MORPHOLOGY AND MECHANISM OF THE INSECT THORAX

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CONTENTS

INTRODUCTION

Nowhere has nature more strikingly displayed her mechanical genius than in the thorax of a winged insect; nowhere else can we find a mechanism so compact, so efficient, so simple, and yet of such varied powers. Locomotion by the coördinated action of three pairs of legs, flight by the unified vibration of two pairs of wings—these are the common functions of the thorax; but, add to them the powers of leaping, grasping, climbing, digging, swimming and many others of which the legs of various insects are capable, and consider that the wings may carry the body forward or backward slowly or with great speed, or keep it hovering almost stationary in the air, while, rubbed upon each other, by some insects they can be made to produce sounds of great volume, and it becomes needless to repeat that the insect thorax is a marvelous bit of machinery.

If we had but to describe the thorax as it is, the task of the anatomist would not be a simple one, but it is always necessary to look beyond the facts that confront us and to discover the more fundamental structures upon which they are reared, an undertaking which requires redoubled effort, but without which there can be no true morphology. An artist may depict the form and color of a building in a manner pleasing to the eye, but, unless he has understood the framework and the principles of its construction, his picture cannot be convincing to the mind.

It is certain that insects did not start out to be either six-legged creatures or winged creatures, and that, during their evolution, the thorax has been continually refashioned to adapt it to the new modes of locomotion. The embryonic history of insects shows that the thorax was first differentiated as the locomotor region of the body by the specialization of its three pairs of segmental appendages as the principal organs of progression, this being accompanied by the reduction of the gnathal appendages to feeding organs, and by the suppression of most of the abdominal appendages (fig. 1). Walking or running on three pairs of limbs instead of on many, now, not only involved a perfection of these appendages themselves, and a considerable amount of reconstruction in the segments bearing them, in order to give the legs better support and their muscles more effective attachment, but it necessitated a remodeling of the general body structure and proportions to effect a proper balance about the newly localized center of gravity. When, at some later period, lateral expansions of the tergal plates began to serve, perhaps, as parachutes, and insects became gliders, it is but natural that the tergal lobes which

eventually became wings should be those of that body region already fixed as the locomotor center. Flight, however, being an entirely new mode of progression, the development of the wings and the perfection of their mechanism meant a further and much greater alteration in the structure of the wing-bearing segments than that which was evolved to accommodate the legs. In a study of the thorax, therefore, we should proceed on the assumption that its elemental structure is to be found in insects that never possessed wings, and that the special

Mth — Prc

Ant — Gc

L — Th

Ab
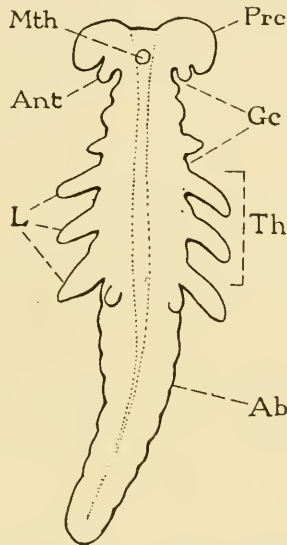
FIG. 1.—Young embryo of an insect, showing its four body regions and their appendages. (Embryo of *Naucoris,* Heymons, 1899.)

The primitive head, or procephalon (*Prc*), bearing eyes, mouth (*Mth*), and antennæ (*Ant*); the jaw region (*Gc*) of three segments, bearing mandibles, first maxillæ, and second maxillæ; thorax (*Th*) of three segments, bearing the legs; abdomen (*Ab*) of at most twelve segments, each but the last with a pair of rudimentary appendages in some insects.

thoracic structures of winged insects are characters that have been superposed on those primarily adapted to progression on three pairs of legs.

Facts and theories should run parallel; in entomology it seems they often diverge. Some theories, however, have served as useful stepping stones, though they themselves have later been swept away by the current; others are illusions of the imagination and land us in mid-stream. There have been many speculations concerning the number of segments in the insect thorax—some anatomists have claimed that there are five and even ten segments represented in its construc-

tion ; embryologists say there are only three. Many entomologists, though they reject the multiple segment theory, have, nevertheless, thought it necessary to postulate four consecutive rings in each of the three segments, conceived to have arisen from four primitive transverse folds of a soft-bodied ancestral form, in which the sclerites of the segment were originally laid down as chitinizations of the integument. This theory at first appeared to have much in its favor, but the more the thoracic skeleton has been studied, especially in connection with the musculature, the more the four-ring theory loses support, and gradually entomologists have relinquished it in favor of the idea that the various sclerites are secondary divisions of primitively simple plates. The last review of the evidence against these theories of thoracic segmentation and annulation is given by Weber (1924), and the theories should now be laid away for the historian, and respected for the fact that they have been helpful.

Recently another theory has been proposed by Feuerborn (1922), which would make the insect thorax a rather complicated assortment of parts derived from four segments. It appears, however, that this conception has been based on a misinterpretation of the facts in the metamorphosis of certain Diptera. Feuerborn's theory has been opposed by Martini (1922) and by Weber (1925, '27) ; particularly by Weber has the evidence put forth in its favor been thoroughly and critically examined and found to be wanting in essential points.

I. FUNDAMENTAL STRUCTURE OF AN ARTHROPOD SEGMENT

The anatomical form of most parts of animals, being a patchwork of changes or modifications that have been adopted in different stages of the animal's evolution, according to its changing needs, consists of a series of characters overlapping or built one upon the other into a concrete whole. The work of the morphologist, therefore, is largely one of analyzing compound structures, of separating them into their component elements, and of determining the chronological order of the evolutionary processes that have combined them. This he must do both from a study of embryology, and by the use of his imagination, guided by a knowledge of comparative anatomy. As a consequence, morphology is largely theoretical, and morphological theories continually supplant one another as new facts throw new light on the subject of animal structure. In the present paper, some of the older views on the structure of the insect thorax are discarded ; but a base is taken from a later theory, combined with selections from others, some new observations are added, and from the mixture the

basic theory is redistilled in a new form. The product, it is hoped, when tested, will be found to be a closer approximation to the truth than any of the ingredients, but it will fail of its purpose if it does not act as a stimulus to the further study of the facts bearing on the evolution of the insect thorax.

PRIMARY SEGMENTATION

In the study of insect evolution, we go back to a soft-skinned, worm-like creature with the body divided into a series of cylindrical parts, or *segments,* each of which bears a pair of lateral or ventro-lateral *appendages.* In an animal of this sort the intersegmental rings are the lines of attachment of the principal longitudinal muscles; in fact, the circular grooves separating the segments, and, therefore, the segments themselves are determined by the muscle attachments—in other words, the body segmentation corresponds with the muscle segmentation. If, at an earlier phylogenetic stage, the animal was unsegmented, it would seem that the body segments, or somites, must have resulted from the division of the muscle layer into muscle segments, or myotomes.

Starting with the insect's ancestor as a soft-skinned, segmented animal, resembling in its segmentation the soft-bodied larvæ of some modern insects, we must believe that its body segments then corresponded with its muscle divisions (fig. 2 A). This type of body division we may call *primary segmentation.* The muscles, extending between the intersegmental rings, are segmental in arrangment. Already, we assume, the creature possesses well-established dorsiventrality and cephalization; *i. e.,* one surface, the back or *dorsum,* is normally uppermost, and the opposite surface, the *venter,* is downward, while, in the usual progression, one end, the head end, is forward.

SECONDARY SEGMENTATION

The modern adult arthropods, unlike their hypothetical ancestors, are in general hard-shelled animals; they have developed an external skeleton formed of calcareous or chitinous matter or both deposited in the ectoderm, and the hardening of the body wall has had a far-reaching consequence on the structure of the segments and on the general mechanism of the animal. The skeletal deposits have taken the form of segmental plates (fig. 2 B), the principal plates in each segment being a dorsal one, or *tergum* (T) and a ventral one, or *sternum* (S). These two plates are separated on the sides of the segment by a membranous *pleural area.* The hardened parts of the

body wall could not occupy the entire length of each segment, for if they did the creature would become a tube that might be compressed or expanded dorsoventrally but that could not move otherwise. A circumferential part of each segment must, therefore, remain flexible.
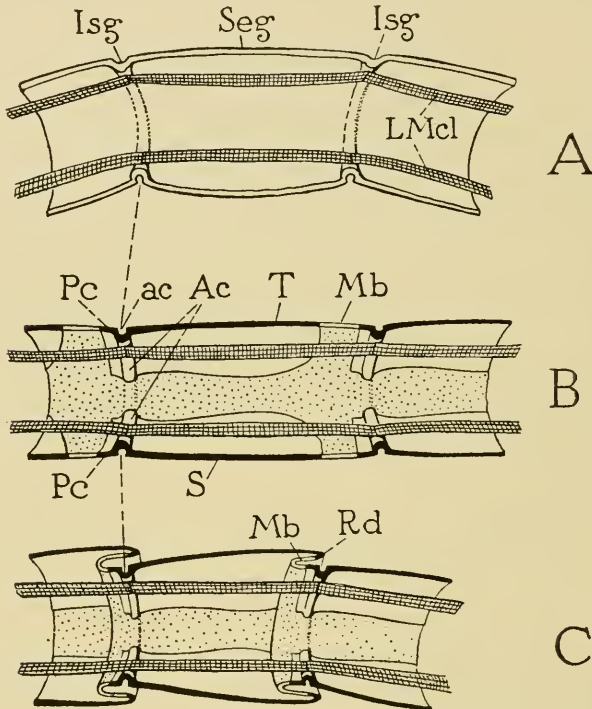

FIG. 2.—Diagrammatic lengthwise sections of a segmented animal, showing primary and secondary segmentation.

A, primary segmentation of soft-bodied animal, with segments (*Seg*) marked by intersegmental rings (*Isg*) to which longitudinal muscles (*LMcl*) are attached.

B, secondary segmentation of insect with hard plates in its body wall—each tergum or sternum (*T, S*) includes part of chitinized intersegmental groove before it, forming antecosta (*Ac*) internally and antecostal suture (*ac*) externally, with a narrow precosta (*Pc*) on anterior margin; posterior unchitinous part of segment becomes secondarily the " intersegmental " membrane (*Mb*).

C, secondary segmentation accompanied by telescoping of the segments, each segmental plate ending in a posterior fold, or reduplication (*Rd*).

The flexibility could not well be at the intersegmental lines, because the muscles are here attached and demand a firm support, for which reason the dorsal and ventral parts of the intersegmental grooves have been hardened and converted into internal ridges (fig. 2 B, *Ac*), each marked externally by a corresponding groove, or suture (*ac*). That each ridge should become continuous with the plate behind it

rather than with the one before it, is decided by the fact that the animal already possesses cephalization. In order to retain the power of cephalic movement when the body wall becomes hardened, the segments must remain capable of being drawn forward by the contraction of their muscles, and this can be accomplished best if the flexible region of each segment is its posterior part. Hence, each intersegmental, muscle-bearing ridge has become continuous with the segmental plate behind it, and usually only a narrow lip extends forward of the ridge and its suture to connect with the preceding membranous area.

Each dorsal or ventral plate of the body wall, *tergum* or *sternum*, now includes: (1) a segmental sclerite of varying extent, the primary tergum or sternum (fig. 2 B, *T, S*); (2) an anterior intersegmental part, consisting of an internal, transverse, sub-marginal ridge, the *antecosta* (*Ac*), marked externally by a corresponding *antecostal suture* (*ac*); and (3) a narrow anterior marginal lip, or *precosta* (*Pc*), belonging to the segment preceding. In the posterior part of each segment, behind the tergum and sternum, is a circular membranous area (*Mb*). In an animal thus constructed, the membranous rings of the body wall are its movable joints, and they are called the "intersegmental membranes"; the longitudinal muscles have become intersegmental in function, since they extend from the antecosta of one plate backward to the antecosta of the plate following. But, a body division of this kind is clearly a *secondary segmentation*. The antecostal ridges, still carrying the muscle attachments, mark the limits of the primitive segments. All adult insects with hard plates in their walls have a secondary segmentation; the soft-bodied larvæ of some insects, such as caterpillars, grubs, maggots, retain a primary segmentation. This difference in the segmental limits between larval and adult insects, and the fact that the membranous "intersegmental" rings of adult insects are the posterior parts of the true segments, has already been noted by Janet (1898), who says: "The name *intersegmental membrane* generally given to such a membrane, justified by its physiological function, is, however, inexact from a morphological standpoint."

Arthropods in general are characterized by another feature of their outer organization, and this is the telescoping of their segments, each segment being partially retracted into the one before it (fig. 2 C). This condition follows naturally from the relation of the muscle attachments to the segmental plates and to the flexible membranous areas. As a result, each tergum or sternum usually ends posteriorly in

a fold, or *posterior reduplication* (*Rd*), which overlaps the anterior part of the segment following.

The segmental appendages, which in their origin are simple out-growths of the body wall, have their bases in the pleural membranes, one on each side of the segment. In the Chilopoda and the Insecta, the pleural areas also contain skeletal plates, the pleurites, but most of these plates are probably derived from a basal part of the appendage. In pterygote insects the pleurites constitute a highly organized *pleuron*.

Entomologists have usually described the various small chitiniza-tions that occur between the principal segmental plates of insects as " intersegmental " sclerites. The only true intersegmental elements, however, are the antecostæ or parts derived from them, such as the phragmata of the dorsum and the intersegmental muscle processes of the venter. Most other so-called " intersegmental " chitinizations belong either to the anterior or the posterior parts of the true seg-mental areas. Examples of sclerites of this sort probably are the neck plates, or cervical sclerites, though their exact morphological status has not yet been determined. Since the anterior ends of the principal dorsal and ventral muscles of the prothorax are attached anteriorly on the back of the head, it would appear, at first thought, that the neck-plates belong to the anterior part of the prothorax. But the post-occipital ridge of the head, and the tentorium, to which the prothoracic muscles are attached, are formed by invaginations between the maxillary and labial segments. It follows, then, that an inter-segmental line has been lost somewhere between the anterior margin of the prothorax and the posterior margin of the labial segment; per-haps its position is indicated by the ends of certain muscles attached on the neck membrane in some insects. It is possible, therefore, that the cervical sclerites are derived from both segments. The two lateral plates constitute an important part of the mechanism for moving the head: their muscles extend to the back of the cranium, and to the tergum of the prothorax. The cervical sclerites of various insects have been described by Verhoeff (1903), Voss (1905), Martin (1916), and Crampton (1917, 1917a, 1926).

II. ELEMENTAL STRUCTURE OF A THORACIC SEGMENT

Though the form of the insect thorax most familiar to entomolo-gists does not present to the eye the basic structure of its parts, it is that on which our nomenclature has been established, and, therefore, it will be necessary to consider first a typical thoracic segment in its definitive state in order to explain the terms in common use applied

to its various parts. The morphologist is often tempted to throw off the nomenclatural shackles that bind him to the past, for new ideas could be much more freely stated if they did not have to be expressed in the terminology of former errors, or, at least, in the language of what we now regard as the misconceptions of a less enlightened earlier age. Yet, a discarding of old names might only set an example for a future generation, which, most likely, would proceed in turn to reject our terms along with our ideas, and adopt a new orismology expressive of its own ideas. After all, even a scientific term usually meets with the fate common to all names, and soon becomes accepted as a label for an object, without significance of derivation, and without respect to the original conception it implied.

GROUND-PLAN OF A THORACIC SEGMENT

We have already seen that a primitive limb-bearing segment presents a dorsum and a venter, in each of which is developed a chitinous plate, the tergum and the sternum, respectively, and a membranous pleural area between the two on each side, in which the limb is implanted, and in which also there are usually present a number of chitinizations, the pleurites, or collectively the pleuron.

The tergum, or notum as the dorsal segmental plate is frequently called, in its typical form is a simple sclerite covering the back of the segment (fig. 3 A, T) and in wingless segments often produced downward on the sides, sometimes overlapping the bases of the legs. The tergum of the mesothorax, and usually that of the metathorax is marked anteriorly by a submarginal antecostal suture (ac) and corresponding internal antecostal ridge (B, Ac), the two setting off a narrow precosta (Pc) from the anterior margin of the principal tergal plate. The tergum of the prothorax, however, always lacks a true antecosta and precosta, these parts apparently having been lost in the " neck." The dorsal muscles of the prothorax that arise posteriorly on the antecosta of the mesotergum thus come to be inserted anteriorly on the head, and to act as muscles for moving the head. The metatergum also sometimes lacks an antecosta and a precosta, but in such cases these parts are found to have been transferred to the mesothorax, and, in the same way, the corresponding elements of the first abdominal tergum may become a part of the metathorax. The antecostæ of the mesotergum, metatergum, and first abdominal tergum commonly develop plates, called *phragmata* (fig. 23 C, $1Ph, 2Ph, 3Ph$), that extend into the thoracic cavity to give increased surfaces for the attachment of the dorsal longitudinal muscles. The rear margin of

any tergum usually forms a transverse fold, or posterior reduplication (fig. 3 B, *Rd*), that of the protergum sometimes widely overlapping the mesothorax.

The sterna of the thoracic segments of insects never have the structure typical of segmental plates, such as that of the more simple thoracic terga, or that of the abdominal sterna of insects, or the sterna of the leg-bearing segments of the Chilopoda. The thoracic sterna have been modified, apparently since an early stage in the evolution of insects, through an alteration in the segmental relations of
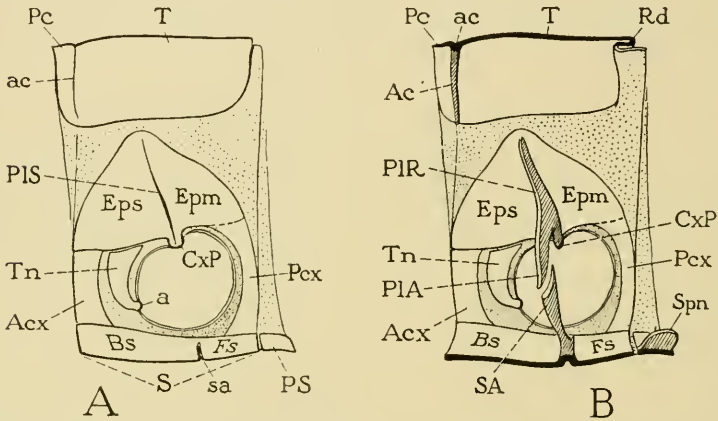

FIG. 3.—Ground-plan of a wingless thoracic segment, showing the usual or typical structure in pterygote insects.

A, external lateral view, left side; B, internal view of right side. *Ac*, antecosta; *ac*, antecostal suture; *Acx*, precoxal bridge; *a*, articulation of trochantin with coxa; *Bs*, basisternum; *CxP*, pleural coxal process; *Epm*, epimeron; *Eps*, episternum; *Fs*, furcisternum; *Pc*, precosta; *Pcx*, postcoxal bridge; *PlA*, pleural arm, or apophysis; *PlR*, pleural ridge; *PlS*, pleural suture; *PS*, poststernum; *S*, sternum; *SA*, sternal arm, or apophysis; *sa*, external root of sternal apophysis; *Spn*, spina; *T*, tergum; *Tn*, trochantin.

the ventral muscles. In the thorax, these muscles are attached not to anterior ridges of the sternal plates, but to processes arising from the posterior parts of the sterna or from intersternal folds or chitinizations of the integument.

It is difficult to select, among the numerous variations in form of the ventral thoracic plates, a structure that may be regarded as " typical " of a thoracic sternum. The most constant sternal landmark consists of a pair of entosternal arms arising either independently from the region between the bases of the coxæ, where their roots are marked externally by two pits in the cuticula, or jointly from a common median base. Since the second condition is the more

frequent in higher insects, the compound, forked apodeme has been named the *furca*, but the presence of two independent processes undoubtedly represents the more primitive condition. In some cases, the sternal arms, or apophyses (figs. 3 B, 4, *SA*), arise from a transverse ridge of the sternum, as in the prothorax of Acrididæ, and the external groove of the ridge then divides the sternum into two parts; but again, a division of the sternum may occur anterior to the bases of the furcal arms. The two parts of the sternum have been called somewhat loosely the sternum and sternellum, but since the first name should be reserved for the entire sternal plate (fig. 3 A, *S*), the terms *basisternum* and *furcisternum* (*Bs* and *Fs*) proposed by Crampton (1909) are to be preferred, though the first sternal sclerite is not " basal " and the furca is not necessarily a process of the second.

In addition to the sternal arms or furca, there is often present in the lower orders of winged insects a median sternal process known as the *spina* (fig. 3 B, *Spn*) situated behind the paired apodemes. Sometimes the spina appears to be carried by the posterior margin of the furcisternum, but typically it is borne on an independent sclerite, the *spinisternum* in Crampton's nomenclature. Another sclerite, the *postfurcisternum,* is found in rare cases between the furcisternum and the spinisternum, or extends as a fold laterally, where it may bear a pair of small processes known as the *furcillæ*. It is probable, however, that both furcisternum and spinisternum are parts of one poststernal region.

In general, then, we may say that the ventral chitinization of a thoracic segment consists of a principal plate, the true *sternum* (fig. 3 A, *S*), and of one or two poststernal sclerites constituting a *poststernum* (*PS*), the latter usually associated with, or incorporated into, the posterior part of the sternum proper. There is reason to believe, as will be shown later (page 21), that the poststernal parts are primary intersegmental elements that once constituted the precosta and antecosta of the sternum following. At any rate, this assumption explains the apparent reversal in the attachments of the ventral thoracic muscles, which, as the poststernal sclerites are lost, become transferred to the posterior parts of the preceding sterna and finally to the furcisternal apodemes.

The two divisions or regions of the sternum proper usually differ considerably in shape and size. The basisternum lies mostly before the bases of the legs (fig. 7 B, *Bs₂*, *Bs₃*,) and may become expanded laterally or fused with a precoxal part of the pleuron (fig. 3 A, *Acx*). Its anterior part is sometimes differentiated as a *presternum,* being separated from the rest by a suture, and an internal ridge simulating

an antecosta, but the ventral muscles are never attached to this ridge. The furcisternum lies between the coxal bases; it is usually narrow, sometimes reduced to a mere base for the furca. When the coxal cavity is closed behind by a postcoxal bridge from the pleuron (fig. 3 A, *Pcx*), the bridge unites below with the furcisternum and is usually continuous with it. In some of the Apterygota and in some species of the higher pterygote orders the coxa of the mesothorax and of the metathorax is articulated ventrally to the sternum by a condyle on the lateral margin of the furcisternum.

The sternal arms, whether they are independent apophyses of the sternum, or are united upon a common base, extend upward and out-
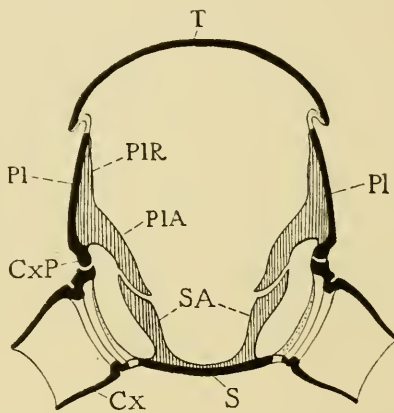

Fig. 4.—Diagrammatic cross-section of wingless thoracic segment of a pterygote insect.

Cx, coxa; *CxP*, pleural coxal process; *Pl*, *Pl*, pleura; *PlA*, pleural apophysis; *PlR*, pleural ridge; *S*, sternum; *SA*, sternal apophyses; *T*, tergum.

ward toward descending apodemes of the pleuron (figs. 3 B, 4, *PlA*), and the two sets of processes are almost always closely associated, in some cases fused, but more generally united by short muscle fibers (fig. 28, *G*). The sternal and pleural arms thus form bridges across the coxal cavities, and the similarity of their position and their com-plimental function suggest a correlation in origin. Neither pair is present in the Apterygota.

The pleuron, though subject to an endless number of minor varia-tions, shows a general plan of structure in the Pterygota which may be simplified to the diagrammatic scheme shown in figure 3 A. In the Apterygota the pleuron is little developed, and does not indicate an evolution toward that of the winged insects, but it does suggest, as will be shown later (page 22), the nature of the structure from which

has been developed the pleural sclerites in both the Apterygota and the Pterygota.

The key to the structure of the adult pterygote pleuron is the *pleural suture* (fig. 3 A, *PlS*), a groove extending upward from above the base of the coxa, and forming internally the *pleural ridge* (fig. 3 B, *PlR*). The pleural ridge is to be identified by the *pleural arm* (*PlA*), which extends inward and ventrally from its lower part, and by the condyle at its ventral end, the *pleural coxal process* (*CxP*), which forms the dorsal articulation of the coxa with the body. The part of the pleuron dorsal to the coxa is divided by the pleural suture and pleural apodeme into an anterior region, the *episternum* (fig. 3 A, B, *Eps*), and a posterior region, the *epimeron* (*Epm*). These two sclerites are thus secondary divisions of a primitive plate, there being no evidence of their origin from separate centers of chitinization. The relation of the pleural arm to the corresponding sternal arm (fig. 3 B, *PlA* and *SA*) has already been noted.

The anterior ventral angle of the episternum is usually extended toward the sternum to form a *precoxal bridge* (fig. 3, *Acx*) before the base of the leg, and often a similar extension from the epimeron forms a *postcoxal bridge* (*Pcx*) behind the leg, the first becoming continuous with the basisternum, the second with the furcisternum. The anterior bridge, however, in some of the lower insects is separated from the episternum and constitutes an independent sclerite, the *anterior laterale,* occasionally divided into an upper and a lower piece. Less frequently is the posterior bridge an independent *posterior laterale.* When all the regions of the pleuron thus far described— episternum, epimeron, precoxal bridge, postcoxal bridge—are well developed, they constitute an arch over the base of the coxa, braced upon the sternum below, from which the leg is suspended by the coxal process at the lower end of the pleural ridge.

In the generalized pterygote pleuron a sclerite known as the trochantin (fig. 3 A, *Tn*) lies before the base of the coxa, but behind the precoxal bridge (*Acx*). The trochantin is usually triangular in form, elongate dorsoventrally, with its upper end touching upon the episternum or fused with the lower part of the latter. Its lower end articulates by a *trochantinal coxal process* (*a*) with the anterior margin of the coxal base. The trochantin is a highly variable sclerite; it is best developed in the Apterygota and in the lower orders of the Pterygota, though it may differ much in closely related species; in the higher pterygote orders it is rudimentary or absent. In some of the Apterygota the trochantin forms an arch over the base of the coxa; only in rare cases does it extend dorsal to the coxa in pterygote

insects as a free sclerite, being usually fused into the lower part of the episternum, or limited to the region between the episternum, precoxal bridge, and the coxa. It is clear that the trochantin is a sclerite of the pleuron that has played a more important rôle in primitive insects, and one now in a state of becoming obliterated in the higher insects. The evidence bearing on its past history will be discussed in the next section of this paper.
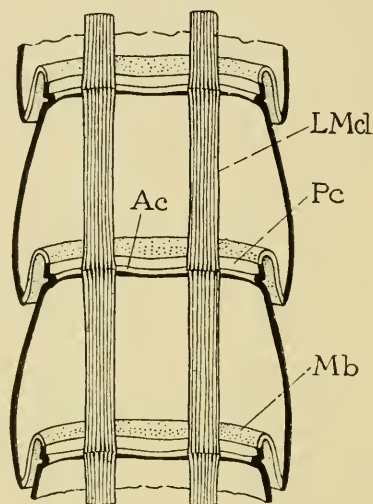

FIG. 5.—Inner surfaces of typical dorsal or ventral segmental plates of insect with secondary segmentation.

Ac, antecosta, or anterior submarginal ridge of segmental plate; *LMcl,* longitudinal muscles, attached to antecostæ; *Mb,* secondary "intersegmental" membrane; *Pc,* precosta, narrow anterior lip of plate, before the antecosta.

EVOLUTION OF THE THORACIC SCLERITES

It is one thing to formulate in a general way a working plan for the study of the thoracic sclerites as they occur in modern adult insects; it is quite another to understand how the structure represented by this plan has been evolved from a more primitive one, and to determine what the primitive structure itself may have been. In pursuing this line of investigation a study of the thorax of the Apterygota should be of assistance, though, as we shall find, the apterygote thorax gives little evidence of having evolved into the pterygote thorax. Yet, the thorax of apterygote insects has preserved certain characters, which, though degenerate in some respects, afford better evidence of the structure of the primitive insect thorax, and therefore

of that of the extinct ancestors of the Pterygota, than is to be found
in the thorax of modern winged insects, or in that of the earliest
winged forms known from the paleontological records.

THE TERGUM

The dorsal plates of the thoracic segments, though highly specialized
in the mesothorax and metathorax of the Pterygota, have been
affected less in the adaptive reconstruction of the thorax than have
either the sternal or the pleural parts. The reason for this is clearly to
be found in the fact that the evolution of the terga is correlated with
the development of the wings, organs of comparatively recent origin,
while the evolution of the sternal and the pleural parts began with the
differentiation of the thorax as the specialized locomotor center of
the body. In general, the dorsal plates of the thoracic segments have
preserved the structure characteristic of the terga of arthropods
having a secondary segmentation, in which the dorsal muscles extend
between antecostal ridges (fig. 5) derived from the primitive inter-
segmental folds (fig. 2). In the prothorax, however, the tergum
always lacks a true antecosta and precosta, and the principal dorsal
muscles are attached anteriorly on the back of the head, as are also
the ventral muscles. By this anatomical arrangement the head be-
comes movable on the body by the action of the prothoracic muscles.

In the Apterygota the thoracic terga are comparatively simple
plates. In *Japyx* (fig. 6 A) the mesotergum and metatergum have
particularly large precostæ (Pc_2 Pc_3), each set off by a distinct ante-
costal suture (ac), and marked by a median pair of prominent setæ,
as is also the precosta of the first abdominal segment (IPc). Verhoeff
regarded the precostal sclerites of *Japyx* as representing terga of
rudimentary intercalary thoracic segments; Enderlein (1907) claimed
that they are but " apotomes " of the following terga; it is now clear
that they are nothing more than unusually large precostæ, since the
dorsal muscles are attached to ridges at their bases. Behind each
principal tergal plate is a membranous area (fig. 10, *Mb*) continuous
with the pleural area on each side of the segment. In the Protura the
tergum of the mesothorax and of the metathorax (fig. 8, *T*) does not
cover the entire back of the segment, there being a large membranous
or weakly chitinous area behind it. This area Berlese (1910) regards
as " intersegmental," but Prell (1913) distinguishes in it two regions,
the first of which he calls the " nothotergite," while the second he
suggests is the homologue of the postnotal plate of certain winged
insects. The postnotum, however, as will be shown later, when

2

present is a development of the precosta normally attached to the tergum following, and the post-tergal region in the proturan dorsum does not appear to be a part of the small precosta behind it in either the mesothorax or the metathorax.

