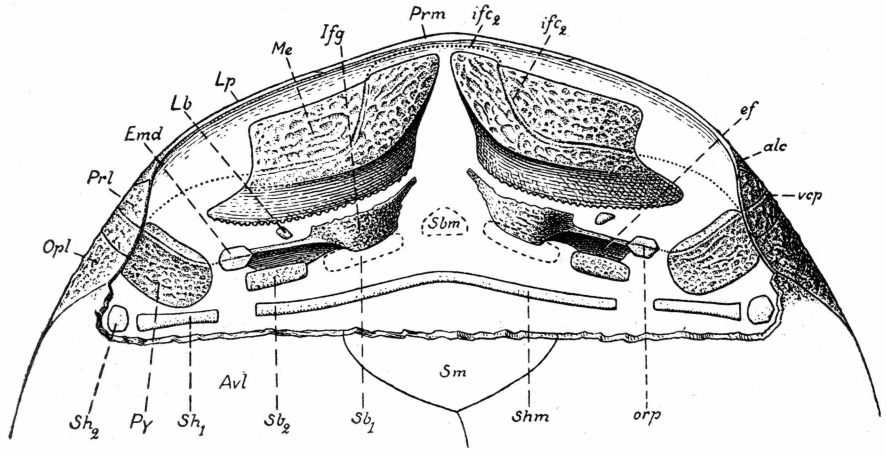


Text-fig. 33. *Bothriolepis canadensis*. Restoration of a somewhat well preserved right infraprelateral plate. External (ventral) aspect. × $^3/_1$.
am, anterior margin; *apl*, area along lateral (dorsal) margin (attached to prelateral and extralateral plates); *mm*, medial (ventral) margin; *vcp*, vertical pit-line of cheek.

The infraprelateral plate has been found preserved only in *B. canadensis* (*Py*, text-figs. 8, 33, 34, 37, 108, 110–114). As already pointed out, it is situated on the lower division of the cheek. More precisely it lies immediately ventro-medially to the posterior part of the prelateral plate and the adjacent anterior part of the extralateral plate and was obviously somewhat in contact with both those plates. It is a small and relatively thick bone, four-sided in shape, and broader (morphologically higher) than long (broad). When in position its axis of breadth (height) passes from in front and laterally in a direction medially and somewhat backwards. Its lateral margin, that is to say its morphologically dorsal margin, was found completely preserved only in one case in which it is developed as shown in text-fig. 33, thus in such a way that in its longer posterior part it is produced into a broad truncated process. The anterior margin is slightly undulating, whereas the posterior and medial (morphologically ventral) margins are convex. The antero-lateral (morphologically antero-dorsal) and postero-lateral (morphologically postero-dorsal) corners are well pronounced, whereas the other two corners (the morphologically antero-ventral and postero-ventral ones) are rounded off. Near its anterior margin the plate throughout its latero-medial (morphologically dorso-ventral) extent is crossed by the vertical pit-line groove of the cheek (*vcp*). Along its lateral (morphologically dorsal) margin there is a broad unornamented area (*apl*) by means of which the plate was loosely attached to the medial faces of the prelateral and extralateral plates. The internal (dorsal) face of the plate is not exposed in anyone of the specimens examined.

Apart from the extralateral plate already described above, the following dermal bones belonging to the visceral skeleton are now known in the *Bothriolepinae*: the mental plate, the inferognathal, the extramandibular plate, the submandibular series of plates and the subhyoideal series of plates.

Before proceeding to a detailed account of these bones, however, we



Text-fig. 34. *B. canadensis*. Restoration showing the dermal bones of the cheek and visceral skeleton in ventral aspect. The foremost part of the ventral wall of the trunk-armour removed. × 4/5.

Avl, anterior ventro-lateral plate; *Emd*, extramandibular plate; *Ifg*, inferognathal; *Lb*, small bone at the angle of the mouth, either a substitution bone in a labial cartilage or a dermal bone developed on the outside of such a cartilage; *Lp*, lateral plate; *Me*, mental plate; *Opl*, extralateral plate; *Prl*, prelateral plate; *Prm*, premedian plate; *Py*, infraprelateral plate; *Sbm*, Sb_1, Sb_2, plates of the submandibular series; *Shm*, Sh_1, Sh_2, plates of the subhyoideal series; *Sm*, semilunar plate; *alc*, antero-lateral corner of head-shield; *ef*, external face of posterior non-biting division of inferognathal (this face lay on the medial side of the posterior parts of Meckel's cartilage; ifc_2, lower infraorbital sensory canal groove; *orp*, oral pit-line; *vcp*, vertical pit-line groove of cheek.

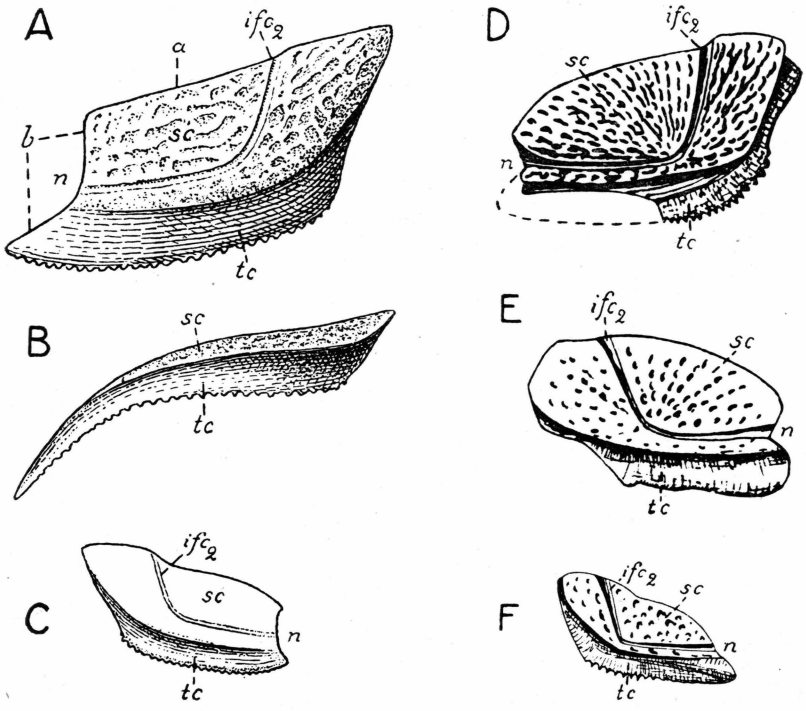
shall first briefly consider the dermal jaw elements of the Brachythoracid and Ptychtodontid Arthrodires which are of much interest to us in this connection. In these two groups, and presumably also in most other Arthrodire groups, the teeth of the upper and lower jaws have been modified into large tooth plates, whereas in Rhenanid Arthrodires they remained independent or were coalesced into numerous small plates.

In the Brachythoracid Arthrodires there are two paired tooth plates in the upper jaw, an anterior and a posterior, which are currently termed the anterior superognathal and the posterior superognathal respectively. The anterior superognathal is attached to the bottom of the nasal capsule of its side, whereas the posterior superognathal, which is the largest one of the two plates, is attached to the ventral margin and to the medial face of the palatoquadrate (Sg_1, Sg_2, text-fig. 67; cf. Stensiö 1934a, pp. 23–26, 35–36, text-figs. 1B, 4, 14; Watson 1934, pp. 440–445). On the other hand, in Ptyctodontid Arthrodires there is only one upper tooth-plate, the posterior superognathal, which extends backwards practically along the whole lower margin of the palatoquadrate and is attached to that endoskeletal element not only along the ventral margin and on the medial side, but also on the lateral side (Sg_2, text-fig. 71B; cf. Gross 1933b, p. 61, pl. 7, figs. 3–4; Watson 1938, pp. 399–400; observations made by the writer on the pala-

toquadrate of *Rhynchodus* described by Gross in 1933b). In both Brachythoracid and Ptychtodontid Arthrodires we find in the lower jaw but one paired dermal jaw bone, the inferognathal. This bone in Brachythoracid Arthrodires is of a complex nature, being formed in them by a tooth plate anteriorly and by an ordinary dermal bone component posteriorly. The tooth component lay largely on the outside of Meckel's cartilage, whereas the ordinary dermal component was situated on the medial side of the said cartilage. As is thus obvious, the inferognathal in Brachythoracid Arthrodires was composed of two divisions, an anterior biting and a posterior non-biting, situated laterally and medially respectively to Meckel's cartilage (*Ifg*, text-fig. 67). The inferognathal in the Ptyctodontid Arthrodires, on the other hand, is probably represented exclusively by the biting division (*Ifg*, text-fig. 71B), which, stretching as far backwards as almost to the posterior end of the lower jaw, extends far downwards on both sides of Meckel's cartilage (cf. Stensiö 1934a, pp. 26, 36, 45–47, text-figs. 4, 14, 24; Stensiö 1938, pp. 30–31, text-fig. 13; observations made by the writer in *Rhynchodus*).

A tooth-plate, or a dermal element, corresponding to the anterior superognathal of the Brachythoracid Arthrodires should be sought for in the *Antiarchi* below the nasal capsule, that is to say far behind the mouth-opening. However, even the most completely preserved *Bothriolepis*-specimens at my disposed did not show the slightest traces of a tooth plate so situated; and everything thus seems to indicate that an anterior superognathal was entirely absent in the *Antiarchi*. This condition is probably to be regarded as secondary and due to the forward migration of the entire jaw apparatus in the group (cf. pp. 29–31 above). During the shifting forwards of the jaw apparatus the anterior superognathal conceivably retained its primary position underneath the nasal capsule, on account of which it became situated as far backwards in the roof of the mouth that it lost its function and disappeared. The absence of the anterior superognathal in Ptyctodontid Arthrodires is presumably also due to the fact that their jaw apparatus is situated much further anteriorly than that of the Brachythoracid Arthrodires (cf. text-figs. 67, 71B).

As may thus be gathered, the mental plate is the only upper dermal jaw element present in the *Antiarchi*. In its position in relation to the mouth-opening and in its morphologically rostro-caudal extent it reminds much of the posterior superognathal of the Brachythoracid and Ptyctodontid Arthrodires. In contradistinction to what is the case with the superognathal in these two Arthrodire-groups, however, it does not consist only of a biting tooth-component (*tc*, text-figs. 35A), but comprises also a considerable sensory canal component (*sc*, text-fig. 35A), which is crossed by the lower infraorbital sensory canal groove (ifc_2) and extends far antero-dorsally above the tooth-component. It is of a more complex nature, therefore, than the superognathal of the Brachythoracid and Ptyctodontid Arthrodires, which

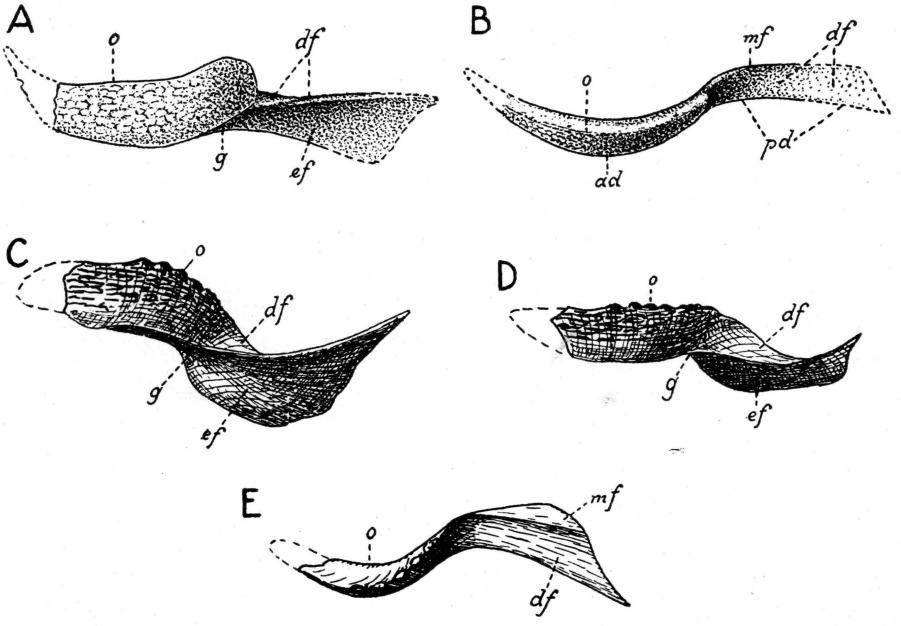


Text-fig. 35. *A*, *B*, a right mental plate of a large individual of *Bothriolepis canadensis* in external and ventral (labial) aspects respectively. × $^2/_1$. *C*, a left mental plate of a fairly small individual of *B. canadensis* in external aspect. × $^2/_1$. *D*, *E*, a right and a left mental plate of *B. cellulosa* in external aspects. From Gross 1941a, × $^3/_2$. *F*, a left mental plate of *Grossilepis tuberculata* in external aspect. From Gross 1941a. × $^2/_1$.
a, dorsal margin; *b*, posterior (lateral) margin; *ifc*$_2$, lower infraorbital sensory canal groove; *n*, lateral notch; *sc*, sensory canal component; *tc*, tooth component.

as pointed out, is only a tooth-plate. As in fact, it seems to be homologous in part with the posterior superognathal of the Brachythoracid and Ptyctodontid Arthrodires and as in addition it is a biting dermal element belonging to the upper jaw in a group of Gnathostome vertebrates, the mental plate cannot possibly have lain loosely in the skin, but must have been firmly connected with the foremost part of the outside and lower margin of the palatoquadrate of its side (cf. pp. 36–37 above). More precisely, it must have been attached to the palatoquadrate with its internal face approximately at the transition between its two components (cf. p. 208 below).

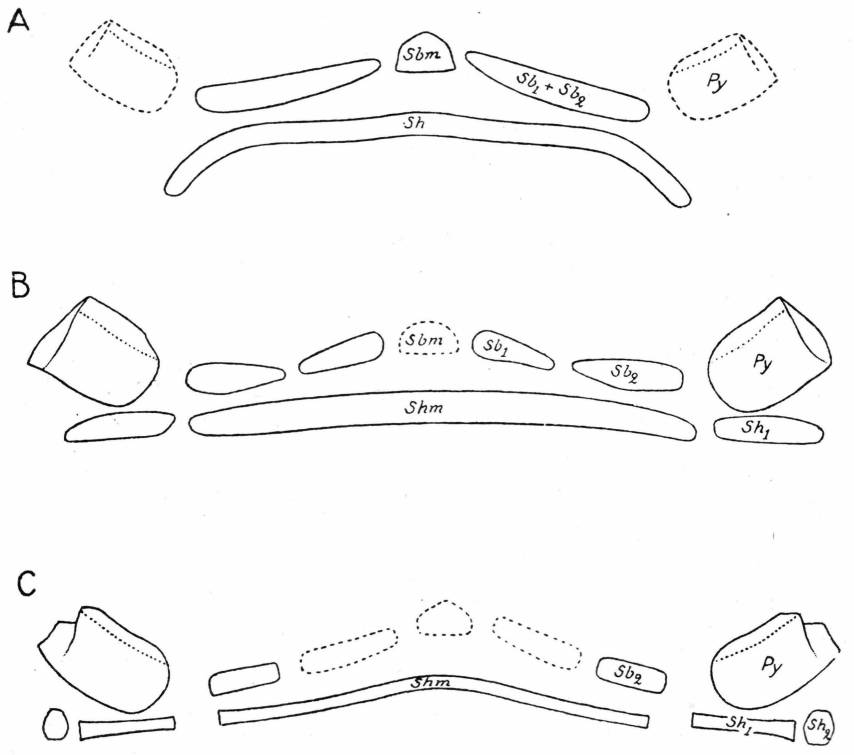
The biting dermal element in the lower jaw of the *Antiarchi*, the inferognathal, is known as yet only in the *Bothriolepinae* in which, as shown by the writer and Gross, in most of its essential characters it is as the correspondingly termed bone in the Brachythoracid Arthrodires. It cannot be doubted any longer, therefore, that is is strictly homologous with that bone (Stensiö 1931, pp. 63–68, 154; Gross 1941a, pp. 39–41).

The mental plate in the *Bothriolepinae* (text-figs. 4, 8, 34, 35, 90, 97, 101, 110, 111, 112B, 113A, 114, 131, 140, 160–162, 168, 169, 234E, 237C) is fairly well known from earlier descriptions by Patten (1904, pp. 116–118, text-fig. 3; 1912, pp. 373–374, text-fig. 254; 1932, text-fig. 5), Stensiö (1931, pp. 60–63, 154, text-figs. 23, 27) and Gross (1933a, p. 42, pl. 5, fig. 11; 1941a, pp. 14, 39, text-figs. 6A, B, 26G and pl. 5, figs. 7, 8; pl. 19, figs. 9). The plate has so far been found preserved both in certain *Bothriolepis*-species (*B. canadensis*, *B. cellulosa*, *B. maxima*) and in *Grossilepis tuberculata*. Contrary to what is the case in *Pterichthyodes* (Traquair 1894–1906, text-fig. 52), *Asterolepis* (Nilsson 1941, pp. 19–21, text-fig. 5B) and *Remigolepis* (text-fig. 16; cf. Nilsson 1941, pp. 19–21, text-fig. 6) the plate does not meet or connect anteriorly (antero-medially) with its antimere, but is always separated from it by an interspace, which at least ventrally was developed for the upward bent symphysial parts of the rami of the lower jaw (text-fig. 114; cf. p. 36 above). As to its general shape (text-fig. 35) the plate is rhomboidal, morphologically longer than high, and in addition at any rate in *B. canadensis*, curved in such a manner that in a morphologically rostro-caudal direction its outer face is convex and its internal face correspondingly concave. According to their morphological relations its four margins may be termed the dorsal, posterior, ventral (labial) and anterior (antero-medial) margins respectively. The dorsal and ventral margins are always longer than the other two, of which the posterior one is shortest. The dorsal margin is mostly slightly concave, but may also be somewhat convex. The anterior part of this margin, situated in front of the lower infraorbital sensory canal groove (*if*c_2), mostly projects a little further dorsally than the posterior longer part, and, besides, it is also marked off from the latter part by a low nick. The postero-dorsal corner generally is well developed in *Bothriolepis* (text-fig. 35A, B, D, E), while it is obtuse and less pronounced in *Grossilepis* (text-fig. 35F). The posterior margin is always concave, sometimes, as for instance in *B. canadensis* and *B. cellulosa*, even deeply concave. In fact this margin forms a more or less deep notch, which is directed laterally and somewhat posteriorly. The postero-ventral corner is always produced into a posterior process. The ventral margin, which participated into the formation of the upper boundary of the mouth opening, is somewhat convex and provided with small, irregular tooth-like cusps. On account the condition that the antero-ventral corner is much rounded off this margin passes over without any definite boundary into the anterior (antero-medial) margin, which may be slightly concave, straight, or even somewhat convex. The ventral part of this margin also took part in the boundary of the mouth-opening and is often equipped with small tooth-like cusps similar to those of the ventral margin. The dorso-medial corner is always well pronounced. The two components of the plate are always marked off from one another externally. The external face of the sensory canal component (*sc*) is ornamented throughout its ex-



Text-fig. 36. *A*, *B*, a left inferognathal of *Bothriolepis canadensis* in external and dorsal (labial) aspects respectively. × 3.7. *C*, *E*, a left inferognathal of *Grossilepis tuberculata*. *C*, in external aspect, *D*, in external and somewhat posterior aspect, and *E* in dorsal (labial) aspect. From Gross 1941a. Approximately × 7.4.
ad, anterior, biting division; *df*, dorsal free face of the posterior, non-biting, division; *ef*, external face of posterior non-biting, division (this face lay on the medial side of the posterior parts of Meckel's cartilage); *g*, groove underneath transition between anterior, biting, and posterior, non-biting, divisions (this groove was occupied by the dorsal margin of Meckel's cartilage, which at this place crossed the inferognathal from the outside to the inside); *mf*, medial free face of posterior non-biting division; *o*, oral margin of anterior biting division; *pd*, posterior, non-biting division.

tent and in addition crossed by a rostral part of the lower infraorbital sensory canal groove (ifc_2). The external face of the tooth-component (*tc*), on the other hand, is completely devoid of ornament and, besides, it is situated at a deeper level than that of the sensory canal component. The posterior part of the tooth-component in all probability was covered on the outside by a thick mass of soft tissue, which formed a sort of labial fold. This labial fold probably continued backwards and downwards behind the angle of the mouth-opening as far as on to the outside of the lower jaw (text-fig. 114). In it lay the supposed labial cartilage and the small labial bone (*Lb*, text-figs. 7, 8, 34, 111) described above in this work (pp. 35–36). At least in *B. canadensis* (Stensiö 1931, *rm*, text-fig. 23C) the internal face of the plate in its lower half is crossed by a low ridge. This ridge cannot have served as a place of insertion for muscles, as maintained by the writer in 1931 (Stensiö 1931, p. 62), but must obviously have had another function. In all probability it was developed for the attachment of the plate to the palatoquadrate and presumably lay along the ventral margin of the palatoquadrate of its side (cf. pp. 91–93 above).



Text-fig. 37. *Bothriolepis canadensis*. *A–C*, restorations of the submandibular and subhyoideal series of bones of three individuals. The infraprelateral plate of both sides also restored. Ventral aspect. *A*, *B*, × $^{9}/_{4}$. *C*, × $^{9}/_{8}$.
Py, infraprelateral plate; *Sbm*, median submandibular plate; Sb_1, Sb_2, lateral paired submandibular plates; *Sh*, undivided subhyoideal plate; *Shm*, median subhyoideal plate; Sh_1, Sh_2, lateral, paired subhyoideal plates.

The inferognathal (= "mandibular bone" in the terminology previously employed by the writer; *Ifg*, text-figs. 8, 34, 36, 107, 110–113, 114; cf. also Gross 1941a, text-fig. 29 and pl. 20, figs. 5–11) is known as yet in two *Bothriolepis*-species (*B. canadensis, B. groenlandica*) and in *Grossilepis tuberculata*. As it has been exhaustively dealt with previously (Stensiö 1931, pp. 63–68, 154; Gross 1941a, pp. 39–41), it is not necessary to enter upon its special characters here. As the corresponding bone in the Brachythoracid Arthrodires, it consists of an anterior biting and a posterior non-biting division situated laterally and medially respectively to Meckel's cartilage. Its posterior non-biting division is developed in essentially the same way as in *Bothriolepis* and *Grossilepis*.

The extramandibular plate (*Emd*, text-figs. 8, 34, 110, 111, 112A, B) is a very small, delicate, paired dermal element which has been met with so far only in *B. canadensis*. This plate was noticed by the writer already in 1931 and was on that occasion described as the plate *Y* (Stensiö 1931, p. 69, text-figs. 25, 26). In a few well preserved specimens at my disposal it lies

close ventrally (medially) to the antero-ventral (antero-medial) corner of the infraprelateral plate, and, as in these specimens it seems hardly to be dislocated, it is likely that it lay on the upper posterior part of the outside of the lower jaw, and thus laterally to the posterior part of the probable fossa of insertion for the m. adductor mandibulae (text-figs. 8, 34). That it would have been so situated is further supported by the fact that, at any rate in some cases, it is crossed in its morphologically longitudinal direction by a pit-line groove (*orp*), which seems to form the ventral continuation of the vertical pit-line (*vcp*) of the cheek, and, as we shall see (pp. 178–179 below), certainly represents a posterior part of the oral pit-line of fishes in general. The plate seems to vary somewhat in shape, but is normally longer than high. As far as is known, it has no homologue in the Brachythoracid and Ptyctodontid Arthrodires. Its presence in the *Bothriolepinae* indicates that the outside of the lower jaw in Placoderms primarily was provided with dermal bones to about the same extent as in Teleostomian fishes.

The submandibular and subhyoideal series of dermal bones have as yet been found completely preserved only in *B. canadensis* (*Sbm*, Sb_1, Sb_2, *Sh*, *Shm*, Sh_1, Sh_2, text-figs. 8, 34, 37; cf. also Patten 1932, text-fig. 5)[1]), where they are present on the ventral side of the head. The submandibular series is beyond question developed in relation to the lower margin of Meckel's cartilages of both sides, whereas, judging from its position, the subhyoideal series seems to have been developed underneath the ventral divisions of the hyoid arches of both sides. The two series of bones seem to be devoid of homologues in the Arthrodires. On the other hand, they are probably comparable to certain bone formations met with in the Acanthodians, Crossopterygians and Actinopterygians. The submandibular series seems thus to correspond nearest to the mandibular dermal rays of the Acanthodians (Watson 1937, pp. 56, 63, 67–68, 75–76, 83, 86, 92, 103–104, 118–119). The subhyoideal series may be of the same nature as the dermal bones on the upper parts of the hyoid arch and the hyoid gill-cover in Acanthodians (Watson 1937, pp. 56–57, 63–64, 68, 76, 119) and probably represents the branchiostegal rays and gular plates in Teleostomian fishes.

The submandibular series of bones (= "postmandibular series", Stensiö 1931, p. 68; *Sbm*, Sb_1, Sb_2, text-figs. 8, 34, 37, 110, 111, 112A–C, 113B, C; cf. also Patten 1932, text-fig. 5) varies much in its development in different individuals. It may be represented only by a relatively short paired plate (Sb_2) below the ventral margin of Meckel's cartilage (text-figs. 8, 34, 37C, 111) or by a longer paired plate ($Sb_1 + Sb_2$), extending along a large part of the lower margin of Meckel's cartilage (text-figs. 37A, 112A). Sometimes it may also consist of two paired plates (Sb_1, Sb_2) below Meckel's cartilage (text-figs. 37B, 110, 112B, C, 113B). Finally, besides one, two or

[1]) A subhyoideal bone has also been observed in *B. groenlandica* (*Sh*, pls. 15, 16).

perhaps more paired elements, it may also in certain cases include also a median unpaired element (*Sbm*, text-figs. 34A, 112A), termed by the writer in 1931 (Stensiö, p. 68) the postsymphysial plate. This plate was situated below and behind the symphysial parts of the lower jaw. All the plates of the series are comparatively delicate and were only very loosely connected with the lower jaw. The paired ones of them are longer than high and somewhat rectangular or oval in outline, whereas the unpaired median postsymphysial plate is broader than high and somewhat pentagonal in shape. The paired plates are often provided with a delicate reticular ornament. As far as is known, the series shows no sensory canal grooves or pit-line grooves.

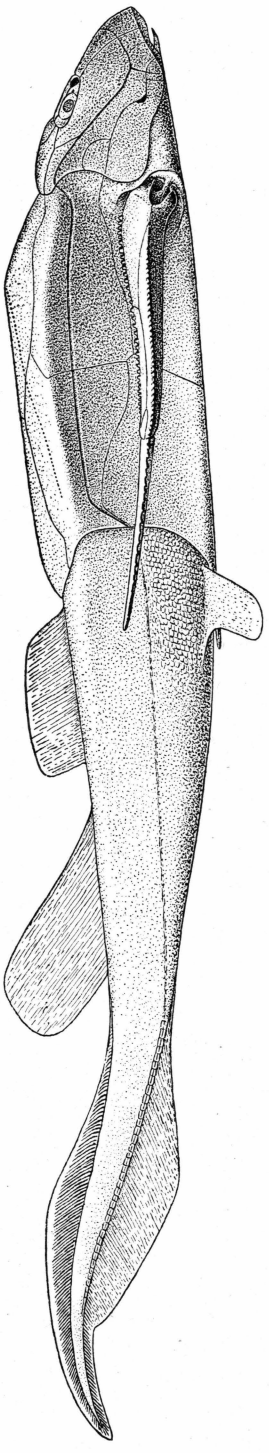
The subhyoideal series (= "ponticular series" of plates, Stensiö 1931, p. 68; *Sh*, *Shm*, Sh_1, Sh_2, text-figs. 8, 34, 37, 110–112, 113B; pls. 15, 16; cf. also Patten 1932, text-fig. 5) is also variable as to its development. In the simplest cases it is formed by a single more or less narrow plate, extending nearly across the whole ventral face of the head (*Sh*, text-figs. 37A, 112A), but in most cases it consists of one broad median unpaired element (*Sbm*), and one or two smaller paired elements (Sh_1, Sh_2), situated close posteriorly to the infraprelateral plate (text-figs. 8, 34, 37B, C, 111, 112C, 113B; cf. also Patten 1932, text-fig. 5). The series may often extend straight across the lower side of the head, but in certain cases its lateral parts are curved backwards so that its anterior margin is convex and its posterior margin concave. Its bone or bone elements may sometimes be very delicate, whereas in other cases they are stronger developed. The series is always completely devoid of ornament.

For further particulars concerning the development of the submandibular and subhyoideal bone series the reader is referred to the description of *B. canadensis* below in this work (p. 269).

Trunk, girdles and fins.

Among the *Bothriolepinae* the trunk has been found completely preserved only in *B. canadensis* (text-figs. 38, 40B, 54, 62; cf. also Patten 1904, pp. 113–114, text-figs. 1, 2; 1912, text-figs. 250, 251, 257; Stensiö 1931, text-fig. 72). In this species it is longer and slenderer (text-figs. 38, 40B, 62C) than in *Pterichthyodes* (Forster-Cooper 1934, text-figs. 1, 2; pl. 2; Watson 1935, text-fig. 27), and probably also than in *Remigolepis* (cf. Part III of this work). However, it is very likely that it was somewhat different in its proportions in other *Bothriolepis*-species.

The specimens of *Bothriolepis canadensis* (text-figs. 38, 40B) and *Pterichthyodes* (text-fig. 61) which have the trunk completely preserved show clearly that the trunk-armour of the *Antiarchi* extended very far backwards and that it surrounded the whole abdominal region with the exception of certain postero-dorsal and lateral parts. As to the caudal extent of the trunk-



Text-fig. 38. *Bothriolepis canadensis*. Restoration of a medium-sized individual in lateral aspect. About one half of the natural size.

armour the *Antiarchi*, therefore, are nearest suggestive of the Dolichothoracid Arthrodires (cf. *Heintz* 1929a, pp. 42–45, figs. 15–16; 1933, fig. 5; 1938, text-fig. 6; Stensiö 1944, pp. 2, etc., and figs. 15–17).

Axial skeleton.

The vertebral column in the *Bothriolepinae* was clearly devoid of ossifications and calcifications. Its arcual elements certainly consisted only of cartilage. Vertebral centra cannot have been present. The notochord must have been well developed throughout the trunk, and, as normally in lower fishes, it must have extended forwards into the basal parts of the endocranium. Because of the presence of the well developed occipital joint between the head and trunk, it is conceivable, however, that, as in the Arthrodires (Stensiö 1925, pp. 96–97; 1934a, pp. 56, 60; Stetson 1930, p. 32), it was fairly weakly developed in the endocranium.

With regard to the general stage of development the vertebral column in *Bothriolepinae* and *Antiarchi* in general was thus probably somewhat as in Arthrodires (Gross 1938b, pp. 189–197) and Palaeozoic sharks in general (Moy-Thomas 1939).

Girdles of the paired fins.

Endoskeletal shoulder-girdle.

The endoskeletal shoulder-girdle must be assumed to have been persisting to some extent in the *Antiarchi*. It consisted certainly only of cartilage and lay entirely within the anterior part of the trunk-armour. Contrary to what is the case in other fishes it was but in slight contact with the pectoral fin, which articulated principally against the trunk-armour (cf. also pp. 148–153 below). There can be no doubt, however, that this condition must be secondary and due above all to the special development of the pectoral fin and its exoskeleton. The endoskeletal shoulder-girdle served as a place of origin for the protractor and retractor (adductor) muscles of the pectoral fin.

Exoskeletal shoulder-girdle or trunk-armour.

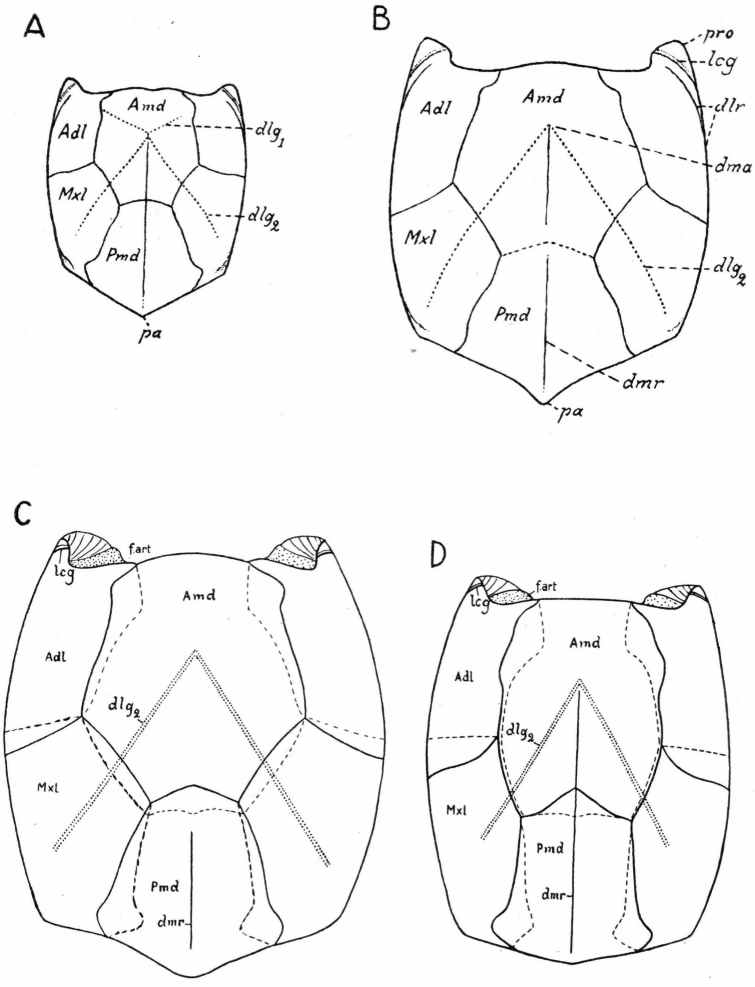
It was shown already in 1931 (Stensiö 1931, pp. 72–107, 109–138, 158–160; cf. also Gross 1941a, pp. 57–69) that the trunk-armour in the *Antiarchi* is homologous with the trunk-armour of the Arthrodires and that the pectoral appendages of the *Antiarchi* are true pectoral fins of a highly specialized type. Since that time it has been established that the Arthrodires have a scapulo-coracoid attached to, or situated inside, the trunk-armour, and that a more or less large pectoral fin articulated against their scapulo-coracoid (Stensiö 1944, pp. 36–69, 77–79; cf. Heintz 1938, pp. 19–25; Gross 1938, p. 199; Stensiö and Jarvik 1939, pp. 265–266; cf. also Broili 1930a; 1933a, b; Watson 1934, p. 448; 1937, p. 137). It is thus fully obvious now that the trunk-armour in both the *Antiarchi*

and *Arthrodires* is simply the exoskeletal shoulder-girdle, which is excessively developed so that it covers an unusually large part, or nearly the whole, of the abdominal region of the trunk.

In its general shape and most of its other general characters the trunk-armour is fairly uniformly developed in all the *Antiarchi*-groups in which it is known in any detail. In all the *Antiarchi*-groups it is thus composed of an unpaired dorsal wall, a paired lateral wall, and a ventral wall, which extends somewhat further backwards than the other walls. The walls meet at more or less pronounced angles, and hence externally they are marked off from each other by two paired ridges, the dorso-lateral ridge (*dlr*, text-figs. 38–40, 283D) and the ventro-lateral ridge (*vlr*, text-figs. 38, 40, 41, 283D), which are situated between the dorsal and lateral walls and between the lateral and ventral walls respectively. The primary number of plates composing the trunk-armour is also the same in all *Antiarchi* groups. The posterior dorso-lateral and posterior lateral plates, which in several of the groups are intimately connected with one another, in the *Bothriolepinae* are completely fused into a single plate, the mixilateral plate (Stensiö 1931, pp. 84–89). The semilunar plate is paired in *Pterichthyodes*, *Asterolepis* and *Remigolepis* (Traquair 1894–1906, text-figs. 38, 52–55; Gross 1931, pl. 5, fig. 4; Nilsson 1941, text-fig. 7; cf. also Part III of this work), but unpaired in *Gerdalepis* (Gross 1941b, pp. 206–207, figs. 6A, 9, 10) and the *Bothriolepinae* (text-fig. 41). In addition it is noteworthy that a small supernumerary plate (*Dx*, text-figs. 248, 249) has been found in a single case in *Bothriolepis*, in the suture between the anterior median dorsal, posterior median dorsal, and mixilateral plates. This plate, which will be described as the supramixilateral plate, is probably a fortuitous formation.

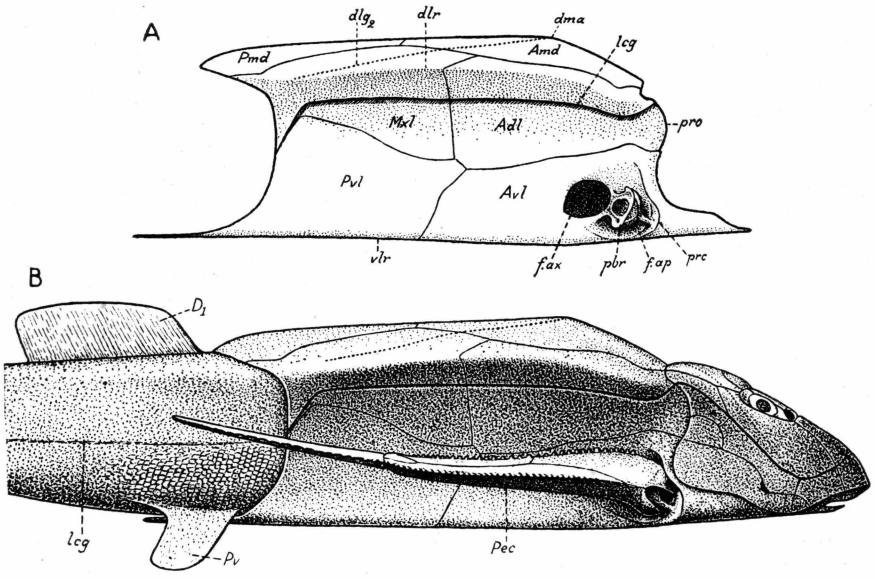
After these general remarks we shall now turn to a detailed description of the walls of the trunk-armour in the *Bothriolepinae*.

The dorsal wall in the *Bothriolepinae* (text-figs. 38–40, 98, 179–183, 249, 261, 264, 283D, 287B, 304, 308) extends backwards to immediately in front of the anterior dorsal fin and is quadrilateral when looked at from above or from below. The anterior margin in its median part, situated above and behind the posterior margin of the head-shield, is generally a little convex, whereas in either lateral part it is produced forwards and takes part in the formation of the processus obstans (*pro*). The paired lateral margin, which is represented by the dorso-lateral ridge (*dlr*), generally is convex. The posterior margin as a whole is slightly convex in *Grossilepis* (text-fig. 39D), but strongly convex in *Bothriolepis* (text-fig. 39A–C). This margin as a rule presents a more or less pronounced posterior median corner or angle (*pa*), which is formed by the posterior median dorsal plate. The dorsal wall is longest in its median part, broadest about at its middle, more precisely, across the points where the dorso-lateral ridges are cut through by the suture



Text-fig. 39. Restorations of the dorsal wall of the trunk-armour of *Bothriolepis canadensis*, *B. cellulosa* and *Grossilepis tuberculata*. All the resotrations in dorsal aspect. *A*, of a very small individual of *B. canadensis*. Nat. size. *B*, of a somewhat larger individual of *B. canadensis*. $^{5}/_{12}$ of the nat. size. *C*, of *B. cellulosa*. From Gross 1941a. About ½ of the nat. size. *D*, of *Grossilepis tuberculata* (Gross). From Gross 1941a. × $^{5}/_{6}$.
Adl, anterior dorso-lateral plate; *Amd*, anterior median dorsal plate; *Mxl*, mixilateral plate; *Pmd*, posterior median dorsal plate; dlg_1, anterior oblique abdominal pit-line groove; dlg_2, posterior oblique abdominal pit-line groove; *dlr*, dorso-lateral ridge; *dma*, tergal angle; *dmr*, dorsal median ridge; *f.art*, articular fossa for paranuchal trochlea; *lcg*, main lateral line-groove; *pa*, posterior angle or corner of posterior median dorsal plate; *pro*, processus obstans.

between the anterior dorso-lateral and mixilateral plates. The breadth in young individuals always is smaller than the length. However, as in several, or perhaps all, of the species it grew proportionally somewhat more than the length, it is normally larger in old individuals than in younger ones (text-figs. 179–183). In very old individuals of certain species, e.g. *B. canadensis*,

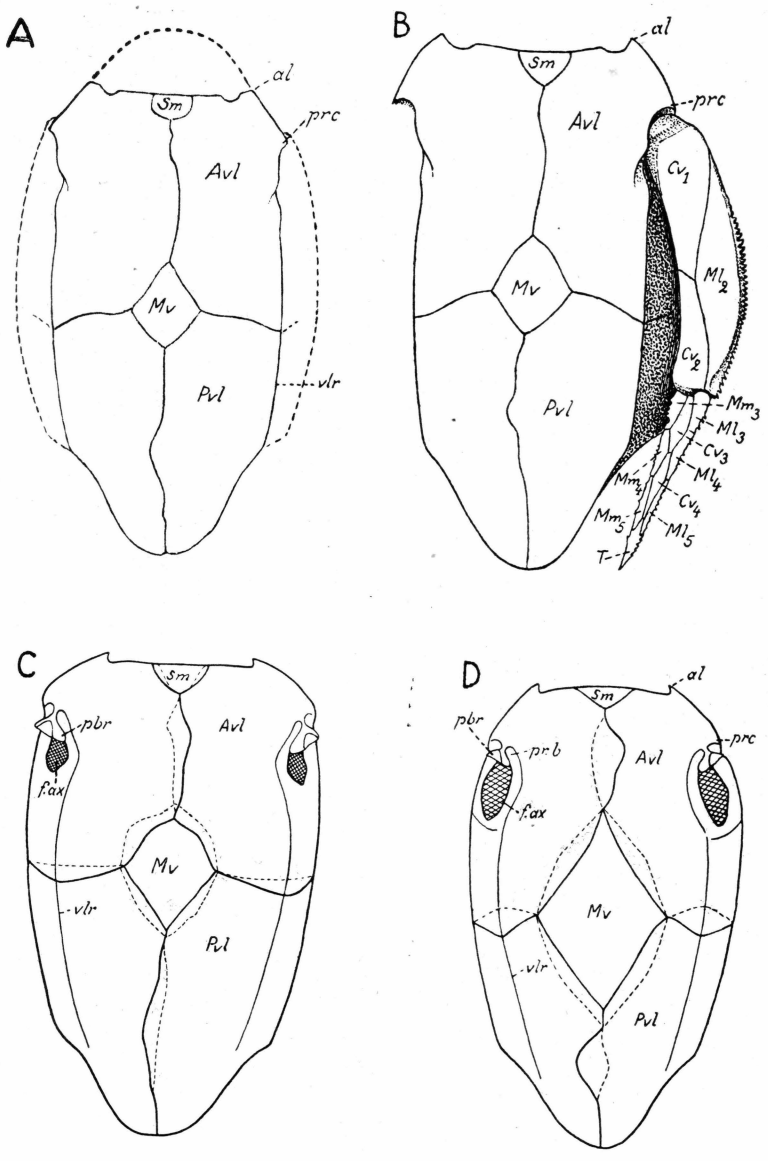


Text-fig. 40. *Bothriolepis canadensis*. *A*, restoration of trunk-armour of a medium-sized individual. Lateral aspect. *B*, restoration of head and anterior part of trunk with pectoral, pelvic, and anterior dorsal fins. Pectoral fin in a maximally retracted position. Squamation also shown. Lateral view. Both figures somewhat more than half the natural size. *Adl*, anterior dorso-lateral plate; *Amd*, anterior median dorsal plate; *Avl*, anterior ventro-lateral plate; D_1, anterior dorsal fin; *Mxl*, mixilateral palte; *Pec*, pectoral fin; *Pmd*, posterior dorsal plate; *Pv*, pelvic fin; *Pvl*, posterior ventro-lateral plate; dlg_2, posterior oblique abdominal pit-line groove; *dlr*, dorso-lateral ridge; *dma*, tergal angle; *f.ap*,fossa articularis pectoralis; *f.ax*, foramen axillare; *lcg*, main lateral line groove; *pbr*, processus brachialis; *prc*, prepectoral corner; *pro*, processus obstans; *vlr*, ventro-lateral ridge.

it is even as large that almost, or practically, it equals the length (text-figs. 182, 183). In outer aspect the wall in all essentials is as in the other *Antiarchi*. It is highest along its median axis, whence it slopes laterally towards the lateral walls (text-figs. 38, 40, 114, 283D, 287B). In front of the tergal angle (*dma*, text-figs. 38–40, 43), which is situated on the anterior half of the anterior median dorsal plate, it slopes also forwards towards the head-shield. Owing to the condition that it is highest along its median axis and slopes towards the sides its dorsal face is divided into right and left halves. In front of the tergal angle (*dma*) these two halves pass over into one another without any definite boundary, whereas behind the tergal angle they are separated by the more or less well developed dorsal median ridge (*dmr*). The wall is of a very different height in various species. It is very low and flat in *B. canadensis* (text-figs. 38, 40, 114, 150B, D, 151; cf. also Stensiö 1931, text-figs. 29B,38 B), in which it meets the lateral wall of either side at angle of about 95–100°. Presumably it was also fairly low and flat inter alia in *B. cellulosa* and *Grossilepis*. In *B. panderi* (Obrutschew 1939, p. 115), *B. maxima* (text-fig. 243H, J) and *B. alvesiensis* it is a little higher, the angle between it and the lateral wall amounting to 100–120°. In *B. gigantea*,

B. obesa, *B. turanica*(Obrutschew 1939, p. 115), *B. groenlandica* (text-figs. 283D, 287) and *B. jarviki* (text-fig. 304) it is still higher, the angle between it and the lateral wall amounting to between 120–145°. Finally, in *B. cristata* and *B. gippslandiensis* (text-fig. 264) it is not only high in itself, but in addition elevated into a high dorsal median crista. As in *Ceraspis* (Gross 1937, pp. 14–19, text-fig. 9, 11), this crista is formed by the excessively developed dorsal median ridge (*dmr*). This ridge (*dmr*) from the tergal angle (*dma*) on the anterior median dorsal plate extends backwards as far as close to, or to, the posterior corner or process (*pa*) of the wall. When normally developed, and thus not elevated into a high crista, this ridge seems mostly to be stronger developed in young individuals (text-figs. 39A, 88, 91, 95–98, 115, 118, 121A, B, 136A, 138A–E, 179, 199–202, 204–206, 263, 280A, C, D, F, 286A–E, 302; pls. 34, 35, 42; pl. 43, fig. 3) than in older ones, in which generally it is less pronounced and sometimes also interrupted on the posterior part of the anterior median dorsal plate and on the adjacent anterior part of the posterior median dorsal plate (text-figs. 39B, C, 101, 109, 116, 117, 119, 120, 121C–M, 122–124, 127–135, 137C, 138F–R, 139–141, 146–149, 154–159, 180–183, 216, 217, 225, 239, 248, 249, 250A, 254A, 281A, B, 284–286; pls. 20–33, 36–41).

In very small individuals of various *Bothriolepis*-species, e.g. *B. canadensis* (pp. 274–281 below), *B. gippslandiensis* (Hills 1931, pp. 217, 219) and *B. groenlandica* (see these species), the outer face of the dorsal wall of the trunk-armour usually presents certain characters which are mostly absent in medium-sized and large individuals, and which are to be regarded, therefore, as special characters of immaturity. These characters are as follows. 1) The presence of a paired low, narrow ridge, the oblique transverse ridge (*otr*, text-figs. 43A, 88, 91, 92, 95, 96–98, 115, 118C, D, F, 199, 202, 204, 280A, 302; pl. 13, fig. 3; pl. 34, figs. 1, 4; pl. 35, figs. 1, 3), which runs off in an antero-lateral direction from the tergal angle (*dma*). This ridge is often developed only for some distance nearest to the tergal angle, but in several cases it is also traceable on to the anterior dorso-lateral plate, more precisely, to somewhere near the processus obstans. 2) The presence of a more or less well-defined paired pit-line groove, the anterior oblique abdominal pit-line groove (dlg_1, text-figs. 39A, 43A, 88, 91, 96, 98, 115, 118, 121A–D, F, G, J, L, 202, 204, 280A, C, D, F; pl. 34, figs. 1, 4; pl. 35, figs. 1, 3), which is situated immediately in front of the oblique transverse ridge (*otr*) and from, or near, the tergal angle (*dma*) extends more or less far antero-laterally on the anterior median dorsal plate, but generally not on to the anterior dorso-lateral plate (cf. pp. 211–214 below). 3) The presence of a paired shallow, fairly broad depression, the oblique transverse depression (*otd*, text-figs. 43A, 91, 95, 96, 263, 280A, 283A, B; pl. 34, fig. 4; pl. 35, figs. 1, 3), corresponding in position and extent to the postlevator thickening (*alr*) of the lower face of the wall. This depression, which thus lies somewhat in front of both the



Text-fig. 41. Restorations of the ventral wall of the trunk-armour. *A*, *B*, of *Bothriolepis canadensis*. × $^5/_{12}$. *B*, of *B. cellulosa*, from Gross 1941a. × $^1/_2$. *C*, of *Grossilepis tuberculata*, from Gross 1941a. × $^5/_6$.

Avl, anterior ventro-lateral plate; Cv_1–Cv_4, ventral central plates 1–4; Ml_2–Ml_5, lateral marginal plaes 2–5; Mm_3–Mm_5, medial marginal plates 3–5; *Mv*, median ventral plate; *Pvl*, posterior ventro-lateral plate; *Sm*, semilunar plate; *T*, terminal plate; *f.ax*, foramen axillare; *al*, antero-lateral corner of anterior ventro-lateral plate and of ventral wall as a whole; *pbr*, processus brachialis; *prc*, prepectoral corner; *vlr*, ventro-lateral ridge.

oblique transverse ridge (*otr*) and the anterior oblique abdominal pit-line groove (dlg_1), from somewhere near the tergal angle (*dma*) extends anteriorly and laterally to the foremost dorso-medial part of the anterior dorso-lateral

plate. 4) Finally, also the presence of an unpaired depression, the posterior transverse depression (*dp*, text-figs. 45A, 88A, 91, 95, 96, 98, 199, 201, 204; pl. 42, fig. 4; pl. 43, fig. 3), situated across the hindmost part of the posterior median dorsal plate, above the dorsal part of the crista transversalis interna posterior (*crtp*). The presence of this depression, and also of the oblique transverse one (*otd*), is certainly due simply to the condition that the dorsal wall in very young individuals is as thin that its upper face to a certain extent reflects the stronger relief of its lower face.

In certain species one or more of the characters of immaturity enumerated above may persist to some extent also in medium-sized and large individuals, but in most species they disappeared pretty soon. In *B. canadensis*, for instance, they are as a rule entirely absent already in those individuals in which the dorsal length of the trunk-armour exceeds 5–6 cm.

