PAPERS
OF
THE ROYAL SOCIETY OF TASMANIA
1930

THE EVOLUTION OF THE CLASS INSECTA.*

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With 19 Text Figures.

(Read 9th June, 1930.)

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*This paper is an amplification of the address of similar title given as the Presidential Address to Section D, Brisbane Meeting, A.A.A.S., May, 1930.

INTRODUCTION.

The subject of this paper is one which is admittedly full of difficulty, yet at the same time one of the profoundest interest, viz., the Evolution of the Insects as a Class from some ancestral type which was not an Insect, but something more primitive in its general structure. In attempting this task, I must first of all classify and pass in review the various theories that have been advanced by famous zoologists or entomologists to account for the origin of this Class, admittedly the highest development within the Phylum Arthropoda. Each main hypothesis will be examined on its merits and tested as to its validity. Having carried out this task, I then propose to state the position as it appears to me and to offer a new theory which attempts to embrace all the known facts of the case.

SECTION I.

EXISTING THEORIES.

One method of examining the theories already put forward about the origin of the Class Insecta would be to keep to strict chronological order and deal with each separate theory as it was presented by its author. This would be a long and, I fear, somewhat tedious process. Moreover, these theories are of very unequal merit, and some of them most certainly do not deserve special treatment, as they have not been worked out with the care and thoroughness which we have a right to demand from any author who would try to bring the scientific world to accept his views. Also, it so happens that a particular theory, after enjoying a period of popularity for a span of years, sinks into oblivion against the greater brilliance of some newer theory. Then, after a further period, another author comes along, refurbishes up the old theory and adds a few more tempting tit-bits to it, and back we swing to the older outlook with a fresh polish on it. Thus, if I attempted the historical method, I should be keeping your minds swinging back and forth between one type of theory and another, and you would merely be studying the trees instead of trying to get a general view of the whole wood.

So I shall attempt in this instance another method, viz., to classify the known theories of the origin of Insects into definite groups. This will enable you to follow the evolution of the theories themselves, even if it does not help you much to follow the evolution of the Insects.

Now, in order to classify and study these theories, let us first of all examine the question of what types of animals may be brought into the question.

Obviously, we may reject from the start all those theories which attempt to derive the Insecta from something very far back and extremely simplified by comparison with them. It does not, for instance, take a very acute mind to put forward the theory that Insects are derived from Annelid Worms! If anyone has done so, no doubt you will all with one accord make the obvious rejoinder "That is too "easy a solution; for it seems highly probable that the "whole of the Phylum Arthropoda is so derived." Nevertheless, I would not altogether reject such a theory. I would only insist that, for it to be taken into account, it must present a fairly complete picture of the lines of evolution of the various groups of Arthropoda from the Annelids, and, in the special case of the Insecta, fill in the wide gap between the creeping worm and the highly specialised flying insect. It is for this one reason that I feel compelled to pass over Walton's theory (1927) of the origin of Insects direct from Polychæta with a few remarks and a reference at the end of this address, to enable those of you who so desire to study the theory for yourselves. Walton simply sets forth the general idea that both the leg and the wing of the insect have been derived from the parapodium of a Polychæt worm, the leg being a specialised development from the neuropodium and the wing from the notopodium. He makes no attempt to explain how it is that, in this case, all the segments of the insect's body do not possess wings and legs; he merely indicates that the wings, being dorso-lateral, could best have come from the notopodium, while the legs, being ventro-lateral, could best have come from the neuropodium. No attempt is made to show the evolution of the intermediate stages between these two extremes, nor to indicate the known fossil types that should surely stand somewhere near the line of evolution; nor is any attempt made to show how the complex musculature of the insect leg or wing could be derived from the extremely simple and, histologically, very different, musculature of the worm. Walton's theory, then, in spite of a certain amount of intriguing suggestiveness, must be put outside the main feast of reason, and must be partaken of, if swallowed at all, as a simple *hors d'œuvre!*

This brings me to my first main proposition, viz., that any theory of the evolution of Insects, to be acceptable, must either show their origin from a lower type of Arthropod, or, if not that, must at least indicate the relationships that exist between Insects and those groups of Arthropods nearest to them. You will note that I ask specifically, not for a derivation from any *living* type of Arthropod, though some authors are so obliging as to offer this type of solution, but at any rate either from some ancient fossil type of Arthropod, or, if not that, then from some carefully reasoned hypothetical common ancestor shared by Insects and some related group or groups. Let us begin with a careful consideration of existing theories concerning the origin of Insects. I shall take first of all those which seek to derive the Insecta from Marine Arthropoda. These can be divided into two groups, as follows:—

I. Descent of the Insecta from Trilobita. *Handlirsch's Theory.*

II. Descent of the Insecta from Crustacea. Various theories culminating in *Crampton's Theory.*

I. HANDLIRSCH'S THEORY.

Handlirsch's Theory of the evolution of Insects from Trilobites was first published in full form in 1908 and was again very ably summarised by the author in 1913. It forms almost a perfect model in completeness of presentation and carefulness of argument, and therefore must merit our fullest attention. The author was a student of the great Austrian entomologist, Brauer, and was therefore originally predisposed towards Brauer's well-known Campodea-Theory. During the course of a long life, he has gained as wide an experience of insects in general as any living man, and he is well known as the author of a monumental work on Fossil Insects (1908), in which his theory is very fully set forth. I propose here to give you a succinct account of the theory itself, and then to offer some criticisms of it.

According to Handlirsch, the winged insects or Pterygota (which he calls Pterygogenea) are the original Insecta, and the ancestral type is to be found in the Order Palæodictyoptera of the Upper Carboniferous. This type carried the fore and hind wings outspread as in the Anisopterous Dragonflies, but it also possessed rudimentary wings on the prothorax, and the abdominal segments were provided with small side-processes of the tergites, known as paranota.

Handlirsch then sets out to prove that the wings of the Pterygota are simply specialisations from the original paranotal or pleural expansions of the tergites found in the Trilobites. This, of course, is not difficult. There are only two possible theories of the origin of insect wings; one theory holds that they were originally gills, and that, therefore, the ancestral winged insect must have been aquatic; the other theory holds that they are lateral expansions of the thoracic nota. The majority of entomologists now support the latter theory; so Handlirsch appears to be on very sound ground here.

Handlirsch then addresses himself to the question as to whether any Trilobite ever existed that could possibly have been the direct ancestor of the Pterygota. His argument on this point runs thus:—We know of Trilobites with few postcephalic segments, as well as Trilobites with many such segments; somewhere between the two extremes there must have been forms in which the segmentation of the body was exactly that required to give rise to the segmentation found in Pterygota. (This we may readily admit, without thereby accepting it as proof that such a form, if it existed, was the actual ancestor of the Insects.) Again, he says, we know of Trilobites with narrow bodies as well as Trilobites with broad bodies; also we know of Trilobites possessing a pair of compound eyes and three ocelli, exactly as in Insects, and at least one genus of Trilobites is also known which possessed a pair of terminal, many-jointed cerci. Further, all Trilobites agree with Insects in possessing only one pair of simple antennæ.

All the above points are well made, as far as they go, and we can admit them as indicating quite clearly *what kind* of Trilobite *might have been* the ancestor of the Pterygota. But none of them prove that any such Trilobite *was* actually the ancestor we are looking for, and I am sure you will all note with me that most of the characters enumerated by Handlirsch are so primitive that there is still quite a long gap to fill between Handlirsch's ancestral Trilobite form and a Palæodictyopterous Insect. This gap Handlirsch very cleverly fills by giving a reconstruction of his idea of what the larva or nymph of a Palæodictyopteron must have been like (figs. 1, 2, 3). When you look at these

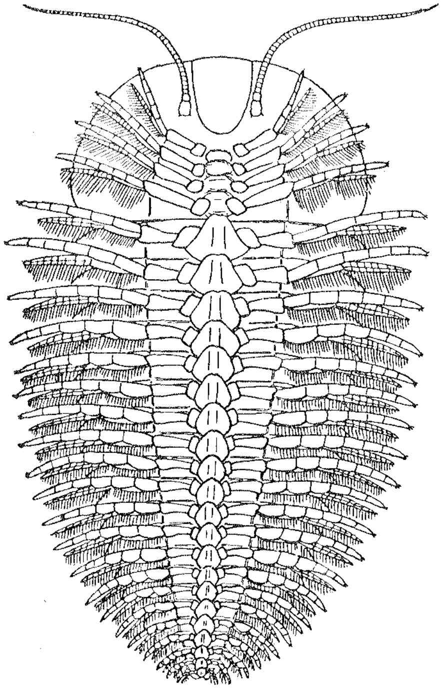

Fig. 1. A Trilobite, *Triarthrus becki,* Green. Ventral view, restoration. After Beecher.

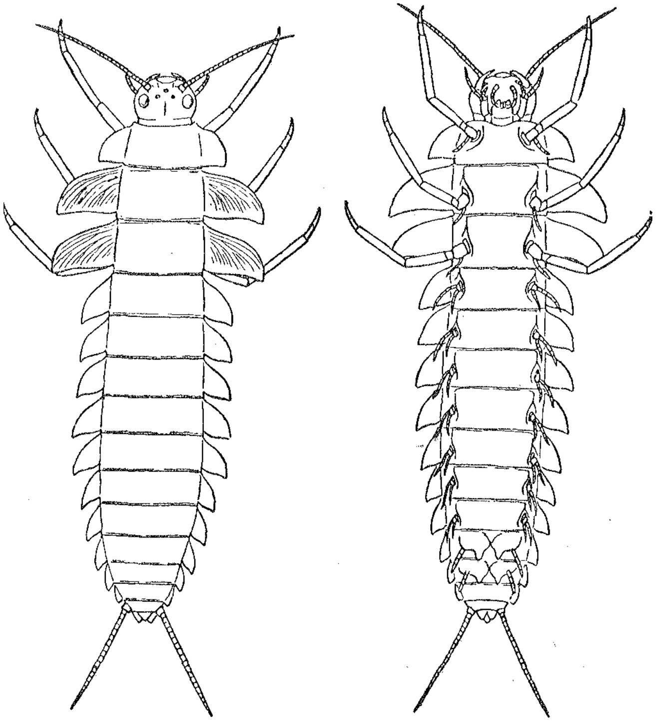

Fig. 2. Reconstruction of the larva of the original ancestor of the Insecta, according to Handlirsch. (Order Palæodictyoptera, Upper Carboniferous.)

Left, dorsal, and right, ventral view. After Handlirsch.

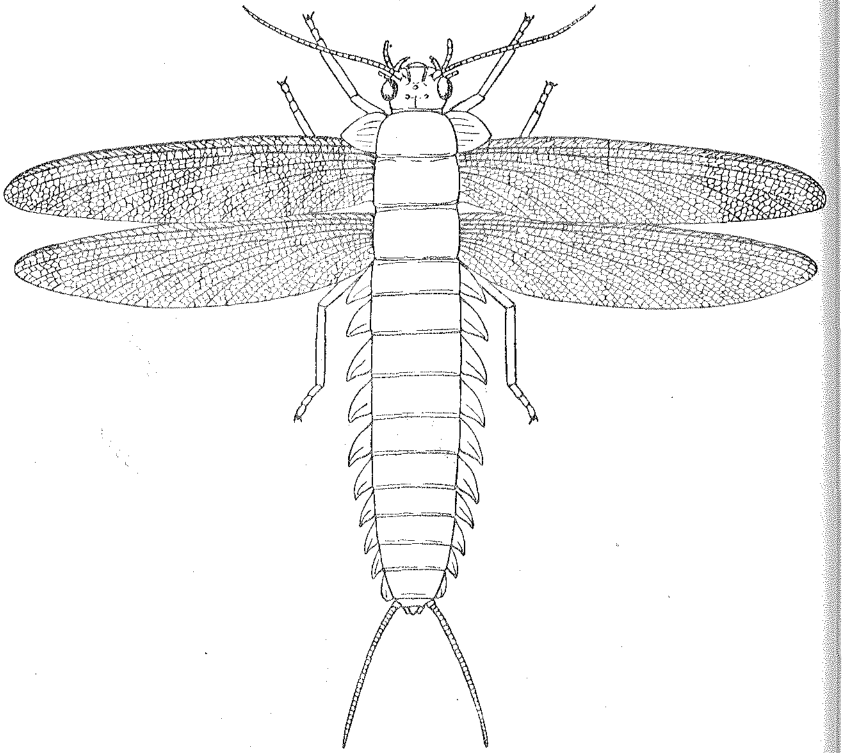

Fig. 3. Reconstruction of the imago of the original ancestor of the Insecta, according to Handlirsch. (Order Palæodictyoptera, Upper Carboniferous.) Dorsal view. After Handlirsch.

three figures side by side, the Trilobite, the larval Palæodictyopteron and the adult Palæodictyopteron, you feel that Handlirsch has presented a good case.

Further, Handlirsch also drives home his argument palæontologically. The Trilobites lived from the Lower Cambrian to the Permian; thus there was an immense period of geologic time during which some shallow-water form of Trilobite could have worked its way up the estuaries into brackish water, thence into fresh water, and finally could have developed into the flying insect. Handlirsch, be it noted, places the origin of the Insecta as not lower than the Lower Carboniferous or, at the earliest, in the Upper Devonian (see fig. 4).

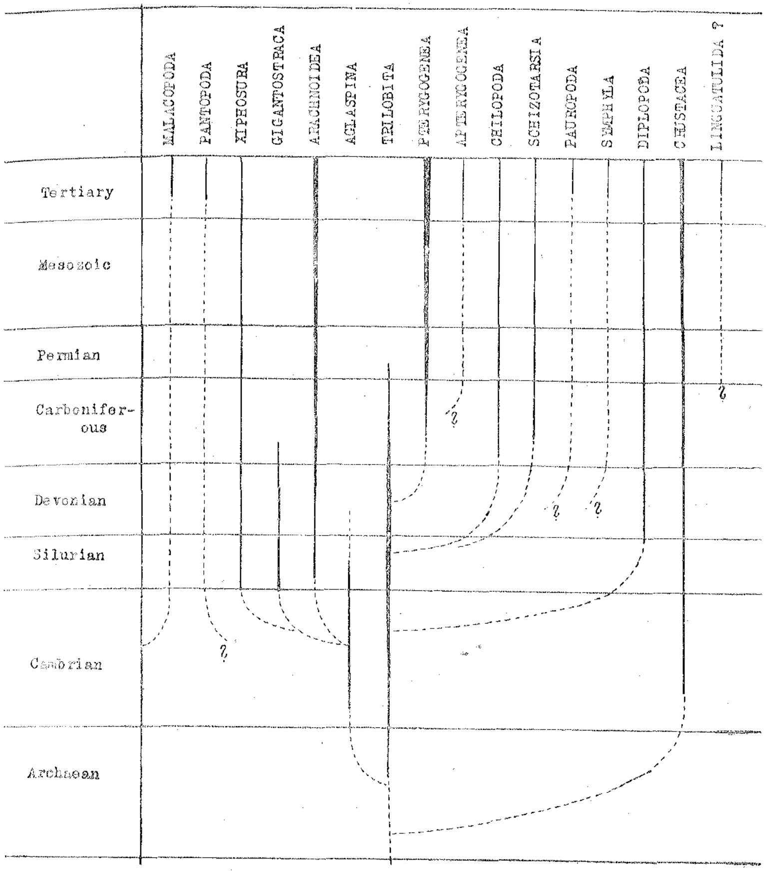

Fig. 4. Phylogeny of the Arthropoda, according to Handlirsch (1913).

Handlirsch's Theory, though primarily devised to explain the origin of Insects, actually covers the whole of the Arthropoda. He casts out the Onychophora as not being true Arthropods, and then boldly claims that all the other Classes of Arthropods, exclusive of the Tardigrades and Pentastomida, are derived from Trilobites.

Before attempting to offer criticisms of this theory in general, let us see how Handlirsch deals with the most obvious criticism of all. It is very hard for any entomologist to believe that the original ancestral type of the Insecta was a winged insect. But, if the ancestral form was not a winged but a primitively wingless insect, then Handlirsch's theory has its very foundation knocked from under it; for it is founded primarily on the evolution of the insect wing direct from the pleuron of the Trilobite. Hence Handlirsch is put into the position of having to defend the thesis that the known Apterygota are degenerate descendants of originally winged insects. This he does in characteristic fashion. He asks the question:—To which of the groups of Apterygota are the Pterygota most obviously allied? The answer, with which we must all agree, is that they are most closely related to the Ectotrophous Thysanura, viz., the Machilidæ and the Lepismatidæ. He then puts aside the Machilidæ, evidently because they were laterally flattened, jumping forms, and centres his argument on the Lepismatidæ, which are dorso-ventrally flattened, running forms which possess definite paranota on the thorax. Then, dealing with the paranotal flaps of *Lepisma*, he quotes (1913) an unpublished observation given to him by Dr. Sulc, who states that the tracheation of the lateral flap of the thoracic notum in this insect can be homologised with the typical tracheation of the larval wing in the Pterygota. Even accepting this observation, he has to confess that the matter is "not proven," though, for his part, he holds that these flaps are not the rudiments but the vestiges of original wings.

Now Handlirsch lays himself open to a serious attack here, and we must drive it home. Careful dissections of the thoracic flaps of *Lepisma* made by Mr. Tonnoir in Canberra show quite clearly that Dr. Sulc's observation is incorrect. The tracheation of these flaps is not of a fixed type; it varies in important details both in individuals, in the different segments of the thorax, and also on right and left sides. Only a person who was determined to find, at all costs, a series of homologues to the six main tracheæ of the insect wing could possibly do so, and even then he would have to choose the most suitable of the many variations and more than stretch a point in homologising the tracheal branches. Thus we must insist that there is really no evidence in favour of Handlirsch's view, and, as we shall see when we come to review the whole problem, there is also an immense mass of evidence against it.

Again, we have another criticism to level against the theory on palæontological grounds. If Handlirsch is right, the Pterygota must be older than any of the Apterygota. This did not give him much trouble, because, at the time that he wrote, the only known fossil Apterygota were Tertiary. So he puts the Pterygota as originating in the Lower Carboniferous, or at the very earliest in the Upper Devonian, and then indicates an origin for the various groups of Apterygota, somewhere in the Carboniferous. But, unfortunately for the theory, I have since been able to prove (1928) that true Collembola, closely resembling living Poduridæ, were present in the peat-bogs of the Lower Devonian, along with Acarids, Crustacea, and the most primitive types of vascular plants. Hence, if Handlirsch's theory is correct, Pterygota must have existed even before that time! This is a thing that nobody could believe; not only because no fossil winged insects are known before the Upper Carboniferous, but also because there were no trees in existence at that time, and little food suitable for anything but a crawling, creeping, or swimming form. I feel myself that this discovery of Lower Devonian Collembola has given Handlirsch's theory a very severe blow indeed.

On minor morphological points, Handlirsch is also open to criticism. He makes no attempt to indicate how the insect mandible has been evolved from the primitive biramous limb of the Trilobite head. No known insect has a mandible with either endopodite, exopodite, or epipodite still present. Surely we are entitled to be given some guide as to the intermediate stages. Further, and this is a grave mistake, in all his figures of Trilobites, Handlirsch entirely ignores the separation of the pygidium from the thoracic region; and I can only conclude that he either overlooked this point, which is a serious one, or desired to carry his ancestral form so far back that its pygidial segments were to be conceived of as being in a primitively unfused condition. For it is obvious, I think, that no form of Trilobite which already had two or more primary body-segments fused together to form a pygidium could possibly be the ancestor of the Insects.

To conclude, then, Handlirsch's theory, fascinating as it is, is not acceptable on many grounds, and we must look elsewhere for our solution.

II. The Descent of Insects from Crustacea.

The idea that Insects are descended from Crustacea can be traced back a very long way. The essential difference between Handlirsch's Theory and all the variations of belief in the descent of Insects from true Crustacea lies in this:—

In the former, the ancestral group is extremely primitive, and the gap to be filled between it and the Insecta is very wide; in the latter, the descent is claimed to be from an already highly organised Crustacean type, by a transference from marine to terrestrial conditions, to a primitive type of wingless Insect. As we shall see in the course of our study, the particular type to which all these theories direct attention is the family Machilidæ, which all are unanimously agreed upon is the most Crustacea-like of Insects.

