

THE THORAX OF THE HYMENOPTERA.

By ROBERT EVANS SNODGRASS,

Of the Bureau of Entomology, United States Department of Agriculture.

1. INTRODUCTION.

There are always two classes of workers concerned in the scientific study of any group of animals who think that the work of the other class is properly but secondary to their own. These are the systematists and the morphologists. In the field of entomology, however, there is now a very large third class of workers who pick out as important only those phases of the subject that have some direct connection with the welfare of mankind. We need not discuss the relative merits of the three, however, because the present paper is a sufficient demonstration of the interdependence of all these branches of entomological research. To wit, the gypsy moth and the brown-tail moth have been for a number of years greatly infringing on human interests and pleasure in certain parts of New England. A most promising means of combating them is the importation and rearing of destructive Hymenopteran parasites. Students of these parasites discover that the thorax presents valuable characters for the determination and classification of species, but they are handicapped in the use of such characters by the lack of reliable studies on the structure of the thorax among parasitic Hymenoptera in general. When, furthermore, the present writer undertook a study of the latter subject, he soon found himself necessarily involved in a general investigation of the Hymenopteran thorax, and especially of that of the lower members—the Tenthredinoidea and Siricoidea. These in turn had to be compared with the more generalized orders of insects to make sure of correct interpretations. Hence, while an unscientific person may be inclined to ask what the study of a cockroach's thorax has to do with the extermination of the gypsy moth in Massachusetts, experience shows that no special branch of entomology can be developed properly unless based on a knowledge of the fundamental structure of insects in general.

The study of the Hymenopteran thorax here presented is a contribution from the United States Bureau of Entomology, prepared under the direction of its chief, Dr. L. O. Howard. The work by the writer has been in the nature of a collaboration with Mr. J. C. Crawford of the United States National Museum and with Mr. H. L. Viereck and Mr. S. A. Rohwer of the bureau, who, as specialists in various groups of the Hymenoptera, have furnished not only the identified specimens from which the dissections and drawings were made, but also the taxinomic plan followed in treating the various species.

The most irreconcilable subject of contention between systematists and morphologists is in the field of terminology. The morphologists, of course, insist that the same anatomical parts should be given the same names in all the orders. The systematists, on the other hand, inheriting from their forerunners in taxonomy a different set of terms in each order, hold that these names should be retained for the sake of convenience, since every new student has to learn them anyway. They think it well enough to let such names remain as they are with the understanding that they are merely handles to the different parts used in description and that they are not supposed to have any morphological significance. Furthermore, the morphologists often make up such cumbrous terms, that, however significant from an anatomical standpoint, they are far too unwieldy for using as the names of organs or parts in specific descriptions. Hence, perhaps complete uniformity will never exist in entomological nomenclature. In the preparation of the present paper, however, no such conflict has arisen, and this for two reasons: First, the lateral and ventral parts of the Hymenopteran thorax have been so little used in specific descriptions that no system of names has yet been given to them; and secondly, the names commonly applied to the back plates are in some cases so glaringly misplaced that even systematists themselves are glad to have their nomenclature revised.

At first sight the thorax of most of the Hymenoptera appears very different from that of all other insects. Not only does it seem impossible to make out the ordinary parts of each segment, but the limits of the segments themselves are obscure. For a true solution of the subject the student must begin with a study of the Tenthredinoidea and Siricoidea and compare their structure with that of the more generalized orders of insects. While some entomologists have separated these two groups as a distinct order from the rest of the Hymenoptera, there can be no doubt that in their thoracic characters they are truly Hymenopteran. Yet, on the other hand, their thorax is so generalized that one can not possibly mistake its morphology in a comparison with the thorax of a grasshopper or stonefly. Hence, if the Phytophaga, so called, had become extinct, the Hymenopteran tree would have been cut off just so much higher above its

base, and the thoracic structure of its various branches would have been much more difficult to decipher.

The Hymenoptera are usually given the highest place in the scale of specialization, yet in almost every feature, members of some other order might be placed ahead of them. The mouth parts of the Hemiptera, the thorax and wings of the Diptera, and the internal organs of many other forms are more specialized than the corresponding parts of the Hymenoptera, while the Tenthredinoidea are certainly more generalized in their adult characters than the lowest members of the Hemiptera, Lepidoptera, or Diptera. These other orders, however, have picked out some one character or group of characters for extreme specialization. The Hymenoptera, on the contrary, have carried nearly *all* their organs to a high state of perfection and specialization. The mouth parts, the thorax, the legs, the wings, the ovipositor or sting, the alimentary canal, the tracheal system—all constitute a group of specialized organs unparalleled in any other order. Added to this is the high development of their instincts and the great diversity of their habits. Hence, there can be no doubt that the order amply merits the place of honor assigned to it.

2. GENERAL STRUCTURE OF THE INSECT THORAX.

It may still be confidently asserted that the thorax of insects consists of three segments, the attempts of various entomologists to make out a contrary case notwithstanding. Those who would elaborate this region of the body into a composite structure of many original segments may be grouped into two classes. The first includes those who look upon each apparent segment as a compound of two or four primitive segments. The second includes those who believe that all but three of the original segments have disappeared, except in some of the lowest insects where their rudiments persist as the intersegmentalia or little sclerites situated between the normal segments. The theory of the first class of speculators derives the consecutive parts of each definitive segment from a series of coalesced primitive segments; that of the second class leaves each modern segment a unit, and only assumes that there were once a great many more such units present. In the study of insects alone neither of these theories seems to be demanded. There is no necessity for supposing that the parts of any segment are anything more than secondary differentiations, or that the intersegmentalia are anything more than secondary products of the principal segments. Embryologists have never discovered more than three metameres in the true thoracic region of any insect.

In this connection it is interesting to note that both of these theories have been urged principally by myriopodists, or by entomologists who have included the Myriopoda largely in their studies. In fact, both theories are really based on the idea that insects are lineal

descendants of the centipedes. The myriopodists find that the different forms of the Chilopoda may be arranged in a series indicating a progressive reduction and disappearance of alternating segments. If this process should be continued far enough and accompanied by the disappearance of most of the legs, together with a few other changes, there would undoubtedly be produced an insect-like creature. Or, again, the same result might be obtained if the reduction in the number of segments were brought about by a combination of the chilopod segments instead of by an obliteration of the supernumerary ones. Hence, the evolution of insects from centipedes may be explained in two ways, but it would seem that the myriopodists simply assume the fact of this evolution which they would so amply explain. While probably few entomologists disclaim a common origin for the Chilopoda and Hexapoda, yet probably few of them admit that a study of insects alone affords any evidence of a lineal descent of the latter from centipedes. While it may be true, then, that the myriopods appear to be evolving into insects, it is not true that insects appear to have descended lineally from centipedes. The alleged relationship seems to be a case of a myriopodan claimant.

The theory that an insect is a centipede which has lost most of its segments by reduction has been elaborated chiefly by Verhoeff, but that author's ideas have been so widely criticised, especially by European entomologists, that the writer will not reiterate the subject here.^a The bulk of opinion favors the notion that the intersegmental plates are secondary sclerites cut off from the front parts of the thoracic segments. Crampton (1909) has given the general term of *intersegmentalia* to all the sclerites that occur between any two segments, while Enderlein (1907) designated the special group apparently derived from the front of any segment as the *apotom* of that

^a The writer has heretofore overlooked the theory of Hagen (1889) that each thoracic segment of modern insects is a composite of *three* primitive segments, the first of which carried the wings, the second the legs, and the third the spiracle. Hagen's reasoning is a good example of the exasperating style of logic such writers always use for closing their argument at both ends. For example, after stating his proposition, he expects the reader to accept its truth simply because it explains the structure of the thorax so nicely, as if this in itself were sufficient evidence. In the first place, the author assumes that there is something to explain, and, in the second place, he gives no reason why the parts have not been produced secondarily from *one* primitive segment, as they so evidently appear to be formed to students of development. The negative argument, that embryos of insects do not indicate any such thoracic composition, is set aside, after the manner of all such writers, by the statement that the condensation of the three segments into one took place so far back in phylogenetic history that even the embryo shows no longer any trace of it. ("Ich miene also, dass diese Cumulation von je drei Segmenten einen so alt erworbenen Zustand darstelle, dass selbst im Embryo der Nachweis nicht mehr vorhanden ist.") This argument must give a feeling of profound peace to all who seek its blissful security. Who enters here leaves all doubt behind and shuts out all pursuit. In this garden of Eden anybody can have all creatures created according to his own private formulas.

segment, those of the thorax corresponding with the "mikrothorax," "stenothorax," and "cryptothorax," of Verhoeff.

It is only in the neck region that a sufficient structure is found to warrant the idea of an extra segment. Many entomologists as well as myriopodists have believed, as first suggested by Huxley, that the sclerites in the walls of the neck, often highly developed in the lower orders, are the rudiments of a fourth thoracic segment. This supposed segment was named by Verhoeff the "*mikrothorax*." But yet, no actual proof has been adduced of the segmental nature of this group of sclerites. Some students of the subject think that the plates in question are derived from the labial segment of the head, others from the front of the prothorax, while still others claim that they arise from both of these sources. No one has discovered a separate neck segment. If the neck sclerites belong to the labial segment, then this segment must carry the name "microthorax" if the term be used at all. To the writer it now seems preferable to dispense with this appellation altogether, and to substitute the term *cervicum*, as used by Crampton (1909), to designate the neck and its plates; distinguishing the latter as the *cervical sclerites*. This involves no theory concerning the nature of these parts. The writer thus retracts whatever doubtful notions on the "microthorax" he may have expressed in former papers (1909, 1910).

The terms used in this paper to designate the principal parts of the body and of each thoracic segment are classified in the following tables. The phragmas, as will be shown later (pp. 57 to 64), are really intersegmental structures, or at least are developed intersegmentally, and hence, should be classed as such, though in adults they become associated with either the segment before or behind them. Since the first segment of the thorax is often so very different from the other two, on account of the reduction of its parts, a wing-bearing segment is given as a complete example of a thoracic segment.

PRINCIPAL PARTS OF AN ADULT INSECT.

Head.—Composed of seven consolidated segments.

Cervicum.—The neck region, including the cervical sclerites, derived perhaps from both the head and the prothorax.

Thorax.—Composed of three segments.

Prothorax.

Anterior phragma.

Mesothorax, including the mesothoracic apotomal plates when present.

Middle phragma.

Metathorax, including the metathoracic apotomal plates when present.

Posterior phragma.

Abdomen.—Composed of ten or more segments, except in Hymenoptera, where the first is transferred to the thorax.

PRINCIPAL PARTS OF A WING-BEARING SEGMENT.

*Dorsum.**Tergum* (*T*).*Notum* (*N*).*Prescutum* (*Psc*).*Scutum* (*Sct*).*Scutellum* (*Scl*).*Postnotum, postscutellum* (*PN*).*Latus.**Pleurum* (*Pl*).*Preepisternum* (*Peps*).*Episternum* (*Eps*) and *episternal paraptera* (*1P, 2P*).*Epimerum* (*Epm*) and *epimeral paraptera* (*3P, 4P*).*Trochantin* (*Tn*).*Venter.**Sternum* (*S*).*Presternum* (*Ps*).*Eusternum* (*Es*).*Sternellum* (*Sl*).*Poststernellum* (*PSl*).*Wing* (*W*).*Wing membrane*, including the axillary membrane (*AxM*).*Wing veins*—*costa* (*C*), *subcosta* (*Sc*), *radius* (*R*), *media* (*M*), *cubitus* (*Cu*), *anals* (*A*).*Axillaries* (*Ax*), *first* (*1Ax*), *second* (*2Ax*), *third* (*3Ax*), and *fourth* (*4Ax*).*Leg* (*L*).*Coxa* (*Cx*).*Trochanter* (*Tr*).*Femur* (*F*), with sometimes *second trochanter*.*Tibia* (*Tb*).*Tarsus* (*Tar*), including *claws* (*Cla*), *pulvilli* (*Pv*), and *empodium* (*Emp*).

In selecting and inventing names for the parts the writer has used those most in harmony with the system established by Audouin (1824), and, in fact, has retained Audouin's names wherever possible. The prefixes *pro*, *mesa*, and *meta* are reserved exclusively for designating the three thoracic segments or their respective parts, while corresponding anterior and posterior parts of any one segment are distinguished by the prefixes *pre* and *post*. Thus, "proscutum" means the scutum of the prothorax, but "prescutum" is the notal subdivision in front of the scutum in any segment. This system leads to a number of hybrid combinations of Latin and Greek terms, but, to avoid them, confuses the significance of the words. Berlese

(1906) distinguishes the four parts of the tergum by the names “acrotergite,” “protergite,” “mesotergite,” and “metatergite,” which offend in both respects at once. The writer believes that it is better to use a mixed term like “postnotum” to designate the plate lying behind the notum in any segment than to create confusion by calling it the “metanotum,” by which term most anyone would understand the notum of the metathorax.

The following are definitions of the terms given in the above tables, together with descriptions of the secondary parts pertaining to each. A special discussion of the morphology of the postnotum and the phragmas is given on pages 53 to 64.

Dorsum.—The back or dorsal surface of any segment, of any part, or of the entire body.

Tergum.—The chitinous plate or plates of the dorsum of any seg-

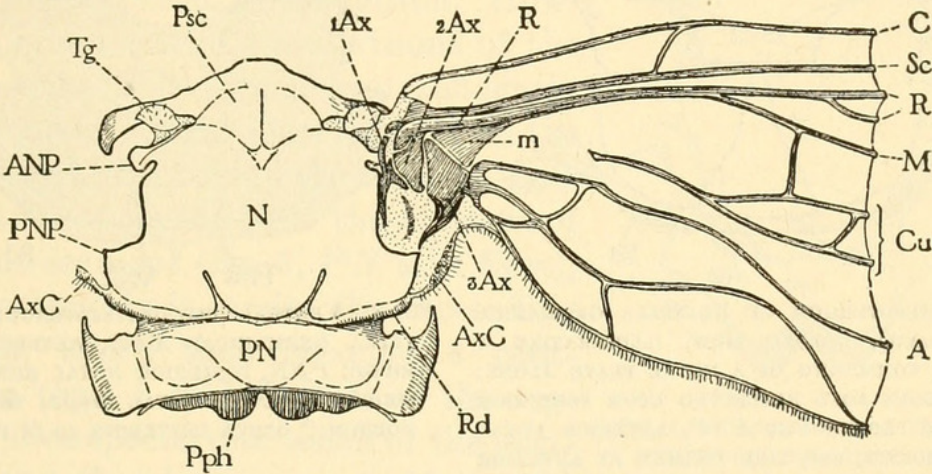


FIG. 1.—MESOTERGUM AND BASE OF RIGHT WING OF TÆNIPTERYX FRIGIDA (STONEFLY), SHOWING THE WING-BEARING NOTUM (N) AND THE POSTNOTUM (PN): A, ANAL VEIN; ANP, ANTERIOR NOTAL WING PROCESS; 1Ax, FIRST AXILLARY; 2Ax, SECOND AXILLARY; 3Ax, THIRD AXILLARY; AxC, AXILLARY CORD; C, COSTA; Cu, CUBITUS; M, MEDIA; m, MEDIAN PLATE OF WING BASE; N, NOTUM; PN, POSTNOTUM; PNP, POSTERIOR NOTAL WING PROCESS; Pph, POSTPHRAGMA; Psc, PRECUTAL DIFFERENTIATION OF NOTUM; R, RADIUS; Rd, POSTERIOR MARGINAL REDUPLICATION OF NOTUM; Sc, SUBCOSTA; Tg, TEGULA.

ment, typically confined to the back, but often extending downward on the sides or even upon the ventral surface. In adult winged insects the tergum of the mesothorax and of the metathorax very commonly consists of an anterior wing-bearing plate, and of a posterior plate having no connection with the wings. These are distinguished as the *notum* and the *postnotum* (fig. 1, N and PN).

Notum.—The primitive tergal plate, being the entire tergum of any segment in nymphal forms, as well as of the prothorax and of the abdominal segments in all adults. In the mesothorax and metathorax of adults, when there are two tergal plates present in each segment, the notum is the anterior or wing-bearing one (figs. 1 and 8, N). The words “tergum” and “notum,” as used by the writer, are, therefore, synonymous except where there is present in the wing-bearing segments a secondary postalar tergal plate. Since “tergum” has

priority over "notum" as a general term, the writer has used the latter in the more restricted sense, and has named the posterior secondary sclerite of the tergum, when present, the "postnotum."

The lateral margins of each wing-bearing notum are produced into the *anterior* and *posterior notal wing processes* (figs. 1, 2, and 4, *ANP* and *PNP*) for the articulation of the wings. The ventral surface very commonly presents three ridges—an *anterior notal ridge* (fig. 3, *ANR*), a *posterior notal ridge* (*PNR*), and a median V-shaped *notal ridge* (*VNR*)—the "entodorsum," having its apex forward. These three ridges form three transverse lines (fig. 2, *anr*, *vnr*, and *pnr*) on the surface of the notum. The first is slightly submarginal on account of the reflexed anterior edge of the notum, while the third is nearly always some distance in front of the posterior edge of the notum,

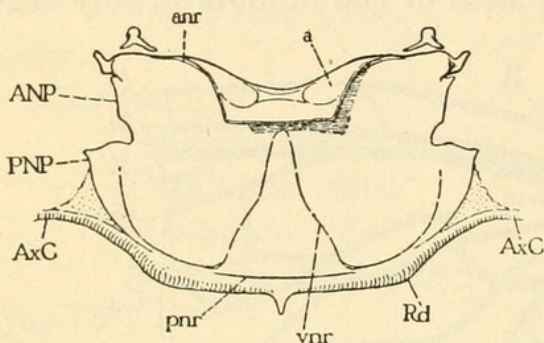


FIG. 2.—MESOTERGUM OF *BLATELLA GERMANICA* (COCKROACH), DORSAL VIEW, ILLUSTRATING A TERGUM CONSISTING OF A NOTAL PLATE ALONE: *a*, CHITINOUS FOLD REFLECTED UPON POSTERIOR EDGE OF PROTERGUM; *ANP*, ANTERIOR NOTAL WING PROCESS; *anr*, LINE FORMED BY ANTERIOR VENTRAL NOTAL RIDGE; *AxC*, AXILLARY CORD; *PNP*, POSTERIOR NOTAL WING PROCESS; *pnr*, LINE FORMED BY POSTERIOR VENTRAL NOTAL RIDGE; *Rd*, POSTERIOR REDUPLICATION OF THE NOTUM; *vnr*, LINE FORMED BY MEDIAN VENTRAL V-SHAPED NOTAL RIDGE.

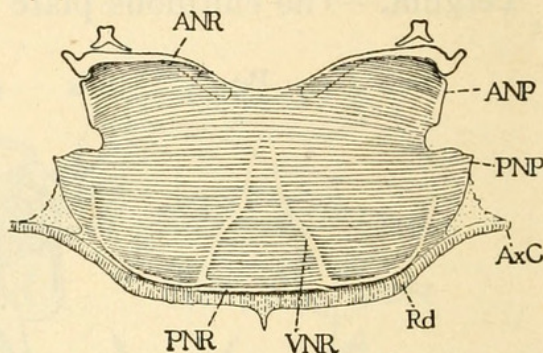


FIG. 3.—VENTRAL VIEW OF MESOTERGUM OF *BLATELLA GERMANICA*: *ANR*, ANTERIOR NOTAL RIDGE; *PNR*, POSTERIOR NOTAL RIDGE; *VNR*, MEDIAN V-SHAPED NOTAL RIDGE, THE "ENTO-DORSUM;" OTHER LETTERING AS IN FIG. 2.

which forms a conspicuous posterior reduplication of varying width (figs. 1, 2, and 3, *Rd*) overlapping the part behind.

