NOTES ON THE RELATIONSHIPS INDICATED BY THE VENATION
OF THE WINGS OF INSECTS.

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(Continued from page 216)

I have pointed out the close resemblance between the Zoraptera and the Psocids in several papers (Crampton, 1921 and 1922) and I would now definitely place the Zoraptera in the order Psocida, assigning to the Zorotypoidea the rank of suborder, or superfamily. The discussion of the origin of the Zoraptera would therefore resolve itself into the question of the origin of the Psocids in general, since what applies to one branch of the Psocids applies to all. A comparison of the wing of the Psocid shown in Fig. 32 with that of the Protorthopteron shown in Fig. 34 would indicate that the Psocids and Protorthoptera are extremely closely related, and in all probability the line of descent of the Psocids branched off from the common stem of the Protorthoptera and Protoblattida. This view is in harmony with the fact that the wings of certain Psocids are suggestive of the type occurring in some Blattids (compare Fig. 65 with Fig. 64) since the Blattids also arose from the common Protorthopteron-Protoblattid stem, and much the same tendencies (i. e. the same genes, determinants, or factors) could enter both the Psocid and Blattid lines of descent, having been inherited from their common ancestry. The wings of the Zoraptera are quite suggestive of a relationship to the Isoptera (and the venation of other Psocids is rather faintly suggestive of Isopteron affinities) and this also would indicate that both Psocids and Isoptera were descended from ancestors very like the Protorthoptera (with the Protoblattida.) The resemblance between the wing of the Psocid shown in Fig. 32, and that of the Mixotermiteoid shown in Fig. 13 may be due to their mutual relationship to the Protorthoptera, but it is quite possible that the point of origin of the Psocid line of development may have been quite close to the point at which the Mixotermiteoid line of development branched off from their Protorthopteron-like ancestors, and the resemblance would therefore be due to consanguinity, rather than to "convergence." The marked resemblance between the wings of such Psocids as *Zorotypus* and the Embiids (with the Plecoptera) has been discussed in several papers (Crampton, 1921 and 1922) and, although both *Zorotypus* and the Embiids are closely related to the Protorthoptera, the resemblance between them is not due solely to their mutual relationship to the Protorthoptera, but is due to a more direct relationship between the Psocids and Embiids (with the Plecoptera), and it is extremely probable that the line of descent of the Psocids branched off near the base of the common Protoblattid-Protorthopteron stem very close to the point of origin of the common ancestors of the Embiids and Plecoptera; and the insects related to the Blattids (with the Isoptera) "took their origin" very near this point also.

The Psocids, Mallophaga, Pediculids, Thysanoptera, and Hemipteroid insects (i. e. Hemiptera and Homoptera) have been grouped in a single superorder, the "Panhomoptera," and a study of the venation of the groups in question would lend weight to the correctness of this grouping. The Psocids were

evidently descended from ancestors very like the Protorthoptera, (with their allies the Isoptera) and the Thysanoptera were apparently descended from ancestors resembling the modified descendant of the Protorthoptera shown in Fig. 35, as may be seen by comparing Fig. 33 with Fig. 35. The mutual resemblance between the wings of certain Psocids and the Thysanoptera has been discussed elsewhere (Crampton, 1922) and need not be described here, so that it is not necessary to do more than call attention to the fact that the relationship between the Psocids and the Thysanoptera is more direct than through the mediation of their mutual relationship to the Protorthoptera (and the Orthopterous descendants of the Protorthoptera.) The Pediculids are apparently quite closely related to the Mallophaga, (and Platypsyllid Coleoptera also) though both are wingless groups, and nothing is known of their more direct winged ancestors, though both were doubtless derived from Psocid-like forms, as is indicated by their general body characters. The Mallophaga in particular are extremely like Psocids in the character of their head structures, thoracic plates, etc., but they are also astonishingly like the members of the Coleopterous group Platypsyllidae in certain respects (and they also have certain features in common with the Hemimerid family of the Dermaptera.) If the Psocids, Dermaptera and Coleoptera are all to be derived from Protorthopteroid ancestors, this complicated interrelationship of the Mallophaga to all of these orders is readily comprehensible; but if this view is inadmissible, the resemblance between the Mallophaga and the Hemimerid Dermaptera, for example, must be regarded as a result of convergent development due to the selective action of similar environmental conditions (ectoparasitism.)

Judging from their general structure, the Thysanoptera are more closely related to the Hemipteroid insects than to the Psocids, but since the Psocids themselves are quite closely related to the Hemipteroids the dual relationship of the Thysanoptera to the Psocids and to the Hemipteroids is quite readily comprehensible. The remarkable parallelism in the venation of a long series of Psocids and Homopterous Hemipteroid insects has been discussed in a previous paper (Crampton, 1922) and the Psocids parallel the Homoptera so closely that it would be very appropriate to designate the Psocids as "Parahomoptera" rather than as "Psocoptera," as is done by certain recent entomologists—especially since all of the Psocoptera are not *Psocus*-winged (e. g. the wings of *Embidopsocus* are nothing like those of *Psocus*) and the designation "Psocoptera" is not at all appropriate for such Psocids as these, while even *Embidopsocus* parallels the venation of certain Homoptera, as was pointed out in the article referred to above.