The dorso-lateral ridge (*dlr*, text-figs. 38–40, 48, 50, 95, 114, 117, 127, 129, 144, 145, 150–156, 226, 227, 243H, I, 249, 251, 256, 259B, 264, 283D, 287B, 288, 289, 304, 308) is generally well pronounced, but may also be somewhat rounded off. In *B. nielseni* (text-fig. 308) it is set nearly throughout its extent with strong, somewhat spine-like tubercles.

The lateral wall of either side of the armour (text-figs. 38, 40, 41, 114; 145B, 150B, D, 151A, 152, 264, 283D, 287B, 304) is always shorter than the dorsal and ventral walls and is so situated that its lateral face is directed laterally and somewhat downwards, and its medial face medially and somewhat upwards. Moreover, it is curved as a whole in such a manner that in a rostro-caudal direction it is a little convex on its lateral face and correspondingly concave on its medial one. In addition it is also arched in a dorso-ventral direction, but this arching is different in individuals species (text-figs. 114, 243H, I). Only its anterior and posterior margins are free. The former of these two margins is convex in its upper part formed by the processus obstans (*pro*), and concave in its ventral part, whereas the posterior margin is concave throughout its extent. The processus obstans is longer and higher (broader) than in *Pterichthyodes*, *Gerdalepis*, *Asterolepis* and *Remigolepis*.

The ventro-lateral ridge (*vlr*, text-figs. 38, 40, 41, 51–53, 145B, 160–163, 164B, C, 165D–F, 166–176, 177C, 264, 283D, 287B, 304) is often fairly pronounced (*B. canadensis*, *B. cellulosa*, *B. groenlandica*, *Grossilepis tuberculata*), but it may also be more rounded off and less conspiracuous (*B. maxima*, *B. gigantea*).

The ventral wall of the trunk-armour (text-figs. 41, 160–163, 164A, 167–169, 171, 175–178, 283D, 287B, 292B; pls. 15–18), as in the other *Antiarchi*, may be regarded as composed of three divisions: a subcephalic division projecting forwards beyond the lateral walls, underneath the posterior parts of the head, a middle, principal division, situated between the lateral walls; and a subanal division, extending backwards beyond the lateral walls, below

the anal opening. As in the *Antiarchi* in general, this wall is longer than the other walls of the armour. It is broadest across the prepectoral corners (*prc*, text-figs. 41, 160–163, 292B; pls. 15–18) of the anterior ventro-lateral plates, where its breadth may almost equal the maximum breadth of the dorsal wall. From this place it decreases in breadth both forwards and backwards mostly, however, in the latter direction. In *B. traquairi* (text-fig. 214), where it narrows much more backwards than in any other *Bothriolepis*-species, its subanal division is particularly narrow. Because of this narrowing both in front of, and behind, the prepectoral corners the wall as a whole (text-fig. 41) is considerably narrower than the dorsal one. Often it is practically flat, but sometimes it may also be a little arched in such a manner that its external face is slightly convex and its internal face slightly concave both in rostro-caudal and transverse directions. The anterior free margin, that is to say the anterior margin of the subcephalic division (text-fig. 41), may be straight, slightly convex or even slightly concave. The antero-lateral corner (*al*) of either side is generally somewhat produced into a more or less marked antero-lateral process. The lateral margin is so directed as to converge backwards towards that of the opposite side. It consists of a prepectoral or subcephalic part, a middle part, and a subanal part, formed by the free lateral margin of the subcephalic division of the wall, the ventro-lateral ridge (*vlr*) and the free lateral margin of the subanal division of the wall respectively. Taken as a whole this margin is convex but presents a more or less deep axial notch below the fossa articularis pectoralis and in addition sometimes a concavity at the transition between its middle and subanal parts, a concavity which in *B. traquairi* (text-fig. 214) is long and particularly clearly developed. The prepectoral or subcephalic part of the margin is always well bounded off anteriorly. This part is directed somewhat forwards and is mostly somewhat convex. At its anterior end it is fairly thin, but, as it increases rapidly in thickness backwards, it is very thick most posteriorly (text-figs. 4, 38, 40B). The main middle part of the margin is well bounded off from the prepectoral one by the prepectoral corner (*prc*). Not considering the axial notch, this part is convex throughout its extent. Its maximal convexity may be situated just behind the axial notch (*B. traquairi*), somewhat behind this notch, or even as far back as at the suture between the anterior and posterior ventro-lateral plates. The subanal part of the margin passes over without any definite boundary both into the middle part of the same margin and into the posterior margin of the wall. It is normally convex with a slight concavity anteriorly, but it may also be fairly straight or a little concave throughout its extent (*B. traquairi*). Finally, the posterior margin of the wall is always short and convex.

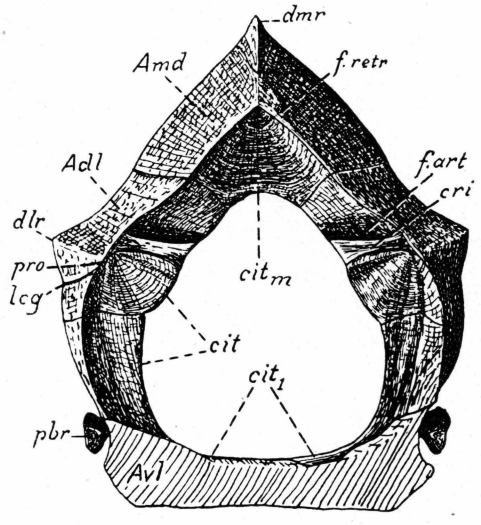
We shall now proceed to an examination of the internal side of the trunk-armour in the *Bothriolepinae*, and in so doing we shall first turn to the crista transversalis interna anterior and the crista transversalis interna posterior

(cf. Stensiö 1931, pp. 72, 79, 80–82, 86, 96–102, 104; Gross 1941a, p. 23). The crista transversalis interna anterior (*cit*, cit_1, cit_2, tex-figs. 48, 49, 51A, 144, 145A, 151, 152, 164A, 165B, C, F, 166E, F; pls. 15, 50, 51, 54) is of a type similar to that in *Asterolepis* (Gross 1931, pl 5, fig. 4) and *Remigolepis* (Stensiö 1931, pp. 96–97; cf. also Part III of this monograph), forming an imperfect anterior boundary of the cavity of the trunk-armour. In many cases it is completely interrupted dorsally, being devoid of a median dorsal division, and in these cases it is thus dorsally exactly as in *Asterolepis*, *Remigolepis* and *Byssacanthus* (Gross 1940b, text-fig. 10A, B). Often, however, it shows also vestiges of a median dorsal division, which is developed on the anterior median dorsal plate. These vestiges include the formation to be described below (pp. 111–112) as the postlevator crista (*cr.pl*, text-figs. 44A, C, 125A–F, 126F, 238A, 250B, 280B, E, 282C, 305A, B) and a floor underneath the posterior part of the levator fossa (text-fig. 265B). When one or both of these formations are present the crest in its development, as we shall see (pp. 109–110 below), approaches the corresponding crest in *Ceratolepis* (text-fig. 42). The lateral, vertical, division of the crest (*cit*), which begins immediately laterally to the anterior median dorsal plate, on the anterior dorso-medial corner of the anterior dorso-lateral plate, and thence extends down along the whole anterior margin of the lateral wall of the trunk-armour, is high throughout its extent. As normally in the *Antiarchi*, it constitutes, therefore, a broad transverse lamina of bone (*cit*, text-figs. 48A, B, D, 49, 144B, C, 145A), which on the upper part of its anterior face bears the articular fossa (*f.art*) for the paranuchal trochlea of the head-shield. This fossa lies just medially to the uppermost part of the processus obstans (*pro*). The ventral, horizontal, division of the crest (cit_1, text-fig. 164A), which is developed on the ventral wall of the trunk-armour, decreases considerably in height in a medial direction and is comparatively low in the greater part of its extent, above all at and near the suture between the anterior ventro-lateral plates. This division (cit_1) was termed by Gross (1941a, p. 23) the postbranchial crest, a term which will also be adopted for it here. It is always straight and crosses the ventral wall of the trunk-armour comparatively far backwards, about at the transition between the subcephalic and middle, principal divisions.

In three of the *Bothriolepis*-species, *B. cellulosa* (Gross 1941, p. 23), *B. maxima* (text-fig. 243A), and *B. groenlandica* (pls. 15, 54) the ventral, horizontal division of the crista transversalis interna anterior is divided into two branches, anterior and a posterior, which are nearly parallel with each other and which have been termed by Gross (1941a, p. 23) the "postbranchial crest", and the "crista transversalis interna anterior" proper. As pointed out by Gross, the "postbranchial crest" must represent the anterior ventral branch of the crista transversalis interna anterior in *Asterolepis* and *Remigolepis*. The opinion advanced by the present writer in 1931 (Stensiö 1931,

p. 97) that the "postbranchial crest" is the homologue of the posterior ventral branch of the crista transversalis interna anterior in *Asterolepis* and *Remigolepis* has thus turned out to be wrong.

For comparison we shall now dwell a little upon the development of the crista transversalis interna anterior in *Ceratolepis*. The crista transversalis interna anterior in this form (text-fig. 42; cf. Gross 1933b, text-fig. 4A) is much more complete than the corresponding crest in *Asterolepis, Remigolepis* and the *Bothriolepinae*. Besides the divisions found developed in those forms,



Text-fig. 42. *Ceratolepis stensiöi* Gross. Trunk-armour in anterior aspect. Subcephalic division of ventral wall removed. From Gross 1933 (1933b). $^3/_4$ of nat. the size.
Adl, anterior dorso-lateral plate; *Amd*, anterior median dorsal plate; *Avl*, anterior ventro-lateral plate; *cit*, crista transversalis interna anterior (lateral, vertical division); cit_1, post-branchial crista (ventral, horizontal division of crista transversalis interna anterior); cit_m, median dorsal division of crista transversalis interna anterior, developed as a floor of the levator fossa; *cri*, infraarticular crista; *dlr*, dorso-lateral ridge; *dmr*, dorsal median ridge; *f.art* articular fossa for paranuchal trochlea; *f.retr*, levator fossa, developed as an anteriorly opening pit (completely bounded laterally, posteriorly and ventrally by the median dorsal part of the crista transversalis interna anterior); *leg*, main lateral line; *pbr*, processus brachialis; *pro*, processus obstans.

it includes also a complete unpaired, median dorsal division. This division (cit_m) is situated on the lower side of the anterior median dorsal plate, connecting the paired lateral divisions of the crest. More precisely, it seems to descend from the lower face of the anterior median dorsal plate mainly along the anterior margin of the postlevator thickenings (*alr*), just in front of the anterior median ventral process (prv_1). It has such a position and extent that it forms complete lateral, posterior, and ventral boundaries of the levator-fossa (*f.retr*), which is, therefore, a large, forward opening pit. It is easily seen that the unpaired median division of the crest in *Ceratolepis* is represented in the *Bothriolepinae* by the postlevator crest (*cr. pl*; p. 112) and

the floor below the posterior part of the levator fossa. Whether these structures in the *Bothriolepinae* actually are vestiges of a primarily complete unpaired median dorsal division of the crista transversalis interna anterior, or whether they form an initial stage towards the development of such a division of the crista transversalis interna anterior, is a question which cannot be answered at present. It is of interest, however, that in this as well as in certain other characters in their trunk-armour the *Bothriolepinae* remind more of the Ceratolepids than of other *Antiarchi*-forms (cf. also pp. 111–115).

The crista transversalis interna posterior in the *Bothriolepinae* (*cr. tp*, text-figs. 46, 47, 88, 92, 102, 106, 136, 137A, B, 143, 146, 150, 151B, 152, 156, 158, 172C, 173, 199, 238B, 240, 305D) in all essentials agrees with the corresponding crest in the *Asterolepinae* and *Remigolepidae*. It is developed around the whole posterior opening of the trunk-armour and throughout is lower and more rounded off than the crista transversalis interna anterior. Its median dorsal part may be more or less concentric with the posterior margin of the posterior median dorsal plate. Sometimes this part is situated close to the posterior margin of the posterior median dorsal plate, sometimes a little in front thereof. In the latter case there is a smooth transverse area between it and the said margin, an area which will be termed here the posterior marginal area (*pma*, text-figs. 46B, C, 47A, C). Laterally to the posterior median dorsal plate the crista runs first latero-ventrally and ventrally along the posterior margin of the trunk-armour. On reaching the ventral wall of the trunk-armour it turns off in a postero-medial direction and passes on to the subanal division of this wall (text-figs. 172C, 173). The lateral and ventral parts of the crest are always well pronounced, whereas the median dorsal part varies considerably in its development in the individual species. This part is thus normally high and well developed in *Bothriolepis canadensis* (text-figs. 46, 47A, 136, 137A, B), somewhat lower and less well marked in *B. cellulosa* and *B. groenlandica* (text-figs. 47C; pl. 36, figs. 3, 4; pl. 42, figs. 1–3; pl. 43, fig. 2; cf. also Gross 1941a, pl. 10, figs. 3, 6), and mostly low and obscure in *B. maxima*, *B. gigantea*, *B. leptocheira*, *B. jarviki* and *Grossilepis tuberculata* (text-figs. 239, 305D; cf. also Traquair 1894–1906, pl. 25, fig. 2; pl. 29, fig. 4; Gross 1941a, pl. 23, figs. 3, 4). Finally, attention should here also be drawn to the condition that, at least in *B. canadensis*, there is a transverse broad thickening (*tvc*, text-figs. 172C, 173) on the posterior ventro-lateral plate immediately in front of the ventral part of the crest here under consideration. This thickening, which is broad, particularly in its medial parts, extends straight across the ventral wall of the trunk-armour.

The remaining structures of the inner side of the trunk-armour of the *Bothriolepinae* to be dealt with in this connection are all found on the dorsal wall, more precisely on the lower (internal) faces of the anterior median dorsal, anterior dorso-lateral, and posterior median dorsal plates. These

structures are as follows: the levator fossa, the postlevator thickening, the postlevator crista, the ventral median ridge and groove, the anterior ventral process and pit, the posterior ventral process and pit, the ventral tuberosity, and the supranuchal area (cf. Stensiö 1931, pp. 72–80).

The levator fossa (*f. retr,* text-figs. 44, 106, 125, 126, 224G–J, 238A, 250B, 254B, 255, 259A, 260, 265A, 268E, F, 280B, E, 281C, D, 282, 305A, B), as we know (Stensiö 1931, pp. 75–77, text-figs. 33, 37), is a median unpaired depression on the anterior median dorsal plate, on which from the anterior margin it extends backwards as far as to underneath the tergal angle (*dma*). Anteriorly it is about equally broad as the anterior margin of the anterior median dorsal plate, but it narrows rapidly backwards towards its posterior end so that it is triangular in its general outline. It is considerably shorter and broader than in *Asterolepis* (Stensiö 1931, text-fig. 37; 1938, pl. 3, fig. 2; pl. 4, fig. 1) and in this respect nearest resembles the corresponding fossa in *Byssacanthus* (Gross 1940b, text-fig. 10A, B), *Ceraspis* (Gross 1937, text-fig. 8) and *Pterichthyodes*[1]). Finally, it is worthy of mention here that it is fairly different in its proportions in the individual species of the *Bothriolepinae.* It may be mentioned, for instance, that it is extremely short and broad in *Bothriolepis gippslandiensis* (text-figs. 44D, 265A; cf. also Hills 1931, pls. 11, fig. 6), but comparatively long and narrow in *B. obesa, B. leptocheira, B. jarviki* (text-figs. 259A, 260, 305A, B), and other species in which the tergal angle (*dma*) is situated relatively far backwards. – As pointed out by the writer on an earlier occasion (Stensiö 1931, pp. 75–76), the levator fossa was probably the place of origin of the levator muscles of the head (see Stensiö 1945, p. 6).

The lateral and posterior boundary of the levator fossa is formed by the paired postlevator thickening (= "antero-lateral ridge", Stensiö 1931, p. 76; *alr,* text-figs. 44, 125, 126, 238A, 250B, 254B, 255, 259A, 265A, 280B, E, 281C, D, 282, 305A, B) and often also by this thickening and the paired postlevator crista (*cr.pl*). The postlevator thickening (*alr*), as normally in the *Antiarchi,* begins underneath the tergal angle (*dma*), from where it stretches in an antero-lateral direction first to the foremost part of the suture between the anterior median dorsal plate and then further on to the anterior dorso-medial part of the dorsal lamina of the anterior dorso-lateral plate. It is always well rounded off and increases rapidly in breadth in an antero-lateral direction. In the majority of the species it is well developed, but in certain species, as for instance *B. maxima, B. gigantea* and *B. obesa* (text-figs. 44C, 238A, 254B, 255, 259A) it is generally low and little conspicuous, and sometimes even almost absent. – Besides in the *Bothriolepinae,* the postlevator thickening is also found in *Asterolepis* (Stensiö 1931, text-fig. 37;

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[1]) Specimens of *Pterichthyodes milleri* from Lethen Bar in the possession of the Swedish Museum of Natural History in Stockholm.

Nilsson 1941, pl. 8), *Pterichthyodes*[1]), *Byssacanthus* (Gross 1941, text-fig. 10A, B), and probably in *Ceraspis* too (Gross 1937, text-fig. 8). On the other hand, it is entirely absent in *Remigolepis*, in which the levator fossa, therefore, is devoid of a clear posterior boundary.

The postlevator crista (*cr. pl*, text-figs. 44A, C, 88A, 106, 125A–E, 126A, D, F, 148, 151B, 158, 199, 224G, H, J, 238A, 250B, 254B, 255, 259A, 268E, F, 280B, E, 281, 282, 305A, B), already referred to above (pp. 109–110), is not constantly developed, but is nevertheless often met with. At least in certain species it is found more frequently in small individuals than in larger ones. When present the crest is usually well marked off from the postlevator thickening (*alr*), and hence it is generally so well distinguishable from that thickening that it cannot be confounded with it. Mostly it is narrow, fairly sharp-edged and well defined, but in certain species (*B. jarviki*, text-fig. 305A, B) it may be broader and more obscure. It begins underneath the tergal angle (*dma*), on the very postero-medial end of the postlevator thickening, of its side, and, running first forwards and slightly laterally, it crosses the most proximal part of the postlevator thickening. At or near the antero-medial margin of the postlevator thickening, and thus at or near the levator fossa, or in the posterior part of this fossa, it turns in a more lateral direction so as to pass along, or close in front of, the distal longer part of the postlevator thickening. It ends at the antero-lateral corner (*a*) of the anterior median dorsal plate, just at the very upper end of the lateral, vertical division of the crista transversalis interna anterior (*cit*). The circumstance that antero-laterally, on either side, it ends just at this place and the condition that it is situated mainly behind the levator fossa show that the crista under consideration actually corresponds to a lateral upper part of the strongly developed median dorsal division (cit_m) of the crista transversalis interna anterior in *Ceratolepis* (cf. pp. 109–110 above and text-fig. 42). In *B. gippslandiensis* (text-fig. 265B; cf. also Hills 1931, pp. 220–221 and text-fig. 7), and fortuitously also in *B. canadensis*, the posterior median part of the levator fossa is provided with a thin bony floor, which in all probability is formed by the posterior parts of the postlevator crests and, therefore, presumably is a homologue of the median upper part of the median dorsal division of the crista transversalis interna in *Ceratolepis*. The postlevator crista is absent in *Gerdalepis*, *Asterolepis*, *Byssacanthus* and *Remigolepis*. It cannot be decided for the time being whether it is regularly absent also in *Pterichthyodes* and *Ceraspis*.

The ventral median ridge (*mvr*, text-figs. 44, 47, 106, 125, 126, 137B, 146, 148, 151B, 158, 224G, H, J, 238B, 240, 250B, 254B, 255, 259A, 268E–G, 280B, E, 281C, D, 282, 305A, B, D; cf. also Gross 1941, text-figs. 8A–C, 10C, 11D, G, 30A–D, 31D) is an unpaired structure, which is present in the *Bothriolepinae* on the anterior and posterior median dorsal plates. In young

[1]) See foot-note on p. 111.

individuals (text-figs. 125, 126A, B, 136, 280B, E) it is developed only for a short distance on the anterior median dorsal plate, underneath the tergal angle (*dma*), and thus between, close in front of, and close behind the postero-medial parts of the postlevator thickenings and the postlevator crests, whereas in older individuals it has normally a much greater rostro-caudal extent. More precisely, in medium-sized and fully mature individuals it practically always extends backwards from the anterior ventral process (prv_1) as far as to about the middle of the posterior ventro-lateral plate (text-figs. 44, 47, 106, 126C–F, 137B, 250B, 254B, 255, 259, 268E, G, 281C, D, 282, 305A, B, D). Often in medium-sized and fully mature individuals the ridge in question streches also more or less far forwards into the levator fossa, sometimes even practically to the anterior margin of that fossa. The median ventral groove (*grm*) is absent in young individuals and began to develop only after that the median ventral ridge had grown fairly far behind the anterior ventral process. This groove (*grm*), which presumably lodged certain rostro-caudally running vessels, in fully mature individuals is traceable from the posterior parts of the anterior median dorsal plate backwards to the anterior or middle part of the posterior median dorsal plate. – The ventral median ridge fortuitously occurs in *Asterolepis* (Stensiö 1938, pl. 2, fig. 3; Gross 1940b, text-fig. 5F), but is always absent in *Remigolepis* and probably also in *Pterichthyodes*, whereas the ventral median groove is absent in all these three genera. Both the ridge and the groove are present in *Ceratolepis* (Gross 1933b, text-fig. 4C), where they are developed about in the same way as in the *Bothriolepinae*. In *Byssacanthus* (Gross 1940b, text-figs. 10G, H) the ridge is excessively developed so that the groove is completely enclosed in it. The groove in *Byssacanthus* thus is a canal in the median ventral ridge. The conditions with regard to the ridge and groove in *Gerdalepis* (Gross 1941b, p. 199) seem to be most suggestive of those in *Byssacanthus*.

The anterior ventral process (prv_1, text-figs. 44, 106, 125, 126, 148, 250B, 254B, 255, 259, 280B, E, 281C, D, 282, 305A, B; cf. Stensiö 1931, text-fig. 33; cf. also Gross 1941a, pl. 8; pl. 9;, fig. 1; pl. 20, fig. 2; pl. 21, fig. 3) is invariably present both in *Bothriolepis* and *Grossilepis*, but is normally fairly short. It is situated on the anterior median dorsal plate exactly underneath the tergal angle (*dma*), more precisely, on the ventral median ridge between the postero-medial ends of the postlevator thickenings (*alr*) and postlevator crests (*cr.pl*), just at the posterior end of, or close behind, the levator fossa. Mostly it is directed almost straight ventrally, but in several cases it may also point ventrally and somesvhat anteriorly. It is pierced by the anterior ventral pit (pt_1), which reaches upwards into it to a point close underneath the tergal angle, being separated from that angle only by a thin layer of bone. This pit decreases rapidly in diatmeter upwards so as to become fairly pointed most dorsally. Its ventral opening, which

sometimes may be fairly large, is always oval and longer than broad[1]). The anterior ventral process and pit are entirely absent in *Asterolepis*, *Pterichthyodes* and *Remigolepis*, whereas in the *Ceraspidae* the pit seems to be represented by a vascular canal which ascends into the anterior part of the high dorsal crest or dorsal spine (Gross 1940b, text-fig. 10H).

The posterior ventral process (*prv*$_2$ text-figs. 46, 47, 136B–F, 137A, B, 238B, 240, 305D; pl. 36, figs. 3, 4; pl. 37, fig. 2; cf. also Stensiö 1931, text-fig. 34; Gross 1941a, text-figs. 11D, F, G, 31D, E; pl. 10, figs. 3, 6; pl. 23, figs. 3, 4) is always well developed in *Bothriolepis* and *Grossilepis*, and so is also the posterior ventral pit (*pt*$_2$). The process, which probably varies in length and shape, descends in an antero-ventral direction from the posterior median dorsal plate, just in front of the crista transversalis interna posterior (text-figs. 46, 47). The pit is situated close in front of, and partly in, the process and penetrates deeply in a postero-dorsal direction into the posterior median plate (text-fig. 46B, C). It is always widest at its opening, from where it decreases in width upwards. Its opening is longer than broad[2]). – The posterior ventral process and pit are both present in *Asterolepis* (Gross 1931, pl. 7, fig. 10A), but they are in this form completely independent of one another, the process being a well-defined spine-like formation, situated entirely behind the pit. The pit, at any rate, is present also in *Gerdalepis* (Gross 1933b, pl. 1, fig. 5; 1941b, p. 200, figs. 2A, 3B) where, however, it is situated behind the apical chamber. Both the structures in question are entirely absent in *Remigolepis*.

The ventral tuberosity (*tb*, text-figs. 46, 47, 106, 136B–F, 137A, B, 151B, 158, 238B, 240, 305D; cf. also Stensiö 1931, text-fig. 34) is a rough unpaired thickening of a nature similar to that of the poriferous area of the premedian plate and the supraotic thickening of the centro-nuchal plate (cf. pp. 54–55, 57–58). It is situated on the ventral (internal) side of the posterior median dorsal plate mainly in front of the posterior ventral pit, between it and the hindmost part of the ventral median groove (*grm*), but it extends also backwards so that it forms the lateral boundaries of the posterior ventral pit. In *B. canadensis*, *B. panderi* (Gross 1941a, p. 20) and *B. groenlandica* it is well developed even in young individuals, whereas in several other species, inter atia *B. cellulosa* (Gross 1941a, p. 20; pl. 10, figs. 3, 6), *B. maxima* (text-figs. 238B, 240) and *Grossilepis tuberculata* (Gross 1941a, p. 43, pl. 23, figs. 3, 4), it is normally weakly developed or absent. This structure is thus not constantly developed among the *Bothriolepinae*. It is always absent in *Asterolepis* and *Remigolepis*. With regard to its position it is suggestive of the crista apicalis of the posterior median dorsal plate in *Gerdalepis* (cf.

[1]) The anterior ventral pit (*pt*$_1$) has a very large rostro-caudal extent in *B. maxima* (text-fig. 238 A). Also in *B. gigantea* it has sometimes a considerable rostro-caudal extent (text-fig. 255).

[2]) The posterior ventral pit (*pt*$_2$) is situated strikingly far forwards in *B. maxima* (text-figs. 238 B, 240).

Gross 1941b, pp. 202–205, fig. 2A), and thus it is not impossible that it may represent a dorsal part of that crest.

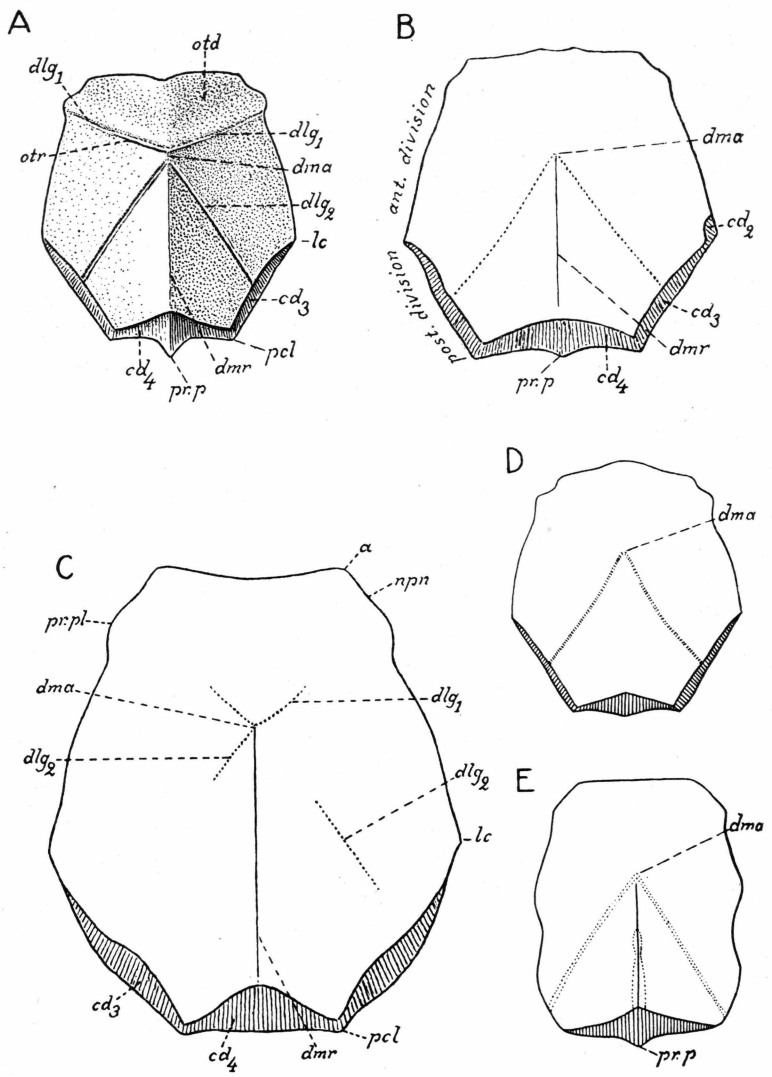
Finally, the supranuchal area (*sna*, text-figs. 44A, C, E, 126B, C, E, F, 238A, 255, 281C, D, 282, 305A) is developed along the anterior margin of the lower face of the anterior median dorsal plate and thus along the anterior end of the levator fossa. It is situated above the obtected nuchal area (*nm*, text-figs. 4, 9, 10, 13, 14, 25A, 26) of the centro-nuchal plate and was in contact with that area, when the head was in a maximally lowered position (cf. p. 24 above). It is normally absent or very obscure in young individuals, but became gradually more pronounced with the proceeding growth of the individuals, on account of which in medium-sized and fully mature individuals of the individual species it is mostly very well marked, at any rate in its lateral parts, immediately medially to the postlevator thickening and postlevator crest. The supranuchal area is met with also in *Asterolepis* (Gross 1931, pl. 7, fig. 11; 1940b, text-figs. 4A–D, 5B, D; Stensiö 1931, text-fig. 37; 1938, pl. 3, fig. 2) and *Remigolepis*. On account of the condition that the anterior end of the anterior median dorsal plate is very narrow in those two forms however, it extends in them, also laterally on to the anterior dorso-lateral plate of each side.

As may be gathered from the above, the special structures of the lower side of the dorsal wall of the trunk-armour are more completely, more constantly, and more uniformly developed in the *Bothriolepinae* than in anyone of the other *Antiarchi*-groups known at present with the exception of the Ceratolepids.

We shall now proceed to the various plates composing the trunk-armour of the *Bothriolepinae*.

The anterior median dorsal plate (*Amd*, text-figs. 38–40, 43, 44, 88, 90–92, 95–98, 101, 102, 106, 109, 114–128, 129–134, 140–143, 146–149, 151, 152, 154–159, 179–183, 199, 200, 202, 204–207, 210, 216, 224, 238A, 247–250, 254–255, 259A, 260, 261, 262B, 263, 264, 265, 268, 280–285, 302, 305A–C, 308) is broad anteriorly, about as in *Pterichthyodes* (Traquair 1894–1906, text-fig. 51), *Gerdalepis* (Gross 1941b, fig. 7), *Ceratolepis*, *Cerapis* and *Byssacanthus* (Gross 1933b, text-fig. 4A, C; 1937, pp. 14–16, text-figs. 8, 11; 1940b, pp. 41–43, text-fig. 10; cf. also text-fig. 42 in the present work), and differs clearly, therefore, from the corresponding plate in *Asterolepis* and *Remigolepis*, which is always narrow anteriorly (Gross 1931, pp. 29–30, text-fig. 14; 1940, pp. 20–27, text-figs. 4A–E, 5; Stensiö 1931, pp. 72–77, 170–172, text-figs. 37, 82; 1938, pp. 12–13, text-figs. 3, 7; Watson 1932, text-fig. 3). In *Bothriolepis* (text-figs. 43A–D, 44A–E, 118–126, 238A, 254A. 260, 262B, 263, 280–285, 305A–C) the plate is as normally in the group, in that its paired lateral margin somewhat behind its middle is provided with a well-marked lateral corner (*lc*). The lateral margin is divided by this corner into two divisions, anterior and posterior, the former of which is always

longer than the latter. The parts of the plate situated anteriorly and posteriorly to a transverse line through the lateral corners (*lc*) will be referred to as the anterior and posterior divisions respectively of the plate (fig. 2A). On the other hand, in *Grossilepis* (text-figs. 43E, 44F, 268; cf. also Gross 1941a, text-fig. 30) the plate is devoid of a lateral corner, or has this corner obscurely or weakly developed. In this genus the anterior and posterior divisions both of the lateral margin and of the plate itself, therefore, as a rule are much less clearly defineable than in *Bothriolepis*. In *Bothriolepis* the plate is broadest across its lateral corners (*lc*) and thence narrows fairly much towards its ends (text-figs. 43A–D, 44A–E); in *Grossilepis*, on the other hand, it is usually broadest fairly far in front of its lateral corners or has a nearly uniform breadth throughout its length (text-figs. 43E, 44F, 268; cf. also Gross 1941a, text-figs. 30B–H). In certain cases in the last-mentioned genus, however, it may also be broadest across its lateral corners and decrease in breadth forwards and backwards from these corners, but even in these cases (text-fig. 268A; cf. also Gross 1941a, text-fig. 30A) it is nevertheless much more uniform in breadth than in *Bothriolepis*. The plate in both the genera is so broad that its maximum breadth exceeds two thirds of its length. The maximum breadth in the majority of species usually amounts to between 75–95% of the length, but in certain species, as for instance *B. hydrophila*, *B. lohesti* and *B. gippslandiensis*, it is normally larger, equalling or exceeding the length. In *B. canadensis*, of which a great number of specimens could be examined, it ranges between 76–112% of the length and in certain specimens may thus exceed the length; in this species however, it exceeds the length only in very large individuals. It could be clearly established that the plate both in *B. canadensis* and in *B. groenlandica* normally grew proportionally more in breadth than in length, on account of which in these two species it is generally broader in large individuals than in smaller ones. As far as I can see, the same probably applies also to other species. Everything seems thus to show that the plate in question in the *Bothriolepinae* in general normally was broader in old individuals than in young ones. The anterior margin of the plate usually is about as broad as the posterior part of the centro-nuchal plate (text-figs. 98, 179C, 180A, 181C, 182), but may also often be broader (text-figs. 247–249, 261). This margin varies much in shape not only in different species, but also in various individuals of the same species (text-figs. 118–126, 280–282, 284, 285, 305A–C). Laterally it is as a rule clearly bounded off from the lateral margin of either side by a fairly well developed antero-lateral corner (*a*). Immediately behind this corner, on the foremost part of the anterior division of the lateral margin, we find a more or less marked concavity or facet, the postnuchal notch (*npn*, text-figs. 43, 44, 118–126, 238A, 247–249, 254, 268, 280–282, 284, 285, 305A–C), bounded behind by an obtuse, rounded lateral process, the external postlevator process (*pr.pl*),



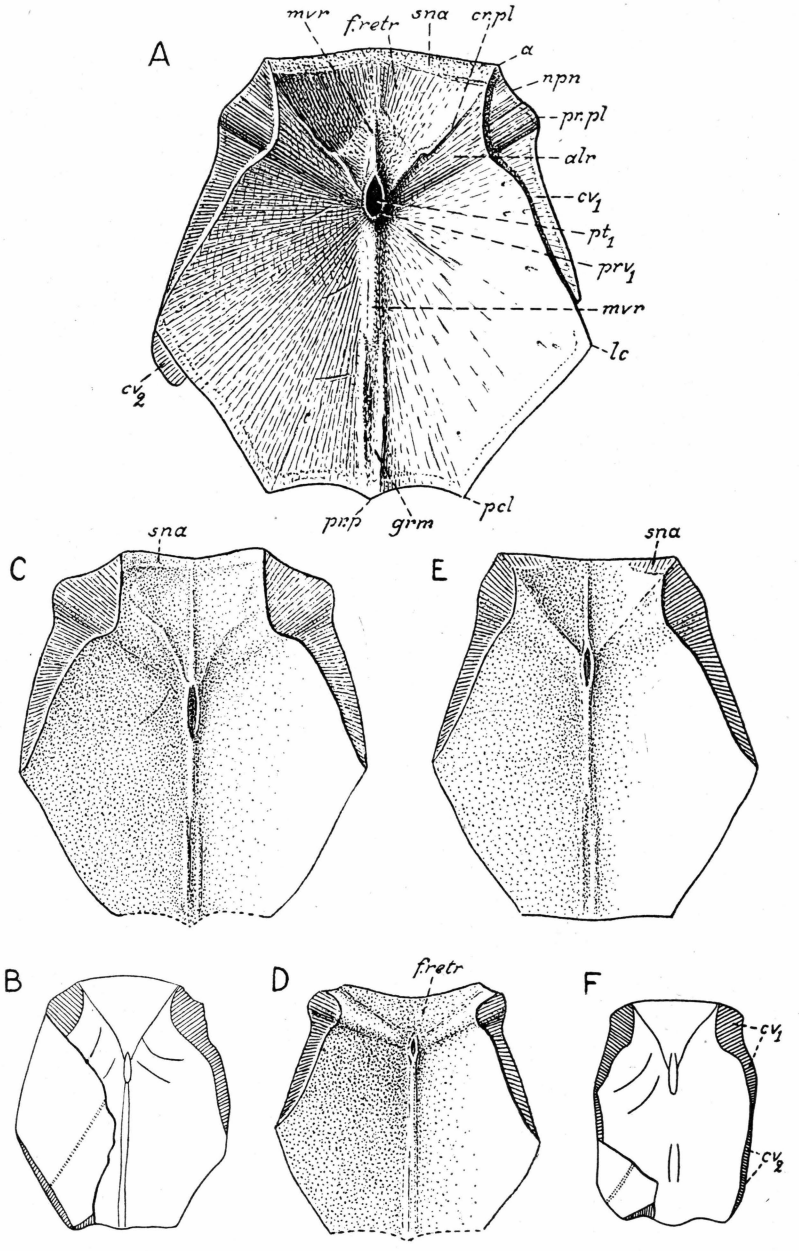
Text-fig. 43. Anterior median dorsal plates of four *Bothriolepis*-species and of *Grossilepis tuberculata*. Dorsal aspect. *A*, of a small individual of *Bothriolepis canadensis*, showing the special characters of young stages. × 5/3. *B*, of a large individual of *B. canadensis*. × 5/8. *C*, of a medium-sized individual of *B. groenlandica*. × 5/9. *D*, of *B. panderi*. From Gross 1941a. × 5/6. *E*, of *Grossilepis tuberculata*. From Gross 1941a. × 5/6.
a, antero-lateral corner; cd_2, cd_3, cd_4, areas overlapped by anterior dorsolateral plate, mixilateral plate and posterior median dorsal plate respectively; dlg_1, anterior oblique abdominal pit-line groove; dlg_2, posterior oblique abdominal pit-line groove; *dma*, tergal angle; *dmr*, dorsal median ridge; *lc*, lateral corner; *npn*, postnuchal notch; *otd*, obliquely transverse depression; *otr*, oblique transverse ridge; *pcl*, postero-lateral corner; *pr.p*, posterior median process; *pr.pl*, external postlevator process.

which lies in the straight antero-lateral continuation of the postlevator thickening (*alr*). Behind this process the anterior division of the lateral margin may be straight, slightly convex or even undulating. This division

of the lateral margin of the plate is thus developed in much the same way as in *Byssacanthus* (Gross 1940b, text-fig. 10), whereas, on the other hand, it differs clearly from the corresponding margin in *Asterolepis* and *Remigolepis*, which generally is somewhat convex throughout its extent and without marked notches or processes[1]). The posterior division of the margin in *Bothriolepis* normally is somewhat convex anteriorly and concave posteriorly, in *Grossilepis* convex throughout. The posterior margin of the plate in most cases is provided with a generally short posterior median process (*pr.p*), and in these cases it is usually concave on either side of the process. When the posterior median process is absent the posterior margin as a whole may be somewhat concave, practically straight, or even a little convex. The upper (external) face of the plate (text-figs. 38–40, 43) bears the anterior part of the dorsal median ridge (*dmr*) or crest. This crest, as we have seen, does not extend forwards on to the anterior margin of the plate, but always ends some distance behind it at a more or less clearly marked angle, the tergal angle (*dma*), already repeatedly referred to, which is situated straight above the anterior ventral process and pit. Like these structures, the tergal angle occupies a somewhat different position on the plate in the various species. In *B. gippslandiensis* (text-figs. 44D, 264, 265) it thus lies strikingly close to the anterior margin of the plate; in the majority of species, such as *B. canadensis*, *B. cellulosa*, *B. ornata*, *B. panderi*, *B. alvesiensis*, *B. hydrophila*, *B. leptocheira*, *B. lohesti*, *B. groenlandica*, *B. jarviki*, and in *Grossilepis*, it is situated further backwards, a little in front of, just at, or slightly behind, the transition between the anterior and middle thirds of the plate (text-figs. 38–40, 43, 121–124, 216, 224, 248, 249, 250A, 260, 262B, 268, 280A, C, D, F, 281A, B, 284, 285, 305A–C); and, finally, in *B. maxima* (text-fig. 238A), *B. gigantea* (text-fig. 254) and *B. obesa* (text-fig. 259A) it is found only a little in front of the middle of the plate. Anterorly to it the median part of the plate slopes more or less forwards. Towards this angle converge the posterior oblique abdominal pit-line grooves (dlg_2) and, in young individuals (text-figs. 43A, 121, 263, 280A, C, D, F) in addition also, the obliquely transverse ridges (*otr*), the anterior oblique abdominal pit-line grooves (dlg_1), and the obliquely transverse depressions (*otd*) above the postlevator thickenings.

As we known since long ago, the anterior median dorsal plate in *Bothriolepis* is normally connected with the anterior dorso-lateral and mixilateral plates in a manner corresponding to thats in *Pterichthyodes* and *Gerdalepis*, that is to say so, that it overlaps the anterior dorso-lateral plate in front of its lateral corner (*lc*), whereas it is overlapped by the mixilateral plate behind the said corner. Besides this normal type of sutural connection, however, we find in *Bothriolepis* also other, anomalous types of the sutural con-

[1]) In certain *Asterolepis*-species, e. g. *A. scabra* (Stensiö 1931, text-fig. 37; Nilsson 1941, text-fig. 10, pl. 8) there are fairly clear indications both of a postnuchal notch and of an external postlevator process. These two formations are probably normally present in *Pterichthyodes*.



Text-fig. 44. Anterior median dorsal plates of five *Bothriolepis*-species and of *Grossilepis tuberculata*. Ventral aspect. *A*, of *B. canadensis*. × $^5/_6$. *B*, of *B. panderi*. From Gross 1941 a. × $^5/_6$. *C*, of *B. gigantea*. Somewhat more than $^5/_{18}$ of the nat. size. *D*, of *B. gippslandiensis*. Restoration based on a photographic reproduction given by Hills in 1931. × $^5/_6$. *E*, of *B. groenlandica*. × $^5/_9$ of the nat. size. *F*, of *Grossilepis tuberculata*. From Gross 1941 a. × $^5/_6$. *a*, antero-lateral corner; *alr*, postlevator thickening; *cr.pl*, postlevator crista; cv_1, area overlapping anterior dorso-lateral plate; cv_2, area overlapping mixilateral plate; dlg_2, posterior oblique abdominal pit-line groove; *f.retr*, levator fossa; *grm*, ventral median groove; *lc*, lateral corner; *mvr*, ventral median ridge; *npn*, postnuchal notch; *pcl*, postero-lateral corner; *pr.p*, posterior median process; *pr.pl*, external postlevator process; prv_1, anterior ventral process; pt_1, anterior ventral pit; *sna*, supranuchal area.

nection between the anterior median dorsal plate and the anterior dorso-lateral and mixilateral plates. As recently shown by Gross (1941a, pp. 18–19) and as will be further demonstrated below in the systematic part of this work, anomalous types of this sutural connection in *Bothriolepis* occur even much more frequently than what could be supposed previously. Out of 130 specimens of *B. canadensis* examined by the writer the sutural connection in question thus appeared to be anomalous in no less tahn 47 specimens, that is to say in about 36% of the material. In *B. canadensis* it could also be established that anomalous types of the sutural connection in question occur only in trunk-armours where the dorsal wall is more than 4,5 cm long, and that these anomalous types are more frequently met with in large individuals than in medium-sized ones. As also in *B. groenlandica* the anomalous types both appeared and became fully pregnent first in smaller medium-sized individuals, one may be justified in concluding that this was the case also in all other *Bothriolepis*-species. The anomalous types of the sutural connection just under consideration in *Bothriolepis* in general in all probability began to develop, therefore, first at a certain definite stage of growth, after which they gradually became more common and more pronounced. Consequently the normal type of the sutural connection of the anterior median dorsal plate characteristic of *Bothriolepis* seems to be constantly found only in very young in dividuals.

The anomalous types of the sutural connection between the anterior median dorsal plate and the anterior dorso-lateral and mixilateral plates observed as yet in *Bothriolepis* are as follows: 1) The anterior median dorsal plate has its normal sutural connections with the two plates laterally to it, with the exception, however, that most anteriorly at the postnuchal notch it both overlaps, and is overlapped by, the posterior dorso-lateral plate. This anomalous type seems to be rather rare, being observed with certainty as yet only in certain cases in *B. cellulosa* (text-figs. 2A, 224E; Gross 1941a, p. 19, text-figs. 8D, 12B) and *B. maxima* (text-figs. 49, 238A). 2) The anterior median dorsal plate overlaps the anterior dorso-lateral plate for a long distance anteriorly, but is overlapped by this plate further posteriorly on one or on both sides, in front of its lateral corner (*lc*). Behind its lateral corner it is overlapped, as normally, by the mixilateral plate. This anomalous type is the one that occurs most frequently in *B. canadensis* (text-figs. 43B, 118C, 119F, 120A, 121F, J, 122A, B, E, 123A, B, D, 124A, 127, 130, 132, 133, 134, 147, 155, 157), but it is often found also in *B. cellulosa* (text-fig. 224C, G; cf. also Gross 1941a, p. 18, text-figs. 8B, 9C, F). In *Microbrachius* this type is the normal one, characteristic of the genus. Otherwise it is fairly often met with in *Remigolepis* (Stensiö 1931, pl. 14, fig. 2; pl. 15, fig. 2) and may also occur in *Asterolepis* (*A. estonica*, Gross 1940, p. 23, text-fig. 4E). 3) The anterior median dorsal plate overlaps the anterior dorso-lateral plate in normal extent. In addition behind its lateral corner, on one or on

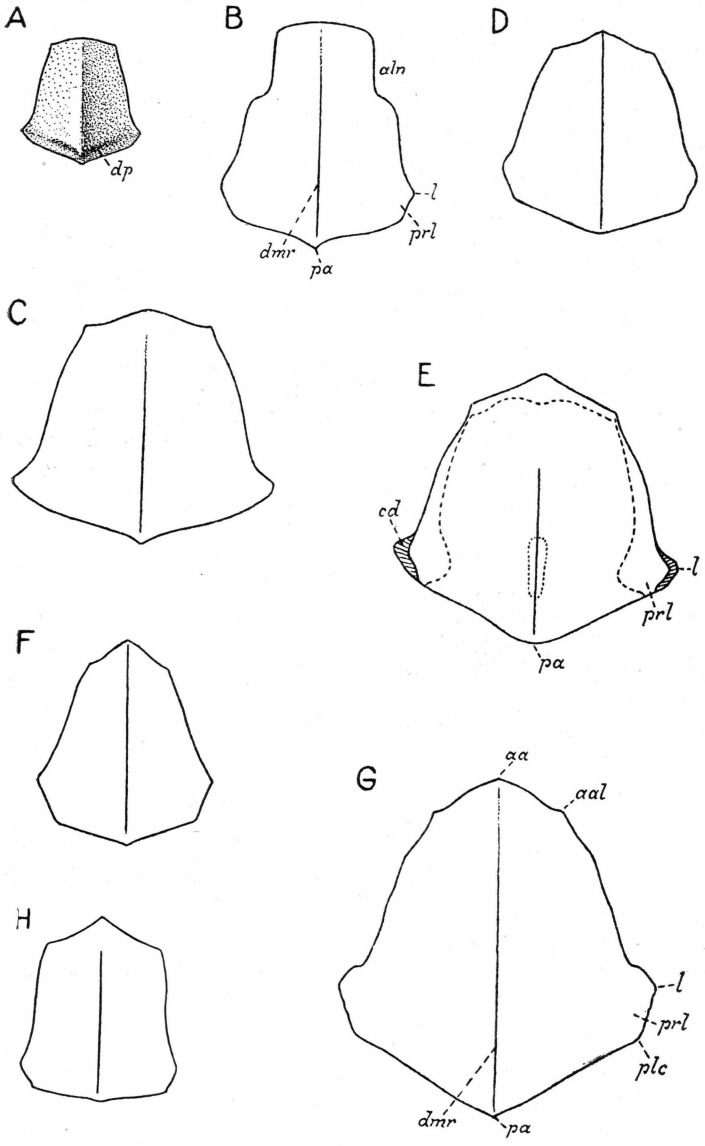
both sides, it overlaps also an anterior area of the mixilateral plate. On one or on both sides it is thus overlapped by the mixilateral plate to a smaller extent than normally. This anomalous type has been found in *B. canadensis*, *B. cellulosa*, *B. maxima*, *B. alvesiensis*, *B. hydrophila*, *B. groenlandica* and *B. jarviki* (text-figs. 101, 109, 115, 118D, 119A, D, 121D, G, M, 122D, 124C, 131, 144B, 159, 224A, 238A, 248, 249, 262B, 282A, 284, 285A, B, D, 305C). As we known, it is characteristic of *Remigolepis* (Stensiö 1931, pp. 77, 170–172, text-figs. 82, 89), but it may occur also in *Gerdalepis* (Gross 1937, pp. 12–14, text-fig. 7A; 1941a, p. 18; 1941b, p. 199). 4) The abnormal sutural connections referred to above as 2 and 3 occur combined. This type has as yet been noticed only in *B. canadensis* (text-figs. 44A, 119E, 120B, 122F, 123C, 124B, 156). 5) The anterior median dorsal plate overlaps the anterior dorso-lateral plate only anteriorly. Further backwards it abuts against the remaining posterior part of the anterior dorso-lateral plate and against the mixilateral plate only with its very lateral edge. Except most anteriorly its sutural connection with the anterior dorso-lateral and mixilateral plates is thus a typical harmony. This anomalous type is very rare, being met with only in one case in *B. cellulosa* (text-fig. 224J; cf. also Gross 1941a, p. 18, text-fig. 8C). It has otherwise been found only in *Grossilepis*.

In *Grossilepis* (text-figs. 44F, 268E, G; Gross 1941a, pp. 42–43, text-fig. 30) the anterior median dorsal plate normally overlaps both the anterior dorso-lateral and mixilateral plates about in the same manner as in *Asterolepis*. However, its overlapping of the mixilateral plate is much less extensive than in *Asterolepis*. Besides this normal type, the anterior median dorsal plate in *Grossilepis* may also show two anomalous types of the sutural connection here in question. These two anomalous types, which have been distinguished and described by Gross (1941a, p. 43), are as follows. *A*) The anterior median dorsal plate overlaps the anterior dorso-lateral plate, but along a very narrow area is overlapped by the mixilateral plate. This abnormal type, which is the normal one in *Bothriolepis*, seems to be fairly common (Gross 1941, pl. 25, figs. 1, 2, 5). *B*) The anterior median dorsal plate overlaps the anterior dorso-lateral plate, whereas it is connected with the mixilateral plate only by means of its very edge; hence it does not overlap the latter plate; nor is it overlapped by it (text-fig. 268F; cf. also Gross 1941a, text-fig. 30B, pl. 21, fig. 3). This abnormal type seems not to be as common as type *B*. As we have already seen, it occurs very rarely in *Bothriolepis* too.

