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UNDER LEDELSE AF LAUGE KOCH

ON THE PLACODERMI OF THE
UPPER DEVONIAN OF EAST GREENLAND

I. PHYLLOLEPIDA AND ARTHRODIRA

BY

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WITH 26 FIGURES IN THE TEXT AND 25 PLATES

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CONTENTS

	Page
Preface	5
Notes on the localities of Phyllolepidids and Arthrodirens in East Greenland ..	7
Material and methods	10
Description of the material:	
Order Phyllolepidida	11
Historical remarks	11
Geological range and geographical distribution	12
Anatomical remarks	13
Terminology	13
General characters	16
Minute structure of the dermal bones	22
Sensory canal system	25
Homologues of the bones of the armour	29
Vertebral column	32
Concluding remarks on the relationships and systematic position of the Phyllolepidids	32
Genus Phyllolepis Ag.	34
<i>Ph. orvini</i> HEINTZ	34
<i>Ph. söderberghi</i> n. sp.	36
<i>Phyllolepis</i> spp.	40
Order Arthrodira:	
Genus Groenlandaspis HEINTZ	54
<i>Groenlandaspis mirabilis?</i> HEINTZ	55
Bibliography	56

PREFACE

Since the publication of the paper "Upper Devonian Vertebrates from East Greenland" in 1931 (STENSIÖ 1931) a gigantic, new material of Upper Devonian Vertebrates has been brought home by the Danish East Greenland expeditions in 1931—33 (SÄVE-SÖDERBERGH 1932a, 1933a). This material has been collected by Dr. G. SÄVE-SÖDERBERGH, Stockholm; Cand. E. NIELSEN, Copenhagen; Mr. H. LETH-PEDERSEN, Copenhagen; Mr. D. LAURSEN, Copenhagen; Fil. mag. E. JOHANSSON, Uppsala; Fil. mag. G. LINDGREN, Uppsala; Kand. T. SÄVE-SÖDERBERGH, Uppsala; Kand. G. WÄNGSJÖ, Uppsala; Fil. kand. E. OHLSSON, Uppsala; and Fil. kand. B. GRANSTRÖM, Uppsala. It comprizes the following groups of vertebrates: *Placodermi*, represented by *Phyllolepida*, *Arthrodira* and *Antiarchi*; *Crossopterygii* represented by Holoptychids and Rhizodontids; *Dipnoi*, *Stegocephalia*, and in addition two other groups of which one perhaps may reveal itself as a new group of the lower *Choanata* (cf. SÄVE-SÖDERBERGH 1934a), whereas the other is so imperfectly known that nothing can be said of its affinities (cf. STENSIÖ 1931, pp. 205—207). Of these groups the *Arthrodira* are very rare, being known only by a few imperfect remains. Rare are also the *Dipnoi* and *Stegocephalia*, of which, however, several specimens are found. More abundantly occur the *Phyllolepida*, but most common are the *Antiarchi* and the *Crossopterygii*, which form the bulk of the new material. The *Antiarchi* are even more common than the *Crossopterygii* and are now in the material available represented by thousands of specimens.

The present work will be published in two parts. The first of these parts will deal with the *Phyllolepida* and *Arthrodira*, the second with the *Antiarchi*.

The *Stegocephali* will be described in full by SÄVE-SÖDERBERGH, who has already published a preliminary description of the material collected up to 1931 (SÄVE-SÖDERBERGH 1932b). The *Dipnoi* and the possibly new group of lower *Choanata* will also be described by SÄVE-SÖDERBERGH. The remaining groups will be described either by the writer or by SÄVE-SÖDERBERGH or by both of us.

Though as yet only a small part of it has been described in detail (SÄVE-SÖDERBERGH 1932b), it is evident that the new material of Upper Devonian Vertebrates from East Greenland is of a high importance from the point of view of comparative anatomy. In fact it is one of the most important materials of fossil vertebrates that has been discovered during later decades.

That both this and so much other important material of fossil vertebrates could be brought home by the Danish East Greenland expeditions, is due to the great interest which the leader of these expeditions, Dr. LAUGE KOCH, has paid to the paleontological research of East Greenland, and the effective way in which he has supported and facilitated the collections by competent persons at the more yielding localities. Vertebrate palaeontology is highly indebted to Dr. KOCH for what he has done in this case.

It is also a great pleasure to express here to Dr. KOCH my personal thanks for entrusting to me the description of the *Placodermi*. In addition I wish also to thank Dr. KOCH most cordially for good collaboration and for great kindness and courtesy in all respects during the work with that material.

My thanks are further due to Dr. G. SÄVE-SÖDERBERGH for valuable information concerning the geology of the Upper Devonian of East Greenland and for his kindness in placing at my disposal the stratigraphical table published in p. 7 of the present paper.

The preparation of the material, which has been difficult and which on account of the great hardness of the rock has taken a very long time, has been carried out by Mrs. A. STENSIÖ, Miss A. BRASCH and Miss B. ARNELL. The drawings have been made by Mr. S. EKBLOM and Mrs. A. STENSIÖ.

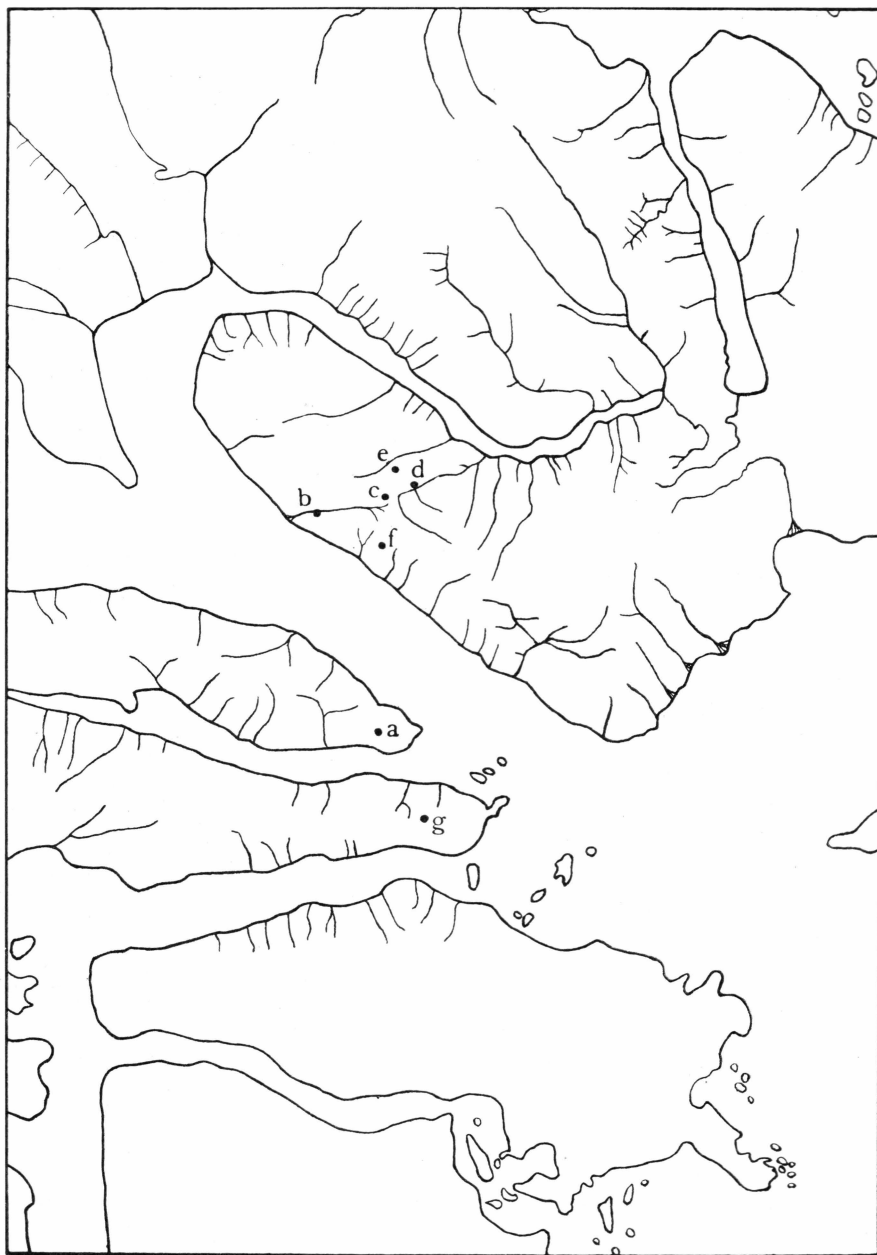
NOTES ON THE FIND LOCALITIES OF PHYLLOLEPIDS AND ARTHRODIRES IN EAST GREENLAND

Remains of *Phyllolepis* are thus far known from five localities (text-fig. 1, *a—e*) viz.: Orvin's locality at Cape Graah (*a*); the bottom of the western part of the Parallel Valley, near the coast (*b*); the S. side of Mt. Sederholm at the Profile Ravine (*c*); the S. side of Mt. Sederholm, opposite the Circus-Mountain (*d*); and the N. side of Mt. Sederholm, Vasti Valley, N. of the Circus Valley (*e*). The first-mentioned of these localities is the one discovered by ORVIN (1930, pp. 16—17; HEINTZ 1930, pp. 36—44; 1932b, pp. 5—17; SÄVE-SÖDERBERGH 1932a, pp. 17—21). The *Phyllolepis* remains, occur all in a single series — the *Phyllolepis*-series (cf. the table below) — which is situated nearest below the *Remigolepis*-series. They are always found associated with remains of *Bothriolepis* and *Holoptychius*.

The *Arthrodira* are, in the material available, represented by a single fragment only. This fragment which is from Mt. Stensiö (*f*) (text-fig. 2) has been collected in the Arthrodire-sandstone series — thus the series following nearest above the *Remigolepis*-series (cf. the table below).

The more precise position of the different localities referred to above is shown in text-fig. 1.

The geological conditions in the Upper Devonian of East Greenland are elucidated by the accompanying table (p. 9) which is quoted from SÄVE-SÖDERBERGH (1934b). In this table all necessary information concerning the different fossiliferous series is to be found.



Text-fig. 1. Sketch-map showing the find localities of *Phyllolepis* and *Grönlandaspis* in the Upper Devonian of East Greenland. *a*, Orvin's locality at Cape Graah; *b*, bottom of the W. part of the Parallel Valley, near the coast; *c*, S. side of Mt. Sederholm, at the Profile Ravine; *d*, S. side of Mt. Sederholm, opposite the Circus-Mountain; *e*, N. side of Mt. Sederholm, in the Vasti Valley, N. of the circus valley; *f*, Mt. Stensiö; *g*, Mt. Celsius (*Groenlandaspis*, collected by ORVIN).

The Development of the Upper Devonian in East Greenland 9
according to Sæve-Söderbergh (1934b).

Age		East Greenland	
		Divisions	Localities
Carboniferous or uppermost Upper Devonian		4. The Upper Sandstone Complex. (Light-grey and brick-red sandstones).	Mt. Celsius: Top of Western part. Gauss Peninsula: Margrethe Valley; the summits of Mt. Nathorst and Mt. Stensiö.
Upper Devonian	Upper Upper Devonian	3. The Arthrodire-Sandstone Series. (Grey marls and sandstones with <i>Grönlandaspis</i> and <i>Crossopterygians</i>).	Mt. Celsius: The uppermost parts. Gauss Peninsula: Margrethe Valley; upper parts of Mt. Nathorst, Mt. Wiman, Mt. Stensiö, Mt. Smith Woodward, and the Remigolepis Ridge.
		2. The Remigolepis Series. (Dark-red, brown and grey marls, dark-grey sandstones, with constant thin layers, with very rich fossil localities: <i>Remigolepis</i> , <i>Holoptychius</i> and other <i>Crossopterygians</i> , <i>Stegocephalians</i> (<i>Ichthyostegids</i>), <i>Dipnoids</i> and probably also new groups of vertebrates.	Mt. Celsius: The middle parts. Gauss Peninsula: S. coast: from the Margrethe Valley as far W. as Mt. Smith Woodward; The inland: the base of Mt. Harder (Mt. Bøggild); middle part of the Remigolepis Ridge; upper part of Mt. Sederholm, and Mt. "Karbon-cirkus"; the N. coast: uppermost parts of Mt. Sederholm; the E. summit of Mt. Victor Madsen. In the W. part of Gauss peninsula consisting of three divisions: c. Red and grey, stratified sandstones and marls. b. Dark-grey, stratified sandstones and marls. a. Dark-red homogenous marl.
		1. <i>Phyllolepis</i> Series (or Lower Sandstone Complex). (Light-red, brown, and light-grey sandstones; with <i>Phyllolepis Bothriolepis grönlandica</i> and <i>Holoptychius</i> in several horizons in the upper part.	Mt. Celsius: The basal parts. Gunnar Andersson Peninsula (Cape Graah). Gauss Peninsula: Along the whole S. coast except in Mt. Stensiö; the inland: in the lower parts of most of the mountains: Remigolepis Ridge, the "Circus Mountainus". Mt. Sederholm; the whole W. part of Gauss Peninsula W. of Mt. Smith Woodward and Mt. Sederholm, the summit of Mt. Victor Madsen excepted. (?) Strindberg Peninsula: Grey sandstones, possibly corresponding to the lower part of the <i>Phyllolepis</i> Series. (?) Hudson Land: Grey and reddish sandstones in the Musk-ox Range, possibly belonging to the <i>Phyllolepis</i> Series. ? W. parts of the Ymer Island, S. of the Dusen Fjord, Geographical Society Island, and Traill Island: light-grey and red sandstones possibly belonging to the <i>Phyllolepis</i> Series: <i>Bothriolepis</i> and <i>Crossopterygii</i> in Mt. Kungaborgen.
	Lower Upper Devonian	Not found in East Greenland.	

MATERIAL AND METHODS

The *Placodermi* known thus far from East Greenland occur as a rule in very hard marls and sandstones. Only certain *Remigolepis* remains are found in a more shaly rock. More precisely the conditions in regard to the matrix are as follows.

The *Phyllolepis*-remains from Cape Graah are embedded in a very hard, white-red sandstone with numerous black-green spots. As this sandstone is fairly porous, the bone-tissue in it has generally been subjected to weathering; the *Phyllolepis*-remains from the localities on Mt. Sederholm are found in a very hard fine-grained, brown-red sandstones, or in a green-red sandstone; and finally the *Phyllolepis*-remains from the bottom of the W. part of the Parallel Valley occur in a very hard grey-red sandstone.

The Arthrodire-remains known thus far are embedded in grey sandstone or in a grey conglomerate.

The bone tissue of the East Greenland Phyllolepid and Arthrodires is in most cases of a blue, blue-white, blue-white and somewhat red or whitish-red colour. In many cases its minute structure is poorly preserved, a condition which is due to the circumstance that its finest vacuities, the cell-spaces and the canaliculi, are not infiltrated with a matrix differing in colour from the bone tissue, but above all to the fact that it is much transformed by pressure in the rock. In several cases, however, the minute structure may also be fairly well preserved, as for instance in the *Phyllolepis*-remains from the localities on Mt. Sederholm (pls. 18—25).

The preparations have been carried out partly with mallet and chisels in the ordinary way, partly by a special dental mallet under a binocular loup. For all finer details the latter method proved indispensable. On account of the circumstance that the bone-tissue always has a colour which differs much from that of the surrounding matrix there were no difficulties in observing details, and the specimens could therefore on the whole be both studied and photographed in a dry condition.

DESCRIPTION OF THE MATERIAL

Placodermi.

Order Phyllolepidi.

Historical remarks.

Only one genus *Phyllolepis* AGASSIZ is as yet known of the *Phyllolepidi*. This genus was established by AGASSIZ in 1844 (p. 67) on an imperfect plate which, as is now known, is the posterior one of the two large, unpaired dorsal plates of the armour. Otherwise descriptions of material of *Phyllolepis* have been published by FRITSCH (1888, pp. 89—90), LOHEST (1888, pp. 155—167), NEWBERRY (1889, pp. 97—98), WOODWARD (1891, p. 314; 1914, pp. 122—123; 1920, p. 31), ROHON (1900, pp. 48—49), HUSSAKOF & BRYANT (1918, pp. 21—22), HEINTZ (1930, pp. 36—42; 1932 b, pp. 5—14), LERICHE (1931, pp. 9—14), and HILLS (1931, pp. 212—213; 1932, p. 852).

With the exception of an almost complete specimen described by WOODWARD in 1914 (1914; 1920) all the material dealt with thus far of the genus consists only of detached and often even very imperfect plates. On account of this circumstance it has been very difficult to arrive at any definite opinion concerning the systematic position and relationships of the genus.

AGASSIZ in 1844 placed *Phyllolepis* among his "Coelacanthes" which otherwise comprized the genera: *Coelacanthus* AGASSIZ, *Macropoma* AGASSIZ, *Holoptychius* AGASSIZ, *Bothriolepis* EICHWALD, *Glyptolepis* AGASSIZ, *Psammosteus* AGASSIZ, *Hoplopygus* AGASSIZ, *Uronemus* AGASSIZ, *Undina* MÜNSTER, *Ctenolepis* AGASSIZ, *Psammosteus* AGASSIZ, *Gyrosteus* AGASSIZ, *Platygnathus* AGASSIZ, *Dendrodus* OWEN, *Lamnodus* AGASSIZ, *Cricodus* AGASSIZ and *Asterolepis* AGASSIZ (cf. the historic account of the Coelacanthids published by STENSIÖ 1921, pp. 43, 44).

ZITTEL in 1887 (1887—90, p. 180) referred *Phyllolepis* with doubt to the *Crossopterygii*, and a somewhat similar view of its relationships seems to have been held by LOHEST in 1888 (pp. 155—167). NEWBERRY in 1889 (p. 97) pointed out certain similarities in the ornamentation in

Phyllolepids and *Holonema* and wrote as follows: "the peculiar style of ornamentation is almost identical with that of *Holonema rugosa*, and I can not but think that these rounded, detached, thin plates were in some way associated with large angular ones, which were united to form a carapace somewhat like that of "*Pterichthys*". Accordingly NEWBERRY seems to have been inclined to assume that *Phyllolepis* was in some way allied to the *Placodermi* (*Antiarchi* + *Arthrodira*).

WOODWARD in 1891 (p. 314) placed *Phyllolepis* and *Holonema* in a common family, *Phyllolepidae*, which he referred to the *Arthrodire*s. And an in the whole similar view was held also by SCHLOSSER in 1918 (p. 44).

In connection with his description of the almost complete specimen of *Phyllolepis* WOODWARD in 1914 pointed out that a certain resemblance existed between *Phyllolepis* and *Drepanaspis*. On account of this he considered *Phyllolepis* akin to the *Drepanaspids* and referred it with these to the *Heterostraci* among the *Ostracoderm*s. This opinion by WOODWARD has later on gained an almost general acceptance (SCHLOSSER 1923, p. 31; HEINTZ 1930, p. 36; 1932 b, pp. 5—14; HILLS 1931, p. 212; 1932, 852; WOODWARD 1920, p. 31; 1932, p. 30; OBRUTSCHEW 1933, p. 99; BROTZEN 1933, pp. 653—654), only the present writer having expressed some doubt of its correctness. This was done in the general account on the *Heterostraci* which in 1927 was given in the monograph on the Spitsbergen Cephalaspids (STENSIÖ 1927, p. 330). After having pointed out certain of the differences between *Phyllolepis* and *Drepanaspis*, my view on the subject at that occasion was summarised in the following way: "Since *Phyllolepis* both is imperfectly known and obviously differs in important features from *Drepanaspis*, it may be very much doubted whether it really pertains to the *Heterostraci* at all. In fact, with the slight knowledge which we have of it at present, I find it very difficult to understand where it may have its nearest allies." That this doubt was justified is shown by the account of the organisation of *Phyllolepis* given below.

That *Phyllolepis* differs considerably from *Holonema*, who is a typical *Arthrodire* has been shown by OBRUTSCHEW (1933) in a paper on *Holonema* (cf. also GROSS 1933, pp. 45—48).

Geological range and geographical distribution.

Phyllolepis is known only from deposits of Upper Devonian age in which it occurs associated with *Bothriolepis* and *Holoptychius* (cf. SÄVE-SÖDERBERGH 1932a, pp. 28—37, 1933a). It has a strikingly wide geographical distribution, remains referable to it having been found in East Greenland, Scotland, England (WALLIS 1928; cf. also SÄVE-SÖDER-

BERGH 1932a, p. 30), Belgium, Western Russia (HECKER, PHILLIPOVA and BARKHATOVA 1932, p. 66), N. Russia (Timan: ROHON 1900, pp. 48—49), New York State U.S.A., and in Victoria and N.S. Wales, Australia (HILLS 1931; 1932).

Anatomical remarks.

Terminology.

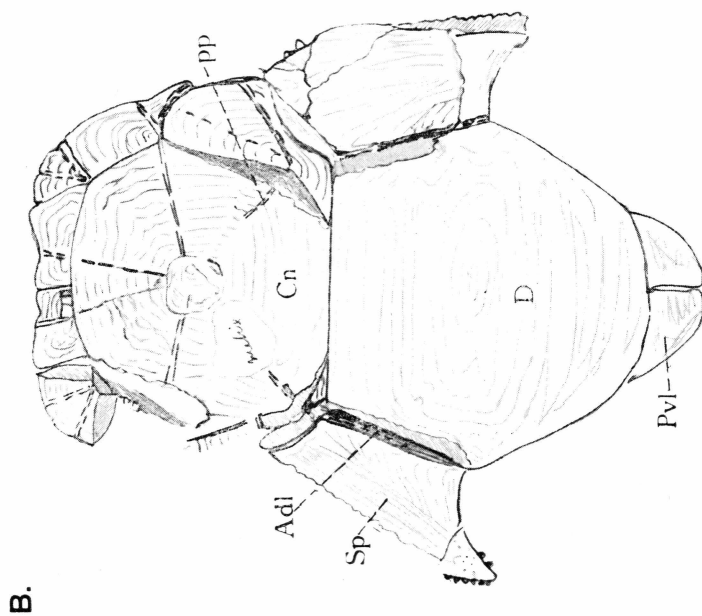
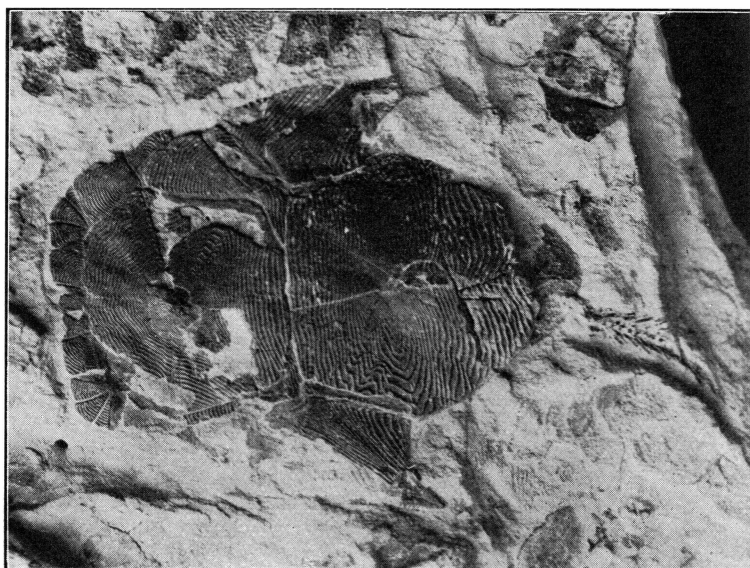
The *Phyllolepis-armour* (text-figs. 2, 6) is in its dorsal part composed of two large unpaired median plates and five paired plates, and in its ventral part of three paired and at least one unpaired plate (text-figs. 2, 6, 24—26). Of its lateral parts which are fairly imperfectly known only two paired plates (text-figs. 2, 6, 22) have as yet been observed with certainty.

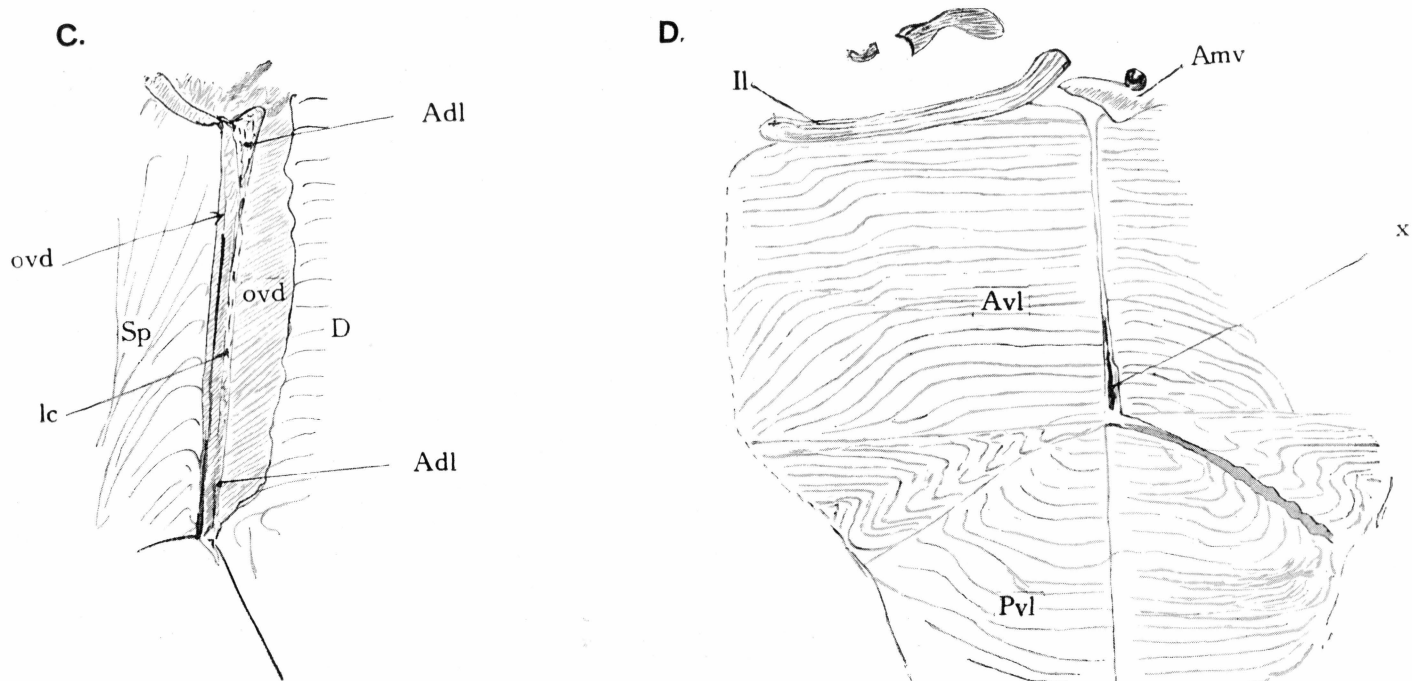
WOODWARD in 1914 purposely avoided the introduction of special terms for the different bones of the *Phyllolepis-armour*. On the other hand in a short notice published in 1920 he calls the four anterior, paired, dorsal plates “marginal plates” and the most posterior, paired lateral plate “cornu”.

In the remarks given on *Phyllolepis* by the present writer in 1927 (STENSIÖ 1927, p. 330) the figure published by WOODWARD in 1920 of *Ph. concentrica* was reproduced, and in the explanation of this figure the large, unpaired posterior dorsal plate was referred to as the median dorsal plate, the large unpaired anterior dorsal plate as the rostral plate, and the paired lateral plate as the cornual plate. This terminology was then adopted by LERICHE in 1931 (pl. 8), who in addition for the four anterior paired dorsal plates employed the term “marginals” introduced by WOODWARD in 1920.

