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THE MORPHOLOGY OF TIPULA REESI ALEXANDER (DIPTERA: TIPULIDAE)

By Bryant E. Rees and G. F. Ferris

This paper is the third of a projected series in which it is planned to consider in detail the morphology of selected representatives of various insect groups. In the preparation of the paper Mr. Rees has been responsible for most of the dissecting and study of specimens and for the preparation of most of the accompanying illustrations and the paper is therefore based primarily upon his work. Mr. Ferris has independently compared all of the illustrations with the material from which they have been derived and has supplemented those of Mr. Rees with a few others. He has also edited and arranged the textual material. The conclusions presented have in the main been arrived at by joint consideration of the various problems, but Mr. Ferris will assume full responsibility for any pronouncements and opinions on disputed questions.

It was the desire of the authors to consider the morphology of a generalized Dipteran as a basis for an understanding of the more specialized members of this Order. Since it is generally assumed that the most generalized Diptera are to be found in the superfamily Tipuloidea recourse was had to species from this group. Out of the material obtainable there was selected a species which seemed to be the most suitable of all that were examined and on the whole the choice has proven to be very fortunate, although certainly even this species could not be entirely understood without reference to others which in some respects are still more generalized. After the work on this species was practically completed it was discovered that the species is apparently undescribed and a formal description of it, prepared by Professor C. P. Alexander, is here included in order to validate its name. The name of the new species is of course to be credited to Professor Alexander.

We wish here to express our thanks to Professor Alexander for his assistance in the identification of our material, for suggestions as to species which might be of aid to us and for supplying us with material of them. Without some of these species we would still be quite in the dark concerning certain obscure points in the morphology of this group. The formal description of the species upon which the work is primarily based follows.

Tipula (Lunatipula) reesi new species

By C. P. Alexander

General coloration yellow; nasus lacking; antennal flagellum weakly bicolored; wings grayish subhyaline, sparsely patterned with brown; obliterative

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band before cord conspicuous; male hypopygium with the basistyle completely separated from sternite; eighth sternite with a conspicuous median lobe and hair brushes, the lateral lobes flattened, margined with strong setae from tuberculate bases.

Male. Length, about 17-18 mm.; wing 16-17 mm.

Female. Length, about 23-24 mm.; wing 17-18 mm.

Described from alcoholic specimens.

Frontal prolongation of head yellow; nasus lacking; palpi yellow, the terminal segment darker. Antennae (male) relatively short; basal three or four segments yellow, succeeding segments weakly bicolored, the basal enlargements of the individual segments slightly darker than the apical pedicels. Head above obscure brownish yellow, the vertex between eyes more darkened.

Mesonotal praescutum brownish yellow, with three clearer yellow stripes, the median one very vaguely divided by a capillary darker vitta; scutal lobes with yellow centers; posterior sclerites of notum yellow. Pleura yellow, vaguely more darkened along the sutures. Certain of the specimens, especially the females, are darker colored, apparently being more or less pruinose in fresh specimens. Halteres with stem yellow, knob infuscated. Legs with coxae and trochanters yellow; remainder of legs obscure yellow, the tips of the tibiae and the terminal tarsal segments more infuscated. Wings grayish subhyaline, vaguely patterned with darker and with whitish subhyaline; stigma brown; very small brown clouds at origin of Rs, end of vein Sc and along m-cu; central portion of cell R_2 weakly darkened; a whitish obliterative band before cord, extending from costa across wing into base of cell M_3; veins pale brown, darker along cord and in the darkened areas. A group of trichia on squama. Venation: Distal end of free tip of vein Sc_2 swollen, as in the group; vein R_3 sinuous; petiole of cell M_1 subequal to m; cell 1st M_2 relatively small.

Abdomen yellow, the tergites with three relatively narrow brown stripes that are narrowly interrupted at the incisures, slightly widened and more conspicuous behind; hypopygium more brownish yellow. Male hypopygium relatively large; tergite almost entirely separated from sternite; basistyle entirely separated, not produced apically. Ninth tergite with the lateral lobes only slightly produced; median lobe sunken, deeply split by a narrow median notch. Outer dististyle a weakly spatulate blade. Inner dististyle heavily sclerotized apically; posterior lobe gently arcuated, its apex darkened and provided with numerous short setae. Eighth sternite with a broad, deep, median incision, at base bearing a gently bilobed cushion that is tufted with a double brush of elongate setae, the more mesal ones of which are microscopically roughened; immediately dorsad of this cushion a triangular median lobe that is densely covered with short curved setae, the apical group longer and more slender; lateral lobes of sternite incurved, flattened, the margins with long conspicuous setae arising from strong tubercles, those of lower edge stronger and more fasciculate, from larger tubercles.

