NOTES ON ARTHRODIRA

BY

A. HEINTZ

Abstract. In the first part of this paper a description is given of Coccosteus minor Miller, a minute form, which in some respects represents an intermediate stage between Coccosteus decipiens and Phlyctænaspis. The material is preserved in the Royal Scottish Museum, Eddinburgh.

The second part deals with the development of the gnathal elements in Coccosteus decipiens and shows that the position of these elements as proposed by Watson is not correct. The reconstruction of the body carapace is discussed in detail and indicates that the reconstruction proposed by Watson is, likewise, probably not altogether accurate.

Further, a description follows of the skin fragments, the stomach contents and the shape of the tail in C. decipiens.

In the last part the discovery of pectoral fin fragments in C. decipiens is described and, in connection herewith, the development of the pectoral fins in Arthrodira discussed.

During my visit to England and Scotland in the Summer 1937 I had the opportunity inter alia of re-studying the large collections of the Devonian Placoderms preserved in the British Museum of Natural History, London, and in the Royal Scottish Museum, Edinburgh. I give below a short account of my investigations.

In this place I wish to express my warmest thanks to Dr. E. I. White of the British Museum and Dr. Stephen of the Royal Scottish Museum for the great kindness they showed me in allowing me to study the collections and in giving me permission to describe some of the material. During my visit they helped me in every possible way and assisted me in all directions. Dr. Stephen has kindly lent me some specimens from the Royal Scottish Museum. And to Dr. White I am especially obliged for the many interesting and instructive discussions about the structure of the Arthrodira.
I. Description of *Coccosteus minor*  
H. Miller.

This minute specimen of Coccosteus is known from the middle Old-Red of Scotland. In addition, uncertain fragments are described from Estonia (Gross 1933). Robert Dick was the first to collect it, and H. Miller described it briefly (1858), under the name *Coccosteus minor* “until such time as some person better qualified furnishes the creature with a more characteristic one.” (H. Miller, 1858, p. 396).

The next to mention *C. minor* was Traquair, in “Old-Red Sandstone Fishes” (1888) where he pointed out, that *C. minor* is “most certainly extremely distinct from the ordinary . . . examples of the genus” (=*C. decipiens*). The following year (1889) in a paper about the structure of *Homostius*, he gives a picture of *C. minor* without, however, any description in the text. Also in Traquair’s paper about the structure of *Coccosteus decipiens* (1890) *C. minor* is mentioned only, but not described. The most complete description of it is given in Woodward’s “Catalogue” (1891), but here without any picture. *C. minor* has since been mentioned by many authors, especially in stratigraphical papers, but it has never been described in detail.

I will therefore try to give a more complete description of it, as this form in many respects is of great interest, showing a number of characteristics, transitional between *Phlyctænaspis acadica* and *C. decipiens* (Heintz 1931, 33).

The question of the “Holotypus” of *Coccosteus minor* appears to be rather complicated, as H. Miller, who proposed the name, neither depicted nor described any particular specimen, which could be chosen as Lectotypus. Traquair in 1889 depicted one very well preserved specimen (Royal Scottish Museum 1254) (Pl. I, 1; fig. 2, 2). Among the material in the Royal Scottish Museum is a quite good specimen labelled "Type" (R. S. M. 1317), (Pl. II, 3; fig. 2, 3), also another specimen, representing only the *MD* plate, is labelled “Figured”. I have, however, not been able to discover who has chosen the mentioned “Type” or figured the *MD* plate, and it is also unknown whether the marked specimens have ever been depicted or described.

---

1 The explanation of letters in the text and in all textfigures, see p. 26.
Fig. 1. Reconstruction of *Coccosteus minor* Miller.
1. Head shield. 2. Dorsal body carapace. 3. Ventral body carapace. 4. Hind part of *MD* plate seen from the inside. 5. Hind part of *MD* plate seen in longitudinal section. 6. *SP* seen from the side and underside. 7. *IL* seen from outside and inside.

It therefore seems most natural to regard the specimen depicted by Traquair in 1889 as Lectotypus for *Coccosteus minor*. It is figured by him on Pl. I, fig. 3, and in this paper on Pl. I, 1; fig. 2, 2.

As a whole *Coccosteus minor* is very similar to *C. decipiens* showing the same plates in the head and body armour which are known in the latter, with almost the same shape and relative position (Pl. I; II; fig. 1; 2). But it is easily distinguished by its minute size. The largest *MD* plate I measured in the Royal Scottish Museum was 34 mm long (in the Br. M. I have seen larger plates), its average length being ca. 28 mm, while the smallest *MD* I have measured in
Coccos teus decipiens was ca. 47 mm, the largest ca. 120 mm. It is not only the size, however, which separates these two forms, but a number of characteristics in the configuration of the single plates, makes it easy to determine C. minor.

As a whole, the sculpture in our form is much finer than that in C. decipiens. Also the sensory canals are finer, often more indistinct.

On the other hand, the single plates seem to be relatively more solid than those in C. decipiens, and the vertebral column is more completely ossified (Pl. I, 1). In many specimens the single plates seem to be more strongly fitted together than is the case in C. decipiens. The SO plate, for instance, is practically always in contact with the head shield, and the Internal and the PSO are always preserved in situ (Pl. I; II, 1, 3; fig. 2). But also a large number of isolated plates of C. minor is known, especially those of the body carapace.

I do not intend to describe below the single plates in the armour of C. minor, as its shape is perfectly seen in the figures and plates, but only to point out the most interesting characteristics in its construction, the characteristics which distinguish it from C. decipiens.

The head shield (Pl. I; II, 1, 3; fig. 1; 2) in its configuration is very reminiscent of that in C. decipiens. A characteristic feature, however, is that the plate in the cheek-region, which in C. decipiens is only loosely attached to the head roof, here seems to be very solidly fixed (Pl. I, 1; II, 1). In this respect, C. minor reminds one of the Arthrodira from Wildungen, where this condition has become a rule. The development of the PM plate is interesting, it is much larger than in C. decipiens and comes in contact with M, PtO and EB (PN). In Phlyctænaspis PM touches M and EB, in C. decipiens it is strongly reduced and only comes in contact with the M plate (Heintz 1931). The same is the case in Dinichthys (Heintz 1932).

