SOME REMARKS ABOUT THE STRUCTURE OF PHLYCTÆNASPIS ACADICA
WHITEAVES

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(WITH 6 TEXT-FIGURES AND 3 PLATES)

The interesting Lower Devonian Arthrodira-Phlyctænaspis acadica Whit., known from Campbellton in Canada, was, for the first time described by Whiteaves in 1882 and 1889 under the name "Coccosteus acadicus". Later a number of beautifully preserved specimens was collected in Canada and studied in England by Traquair (who proposed the name Phlyctænaspis) (1890, 1, 1890, 2, 1891, 1893) and Woodward (1892, 1, 2).

During my visit to England in 1930, I had the privilege of examining the large material of this form, preserved both in the British Museum in London and in the Royal Scotch Museum in Edinburgh and already after a short examination I understood that, with our recent knowledge of Arthrodira and especially Acanthaspida, the structure of Phlyctænaspis could be much more completely worked out. Thanks to the courtesy of Dr. Er. I. White, British Museum, and Dr. Grimshaw, Edinburgh Museum, I have received in Oslo for a renewed study the whole Phlyctænaspis material from these two museums. I have now the pleasure to express my deep gratitude to Dr. White and Dr. Grimshaw for their great generosity.

As seen from the following paper I have been successful in finding some new points in the structure of Phlyctænaspis.

The Head Shield.

The head roof of Phlyctænaspis acadica is well known. It is described and depicted in the papers of Whiteaves, Traquair, Woodward, Jaekel and finally discussed by Stensiø (1925). As is known, it represents a typical Arthrodira head roof, with all plates and sensory canals clearly developed. The best picture of the head...
roof is given by Woodward in his paper. "On the lower Devonian fish fauna of Campbellton" (1892, 2). The specimen depicted in this paper (British Museum P. 6555) is especially interesting, as it shows some plate fragments in front of the orbital openings, on both sides of the rostro-pineal plate. Woodward has called these plates as the probable "pre-maxilla" (an older name for the plate, which we now call the post-rostral (Gross 1931) or post-nasal (Heintz 1932). In 1925 Stensiø made a schematic reconstruction of the head roof of Phlyctænaspis acadica, based on a study of the same specimen P. 6555 in the British Museum. Stensiø agrees with Woodward, that the plates in front of the head are the right and left "pre-maxilla" (post-nasal), but he proposed to call them the "plates L." According to Stensiø these plates in Phlyctænaspis acadica have an unusual position. Unlike the conditions in all other forms they are situated between the rostro-pineal, pre-orbital and post-orbital plates in such a way, that the orbital incut is placed between the plates "L" and PtO, and the nostrils between "L" and the rostral plate. Thus PrO takes no part in limiting the orbital opening. In no other Arthrodira is such an arrangement of the plates round the orbits known. It was therefore with the greatest interest that I started the investigation of the specimen in question, which was kindly sent to me by Dr. White. The first glance seems to prove that Stensiø was right. On both sides, in the incut between the R, PrO and PtO plates, were placed some tuberculated plates, which correspond quite well with the picture given by Stensiø (1925, fig. 21). But after a more detailed examination, and especially after I had carefully worked out the single plates, I came to another result. I was able to work out not less than 6 or 7 different plates on each side of the rostro-pineal (Pl. I). This discovery is especially interesting, as the plates found in this region, are not known before in any other Acanthaspida.

The largest plate, which is completely preserved, on the right side of the head roof, and only present as a fragment on the left side, is doubtless the sub-orbital plate (SO, fig. 1 & 2, Pl. I). It was not known before in other Acanthaspida except in Euryaspis brachycephalus Br., where a doubtful fragment was determined by Bryant (1932) as an probable SO plate (Pl. VII, 1).

