A FURTHER CONTRIBUTION TO THE PROBLEM OF SEGMENTATION IN THE ARTHROPODA.

J. M. REYNOLDS.

ABSTRACT.

The problem of the condition of segmentation in the primitive Arthropoda is an important one, and especial interest attaches to it because of Tillyard's new few-segmented ancestor theory. There are reasons for believing that few-segmented larvae have not the phylogenetic significance that Tillyard attaches to them, nor is phylogenetic segment loss necessarily to be found in ontogeny as he supposes. In the latter case three separate aspects have to be considered (a) true anamorphic forms which never develop such segments. (b) forms with embryonic development or with larval segment differentiation which fail to differentiate such segments. (c) excalated segments which occur in the middle of a series of segments and whose loss is likely to be shown in ontogeny. The more immediate Arthropod ancestor can be discussed, but the pre-Arthropod form is dangerous to postulate in the present state of our knowledge, or analysis of it. Three solutions of the former problem have been suggested (a) Carpenter's twenty-two-segmented ancestor theory, an analysis of which, in the light of modern knowledge, suggests that it deserves serious attention. (b) Lankester's freely-segmented ancestor theory, which is consistent with the facts, and the one which may prove to be correct. (c) Tillyard's few-segmented ancestor theory, which is at variance with the facts, and necessitates improbable assumptions. Tillyard's theory deriving progoneate and opisthogoneate Arthropoda by differential segment interpolation from a common ancestor with a single gonopore, is unsatisfactory because of the unlikely structure that it involves for internal organs. Finally, the mode of tagma formation postulated by Tillyard for his segmentation theory seems to be contrary to embryological evidence; to be unsupported by morphology; and to be inadequate as an explanation of available data.

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INTRODUCTION.

Since metamerism forms the basis of the structure of most of the higher Invertebrata, and is also prominent in the highly evolved phylum Chordata, it will scarcely be denied that problems concerning the fundamental principles of metamerism are of real and general zoölogical interest. Tillyard's theory (1930) strikes at the root of all accepted conceptions of Arthropod metamerism, so it is obvious that, if he is right, our ideas require drastic revision and, if he is wrong, it is most desirable that the fallacies in his arguments should be exposed. This, then, must be my excuse for making a renewed attack on Tillyard's theory, which he has recently (1935) modified and extended. Because his interpretation of the progress of metamerism in the Arthropoda has been confined to its bearing on the origin of Insecta, his work has tended to escape both general notice and serious attention, by those responsible for the spreading of zoölogical knowledge. As a striking example of this, I may refer to a recent textbook on Invertebrata, by Borradaile, Potts, Eastham and Saunders (1932, revised 1935), in neither edition of which is there even a reference to Tillyard's revolutionary theory. Now, although I am not in agreement with Tillyard, I cannot but feel that the careful and skilful way in which he has expounded his theory, and the detail with which he has tried to substantiate it, entitle it to close consideration. This was especially true when Borradaile's book was published, for I do not think that there had been any attempt made at a comprehensive criticism of Tillyard's theory, until my recent paper (1935). (It is true that there had been a brief, but very inconclusive and sketchy criticism by Raymond, Petrunkevitch and Carpenter (1931), but Tillyard answered this satisfactorily (1932)). I wish, here, to elaborate the views which I expressed in 1935, and also to deal with one of Tillyard's late papers (1935) which appeared just after mine.

That the course of metamerism offers a problem on which finality cannot readily be reached, is true, but one can at least try to show in which direction the balance of evidence points, and also try to suggest the most useful lines along which further enquiry should be made. Palaeontology has already shown us that, quite apart from the imperfection of the geological record, the antiquity of the Invertebrata makes it likely that we shall wait in vain for any lineage series, linking together the classes of its phyla. We must, then, resign ourselves to the fact that these phylogenetic problems can only be settled by logical inferences drawn from relevant data. That all the necessary data is yet available, is unlikely, but that only means that we must be more careful in our use of what data we already have. There is a modern tendency to regard such attempts to reconstruct phylogenies as vague, valueless, speculation; but to this I cannot agree—it should be possible to reach reasonable conclusions by the honest use of a scientifically-trained critical faculty.

SIGNIFICANCE OF FEW-SEGMENTED DEVELOPMENTAL FORMS.

Tillyard's paper (1935) assumes that the ancestor of the Myriapoda-Insecta complex was few-segmented—that is to say, he relies upon the arguments in his original paper (1930) as sufficient proof of this, without supplying any additional evidence. Those arguments I have already criticized (1935), but as I wish to add further comments, it will be necessary briefly to summarize Tillyard's evidence. It is impossible to do him full justice in such a summary, so for a truer understanding of his arguments, reference should be made to his original paper.

Tillyard regards the few-segmented nauplius as evidence of a few-segmented condition in ancestral Crustacea; whilst in its developmental addition of segments he sees a recapitulation of the evolutionary stages which lead up to the modern Crustacea, with their greater number of segments. Tillyard attaches a similar significance to the anamorphosis of Myriapoda and Protura. My view is that such few-segmented developmental stages are inevitable from the manner in which segments are formed, and I previously quoted Annelida in my support. It has since occurred to me that it is perhaps better to keep within the Arthropod phylum, which can be done by considering the Onychophora. In these animals the segments are developed from front to back, new segments being differentiated from the posterior region one by one (Sedgwick, 1885). In this case it is obvious that, however many segments their ancestors had possessed, the early developmental stages of modern Onychophora would be few-segmented, simply because the segments are formed in this gradual way. Nor do I see any reason to expect that segments should appear simultaneously in any of the other Arthropod classes. It is, then, not reflections of an animal's few-segmented ancestors that are to be seen during the gradual increase in the number of segments during Arthropod ontogeny, but simply the inevitable terms in a series dictated by the manner in which the structure of the adult is formed from an unsegmented mass. For this reason I cannot agree that any importance can be attached to the few segments possessed by nauplii or newly-hatched Myriapoda. Surprise may be expressed that these active larvae do not have their metamerism so hurried on, that when hatched they have the complete series of segments in an elementary form, leaving the full development of the segments to continue with growth; but Raw (1927) makes a suggestion which meets the case. He says that segments probably need to attain at least a certain minimum size before they are practicable structures, so that small creatures such as nauplii and Pauropod larvae would be likely to have a few fairly-well-developed segments, rather than a larger number of relatively inefficient ones. When the natatory appendages of the nauplius and the ambulatory appendages of a young Pauropod are remembered, it seems only fair to admit that this argument may have some weight.

In the development of some Branchiopod nauplii, an early stage may be seen when the larva has a large number of minute annulations, and some zoölogists have regarded them as traces of ancestral forms with many segments. This is an important point, because if they are right, as much damage is done to my views as to Tillyard's. The damage to Tillyard's theory is obvious, since this annulated larva is supposed to show a freely-segmented ancestor, while Tillyard regards the nauplius as evidence of a few-segmented ancestor. The damage to my theory is less evident, but quite as real, because if this annulation does show a primitive, many-segmented, condition, then traces of that condition do appear early in development, before the fewer-segmented stages — a thing which I regard as mechanically impossible. However, the explanation seems to be that no coelom sacs are associated with these annulations (Claus 1886), which are, therefore, not true segments at all. Rather should they be regarded as mere wrinkles, such as the annuli found non-segmentally on *Peripatus*. It is only fair to add that it has been shown by Balfour (1880) in the Araneae, and by Wheeler (1893) in the Orthoptera, that segmentation may appear in the ectoderm before it does so in the mesoderm. But although it is true that here we have, for a time, ectodermal divisions which are truly segmental, and yet which are not associated with separate mesodermal masses; their true nature is ultimately shown by a correlated mesodermal segmentation—which is not the case in the Branchiopod nauplius. Of course it might still be claimed that the Branchiopod annulations are of segmental value, but that the corresponding mesodermal masses here fail to differentiate. But I do not think that this explanation can be correct because an ectodermal area covered by a number of annuli eventually forms a single segment. This means that, if the annuli be regarded as reminiscent of ancestral segmentation, modern segments are of multiple origin—a most unlikely thing, for which I know of no evidence. Thus the pseudo-segmented condition of the Branchiopod nauplius is not to be given any phylogenetic significance.