Since the wings of the Psocids parallel those of the Homoptera so remarkably closely (apparently due to the inheritance of many common genes, determinants or factors from a common source) we would expect that if the Psocids were derived from ancestors closely related to the common Protorthopteron-Protoblattid stem, the Homoptera would also be derived from ancestors extremely similar to these forms, and indeed, certain Homopterous wings are very suggestive of those of certain Protorthoptera, while such a Homopterous wing as the one shown in Fig. 58 approaches quite closely that of the descendant of the common Protorthopteron-Protoblattid stem shown in Fig. 59, and a surpris-

ingly large number of anatomical features of Hemiptera are "Blattoid." In fact, it would be quite impossible to derive such a type as the Homopterous wing shown in Fig. 58 from that of *Eugereon* (Fig. 41) which is supposed to represent the type ancestral to the Homoptera and Hemiptera (Heteroptera), so that it is much more probable that the ancestors of the Homoptera and Hemiptera were very like the common Protorthoptera-Protoblattid stem, and the common ancestors of the Homoptera and Hemiptera apparently arose at the point where the common stock of the Protorthoptera and Protoblattida began to diverge from the Palaeodictyoptera, and *Eugereon* doubtless branched off from the same point, or very near it. *Eugereon*, however, is more like the Palaeodictyoptera (compare figs. 41 and 30), and it possibly may be regarded as a specialized Palaeodictyopteron. In stressing the close relationship of the primitive Homoptera to the common Protorthopteron-Protoblattid stock, I would not minimize the fact that the Homoptera have also taken over traits from the Palaeodictyoptera into their line of development, but these are to be regarded more as persistent features coming up from the common stock which gave rise to both Palaeodictyoptera and the Protorthoptera-Protoblattida—and the Homoptera apparently arose at the point where these two lines began to diverge from their common ancestry. The line of development of the Megasecoptera also apparently branched off near this point, so that the ancestors of the Homoptera were doubtless related to the Protoblattid-Protorthopteron stock, and to the Megasecoptera, Protohemiptera and Palaeodictyoptera as well. The line of development of the Hemipteroids, however, apparently parallels that of the Protoblattid-Protorthopteron stem and the forms descended from it such as the Psocids, etc. and the Hemipteroids also approach the Neuropteroid types (which were derived from a similar source) in many respects.

The Psocids, and their allies the Hemipteroids, etc., parallel the Neuropteroid insects quite closely in many respects, as was mentioned above, and I am convinced that this parallelism is due to the inheritance of the same genes, determinants or factors (albeit these are modified by differing factors in the different orders) from a common source, rather than that the marked resemblance between the forms in question is due to "convergence" (i. e. the similarity is the result of consanguinity rather than to the operation of similar environmental influences). The resemblance between the wings of the Homoptera and the Lepidoptera is well known, and the similarity between the wing of the Psocid shown in Fig. 32 and that of the Lepidopteron shown in Fig. 54 is unmistakable. The resemblance between the Psocid shown in Fig. 32 and the Trichopteron shown in Fig. 25 is quite marked, and the resemblance between the Psocid, Homopteron and Trichopteron wings shown in Figs. 40, 39 and 38 is very striking, as is also the resemblance between the wing of the Homopteron shown in Fig. 36 and the Trichopteron shown in Fig. 37 (or the Mecopteron shown in Fig. 52). The most instructive and important resemblance, however, is that between the Psocid shown in Fig. 65 and the Hymenopteron shown in Fig. 66, and when these two wings are compared together, and that of the Hymenopteron shown in Fig. 66 is compared with the Homopterous wing shown in Fig. 68, it would appear very probable that the veins interpreted as the fourth and fifth branches of radius in the sawflies, are merely cross veins between the radial

sector and media. Similarly, a comparison of the median and cubital veins in Figs. 66 and 65 would suggest a different interpretation of these veins in the sawflies than the one usually accepted. The venation of certain Psocids (Fig. 40) is very suggestive of that of certain Neuroptera (compare Fig. 40 with Fig. 51; Fig. 31 with Fig. 28, etc.) and Coleoptera, as is also true of certain Homoptera. From the foregoing, it should be quite evident that the lines of descent of the Psocids and their allies the Homoptera, parallel the lines of descent of the insects descended from Neuroptera-like forbears, quite closely, and the forms allied to the Psocids were probably derived from a common source with the Neuropteroid insects (i. e. from Protorthoptera-like forbears.)

