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[FROM AMERICAN JOURNAL OF SCIENCE, VOL. XXI, JUNE, 1931.]

DISCUSSION AND COMMUNICATIONS.

THE EVOLUTION OF THE CLASS INSECTA.

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I. THE VIEWS OF A PALEOENTOMOLOGIST.

Doctor Tillyard divides his work into two sections: in the first he attempts to show that the existing theories of the origin of the insects are untenable, and in the second he proposes a new theory designed to explain the descent of the insects more satisfactorily.

The first theory considered is that of Handlirsch, who derives the Pterygota directly from the trilobites, treating the Apterygota as specialized descendants of the winged forms. Tillyard objects to this hypothesis on several morphological points and particularly on paleontological grounds; for the presence of Collembola in the Lower Devonian shows that the Apterygota existed before the Pterygota, which appear in the Upper Carboniferous. The second theory advocates the descent of the insects directly from the Crustacea. This has been advanced in various forms and supported by several investigators, particularly Crampton, who has published a long series of papers on the subject. From the studies of the comparative external morphology of the arthropods, Crampton has attempted to show that the ancestor of the insects was a relative of the Syncarida. Tillyard reviews the evidence and concludes that "*so far*, there appears to be no inherent impossibility that the insects may not have been descended from Syncarida or some closely related group, but that it does not appear very likely." Further on, however, Tillyard claims that the internal morphology of the insects and Crustacea disproves such a relationship. The third theory is generally associated with Versluys, who derives the aquatic arthropods from the terrestrial Onychophora, through the myriopods. His hypothesis is largely concerned with the arachnids, and Tillyard dismisses it briefly, since Versluys admits that the theory is still unsatisfactory to himself regarding the insects and Crustacea. The fourth existing theory is that which derives the insects from the myriopods. This was originally proposed by Brauer, who believed that the larva of the Thysanuran *Campodea* was a representative of the type intermediate between the insects and the chilopods. Associated with this view are several other theories connecting the insects with the Symphyla.

* The undersigned asked Doctors Carpenter, Raymond, and Petrunkevitch to discuss R. J. Tillyard's very valuable paper, "The Evolution of the Class Insecta" (Roy. Soc. Tasmania, Papers and Proc., 1930, pages 1-89), the idea being to get various students of the Arthropoda to express their opinions as to the genesis of these invertebrates. It will be seen that finality along all lines of classification is not yet obtainable, mainly because of the lack of necessary fossil evidence, which may be a long time in coming to light. CHARLES SCHUCHERT.

Tillyard finds the latter explanation the most promising of all those which have been proposed, but rejects it because of the difference in the position of the genital openings in the insects and Symphyla.

The new theory which Tillyard proposes is based upon the acceptance of the four following points: 1) The Apterygota are not descended from original winged forms, but are more primitive than the Pterygota. 2) The Thysanura Ectotrophica are the immediate ancestors of the pterygote insects. 3) The Thysanura Entotrophica are closely related to the Thysanura Ectotrophica and therefore very close to the main evolutionary stem of the Pterygota. · 4) The Collembola and Protura are much further removed from the Pterygota than the Thysanura. His theory is developed as follows:

From a study of the segmental appendages of the Crustacea, Tillyard is led to agree with the usual view that the Crustacea at some time in their past had an ancestor which is now represented in modified form by the nauplius larva, and that what we may call the nauploid ancestor of the Crustacea was essentially a simpler type of arthropod than any other existing crustacean. If we accept the fact that all the Crustacea have been evolved from a nauploid ancestor, we must *a fortiori* accept the fact that all myriopods have also evolved from a simpler ancestral type with few original somites. The appendages and segmentation of the Crustacea and Collembola indicate that the Collembola have "as much right to be classed as Myriopods as the Pauropods." Accordingly, the Pauropoda, Symphyla, and insects have been derived from a common ancestor. From a study of the walking legs in the arthropods, Tillyard finds there is no evidence for the evolution of the walking legs of the terrestrial arthropods from the swimming limb of the marine arthropods; but there is an indication of relationship to the Symphyla. From a viewpoint of the reproductive organs this relationship of the insects with the Symphyla seems improbable, for the former are opisthogoneate, and the latter progoneate. But Tillyard finds that the lines of evolution of the reproductive systems in the progoneate myriopods and insects converge; so that the common ancestor of the two would possess an intermediate type. The respiratory system of the arthropods does not show any evidence that the tracheate arthropods are of monophyletic origin; there is every indication that the terrestrial forms originally breathed directly through the cuticle. The alimentary tract of the insects is closest to that of the myriopods, and the ectodermal Malphigian system is common to the insects and myriopods only. The circulatory system shows no definite relationships, except that the insects' type could not have been derived from that of the Crustacea. Finally, the embryological development of the insects is closest to that of the myriopods.

Briefly, then, Tillyard's theory is that the Pterygota have been descended from the Apterygota, the lowest form of which is the Collembola-type; the Collembola stock have been derived from the progenitor of the chilopods; and this progenitor is a development of the ancestor of the diplopods. The common ancestor of the Diplopoda, Chilopoda, and Insecta, Tillyard calls the "Protaptera."

Expressed in its lowest terms, as above, Tillyard's theory does not seem to be very new. In his treatment of the theories which have been previously advanced, he has omitted reference to several papers, notably those of Kingsley, Heymons, Korscheldt, and Tothill, in which views much like the one he proposes are upheld. Tothill, for example, in his "Ancestry of the Insects" (this Journal, **42**, 373, 1916) concluded that the Pterygota originated from the Apterygota, and that the Apterygota "arose from an ancient Chilopod stock." Aside from mere wording this is the same view as that of Tillyard, who advocates their origin from some unknown form which gave rise to the chilopods. Tothill, also, concluded that the diplopods, being progoneate, were less closely related to the insects than the chilopods, and he likewise placed the Onychophora outside the hexapod complex. In fact, a phylogenetic "tree" based upon Tothill's conclusions would be quite identical with the one which Tillyard uses to illustrate his theory. Tothill assigned no name to the common ancestor of the Diplopoda, Chilopoda, and Insecta, as Tillyard has done (Protaptera); he merely suggests that the common ancestor was "very likely, though by no means certainly, derived from ancient generalized trilobites." In this latter conception he *may* differ from Tillyard; but I have been unable to find any statement in Tillyard's paper as to where he would derive his Protaptera or what relation it had with the nauploid ancestor of the Crustacea. Of course, Tillyard has entered further into the question than the others, and has been able to profit by recent investigations on the subject. But I consider that Tillyard is incorrect in stating that "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"; for Tothill, at least, used as many embryological data as Tillyard has. At any rate, if Tillyard's conception of the relationship between the hexapods and the other existing arthropods is accepted, Tothill and his predecessors should be given due credit for already having expressed the same view.

There are a few minor points on which Tillyard is open to correction. In his discussion of the tarsal segmentation, for example, he states that the Megasecoptera had three tarsal segments; although Lameere has described five segments in some of the Commentry specimens. He also states that the "Plectoptera, both fossil and recent, have five-segmented tarsi"; whereas, as a matter of fact, the number varies in this group from one to five. These particular points may not affect his conclusion.

Regardless of the increased activity during recent years in insect paleontology and related subjects, practically no contribution has been made to the question of the origin of the insects. We are still faced by the fact that the very earliest insects known possess appendages which are like those of existing insects, and which show no approach to those of other arthropods. Unfortunately, also, we know very little of the smaller Crustacea of the early Paleozoic; unquestionable fresh-water deposits have not been found below the Upper Silurian, and it is probably fresh-water arthropods of the Ordovician and Silurian that were particularly concerned with the origin of the insects and other terrestrial arthropods. So much time has elapsed subsequently that all our existing types have become specialized in many ways, while the groups which may have been most intimately involved with the insects have long since been extinct. In my opinion, all theories of the origin of the insects will remain questionable until we know more details of these extinct forms.