Finally, the notum is commonly more or less divided into three regions by topographical differentiation or by transverse lines or sutures, independent of those formed by the ventral ridges. The first subdivision is the *prescutum*, the second the *scutum*, and the third the *scutellum*. These are best marked in the higher forms, as illustrated by the mesotergum of a crane-fly (fig. 4, *Psc*, *Sct*, *Scl*), and are clearly not homologous in all the orders, because they do not always bear the same relation to the more fixed characters of the notum. In the Hymenoptera the notum is actually cut into two separate pieces by a suture crossing it in front of the apex of the V-shaped ridge (pl. 10, fig. 46, *k*). In the lower orders the differentiations of the notum are largely topographical. In the cockroach (fig. 2) there are no divisions corresponding with those of the crane-fly (fig. 4),

though in the stonefly (fig. 1) a prescutal region (*Psc*) is distinctly marked off from the rest. The cord-like thickenings of the basal membranes of the wings (figs. 1, 2, 3, and 4, *AxC*) arise from the posterior angles of the notum, at the ends of the posterior reduplication.

Postnotum (*PN*).—The posterior transverse postalar sclerite of the mesotergum and metatergum (figs. 1, 4, and 5, *PN*), developed best in those segments that have the wings best developed as organs of flight, though not present in either segment of the Isoptera. It is absent in the mesothorax of Orthoptera, Euplexoptera, and Coleoptera, and is greatly reduced or absent in the metathorax of species having the hind wings reduced. That of the metathorax is generally fused with the first abdominal tergum in Orthoptera, Euplexoptera, and Hymenoptera.

The postnotum is ordinarily called the "postscutellum," since it lies immediately behind the scutellum of the notum. However, it is not one of the divisions of the notum, since it is formed independently as a secondary tergal chitinization in the dorsal membrane behind the notum. Laterally it is connected with the epimera of the same segment (fig. 5, *PN* and *Epm*), while posteriorly it carries the succeeding phragma, which thus becomes a postphragma (figs. 1 and 4, *Pph*) of the segment. (See special discussion of the postnotum and the phragmas, pp. 53 to 64.)

Phragmas (*Ph*).—The internal, vertical, transverse plates developed from the intersegmental folds between the terga (figs. 15 and 16, *2Ph*, *3Ph*). There are commonly three phragmas present, the anterior, the middle, and posterior, originating between the prothorax and the mesothorax, between the mesothorax and metathorax, and between the metathorax and the first abdominal segment respectively. In the adult stage the phragmas are not independently intersegmental, each being connected with either the tergum behind it or the one in front of it. The first, when present, is always fused with the front edge of the mesonotum. The second is likewise fused with the front of the metanotum in Orthoptera, Euplexoptera, and Coleoptera, but when present in the other orders it is connected with the postnotum of the mesotergum. The third is always connected with the meta-postnotum even when this plate is fused with the first abdominal tergum. If the postnotum is absent there is likewise no phragma.

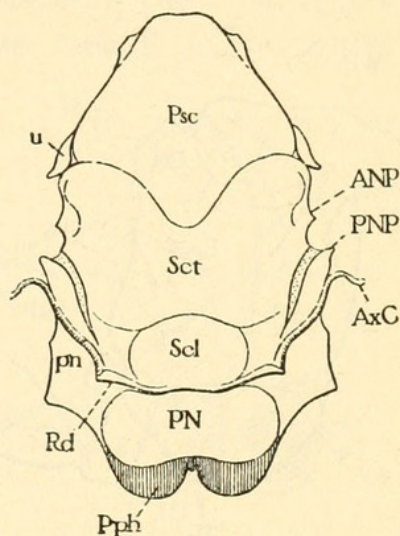


FIG. 4.—MESOTERGUM OF *HOLORUSIA GRANDIS* (CRANEFLY), SHOWING DIVISION OF NOTUM INTO THREE PARTS (*Psc*, *Sct*, AND *Scl*), BACK OF WHICH IS POSTNOTUM (*PN*): *AxC*, AXILLARY CORD; *ANP*, ANTERIOR NOTAL WING PROCESS; *PN*, *pn*, POSTNOTUM; *PNP*, POSTERIOR NOTAL WING PROCESS; *Pph*, POSTPHRAGMA; *Psc*, PRESCUTUM; *Rd*, POSTERIOR REDUPLICATION OF NOTUM; *Scl*, SCUTELLUM; *Sct*, SCUTUM; *u*, LOBE OF PRESCUTUM BEFORE BASE OF WING.

Thus, in adults, any phragma may be spoken of either as a *prephragma* (*Aph*) or as a *postphragma* (*Pph*) of the segment to which it is attached. In those orders having a postnotum in the mesothorax the tergum of this segment carries both a prephragma and a postphragma, while the metatergum has only a postphragma. In the other orders the metatergum bears two phragmas while the mesotergum has only a prephragma.

Latus.—The side of any segment, of any part, or of the entire body—the lateral area between the dorsum and the venter. The writer introduced this term, in the sense here defined, in a former paper (1910), because, if the term “pleurum” is used to designate the chitinous parts of the side of any segment, it is evident that another is needed to refer to the side of the segment itself, which should include both the membranous and

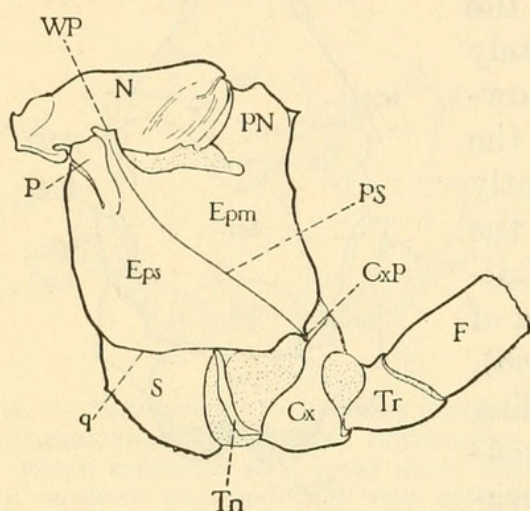


FIG. 5.—METATHORAX OF TÆNIPTERYX FRIGIDA (STONEFLY), LEFT SIDE, WINGS REMOVED: *Cx*, COXA; *CxP*, PLEURAL COXAL PROCESS; *Epm*, EPIMERUM; *Eps*, EPISTERNUM; *F*, BASE OF FEMUR; *N*, NOTUM; *P*, EPISTERNAL PARAPTERUM; *PN*, POSTNOTUM; *PS*, PLEURAL SUTURE; *q*, STERNOPLEURAL SUTURE; *S*, STERNUM; *Tn*, TROCHANTIN; *Tr*, TROCHANTER; *WP*, PLEURAL WING PROCESS.

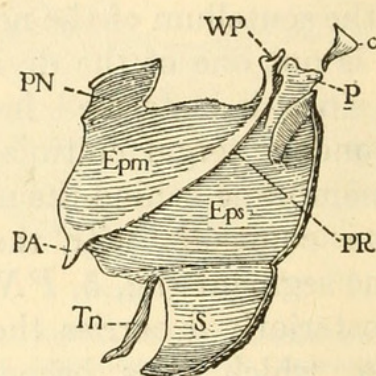


FIG. 6.—LEFT METAPLEURUM OF TÆNIPTERYX FRIGIDA (STONEFLY), INTERNAL: *c*, SCLERITE CONNECTING PARAPTERUM (*P*) WITH HEAD OF COSTAL VEIN OF WING; *Epm*, EPIMERUM; *Eps*, EPISTERNUM; *P*, EPISTERNAL PARAPTERUM; *PA*, PLEURAL ARM; *PN*, LATERAL PART OF POSTNOTUM, CONTINUOUS WITH EPIMERUM; *PR*, PLEURAL RIDGE; *S*, STERNUM; *Tn*, TROCHANTIN; *WP*, PLEURAL WING PROCESS

the chitinous parts. The adjective “lateral” follows from “latus,” just as does “dorsal” from “dorsum” and “ventral” from “venter.”

Pleurum (*Pl*).—The chitinous plate or plates of the latus of any segment, often partially crowded out by lateral encroachments of the tergum or sternum, especially in the prothorax. A typical adult pleurum of the mesothorax or metathorax covers most of the latus and presents externally a vertical or oblique *pleural suture* (fig. 5, *PS*) extending from the base of the *wing process* (*WP*) above to the *coxal process* (*CxP*) below. This divides the pleurum into an anterior or ventral *episternum* (*Eps*) and a posterior or dorsal *epimerum* (*Epm*). Internally there is a heavy *pleural ridge* (fig. 6, *PR*) along the line of the pleural suture, which gives off a *pleural arm* (*PA*) at or near its lower end. At the upper end of the epi-

sternum are one or two *episternal paraptera*, small plates connected with the head of the wing and giving insertion to the extensor and pronator muscle of the wing. At the upper end of the epimerum there is likewise frequently one and very rarely two *epimeral paraptera*. The metapleurum of the stonefly, shown in figure 5, has only one parapteral plate (*P*), situated just in front of the wing process and not entirely disconnected from the episternum.

Audouin (1824) first described the "paraptère" as a little plate of the pleurum situated in front of the wing base. The present writer, in a former paper (1909), applied the term in the plural to the series of little subalar pleural plates both before and behind the wing process, as defined here. Some authors have supposed that Audouin referred to the tegula in describing the "paraptère," but his description shows clearly what he meant. (The present writer has fully discussed this subject in a former paper, 1910, footnote *a*, pp. 20 and 21.)

Ventrad to the episternum and in front of the coxa is a variable plate called the *trochantin* (fig. 5, *Tn*). It is best developed in the lower orders, where it articulates by its lower end with the ventral rim of the coxa; but it is often rudimentary or is fused with the lateral precoxal part of the sternum. In cases where the coxa appears to articulate ventrally with the sternum, it may be that the articulation is really with the absorbed trochantin.

In the Orthoptera and Euplexoptera there is very often present a plate lying before the episternum which the writer (1909) has termed the preepisternum (fig. 7, *Peps*). In a few cases it forms a continuous band from the front of the episternum to the front of the sternum (presternum). It was described by Verhoeff (1903) as the "katopleure." When the preepisternum does not reach the sternum there is very frequently a plate lying between it and the sternum (fig. 7, *x*). In a former paper on the thorax the writer (1909) followed the prevalent custom, especially among German entomologists, of regarding these plates as separated presternal sclerites (the "Vorplatten" of the Germans). Crampton (1909), however, has elaborated the following theory based principally on a study of the Blattidæ and Euplexoptera. He supposes that in a primitive form the chitin was continuous across the ventral surface

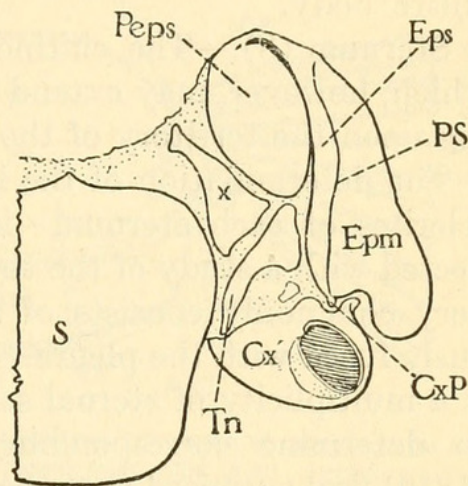


FIG. 7.—RIGHT HALF OF MESOPECTUS OF SPONGIPHORA APICIDENTATA (EARWIG): *Cx*, COXA; *CxP*, PLEURAL COXAL PROCESS; *Epm*, EPIMERUM; *Eps*, EPISTERNUM; *Peps*, PREEPISTERNUM; *PS*, PLEURAL SUTURE; *S*, STERNUM; *Tn*, TROCHANTIN; *x*, PLATE BETWEEN THE STERNUM AND PREEPISTERNUM.

of the segment from one pleural suture to the other. This was then divided by sutures into a sternal sclerite, an episternal sclerite, a trochantin, and a large plate lying between the sternum and the episternum, which Crampton calls the "laterale." Finally, this is supposed to have differentiated into an "episternal laterale" adjoining the episternum (fig. 7, *Peps*) and into a "sternal laterale" (*x*) adjoining the sternum. A study of adult insects furnishes plenty of facts for illustrating such a theory, and it certainly looks reasonable, but the writer would not urge it without knowing whether there are any facts of development that would contradict it. Since neither of the plates in question (*Peps* and *x*) occur in the Hymenoptera, however, a decision on their nature or origin is immaterial to the present paper.

Venter.—The under surface of any segment, of any part, or of the entire body.

Sternum (*S*).—The chitinous parts of the venter of any segment, which, however, may extend upward in the latera, thereby encroaching upon the territory of the pleura.

The determination of the homologies of the sternites—that is, the sclerites of each sternum—is the most unsatisfactory subject connected with a study of the thorax. In the higher orders the sternum very commonly consists of a single ventral sclerite often continuously fused with the pleura. But in many of the lower orders there is a multiplicity of sternal sclerites, and it is often a difficult matter to determine corresponding parts in different forms. MacLeay (1830) first surmised that there are four sternites corresponding with the four parts of the tergum, and he named them the "præsternum," "sternum," "sternellum," and "poststernellum." Comstock and Kochi (1902) adopted the same nomenclature. Crampton (1909), however, has made a more careful study of the sternal anatomy, and, while he discovers four transverse parts, he names them the "præsternum," "basisternum," "furcisternum," and "spinisternum," because, as he says, only the first coincides with the divisions recognized under the earlier set of names. Crampton's system eliminates the inconvenience of calling both the entire ventral chitination and its principal subdivision the "sternum." The writer, however, would prefer to substitute the word *eusternum* for the second subdivision (as given in the table, page 42) so as to retain the original names even though with an altered significance as to the limits of the sclerites to which they are applied.

Each thoracic sternum almost invariably has a forked apodeme projecting upward from its inner surface. This is commonly known as the *furca* or "entosternum." The *furca*, according to Crampton, is carried by the third sternite, the "furcisternum" of his nomenclature.

The posterior part of the prosternum frequently bears a long internal spine projecting posteriorly, hence the name "spinisternum" of Crampton.

Wings.—In immature stages the wings appear to be hollow expansions of the back plates of the mesothorax and metathorax. In adults the upper surface of each is continuous by membrane with the edge of the notum and the lower surface with that of the pleurum. Each is more firmly hinged to the wing processes of the notum by two small axillary sclerites, and is pivoted upon the wing process of the pleurum by another.

Wing membrane.—The appressed dorsal and ventral walls of the original wing sac, forming the *cells* between the chitinous veins and the thin *axillary membrane* between the axillaries. The second is

nearly always bordered posteriorly by a conspicuous ligament-like thickening, the *axillary cord* (figs. 1, 8, and 10, *AxC*) arising typically from the posterior angles of the notum at the outer ends of the posterior reduplication (figs. 1, 2, and 3, *AxC* and *Rd*). Sometimes the axillary membrane forms a large lobe or a pair of lobes, called the *alula*, at the posterior angle of the wing base.

On its anterior edge is a hairy pad, the *tegula* (*Tg*), which, in the front wing, is sometimes developed into a large scale overlapping the root of the wing.

Wing veins.—The writer adopts the Comstock-Needham (1898) system of wing venation and nomenclature for morphological purposes, but he does not advocate its use by systematists for descriptive purposes. A vein that is evidently a compound of several original veins must, according to this system, be named as the sum of all its components. Thus results such appellations as $Sc + R + M$, or $Cu_1 + Cu_2 + M_4 + 1stA + 2dA + 3dA$ for names of veins in the Hymenopteran wing. Combinations of this sort are certainly too cumbrous to be practical—a systematist should not be required to use such complex terms when he wants to mention a particular vein of the wing. Hence, while this system may be used to show the morphology of

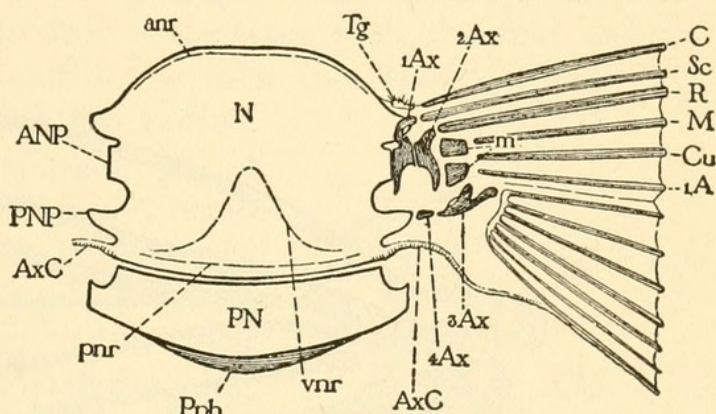


FIG. 8.—THEORETICAL DIAGRAM OF A WING-BEARING TERGUM AND BASE OF WING: *1A*, FIRST ANAL VEIN; *ANP*, ANTERIOR NOTAL WING PROCESS; *anr*, LINE OF ANTERIOR VENTRAL NOTAL RIDGE; *1Ax*, *2Ax*, *3Ax*, *4Ax*, FIRST, SECOND, THIRD, AND FOURTH AXILLARIES OF WING BASE; *AxC*, AXILLARY CORD; *C*, COSTA; *Cu*, CUBITUS; *M*, MEDIA; *m*, MEDIAN PLATES OF WING BASE; *N*, NOTUM; *PN*, POSTNOTUM; *PNP*, POSTERIOR NOTAL WING PROCESS; *pnr*, LINE OF POSTERIOR VENTRAL NOTAL RIDGE; *Pph*, POSTPHRAGMA; *R*, RADIUS; *Sc*, SUBCOSTA; *Tg*, TEGULA; *vnr*, LINE OF MEDIAN VENTRAL V-SHAPED NOTAL RIDGE.

any vein, taxinomists, especially in the Hymenoptera, will probably continue the use of more convenient, though less significant, individual names for the veins. An unfortunate thing in this connection is that systematists in different orders have, in many cases, used the same names for entirely different veins.

Axillaries (*Ax*).—The little sclerites at the base of the wing which hinge the latter to the notum and pleurum. Many individual names have been given to these sclerites by different students, but the writer has selected the general term of *axillaries* proposed by Strauss-Dürckheim (1828) for those of the hind wing of *Melolontha*, distinguishing the individual plates as the *first*, *second*, *third*, and *fourth*. The fourth is usually absent except in Orthoptera and Hymenoptera, but the other three are of almost universal occurrence in all the winged orders except the mayflies and dragonflies.

