

26. *The SYSTEMATIC POSITION of the TRILOBITES.* By H. M. BERNARD, Esq., M.A., F.L.S., F.Z.S., of the Huxley Research Laboratory, Royal College of Science, London. (Communicated by Dr. HENRY WOODWARD, F.R.S., P.G.S. Read March 7th, 1894.)

It is now just fifty years since Burmeister¹ wrote that he "was convinced" that the reasons he afforded would be "deemed sufficiently conclusive to satisfy the unprejudiced reader" that "the trilobites were a peculiar family of the crustacea, nearly allied to the existing phyllopoda, approaching the latter family most nearly in its genus *Branchipus*, and forming a link connecting the phyllopoda with the pœcilopoda." Burmeister's reasoning has not, however, been generally considered satisfactory, and his claim that the trilobites are related to the phyllopoda, though recognized as possible,² appears somewhat to have waned before the claim put forward by others that they are primitive isopods. But this latter relationship had already been shown by Burmeister to be highly improbable, and this judgment is fully endorsed and further enforced by Gerstaecker, whose monumental review of the crustacea in Bronn's 'Klassen und Ordnungen des Thierreichs' gives special weight to his opinion.³ In the absence of any certain knowledge as to the character and arrangement of the limbs, Gerstaecker, while recognizing trilobites as crustacea, declines to adopt any special relationship: that is, he is evidently not convinced by Burmeister's reasoning. And it must indeed be admitted that Burmeister's arguments were, in themselves, far from conclusive, even when correct as far as they went. Since the appearance of the 5th volume of Bronn's 'Klassen und Ordnungen' in 1879, however, further facts have come to light which completely justify the conclusions of Burmeister, so far, that is, as to the trilobites having been primitive phyllopods.

My own study of the phyllopod *Apus* brought me, from the purely zoological standpoint and along an entirely different line of reasoning, to very nearly the same conclusion as Burmeister, or, more strictly, to that adopted by Linnæus,⁴ who decided in favour of classing the trilobites with *Monoculus Apus*. I endeavoured to show⁵ that *Apus* was the ancestral form of all existing crustacea (excluding the ostracoda), and, as such, might be expected to throw light on the trilobites. About the same time as my book was published there appeared a long and very valuable paper on the

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

² Lang's 'Text-book of Comparative Anatomy,' English translation, p. 415.

³ See further the note at the end on the isopod relationship.

⁴ A summary of the different views which have from time to time been put forward as to the systematic position of the trilobites is given by Walcott in his short but invaluable paper: 'The Trilobite: New and Old Evidence relating to its Organization,' Bull. Mus. Comp. Zool. Harvard, vol. viii. (1880-81).

⁵ 'The Apodidæ, a Morphological Study,' Nature Series, Macmillan, 1892.

genealogy of the crustacea¹ from the pen of Prof. Carl Grobben, of Vienna, whose well-known researches into the anatomy and embryology of the crustacea lend special weight to his conclusions. Prof. Grobben, after reviewing an immense array of facts and arguments, arrives at the conclusion that all the existing crustacea can be deduced from an *Apus*-like ancestral form.

Since the publication of these conclusions, I have been studying the organization of the trilobites themselves, and I wish here to express my warmest thanks to Dr. Henry Woodward, F.R.S., to Prof. Judd, F.R.S., and to Prof. G. B. Howes, for kindly placing specimens at my disposal for examination, and further to Mr. W. I. Last, Keeper of the Mechanical Department at the South Kensington Museum, for the kindly and invaluable assistance he rendered me in fitting up for me a small sandblast, by means of which I have been endeavouring to 'develop' the fossils.

I. The great variability in the number of the segments shown by the trilobites need hardly be again insisted upon as a feature connecting them with the phyllopoas. Of still greater importance is the gradual diminution of the size of the segments posteriorly, which remarkable feature the trilobites share with *Apus*. I have endeavoured to show (*op. jam cit.*) that this feature is explicable by assuming that *Apus* is the 'Protonauplius' of authors, in which a very large number of segments commence to develop, many of which, however, at the posterior end of the body, remain fixed in a rudimentary condition. This explanation of the morphology of *Apus* is, it seems to me, evident if we compare the adult with the developing larva. The adult is but the *grown, not metamorphosed*, larva—grown by the continual development of segments from before backwards, until at a certain stage this process becomes fixed, and we have the adult *Apus* with a number of fixed rudimentary segments.² This fixation of a number of undeveloped segments is visible in many trilobites.

In the early *Olenellus* these rudimentary posterior segments are still free (*i. e.* do not form a pygidium). As a rule, however, they form the plate-like pygidium characteristic of the trilobites. This specialization seems to have set in very early; for instance, in *Microdiscus* we find a pygidium apparently consisting of only a few segments differing little in size from those of the trunk, whereas a review of the pygidia of the whole order leaves little doubt that this organ was originally composed of a number of larval segments which diminished gradually in size and development from before backward.

That animals closely resembling *Apus* were extant in earliest

¹ Sitzungsber. d. k. Akad. Wissensch. Wien, vol. ci. (1892) pt. i. pp. 237-274.

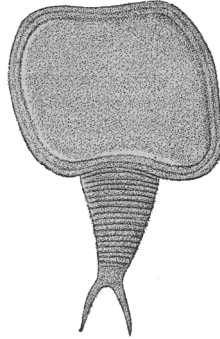
² In a recent systematic paper on the genus *Apus* (*Z. w. Z.* 5, pt. 1), Dr. Braem records a remarkable inconstancy in the number of limbless tail-segments within one and the same species. In *A. canceriformis* the number varies from 5 to 8; in *A. numidicus* from 10 to 14; in *A. productus* from 4 to 6; in *A. externus* from 5 to 6. This fact is quite in keeping with the undifferentiated (that is, embryonic) condition of the posterior region of the body.

times we now know for certain, not only from the existence of rich remains of phyllopods with shields closely resembling that of *Apus*.¹ but further from the remarkable Cambrian *Protocaris Marshi*² (fig. 1), which apparently possessed the same peculiar character of the posterior segmentation as *Apus*, and which I should like to call *Apus Marshi*.

Again, the extinct *Echinocaris* takes its name from a feature which it possessed in common with *Apus*. The posterior cylindrical (and apparently limbless) segments are provided with a ring of spines slightly anterior to the posterior edge of the segment. Serrated posterior edges of these segments occur very generally in the copepoda, and a variation of the arrangement in *Echinocaris* occurs in some stomatopoda, and perhaps on the dorsal sides of other crustacea (not phyllopods). It is, however, very marked in the phyllopods *Apus*

and *Estheria*, in the former of which it repeats almost exactly the arrangement in *Echinocaris*, there being a complete ring of sharp spines round each of the posterior segments, slightly in front of its posterior edge. In both *Echinocaris* and *Apus*, further, this special ring of spines is not developed on the anal segment. Moreover, the shell of *Echinocaris* has lateral markings which involuntarily suggest the markings caused by the shell-gland on the carapace of *Apus*. In addition to two caudal cirri, *Echinocaris* had the median prolongation of the anal segment which is characteristic of so many of the Apodidæ (*Lepidurus*).³

Fig. 1.—*Protocaris Marshi*,
Walcott.



II. The formation of the head by the gradual incorporation of trunk-segments is now very clearly shown in Walcott's detailed description of the Cambrian trilobites of North America. The composition of the head out of five somites is, as is well known, a crustacean characteristic, although no crustacean now shows this

¹ See 'Monograph of the British Palæozoic Phyllopoda,' pt. i. T. R. Jones and H. Woodward, Palæont. Soc. 1888. See also the paper by Clarke ('American Naturalist,' 1893, p. 793) on the carapace of *Rhinocaris*. It seems to me that the remarkable double suture which he describes for this interesting Devonian crustacean points back to the univalve condition of the original carapace. It is easy to deduce both forms of the carapace, that with a single median, and that with a double suture, from an *Apus*-like shield; whereas it would be difficult to arrange these carapaces in any other order of development.