As normally in the *Antiarchi*, the anterior median dorsal plate in *Bothriolepis* and *Grossilepis* generally is overlapped by the posterior median dorsal plate. However, in *B. maxima* it may also to a certain extent overlap the posterior median dorsal plate (text-fig. 238A, cv_3).

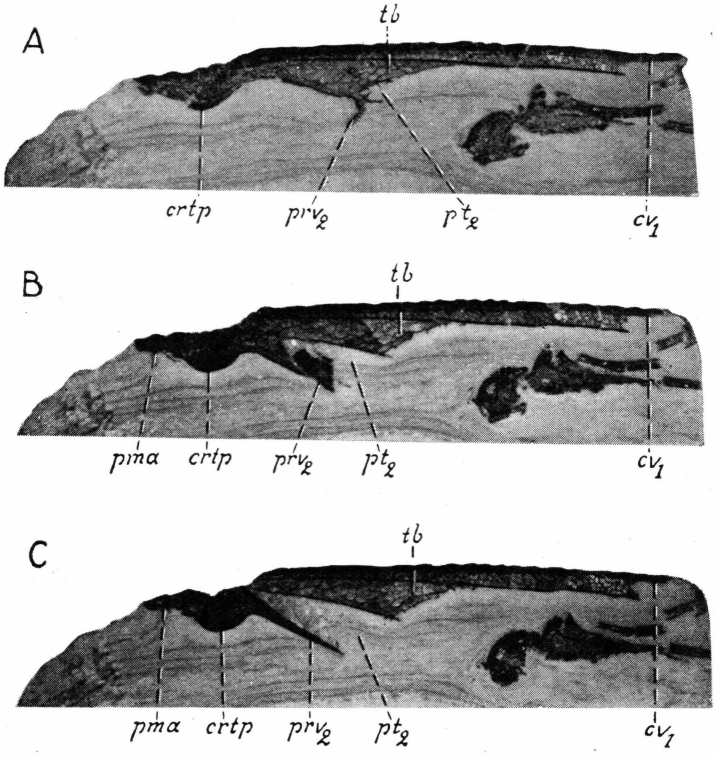
The posterior median dorsal plate (*Pmd*, text-figs. 38–40, 45–47, 88, 90–92, 95–98, 101, 102, 106, 109, 115–117, 127–143, 146–149, 151B, 154–159, 199–201, 207, 217, 225, 231A, 238B, 239, 248, 249, 264, 269, 286, 287A,

305 D, 308) is of fundamentally the same shape as in other *Antiarchi*-forms. It is thus four-sided, but, as in many cases it narrows considerably forwards, it often tends to be somewhat triangular in outline. Postero-laterally on either side it is always produced into a well pronounced, lateral process (*prl*, text-figs. 45, 47), which mostly is broad and generally ends with a marked lateral corner (*l*). In *B. canadensis* (text-figs. 137 C, 138, 139) and *B. groenlandica* (text-figs. 286, 287 A) it is obvious that during its growth the plate increased proportionally somewhat more in breadth than in length. As this seems to have been the case in several other *Bothriolepis*-species too, we may be justified in concluding that the plate in question in the *Bothriolepinae* in general normally is somewhat broader in fully mature individuals than in immature ones. The plate is always broadest across the lateral corners (*l*) of its lateral processes (*prl*), where its breadth seems never to be less than three fourths of the length. It is very variable, however, as to its breadth. In certain species it is narrower than long both in immature and mature individuals, in other species it is about as broad as long or broader than long in all stages of growth of the individuals, whereas, finally, in several species it is normally narrower than long in immature individuals, but broader than long in fully mature individuals. In *B. groenlandica* (text-figs. 45 F, G, 47 C, 286, 287 A), *B. ornata* (text-fig. 217), and at least to some extent also *B. jarviki* (text-fig. 305 D), the plate is mostly considerably narrower in its foremost parts, in front of its lateral processes (*prl*), than what is usually the case in the other species. In consequence both of this and of its usually fairly small maximum breadth the plate as a whole in the said three species is often of a strikingly narrow type. The anterior margin of the plate varies considerably in shape both in different species and in various specimens of the same species. It is often more or less produced into an anterior corner or angle (*aa*), but it may also frequently be more or less convex and devoid of an anterior corner or angle (text-figs. 45, 47). The antero-lateral corner (*aal*) is always well developed. The by far longer anterior part of the lateral margin situated in front of the lateral process (*prl*) normally as a whole is a little convex, often, however, with a slight concavity at the anterior end and just in front of the lateral process. Anteriorly on one or on both sides this part of the lateral margin may not rarely present a more or less deep notch, the mixilateral notch (*aln*, text-figs. 45 B, 138 M, P, Q, 139 A–D, 286 F, G, 287 A), which fortuitously (*B. canadensis*) may be represented by two or more smaller notches (text-fig. 138 Q). The hindmost part of the lateral margin situated on the lateral process is often somewhat long and a little concave or convex, but may also not rarely be very short and convex (text-figs. 45, 47). The postero-lateral corner (*plc*) is mostly well marked, but may also sometimes be somewhat rounded off. The posterior margin is always convex and generally produced into a more or less pronounced posterior median corner (*pa*), which sometimes may tend to be elongated into a short



Text-fig. 45. Restorations of posterior median dorsal plates of four species of *Bothriolepis*, and of *Grossilepis*. Dorsal aspect. *A*, of a very small individual of *Bothriolepis canadensis*. × $^5/_3$. *B*, of a medium-sized individual of *B. canadensis*. × $^5/_6$. *C*, of a large individual of *B. canadensis*. × $^5/_9$. *D*, of a small individual of *B. cellulosa*. From Gross 1941a. × $^5/_3$. *E*, of a large individual of *B. cellulosa*. From Gross 1941a, × $^5/_9$. *F*, of a small specimen of *B. groenlandica*. × $^5/_6$. *G*, of a large individual of *B. groenlandica*. × $^5/_9$. *H*, of *Grossilepis tuberculata* from Gross 1941a. × $^5/_6$.

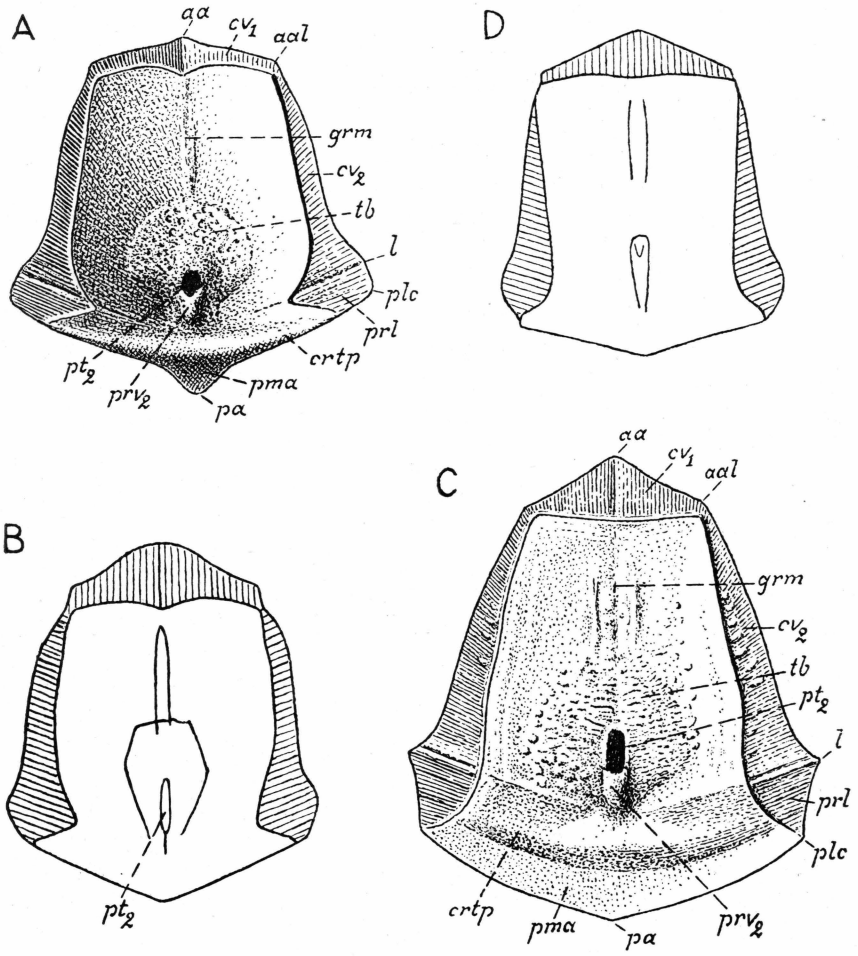
aa, anterior corner or angle; *aal*, antero-lateral corner; *aln*, mixilateral notch; *cd*, area overlapped by mixilateral plate; *dmr*, dorsal median ridge; *dp*, groove above the median dorsal part of the crista transversalis interna posterior (normally present only in very young individuals); *l*, lateral corner or angle; *pa*, posterior corner or angle; *plc*, postero-lateral corner; *prl*, lateral process.



Text-fig. 46. *Bothriolepis canadensis.* A–C, three rostro-caudal sections through the median part of a posterior median dorsal plate. *A*, the most lateral, *C*, the most medial one of the sections. × $^{2}/_{1}$.
crtp, crista transversalis interna posterior; cv_1, area overlapping posterior median dorsal plate; *pma*, posterior marginal area; prv_2, posterior ventral process; pt_2, posterior ventral pit; *tb*, ventral tuberosity.

process, whereas in other cases it may be almost reduced. In *B. groenlandica* it may sometimes even be entirely absent. In one specimen of *B. canadensis*, where, the corner in question is absent, the median part of the posterior margin of the plate is occupied by a marked concavity (text-fig. 137A, B).

The posterior median dorsal plate normally overlaps both the anterior median dorsal plate and the mixilateral plate, quite as is the case in *Pterichthyodes*, *Asterolepis* and *Remigolepis*. It is now fully clear, however, that it may vary considerably with regard to its connection with the mixilateral plate and that this is the case particularly when it exhibits a mixilateral notch. Along this notch it may sometimes abut against the mixilateral plate only with its very lateral edge, whereas in other cases it slightly overlaps the mixilateral plate, or else connects with that plate in a more complicated manner. Even when devoid of a mixilateral notch it may sometimes in *B. cellulosa* (text-figs. 45E, 225E; cf. also Gross 1941a, p. 20, text-figs. 11D, 12C), *B. maxima* (text-fig. 239) and *B. groenlandica* (text-fig. 286F, J, K)



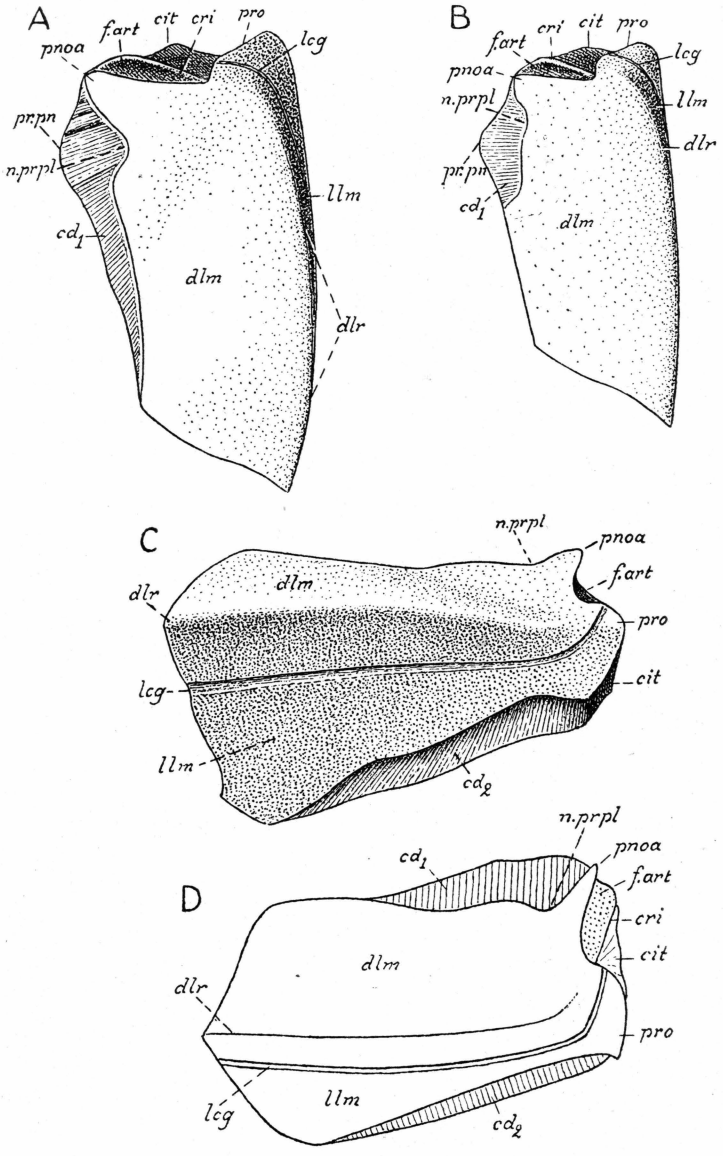
Text-fig. 47. Restoration of the posterior median dorsal plate of four species. Ventral aspect. *A*, of an individual of *B. canadensis* in which the ventral median groove is just developing. × $^3/_2$. *B*, a large individual of *B. panderi*, from Gross 1941a. × $^1/_2$. *C*, of al medium-sized individual of *B. groenlandica*. × $^1/_1$. *D*, of *Grossilepis tuberculata*, from Gross 1941a. × $^1/_1$.

aa, anterior corner; *aal*, antero-lateral corner; *crtp*, crista transversalis interna posterior (median dorsal part); cv_1, area overlapping anterior median dorsal plate; cv_2, area overlapping mixilateral plate; *grm*, ventral median groove; *l*, lateral corner; *pa*, posterior corner or process; *plc*, postero-lateral corner; *pma*, posterior marginal area; *prl*, lateral process; prv_2, posterior ventral process; pt_2, posterior ventral pit; *tb*, ventral tuberosity.

both overlap, and be overlapped by, the mixilateral plate. In *B. maxima* and *B. groenlandica* its overlapping by the mixilateral plate may often be so considerable that from the antero-lateral corner (*aal*) et extends backwards to a point on the lateral process (*prl*) somewhat behind the lateral corner (*l*). As has been pointed out, the plate in *B. maxima* is sometimes a little overlapped anteriorly by the anterior median dorsal plate (text-fig. 239, cd_1).

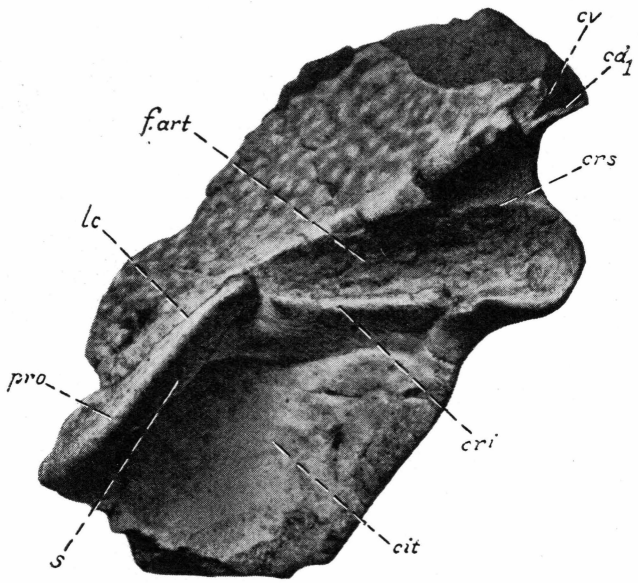
Those plates in the *Bothriolepinae* which take part in the formation of the lateral wall of the trunk-armour, that is to say the anterior dorso-lateral, mixilateral, anterior, ventro-lateral and posterior ventro-lateral plates, are mostly much crushed and compressed, and hence they are not nearly as completely known as the anterior and posterior median dorsal plates. As normally in the group, these plates consist of two laminae. The anterior dorso-lateral and mixilateral plates are thus composed of dorsal and lateral laminae, meeting at the dorso-lateral ridge, whereas the posterior and posterior ventro-lateral plates consist of lateral and ventral laminae, connected at the ventro-lateral ridge. As in *Pterichthyodes*, *Asterolepis* and *Remigolepis* (Traquair 1894–1906, pp. 103–104; Stensiö 1931, text-figs. 84, 85; 1938, p. 14, text-fig. 5; cf. also the account of the *Remigolepidae* in Part III of this monograph), the four plates here under consideration may vary considerably in their proportions in different individuals of one and the same species. In certain cases the anterior dorso-lateral and anterior ventro-lateral plates may thus be relatively short and broad and the mixilateral and posterior ventro-lateral plates relatively long and narrow, whereas in other cases these plates are developed in the reverse way (text-figs. 48, 50, 51, 53, 153, 166, 174, 179–183, 227, 238C, 270, 288, 289, 291; cf. also Gross 1941a, text-figs. 13, 14, 32–35). The anterior and posterior median dorsal plates are also influenced to some extent by these variations. This is particularly the case with the posterior median dorsal plate, which is clearly longer and narrower in those individuals where the mixilateral and posterior ventro-lateral plates are long than in those individuals where these two plates are short.

The anterior dorso-lateral plate (*Adl*, text-figs. 38–40, 48, 49, 88, 90–92, 95–98, 101–102, 106, 109, 115–117, 127–134, 140–149, 151, 152, 154–159, 179–183, 226, 238C, 247–249, 261, 264, 270A–C, 288, 308) in its general characters is much as in the other *Antiarchi*. However, it is normally broadest across its posterior part, and not, as in *Asterolepis*, *Pterichthyodes* and *Gerdalepis* (Gross 1941b, text-fig. 11; exception cf. Gross 1933b, text-fig. 1C), across its anterior part. The dorsal lamina always is broadest across its foremost part, more precisely, across the dorso-lateral ridge and the internal postlevator process (*pr. pn*, text-fig. 48) to be described below. Its lateral lamina is highest across its hindmost part somewhat in front of the suture with the mixilateral plate, and not, as in *Asterolepis*, *Pterichthyodes* and *Gerdalepis*, across its middle or foremost parts. The latter lamina is of a fairly different relative height in the various species. In several species, e.g. *Bothriolepis canadensis* (text-figs. 48C, 144A, 145B), *B. cellulosa* (text-fig. 226), *B. obesa* (text-fig. 259B), *B. cristata* (Traquair 1894–1906, pl. 31, fig. 2), *B. jarviki* (text-fig. 304), and perhaps also *B. alvesiensis*, it is thus relatively high and short, whereas in other species, such as *B. maxima* (text-fig. 238C), *B. gigantea*, *B. groenlandica* (text-fig. 287B, 288) it is low and long. When looked at from above the anterior margin of the plate is a little



Text-fig. 48. Restorations of four anterior dorso-lateral plates. *A*, *B*, *C* of *B. canadensis* in dorsal and lateral aspects. × $^5/_4$. *D*, of *Grossilepis tuberculata*, in dorso-lateral aspect. Gross 1941a. × $^5/_3$.

cd_1, area overlapped by anterior median dorsal plate; cd_2, area overlapped by anterior ventro-lateral plate; *cit*, vertical part of the crista transversalis interna anterior, forming an anterior transverse lamina; *cri*, infraarticular crest; *dlm*, dorsal lamina; *dlr*, dorso-lateral ridge; *f.art*, articular fossa; *lcg*, main lateral line groove; *lm*, lateral lamina; *n.prpl*, notch in the dorsal margin of the ornamented area for the external postlevator process (*pr.pl*) of the *Amd*-plate; *pnoa*, postnuchal ornamented corner; *pro*, processus obstans; *pr.pn*, internal postlevator process.



Text-fig. 49. *Bothriolepis maxima.* A fragmentary right anterior dorso-lateral plate in anterior and somewhat medial view, showing the dorsal portion of the upper vertical part of the crista transversalis interna anterior with the articular fossa fot he paranuchal trochlea and the medial face of the processus obstans with the area of »Siebknochen«. Specimen No. P. 3357 in the Swedish Museum of Natural History, Stockholm. × $^1/_1$. cd_1, area overlapped by anterior median dorsal plate; *cit*, upper vertical part of crista transversalis interna anterior, forming an anterior transverse lamina; *cri*, infraarticular crest; *crs*, supraarticular crest; *cv*, area overlapping an anterior lateral area of the anterior median dorsal plate; *f.art*, articular fossa for paranuchal trochlea; *lc*, main lateral line groove; *pro*, processus obstans; *s*, »Siebknochen«-area on lower (internal) face of processus obstans.

concave, or sometimes almost straight, in its uppermost part, which lies dorsally to the processus obstans (text-fig. 39). The processus obstans (*pro*, text-figs. 48, 49), as in the other *Antiarchi*, is formed both by the dorsal and lateral laminae of the plate, and, as already pointed out, projects freely forwards laterally to the upper part of the vertical, lateral division of the crista transversalis interna anterior (*cit*), immediately below the articular fossa (*f.art*) for the paranuchal trochlea of the head-shield (text-figs. 49, 144C, 145A). This process constantly is much broader than in *Asterolepis* (cf. Gross 1933b, text-fig. 3) and *Remigolepis* (cf. Part III of this work), but it is probably not quite as broad as in *Microbrachius* (cf. Watson 1935, text-fig. 28). It extends downwards to the anterior, ventral end of the area (cd_2), overlapped by the anterior ventro-lateral plate, and thus reaches as far ventrally that to some extent it forms an anterior boundary of that area. Contrary to what is the case in *Asterolepis* (Gross 1933b, text-fig. 3A) it was not overlapped in its ventral part by the postmarginal plate, but articulated only against the subobstantic area (*soa*) of the head-shield, which it covers completely when the head is in a maximally lowered position. In *B. canadensis*

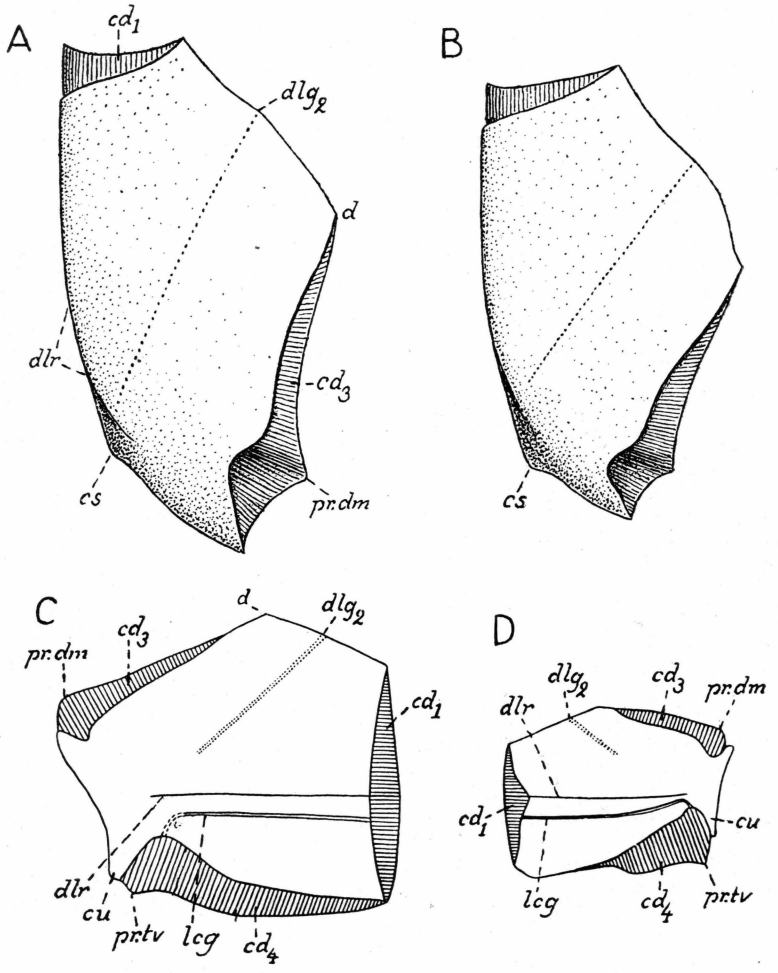
and *B. maxima* the medial (internal) face of the process is provided with a fairly large "Siebknochen"-area (*S*, text-fig. 49; cf. Gross 1931, pp. 16–19; 1935, pp. 23–24) in its dorso-medial and middle parts, whereas it is devoid of "Siebknochen" on its ventro-lateral part. A corresponding "Siebknochen"-area was certainly present also in other *Bothriolepinae*. As is obvious from the extent of this "Siebknochen"-area and from the distribution of "Siebknochen" on the subobstantic area (cf. pp. 46–47 above), the processus obstans was in real articular connection only with the longer posterior part of the subobstantic area. The part of the crista transversalis interna anterior (*cit*, text-figs. 48, 49) which lies on the plate here under consideration is so strongly developed that, as we have seen (pp. 108–110 above), it forms a broad transverse lamina of bone. This condition beyond question is due to the fact that this part of the crest bears the strong and broad articular fossa for the paranuchal trochlea of the head-shield. This fossa (*f.art*, text-figs. 48, 49, 144, 145A) stretces across the uppermost broadest part of the crista transversalis interna just medially to the upper (dorso-medial) margin of the processus obstans and lies so that, as in other *Antiarchi*, its axis of length is transversal and practically horizontal. As is clearly seen in *B. canadensis* (text-figs. 144C, 145A) and *B. maxima* (text-fig. 49), it is highest at its medial end, lowest at its lateral end, and not the reverse, as in *Asterolepis* (Gross 1931, pl. 5, fig. 4) and *Remigolepis* (cf. Part III of this work). With regard to its shape it is thus fully in harmony with the paranuchal trochlea (cf. p. 63). In *B. canadensis* it is bounded only by an infraarticular crest (*cri*), in *B. maxima*, on the other hand, also by a supraarticular crest (*crs*). The dorsal (dorso-medial) margin of the plate as a whole is more or less convex anteriorly, but somewhat concave posteriorly. The convexity in its foremost part is due to the fact that it is mostly produced there into a broad, rounded dorso-medial process (*pr.pn*, text-fig. 48A, B, D), which, as it is overlapped by the external postlevator process (*pr.pl*) of the anterior median dorsal plate, will be referred to as the internal postlevator process. This process on its lower side shows a thickening which lies in the straight lateral continuation of the postlevator thickening (*alr*) of the anterior median dorsal plate, constituting the antero-lateral part of that thickening. The process seems normally to be present in *Bothriolepis*, whereas, on the other hand, it is often obscure or absent in *Grossilepis*. The posterior margin of the plate is divided by a marked posterior corner at the dorso-lateral ridge into an upper and a lower part, corresponding to the dorsal and lateral laminae respectively of the plate. The upper part of this margin, which faces posteriorly and somewhat medially, may be fairly straight, a little convex, or else somewhat convex medially and concave laterally. The ventral part of the same margin, which faces fairly straight backwards, or backwards and more or less ventrally, may be fairly straight, a little concave or a little convex. Finally, the ventral margin of the plate is always directed downwards and a little for-

wards. It is often somewhat concave anteriorly and convex posteriorly, but it may also as a whole be convex or almost straight. The corners of the plate are always clearly distinguishable, but may often be more or less rounded off.

Just opposite the base of the internal postlevator process the area (cd_1) overlapped by the anterior median dorsal plate generally extends more or less far laterally into the upper margin of the exposed ornamented area of the plate, forming a more or less marked notch-like depression (*n.prpl*, text-fig. 48A, B). This notch-like depression is developed for the external postlevator process (*pr.pl*) of the anterior median dorsal plate. When the last-mentioned plate is in its position and fills up the notch-like depression here in question the anterior dorso-medial corner of the exposed ornamented area of the plate seemingly constitutes an anterior dorso-medial process. This seeming process (*pnoa*, text-figs. 39, 48, 49, 98, 101, 129, 144, 145C, 179–183, 226, 238C, 247–249, 270A–C, 288), which is received by the postnuchal notch (*npn*) of the anterior median dorsal plate, will be referred to as the postnuchal ornamented corner.

The sutural connections between the anterior dorso-lateral plate and the anterior median dorsal plate have already been dealt with above (pp. 118–121), and, as we have seen, they, are somewhat different in *Bothriolepis* and *Grossilepis* and by far not as constant as has previously been assumed. With regard to its sutures with the other adjacent plates the anterior dorso-lateral plate is on the whole as normally in the *Antiarchi*, that is to say, it overlaps the mixilateral plate and is normally overlapped by the anterior ventro-lateral plate. However, at least in *B. groenlandica* (text-fig. 288), *B. maxima* (cf. p. 451) and *B. canadensis* (text-fig. 48C) it is not simply overlapped by the anterior ventro-lateral plate, but also at the same time overlaps that plate for a considerable stretch behind the processus obstans. This overlapping is particularly well developed in *B. groenlandica*, whereas it is mostly less pronounced in *B. canadensis*. This complicated type of sutural connection between the plate in question here and the anterior ventro-lateral plate will certainly be found also in other *Bothriolepis*-spices. The connection with the distalmost part of the anterior ventro-lateral plate in *B. canadensis*, *B. groenlandica* and *Grossilepis tuberculata* often is only a harmony. In several cases the very posterior ventral corner of the plate is in contact with the antero-dorsal corner of the posterior ventro-lateral plate, whereas in other cases it is probably entirely separated from that corner by the mixilateral and anterior ventro-lateral plates.

The mixilateral plate (*Mxl*, text-figs. 38–40,50, 88, 90–92, 95–98, 101, 102, 106, 109, 115–117, 127–134, 137A, B, 140–143, 146–150, 151B, 152–159, 179–183, 227, 238F, G, 248, 249, 256, 259B, 261, 264, 270D–J, 289, 304) in *Bothriolepis* extends considerably further dorso-medially in the dorsal wall of the trunk-armour than what normally it does in *Grossilepis* (text-fig. 39; cf. also Gross 1941a, text-figs. 17, 36). In *Bothriolepis* its dorsal



Text-fig. 50. Restorations of the mixilateral plate in three *Bothriolepinae*. *A*, *B*, of *Bothriolepis canadensis*, in dorsal aspect. × $^1/_1$. *C*. of *B. cellulosa* in lateral aspect (much flattened). From Gross 1941a. × $^1/_1$. *D*, of *Grossilepis tuberculata*. From Gross 1941a. × $^1/_1$. cd_1, area overlapped by anterior dorso-lateral plate; cd_3, area overlapped by mixilateral plate; cd_4, area overlapped by posterior ventro-lateral plate; *cs*, corner between the dorsal and lateral laminae; *cu*, postero-ventral ornamented corner; *d*, dorsal corner; dlg_2, posterior oblique abdominal pit-line groove; *dlr*, dorso-lateral ridge; *lcg*, main lateral line-groove; *pr.dm*, medial dorsal process; *pr.tv*, postero-ventral process.

lamina is clearly broader than the exposed ornamented area of the dorsal lamina of the anterior dorso-lateral plate, whereas, in *Grossilepis*, on the other hand, its dorsal lamina is about equally broad as, or only slightly broader than, the said area of the dorsal lamina of the anterior dorso-lateral plate. The plate is always broadest at a transverse plane across its dorsal corner, (*d*) and this also applies to its dorsal lamina. The lateral lamina sometimes is highest close to its anterior end (*Bothriolepis canadensis, B. cellulosa*), sometimes at its posterior end (*B. groenlandica*), but may also be of about

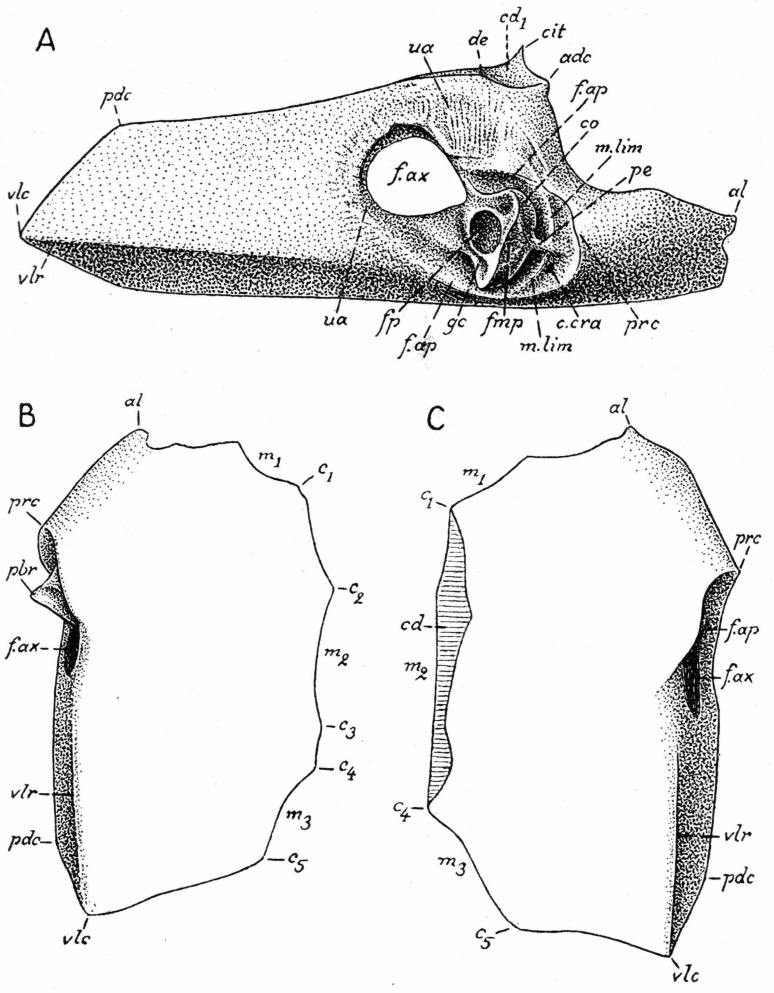
the same height anteriorly and posteriorly (*B. obesa, Grossilepis tuberculata*). As to its height in the various species this lamina is approximately as the corresponding lamina of the anterior dorso-lateral plate. It is thus comparatively high in proportion to its length for instance in *B. canadensis* (text-figs. 150B, D, 152, 153F, G), *B. cellulosa* (text-figs. 50C, 227), *B. obesa* (text-fig. 259B), *B. cristata* (Traquair 1894–1906, pl. 31, fig. 2), *B. jarviki* (text-fig. 304) and perhaps also *B. alvesiensis* (text-fig. 251), but relatively low for instance in *B. maxima, B. gigantea* (text-fig. 256) and *B. groenlandica* (text-figs. 287B, 289). The anterior margin of the plate as a whole normally is somewhat convex with a more or less marked anterior corner at the transition between the dorsal and lateral laminae. The dorsal margin is divided by the more or less pronounced dorsal corner (*d*) into anterior and posterior divisions, connected with the anterior and posterior median dorsal plates respectively. The anterior one of these divisions may be a little undulating in different ways, or else practically straight, whereas the posterior division is more varying in its configuration, being as a whole convex, concave, fairly straight, or slightly undulating. In its hindmost part the latter division is often produced dorso-medially into a medial dorsal process (*pr.dm*), which is situated underneath, and is covered by, the lateral process (*prl*) of the posterior median dorsal plate (text-figs. 50, 137A, B, 150A, C, 151B, 153A–E, 227, 270D–J, 289). The medial dorsal process is mostly well developed, but may also be obscure or absent (*B. groenlandica, Grossilepis tuberculata*). The posterior margin of the plate is always more or less concave. Finally, the ventral margin of the plate may be somewhat convex, somewhat concave, fairly straight or undulating. The postero-ventral corner of the plate is mostly produced downwards into a broad, more or less marked process, the postero-ventral process (*pr.tv*), which is overlapped by the postero-dorsal corner of the posterior ventro-lateral plate. The other corners of the plate are also well pronounced. The postero-dorsal one may often be extended into a process, more or less clearly bounded off from the medial dorsal process (*pr.dm*). The dorsal lamina of the plate is crossed on its outside by the posterior part of the posterior oblique abdominal pit-line groove (dlg_2). The dorso-lateral ridge (*dlr*) does not extend as far back as to the posterior margin of the plate, but disappears always some distance in front of this margin. Opposite the bases of both the medial dorsal process (*pr.dm*) and the postero-ventral process (*pr.tv*) the exposed ornamented area of the plate is always relatively narrow, much narrower than in front, and narrower also than across its hindmost part. That this is so is due to the fact that the area under consideration at this place has two pronounced notches a dorsal one, developed for the lateral process (*prl*) of the posterior median dorsal plate, and a ventral one, occupied by the dorsal corner (*dc*, text-figs. 40, 53, 264, 287B, 304) of the posterior ventro-lateral plate. When the plate is in its natural position in the lateral wall of the trunk-armour, the part of its ornamented

area that lies behind the ventral one of the two notches just mentioned extends downwards as a process-like formation behind the dorsal corner of the posterior ventro-lateral plate. This process-like formation, which will be termed the postero-ventral ornamented corner (*cu*), is somewhat differently developed in various species, being relatively small in *B. canadensis* (text-fig. 153F, G), *B. cellulosa* (text-figs. 50C, 227), *B. obesa* (text-fig. 259B), *B. gippslandiensis* (text-fig. 264), *B. groenlandica* (text-figs. 287B, 289), and *Grossilepis tuberculata* (text-figs. 50D, 270D–F), but relatively large in *B. maxima* and *B. alvesiensis*? (text-fig. 251).

The sutural connection of the mixilateral plate with the anterior and posterior median dorsal plates has already been exhaustively described above (pp. 118–121, 124–125) and it is, therefore, superfluous to enter upon it here. As we have seen, this sutural connection is not only differently developed in *Bothriolepis* and *Grossilepis*, but is also much more variable in the various *Bothriolepis*-species than what could be supposed previously (cf. also below pp. 211–214). As normally in the *Antiarchi*, the plate both in *Bothriolepis* and *Grossilepis* is overlapped by the anterior dorso-lateral plate. In *Bothriolepis*, as in other *Antiarchi*, it is overlapped also by the posterior ventro-lateral plate, but in certain *Bothriolepis*-species (*B. maxima*, *B. groenlandica*) we find that its relations to the posterior ventro-lateral plate may be more complicated in that at the same time it may both be overlapped by, and to some extent also overlap, the posterior ventro-lateral plate (*pdc*, text-fig. 289). In *Grossilepis* the plate varies much more as to its connection with the posterior ventro-lateral plate than in *Bothriolepis*. In *Grossilepis* it is often overlapped by the posterior ventro-lateral plate only in its posterior half, whereas anteriorly it meets that plate only with its very ventral edge, without any overlappings. In other cases, as in *Bothriolepis*, it may be overlapped by the posterior ventro-lateral plate practically along its whole ventral margin. Finally, when attached anteriorly to the posterior ventro-lateral plate only by its very edge, it may posteriorly both overlap, and be overlapped by, that plate (Gross 1941a, pp. 45–46).

The anterior ventro-lateral plate (*Avl*, text-figs. 4, 8, 34, 38, 40, 41, 51, 52, 160–169, 173, 175, 176, 178, 241, 242, 243A, 270K, 290, 291, 292B, 304) in its general shape is essentially as in other *Antiarchi*. Its most distinctive characters are as follows. It is broadest as a rule at a transverse plane approximately through or near its antero-dorsal corner (*adc*), and not fairly far behind this corner, as is normally the case in *Pterichthyodes*, *Asterolepis* and *Remigolepis*. The lateral lamina is always highest at, or in front of, its dorsal corner, but not about equally high throughout its length, as in *Gerdalepis* (Gross 1933b, text-fig. 1C, D; 1941b, text-fig. 11), or highest in its posterior part, as in *Pterichthyodes* (text-fig. 61; cf. also Traquair 1894–1906, text-fig. 36; Watson 1935, text-fig. 27), *Asterolepis* (Traquair 1894–1906, text-fig. 39; Gross 1931, text-figs. 11, 18; Nilsson 1941, text-fig. 8)

and *Remigolepis* (cf. Part III of this work). The ventral lamina is broadest along a transverse line through its prepectoral corner (*prc*) or close behind this corner (text-figs. 41, 51B, C, 52, 166A–D, 291, 292B), but not across its middle or further posteriorly, as in the *Pterichthyodes*, *Asterolepis* and *Remigolepis*. In the normal way characteristic of the *Antiarchi* in general the ventral lamina in most cases is somewhat broader in the plate of the right side than in that of the left side. In the position of its total maximum breadth, in the position of the maximum height of its lateral lamina, and in the position of the maximum breadth of its ventral lamina the plate thus clearly differs from the corresponding one in *Pterichthyodes*, *Asterolepis* and *Remigolepis*, whereas, on the other hand, in all these characters it approaches the one in *Ceraspis* (Gross 1937, text-figs. 10B, C, 11B). The anterior margin of the lateral lamina of the plate is more or less concave and, as normally in the *Antiarchi*, it passes over ventrally into the free lateral (dorso-lateral) margin of the subcephalic division of the ventral lamina (text-figs. 4, 40, 51). The dorsal margin of the plate normally as a whole is a little convex and may often on the external edge, near its anterior end, show a low corner, the dorsal corner (*de*) already referred to. The posterior margin of the plate, which is formed by both the lateral and ventral laminae, as a whole is convex with a marked corner, the posterior ventro-lateral corner (*vlc*, text-figs. 51B, C, 52), at the ventro-lateral ridge and thus at the transition between the two laminae. As to its detailed configuration this margin is very variable. The free anterior and lateral margins of the subcephalic division of the ventral lamina have already been dealt with above in the general description of the ventral wall of the trunk-armour (pp. 106–107), and it is, therefore, superfluous to enter upon them here. Finally, the ventro-medial margin of the plate, that is to say the medial margin of the ventral lamina, may for the description be regarded as consisting of three divisions, an anterior (m_1), connected with the semilunar plate, a middle (m_2), connected with the corresponding division of the plate of the opposite side, and a posterior (m_3), connected with the median ventral plate (text-figs. 41, 51B, C, 52, 166A–D, 270K, 291, 292B). The anterior one (m_1) of these divisions is shorter than the other two. It is always shorter and more medially directed than in *Pterichthyodes*, *Asterolepis* (cf. Traquair 1894–1906, text-figs. 35, 38, 52, 53–55; Stensiö 1931, text-fig. 52; Nilsson 1941, text-fig. 7) and *Remigolepis* (cf. Stensiö 1931, text-fig. 87; cf. also Part III of this work) in which it seems also to be situated more on the anterior than on the medial margin of the ventral lamina. This division in the *Bothriolepinae* has much the same position as the corresponding one in *Gerdalepis* (Gross 1941b, text-figs. 9, 10A), but is of a different shape. The middle division (m_2) in *Bothriolepis*, as in the *Antiarchi* in general, normally is longer than the other two, whereas in *Grossilepis* (text-figs. 41D, 270K; cf. also Gross 1941a, text-figs. 34, 37) it always is shorter than the posterior one. This latter division (m_3) in *Both-*



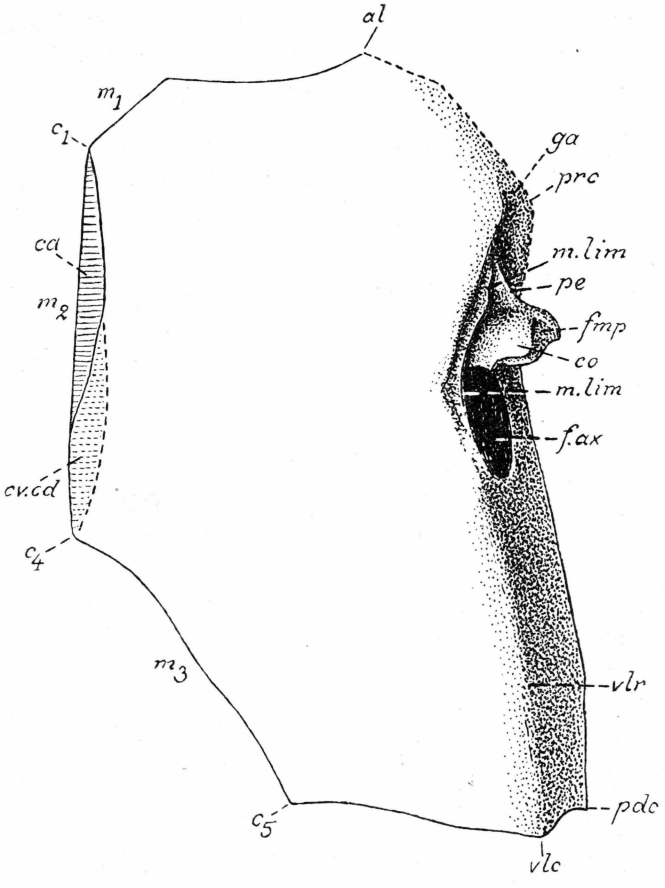
Text-fig. 51. *Bothriolepis canadensis*. Restorations of three anterior ventro-lateral plates. *A*, of a right plate in lateral and somewhat ventral aspect. × $^5/_3$. *B*, of a right plate in ventral aspect. × $^5/_4$. *C*, of a left plate in ventral aspect. The processus brachialis of this plate missing. Slightly enlarged.

adc, antero-dorsal corner of lateral lamina; *al*, anterior lateral corner of subcephalic division of ventral lamina; c_1, corner between anterior (m_1) and middle (m_2) divisions of medial margin of ventral lamina; c_2, c_3, corners on middle division (m_2) of medial margin of ventral lamina; c_4, corner between middle (m_2) and posterior (m_3) divisions of medial margin of ventral lamina; c_5, posterior medial corner of ventral lamina (= posterior ventro medial corner of the plate as a whole); *cd*, area overlapped by right anterior ventro-lateral plate; cd_1, area overlapped by anterior dorso-lateral plate; *cit*, crista transversalis interna anterior and its area of connection with ventral end of same crista on anterior dorso-lateral plate; *co*, pars condyloidea of processus brachialis; *c.cra*, opening of a canal; *de*, dorsal corner or angle; *f.ap*, fossa articularis pectoralis; *f.ax*, foramen axillare; *fmp*, protractor area; *fp*, funnel pit; *gc*, groove dorsally and ventrally to the funnel pit; m_1, anterior division of medial margin of ventral lamina, connected with semilunar plate; m_2, middle division of medial margin of ventral lamina, connected with anterior ventro-lateral plate of opposite side; m_3, posterior division of medial margin of ventral lamina, connected with median ventral plate; *m.lim*, dorsal and ventral margo limitans, in all probability developed for attachment of articular capsule; *pbr*, processus brachialis; *pdc*, postero-dorsal corner of lateral lamina; *pe*, pars pedalis of processus brachialis; *prc*, prepectoral corner; *ua*, unornamented area postero-dorsally to fossa articularis pectoralis and around foramen axillare; *vlc*, posterior ventro-lateral corner; *vlr*, ventro-lateral ridge.

riolepis generally has about the same relative length as in *Pterichthyodes*, *Asterolepis* and *Remigolepis*, whereas in *Grossilepis* it is much longer than in the said three genera, and much longer even than the other two divisions. The ventro-lateral ridge (*vlr*), as normally, is traceable forwards as far as to underneath the anterior part of the fossa articularis pectoralis (*f.ap*). This fossa (*f.ap*), the processus brachialis (*pbr*), and the structures related to them (text-figs. 4, 40, 51, 52, 145B, 163–166, 241, 242, 243A) agree in most respects with the corresponding formations in *Asterolepis* and only little needs therefore to be said concerning them here (cf. Gross 1931, pp. 39–42, pl. 5, fig. 6; pl. 7, fig. 14; 1940b, pp. 28–30, text-fig. 7; Stensiö 1931, pp. 92–102, text-figs. 40–44). The fossa articularis pectoralis in certain species (text-figs. 4, 40, 51A, 145B, 164C, 165D, F, 166E, F) is well bounded off anteriorly, whereas in other species (text-figs. 52, 241) there is a broad groove (*ga*) which, as in *Asterolepis* (cf. Gross 1931, pl. 7, fig. 14; 1940, text-fig. 7D; Stensiö 1931, text-figs. 41, 42), leads forwards on to the broad lateral margin of the subcephalic division of the ventral lamina of the plate. The dorsal division of the margo limitans (*m.lim*), at least in *B.canadensis* (text-figs. 4, 40, 51A, 165D–F, 166E, F), is weaker developed than in *Asterolepis*. The groove (*gc*, text-figs. 4, 40, 51, 164C, 166E) around the external opening of the funnel pit (*fp*) in both *B. canadensis* and *B. maxima* is shallow and usually interrupted laterally, whereas it is deep in its dorsal and ventral medial parts. When interrupted laterally it is in fact represented only by deep dorsal and ventral pits. Finally, the external opening of the canal *c.cra* generally lies nearer to the pars pedalis (*pe*) of the processus brachialis (text-figs. 4, 40, 51A, 164C, 165F, 166E, F) than what it does in *Asterolepis*.

As to its sutural connections the anterior ventro-lateral plate on the whole is as normally in the *Antiarchi*. However, the following abnormal conditions have been observed. At least sometimes in *B. maxima* (*cv.cd*, text-fig. 52; cv_2, text-fig. 243A) the plate of the right side does not simply overlap that of the left side, but is also overlapped by it posteriorly. In certain species (*B. groenlandica, B. canadensis*) the plate does not only overlap the anterior dorso-lateral plate, but at the same time is also more or less overlapped by that plate (cf. p. 130 above). In several species it often abuts posteriorly against the anterior dorso-lateral plate only with its very dorsal edge. Not rarely it is in contact at its postero-dorsal corner with the mixilateral plate. In some cases it overlaps the semilunar plate, while in other cases its attachment to that plate is developed as a harmony.