The first clear enunciation of the theory of descent from Crustacea was that by Hansen (1893), who received support from Ray Lankester (1904), G. H. Carpenter (1903, 1905), and Börner (1909). The basis of Hansen's theory may be stated in his own words (1893, pp. 427, 428):—

"I regard the maxillæ in *Machilis* as decidedly homo-"logous with the maxillæ (second pair of maxillæ of "authors) in the Malacostraca, and the labium as homo-"logous with the maxillipedes and agreeing in many "respects with these appendages in the case of the groups "mentioned." (The groups referred to are the Isopods and, more especially, the Amphipods.)

"The hypopharynx" (i.e., in *Machilis*) "is conspicuous " . . . . and homologous with the hypopharynx (para-"gnathi) in the Malacostraca. The organs which are "termed 'paraglossæ' by authors have nothing to do with "the hypopharynx. . . . . I regard these 'paraglossæ' as "homologous with the maxillulæ of Crustaceans."

Hansen's theory was more fully developed by Carpenter (1903, 1905). We might here note that Hansen used the term "endopodite" to include both the basal segments ("protopodite" of authors) and inner ramus ("endopodite" of authors) but we shall follow the usual terminology and restrict the term to the inner ramus.

The complete theory of Hansen and Carpenter may be considered to comprise the following points:—

(a) The compound eyes of Insects are morphologically the same as the compound eyes of Crustacea and belong to the same head-segment.

(b) The antennæ of Insects are homologous with the antennules or first antennæ of Crustacea.

(c) The second antennæ, or antennæ, of Crustacea are entirely suppressed in the Insecta, the segment which originally bore them being the intercalary or third head-segment.

(d) The mandibles of Insects are homologous with those of Crustacea, and have been directly derived from them by loss of the endopodite.

(e) The superlinguæ or maxillulæ of Insects are homologous with the first maxillæ, or maxillulæ, of Crustacea.

(f) The hypopharynx of Insects is homologous with the paragnaths of Crustacea, and has nothing to do with the maxillulæ or paraglossæ.

(g) The first maxillæ of Insects are homologous with the second maxillæ, or maxillæ, of Crustacea.

(h) The typical head of a Crustacean is therefore composed of six fused segments, three pre-oral and three post-oral, to which the first thoracic segment becomes sometimes closely applied, its appendages then becoming the first maxillipedes.

(i) The typical head of an Insect is composed of seven fused segments, three pre-oral and four post-oral, the seventh representing the first thoracic of Crustacea, and its appendages being fused together to form the labium or second maxillæ.

It might be noted that the Machilidæ are held to be the most primitive of all Insects, on this theory, on account of their general close resemblance to Crustacea, the similarity of their mandibles with certain types found in the Crustacea (especially the Cumacea), the possession of large compound eyes (absent in other groups of Apterygota), and the presence of the coxal styles on the middle and hind legs. These styles are considered to represent either a Crustacean exopodite (Hansen) or an epipodite.

Hansen's Theory appeared to receive great additional support when Folsom (1900) announced the discovery of the embryonic maxillulary or superlingual segment in the embryo of *Anurida*, one of the Collembola. Unfortunately this discovery was later on proved to be based upon a misconception, and Folsom himself withdrew his claim. The position at the present day is that nobody has ever seen more than six primitive segments in the embryonic head of an insect. It is only fair to state that the embryology of the head of *Machilis* has not yet been fully investigated, although this is one of the insects in which the maxillulæ are best developed.

Hansen's position has been attacked in detail by Crampton (1917 *et seq.*). This author, himself a firm believer in the descent of Insects from Crustacea, is nevertheless convinced that the head of an Insect consists of only six segments, and that Hansen committed a grave error when he homologised the superlinguæ or maxillulæ of Insects with the first maxillæ or maxillulæ of Crustacea. The difference between Hansen's and Crampton's interpretations of the segmentation and appendages of the Insect head is best exhibited in tabular form (Table A).

TABLE A.

TABLE SHOWING SEGMENTATION AND APPENDAGES OF THE HEAD IN CRUSTACEA AND INSECTA ACCORDING TO (A) HANSEN, (B) CRAMPTON.

SEGMENT.	(A) APPENDAGES, HANSEN, 1893.		(B) APPENDAGES, CRAMPTON, 1922.	
	CRUSTACEA.	INSECTS.	CRUSTACEA.	INSECTS.
1.	(Compound Eyes)	(Compound Eyes)	(Compound Eyes)	(Compound Eyes)
2.	1st Antennæ	Antennæ	1st Antennæ	Antennæ
3.	2nd Antennæ	(Absent)	2nd Antennæ	(Absent)
4.	Mandibles	Mandibles	Mandibles	Mandibles
	—	—	(Paragnaths)	(Maxillulæ)
5.	1st Maxillæ	Maxillulæ	1st Maxillæ	1st Maxillæ
6.	2nd Maxillæ	1st Maxillæ	2nd Maxillæ	2nd Maxillæ
7.	1st Maxillipedes	2nd Maxillæ	—	—

It will be seen from the above that Crampton challenges Hansen's conclusions as to the nature of the insect maxillulæ, and will not allow that they are true segmental appendages at all. He severely attacked Folsom's embryological studies also. In his view, the maxillulæ of Insects are the exact homologues of the paragnaths of the higher Crustacea, which are also not considered to be true segmental appendages. It

therefore follows that the first and second maxillæ of Insects are the homologues of the first and second maxillæ of Crustacea, and the two types of head are both composed of six fused segments and are even more closely similar than Hansen imagined.

I think Crampton has proved his case very fully; and, personally, in common with almost all modern entomologists, I accept the thesis that the Insect head is composed of six segments and that the maxillulæ are homologous with the paragnaths of Crustacea. I do not agree, however, that this proves the descent of Insects from Crustacea; it only proves community of origin. One need only point out that the heads of Trilobites and of many Myriopods also have six segments to see the fallacy of Crampton's argument. Insects may, or may not, be descended from Crustacea. If they are, then a much more detailed proof of that descent is still required.

This detailed proof Crampton has attempted to supply, in a long series of papers, all directed towards the same end. He started off with the idea that the Tanaidacea, Isopoda, and Cumacea had a common ancestry with the Insecta (1920), but modified this after a fuller study of the mandibles (1922) to a theory of the descent of Insects from a common ancestor intermediate between the Mysidacea and Syncarida. His later studies appear to have attracted him more and more towards the Syncarida as the actual ancestors of Insects, and, although I have not yet received a copy of his latest paper, I understand that he now considers the Bathynellidæ to be the most probable ancestors of the Insecta.*

It is not, of course, at all easy to deal with a theory which is still in process of modification. Let us, however, make the attempt, by instituting a detailed comparison between the Machilidæ, which are claimed to be the most primitive of all known Insecta, and the Syncarida, with a Bathynellid taken as type (figs. 5, 6).

It will be seen that Crampton's argument, as indeed all other arguments in favour of the Crustacean descent of

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*In a more recent communication, received after this was written, Dr. Crampton further modifies his position, merely claiming that Insects are derived "from Crustaceoid ancestors." What this means actually I am not quite clear, unless his word "Crustaceoid" really means "Crustacean." It would appear to involve the abandonment of any claim that Insects are descended from any higher type of Crustacea, and the substitution of a more general claim that they are descended from a more primitive Crustacean type.—R.J.T.

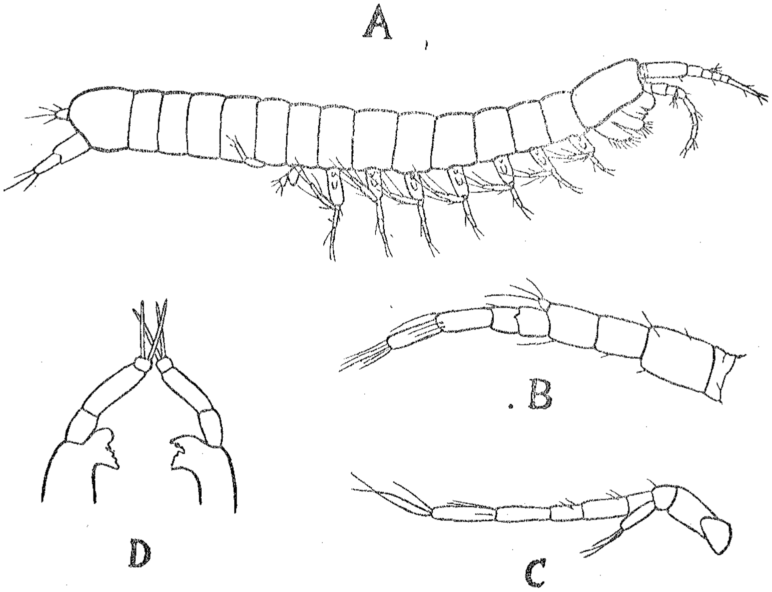

Fig. 5. *Bathynella natans,* Vejd. Class Crustacea, Order Syncarida, family Bathynellidæ. A, lateral view of male; length 2mm. B, first antenna of same. C, second antenna of same. D, mandibles of same, with endopodites and incisor and molar areas. After Calman.

Insects, deals only with the exoskeleton, i.e., the segmentation and appendages. The details of embryology and the form of the various systems of internal organs are not taken into account. Here, then, I must make a definite demand, viz., that before any theory of the Crustacean ancestry of Insects can be accepted, it must indicate the lines of evolution of the Insectan type of embryology and of the Insectan types of internal systems of organs from those of Crustacea. And this demand must all the more be carefully fulfilled if, after our examination of the case based on external characters only, it appears that a Crustacean ancestry of Insects is at all probable.

Let us consider, first of all, the *segmentation* of the body. In the Syncarida we have six fused head-segments, eight thoracic segments, and six abdominal segments, plus a telson. This gives a total of twenty complete somites. For the primitive Insect, we count again six fused segments for the head, three for the thorax, and eleven for the abdomen, plus a telson; the total is again twenty. All that is necessary, then, for a Bathynellid to become a Machilid, as far as segmentation is concerned, is for the last five thoracic segments to change their function and become abdominal, with consequent reduction of their appendages to vestiges! It looks so simple, put thus, that one may well be tempted to ask: Where is the evidence that such a vast change as this ever took place, and where are the intermediate forms to be found? The reply to this is that the Machilidæ themselves possess reduced appendages on most of their abdominal segments. Unfortunately, the Bathynellidæ only possess abdominal appendages on the first and sixth segments, whereas in the Machilidæ the abdominal appendages, though reduced, occur on all, or nearly all the segments. Thus, on this point alone, the Bathynellidæ cannot be the ancestors of the Machilidæ; and the latter, if descended at all from Syncarida, must have been derived from a form with a complete series of abdominal appendages! Here one may well interpose and ask: Why not, then, be quite logical, and derive the Machilidæ from a Myriopod?

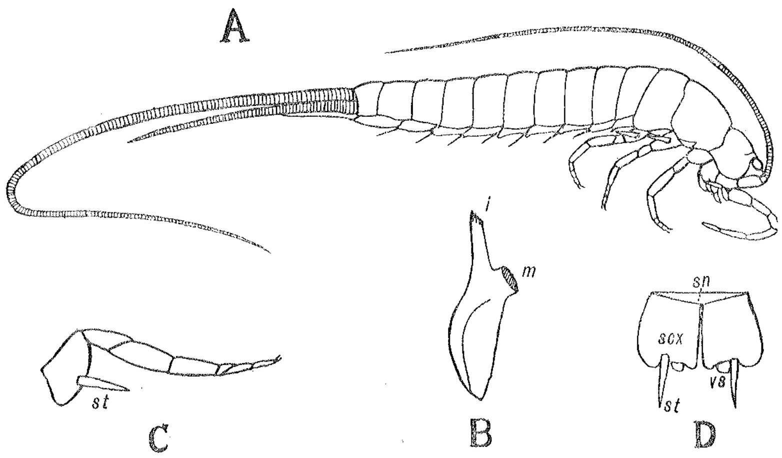

Fig. 6. *Nesomachilis maoricus,* Till. Class Insecta, Order Thysanura, family Machilidæ. A, lateral view of female; length 55 mm., excluding tail-filaments. B, mandible of same, showing incisor (*i*) and molar (*m*) areas. C, middle leg of same, showing coxal style (*st*). D, fifth abdominal sternite of same, showing subcoxa (*scx*), sternum (*sn*), styles (*st*), and exsertile vesicles (*vs*).

Next let us consider the appendages. The first thing that we note is that almost all Crustacea, including the Syncarida, possess *two pairs of antennæ* (fig. 5, B, C). Insects and Myriopods, on the other hand, have only the first pair. If the Machilidæ are derived directly from Bathynellidæ or any other form of Syncarida, we may ask, where is the evidence of the suppression of such a functionally active appendage as the Crustacean second antennæ? In the embryology of Insects, the intercalary segment, corresponding with the Crustacean segment bearing the second antennæ, is practically suppressed; in fact, it is only *inferred* from the composition of the embryonic brain and the presence of a pair of cœlomic sacs. At no stage does it appear as a well-defined embryonic segment, and at no stage is there any sign of embryonic appendages.

We may well ask: Is it possible to believe that this can be so, if Insects are really derived directly from a high type of Crustacean in which this segment and its appendages are strongly developed both in the embryo and the adult? Why not, again, be more logical, and derive the Insects direct from more primitive terrestrial forms in which this segment and its appendages have never yet been found complete?

Our difficulties are not over with the second antennæ. We come next to the *mandibles* (figs. 5D, 6B), one of Crampton's strongest points. His work (1922) in comparing the primitive Machilid mandible with that of Crustacea has been carefully done and is of great interest. He stresses the point that the insect mandible has never, in any known form, possessed more than a single segment, corresponding with the coxopodite of a typical Crustacean limb. He then clearly differentiates the separate incisor and molar areas in the mandible of *Machilis*, and compares them with similar areas found in certain Crustacean mandibles, notably in those of *Asellus* (Isopoda), *Diastylis* (Cumacea), *Apseudes* (Tanaidacea), *Stegocephalus* (Amphipoda), etc. Curiously enough, all these mandibles, except that of the Cumacean *Diastylis*, possess well-developed endopodites, and so do the mandibles of *Bathynella* (fig. 5D) and other Syncarida, not definitely considered by Crampton in his argument. So he has either to hold that *Machilis* is descended from the Cumacea, or from some Decapod form with a similar type of mandible, or else derive them from one of the other groups by loss of the mandibular endopodite.

To all this argument one can only reply, that it *may* be so, or *may not!* Where is the proof, in insect embryology or morphology, that the insect mandible ever possessed the original form of a complete Crustacean appendage, or even merely possessed an endopodite? I confess that I find no evidence for it anywhere. It is all purely plausible assumption. It appears to me just as logical to argue that incisor and molar areas have been differentiated in Arthropod mandibles more than once in the course of evolution. I will not deny that Crampton *may be* right; all I would say is that other explanations *may be* right also, and that he has not fully proved his case.

Crampton then deals with the first maxillæ (1922) and derives these from a complete, typical Crustacean appendage. Incidentally, one notes here that he requires three basal segments, coxopodite, basipodite, and ischiopodite, for his primitive Crustacean type, as indicated in Table B; whereas, in dealing with the mandible, he does not hesitate to demand a type with only a single basal segment, and argues that any apparent division of it is purely secondary. So the mandibular endopodite arises, according to Crampton, from the basal segment, while in the first maxilla it arises from the third!

TABLE B.

TABLE SHOWING HOMOLOGIES BETWEEN PARTS OF THE CRUSTACEAN AND INSECTAN MAXILLA (AFTER CRAMPTON).

PART.	IN CRUSTACEA.	IN INSECTA.
First or Basal Segment.	Coxopodite.	Cardo.
Second Segment.	Basipodite.	Stipes.
Its gnathobase.	(Endite)	Lacinia.
Third Segment.	Ischiopodite.	Palpifer.
Its gnathobase.	(Endite)	Galea.
Exopodite (from basipodite).	Exopodite.	Absent.
Endopodite (from ischiopodite).	Endopodite.	Palpus.

Table B shows clearly the homologies of the parts of the Crustacean and Insect maxillæ, as given by Crampton. It must be remembered that Hansen should be given the credit for pointing out the incorrectness of the idea that the maxillary palp was the Crustacean exopodite. We can agree with Crampton that the cardo and stipes of an insect maxilla correspond with the two basal segments of the Crustacean appendage, and that the exopodite is absent.

But one may reasonably doubt whether the palpifer of the insect maxilla is an original segment, seeing that it is very seldom differentiated at all in the Insects. Moreover, as nobody has ever seen even a vestige of an undoubted exopodite in any Insectan appendage, why not go at once to the root of the argument and ask: Why is it necessary at all to have to derive any insect appendage from the biramous type found in the Crustacea? Is not this begging the whole question?

The matter appears to resolve itself into this, that, granted that the insect maxilla has been derived from the Crustacean maxilla, the mode of reduction is clear. But the fact that the lacinia and galea are gnathobases does not prove that the appendage was originally of Crustacean type; it merely proves that it is a primitive appendage modified as a jaw. Unless we tacitly assume the origin of Insecta from marine types, such a primitive appendage need never have been biramous at all.

Turning next to the insect leg, we note that here again the supporters of a Crustacean ancestry would have us believe that it has been derived from a typical biramous appendage by loss of the exopodite. In this case, the coxal styles of *Machilis* have been brought into the argument and are claimed to be either exopodites, or, alternatively, epipodites of the primitive appendage, according to whether we accept the coxa as the original second segment of the insect leg or the original basal segment. In either case, we might reasonably expect it to occur on all three pairs of legs, instead of on only two, and we should certainly expect it to be present in the newly hatched larva, though this does not seem to have been determined as yet. May we not fairly ask: Is not this style perhaps merely a spur, not an exopodite or epipodite at all? Such spurs are known to occur on other segments of the legs of insects, notably the tibia; but epipodites are not known to occur at all in Insecta, with this sole possible exception. And, if these styles have any significance at all, what about the long series found in *Scolopendrella* (figs. 9, 15)?

Crampton also compares the terminal appendages of the Insecta with those of the higher Crustacea. There can be no doubt that the cerci of Insects are homologous with the uropods of Crustacea, and that both forms possess a telson. But this does not prove descent of Insects from Crustacea. True cerci are present in the Symphyla as well as in many Insects; why should not the Insectan cerci be developed from older organs in the Myriopoda?

Fig. 7 exhibits the phylogeny of Insects and their allies, as conceived by Crampton (1920).

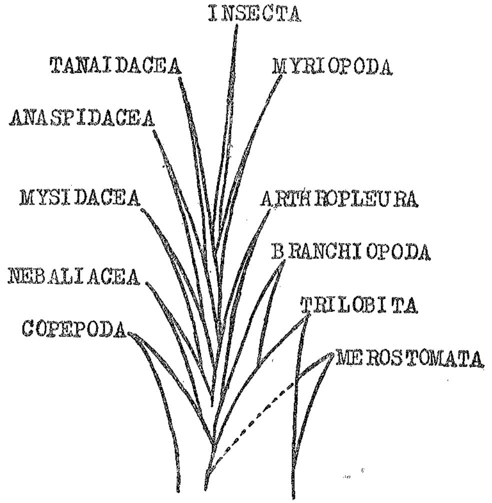

Fig. 7. Phylogeny of Insects and their nearest allies, according to Crampton (1920).

The outcome of all that Crampton has written appears to me that, *so far*, there appears to be no inherent impossibility that the Insecta may have been descended from Syncarida or some closely allied group, but that it does not appear to be very likely. We must also remember that Crampton has not made use of any characters except just those which serve his argument, and that these have all been selected from the rather narrow field of external morphology. Even within that field, we await from Crampton an explanation of the complete loss of the second antennæ in Insecta, as well as a detailed explanation of an equally bad crux, viz., how any form in which a specialisation of the postcephalic region already into a thorax with eight somites and an abdomen with six or seven could possibly be transformed into one of the Insect type! And, as I have already remarked, the more convincing Crampton can make his reply on these points, so much the more must we then demand from him additional proof of his theory by a rigid examination of the various systems of internal organs, all of which must show a reasonable possibility of evolution from the Syncarid or allied Crustacean type to the primitive Insectan type.

As an alternative theory is being put forward later on in this paper, I need only refer the reader to the arguments there developed in connection with the embryology and the various internal organs, for him to see how impossible it is, when these are considered, for us to accept any group of Crustacea as in any way the immediate ancestors of the primitive Insecta. And, as the theory of a Crustacean origin fails badly on these points, it must be adjudged to fail altogether.

