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THE EVOLUTION OF THE CLASS INSECTA.*

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With 19 Text Figures.
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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, refurnishes 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 Polychaeta 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 Polychaet 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 rea-
son, and must be partaken of, if swallowed at all, as a simple
*hors d'oeuvre!*

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 Trilobites. *Handlirsch's
Theory.*

II. Descent of the Insecta from Crustacea. Various
theories culminating in *Crompton'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
fulliest 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 Pterygogena) are the original Insecta, and
the ancestral type is to be found in the Order Paleodictyoptera
of the Upper Carboniferous. This type carried the
fore and hind wings outspread as in the Anisopterus

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
paranatal 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 segmen-
tation 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 possess-
ing 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 Paleodictyopterous Insect. This gap
Handlirsch very cleverly fills by giving a reconstruction of
his idea of what the larva or nymph of a Paleodictyopteron
must have been like (figs. 1, 2, 3). When you look at these
Fig. 1. A Trilobite, *Triarthrus beckii*, Green. Ventral view, restoration. After Beecher.

Fig. 2. Reconstruction of the larva of the original ancestor of the Insecta, according to Handlirsch. (Order Palaeodictyoptera, Upper Carboniferous.) Left, dorsal, and right, ventral view. After Handlirsch.
three figures side by side, the Trilobite, the larval Palaeodictyopteron and the adult Palaeodictyopteron, you feel that Handlirsch has presented a good case.

Further, Handlirsch also drives home his argument palaeontologically. 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 Insects as not lower than the Lower Carboniferous or, at the earliest, in the Upper Devonian (see fig. 4).

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 Machilidae and the Lepismatidae. He then puts aside the Machilidae, evidently because they were laterally flattened, jumping forms, and centres his argument on the Lepismatidae, 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. Sulp, 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. Sulp'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 palaeontological 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 Collombola, closely resembling living Poduridae, 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 Collombola 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:
The evolution of the class Insecta

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 Machilidae, which all are unanimously agreed upon as 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 homologous with the maxillæ (second pair of maxillæ of "authors) in the Malacostraca, and the labium as homologous with the maxillipeds 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 (paragnathi) 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 maxillæ of Crustacea."

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 superlingüæ 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 maxillæ or paraglossæ.

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

(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 Machilidae 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 Cumaceae), the possession of large compound eyes (absent in other groups of Aptyrygota), 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 maxillulillary 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 posi-
tion 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 maxillulae 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 superlingue or maxillula of Insects with the first maxilla or maxillula 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>
<thead>
<tr>
<th>SEGMENT</th>
<th>(A) APPENDAGES, HANSEN, 1893</th>
<th>(B) APPENDAGES, CRAMPTON, 1922</th>
</tr>
</thead>
<tbody>
<tr>
<td>CRUSTACEA</td>
<td>INSECTS.</td>
<td>CRUSTACEA</td>
</tr>
<tr>
<td>1. (Compound Eyes)</td>
<td>(Compound Eyes) Antennae</td>
<td>(Compound Eyes)</td>
</tr>
<tr>
<td>2. 1st Antennae</td>
<td>Antennae</td>
<td>1st Antennae</td>
</tr>
<tr>
<td>3. 2nd Antennae</td>
<td>(Absent)</td>
<td>2nd Antennae</td>
</tr>
<tr>
<td>4. Mandibles</td>
<td>Mandibles</td>
<td>Mandibles</td>
</tr>
<tr>
<td>5. 1st Maxillae</td>
<td>Maxillae</td>
<td>(Paragnaths) (Maxillae)</td>
</tr>
<tr>
<td>6. 2nd Maxillae</td>
<td>1st Maxillae</td>
<td>1st Maxillae</td>
</tr>
<tr>
<td>7. 1st Maxillipedes</td>
<td>2nd Maxillae</td>
<td>2nd Maxillae</td>
</tr>
</tbody>
</table>

It will be seen from the above that Crampton challenges Hansen's conclusions as to the nature of the insect maxillulae, and will not allow that they are true segmental appendages at all. He severely attacked Folsom's embryological studies also. In his view, the maxillulae 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 maxillae of Insects are the homologues of the first and second maxillae 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 maxillulae 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 Bathynellidae to be the most probable ancestors of the Insects.*

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 Machilidae, which are claimed to be the most primitive of all known Insects, 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.
THE EVOLUTION OF THE CLASS INSECTA

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Fig. 5. Bathynella natans, Vejd. Class Crustacea, Order Syncarida, family Bathynellidae. A, lateral view of male; length 28 mm. 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 Machilide themselves possess reduced appendages on most of their abdominal segments. Unfortunately, the Bathynellidre only possess abdominal appendages on the first and sixth segments, whereas in the Machilide these appendages, though reduced, occur on all, or nearly all the segments. Thus, on this point alone, the Bathynellidae cannot be the ancestors of the Machilide; 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 Machilide from a Myriopod?