Also the Internal is relatively large, somewhat shorter, but broader than in C. decipiens (I, Pl. I; II; fig. 1; 2). The SO is probably the plate which in its development differs mostly from that in C. decipiens. Its front part is relatively very broad covered with tubercles, while the hind part is more slightly developed. As a whole SO is reminiscent of the corresponding plate in Phlyctænaspis acadica, where, however, the front part is still shorter and broader (Heintz 1933, fig. 1). It is also interesting to notice the development of tubercles on the anterio-
Fig. 2. Parts of the head shields of *Coccosteus minor* Miller.

3. Specimen Nr. 1317, R. Sc. Mus. Edinb. Specimen is labelled as “Type”.

ventral margin of the plate; in some specimens they become large, long and pointed forming a row of more or less strongly developed “teeth” (*SO*, Pl. I, I; II, I; fig. 1; 2).

The *PN* (=post-rostral, Gross) is present in many specimens. It is a comparatively large thick plate, which comes in contact with *R*, *SO* and *PrO*. It did not show any incuts for the nostrils, known in *C. decipiens*, nor the continuation of the Supra-orbital sensory canal, known both in *C. decipiens*, *Dinichthys* and some of the Wildungen Arthrodira. On this plate the tubercles also are very distinctly developed having a still more tooth-like outline than is the case in *SO*; especially those along the ventral margin are large (*PN*, Pl. II, I; fig. 1; 2, 1, 3).

Almost the same can be observed in the *R* plate, which otherwise is very similar to the corresponding plates in *C. decipiens* and
Phlyctænaspis acadica. Here again real “teeth” are developed on the anterio-ventral margin (R, Pl. I, 1, 2; II, 1; fig. 1; 2).

The function and significance of these sets of teeth are difficult to understand. They were situated in front, and dorsally to the mouth opening, and could thus hardly be used as real teeth. So far as I am aware no corresponding structures are known in other Arthrodira.

The other plates in the head roof of C. minor are quite similar to those in C. decipiens. Their configuration and position are clearly seen on Pl. I; II and fig. 1, 1; 2.

The gnathal elements are imperfectly known. Among the material in the Royal Scottish Museum I did not find any specimens distinctly showing them. In the Lectotype (IG, Pl. II, 1; fig. 2, 1) in the orbital opening, I noticed two long and narrow bones with a row of more or less strongly developed teeth. They may probably represent the front parts of both the IG plates. As mentioned above, they are very weak and narrow, more reminiscent of the IG I described in Phlyctænaspis acadica (1933, Pl. II, 3, 4), than of those in C. decipiens.

In some other specimens a small smooth plate with a row of teeth along one margin has been observed (SG, Pl. I, 2). It is most probable that we have here to do with the PSG elements. This plate is also reminiscent of the plate I described in Phl. acadica as a probable PSG plate (Heintz 1933, Pl. II, 2).

The gnathal elements in C. minor were apparently neither so strongly developed nor so completely ossified, as those in C. decipiens, for which reason they are only very seldom preserved in the fossil.

The body carapace (Pl. I, II; fig. 1, 2 7) is also very similar to that in C. decipiens, at the same time showing some characteristics reminiscent of Phlyctænaspis.

MD is slightly narrower, than in C. decipiens, running posteriorly into a distinct and comparatively long spine (Pl. I, 1; fig. 1, 2, 4, 5). This spine is directed a little upwards, its posterior part is completely rounded in cross-section, indicating that the spine protuded somewhat through the skin, forming a real spine. The ridge on the ventral side of MD is always present, but was broken off in all the specimens I have examined, thus preventing me from determining its exact size. The sensory canals on the dorsal side of MD were indistinct.

The AL plate (Pl. I, 1; II, 1; fig. 1, 2) is shorter and broader than that in C. decipiens, more reminiscent of that in Phlyctænaspis and in Jaekelaspis (Gross 1933, 37, Heintz 1929, 33). The four
consolidated ridges, which in Acanthaspida run from the centre of the plate to the four corners are distinctly seen in our form (but never in \textit{C. decipiens}). The lower part of \textit{AL} is somewhat concave, similar to \textit{Phlyctænaspis} and \textit{C. decipiens}, while, on the contrary, the upper larger part is slightly convex giving the whole plate a S-shaped outline in section. The “inner wing” in \textit{AL} (Heintz 1931, 32) is faintly developed, but more distinct than in \textit{Phlyctænaspis acadica} (Heintz 1933). Especially characteristic is the very large lower margin of \textit{AL}, to which the \textit{SP} is attached. Once more a condition reminiscent of that in \textit{Phlyctænaspis}.

The \textit{IL} plate is very large and is perfectly preserved in a number of specimens (Pl. I; II, 2; fig. 1, 3, 7). It is slightly broader in the lateral part, than the corresponding plate in \textit{C. decipiens} and much broader than that in \textit{Phlyctænaspis} (comp. Heintz, 1931, fig. 9, 11, 1933, fig. 3, 5), and it is remarkable to notice that in shape and sculpture (rows of minute tubercles) it is reminiscent of \textit{AL} in \textit{Dinichthys} (Heintz, 1932, fig. 62).

The \textit{SP} (Pl. I; II; fig. 1, 2, 3, 6) is one of the most characteristic plates in \textit{C. minor}, distinguishing it sharply from \textit{C. decipiens} and connecting it with \textit{Phlyctænaspis}.

It is pointed at the posterior end, almost twice as long as that in \textit{C. decipiens}, while it is shorter than \textit{SP} in \textit{Phlyctænaspis} and not so flat as the latter. Similar to Acanthaspids and Coccosteids it is connected to \textit{AL}, \textit{IL} and \textit{AVL}.

The \textit{PL} is small, however, comparatively larger than in \textit{C. decipiens}, but its outline is more similar to the Coccosteids than that of the Phlyctænaspids. The ventral corner is overlapped by the anterio-dorsal offshoot of \textit{PVL} exactly as is the case in \textit{C. decipiens}.