HEINTZ in 1932 also adopted the terms suggested by the present writer in 1927, but in addition he introduced also the following new ones: “Prärostralplatte” for the most anterior, paired, dorsal plate; “Ocularplatte” for the third, paired, dorsal plate, counted from in front; and “Branchialplatte” for the fourth, paired dorsal plate, counted from in front. These as well as the other terms employed by the writer and HEINTZ, were all chosen on the assumption that the *Phyllolepis-armour* at least in regard to its general composition was somewhat comparable to that in the *Heterostraci*. Since now, as we shall see, this is not the case, but *Phyllolepis* has revealed itself as a Placoderm, the terms just referred to are too inadequate to be retained. In such circumstances I have suggested the following ones (cf. also text-figs. 2, 6).

Marginal plate 1, marginal plate 2, marginal plate 3 and marginal plate 4 ($M-M_4$) for the four most anterior paired dorsal plates counted from in front; median cephalic plate (Cn) for the anterior, median, unpaired, dorsal plate; median dorsal plate (D) for the posterior, median





Text-fig. 2. *Phyllolepis concentrica* AGASSIZ. A, The complete specimen in the Brit. Mus. figured and described by WOODWARD in 1914 and 1920. Dorsal view. Approximately one half of the nat. size. B, Sketch of the specimen figured in A. Somewhat diminished. C, part of the dorsal side showing the narrow anterior dorso-lateral plate overlapped by the median dorsal plate and a lateral plate. Somewhat enlarged. D, part of the ventral wall of the armour. Approximately nat. size. Sketches kindly placed at my disposition by SÄVE-SÖDERBERGH¹⁾. *Adl*, anterior dorso-lateral plate; *Amv*, anterior median ventral plate; *Avl*, anterior ventro-lateral plate; *Cn*, median cephalic plate; *D*, median dorsal plate; *Il*, intero-lateral plate; *Pvl*, posterior ventro-lateral plate; *Sp*, spinal plate or anterior lateral plate or anterior lateral plate fused with the spinal; *lc*, main lateral line; *ovd*, overlapped areas; *pp*, groove probably corresponding to the posterior head-line of pit organs in fishes in general; *X*, possibly remains of the posterior median ventral plate.

¹⁾ See foot-note on p. 21 below.

unpaired, dorsal plate; anterior dorso-lateral plate (*Adl*) for the plate situated immediately laterally to the median dorsal plate; spinal plate (*Sp*) for the laterally protruding plate found preserved in *Phyllolepis concentrica* (text-figs. 2, 8); intero-lateral plate (*Il*) for the most anterior paired ventral plate; anterior ventro-lateral plate (*Avl*) for the second paired ventral plate counted from in front; posterior ventro-lateral plate (*Pvl*) for the most posterior paired ventral plate; and finally anterior median ventral plate (*Amv*) for the unpaired ventral plate.

General characters.

The knowledge which we now possess concerning the armour of *Phyllolepis* shows that this (text-figs. 2, 6) is composed of two divisions, a cephalic division and a trunk division, the latter of which, in a corresponding way as in the *Antiarchi* and *Arthrodira*, covers the anterior broad division of the trunk.

The cephalic division consists dorsally of the four paired marginal plates (M_2 — M_4 , text-figs. 2, 6) and the unpaired median cephalic plate (*Cn*, text-figs. 2, 6). Ventrally there were probably also certain ossified elements, but these are still so imperfectly known (text-fig. 2B) that nothing can be said of them.

The marginal plates 1 and 2 (M_1 , M_2 , text-figs. 2, 6, 16, 17) are situated in front of the median cephalic plate (*Cn*), which previously has been compared (STENSIÖ 1927, p. 433; HEINTZ 1932b) to the rostral plate of the Pteraspids and Drepanaspids among the *Heterostraci* (*R*, text-figs. 3—5). Neither in the Pteraspids nor in the Drepanaspids, however, there are any small plates in front of the rostral plate (text-figs. 3—5) for, as is well known (KIAER 1928), the rostral plate in these groups forms not only the rostral end of the armour but also the upper boundary of the anterior part of the mouth. In addition the rostral plate in these groups bears on its ventral side the tooth-bearing area called by KIAER (1928) "the maxillary tooth plate". The marginal plate 4 (M_4 , text-figs. 2, 6, 19) resembles both in regard to its position and shape the paranuchal of the Arthrodirens (GROSS 1932; externo basal, HEINTZ 1932a), and characteristic of it is also, that on its ventral side it has a deep pit (*d*, text-fig. 19B, pl. 5, fig. 3) which seems to correspond to the canal in the Arthrodirens which perhaps may have lodged the ductus endolymphaticus (cf. OBRUTSCHEW 1929, p. 299; HEINTZ 1931, text-fig. 3; STENSIÖ 1934).

The median cephalic plate (*Cn*, text-figs. 2, 6, 20, 21) has on its lower face a shallow, but nevertheless fairly distinct median longitudinal groove (*gr*) which at its posterior end is of a similar breadth as the anterior part of the levator fossa (*f.retr*, text-fig. 15) to be described below on the median dorsal plate. On the other hand this plate shows no traces

whatever of having had any so-called "maxillary tooth-plate", and it is clear that it cannot have entered into the boundary of the mouth as the rostral plate of the *Heterostraci*, but that it must have been situated above the posterior parts of the endocranium.

The plates now dealt with on the dorsal side of the head are provided with relatively broad, overlapping and overlapped areas in a somewhat corresponding way as the dermal bones of the head in the *Placodermi*. On the other hand the dermal bone-plates covering the head in the *Heterostraci* have no or only very slightly developed areas of that kind.

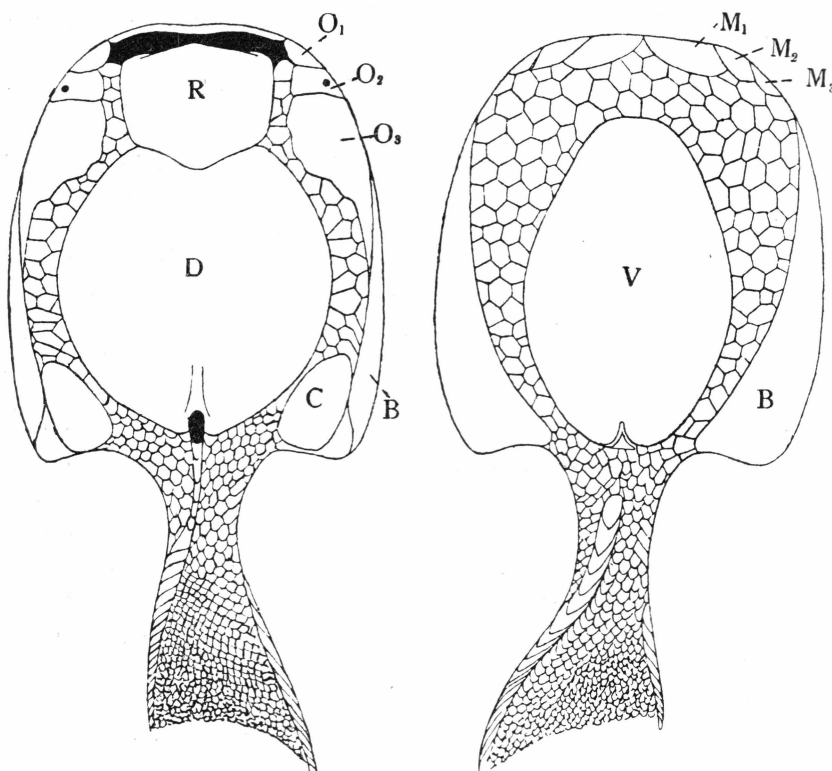
The disposition of the sensory canal system (cf. the account of that below) and the absence of orbital incisures on the anterior marginal plates show that the anterior parts of the endocranium either was devoid of external dermal bones or was protected only by vestigial dermal bones, which were situated so loosely in the skin that, during the decaying of the soft tissues, they became detached and got lost. As is obvious from the considerable length of the median cephalic plate the postorbital parts of the endocranium, particularly the otic region of this, must have been strikingly long; and in this respect therefore the endocranium was of a similar type to that in the *Arthroires* (cf. STENSIÖ 1925a, and 1934).

As far as can be judged from the conditions known the head was not or only very slightly moveable against the trunk. In any case the head armour and trunk armour do not show any distinct traces of articulation as they do in the *Antiarchi* and in the majority of the *Arthrodira*.

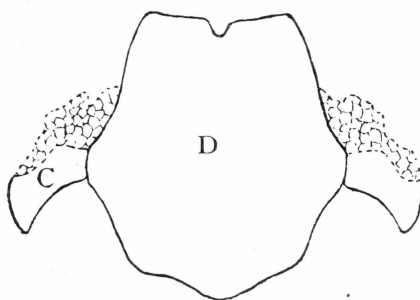
Finally it should be mentioned in this connection that from the construction of the armour in general we are led to the conclusion that the gills were situated below the head as in the *Placodermi* (cf. HEINTZ 1932a, pp. 199—202; STENSIÖ 1934) and not behind this in the anterior part of the trunk armour as in the *Heterostraci* (text-figs. 3—5). Expressed in another way: the gill apparatus was in *Phyllolepis* short and subcranial as in the *Placodermi*, whereas in the *Heterostraci* it is long and mainly postcranial.

The trunk division of the armour is, in regard to its position, extent and composition, clearly of the Placoderm-type (text-figs. 2, 6). Thus it covers the anterior, broad, postbranchial divisions of the trunk and consists of plates of which at least many seem to have exact homologues in the *Arthrodira* (cf. the account of the homologues of the bones of the armour below in this paper).

The median dorsal plate (*D*, text-figs. 2, 6, 14, 15) is large and well developed. Along each lateral margin and along an adjacent part of the anterior margin it has on its ventral face an area (*w*, text-fig. 16) which overlaps the anterior dorso-lateral plate. In addition it displays on its ventral face a fairly distinct levator fossa (*f.retr*, text-fig. 15) of a similar type as that in the *Antiarchi* (STENSIÖ 1931, p. 75) and a median long-



Text-fig. 3. *Drepanaspis gemündenensis* TRAQUAIR. A, in dorsal, B, in ventral view. After TRAQUAIR 1904 (slightly altered). C, cornual plate; D, median dorsal plate; M_1-M_3 , oral plates (belong to the ventral side of the mouth and correspond to the oral plates in the Pteraspids); O_1-O_3 , ocular plates; R, rostral plate; V, ventral plate. B, branchial plate.

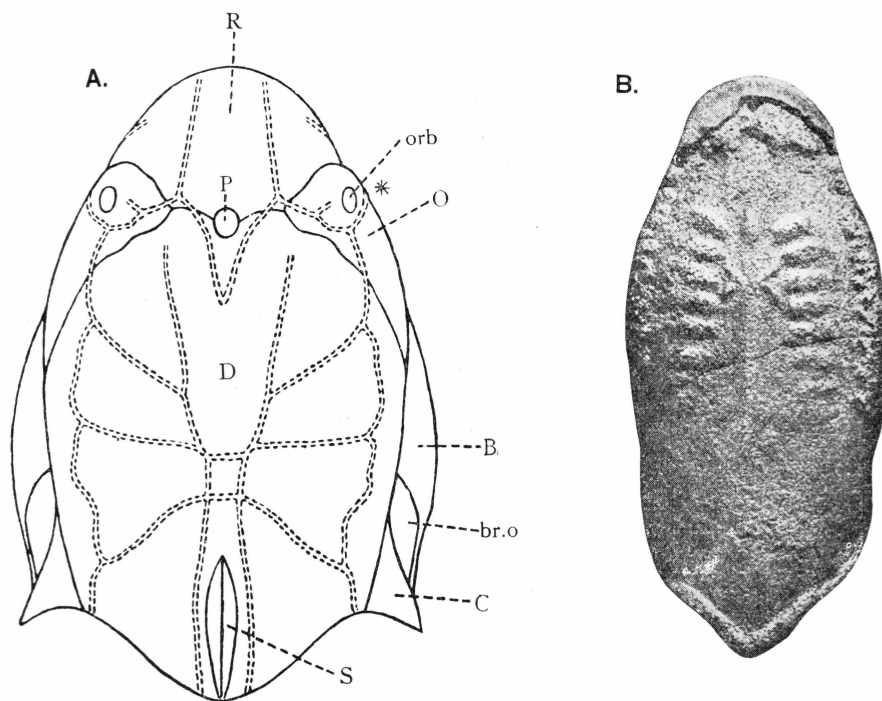


Text-fig. 4. *Psammosteus taylori* TRAQUAIR. After HEINTZ 1932 from WOODWARD 1911. C, cornual plate; D, median dorsal plate.

itudinal groove (*grm*) bounded on each side by a low longitudinal ridge (*r*). On the other hand no median longitudinal keel, or no median ventral process, is to be found on the ventral face of the plate. In regard to the

development of its ventral face the plate therefore shows a striking agreement with the anterior median dorsal plate of the *Antiarchi* (cf. STENSIÖ 1931, p. 75, and text-figs. 33, 37) whereas in other respects it is more suggestive of the median dorsal plate in the *Arthrodira*.

Of particular interest is that an anterior dorso-lateral plate (*Adl*, text-figs. 2, 22) has now been discovered both in *Phyllolepis concen-*



Text-fig. 5. *Pteraspis primaevus* KIAER. Reconstruction in dorsal view. After KIAER 1928. B, *Poraspis cylindrica* KIAER & HEINTZ. Impression of the ventral face of the dorsal shield. After KIAER & HEINTZ 1932.

B, branchial plate; C, cornual plate; D, median dorsal plate; O, orbital plate; P, pineal plate; R, rostral plate; S, dorsal spine; br.o, branchial opening; orb, orbital opening.

*trica*¹⁾) and among the material from East Greenland. This plate, which is long and narrow, has only a very narrow exposed area, which in its

¹⁾ SÄVE-SÖDERBERGH has recently, during a visit to the British Museum, examined the complete specimen of *Ph. concentrica* described by WOODWARD in 1914 and 1920. In this specimen he has discovered the anterior dorso-lateral plate approximately in its natural position, laterally to the median dorsal plate, and several other new plates which already had been found detached in the East Greenland material. Text-fig. 2 is a sketch of this specimen kindly placed at my disposal by SÄVE-SÖDERBERGH.

longitudinal direction is crossed by the lateral line groove (*lc*). It is overlapped dorsally by the median dorsal plate, which for this purpose has a fairly distinct overlapping area (*ov*, text-fig. 15), and ventrally by another plate, which either is the anterior lateral plate or a compound plate arisen by the fusion of the anterior lateral plate and the spinal plate. On its anterior face the plate has a shallow indistinct elevation (*c*, text-fig. 22) which perhaps may be a vestigial condyle, indicating that originally there may have been an articulation between the head and trunk of a similar type as in the *Arthrodira*. — As we find from the details given and from the figures cited the anterior dorso-lateral plate is very suggestive of the similarly termed plate in the Arthrodires in general, but particularly of that in certain Acanthaspids from the Lower Old Red of Podolia in Poland (text-fig. 23).

The structure of the lateral wall of the trunk armour, ventrally to the anterior dorso-lateral plate, is still very imperfectly known (text-figs. 2, 6). Above all it is impossible to make out whether there is an independent anterior lateral plate or whether this has fused with the spinal plate. It is also uncertain whether a posterior dorso-lateral and a posterior lateral plate were present.

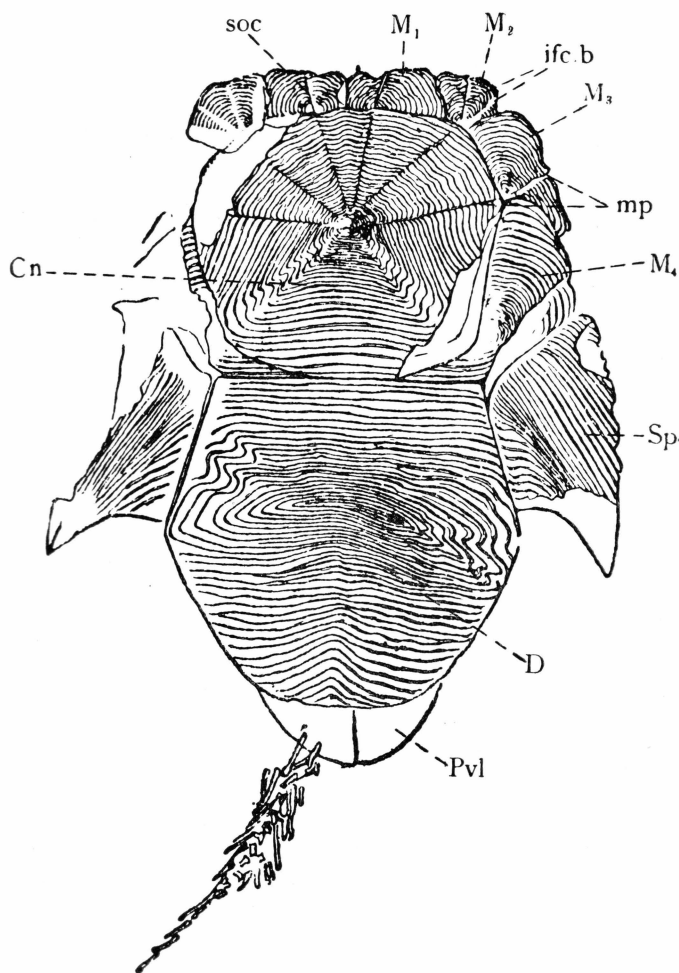
The supposed spinal plate (*Sp*, text-figs. 2, 6) projects much laterally to the other parts of the lateral wall of the trunk armour. Whether it is independent or fused with the anterior lateral plate cannot be decided, as has already been pointed out. In regard to its size and development it is mostly suggestive of the spinal of the Acanthaspids.

The ventral wall of the trunk armour (text-figs. 2, 24) is strikingly flat. It is composed of three paired plates the intero-lateral (*Il*) the antero-ventro-lateral (*Avl*) and the postero-ventro-lateral (*Pvl*) and at least of one unpaired median plate — the anterior median ventral (*Amv*). If a posterior median ventral plate was present, which is still very uncertain, this plate must have been very narrow and at least to a large extent overgrown on the outside by the antero-ventro-lateral and the postero-ventro-lateral (cf. text-fig. 2 *D*, the bone lettered *X*).

The intero-lateral (*Il*, text-fig. 2) is both in regard to shape and position suggestive of the similarly termed bone in the Arthrodires (cf. HEINTZ 1929a, text-figs. 16, 26, 33, 34, 36; 1929b, text-fig. 5; 1931, text-fig. 11; 1933, text-fig. 3) and so are also the antero-ventro-lateral (*Avl*, text-figs. 2, 24) and postero-ventro-lateral (*Pvl*, text-figs. 2, 24). On the other hand the anterior median ventral plate (*Amv*, text-fig. 2) is much shorter than that in the Arthrodires and therefore on the whole somewhat as the unpaired semilunar plate in *Bothriolepis* (cf. STENSIÖ 1931, p. 107, text-fig. 53). Here it should be pointed out that the plate described by LERICHE in 1931 (pp. 11, 12, foot-note on p. 13; text-fig. 3; pl. 2, figs. 1—3; pl. 3, fig. 1) and HEINTZ in 1932 (pp. 11—12; text-

figs. 5, 7; pl. 1, fig. 2; pl. 2, fig. 1) as a "cornual" (spinal) plate is in fact an antero-ventro-lateral plate.

Both the antero-ventro-lateral plate and the postero-ventro-lateral plate lack completely a vertically ascending lamina along their lateral margins, and it is therefore clear that they did not enter in the formation of the lateral wall of the trunk armour. The postero-ventro-lateral plate seems also to lack completely indication of overlapping or overlapped



Text-fig. 6. *Phyllolepis concentrica* AGASSIZ. Head and anterior part of trunk in dorsal view. After WOODWARD 1920.

Cn, median cephalic plate; *D*, median dorsal plate; *M*₁—*M*₄, marginal plates 1—4; *Pvl*, postero-ventro-lateral plate; *Sp*, Supposed spinal plate perhaps including the anterior lateral plate; *ifc.b*, perhaps the postero-medial branch of the infraorbital groove; *mp*, possibly middle head-line of pit organs; or else postero-medial branch of the infraorbital groove; *soc*, supraorbital sensory groove.

areas along its lateral margin. On the other hand the antero-ventro-lateral plate probably has a slightly developed overlapping area along its lateral margin, an area which, if it is really present, must have overlapped a lateral element of its side. This overlapping was conceivably the only connection between the ventral and lateral walls of the trunk armour, which therefore in this respect was as in the more specialised *Euarthrodires* (cf. HEINTZ 1929a, text-fig. 15A; 1931, figs. 11, 12; 1932a, text-fig. 67; GROSS 1932) and not as in the *Acanthaspids* (HEINTZ 1929a, text-figs. 9, 11, 15; 1929b, text-fig. 6; 1933, text-fig. 5) and *Antiarchi* (STENSIÖ 1931, text-fig. 32).

As will appear from the above account and from the figures cited, the bones in the trunk-division of the *Phyllolepis*-armour have wide and well developed overlapping and overlapped areas of a similar type as those in the corresponding division of the *Arthrodira*-armour. In this connection it should also be pointed out that the mode of overlapping of the various plate is on the whole as in the *Arthrodires*.

Contrary to what is the case in practically all *Heterostraci* (exception *Ctenaspis* KIAER 1930, p. 4) the external dermal bones in *Phyllolepis* lack completely a coating of dentine and enamel and in this respect therefore *Phyllolepis* is also decidedly in accord with the *Placodermi* and not with the *Heterostraci*.

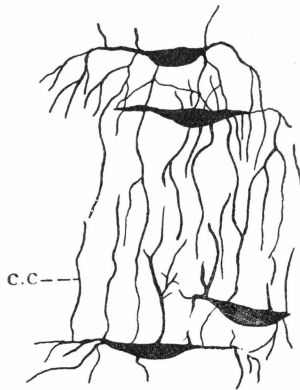
Finally it is also noteworthy that in regard to its ornament the armour in *Phyllolepis* is not as that in the *Heterostraci* but fairly much as that in *Holonema* (OBRUTSCHEW 1933, pl. 5; cf. also GROSS 1933, pl. 5, fig. 1) and certain *Acanthaspids* such as *Lunaspis* (BROILI 1929, text-fig. 1 and pls. 1, 2; 1930, text-fig. 2; GROSS 1933, pl. 4, figs. 2—4; pl. 5, fig. 1).

Minute structure of the dermal bones.

The dermal bones may be considered to be composed of three layers: a basal layer, a middle layer and a superficial layer, of which, however, the superficial layer is imperfectly developed and in most cases even not clearly distinguishable from the middle one. All the layers contain typically developed cell-spaces, a fact which is of much importance, as alone it shows that *Phyllolepis* cannot be referred to the *Heterostraci*, which, as is well known, lack entirely cell-spaces in their bone-tissue.

The basal layer (*bl*, pls. 19—23) is in certain places thick and well developed, in other places thin and not well distinguishable from the middle layer. As far as is known it is as a rule thin in the central parts of certain larger plates, but it may also be thin in certain other places and in certain smaller plates. It is laminate in structure with the laminae parallel with the basal face, but the lamination is often somewhat obscure,

which probably is due to the circumstance that the fibres in two adjacent laminae cross each other at a very small angle. In this connection it should also be pointed out that the ground-substance in the different laminae is very rich in fibres. Cell spaces are met with in a great number and are as a rule flatter on their outer than on their inner (basal) face (text-fig. 7; pl. 18, fig. 2; pl. 22, fig. 2). The cell-spaces are in communication with neighbouring ones by means of several branching canaliculi (*c. c.*, text-fig. 7; pl. 18, fig. 2; pl. 22, fig. 2). In several places these canaliculi are filled by a dark matrix, and in such places they appear in transverse sections as black dots (pl. 21; pl. 22, fig. 1). In many places canals which lodged fibres of Sharpey are seen to pierce the basal layer in a more or less oblique direction. Finally it should be



Text-fig. 7. *Phyllolepis* sp. Cell-spaces from the basal layer in transversal section; Magnification about $\times 500$ diam.

c.c., canaliculi.

added here that the basal layer is perforated by several vascular canals (*hav*, pls. 21, 23) which ascend more or less vertically to the middle layer. These vascular canals are probably at least in most cases true Haversian canals, but the laminae around them are often fairly indistinct (cf. MOODIE 1926, pp. 78—80). In such cases, however, it is always clearly seen that the cell-spaces have a concentric arrangement in relation to the canals and that their canaliculi are disposed so as to radiate towards the lumen of the canals.

The middle layer (*ml*, pls. 19, 20, 23—25) which is thick, is characterized particularly by the abundance of canals in it, canals which frequently anastomose with each other forming a complicated system. These canals which are of about a similar width as the bone trabeculae separating them, or sometimes even a little wider than these, have a somewhat different disposition not only in different plates but also in several cases at a different depth and in different places of the same plate.

In order to elucidate more in detail what has just been said concerning the middle layer we shall turn to the median dorsal plate in which that layer is best known at present. The middle layer of this plate may be considered to consist of two divisions, a basal one and a superficial one. In the central parts of the plate the basal division is characterised by the presence of a number of very regular flat plexus of canals. Each such plexus which is separated from the one nearest basally and superficially to it by a fairly thick bony wall and which is in communication with the one nearest basally and superficially to it only by relatively few branches, consists of regularly polygonal and uniformly large meshes, all of which are situated approximately at the same level. Basally in the central parts of the plate the basal division passes over into the basal layer which there may be either very thin or else indistinctly developed. Towards the margins of the plates the basal division of the layer is composed only of a few, probably only two or three plexus, which differ from those of the central parts in having their meshes long and disposed so as to produce a distinct radiate structure in the bone tissue. The superficial division of the layer in the plate under consideration differs from the basal division by a more irregular arrangement of its vascular canals.

The bone trabeculae separating the vascular canals of the middle layer are as a rule composed of laminae concentric with the canals. The majority of the canals are therefore Haversian canals. Cell-spaces are found in all the trabeculae, though they are less common and less completely filled with matrix than in the basal layer. In shape they may be either somewhat sphaeroid or flat, but their superficial and basal face have almost approximately a similar arching. They are always provided with several canaliculi.

The superficial layer (*sl*, pls. 19, 20) is present only in the ridges forming the ornament of the bones. It is mostly so imperfectly developed that it may be doubted whether we are really justified in distinguishing it from the middle layer. That this has nevertheless been done here is due to the circumstance that macroscopically the ridges are more solid and not so rich in wide canals or in canals in general as the parts below them which belong to the middle layer. In none of the sections made I have found the layer typically developed, but, as is clear from what has just been said, it is characterized by a somewhat more solid character than the middle layer, owing to the fact that it often contains fewer and finer canals than that layer. Characteristic of it is in addition that its canals often turn upwards to and open on the external face of the bones. The trabeculae separating the vascular canals are in essentials as those in the middle layer. Laminae parallel with the external face were not to be found for any stretch worth mentioning in the sections

studied by the writer, but whether this condition is typical or not I am at present unable to decide. Noteworthy is, however, that HILLS (1931, text-fig. 3, and p. 213) both figured and described such laminae in the *Phyllolepis* plates from Victoria, Australia. Cell-spaces are fairly often found in the layer, under discussion, but these cell-spaces are so imperfectly filled with matrix, that little can be established concerning their shape. It is very conceivable, however, that they did not differ fundamentally from those in the middle layer.

