

NEW RESTORATIONS OF THE HEADS OF  
*PHARYNGOLEPIS OBLONGUS* KIAER AND  
*PHARYNGOLEPIS KIAERI* SP.NOV., WITH A  
NOTE ON THEIR LATERAL-LINE SYSTEMS

BY

IAN C. SMITH

(Zoology Department, The University of Glasgow, Scotland.)

CONTENTS.

	Page
Introduction . . . . .	373
Materials and Methods . . . . .	376
The Cranial Roof of <i>Pharyngolepis</i> . . . . .	377
Descriptions of the Species	
<i>Pharyngolepis oblongus</i> KIAER . . . . .	380
<i>Pharyngolepis kiaeri</i> sp. nov. . . . .	384
Discussion . . . . .	389
Note on the Sensory-line System . . . . .	396
Acknowledgements . . . . .	401
References to Literature . . . . .	401
Plates I—VI . . . . .	403

**Introduction**

The work on which this paper is based forms part of a wider study of the Norwegian and Scottish genera of the Order Anaspida, and arises out of an attempt to use the Norwegian material as a standard of reference for the less well preserved Scottish forms, *Birkenia* and *Lasanius* (TRAQUAIR 1899, 1905), and more directly from an attempt

to resolve the structure of the dermal cranial roof and to locate the nasohypophysial and pineal foramina in *Birkenia*. In the course of this work it has become apparent that new descriptions of the cranial roof of the Norwegian Anaspids are required: in this paper the cranial roof of one genus, *Pharyngolepis*, is re-described together with a description of a newly recognized species, *Pharyngolepis kiaeri* sp. nov.

The Norwegian genera, *Pharyngolepis*, *Pterygolepis* (= *Pterolepis*) and *Rhyncholepis*, were very carefully described by KIAER in his original monograph on these forms, (KIAER 1924) but until recent times no further work has been done on them and, indeed, very little on Anaspid morphology in general. STENSIÖ (1939) reviewed the existing knowledge of the group fairly extensively in a paper dealing with a newly discovered Canadian Anaspid, *Endeiolepis*, and also earlier in «The Downtonian and Devonian Vertebrates of Spitsbergen — Cephalaspidae» (STENSIÖ 1927) and in «The Cephalaspids of Great Britain» (STENSIÖ 1932). In a new work, STENSIÖ (1957) has discussed many aspects of Anaspid morphology of general importance from the point of view of their status as Ostracoderms and has given new restorations of the head and branchial regions of *Pterygolepis* in particular, which must certainly form the basis for all subsequent work on other Anaspids.

The histology of the Anaspid exoskeleton was described by GROSS (1938) in a valuable contribution dealing mainly with detached scales from the Downtonian of S. Wales, and ROBERTSON (1937) has described still older scales from the Ludlow of Oesel; but the scales of Anaspids are, as a rule, too badly preserved for a general histological survey of the order to be made. For example, little or no structural detail can be made out in the scales of any specimen of *Birkenia* yet examined (TRAQUAIR 1899; STETSON 1928). It is clear, however, from earlier work and from sections which have recently been prepared by Dr. T. Ørvig and the writer that *Pterygolepis* scales resemble those of the Welsh and Oesel material quite closely (Plate VI). There is every reason to believe that the very slight degree of ossification in the greater part of the exoskeleton of *Lasanius* and the apparent absence of all dermal bone in *Endeiolepis* is no more than an extreme manifestation of the tendency towards exoskeletal reduction which is characteristic of the Anaspia as a whole (STENSIÖ 1939), that *Lasanius* and *Endeio-*

*lepis* are, in other words, very specialized and not primitive (c.f. KIAER 1924; STENSIÖ 1927). A closely parallel case is seen in the Pertromyzontids which, although related to both the Anaspids and the Cephalaspids, must have taken their origin quite early from some intermediate ancestral group (probably nearer to the Cephalaspids than to the Anaspids) and which subsequently underwent, in many respects, a reductional evolution developing, or accentuating, many characters similar to those of the Anaspids (see STENSIÖ 1957).

Since TRAQUAIR's original description (TRAQUAIR 1899) *Birkenia* has been re-examined on very few occasions (STROMER 1926, 1930; STETSON 1928) which is not surprising in view of the difficulty of the material. This species is not uncommon but is normally poorly preserved — as impressions or highly carbonized compressions, almost always lateral. KIAER (1924) rightly considered that in the arrangement of the plates and scales of its exoskeleton, *Birkenia* is much more complex than any of the other known armoured Anaspids; nevertheless, with regard to the pattern of the cranial roof and the presence of a discontinuity in the dorso-lateral squamation of the trunk, this genus seems to have much in common with *Pterygolepis* — perhaps enough to justify the inclusion of *Pterygolepis* in the family *Birkeniidae*, or in a super-family *Birkeniiformes* (c.f. KIAER 1924; STENSIÖ 1957). It is already clear that STETSON's reconstruction of the cranial roof in *Birkenia* is inaccurate, notably with regard to the position of the nasohypophysial and pineal foramina. The foramen which STETSON called the «nostril» is almost certainly the pineal foramen and his «pineal opening» is probably an artefact; nor is the shape of the «pineal plate» in his drawing quite correct, it is actually much more like that of *Pterygolepis* (see KIAER 1924). The trunk squamation of *Birkenia* has several hitherto unrecognized peculiarities in the orientation of the scales in various areas, this is important because of the association between the arrangement of the scales and the arrangement of the myotomes. This matter will, however, be considered more fully on another occasion and before a new restoration of this important species is completed, some new material is urgently needed since, apart from the generally poor preservation, many of the existing specimens are badly weathered and covered with a thick layer of «rust».

### Materials and Methods

The specimens examined in the course of this work consisted of a large collection of the genera of Norwegian Anaspidida mostly belonging to the Palaeontological Museum, University of Oslo and a few to the Swedish Museum of Natural History, Stockholm. In addition, I had at my disposal another large collection of the two Scottish genera of Anaspidida borrowed from the Royal Scottish Museum, Edinburgh; the Geological Survey; Edinburgh; the Kelvingrove Museum, Glasgow; the Hunterian Museum, University of Glasgow; and the Palaeontological Institute, University of Uppsala. I am most grateful to the authorities of all these museums and institutes who have so generously allowed me the use of some or all of their Anaspid collections. With one exception, certain specimens of Norwegian Anaspidids only are described and figured in this paper, their catalogue numbers appear in the appropriate sections.

All the Norwegian Anaspid material originated from the Rudstangen (? Downtonian) locality at Ringerike, S. Norway, and the rock in which they are preserved is a very fine-grained, greenish-grey sandstone. The fossils are always strongly compressed and are sometimes quite flat (see KIAER 1911). Remains of exoskeletal material are usually present in a brown, translucent form in which, in most cases, little histological detail can be made out.

The Scottish material is derived from several (? Downtonian) localities in Lanarkshire, Ayrshire and Dumfriesshire in the south of Scotland (see TRAQUAIR 1899; PEACH & HORNE 1899). They are present in rock which varies from light-coloured, rather loose sandstone to fine-grained, light to dark grey or almost black shales.

The fossils were examined in strong illumination with a binocular loupe using 95 % alcohol, xylol or oil of aniseed as wetting fluids. Photographs of suitable specimens immersed in xylol or oil of aniseed were taken under powerful arc-lamp illumination at magnifications depending on the size of the specimen and the area under investigation. In many cases, a red filter was used in conjunction with a small aperture on the camera, and a prolonged exposure (up to two hours) was given in order to reduce all uneven reflections from the matrix

to a minimum and to enhance details on the fossil as far as possible. The photographs, printed on suitable matt paper, were outlined in indian-ink and difficult details were added from inspection of the fossil under the binocular loupe; the outlined photograph was then traced, and on such tracings the restorations figured in this paper are based. To obtain an estimate of the perspective foreshortening, the restorations were further traced on to thin wax-sheets which were then empirically moulded into the supposed shape of the cranial roof in its natural condition, these models were photographed in plan and side elevation and drawings were made from them.

Little or no preparation of the material was required although it was necessary to clean parts of some fossils with fine needles under the binocular loupe.

The work was carried out entirely in the Palaeozoology Department of the Swedish Museum of Natural History, Stockholm and I am most grateful to Professor E. A. Stensiö for all the help and facilities which were given me during my visits.

### **The Cranial Roof of *Pharyngolepis***

Because of the impossibility of homologizing the plates of the cranial roof in Anaspida with those in Cephalaspida or any other group of lower vertebrates, the dermal plates of the cranial roof in *Pharyngolepis* (except the numerous small scales in the occipital division) are designated by means of letters, thus *G* to *Z* with e.g. *K* and *K<sup>a</sup>* etc. where a plate is apparently subdivided longitudinally; and *K*, *K<sub>2</sub>* etc. where a plate seems to be divided transversely by a groove or sensory-line canal. This is possible because, whilst two species are involved, the form and arrangement of the plates is fundamentally the same in both. Whilst this lettering of the plates is necessary both to describe the sensory-line system and to compare the cranial roofs of the several specimens, it must be emphasized that it has no morphological significance in itself and is not intended to imply any homologies whatever outside this particular genus. It is hoped, however, that studies now proceeding will enable at least some true homologies to be established amongst the Anaspid forms; in this connection the recognition of parts of a sensory-line system in *Pharyngolepis* has an added

importance. STETSON (1928) and, to some extent, KIAER (1924) have given names to certain plates on the cranial roof of Anaspids but, for the reasons given above, these systems of nomenclature must be regarded as unsound at present.

Text Figures 1 A and 1 B are drawings of the cranial roofs of two specimens of *Pharyngolepis oblongus* and Text Figure 2 is a drawing of the only example of *Pharyngolepis kiaeri*. All three figures have been made directly from the photographs of the fossils and represent the dermal plates in basal (internal) view, horizontally flattened. The diagnoses of the two species are based on these figures and on the unrestored photographs (Plates I–IV). It is interesting to compare Text Figures 1 A and 2 with Text Figures 3 A, 3 B, and 4 A, 4 B in which an attempt has been made, with the use of wax-plate models, to restore the cranial roof, in dorsal and lateral aspects respectively, of the two species. In the restorations the differences between the species are emphasized and, in addition to other features, the relatively short pre-nasal and long post-nasal divisions of the cranial roof in *Pharyngolepis oblongus* contrast sharply with the relatively much longer pre-nasal division, and the relatively shorter post-nasal division of *Pharyngolepis kiaeri*.

The individual plates and scales are not here described in detail since their form and arrangement will be sufficiently clear from the figures, and the diagnoses draw attention to points of special importance. It is, however, of value to make a brief comparison of the new restorations with those figured by KIAER (1924, Fig. 20, p. 44; Fig. 26b, p. 55). It is at once obvious that KIAER was unsuccessful in resolving plates *S*, *T–T*, whilst plates *U* and *V* are incorrectly drawn for the following reason: in Specimen E. 1039 (KIAER 1924, Fig. 20) the bone substance that is actually preserved does indeed make a deep caudal notch in plate *V* and, at first sight, this seems to be the limit of the plate. But, in fact, the suture lies more anteriorly leaving a broad V-shaped area posterior to the suture from which the bone has disappeared. It is also clear from Fig. 26b that KIAER did not correctly identify the pineal foramen but confused it with the opening that is actually the nasal part of the nasohypophysial foramen; nevertheless, reference to KIAER's Figure 20 shows that he did observe the true pineal foramen. The anterior margin of the hypophysial part of the nasohypophysial foramen in KIAER's Figures 20 and 26b has been given

an arched form instead of the practically straight margin which is correct; once again the error can be traced to Specimen E. 1039 in which this margin is damaged. I have found no justification for the rather regular, lozenge-shaped occipital scales illustrated by KIAER in Figure 26b, it is certainly possible that from the exterior side they had this appearance but the only available specimens with this part of the cranial roof in a well preserved condition display the basal (internal) faces of the scales, and in this aspect they are somewhat irregularly rhomboidal and closely fitting without, as far as one can judge, any overlapping. Another matter of some importance is that, as noted by KIAER, the circum-orbital plates have a thickened basal (internal) ridge surrounding the foramen; but from KIAER's Figure 26b these ridges could be mistaken for a ring of separate elements — such a mistake seems already to have occurred (see BYSTROW 1955, Fig. 39, p. 513). Whether a sclerotic ring was also present is still questionable. It also seems now quite certain that KIAER's restoration (Fig. 26b) contains features of both *Pharyngolepis oblongus* and *Pharyngolepis kiaeri*, this is again referred to on p. 384.