² Walcott, 'On the Cambrian Faunas of North America,' Bull. U.S. Geol. Surv. No. 10, vol. ii. 1884-1885.

³ See James Hall's figures, 'Natural History of New York,' pls. xxix.-xxx, vol. vii. (1888).

primitive segmentation of the head-region. It is even quite obscured in *Apus*, and can only be gathered from the number of cephalic appendages.

The head-region of the trilobites is also, as a rule, so specialized that it is no longer possible to make out its exact segmentation. Although five seems to be the usual number of component segments, four forming the glabella, and the fifth the 'occipital ring,' trilobites occur in which all traces of segmentation have disappeared from the glabella, while again, on the other hand, others appear to have six segments forming the head. Barrande has tabulated the apparent segmentation of the heads of the Silurian trilobites of Bohemia (vol. i. pp. 195-7). The numbers range from 2? to 6. There is no reason why the trilobites should not show great variation in the number of the segments composing the head; indeed, the conclusions at which we have arrived concerning their systematic position would lead us to expect such variation. Fortunately, in the ancient Cambrian forms, such as *Microdiscus* and *Olenellus*, the segmentation of the head is so clear that it is almost impossible to misunderstand it. A study of these forms seems indeed to show us the crustacean head in making.

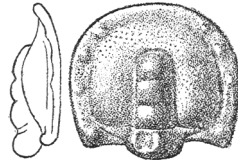
Commencing with *Microdiscus* (fig. 2), we find that it has only four distinct segments embraced by the head-shield. The fourth segment, further, shows traces of quite recent incorporation into the head (see fig. 2, profile). So that this form points back to the time when there were only three segments forming the head-region. There are other trilobites with apparently only four segments in the head (e. g. *Triarthrus Beckii*), which on that account ought, perhaps, to be classed with *Microdiscus* as a group distinct from those with five segments. On the

other hand, many trilobites with five head-segments show signs of having arisen from those with only four head-segments, inasmuch as the fifth very often bears the appearance of having been recently incorporated; it frequently retains its strong resemblance to the trunk-segments, and is seldom completely merged with the glabella.

We may, then, safely conclude from the study of adult forms alone: (1) that *Microdiscus* was preceded by a form with three head-segments; (2) that forms with four head-segments, of which examples such as *Microdiscus* have been preserved, preceded the forms with five head-segments; (3) that forms with six head-segments (*Ogygia* and the related *Limulus* and Eurypterids) are to be derived from those with five head-segments.

The formation of the head-region by the fusion and gradual in-

Fig. 2.—Head-shield of *Microdiscus Meeki*, showing head of four segments, the fourth only partially incorporated in the head.



[From Walcott, Tenth Report U.S. Geol. Surv. (1890) pl. lxxxi.]

corporation of somites, which is quite obscured in the development of the crustacea, is still perfectly clear in the development of the trilobites, *e. g.* in that of *Olenellus* described and figured by Walcott.¹ This trilobite, with five head-segments in the adult, arose almost certainly from a form with four head-segments; the youngest stage observed has only four segments, with their own characteristic pleuræ, the posterior pairs being bent backward, as terminal pleuræ usually are (fig. 3). When the fifth head-segment appears, it does so as a trunk-segment, *i. e.* with typical trunk-pleuræ; that is, with pleuræ which run out laterally in the transverse plane (see figs. 4 & 5, p. 416). These pleuræ of the fifth head-segment only gradually become incorporated into the head-shield, and in some species their points seem to persist on each side in the middle of the posterior margin of the cephalic shield.

These figures of the developing *Olenellus* are further of special interest because they show without doubt that the segmentation of the head was still very distinct, *i. e.* the fusion of the segments was only of recent occurrence. We find the head-segments diminishing in size from front to back (fig. 4 *a*, p. 416), which is typical of the development of segmented animals when the segments do not belong to a highly specialized region. This early developmental stage no longer appears in the metamorphoses of the crustacea.

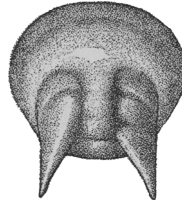
It appears to me, then, that we have, in the trilobites *Microdiscus* and *Olenellus*, two consecutive stages in the development of the crustacean head. But, at the same time, although *Microdiscus*, with its head of four segments, is, in this respect, an older type than *Olenellus*, with its head of five segments, in other respects (for example, in its pygidium) it is more specialized.

III. The two chief characteristics of the head of these primitive crustacea are (1) the bending round ventrally of the first segment, so that the labrum and mouth face posteriorly; and (2) the cephalic shield.

1. In my endeavour to trace the possible origin of the crustacea from their annelidan ancestor, I laid special stress upon this bending round of the mouth for the purpose of using the parapodia as mouth-organs. I had shown, at first without reference to the trilobites,

¹ 'Fauna of the *Olenellus*-zone' (see especially pl. 4, xxxvi.) in U.S. Geol. Surv. Tenth Report (1890). See also S. W. Ford, 'Embryonic Forms of Trilobites,' Amer. Journ. Sci. ser. 3, vol. xiii. (1877) p. 265, and vol. xxii. (1881) p. 250; some of Walcott's figures are taken from these papers.

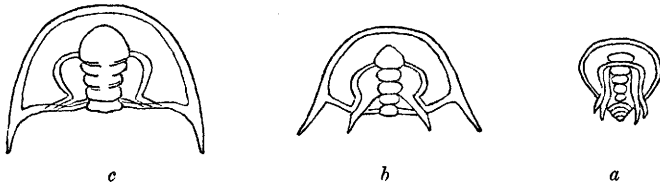
Fig. 3.—Youngest stage of *Olenellus* asaphoides ($\frac{1}{8}$ mm.) seen by Walcott.



[This shows the four head-segments with the anal segment; the cephalic shield apparently consists of the pleuræ of the 1st-4th segments.]

and solely from an examination of the external and internal structure of *Apus*, that such bending round must have taken place in the ancestral crustacean ('The Apodidæ,' *op. supra cit.*). But, having only *Apus* as a guide, I had to leave the question undecided as to how many segments actually turned over, *i. e.* into or towards

Fig. 4.—*Olenellus asaphoides*, after Ford.



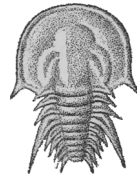
[The order has been accidentally reversed.]

- a* = Embryonic form: head composed of five segments, which diminish in size from before backward.
- b* = A further stage of the same.
- c* = Pleuræ of the fifth segment beginning to take part in the formation of the head-shield.

the horizontal plane. Finding the mandibles (belonging to the third segment) arranged dorso-ventrally, I have since been inclined to think that the third segment remained more or less completely in the transverse plane. I should therefore have assigned the chief part in the formation of the bend to the first and second segments.

A study of *Olenellus*, in which the segmentation of the head is especially distinct, shows us that such a bending round did actually take place, but that it was primarily confined to one, *i. e.* to the first, segment. By the bending round of the first segment, so that the labrum and mouth point backward, thus apparent in the trilobites, we can, as I have shown, obtain an explanation of the pre-oral position of the antennæ in the crustacea, and, further, of the bend in the alimentary canal also characteristic of the group, and especially marked in *Apus* and *Limulus*. In this latter animal, indeed, the backward bend of the œsophagus has been secondarily exaggerated. The same may also have taken place in *Apus*. If so, it must be attributed to the gradual backward growth of the mouth, so as to allow a greater number of limbs to function as mouth-parts. In *Limulus* the basal plates of five pairs of limbs

Fig. 5.—*Young specimen of Olenellus asaphoides*.