Holotype, alcoholic male, Stanford University, California, May 6, 1938 (B. E. Rees). Allotopotype, alcoholic female. Paratypes, alcoholic material of both sexes; material preserved in the author's collection and in the Natural History Museum, Stanford University.

I take great pleasure in naming this crane fly in honor of the collector and co-author of the accompanying morphological study of the species. The fly is closest to *Tipula (Lunatipula) aequalis* Doane, *T. (L.) planicornis* Doane and *T. (L.) tingi* Alexander, all of which likewise have the nasus lacking. All of these species are well distinguished among themselves by the details of structure of the male hypopygium. In the above description, morphological discussions have been purposely curtailed since Mr. Rees will have treated all such in detail.

MORPHOLOGY OF TIPULA REESI ALEXANDER

Introductory Note

While, as we have remarked, the superfamily Tipuloidea is usually considered to contain the most generalized of the Diptera, the fact still remains that in many respects the members of this group are far from being ideal expressions of what the primitive Dipteran must have been. It may very well be that somewhere among the thousands of species of this superfamily there exists one in which all parts of the body are equally generalized, but certainly in the species that we have been able to examine this is not the case. We would conclude, from what we have seen, that it would be necessary to put together at least a half dozen flies from widely different families in order to obtain such a generalized species. The highly specialized Tabanidae, for example, retain mandibles, which are lost in the more generalized Tipulidae. In certain of the Tipuloidea the maxillae retain a generalized condition, but in the species here treated a very specialized condition of these structures is present. The most generalized genitalic structures of a male that we have seen have been in a species of the Stratiomyidae, while certainly in the Tipulidae they present remarkable specializations, while in the supposedly very primitive Tanyderidae they are by no means generalized.

It is evident therefore that not until a very considerable number of species of Diptera have been investigated will we have any thoroughly sound basis for a comparative morphology of the Order. As a beginning the species here considered is quite favorable. With the morphology of species of the Neuroptera and Mecoptera understood it is possible to proceed to *Tipula* without encountering any very marked difficulties.

THE HEAD (FIGURES 72-75)

The elongation of the head in this species is due entirely to elongation of the clypeal and genal areas. No epistomal (= clypeo-frontal) suture and no anterior tentorial pits are present, consequently the proximal delimitation of the clypeus is not indicated in this species, but in others, as in the genus *Limonia*, the anterior tentorial pits are clearly evident, being situated just below the antennal foramina. On this basis the entire front of the head from just distad of the antennal foramina to the apex is of clypeal derivation. Separation of the clypeus from the genae is at the most indicated by an exceedingly faint depression. At the apex of the genal area is a small, partially detached plate which lies in the position ordinarily assumed by the subgena. It is here (Figure 72B) designated as that piece, but with some reservations and it may be merely a secondary lobe of the gena.

The head capsule is closed behind by the approximation of the genal and postgenal areas along the median line from the occipital foramen to the base of the labium, but other than this median suture no sutures are present and the areas of the epicranium can be defined only as general regions.

The Labrum (Figures 72A, 75C)

The labrum is a small lobe at the apex of the clypeus, from which it is definitely set off by a suture. At its apex it bears on each side a small lobe. Peterson (1916) identified these lobes as the epipharynx, but we are unable to regard them as being this structure and they are here designated (Figure 75C) merely as labral lobes. We consider that the epipharynx as a distinct structure is not present.

The Mandibles

In this group the mandibles are entirely lacking.

The Maxillae (Figures 72, 73E, 75D)

Peterson (1916) has shown that all Diptera having functional mouthparts possess maxillae, which, however, may be greatly reduced and modified. The problems having to do with them involve the homologies of the remaining reduced and modified structures. In the species here under consideration the loss of parts has been carried to an extreme degree and it is only by reference to other and less modified species of the Tipuloidea that they can be understood. In *Dactylolabis montana* (Figure 74C) the posterior wall of the rostrum is membranous and in this membrane there lie two elongated sclerotized areas that seem definitely to represent the stipes of the maxillae. To the apices of these pieces articulate the maxillary palpi. A similar situation exists in *Pedicia calcar*, although here it is complicated by the fusion of these stipital parts into a single median plate.

In *Tipula reesi*, as in many other Tipulidae, the elongation and extension of the genal areas has displaced the stipes from the area which it occupies in the more generalized forms and consequently an entirely new situation has arisen (Figure 73E). The stipes—at least as an external sclerite—is entirely lacking. Furthermore, in this species all the other parts of the maxilla excepting only the palpi have been lost, although the palpi are retained in their generalized five-segmented condition. Articulating with the base of the palpi is the apex of an apodeme which is attached also to the wall of the head by a very small surface area just at the base of the first palpal segment. From thence it passes to the meson where it meets its companion from the opposite side and the two form a huge medial apodeme which extends upward into the head cavity. The identity of this apodeme immediately comes into question.