Finally, a few comments on the nature of the sutures and grooves between the plates and scales of the cranial roof and adjacent areas may usefully be made. Between plates *Q* and *Q<sup>a</sup>* there is a very deep groove, probably separating the plates completely; basally (internally) there is a ridge along each side of this groove. It would be incorrect to regard this groove as a suture corresponding, for example, to those between plates *U* and *V*; *Q<sup>a</sup>* and *V* etc. It does, however, seem to correspond to the grooves between plates *X* and *W* (which also have a thickened ridge of bone along their common margins), *G* and *P*, *O* and *K*, and probably to that between *J*, *K*, *L*, *M* and *J<sub>2</sub>*, *K<sub>2</sub>*, *L<sub>2</sub>*, *M<sub>2</sub>* (see Text Figure 2) etc. Plates *R* and *R<sup>L</sup>* are loosely articulated together and the suture between plates *R<sup>L</sup>* and *X* was probably not rigid, thus suggesting a certain flexibility of the snout region; a flexibility of this kind is in agreement with STENSIÖ's view that the Anaspids had suctorial mouths.<sup>1</sup> The V-shaped groove in plate *H*, the

<sup>1</sup> STENSIÖ (1957) points out that the mouth cannot have been fringed, as in e. g. KIAER's reconstructions of the Norwegian Anaspids, by free margins of bone, either cranial elements or ventral visceral scales; but there must have been soft tissues extending past the bone margins to form an oral opening. In the absence of any true jaw elements, a suctorial mouth with or without a rasping tongue is a strong probability for all Anaspids.

groove between plates  $Q$  and  $Q^a$ , and that running transversely from plate  $H$  to the lateral margin of the cranial roof are all constant features of all the specimens of *Pharyngolepis* examined (see further the note on the sensory-line system).

All other details may readily be understood from the figures, diagnoses and descriptions of the species.

### Descriptions of the species

*PHARYNGOLEPIS OBLONGUS* KIAER (Text Figures 1A, 1B, 3A, 4A, 5 and 6; Plates I–III) *Diagnosis*: — orbital openings anterior to the mid-transverse line of the bony skull roof; the entire nasohypophysial foramen situated between the orbits. Occipital division of the cranial roof with numerous, irregularly rhomboidal scales; ill-defined and

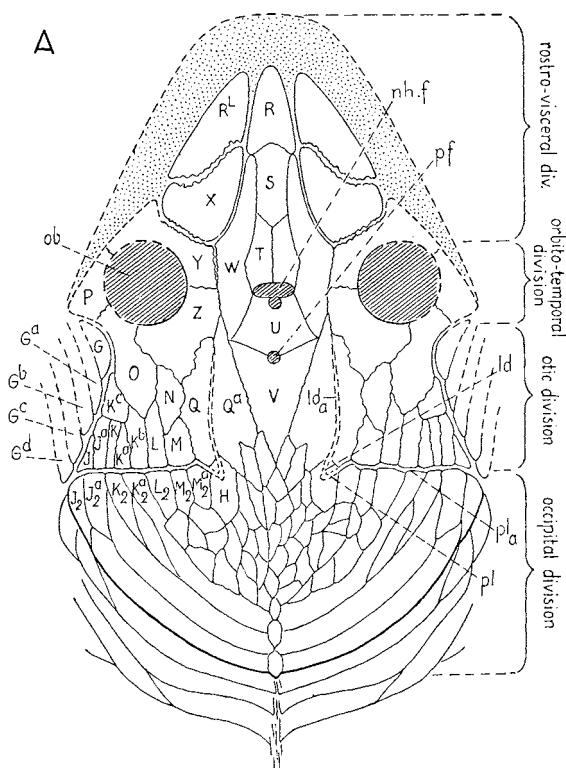


Fig. 1 A. *Pharyngolepis oblongus* KIAER; dermal cranial roof of Specimen E. 0122 (Pal. Mus. Oslo — counterpart of the lectotype) flattened in the horizontal plane and seen in basal (internal) view. The stippled area indicates soft tissues extending beyond the margins of the plates and scales. The major exoskeletal plates are lettered G — Z as explained in the text and the four divisions of the cranial roof are indicated; other letters,  $ld$  and  $ld_a$  = cranial part of the dorsal lateral-line groove;  $nh.f$  = nasohypophysial foramen;  $ob$  = orbit;  $pf$  = pineal foramen;  $pl$  and  $pl_a$  = posterior pit-line groove. (see also Plate I). X 2.7.



rounded posteriorly. Plates bordering the groove between the otic and occipital divisions of the cranial roof considerably more subdivided than in *Pharyngolepis kiaeri*, never fewer than 5 and frequently as many as 7. The lateral post-orbital emargination of the cranial roof is filled by several (about 5) separate plates (the *G* series). The ventrolateral scales of the cheek and ventral visceral exoskeleton (see Text Figure 5) large, rhomboidal, increasing in size ventrally and, especially, posteriorly.

In addition there are several other specific characters of *Pharyngolepis*

*oblongus*: measured on the flattened head, the greatest width of the cranial roof is between plates  $J_2-J_2$  in the occipital division posterior to the transverse groove  $pl_a$  separating the otic and occipital divisions of the cranial roof. The rostral part of the rostro-visceral division is narrow, broadening out nearly uniformly to plates  $P-P$  in the orbito-temporal division at an angle of  $74^\circ$  to  $78^\circ$ . Plate  $U$  is large and meets  $Q^a$  laterally, plate  $V$  has acute anterior angles. The apex of the V-shaped groove in plate  $H$  lies one third, or a little more, of the distance from the posterior to the anterior end of the cranial roof. The length to breadth ratio of the plate complex  $R, S, T, U, V, W$  is about  $3 : 1$ , of plate  $R$  it is between  $1\frac{3}{4} : 1$ , of plate  $R^L$  it is about  $2\frac{1}{2} : 1$ , and of plate  $X$  about  $1\frac{1}{2} : 1$ .

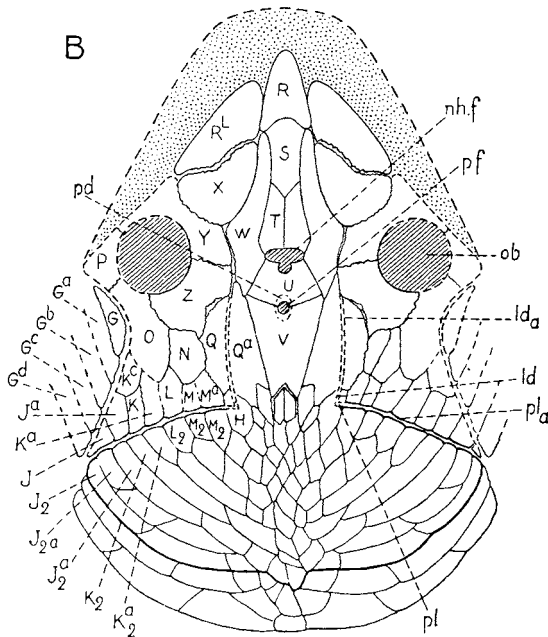


Fig. 1 B. *Pharyngolepis oblongus* KIAER; dermal cranial roof of Specimen E. 1039 (Pal. Mus. Oslo) flattened in the horizontal plane and seen in basal (internal) view. (see also Plate II).  $\times 2$ .  $pd$  = pineal depression; other lettering and shading as in Text Fig. 1 A.

*Lectotype*: — a large and well preserved specimen with the dorsal side of the head and trunk exposed in basal (internal) view, Specimen E. 1152 (Pal. Mus. Oslo) figured by KIAER 1924 in Plate VIII, Figure 1, and Plate IX, Figure 1; and the counterpart of E. 1152, Specimen E. 0122 (Pal. Mus. Oslo), figured in this paper in Plate I.

*Material*: — in addition to the counterpart of the lectotype, two other specimens of *Pharyngolepis oblongus* which display parts of the head region have been available for study; they are E. 1039 (Pal. Mus. Oslo), figured by KIAER 1924 as Figure 20, p. 44 and in this paper in Text Figure 1A and Plate II. It consists of part of a cranial roof, mostly median to the orbital foramina with a small area of the squamation of the right cheek. The other specimen is E. 1068 (Pal. Mus. Oslo) figured by KIAER 1924 in Plate IX, Figure 2 and Plate XI, Figure 1; and in this paper in Text Figure 5 and Plate III.

*Description*. All three specimens are rather large but E. 1039 is the biggest and its estimated length, based on the head length, is in the region of 250 mm; KIAER's figures for the total length of *Pharyngolepis oblongus* range from 190 to 200 mm only. The length of the head of E. 1039 is approximately 38 mm, the width across the orbital division at its widest part is about 23 mm, from the tip of plate *R* to the anterior margin of the orbit is about 14 mm; from the tip of plate *R* to the pineal foramen, 17 mm; and to the angle of the V-shaped groove in plate *H* about 24 mm. Plate *V* in this specimen has an unusual shape, its posterior end is notched, giving rise to a «butterfly-like» appearance — two small, rhomboidal scales fit into the notch. The anterior occipital scales in this specimen are, on the whole, much more regular than in any of the others — but this is perhaps a function of its size or age. The pineal opening has the same relative position and size as in the other specimens but it can be seen here that, viewed from the interior of the head, the actual foramen pierces a larger, oval, longitudinally arranged depression which must have contained the bulk of the pineal body (Text Figure 1B, *pd*).

Specimen E. 0122 is a counterpart bearing the dorsal side only of the head and body (the tail is missing) of a *Pharyngolepis* whose total length is estimated at about 193 mm (the preserved part measures 145 mm) in which the scales and dermal plates are mostly present but in a considerably altered condition as far as their composition is

concerned. The length of the cranial roof is 29 mm, the estimated width across the orbito-temporal division is 19.5 mm; the maximum width of the cranial roof is 20.5 mm. The length from the tip of plate *R* to the anterior margin of the orbit is 10.25 mm, the length from the tip of plate *R* to the pineal foramen is 14 mm, and to the angle of the V-shaped groove in plate *H* 20.25 mm. From this specimen one can gain an excellent idea of the dorsal aspect of *Pharyngolepis oblongus*; the dorsal scales lie in a practically parallel-sided strip from just behind the cranial roof to the end of the series of dorsal ridge scales, and have a nearly constant breadth of 21 mm. If we allow for the natural arching of the dorsal scales, which are here laid almost flat, we obtain a picture of a parallel-sided, rather narrow-backed form — in this case the breadth across the back could have been no more than 17 or 18 mm, possibly less.

Specimen E. 1068 (Text Figure 5) provides an interesting comparison with the previous specimen, here the animal is preserved in a lateral compression with only the right and central median part of the cranial roof flattened out horizontally; it is a little smaller than E. 0122, i.e. about 188 mm. From the branchial region to the anal fin the depth is fairly constant at 35 mm, the thickness of the compression is only about 5.5 mm. Even allowing for a factor of 3 or a little more for the extent of the compression, *Pharyngolepis oblongus* can not have been as rounded in cross section as KIAER believed but must, on the contrary, have been a laterally compressed, deep-bodied form with a depth of about twice its thickness. This conclusion seems to be amply confirmed by similar measurements on other specimens.

Measurements on the head of E. 1068 are rather difficult because of the small part that is preserved, but the width across the orbito-temporal division seems to be about 14.5 mm; the length of the head is perhaps about 21.5 mm.

The importance of this specimen lies in the fact that, whilst it can be identified as a specimen of *Pharyngolepis oblongus*, much of the lateral and ventral parts of the head and immediately post-cranial scales are present.

*Remarks.* In KIAER's reconstruction of *Pharyngolepis oblongus* (KIAER 1924, Fig. 37, p. 81) it will be noticed that the squamation of the cheek and ventral visceral exoskeleton does not agree with that

described above. We must, I think, believe that KIAER used the specimen of *Pharyngolepis kiaeri* (E. 1116 + E. 1043) for parts of his reconstruction, this would account for the discrepancies. A number of characters are involved including the size and shape of plate G, in *Pharyngolepis oblongus*, unlike *Pharyngolepis kiaeri*, there are several smaller plates comprising the G series.