(One further case, for which no explanation seems to have been advanced, is found in the Pauropoda. According to Harrison (1914) the larva hatches with fewer apparent segments than can be distinguished on the embryonic membrane. But this segmentation of the embryonic membrane is not sufficient to support the idea that it is a developmental trace of a more-freely-segmented ancestor, since it shows less segments than the *adult* attains, although more than possessed by the *first-stage larva.* Since I know of no confirmation of the observation, I am inclined to think that little significance should be attached to it, but the relatively few segments possessed by the Pauropoda suggest that the first stage larva may possibly consist of more segments (as shown by the embryonic membrane—their "loss" being due to fusion) than is apparent).

SEGMENT LOSS.

Closely related to the question just discussed, is one which Tillyard (1930) uses as apparent support for his theory. He asks why, if he is wrong and modern Arthropoda have come from more-freely-segmented ancestors, is there no trace of such reduction to be seen in the development of certain few-segmented forms? The answer to this query involves the investigation of the somewhat complex problem of segment loss which, though both interesting and important, has not, I think, yet been properly faced or suitably discussed. The complexity of this problem can be reduced by considering separately two of its aspects which require rather different explanations. Although the two groups into which I am dividing the problem grade into one another, I feel that the principles involved in the "loss" of segments in *typical* examples of each of these groups are so different that they cannot satisfactorily be considered together. The essential differences are well illustrated by the nauplius and the Diplopod larva respectively. In the former the adult condition is attained by the *differentiation* of the trunk, whilst in the latter it is attained by the *addition* of new segments. Thus in the nauplius segments are elaborated out of material which is present before full segmentation, whilst in the Diplopod new units are formed from material which is created only as, and when, required. The truth of this is shown by Pflugelfelder (1933) in his histological account of the development of segments in the Diplopod, *Platyrrhacus.* Now it can hardly be expected that the failure to show the full complement of ancestral segments would be expressed in the same way in two groups which attain their posterior segments in ways so different from one another. But, having established this distinction, I would make it clear how complete is the gradation between the two groups, by recalling that *before hatching* the Diplopod has a few segments differentiated out of an unsegmented mass, and that it is only *after hatching* that it adds segments from newly-formed material.

Curiously enough, the two examples (*Pauropus* and *Collembola*) whose few-segmented condition Tillyard challenges his critics to explain, fall one into each of my two groups.

Let us first consider *Pauropus*. This is an anamorphic form which attains in the adult condition a number of segments (18) which is admittedly less than is usually found in Myriapoda (20 at least), yet in whose development there are no traces of what anyone would regard as segment loss. This, says Tillyard, shows that their ancestors were not freely-segmented; but I cannot agree. Since the posterior segments of the Pauropoda are not formed simultaneously, nor differentiated out of an unsegmented terminal region, but are formed from material expressly made for the purpose, when required (the truth of this is clearly shown by Harrison (1914) in his description of the development of *Pauropus*), it is surely probable that, in attaining their adult condition, forms with fewer segments than their ancestors will fail to manufacture the lost segments, rather than make material which is subsequently to be lost. This would explain why no traces of freely-segmented ancestors are to be found in the development of any relatively few-segmented forms belonging to that one of my two groups in which the posterior segments are *added*.

Tillyard's other example is Collembola, a group of Insecta whose adults, by differentiation from an unsegmented mass, attain only nine post-cephalic segments, instead of the normal Insectan complement of fourteen. Tillyard (1930) claims that Collembola show no trace of reduction of segments during development, and that they must, therefore, have come from few-segmented forms. (He has rather spoilt his argument now (1935) by postulating that Collembola came from even-fewer-segmented ancestors, and yet saying that no trace of such ancestors is, or should be expected, to be seen in the development of modern Collembola, since their present condition of segmentation has obtained since the Devonian.* Well

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* Actually, no complete abdomen of the Devonian Collembolan, *Rhyniella*, has been found, so there is nothing to *prove* its condition of segmentation. Even Scourfield's recent discoveries (unpublished), of which he has kindly sent me tracings, provide no evidence on this point.

surely if he cannot find developmental traces of the ancestral stages required for his phylogeny, it is unreasonable for him to expect his opponents to find their ancestral stages either). But although I think that this retort is sufficient to discount any significance that Tillyard may attach to the few-segmented condition of the Collembola, it avoids the real issue, which is that of the failure of full ancestral segmentation to appear in forms which develop their segments from an unsegmented embryonic mass. I wish, therefore, to discuss the problem fully, though without feeling that Tillyard's original challenge any longer necessitates an answer.

If we first consider *Limulus* it may appear that segments are formed, and secondarily lost, but that, I think, is only an illusion. The interesting region is the metasoma, which consists of an unsegmented mass representing six original segments, all of which were possessed by its allies the Eurypterida, and four of which were possessed by some Synxiphosura (Savory 1935). But in *Limulus* there are *developmental* traces of two "segments" which are later lost, or rather "fused". Here, then, it would seem that ancestral segments are made during development only to disappear in the adult, but that is hardly the truth. When it is said that traces of these segments occur in development, all that is meant is that coelom sacs appear (actually Iwanoff 1933, also figures slight traces of two other mesodermal masses), and not that other segmental structures (such as terga and sterna, appendages and neuromeres) are to be found. But the loss of identity of these coelom sacs in the adult is not to be regarded as notable, since that is the usual fate of the coelom in the Arthropoda. What should be stressed is that, although these coelom sacs do appear, they fail to produce their usual effects—the formation of the surrounding segmental structures. Thus the few-segmented condition of present forms is seen to be reached during development by a failure to differentiate ancestral segments, rather than by their early formation and later loss. Before leaving *Limulus* I may point out that, just as we see in the *unsegmented* metasoma a sign of its more-freely-segmented ancestors, so should we see in the *unsegmented* trunk of the nauplius the sign of its freely-segmented ancestors—a sign whose validity is the more readily accepted since the nauplius trunk eventually *differentiates* into many segments.

It must be admitted, however, that where segmentation is less profuse than in ancestral forms, it is usually possible to trace rudimentary coelom sacs for some of the "lost" segments, and also there tends to be a region of the body which, although unsegmented, is not a segment. Thus in the Araneae the unsegmented opisthosoma presumably represents twelve originally free abdominal segments, although only about ten of them are visible as mesodermal masses in embryology (Sivickis and Fileoto 1928). I would draw especial attention to the unsegmented region of this second of my groups, because it differs so markedly from the condition in my first group, where "lost" segments have no material representation.

If I be challenged to explain the condition of the Collembola, I should say that there are two possibilities. It may be that careful embryological work would show traces of mesodermal masses at the end of the abdomen, showing that the Collembola belong to group two, and come from more-freely-segmented ancestors. Those workers who have done research on Collembolon development do not seem to have paid much attention to this point, and indeed I have not yet found a paper which makes it clear whether the last "segment" of the abdomen is truly a segment, or only a telson. The other possibility is that the Collembola were originally anamorphic (the Protura suggest that the Apterygota developed in this way in the comparatively recent past) and that they were reduced to their present condition of segmentation by loss as in my group one. This would account for their failure to show traces of ancestral segments, although their development is now embryonic.