In *Lepisma* the lateral margins of the thoracic terga are somewhat produced above the bases of the legs, in *Machilis* they form free lobes reaching down on the sides of the segments and overlapping the
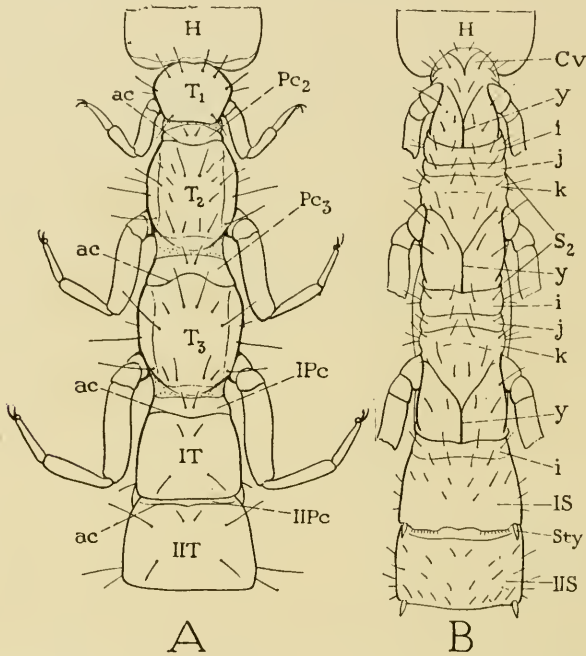

FIG. 6.—Thorax of *Japyx sp.*, with base of head and of abdomen.

A, dorsal view, showing larage precostæ (*Pc*) of mesotergum (*T₂*), metatergum (*T₃*), and first abdominal tergum (*IT*). B, ventral view, showing anterior apotomal folds (*i, j, k*) of sterna, and sutures (*y*) of Y-shaped ridges of thoracic sterna.

leg bases, but there is no reason for believing that these tergal extensions in the Thysanura have any phylogenetic relation with the tergal lobes from which the wings of pterygote insects are presumed to have evolved.

In the Pterygota, the terga of the thorax reach their highest degree of development in the second and third segments, where they present numerous specializations fitting them to their functions of supporting the wings and of giving efficient attachment to the principal muscles that move the wings. The features of the wing-bearing terga, how-

ever, will be described in the discussion of the structure of a wing-bearing segment (page 45). The pterygote protergum shows various modifications of form, but none of its characters is to be homologized with the special structures of the mesotergum or metatergum, a fact indicating that the rudimentary wing lobes of the prothorax of the Palæodictyoptera (fig. 19) were never developed into movable appendages in later insects.

<center>THE STERNUM</center>

The most important thing to be noted in a study of the sterna of the insect thorax is the fact that the ventral longitudinal muscles,
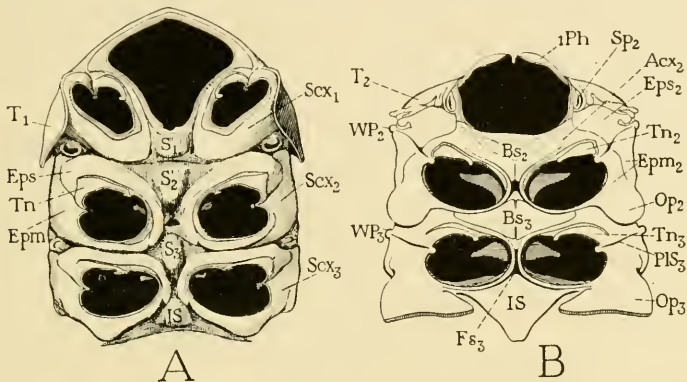

Fig. 7.—Pleuro-sternal parts of thorax of a cicada (*Tibicina septcndecim*).

A, ventral view of thorax of mature nymph, legs removed, showing the pleural parts continuous around inner sides of coxal cavities, suggesting that each pleuron represents a basal, or subcoxal, segment (*Scx*) of a leg (see figs. 15 B, 16 D). B, ventral view of mesothorax and metathorax of adult, showing pleural folds on inner sides of coxal cavities persisting as chitinous ridges on edges of sterna.

except in the Protura, extend between posterior parts of the sternal sclerites, and are never attached as they are in the abdomen, or as are the dorsal muscles of both thorax and abdomen, to anterior ridges of the segmental plates. The ventral musculature is greatly reduced in the thorax of all adult pterygote insects, but in holometabolous larvæ (Coleoptera, Lepidoptera, Diptera) the sternal muscles of the thorax are developed in proportion to the rest of the body musculature, and include large latero-ventral bands of fibers continuous with the muscle bands of the abdomen. In the Protura, according to Berlese (1910), the longitudinal musculature is complicated in a manner characteristic of primitive forms, and presents features suggestive of the musculature of larvæ of holometabolous insects. The ventral muscles, for example, consist of two latero-ventral bands of fibers continuous

through the abdomen and thorax. In the abdomen, except in the first segment, the fibers are attached to antecostal ridges of the sterna, and in the thorax to the anterior margins of the sternal plates, except in the prothorax where they are inserted anteriorly on the head. Here is unquestionably a uniformly primitive condition of the ventral musculature. It is probably of no phylogenetic significance that, anterior to the fifth abdominal segment, the fibers of these muscles are of the length of two segments and are attached to alternate sterna.

The sternal chitinization of each thoracic segment of the Protura, according to Berlese (1910) and Prell (1913), consists of two plates (fig. 8), one lying before the bases of the legs, the other between and behind them. In the mesothorax and metathorax the second sternal plate bears a median apodemal ridge, which in the Eosentomidæ is forked anteriorly and has the form of a **Y** with the arms extending toward the bases of the coxæ.

In *Japyx* the principal part of the sternal region in each thoracic segment consists of a large quadrate plate conspicuously marked externally by the lines of a **Y**-shaped ridge on the inner surface (fig. 6 B, y). The arms of the ridge extend outward and forward to the bases of the legs, where each becomes continuous with a basal ridge of the coxa and constitutes a sternal coxal articulation. The anterior part of each sternum consists of a semimembranous area (fig. 6 B, k) indistinctly separated from the rest, and bearing four prominent setæ in a transverse row. Before this area there are two well-marked sternal folds (i, j) that appear as replicas of it, each bearing likewise four setæ similarly placed. A single fold with four setæ occurs between the metasternum and the first abdominal sternum (IS). These sternal folds, the sternal "apotomes" of Enderlein (1907), the "intersternites" of Crampton (1926), are usually regarded as intersegmental, but that they belong to the sternum following is shown by the fact that the anterior margin of the first one of each thoracic set, as seen in side view (fig. 10, i), coincides with the line of the antecostal suture of the tergum (ac) of the same segment. A striking feature of the sternal structure in the thorax of *Japyx* is the reversed overlapping of the sternal plates, the posterior edge of each principal plate being covered externally by the anterior fold of the sternum following. The posterior ends of the median ridges of the sternal apodemes project as free processes into the body cavity.

There are no continuous bands of longitudinal muscle fibers in the thorax of *Japyx*, as there are in the Protura. Grassi (1886) says, in both *Japyx* and *Campodea* the longitudinal ventral muscles of the thorax are not recognizable with certainty. In this respect these

forms resemble the adults of winged insects, though it would be diffi-
cult to homologize individual sternal muscles in the two groups. In
each thoracic segment of *Japyx* a pair of divergent muscles goes for-
ward from the arms of the sternal apodeme to the posterior edge of
the sternal plate preceding. These muscles clearly act as retractors
of the anterior sclerite, their action in this capacity being made possi-
ble by the reversed overlapping of the adjoining sternal parts, and the
flexibility of the folds between the chitinous plates. The median ridge
of the **Y**-apodeme gives origin to muscles that go obliquely outward
to the coxæ, and other coxal muscles of the sternum are attached
between the arms of the apodeme. The dorsal muscles of the coxæ
arise on the tergum.

The sternal apodeme of the Protura and of the entognathous Thy-
sanura is evidently a homologous structure in both groups. It consists
of a median ridge in *Acerentomon* and *Campodea* (Grassi), but is
forked anteriorly in *Eosentomon* and *Japyx*. This apodeme can
scarcely be a prototype of the furca of the Pterygota, because the
median base of the furca is clearly a secondary development in the
higher winged insects, the arms, developed from lateral sternal inva-
ginations, being the primitive elements of the furca.

The thoracic musculature of *Lepisma* and *Machilis* is complicated,
especially so is that of *Machilis,* but, while a thorough study of it
would make a valuable contribution to our knowledge of the Thysa-
nura, it does not appear, from a superficial examination, that it would
throw any light on the evolution of the sternal musculature in the
Pterygota. The Thysanura do show, however, that the ventral longi-
tudinal muscles of the thorax have become attached to the posterior
margins of the sterna, which latter apparently have absorbed the ante-
costal ridges following, since antecostæ and precostæ are not present
in the typical position on any of the thoracic sterna, or on the first
abdominal sternum.

The larvæ of pterygote insects with complete metamorphosis have
in most cases a primary segmentation of the body, in which the attach-
ments of the longitudinal muscles are at the intersegmental grooves.
Even where segmental plates are present in the body wall, as in the
larvæ of some beetles (fig. 25), the areas of the muscle attachments
may be non-chitinous, but wherever a costa is formed (*ac*) it is in
the intersegmental fold and is attached to the segmental plate follow-
ing it.

In the larva of *Dytiscus marginalis,* as described by Speyer (1924),
a pair of furcal arms arises on each sternal region of the thorax
between the legs, and each pair is supported on a transverse ridge, or

infold of the sternal wall. An inflection of the integument between the prothorax and the mesothorax, and one between the mesothorax, and the metathorax form intersegmental folds between the thoracic sterna. The fold between the first and second segments bears laterally on each side a small process, the furcilla, and medially an unpaired process (the spina) ; the fold between the second and third segments has only a median process. The musculature of the *Dytiscus* larva, Speyer shows, is primitive in many ways ; both abdomen and thorax, for example, are traversed by continuous latero-ventral bands of muscle fibers. In the abdomen the fibers of these muscles are attached to anterior folds of the sterna, except in the first segment where all but one pair are inserted anteriorly on posterior parts of the metaster- num, either on the furcal arms and the supporting ridge, or on lateral points corresponding in position with the furcillæ of the first inter- sternal fold of the thorax. In the thoracic segments the ventral muscles are attached to the furcal arms, to the furcillæ, to the median process, and to a transverse ligament at the posterior edge of the segment, except in the prothorax where one set ends on the back of the head and another on the cervical sclerites. Without going farther into details of Speyer's account, it is clear that the sternal thoracic muscles in the larva of *Dytiscus* are attached either to posterior parts of the sterna, or to processes (furcillæ and spina) of intersegmental folds. The folds, Speyer says, appear to be derived from the anterior part (acrosternite) of the sternum following in each case.

In the adult of *Dytiscus* (Bauer, 1910), the principal ventral muscles of the thorax consist of paired bundles of longitudinal fibers extending between the sternal apophyses, and from the prosternal apophysis to the back of the head. This is the general condition of the longitudinal ventral musculature in the thorax of adult Pterygota, except that where median apophyses are present some of the muscles are attached to them.

A study of both the Apterygota and the Pterygota, therefore, ap- pears to indicate that the first step in the evolution of the thoracic sterna consisted of a union or close association of the points of attachment of the ventral muscles with the sternal plates preceding. It may be questioned whether the folds bearing the muscle attach- ments in the thoracic region ever formed antecostæ of the sterna following, as they do in the abdomen, but it is reasonable to suppose that they did, considering that the sterna of the Chilopoda are of uni- form structure in all the limb-bearing segments, and that the ventral thoracic muscles of the Protura are attached to the anterior margins of the sterna (Berlese). Chitinizations of the intersegmental folds

bearing the ventral muscle attachments have thus come to form apparent *posterior* elements of the sterna, or have been incorporated into the posterior parts of the sterna, and in this respect, as pointed out by Weber (1924), the sternal structure in the thorax is comparable to the tergal structure in those segments where a postnotal plate and phragma, originally intersegmental or a part of the succeeding tergum, become a part of the preceding tergum. By analogy, the intersegmental or posterior part of the definitive sternum may be termed the *poststernum* (fig. 3 A, *PS*). That the poststernal part in each segment, which sometimes consists of two parts (postfurcisternite and spinisternite of Crampton) is a true intersegmental element has been effectively stated by Weber (1924), who says: "One may conclude with all appearance of truth that the postfurcasternite has arisen from the membranous region between the true sterna, perhaps as a result of the muscles attached to it, and that it is a structure in every way similar to the postnotum of winged insects, though doubtless of older origin." Where two postfurcal sclerites are present, the second, or spinisternum, Weber believes, is only a detached piece of the first comparable to the phragma of a postnotum. Again, reviewing the prothoracic structure of the Neuroptera, Trichoptera, and Lepidoptera, in his paper on the thoracic skeleton of the Lepidoptera, Weber (1924 a) says: "The fourth section of the sternum, the *postfurcasternite,* is usually clearly separated from the furcasternite and is obviously a secondary structure. In *Sialis* it is only suggested, in the Trichoptera it is a distinct posterior appendage of the sternum, in *Hepialus* it becomes extremely long, and here there begins the formation of a posteriormost and likewise secondary piece of the sternum, which may be identified with the spinisternite of Crampton. This sclerite borders so closely on the mesosternum that it becomes a question whether it should be reckoned as a part of this sclerite or of the prosternum."

The poststernal sclerites, however, are not generally persistent elements of the sterna, for in most insects they are either lost or become indistinguishably fused into the posterior edges of the true sternal plates. Some of the ventral muscles that remain in the adult stage are attached to the spina, if this process is present; the attachments of the others become transferred to the posterior part of the sternum, where, in the Pterygota, they are carried mostly by the furcal arms. The development of the furcal arms, or lateral sternal apophyses, has differentiated the primitive sternal plate into basisternum and furcisternum, but the presence of these processes is a character of the Pterygota, there being no trace of them or other homol-

ogous sternal apodeme in any of the Apterygota. While, therefore, the general structure of the thoracic sterna has been developed in connection with the specialization of the thorax as the locomotor center of the insect body, the special structure of the thoracic sterna of winged insects has evolved within the pterygote group, probably as an adaptation to an indirect function in connection with the wings. Though Crampton (1926) distinguishes a basisternum and a furcisternum in some of the Thysanura, the structures separating the sternal regions so named, such as the Y-shaped ridges of *Japyx* (fig. 6 B, *y*) are not to be homologized with the sternal apophyses of the Pterygota.

<center>THE PLEURON</center>

The pleuron of a thoracic segment offers a more difficult problem in morphology than does either the tergum or the sternum, and the question of the origin of its sclerites has been the subject of much speculation and discussion. Our prevalent ideas concerning the structure of the pleuron have been derived largely from a study of the pterygote thorax, but, since the pleurites as they occur in a winged insect are certainly not primary elements in the wall of any primitive segment, we see, undoubtedly, in the thoracic pleuron of winged insects a highly specialized structure. A study of the apterygote thorax, therefore, might give more valuable suggestions concerning the basic structure of the pterygote pleuron than are to be had from a knowledge of the pterygote pleuron itself, since the pleural structure of the Apterygota should be less removed from the common ancestral structure than is that of the Pterygota.

The largest number of pleural sclerites is found in the Protura. In the mesothorax and metathorax of *Eosentomon,* as described by Prell (1913), there are nine principal plates on each side of the segment between the tergum and the sternum (fig. 8). Four of these (*a, b, c, d*) are more dorsal than the others and constitute a series of *tergopleurites,* according to Prell's interpretation. Four others (*e, f, g, h*) form a ventral series believed by Prell to represent the true pleural plates of other insects. Since Crampton (1914) has named the corresponding area in Pterygota the *eupleuron,* the series of plates having an analogous position in *Eosentomon* and other Apterygota may conveniently be termed the eupleural sclerites. The ninth plate in the general pleural area of *Eosentomon* (*Tn*) is a semicircular chitinization over the dorsal half of the coxa (*Cx*), and this sclerite Prell calls the *trochantin,* since its anterior part is clearly the homologue of the usual trochantinal sclerite of pterygote insects. It is

important to note that the eupleural and trochantinal sclerites of *Eosentomon* form a group of small plates arched over the coxal base, and that in this way they correspond with the pleurites in a pterygote pleuron. It may be questioned whether the plates of the eupleural series in *Eosentomon* are to be identified individually with specific pleural sclerites of winged insects, as Prell suggests, but it is true, at least, that they occur in homologous parts of the pleural area. There can be little doubt, however, that the trochantin is the same sclerite in both insect groups. In *Eosentomon* its anterior part tapers downward and ends in a recurved point articulating with the anterior
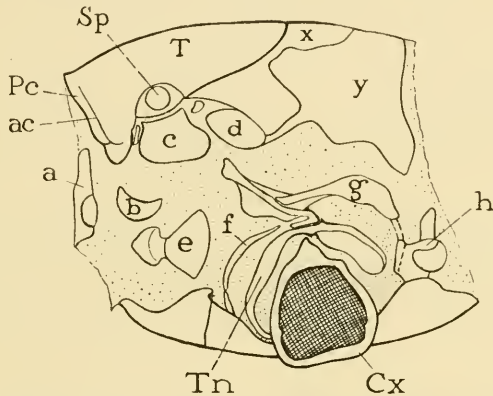

Fig. 8.—Mesothorax of a proturan, *Eosentomon germanicum*. (Figure from Prell, 1913, but differently interpreted, and re-lettered.)

The dorsum contains a tergum (T) with narrow precosta (Pc) separated by antecostal suture (ac), and two posterior weakly chitinized regions (x, y). The pleural area contains a dorsal series of tergo-pleurites (a, b, c, d), a ventral group of true pleurites (e, f, g, h) about the base of the coxa (Cx), and a trochantin (Tn) arched over the coxa.

ventral rim of the coxal base, while its dorsal part, Prell says, articulates both with the dorsal edge of the coxa and with the median pleural plate (g) above it.

In the Chilopoda, the pleural regions of the leg-bearing segments contain a number of small sclerites. The more dorsal plates in each segment are probably tergopleurites, but those immediately above and before the base of the leg would appear to represent the eupleural and trochantinal sclerites of the Protura. In *Lithobius forficatus,* as figured by Verhoeff (1903), there are two sclerites lying dorsal to the base of the coxa (fig. 9), of which Verhoeff calls the upper one (o) the "anopleure," and the lower (Tn) the "katopleure." A third (p), lying before the coxa, Verhoeff regards as the "trochantin";

and a fourth (q), apparently forming the dorsal part of the coxa (Cx), he calls the "coxopleure." When compared with *Eosentomon* (fig. 8), it appears more likely that the plate over the coxa in *Lithobius* should be the trochantin, of which the more ventral sclerite (p) may
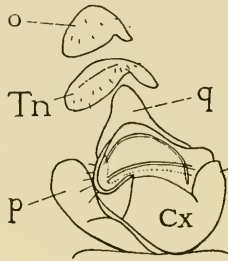

FIG. 9.—Coxa and pleurites of one segment of a centipede, *Lithobius forficatus*. (Verhoeff, 1903.)

Cx, coxa; *o*, eupleural sclerite (anopleure of Verhoeff); *p*, precoxal sclerite; *q*, coxal sclerite (coxopleure of Verhoeff); *Tn*, trochantin (katopleure of Verhoeff).

be a part, though the latter might correspond with the precoxal sclerite (f) in *Eosentomon*. In *Lithobius sp?* (fig. 32 B) there is only one plate dorsal to the coxa. Though the Chilopoda and the Protura cannot be regarded as related except indirectly through some remote common
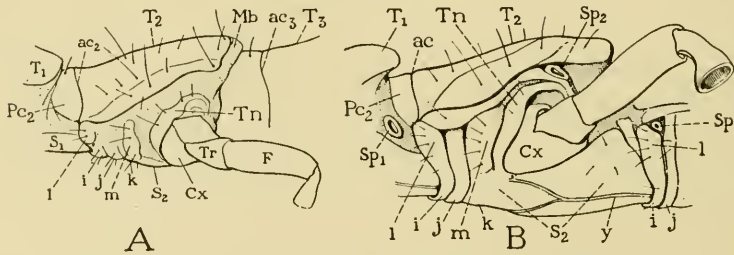

FIG. 10.—Lateral view of mesothorax of Japygidæ.

A, *Japyx sp.*, pleural region occupied by trochantin (Tn) curving over base of coxa (Cx), and by two lateral extensions (l, m) from apotomal folds (i, k) of sternum. (Spiracles not seen in this species.)

B, *Heterojapyx sp.* (large species from Australia), showing spiracles. Sp_3, prothoracic spiracle; Sp_2, mesothoracic spiracle; a metathoracic spiracle in corresponding position; Sp, first metathoracic spiracle, at upper end of pleural apotomal folds. Other lettering as on figure 6.

ancestor, yet it does not appear impossible that their pleural sclerites may have been derived from the same basic structure.

In the Japygidæ, the pleural structure appears, at first sight, to have little in common with that of the Protura. In some forms (fig. 10 B) there is a tergopleural fold in the mesothorax and meta-

thorax immediately below the edge of the tergum, above and behind which is the segmental spiracle (Sp_2). Arching over the base of the coxa is a chitinized fold which should represent the trochantin (Tn), though it is continuous basally with the sternum before the articulation of the latter with the coxa (Cx). Anterior to the trochantin are two or three chitinized pleural areas (A, B, l, m) continued from the apotomal folds of the sternum (i, j, k). The apotomal folds constitute a specialization in the Japygidæ, but the true pleural parts apparently are reduced to the trochantinal fold over the coxa.

In *Lepisma* the thoracic pleural regions have well-defined chitinous plates. In the mesothorax and metathorax, two sclerites (fig. 11, r, Tn) arch concentrically over the base of the coxa, while a third
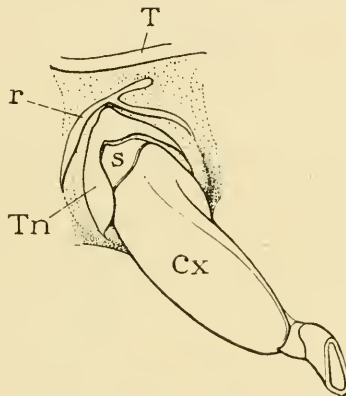

Fig. 11.—Mesothoracic pleuron, edge of tergum, and base of leg of *Lepisma*.

Cx, coxa; r, eupleural sclerite; s, sclerite on base of coxa; Tn, trochantin; T, tergum.

smaller one (s) is attached to the rim of the coxa itself. The first is evidently a sclerite of the eupleural series. It is a narrow chitinous band, with a short dorsal arm projecting upward and posteriorly, to the end of which is attached a muscle. The second sclerite (Tn) has the position of the trochantin in *Eosentomon* (fig. 8), though it fits closely over the upper end of the coxa, and has no special articular points with the latter. It is larger than the dorsal sclerite, triangular over the coxa, and expanded again where it overlaps the anterior angle of the coxal base. The third sclerite (s) is a small triangular piece closely attached to the base of the coxa, and is probably a detached piece of the latter. It suggests Verhoeff's " coxopleure " in *Lithobius* (fig. 9, q), but is apparently not the sclerite so designated by Verhoeff in *Lepisma*. In the prothorax, the same pleural sclerites are present, though they are here less distinct and not easily separated.

The pleural pattern of *Lepisma* is surprisingly similar to that of *Lithobius* (fig. 9), and is one also that conforms with the pleural pattern in *Eosentomon* (fig. 8), except that the eupleural series of plates is represented by a single sclerite in *Lepisma* (fig. 11, *r*). It is not implied, however, that *Lithobius* and *Lepisma* have any immediate relationship, or that either is descended from *Eosentomon*, but that through the disintegration of a primitive chitinization in the pleural region of a common ancestor, there have resulted the pleural patterns of *Eosentomon*, *Lithobius* and *Lepisma*.

The pleuron of *Machilis* has little resemblance to that of the other Apterygota. It consists of a single, small, triangular plate (fig. 12, *t*)
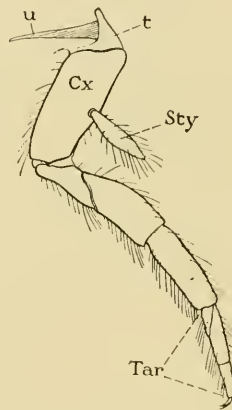

FIG. 12.—Left mesothoracic leg and pleural sclerite of *Machilis*, anterior view. *Cx*, coxa; *Sty*, stylus; *t*, pleural sclerite, *Tar*, tarsus; *u*, apodeme of pleural sclerite.

closely attached to the base of the coxa, but extending dorsally to the base of the lateral fold of the tergum. Many writers, probably following Hansen (1893), designate this sclerite the trochantin (or subcoxa), and its close connection with the coxa would suggest its trochantinal nature. Its basal angles are continued into a fold that surrounds the base of the coxa; its triangular lateral surface is marked by a vertical groove in which a deep invagination forms a long, slender, internal arm (*u*) to which is attached a muscle from the tergum. Crampton (1926) assumes that the plate belongs to the eupleural series, and that its areas before and behind its external suture are equivalent to the episternum and epimeron of pterygote insects. It is suggested by Prell that the median plate in the eupleural series of *Eosentomon* is likewise the common fundament of the

pterygote episternum and epimeron. It may be questioned, however, whether these are cases of actual homology or of resemblances in structures arising independently in response to similar demands. There is no evidence of lineal or connected relationship between the Protura, *Machilis,* and the Pterygota.

A study of the pleura of *Eosentomon, Japyx,* and *Lepisma* leads to the generalization that the pleurites of the Apterygota comprise a eupleural series of chitinizations arched over the base of the coxa, and a trochantinal sclerite in immediate contact with the coxa, while with them there may be associated a sclerite derived from the coxal base. A suggestion of the same pattern is to be found in the pleura of the Chilopoda. In *Machilis* the pleurites are reduced to a single plate, the identity of which is obscure—it might be the trochantin, or it might be a sclerite of the eupleural series. In the Collembola the thoracic pleurites are but poorly developed. Crampton (1926) finds a trochantin closely associated with the coxa, and a pleural sclerite lying above the coxa, but of the collembolan sclerites in general, he says, they "are too weakly developed, and too unsatisfactory in nature to afford much evidence of relationships to other forms." The line of descent of the Collembola, Crampton believes, "leads off in a direction having no especial bearing on the evolution of the higher forms." The present writer would add that the same may as truly be said of any of the apterygote groups. There is no suggestion, for example, in the Apterygota of the probable steps in the evolution of the pterygote pleuron; rather, each pleural pattern in the Apterygota appears to have resulted independently from the disintegration of a more concrete earlier structure. Reasons will later be given for believing that the structure of the pterygote pleuron is correlated with the wings, and that it has been developed in the extinct and unknown line of descent that led to the winged insects.

The typical structure of the pterygote pleuron has already been described and shown diagrammatically in figure 3. A more generalized condition, however, is to be found in the prothorax of the Plecoptera (fig. 13). Here there is a dorsal eupleural sclerite, or *anapleurite* (*Apl*), and a trochantinal sclerite (*Tn*) intervening between the anapleurite and the coxa, and articulating both anteriorly and dorsally with the coxa (C, *a, b*). The anapleurite is divided by an external suture and an internal ridge into an anterior episternal region and a posterior epimeral region.

The more usual pleural structure in the Pterygota includes a precoxal bridge from the episternal part of the anapleurite to the basisternum, and often also a postcoxal bridge from the epimeral region

to the furcisternum. This chitinous arch constitutes the *eupleuron* (Crampton, 1914), and it is clear that it corresponds closely with the eupleural series of sclerites in *Eosentomon* (fig. 8), though not necessarily in identity of individual plates. The " typical " trochantin of the pterygote pleuron (fig. 3, *Tn*) is excluded from the dorsal, or pleural, articulation of the coxa (*CxP*), but there are many insects in which it extends posteriorly to the articulation and takes part in the formation of the articular condyle (figs. 7, 14, 15 B, *Tn*), and, as we have seen, in the plecopteran prothorax (fig. 13), it intervenes entirely between both episternum and epimeron, and the coxa, and carries the dorsal condyle of the coxal articulation as well as the anterior one.
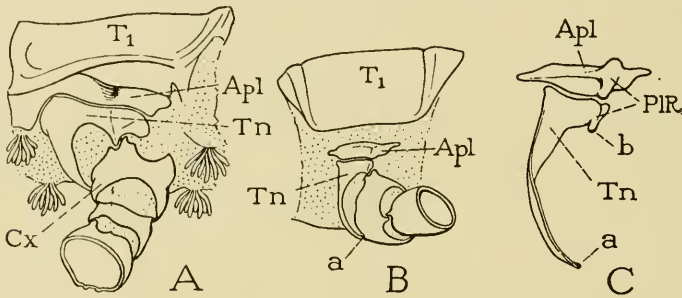

FIG. 13.—Prothorax of Plecoptera. (Proc. U. S. Nat. Mus., 1909.)

A, left side of prothorax and base of leg of nymph of *Pteronarcys;* pleuron composed of a dorsal anapleurite (*Apl*) of eupleural arch, and of a trochantin (eutrochantin of Crampton) carrying both anterior and dorsal articulations of coxa (C, *a, b*).

B, same parts of nymph of *Perla.*

C, inner view of right prothoracic pleural plates of nymph of *Perla; a,* anterior articulation of coxa; *Apl,* anapleurite; *b,* dorsal articulation of coxa; *PlR,* pleural ridge; *Tn,* trochantin.

We may conclude, therefore, that the basic structure of the pterygote pleuron, as shown at A of figure 15, is identical in plan with that of the apterygote pleuron, as exhibited in *Eosentomon* (fig. 8), and that the pleuron in each group consists of a eupleural series of sclerites, and of a trochantinal sclerite arching concentrically over the base of the coxa.