[The pleuræ of the fifth head-segment are seen to resemble those of the trunk-segments.]

function as jaws, a specialization further developed in the Eurypteridæ, in which the most posterior of these becomes the most powerful.

The great development of the glabella in many trilobites may perhaps be due in some cases to the great development of the œsophagus as a 'masticatory stomach,' or, again, of the mid-gut diverticula ('liver'), which almost certainly occupied this part of the body (cf. *Limulus* and *Apus*).

My theoretical deduction of all crustacea from an annelid in which the anterior end was bent round ventrally, so as to allow of its appendages to function as jaws, is thus fully confirmed by these early trilobites.

2. The head-shield seems to have been a characteristic of all the earliest crustacea. I endeavoured (in 'The Apodidæ') to explain it as starting from the lateral projections which would be necessarily caused by the sharp bending round of the first segment. A careful study of the series of under-surfaces of the heads (especially of *Dalmanites socialis* and *Paradoxides bohemicus*) figured by Barrande¹ has confirmed me in this supposition.

Still more conclusive evidence, however, on this point is yielded by the developmental history of *Sao hirsuta*, also given in Barrande's classical work. Stages 1-8 show the first segment produced on each side into points curving backwards round the outer edges of the cephalic shield (see fig. 6). In stage 9 this is nearly obscured, while the head-shield of the adult is very highly specialized and shows no traces of its origin.

The head-shield thus almost certainly originated in the first segment, as a pair of lateral projections due to the sharp bend in that segment. The backward growth of these projections, *i. e.* their repetition on the following segments as pleuræ, was a natural process.

In *Microdiscus* the head-shield extends backward through three segments, the fourth segment being not yet quite incorporated into it. When five segments became definitely fixed as the normal number of head-segments, the head-shield ran back to the posterior edge of the fifth segment. Not only, however, does this fifth segment often appear like a trunk-somite, but the transverse strip of the head-shield belonging to it very often appears, as above noted, to be a pair of pleuræ belonging to the trunk-segments, fused along their anterior edges with the cephalic shield.

This fact, namely, that the comparatively recent incorporation of the pleuræ of the fifth head-segment is still visible, helps us to understand the morphology of the head-shield. As above suggested, we

Fig. 6.—*Sao hirsuta*, after Barrande.

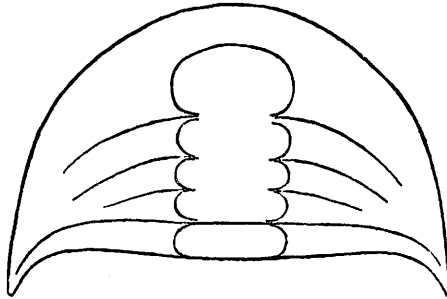


[Early stage, showing lateral projections as due to bending of first segment.]

¹ 'Système silurien de la Bohême,' vol. i. (1852) Trilobites, pls. 2 A and 2 B.

may safely describe it as consisting of the fused lateral projections of the cephalic segments. The first pair, I think, were the lateral projections which would naturally be formed by the bending round of the first segment. This first pair of projections would give rise to a second pair belonging to the second segment. I say 'would give rise' because, from the method of development of segmented animals, the metameric repetition of special structures is a well-known fact. We can thus suppose three pairs of 'pleuræ,' diminishing in size, developed on the 2nd, 3rd, and 4th segments

Fig. 7.—Diagram showing the probable composition of the head-shield.



as metameric repetitions of the lateral projections of the first segment. This stage seems indeed to be represented in the larval *Olenellus* (fig. 3, p. 415), in which we have the head-shield composed of the secondarily enlarged lateral projections of the first segment, and three pairs of pleuræ. These posterior pleuræ of the posterior developing head-segments slope directly backward, just as do the pleuræ of the posterior tail-segments, which are also rudimentary. I consider this latter point of great morphological importance, as it seems to show that the head-shield was a structure *sui generis*.

This head-shield, composed of the pleuræ of four segments, in the same way gave rise in the trilobites to large pleuræ on the subsequently developed trunk-segments, these pleuræ generally diminishing in size from front to back. If the first pair of these pleuræ fuse with the head-shield, as above described, we should get a head-shield composed of (1) the lateral projections of the first segment, (2) the pleuræ of the second, (3) the smaller pleuræ of the third segment, (4) the still smaller pleuræ of the fourth segment, (5) the pair of the large pleuræ of the most recently incorporated trunk-segment forming the fifth cephalic segment. This origin is further illustrated by the diagram (fig. 7). That diagram finds ample justification in the series of figures 3, 4, 5, and 6, in which we trace the rise of the fifth cephalic segment, with the gradual development and incorporation into the head-shield of its pleuræ, which are typical trunk-pleuræ.

It is further of especial interest to note that the lines of fusion between the lateral projections of the first segment and the pleuræ of the second segment apparently correspond with the posterior halves of the mysterious cephalic sutures. Many trilobites have these sutures running out laterally, as if dividing the shield into two somewhat similar pleuræ (e. g. *Cromus intercostatus* and *Dalmmites*).¹ The symmetry of the line itself has, however, been broken by the wandering backwards of the eye-tubercle, which, as we shall see, belonged originally to the first segment, and wandered only secondarily on to its lateral projections. The larval forms of *Olenellus* (fig. 3, p. 415) show how this line might run almost straight backwards when the first pair of projections are very largely developed in comparison with the pleuræ of the following segments, which, like the pleuræ of the rudimentary tail-segments, may slope backwards.

The retention of the line of fusion² between the anterior edges of the pleuræ of the second head-segment with the lateral projections of the first segment, as a line of weakness through the thick dorsal head-shield, may have been useful for ecdysis. The thin ventral membrane would no doubt have split easily; but, for the drawing out of the limbs, etc., it is necessary to open up the dorsal surface. This would have been extremely difficult in the case of the trilobites, unless special provision had been made for it. Both *Limulus* and *Apus* are said to moult by splitting along the frontal edge. In the trilobites, the splitting generally appears to have left the frontal edge on each side of the glabella and to have run back to the eyes; it then followed the line along the inner posterior edges of the eyes, which, as above stated, may well have been the original line of fusion of the first and second pairs of pleuræ forming the head-shield.

IV. In endeavouring to deduce *Apus* from a carnivorous annelid, by the bending round of the first segment, I had assumed that the eyes were originally on the prostomium (as they are typically in carnivorous annelids), and that when this was bent round ventrally they wandered up on to the dorsal surface of the first segment. Clear traces of this wandering of the eyes from the ventral on to the dorsal surface can still be found in the development of *Apus*, the eyes showing a gradual dorsal displacement during development. I brought forward also some morphological evidence in favour of this dorsal wandering of the eyes of *Apus*; for instance, the position and shape of the brain and antennal nerves seem best explained on the assumption that the brain had been dragged out of its original

¹ An almost similar suggestion was made by M'Coy, 'On the Classification of some British Fossil Crustacea,' *Ann. & Mag. Nat. Hist.* ser. 2, vol. iv. 1849, who concluded, from the position of the eyes as belonging to the first 'ring,' that the suture running posterior to them was the line of junction of the first and second rings. He claimed the whole sutures as such. I would, however, only claim the posterior portions of the suture, believing that the anterior lobe of the glabella certainly belongs to the first segment.

² S. W. Ford, *Am. Journ. Sci.* ser. 3, vol. xiii. (1877) p. 267, if I understand him aright, states that this fusion is incomplete in the youngest stages.

prostomial position (which has been retained in *Limulus*) by such a movement of the eyes. I further thought that the water-sacs over the eyes of *Apus* might be evidence of this wandering, these water-sacs being perhaps the integumental fold round the base of the prostomium, which had been drawn back into pockets by the eyes, in which pockets the eyes were consequently situated (fig. 8, p. 421). This sinking-in of the eyes into pockets under the cuticle has been shown by Grobben to be very common among the lower crustacea. It is found in the Cladocera, Estheridæ, *Argulus*, and in the larval cripipedes, and must, therefore, be considered of very remote origin.