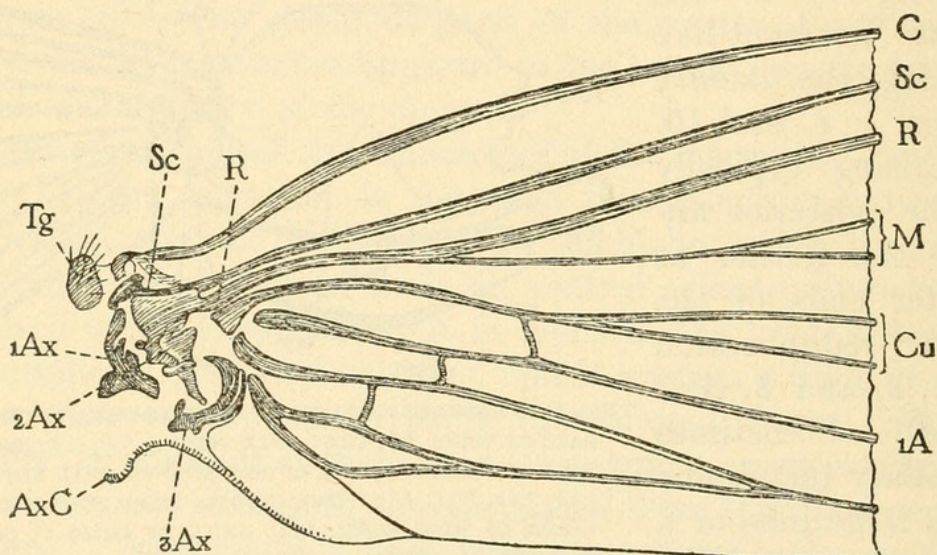


FIG. 9.—BASE OF FRONT WING OF *ASYNARCHUS PUNCTITISSIMUS* (CADDICEFLY): *1A*, FIRST ANAL VEIN; *1Ax*, *2Ax*, *3Ax*, FIRST, SECOND, AND THIRD AXILLARIES; *Ax C*, AXILLARY CORD; *C*, COSTA; *Cu*, CUBITUS; *M*, MEDIA; *R*, RADIUS; *Sc*, SUBCOSTA; *Tg*, TEGULA.

The axillaries, their relations to the back and to the base of the wing, are shown diagrammatically by figure 8. The first (*1Ax*) nearly always has a curved anterior neck which rests upon the anterior notal wing process (*ANP*), while its body is hinged to the edge of the notum back of the latter. Its anterior end is associated with the base of the subcosta (*Sc*). The second (*2Ax*) is the pivotal sclerite of the wing base, since it rests and turns upon the wing process of the pleurum. Its anterior end is associated with the base of the radius (*R*). The third axillary (*3Ax*) is associated with the bases of the anal veins, except with the first (*1A*) when this vein is separated from the others, as it is in the Orthoptera. The *flexor muscle* is attached to this sclerite, which serves also to plicate the wing of those forms that fold the anal region. When the fourth axillary (*4Ax*) is present it articulates with the posterior wing process of the notum (*PNP*), and intervenes between the latter and the third axillary. When it is absent

the third articulates more or less directly with the posterior process. Distad to the second axillary, and associated with the bases of the media (*M*), the cubitus (*Cu*) and the first anal (*1A*), when these veins are distinct at their bases, are one or two small *median plates* (*m*) which are not of constant occurrence, and which vary much in different forms when they are present. It will be observed that the base of the costa is not associated with any of the axillaries. The membrane of the wing base directly connects this vein with one or both of the episternal paraptera, upon which is inserted the *extensor muscle* of the wing, called also the “pronator” because, while it turns the wing forward, it at the same time depresses the anterior edge.

The diagram, figure 8, is constructed from a study of all the orders, for no one form shows all the parts of the wing so generalized. Many, however, approximate it. The stonefly shown in figure 1 is very simple. In it the subcosta (*Sc*) articulates with the first axillary (*1Ax*), the radius (*R*) is continuous with the second (*2Ax*). The media (*M*) fuses basally with the radius, but a distinct median basal plate (*m*) is present. The cubitus (*Cu*) does not reach the wing base, and there is no separate first anal. The other anals (*A*) are connected with the third axillary (*3Ax*), which is articulated directly to the posterior wing process (*PNP*), the fourth axillary being absent. The wing of the caddicefly, shown in figure 9, is likewise very generalized, though it not only lacks a fourth axillary, but has also no median plates. The media (*M*) is here, again, fused with the base of the radius (*R*), which is continuous with the second axillary (*2Ax*). The subcosta (*Sc*) articulates, by a prominent basal knob, with the first axillary (*1Ax*). The cubitus (*Cu*) and the first anal (*1A*) reach the base of the wing as separate veins, while the other anals are associated with the third axillary (*3Ax*).

The first, third, and fourth axillaries are developed in the dorsal wall of the wing sac. The second is formed from united dorsal and ventral elements. The latter is clearly shown as a separate piece in the wing of *Tænipteryx frigida* (fig. 10, *2Ax*), and has attached to its posterior end the large internal chitinous *axillary disc* (*AxD*). The ventral part articulates with the pleural wing process, while the dorsal part (fig. 1, *2Ax*) carries the radius (*R*), which is but weakly developed below. The axillary disk (fig. 10, *AxD*) is of very general occurrence and bears the dorsal insertion of the *coxo-axillary muscle*, whose lower end is attached to the rim of the coxa of the same segment. The disk is very commonly attached to the second

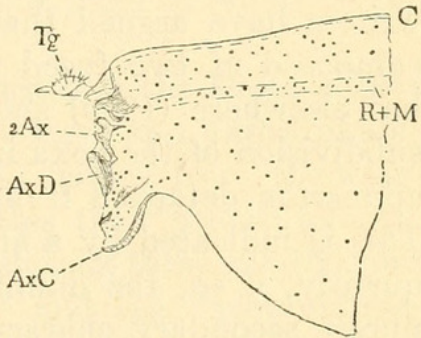


FIG. 10.—VENTRAL SURFACE OF BASE OF FRONT WING OF TÆNIPTERYX FRIGIDA (SEE FIG. 1): *2Ax*, VENTRAL ELEMENT OF SECOND AXILLARY; *AxC*, AXILLARY CORD; *AxD*, AXILLARY DISK; *C*, COSTA; *R+M*, BASAL TRUNK OF RADIUS AND MEDIA; *Tg*, TEGULA.

axillary, but is sometimes carried directly by the axillary membrane, while in a genus of beetles (*Cyllene*) it is attached to a special process of the postnotum. In the honey bee the coxo-axillary muscle is inserted upon a sclerite which appears to be an epimeral parapterum.

Legs.—In adults the legs are attached to the ventrolateral regions of each thoracic segment, typically between the pleurum and the sternum, and behind the middle of the segment. The basal segment or *coxa* (figs. 5 and 7, *Cx*) is articulated above to the pleural coxal process (*CxP*) at the lower end of the pleural suture (*PS*), and below to the lower end of the trochantin (*Tn*). If the trochantin is absent, as it generally is in the higher orders, the coxa either has no ventral articulation or it articulates with a knob of the sternum. When the trochantin appears to be absent it might, of course, simply be fused with the sternum, in which case the apparent sternal coxal process may be really the trochantinal condyle.

The coxa is a double structure in the mesothorax and metathorax of Neuroptera, Mecoptera, Trichoptera, and Lepidoptera. Some writers have argued that this is evidence of each segment's being composed of two fused primitive segments. The writer, however, has elsewhere (1909) shown reason for believing that the posterior subdivision of the coxa in such cases is simply the lower part of the epimerum detached from the latter and fused upon the true coxa. This is indicated by a study of larval and pupal forms, and consequently, if so, the double nature of the coxæ in these orders is a purely secondary character and can have no morphological significance, unless, indeed, it be assumed that the simple larval coxæ are specialized and that in the pupal and adult stages the legs revert to a more primitive ancestral character.

The next joint of the leg, the *trochanter* (fig. 5, *Tr*), is apparently double in some of the Hymenoptera, but in such cases it looks more reasonable to regard the "*second trochanter*" as a basal subdivision of the third joint or *femur* (*F*).

The characters of the *tibia* (*Tb*) and *tarsus* (*Tar*) are too familiar to require any special discussion here. The under surface of each tarsal joint is sometimes provided with a pair of small cushion-like pads, which were named the *pulvilli* (*Pv*) by Kirby and Spence (1826). Most authors, however, would understand by "the pulvilli" only those pads of the terminal segment occurring at the bases of the claws. The terminal segment frequently bears also a median fleshy appendage between the claws, which is known as the *empodium* (*Emp*). All of these soft appendages of the tarsus enable the insect to adhere to smooth surfaces by a sticky liquid excreted upon them. The Hymenoptera possess only the median appendage of the terminal segment.

3. MORPHOLOGY OF THE POSTNOTAL PLATES (POSTSCUTELLA) AND THE PHRAGMAS.

Almost all writers have recognized under some name the postnotal sclerites of the thoracic terga. The nomenclature current amongst Hymenopteran systematists, however, attaches the name "postscutellum" to the plate on the surface of the dorsum immediately following the mesoscutellum (pl. 14, fig. 63, N_3), but which, in this order, is the metanotum, since it carries the hind wings. This mistake has arisen from the fact that the earlier students of these insects were ignorant of the fact that the true postscutellum (the postnotum) of the mesothorax is deeply invaginated and entirely concealed within the body between the mesothorax and the metathorax. A further consequence of this error is the application of the name "metathorax" to the propodeum or first abdominal segment (*IT*) of the thoracic mass, in spite of the fact that it has no connection whatever with the hind wings. The incorrectness of such a nomenclature is at once apparent when it is seen that it assigns both pairs of wings to the mesothorax.

The usual interpretations of the back sclerites in the Diptera have been more correct because there is present a large and unmistakable postnotal plate in the mesothorax (fig. 4, *PN*) distinct from the wing-bearing metanotum. Lowne (1892) calls this the "postscutellum" in the blow-fly. Crampton (1909) distinguishes its three subdivisions in the Tipulidæ as the "mediophragmite" and the "pleurophragmites." Berlese (1906), however, confuses it with the metathorax in both *Tipula* and *Calliphora*.

Various names have been given by different authors to this postnotal plate. Chabrier (1820) called it the "cloison costale." Strauss-Durckheim (1828) called that of the metathorax in *Melolontha* the "tergum." Amans (1885) included both the postnotum and the attached phragma under the name of "subpostdorsum." Kolbe (1889) applied the term "phragma" to both the postnotum and its phragma. Audouin (1824) first used the term "postscutellum" in describing the tergum of *Dytiscus*, but he did not correctly distinguish the parts anatomically, as the present writer has elsewhere shown (1909), yet, the term *postscutellum* may very appropriately be given to the tergal plate following the scutellum when the latter is present. However, as will be shown later, the postscutellum in this sense is not one of the subdivisions of the notum, corresponding with the pre-scutum, scutum, and scutellum, but is a separate plate developed independently back of the true notum. Therefore, the writer formerly (1909) adopted the term "pseudonotum," used by Verhoeff (1903) in the Euplexoptera (Dermaptera), as a general term, but suggested as an alternative the name *postnotum*. Since, however, Verhoeff did not

define "pseudonotum" as a general term, the name "postnotum" is used as such in the present paper, while "postscutellum" is used as an alternative in the higher orders where the scutum and scutellum are well differentiated.

The simplest thoracic terga occur amongst nymphal and larval forms. The nymph of a stonefly (fig. 11) has each segment protected above by an undivided notal plate, those of the mesothorax and metathorax carrying the rudiments of the wings. Between these dorsal plates are wide white membranous areas, which, as shown by sections (fig. 14 Mb_1 , Mb_2 , Mb_3), belong to the posterior parts of the segments *because they lie in front of the intersegmental constrictions*. The dorsum of each thoracic segment of this nymph consists, therefore, of a chitinous notum (N) and of a non-chitinous postnotal membrane (Mb).

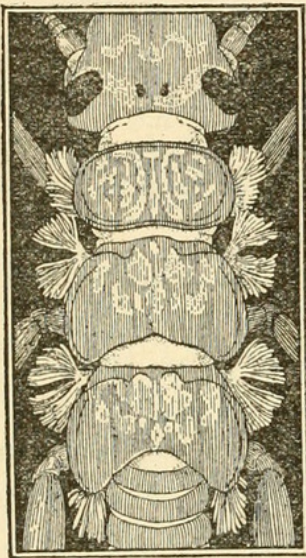


FIG. 11.—NYMPH OF A STONEFLY, DORSAL VIEW, SHOWING WIDE POSTNOTAL MEMBRANOUS AREAS, WHICH, IN THE MESOTHORAX AND METATHORAX OF THE ADULT, ARE OCCUPIED BY THE POSTNOTAL PLATES.

Amongst winged adults the simplest terga are probably to be found in some of the smaller cockroaches. A good example is afforded by the mesothorax of *Blatella germanica* in the dorsum of which there is but one plate present, and this one is unquestionably the true notum (fig. 2), since it carries the wings and has the axillary cords (AxC) arising from the outer ends of its posterior reduplication (Rd). On the sides are the two wing processes (ANP and PNP) separated by a deep emargination. On its anterior part is a thin flap (a) which is attached to the pronotum, being reflected upon the posterior overlapping part of the latter from the anterior phragma. The surface is gently convex and there are no divisions into subsclerites corresponding with those of the

higher orders, though there are several lines on the surface due to the internal ridges shown in figure 3. There is no postnotal plate present. The notum of the metathorax is almost identical with that of the mesothorax, and, if there is a postnotum present, it is fused with the first abdominal segment. In the Isoptera, likewise the terga of the wing-bearing segments consist each of a single notal plate, which, however, is often greatly constricted in the middle by the deep lateral emarginations.

In almost all other adult winged insects the tergum consists of two plates in those segments that have the wings well developed as organs of flight. The anterior plate is the true *notum*, being identical with the entire nymphal tergum, since it alone carries the wings. The posterior plate is the *postnotum* and is not represented in the nymphal tergum. The Ephemera, Odonata, Plecoptera, Neuroptera, and

others (except the Isoptera), having the wings equally developed, possess a well-developed postnotum back of each wing-bearing plate. In the Diptera and the higher Lepidoptera the postnotum of the metatergum is reduced or obliterated. In the Tenthredinoidea and Siricoidea it is distinct in each segment. In the other Hymenoptera the postnotum of the mesothorax is hidden by invagination within the body, while that of the metathorax is usually fused with the first abdominal tergum. In the mesothorax of the Orthoptera, Euplexoptera, and Coleoptera, where the front wings are developed as protective structures rather than as organs of flight, the postnotum is lacking, or is possibly represented in a very rudimentary condition in a few species by two small plates yoking the mesonotum to the metanotum.

The writer (1908, 1909) has heretofore contended that the Orthoptera have no postnotum in either segment. Crampton (1909) opposes this with the statement that "the postscutellum of *Gryllus domesticus* is quite well developed." Other writers, including Voss (1905), have likewise described a postnotum under some name in the metathorax of various members of the Orthoptera, but in all such cases the sclerite referred to is actually, i. e., by anatomical continuity, a part of the first abdominal segment. The present writer has examined species of *Gryllus*, *Gryllodes*, and *Nemobius* and finds that there is in each an anterior subdivision of the apparent first abdominal tergum, to the internal surface of which are attached the posterior ends of some of the longitudinal dorsal muscles of the metathorax, especially two lateral bands. Hence, this may be taken as evidence that the subsclerite in question is the true postscutellum or postnotum of the metathorax. It is largest in *Nemobius*, but is more distinct from the first abdominal tergum in *Gryllus* than in the other two genera, while in *Gryllodes* it is so small and so intimately a part of the abdominal tergum that it certainly taxes one's credulity to believe it is anything else. In *Blatella* there are two small lobes, situated laterally upon the front edge of the first abdominal tergum, to which are attached the posterior ends of some of the lateral longitudinal muscles of the metanotum. By the same reasoning, as in the case of the Gryllidæ, these lobes may be argued to be rudiments of the metapostnotum in the Blattidæ. In the Acridiidæ the first abdominal tergum presents a large subdivision extending downward on the sides before the lateral tympana of this segment. A longitudinal section of *Triemerotropus maritima* (fig. 12) shows that, to the middle of this apparent subdivision (PN_3) of the first abdominal tergum (IT), is attached the posterior phragma ($3Ph$), and that upon this plate and the phragma are inserted the posterior ends of the great dorsal longitudinal muscles of the metathorax ($DMcl$). Finally, in the Locustidæ (fig. 13) there is a conspicuous arched anterior subdivision (PN_3) of the

apparent first abdominal tergum (*IT*), which fits closely into the concavity under the posterior edge of the metanotum (*N*₃).

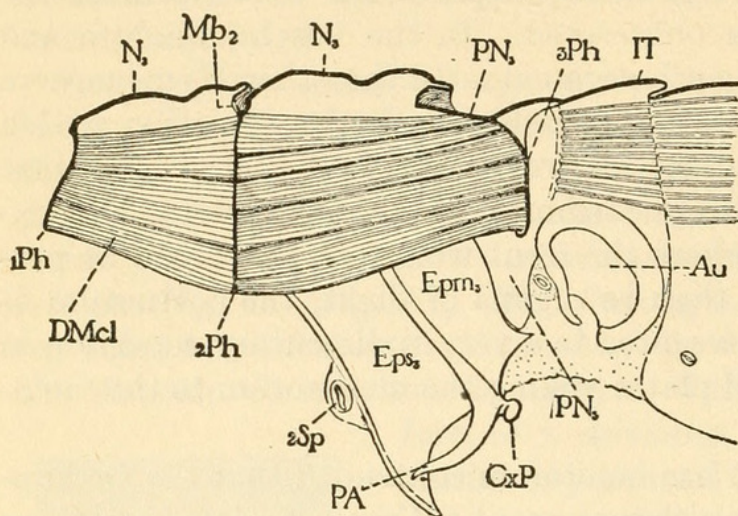


FIG. 12.—LONGITUDINAL SECTION THROUGH BACK OF MESOTHORAX, METATHORAX, AND BASE OF ABDOMEN OF A LOCUST (*TRIMEROTRYPUS MARITIMA*): *Au*, "AUDITORY ORGAN;" *CxP*, COXAL PROCESS OF METAPLEURUM; *DMcl*, DORSAL LONGITUDINAL MUSCLES; *Epm*₃, EPIMERUM OF METATHORAX; *Eps*₃, EPISTERNUM OF METATHORAX; *IT*, FIRST ABDOMINAL TERGUM; *Mb*₂, POSTNOTAL MEMBRANE OF MESOTHORAX; *N*₂, MESONOTUM; *N*₃, METANOTUM; *PA*, PLEURAL ARM; *PN*₃, PLATE FUSED WITH FIRST ABDOMINAL TERGUM (*IT*), WHICH IS PROBABLY THE POSTNOTUM OF METATHORAX; *1Ph*, *2Ph*, *3Ph*, ANTERIOR MIDDLE AND POSTERIOR PHRAGMAS; *2Sp*, SECOND THORACIC SPIRACLE.

