

26. SUPPLEMENTARY NOTES on the SYSTEMATIC POSITION of the TRILOBITES. By HENRY M. BERNARD, Esq., M.A. Cantab., F.L.S., F.Z.S. (Communicated by Dr. HENRY WOODWARD, F.R.S., P.G.S. Read April 24th, 1895.)

SINCE I had the honour of reading a paper on this subject before the Geological Society (printed in this Journal, vol. 1. 1894, p. 411) two other papers have appeared in America, giving further details as to the appendages and structure of *Triarthrus*.¹ Both papers are by Dr. C. E. Beecher. The earlier, describing the pygidial limbs, appeared in time to be briefly mentioned in a footnote in my own paper just referred to. The more recent has but now appeared, and gives an account of the ventral structure of *Triarthrus*. These two papers seem to me to contain matter of perhaps even greater morphological interest than the discovery of the antennæ.

The Metastoma.—Taking the new evidence, not in the order of its appearance, but in the order of the parts referred to, the metastoma, 'now revealed for the first time,' is described and figured by Dr. Beecher as a small, convex, arcuate plate just posterior to the extremity of the hypostoma. A small arcuate plate projecting backwards, as shown in Dr. Beecher's figures, is the exact form that the labium or lower border of the mouth must have assumed, when the first segment of the hypothetical annelid ancestor bent round so that the mouth opened posteriorly for the new method of feeding. But such a metastoma, as I have already argued, would be a disadvantage: it would form a barrier in the way of food being pushed into the mouth by the 'gnathobases.' In *Apus* we accordingly find the metastoma modified into two lobes placed laterally and squeezed in between the mandibles and maxillæ. This arrangement leaves the middle passage to the mouth open, while it prevents food-particles from escaping laterally between the biting-limbs. In *Triarthrus* we find the first stages of this modification; the primitive metastoma is not yet obliterated in the middle line, but the lateral lobes are beginning to develop.

Again, in the position of the labium, in front of, or at least in a line with² the jaw-pieces of the second pair of appendages, *Triarthrus* has retained a very primitive feature. It is obvious that, on the bending round of the first segment for the pushing of food into the mouth, no pair of parapodia would at first be in exact position

¹ 'The Appendages of the Pygidium of *Triarthrus*,' Am. Jour. Sci. ser. 3, vol. xlvii. (1894) p. 298; and 'Further Observations on the Ventral Structure of *Triarthrus*,' American Geologist, vol. xv. (1895) p. 91.

² I see no reason for doubting that the relative position of these parts as shown in Dr. Beecher's figures is the natural one. The metastoma and the limbs inserted near it could not well move apart without tearing the cuticle. I do not think that the chitin would be likely to stretch very much, as Dr. Beecher suggests, except in the sense of smoothing out folds. But such a stretching would, I think, reveal the true relations of the parts to one another.

to function as jaws. The appendages of the 2nd segment, which would be the nearest to the mouth in its new position, must still at first have been behind the labium.

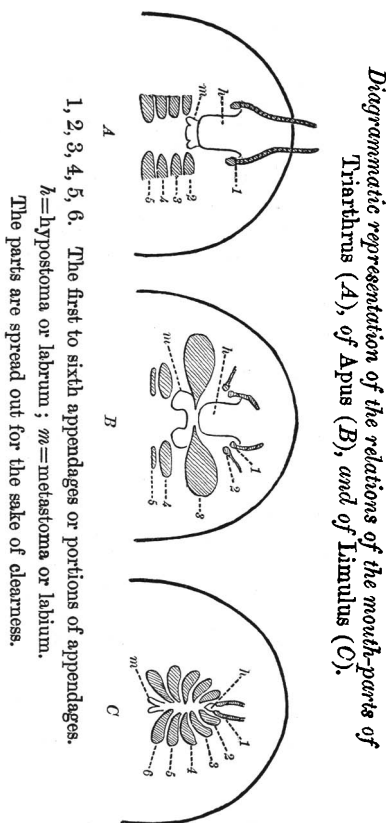
In *Apus* we find a high degree of specialization; the greatly developed lateral lobes of the labium have grown backward so as to overlap posteriorly the jaw-pieces of the third pair of appendages, which are developed as enormous mandibles.

In *Limulus* we find a still further specialization. The labial lobes have been forced back still farther, and appear as two small appendages behind the jaw-pieces of the sixth pair of appendages. Lastly, the large metastoma of the Eurypterids is probably a further adaptation of the same labial lobes situated also behind the sixth pair of appendages.