In comparing the eyes of trilobites with those of *Apus*, the following points are noteworthy:—

(a) The eyes, in most trilobites, are found at varying distances from the glabella, on the 'checks' of the head-shield. *Olenellus*, however, shows that the eyes originally belonged to the glabella, and further, to the first segment. The ocular tubercle in *Olenellus* is seen branching off from this segment and bending round backwards along the posterior edge of the pleuræ of the first segment (see figs. 4 & 5, p. 416). The eyes never cross the great cephalic sutures.

(b) The fact that, in the trilobites, the eyes wandered laterally off the glabella (which is shown also in the development of *Sao hirsuta*¹) and took up the most varied positions on the 'checks' of the cephalic shield, seems to show that they had no fixed hereditary locus on the dorsal surface.

(c) Many of the early trilobites, e. g. *Paradozoides*, show, in addition to the four more or less clear segmental constrictions between the five segments composing the head, traces of a constriction lying anteriorly, on what is apparently the first segment. If this was a true segmental constriction, then, in these cases, we should have six segments forming the head, which, it must be admitted, is a possible variation. The head-region of *Ogygia* is apparently, and of *Limulus* is certainly, composed of six segments; and the secondary fusion of the anterior trunk-segment with the typical number five is what we might expect from the whole process of the formation of the head out of fused segments. But there is another interpretation which requires no more than the normal five head-segments, namely: these anterior infoldings are the openings into pockets into which the eyes have sunk beneath the outer cuticle, pockets homologous with the water-sacs over the eyes of *Apus*. It is true that in *Apus* the pore opening into these sacs is unpaired and median. The paired condition of the pores in the trilobites might be due to the wandering apart of the eyes laterally, which has so evidently taken place (cf. *Olenellus*). These infoldings in the trilobites are nearly always found in a direct line with the eyes, and seem ultimately to disappear from the glabella of later trilobites. I would like to suggest, further, that the pores found just in front of the eyes of some trilobites² (pl. xxiv. fig. 30, Barraude), or in the

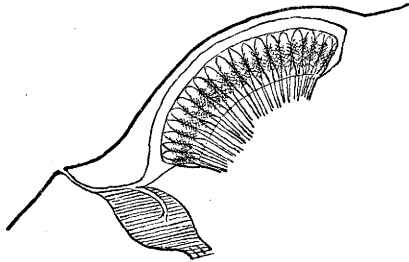
¹ Korschelt & Heider, 'Vergleichende Entwicklungsgesch.' 1892, p. 512.

² See Woodward, 'On the Nature of certain Pores observable in the Cephalon or Head-shield of some Trilobites,' App. to Monogr. in Palæont. Soc. vol. xxxviii. 1884.

furrow between the glabella and cheek in trilobites which appear to be eyeless, may be the same structures, only closer to the eyes. Perhaps too the curious marks on each side of the glabella in *Phacops Volborthii* and *Ph. fecundus* may also come under the same head: that is, they may all be openings, or the remains of openings, into water-sacs over the eyes.

(d) According to this interpretation of the facts, water-sacs must have originally been present over the eyes of all these primitive crustacea, completely degenerating, however, in later forms. The trilobites afford some interesting, though indirect and not conclusive, evidence on this point. As is well known, in the earliest trilobites the 'eye-membrane' is generally wanting. Gerstaecker¹ would account for this as due to the enormous pressure to which the Lower Silurian fossils were exposed. I would suggest, as a more probable interpretation, that the eye proper was not in actual contact with the outer cuticle, but lying in a pocket which would fall away from the outer cuticle as the animal tissues decayed. In *Apus*, the eye, not being attached to the outer cuticle, but belonging to the thin cuticle of the water-sac (see fig. 8), easily falls away from the former in the process of section-cutting; only as the water-sacs degenerated (as they have done in the higher crustacea), and as the eyes became secondarily attached to the external cuticle, would they be preserved.

Fig. 8.—Diagram of the eye of *Apus*.



[The eye is sunk beneath the surface in a water-sac, and is therefore not in contact with the outer cuticle]

We may, then, suppose that in the earlier trilobites the external cuticle was differentiated, above where the eyes were situated in the water-sacs, so as to form a kind of thin and membranous cornea, which would be easily destroyed. This would explain the frequent collapse of the 'eye-membrane.' Again, in other trilobites, the external cuticle above the eyes may have shown no such differentiation into a smooth membranous cornea, the eyes lying in the water-sacs under a generally transparent cuticle. These trilobites would now appear to have been blind, whereas their eyes were more probably in pockets under the external cuticle. *Microdiscus* has no eyes visible. It is interesting to note M'Coy's observation (quoted by Dr. Woodward, *op. supra cit.*) that the pores above mentioned are most obvious in 'blind' trilobites.

(e) The eyes which do appear in trilobites show very marked differences, which Burmeister, with great ingenuity, endeavoured to

¹ Bronn's 'Klassen und Ordnungen,' vol. v. p. 1163.

show might be due to the presence or absence (presumably through post-mortem destruction) of a thin membranous cornea, which he assumes covered the eyes of the trilobites, similar to that which covers the eye in *Branchipus*. I have always considered this membranous cornea of *Branchipus* as indicative of the former presence of a water-sac, which secondarily disappeared as the eye became stalked; otherwise it seemed difficult to explain why the eye itself did not belong to the external cuticle represented by the cornea. In the same way, among some of the later trilobites, the water-sac probably degenerated secondarily, leaving the eye in contact with, but not strictly belonging to, the outer cuticle, which may have covered the eye like a thin membrane. This whole subject is, however, beset with great difficulties, so that it is impossible as yet to come to any definite conclusion; for while, on the one hand, the so-called faceted eyes of trilobites, showing round projecting single eyes arranged at some distance from one another, remind one strongly of the tips of crystalline cones,¹ such as occur in the eyes of *Apus* (see fig. 8, p. 421), on the other it is clear from Clarke's² researches that these were certainly in some cases true corneal lenses, apparently belonging to the outer cuticle, and, indeed, somewhat elaborate structures.

Further, the eye of *Limulus* is a great difficulty; here we have no trace of a water-sac, nor of corneal lenses, while the bodies which appear analogous to the crystalline cones are simply inward projections of the outer cuticle. In discussing the eye of *Apus*, I was led to the conclusion that the eye of *Limulus* was the more primitive, a conclusion also arrived at by Watase.³ If this is so, then these eyes certainly belong to the external cuticle primarily, and not secondarily by the degeneration of a water-sac. The only way out of the difficulty, it seems to me, is to assume that while, in some cases, the eyes, in travelling backwards, passed beneath a fold of the cuticle into deep pockets, as above described, in others the folds themselves degenerated secondarily, leaving the eyes once more on the free exterior surface of the head.

V. Behind the eyes of *Apus* there occurs, in all species of the Apodidæ that I have examined, the well-known 'dorsal organ,' which in *Apus* appears to be an excretory organ.⁴ It is often raised on a slight plateau above the surrounding cuticle; the cuticle of the plateau itself is extremely thin, and likely to collapse easily during the early stages of fossilization. Did such an organ occur on the dorsal surface of the head of the trilobites? Fig. 9 (p. 423) shows us that, in the Cambrian trilobite *Olenellus asaphoides*, there was such an organ, of essentially the same shape as that in *Apus*, but apparently shifted farther back than in *Apus*, that is, on to the fifth segment. In

¹ See Packard, 'The Structure of the Eye of the Trilobites,' in the 'American Naturalist' for 1880.