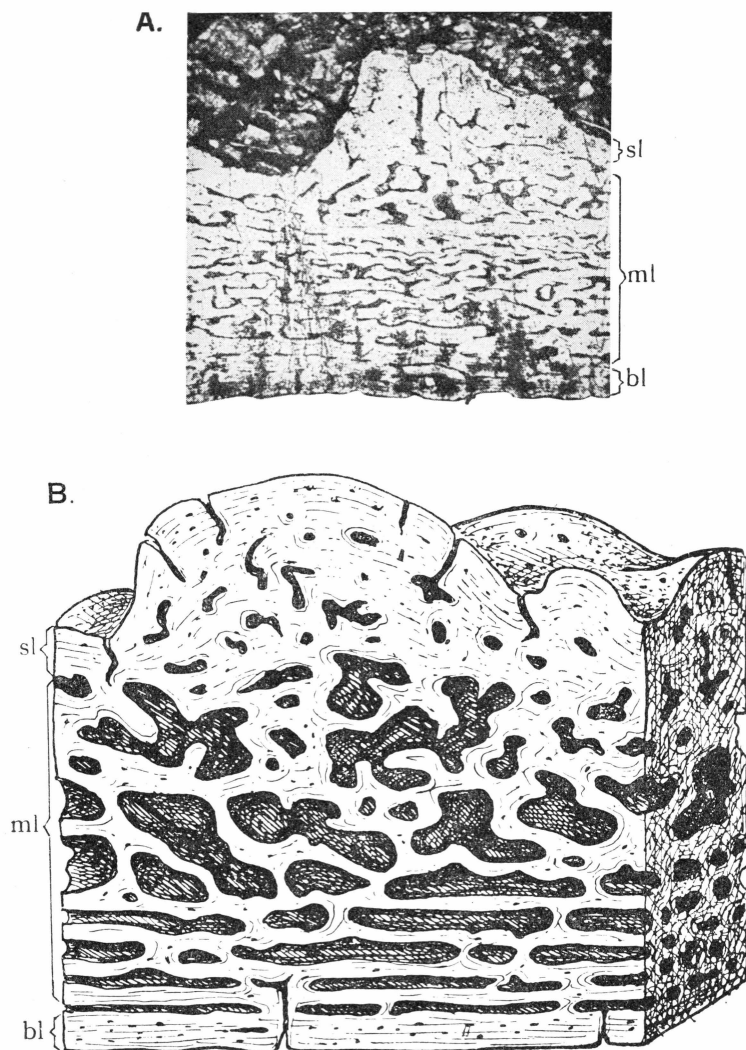
As may be gathered from the above description *Phyllolepis* resembles in the minute structure of its dermal bones decidedly the Placodermi (cf. text-figs. 8, 9). Among these it approaches in the respect under consideration particularly the *Arthrodira* (cf. HEINTZ 1929a, pp. 27—30; pls. 22—24; GROSS 1930, pp. 15—17; 1931, pp. 8—20), agreeing with these in the following characters (text-fig. 8): in the structure and development of the basal layer; in the mode of transition of the basal layer in the middle layer in places; in the structure of the middle layer as a whole; in the presence in the middle layer of a basal and a superficial division (HEINTZ 1929a, p. 27); and in the development of the superficial layer, as this is very thin as in certain Arthrodires (*Jaekelaspis*, HEINTZ 1929a, pl. 22, fig. 5)¹). For comparison with the conditions in the Arthrodires more closely the reader is referred to text-fig. 8 which shows sections through the dermal bones of certain Acanthaspids. — In the *Antiarchi* (text-fig. 9) the basal layer is more distinctly developed, the middle layer is provided with larger cavities and less uniform, and the superficial layer is much better developed than in *Phyllolepis*.

The knowledge which we now possess concerning the structure of its dermal bones thus shows beyond question that *Phyllolepis* cannot be referred to the *Heterostraci*, but that it certainly pertains to the *Placodermi* among which it seems to show the greatest agreements with the Arthrodires.

Sensory canal system.

The sensory canal system in *Phyllolepis* was first discovered and figured by WOODWARD in 1914 (pp. 122—123), who, however, did not give any special description of it. As in the *Placodermi* and *Elasmobranchii* it consists of open grooves. At present, however, it is very imperfectly known, only certain dorsal parts of it, more precisely the parts situated on the median cephalic plate, the marginal plates and the anterior dorso-lateral plate, being preserved. On account of this a more exact interpretation of it cannot be given as yet.

¹) In several Arthrodires (*Coccosteus livonicus*; GROSS 1930, pl. 2, fig. 12) the tubercles on the outside of the dermal bones may be composed in part of dentine. Dentine may, however, also be absent in certain Arthrodires (among others certain forms from Wildungen).

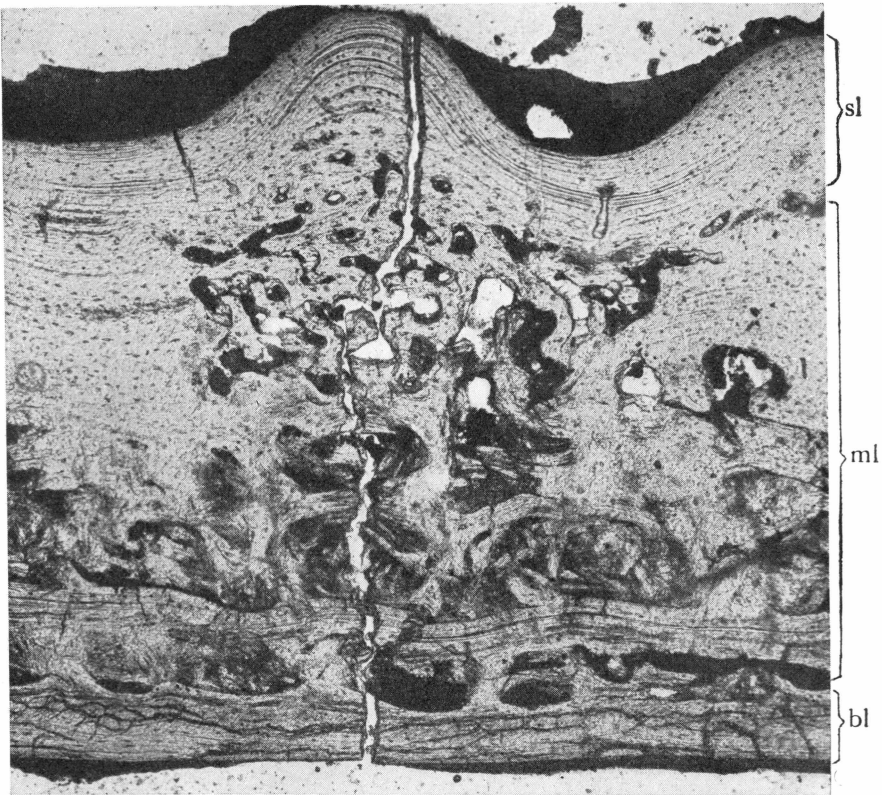


Text-fig. 8. *Arctaspis hoeli* HEINTZ. A, transverse section through a part of a dermal bone. $\times 30$ diam. B, restoration of microscopic structure of a part of a dermal bone. $+ 50$ diam. After HEINTZ 1929a.

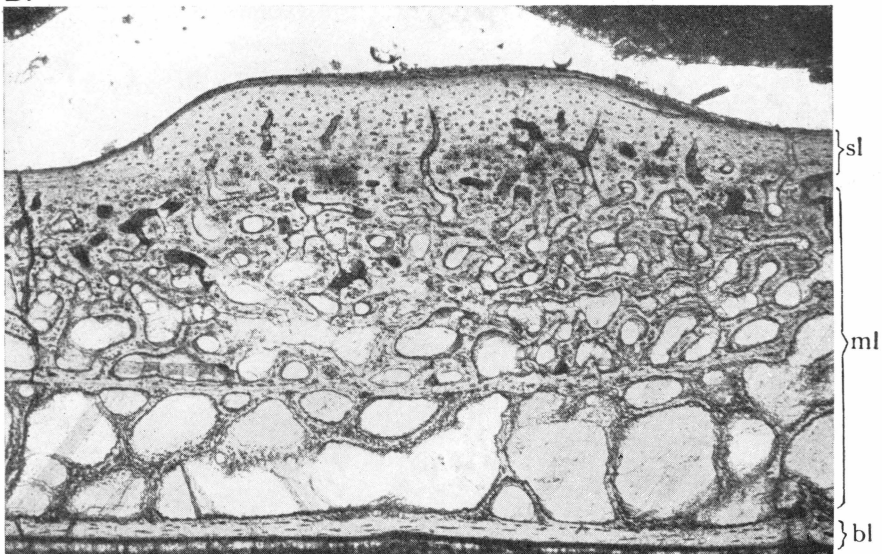
bl, basal layer; *ml*, middle layer with its two divisions; *sl*, superficial layer.

The supraorbital canal is no doubt represented by the most anterior and most medial paired groove on the head (*soc*, text-figs. 2, 6, 16, 20; pl. 1, figs. 2—5; pl. 2; pl. 4, fig. 3). This groove has its posterior end close to the centre of the median cephalic plate (*Cn*) where, at least in a few cases, it meets its fellow of the other side. From there it goes forwards and somewhat laterally on to the marginal plate 1 (*M₁*), which it crosses. In front of the last-mentioned plate it certainly went forwards in soft tissue.

A.



B.



Text-fig. 9. A, *Bothriolepis cellulosa*. Transverse section through a dermal bone. B, *Bothriolepis canadensis*. Transverse section through a dermal bone of a young specimen. $\times 50$ diam.

bl, basal layer; *ml*, middle layer; *sl*, superficial layer.

The paired groove following nearest behind the one just dealt with is always present on the marginal plate 2, on which it consist of two branches on anterior and a posterior which join each other most medially (*ifc.b*, text-figs. 2, 6; *ifc*, 17; pl. 8, fig. 2; pl. 13, fig. 1). In several cases it did not extend postero-medially on to the median cephalic plate (pl. 4, fig. 3; cf. also LERICHE 1931, pl. 1, fig. 1; HEINTZ 1932, text-fig. 7 and pl. 1, fig. 1); in other cases more or less distinct traces are found of it, there too, e. g. in the specimens, figured in text-fig. 20, pl. 2, and pl. 6, fig. 2. In *Phyllolepis concentrica* it would according to WOODWARD (1914; 1920) extend uninterrupted from the marginal plate 2 postero-medially on to the central part of the median cephalic plate (text-fig. 6) whereas according to SÄVE-SÖDERBERGH (text-fig. 2) it would end already at the boundary between the marginal plate 2 and the median cephalic plate, thus without continuing on to the last-mentioned plate.

From its position it is fairly probable that the groove here under discussion represents the dorso-medial branch of the infraorbital groove of the Arthrodires (text-fig. 10; cf. also STENSIÖ 1925a, pp. 168—169, 177) and *Antiarchi* (cf. text-fig. 11; STENSIÖ 1931, pp. 143—144), but the possibility is of course also to be taken earnestly into account that it is a structure without any direct homologue in other forms.

The third paired groove counted from in front (*mp*, text-figs. 2, 6, 18, 20; pl. 1, fig. 6; pl. 2; pl. 4; pl. 6, fig. 2; pl. 16, fig. 1) begins in all species in which it is known on the median cephalic plate (*Cn*), close to the centre of this plate and not so very far postero-laterally to the other grooves. It goes in a lateral and only slightly anterior direction to the marginal plate 3 (*M₃*) on which it pretty soon bifurcates into an anterior branch which forms a fairly straight continuation of the unbranched groove and goes to the lateral margin of the plate, and a posterior branch which goes postero-laterally to the posterior end of the plate. After having left the marginal plate 3 (*M₃*) both these branches certainly continued at least a short stretch in soft tissue. — As far as can be judged the medial unbranched part of the groove described may correspond to the middle head-line of pit-organs in fishes in general or possibly to the postero-medial branch of the infraorbital groove of the *Arthrodira* and *Antiarchi* (cf. STENSIÖ, loc. cit.). If the first of these alternatives would turn out to be true the anterior branch of the groove would be the most posterior part of the infraorbital canal and thus the otic part of this canal (SÄVE-SÖDERBERGH 1933b, p. 7), whereas the posterior branch would represent the most anterior part of the main lateral line that was supplied by the n. glossopharungeus and thus the post-otic canal (SÄVE-SÖDERBERGH 1933b, p. 7). On the other hand if the second alternative revealed itself to be true both the branches of the groove under consideration would belong to the infraorbital canal

and the anterior one of them would then be the posterior portion of the postorbital part of this canal whereas the posterior branch would correspond to an anterior portion of the postotic part of the same canal.

In the Greenland species and in *Ph. concentrica* we find a fourth paired sensory canal groove which is situated on the marginal plate 4 (*lc*, text-figs. 2, 19; pl. 5; pl. 7, fig. 1; pl. 18), which it crosses from the boundary towards the median cephalic plate in an antero-lateral direction to the very lateral margin. Laterally to this margin, which it reaches fairly close behind the marginal plate 3, it certainly continued for a stretch in soft tissue. In the Greenland species I have found no antero-medial branch from it, whereas according to SÄVE-SÖDERGERGH (text-fig. 2) it would have such a branch which would be situated on the postero-lateral part of the median cephalic plate.

As far as can be judged we are in the fourth groove just described concerned with the posterior main part of the cephalic division of the main lateral line. The medial branch from the groove observed by SÄVE-SÖDERBERGH in *Ph. concentrica* seems to correspond well to the posterior head line of pit organs in the Arthrodires (cf. text-figs. 10, 11; cf. also STENSIÖ 1925a, text-fig. 24 and p. 179).

Of the trunk-division of the main lateral line groove the part situated on the anterior dorso-lateral plate is present both in *Ph. concentrica* (text-fig. 2) and in the Greenland species (text-figs. 2, 22; pl. 7, fig. 3; pl. 8, fig. 3; pl. 17, fig. 1).

From the position and extent of the supraorbital groove and from the existence of a probable postero-medial branch of the infraorbital groove it is obvious that the eye must have been situated somewhere in front of the marginal plate 2 (M_2) or in front of the suture between this and the marginal plate 1 (M_1).

Though our knowledge of it is still imperfect it is not difficult to see that the sensory canal system is of the *Placodermi*-type and mostly in agreement with that in the Arthrodires.

Homologues of the bones of the armour.

Already from what has been set forth above it may easily be gathered that with regard to the bones of its armour *Phyllolepis* is on the whole as a Placoderm which in most respect approaches the Arthrodires. In order to elucidate more in detail this agreement between *Phyllolepis* and the *Placodermi* an account is here given of the homologues of the various bones in the armour of *Phyllolepis*.

As it bears the posterior part of the supposed supraorbital groove, and the possible dorso-medial branch of the infraorbital groove, the groove which possibly represents the middle pit-line of the head and in addition perhaps also a part of the posterior head line, the median cephalic

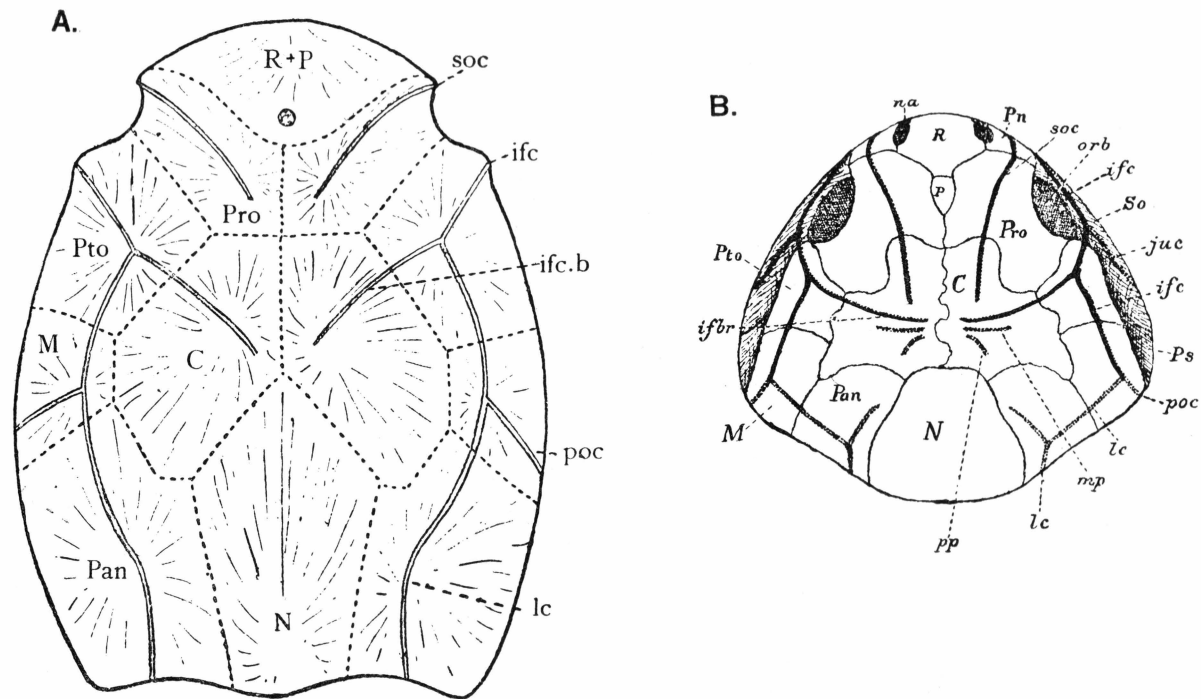
plate (*Cn*, text-figs. 2, 6) corresponds to both the nuchal plate and the central plates of the Arthrodires (text-fig. 10), and at least in part to the median nuchal plate of the *Antiarchi* (text-fig. 11; cf. also STENSIÖ 1931, p. 153). From its relations to the supposed supraorbital sensory groove it is highly probable that the marginal plate 1 (M_1 , text-figs. 2, 6) represents at least a part of the preorbital of the Arthrodires (text-fig. 10), whereas the marginal plate 2 (M_2 , text-figs. 2, 6) on account of the fact that it bears a part of the supposed infraorbital groove seems to be comparable at least to a part of the postorbital of the Arthrodires (text-fig. 10) and to the postmedian plate of the *Antiarchi* (text-fig. 11; cf. also STENSIÖ 1931, pp. 151—152). Finally the marginal plates 3 and 4 (M_3 and M_4 , text-figs. 2, 6) have approximately similar relations to the sensory canal system as the marginal and paranuchal plates respectively of the Arthrodires, and it is therefore conceivable that they correspond at least to the dorso-medial parts of these plates (text-fig. 10)¹).

If the bones just dealt with have the homologues suggested, it follows that a considerable rostral part of the head must be destitute of dermal bones and that the orbit must have been situated close in front of the suture between the marginal plates 1 and 2 (M_1 and M_2). On the other hand, if the sensory groove supposed to be the middle pit-line of the head should reveal itself as the postero-medial branch of the infraorbital groove, and if what has been considered as this branch would be a structure *sui generis*, the marginal plate 3 (M_3) would of course represent the postorbital of the Arthrodires, whereas the marginal plate 2 (M_2) would not be comparable to any Arthrodire plate. The orbit would in this latter case have been situated somewhat in front of the marginal plate 2 (M_2).

The median dorsal plate (*D*, text-figs. 2, 6) and the anterior dorso-lateral plate (*Adl*, text-figs. 2, 6, 22) are probably the exact homologues of the similarly termed plates in the Arthrodires, and so are probably also the intero-lateral, the anterior ventro-lateral, the posterior ventro-lateral and the anterior median ventral plate. Possibly this is the case also with the spinal plate, unless this comprises also the anterior lateral plate of its side, but anything concerning this question cannot be decided at present. Whether any homologues of the posterior dorso-lateral and posterior lateral plates of the Arthrodires were present is unknown.

From what has been set forth here we see that in regard to the homologues of the plates in its armour *Phyllolepis* reveals itself as a Placoderm most closely related to the *Arthrodira*.

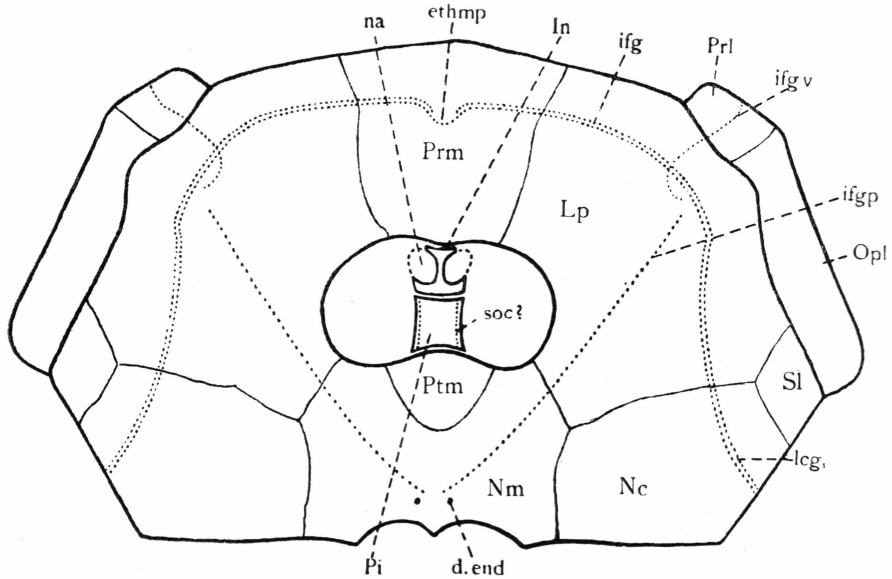
¹) A support for the opinion that the marginal plate 4 corresponds to the paranuchal (externo-basal HEINTZ 1932a) of the Arthrodires is also found in the fact that, as pointed out above, it has on its lower side a deep pit which seems to correspond to the canal in the Arthrodires, that probably was developed for the ductus endolymphaticus.



Text-fig. 10. Dermal cranical roof with sensory canal grooves. A, of *Svalbardaspis typica* HEINTZ. After HEINTZ 1929. B, of *Cocosteus decipiens* AGASSIZ. After STENSIÖ 1925a. C, central plate; M, marginal plate; N, nuchal plate; P, pineal plate; Pan, paranuchal plate; Pn, postnasal plate; Pro, preorbital plate; Pto, postorbital plate; R, rostral plate; ifc, infraorbital sensory groove; ifbr, postero-medial branch of the infraorbital sensory groove; lc, cephalic division of the main lateral line; mp, middle pit-line of the head; poc, preopercular sensory groove; pp, sensory groove, probably corresponding to the posterior pit line of the head in fishes in general; soc, supra-orbital sensory groove.

Vertebral column.

In the almost complete specimen of *Phyllolepis concentrica* described by WOODWARD (text-fig. 6 in the present work; cf. WOODWARD 1920, p. 31) there are ossified remains of neural and haemal arches. As neither any detailed figure nor any detailed description has been given of these skeletal elements it is impossible to ascertain whether they are *Arthrodira*-like or not. In any case it is evident, however, that the presence of these elements is a character which hitherto is unknown in the *Hetero-*



Text-fig. 11. *Bothriolepis canadensis*. Dermal cranial roof and cheek-bones. After STENSIÖ 1931.

ln, prepineal plate; *Lp*, lateral plate; *Nc*, lateral nuchal plate; *Nm*, median nuchal plate; *Opl*, opercular plate (postsuborbital); *Pi*, pineal plate; *Prl*, prelateral plate; *Prm*, premedian plate; *Ptm*, postmedian plate; post-median plate; *Sl*, sufflaminal plate; *d.end*, opening probably for the ductus endolymphaticus; *ethmp*, pit-line uniting the main division of the infraorbital sensory canal grooves; *ifg*, infraorbital sensory canal groove (main division); *ifgp*, subrostral pit-line (division of the infraorbital sensory canal groove); *lcp*, cephalic division of the main lateral line groove; *na*, external nasal aperture; *soc?*, groove conceivably caused by the supraorbital sensory canal.

straci. With regard to the development of the vertebral column *Phyllolepis* is therefore in fact at a corresponding stage of development as the *Arthrodi*res.

Concluding remarks on the relationships and systematic position of the *Phyllolepis*s.

WOODWARD (1914, 1920), LERICHE (1931), HEINTZ (1932b), BROTZEN (1933) and others have compared *Phyllolepis* to certain forms among

the *Heterostraci* such as *Psammosteus* and *Drepanaspis* and placed it among the *Heterostraci*. The researches now carried, have shown, however, that it has nothing whatever to do with these, but that it must be a Placoderm, thus a form related to the *Antiarchi* and *Arthrodira*.

If we try here to summarise the most important of the characters which *Phyllolepis* has in common with the Placoderms these would be as follows. 1) The subdivision of the armour into a cephalic division and a trunk-division; 2) the general structure of the armour; 3) the shape and development of several of the plates in the armour; 4) the position of the gills underneath the head and not behind this; 5) the structure and disposition of the sensory canal system; 6) the structure of the dermal bone-tissue and particularly the presense of cell spaces in this; and finally 7) the presence of neural and haemal arches in the vertebral column.

Among the Placoderms *Phyllolepis* shows agreements both with the *Antiarchi* and *Arthrodira*. With the *Antiarchi* it agrees mainly in the configuration of the lower face of the median dorsal plate; on the other hand with the *Arthrodira* it has a number of important characters in common, viz. 1) The shape and development of many of the plates in the armour; 2) the presence of a large, probably Acanthaspid-like spinal plate; 3) the disposition of the sensory canal system; 4) the minute structure of the dermal bones; and 5) the presense of ossified neural and haemal elements in the vertebral column. It is therefore beyond question most closely related to the Arthrodirens among which it seems to approach mostly the *Acanthaspida*. As, however, it differs fairly much from the Arthrodirens above all in the fusion of the central plates with the nuchal plate into a median cephalic plate, in the presence of a long sensory canal groove which possibly represent the middle head line of pit organs, and in the absence or possibly slight development of the posterior median ventral plate I have found it most convenient at least at present to erect a special group for it among the Placoderms, a group which I have called *Phyllolepida* and which has been given the rank of an order. As the order *Phyllolepida* as thus defined is more closely related to the order *Arthrodira* than to the *Antiarchi* the classification of the *Placodermi* as far as they are known will be as follows.

Placodermi.

Grupp A.

Order *Antiarchi*.

Grupp B.

1. Order *Phyllolepida*.

2. Order *Arthrodira*.

The absence of the anterior part of the dermal cranial roof, the probable absence of lateral dermal bones on the head and the absence or vestigial development of the posterior dorso-lateral plate, the posterior lateral plate and the posterior median ventral plate show clearly that *Phyllolepis* is a highly specialised form which in regard to its armour has to a certain degree undergone a regressive development.

As has been shown by the writer in a recent work (STENSIÖ 1934) and by BROILI (1934) the *Placodermi* are beyond question true gnathostomes, which in some way are related to the ancestors of the Elasmobranchs.

Genus *Phyllolepis* AGASSIZ.

Syn. *Pentagonalepis*, LOHEST, M. 1888.

Diagnosis. — Head and trunk armour probably fairly rigidly connected with each other. Anterior bones of the dermal cranial roof probably completely reduced; the remaining bones of the dermal cranial roof consisting of an unpaired large median cephalic plate and four paired marginal plates. In the trunk carapace: a median dorsal plate, a paired antero-dorso-lateral plate, a spinal plate, a paired intero-lateral plate, a paired anterior ventro-lateral plate, a paired posterior ventro-lateral plate and an unpaired anterior median ventral plate known thus far. Sensory canal system represented by open grooves converging on the top of the head towards the centre of the median cephalic plate. Ornament of the external dermal bones consisting of rounded continuous ridges, often with a disposition concentric with the margins of the bones.