We can thus trace through *Triarthrus*, *Apus*, and *Limulus* A, B, C, *m*) the gradual modification of the labium from its primitive condition as a ridge-like posterior border of the mouth, such as the 'bent annelid' theory demands, into the pair of specialized and enigmatical lobes such as is found in the last-named animal. We can also trace equally clearly through the same series the gradual translocation of the labium, or rather of its lateral lobes, as they travelled backwards from their primitive position in front of the second pair of appendages to their extreme position behind the sixth pair.

The Mouth-formula.—The original similarity of the limbs of the head and of the trunk, which the annelidan theory demands, is still found in *Triarthrus*.

Passing by the first pair, each of which was probably from the first nothing more than the cirrus of a notopodium, as is frequently the case in the chaetopods, we find all the following appendages (excluding those of the pygidium) structurally alike.



This is no longer the case in *Apus*. But, as I have endeavoured to show, the conditions there found can be traced in detail from such a hypothetical primitive condition. The head-limbs, in developing their jaw-pieces, did not require the dorsal portions of the parapodia; these, however, in some cases persist as vestiges. On the trunk, on the other hand, the dorsal portions of the parapodia were most needed and developed as locomotory appendages.

Here again, then, in this primitive homogeneity of the head- and trunk-appendages, *Triarthrus* ranks far below *Apus*, in which certain of the appendages near the mouth are already structurally modified for co-ordinated action as jaws and maxillæ, and accordingly form a group apart from the thoracic limbs.

Dr. Beecher's figures seem to show a tendency in the jaw-pieces of the head-limbs of *Triarthrus* to become more and more powerful as we recede from the mouth; those of the fifth pair appear as the largest (*A*, p. 353). This cannot be considered as a mere accident, inasmuch as we find the same gradual increase in the size of the jaws distinctly marked in *Limulus* (*C*, p. 353), and enormously pronounced in *Eurypterus*. In these two animals the maximum of size is reached in the sixth pair of appendages. According to the browsing annelid theory, the pair of jaw-pieces nearest the mouth (that is, of the second appendages) would, one would think, develop to be the largest. Yet in no case does this happen. It is, however, typical of many chætopods that the first pair of appendages is reduced to little more than the cirrus of the notopodium; the second pair, complete as far as form goes, is often small, while the third and following pairs increase in size until a maximum is reached. It is obvious, then, that if such a chætopod took to browsing in the manner described, the limbs which were first ranged on each side of the mouth would necessarily show this gradual increase in size.

On this primitive condition the arrangement of the jaws in *Apus* (*B*, p. 353) is a striking advance in specialization. We there find that the smaller jaw-pieces of the second pair of appendages were allowed to atrophy in favour of the larger and more powerful jaw-pieces of the third appendages, which became true biting-jaws working within the mouth-aperture—that is, between the labrum and the labial lobes. This arrangement amounted to a practical monopoly of the mouth-aperture by a single pair of mandibles; while the following pairs, divorced from any close connexion with the mouth, and being, compared with the mandibles, of secondary importance, show either no great specialization or even degeneration (*B*, 5, p. 353).

This striking specialization of the mouth-parts found in *Apus* must have had some advantages over the simpler and more primitive (annelidan) condition found in *Triarthrus* and *Limulus*. It is not improbable that the single pair of highly specialized jaws, their cutting edges working between the labrum and the labium—that is, well within the mouth-aperture—are in many respects far more efficient instruments for alimentation on which growth and multi-

plication ultimately depend than a number of pairs of jaws grouped around, that is, necessarily in less close association with, the mouth. Another advantage, however, might be found in that the atrophy of the jaw-pieces of the second pair of appendages would release their dorsal branches to become specialized as sensory feelers. Although this latter specialization can hardly be said to have taken place in *Apus*, we know, from the great development of the second antennæ in the higher crustacea, that this pair of appendages, rejected as jaws, have become most efficient sensory organs.

Triarthrus represents the primitive type of mouth-formula, which is handed on somewhat specialized to the other merostomata. *Apus*, however, branched off and by developing the jaw-pieces of the third pair of appendages as specialized mandibles started the type of mouth-parts belonging to the crustacea proper. That the mouth-formula of *Apus* is the origin of the mouth-formulæ of the higher crustacea admits of little doubt when the other primitive features in its organization are taken into account.