As usual the SO is composed of a handle (hd. fig. 1) and a blade (bd. fig. 1). The handle is here unusually short and blunt, the blade relatively broad and long. The lower margin of SO is not so straight as
in other forms, but is composed of two parts (a—b & b—c, fig. 1), placed at an obtuse angle to each other. The hind margin (c—d) is straight, the upper (d—e) is convex. From the upper front angle (e) the limit runs in a concave arch to the top of the handle (a). The whole plate is not so plane as is the case in other forms: The surface of the relative narrow brim along the lower margin of the blade and handle is placed nearly perpendicular to the surface of the upper part of the plate, the whole plate being more or less strongly bent along the line a—c (fig. 1). As usual a three branched sensory canal is clearly seen on SO. The upper branch (s1), which is badly preserved in our specimen (fig. 1, Pl. I, 1), runs from the upper front angle downwards, almost perpendicular to the lower margin of the plate. When reaching the lower, bent part of the plate, it branches into two, the one (s2) running onto the handle crossing its front point, the other (s3) running obliquely downwards and backwards and crossing the hind limit of the plate. The two lower canals are unusually deep, looking like real clefts or splits. The whole plate is covered with tubercles, which correspond exactly with those on the head and body carapaces. Unfortunately the configuration of the plate on the inside is unknown. Compared with other Arthrodira the relative size of SO in Phlyctænaspis acadica is unusually small and it is only in Homostius that a somewhat corresponding condition can be found.

In front of the handle of the SO plate, between it and the rostral plate are placed fragments of one (or two?) comparatively small plates (PN? fig. 2, Pl. I, 1, 2, 4). It is, however, so badly preserved, that it is impossible to reconstruct its form and size, but according to its position between the handle of SO and the rostral we evidently here have to deal with the post-nasal plate, or another homologue plate. Thus, in reality, the post-nasal or STENSIO'S plate “L” in Phlyctænaspis was situated exactly in the same place as in all other Arthrodira.
In the space between the sub-orbital and post-nasal on one side and rostro-pineal, pre- and post-orbital plates on the other, we find a group of plates more or less strongly crushed and pressed together, which STENSIØ regarded as the plate "L" (post-nasal). It is especially well-preserved on the right side of the head roof (Pl. I, 1, 3), where it can easily be seen that it consists of 4 plates: Two are seen from the outside (a, b fig. 2, Pl. I, 1, 3), they are thick and covered with tubercles, like all the other plates in Phlyctænaspis. The two others are almost completely covered by the two first, and only a narrow border showing their interior can be seen (c, d fig. 2, Pl. I, 1, 2, 3). The two first are of the same size, quite strongly convex, especially along the outside. Here the plates are broken off, thus only the impression of their interior is seen on the stone, showing some remarkable small folds. According to the position, shape and the presence of these folds, we can hardly doubt, that we here have to do with the sclerotic plates. The two upper (a & b) almost entirely cover the two lower (c & d). The plates on the left side of the head roof (Pl. I, 1) are not so well preserved, but also here we can more or less clearly recognize all the 4 plates (a, b, c, d Pl. I, 1, 2) only they are more strongly crushed and dislocated. Thus the plates, which STENSIØ regarded as the post-nasal, are in fact the sclerotic plates. They are, compared with the sclerotic plates known in other Arthrodira, unusually large and solid. As a rule, in other forms they are much narrower, and especially much thinner, and never have the tuberculated ornamentation so strongly developed. The sclerotic plates in Phlyctænaspis are so large that they would quite fill up the orbital openings if arranged as in other Arthrodira. Thus it is obvious that the sclerotic ring in Phlyctænaspis must form something like a more or less strong capsule protruding from the orbital opening of the head roof, similar to, for instance, the "telescope" eyes in some fishes and birds (fig. 2).

The configuration of the rostro-pineal plate in our specimen also shows some new points. As far as I know it has not hitherto been observed that the front part of the rostral plate and especially the outside front angles are quite strongly bent downwards (fig. 2 R, Pl. I, 1).

The position of the nostrils, which in other Arthrodira are placed between the R and PN plates, cannot be fixed with certainty. It is, however, possible, that they were placed immediately behind...
the front side angle of R, where a somewhat indistinct impression is developed (x, fig. 2, Pl. I, 1, 4).

The hind, pineal part of the RP plate, was well-known from the interior, where in some specimens a clearly fanshaped impression was observed (Woodward, 1892, 2). In our specimen, I was also able to find the pineal fontanel from the outside. It is placed very low down, just in the lower hind angle of the plate, on the limit between the sculptured upper part and the overlapping margin, which was covered by the C plates (Pl. I, 1). In complete specimens this fontanel was probably covered by the upper margins of the C plates, but in our specimen it is distinctly seen, as the RP plate is removed slightly upwards, thus losing its connection with the C plates. Compared with the fontanel in other forms, that in Phylctænaspis is unusually large.