I have grouped the Neuroptera, Coleoptera, Strepsiptera, Hymenoptera, Mecoptera, Diptera, Siphonaptera, Trichoptera and Lepidoptera into a superorder called the "Panneuroptera," which corresponds to the Holometabola, or to the Endopterygota of various investigators, and I have here retained the term Panneuroptera merely for the sake of a uniform method of designating the superorders in general. Although the body structures of the adult Coleoptera and Hymenoptera are somewhat more primitive than those of the Neuroptera in general, the Neuroptera have nevertheless retained the wings in a condition more closely approximating the original state for the superorder as a whole, and since the members of the superorder Panneuroptera were all evidently derived from the same (or nearly the same) source, the venation of the Neuroptera may be used to illustrate the origin of the members of the superorder indicated by a study of their wings—which are the only features sufficiently well preserved to compare the structures of their fossil precursors with those of their modern descendants. The wing of the Neuropteran shown in Fig. 53 is strikingly like that of the Palaeodictyopteron shown in Fig. 56, and the ancestors of the Neuroptera were undoubtedly like the Palaeodictyoptera in many respects—but this is not the whole story, since the Neuropteran shown in Fig. 20, for example, exhibits many Protoblattid and Protorthopteran features (compare it with Figs. 11, 15, 19, etc., or Fig. 53 with 55, etc.) which cannot be passed over in silence. The only logical explanation for this dual resemblance in fundamental details, is that the line of development of the Protorthoptera-Protoblattida began to diverge from that of the Palaeodictyoptera, as both emerged from their common ancestral group, which in turn was derived from ancestors which combined in themselves the primitive characters of the Palaeodictyoptera, Protodonata, etc. Not only did the Neuroptera arise at the point where the Protoblattida-Protorthoptera began to diverge from the Palaeodictyoptera, but the ancestors of the Isoptera doubtless also arose at or very near this same point (as is also true of the origin of the lines of development of several other forms, such as the Plecoptera, the Megasecoptera, and probably the Synarmogoida, and even the common ancestors of the Hemiptera-like forms) and this doubtless accounts for the fact that the neururation of such a Neuropteran as the one shown in Fig. 16 resembles that of the Isopteran shown in Fig. 12 so closely (if the form in question is really a Neuropteran as Handlirsch and others claim) since all of these have inherited many genes, determinants or factors from a common source, and this causes their lines of development to parallel each other very closely. Whether this explanation is valid or not, the fact

remains that the lines of development of the Neuroptera and their immediate relatives very closely parallel those of such insects as the Protorthoptera, which were descended from the common Protoblattid-Protorthopteran stock, and the explanation given above is as logical as any, since it takes all of the known facts of comparative anatomy into consideration, and none of these facts would militate against this view.

The Dermaptera were apparently descended from the common Protorthopteran-Protoblattid stem, and their line of development parallels that of the Protorthoptera and the Orthoptera remarkably closely. Similarly, the wings of certain Coleoptera are strongly suggestive of those of certain Protorthoptera (e. g. *Probuvis speciosa*). I do not find much support, however, in the study of the known types of wings in the two groups for my contention that the Coleoptera and Dermaptera are very closely related (which is based upon a comparison of the general structures of the body), although I feel certain that the relationship between the Coleoptera and the Dermaptera is much more intimate and direct than through the intermediation of their mutual relationship to the Orthoptera and the Protorthoptera. The larvae of the Coleoptera are so like those of the Neuroptera that I have been unable to find any character which will unfailingly distinguish between the two in every case, and the venation of the Coleoptera (fig. 72) is certainly in harmony with the view that the Coleoptera are extremely closely related to the Neuroptera* (fig. 69) —and the usually accepted view that the Holometabola are a natural assemblage is apparently correct. Since the Coleoptera are the next of kin to the Neuroptera and Hymenoptera, the line of development of the Coleoptera (which branched off at the base of the common Holometabolous stem), like that of the Neuroptera, should arise at the point where the line of development of the Protorthoptera-Protoblattida began to diverge from that of the Palaeodictyoptera, but I have not been able to find any Palaeodictyoptera which approach the Coleoptera remarkably closely in their wing venation, and the line of development of the Coleoptera must apparently be regarded as paralleling that of the descendants of the original Protorthopteran-Protoblattid stock on the one side, and the Holometabola on the other—with their closest affinities with the Holometabola in general and the Neuroptera and Hymenoptera in particular. The relationship of the Coleoptera to the Psocids and Homoptera, or to the Plecoptera and Embiids, is not readily apparent from a comparison of the wings available for study (although such Psocids as *Sphaeropsocus kuenowi*, for example, resemble the Coleoptera in some respects) and the relationship of the Coleoptera to these forms (and to the Blattids and Isoptera as well) can be more profitably discussed with other features than the wing veins.

The resemblance between the wings of the Hymenoptera and the Psocids and Homoptera (compare Figs. 66 and 65) has already been discussed (as has also the resemblance between the wings of certain Neuroptera and Psocids), but the closest affinities of the Hymenoptera as indicated by their wing venation

*Since the foregoing was written, Dr. Forbes has shown me some of his figures of Coleopterous venation which very clearly indicate a close relationship between the Coleoptera and the Neuroptera, and he also called my attention to the fact that Fig. 72 which was based upon a figure by Handlirsch, does not accurately represent the condition of the cross veins etc., in *Omma*.