The Appendages of the Trunk and Pygidium.—Burmeister,¹ in his restoration of the trilobite, figured the under-surface as provided with two complete series of many-lobed phyllopodan appendages, which, however, did not extend to the rudimentary pygidial segments. Actual discovery of portions of filamentous limbs apparently finally disposed of Burmeister's restoration. It was obvious, however, that if the trilobites were related to *Apus*, the limbs of the fused rudimentary pygidial segments might have been phyllopodan, as they are in *Limulus*. On the other hand, Walcott's restoration, partly based upon Hall's discovery of the underside of *Asaphus*, showed them to be filamentous. On the whole, then, while firmly believing that the trilobites must have at one time had phyllopodan appendages, I was inclined to believe that the limbs in the trilobites, being filamentous in the developed segments, might also appear as such from the first, it not being necessary to assume that they passed through any phyllopodan stage in their ontogenetic development. After all, Burmeister's restoration has been so far justified that one trilobite² is now known to have had phyllopodan limbs, not in the thorax, where he placed them, but in the pygidial segments, where he left them out.

This discovery fully justifies the explanation which I have offered of the morphology of the posterior region of *Apus*, and the homologizing of that region with the pygidial region in the trilobites. In both cases we have a fixation of larval conditions. We now know, then, that the common racial form of both *Apus* and the trilobites possessed phyllopodan appendages, which in the former

¹ 'Die Organisation der Trilobiten aus ihren lebenden Verwandten entwickelt,' Berlin, 1843; Engl. transl. edited by T. Bell & Edw. Forbes, Ray Soc. 1846.

² Since this was written Dr. Beecher has discovered that the pygidial limbs of *Trinucleus* show essentially the same characters; see Am. Journ. Sci. ser. 3, vol. xlix. (1895) p. 307.

case, while persisting as swimming-plates, are anteriorly adapted for clinging to weeds, and in the latter case were early changed into filamentous crawling-legs.

In my former paper I suggested two possible genealogies, one in which the trilobites appeared as offshoots specialized for a creeping manner of life, from the main crustacean stem, and the other in which *Apus* and the higher crustacea are deduced from the trilobites by a secondary loss of pleuræ along the trunk-segments. The persistence in *Apus* of cylindrical trunk-segments but loosely bound together inclined me to pronounce strongly in favour of the former. This choice is now amply justified. Not only in the form of the segments, but in their number and in the character of the appendages, *Apus* stands far below the trilobites. *Apus*, in spite of the specialization of its mouth-parts, in the possession of traces of over sixty cylindrical body-segments, and of its but slightly modified leaf-like limbs, is clearly in the direct line of descent between the original annelidan ancestor of the whole group and the higher crustacea. The trilobites, on the other hand, while retaining the homogeneity of the head and trunk-limbs, and other primitive annelidan characters which have been lost in *Apus*, are yet specialized by the great reduction in the number of body-segments, by the development on every segment of large pleuræ, and by the early modification of the phyllopodan appendages.

The trilobites, therefore (as exemplified by *Triarthrus*), in spite of their extremely primitive mouth-formula, do not stand in the direct line of descent of the crustacea, but are lateral offshoots, specialized for a creeping manner of life.

Specialization of the Limbs.—In the modification of the original phyllopodan appendages it is the endopodites in both *Apus* and the trilobites which are most modified. The exopodite, which I think was the original notopodial cirrus, retains in both cases its phyllopodan specialization as a swimming-organ.

Triarthrus possessed the gnathobases on the trunk-limbs, somewhat as we find in *Apus*. This, as I endeavoured to show in my former paper, was rendered highly probable by an examination of Walcott's results,¹ and by a comparison of his sections of *Calymene* with sections of *Apus*. This point is now set at rest. The phyllopodan limbs of the larval segments, in developing into walking-legs, retained throughout their whole length the gnathobases which, round the mouth, become the jaws. Dr. Beecher has accordingly given an emended diagrammatic section—emended, that is, from Walcott's well-known figure in his classical paper just quoted. If I might be allowed to suggest a further emendation, it would be in the direction of making the line of insertion of the limb much longer transversely. Walcott's sagittal sections, compared with sagittal sections of *Apus*, appear to me to leave no doubt that the

¹ 'The Trilobite: New and Old Evidence relating to its Organization,' Bull. Mus. Comp. Zool. Harvard, vol. viii. 1880-81.

dorsal skin of the leg passed proximally into the under surface of the pleura, and, on the other hand, that the gnathobase was joined to the body somewhat farther in towards the median line.