None of the other side plates of the head, can with certainty be determined in the above-described specimen. Seen between, and partly behind the sclerotic plates, however, are fragments of some other plates, which unfortunately are so badly preserved, that it is impossible to determine what they are.

In the other specimen P 6577a in the British Museum, however, two other head plates are clearly seen (Pl. II, 1). The specimen shows the right front part of the ventral carapace (right AVL, AMV and IL) in its natural connection. In front and beneath it is the hind and central part of the head roof seen from the inside (right EB, C and M). The greatest part of the plates themselves are broken off, thus only the impression of their tuberculated surfaces is left. In the centre, above the front part of IL, the C plate is placed; more to the left is the EB and slightly upwards M. Thus the right (on the Pl. II it is the left) outside margin of the head roof is distinctly seen. On its outside hind
corner partly limiting M and partly EB, a small triangular plate is situated (on Pl. II it is seen from the inside) (PM, Pl. II, 1). This plate which must be regarded as the post-marginal, fills up the incut always found in this place in all head roofs of *Phlyctænaspis acadica*. As is known, Traquair described the corresponding plate in *Phlyctænaspis angelica* (1894), and called it angulare.

The second plate is relatively long and narrow and is placed along the outside margin of the head roof (X, Pl. II, 1). Its front part is narrow showing some indistinct ridges, the hind part was doubtless broader, but in our specimen, only the lower part of the plate is preserved, as the upper is broken off, and only an indistinct impression on the stone shows that the plate was originally broader. Along its hind margin runs a remarkable semi-circular impression.

It is difficult to determine with which plate in other *Arthrodira* this corresponds. According to its position along the M and PM plates it seems natural to regard it as an internal, whereas, compared with *Coccosteus* it is too broad and large to represent that plate. It can also hardly be regarded as a sub-orbital, as its outline and position do not correspond with the SO we have described in the specimen P. 6555 in the British Museum. It may perhaps, represent the post-sub-orbital, however, as this plate it is also too large and long. At present therefore it seems impossible to determine it with certainty.

Of greater interest is the presence of the gnathal elements, which were found among the material from the Edinburgh Museum. Even Traquair in 1894 pointed out the presence of these plates and remarked, that they must belong to *Phlyctænaspis acadica*. In all three fragments are known (Pl. II, 2, 3, 4). Two of them represent parts of some long and narrow plates which I regard as fragments of the infero-gnathal plates (Pl. II, 3, 4). One is narrower in front and becomes broader to the rear (3), the other, on the contrary, is broader in front and narrower to the rear (4). On the somewhat bent upper front margin is developed a number of smaller and larger, conical, quite long “teeth”. Unfortunately I was unable to study their microscopical structure, because of the moderate material, but an investigation under a strong lens made it possible to state that their structure is quite similar to that in *Coccosteus* — compact teeth without any pulpa cavity. On the whole the larger teeth are placed in the front part of the jaw, decreasing gradually backwards and finally the hind part of the plate is completely toothless.
As far as one can see, the plate is very thin, not thicker than the basal part of the "teeth". Probably the hind part, corresponding with the "blade" in other forms, either consists of cartilage, or is only very imperfectly ossified. If this is the case it explains why the hind part of IG is not preserved, but only the front part, which corresponds with the functional portion and carries "teeth".

The third fragment represents, as far as I can judge, a complete small plate (Pl. II, 2). It is almost triangular, with one very short, and two comparatively long sides. One of these is slightly concave, the other somewhat convex. Along the convex and the short side are placed relatively large "teeth". They are directed downwards, nearly perpendicular to the surface of the plate, (they are, therefore, not particularly clearly seen on the photographs), quite irregularly arranged not always parallel to each other, and with larger and smaller teeth placed side by side, without any system. The outline and structure of these "teeth" correspond exactly with those in the infero-gnathal plate described above. It is impossible with certainty to determine which of the gnathal elements our plate represents. In my opinion, however, it must be one of the supra-gnathal elements, probably the postero-supra-gnathal. The plate is very thin and it is not impossible that it was strengthened with the help of cartilage.

