EXPLANATION OF PLATE I.

Fig. 1. Diagrammatic figure of the posterior respiratory organ of a dipterous larva indicating the several diagnostic characters. *Diameter of circular plate. 1, 2, 3, 4, first, second, third and fourth interspiracular spaces of left stigmal plate. I, II, III, dorsal, median and ventral slit-like spiracles, respectively, of right stigmal plate. IV, the left circular plate or "button."

Fig. 2. The micro-protractor showing arrangement of ruled angles. The various possible combinations from 5° to 360° indicated by the concentric lines.

A PHYLOGENETIC STUDY OF THE MESOTHORACIC TERGA AND WING BASES IN HYMENOPTERA, NEUROPTERA, MECOPTERA, DIPTERA, TRICHOPTERA AND LEPIDOPTERA.[1]

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In several papers dealing with the phylogeny of insects, the Hymenoptera, Neuroptera, Mecoptera, Diptera, Siphonaptera, Trichoptera, Lepidoptera and their allies were grouped in a superorder called the "*Panneuroptera.*" A portion of the evidence for such a grouping, based upon the study of the genitalia of males, has already been presented in Psyche, Vol. 25, p. 47, and in the Proc. Ent. Soc. Washington, Vol. 21; and in the present paper, I would briefly review the evidences of relationships indicated by the nature of the mesothoracic terga and wing bases in these insects. The terminology here adopted is that previously applied to the terga and wing bases of the Embiidæ, Plecóptera, Coleoptera and Dermaptera (Psyche, Vol. 25, p. 4), the Blattidæ, Plecoptera and Neuroptera (Jour. N. Y. Ent. Soc., Vol. 24, p. 1), the Orthoptera (Ann. Ent. Soc. America, Vol. 11, p. 347), and the Hymenoptera and Diptera (Jour. N. Y. Ent. Soc., Vol. 22, p. 248).

In the lower insects, the metathorax is subequal in size to the mesothorax, and in a few instances is even larger than the mesothorax. In the insects here considered, however, the mesothorax is usually the larger of the two, and since the metathorax becomes

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reduced to a narrow transverse band in the tergal region of the Diptera, I have restricted the present discussion to the mesonotum alone, since it is usually well developed in most of the insects of this group.

In the mesonotum of the insects here discussed, there is a tendency for the prescutum ("psc," Figs. 1, 3, 5, and 6) to become prolonged further backward into the scutal region "sc," thereby becoming longer than broad, while in the lower insects it is frequently broader than long. On the other hand, the scutellum, "sl," which may become very narrow and prolonged far forward into the scutal region, "sc," in such lower insects as the Blattidæ, etc., in the insects here discussed tends to become somewhat broader than long. The mesothoracic postscutellum, "psl," is usually undeveloped in such lower insects as the Blattidæ, Mantidæ, Acrididæ, Dermaptera, Coleoptera, etc., but in the Embiidæ and Plecoptera it is quite well developed, as in the insects under consideration. The mesothoracic tegula "t" is frequently quite large in the insects under discussion, and is usually developed only in the mesothorax, while in the lower forms, it is usually small, or not developed in the mesothorax, although in some cases it may be developed in both meso and metathorax in the lower insects. The sclerite labeled "a" in Figs. 1, 2, 4, etc., is usually not well developed in lower insects, while in many of the higher insects it is quite large, its better development in the latter insects being probably correlated with the superior powers of flight in the higher forms. I have not observed the middorsal suture "ms" in many lower insects (excepting the Plecoptera and Embiidæ), while it appears to be present in many of the higher insects, although it is not present in all of them.

As may be seen from the accompanying diagrams (Plate II) the general plan of the sclerites is relatively simple, and is adhered to quite closely by most of the insects here shown. It is thus a much simpler matter to compare the different insects together in attempting to trace their paths of development than is the case with the wing venation, where the complex and intricate patterns, with their bewildering array of modifications, make it very difficult to trace out the paths of development followed by the different groups of insects, unless one has practically all of the intermediate stages; and even then he may be led astray by the study of only one set of structures, unless it be confirmed by an examination of many others from different parts of the body, since insects which are primitive in respect to one particular feature, may be relatively highly specialized with regard to certain other features, and the same set of structures is not always equally well developed in all insects. On this account, it has been a source of great surprise to me that those who attempt to trace the lines of development of insects confine their attention almost entirely to the difficult wing venation, neglecting other no less vital features (which due to their simpler arrangement are much easier to study), and they are apparently unmindful of the fact that, due to the different degree of development of a set of structures in different insects, no *one* set of structures can be relied upon for such a study, since the evidence must be drawn from *all available sources*, the evidence drawn from one source merely serving to check that drawn from other sources. On this account, I would present the evidence furnished by a study of the terga and wing bases as merely a portion of the evidence of relationships based upon the study of as many and as widely differing structures as possible, in an effort to determine the lines of descent and the interrelationships of the insects comprising the superorder "Panneuroptera."