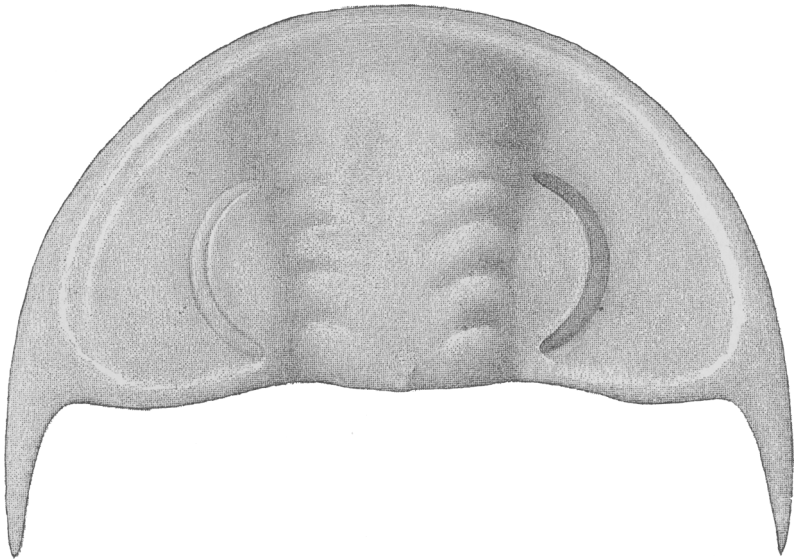
² 'Structure and Development of the Visual Area in the Trilobite *Phacops Rana*. Green,' Journ. Morph. vol. ii. (1889).

³ 'Morphology of the Compound Eyes of Arthropods,' Journ. Roy. Micr. Soc. 1890, p. 318.

⁴ 'The Apodidæ,' p. 304.

Apus its exact position with reference to the segmentation is difficult to ascertain. As some evidence of this wandering backwards of the organ in the trilobites, I would draw attention to the sloping backwards of the lines of constriction between the posterior head-segments shown in fig. 9; and further to the fact that Walcott describes a tubercle on the fourth (last) head-segment of *Microdiscus*, whereas, where five segments form the head, it is generally found on the fifth. *Asaphus* seems to form an exception, for the tubercle (?) appears to occur on the fourth segment, and not on the fifth.

Fig. 9.—Head-shield of *Olenellus* (*Mesonacis*) *asaphoides*, showing the oval 'dorsal organ' on the fifth cephalic segment.



[From Tenth Report U.S. Geol. Surv. (1890) pl. xc.]

This organ seems, in the trilobites as in the crustacea, to have been very early modified. It develops in the former into a slightly conical prominence in *Isotelus*, or into a long sharp spine, *e. g.* in *Olenellus Bröggeri*. Traces of it appear in very many Cambrian and Silurian trilobites, for example, in species of *Dalmanites*, *Asaphus* (on the fourth segment), *Cheirurus*, *Bronteus*, *Proetus*, *Cyphaspis*, *Acidaspis* (either as a median spine or as a circumvallate pit between two lateral spines), *Conocephalites*, *Hydrocephalus*. In the Carboniferous trilobites figured in Dr. Woodward's monograph,¹ traces of it are marked in species of *Phillipsia* and *Griffithides*. In many of these it occurs as a round mark, the exact nature of which is difficult to ascertain. In *Olenellus Bröggeri* and in some species of *Sao* and *Acidaspis*, as above stated, it is produced into a sharp median spine. That all these structures are modifications of the oval patch on the

¹ Palæont. Soc. vols. xxxvii. & xxxviii.

head of *Olenellus* there can, I think, be no doubt, and as little, all things considered, that this oval patch on the head of *Olenellus asaphoides* is homologous with the oval patch on the head of *Apus*. If so, it was, in all probability, originally excretory, and its transformation into a spine suggests that this spine was poisonous. It is, further, interesting to note that this median head-tubercle or spine tends to be repeated on the trunk-segments.

VI. The alimentary canal of the trilobites, as is well known, has been found more than once as a cast within the animal, due, according to Barrande,¹ to its having been filled with argillaceous matter, which suffered no change if the matrix of the fossil happened to be sand. In this connexion, I might mention that I have a series of sections of *Apus cancriformis* in which the alimentary canal is full, almost to distension, of fine grit.

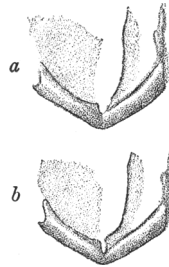
Burmeister, arguing from analogy, placed the anus of the trilobites terminally, as indeed he was quite justified in doing, considering that he correctly interpreted the pygidium as composed of fused segments. I do not quite understand the figure given by Burmeister (*op. cit.* pl. v. fig. 4), which seems to represent an anal aperture in *Asaphus tyrannus*. If this be so, the anal segment in this animal seems to be greatly specialized, and the position of the aperture figured (on the ventral surface of the segment) may have been secondarily acquired. I have myself discovered, by means of the sand-blast, clear traces of an anus in *Calymene Blumenbachii* (see fig. 10, *a* & *b*), and it is situated terminally, as one would expect. This position of the anus could further be gathered from what is known of the course of the alimentary canal. Barrande (p. 229) describes it as running backwards "jusqu'à l'extrémité de l'axe, vers le bord postérieur du pygidium."

VII. With regard to the limbs of the trilobites, the most important recent discovery² has been that of antennæ in *Triarthrus Beckii*

¹ 'Système silurien de la Bohême,' vol. i. (1852) p. 229.

² W. D. Matthew, 'On Antennæ and other Appendages of *Triarthrus Beckii*,' Amer. Journ. Sci. ser. 3, vol. xlvi. (1893) p. 121. By the kindness of Dr. Henry Woodward I have been able to examine a specimen with antennæ, presented to him by Prof. Marsh and exhibited by him in the Natural History Museum at South Kensington. I have no word to add to Mr. Matthew's careful description.

Fig. 10.—*Pygidium* of *Calymene Blumenbachii*.



a = Under surface, showing the torn edge of the ventral membrane running posteriorly towards the median anus.

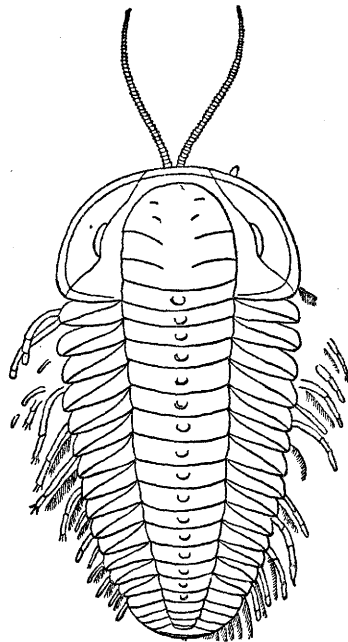
b = The same, as first revealed by the sand-blast. The projecting portion of the membrane bounding the anus anteriorly was accidentally broken off.

(fig. 11). These antennæ, as far as can be ascertained, were attached on each side of the labrum,¹ and may be assumed to have belonged to the first segment, that is, they were homologous with the first antennæ of *Apus*. These very pronounced antennæ were evidently specialized in this particular trilobite; but we may naturally infer from them that all trilobites had appendages on the first segment which were, as a rule, sensory organs. The exact form which they assumed is a matter of little morphological importance. In some they may have developed pincers (cf. *Limulus* and *Pterygotus*²), but in the majority of cases they more probably remained purely sensory.

As to the appendages of the following head-segments, we should probably find every grade of specialization, from the lowest trilobites upward. The simplest would be that stage in which the head-appendages did not differ either one from the other or from those of the trunk: all alike being, in all probability, membranous lobes deducible from the parapodia of their annelidan ancestors. The ventral portions of these were, in all probability, masticatory ridges, and pre-eminently specialized as such in the region of the mouth. Dr. Woodward's discovery of one of these head-appendages in *Asaphus platycephalus*³ shows the basal masticatory ridge, while the dorsal portion is developed into a jointed cirrus-like process (cf. *Pterygotus*). In some trilobites all

the four pairs of posterior cephalic appendages may have presented this character, the masticatory plates being about equally developed (as in *Limulus*), whereas the dorsal portions were either sensory organs or walking-limbs. *The great interest which attaches*

Fig. 11.—*Specimen of Triarthrus Beckii, showing the antennæ.*
(After Beecher.)