As these plates are the first fragments of the gnathal elements known in Acanthaspida, they are of rather great interest.

The body carapace.

Much attention has not earlier been paid to the reconstruction of the body carapace in Phlyctænaspis acadica. Two plates were depicted by Whiteaves (1889), a diagrammatic reconstruction of the ventral shield is given by Traquair (1893), and finally Woodward wrote (1892, 1) some remarks about the position and shape of the spinal in this form. Our more thorough knowledge of the structure of the body carapace in Acanthaspida, however, also allows us to understand better the configuration of the carapace in Phlyctænaspis, which is a typical representative of this group. Most useful for the comparison is the new Acanthaspis from the lower Devonian in Overath recently described by Gross (1933, 1).

The body carapace in Phlyctænaspis acadica is in many respects reminiscent of that in Jaekelaspis from Spitsbergen on one hand and that in Coccosteus decipiens on the other. The body carapace in our
form is very seldom found more or less complete and as a rule, only isolated plates, or some few plates connected to each other, can be found among the material. We will therefore first describe the single plates and finally try to give a reconstruction of the whole carapace.

The median-dorsal plate is as usual the largest (MD, fig. 3, 5, Pl. III, 1, 2), and varies quite strongly in outline. The pictures on fig. 3 and 5 must be regarded as the most typical. Some specimens, however, are of the same breadth throughout their whole length and are slightly bent from side to side, while others, on the contrary, are much narrower in the front part and sharply bent from side to side thus forming a crest along the median line. This crest is especially strongly developed in the hind part of the plate, from the ossification centre, which is the highest point (s, fig. 3, 5, Pl. III, 1, 2) and backwards; forwards the crest becomes gradually lower and at the rear it runs abruptly downwards, forming something like a step, which in some specimens can be very distinctly developed.

Most of the MD plates measure in length between 6 and 9 cm but I have also found some few plates only from 2 to 5 cm long. These small plates are comparatively narrow in front, and strongly bent from side to side, with a distinct crest on the median line, thus belonging to the second type of plates I mentioned. As all these different types of MD plates, however, are connected to each other through a number of transitional forms, I propose preliminarily to regard them as individual variations of one and the same species *Phlyctænaspis acadica* of different age.

From the inside the median crest is only moderately developed, and in reality, only in the region of the ossification centre is something like a broad, flat ridge seen. Thus in the configuration of the MD plate, *Ph. acadica* corresponds very well with *Jaekelaspis* from Spitsbergen (Heintz, 1929, 1).

The antero-dorso-lateral plate (ADL, fig. 3, 5, Pl. III, 1, 2) is slightly bent along a line running from the basis of the condylus to the middle protruded part of the hind margin. This line is always clearly marked with the help of a small, narrow ridge. The sensory canal, also starting from the basis of the condylus, runs more obliquely downwards. Thus the above-mentioned ridge, and the sensory canal compose two distinctly, diverging lines, running from the condylus backwards, and represent two very characteristic
Fig. 3. The plates of the dorsal part of the body carapace in *Ph. acadica* from the outside ca. × 3/4. **ADL** — antero-dorso-lateral plate. **AL** — antero-lateral plate. **IL** — interolateral plate. **MD** — median-dorsal plate. **PDL** — postero-dorso-lateral plate. **PL** — postero-lateral plate. **Sp** — spinal plate. **a**—**b** — upper, **b**—**d** — front, **d**—**c** — lower and **c**—**k** — hind margins of the **AL** plate. **h** — ossification centre of **AL**.