Though we may see, then, a fundamental identity of structure in the pleuron throughout the entire hexapod group, the evolution of the pleural sclerites has been quite different in the Apterygota and Pterygota. In the former, the sclerites show a tendency to reduction in different ways in different families, and the reduction, usually ending in obliteration of some of the sclerites, has produced the various and apparently unrelated pleural patterns characteristic of

the Apterygota. In the Pterygota, on the other hand, the pleuron
has evolved along a definite, constructive line. In the lower orders
of winged insects it may consist, as in the Apterygota, of a number
of separate sclerites, but in the higher orders it becomes a continuous
plate, resting below upon the sternum, giving a solid point of suspen-
sion for the leg, and, in the wing-bearing segments, a support for the
wing, and for the tergum also, since the latter must be braced against
the downward pull of the tergo-sternal muscles in order that these
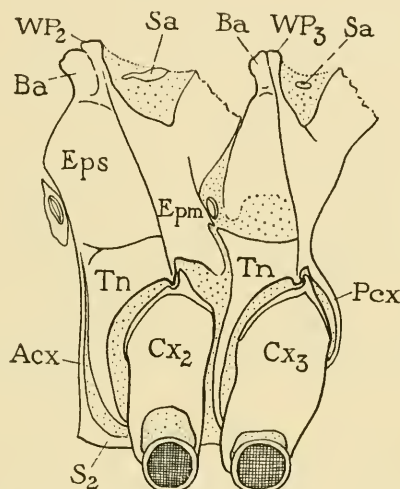muscles may function as elevators of the wings.

Fig. 14.—Mesopleuron and metapleuron of *Psocus venosus*.

The dorsal part of trochantin (Tn) of mesothorax here united with episternal
part (Eps) of anapleurite (fig. 13, Apl); postarticular part of trochantin
(fig. 13, Tn) either absent or fused with epimeron (Epm); basalares (Ba, Ba)
not separated from episterna.

The evolution of the pterygote pleuron has included principally a
development of the eupleural arch, and particularly of its anapleural
region. With the latter has been united the dorsal part of the tro-
chantin, as shown by Crampton (1914) and by Weber (1924). The
resulting plate, bearing the dorsal articulation of the coxa, has been
strengthened by an internal ridge extending upward from the coxal
condyle, the external suture of which separates the definitive epister-
num and epimeron. There is perhaps no evidence as to whether the
part of the trochantin posterior to the coxal articulation (fig. 13,
A, B, C) has been absorbed by the epimeron, or has been independently
lost, but there is abundant evidence of the fate of its pre-articular

part. The part dorsal to the coxa unites partially or completely with the eupleural region above it, in the second case becoming a part of the definitive episternum, while the part before the coxa may separate from the supracoxal part to become a free plate (fig. 7 B, Tn_2), the sclerite ordinarily known as the trochantin (fig. 3, Tn). In the higher orders of the Pterygota, the trochantin becomes rudimentary or disappears entirely, and it is subject to much variation even in those orders where it is best developed. It is clear that the trochantin is a sclerite that has played a much more important part in the pleural mechanism of the earlier insects, and that it is now in process of degeneration.
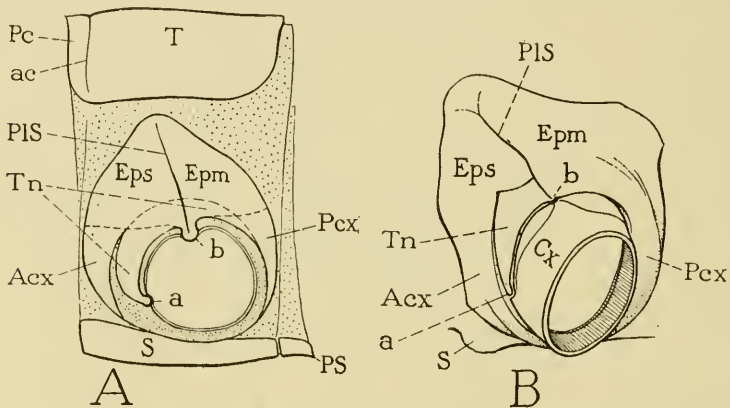

FIG. 15.—Theoretical composition of the pleuron, suggesting its origin from a subcoxal segment of the leg.

A, diagrammatic lateral view of a wingless segment, showing pleuron consisting of a eupleural arch (Acx, Eps, Epm, Pcx), and of a trochantinal arch (Tn), the latter fused dorsally with anapleurite (fig. 13, Apl) to form the definitive episternum and epimeron (Eps, Epm).

B, mesothoracic pleuron and base of coxa of mature nymph of cicada (*Tibicina septendecim*), showing parallelism in structure with A, and suggesting the origin of the pleuron from a subcoxal leg segment.

The foregoing review shows that there is a basic unity of structure in the pleural parts in both the Apterygota and the Pterygota, since in each group the pleurites fall into a eupleural and a trochantinal arch concentric over the base of the coxa. For practical purposes it is perhaps enough that we can trace the approximate evolution of the pleurites in their various modifications, but a deeper understanding of the thorax demands an explanation of the origin and nature of the pleurites themselves.

The pleural sclerites have been regarded as intrinsic elements of the lateral walls of the segments, but their variability and their general weak development in the Apterygota, would indicate that the plates

are of little use in wingless insects, and that they are in a state of degeneration in the Apterygota. It is, therefore, reasonable to suspect that the pleurites are derivatives of some earlier structure, which has become degenerate in the Apterygota, but which, in the wing-bearing segments of the Pterygota, has undergone a new development by which it has become remodeled into an essential part of the wing mechanism.

From a comparative study of the appendages of the Arthropoda, Hansen (1893) concluded that the coxa is the second segment of the primitive arthropod limb, and that, in insects, the rudiment of the true basal segment is the trochantin. It was later claimed by Heymons (1899), however, that the trochantin is only a small part of the original basal segment, the major part of which has formed the other pleural sclerites. This assertion Heymons based on a study of the development of the thorax in the Hemiptera. In the embryo, he says, the basal part of the leg divides into a proximal and a distal part, the second becoming the coxa, while the first flattens out and forms those parts of the thorax with which the leg articulates. The basal piece of the limb, or hypothetical basal leg segment, Heymons designated the *subcoxa*.

The idea that the arthropod limb in general includes a subcoxal basal segment has been particularly elaborated by Börner. According to Börner's most recently expressed view (1921), the subcoxa is retained as a free basal segment of the limb only in the Pentapoda (Pycnogonida); in other arthropods it is either incorporated into the body wall, forming the pleuron in Insecta and in some Crustacea, and in other Crustacea a part of the sternum, or it has entirely disappeared, as in the Arachnida.

Crampton and Hasey (1915) have opposed the theory of the subcoxal origin of the pleural plates in insects, pointing out that Heymons misinterpreted some of the elements in the pleuron of *Nepa*, and that according to his statement the epimeron is not included in the subcoxa of the Hemiptera, though Heymons says that the subcoxal region includes both the episternum and the epimeron in Blattidæ. The hemipteran species that Heymons studied are, indeed, not good forms on which to base a study of the pleuron, for in *Naucoris*, one of his examples, the epimeron of the metathorax is rudimentary, and the episternum of the mesothorax is united with the sternum. In each segment, therefore, only a single pleural plate is evident in both nymph and adult, and a failure to recognize these conditions might give the impression that a single pleural plate in *Naucoris* is the equivalent of the episternum and epimeron in gen-

3

eralized insects. Heymon's general conclusion is that the pleural parts of adult insects may not correspond exactly in their entire extent with the subcoxal leg segment of the embryo, but that they are either in part or principally derived from it. The subject needs further support from embryology; but the subcoxal theory is now generally accepted in one form or another by most European students of insect morphology, though some follow Hansen in regarding the trochantin alone as representing the subcoxa.
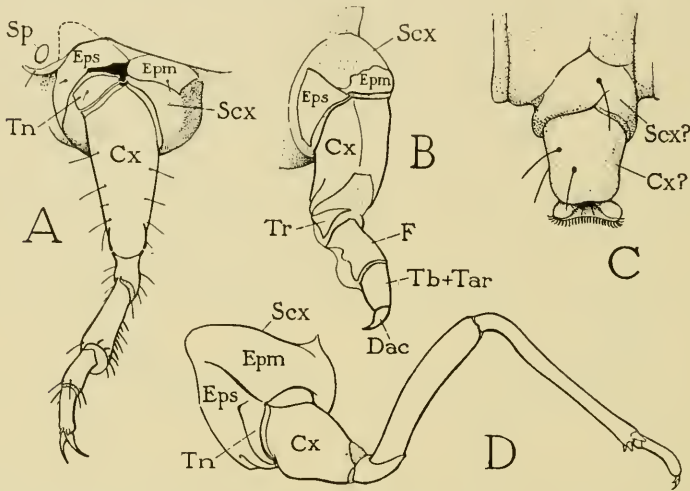

FIG. 16.—Legs and pleural parts of immature insects, suggesting that the pleural sclerites belong to a basal, subcoxal segment of the leg (*Scx*).

A, middle leg and pleural sclerites of larva of *Scarites* (Carabidæ).
B, middle leg and pleural sclerites of larva of *Pteronidea ribesi* (Tenthredinidae).
C, abdominal leg of a caterpillar (Lepidoptera).
D, hind leg and pleuron of mature nymph of *Tibicina septendecim* (Homoptera).

Students of other groups of Arthropoda also recognize a subcoxal segment, or *pleuropodite*, as the true base of the primitive limb (fig. 42 A). Some of the Acarina furnish particularly suggestive examples of structures that appear to be subcoxal leg segments. In the ticks (Ixoidea) each leg is articulated to a large basal piece (fig. 17, *Scx*) expanded on the ventral surface of the body, but continued over the base of the coxa as a narrow arch in the pleural surface. These leg bases are provided with tergal muscles *(Dermacentor, Amblyomma)*, and those of the first pair at least are capable of a slight rotary motion on their transverse axes. Each, moreover,

bears the basal attachments of the abductor and adductor muscles of the coxa *(Cx)*. In short, either the facts are most deceptive, or the ticks have retained subcoxæ in the form of functional leg bases.

A recent writer, Becker (1923, 1924), would, in a manner, reverse the relations between the pleuron and the base of the leg, since he claims that in the Chilopoda and the Insecta the coxa and trochanter are derived from the pleuron, the latter being a primary part of the thoracic wall. Becker's claim, however, may be simply another way of stating that the pleuron and the base of the leg are parts of the same structure.

Though it must be admitted that direct evidence for the derivation of the insect pleuron from the base of the limb is still insufficient,
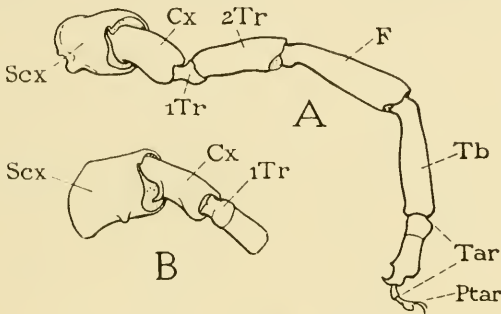

Fig. 17.—Legs of Acarina.

A, hind leg of *Amblyomma tuberculatum*, ventral view; B, base of hind leg of *Dermacentor variolatus*. *Cx,* coxa; *F,* femur; *Ptar,* pretarsus; *Scx,* subcoxa, or ventral plate of body wall bearing free part of limb; *Tar,* tarsus; *Tb,* tibia; *1Tr,* first trochanter; *2Tr,* second trochanter.

there are many facts that may be adduced as circumstantial evidence. In a cicada nymph, for example, each leg is attached to a large, oval, subcoxal, latero-ventral area of the body wall between the tergum and the sternum of its segment (fig. 7, A, *Scx*). The lateral part of each area is occupied by the pleural sclerites (figs. 7 A, 15 B, 16 D), and the precoxal and postcoxal parts (fig. 15 B, *Acx, Pcx*) are continuous in a semi-membranous fold around the mesal side of the base of the coxa (fig. 7 A). Even in the adult, the mesal subcoxal fold is quite distinct from the true sternum (fig. 7 B), though it is here chitinized and appears as an elevated marginal rim of the sternum. This structure recalls Heymons' statement that the adult sternum in the Hemiptera includes the ventral part of the subcoxa. The pleurites of a young cricket (fig. 26 A) and of other Orthoptera in the first instar likewise give the impression of belonging to a basal leg seg-

ment flattened out in the lateral wall of the body segment. In some holometabolous larvæ, as in the larva of a carabid beetle (figs. 16 A, 25), or in a sawfly larva (fig. 16 B), the thoracic legs are carried on subcoxal mounds *(Scx)* of the body wall, which have the appearance of being the true bases of the legs, and in which are situated laterally the pleural sclerites.

To trace the evidence of subcoxal elements in the abdominal segments of adult and larval insects (fig. 16 C) would take us beyond the limits of a paper on the thorax, but the contention by Börner (1909) that the gills of mayfly nymphs are homologues of the thoracic legs, and that their basal supports are subcoxæ is too interesting to pass over. Dürken (1909), it is true, has shown that the musculature of the gill does not fit with Börner's interpretation; but if Börner had compared the gill muscles, not with the tergal promotors and remotors of the coxæ, but with the coxal abductors and adductors, which should arise within the subcoxæ, there might be less objection to his homology of the skeletal parts. The general subject of the musculature of the leg base, however, will be given special attention in a following section (page 83), wherein it will be shown that the coxa appears to possess muscles that should belong to two leg segments.

Börner rightly says that an arthropod limb, in order to be an effective instrument of locomotion, must be able to turn forward and backward on its base. If a subcoxal segment was the primitive base of the limb, it, therefore, moved upon a vertical axis in the pleural membrane between tergum and sternum. Börner assumes also that the coxa moved in the same manner as the subcoxa; but this would give a double-jointed movement of the limb base in one plane. More reasonable does it seem that the primitive coxa moved in a vertical plane on a horizontal axis between anterior and posterior articular points on the subcoxa, thus duplicating the movement of the following coxo-trochantinal joint, rather than that of the limb with the body. When the subcoxa then became a fixed part of the body wall, its function as the leg base necessarily devolved upon the coxa, and the latter, taking over the promotor and remotor muscles of the subcoxa, shifted its axis from the horizontal to an oblique position and finally to a vertical one.

The subcoxal theory, then, as proposed in this paper, assumes that the coxa originally articulated with the hypothetical basal segment of the limb (fig. 18 A, *Scx*) by an anterior articulation *(a)* and a posterior articulation *(b)*, and that, in insects, the lateral walls of the subcoxa have furnished the pleural sclerites of the thorax, while the
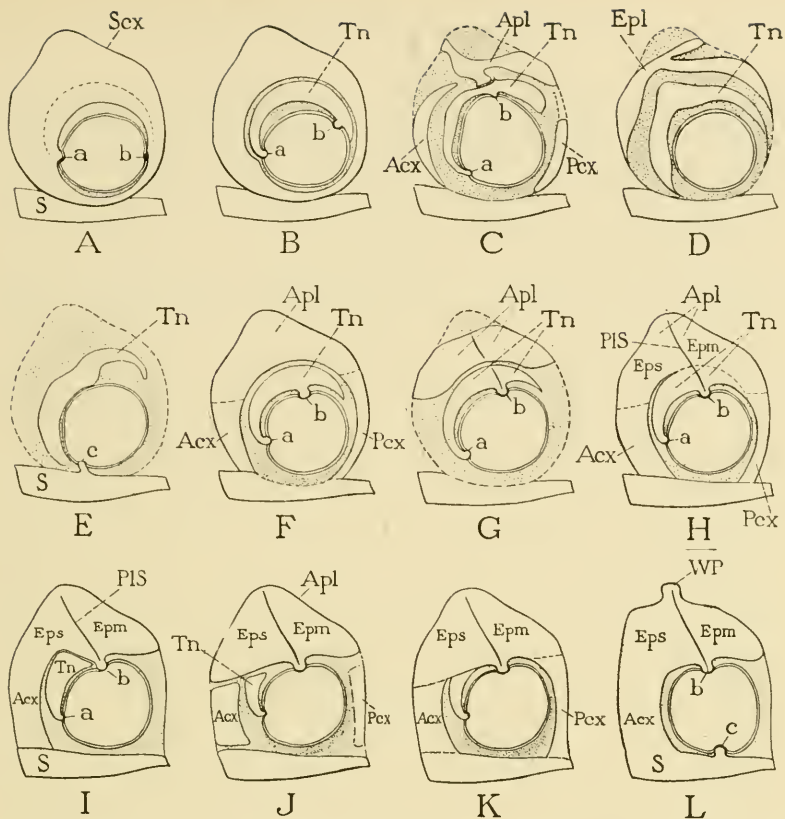
Fig. 18.—Diagrams outlining the possible origin and evolution of the thoracic pleurites from a subcoxal segment of the leg.

A, the theoretical subcoxa (*Scx*) as a primitive basal leg segment, with anterior and posterior coxal articulations (*a, b*) on a horizontal axis. *S,* sternum.

B, theoretical separation from subcoxa of a supra-coxal, trochantinal sclerite (*Tn*) bearing the coxal articulations (*a, b*).

C, subcoxa flattened into pleural wall of segment; its basal chitinization broken up into a series of eupleural sclerites (*Acx, Apl, Pcx*) forming an arch over coxa concentric with the trochantin (*Tn*); posterior articulation of coxa (*b*) dorsal in position. (*Eosentomon,* fig. 8.)

D, pleuron consisting of a eupleural sclerite (*Epl*) and a trochantinal sclerite (*Tn*), concentric over coxa. (*Lepisma,* fig. 11.)

E, subcoxal part of pleuron with a single sclerite, the trochantin (*Tn*); coxa articulated to sternum. (*Japyx,* fig. 10.)

F, theoretical primitive pterygote pleuron, consisting of a eupleural subcoxal arch (*Acx, Apl, Pcx*) based on sternum, and of a trochantin (*Tn*) carrying anterior and dorsal articulations of coxa (*a, b*).

G, prothoracic pleuron of Plecoptera (fig. 13), consisting of anapleurite (*Apl*) of eupleural arch, and of trochantin (*Tn*).

H, usual structure of pterygote pleuron: trochantin (*Tn*) fused dorsally with eupleural arch, and united areas divided by pleural suture (*PlS*) into episternum and epimeron (*Eps, Epm*).

I, ventral part of trochantin (*Tn*) a free sclerite by separation from part reunited with eupleuron; postcoxal part of eupleural arch lacking. (Blattidæ.)

J, precoxal and postcoxal parts of eupleural arch forming independent plates (*Acx, Pcx*).

K, eupleural arch complete, united below with sternum.

L, episternal, precoxal, and basisternal regions continuous; postcoxal part of eupleural arch lacking; sternum with secondary articulation with coxa (*c*).

median ventral rim has either become membranous, or has united with the edge of the sternum. In the Acarina, the ventral part of the subcoxa has formed the large plate in the ventral wall of the body to which the leg is attached, while the lateral part has been reduced to a narrow arch over the coxal base.

The assumed change in the coxal axis from a horizontal to an oblique position, when the coxa became the functional base of the limb, suggests a reason for the detachment of a supra-coxal piece, the trochantin (fig. 18 B, Tn), from the body of the subcoxa, for it is clear that the displacement of the axis would be facilitated if the part of the subcoxa bearing the articular condyles became a free sclerite. Börner's view that the ventral articulation of the coxa was originally with the sternum, and that the trochantin is derived from the sternum is contradicted by the fact that in Protura (fig. 8) and in the prothorax of Plecoptera (fig. 13) the trochantin is a free sclerite bearing both the anterior (ventral) and the dorsal articulations of the coxa. In scattered cases, in both the Apterygota and the Pterygota, the coxa is articulated ventrally to the sternum, but in most such instances this is clearly a secondary condition. That the primitive axis of the coxa was horizontal is attested, furthermore, by evidence, to be presented later, that the primitive musculature of the coxa consisted of abductor and adductor muscles. In the head, the mandible retains this form of articulation, and a simple abductor-adductor musculature.

It is not difficult to imagine the probable evolution of the basal part of the subcoxa into the eupleural sclerites. In the Apterygota and in the Chilopoda, this part of the subcoxa has broken up into small plates forming various patterns in different families. In *Eosentomon*, probably three at least of the ventral series of pleurites (fig. 8, f, g, h) belong to the leg base, and may be supposed to be remnants of the eupleural part of the subcoxa (fig. 18 C). These sclerites, as Prell (1913) has pointed out, correspond in position with the divisions of the pterygote pleuron (fig. 18 J), one being supracoxal in position *(Apl)*, and the other two *(Acx, Pcx)* precoxal and postcoxal. In the Chilopoda (figs. 9, 32 B), the pleural pattern is variable, and perhaps has little relation to that in any insect, but apparently there are to be distinguished in it both eupleural and trochantinal sclerites. In the Thysanura there is little uniformity in the pleural structure: *Lepisma* (figs. 11, 18 D) has a single eupleural plate; in *Japyx* (figs. 10, 18 E) the only true pleural chitinization appears to be the trochantin; in *Machilis* (fig. 12) one plate is present over the coxa, but its relation to the pleurites of other Apterygota is not clear.

In the Pterygota, the eupleural arch of the subcoxa is commonly differentiated into three regions, one forming a supracoxal plate, or *anapleurite* (fig. 18 F, *Apl*), lying above the coxa, and the others a *precoxal plate (Acx)* and a *postcoxal plate (Pcx)* lying before and behind the coxa, respectively. The anapleurite is the primitive basis of the episternum and epimeron, and is seldom undeveloped; the other two are variable, and one or both may be lacking. In the pro- thorax of Plecoptera (figs. 13, 18 G), the anapleurite *(Apl)* of the eupleuron, and the trochantin *(Tn)* are present and entirely separate from each other, the latter carrying both the anterior and the dorsal (posterior) articulations of the coxa *(a, b)*. In other pterygote forms, however, the dorsal part of the trochantin, with the dorsal articular condyle of the coxa *(b)*, is united with the anapleural region of the eupleuron (fig. 18 H). The free anterior part of trochantin may remain continuous with its dorsal part (H), but usually it separates from the latter, which becomes an integral part of the episternum, and constitutes a free sclerite lying before the coxa (I, J, K, *Tn*). The anterior trochantinal piece, however, becomes rudimentary or is lost entirely in most of the higher insects. The coxa then often ac- quires a secondary ventral articulation with the furcisternum (L, *c*). In a few insects the ventral rim of the subcoxa persists as a fold around the mesal side of the coxal base (fig. 7), but generally it is not distinguishable, and the precoxal and postcoxal parts of the sub- coxa (fig. 18 H, *Acx, Pcx*) appear as ventral extensions from the episternum and epimeron to the sternum, which, if chitinized, form plates or bridges (J, K). The precoxal bridge is usually best de- veloped (I), the posterior one being frequently lacking. Both may become confluent with the pleural plates above and with the sternal plates below, uniting all these parts into a continuous chitinization surrounding the coxal cavity *(K)*, but the postcoxal bridge may be absent, leaving the coxal cavity " open " behind (L). The numerous other variations of the pterygote pleuron familiar to students of the thorax need not be detailed here, for it will be clear that all are but modifications of the basic structure given above.

THE SPIRACLES

It seems most reasonable to suppose that the spiracles of primitive insects were situated in the pleural regions of the segments, between the edges of the terga and the bases of the limbs. From this neutral position, then, the tracheal branches from each spiracle went to the dorsal and ventral parts of the segment, and the dorsal and ventral

muscles of the spiracular closing apparatus were attached to the tergum and the sternum of the same segment.

Embryologists give us little information concerning the exact position of the spiracles in the embryo with relation to the segmental plates. Lehmann (1925) states that the tracheal invaginations of a phasmid, *Carausius morosus,* appear laterally on the bases of the appendages close to the anterior margins of the segments. Heymons (1895), describing the development of *Forficula* and *Gryllus,* says the spiracles arise as pits on the anterior lateral parts of the spiracle-bearing segments, soon after the appearance of the segmental appendages. Wheeler (1889) says the tracheal invagination on the thorax of *Leptinotarsa decemlineata* are situated at the bases of the legs near the anterior edges of the somites to which they belong; those of the abdomen, however, are placed near the middle of the lateral half of each segment.

In modern adult insects the location of the spiracles is too variable to serve as an index of what the primitive position of the spiracles may have been, for the adult spiracles may lie in the terga, in the pleural membranes, or in the sterna, and these variations occur within the orders, and often on different segments of the same species. It can be stated as a general rule that the abdominal spiracles lie in a line along each side of the body; especially is this true of the spiracles of embryos and larvæ of most holometabolous insects (Lepidoptera, Hymenoptera, Diptera). In many cases, therefore, where the abdominal spiracles of the adult are located in lateral or ventro-lateral areas of the terga, or in lateral parts of the sterna, it would appear that the segmental chitinizations have simply extended from one direction or the other over the spiracular areas to include the spiracles in the definitive segmental plates. In other cases, again, it is possible that there may have been a dorsal or ventral migration of the spiracles, for often the first abdominal spiracle is considerably out of line with those following. In adult Coleoptera, the abdominal spiracles are commonly situated on the dorsal plane of the body, where they may be contained in lateral parts of the terga, in the pleural membranes, or in upturned lateral parts of the ventral plates. In the Scarabæidæ often the spiracles of the first three or four segments are in the pleural membranes, while those following are in the lateral sternal plates. In adephagous larvæ the spiracles (fig. 25, *Sp*) lie in lateral parts of the dorsum, the ventral limits of which are marked on each side by a lateral fold (*a, a*) extending through abdomen and thorax. In adults of this group the abdominal spiracles are inclosed in marginal plates of the terga. In lampyrid larvæ the spiracles are on

ventro-lateral plates of the abdomen, beneath the projecting edges
of the terga, which in the adults are fused with the lateral edges of
the sterna and reflected dorsally. Since the homology of the so-called
" pleural " sclerites in the abdomen of the Coleoptera is not known,
the morphological position of the spiracles in this order cannot be
exactly stated, but the nature of the variations in the location of the
spiracles suggests that there has occurred, in some cases, dorsal and
ventral migrations of the spiracles themselves from a primitive site
in the pleural membranes.

The spiracles of the thorax in adult insects usually occur at vary-
ing levels on the sides, *between* the chitinous pleura. They appear,
therefore, to be intersegmental in position. In embryonic and larval
stages, however, the thoracic spiracles are usually well within the
limits of the segments. In the typical Chilopoda (Pleurostigma) the
spiracles are in the pleural membranes and generally in the posterior
parts of the segments. In the Protura they lie in small plates in the
lateral margins of the mesothoracic and metathoracic terga (fig. 8,
Sp.). The tracheal branches from each abdominal spiracle in insects
are distributed mostly within the segment of the spiracle, and the
muscles of the closing apparatus of an abdominal spiracle arise from
the tergum and the sternum of the same segment. There can be little
doubt, therefore, that all spiracles are segmental organs, as claimed
by Lehman (1925) in his recent review of the insect tracheal system,
in which also he gives reasons for believing that the primitive tracheal
invaginations of insects may represent the ectodermal parts of the
ducts of the nephridial organs (nephromixia) of *Peripatus*. The
apparent intersegmental positions of the thoracic spiracles are evi-
dently the result of secondary displacements, which in many cases
can be traced during development, though some writers (Comstock,
1924, Keilin, 1924, de Gryse, 1926) have argued that all spiracles
are intersegmental in origin, and that their segmental positions are
owing to secondary migrations. A spiracle could not be truly inter-
segmental in a soft-bodied insect without interference with its func-
tion, and the idea of any organ or set of organs other than folds for
muscle attachments being intersegmental is at variance with our con-
ception of the nature of metamerism.

The typical number of spiracles in insects is ten pairs, two pairs
being thoracic and eight abdominal. There is much reason from
developmental studies for regarding the usual first pair of spiracles as
belonging to the mesothorax, and the second to the mesothorax, and
for believing that their intersegmental positions, or the occasional
prothoracic position of the first are due to forward migrations. Yet,

it is disconcerting to observe that the dorsal muscle from the closing lever of the first spiracle of a caterpillar is attached dorsally to the lateral margin of the protergal shield, and still more so to find that there is a spiracle in the prothorax of *Japyx* and related genera in addition to one in the mesothorax.

The usual absence of prothoracic spiracles in adult insects has never been satisfactorily explained. Though Wheeler (1889) says the tracheal invaginations of the first thoracic segment in the embryo of the potato beetle (*Leptinotarsa decemlineata*) are small, and soon close over and disappear, and though Cholodkowsky (1891) mentions the presence of a pair of such invaginations in each segment of the embryo of *Blatta,* students of insect embryology in general have not been able to find traces of spiracles or tracheal pits in the prothorax at any stage of development (Lehmann, 1925). In *Smynthurus,* one of the Collembola, the single pair of spiracles present is located in the neck. Perhaps these are the prothoracic spiracles. In *Campodea* and *Japyx,* and related genera, there is a pair of spiracles on each of the thoracic segments; in *Japyx* there is an additional pair on the metathorax. In *Heterojapyx* the first spiracle (fig. 10 B, Sp_1) is on the side of the prothorax posterior to the base of the leg, the mesothoracic spiracle (Sp_2) lies between a dorsal (tergopleural) scelerite of the pleuron and the edge of the tergum, the corresponding spiracle of the metathorax has a similar position, while the fourth spiracle (Sp) lies latero-ventrally before the base of the hind leg, between the lateral ends of the first and second apotomal folds of the pleuron. The significance of the number and position of the thoracic spiracles of *Campodea* and *Japyx* is by no means clear. The dorsal spiracles that occur on the prothorax and at the posterior end of the abdomen in the larvæ of Diptera are probably special larval organs, since the eight normal lateral spiracles appear on each side of the abdomen in some forms (*Rhagoletis, Braula*) toward the end of the larval period.

The second thoracic spiracles are very small in some adult insects; in certain larvæ they are lacking. In caterpillars and in the larvæ of beetles, the site of each is marked externally by a minute disc in the cuticula just behind the intersegmental fold between mesothorax and metathorax, and the disc is connected by a degenerate tracheal strand with the main lateral trunk of the respiratory system; in the adults, these spiracles are restored as functional organs. The thoracic spiracles usually differ from the abdominal spiracles in some manner, either in the relative positions of their parts, in their structure, or in the type of their closing apparatus, a condition as yet unexplained.