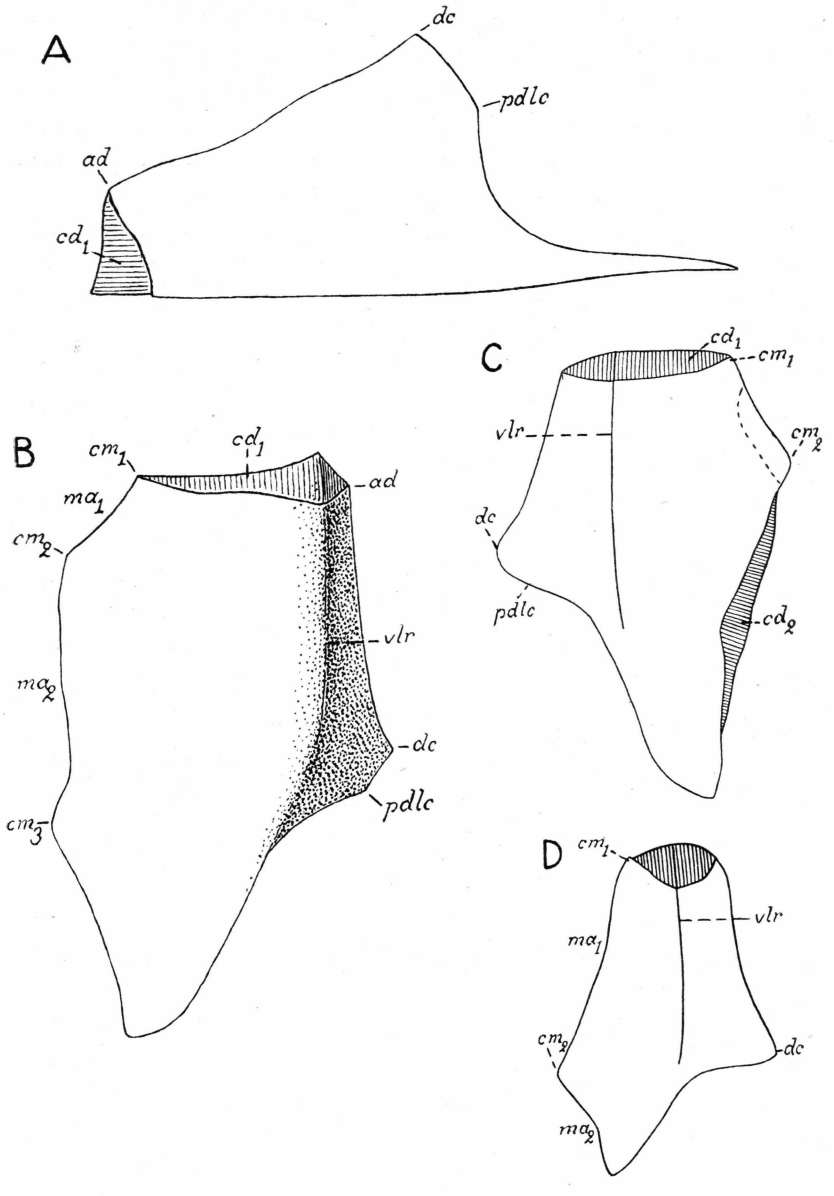
The posterior ventro-lateral plate (*Pvl*, text-figs. 38, 40, 41, 53, 150, 160–162, 164A, 167–178, 238H, 264, 270L, M, 287B, 290, 292, 304) in its general characters agrees with the corresponding plate in the other *Antiarchi* and, as in them, it is as a whole broadest at a transverse plane through the dorsal corner (*dc*) of its lateral lamina. This lamina is highest along a vertical line from its dorsal corner (*dc*) down to the ventro-lateral



Text-fig. 52. *Bothriolepis maxima.* Restoration of a left anterior ventro-lateral plate in ventral aspect, based on the specimen shown in fig. 242. × $^1/_2$ of the nat. size.
al, anterior lateral corner of subcephalic division of ventral lamina; c_1, corner between anterior (m_1) and middle (m_2) divisions of medial margin of ventral lamina; c_4, corner between middle (m_2) and posterior (m_3) divisions of medial lamina; c_5, posterior medial corner of ventral lamina (= posterior ventro-medial corner of the plate as a whole); *cd*, area overlapped by right anterior ventro-lateral plate; *co*, pars condyloidea of processus brachialis; *cv.cd*, place where the plate is not only overlapped but also overlaps the corresponding plate of the opposite side; *f.ax*, foramen axillare; *fmp*, protractor area; *ga*, groove leading from fossa articularis pectoralis forwards on to lateral margin of subcephalic division of ventral lamina; m_1, anterior division of medial margin of the ventral lamina, connected with semilunar plate; m_2, middle division of medial margin of ventral lamina, connected with anterior ventro-lateral plate of opposite side; m_3, posterior division of medial margin of ventral lamina, connected with the posterior median dorsal plate; *m. lim*, ventral margo limitans; *pdc*, posterior dorsal corner of lateral lamina; *pe*, pars pedalis of processus brachialis; *prc*, prepectoral corner; *vlc*, posterior ventro-lateral corner; *vlr*, ventro-lateral ridge.

ridge (*vlr*), but its height at this place in various species is fairly different in proportion to its length and may also vary considerably in different specimens of one and the same species. From its dorsal corner the lamina decreases in height both backwards and forwards. At its anterior end, how-

ever, it is about equally high as, or higher than, the posterior margin of the lateral lamina of the anterior ventro-lateral plate, and not considerably lower than that margin, as in *Pterichthyodes*, *Gerdalepis*, *Asterolepis* (Traquair 1894–1906, text-figs. 36, 39; Gross 1931, text-fig. 11; 1933b, text-fig. 1C, D; 1941b, text-fig. 11; Watson 1935, text-fig. 27) and *Remigolepis* (Stensiö 1931, text-fig. 81). The ventral lamina, as normally in the group, is usually a little broader in the plate of the left side than in that of the right side. As in other *Antiarchi*, this lamina is also broadest at a transverse line across the ventro-lateral ridge (*vlr*) and the middle medial corner (cm_2) of its medial margin, that is to say the corner that is developed just behind the median ventral plate (*Mv*). On account of the fact that this corner (cm_2) generally is situated much further forwards in *Bothriolepis* than in *Grossilepis* (text-fig. 53) the maximum breadth of the lamina as a rule lies considerably further anteriorly in the former genus than in the latter one. However, the maximum breadth of the lamina was also situated fairly far backwards in those of the *Bothriolepis*-species (*B. maxima* and others) in which the median ventral plate is large. The subanal division of the ventral lamina, which extends freely backwards beyond the lateral lamina, is well developed and as a rule about as long relatively as in most other *Antiarchi*-forms. The anterior margin of the plate, which is formed by both the lateral and ventral laminae, is as a whole convex, often with a more or less clearly developed corner at the transition between its lateral and ventral divisions. The dorsal margin posteriorly near its posterior end rises into a rounded or pointed dorsal corner (*dc*, text-fig. 53), which in certain species (e.g. *B. groenlandica*, text-figs. 287B, 290, 292A) is produced into a dorsal process. By this corner or process the dorsal margin is subdivided into two divisions, a long anterior, and a short posterior, which are somewhat variable in their configuration. The postero-dorsal corner (*pdlc*) is often obscure or absent. The posterior margin of the lateral lamina is always clearly concave and passes over ventrally into the lateral margin of the subanal division of the ventral lamina. This latter margin normally is a little convex or fairly straight and passes over without any boundary into the short convex posterior margin of the same division of the ventral lamina. Finally, the ventro-medial margin of the plate, thus the medial margin of the ventral lamina, consists of anterior and posterior divisions, separated by the middle medial corner (cm_2), already referred to. The anterior one (ma_1) of these two divisions is connected with the median ventral plate. As in other *Antiarchi*, this division in *Bothriolepis* usually is much shorter than the posterior one (ma_2), whereas in *Grossilepis*, on the other hand, it is about equally long as, or longer than, that division. As to its configuration it is mostly a little concave, but may also be straight, a little convex, or somewhat undulating. The posterior division (ma_2) of the margin is very variable as to its development, but regularly is straighter on the right plate than on the left one. At or behind its middle it usually forms



Text-fig. 53. Restorations of four posterior ventro-lateral plates. *A*, *B* of a left plate of *Bothriolepis canadensis* in lateral and ventral aspects. × $^{2}/_{1}$. *C*, of a right plate of *B. cellulosa* in external aspect. From Gross 1941a. × $^{1}/_{1}$. *D*, of a flattened left plate of *Grossilepis tuberculata* in external aspect. From Gross 1941a. × $^{1}/_{1}$.

ad, antero-dorsal corner of lateral lamina; cd_1, area overlapped by anterior ventro-lateral plate; cd_2, area overlalpped by left posterior ventro-lateral plate; cm_1, antero-media corner of ventral lamina; cm_2, middle corner of ventral lamina just behind median ventral plate; cm_3, posterior medial corner of ventral lamina; *dc*, dorsal corner of lateral lamina; ma_1, anterior division of medial margin of ventral lamina, connected with median ventral plate; ma^2, posterior division of medial margin of ventral lamina, connected with corresponding division of medial lamina of posterior ventro-lateral plate of opposite side; *pdlc*, postero-dorsal corner of lateral lamina; *vlr*, ventro-lateral ridge.

a broad rounded process or angular corner, the posterior medial corner (cm_3), which is more pronounced on the plate of the left side than on that of the right side. This corner is more or less clearly developed also in other *Antiarchi*-forms (Traquair 1894–1906, text-figs. 35, 38, 47, 52, 55; Gross 1941 b, text-fig. 9; Nilsson 1941, text-fig. 7; Stensiö 1931, pl. 11, fig. 2; pl. 21, fig. 1; pl. 26, figs. 1, 4, 6, 7).

With regard to its sutural connections with the anterior ventro-lateral and medial ventral plates as well as regarding its connection with the corresponding plate of the opposite side the posterior ventro-lateral plate is essentially as in other *Antiarchi*. Thus it is overlapped by the anterior ventro-lateral plate, but overlaps the median ventral plate[1]). Ventrally the plate of the left side overlaps the corresponding plate of the right side on a more or less long stretch behind the middle medial corner (cm_2), whereas furthest caudally the two plates meet only edge at edge without any overlappings. Most posteriorly the two plates may even be a little apart from one another with their subanal divisions. The sutural connection of the plate with the mixilateral plate has already been dealt with in full above (p. 133). However, it may be pointed out here that process-shaped dorsal corner (*dc*) in *B. groenlandica* fits into a pit in the mixilateral plate (*pdc*, text-figs. 287B, 289). Finally, it may be mentioned that at its antero-dorsal corner the plate may sometimes be in contact with the anterior dorso-lateral plate of its side.

The semilunar plate (*Sm*, text-figs. 8, 12, 34, 41, 110, 112A, B, 113A, C, 160–162, 164A, 167–169, 176, 262C, 292B), as we know, is a small unpaired median plate situated in the foremost part of the suture between the anterior ventro-lateral plates. In these respects it agrees with the semilunar plate in *Gerdalepis* (Gross 1941 b, pp. 206–207, text-figs. 9, 10A). However, in contrast to that plate it is not five-sided, but triangular or semicircular in shape. At least in *B. canadensis* it is highly variable. In this species it may be either a little overlapped by the anterior ventro-lateral plates, or else it may be connected with those plates only by its postero-lateral edges. In *B. maxima* it may at least sometimes be considerably overlapped by the anterior ventro-lateral plate (cv_1, text-fig. 243A). As pointed out by Gross (1941 b, p. 207), the semilunar plate in the *Bothriolepinae* and in *Gerdalepis* reminds of the anterior median ventral plate in Arthrodires, whereas the paired, broad semilunar plate in *Asterolepis*, *Pterichthyodes* and *Remigolepis* (Traquair 1894–1906, text-figs. 35, 38, 53–55; Gross 1931, p. 35, pl. 5, fig. 4; pl. 7, figs. 5–7; Stensiö 1931, pp. 105–106, text-figs. 52, 53; Nilsson 1941, text-fig. 7, pl. 1; cf. also Part III of this work), which is attached mainly to the anterior margin of the anterior ventro-lateral plate, is suggestive of the intero-lateral plate of the Arthrodires (see below the Addenda).

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[1]) In *B. maxima* it may sometimes also be somewhat overlapped by the median ventral plate (cd_3, text-fig. 238 *H*).

The median ventral plate (*Mv*, text-figs. 41, 150B, 160–162, 164A, 167–169, 171B, 173, 175–178, 214, 238J, 292B; pl. 56, figs. 2–4; pl. 57, fig. 1; cf. also Traquair 1894–1906, pl. 24, fig. 5; Gross 1941a, pp. 24, 49, text-figs. 16, 18, 37) is of the ordinary quadrilateral and more or less clearly rhombic shape characteristic of the *Antiarchi* in general. In the majority of the *Bothriolepis*-species it is comparatively small, of a somewhat similar size in proportion to the adjoining plates and the ventral wall of the trunk-armour as normally in *Pterichthyodes, Gerdalepis, Asterolepis* (Traquair 1894–1906, text-figs. 35, 38, 53–55; Gross 1931, p. 35, pl. 8, fig. 18; 1941b, text-fig. 9; Nilsson 1941, text-fig. 7), *Remigolepis* (Stensiö 1931, text-fig. 87, pl. 11, fig. 2; pl. 14, fig. 1; pl. 23, fig. 1; pl. 25; cf. also Part III of this work) and *Ceraspis* (cf. Gross 1937, text-fig. 10C), but in certain *Bothriolepis*-species (*B. maxima* and presumably also *B. leptocheira* and *B. hydrophila*) and *Grossilepis* it was much larger. At least in *Grossilepis* it must have been about as large relatively as in *Ceratolepis* (cf. Gross 1933b, text-fig. 4E). More precisely, in *Grossilepis* it was of such a considerable size that its length must have amounted to nearly one half of the total length of the ventral wall of the trunk-armour, whereas its breadth exceeded one half of the total breadth of the said wall of the trunk-armour (text-fig. 41D; cf. Gross 1941a, text-figs. 34, 35, 37). In *Bothriolepis*, and in *Grossilepis* as well, it seems normally to be longer than broad, but in *Bothriolepis*, at any rate, it may sometimes be nearly as broad as it is long (text-figs. 178, 292B). The anterior and posterior divisions of the plate, that is to say those parts of the plate that are situated respectively in front and behind a line through its lateral corners, are sometimes a little differently developed in different species. In *B. canadensis* the anterior one of these two divisions is thus always a little longer and mostly also a little more pointed than the posterior one (text-figs. 41A, B, 161, 162, 164A, 167, 171B, 175, 176, 178), whereas in *B. cellulosa* (text-fig. 41C) the reverse condition is said by Gross (1941a, p. 24, text-figs. 16, 18) to be predominant. In *B. groenlandica*, on the other hand, the condition in this respect seems to be such that the two divisions are mostly so equally developed that, when the plate is found detached, it is impossible to decide which one of them is the anterior or posterior one (pl. 56, figs. 2–4; pl. 57, fig. 1). The margins of the plate normally are slightly convex and, besides, frequently also somewhat undulating. The four corners of the plate are mostly well marked, but may not rarely be somewhat rounded off. As normally in the *Antiarchi*, the plate is always overlapped by both the anterior and posterior ventro-lateral plates. In *B. cellulosa* its anterior overlapped areas may perhaps often be a little broader than its posterior ones, whereas in *B. canadensis* and *B. groenlandica* all overlapped areas seem to be about equally broad. In *B. maxima* the plate may both be overlapped by, and slightly overlap, the posterior ventro-lateral plate (cd_3, cv_1, text-fig. 238A).

Finally, the supramixilateral plate (*Sx*, text-figs. 248, 249) is a supernumerary element, which has been met with so far only on the left side in a single trunk-armour of *B. alvesiensis*. The plate, which is clearly seen in a reproduction given by Traquair (1894–1906, pl. 26, fig. 1), is situated at the corner between the anterior median dorsal, posterior median dorsal, and mixilateral plates, where it fills up distinct notches on all of these three adjoining plates. The deepest one of these notches, however, is the one situated on the anterior part of the lateral margin of the posterior median dorsal plate, that in all respects is as a large mixilateral notch (cf. pp. 122–125). The plate here in question is about twice as long as broad with well rounded off corners. As the plate is represented only by an impression of its dorsal face no details could be made out concerning its sutural connections. The comparatively frequent occurence of a large supramixilateral notch on the posterior median dorsal plate in several *Bothriolepis*-specis renders it likely that a supramixilateral plate was fortuitously developed also in other species than *B. alvesiensis*.

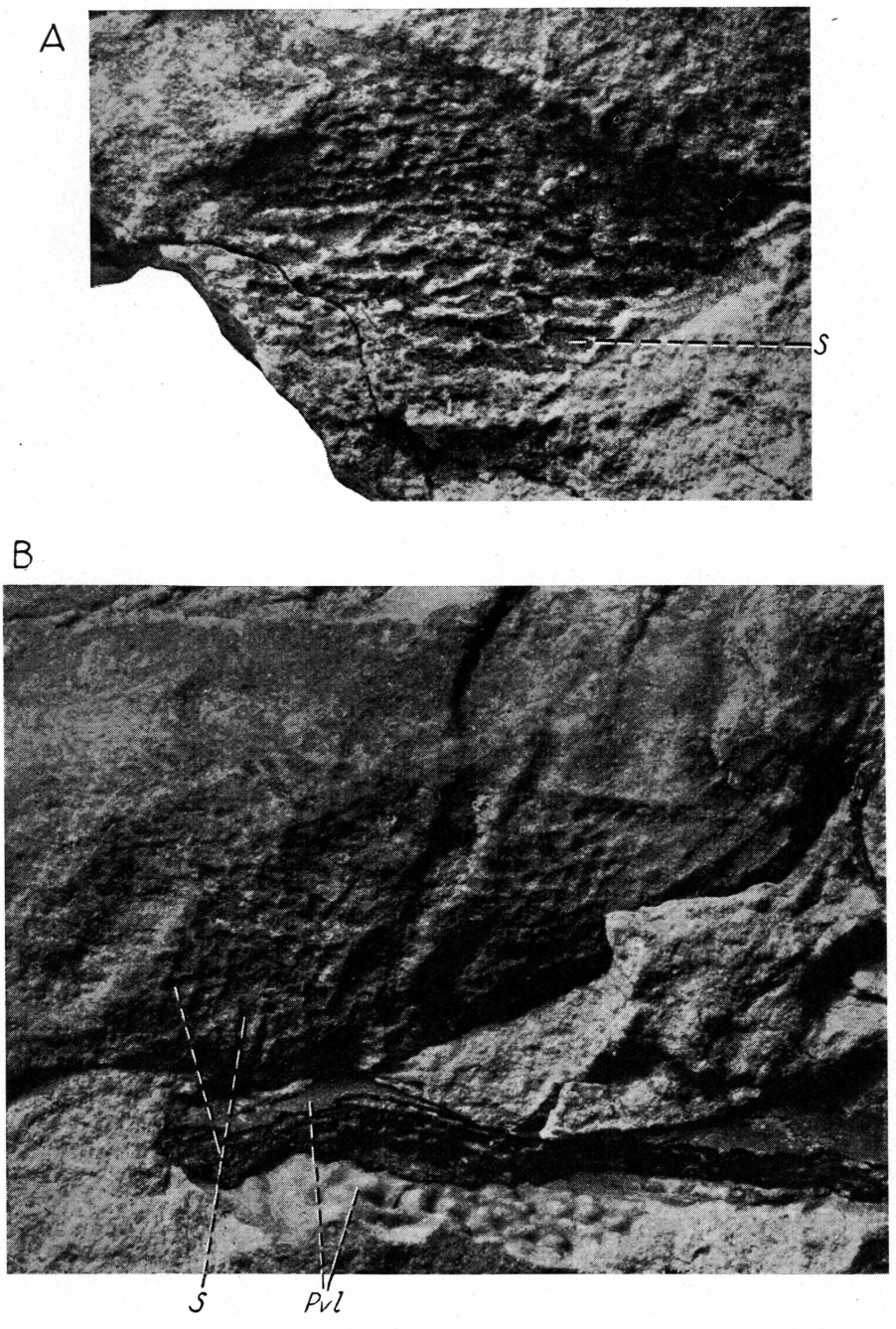
Pelvic girdle.

The normal occurrence of a pelvic girdle and a pelvic fin in Arthrodires proves that these structures must have existed and been well developed already in the primitive ancestors of the Placoderms. In these circumstances we must assume, of course, that a pelvic girdle and a pelvic fin were present also in primitive *Antiarchi*, which, as we now know (cf. p. 222), must be derived from some primitive group of Arthrodires, presumably nearest akin to Euarthrodires. However, it is possible that the pelvic girdle was much reduced in several of the Middle Devonian and Upper Devonian *Antiarchi*-forms.

Since, as we know (cf. pp. 160–162; cf. also Stensiö 1931, p. 138), they shon remains of a pelvic fin, the *Bothriolepinae* must have had a pelvic girdle. Their pelvic girdle probably lay in the hindmost ventral part of the abdominal region, close behind the lateral wall of the trunk-armour and thus above the anterior portion of the subanal division of the trunk-armour. It was certainly formed only of endoskeleton, which seems to have consisted entirely of cartilage.

Unarmoured posterior division of trunk. Squamation.

The unarmoured posterior division of the trunk in the *Bothriolepinae* is fundamentally as in the other *Antiarchi*, that is to say it comprises the hindmost dorsal and lateral parts of the abdominal region and the whole caudal region. Up till now it has been found preserved only in *B. canadensis* (text-figs. 38, 40B, 62C; cf. also Patten 1904, pp. 113–114, text-figs. 1, 2; 1912, text-figs. 247–251; Stensiö 1931, pp. 107–109, text-figs. 54, 72), where it is longer and more slender than in *Pterichthyodes* (text-fig. 61; cf. Traquair 1894–1906, text-figs. 34–36, 51, 52; Forster-Cooper 1934, text-figs. 1, 2,

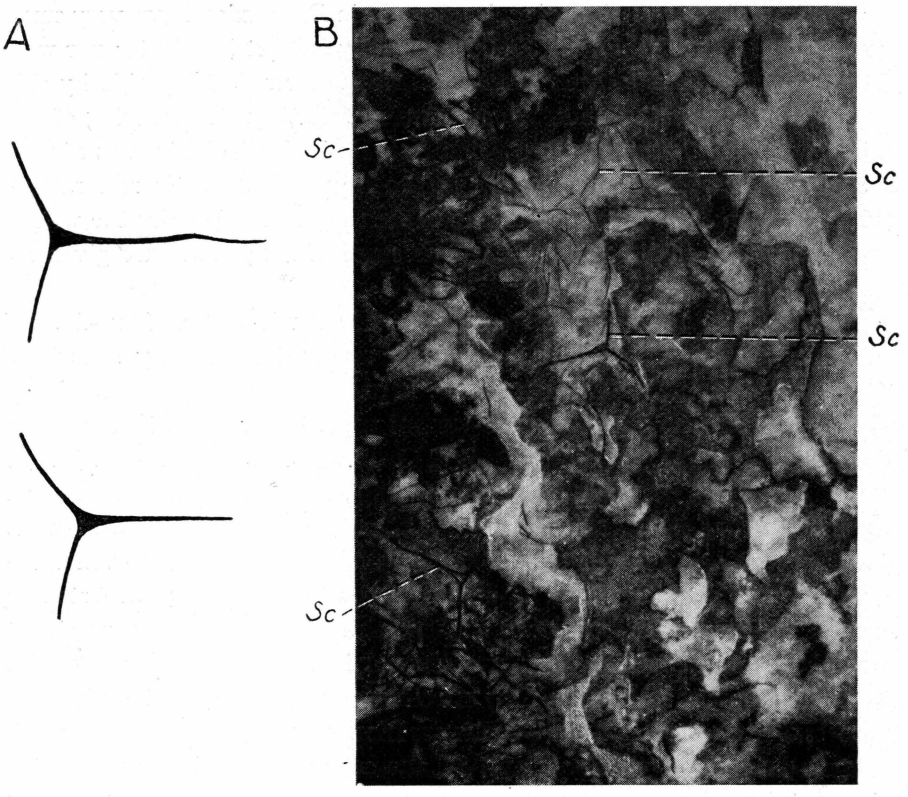


Text-fig. 54. *Bothriolepis canadensis*. *A*, *B*, impressions of scales from the lower parts of the flanks just behind the trunk-armour. Specimens Nos. P. 2482 and P. 2672 respectively in the collections of the Swedish Museum of Natural History in Stockholm. × $^{4}/_{1}$.
Pvl, fragmentary remains of subanal divisions of posterior ventro-lateral plates; *S*, impressions of scales.



Text-fig. 55. *Bothriolepis canadensis*. A part of the scale-covering of the foremost part of the ventral side of the caudal region close behind the ventral wall of the trunk-armour (*Ta*). The scales all seen from the outside and, therefore, showing their ornament. Specimen No. 2287 in the Swedish Museum of Natural History in Stockholm. Same specimens as in text-figs. 56, 59, 60, 133 and 175. × $^{10}/_{1}$.

pl. 2; Watson 1935, text-fig. 27), and probably also than in *Remigolepis* (cf. Part III of this monograph). Whether, as stated by Patten (1904, p. 113), it is actually triangular in cross-section could not be ascertained on the material available to the writer.



Text-fig. 56. *Bothriolepis canadensis*. *A*, restorations of two 3-radiate highly vestigial scales of the pelvic fin. × $^{20}/_{1}$. *B*, a part of a ventral fin showing a few more or less deficient 3-radiate, highly vestigial, scales. Specimen No. P. 2287 in the possession of the Swedish Museum of Natural History in Stockholm. Same specimens as in text-figs. 55, 59, 60, 133 and 175. × $^{10}/_{1}$.
Sc, 3-radiate vestigial scales and fragments of such scales in their positin in the carbonaceous blackish mass representing the pelvic fin.

The squamation in the *Bothriolepinae* was higly reduced, and it is not impossible that in certain of the representatives of the subfamily it may even have been totally absent. At present it is known in only *Bothriolepis canadensis*, where it persists on the flanks an on the ventral side of the caudal region of the trunk nearest behind the trunk-armour (text-figs. 38, 40B, 54, 55, 59, 60). In addition in this species it is represented by a rostro-caudal row of scales (*Ls*, text-figs. 38, 62), developed in relation to the main lateral line along the ventral margin of the body axis of the caudal fin, and by certain peculiarly shaped elements on the pelvic fin (text-fig. 56). The other parts of the unarmoured division of the trunk, thus the hindmost dorsal part of the abdominal region nearest to the anterior dorsal fin and almost the whole caudal region, are completely devoid of all formations of hard tissue and are in their fossil condition preserved only as a thin carbonaceous film of a blackish or somewhat brownish appearance.

All the scales, or vestiges of scales, present in *B. canadensis* are very small and delicate (text-figs. 54–56, 59, 60, 62). They are not imbricate; nor were they firmly attached to each other in other manners, but lay side by side in the skin. It is easily understood, therefore, that by the decaying of the skin they mostly became loose and got lost. No indications of scales of such a considerable size as those shown by Patten in one of his restorations (1904, text-fig. 1) were to be found in the material examined by the writer, and, in fact, no statements as to the presence of such scales are given by Patten himself.

The scales of the flanks nearest behind the trunk-armour (text-fig. 54) on the whole are of a somewhat uniform size and are mostly somewhat rhombic or, at least, four-sided in shape. In places they show also a tendency to a disposition in obliquely dorso-ventral rows. The scales of the ventral side of the caudal region nearest behind the trunk-armour (text-figs. 55, 59, 60), on the other hand, are of a much varying size and shape. Some of them are developed as small irregular plates, others as small tubercles somewhat reminding of Acanthodian scales. Several of these scales may even have more or less lobated margins in such a manner that they are somewhat stellate in outline. These scales are all irregular in their disposition, or more precisely, they show no indications of being disposed in rows. Whereas anteriorly, just behind the trunk-armour, they are situated close together, they become more scattered caudally, finally disappearing completely already a short distance behind the trunk-armour. All the scales in question are provided with a tubercular ornament. The smallest ones of them have only one tubercle, whereas the larger ones bear a few tubercles.

The scales developed in relation to the main lateral line on the body axis of the caudal fin (*Ls*, text-figs. 38, 62) form a continuous row. They are all longer than high and grooved in a longitudinal direction on their outside for the lateral line.

Finally, the dermal elements on the pelvic fin (*Sc*, text-fig. 56) have been found preserved only in a single specimen of *B. canadensis*. They are very small and seem mostly to be situated far apart. They are usually 3-radiate in shape, resembling spiculae of sponges. As they occur only in the fold interpreted as a pelvic fin and are found in the folds of both the right and left sides, they must beyond question be formations belonging to this fin-fold. Because of their peculiar shape they cannot possibly be ceratotrichia, and the only plausible explanation of them at present is, therefore, that they are scales in highly vestigial condition.

Besides in the *Bothriolepinae*, the squamation among the *Antiarchi* was highly reduced or absent also in *Asterolepis*, *Microbrachius*, the *Ceraspidae*, and in addition in one species of *Pterichthyodes* (*P. cancriformis*, Forster-Cooper 1934, pp. 25–29, text-fig. 2, pl. 2). On the other hand, the squamation is comparatively well developed on the whole posterior unarmoured

division of the trunk in *Pterichthyodes milleri* (text-fig. 61; cf. also Traquair 1894–1906, text-figs. 34–36; Forster-Cooper 1934) and *Remigolepis* (Stensiö 1931, pp. 108, 178; cf. also Part III of this monograph).

For comparison we may mention here that the Arthrodires show a similar trend towards a complete reduction of the squamation of the trunk as do the *Antiarchi*.

In this connection it should also be mentioned that an anal plate is developed in *B. canadensis*. This plate, whose presence was recorded already by Patten, is situated just above the hindmost part of the subanal division of the ventral wall of the trunk-armour. In the material examined by the writer it was met with only in one specimen, where it is longer than broad. A photographic reproduction of it was given in 1931 (Stensiö 1931, text-fig. 54).

Paired fins.

Pectoral fin.

The detection of an endoskeleton in the pectoral appendage of *Bothriolepis* made in 1931 (Stensiö 1931, pp. 111–113, text-fig. 55, pl. 2, figs. 5, 6) proved convincingly that this appendage is a pectoral fin of the same nature as that of fishes in general. The fact that the pectoral appendage of the *Antiarchi* is a real pectoral fin seems quite natural now, however, since it has been shown that a true pectoral fin was present also in widely different groups of Arthrodires (Broili 1930a, b; 1933a, b; Watson 1934, p. 448, p. 137; Heintz 1938, pp. 19–25; Gross 1938, p. 199; Stensiö & Jarvik 1939, pp. 265–266; Stensiö 1944, pp. 36–69, 77–79) and since, therefore, it must be postulated that such a fin was developed already in the common ancestors of all groups of Arthrodires, and thus also in the ancestors of the *Antiarchi* which, as is now clear (cf. pp. 219–222), are to be sought for among primitive Arthrodires.

In its general appearance the pectoral fin of the *Antiarchi* is widely different from the corresponding fin in other fishes, a condition due above all to the unique development of its exoskeleton. At a closer analysis it may be characterized as mesorachic and extremely stenobasal, whereas that of the Brachythoracid and Rhenanid Arthrodires is pleurorhachic and eurybasal (Gross 1941a, pp. 67–69). With regard to its general structural type it is thus such that it can hardly be directly derived from a Brachythoracid-like one (cf. Gross 1941a, loc. cit.), but nearest from a pectoral fin modified in an archipterygium-like manner. Consequently it may readily be imagined to have arisen from such a basally concentrated pectoral fin as that of the *Acanthothoraci* (Stensiö 1944, pp. 66–69). Everything thus goes to prove now, that with regard to the structure of the pectoral fin the *Antiarchi* and

Arthrodires actually are much closer to each other than what was maintained by Gross (1941a, loc. cit.; cf. below pp. 221–222).

Though, as just mentioned, it may be assumed to have arisen nearest from a fundamentally archipterygium-like fin and exhibits clear archipterygium-like characters, the pectoral fin of the *Antiarchi* is nevertheless so highly transformed and specialized that, as urged by Gross (1941a, p. 68), it may be considered to represent a type of its own, a type which has been termed by Gross (1931, p. 52) the arthropterygium-type.

As is well known since long ago, the pectoral fin of the *Bothriolepinae* is subdivided into two segments, a proximal longer and a distal shorter, which were in real articular connection with each other. Like that in *Pterichthyodes Gerdalepis, Asterolepis* and *Microbrachius* it differs, therefore, considerably from the corresponding fin in *Remigolepis*, which is unsegmentated and in consequence of this relatively slightly specialized in its exoskeleton (cf. Stensiö 1931, pp. 113–138, 178, text-figs. 80, 88; cf. also Part III of this work). Taken as a whole the pectoral fin in the *Bothriolepinae* is long and comparatively slender. In *Bothriolepis*, and conceivably also in *Grossilepis*, it is always longer in proportion to the trunk-armour than what is the case in *Pterichthyodes, Gerdalepis* (Gross 1941b, text-fig. 9), *Asterolepis, Microbrachius* and *Remigolepis*. When lying alongside the body-wall it reaches in *Bothriolepis* as far backwards as to, or even somewhat beyond, a transverse plane through the posterior end of the ventral wall of the trunk-armour (text-figs. 38, 40B, 41B, 161, 167, 179–183, 261, 264, 308; pls. 15–18, 70), whereas in *Pterichthyodes, Gerdalepis, Asterolepis, Microbrachius* and *Remigolepis*, on the other hand, it ends quite far in front of the said transverse plane.

The endoskeleton of the pectoral fin in the *Bothriolepinae* and *Antiarchi* in general was developed as an internal central axis. As it consisted of cartilage, generally devoid of lime-salts, it could not be preserved in the fossils, However, as is well known (Stensiö 1931, p. 111, text-fig. 55, pl. 2, figs. 5, 6), remains of it have been met with in some cases in *Bothriolepis canadensis*, but in these cases it was lined by a superficial crust of a hard lime-bearing tissue, a crust which was resistible enough to become fossilized. In these cases it is thus not the cartilage itself that is preserved, but its lining of hard lime-bearing tissue. This tissue is of a considerable interest, since, as pointed out by the writer (Stensiö 1931, p. 111), it is somewhat intermediate in minute structure between true bone and calcified cartilage of the prismatic type occurring in Selachians. In thin sections it is found to contain minute spaces which probably are cell-spaces. The lime around each such probable cell-space is deposited in concentric layers, which seem to be destitute of fibres and which both in this and other respects are such that they cannot possibly be interpreted as Haversian lamellae. In thin section the tissue is, therefore, of such a general appearance as to convey the impression that it

is composed of small globules built up of concentric layers around the various probable cell-speces.

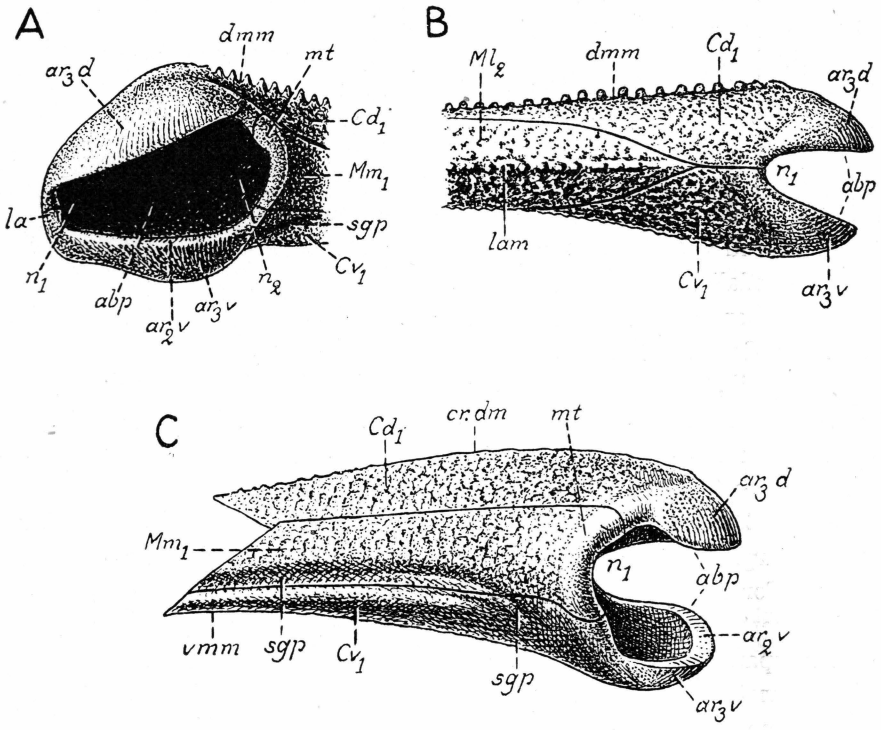
The most complete lime-incrusted element of the endoskeleton of the pectoral fin found preserved in *B. canadensis* (Stensiö 1931, text-fig. 55) lies in the foremost part of the proximal segment and is presumably somewhat in its natural position in the segment. With its anterior end this element is situated fairly close behind the pars condyloidea of the processus brachialis (cf. p. 136; cf. also text-figs. 51, 164b, 165, 166). From near the said part of the processus brachialis it extends distally not quite to the middle of the segment and thus is rather short. It is much narrower than the segment and does not, therefore, by far fill up the interior of it. Judging from its position in the segment, from its relatively slight distal extent and from the fact that lime-incrusted pieces of endoskeletal nature sometimes occur also in the distal parts of the segment, it is likely that the element in question does not constitute the whole endoskeletal axis, but that it represents only a proximal part of a long endoskeletal axis, extending distally through the whole proximal segment and from it also into the distal segment. It could not be established whether the element was covered by a lime-crust also at its anterior end. If this was not so, however, the cartilaginous interior part must have extended somewhat proximally beyond the line-crust representing the element in the fossil condition, and consequently the element may very well have articulated against the pars condyloidea of the processus brachialis. In such a case it cannot possibly have articulated against the pars condyloidea itself, which, as it belongs to the anterior ventro-lateral plate, is formed by dermal bone, but against a cartilage which can only have been situated in the funnel pit (*fp*, text-figs. 4, 51A, 166E, F), of the pars condyloidea. Such a cartilage situated in the funnel pit of the processus brachialis may well be imagined to have been present and would explain why the funnel pit is always so wide and well developed. Since this pit extends inwards through the whole processus brachialis and from it continues even into the lateral lamina of the anterior ventro-lateral plate itself (cf. Stensiö 1931: the two series of sections reproduced in text-figs. 43–48) the possible cartilage situated in it could without difficulty be interpreted as a part of the endoskeletal shoulder-girdle, secondarily separated off by the excessive development of the processus brachialis (see the Addenda). Be this as it may, the lime-incrusted axial element here in question in its fossil condition probably has no direct contact with the pars condyloidea of the processus brachialis. The medial side of the elements is developed as a broad proximo-distally passing groove, which gradually becomes shallower distally, finally disappearing entirely towards the distal end of the element. This groove in all probability was the insertion area of the tendon or tendons of the retractor (adductor) group of muscles of the pectoral fin. The lateral side of the element is throughout its extent convex in a dorso-ventral direc-

tion. In cross-section the element is crescent-shaped in its anterior and middle parts, but oval near, and at, its distal end (cf. Stensiö 1931, pl. 2, figs. 5, 6).

As may be gathered from the above, the endoskeletal axis of the pectoral fin in the *Bothriolepinae* and *Antiarchi* in general consisted of cartilage, which at least sometimes in the *Bothriolepinae* was partly lined externally by a hard lime-bearing tissue. The axis probably extended throughout, or almost throughout, the whole length of the interior of the fin and may conceivably have been subdivided into a few elements. The most proximally situated one of these elements may be suspected to have articulated against a cartilage in the funnel pit of the processus brachialis, a cartilage, primarily forming part of the endoskeletal shoulder-girdle, but detached from it by its enclosure in the exoskeleton. The most distal one of the elements in question in the *Bothriolepinae*, *Pterichthyodes*, *Gerdalepis*, *Asterolepis* and *Microbrachius* probably lay in the distal segment of the fin, and must, therefore, in these forms, be assumed to have articulated against the one nearest proximally to it, that is to say the distalmost one of the proximal segment. In *Remigolepis*, on the other hand, no articulation was, of course, developed between the two distalmost elements of the axis, but all the elements of the axis must there have been fairly rigidly connected with each other.

The exoskeleton of the pectoral fin in the *Bothriolepinae*, as in other *Antiarchi*, forms a complete pectoral fin-armour. Like in *Pterichthyodes*, *Gerdalepis* (Gross 1941b, p. 208, text-fig. 9), *Asterolepis* and *Microbrachius*, it consists of a proximal and a distal segment, which articulated against each other, and which may be referred to as the proximal and distal segments respectively of the pectoral fin-armour.

The proximal segment of the pectoral fin-armour (text-figs. 38, 40B, 41B, 57, 98, 180A, 181C, 182, 194–196, 228A, B, 243B–G, 257, 261, 262D, 264, 271A, B, 293, 294, 306, 308) is a somewhat tube-like formation, open at the proximal and distal ends. It is not round, however, but of such a shape that, except most anteriorly, its lateral margin is low and edge-shaped, whereas its medial margin is comparatively high. In cross-section it is, therefore, like a low triangle with the base medially and the point laterally. On account of this shape it may be regarded as built up of three walls, dorsal, ventral and medial. The dorsal and ventral walls at their transition into each other form the sharp-edged lateral margin of the segment. The medial wall externally is bounded off from the dorsal wall by a well developed dorso-medial margin and from the ventral wall by a ventro-medial margin, generally more or less rounded off and distally sometimes slightly developed or almost absent. The segment is highest near its proximal end, where its height may equal its breadth, but decreases in height distally, so that its distal end is fairly low (text-figs. 38, 40B, 57, 196, 243D–G). It is broadest about at its middle or somewhat further distally and is always much longer than broad. However, in the various species it is always longer



Text-fig. 57. *Bothriolepis canadensis.* Restorations showing the proximal end of the exoskeleton of the proximal segment. *A*, in proximal aspect. *B*, in lateral aspect. *C*, in medial aspect. × 3/2.

Cd_1, dorsal central plate 1 (dorsal articular); Cv_1, ventral central plate 1 (ventral articular); Ml_2, lateral margin plate 2 (lateral marginal); Mm_1, med⁷al marginal plate 1 (axial plate); *abp*, proximal brachial aperture; ar_3d, external articular area of dorsal central plate 1; ar_2v, ar_3v, marginal and external articular areas respectively of ventral central plate 2; *cr.dm*, crest on dorso-medial margin (*dmm*) formed by the fusion of spines; *dmm*, dorso-medial margin; *la.m*, lateral margin; *mt*, postarticular thickening; n_1, lateral corner of proximal brachial aperture, probably for protractor muscle of pectoral fin or for tendon of this muscle; n_2, medial corner of proximal brachial aperture, for nerves and vessels to interior of pectoral fin and probably also for tendon or tendons of retractor muscles of pectoral fin; *sgp*, pectoral pit-line groove; *vmm*, ventro-medial margin.

in proportion to its breadth in young individuals than in older ones. In most species it is about 5 times as long as broad in young individuals and 4–3 1/3 times as long as broad in fully mature individuals, but in several species it is of a longer and slenderer shape. In *B. groenlandica*, for instance, it is about six times as long as broad in small individuals and about four and a half times as long as broad in fully mature individuals; in mature individuals of *B. maxima* it is even almost five times as long as broad. The opening at its proximal end, the proximal brachial aperture (*abp*, text-figs. 57, 189D, 190A–D, 191C, D, 196), is developed for the articulation against the trunk-armour (exoskeletal shoulder-girdle) and embraces the pars pedalis (*pe*) of the processus brachialis. This opening in all essentials

agrees with the corresponding one in *Asterolepis ornata* (cf. Gross 1931, pl. 5, figs. 1–3; pl. 6, figs. 1, 2; 1933a, text-fig. 17, 21). It is thus much broader than high, higher medially than laterally, and so situated that its axis of breadth passes from above and medially in a direction laterally and a little ventrally (text-fig. 57A). Because of its considerable breadth it is not confined to the very proximal end of the segment only, but extends also somewhat on to both the medial and lateral sides of it. Only the middle parts of its dorsal and ventral margins participated in the articular connection with the pars pedalis of the processus brachialis, and only these parts of the said margins, therefore, are thick and formed of "Siebknochen" (cf. Stensiö 1931, text-figs. 41, 44). The other parts of the dorsal and ventral margins are fairly thin, and so are also the lateral and medial margins of the aperture (text-figs. 57A, C, 196B, 297C, D). The medial margin, however, on its outside is normally strengthened by a broad rounded dorsi-ventral ridge, the postarticular thickening (*mt*, text-figs. 57A, C, 190B, C, 191D, 194, 195, 196B, 244E, 300), which from the dorsal central plate 1 descends across the medial marginal plate 1, usually from it continuing on to the ventral central plate 1. For not preventing the protraction and retraction of the pectoral fin the aperture here under consideration is considerably broader, of course, than the pars pedalis of the processus brachialis, but, as is clearly seen in *B.canadensis*, its breadth exceeds considerably the maximal one necessary for extreme protractions and retractions. Even when the segment is in a maximally protracted or retracted position there is always, therefore, a lateral and a medial corner respectively of the aperture, which are not occupied by the pars pedalis of the brachial process. On account of this considerable breadth the aperture cannot possibly have been developed only for the articulation with the pars pedalis, but must have had other functions as well. Its lateral corner (n_1, text-figs. 57, 190A, D, 191C, 196A) probably served as an entrace for the protractor muscle or its tendon into the interior of the segment, whereas the medial corner (n_2), text-figs. 57, 190B, C, 191D, 196B), which is situated opposite the foramen axillare (*f.ax*) in the lateral lamina of the anterior ventro-lateral plate, must have been traversed by the main nerves and vessels for the whole interior of the fin and, besides, possibly also by the tendon or tendons of the retractor muscle of the fin. The nerves and vessels which entered the interior of the fin through the last-mentioned corner (n_2) of the aperture emerged from the trunk-armour (exoskeletal shoulder-girdle) through the foramen axillare. The protractor muscle, which certainly was fairly small, probably took origin on the protractor area (*fmp*, figs. 51, 52) of the processus brachialis. The retractor muscle may be suspected to have taken origin on the principal part of the endoskeletal shoulder-girdle, situated inside the trunk-armour, medially to the anterior ventro-lateral plate (cf. above p. 100). Two smaller muscles, serving for a slight raising and lowering of the pectoral fin, probably originated in the grooves *gc*, dorsally and ventrally to the funnel pit (fig. 51A).

Both these muscles, however, lay within the proximal segment and thus did not enter the proximal brachial aperture. The distal opening of the segment just under description will be termed the distal brachial aperture. This opening is always low and broad and is also developed much in the same way as in *Asterolepis ornata*.

The distal segment of the pectoral fin-armour (text-figs. 38, 40B, 41B, 98, 180A, 181C, 182, 195, 198, 228C–E, 261, 264, 293A, B, 295, 306, 308; cf. also Gross 1941, text-fig. 44), as in *Pterichthyodes*, *Gerdalepis* and *Asterolepis*, is nearest suggestive of a spear-head, decreasing in height and breadth distally and ending into a pointed apex. In cross-section in certain species it is considerably broader than high, in other species more circular. Its lateral and medial margins are often developed as sharp crests, bounded off from the dorsal and ventral faces of the segment by dorsal and ventral longitudinal groove-like depressions, the dorsal and ventral marginal grooves. The lateral margin lies in the straight distal continuation of the lateral margin of the proximal segment, whereas the medial margin forms the direct posterior continuation of the dorso-medial margin of the proximal segment, and not of the ventro-medial one, as one would be most inclined to assume. The opening in the proximal end of the segment, the antibrachial aperture, is broad and low. Through it the endoskeletal axis of the pectoral fin penetrated into the distal segment. This opening was also traversed by nerves and vessels, and by the tendons of the flexor muscles of the distal segment.

The pectoral fin-armour of the *Bothriolepinae*, like that of the other *Antiarchi*, bears two rows of spines, a medial and a lateral. The medial row is developed along the dorso-medial margin of the proximal segment and along the medial margin of the distal segment, whereas the lateral row extends along the lateral margins of both the proximal and distal segments. Besides these two rows of spines, a third ventro-medial row may fortuitously be found on the most proximal parts of the ventro-medial margin of the proximal segment (text-fig. 197F). The last-mentioned row is very slightly developed and has thus far been observed only in *B. canadensis*.

The detailed development of the medial and lateral rows of spines is known only in the *Bothriolepis*-species in which it is as follows. Both these rows are relatively stronger developed in young individuals than in older individuals, but particularly than in fully mature individuals (text-figs. 41B, 98, 180A, 181C, 182, 193, 194, 195, 293, 294, 295, 296). Their spines on the proximal segment in young individuals are also normally fewer, relatively larger, and more independent from each other at their bases than in more mature individuals. With the proceeding growth of the individuals the spines of both the rows tended more or less to fuse with each other a their bases or in their basal parts. This tendency of fusion of the spines is much more pronounced, however, on the proximal segment than on the distal one. The proximal ones of the medial spines of the proximal segment in fully mature individuals are occasionally (*B. canadensis*, text-figs. 182, 194C; *B. jarviki*, pl.

73, fig. 2) or normally (*B. maxima*, text-figs. 244A, 245A; *B. groenlandica*, text-figs. 294A, B, 296) completely coalesced with each other into a more or less clearly serrated or smooth-edged dorso-medial crest (*cr.dm*). The lateral spines of the proximal segment in the majority of species remain independent in their distal longer parts. In *B. maxima*, however, in which they are in a somewhat reduced condition, they are often fused on the posterior part of the proximal segment into a distinct lateral crest (*cr.l*, text-fig. 246). There is reason to suspect that a similar fusion of lateral spines may have taken place also in *B. gigantea*.

The medial spines in several of the *Bothriolepis*-species, such as *B. canadensis* (text-figs. 40B, 57A, B, 190D, E, 196), *B. cellulosa*, *B. maxima* (text-fig. 243E–G) and *B. groenlandica* (text-figs. 294, 296), point dorsally or dorsally and a little medially on the proximal parts of the proximal segment, whereas they point straight medially on the hindmost part of the proximal segment and on the whole distal segment too. In other *Bothriolepis*-species, such as *B. panderi* (text-fig. 232) and *B. jarviki* (pl. 72, fig. 2; pl. 73, fig. 2), on the other hand, these medial spines of the proximal segment are all directed almost straight medially. The lateral spines are always directed straight laterally both on the proximal and distal segments. Both the medial and lateral spines may be straight or more or less curved. The medial ones incline in a proximal or distal direction, but may also be bent laterally; the lateral ones incline in a proximal or distal direction, but are usually not or only slightly curved upward or downward.

The articulation of the two exoskeletal segments of the pectoral fin against each other, and the articulation of the proximal one of these two segments against the trunk-armour (the exoskeletal shoulder-girdle), are in all essentials as in *Asterolepis ornata* (Gross 1931, pp. 39–45), on account of which it is superfluous to enter upon them here. When situated alongside the body wall the pectoral fin occupied the position shown in text-figs. 38 and 40B. From this position it could not be lowered any further, whereas on the other hand, it could be raised as much that the middle part of the distal segment was approximately on a level with the postero-dorsal corner of the lateral wall of the trunk-armour. Previous restorations in which it is shown in a lower position when fully adducted to the trunk-armour are wrong[1]).

As is now fully clear from its position and articulation with the trunk-armour (exoskeletal shoulder-girdle), the pectoral fin must have functioned as a regulator of the movements upwards, downwards and towards the sides. At the same time it served also as an organ of floating and balance. To a certain extent it was, of course, also an organ of propelling.

As has been pointed out already above (pp. 7–10), the new terminology of the bones of the pectoral fin recently introduced by Gross (1941a, pp. 25–

[1]) This applies also to the restoration of *Pterichtyodes* given by Watson in 1935 and reproduced here in text-fig. 61.

31, 49–54, 57–60) has been adopted in this work. For an explanation of this new terminology the reader is referred to table I on pp. 8–9 above, in which also the previous terminologies are given for comparison.