The ventral carapace (Pl. II, 2; fig. 1, 3) corresponds entirely to that in \textit{C. decipiens} or \textit{Phlyctænaspis}. The \textit{AVL} was connected by its anterio-lateral margin to \textit{IL} and \textit{SP}. Its somewhat curved posterio-lateral margin corresponds in its shape to the posterio-lateral margin of the \textit{AL} plate. As I have already pointed out in the description of \textit{C. decipiens} (1931) and \textit{Phl. acadica} (1933), these plates do not overlap each other, but may only touch each other on their inner sides. It is, however, very probable, as Watson (1934) has pointed out in \textit{C. decipiens}, that they are divided from each other by a narrow slit. I shall discuss this question in greater detail later on.
The AMV, PMV and PVL are almost diminutive copies of the corresponding plates in *C. decipiens*. The PVL is probably slightly narrower, and its posterio-lateral corner is drawn out into a longer “spine” (Pl. I, 1; II, 2; fig. 1, 3).

I have observed a very unusual pair of plates in three specimens of *C. minor* (Pl. I, 2; II, 1, 3; fig. 1; 2, 1). They are placed in the opening between the head and the body carapace, more precisely, between the hinder margin of *MB* and the front margin of *MD*. They represent two tuberculated small plates broader on one side, narrowing towards the other and they more or less completely fill out the opening between *MB* and *MD*. In one specimen a sensory canal(?) was apparent running along the longitudinal axis of the plate (Pl. II, 1; fig. 2, 1).

The presence of such plates has never been observed in any other Arthrodira. In fact, it is very remarkable that any plates have been situated in this region, as they will only prevent the movement of the head shield up and down. It is not excluded that they are only plates or plate-fragments, which are removed, and really belonged to another part of the carapace. It is however, difficult to determine what other plates they may represent. Two of the specimens, where I found these plates, are very well preserved with all the other plates present in their natural positions. These two plates are not similar to any of the others in the carapace, they are completely symmetrically situated, on both sides of the median line of the animal, and the right and left plates are absolutely similar. This indicates that very probably we have here to do with two new plates, which hitherto have not been observed. Perhaps more careful investigations of other specimens of *Coccosteus*, may reveal more of these plates.

The inner skeleton is more imperfectly known in our form. The spinal column, which is preserved in some specimens (Pl. I, 1) seems to be somewhat stronger ossified than in *C. decipiens*; the neural and hemal arches, on the contrary, are more indistinct. The pelvic girdle is also known and is represented by two narrow S-shaped bones (Pl. I, 1). No fin-rays supporting the median-dorsal or pelvic fins have ever been observed. Also the sub-median-dorsal plate and the plate supporting the anal fin(?) is unknown in *C. minor*.

As we have seen, *C. minor* in the majority of its characteristics corresponds closely to those in *C. decipiens*. In some, however,
it shows a relation to *Phlyctænaspis* and we may therefore regard it as a more "primitive" form. In the row of development *Jaekelaspis Dinichthys* (comp. Heintz 1931, 33) it must be placed between *Phlyctænaspis* and *C. decipiens* (fig. 7, 3).

Finally, I shall give a new definition of *C. minor*, which, however, only represents a somewhat enlarged and altered classical definition given by Woodward (1891).

**Coccosteus minor** H. Miller (1858) is a very small species, with a carapace attaining a maximum length of about 50–70 mm. The cranial shield is broader than long. *PN* relatively large. On the anterio-ventral margin of *R, PN* and *SO* tooth-like tubercles are developed, *SO* broad in the front part. *PSO* small. *I* short and broad. *PM* large, touching *PoO, M, I* and *EB*. The gnathal elements imperfectly known, it seems that the *IG* teeth are very slender and sharply pointed. The *MD* plate about twice as long as broad, gradually tapering posteriorly into a long, blunt point. *AL* relatively broad and short, four distinctly developed consolidated ridges running from the centre of the plate to each corner. The hind wing very moderately developed. The ventral margin coming in contact with *SP* is very long. *SP* relatively long. *IL* large, broad in its lateral part. *PVL* twice as long as broad, at each posterior-lateral angle protruding into a short spine. Tuberculation numerous, of minute size, never confluent and not arranged in definite lines. Column and pelvic girdle are well ossified. Middle Old-Red Sandstone, Scotland (Caithness and Orkney) and probably Baltic states (Estonia).

**II. Remarks on Coccosteus decipiens AG.**

In 1931 I published a description of *C. decipiens*, chiefly based on my studies of the collections in the British Museum and in the Royal Scottish Museum, where I gave a new reconstruction of this form. In 1934 Professor Watson published a paper on the "Interpretation of Arthrodira", where, in a discussion of the structure of *Coccosteus*, he pointed out some mistakes, which, in his opinion, I had made in my reconstruction. Finally in 1935 he published a new reconstruction of *Coccosteus*.

With regard to the mechanism of the jaw in Arthrodira, I completely agree with Prof. Watson in his conclusion, a conclusion, which
is thoroughly in accordance with Stensio's investigation (1934). But in some other points it seems to me, that Watson's reconstruction is not altogether accurate, not giving a true picture of the structure of *Coccosteus decipiens*. The most detailed examination of the material in London and especially in Edinburgh, has, as far as I can judge, supported my reconstruction of 1931. I shall below briefly try to state my opinion and at the same time describe some new details, which I have discovered in the structure of *C. decipiens*.

The Head shield.

In Watson's reconstruction (fig. 4, 2) the head shield is depicted shorter and higher than in mine, the Internal in my opinion, is too broad and the *PtO* too small. But it is quite impossible, however, to discuss such details, as the plates will always diverge to some extent.

The greatest difference between Watson's and my reconstruction lies in the position and shape of the gnathal elements. In the drawing by Watson the supra-gnathal elements are not altogether distinct, as he has only depicted them from the ventral (palatal) surface, not giving any drawing showing them from the lateral-, anterior- and inner sides. The description alone does not give a sufficiently clear picture of them.