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II. THE VIEWS OF A STUDENT OF PALEOZOIC CRUSTACEA.

The student of insects who tries to determine their origin is confronted by a situation hardly paralleled in any other group. The insects are highly specialized for life in the air, yet an attempt must be made to show their derivation from creatures highly specialized for life in the water or on land. If bats were the only known mammals, and vertebrate fossils unknown, we should probably try to show how bats might have been derived from fishes of types now living. The situation would present about the same sorts of problems which now confront the student of the ancestry of insects.

Modern studies of fossil insects, stimulated by the compilations of Handlirsch, have resulted in important contributions to knowledge of the wings. Relationships, as indicated by the venation, are gradually coming to be understood. But unfortunately the study of the comparative anatomy of wings gives no clue to their origin. Some unusually well-preserved specimens of fossil insects do retain parts of the body and of the appendages. These have, however, been interpreted as showing the characteristics of modern representatives of the group. Apparently the oldest Pennsylvanian insect was just as much an insect as any modern form.

This in itself should not, however, be discouraging. The oldest tetrapods are just as completely tetrapods as any modern animal, yet the study of the crossopterygians has pretty nearly solved the problem of the origin of terrestrial vertebrates. The origin of the insects will not be understood until much more is known about the other arthropods of the early and mid-Paleozoic, particularly of the non-marine forms of the Silurian, Devonian, and Mississippian. It is not likely that the study of trilobites or other marine creatures will be of much assistance.

The conditions being such, the entomologist must realize that the solution of his problem awaits the discovery and interpretation of much more material. In the meantime, he can accelerate progress by keeping the question before the attention of paleontologists; by intensive comparative studies, aided perhaps by a little imagination, of the scanty material representing bodies and appendages of Carboniferous and Permian insects; and by deducing the probable anatomy of the ancestor from the morphology of recent insects.

The last is what Tillyard has done in the article now under review, and what Crampton had done by another method and from another standpoint. Studies along these lines by all students having a comprehensive knowledge of insects should be encouraged, but for the present there should be no great amount of competition among the various theories proposed. No decision as to which is correct is possible.

I have been asked to review Doctor Tillyard's paper from the standpoint of one interested in the Paleozoic crustaceans. Handlirsch's theory of the origin of insects from the trilobites receives a very fair presentation, Tillyard showing, in fact, a much more sympathetic attitude toward it than can be achieved by the present writer. His review is important chiefly in that it appears to indicate that some of the fundamentals of trilobitan and, therefore, of crustacean anatomy are not clear in Tillyard's mind. He has produced, with attribution to Beecher, an extremely inaccurate figure of a trilobite showing sternites and appendages, constructed apparently by combining the observations of Beecher with the somewhat fanciful deductions of Jaekel. It should be noted that there is no evidence for the presence of sternites in any trilobite. This figure indicates that the inner end of the protopodite articulates with a basal segment near the median line, whereas there is abundant evidence that the inner ends were free, the real articulation being with an appendifer near the outer end. This is particularly important in tracing the origin of mandibles of insects. There is no reason why they should show any trace of "exopodites, endopodites, or epipodites," if they are modifications of the gnathites of trilobites.

Another and less important point is the insistence on the importance of the pygidium of the trilobite as evidence against their inclusion among the ancestors of the insects. Barrande pointed out, and I have repeatedly stressed, the fact that segments were not fused to form the pygidium of the trilobite. On the contrary, segments were freed from the anterior margin of the pygidium to form the thorax. In several families the pygidium was broken down until it consisted of only the anal segment. Such a trilobite may have been in the ancestral line of the insects.