Next let us consider the appendages. The first thing that we note is that almost all Crustacea, including the Syncarida, possess two pairs of antennae (fig. 5, B, C). Insects...
and Myriopods, on the other hand, have only the first pair. If the Machilidae are derived directly from Bathynellidae 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 coelomic 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 Machilid, and compares them with similar areas found in certain Crustacean mandibles, notably in those of Asellus (Isopoda), Diastylis (Cumacea), Aeneides (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 either to hold that Machilid 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 Insect Maxilla (after Crampton).**

<table>
<thead>
<tr>
<th>PART</th>
<th>IN CRUSTACEA</th>
<th>IN INSECTA</th>
</tr>
</thead>
<tbody>
<tr>
<td>First or Basal Segment.</td>
<td>Coxopodite.</td>
<td>Cardo.</td>
</tr>
<tr>
<td>Its gnathobase.</td>
<td>(Endite)</td>
<td>Lucina.</td>
</tr>
<tr>
<td>Third Segment.</td>
<td>Ischiopodite.</td>
<td>Palpifer.</td>
</tr>
<tr>
<td>Its gnathobase.</td>
<td>(Endite)</td>
<td>Galea.</td>
</tr>
<tr>
<td>Exopodite (from basipodite).</td>
<td>Exopodite.</td>
<td>Absent.</td>
</tr>
<tr>
<td>Endopodite (from ischiopodite).</td>
<td>Endopodite.</td>
<td>Palpus.</td>
</tr>
</tbody>
</table>

Table B shows clearly the homologies of the parts of the Crustacean and Insect maxilla, 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).

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 Synneurida 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 Insects. 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:—


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 Palaeozoic 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 Paphigmani, the Solifugae, 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 chelicerae, 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 opisthognoneate. One side-branch of the progoneate forms developed chelicerae 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 Hainlirsch'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

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Fig. 8. Phylogeny of the Arthropoda, according to Versluys (1928, in litt.).
which no tracheae 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, Insects, and terrestrial Arachnida 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 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:**

—1 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 antennae 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* larva. 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 Crayfishes outside the Insecta, and thus brought the Symphyla into the question. Thus a school of writers arose who claimed that Scolopendra and Crayfishes (figs. 8, 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
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 this 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 that the difficulty created by the fact that the Symphyla are protozoans while the Insects are epiephagenous, 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 Craypods; in particular, the Y-shaped suture which separates the epipharynx from the frons in many primitive Insects is present in Scolopendrella.

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

(3) There are two pairs of maxillae present, as in Insects, though other groups of Progonota (Diplopoda, Pauropoda) 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 eneural ventral one (fig. 15, vs). Though the abdominal legs are absent in the Thysanura, movable styles and ventral ones occur throughout that group of Insects.

*G. H. Carpenter (1891), however, maintains that Polyxenus, a primitive Diplopoda, has two pairs.

(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 Sphagidae.

(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 Craypods itself has only thoricuine spiracles, the Collembolan family Sminturines has a pair of head tracheae only.

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

(10) A pair of anal glands open at the tips of the cerci (fig. 9, pl). Similar glands occur in the Thysanura Anelytta (fig. 12 pl).

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 tergite (fig. 9, gp).

With regard to the above three characters, in which the Symphyla differ markedly from the Insects, 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 it appears at first sight; for we have to remember that we do not yet know anything about the embryology of the Sym-
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 propodeate 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 (1903-9) has brought a fresh interest into the problem by the study of his new family Prejapygidae, and particularly by his detailed account of the genus Analognus (fig. 13), which should be compared with the Japygidae also (fig. 11). This extraordinary insect appears 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 Scelopendrella on the other. Further, a pair of anal glands are developed exactly as in Scelopendrella 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 propodeate 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 Crampston's Theory, in spite of some excellent points, has not been clearly presented and fails to make a strong appeal; that
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 Pterygota insects.
3. The Thysanura Ectotrophica are closely related to the Thysanura Entotrophica, and therefore very close to the main evolutionary stem of the Pterygota.
THE EVOLUTION OF THE CLASS INSECTA