Let us now turn our attention to those theories which seek to derive the Insects from terrestrial Arthropoda. All such theories must have one of two aims: they must either attempt to derive Insects from Myriopoda, or they must go farther back and attempt to derive both insects and Myriopods through a common ancestor from the Onychophora. We may therefore classify them as follows:—

III. The General Theory of the Terrestrial Origin of Arthropoda—*Versluys' Theory.*

IV. The Theory of Descent of Insects from Myriopoda —*Brauer's Campodea Theory.*

III. VERSLUYS' THEORY.

This very interesting theory has been set forth in much detail in a series of papers by Versluys and Demoll (1914-1922). Though it is primarily concerned with the evolution of the Arachnida, it has to be taken account of as an important theory which bears on the possible line of evolution of Insects. For that reason I propose to give a short account of it here and to offer some criticisms.

The theory starts off with the well-known thesis of Ray Lankester (1881) that *Limulus* is a marine Arachnid. Ever since Ray Lankester propounded that thesis, it has been universally accepted that *Limulus* is a true Arachnid and a remnant of the otherwise extinct group of Merostomata, to which the Palæozoic fossil Eurypterids belonged. It has also been fairly generally accepted that the marine fossil groups, Eurypterids and Trilobites, were the ancestral forms of all the principal groups of Arthropoda, leaving *Peripatus* out of account. In particular, the Scorpions and their allies are held to be terrestrial descendants of marine Arachnid ancestors, and the old group Tracheata, which was formed to include all the tracheate air-breathing Arthropods, is now believed to have no foundation as a monophyletic group.

The above statement is, I think, a fair summary of the orthodox view held by most zoologists since Ray Lankester published his theory.

Now Versluys and his colleague contest this view. They are in entire agreement with Ray Lankester concerning the Arachnid affinities of *Limulus* and the Eurypterids; but they hold that the deduction that the terrestrial Arachnids are descended from marine forms is entirely wrong, and that, on the contrary, these huge marine types are themselves specialised offshoots from more primitive terrestrial forms allied to the Scorpions. This conclusion is come to by an interesting series of deductions, as follows:—

(a) An analysis of the external characters of Scorpions and Eurypterids indicates that they were very closely allied.

(b) But even more primitive forms than Scorpions still live on the land, e.g., the Palpigradi, the Solifugæ, and the Chernetidea, in which the thorax has two free segments and the differentiation between pre- and post-abdomen is not so marked.

(c) Also a careful study of the structure of the eyes of *Limulus* and Scorpions indicates that the former must have been derived from the latter, not *vice versa*; i.e., the change in form must have been preceded by a change of living, from air to seawater, and not *vice versa*.

(d) In general, the appendages of Eurypterids and *Limulus* are more specialised than those of Scorpions, and their respiratory appendages are nothing more than slightly modified sternites.

As far as this argument goes, I believe Versluys has made out a good case. But he now takes another very big step. It being proved that the Arachnida were originally terrestrial tracheate forms, he now goes on to trace them back to a common ancestor with the Progoneate Myriopods, on the ground of the forward position of the genital opening, common to both groups. As the Arachnida never developed true mandibular jaws, of the type found in Myriopods and Insects, this conclusion involves also the branching-off of the Arachnida from the ancestral terrestrial tracheate stem at a period earlier than the evolution of the true Progoneate Myriopods. This clearly involves the derivation of the three groups, Arachnida, Myriopoda, and Insecta, from an exceedingly primitive type of terrestrial tracheate Arthropod. Such primitive ancestral group, according to Versluys, can be nothing else than the Onychophora! Incidentally, the unity of the old group Tracheata is affirmed, and all living Arthropods must be derived from it!

Versluys also holds that organs like the compound eye, the cheliceræ, and the compound or segmented fore-brain can only have arisen once in each case. So the present-day Peripatoids are the remnant of the original tracheate stem, before any of these organs were formed. Then arose, as a specialisation from the Onychophora, exceedingly primitive Myriopod types, both progoneate and opisthogoneate. One side-branch of the progoneate forms developed cheliceræ and gave origin to all known Arachnida, including the Pycnogonida. The main stem went on and developed a more complex fore-brain. Before the compound eye was formed, most of the existing Myriopod groups branched off from it. Then came the highest groups of all, with the compound eyes well formed. Of these, the highest expression is the Insecta, while the Trilobites and Crustacea are much more primitive side-branches that took to the sea!

The above phylogeny can be graphically expressed as in fig. 8. Incidentally, I would like you to note that the portion of Versluys' Theory which deals with the Insects is a kind of inversion of Handlirsch's and Crampton's Theories, in so far as he would derive both Trilobites and Crustacea from a terrestrial ancestor preceding Insects and Myriopods.

In considering the evolution of Insects, I do not feel called upon to criticise very fully that portion of Versluys' Theory which deals with the Arachnida. I can only say that his papers are well worth reading for the wealth of detailed study of primitive Arachnidan types contained in them. But we must join issue on those main points which lie outside his survey of the Arachnida, viz., on the unity of the old group Tracheata, on the monophyletic origin of various complex organs, and on the derivation of Trilobites and Crustacea from terrestrial forms. Let me briefly indicate my main criticisms:—

(1) *The Tracheata*:—I consider that Versluys' main theory could well stand by itself, without seeking to bolster up this old, discarded group. If we follow the Insects back to the most primitive forms, we come to a few simple types in

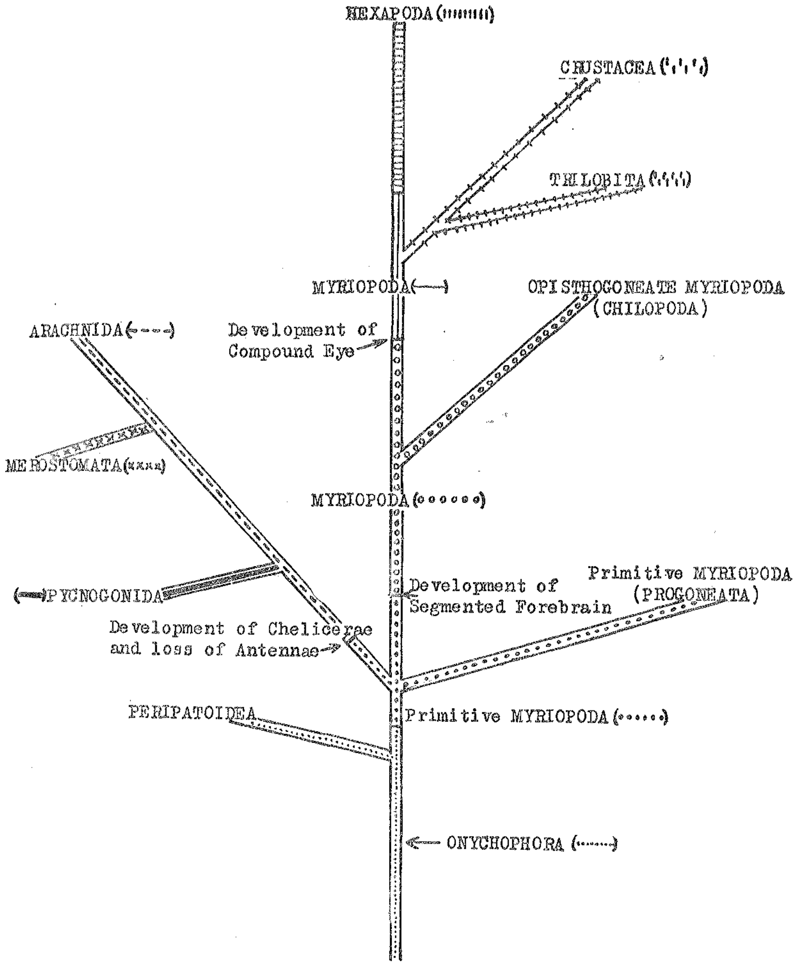

Fig. 8. Phylogeny of the Arthropoda, according to Versluys (1928, *in litt.*).

which no tracheæ are developed. How do such forms breathe? Obviously, through their integument. The formation of a tracheal system was, in the first instance, an attempt to increase the respiratory surface of the integument at those points where it was already most permeable. The same is true of the Myriopoda. Why, then, should we demand a tracheate common ancestor for all terrestrial forms of Arthropoda? Is not the structure of the tracheal system in *Peripatus* an eloquent witness to this very thing? How could the various tracheal systems of Onychophora, Myriopoda, Insecta, and terrestrial Arachnids have arisen, unless we grant a common ancestor that breathed through the integument only?

I would go so far as to say that it is no more necessary to insist on a common tracheate ancestor for all terrestrial Arthropods than it is to insist on a common gill-bearing ancestor for all marine forms.

(2) *The Compound Eye*:—It seems certain that this organ was originally formed from an aggregation of separate simple eyes. The fact that many of the larger types of Chilopods possess such assemblages of eyes on each side of the head should make it a matter of little surprise to us that in one group, the Schizotarsia, true compound eyes of the type found in Insects occur. In this and other characters there can be no doubt whatever that *Scutigera* and its allies are very highly specialised Chilopods. This, however, does not mean that *Scutigera* lies anywhere along the line of evolution of the Insects, nor of the Crustacea, nor of the Trilobites. Though the detailed structure of the compound eyes of Insects and Crustacea is extraordinarily similar, I fail to see myself why two such similar structures should not have arisen independently, given that the original elements, the simple eyes, were being developed over and over again in more primitive groups. The fact that the most primitive compound eye in Crustacea was almost certainly of the stalked type seems to rule out entirely a monophyletic origin for these organs in Insects and Crustacea; for compound eyes in Insects are without exception sessile. But the same fact does not preclude the derivation of the Crustacean stalked eye from the Trilobite eye, since the position of the latter on the free cheek would appear to be exceptionally favourable to the development of a stalked type.

It seems reasonable to conclude that compound eyes arose on four separate occasions during the evolution of the Arthropoda—

(a) in the Arachnida;
(b) in the Trilobite-Crustacean ancestor;
(c) in the Schizotarsia; and
(d) in the Insecta.

(3) *The descent of Trilobites and Crustacea from a terrestrial common ancestor with the Insects and Myriopoda*:—I do not propose to refute this in detail, because Professor Versluys himself, in a carefully reasoned statement setting forth the main points of his theory, and sent to me with permission to publish it, agrees that his "hypothetical evolution" is still unsatisfactory as regards its treatment of the Insecta and Crustacea. He explicitly mentions that he has not yet overcome the difficulty of accounting for the presence of two pairs of antennæ in the Crustacea against only one in Insects and Myriopods, and also how the genital openings in Crustacea and Insects came to be so differently placed.

I think we can conclude that Versluys' Theory, interesting as it is in regard to the evolution of the Arachnida, does not give us the proof that we are searching for about the origin of Insects. It is chiefly presented here as an offset to Handlirsch's and Crampton's theories, of which it is, as regards the evolution of Insects, the very antithesis.

IV. THE DESCENT OF INSECTS FROM MYRIOPODA.

From very early times there has existed a not very clearly defined belief in the descent of Insects from Myriopods. The first clear direction was given by Brauer (1869-70) in his well-known Campodea Theory. Brauer claimed that all living insects were descended from a type very similar to the existing genus *Campodea* in the Order Thysanura, and that this type was still preserved in many primitive larval forms of winged insects; these forms he termed *campodeiform* larvæ. The Campodea-type was derivable from the Chilopoda, and these latter in their turn from Onychophora.

Brauer's theory of the primitiveness of the campodeiform type of insect larva has been widely accepted, but his derivation of Insecta from Chilopoda has met with little or no support.

Packard (1898) saw clearly that Insects could not be derived either from Diplopoda or Chilopoda, though he held that the latter were the nearest large group of Arthropoda to the true Insecta.

Brauer's theory led to a search by many authors for relatives of *Campodea* outside the Insecta, and thus brought the Symphyla into the question. Thus a school of writers arose who claimed that *Scolopendrella* and *Campodea* (figs. 9, 10) were very closely related. Amongst these we may mention Packard, Ryder, Grassi, Haase, and Pocock. The last-named (1893) elevated the Symphyla to the position of an independent Class, and claimed that it was the "living

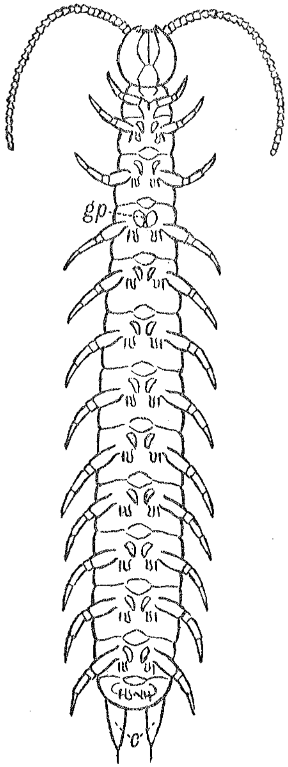

Fig. 9. *Scolopendrella* sp., Australia. Class Progoneata, Order Symphyla, family Scolopendrellidæ. Length 6 mm. Ventral view, showing cerci (*c*) and gonopores (*gp*). Note the presence of styles and exsertile vesicles on most of the abdominal segments.

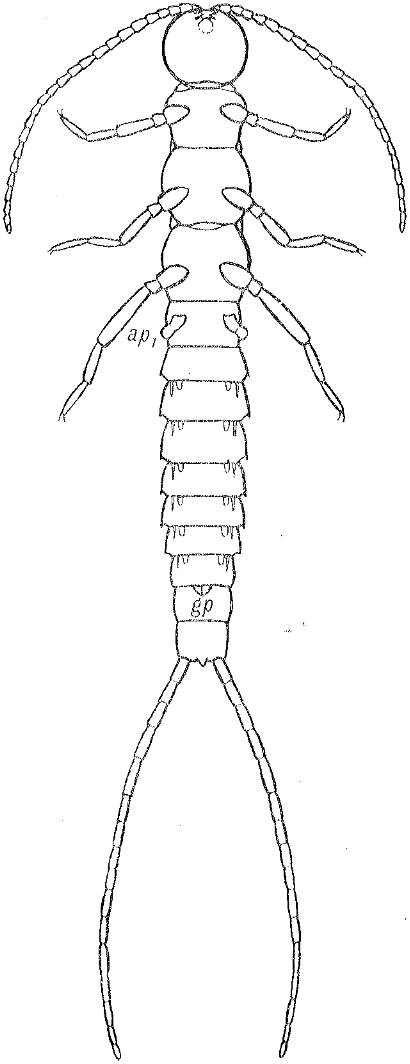

Fig. 10. *Campodea philpotti*, Till. Class Insecta, Order Thysanura, family Campodeidæ. Length 7 mm, excluding cerci. Ventral view, showing appendages of first abdominal segment (*ap* 1) and gonopore (*gp*). Note the presence of styles and exsertile vesicles on some of the abdominal segments, also the long, many-segmented cerci.

"form that comes nearest to the hypothetical ancestor of the "two great divisions of tracheates," i.e., of Myriopods and Insects. Thus all previous nebulous ideas as to the derivation of Insects from Myriopods became crystallised in this single theory. It is true that Pocock himself held that both Myriopods and Insects had descended from *Scolopendrella*. Packard strongly combated this view; he held that *Scolopendrella* was a remnant of an otherwise extinct group from which the Insects had descended, and which partially filled the wide gap between *Peripatus* and the Insects. Schmidt (1895) put the Symphyla between the Diplopods and the Pauropods, thus removing them further from the Insects. Packard recognises the difficulty created by the fact that the Symphyla are progoneate while the Insects are opisthogoneate, but he does not consider that sufficient to overthrow the theory.

Let us now consider a number of points for and against the theory:—

(1) The general form of the head in *Scolopendrella* closely resembles that of *Campodea*; in particular, the Y-shaped suture which separates the epicranium from the frons in many primitive insects is present in *Scolopendrella*.

(2) The antennæ are elongated, many-segmented and moniliform, thus differing from those of any other Myriopoda and very closely resembling the antennæ of *Campodea*.

(3) There are two pairs of maxillæ present, as in Insects, though other groups of Progoneata (Diplopods, Pauropods) apparently possess only one.*

(4) All the legs except the first pair are four-segmented, and the tibio-tarsus ends in a claw plus an empodium. Thus they closely resemble the legs of Collembola, though they are of more primitive type in lacking the marked differentiation of femur and tibia.

(5) At the base of each leg there is a movable style (fig. 15, *st*) and, alongside this, an eversible ventral sac (fig. 15, *vs*). Though the abdominal legs are absent in the Thysanura, movable styles and ventral sacs occur throughout that group of Insects on a varying number of abdominal segments (figs. 6, 10, 12, *st*, *vs*).

(6) The last segment of the abdomen carries a pair of unsegmented cerci (fig. 9, *c*). Similar organs occur in all the Thysanura, and they are unsegmented in the Japygidæ.

(7) Malpighian tubules are present, two in number, and open into the anterior end of the hind-gut, as in Insects generally.

(8) The tracheal system opens by a single pair of stigmata situated in the head. Although *Campodea* itself has only thoracic spiracles, the Collembolan family Sminthuridæ has a pair of head tracheæ only.

(9) The alimentary canal resembles that of *Campodea* closely, and rectal glands are present.

(10) A pair of anal glands open at the tips of the cerci (fig. 9, *gl*). Similar glands occur in the Thysanuran *Anajapyx* (fig. 12 *gl*).

This is a formidable list of resemblances. Let us now consider the differences:—

(1) The mandibles are two-segmented. No known insect has this primitive character.

(2) The tergites and sternites of the body-region do not coincide. There are apparently only thirteen sternites, twelve bearing legs and the thirteenth being the anal segment. The number of tergal plates is fifteen or sixteen.

(3) The gonoducts are directed forward and open into a pair of closely opposed gonopores placed on a raised median area *on the fourth abdominal sternite* (fig. 9, *gp*).

With regard to the above three characters, in which the Symphyla differ markedly from the Insecta, I would say that the possession of two-segmented mandibles need not surprise us in so primitive a form. Nor does such a character necessarily remove its possessor from being considered as a direct ancestor of Insects. The lack of agreement between tergites and sternites is, perhaps, of less importance than appears at first sight; for we have to remember that we do not yet know anything about the embryology of the Sym-

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*G. H. Carpenter (1905), however, maintains that *Polyxenus*, a primitive Diplopod, has two pairs.

phyla, and it may well be that a sternite without legs has become suppressed near the head end, while it seems highly probable that the original embryonic anal segment never carried legs (*cf.* the Pauropoda) and so the supposed last segment may be in reality two. This would bring the total number of abdominal segments up to fifteen for both sternites and tergites, which is exactly the number obtained by adding the number of thoracic and abdominal segments in the Protura. But the third character, the progoneate position of the genital opening, remains still a bad stumbling block, and it is on this character that the theory of the origin of Insecta from Symphyla goes to pieces. It is, I think, fairly safe to say that, but for this one serious fault, there has never been presented any theory of the origin of insects having so many definite points in its favour.

Though there has been a marked tendency amongst many modern entomologists to turn away from the Myriopoda as possible ancestors of the Insecta, we may note that Silvestri (1901-9) has brought a fresh interest into the problem by the study of his new family Projapygidæ, and particularly by his detailed account of the genus *Anajapyx* (fig. 12), which should be compared with the Japygidæ also (fig. 11). This extraordinary insect apears to come even closer to the Symphyla than does *Campodea.* The cerci are short and only divided into a small number of segments, thus bridging the gap between the type found in *Campodea* on the one hand and the type found in *Scolopendrella* on the other. Further, a pair of anal glands are developed exactly as in *Scolopendrella* and open at the tips of the cerci. Thus, in spite of the difficulty that still remains, and to many still appears insuperable, regarding the progoneate position of the genital openings in the Symphyla, one may say that new interest has been aroused in this old theory, even though the final proof of descent is still lacking.