It will be noticed that, while I have tried to show that few-segmented forms attain that condition by a failure to reproduce ancestral segments, I have restricted my remarks to posterior segments. (It may be of interest to note that posterior segments may be "lost" in another way. In *Pieris* (Henson 1932) part of the tenth and the whole of the eleventh abdominal segments "disappear" owing to their invagination into the rectum.) I had good reasons for making the above restriction, because it is well known that, quite contrary to the principles that I have established, in some cases the phenomenon of excalation occurs. Thus the tritocerebral segment of the Insectan head and the pre-genital segment of Arachnida, have fleeting embryonic representation, before disappearing in the adult. But this is not really any contradiction of my views, because both of these lie in the midst of a series of segments, which quite alters the case. For, since segments are formed one by one from the posterior and pushed forwards, the segments behind excalated segments could not be differentiated until the animal had disposed of the material for the excalated segment. Excalated segments are not just dropped out of the animal suddenly, they simply become of less importance, so that their material is likely to remain in a more or less reduced condition, and such of it as does remain must be marked off in development, so that it shall not impede the formation of the following segment. The case of the posterior segments is quite different, since they are the last to come from the zone of segment addition (group I) or the region of segment differentiation (group II) and are not followed by other segments. That it is the final members of the series which do not appear, is particularly well shown in *Limulus,* in whose metosoma the last few segments are not even represented by coelom sacs; and Cannon (1924) comments on a similar gradation in the development of *Estheria.*

The Trilobita are of especial interest since they show the essential processes of both my two groups working together in an animal. The formation of the new material for segments goes on at the posterior of the pygidium, as in group I, whilst the differentiation of segments goes on at the anterior of the pygidium (Raymond 1920) as in group II. That the formation of the pygidium is, therefore, due to the addition of segmental material being more rapid than is the differentiation of segments, I have already shown in my previous paper (1935) in which further evidence for such a view may be found. I should like, however, to insist that the way in which the pygidium behaves, and is formed, contradicts those who regard it as a mere consolidation of the originally free posterior segments—such as occurs in some Isopod Crustaceans. *In the adult* the pygidium undoubtedly does represent undifferentiated segments which were free in the animal's ancestors, but *during development* the pygidium is successively composed of a different series of segments (often the number composing it varies at each moult (Raw 1927)), so that the pygidium of one instar cannot be considered to be homologous with that of another instar, even within a species, let alone from species to species.

ANCESTRAL SEGMENTATION.

I am doubtful whether any useful purpose can be served by discussing the condition of the segmentation of the earliest members of the Annelid-Arthropod complex. As usual, there are two diametrically opposed views: (a) That few segmented larvae such as the trochophore show the ancestral segmentation (Carpenter 1905)—but the reasons which I have already given for refusing such significance to the nauplius, are equally applicable here; and (b) That adult Annelida, with their large but indefinite number of segments show the ancestral condition (Raw 1927), since these are undoubtedly on a lower evolutionary level than the fewer-segmented Arthropoda. But although we may agree that the Annelida belong to a lower evolutionary *level,* they do not necessarily lie on the evolutionary *path* of the Arthropoda, which discounts such evidence.

But, if we must admit that because of our present lack of knowledge (or perhaps because of our failure to apply adequate critical analysis to the available knowledge) the problem of the ancestor of the Annelid-Arthropod complex must remain unsolved, there is no reason to abandon the discussion of the segmental condition of the more immediate ancestor of the six main groups of the Arthropoda—Arachnida, Crustacea, Insecta, "Myriapoda", Onychophora, and Trilobita. The two extreme possibilities just outlined for the original ancestor remain, but there is added a compromise in the form of Carpenter's twenty-two-segmented ancestor, from which both fewer-segmented and more-freely-segmented forms have been claimed to have arisen. In my previous paper I regret to say that I was so under the influence of modern authors that I spoke of Carpenter's theory (1903 and 1905) as having been sufficiently discredited by Tillyard (1930), and said that it was, therefore, not entitled to the space which its discussion would require. That estimate I now feel to have been unfair, and so I wish to make amends by reviewing Carpenter's theory here, and claiming for it the right to serious consideration, and a more adequate criticism and appraisal than it seems to have received in the past.

Since Carpenter's theory depends upon the establishment of segmental correspondence between the Arthropod classes, the first problem is to find those forms in each class whose segmentation may justly be regarded as typical of that class—or, more strictly, those members from whom all other members of the class are likely to have derived their segmentation. Now this can be done in two ways—the first of which, though obviously unscrupulous, is probably the better of the two. It is to choose as examples of "typical" segmentation, simply those animals which suit one's theory best! It may seem an unprincipled thing to do, but as long as one admits that one is doing it there is no risk of misleading people. Anyway it would not be seriously suggested that the phylogeny of the Arthropoda can be determined solely on the basis of segmentation, so any such theory will inevitably be checked by other data. Thus it would seem best to make out as strong a case as possible from data strictly relevant, showing how, and where, minor modifications could be made without fundamentally damaging the theory; and above all it should be admitted that certain alternatives depend for their solution, on the discovery of further data. It may now be asked, why the checking of one's data should not be done by oneself, which brings us to the second method which, though apparently fairer than the first, is actually liable to lead to far worse abuses. That is to seek in each class the animals which, on a balance of characters, are to be regarded as generalized. Where there is general agreement on the matter, among competent authors, it would be unwise not to accept their decision, since it would probably mean basing one's argument on an insecure foundation. But it is not often that such agreement can be found, with the result that one has got to determine *for oneself* which animal is most generalized. Now to do this adequately in a *single case* requires a review of all aspects of any possible candidates—taking into account morphology, embryology, palaeontology, etc.—which is clearly beyond the scope of most writers. (This will readily be admitted, if it be remembered that there is, as yet, no general agreement, even among students of Crustacea, as to the form of the primitive Crustacean appendage.) The result is that, adequate discussion being out of the question, the writer chooses such facts as may seem significant to him, and draws from them his conclusions as to which animals are primitive in the various groups. Of how little value such conclusions are, hardly requires stressing, yet when used to support a main theory, they tend to assume a spurious significance. I cannot, therefore, too strongly deprecate the bolstering up of a theory by a *selection* of facts which apparently support it, because such a method is liable to give a false idea of that theory's consonance with data, other than that on which it is primarily built. In other words a partial discussion of data is a great deal more misleading than its complete omission.

In considering Carpenter's theory then, let us either adopt forms whose primitiveness is vouched for by general opinion, or in the absence of these, choose those which suit his theory best—and if further data be required, let us either discuss it fully, or freely admit the need for its further discussion. To save space the evidence is provided in the usual tabular manner, and should be used in conjunction with the comments that follow. (See Table I.)

Table I.

	INSECTA	CRUSTACEA	ARACHNIDA
	Machilis sp.	Nebalia sp.	Scorpio sp.
1.	Occular. Eyes?	Occular. Eyes?	Rostral. Rostrum?
2.	Antennal. Antennae	Antennular. Antennules	Cheliceral. Chelicerae
3.	Tritocerebral	Antennal. Antennae	3d Prosomal. Pedipalpi
4.	Mandibular. Mandibles	Mandibular. Mandibles	4th Prosomal. Legs
5.	Maxillary. Maxillae	Maxillulary. Maxillulae	5th Prosomal. Legs
6.	Labial. Labium	Maxillary. Maxillae	6th Prosomal. Legs
7.	1st Thoracic. Legs	1st Thoracic. Natatory Leg	7th Prosomal. Legs
8.	2d Thoracic. Legs	2d Thoracic. Natatory Leg	Pregenital. Chilariae?
9.	3d Thoracic. Legs	3d Thoracic. Natatory Leg	Genital. Operculum
10.	1st Abdominal. Styles	4th Thoracic. Natatory Leg	2d Mesosomal. Pectines
11.	2d Abdominal. Styles	5th Thoracic. Natatory Leg	3d Mesosomal. Lungs
12.	3d Abdominal. Styles	6th Thoracic. Natatory Leg	4th Mesosomal. Lungs
13.	4th Abdominal. Styles	7th Thoracic. Natatory Leg	5th Mesosomal. Lungs
14.	5th Abdominal. Styles	8th Thoracic. Natatory Leg	6th Mesosomal. Lungs
15.	6th Abdominal. Styles	1st Abdominal. Pleopods	1st Metasomal
16.	7th Abdominal. Styles	2d Abdominal. Pleopods	2d Metasomal
17.	8th Abdominal. Styles	3d Abdominal. Pleopods	3d Metasomal
18.	9th Abdominal. Styles	4th Abdominal. Pleopods	4th Metasomal
19.	10th Abdominal. Styles	5th Abdominal. Pleopods	5th Metasomal
20.	Anal. Cerci	6th Abdominal. Pleopods	6th Metasomal
21.	Telson. Caudal ramus	7th Abdominal	Telson. Poison Spine
22.		Telson. Furca	
23.			
24.			
25.			