Only three species, *Ph. concentrica* AGASSIZ, *Ph. undulata* LOHEST and *Ph. orvini* HEINTZ have hitherto been known of the genus¹).

Phyllolepis orvini HEINTZ.

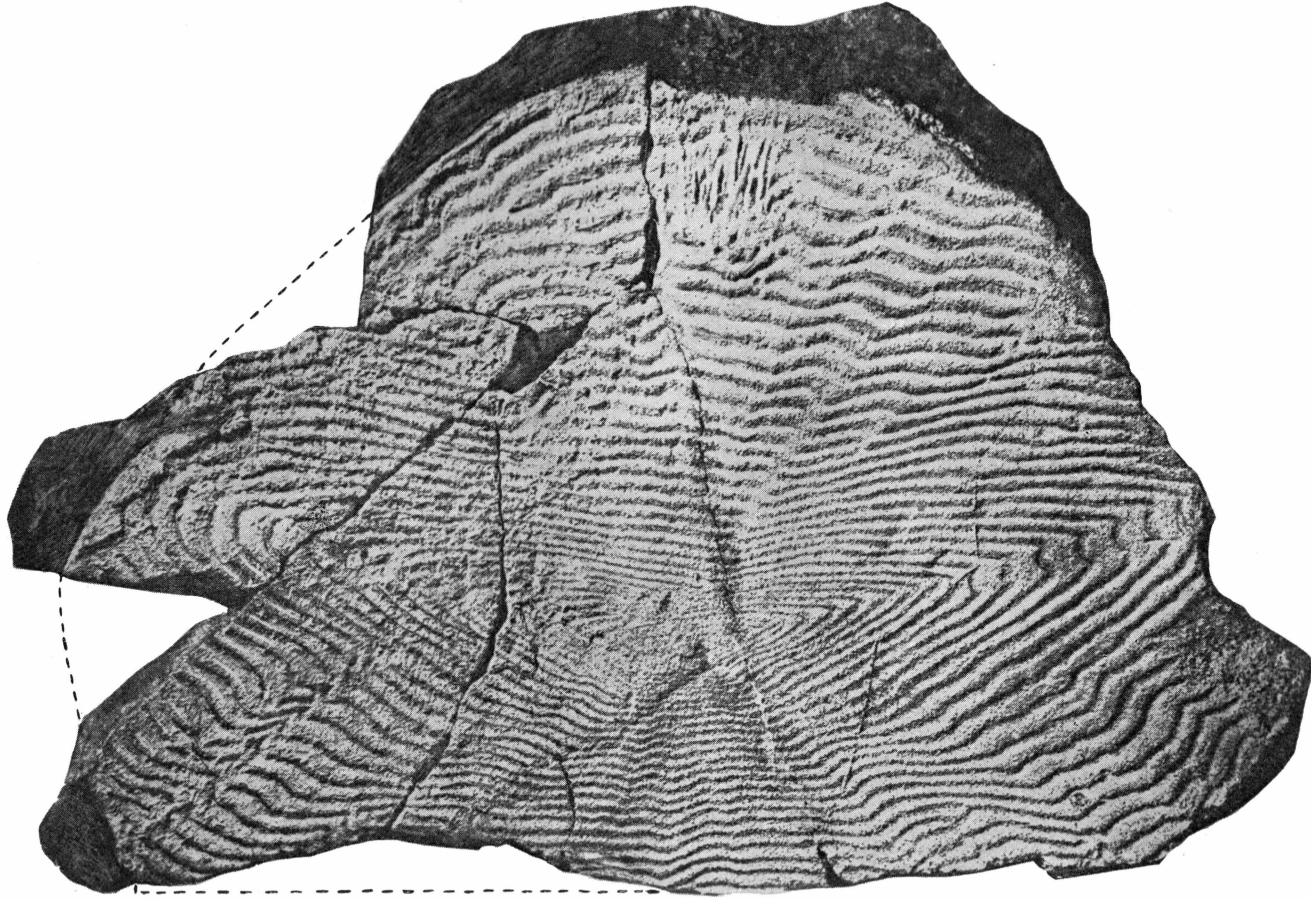
(Text-figs. 12, 13).

Diagnosis. — A very large *Phyllolepis*, probably with a relatively short, broad and flat armour. Median dorsal plate probably much broader than long, the proportions between its breadth and length possibly being approximately 3:2. The ornament of the median dorsal plate consisting of ridges, disposed in such a way that those of the anterior and posterior halves meet at a strikingly acute angle.

Material. — Under this species name only a single plate, the median dorsal plate figured by HEINTZ (1930), is dealt with (text-fig. 12, 13). This plate is chosen as a holotype.

Description. — The plate under consideration here is of a large size, its length in the present state of preservation being 11 cm and

¹) A fourth species was established by LOHEST (1888, pp. 157—158) but this species is now considered as a synonym of *Ph. undulata* (LERICHE 1931).



Text-fig. 12. *Phyllolepis orvini* HEINTZ. Median dorsal plate. Holotype. After HEINTZ 1930. Somewhat diminished.

its breadth 16.5—17 cm; and it is therefore clear that the species attained a very large size. It is very likely, however, that an anterior part is missing and that the length therefore was larger than 11 cm. And if this be so the plate would obviously have been more round in shape than what has been supposed by HEINTZ. It is therefore reason to assume that the plate did not differ so very much from the corresponding one in *Ph. söderberghi* to be described below.

The ornament of the plate consists of ridges in the normal way. Of these ridges those which are concentric with the anterior margin begin to curve backwards already close to the median line of the plate and continue with this curvature in such a way that they pass over without any boundary into those concentric with each antero-lateral margin. Therefore we have here in fact only anterior ridges with a disposition somewhat concentric with the anterior and antero-lateral margins and posterior ridges which are somewhat concentric with the postero-lateral margins. The anterior and posterior ridges thus formed meet each other at very acute angle.

Nothing is known thus far concerning the lower face or of the overlapping areas of the plate.

Remarks. — *Ph. orwini* is not well distinguished from *Ph. söderberghi*. It is characterized particularly by the ornament of its median dorsal plate.

Geological horizon and locality. — The *Phyllolepis* Sandstone Series. Orwin's locality at Cape Graah.

Phyllolepis söderberghi n. sp.

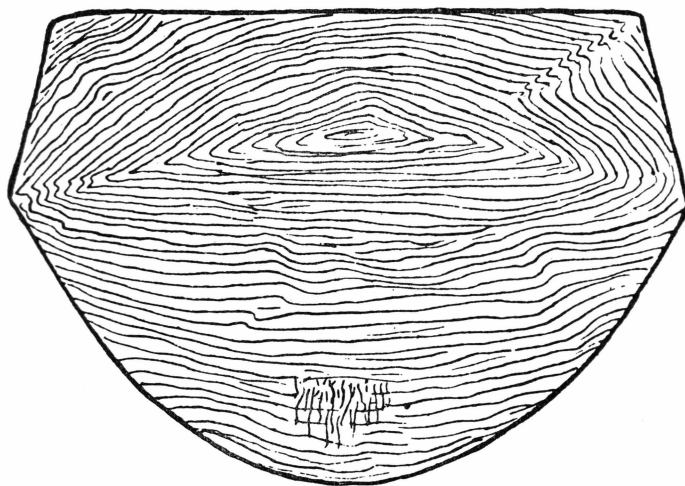
(Text-figs. 14, 15; pls. 9—11).

Diagnosis. — A very large *Phyllolepis* probably with a relatively broad and flat armour. Median dorsal plate almost as long as broad, of a somewhat pentagonal shape, and ornamented with ridges disposed in such a way that those concentric with the anterior margin and those concentric with each antero-lateral margin are fairly well distinguishable from each other and that those concentric with the last-mentioned margin meet those of the posterior part of the bone, which are fairly transversal, at a somewhat obtuse angle.

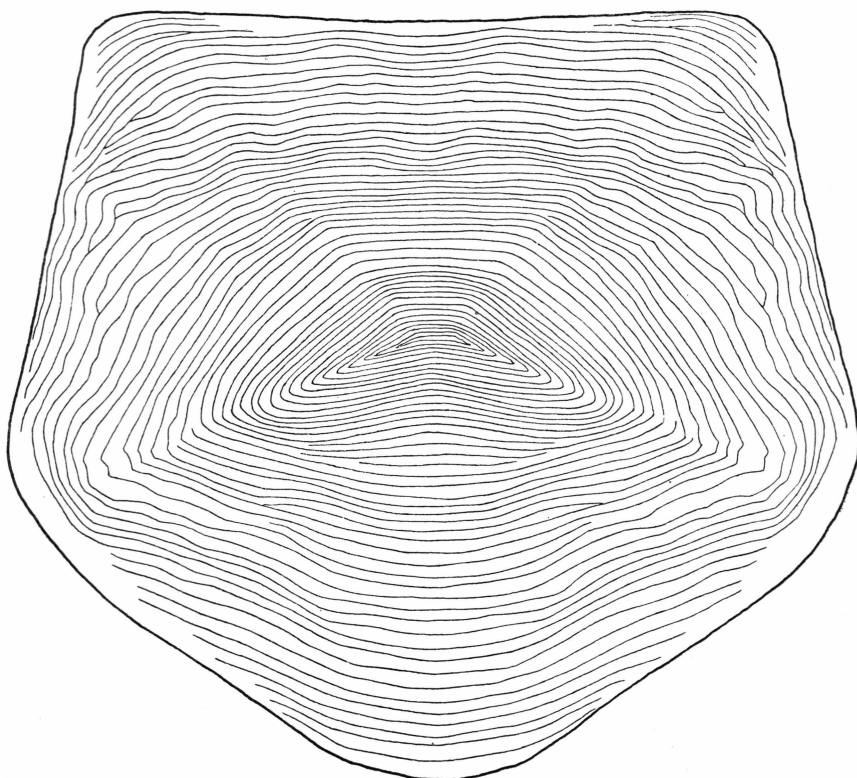
Material. — The material referable to this species with certainty consists only of two median dorsal plates (nos. 427d, e; 431c, d) of which the one (no. 427d, e) shown in pls. 9 and 10 is chosen as a holotype.

Description. — The holotype is large, measuring not less than 15,5 cm. in length and 17,4 cm in breadth. The other plate is smaller, its corresponding dimensions being 9.2 cm and 10.3 cm respectively. As is clear from these measurements the species attained a very large size.

The two median dorsal plates present (text-fig. 14; pls. 9—11) agree



Text-fig. 13. *Phyllolepis orvini* HEINTZ. Restoration of median dorsal plate. As the anterior part seems to be missing the extent of the plate in a rostro-caudal direction may have been longer than in this restoration. Much diminished. Mainly after HEINTZ 1932.



Text-fig. 14. *Phyllolepis söderberghi* n. sp. Median dorsal plate in dorsal view. After the holotype. Approximately $\frac{2}{3}$ of the nat. size.

well with each other in regard to shape, both being pentagonal with the corners somewhat rounded off. The anterior margin may be slightly concave almost straight. The antero-lateral margin is fairly short, corresponding in length only to a little more than one half of the anterior margin; and finally each postero-lateral margin, which as a whole is slightly convex, is somewhat, though not so very much shorter than the anterior margin. With regard to their general shape it should also be mentioned here that both the plates are strikingly flat, their upper face being only slightly convex and their lower face only slightly concave.

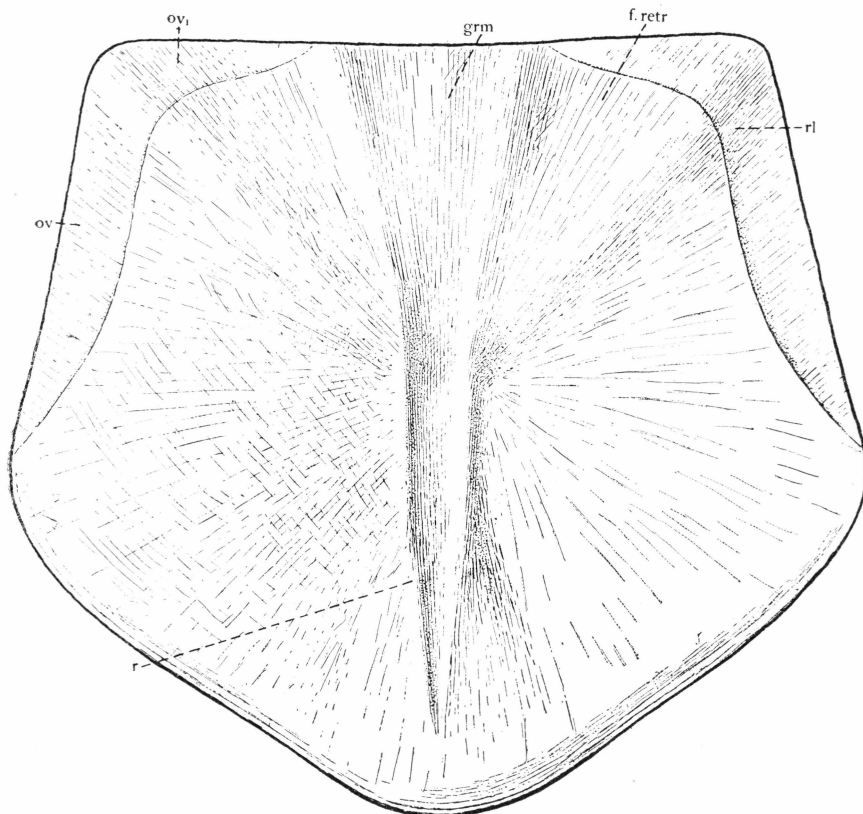
On both the plates the lower face (text-fig. 15; pl. 10; pl. 11, fig. 2) was exposed by etching with acid, and by this it became clear that this face displays certain details of interest. More precisely we find on it, as has already been pointed out above (pp. 20—21), a lateral overlapping area, a levator fossa and a median longitudinal groove.

The lateral overlapping area (*ov*, text-fig. 15; pl. 10; pl. 11, fig. 2) which is broad but not particularly well developed, is situated along the antero-lateral margin and along the lateral part of the anterior margin (*ov*₁). From its shape it is easily seen that it must have overlapped the anterior dorso-lateral plate; and accordingly we have here similar sutural connections between the median dorsal plate and the anterior dorso-lateral plate as in the *Arthrodires*.

The levator fossa (*f.retr*, text-fig. 15; pl. 10; pl. 11, fig. 2) which is situated on the anterior third of the bone, has its widest part directed forwards. Though being shallow it is fairly conspicuous. On each side it is bounded by a low rounded ridge (*rl*) which from a point near the median line goes forwards and laterally to the antero-lateral corner of the bone. In regard to both shape and position it is so suggestive of the levator fossa in the *Antiarchi* (cf. STENSIÖ 1931, pp. 75—77) that it is likely that it must have had at least a similar function as this. As, however, the head was not or perhaps only very slightly moveable against the trunk the musculature which gave rise to it must have been much less well developed than in the *Antiarchi*.

Finally the median longitudinal groove (*gm*, text-fig. 15; pl. 10; pl. 11, fig. 2) is almost as long as the bone, beginning already at the anterior margin and extending through the levator fossa and behind this backwards almost as far as to the posterior end of the bone. It is bounded on each side by a low, longitudinal ridge (*r*) and characteristic of it is otherwise that it is broadest at its anterior end, narrowing from there rather rapidly throughout the levator fossa. Behind that fossa it narrows only very slowly and gradually backwards. Both in its position and development as a whole it resembles much the median dorsal groove on the lower face of the anterior median dorsal plate in *Bothriolepis canadensis* and other *Bothriolepis* species (cf. STENSIÖ 1931, p. 75, and text-fig. 33).

The ornament of both the plates referred to the species is very similarly developed. In the normal way it consist of ridges (text-fig. 14; pl. 9; pl. 11, fig. 1). Contrary to what is the case in *Ph. orvini* the ridges concentric with the anterior margin and the ridges concentric with each antero-lateral margin are fairly well distinguishable from each other, the transition between them taking place fairly suddenly. In addition



Text-fig. 15. *Phyllolepis söderberghi* n. sp. Median dorsal plate in ventral aspect. Approximately $\frac{2}{3}$ of the nat. size.

f. retr, levator fossa; *grm*, median longitudinal groove; *ov*, *ov₁*, areas overlapping the anterior dorso-lateral plate; *r*, ridge bounding the median longitudinal groove; *rl*, ridge bounding the levator fossa.

the ridges concentric with each antero-lateral margin meet the ridges of the posterior parts of the upper face, which are fairly transversal, at a more obtuse angle than in *Ph. orvini*.

Remarks. — *Ph. söderberghi* is distinguished from *Ph. orvini* in the shape and ornament of the median dorsal plate.

Geological horizon and locality. — The *Phyllolepis*-sandstone series. S. side of Mt. Sederholm, at the Profile-ravine in the Parallel Valley.

Phyllolepis spp.

(Text-figs. 16—26; pls. 1—8, 12—17; pl. 18, fig. 1).

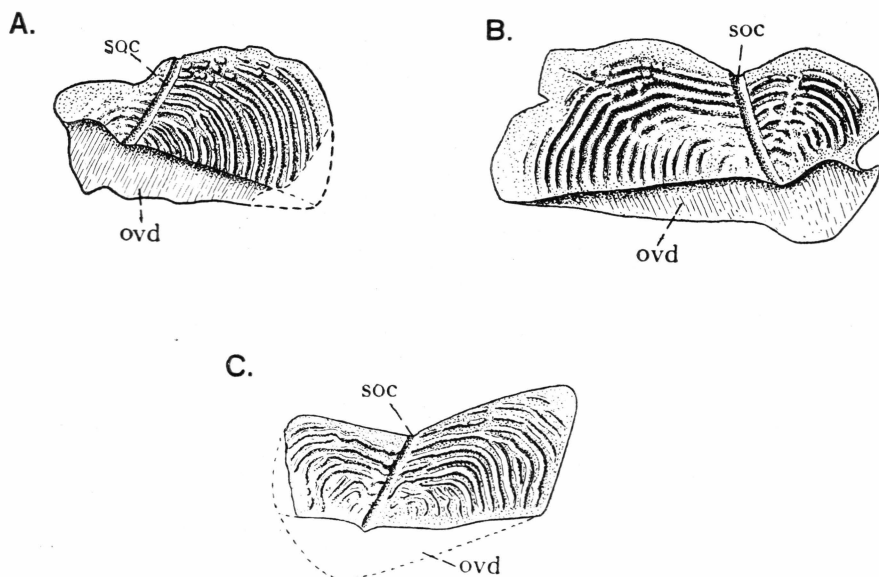
Material. — Under this title I describe all the *Phyllolepis* plates available which at present cannot be referred either to *Ph. orvini* or to *Ph. söderberghi* (nos. 400—417, 419—422, 424, 425, 427a, b, c, 429—430, 431a, b, 432—434, 436, 437, 439—442, 444—448, 450, 452, 454, 455, 458—460). These plates form the bulk of the *Phyllolepis*-material collected thus far.

Description. — The plates to be described here are dealt with in the following order: the marginal plates 1, 2, 3, and 4; the median cephalic plate, the anterior dorso-lateral plate, the anterior lateral plate, the spinal plate, the anterior and posterior ventro-lateral plate and finally five plates the position of which in the armour is still unknown.

The marginal plate 1 is represented by two types which for the sake of brevity we may refer to as type A and type B. In type A (text-fig. 16A; pl. 1, figs. 4, 5; M_1 , pl. 2) the part of the plate situated medially to the supraorbital sensory groove (*soc*) reaches much less forwards than the part situated laterally to the same groove, whereas in type B (text-fig. 16B, C; pl. 1, figs. 2, 3) it has almost the same forward extent as that. Both the types were overlapped posteriorly along the posterior margin by the median cephalic plate, for which they have a broadly triangular overlapped area (*ovd*). Characteristic for both the types of plates is in addition that laterally they overlapped the marginal plate 2. They must therefore both be provided with an overlapping area along their lateral margin, but this area has not as yet been observed. The ornament and the other details to be seen in the two types of plates are so well displayed by the figures cited that a description of them is superfluous.

Of type A two specimens (nos. 429, 431) are known which both are from the S. side of Mt. Sederholm. Of type B there are two specimens one of which (no. 424) is from the S. side of Mt. Sederholm whereas the other (no. 401) is from Orvin's locality at Cape Graah.

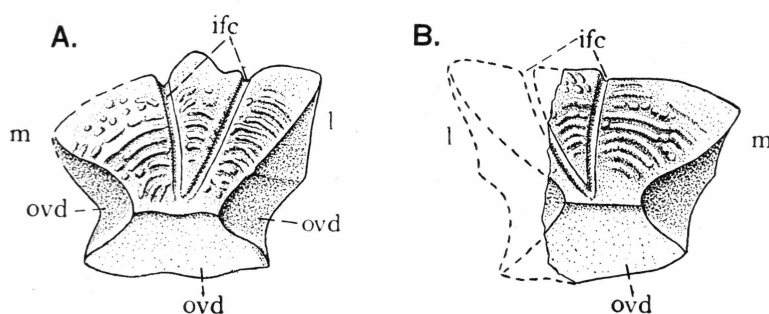
The marginal plate 2 (text-fig. 17; M_2 , pl. 1, fig. 2; pl. 8, fig. 2; pl. 13, fig. 1) is still imperfectly known, the specimens present of it (nos. 400, 424, 427a) being incompletely preserved. The plate is broadest at its anterior margin from where it narrows backwards as far as close in front of the posterior end, there increasing somewhat in breadth again. On account of this its lateral and medial margins are concave. Its anterior and posterior margins are both somewhat convex, the former, however, more so than the latter. Wide overlapped areas (*ovd*) are present along the medial margin, along the posterior margin and along the lateral margin. These areas, which are continuous with each other, are overlapped by the marginal plate 1, by the median cephalic plate



Text-fig. 16. *Phyllolepis* spp. Marginal plate 1. A, of type A from the S.side of Mt. Sederholm. B, of the type B (from the S.side of Mt. Sederholm); C, of type B (no. 401) from Orvin's locality at Cape Graah. Approximately natural size. *soc*, groove for a part of the supraorbital sensory canal; *ovd*, overlapped areas.

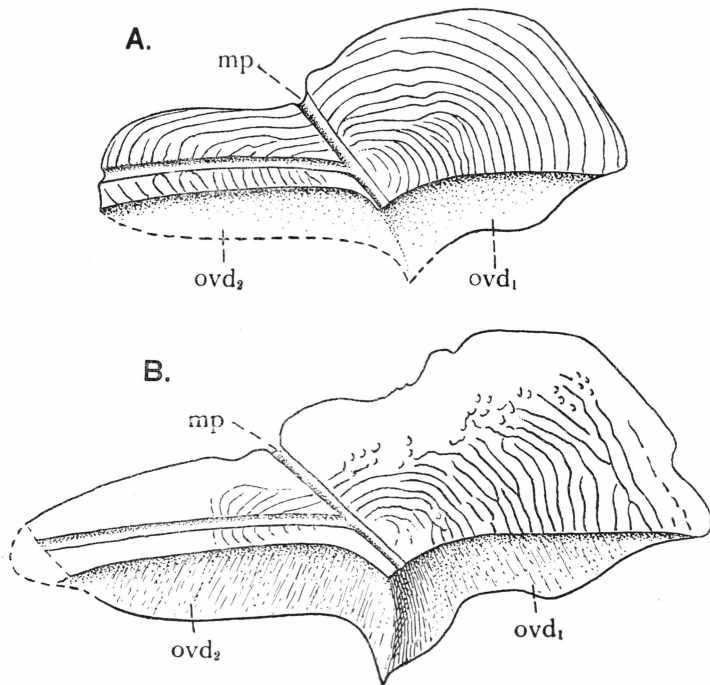
and by the marginal plate 3 respectively. The freely exposed part of the upper (external) face is somewhat nearer to its lateral than to its medial margin crossed by a V-shaped groove (*ifc, ifc.b*) which, as has already been pointed out (p. 28, above), lodged a part of the probable infra-orbital sensory canal.

The marginal plate 3 (text-fig. 18; pl. 1, fig. 6; pl. 4, figs. 1, 2; pl. 16, fig. 1) is in regard to its shape in all the specimens available (nos. 400, 404, 408, 410, 415, 454, 458) of a similar type as that figured



Text-fig. 17. *Phyllolepis* spp. Marginal plate 2. A, from the S.side of Mt. Sederholm (no. 427); B, from Orvin's locality at Cape Graah (no. 400). Approximately nat. size. *ifc*, groove for a part probably of the infraorbital sensory canal; *l*, lateral; *m*, medial margin; *ovd*, overlapped areas.

and restored by HEINTZ (1932b, text-fig. 7; pl. 2, fig. 3). Thus it is much broader in its anterior than in its posterior part, and it differs therefore distinctly from the corresponding bone in *Ph. concentrica* (cf. text-figs. 2, 6) which narrows only rather little backwards. Along its postero-medial margin it has large overlapped area which in its anterior part (*ovd*₁) is overlapped by the median cephalic plate and in its posterior part (*ovd*₂) by the marginal plate 4. The freely exposed part of the upper (external) face is ornamented with ridges concentric with the antero-medial and antero-lateral margins. In certain of the specimens the ridges



Text-fig. 18. *Phyllolepis* spp. Marginal plate 3. A, from Orvin's locality at Cape Graah (no. 408). B, from the S. side of Mt. Sederholm in the Vasti valley (no. 458b). *mp*, groove probably for a part of the middle head-line; *ovd*₁, area overlapped by the median cephalic plate; *ovd*₂, area overlapped by the marginal plate 4.