Our survey of the main theories has now brought us to the position that no fully acceptable theory of the evolution of the Class Insecta has yet been presented. We may say that Handlirsch's Theory attracts many because of the brilliance and lucidity of its presentation; that Crampton's Theory, in spite of some excellent points, has not been clearly presented and fails to make a strong appeal; that

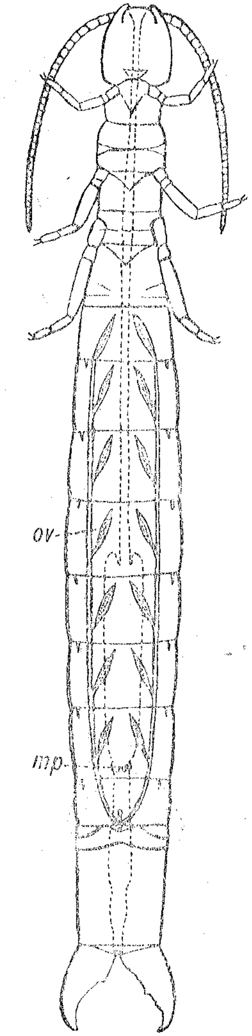

Fig. 11. *Heterojapyx gallardi,* Till. Class Insecta, Order Thysanura, family Japygidæ. Length 40 mm. Diagrammatic ventral view of female, with the reproductive system consisting of seven pairs of segmentally arranged ovaries (*ov*). Alimentary system shown by means of dotted lines; the small Malpighian tubules are shown at *mp*. Note the unsegmented forceps-like cerci (cf. those of *Scolopendrella,* fig. 9), the position of the gonopore, and the presence of styles on some of the abdominal segments.

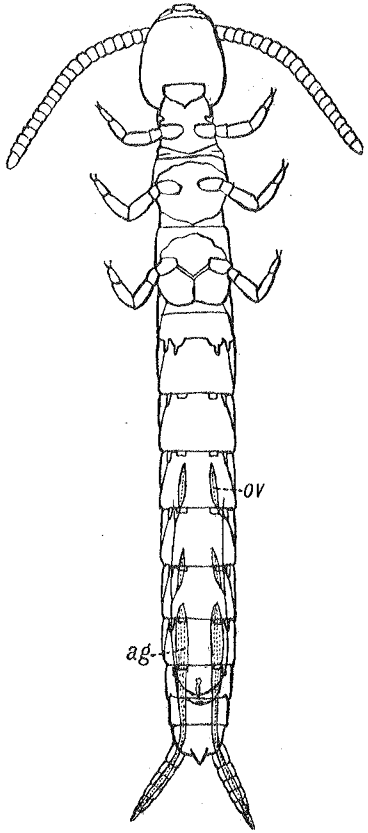

Fig. 12. *Anajapyx vesiculosus*, Silv. Class Insecta, Order Thysanura, family Projapygidæ. Length 2 mm. Diagrammatic ventral view of female, with reproductive system consisting of two pairs of ovaries (*ov*). The anal glands (*ag*) are shown with their ducts opening at the ends of the cerci (cf. *Scolopendrella*, fig. 9). Note the appendages of the first abdominal segment (cf. *Campodea*, fig. 10), also the styles and exsertile vesicles on the following segments. After Silvestri.

Versluys' Theory has not been given any particular attention by entomologists; and, finally, that probably the most attractive theory of all, viz., the origin of Insects from a common stock with the Symphyla, has fallen to the ground owing to the apparently insuperable difficulty of explaining the differences in the position of the genital openings. The final verdict on all these theories must be "Not Proven."

SECTION II.

A NEW THEORY OF THE DESCENT OF THE CLASS INSECTA.

We are now in a position to ask: Do we know enough about the Arthropoda in general, and about primitive insects in particular, to attempt to construct any theory concerning the descent of the Class Insecta which might be acceptable to modern entomologists? I think we do; but we must be prepared to take a somewhat wider view of the problem than has hitherto been the case.

To my mind, a theory of the Evolution of the Insecta, to be acceptable, must satisfy the following conditions:—

(1) It must indicate, without any wide break, the line of evolution followed, not only by the external form, segmentation and appendages, but also by the various internal organs;

(2) It must also indicate the way by which the very highly specialised type of embryological development found in the Insecta has been attained; and

(3) It must account for the "aberrant" primitive groups of Insecta, viz., the Collembola and Protura, as well as showing the line of evolution leading to the Thysanura and the Pterygota.

Let us, then, first of all ask: On what acceptable foundation are we to base our new theory?

The following points appear to me to be a sound basis to work upon:—

(1) *The Apterygota are not descended from originally winged forms, but are more primitive than the Pterygota.* All theories of descent for the Insecta admit this, except Handlirsch's. In view of the recent discovery of Collembola in the lower Devonian peat-bogs, can we any longer doubt that Handlirsch is here in error?

(2) ***The Thysanura Ectotrophica are the immediate ancestors of all Pterygote insects.***

(3) ***The Thysanura Entotrophica are closely related to the Thysanura Ectotrophica, and therefore very close to the main evolutionary stem of the Pterygota.***

(4) *The Collembola and Protura are much further removed from the Pterygota than are the Thysanura.*

Those who would now follow me into the details of my new theory are asked to accept these four main propositions, if not as self-evident axioms, at any rate as so soundly based that they may be taken as the groundwork of our theory.

It follows from these four points that we shall nowhere be concerned in this theory with the origin of wings or of winged insects. What we are concerned with is the interrelationship of the three great groups of Apterygota, viz., the Collembola, the Protura, and the Thysanura, and the nature of their common ancestors. I take leave to think that this subject is wide enough for the founding of a sound theory, and that it is also of the most intense interest to all entomologists.

In working out the details of my theory, I must, perforce, begin with the more obvious arguments involving the comparative morphology of known forms. These will, however, be extended to include a survey of the evolution of the chief internal organs and of the embryology, and due regard will be paid to the principle that no violence must be done to the known geological record, imperfect as it may actually be. Further, the ontogenetic stages indicated in the various larval changes will be given due consideration.

SEGMENTATION AND THE SEGMENTAL APPENDAGES.

T. H. Huxley (1859) once remarked—"I venture to "think it a matter of no small moment if it can be proved "that a Lobster, a Cockroach, and a Scorpion are composed "of the same number of primitive somites." He did not, however, as some think, actually call attention to the existence of such a correspondence. Let us grant at once that, if this correspondence actually does exist, then momentous conclusions must flow from it. Ray Lankester (1904) and G. H. Carpenter (1905) have followed this line of argument up, and the latter author presents a table showing the numerical correspondence of segmentation in all the chief groups of Arthropoda.

In making this comparison, Carpenter finds that the Leptostraca are the Crustacean group which agrees exactly in segmentation with the primitive Insect, and assigns twenty-two somites to each. He also assigns the same number of somites to the Symphyla, the genus *Polyxenus* amongst the Diplopoda, and to the Scorpions, and *Limulus* amongst the Arachnida. For the Onychophora, the Trilobites, and the Branchiopoda amongst Crustacea the number of somites is highly variable; this he regards as a secondary character. The Chilopoda also have an excessive segmentation, and the primitive genus *Lithobius* is credited with twenty-four somites, the minimum for the Class. The Malacostraca amongst the Crustacea fall one segment short of the requisite number for Insects and Leptostraca; this is explained by a fusion of the original sixth and seventh abdominal somites.

Carpenter presents an attractive case. If it were fully proved, there could be nothing for it but to accept the number of twenty-two somites as the ancestral condition for the whole Phylum Arthropoda, and therefore to regard such groups as the Tardigrada, the Pycnogonida, the Pauropoda, and the Collembola as greatly reduced forms.

But there are grave weaknesses in Carpenter's thesis. First of all, he has followed Hansen in accepting seven somites for the head region in Insecta, Symphyla, and Diplopoda, by regarding the superlinguæ or so-called maxillulæ as the paired appendages of a definite somite. I think there can be no doubt that Crampton is correct in his claim that these organs are the homologues of the paragnaths of the higher Crustacea, and that therefore the head in Insects and Symphyla is only composed of six segments. This brings the insect head into agreement with that of the Trilobites and Crustacea in general; but, at the same time, it throws out of gear the correspondence with the Leptostraca, which are now seen to possess one more somite than the Insects and Symphyla. Further, it does not appear that Carpenter has paid attention to the inequality in number of tergites and sternites in the Symphyla. Before it can be definitely asserted that this group has the same number of somites as the Insects, we must know something about the formation of its embryonic somites. Such knowledge is still completely lacking.

We are thus faced with the position that the supposed proof of the existence of an original number of somites common to the whole Arthropod stock appears somewhat forced, and we are no longer at all bound to accept it or to incorporate it in any theory of the evolution of the Class Insecta. We may, however, still allow a considerable degree of importance to the very close correspondence in segmentation between the Malacostraca, the typical Insecta, and perhaps the Symphyla, as indicating the possibility, though by no means the certainty, that these three groups may have been descended from a common ancestor.

In developing my new theory, I propose to examine this problem of segmentation from an entirely different viewpoint. We know that all Crustacea pass through a *Nauplius*-stage, either as a free-swimming larva, or within the embryo. It is by now generally agreed that the universal occurrence of such a stage in the Crustacea is a record, preserved in the ontogeny, of the phylogenetic fact that, at some period in their past history, the Crustacea had an ancestor which *is now represented in a modified form* by the *Nauplius* larva. The chief modifications, of course, must be connected with larval existence, viz., small size, lack of development of certain organs not needed for larval life (e.g., the reproductive system), probable secondary reduction of the number of postcephalic somites, and also possible specialisations of certain organs, e.g., the appendages, suitable for the modified conditions of larval life. Making due allowance for all these, one can scarcely resist the conclusion that what we may call the *Nauplioid ancestor* of the Crustacea was essentially a simpler type of Arthropod than any existing Crustacean, and that it had a simpler segmentation, with fewer somites both in the head and in the postcephalic region.

Although the other marine groups of Arthropoda do not possess a definite *Nauplius*-larva, they possess evidence in their ontogenies leading to the same conclusion as the above. The Trilobites went through a succession of larval stages in which the number of segments was increased from stage to stage, and the earliest of these was most like the *Nauplius*-larva of the Crustacea. The Merostomata, as exemplified by *Limulus*, also go through a larval stage called the "Tri-" lobite-larva," from which the adult form is reached by addition of further somites.

Further, there are a few of the more highly evolved forms amongst the Crustacea in which the whole of the original larval history is, so to speak, telescoped into the embryonic period, so that they hatch out from the egg as a small edition of the adult form. Examples of this are to be found in the Crayfishes and also in the Syncarida.

Now when we turn to the terrestrial Arthropoda (leaving out of account for the present the Onychophora), we do not find any evidence of the existence of a Nauplioid ancestral type, but we do find clear evidence of the evolution of these types from ancestors which had simpler segmentation. This is most clearly seen in the Myriopoda. In this great group, all the Progoneate forms, viz., the Diplopoda, the Pauropoda, and the Symphyla, pass through a series of larval stages with gradual addition of somites. It is to be noted that the segments are not added to the posterior end of the body, but are interpolated between either the anal segment and the one originally before it (as in Diplopoda) or between the preanal segment and the one before it (as in Pauropoda), and that they may be added either singly or in groups, as many as five at a time in forms like *Julus* with many segments. This phenomenon is called *anamorphosis*, and I wish to direct attention to it here as of great importance in our new theory. In the Opisthogoneata, the Schizotarsia and a number of the Chilopoda are also anamorphic.

Contrasted with these numerous anamorphic forms, we find a certain number only of the Chilopoda in which, as in the Crayfishes and Syncarida, the whole of the larval development is telescoped into the embryonic period, and the young larva emerges with the full number of segments proper to the adult. This phenomenon is called *epimorphosis.*

Now it seems clear to me that, if we accept the fact that all Crustacea have been evolved from a Nauplioid ancester, we must *a fortiori* accept the fact that all Myriopoda have also been evolved from a simpler ancestral type with fewer original somites.

One sees no escape from this conclusion, particularly when one studies a primitive group of Myriopoda like the Pauropoda (fig. 13), in which the adult number of somites is considerably less than is found in other groups. If there were any truth, for instance, in the fundamental proposition of Carpenter, that the original ancestor of all Arthropoda possessed twenty-two (or shall we say, following Crampton's modification, twenty-one?) somites, then some record of this reduction should be preserved in the ontogeny of the

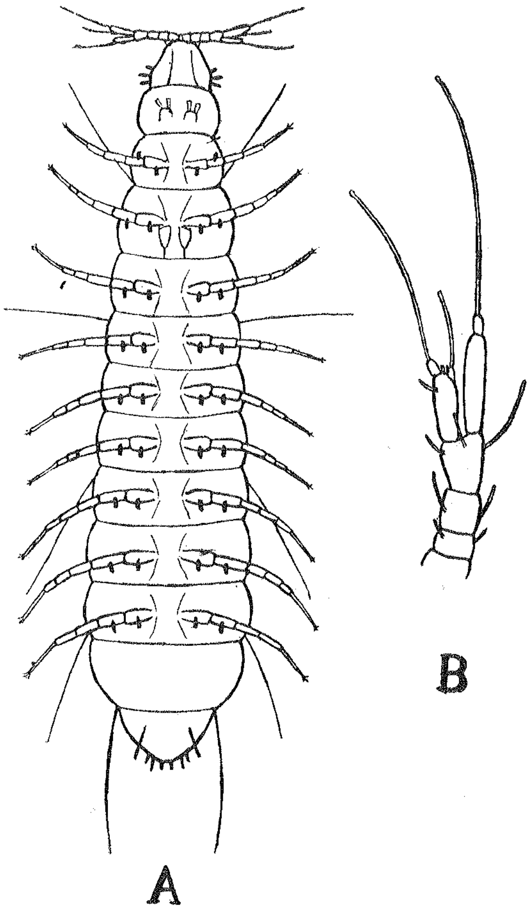

Fig. 13. *Pauropus amicus*, L. Harr. Class Progoneata, Order Pauropoda, family Pauropodidæ. Length 1.6 mm. A, ventral view; length 1.6 mm. B, antenna. After L. Harrison (1914).

Pauropoda! So far is this from being the case that the Pauropoda are not even epimorphic, but just as anamorphic in their development as any genus of Diplopoda with abundant segmentation. We owe to L. Harrison (1914) a clear account of the larval stages of Pauropoda. An analysis of his paper made by me for the purposes of this argument gives us the following Table, which is highly instructive:—

TABLE C.

ANALYSIS OF THE SEGMENTATION IN THE ONTOGENETIC STAGES OF THE PAUROPODA.

	SEGMENT.	Hexapod Larva.	10-Legged Larva.	12-Legged Larva.	16-Legged Larva.	Adult or Imago.
Head.	1.	Oc.	Oc.	Oc.	Oc.	Oc.
	2.	Ant.	Ant.	Ant.	Ant.	Ant.
	3.	—	—	—	—	—
	4.	Md.	Md.	Md.	Md.	Md.
	5.	Mxl.	Mxl.	Mxl.	Mxl.	Mxl.
	6.	—	—	—	—	—
	7.	1st Legs	1st Legs	1st Legs	1st Legs	1st Legs
	8.	2nd Legs	2nd Legs	2nd Legs	2nd Legs	2nd Legs
	9.	3rd Legs	3rd Legs	3rd Legs	3rd Legs	3rd Legs
	10.	—	—	—	—	4th Legs
	11.	—	—	—	4th Legs	5th Legs
	12.	—	—	—	5th Legs	6th Legs
	13.	—	—	4th Legs	6th Legs	7th Legs
	14.	—	4th Legs	5th Legs	7th Legs	8th Legs
	15.	—	5th Legs	6th Legs	8th Legs	9th Legs
	16.	Preanal	Preanal	Preanal	Preanal	Preanal
	17.	Anal	Anal	Anal	Anal	Anal

It will be seen that the young Pauropod hatches out as a six-legged larva having a total of only six somites behind the head. We must be careful not to jump to the conclusion that this larva represents an *insectan* stage in the ancestry of Pauropoda. That this is not so will be gathered at once from the fact that the first body-segment does not carry legs. Thus the legs of the young Pauropod larva are not homologous with the thoracic legs of the Insecta, but are on the second, third, and fourth postcephalic segments instead of on the first, second, and third. We may also recall that the young Diplopod hatches out as a larval form having three pairs of legs, but that these are usually on the first, third, and fourth segments, thus differing in arrangement both from the Pauropod and the Insect types.

It will, therefore, be clear that we may not claim, from this larval development, that either Diplopoda or Pauropoda have passed through a Hexapod or Insectan stage in their ancestry. All we may claim is that they have passed through an ancestral stage with fewer somites and fewer pairs of appendages than they now possess, and that a reduction of this original number of appendages, whatever it may have been, to three pairs in the first larval stage has been accomplished in several different ways, evidently because the small first instar larval form could best get along with three pairs, though not necessarily the *same* three pairs.

Now let us try to get some idea of what this primitive ancestor was like.

In the *Nauplius*-larva of the Crustacea, the head is well-formed, and consists of four segments, viz., the ocular, the first antennal, the second antennal, and the mandibular. Three of these are preoral and one postoral. In the passage to the *Metanauplius*-larva, there is a zone of addition behind the mandibular segment, as well as a zone of addition at the posterior end of the body.

Now it seems to me that the correct interpretation to put on this is that, whatever number of postcephalic segments there may have been present in the original ancestor of the Crustacea, there can be no doubt that the head originally possessed only four segments. Thus there can only have been one pair of jaws, and the mouth must have been closed from below *by a flap or process of the mandibular segment.*[*]

If we now compare this Nauplioid condition of the ancestral Crustacean head with the head of *Peripatus*, we find a close similarity. The ocular segment is the same in both. The second segment in *Peripatus* carries the antennæ, which are homologous with the first antennæ of Crustacea. The third segment in *Peripatus* carries the jaws, which are homologous with the second antennæ of Crustacea; and the fourth segment carries the oral papillæ, which are the homologues of the Crustacean mandibles. No true appendages close the mouth from below, but the orifice is protected by papilliform ridges.

It is here that I wish to introduce the first point in my theory which I think is entirely new, viz., that the so-called maxillulæ or superlinguæ of Insects, together with their median process the hypopharynx, and the paragnaths of the Crustacea, are not only *not true appendages*, but *represent definitely the ancestral lower lip of the mouth when the head was in the four-segmented condition.* I can see no other reason for their existence, from the point of view of evolution, nor can I find any other explanation of their embryonic development from the mandibular somite. They are certainly not original portions of the mandibles, budded off; for their rudiments appear separately and between the bases of the rudiments of the mandibles. If we accept this solution, we are able to understand at once the present condition of the mouth in the Insecta and Crustacea. It has evidently been enlarged by the subsequent addition of two more pairs of appendages. In the Insecta, the paired glands of the second maxillæ must originally have opened on to the exterior, beneath the head. Their ducts have now been forced up into a position apparently within the mouth, and function as salivary glands; but the fact that they open below and not above the hypopharynx is an indication that they did not originally belong to the mouth at all.

If the above interpretation is correct, one might also venture on a prophecy:—Somewhere in the Pre-Cambrian rocks there must exist an ancestor of Trilobites and Crustacea, and probably of Eurypterids also, in which the head was composed of only four segments, as in the Onychophora. This ancestor may quite well be much larger than *Peripatus*, though, in my opinion, it will probably exhibit appendages composed of only a single segment. I believe that remains of such an ancestor are already being unearthed near Adelaide; but they are in such ancient rocks and have undergone so much contortion that they will be very difficult to interpret.

Returning now to the question of the segmentation of the postcephalic region in our ancestral form, it is clear that we have no definite evidence in favour of any fixed number of segments. I would be content to claim that Arthropods in general have been descended from forms with fewer segments than are to be found in the adults of higher groups to-day, without specifying the exact number. If we again study our Pauropod Table (Table C), we see that the adult Pauropod has a total of *twelve* postcephalic somites. To reach this condition it has to pass through larval stages with successively six, eight, nine, and eleven postcephalic somites. In the Symphyla, a larval stage with six pairs

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[*] The presence of the *mandibular grooves* on the heads of many Crustacea, including Syncarida, may also be evidence in favour of this.

of legs is known, but the full larval history has not yet been worked out.

Let us now summarise the above results with a view to a further application of them to the problem of insect ancestry:—

(1) In marine Arthropoda, forms with free-living larval stages are more primitive than forms that hatch with the full number of adult somites. A Nauplioid ancestor is indicated, with fewer somites than in recent dominant groups.

(2) In terrestrial Arthropoda, anamorphic forms are more primitive than epimorphic. Again, an ancestor with fewer somites is indicated, but not necessarily a Hexapod ancestor.

(3) In cephalisation, a stage with the head composed of only four fused segments was reached very early in the evolution of the Arthropoda. Amongst terrestrial Arthropoda, the Onychophora are a relict of this stage of evolution, though they are specialised in having attained an epimorphic development and in possessing a large though indeterminate number of postcephalic somites.