Traits in the plate (Pl. III, 1, 2). The condylus itself is moderately developed, but nevertheless is larger than in *Jaekelaspis*. The overlapping margins, especially the one covered by **AL**, are very broad, a condition similar to that in *Coccosteus* (Heintz, 1931). From the inside the plate is quite smooth showing only an indistinct ridge which continues to the condylus. From the description above it is obvious that **ADL** in *Ph. acadica* is remarkably like that in *Acanthaspis heintzi*, described by Gross (1933, 1).
The postero-dorso-lateral plate (PDL, fig. 3, 5, Pl. III, 1, 2) in our form is also almost identical with that in *Acanthaspis heintzi* Gross. It is of about the same size as ADL, also bent along the longitudinal line, which divides it into two almost equal parts. The sensory canal — an immediate prolongation of that on the ADL plate — runs on the lower part of the plate. The overlapping margins are also here very big and similar to ADL, the lower being particularly broad. It is divided into two parts, the front, short one (fig. 3, PDL, a) overlapped by the upper hind corner of AL, and the hind, larger one (fig. 3, PDL, b) covered by PL. From the inside a quite distinct transversal ridge runs along the hind margin of the plate. It composes a part of the consolidated ring, running round the hind opening of the body carapace, and is well-known not only in *Acanthaspida*, but also in *Antiarchi*.

The antero-lateral plate (AL, fig. 3, 4, 5 Pl. III, 1) is relatively large. It was for the first time described and depicted by Whiteaves (1889, Pl. IX, fig, 4), but he regarded it as a median plate. Traquair, however, has already pointed out that this is not the case and that we here have to do with a side plate of the body carapace. It is almost quadrangular (fig. 3, 4) with a clearly-marked ossification centre (h), from which more or less distinctly developed ridges run to the four corners (a, b, c, d) of the plate. They compose a cross like figure (a—h—d and c—h—b) characteristic not only in *Phlyctænaspis*, but also in other *Acanthaspida* (Heintz, 1929; Gross, 1933, 1). It can be mentioned here that also in *Coccosteus minor* the cross ridges on AL are clearly developed.

These four consolidated ridges divide the whole plate into four triangular portions (fig. 3, 4, 5, Pl. III, 1) the upper (a—h—b), the front (b—h—d), the lower (d—h—c) and finally the hind (c—h—a). These 4 sections differ from each other because of their sculpture: On the upper and lower triangles the single tubercles are comparatively large and distinctly arranged in longitudinal rows, running more or less paralleled to the outside margin of the plate. The hind triangle is covered with smaller tubercles, unevenly arranged. Finally, the front triangle shows a more complicated structure, with two other indistinct ridges (h—f and h—g). They divide the whole section into three parts: The lower (d—h—g) is long and narrow covered with closely-set small tubercles. The next (g—h—f) is somewhat broader and shorter, with larger tubercles in rows running parallel to the
outside margin. Finally, the upper (f—h—b) is again covered with smaller tubercles. The front triangle (d—h—b) also shows other interesting features. Almost in the middle of its front margin a clear offshoot (f) is developed and into its point runs the above mentioned ridge h—f. In addition, the whole front triangle is distinctly bent inwards, along the line b—h and h—d, thus forming a quite broad brim, directed into the central part of the carapace (fig. 5, A, AL). As we shall see later, the hind margin of IL was attached to the basal part of this "brim" (f—g—d), indicating that we here have to do with a part of AL, which must correspond with the "hind wing" in *Dinichthys* (Heintz, 1932, 2).

In my paper "Untersuchungen über den Bau der Arthrodira" (1932, 1) I have discussed the gradual change of the outline of AL in different *Arthrodira*. I have described a series: *Coccosteus-Dinichthys-Stenognathus-Heterostius*, and have shown how the configuration of AL in these forms gradually develops in one direction. Now we are able to add to these series some new links, showing the first and most primitive stage of this interesting line of development. In *Jaekelaspis* and *Eleganthaspis* from the lower Devonian of Spitsbergen (and perhaps *Lunaspis*) we find the crossformed ridges on AL well developed, but with the front triangular portion not bent inwards (cf. Heintz, 1929, 1, fig. 8, 9, 11, 13, Pl. IV, 2, Pl. XVI). The hind side margin of the IL plate, comes in contact with the lower part of the front margin of AL in such a way that a sharp angle is formed between the surface of AL and IL (Heintz, 1929, 1, fig. 8 A, 9 B, 12 A, 13 A, 14 B). This condition may be regarded as the most "original". The next stage in the development we find in *Phlyctænaspis acadica*, where, as

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1 On this figure the letter "b" should be placed instead of letter "e".
mentioned, the front triangle shaped portion of AL is bent inwards. Hereby the surface of IL, which comes in contact with this part of AL, composes an immediate prolongation of the lower front part of AL and they are also placed on the same plane. In spite of the front part of AL being bent inwards, it is still covered with tubercles, as for instance in *jaekelaspis*. The next step can be found in *Coccosteus decipiens*. The inwardly bent front triangular part of AL is here strongly reduced and removed far inwards, and has totally lost its tuberculation. The quite large IL with its hind side margin comes in contact with this inwardly-placed part of AL, which I have called "the hind wing". The following stages in the gradual change of the AL plate I have, as mentioned, discussed before (Heintz 1932, 1).