TABLE I.—(Continued.)

	DIPLOPODA	CHILOPODA	SYMPHYLA
	POLYXENUS SP.	LITHOBIUS SP.	SCOLOPENDRELLA SP.
1.	Occular. Eyes?	Occular. Eyes?	Occular? Eyes?
2.	Antennal. Antennae	Antennal. Antennae	Antennal. Antennae
3.	Tritocerebral	Tritocerebral	Tritocerebral?
4.	Mandibular. Mandibles	Mandibular. Mandibles	Mandibular. Mandibles
5.	Maxillary. Maxillae	Maxillary. Maxillae	Maxillary. Maxillae
6.	Labial. Labium	Labial. Labium	Labial. Labium
7.	1st Abdominal	1st Abdominal. Poison Claws	1st Abdominal. Legs
8.	2d Abdominal. Legs	2d Abdominal. Legs	2d Abdominal. Legs
9.	3d Abdominal. Legs	3d Abdominal. Legs	3d Abdominal. Legs
10.	4th Abdominal. Legs	4th Abdominal. Legs	4th Abdominal. Legs
11.	5th Abdominal. Legs	5th Abdominal. Legs	5th Abdominal. Legs
12.	6th Abdominal. Legs	6th Abdominal. Legs	6th Abdominal. Legs
13.	7th Abdominal. Legs	7th Abdominal. Legs	7th Abdominal. Legs
14.	8th Abdominal. Legs	8th Abdominal. Legs	8th Abdominal. Legs
15.	9th Abdominal. Legs	9th Abdominal. Legs	9th Abdominal. Legs
16.	10th Abdominal. Legs	10th Abdominal. Legs	10th Abdominal. Legs
17.	11th Abdominal. Legs	11th Abdominal. Legs	11th Abdominal. Legs
18.	12th Abdominal. Legs	12th Abdominal. Legs	12th Abdominal. Legs
19.	13th Abdominal. Legs	13th Abdominal. Legs	13th Abdominal. Reduced Legs
20.	14th Abdominal. Legs	14th Abdominal. Legs	14th Abdominal. Cerci
21.	Anal	15th Abdominal. Legs	Anal
22.		16th Abdominal. Legs	
23.		17th Abdominal. Genital Legs	
24.		Anal	
25.			

TABLE I.—(Concluded.)

	PAUROPODA	ONYCHOPHORA	TRILOBITA
	PAUROPUS SP.	PERIPATUS CAPENSIS	GENERAL
1.	Occular? "Eyes"?	Antennal. Antennae	Occular? Eyes? ....
2.	Antennal. Antennae	Mandibular. Jaws	Antennal. Antennae.
3.	Tritocerebral?	3d Cephalic. Oral Papillae.	3d Cephalic. Biramous Leg.
4.	Mandibular. Mandibles ...	1st Abdominal. Legs	4th Cephalic. Biramous Leg.
5.	Maxillary. Maxillae	2d Abdominal. Legs	5th Cephalic. Biramous Leg.
6.	Labial. Labium	3d Abdominal. Legs	6th Cephalic. Biramous Leg.
7.	1st Abdominal. Reduced Legs	4th Abdominal. Legs	....
8.	2d Abdominal. Legs	5th Abdominal. Legs	Variable number of
9.	3d Abdominal. Legs	6th Abdominal. Legs	thoracic segments;
10.	4th Abdominal. Legs	7th Abdominal. Legs	each bearing a pair
11.	5th Abdominal. Legs	8th Abdominal. Legs	of biramous legs.
12.	6th Abdominal. Legs	9th Abdominal. Legs	....
13.	7th Abdominal. Legs	10th Abdominal. Legs	Variable number of
14.	8th Abdominal. Legs	11th Abdominal. Legs	"fused" pygidial
15.	9th Abdominal. Legs	12th Abdominal. Legs ...	segments; each
16.	10th Abdominal. Legs	13th Abdominal. Legs	bearing a pair of
17.	11th Abdominal	14th Abdominal. Legs	biramous legs.
18.	Anal	15th Abdominal. Legs	....
19.	....	16th Abdominal. Legs	Terminal segment
20.	....	17th Abdominal. Legs	may bear uniramous
21.	....	Anal. Anal Papillae	"cerci."
22.	....	1st Embryonic	....
23.	....	2d Embryonic	May be a "Telson"
24.	....	....	or Median Caudal
25.	....	....	process.

(1) Insecta. (a) The pre-occular segment suggested by Wiesmann's (1926) discovery of a pair of coelom sacs in that position during the development of *Carausius,* has not been included, because its bearings on the comparative morphology of Arthropoda are so important and revolutionary that it seems difficult to accept his conclusions, without confirmation. The possibility of the existence of such a segment, must, however, be borne in mind for his paper provides evidence which it would be unreasonable to ignore. The sacs appear from the first in a pre-oral position which argues against their segmental nature, and would seem to relate them rather to a "prostomial" region. In Annelida the prostomium is not, of course, regarded as a segment (Goodrich 1897), but that is because no coelom sacs are associated with it. The coelom sacs under discussion *may* have arisen secondarily in answer to the muscular needs of the labrum, but I know of no parallel to such a process, within the Arthropoda (though there is a *possibility* of a similar condition in the Arachnida, as I shall show later (page 45)). Finally, I would suggest that if this segment be shown to be present in other Insecta, it will be found in all other Arthropod groups with the possible exception of the Arachnida, and the probable exception of the Onychophora. (b) The occular segment (or pre-antennal) has been shown to be represented by coelom sacs (Wiesmann 1926) or mesodermal masses (Paterson 1935), but the eyes are not necessarily its appendages. (c) The tritocerebral segment is too well-known to require comment, other than it is usually embryonic but that it may be represented by vestiges in some adults (e.g. *Dissosteira*—Snodgrass 1928). (d) Hansen's claim (1893) for the segmental nature of the "maxillulae" has not met with general acceptance. The embryological evidence seems against it, since Folsom's claim (1899) for a coelom sac for this "segment" in Collembola has not been substantiated. Thus Filipcenko found no trace of it in *Isotoma,* whilst modern workers in insect embryology fail to find evidence for it in the Pterygota. Since morphological data alone, does not seem to be valid evidence, I have not included a maxillular segment in my table. (e) Eleven segments seem to be the number contained in the insect abdomen (Wiesmann 1926, Henson 1932, and Paterson 1935). The telson of Protura has often been mistaken for a twelfth segment, but is, of course, not a true segment at all.

(2) Crustacea. (a) The occular segment here offers the

same problems as it does in the Insecta. (b) The limbless abdominal segment of the Leptostraca is probably fused with the preceding one in Eumalacostraca—as observed in the Schizopoda by Sars (1885). (c) The choice of a Malacostracan as a "typical" Crustacean is probably not in accord with the general view, but I do not think that sufficient evidence is yet available (or the discussion of it suitably undertaken) to show that the Entomostraca have a greater right to be regarded as "typical" Crustacea. Undoubtedly, however, this is a point on which adequate discussion, by competent authors, is required.