III. SPECIAL STRUCTURE OF A WING-BEARING SEGMENT

While the perfection of the legs as walking appendages affected principally the lower pleural and the sternal parts of the thoracic segments, the development of the wings as efficient organs of flight involved changes mostly in the tergal and the upper pleural regions of the two segments concerned, though the increased importance of the tergo-sternal muscles, and the need of solidarity in the wing-bearing part of the thorax have had a general effect on the entire thoracic structure.

Flying insects have evolved along two quite different lines, but the similarity in their general structure, and in the structure of the wings themselves shows that both resulting groups are descendents of a common ancestral form, which form had all the features distinguishing the Pterygota from the Apterygota. The two lines of differentiation in the Pterygota have been established through the adoption of different mechanisms for moving the wings. Among modern insects, one pterygote group is represented only by the Odonata, the other includes the rest of the winged orders.

In the non-odonate insects there are few special wing muscles, the muscles that effect the movement of the wings being chiefly the longitudinal dorsal muscles of the terga, the tergo-sternal muscles, and a set of muscles that originally were muscles of the coxæ. The tergal and the tergo-sternal muscles move the wings indirectly by the production of alternating changes in the shape of the thorax; the other muscles are more closely connected with the wings in the adult, but, being leg muscles in origin, they also are not primary wing muscles. It thus appears that when wings were developed and first became mobile appendages, they were moved by muscles already present in the segments bearing them. Only a few special wing muscles have since been acquired by most insects. In the Odonata, however, the wings are moved entirely by muscles inserted directly on the wing bases, and it is impossible to trace any homology between these muscles and the wing muscles of other insects. According to Poletaiew (1881) the wing muscles of the dragonflies are formed and developed during the nymphal stages of these insects. The wing mechanism of the Odonata, therefore, must be one secondarily acquired through the development of special wing muscles, which have supplanted the primitive musculature of the wing-bearing segments. For this reason, the following descriptions of the structure of a typical wing-bearing segment will be based on that of the mesothorax and metathorax of non-odonate insects.

GROUND-PLAN OF A WING-BEARING SEGMENT

Though the general structure of the thorax was determined through the specialization of this region of the body as the locomotor center of the insect, and through the transformation of the subcoxæ into chitinous pleura, probably long before the wings appeared, the special features of the thoracic segments in winged insects have undoubtedly been evolved as characters correlated with the development of the wings.

The paleontological history of insects shows that lateral tergal lobes were present on the prothorax of many of the earliest known winged
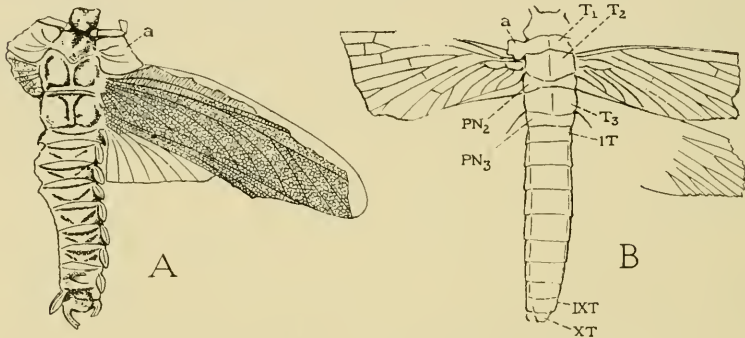

Fig. 19.—Carboniferous insects with tergal lobes on the prothorax (Palæodictyoptera).

A, *Stenodictya lobata* Brong., with large lobes (*a*) on protergum. (Brongniart, 1890.) B, *Eubleptus danielsi* Handlr. (drawn from specimen No. 35576, labeled holotype, in U. S. Nat. Mus.), showing small protergal lobe (*a*), well-developed postnotal plates (*PN₂*, *PN₃*) in mesothorax and metathorax, and ten abdominal segments.

species (fig. 19) ; but there is no fossil insect known from the geological period, probably the Silurian, when the wings were in the course of development. There can be little doubt, however, that the wings were evolved from lateral lobes of the dorsum in the mesothorax and metathorax. We can only speculate as to what service these lobes were to insects during their early stages of evolution. The most popular explanation is that they were gills, and that the tracheæ, which mark later the courses of the wing veins, penetrated the lobes first for respiratory purposes. This theory implies that the ancestors of winged insects passed through an aquatic period in their evolution after having acquired a tracheal system during a previous period when they dwelt on land. Osborn (1905), in proposing this explanation of the origin of insect wings, suggests that insects lived in the

water during the Silurian age, and that the aquatic progenitors of the
Pterygota were themselves descendents of primitive terrestrial tra-
cheates of Ordovician times. This theory of the origin of insect
wings is pretty safe from destructive criticism, but for the same
reason little direct evidence can be shown in its favor. Bats and flying
squirrels have not needed a baptism for the acquisition of wings, but
their wings do not contain tracheæ. On the other hand, it is perhaps
not certain that, phylogenetically, the veins of insect wings were pre-
ceded by the tracheæ. The Silurian insects, known only as the neces-
sary ancestors of post-Silurian insects, do not attest an adaptation to
life in the water in any of their descendents. If they were aquatic,
they have left no direct descendents; and existing insects bear no
stamp of an aquatic ancestry. The abdominal gill lobes of nymphs
of Ephemerida, often cited as possible homologues of the hypothetical
thoracic gill lobes from which the wings might be supposed to have
developed, have been shown by Dürken (1907), from a study of their
musculature, to have nothing in common with the wings. The oldest
known insects are distinctly terrestrial, and they likewise give no
evidence of a recent emergence from a water environment, except as
adults from aquatic nymphs. For a more complete discussion of the
arguments that have been made in favor of a gill origin of the wings,
and of the facts indicating their paranotal origin, the student is re-
ferred to the paper by Crampton (1916) on this subject, in which
will be found also a long bibliography.

If the gill theory of wing origin in insects is found eventually
unacceptable in any form, it should not be hard to believe that the
wing lobes in earlier stages enabled their possessors to glide through
the air from elevated situations, and that the lobes were thus organs
of sufficient importance to demand a considerable degree of recon-
struction in the pleura, or subcoxal chitinizations, of the segments
bearing them. There is no evidence that prothoracic lobes were ever
developed into wing-like or even movable appendages, and there is no
proof that they were present in the true ancestors of winged insects,
or that the wing lobes are their homologues in any case. Yet, con-
sidering the essential identity of structure between the prothoracic
pleuron and the pleura of the wing-bearing segments, it becomes evi-
dent that all the thoracic pleura must owe their specialized form to
some common guiding influence, and that this influence must have
determined the basic structure of the pterygote thoracic pleuron be-
fore the dorsal lobes of the mesothorax and the metathorax evolved
into true wings. A reasonable postulate, therefore, is that the deter-

mining factor of the pleural structure in the thorax was the presence of potential wing lobes on each of the thoracic segments.

Carpentier (1921), in his study of the pleura of wingless Orthoptera, shows that the pleuron of the prothorax is identical in structure with the pleura of the other two thoracic segments, a condition suggestive of the former presence of wings on the prothorax, though
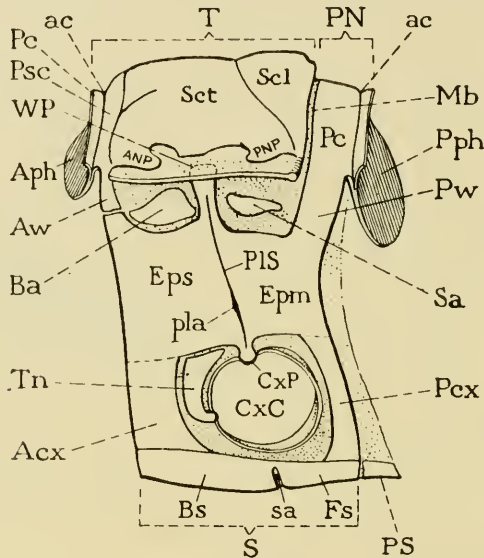

FIG. 20.—Diagrammatic structure of a wing-bearing segment with a phragma attached to each end; wing cut off at base; coxa removed.

ac, antecostal suture; *Acx*, precoxal bridge; *ANP*, anterior notal wing process; *Aph*, anterior phragma; *Aw*, prealar process, or bridge; *Ba*, basalare, episternal epipleurite; *Bs*, basisternum; *CxC*, coxal cavity; *CxP*, pleural coxal process; *Epm*, epimeron; *Eps*, episternum; *Fs*, furcisternum; *Mb*, remnant of intersegmental membrane; *Pc*, precosta; *Pcx*, postcoxal bridge; *pla*, external root of pleural apophysis; *PlS*, pleural suture; *PN*, postnotum (postscutellum); *PNP*, posterior notal wing process; *Pph*, posterior phragma; *PS*, poststernum; *Psc*, prescutum; *Pw*, postalar bridge; *S*, sternum; *Sa*, subalare, epimeral epipleurite; *sa*, external root of sternal apophysis; *Scl*, scutellum; *Sct*, scutum; *Tn*, trochantin; *WP*, pleural wing process.

Carpentier does not commit himself to this conclusion. The mental picture of a pair of fully-developed wings on each of three consecutive segments, however, is not convincing as a mechanical reality; but the degree of development in the prothoracic pleura may be taken to mean that the paranotal lobes of the prothorax once reached a stage of development in which they, as well as those of the mesothorax and metathorax, required the support of the pleura. Beyond this stage, the lobes of the second and third segments were evolved

into freely movable wings, while those of the prothorax degenerated and were lost. In harmony with this view is the difference in structure between the tergum of the prothorax and that of a wing-bearing segment, and the differences in the segmental musculature. As the skeletal parts of the mesothorax and metathorax responded to the demand for mobility in the tergal lobes, the segmental muscles capable of moving the latter were developed accordingly.

The general structure of a wing-bearing segment is shown diagrammatically in figure 20. The dorsum of the segment may be occupied only by the true tergal plate *(T)*, or *notum*, as the tergum of a thoracic segment is often called ; but the segment in which the wings are best developed usually has also a second smaller plate, the *postnotum (PN)*, lying immediately behind its true tergum. On the sides of the segment are the usual pleural plates of pterygote insects, the episternum *(Eps)* and epimeron *(Epm)*, separated by the pleural suture *(Pls)*. At the upper end of the latter the dorsal edge of the pleuron is produced into a special *pleural wing process (WP)*, which forms a fulcrum against the wing base. The tergum is often supported on the pleura by arms extending from its anterior lateral angles to the corresponding dorsal angles of the episterna, each arm constituting a *prealar bridge (Aw)*. The postnotum, when present, is generally connected likewise by lateral extensions with the epimera, each extension forming a *postalar bridge (Pw)*. Between the wing base and the upper edge of the pleuron there is an ample membrane in which are situated several small epipleural plates *(Ba, Sa)*. The ventral parts have no distinctive features in the wing-bearing segments and have been sufficiently treated in the description of the fundamental structure of the thoracic sterna (page 17). The details of the wing-bearing tergum, and certain features of the pleuron, however, need a more extensive special examination.

STRUCTURE OF A WING-BEARING TERGUM

The tergum of a wing-bearing segment preserves in its basic structure the elemental composition of the tergal plate in any segment where secondary segmentation has been established (fig. 2 B, C). It includes the intersegmental antecostal ridge preceding (fig. 21 B, *Ac*), and a precosta (A, B, *Pc*) demarked externally by the antecostal suture (A, *ac*). Its posterior edge is reflected ventrally in a marginal fold, or posterior reduplication (B, *Rd*). Between the tergum and the following precosta there is a transverse membranous area (fig. 23 B, *Mb*), functionally intersegmental, but which is morpho-

logically the posterior part of the segment. Only in larval insects is
the primary body segmentation (fig. 23 A) found in the thorax, and
even here the union of the primitive terga with the chitinized inter-
segmental fold may establish a typical secondary segmentation. In
the larva of *Scarites* (fig. 25), the fold between the protergum and
the mesotergum is chitinized and united with the latter, forming thus
an antecosta of the mesotergum. From the antecosta of each of the
wing-bearing segments, and from that of the first abdominal segment
there is usually developed a pair of thin chitinous lobes, the two
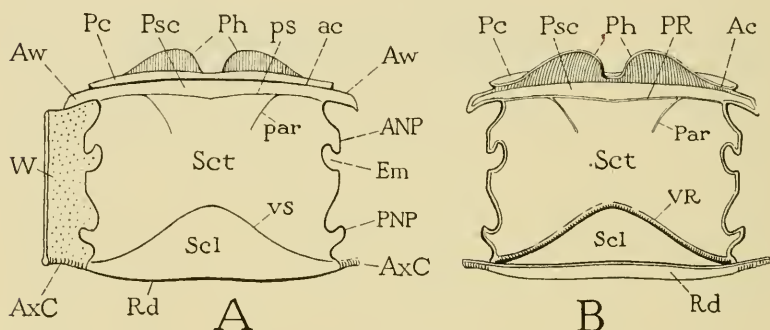constituting a *phragma* (fig. 21, *Ph*), which projects into the cavity

Fig. 21.—Diagrammatic structure of a wing-bearing tergum, not including a
postnotum.

A, dorsal; B, ventral. *Ac,* antecosta; *ac,* antecostal suture; *ANP,* anterior
notal wing process; *AxC,* axillary cord; *Aw,* prealar process; *Em,* lateral
emargination of tergum; *Par,* parapsidal ridge; *par,* parapsidal suture; *Pc,*
precosta; *Ph,* phragma; *PNP,* posterior notal wing process; *PR,* ridge between
prescutum and scutum; *ps,* prescuto-scutal suture; *Psc,* prescutum; *Rd,* posterior
reduplication of tergum; *Scl,* scutellum; *Sct,* scutum; *VR,* ridge between
scutum and scutellum; *vs,* scuto-scutellar suture; *W,* base of wing.

of the thorax and furnishes an increased surface for the attachment
of the dorsal longitudinal muscles.

   The wings are hollow outgrowths from the lateral parts of the
dorsum in each segment, between the prealar bridges and the posterior
edge of the tergum (fig. 21 A, *W*). The posterior margins of the
wings, therefore, are direct continuations from the posterior fold
(Rd) of the tergum. The dorsal wall of each wing is continuous with
the lateral margin of the tergum, the ventral wall is reflected into the
pleural subalar membrane. The wings become movable by the mem-
branization of their bases. The lateral edges of the adult tergum are
produced into small lobes to support the dorsal articular elements of
the wings; generally there are two lobes on each side, an *anterior*

notal wing process (fig. 21, *ANP*), and a *posterior notal wing process (PNP)*, though the latter is frequently lacking. Behind the first wing process there is a deep *lateral emargination* of the tergum *(Em)*.

The surface of the wing-bearing tergum is differentiated into several areas, some being limited by the sutures of internal ridges, others being merely topographical in nature. The internal ridges are, therefore, the features of greatest importance in a study of the tergum. The most constant apodemal ridge has the form of an inverted *V* (fig. 21 B, *VR*), the arms of which arise near the posterior angles of the tergum and converge forward, the apex being usually behind the center of the tergum. This apodeme, which may be designated the *V-ridge,* forms a strong brace in the posterior part of the tergal plate, and sets off a posterior area of the tergum called the *scutellum (Scl)*. All the muscles of the tergum arise upon the prescutellar area. The rear margin of the scutellum is deflected in the posterior reduplication *(Rd),* and its ends are prolonged in the axillary cords of the wings *(AxC)*.

On the anterior part of the tergum, behind the antecostal suture *(ac)*, there is often differentiated a narrow transverse strip, called the *prescutum* (fig. 21, *Psc*). The area is sometimes limited by a distinct suture (A, *ps*), with a corresponding internal ridge (B, *PR*), but the prescutum is seldom as definitely marked as the scutellum, and its separation from the rest of the tergum may be faint or obsolete. Anteriorly the prescutum is deflected into the antecostal suture (A, *ac*) over the base of the phragma *(Ph),* beyond which is the precosta *(Pc),* or anterior lip of the phragma base, always narrow, sometimes scarcely perceptible, except when enlarged to form a postnotum of the preceding segment (figs. 22, 23). Laterally, the prescutum ends in the prealar bridges (fig. 21 A, *Aw*), if such processes are present.

The application of the term " prescutum " as given here follows the evident intent of Audouin (1824), who defines the " praescutum " as " la pièce la plus antérieure," and adds that " elle est quelquefois très grande et cachée ordinairement en tout ou en partie dans l'interieur du thorax." This is the part, however, called " acrotergite " by Berlese, and " pretergite " by Crampton (1919). As will be shown later, the triangular area of the tergum in some insects, usually regarded as a part of the prescutum (" protergite " of Berlese), is apparently a part of the scutum.

The area of the tergum between the prescutum and the scutellum is the *scutum (Sct)*. The topography of the scutum is variable; its surface is often cut by sutures which arise from the secondary de-

4

velopment of ridges on its under surface. The most important of these ridges are two known as the *parapsides* (fig. 21 B, *Par*), which arise laterally from the prescuto-scutal suture and converge poster-iorly a varying distance in the scutum. The lateral margins of the scutum bear the anterior and the posterior wing processes *(ANP, PNP)*, and are notched just behind the former by the lateral emar-ginations *(Em)*. The wings *(W)* are extensions from the scutum and scutellum, their posterior, thickened edges (the axillary cords) being continued from the narrowed ends of the scutellum.

THE POSTNOTAL PLATES

Though the terga of the wing-bearing segments have acquired no new elements to enable them to play their parts in the wing mechan-ism, they have, however, in most cases lost the simplicity of segmental plates through a redistribution of some of the primitive elements. A primitive dorsal plate, bearing the wings and preserving the struc-ture of a typical tergum, with an antecosta or phragma at the anterior end, occurs in the mesothorax and metathorax of Isoptera, and in the mesothorax of Orthoptera, Euplexoptera, and Coleoptera. In nearly all other instances, the dorsum of a winged segment contains two plates (fig. 22A), the first being the true tergum, or notum *(T)*, the second the postnotum *(PN)*. The postnotum occurs in typical form only in the adult insect ; it consists of the greatly enlarged pre-costa, together with the antecosta and phragma, of the following tergum usually more or less separated from the latter and closely asso-ciated with the preceding tergum. The altered relation in the tergal parts of the wing segments is probably the result of a secondary modification, for, as we shall see, it constitutes a structure correlated with efficiency of wing motion. Presumably all the thoracic terga of the wingless ancestors of the Pterygota had the usual form of seg-mental plates (fig. 5), still retained in those of the Apterygota.

The nature of the redistribution of the tergal parts in segments having a postnotum is explained diagrammatically in figure 23. At A is shown the original primary segmentation, with the dorsal mus-cles *(LMcl)* attached to the intersegmental folds. In B the folds are chitinized to form antecostæ *(Ac)*, each with a small precosta *(Pc)* before it. The posterior membranous parts of the segments *(Mb)* now become the flexible " intersegmental " regions, and the segmen-tation is typically secondary. Let us suppose that the dorsal plates (C, T_1–IT) are the terga of segments from the prothoracic to the first abdominal, inclusive, and that each antecosta has a phragma

(1Ph, 2Ph, 3Ph) bearing the muscle attachments. At C, a condition is given in which the antecosta of the first abdominal tergum *(IT)*, with its phragma *(3Ph)* and the precosta are separated from the principal part of the abdominal tergum and are more closely connected with the tergum of the metathorax *(T₃)*. The abdominal precosta and antecosta, or the base of the phragma, here constitute, then,
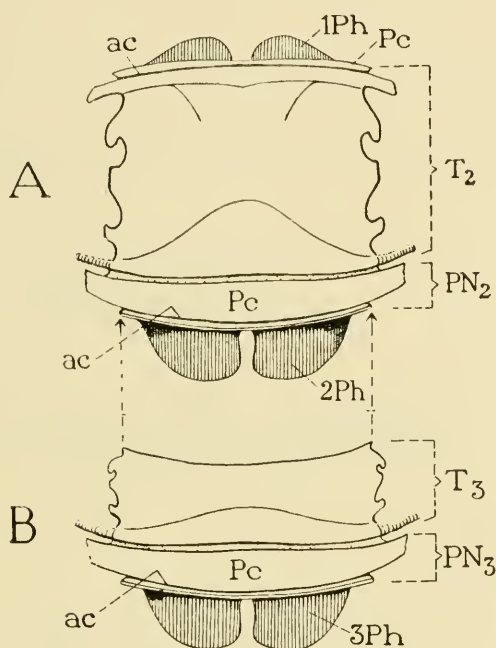

Fig. 22.—Diagram of wing-bearing terga with postnotal plates.

A, tergal plates of mesothorax; B, tergal plates of metathorax. Each postnotum *(PN₂, PN₃)* consists of precosta *(Pc)* and narrow postcostal piece detached from following tergum, with a phragma *(Ph)* developed from the antecostal ridge, the base of which is marked externally by the primarily intersegmental antecostal suture *(ac)*.

the postnotum *(PN₃)* of the metathorax. The latter segment is now provided with two phragmata, an anterior phragma *(2Ph)*, and a posterior phragma *(3Ph)*, and its dorsal muscles become segmental instead of intersegmental. The relations between the mesothorax and the metathorax are here (C) of the normal type. The condition represented is characteristic of the Orthoptera, Euplexoptera, and Coleoptera, though in the first two orders the postnotum of the metathorax usually retains its connection with the first abdominal tergum.

In most other insects a postnotum is present in each of the wing-bearing segments, as given at D of the figure. In this case the mesothorax is provided with an anterior phragma *(1Ph)* and a posterior phragma *(2Ph)*, while the metathorax has only a posterior phragma *(3Ph)*. The first phragma *(1Ph)* is never transferred to the protergum. If the base of the middle phragma *(2Ph)* retains its connection also with the metatergum, the mesotergum and metatergum
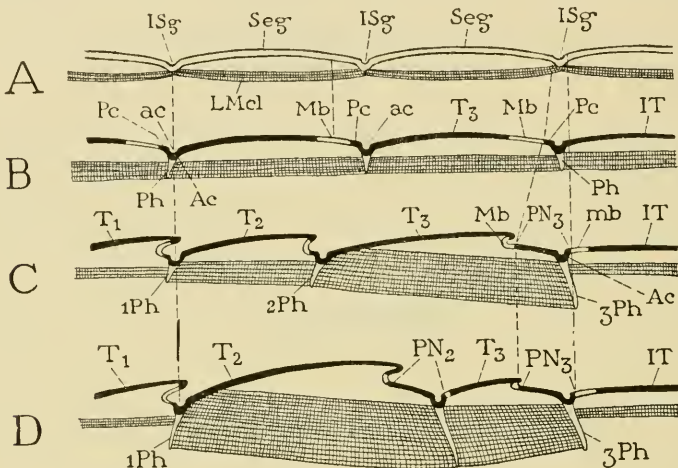

Fig. 23.—Diagrammatic lengthwise sections showing the nature of the phragmata and the thoracic postnotal plates.

A, primary segmentation in non-chitinous segments *(Seg)*, with longitudinal muscles *(LMcl)* attached at intersegmental rings *(Isg)*.

B, secondary segmentation: each tergal plate *(T)* including the chitinized antecosta *(Ac)* and narrow precosta *(Pc)*; antecostæ bearing phragmata *(Ph)*; the antecostal sutures *(ac)* are the original intersegmental grooves (A, *Isg*).

C, thorax with metathoracic wings chief organs of flight: third phragma *(3Ph)* separated from first abdominal tergum *(IT)* by secondary membrane *(mb)*, and its precosta (B, *Pc*) enlarged to form the pre-phragma part in a postnotal plate *(PN3)* of metathorax.

D, thorax with mesothoracic wings chief organs of flight: each wing-bearing segment with a postnotal plate *(PN2, PN3)* and a posterior phragma; the postnotal plates prevent telescoping of the segments (fig. 2 C).

are said to be "fused." Comparing C and D with A in figure 23, it is clear that the part of postnotal plate before the phragma belongs to the posterior part of the primary segment in which it occurs, and that only the narrow posterior lip of the phragma base has come from the following segment. It is thus true, as Berlese (1909) has shown, that the postnotum of a winged segment is the "acrotergite" of the tergum following.

The variation in the connections of the phragmata is correlated with the specialization of one pair of wings or the other as the chief organs

of flight. If flight devolves principally upon the hind wings, as it does in the Orthoptera, Euplexoptera, and Coleoptera, the second phragma, is attached to the anterior part of the metatergum, and the third phragma, though it may not be separated from the first abdominal tergum, becomes functionally a part of the metatergum through the forward extension of its precosta as a postnotal plate of the meta-thorax. Where the fore wings are the most highly developed for flight, as they are in the majority of insects, the second phragma goes to the mesotergum. In other words, the segment containing the largest wing muscles has a phragma at each end, an arrangement which concentrates the force of the muscles upon the tergum of this one segment.

The postnotal plates are probably contemporaneous in their origin with the acquisition of motion by the wings. They are well developed in the oldest known fossil insects; in the Palaeodictyoptera there is a large postnotum behind each of the wing-bearing terga (fig. 19 B, PN_2, PN_3). The statement by Handlirsch (1908) that there are eleven abdominal segments in this group appears to be the result of counting the postnotum of the metathorax as the first abdominal ter-gum. In the Isoptera postnotal plates are lacking, but this condition is here correlated with the degeneration of the dorsal thoracic muscles and the weak nature of the termite flight. Postnotal plates are present in the Ephemerida and Odonata, though in the latter also the dorsal muscles have been lost.

It is not difficult to see a reason for the development of postnotal plates in wing-bearing segments. Where the primitive tergal plates are separated by membranous areas of the posterior parts of the seg-ments (fig. 2 B, 23 B, Mb), a contraction of the dorsal muscles causes an overlapping of the terga (fig. 2 C), a result which must be counter-acted if the muscles are to produce motion in the wings. The inter-segmental membranes, therefore, must be reduced or obliterated, and their suppression has been accomplished in most cases by a forward extension of the precostal margins (fig. 23 C, D) until the resulting postnotal plate and the tergum in each segment form an uninterrupted arch between consecutive phragmata. The force of the muscle con-traction is now expended against the tergal arch, with the result that its upward flexion gives a down-stroke to the wings. Thus, also, the longitudinal dorsal muscles become antagonists to the tergo-sternal muscles, if the latter muscles previously existed, or they call for the development of such muscles, which then become elevators of the wings.

MODIFICATIONS OF THE WING-BEARING TERGA

The structural variations in the terga of the mesothorax and meta-thorax of winged insects have furnished a problem that has caused much vexation to those who would like to have the parts of the terga in all insects conform with one simple plan of organization. The tergal parts probably do represent one plan of structure, but they do not always agree with the usual system of nomenclature applied to them. The trouble is that the fundamental structure, easily recognized in some cases, is so obscured in others that parts which appear to be the same in different insects are really not so.

The wing-bearing tergum, as we have seen (fig. 21), has an ante-costa (B, Ac) on its front margin bearing a phragma (Ph), the base of which is marked externally by the antecostal suture (A, ac). The precosta (Pc), or anterior lip of the phragma base, before the meso-thoracic tergum is but a narrow strip, often indistinguishable; that before the metatergum, however, is enlarged to form a postnotal plate of the mesothorax if the fore wings are chiefly functional in flight, and the precosta of the first abdominal tergum becomes usually a postnotal plate of the metathorax. Behind the antecostal suture in a tergum that retains the precosta and phragma preceding, there is usually differentiated a narrow prescutum (Psc) ending laterally in the prealar bridges or other lobes before the bases of the wings. A triangular scutellum (Scl) is set off on the posterior part of the tergum by the suture of the V-ridge (vs or VR), and the part of the tergum between the prescutum and the scutellum is the scutum (Sct). The difficulties encountered in the study of the wing-bearing terga of different insects arise from the obscuring of these landmarks, either through a partial or complete suppression of the marks them-selves, or from their being subordinated to characters of secondary development.

The prescutum occurs in typical form in most of the Orthoptera, where it consists of a narrow transverse area of the anterior part of the tergum (fig. 24 B, C, Psc), ending laterally in the prealar pro-cesses, and usually expanded at the antero-lateral angles of the scutum. In *Blatta* the prescutum is separated from the scutum by a faint suture and internal ridge; in the Acrididae (fig. 24 C) it is demarked rather by the line of declivity at the anterior margin of the scutum; in *Gryllus* (B) it is scarcely distinct from the scutum medially. In Lepidoptera there is usually a small triangular prescutal plate in the mesothorax (G, Psc) set into a notch in the anterior border of the scutum. In the metathorax of Coleoptera the prescutum reaches its highest develop-

ment (H, *Psc*), its median part being here often expanded posteriorly until it almost meets the apex of the scutellum (*Scl*). In Tipulidæ (D) and Tenthredinidæ (I), the prescutum is reduced to a narrow band (*Psc*) surrounding the convex anterior margin of the scutum, and extending backward on the sides to the bases of the wings. In some cases,
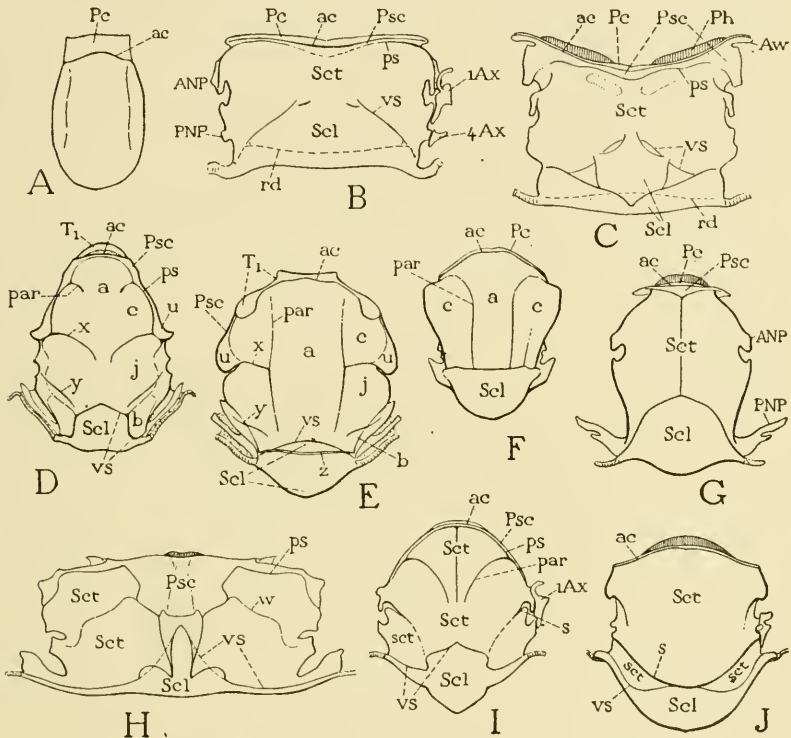

Fig. 24.—Modifications of the wing-bearing tergum.