The postero-lateral plate was earlier unknown in *Acanthaspida*. The first to discover it was Gross, who in his recent paper describes it in *Acanthaspis heintzi* (Gross, 1933, 1). I was also fortunate to find this plate in *Ph. acadica*. It is a somewhat long, narrow bone, in shape very similar to that described by Gross (PL, fig. 3, 5, Pl. III, 2). Apparently due to its small size, this plate is very seldom preserved in *Phlyctænaspis acadica*, and among the whole of the extensive material from the British and Edinburgh Museums I was only able to find two more or less complete plates. The shape of this plate, which was strongly connected to PDL and PVL and partly to the upper hind corner of AL, is seen on fig. 3 and 5 and on Pl. III, 2. From the inside PL is smooth, only with a thickened ridge, running along its hind margin.

The spinal plate is comparatively short and broad (Sp fig. 3, 5, 6, Pl. II, 1). I was not able to find either on its inner or its outer margins, any traces of spikes which are so common in many other *Acanthaspida*. It is not often that we find Sp in its natural contact with the AL or AVL plates. As a rule it is preserved either absolutely isolated, or removed from its natural position, a circumstance especially remarkable when we remember that in the majority of other *Acanthaspida*, the spinal is practically always found connected to AVL and sometimes to AL as well. We must therefore suppose that Sp in *Ph. acadica* was not so strongly combined to the neighbouring plates as in other *Acanthaspida*, a condition which certainly must be brought in connection with the absence of the "post-spinal-lamels" (Heintz, 1929, 1) — bony lamels, which in many other
Acanthaspida connect AL, AVL and IL together and divide the cavity in Sp from the body cavity.

The intero-lateral plate (IL fig. 3, 5 A, 6, Pl. II, 1) is comparatively large. As usual it is sharply bent along the longitudinal axis, thus forming two parts, one dorsal (fig. 3, 5 A) and one ventral (fig. 6 Pl. II, 1). The ventral part is an immediate prolongation of the AVL plate and comes also partly in contact with AMV. It is sculptured, as are all the other parts of the carapace, with even small tubercles. The dorsal part is narrow in front and broader towards the rear. On the hind side margin we find a rounded incut where the lower front part of AL fits in perfectly. The front part of the dorsal surface of IL is sculptured not with tubercles, but with narrow ridges, running obliquely upwards and backwards. It is interesting to point out, that corresponding sculpture is found on IL in Dinichthys (Heintz 1932, 2) and Homostius (Heintz, in print). The oblique ridges on IL is perhaps a trait characteristic for this plate in Arthrodira.

The ventral carapace is well developed. As is known, Traquair was the first to give a reconstruction of it (1893), which, however, is not correct in all parts. The shape of the single plates is clearly seen on fig. 6. We can only point out here the unusual shape and size of MV and especially AMV. The hind part of the outside margin of AVL is more or less strongly bent upwards (fig. 5). This curve is still more distinct in the PVL plate, where the outside
Fig. 6. The plates on the ventral part of the body carapace in Ph. acadica. From the outside ca. × 3 3/4. AMV—antero-median-ventral plate. AVL—antero-ventro-lateral plate. IL—intero-lateral plate. MV—median-ventral plate. PVL—postero-ventro-lateral plate. Sp—spinal. x—y—outside front margin of AVL, y—z—side margin of AVL.

margin is strongly curved upwards (fig. 5) and comes in contact with the PL plate. We can also notice that the shape of PVL is incorrectly depicted by TRAQUAIR, as its hind margin is rounded but not incut.