(Figs. 66 and 67) in addition to other features, lie with the Neuroptera (Figs. 69 and 51) and Coleoptera (fig. 72). The evidence of the venation etc., might therefore be taken to indicate that the Hymenoptera, with the Neuroptera and Coleoptera, arose from ancestors whose lines of descent sprang from the point where the common Protorthopteran-Protoblattid stem began to diverge from the Palaeodictyoptera (although no Palaeodictyopterous types which approach the Hymenoptera very closely have yet been found—though the Palaeodictyoptera approach the Hymenoptera's near relatives, the Neuroptera, very closely), and the line of descent of the Hymenoptera parallels that of the Psocids and other forms descended from the common Protorthopteran-Protoblattid stock on the one side, and the Holometabolous types on the other—with their closest affinities with the Holometabola in general, and the Neuroptera and Coleoptera* in particular. The Coleoptera, Neuroptera and Hymenoptera appear to be the most primitive representatives of the Holometabola, and of these, the Coleoptera are a rather aberrant group not as closely related to the higher Holometabola as the Neuroptera and Hymenoptera are, in certain respects. The ovipositor of such Hymenoptera as *Xyela* is astonishingly like those of the Neuropteran *Raphidia*, but the genitalia of male sawflies are extremely like those of male Mecoptera and Diptera (and somewhat less like those of male Trichoptera and Lepidoptera). The Hymenoptera are a cerci-bearing group, while the Neuroptera are not, and the larvae of sawflies are rather more suggestive of those of the Trichoptera and Mecoptera which are cerci-bearing groups, so that in these and certain other particulars, the Hymenoptera appear to lead to the Mecopteroid Holometabola (i. e. the Mecoptera, Diptera, Siphonaptera, Trichoptera and Lepidoptera), but on the whole, I am somewhat more inclined to regard the Neuroptera as slightly nearer the precursors of the Mecopteroid Holometabola than the Hymenoptera are. The venation of the wings of certain Homoptera is extremely like that of certain Hymenoptera (as has been mentioned before) and the ovipositor and terminal segments of a Cicada are extremely like those of the Hymenopteran *Sirex*, for example; similarly, the wings of the Psocids are very like those of certain sawflies (as was mentioned before) and the general characters of the Psocids are very suggestive of affinities with the sawflies (and their relatives the Neuroptera). There are also resemblances between the Hymenoptera and the Embiids (with their relatives the Plecoptera); and the Blattids, and their relatives the Isoptera, are apparently extremely like the ancestors of the Hymenoptera. How can we account for this complicated interrelationship indicated by many features of the body, and supported by the evidence of the wing-venation as well? The only satisfactory answer so far as I can see, is to admit that all of these forms arose from ancestors occupying a position at or near the point where the common Protorthopteran-Protoblattid stem began to diverge from the Palaeodictyoptera. This view would be supported by the evidence of the wing-venation, and would be in harmony with a great number of facts which cannot be explained on any other grounds, so that in the absence of any

*The head capsule, neck plates, terga, ovipositor, etc., of certain Hymenoptera are astonishingly like those of certain Neuroptera, while the mouthparts, male genitalia, etc., of the Hymenoptera are more like those of the Coleoptera, and the same is true to some extent, of the wings.

known facts which would tend to controvert it, I feel that we are safe in adopting this view.

As was mentioned above, the Mecopteroid Holometabola (i. e. the Mecoptera, Diptera, Siphonaptera, Trichoptera and Lepidoptera) are slightly more closely related to each other than they are to the Neuropteroid Holometabola (i. e. the Hymenoptera, Neuroptera and Coleoptera), and their closest affinities are possibly with the Hymenoptera and Neuroptera, while the Coleoptera are slightly further removed from them in many anatomical features. Tillyard, 1919, seems to be inclined to regard the Mecoptera as the nearest living representatives of the types ancestral to the Holometabola in general, but from a study of the general anatomy of the forms in question, I am more inclined to regard the Coleoptera, Neuroptera and even the Hymenoptera, as more primitive (anatomically) than any Mecoptera I have studied, although everyone who has gone into the matter at all deeply will readily admit that the Mecoptera have remained as primitive as any of the *higher* Holometabola (i. e. the Diptera, Lepidoptera, Trichoptera, etc.) in most of their external features at any rate.

Tillyard, 1919, would derive the primitive Lepidopterous venation shown in Fig. 54 and the primitive Trichopterous venation shown in Fig. 37, from that of the insect shown in Fig. 52, which he calls a "Paramecopteran"; and he would derive the primitive Dipterous venation shown in Fig. 61, from that of the insect shown in Fig. 60, which he calls a "Paratrichopteran." If the "Paramecoptera" and "Paratrichoptera" of Tillyard actually represent distinct orders (which I seriously doubt) it would be preferable to call the insect shown in Fig. 60 a "Paramecopteran" (instead of a "Paratrichopteran") since its venation is so nearly identical with that of other Mecoptera (such for example as the one shown in Fig. 57) that it does not seem worth while to place it in a distinct order from the Mecoptera, especially since the wings are the only anatomical features known. Similarly, it would be preferable to call the insect shown in Fig. 52 a "Paratrachopteran" (instead of a "Paramecopteran") if it is to be considered as representing a distinct order, since its venation parallels that of the Trichopteran shown in Fig. 37, for example. The insect shown in Fig. 52, however, is so much like the insects which Tillyard calls "Protomecoptera" and the primitive Mecopterous types, that I am inclined to regard it also as a primitive representative of the order Mecoptera. If the view that the so-called "Paramecoptera" and "Paratrachoptera" are merely types of Mecoptera is correct, Tillyard's derivation of the Lepidoptera, Trichoptera, and Diptera is quite in accord with the views of others who have also derived the Lepidoptera, Trichoptera and Diptera from Mecopterous, or Mecoptera-like forbears. I cannot help but feel, however, that the ancestors of the Trichoptera, Lepidoptera, Diptera, etc., were not pure Mecoptera alone, but that the ancestors of some of these at least, were more of the nature of the common ancestors of the Mecoptera and Neuroptera (with the Hymenoptera.) Thus, for example, the primitive type of Lepidopterous wing shown in Fig. 54 might very readily be derived from a type of wing essentially like that of the Neuropteran shown in Fig. 51 (and many features of the body in general would bear out this assumption), and certain features of the Diptera, for example, point to a very close relationship between them and the Neuroptera (with the Hymenoptera) as well as the Mecoptera, and many