In some of the specimens from Edinburgh the gnathal elements are well preserved, and can be studied from various sides. Especially one piece, which I have partly prepared, shows all the 6 gnathal plates almost in their natural relation. In fig. 3, 6 one can clearly see the single elements. The left *ASG* is relatively broad in the front, and shows a double row of teeth-like tubercles on the anterior surface. Both the *PSG* are seen from the ventral side, their basal parts are not exposed. But it is obvious that we also here have two rows of tooth-like tubercles, and teeth also along the ventral ridge. According to Watson's description, it is obvious that the supra-gnathal elements have also two somewhat diverging rows of teeth. In other hitherto known *Coccosteus* specimens, the double row of teeth in the *PSG* have earlier been described in *C. livonicus* by Gross (1930, 1933), in *C. trautscholdi* by Obrouch (1931). I have, myself, seen the gnathal elements in *C. canadensis* developed in the same manner. In fig. 3 are depicted *ASG* and *PSG* from these three *Coccosteus* specimens.
In all of them one can see that PSG has distinctly developed the double row of teeth placed in a vertical position. Along the lower margin however, the teeth are not developed. In ASG no teeth can be seen in C. canadensis (fig. 3, 4, 5), but in C. livonicus (fig. 3, 1), one row is placed along the anterior margin. It seems, therefore, quite obvious that originally the supra-gnathal elements in the Coccosteids had well developed teeth in two rows, which, as Watson points out, corresponds to the double row of teeth in the infero-gnathal. This set of teeth, seems to have been of a grasping character. In the full grown Coccosteus however, both the supra-gnathal and infero-gnathal elements developed sharp cutting edges, thus completely changing the function of the “set of teeth” from grasping to cutting. In C. minor it seems, that the grasping function is maintained through out the whole of life: in this form one can usually see the relatively sharp and long “teeth”. The gnathal elements in this form are, however, hitherto imperfectly known. In C. decipiens the teeth are dominant in the younger specimens, the cutting edges becoming stronger and more developed in older individuals. The teeth are, however, still to be found in ASG and PSG in all specimens. In the larger Coccosteus, as in C. livonicus, the cutting edges are absolutely dominant. But we can still find the vertical rows of teeth both in the front margin of ASG and two vertical rows in PSG (fig. 3, 2). In C. canadensis the teeth in all cases in the full-grown specimens — have completely disappeared from ASG, but are still preserved in two rows in PSG (fig. 3, 4, 5). Finally, in Dinichthys the double row of teeth have also disappeared from PSG, and only along the posterior margin of it may traces of teeth still be observed. (In some species of Dinichthys, however, teeth can also be found in ASG.) Corresponding to this change the teeth of the infero-gnathal have gradually been replaced by cutting-edges, the teeth in the anterior edge having kept for the longest time, and may still be found in Dinichthys and other Arthrodira from upper Devonian.

Watson in his description and figures (3 & 4) pointed out that in Coccosteus “the supra-gnathals placed in their correct position . . . are very widely separated from one another” and that “in Dinichthys a reconstruction found on Heintz’ figures shows that they are even more widely separated”. I can hardly understand how Watson could draw such a conclusion according to my drawings. His figure 4, depicting Dinichthys head from above, with the gnathal elements in
Fig. 3. Gnathal elements in different Coccosteus species.

“natural position” taken from “Heintz figures without modification” is certainly wrong in my opinion. So far as I can judge, in all my drawings it is absolutely obvious that the supra-gnathal elements are not so small in relation to the head as is shown by Watson. My figure 81, a front view of the reconstructed head in Dinichthys is in complete agreement with all my other figures, and so far as I can conclude from the enormous material in the American Museum and the splendidly preserved material in Cleveland Museum, quite correct. The marvellous carapace of Dinichthys, mounted by the late Professor Hyde in Cleveland consisting of the bones of one single
specimen, shows the relation between the gnathal elements and the head roof closely corresponding to my reconstruction in fig. 81. Also with regard to Coccosteus, I am sure that Professor Watson is mistaken. His fig. 3 showing "the Supro-gnathals in their natural position" does not seem to be exact. The gnathal elements are depicted too small and too far removed from each other. So far as I could see, in all specimens of Coccosteus where the gnathal elements were preserved, they were much larger in relation to the head shield. (In Watson's picture the head shield and gnathal elements are taken from different specimens.)

The distance between the right and left ASG must have been relatively very short. Firstly, we have seen that this distance is very short in Dinichthys; secondly in the Wildungen Arthrodira with well preserved gnathal elements in situ, the ASG almost touch each other (Gross 1930, Stensiö 1934); thirdly, in many well preserved specimens of Coccosteus, they are situated close to each other. Finally, the position of the infero-gnathals points in the same direction. Watson supposed that both in Dinichthys and Coccosteus "the anterior ends of the infero-gnathals . . . were very widely separated from one another". As we know, in the Wildungen forms this is not the case, and in Leiosteus, for instance, Jaekel, and in the later time Gross (1930) and Stensiö (1934) have found ossified rostral parts of the Meckelian cartilage, which kept the right and left rami closely together. In the collection of Professor Hyde, Cleveland, is one specimen of Dinichthys, with corresponding ossifications in the front part of the infero-gnathal, showing that the infero-gnathals were placed quite closely to each other. In one specimen of Coccosteus decipiens from Edinburgh, I have been successful in finding two parts of the same kind of ossification (Pl. III, 4, D), clearly indicating that also in Coccosteus the infero-gnathals were not widely separated, as proposed by Watson. The same specimen also showed all the gnathal elements practically in situ, thus in the best possible way supporting my view that the ASG were situated very close to each other. Also the "medio-supra-gnathal" is distinctly seen in this specimen (Pl. III, 4, B). According to Stensiö's description of Pholidosteus, it can hardly be doubted that this element corresponds to the rostral process and internasal wall in Pholidosteus and that Watson was right when he regarded it as lying between the spherical olfactory capsules. In my specimen, on the right side, some fragments of these capsules are still preserved (Pl. III, 4, A).
At the same time, we may therefore suppose that also in *Coccosteus decipiens*, as in a number of other known Arthrodira, the antero-supra-gnathal elements on the right and left side of the head were situated comparatively close to each other. The same was the case with the points of the infero-gnathals, in some forms they are still connected with the ossified front parts of the Meckelian cartilage, thus in this respect the reconstruction by Watson is erroneous.

The body carapace.