*PHARYNGOLEPIS KIAERI* sp. nov. (Text Figures 2, 3 B, 4 B, and 8; Plates IV A, IV B, V 1).

*Diagnosis:* — orbital openings situated on the mid-transverse line of the cranial roof; the pineal foramen lies between the mid-parts of the orbital openings but posterior to the midtransverse line of the cranial roof; the nasal part of the nasohypophysial foramen

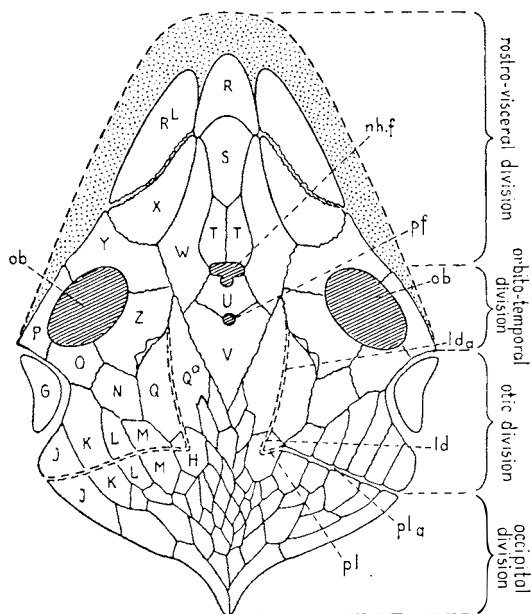


Fig. 2. *Pharyngolepis kiaeri* sp. nov., dermal cranial roof of Specimen E. 1043 (Pal. Mus. Oslo) flattened in the horizontal plane and seen in basal (internal) view. Drawing based on specimens E. 1116 and E. 1043 (Pal. Mus. Oslo). Lettering as in Text Fig. 1. (see also Plate IV A and B). X 2.8.

lies just between the orbits anterior to the mid-transverse line of the cranial roof; the hypophysial part of the nasohypophysial foramen opens just anterior to a line drawn through the anterior margins of the orbits. The posterior boundary of the cranial roof is rather well defined with an acute posterior angle; the small, irregularly rhomboidal scales in the occipital division of the cranial roof less numerous than in *Pharyngolepis oblongus*. Plates bordering the groove  $pl_a$  between the otic and occipital divisions of the cranial roof

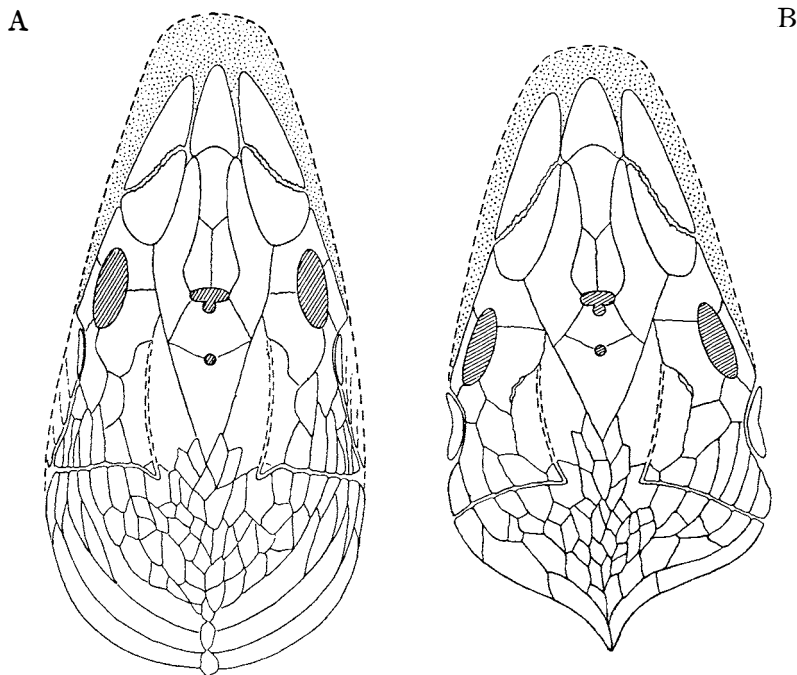


Fig. 3. *Pharyngolepis*, attempted restorations of the cranial roof in dorsal aspect drawn from wax-plate models. A, *Pharyngolepis oblongus* KIAER, X 2.7; B, *Pharyngolepis kiaeri* sp.nov., X 2.8.

are rather few (not more than 6 in the holotype). The lateral post-orbital emargination in the otic division is largely filled by a single, rather large plate, *G*. The latero-ventral scales of the cheek and ventral visceral exoskeleton are small, rather uniform in size, lozenge-shaped and very numerous. There is, incidentally, neither in this species nor in *Pharyngolepis oblongus* a sharp demarkation between the cheek and ventral visceral scales (referred to in this paper as scale fields *c* and *d* respectively).

The following characters are also typical of this species: measured on the flattened head, the greatest width of the cranial roof is across plates *P* – *P* in the orbito-temporal division. The rostral part of the rostro-visceral division is narrow and broadens out almost uniformly to plates *P* – *P* at an angle of 60°. Plate *U* is small, not meeting

$Q^a$  laterally; plate  $V$  has truncated anterior angles. The apex of the V-shaped groove on plate  $H$  lies at less than one third of the length from the posterior to the anterior end of the cranial roof – or, if the posterior angle of the cranial roof is rounded off, at less than one quarter of the length. The length to breadth ratio of the plate complex  $R, S, T, U, V, W$  is about  $2\frac{1}{2} : 1$ , that of plate  $R$  is about  $1\frac{1}{4} : 1$ , of plate  $R^L$  about  $3\frac{1}{2} : 1$ , and of plate  $X$  about  $2\frac{1}{4} : 1$ .

*Holotype*. — one nearly complete specimen with the counterpart of the head and anterior part of the trunk; Specimens E. 1116 and E. 1043 (Pal. Mus. Oslo). E. 1116 is figured by KIAER (1924) in Plate X, Fig. 1.

*Material*. — the only material referable to the species consists of the holotype and its counterpart.

*Description*. The specimen, which is fairly complete, passes through the rock matrix from one side to the other with the greater part of the ventral surface hidden and the distal parts of the tail are missing; in this specimen a short section of vertebral column has been observed with the aid of an X-ray examination (SMITH 1956). The head and trunk regions are preserved on one side of the matrix in an almost dorso-ventral position, a considerable part of the squamation of the cheek and ventral visceral exoskeleton is present on the right side but otherwise only the dorsal surface is visible. On the reverse side of the matrix the posterior part of the trunk and the proximal part of the tail are laterally flattened with the right side exposed. The total length of the specimen is approximately 135 mm, the length of the anterior piece is 92 mm. The length of the cranial roof is 28 mm and its maximum width, which cannot be determined exactly, seems to be about 20.5 mm. The distance from the tip of plate  $R$  to the anterior margin of the orbit is 12 mm, that from the tip of plate  $R$  to the pineal foramen is 12.5 mm, and to the angle of the V-shaped groove on plate  $H$  is 19.5 mm.

*Remarks*. KIAER referred this specimen to the species *Pharyngolepis oblongus* which it closely resembles in many respects and, indeed, no differences have been detected other than in the cranial roof and adjacent areas of exoskeleton where, however, there are several characters, mostly those of relative proportions, in which it differs quite consider-

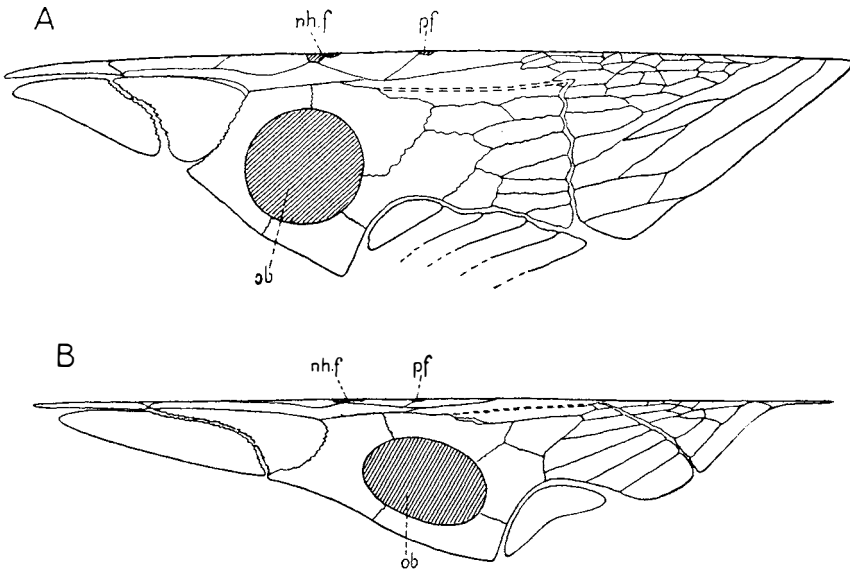


Fig. 4. *Pharyngolepis*, attempted restorations of the cranial roof from the side using same models as in Text Fig. 3. A, *Pharyngolepis oblongus* KIAER, X 4.5; B, *Pharyngolepis kiaeri* sp. nov., X 3.75.

ob = orbit; nh.f = nasohypophysial foramen; pf = pineal foramen.

ably from *Pharyngolepis oblongus* and which do not seem to be result of the state of preservation. The possibility that we are here concerned with sexual dimorphism can certainly not be ignored but, in the absence of any positive indications, can probably be discounted. Nor is there any evidence of continuous variation within *Pharyngolepis oblongus* and, in the circumstances, it seems most likely that E. 1116 and E. 1043 truly represent a new species. KIAER mentioned the possibility of a second species of *Pharyngolepis* with reference to a small specimen having only 12 branchial openings instead of the usual 15 (KIAER 1924, pp. 61 and 134). I have had the opportunity to examine this specimen (now E. 1036, Pal. Mus. Oslo) but there are no means by which to associate it with one species or the other, or to erect for it a new species; it may be a variation of one or other of the species described or a juvenile form and for the present it must remain included in the species *Pharyngolepis oblongus*.

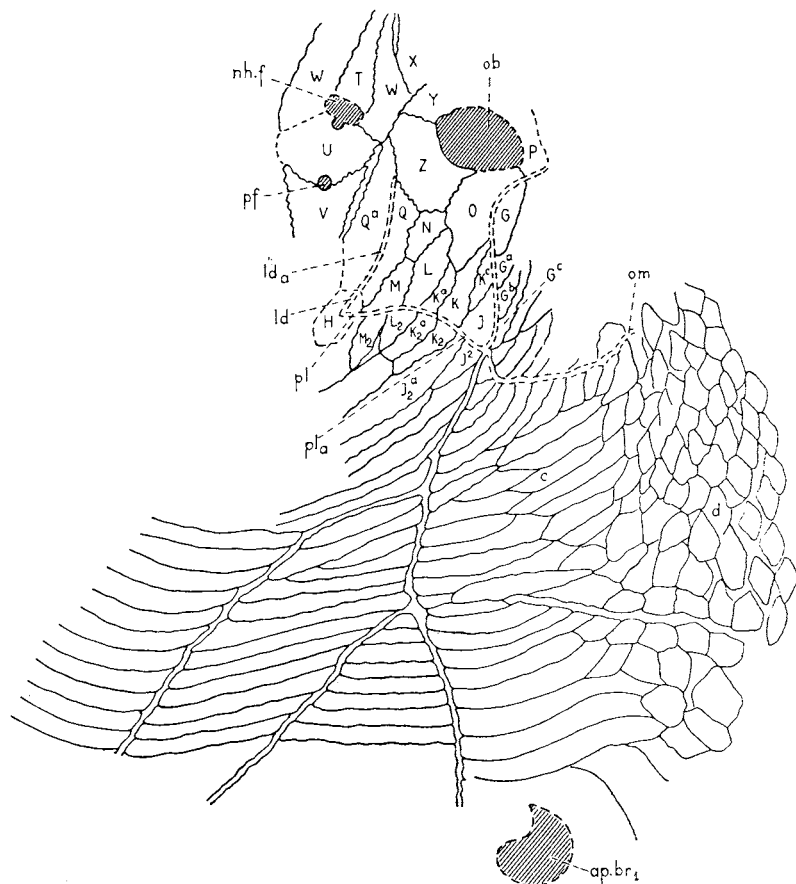


Fig. 5. *Pharyngolepis oblongus* KIAER, part of the cranial roof and adjacent areas of exoskeleton of Specimen E. 1068 (Pal. Mus. Oslo). X 3.6.