In this connexion it is impossible to avoid noticing the remarkable length and filiform character of these gnathobases on the trunk-limbs of *Triarthrus*. If the appearances are not deceptive, it looks as if some differentiation had already taken place between the jaw-pieces of the limbs nearer the mouth and those of the limbs farther off; this supposition being further justified by the fusion of a certain number of segments to form a head-region. The filiform character of the gnathobases of the thorax requires further elucidation.

There appear to be no traces of gills on the limbs of *Triarthrus*. Their absence seems to allow of the exopodites being attached higher up on the limb than is the case in *Apus*, in which a well-developed gill persists. In *Limulus* both gills and exopodites have vanished from the walking-limbs, except from the last pair, which have rudimentary exopodites. But in this case the gill portions of the phyllopodan abdominal (pygidial) appendages are greatly specialized. It is possible that, when the pygidial or the transitional limbs of *Triarthrus* are further unravelled, gills may be discovered. This expectation is justified by the presence of larval phyllopodan limbs at the extreme end of the body, indistinguishable, so far as their ventral edges go, from the larval limbs of *Apus*, which we know had gills inserted on their dorsal edges. It is true that gills are not shown on the limbs figured by Claus and copied by Beecher,¹ but they are quite distinct on the smallest rudimentary limb on a specimen of *Apus productus* ('*Apodidæ*,' fig. 10). The presence of typical phyllopodan appendages necessitates the assumption that gills have somewhere to be taken into account. It seems hardly likely that they should have completely vanished along the whole length of the body. Somewhere in the series between the developed crawling-legs and the larval phyllopodan limbs, gills of some kind, however rudimentary, must surely have existed. In some trilobites they may have been better developed than in *Triarthrus*, and Walcott's interpretation of his sections is, in this respect, by no means necessarily incorrect.

Former presence of Setæ on the Appendages.—The appendages of *Triarthrus* show very distinct traces of the former presence of setæ. Those, however, which are personally of most interest to me are figured by Dr. Beecher as tufts of stiff setæ on the dorsal edges of the exopodites, near their attachments to the coxopodite on the 4th and 5th head-limbs. In view of the very primitive annelidan characters of the limbs above insisted upon, these setæ, allowing for some shiftings of position, may well be the derivatives of the parapodial setæ of the chaetopodan ancestral form. In my endeavours to

¹ 'The Appendages of the Pygidium of *Triarthrus*,' Am. Journ. Sci. ser. 3, vol. xlvii. (1894) pl. vii. fig. 4.

deduce *Apus* from a chætopod I assumed the former presence of such setæ, and, finding the shell-gland opening on the dorsal branch of the 5th head-limb, I suggested that this gland might be a derivative of a setiparous gland. Here is not the place to enter upon this rather difficult discussion, especially as I have gone into the subject at length elsewhere.¹ I will only add that the discovery of tufts of setæ on the limbs of *Triarthrus*, which are in many respects very primitive, in practically the very spot where, in *Apus*, I assumed their former presence, may, I think, fairly be claimed as one more slight confirmation of my general argument.

Head-Segments.—Dr. Beecher corrects me in my suggestion that *Triarthrus* may have had only four segments in its head-region. There are five pairs of limbs apparently attached under the head-shield. This would, however, make no difference to the general drift of my argument that the gradual building-up of the crustacean head can be traced in the trilobites. The gradual incorporation of body-segments, probably associated with the specialization and co-ordinated movements of mouth-limbs, undoubtedly took place, and it did not stop with the trilobites, but continued till in *Limulus* and the Eurypterids six segments fused to form a head-region. In the case of *Limulus* the whole of the rest of the body corresponds to a pygidium with persistent phyllopodan appendages. In the Eurypterids, on the other hand, the posterior segments remained free, as they were also in the earliest known trilobites (*Olenellus*).

Phylogenetic Conclusions.—Summing up our comparison of the new and important facts described by Dr. Beecher with the known conditions of *Apus*, we find that the crustacea can now be linked, step by step, with the chætopod annelids. The line of development is practically that which I sketched in my former paper, but we are now in a position to supplement that scheme by additional details which bring it still closer to the actual order.

The common ancestor of *Apus* and *Triarthrus* had a many-segmented cylindrical body, the former still showing traces of more than sixty segments. A large prostomium bent round towards the ventral surface, so that the mouth opened downwards and backwards; each segment except the first was provided with a pair of swimming leaf-like appendages, richly provided with setæ; each such appendage carried on its dorsal edge a gill and an exopodite. The appendages of the first segment were simply cirrus-like, and they pointed downwards on each side of the ventrally-placed prostomium. Such an animal is a typical chætopod annelid, with the first segment bent round ventrally. We gather from later specializations that this bending was for the purpose of using the parapodia nearest the mouth to push in the food.