(3) Arachnida. (a) The embryonic existence of the rostral segment has been shown by Wallstabe (1908), confirming Jawarowski's description (1891), though Sivickis and Fileoto (1928) did not find a rostral segment in *Latrodectus*. Further, the cases quoted refer to work on the Araneae, but in the more primitive group, Xiphosura, Iwanoff (1933), in his very thorough work on the embryology of *Limulus*, found no trace of a rostral segment. It is, therefore, possible that Balfour (1880) was correct in his assumption that the rostral "segment" of Araneae is secondary, because of its late differentiation from the cheliceral segment. Finally, Police (1933) figures distinct coelom sacs associated with the rudiments of the rostrum in *Theridium* (Araneae), and consequently not only considers the existence of the rostral segment to be proved, but also regards the paired rudiments of the rostrum to be its appendages. (b) The embryonic status of the pre-genital segment is too well established to require discussion (e.g. Iwanoff 1933). According to the author cited, its appendages are the chilariae, though that is not the general view.

(4) Diplopoda. (a) The occular segment offers the same problems here as in Insecta, and a coelom sac for this region has been shown clearly by Pflugelfelder (1932). (b) The presence of a tritocerebral coelom sac has been shown by Robinson (1907) and Pflugelfelder (1932). It is remarkable, however, that the latter attributes the antennae to this segment. Robinson does not do so, and seems more likely to be correct, for Pflugelfelder's view would place the Diplopoda in a very different morphological category from the Chilopoda and Insecta. Nevertheless it would be wrong to ignore Pflugelfelder's work, and this is a point which requires confirmation, although it will not affect the *number* of segments in

my table. (c) The maxillulae (Carpenter 1905) offer the same problems here as in Insecta, again there being no embryological evidence for a maxillular segment. (d) Carpenter (1905) claimed to have dissected out both pairs of maxillae in *Polyxenus,* but they seem usually to be fused to form the gnathochilarium. The compound nature of the gnathochilarium has been shown embryologically by Pflugelfelder (1932) in *Platyrrhacus,* but Robinson (1907) claims that in *Archispirostreptus* the first maxillae are vestigeal and that the gnathochilarium is formed from the second maxillae only. (e) *Polyxenus* is the only form with so few segments in the abdomen.

(5) Chilopoda. (a) The head presents the same problems here as in Insecta. The occular segment (with vestigeal or rudimentary appendages of a non-occular nature) and the tritocerebral segment (a very faint trace, consisting of little more than a neuromere) were found embryologically in *Scolopendra* by Heymons (1901), who did not find coelom sacs for the maxillulae or for a pre-occular segment. (b) There do not seem to be any Chilopoda which have few enough abdominal segments to reduce the total number of segments below twenty-four.

(6) Symphyla. (a) Since the embryology of Symphyla has not been worked out, it seems fair to assume, on morphological grounds, that they possess occular and tritocerebral segments, until it is proved otherwise. According to an account of their sense-organs in the Journal of Entomology, Claremont (1928-1929) small eye-like structures were observed in Symphyla by Grassi (1885) but neither Hansen (1903) nor Williams (1907) found them. Wood-Mason (1883) found pitted structures in a suggestive position, but made no histological investigation. It is quite possible that eyes have been lost by these creatures since they are very small, and of a retiring habit. (b) The lack of correspondence between tergites and sternites makes the determination of the number of abdominal segments difficult. It is possible that too many segments are shown in the table, but it is not likely that there are too few. Embryological investigation is required to settle this, and many other points regarding the Symphyla.

(7) Pauropoda. (a) The head offers the same problems here as in Symphyla. Pauropoda do not appear to have any eyes, although Harrison (1914) mentions some eye-like structures. Hilton (1928-1929) makes no mention of them in his account of the sense organs of the Pauropoda, nor do his

drawings suggest their presence. The same possibility of their secondary absence applies here as in Symphyla. (b) According to Harrison (1914) twelve segments are clearly marked off by ventral sutures, but tergites are not very useful, owing to their tendency to fuse in pairs, or to be lost altogether. It is clear that Pauropoda possess fewer segments than do the Symphyla, but embryological investigation is clearly necessary.

(8) Onychophora. (a) There is no embryological evidence for an occular segment, and there is reason to believe that none will be found. The eyes of *Peripatus* resemble those of Annelida, rather than those of other Arthropoda (Sedgwick 1885). (b) *Peripatus capensis* is the only Onychophoran which has so few segments, and its condition is unlikely to be primitive, since there is embryological evidence of at least two segments, behind the last found in the adult (Sedgwick 1887).

(9) Trilobita. (a) The occular segment is assumed for morphological reasons, since embryology cannot be invoked for confirmation. (b) According to Crampton (1928) the first pair of biramous appendages lie beside the hypopharynx and paragnaths, and are thus beside the mouth, and must, therefore, have acted as mandibles. On the assumption that the Trilobite head can be directly homologized with that of Crustacea, Crampton considers that the first pair of biramous appendages in Trilobita are homologous with Crustacean mandibles, which would mean that a pair of pre-oral appendages (homologous with Crustacean antennae) have been lost. If this is true, an extra segment must be added to the Trilobite head in my table. Since, however, it is well-known (Goodrich 1897) that segments have passed from a post-oral to a pre-oral position during the evolution of the Arthropoda (they actually do so during the development of the nauplius), it seems probable that the first pair of biramous appendages in Trilobita are actually homologous with Crustacean antennae, although occupying the position of Crustacean mandibles. In other words, the pre-oral shift of cephalic segments has not proceeded so far in Trilobita, as it has done in the Crustacea. (c) This is one of the two most unsatisfactory of the groups as regards trunk segmentation, because the choice of any particular form as illustrative of "typical" segmentation seems quite arbitrary. There is an *apparent* range (in which of course suitably segmented forms are to be found) from forms with very many segments, to forms with very few segments. I say apparent because the so-called few-segmented forms like *Agnostus,* have a pygidium which may (Reynolds 1935) be

formed of many "fused" segments, so that it is possible that such "few-segmented" forms actually had more segments than is commonly supposed. Carpenter (1903) gave a table showing (statistically) the tendency for earlier Trilobites to have fewer segments than later forms, but I am not in a position to say whether modern data would support such a view. Anyway, one of the oldest Cambrian Trilobites—*Nevadia weeksi*—has twenty-eight thoracic segments, and a small, apparently unsegmented, pygidium (Walcott 1910), which seems to discount the value of Carpenter's statistical data.

When Carpenter (1903 and 1905) proposed the theory which the foregoing data is supposed to support, he tried to show that the segmental correspondence between the Arthropod groups was exact. Now this could only be done by the use of (a) much very doubtful data (especially as many embryological problems had not then been solved), and worse still (b) by the selection of just those facts relevant to segmentation which suited him best.

This quite naturally militated against the general acceptance of his views, and tended to obscure their underlying significance. For I believe that the table which I have drawn up, although not showing exact segmental correspondence, and although certain of its features are subject to confirmation, is none the less impressive. Huxley (1858) said "I venture to think it a result of no small moment if it can be proved that a Lobster, a Cockroach, and a Scorpion are composed of the same primitive number of somites", and it must surely be agreed that it would be a remarkable coincidence if three such distinct groups as Insecta (20), Crustacea (21) and Arachnida (20), had reached such conditions of segmentation independently, either from few-segmented or many-segmented ancestors. The improbability of such a coincidence is not lessened when it is seen that hints of a similar condition are to be found in at least two of the three remaining Arthropod groups. Although the Myriapoda is admittedly a heterogeneous group, it is sufficiently compact for one to assume that the segmentation of the ancestors of one of its groups, did not differ markedly from the segmentation of the ancestors of the other groups. Therefore, Symphyla (?21), Polyxenus (21) among the Diplopoda, and Lithobius (24) among the many-segmented Chilopoda, may well be reminiscent of an "about-twenty-segmented" Myriapod ancestor. The small size of the Pauropoda is surely sufficient excuse for their possession of slightly fewer segments? On the other hand, I have shown that *Peripatus capensis* can hardly be claimed to show the possibility of such a twenty-one-segmented ancestor for the Onychophora; and the Trilobita give no real hint of an "about-twenty-segmented" ancestral condition—though I have shown that even in them the possibility cannot be ruled out.