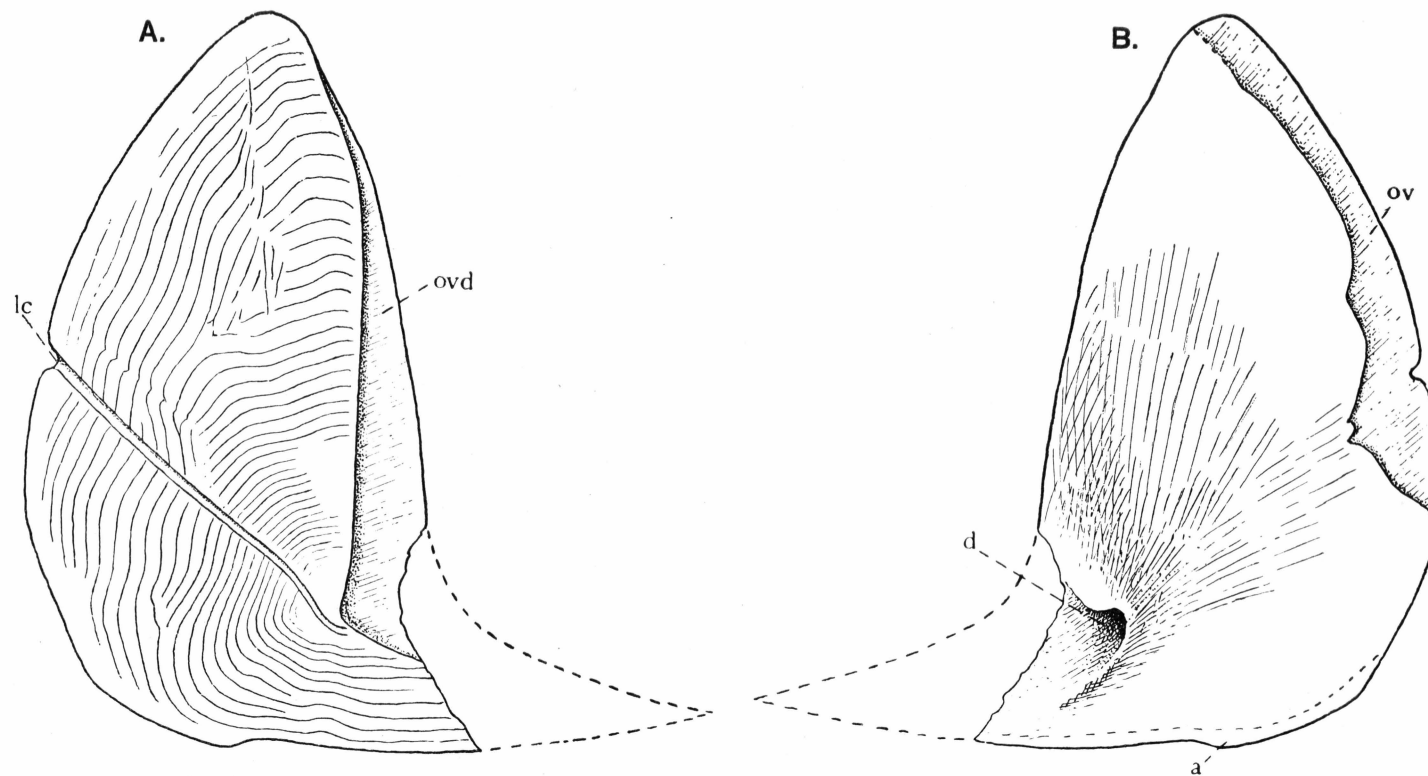
are present as far laterally as to the very antero-lateral margin (text-fig. 18A; pl. 1, fig. 6); in other specimens there is a smooth zone along the lateral margin at least of the posterior broad part of the bone (text-fig. 18B; pl. 16, fig. 1). The character of the ornament otherwise is shown by the figures cited. The freely exposed part of the upper (external) face is, as described by HEINTZ (1932b), crossed by two sensory canal grooves which meet each other somewhat laterally to the overlapped area, thence being continued medially by a single groove which goes

in a postero-medial direction on to the median cephalic plate. This groove may, at least provisionally, be considered as an equivalent of the middle head-line of pit-organs in fishes in general.

The marginal plate 4 (text-fig. 19; pl. 5; pl. 7, fig. 1; pl. 18, fig. 1) is among the material represented by rather many specimens (nos. 414, 415, 424, 433, 436, 437, 439, 440, 460) most of which, however, are fairly imperfectly preserved. In regard to its general shape it is rather suggestive of the corresponding plate in *Ph. concentrica* (text-figs. 2, 6). Thus it has a fairly much convex lateral margin, a somewhat convex posterior margin which merges without any boundary into the lateral margin, and a medial margin which consists of an anterior part medially directed and a posterior part anteriorly directed. With a posterior medially directed process the plate extends behind the median cephalic plate quite as in *Ph. concentrica*. Along the medial margin on the upper (external) face it has a well developed but not particularly broad area (*ovd*) which is overlapped by the median cephalic plate, and along the anterior part of the lateral margin on the lower (ventral) face an area (*ov*) which with its anterior part overlapped a posterior part of the marginal plate 3 and behind this perhaps another small plate. Along the posterior margin on the ventral face there is also a narrow zone (*a*) which seems to have been situated dorsally to the anterior margin of the median dorsal plate and which probably was fairly rigidly attached to this margin. On the lower (ventral) face of the bone somewhat laterally to the reentering angle of the medial margin we find a deep somewhat oblong fossa (*d*) which is situated at a somewhat corresponding place as the canal in the Arthrodires (cf. OBRUTSCHEW 1929, p. 299; STENSIÖ 1934, p. 32) which possibly lodged the ductus endolymphaticus and which therefore probably corresponds to this canal. The freely exposed part of the upper (external) face of the bone is, as in *Ph. concentrica*, ornamented with ridges concentric with the lateral and posterior margins. In addition this part of the upper face is crossed by a sensory groove which goes from the lateral margin in postero-medial direction towards the reentering angle of the medial margin. This sensory groove (*lc*) possibly represents the cephalic division of the main lateral line (cf. p. 29 above).

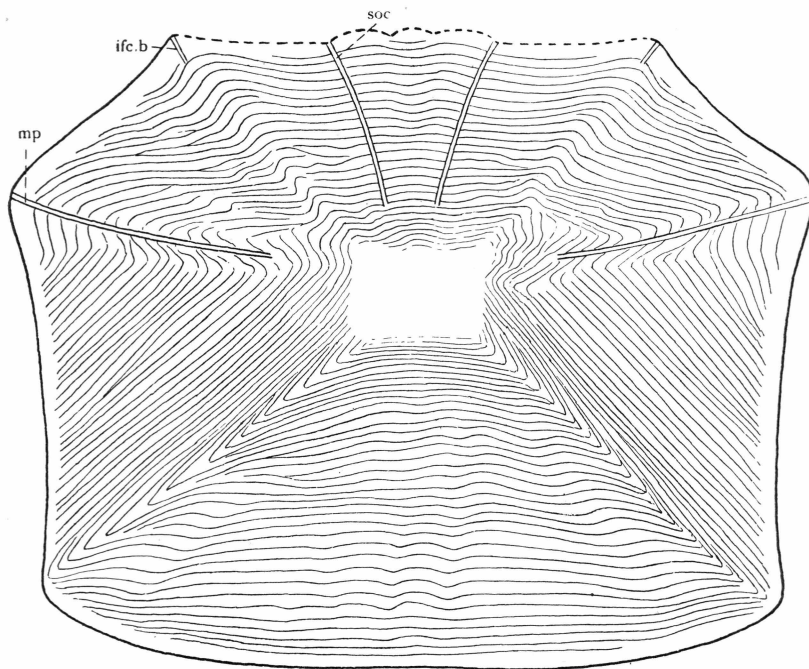
Concerning the marginal plate 4 it should also be mentioned here that this in the material from Orvin's locality (nos. 414, 415; pl. 18, fig. 1) at least in several cases seems to be a little broader in proportion to its length than what is the case in the material from Mt. Sederholm (nos. 436, 437, 440; pl. 5; pl. 7, fig. 1).

The median cephalic plate (text-figs. 20, 21; pls. 2, 3; pl. 4, fig. 3; pl. 6, fig. 2) is of an in the whole similar shape as in *Ph. concentrica* though, at least in several cases, it may perhaps be a little broader in



Text-fig. 19. *Phyllolepis* sp. Restoration of the marginal plate 4. A, in dorsal view. B, in ventral view. Approximately nat. size.
a, zone situated dorsally to and somewhat rigidly attached to the median dorsal plate; *d*, fossa perhaps corresponding to the canal in the Arthrodiros, which probably lodged the ductus endolymphaticus; *ov*, area overlapping at least the posterior part of the marginal 3 and in addition perhaps another plate; *ovd*, area overlapped by the median cephalic plate; *lc*, groove probably representing the cephalic division of the main lateral line.

proportion to its length. On it we may distinguish an anterior unpaired margin, a paired antero-lateral margin, a paired lateral margin and a posterior unpaired margin. The anterior margin, which is fairly long has a short, obtuse, median process, bounded on each side by a shallow emargination. Along this margins lie the marginal plates 1 and at least the main part of the marginal plates 2. The antero-lateral margin which is the shortest of all the margins, seems mostly to be slightly concave. Along it lies the anterior wide part of the marginal plate 3. The lateral

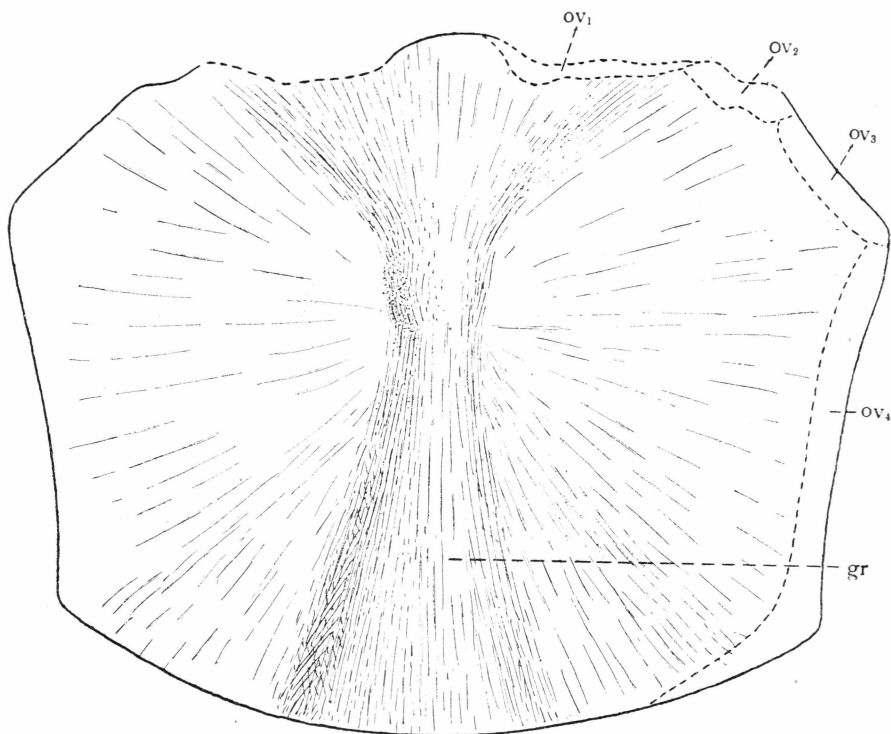


Text-fig. 20. *Phyllolepis* sp. Median cephalic plate in dorsal view. Approximately $\frac{2}{3}$ of the nat. size.

ifc.b, vestigial groove probably representing a part of the postero-medial branch of the infraorbital sensory canal; *mp*, groove, probably representing a part of the middle head-line of fishes; *soc*, groove probably representing a posterior part of the supra-orbital sensory canal.

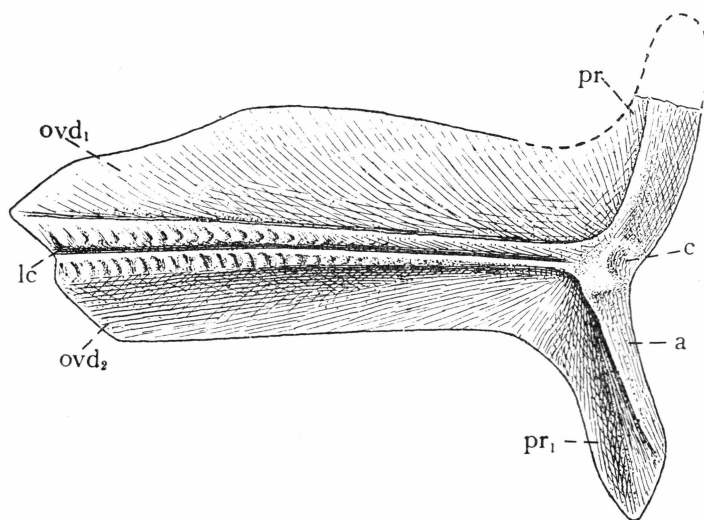
margin, which is fairly long, is always somewhat concave; it abuts against the anterior part of the marginal plate 4. Finally the posterior margin which is the longest of all is always somewhat convex. With its lateral part on each side it meets the posterior part of the marginal plate 4, whereas with its most medial part it is in contact with the median dorsal plate.

As we know from the description of the marginal plates the median cephalic plate overlaps all these, and it is therefore in this respect in the



Text-fig. 21. *Phyllolepis* sp. Median cephalic plate in ventral view. Somewhat diminuted.

gr, median groove; *ov1—ov4*, overlapping areas (imperfectly preserved).



Text-fig. 22. *Phyllolepis* sp. Restoration of the anterior dorso-lateral plate in lateral view. Slightly diminished.

a, anterior face; *c*, low condyle; *lc*, lateral line groove; *ovd1*, dorsal overlapped area; *ovd2*, ventral overlapped area; *pr*, dorsal process; *pr1*, ventral process.

main as the central plates and the median nuchal plate (median basal) of the Arthrodires (cf. HEINTZ 1932a, text-fig. 9). Of its overlapping areas only certain parts are to be seen (ov_1 — ov_4 text-fig. 21; ov , pl. 3) on its lower face along the anterior and antero-lateral margins. On the posterior half of the lower (ventral) face of the bone there is a median shallow groove (gr , text-fig. 21; pl. 3) which is fairly badly defined laterally. This groove is broadest at its posterior and anterior ends. At the latter end it corresponds in breadth approximately to the breadth of the most anterior part of the median longitudinal groove on the lower face of the median dorsal plate. Otherwise the development of the lower face is imperfectly known. The upper (dorsal) face is fairly completely preserved in several of the specimens. It is ornamented with ridges (text-fig. 20; pl. 2; pl. 4, fig. 3; pl. 6, fig. 2) which are in the whole concentric with the anterior, the antero-lateral and the posterior margin. On the other hand laterally there is a triangular area on which the ridges pass from in front and medially backwards and laterally to each lateral margin. A similarly ornamented lateral area is also found both in *Ph. concentrica* (text-figs. 2, 6) and *Ph. undulata* (LERICHE 1931, pl. 1, fig. 1) though in both these species it is not so well developed and less conspicuous. On the upper face of the plate, we find also two well developed paired sensory canal grooves (soc , mp) and vestiges of a third such groove ($ifc.b$, text-fig. 20; pl. 2; pl. 6, fig. 2) situated between the other two on each side. Accordingly there is an anterior, a middle and a posterior sensory canal groove, though the middle one is very imperfectly developed. As has already been mentioned in the general account (pp. 25—29) these grooves most probably represent respectively: a part of the supra-orbital groove of the Arthrodires, a postero-medial branch of the infra-orbital groove of the Arthrodires and the middle head line of pit organs in fishes in general. It is not impossible, however, that the second groove from in front, which is very vestigial, may be a structure *sui generis*: and if this would be so, the most posterior groove would probably correspond to the postero-medial branch of the infraorbital groove in the Arthrodires.

The anterior dorso-lateral plate (text-fig. 22; pl. 7, figs. 2, 3; pl. 8, fig. 3; pl. 17, fig. 1) is represented by three specimens (nos. 419, 433, 441) all of which are more or less imperfectly preserved. It is narrow in proportion to its length, its breadth constituting only approximately one half of the length. The antero-dorsal corner is produced into a fairly strong dorso-medial process (pr) which was situated underneath the anterior lateral part of the median cephalic plate, which is so imperfectly preserved that nothing certain can be said of its length and exact shape otherwise. In a similar way the antero-ventral corner was also produced in a ventral process (pr_1). With regard to its proportions and general

shape the plate resembles the correspondingly termed plate of certain Acanthaspids from the Lower Old Red of Podolia (text-fig. 23) which also is strikingly narrow and much narrower than that in the Arthrodires in general.

At the anterior end of the anterior dorso-lateral plate we find a fairly well developed anterior face (*a*, text-fig. 22; pl. 8, fig. 3) with a low fairly indistinct transverse elevation (*c*) which perhaps may be an articulation condyle in a much reduced stage. If this is so, *Phyllolepis* would of course originally have had a similar articulation between the head and trunk as the Arthrodires¹). The dorsal process of the bone was overlapped by the anterior median dorsal plate throughout its extent. The external face of the bone shows otherwise an overlapped area both along its dorsal (*ovd*₁) and along its ventral margin (*ovd*₂) the former of which is much broader than the latter. The dorsal area was overlapped by the median dorsal plate, the ventral area by the anterior lateral plate or, if this was fused to the cornual plate, by the compound plate thus formed (cf. below the account of the anterior lateral plate). Accordingly we find that the plate agrees with the similarly termed one in the Arthrodires not only in its general shape, but also in the way in which it is overlapped by the adjacent plates dorsally and ventrally to it. The freely exposed part of the external (lateral) face is very narrow, so narrow indeed that it could easily be overlooked if the plate was in its natural position in the armour. As in the Arthrodires this face is crossed in its longitudinal direction by the main lateral line (*lc*), which, is developed as a groove. Dorsally and ventrally to the lateral line groove, the face is ornamented with short transverse (dorsi-ventral) ridges, which may be somewhat curved or undulating. The internal (medial) face which is somewhat concave in a transverse direction, shows along its posterior margin certain indistinct traces of a narrow area (*ov*, pl. 7, fig. 2) which perhaps may be an overlapping area; and if this really is so, this would of course mean that a small, vestigial, posterior dorso-lateral plate was present in the trunk armour. In any case there seems to be some reason to suspect that such a plate might have been present.

The anterior lateral plate is not known thus far. At any rate it cannot be identified among the material at hand.

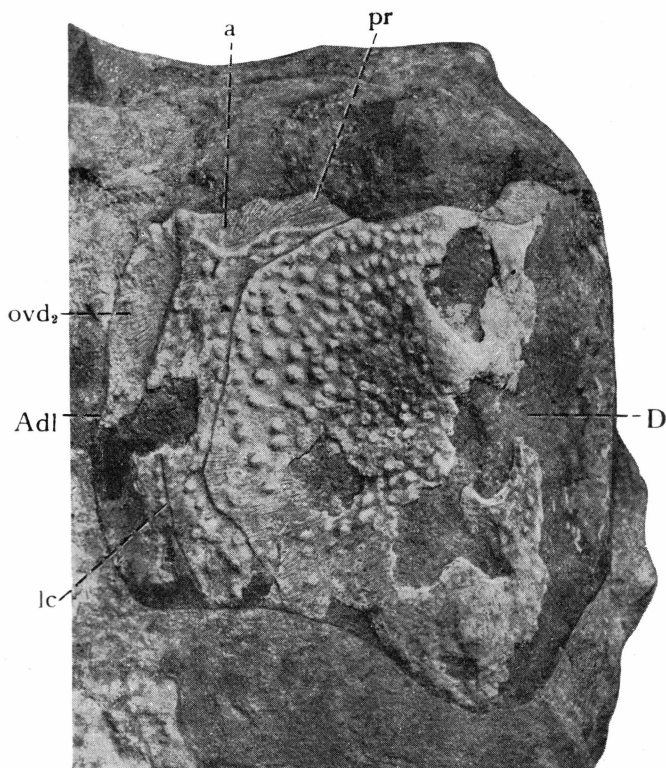
Any plate comparable to the spinal (or cornual) of *Ph. concentrica* is not known, since the plate described as such by HEINTZ (1932b, pl. 1, fig. 2; pl. 2, fig. 1) as we shall see is an anterior ventro-lateral plate.

The ventral wall of the trunk-carapace is still imperfectly known.

¹) In this connection it should be mentioned that the articulation between the head and the trunk-armour is much or entirely reduced in the Acanthaspids from Podolia (according to kind information from Dr. BROTZEN, who is describing these forms).

The most complete specimen of it found preserved hitherto (text-fig. 24, pl. 12) displays well the anterior and posterior ventro-lateral plates of both sides in their natural position in relation to each other (no. 421). The intero-lateral plates and the median ventral plates are not represented in the material available.

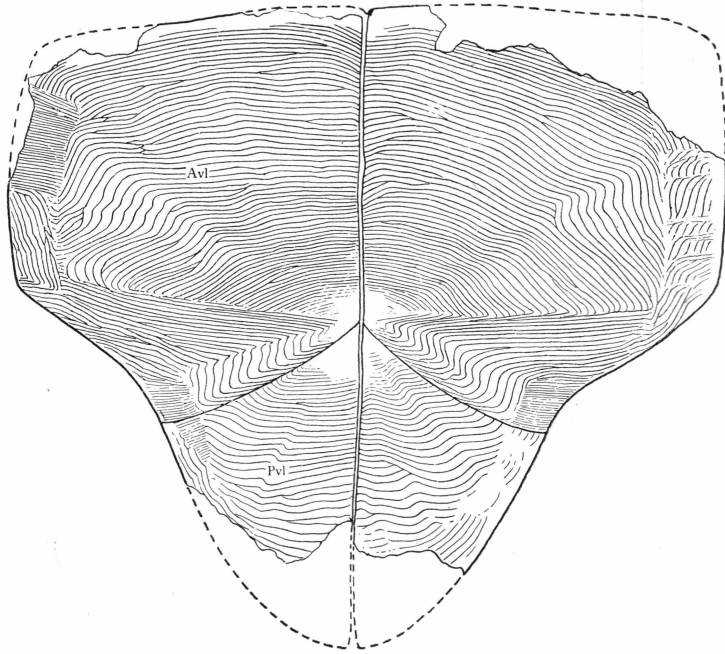
The anterior ventro-lateral plate (*Avl*, text-figs. 24, 25; pl. 6, fig. 1; pl. 12; pl. 13, fig. 2; pls. 14, 15) is very large, measuring from approx-



Text-fig. 23. Acanthaspid from the Lower Old of Podolia. Anterior dorso-lateral plate, in its natural connection with the median dorsal plate. Approximately $\times 2$ diam. *Adl*, anterior dorso-lateral plate; *D*, median dorsal plate; *a*, anterior face; *lc*, main lateral line (groove); *ovd₂*, ventral overlapped area; *pr*, dorsal process.

imately 13.5—16.5 cm in breadth and from approximately 15—18 cm in length. It is broadest in its anterior two thirds in which its breadth is fairly uniform, then in its posterior third rapidly decreasing in breadth as far as to its posterior end at which its breadth is only approximately one half of the maximum breadth. The anterior margin which is long, seems to be fairly straight; the medial margin which is approximately as long as the anterior one, has at least on the plate of the left side a

low medial process (text-fig. 25; pl. 15); the lateral margin, which is the longest of all, is in its anterior two thirds somewhat convex or fairly straight, in the posterior third concave; finally the posterior margin, which is the shortest one, is straight and directed not only posteriorly but also somewhat medially. The bone is slightly bent in such a way that it is a little concave in a transverse direction on the dorsal (internal) face and correspondingly convex on the ventral (external) face. In addition the posterior narrower part lies not in the same level with the anterior



Text-fig. 24. *Phyllolepis* sp. Preserved parts of the ventral wall of the trunk carapace. Ventral view. Approximately one fourth of the nat. size.

Avl, anterior ventro-lateral plate; *Pvl*, posterior ventro-lateral plate.

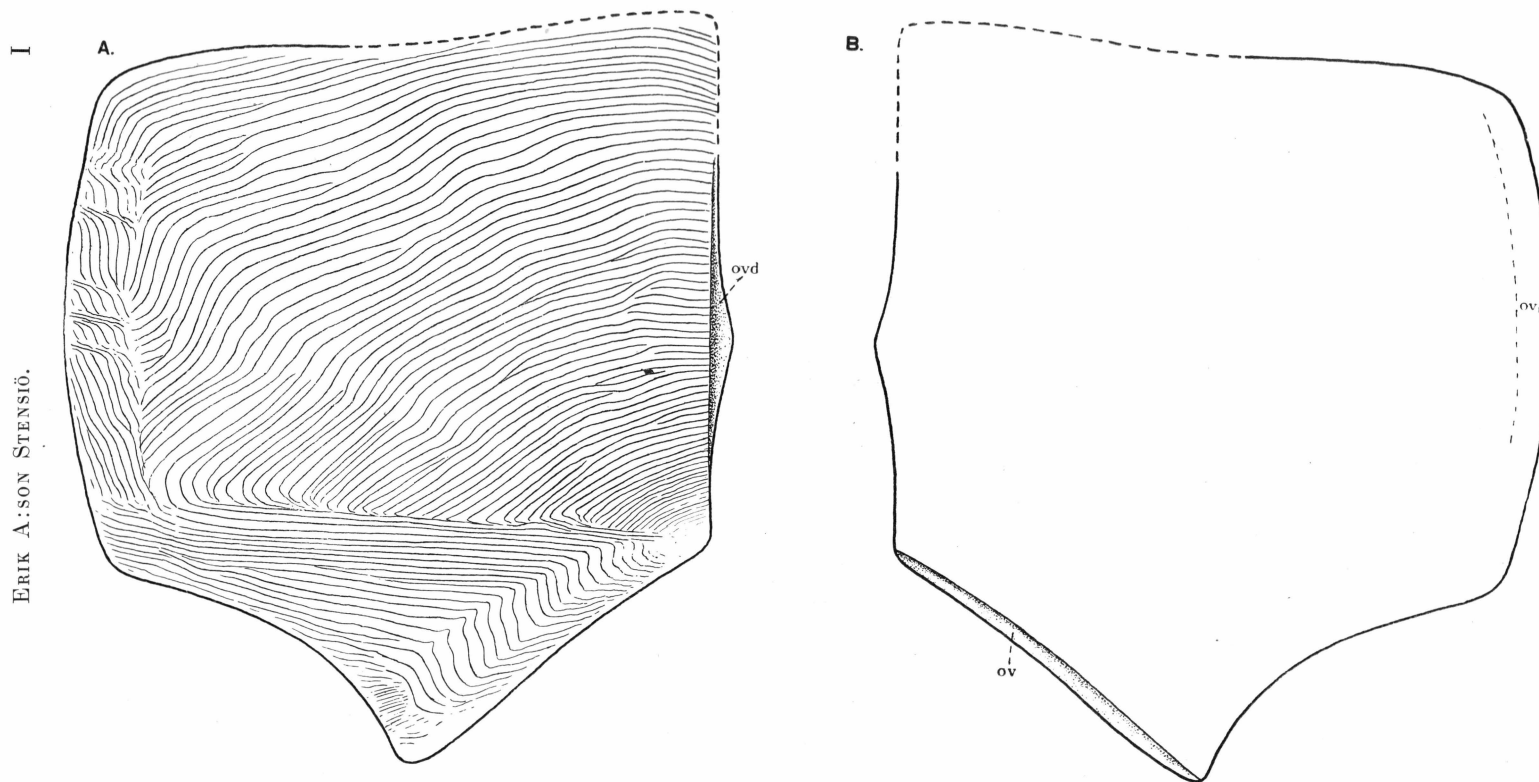
broader part, but somewhat higher than this. The plate of the left side bears along its medial margin a narrow overlapped area (*ovd*, text-fig. 25; pl. 14) which shows that this plate was to a certain extent overlapped by its fellow of the right side; and accordingly we find here that the anterior ventro-lateral plates at least to a certain extent overlapped each other in a similar way as the corresponding plates in the *Antiarchi* (STENSIÖ 1931, p. 102). Along the posterior margin there is a narrow but very distinct area (*ov*, text-fig. 25; pl. 15) for the overlapping of the posterior ventro-lateral plate. Possibly narrow but very slightly developed overlapping areas are present also along the anterior two thirds of the lateral margin of the plate, but the remains of these possible

areas are very obscure (*ov*, pl. 15). If there really was an overlapping area here, this would mean that the ventral wall of the trunk-armour was at least somewhat firmly attached to the lateral and dorsal parts of this armour. On the other hand if I am mistaken in this case, if there was no overlapping area along the lateral margin, the ventral wall of the trunk-armour would of course have been without any firm connection with the other parts of the trunk-armour, for, as we shall see, the posterior ventral plate was certainly not in any direct contact with these.

The ornament of the anterior ventro-lateral plate is characteristic (text-fig. 25; pl. 6, fig. 1; pl. 12; pl. 13, fig. 2; pl. 14). On the anterior two thirds of the plate it consists of ridges which are transverse in the main, but which laterally curve somewhat backwards. In certain cases these transverse ridges are present to the very anterior and lateral margins, in other cases there is a distinct marginal zone along the anterior margin and the anterior two thirds of the lateral margins on which the ridges are concentric with the said margins. In the first mentioned cases we find often between the lateral parts of the long ridges other shorter ones which cross only a lateral part of the plate along the very lateral margin, the total number of ridges close to the lateral margin thus being much greater than more medially. On the posterior third of the ventral (external) face the ridges are arranged in such a way as to pass from in front and laterally in a backward and medial direction. On this third they may also be curved so as to meet the posterior margin at an almost right angle. The other characters of the ornamentation are well shown in the figures quoted, and therefore I do not enter upon them more in detail here.