A, mesotergum of *Japyx*, consisting of a simple segmental plate with a large precosta (*Pc*) separated by an antecostal suture (*ac*). B, metatergum of *Gryllus assimilis*, area behind antecostal suture (*ac*) partially divided into prescutum (*Psc*), scutum (*Sct*), and scutellum (*Scl*). C, mesotergum of *Melanoplus femur-rubrum*. D, mesotergum of *Holorusia rubiginosa*; prescutum (*Psc*) a narrow band terminating on each side in prealar lobe (*u*); scutum marked by three pairs of sutures (*par, x, y*); *a, c, j, b*, attachments of tergal muscles (fig. 34 D, *A, C, J, B*). E, mesotergum of *Tabanus atratus*: prescutum (*Psc*) fused medially with scutum; parapsidal sutures (*par*) extended posteriorly; scutellum divided by secondary groove (*z*). F, mesotergum of *Cynips*: prescutum and scutum fused; parapsidal sutures (*par*) cut the scutum lengthwise into three parts (*c, a, c*). G, mesotergum of *Phassus argentiferus*. H, metatergum of *Calosoma scrutator*: scutum divided medially by approximation of prescutum and scutellum, and each half divided by suture (*w*) into anterior and posterior part (*Sct, Sct*). I, mesotergum of *Pteronidea ribesi*: prescutum (*Psc*) very narrow; parapsidal sutures (*par*) of scutum convergent; scutum cut by lateral sutures (*s*). J, mesotergum of *Apis mellifica*: prescutum and scutum united; scutum divided by secondary suture (*s*) into three parts (*Sct, sct, sct*).

even in segments having an anterior phragma, the prescutum entirely loses its individuality, as in the cicada and in the higher Hymenoptera (fig. 24 F, J). In the higher Diptera, remnants of the prescutum are distinguishable at the sides of the scutum (E, Psc) terminating in prealar lobes (u) corresponding with those of the Tipulidæ (D), but anteriorly the prescutum is not discernible in those Diptera in which the protergum (E, T_1) is fused with the mesotergum.

A prescutum is generally lacking as a defined area in metathoracic terga that have parted with the middle phragma (fig. 22, T_3), but this condition probably does not mean necessarily that the entire prescutal region has become detached with the phragma.

The separation of the scutellum from the scutum by the V-ridge and its suture is usually a very distinct one (fig. 24 D-J), but in some groups the boundary between these two areas of the tergum also is difficult to determine. In Blattidæ, the scutellum is of typical form, though its median part extends forward in a long narrow triangle almost to the prescutum. In $Gryllus$ (fig. 24 B) the lateral arms of the V-ridge do not meet, and the scutum and scutellum are continuous medially. In Acrididæ, the V-ridge (C, vs) is interrupted by another ridge of similar shape but turned in the opposite direction. The arms of this second ridge, converging medially and posteriorly, bound the posterior margins of the shield-shaped elevation of the scutellum (Scl) that lies between the bases of the folded wings. A similar condition exists in the mesotergum of Hemiptera and Coleoptera. In the higher Diptera, the position of the V-ridge is less noticeable externally (E, vs) than is the secondary suture (z) that forms a deep groove across the anterior end of the scutellum. In the Tenthredinidæ a pair of sutures extends inward and posteriorly from the lateral emarginations of the mesotergum (I, s), which sutures become a continuous cleft in some of the higher Hymenoptera (J, s) that cuts the tergum into two pieces, the second of which includes the scutellum (Scl) and the posterior lateral parts of the scutum (sct, sct). Systematists, for convenience, usually designate this secondary suture as the division between scutum and scutellum, a disposition entirely wrong from a morphological standpoint.

While, then, in terga of simple construction, it is not difficult to identify homologous regions if the internal structure is examined, complications are encountered within some of the orders, especially in the scutum (fig. 24 D-J), which have led to widely different interpretations. The following considerations, however, suggest an explanation of these tergal modifications which gives a simplified con-

ception of their nature, and which when logically carried out does not lead to conflicting results.

In the mesothorax of Tipulidæ, the tergal area between the prescutum (fig. 24, D, *Psc*) and the scutellum *(Scl)* is partially divided into several regions by pairs of oblique lateral sutures. The sutures constituting the first pair *(par)* extend inward and posteriorly a short distance from the lateral parts of the prescuto-scutal suture *(ps)*; those of the second pair *(x)* arise before the bases of the wings and converge posteriorly and medially; those of the third pair *(y)* go from the region of the wing base posteriorly and medially toward the median field of the scutellum. Each suture is the external line of a corresponding internal ridge, and the spaces between the ridges are areas of muscle attachments. The anterior ends of the dorsal longitudinal muscles are attached on the median area *(a)* between the first pair of ridges *(par)*. The tergo-sternal muscles (fig. 34 D, *C*) are attached laterally on the spaces *(c)* behind these ridges; the tergo-meron muscles (fig. 34 D, *J*) are attached on the lateral areas *(j)* between the second and third ridges; and the tergo-phragma muscles (fig. 34 D, *B*) are attached behind the third ridges. These lateral tergal muscles in the Diptera all act as elevators of the wings.

The first pair of lateral tergal ridges in the Tipulidæ (fig. 24 D, *par*) are clearly the homologues of the so-called parapsides, or parapsidal ridges, of other insects (E, F, I, *par*), which are usually regarded as defining a median triangular posterior extension of the prescutum (the *protergite* of Berlese). It is here proposed, however, that the parapsides are merely secondary ridges of the scutum, and that the median area between them is, therefore, a part of the scutum. The ridges are correlated with the extension of the anterior ends of the dorsal longitudinal muscles on the tergum: as these muscles enlarge, their anterior bases encroach first upon the prescutum, then upon the scutum (fig. 29, *A, A*), and they may finally come to occupy almost the entire median field of the latter (fig. 34 D, *A, A*). In the higher Diptera, in which the median part of the prescutum and scutum are not distinct (fig. 24 E), the anterior ends of the parapsidal sutures *(par)* are obsolete; their posterior ends unite with the next pair of lateral sutures *(x)*. In Cynipidæ, the parapsidal sutures (F, *par*) extend backward to the scuto-scutellar suture and cut the scutum lengthwise into three areas *(c, a, c)*. In the mesothorax of Cicadidæ and Tenthredinidæ, the parapsidal sutures define an anterior median triangular area of the scutum; in the former (fig. 29), the prescutum is not distinct, but in the latter family it is present though very narrow (fig. 24 I, *Psc*). In the mesothorax of Lepidop-

tera the scutum is strengthened by a median ridge on its inner surface, forming a median suture externally (fig. 24 G).

The mechanism of the wing-bearing tergum and its functional evolution in connection with the wings have been well protrayed in recent papers by Weber (1924, 1925). The tergum must be so constructed that it will bend upward in response to the contraction of its dorsal longitudinal muscles, in order to give the down-stroke to the wings. The evident purpose of the parapsidal ridges, when present, and of the V-ridge, as Weber points out, is to conduct the flexion of the tergum in an even curve toward the middle from the two ends of the segment, for without these gradient braces the pull of the muscles would simply deflect the anterior and posterior parts of the tergal plate, in most cases. In the higher Hymenoptera, however, the tergum becomes strongly chitinized and rigid. Here flexibility is supplied by the development of a secondary suture, which cuts across
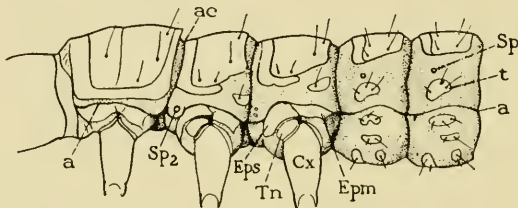

FIG. 25.—Thorax and base of abdomen of larva of *Scarites* (Carabidæ).

a, a, pleural fold; *ac,* antecostal suture of mesotergum; *Cx,* coxa; *Epm,* epimeron; *Eps,* episternum; *Sp,* spiracle; *t,* tergopleurites; *Tn,* trochantin.

the posterior part of the scutum (fig. 24 J, *s*) and divides the tergum into two pieces movable upon each other.

THE PLEURON OF A WINGED SEGMENT

The rôle of the pleuron in connection with flight is a more passive one than is that of the tergum, the chief function of the pleura in a wing-bearing segment being to support the bases of the wings and the tergal plates. The pleuron of a winged segment, therefore, shows fewer variations in relation to the wings than does the tergum, and the pleura of the mesothorax and metathorax do not differ in basic structure from the pleuron of the prothorax, though the actual difference may often be considerable on account of the degenerative tendency of the prothorax, and especially of the prothoracic pleuron.

The wing support of the pleuron of a winged segment consists of a short thick arm, the *pleural wing process* (fig. 20, *WP*), extending upward from the dorsal edge of the pleuron above the pleural suture

(PlS). It is braced internally by the upper end of the pleural ridge. The tergum does not always rest upon the pleura of its segment, but, when it does, the supports consist of the anterior lateral processes of the tergum that form the prealar bridges *(Aw)* to the episterna, and of the lateral extensions of the postnotum *(PN)* to the epimera that constitute the postalar bridges *(Pw).* These props give effective resistance to the downward pull of the tergo-sternal and the tergo-coxal muscles.

The episternum and the epimeron (fig. 20, *Eps, Epm*) undergo numerous variations in form, and various subdivisions into secondary sclerites in the mesothorax and metathorax of the different winged orders, but their modifications are in general easy to follow, and are so well understood that they need not be reviewed here. The precoxal and postcoxal elements *(Acx, Pcx)* are usually well developed, though the second is generally the smaller, and may be absent. The trochantinal plate *(Tn)* is best developed in the more generalized Pterygota (figs. 13, 14, *Tn*), but shows always a tendency toward reduction, and is lost in the higher orders.

The small sclerites lying in the pleural membrane immediately beneath the base of the wing (fig. 20, *Ba, Sa*) serve in the adult as insertion points for two important muscles of the wings (figs. 28, 30 A, *E, F*). There are at most two of these sclerites above the episternum, and two above the epimeron, but more usually there is only a single plate in each position, one before the pleural wing process, the other behind it. Many entomologists, supposedly following Audouin(1824), have called the episternal sclerite the " parapteron," and Audouin says of the plate that he defines by this name, " elle a des rapports avec l'episternum et avec l'aile, toujours elle s'appuie sur l'episternum, se prolonge quelquefois inferieurment le long de son bord antérieure, ou bien, devenant libre, passe au devant de l'aile, et se place même accidentellment au-dessus." It is possible, therefore, that Audouin in some cases confused the plate ordinarily beneath the wing with the tegula, though of his " paraptere " he says, " toujours elle s'appuie sur l'episternum." Crampton (1914), however, claiming that Audouin first applied the term " parapteron " to the tegula, designates the episternal plates the *basalares (Ba)*, and the epimeral plates the *subalares (Sa).* These terms commemd themselves because they carry specific distinction, though all the plates are subalar in position. Voss (1905) and other German writers call the sclerites the " pleural hinge plates " (Pleuralgelenkplatten), but they are not true articular elements of the wing base. Collectively, we may call the plates the epipleurites.

appendage through the membranization of its basal part, and which has become movable in a definite manner through the close association of certain chitinous points in its base with special points on the edges of the tergum and pleuron of its segment. The wing is a secondary structure, acquired long after the legs were fully developed and the subcoxæ transformed into chitinous pluera. The first movements of the wings were made probably through successive alterations in the shape of the thorax produced by the contractions of body muscles already present; and insects in general have developed few muscles particularly for the movement of the wings. The Odonata stand alone among modern insects in having acquired special sets of wing muscles attached directly to the bases of the wings, which have completely replaced the older thoracic muscles. Since the dragonflies represent an ancient group of insects, it must be supposed that they developed their peculiar thoracic musculature during an early period of their history. According to Poletaiew (1881) the wing muscles of modern Odonata are formed in the individual during the postembryonic stages of growth and attain their definitive form only in the last nymphal instar.

GENERAL STRUCTURE OF THE WINGS

The insect wing is a flattened, double-layered expansion of the body wall, and, therefore, its own walls consist of the same elements as the body wall—cuticula, hypodermis, basement membrane—and its lumen contains tracheæ, nerves, and liquid of the body cavity.

Development of the wings.—Though the adult wing preserves the basic structure of the hollow immature wing pad, the progressive changes that take place within it during its growth so alter its tissues that the fully formed wing becomes practically a lifeless appendage serving as a propeller in the mechanism of flight. The histological details of the development of the wings, the formation of the wing tracheæ, and the relations of the tracheæ to the veins have been described by Weismann (1864), Gonin (1894), Mayer (1896), Comstock and Needham (1899), Mercer (1900), Tower (1903), Powell (1903), Marshall, (1915). The principal studies of the origin of the wing tracheæ from the trachea of the wing base are those of Chapman (1918), and Beck (1920).

The wings of insects with incomplete metamorphosis appear in the second or third nymphal instar as hollow, flattened outgrowths of the lateral parts of the dorsum in the mesothorax and metathorax, and they grow externally in the same manner as do the legs, mouth parts, or other appendicular organs of the body. In insects with complete

metamorphosis the wings develop beneath the cuticula, usually in pouches of the hypodermis, their rudiments appearing first in different insects from a late embryonic period to the last larval stage. They are everted from the hypodermal pockets during the prepupal stage of the larva, and become exposed as external organs with the shedding of the last larval skin.

The relation between wing tracheæ and vein channels in wings that develop on the exterior of the body would appear to indicate that the positions of the veins are determined by the original courses of the tracheæ, and this consideration has given weight to the idea that the wings originated as gills. In the Holometabola, however, the vein channels are defined in advance of the growth of the tracheæ, and the latter, when formed, do not always enter veins corresponding with those they occupy in insects with incomplete metamorphosis. Development in the Holometabola, therefore, shows that veins may be laid down along definite lines in the wing without the guidance of tracheæ, and that the tracheal courses have no fixed relation to particular veins. The conditions met with in the Holometabola may easily be explained as secondary, but they allow us to question if tracheæ necessarily did determine vein formation or the vein positions in the phylogenetic development of the wings. Since the growing wing is a functionless organ in all insects, and follows a more or less aberrant course in its development, its ontogenetic stages are likely to have become adapted to the conditions of growth, and, for this reason, they cannot be taken as representative of the sequence of steps in the evolution of the wing. The veins may have originated independently as strengthening ribs in the primitive wing lobe, limiting to their channels, as the intervening areas became flattened, the courses of the tracheæ and the nerves penetrating the wing.

The adult wing.—The fully formed wing has the same fundamental structure in all insects, regardless of the method of development, or of the specialized form it attains in the imago. The wing of a roach developed externally arrives at the same structural pattern as that of a moth developed internally; the elytron of a beetle, the halter of a fly retain each the unmistakable features of a wing.

The typical wing of modern insects extends laterally from the edge of the dorsum where its base is articulated to the tergum above and to the wing process of the pleuron below. Its anterior margin arises behind the prealar bridge of the tergum, if this process is present (fig. 21A, *Aw*); its posterior margin is continuous with the posterior fold *(Rd)* of the tergum. The area of the wing is traversed

by the *veins* and *cross-veins;* the thin intervening spaces, or *cells,* are occupied by the *membrane* of the wing. The wing base contains a number of small sclerites, the *axillaries,* or *pteralia* (fig. 27, *Ax*). At the base of the anterior margin of the wing there is usually a thickening, the *tegula (Tg),* commonly having the form of a small hairy pad, but sometimes developed into a large flat lobe overlapping the base of the wing. The rear margin of the basal membrane of the wing is generally corrugated and thickened, forming a posterior ligature of the wing, the *axillary cord (AxC).* The wing is held in
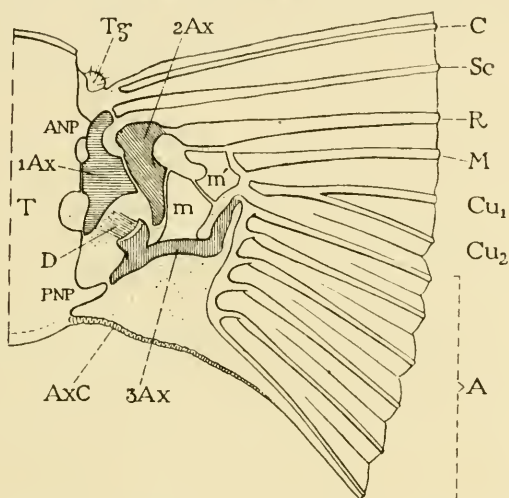
FIG. 27.—Diagrammatic structure of the wing base and its articulation with the tergum.

A, anal veins; *ANP,* anterior notal wing process; *1Ax,* first axillary; *2Ax,* second axillary; *3Ax,* third axillary; *AxC,* axillary cord; *C,* costa; *Cu₁,* first branch of cubitus; *Cu₂,* second branch of cubitus; *D,* flexor muscle of third axillary; *M,* media; *m, m′,* median plates of wing base; *PNP,* posterior notal wing process; *R,* radius; *Sc,* subcosta; *T,* tergum; *Tg,* tegula.

various positions when at rest, but with most insects it can be flexed posteriorly against the sides of the body. When extended it is capable of a free up-and-down motion, and of a slight rotary motion on its long axis. The posterior part, or anal area, of the wing in some insects when flexed can also be folded or plicated along the lines of the veins. In two orders of insects the distal part of the wing can be variously folded.

The nomenclature of the wing veins given in figure 27 is that of Comstock and Needham, except that the vein ordinarily called " first anal " is represented as a proximal branch of the cubitus. (See Imms, 1924, fig. 28). A study of the wing base shows that this vein

does not belong with the anal group attached to the third axillary,
but that it is associated with, or attached to, the base of the cubitus.
Its relation to the cubitus has been demonstrated by Tillyard (1919),
who designates it the second branch of cubitus, and by Karny
(1925), who calls it the " cubital sector." In the adult insect, the
first vein of the wing, the *costa (C)*, when present, usually lies in the
anterior margin of the wing. The second vein, the *subcosta (Sc)* is
associated at its base with the head of the first axillary sclerite *(1Ax)*.
The third vein, *media (M)*, is usually associated with one or two
small *median sclerites (m, m')* of the wing base. The fourth vein,
the *cubitus (Cu)* has no particular basal connections. The following
veins, the *anals (A)* are definitely attached to the third axillary *(3Ax)*
or to an arm of the latter.

The axillary plates of the wing base play an important part in the
mechanism of the wing, for they not only serve to attach the wing to
the body, but they determine the effect of the muscles that act upon
the base of the wing. Three of these sclerites are almost always
present, and have definite relations to one another, to the bases of the
veins, and to the adjoining parts of the thorax. The first one, the
first axillary, or *notopterale,* (fig. 27, *1Ax*), is a flat sclerite of the
dorsal membrane of the wing base, and is possibly to be regarded as
a tergal chitinization. It is hinged by its inner margin to the edge of
the tergum, and has its anterior part supported by the anterior notal
wing process *(ANP)*. Its anterior extremity is usually more or less
closely associated with the base of the subcostal vein *(Sc)*. By its
outer margin it articulates along an oblique line with the second
axillary. The *second axillary,* or *intraalare (2Ax),* has both a dorsal
and a ventral surface in the wing base, and may be derived from the
proximal end of the radial vein *(R)*, with which it is continuous.
By the inner oblique margin of its dorsal part it articulates with the
outer edge of the first axillary. Its ventral plate (fig. 30 A, *c*) has a
convex surface that rests upon the wing process of the pleuron when
the wing is extended. A tendon-like connection *(b)* with the subalar
sclerite *(Sa)* below it makes the second axillary the objective of the
subalar muscle *(F)* of the coxa. The *third axillary,* or *basanale*
(fig. 27, *3Ax*), though developed mostly in the dorsal membrane of
the wing, has also a ventral surface. It articulates with the posterior
notal wing process of the tergum *(PNP)*, except when a fourth
axillary is present. Its long axis is obliquely transverse, and a lobe
on its anterior margin gives attachment to the principal flexor muscle
of the wing (fig. 30, A, *D*). The bases of the anal veins are associated

with the distal end of the third axillary. A *fourth axillary* is some-
times present (Orthoptera, Hemiptera, Hymenoptera), but it is
always a small sclerite of the dorsal surface of the wing base, inter-
vening between the inner end of the third axillary and the edge of
the tergum (fig. 24 B, *4Ax*). It is perhaps a detached piece of the
posterior notal wing process. Lying in the space between the second
axillary, the distal part of the third axillary, and the bases of the
median and cubital veins, there are usually two sclerites of less
definite form which may be termed the *median plates* of the wing base
(fig. 27, *m, m'*). These sclerites serve to connect the median field of
the wing with the true axillaries.

THE WING MUSCLES AND THE MECHANISM OF WING MOTION

The mechanism of insect flight was carefully studied by entomol-
ogists in the early part of the last century. Noteworthy papers pub-
lished on the subject at that time are those of Chabrier (1820-'22),
Jurine (1820), and Straus-Dürckheim (1828). Chabrier's work, the
first of any importance on the wing structure of insects, contains
detailed descriptions of the skeletal anatomy of the thorax, the struc-
ture and articulation of the wings, and the muscles and mechanism
of flight—an extensive piece of original investigation, remarkable
for its accuracy and for the understanding shown by the author for
his subject. Following a general account, there is given detailed
descriptions of the entire wing mechanism in Coleoptera *(Melolon-
tha),* Odonata *(Aeschna),* and Hymenoptera *(Bombus).* Jurine's
paper, which describes the wing mechanism of Hymenoptera, ap-
peared after the first section of Chabrier's work was published. The
great work of Straus-Durckheim (or Straus-Dürckheim, as his sig-
nature appears beneath the dedication to Cuvier), published under
the title, "Considérationes générales sur l'anatomie comparée des
animaux articulés," is devoted principally to a study of *Melolontha
vulgaris.* It is one of the finest monographs ever written on insect
anatomy, and is accompanied by figures unsurpassed in clarity of
detail by any methods of modern illustration. The thorax, the wing
muscles, and the mechanism of flight are given full attention. These
early works, unfortunately, are somewhat difficult for present-day
students to read, because their authors used mostly individual sys-
tems of nomenclature, none of which has been closely followed by
later entomologists.

The modern study of the wing mechanism begins with Lendenfeld
(1881) and Amans (1883,'84, 1884, 1885), though again the nomen-

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clature of these writers has not been generally adopted. Lendenfeld
details the wing structure and all parts concerned with the wing
action in the Odonata ; Amans gives a comprehensive comparative
study of the wing mechanism in the principal orders of insects.
Following these papers, accounts of the structure, musculature, and
mechanics of the wings of various insects are contained in the works
of Luks (1883), Janet (1899), Petri (1899), Voss (1905, 1912),
Dürken (1907), Berlese (1909), Snodgrass (1909), Bauer (1910),
Gröschel (1911), Stellwaag (1910, 1914), Crampton (1914),
DuPorte (1920), Weber (1924, 1925). The nature of the wing
movements in insects has been studied particularly by Marey (1869,
1869,'72), Lendenfeld (1903), Stellwaag (1910, 1914), and Voss
(1913,'14).

The wing of most insects has four cardinal movements: *elevation,
depression, flexion, extension.* In addition, the wing is capable of a
slight *rotation* on its long axis. Elevation and depression are vertical
movements effected primarily by the longitudinal and oblique tergal
muscles, and the tergo-sternal muscles of the thorax, but the coxal
muscle of the epimeron becomes a strong accessory depressor of the
wing in the adult. The flexor of the wing is the muscle of the third
axillary sclerite of the wing base; the extensors are chiefly the mus-
cles of the basalar and subalar sclerites. The partial rotary movement
of the wings may be a mechanical result of the wing structure and
of the reaction of the wing surfaces to pressure of the air during
flight, but probably it is controlled by the epipleural muscles.

The tergal and tergo-sternal muscles of the thorax that principally
effect the elevation and depression of the wings are known as the
indirect wing muscles, because they produce wing movements through
causing alternating changes in the shape of the thorax. The depres-
sors consist of the pair of great dorsal longitudinal muscles, typically
stretched between the phragmata (fig. 28, *A*), but often so large that
they encroach a varying distance upon the anterior part of the scutum
(fig. 29, *A, A*). The oblique dorsals, extending laterally from the
posterior part of the scutum to the posterior phragma (fig. 28, *B*),
are probably accessory to the longitudinals in some cases, but in others
their positions become so nearly perpendicular to the tergum (figs. 29,
34 D, *B*) that they must act as elevators of the wings. These mus-
cles are of extraordinary size in the cicada (fig. 29, *B*). The usual
elevators of the wings include always the pair of large vertical mus-
cles in the anterior part of the thorax (figs. 28, 29, *C*), attached
dorsally to the scutum laterad of the longitudinals, and ventrally to

the basisternum anterior to the coxa, but other muscles are often accessory to these. As just noted, the oblique dorsals may be wing elevators. In the mesothorax of Diptera the remotor of the coxa, which arises dorsally on the scutum and is attached ventrally on the meron of the coxa, becomes a wing elevator through the transfer of the meron from the coxa to the wall of the segment (fig. 34 D, J).

The epipleural (basalar and subalar) coxal muscles, and the muscles of the third axillary constitute the *direct wing muscles,* so called because they act more immediately on the wing, though the epipleural
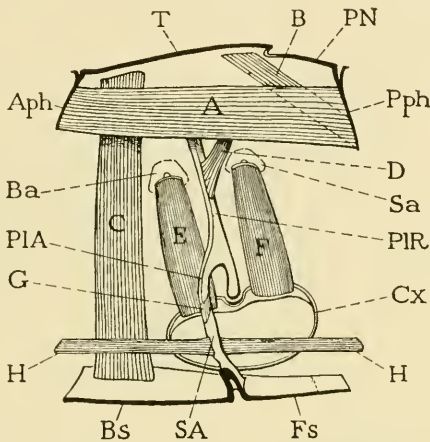

Fig. 28.—Diagram of the principal muscles of a wing-bearing thoracic segment, exclusive of the leg muscles, right side, internal view.

A, dorsal longitudinal muscle attached to successive phragmata, indirect wing depressor; *B,* oblique dorsal muscle from scutum to posterior phragma; *C,* tergosternal muscle from scutum to basisternum, indirect wing elevator; *D,* wing flexor of third axillary sclerite; *E,* basalar muscle of coxa, direct extensor of wing; *F,* subalar muscle of coxa, direct extensor and depressor of wing; *G,* pleuro-sternal muscle from pleural apophysis to sternal apophysis; *H,* longitudinal ventral muscles attached to sternal apophyses.

muscles are not inserted directly on the wing base, and, as we have seen, are primarily muscles of the leg. The basalar muscle (figs. 28, 30 A, E) arises ventrally on the lateral rim of the coxa *(Cx)* anterior to the pleural articulation; an anterior branch (fig. 30A, E') may arise on the basisternum, on the precoxal bridge, or on the episternum. Since the basalar plate (fig. 30 A, *Ba*) or the corresponding basalar lobe of the episternum is connected with the anterior angle of the wing base by a ligament-like thickening of the uniting cuticula *(a),* its muscles have a direct functional relation with the anterior part of the wing base. The subalar muscle (figs. 28, 30 A, F) arises, in typical cases, from the coxal margin posterior to the pleural articu-

lation, and the ligamentous connection (fig. 30 A, *b*) between the subalare *(Sa)* and the second axillary *(2Ax)* gives this muscle a functional relation to the median or posterior part of the wing base. The muscle of the third axillary (figs. 28, 30 A, *D*), often with several branches, arises from the pleural ridge or from neighboring parts of the pleuron, and goes obliquely dorsally and posteriorly to its insertion on the muscle process of the third axillary *(3Ax)*. In the Diptera there are two small muscles inserted on the first axillary, and in many insects there are various other small muscles associated with the wing base, but all of these muscles are of secondary importance and probably of a secondary origin.

It is difficult to demonstrate the action of the wing mechanism in a dead insect, but, allowing for much greater efficiency of the apparatus under the tension of living muscles, a pretty fair understanding of the various wing motions may be obtained from a study of freshly killed specimens. Take some large Diptera, for example (Syrphidæ, Muscoids). The wings of the dead fly are usually flexed. A lengthwise compression of the back of the mesothorax partly extends the wings and gives to each a downward motion accompanied by a strong deflection of the costal margin. A vertical compression of the thorax elevates the wings, and most strongly the costal margins. If a piece is cut out of the middle of the tergum, the wings no longer respond to pressure on the thorax in either direction, showing that the movements of the tergum, though slight, are sufficient to produce the wing motions. It is evident, too, that the nature of the wing articulation produces, in part at least, the compound character of the wing movements, but these movements are greatly accentuated by the action of other parts of the mechanism. The most decisive movement in the wing results from a downward pressure on the second axillary sclerite of the wing base, the wing being immediately extended, while the hind margin turns downward until the plane of the wing is almost vertical, with the costal margin uppermost. Complete extension of the wing in a horizontal plane results from pressure on the basalar plate or basalar lobe of the episternum. The wing of the freshly killed insect can thus be made to perform most of its movements by pressure on various parts of the thorax, and an understanding of the wing mechanism then becomes a matter of determining what muscles may produce the movements observed.

Since the Odonata, the Ephemerida, and the Palæodictyoptera do not flex the wings, the apparatus of elevation and depression by means of the indirect wing muscles was undoubtedly the first part

of the wing mechanism to be developed by insects; but, in studying
the movements of the wings of other insects, it will be most con-
venient to begin with those movements made in the horizontal plane,
which are effected principally by the direct muscles.