other facts would indicate that the ancestors of the higher Holometabola were pre-Mecopterous forms combining in themselves Mecopterous, Hymenopterous, and Neuropterous features, rather than that the ancestors of the higher Holometabola were simple Mecoptera. Insects which have retained certain anatomical features in a primitive condition are frequently fairly highly specialized in other anatomical features, and until more is known of the general anatomy of *Belmontia*, it would be unwise to attempt to derive all of the higher Holometabola from the insect whose wing is shown in Fig. 52, especially since a study of the body in general (e. g. head and mouthparts of Micropterygid Lepidoptera, etc.) would point to an ancestry for many of the higher Holometabola in forms which are fundamentally more primitive than the Mecoptera (to which group I believe that the insect shown in Fig. 52 belongs.) The line of development of the Diptera parallels that of the Mecoptera remarkably closely, and the two apparently merge as we trace them back to a common source, and in the same way, the line of development of the Lepidoptera parallels that of the Trichoptera remarkably closely, and these two lines of descent also appear to merge as we trace them back to their common ancestry. The lines of descent of the higher Holometabola mentioned above, parallel each other extremely closely, and as we trace them all back to their common source, they are joined by the lines of descent of the Hymenoptera, Neuroptera, etc., and all of these apparently lead back to ancestors occupying a position at or near the point where the common stem of the Protorthoptera and Protoblattida began to diverge from the Palaeodictyoptera. Since the lines of development of the Psocids and Homoptera arose at the same point, both of these groups could readily exhibit characters in common with the Lepidoptera and Trichoptera, having inherited the same tendencies from their common ancestry—and the Protorthoptera have apparently retained more of the characters of this common ancestry than any other group of insects. It would be possible to group the higher Holometabola (i. e. the Mecoptera, Diptera, Lepidoptera, Trichoptera, etc.) in a superorder (Panme-coptera) distinct from the lower representatives of the Holometabola, but it is preferable to group them all in a single Holometabolous group (Panneuroptera) including the Neuroptera, Coleoptera, etc., as well.

The Strepsiptera are a type of Holometabolous insects whose affinities are rather difficult to determine, although the usual view that they are closely related to the Coleoptera is doubtless correct. There are a few points of resemblance between the wings of the Strepsiptera and those of certain Trichoptera, as may be seen by comparing Fig. 74 with Fig. 73, and in their general anatomy they also exhibit some Hymenopteroid features. Many features of the body (particularly of the abdominal region) of the Hemipteroid insects are extremely suggestive of a relationship to the Strepsiptera, and the wing of the Hemipteroid insects shown in Fig. 75 resembles that of the Strepsipteron shown in Fig. 74 in some respects, while the venation of the Hemipteroid insect shown in Fig. 71 is even more similar to the Strepsipteron shown in Fig. 74. The Psocids also approach the Strepsiptera in certain features. The venation of the Coleopterous wing shown in Fig. 70 is somewhat suggestive of the Strepsiptera (Fig. 74), but the resemblance is not very striking, and the relationship between the Strepsiptera and the Coleoptera is better illustrated by the character of the larvae, and cer-

tain features of the adult anatomy. The wing of the modified descendant of the Protorthopteran-Protoblattid stem shown in Fig. 48 exhibits certain features suggestive of a relationship to the Strepsiptera (Fig. 74), but it is quite possible that any resemblance between the venation of the Strepsiptera and Dermaptera is due to their mutual relationship to the Coleoptera—for I still believe that the Coleoptera are closely related to the Dermaptera as well as to the Neuroptera, since they are anatomically intermediate between the two in their general body structures, although the wings available for comparison do not show this very strikingly. It is very probable that the line of development of the Strepsiptera branched off near the base of the Coleopteron stem, and took over in its line of development certain features inherited from the ancestors of the Coleoptera, which occupied a position close to the common stem of the Protorthoptera and Protoblattids, and were therefore related to the Dermaptera also, since these branched off from the common Protorthopteran stock at the point where the line of development of the Coleoptera arose. Any resemblance between the Strepsiptera and the Hemipteroid insects, is possibly due to the inheritance of common factors from their forbears in or near the common Protorthopteran-Protoblattid stock from which they all arose, although the resemblance between the Strepsiptera and Trichoptera is apparently due to a more direct connection than through the intermediation of the Protorthopteroid forms.