Peterson (1916, p. 38) regarded this apodeme as being identical with the fused stipites of the maxillae, notwithstanding the fact that it is not a surface structure. Such an identification seems to us quite untenable and we have cast about for some more satisfactory explanation. We believe that to arrive at some such explanation it is necessary to go far outside the Diptera for a beginning.

In the generalized maxilla (Snodgrass, Principles of Insect Morphology, p. 42, Figure 79) there are various muscles, but there is one which seems to be especially persistent and to have usually a well developed apodeme, that being the muscle which Snodgrass has called the "cranial flexor of the lacinia," which originates on the tergal wall of the head and inserts at the inner basal angle of the lacinia. This is apparently the most persistent of all the muscles of the maxilla, for it occurs even in such diverse forms as *Japyx* and the weevils.

In *Panorpa nuptialis* (Ferris and Rees, 1939, Figure 39) the apodeme of this muscle is present and divides apically into two branches, one of which at least extends into the lacinia. If we turn to the Tipulid, *Limonia sciophila*, we find a situation which is very similar to that in the Mecoptera, but with a slight modification. In this species the stipes is lacking, but the palpus and one terminal lobe of the maxilla are retained. A long apodeme, similar in position to that seen in the Mecoptera is present and is apically branched (Figure 74A). One long branch extends into the maxillary lobe, and for this reason we would identify that lobe as the lacinia. The other branch, which is merely a point, articulates to the first segment of the maxillary palpus. The apodemes from the opposite sides meet and are fused proximally for a short distance. The muscles which they serve have not been seen in the material at hand, but they evidently originate on the tergal wall of the head close to the occipital foramen.

We see no reason whatsoever to regard these apodemes as other than those

of the "cranial flexors of the lacinia." If we turn from this to *Tipula* we have what are evidently the same apodemes, differing only in that they are fused for practically their entire length and that the lacinial branch is lost, since no lacinial lobe is present.

We therefore consider that the median apodeme in this case is not the stipes and has nothing to do with the stipes. It is composed of the persistent, fused cranial flexor apodemes of the lacinia, which with the loss of the laciniae have taken on new functions. In the higher Diptera an apodeme that seems certainly to be this is present and passes through various modifications of form and function.

The Labium (Figures 72, 73)

As is well known, the labium of the Diptera presents certain problems concerning which there has been much divergence of opinion. We hold, however, that if we go back to the Mecoptera for a starting point these difficulties are easily resolvable, for the conditions which appear in the Diptera seem merely to be developments of tendencies that are initiated in this other Order.

If the reader will refer to the earlier paper in this series (Ferris and Rees, 1939) in which the morphology of a Mecopteran is discussed, the situation will be found much clarified. It is evident that in this Mecopteran the labium is much reduced; the glossae and paraglossae are suppressed; the prementum is represented merely by two partially fused pieces that may be regarded as the palpigers, upon the base of each of which there inserts a large apodeme; and the mentum is represented merely by a small plate. It should be noted above all that the labial palpi are but two-segmented and that the basal segment tends to be much swollen, its ventral surface being entirely membranous. It may be added that there is but a single muscle inserting on the palpus.

Coming back to our Tipulid we can see how little different it really is from the Mecopteran. The mentum has disappeared entirely. The prementum is a small sclerotization which is little more than a point of insertion for the huge, fused labial apodemes, with in addition two small, curved pieces to which the palpi articulate and which may be regarded as the palpigers. The two-segmented condition of the palpi is clearly indicated, but both segments are swollen and bulbous and both are entirely membranous except for small dorsal, sclerotized areas. The membranous ventral area has developed a set of peculiarly Dipteran structures, the pseudotracheae, but beyond this there is nothing that is not merely a continuation of the developments seen in the Mecoptera. Crampton, it may be added, has noted that pseudotracheae occur in certain Mecoptera.

It would be pointless, we believe, to review here the history of the controversy concerning the nature of the terminal lobes or "labella" of the Diptera, the lobes which we here regard as being the labial palpi. For one thing, we are unable to see why such a controversy should ever have arisen concerning a situation that seems to be so simple and uncomplicated! Crampton, in two papers (1923, 1925) especially, has reviewed the matter and stated the case for regarding these structures as the labial palpi. Snodgrass (Principles of Insect Morphology, p. 319) has set forth one last objection to Crampton's views, stating that while labial palpi "are typically provided with antagonistic muscles, the lobes of the fly labium have usually each only one muscle inserted directly upon it." But this last argument fails, for in *Panorpa nuptialis*, at least, the labial palpi have each but a single muscle.