Tillyard attaches great importance to his determination of the presence of the Collembola in the Devonian Rhynie chert. To me the evidence for that identification is not entirely convincing. The material is very scanty, Tillyard himself stating that only two specimens are of any importance, a fragment of a head showing an antenna 0.254 mm. long, and a minute pair of mandibles. His determination is based almost entirely on the former. The Rhynie chert has produced thousands of fragments of a little crustacean which was described by Scourfield. It seems rather a remarkable coincidence that the antennae of this little creature, *Lepidocaris rhyniensis,* should be so similar to those of the "insect."

The antenna of the supposed collembolid springs from the side of the head, and has been interpreted as having four segments, although Tillyard states that the third and fourth are only imperfectly divided, the suture between them being very indistinct. Hence the appearance is that of a three-segmented antenna. The first segment is the shortest, the outer one (or two?) making up about three-fifths of the total length.

The antenna of the associated crustacean has three segments, the first shortest, and the distal one about half the total length. The latter does not show a transverse suture, but there is a lateral projection which might be taken as an indication of the location of such a suture. It likewise is attached to the head.

There are, to be sure, recognizable differences in the proportion of the parts of the two sorts of antennae, and particularly in the outline of the distal segment. Considering, however, that a crustacean with the same type of antenna, attached in the same way, is known from the same locality as the one called an insect, it appears likely that the appendage belongs to a crustacean rather than to an insect. The reference to the latter class appears to be based merely upon its general appearance. The associated mandibles and jaws also figured by Tillyard may just as well be interpreted as appendages of crustaceans as of insects.

The greater part of that portion of the memoir under review which deals with Crustacea consists of a criticism of Crampton's papers. Since Crampton has, in the absence of fossils, been forced to compare living crustaceans with living insects, too much in the way of connecting links and absolute proof cannot be demanded of him. How, in the absence of fossils, could we connect bats with fish? Crampton has done a very useful piece of work which shows that there is a real possibility that the insects may have been derived from some as yet unknown member of the Crustacea.

The only serious objection to a crustacean ancestor which Tillyard raises is that insects have no second antennae. This objection has real force if an attempt is made to derive the insects from any of the modern crustaceans; Crampton has apparently given up any attempt to do this. It might be mentioned that the hypothetical crustacean ancestor need not have been aquatic. No terrestrial crustacean, a descendant of the trilobites retaining a single pair of antennae, is known, but such may have existed.

With Tillyard's ideas about the segmentation of arthropods, and especially about the possible importance of a mystic number twenty-two (or twenty-one), the present writer is in hearty agreement. To state, however, that the head of the primitive crustacean had only four segments is to pass entirely into the realm of theory. There is no evidence for it beyond the condition found in the nauplius of the modern crustacean. That the nauplius is strictly indicative of the form of the ancestor of the whole group is questionable. We know a simpler larva in the protaspis of the trilobite, compared with which the nauplius as we know it now is specialized. Such evidence as we possess as to the primitive condition of the head of the crustacean is gained from fossils of mid-Cambrian age. In this fauna we have the trilobite *Neolenus* with five pairs of appendanges on the head, the haplopod crustacean *Marrella* with five pairs, the branchiopods *Burgessia* and *Waptia* with five pairs, the xenopod *Sidneyia* with five pairs, and the phyllocarid *Hymenocaris* with five pairs. Although the diversity of crustaceans existing in mid-Cambrian times shows that even that early day was far removed from the time of the primitive crustacean, yet the presence in all these diverse groups of the same number distinctly suggests its primitiveness. One cannot deny, of course, the possibility of the existence of a pre-Cambrian ancestor with only four segments in the head. That its appearance should have been onychophoran does not seem plausible, especially in view of the recent information about *Aysheaia*. (Hutchinson, Proc. U. S. Nat. Mus., **78**, 22, 1930.)

The only other point made by Tillyard on which I shall comment is his query, "Is there any real evidence of descent of the terrestrial uniramous walking leg from the marine biramous appendage of the Trilobites and Crustacea?"