The total reconstruction of the body carapace is given on fig. 5 A, B and C. It is interesting to study the contact between the AL and AVL plates, which shows a condition homologous to that in Coccosteus decipiens (HEINTZ, 1931). The basal part of AL (d—c, fig. 3) comes in contact with Sp, and also, on the other hand, touches the front part of the outside margin of AVL (x—y, fig. 6). Thus the point c on AL and the point y on AVL come in contact and at the same time point z (fig. 6) on AVL touches point k (fig. 3) on AL, (because PVL overlaps the lower part of PL) with the result that the arched hind margin of AL (a—k, fig. 3) coincides with the
arched margin y—z on the AVL (fig. 6). Similar to Coccosteus, no overlapping margins are developed on these parts of AL or AVL, the contact between these two plates being quite weak, as, in fact, they just touch each other with the inner side of their margins. It is the only place in the whole head and body carapace, where such a connection between two plates is developed. In reality, if we remember that the carapace plates are placed in the skin, we have in this place a fold in the skin. The plates are developed both in the upper and lower part of this fold, and touch along the bent line of the fold. The spinal must also be regarded as a double bent plate, lying in a fold of skin and forming an immediate prolongation of the above-mentioned fold. Thus we must accept that on both sides of the body carapace in Phlyctænaspis a fold of skin was developed which stretched from the front point, directly behind the gill openings, backwards, and partly upwards (fig. 5, B) nearly to the middle of the carapace. It is obviously most natural to regard this fold as homologous to the fin folds in other fishes, and the spine of Arthrodira as homologous to the pectoral fins in other fishes, a proposition earlier expressed by Stensio (1931).

When looking at the total reconstruction of the body carapace in Phlyctænaspis we can clearly see that the cross section in the front and the hind part show different pictures: In the front it is almost triangular, in the hind part, seven-sided (fig. 5, A & C). It is also of interest to notice that the basal part of the spinal (fig. 3, d—c, fig. 6, x—y) is placed with the front point (d or x) lying lower than the hind (c or y), with the result that the position of the whole spinal is not horizontal (not in the same plane as the ventral shield), but is directed somewhat obliquely upwards. This again is a condition similar to that known both in Acanthaspida (Heintz, 1929, 1, 2) and Coccosteus (Heintz 1932, 1).

The body scales.

In the stones, with the remnants of Ph. acadica, is often preserved a great number of smaller plates and differently shaped scales (Pl. III, 3, 4, 5, 6). They are either found isolated, or lying more or less near each other forming relatively large groups (Pl. III, 6). I have never seen them, however, arranged in any kind of regular pattern but in some specimens of Ph. acadica, where the body carapace was more or less completely preserved, I observed a great
number of these small scales placed behind the MD plate (Pl. III, 6). This led me to suppose that these scales belong to *Ph. acadica* and have probably covered the hind part of the body and tail in this form. As is known, only in one *Arthrodira — Lunaspis heroldi* Bröili (1930) (an *Acanthaspid*) scales are observed covering the hind part of the body, otherwise in no other *Arthrodira* have body scales been found.

Among our material we can distinguish between 4 different types of scales:

1. The greatest number comprises more or less rhomboidal or sometimes more quadrangular scales, without any clear traces of overlapping margins and with typical *Phlyctænaspis*-like tuberculated sculpture on the outside (Pl. III, 6, a, a).

2. More rare, are some more or less oblong triangular scales with clearly overlapping margins along both the longitudinal sides from the inside (Pl. III, 5). They are strongly arched from the outside, but smooth from the inside, and are thus quite thick and solid. From the outside they are sculptured with large tubercles (Pl. III, 5, 6 b, Pl. II, 6, 7).

3. Also the next type, the fulcra-like, quite big scales are comparatively seldom to be found. They are much bent along the longitudinal axis with a deep incut in the hind margin (Pl. III, 4).

4. The last type is also not very common. They are quite large, thin, roundish scales, smooth on the inside, but on the outside covered with concentrically arranged tubercles (Pl. III, 3).