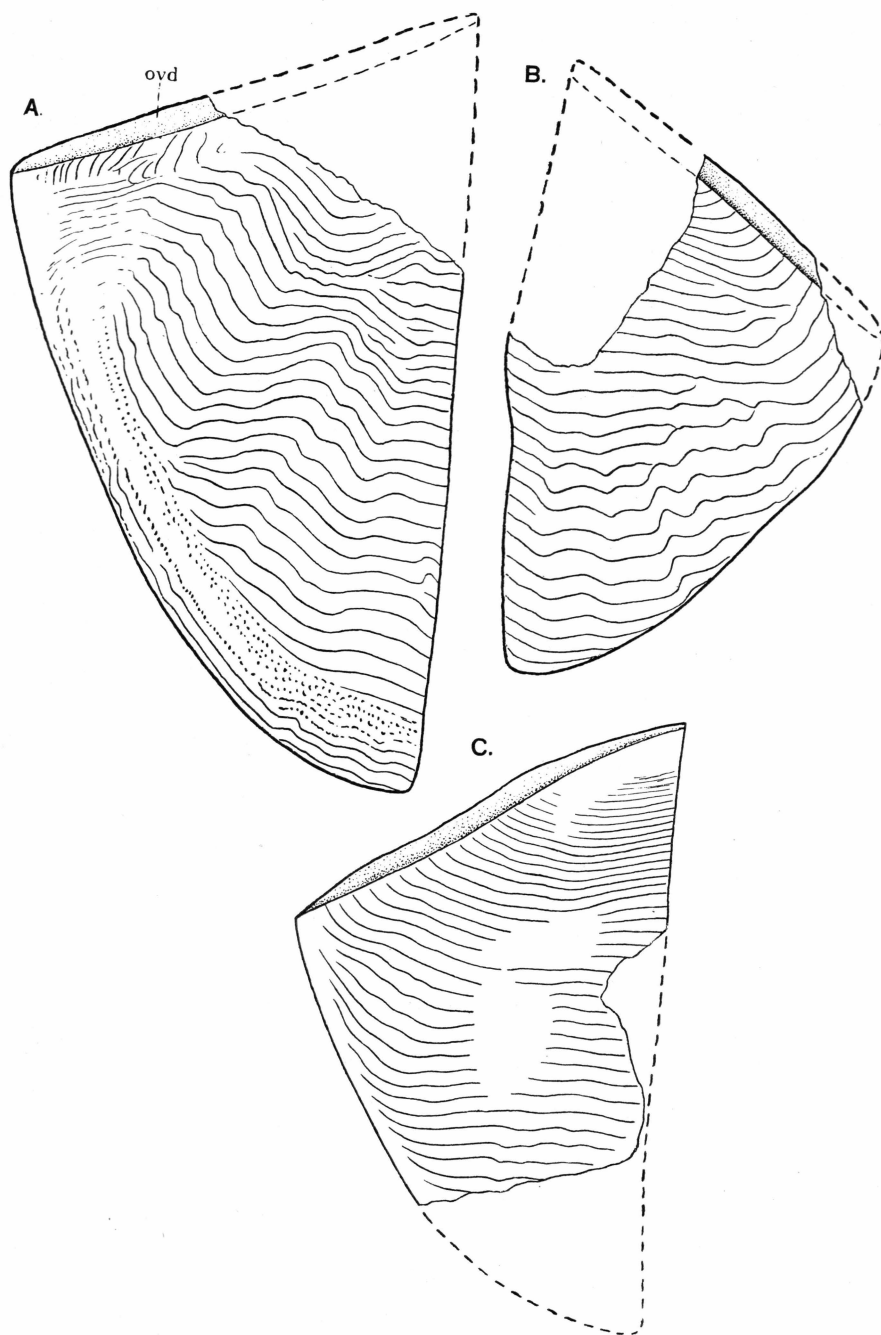
The plate described by LERICHE 1931 (pl. 2, figs. 1—3) and by HEINTZ (1932b, text-fig. 5; pl. 1, fig. 2; pl. 2, fig. 1) as a cornual plate agrees so completely with the plate just dealt with above under the term of anterior ventro-lateral plate, that it cannot be doubted that it is such a plate. And accordingly a real spinal (cornual) plate is at present unknown not only in *Ph. undulata* but also in the Greenland species.

The posterior ventro-lateral plate (*Pvl*, text-figs. 24, 26; pl. 12, 15; pl. 16, fig. 2; pl. 17, figs. 1, 2) is not by far as large as the anterior ventral plate. Roughly taken it is of a triangular shape with one margin directed latero-anteriorly, one margin laterally and one margin medially. The latero-anterior margin, which is the shortest one, is practically straight, and so is also the medial margin, which is the longest of the three, whereas the lateral one is fairly much convex. As a whole the plate is curved in such a way that the ventral (external) face is somewhat convex in a transverse direction and the dorsal (internal) face correspondingly



Text-fig. 25. *Phyllolepis* sp. Anterior ventro-lateral plate. A, in external (ventral), B, in internal (dorsal) view. Restoration after the specimens figured in pls. 14, 15 (no. 454). Approximately $\frac{2}{3}$ of the nat. size.

ov, area overlapping the posterior ventro-lateral plate; *ov₁*, area probably overlapping a lateral part of the lateral wall of the trunk armour; *ovd*, area overlapped by the right anterior ventro-lateral plate. This area has been drawn here by a mistake: it should be on the corresponding plate of the left side only.



Text-fig. 26. *Phyllolepis* sp. Posterior ventro-lateral plate. A, a specimen from Orvin's locality at Cape Graah (the specimen figured in pl. 16, fig. 2 no. 420); B, a second specimen from Orvin's locality at Cape Graah (the specimen figured in pl. 17, fig. 1; no. 419); C, a specimen from the N. side of Mt. Sederholm (the specimen figured in pl. 17, fig. 2; no. 454b). Somewhat diminished. *ovd*, area overlapped by the anterior ventro-lateral plate.

concave in the same direction. Along the latero-anterior margins there is a narrow area (*ovd*) which was overlapped by the anterior ventral plate. Otherwise neither any overlapped nor any overlapping areas seem to be present on the plate. The ornament consists of undulating ridges which are disposed so as to pass from in front and laterally in a medial and backward direction. In certain of the specimens there is a zone along the lateral margin with ridges somewhat concentric with that margin or with a few such ridges and tubercles, in other specimens this marginal zone is entirely absent. In regard to the ornament the plate under consideration is thus among the material represented by two types, both of which are met with not only at Orvin's locality at Cape Graah, but also at Mt. Sederholm. As it is strikingly flat and as it has no lateral lamina which ascends from it the posterior ventro-lateral plate did not extend upwards on to the lateral face of the trunk, but is entirely confined to the ventral face of this.

Of the plates the position of which in the armour is still uncertain only two are so well preserved that a description of them is worth while. One of these plates is shown in pl. 1, fig. 1, and pl. 8, fig. 1; the other in pl. 17, fig. 3. The first-mentioned one is four-sided and has along one of its margin a distinct overlapped area (*ovd*). Whether in addition it was provided with any overlapping area cannot be decided. Its characters otherwise are well displayed by the figures. The other plate which possibly is only a fragment of a larger plate and which bears strong spine-like tubercles may perhaps be a part of a spinal plate.

Remarks. Any certain determination of the plates described here as to species is at present impossible, but it is highly probable that they belong to both *Ph. orvini* and *Ph. söderbergi*.

Geological horizon and localities. — The *Phyllolepis* sandstone series. Orvin's locality at Cape Graah; S. side of Mt. Sederholm (opposite Mt. Carbon Circus; at the Profile Ravine in the Parallel valley; the bottom of the Parallel valley near the coast); N. side of Mt. Sederholm (the Vasti valley N. of the Circus valley).

Order **Arthrodira.**

Genus **Groenlandaspis** HEINTZ.

This genus, which was erected by HEINTZ in 1932 (1932b, pp. 18—24) is still very imperfectly known, nothing new material of any importance referable to it being discovered by the Danish East Greenland expeditions. I have therefore nothing to add to the diagnosis given by HEINTZ (1932b, p. 24) but simply quote this: "... Ziemlich grosse Form. Die Plattengrenzen des im hinteren Teile ausgebuchteten Kopfpanzers sind schwer zu finden. Die MB (nuchal plates) — schmal, long, schwach ver-

dict. Die EB (paranuchals) — gross, mit grosser Fossa condyli und zwei verdichten Leisten. Der Abstand zwischen den Fossae relativ klein”.

“Der Rumpfpanzer besteht aus ganz isolierten¹⁾ Platten. Die MD (median dorsal) sehr schmal und lang mit schwachem medianem Kiel. Die ADL (anterior dorso-laterals) mit kräftig ausgebildeten Kondyli, ohne ausgeprägten, verdichten Leisten. Die AL (anterior laterals) ungewöhnlich gross und bildet allein den Kontakt zwischen dem Rücken- und Bauchpanzer. Die IL (intero-laterals) auch kräftig ausgebildet, besonders im oberen Teil. Keine Spuren von einer Spinalen bekannt. Bauchpanzer flach und gross.”

Only a single species *G. mirabilis* HEINTZ is known thus far of the genus.

Groenlandaspis mirabilis? HEINTZ.

(Pl. 8; fig. 4).

Material. — To this species only a single fragmentarily preserved plate (no. 580) may be referred with certainty.

Description. — The plate just mentioned (pl. 8, fig. 4) shows traces of an overlapped area on one side. Its ornament consists of numerous, fairly closely set tubercles, which are low, obtuse and pretty rounded. The microscopic structure of these tubercles could not be studied in a thin section, but from their appearance, when the plate was submerged into xylol or oil of aniseed, it is likely that in their most distal parts they consist of a dentine-like tissue.

Remarks. — Any certain determination as to species of the plate here under description is of course impossible. That I have provisionally referred it to *G. mirabilis* is due to the circumstance that in regard to its ornament it shows a certain at least superficial agreement with that species (cf. HEINTZ 1932b, pl. 5, figs. 1, 2, 5; pl. 6, fig. 1).

Geological horizon and locality. — The Arthrodire-Sandstone Series. E. side of Mt. Stensiö.

¹⁾ By this expression HEINTZ probably means that the plates are not fused, but independent and united with each other by distinct sutures.

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EXPLANATION OF PLATES

Only Ilford special rapid panchromatic plates have been used. The macro-photos have been taken with Zeiss Tessar objectives F. 36 cm. 1:6.3 and F. 25 cm 1:6.3. As a rule the Ilford gamma filter gave the most satisfactory results.

All the specimens figured belong to the Geol. Survey of Greenland (G.G.U.), Copenhagen.

Plate 1.

Phyllolepis spp.

- Fig. 1. Plate the position of which cannot be ascertained. Impression of the external side. Specimen no. 442. Nat. size.
- Fig. 2. Marginal plate 1 and a fragment of marginal plate 2 of the left side. Impression of the external side. Specimen no. 424b. Nat. size.
- Fig. 3. Marginal plate 1, imperfectly preserved. Cast of an impression of the exposed area. Specimen no. 401. Nat. size.
- Figs. 4, 5. Marginal plate 1 of the right side in two stages of etching. In fig. 2 almost all the bone tissue has been removed so as to show the impression of the outer face. Specimen no. 429. Nat. size.
- Fig. 6. Marginal plate 3 of the left side. Cast of an impression of the external face. Specimen no. 408. Nat. size.

Explanation of letters.

M_1 , marginal plate 1; M_2 , marginal plate 2; *ifc.b*, sensory groove, probably representing the postero-medial branch of the infraorbital groove of the Arthroires; *mp*, sensory groove, representing a part probably of the middle head-line of pit organs in fishes in general; *ovd*, *ovd*₁, *ovd*₂ overlapped areas; *soc*, supraorbital sensory groove.

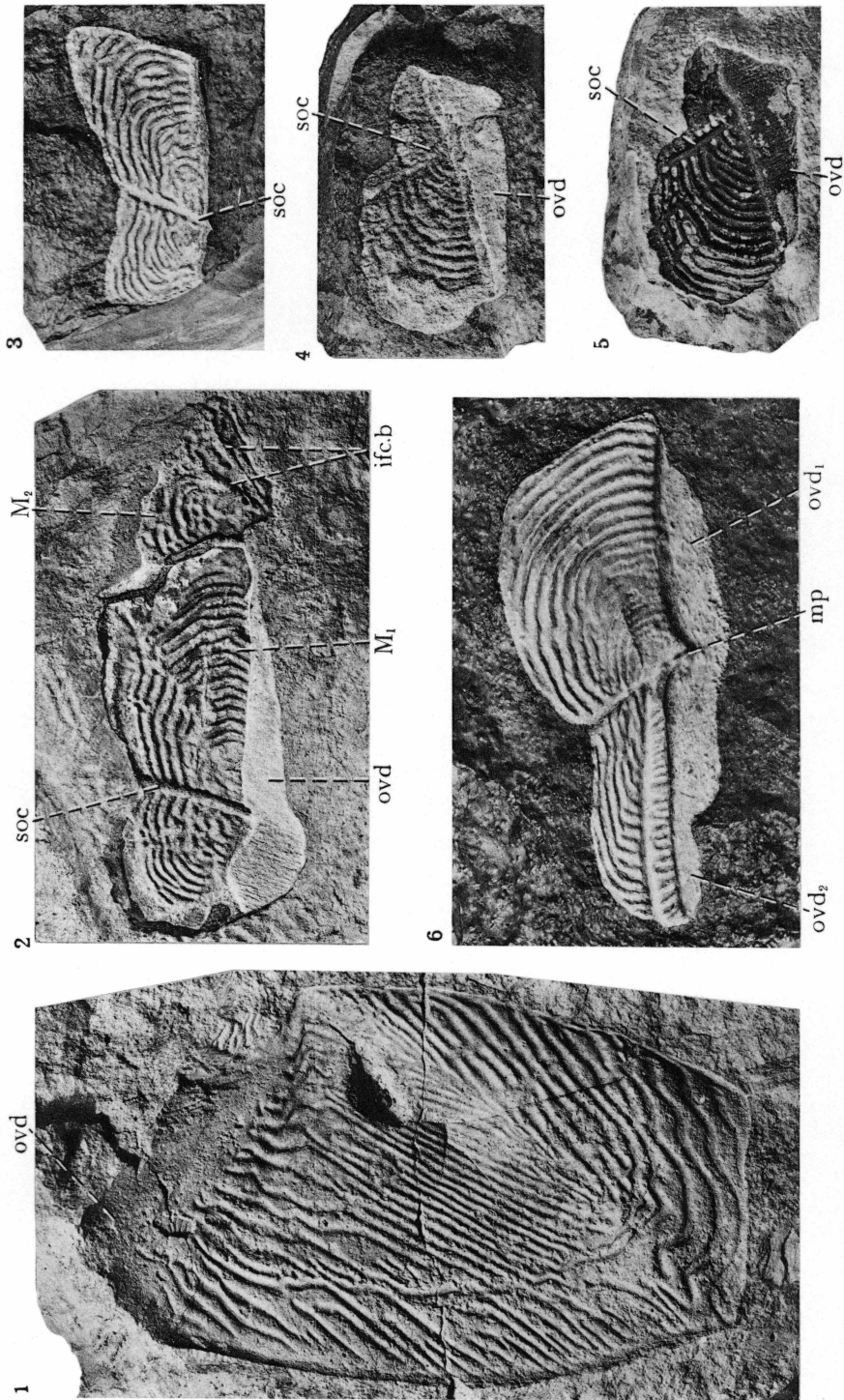


Plate 2.

Phyllolepis sp.

Median cephalic plate and parts of marginal plate 1 of the left side, preserved mainly as impressions of the external sides. Specimen no. 431a. Nat. size.

Explanation of letters.

Cn, median cephalic plate; *M*₁, marginal plate 1; *ifc.b*, vestiges of the sensory groove which probably represents the postero-medial branch of the infraorbital groove in the Arthroires; *mp*, sensory groove, representing a part probably of the middle head-line of pit-organs in fishes in general; *soc*, supra-orbital sensory groove.

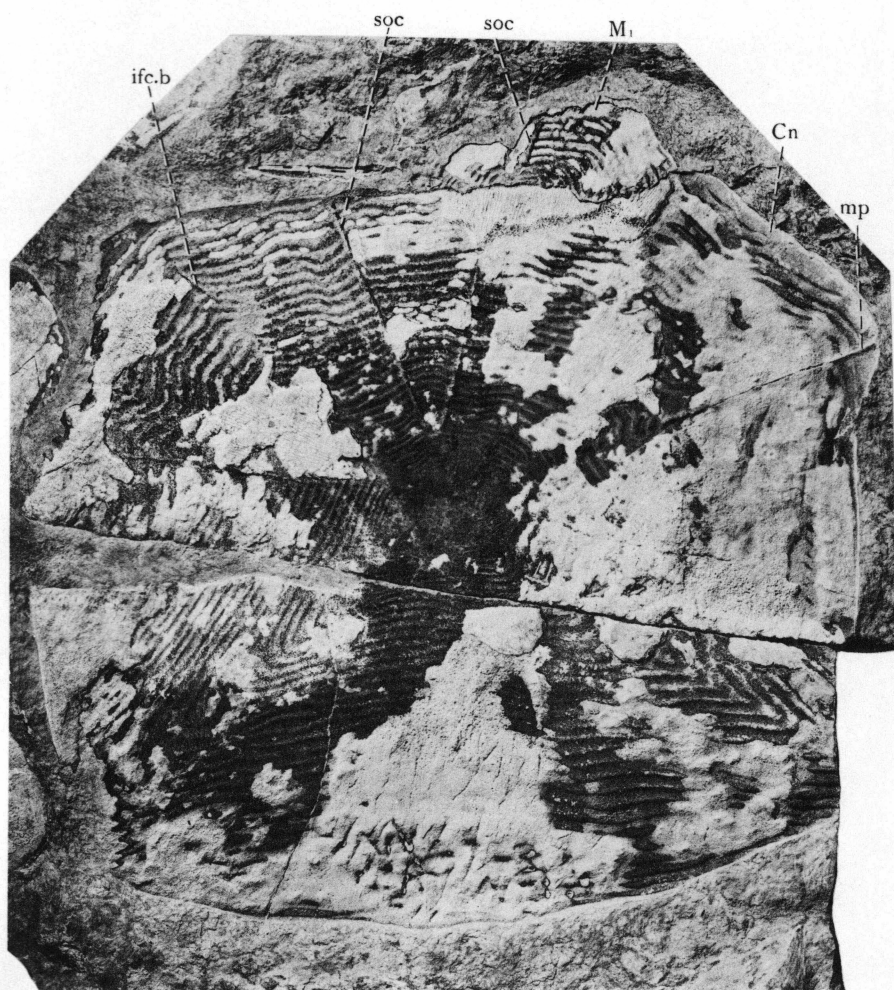


Plate 3.

Phyllolepis sp.

Median cephalic plate, preserved mainly as impression of the lower (internal) face.
Specimen no. 459. Nat. size.

Explanation of letters.

gr, median groove; *ov*, overlapping areas.



Plate 4.

Phyllolepis sp.

- Fig. 1. A fragmentary marginal plate 3 of the left side preserved mainly as impression of the external face. Specimen no. 454b. Nat. size.
- Fig. 2. A fragmentary marginal plate 3, preserved as impression of the external face. Specimen no. 410. Nat. size.
- Fig. 3. An imperfect median cephalic plate seen from the dorsal (external) face. Specimen no. 409b. Nat. size.

Explanation of letters.

mp, part of a sensory groove, probably corresponding to the middle head-line of pit organs in fishes in general; *ovd*₁, *ovd*₂, overlapped areas; *soc*, supraorbital sensory groove.

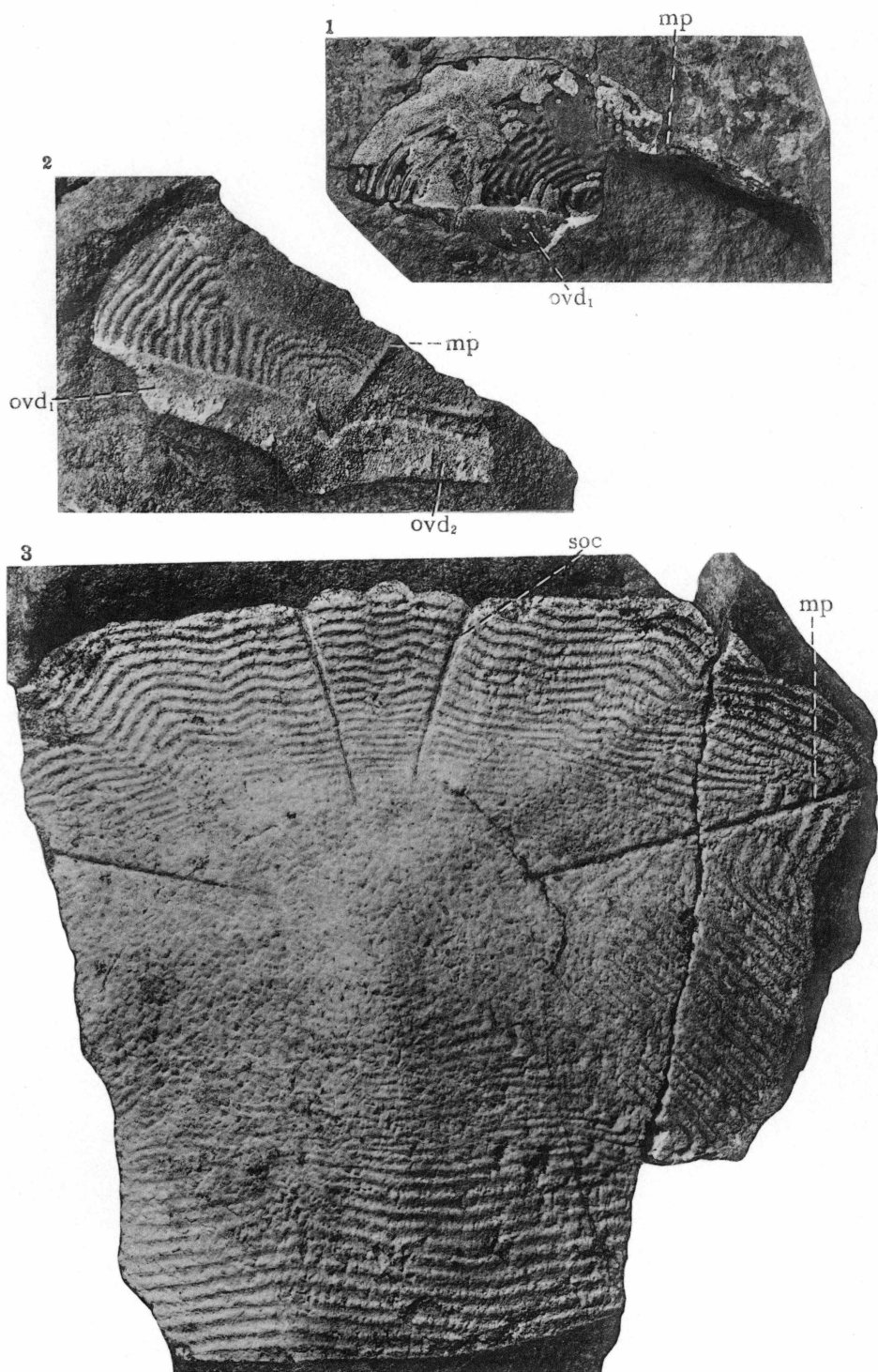


Plate 5.

Phyllolepis sp.

- Fig. 1. Somewhat imperfect marginal plate 4 from the left side. Impression of the external face. Specimen no. 460. Nat. size.
- Fig. 2. Somewhat imperfect marginal plate 4 from the left side. Impression of the external face. Specimen no. 440. Nat. size.
- Fig. 3. Same marginal plate as in fig. 2. Impression of the internal (ventral) face. Specimen no. 440. Nat. size.

Explanation of letters.

d, pit conceivably for the ductus endolymphaticus; *lc*, sensory groove probably representing a part of the cephalic division of the main lateral line; *ov*, overlapping area; *ovd*, overlapped area.

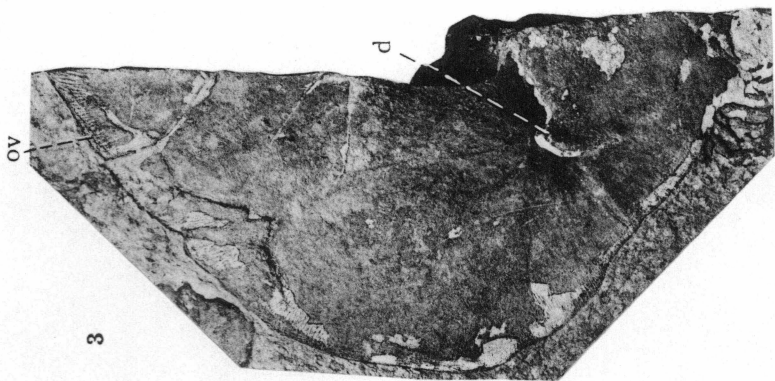
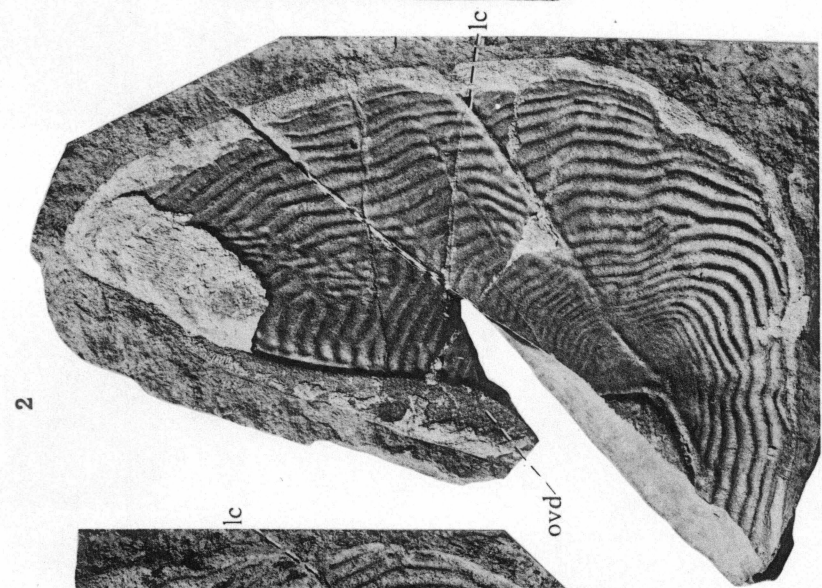
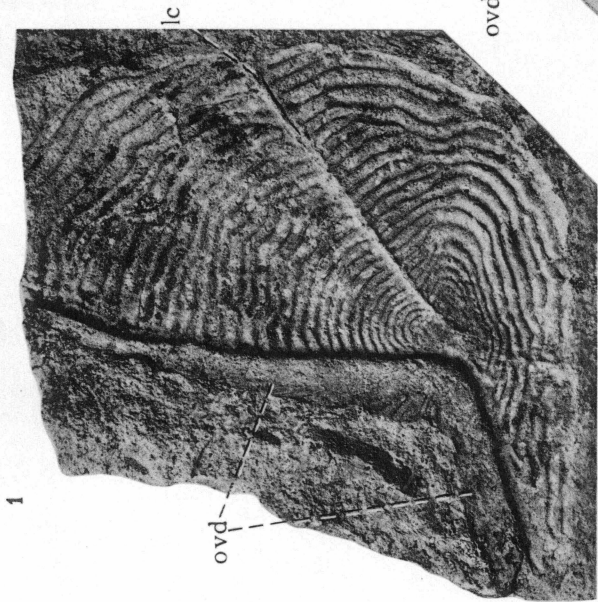


Plate 6.