These free-swimming browsing annelids early developed pleuræ on a few of the most anterior segments. Such pleuræ were formed

¹ 'Comparative Morphology of the Galeodidæ,' § Excretion. Read before the Linnean Society, February 1895. (In the press.)

before any great specialization of the mouth-limbs took place. All we can safely postulate with regard to these pleuræ, judging again from later specializations, is that they were protective, and perhaps originally only for the protection of the larvæ with but few segments; this might account for their limitation in many subsequent forms to the head-segments alone. In the meantime the body was shortening by the fixation, at its posterior end, of a certain number of segments in a rudimentary condition.

From these primitive crustacean-annelids a group branched off, their specialization being the continuation of the original head-pleuræ along the whole length of the body. This was in adaptation to a crawling manner of life, the limbs on the developed segments becoming modified into legs. These, the trilobites, were, in fact, as I ventured to call them three years ago, browsing armoured annelids. In direct line with these arose *Limulus* and the Eurypterids, the last-named being specialized by the secondary degeneration of the pleuræ.

The main branch developed the pleuræ primarily on five segments only, where they formed a head-shield, which grew back as a fold over the posterior segments. The trunk-segments remained cylindrical, and the trunk-limbs persisted as swimming-plates. The limbs near the mouth, on the other hand, became greatly specialized, the most important modification being the rejection of the second appendages as jaws, leaving them free to become sensory feelers, and the great development of the jaw-pieces of the third pair as mandibles, working well within the mouth-aperture. The process of shortening the body by the fixation of a still larger number of the inherited body-segments in a larval condition became more and more marked. Such a development answers to *Apus*, from which animal all the higher crustacea can be deduced.

DISCUSSION.

The PRESIDENT remarked that Mr. Bernard's paper dealt with some additional points of structure observed in certain trilobites recently described by Dr. C. E. Beecher, and he suggested that, in all probability, the very small, rudimentary, paired appendages, attached to the posterior segments in *Triarthrus* and *Trinucleus*, indeed even the fringes of setæ on the exopodites generally (like the similar setaceous appendages in *Mysis*), may have served as branchial appendages. Again, although there does not appear to have been a pair of very large and specialized jaws in the trilobites, as seen in *Apus*, we may feel certain that 2 or 3 pairs of the anterior appendages in trilobites had already been differentiated to serve as simple jaw-feet.

He referred to the Author's important observation made in his former paper as bearing on the resemblance of *Apus* to trilobites—namely, that at a certain stage a number of the hinder segments in both had become fixed as a series of not fully developed and still rudimentary segments.

Judging from the occurrence of *Protocaris Marshii* (an early *Apus*) with *Olenellus* in Lower Cambrian rocks, the ancestors of *Apus* must have been contemporary with those of the trilobites, and such a form as *Protocaris* may have given origin to the Phyllocarida of the Palæozoic rocks, which they somewhat resemble, save that the latter have a much smaller number of segments. The great number of segments in *Apus* and in some trilobites was a very annelidan character.

Dr. J. W. GREGORY thought that all palæontologists would be glad that appendages in trilobites had been found and described by so careful a worker as Dr. Beecher. He thought that the new facts described confirmed the view of the close alliance of trilobites with the phyllopods for which Mr. Bernard had contended, but he still doubted whether its descent from an annelid was sufficiently proved. The limbs of *Apus* seemed to him more to resemble arthropod appendages than annelidan parapodia.

Mr. E. T. NEWTON also spoke.

The AUTHOR stated, in reply, that there seemed to be no escape from the conclusion that the immediate ancestors of *Apus* (and consequently of the trilobites) possessed between 60 and 70 segments; that is, they were annelids. Further, what we now know of *Apus* and of the trilobites enables us to trace step by step the course of the transformation of the chaetopod into the crustacean.

It was not contended that *Apus* was an ancestral form of the trilobites, only that in its enormous number of trunk-segments, and in their cylindrical form, *Apus* had retained primitive annelidan characters which the trilobites had lost. On the other hand, as was shown in the paper, the trilobites (as represented by *Triarthrus*) had retained annelidan characters which had been lost in *Apus*. The position adopted by the Author in his previous paper was now fully confirmed,—the trilobites were to be regarded as fixed stages in the development of *Apus* from a chaetopod, specialized for a creeping manner of life.