The foregoing facts may be briefly summarized as follows. Of the higher insects, the Mecoptera, Diptera, Siphonaptera, Trichoptera and Lepidoptera are extremely closely related, as are the Neuroptera, Coleoptera (with the Strepsiptera?), and Hymenoptera, and all of these insects form a natural group of Neuropteroid insects comprising the superorder *Panneuroptera* (also called Sialomorpha or Sialoformia) corresponding to the Holometabola or Endopterygota of entomologists in general.) Of the remaining higher insects, the Psocids (Parahomoptera), which are here regarded as including the Zoraptera as a suborder or superfamily of the Psocids, the Mallophaga (Lipoptera), and Pediculids (Ellipoptera), are quite closely related, and the Hemiptera, with the Homoptera, are quite closely related to the Thysanoptera, and all of these have been grouped in a Hemipteroid or Psocid superorder called the *Panhomoptera* (also called the Psocomorpha or Psociformia). The lines of development of these Neuropteroid and Psocid superorders parallel one another so closely (due to the inheritance of many factors in common from their forbears, which occupied a position intermediate between the Protoblattid-Protorthopteran stock and the Palaeodictyoptera) that it has seemed advisable to group them all in a larger subdivision of winged insects called the "*Neuropteradelphia*," which comprises all of the so-called higher insects. In most of these "higher" insects, the fore wings are larger than the hind ones, and most of them exhibit no marked tendency toward development of an anal fan. Wings held along abdomen when at rest.

The Blattids (Palaeoptera) and Mantids (Eudictyoptera) are so closely related that they are placed in a single order called the "Dictyoptera" (a term originally applied to the Neuroptera and Odonata) by some recent investigators, and it is largely a matter of personal preference whether they are divided into two orders, or are grouped into one, although if their immediate relatives, the Isoptera, are regarded as a distinct order, they also may be regarded as represent-

ing two distinct orders. The Blattids, Mantids, and Isoptera have been grouped into a Blattoid superorder called the *Panisoptera* (Blattomorpha or Blattiformia), and the Protoblattids (Propalaeoptera) are also placed in this superorder provisionally. The saltatorial Orthoptera (with which the Grylloblattids may be included) are extremely closely related to the Phasmids (Cheleutoptera), and, with the Dermaptera, these three types have been grouped into an Orthopteroid superorder called *Panorthoptera* (Gryllomorpha, or Grylliformia.) The Protorthoptera are so closely related to the Orthoptera, that they might also be included in this superorder. If the Protorthoptera are grouped with the members of the Orthopteroid superorder, and the Protoblattids are grouped with the Blattoid superorder, it is evident that the lines of development of the lowest representatives of the two superorders (i. e. the Protoblattids and Protorthoptera) quickly merge as we trace their lines of descent a little further back, and this might be taken to indicate that it is preferable to combine the two superorders into a single Orthopteroid superorder (*Panorthoptera*.) The Plecoptera and Embiids (Platyptera) are so closely related that they have been grouped in a Plecopteroid superorder called the *Panplecoptera* (Perlomorpha or Perliformia), and the fossil Hadentomoids (Proplatyptera) might also be grouped in this superorder, but it is preferable to wait until more is known of these fossil forms before attempting to determine definitely where to place them. The Blattoid, Orthopteroid and Plecopteroid superorders are so closely related that it is advisable to group them into a division of winged insects called "*Orthoptera-delphia*." In the members of this group, the fore wings are usually smaller than the hind wings. There is a tendency toward development of an anal fan, and the wings are capable of being folded along the abdomen.

The Ephemera (Archiptera or Plectoptera) have preserved in their "larval" stages, certain features which indicate that they are among the most primitive of living Pterygota, and with the Odonata (Pseudoneuroptera or Paraneuroptera) they constitute a primitive group of insects which branched off from the Pterygotan stem at an early period, to follow their own paths of specialization. Although the Ephemera are not as closely related to the Odonata as might be expected from certain resemblances to the Thysanoura, which both exhibit, the Ephemera and Odonata may be grouped in the Ephemeroïd superorder *Panarchiptera* (Ephemeromorpha or Ephemeriformia), for the sake of convenience. The Protodonata would also be included in this superorder, since they appear to be merely primitive Odonata, hardly worthy of ordinal rank. The Protephemera (Protarchiptera) are so closely related to the Ephemera that they might possibly be placed in the same superorder with them, but it is preferable to wait until more is known of the fossil forms before attempting to group them definitely. The Palaeodictyoptera were formerly placed in the Ephemeroïd superorder, but it is preferable to place them in a Palaeodictyopteroid superorder (*Panpalaeodictyoptera*) which would probably also include the Synarmogoida etc., but so little is known of the fossil forms, that much more investigation is needed before we are able to group them definitely. The Ephemeroïd superorder and the Palaeodictyopteroid superorder constitute the division of winged insects called "*Archipteradelphina*." The wings of the members of this division tend to remain subequal in size, and are usually incapable of being

folded along the body (i. e. are held out from the body when at rest.) True anal fan lacking in practically all of these insects.

If we were able to make a detailed study of the immediate precursors (or even the earliest representatives) of the various orders of living insects, they would doubtless exhibit so many features in common, that it would be extremely difficult to separate them into well defined superorders, and even when we are dealing with living insects alone, the persistence of "synthetic" types, or forms annectant between several orders, makes it very difficult to determine the group with which the forms in question have their closest affinities. The wings of some of the fossil forms sufficiently well preserved for study, combine in themselves so many features common to a large number of recent orders, that when these fossils are included in any grouping of insects into superorders or larger divisions, these groupings are found to intergrade because of the fact that some of these intermediate fossil forms might as readily be included in one group as another, and it is only when we restrict our consideration to living forms alone, that the superorders and divisions are at all clearly defined. In fact, it would be entirely possible to use a different method of grouping insects than the one proposed above, but the grouping of winged insects into the higher orders (Neuropteradelphia), lower orders (Orthopteradelphia) and archaic forms (Archipteradelphia) emphasizes the fact that the lines of development of some "hang together for a longer time" than others do, in "travelling along the road to specialization," and I have attempted to give expression to the same idea in grouping the members of these divisions into superorders.