Watson's reconstruction of the body armour in *Coccosteus decipiens* cannot, in my opinion, be regarded as correct. Firstly, the relation between the breadth of *MB* and *MD* is certainly wrong, as these two plates in reality are almost equally broad, *MB* being slightly broader, with the result that the fish in side view shows the posterior ventral corner of *MB* placed just below the anterior ventral corner of *MD*. In all hitherto proposed reconstructions (Traquair, Woodward, Jaekel, Stromer, Heintz) this is always the case. In Watson's, however, the posterior ventral corner of *MB* is placed far beneath the corresponding corner in *MD* (fig. 4, z).

The second mistake is the position of the plates in the ventral carapace. In the text, Watson himself points out that the ventral surface is "nearly flat". In the reconstruction, however, the plates of the ventral carapace are depicted so strongly bent, that even the posterior-median-ventral is very distinctly seen (fig. 4, 2; *PMV*). *AVL* gets a remarkably, upwardly curving hinder corner, and *PVL* is strongly curved throughout the whole breadth. It can hardly be doubted that this picture is incorrect. In all earlier proposed reconstructions the ventral shield was never depicted in such an unusual way. In side view, one can never see any traces of *PMV*, and only the antero-lateral corner of *PVL* curves slightly upwards. This mistake in the reconstruction by Watson is in connection with the erroneous position of *AL*. As I have pointed out in my reconstruction of *Coccosteus* (1931, pg. 304 305) and later on in a description of *Phlyctænaspis acadica* (1933), *AL* in these forms is always more or less strongly S-shapedly bent. If we draw a straight line from the antero-ventral corner of *AL* (fig. 4, 1, b) to its posterior corner (d) the whole plate becomes divided into two more or less triangular parts. The upper one b a d is more or less convex, the lower one b c d, on the
NOTES ON ARTHRODIRA

Fig. 4. Coccosteus decipiens Ag.
contrary, concave. The $SP$ is fastened to the ventral margin of $AL$ (fig. 4, 1, b c) and this margin runs obliquely backwards and outwards.

This condition is especially distinctly developed in the oldest known Arthrodira $Acanthaspida$, for instance, in $Jaekelaspis decipiens$ from Spitsbergen (Heintz 1929, 1) (fig. 7, 1). In $Phlyctænaspis$ it is also obvious, but here the lower triangle of $AL$ is more reduced (Gross, 1933, Heintz, 1933) (fig. 7, 2). Also $C. minor$ shows the same condition (fig. 7, 3), and in $C. decipiens$ it is seen in practically every specimen, which is not too strongly compressed (fig. 7, 4). This curvature of $AL$ is thus inherited from the $Acanthaspids$ and is connected with the development of the large $SP$. Watson, however, does not accept this configuration of $AL$, and, so far as I can understand him, regards $AL$ as an evenly convexly curved plate. This results in the fact that in his reconstruction the posterior corner of $AL$ (d), which touches the $PL$ plate, is lifted too high up on the side of the body carapace, and $PL$ reaches almost to the medium line of the fish. To be able to get $PVL$ in contact with $PL$, when $AL$ and $PL$ are placed in such an unnatural position, Watson was forced to bend the ventral carapace so violently, that from being flat, it became quite semi-circular in section. Trials with paper models, proposed by Watson himself, will easily show that his reconstruction is altogether impossible. Before giving my reconstruction in 1931, I made a number of models of $Coccosteus'$ carapace. To control Watson's reconstruction, I carefully measured a number of well preserved specimens in the Royal Scottish Museum, again making a new reconstruction. This one did show me that the only possible position of the plates in the body carapace in $Coccosteus$ corresponds almost with the one proposed by me in 1931. This is also obvious according to my figure showing a specimen in the British Museum (P 180) (fig. 4, 1), with all the plates from the left side of the body in natural connection with each other. If we imagine two lines in the body of $Coccosteus$, one running along the dorsal side of the carapace, the other along the ventro-lateral margin, they become more or less parallel. If we then could "roll out" the carapace and place it on a plane, these two lines would still run more or less parallel to each other. Such a "rolled out" carapace represents the specimen in fig. 4, 1. The dorsal line is here easily drawn, running along the median line of $MD$, and the ventro-lateral line would then run more or less parallel to it. The front point of this line is clear, being the anterio-ventral point
of \textit{AL} (b). If we trace a line from this point parallel to the upper line, it will run through the posterior point of \textit{AL} (d) and through the posterior point of \textit{PL}, in other words exactly similar to my reconstruction. If, however, we follow Watson's figure, the above-mentioned line from point “b” will run almost along the spinal obliquely downwards. It is easily understood that this line can never become parallel to the upper one, in that case it would be necessary to undertake a quite impossible deformation of the whole body carapace.

Further on, Watson points out that “there can be little doubt that a large pear-shaped opening facing chiefly downward separated the lateral and ventral parts of the carapace immediately behind the spinal and in front of... the connection... made by \textit{PL} and \textit{PVL} plates”. In other words, Watson means that \textit{AL} and \textit{AVL} were connected only in the front part, and were widely separated in the hinder. In my papers on \textit{Coccosteus} and \textit{Phlyctænaspis} I have thoroughly discussed the question of the connection of \textit{AL} and \textit{AVL} and have come to the result that the hinder parts of these plates are not connected to each other as other plates in the carapace and that they do not overlap each other, but only touch each other on their inner sides. In fact this explanation shows that the hinder parts of these two plates are only kept together by the skin. I have explained this unusual condition by the fact that the basal part of \textit{AL} and the lateral part of \textit{AVL}, together with \textit{SP} form “ossified” lateral skin folds homologous to the pectoral fins in other fishes. It is therefore very probable, that Watson is right in his opinion that there really was an opening between \textit{AL} and \textit{AVL}. But, on the other hand, this opening was not “large and pear-shaped”; but only a relatively narrow slit. In the following chapter, on the pectoral fins in Arthrodira, I shall discuss this question more in detail.