The Neuroptera appear to be as primitive as any of the insects here considered, and a study of their structures may therefore be taken as the basis for that of the other forms, although the Neuropteron shown in Fig. 5 is not as primitive as the Sialidæ, etc., and was chosen largely to illustrate the tendency among certain Neuroptera toward the development of the type of tergum and wing base occurring in some Mecoptera and Diptera. In the Neuroptera (Fig. 5) the prescutum "psc" and scutellum "sl" tend to assume a triangular outline, and the apices of the triangles approach each other near the middle of the tergal plate in which these sclerites occur. The same tendency is apparent in the sawflies (Fig. 1) and in both sawflies and Neuroptera the prescutum "psc" (Figs. 1 and 5) is divided by the middorsal suture "ms" into two symmetrical halves.

As is indicated by the extent of the broad black line bounding the stumps of the cut off wings in Figs. 1, 2 and 4, the base of the wings is comparatively broad in the sawflies, Trichoptera, Lepidoptera, and lower Neuroptera, although in the Neuropteron shown in Fig. 5 this is not the case, due to the fact that it was chosen to illustrate the tendency in some Neuroptera for the wing base and tergum to approach the condition occurring in certain Mecoptera and Diptera. In both the Trichoptera (Fig. 2) and the Lepidoptera (Fig. 4) there is a marked tendency for the tegula "t" to become large—a tendency which is somewhat less developed in the Hymenoptera (Fig. 1) and in certain Neuroptera, although there are evidences of it in these insects as well. The tegula, however, is best developed in the Trichoptera and Lepidoptera, and in these insects the region labeled "s" (Figs. 2 and 4) is very similar in outline, as is true of the incision in the margin of the region immediately behind that labeled "s." In both Trichoptera and Lepidoptera (Figs. 2 and 4) the alar ossicle labeled "n" is comparatively well developed, as is also true of the sclerite labeled "a"; and in both Trichoptera and Lepidoptera, there is a marked tendency toward the formation of a membranous area "ma" (Figs. 2 and 4) in the postscutellar region "psl."

The above-mentioned similarities between the Trichoptera and Lepidoptera are in full accord with the evidence of close relationship drawn from other sources, such as the presence of a coiled proboscis in such Trichoptera as *Plectrotarsus gravenhorsti*, the lepidopteroid character of the venation and wing-outlines of certain Trichoptera, the similarity in the antennæ, legs, genitalia, outline of the abdomen, and other features which point very clearly to a community of descent, or a merging of the lines of descent of the Lepidoptera and Trichoptera as they are traced back to their point of origin; and (as has been pointed out in a paper soon to be published in the Trans. Ent. Soc. London, dealing with the phylogeny and interrelationships of the higher insects) these anatomical features of the adult insects, as well as the study of larval characters, clearly point to the Trichoptera rather than the Mecoptera as the stem forms from which Lepidoptera have sprung, despite the efforts of Handlirsch and Tillyard to emphasize the mecopteroid character of the venation of the lepidopterous wing. The Mecoptera are also related to the Lepidoptera, but less closely than the Trichoptera are, and I am more inclined to regard the lines of descent of the Mecoptera, Trichoptera, and Lepidoptera as springing off from a common point of a stem resembling the Neuroptera very closely, though the lines of descent of the Trichoptera and Lepidoptera appear to merge in a single line as we trace them back to this common point of origin.