*c* = cheek exoskeleton; *d* = ventral visceral exoskeleton; *ap.br*<sub>1</sub> = first branchial opening; *ld* and *ld*<sub>a</sub> = cranial part of the dorsal lateral-line groove; *nh.f* = nasohypophysial foramen; *ob* = orbit; *om* = sensory-line groove on cheek exoskeleton; *pf* = pineal foramen. Note the large, rhomboidal scales in scale-field *d* increasing in size ventrally. (see also Plate III).

On the basis of all the characters described, the three specimens referred to the species *Pharyngolepis oblongus* fall into a compact group with no overlapping of characters of *Pharyngolepis kiaeri*. On the other hand, the number, arrangement, and general shape of the head



plates is fundamentally the same in the two species as can be seen from Text Figures 1 and 2, except in the case of the scales on the occipital division of the cranial roof, the plates bordering the groove *pl<sub>a</sub>* and, as already emphasized, the scales of the cheek and ventral visceral exoskeleton. The position of the orbits, pineal and nasohypophysial foramina and the position of the greatest width of the cranial roof, together with the rostral angle and the relative proportions of certain parts of the cranial roof provide the major differences.

### Discussion

The dermal elements of the skull roof, cheek and supra-trematic parts of the branchial region of an armoured Anaspid are basically comparable with the exoskeleton of the cephalic shield of a Cephalaspid in general features although the exoskeleton of the cephalic shield is frequently more extensive caudally (e. g. *Thyestes*, *Dartmuthia*, *Tremataspis*). The orbital openings and nasohypophysial and pineal foramina in both groups lie in corresponding positions and the part of the cranial roof anterior to the nasal opening in Anaspids is, as in Cephalaspids, of visceral origin but covered by dermal plates which include the so-called «rostral» plates — i. e. those situated on the rostral part of the visceral endoskeleton, morphologically sub-ethmoidal (STENSIÖ 1927, 1939, 1957). The nasohypophysial and pineal foramina pierce the median (ethmoidal) part of the orbito-temporal division of the cranial roof. The dorsal and lateral sides of the exoskeleton of the adult Cephalaspid shield form a continuous piece of bone (STENSIÖ 1957, p. 188) whilst the corresponding exoskeletal parts in Anaspids are composed of a considerable number of small, rhomboidal scales and larger plates. The mouth in both groups is sub-terminal and the ventral visceral exoskeleton in Anaspids (*Rhyncholepis* is a notable exception) resembles that of Cephalaspids rather closely in being made up of a large number of small dermal elements which, like the exoskeleton of the cheek and pre-branchial regions also of Anaspids, was undoubtedly a flexible area. The nature of the ventral visceral squamation in Cephalaspids indicates that the internal structures — cartilages and muscles — were adapted for producing a flow of water through the pharyngeal region and over the gills; the

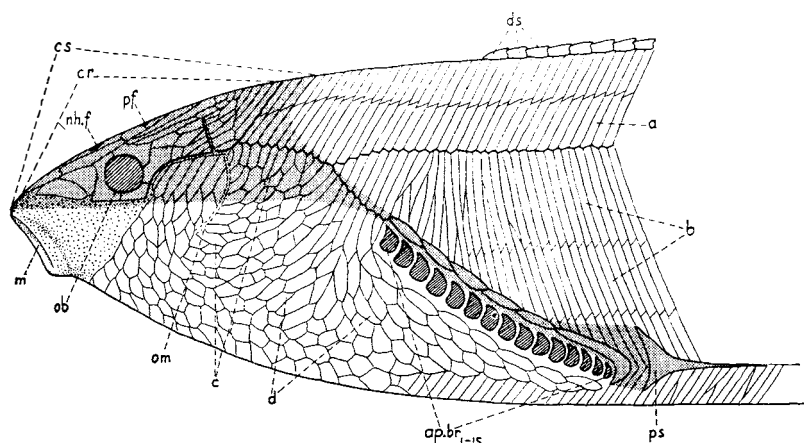


Fig. 6. *Pharyngolepis oblongus* KIAER, an attempted new reconstruction of the head and anterior end of the body in lateral view: modified after KIAER 1924, Text Fig. 37; and STENSIÖ 1957, Text Fig. 127A. The area *cs* (shaded) indicates the approximate extent of the exoskeleton which corresponds to the cephalic shield of a Cephalaspid and includes the cranial roof (*cr*), the pectoral spine (ventro-lateral scute) apparatus (*ps*), and the strip of exoskeleton above the branchial openings (*ap.br.1-15*). The stippled area indicates soft tissues free from exoskeleton which extend forwards to form the actual mouth. Other lettering : *c* = cheek exoskeleton; *d* = ventral visceral exoskeleton; *ds* = dorsal ridge scales; *nh.f* = nasohypophysial foramen; *m* = oral opening; *ob* = orbit; *om* = sensory-line groove on the cheek exoskeleton; *pf* = pineal foramen. X 1.6.

combined areas of flexible squamation in Anaspids overlay regions which had both this function and that of accommodating, like the corresponding regions in modern Petromyzontids (in which, however, the exoskeleton is absent), sucking mouth-parts and a rasping tongue (STENSIÖ 1957, p. 227). It is interesting to note in this connection that amongst the Cephalaspids, the primitive *Aceraspidae* also possessed a rasping tongue mechanism (STENSIÖ 1957; see also the footnote on p. 379).

In Text Figure 6 an attempt has been made to indicate the areas of exoskeleton in an Anaspid (*Pharyngolepis oblongus*) which correspond to the cephalic shield and ventral visceral exoskeleton of Cephalaspids. Apart from the lesser breadth of the heads and the

more numerous dermal elements in the Anaspids, the most obvious difference is in the position of the branchial openings. STENSIÖ (1957) has already shown that by reference to a form such as *Tremataspis* in which the cephalic shield is oval in cross section and is produced back as far as the anal opening, and that by assuming the loss in Anaspids of several (three) anterior gill-pouches together with a small backward shift of the remainder, a correlation can be made. The thickened bony flanges external to the eyes and dorso-lateral to the branchial openings in the majority of Cephalaspids are clearly secondary formations.

It is most probable that in Cephalaspids, whilst the usual number of branchial openings is ten with a reduced eleventh, a much larger number was primitively present and that they extended further back on the ventral side of the pharyngeal region but have been eliminated by the development of the post-branchial wall of the cephalic shield. The evolution of a cephalic shield and the fusion of the lateral halves of the visceral endoskeleton in the median line to form a post-branchial wall imposed a limit on the branchial region in Cephalaspids. Additional branchial openings developed, however, during ontogeny in some Anaspids and, if STENSIÖ is correct in believing that the first three, pro-otic, gills of the Cephalaspid series (pre-spiracular, spiracular and hyoidean) have disappeared from Anaspids, then the persisting 6-8 branchial openings in *Lasanius* and 8 in *Birkenia* should be the same as the openings of the branchial chambers  $k_4-k_{11}$  in Cephalaspids (see e. g. STENSIÖ 1957, Text Fig. 116). But *Pharyngolepis* for example, with its usual total of 15 branchial openings, must have retained eight additional, primitive, vagal-innervated gills, thus resembling the Heterostraci and Myxinoids. In adult Myxinoids the region of branchial openings frequently extends far back along the flanks and there is never a limiting post-branchial wall. In larval Myxinoids, e. g. *Bdellostoma* (see DEAN 1899; STENSIÖ 1927, 1957) the branchial region is short and the primordia of the developing visceral endoskeleton diverge backwards on either side of the head and have the potentiality for unlimited backward growth. The larval head of Myxinoids is considerably flattened dorso-ventrally and, in many respects, resembles a Pteraspid such as *Simopteraspis primaeva* KIAER (Text Fig. 7) to a striking degree. In *Simopteraspis*, as in Pteraspids

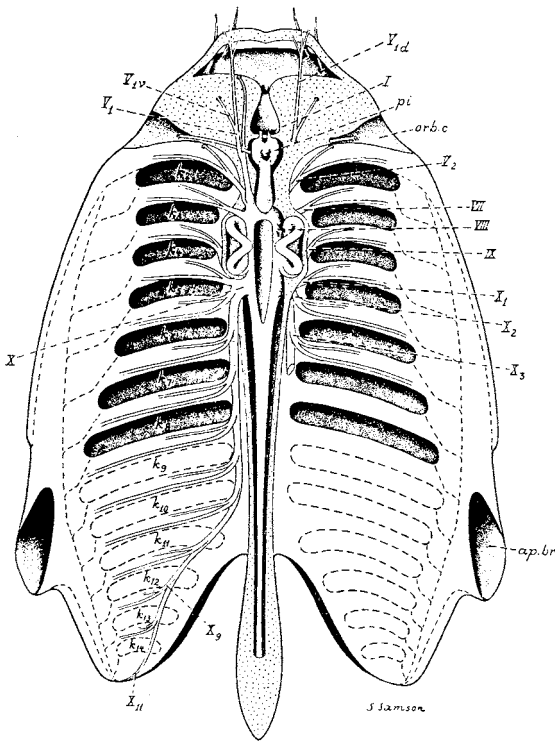


Fig. 7. *Simopteraspis primaeva* (KIAER), an attempted reconstruction of the endocranium to show the number and arrangement of the branchial chambers. A limiting post-branchial wall is absent. After STENSIÖ 1957, Text Figure 200. X 3.3. *ap.br.* = branchial aperture;  $k_2 - k_{14}$  = branchial chambers;  $V_1$  = profundus nerve;  $V_{1d}, V_{1v}$  = dorsal and ventral branches respectively of the profundus nerve;  $V_2$  = trigeminal nerve; VII = facialis nerve; VIII = auditory nerve; IX = glossopharyngeus nerve;  $X_1 - X_{11}$  = branchiomeric branches of the vagus nerve; *orb.c.* = orbital cavity; *pi* = pineal organ.

in general, there may have been up to 15 branchial chambers with no union between the posterior parts of the visceral endoskeleton of both sides, i. e. no post-branchial wall. The Anaspids with branchial openings ranging from as few as 6 (in *Lasanius*) to as many as 15 (in *Pharyngolepis*) clearly resembled the Heterostraci and Myxinoids in having no posterior limit to the branchial region, and STENSIÖ's idea of a post-branchial wall in *Pterygolepis* (STENSIÖ 1957, Fig. 127B) must be incorrect; we should rather expect an arrangement of gills more nearly resembling that in the Heterostraci in which the two halves of the visceral endoskeleton remain independent posteriorly and separate medially. The

pericardial cartilage of Petromyzontids is the homologue of the post-branchial wall in Cephalaspids; in both these groups the two halves of the posterior visceral endoskeleton have come together and joined

so that the branchial openings are limited posteriorly and fixed in number — ten plus a reduced eleventh in Cephalaspids; seven, with the three anterior ones absent in Petromyzontids.

KIAER was unable to decide the location of the otic capsules in any of the Norwegian Anaspids and the matter still remains in doubt although in *Pharyngolepis* they must have underlain approximately plates *Q*, *Q<sup>a</sup>*, *L*, *M*, *N*, *O*. In one specimen of *Pterygolepis* a pair a lateral depressions are present posterior to the orbital openings on the cranial roof and may be due to the dermal elements having been crushed down on the otic capsules; and in *Lasanius* the capsules themselves, which had a perichondral ossification and were not covered by thick dermal plates, have been identified with even some indication of the actual form of the labyrinth in several specimens. Full descriptions of these two cases will be given on other occasions.