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

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 surely 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 Pterygota, viz., the Collembola, the Protura, and the Thyrsanura, and the nature of their common ancestry. 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 such correspondence actually does exist, then momentous conclusions must flow from it. Ray Lankester (1894) and G. H. Carpenter (1895) 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 Lepidoptera 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 Palaeonpus amongst the Diplopoda, and to the Scorpions, and Lanius 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 Ophiophora also have an excessive segmentation, and the primitive genus Leptobrachus is credited with twenty-four somites, the minimum for the Class. The Malacostraca amongst Crustacea fall one segment short of the requisite number for Insects and Lepidoptera; 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 Euryopida, 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 Huxley in accepting seven somites for the head region in Insecta, Symphyla, and Diplopoda, by regarding the superlingua or so-called mandibles as the paired appendages of a definite somite. I think there can be no doubt that Carpenter 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 Symphyla in general; but, at the same time, it throws out of gear the correspondence between the Lepidoptera, 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 Mollusca, the Echinodermata, 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 egg. 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 postephalic 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 postephalic 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 Tribolites 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 Nauplioid 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 Crayfish and also in the Siphonacea.

Now when we turn to the terrestrial Arthropoda (leaving out account for the present the Insecta), 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 Procrustata, 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 penultimate 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 Ophiuroidea, the Scyphozoa, 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 Siphonacea, the whole of the larval development is telescoped into the embryonic period, and the young larva emerges with the full number of somites proper to the adult. This phenomenon is called gnomorphosis.

Now it seems clear to me that, if we accept the fact that all Crustacea have been evolved from a Nauplioid ancestor, we must accept that the 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
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.**

<table>
<thead>
<tr>
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<th></th>
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<tbody>
<tr>
<td>6.</td>
<td>—</td>
<td>1st Legs</td>
<td>1st Legs</td>
<td>1st Legs</td>
<td>1st Legs</td>
</tr>
<tr>
<td>7.</td>
<td>Ant.</td>
<td>2nd Legs</td>
<td>2nd Legs</td>
<td>2nd Legs</td>
<td>2nd Legs</td>
</tr>
<tr>
<td>8.</td>
<td>2nd Legs</td>
<td>2nd Legs</td>
<td>2nd Legs</td>
<td>2nd Legs</td>
<td>2nd Legs</td>
</tr>
<tr>
<td>9.</td>
<td>3rd Legs</td>
<td>Ant.</td>
<td>3rd Legs</td>
<td>3rd Legs</td>
<td>3rd Legs</td>
</tr>
<tr>
<td>10.</td>
<td>—</td>
<td>—</td>
<td>4th Legs</td>
<td>4th Legs</td>
<td>4th Legs</td>
</tr>
<tr>
<td>11.</td>
<td>—</td>
<td>—</td>
<td>4th Legs</td>
<td>4th Legs</td>
<td>4th Legs</td>
</tr>
<tr>
<td>12.</td>
<td>—</td>
<td>—</td>
<td>5th Legs</td>
<td>5th Legs</td>
<td>5th Legs</td>
</tr>
<tr>
<td>13.</td>
<td>Preanal</td>
<td>Preanal</td>
<td>Preanal</td>
<td>Preanal</td>
<td>Preanal</td>
</tr>
</tbody>
</table>

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 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 Meconaclellus-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 antennae, which are homologous with the first antennae of Crustacea. The third segment in Peripatus carries the jaws, which are homologous with the second antennae of Crustacea; and the fourth segment carries the oral papillae, which are the homologues of the Crustacean mandibles. No true appendages close the mouth from below, but the oticles are 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 maxillule or submaxillipedia of Insects, together with their median process the hypopharynx, and the paragnathus

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

of the Crustacea, are not only not true appendages, but represent definitely the ancestral second 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 Insects and Crustacea. It has evidently been enlarged by the subsequent addition of two more pairs of appendages. In the Insects, the paired glands of the second maxilla 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 theyopen 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 Crusta­ceae, and probably of Eurypterids also, in which the head was composed of only four segments, as in the Echinoderms. 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 Arthropod in general have 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 Panuliform Table (Table C), we see that the adult Panuliform 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 Symphyyla, a larval stage with six pairs
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. Among 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 superlingum 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 maxillae 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>
<thead>
<tr>
<th>SEGMENT</th>
<th>CRESTACEA</th>
<th>ARACHNIDA</th>
<th>ARTHROPODA</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>(Eyes)</td>
<td>(Eyes)</td>
<td>(Eyes)</td>
</tr>
<tr>
<td>2.</td>
<td>Antennae</td>
<td>1st Antenna</td>
<td>Antennae</td>
</tr>
<tr>
<td>3.</td>
<td>2nd Antennae</td>
<td>(Antennae)</td>
<td>Antennae</td>
</tr>
<tr>
<td>4.</td>
<td>Oral Pupillae</td>
<td>Mandibles</td>
<td>Pedipalps</td>
</tr>
</tbody>
</table>