The question hence arises, in making an interpretation of these parts in the Orthoptera, whether the true postnotum of the metathorax has been fused with the first tergum of the abdomen, or whether the posterior ends of the dorsal muscles and the phragma, when present, have become attached to the first abdominal tergum. Since the middle phragma, as will presently be shown, is in some orders attached to the posterior edge of the

mesothorax and in others to the anterior edge of the metathorax, there would seem to be no logical reason why the posterior phragma should not sometimes be attached to the front of the first abdominal tergum. Woodworth (1909), in fact, argues that the phragmas really belong in all cases to the segment following them. The writer, however, believes that the phragmas are intersegmental, or are composed of lamellæ derived from both segments, and that they become secondarily more solidly associated with the one segment or the other. Berlese (1906) regards the plate in question in the Orthoptera as the "acrotergite" of the first abdominal segment, but he homologizes it

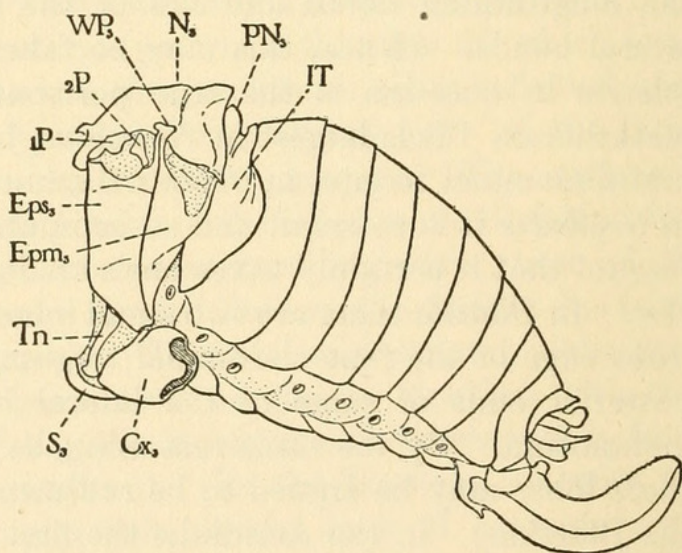


FIG. 13.—METATHORAX AND ABDOMEN OF A LONG-HORNED GRASSHOPPER (*SCUDDERIA FURCATA*), SHOWING THE APPARENT POSTNOTUM OF THE METATHORAX (*PN*₃) INTIMATELY FUSED WITH THE FIRST ABDOMINAL TERGUM (*IT*): *Cx*₃, METACOKA; *Eps*₃, *Epm*₃, EPISTERNUM AND EPIMERUM OF METATHORAX; *IT*, FIRST ABDOMINAL TERGUM; *N*₃, METANOTUM; *1P*, *2P*, EPISTERNAL PARAPTERA; *PN*₃, THE APPARENT POSTNOTUM OF METATHORAX; *S*₃, METASTERNUM; *Tn*, TROCHANTIN; *WP*₃, PLEURAL WING PROCESS.

with the metapostnotum of some other orders, such as the Coleoptera, which he also refers to the abdomen. In the Coleoptera the postnotum of the metatergum is a very distinct plate. While it is sometimes attached to the front of the abdomen, it seldom appears in this order to be a part of the abdominal tergum, and it nearly always retains a connection with the epimera of the metathorax.

With regard to the so-called "postscutellum" of the metathorax in the Orthoptera, then, the writer reiterates his former statement, that it is, by anatomical continuity, a part of the first abdominal tergum. Theoretically, it may be the postnotum of the metathorax, but reason should be shown why the dorsal muscles of the metathorax and even the posterior phragma may not, in some cases, be attached to the first abdominal tergum, just as these muscles of the mesothorax (fig. 12, *DMcl*) and the middle phragma (*2Ph*) are, in many cases, attached to the front of the metathoracic tergum (*N₃*). The Mantidæ and Phasmidæ do not show any anterior subdivision of the first abdominal tergum, nor do they have any trace of an independent postnotum in either segment. Hence, the Orthoptera do not have a postnotum at all in the mesothorax and, if they have this plate in the metathorax, it is developed best in the higher families and always apparently as an intimate part of the first abdominal tergum.

This brings us to the question concerning the nature of the phragmas and the reason for their relation to the postnotal plates stated on page 45. The phragmas, as already described, are the internal transverse plates descending into the body cavity from between the thoracic and first abdominal terga. There are consequently never more than three of them present; often only one or two are well developed, while in some cases there are no traces of any phragmas at all. Kirby and Spence (1826) named them the "prophragma," the "mesophragma," and the "metaphragma," but, since their connections with individual segments are secondary and variable, it seems best to call them the *anterior*, *middle*, and *posterior* phragmas. Each is composed, in its upper part at least, of two closely appressed or fused laminae, and, in the adult stage, is attached to one of the two adjoining terga or to both. The first or anterior phragma is always, so far as the writer has observed, attached to the front of the mesotergum. The second or middle phragma is sometimes attached to the posterior edge of the mesotergum and sometimes to the anterior edge of the metatergum, or, when these two plates are anchylosed, to both of them. The third is always, unless the Orthoptera constitute an exception, attached to the posterior edge of the metatergum, or to both this plate and the first abdominal tergum when these two parts are anchylosed.

That this association of the phragmas in the adult stage with one or the other of the adjoining terga is a secondary condition is suggested by a study of figures 14, 15, and 16. The section through

the back plates of the nymph of a stonefly (fig. 14) shows that the dorsal muscles (*DMcl*) are segmentally arranged, being attached to the anterior and posterior parts of the same segment, i. e., just back of and just before the intersegmental constrictions. The corresponding sections of adult stoneflies (figs. 15 and 16) indicate that the phragmas (*2Ph* and *3Ph*) are simply downward ingrowths from the deepest parts of the intersegmental grooves to accommodate the increased thickness of the dorsal muscles (*DMcl*). Hence, the phragmas appear to be truly intersegmental in their origin, and it may easily be imagined that the common bilaminate structure results

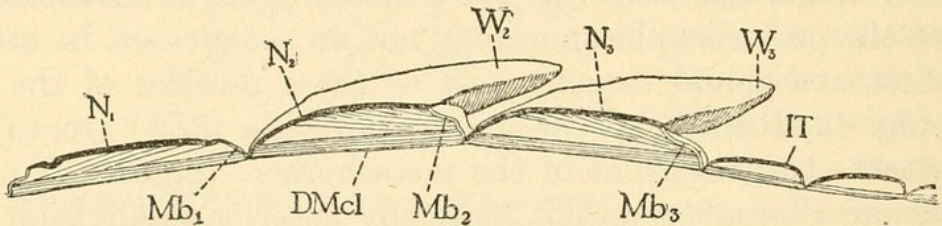


FIG. 14.—LONGITUDINAL SECTION THROUGH BACK OF THORAX AND BASE OF ABDOMEN OF A STONEFLY NYMPH (*ISOGENUS*), SHOWING EACH BACK PLATE OF THE THORAX SEPARATED FROM THE ONE BEHIND IT BY A WIDE POSTNOTAL MEMBRANE: *DMcl*, DORSAL LONGITUDINAL MUSCLES; *IT*, FIRST ABDOMINAL TERGUM; *Mb1*, *Mb2*, *Mb3*, POSTNOTAL MEMBRANES; *N1*, PRONOTUM; *N2*, MESONOTUM; *N3*, METANOTUM; *W2*, FRONT WING; *W3*, HIND WING.

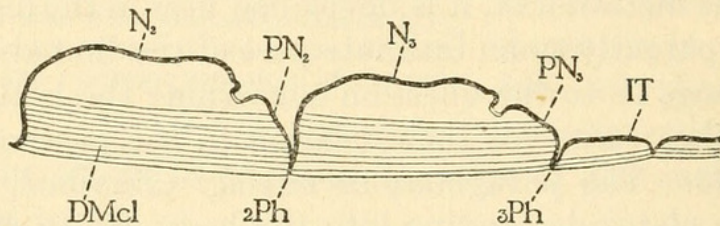


FIG. 15.—LONGITUDINAL SECTION THROUGH BACK OF MESOTHORAX, METATHORAX AND BASE OF ABDOMEN OF AN ADULT STONEFLY (*ALLOPERLA*) SHOWING POSTNOTAL PLATES (*PN2*, *PN3*) OCCUPYING POSITION OF POSTNOTAL MEMBRANES (*Mb2*, *Mb3*) IN FIG. 14: *2Ph*, *3Ph*, SECOND AND THIRD PHRAGMAS; OTHER LETTERING AS IN FIG. 14.

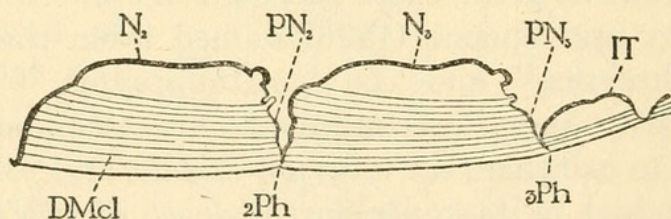


FIG. 16.—CORRESPONDING SECTION THROUGH ANOTHER ADULT STONEFLY (*TÆNIPTERYX FRIGIDA*), SHOWING SAME THING AS FIG. 15: LETTERING AS IN FIGS. 14 AND 15.

from an apposition and fusion of the infolded surfaces of the adjoining terga, thus increasing the depth of the phragmas.

In such forms as *Alloperla* (fig. 15) and *Tænipteryx* (fig. 16) it is seen that there is no movable articulation between the mesotergum and the metatergum, the two being united in the middle phragma (*2Ph*). But in most insects there is more or less motion possible between these two parts due to an intervening membranous area, as in the Orthoptera and Coleoptera. Fig. 12, representing a longitudinal section through the back of a grasshopper, shows that while the middle phragma (*2Ph*) is solidly attached to the front of the metanotum (*N3*), it is separated from the mesonotum (*N2*) by a narrow mem-

brane (Mb_2). Hence, while the latter would ordinarily be called the "intersegmental membrane," it is clear that it lies before the original intersegmental line and really belongs to the posterior part of the mesodorsum. The same must be true of the membrane between the prothorax and the mesothorax, since the anterior phragma ($1Ph$) is solidly attached to the front of the mesotergum. In other insects, where the middle phragma is attached to the posterior edge of the mesotergum, the "intersegmental membrane" behind it must really belong to the front of the metadorsum. Therefore, in general, if the phragmas are truly intersegmental structures, the real intersegmental lines pass through them, where phragmas are present, and the deepest part between the two laminae of any one is the true demarkation between the segments adjoining it. Woodworth (1909) is inclined to doubt this view, holding that "a more reasonable position would seem to be that the infolding for the attachment of intersegmental muscles marks the posterior boundary of the prescutum, that the phragma belongs entirely to the following segment, and that with the completion of the chitinization of the articular membrane, the division is lost somewhere immediately anterior to the phragma." Thus he claims that "the anterior phragma is mesoprescutal; the posterior is a part of the first abdominal segment." The present writer objects to this theory on the ground that, as he thinks, the facts do not substantiate it, but demonstrate the opposite view stated above.

The function of the phragmas is to give an increased surface of attachment for the longitudinal muscles of the back. These muscles are greatly developed in the wing-bearing segments of nearly all strong-flying insects (the dragon flies excepted) because they are the ones that produce the downward stroke of the wings during flight, the upward stroke being produced by the vertical muscles of the thorax. When the latter muscles contract they depress the back plates, which in turn pull down the bases of the wings, thereby throwing up the distal parts of these organs, the fulcrum being the wing processes of the pleura. The succeeding contraction, then, of the longitudinal muscles restores the shape of the thorax and consequently elevates the back plates, which, by the same mechanism as before, force the wings downward. It is thus seen that the phragmas have an important association with the function of the wings. The other elements in the wing motion are produced by smaller muscles inserted directly upon the wing bases, but these are not material to the present discussion.

Furthermore, there is a relationship between the phragmas and the postnotal plates which, in general, may be stated as follows: When a phragma is associated with the posterior part of a segment it is attached to a postnotal plate of the tergum, which plate is usually otherwise lacking. Or, conversely, when the tergum of either segment possesses a postnotal plate it usually possesses also a post-

phragma. Consequently, in the case of the mesothorax a postnotum is present in most cases only when the middle phragma is present and attached to the mesotergum; in the case of the metathorax, a postnotum is present in most cases only when the posterior phragma is present. The anterior phragma being never attached to the protergum, the prothorax never possesses a postnotum. The postnotum is lacking in the mesothorax of Orthoptera, Euplexoptera, and Coleoptera, in which orders the middle phragma is attached to the front of the metatergum. It is greatly reduced or obliterated in the metathorax of the Diptera and in most of the higher Lepidoptera, which have but a weakly developed posterior phragma or none at all. On the other hand, it is present in both segments of the Ephemera, Odonata, Plecoptera, Corrodentia, Neuroptera, Trichoptera, and the lower Lepidoptera, while it is well developed in the mesothorax of the higher Lepidoptera, and reaches its greatest size in the mesothorax of the Diptera, which have an extremely large middle phragma attached to this segment. In the Tenthredinoidea and Siricoidea of the Hymenoptera it is well developed in each segment; in the other Hymenoptera the postnotum of the mesothorax becomes buried between the segments, while that of the metathorax fuses with the first abdominal tergum.

If, now, we compare this distribution of the postnotum through the various orders with the development of the wings, it at once becomes evident that the postnotum is present in those segments that have the wings developed as organs of flight and that its size varies directly with the development of the power of flight. Thus, the front wings of the Orthoptera, Euplexoptera, and Coleoptera are developed principally as protective organs, while in the higher Lepidoptera and Hymenoptera they are the principal, and in the Diptera the only, organs of flight. In the other orders that use the two wings more equally, the postnotal plates are about equal in the two segments, except the Isoptera, which, as has already been stated, do not possess a postnotum in either segment.^a

The Hemiptera appear to be somewhat contradictory to the above statements in some ways. *Belostoma*, for example, and probably all

^a Each wing-bearing tergum of the Isoptera consists of only one plate which, though in some cases almost cut by the deep lateral emarginations into two parts, the "antedorsum" and "postdorsum" of Enderlein (1903), is yet clearly the notum because of the wing attachments to it. The writer has examined representatives of *Termopsis*, *Calotermes*, *Copritermes*, *Microtermes*, *Armitermes*, and *Eutermes* but has found no trace of a postnotum in either segment. A very small set of dorsal longitudinal muscles is present attached to the front and rear of each segment, just as in the stonefly nymph. On the other hand the lateral dorso-ventral muscles are very large and extend from the anterior part of the notum to the epimeral plate of the coxa on each side. Each coxa has the appearance of being double—a distinctive character of the Neuroptera, Mecoptera, Trichoptera, and Lepidoptera. This and the absence of the postnotal plates would separate the Isoptera from the Corrodentia, with which they are frequently associated.

the Heteroptera, has a large postnotum in the mesothorax which carries the middle phragma, but it is deeply fused mesially into the front of the metanotum and looks like a prescutum of this segment. For this reason the writer made the erroneous statement in a former paper (1909) that the Belostomidæ have no postnotum in the mesothorax. However, that the plate in question is such is amply proven by its solid lateral connections with the mesepimera. *Cicada*, on the other hand, has a much smaller postnotum in the mesothorax, but the very large middle phragma is solidly attached to the lateral parts of this segment. In both *Cicada* and *Belostoma* the great mass of the thoracic muscles is in the mesothorax, though, judging from analogy with beetles, one would suppose that in *Belostoma*, at least, the hind wings must do most of the flying.

In general, however, it is evident that the attachment of a phragma to the posterior part of either segment and its size are dependent upon the development of the power of flight in that segment, and that the postnotal plates are developed to support the phragmas. There are, of course, many apparent minor exceptions to this where a comparatively large postnotum is present bearing only a small or even a rudimentary phragma. But, in such cases, the dorsal muscle fibers are attached posteriorly to the postnotum itself, which thus serves as both postnotum and phragma.^a In fact, many writers have made no distinction between the phragmas and the surface plates to which they are attached, defining the "prescutum" as the exposed part of the prephragma and the "postscutellum" as the exposed part of the postphragma of any segment. The present writer, however, for reasons based on the following facts, prefers to distinguish between the phragma and its surface support.

The reader's attention has already been directed to figure 11, showing the back of a stonefly nymph, in which each thoracic tergum consists of a simple notal plate separated from the one behind by a wide membrane. Figure 14 is a longitudinal section through the back of a similar form. The depressions mark the constrictions between the segments. It is, hence, evident that the membranes (Mb_1 , Mb_2 , Mb_3) are not truly intersegmental, but are postnotal in position, since they occur between the notal plates (N_1 , N_2 , N_3), and the posterior limits of the segments. If, now, this figure be compared with figures 15 and 16, showing corresponding sections through the mesothorax and metathorax of adult stoneflies, it will be seen that the postnotal membranes are mostly replaced by postnotal chitinizations

^aThe Odonata constitute a very prominent exception to many of the above statements. They have large postnotal plates in each wing-bearing segment but possess neither phragmas nor longitudinal thoracic muscles. Their wings are moved entirely by the great dorsoventral muscles which are inserted by means of stalked disks upon the bases of the wings themselves and upon the adjoining parts of the nota. It may be that the postnotal plates here serve the purpose of lengthening the terga so as to give more space for the play of the wings.

(PN_2 , PN_3), which form conspicuous wide transverse plates on the surface of the dorsum behind the wing-bearing nota. In *Alloperla* (fig. 15) they are weakly continuous with the notal plates, but in almost all insects, where they occur, they are separated from the latter by narrow membranous sutures, as in *Tæniopteryx* (fig. 16). Therefore, it is clear that the so-called "postscutellum" is not a differentiation of the true notum, as is the prescutum, scutum, or scutellum, but is an additional plate, and, hence, the writer's ground for designating it by the more generally significant term of "postnotum."

Again examining figure 14 it will be seen that the dorsal longitudinal muscles ($DMcl$) are truly segmental at this stage of development. Woodworth (1909), however, thinks otherwise, for he says, "The great dorsal muscle of flight for which the phragma was developed is probably only a dorsal intersegmental muscle. These extend from the anterior edge of one segment to the corresponding part of the next." The writer can not see how the annular constrictions of any nymphal form can be anything else than the intersegmental lines. They certainly appear to correspond with the grooves between the embryonic somites. Moreover, the muscle somites of the embryo correspond with the body somites. This is true even in adults. If the thoracic and abdominal terga of *Machilis* be removed there are uncovered muscular segments exactly corresponding with the chitinous segments. As has already been pointed out, the postnotal membranes of the nymph (fig. 14, Mb) are not "intersegmental," but lie before the true intersegmental grooves. For this reason the longitudinal muscles of any segment may pull the succeeding segment forward, by their contraction, just as if their posterior ends were inserted upon the anterior edge of the latter segment.

If the ancestral insects were wingless creatures, as is universally conceded, then it must be assumed that the primitive function of the longitudinal muscles was the movement of the segments, principally the retraction of each into the preceding segment for purposes of locomotion or respiration. It follows next, as a corollary to this, that the part these muscles play in the movement of the wings in modern insects has secondarily devolved upon them in the mesothorax and metathorax. Now, in order that the contraction of these muscles may change the shape of these two segments instead of telescoping them, it is clear that the postnotal membranes must be obliterated in some way, so that the chitinous parts shall abut against each other. We can imagine that this might be effected in three ways: (1) By a posterior extension of each notum till it should meet the succeeding notum, (2) by a chitinization of the postnotal membranes, or (3) by a shortening of these membranes. There is no evidence that the first has ever happened—no insect shows a posterior prolongation of the notum behind the scutellum, which would be a true postscutellum, though the scutellum itself is often enlarged

so as to *overlap* the segment behind. The second process has taken place in those segments of all species that have a postphragma, including many that have only a rudimentary phragma, and has resulted in the formation of the postnotum wherever this sclerite occurs. The third process may be supposed to have taken place in the mesothorax of those orders that have no postphragma and no postnotum in this segment, and in which the notum lies close to that of the succeeding segment, if indeed it is to be assumed that this condition is primitive in such cases and not secondary. The reduction or absence of the postnotum in the metathorax is, of course, a secondary modification consequent upon the reduction of the hind wings. The anterior phragma and the posterior phragma are constant in their attachment to the front of the mesotergum and the back of the metatergum, respectively, while the middle phragma is assigned to the segment most in need of it. When the front wings are used in flight as much as the others or more the middle phragma is attached to the mesotergum; when the hind wings are the chief organs of flight it is attached to the metatergum. Thus it results that the principal flight segment is always provided with both a prephragma and a postphragma, while the other is left with only a prephragma or a postphragma. In this way the longitudinal muscles of this favored segment are enabled to act most forcibly on the tergum, though at the expense of some of the power of the muscles of the other segment. In the higher Hymenoptera this specialization has been carried so far that the metathoracic muscles are rudimentary, while the great mesothoracic mass of muscles effects the thorax as a whole, producing the motion of both pairs of wings.