The dermal plates and scales of the cranial roof of *Pharyngolepis* are ornamented with small bony tubercles which are irregularly spaced but which on the larger plates are arranged in rows radiating from the centres of ossification; in the smaller plates and scales such a distribution can generally not be made out. A «mucous-canal» system (see STENSIÖ 1957, pp. 266–267<sup>1</sup>) is slightly developed on some of the cranial plates e.g. on plates *T*, *W* etc. but it is too inconsiderable compared with that in e.g. *Pterygolepis* for a description to have any value. On the trunk scales the tubercles are arranged in irregularly spaced rostro-caudal rows, obliquely transverse to the vertical axis of the scales; a similar pattern is to be seen on the trunk scales of *Pterygolepis* and also in *Rhyncholepis* but in the latter genus the rows

<sup>1</sup> STENSIÖ (loc. cit.) and STENSIÖ & ØRVIG (unpublished) point out that the system of grooves or canals present on the dermal exoskeleton of Ostracoderms was quite clearly not a mucous canal system. The grooves surround, in fact, the individual scale elements which have fused to form larger plates or shields, the bottoms of the grooves lie lower than the depth of the dentinous layer and communicate with the channels and cavities of the basal layer of the exoskeleton. Thus the grooves could contain nerve-endings and blood-vessels which could not penetrate the dentinous layer, and from these grooves the epidermis could regenerate over the compact surface of the exoskeleton. In Anaspida, the outer, compact layers have been lost from the exoskeleton and the grooves are consequently shallow, but still visible though no longer essential since nerves and blood-vessels were able to penetrate all parts of the exoskeleton (Plate VI).

are more pronounced because of the very much smaller size of the tubercles, and the closer spacing of the rows. An appearance suggesting parallel fibres is the result. The same pattern of tubercles is not generally obvious in *Birkenia* since the tubercles are more randomly scattered on the scales; the arrangement of the tubercles on the trunk scales of some specimens of *Pterygolepis* is a little reminiscent of that in *Birkenia* (see Plate V 1 - 4). As STENSIÖ (1957) has pointed out, the scale with fine rows of tubercles and strong basal ridges was probably present in *Jamoytius kerwoodi* WHITE (1946) and the markings interpreted by WHITE as muscle-fibres are, in fact, more likely to be the remains of tubercle rows; the structures which WHITE called myocommata are the thickened, basal, dorso-ventral ridges of the scales. This view is much more in keeping with the state of preservation of *Jamoytius* than the belief that traces of soft tissues have survived in a recognizable form. Reference to an approximately contemporary form, *Lasanius*, from almost the same locality (Logan Water, Lanarkshire), without any consideration of the taxonomic status of *Jamoytius*, reinforces this opinion. For the mostpart, the exoskeleton of *Lasanius* was in a still greater state of reduction and only the merest traces of the basal, dorso-ventral ridges of the scales can be seen in a few, favoured specimens, rows of tubercles are not seen. Of non-calcified internal structures there remain in *Lasanius* only slight traces of a vertebral column and, in one or two examples, what has been taken to be intestine, stained doubtless by its bituminous contents. For the rest, where they remain, the soft tissues form a thin, undifferentiated, carbonized film on the matrix.

A final point of interest connected with the exoskeleton concerns STENSIÖ's suggestion (STENSIÖ 1939) that the dermal cranial roof in Anaspids may not have consisted of fully independant plates. In *Pharyngolepis* the sutures between the plates and scales do, as far as one can judge from imperfect specimens, pass right through the hard tissues but it is possible that some of the grooves on the head e. g. that between plates  $Q$  and  $Q^a$  may originally not have been so deep (in the fossils the matrix is frequently seen in the grooves between plates  $Q$  and  $Q_a$  but this could be the result of a fracture along the line of the groove). In this respect *Pharyngolepis* does seem to differ in some degree from *Pterygolepis* (and probably from *Rhyncholepis*



also) but none of the specimens is complete enough for a definite conclusion to be reached. The matter is, however, of some importance in assessing the extent of the homology between Anaspid and Cephalaspid cranial roofs.

### Note on the Sensory-line System of *Pharyngolepis*

The exoskeleton in Anaspids is represented by only a single, rather thick isopedine layer which was situated in the *stratum compactum* of the corium. The outer layers of the corium were without hard tissue of any kind. Consequently the exoskeleton of Anaspids corresponds to the basal layer only of the exoskeleton in Cephalaspids and Heterostraci, (see further GROSS 1938; STENSIÖ 1939; and the footnote on p. 393 of this paper). The sensory-lines of Anaspids, which the evidence suggests were probably always pit-lines, lay rather superficially in the epidermis and outer parts of the corium and could not, therefore, as a rule cause any grooves to form on the exoskeleton. Exceptions to this rule are, however, found in *Pharyngolepis* where in certain areas the sensory-lines have apparently left markings on the exoskeleton (see Text Figures 8 and 10), this has most likely occurred in places where the corium was particularly thin. These markings are as follows (see Text Figure 8) : firstly, two pit-line grooves meeting at an angle on plate *H*, a longitudinal pit-line groove (*ld*) and a transverse one (*pl*). Associated with these grooves are two more, very consistent, grooves one of which (*ld<sub>a</sub>*) lies between plates *Q* and *Q<sup>a</sup>* and seems to form an anterior continuation of *ld* the other (*pl<sub>a</sub>*) is a transverse groove, sometimes deep, sometimes shallow, which runs from *pl* to the lateral margin of the cranial roof between the otic and the occipital divisions of the cranial roof. The groove *pl<sub>a</sub>* may cross the centres of ossification of plates *J*, *K*, *L*, *M* (as shown on the left side of Text Figure 8) or it may pass more deeply between fully indipen-

view. X 2.8. *a*, *b* = dorso-lateral and lateral scale-fields respectively; *ds* = dorsal ridge scales; *ld* and *ld<sub>a</sub>* = cranial part of dorsal-lateral-line groove; *ll* = pit-line groove belonging to the main lateral-line; *om*, *cb*, *vp* = sensory-line grooves on the cheek and ventral visceral exoskeleton; *pl* and *pl<sub>a</sub>* = grooves corresponding to the posterior pit-line of fishes; *pm* = mandibular plate (see further STENSIÖ 1957, p. 227). For lettering of the cranial roof plates see also Text Figure 2.



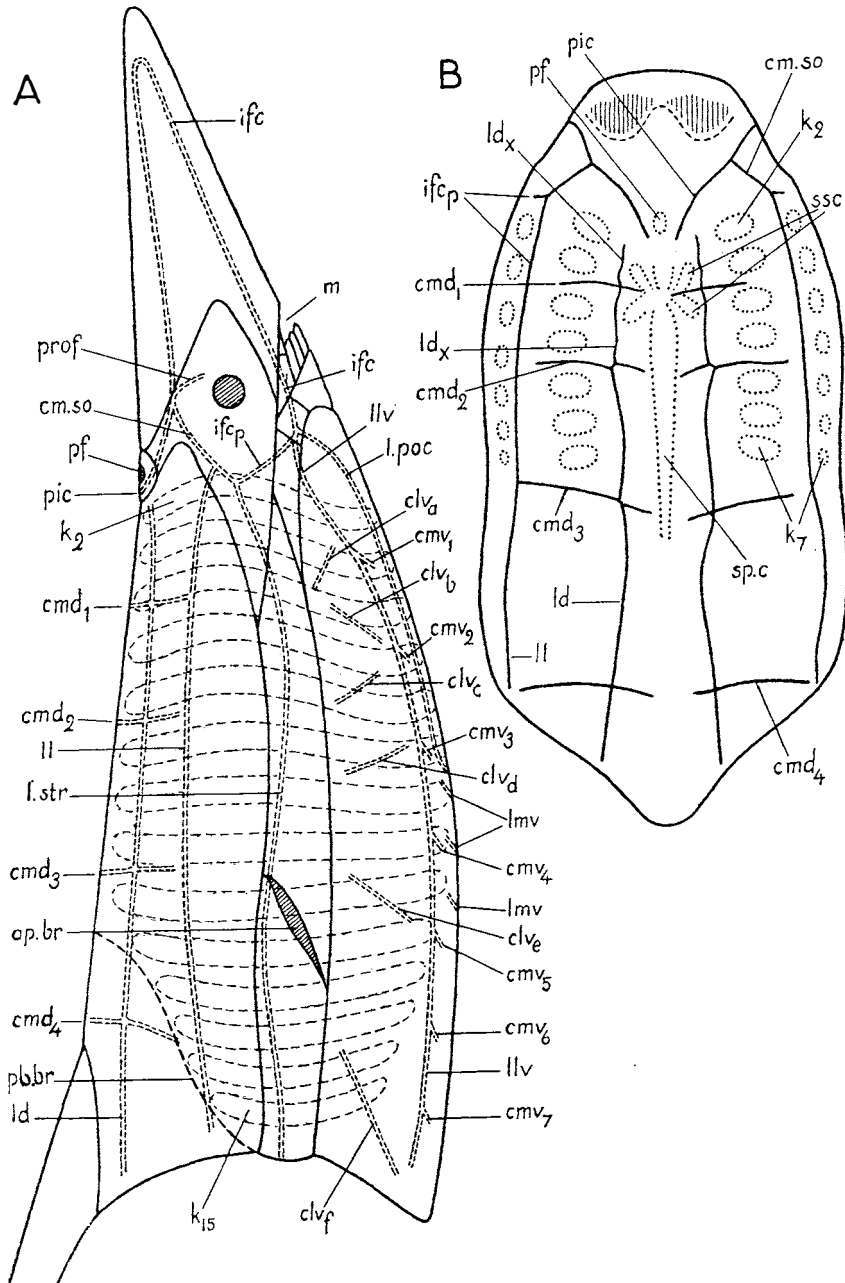


Fig. 9. The text next page.

dant plates  $J$ ,  $J^a$ ,  $K$ ,  $K^a$  etc. (as shown on the right side of Text Figure 8). The grooves  $ld$  and  $ld_a$  of *Pharyngolepis* may be compared with the canal  $ld_x$ , the anterior part of the dorsal lateral-line canal, in a Heterostracan such as *Poraspis polaris* (Text Figure 9 B), and they are found to correspond closely in position;  $ld$  and  $ld_a$  may thus be identified with reasonable certainty as part of the dorsal lateral-line system lying on the cranial roof. The transverse grooves  $pl$  and  $pl_a$  are also seen to have a morphological position closely similar to  $cmd_2$  in *Poraspis polaris*, both running transversely across the cranial roof posterior to the ear (see p. 393). Consequently,  $pl$  and  $pl_a$  are most probably homologous with the so-called «supra-temporal commissure» of *Petromyzon* and with the posterior pit-line of fishes in general (see *inter alia* ALLIS 1889; JARVIK 1948; JOHNSTON 1905; STENSIÖ 1957).

Secondly, in the specimen of *Pharyngolepis kiaeri* (Text Figures 8 and 10) behind the cranial roof in the scale-field  $a$  is an irregular series of short, shallow pit-line grooves ( $ll$ ). These pit-line grooves lie more or less transversely across the scales but in a few instances they appear to lie across the hiatus between two scales. It is quite clear from the position and alignment of this series of pit-line grooves

*Fig. 9.* The sensory-line system in Heterostraci. A, diagram of a generalized pteraspidomorph heterostracan in which a compilation of all the known sensory-line canals and pit-line grooves in Heterostraci, taken from various sources, has been laid in, and is seen in lateral view. Outline of the diagram based on WHITE's restoration of *Pteraspis rostrata* v. *toombsi* WHITE 1935. B, *Poraspis polaris* KIAER, dorsal disc of the carapace to show sensory-line canal system. After KIAER 1932; lettering after STENSIÖ 1957.  $ap.br$  = branchial apperture;  $clv_{a-f}$  = hypotrematic transverse commissural sensory-lines;  $cmd_{1-4}$  = dorsal post-orbital transverse sensory-line commissures;  $cmd_2$  = sensory-line canal corresponding to the posterior pit-line of fishes in general;  $cmv_{1-6}$  = ventral post-orbital transverse sensory-line commissures;  $cm.so$  = supra-orbital transverse sensory-line commissure;  $ifc$ ,  $ifc_p$  = infra-orbital sensory-line canal;  $k_2$  —  $k_{15}$  = branchial chambers;  $ld$  = dorsal lateral-line canal;  $ld_x$  = cranial part of dorsal lateral-line canal;  $ll$  = main lateral-line canal;  $llv$  = ventral longitudinal sensory-line canal;  $lmv$  = median ventral sensory-line canal;  $l.poc$  = post-oral ventral sensory-line canal;  $l.str$  = supra-trematic sensory-line canal;  $m$  = oral opening;  $pb.br$  = probable posterior limit of visceral endoskeleton;  $pf$  = pineal foramen;  $pic$  = pineal sensory-line canal;  $prof$  = «profundus» sensory-line canal;  $soc$  = supra-orbital sensory-line canal;  $sp.c$  = spinal cord;  $ss.c$  = semicircular canals.