(4) During the four-segmented head stage of Arthropoda, the paragnaths, or, alternatively, the superlinguæ and hypopharynx, were developed as a non-appendicular lower lip to the mouth, closing it from below. They belong to the last of the four then existing head-segments, i.e., the mandibular.

(5) Later evolution of the head-capsule produced either five-segmented heads (Diplopoda, Pauropoda), or six-segmented heads (Trilobites, Crustacea, Chilopoda, Insecta). In such cases the mouth-cavity became enlarged and closed below by the maxillæ or labium, so that the hypopharynx, when developed, appears as an internal *tongue* within the mouth, and the salivary glands, originally having ducts opening external to the mouth, open instead beneath the hypopharynx, within the mouth. Tables D and E are attempts to exhibit these results in concise form.

TABLE D.

TABLE OF COMPARISON OF THE APPENDAGES OF THE HEAD SEGMENTS IN VARIOUS GROUPS OF ARTHROPODA.

A. FOUR AND FIVE-SEGMENTED HEADS.

SEGMENT.	ONYCHOPHORA Embryo and Adult.	CRUSTACEA Nauplius Larva.	ARACHNIDA Embryo and Adult.	DIPLOPODA. PAUROPODA.
1.	(Eyes)	(Eyes)	(Eyes)	(Eyes)
2.	Antennæ	1st Antennæ	(Rostrum)	Antennæ
3.	Jaws	2nd Antennæ	Cheliceræ	(Intercalary)
4.	Oral Papillæ	Mandibles	Pedipalps	Mandibles
5.				1st Maxillæ

TABLE E.

TABLE OF COMPARISON OF THE APPENDAGES OF THE HEAD SEGMENTS IN VARIOUS GROUPS OF ARTHROPODA.

B. SIX-SEGMENTED HEADS.

SEGMENT.	TRILOBITES.	CRUSTACEA. Adult.	SYMPHYLA. Adult.	CHILOPODA. Embryo and Adult.	INSECTA. Embryo and Adult.
1.	(Eyes)	(Eyes)	(Eyes)	(Eyes) (pre-antennæ)	(Eyes)
2.	Antennæ	1st Antennæ (Antennules)	Antennæ	Antennæ	Antennæ
3.	1st Maxillipedes	2nd Antennæ (Antennæ)	(Intercalary)	(Intercalary)	(Intercalary)
4.	2nd Maxillipedes	Mandibles	Mandibles	Mandibles	Mandibles
5.	3rd Maxillipedes	1st Maxillæ (Maxillulæ)	1st Maxillæ	1st Maxillæ	1st Maxillæ
6.	4th Maxillipedes	2nd Maxillæ (Maxillæ)	2nd Maxillæ	2nd Maxillæ	2nd Maxillæ

Let us now turn our attention to the Insecta.

The whole of this Class, with the exception of the Collembola and Protura, may be placed as definitely *epimorphic* in their ontogeny, i.e., the young larva hatches out with the same number of somites as the adult. One may, for the purposes of this discussion, omit those very highly specialised types which have passed even beyond epimorphosis, in that a reduction of some of the original somites may have taken place either in the adult or in both larva and adult, e.g., in the reduction of the number of definite abdominal segments to less than ten. Also we may leave out of account the problematical interpretation of certain so-called "protopod" larvæ in parasitic Hymenoptera.

In the Protura, there is a definite *anamorphic* type of ontogeny. The young larva hatches out with only nine abdominal segments, and three more are added in the form of small annular somites to form the adult abdomen with twelve segments.

If the Collembola were truly epimorphic, they ought either to hatch out with the full number of somites characteristic of the Insecta, or else show indications, either in their embryology or in the course of larval development, of the reduction which has taken place. There is, however, no sign of this at any stage. The embryonic development proceeds up to the formation of six abdominal segments only; the larva hatches in that stage, and the adult retains exactly that number of segments. I propose to term this type of ontogeny ***protomorphic.***

If we compare this with the larval stages of the Pauropoda (Table C), we shall see that the Collembola appear to have stopped short, as far as their postcephalic segmentation is concerned, at the stage indicated by the twelve-legged larva of the Pauropoda. Now about the only fact known concerning the ontogeny of the Symphyla is that they also pass through a twelve-legged larval stage. As the presence of two pairs of maxillæ and definite hypopharynx and maxillulæ have been proved for this group, we can now make an even closer comparison and say that the Collembola possess exactly the segmentation of the twelve-legged larvæ of Symphyla. The only difference lies in the appendages, all of which are retained in the Symphyla, including a pair of unjointed cerci.

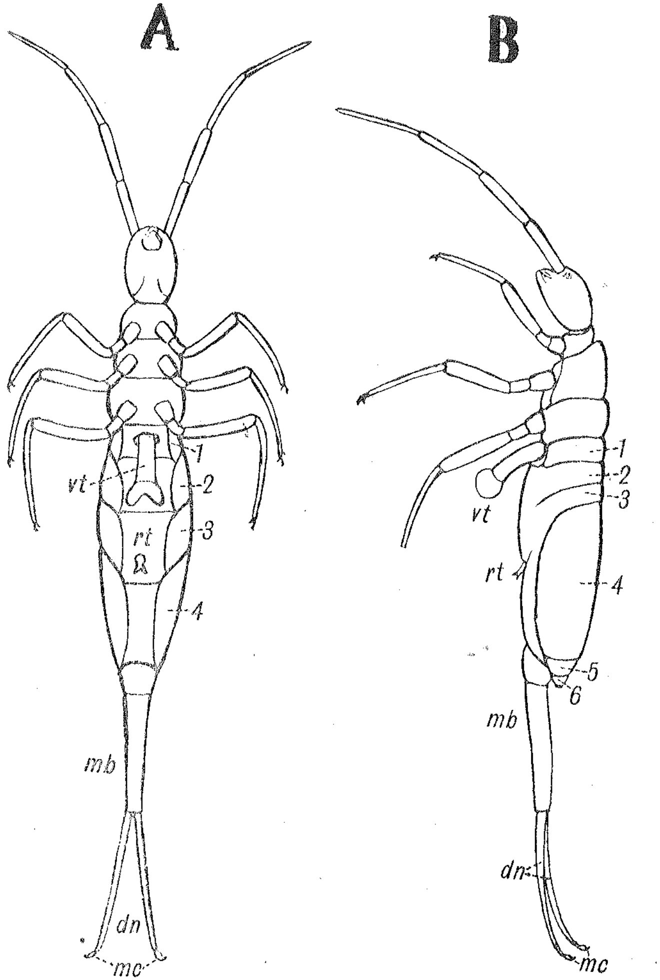

Fig. 14. Diagrammatic view of a Collembolon, family Entomobryidæ. A, ventral view, B, lateral view, showing the abdominal segments, numbered 1-6, the catch or retinaculum (*rt*), ventral tube (*vt*), and the parts of the spring or furcula, viz., manubrium (*m*), dens (*d*), and mucro (*mc*).

Further support for this view is obtained when we come to study the development of the appendages in Collembola (fig. 14). In the embryo, all the postcephalic segments show the rudiments of appendages except the last two, viz., the preanal and anal. This is an exact parallel to the condition of the postcephalic region in the twelve-legged larva of Pauropoda. Before hatching, the appendages of the second abdominal segment (fifth postcephalic) disappear. In the newly hatched larva, the appendages of the first abdominal segment (fourth postcephalic) become fused to form the *ventral tube* (fig. 14, *st*); those of the third abdominal segment (sixth postcephalic) also fuse to form the *catch* or *retinaculum* (fig. 14, *st*), and those of the fourth abdominal segment (seventh postcephalic) remain very large and are only partially fused to form the large *spring* or *furcula*; this organ has a fused basal portion or *manubrium* (fig. 14, *m*), a pair of elongate *dentes* (*d*) and small terminal portions or *mucrones* (*mc*).

Thus, of all the original paired appendages of the postcephalic region in Collembola, only one pair, those of the fifth segment, have been lost.

In the twelve-legged larva of Pauropoda, it is also true that only one pair of original postcephalic appendages disappear; only, in this case, it is the first pair, not the fifth.

In the twelve-legged larva of the Symphyla, none of the appendages of the postcephalic region degrades except those of the preanal segment, which appear to be partially atrophied. The anal segment bears a pair of short cerci, which are absent in Collembola and Pauropoda.

The result of this survey of the Collembola is most interesting. They are classified as Insecta; but, according to our analysis, *they have just as much right to be classed as Myriopoda as have the Pauropoda.* The only difference is that, while they retain all their original appendages except one pair, only the first three postcephalic appendages remain as functional walking-legs; *the remainder are modified to serve other functions.*

The conclusion appears to be irresistible that, unless the Collembola are not true Insects, then the Insecta, Pauropoda, and Symphyla have all been derived from a common ancestor with segmentation similar to that of Collembola.

Table F presents in tabular form the results of our analysis of the ontogeny of the groups under discussion, together with the Arachnida and Tardigrada.

TABLE F.

ANALYSIS OF THE TYPES OF POSTCEPHALIC SEGMENTATION IN VARIOUS GROUPS OF ARTHROPODA.

PROTOMORPHISM:—The preservation of an original condition with few body segments, without change from embryo to adult.

ANAMORPHISM:—The formation of few body segments in the embryo, with addition of further segments during larval life, the full number being reached at a late larval or adult stage.

EPIMORPHISM:—The formation of the full number of body-segments while still in the embryonic condition.

GROUP.	PROTOMORPHIC.	ANAMORPHIC	EPIMORPHIC.
TARDIGRADA	All forms (?)	——	——
ONYCHOPHORA	——	——	Peripatoidea
MYRIOPODA	——	Pauropoda Symphyla Diplopoda Chilopoda (part) Schizotarsia	Chilopoda (part)
INSECTA	Collembola	Protura	Thysanura Pterygota
TRILOBITA	——	All forms	——
CRUSTACEA	——	Most forms	Syncarida, etc.
ARACHNIDA	Pycnogonida (?)	Xiphosura	Scorpionida Araneina, etc.

THE EVOLUTION OF THE WALKING-LEG.

We can scarcely be wrong in deriving the walking-leg in Insects and Myriopods from an originally unsegmented process such as is found in many Annelid worms. The first truly Arthropodan stage may be envisaged as a still simple, unsegmented, short appendage provided with two sets of opposable muscles, extensors and flexors, and ending in one or two claws. This stage is represented in the limbs of Tardigrades. The next stage consists in a slight elongation of the leg, with annulation of a primitive type, as is to be seen in *Peripatus*. With further elongation comes the differentiation of the definitive segments, each having its chitinous exoskeleton somewhat hardened in comparison with the chitin of the joint, and thus for the first time becoming a definite unit in the leg mechanism. The walking-legs of both Insects and Myriopods are of this type, but show a wide range of evolution, both in the number of the segments and in their individual specialisations.

Comparing the walking-leg of the typical Myriopod with that of an Insect we are at once struck with the fact that the

Myriopod leg is of a more primitive type in not having the marked specialisation of femur and tibia which is to be found throughout the adult stages of most Insects. Let us then, first of all, follow out the evolution of the walking-leg in the various groups of Myriopoda.

The simplest type of Myriopod leg is that found in the Symphyla (fig. 15). It is usually stated to consist of five segments. We propose, however, in this paper, to consider that the leg proper starts with the coxa, as it does in the Insecta. The coxa of an insect shows a definite articulation with the sternal and pleural regions of the thorax. A careful examination shows that the segment which has this articulation in the Symphyla is the rather large, stout segment (*cx*) which is fourth from the distal end. Further, this segment is articulated with a kind of slightly chitinised socket, from the pleural portion of which there is developed a long, slender, curved apodeme (fig. 15, *ap*). From the sternal part of this socket are developed the ventral sac (*vs*) or eversible vesicle, and the style (*st*). I propose to call all this region the *subcoxa*. The sternal part is clearly homologous with the *subcoxal plate* in the abdominal segments of *Machilis* (fig. 6, D, *scx*); for this plate also bears the ventral sac and the style in that family, and lies behind the true sternum, which is a weakly chitinised, triangular plate (fig. 6, D, *sn*). In our view, then, the leg proper begins with the coxa, and the number of segments must be counted from that as the basal segment.

A comparison of the four-segmented leg of *Scolopendrella* (fig. 15) with the four-segmented leg of a Collembolan (fig. 14) will here prove useful. In the latter, the four segments are known as the coxa, trochanter, femur, and tibio-tarsus; these names, therefore, may also be used for the four segments of the leg in Symphyla. It is worth noting that the tibio-tarsus in Collembola ends in a well-developed claw and an empodium; the tibio-tarsus of *Scolopendrella* also ends in a claw and an empodium.

Returning to the legs of Myriopoda, we find the next stage, a six-segmented leg, in the Pauropoda and some of the Diplopoda. This condition appears to have arisen by the interpolation of two short segments between the original femur and tibio-tarsus of a four-segmented leg of Symphylan type, as in the Oniscimorphous Diplopoda. In the higher groups of Diplopoda, the distal segment becomes divided into two, giving a seven-segmented leg. In some cases, there ap-

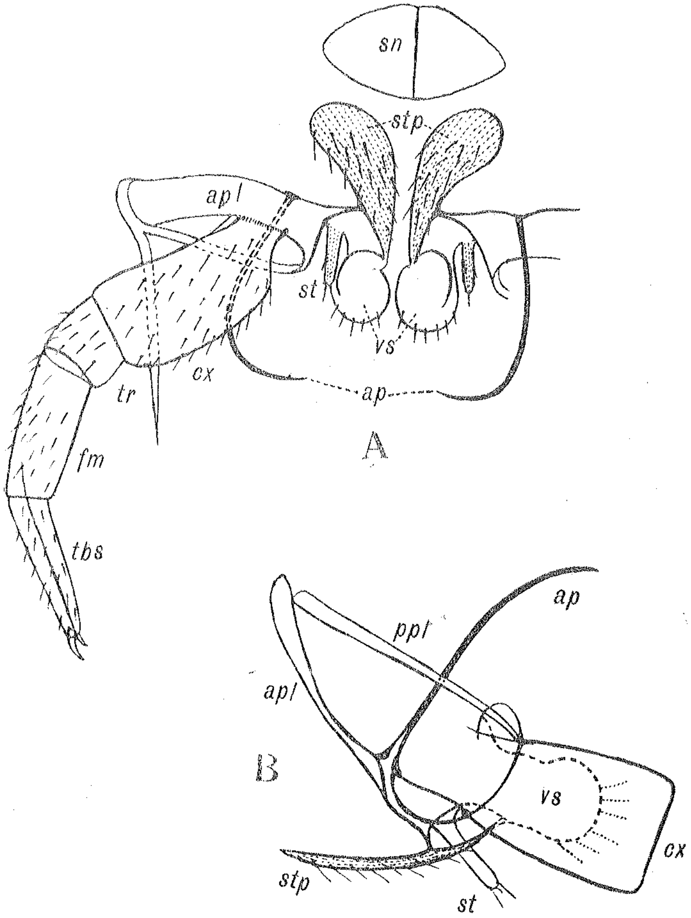

Fig. 15. Sternal region and leg in *Scolopendrella* sp., Australia. Class Progoneata, Order Symphyla, family Scolopendrellidæ. A, ventral view, drawn from a cleared and mounted KOH preparation stained in eosin. B, lateral view, drawn from an unmounted KOH preparation stained in eosin and cleared in clove oil, to show correct position of parts. *ap*, apodeme; *apl*, anterior pleural process, *ppl*, posterior pleural process, and *stp*, sternal process of the subcoxa; *cx*, coxa; *fm*, femur; *sn*, sternum; *st*, style; *tbs*, tibiotarsus; *tr*, trochanter; *vs*, exsertile vesicle. In B, all segments of the leg are omitted except the coxa, and the exsertile vesicle is indicated by dotted lines as it lies behind the coxa.

pears to be a further subdivision, more or less complete, of the distal segment, so that the highest type of leg evolved in this group may be said to be eight-segmented. The Diplopoda are also remarkable for the approximation of the two coxæ, which remain large, and in the setting-apart, in the males, of one pair of legs to form the copulatory organs.

Turning next to the Opisthogoneate Myriopods, we have to determine which is the true coxa in the Chilopoda. There are two more or less well defined, small, ring-like segments at the base of the leg, the first of which frequently bears a small style resembling that of the coxa of *Machilis*. This should therefore be the coxa, and the second short segment should be the trochanter. Following this are five well developed segments, so that we may call the typical Chilopodous leg seven-segmented. In some groups, however, the distal segment is either more or less completely subdivided into two, so that the highest development is again an eight-segmented leg.

A very remarkable and high degree of specialisation of the legs is attained by the Schizotarsia, an aberrant offshoot of the Chilopoda. In these the two distal segments of an originally seven-segmented leg become greatly elongated and very slender; each is subdivided into a number of annuli or secondary segments. This condition is usually spoken of simply as "multi-articulate," but the original point of division between the two distal segments proper is easily seen at an elbow near the middle of the annulated portion. The animal walks or runs by means of the first five segments of each leg only, and uses the two distal ones in a most extraordinary manner. It captures its prey by leaping upon it and enclosing it in a veritable basket or cage of legs; while devouring its prey at leisure, it keeps the terminal segments of its legs vibrating at a rapid rate, thus producing a misty effect and rendering itself almost invisible! A further interesting point is that a true "breaking-joint" is formed between trochanter and femur, thus enabling the animal to escape with ease if one of its long legs is either caught in a crevice or seized upon by an enemy.

It will be seen from the above account that the line of evolution of the Myriopod leg, after the Symphylan stage, cannot be homologised segment for segment with the Insect leg.

Turning now to the evolution of the Insect leg, we take up the story again at the Collembola (fig. 14), in which the comparison with the leg of the Symphyla is very close. This leg is four-segmented, and the tibio-tarsus ends in a claw plus an empodium. The subcoxal region is extremely primitive, with very slight chitinisation. The next stage is to be found in the five-segmented legs of Protura and Thysanura Entotrophica; the additional segment is formed by subdivision of the tibio-tarsus into distinct tibia and tarsus. In the Protura, the specialisation of femur and tibia, which is strongly marked in most adult insects, is not at all marked, so that these primitive insects are closer to the Myriopoda in this character than other insects. The Projapygidæ (fig. 12) are somewhat more specialised in this respect; the Japygidæ (fig. 11) a little in advance of the Projapygidæ; and the Campodeidæ (fig. 10) are slightly in advance of the Japygidæ.

No group of Insects now exists with a six-segmented leg which has not been attained by reduction; the few types in which the tarsus is at present two-segmented can all be proved to be reductions from a type in which the tarsus was originally three-segmented. Within the Thysanura, the distinction between the two groups Entotrophica and Ectotrophica is most marked; all the former have the tarsus simple, while in the latter it is never less than three-segmented. A few forms of Lepismatidæ are known in which the leg is eight-segmented (tarsus four-segmented) but these are obviously secondarily derived from forms having the typical seven-segmented legs of the Ectotrophica.

The Pterygota appear at first sight to centre round two distinct lines, one having the tarsus three-segmented and the other five-segmented. To the former would belong the fossil orders Palæodictyoptera and Megasecoptera, and also a number of recent groups (Dermaptera, Plecoptera, Copeognatha, Hemiptera, etc.). Handlirsch, who regards the Palæodictyoptera as the ancestral type of the Insecta, would also claim that this three-segmented condition of the tarsus is the primitive condition. But we have very clear evidence from the fossil record that the three-segmented condition has been secondarily derived from a five-segmented one in Perlaria and Copeognatha, and there is some evidence that the three-segmented condition in Odonata may also be a reduction. I am therefore inclined to consider the five-segmented condition of the tarsus as the primitive form for Pterygota, especially as the Plectoptera, both fossil and recent, have five-segmented tarsi.

Here let us pause once more to collect into tabular form our analysis of the evolution of the walking-leg in terrestrial Arthropoda (Table G).

The next stage of our analysis brings us to the question of the relationship of the typical uniramous legs of terrestrial Arthropoda to the primitive biramous types of marine Arthropoda. We have to ask the question: Is there any real evidence of descent of the terrestrial uniramous walking-leg from the marine biramous appendage of Trilobites and Crustacea?

TABLE G.

TABLE SHOWING EVOLUTION OF THE TYPES OF WALKING-LEG IN ANNELIDA AND ARTHROPODA.