Thus it is possible to see a reason for the fundamental structure of the wing-bearing thoracic terga, a structure which follows logically from the assumption that the flight function has been secondarily acquired, and that extra parts had to be added to the primitive notal plates to enable the longitudinal muscles to depress the wings by elevating the notal plates, instead of pulling the segments together, which latter was their original function. Furthermore, the strain of these muscles on the notum must be held partly responsible for the modifications of this plate. However, since the function of elevating the wings devolved upon the primitive vertical muscles of the mesothorax and metathorax, it can not be doubted that the primary cause of the modifications of the notal plates is to be traced to this latter source.

The foregoing is a brief review of a subject that might be studied and illustrated in much greater detail. The basis of the writer's information is contained in his former paper (1909) on the thorax of insects, in which, however, he would now make certain modifications mentioned in the present paper. It is hoped that enough new material is given here, first, to substantiate the claim that each wing-bearing tergum of the insect thorax is not composed of four con-

secutive elements, as so often described, but consists of one principal wing-bearing plate and of a secondary postalar plate, the first of which becomes differentiated into the secondary regions termed prescutum, scutum, and scutellum; and, second, to show a logical reason for this structure, based on the necessity for it, arising when the primitive segmental muscles had to take on them the newly acquired duties of moving the wings.

4. STRUCTURE OF THE HYMENOPTERAN THORAX.

This paper is designed especially to elucidate the external morphology of the thorax of the nonaculeate Hymenoptera. Therefore the Aculeata have been illustrated by only three forms selected from three representative families. The writer has, furthermore, made no attempt to apply the facts of anatomy to the classification of the families. This must be done by systematists who are widely acquainted with the comparative structure of all the different parts of the body. Writers who become intimately acquainted with one set of characters are ever prone to reconstruct classifications on a basis of their specialty and are as often misled by the narrowness of their horizon. Any system of taxonomy or phylogeny must be founded on a consideration of all the characters of all the forms concerned.

The following is a list of the species studied, arranged according to the present classification by Hymenopteran systematists:

I. TENTHREDINOIDEA.

PAMPHILIDÆ.

Bactroceros pallimacula (Norton).—fig. 17.

TENTHREDINIDÆ.

ARGINÆ.

Arge, species.—figs. 10–12, 14, 15.

NEMATINÆ.

Lygænematis erichsoni (Hartig).—fig. 18.

DOLERINÆ.

Dolerus aprilis Norton.—fig. 13.

CIMBICINÆ.

Trichiosoma lanuginosa Kirby.—figs. 16, 19.

II. SIRICOIDEA.

SIRICIDÆ.

Tremex columba (Linnæus).—figs. 1–9.

III. ICHNEUMONOIDEA.

BRACONIDÆ (Of the numerous subfamilies of this group the following two have been selected as the ones most likely to show the extremes of variation).

BRACONINÆ.

Eurobracon penetrator (Smith).—fig. 20.

APHIDIINÆ.

Diæretus piceus (Cresson).

III. ICHNEUMONOIDEA—Continued.

CAPITONIIDÆ. (This family consists of at most four genera, of which *Capitonius* is the best known).

Capitonius ashmeadii Dalla Torre.—fig. 21.

EVANIIDÆ. (This family includes three subfamilies—the Evaniinæ, Aulacinæ, and Fœninæ.)

AULACINÆ.

Odontaulacus editus (Cresson).—fig. 22. a

ICHNEUMONIDÆ.

OPHIONINÆ.

Erymotylus macrurus (Linnæus).—figs. 23, 33.

TRYPHONINÆ.

Metopius pollinatorius (Say).—fig. 24.

PIMPLINÆ.

Megarhyssa lunator (Fabricius).—fig. 25.

CRYPTINÆ.

Cryptus extrematus Cresson.—fig. 26.

ICHNEUMONINÆ.

Trogus lutorius (Fabricius).—figs. 27, 29, 30, 32.

Allomya debellator (Fabricius).—fig. 28, 31.

IV. CHALCIDOIDEA. (According to Ashmead there are fourteen families in this group. The following eight are selected to show the range in variation of thoracic structure.)

TORYMIDÆ.

TORYMINÆ.

Syntomaspis racemariæ (Ashmead).—fig. 34.

CHALCIDIDÆ.

LEUCOSPIDINÆ.

Leucospis affinis Say.—figs. 35–39.

EURYTOMIDÆ.

EURYTOMINÆ.

Eurytoma diastrophii boltenii Riley.—fig. 46.

MISCOGASTERIDÆ.

TRIDYMINÆ.

Hemadas nubilipennis (Ashmead).

ENCYRTIDÆ.

EUPELMINÆ.

Cerambycobius cushmani Crawford.—figs. 40, 41.

ENCYRTINÆ.

Microterys, species.—figs. 42, 43.

PTEROMALIDÆ.

PTEROMALINÆ.

Catolaccus incertus Ashmead.—fig. 44.

ELASMIDÆ.

Elasmus atratus Howard.

IV. CHALCIDOIDEA—Continued.

EULOPHIDÆ.

APHELININÆ.

Coccophagus lecanii (Fitch).—fig. 45.

Prospaltella berlesii (Howard).—fig. 47.

EULOPHINÆ.

Dimmockia incongruus (Ashmead).—fig. 48.

V. CYNIPOIDEA.

FIGITIDÆ.

FIGITINÆ.

Figites floridanus Ashmead.—fig. 50.

ENCOILINÆ.

Hexaplasta, species.—fig. 49.

CYNIPIDÆ.

CYNIPINÆ.

Rhodites mayri Schlechtendal.—fig. 51.

VI. PROCTOTRYPOIDEA. (The following four families are selected as representative of the seven families comprising this group.)

HELORIDÆ.

HELORINÆ.

Helorus paradoxus (Provancher).—fig. 58.

PROCTOTRYPIDÆ.

Proctotrypes caudatus Say.—figs. 53, 57.

DIAPRIIDÆ.

DIAPRIINÆ.

Tropidopria conica (Fabricius).—fig. 59.

SCELIONIDÆ.

TELENOMINÆ.

Telenomus ashmeadi Morrill.—fig. 60.

VII. ACULEATA. (The following three aculeate families have been selected as representative of the superfamilies included under this head.)

CEROPALIDÆ (formerly POMPILIDÆ).

Pepsis formosa Say.—fig. 61.

MYRMECIDÆ.

Pogonomyrmex transversus (Smith).—fig. 62.

APIDÆ.

Apis mellifera Linnæus.—fig. 63.

1. THE THORAX OF TREMEX COLUMBA AND THE TENTHREDINOIDEA.

Before undertaking a comparative study of the Hymenopteran thorax it is most important to become thoroughly acquainted with the thoracic structure in one of the more generalized members of the order. In most of the higher families the original structure is so obliterated, while secondary characters are so prominent, that the

student of any one group is almost sure to be misled in his interpretations of the morphology. The writer has selected the horntail, *Tremex columba*, as the subject of a preliminary description, both because its thorax is very generalized in structure and because it is a large and widely distributed species.

Figure 1 on plate 1 shows a side view of the thorax and the base of the abdomen, the wings being entirely removed and the legs detached from their basal joints or coxæ (Cx_1 , Cx_2 , Cx_3). Since the latter are unmistakable landmarks, they make good starting points for a morphological orientation. The plate to which the first coxa (Cx_1) is attached is the propleurum, consisting in *Tremex* entirely of the proepisternum (Eps_1). Each curves mesally over the ventral surface of the prothorax, so that the two almost meet along the midline (2, Eps_1) in front of the small prosternum (S_1). Above these episternal plates is the large protergum (1, N_1), forming a cap over the anterior end of the mesothorax. Just behind its lateral margin on each side is a small sclerite containing the anterior thoracic spiracle (1 Sp). It will be noticed that the pronotum is associated much more closely with the mesothorax than it is with the pleural and sternal parts of its own segment, these latter, which together constitute the propectus, forming a loose suspensorium for the front legs.

Between the front coxa and the middle coxa on each side are the plates of the mesopleurum—the mesepisternum (Eps_2) and the mesepimerum (Epm_2). They are separated by the distinct mesopleural suture (PS_2) extending upward and forward from the articulation of the coxa into the mesopleural wing process (WP_2) which supports the front wing from below. The small irregular sclerite lying before the wing process is the parapterum of the mesothorax (P_2). The episternum (Eps_2) is not separated in *Tremex* from the mesosternum (S_2), though in many other species the two are divided by a distinct suture. Above the mesopleura is the mesonotum (N_2), consisting principally of the scutum (Sct_2) and the scutellum (Scl_2). Beneath the posterior edge of the latter is seen a part of the mesopostnotum (PN_2), whose lateral parts are attached to the mesepimera (Epm_2).

Between the mesocoxa (Cx_2) and the metacoxa (Cx_3) are the two plates of the metapleurum, the metepisternum (Eps_3) and the metepimerum (Epm_3), separated by the oblique metapleural suture (PS_3). The last ends above in the slender metapleural wing process (WP_2) which supports the hind wing. In front of it is the small parapterum of the metathorax (P_3). Between the latter and the mesepimerum (Epm_2) is a small sclerite containing the posterior thoracic spiracle (2 Sp). Above the metapleura are three dorsal sclerites (N_3 , PN_3 , and IT). The first is the metanotum (N_3) and carries the hind wings. The second is the metapostnotum (PN_3), though it is more closely attached to the plate following it than to the metanotum. The third is the first abdominal tergum (IT) containing the first

abdominal spiracles (*ISp*). Both the metapostnotum and the first abdominal tergum are divided along the median dorsal line into two lateral plates (6, *PN*₃ and *IT*). The metasternum, like the mesosternum, is continuously fused with the episterna of its segment.

The thoracic homologies, as presented in the above account, certainly seem indisputable when the parts of each segment are compared with those of any of the generalized orders of insects. For example, compare the mesothorax of *Tremex* with either segment of an adult stonefly such as *Tæniopteryx frigida* (fig. 5). The two pleural plates (*Eps* and *Epm*) of *Tæniopteryx*, separated by the pleural suture (*PS*), are identical with those of the mesothorax of *Tremex* (1). The pleural suture (*PS*) in each case extends from the coxal articulation into the wing process (*WP*). The parapterum (*P*) lies before the latter in both, though it is attached to the episternum in the stonefly. The notum (*N*) is unquestionably the same plate in each case, and the postnotum (*PN*) in each is connected with the posterior angles of the epimera (*Epm*). The ventral parts are different in that the sternum (*S*) of the stonefly is separated from the episternum (*Eps*) by a suture (*q*), and the coxa (*Cx*) is articulated below to a sclerite, the trochantin (*Tn*), which does not occur in *Tremex*. It will be shown later that many Hymenoptera, however, possess a sterno-pleural suture on each side corresponding with that of *Tæniopteryx*. The structure of the metathorax of *Tremex* but duplicates that of the mesothorax, the differences being simply in the size and the shape of the parts.

Marlatt (1896) has described and figured the thorax of a sawfly, *Lygænematus* (*Pachynematus*) *erichsonii*. He calls the large mesepisternum (18, *Eps*₂) the "epimeron" of the mesothorax, while he calls the true mesepimerum (*Epm*₂) a "posterior plate of the epimeron." In the metathorax he calls the episternum (*Eps*₃) the "epimeron," while he does not name the true epimerum (*Epm*₃) of this segment. The plates of the first abdominal tergum he calls the "scutellum" of the metathorax, but does not say how they come to carry the first abdominal spiracles (*ISp*). The writer can produce no argument against these interpretations so effective as that to be derived from a comparison of the sawfly (18) with a stonefly (fig. 5) or a grasshopper (fig. 13). Systematists in general, who have attempted to explain the thoracic anatomy of the Hymenoptera, have made so many inconsistent applications of anatomical names that space can not be given here to a review of their works.

We may now more conveniently make a detailed study of each part of the thorax separately and at the same time note the modifications that occur in the Tenthredinoidea, for some of them are, in some ways, more generalized than *Tremex*.

The **pronotum**, as already stated, appears to belong to the front of the mesothorax rather than to the prothorax. Its posterior lateral angles are more or less produced toward the bases of the wings, often forming a distinct lobe (1, N_1 , w) on each side partially overlapping the first spiracle ($1Sp$). In other families it usually completely covers and conceals the spiracle.

The **propectus** is always very loosely connected with the pronotum by membrane, and its lateral parts reach forward in the walls of the neck to the base of the head. In *Tremex*, as already described, the propleurum consists of the episternal plates alone (1, 2, Eps_1), but many other forms show at least a trace of an epimerum. In a species of *Arge* (12) both pleural plates (Eps_1 and Epm_1) are well developed and are separated by a distinct pleural suture (PS), just as in any other segment. *Lygænematus erichsonii* (18) also possesses a comparatively large proepimerum (Epm_1). The posterior angle of the epimerum is produced internally as a large epimeral arm (12, $EpmA$), but when the epimerum is absent this arm appears to arise from the episternum (2). This internal process is apparently not the homologue of the pleural arm of other segments (9, PA), since it does not arise from between the pleural plates.

The prosternum (2, 12, S_1) is a small plate lying between the front coxæ (Cx_1) and behind the ventral parts of the episterna (Eps_1). It carries two internal apodemes constituting the anterior or prosternal furca (2, Fu). In *Tremex columba* a small plate (2, d) lies between the prosternum and the coxa on each side, and in *Arge* there is a smaller one on the side (12, e) between the coxa, the sternum, and the episternum.

Many entomologists regard the prothoracic plates that the writer calls the episterna as the prosternum. Most of them, however, apparently do not observe that the true prothoracic sternum lies behind these plates and between the bases of the coxæ. Berlese (1906) defines the lateral part of each pleural plate as the "episternum" and the ventral part as the "mesosternite" of the mesosternum. The true prosternum he calls the "metasternite." In studying *Scolia rufifrons* he finds two other parts, which are illustrated as well by *Scolia dubia* (fig. 17), the first being a median subdivision (A and B, n) of the episternum (Eps), which he calls the "prosternite," the second a median sclerite (l) in the ventral wall of the neck, which he calls the "acrosternite." Thus Berlese is able to establish in the Hymenopteran prothorax the four consecutive parts which he thinks are the primitive elements of every sternum. The only contrary argument to this homology is that appearances are too strongly against it. The lateral ridge (fig. 17 A, j) simply marks the line where the edge of the pronotum laps over the episternum, while

Berlese's interpretations of the other parts (*l* and *n*) appear purely fanciful to the writer of this paper.

Cervical sclerites are of unusual occurrence in the Hymenoptera. A small chitinous piece occurs on each side of the neck in the honey bee (63, *i*) just below the anterior knob of the proepisternum (*Eps*₁). The ventral plate in the neck of *Scolia dubia* (fig. 17 B, *l*) appears to be a cervical sclerite rather than a prothoracic sternite. In *Dolerus aprilis* there is a small dorsal cervical (13, *g*). Crampton (1909), from a study of *Dolerus*, concludes that the plate called the proepisternum (*Eps*₁) in this paper is really in large part a lateral cervical sclerite. In *Dolerus aprilis* (13) it presents a small posterior subdivision (*eps*₁) just in front of the pleural suture (*PS*) which separates it from the small epimerum (*Epm*₁). This small piece (*eps*₁) alone Crampton thinks is the true prothoracic episternum, the larger anterior part (*Eps*₁) being a lateral cervical sclerite. The slender sclerite

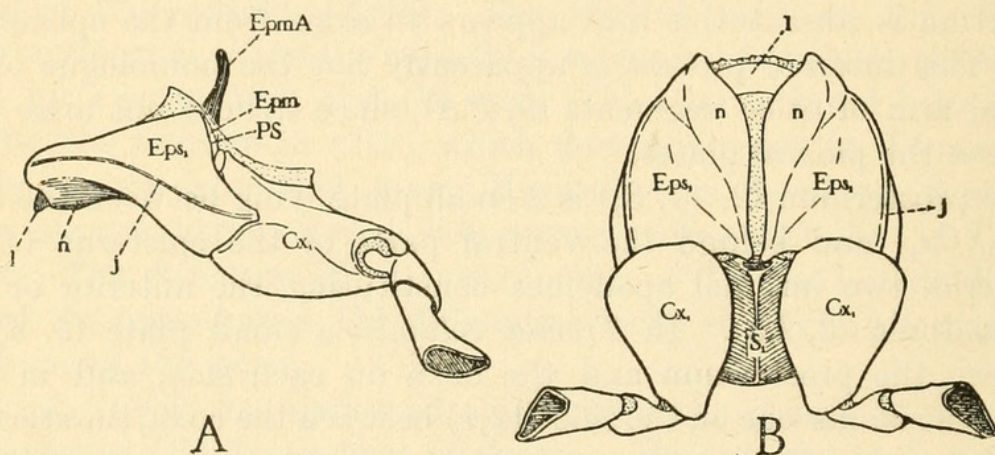


FIG. 17.—PROPECTUS OF *SCOLIA DUBIA*; A, LATERAL VIEW; B, VENTRAL VIEW: *Cx*₁, PROCOXA; *Epm*₁, EPI-MERUM; *EpmA*, EPIMERAL ARM; *Eps*₁, EPISTERNUM; *j*, RIDGE ON SIDE OF EPISTERNUM WHERE EDGE OF PRONOTUM OVERLAPS IT; *l*, VENTRAL CERVICAL SCLERITE; *n*, VENTRAL SUBDIVISION OF EPISTERNUM; *PS*, PLEURAL SUTURE; *S*₁, PROSTERNUM.

(*f*) along the upper edge of the latter he regards as a dorsal cervical. Hence, in all other forms he terms the large latero-ventral prothoracic plate, where it is not subdivided into two parts (*Eps*₁ and *eps*₁), the “cervico-propleuron.” While *Dolerus* may not be a unique example of the subdivision of the lateral propectal plate, it is certainly exceptional, and, to the writer of this paper, the structure of one genus does not seem a sufficient basis for so wide a generalization. The corresponding parts in *Arge* (12) certainly look much more primitive than those of *Dolerus* (13), and the plates (*Eps*₁ and *Epm*₁) on opposite sides of the pleural suture (*PS*) certainly here suggest that they are the episternum and the epimerum of the prothorax and nothing more. It is, then, simply a question of condensation *versus* differentiation. Is *Dolerus* primitive and have the simpler forms been produced by a complete fusion of the original parts, or is *Arge* primitive and has *Dolerus* secondarily acquired its

more complicated structure? The reader may take his choice. The writer adopts the second view because it is the simpler.

The **mesotergum** of *Tremex* (1) consists of a notum (N_2) and a postnotum (PN_2). The first is the large plate of the back, consisting of the mesoscutum (Sct_2) and mesoscutellum (Scl_2). The second (PN_2) is, in the normal condition, mostly hidden beneath the posterior edge of the scutellum, but when the metathorax is removed from the mesothorax the postnotum of the latter is found to be mostly invaginated into the groove between the two segments, for it is now seen to be a distinct plate (3, 4, PN_2) carrying a large two-lobed postphragma (Pph_2) projecting far backward through the metathoracic cavity.

On the anterior edge of the mesonotum is a prephragma (3, 4, Aph_2), while the lateral margins form the anterior and the posterior notal wing processes (ANP and PNP). On the under surface is a well-developed V-shaped entodorsal ridge (4, VNR) which forms the line (3, vnr) on the surface separating the scutum (Sct_2) from the scutellum (Scl_2). There is no prescutal division of the mesonotum in *Tremex*, though in many of the sawflies there is a distinct mesopre-scutum (10, 16–19, Psc_2) defined by a V-shaped suture (h). A small lobe on the posterior margin of the scutellum (3, o) might reasonably be termed the postscutellum if this name did not already belong to the postnotal plate.