The flexion of the wing is easiest to understand. When the wing,
the hind wing of a grasshopper for example, is turned back toward
the side of the body, the distal end of the third axillary (fig. 27, $3Ax$)
turns upward, inward, and forward, carrying with it the anal area
of the wing, which is folded and laid against the side of the abdomen.
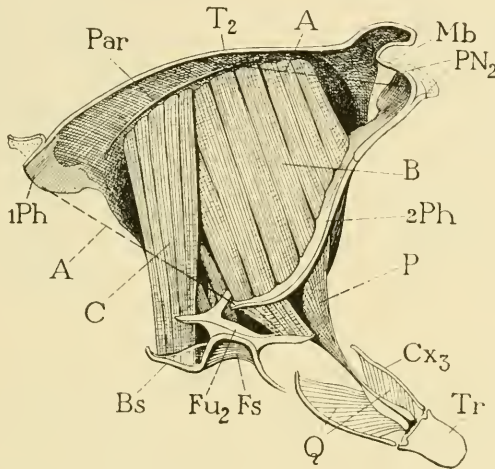In life, the beginning of this action results probably from the natural

Fig. 29.—Muscles of right half of mesothorax of cicada (*Tibicina septen-
decim*), with metathoracic coxa.

A, A, position of longitudinal dorsal muscle; *B,* oblique dorsal muscle; *C,*
tergo-sternal muscle; *P,* thoracic branch of depressor of trochanter of hind leg
(*Tr*); *Q,* coxal part of depressor of trochanter.

elasticity of the wing base, which latter partially flexes when the
muscles of extension are relaxed, but the contraction of the muscle
of the third axillary undoubtedly completes the folding, and holds
the wing tight against the body in its final position. The anterior
part of the wing necessarily follows the anal area, but its movement
is acclerated by the articular relations of the axillaries. The median
plate *(m),* affected by the motion of the third axillary, pushes the
second axillary *(2Ax)* medially and revolves it to a longitudinal posi-
tion over the first axillary, as the latter *(1Ax)* turns vertically on its
hinge with the tergum. By these multiple movements in the basal
elements of the wing, the anterior veins overtake the anals and are
folded above them against the side of the body. The flexion of the

wing is simpler in wings with a small anal area, but is essentially the same in all insects.

In the Dermaptera and the Coleoptera the distal parts of the flexed wings are mechanically folded transversely in order that the wings may be concealed beneath the shorter elytra. The various types of this folding in the wings of Coleoptera have recently been described by Forbes (1926).

The positions of the axillaries relative to one another in the flexed wing are quite different from those which they have in the extended wing. The extension of the wing involves a restoration of the axillaries to a horizontal plane, in which the sclerites again assume their former relations. The key to the transposition from one state to the other is in the position of the second axillary. If this sclerite is forcibly depressed, all the axillaries go back to the horizontal plane, and the wing is necessarily spread. The depression of the second axillary is evidently accomplished by the contraction of the subalar muscle (fig. 30 A, F), since the subalar sclerite is closely connected with the ventral plate (c) of the second axillary. The epimeral muscle of the coxa (fig. 26 B, F), therefore, in the adult insect (fig. 30 A) becomes the *posterior extensor of the wing* (Straus-Dürckheim, Bauer). The final, complete extension of the wing is probably brought about by the contraction of the basalar muscles (fig. 30 A, E, E'), since the basalar sclerite, or corresponding lobe of the episternum, is in intimate connection with the anterior angle of the wing base. The basalar muscles are, therefore, the *anterior extensors of the wing*. Their function in this capacity, however, is sometimes difficult to demonstrate.

The wings in extension are ready to be acted upon by the indirect muscles of elevation and depression. These are principally the longitudinal and oblique dorsal muscles, and the vertical tergo-sternal muscles. The last (figs. 28, 29, 30 B, C), by contraction, flatten the arch of the tergum (T), and the movement in the edges of the latter, bearing downward on the bases of the wings mesad of the pleural fulcra, gives the up-stroke to the distal parts of the wings (fig. 30 B). The longitudinal dorsal muscles (A) now act as antagonists to the verticals, since by their contraction they pull upon the two ends of the tergum and restore the curvature of the latter. The upward movement in the lateral tergal margins gives the down-stroke to the wings (fig. 30 D). The function of the oblique dorsal muscles (fig. 28, B) is not clear in all cases. Ordinarily these muscles appear to be accessory to the longitudinals; in the Diptera (fig. 34 D, B), however,

they are clearly elevators of the wings, and in the cicada (fig. 29, *B*) their great size would indicate that they are the principal wing elevators.

The thoracic musculature of the Diptera is highly specialized in order to give power and efficiency to the wing movements, but at
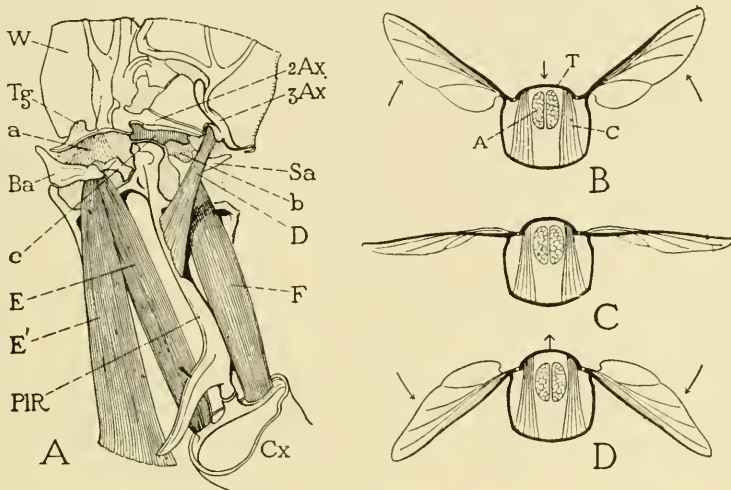

FIG. 30.—Mechanism of wing motion.

A, direct wing muscles of right fore wing and associated parts in a grass-hopper (*Dissosteira*). *a*, tendinous thickening of cuticula uniting basalar sclerites (*Ba*) with anterior part of wing base; *2Ax*, second axillary; *3Ax*, third axillary; first and fourth axillaries removed; *b*, tendinous thickening of cuticula uniting subalar sclerite (*Sa*) with ventral plate (*c*) of second axillary; *Ba*, anterior basalare; *c*, ventral plate of second axillary; *Cx*, coxa of middle leg; *D*, muscle of third axillary, flexor of wing; *E*, basalar muscle to coxa, with branch (*E'*) to basisternum, extensor and deflexor muscles of wing; *F*, subalar muscle to coxa, extensor and depressor of wing; *PlR*, pleural ridge; *Sa*, subalare; *Tg*, tegula; *W*, base of fore wing, elevated.

B, C, D, diagrammatic illustration of action of indirect wing muscles in flight as seen in cross-section of thorax through bases of wings, anterior view. *A*, dorsal longitudinal muscles, attached to phragmata (see fig. 28); *C*, tergo-sternal muscles; *T*, tergum. The wings are elevated indirectly (B) by depression of tergum caused by contraction of tergo-sternal muscles; they are depressed (D) by elevation of tergum produced by contraction of longitudinal muscles.

the same time it is greatly simplified in comparison with that of an orthopteroid insect. In each side of the mesothorax there are three large, oblique dorsoventral muscles which serve as elevators of the wings (fig. 34 D). The first is the ordinary tergo-sternal muscle(*C*) attached below on the basisternum; the second (*J*) is the remotor of the coxa, attached below on the meron, which in the Diptera becomes a wing elevator through the transfer of the meron of the

middle coxa (fig. 34 B, C, D, Mer_2) to the thoracic wall; the third (D, B) is the oblique dorsal muscle attached ventrally on the lateral extremity of the postnotum.

The tip of each vibrating wing describes a figure-8 curve, if the insect is held stationary, showing that the wing in motion undergoes alternating partial rotations on its long axis. Some writers have claimed that this movement results entirely from the pressure of the air on the wing surfaces as the wing vibrates, the flexible posterior margin of the wing being mechanically turned upward during the down-stroke, and downward during the up-stroke. The rotary motion of the wings, however, is necessary to give the forward movement to the insect in the air, and, as may be seen well in the wing of a fly, the nature of the wing articulation causes a deflection of the costal margin to accompany the down-stroke produced by the muscles of the tergum. In some insects, also, pressure at the anterior root of the wing base deflects the costal margin, and for this reason the basalar sclerite and its muscles have been termed the " pronator apparatus " of the wing (Amans). A strong posterior deflection of the wing accompanies pressure on the second axillary in Diptera, and it cannot be doubted, therefore, that in swiftly flying insects the muscle of the subalar sclerite, which pulls finally upon the second axillary, plays an important part in the posterior rotation of the wing during the up-stroke. The subalar muscle, therefore, would act as extensor, depressor, and rotator of the wing.

The mechanism for the control or modification of forward flight is not definitely known. Those who attempt to explain the tropistic reactions of insects usually assume a differential nervous regulation of the muscles on the two sides of the body; but this explanation could hardly apply to the indirect muscles of flight. It is probable, then, that the insect determines its course through the air by the control of its direct wing muscles, or by changing the slant of the body or the position of the legs, as suggested by Jousset de Bellesame (1879). Some insects are able to arrest their forward flight and suddenly reverse or go sidewise, without perceptibly changing the position of the body, and some are well known for their hovering powers. It is difficult to conceive how a wing structure and wing mechanism so clearly adapted to forward flight can also propel the insect backward or sidewise. The act of hovering on vibrating wings is explained by Straus-Dürckheim (1828) as accomplished through a continued contraction of the subalar muscles, thus checking the

rotatory motion of the wings and preventing their forward drive. The lifting power, then, needs only to counterbalance the weight of the insect's body.

The wing musculature of the Ephemerida shows clearly that the mayflies belong to the non-odonate branch of the Pterygota. Their thoracic musculature, according to the account of Dürken (1907), includes typical longitudinal and oblique tergal muscles (fig. 28, A, B), and tergo-sternals (C), the two sets constituting indirect depressors and elevators of the wings. The mayflies, however, do not flex the wings, and as a consequence the episternal and epimeral coxal muscles retain their primitive function as movers of the coxæ. The principal difference in the thoracic musculature of the Ephemerida and that of Orthoptera is in the greater number of muscles that arise on the epimeron, or on the epimeral region of the pleuron. There is no question of the truth of Dürken's statement that the musculature of the mayflies clearly separates the Ephemerida from the Odonata, but his claim that it separates them also from the Orthoptera does not appear to be warranted by his own descriptions. The Ephemerida are certainly, however, the most primitive of the non-odonate branch of the Pterygota.

The highly specialized wing musculature of Odonata has been described by Poletaïew (1881) and by Lendenfeld (1881). The usual tergal and tergo-sternal muscles are completely lacking in the thorax of the dragonflies, and each wing is provided with a set of direct muscles which effect all its movements. These muscles are of secondary development in the nymph, according to Poletaïew. They comprise identical sets of muscles in each of the wing-bearing segments, alike in all dragonflies. According to the elaborate descriptions of Lendenfeld, there are eight muscles to each wing. One of each set arises on the tergum, the others arise from ventral marginal ridges of the pleura or from processes of these ridges; they are all inserted either on the bases of the wing veins or on plates directly associated with the wing base.

In the Isoptera the dorsal longitudinal muscles of the thorax are degenerate, but the direct wing muscles, which are highly developed, show that the termite thoracic musculature is of the orthopteroid type. Fuller (1925) describes the muscles of the thorax of winged termites, but he does not explain how flight in these insects is sustained, even feebly, by a mechanism in which the principal motor elements appear to be lacking.

V. THE LEGS AND THEIR MUSCLES

In discussing the anatomy of an insect's leg, it will be convenient to limit the application of the term "leg" to that part of the appendage which ordinarily forms the free movable limb, ignoring for the present the theoretically basal subcoxa, but including the coxa in all cases, even when the latter is firmly fixed to the body wall.

STRUCTURE OF AN INSECT'S LEG

The typical and usual parts of the leg of an insect (fig. 31 A) are the *coxa (Cx)*, the *trochanter (Tr)*, the *femur (F)*, the *tibia (Tb)*,
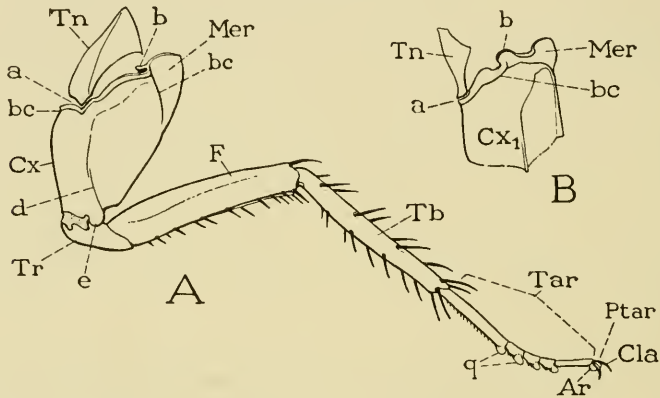

Fig. 31.—Structure of an insect leg, as represented by that of a roach (*Periplaneta americana*).

A, left mesothoracic leg and trochantin, anterior view; B, base of prothoracic coxa, with trochantin. *a*, articulation of coxa with trochantin; *Ar*, arolium; *b*, articulation of coxa with pleuron; *bc*, basicostal suture; *Cla*, claw; *Cx*, coxa; *d*, anterior coxal suture; *e*, anterior coxo-trochanteral articulation; *F*, femur; *Mer*, meron; *q*, ventral pads of tarsal segments, tarsal euplantulæ; *Tar*, tarsus; *Tb*, tibia; *Tn*, trochantin; *Tr*, trochanter.

the *tarsus (Tar)*, and the *pretarsus (Ptar)*. The several divisions of the leg are known as segments, or joints; the term *segment* will here be used for each piece of the leg, and the word *joint* limited to the articulation between adjoining segments. The surfaces of the leg are oriented for descriptive purposes when the limb is extended at right angles to the body, the outer surface then being dorsal, the inner ventral, and the other two anterior and posterior.

The movable base of the leg is ordinarily the coxa. The base of the coxa is inserted into a membranous area of the body wall between the pleuron and the sternum, which permits of whatever motions the closer articulations of the coxa with the surrounding chitinous parts allow. In pterygote insects the coxa is nearly always attached by an

articular surface on its outer basal rim (fig. 33 A, *b*) to the coxal process of the pleuron (fig. 4). In most of the lower orders, the coxa has also an anterior articulation with the ventral end of the trochantin (fig. 31, *a*), but when the trochantin is absent, the coxa is suspended from the pleural process alone, except where it becomes articulated ventrally to a process of the furcisternum. Sometimes the coxa is not movable, as in the thoracic legs of caterpillars, and in the meta-thoracic leg of adult beetles. The leg, however, is always movable at the coxo-trochanteral joint, and if the coxa is distinguished as the leg *basis,* the part of the limb beyond it is the *telopodite.*

The joints of the leg consist of membranous rings of the leg wall between the chitinized areas that constitute the leg segments. Some-
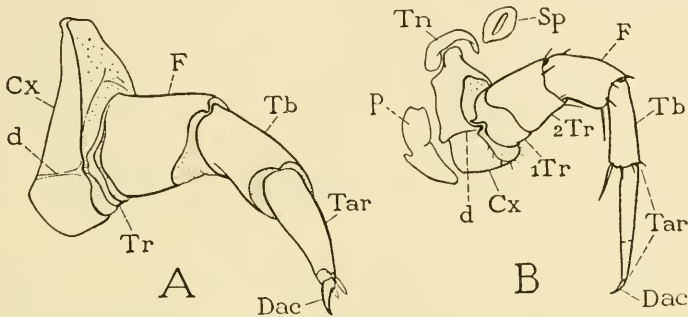

FIG. 32.—Leg of a caterpillar, and of a centipede.

A, left prothoracic leg of *Estigmene acraea*, anterior view; B, leg of *Lithobius sp.* Note similarity of structure in the coxæ (*Cx*), and in the dactylopodite-like terminal claws (*Dac*); trochanter (*Tr*) rudimentary in the caterpillar, represented by two segments in the centipede (*1Tr, 2Tr*).

times there is no close association between adjacent segments, but usually at one or two points the segments are hinged by chitinous processes, or condyles, or by other articulating surfaces on their opposing margins. Hinged joints are either *monocondylic* or *dicondylic,* according as they have one or two articular points. A single hinge is typically dorsal; in dicondylic joints, one hinge is anterior and the other posterior, except at the trochantero-femoral joint where the hinges, if present, are dorsal and ventral.

The structure of the hinges between the leg segments varies much at different joints and in different insects. Sometimes the two opposing surfaces simply touch by their points. In other cases the hinge is of the ball-and-socket type, a condyle of one surface fitting into a socket of the other, and in dicondylic joints of this kind the two hinges are frequently reversed in structure, but the condyle of the anterior

hinge is generally on the proximal of the two articulating segments. The coxo-trochanteral joint is always dicondylic. In the telopodite, dicondylic hinges are characteristic of the legs of adult insects, mono-condylic are usual in the legs of larvæ (fig. 32 A), but in the larvæ of Neuroptera and Trichoptera, the femero-tibial joint is dicondylic. An occasional special, or perhaps generalized, type of hinge consists of a flexible chitinous bar continuous from one segment to the other.

The Coxa.—In its most symmetrical form, the coxa has the shape of a short cylinder or truncate cone (fig. 31 A, *Cx,* fig. 33 A). Its proximal end is girdled by a submarginal *basicostal suture* (*bc*), which forms internally a low, circular ridge, or *basicosta* (fig. 33 A, *Bc*), and sets off a marginal flange, or *basicoxite* (*Bcx*), termed the coxomarginale by Crampton and Hasey (1915). The basicosta strengthens the base of the coxa, and serves also for the attachment of some of the coxal muscles. On the mesal half of the coxa, the basicosta is usually weak and often confluent with the coxal margin; on the outer surface, however, it commonly forms a strong ridge, (fig. 33 B, *Bc*), and in some cases a wide ledge (C) upon which muscles of this region are attached (fig. 37 B). The trochanteral muscles that arise within the coxa are attached distal to the basicosta (fig. 35 A).

The coxa has three constant articular surfaces, one proximal on the outer margin of its base (fig. 33 A, *b*) articulating with the coxal process of the pleuron, and two distal, one anterior (*e*) and the other posterior (*f*), by which the trochanter is hinged to the coxa. The pleural articular surface (*b*) is formed by an inflection of the wall of the basicoxite, and is supported on the basicosta (fig. 33 B, C). Besides these articulations, there is usually an anterior basal articulation with the ventral extremity of the trochantin (fig. 31 A, *a*), if the trochantin is present; when the trochantin is absent, there is sometimes a ventral articulation between the coxa and the furci-sternum (fig. 18 I, *c*).

The walls of the coxa are often strengthened by internal ridges, the lines of which appear as sutures on the external surface. One ridge extending from the basicosta to the anterior trochantinal articulation, marked externally by a corresponding suture (fig. 33 A, *d*) is more constant than the others, though the position of its proximal end varies. In the legs of centipedes (fig. 32 B) and of caterpillars (A) it extends basally to the middle of the anterior margin of the coxal base. In the fore leg of a grasshopper (fig. 33 D, *d*) the ridge has a similar position, ending at the articulation of the trochantin

(Tn) with the coxa. This position suggests that the ridge may be a primitive coxal structure forming a brace between the anterior trochantinal and trochanteral articulations. In many cases, however, the ridge extends basally to the pleural articulation (fig. 33 A, d'),
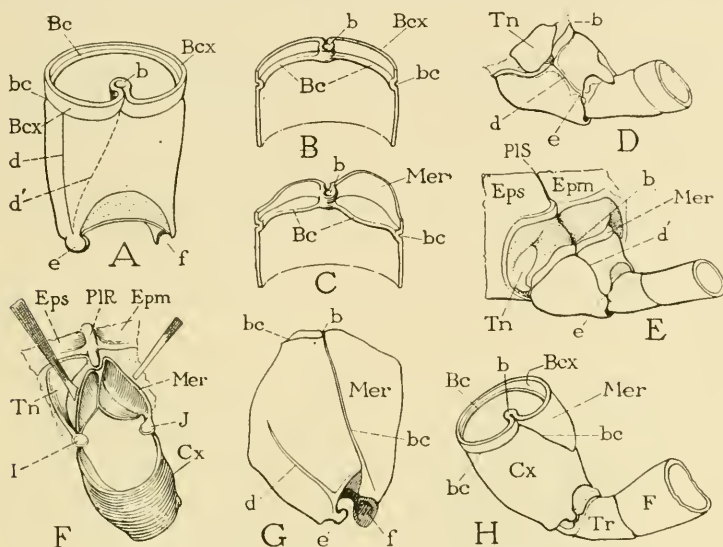

Fig. 33.—Structure of the coxa.

A, diagram of coxal structure, lateral view, showing marginal basicoxite (Bcx) separated from body of coxa by internal basicostal ridge (Bc) and external basicostal suture (bc): b, pleural articulation; d, d', varying positions of anterior coxal suture; e, f, anterior and posterior trochanteral articulations.

B, basal part of external wall of coxa, inner surface: showing pleural articulation (b) supported on basicosta (Bc).

C, same parts of a coxa with part of basicoxite posterior to pleural articulation (b) enlarged to form the basal coxal lobe known as the meron (Mer).

D, base of fore leg of grasshopper $(Dissosteira)$: anterior suture (d) extending between trochantinal and trochanteral articulations.

E, middle leg of same; anterior suture (d') continuous above with pleural suture (PlS).

F, base of right middle coxa and associated pleural parts, inner view, of cicada $(Tibicina septendecim)$: showing point of attachment of promotor muscle (I) on trochantin (Tn), and of remotor (J) on meron (Mer).

G, middle coxa of peach borer moth $(Aegaria exitiosa)$: meron (Mer) greatly enlarged; anterior suture (d) partly suppressed.

H, Diagram of coxal structure with meron (Mer) extended distally, and anterior suture (A, d) lacking.

as in the middle leg of a grasshopper (E, d'), and its suture then falls in line with the pleural suture (PlS). The latter condition has given rise to the idea that the coxa is formed of an anterior and a posterior part corresponding with the episternum and the epimeron, but it is clear that this conception is based on a superficial character, which is also a variable one. The coxal ridge is sometimes incomplete basally

(fig. 33 G, *d*), and probably in the majority of insects it is lacking (H).

The inflection of the outer wall of the basicoxite to form the pleural articular surface of the coxa (fig. 33 A, *b*) divides the basicoxite externally, and the two lateral basicoxal parts often beome enlarged in the form of two lobes on the coxal base (fig. 33 C), one before the pleural articulation, the other behind it. The posterior lobe, which is usually larger than the other, is the *meron* (*Mcr*), though, as presently will be shown, quite different parts of the coxa have been confused under this term. The basicoxal lobes are well developed on the middle and hind legs of a cicada (figs. 16 D, 33 F), the meron of the hind leg of an adult cicada bearing a large hollow spine-like process.

The meron is often much enlarged through being extended distally on the posterior part of the coxa (figs. 31 A, 33 H), but even if it reaches almost to the end of the coxa (figs. 33 G, 34 A), it still preserves the relation of a basal lobe to the rest of the coxa, for it never takes part in the trochanteral articulations. The suture limiting the meron is always an extension of the basicostal suture (*bc*), and its internal ridge separates the bases of the coxal muscles of the meron from those of the trochanteral muscles attached within the body of the coxa. By this test, the meron of a coxa lacking a true lateral suture (fig. 33 H), and the posterior part of a coxa divided by this suture (E, *d′*) should be easily distinguished, but the mistake of identifying one with the other has often been made. In the middle and hind legs of Blattidæ (fig. 31 A), the distal part of the basicostal suture (*bc*) defining the elongate meron is obsolete, giving the meron the appearance of being a part of the coxa, but in Termitidæ, with a similar meron, the suture is complete, and the meron is a typical basicoxal lobe.

In adult Neuroptera, Mecoptera, Trichoptera, and Lepidoptera, the meron of the middle and hind legs is particularly large, often reaching to the distal end of the posterior face of the coxa (figs. 33 G, 34 A, *Mcr*), though in the larval stages it is an inconspicuous lobe on the coxal base, or is not distinguishable (Lepidoptera). The growth of the meron takes place during the pupal stage, and its apparent continuity at this time with the epimeron above it, in Neuroptera and Trichoptera, led the writer, in a former paper (1909), to the conclusion that the adult meron in these orders is derived from the epimeron. A study of the musculature, however, shows the identity of the large adult meron with the inconspicuous

posterior basicoxal lobe of the larva. The continuity of the meron and the epimeron during the pupal stage is, therefore, but a secondary and temporary union of these parts in the Neuroptera and Trichoptera, as claimed by Crampton and Hasey (1915), but it fore-
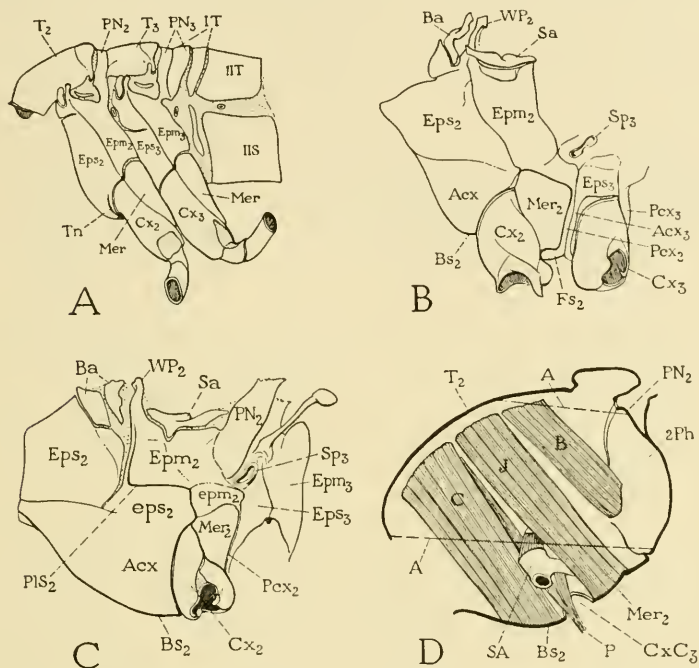

FIG. 34.—Modifications by which the mesothoracic meron, normally a basal lobe of the coxa, in the Diptera becomes a plate of the body wall.

A, mesothorax, metathorax, and base of abdomen of *Panorpa consuetudinis*: meron (*Mer*) forming a large lobe on posterior face of each coxa.

B, mesothoracic and metathoracic pleura and coxæ of a tipulid fly (*Holorusia grandis*): meron of mesothorax (*Mcr₂*) a large coxal plate projecting into pleural wall.

C, mesothoracic and metathoracic pleura and middle coxa of horse fly (*Tabanus atratus*): mesothoracic meron (*Mer₂*) detached from coxa (*Cx₂*), and incorporated into body wall.

D, median section of thorax of a syrphid fly (*Eristalis tenax*): the remotor muscle of middle coxa (*J*) becomes a wing elevator, by transfer of the meron (*Mcr₂*) from coxa to body wall.

shadows a permanent displacement of the meron in the mesothorax of Diptera.

The meron region of the coxa bears the ventral attachment of the subalar epipleural muscle (fig. 37 B, *F*), and of the remotor of the coxa (*J*). A plate in the ventrolateral wall of the mesothorax of Diptera, lying above and behind the base of the coxa, constituted a

puzzle for insect morphologists until it was shown by Crampton and Hasey (1915) and by Crampton (1925, 1925a) to be the meron of the middle leg. In the Tipulidæ, the plate in question (fig. 34 B, Mer_2) is attached to the middle coxa (Cx_2) and is quite distinct from the postcoxal bridge of the mesothorax (Pcx_2). To its upper part is attached the muscle from the subalar plate (Sa), and to its lower part the tergal remotor of the coxa. The plate is, therefore, the meron, and its relations to the coxa are the same as those of the meron in *Panorpa* (fig. 34 A), though it forms a part of the segmental body wall in the Tipulidæ. In the higher Diptera, the corresponding plate (fig. 34 C, Mcr_2) is detached from the coxa, and is closely united with a part of the epimeron above it (cpm_2), and with the very narrow postcoxal bridge (Pcx_2) behind it. The body of the coxa (Cx_2) is independently movable on a vertical axis. The base of the subalar muscle in the higher Diptera has migrated upward upon the true pleural region, and is attached to the horizontal part of the pleural ridge behind the base of the pleural arm. The remotor muscle of the coxa (fig. 34 D, J), however, remains attached ventrally to the transposed meron (Mcr_2) and becomes thus an elevator of the wings, being the middle muscle of the three large wing elevators (C, J, B) in each side of mesothorax. The transposition of the mesothoracic meron in the Diptera from the coxa to the body wall is clearly a device for increasing the power of flight by transferring one of the leg muscles to the service of the wing.

The trochanter.—The trochanter is ordinarily a small segment, usually fixed more or less firmly to the base of the femur (fig. 31 A, Tr). Structurally it resembles the coxa, having a strong basicostal ridge (fig. 35 A, g) bearing the coxal articulations, but its motion is limited by the latter to movements in a vertical plane. Being the base of the telopodite, however, its articulation with the coxa is one of the important hinges of the insect leg. The ventral lip of the trochanter base usually projects into the coxa as a strong process for the attachment of the extensor muscles (fig. 35 A, P, Q). The trochantero-femoral joint, though usually having but little motion, differs from all other joints of the insect leg in that, when movable, it bends forward and backward on a vertical axis. A reductor muscle of the femur (fig. 35 A, R) arises in the trochanter and is inserted on a basal thickening (basicosta) of the femur (i). By this character, the true trochantero-femoral suture may be identified where it might otherwise be confused with certain other sutures that sometimes occur near it.

In a few insects the trochanter appears to be double. In some of the Hymenoptera (Ichneumonidæ, Braconidæ), for example, two pieces of the leg occur between the coxa and the femur which are called " first trochanter " and " second trochanter." That the first alone is the trochanter (fig. 35 B, Tr), however, is shown by the fact that the reductor femoris muscle (R) is inserted on a plate (i) inflected from the base of the second (F'). The latter is, therefore, a basal subsegment of the femur (F), separated by a secondary suture
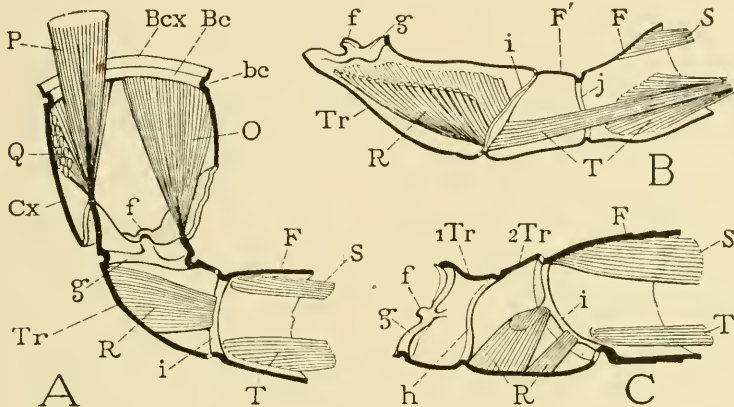

FIG. 35.—Structure and musculature of the coxa, trochanter, and base of femur.