(x Present.)

TYPE.	ANNELIDA.	TARDIGRADA.	ONYCHOPHORA.	MYRIOPODA.	INSECTA.
Unsegmented Process	x				
Simple Leg with Claws		x			
Simple Leg with Claws and primitive annulations			x		
Four-segmented Leg with single tibiotarsus				x Symphyla	x Collembola
Five-segmented Leg with separate tibia and tarsus					x Protura x Thysanura Entotrophica
Six-segmented Leg				x Pauropoda x Diplopoda	
Seven-segmented Leg				x Diplopoda x Chilopoda	x Thysanura Ectotrophica x Pterygota (some)
Seven-segmented Leg with secondary annulations				x Schizotarsia	
Eight-segmented Leg				x Diplopoda x Chilopoda	x Thysanura Ectotrophica (some)
Nine-segmented Leg					x Pterygota (most)

This brings us at once to the much-debated question of the coxal styles of Machilidæ (fig. 6, C, *st*). According to those who support the descent of Insects from Crustacea, these styles are either true exopodites or true epipodites. If the original basal segment of the leg in *Machilis* is the subcoxa (fig. 6, D, *scx*), then the style *may be* a true exopodite, as it is borne on the second segment (coxa). If, however, the coxa is the true basal segment, then the style cannot be an exopodite, though it *might be* an epipodite. In either case, the presence of similar styles on most of the abdominal segments of Machilidæ, and, indeed, of most abdominal segments in the Thysanura, has been claimed as additional evidence of the descent of these insects from Crustacea. Let us examine the position more closely.

It seems clear that the abdominal styles in Machilidæ are not the homologues of the coxal styles of the second and third thoracic segments; for the abdominal styles are borne on the subcoxa (fig. 6, D, *scx*) and must therefore be the homologues of the styles found in *Scolopendrella* (fig. 15, *st*). These styles are situated just externally to the *exsertile vesicles* (*vs*) in both cases.

The double homology of coxal style and ventral sac is quite inexplicable except on the ground that the Symphyla and Machilidæ were derived from a common ancestor.

Further, we have to note the occurrence in Chilopoda and Schizotarsia of small coxal styles on most of the legs. These are clearly homologous with the coxal styles of Machilidæ. But these groups have not developed the subcoxal styles and sacs. Hence we may safely conclude that both types of style are not remnants of original epipodites, or exopodites, but merely a special development which took place at some stage in the evolution of the common ancestor of Myriopods and Insects, and were carried over into certain ancient types of both Classes.

As there is not a particle of other evidence throughout the Myriopoda and Insecta for the occurrence of either an exopodite or an epipodite, I think we are entitled to conclude that there is really no evidence whatever for the evolution of the walking-leg of the terrestrial Arthropod from the biramous swimming limb of the marine Arthropod.

We see, then, that the course of our investigation has again forced us into the position of maintaining some kind of relationship between the Symphyla and the Apterygota, although we are no longer thereby put into the position of the original supporters of this theory, in so far as it involved them in acceptance of the Symphyla as the nearest approach to the ancestral group of the whole of the Insecta.

Our conclusions may be stated as follows:—

(1) No evidence exists for the origin of the walking-leg of Myriopoda and Insecta from a biramous type of limb.

(2) Coxal styles occur in Chilopoda, Schizotarsia, and the Machilidæ.

(3) Subcoxal styles and eversible ventral sacs occur in Symphyla and Thysanura. Subcoxal styles also occur in Protura.

REPRODUCTIVE SYSTEM; THE PROBLEM OF THE POSITION OF THE GONOPORE.

Having thus arrived at a point where it is idle to shut our eyes to the fact that the evidence so far disclosed points to a much closer hereditary connection between Myriopoda and Insecta than between Crustacea and Insecta, we come now right up against the old crux, which may be stated as follows:—

All the older types of Myriopoda are progoneate. The Chilopoda and Schizotarsia are, it is true, opisthogoneate, but nobody proposes to derive the Insecta from either of them. All the Insecta are opisthogoneate. How can one bridge the gap between the progoneate Myriopods and the opisthogoneate Insecta?

It has long appeared to me that this problem is almost insoluble, if we are not to go back nearly to an Annelid ancestor with paired segmental gonads and gonoducts. However, a new solution now presents itself as the outcome of the present analysis, and I shall try to explain it clearly herewith.

In the following discussion, all segments will be reckoned from the head backwards as *postcephalic*, without regard to the presence of the thorax in the Insecta, since it is admitted that the thoracic region of an insect is composed of the first three original postcephalic segments of a more primitive type.

On the above reckoning, the Collembola possess *nine* postcephalic segments. If my theory that they are more primitive than other Myriopoda and Insecta, as regards their segmentation, is correct, then they never had more than nine postcephalic segments.

The gonopore in Collembola opens on the eighth postcephalic segment. In the Thysanura and most Pterygota the male duct opens on the twelfth postcephalic segment, the female on the eleventh. In the Plectoptera, however, the female ducts, which are paired, open on the tenth postcephalic segment. In the Protura the genital ducts open between the last two segments, i.e., the fourteenth and fifteenth postcephalic. In the Chilopoda, they open on the last segment. All these variations are included in the one term *opisthogoneate.*

In Diplopoda the genital ducts open on the third postcephalic segment; there are also, in the male, accessory copulatory structures either on the last segment, or on the seventh or eighth. The Pauropoda also have the genital ducts opening on the third postcephalic segment; the Symphyla on the fourth. Both these conditions are classed as *progoneate.*

Now nobody denies that Plectoptera and the rest of the Pterygota had a common ancestor because the female ducts in the former open one segment in front of their position in other Pterygota. Nor would they deny the unity of the Class Insecta on the ground that the position of the gonopore, though opisthogoneate, was not the same in Collembola, or in Protura, as it is in the Thysanura or the Pterygota.

Thus the issue as between the term "progoneate" and the term "opisthogoneate" is seen to be essentially one of degree. Granted that the divergence between the position of the gonopore in Symphyla and in Thysanura is too great to be "jumped," we may nevertheless ask *what amount of divergence would be permitted* for the present objection to the postulation of a common ancestor to be overcome? The reply must be, unless we are to be entirely illogical, that a similar amount of divergence must be permitted as is already accepted within one of the two divergent groups, say, the opisthogoneate. In this group the most forward position for the gonopore is actually to be found in the Collembola, strange as this may seem; for they have the genital opening on the eighth postcephalic somite!

Now the most backward position of the gonopore in the Progoneata lies on the fourth postcephalic segment. Hence

(1) *The original condition in the protomorphic ancestor of both progoneate and opisthogoneate forms*:—Even if we grant that the original terrestrial ancestor of Myriopoda and Insecta had a number of postcephalic somites *not less than the Collembola,* it is not required that functional gonads need have been present on any somites except the fourth to eighth postcephalic inclusive. Fig. 16, A shows this condition. Each gonad discharged its products through its own segmental duct, as indicated above.

(2) *Evolution of the primitive progoneate type*:—This would be accomplished by the fusion of all the ducts along each side into a single gonoduct opening forwards into the original pore of the fourth postcephalic somite. The remaining pairs of gonopores must have become vestigial and later on disappeared. Probably also the most anterior pair of gonads (those of the fourth postcephalic somite) also became vestigial and later on disappeared. Fig. 16, B shows this condition.

(3) *Evolution of the primitive opisthogoneate type*:—This would be accomplished by a fusion of all the ducts along each side, similar to that in (2), but opening backwards into the original pores of the eighth postcephalic somite, instead of forwards into the fourth. As in (2), all the remaining pairs of gonopores must have become vestigial and later on disappeared. Fig. 16, C shows this condition.

(4) *Stages in the Evolution of the progoneate type*:—It would appear probable that, during anamorphic evolution of the progoneate type, the original pair of gonads in the fourth postcephalic somite has degraded and disappeared; at the same time, probably at least three extra pairs of gonads have been developed posteriorly, in the ninth to the eleventh postcephalic somites, during anamorphosis, either during a single interpolation of three segments, or during two stages of addition, of two segments followed by one more (as in the larval development of Pauropoda). Fig. 17, B shows this intermediate or Proto-pauropod stage. From it, there can easily be developed the adult condition found in the Pauropoda (fig. 17, C) in which the ducts have been extended forward one segment (probably by ectodermal additions) so as to open into the third postcephalic somite, while the gonads of the fifth and sixth segments appear to have been lost, and the remaining pairs have combined into two groups, each extending through several segments, and thus partially obscuring the original segmental arrangement.

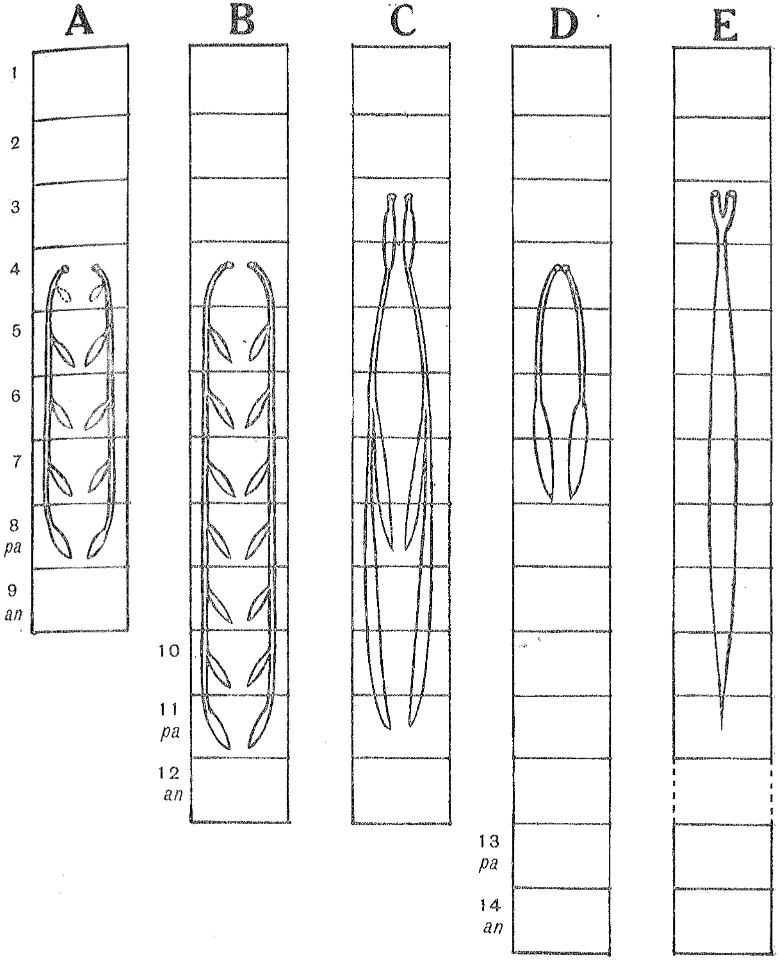

Fig. 17. Further Evolution of the Progoneate Type of Reproductive System. Diagrammatic. A, ancestral progoneate (as in fig. 16, B). B, intermediate or Proto-pauropod stage, leading to C. C, Pauropoda. D, Symphyla. E, Diplopoda. The numbers indicate postcephalic somites; *an*, anal, and *pa*, preanal somite. All diagrams represent female organs.

In the Symphyla (fig. 17, D), the original position of the gonopores is retained, but there is a very great reduction in the gonads; apparently only those of the sixth and seventh postcephalic somites have been retained, and these are fused on each side, so as to obliterate the original segmental arrangement.

The Diplopoda (fig. 17, E), like the Pauropoda, have specialised in the forward movement of the gonopores, but appear to have retained a larger number of the original pairs of gonads; these, however, have all become fused together to form one great, elongated gonadial chamber. The paired ducts have also fused, except towards the gonopores, where they remain separate.

How close these hypothetical stages in the evolution of the reproductive systems of the various types of Progoneata actually come to the truth can only be discovered by very careful examination of the embryonic and larval development of the gonads in existing types. This has, apparently, not yet been attempted. If, however, my new theory at all approximates to the actual course of evolution of the ancestors of Myriopoda and Insecta, such a study as this should yield many points of evidence in its favour, or, alternatively, offer evidence demanding some reconstruction of its details.

(5) *Stages in the Evolution of Opisthogoneate types*:—Starting from the ancestral protomorphic opisthogoneate type already envisaged (fig. 16, C), we have to follow out four distinct lines of evolution as follows:—

(a) *The Collembola* (fig. 16, D, E):—Here the intermediate stage may be conceived of as an enlargement of the five gonads on each side to a stage in which their separate ducts become obliterated (fig. 16, D). This may be termed the Proto-collembolan stage. The condition of the male gonads in Poduridæ is a little further advanced (fig. 16, E), the gonads on each side forming a huge convoluted mass projecting as far forwards as the mesothorax, but still showing definitely its origin from five originally distinct gonads. In the females fusion proceeds further, and apparently all signs of the original segmental arrangement are lost.

It is important that the embryonic formation of the testes in some primitive Podurid should be worked out completely, so as to determine which five postcephalic somites actually produce the paired gonads.

We must note that, as there has been no anamorphosis in the Collembola, the evolution of the gonads must have been comparatively simple, and has only involved the original elements present in the hypothetical ancestor of both progoneate and opisthogoneate types.

(b) *The Protura* (fig. 18, A, B):—For the evolution of this type, we require two anamorphic stages. In the first, the original five pairs of gonads were retained, and the position of the gonopores was probably pushed backwards to between the anal and preanal segments. By interpolation of three more segments just anterior to these, without development of extra gonads within them, we reach what we may term the *Proto-proturan Stage* (fig. 18, A), originally an adult condition, but now represented by the larval form with

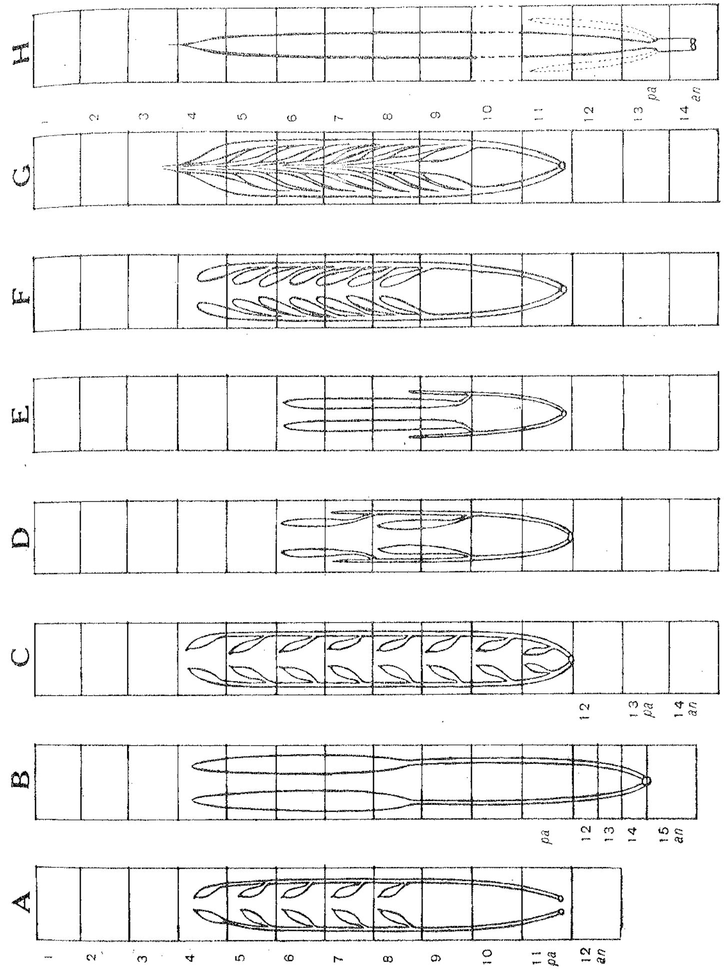

Fig. 18. Further Evolution of Opisthogoneate Types. Diagrammatic. A-B, Proturan line. C-G, Thysanuran-Pterygotan line. H, Chilopoda. A. Proto-proturan stage, intermediate between ancestral type (fig. 16, C) and B, Protura. C, Proto-thysanuran stage, leading to Japygidæ (fig. 11) by loss of last pair of gonads. D, Projapygidæ (fig. 12). E, Campodeidæ. F, Machilidæ. G, typical primitive Pterygote type. H, Chilopoda: the accessory glands are shown by dotted lines to indicate the extent of the additional posterior portion of ectodermal origin. Numbers indicate postcephalic somites; *an*, anal, and *pa*, preanal somite. All diagrams represent female organs.

nine abdominal segments. Either before or after this stage was reached, the paired gonads must have become fused into two elongate organs of the type now existing in the Protura. The present Proturan stage (fig. 18, B) has been reached simply by a second anamorphic development, resulting in the addition of three ring-segments just in front of the anal segment.

(c) *The Thysanura and Pterygota* (fig. 18, C-G):—The evidence favours a common ancestor for these two groups, which we may term the Proto-thysanuran stage (fig. 17, C). It must have had eight pairs of gonads, and must also have been developed anamorphically from the ancestral protomorphic opisthogoneate type (fig. 16, C) by the addition, either at a single stage or at two, of three additional somites in front of the preanal.* From this type, the Japygidæ (fig. 11) evolved simply by loss of the most posterior pair of gonads: the segmental condition of the other seven remains complete to the present day in the females, and the only other specialisation is the union of the two original gonopores on the preanal segment. The Projapygidæ (*Anajapyx*, fig. 18, D) show a further stage of reduction, the gonads being reduced to two pairs only; each of these two, however, is probably composed of two or more of the original segmental gonads. The end development of this line is to be found in the Campodeidæ (fig. 18, E), where all the remaining gonads on each side are fused into a single elongate organ.

The Machilidæ and Lepismatidæ apparently constitute another line of development, in which (fig. 18, F) the original seven pairs of gonads retained in the Japygidæ lose their segmental arrangement and become more crowded together (Machilidæ). In the Lepismatidæ, either there is a secondary reduction to five pairs only, or, just possibly, these five pairs may actually represent the original five pairs of the ancestral protomorphic type, carried over unchanged.

It is interesting to note that, on this new theory, the two lines of evolution of the reproductive organs in the Thysanura Entotrophica and Thysanura Ectotrophica are seen to be distinct, but quite closely related.

Turning next to the Pterygota (fig. 18, G), the line of evolution follows closely that of the Thysanura Ectotrophica, but apparently the whole eight original pairs of gonads are retained, though their segmental condition is lost. The condition found in the females of Plectoptera, in which the two oviducts open separately on the tenth postcephalic somite instead of on the eleventh, is quite possibly not primitive, but a secondary development correlated with the necessity, in these delicate and short-lived insects, for freeing large masses of eggs as quickly as possible.

(d) *The Chilopoda and Schizotarsia* (fig. 18, H):—What little is known about the gonads in this group indicates that they have pursued their own line of evolution quite independently of that of the Insecta. It is not possible to indicate the stages in its development very closely, but an examination of the female reproductive organs in the more primitive groups ought to afford some evidence of it. In the best-known form, *Scolopendra*, the whole of the original gonads are fused together to form an elongated single organ (fig. 18, H). This organ lies in the middle line, below the alimentary canal and above the central nervous system. Its form appears to be correlated with the great elongation and narrowing of the animal's body. The gonopores open together on the last segment; probably the extension backwards from the original position on the preanal segment has been accomplished by the formation of a secondary ectodermal portion of the ducts, posterior to the entry of the two accessory glands (fig. 18, H, dotted portions); or, alternatively, the true anal segment may be vestigial, as in most Insecta.

Before leaving this subject of the reproductive system, it will be as well to say a few words about the Crustacea. In this Class in general, the gonopores may open in any position from the first to the nineteenth postcephalic somite. The posterior position is, however, very unusual, and is only to be found in certain Branchiopoda in which a very large addition of somites has taken place. Such types, of course, do not enter into the discussion of the origin of Insecta in any case. *All the types of Crustacea which can possibly come into the discussion are classifiable as progoneate types, in contrast with the Insecta.* Moreover, none of them shows the primitive segmental arrangement of gonads required of the ancestor of the Insecta. Take, for instance, the Syncarida. In this group the ovaries form an elongate mass running from the posterior part of the thorax into the abdomen; the oviducts open on the inner faces of the coxopo-

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*Possibly the undeveloped, annular nature of the ninth abdominal segment in Japygidæ is evidence that it was the last segment to be added anamorphically in the ancestor of Thysanura.

dites of the sixth pair of thoracic limbs. The testes are long slender tubes with their vasa deferentia opening on the sternal surface of the last thoracic somite. Thus in the Syncarida the gonopores of the female belong to the sixth postcephalic somite, those of the male to the eighth!