¹ [While this paper was passing through the press, a paper appeared by Walcott, 'Note on some Appendages of the Trilobites,' Geol. Mag. June 1894, p. 246, which contains a figure of a *Triarthrus*, showing the attachment of these antennæ in exactly the position which the first antennæ occupy in *Apus*. As to the great importance of this, see my note in 'Nature,' vol. xlvi. (1893) p. 582.—H. M. B., June, 1894.]

² And, according to Laurie, *Stimonia*, 'The Anatomy and Relations of the Eurypteridæ,' Trans. Roy. Soc. Edin. vol. xxxvii. pt. ii. (1893) p. 509.

³ Quart. Journ. Geol. Soc. vol. xxvi. (1870) p. 486.

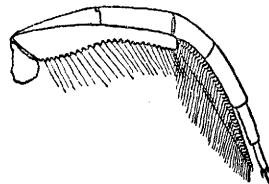
to *Apus* lies in the fact that in this form we have the specialization of the mouth-parts which remained typical of the later crustacea. In *Apus* the second antennæ degenerated, that is, as compared with the anterior pair, their ventral masticatory portions almost, if not entirely, disappearing. In the third pair of limbs it is the dorsal portion which entirely disappears, while the ventral develops into a large fleshy jaw. In the last two limbs the dorsal portions persist in a rudimentary condition, while the ventral are masticatory ridges, second in importance only to the 'mandibles.' On the trunk the masticatory portion of the limbs progressively gives up its function, while the dorsal portions develop primarily as organs of locomotion.

There is no reason to believe that any trilobites possessed this formula for the cephalic appendages. Certainly in the older trilobites, in which we find the head-region either incomplete as to the number of the segments, or with the typical number of segments but not very closely fused together, it was not likely that the limbs of these segments were specialized like those of *Apus* and the higher crustacea, in which the head-segments are fused beyond all further recognition as such. Judging, indeed, from those merostomata whose cephalic limbs we know anything about, there is reason to believe that the trilobites tried almost every possible masticatory formula.

As to the limbs of the trunk, Burmeister assumed that they were membranous 'lobes' like those of *Apus* and *Branchipus*. Recent discoveries, however, show that the ambulatory portion of the leg was filiform; yet Burmeister was not far from the truth. The limb of the trilobite, according to Walcott's sections, was a biramose appendage, with a gill, a cirrus (exopodite), and a locomotory 'endopodite,' and, what is of equal, if not of greater importance, a flat, membranous, basal portion.

Commencing with the distal portion of the leg, Walcott's claim that it was biramose has now been fully confirmed by the discovery of specimens of *Triarthrus Beckii* showing appendages.¹ In these beautiful specimens we have the distal portions of the limbs shown us closely resembling those of *Apus*, only in *Apus* the two branches are flat and membranous for swimming, while in *Triarthrus* they are apparently longer and narrower and secondarily jointed, for crawling. As all who have examined *Apus* know, the two branches are arranged side by side exactly as we find in *Triarthrus* (fig. 12), the exopodite being behind the endopodite.

Fig. 12.—Limb of *Triarthrus Beckii*. (After Beecher.)



¹ See Walcott's valuable paper quoted above, and also the more recent paper by Matthew, and further Dr. C. E. Beecher, 'On the Thoracic Legs of *Triarthrus*,' Amer. Journ. Sci. ser. 3, vol. xlv. (1893) p. 467.

It is only when the limb is flattened out under a cover-glass that the exopodite assumes its true morphological position as a dorsal appendage of the endopodite, branching off laterally in the transverse plane. Further, the flat rowing exopodite of *Apus* is supplied with a fringe of sensory hairs. These hairs are very marked on the exopodite of *Triarthrus*, which, as above noted, has the same position with reference to the endopodite as in *Apus*.

Proximally to these two branches, *Apus* has a gill on the dorsal side of the limb. This organ is either not uncovered in any of the described specimens of *Triarthrus*, or else was quite rudimentary in these animals. But Walcott's researches have led him to the conclusion that the trilobites possessed gills in the typical place, and often, in adaptation no doubt to their manner of life, highly specialized structures.

Fig. 13.—Section of *Calymene senaria*. (After Walcott.)

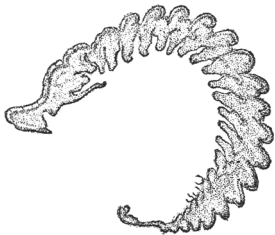
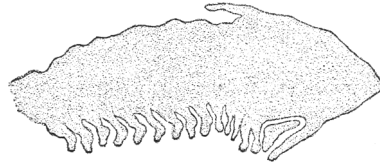


Fig. 14.—Corresponding section through *Apus* (*Lepidurus*) *spitzbergensis*, Bernard.



So far, then, we have the limbs of the trilobites fundamentally of the same type as those of *Apus*. But the question of prime importance still remains to be answered—were the trilobite-legs phyllopodan, or, considering their more filamentous distal portions, do they show any traces of having been originally membranous appendages with broad transverse insertions?

Walcott's figures appear to me to leave no doubt on this point. The sections (figs. 13 & 15, from Walcott) are almost exactly paralleled by longitudinal sections of *Apus* (figs. 14 & 16), so far, that is, as the section through the limbs is concerned. The limb of *Apus* has a long transverse attachment, partly to the ventral and partly to the lateral surface of the body. Sagittal sections cut laterally (fig. 16, p. 428) show the divisions between the limbs running high up the sides of the body as in the corresponding section of *Calymene senaria* (fig. 15, p. 428). Fig. 13 shows a section through the same trilobite, and fig. 14 one through *Apus*, passing through the lobate basal portion of the limbs farther in, that is, nearer to the median plane. On comparing the four sections here given, we thus have, in both animals, the attachments of the limbs occurring not only in tangential sections, but in those taken much farther in towards the median line. This can have but one explanation, namely,

that the limbs in *Calymene*, as in *Apus*, had long transverse lines of attachment. Further, the shape of the limbs of *Apus* in section is almost exactly the same as the sections of the limbs shown in *Calymene senaria*. This comparison with the section of *Apus* makes it very clear that the section (fig. 13) passed through the membranous basal portions of the limbs of *Calymene*, and does not contain longitudinal sections of the legs themselves, showing traces of joints, as Walcott very naturally, but I think erroneously, infers.

Fig. 15.—*A more tangential longitudinal section of Calymene senaria.* (After Walcott.)

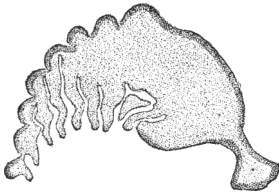
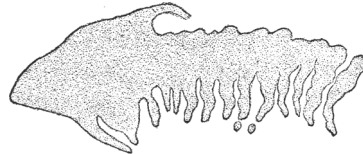


Fig. 16.—*Corresponding section of Apus (Lepidurus) spitzbergensis.* Bernard.



That the limbs in the trilobites had long transverse insertions, as in *Apus*, seems to me also to be established by fig. 17 (from Walcott), which represents a rolled-up *Calymene senaria* with a portion of the dorsal test broken out, showing a cast of the ventral surface. From this we see that the limbs were certainly, at their origin at least, membranous lobes which sloped forward, as shown in fig. 13 (p. 427). Walcott himself does not seem to have allowed for this forward slope, in concluding from his sections that the membranous lobe had but comparatively a short transverse attachment, the limb afterwards swelling out transversely into a flat triangular basal piece. If the plane of transverse section passed through the apex of one of the bent¹ black lines representing the lines of insertion of the limbs in fig. 17, we should get exactly the appearance adopted by Walcott in his ideal restored section, *i. e.* a broad basal joint with narrow attachment. Further, Walcott's own sections show in other places that the line of insertion was in reality not so short.