Phyllolepis sp.

- Fig. 1. Anterior part of a left anterior ventro-lateral plate in external view. Cast of an impression. Specimen no. 415. Approximately $\frac{2}{3}$ of the nat. size.
- Fig. 2. Imperfect median cephalic plate in external view. Cast of an impression. Specimen no. 415. Approximately $\frac{2}{3}$ of the nat. size.

Explanation of letters.

ifc.b, sensory groove, probably representing a part of the postero-medial branch of the infraorbital groove of the Arthrodiros; *mp*, sensory groove probably representing the middle head-line of fishes in general.

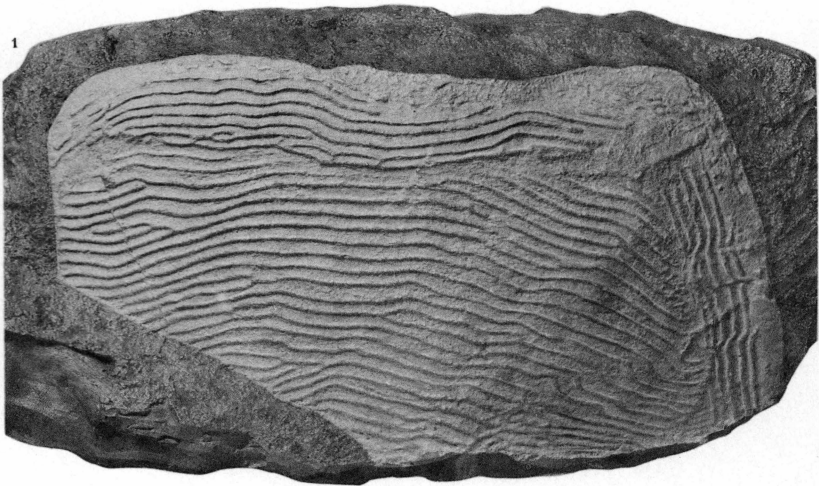


Plate 7.

Phyllolepis sp.

Fig. 1. Imperfect marginal plate 4 of the right side. Impression of the external face. Specimen no. 436. Nat. size.

Figs. 2, 3. Imperfect anterior dorso-lateral plate in counterpart. Fig. 2 shows parts of the medial face, preserved as impressions. Fig. 3 shows parts of the lateral (external) face preserved as impressions. Specimen no. 441. Nat. size.

Explanation of letters.

lc, sensory groove probably representing a part of the cephalic division of the main lateral line; *lc*₁, main lateral line; *ov*, overlapping area; *ovd*, *ovd*₂ overlapped areas; *pr*, dorsal process of the anterior dorso-lateral plate.

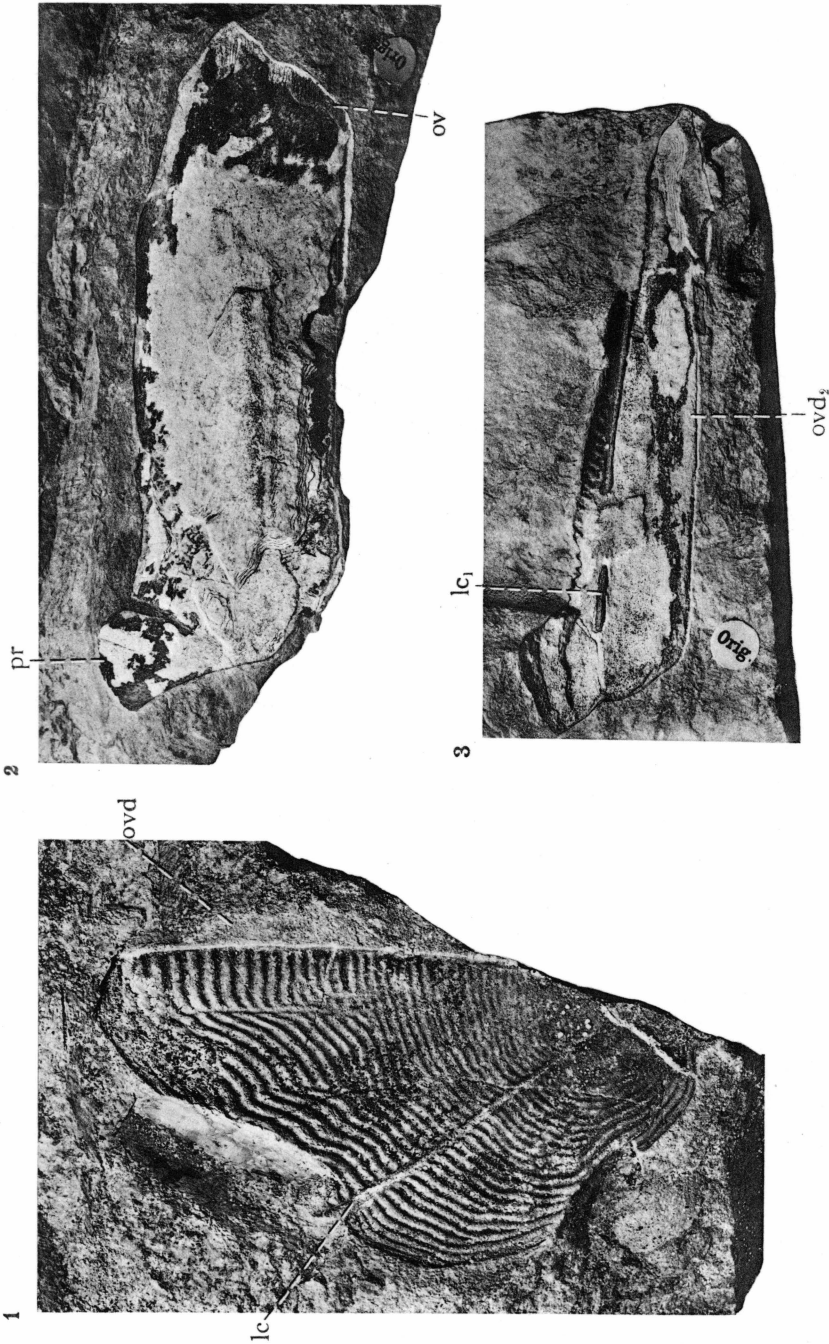


Plate 8.

- Fig. 1. *Phyllolepis* sp. Plate the position of which is still unknown. Preserved mainly as impression of the external face. Specimen no. 439. Nat. size.
- Fig. 2. *Phyllolepis* sp. Almost complete marginal plate 2 of the left side. Impression of the external face. Specimen no. 427. Nat. size.
- Fig. 3. *Phyllolepis* sp. Anterior dorso-lateral plate of the left side preserved as impression of the external and anterior faces. A posterior part missing. Specimen no. 433. Nat. size.
- Fig. 4. *Groenlandaspis mirabilis?* HEINTZ. Fragmentary plate. Specimen no. 580. Nat. size.

Explanation of letters.

a, anterior face of the anterior dorso-lateral plate; *c*, elevation, perhaps representing a vestigial articulation trochlea; *ifc.b*, sensory groove, perhaps representing a part of the postero-medial branch of the infraorbital groove of the Arthrodiros; *lc*, main lateral line; *ovd*, *ovd*₁, *ovd*₂ overlapped areas; *pr*₁, ventral process.

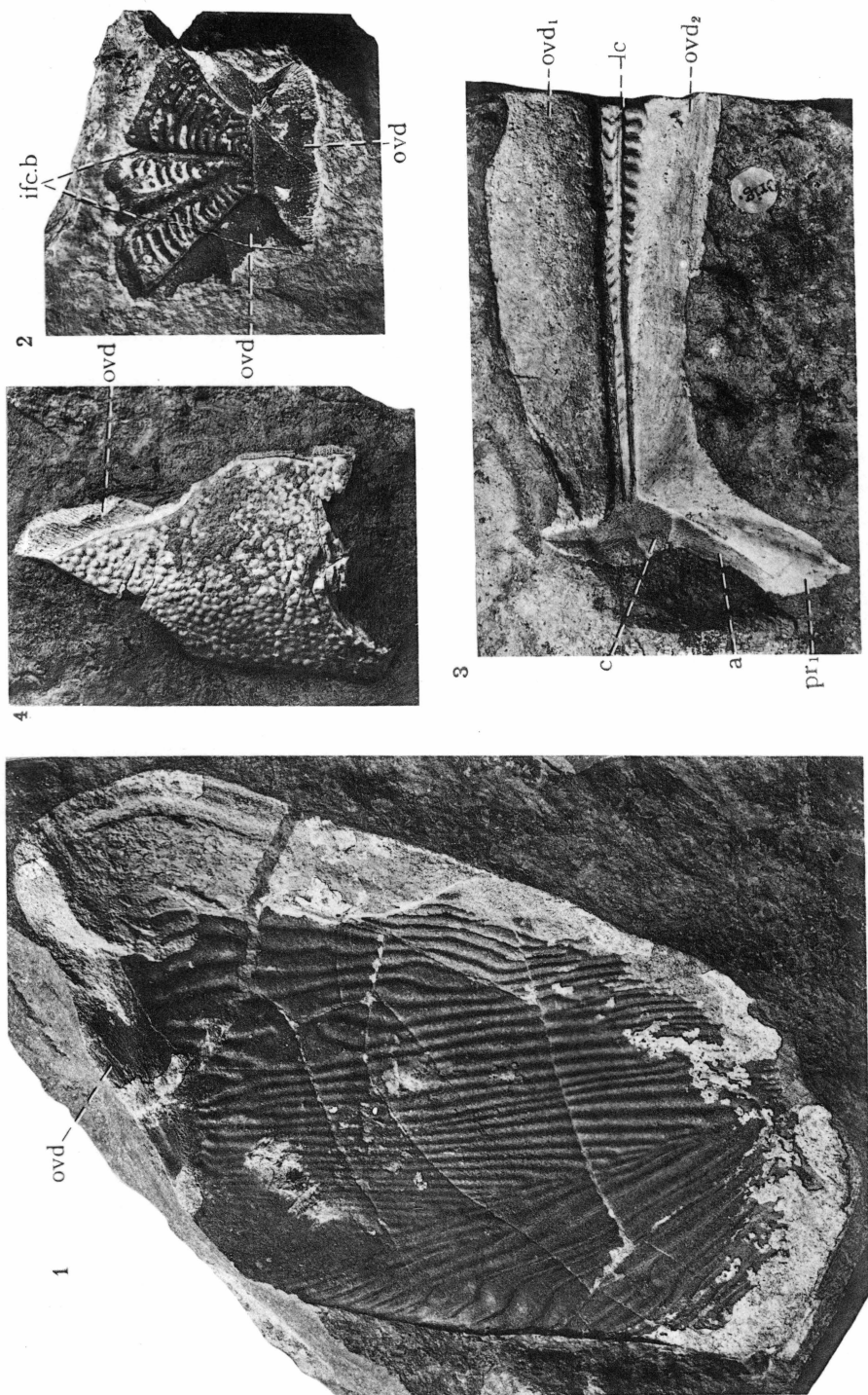


Plate 9.

Phyllolepis söderberghi n. sp.

Median dorsal plate, showing in places impressions of the external face. Specimen no. 427 (same as in pl. 10). Somewhat more than one half of the nat. size.

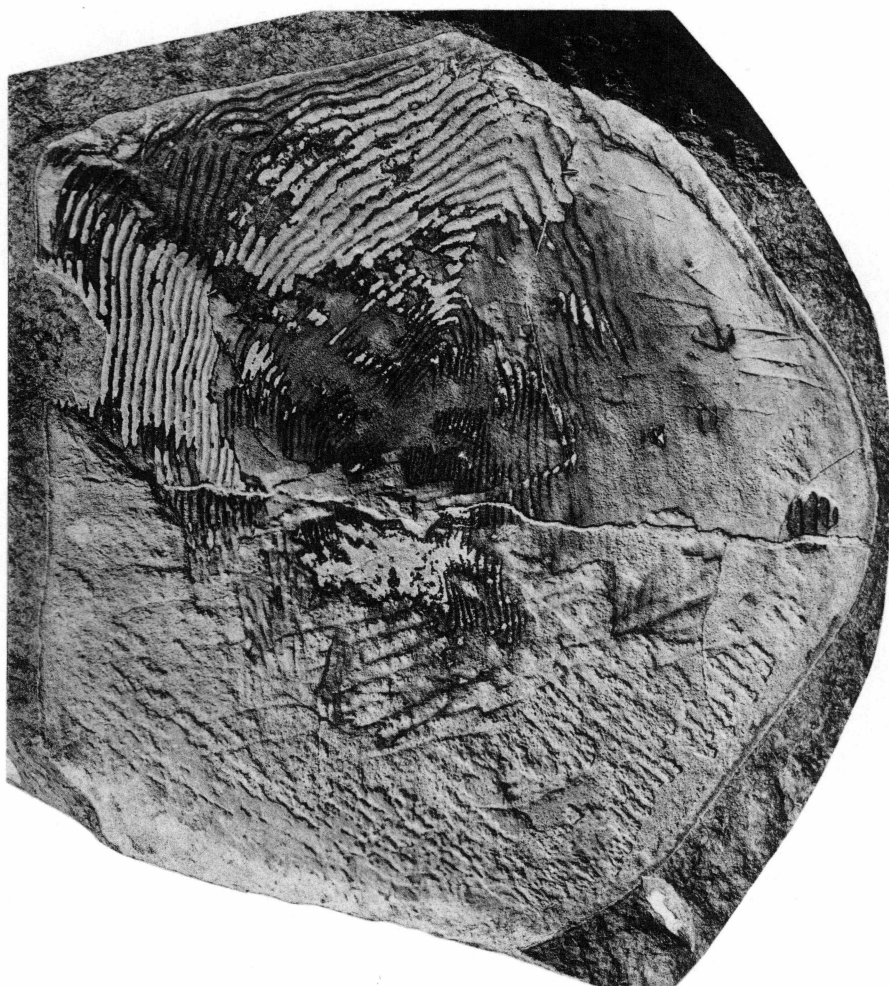


Plate 10.

Phyllolepis söderberghi n. sp.

Median dorsal plate. Impression of the ventral face. Counterpart of the specimen in pl. 9 (no. 427). Somewhat more than one half of the nat. size.

Explanation of letters.

f.retr, levator fossa; *grm*, median longitudinal groove; *ov*, *ov*₁, area overlapping the anterior dorso-lateral plate; *r*, ridge bounding the median longitudinal groove; *rl*, ridge bounding the levator fossa.

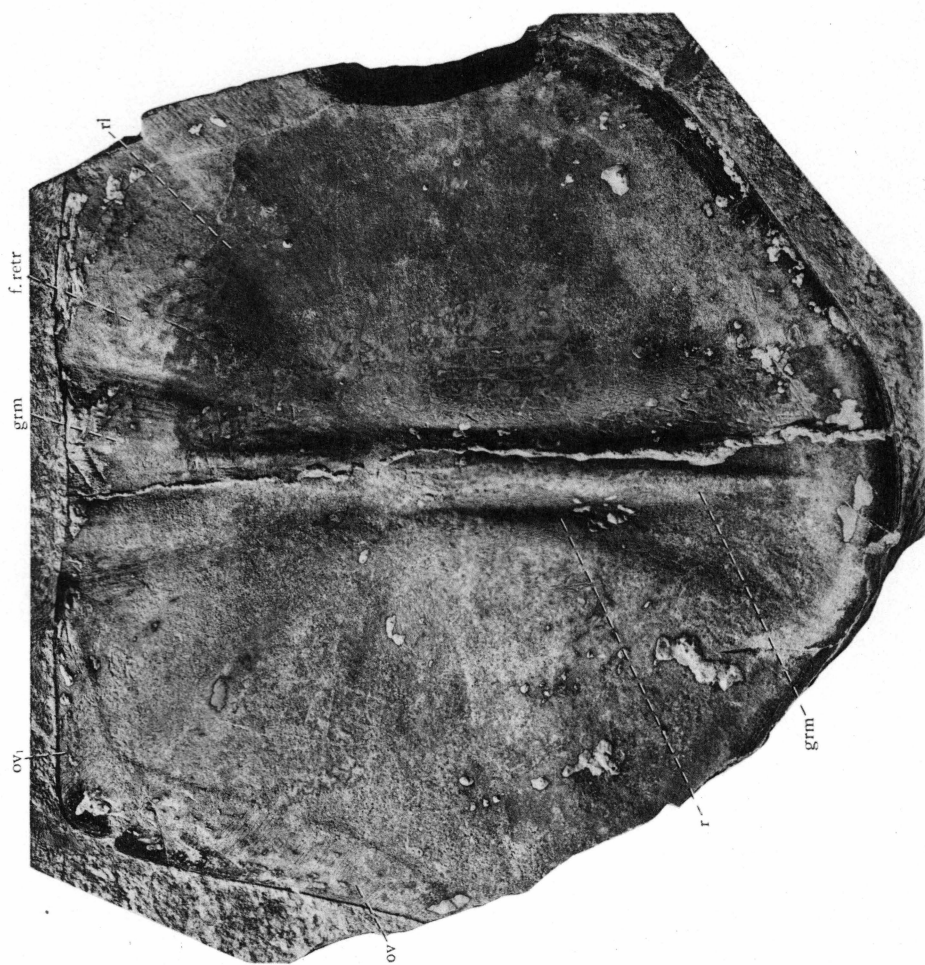


Plate 11.

Phyllolepis söderberghi n. sp.

Figs. 1, 2. Median dorsal plate in counterpart. Fig. 1 showing the dorsal and fig. 2 the ventral face. Specimen no. 431. Nat. size.

For explanation of letters see pl. 10.

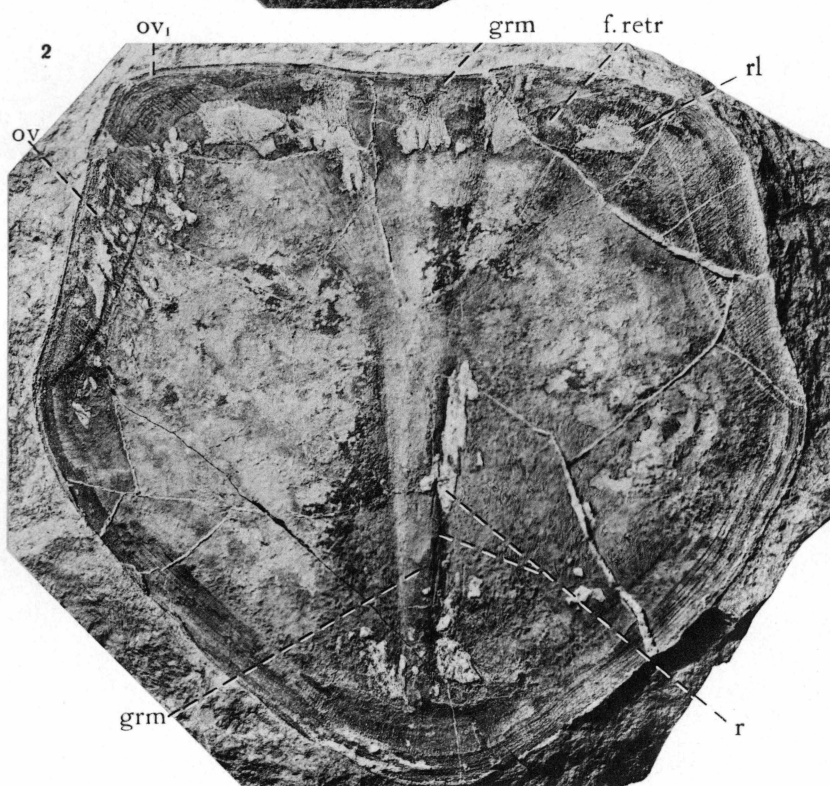


Plate 12.

Phyllolepis sp.

Part of the ventral wall of the trunk armour showing the anterior and posterior ventro-lateral plates in their natural position in relation to each other. Ventral view. Cast from an impression which could not be removed from the rock at the find locality (Cape Graah). Specimen no. 421. Somewhat more than one third of the nat. size.

Explanation of letters.

Avl, anterior ventro-lateral plate; *Pvl*, posterior ventro-lateral plate.

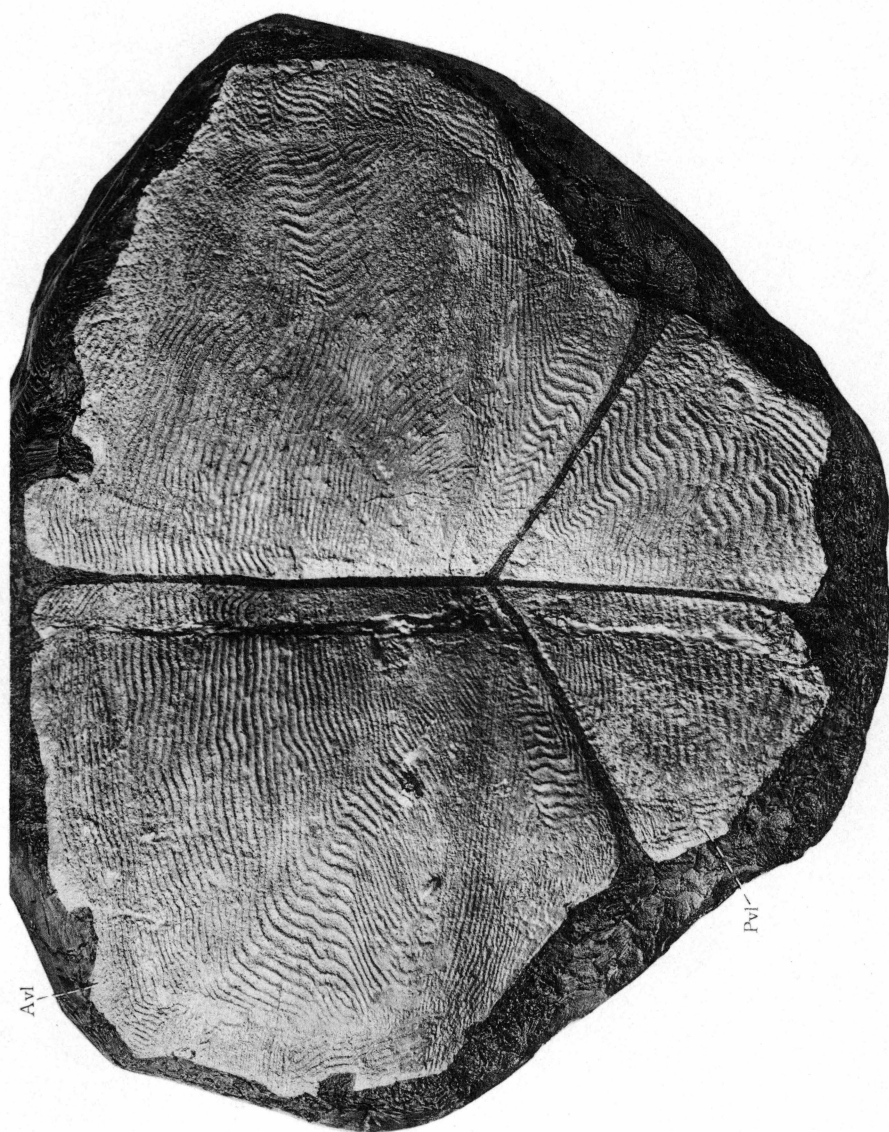


Plate 13.

Phyllolepis sp.

- Fig. 1. Fragmentary marginal plate 2 of the right side. Impression of the external face. Specimen no. 400. Nat. size.
- Fig. 2. Imperfect anterior ventro-lateral plate of the left side preserved mainly as impression of the ventral (external) face. Specimen no. 424. Nat. size.

Explanation of letters.

ifc.b, sensory canal grooves, probably represents a part of the postero-medial branch of the infraorbital groove of the Arthrodire; *ovd*, overlapped areas.

2

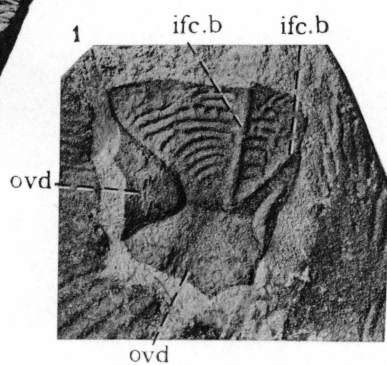


Plate 14.

Phyllolepis sp.

Anterior ventro-lateral plate of the left side, preserved mainly as impression of the external (ventral) face. Specimen no. 454 (same as in pl. 15). Nat. size.

For explanation of letters see pl. 15.



Plate 15.

Phyllolepis sp.

Anterior ventro-lateral plate (*Avl*) and posterior ventro-lateral plate (*Pvl*) of the left side, preserved as impression of the dorsal (internal) face. The anterior ventro-lateral plate is counterpart of the plate shown in pl. 14 (specimen no. 454). Nat. size.

Explanation of letters.

Avl, anterior ventro-lateral plate; *Pvl*, posterior ventro-lateral plate; *ov*, area overlapping the posterior ventro-lateral plate; *ov*, the area along the postero-medial margin overlapping the posterior ventro-lateral plate; the other area possibly overlapping the spinal plate or a correspondingly situated plate of the lateral wall of the trunk armour; *ovd*, overlapped area (pl. 14).



Plate 16.

Phyllolepis sp.

- Fig. 1. Left marginal plate 3 preserved in part as impression of the medial face. Specimen no. 458. Nat. size.
- Fig. 2. Left posterior ventro-lateral plate, preserved as impression of the ventral (external) face. The antero-medial corner lacking. Specimen no. 420. Nat. size.

Explanation of letters.

ovd, *ovd*₁, overlapped areas.