Of course, one *can* still claim that such segmental resemblances are pure coincidence, but I must confess that I find it difficult to believe that four of the six Arthropod groups should arrive *independently* at an "about-twenty-segmented" condition. If it could be shown that such a number of segments were mechanically desirable, the coincidence would be less remarkable, but this does not seem possible. It does not appear probable that an aquatic Eurypterid swimming with a single pair of paddles; a terrestrial Insect walking on three pairs of legs, or flying with two pairs of wings; an aquatic Crustacean swimming with many pairs of limbs, or crawling with several pairs of legs on the sea-bottom; a worm-like *Peripatus* crawling on stumpy protrusions; and a Millipede scrambling about on numerous pairs of legs—should all be most satisfactory when composed of about twenty segments! And, even if this were believed, a little thought would show that such an idea is unsound, because whilst about twenty segments may be the general plan in each group, segments are "lost" or "fused", without any apparent ill-effect to the animals concerned. Some deeper significance must then be sought, if we are not willing to admit that this segmental condition is due to pure chance—and if that significance is not one of common ancestry, some entirely new hypothesis is necessary.

I have tried to put Carpenter's theory fairly, in its strongest form, and freed from its usual encumbrance of a straining after exact segmental correspondence. Whether it is true or not, frankly I do not pretend to decide, but I maintain that its claim must be seriously admitted, until an adequate criticism is made of the theory, as I have put it.

Carpenter's theory having had its due, we can turn to the two remaining theories regarding the segmentation of the more immediate Arthropod ancestor. The many-segmented theory was expounded by Lankester (1905), and I have shown that it is probably consistent with the facts in the Myriapod-Insect group (1935). Until it is decided which type of Crustacean (Entomostracan or Malacostracan) is more primitive in its segmentation, the Crustacea can hardly be brought into the argument. The Trilobita are probably in favour of this freely-segmented ancestor theory, as I have shown (1935). The information provided by the Onychophora can be used to support this theory rather better than it could to support Carpenter's, since the form with fewest segments (*Peripatus capensis*) shows embryonic signs of having come from more freely-segmented ancestors. Finally the Arachnida may be said to support the theory of gradual reduction of segment members, as will be shown later (page 51). On the whole, therefore, this theory does not seem to be at variance with the facts, and may well be the one on which it is necessary to fall back. Although rather little definite evidence can be put forward in support of this theory, I shall show that the few-segmented ancestor theory is unlikely to be correct, so if Carpenter's theory also be rejected, the many-segmented theory remains as the only tenable one.

As for the few-segmented ancestor theory, I have already shown that the facts on which Tillyard bases it are capable of other, and to my mind more probable, explanations; but this, of course, does not necessarily mean that it is incorrect. I must confess that I am unable, at present, to find evidence in favour of a few-segmented ancestor, but I am not prepared to dismiss it altogether, as an impossible hypothesis. However, I do wish to discuss the difficulties into which Tillyard has been led by the form in which he has recently worked out his few-segmented ancestor theory. His hypothetical Myriapoda-Insecta ancestor (see Table II) has only four post-

TABLE II.

Tillyard's Hypothetical Myriapod-Insect Ancestor—Postcephalic Segments.

Name of Segment	Postcephalic Position	Features
A	1	Paired walking legs.
B	2	Paired walking legs.
Y	3	Paired walking legs, and paired gonopores.
Z	4	No appendages. Anus.

cephalic segments, and yet all but one is quite distinct from the others in its structure, and in the function which it performs. But if the animal represents so primitive a stage in metamerism that only four trunk segments had appeared, I do not believe that those segments would be notably different from one another, either in form or function. Thus, if Tillyard regards his hypothetical ancestor as primitively few-segmented (as I think he does), it seems to me he is postulating, for its trunk segments, a specialization of structure and function, which is incredible. Further, his ancestor must have had a complicated six-segmented head attached to a primitively few-segmented trunk. It is little use claiming that the head of the hypothetical ancestor was generalized, because the various groups of the Myriapoda-Insecta are supposed to have arisen *independently* from this hypothetical ancestor, and the resemblances between the Myriapod-Insect heads (see Table I) seem far too great to admit the possibility that they were evolved *separately* from an unspecialized head. I will not labour this point, because I do not think that anyone will disagree with me, but I must insist on the unlikelihood of the Myriapoda-Insecta ancestor having evolved a complicated six-segmented head (complete with excalated tritocerebral segment) whilst still possessing only four trunk segments.

Tillyard has only worked out his theory of increasing segmentation in the Myriapod-Insecta, but his use of the nauplius in support shows that he believes the same process to have occurred in Crustacea, whilst he would presumably extend it to the other Arthropod classes also—since it would be strange if these differed from one another in so vital a particular as the process of metamerism. It is fair, then, to check Tillyard's theory by seeing if it is applicable to classes other than the Myriapoda-Insecta (I have shown (1935) that here the evidence is at least equally consistent with a *decrease* in segment numbers). The Arachnida seem to behave in exactly the opposite way from that postulated by Tillyard. Far from the number of segments increasing throughout the group, it has become fewer, at least as far as external representation is concerned. Since the Scorpiones seem to have been represented by aquatic forms in the Silurian (Pocock 1901), they may well claim to be representative of primitive forms, especially as regards their segmentation, since in this respect they resemble the ancient Eurypterida. The number of segments in the opisthosoma of Scorpiones is twelve, a number which is not merely never exceeded in the Arachnida, but which is seldom attained amongst the higher forms (e.g. Opiliones show only ten opisthosomal segments). The Arachnida, then, provide no evidence that Tillyard's theory of increasing segmentation is correct. In the Crustacea the evidence is less certain, but a review of the main groups of the Class is instructive. Within the Branchiopoda there is little doubt that it is reduction that has occurred, since it is in the specialized forms, such as the Cladocera, that segments are few in number. The unsegmented abdomen of the Cirripedia is eloquent evidence of a failure to differentiate segments externally (as was explained for the metasoma of *Limulus*) and not a sign of a primitively few-segmented condition; and the same applies to the Ostracoda. The Copepoda show complete stability of segment numbers, which is the more surprising since their tagmata are differently composed in different families. This, of course, sheds no light, one way or the other, on the question under discussion. Finally the Malacostraca cannot be said to show an increase in segment numbers; indeed there is a "loss" of a terminal segment in passing from the Leptostraca to the Eumalacostraca. The evidence supplied by the Onychophora has been sufficiently discussed in connection with Carpenter's theory, and seems hardly certain enough to be useful (though they seem against Tillyard's views), and I have shown (1935), that the Trilobita are probably opposed to Tillyard's views.

To sum up all that I have said about Tillyard's few-segmented theory, I would suggest that it is not supported by the available evidence, and that the form in which he has proposed it raises difficulties which place a severe strain upon one's credulity.

THE GONOPORE IN RELATION TO SEGMENTATION.