In order, then, for the Syncarida to be the ancestral group to the Thysanura, it is necessary to postulate a lost type of Syncarid in which the gonopores of the two sexes were placed much farther back; to wit, in the female, no less than five segments back, and in the male, four! There is not the slightest evidence that such a type ever existed; whereas there is plenty of evidence that both progoneate and opisthogoneate types of terrestrial Arthropoda arose from a single stem.

One is not surprised that no advocate for the Crustacean origin of Insects has ever yet been bold enough to mention the gonads!

As for the Trilobites, nothing whatever is known about their reproductive system, so it is idle to speculate. Probably their gonads remained segmental, with many paired gonopores. They were certainly quite primitive enough to have been *possible* ancestors of almost any group of higher Arthropoda; but we have already seen that Handlirsch's method of filling in the intermediate stages is not acceptable, and there does not appear to be any other suggestion worth considering.

The Onychophora are already almost as highly specialised opisthogoneate types as the Chilopoda. Therefore no Peripatoid type can possibly have been the ancestor of such a form as *Japyx*, which has retained segmental gonads. Unless some evidence can be brought forward giving a direct evolutionary connection between Onychophora and primitive Myriopodan types, it would appear to be useless to bring them into the argument at all.

We may reasonably conclude this stage of our argument by presenting a somewhat diagrammatic "phylogenetic tree" embodying the combined results of our analysis of the evolution of the body-segmentation, of the walking-leg, and of the reproductive system. It would be almost impossible to indicate, in a single diagram, the evolution of a series of groups based on the study of these three characters, if it were not that they reinforce one another in a very complete manner. The result is to be seen in fig. 19.

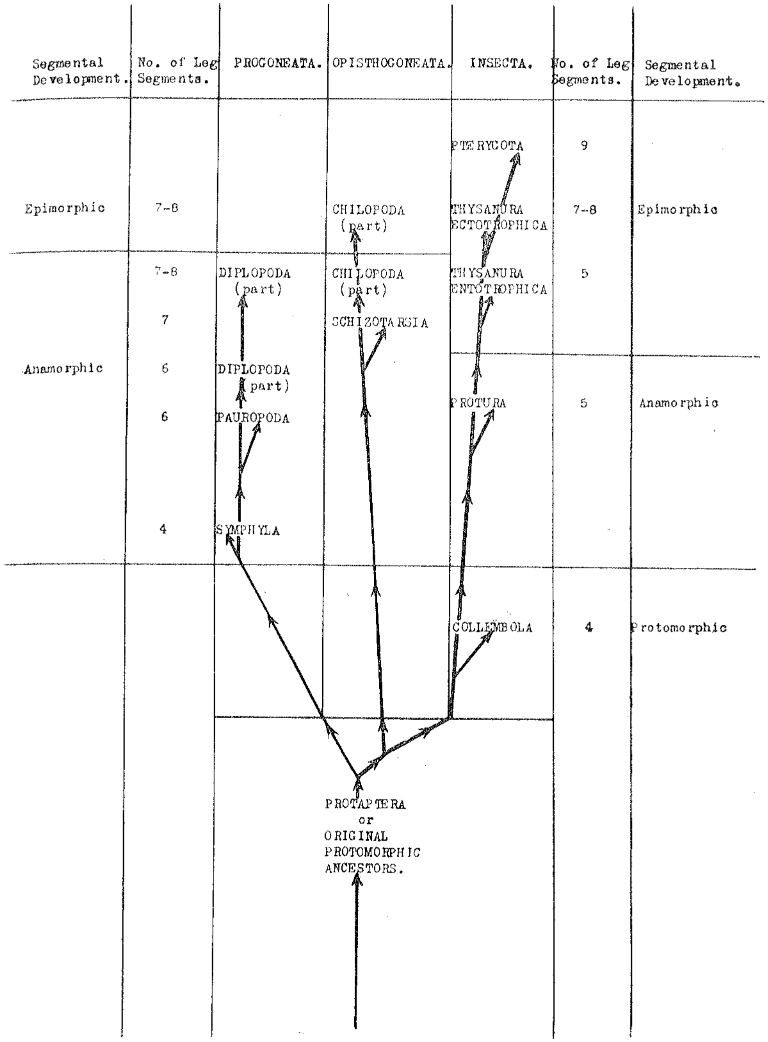

Fig. 19. Phylogeny of the Insecta according to the New Theory. The thick, arrowed lines indicate the courses of evolution. The type of segmental development and form of walking-leg are indicated in vertical columns on either side of the phylogenetic tree.

We have now set out the main lines of our new theory, and must proceed to test it along the same lines that I have indicated for existing theories. That is to say, we must consider the various systems of internal organs, the embryology and the geological record of the groups under consideration, and see how far the evolutionary record in each case either supports or conflicts with the theory.

THE RESPIRATORY SYSTEM.

This is considered first because it appears to be, next to the segmentation and appendages, the system which has already given rise to most discussion.

Generally speaking, marine Arthropods breathe by means of external gills, which may, or may not, be secondarily covered for protection, while terrestrial Arthropods breathe by means of an internal system of tracheæ or air-tubes, developed from invaginations of the ectoderm. Nobody would to-day, as far as I know, postulate a single great monophyletic group Branchiata for all the gill-bearing forms. On the other hand, Versluys (1914-1922) has resurrected the old group Tracheata for all the tracheate forms, and claims that it is a monophyletic group. Let us examine the position afresh.

How far is Versluys justified in his contention?

I have indicated, in my criticism of Versluys' Theory, that it would appear that he has made out a good case for the terrestrial Arachnida being actually more primitive than the marine forms. At first sight, the geological record would appear to deny this. But we have to remember that fossil records of land animals living before the Lower Devonian are extremely scarce, so that it is fair to assume that we know relatively little of what terrestrial life was like during the Cambrian and pre-Cambrian periods. The discovery of an abundant fossil fauna of Acarina in the Lower Devonian peat-bogs, associated with small Crustacea and also with true Collembola, should make us pause before asserting that the geological record is against Versluys. For the Acarina are undoubtedly very highly specialised; they stand above the epimorphic groups of terrestrial Arachnida and are remarkable for having undergone considerable reduction both in the larval and adult conditions. The loss of abdominal segmentation, of demarcation between cephalothorax and abdomen, and specialisation of mouth-parts, are all specialised adult characters, while the secondary reduction of the larval legs to three pairs (proved by the embryonic development of *four* pairs in at least one primitive form) is a specialisation unparalleled within the Class.

But when Versluys wishes to assert that the Arachnid tracheal system arose monophyletically with that of other terrestrial Arthropods, I disagree with him entirely. This assertion involves the evolution of all types of Arthropod tracheation from that of Onychophora, which is, to me, unthinkable.

Let us, first of all, clear the ground, by removing from the argument all obviously secondarily derived structures, whether of tracheæ or gills. In this category come—

(a) all tracheal gills developed in various groups of Insect larvæ, and

(b) all so-called "tracheal systems" developed in terrestrial groups of Crustacea, such as the Oniscoid Isopoda.

As regards (a), the fact that all these gills contain tracheæ is definite proof of their secondary nature, and is incidentally proof that all groups that possess such organs are *secondarily* aquatic and not primarily so. As regards (b), it is clear that, morphologically, these structures are in the nature of pseudotracheæ and not tracheæ, and the fact that they are borne on the exopodites of the pleopods, which are obviously marine developments, is as strong a proof of their secondary nature as is the possession of tracheæ in the gills of aquatic insect larvæ.

Thus we dispose of two points, viz.:—

(1) The occurrence of aquatic insect larvæ with tracheal gills does not prove that the insects were aquatic in origin, but reinforces the belief that they were terrestrial.

(2) The supposed "tracheal system" of Oniscoidea is not only *no proof* of the origin of Insecta from Crustacea, but is definitely against it; for it is obvious that no Insect tracheal system has been developed from such a system as is found in the Oniscoidea.

Now there are clearly three main systems of respiration within the Arthropoda, viz.:—

(1) through the cuticle,

(2) by means of gills, and

(3) by means of tracheæ.

Primitive forms are known, both marine and terrestrial, which breathe directly through the cuticle. The primitive gill of a marine Arthropod is a specialised outgrowth of the cuticle, either from part of a somite, or part of an appendage. It is therefore of the nature of an evagination designed to increase the amount of permeable surface presented to the oxygen-carrying medium, i.e., salt-water. In the case of an appendage, further advantage is gained by the ability to wave it to and fro. The primitive trachea, as seen in the Onychophora, for example, is an invagination of the cuticle, designed to increase the amount of permeable surface and also to bring the air into closer contact with the various internal organs in need of oxygen. One need scarcely be surprised that, in the case of an animal with such a soft cuticle as *Peripatus*, no definite segmental arrangement of the tracheal system was evolved.

It should be clear, then, that there is no more necessity to demand a monophyletic origin of all tracheate Arthropoda from an original tracheate form than there is to demand a monophyletic origin of all gill-bearing marine forms from a single gill-bearing marine type. On the other hand, there is plenty of evidence available to show that the original terrestrial types of Arthropod possessed no tracheæ at all, but simply breathed through their cuticle.

The Collembola, which, on my new theory, are the most primitive of all Insects, and, in some ways, notably in their protomorphism, more primitive than any existing Myriopoda, are entirely without tracheæ except in the case of the highly specialised family Sminthuridæ, in which a single pair of tracheæ occurs in the head region. I submit that, if Collembola were descended from tracheate forms, any type which now possessed a tracheal system would not have been the most highly specialised type, but one of the more primitive forms; nor would the tracheæ have been in the head, but in some segment which would have clearly indicated a reduction from the original postcephalic segmental system, as exhibited, for instance, in the more primitive Thysanura or Pterygota.

The Pauropoda have no tracheal system either. Here again we are dealing with a group which, on my new theory, is extremely archaic, being as old, almost, on the progoneate side, as the Collembola are on the opisthogoneate side.

The tracheal system of Diplopoda, with its tufts of fine tubules passing inwards from each spiracle, does not appear to be monophyletic with that of the Insecta or of the Chilopoda.

The tracheal system of the Chilopoda may have originated from the same stem as that of the Thysanura, or it may have arisen independently. Its highest expression, in the Schizotarsia, is of a type without parallel in any of the higher Insecta, where the tendency, indeed, is strongly towards reduction of the tracheal system.

The Protura possess a tracheal system with thoracic spiracles only. This is quite in line with my theory if we consider that the most primitive Insecta had no tracheæ, the intermediate anamorphic types only a partially developed (thoracic) system, and the higher types, Thysanura and Pterygota, a much more complete system.

It is still quite permissible to argue that the tracheal system of the Campodeidæ is a reduction from a more complete system present in the ancestral Thysanuran. Indeed, on my new theory, this is more probable than that the Campodeidæ show a primitive system comparable with that of Protura. For the series Japygidæ-Projapygidæ-Campodeidæ is, on my new theory of the evolution of the reproductive organs, a complete reduction series, and the presence of two thoracic and one abdominal pairs of spiracles in *Anajapyx* points in exactly the same direction.

On the other hand, I would regard the tracheal system of the Symphyla as extremely primitive, and as one of the very first attempts to develop a tracheal system of the Diplopod type, with numerous fine tubules not anastomising within the body. In this, as in many other characters, I consider the Symphyla to be much more primitive than the Campodeidæ. It is evident that there has been a considerable amount of convergence between the two groups, giving a superficial appearance of much closer relationship than really exists.

When we turn to the marine series, we find small, primitive types of Crustacea without any special gill-formation, but breathing only through the cuticle. In the higher types, especially in the Malacostraca, the gill-series is of high complexity. Particularly we must take account of the gills of Syncarida, as these have been considered as possible ancestors of the Insecta. In this group, the gills are provided on the epipodites of the thoracic legs, and show a progressive reduction from the primitive Anaspididæ, through the Koonungidæ to the Bathynellidæ. There can be little doubt that the last-named family is the most debased and specialised of the Syncarida, both on account of reduction of its appendages and also in its remarkable habits of living. So, then, if we are to derive the Insecta from Syncarida, we must picture them as having passed from marine to estuarine waters, thence to fresh-water rivers, thence to cave-waters and wells as Bathynellid-like forms; thence they must have emerged as cave-dwellers in the form of Machilidæ, with the vestiges of their original gills still in the form of coxal styles! Obviously a most fascinating theory, but scarcely a convincing one! The only position to which I am willing to relegate it is one in which the Syncarida must be considered as the ancestors of the whole Myriopod-Insectan complex, and I am afraid that this would take the ancestor too far back, both geologically and as regards its segmentation, to keep it within practical considerations. If any worker in these fields considers that there is a good case for a Syncarid ancestry of Insects, then such a theory must take a definitely opposed stand to my new theory of the protomorphic origin of Insects and Myriopods, and must regard forms like Collembola and Pauropoda as having evolved from ancestors having the exact segmentation of Syncarids. This, I venture to suggest, would be extremely difficult to maintain.

Further, any supporter of the Syncarid or, more generally, the Crustacean origin of Insects must admit my argument in favour of the Insects having evolved from types without a tracheal system. But this, again, throws them back on a consideration of Collembola and Pauropoda as very primitive types, and places them somewhat on the horns of a dilemma.

THE ALIMENTARY SYSTEM.

A very simple evolutionary line can be established for the digestive system of Onychophora, Myriopoda, and Insecta. In *Peripatus*, the endodermal region, or mid-gut, occupies most of the length of the digestive tube, while short ectodermal portions, covered with an extremly fine chitinous cuticle, form the fore-gut anteriorly and the hind-gut posteriorly. This type of digestive tube persists in the Myriopoda, with a tendency towards slight lengthening of the fore- and hind-guts at the expense of the mid-gut. In the Insects the mid-gut region becomes further shortened, and the lengthened regions of fore- and hind-gut tend towards differentiation of parts, which, however, vary greatly according to the group of insects under consideration, and the type of food consumed. In primitive Insects, there is never any development of an ectodermal stomach or gizzard, of the type found in Crustacea.

In the Crustacea, from the earliest types onwards, there is a marked shortening of the mid-gut region and a high stage of development of the fore-gut. The latter becomes differentiated into the œsophagus and stomach, or gizzard, the latter being developed *within the head;* and there is a marked bend in the course of the œsophagus upwards and forwards into the head before reaching the stomach.

If, then, the Insecta are derived from Crustacea, the whole of this important development of the fore-gut must have become degraded and then must have entirely disappeared! Not a trace of it is left, in any primitive Insect.

Further, in Crustacea there is developed, from the anterior portion of the mid-gut in the embryo, a voluminous set of hepatic cæca, or a liver. This type of organ is also quite unknown in the Insecta. The corresponding portion of the embryonic mid-gut in Insects has been proved only to develop up to a certain point, and the two glandular pockets formed by it are only transitory structures and soon disappear. One would certainly expect to find a greater development of the liver, *if* Insects are derived from any group of higher Crustacea, though the condition found is not incompatible with a derivation from some early type of proto-Crustacean, such as the Nauplioid ancestor already postulated.

The evidence would point strongly to a close relationship of Myriopoda and Insecta, with a possible, but by no means certain, derivation from Onychophoroid forms; any relationship indicated with Crustacea is seen to be, by comparison, a much more distant one.

THE EXCRETORY SYSTEM.

In the Crustacea the most important excretory organs are the paired antennary and maxillary glands. The former open at the base of the second antennæ. In Branchiopoda, they develop before the maxillary glands, and function during larval life; they then atrophy, and their function is taken on by the maxillary glands. They become the "green glands" of the Decapoda. The maxillary glands open at the base of the first maxillæ; in Decapoda, they sometimes precede the antennary glands in functioning, thus reversing the order found in the Branchiopoda. In this latter group they become the "shell-glands."

In the Syncarida, a single pair of excretory glands is well developed behind the mandibles. These would appear to be homologous with the maxillary glands of other Crustacea, but their ducts have not yet been traced with certainty.

No Crustacean is known with any trace of Malpighian tubules.

The essential excretory organs of terrestrial Arthropoda (exclusive of the Onychophora, which still retain the nephridia of Annelids) are known as *Malpighian tubules.* They occur in terrestrial Arachnida, in Myriopoda, both Progoneata and Opisthogoneata, and in Insecta. Those of Arachnida are shown by embryology to be special developments of the endoderm, and form diverticula of the hinder end of the mid-gut. Those of Myriopoda and Insecta agree in being of ectodermal origin, and form diverticula of the anterior portion of the hind-gut. Thus it is only in the Myriopoda and Insecta, amongst all the groups of Arthropoda, that true *ectodermal* Malpighian tubules are developed.

There could scarcely be a more striking testimony to the essentially close relationship between Myriopoda and Insecta than this.

If it be objected that certain Insecta, e.g., *Japyx,* do not possess Malpighian tubules, and that, therefore, they must be regarded as organs specially developed within the Class, I would reply that I have myself dissected *Heterojapyx* and have found there a set of six short diverticula at the anterior end of the hind-gut. These are evidently Malpighian tubules in a reduced form. Probably a transverse sectioning of the same region in *Japyx* would reveal their presence.

Silvestri (1905) has demonstrated the presence of six short Malpighian tubules in the family Projapygidæ (*Anajapyx*). The Protura also have six very short ones, in the form of small papillæ. The Campodeidæ have sixteen very short tubules, but the Thysanura Ectotrophica have them well developed though variable in number. The Collembola alone do not possess them and apparently have never possessed them at all; these forms carry on their excretion, apparently, entirely through the cuticle.

In the Myriopoda, the Pauropoda agree with the Collembola in possessing no Malpighian tubules. The Symphyla have two, well-developed; the Chilopoda and Schizotarsia two to four; the Diplopoda are apparently variable, but with not more than four.

It would thus appear that Malpighian tubules probably developed *in the common ancestor of Myriopoda and Insecta* at a stage later than the differentiation of the two most primitive groups, Collembola and Pauropoda.

This does not in itself definitely disprove an *ultimate* origin of both groups from some very primitive form of Crustacea, such as the hypothetical Nauplioid ancestor. But it appears to me to be much opposed to the theory of descent from any of the higher Crustacea, more particularly as not only the antennary glands of the latter Class, but also the appendages connected with them, are nowhere to be found in the Insecta. Small maxillary glands are known to exist in Collembola and Protura, but they do not exercise an excretory function.

THE CIRCULATORY SYSTEM.

In all Arthropoda the heart is an elongated dorsal vessel, supported by segmentally arranged alary muscles and having paired segmental ostia with valves to allow only ingress and not egress of the blood. This dorsal organ lies in the thorax and abdomen, and opens by means of the dorsal aorta into the head. In Insecta and most Myriopoda there are no closed circulatory vessels beyond the heart and dorsal aorta. Some of the higher Myriopoda, however, e.g., Chilopoda and Schizotarsia, have a well-developed arterial formation. In the Insecta and the lower groups of Myriopoda, the blood for the most part circulates in an open hæmocœle or blood-cavity, and only its forward dorsal movement is controlled by the heart and aorta. This type of circulatory system must be regarded as quite primitive, and closely resembling that of the Onychophora; probably the evolution of the tracheal system robbed the blood of a large share of one of its chief functions, that of oxygenation of the tissues, and thus prevented further development of the closed circulatory system.

Arterial development is found to a greater or less degree in most types of Crustacea, and it is clear that types like the Branchiopoda and Syncarida, not to mention the higher Malacostraca, are far in advance of the Insecta in their circulatory systems. In *Bathynella* the short heart is reduced to a position in the fourth thoracic somite. Other Syncarida also have the heart shortened, and this can even be seen to some extent in the more primitive Leptostraca. On this ground alone it would appear impossible to derive the Insecta or Myriopoda from any of the higher Crustacea.