The dermal bones forming the proximal segment of the fin-armour (text-figs. 40B, 41B, 57, 98, 180A, 181C, 182, 194–196, 228A, B, 243A–G, 257, 261, 262D, 264, 271A, B, 293, 294, 306, 308) in their disposition and shape are fundamentally as in *Pterichthyodes*, *Gerdalepis* and *Asterolepis* (cf. Traquair 1894–1906, text-figs. 34–38, 51–53; Gross 1931, text-figs. 9, 11, 12; pl. 5, figs. 1–3; pl. 6, figs. 1, 2; 1933a, text-fig. 17; 1941a, pp. 25–31, 49–54, text-figs. 19–24, 38–43, 45; 1941b, text-fig. 9; Stensiö 1931, pp. 114–132, text-fig. 55–56; Nilsson 1941, text-figs. 7, 13). In contradistinction to what is the case at least in *Pterichthyodes* and *Asterolepis*, the dorsal central plate 2 (Cd_2), however, is only a small bone, confined in its extent to the most distal part of the segment. In consequence of this the dorsal central plates 1 (Cd_1) and 2 (Cd_2) do not meet in a suture, as they do in *Pterichthyodes* and *Asterolepis*, but are widely separated from one another by the lateral and medial marginal plates 2 (Ml_2, Mm_2), which meet on the dorsal side of the fin, forming a long proximo-distally running suture. With the exception of the dorsal central plate 2 (Cd_2), all the plates of the proximal segment are longer in proportion in their breath or height than the corresponding ones in *Pterichthyodes* and *Asterolepis*. As in these two genera, both the dorsal and ventral central plates 1 (Cd_1, Cv_1) are provided with a medial lamina, which participates in the formation of the medial wall of the proximal segment. Contrary to what is the case in *Pterichthyodes* and *Asterolepis*, however, the medial lamina of the ventral central plates 1 is usually fairly low and indistinct in its posterior part or else represented only by its anterior part (text-figs. 57C, 190B, C, 191D, 196B; cf. also Gross 1931, pl. 5, fig. 3; pl. 6, fig. 2; 1933a, text-figs. 17, 21; Stensiö 1931, text-figs. 59, 60, 62). The articular areas of the dorsal and ventral central plates 1, are essentially as in *Pterichthyodes* and *Asterolepis* and thus are three on each plate (text-figs. 57, 193, 196B, 197, 296, 297, 307): an internal, spheroidal one ($ar_1 d$, $ar_1 v$) for the articulation against the pars conduloidea of the processus brachialis; a marginal, horizontally situated, plane one ($ar_2 d$, $ar_2 v$) for the articulation against the upper and lower sides respectively of the pars pedalis of the processus brachialis; and, finally, an external, spheroidal one ($ar_3 d$, $ar_3 v$) for the articulation against the walls of the fossa articularis pectoralis dorsally and ventrally respectively to the base of the pars pedalis of the processus brachialis. The last-mentioned one ($ar_3 d$) of the three articular areas is situated along the proximal margin, the articular margin, of the plates, but is not nearly as broad as that margin. Behind it there is on the two plates an unornamented more or less large area, the postarticular smooth area, which also extends medially on to the medial laminae of the plates. The lateral margin of the two plates in its foremost part shows a more or less marked angle, the lateral angle (*la*), by means of which it is divided into

an anterior and a posterior division. With the anterior one (a_1) of these two divisions, at which they are strikingly thick (text-figs. 57A, C, 193H, 297C, D), the two plates meet and form a suture with one another, whereas with the posterior division (a_2) they are suturally connected to the lateral marginal plate 2 (Ml_2).

Turning to the dermal bones composing the distal segment of the pectoral fin-armour (text-figs. 40B, 41B, 98, 180A, 181C, 182, 195, 198, 228C–E, 293A, B, 295, 306; cf. also Gross 1941a, text-fig. 44) we find that they are normally more numerous than in *Asterolepis*, *Gerdalepis* and *Pterichthyodes*. Each of the longitudinal series of bones in this segment in the *Bothriolepinae* in most cases nearest proximally to the terminal plate presents one or two elements more than what they do in the three genera just referred to. The maximal number of independent elements observed as yet in the dorsal central, ventral central, lateral marginal, and medial marginal series of the distal segment thus amounts to 4, 2, 3, 4 respectively in the *Bothriolepinae*, whereas it is 1, 1, 2, 2 in *Asterolepis*, and 2, 2, 3, 2 in *Pterichthyodes*. On account of this generally larger number of elements in its longitudinal bone series the distal segment of the fin-armour in the *Bothriolepinae*, of course, also normally comprises a larger number of transversal zones of bones than what is the case in *Asterolepis* and *Pterichthyodes*.

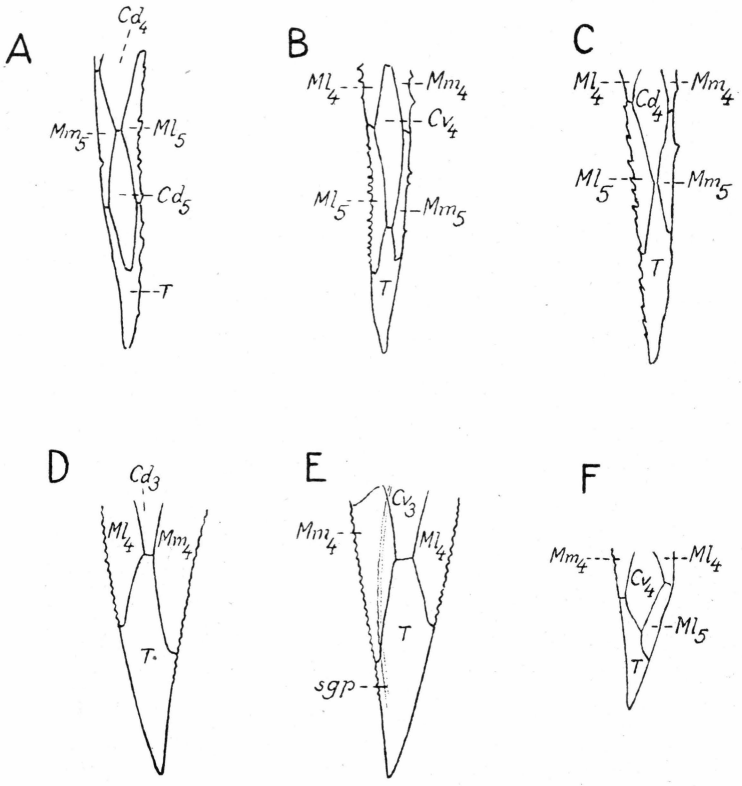
In his most recent work on *Bothriolepis* Gross (1941a, pp. 60–65) paid much attention to the variations in the number of dermal bones and transverse zones of bones respectively in the distal segment of the pectoral fin-armour. He arrived at the opinion that the terminal plate gave rise to distal bone elements by a process of desintegration, a sort of "Sprossung" and wrote concerning this as follows (p. 63): "Der Vergleich der Distalglieder hat uns gezeigt, dass sie stets nach dem gleichen Prinzip gebaut sind; sie bestehen aus einer wechselnden Zahl von Zonen, die sich aus je vier Knochen zusammensetzen. Die Anzahl der Zonen nimmt mit der phylogenetischen Entwicklung anscheinend zu (*Asterolepis* – *B. cellulosa* – *B. canadensis*), doch verschieden rasch innerhalb der Gattungen und Arten. Bei *Asterolepis* haben wir nur eine abgeschlossene Zone (3.), bei *Bothriolepis* drei (3.–5.). – – Die Terminalplatte is nicht ein Knochen unter anderen, sondern sie ist eine Art Sprossungskegel, gewissermassen vergleichbar der Knospe einer höheren Pflanze. Sie ermöglicht die phylogenetische Streckung des Distalgliedes, indem sie proximal immer neue Zonen abgliedert, distal aber ihr Wesen behält, nur bald diesem, bald jenem Typus, bald länger, bald kürzer seiend. Voraussetzung der Sprossung ist anscheinend die Streckung bis zu einer innerhalb der Arten festgelegten relativen Länge, bei der kein zu grosser Unterschied zwischen der neuen Zone und der proximal vorausgehenden Zone auftreten darf. Ist diese Länge erreicht, dann zerfällt das Proximalende der Terminalplatte in die vier Knochen einer neuen Zone, wobei meistens die Marginalia den Centralia vorauseilen, da sie ja auch räum-

lich den Centralia vorausgehen. Anscheinend erfolgt kein Zerfall, wenn die Terminalplatte sehr kurz ist; zur Individualisation der Zonen-Knochen gehört eine bestimme Grösse; nur die Terminalplatte kann dehr gross bis sehr klein sein."

The conditions in *B. canadensis*, which are now well known (cf. pp. 363–374 below), do not afford any evidence in favour of Gross's opinion just referred to. If a disintegration of elements has taken place from the terminal plate in the manner presumed by Gross the number of plates in the distal segment of such a species as *B. canadensis* be expected, of course, generally or at least often, to be smaller in young individuals than in fully mature ones. Expressed in another way the plates of the distal segment in *B. canadensis* would then be expected to have increased in number with the proceeding growth of the individuals. However, this is not the case. The variations as to the number of elements clearly appear to be completely independent of the age and size of the individuals. Besides, in both *B. canadensis* and other *Bothriolepis*-species (Gross 1941a, p. 65) it is often so that the plates of the distal segment tend to fuse and thus to become reduced in number in older individuals. It seems also very unlikely from other points of views that the terminal plate would have been able to undergo repeated distintegrations in the manner supposed by Gross. As far as may be judged at present, there are thus no indications whatever, that the increase in number of elements in the distal segment of the fin-armour in *Asterolepis – Pterichthyodes – Bothriolepis* would have taken place by a disintegration from the terminal plate. On the other hand, Gross is certainly right in comparing the increase in number of the dermal elements and transverse zones of these elements to the procedure which in Tetrapods causes the hyperphalangy (Gross 1941a, pp. 64–65). A similar phenomenon is otherwise met with also in the axial skeleton of the pectoral fin of Dipnoans in which the central axis is subdivided into a great number of short joints.

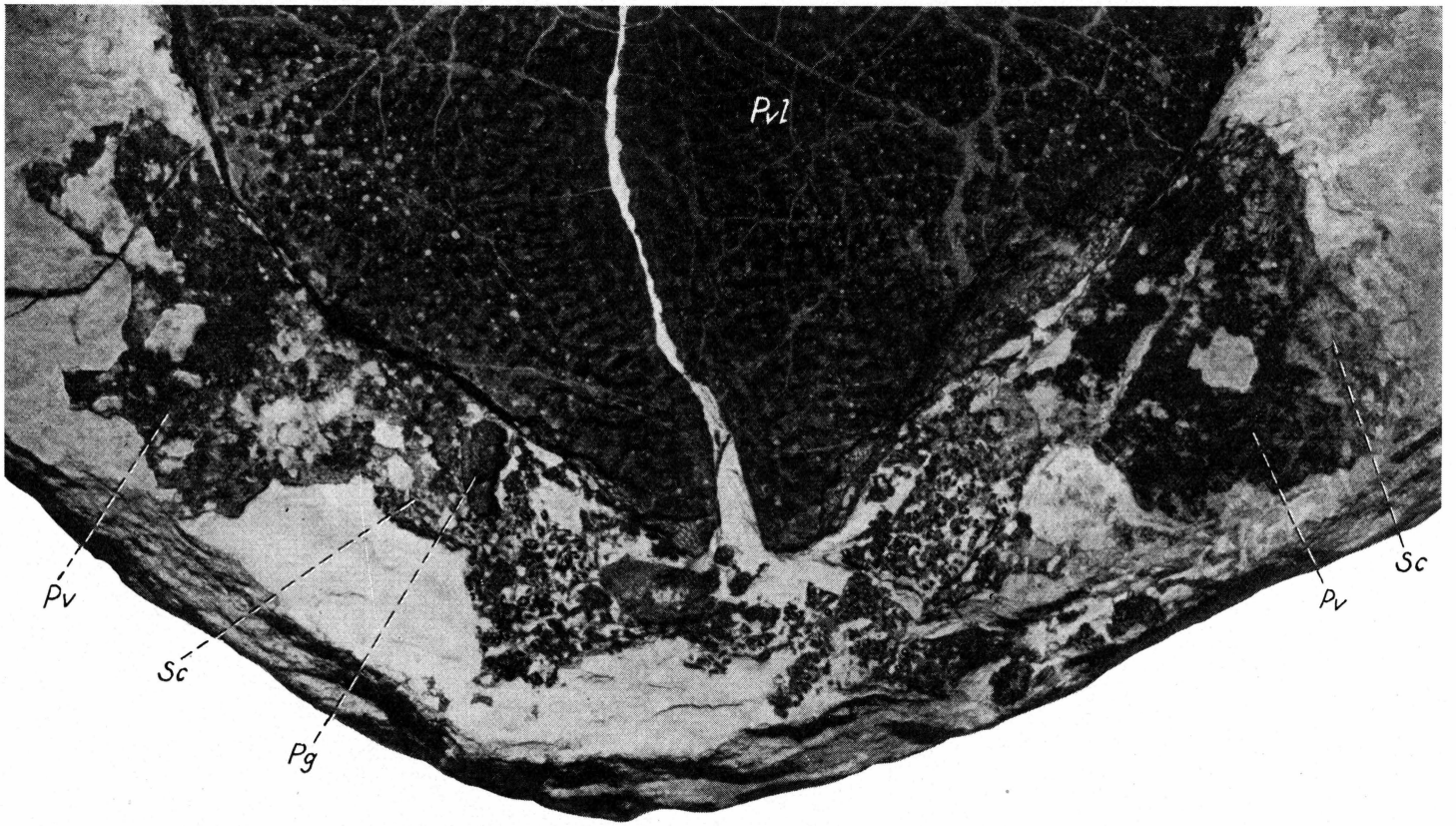
Apart from their greater number the bones of the distal segment in the *Bothriolepinae* are fundamentally as those in *Asterolepis*, *Pterichthyodes* and *Gerdalepis* (Traquair 1894–1906, text-figs. 34–38, 51–55, Gross 1931a, pp. 37–38, 43–44, text-figs. 9, 11, 12, pl. 6, figs. 3, 4; pl. 7, figs. 1, 2; pl. 8, figs. 1–13; 1941a, pp. 28–31, 53–54, 65–67, text-figs. 23C–E, 24, 43C–H, 44; 1941b, p. 208, text-fig. 9; Stensiö 1931, pp. 124–137, text-figs. 57, 58, 63, 66–69; Nilsson 1941, text-figs. 13, 21). The most proximal ones of them are developed almost in the same way as the corresponding ones in *Asterolepis*. The anconeal processes of the lateral and medial marginal plates 3 (Lm_1, Mm_1) – the lateral and medial anconeal processes (*pal*, *pam*, text-figs. 198, 228C–E, 295) – are both present.

The terminal plate in *Bothriolepis* (*T*, text-figs. 41B, 58A–C, 98, 195, 198, 228C–E, 295, 306), as recently pointed out by Gross (1941a, pp. 60–63, text-figs. 44, 45E–K), has mostly a characteristic shape, differing both



Text-fig. 58. Terminal parts of distal pectoral fin-segment, showing different types of terminal plates. *A*, *B*, of two individuals of *Bothriolepis canadensis*. Terminal plate of the normal *Bothriolepis*-type in dorsal and ventral aspects respectively. In both cases of the right pectoral fin. *C*, of *B. canadensis*. Terminal plate of the *Asterolepis*-type. Dorsal aspect. Left pectoral fin. *D*, *E*, of *Asterolepis ornata*. Left pectoral fin in dorsal and ventral aspects respectively. From Gross 1941a. *F*, of *Pterichthyodes milleri*. Left fin. Ventral aspect. From Gross 1941a.
Cd_3–Cd_5, dorsal central plates 3–5; Cv_3–Cv_4, ventral central plates 3–4; Ml_4, Ml_5, lateral marginal plates 4, 5; Mm_4, Mm_5, medial marginal plates 4, 5; *T*, terminal plate; *sgp*, pectoral pit-line groove.

from that in *Asterolepis* and from that in *Pterichthyodes* (text-fig. 58D–F). On its dorsal side it normally bifurcates proximally into two processes, a lateral and a medial, which together embrace the distal half of the most distal plate (Cd_5 or Cd_6) of the dorsal central series, whereas on its ventral side it is produced into a long process projecting proximally between, and separating, the distal halves of the most distal elements of the lateral and medial marginal series. In those cases when the dorsal central series of the distal segment consists only of two independent elements (Cd_3, Cd_4, text-fig. 58C), however, the terminal plate also on its dorsal side has a median proximally projecting process similar to that of the ventral side. In these cases the terminal plate is of a the same type, therefore, as in *Asterolepis*. An examination of the variations of the terminal plate in *Bothriolepis* (cf. pp. 373–374 below) thus clearly proves that, as maintained by Gross, the proximal processes



Text-fig. 59. *Bothriolepis canadensis*. Posterior part of the ventral wall of a trunk-armour with remains of the squamation and of the ventral side and of the pelvic fins. Ventral aspect. The pelvic fins represented mainly only by a blackish-brown felt-like carbonaceous film in consequence of which they are darker than the scale-covered part of the ventral side of the trunk. × 2.4. Specimen No. P. 2287 in the Swedish Museum of Natural History in Stockholm em as(espciment n as iext-figs. 55, 56, 59, 60, 133, 175).
Pg, skeletal element probably belonging to pelvic fin; *Pv*, pelvic fin; *Pvl*, posterior ventro-lateral plate; *Sc*, remains of 3-radiate vestigial scales of pelvic fins.

of this plate are potential serial homologues of the elements of the various longitudinal series situated further proximally in the fin-armour.

Pelvic fin.

The pelvic fin is known since long ago in the Brachythoracid Arthrodires, and has in more recent years been found also in other groups of Arthrodires (cf. Woodward 1891b, pp. 282, 289; 1922, p. 35; Dean 1896, p. 162; 1909, pp. 282–287; Jaekel 1903, p. 111; Stensiä 1925, p. 179; Heintz 1931, pp. 311–312; 1938, pp. 18–19; Jaekel 1929, pl. 10, fig. 2; Gross 1933b, p. 60; Watson 1934, pp. 447–448, 457; 1938, pp. 404–405; Gross 1938, pp. 201–202; Broili 1930a, pp. 15–16; 1933b, p. 428; Moy-Thomas 1939a, p. 22). It is obvious, therefore, that the pelvic fin must have been developed in Arthrodires in general. Under these conditions it must be assumed that this fin was present already as early as in the primitive Arthrodire-forms from which the *Antiarchi* are derived. Accordingly it is only quite natural that the pelvic fin itself or vestiges of this fin, are found persisting also in the *Antiarchi*.

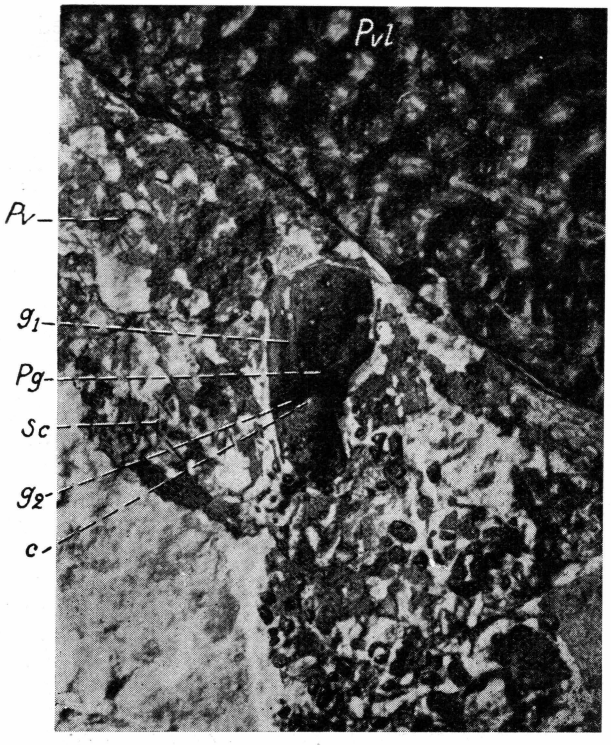
Became of the fact that the whole unarmoured division of their trunk is very rarely preserved the *Antiarchi* are still very imperfectly known as to their pelvic fin. As a rule there is no possibility even to make sure whether the pelvic fin persisted or not. Structures which are of such a nature that they may be regarded as remains of a pelvic fin are known at present only in two *Antiarchi*-species, *Pterichthyodes milleri* and *Bothriolepis canadensis*. In *P. milleri* these structures are shown in a dorso-ventrally flattened specimen reproduced by Forster-Cooper some years ago (1934, text-fig. 1). They consist there of fragments of a paired fold-like structure situated laterally to, and immediately behind, the subanal division of the ventral wall of the trunk-armour. No attention was paid to them by Forster-Cooper, and they seem also to have been overlooked by subsequent writers, dealing with *Pterichthyodes*. In *B. canadensis* pelvic fin formations were noticed already by Patten (1904, p. 114, text-fig. 1; 1912, p. 371, text-figs. 247, 248, 250), who described them as "frills". These "frills", which are also paired fold-like structures just behind the lateral walls of the trunk armour, were discussed by the present writer in 1931 (Stensiä 1931, p. 138) and were then interpreted by him as true pelvic fins, an interpretation, which, as we shall see, has now gained a further strong support. Everything seems decidedly to show, therefore, that *Bothriolepis* possessed a somewhat well developed pelvic fin.

As may be gathered from what has been set forth above, the pelvic fin in *Bothriolepis* was a fold-like structure, projecting laterally from the lower part of the unarmoured division of the trunk close behind the trunk-armour, above and a little behind the subanal division of the posterior ventro-lateral

plate. Accordingly it projected laterally from the unarmoured division of the trunk in the lowermost part of, and just behind, the large notch which is always developed in the posterior margin of the lateral wall of the trunk-armour (text-figs. 38, 40).

The materal of *B. canadensis* available to the writer on the whole is much more poorly preserved as regards the pelvic fin than that dealt with by Patten. However, it includes a specimen which shows the pelvic fin of both sides in another state of preservation than the ordinary one and which consequently is of much interest. This specimen (text-figs. 55, 56, 59, 60, 133, 175), which is embedded in a nodule, is fairly complete, wanting only little more than a large anterior part of the head-shield. It displays inter alia the ventral wall of the trunk-armour, considerable parts of both the pelvic fins, and the squamation of the foremost part of the ventral face of the trunk just behind the trunk-armour. The pelvic fin (*Pv*, text-figs. 59, 175) forms a thin fold, which protrudes fairly far laterally to the subanal division of the posterior ventro-lateral plate, a fold which probably was fairly stiff. This fold is well defined anteriorly, whereas posteriorly it seems to have passed over gradually into the lateral wall of the trunk. There is no evidence of of ceratotrichia, but the fin in its fossil condition consists of a fairly thick carbonaceous mass, somewhat felt-like in structure and brownish-black in colour. In this mass are embedded the peculiar 3-radiate exoskeletal structures (*Sc*, text-figs. 56, 59, 60) described above (p. 146), which conceivably are highly vestigial scales. By the absence of other exoskeletal formations the pelvic fin-folds are clearly distinguiswable from the adjacent parts of the flanks and the lower side of the unarmoured division of the trunk, which, as we have seen (pp. 145–147 above), are covered with small foursided or irregular scales and dermal tubercles.

In the hindmost basal part of the right pelvic fin, just at the transition to the scale-covered part of the lower side of the trunk, in the specimen of *B. canadensis* dealt with just above we notice a small bone, probably detached, which is of a certain interest. This bone (*Pg*, text-figs. 59, 60, 175) consists of a solid tissue, resembling that of a dermal bone, but does not show any signs of ornament, at least not on the side, that is exposed. It is of an oblong shape and broadest at the end which is nearest to the ventral wall of the trunk-armour. At this end it is somewhat convex, whereas at its opposite end it is more truncated. On its anterior broadest part it presents a longitudinal groove (g_1), situated along its antero-laterally directed margin, and at the posterior end of this groove there is another, oblique transverse groove (g_2), which leads to a canal (c), penetrating into the interior of the bone. In spite of its solid structure it is impossible to decide whether the bone here under consideration is of exoskeletal or endoskeletal origin. Be this as it may, it is conceivable, however, that somehow it belongs to the pelvic fin.



Text-fig. 60. *B. canadensis*. A posterior part of the right pelvic fin of the specimen reproduced in text-figs. 55, 56, 59, 60, 133, 175. Ventral aspect. × $^{5}/_{1}$.
Pg, bone-element probably belonging to pelvic fin; *Pv*, right pelvic fin; *Pvl*, right posteiror ventro-lateral plate; *Sc*, remains of 3-radiate vestigial scales of pelvic fins; *c*, opening of a canal in the plate *Pg*; g_1, marginal groove; g_2, oblique transverse groove leading from opening *c*.

The pelvic fin in *B. canadensis* has recently been dealt with by Denison (1941), who has examined the well preserved material in Patten's collections at Dartmouth. According to him the pelvic fin was probably differently developed in the two sexes of *Bothriolepis*. In one of the sexes it would be of small size and little complicated in its shape, in the other sex, on the other hand, it would be large, with a large "frill", and very complicated in structure. In the latter sex it was said to be developed is such a manner that it may be suspected to have served either as a clasper, comparable to that in Elasmobranchs, or as a brood pouch. The pelvic fin described above by the present writer would obviously be of the small, simple type.

Denison bases his description of the pelvic fin mainly on the petrographic characters of the rock-types filling up the fin in the fossils, thus on conditions which are far from reliable. His opinions, therefore, to a large extent are very doubtful. As his description is difficult to follow and as the reproductions accompanying his account are obscure, a proper criticism of his interpretations in this case cannot be given without access to his material.

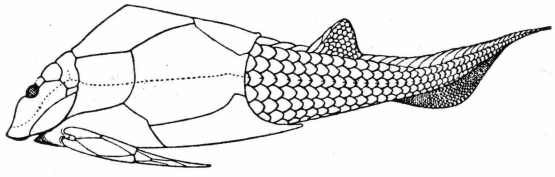
Unpaired fins.

Dorsal fins.

An anterior and a posterior dorsal fin are known in *Bothriolepis canadensis* and it is conceivable, therefore, that the *Bothriolepinae* in general, or at any rate the *Bothriolepis*-species, were equipped with two dorsal fins. In *Pterichthyodes*, on the other hand, there is, as we know (text-fig. 61; cf. also Traquair 1894–1906, text-figs. 34, 36, 51; Forster-Cooper 1934, text-fig. 1 and pl. 2; Watson 1935, text-fig. 27), only one dorsal fin, representing the posterior one of the two in *Bothriolepis*. The anterior dorsal fin in *Pterichthyodes* has been transformed into a few large unpaired dorsal ridge scales (text-fig. 61).

The anterior dorsal fin in *B. canadensis* (text-figs. 38, 40B; cf. Patten 1904, text-figs. 1, 2; 1912, text-figs. 247, 251) is situated close behind the dorsal wall of the trunk-armour. In the material available to the writer it is very deficiently preserved, and hence nothing can be said of its shape. According to Patten it is low, longer than high, and completely devoid of scales and other exoskeletal structures. Its endoskeleton must have consisted entirely of cartilage.

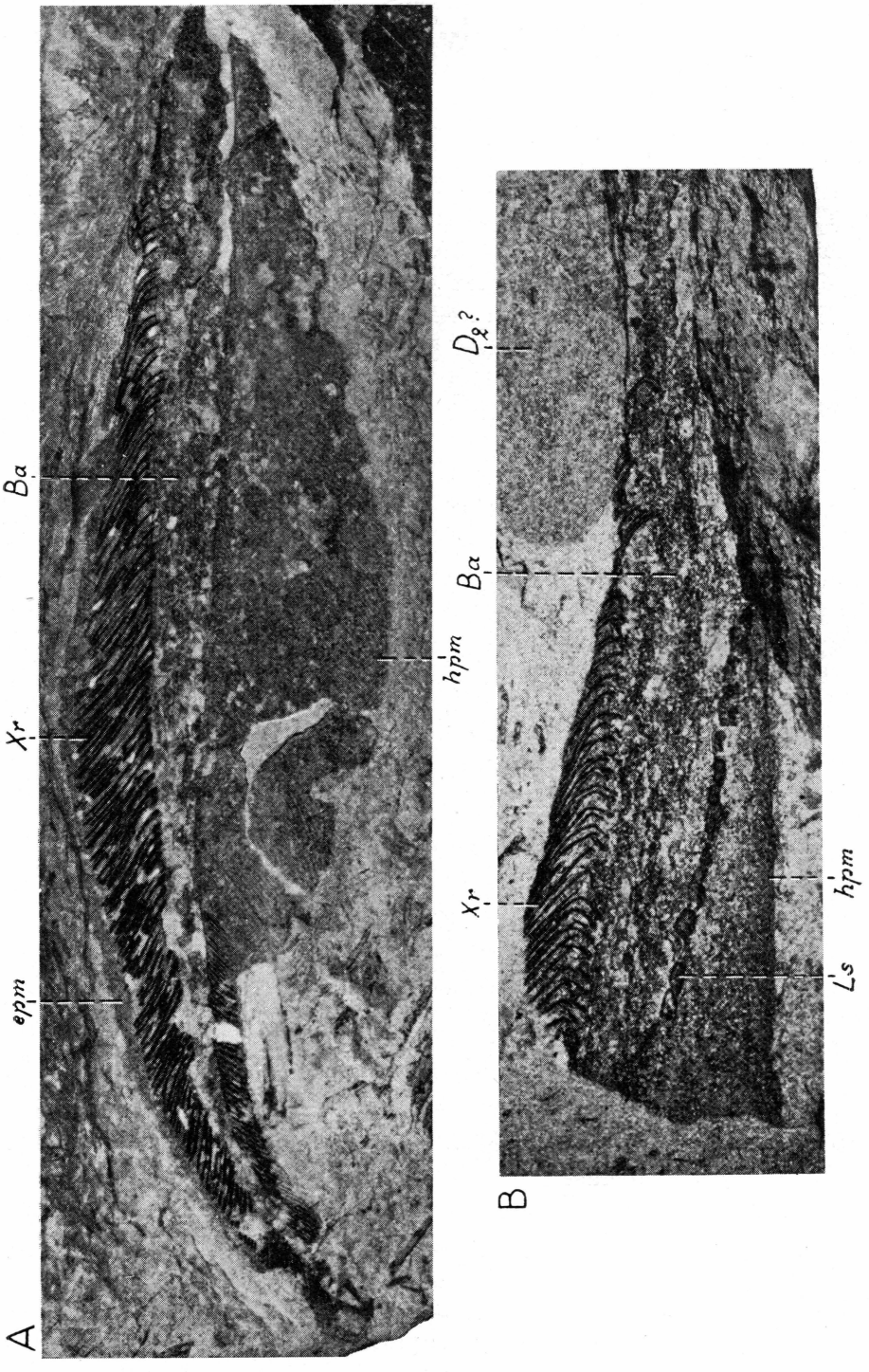
The posterior dorsal fin in *B. canadensis* (text-figs. 38, 62C) is normally about as high as it is long (cf. Stensiö 1931, text-fig. 72; Patten 1904, text-figs. 1, 2; 1912, text-figs. 247–251), but in some individuals (text-fig. 62B) it may probably be somewhat longer in proportion to its height. In contrast to what is the case with the corresponding fin in *Pterichthyodes* (text-fig. 61) it has no spinelike formation at its anterior margin and, besides, it is also completely without scale-covering. In well preserved



Text-fig. 61. Restoration of *Pterichthyodes milleri* in lateral aspect. From Watson 1935. The position of the pectoral fin in this restoration is wrong (cf. p. 154 above and text-figs. 38, 40 *B*).

specimens its membrane shows a delicate proximo-distally disposed striation, which certainly was caused by decayed ceratotrichia (cf. Stensiä 1931, pp. 139–140). The endoskeleton of the fin must have consisted of cartilage without lime-incrustations.

The Petalichthyid, Stegoselachian and Rhenanid Aarthrodires have only one dorsal fin, corresponding to the posterior one of the *Antiarchi*. As an anterior dorsal fin seems to occur however, in the Brachythoracids in general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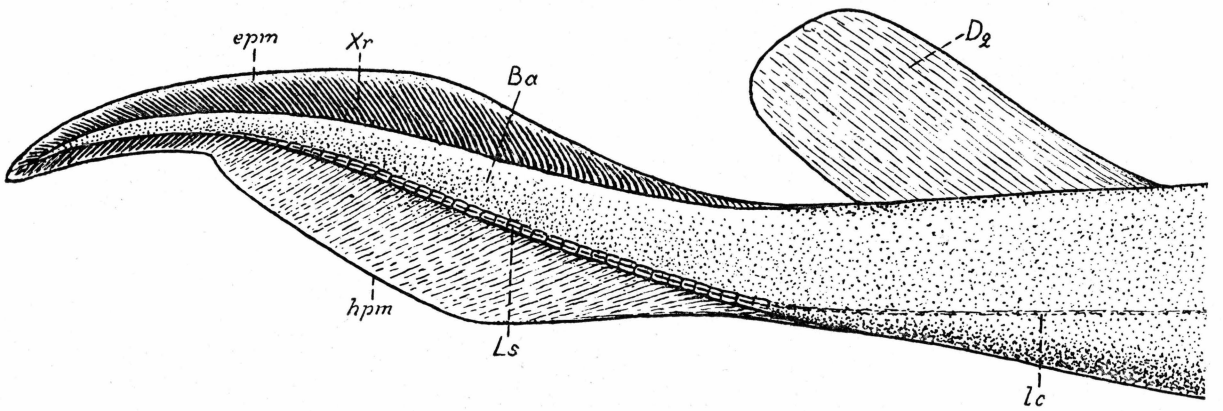


Text-fig. 62. *Bothriolepis canadensis*. *A*, an almost complete caudal fin showing the shape of the epichordal and hypochordal fin-membranes. Specimen No. P. 2674 in the Swedish Museum of Natural History in Stockholm. ×2. *B*, a deficient caudal fin showing parts of the fin-membranes and a part of the body-axis with a longitudinal row of scales developed in relation to the main lateral line groove. Specimen No. P. 2875 in the Swedish Museum of Natural History in Stockholm. × 2. *C*, restoration of the hindmost parts of the caudal region with the posterior dorsal and caudal fins. × 2. *Ba*, body axis; D_2, posterior dorsal fin; *Ls*, row of small scales, developed in relation to the main lateral line groove of the trunk; *Xr*, lime-impregnated rods, probably excessively developed ceratotrichia; *epm*, epichordal fin-membrane; *hpm*, hypochordal fin-membrane; *lc*, main lateral line groove.

(Heintz 1931, p. 309, text-fig. 12) and in *Rhamphodopsis* among the Ptycdontids (Watson 1938, pp. 401, 403, text-fig. 1) it may be presumed that the primitive ancestral forms of the Arthrodires, and thus also the ancestors of the *Antiarchi*, were equipped with two well developed dorsal fins.

Anal fin

The anal fin is absent both in *Bothriolepis* (text-figs. 38, 62) and *Pterichthyodes* (text-fig. 61), and it is highly probable, therefore, that it was absent in the *Antiarchi* in general. The absence of this fin in *Antiarchi*, however, is certainly secondary and due to the adaption of the group to a pronounced benthonic mode of living.

It may be mentioned for comparison that an anal fin was certainly present in Brachythoracid Arthrodires, but absent in Rhenanids and other highly benthonic Arthrodire forms.

Caudal fin.

The caudal fin of the *Bothriolepinae* has been found preserved only in *B. canadensis*. In this species (text-figs. 38, 62), as we know since long ago (Patten 1904, pp. 113–114, text-figs. 1, 2; 1912, text-figs. 247–251; Stensiä 1931, pp. 140–141, text-fig. 72), it is clearly heterocercal, long and relatively low. In its general proportions it agrees fairly well with the corresponding fin in *Pterichthyodes milleri* (text-fig. 61; cf. also Watson 1935, text-fig. 27), whereas it is longer and lower than that in *Pterichthyodes cancriformes* (Forster-Cooper 1934, pl. 2, figs. 1, 2). Its body axis is long and slender, but, contrary to what is the case in *Pterichthyodes* (text-fig. 61), it does not extend quite to the caudal tip of the fin. Its hindmost part is more or less clearly bent downward. The epichordal lobe was developed as a real functioning membrane, the epichordal membrane (*epm*, text-fig. 62), and not as a series of large unpaired ridge-scales, as in *Pterichthyodes* (text-fig. 61), a condition which together with the relatively slight upward bend of the longer anterior part of the body axis effects that the fin as a whole is somewhat less heterocercal in appearance than in *Pterichthyodes*. The epichordal membrane (*epm*) begins somewhat behind the posterior dorsal fin and extends backwards to the very caudal tip of the body axis, behind which it is continuous with the hypochordal fin-membrane. It is highest about at it middle, where its height is almost equal to that of the foremost part of the body axis, lowest at its anterior end. The hypochordal membrane (*hpm*, text-fig. 62) is developed along the whole ventral margin of the body axis and extends, therefore, further backwards than in *Pterichthyodes*. Its hindmost part continuous with the epichordal membrane, however, is low and clearly marked off from the longer anterior part, which, as in *Pterichthyodes*, is comparatively high. The epichordal lobe and the hindmost low part of the hypochordal lobe are strengthened with paired lime-impreg-

nated rods (*Xr*, text-fig. 62), a little laterally bent and somewhat expanded at their bases. These rods were previously interpreted by the writer as vestigial ridge-scales, but, as at the transition between the posterior low and anterior high parts of the hypochordal membrane they pass gradually over into a striation, which obviously is to be regarded as markings of decayed ceratotrichia, it seems almost certain that they are simply excessively developed ceratotrichia, impregnated with lime-salts. A further support for this opinion of their nature is the fact that they are much more numerous than what they might be expected to have been in case they were vestiges of ridge scales. Ceratotrichia were thus developed in both the epichordal and hypochordal membranes of the fin. The horizontal part of the epichordal and hypochordal membranes behind the body axis is low, but is always clearly developed. Apart from the longitudinal row of scales developed along the ventral margin of the body axis in relation to the main lateral line (cf. pp. 145–146) the caudal fin is completely without scale-covering.

* * *

As may be gathered from the account given just above, with regard to the development of its unpaired fins *Bothriolepis* is clearly distinguished from *Pterichthyodes* in the following fundamental characters: 1) the presence of a real functioning anterior dorsal fin instead of a series of unpaired dorsal ridge-scales; 2) the absence of a spine-like formation at the anterior margin of the posterior dorsal fin; 3) the less pronounced heterocercal shape of the caudal fin as a whole; 4) the presence of a well developed functioning epichordal membrane in the caudal fin, instead of a series of dorsal ridge-scales; 5) the further backward extent of the hypochordal membrane of the caudal fin and the fact that the hypocordal and epichordal membranes meet and are continuous with each other behind the extremity of the body axis; 6) and finally, the excessive development and lime-impregnation of the ceratotrichia in the whole epichordal membrane and in the hindmost low part of the hypochordal membrane of the caudal fin. – The total absence of scales or dermal tubercles on the membranes of the unpaired fins in *Bothriolepis* is no character specially distinctive of this genus, for the membranes of the corresponding fins are devoid of scales in one of the *Pterichthyodes*-species (*Pt. cancriformis,* Forster-Cooper 1934) and may with good reason be suspected to have been without scales also in several other *Antiarchi*-forms.

In character No. 1 of the six enumerated above *Bothriolepis*, as we have already seen (pp. 165–166), has certainly retained a more primitive condition than *Pterichthyodes*. It is also not impossible that it may be more primitive than *Pterichthyodes* in characters Nos. 3, 4 and 5 too, for, as is well known, the caudal fin seems normally to be only fairly slightly heterocercal in the Arthrodires and may, therefore, be assumed in the primitive ancestors of the Arthrodires to have been almost symmetric with both an epichordal and an hypochordal membrane. In character No. 6, on the other hand,

Bothriolepis is clearly more specialized than *Pterichthyodes*, and it is highly probable that it is so also in character No. 2.

Soft internal structures.

In a paper published a few years ago Denison (1941) described certain formations in *Bothriolepis canadensis* which he interpreted as remains of soft internal structures. These formations, some of which have already been noticed and discussed by Patten (1904, p. 116, text-fig. 2; 1912, pp. 371–372, 379–380, text-figs. 251, 253, 254, 256), are found within the head- and trunk-armour.

As far as may be judged from the material available to the writer, Denison is probably right in considering a concentric formation in the interior of the trunk-armour as remains of the alimentary canal. And he is probably also right in concluding that the intestine was equipped with a spiral valve of the "scroll type", developed much as in the *Carcharinidae* and *Sphyrnidae* among the Elasmobranchs. His interpretations of the formations in the head, on the other hand, seem very doubtful. It may possibly be true that there are certain traces of the oesophagus, but the paired formation which extends backwards from the foremost part of the ventral side of the gill-region into the foremost ventral part of the trunk-armour cannot possibly be the cast of a paired lung, as maintained by him. This paired formation reached so far forwards underneath the visceral arches that it would have been in communication with the hindmost basal part of the mouth-cavity about opposite the jaw articulation, and thus either in front of the basibranchial series of elements, or else by a canal through or between some of the foremost basibranchial elements (cf. text-figs. 7, 8, 34). Hence in its position and in its relations to the visceral endoskeleton it is quite different from an air bladder or lung, which, as we know (Rauther 1937, pp. 884–890; Marcus 1937, pp. 919–926), arises from material belonging to reduced gill pouches situated behind the fifth branchial arch. As thus it cannot be an air bladder or lung, the formation under consideration may be either a cast of some sort of accessorial gill, or, more probably, simply a mud-filling in the lower part of the gill chamber, which, as may be understood from the account given above (pp. 21, 39, 40) must have been closed laterally by the gill cover with its bones, and ventrally to that by soft tissue, so that it opened only posteriorly.

Finally it should be pointed out here that the nasal cavity cannot have had the shape of the matrix which Denison has found in its place. This matrix fills up not only the nasal cavity, but occupies the whole preorbital recess, thus the space occupied by the whole anterior dorsal part of the ethmoidal region, including the nasal capsules (cf. text-figs. 6, 7, 9, 13–15).

Ornament.

The ridges and tubercles forming the ornament in the *Bothriolepinae* normally consist of bone-tissue rich in cell-spaces. However, it was noticed by the writer that the ridges and tubercles on the median part of the anterior median dorsal plate in *B. canadensis* may sometimes be formed most superficially of a solid tissue completely devoid of cell-spaces, a tissue which in some respects is suggestive of dentine.

As pointed out by Gross (1941 a, pp. 5, 33–34), *Bothriolepis* and *Grossilepis* differ considerably from one another in their ornament. *Bothriolepis*, as is well known since long ago, has a fundamentally reticular ornament, highly suggestive of that in *Remigolepis* (Stensiö 1931, pp. 183–185, 187, 189, 191; cf. also Part III of this work), whereas *Grossilepis*, on the other hand, shows a rather typical tubercular ornament, according to Gross reminiscent of that in *Asterolepis ornata*.

In the three *Bothriolepis*-species *B. canadensis*, *B. gippslandiensis* and *B. groenlandica*, of which a large material has now been investigated (cf. p. 229; cf. also Hills 1931, pp. 216–217), the interesting fact could be established that the ornament is very uniformly and equally developed in small individuals, but that with the proceeding growth of the individuals it gradually underwent more or less considerable transformations leading to such a result that in medium-sized, and particularly in large, individuals it became not only more or less different from what it was in the small individuals, but also of a different type in each one of the three species.

For the purpose of illustrating what has been said just above concerning the transformation of the ornament during the growth in *B. canadensis*, *B. gippslandiensis* and *B. groenlandica* the following details may be given here.

In small individuals of the three species just under consideration (cf. pp. 376, 521, 581; text-figs. 88, 90, 91, 95–97, 115, 199–206, 280 A, 302; pl. 3, fig. 2; pl. 6, fig. 1; pl. 11, fig. 6; pl. 13, fig. 3; pl. 34, figs. 1, 4; pl. 35, figs. 1, 3; pl. 43, fig. 3; cf. also Hills 1931, pp. 216–217) the ornament consists of a strikingly regular network of anastomosing ridges, a network with small meshes, fairly uniform in size and outlines. The ridges are delicate, but well marked. All of them are continuous throughout their extent between their points of anastomoses and, besides, often have a practically uniform thickness. They are either without distinct swellings and elevations, as in *B. groenlandica* (text-fig. 302), or else exhibit tubercular elevations at their points of union, as in *B. canadensis* (text-figs. 199–203, 205). The ridges of the individual bones show no indication of a concentric or radiating disposition.

In large individuals of the three species in question, on the other hand, the ornament is developed mainly as follows (text-figs. 10, 25 A, 76, 154–159; pl. 2; pl. 3, fig. 1; pls. 4, 5, 7, 22, 25, 28–31, 33; pl. 37, fig. 1; pls. 38–41; pls. 44–49; cf. also Hills 1931, pp. 216–217). Normally it is relatively coarser

and often also more irregular than in small individuals. Mostly it shows also a trend to become tubercular, a trend which is slightly pronounced in *B. groenlandica*, more pronounced in *B. canadensis*, but most so in *B. gippslandiensis*. This trend in *B. canadensis* has often led to a partial, in *B. gippslandiensis* normally even to a complete, breaking up of the ridges into tubercles. In *B. groenlandica* the network of anastomosing ridges persits to the same extent as in small individuals, but with the modifications that the meshes of the network are a little more varying in size and shape, that the ridges are somewhat more varying in width and height, and that the points of anastomoses of the ridges may be little raised in places into tubercle-like elevations. In *B. canadensis* the network of anastomosing ridges may also persist to a similar extent as in small individuals, but it may also often be clearly retained only on the central parts of several of bones, whereas on the marginal parts of the bones it is more or less completely reduced, the anastomoses between the ridges being sparse or absent there. In both these cases, however, the meshes of the network are very variable as to size and shape. Moreover, in *B. canadensis* the ridges are always clearly nodose, and, besides, their points of anastomoses are elevated into tubercles, usually stellate at their bases. A more or less great number of the ridges in *B. canadensis* are also subdivided into shorter pieces, undulating or vermiculating, and into tubercles, stellate at their bases. In all of the three species under consideration the ridges, or their derivates, on the marginal parts of the bones are mostly disposed more or less concentrically or radiatingly, or both these ways at the same times, whereas on the central parts of the bones, on the other hand, they retain a more or less regular reticular disposition. This different development of the ornament of the marginal and central parts of the bones seems to be due to a much more rapid growth of the peripherical parts of the bones in older individuals than in younger ones, and accordingly we are here probably concerned with a correlative relation between the disposition of the ornament and the growth of the bones similar to that in Stegocephalians (Bystrow 1935; Säve-Söderbergh 1937).

As may be gathered from what has just been set forth, the ornament in *B. canadensis*, *B. gippslandiensis* and *B. groenlandica* during the growth of the individuals underwent such a transformation that in these three species we are justified in distinguishing an immature and a mature type or ornament. Judging from its characters in the other *Bothriolepis*- species and in *Grossilepis tuberculata*, the ornament in them must also have undergone a transformation during the growth of the individuals corresponding to that of the three species just dealt with. An immature and a mature type of ornament are therefore distinguishable in the *Bothriolepinae* in general.

The immature and mature types of ornament differ only slightly from each other in certain *Bothriolepis*-species, as for instance *B. ornata*, *B. max-*

ima and *B. groenlandica*, whereas they show considerable differences in other *Bothriolepis*-species, such as *B. canadensis*, *B. panderi* and *B. lohesti*, but above all *B. gippslandiensis*. It is fully obvious, therefore, that the mature type of ornament in the various species represents very different stages of transformation of the immature type. It deserved also to be emphasized in this connection that medium-sized individuals of the various species exhibit all stages of transition between the immature type and the mature type characteristic of each species, and that the immature type sometimes may persist fairly unchanged both in medium-sized and large individuals.

In *B. canadensis*, of which a particularly large material was examined by the writer (cf. pp. 376–385 below), the ornament varies exceedingly as to its details even in individuals of about the same size. The conditions in this species show clearly that the range of variation of the ornament in the *Bothriolepis*-species generally is much wider than what could be supposed hitherto.

From our knowledge of its development at various stages of growth it is fully obvious now that the ornament in the *Bothriolepinae*, or at any rate in *Bothriolepis*, cannot be used as a species character when we are dealing with small individuals, since normally it is very alike in small individuals of all species. On the other hand, it may often be of a good help for the determination of medium-sized, but above all of large, individuals.

Sensory canal system.

The sensory canal system in the *Bothriolepinae* could be studied in detail in *Bothriolepis* in which, therefore, it is very well known now both as to its disposition and as to its variations. It is also somewhat well known in *Grossilepis* (Gross 1941a, pp. 33–57), where in essentials it is as in *Bothriolepis*.

In *Bothriolepis* the pit-line grooves of the dorsal side of the armour, that is to say the pit-line grooves on the head-shield and on the dorsal wall of the trunk-armour, as a rule are deeper and more conspicuous in young individuals (text-figs. 199, 200, 202, 205, 206) than in fully mature ones (text-figs. 154–159). In addition it was found in *Bothriolepis* that two pit-line grooves of the dorsal side of the armour, the anterior oblique cephalic pit-line groove (*ifc.*b_1) and the anterior oblique abdominal pit-line groove (*dlg*$_1$), which often or even normally are present and well developed in young individuals, generally disappeared during the proceeding growth so that as a rule they are absent in fully mature individuals (cf. pp. 177, 185–186).

The investigations of the sensory canal system of the *Bothriolepinae* carried out in this work has led to the detection of certain sensory canal grooves, previously unknown, and to new interpretations of several of the sensory canal grooves, interpretations which differ considerably from the older ones given by the writer in 1931 (Stensiö 1931, pp. 141–150). Under

these conditions and in view of the fact that new terms have to be introduced for several of its grooves the sensory canal system will be fairly exhaustively dealt with here.

The supraorbital sensory groove (soc_1, soc_2) is here defined somewhat differently than in 1931 (Stensiö 1931, p. 142). It will now be considered to comprise two sections, a posterior paired one and an anterior median unpaired one. The posterior paired sections (soc_1, text-figs. 21C, 30D, 65, 104, 114; cf. Stensiö 1931, text-figs. 11, 74) is the vestigial groove which was interpreted by the writer in 1931 as the supraorbital sensory canal groove. As is now obvious, this section is mostly situated on the posterodorsal sclerotic plate, more precisely along the medial margin of this plate, but may it sometimes also be found along the lateral margin of the pineal plate. The anterior unpaired section (soc_2, text-figs. 4, 6, 7, 9, 10, 14, 20Al 65, 82–85, 114, 208, 209, 219, 220, 233A, B, E, 235A, 247, 249, 252A, 253A, B, 266, 267A–C, 273B, 274, 275, 303A) is a pit-line groove on the premedian plate, where it forms a commissure between the anterior parts of the upper infraorbital grooves (ifc_1; cf. p. 173 below) of both sides. Accordingly it is situated far in front of the posterior section and, at any rate in the fossils, has no connection with that section. As is already well known (Stensiö 1931, text-fig. 7D, E), it is very variable as to its configuration and delvelopment otherwise. It is generally transverse and arched in such a manner that it is convex on its posterior side and correspondingly concave on its anterior side (text-figs. 9, 10, 14, 20, 65A), but in certain species it may sometimes, or often, be rostro-caudally produced and extend some distance backwards on the premedian plate (figs. 65B, 233A, B, 235A, 253B). The facts that contrary to the adjacent parts of the upper infraorbital grooves (ifc_1) it is a shallow pit-line and that it extends more or less backwards on the premedian plate have caused that it is regarded here not as a commissural part of the upper infraorbital grooves, but as an anterior vestigial part of the supraorbital sensory grooves, which must be assumed primarily to have reached forwards so that they were in connection with the infraorbital grooves quite as is the case in Euarthrodires (cf. text-figs. 66, 67). They may then have fused for some distance most anteriorly on the snout in the manner shown in text-fig. 65B, after which their middle part became reduced, so that only a supraorbital section, and the anterior unpaired section were left (fig. 65A, B). – In *Pterichthyodes*, *Asterolepis* and *Remigolepis* we know so far only the anterior unpaired section of the supraorbital sensory canal groove.