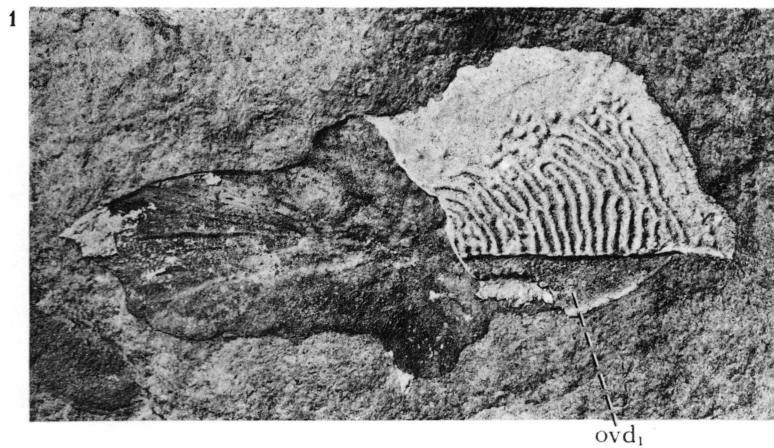
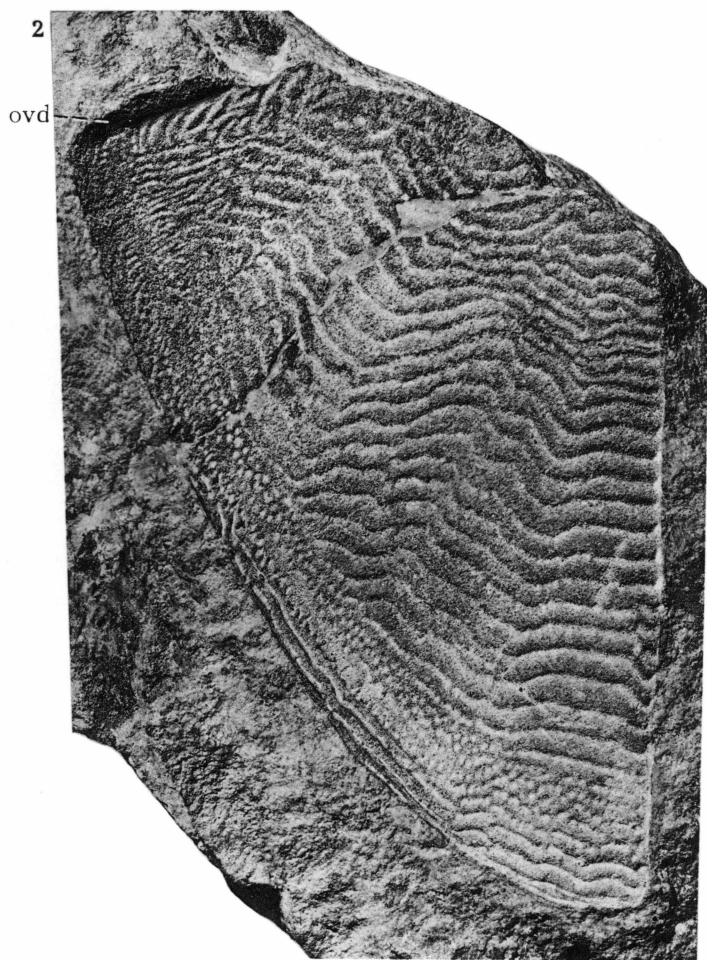


Plate 17.

Phyllolepis sp.

- Fig. 1. Impressions of the external face of an imperfect left anterior dorso-lateral plate and of an imperfect right posterior ventro-lateral plate. Specimen no. 419. Nat. size.
- Fig. 2. Imperfect left posterior ventro-lateral plate preserved as impression of the ventral (external) face. Specimen no. 454. Nat. size.
- Fig. 3. Fragmentary plate the position of which is still unknown. Impression of the external side. Specimen no. 455. Nat. size.

Explanation of letters.

Adl, anterior dorso-lateral plate; *Pvl*, posterior ventro-lateral plate; *lc*, main lateral line; *ovd*, *ovd*₂, overlapped areas.

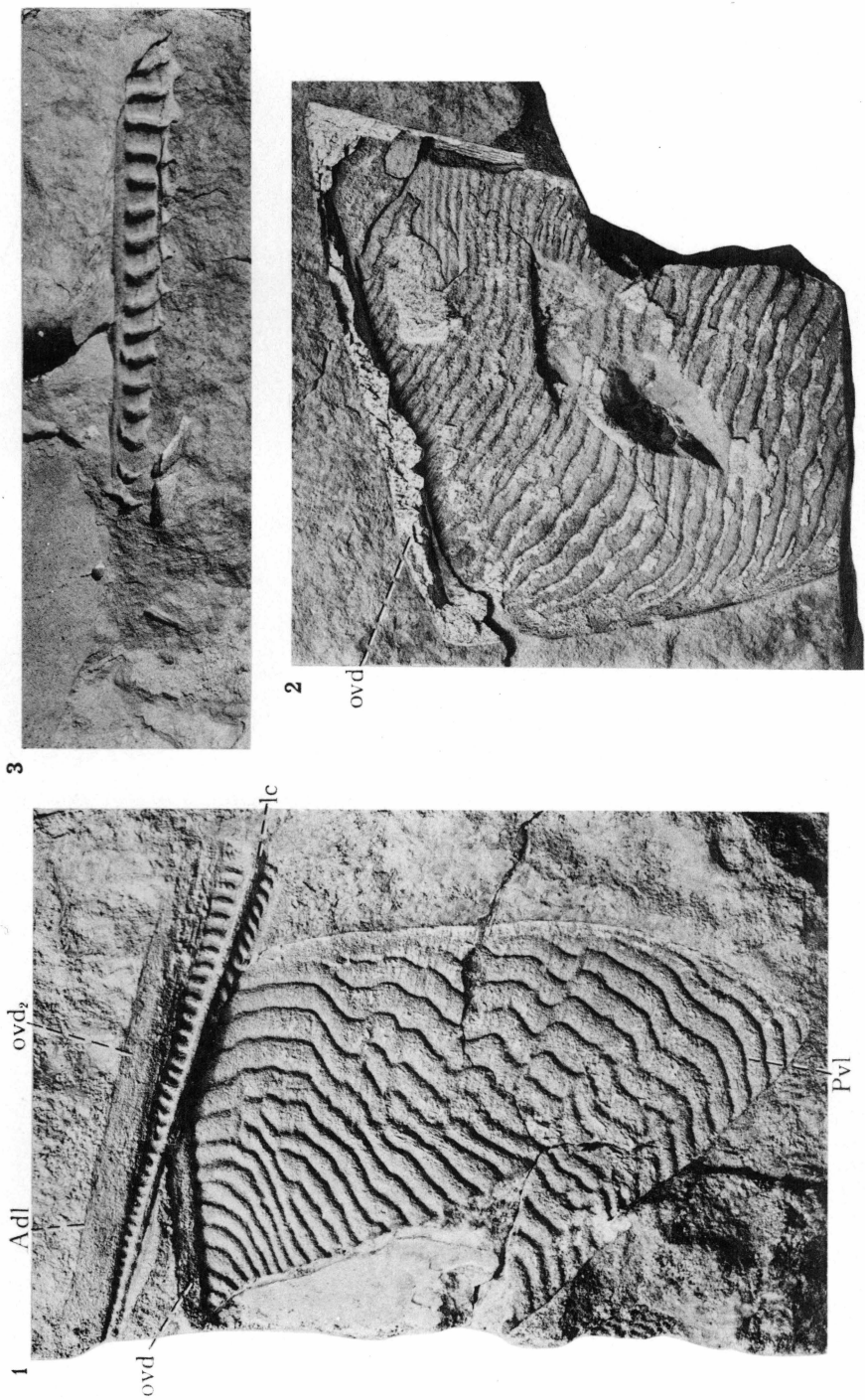


Plate 18.

Phyllolepis sp.

Fig. 1. Imperfect marginal plate 4 (right). Specimen no. 415. Natural size.

Fig. 2. Part of the basal layer showing cell-spaces with canaliculi. The base of basal layer upwards. $\times 500$ diam.

Explanation of letters.

c.c., canaliculi; *c.sp.*, cell-spaces; *lc*, lateral line groove, probably representing a part of the cephalic division of the main lateral line; *ovd*, overlapped area.

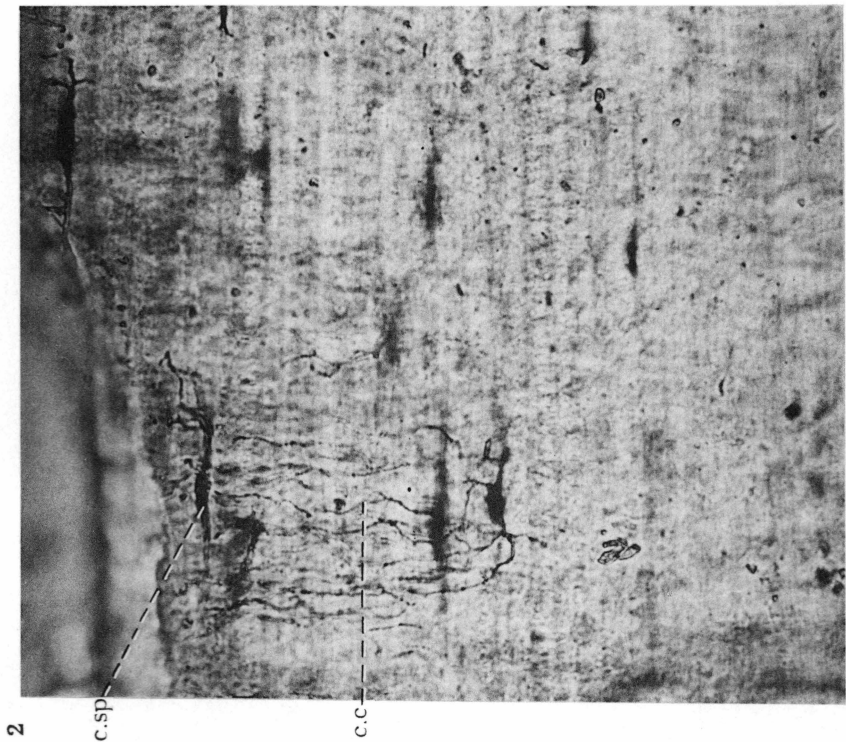
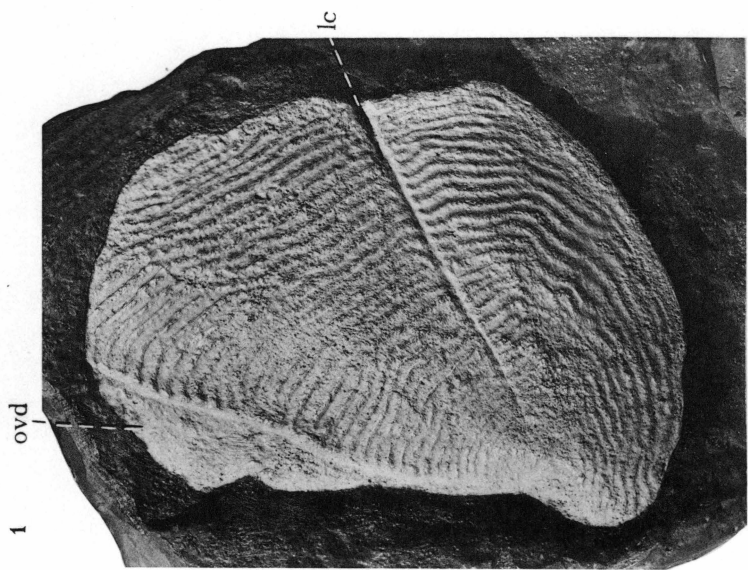


Plate 19.

Phyllolepis sp.

Figs. 1, 2. Vertical sections through dermal bones. In fig. 1 the basal layer is very distinctly developed, whereas in fig. 2 it is less well developed. $\times 50$ diam.

Explanation of letters.

bl, basal layer; *m*, dark zone in the matrix; *ml*, middle layer; *sl*, superficial layer.

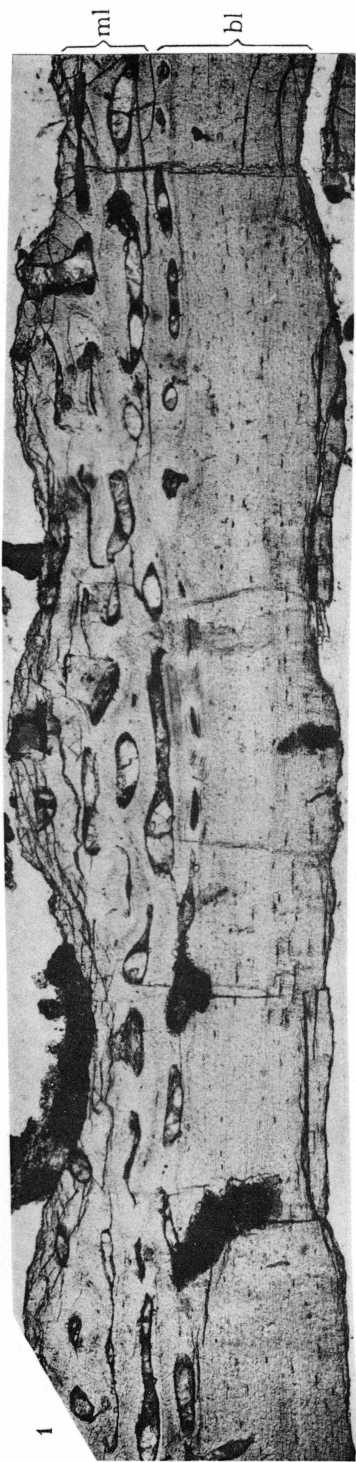
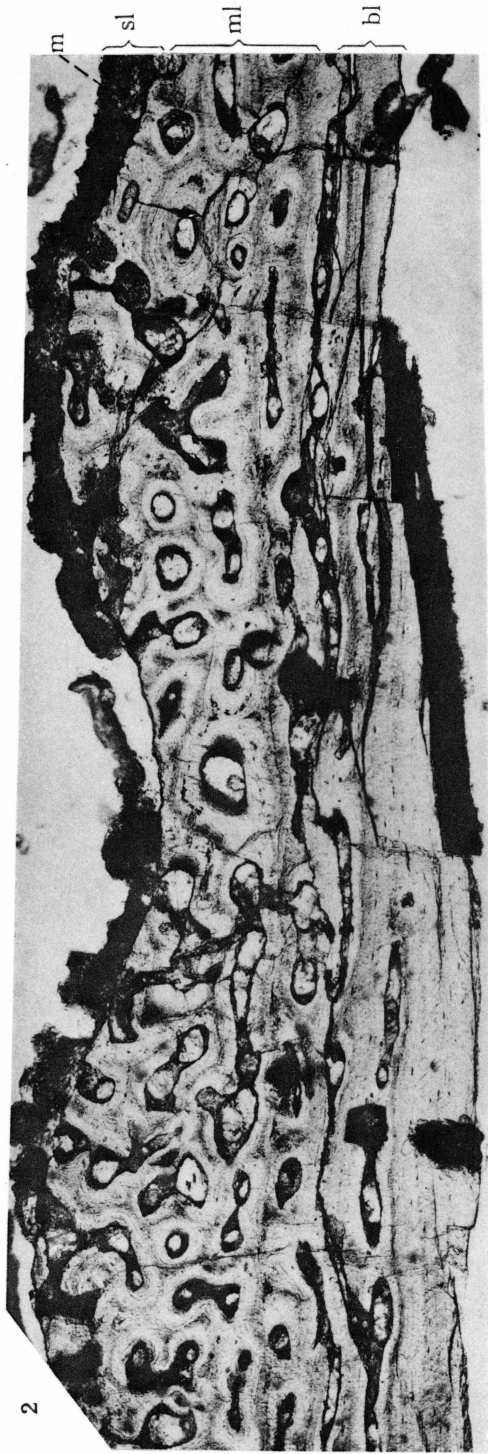


Plate 20.

Phyllolepis sp.

Vertical section through a part of a bone in which the basal layer is slightly developed
or absent. $\times 50$ diam.

Explanation of letters.

bl, basal layer; *ml*, middle layer; *sl*, superficial layer.



Plate 21.

Phyllolepis sp.

Horizontal section through the basal layer of a dermal bone; at *b*, a spot at which the canaliculi are particularly well filled with a dark matrix. $\times$ 250 diam.

Explanation of letters.

b, spot at which the canaliculi of the cells are particularly well filled with a dark matrix; *c.c.*, canaliculi; *c.sp.*, cell-spaces; *hav*, Haversian canal.

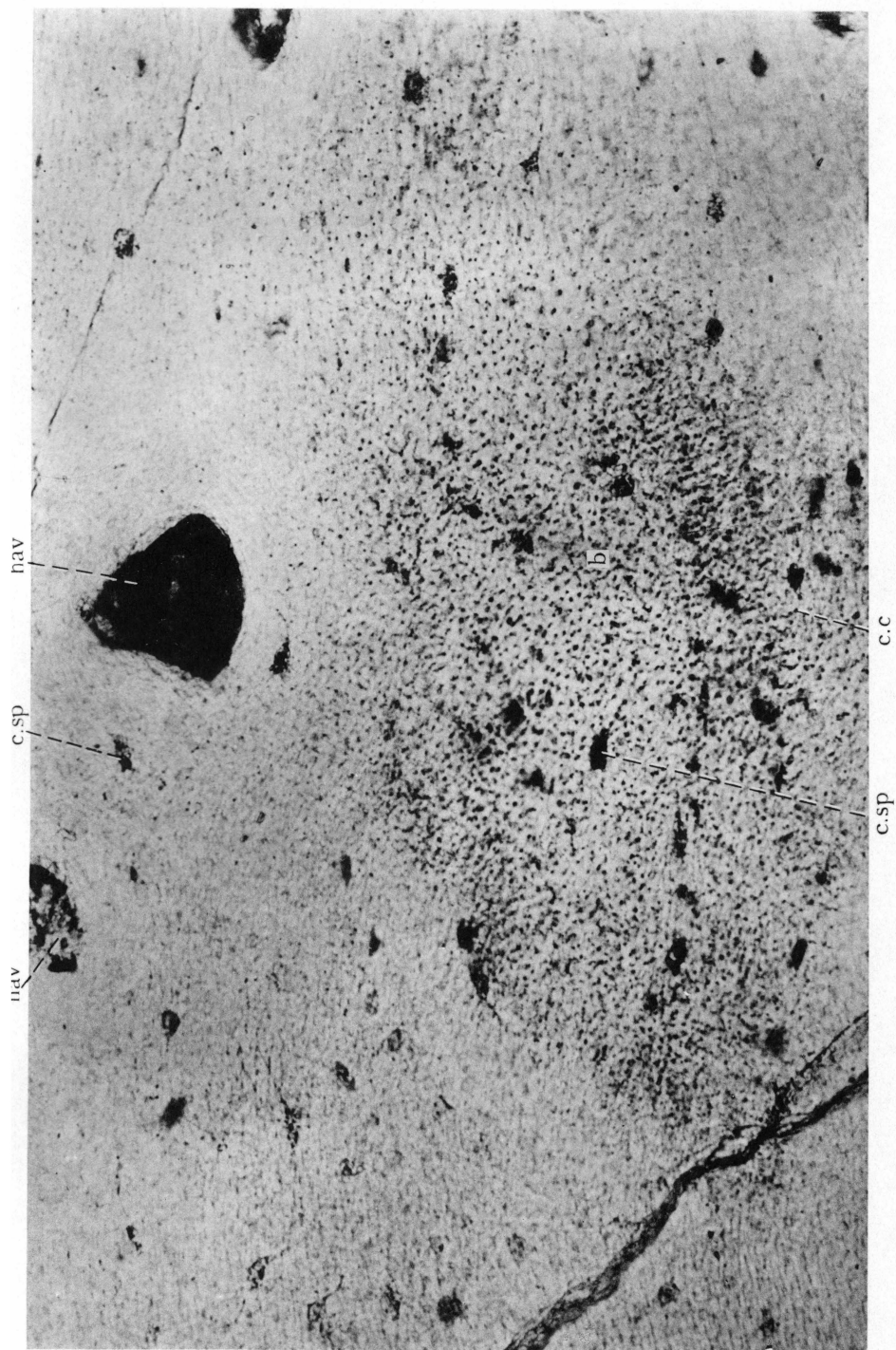


Plate 22.

Phyllolepis sp.

- Fig. 1. Horizontal section through a part of the basal layer in which the canaliculi of the cell-spaces are partly filled with matrix. $\times 250$ diam.
- Fig. 2. Vertical section through a part of the basal layer. The cell-spaces are well shown. $\times 250$ diam.

Explanation of letters.

c.c., canaliculi of cell-spaces; *c.sp.*, cell-spaces.

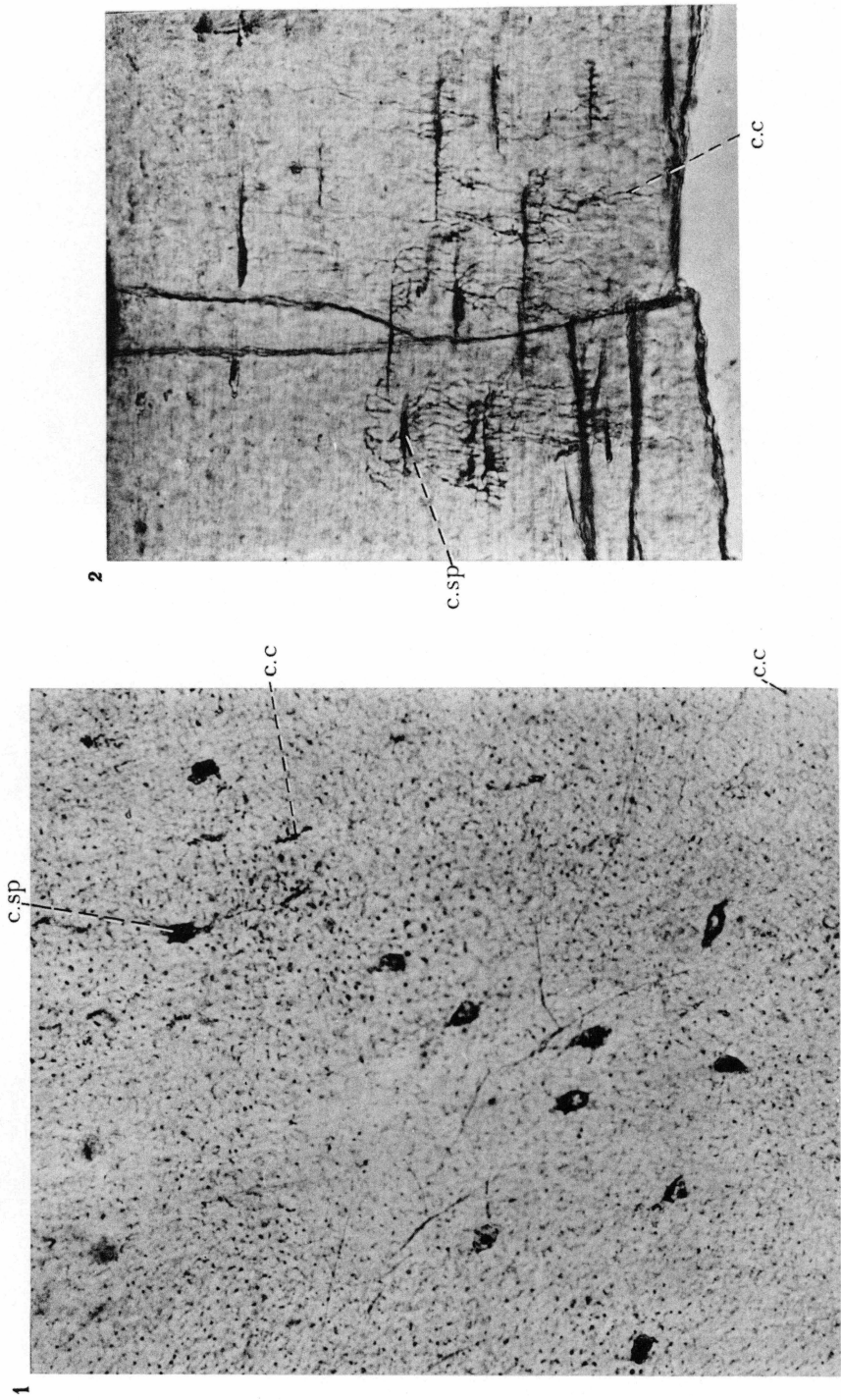


Plate 23.

Phyllolepis sp.

Horizontal section through the most basal part of the middle layer at a place at which the vascular system of this forms fairly regular plexus. In places, particularly at the right upper corner, the basal layer shown. $\times 50$ diam.

Explanation of letters.

bl, basal layer; *hav*, Haversian canals and other vascular canals; *ml*, middle layer.

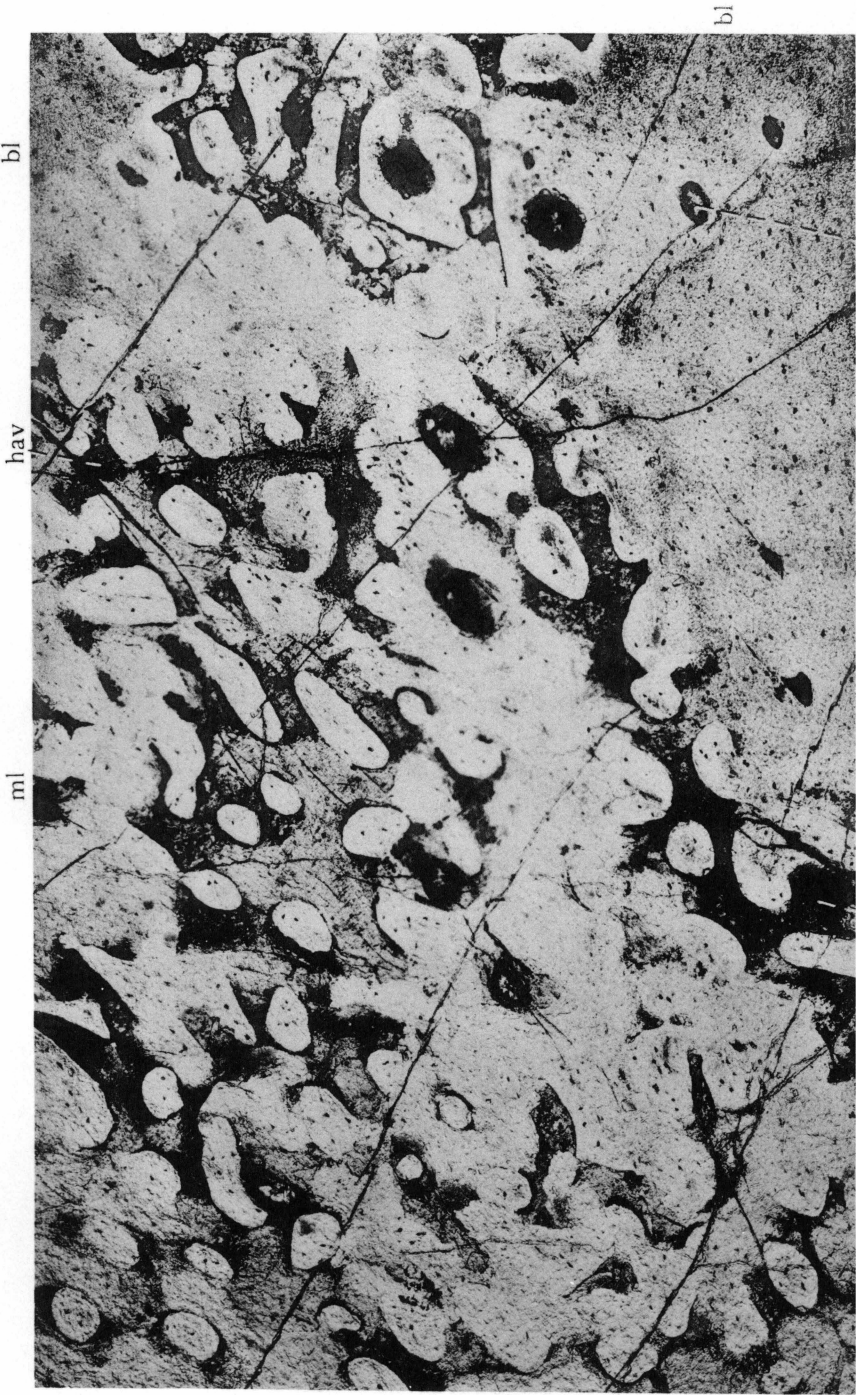


Plate 24.

Phyllolepis sp.

Section through a part of the middle layer. The section shows the laminate structure of the bone around the Haversian canals and in certain places cell spaces. $\times 250$ diam.

Explanation of letters.

c.sp, cell-spaces; *hav*, Haversian canals and in places perhaps other canals.



Plate 25.

Phyllolepis sp.

Section through the middle layer showing the radiate arrangement of the canaliculi
in a zone around the Haversian canals. $\times$ 250. diam.

Explanation of letters.

c.c., canaliculi; *hav*, Haversian canals.