The mesothoracic terga and wing bases of tipulid Diptera and the *Bittacus*-like Mecoptera are strikingly similar (Figs. 3 and 6). In both of these types of insects, the mesothoracic terga become very elongate, and the wing bases become shifted backward by the elongation of the prescutal region "psc" (Figs. 3 and 6). The wing bases are also rather narrow or constricted in these insects, as is indicated by the extent of the broad black line bordering the cut off wings in Figs. 3 and 6. A similar tendency is shown in the Neuropteron depicted in Fig. 5, and it is quite possible that the nemopterid Neuroptera resemble the common ancestors of Mecoptera and Diptera in some respects, especially in the evident tendency toward the elongation of the head region and the reduction of the hind wings to narrow ribbon-like structures, which is carried still further in the Diptera. The outline of the scutellum "sl" is very similar in the Dipteron and Mecopteron shown in Figs. 3 and 6, and the bulging region bearing the label "psl" in Fig. 3 apparently corresponds to the median region labeled "mt" in Fig. 6. The sclerites designated as "prt" in Fig. 3 probably correspond to those bearing the same label in Fig. 6. The prescutal region "psc" tends to assume a similar outline in both insects, the tegula "t" is small in both, and the alar ossicle "n" is not greatly developed in either of these insects. The outline of the tergum, and the nature of the wing bases as well as the features mentioned above would indicate a close relationship between the tipulid Diptera and the *Bittacus*-like Mecoptera, and this is borne out by the nature of the head, antennæ, mouthparts, legs genitalia and character of the abdomen in the two groups, so that the marked similarity in appearance between *Bittacus* and the lower Diptera is not merely a superficial resemblance, but extends to the more minute details as well. I would therefore maintain that the lines of development of the Mecoptera and Diptera merge as we trace them back to their common origin, and the Neuroptera appear to be as much like the common stock as any other insects, from which the lines of development of the Trichoptera and Lepidoptera, and the Mecoptera and Diptera, have sprung.

The tergum of the Hymenoptera (Fig. 1) is as much like that of the Neuroptera (Fig. 5) as any, and in general, the Hymenoptera seem to be quite closely related to the Neuroptera. The line of development of the Hymenoptera therefore probably arose near the base of the neuropteroid stem, though the Hymenoptera are in some respects intermediate between the Neuroptera and the Psocidæ. The Hymenoptera have many characters suggestive of affinities with the Mecoptera, although the Mecopteron shown in Fig. 3 is not so well suited as *Panorpodes* and other primitive Mecoptera for demonstrating this relationship. Since the mecopteron line of development originated at a point quite far down on the main neuropteron stem, it is merely to be supposed that the Mecoptera will show evidences of a rather close relationship to the Hymenoptera, which also occupy a position far down this main stem, and similarly, since the Trichoptera branched off from this main stem very near the point of origin of the Mecoptera, both Trichoptera and Mecoptera show indications of affinities with the Hymenoptera as well as with the Neuroptera; but the resemblances between the Hymenoptera, Mecoptera and Trichoptera are the most patent in the larval stages of these insects. Since the Hymenoptera resemble Mecoptera in some respects, and since the Diptera also resemble Mecoptera in many respects, it is to be expected that there will be certain points of resemblance between the Hymenoptera and Diptera also; but I do not consider that the Hymenoptera and Diptera are as closely related as MacGillivray and other students of the wing venation have been led to suppose, from their studies of this one set of structures alone. That the Siphonaptera (the fleas) were descended from Diptera-like ancestors is admitted by practically all recent investigators; but since these forms are wingless, it has not seemed advisable to include a study of their terga in a paper dealing largely with the wing-bases.

The evidence of relationships among the insects here discussed, as indicated by a study of the terga and wing bases, is in full accord with the evidence from other structures as well, and the conclusions here reached may be briefly summarized as follows. The Neuroptera are as primitive as any representatives of the superorder (the Panneuroptera), and probably have departed as little as any from the condition typical of the forms ancestral to the group as a whole. The Hymenoptera are also very primitive, and occupy a position far down on the main neuropteroid stem. The Mecoptera and Trichoptera arose from neuropteroid ancestors, and are also related to the Hymenoptera. The line of development of the Diptera merges with that of the Mecoptera, and the line of development of the Lepidoptera merges with that of the Trichoptera as all of these are traced back to the common neuropteroid stem. The Trichoptera are probably a little more closely related to the Neuroptera than to the Mecoptera, but their line of descent branched off from the common neuropteroid stem very near to the point of origin of the mecopteron line of development on the same neuropteroid stem. There are some reasons for regarding the Mecoptera as the stem forms from which the lines of development of the Diptera, Trichoptera and Lepidoptera have sprung; but the Neuroptera are on the whole as near as any, to the ancestral forms from which all of these insects are descended.