A, diagram of typical musculature of coxa, trochanter, and base of femur; B, trochanter and base of femur of an ichneumonid (*Megaryssa*), showing basal subdivision (F') of the femur (F); C, trochanter and base of femur of middle leg of dragonfly nymph (Aeschnidæ), showing double structure of the trochanter ($1Tr$, $2Tr$).

Bc, basicosta of coxa; *bc*, basicostal suture; *Bcx*, basicoxite; *Cx*, coxa; *F*, femur; *F'*, basal subdivision of femur; *f*, posterior coxo-trochanteral articulation; *g*, basicosta of trochanter; *h*, ridge between subdivisions of trochanter; *i*, basicosta of femur; *j*, femoral ridge setting off basal subdivision of femur; *O*, levator muscle of trochanter; *P*, thoracic branch of depressor of trochanter; *Q*, coxal branch of depressor of trochanter; *R*, reductor muscle of femur; *S*, levator of tibia; *T*, depressor of tibia; *Tr*, trochanter; *1Tr*, *2Tr*, first and second subdivisions of trochanter.

and ridge (j). A branch of the tibial flexor (T) crosses the ridge and is attached at the anterior end of the true femoral base.

In the Odonata, both nymphs and adults, there appear likewise to be two trochanteral segments (fig. 35 C, $1Tr$, $2Tr$). The structural relations here, however, are quite different from those in the hymenopteran leg (B). The reductor femoris muscle (R) of the dragonfly arises in the second trochanter, and the ridge (i) upon which it is inserted is clearly the basicosta of the femur (F). The ridge (h) with its external suture between the two parts of the trochanter is, therefore, a trochanteral structure, and its presence furnishes a

reason for believing that in the dragonflies the two parts of the tro-
chanter ($1Tr$, $2Tr$) represent two primitive segments of the leg, as
claimed by Verhoeff (1903 a, 1903 b). Gründberg (1903), on the
other hand, sees here only a secondary division of the trochanter,
and he would homologize the dividing ridge (h) with the more basal
ridge of the trochanter in other insects. He fails to note, however,
that the latter ridge (g) is also present and well developed in the
Odonata, and bears the coxal articulations (f). Verhoeff calls the
first trochanter the " true trochanter " and the second the " prae-
femur." He believes that the first disappears in most insects other
than the Odonata, and that the so-called trochanter of insects is the
homologue of the praefemur of the Chilopoda. The disappearance
of the first trochanter segment, however, would involve a replace-
ment of the articular elements in the coxo-trochanteral joint, an un-
likely transformation. It seems more reasonable, therefore, that the
two trochanteral segments have been united into one in most insects
(fig. 42). The basal lip of the trochanter (fig. 35 A), when un-
usually wide, often gives the trochanter a false appearance of being
a double segment.

The femur.—This, the third segment of the insect leg (fig. 31 A,
F), is usually the longest and strongest part of the limb; but it
varies in size from that of the huge hind femur of leaping Orthoptera
to that of the small femoral segment in the leg of a sawfly larva
(fig. 16 B), which is much inferior to the coxa. The femoro-tibial
joint, or " knee " of the insect leg, is typically dicondylic in adult
insects and in the nymphs of Hemimetabola; but in holometabolous
larvæ it is usually monocondylic (figs. 16 A, 32 A), as it is in the
Chilopoda (fig. 32 B). In the larvæ of Neuroptera and Trichoptera
it is dicondylic.

The tibia.—The tibia (fig. 31 A, Tb) is characteristically a slender
segment in adult insects, only a little shorter than the femur, or the
combined femur and trochanter. Its proximal end forms a more or
less distinct " head " bent toward the femur, a device which allows
the tibia to be flexed close against the ventral surface of the femur,
and one often not expressed sufficiently in insect drawings to suggest
the essential mechanism of the femoro-tibial articulation. The tibio-
tarsal joint is dicondylic in adult insects, unless articular points are
lacking, but it is always monocondylic in holometabolous larvæ.
Sometimes the tibia and tarsus are united, forming a tibio-tarsal
segment (figs. 16 B, 43 B).

The tarsus.—In adult insects, the tarsus comprises from one to
five small pieces (fig. 31 A, Tar). In holometabolous larvæ, however,

it consists of a single leg segment (figs. 16 A, 32 A, 41 B, *Tar*), as it does in adult Protura (fig. 41 A), which segment is probably the propodite of the generalized arthropod limb (fig. 42). The subsegments, or articles, of the adult tarsus, conveniently called tarsal " segments," therefore appear to be subdivisions of a single primitive shaft; they have no articular hinges with each other, though they are usually freely movable by inflected connecting membranes (fig. 39), and they never have individual muscles. The tarsus is moved as a whole by muscles inserted upon its base, or by tension of the claw muscles on the tendon which traverses it (fig. 39, *x*). Tarsi having fewer than five segments, therefore, represent either a stage of progress in the division of the primitive segment, or a retrogressive condition in which some of the articles of a five-segmented tarsus have been lost or have coalesced. The tarsi of the Apterygota may be supposed to be of the first class, as may likewise those of the Odonata with three segments, but in the rest of Pterygota, the adult tarsus appears to have been standardized with five segments, and all reductions from this number are most likely of a secondary nature.

The basal segment of the tarsus is often larger than the others, and is distinguished as the *basitarsus,* metatarsus, or planta, the first term being preferable. On the under surfaces of the segments, except the last, there are sometimes small pads, the *euplantulæ* (Crampton, 1923), or tarsal pulvilli (fig. 31 A, *q*).

The pretarsus.—Entomologists generally have not found it necessary to refer collectively to the terminal parts of the insect leg (fig. 31 A, *Ar, Cla*), and consequently we have no satisfactory name for the group of organs at the end of the tarsus, which in some cases might appropriately be termed the " foot," but not with those insects that place a part or all of the tarsus on the supporting surface. The group of terminal foot structures is called the *unguis* or *ungula* by Schiödte, the *prætarsus* by de Meijere, the *articularis* by MacGillivray, and the *Krallenglied* by Arnhart. Since de Meijere (1901) has given the most comprehensive description of the parts in question, his name for them, *prætarsus,* is adopted in the Americanized form of " pretarsus " in the present paper, though not without regret that de Meijere did not invent a more fitting term.

In its simplest form the terminal part of the insect leg consists of a small, claw-like segment similar to the dactylopodite of a crustacean or chilopod limb (fig. 32 B, *Dac*). A pretarsus of this kind occurs in adult Protura (fig. 41 A), in some Collembola, in the larvæ of most beetles (fig. 43), and in the larvæ of Lepidoptera (figs. 32 A, 41 B) and Tenthredinidæ (fig. 16 B). A one-clawed

pretarsus is found also in a few adult pterygote insects, as in the
Coccidæ, Pediculidæ, and the mammal-infesting Mallophaga, but the
structure of the foot in such cases has probably resulted secondarily
from the suppression of one claw in an original pair of claws.

The pretarsus of an adult insect, in its typical form (fig. 36 A, B),
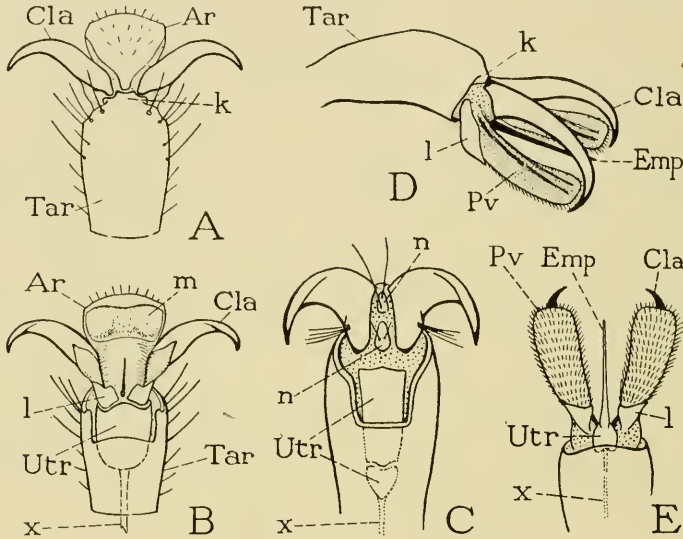arises from the end of the last tarsal segment by a membranous base,

FIG. 36.—Structure of the insect foot (pretarsus).

A, end of tarsus (*Tar*) and foot of a roach (*Periplaneta americana*), dorsal
view: claws (*Cla*) articulated to unguifer process (*k*) on end of last tarsal
segment; arolium (*Ar*), a median lobe between claws.

B, the same, ventral view; showing ventral pad (*m*) of arolium, auxiliary
plates (*l*) at bases of claws, and unguitractor plate (*Utr*) to which is attached
tendon (*x*) of retractor muscles of claws (fig. 39, *X*).

C, foot of a cicada (*Tibicina septendecim*): arolium lacking, or represented
by small plates (*n*) between claws.

D, foot of an asilid fly, lateral view: arolium lacking; lateral, lobe-like
pulvilli (*Pv*) arising from auxiliary plates (*l*) beneath claws, and median
spine-like empodium (*Emp*) arising from unguitractor plate.

E, the same, ventral view.

upon which are supported a pair of movable lateral *claws* (*Cla*), and
a median lobe, the *arolium* (*Ar*). The claws are hollow, multicellular
organs, their cavities being continuous at their bases with the lumen
of the base of the pretarsus. Each is articulated dorsally to the
unguifer (A, *k*), a median process of the distal end of the last tarsal
segment (*Tar*). The arolium, likewise a hollow lobe, is a direct
continuation of the median part of the pretarsal base; it may be
entirely membranous, or its walls may be partly chitinous. On the

ventral surface is a large basal plate, the *unguitractor* (B, *Utr*), which is partially invaginated into the end of the tarsus (*Tar*), where the flexor, or retractor, "tendon" of the claws (*x*) is attached to its proximal end. The unguitractor may consist of two pieces (C, *Utr*), or sometimes there is a second plate, the *planta,* distal to the unguitractor at the base of the arolium, and there may be lateral plates, the *auxiliæ* (*l*), at the bases of the claws. In the honeybee, a transverse chitinous band lies beyond the planta in the ventral wall of the arolium.

All parts of the pretarsus are subject to much variation. The claws sometimes have each two points; sometimes the claws are of unequal size, one claw becoming reduced and occasionally obliterated, the result being a one-clawed foot. Again, both claws become very small, and both may be lacking. In the Physopoda, the claws are minute, and the foot consists principally of the large bladder-like arolium. In some of the Thysanura there is a third, median claw between the two lateral claws, well developed though small in *Lepisma* (fig. 44, C, D, *Dac*) rudimentary in *Japyx* (fig. 44 A, *p*). This median claw is probably not analogous to the lateral claws, being more likely a remnant of the primitive dactylopodite. The pretarsus of first-stage larvæ of Meloid beetles, the triungulins, also apparently has three claws, a large median one and two slender lateral ones; but there is some doubt as to the nature of the lateral claws of the triungulin foot, Böving (1924) pointing out that they are claw-like setæ rather than true claws. In a lampyrid larva with three claws on each foot, the lateral claws appear to be outgrowths of the dactylopodite, since they have no articulations with the tarsus.

The arolium (*Ar*) varies in size and in form from a small simple lobe to a large complex appendage; or again it may be rudimentary or entirely lacking (fig. 36 C). In the Diptera there are two lateral ventral foot lobes, the *pulvilli* (fig. 36 D, E, *Pv*), which arise from the auxiliæ (*l*), one beneath the base of each claw. The arolium is rudimentary or absent in most Diptera; only in the Tipulidæ, according to de Meijere, is it well developed. In other families a median process, the *empodium* (*Emp*), or "processus plantaris" of de Meijere, is commonly developed from the distal end of the unguitractor plate. The empodium may be spinelike (fig. 36, D, E), or lobelike and similar to the lateral pulvilli.

MUSCLES AND MECHANISM OF THE LEG

Though the legs of different insects are adapted in their structure to a great variety of uses, their motions are made according to the

simplest of mechanical principles, for, with the exception of the movements of the coxa on the body, the action at each of the flexible joints is merely that of a hinge working in a single plane.

In insects, and in most other arthropods, the functional base of the leg is the coxa, and the appendage as a whole moves on the articulation of the coxa with the body. In the more generalized orders, where the coxa is suspended freely from the pleuron, the leg may swing forward and backward on a transverse (or vertical) coxal axis
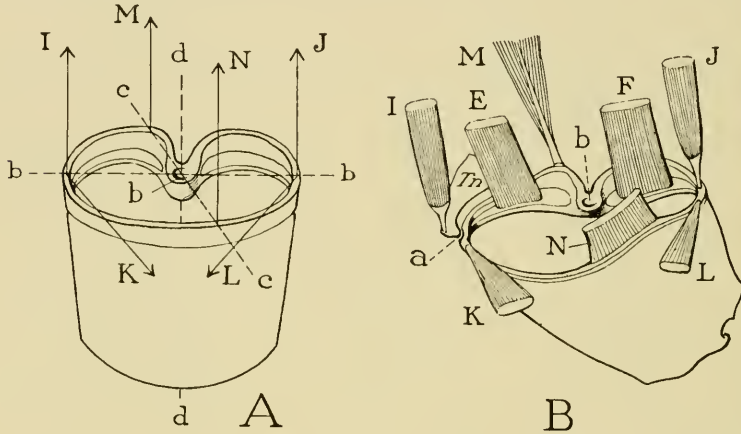

FIG. 37.—The cardinal axes of motion, and the corresponding muscles of a coxa freely articulated to the pleuron.

A, diagram of the mechanism of coxal motion on the pleural articulation (*b*), inner view. The cardinal movements are: (1) *abduction* and *adduction* on longitudinal axis (*b b*) by means of abductor and adductor muscles (*M, N*); (2) *promotion* and *remotion* on transverse axis (*c c*) by promotor and remotor muscles (*I, J*); and (3) *rotation* on vertical axis (*d d*) by anterior and posterior rotator muscles (*K, L*).

B, diagram of coxal musculature, inner view of base of right coxa: *E, F*, basalar and subalar muscles of wing attached on coxa (fig. 28); *I*, promotor of coxa, tergum to trochantin; *J*, remotor, tergum to coxa; *K*, anterior rotator, sternum to coxa; *L*, posterior rotator, sternum to coxa; *M*, abductor, episternum to coxa; *N*, adductor, sternum to coxa.

(fig. 37 A, *cc*), outward and inward on a longitudinal axis (*bb*), or it may turn in the plane of its base on an axis through the middle of the coxa (*dd*). The possible elemental movements of the coxa and of the leg as a whole are, therefore, *promotion* and *remotion, abduction* and *adduction,* and *rotation;* but, if the coxa has a free articulation, the actual movements of the leg base are unlimited, since, by simultaneous contraction of two or more sets of the coxal muscles, there may result compound movements in any direction. In conformity with its motile possibilities, the coxa has a much more elaborate musculature than that of any other segment of the leg: where

its movements are unrestricted, it is provided with antagonistic sets of muscles corresponding with its three primary axes of motion. It has *promotors* and *remotors* (fig. 37 A, *I, J*), *abductors* and *adductors* (*M, N*), and *anterior* and *posterior rotators* (*K, L*).

If the coxa represents the base of the primitive arthropod limb, we have only to assume that its muscles were directly fitted to its needs. We have seen, however, that there is reason for believing that the original limb had its base in a subcoxal segment, which became incorporated into the pleural wall of the body to form a support for the rest of the limb, the latter acquiring a new functional base in the coxa. This theory can not be supported on external features alone; the transformations that it assumes could not but involve changes in the leg musculature, and it must be shown at least that there is nothing in the arrangement of the muscles in modern insects that is incompatible with the theory—if positive evidence can be found of shiftings in the muscle attachments in accord with the assumed changes in the skeletal parts, the theory will be so much the more acceptable.

A primitive segmental limb, perhaps of a parapodial nature, must have turned forward and backward on its base in the lateral wall of its segment. It, therefore, possessed promotor and remotor muscles, probably dorsal and ventral promotors (fig. 38, A, *I, K*) and dorsal and ventral remotors (*J, L*). According to Börner (1921) the parapodium of an annelid worm (*Nereis*) has a musculature of this sort by which it is turned anteriorly and posteriorly. If, then, the arthropod subcoxa turned on a vertical axis, it follows that the coxal movement on the subcoxa was most probably in a vertical plane on a horizontal axis. The coxa, therefore, had abductor and adductor muscles (*M, N*) arising on the dorsal and the ventral wall of the subcoxa.

Something analogous at least to this theoretical musculature of the primitive limb base (fig. 38 A) may be seen in the Acarina. In the Ixodidæ the movable part of each leg is supported on a large basis that spreads out as a wide plate in the ventral wall of the body (fig. 17, *Scx*), but which also is narrowly continuous around the dorsal side of the first free segment of the leg. These leg bases are provided with anterior and posterior dorsal muscles, and the bases of the first pair of legs in *Dermacentor* and *Amblyomma* at least are slightly movable in the living tick, turning on an obliquely transverse axis. The next piece of the leg is a free, cylindrical segment (*Cx*), hinged to the basis by anterior and posterior articulations on an axis at right angles to that of the basis with the body, the anterior

articulation being at the ventral anterior angle, and the axis extending obliquely dorsally and posteriorly to the rear articulation. The third segment, a small trochanter-like piece ($1Tr$), is hinged to the second on a longitudinal axis with typical coxo-trochanteral articulations. The structure of the proximal part of the acarine leg, therefore, strongly suggests that the ventrally expanded basis is the subcoxa, and that the following two segments are the coxa and the first trochanter. Though the axis of the subcoxo-coxal joint is somewhat oblique, its movements are essentially those of abduction and adduction, since the coxal muscles consist of dorsal and ventral antagonists, both attached here on the ventral plate of the subcoxa, probably on account of the reduction of the lateral wall of the latter. The obliquity of the subcoxo-coxal hinges in the Acarina is clearly an adaptation to allow the legs to move in the plane of the flattened body.

Assuming, then, a subcoxal segment functioning as the leg base at some remote time in the ancestry of insects, we must postulate either that the present coxal musculature is a new development, or that it has been evolved through a transfer of the subcoxal muscles to the coxa. There is no evidence in support of the first supposition; there is nothing to contradict the possibility of the second. Abundant evidence is at hand to show that the bases of insect muscles may undergo considerable migrations. If the dorsal promotor and remotor muscles of the subcoxa (fig. 38 A, I, J) were transferred to the coxa, they would become promotors and remotors of the coxa (B) when the posterior coxal articulation (A, b) assumed its dorsal lateral position (B, b); but a transfer of the ventral promotors and remotors of the subcoxa (A, K, L) to the coxa (B) would convert these muscles into anterior and posterior rotators of the coxa. The dorsal promotor (I), however, remains attached to the trochantin (B, Tn), a piece of the subcoxa, as long as this sclerite persists; only when the trochantin is greatly reduced or is lacking does it become attached to the coxa. The flexibility of the free part of the trochantin, or its detachment from the rest of the pleuron allows the trochantinal muscle to function as a coxal promotor. The trochantinal hinge with the coxa (a) thus becomes a lifting point rather than an articulation, as has been noted by Crampton.

The primitive abductors and adductors of the coxa (fig. 38 A, B, M, N) retain their original function, but the second becomes attached to the sternum with the suppression of the ventral wall of the subcoxa and is eventually supported on the sternal apophysis (SA) to give it more efficient action. The forward migration of the posterior coxal articulation to a mid-lateral position (B, b) has

crowded the base of the coxal abductor (M) to the forward part of
the eupleural region of the subcoxa, which later becomes the epister-
num, and upon this plate arise the abductors of the coxa in all
modern insects, except where the pleurum becomes rudimentary.
Placed at a mechanical disadvantage by the new position of the coxal
articulation, the abductor has regained efficiency in part from the
inflection of the pleural articular surface toward the center of the
coxal base (fig. 37 A).

The above outline of what may have taken place in the theoretical
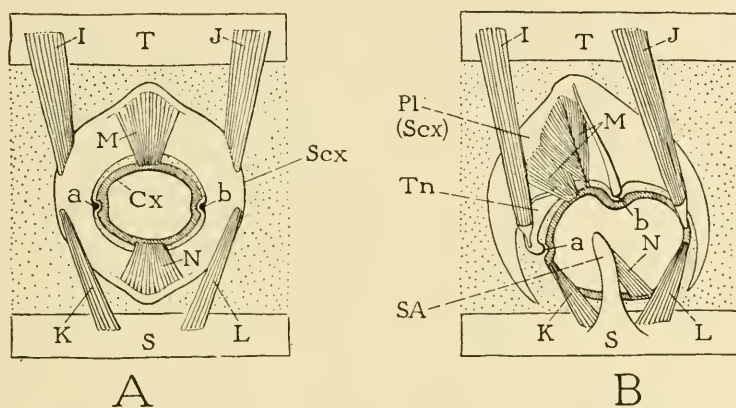transformation of the leg base is purely hypothetical, but it accounts

Fig. 38.—Theoretical derivation of modern coxal muscles from primitive
coxal and subcoxal muscles.

A, Diagram of theoretical primitive musculature of subcoxa and coxa:
a, b, horizontal axis of coxa on subcoxa; I, J, tergal promotor and remotor
muscles of subcoxa; K, L, sternal promotor and remotor muscles of subcoxa;
M, N, abductor and adductor muscles of coxa, arising within subcoxa.

B, muscles transposed, posterior coxal articulation (b) shifted to dorsal posi-
tion: I, becomes promotor of coxa; J, becomes remotor of coxa; K, L, become
rotators of coxa; M, N, remain abductor and adductor of coxa.

for the present complicated musculature of the coxa in the more
generalized pterygote insects, and it explains those features that give
the coxal musculature an appearance of having been secondarily
adapted to the purposes of the coxa.

A typical generalized coxal musculature of the leg of a wing-
bearing segment is shown at figure 37 B; it is approximately that
of the middle leg of a grasshopper (Acrididæ), except that some of
the single muscles in the figure are represented by several groups of
fiber bundles in the grasshopper. The principal tergal promotor (I)
is nearly always a single muscle inserted below on the trochantin
(Tn), or on the anterior coxal rim when the trochantin is absent.

The remotor (J) may comprise several tergal muscles inserted on the meron region of the coxa. Besides the principal abductor (M), there are usually several smaller muscles from the episternum to the anterior lateral part of the coxal rim, some of which are probably accessory promotors. The adductor (N) and the rotators (K, L) arise upon the sternum or upon the sternal apophysis. The posterior rotator may be broken up into a group of muscles. In addition to the muscles just described the coxal musculature of a wing-bearing segment includes the epipleural muscles (E, F), already described in connection with the wings. The first (E) may be regarded as a part of the abductor system of the leg in its origin, but the second (F), having no representative in the prothorax, would appear to be a secondarily developed muscle. Both the epipleural muscles are present in nymphal Orthoptera, where they apparently function as leg muscles, since the basalar and subalar plates are here not separated from the pleuron (fig. 26 B).

The actual arrangement of the coxal muscles and their attachments to the base of the coxa are seldom so diagrammatically simple as shown in figure 37 B. There are likely to be several muscles in each set, and again it is not always possible to find a representative of each group. The coxa itself is usually turned more or less at an angle to the body, and its base is seldom a symmetrical plane at right angles to its length. It is, therefore, often difficult to determine the exact function of any particular muscle or set of muscles. Moreover, it appears that the action of individual muscles may be changed in consequence of modifications in the coxal articulations. When the coxa, for example, is hinged to the sternum, and has its motions limited to a forward and backward turning on a transverse or vertical axis, its musculature is correspondingly reduced, and such muscles as remain become either promotors or remotors. In the Dytiscidæ the hind coxæ are immovable, constituting solid bases for the telopodites of the hind legs, which are the swimming organs. In *Dytiscus,* according to Bauer (1910), each hind coxa retains, besides the subalar wing muscles, only two of the normal coxal muscles, and these, having their origin on the tergum, serve probably as accessory elevators of the wings. Since the data for a comparative myology of insects are not yet at hand, no attempt can be made here to follow the modifications of the coxal musculature in the various groups of insects.

In the telopodite, or that part of the leg beyond the coxa, the joints bend either forward and backward, or up and down. The most precise terms for the motions at the two types of joints are *produc-*

tion and *reduction,* and *elevation* and *depression,* respectively. Joints of the first type are provided with *productor* and *reductor muscles;* those of the second type with *levator* and *depressor muscles.* Some writers use the terms " flexor " and " extensor," or " abductor " and " adductor " as synonymous with levator and depressor, regardless of the nature of the respective movements ; others call that muscle the " extensor " which accomplishes the principal work of the leg segment distal to the joint, and name its antagonist the " flexor." The last system is appropriate for designating function, but for ana-
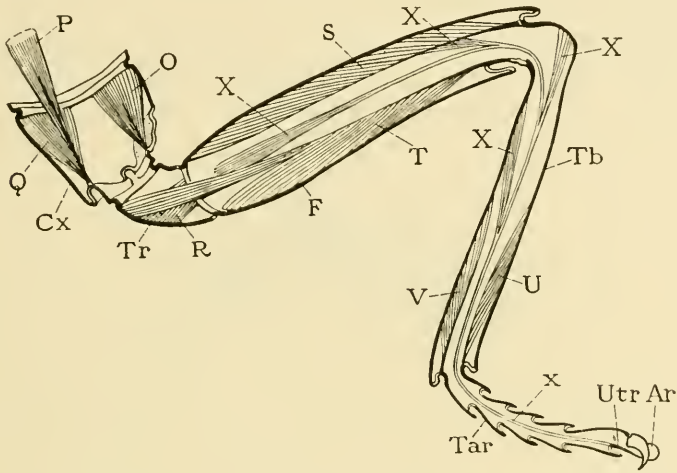

FIG. 39.—Diagram of typical leg musculature, left leg, anterior view.

O, levator of trochanter ; *P, Q,* thoracic and coxal branches of depressor of trochanter ; *R,* reductor of femur ; *S,* levator of tibia ; *T,* depressor of tibia ; *U,* levator of tarsus ; *V,* depressor of tarsus ; *X, X, X, X,* branches of depressor of pretarsus (retractor of claws) ; *x,* tendon of claw retractor muscles, attached to unguitractor plate (*Utr*).

tomical descriptions " levator " and " depressor " are to be preferred, because they lead to no ambiguity and can be applied always to homologous muscles. In the telopodite of the insect leg, only the trochantero-femoral joint bends forward and backward, the other three are movable in a vertical plane.

The muscles that move the trochanter are also levators and depressors of the entire telopodite, since the trochanter usually has but little if any motion on the femur. The levator of the trochanter (figs. 39, 40, *O*) arises in the dorsal part of the coxa and is inserted on the dorsal lip of the trochanter base, usually by a chitinous tendon. The depressor, in pterygote insects, has both coxal and thoracic

branches. The coxal branch (Q) spreads out in a broad fan on the ventral wall of the coxa; the thoracic branch (fig. 39, P) includes one or two long muscles from the tergum, one from the arm of the pleural ridge, and sometimes one from the episternum (fig. 26 B, P), the fibers from all sources converging upon a large apodeme that arises from the ventral lip of the trochanter or from the articular membrane close to it. The great size of the depressor muscles of the trochanter gives the leg a strong movement of extension, which is that by which it accomplishes its principal work. The ample membrane above the trochanteral articulation allows the trochanter and femur to be freely flexed upward.

The trochantero-femoral joint of the insect leg, though usually having little if any motion, is often slightly movable and sometimes freely so, as in the bees. Its movements are always forward and
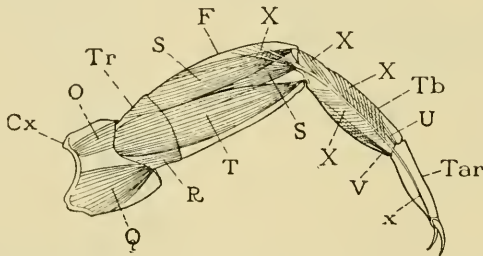

FIG. 40.—Muscles of right hind leg of *Japyx*, posterior view (lettering as on fig. 39).

rearward (production and reduction). In the higher Crustacea, which have two articulated trochanteral segments (basis and ischium, fig. 42 A), the second trochanter and the femur are each provided with productor and reductor muscles (Schmidt, 1915). In the Chilopoda and Hexapoda the second trochanter, or the single compound trochanter of most Hexapoda, has no muscles, but it contains a reductor femoris (figs. 35, 39, R) inserted on the posterior rim of the femoral base. In the leg of a caterpillar (fig. 41 B) a very small femoral reductor (R) goes from the upper anterior end of the incomplete trochantin (Tn) to the upper posterior part of the base of the femur. In the Protura, Prell (1912) describes a reductor femoris arising within the distal end of the coxa (fig. 41 A, R). Ordinarily the femur has no other muscle than the reductor, but both Berlese (1909) and Prell (1912) describe in the Protura a levator of the femur arising in the base of the coxa (fig. 41 A, lf). Berlese describes also a femoral depressor, but Prell does not mention or figure such a muscle.