\textbf{The body behind the carapace.}

Behind the body carapace in \textit{Coccosteus}, only the following more or less complete parts of the inner skeleton have hitherto been described: the neural and hemal arches; supporters for the median-dorsal fin; two doubtful plates, which perhaps have supported a second dorsal fin and an anal fin; and the pelvic girdle with traces of the pelvic fins (5 rays). When studying the collection
in Edinburgh, I was successful in finding traces of the skin-covering in *Coccosteus*. In the *Coccosteus* specimen preserved in grey sandstone as black fragments, I discovered that on the posterior point of *MD* and *PVL* one could see dark shadows following the configuration of the column, thus indicating the shape of the body (fig. 4, 3). Unfortunately, these shadows became gradually more indistinct posteriorly, almost disappearing in the caudal region. They are especially distinct in the hinder part of *MD* and on the dorsal fin. Through binoculars one could see some minute black "scales" arranged in more or less regular rows, but without touching each other. I suppose a careful investigation of any one of these "black" specimens might reveal fragments of skin and traces of the outline of the body form. In some better preserved specimens, however, showing the fish as white bones in red sandstone, I also discovered fragments of skin. Here they were present as distinct minute scales lying quite close to each other (Pl. III, 3), reminiscent of the placoid scale-covering in the Elasmobranchii. As is known, hitherto only some isolated scales in *Phlyctænaspis* (Heintz 1933) and a complete scale-covering in *Lunaspis* have been discovered. *Lunaspis*, however, as is shown by Gross (1937) does not belong to the real Arthrodira, but to the Petalichtida. The late Professor Hyde showed me some small scales which he supposed belonged to the skin-covering in *Dinichthys*. They were much larger than those in *Coccosteus*, but reminiscent of the latter in shape.

In a few specimens in Edinburgh I discovered some remarkable traces, which I can only explain as stomach-content in *Coccosteus*. They made a somewhat oblong more or less irregular shaped mass consisting of various minute fragments, cemented together (Pl. III, 2, e). I found them always immediately behind the column, usually posteriorly to the body carapace, but always in front of the pelvic girdle.

I also found two other interesting points in connection with the development of the inner skeleton. As is known, the anterio-ventral point in the pelvic girdle is always found immediately behind the posterio-lateral point in the *PVL* plate. This point in *Coccosteus decipiens* is as a rule drawn out into a short "spine" (fig. 4, 1), in *C. minor* this "spine" is still stronger developed (fig. 1, 3). This "spine" is situated exactly in the limit between the lateral and ventral parts of the body, in the lateral skin fold. The position of the pelvic girdle indicates that the pelvic fins began almost from this point run-
ning backwards, more or less along the lateral-ventral margin of the body. Thus it seems that the “spine” in \textit{PVL} indicates the starting point of the pelvic fins and, perhaps, is the last remains of a larger spine supporting the fins in older forms. The same may also be the truth about the pointed posterior end of the \textit{MD} plate. In \textit{C. minor}, as pointed out above, we have here a real, and relatively long “spine” directed slightly upwards. In \textit{C. decipiens} this “spine” is shorter, but still quite distinct, perhaps being the starting point of the dorsal fin (fig. 4, 1, 3).

Another observation concerning the caudal region: as a rule it is supposed that the neural and hemal arches are practically of the same size in the caudal region of \textit{Coccosteus} (Traquair, Woodward, Jaekel, Stromer, Heintz, Watson). According to this circumstance, the conclusion was usually drawn that the caudal fin in \textit{Coccosteus} was diphycercal. Jaekel has even depicted it as whip-shaped.

In some specimens in Edinburgh I discovered, however, that the hemal arches slightly behind the “anal” plate become distinctly larger than the neural (*fig. 4, 4), indicating, that the tail in \textit{Coccosteus} was perhaps still heterocercal. An investigation of a greater number of specimens may solve this interesting question.

\section*{III. The Pectoral Fins in Arthrodira.}

The question about the presence or absence of pectoral fins in Arthrodira has hitherto not been solved with absolute certainty. The older authors, as Miller, Agassiz, v. Koenen, Trautschold and Newberry took it for granted that Arthrodira, similar to all other fishes, had well developed pectoral fins. H. Miller in his reconstruction of \textit{Coccosteus} placed the \textit{SO} as fins at the sides of the body. Trautschold regarded plates of \textit{Psammosteus} as pectoral fins in the larger Coccosteids from Russia (\textit{C. trautscholdi} (Eastm.)).

Later scientists, however, have reached quite the opposite result. Traquair, Woodward, Dean and others regarded Arthrodira as forms without pectoral fins and in all reconstructions they are depicted without these fins. On the contrary, Jaekel since 1902, has advocated the opinion, that all Arthrodira had pectoral fins. He supported this opinion, by the fact that both the pelvic girdle and traces of the pelvic fins have been found in some Arthrodira, indicating that also
the pectoral fins must have been present, and he considered that the deep incuts on the side of the body carapace between the dorsal and ventral shields were caused by the pectoral fins.

Stensiö pointed out that the ancestors of the Arthrodira must have had both pectoral and pelvic fins, and that the SP in *Acanthaspida* apparently was homologous to the pectoral fins. If the younger representatives of the Arthrodira do not have any pectoral fins they must have been secondarily reduced.

In my paper on *Phlyctænaspis* (1933) I also pointed out that SP, together with the antero-ventral part of AL and the anterio-lateral part of AVL really form an "ossified" skin-fold and must be regarded as homologous to the pectoral fins in other fishes.

When discussing the pectoral fins in *Dinichthys* I noted the unusual slit between the AL and AVL in this and many other forms, and emphasized that this slit can hardly be understood without accepting the presence of the pectoral fins. But later on I mentioned that "there are some other circumstances making the presence of pectoral fins problematic". For instance in Acanthaspida "... the body carapace extends very far downwards and no cleft between the dorsal and ventral armours is developed. If in these forms we place the pectoral fins behind the body carapace, they will be too far back and too close to the pelvic fins".

Watson (1934) mentioned of the pectoral fins that "no trace whatsoever is to be seen of pectoral fins in *Coccosteus*. In *Dinichthys*, however, ... the notch ... between the dorsal and ventral division of the body armour, has no explanation other than the presence of pectoral fin ... It is ... impossible to account for the well-developed spine on the early Acanthaspids, which is exactly similar to an Acanthodian fin-spine, except by derivation from the ancestor with functional pectoral fins bearing spines ... The movable arm of Antiarchi would thus represent the pectoral fin of the ancestor, the only relic of which that persists in Arthrodires being the spine. Thus if *Dinichthys* actually possessed a pectoral fin it must have redeveloped it by further elaboration of a limb but which in some of its ancestors never developed into a movable structure".