### Table E

<table>
<thead>
<tr>
<th>SEGMENT</th>
<th>CHILOPODA</th>
<th>INSECTA</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>(Eyes)</td>
<td>(Eyes)</td>
</tr>
<tr>
<td>2.</td>
<td>Antennae</td>
<td>Antennae</td>
</tr>
<tr>
<td>3.</td>
<td>1st Maxillae</td>
<td>Antennae</td>
</tr>
<tr>
<td>4.</td>
<td>2nd Maxillae</td>
<td>Pedipalps</td>
</tr>
<tr>
<td>5.</td>
<td>3rd Maxillae</td>
<td>Mandibles</td>
</tr>
<tr>
<td>6.</td>
<td>4th Maxillae</td>
<td>Pedipalps</td>
</tr>
<tr>
<td></td>
<td>5th Maxillae</td>
<td>Mandibles</td>
</tr>
<tr>
<td></td>
<td>6th Maxillae</td>
<td>Mandibles</td>
</tr>
</tbody>
</table>
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 purpose 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" larva in parasitic Hymenoptera.

In the Protura, there is a definite neumoorphic 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 maxillae and definite hypopharynx and maxillula 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 larva of Symphyla. The only difference lies in the appendages, all of which are retained in the Symphyla, including a pair of unjointed cerci.

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 condi-
tion of the postcephaline region in the twelve-legged larva of Pauropoda. Before hatching, the appendages of the second abdominal segment (fifth postcephaline) disappear. In the newly hatched larva, the appendages of the first abdominal segment (fourth postcephaline) become fused to form the ventral tube (fig. 14, a); those of the third abdominal segment (sixth postcephaline) also fuse to form the caudal or recticuta (fig. 14, b), and those of the fourth abdominal segment (seventh postcephaline) remain large and are only partially fused to form the large spring or forçade; this organ has a fused basal portion or manubrium, a pair of elongated denticles (d), and small terminal portions or manubriums (e).

Thus, of all the original paired appendages of the postcephaline region in Collombola, 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 postcephaline appendages disappear; only, in this case, it is the first pair, not the fifth.

In the twelve-legged larva of the Symphyla, some of the appendages of the postcephaline region degrades except those of the proanl segment, which appear to be partially atrophied. The anal segment bears a pair of short cerci, which are absent in Collombola and Pauropoda.

The results of our survey of the Collombola is most interesting. They are classified as Insects; 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 postcephaline appendages remain as functional walking-legs in the adult stage, which appear to be partially atrophied. The anal segment bears a pair of short cerci, which are absent in Collombola and Pauropoda.

The conclusion appears to be irresistible that, unless the Collombola are not true Insects, they should be classed neither with the Collombola nor with the Arachnida. Insects, Pauropoda, and Symphyla have all been derived from a common ancestor with segmentation similar to that of Collombola.

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

<table>
<thead>
<tr>
<th>GROUP</th>
<th>PTEROPODA</th>
<th>ANIMORPHA</th>
<th>EPHORPHA</th>
</tr>
</thead>
<tbody>
<tr>
<td>PTEROPODA</td>
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<td>—</td>
</tr>
<tr>
<td>ANIMORPHA</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>EPHORPHA</td>
<td>—</td>
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<td>—</td>
</tr>
<tr>
<td>ARACHNIDA</td>
<td>—</td>
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<td>—</td>
</tr>
<tr>
<td>SCORPIONA</td>
<td>—</td>
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<tr>
<td>HOPPIDA</td>
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<tr>
<td>SPRINGIDA</td>
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<tr>
<td>PERIPATIDA</td>
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</tr>
<tr>
<td>PERIPLUGA</td>
<td>—</td>
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</tbody>
</table>

### The Evolution of the Walking-Leg

We may safely be wrong in deriving the walking-leg in Insects and Myriopoda from an originally unsegmented process such as is found in many Annulid worms. The first truly Arthropod stages may be envisaged as a still simpler, unsegmented, short appendage provided with two sets of apposable muscles, extensions and flexors, and ending in one or two claws. This stage is represented in the limbs of Tardigrada. The next stage consists in a slight elongation of the leg, with accretion of a primitive type, as it is to be seen in Peripatida. With further elongation comes the differentiation of the definitive segments, each having its chitinous coxa 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 Myriopoda are of this type, but show a wide range of evolution, both in the number of the segments and in their individual specializations.