The evidence points to the early forms of Myriopoda and Insecta having had a very primitive form of circulatory system, and their descendants having preserved this primitive type with little modification beyond increase or decrease of the number of segmental divisions of the heart. Collembola have a six-chambered heart, the divisions being in the second to seventh postcephalic somites. It seems probable that the anal and preanal somites originally did not develop such chambers and that the dorsal aorta originally belonged to the first postcephalic somite. Thus the type of heart found in Collembola may be the exact ancestral type. With the evolution of anamorphic types, the number of chambers would be increased. The probable maximum development in the Insecta is that found in *Periplaneta*, where the heart is said to have no less than thirteen chambers. Most of the Pterygota, however, have less than this, the usual number being seven to ten, while there are instances of reduction to three, or even to a single chamber.

THE CENTRAL NERVOUS SYSTEM.

There is little to gain from a study of the central nervous system in the groups under discussion. It is evident that this system shows a wider divergence in passing from the more primitive to the higher types of Crustacea than it does in the Myriopoda and the Lower Insecta. In the lower Crustacea the two longitudinal nerve-cords are wider apart, the connectives better developed, and the component ganglia of the subœsophageal complex more distinct than in any Insect type. By the time that the Malacostraca are reached, however, the evolution appears to have passed beyond that of the lower Insecta; the longitudinal cords are well fused together, the connectives obliterated, and the subœsophageal ganglion has begun to incorporate within itself the more anterior of the thoracic ganglia. How far this process has gone in Syncarida it does not appear possible to determine. Of *Parabathynella*, Calman (1917) states that "the central nervous system is remarkably bulky in comparison with the "other organs. The ventral nerve-cord shows some degree of longitudinal concentration (not very fully de"scribed), and the ganglia are indistinctly defined from the "connectives."

The higher Insects, of course, develop an extreme concentration of the central nervous system and a more complex brain than can be found anywhere within the Crustacea.

THE SENSE ORGANS.

We need only consider here the *eyes* and the *antennæ*.

(1) *The Eyes*:—The Arthropod eye began as a pit-like depression in the ectoderm, from which there was evolved a type of simple eye similar to that found in many Myriopoda and also in the larvæ of some Insects. This simple type, called an *ocellus*, has the hypoderm layer composed still of a single layer of cells, but those that border the pit become differentiated into vitreous-body cells and retinal cells, the latter secreting rods. The lens is formed simply by thickening of the cuticle over the pit.*

From this simple type we can derive all the types of compound eyes found in Arthropoda. I have already considered the problem of the evolution of this organ in Arthropoda, in dealing with Versluys' Theory (p. 26) and can only repeat my conclusion that compound eyes have been formed at least four times within the Phylum, independently of one another, viz., in the Myriopoda (*Scutigera*), in the Insecta, in the Crustacea (primitively a stalked type), and in the Arachnida.

(2) *The Antennæ*:—A comparison of the antennæ of the Onychophora, Myriopoda, and Insecta appears to indicate very clearly the line of evolution of these organs. Probably originally a pair of unsegmented processes, they first of all became annulated. In that stage, with only slight elongation, they are to be seen in *Peripatus* to-day. Right at the very base of the Myriopod-Insectan stem they would appear to have evolved into a higher type, in which the annuli had become definite segments. Only the basal segment, or scape, receives the insertion of the antennary muscles. The primitive number of segments would appear to have been only three, viz., scape, pedicel, and distale. The earliest known fossil Insecta, viz., the Lower Devonian Collembola, have the

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*Except in the Onychophora, where it is a separate body below the cuticle.

distale indistinctly divided into two subsegments, thus foreshadowing the normal Collembolan development of four segments.

The four-segmented condition must also have been the original one for the ancestors of Progoneata; for we find in the Pauropoda that the antennæ have four simple segments surmounted by two *which both spring from the fourth,* thus furnishing the only example in the whole of the Myriopod-Insectan series of a truly biramous antenna! In Diplopoda two segments are added *in series*, making six in line as the basic type for this group—more being added in the higher forms.

The condition of the antennæ in Pauropoda has not yet, as far as I am aware, been advanced by any author as evidence of descent from Crustacea; howbeit, we may be sure that, if the Pauropoda had been Insecta, it would have been so advanced. Let us examine such a claim to see how much it is worth.

The antennules or first antennæ of Syncarida consist normally of three well-developed basal segments followed by two rami; the internal ramus is well developed, and is in the form of a flagellum with many annular segments; the external ramus is shorter and composed of few segments. In the Bathynellidæ the internal ramus is shortened to five segments, while the external ramus is a mere stump. The second antennæ are somewhat like the first, but the external ramus is never well developed; it may be formed of a single well-developed segment, or be reduced to a stump or scale.

In the Pauropoda, the whole of the antenna is held in a position *transverse to the body axis.* The Syncarida have the first two segments pointed forward and the remainder transverse.

To develop the Pauropod type of antenna from that of the Syncarida one would have to assume that the ancestral form was even more degraded than *Bathynella.* Both internal and external rami would be reduced to a single segment; but, incidentally, an additional basal segment must have become developed, for the rami of the Pauropod antenna arise from the fourth, not the third segment.

Admitting that this *might* have happened, we have then to face the fact that *in no other character do the Pauropoda approach the Syncarida.* The anamorphic development of the Pauropoda and the fact that, even in the adult form, their segmentation does not agree with that of the Syncarida, must surely put them clean out of court as a possible connecting link with Crustacea.

In the Protura the antennæ appear to have been lost. This is noteworthy as indicating that these organs were probably very short in the hypothetical proto-Proturan ancestor. Many Insect larvæ have the antennæ so short that little more is needed for complete suppression. In many of the higher Insecta and Myriopoda, however, a long antenna or "feeler" is developed, with very numerous flagellar segments, all originally evidently annulations of the single elongated distale or its primary subdivisions.

There would appear, then, to be no evidence whatever for the derivation of the Insect antenna from the first antenna of Crustacea, and a great deal of evidence to show that it was never anything but a uniramous appendage similar to a primitive leg.

(3) *The Second Antennæ*:—The only types of Crustacea in which these are lost are certain Branchiopoda and Oniscoid Isopoda. Nobody, however, proposes to derive the Insecta from such types. The entire absence of these organs, which are of great importance in the Crustacea, is a grave difficulty which must be overcome before any theory of the origin of Insecta from Crustacea can be acceptable.

EMBRYOLOGY.

None of the theories so far put forward concerning the origin of the Class Insecta appear to have taken into account the evidence from Embryology. It is clear, however, that an acceptable theory must not do violence to the established facts in the embryology of the groups concerned which bear definitely on the course of evolution. For that reason, I shall content myself with a study of two outstanding points in the embryology of Insects and related groups, and shall try to discover how they bear on theories of their origin:—

(1) *The Evolution of the Cœlome*:—The Arthropoda in general are remarkable for the great reduction of the secondary body-cavity or *cœlome,* which makes way for an entirely different type of cavity called the *hæmocœle,* developed by the shrinking apart of ectoderm from endoderm, the space between being filled with blood. This reduction must be regarded as fundamental for Arthropoda; for it is seen to be already in quite an advanced stage in the Onychophora. In

this group the original cavities of the mesodermal somites divide into dorsal and latero-ventral portions. From the walls of the dorsal portions are formed the lateral walls of the heart and the pericardial septum, while, below these, in certain somites only, another portion persists and gives rise to the gonads. The latero-ventral portions become the excretory organs or nephridia.

Now, both in Myriopoda and in Insecta, the portion of the cœlome forming the nephridia degenerates; but the dorsal portion behaves very much as in *Peripatus*. The choking-up of the primitive cœlome is also to a large extent brought about by the formation of the voluminous *fat-body* from the cells of its inner wall.

The *fat-body* reaches an enormous development in many of the larvæ of Holometabolous Insects. *It is a development entirely confined to Myriopoda and Insecta.* It may, then, rightly be claimed as strong evidence of the essential unity of origin of the two groups, as set out in my new theory.

When we turn to the Crustacea, we find a complete absence of the development of a fat-body, together with an even more marked degradation of the original cœlome. Correlated with this is the higher development of the hæmocœle with its definite arterial and venous systems.

It would not be easy to establish the possibility of the evolution of the condition of the cœlome and hæmocœle as found in the Insecta and Myriopoda from even a primitive type of Crustacean. Evolution from any higher type, such as the Syncarida, becomes even more difficult to imagine, and I think we can safely claim that the evidence afforded by the embryology of the cœlome is opposed to it.

(2) *The formation of the embryonic envelopes (amnion and serosa)*:—In the embryology of all Insecta so far examined, from the primitive *Machilis* and *Lepisma* right up to the highest Pterygota, the embryonic area becomes invaginated into the yolk. The opening of this invagination is called the *amniotic pore.* In *Machilis* it remains large; in *Lepisma* it is small but remains open; in the higher Insecta it becomes completely closed. The inner limb of the fold forms the inner embryonic membrane or *amnion*; the outer forms the outer embryonic membrane or *serosa.* As the invagination is not completely closed in such a type as *Machilis*, the amnion cells come to cover the posterior half of the egg as well as the immersed embryo, while the serosa cells cover the anterior half of the egg.

The formation of these embryonic envelopes is almost unique within the Arthropoda. But in the Myriopoda (*Scolopendra*) there is found a condition closely analogous to that found in *Machilis*. The embryonic area becomes infolded into the yolk; but this infolding is only temporary, and straightens out again when most of the yolk has been absorbed. Now, in *Machilis*, when the embryo becomes exserted after the original invagination, the anteriorly situated serosa gives way to the posteriorly situated amnion and decreases in size to form the so-called *dorsal organ.* In *Scolopendra* there is an analogous but less marked formation of a corresponding dorsal organ, in the neck region of the embryo; this may rightly be regarded as the first rudiment of a true serosa.

Nothing resembling the above processes is to be found in the Crustacea. We must therefore conclude that, on the evidence, the Myriopoda are most closely related to the ancestral type of Insecta. If the Insecta have been derived from any type of Crustacea, then it would appear inevitable, on the evidence of the embryology, that the Myriopoda were also derived with them by a common ancestor.

THE GEOLOGICAL RECORD.

We must preface this section with the remark, which is, of course, a truism, that we are here dealing with an incomplete record. But, although admittedly incomplete, our knowledge of fossil Arthropoda, and more particularly of fossil Insects, has progressed very greatly during the past twenty years. Table H is an attempt to present this knowledge in a form that can be easily assimilated.

In order to aid our understanding of the Table, let us picture to ourselves the primitive Palæozoic world which was the seat of our evolutionary drama. Admittedly long before the dawn of the Cambrian Period the seas were filled with living things; marine animals, at any rate, had reached a high degree of complexity in the Lower Cambrian. Terrestrial forms came later. Except for the highly probable occurrence of Onychophora (*Aysheaia*), there are no terrestrial Arthropod groups represented in the record until the Scorpions appear in the late Ordovician. Closely following these appear, in the Lower Devonian, Diplopoda belonging to extinct groups, Collembola and Acarina very similar to existing forms, and perhaps also Thysanura.

TABLE H.

GEOLOGICAL RECORD.

(x Present.)

GROUP.	CAMBRIAN.	ORDOVICIAN.	SILURIAN.	DEVONIAN.	CARBONIFEROUS.	PERMIAN.
ANNELIDA	x	....	.. ....	....	....	....
ONYCHOPHORA	x? (*Aysheaia*)	....	....	....	....	....
TRILOBITA	x	....	....	....	....	..x
CRUSTACEA	x	....	....	x Leptost	raca .... x Syncarida	....
MEROSTOMATA	x	....	....	....	....	....
TERRESTRIAL ARACHNIDA		x..	....	.... x Acarina	.. ..	....
DIPLOPODA				x	....	....
CHILOPODA					x	....
COLLEMBOLA				x	....	....
THYSANURA				x? (*Rhyni*	*ognatha*)	....
PTERYGOTA					x..	....

Winged Insects, however, which of all insect forms are much the most likely to be preserved as fossils, do not appear until the Upper Carboniferous. Even if this record is not complete, and the Pterygote insects really existed in the Middle or Lower Carboniferous, to me it seems quite impossible to conceive that they existed in the Lower Devonian, when there were no trees on the earth at all, and only a few of the first exceeding primitive vascular plants had begun to appear on the land. One can conceive of forms like *Peripatus* living under rocks in a primitive world where fungi, algæ, and such-like simple plant-forms were the only vegetative covering; one can admit that Scorpions may have lurked in the crevices, Thysanura may have run or jumped about there, and Collembola and Acarina may have worked away amongst the débris as they do to-day. But it seems hardly possible to admit the Pterygota to a place in the Lower Devonian landscape!

Let us admit, then, that the discovery of Collembola in the Lower Devonian peat-bogs has dealt a hard blow at that part of Handlirsch's Theory which would make the various groups of Apterygota degraded side-branches from an older Pterygote stem. This part of Handlirsch's Theory must fail because it does violence to the known geological record. We must, of course, recognise, in justice to the talented author himself, that Handlirsch did not know of these Devonian fossils, which were only worked out nearly twenty years after he first published his theory. Further, the new facts appear to me to be fatal to the whole of Handlirsch's Theory, since, to be at all logical, it demands that the winged insects must have preceded the wingless forms.

Almost any other theory would be tenable on the geological record. The Myriopoda go back as far as the beginnings of the Insecta; the Onychophora probably well beyond them. The marine Crustacea are so ancient that even comparatively highly organised forms like the Syncarida were well represented in the Carboniferous, and quite probably in the Devonian also. Admittedly there is not much of a margin here for derivation of Insects from Syncarida or Leptostraca; but we must not press this too hard, because we still have a very imperfect fossil record of these groups.

Thus the sole definite conclusion that we appear entitled to draw from the geological record is that the Pterygota were the latest and most highly organised of all the groups of Arthropoda, and that Apterygote forms most certainly preceded them.

SUMMARY OF THE CHARACTERS OF THE HYPOTHETICAL PROTOMORPHIC ANCESTOR.

(1) *External Morphology*:—Body composed of at most fifteen somites plus telson. Of these, five belonged to the head and ten to the abdomen, but the first abdominal somite became added to the head before the Symphyla and the first true Insecta branched off.

Head segments fused into a capsule. Third segment (intercalary) already degraded and without appendages. Only simple eyes present. A single pair of short antennæ, probably with only three segments (scape, pedicel, and distale). Mandibles with at most only two segments. Maxillæ formed from simple walking-legs with gnathobases developed. Superlinguæ and hypopharynx well developed, indicating an even more primitive ancestral stage, in which the head was composed of only four segments and the mouth was closed posteriorly by these organs, and not by any segmental appendages.

Abdomen, or postcephalon, with each segment carrying a pair of simple walking-legs, except the last,* in which these appendages were directed backwards as cerci. Each leg with only four segments, viz., coxa, trochanter, femur, and tibiotarsus. The cerci were probably one-segmented processes, as in Symphyla and Japygidæ.

Respiration was carried out through the integument, which was composed of very soft chitin.

The reproductive organs consisted of probably only five pairs of segmental gonads, each opening by a duct at the base of its corresponding appendage; these were on the fourth to eighth postcephalic somites.

The alimentary canal consisted of a simple, straight tube, with short fore- and hind-gut regions and a considerably longer mid-gut, without diverticula. Small pockets, probably originally two only, at the anterior end of the hind-gut, served for lodgment of uric acid crystals and formed the rudiments of the future Malpighian tubules or excretory organs.

Heart probably only with six chambers (in second to seventh postcephalic somites), each with paired ostia and valves. A dorsal aorta present, leading into the head. No other closed vessels. Pericardial cavity and alary muscles present.

A large hæmocœle and well-developed fat-body present.

Central nervous system with supraœsophageal ganglion composed of three pairs of ganglia, subœsophageal ganglion composed of the two (or alternatively three) pairs of ganglia supplying the mandibles and maxillæ, and nine pairs of postcephalic ganglia, united by paired longitudinal connectives and transverse commissures.

Embryo with formation of primitive somites to full number present in the adult, but third cephalic somite already degrading and not forming appendage-rudiments. Larva hatched in a form closely resembling adult, which is reached by few ecdyses and with little change beyond increase in size and maturation of gonads.

Probable geological horizon.—Upper Silurian.

Probable ecology.—Terrestrial, dwellers in moist places, feeding on primitive plant-life.

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*Or, alternatively, the cerci belonged to the *preanal* segment and the last segment bore no appendages. This point could be definitely determined by reference to the embryology of the Symphyla.

SUMMARY OF THE MAIN LINES OF EVOLUTION FROM THE HYPOTHETICAL PROTOMORPHIC ANCESTOR.

(1) *The First Dichotomy*:—The first dichotomy was that into Progoneate and Opisthogoneate forms, by union of gonoducts on each side to open either into the most anterior genital somite (*progoneate*, fourth postcephalic somite) or the most posterior (*opisthogoneate*, eighth postcephalic segment). Intermediate forms all died out. The dichotomy was probably complete by the beginning of the Devonian period. The Collembola are a remnant of the original opisthogoneate stock, but further specialised by the adaptation of the hexapod mode of progression, aided by specialisation of the appendages of the fourth to seventh postcephalic segments to form a complex jumping or springing apparatus (ventral tube, catch, and spring). The corresponding progoneate type has been lost.

(2) *Evolution of the Progoneata*:—Increase of size was attained by the addition of further postcephalic somites anamorphically. The oldest types still extant are the Symphyla and the Pauropoda, which probably evolved in the Middle or Upper Devonian. Probably as a side specialisation from a Pauropoid ancestor the whole of the Diplopoda arose. In these two groups there is a tendency for the abdominal tergites to fuse together in pairs.

(3) *Evolution of the Opisthogoneata*:—Increase of size was also at first correlated in this group with the anamorphic addition of new postcephalic somites. Development, however, was more rapid than in the Progoneate types, tending to eliminate all the early anamorphic types and to replace them by epimorphic forms. There was no early tendency towards fusion of tergites; but a definite dichotomy, already begun or foreshadowed by the Collembola, into *Myriopod types* and *hexapod types*, became gradually intensified and gave rise to the two distinct lines of Opisthogoneata and Insecta. The Opisthogoneata remained anamorphic up to a time when the Chilopoda were fairly well developed; but the higher types of this group became epimorphic. The basic anamorphic type had a six-segmented leg; this gave rise to higher forms with seven to eight-segmented legs, and from the former of these arose the Schizotarsia with "multi-"articulate" tarsi. Compound eyes, which were never fully evolved in the Progoneata, were just achieved at the very top of the Opisthogoneata line (*Scutigera*).

(4) *Evolution of the Insecta*:—The hexapod tendency set in even before anamorphosis, and produced the Collembola in the Lower Devonian. The advantages of the hexapod mode of progression made this line evolve more rapidly than either of the others, and so the anamorphic stages were passed through more rapidly. Only a single small anamorphic group of primitive Insecta is left, viz., the Protura, distinguished by the loss of their antennæ. Leaving the Collembola and Protura as lowly side-branches, the main stem passed upwards to a level somewhat higher than that of the Symphyla on the Progoneate side, possessing five-segmented legs, but already fully epimorphic.* These were the Thysanura Entotrophica. Their evolutionary line is probably represented by the progression Japygidæ-Projapygidæ-Campodeidæ. They must have existed somewhere in the Devonian. At a slightly higher level, they produced a more vigorous type with three-segmented tarsi, exserted mouth-parts, and a more complete tracheal system. These were the Thysanura Ectotrophica. They divided into two main types, the dorso-ventrally flattened running types (Lepismatidæ) and the laterally flattened jumping types (Machilidæ); the latter developed compound eyes. Apparently about the same time the Lepismatoid types again ran ahead of the Machiloid, developing compound eyes and a five-segmented tarsus, and from such an ancestral form arose the whole of the Pterygota.

This Summary should be read in conjunction with fig. 19. The following indicates the Classification which should be adopted, on the basis of the new theory:—

I. Class PROGONEATA.	II. Class OPISTHOGONEATA.	III. Class INSECTA.
Sub-classes.	Sub-classes.	Sub-classes.
SYMPHYLA.	CHILOPODA.	COLLEMBOLA.
PAUROPODA.	SCHIZOTARSIA.	PROTURA.
DIPLOPODA.		THYSANURA.
		PTERYGOTA.

Note:—The name "*Protentomon*" has already been used for the hypothetical ancestor of the Class Insecta, based on more than one theory, so I hesitate to use it again in this address. Perhaps the best name that I could suggest for the common protomorphic ancestors of all the Myriopoda and Insecta, as here worked out, would be PROTAPTERA. Such a group would have the status of a Class. The term PROTOCOLLEMBOLA is a little too specialised, to my mind, and too cumbersome also.

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*See note at bottom of p. 64.

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