The next angle from which I wish to view segmentation, is that of Tillyard's gonopore theory. I do not propose to discuss how the gonopore problem itself is to be solved, because that lies outside the scope of the present paper. My reason for criticizing Tillyard's gonopore theory, here, is that it has a direct bearing upon the process of segmentation, and also it appears so attractive that, if substantiated, it would form a very strong piece of evidence in favour of his general theory of segmentation. It is in respect of the gonopore position that Tillyard's recent paper (1935) is most modified as compared with his original paper (1930). His new solution of the gonopore problem is ingenious, and the more striking since it shows, for the first time, how progoneate and opisthogoneate forms might be directly related to one another. Before dealing with Tillyard's theory I must, of course, outline it, but again reference should be made to his paper to do the theory full justice.

He points out that the Pauropoda hatch with only five post-cephalic segments (Harrison 1914), so that although they belong to the "Progoneata", the segment on which the genital duct of the first instar opens, is antepenultimate. Had the Pauropoda hatched with only four post-cephalic segments, the gonopore would have been on the penultimate segment, as it is in the "opisthogoneate" Chilopoda. Tillyard believes that the ancestor of the Myriapod-Insect complex was this hypothetical form with a four-segmented abdomen (see Table II), and that from it, the Opisthogoneata evolved by the addition of segments in front of the genital segment, whilst the Progoneata evolved by the addition of segments behind the genital segment. (I may say that, in my 1935 paper, I anticipated that Tillyard would reach these conclusions, although I expressed the opinion that zoölogists would not readily accept them. I briefly criticized the Pauropod gonopore theory then, but not fully, because I was unaware at the time that Tillyard had formulated it, let alone that he was about to publish it.)

My first objection to his theory is that it implies that the ancestral Myriapoda-Insecta had not got segmental gonads. Indeed, Tillyard states this as a fact, and claims that in doing so, he is deferring to those who criticized him for making the opposite assumption in his original paper. For myself, I find it hard to believe that the gonads of metameric animals were not originally segmental, especially when other internal organs are considered. The segmental ganglia of the nervous system may perhaps be interpreted as a direct response to local muscular and sensory needs, but the same can hardly be said of the heart. In both Myriapoda and Insecta, the heart can be shown to be segmented (in certain primitive forms) by the possession of paired ostia right up to the front of the abdomen in the former case, and into the thorax in the latter. Thus it is to be presumed that the heart would have been at least three-segmented in Tillyard's ancestor. If, then, the heart was segmented, how is it that the gonads were not segmented also? I think the answer is hard to find.

Within the Myriapoda-Insecta complex it is true that none of the gonads of the Myriapoda show the segmental condition in the adult, but all the same each gonad is formed from segmental mesodermal contributions (Heathcote 1888), and the same is true of the Insecta. (The germinal cells themselves do not have a segmental origin, but they become located in several successive segmental mesodermal masses during development, so that the gonads themselves arise metamerically (Cannon 1924—Crustacea: and Wheeler 1893—Insecta)). Further, in the Insecta there is to be found the evidence on which Tillyard's original segmental gonopore theory was built. In the Apterygota—which as I have shown (1936), and as Tillyard believes, are probably the primitive Insecta—there are clear signs of segmental gonads. In Japygid Thysanura the ovaries have seven segmentally arranged lobes (Grassi 1888), and in Machilis the ovary has seven ovarioles (nearly segmentally arranged) (Oudemans 1888); whilst the bunches of ovarioles in the Pterygota seem suggestive. Also Wheeler (1893) found germ cells in six or more of the abdominal segments of Orthopteron embryos, which seems a further proof of the segmental nature of Insect gonads.

But, of course, these arguments are of little use against Tillyard, because he would probably retort that all modern segmentation of the gonads of the Myriapoda-Insecta, arose owing to segmental contributions to organs during the addition of the pre-gonopore or post-gonopore segments; and that such segmentation has, therefore, no ancestral significance. (Since, as we have already seen, he would extend his few-segmented ancestor to the other Arthropod groups, evidence drawn from them would be equally susceptible to the same explanation. I shall not, therefore, waste space by considering the evidence afforded by Arthropod classes other than the Myriapoda-Insecta.)

But, whilst we may admit that the new segments might well have added further gonads, it is a little difficult to believe that only a segmental mass of genital material in a coelom sac would be produced, *without the segmental duct.* (It seems unwise to deny that each gonad originally had a duct, when one considers the Onychophora. Here the coelomoducts of the segmental "nephridia" clearly originally acted as genital ducts, since the gonads actually open through the last of them.) Where a number of segmental gonads are already present, there is nothing remarkable in longitudinal fusion occurring, so that all genital products shall be shed through a common duct (indeed this obviously happened in the Onychophora, as is shown by the development of Peripatus —Sedgwick 1887), but it is less plausible that, as new segments are added, their genital material shall be fused to the original gonad, without showing any trace of their own ducts. In any case it would be a little strange for an originally non-segmental structure to receive segmental additions.

There still remains to be discussed the difficulty created by the diversity of the gonopore position, within the progoneate and opisthogoneate groups themselves. It will be sufficient to consider the latter only, since the problems are similar in both. In the "Opisthogoneata" the gonopore may open terminally (Chilopoda); penultimately (Collembola and Protura); or two or three segments from the end of the abdomen (most Pterygota). Further, the Pterygote condition is rather more complicated than seems generally to be realized. The female reproductive system appears originally to have opened by paired gonopores on the tenth post-cephalic segment. Thus in the Ephemeroptera (which are the only Insectan group to retain the paired gonopores in the adult) the female ducts open on the seventh abdominal segment. Similarly in the early development of the Trichoptera (Dodson 1935) the mesodermal rudiments of the genital ducts end against the ectoderm of the seventh abdominal segment, and the more posterior position of the adult gonopore is only attained by ectodermal invagination—surely a secondary process. Finally, perhaps the most convincing evidence of all is provided by Wheeler (1893), who finds in *Xiphidium* that the female mesodermal duct is derived from the mesodermal sac of the seventh segment of the abdomen, opening between that segment and the next. But it is when the male gonopore is considered that the most surprising conclusion is reached. It is well-known that the male gonopore tends to open more posteriorly than the gonopore of the female, but it appears that not only is this true, but that the terminal part of the genital ducts originate from different mesodermal sacs in the two sexes. Thus Wheeler found that in the male *Xiphidium* the genital duct came from the tenth abdominal mesodermal sac (as distinct from the seventh in the female), opening between that segment and the ninth. From this it would seem that the gonopore and the terminal genital ducts have fundamentally different positions and origins in the two sexes. The truth of this is made even more clear by Wheeler's discovery that, in the early development of the female, rudiments of the male ducts (in the tenth abdominal segment) coexist with the female ducts (in the seventh abdominal segment). To produce gonopores placed at such different segmental distances from the posterior end of the body, and in positions varying according to the sex of the animal, the "Pauropod" ancestor would need to have been modified by processes other than the simple one of pre-gonopore or post-gonopore segment addition. To deal with this point it will be necessary to discuss the general question of tagma formation.

TAGMA FORMATION IN RELATION TO THE GONOPORE POSITION.

Tillyard grants the necessity for explaining why the gonopore is not always penultimate in "Opisthogoneata" and claims that some of the segments have been added in front of, and others behind, the gonopore of his hypothetical ancestor, in the varied proportions necessary to produce the different opisthogoneate groups of today. Indeed, he even goes so far as to suggest (1935) from which segments of the hypothetical ancestor (see Table II), these additional segments have arisen in the various regions of each of the opisthogoneate groups. But if the gonopore position has been reached by such evolutionary steps, there should surely be some trace of the process in the animals' ontogeny? In fact, if segments were added in two different ways during phylogeny, they must surely still be added in the same way during ontogeny—if the gonopore is to be in the new position? At all events, if they are not, it would be necessary for Tillyard to explain how the change-over was effected—but he has not yet made any suggestions. With regard to the development of opisthogoneate forms, I know of no evidence that developmental segment addition is to be found in both pre-gonopore and post-gonopore regions. The evidence from the Insecta alone, is sufficient to cast considerable doubt on his theory. All workers seem to be agreed that the differentiation of new segments proceeds from the front to back steadily; new segments being added from the posterior (e.g. Thomas 1936). Even if there were exceptions (which seems rather doubtful) Tillyard's theory must explain the case cited and many other similar ones.