The appended diagrams will serve to illustrate graphically the lines of descent of the principal orders of winged insects, which have been represented in three groups for the sake of simplicity, since if all were given in one figure, there would result a confusing crossing of lines, since the various lines of descent converge from three different directions forming a "bush-like" figure represented as though drawn "in three dimensions," and it is preferable to simplify such a figure by giving its component parts in three sections, as represented in the diagrams. The "Prodictyoptera" are the common ancestors (or common stem) of the Protorthoptera and Protoblattids; the designation "Prodictyoptera" is used for the sake of brevity in the diagrams.

ABBREVIATIONS.

C. ...Costal vein; Sc. ...Subcostal vein; Rs. ...Radial sector; R₁, R₂, R₃, R₄, and R₅. .Branches of Radial Vein; M₁, M₂, M₃ and M₄. .Branches of Median vein; Cu. ...Cubital veins; A. ...Anal veins.

EXPLANATION OF PLATES.

- Fig. 1. Forewing of fossil Megasecopteran *Corydaloides scudderi*, redrawn from Handlirsch, 1908.
- Fig. 2. Forewing of fossil Orthopteron *Locustopsis elegans*, redrawn from Handlirsch, 1908.
- Fig. 3. Forewing of fossil Synarmogoidan *Synarmoge ferrarii*, redrawn from Handlirsch, 1920.
- Fig. 4. Forewing of fossil Sypharopteroidan *Sypharoptera pneuma*, redrawn from Handlirsch, 1920.
- Fig. 5. Forewing of fossil Protorthopteron (?) *Elcanopsis sydenienis*, redrawn from Tillyard, 1918.
- Fig. 6. Forewing of Protorthopteron *Limopterum ornatum*, redrawn from Handlirsch, 1920.
- Fig. 7. Forewing of fossil Reculoidan *Recula parva*, redrawn from Handlirsch, 1920.
- Fig. 8. Forewing of Plecopteran *Isogenus* sp., redrawn from Comstock, 1918.
- Fig. 9. Forewing of fossil Hapalopteroidan *Hapaloptera gracilis*, redrawn from Handlirsch, 1920.
- Fig. 10. Forewing of fossil Mantid *Petromantis rossica*, redrawn from Handlirsch, 1908.
- Fig. 11. Forewing of fossil Protorthopteron *Gyrophlebia longicollis*, redrawn from Handlirsch, 1920.
- Fig. 12. Forewing of Isopteran *Hodotermes mossambicus* redrawn from Handlirsch, 1908.
- Fig. 13. Forewing of fossil Mixotermitoidan *Geroneura wilsoni*, redrawn from Handlirsch, 1908.
- Fig. 14. Forewing of fossil Mantid *Palaeomantis schmidtii*, redrawn from Handlirsch, 1920.
- Fig. 15. Forewing of fossil Protoblattid *Protophasma dumasi*, redrawn from Handlirsch, 1920.
- Fig. 16. Forewing of fossil Neuropteran (?) *Gigantotermes excelsus*, redrawn from Handlirsch, 1908.
- Fig. 17. Forewing of fossil Mixotermitoidan *Mixotermes ligauensis*, redrawn from Handlirsch, 1908.
- Fig. 18. Forewing of Embiid *Donaconethis abyssinica*, redrawn from Comstock, 1918.
- Fig. 19. Forewing of fossil Protorthopteron *Spaniodera ambulans*, redrawn from Handlirsch, 1920.
- Fig. 20. Forewing of fossil Neuropteran *Nymphites braueri*, redrawn from Handlirsch, 1920.
- Fig. 21. Forewing of fossil Hadentomoidan *Hadentomum americanum*, redrawn from Handlirsch, 1920.
- Fig. 22. Forewing of Plecopteran *Zelandobius confusus*, redrawn from Tillyard.