The **mesopectus** of *Tremex* (5) consists of three principal plates, the combined sternum and episterna, and the two epimera. In many of the Tenthredinoidea, however, there are distinct sterno-pleural sutures, ventrad to the articulations of the mesocoxæ (10, 14, 16, 19, q), which separate the ventral sternum (S_2) from the lateral episterna (Eps_2). On the interior surface of the mesopleurum (9) is seen the heavy pleural ridge (PR) following the line of the pleural suture (1, PS_2), forming the wing process (9, WP) above and the coxal process (CxP) below. Just above the latter it gives off the small pleural arm (PA). In this view the parapterum (P) is seen to support a disk (PD). Upon this disk is inserted the upper end of the pronator muscle of the wing, the parapterum being connected with the head of the costal vein. In most of the sawflies there are two episternal paraptera in the mesothorax (10, 16, 18, 19, $1P$ and $2P$), but in other Hymenoptera the first is lacking. For this reason the single one present will be designated the second parapterum ($2P$). Fig. 5 on plate 1 gives a dorsal view of the interior of the mesopectus, showing the large furca (Fu) of the mesosternum (S_2).

The **metatergum** of *Tremex* consists of a narrow notum (1, 6, N_3) carrying the hind wings, and of two small postnotal plates (PN_3) attached to the first abdominal plates. The metanotum is very simple in all the Hymenoptera. In the Siricoidea and Tenthredi-

noidea it presents two little oval lobes on the dorsal surface called the cenchri (6, 11, *p*). The postnotum is always narrow, but in the Tenthredinoidea it is continuous across the back and is usually fused laterally with the epimera (11, 17, 18, 19, *PN*₃). In all of the Hymenoptera it is more closely attached to the first abdominal tergum than to the metanotum, and, in the higher forms, is often indistinguishably fused with the former.

The **metapectus** of *Tremex* (7) is very similar to the mesopectus (5) except that it is smaller. As in the latter, there are no sternopleural sutures, though in some of the Tenthredinoidea such sutures are present (11, *q*). The interior of the pleurum (8) is identical in structure with that of the mesothorax (9). Its external appearance has already been sufficiently described (1, *Eps*₃, *Epm*₃). The metafurca (7, *Fu*) is somewhat simpler in structure than the mesofurca (5, *Fu*).

The **first abdominal tergum** would scarcely be deserving of a special description in the Siridoidea and Tenthredinoidea were it not for the fact that it is intimately fused into the thorax in all the other Hymenoptera and constitutes the co-called "median segment," "propodeum," or "epinotum." In *Tremex* (1, 6, *IT*), as already described, it consists of two plates, but in most forms it is continuous across the back and always carries the first abdominal spiracles (*ISp*) laterally, in the Tenthredinoids often in a special lateral subdivision (11, 17, 18, 19, *It*).

2. MODIFICATION OF THE THORAX.

In the general study of the Hymenopteran thorax it is found that the structural departures from the comparatively simple thorax of *Tremex* and the Tenthredinoidea consist of progressive modifications along several lines. The chief of these may be stated under the following nine heads:

1. *The separation of the pronotum from the propectus and its attachment to the front of the mesothorax.*

The disassociation of the pronotum from the rest of the prothorax is evident even in the sawflies, as shown by *Bactroceros* (17), *Lygænematus* (18), and *Trichiosoma* (19). In the higher families, such as the bees (*Apis*, 63), it appears to be an integral part of the mesothorax. Its lateral parts nearly always reach far down on the sides, fitting into the angle between the base of the procoxa and mesopleurum. In the honey bee the lower ends extend mesally over the ventral surface till they meet on the midline so that the pronotum forms a complete collar about the front of the mesothorax. In *Proctotrypes caudatus* (57) the lower parts of the pronotum (*N*₁) not only meet each other, but they fuse into a wide ventral plate between the prosternum and the mesosternum, above the bases of the front coxæ. The pronotum in this case forms an entire annulus (54, *N*₁) surrounding the front of the mesothorax and inclosing the propectus (53, *S*₁ and *Eps*₁).

The propectus is freely movable on account of its membranous connection with the rest of the thorax. It serves both as a suspensorium for the front legs and as a support for the head, its lateral episternal parts being produced forward in the side walls of the neck as two processes which loosely articulate with the occiput (1, 2, 12, 13, 53, *v*). The evolution of the pleurum has already been indicated in the description of *Tremex*. In *Arge* (12) the episternum (Eps_1) and the epimerum (Epm_1) are well differentiated and are separated by a distinct pleural suture (PS). The epimerum is also present in *Dolerus* (13), *Lygænematus* (18), and others, but in general it is either absent or very rudimentary, the propleurum consisting of a single plate, the episternum, as in *Tremex* (1, Eps_1), *Leucospis* (36), and *Proctotrypes* (53). In *Dolerus* (13) there is a posterior subdivision (eps_1) of the episternum (Eps_1).

2. *The separation of the mesonotum into an anterior and a posterior plate by a transverse membranous suture.*

The mesonotum of *Tremex columba* is divided into a scutum (3, Sct_2) and a scutellum (Scl_2) by the line (*vnr*) of the entodorsal ridge (4, *VNR*). In some of the Tenthredinidæ there is an indistinct sutural line on each side, anterior to this ridge, extending toward the lateral emarginations of the notum (16, 17, 19, *k*). In nearly all the higher families of the Hymenoptera these two lines are continuous over the dorsum and constitute a distinct transverse suture (*k*) cutting the notum into two parts. This is shown in all the figures representing the mesonotum of the families from the Braconidæ (20) to the Apidæ (63). It is especially illustrated in *Erymotylus* (33, *k*), *Leucospis* (37, *k*), *Cerambycobius* (41, *k*), *Microterys* (42, *k*), *Eurytoma* (46, *k*), and *Proctotrypes* (55, *k*). This division of the mesonotum is so complete that in most cases it actually comes apart along this suture into two distinct plates, which are normally connected only by membrane. The posterior plate in some species has two flat apodemes on its front margin which slip under the posterior edge of the anterior plate. The anterior notal wing processes always arise from the sides of the first plate just in front of the lateral ends of the transverse suture (33, 46, 55, *ANP*), while the posterior processes (55, *PNP*) are situated on the edges of the posterior plate. The posterior notal plate may be called the scutellum (Scl_2), though it is clear that it is more than the equivalent of the scutellar division of the mesonotum of *Tremex* (3, Scl_2), which is defined by the line (*vnr*) of the entodorsal ridge (4, *VNR*). In a former paper the writer (1909) has demonstrated the impossibility of drawing strictly homologous lines between the subdivisions of the notum in different families and orders. The posterior edge of the scutum is generally differentiated as a marginal ridge or lobe bearing the axillary cords of the wing bases at its extremities. Such a subdivision as this might appropriately be called

the "postscutellum," but this term is preoccupied by the postnotum as used by most authors.

The anterior mesonotal plate is the scuto-prescutum, though the division into these two parts is often obscured. In most of the Tenthredinoidea there is present a distinct prescutum (10, 16-19, *Psc*₂), separated by a V-shaped suture (*h*) from the scutum (*Sct*₂). A similar prescutum is present also in some of the Ichneumonidæ, such as *Megarhyssa lunator* (25, *Psc*₂). In others, however, such as *Erymotylus macrurus* (33), the sides of the suture (*h*) extend backward toward the scutoscutellar suture (*k*) without meeting. In a great many of the Hymenoptera these separated halves of the scuto-prescutal suture form two distinct longitudinal lines on the anterior notal plate which subdivide the latter into a median and two lateral or parapsidal areas (*Euurobracon*, 20; *Odontaulacus*, 22; *Erymotylus*, 33; *Syntomaspis*, 34; *Eurytoma*, 46; *Tropidopria*, 58). The sutures are commonly called the *parapsidal sutures*, and the entire front plate for convenience may, in such cases, be called the scutum, as it is ordinarily termed. Yet it is evident that the median area (33, 46, *Psc*₂) is the prescutum prolonged posteriorly to meet the scutellum (*Scl*₂), and that the parapsides are the separated halves of the true scutum (*Sct*₂). In some forms, now, these parapsidal sutures (*h*) are absent, as in *Tremex* (3), *Trogus* (27), *Leucospis* (37), *Microterys* (42), *Coccophagus* (45), *Proctotrypes* (55), *Telenomus* (60), *Apis* (63), and others. In such cases it is to be supposed that the prescutal and scutal plates are fused, and while, for convenience, the anterior plate of the notum may be called the "scutum" it must be remembered that it is really a scuto-prescutal sclerite. In the Hymenoptera the anterior phragma is always attached to the anterior edge of the mesonotum and constitutes a prephragma of the mesothorax (3, 4, 10, 16, 30, 31, 37, 43, 52, 55, *Aph*₂).

3. *The concealment of the mesopostnotum and its phragma by invagination within the cavity of the thorax.*

The Tenthredinoidea (*Arge*, 10; *Trichiosoma*, 16, 19; *Lygænematus*, 18; and *Bactroceros*, 17) possess a distinct postnotum in the mesothorax (*PN*₂), consisting of an exposed transverse plate behind the scutellum (*Scl*₂) connected laterally with the mesothoracic epimera (*Epm*₂). It is visible externally also in *Tremex* (1, *PN*₂), but is less exposed here than in the Tenthredinoids. In all the other Hymenopteran families, however, it is normally concealed from view beneath the metanotum, for it is entirely invaginated into a pocket between the mesothorax and the metathorax, but when the mesotergum is removed from the surrounding parts the postnotum (*PN*₂) and its phragma (*Pph*₂) are brought to light (*Trogus*, 30; *Alomya*, 31; *Leucospis*, 37; *Proctotrypes*, 55). Lateral arms of the the postnotum usually maintain a hidden connection with the pos-

terior upper angles of the epimera. In *Apis* the median part of the postnotum is lacking, but the lateral parts remain as two arms attaching the postphragma to the angles of the mesothoracic epimera. The postphragma (Pph_2) is of variable size, but it is usually large and often projects through the metathorax far back into the cavity of the propodeum.

4. *The reduction of the metanotum to a simple transverse plate carrying the hind wings.*

In the Tenthredinoidea and Siricoidea the metanotum (1, 6, 11, 17, 18, 19, N_3) is a plate with more or less differentiation in its various parts and presents two little dorsal prominences called the *cenchri* (6, 11, $p.$). In the higher families, however, it is usually a very simple narrow plate (20, 26, 28, 57, 60, 63, N_3) lying between the mesonotum (N_2) and the metapostnotum (PN_3), the latter being often indistinguishably fused with the front of the propodeum (IT). Except in wingless forms the metanotum remains an individually separate plate of the dorsum, and may always be identified by the fact that it carries the hind wings laterally.

5. *The fusion of the metapostnotum with the propodeum or first abdominal segment.*

In the Tenthredinidæ the postnotum of the metathorax is a narrow transverse sclerite (11, 18, 19, PN_3) lying between the metanotum (N_3) and the first abdominal tergum (IT), though usually attached to the latter. In *Arge* (11) and *Trichiosoma* (19) it is continuous laterally with the metathoracic epimera (Epm_3). In *Tremex* (1, 6, PN_3) it consists of two narrow plates associated with the front of the first tergal plates of the abdomen (IT). In most of the other Hymenoptera, however, it constitutes a simple dorsal transverse yoke between the posterior angles of the metapleura. (*Trichiosoma*, 19; *Euurobracon*, 20; *Erymotylus*, 23; *Cryptus*, 26; *Proctotrypes*, 57; and *Pepsis*, 61.) While in such cases the metapostnotum is a distinct though often narrow sclerite between the metanotum in front and the propodeum behind, it is nearly always fused with the latter. In the highest phase of its evolution it becomes indistinguishably merged into the front of the propodeum (*Odontaulacus*, 22; *Syntomaspis*, 34; *Catolacus*, 44; *Coccophagus*, 45; *Dimmockia*, 48; *Rhodites*, 51; *Telenomus*, 60; *Apis*, 63). In such cases the dorsum of the thorax consists of five plates (see *Syntomaspis racemariæ*, 34, or *Dimmockia incongruus*, 48)—the pronotum (N_1), the mesoscuto-prescutum (Psc_2 and Sct_2), the mesoscutellum (Scl_2), the metanotum (N_3), and the propodeum (IT), including the metapostnotum. This suppression of the metapostnotum as an individual plate, together with the concealment of the mesopostnotum, has led to a very erroneous nomenclature on the part of Hymenopteran systematists. For example, according to the ordinary application of names to the back plates of any such species

as the examples cited above, the metanotum is called the "postscutellum of the mesothorax," while the propodeum, the true first abdominal segment, is called the "metathorax." Many systematists, of course, recognize the impropriety of such a nomenclature from an anatomical standpoint, but are still constrained from making a change on account of the confusion it would create in taxinomic literature. The object of the present paper is simply the determination of the true morphology of the plates as far as this can be done by a comparative study. As already pointed out in the introduction and elsewhere, morphological terms may often be too awkward for use in systematic descriptions. For example, in those species in which the metapostnotum and the first abdominal tergum are fused this combined plate may for convenience still be called simply the propodeum, though in other forms the first abdominal tergum alone receives this name.

6. *The fusion of the first abdominal segment with the metathorax and its complete incorporation into the thoracic division of the body.*

This character of the Hymenoptera is now so well known that it scarcely needs any discussion here. It is interesting to observe, however, that in such a form as *Sirex* (1) the first abdominal tergum (*IT*) is but slightly separated from the second segment (*II*), and the same is true in the Tenthredinidæ (18, 19). In *Bactroceros* (17) it is more distinctly separated from the rest of the abdomen, but is still most evidently the first abdominal tergum (*IT*). In all the Hymenopteran families above the Tenthredinoidea and Siricoidea, however, it certainly appears to be a part of the thorax, though it of course always carries the first abdominal spiracles (*ISp*). Its fusion with the metapostnotum has already been described. Laterally it fuses with the metapleura (*Pl*₃ and *pl*₃) in most of the higher families (20, 22, 24, 45), the line of separation being sometimes entirely obsolete (21, 50, 51).

This transferred abdominal segment was first called the "segment mediaire" by Latreille (1821), but the name "propodeon" given to it by Newman (1833) is more convenient to use. Emery (1900), and Wheeler (1910) following him, call it the "epinotum" in ants. One of the few modern authors who have argued that it belongs to the thorax is Marlatt (1896), who, following Westwood (1838) calls it the "metascutellum." A voluminous account of the history of the discussion concerning this plate is given by Gosch (1883).

7. *The formation of a single large mesopleural plate on each side by the narrowing of the mesepimerum and the suppression of the mesopleural suture, and its secondary division into an upper and a lower plate.*

In many of the Hymenoptera the pleurites are developed in a most typical form in both the mesothorax and the metathorax. Such is the case in all of the Tenthredinoidea and Siricoidea (1, 17, 18, 19) where a distinct episternum (*Eps*₂, *Eps*₃) and epimerum (*Epm*₂,

*Epm*₃) are present in each of these segments. The same is true of the mesopleurum of some of the Chalcidoidea (34, 37, 45, 47, 48), in which the episternum (*Eps*₂) and epimerum (*Epm*₂) are equally developed and are separated by a distinct pleural suture extending from the coxal articulation to the wing process (*WP*₂) just as in *Tremex* (1, *PS*₂). In the Chalcids and some other forms, however, the mesopleurum is complicated by the presence of a plate (*Ppct*) in front of the episternum, but this will be described later.

In the rest of the Hymenoptera there is a distinct tendency toward the reduction of the mesepimerum and the obliteration of the mesopleural suture with the result that the mesopleurum comes to consist of one large plate (50, 51, 52, *Pl*₂) carrying the wing articulation (*WP*₂) above and the coxal articulation below. In the Ichneumoidea the mesepimerum (20–28, 31, 32, *Epm*₂) is a narrow, though usually perfectly distinct, plate on the posterior edge of the large mesepisternum (*Eps*₂), being widest, amongst the species figured, in *Odontaulacus editus* (22). The suture separating this plate from the episternum is either a distinct line (20, 22, 23, 25, 26, 28) or is marked by a series of quadrate pits (21, 24, 27). In any case it can be identified as the pleural suture by examining the interior face of the thoracic wall, for its course is here marked by a distinct pleural ridge (32, *PR*) extending from the coxa to the wing process (*WP*₂).

The degeneration of the mesepimerum appears to the writer clearly demonstrated by this series of forms (1, 17–28) just described. When, now, it is found that, amongst the Cynipoidea (49–52) and some of the Proctotrypoidea (59), there is no trace of this kind of a subdivision of the pleurum, the conclusion is inevitable that the true episternum and epimerum are indistinguishably fused. Finally, therefore, when other subdivisions of the mesopleurum are discovered the conclusion that these latter are of secondary formation seems equally certain. In a few cases, already pointed out, the mesopleurum consists of one undivided plate (50–52, *Pl*₂), but it more frequently (*Hexaplasta*, sp., 49; *Proctotrypes caudatus*, 57; *Tropidopria conica*, 59) becomes differentiated into an upper wing-bearing part (*Pl*₂) and a lower leg-bearing part (*pl*₂) by a horizontal or oblique suture. This suture, moreover, is usually near the middle of the pleurum and is always above the articulation of the coxa. Hence, it can not be confused with the sterno-pleural suture (10, 16, 23, 27, *q*) which is always below the coxal articulation. Yet nearly all writers on the Hymenopteran thorax have called this lower mesopleural plate the “mesosternum.” To be sure, in nearly all the higher families as well as in some of the lower forms, it is entirely continuous with the sternum, but those species having a sterno-pleural suture clearly demonstrate where the true division between the sternum and the pleurum occurs when it is present.

In some of the Aculeata (*Pepsis*, 61) in which the mesepimerum (Epm_2) is still distinct, the episternum alone is divided into dorsal and ventral plates (Eps_2 , eps_2). In the honey bee (*Apis*, 63) the epimerum (Epm_2) is well developed above, but reaches only about half way down from the wing process (WT_2) to the base of the middle leg. In a worker ant (*Pogonomyrmex*, 62) the upper pleural plate (Pl_2) is continuously fused with the mesoscutum (Sct_2) and, in this case, might just as reasonably be called a part of the mesonotum, as may the lower plate (pl_2) in other forms be called a part of the mesosternum. In *Pogonomyrmex* (62) the latter plate (S_2) is, however, demarked from the pleurum by a suture.

8. *The formation of a prepectal plate in the mesothorax cut off from the anterior parts of both the mesosternum and the mesopleura.*

This character reaches its highest development in the Chalcidoids. The plate in question ($Ppct_2$) is specially well shown in such species as *Catalaccus incertus* (44), *Coccophagus lecanii* (45), and *Dimmockia incongruus* (48), in all of which species it forms a conspicuous plate on the side of the thorax lying between the pronotum (N_1) and the mesepisternum (Eps_2). An examination of the ventral aspect of the thorax, however, shows that this pleural sclerite ($Ppct_2$) on each side is only the lateral part of a plate that is continuous across the ventral surface in most cases. This is specially well shown by *Prospaltella berlesii* (47), where the plate ($Ppct_2$) forms an anterior subdivision of the entire mesopectus. Hence the writer has given it the name of *prepectus*, signifying that it is derived from the anterior parts of both the sternum (S_2) and the episterna (Eps_2).