Comparing the walking-leg of the typical Myriopoda 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 Insects. 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 broad, stout segment (ex) 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 (ve) or eversible vesicle, and the style (st). We propose to call all this region the subcoxa. The sternal part is clearly homologous with the subcoxa of the four-segmented leg of the Holometabola (fig. 6, D, en); 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, en). 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 Neoscolopendrella (fig. 15) with the four-segmented leg of a Colembolan (fig. 14) will have proved useful. In the latter, the four segments are known as the coxa, trochanter, femur, and tibia-tarsus; these names, therefore, may also be used for the four segments of the leg in Symphyla. It is worth noting that the tibia-tarsus in Colembola ends in a well-developed claw and an apodeme; the tibia-tarsus of Neoscolopendrella also ends in a claw and an apodeme.

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 interposition of two short segments between the original femur and tibia-tarsus of a four-segmented leg of Symphylan type, as in the Onychipodous Diplopoda. In the higher groups of Diplopoda, the distal segment becomes divided into two, giving a seven-segmented leg. In some cases, there ap-

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Fig. 15. Sternal region and leg in Neoscolopendrella sp., Australia. Class Prostigmata, Order Symphyla, family Neoscolopendrillid. A, ventral view, drawn from a cleared and mounted KOH preparation stained in eosin. B, lateral view, drawn from a cleared and mounted KOH preparation stained in eosin and cleared in clove oil, to show correct position of parts. ap, apodeme; an, anterior pleural process; en, posterior pleural process; ap, anterior process of the subcoxa; cx, coxa; ex, exsertile vesicle; st, style; tr, trochanter; vs, ventral vesicle. In B, all segments of the leg are omitted except the coxa, and the apodeme 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 coxa, 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 Ophiogonogenate Myriopoda, 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 Mesobhina. 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 Schizobunia, 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.
of the tarsi 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 biramous 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 biramous walking-leg from the marine biramous appendages of Tillybites and Crustacea?

**Table G.**

<table>
<thead>
<tr>
<th>TYPE</th>
<th>CRUSTACEA</th>
<th>ANNEEIDA</th>
<th>MYRIAPODA</th>
<th>INSECTA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Simple Leg with Claw</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Four-segmented Leg with simple coxal styles</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Five-segmented Leg with simple tibia and tarsus</td>
<td>Symphyla</td>
<td></td>
<td>Collembola</td>
<td></td>
</tr>
<tr>
<td>Six-segmented Leg</td>
<td>Pauropoda</td>
<td></td>
<td>Protura</td>
<td></td>
</tr>
<tr>
<td>Seven-segmented Leg</td>
<td>Chilopoda</td>
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<td>Chilopoda</td>
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<tr>
<td>Eight-segmented Leg</td>
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<td>Symphyla</td>
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<tr>
<td>Nine-segmented Leg</td>
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<td>Pauropoda</td>
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(For reasons.)

This brings us at once to the much-debated question of the coxal styles of Machilids (fig. 6, D, etc.). 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 Machilids is the abdomen (fig. 6, D, etc.), then the style may be a true exopodite, as it is borne on the second segment (cox.) 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 Machilids, and, indeed, of most abdominal segments in the Thysanura, has been claimed as additional evidence of the descent of those insects from Crustacea. Let us examine the position more closely.

It seems clear that the abdominal styles in Machilids are not the homologues of the coxal styles of the second and third thoracic segments; for the abdominal styles are borne on the abdomen (fig. 6, D, etc.) and must therefore be the homologues of the styles found in Scopelaspides (fig. 15, 3). These styles are situated just externally to the epipodites ventralis (ev) in both cases.

The double homology of coxal and ventral style is quite inexplicable except on the ground that the Symphyla and Machilids 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 Machilids. 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 epipodites, but merely a special development which took place at some stage in the evolution of the common ancestor of Myriopoda and Insecta, 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 epipodite 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 Pterygota,
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) Coxlal styles occur in Chilopoda, Schizotarsia, and the Machilidae.

(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 Myriopoda and the opisthogoneate Insecta?

It has long appeared to me that this problem is almost insurmountable, 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 gonopores in Collembola open 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 Plecoptera, 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 respiratory 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 Pterygota 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 terms "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 hagiologic, 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 Progonata lies on the fourth postcephalic segment. Hence
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 Collombola, 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.