Dr. White in the British Museum had made a model of *Coccosteus*, where the pectoral fins were placed immediately behind the SP. According to him, *Coccosteus* with its heavy-armoured head and with probably a more or less homocercal tail could not raise itself from
the bottom if it had not any pectoral fins. This supposition seems to be absolutely correct, and we must accordingly expect that in all Arthrodira, where SP is not developed as a large flat spine, it can to some extent be replaced by the soft pectoral fins.

I therefore especially carefully examined all the specimens of *Coccosteus decipiens* in the British Museum and in the Royal Scottish Museum hoping to find fragments of the pectoral fins. My investigation was successful as in a few specimens of *C. decipiens* in the Royal Scottish Museum, I happened to find real fragments of the pectoral fins.

In several specimens, bits of skin were present lying on both sides of the more or less complete ventral shield just behind the SP. These skin-fragments do not show the exact shape of the fins, or indicate their size, as they are too poorly preserved. But they state with certainty the presence of the pectoral fins in *Coccosteus decipiens*, and show that they were covered with the same kind of scale as the body at the back of the armour (Pl. III, 1).

In one specimen I even succeeded in finding not only skin fragments, but also some fin-rays (fig. 5) (R. S. M. 1882—60—3). There were 6-7 in number, placed one beside the other, protruding through the opening between AVL and AL directly behind SP. They were only preserved on one side, and in outline they seemed very similar to the other "rays" known in *Coccosteus* median dorsal fin-rays, and rays in the pelvic fins. They were probably cartilaginous elements only superficially calcified or ossified.

The question may arise whether these rays do not only represent replaced parts of the inner skeleton? I suppose this is not very likely. Firstly, the specimens in question are relatively very well preserved. It would therefore be very remarkable if parts of the neural or hemal arches, or rays of the dorsal or pelvic fins were removed so far forwards. Secondly, the preserved rays are placed very regularly the one beside the other, not giving an impression of having been destroyed or replaced. The circumstance that the
fin-rays have never before been found in any other specimen of *Coccosteus* does not prove that they have not existed in the living fish, especially when we take into consideration that also rays of the pelvic fins have only been found in a very few specimens and are always badly preserved. The rays of the pectoral fins in *Coccosteus* were probably mostly cartilaginous, and only exceptionally became somewhat ossified or calcsifed, thereby accounting for the fact that as a rule they are not found in the fossils, or only exist as indistinct fragments.

In support of my supposition regarding the fin-rays in *Coccosteus decipiens*, I might mention that as early as in 1932 I described some fragments of fins in an American Arthrodire strongly reminiscent of those mentioned above in *Coccosteus*. In addition, I can mention that the late Professor Hyde, showed me in a perfectly preserved ventral carapace in *Dinichthys*, some rays placed immediately behind the *SP*. In shape and arrangement they thoroughly correspond to the rays in *Coccosteus*. In my opinion, this seems to prove that *Coccosteus decipiens* have possessed real, well-developed pectoral fins, supported by cartilaginous fin-rays, placed directly behind the *SP* situated in the opening between the posterior part of *AL* and *AVL*.

Now, however, the question has arisen how have the pectoral fins been developed in the Acanthaspids?

The real movable fins with fin-rays are only known in the later paleozoic fishes as *Dipnoi, Crossopterygii* and *Actinopterygii*. The oldest Devonian sharks had fin-rays, but their fins were certainly only slightly movable. *Acanthodei* in fact the oldest known representative of the Gnathostomi had only fins with a stiff spine in front and a membrane stretched out behind. The Agnatha show various degrees of differentiation of the lateral fin-folds into more or less well-developed pectoral fins, but no real rays have hitherto been observed.

It seems, therefore, most plausible to suppose that the lateral fin-folds in the non-armoured ancestor of *Arthrodira* were already differentiated as pectoral and pelvic parts formed of unmovable fin membrane and probably supported in front by a more or less strongly developed spine, at any rate in the pectoral fin (almost as in the *Acanthodei*).

We do not know anything about the development of the armour in the Arthrodira, how the un-armoured ancestors became changed
Fig. 6. A trial to reconstruct the shape and position of the pectoral and pelvic fins in *Jaekelaspis* (1) and *Coccosteus* (2). Both fishes seen from the ventral side.

into an heavy armoured "Acanthaspid". In the *Acanthaspida* however, traces of the lateral skin-folds and also the median skin-fold are distinctly seen. The unmovable pectoral fin with its supporting spine in front has become changed into the "spine" in the *Acanthaspida*. From the hind limit of this spine a more or less short and poor skin-fold was developed running as far as to the posterior corner of *AL* and *AVL* (fig. 6, 1). Thus these two plates were not connected with each other like all the other plates in the carapace, but only touched each other with their inner margins, and were fused together with a slightly developed skin-fold (Heintz 1931, 33). The limits between the ventral and lateral parts of the carapace, behind the spine, indicate the continuation of the lateral skin-fold. The pelvic fins were probably developed as badly differentiated lobes along this
Fig. 7. Gradual change in the shape of AL and SP in different Arthrodira:

line directly behind the posterio-lateral corner of the carapace. The pectoral fin, which was partly formed of the SP (in front), partly, of the anterio-lateral parts of AL and AVL and, finally, of a more or less short "membrane" serving as a gliding apparatus for the fish during swimming, corresponds in origin and function to the different kinds of "spines" known in the Agnatha (Cephalaspids, Pteraspids) and Acanthodii.