That the posterior paired section (soc_1) of the supraorbital sensory canal groove was supplied by the n. ophthalmicus lateralis is fairly certain. On the other hand, it is very doubtfull whether this was the case also with the anterior unpaired section. It is not quite impossible, therefore, that as main-

tained by the writer in 1931, the latter section may be an ethmoidal commissure of the upper infraorbital grooves (ifc_1).

The infraorbital sensory groove (ifc_1, ifc_2), as here defined, consists of two paired grooves on either side of the head. These two grooves, which are connected with each other by means of the dorsal part of the groove *vcp*, will be referred to as the upper and lower infraorbital grooves respectively.

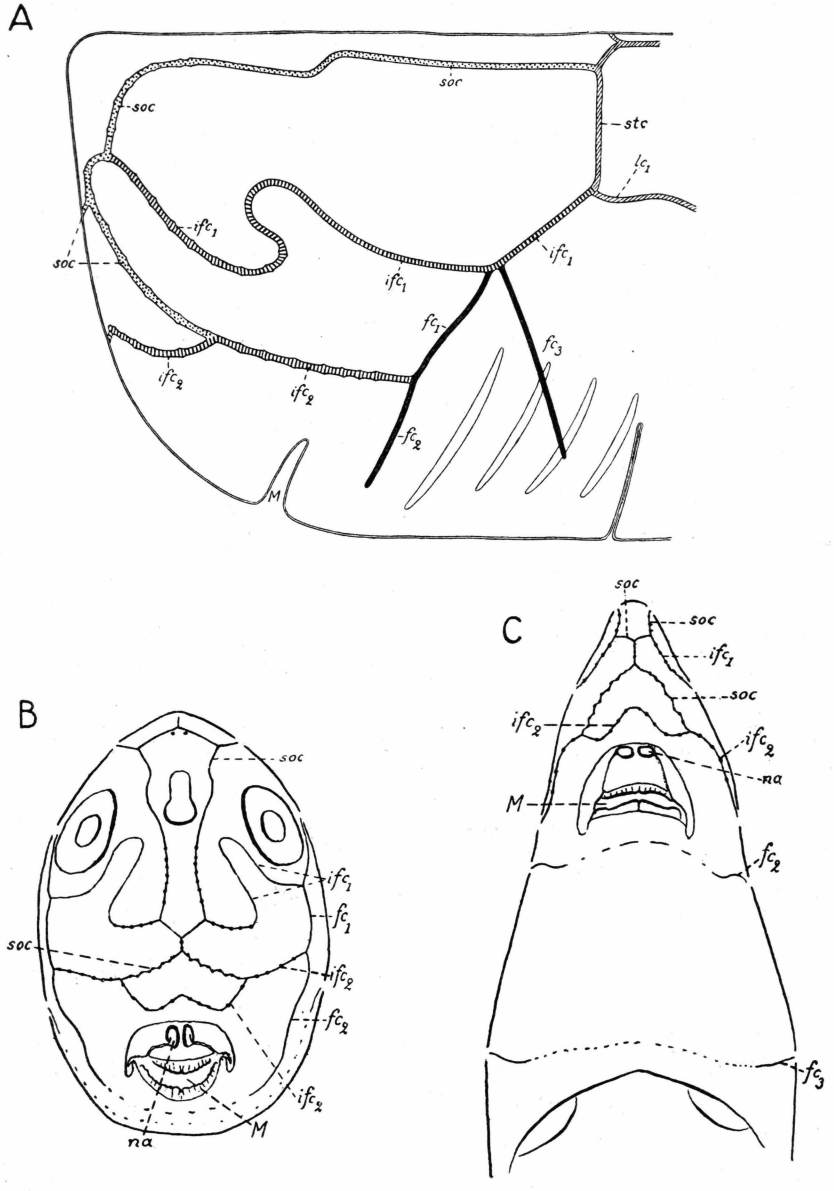
The upper infraorbital groove (ifc_1, text-figs. 4, 6, 7, 9, 10, 14, 24, 27–29, 65, 82–84, 89, 98–100, 114, 208, 209, 219, 223, 229, 233A, B, E, H, 234A, 235A, 247, 249, 252, 253A, C, D, 266, 267F–J, 273B, 274, 277, 303A, B, E) is here considered to extend from the anterior unpaired section of the supra-orbital groove (soc_2) backwards as far as to the pit-line groove *mpg* on the hindmost part of the paranuchal-marginal plate, where it passes over into the cephalic division of the main lateral line groove (*ptc*). It constitutes the chief part of the groove which was interpreted as the infraorbital groove in 1931 (Stensiö 1931, p. 142) and throughout its extent lies on the upper side of the skull-roof. Normally it is of a deep type, but sometimes it may be shallow or absent some distance nearest behind its connection with the groove *vcp* (text-figs. 24F, 82B, 83C, 89E, 208B, 209, 221E, 267H, 274B, 277A, B; cf. Gross 1941a, text-figs. 3E, 27C). At this place it seems in certain cases (text-figs. 82B, 89E, 208B, 221E, 267H; cf. Gross 1941a, text-fig. 3E) to be replaced by the semicircular pit-line groove (*cir*). Most anteriorly it passes over more or less into the unpaired median section (soc_2) of the supraorbital groove. From this groove it runs laterally and backwards to the groove *vcp* near or at which it takes an on the whole posterior course. In this posteriorly running part it makes first a more or less distinct lateral bend and then a long shallow medial curve, after which most posteriorly it bends somewhat laterally, passing over into the cephalic division of the main lateral live groove (*ptc*). Together with the corresponding groove of the opposite side and the anterior median (soc_2) section of the supraorbital groove it forms a continuous sytem of grooves along the lateral and rostral margins of the whole head-shield. This system of grooves in different specimens of one and the same species varies considerably as to its position in relation to the said margins of the head-shield, but despite this it is obvious, however, that in certain species, as for instance *B. panderi*, *B. maxima* and *B. gigantea*, it generally runs nearer to the rostral and lateral margins of the shield than in others, e. g. *B. canadensis*, *B. cellulosa*, *B. alvesiensis*, *B. groenlandica* and *Grossilepis tuberculata*. On account of its position on the head the upper infraorbital groove was certainly innervated, as normally in fishes, by branches from the n. buccalis lateralis, including the n. oticus lateralis.

The lower infraorbital groove (ifc_2, text-figs. 4, 7, 8, 34, 35, 114) is situated entirely on the lower side of the head, anteriorly and antero-laterally, that

is to say morphologically dorsally to the opening of the mouth. It lay to a great extent in the skin, and hence considerable parts of it are missing in the fossils. This groove was presumably in communication with the groove *vcp* (text-figs. 8, 34, 114) ventrally to the prelateral plate (*Prl*), between that plate and the infraprelateral plate (*Py*), from where it passed forwards and medially in the skin on to the mental plate (*Me*), which it reached at the middle of the posterior margin. On the mental plate, where it is developed as a shallow pit-line groove, it first runs medially and somewhat anteriorly, then rather rapidly turning in an antero-medio-dorsal direction. With this latter course it crosses the dorsal margin of the plate not so very far postero-laterally to the antero-dorsal corner, after which it continued in the skin between the mental plate and the rostral margin of the head-shield. In this part of its course it may perhaps have anastomosed with the corresponding groove of the other side so that an ethmoidal commissure was formed. From its position in relation to the mouth-opening and the upper jaws it is obvious that the groove here in question could only have been innervated by branches from the n. buccalis lateralis. It is beyond question, therefore, that it must represent a division of the infraorbital sensory canal. As may be gathered, it is identical with the subrostral pit-line (*ifgv*) of my description in 1931 (Stensiö 1931, pp. 144–146), exclusive, however, of the semicircular pit-line groove and the pit-line *vcp*. The groove is known thus far only in the *Bothriolepinae*.

The dorsal part of the groove *vcp* which connects the upper and lower infraorbital grooves may perhaps also form part of the infraorbital groove. At present, however, I am most inclined to believe that this is not the case, but that the said part of the groove *vcp* is of the same nature as the ventral part of the same groove and as the groove *orp* (see p. 179 below). If this opinion of mine is true it follows, of corse, that the upper and lower infraorbital grooves are not directly continuous with one another as normally in Arthrodires (text-figs. 66–69, 72–74) and most other fishes, but that we are concerned here with conditions reminding nearest of those in recent Holocephalians and *Rajiformes* (text-fig. 63; cf. Cole 1896, pl. 1; Allis 1934, pp. 383–385; Holmgren 1942, pp. 19–24, fig. 18). The two infraorbital grooves in the *Antiarchi*, however, differ considerably from those in Holocephalians and *Rajiformes* above all in that both are situated morphologically ventrally to the nasal aperture. The two grooves of the infraorbital canal in the *Antiarchi* must, therefore, have arisen independently of those in Holocephalians and *Rajiformes* and thus beyond doubt are only analogues of them.

The deep short sensory groove (*ptc*) forming the direct posterior continuation of the upper infraorbital groove (ifc_1), behind the pit-line groove *mpg*, will here be provisionally interpreted as the cephalic division of the main lateral line (*ptc*, text-figs. 4, 6, 7, 9, 10, 14, 27–29, 65, 82–84,



Text-fig. 63. *Chimaera monstrosa*. Outlines of head with the sensory canal system. *A*, in lateral, *B*, in anterior and, *C*, in ventral aspect. *A*, from Cole 1896. *B*, *C*, from Garman 1888, but with interpretations mainly according to Cole 1896 and Allis 1934. *M*, mouth-opening; fc_1, fc_2, fc_3, grooves innervated by lateralis branches, leaving the endocranium associated with the n. facialis. These grooves in the writer's opinion are possibly comparable to the vertical pit-line of the cheek (fc_1), to the oral canal or pit-line (fc_2), and to the jugal canal or pit-line (fc_3) respectively of fishes in general; ifc_1, ifc_2, dorsal and ventral infraorbital sensory canal grooves (= inner and outer buccal grooves in Cole's terminology); lc_1, cephalic division of main lateral line; *na*, nasal aperture; *soc*, supraorbital sensory canal groove; *stc*, supratemporal cross-commissure.

98–100, 208, 209, 219, 223, 229, 233A, 247, 249, 252, 253A, 266, 267M, N, 273, 274, 279, 303E). The groove in question (*ptc*) is always of a deep type and was in communication posteriorly with the main lateral line groove (*lcg*) of the trunk. As has been pointed out above (p. 55), it was probably innervated by a nerve-branch traversing the canal *c.lat* (text-fig. 15A, B; Stensiö 1931, text-figs. 5, 16B), which passes off in a dorso-lateral direction from the upper postero-dorsal corner of the otico-occipital depression. Judging from its position this nerve branch may very well have been given off from the vagus ganglionic complex.

The posterior oblique cephalic pit-line groove (*ifc. b*, text-figs. 4, 6, 7, 9, 10, 14, 21C, 24, 25A, 26, 65, 76–84, 93, 94, 98, 99, 114, 203, 208, 209, 219, 221, 222, 229, 230, 233A, H, 234A, 237A, 247–249, 252, 253A, D, E, 258, 266, 267F–J, M, N, 273, 274, 277, 278, 203B–D), as here defined, is identical with the oblique pit-line groove of the head of my description in 1931 (Stensiö 1931, pp. 143–144), exclusive of the very hindmost hook-shaped part, which, as will be shown below (pp. 180–184), must represent the posterior pit-line of the skull-roof. In the restricted sense here taken the groove, together with the semicircular groove (*cir*) seems to correspond so closely to the pit-line in the Euarthrodires and Phyllolepids known as the dorso-medial branch (*ifc. b*, text-figs. 66, 67A) of the infraorbital groove (Stensiö 1925, pp. 168–169, 177; 1931, p. 144; 1936, p. 25, foot-note; Allis 1934, pp. 399–409) that it can hardly be doubted any longer that it is actually homologous with it (see the Addenda). It begins on the lateral plate somewhat behind the semicircular pit-line groove (*cir*), from where it runs in a posterior and medial direction on to the centro-nuchal plate, crossing the suture between this plate and the lateral plate at or somewhat behind the middle. On the centro-nuchal plate it continues backwards and medially to a point somewhat in front of the external opening of the canal for the endolymphatic duct ($d.end_2$), where it connects with the posterior pit-line (*pp*) of its side. In most cases it is not quite straight, but arched a little laterally, whereas in other cases it may also be arched in the reverse way. In the majority of the *Bothriolepis*-species it is invariably present, but in certain species, as for instance *B. groenlandica* (text-fig. 277E; pl. 9, fig. 4) it may occasionally be absent. Otherwise it deserves to be mentioned here that in certain cases it may have a more or less abnormal position. Thus in some cases it may begin on the paranuchal-marginal plate, instead of on the lateral plate, and in these cases it passes on to the centro-nuchal plate without crossing the lateral plate (text-figs. 222H, 267K; pl. 9, fig. 1; Gross 1941a, text-figs. 1D, 25E)[1]. In other cases it may not rarely arch as much laterally as to reach the centro-nuchal plate at or near its

[1]) In some of these cases we are probably concerned with a completely developed middle pit-line of the skull-roof and not with the posterior oblique cephalic pit-line (cf. pp. 179–180, and text-figs. 65, 208 *A*, 209).

lateral corner (text-figs. 24E, 26L, 93A, 219A, 252B, 267G, L; Gross 1941a, text-figs. 7F, 25A–C). Besides in the *Bothriolepinae*, the oblique cephalic pit-line groove has thus far among the *Antiarchi* been found only in a single *Asterolepis*-species (*A. orcadensis*; Watson 1932, p. 162, text-fig. 3 and pl. 4, fig. 1). As, however, it occurs also in several groups of Arthrodires such as Dolichothoracids (Heintz 1929a, text-figs. 19, 20, 24, 25; 1929b, text-figs. 1, 2; Stensiö 1945: central sensory groove, p. 48, figs. 8, 9, 11), Brachythoracids (text-figs. 66, 67A), and Phyllolepids (Stensiö 1936, text-fig. 9) it was probably present in all primitive *Antiarchi*. It may be expected, therefore, that it will be detected in a more or less vestigial condition in several other *Antiarchi*-forms, above all the geologically oldest ones.

In small individuals there is usually also an anterior oblique cephalic pit-line groove (*ifc.b*$_1$, text-figs. 26L, 84A, B, 88B, 90, 91, 93A–E, 95, 96, 219A). This pit line groove, which is very shallow, is situated anteromedially to the posterior oblique cephalic groove (*ifc. b*). It begins on the lateral plate somewhat medially to the posterior one and runs backwards and medially close to the postero-ventral part of the orbital fenestra. During its passage backwards it converges towards the posterior oblique cephalic groove. It terminates on the posterior median part of the centro-nuchal plate, close in front of the transition between the posterior oblique cephalic groove and the posterior pit-line (*pp*) of the skull-roof, and does not anastomose either with these two pit-line grooves or with its fellow of the other side. Its lateral boundary is often well marked, being formed by a more or less marked ridge (text-figs. 88B, 91, 96, 219A), already observed and described by Gross (1941a, pp. 8, 34, 35, text-figs. 1D, 7F, 25A, B, E). The groove is normally absent in medium-sized and fully mature individuals, but sometimes more or less considerable vestiges of it may persist also in individuals of these two orders of size (text-figs. 76B, 82B, 93N, 208B, 252A, 253A, 267J–L, 303D). As to its innervation and nature this pit-line groove seems to have been as the posterior oblique cephalic pit-line groove (*ifc. b*). Unless it turns out to represent the anterior pit-line of the skull-roof, or the profundus groove, which is very unlikely (cf. Stensiö 1945, pp. 46, 48, 50), it is thus simply a medial oblique cephalic groove, arisen by a longitudinal subdivision of the posterior oblique one (*ifc.b*).

The posterior oblique cephalic pit-line groove (*ifc.b*) and its homologue in the Arthrodires, the central sensory groove (Stensiö 1945, p. 48), according to Holmgren (1942, pp. 14–15), represent the trigeminal placode in embryos of *Squalus*, *Amia* and *Lepidosteus*, and the pineal line of neuromasts in *Petromyzon*. This would thus apply also to the anterior oblique cephalic pit-line groove of the *Antiarchi*. As is now known (Stensiö 1945, pp. 48, 50), however, the opinion by Holmgren just referred to does not seem to be retainable, for at least in the *Dolichothoraci* the single oblique cephalic groove

of each side (the central groove) seems to have been supplied by branches from the n. ophthalmicus lateralis.

The semicircular pit-line groove (*cir*, text-figs. 4, 6, 7, 9, 10, 14, 24, 65, 82–84, 89, 208, 209, 219, 221, 233A, H, 247, 249, 252B, 253A, 266, 267F–J, 273B, 274, 277, 303B; cf. also Gross 1941a, text-figs. 3, 7, 27, 29), already repeatedly referred to, is a short groove, more or less clearly semicircularly arched, which is situated on the lateral plate medially to the foremost part of the upper infraorbital groove (ifc_1) and antero-laterally to the anterior end of the anterior oblique cephalic pit-line groove (*ifc. b*). It is invariably shallow, and may fairly often be absent on one or on both sides. Normally it is quite separated from the upper infraorbital groove, but in a few cases it may be connected at its anterior end with that groove, just opposite the groove *vcp* (text-figs. 80C, 221C; Gross 1941a, text-figs. 3E, 7D, 29, pl. 1, fig. 1; pl. 18, fig. 1), so that at least seemingly it is continued by the last-mentioned groove. In a few cases it may, as already pointed out (p. 173), probably even substitute the adjacent part of the upper infraorbital groove. Previously it has been known only in the *Bothriolepinae*, but recently it has been recorded by Gross (1941a, p. 11) also in *Asterolepis ornata*.

In 1931 the semicircular pit-line groove was held by the writer to be the dorsal part of what on that occasion was termed "the subrostral pit-line" (Stensiö 1931, pp. 144–146), that is to say a dorsal part of the groove lettered *vcp* in this work. As normally it is not connected with the groove *vcp* and as it lies in the anterior continuation of the oblique cephalic pit-line groove (*ifc.b*), however, it seems most likely at present that it represents instead the foremost part of the latter pit-line groove (*ifc.b*).

We shall now turn to the grooves lettered *vcp* and *orp*, which, as is now obvious, must have been continuous so that they formed a single groove, which from the upper infraorbital groove (*ifc*) went almost down to the morphologically upper posterior part of the outside of the lower jaw (text-figs. 4, 7, 8, 34, 65B, 114). The groove *vcp* is the dorsal one of the two grooves and has been known since long ago. In 1931 it was considered, together with the semicircular groove (*cir*) and the lower infraorbital groove (*ifc*), to form part of what was called "the subrostral pit-line" (*ifgv*, Stensiö 1931, pp. 144–146).

The groove *vcp* (text-figs. 4, 6–10, 14, 24, 31A, C, 33, 34, 37, 65, 77A, 81A, B, 82–84, 89, 98, 100, 108, 112B, 114, 208, 209, 219, 221, 233A, H, 234A, 247, 249, 252, 253A, C, D, 266, 267F–J, 273B, 274, 277, 303B) is connected dorsally with the upper infraorbital groove about opposite the anterior end of the semicircular pit-line groove (*cir*). It runs first more or less antero-laterally, or sometimes even fairly straight laterally, across the lateral division of the lateral plate to the prelateral notch (*nprl*), thence passing on to the prelateral plate (*Prl*). After crossing this plat it continues

in a medial and somewhat posterior direction along the anterior margin of the infraprelateral plate (*Py*). Medially (morphologically ventro-medially) to the infraprelateral plate it seems to have passed over into the groove *orp*. In its dorsal part situated on the lateral plate it is normally of a deep type, whereas on the prelateral and infraprelateral plates it is shallow. On the infraprelateral plate it is also very narrow, because of which it may easily be overlooked there. Except most dorsally, the groove *vcp* is thus developed as a typical pit-line.

The groove *orp* (text-figs. 8, 34, 65B, 111, 114), which is very shallow and narrow, crosses the extramandibular plate (*Emd*) in a morphologically longitudinal direction, after which it must have continued some distance forwards in the skin. Throughout its extent it was thus situated along the outside of the oral margin of the lower jaw.

On account of their course and position in relation both to the exoskeleton and endoskeleton (text-figs. 4–8, 34, 114) the lower part of the pit-line *vcp*, situated on the infraprelateral plate, and the entire pit-line *orp*, were certainly innervated by lateralis branches which had their exit from the endocranium together with the n. facialis, and so was probably the case also with the dorsal part of the pit-line groove *vcp*, situated on the lateral and prelateral plates (cf. Stensiö 1931, p. 144–146). According to its position on the cheek the pit-line *vcp* probably represents the vertical pit-line of the cheek in fishes in general, whereas the pit-line *orp* is clearly homologous with the oral (mandibular) groove or pit-line in Selachians and several other groups of fishes[1]). The two pit-line grooves in question will, therefore, be referred in this work as the vertical pit-line groove of the cheek (*vcp*) and the oral pit-line groove (*orp*) respectively. As may easily be gathered from a comparison of text-figs. 4, 7, 8, 34 and 114 with text-fig. 63, they are strikingly suggestive of the grooves fc_1 and fc_2 in *Chimaera* (cf. also Cole 1896, pl. 1; Allis 1934, p. 384, text-fig. 9). – The two pit-line grooves here in question at present are known only in the *Bothriolepinae*.

The preopercular and jugal grooves have probably been completely reduced. At any rate there are no vestiges of them either in the *Bothriolepinae* or in the other *Antiarchi*-forms.

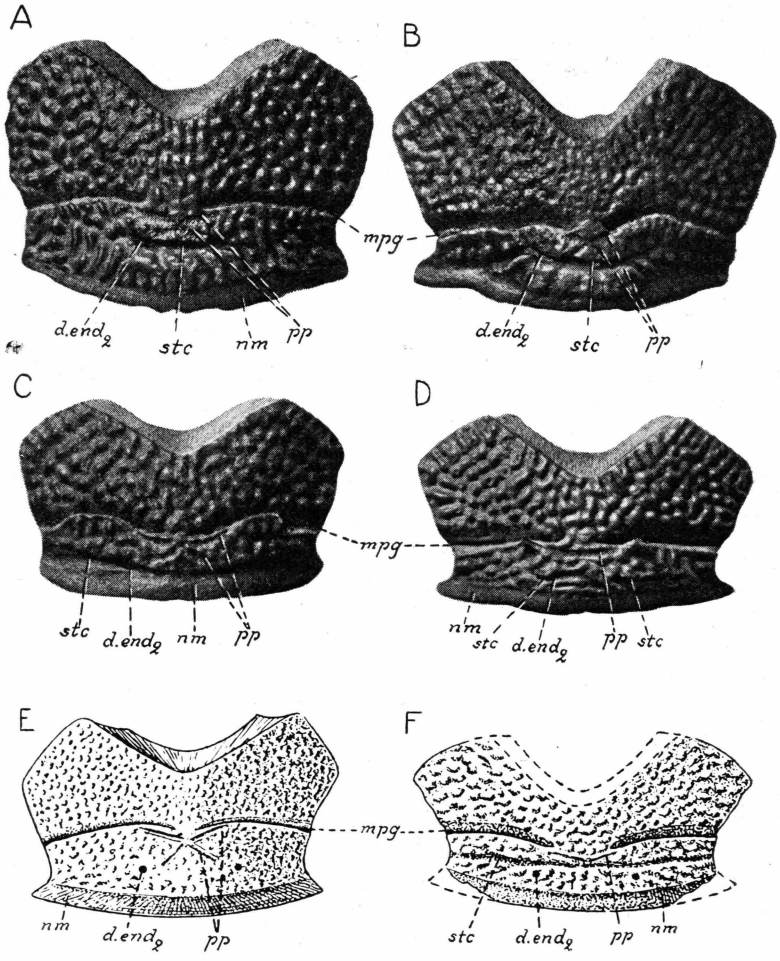
The middle pit-line groove of the skull-roof (*mpg*, text-figs. 4, 6, 9, 10, 14, 27–29, 65, 76, 82–84, 99, 100, 208, 209, 219, 223, 233A, 247, 249, 266, 267N, P, Q, 273B, 274, 279) was first noticed and described by Gross (1933a, p. 42, text-fig. 22; 1940b, text-fig. 14E; 1941a, pp. 8–9, 36, text-figs. 2, 7, 26, 29II), but was interpreted by him as a lateral part of the posterior pit-line. Passing off from the point of union between the upper infraorbital (*ifc*) groove and the cephalic division of the main lateral line

[1]) The part of the pit-line groove *vcp* situated on the lateral and prelateral plates may perhaps also be interpreted as a part of the infraorbital sensory groove.

groove (*ptc*) on the postero-lateral part of the medial division of the paranuchal-marginal plate it runs in a direction medially and posteriorly, normally terminating already a short distance from the said two main sensory canal grooves. As a rule, therefore, it is very short. In one specimen of *B. canadensis* (text-figs. 208A, 209) it is seen, however, that on the right side, after passing medially and posteriorly for a short distance, it turns almost straight medially and continues in that direction as far medially as on to the median posterior part of the centro-nuchal plate, where it anastomoses with the anterior end of the pit-line groove *pp* of its side. In this single case it is rather well marked, but normally, when represented only by a short lateral part, it is always very shallow. It is no wonder, therefore, that it has been overlooked previously. In some species it is fairly constantly met with, in others it seems to be more occasionally developed.

From what has just been set forth concerning its position and relations to the other sensory canal grooves it is obvious that the pit-line here under consideration must be a vestige of the deep transverse groove in *Pterichthyodes*, *Asterolepis* and *Remigolepis* that is developed as a more or less complete cross-commissure on the posterior part of the head-shield somewhat in front of the external openings of the canals for the endolymphatic ducts (*mpg*, text-fig. 64; Gross 1931, pl. 4, figs. 5, 7; pl. 12, fig. 7; 1933a, text-figs. 14, 16; 1933b, text-fig. 3B; 1940b, text-figs. 8B, 14F; Stensiö 1931, pp. 146–149, text-figs. 13, 80; Stensiö 1938, text-figs. 1, 2, 7, 9). Since now, as will be demonstrated below, the cross-commissural groove in *Pterichthyodes*, *Asterolepis* and *Remigolepis* just referred to represents the middle pit-line of the skull-roof of fishes in general, the shallow and mostly very short pit-line here in question in the *Bothriolepinae* cannot, of course, be interpreted as anything else but a vestigial middle pit-line.

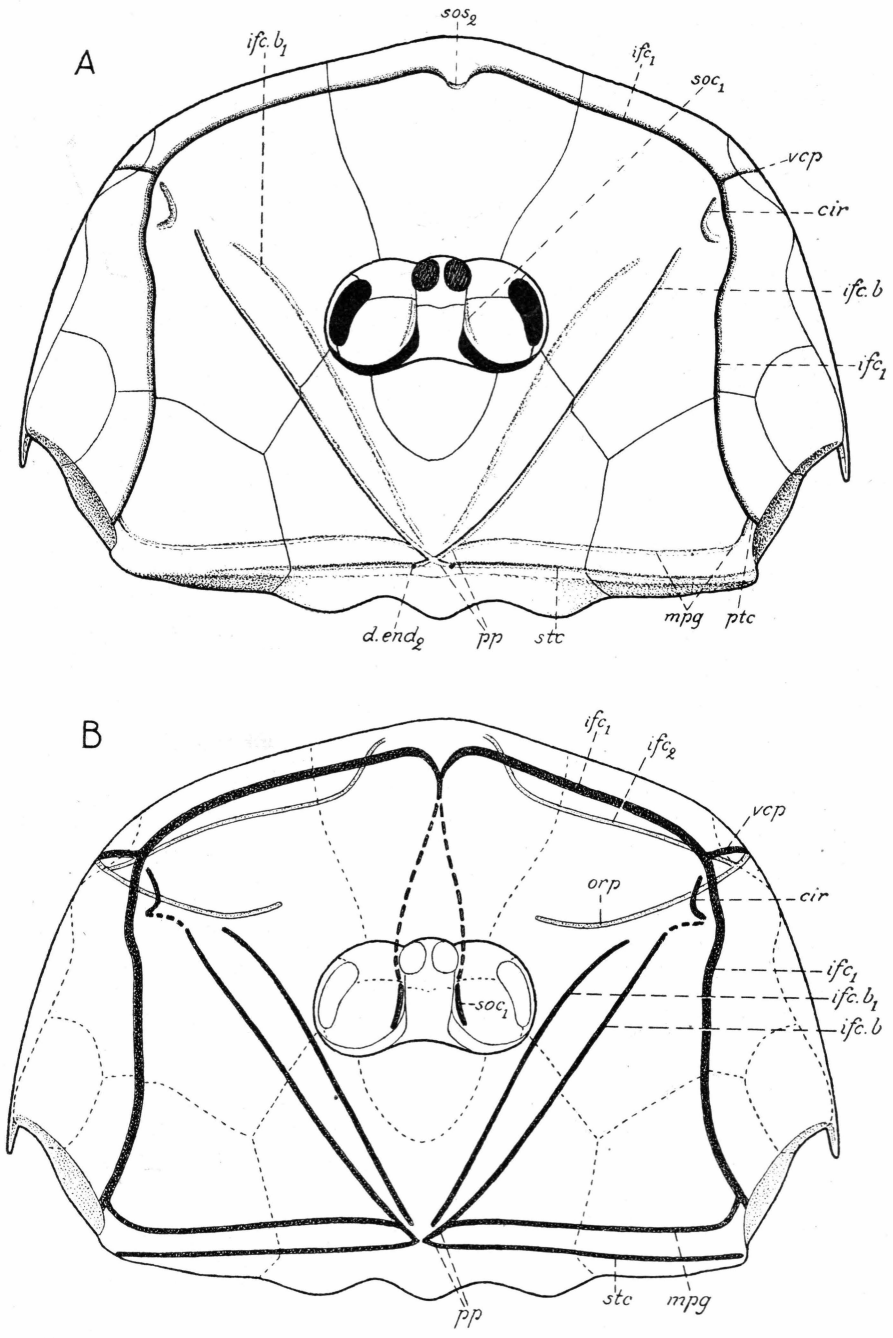
The posterior pit-line prove of the skull-roofs (*pp*, txt-figs. 6, 9, 10, 14, 25A, 26, 65, 76, 77B, C, 78C, 82–84, 93, 94, 208, 209, 219, 222, 233A, 236A, 237A, 247, 249, 252A, 253A, E, 258, 266, 267K–M, 273B, 274, 278, 303C, D) lies on the posterior median part of the centro-nuchal plate close in front of the external openings of the canals for the endolymphatic ducts ($d.end_2$). It consists of two sections, both of which are narrow and shallow. The anterior section is connected with the posterior oblique cephalic pit-line groove (*ifc.b*) and forms the straight postero-medial continuation of that groove. The posterior section, on the other hand, passes off at a sharp lateral bend from the anterior one and runs in a postero-lateral direction towards the external opening of the canal for the endolymphatic duct ($d.end_2$), ending at or near this opening. Taken as a whole the pit-line is thus shaped like a couchant V, with the point medially. Normally both sections are present, but in *B. maxima* (text-fig. 236) and in *B. gippslandiensis* (text-fig. 26H) the posterior section seems usually to be absent. In *Bothriolepis* the two sections are as a rule connected with one another (text-figs. 26A–K), whereas



Text-fig. 64. *A–D.* Four centro-nuchal plates of *Asterolepis ornata*, in dorsal aspect. × $^5/_4$. *E, F,* centro-nuchal plates of *Asterolepis säve-söderberghi*. Dorsal aspect. From Stensiö 1938. *E, F,* × $^5/_4$.
d.end$_2$, external opening of canal for the ductus endolymphaticus; *mpg*, middle pit-line groove; *nm*, obtected nuchal area; *pp*, posterior pit-line groove; *stc*, supratemporal pit-line groove.

this is normally not the case in *Grossilepis* (text-figs. 26L, 267K–M; cf. also Gross 1941a, text-fig. 25). Finally, it deserves to be mentioned here that the pit-line in several of the *Bothriolepis*-species normally meets and anastomoses with that of the opposite side by means of its medial corner, formed by the transition between its two sections (text-fig. 26), but that no such connection or anastomosis has been met with in *Grossilepis* (text-figs. 26L, 267K–M; cf. Gross 1941a, text-fig. 25).

That now the groove here under consideration actually is the posterior pit-line groove of the skull-roof is obvious from certain conditions in *Asterolepis*, which will, therefore, be dealt with here.



Text-fig. 65. *Bothriolepis canadensis*. *A*, restoration of the sensory canal grooves and pit-line grooves observed on the dorsal side of the head. *B*, restoration of the sensory canal grovves and pit-line grooves of the head observed as yet. The head shield drawn as if transparent, so that it shows the ventral grooves. The probable primary course of the supraorbital and posterior oblique cephalic grooves shown with broken lines. × 4/3.
cir, semicircular pit-line groove, probably constituting an anterior part of the pit-line

As is seen from text-fig. 64, the *Asterolepis*-species exhibit three pit, lines, *mpg, pp* and *stc,* on the posterior part of the head-shield (cf. also Stensiö 1931, text-fig. 13; Stensiö 1938, text-figs. 1, 2, 7, 9; Gross 1940b-text-figs. 8,B 14F; 1941a, p. 8). The foremost one, *mpg,* of these pit-line grooves is the one which extends laterally on to the paranuchal-marginal plate, where it is connected with the upper infraorbital groove (ifc_1) and the cephalic division of the main lateral line groove (*ptc*) at their transition into one another. This groove (*mpg*), which is invariably present and often may form a complete cross-commissure between the main longitudinal grooves of both sides, is situated somewhat in front of the external openings of the canals for the endolymphatic ducts ($d.end_2$). It is always deep, almost as deep as the upper infraorbital groove (ifc_1) and the postotic (*ptc*) grooves and opens upwards and forwards. The groove, *pp,* following nearest backwards, lies on the medial part of the centro-nuchal plate close behind the groove *mpg.* In *Asterolepis ornata, Asterolepis säve-söderberghi* and, probably, also in other species (*A. orcadensis* Watson 1932, pp. 162–163, text-fig. 3 and pl. 4, fig. 1) it is constantly present, but despite this it has been detected only recently (Stensiö & Säve-Söderbergh 1938, *ppg,* text-figs. 1, 2, 7, 9; Gross 1940b, pp. 31, 54–58; *ifc.b,* text-figs. 8B, 14F; 1941a, p. 8), a circumstance which is due to the fact that mostly it is very shallow and obscure. It consists of two divisions, an anterior one, which begins immediately behind the pit-line *mpg* and runs medially and somewhat backwards, and a posterior one, which from its connection with the anterior one turns off in a direction backwards and laterally towards the external opening of the canal for the endolymphatic duct ($d.end_2$) of its side. As to its shape the pit-line *pp* is thus developed as a couchant V with its point medially. By this medially directed point between its two divisions it is mostly connected with the corresponding pit-line of the other side. In some cases it is represented by one of its sections, either the anterior or posterior one. The posterior section may anastomose with, and pass over into, the groove *stc.* Consequently the pit-line groove in question is developed almost exactly as the one in the *Bothriolepinae* above described as the posterior pit-line groove of the skull-roof. It must thus beyond question be the exact homologue of

groove *ifc.b*; ifc_1, upper infraorbital groove, representing inter alia the otic section of the infraorbital canal of fishes in general; ifc_2, lower infraorbital groove, representing the infraorbital and ethmoidal sections of the infraorbital sensory canal of fishes in general; *ifc.b,* posterior oblique cephalic pit-line groove; $ifc.b_1$, anterior oblique cephalic pit-line groove (normally present only in very small individuals); *mpg,* middle pit-line groove of skull-roof (normally only a very short lateral part developed); *orp,* oral (mandibular) pit-line groove; *pp,* posterior pit-line groove of skull-roof, continuous with posterior oblique cephalic pit-line groove (*ifc.b*); *ptc,* cephalic division of main lateral line; soc_1, posterior section of supraorbital sensory groove, developed as a very shallow pit-line; soc_2, anterior median section of the supraorbital sensory canal grooves, developed as an unpaired median pit-line groove, the anterior median pit-line; *stc,* supratemporal groove, representing the supratemporal cross-commissure of fishes in general; *vcp,* more or less deep groove, probably representing the vertical pit-line of the cheek in fishes in general.

that pit-line in the *Bothriolipinae* and has, therefore, to be termed in the same way as it. Finally, the pit-line groove *stc*, the hindmost one of the three pit-lines grooves here under consideration in *Asterolepis*, was first noticed in 1931 (Stensiö 1931, pp. 148–149; *ppg*, text-figs. 13C–M; cf. also Stensiö 1938, *ppg*, text-fig. 9) and has recently been dealt with by Gross (1940b, pp. 31, 56–58; *stc*, text-figs. 8B, 14). This pit-line groove (*stc*), which, like the groove *mpg*, is transversal, passes close to or just across the external openings of the canals for the endolymphatic ducts. Otherwise it varies much in its development. In certain cases it is thus paired, in other cases unpaired. In most cases it is short, occupying only a median part of the centro-nuchal plate, in other cases it crosses almost the whole centro-nuchal plate, and, finally, in certain cases it is so long that it extends on to the paranuchal-marginal plate of either side. In some cases it may be deep and well marked, in others narrow and shallow. Not rarely it may be entirely absent. As we thus find, it is much more variable and much less constant than the other two.

As may be gathered from what is now known of it, the pit-line groove *mpg* in *Asterolepis* and other *Antiarchi* cannot represent either the anterior pit-line of fishes in general or the pit-line groove *ifc. b* of the Arthrodires. It cannot either be the equivalent of the posterior pit-line groove of the skull-roof, as maintained by the writer in 1931 (Stensiö 1931, pp. 146–149, *mpg*, text-fig. 13) and quite recently also by Gross (1940b, p. 31, *pp*, text-figs. 8B, 14F), but must instead be interpreted as the middle pit-line groove of the skull-roof (cf. Stensiö 1938, text-figs. 2, 9), an interpretation which is fully in accord with its position far backwards on the head-shield. As this is so, it follows, of course, that the pit-line grooves *pp* and *stc* in both *Asterolepis* and other *Antiarchi* simply represent the middle pit-line of the skull-roof and the supratemporal cross-commissure respectively.

After this digression to *Asterolepis* and the *Antiarchi* in general we shall now return to the *Bothriolepinae* and nearest to their supratemporal cross-commissure.

The supratemporal cross-commissure (*stc*, text-figs. 6, 9, 25A, 26A, K, 65, 76, 77, 78C, 79, 80C, 81B, C, 82–84, 91, 93, 94, 99, 100, 102, 109, 208, 209, 233A, 247, 249, 274A, 278C–E, 303D; cf. also Gross 1941a, pl. 3, figs. 5–7; pl. 4, figs. 4, 5; pl. 19, figs. 11, 14) is frequently present in the *Bothriolepinae*, but, being shallow and obscure, it has long escaped attention. As to its position, essential characters and variations it is much as in *Asterolepis* (cf. pp. 183–184 above) because of which a description of it is superfluous here. From the external opening of the endolymphatic duct ($d.end_2$), or from the median posterior part of the centro-nuchal plate, it may often extend laterally as far as to the hindmost lateral part of the paranuchalmarginal plate.

The main lateral line (*lcg* or *lc*, text-figs. 38–40, 48, 50C, D, 62B, C,

144, 145B, C, 150D, 153F, G, 164C, 226, 227, 238C, F, 251, 256, 259B, 264, 270A–F, 287B, 288, 289) was connected anteriorly with its cephalic division (*ptc*) situated on the head-shield. It begins at the anterior margin of the dorsal lamina of the anterior dorso-lateral plate, more precisely at the dorso-medial margin of the processus obstans (*pro*), and first runs latero-ventrally and somewhat backwards across the basal part of the processus obstans down to the lateral wall of the trunk-armour. There it passes backwards on the upper halves of the lateral laminae of the anterior dorso-lateral and mixilateral plates. On the lateral lamina of the mixilateral plate it gradually bends upwards until just above the dorsal corner of the posterior ventro-lateral plate, where it bends down rather abruptly, following the suture-line between the mixilateral and posterior ventro-lateral plate postero-ventrally as far as to the posterior margin of the lateral wall of the trunk-armour. On account of this downward bend it reaches the unarmoured posterior division of the trunk somewhat ventrally to the level at which it is mainly situated on the trunk-armour. On the unarmoured posterior division of the trunk it can be traced only on the caudal fin, where it passes backwards along the ventral margin of the body-axis of the fin, close to the hypochordal fin-membrane (text-fig. 62B, C). At any rate in this part of its course, in *B. canadensis*, as we have seen (cf. pp. 145–146), it is situated in a row of small oblong scales, semi-cylindrical in cross-section, (*Ls*, text-fig. 62). Throughout its extent it is developed as a groove, which is deep on the trunk-armour, but probably shallower behind that armour. On the trunk-armour its openings are directed laterally and fairly much ventrally.

The dorsal lateral line in fishes in general is represented in the *Bothriolepinae* by two paired shallow pit-line grooves, an anterior and a posterior, which according to their position and oblique course will be termed here the anterior and posterior oblique abdominal pit-line grooves respectively.

The anterior oblique abdominal pit-line groove (*dlg*$_1$, text-figs. 39A, 43A, C, 88, 91, 95–97, 98, 101, 102, 115–117, 118A, C, D, F, 121A–D, F, G, J, L, 142, 179A–C, F, 202, 204, 254A, 261, 262B, 263, 280A, C, D, F, 302; pl. 13, fig. 3; pl. 34, figs. 1, 4; pl. 35, figs. 1, 3) was noticed by Traquair and is also shown in some of his reproductions and restorations (Traquair 1888b, pl. 18, fig. 4; 1895, pl. 8; 1894–1906, p. 125, text-fig. 62; pl. 24, fig. 1; pl. 30, figs. 1–3), but its nature of a pit-line groove was not perceived by him. The groove frequently, or normally, is present in young individuals, but then disappeared pretty soon in later stages of growth and, therefore, is generally absent in older individuals. Vestiges of it are met with fairly frequently in smaller medium-sized individuals, but are usually rare in fully mature individuals. The groove is thus clearly a formation characteristic of young individuals (cf. pp. 104–106 above). When completely developed it extends backwards and medially from the foremost part of the dorsal lamina

of the anterior dorso-lateral plate, near the dorsal part of the processus obstans, to the tergal angle (*dma*) of the anterior median dorsal plate, where, at least in many cases, it seems to anastomose with the corresponding groove of the opposite side. At the suture between the anterior dorso-lateral and anterior median dorsal plates it lies usually close behind the external postlevator process (*pr.pl*) of the latter plate. In small individuals, in which the oblique transverse ridge (*otr*) of the dorsal wall of the trunk-armour is present and well developed, it always passes immediately in front of, and parallel with, this ridge, which thus forms its posterior boundary. It is generally very shallow and obscure, and it is no wonder, therefore, that it has been overlooked up till now. However, in certain cases it may be so well pronounced (text-figs. 88B, 202, 254A, 302) that its nature of a pit-line is fully obvious. Mostly it is imperfectly developed, being represented only by middle or posterior parts. Besides in the *Bothriolepinae*, it has so far been met with only in *Remigolepis* (cf. Part III of this work).

The posterior oblique abdominal pit-line groove (*dlg*$_2$, text-figs. 38–40, 43, 50, 98, 118–124, 153, 179–183, 199, 200, 202, 206, 207, 216, 224, 227, 238G, 248, 249, 250A, 251, 254A, 256, 259B, 261, 262B, 263, 264, 268, 270D, 280A, C, D, F, 284, 285, 287B, 289), as here defined, is the pit-line groove described by the writer in 1931 (Stensiö 1931, p. 149) as "the oblique pit-line of the trunk". Contrary to what is the case with the anterior oblique one this pit-line groove (*dlg*$_2$) in the *Bothriolepis*-species, and in *Grossilepis*, is present not only in young individuals, but also in medium-sized and fully mature ones. Moreover, it is generally well pronounced and easy to observe, because of which it has been known since long ago. It begins at the tergal angle (*dma*), slightly behind the posterior end of the anterior oblique pit-line groove (*dlg*$_1$), and is there mostly connected with the corresponding grove of the opposite side. On the other hand, it seems never to be connected with the anterior oblique groove (*dlg*$_1$). In *Bothriolepis* it normally runs in a postero-latero-ventral direction towards the posterior ventral part of the dorsal lamina of the mixilateral plate, crossing the suture between the anterior median dorsal and mixilateral plates about at, or somewhat behind, its middle. In four cases in *B. canadensis* it has been found to have an abnormal course. In two of these cases (text-fig. 211; Robertson 1938, p. 300) it passes fairly straight backwards from the tergal angle on to the posterior median dorsal plate, terminating on the hindmost part of that plate, near the dorsal median ridge, instead of as normally on the mixilateral plate; in the other two cases (text-figs. 123C, 210) on one side it takes a lateral and somewhat anterior course and passes on to the dorsal lamina of the anterior dorso-lateral plate. On account of the fact that on the latter plate it lies strikingly far forwards it is not impossible that in these two cases it may be fused in its lateral part with a vestige of the anterior oblique abdominal pit-line (*dlg*$_1$). In some cases in *B. canadensis* it may also be

double throughout, or in part (text-fig. 207). In *Grossilepis* (text-figs. 39D, 43E, 268; cf. Gross 1941a, pp. 34, 42–43, 46 and text-fig. 30C–E, G, H) it begins also at the tergal angle, but has always a more posterior course than in *Bothriolepis*. On account of this in *Grossilepis* it reaches the mixilateral plate after crossing either the postero-lateral corner of the anterior median dorsal or the hindmost part of the suture between the mixilateral and anterior median dorsal plates. However, in *Grossilepis* it may often pass so straightly backwards that it does not reach the mixilateral plate, but instead terminates on the hindmost part of the posterior median dorsal plate. Both in *Bothriolepis* and *Grossilepis* it may occasionally be imperfectly developed or absent on one or on both sides. At least in *Bothriolepis* it is clearly deeper and more complete in young individuals than in older ones.

In *B. cellulosa*, *B. panderi* and a new species (*B. obrutschewi* n. sp according to informations by Gross) there is a short dorso-ventral pit-line groove (Gross 1941a, pp. 21, 22, *dpx*, fig. 13B) on the posterior upper part of the lateral lamina of the mixilateral plate. As maintained by Gross, this pit-line is presumably the postero-ventral end of the posterior oblique abdominal pit-line groove.

Besides in the *Bothriolepinae*, the posterior oblique abdominal pit-line groove among the *Antiarchi* is found also in *Remigolepis* (Stensiö 1931, pp. 149, 183, text-figs. 80, 82, 85; cf. also Part III of this work), *Asterolepis* (Gross 1940b, p. 22, text-figs. 4F, 5A) and *Cypholepis* (Gross 1931, pl. 4, fig. 16). In *Remigolepis* it is approximately as completely developed as in the *Bothriolepinae*. In *Asterolepis* it is present in certain cases, but is then represented only by a short anterior part near the tergal angle. Finally, in *Cypholepis* it is developed at least nearest the tergal angle, but it is conceivable, however, that in this form it reached much further backwards. A homologue of the pit-line groove in question is also met with in certain Arthrodires (Heintz 1932b, text-fig. 10).

In this connection it should also be mentioned that in one case, on the left side of a large anterior median plate of *Bothriolepis gigantea* (text-fig. 254A; cf. also Traquair 1894–1906, pl. 24, fig. 1), there are certain indications of a middle, mainly transverse dorsal abdominal pit-line groove (*dlgm*).

The subcephalic abdominal pit-line (*sg*, text-fig. 160) is a ventral pit-line groove, situated on the subcephalic division of the ventral wall of the trunk-armour, and has not been observed before in the *Bothriolepinae* It is known so far only in two cases, in one specimen of *Bothriolepis canadensis* and one specimen of *B. maxima*, where it appears as a broad, distinct groove on the subcephalic division of the anterior ventro-lateral plate. More precisely, from a point medially to the prepectoral corner (*prc*) it extends in a direction medially and somewhat forwards. In the specimen of *B. canadensis* it ends just at the suture between the anterior ventro-lateral and se-

milunar plates without continuing on to the latter plate, whereas in the specimen of *B. maxima* its medial end lies further backwards on the anterior ventro-lateral plate. Although it is thus situated entirely laterally to the semilunar plate, it must nevertheless correspond to the subcephalic pit-line groove in *Asterolepis* that crosses the semilunar plates in a mainly transverse direction (Stensiö 1931, *sg*, p. 150, text-fig. 52; Gross 1941b, p. 207, text-fig. 10D, E; Nilsson 1941, text-fig. 7). The fact that a corresponding ventral groove, situated on the anterior ventro-lateral plate, occurs also in Brachythoracid Arthrodires (Heintz 1932, p. 126, text-fig. 11) shows that the subcephalic abdominal pit-line in *Bothriolepis* and *Asterolepis* is no occasional structure, but must be a vestige of a transverse ventral pit-line which in primitive Placoderms lay on the foremost part of the ventral wall of the trunk-armour (cf. Gross 1941b, p. 207).

Finally, the pit-line groove of the pectoral fin, the pectoral pit-line groove (*sgp*, text-figs. 57A, C, 190B, C, 191D, 195B, 196B, 228B, 243C, D, 244E, 271A, 293B, 299A), as we know, is present both in *Bothriolepis* (Stensiö 1931, pp. 149–150, text-figs. 62B, 63D; Gross 1933a, text-figs. 21A, 23A; Gross 1941a, text-fig. 23B) and *Grossilepis* (Gross 1941a, text-fig. 43A), but has in them a position somewhat different from that in *Asterolepis* (cf. Gross 1931, pl. 5, figs. 2, 3; pl. 6, figs. 1–4; 1933a, text-fig. 17:1; Stensiö 1931, pp. 149–150, text-fig. 61A, C, 65A; Nilsson 1941, text-figs. 16, 17B, D). On the proximal segment it runs much lower down, much nearer to the ventro-medial margin of the segment, than in *Asterolepis*, whereas on the distal segment it follows approximately the medial margin of the segment, so that throughout its extent on the latter segment it lies somewhat further medially than in *Asterolepis*. At any rate in *Bothriolepis* it varies somewhat as to its position in relation to the medial marginal plate 1 and the ventral central plates 1 and 2. – As pointed out previously, the pectoral pit-line groove is a formation analogous to the scapular and postcapular branches of the lateral line in the *Rajiformes* (cf. Ewart & Mitchell 1892, pp. 96–97).