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.

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.

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.

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, B), like the Panopoda, have specialized 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 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 our 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 Poduridae 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 Poduridae 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 Proturan (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 genual 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...
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 Phrygopida (fig. 18, C-G)—The evidence favour a common ancestor for these two groups, which we may term the Proto-thysanuran stage (fig. 18, C). It must have had eight pairs of gonads, and must also have been developed anamorphically from the ancestral postembryonic ephippiosomite 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 Japygidae (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 Phryngepidae (Anopygidae, 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 Campodeida (fig. 18, E), where all the remaining gonads on each side are fused into a single elongate organ.

The Machilide and Lepismatide apparently constitute another line of development, in which (fig. 18, F) the original seven pairs of gonads retained in the Japygidae lose their segmental arrangement and become more crowded together (Machilide). In the Lepismatide, either there is a secondary reduction to five pairs only, or, just possibly, those five pairs may actually represent the original five pairs of the ancestral postembryonic 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 Evacophagica and Thysanura Ectocryptica are seen to be distinct, but quite closely related.

Turning next to the Phrygopida (fig. 18, G), the line of evolution follows closely that of the Thysanura Ectocryptica,
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 opisthongenate 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 opisthongenate 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.
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 tracheae 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 Arachnida in the Lower Devonian post-lim, associated with small Crustacea and also with true Ciliophora, 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 specialization unparalleled within the Class.

But when Versluys wishes to assert that the Arachnoid 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, unthinkably.

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

(a) all tracheal gills developed in various groups of Insect larvae, 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 tracheae is definite proof of their secondary nature, and it incidentally proves 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 pseudotracheae and not tracheae, 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 tracheae in the gills of aquatic insect larvae.

Thus we dispose of two points, viz.—

1. The occurrence of aquatic insect larvae 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 Oniscidea 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 Oniscidea.

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

1. by means of tracheae,

2. by means of gills, and

3. by means of tracheae,
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 Oligostraca, for example, is an evagination 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 Porifera, 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 Arthropods 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 Arthropoda possessed no tracheae 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 Myriapoda, are entirely without tracheae except in the case of the highly specialised family Protura, in which a single pair of tracheae 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 tracheae have been in the head, but in some segment which would have clearly indicated a reduction from the original psephophorous segmental system, as exhibited, for instance, in the more primitive Thysanura or Protura.

The Panorpidae 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 prosome side, as the Collembola are on the epipteronate 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 Schizomidae, 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 tracheae, 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 Chilopoda is a reduction from a more complex system present in the ancestral Thysanura. Indeed, on my new theory, this is more probable than that the Chilopoda show a primitive system comparable with that of Protura. For the series Japygidae-Projapygidae-Campodeidae is, on my new theory, the evolution of the reproductive organs, a complete reduction series, and the presence of two thoracic and one abdominal pair of spiracles in Anaspidae 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 Diplopoda type, with numerous fine tubules not anastomosing with each other. This is quite in line with my theory that the Symphyla should be more primitive than the Cam- podeidae. 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 Anaspidae, through the Kooc-
and associate this with the Bathynellidae. 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 Insects 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 Mochlididae, with the vestiges of their original gills still in the form of exhalent 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 Insecta. Further, any supporter of the Syncarid doctrine 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 one back on a consideration of Collemboidea and Porcellio (now 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 Porcellio, the endodermal region, or mid-gut, occupies most of the length of the digestive tube, while short ecdysozoal portions, covered with an extremely 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 to shortening of the fore- and hind-guts at the expense of the mid-gut. In the Insecta 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 accord-

ing to the group of insects under consideration, and the type of food consumed. In primitive Insecta, there is never any development of an ecdysozoal 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 oesophagus and stomach, or gizzard, the latter being developed within the head, and there is a marked bend in the course of the oesophagus upwards and forwards into the head before reaching the stomach.

If, then, the Insects 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 caeca, or a liver. This type of organ is also quite unknown in the Insects. The corresponding portion of the embryonic mid-gut in Insecta 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-Crustacea, such as the Nampliaid annelid 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 Opheliophorid 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 antennae. In Branchiopoda, they develop before the maxillary glands, and function during larval life; they then atrophy, and their function is taken over by the maxillary glands. They become the "green glands" of the Decapoda. The maxillary glands open at the base of the first maxillae; 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. Those would appear to be homologous with the maxillary glands of other Crustacea, but their ducts have not yet been traced with certainty.