Abbreviations.

a. = Adanal process or ossicle (adanale).
j. = Juxtategula.
m. = Median ossicle (medipterale).
ma. = Membranous area of postscutellum.
ms. = Middorsal suture.
mt. = Meditergite.
n. = Notopteral ossicle (notopterale).
pa. = Prealar bridge (prealare).
pf. = Prescutal fontanelle.
po. = Posttergite.
prt. = Pretergite.
ps. = Parascutellum.
psc. = Prescutum.
psl. = Postscutellum.
pt. = Parategula.
ptg. = Postalare or pleurotergite.
s. = Suralare.
sc. = Scutum.
sl. = Scutellum.
so. = Scutal organ.
t. = Tegula.

Explanation of Plate II.

Fig. 1. Mesonotum and wing-base of the Hymenopteron *Cephaleia.*

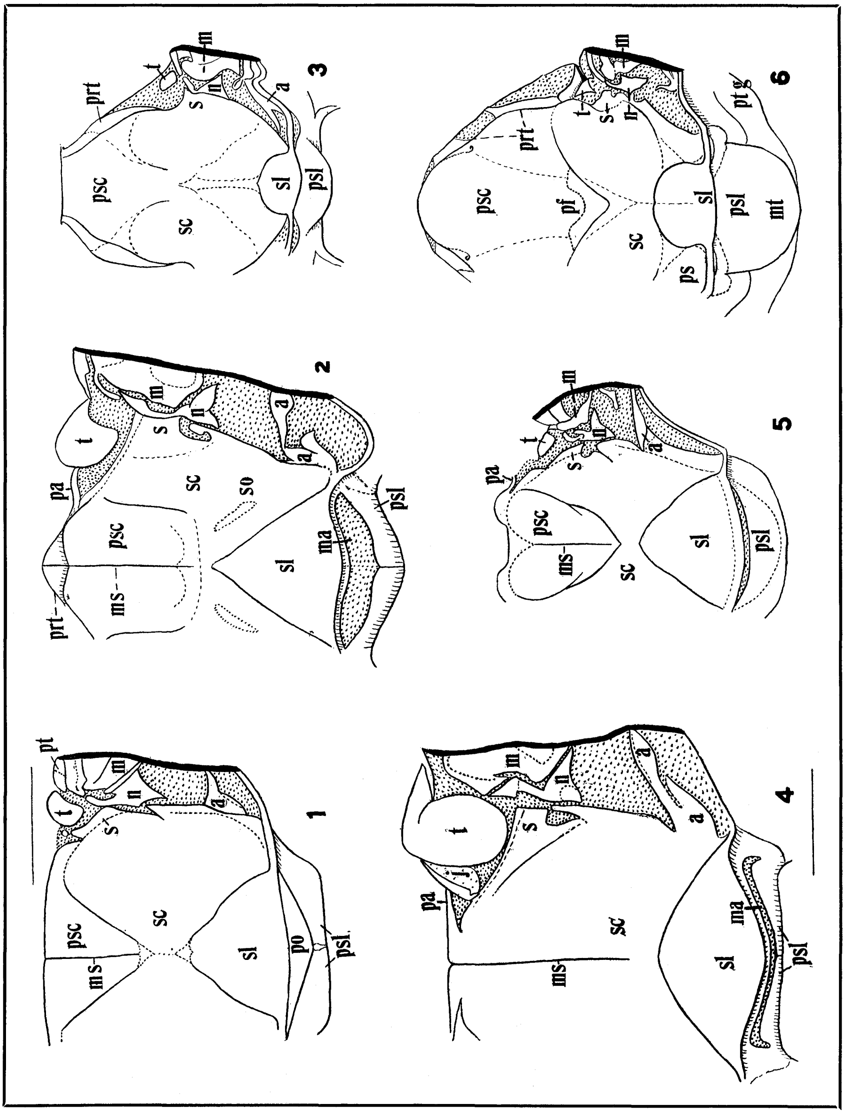
Fig. 2. Mesonotum and wing-base of the Trichopteron *Neuronia.*