The beginning of the mesoprepectus is to be found in the Ichneumonidæ, in nearly all members of which the anterior part of the mesopectus is differentiated as a subsclerite (23-28, 31, 32, $Ppct_2$), marked off by a suture from the sternum (S_2) and the episternum (Eps_2). In the Chalcid, *Leucospis affinis* (35, 37, 39), the median part of the prepectus is not entirely cut off from the front of the mesosternum (S_2). In *Microterys*, sp. (43) there are two prepectal plates, one on each side ($Ppct_2$, $Ppct_2$), which are not connected in front of the sternum, but this is most evidently a secondary reduction. In *Cerambycobius cushmani* (40, 41) the prepectus occurs in a distorted condition ($Ppct_2$) on account of the curious shape of the mesopleurum. Though the prepectus has something of the appearance of the preepisternum (see p. 47) of the more generalized orders of insects, especially if we assume a continuity between the preepisterna and the presternum, yet the phylogenetic gap between them is too great to permit of the homologizing of one with the other. The prepectus of the Hymenoptera appears to be a purely secondary production within this order.

9. *The obliteration of the metapleural suture resulting in the formation of a single metapleural sclerite, which becomes divided again into an upper and a lower plate.*

The evolution of the metapleurum is parallel with that of the mesopleurum. In the Tenthredinoidea and Siricoidea (1, 8, 11, 17, 18) it consists of two approximately equal plates, the episternum (Eps_3) and the epimerum (Epm_3) separated externally by the plural suture (1, 11, PS_3) and internally by the pleural ridge (8, PR). In all the other Hymenoptera, however, the metapleural suture is obliterated, and the metapleurum consists either of one single plate (34, 40, 44, 45, 48, 49, 50, 51, 57, 59, 60, 62, Pl_2) or it becomes more or less divided into a dorsal wing bearing part and a ventral leg-bearing part (20, 23–28, 61, 63, Pl_3 and pl_3). In *Trichiosoma lanuginosa* (19) there is a suggestion of this dorsal and ventral subdivision even before the pleural suture has disappeared, resulting in the formation of four subsclerites (Eps_3 , eps_3 and Epm_3 , epm_3). It has already been shown that the upper parts of the metapleura are nearly always fused with the lateral parts of the metapostnotum (PN_3), but besides this they are nearly always fused also with the sides of the propodeum (IT). In many cases, therefore, all four of these parts, the metapostnotum (PN_3), the propodeum (IT), and the two metapleura (Pl_3) are fused into one large piece in which sometimes all traces of sutures are obliterated (21, 50, 51).

3. SUMMARY OF THORACIC CHARACTERS.

As a result of these various modifications the thoracic division of the body in the higher Hymenoptera looks very different in its composition from that of all other insects. By the rearrangement of some of the parts and the consolidation of others the original metameral structure is obscured, and the thoracic walls come to be made up of seven distinct chitinous plates having but little evident relation to the original four segments. This remodelled structure is well shown by the Proctotrypid, *Helorus paradoxus* (58). The parts may be specified as follows: (1) the propectus, consisting of the prosternum and the proepisterna (Eps_1), which supports the head and carries the front legs; (2) the protergum, or pronotum (N_1), forming a cap over the front of the mesothorax; (3) the scuto-prescutal plate of the mesonotum (Psc_2 and Sct_2) carrying the anterior dorsal articulations of the front wings; (4) the scutellar plate of the mesonotum (Scl_2), separated from the preceding by the suture (k) and carrying the posterior articulations of the front wings; (5) the mesopectus, consisting of the fused mesosternum (S_2) and mesopleurites (Eps_2 , and Epm_2), supporting the front wings from below and carrying the middle legs; (6) the metanotum (N_3) carrying the dorsal attachments of

the hind wings; and (7) the posterior composite mass of the thorax, consisting of the metapostnotum (PN_3) and the first abdominal tergum (IT) above, of the metapleura (Pl_3) on the sides, and of the metasternum below, carrying the first abdominal spiracles (ISp), the pedunculate part of the abdomen (II , III) and the hind legs (Cx_3), and supporting the hind wings on the metapleural wing processes (WP_3).

The wingless Hymenoptera have the thorax the most highly specialized and, at the same time, the most simplified. In the apterous forms of Mutillidæ and the workers of Formicidæ (62) the propectus is detached in the usual fashion from the rest of the thorax and the protergum is separated from the mesothorax, at least on the sides, by a cleavage suture, but otherwise the thoracic walls are solid. The back sclerites (62, Sct_2 , Scl_2 , N_3 , PN_3 and IT) form one continuous plate from the protergum (N_1) to the second abdominal segment (II). The indistinct line (k) across the back appears to be the scuto-scutellar suture. The lateral margins of the dorsal plates, are indistinguishably fused with the pleurites and these latter are continuous with the sterna. The mesopleurum is partially divided by an impressed line (r) into an upper plate (Pl_2) continuous with the mesoscutum (Sct_2) and into a lower plate (pl_2) carrying the middle coxa (Cx_2). This sort of subdivision of the mesopleurum has been pointed out in other forms (59). The mesepisternum alone is frequently so divided (*Pepsis*, 61, Eps_2 , eps_2). The first spiracle of the worker ant is situated as usual behind the angle of the protergum (62, $1Sp$), the second ($2Sp$) is inclosed in the posterior margin of the upper mesopleural plate (Pl_2). The first abdominal spiracle (ISp) is located on the side of the propodeal region (IT).

Other authors have made different interpretations of the morphology of the ant thorax. Janet (1898) calls the proepisternum (62, Eps_1) the "prosternum" and the lower parts of the pleura of the other two segments the "mesosternum" and the "metasternum". Nassanoff (1889), Emery (1900), and Berlese (1908) name these parts in the same way. The writer has already stated the argument against such a disposition of these plates (see pp. 77 and 78). The pleurum of any segment lies normally between the base of the wing and the base of the leg, and it is inconceivable why a line midway between these points should be regarded as the sterno-pleural suture. At least some strong reason should be given for imagining such a distortion to have taken place that would put it there. In the lower Hymenoptera, as already shown, the true sterno-pleural sutures lie ventrad to the articulations of the coxæ (10, 11, 14, 16, 27, q). In most of the higher forms these sutures disappear though they recur in many scattered cases (40, 43, 50, q). Therefore, the line on the middle of the side can be nothing else than a secondary subdivision of the pleurum itself.

The application of anatomical terms to the back plates of the ant thorax by Nassanoff (1889) is such as to indicate that this author's ideas of the thoracic morphology or nomenclature are quite different from those of the present writer. When the same words are used in different senses by two writers an argument on the subject is likely to be very meaningless. The present writer agrees with Janet (1898) in his nomenclature and morphology of most of the thoracic sclerites, except with respect to the limits of the sternum. It is only by dissociating the parts of the thorax, as Janet did, that their true relations become apparent.

Finally, the work of Emery (1900) on the thorax of ants must be given a special discussion because Emery's views have been adopted by Wheeler (1910) in his recent comprehensive work on ants. Emery bases his ideas of the formicoid thorax on a study of the female *Streblognathus æthiopicus*. The present writer has not had access to a specimen of this species but the principal thoracic characters are similar in most of the Ponerine genera. Text figure 18 shows the left side of the thorax of *Leptogonys* (*Lobopelta*) *elongata*. The prothorax (N_1 , Eps_1) and the dorsal plates of the other segments (Psc_2 , Sct_2 , Scl_2 , N_3 , IT) do not differ from those of other Hymenoptera. In the mesopleurum, however, the limits of the epimerum (Epm_2) are almost obliterated, yet a comparison with *Pepsis* (61, Epm_2) leaves no doubt that the indistinctly marked subdivision (fig. 18, Epm_2) along the upper part of the posterior margin of the pleurum is the true mesepimerum. A small but distinct internal ridge attests that the faint line (PS_2) is the true pleural suture, though it fades out before it reaches either the wing process (WP_2) or the coxal process. The episternal area is divided by an oblique furrow (r) into an alar and a coxal region (Eps_2 and eps_2) while, again, the dorsal part of the latter is partially cut off by a longitudinal furrow (z). Now, Emery names

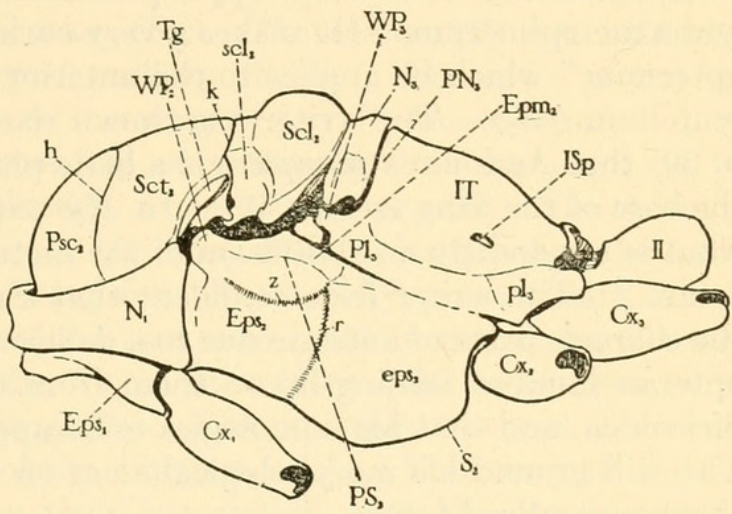


FIG. 18.—LATERAL VIEW OF ANT THORAX (*LEPTOGONYNS ELONGATA*): Cx_1 , Cx_2 , Cx_3 , COXÆ; Epm_2 , MESEPIMERUM; Eps_1 , PROEPISTERNUM; Eps_2 , eps_2 , UPPER AND LOWER SUBDIVISIONS OF MESEPISTERNUM; h , SCUTO-PRESCUTAL (PARAPSIDAL) SUTURE; II , SECOND ABDOMINAL SEGMENT; ISp , FIRST ABDOMINAL SPIRACLE; IT , PROPODEUM (FIRST ABDOMINAL TERGUM); k , SCUTO-SCUTELLAR SUTURE OF MESONOTUM; N_1 , PRONOTUM; N_3 , METANOTUM; Pl_3 , pl_3 , UPPER AND LOWER SUBDIVISIONS OF THE METAPLEURUM; $P N_3$, METAPOSTNOTUM FUSED WITH IT ; $P S_2$, MESOPLEURAL SUTURE; Psc_2 , MESOPRESCUTUM; r , LATERAL SUTURE OF MESEPISTERNUM; S_2 , MESOSTERNUM; Scl_2 , PRINCIPAL PART OF MESOSCUTELLUM; scl_2 , ANTERIOR SUBDIVISION OF MESOSCUTELLUM; Sct_2 , MESOSCUTUM; Tg , TEGULA; WP_2 , WP_3 , PLEURAL WING PROCESSES; z , DORSAL SUTURE OF MESEPISTERNUM.

The prothorax (N_1 , Eps_1) and the dorsal plates of the other segments (Psc_2 , Sct_2 , Scl_2 , N_3 , IT) do not differ from those of other Hymenoptera. In the mesopleurum, however, the limits of the epimerum (Epm_2) are almost obliterated, yet a comparison with *Pepsis* (61, Epm_2) leaves no doubt that the indistinctly marked subdivision (fig. 18, Epm_2) along the upper part of the posterior margin of the pleurum is the true mesepimerum. A small but distinct internal ridge attests that the faint line (PS_2) is the true pleural suture, though it fades out before it reaches either the wing process (WP_2) or the coxal process. The episternal area is divided by an oblique furrow (r) into an alar and a coxal region (Eps_2 and eps_2) while, again, the dorsal part of the latter is partially cut off by a longitudinal furrow (z). Now, Emery names

the coxal subdivision of the episternum (eps_2) the "mesosternum," while the part of the upper plate above the groove (z) he calls the "epimerum" and the part below the "episternum." A person who has studied ants alone may be excused for making such an interpretation as this, but, in the light of a comparative study of all the Hymenoptera, the writer can not see how the sutures (r) and (z) can be anything other than secondary grooves in the mesepisternum. The writer has not observed a metapleurum in the ants constructed as in Emery's figure of *Streblognathus*. In *Leptogonys* and other Ponerines examined the metapleurum (Pl_3 and pl_3) is very indefinitely demarked from the propodeum (IT), and the metapostnotum (PN_3) is not distinct from either. Emery calls the lower part of the metapleurum the "metasternum" while in the upper part he finds both a metepisternum and a metepimerum. He makes a very curious use of the word "parapternum" which he applies to the anterior subdivision of the mesoscutellum (scl_2). The writer has shown elsewhere (1910, footnote *a*, p. 20) that Audouin's *paraptère* is a little plate in the pleurum before the base of the wing (see p. 47). In *Myrmica piriformis* Emery calls what is apparently a subdivision of the metanotum the "metaparapterum." The writer feels confident that Emery's interpretations of the thoracic parts of ants are due to a deficient study of other Hymenopteran families leading up to them from the Tenthredinoidea and Siricoidea, and that his homologies must appear erroneous to anyone who will ground his morphological ideas on the thoracic structure of these generalized forms.

5. WINGS, THEIR VENATION AND ARTICULATION.

A comprehensive study of the wings is beyond the scope of the present paper, but there are some interesting points brought out in a study of the evolution of their basal parts. The Hymenopteran venation is so different from that of all other insects that any scheme of homology with the other orders involving the branches of the veins is purely speculative. The Comstock-Needham system of nomenclature as applied to the front wing of *Sirex flavicornis* is shown by figure 74. It assumes that the fourth and fifth branches of the radius (R_4 and R_5) have been bent back toward the posterior edge of the wing and fused with the neighboring branches of the media and that the third and fourth branches of the media (M_3 and M_4) have been likewise turned back and united with the cubitus (Cu), while this last vein fuses with the first anal ($1A$). If all the terminal branches of the veins in this wing were to be designated according to the veins that unite in their formation, they would have to be given, in many cases, names entirely too long for practical purposes. For this reason Hymenopteran systematists have not commonly adopted the Comstock-Needham nomenclature, but continue to use that of Cresson (1887). Figure 76 shows the front wing of an Ichneumonid,

Megarhyssa lunator, with the veins named according to the Cresson nomenclature, while figure 75 shows the same wing of *Sirex flavicornis* (74) named by this system as modified to suit the Siricoidea and Tenthredinoidea by Mr. S. A. Rohwer, of the United States Bureau of Entomology. Figure 77 is the front wing of *Leucospis affinis*, and the names applied to the rudiments of its veins are those in use by students of the Chalcidoidea.

The base of the Hymenopteran wing shows an increasing tendency, as the higher families are approached, toward a condensation of the bases of the first five veins. A very generalized wing base is found in the Pamphiliid, *Itycorsia discolor* (64). The costal vein (*C*) consists basally of two little chitinous pieces (*C* and *C*). The subcosta (*Sc*) is well developed, and articulates with the first axillary sclerite (*1Ax*) by a large and contorted base (*Sc*). The radius (*R*) is continuous at its base with the second axillary (*2Ax*). The media is not an independent vein basally in the wing of any Hymenopteran and, by the Comstock-Needham scheme of venation, it is supposed to be fused with the radius, forming a compound vein (*R + M*), which is the principal anterior vein of the wing (74). Nevertheless the little median plate (*m*) of the wing base is generally present with which both the media and the cubitus are associated in the wings of more generalized insects (see fig. 8). The cubitus (*Cu*) is likewise combined with the base of the radius. Consequently the next two veins that enter into the base of the wing are anals. They may be known as such, furthermore, by their association with the third axillary (*3Ax*). Since an apparent branch (74, *2A*) of the first anal is regarded at the true second anal, the second one at the base of the wing is called the third anal (*3A*).

The front wing of *Sirex flavicornis* (65) shows a few structural departures from that of *Itycorsia*. There is only one basal piece of the costa (*C*), and the enlarged base of the subcosta (*Sc*), articulating with the first axillary (*1Ax*), is separated from the shaft of the subcostal vein. These differences are more pronounced in *Tremex columba* (66), one of the Siricidæ. The shaft of the subcosta is not present as a vein, though its site is marked by a short branching trachea (*Sc*). The basal part (*Sc*), however, is very large and conspicuous. In *Megarhyssa lunator* (67), an Ichneumonid, there are no traces of the subcostal shaft, but its basal part (*Sc*) is present and articulates with the first axillary (*1Ax*). In *Pepsis* (69), one of the Ceropalidæ (Pompilidæ), the base of the subcosta (*Sc*) forms a large mass at the humeral angle of the wing, with which is fused the basal part of the radius (*R*). This is evident from the articulation with both the first (*1Ax*) and the second axillary (*2Ax*). Finally, in the Chalcid, *Leucospis* (68), and in the honey bee, *Apis* (70), the basal remnant of the subcosta (*Sc*) forms a large and conspicuous scale-like plate on the humeral angle of the wing base. It looks like a

secondary tegula, but it can not be confused with this organ, because the tegula is present also and overlaps the subcostal scale.

In the hind wing the bases of the subcosta and radius are generally fused into one large humeral mass, as shown in *Tremex columba* (71, *Sc* and *R*), *Apis mellifera* (72), and *Leucospis affinis* (73).

The details of the axillaries of *Tremex columba* and of *Apis mellifera* are shown by figure 19. The first axillary (1*Ax*) always articulates with the anterior wing process of the notum (fig. 8, *ANP*), while its anterior neck articulates with the base of the subcostal vein. The second axillary (2*Ax*) rests below upon the wing process of the pleurum and is associated with the base of the radial vein. Its inner

edge articulates with the body of the first axillary and its posterior end is usually articulated to the third. A muscle disk (fig. 19, *A*, *B*, *AxD*) or some sort of muscle-bearing sclerite is usually attached to its posterior end by a long tendon-like stalk and carries the upper end of the slender coxo-axillary muscle, whose lower end is attached to the upper rim of the coxa of the same segment. The third axillary (3*Ax*) is associated with the bases of the anal veins and carries the insertion of the flexor muscles of the wing. It nearly always presents a special lobe for the accommodation of these muscles and is often provided with an accessory sclerite (fig. 19, *B*, *C*, 3*ax*). The fourth axillary (4*Ax*) is always smaller and sim-

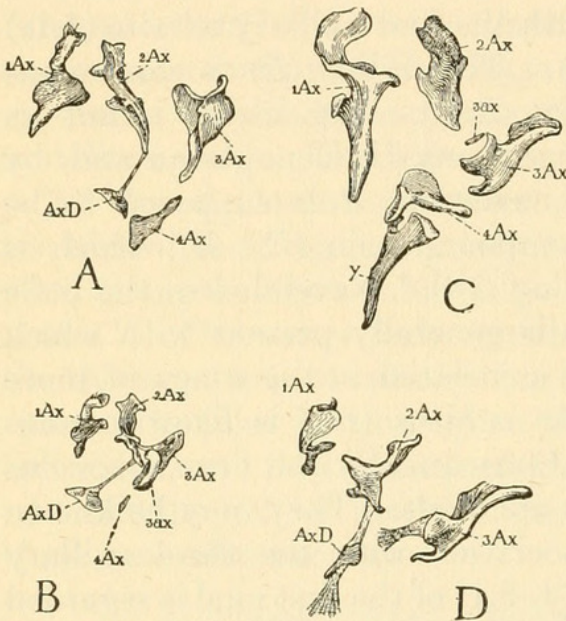


FIG. 19.—AXILLARY SCLERITES; *A*, OF FRONT WING OF *TREMEX COLUMBA*; *B*, OF HIND WING OF *TREMEX COLUMBA*; *C*, OF FRONT WING OF *APIS MELLIFERA*; *D*, OF HIND WING OF *APIS MELLIFERA*: 1*Ax*, FIRST AXILLARY; 2*Ax*, SECOND AXILLARY; 3*Ax*, THIRD AXILLARY; 3*ax*, ACCESSORY SCLERITE OF THIRD AXILLARY; 4*Ax*, FOURTH AXILLARY; *AxD*, DISK OF COXO-AXILLARY MUSCLE ATTACHED TO SECOND AXILLARY; *y*, MUSCLE-BEARING SCLERITE ATTACHED TO FOURTH AXILLARY OF FRONT WING IN *APIS MELLIFERA*.

pler than the others. It is present in the front wing of most of the Hymenoptera and in the hind wing of many of them. It is generally absent in other insects except the Orthoptera. When present, it forms the hinge plate of the wing articulating with the posterior wing process of the notum (fig. 8, *PNP*). It is absent in the hind wing of *Apis* (72 and fig. 19 *D*) and in the hind wing of *Leucospis* (73). In these cases the third axillary (3*Ax*) is associated with the posterior wing process. In the honey bee the fourth axillary of the front wing has a large accessory sclerite (70 and fig. 19 *C*, *y*) associated with it, upon which is inserted a slender muscle attached to an arm of the sternal furca.