No Crustacea 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 Protozoa and Opisthobranchidae, 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 appear to have an 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 Heteroprepus 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 Proopterygidae (Anura- japyx). The Proctura also have six very short ones, in the form of small papillae. The Campodeidae have sixteen very short tubules, but the Tymenura Heterochora 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 Symphyllida 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 Nauplius 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 aitae 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 hemocele 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 Branchipoda and Syncarida, not to mention the higher Malacostraca, are far in advance of the Insecta in their cir-
The Evidence points to the early forms of Myriopoda and Insecta having had a very primitive form of circulatory system, and their descendents 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 Pentoptera, where the heart is said to have no less than thirteen chambers. Most of the Pterygotes, 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. The central nervous system of the 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 cephalon, receives the insertion of the antennary muscles. The primitive number of segments would appear to have been only three, viz., scape, pedicel, and distal. The earliest known fossil Insecta, viz., the Lower Devonian Collembola, have the 6-chambered heart, the divisions being in the second to seventh postcephalic somites. 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 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 antennae.

(1) The Eyes.—The Arthropod eye began as a pit-like depression in the ecdcrner, from which there was evolved a type of simple eye similar to that found in many Myriopoda and also in the larvae of some Insecta. This simple type, called an ocellus, has the hypodermal layer composed still of a single layer of cells, those that border the pit becoming differentiated into vitreous-body cells and retinal cells, the latter secreting the cuticle. 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 Arthropods. I have already considered the problem of the evolution of this organ in Arthropods, in dealing with Vorobyov's Theory (p. 38) and can only repeat my conclusion that compound eyes have been formed at least four times within the Phyllum, 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 Antennae.—A comparison of the antennae of the Odonopera, 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 cephalon, receives the insertion of the antennary muscles. The primitive number of segments would appear to have been only three, viz., scape, pedicel, and distal. The earliest known fossil Insecta, viz., the Lower Devonian Collembola, have the...
distal indistinctly divided into two subsegments, thus foreboding the normal Collumbolan 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 antennae have four simple segments surrounded by two which both spring from the fourth, thus furnishing the only example in the whole of the Myriopod-Insecta 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 antennae 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 Insects, it would have been so advanced. Let us examine such a claim to see how much it is worth.

The antennules or first antennae of Syncarida consist normally of three well-developed basal segments followed by two rami; the internal ramius is well developed, and is in the form of a flagellum with many annular segments; the external ramius is shorter and composed of few segments. In the Bathynellidae the internal ramius is shortened to five segments, while the external ramius is a mere stump. The second antennae are somewhat like the first, but the external ramius 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 ramus of the Pauropod antenna arises 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 amorphous 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 antennae 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 larvae have the antennae so short that little more is needed for complete suppression. In many of the higher Insects and Myriopoda, however, a long antenna or "feeler" is developed, with very numerous flagellar segments, all originally evidently annotations of the single elongated distal or its primary subdivisions.

There would appear, then, to be no evidence whatever for the derivation of the Insect antennae 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 Antenna:—The only types of Crustacea in which these are lost are certain Branchiopoda and Onychia and 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 Insects 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 Cavity:—The Arthropoda in general are remarkable for the great reduction of the secondary body-cavity or coelome, which makes way for an entirely different type of cavity called the hemocoel, 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 Ophiurophora. 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 coelome from the cells of its inner wall.

The fat-body reaches an enormous development in many of the larvae 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 coelome. Correlated with this is the higher development of the hemocoel with its definite arterial and venous systems.

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

(3) The formation of the embryonic envelopes (amnion and serosa):—In the embryology of all Insects so far examined, from the primitive Neuroptera and Lepisma right up to the highest Pterygota, the embryonic area becomes involuted into the yolk. The opening of this invagination is called the amnion pore. In Mischidae 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 Mischidae, 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 (Scelopendra) there is found a condition closely analogous to that found in Mischidae. The embryonic area becomes involuted into the yolk; but this involution is only temporary, and straightens out again when most of the yolk has been absorbed. Now, in Mischidae, when the embryo becomes excoriated after the original invagination, the anteriorly situated amnion and serosa is in time to form the so-called dorsal organ. In Scelopendra 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 amnion.