Fig. 3. Mesonotum and wing-base of the Mecopteron *Bittacus.*

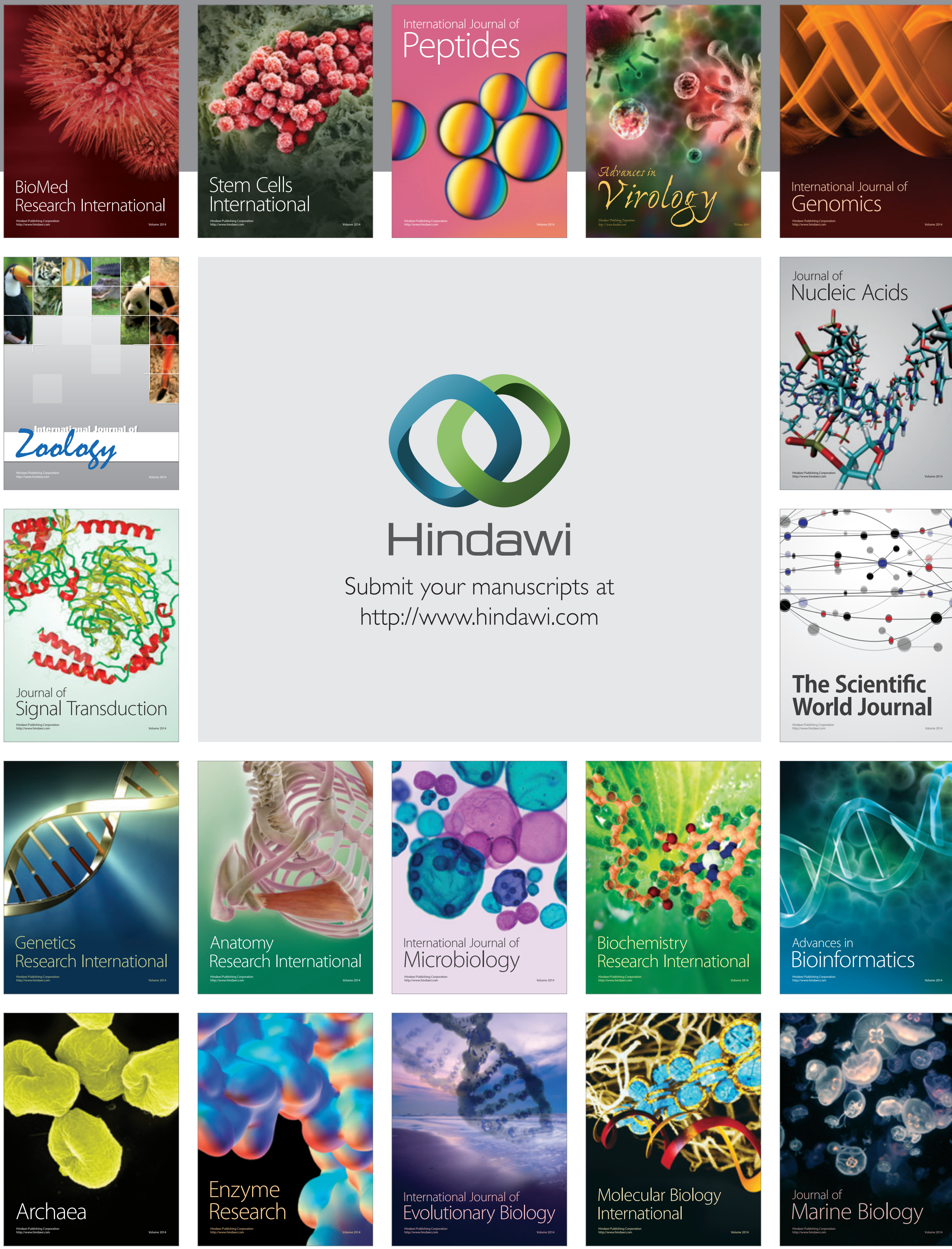
Fig. 4. Mesonotum and wing-base of the Lepidopteron *Phassus.*

Fig. 5. Mesonotum and wing-base of the Neuropteron *Nemoptera.*

Fig. 6. Mesonotum and wing-base of the Dipteron *Tipula.*



Crampton—Mesothoracic Terga and Wing-Bases.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