Fig. 17.—*Enrolled Calymene.* (After Walcott.)



[The dorsal test is broken, showing a cast of the inner ventral surface.]

Judging, then, from these valuable sections compared with trans-

¹ I cannot be quite sure whether I am interpreting the figure correctly; part of the lighter lines may be meant to represent dorsal muscular apophyses. This, however, would not affect the main argument.

verse and longitudinal sections of *Apus*, I am convinced that the basal regions of the limbs of trilobites were membranous lobes with long transverse insertions, which probably passed laterally into the membranous under-surfaces of the pleuræ. Fig. 15 is, I think, completely explained by this supposition.

These membranous basal plates probably projected inwards towards the ventral median line all along the trunk, as they still do in *Apus*, perhaps as segmental repetitions of the masticatory plates round the mouth. In *Apus*, I believe, they are still functional, and serve to push food forward towards the head and mouth. The anterior pairs are armed with teeth, and foreshadow the maxillipedes of the higher malacostraca.

We conclude, then, that the limbs of the trilobites, in spite of their development of filiform ambulatory legs, were originally membranous lobes, and that their basal regions persisted as such. This is of primary importance, as it places their affinity with the phyllopods beyond question.¹

Of equal importance is the fact which I have elsewhere already insisted upon, that the limbs of the trilobites show the same gradual diminution in size from front to back which we find in *Apus*, the most posterior being quite minute and rudimentary. If my explanation of this remarkable phenomenon be correct, namely: that these posterior segments are fixed in an undeveloped larval condition, then these early phyllopods were clearly not very far removed from ancestors with a very much richer segmentation than they themselves possess, or than *Apus* possesses. *Apus cancriformis* develops, or commences to develop, upwards of sixty segments, and may thus well be descended from a form with seventy to eighty, or even a hundred segments.

SUMMARY.

It is now possible, from the foregoing considerations, to fix with great probability the zoological position of the trilobites. The bending round ventrally of the first segment, the great labrum with antennæ attached at its sides, the 'wandering' of the eyes, the pores (pointing to the probable presence of water-sacs), the head with a varying and progressively increasing number of segments, the dorsal organ, the rudimentary character of the posterior segments, and the gradual diminution in size, with the essentially lobate or phyllopodan type, of the limbs, all serve to connect the trilobites with *Apus*.

This relationship cannot, however, be considered as direct. *Apus*, on account of its richer segmentation, the absence of pleuræ on the

¹ [Since this paper was read, Dr. Beecher has described the 'Appendages of the Pygidium of *Triarthrus*,' Amer. Journ. Sci. ser. 3, vol. xlvii. p. 298, April, 1894. *The limbs of the rudimentary pygidial segments of Triarthrus are almost indistinguishable from the rudimentary limbs of the larval segments in a growing Apus, which till now were unique among the limbs of arthropods.* The limbs of trilobites, whatever their adult form, were therefore beyond question developments of originally phyllopodan appendages. Their transitions from front to back, that is, from filamentous to membranous, is also exactly paralleled in *Apus*, see figs. 9, 4, 5, and 10 in 'The Apodidæ.'—H. M. B., June, 1894.]

trunk-segments, and its more membranous parapodia-like limbs, must be assumed to lie in the direct line upwards from the original annelidan ancestor towards the modern crustacea. The trilobites then must have branched off laterally from this line either once or more than once, in times anterior to the primitive *Apus*, as forms specialized for creeping under the protection of a hard imbricated carapace. This carapace was obtained by the repetition, on the trunk-segments, of the head-shield which, as we have already seen, almost certainly existed as a structure *sui generis* in earlier forms, and, somewhat modified, has been retained as such in the early crustacea proper ('*Aspidophora*').

Reading downwards, we should arrange the relationship as follows:—

A richly segmented annelidan ancestor, with the first segment bent round, so that the labrum and mouth point backwards, in order that the parapodia may function as mouth-parts; projections due to this bending round occur at the sides of the first, or flexed, segment.

The second segment fuses with the first to form a head of two segments. The lateral projections, secondarily specialized, are repeated on the second segment as pleuræ, which fuse with the lateral projections of the first segment.

Three segments form the head-region, and two pairs of pleuræ fuse with the lateral projections to form a head-shield.

Four segments form the head-region, and their lateral projections form the head-shield. This head-shield *is not* repeated as pleuræ along the trunk-segments.

→ *Microdiscus* and other trilobites which have only four segments in the head, and in which the head-shield *is* repeated as pleuræ along the trunk-segments.

Five segments form the head-region, their pleuræ forming the head-shield, which *is not* repeated as pleuræ along the trunk-segments.

→ *Olenellus* and other trilobites with five head-segments. These may either be deduced from trilobites with four head-segments, or have branched off independently from the main stem. The pleuræ are repeated along the trunk-segments for a creeping manner of life. With various formulæ of the cephalic limbs.

Head-shield developing backwards as a carapace. *Apus*.

→ Trilobites (e. g. *Ogygia*) with six segments forming the cephalic region, due probably to the association of the powerful limbs¹ of the sixth segment with the mouth-parts.

Modern crustacea.

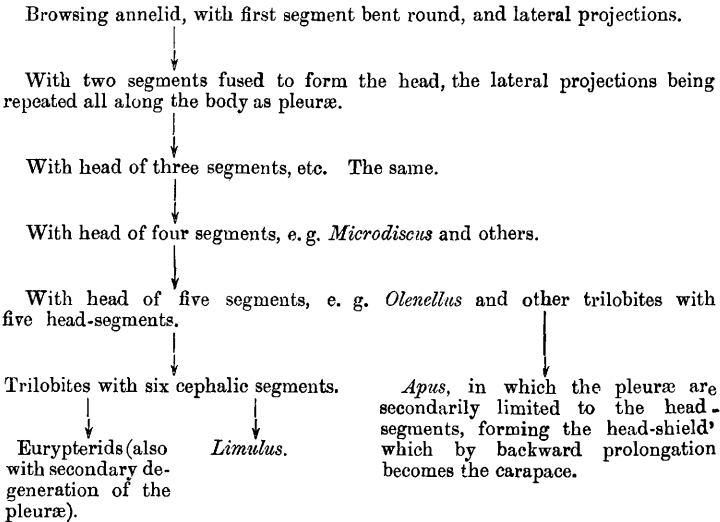
→ *Limulus*.

→ Eurypterids (with secondary degeneration of the pleuræ).

¹ Compare the special development of the first trunk-limbs of *Apus*, and of *Calymene* according to Walcott's restoration.

In this provisional classification we have assumed that *Microdiscus* and *Olenellus* branched off, perhaps independently, from the main stem, as forms specialized for creeping—by the development of the pleuræ along the whole length of the body. It is obvious, of course, that there is an alternative scheme, namely, that which assumes that *Microdiscus* and *Olenellus* stand more or less in the direct line, and that *Apus* branched off from *Olenellus* (each having five head-segments). *Apus* in this case would be a later specialization, characterized by a failure to develop the pleuræ (for example, the Eurypterids) along the trunk-segments, perhaps in adaptation to a more free-swimming manner of life. In that case, its cylindrical vermiform body would be a return to ancestral conditions.

The classification would then be as follows:—



For my own part, I find the former classification the more acceptable. The repetition of the head-shield as pleuræ along the trunk-segments, seems to be the *specialization* which characterizes the trilobites. If *Apus* cannot show the primitive segmentation of the head, no trilobite can show the vermiform body and the rich segmentation of *Apus*.