I have prepared some microscopical sections of these scales and plates to prove that they really belong to *Phlyctænaspis*. Their microscopical structure seems to correspond exactly with that in the head and body plates in *Phlyctænaspis*. We find the same three layers: The outside layer, with typically developed tubercles (Pl. II, 6, a), the median layer with more or less strongly developed vascular canals (Pl. II, 6, b), and, finally, the basal layer, with typical bone lamels (Pl. II, 6, c). The arrangement of the single lamels, vascular canals and bone cell cavities corresponds exactly with that in the plates of *Phlyctænaspis*. Particularly distinct in the outside layer of the tubercles are the characteristic unipolar bony cell cavities (described by Gross 1930, 1932, 2) (Pl. II, 5, 6, 7).

As mentioned above the scales have in no cases been found in their original connection with each other, thus making it difficult to
determine with certainty how they were arranged in the body of Phlyctænaspis. It is only obvious that the fulcra-like scales (Pl.III, 4) were placed along the median line of the body, perhaps forming the basal part of the median fin.

As is known, Acanthaspida must be regarded as a "primitive" central group of Arthrodira, from which all the other forms radiate. Therefore, the new points regarding the structure of this group are always of some general interest.

They show us on one side some likeness between Acanthaspida and the second group of Placoderma — Antiarchi. As already pointed out by Gross and myself, Acanthaspida, among all other Arthrodira, shows the greatest resemblance to Antiarchi — in the general shape of the body carapace, in the presence of spine, which is probably directly homologous to the actinopterygium in Antiarchi and in the remarkable correspondence in form with the PL plate. We can now add to these characteristics two new: 1) A strongly development of the sclerotic rings in both forms\(^1\) and 2) that the hind part of the body is covered with quite solid scales.

These characteristics can in no cases, however, be taken as evidence that Acanthaspida are descended from Antiarchi or the opposite. They show only that these two groups are descended from one and the same ancestor and are more or less closely related.

On the other hand, the new facts concerning Phlyctænaspis give us the possibility in some cases of understanding better the development of the shape of the different plates in Arthrodira. Thus we now know, that originally the sclerotic plates were larger and solid like the plates in the head roof and covered with the ordinary sculpture. In younger forms they are somewhat reduced, thinner and narrower and have lost their sculpture. It also appears that the scale-cover of the body becomes reduced in more specialized Arthrodira.

It is a great pity that the gnathal elements are only known as fragments in Phlyctænaspis, as a more thorough knowledge of the jaw elements in this form, should certainly help us to understand the structure of the mouth in Arthrodira and the relation of their to other fishes.

\(^1\) It must, however, be pointed out, that there are only 3 sclerotic plates in Antiarchi, in Arthrodira — 4.

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PLATES
Plate I.

The head carapace of Phlyctænaspis acadica Wht. British Museum Nr. P 6555.
1. The front part of the head roof.
2. The left orbit enlarged.
3. The right orbit enlarged.
4. The left part of the head roof photographed from the front.

Plate II.


2. The gnathal plate (PSG?) in *Ph. acadica*. Edinburgh Museum 1897/51/125. ca. × 3.5.

3. A fragment of the infero-gnathal plate in *Ph. acadica*. Edinburgh Museum 1897/51/125. ca. × 3.5.

4. Another fragment of the infero-gnathal plate in *Ph. acadica*. Edinburgh Museum. 1897/51/126. ca. × 3.5.

5. Some unipolar bone cell cavities in the tubercles of a carapace plate in *Ph. acadica*. ca. × 300.

6. Cross section of a scale in *Ph. acadica*. ca. × 30. a. — outside layer, b. — vascular layer, c. — basal layer.

7. Tubercles with unipolar cells from a scale in *Ph. acadica*. ca. × 100.

8. Tubercles with the unipolar cells from a body plate in *Ph. acadica*. Compare with the structure of the scale. ca. × 100.
A. Heintz: Phlyctænaspis.

Pl. II.
Plate III.


3. A roundish thin plate in *Ph. acadica*. British Museum P. 7084. ca. × 2.

4. A fulcra like scale in *Ph. acadica*. British Museum P. 6559 b. ca. × 2.

5. A long narrow scale in *Ph. acadica*. Edinburgh Museum Nr. 1897/51/125. ca. × 4.

6. A plate with many body scales situated behind the median-dorsal plate (MD). a — rhomboidal scale, b — long, narrow scale. Edinburgh Museum 1897/51/128. ca. × 1.