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 amnial type of Insecta. If the Insects 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 prefix 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 II 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 Palaeozoic world which was the seat of our evolutionary drama. Admittedly long before the end 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 Ogygophora (Athyoeus), 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, Calonebra and Acrorida very similar to existing forms, and perhaps also Thaniatura.
Winged Insects, however, which are not, the most likely to be preserved as fossils, do not appear until the Upper Carboniferous. Even if this record is not complete, and the Apterygota 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 encroaching primitive vascular plants had begun to appear on the land. One can conceive of forms like Pterygota living under rocks in a primitive world where fungi, algae, and such-like simple plant-forms were the only vegetation covering; one can admit that Scorpions may have lurked in the crevices, Thysanura may have run or jumped about there, and Collembola and Astacina may have worked away amongst the debris 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 post-lags has dealt a hard blow at that part of Handlirsch's Theory which would make the var-

### TABLE II. GÉOLOGICAL RECORD.

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<td>ANNELIDA</td>
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<tr>
<td>ONYCHOPHORA</td>
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<td>TETRAPODA</td>
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<td>TREVIRANUS</td>
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<td>COLEMBOLA</td>
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<td>TREVIRANUS</td>
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<td>PTERIGOTA</td>
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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 Pterygota 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 encroaching primitive vascular plants had begun to appear on the land. One can conceive of forms like Pterygota living under rocks in a primitive world where fungi, algae, and such-like simple plant-forms were the only vegetation covering; one can admit that Scorpions may have lurked in the crevices, Thysanura may have run or jumped about there, and Collembola and Astacina may have worked away amongst the debris 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 post-lags has dealt a hard blow at that part of Handlirsch's Theory which would make the var-

Almost any other theory would be tenable on the geological record. The Myriopoda go back as far as the beginning of the Insecta; the Onychophora probably well beyond them. The marine Crustacea are so ancient that even comparatively highly organized forms like the Syncarida were well represented in the Carboniferous, and quite probably in the Devonian also. Admittedly there is not much of a snag in here for derivation of Insects from Syncarida or Leptotanaceae; 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 Apterygota forms must certainly preceded them.

**SUMMARY OF THE CHARACTERS OF THE HYPOTHETICAL PTERYGOTIC ANCESTOR.**

(1) Externally 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 Synymphal stage and the first true Insecta branched off. Head segments fused into a capside. Third segment (intercalary) already degraded and without appendages. Only single eye present. A single pale of short antennae, probably with only three segments ( scape, pedicel, and distais). Mandibles with at most only two segments. Maxillae formed from simple walking-legs with granulatus developed. Supra- lingue and hypopharynx well developed, indicating an even more primitive synnathial 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, trochantar, femur, and tibia-tarsus. The cerci were probably one-segmented processes, as in Lysiphylus and Japygidae.

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 appendages; there 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.

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

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

Central nervous system with supraesophageal ganglion composed of three pairs of ganglia, subesophageal ganglion composed of the two (or alternatively three) pairs of ganglia supplying the mandibles and maxilla, and nine pairs of postcephalic ganglia, united by paired longitudinal connectives and transverse commissuraries.

Embryo with formation of primitive somites to full number present in the adult, but third cephalic somite already degenerating 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.

*Or, alternatively, the cerci belonged to the presad segment and the last segment bore no appendages. This point could be definitely determined by reference to the embryology of the Lysiphylus.
(4) Evolution of the Insects.—The hexapod tendency set in even before anamorphism, 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 antennae. Leaving the Collembola and Protura as lower side-branches, the main stem passed upwards to a level somewhat higher than that of the Symphyta on the Prothorax side, possessing five-segmented legs, but already fully epimorphic. These were the Taphana Ectotrophiea. Their evolutionary line is probably represented by the progression Nymphidae—Protapterida—Crabronidae. They must have existed somewhere in the Devonian. At a slightly higher level, they produced a more vigorous type with three-segmented tarsi, exerted mouth-parts, and a more complete tracheal system. These were the Taphana Entrotrophiea. They divided into two main types, the dorso-ventrally flattened running types (Leguminidae) and the laterally flattened jumping types (Machilidae); 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
II. Sub-class
III. Sub-class

PROGONATA. OPISTHOCONATA. INSECTA.

Sub-class...

SYMPHYLA. CHILOPODA. COLLEMBOLA.
PAUROPODA. SCHIZOTARSIA. PROTURA.
DIPLOPODA. PHYTHANURA.
PTERYGOTA.

Note:—The name "Protendomor" 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 protomorph ancestor of all the Myriapoda and Insecta, as here worked out, would be PROTOPTERTIUM. Such a group would have the status of a Class. The term PROTOCOLEMBOLA is a little too specialised, to my mind, and too cumbersome also.

REFERENCES