It seems to me, therefore, that the trilobites, studied in the light of new discoveries, especially of those which we owe to American investigators, yield the most interesting and important evidence as to the origin of the crustacea. Stripped of their pleuræ and of the expansion of the head-shield, we have, in the early trilobites (e. g. *Olenellus*), long segmented animals tapering at the posterior end. The first segment is bent round ventrally, so that the large labrum points backwards. The appendages of the first segment appear to have functioned as sensory organs and to have pointed downwards, being inserted at the sides of the labrum. The following segments were provided with membranous lobate appendages carrying, on their

dorsal edges, gills and sensory cirri, and distally specialized into locomotory organs. The alimentary canal ran through the whole length of the body, bending round anteriorly to open through the mouth.

The trilobites may thus be briefly described as *fixed specialized stages in the evolution of the crustacea from an annelidan ancestor, which bent its mouth round ventrally so as to use its parapodia as jaws.*

Postscript on the Relation of the Isopods to the Trilobites.

[The suggestion that the isopods are the modern representatives of the trilobites must be judged on its own merits. The argument in the foregoing paper is not in any way affected by it. The relationship between *Apus* and the trilobites would remain intact, the question being merely the following, "Can the isopods be deduced directly from trilobites with five head-segments, that is, can they be drawn from the main crustacean stem below *Apus*, or have they branched off from the higher crustacea above *Apus*?" The former is practically the position taken up by MacLeay¹ (referred to by the President in the discussion which followed the reading of the above paper). That able observer recognized the relationship between *Apus* and the trilobites, but placed the latter between *Apus* and the amphipods, probably without any clear notion of what we now mean by descent.

I am myself disposed to think that the isopods and amphipods are but repetitions of the same process above *Apus* as that which is illustrated by the trilobites below *Apus*. If the trilobites were primitive crustacea lower than *Apus*, specially adapted to a creeping mode of life, the isopods may be crustaceans higher than *Apus* adapted to the same mode of life, and therefore closely resembling the trilobites. The well-developed anteriorly-placed antennæ, the unmistakably crustacean mouth-formula, the sharp division into thorax and abdomen, show the isopods to be crustacea above *Apus*. Hence I cannot help thinking that they are related to the trilobites, not directly, but indirectly through *Apus*.—June, 1894.]

DISCUSSION.

The PRESIDENT complimented the Author on the clear manner in which he had shown the homologies between the ancestral form *Apus* and the trilobita. He called attention to W. S. MacLeay's 'Observations on Trilobites,' published in 1839, in which MacLeay had proposed to place the trilobita between the entomostraca and xiphosura on the one hand and the isopoda and amphipoda on the other. He thought that MacLeay deserved credit for his acute insight into the relations of these forms, and that, too, at a time when but

¹ W. S. MacLeay, 'Observations on Trilobites, founded on a Comparison of their Structure with that of living Crustacea,' in Murchison's 'Silurian System,' pt. ii. 1839, pp. 666-669.

little advance had as yet been made in the study of the arthropoda. While he agreed with Mr. Bernard that the earlier trilobites presented forms with very numerous segments, he pointed out that the later ones showed signs of advance—in having fewer free thoracic rings and a well-developed pygidial shield. He had always cherished the idea that the isopoda might have branched off at some distant time from the trilobita, and he drew attention to such points of structure as the pores in the free cheeks, which were present in such isopods as *Sphæroma* and *Serolis*, and in such trilobites as *Phillipsia*, *Griffithides*, *Ampyx*, and *Trinucleus*. The way in which the neck-segment is folded around the glabella and forms the free cheeks in both isopods and trilobites must also be deemed significant.

The discovery of such well-preserved limbs, by Dr. Beecher, in *Triarthrus Beckii* justified the Author in regarding at least these earlier trilobites as extremely entomostracan in character.

The Rev. T. R. STEBBING agreed with the Author in thinking that the trilobites have little connexion with the isopods, though the resemblance is sometimes striking, and is often favoured rather than otherwise by the character and position of the eyes. But, whereas the isopods are distinctly malacostracan, with a number of segments never exceeding twenty-one, the number of segments in a trilobite varies as readily as the fashion of a lady's dress. Moreover, in many isopods the mandibles are stout and the limbs either strong or long and prominent, making it improbable that the body of the animal should be fossilized without leaving any trace of the appendages, as appears to have happened with the majority of the trilobites. On the other hand, *Apus* and *Lepidurus* seem to have still less claim to any close alliance with the trilobites, the two groups being quite devoid of any general resemblance, the phyllo-pods in question having a large carapace extending back over the segments of the thorax, on which the head-shield of the trilobite never encroaches. The tail or pleon of the trilobite is, as a rule, transverse and compact, that of the phyllopod elongate and flexible. Of the phyllopod limbs many are lamellar, while in Walcott's restoration of the trilobite *Culymene senaria* there is a continuous series of legs, all slenderly articulated. If mere guesses are allowable, the suggestion may be hazarded that of living animals the group nearest the trilobites may be the myriapods, as these have a long series of slenderly articulated legs, and segments both numerous and variable in number. The still prevailing obscurity of the subject is illustrated by the fact that Walcott compares certain appearances in his sections of Silurian trilobites with the spiral branchiæ of a whale-louse, a parasitic amphipod of probably quite modern development. In the figure of a specimen of *Triarthrus Beckii*, a pair of antennæ are represented projecting straight forward from the centre of the head-shield. It may well be wondered where the points of attachment of antennæ so placed are to be found on the underside of the trilobite's head.

Prof. G. B. HOWES said that he believed the discovery of the terminal anus in the trilobite dealt the death-blow to the association

of the trilobites with the arachnoid series. He advanced reasons for accepting the Author's homology of the median cephalic pore of the trilobites with the aperture of the dorsal gland of *Apus*, and for believing that in the latter we are dealing with an organ early differentiated in the crustacean series, but now for the most part lost—the 'dorsal organ' of embryologists being its vestigial homologue. He believed that the facts and arguments brought forward by the Author of the paper proved the trilobites to be crustacea, and fully justified their association with *Apus* as an early offshoot on the crustacean line. He considered that in demonstrating the progressive fusion of head-segments among the trilobites the Author had shown those animals to have so far undergone a parallelism of modification to all other great groups of arthropods. If, as he believed, the degree of this fusion was the surest guide to the position of any one member in an arthropod series, that being the higher in proportion as the fusion is numerically the greater, the places customarily assigned to the Scorpionidæ and the Araneidæ by the advocates of the *Limulus*-an-arachnid theory must be transposed—the scorpions becoming the culminating members of the arachnoid series. Judged from this standpoint, the superficial resemblances between *Limulus* and *Scorpio* appeared to him closely akin to those between, say, the flying squirrels and *Galeopithecus*, or between the *Rana jerboa* and *Bufo jerboa* of Borneo, and suggestive of isomorphism by convergent modification. To definitely assert that *Limulus* is an arachnid appeared to him on a par with saying that the 'flying lemur' is a squirrel, and the *Bufo jerboa* a frog.

Mr. MALCOLM LAURIE also spoke.

The AUTHOR, in reply, said that none of the objections dealt with points of any morphological importance. The head-shield in *Apus* developed by backward prolongation into a carapace, and in the trilobites gave rise to the pleuræ by segmental repetition, as any prominent cuticular structure might be repeated. It was enough that the antennæ in both were inserted at the sides of the labrum, and that the trunk-limbs were of the same type, with 'endopodite,' 'exopodite,' and gills, and, what was still more important, with broad lines of insertion. That the trilobites might be myriapods could not have been seriously suggested. The subject was necessarily speculative, and the value of a speculation depended upon the evidence in its favour; in the present case, all the available evidence tended to establish the affinities proposed.