- Fig. 23. Hindwing of fossil Protoblattid *Eucaenus ovalis*, redrawn from Handlirsch, 1920.
- Fig. 24. Hindwing of fossil Protoblattid *Protophasma dumasi*, redrawn from Handlirsch.
- Fig. 25. Forewing of Trichopteron *Beracodes minuta*, redrawn from Ulmer, 1907.
- Fig. 26. Hindwing of Isopteron *Mastotermes darwinensis*, redrawn from Comstock, 1918.
- Fig. 27. Hindwing of Mantid *Metallucetra splendida*, redrawn from Handlirsch, 1908.
- Fig. 28. Forewing of Neuropteron *Coniocompsa vesiculigera*, redrawn from Enderlein, 1908.
- Fig. 29. Hindwing of fossil Protorthopteron *Sthenaropoda fischeri*, redrawn from Handlirsch, 1920.
- Fig. 30. Forewing of fossil Palaeodictyopteron *Homothetus fossilis*, redrawn from Handlirsch, 1908.
- Fig. 31. Forewing of Psocid *Archipsocus brazilianus*, redrawn from Enderlein.
- Fig. 32. Forewing of Psocid *Amphientomum paradoxum*, redrawn from Tillyard, 1918.
- Fig. 33. Forewing of fossil Thysanopteron *Palaeothrips fossilis*, redrawn from Scudder, 1890.
- Fig. 34. Forewing of fossil Protorthopteron *Lepium elongatum*, redrawn from Handlirsch, 1920.
- Fig. 35. Forewing of Orthopteron *Dionconema ornata*, redrawn from Handlirsch, 1908.
- Fig. 36. Forewing of Homopteron *Dictyophora europaea*, redrawn from Handlirsch, 1908.
- Fig. 37. Forewing of Trichopteron *Ryacophila*, redrawn from several sources.
- Fig. 38. Forewing of Trichopteron *Chaetopteryx villosa*, redrawn from Tillyard, 1919.
- Fig. 39. Forewing of Homopteron *Bothriocera prosignoretii*, redrawn from Metcalf, 1913.
- Fig. 40. Forewing of Psocid *Calopsocus infelix*, redrawn from Enderlein, 1903.
- Fig. 41. Forewing of fossil Protohemipteron *Eugereon boeckengi*, redrawn from Handlirsch, 1920.
- Fig. 42. Hindwing of Blattid *Periplaneta australasiae*, redrawn from Handlirsch, 1908.
- Fig. 43. Hindwing of Blattid *Chorisneura nigrifrons*, redrawn from Handlirsch, 1908.
- Fig. 44. Hindwing of Blattid *Diaphana fieberi*, redrawn from Handlirsch, 1908.
- Fig. 45. Hindwing of Orthopteron *Tettix subulata*, redrawn from Handlirsch, 1908.
- Fig. 46. Hindwing of Plecopteron *Eusthenia spectabilis*, redrawn from Comstock, 1918.
- Fig. 47. Hindwing of Homopteron *Myndus*, redrawn from Metcalf, 1913.
- Fig. 48. Hindwing of "an earwig" (Dermapteron) redrawn from Comstock, 1918.
- Fig. 49. Hindwing of Phasmid *Xeroderus kirbyi*, redrawn from Handlirsch, 1908.

- Fig. 50. Hindwing of fossil Palaeodictyopteron *Lamproptilia grandeuryi*, redrawn from Handlirsch, 1908.
- Fig. 51. Forewing of Neuropteran *Austrosialis ignicollis*, redrawn from Tillyard, 1919.
- Fig. 52. Forewing of fossil Mecopteron (?) *Belmontia mitchelli*, redrawn from Tillyard, 1919.
- Fig. 53. Forewing of Neuropteran *Protohermes davidi*, redrawn from Tillyard, 1919.
- Fig. 54. Forewing of Lepidopteron *Eriocrania semipurpurella*, redrawn from Tillyard, 1919.
- Fig. 55. Forewing of fossil Blattid *Polyetoblatta caloptyx*, redrawn from Handlirsch, 1908.
- Fig. 56. Forewing of fossil Palaeodictyopteron *Fouquea sauvagei*, redrawn from Handlirsch, 1908.
- Fig. 57. Hindwing of Mecopteron *Panorpodes carolinensis*, redrawn from Tillyard, 1918.
- Fig. 58. Forewing of Homopteron *Hotinus*, redrawn from Handlirsch, 1908.
- Fig. 59. Forewing of fossil Blattid *Aisoblatta orenburgensis*, redrawn from Handlirsch, 1908.
- Fig. 60. Forewing of fossil Mecopteron *Austropsyche superba*, redrawn from Tillyard, 1919.
- Fig. 61. Forewing of Dipteron *Protoplasa fitchii*, redrawn from Tillyard, 1919.
- Fig. 62. Forewing of fossil Odonatan *Protagrion audouini*, redrawn from Handlirsch, 1908.
- Fig. 63. Forewing of fossil Protephemerid, *Triplosoba pulchella*, redrawn from Handlirsch, 1920.
- Fig. 64. Forewing of Blattid *Diaphana fieberi*, redrawn from Handlirsch, 1908.
- Fig. 65. Forewing of Psocid *Caecilius*, redrawn from Enderlein, 1903.
- Fig. 66. Forewing of Hymenopteron *Xyela julii*, redrawn from Macgillivray, 1906.
- Fig. 67. Hindwing of Hymenopteron *Neurotoma fasciata*, redrawn from Macgillivray, 1908.
- Fig. 68. Forewing of fossil Homopteron *Mesojassus ipsviciensis*, redrawn from Tillyard, 1920.
- Fig. 69. Forewing of Neuropteran *Stenosialis australiensis*, redrawn from Tillyard, 1919.
- Fig. 70. Hindwing of Coleoptera *Philonthus*, redrawn from Handlirsch, 1908.
- Fig. 71. Forewing of Homopteron *Toxoptera graminum*, redrawn from Patch, 1909.
- Fig. 72. Hindwing of Coleopteron *Omna stanleyi*, redrawn from Handlirsch, 1908.
- Fig. 73. Hindwing of male Trichopteron *Lepocella punctata*, redrawn from Ulmer, 1907.
- Fig. 74. Hindwing of fossil Strepsipteron *Paraxenos eberi*, redrawn from Handlirsch.
- Fig. 75. Hindwing of Hemipteron *Cyphostelhus tristriatus*, redrawn from Handlirsch, 1908.