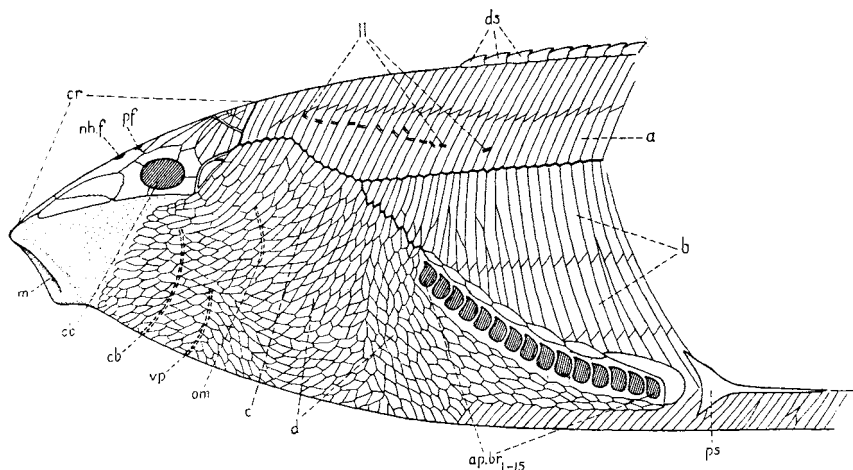


Fig. 10. *Pharyngolepis kiaeri* sp.nov., an attempted reconstruction in lateral view of the head and anterior end of the body and the sensory-line system. X 2. *a* = dorso-lateral scale-field; *ap.br.1-15* = branchial apertures; *b* = lateral scale-field; *c* = cheek exoskeleton; *cr* = cranial roof; *d* = ventral visceral exoskeleton; *ds<sub>1</sub>* = first dorsal ridge scale; *ll* = pit-line grooves corresponding to part of the main lateral-line; *m* = oral opening; *nh.f* = nasohypophysial foramen; *ob* = orbit; *om*, *vp*, *cb* = sensory-line grooves on cheek and ventral visceral exoskeleton; *pf* = pineal foramen; *ps* = pectoral (ventro-lateral scute) apparatus. The stippled area indicates the region of soft tissues around the mouth.

that they belong to the main lateral-line, and are homologous with part of *ll* in *Poraspis polaris* and other Heterostraci (Text Figure 9). Although not marked on the exoskeleton, the main lateral-line of *Pharyngolepis* probably continued back on the scale-field *b* (see Text Figure 10) towards the tail. The pit-line grooves (*ll*) were observed, but not identified by KIAER (1924) and can be seen in his Figure 37, p. 81.

Running almost vertically downwards on the ventral visceral exoskeleton and partly on the cheek (scale-fields *c* and *d* in Text Figure 10) in the specimen of *Pharyngolepis kiaeri* there are three rather faint grooves which have most probably been caused by sensory-lines; in succession from the posterior they are *om*, *vp*, and *cb*. The groove *om* is a most directly ventral to the end of *pl<sub>a</sub>* and a corresponding groove seems to have been present in *Pharyngolepis oblongus* (Text Figures 5 and 6, *om*), *vp* lies at about the level of

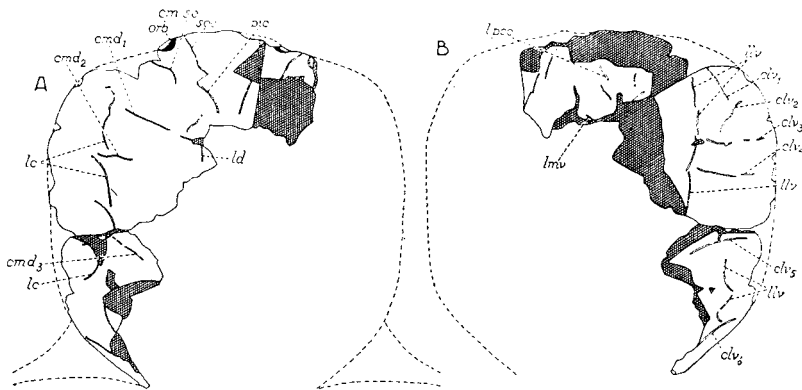


Fig. 11. *Amphiaspis argos* OBRUTSCHEV; showing the sensory-line grooves of the carapace in dorsal (A) and ventral (B) views. From OBRUTSCHEV 1939, after STENSIÖ 1957. X approximately  $\frac{1}{6}$ .  $clv_{1-6}$  = hypotrematic transverse commissural sensory-lines;  $cmd_{1-3}$  = dorsal, post-orbital, transverse sensory-line commissures;  $cmd_2$  = sensory-line groove corresponding to the posterior pit-line of vertebrates in general;  $cm.so$  = supra-orbital transverse sensory-line commissure;  $l.c.$  = main lateral-line groove;  $ld$  = dorsal lateral-line groove;  $llv$ ,  $lmv$  = lateral and medial ventral sensory-line grooves respectively;  $l.poc$  = post-oral sensory-line groove;  $orb$  = orbit;  $pic$  = pineal sensory-line groove;  $so.c$  = supra-orbital sensory-line groove.

the anterior end of the plate *G*, and the groove *cb* is approximately level with the posterior margin of the orbit. Each of these grooves crosses fields of small, rhomboidal scales and it is difficult to make certain of their exact relationships to the scales, but in some cases (even in the same groove) they appear to cross centres of ossification whilst elsewhere they run between individual scales. In the more typical Heterostraci there are no sensory-lines corresponding in position to the grooves *om*, *vp*, and *cb* but in a peculiar and little-known form, *Amphiaspis argos* OBRUTSCHEV (1939) there is a series of six short, rather irregularly arranged sensory-line grooves situated ventrolaterally (see Text Figure 11). This series has been denoted by STENSIÖ (1957) as  $clv_a - clv_f$ . Without entering into a detailed discussion on this *clv* series in the present paper, it may be mentioned that the grooves *om*, *vp* and *cb* in *Pharyngolepis* appear to represent three members of the *clv* series in *Amphiaspis*.

In view of the relationships of the grooves *om*, *vp* and *cb* and espe-

cially of  $ld_a$  and  $pl_a$  to the dermal elements, it is not inconceivable that some of the other sutures and hiatuses between plates and scales in *Pharyngolepis* also housed sensory-lines.

### Acknowledgements

In addition to the acknowledgements already made earlier in the paper, I would like to thank the scientific and technical staff of the Palaeozoology Department of the Swedish Museum of Natural History, Stockholm, for very much help and kindness; in particular I wish to thank Dr. T. Ørvig for instruction in the art of preparing thin sections of fossil material; Mr. U. Samuelson for the photographic part of the work without which this paper could not have been prepared; and Mrs. S. Samson and Mr. S. Eklblom for skillful assistance with the drawings. I would also like to thank Professor E. A. Stensiö, Professor A. Heintz, and Dr. T. Ørvig for advice and criticism during the course of preparation of this paper.

The work was done whilst I was on leave of absence from the University of Glasgow and during part of the time I held a scholarship from The Swedish Institute for Cultural Relations, I am most grateful to both these bodies for having given me the opportunity to carry out this research.

### REFERENCES TO LITERATURE

- ALLIS, E. P. 1889: The anatomy and development of the lateral-line system in *Amia calva*. J. Morphol. Vol. II, No. 3. pp. 463–566.
- BYSTROW, A. P. 1955: On the microstructure of the armour in Silurian and Devonian agnathous vertebrates. In the memorial volume to L. S. BERG. Acad. Sci. U. S. S. R.: Leningrad. (in Russian).
- DEAN, B. 1899: On the embryology of *Bdellostoma stouti*, etc. Festschr. zum siebsigsten Geburtstag von C. von Kupfer. Jena. pp. 221–276.
- GROSS, W. 1938: Der Histologische Aufbau der Anaspiden-schuppen. Norsk Geologisk Tidsskrift, Bd. 17, pp. 191–196.
- JARVIK, E. 1948: On the morphology and taxonomy of the Middle Devonian Osteolepid fishes of Scotland. K. Svenska Vetenskapsakad. Handl. Ser. 3, Bd. 25, No. 1, pp. 301.
- JOHNSTON, J. B. 1905: The cranial nerve components of *Petromyzon*. Morph. Jahrb. Bd. XXXIV, Heft 2, pp. 149–203.
- KIAER, J. 1911: A new Downtonian fauna in the sandstone series of the Kristiania area. Videnskapselskapets Skrifter. 1. Mat.-Naturvid. Klasse 1911, No. 6.

- KIAER, J. 1924: The Downtonian fauna of Norway. 1 Anaspida. Videnskaps-selskapets Skrifter 1. Mat.-Naturvid. Klasse, 1924, No. 6.
- 1932: The Downtonian and Devonian vertebrates of Spitsbergen. 4. Suborder Cyathaspida. Skrifter om Svalbard og Ishavet; Vol. 52, pp. 1–26.
- LEHMAN, J. P. 1952: Etude complémentaire des Poissons de l'éotrias de Madagascar. K. Svenska Vetenskapsakad. Handl. Ser. 4, Bd. 2, No. 6, pp. 201.
- OBRUTSCHEV, D. 1939: Devonian fishes from Euroyka river. U. S. S. R. Acad. Sci. OBRUTSCHEV Jubilee, Vol. 2, pp. 315–330.
- PEACH, B. N. & HORNE, J. 1899. The Silurian rocks of Britain. Vol. 1, Scotland. Mem. Geol. Survey U. K.
- ROBERTSON, G. M. 1937: Anaspida from the Ludlow of Oesel. J. Palaeontol. Vol. 11, No. 3, p. 256.
- SMITH, I. C. 1956: A note on the axial skeleton of the Anaspid *Pharyngolepis* sp. Arkiv. för Zoologi; Ser. 2, Bd. 9, No. 6, pp. 573–577.
- STENSIÖ, E. A. 1927: The Downtonian and Devonian Vertebrates of Spitsbergen. Pt. 1, Cephalaspidae. Skrifter om Svalbard og Ishavet. No. 12, Oslo.
- 1932: The Cephalaspids of Great Britain. London: British Museum (Natural History).
- 1939: A new Anaspid from the Upper Devonian of Scaumenac Bay in Canada. K. Svenska Vetenskapsakad. Handl. Ser. 3, Bd. 18, No. 1 pp. 1–25.
- 1957: Les Cyclostomes Fossiles ou Ostracodermes. in *Traité de Zoologie*, Masson et Cie : Paris (in the press).
- STETSON, H. C. 1928: A restoration of the Anaspid *Birkenia elegans* TRAQ. J. Geol. Vol. XXXIV, No. 5, pp. 458–470.
- STROMER, E. 1926: Weitere Bemerkungen ü. die ältesten bekannten Wirbeltiere-Reste, besonders ü. die Anaspida. Sitzungb. der Bayerischen Akad. der Wiss. Mat.-naturwiss. Abt. Jahrg. 1926, pp. 9–20.
- 1930: Neues ü. die ältesten u. primitivsten Wirbeltiere, besonders die Anaspida. Sitzungb. der Bayerischen Akad. der Wiss. Mat.-Naturwiss. Abt. Jahrg. 1930, pp. 107–121.
- TRAQUAIR, R. H. 1899: Report on fossil fishes. Trans. Roy. Soc. Edin. Vol. XXXIX, Pt. III (No. 32), pp. 827–864.
- 1905: Supplementary report on fossil fishes. Trans. Roy. Soc. Edin. Vol. XL, Pt. IV (No. 33), pp. 879–888.
- WHITE, E. I. 1935: The Ostracoderm *Pteraspis* KNER and the relationships of the Agnathous vertebrates. Phil. Trans. Roy. Soc. London, Ser. B, No. 527, Vol. 225, pp. 381–457.
- 1946: *Jamoytius kerwoodi*, a new chordate from the Silurian of Lanarkshire Geol. Mag. Vol. LXXXIII, No. 2, pp. 89–97.