The musculature of the femoro-tibial joint is variable. In adult insects, except Protura, however, it consists of a levator and a depressor of the tibia (fig. 39, *S, T*), the former often double (fig. 40, *S, S*). Both muscles are large and arise within the femur, though the depressor commonly has an anterior branch arising on the ventral wall of the trochanter (fig. 39, *Tr*). The fibers are usually inserted on apodemes springing from the dorsal and ventral lips of the tibial base, or arising from the membrane of the knee joint, the base of the depressor apodeme often forming a large chitinous plate in the ventral membrane of the joint. In the Protura, according to Prell (1912), there are no levator muscles in the telopodite beyond the trochantero-femoral joint, though Berlese describes a levator (abductor) of the tibia and of the tarsus. The depressor of the tibia in the Protura (fig. 41 A, *T*) consists of several branches arising in the femur and in the trochanter. In the leg of a caterpillar the tibia has a levator (fig. 41 B, *S*) arising in the base of the femur, and a depressor of three large branches (*T*), two branches from the femur and one from the trochanter, the group suggesting that of the tibial depressors in *Eosentomon* (A, *T*). Apparently all insect larvæ have both levator and depressor muscles of the tibia regardless of whether the femoro-tibial articulation is dicondylic or monocondylic.

The tarsus of typical adult insects is provided with both levator and depressor muscles arising within the tibia (figs. 39, 40, *U, V*). In the Protura (Prell, 1912) there is no tarsal levator, and the depressor usually arises by several heads in the tibia, femur, and trochanter, the distribution varying according to the species. In *Eosentomon* there is but one long depressor of the tarsus with its origin in the trochanter (fig. 41 A, *V*). In the caterpillar of *Estigmene* (fig. 41 B) there is no tarsal levator, but a simple depressor (*V*) arises on the anterior ventral wall of the tibia. In all insect larvæ the tibio-tarsal joint is either monocondylic or lacks articular points. In a trichopteran larva, as figured by Börner (1921), the tarsus has only a depressor muscle; but in coleopteran larvæ with a tarsus distinct from the tibia, there are both levators and depressors of the tarsus (fig. 43 A, *U, V*). In adult insects the tarsus is freely flexed upward, but can usually be extended only in line with the axis of the tibia; in larval insects the tarsus has a greater downward motion.

The subsegments of the tarsus are never provided with muscles, evidence that the articles are not true segments. Du Porte (1920) has described and figured levator muscles of the tarsal subsegments in *Gryllus*, but this is certainly an error. Likewise, muscles of the foot, or pretarsus, never have their origin in the tarsus in insects,

though in some other arthropod groups the muscles of the dactylopo-
dite arise in the propodite.

The insect pretarsus is provided only with depressor muscles, called
usually flexor or retractor muscles of the claws, and in this feature
it resembles the terminal leg segment of the Chilopoda. In the
Crustacea, Pycnogonida, and Arachnida, however, the dactylopodite
has both levator and depressor muscles. Du Porte (1920) describes
an " extensor " of the claws in *Gryllus,* but here again his observation
is clearly at fault.

In insects and in the chilopods, the pretarsal muscles have their
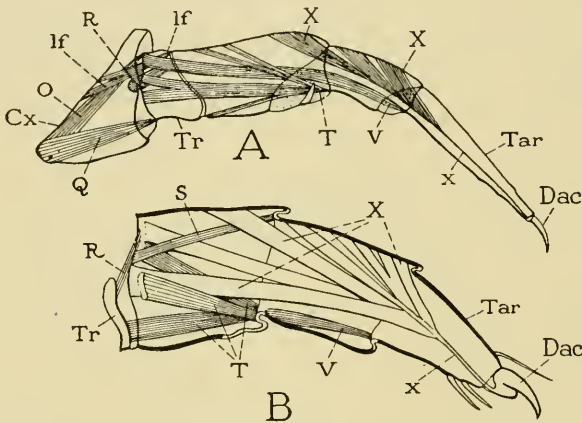origin in the leg segments proximal to the tarsus, and they are all

FIG. 41.—Leg of proturan and of caterpillar, showing similarity of musculature.

A, hind leg of *Eosentomon germanicum* (Prell, 1912) ; B, right hind leg of
caterpillar of *Estigmene acraea,* posterior view. (Lettering as on fig. 39, except
lf, levator of femur.)

inserted on a long " tendon " arising on the base of the pretarsus and
extending through the tarsus (fig. 39, x). In insects, the fibers of
the pretarsal muscles form several or numerous bundles (figs. 39, 40,
41, 43, X) arising in the tibia and the femur, and sometimes in the
trochanter, the number of the bundles and the points of their origin
varying much in different species. Where the pretarsus has the form
of a simple dactylopodite, as in Protura (fig. 41 A) and in certain
holometabolous larvæ (figs. 41 B, 43), the apodeme, or " tendon,"
of the pretarsal muscles arises directly from its base—in *Lepisma*
it arises from the base of the median claw (fig. 44 C, E, x) ; but in
other insects in which there is a special unguitractor plate, the tendon
arises from the proximal end of this sclerite (figs. 36 B, 39, 44 B, *Utr*).
The pull of the muscles on the unguitractor plate turns the claws

downward on their dorsal articulations with the unguifer process at the end of the tarsus (fig. 36 A, D, *k*). The claws are extended by the elasticity of their basal connections when the flexor muscles relax, or by the weight of the insect on the supporting surface.

MORPHOLOGY OF THE LEG

Entomologists can not resist the temptation of endeavoring to trace the evolution of the insect leg from a biramous appendage such as is supposed to have been the ancestral form of all arthropod limbs. The plan of this hypothetical generalized appendage, as conceived principally by the carcinologists (fig. 42 A), includes a basal stalk, or
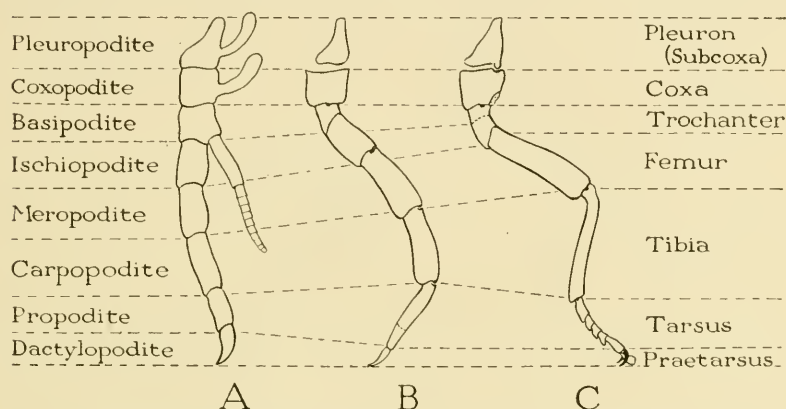

Fig. 42.—Diagram suggesting homologies of segments in arthropod limbs.

A, generalized crustacean limb; B, leg of a chilopod (centipede) ; C, leg of an insect.

protopodite, and two distal branches, an *exopodite* and an *endopodite.* The stalk is divided into three segments (formerly only two were recognized), a *pleuropodite,* a *coxopodite,* and a *basipodite.* The exopodite has a number of small subdivisions, fortunately not named individually ; the endopodite consists of five segments, an *ischiopodite,* a *meropodite,* a *carpopodite,* a *propodite,* and a terminal *dactylopodite.* The basal two segments of the stalk may bear external appendages called *epipodites;* lobes on the inner margins of the segments are *endites.*

The only fact that can be construed as evidence of a biramous origin of insect appendages is the presence of styli on the coxæ of the middle and hind legs of *Machilis* and related genera (fig. 12, *Sty*). No insect appendage develops in the embryo with a biramous struc-

ture ; the lobes of the maxillæ are now recognized as being endites of a uniramous stalk. The leg styli of *Machilis* have apparent homologues in similar styli on the legs of Symphyla, in the paired styli occurring on a number of the abdominal segments of *Machilis, Lepisma, Japyx,* and other thysanuran genera, and in those of the ninth abdominal segment of the males of certain pterygote insects. The abdominal styli of *Lepisma* are said by Heymons (1897) to appear and to develop during the postembryonic life of the insect, a period rather late for a primitive organ to become first apparent. Moreover, the leg styli of *Machilis* and *Scolopendrella* occur on the coxæ, while the seat of a true exopodite is the basipodite, a segment either lacking in most insects or included in the trochanter (fig. 42 C). There is, therefore, reason for doubting that the styli of insects are exopodites. Unquestionably they are organs possessed by the ancestors of both the Apterygota and the Pterygota, but that they are other than secondary structures is yet to be demonstrated.

When the exopodite disappears from a biramous limb, as it commonly does in the evolution of an appendage that takes on a special function, there is left a uniramous shaft of eight segments. The basal segment, pleuropodite, or subcoxa (fig. 42), according to the theory adopted and elaborated in this paper, becomes incorporated into the body wall to form the pleuron in the Insecta and Chilopoda. In the Crustacea, Borradaile (1917) says, the pleuropodite " may or may not have originally existed as a free joint in every biramous limb, but has now always disappeared, either by fusion with the trunk or with the second joint, or perhaps sometimes by excalation." In the Arachnida the pleuropodite has entirely disappeared. In the Pantapoda (Börner), and in the Acarina it apparently remains as a basal segment or support of the leg. In those arthropod groups that lose the pleuropodite, or subcoxa, as a free part of the limb, the rest of the appendage with its new base in the coxopodite becomes the functional leg.

In entomological terminology the pleuropodite (subcoxa) becomes the pleuron (fig. 42 C), the coxopodite is the coxa, the basipodite and the ischiopodite united form the trochanter, the meropodite is the femur, the carpopodite is the tibia, the propodite the tarsus, and the dactylopodite the pretarsus. This, at least, is a reasonable scheme of homology, though confessedly a theoretical one, and may be applied consistently in the several arthropod groups. The leg segmentation of a chilopod (fig. 42 B) conforms with it, as does also that of the Acarina (fig. 17) and the Arachnida. Exceptional opinion will be noted presently.

There is such uniformity of structure in the articulation between the usual first and second segments of the leg that this joint may be taken as invariably separating the coxa and the first trochanter. There is no apparent reason for doubting that the second and third segments of the chilopod leg (fig. 42 B) correspond with the basipodite and ischiopodite of the crustacean leg (A). The first of these segments lacks muscles in the Chilopoda, but this is explained by Verhoeff (1903a) as a device for allowing the leg to be broken off without injury to the animal, the natural break taking place at the base of the segment in the Pleurostigma and at the distal end in the Notostigma. In insects there is reason for believing, as already shown (page 78), that the basipodite and ischiopodite, or first and second
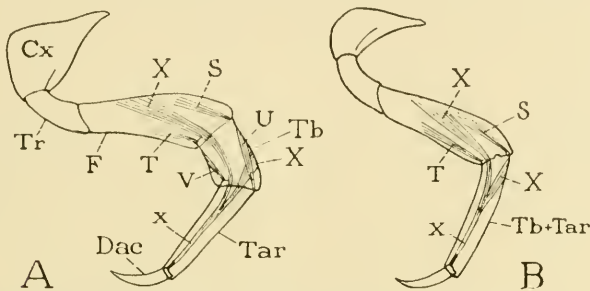

FIG. 43.—Segmentation and musculature of legs of coleopteran larvæ. (Figures from Jeannel, 1925, but differently interpreted, and re-lettered.)

A, leg of larva of *Trechus*, with usual six segments; B, leg of larva of Bathisciinæ, with five segments. *Cx*, coxa; *Dac*, dactylopodite; *F*, femur; *S*, levator of tibia, *T*, depressor of tibia; *Tar*, tarsus; *Tb*, tibia; *Tb + Tar*, tibio-tarsus; *U*, levator of tarsus; *V*, depressor of tarsus; *X, X*, branches of depressor of dactylopodite; *x*, tendon of *X*, inserted on base of dactylopodite.

trochanter, have united to form the usual single trochanter (fig. 42 C). The presence of a reductor femoris muscle in the trochanter identifies the trochantero-femoral joint with that between ischiopodite and meropodite in Crustacea and Chilopoda (A, B).

The principal bend, or "knee," in the telopodite of the arthropod leg is regarded by Börner as being in all cases the joint between meropodite and carpopodite. Jeannel (1925) takes exception to this view, since he believes that in insects the tibia and the tarsus are subdivisions of the propodite, and that the carpopodite has been lost from the leg of all insects, except in those coleopteran larvæ of the Adephaga group that have six segments in the leg (fig. 43 A). In other larvæ, he claims, the six segments result from a division of the propodite into tibia and tarsus. Jeannel would find a remnant of the carpopodite in the small sclerite of the ventral membrane of the

knee joint to which the flexor muscle is here often attached. As already pointed out, however, this interpretation seems entirely unnecessary, since there is no evidence that the tibia and tarsus are not primitive limb segments, as the tarsal muscles indicate. In coleopteran larvæ with a five-segmented leg (fig. 43 B), therefore, it is most probable that the tibia and tarsus are united, as also is indicated by the attachment of the first branch of the pretarsal muscle (X). Muscle insertions in many places are upon small chitinizations of an articular membrane, rather than directly upon the part to be moved by the muscle.

The idea that the pretarsus of the insect represents a primitive leg segment has not been generally accepted, some entomologists regarding it as a sixth segment of the tarsus, while others see in the terminal
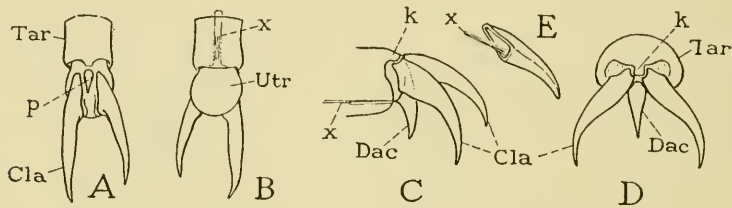

FIG. 44.—Terminal foot structures of Thysanura.

A, hind claws and end of tarsus of *Japyx*, dorsal view, showing rudimentary median claw (*p*). B, same, ventral view, showing large unguitractor plate (*Utr*). C, foot of *Lepisma*, lateral, with dactylopodite-like median claw (*Dac*) to which is attached tendon (*x*) of depressor muscle. D, same, end view. E, median claw, or dactylopodite, of *Lepisma*, with piece of depressor tendon (*x*).

structures only special developments of the last tarsal segment. The present writer, however, would now adopt the view so well stated and so fully illustrated by de Meijere (1901), that the pretarsus, including the claws, the arolium, and all accessory parts of the foot is a development of the dactylopodite of the generalized arthropod limb.

A pretarsus having the form of a simple claw-like dactylopodite occurs in the Protura, in some of the Collembola, in caterpillars, sawfly larvæ, and in most beetle larvæ. In the Lepismidæ each pretarsus has three claws, there being a slender decurved median claw between the two lateral claws (fig. 44 C, D, *Dac*). The median claw is a hollow structure (E) with the unguitractor tendon (*x*) attached to its base, and, if the lateral claws were lacking, it would constitute a miniature but typical dactylopodite. In *Japyx* the ventral part of the pretarsus apparently has become developed into a large unguitractor plate (fig. 44 B, *Utr*), while a point that is perhaps its tip remains

as a rudimentary median claw (p). In *Campodea* and *Machilis* the
median claw has disappeared and only the lateral claws remain. The
median arolium of many pterygote insects might be regarded as the
transformed body of the dactylopodite, though it appears more likely
that arolium, empodium, and pulvilli are all secondary formations.

The origin of the two lateral claws of the insects pretarsus should
be determined by a study of the transformation of a single-clawed
larval pretarsus, such as that of a caterpillar, into the two-clawed
structure of the adult, but this has not been done. De Meijere believes
that the claws are merely outgrowths of the base of the dactylopodite,
though he admits no evidence of this has been found in insects, but
he points out that the possibility of claws arising thus is shown by
the presence of dorsal claw-like structures on the dactylopodite of
certain isopods (*Iaera, Janira, Munna*). The articulation of the claws
to the end of the tarsus might suggest that they belong to the tarsus,
as claimed by Jeannel (1925), but the fact that the cavities of the
claws open through their wide bases into the lumen of the pretarsus
shows that the claws belong to the terminal segment. The tarsal
articulation of the claws, then, becomes of no more significance than
the articulation of any other leg segment to the segment proximal
to it. That the claws are not transformed setæ is demonstrated by
their multicellular structure, and by the frequent occurrence of true
setæ upon them.

There still remains to be discussed the question as to what was the
nature of the first articulations between the segments of the insect
leg. Börner (1921) believes that the double, or dicondylic, hinge is
the primitive one, and that the single articular point, or monocon-
dylic hinge, has resulted from a dorsal migration and union of
anterior and posterior condyles. Prell (1912) argues the reverse,
basing his claim on the fact that the joints of the telopodite in the
Protura have each a single dorsal articulation, and are provided with
flexor muscles only. The coxo-trochanteral joint is so constantly
dicondylic in arthropods that there is no reason for supposing it ever
had any other structure; but the common occurrence of monocondylic
articulations at the other joints in the legs of larvæ of holometabolous
insects, and their association with a dactylopodite-like end segment,
as in the Chilopoda (fig. 32), furnishes a basis for believing that the
primitive joints in the telopodite of the insect leg were of the mono-
condylic type. Further evidence of this is to be seen in the fact that
the segments of the maxillary and labial palpi are provided each with
only one muscle, a condition seldom found in connection with dicon-
dylic joints.

Though the leg of a caterpillar, both in its structure, as compared with the leg of a centipede (fig. 32), and in its musculature, as compared with that of a proturan (fig. 41), irresistibly suggests that it is a primitive organ, it must yet be noted that, in the larvæ of Neuroptera and Trichoptera, the adults of which certainly stand below the Lepidoptera, the legs have a dicondylic knee joint and two terminal claws. The same apparent phylogenetic discrepancy is to be observed in the Coleoptera, where the larvæ of most Adephaga have two claws, and those of other groups only one claw. It should be recognized, however, as shown by Berlese (1913), that the larvæ of different insects do not necessarily represent equivalent ontogenetic stages, nor, therefore, equivalent phylogenetic stages. The larvæ of more generalized adults are likely to have acquired many adult characters, while those of more highly specialized adults may be of an earlier ontogenetic stage and, consequently, may retain more primitive characters.

VI. SUMMARY (EVOLUTION OF THE THORAX)

A brief review of the principal points elaborated in the preceding discussions may be presented in the form of an outline of the probable evolution of insects, since the specializations of the thorax and its appendages constitute the most distinctive characters of insects.

1. In the primitive, segmented, but soft-bodied ancestors of the arthropods, the limits of the body segments coincided with the lines of attachment of the principal dorsal and ventral longitudinal muscles. Modern adult arthropods, however, with solid body wall plates, have developed a secondary segmentation, to allow a forward contraction of the body, through the union of the muscle-bearing ridges of the body wall with the segmental plates following, thus converting the membranous posterior parts of the segments into the functional but secondary intersegmental areas.

2. In the evolution of insects, as shown by ontogeny, and probably of all arthropods, the earliest differentiation in the long, segmented body consisted of the union of the anterior two or three segments to form a primitive head, or procephalon, containing the first three nerve centers condensed into a brain.

3. The distinctive character of insects began with the development of the thorax as the locomotor center of the body, this being accompanied by the reduction of the appendages on most of the segments following, and the transformation of those on the three segments immediately preceding into gnathal organs, the segments of which later unite with the procephalon to form the definitive head. The newly

localized center of gravity from now on determined the general form and proportions of the body parts. The specialization of the thorax before wings appeared consisted of structural changes better adapting its segments to the functions of supporting the legs and of giving more efficient attachment and action to the leg muscles.

4. The limbs of primitive arthropods were probably rather simple appendages growing outward from the lateral or pleural areas of the segments between the dorsum and the venter. They probably turned forward and backward on their bases, each being moved by promotor and remotor muscles, fibers of each set arising on the dorsum and on the venter, or on the tergum and the sternum when segmental plates were developed. The second segment of the limb most likely moved in the opposite direction from the basal one, *i. e.,* it turned dorsally and ventrally by a longitudinal axis on the first, and was provided with abductor and adductor muscles. The third segment moved in the same plane as the second, on a longitudinal axis with the latter. The proximal three segments of the primitive limb were the subcoxa, the coxa, and the first trochanter.

5. As the evolving limb came to need more solid support, the subcoxa became flattened out in the pleural wall of its segment, and lost its power of motion. A dorsal piece of the distal rim of the subcoxa, bearing the anterior and the posterior articulations with the coxa, separated from the basal part, and the ventral region of the latter degenerated, or united with the edge of the sternum. The subcoxa thus became reduced to a basal eupleural arch and a distal trochantinal arch, the two lying concentrically over the base of the coxa, and having now the status of chitinous elements in the pleural wall of the body segment.

6. The coxa, thus forced to replace the subcoxa as the functional base of the limb, had to adapt itself to its new responsibilities. By a shifting of its posterior articulation with the trochantin to a dorsal position, it preserved for the limb the power of forward and backward movement. With the change, however, the coxa, acquired in addition the possibility of a partial rotary motion, but, while it retained its transverse movements, its abductor muscles lost efficiency through the altered position of the articulation. The assumption by the coxa of the former duties of the subcoxa involved a transfer of the subcoxal muscles to the coxa. The dorsal promotor and remotor muscles functioned still as such when attached to the coxa, but the ventral muscles became rotary muscles, since the coxa was now free to turn on its dorsal articulation. The abductor and adductor muscles of the coxa, the first retaining its origin on the subcoxa (now

the pleuron), but the second being transferred to the sternum, still act in their original capacities. The dorsal promotor is the last sub-coxal muscle to be given over to the coxa, being retained by the trochantin until this sclerite becomes rudimentary or disappears.

7. Before the wings appeared, or while they were developing into organs of flight, the tendency of the subcoxa, now the chitinous pleuron of the segment, apparently was to break up into various pieces that would allow flexibility to the lateral segmental wall. In the Apterygota, the eupleural and trochantinal arches remain separate, and both have become variously reduced. In the Protura the eupleural arch has broken up into a number of sclerites corresponding in a general way with the eupleural plates of the Pterygota, perhaps indi-cating that the proturan ancestors were nearly related to the ancestors of the Pterygota; but in the other Apterygota the eupleuron has become degenerate, and suggests no evolution toward the pleural pattern of the Pterygota. In the early Pterygota, the eupleural arch became divided into a dorsal plate, an anterior plate before the coxa, and a posterior plate behind the coxa. The trochantin, still carrying the coxal articulations, remained an independent sclerite for a while, but its dorsal part later united with the dorsal eupleurite. The com-pound plate thus formed then became strengthened by an internal ridge extending upward from the dorsal articulation of the coxa, and the corresponding external suture divided the plate into epister-num and epimeron. The anterior part of the trochantin has become detached in many insects to form a free sclerite still bearing the anterior coxal articulation. In the higher pterygote groups the evolu-tion of the pleuron has been toward a reunion of the sclerites to form a solid segmental wall, especially in the wing-bearing segments. Where the free remnant of the trochantin is lost, the coxa may ac-quire a ventral articulation with the sternum, as in some of the Apterygota.

8. When the thorax became set apart as a locomotor region, the overlapping of its segmental plates and the telescoping of its segments became a handicap to its functional development. To counteract its mechanical weakness, the muscle-bearing parts of the sterna were transferred from the anterior margins of the sternal plates to the posterior margins of those preceding, thus bringing about a reversal in the segmental relations of the ventral muscle attachments in the thorax from those in the abdomen. When furcal arms were later developed, the muscle attachments were farther transferred in part or entirely to these processes, and the poststernal parts were then lost or absorbed into the posterior margins of the principal sternal plates.

9. The wings, developed as lateral outgrowths of the dorsum, entailed the development of a second set of modifications in the thoracic structure, superposed on those already acquired in connection with the development of legs as efficient organs for terrestrial or arboreal progression. The wing lobes served at first probably as planing surfaces that enabled their possessors to glide through the air from elevated positions; there is no good evidence that they ever had any other function.

10. The wings of all insects except the Odonata are still moved principally by muscles present in the thorax when the wing lobes were first acquired. The evolution of the wings involved the development of a supporting apparatus from the dorsal part of the pleuron, changes in the terga bearing them, and a general consolidation of the mesothorax and metathorax. Since the up-and-down motions of the wings are produced by movements of the terga, the development of wing motion demanded from the first a suppression of the flexible overlapping of the terga, and this was accomplished, as in the sterna, by a transfer of the precostal margins of the third and fourth terga, together with their muscle-bearing ridges or phragmata, to the segments preceding, where they constitute the postnotal plates. The dorsal longitudinal muscles could now effect an upward bending of each tergum, giving a down-stroke to the wings, and the tergo-sternal muscles could act antagonistically as elevators of the wings by flattening the tergal arches. Since the wings have not been developed alike in the two wing-bearing segments of all the orders, the tergal readjustments vary accordingly.

11. The ridges on the under surfaces of the wing-bearing terga have been developed in response to the needs of the terga as parts of the wing mechanism. The tergal areas between the ridges, defined on the exterior by the corresponding sutures, are therefore in no sense primitive component elements of these terga, and are not to be homologized with tergal " divisions " in the other segments.

12. But few new muscles have been developed in most insects in connection with the wings. In the Odonata, however, the primitive musculature has been suppressed, and has been replaced by sets of special wing muscles attached directly to the wing bases. The Odonata, therefore, represent a highly specialized line of descent that branched off from the main pterygote stem at an early period, but apparently since the time of the oldest insects known from the paleontological records.

13. The legs of insects have undergone an evolution that has resulted in the typical leg structure of the adult, but various developmental stages are preserved in the legs of some of the lower insects, and in those of certain larval forms. The third and fourth segments of the primitive limb, the basipodite and the ischiopodite, have united into a single small segment, the trochanter. The trochantero-femoral joint, when movable, preserves its vertical axis of motion, with dorsal and ventral articulations. A reductor femoris muscle persists, but there is no productor. The femoro-tibial and tibio-tarsal joints have lost their primitive monocondylic structure in most adult insects, and have become dicondylic through the development of anterior and posterior articulations, with the acquisition of levator muscles. The tarsus, or propodite of the primitive limb, has become fragmented into a series of sub-segments, typically five, but none of these sub-segments have acquired muscles. The terminal leg segment, the dactylopodite, has developed into the complicated pretarsus of most adult insects through the suppression of the original median claw, and the development of lateral claws, a median arolium, or various other accessory lobes. A levator muscle of the dactylopodite is lacking in all insects; the depressor, with branches arising in the tibia, femur, and even the trochanter, is retained as the " retractor " of the claws, the fibers of its branches being inserted on the retractor apodeme, or " tendon," attached to the unguitractor plate in the base of the pretarsus, possibly a remnant of the original dactylopodite.

ABBREVIATIONS USED ON THE FIGURES

A, anal veins.
longitudinal dorsal muscle, indirect depressor of wing.
Ab, abdomen.
Ac, antecosta.
ac, antecostal suture.
Acx, precoxal bridge.
ANP, anterior notal wing process.
Ant, antenna.
Aph, anterior phragma.
Apl, anapleurite.
Ar, arolium.
Aw, prealar process, or bridge.
Ax, axillaries. *1Ax*, first axillary; *2Ax*, second axillary; *3Ax*, third axillary; *4Ax*, fourth axillary.

B, oblique dorsal muscle.
Ba, basalare, episternal epipleurite (parapteron).
Bs, basisternum.

C, costa, first vein of wing.
tergo-sternal muscle, indirect elevator of wing.
Cla, claw.
Cu, cubitus, fifth vein of wing.
Cv, cervix, neck.
Cx, coxa.
CxC, coxal cavity.
CxP, pleural coxal process (*b*).

D, muscle of third axillary, flexor of wing.
Dac, dactylopodite.

E, basalar coxal muscle, direct extensor of wing.

Epl, eupleuron.

Epm, epimeron.

epm, subdivision of epimeron.

Eps, episternum.

eps, subdivision of episternum.

F, subalar coxal muscle, direct extensor and depressor of wing.
femur.

Fs, furcisternum.

Fu, furca, the sternal apophyses united on median base.

G, muscle from pleural apophysis to sternal apophysis.

Gc, jaw segments of head, gnathocephalon.

H, head.
longitudinal ventral muscle.

I, promotor muscle of coxa.

I-XII, abdominal segments.

IS, first abdominal sternum.

ISg, intersegmental groove.

IT, first abdominal tergum.

J, remotor muscle of coxa.

K, anterior rotator muscle of coxa.

L, leg.
posterior rotator muscle of coxa.

LMcl, longitudinal muscles.

M, abductor muscle of coxa.
media, fourth vein of wing.

Mb, " intersegmental " membrane.

mb, secondary " intersegmental " membrane behind base of phragma.

Mer, meron.

Mth, mouth.

N, adductor muscle of coxa.

O, levator muscle of trochanter.

Op, operculum.

P, thoracic branch of depressor muscle of trochanter.

Par, parapsis, parapsidal ridge.

par, parapsidal suture.

Pc, precosta, anterior marginal lip of segmental plate before antecostal ridge and suture.

Pcx, postcoxal bridge.

Ph, phragma.

Pl, pleuron.

PlA, pleural apophysis.

pla, external root of *PlA.*

PlR, pleural ridge.

PlS, pleural suture.

PN, postnotum (postscutellum) postalar tergal plate of winged segment, bearing phragma, consisting of precosta and posterior lip of phragma, usually detached from following tergum.

PNP, posterior notal wing process.

Pph, posterior phragma.

PR, ridge between prescutum and scutum.

Prc, procephalon (primitive head, not including jaw segments).

PS, poststernum (postfurcisternum and spinisternum).

ps, prescuto-scutal suture.

Psc, prescutum.

Ptar, pretarsus.

Pw, postalar bridge.

Q, coxal part of depressor muscle of trochanter.

R, radius, third vein of wing.
reductor muscle of femur.

Rd, posterior fold, reduplication, of tergum.

rd, anterior ventral margin of *Rd.*

S, levator muscle of tibia.
sternum.

SA, sternal apophysis.

Sa, subalare, epimeral epipleurite (parapteron).

sa, external root of sternal apophysis.

Sc, subcosta, second vein of wing.

Scl, scutellum.

Scx, subcoxa.

Sct, scutum.

sct, subdivision of **scutum**.

Seg, segment.

Sp, spiracle.

Spn, spina, median process of post-sternum.

Sty, stylus.

T, depressor muscle of tibia. tergum.

Tar, tarsus.

Tb, tibia.

Tg, tegula.

Th, thorax.

Tn, trochantin.

Tr, trochanter.

U, levator muscle of tarsus.

V, depressor muscle of tarsus.

VR, ridge between scutum and **scutellum**.

vs, scuto-scutellar suture.

WP, pleural wing process.

X, depressor muscle of dactylopodite, retractor of claws.

x, "tendon" of *X*.

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