Summing up what has been set forth just above we find that with regard to their sensory canal system the *Bothriolepinae* differ from *Pterichthyodes*, *Asterolepis* and *Remigolepis* in the following characters: 1) The presence of a posterior paired vestigial section (soc_1) of the supraorbital groove; 2) the presence of a lower infraorbital groove (ifc_2); 3) the constant presence of a posterior oblique cephalic pit-line groove (*ifc.b*); 4) the presence of an anterior oblique cephalic pit-line groove ($ifc.b_1$), often well developed in small specimens, but generally absent in medium-sized and large specimens; 5) the presence of a semicircular pit-line groove (*cir*); 6) the presence of a vertical pit-line groove on the cheek (*vcp*); 7) the presence of an oral pit-line groove (*orp*); 8) the presence of an anterior oblique abdominal pit-line

groove[1]); 9) the usually vestigial development of the middle pit-line groove (*mpg*) of the skull-roof; and 10) the fact that the groove of the supratemporal cross-commissure, though often present, is shallow and obscure. In characters nos. 1–3 and 5–8 the *Bothriolepinae* have certainly retained more primitive conditions than *Pterichthyodes*, *Asterolepis* and *Remigolepis*. Their pit-lines were almost all so well developed and deep that they gave rise to distinct grooves on the underlying dermal bones, whereas several of the pit-lines in *Pterichthyodes*, *Asterolepis* and *Remigolepis* normally were more reduced, shallower and so superficial in position that they were unable to cause any markings on the underlying exoskeleton. As to the characters nos. 4, 9 and 10 the *Bothriolepinae* are probably more specialized than *Pterichthyodes*, *Asterolepis* and *Remigolepis*.

As is also obvious from what has been set forth here, the sensory canal system in the *Antiarchi* in general, but particularly in the *Bothriolepinae*, in several important characters is highly suggestive of that in the Arthrodires. As that of the Arthrodires and Acanthodians it is, taken as a whole, of a specialized Elasmobranchian type (cf. Stensiö 1931, p. 150).

Finally, it may be mentioned here that the principal sensory canal grooves in the *Bothriolepinae*, and in the other *Antiarchi* as well, are mostly very deep (cf. Stensiö 1931, text-fig. 6). On account of this it is not guite impossible that they were covered by the epidermis and the non-ossified superficial layer of the corium and thus perhaps were real closed canals opening outwards by means of pores piercing the superficial parts of the skin.

Remarks on the homologies of the dermal bones of the head and trunk in the Bothriolepinae and Antiarchi in general.

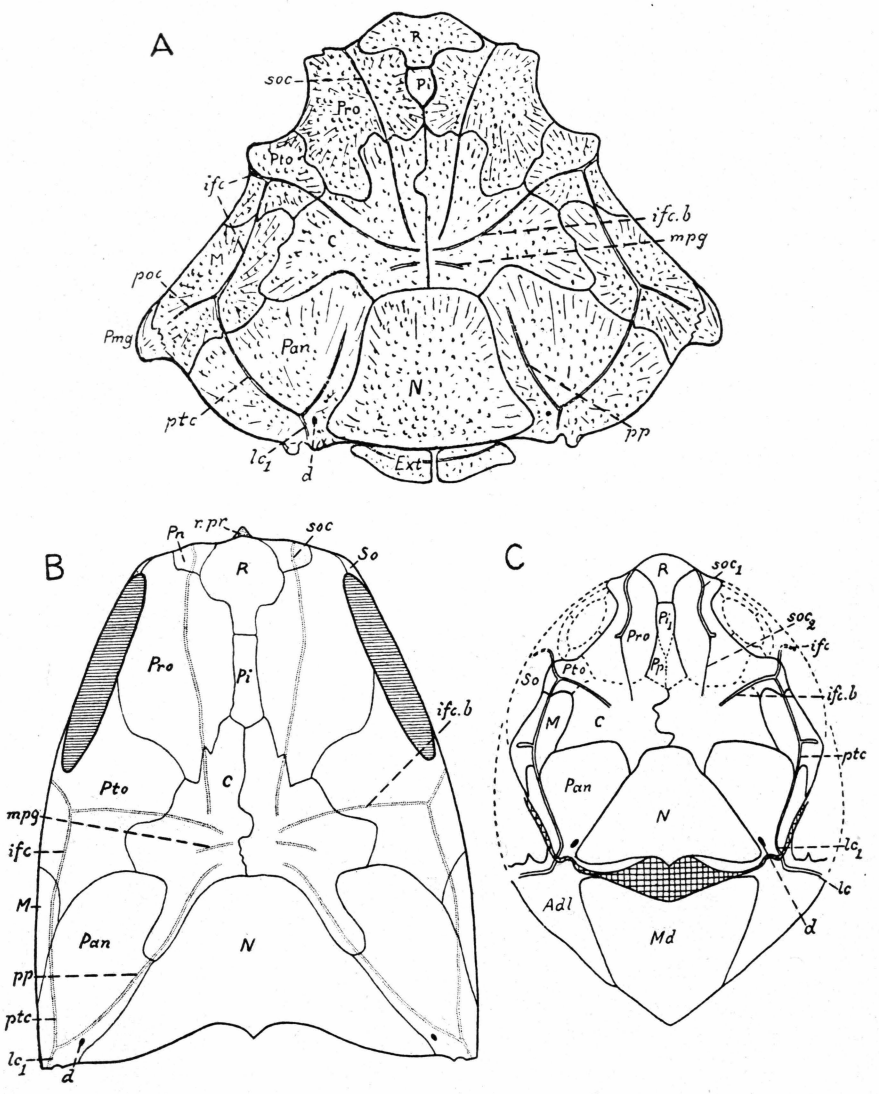
The head of the *Antiarchi*, as we have seen (cf. pp. 24–98), is of a highly specialized Arthrodiran type and must be assumed to have arisen from a primarily Euarthrodire-like head which in general appearance was somewhat as in *Coccosteus*, *Rhachiosteus* or *Pholidosteus* (text-figs. 66, 67). Its phyletic development from such an Euarthrodire-like head, as already pointed out (pp. 29–31, 85–86), may be assumed to have taken place somewhat in the following way. In consequence of an adaption of the animals to a pronounced benthonic mode of living the eyes migrated to the dorsal side of the skull-roof and became situated close to one another, causing thereby a considerable narrowing of the interorbital wall. A mass of tissue which lay on the rostral and lateral sides of the snout, ventrally and postero-latero-ventrally to the nasal apertures, but chiefly dorsally to the ethmoidal sections of the infraorbital sensory canal grooves, was produced forwards and laterally and developed into a large rostral fold which swung upwards, forming an anterior continuation of the skull-roof in front of the nasal apertures. To this rostral

[1]) This pit-line groove, which generally is found only in young individuals, has now been noticed also in *Remigolepis*.

fold were also added certain upper parts of the cheeks, which entered in the formation of the antero-lateral parts of the skull-roof. The rostral fold, completed in this way, developed to such an extent as ultimately to constitute the whole preorbital division of the skull-roof and to be supported by a powerful outgrowth, a sort of rostral process, from the basal parts of the ethmoidal region of the endocranium. The excessive development of the rostral fold, which thus resulted in the formation of a secondary snout in front of the primary one, naturally caused a considerable change in the position of the external nasal apertures. These apertures primarily lying on the anterior rostral face of the ethmoidal region and almost terminally, were pushed upwards and backwards so as ultimately to be situated on the dorsal side of the head, between the foremost parts of the orbits, and thus far behind the rostral end of the secondary snout. In connection with these changes in position of the external nasal apertures the nasal capsules shifted backwards and upwards, on account of which to a large extent they came to be situated in the foremost part of the interorbital wall. While all these transformations were in progress in the cranium, the jaw apparatus migrated forwards so that ultimately it was situated entirely underneath the preorbital division of the skull, and thus entirely in front of the orbits. The mouth-opening was shortened into a transverse slit, but retained a ventral position comparatively far behind the tip of the secondary snout; taken as a whole it developed in a manner somewhat similar to that in recent *Rajiformes*. The upper jaws and certain lower parts of the mass of tissue primarily belonging to the rostral and lateral faces of the ethmoidal region, together with certain anterior and lower parts of the cheek, were bent downwards so as to participate into the formation of the ventral side of the head. In consequence of the forward migration of the jaw apparatus the remaining laterally and ventrally directed parts of the cheek were much shortened. Owing to the flattening of the foremost part of the head as a whole the posterior laterally directed part of the cheek also became very low. Finally, the principal part of the otic region and the occipital region, together with the corresponding parts of the skull-roof, were highly shortened.

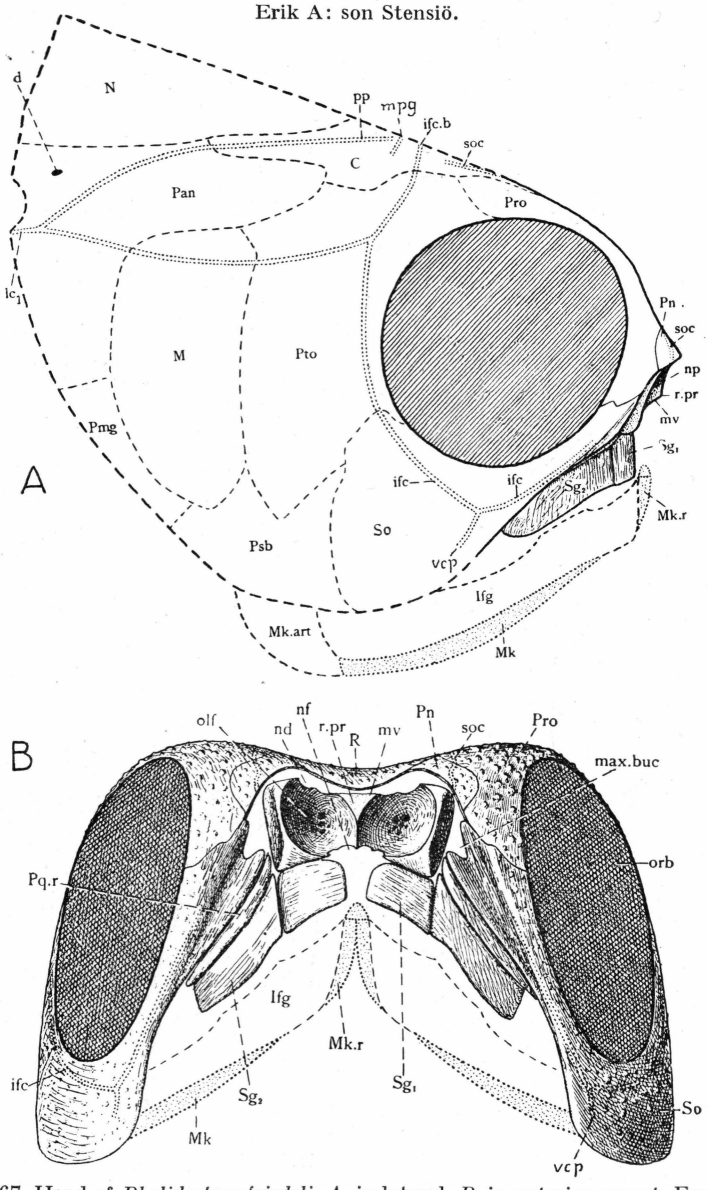
As has been demonstrated above in this work (31–33), the *Antiarchi* resemble Rhenanid Arthrodires in the development of the preorbital division of the cranium, in the position of the external nasal apertures close to one another on the dorsal side of the head and between the orbits, and in the preorbital position of the jaw apparatus. It is fully obvious, however (cf. p. 33), that all these resemblances between the two groups are parallelisms. In the shortening and development of the postorbital division of the cranium and in the position of the jaw apparatus the *Antiarchi* are also reminiscent of Ptyctodontid Arthrodires.

The considerable transformations outlined above that have taken place in the *Antiarchi* during their evolution from primarily Euarthrodire-like



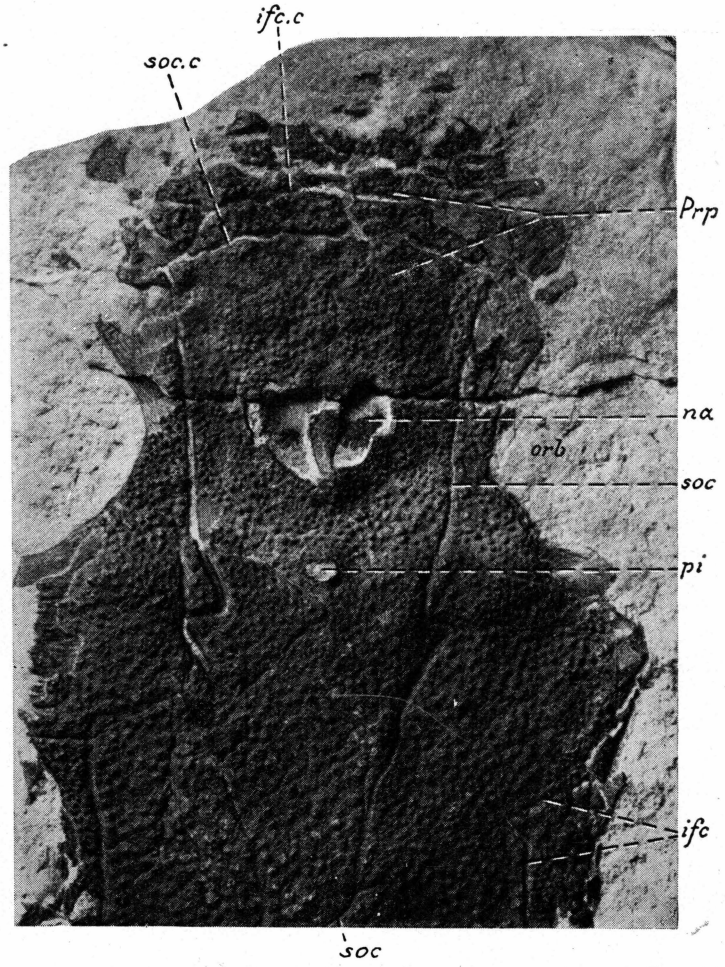
Text-fig. 66. Skull-roofs of three *Brachythoracid Arthrodires*. Dorsal aspect. *A*, of *Coccosteus decipiens*. From Heintz 1931, somewhat altered and with the extrascapular plates restored after those in *C. minor* (Heintz 1938). *B*, of *Pholidosteus friedeli*. From Stensiö 1934 and 1936. *C*, of *Rhachiosteus pterygiatus*. The dorsal wall of the trunk-armour also shown. From Gross 1938.

Adl, anterior dorso-lateral plate; *C*, central plate (complex plate); *Ext*, extrascapular plate; *M*, marginal plate; *Md*, median dorsal plate; *N*, nuchal plate (»median basal«); *Pan*, paranuchal plate (»externo-basal«); *Pi*, pineal plate; Pi_1, pineal plate; *Pmg*, postmarginal plate; *Pn*, postnasal plate; *Pp*, perhaps postpineal plate (in *Rhachiosteus*); *Pro*, preorbital plate; *Pto*, postorbital plate; *R*, rostral plate; *So*, suborbital plate; *d*, opening for canal of ductus endolymphaticus; *ifc*, infraorbital sensory groove; *ifc.b*, central sensory canal groove; *lc*, main lateral line-groove; lc_1, cephalic division of main lateral line; *mpg*, middle pit-line groove of skull-roof; *pp*, posterior pit-line groove of skull-roof; *ptc*, postotic sensory canal groove; *r.pr*, rostral process of internasal wall; *soc*, supraorbital groove; soc_1, anterior deep part of supraorbital sensory canal groove (in *Rhachiosteus*); soc_2, posterior part of supraorbital sensory canal groove, developed as a shallow pit-line (in *Rhachiosteus*).



Text-fig. 67. Head of *Pholidosteus friedeli*. *A*, in lateral, *B*, in anterior aspect. From Stensiö 1934a.

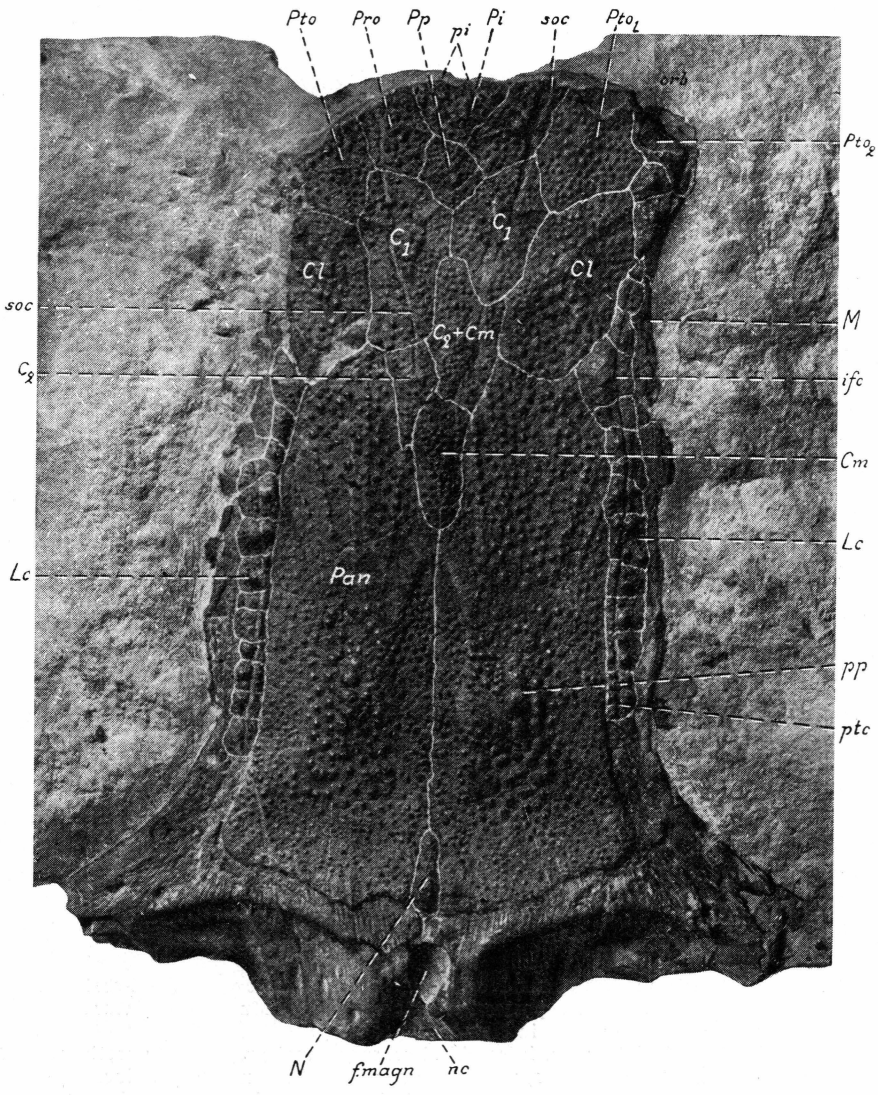
C, central plate (complex plate); *Ifg*, inferognathal; *M*, marginal plate; *Mk*, Meckelian cartilage; *Mk.art*, pars articularis of Meckelian cartilage (ossified); *Mk.r*, rostral part of Meckelian cartilage (ossified); *N*, nuchal plate (»median basal«); *Pan*, paranuchal plate (»externo-basal«); *Pmg*, postmarginal; *Pn*, postnasal plate; *Pq.r*, rostral part of palato-quadrate; *Pro*, preorbital plate; *Psb*, postsuborbital; *Pto*, postorbital; *R*, rostral plate; *So*, suborbital; Sg_1, anterior superognathal; Sg_2, posterior superognathal; *d*, external orifice of canal for endolymphatic duct; *ifc*, infraorbital sensory canal groove; *ifc.b*, central sensory canal groove; lc_1, cephalic division of main lateral line; *max.buc*, foramen for the r. maxillaris V, and the n. buccalis lateralis, and for vessels; *mpg*, middle pit-line groove of the skull-roof; *mv*, internasal wall, *nd*, notch in the dorsal wall of the nasal pit; *nf*, notch in the ventral wall of the nasal pit, perhaps corresponding to the nasal fortanelle of Selachians; *np*, nasal pit; *olf*, foramina for the exit of the olfactory nerves into the nasal cavity; *orb*, orbit; *pp*, posterior pit-line groove of skull-roof; *r.pr*, rostral process; *soc*, supraorbital sensory groove; *vcp*, possibly vertical pit-line groove of cheek.



Text-fig. 68. *Asterosteus stenocephalus* Newberry. Anterior part of the skull-roof in dorsal view. Specimen No. 268 G in the possession of the American Museum of Natural History in New York. × $^3/_2$.

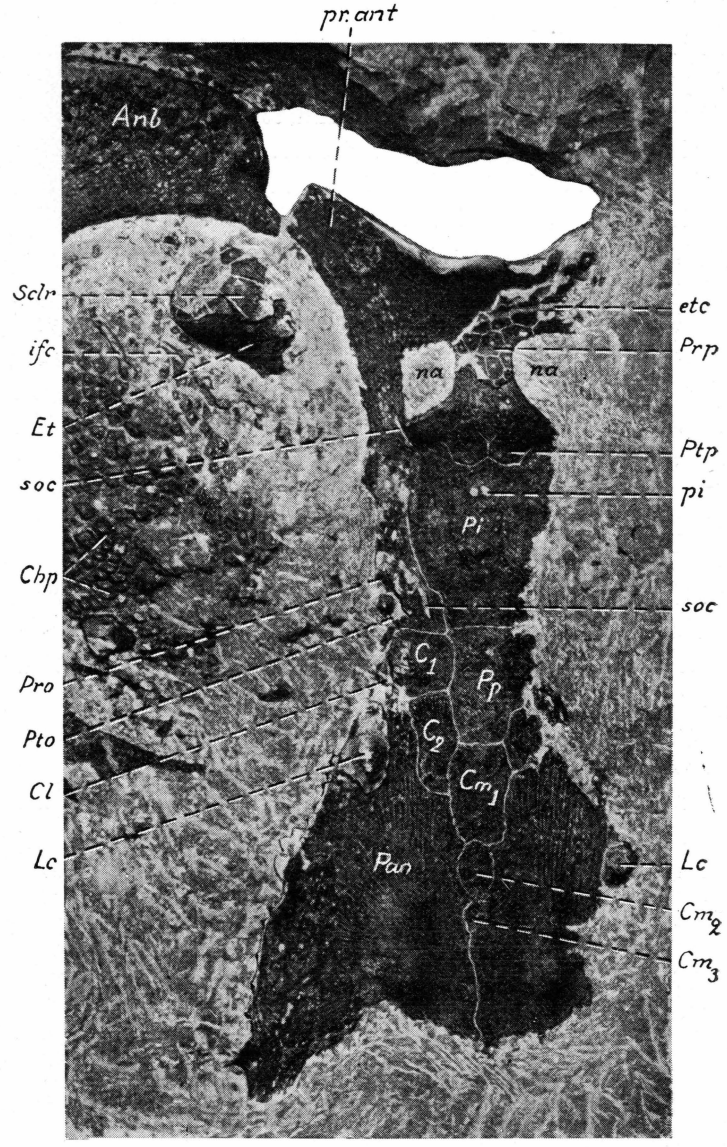
Prp, prenasal dermal plates; *ifc*, infraorbital sensory canal groove (otic section); *ifc.c*, anterior ethmoidal commissure; *na*, nasal opening; *orb*, orbital notch; *pi*, pineal opening; *soc*, supraorbital sensory canal groove; *soc.c*, posterior ethmoidal sensory canal commissure.

ancestors, of course, have also caused several modifications in the development of the sensory canal system of the head. Owing to the strong narrowing of the interorbital wall the interorbital part of the exoskeletal skull-roof was reduced laterally on either side so that the interorbital section of the supraorbital sensory canal groove (soc_1) became situated in the skin above the medial part of the eye-ball. This section of the supraorbital canal was also much reduced and lost its connection anteriorly with the anterior sections of the same groove (text-fig. 65B). Generally it gained secondary relations to the postero-dorsal sclerotic plate, but sometimes it became also situated above the lateral part of the pineal plate. The section of the groove



Text-fig. 69. *Asterosteus stenocephalus* Newberry. Cranium, wanting its prepineal parts Dorsal aspect. Specimen No. 314 in the possession of the American Museum of Natural History in New York. Approximately × $^1/_1$.

C_1, C_2, anterior and posterior central plates proper, developed in relation to supraorbital sensory canal groove; C_2+Cm, posterior central plate proper, probably fused with a median central plate; *Cl*, lateral central plate, situated laterally to supraorbital sensory canal groove; *Cm*, median plate central; *Lc*, independent lateral sensory canal components of postorbital, marginal, and paranuchal plates; *M*, marginal plate (component not related to the infraorbital sensory canal groove); *N*, nuchal plate; *Pan*, paranuchal plate (the medial component, not related to the sensory canal system; *Pi*, pineal plate; *Pp*, postpineal plate; *Pro*, preorbital plate, Pto_1, Pto_2, postorbital plates; *f.magn*, foramen magnum of endocranium; *ifc*, infraorbital sensory canal groove; *nc*, posterior opening of space for notochord in cranial basis; *orb*, orbital notch; *pi*, pineal aperture; *pp*, a short transverse pit-line, possibly the posterior pit-line of the skull-roof; *ptc*, postotic sensory canal groove; *soc*, supraorbital sensory canal groove.



Text-fig. 70. *Jagorina pandora* Jaekel. Parts of the skull in dorsal aspect. The lateral and posterior parts of the skull-roof covered by matrix which could not be removed without damaging the endocranium. The ornament and the outer layers of the dermal bones mostly not preserved. Specimen belonging to the Geol.-Palaeontological Institute of the University of Berlin. × $^2/_1$.

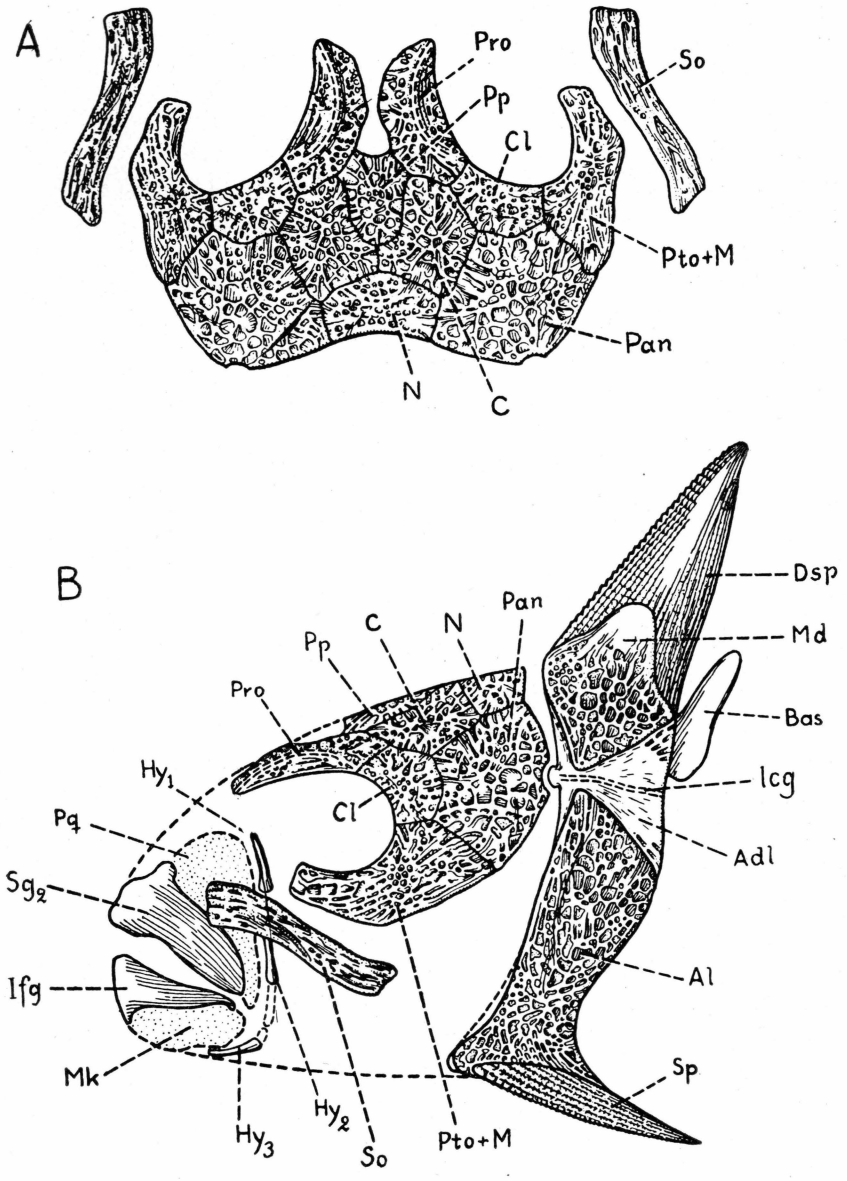
Anb, antorbital ossification for the support of the large pectoral fin (only a proximal part shown); C_1, C_2, anterior and posterior central plates proper, developed in relation to the supraorbital sensory canal groove; *Cl*, lateral central plate, situated laterally to the supraorbital sensory canal groove (not well exposed); Cm_1–Cm_3, median central plates; *Chp*, scale-like dermal plates of anterior part of cheek; *Et*, ossified endoskeletal tube around eye-ball; *Lc*, independent lateral sensory canal components of paranuchal, marginal and postorbital plates; *Pan*, paranuchal plate (medial component, not related to the sensory canal system); *Pi*, pineal plate; *Pp*, postpineal plate; *Pro*, preorbital plate; *Prp*, prenasal plates; *Pto*, postorbital, or postorbitals, imperfectly exposed; *Ptp*, postnasal plates; *Sclr*, dermal sclerotic plates; *etc*, one of the two ethmoidal cross-commissural sensory canal grooves; *ifc*, infraorbital sensory canal groove (infraorbital section); *na*, nasal aperture; *pi*, pineal aperture; *pr.ant*, antorbital process; *soc*, supraorbital sensory canal groove.

in question following nearest in front of the interorbital section just dealt with disappeared completely (text-fig. 65B), whereas the very foremost section (soc_2) seems to have persisted and to have fused with that of the opposite side into an anterior median groove, which was transformed into a pit-line groove connecting the upper infraorbital grooves (ifc_1) of both sides. The anterior division of the infraorbital groove became subdivided into an upper part, situated on the dorsal face of the head, and a lower part, situated on the lower side of the head. In consequence of the modifications in the lateral parts of the head the lower part of the infraorbital groove (ifc_2) lost its direct connection with the upper infraorbital groove (ifc_1, figs. 4, 65). In connection with the said modifications in the lateral parts of the head the vertical pit-line groove of the cheek was extended both upwards, on to the skull-roof, and downwards, on to the lower side of the head. This pit-line groove also gained connection with the upper and lower infraorbital grooves and thus ultimately developed in a manner somewhat corresponding to that in recent Holocephalians and *Rajiformes* (text-fig. 63; cf. also Holmgren 1942, pp. 22–24, figs. 17, 18). The middle and posterior pit-line grooves, and the supratemporal groove, were all pushed close together on the short postorbital division of the head-shield. The cephalic division of the main lateral line was much shortened.

As may readily be understood from what has just been advanced, the dermal bones of the head must on the whole be much higher specialized in the *Antiarchi* than what they are in Euarthrodires and several other groups of Arthrodires. That this is so was shown to some extent already in 1931 (Stensiö 1931, pp. 150–155), but will now be further elucidated in the subsequent account.

After these general remarks we shall now proceed to a discussion of the individual dermal bones in the head-shield and trunk-armour of the *Antiarchi*.

The premedian plate cannot be directly compared to any one of the single independent plates which occur on the rostral parts of the ethmoidal region in the Euarthrodires (cf. text-figs. 66, 67). This plate must, therefore, have arisen as such in connection with the formation of the preorbital division of the head-shield. Its position and relations to the sensory canal system indicate that its larger anterior part was represented in Euarthrodires only by a mass of soft tissue which lay on the median part of the rostral face of the ethmoidal region, just below the external nasal apertures (cf. text-fig. 67). Besides, it is not impossible that the plate in its posterior part may also include homologues of the postnasal plates (*Pn*, text-figs. 66B, 67) of the Euarthrodires. In Rhenanid Arthrodires it is represented by the small prenasal plates (*Prp*, text-figs. 68, 70), situated behind, and just in front of, the posterior one (*soc.c*, text-fig. 68) of the two transverse commissural sensory canal grooves which are found on the foremost ethmoidal part of the skull-roof. This posterior transverse commissural groove (*soc.c*) probably



Text-fig. 71. A Ptyctodontid Arthrodire, *Rhamphodopsis trispinatus* Watson. *A*, the dermal bones of the head spread out into one plane and viewed from above. *B*, reconstruction of the head and trunk-armour in lateral aspect. From Watson 1938, but with a different interpretation of the head-bones. × $^{2\cdot7}/_{1}$.

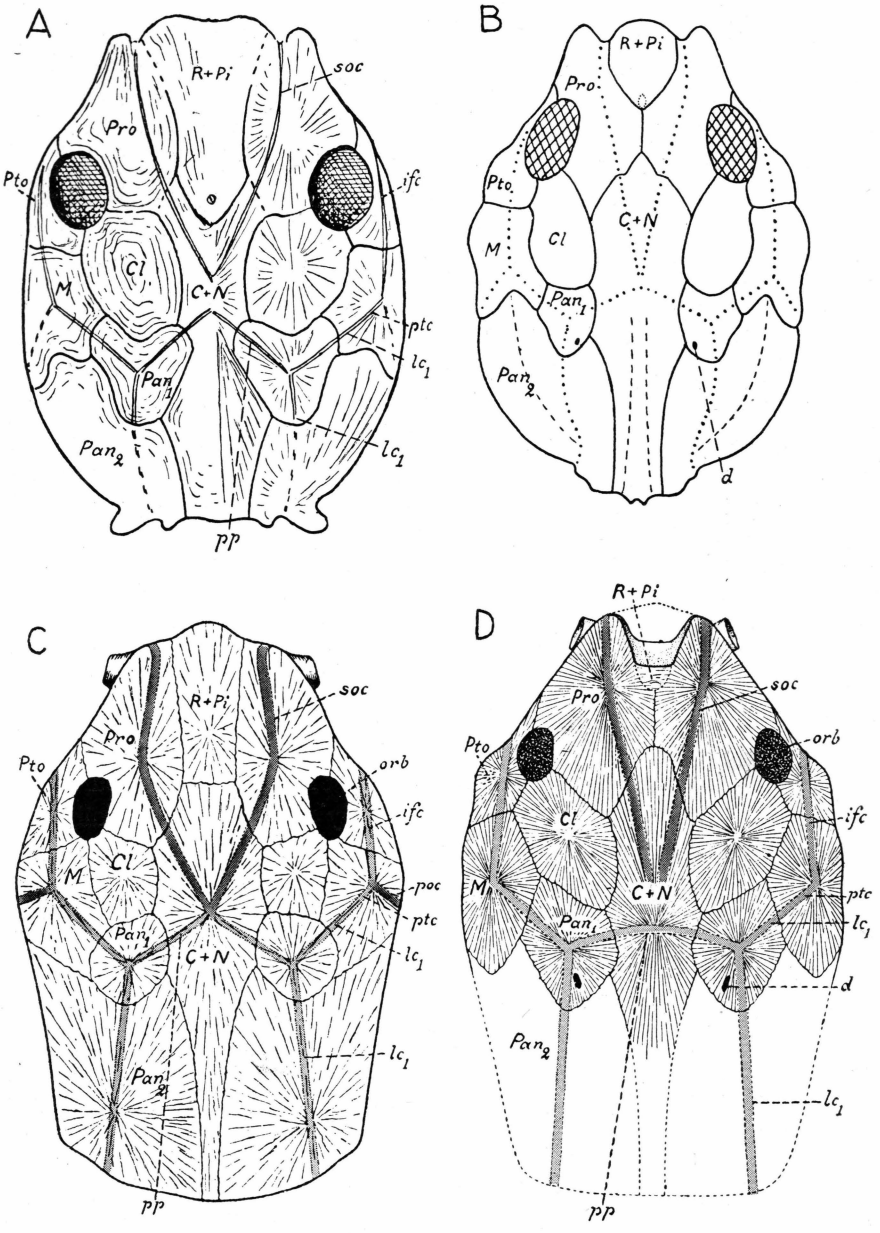
Adl, anterior dorso-lateral plate; *Al*, antero-lateral plate; *Bas*, basal plate of anterior dorsal fin; *C*, central plate proper; *Cl*, lateral central plate; *Dsp*, spine of anterior dorsal fin; Hy_1–Hy_3, ossifications of hyoid arch; *Ifg*, inferognathal; *Md*, median dorsal plate; *Mk*, Meckel's cartilage; *N*, nuchal plate; *Pan*, paranuchal plate; *Pp*, postpineal plate (= plate *Y* of Watson's description); *Pq*, palatoquadrate; *Pro*, preorbital plate; *Pto*+*M*, postorbital plate, probably fused with marginal plate; Sg_2, posterior superognathal; *So*, probably a suborbital plate; *Sp*, pectoral fin-spine; *lcg*, main lateral line groove.

corresponds to the rostral parts of the upper infraorbital grooves in the *Antiarchi*, whereas the anterior transverse commissure (*ifc.c*, text-fig. 68) presumably is comparable nearest to the ethmoidal parts of the lower infraorbital grooves in the *Bothriolepinae*. The condition that the two ethmoidal commissures in Rhenanid Arthrodires lie on the rostral part of the dorsal face of the snout clearly proves that the anterior part of the preorbital division of the skull-roof in these Arthrodires includes skeletal elements the homologues of which in the *Antiarchi*, as we shall see (cf. p. 208 below), are situated on the lower side of the head, between the rostral margin of the head-shield and the mouth-opening. The transformation of the anterior median part of the preorbital division of the skull-roof in this respect has thus proceeded much further in Rhenanid Arthrodires than in *Antiarchi* (cf. pp. 31–33 above).

That the foremost part of the dorsal side of the ethmoidal region which represents the rostral face of the snout in Euarthrodires is completely covered by exoskeleton in two so widely different groups of Placoderms as *Antiarchi* and Rhenanid Arthrodires is of much interest. This fact necessitates the assumption that the snout in primitive Placoderms in general must have been completely covered by dermal bones on all its outer faces. The absence of exoskeleton on more or less extensive rostral parts of the head in several of the specialized Arthrodire groups known to us, therefore, certainly is secondary and due to reduction. In these circumstances it follows, of course, that the premedian plate cannot possibly be a quite new skeletal formation developed within the *Antiarchi*-group, but must have arisen from certain of the rostral exoskeletal elements which existed in the primitive Arthrodiran ancestors of that group.

The rostral plate, as we now know, is a small, median, unpaired T-shaped bone, situated mainly between and behind the external nasal apertures, on the primary rostral part of the snout. Both in its shape and in its position it agrees, therefore, so completely with the rostral plate of the Brachythoracid and Dolichothoracid Arthrodires (Stensiö 1931, p. 151; 1942, pp. 11–12) that beyond question it is homologous to it (*R*, textfigs. 66, 67B). Accordingly it is also a strict homologue of the rostral component of the rostro-pineal plate of the Petalichthyid Arthrodires (*R*+*Pi*, text-fig. 72). In Rhenanid Arthrodires it is represented by several small plates (*Ptp*, text-figs. 68, 70), which are situated between, and just behind, the external nasal apertures and the most posterior ones of which may show

Text-fig. 72. Restorations of the skull-roofs of four *Petalichthyid Arthrodires*. Dorsal aspect. *A*, of *Lunaspis arctica* Heintz. From Heintz 1937. *B*, of *Lunaspis* (based on *L. broilii* Gross and *L. prümensis*). From Gross 1937. *C*, of *Macropetalichthys rapheidolabis*. From Stensiö 1925. *D*, of *Epipetalichthys wildungensis*. From Stensiö 1925. The interpretation of the bones in part different from that given by Gross and Heintz in 1937. *Cl*, lateral central plate, primarily probably developed in relation to a posterior medial part of the pit-line groove *ifc.b* in Arthrodires in general; *C*+*N*, centro-nuchal plate, formed by the fusion of the homologues of the following places of certain other Arthrodires:



1) the postpineal plate (*Pp*, text-figs. 69, 70, 71) of the Rhenanids and Ptyctodontids; 2) the central plates proper (*C*, text-figs. 69, 70, 71) of both sides of the Rhenanids and Ptyctodontids; 3) the median central plates (*Cm*, Cm_1–Cm_3) of the Rhenanids; 4) the nuchal plate (*N*, text-figs. 66, 67, 69, 71) of the Euarthrodires, Ptyctodontids and Rhenanids; and 5) the medial extrascapulars of the Brachythoracids; *M*, marginal plate; Pan_1, Pan_2, anterior and posterior paranuchal plates respectively; *Pro*, preorbital plate; *Pto*, postorbital plate; *Pto*, postorbital plate[1]); rostro-pineal plate; *d*, external opening of canal for endolymphatic duct; *ifc*, infraorbital sensory canal; lc_1, cephalic division of main lateral line; *orb*, orbit; *pp*, canal corresponding to the posterior pit-line of the skull-roof of fishes in general; poc_1, probably a dorsal part of the prepercular canal; *ptc*, postotic sensory canal; *soc*, supraorbital canal.

[1]) See foot-note on next page (p. 200).

a paired disposition. As will be shown below (pp. 201–205), the rostral plate in Placoderms normally is the foremost element of a median unpaired series of bones which from the tip of the snout extends more or less continuously backwards to the posterior margin of the skull-roof.

The pineal plate, as we know (Stensiö 1931, p. 150), is doubtless in the main the strict homologue of the similarly termed plate in Brachythoracid, Dolichothoracid and Rhenanid Arthrodires (*Pi*, text-figs. 66, 68–70) and also most certainly corresponds to the pineal component of the rostro-pineal plate in Petalichthyid Arthrodires (*R*+*Pi*, text-fig. 72). In Arthrodires it is normally the second plate from in front of a median unpaired series of plates (cf. the account of the rostral plate just above and pp. 201–205 below).

The lateral plate is certainly (cf. also 70–74) of a very complex nature. Judging from its position in the head-shield and from its relations to the sensory canal system, its homologiues are probably somewhat as follows. Its foremost portion, developed in relation to the foremost part of the upper infraorbital groove (*ifc*$_1$), is of a nature corresponding to that of the anterior parts of the premedian plate (cf. pp. 196–197). This portion lay in a mass of tissue whose homologue in Euarthrodires was situated just ventro-laterally and postero-laterally to the external nasal aperture (text-fig. 67). In Rhenanid Arthrodires, on the other hand, it is represented by the lateral ones of the small plates (*Prp*, text-figs. 68, 70) which lie just in front of, and behind, the lateral part of the posterior ethmoidal commissure (*soc.c*) and the adjoining foremost part of the sensory canal groove, laterally to the connection of that commissione with the supraorbital groove (*soc*). As the anterior parts of the premedian plate, the foremost portion of the lateral plate thus probably is no new formation arisen within the *Antiarchi*-group, but must be assumed to have been formed by certain exoskeletal elements present in the primitive Arthrodiran ancestors of the group (cf. p. 198 above). The antero-lateral portion of the lateral plate which (in the *Bothriolepinae*) bears the upper part of the vertical pitline of the cheek (*vcp*) was conceivably formed in a mass of tissue which primarily entered in the formation of the cheek. This part of the plate may probably, therefore, represent a component of the suborbital of the Euarthrodires (text-figs. 66B, 67) and a number of the small dermal plates which cover the upper parts of the cheek in Rhenanid Arthrodires (*Chp*, text-fig. 70; cf. also Broili 1933a, text-fig. 3). Finally, on account of its relations to the oblique cephalic pit-line groove (*ifc.b*) the posterior main portion of the lateral plate must in the first place

[1]) This plate in Petalichthyid Arthrodires was erroneously interpreted as a suborbital by Gross (1937, pp. 49, 51, 54, 59, 64, text-figs. 24–26, 28) and Heintz (1937, pp. 4–8, text-figs. 1,2). That in this plate we are actually concerned with the postorbital plate was shown already in 1925 (Stensiö 1925, pp. 147–148, text-figs. 3, 5, 8). The plate is to a large extent situated on the postorbital process of the endocranium, and the sensory canal traversing it was innerwated by nerve-branches which pierced the post-

comprise the homologue of the postorbital plate of the Euarthrodires (*Pto*, text-figs. 66, 67 A) and the equivalents of the postorbital plate in the Petalichthyid[1]) and Rhenanid Arthrodires (*Pto*, Pto_1, text-fig. 69; *Pto*, text-fig. 72). In addition it may probably include a component representing a lateral or antero-lateral part of the central plate of the Euarthrodires (*C*, text-figs. 66, 67 A) and at least the lateral central plate (*Cl*, text-figs. 69–72) of the Ptyctodontid, Petalichthyid[1]) and Rhenanid Arthrodires.

Summing up what has just been set forth here concerning it we thus find that the lateral plate in all probability is composed of four principal components: 1) an anterior component, developed in relation to an anterior part of the upper infraorbital sensory canal groove and probably preformed in primitive Arthrodires in general by certain bone plates situated on the rostral face of the ethmoidal region just below, just posteriorly, and somewhat postero-ventrally, to the external nasal aperture of either side; 2) an anterior lateral component, developed in relation to the upper part of the vertical pit-line of the cheek, which represents a part of the suborbital of the Euarthrodires and several of the dorsal small cheek-plates occurring on the cheek of the Rhenanid Arthrodires; 3) a main posterior component, representing the postorbital or its equivalents in the Arthrodires; and, finally, 4) a hindmost component, which represents an antero-lateral part of the central plate of the Euarthrodires and the whole lateral central plate of the Ptyctodontid, Petalichthyid and Rhenanid Arthrodires. Whether it includes also a vestige of the preorbital plate of the Arthrodires is difficult to say, but it seems very unlikely that this is the case. The homologue of the last-mentioned plate of the Arthrodires has probably been completely reduced in consequence of the migration of the eyes to the dorsal side of the head and in consequence of the excessive narrowing of the interorbital wall caused by that dorsal migration of the eyes. A strong evidence in favour of this veiw is the vestigial condition and variable position of the posterior section (soc_1) of the infraorbital sensory canal groove. By the reduction of the homologue of the preorbital plate this section of the supraorbital groove lost its ordinary connection with the exoskeletal skull-roof and became variable as to its position. As we have seen (pp. 172–173 above), it may lie along the lateral margin of the pineal plate or on the medial part of the postero-dorsal sclerotic plate. Sometimes it was probably also situated in the skin, between the pineal plate and the postero-dorsal sclerotic plate.

The postpineal plate, generally known up till now under the term

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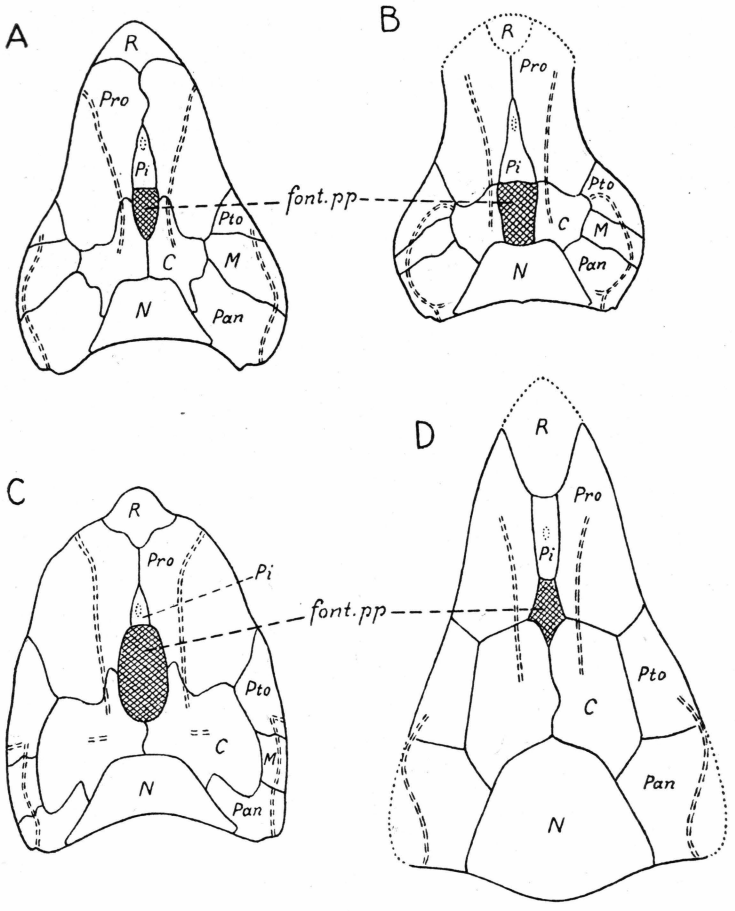
orbital process. These nerve branches were certainly given off from a nerve which corresponded to the r. oticus lateralis of fishes in general. This being so, it follows, of course, that the plate (*Cl*) considered by Gross and Heintz as the postorbital must be the homologue of the lateral central plate of the Rhenanids and Ptyctodontids (*Cl*, text-figs. 69, 70, 71).

[1]) Cf. foot-note [1]) on preceeding page (p. 200).

of postmedian plate, was considered by the writer in 1931 to be represented in Euarthrodires either by certain postero-medial parts of the postorbitals or by certain antero-medial parts of the central plates fused into an unpaired median plate (Stensiö 1931, pp. 151–152). However, a somewhat different and more satisfactory explanation of the nature of this plate can now be given than what was the case on that occasion. Already a cursory glance at text-figs. 69, 70 and 71 may suffice to make clear that the postpineal plate in all probability is the strict homologue of an unpaired median element invariably present in the Rhenanid and Ptyctodontid Arthrodires, an unpaired median element (*Pp*) which in Rhenanids lies immediately behind the pineal plate (text-figs. 69, 70) and in Ptyctodontids just behind the gap in the skull-roof primarily occupied by the completely reduced pineal plate (text-fig. 71). This element in Rhenanids and Ptyctodontids, which will also be termed postpineal plate, is situated in such a way behind the pineal plate that it extends more or less far backwards between the central plates proper (*C*, C_1, C_2) and is bounded laterally by the posterior parts of the preorbital plates and behind them by the central plates proper. In *Asterosteus* and *Rhamphodopsis* (text-figs. 69, 71) its posterior boundary is also constituted by the central plates proper, whereas in *Jagorina* (text-fig. 70) it is bounded posteriorly by the foremost one (*Cm*) of a series of three median unpaired central plates (Cm_1–Cm_3) which follows behind it.

In *Asterosteus* and *Jagorina* (text-figs. 69, 70) we see clearly that the postpineal plate (*Pp*) is an element belonging to an unpaired median series of bones that from in front backwards is composed of the following plates: 1) the pineal plate (*Pi*), 2) the postpineal plate (*Pp*), 3) one ore more median unpaired central plates (*Cm*, Cm_1–Cm_3), and 4) a small nuchal plate (*N*) situated near or at the posterior margin of the skull-roof. A closer analysis shows that a corresponding median unpaired series of bones actually occurs in all groups of Arthrodires and, besides, also in the *Antiarchi*. The presence of a median unpaired series of bones in the exoskeletal skull-roof is thus a characteristic feature of Placoderms in general. As a wider knowledge of this unpaired median series of bones in Arthrodires helps considerably in elucidating the homologies not only of the postpineal plate, but also of several other plates of the skull-roof of the *Antiarchi*, we shall enter briefly upon its development in various groups of non-Rhenanid Arthrodires.