Manuscript received Sept. 3, 1957.

Printed December 1957.

## PLATES I–VI

(None of the plates are retouched).

PLATE I.

*Pharyngolepis oblongus* KIAER; counterpart of the lectotype. Most of the cranial roof and anterior dorsal trunk squamation is seen in basal (internal) view. Same specimen as in Text Figure 1A. The tubercles on the surface of the plates and scales are visible but most of the underlying bone is missing. Downtonian, Ringerike, Norway. Specimen E. 0122 (Pal. Mus. Oslo). X 3.2. Photographed in xylol.  $ds_f$  = first dorsal ridge scales;  $ld_a$  = cranial part of the dorsal lateral-line groove;  $nh.f$  = nasohypophysial foramen;  $ob$  = orbit;  $os$  = scales of the occipital division of the cranial roof;  $pf$  = pineal foramen;  $pl_a$  = posterior pit-line groove.



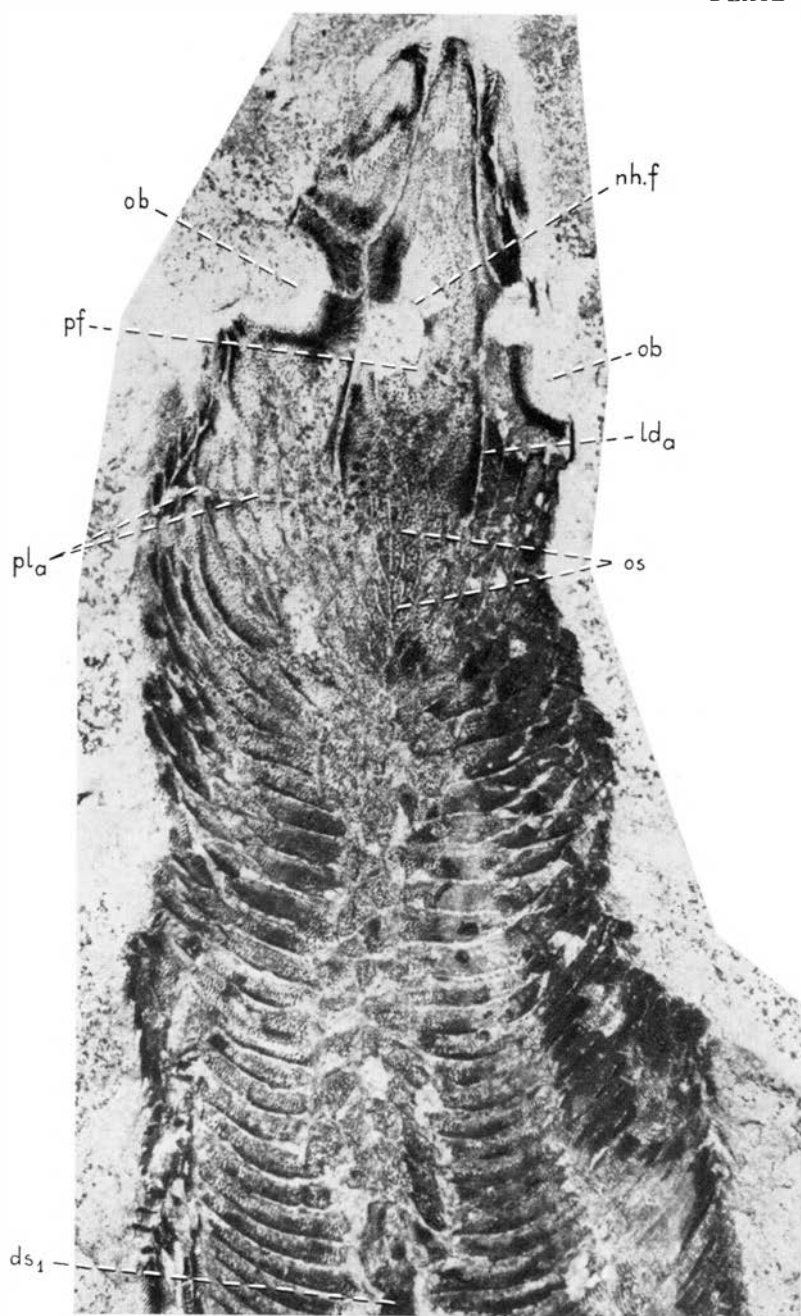


PLATE II.

*Pharyngolepis oblongus* KIAER; part of cranial roof and ventral visceral exoskeleton of the left side in basal (internal) view of Specimen E. 1039 (Pal. Mus. Oslo), Downtonian, Ringerike, Norway. Same specimen as in Text Figure 1B. Much of the bone substance is missing but the surface tubercles are visible. X 4.5. Photographed in 95 % alcohol.  $d$  = ventral visceral exoskeleton;  $H$  = small hexagonal plate carrying pit-line grooves;  $ld$ ,  $ld_a$  = cranial part of dorsal lateral-line groove;  $pl$ ,  $pl_a$  = posterior pit-line groove; other lettering as in Plate I.

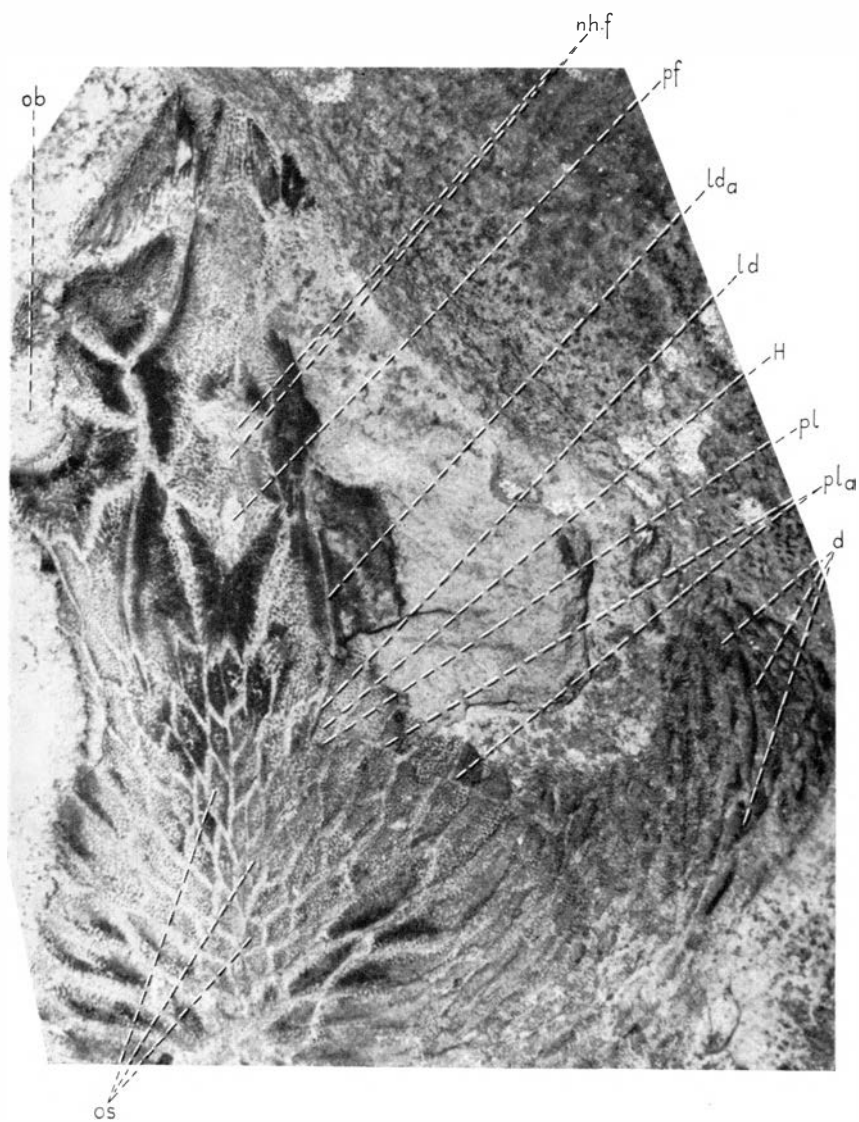


PLATE III.

*Pharyngolepis oblongus* KIAER; mid-median and left side of cranial roof of Specimen E. 1068 (Pal. Mus. Oslo) with adjacent areas of scales including most of the cheek and ventral visceral exoskeleton in basal (internal) view. In general only the superficial tubercles have retained bone substance. Same specimen as in Text Figure 5. Downtonian, Ringerike, Norway. X 3.3. Photographed in xylol. *a, b* = dorso-lateral and lateral scale-fields respectively; *c, d* = cheek and ventral visceral exoskeleton respectively; *ap.br<sub>1</sub>* = first branchial opening; *om* = sensory-line groove on cheek and ventral visceral exoskeleton; other lettering as in Plate I.

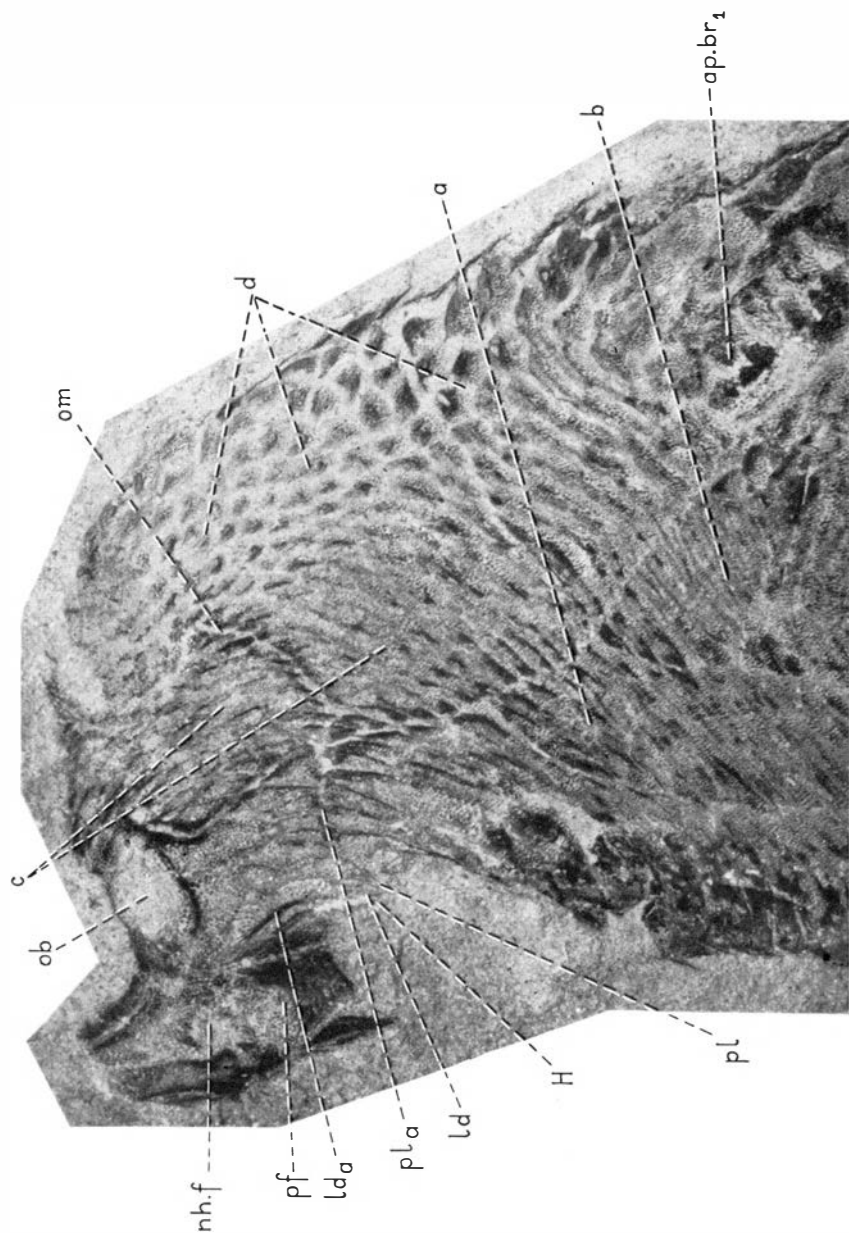


PLATE IV A.