In younger forms a very marked change takes place. The SP becomes more and more reduced, while, on the contrary, the opening between the posterior part of AL and AVL becomes gradually stronger developed, naturally indicating, that the posterior, more or less membranous part of the pectoral fin, which in the Acanthaspida was very short, became gradually larger and more important to the fish as an organ of equilibrium. In Phlyctænaspis, the SP plays a dominant rôle (fig. 7, 2), in C. minor however, it is strongly reduced (fig. 7, 3), but is still quite large, and together with parts of AL and AVL forms an effective gliding plane. However, the real soft pectoral
fin forming a prolongation of the front part of the carapace, is here already large and playing an important rôle. In *Coccosteus decipiens* the "spinal" is of hardly any use as a gliding apparatus, or as an organ of equilibrium (fig. 6, 2; fig. 7, 4). The strongly developed soft pectoral fins, supported by fin-rays, are the only effective equilibrium organ. The dorsal- and ventral carapace are still connected behind the pectoral fins, a circumstance which is sure to diminish the movability and size of the fins. Finally, in *Dinichthys* (fig. 7, 5) the connection between the *PL* and *PVL* ceases altogether. The pectoral fins, supported by firmly developed rays, have now completely lost the "spine" in front which is changed into a small bone connecting the dorsal- and ventral carapace, and they are not prevented in their movements by the carapace-connection behind them.

The changes of the pelvic fins apparently also took place together with the differentiation of the pectoral and from a slightly differentiated skin-fold in the *Acanthaspida* (fig. 6, 1) slowly developed into distinct fins supported by the fin-rays and the ossified pelvic girdle (fig. 6, 2).

The changes in the development of the fins in the Arthrodira, sketched in this paper, must certainly be regarded as an attempt, in a very generalized way, to show how the alterations may have taken place. No details of this "series" are known and the proposed explanation is a more or less theoretical one only.

Paleontologisk Museum,
October 1937.
Explanation of the Letters.

In all the textfigures and plates as also in the text the same letters refer to the same things.

\begin{itemize}
\item \textit{ADL} = Antero-Dorso-Lateral.
\item \textit{AL} = Antero-Lateral.
\item \textit{AMV} = Antero-Median-Ventral.
\item \textit{ASG} = Antero-Supra-Gnathal = Rostro Gnathale.
\item \textit{AVL} = Antero-Ventro-Lateral.
\item \textit{C} = Central.
\item \textit{cl} = Vertebral column.
\item \textit{D} = Rostral, ossified part of Meckelian cartilage.
\item \textit{EB} = Externo-Basal = Externo-Occipital = Paranuchal.
\item \textit{e} = impression of the stomach.
\item \textit{f} = Fragments of pectoral fin.
\item \textit{ha} = hemal arches.
\item \textit{l} = Internal.
\item \textit{IG} = Infero-Gnathal = Mandibulare.
\item \textit{IL} = Intero-Lateral.
\item \textit{lIL} = left Intero-Lateral.
\item \textit{IPDL} = left Postero-Dorso-Lateral.
\item \textit{MB} = Median-Basal = Median Occipital = Nuchale.
\item \textit{MD} = Median-Dorsal.
\item \textit{M} = Marginal.
\item \textit{na} = Neural arches.
\item \textit{P} = Pineal.
\item \textit{PDL} = Postero-Dorso-Lateral.
\item \textit{PL} = Postero-Lateral.
\item \textit{pl} = pelvic girdle.
\item \textit{PM} = Post-Marginal.
\item \textit{PMV} = Postero-Median-Ventral.
\item \textit{PN} = Post-Nasal Sub-Rostral.
\item \textit{PrO} = Pre-Orbital.
\item \textit{PSG} = Postero-Supra-Gnathal = Orbito-Gnathal.
\item \textit{PSO} = Post-Sub Orbital.
\item \textit{Pto} = Post-Orbital.
\item \textit{PVL} = Postero-Ventro-Lateral.
\item \textit{R} = Rostral.
\item \textit{rIL} = right Intero-Lateral.
\item \textit{rPDL} = right Postero-Dorsal-Lateral.
\item \textit{SG} = Supra-Gnathal elements.
\item \textit{smd} = sub-median-dorsal.
\item \textit{SO} = Sub-Orbital.
\item \textit{SP} = Spinal.
\item \textit{x} = New plates placed between \textit{MB} and \textit{MD}.
\end{itemize}
NOTES ON ARTHRODIRA

Literatur.


MILLER, H. 1858. The cruise of the Betsey etc. Edinburgh.


— 1890. 1. Homosteus Asmuss, compared with Coccosteus Agassiz. Geol. Mag. (3) 6.


Printed June 2nd, 1938.
Plate I.

*Coccosteus minor* H. Miller. Middle Old Red sands. Scotland.

Fig. 1. Nearly complete carapace, part of the column and pelvic girdle. Ca. \( \times 2 \) (the same as in text-fig. 2, 2).

2. Head shield and strongly crushed body carapace. The *SG* elements and *IL* plates especially clearly seen. The minute plates (\( x \)) between *MB* and *MD* well preserved. \( \times 2 \).
A. Heintz: Notes on Arthrodira.

Pl. 1.

Norsk geol. tidsskr. 18.
Plate 2.


Fig. 1. Nearly complete head shield and left side of the dorsal shield. *IG, I* and *PM* clearly seen. The minute plates placed between the head and body carapace (x) especially well preserved. Ca. × 2.5 (the same spec. as in text-fig. 2, 1).


3. A part of the nearly completely preserved head and dorsal shield in a small specimen. The minute plates placed between the head and body carapace (x) are clearly seen. Ca. × 3.

Specimen Nr. 1317. Caithness(?).
Plate 3.

*Coccosteus decipiens* Ag. Middle Old Red sands. Scotland.


Fig. 1. Left side of the ventral carapace in specimen 1893, 107,30. One can see the *SP* and *AVL* at the top, and *PL* straight beneath. The fragments of skin covering the pectoral fin are clearly seen (*f*). Ca. × 2.5.

2. Median part of the specimen 1888, 61,45, showing the stomach contents. Ca. × 1.2.

3. A portion of skin from the part of the body immediately behind the body carapace. Ca. × 12. Specimen 1892, 8,33.

4. The front part of the ventral carapace in a specimen showing the gnathal elements and nasal part of the animal in situ. The head shield is removed and placed in front of the ventral carapace, with the rostral part posteriorly. A Olfactory capsules. *B* = Internasal wall = Median-Supra-GnathaL. *D* = Rostral ossified part of the Meckelian cartilage. Ca. × 1.2. Specimen without Nr.
A. Heintz: Notes on Arthrodira.

Pl. 3.

Norsk geol. tidsskr. 18.