6. BIBLIOGRAPHY.

The following list includes only those works on the thorax which are referred to in this paper:

1885. AMANS, P. A., Comparisons des organes du vol dans la serie animale.—Ann. Sci. Nat., ser. 6, Zool., pt. 19, pp. 9-222, pls. 1-8.
1824. AUDOUIN, V., Recherches anatomiques sur le thorax des animaux articules et celui des insectes hexapodes en particulier.—Ann. des Sci. Nat., vol. 1, pp. 97-135, 416-432.
1906. BERLESE, A., Gli Insetti, loro organizzazione sviluppo, abitudini e rapporti coll'uomo.—Societa Editrice Libreria, Milan.
1820. CHABRIER, J., Essai sur le vol des insectes.—Mem. du Mus. d'Hist. Nat., vol. 6, pp. 410-472, pls. 18-21.
1902. COMSTOCK, J. H., and KOCHI, C., The Skeleton of the head of insects.—Amer. Nat., vol. 36, pp. 13-45, 29 figs.
1898. COMSTOCK, J. H., and NEEDHAM, J. G., The wings of insects (IX. The venation of the wings of Hymenoptera. X. The tracheation of the wings of Hymenoptera).—Amer. Nat., vol. 32, pp. 413-422.
1908. CRAMPTON, G. C., Ein Beitrag zur Homologie der Thorakel-Sclerite der Insekten.—Inaug. Diss., Berlin.
1909. ——— A contribution to the comparative morphology of the thoracic sclerites of insects.—Proc. Acad. Nat. Sci. Phila., pp. 3-54, 21 text figs., pls. 1-4.
1887. CRESSON, E. T., Synopsis of the families and genera of Hymenoptera of America north of Mexico.—Trans. Amer. Ent. Soc., Phila., Supplementary vol. for 1887.
1900. EMERY, C., Intorno al Torace delle Formiche.—Bull. Soc. Ent. Ital., vol. 32, pp. 103-119, 14 figs.
1903. ENDERLEIN, G., Über die Morphologie, Gruppierung und systematische Stellung der Corrodentien.—Zool. Anz., vol. 26, pp. 423-437, 4 text figs.
1907. ——— Über die Segmental-Apotome der Insekten und zur Kenntnis der Morphologie der Japygiden.—Zool. Anz., vol. 31, pp. 629-635, 8 figs.
1883. GOSCH, C. C. A., On Latreilles theory of "Le Segment mediaire;" a contribution to the history of entomology.—Kroyers Nat. Tidsskrift, (3), vol. 13, pp. 475-531.
1889. HAGEN, H., Ueber die früheren Zustände der Libellen nebst Andeutung über Bildung des thorax.—Stettin Ent. Zeit., vol. 50, pp. 162-167.
1898. JANET, C., Anatomie du corselet de la *Myrmica rubra* reine.—Mem. de la Soc. Zool. de France, vol. 11, pp. 393-450, 25 text figs., pl. 6.
1826. KIRBY, W., and SPENCE, W., An introduction to entomology, vol. 3, London.
1889. KOLBE, H. J., Einführung in die Kenntnis der Insekten, Berlin.
1821. LATREILLE, P. A., De quelques appendices particuliers du thorax de divers insectes.—Mem. du Mus. d'Hist. Nat., vol. 7, pp. 1-21.
1892. LOWNE, B. T., The anatomy, physiology, morphology, and development of the blow-fly, 2 vols., London (Thorax in vol. 1, pp. 154-209).
1830. MAC LEAY, W. S., Explanation of the comparative anatomy of the thorax of winged insects, with a review of the present state of the nomenclature of its parts.—Zool. Journ., vol. 5, pp. 145-179, pls. 5, 6.
1896. MARLATT, C. L., Revision of the Nematinae of North America.—Bull. No. 3, tech. ser., U. S. Dep. Agric., Bureau of Entomology.
1889. NASSANOFF, N. W., Materials for the anatomy of the ant (*Lasius flavus* Fabr.).—Proc. Zool. Mus. Univ. of Moscow, vol. 4, pt. 1.
1833. NEWMAN, E., Osteology, or the external anatomy of insects. I. On the primary parts of insects.—Ent. Mag., vol. 1, pp. 394-413.

1866. PACKARD, A. S., Jr., Observations on the development and position of the Hymenoptera, with notes on the morphology of insects.—Proc. Bost. Soc. Nat. Hist., vol. 10, pp. 279–295, 4 figs.
1908. SNODGRASS, R. E., A comparative study of the thorax in Orthoptera, Euplexoptera, and Coleoptera.—Proc. Ent. Soc. Wash., vol. 9, pp. 95–108, pls. 2–5.
1909. ——— The thorax of insects and the articulation of the wings.—Proc. U. S. Nat. Mus., vol. 36, pp. 511–595, 6 text figs., pls. 40–69.
1910. ——— The anatomy of the honey bee.—Bull. No. 18, tech. ser., U. S. Dep. Agric., Bureau of Entomology.
1828. STRAUS-DÜRKHEIM, H., Considerationes generales sur l'Anatomie comparee des Animaux Articulés.—Royal Institute of France, 435 pp., 19 pls.
1903. VERHEOFF, K. W., Beiträge zur vergleichenden Morphologie des Thorax der Insekten mit Berücksichtigung der Chilopoden.—Nova Acta. Abh. der Kaiserl. Leop.-Carol. Deutschen Akad. der Naturf., vol. 81, pp. 63–109, pls. 7–13.
1905. VOSS, F., Ueber den Thorax von *Gryllus domesticus*, mit besonderer Berücksichtigung des Flügelgelenks und dessen Bewegung.—Zeitschr. f. Wiss. Zool., vol. 78, pp. 268–521, 654–759, pls. 15, 16, 24.
1838. WESTWOOD, J. O., On the comparative structure of the scutellum and other terminal dorsal parts of the thorax of winged insects.—Ent. Mag., vol. 5, pp. 459–469.
1910. WHEELER, W. M., Ants, their structure, development, and behavior.—Columbia University Press.
1909. WOODWORTH, C. W., Review of three papers on the thorax of insects by R. E. Snodgrass.—Science, new ser., vol. 30, no. 764, Aug. 20, pp. 243, 244.

7. EXPLANATION OF PLATES.

Abbreviations.

The figures 1, 2, 3, etc., placed before an abbreviation signify first, second, third, etc.; the figures 1, 2, and 3 placed after and below an abbreviation refer the latter to the prothorax, mesothorax, or metathorax, respectively, except on the wings where they indicate branches of the veins; the Roman numerals I–X designate the abdominal segments or their respective parts. A subdivision of any part is indicated by a duplicate of its symbol in lower case letters.

A, anal vein.

ANP, anterior notal wing process.

ANR, anterior ventral notal ridge.

anr, line on surface of notum formed by ANR.

Aph, prephragma of any segment.

Ax, axillary sclerites of wing base. *1Ax*, *2Ax*, *3Ax*, *4Ax*, first, second, third, and fourth axillaries.

AxC, axillary cord, the ligament-like thickening of posterior edge of axillary membrane of wing.

AxD, axillary disk, usually attached to second axillary and bearing insertion of coxo-axillary muscle.

AxM, axillary membrane, the membrane of the wing base.

C, costa.

Cer, cervicum.

Cu, cubitus.

cv, cross vein.

Cx, coxa.

CxP, coxal process of pleurum.

Em, lateral emargination of notum.

Emp, empodium.

- Epm*, epimerum.
epm, subdivision of epimerum.
EpmA, epimeral arm.
Eps, episternum.
eps, subdivision of episternum.
Es, Eusternum.
F, femur.
Fu, furca (entosternum.)
H, head.
ISp, first abdominal spiracle.
IT, first abdominal tergum, called the propodeum in Hymenoptera when transferred to thorax.
it, subdivision of propodeum (*IT*).
L, leg.
M, media.
m, small median plate or plates of wing base.
Mb, "intersegmental" membrane.
m-cu, medio-cubital cross vein.
m-m, median cross vein.
N, notum.
P, parapterum: *1P*, *2P*, first and second or episternal paraptera; *3P*, *4P*, third and fourth or epimeral paraptera.
PA, pleural arm, process of pleural ridge.
Pct, pectus, the sternum and pleura together of any segment.
PD, pronator disk.
Peps, preepisternum.
Ph, phragma: *1Ph*, *2Ph*, *3Ph*, first, second, and third phragmas.
Pl, pleurum.
pl, subdivision of pleurum.
PN, Postnotum (postscutellum, pseudonotum).
pn, subdivision of postnotum.
PNP, posterior notal wing process.
PNR, posterior ventral notal ridge.
pnr, line on surface of notum formed by *PNR*.
Ppct, prepectus.
Pph, postphragma of any segment.
PR, internal pleural ridge (entopleurum).
PS, pleural suture, separating episternum and epimerum along line of internal pleural ridge.
Ps, presternum.
Psc, prescutum.
PSl, poststernellum.
Pv, pulvillus.
R, radius.
Rd, posterior reduplication of edge of notum.
r-m, radio-medial cross vein.
S, sternum.
Sc, subcosta.
Scl, scutellum.
scl, subdivision of scutellum.
Sct, scutum.
Sl, sternellum.
Sp, spiracle (*1Sp*, *2Sp*, first and second thoracic spiracles; *ISp*, first abdominal spiracle).
T, tergum (*IT*, first abdominal tergum, the propodeum when fused with the thorax).

Tar, tarsus.

Tg, tegula.

Tn, trochantin.

TnC, coxal process of trochantin.

Tr, trochanter.

VNR, ventral V-shaped ridge of notum (entodorsum).

vnr, line on surface of notum formed by *VNR*.

W, wing.

WP, wing process of pleurum.

Miscellaneous lettering.

a, reflected edge of anterior lamina of prephragma.

b, reflected edge of posterior lamina of postphragma.

c, small plate intervening between parapterum and head of costal vein.

d, plate articulating between prosternum and coxa of *Tremex columba*.

e, accessory precoxal plate.

f, cervical sclerite.

g, dorsal cervical sclerite.

h, parapsidal suture.

i, cervical sclerite of honey bee.

j, lateral episternal ridge of *Scolia dubia*, marking the line where the pronotum overlaps the propleurum.

k, scuto-scutellar suture.

l, ventral cervical sclerite of *Scolia dubia*.

m, median plate or plates of wing base.

o, lobe on posterior margin of scutellum.

p, cenchri.

q, sterno-pleural suture.

r, median episternal groove.

u, prealar lobes of prescutum in *Holorusia*.

v, occipital process of propleurum.

w, posterior lobe of pronotum covering the first spiracle.

x, small plate between the presternum and the preepisternum in generalized segment.

y, accessory sclerite of the fourth axillary (4*Ax*) in the honey bee.

z, dorsal episternal groove.

Numbering.

The following are the names of the wing veins on plate 16, as used by Cresson in the Ichneumonidæ (76), transferred to a Siricoid wing (75), and the names current amongst systematists for the veins of a Chalcidoid wing (77):

1, costal vein.

2, subcostal.

3, radial.

4, median or externo-median.

5, anal, submedian, or interno-median.

6, subanal.

7, basal.

8, transverse radius.

9, cubital.

10, transverse cubital.

11, transverse cubital.

12, transverse cubital.

13, transverse medial.

- 14, discoidal.
- 15, subdiscoidal.
- 16, first recurrent.
- 17, second recurrent.
- 18, transverse vein in anal cell.
- 19, stigma.
- 20, submarginal.
- 21, marginal.
- 22, postmarginal.
- 23, stigmal.
- 24, intercostal.

PLATE 1.

- Fig. 1. *Tremex columba* (Siricidæ), thorax and base of abdomen.
 2. *Tremex columba*, propectus, ventral, left coxa removed.
 3. *Tremex columba*, mesotergum, dorsal.
 4. *Tremex columba*, mesotergum, ventral.
 5. *Tremex columba*, lateral and ventral parts of mesothorax, from above, tergum removed.
 6. *Tremex columba*, terga of metathorax and first abdominal segment, dorsal.
 7. *Tremex columba*, lateral and ventral parts of metathorax, from above, tergum removed.
 8. *Tremex columba*, left metapleurum, hind coxa, and attached part of first abdominal tergum, internal.
 9. *Tremex columba*, left mesopleurum and middle coxa, internal

PLATE 2.

- Fig. 10. *Arge*, sp. (Tenthredinidæ), mesothorax, left side.
 11. *Arge*, sp., metathorax and first abdominal tergum (propodeum), left side.
 12. *Arge*, sp., propleurum, sternum, and front leg, left side.
 13. *Dolerus aprilis* (Tenthredinidæ), propleurum and base of first leg, left side.
 14. *Arge*, sp., mesopectus, ventral.
 15. *Arge*, sp., metapectus, ventral.
 16. *Trichiosoma lanuginosa* (Tenthredinidæ), mesothorax, left side.

PLATE 3.

- Fig. 17. *Bactroceros pallimacula* (Pamphilidæ), thorax and base of abdomen.
 18. *Lygænematus erichsonii* (Tenthredinidæ), thorax and base of abdomen.
 19. *Trichiosoma lanuginosa* (Tenthredinidæ), thorax and base of abdomen. (See also fig. 16, pl. 2.)

PLATE 4.

- Fig. 20. *Euurobracon penetrator* (Braconidæ), thorax and base of abdomen.
 21. *Capitoniuss ashmeadii* (Capitoniidæ), thorax and base of abdomen.
 22. *Odontaulacus editus* (Evaniidæ), thorax and base of abdomen.

PLATE 5.

- Fig. 23. *Erymotylus macrurus* (Ichneumonidæ), thorax and base of abdomen. (See also fig. 33, pl. 7.)
 24. *Metopius pollinctorius* (Ichneumonidæ), thorax and base of abdomen.
 25. *Megarhyssa lunator* (Ichneumonidæ), thorax and base of abdomen.

PLATE 6.

- Fig. 26. *Cryptus extrematus* (Ichneumonidæ), thorax and base of abdomen.
27. *Trogus lutorius* (Ichneumonidæ), thorax and base of abdomen. (See also figs. 29, 30, 32, pl. 7.)
28. *Alomya debellator* (Ichneumonidæ), thorax and base of abdomen. (See also fig. 31, pl. 7.)

PLATE 7.

- Fig. 29. *Trogus lutorius* (Ichneumonidæ), thorax and base of abdomen, legs removed, ventral.
30. *Trogus lutorius*, mesotergum, left side.
31. *Alomya debellator* (Ichneumonidæ), mesothorax, left side.
32. *Trogus lutorius*, left mesopleurum, internal.
33. *Erymotylus macrurus* (Ichneumonidæ), mesotergum, dorsal.
34. *Syntomaspis racemariæ* (Chalcidoidea), thorax and base of abdomen.

PLATE 8.

- Fig. 35. *Leucospis affinis* (Chalcidoidea), left side.
36. *Leucospis affinis*, prothorax, anterior.
37. *Leucospis affinis*, mesothorax, left side.
38. *Leucospis affinis*, left metapleurum and left half of propodeum, internal.
39. *Leucospis affinis*, left mesopleurum, internal.

PLATE 9.

- Fig. 40. *Cerambycobius cushmani* (Chalcidoidea), thorax and base of abdomen.
41. *Cerambycobius cushmani*, thorax and propodeum, dorsal.
42. *Microterys*, sp. (Chalcidoidea), thorax and base of abdomen, dorsal.
43. *Microterys*, sp., mesothorax and metathorax, ventral.
44. *Catolaccus incertus* (Chalcidoidea), thorax and base of abdomen.

PLATE 10.

- Fig. 45. *Coccophagus lecanii* (Chalcidoidea), thorax and base of abdomen.
46. *Eurytoma diastrophii boltenii* (Chalcidoidea), mesotergum, dorsal.
47. *Prospaltella berlesii* (Chalcidoidea), mesopectus and metapectus, ventral.
48. *Dimmockia incongruus* (Chalcidoidea), thorax and base of abdomen.

PLATE 11

- Fig. 49. *Hexaplasta*, sp. (Cynipoidea), thorax and base of abdomen.
50. *Figites floridanus* (Cynipoidea), thorax and base of abdomen.
51. *Rhodites mayri* (Cynipoidea), thorax and base of abdomen. (See also fig. 52, pl. 12.)

PLATE 12.

- Fig. 52. *Rhodites mayri* (Cynipoidea), mesothorax, left side.
53. *Proctotrypes caudatus* (Proctotrypoidea), propectus, ventral.
54. *Proctotrypes caudatus*, pronotum, ventral.
55. *Proctotrypes caudatus*, mesotergum, left side.
56. *Proctotrypes caudatus*, left mesopleurum, internal.
57. *Proctotrypes caudatus*, thorax and base of abdomen.

PLATE 13.

- Fig. 58. *Helorus paradoxus* (Proctotrypoidea), thorax and base of abdomen.
59. *Tropidopria conica* (Proctotrypoidea), thorax and base of abdomen.
60. *Telenomus ashmeadii* (Proctotrypoidea), thorax and base of abdomen.

PLATE 14.

- Fig. 61. *Pepsis formosa* (Ceropalidæ, formerly Pompillidæ), thorax and base of abdomen.
62. *Pogonomyrmex transversum* (Formicidæ), thorax and base of abdomen.
63. *Apis mellifera* (Apidæ), thorax and base of abdomen.

PLATE 15.

- Fig. 64. *Itycorsia discolor* (Pamphiliidæ), base of front wing.
65. *Sirex flavicornis* (Siricidæ), base of anterior half of front wing.
66. *Tremex columba* (Siricidæ), base of front wing.
67. *Megarhyssa lunator* (Ichneumonidæ), base of first wing.
68. *Leucospis affinis* (Chalcidoidea), base of front wing.
69. *Pepsis*, sp. (Ceropalidæ), base of anterior half of front wing.
70. *Apis mellifera* (Apidæ), base of front wing.
71. *Tremex columba*, base of hind wing.
72. *Apis mellifera*, base of hind wing.
73. *Leucospis affinis*, base of hind wing.

PLATE 16.

- Fig. 74. *Sirex flavicornis* (Siricidæ), front wing, veins named according to Comstock-Needham system.
75. The same, veins named according to Cressonian system.
76. *Megarhyssa lunator* (Ichneumonidæ), front wing.
77. *Leucospis affinis* (Chalcididæ), front wing.



Snodgrass, R. E. 1910. "The thorax of the Hymenoptera." *Proceedings of the United States National Museum* 39(1774), 37–91.

<https://doi.org/10.5479/si.00963801.39-1774.37>.

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DOI: <https://doi.org/10.5479/si.00963801.39-1774.37>

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