*Figure 1.* *Pharyngolepis kiaeri* sp. nov., holotype. Cranial roof and part of the cheek and ventral visceral exoskeleton of the right side and anterior dorsal trunk squamation of Specimen E. 1043 (Pal. Mus. Oslo) seen in basal (internal) view. Same specimen as in Text Figure 8. Downtonian, Ringerike, Norway. X 3.3. Photographed in 95 % alcohol.

*Figure 2.* Part of a latex impression of the same specimen to show some details in the region of the orbit. X 3.3. Photographed dry and lightly smoked with ammonium chloride. *om*, *vp*, *cb* = sensory-line grooves on the cheek (*c*) and ventral visceral (*d*) exoskeleton; *ll* = pit-line grooves on scale-field *a* belonging to the main lateral-line; *b* = lateral scale-field; *mp* = mandibular plate; other lettering as in Plate I.

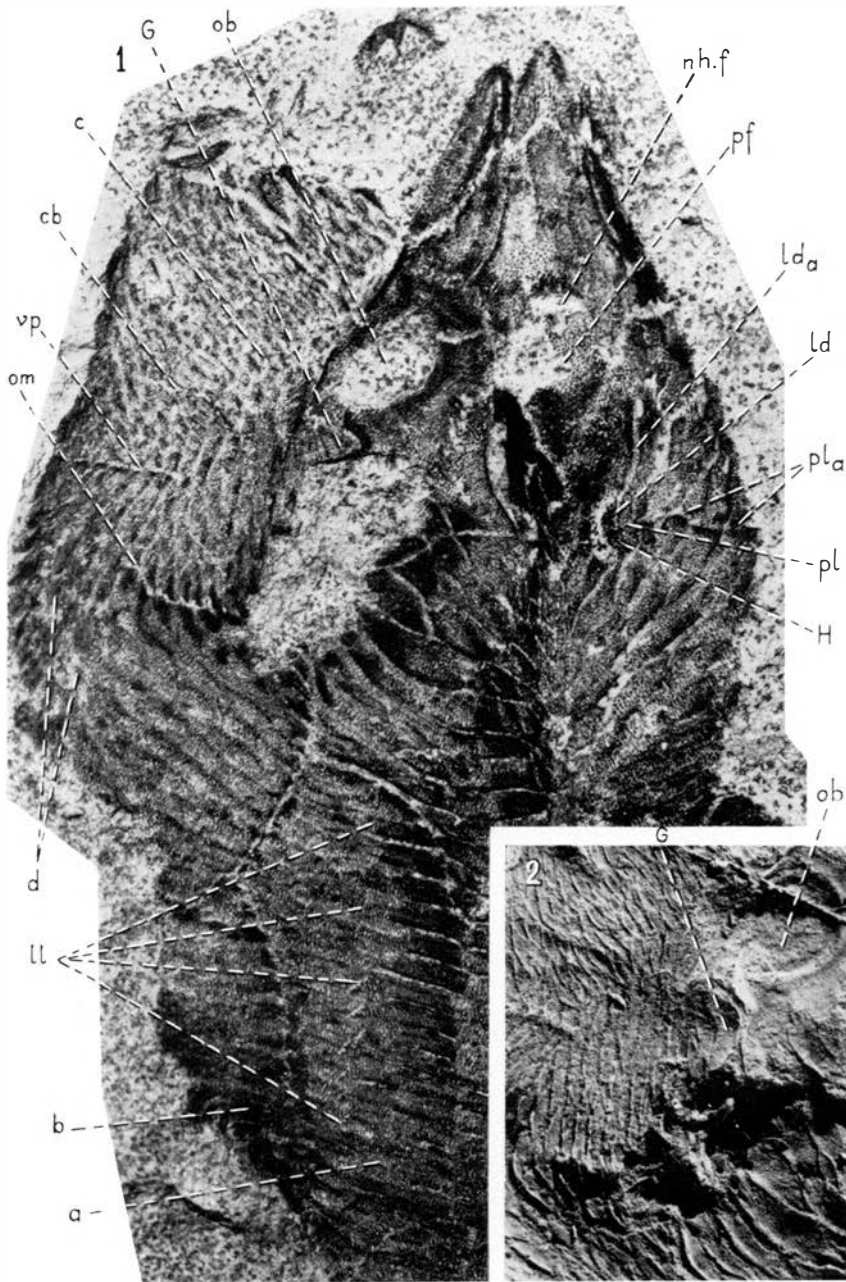


PLATE IV B.

*Pharyngolepis kiaeri* sp.nov., counterpart of the holotype. Specimen E. 1116  
(Pal. Mus. Oslo).



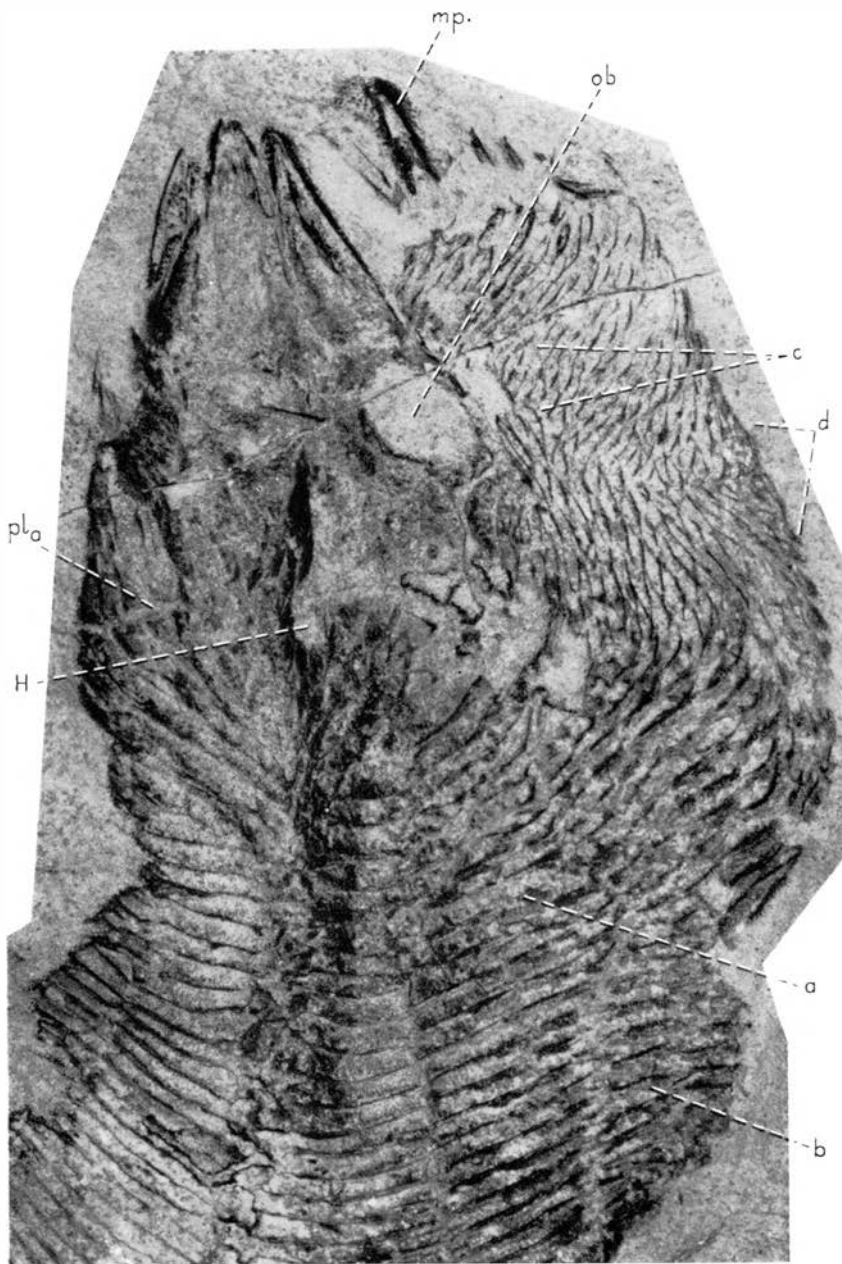


PLATE V.

Superficial features of the exoskeleton of certain Anaspids. 1. *Pharyngolepis kiaeri* sp. nov. Specimen E. 1043 (Pal. Mus. Oslo); 2, *Rhyncholepis parvulus* KIAER. Specimen E. 0177 (Pal. Mus. Oslo); 3, *Pterygolepis nitidus* (KIAER). Specimen E. 0567 (Pal. Mus. Oslo); 4, *Birkenia elegans* TRAQ. Unnumbered specimen in the Kelvingrove Museum, Glasgow.

Exoskeleton in basal (internal) view; all X 15, photographed in xylol. The specimens from Ringerike all retain a certain amount of bone substance on the scales which is brownish and translucent, the specimen of *Birkenia* is, except for some highly carbonized remains, an impression in the rock matrix. *lr* = longitudinal, basal ridges of the scales; *st* = superficial tubercles of the exoskeleton.

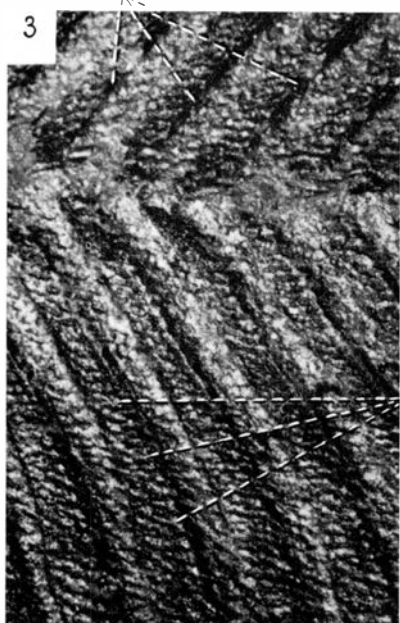
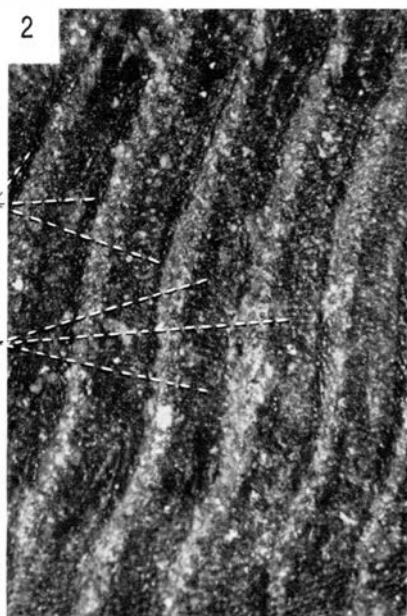
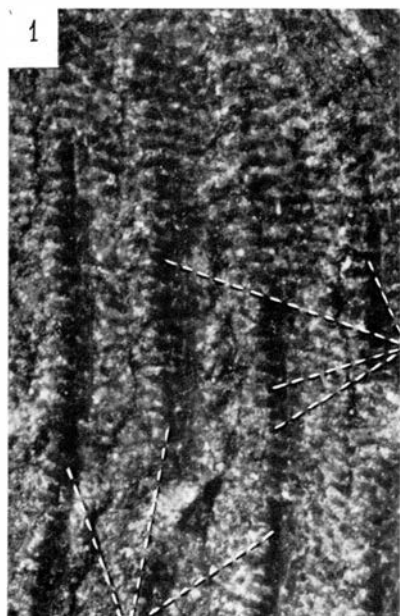


PLATE VI.

*Pterygolepis nitidus* (KIAER), thin section from a dorsal ridge scale of Specimen E. 1041 (Pal. Mus. Oslo) to show the hard tissue of the exoskeleton. Outer margin to the left. X 295. The complete specimen is figured by KIAER (1924) in Plate V.