Turning first to Ptyctodontid Arthrodires (text-fig. 71) we find in them that the unpaired median series of bones of the skull-roof consists only of two plates, the postpineal (*Pp*) and the nuchal (*N*), whereas all its plates in front of the postpineal plate have become entirely reduced. In Petalichthyid Arthrodires (text-fig. 72) the bone-series in question is much more complete and may often also extend uninterrupted throughout the whole length of the skull-roof. In this Arthrodire group, however, it is represented only by two bones, the rostro-pineal plate and the centro-nuchal plate. The



Text-fig. 73. Skull-roofs of certain Brachythoracid Euarthrodires with a postpineal fontanelle. Dorsal aspect. *A*, of *Belesteus pusillus* Gross. *B*, of *Tremastoteus fontanellus* Gross. *C*, of *Brachyosteus dietrichi* Gross. *D*, of *Brachydirus carinatus* Gross. All the figures from Gross 1932a.

C, central plate (complex plate); *M*, marginal plate; *N*, nuchal plate; *Pan*, paranuchal plate; *Pi*, pineal plate; *Pro*, preorbital plate; *Pto*, postorbital plate; *R*, rostral plate; *font.pp*, postpineal fontanelle.

rostro-pineal plate ($R+Pi$) is developed in such a manner as to position, extent and other characters that it must include homologues of both a rostral plate and a pineal plate. The centro-nuchal plate ($C+N$), as has already been pointed out to some extent by Gross (1937, pp. 51–59) and Heintz (1937, pp. 7–8), is a very complex bone, which in all probability includes the homologues of the following elements (cf. text-figs. 66A, 69–71): 1) the postpineal plate of the Rhenanids, Ptyctodontids, and *Antiarchi*; 2) the central plates proper (C, C_1, C_2) of the Rhenanids and Ptyctodontids; 3) the median central plates of the Rhenanids and Ptyctodontids; 4) the nuchal plate of the Rhenanids, Ptyctodontids and Euarthrodires; and finally, 5)

the medial extrascapular elements of the *Brachythoraci* (Stensiö 1945, pp. 41, 42, 53–55, 57, 64). The postpineal plate, and the other plates behind it of the median unpaired series, in the Pelalichthyids have thus fused together into a long unpaired bone into which the central plates proper of both sides have also been included. In the Brachythoracids (text-figs. 66, 67) the series in question is composed of three plates, the rostral plate (*R*), the pineal plate (*Pi*), and the nuchal plate (*N*). The same is also the case in the Dolichothoracids (Stensiö 1942, pp. 4–17; 1945, pp. 41–42, 53–55, 57, 64), but the nuchal plate in them in addition includes medial extrascapular elements and thus is a nuchalo-extrascapular. The postpineal and median central plates both in Brachythoracids and Dolichothoracids have probably fused together with adjoining bones. In certain Brachythoracids, as for instance *Dinichthys* (Heintz 1932b, text-fig. 43), *Pachyosteus* (Gross 1932a, text-fig. 4A–E), *Rhinosteus* (Gross 1932a, text-fig. 6A, B), *Leiosteus* (Gross 1932a, text-fig. 8D) and *Homostius* (Heintz 1934, text-figs. 1–3), and possibly also in the Jaekelaspid Dolichothoracids (Heintz 1929b, text-fig. 1), the postpineal plate is thus presumably fused with the pineal plate, while in other Brachythoracids, e.g. *Coccosteus* (text-fig. 66A; cf. also Heintz 1938, text-fig. 1), and probably also in several Dolichothoracids (Heintz 1929b, text-fig. 2), it seems to form part of one, or of both, the preorbital plates[1]). Finally, in the Brachythoracid form *Rhachiosteus* (text-fig. 66C) it may perhaps be independent. The homologues of the median central plates of the Rhenanids following nearest behind the postpineal plate have in Euarthrodires probably fused together somewhat alternatingly with the right and left central plate. Such an alternating fusion of them with the central plates would explain the often strongly undulating course of the suture between the central plates in several Brachythoracids. Another fact which is of interest to us in this connection as it seems to support the opinion here maintained that at least a homologue of the postpineal plate enters in the formation of the exoskeletal skull-roof of the Brachythoracids is the condition that the exoskeletal skull-roof in *Belosteus*, *Trematosteus*, *Brachyosteus*, and *Brachydirus* exhibits a postpineal fontanelle. This fontanelle (*font.pp*, text-fig. 73; cf. also Gross 1932a, text-figs. 13, 14B, 15B, E, 16C) is situated behind the pineal plate and between the postorbital and central plates in such a manner that it corresponds exactly to a completely reduced postpineal plate, which before its reduction probably formed part of the pineal plate. In *Trematosteus* the fontanelle extends as far backwards as to the nuchal plate (text-fig. 73B), because of which in this genus it seems to represent not only a reduced postpineal plate, but also one or more reduced small median central plates. Turning to the Phyllolepid Arthrodires (Stensiö 1936, pp. 27–28, text-figs. 2, 3, 9, 23, 24) we find in them that the unpaired median series of bones is represented only by the large median unpaired cephalic plate, which is

[1]) In *Coccosteus minor* (Heintz 1938, text-fig. 1) the postpineal plate seems to be included into the left preorbital.

of a complex origin. This plate in Phyllolepids probably comprises homologues of the median central plates, the nuchal plate, the central plates proper of both sides, the lateral central plates of both sides, and the medial extrascapulars (cf. text-figs. 69, 70). Finally, in the *Antiarchi* the unpaired median bone series is very complete, being formed of 1) the complex premedian plate (cf. pp. 196–198 above), 2) the rostral plate (cf. p. 198 above), 3) the pineal plate (cf. pp. 198–200 above), 4) the postpineal plate, and 5) the centro-nuchal plate (cf. pp. 205–206 below).

As may be gathered from the account just given, the postpineal plate of the *Antiarchi* must obviously be considered as a strict homologue of the independent postpineal plate of Rhenanid and Ptyctodontid Arthrodires. As we have seen, it is conceivably homologous also to an anterior median component of the centro-nuchal plate of the Petalichthyids and to a component in the skull-roof of the Euarthrodires that forms part either of the pineal plate or of one of the preorbital plates. In certain Brachythoracid Arthrodires and in the Phyllolepid Arthrodires its homologue has been completely reduced.

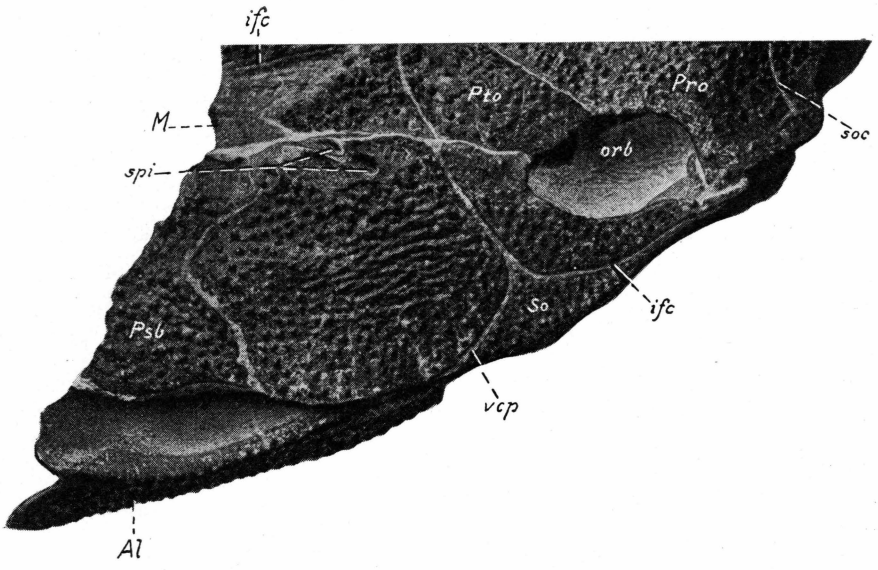
The centro-nuchal plate of the *Antiarchi* has such relations to the sensory canal system that, as we have seen, it bears the hindmost parts of the oblique cephalic pit-line grooves (*ifc.b*, *ifc.b*$_1$) of both sides, mostly (non-*Bothriolepinae*) the median parts of the middle pit-line grooves (*mpg*) of both sides, the posterior pit-line grooves (*pp*) of both sides, and, besides, usually also the medial parts of the supratemporal groove (*stc*). On account of these relations to the sensory canal system and on account of its position and relations otherwise it is fully clear that the centro-nuchal plate must be a complex bone, formed by the fusion together of the homologous of the following bones in the Arthrodires: 1) the median central plates (*Cm*, *Cm*$_1$–*Cm*$_3$, text-figs. 69, 70) in Rhenanids, 2) the central plates proper of both sides in Rhenanids (*C*$_1$, *C*$_2$, text-figs. 69, 70) and Ptyctodontids (*C*, text-fig. 71), and parts of the complex central plates of both sides in Euarthrodires, 3) the nuchal plate proper in Rhenanids, Ptyctodontids and Euarthrodires (*N*, text-figs. 66, 67 A, 69, 70, 71, 73), and 4) certain or all of the medial elements which form the extrascapular plates of both sides in Euarthrodires (*Ex*, text-fig. 66 A). Worthy of notice is that as to its outlines the plate is almost exactly as the two central plates proper (*C*) and the nuchal plate (*N*) in the Ptyctodontids taken together (text-fig. 71).

As we thus find, the centro-nuchal plate of the *Antiarchi* is largely comparable to the centro-nuchal plate in both Petalichthyid and Phyllolepid Arthrodires (cf. pp. 202–204) with regard to its principal components, the central plates, the nuchal plate, and the medial extrascapular elements. It differs from the centro-nuchal plate of the Petalichthyids, however, in the absence of a postpineal component, and from the centro-nuchal plate of the Phyllolepids at least in the absence of lateral central components.

The paranuchal-marginal plate as to position and shape agrees somewhat well with the paranuchal plate of the Ptyctodontids and Euarthrodires (*Pan*, text-figs. 66, 67A, 71, 73), the two separate paranuchal plates of the Petalichthyids (Pan_1, Pan_2, text-fig. 72), and the various elements representing the paranuchal in the Rhenanids (*Pan*, *Lc*, text-figs. 69, 70). In view of the fact that it bears the lateral part of the middle pit-line groove of the skull-roof (*mpg*) it is possible, however, that it represents not only the paranuchal, but also the marginal plate of the Euarthrodires and Petalichthyids (*M*, text-figs. 66, 67A, 72, 73) and the numerous marginal elements of the Rhenanids (*M*, *Lc*, text-fig. 69). Finally, as in many cases it is crossed by the lateral parts of the supratemporal pit-line groove, it also includes certain lateral extrascapular elements. As far as may be judged, it is thus of a complex nature (Stensiö 1945, pp. 55, 59).

The postmarginal plate in all probability is strictly homologous to the similarly termed plate in the Euarthrodires (*Pmg*, text-figs. 66A, 67A). That it persists and is well developed in *Pterichthyodes, Gerdalepis, Asterolepis* and the *Bothriolepinae* is due to the condition that in them it enters to some extent into the formation of the subobstantic area. In *Remigolepis*, where the subobstantic area is formed solely by the paranuchal-marginal plate, it is entirely absent.

The prelateral and extralateral plates belong to the cheek and the opercular fold. As we know, both these plates are present together only in the *Bothriolepinae*, whereas in *Pterichthyodes, Gerdalepis, Asterolepis* and *Remigolepis* there is but one large extralateral plate, covering both the cheek and the opercular fold. At a cursory glance the prelaterel and extralateral plates of the *Bothriolepinae* seem together to represent the single large extralateral plate in *Pterichthyodes*, *Gerdalepis*, *Asterolepis* and *Remigolepis*, but a closer examination of their position in relation to each other seems to show that the extralateral plate is strictly homologous in all the forms referred to. As has been pointed out above (pp. 88–89), the extralateral plate of the *Bothriolepinae* with its antero-dorsal part extends fairly far forwards on the medial side of the prelateral plate, where it is attached to almost the entire margin of the prelateral notch medially to the prelateral plate. Judging from this, it is not inconceivable, of course, that an extralateral plate of the *Bothriolepis*-type might have become produced forwards so that it completely filled up the prelateral notch medially to the prelateral plate and that, therefore, it overtook the function also of the prelateral plate. It is thus, as we find, not inconceivable that an extralateral plate of the *Pterichthyodes-Gerdalepis-Asterolepis-Remigolepis* type may have evolved directly from one of a *Bothriolepis* type and that in consequence of this the prelateral plate lost its function and was reduced completely. Be this as it may, it is clear, however, that on account of its position in relation to the jaw apparatus and to the vertical pit-line of the cheek the prelateral plate is nearest comparable to an upper middle postorbital part of the sub-



Text-fig. 74. *Coccosteus canadensis*. Cheek-bones of the right side of a specimen in the possession of the Swedish Museum of Natural History in Stockholm. The posterior part of the postsuborbital missing. Approximately × $^1/_1$.
Al, intero-lateral plate; *M*, marginal; *Pro*, preorbital plate; *Pto*, postorbital plate; *Psb*, postsuborbital; *ifc*, infraorbital sensory canal groove; *orb*, orbit; *soc*, supraorbital sensory groove; *spi*, possible spiracular opening; *vcp*, vertical pit-line of cheek, previously interpreted as a jugal groove.

orbital of the Euarthrodires (*So*, text-figs. 67, 74) and to certain of the upper small postorbital cheek-plates in *Gemündina* (Broili 1933a, text-figs. 1, 3, 4), whereas the extralateral plate probably represents the hindmost part of the suborbital and the whole of the postsuborbital and internal plates in the Brachythoracids (*Psb*, *So*, text-figs. 67A, 74), and the two posterior plates of the lateral side of the head in *Gemündina* (Broili 1933a, text-figs. 1, 3, 4). Of much interest in this connection is the fact that the spiracular opening at least in Brachythoracid Euarthrodires seems to be situated just above, or in, the very dorsal part of, the suborbital plate (*spi*, text-fig. 74) and thus in them presumably had a position in relation to the cheek-opercular bones fundamentally similar to that in the *Antiarchi*.

Since it is crossed by the lowermost part of the vertical pit-line of the cheek (*vcp*), the infraprelateral plate seems to be an equivalent of a ventral postorbital part of the suborbital of the Brachythoracids (*So*, text-figs. 67A, 74) and of a considerable part of the foremost large cheek plate in *Gemündina* (Broili 1933a, text-figs. 1, 3) which lies ventro-laterally to the eye.

As the Ptyctodontids, the *Antiarchi* seem to be completely devoid of an element corresponding to the anterior superognathal of the Brachythoracids (cf. pp. 90–92 above).

The mental plate, as we have seen (pp. 94–95 above; cf. also Stensiö 1931, pp. 62–63, 154), is composed of both a tooth-component and a sen-

sory canal component. As has already been shown above (pp. 173–174), the tooth-component had such a position in relation to the palatoquadrate that it must be supposed to be a homologue of the posterior superognathal of the Brachythoracids (Sg_2, text-fig. 67) and of the large superognathal of the Ptyctodontids (Sg_2, text-fig. 71). The sensory canal component, which is developed in relation to the foremost parts of the lower infraorbital groove (ifc_2), corresponds to those elements in the Rhenanid Arthrodires (text-figs. 68, 70) which lie somewhat postero-laterally to the anterior ethmoidal cross-commissure (*ifc.c* text-fig. 68) and thus perhaps inter alia also to an antero-dorsal part of the foremost large cheek plate in *Gemündina*, which lies just antero-ventrally to the orbit (cf. Broili 1933a, text-figs. 1, 3, 4). The homologues of this component are to be sought for in the Brachythoracids (text-fig. 67) partly in the mass of soft tissue which lay on the postero-ventral parts of the snout, partly in the suborbital division of the suborbital plate. Consequently the component in question is no new formation, arisen within the *Antiarchi*, but is derived from bones which in primitive Placoderms covered the postero-latero-ventral parts of the snout and the foremost part of the cheek, ventrally to the orbital opening. As far as may be judged at present, the component under discussion thus includes both certain anterior elements, which perhaps to some extent are comparable to the postrostrals of the Crossopterygians, and certain posterior elements which represent the anterior infraorbital elements in Teleostomian fishes in general.

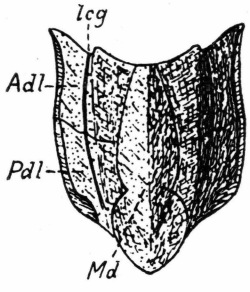
The inferognathal, as we now know (Stensiö 1931, pp. 63–68, 154); Gross 1941a, pp. 39–41; cf. also pp. 93, 96), almost in all its fundamental characters agrees with that of the Brachythoracids, and it is fully obvious, therefore, that it must be strictly homologous that bone. It corresponds certainly also to the inferognathal of the Ptyctodontid Arthrodires. In the Rhenanids there is no inferognathal, but only independent teeth or small tooth-bearing plates.

The extramandibular plate is completely without a bony homologue in the Euarthrodires and Ptyctodontid Arthrodires. In the Rhenanid Arthrodires it may perhaps be represented by certain small scale-like plates on the outside of the lower jaw.

The submandibular series of bones, as we have seen (p. 97 above), seems to correspond nearest to the mandibular dermal rays of the Acanthodians (cf. Watson 1937, pp. 56, 63, 67–68, 75–76, 83, 86, 92, 103–104, 118–119), whereas the subhyoidean series of bones seems to be of a nature similar to that of the dermal bones on the outside of the upper parts of the branchial arches of the Acanthodians (cf. Watson 1937, pp. 56–57, 63–64, 68, 76, 119).

We shall now proceed to the trunk-armour. As is well known (cf. pp. 100–101 above), this armour is developed in relation to the pectoral fins, and hence, like that of the Euarthrodires, it is simply to be regarded as the exoskeletal shoulder-girdle. With regard to its considerable extent on the

trunk it is nearest as in the Dolichothoracid Arthrodires (cf. Heintz 1929a, pp. 33–46, text-figs. 8–11, 15, 16, 22; 1929b, text-fig. 5; 1933, pp. 133–141, text-figs. 3, 5, 6; Stensiö 1944). Of its various bones the anterior dorso-lateral, the posterior dorso-lateral, the posterior lateral, the posterior ventro-lateral and the median ventral plates are all clearly homologous to the correspondingly termed bones in the Arthrodires. In the *Bothriolepinae* the posterior dorso-lateral and the posterior lateral



Text-fig. 75. *Prosphymaspis constricta* (Gross). Trunk-armour in dorsal aspect. From Gross 1933b. × $^2/_1$.
Adl, anterior dorso-lateral plate; *Md*, median dorsal plate; *Pdl*, posterior dorso-lateral plate; *lcg*, main lateral line groove.

plates, as is well known, have always fused together into a mixilateral plate. A tendency towards the development of a mixilateral plate is met with also in *Pterichthyodes*, *Gerdalepis* and *Asterolepis*, but normally the posterior dorso-lateral and lateral plates in them are imperfectly fused. In *Remigolepis* the posterior dorso-lateral and lateral plates are always quite independent elements.

The anterior and posterior median dorsal plates are so developed and have such relations to the adjoining plates that they may be assumed together to represent the median dorsal plate of the Arthrodires. A strong evidence in favour of this assumption is the fact that in a small Dolichothoracid, *Prosphymaspis constricta* (text-fig. 75), described by Gross (1933b, p. 25, text-fig. 6A; 1937, pp. 23–25), the median dorsal plate is imperfectly subdivided into an anterior and a posterior division, which resemble the anterior and posterior median dorsal plates respectively in the *Antiarchi* and probably represent two primarily independent primordia (Stensiö 1944, pp. 25–26).

The anterior ventro-lateral plate in its lateral lamina must be assumed to include a component corresponding to the anterior lateral plate of the Arthrodires and thus certainly is a complex plate (cf. Stensiö 1931, p. 155). In the *Bothriolepinae*, where in certain cases it is crossed anteriorly on its ventral face by a transverse subcephalic abdominal pit-line groove (cf. pp. 187–188), and in *Gerdalepis* (cf. Gross 1941b, p. 207), it may per-

haps anteriorly in its ventral lamina include also a component representing the intero-lateral plate of the Arthrodires (cf. the Addenda).

The semilunar plate is of two types, which seem to be of a somewhat different origin (cf. Gross 1941b, pp. 206–207; cf. also below the Addenda). The small unpaired median type found in the *Bothriolepinae* and in *Gerdalepis* thus probably represents the anterior median ventral plate of the Arthrodires in general. The paired broad type, occurring in *Pterichthyodes*, *Asterolepis*, and *Remigolepis*, on the other hand, presumably includes the homologues of the intero-lateral plate and the adjacent half of the anterior median ventral plate of the Arthrodires, for, as we now know, the anterior median ventral plate is paired in certain Arthrodires (Stensiö 1944, p. 35, figs. 15, 17B), a fact which probably involves that in Arthrodires in general it arose from paired primordia.

Finally, the supramixilateral plate, as we have seen, is certainly a fortuitous formation in the *Antiarchi* and hence in all probability has no homologue in the Arthrodires.

Summing up what has been set forth in this chapter we find that out of 26 dermal bones belonging to the head and trunk-armour in the *Antiarchi* no less than 10 appear to be clearly identifiable and in all probability also strictly homologous to certain ones in the Arthrodires. These 10 bones are as follows: the rostral plate, the pineal plate, the postpineal plate, the postmarginal plate, the inferognathal, the anterior dorso-lateral plate, the posterior dorso-lateral plate, the posterior lateral plate, the posterior ventro-lateral plate, and the median ventral plate. All these ten bones also in their shape and development otherwise retain several of their primary Arthrodiran characters. At least 7 of the remaining dermal bones of the head and trunk-armour in the *Antiarchi* are of such a nature that they may easily be imagined to have developed either by fusion of certain bones or bone components in the Arthrodires, or by subdivision of certain Arthrodiran bones, or by both these procedures combined. These bones are: the centronuchal plate, the paranuchal-marginal plate, the mental plate, the extramandibular plate, the anterior median dorsal plate, the posterior median dorsal plate, the anterior ventro-lateral plate and the semilunar plate. Several, or more precisely 5, of the dermal bones in question in the *Antiarchi*, viz. the premedian plate, the lateral plate, the prelateral plate, the extralateral plate, and the infraprelateral plate, throughout, or at any rate in considerable parts, are difficult to compare to any definite bones, or bone elements, in the Arthrodires, but all of them are such, however, that notwithstanding this they can have arisen only by transformations of certain bones, or bone components, occurring primitive Arthrodires. Though highly specialized and modified these bones must thus also be of an Arthrodiran origin. Finally, homologues of the submandibular and subhyoideal bone-series of the *Antiarchi* may very well be imagined to

have been present in the primitive Arthrodires, in which the exoskeleton on the lower side of the head certainly was more completely developed than what it is in the Arthrodire-groups known to us at present.

With regard to the dermal bones of the head and trunk-armour the *Antiarchi* thus appear to be fundamentally as Arthrodires. In this respect they agree actually so closely with Arthrodires, above all with Euarthrodires and Ptyctodontids, that it is fully clear that they must not only have arisen from a common stock with the non-Rhenanid Arthrodires, but also that in fact they constitute a highly specialized group of Arthrodires. As in most respects they approach the Euarthrodires, they may probably be descendents of some primitive branch of this group of Arthrodires (cf. pp. 25–35).

On the changes of certain characters in the Bothriolepinae during the growth.

As we have seen from the general account here given of their organization, the *Bothriolepinae* underwent considerable changes during their growth. In consequence of these changes young and mature individuals always differ considerably from each other in several of their characters. Certain formations were entirely reduced during the growth, whereas others appeared. The various divisions of the armour and several of the dermal bones underwent considerable changes in their proportions in connection with their increase in size. The ornament was much transformed and often became also disposed in a manner different from that in young individuals. The growth changes are thus so considerable that they are of much importance from a taxonomic point of view, on account of which a brief summary of them deserves to be given here.

The special characters of immaturity distinctive of very young individuals occur in their typical development only in very small specimens, in *Bothriolepis, canadensis* for instance, as a rule in those specimens only in which the dorsal length of the trunk-armour is less than 4 cm. These characters are as follows. The exoskeletal bones are mostly fairly delicate. The orbital fenestra is comparatively large in proportion to the size of the head-shield. The dorsal wall of the trunk-armour is clearly narrower than long. The dorsal median ridge of the trunk-armour in the non-crested species is continuous from the tergal angle throughout its extent backwards and, besides, as a rule is also well pronounced and often sharp-edged. The position of the postlevator thickening and the position of the dorsal median part of the crista transversalis interna posterior normally, or at least often, are marked by correspondingly situated depressions on the outside of the dorsal

wall of the trunk-armour. The pit-line grooves are mostly relatively deep and distinct; these grooves also as a rule are not interrupted; nor do they otherwise show any distinct signs of reduction. The anterior oblique cephalic pit-line groove, the anterior oblique abdominal pit-line groove and the oblique transverse ridge behind the last-mentioned groove are frequently or, in certain species, perhaps even normally present. On the lower side of the dorsal wall of the trunk-armour the postlevator crest is often met with, especially in some species. Concerning the other structures on the lower side of the dorsal wall of the trunk-armour it should be mentioned, that the ventral median ridge is imperfectly developed and is represented only by a short piece in front of the anterior ventral pit and by a somewhat longer piece behind the said pit, and that the ventral median groove and the supranuchal area have not developed. The premedian plate is normally shorter than it is broad. The postpineal plate and the centronuchal plates are both mostly relatively short and broad; this particularly applies to the postpineal plate, which often may be strikingly short in proportion to its breadth. The posterior margin of the centro-nuchal plate presents a median marked angle, but no lateral notches or convexities and thus normally is little complicated as to its configuration. The lateral division of the paranuchal-marginal plate normally is relatively broad as compared to the medial division of the same plate. The anterior and posterior median dorsal plates both are mostly relatively longer in proportion to their breadth than in fully mature individuals. The posterior median process of the anterior median dorsal plate generally is strongly developed. The sutural connections between the dermal bones as a rule are little complicated. The sutural connection of the anterior median dorsal plate with the anterior dorso-lateral and mixilateral plates always, or at least only with rare exceptions, is the normal one characteristic of the genera. The ornament consists of a very regular network of continuous anastomosing ridges. These ridges are mostly of a fairly uniform width. In certain species they are also of a fairly uniform height without distinct nodose swellings or tubercular elevations; in other species they are provided with tubercular elevations at their points of union, and, therefore, are both higher and thicker at those points than in their other parts. They are not interrupted or subdivided into shorter pieces or tubercles; and they show no clear indications of concentric or radiating dispositions. The meshes between them generally throughout, or for the most part, are of a nearly uniform size. The ornament is thus much the same in small specimens of all species.

Already pretty soon during the growth of the individuals several changes began to take place in the immature characters. The exoskeletal bones increased in thickness, in consequence of which the depressions and grooves on their outside, corresponding to thickenings or ridges on their inside, normally began to disappear. The orbital fenestra diminished gradually in size. The dorsal wall of the trunk-armour became broader. The dorsal median

ridge usually became less pronounced and interrupted; sometimes it tended even to disappear in certain parts or throughout. The anterior oblique cephalic pit-line groove, the anterior oblique abdominal pit-line groove, and the oblique transverse ridge behind the last-mentioned groove were normally pretty soon completely reduced. In some of the species the postlevator crista also frequently disappeared. The ventral median ridge grew in anterior and posterior directions, more so, however, in the latter than in the former direction, and in connection with the backward growth of this ridge the ventral median groove began to develop. Also the supranuchal area began gradually to appear. The premedian plate normally increased proportionally more in length than in breadth. The postpineal and centro-nuchal plates both usually grew relatively much in length. The posterior margin of the centro-nuchal plate often got a complicated configuration. The lateral division of the paranuchal-marginal plate mostly decreased somewhat in relative breadth. The anterior and posterior median dorsal plates, on the other hand, normally increased proportionally more in breadth than in length and thus as a rule became broader. The posterior median process of the anterior median dorsal plate decreased in relative size and not rarely became reduced completely. The sutural connections between the dermal bones developed so that in many cases they became more or less complicated, in consequence of which inter alia also abnormal types of the sutural connection of the anterior median dorsal plate with the anterior dorso-lateral and mixilateral plates began to appear. The ornament was gradually transformed. Its ridges becames more irregular and often also more or less clearly nodose and elevated into tubercles. Besides, the ridges also often tended to be dissolved into shorter pieces or tubercles and to become more or less radiatingly or concentrically disposed, particularly on the marginal parts of the bones. This process of transformation of the ornament came to a standstill at very different stages in the individual species. The mature type of ornament, therefore, in certain species differs fairly slightly from its immature type, whereas in other species it is very different from that type, being largely, or practically entirely, tubercular.

In half-mature specimens all stages of transition between immature and mature characters are met with, and such specimens are, therefore, very variable in many of their characters.

The mature characters, which as a rule are typically developed only in full-grown individuals of the individual species, are as follows. The exoskeletal bones normally are thick and well developed. External depressions or grooves corresponding to thickenings or ridges on the inside of the bones are generally absent. The orbital fenestra is much smaller in proportion to the size of the head-shield than in young individuals. The dorsal median ridge of the non-crested species is often obtuse and slightly marked and may not rarely be interrupted or even entirely absent. The anterior oblique

cephalic pit-line groove, the anterior oblique abdominal pit-line, and the oblique transverse ridge just behind the latter groove are normally absent. The postlevator crista in some of the species is more rarely present or else is obscure. The ventral median ridge is developed as far backwards as to the middle of the posterior median dorsal plate and may often also extend far forwards into the levator fossa. The ventral median groove is clearly developed on the posterior parts of the ventral median ridge. The premedian, postpineal and centro-nuchal plates usually are longer in proportion to their breadth than in young individuals, but this is particularly the case with the premedian plate, which, at least in mature individuals of certain species, normally is longer than broad. The posterior margin of the centro-nuchal plate is often of a fairly complicated shape. The lateral division of the paranuchal-marginal plate frequently or, perhaps, normally is narrower in proportion to the medial division of the same plate than what it is in young individuals. The anterior and posterior median dorsal plates are normally considerably broader in proportion to their length than in young individuals. The posterior median process of the anterior median dorsal plate is relatively small or absent. The sutural connections between the dermal bones are often fairly complicated. Abnormal types of the sutural connections of the anterior median dorsal plate with the anterior dorso-lateral and mixilateral plates are frequently met with. The ornament is coarser and more irregular than in young individuals. The ridges are often more or less nodose and, at least in places, elevated into tubercles. On the marginal parts of the bones they are disposed more or less clearly radiatingly or concentrically. In several species they are also interrupted or subdivided into longer and shorter pieces and tubercles and to a large extent devoid of anastomoses. Finally, in certain species they are largely, or almost entirely, dissolved into tubercles. The ornament in mature individuals is thus often more or less clearly tubercular and, therefore, mostly very different from that in immature individuals.

Remarks on the relationships between the Bothriolepinae and other Antiarchi and on the relationships of the Antiarchi with the Arthrodires.

The *Antiarchi*-forms distinguished and described up to 1931 were classified by the writer (Stensiö 1931, pp. 156–158) as follows.

Antiarchi.

Family **Remigolepidae.**
Genus: *Remigolepis.*
Family **Asterolepidae.**
Subfamily Asterolepinae.
Genera: *Asterolepis, Pterichthyodes.*

Subfamily Microbrachiinae.
Genus: *Microbrachius.*
Subfamily Bothriolepinae.
Genus: *Bothriolepis.*
Family uncertain: Genus *Cypholepis.*

Since 1931 the comprehension of the *Antiarchi* has been much widened through recearches by Gross. Gross has thus (1933b, pp. 20–22; 1937, pp. 14–19; 1940, pp. 38–44) shown that the previously known genera *Ceraspis* and *Byssacanthus* actually are *Antiarchi*-forms. These two genera and a new one, *Ceratolepis* Gross (1933b, pp. 16–19) were classified by him into a common new family, *Ceraspidae.* Moreover, he has also described a new genus *Taeniolepis* Gross (1932b, p. 35; 1933a, pp. 43–44) the affinities of which are still uncertain. Finally, he has established (Gross 1941b) that the *Antiarchi*-remains previously known as *Pterichthys rhenanus* Beyrich, *P. lüdenscheidensis* Gross and *P. dohmi* Gross do not belong to *Pterichthyodes* at all, but in fact represent a genus of their own for which the previous genus-name *Gerdalepis* Hoffmann has to be reintroduced.

The classification given by the writer in 1931 was adopted by Gross (1932b, 1933a) and since then has been retained on the whole until 1940, when it was modified by Berg (1940, 115–116, 365–366) in the following way:

Pterichthyes *(Antarchi).*

Order 1. **REMIGOLEPIFORMES.**
Family **Remigolepidae** Stensiö.
Genus: *Remigolepis.*

Order 2. **ASTEROLEPIFORMES.**
Family 1. **Asterolepidae.**
Genera: *Asterolepis, Pterichthys* (*Pterichthyodes*).
Family 2. **Microbrachiidae.**
Genus: *Microbrachius.*
Family 3. **Bothriolepidae.**
Genus: *Bothriolepis.*
Family 4. **Ceraspidae.**
Genera: *Ceraspis, Ceratolepis.*

The genus *Remigolepis*, as we know, represents a group of its own among the *Antiarchi.* It differs from *Pterichthyodes, Gerdalepis, Asterolepis, Microbrachius*, and the *Bothriolepinae* in the absence of the postmarginal plate, in the development of the mental plate, in the absence of a joint in the pectoral fin, and in the development of the pectoral fin-armour. Though resembling the *Bothriolepinae* with regard to the presence of the anterior and posterior oblique abdominal pit-line grooves and the general characters of

its ornament it cannot possibly be nearer akin to them (cf. Stensiö 1931, pp. 156–158).

Pterichthyodes and the *Bothriolepinae* agree in the following characters: 1) the development of their premedian plate and, in consequence of this, 2) at least to a certain extent also the structure of their jaw apparatus; 3) the shape of the rostral plate and, in consequence of this, probably also 4) the development of their anterior sclerotic plate and the boundary of their external nasal aperture; 5) the shape of the pineal plate; 6) the general outlines of the anterior median dorsal plate; and, 7) finally, often (*Pterichthyodes* and *Bothriolepis*) the sutural connections of the anterior median dorsal plate with the mixilateral plate. They differ, however, considerably from each other in the following characters: 1) the breadth of the postorbital division of their head-shield in proportion to the posterior regions of the endocranium; 2) the development of the obstantic margin of the head-shield and the development of the obstantic part of the occipital articulation; 3) the shape of the postmarginal plate; 4) the development of the dermal bones of the cheek; 5) the connection of the posterior dorso-lateral plate with the posterior lateral plate; 6) the development of the semilunar plate; 7) the development of the sensory canal system; 8) the development of the pectoral fin; 9) the development of the pectoral fin-armour; 10) the development of the dorsal fins; and finally 11) the development of the caudal fin. In some of the latter characters, as for instance nos. 1, 5, 8 and 9 the *Bothriolepinae* are clearly more specialized than *Pterichthyodes*, whereas, at least in the characters nos. 7, 10, and 11, on the other hand, they are conceivably more primitive than that genus. The characters nos. 7, 10 and 11 beyond question show that the *Bothriolepinae* cannot be direct descendants from *Pterichthyodes*. Their many important agreements with *Pterichthyodes* renders it likely, however, that they might have evolved from ancestors which were somewhat closely akin to that genus.

Gerdalepis, as we now know (Gross 1941b), is a highly interesting genus. It resembles *Pterichthyodes* in several characters, but clearly differs from it and from all other *Antiarchi*-forms known at present in the presence of a special chamber, the apical chamber, in the dorsal part of its trunk-armour. Otherwise it differs from *Pterichthyodes* in the general shape of its trunk-armour and in the presence of a median unpaired semilunar plate. However, in several other respects it agrees fairly well with that genus, and it is thus easily accounted for that it has been confounded so long with *Pterichthyodes*. As far as it is known for the time being, *Gerdalepis* reminds of the *Bothriolepinae* in the following characters: 1) the shape of the rostral plate and therefore probably also 2) the development of the anterior sclerotic plate and the boundary of the external nasal aperture; 3) the shape of the pineal plate; 4) the development of the semilunar plate; 5) and sometimes also the sutural connection of the anterior median dorsal plate with the mixi-

lateral plate. Finally, it is worthy of notice here that in the general shape of its trunk-armour and in a few other characters *Gerdalepis* seems to some extent to approach the *Ceraspidae*.

Whereas the *Bothriolepinae* thus in some way or other seem to be somewhat akin to *Pterichthyodes* and *Gerdalepis* their relationships with *Asterolepis* are clearly much more distant. They differ considerably from *Asterolepis* in the following characters: 1) the stronger development of the nasal capsules and of the lateral dorsal parts of the ethmoidal region of the endocranium; 2) the development of the rostral part of the presumed rostral process of the ethmoidal region of the endocranium; 3) the larger breadth of the postorbital division of the head-shield in proportion to the posterior regions of the endocranium; 4) the development of the posterior lateral part of the lower side of the head-shield; 5) the development of the premedian plate; 6) the development of the jaw apparatus; 7) the shape of the pineal plate; 8) the development of the obstantic margin of the head-shield and the development of the obstantic part of the occipital articulation; 9) the shape of the postmarginal plate; 10) the shape of the anterior median dorsal plate; 11) the development of the lower side of the anterior and posterior median dorsal plates; 12) the complete fusion of the posterior dorso-lateral and posterior lateral plates into a mixilateral plate; 13) the development of the semilunar plate as a median unpaired bone; 14) the more complete development of the sensory canal system and the more intimate connections between the pit-lines and the underlying dermal bones; 15) the stronger development of the pectoral fins; and, finally 16) the development of the pectoral fin-armour. In nos. 3, 12, 15 and 16 of these characters the *Bothriolepinae* are certainly more specialized than *Asterolepis*. On the other hand, in characters Nos. 2, 4, 5, 6 and 14, they are beyond question more primitive than *Asterolepis*, a fact which proves that they cannot be derived from, or be more closely related to, that genus. With regard to the nasal capsules, the anterior parts of the presumed rostral process, the premedian plate, the jaw apparatus, the pineal plate, and to a certain extent also with regard to the anterior median dorsal plate, *Asterolepis* agrees mostly with the *Remigolepidae*.

Microbrachius and the *Bothriolepinae* agree in the following respects: 1) the development of the premedian plate and, in consequence of this, 2) at least to a certain extent also in the development of their jaw apparatus; 3) the development of the obstantic margin of their head-shield and the development of the obstantic part of their occipital articulation; 4) the shape of the postmarginal plate; 5) to a certain extent the sutural connection of the anterior median dorsal plate with the adjoining plates laterally to it; and presumably also 6) the breadth of the postorbital division of the head-shield in proportion to the posterior regions of the endocranium. The main characters in which *Microbrachius* and the *Bothriolepinae* differ from each

other, as far as our knowledge goes, are only as follows: 1) the relative size of the head in proportion to the trunk-armour and 2) the size of the pectoral fins. As far as may be judged at present, everything seems thus to indicate that *Microbrachius* and the *Bothriolepinae* are fairly closely akin.

As may be gathered from the above statements, the *Bothriolepinae* among the forms discussed are nearest akin to *Microbrachius*, but seem also in some way or other to be somewhat related to *Pterichthyodes* and *Gerdalepis*. Their relationships with *Asterolepis*, on the other hand, are much more distant. In these circumstances it is obvious that the *Bothriolepinae* must be grouped much nearer to *Microbrachius* and *Pterichthyodes* than what the writer did in 1931 (Stensiö 1931, pp. 156–158).

We shall now proceed to a comparison of the *Bothriolepinae* with the genera *Ceraspis* Schlüter, *Byssacanthus* Agassiz and *Ceratolepis* Gross which, as pointed out above (p. 215), were classified by Gross in the family *Ceraspidae* (Gross 1937, pp. 14–19; 1940, pp. 38–44). These genera at present are very imperfectly known and very little can, therefore, be made out concerning their organization. It is even likely that they will turn out to be so different from each other that each of them represents a family of its own. Their kinship with the other better known *Antiarchi*-forms is very obscure. *Ceraspis* resembles the *Bothriolepinae* in the shape of the lateral lamina of its anterior ventro-lateral plate (Gross 1937, text-fig. 10B) and in the condition thats its dorsal crest, just as in the crested *Bothriolepis*-species, is formed by both the anterior and posterior median dorsal plates (Gross 1937, text-figs. 9, 11). In *Byssacanthus* the anterior median dorsal plate (Gross 1940b, pp. 38–44, text-fig. 10), in its general shape, and in most of its details as well, is almost exactly as in *Bothriolepis*. The tergal angle, however, is produced into a high dorsal spine. Of much interest is also that the median part of the plate, below and behind the dorsal spine, is very thick and houses a median, rostro-caudally passing vascular canal from which a branch is given off upwards into the interior of the dorsal spine. This thick median part with its rostro-caudal canal obviously corresponds to the ventral median ridge and the ventral median groove of the *Bothriolepinae*, whereas the branch of the canal ascending into the interior of the dorsal spine presumably represents the anterior ventral pit of the *Bothriolepinae* (cf. pp. 113–114 above). As to its sutural connections the anterior median dorsal plate in *Byssacanthus* is of the *Remigolepis*-type, which, as we have seen, is not infrequently met with also in *Bothriolepis*. Finally, *Ceratolepis* (Gross 1933b, pp. 16–19, text-fig. 4) reminds of the *Bothriolepinae* in the development of the structures on the lower side of its trunk-armour. The crista transversalis interna anterior in this genus is provided with an unpaired median dorsal part (text-fig. 42; cf. also pp. 108–112), which forms complete posterior and ventral boundaries of the levator fossa and which seems to be represented in the *Bothriolepinae* by the postlevator

crest and the vestigial floor, sometimes present underneath the posterior part of the levator fossa (cf. pp. 108–112). In addition in *Ceratolepis* there is also a ventral median ridge and a ventral median groove somewhat similar to the correspondingly termed ones in the *Bothriolepinae*. In certain of their characters known so far the *Ceraspidae*, as we thus find, are clearly suggestive of the *Bothriolepinae*, and it may be strongly suspected, therefore, that in some way or other they are related to those *Antiarchi*-forms. As has been pointed out (p. 216), they remind also somewhat of *Gerdalepis*.

Nothing could be ascertained concerning the affinities of the *Bothriolepinae* to the two genera *Cypholepis* Gross and *Taeniolepis* Gross, of which for the time being only very fragmentary remains are known (cf. Gross 1933a, pp. 43–44).

According to what can be made out at present concerning their relationships the *Antiarchi* may now be provisionally classified somewhat as follows.

Group A. **REMIGOLEPIFORMES** Berg 1940.
Family **Remigolepidae.**
Genus: *Remigolepis.*

Group B. **ASTEROLEPIFORMES** Berg 1940.
Family 1. **Asterolepidae.**
Genus: *Asterolepis.*

Family 2. **Pterichthyodidae** nov. fam.
Subfamily Pterichthyodinae.
Genus: *Pterichthyodes.*
Subfamily Gerdalepinae.
Genus: *Gerdalepis.*

Family 3. **Bothriolepidae.**
Subfamily Microbrachiinae.
Genus: *Microbrachius.*
Subfamily Bothriolepinae.
Genera: *Bothriolepis, Grossilepis.*

Family 4. **Ceraspidae** (perhaps related to the *Bothriolepidae*).
Subfamily Ceraspinae.
Genus: *Ceraspis.*
Subfamily Byssacanthinae.
Genus: *Byssacanthus.*
Subfamily Ceratolepinae.
Genus: *Ceratolepis.*

Incertae sedis.
The genera: *Cypholepis, Taeniolepis.*

As early as in 1931 it was shown by the writer that the *Antiarchi* cannot be Ostracoderms (Stensiö 1931, pp. 158–160). On this occasion the writer also advanced the opinion that the *Antiarchi* must be closely allied to the Arthrodires. The latter opinion has recently to some extent been critisized by Gross (1941a, p. 69), who writes as follows concerning the development of the pectoral fin and the other characters of the *Antiarchi*. "Aus diesen Erwägungen kommen wir zu dem Schluss, dass die *Antiarchi*-Brustflosse auf eine stenobasale, mesorhachische Brustflosse, die vielleicht ein Archipterygium war, zurückgeht. Die Brustflosse der Arthrodira war dagegen eine eurybasale, pleurorhachische Flosse. Diese grosse Unterschiede im Bau der Brustflosse beider Placodermen-Stämme beweisen uns, dass die Trennung von gemeinsamen Vorfahren sehr weit zurück gelegen haben muss, wir können sie nich als nahverwandte Gruppen betrachten. Dasselbe beweisen uns die weitgehenden Differenzierungen im Bau des Kopfes, in der Lage der Hauptsinnesorgane, im Bau der Mundregion, in der Konstanz der Baupläne des Kopf- und Rumpfpanzers innerhalb beider Stämme. Die *Antiarchi* sind im Bau des Kopfes und der Gliedermassen viel differenzierter und spezialisierter als die Arthrodiren, sie haben sich viel weiter von der gemeinsamen Wurzel entfernt. Nur ihr Aussenskelett, das diese differenzierten Körperteile umschliesst, ist in Bezug auf die Gestalt und die Anordnung der Platten, die sich noch vielfach leicht auf einen Hexagonalplatten-Panzer zurückführen lassen, ursprünglich geblieben. – Histologisch sind die *Antiarchi* fortgeschritten, wie die weite Verbreitung von Resorptionserscheinungen, das Fehlen dentinartiger Knochenschichten und die Herausbildung sekundärer Osteone zeigen". – The results gained from the researches carried out in this work clearly prove, however, that in spite of their many specializations the *Antiarchi* are actually much closer akin to the Arthrodires than what was assumed by the writer in 1931.

As we have seen from the account here given of them, the *Antiarchi* agree with the Arthrodires in a great number of characters of which the most important ones may be summarised as follows. 1) The general development of the endocranium and the proportions of certain of its regions; 2) the morphological position of the nasal capsules and external nasal apertures in relation to each other, to the primary tip of the snout, to the ethmoidal region as a whole, and to the orbitotemporal region; 3) the general development of the visceral endoskeleton; 4) the development and position of Meckel's cartilage; 5) the presence and position of the spiracle and the spiracular aperture; 6) the normal absence of dermal bones on the lower side of the endocranium; 7) the general type of the head-shield and the general pattern of its bones and sutures; 8) the presence in the head-shield of such bones as the rostral, pineal, postpineal and postmarginal plates, strictly homologous with the similarly termed Arthrodire-bones; 9) the presence of such plates in the head-shield as the centro-nuchal and paranuchal-

marginal, whose homologues with Arthrodire bones are easily perceived; 10) the development of the gill-cover and the fact that the gill-cover is of a mandibular origin; 11) the general type of development of the dermal bones of the cheek and gill-cover; 12) the development of the tooth component of the mental plate and the fact that this component in all respects is as a posterior superognathal; 13) the presence of an inferognathal and the shape, position, and relations of this element; 14) the presence, position and general type of the trunk-armour; 15) the fact that the trunk-armour is composed of plates most of which are strictly homologous in the two groups; 16) the general development of the sensory canal system and the presence of certain pit-line grooves specially characteristic of Arthrodires; 17) the general shape of the caudal region; and finally; 18) to a certain degree the general shape of the caudal fin. – The agreements enumerated prove convincingly that the *Antiarchi* must be closely allied to the Arthrodires. Besides, these agreements show also that the *Antiarchi* must be derived from primitive Arthrodire forms, which presumably were nearest allied to the ancestors of the *Brachythoraci* and *Dolichothoraci*. On the other hand, as we have seen (pp. 36, 190, 202–205), the *Antiarchi* in certain characters, such as the shape and structure of the postorbital division of their head-shield, the preorbital position of their jaw apparatus, and the presence of but one superognathal in their upper jaw, are also suggestive of the Ptyctodontids (*Rhamphodopsis*), and thus in some way or other they may probably be related also to that group of Arthrodires (cf. Stensiö 1944, pp. 73–76).

With regard to the dorsal position of the nasal apertures between the orbits, the presence of a special preorbital division of the cranium in front of the nasal apertures, and the position far forward of the jaw apparatus the *Antiarchi*, as we have seen (pp. 21, 30–33, 190, 196–202), exhibit conditions somewhat analogous to those in Rhenanid Arthrodires; and hence in these respects the *Antiarchi* actually are not more aberrant from typical Arthrodires than what are the Rhenanids.

Gross in 1941 (1941 a, pp. 67–69) emphasized the great structural difference between the pectoral fin of the *Antiarchi* and the corresponding fin of the Arthrodires, and, as we have seen from the quotation given above on pp. 219–220, because of this was led to the conclusion that the *Antiarchi* are far apart from the Arthrodires. At that time our knowledge of the pectoral fin of the Arthrodires was very slight. Recently it has been shown (see p. 147), however, that the pectoral fin of the *Acanthothoraci*, and probably also that of the *Dolichothoraci*, was narrow-based with a highly concentrated endoskeleton, perhaps of a mesorhachic type (Stensiö 1944, pp. 66–69). As thus it is evident now that the primarily pleurorhachic and eurybasal pelvic fin of the Arthrodires in certain of the groups was modified into a type more or less approaching that of the *Antiarchi*, it follows, of course, that with regard to the structure of their pectoral fin the *Antiarchi* are not

so fundamentally different from the Arthrodires as maintained by Gross. It may be mentioned for comparison here that paired fins of pleurorhachic and mesorhachic types, and of types more or less transitional between these two types, are met with also in the Elasmobranchs proper (Moy-Thomas 1939a, pp. 4–9, figs. 2, 3), which shows that the paired fins of this group too could easily be modified in a manner corresponding to that in Arthrodires. As may thus be gathered, Gross has highly overrated the importance of the structural difference in the pectoral fin of the *Antiarchi* and Arthrodires. Everything goes now to prove that the pectoral fin in certain Arthrodires was of a type which may very well be imagined to have given rise to the excessively specialized pectoral fin of the *Antiarchi*.

The exoskeleton of the pectoral fin in the *Antiarchi* was certainly formed by a fusion of the scales covering the pectoral fin of the primitive Arthrodires. It may be of interest in this connection that the spinal plate of certain Arthrodires (Stensiö 1944, pp. 49–50, 78–79), which was formed by a fusion together of the scales of the foremost vestigial part of the pectoral fin, to a certain extent is a formation analogous to the pectoral fin-armour of the *Antiarchi*.

Summing up what has been set forth above, we thus find that the *Antiarchi* are not only very closely allied to the Arthrodires, but in fact form a highly specialized group of Arthrodires.

In accordance with the results thus gained concerning the relationships of the *Antiarchi* and in view of the results put forward in two previous papers by the writer (Stensiö 1944; 1945) the Arthrodires may now be provisionally classified somewhat as follows.

Arthrodira.

Division A. **Euarthrodira**
- Order 1. *Brachythoraci*
  - Suborder a. *Pachyosteomorphi*
  - Suborder b. *Coccosteomorphi* (*Coccosteus*, *Pholidosteus*)
- Order 2. *Dolichothoraci* (*Acanthaspida*)
- Order 3. *Acanthothoraci*
- Order 4. *Petalichthyida*
- Order 5. *Stegoselachii*
- Order 6. *Phyllolepida*
- Order 7. *Ptyctodontida*

Division B. **Antiarchi**

Division C. **Rhenanida.**