Tillyard does not state his position explicitly, but this is what one gathers:

The ancestor of the trilobites, crustaceans, and eurypterids had appendages consisting of a single segment only (p. 43).

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

Whether by this he means that after the time of the pre-Cambrian ancestor there was a differentiation of arthropods into two lines, one terrestrial, with uniramous limbs, the other aquatic, with biramous appendages, is not clear. At any rate, he appears to have reverted to Walton's theory, which he affects to consider somewhat far-fetched.

It is a question whether any deduction from comparative morphology can be proved. All that we know is that parallelisms are seldom exact. No one who has any real knowledge of the paleontological evidence will question that terrestrial arachnids with uniramous limbs arose from aquatic forms with biramous appendages. Unless all inferences from the structure of insects and myriopods are at fault, it will be extremely difficult to prove that terrestrial and aquatic arthropods have pursued different paths of evolution since the beginning of the Cambrian. According to Tothill (this Journal, 42, 373-387, 1916), the rudiments of the first and second maxillae of the embryos of insects are bifurcated, and may indicate that these appendages at least were probably biramous in the ancestor of the insects.

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III. REFLECTIONS ON THE EVOLUTION OF THE ARTHROPODS, BY A STUDENT OF LIVING AND FOSSIL ARACHNIDS.

Tillyard's theory is a substantial contribution to the problem of the evolution of the arthropods, even though it deals primarily with the class Insecta. If their relationship to other classes of arthropods were more clearly understood, and if their origin were explained in a satisfactory manner, the origin of the other classes would become less of an enigma. Tillyard has brought together in juxtaposition the characters of all classes of arthropods and included in his analysis all external and internal structures. His recognition of three types of postcephalic segmentation in arthropods (p. 49) and his separation of the insects from the classes commonly comprised under Myriopoda are well grounded. Unfortunately, though naturally, in discussing segmentation Tillyard follows the usual method of homologising segments in accordance with their numerical position relative to the first cephalic segment. Is this principle correct? Most students of arthropods accept it without reservation. Yet if it could be shown that there are exceptions to it, the validity of the principle itself would be greatly impaired. We know so-called evanescent segments. They are usually interpreted as segments which have been once present, but have been subsequently lost. Now, the same segments could be interpreted as abortive attempts at the formation of *new* segments. Buxton and I have shown independently that a new segment is formed in the scorpion through a subdivision of an embryologically single somite. Moreover, in the case of vertebrates the numerical value of a segment is quite useless, would make it impossible to homologise such a structure as the shoulder-girdle even within the limits of the same class, and is not considered to be a valid objection under any circumstance. In considering segmentation in arthropods there is an added difficulty of deciding *what is* and *what is not* a segment. Thus Tillyard considers the first segment in all arthropods to be the ocular one. But I have tried to show that the median eyes of spiders and their lateral eyes belong to two different segments, and Schimkewitsch has shown the presence of a median and two pairs of parietal ganglia in spider embryos. It appears, therefore, that the head of arachnids is composed, not of four segments as Tillyard assumes, but of five and possibly of eight. In view of such difficulties it would be a real step forward if it were possible to find truly homologous structures in arthropods, regardless of their numerical position. I have tried to show that the cardio-aortic valve may be recognized as such a structure. Perhaps it will be possible some day to establish the homology of other structures, especially if we bear in mind what seems to be a general principle, namely, that the least useful structures are the ones which are also least subject to evolutionary change. Witness the disposition of spines and bristles.

The inclusion of Tardigrada in the phylum Arthropoda is unfortunate inasmuch as neither their structure nor their development shows truly arthropod features. The inclusion of Xiphosura and Pycnogonida in the class Arachnida is also unfortunate. It is better to raise both to the rank of separate classes because of the many peculiar features proper to them and not encountered in any known Arachnida.

Tillyard's paper has the value more of an analysis and criticism of former theories than of a working hypothesis. Not until a new principle underlying homologous structures and segmentation in arthropods will be found, can we hope to unravel their evolution.

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