But Tillyard does not discuss embryological evidence in this connection, and I feel that his morphological arguments lead him to untenable conclusions. He maintains that tagmata are capable of independent segmentation (1932), and in a letter he suggested that they have arisen from single segments. He says, for example, that the ordinary Crustacean head has been reached by segment interpolation behind the four-segmented nauplius head, independently of the posterior trunk segments. He gives no evidence for such a view, and the embryological evidence seems quite to the contrary. The development of the *Estheria* nauplius (Cannon 1924) gives no hint that segments are formed other than in a front to back sequence, and provides no grounds for believing that the maxillulary and maxillary segments did not originally belong to the trunk series. Hsü (1933) states that, in *Chirocephalus*, segments are developed in a front to back sequence, and his illustrations give no hint of the break which would occur if the head tagma segmented independently. Unless Tillyard can substantiate his claim for "two zones of segment addition" in a nauplius, by embryological evidence, I cannot see that this larva provides proof of the independent segmentation of tagmata.

The Onychophora certainly do not have two zones of segment addition (Sedgwick 1885 and 1887), but as they can hardly be said to have tagmata, they do not enter into the discussion.

The Trilobita are particularly inimical to any theory of the independent segmentation of tagmata, because, as I have already shown, whether a segment will belong to the thorax or to the pygidium is not evident until the end of development (Raymond 1920). Nor is there any evidence that the cephalic segments are added except from the posterior.

Even purely morphological evidence can hardly be said to favour Tillyard. In the Copepoda, there are always sixteen trunk segments, but the segments are grouped into tagmata differently in different families. Now it would be straining credulity too far to claim that the tagmata in these cases attained their present condition by independent segmentation, and yet contrived so that the extra segment addition to one tagma was compensated by a lesser segment addition to the other. It seems more reasonable to suggest that an original definite number of segments have been grouped into tagmata by independent morphological modifications in the Copepod groups.

In the Arachnida, the primitive Eurypterida such as *Strabops* have the opisthosoma undifferentiated into mesosoma and metasoma (Savory 1935); the Xiphosura have the opisthosoma divided into a six-segmented mesosoma and a six-segmented mesosoma; whilst many Arachnida retain the undifferentiated opisthosoma. From this evidence, it could hardly be suggested that the tagmata of the Arachnid opisthosoma have arisen by segment interpolation; it seems rather that the pre-existing segments have been grouped into morphologically distinct areas. It is true that the free segments at the end of the prosoma in Solifugae *might* be interpreted as recent additions from the posterior of that tagma, but they may equally well be regarded as reminiscent of ancestors, all of whose prosomal segments were free. Embryology would seem to be the only means of deciding; indeed it might even show that the freedom of the prosomal segments of Solifugae was secondary, as is the case in the two free anterior cephalic segments of Schizopoda (Borradaile 1935). It is notable, however, that if the segments of Pycnogonida are to be homologized with those of Arachnida, it must be assumed that an extra leg-bearing segment has been interpolated in the prosoma of the Pycnogonida. Calman and Gordon (1933) have suggested that this must be the case since decapodous Pycnogonida (with a second extra pair of walking legs) and even dodecapodous forms (with yet a third extra pair of walking legs) have been found. Further there are various species of these abnormal forms, which seem to have been derived independently from separate normal species. It would certainly seem that, here, segments have been interpolated, though I would suggest that if this be true, traces of such interpolation will be found in the development not only of the abnormal forms, but also in the development of the normal forms, since they appear to have arisen from the Arachnida by the interpolation of a prosomal segment, bearing walking legs.

There seems, then, no evidence (apart from the Pycnogonida) for independent zones of segment addition among the Arthropoda; indeed the opposite conclusion seems more probable from the analysis that I have made. Since such zones are necessary to Tillyard's gonopore theory, and indeed to his whole conception of the process of segmentation in the Arthropoda, it must be admitted that unless he can provide convincing evidence in his favour, his theory must fall. That he has not done so, I think I have shown; and I also think that I have provided sufficient reason for believing that the evidence does not exist.

Finally, even if such pre-gonopore and post-gonopore segment addition *could* be demonstrated, it is surely inconceivable that the proportion of segments formed in each position should be different in the two sexes—and this is what would be required to evolve the Pterygote Insecta with their female gonoduct from the seventh somite, and their male gonoduct from the tenth somite. In any case the co-existence of male and female ducts in different segments in the same animal (Wheeler—Xiphidium) shows that the derivation of the Insect gonopore cannot have been the simple process that Tillyard postulates. Indeed it provides excellent reasons for believing that the original Insecta had segmental ducts. This criticism I regard as fatal to Tillyard's recent gonopore theory.

CONCLUSION.

I am afraid that this whole paper constitutes what must appear to be a rather severe attack on my former friend the late Doctor Tillyard, whose tragic death occurred after this paper was written. It may rather be considered a compliment that his theory should need such prolonged and detailed criticism. Indeed it is the skill and care with which his theory has been propounded that makes it both attractive and formidable; necessitating consideration and criticism from all possible points of view. I hope that the supporters of Doctor Tillyard's theory will agree that at least a fair proportion of my criticism is well-founded, *in so far as it deals with his theory as now propounded,* because that is all that I would claim. If it can be shown that his theory can rise above my criticisms, they will not have been in vain, because they will have served to produce the expression of it in more satisfactory terms, and to get it freed from some of the difficulties that are created by its present form. It is a matter for deep regret that this paper cannot be answered by Doctor Tillyard, but I hope that one of his supporters will undertake the defense which he would, no doubt, ably have made. But, if my criticisms cannot be answered, I am sure that it will be agreed that the sooner the fallacies of an untenable theory are exposed, the better. In either case, then, it is hoped that this survey of the problems connected with Arthropod segmentation will serve to throw light on some of the rather hazy ideas that exist at the present, and to clear the way for further investigation.

I make no apology for those places where I have not substituted theories for those which I have sought to destroy by my criticisms, because I firmly believe that the exposure of fallacies is a useful thing in itself. For incorrect theories tend to obscure the need for further work on a problem, whilst their criticism shows the futility of continuing along such lines, and stresses the need for a fresh viewpoint; whilst the premature formulation of a new theory may easily re-create the undesirable conditions which criticism has just removed.

SUMMARY.

(1) The importance of the segmentation problem, and the need for a careful consideration of Tillyard's few-segmented ancestor theory.

(2) The reasons why few-segmented larvae are not to be given phylogenetic significance.

(3) Phylogenetic segment "loss" is not necessarily to be found in ontogeny. (a) True anamorphic forms never develop such segments. (b) Forms with embryonic development or with larval segment differentiation, fail to differentiate such segments. (c) Excalated segments occur in the midst of a segment series, and their loss is likely to be shown in ontogeny.

(4) The more immediate Arthropod ancestor is discussed. (a) Carpenter's twenty-two-segmented ancestor theory is reviewed in the light of modern knowledge, and it is suggested that this theory deserves serious consideration. (b) Lankester's freely-segmented ancestor theory is shown to be consistent with the facts, and to be the one which may prove to be correct. (c) Tillyard's few-segmented ancestor theory is shown to be at variance with the facts, and to necessitate improbable assumptions.

(5) Tillyard's gonopore theory is criticised in relation to the unlikely structure that it necessitates for internal organs.

(6) The mode of tagma formation postulated by Tillyard for his segmentation theory is shown to be contrary to embryological evidence; to be unsupported by morphology; and to be inadequate as an explanation of available data.

(7) The value of destructive criticism, apart from reconstruction, is emphasized.

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College of Technology,
Leicester, England.