The pseudotracheae in some flies present an extraordinarily complicated pattern, but in this species (Figure 73C) they are very simple.

The Pharynx (Figure 75A, B)

The pharynx in this species is very highly developed, forming a tubular structure in which apparently both dorsal and ventral walls are more or less sclerotized, and which extends almost to the occipital foramen. The ventral

floor is continued onto the oral surface of the labium as a narrow median plate. There is no evidence of a hypopharynx.

The Tentorium

In this species the tentorium is entirely lacking.

THE THORAX (FIGURES 76-81)

In common with most Diptera, the most distinctive feature of the thorax is the enormous enlargement of the mesothorax and the reduction of the metathoracic elements.

The Cervix (Figure 76)

The neck region bears on each side a large cervical sclerite which articulates anteriorly with the occipital condyle of the head and posteriorly with the episternum of the prothorax. Just below this sclerite is a very small, slender piece that probably represents the other of the usual pair of cervical sclerites.

The Prothorax (Figures 76, 78, 79)

The pronotum is relatively large and at the sides so fused with the propleurum that it is impossible to be certain where the parts merge. The episternum is rather well defined, as is the pleural fold, but the epimeron merges indistinguishably into the dorsal region. No trochantin is present. The sternum is quite large and expands behind the coxae into a somewhat sagittate area at the lateral borders of which are the very distinct sternal apophyseal pits. The sternite is folded lengthwise into an inverted V-shape. The pleural and sternal apophyses of the corresponding sides are closely fused and form continuous braces between the sternite and the pleurites.

The Mesothorax

While the mesothorax is enormously enlarged it presents no other unusual modifications. In fact the correspondence with *Panorpa nuptialis* is exceedingly close.

The notum (Figure 81) is diagrammatically clear and calls for no special comment other than to note the extreme development of the postnotum and its large lateral extensions which form broad laterotergites.

The only difficulties in regard to the pleural elements have to do with matters of terminology and not with questions of homology (Figure 76).

The pleural fold extends directly from the coxal condyle to the apex of the pleural wing process. The epimeron is very large and is divided by a faint transverse fold or suture into a superior anepimeron and an inferior katepimeron. The latter is continued as a very narrow band around the posterior border of the coxal foramen to the ventral surface of the body, this band constituting the postcoxale.

The episternum likewise is divided by a depression or suture into a superior and an inferior piece. This depression is very probably the homologue of the pleural cleft seen in the Neuroptera (Ferris and Pennebaker, 1939). It has been called by others the anapleural suture when it occurs in the Diptera.

The identity of the piece immediately below the "anapleural suture" comes into question. It has been called in the Diptera the "katepisternum." If the reader will refer to the figures of the thorax of a Neuropteran presented in an earlier number of this journal (Ferris and Pennebaker, 1939), there will be found what is here considered to be the actual key to the structures of the thorax of the Diptera.

It will be noted in the figure of this Neuropteran (*Agulla adnixa*) that the pleural cleft sets off two parts, the superior anepisternum and an inferior piece which is in turn divided into a superior or anterior area and an inferior or posterior area by a line, there called the "pleural costa," which is the exterior indication of an internal ridge. This line rises at or close to the pleural fold and continues around to the posterior side of the body. In *Agulla* the inferior or posterior area occupies the greater part of the region between the coxa and the pleural cleft and it was regarded in this species as being the katepisternum. The area anterior to the pleural costa was regarded as the preepisternum.

However, it is evident, on comparing *Tipula* with *Agulla*, that in the former there has been a change in the relative size and importance of these two areas. The part called the anepisternum in *Agulla*, and which there forms a conspicuous feature of the lateral aspect of the mesothorax, is here relegated to the ventral side of the body while the part called the preepisternum in *Agulla* is here the conspicuous element of the lateral aspect.

A purely nomenclatorial difficulty is thereby introduced, which in part has its roots in an unsatisfactory basic terminology for these thoracic parts. The use of the term "episternum" for parts that fundamentally are not above the sternum and in fact in several Orders have nothing at all to do with the sternum is a survival from a point of view that is now unacceptable and that is morphologically unsound. There is also a problem of priority in usage.

We have elected here to use the terminology which was employed in the paper on *Agulla*. In this the large area just above and anterior to the mesothoracic coxa becomes the preepisternum. The small area posterior to the pleural costa on the ventral surface of the mesothorax becomes the anepisternum. The terms thus become absurdities—although the homologies are maintained—but if these terms are not employed it becomes necessary to introduce a new term for the area here called the anepisternum, thus confusing the matter still more.

The interpretation of the ventral elements of the mesothorax is merely an extension of the interpretation of the lateral elements.

If we turn to the ventral side of the thorax (Figure 78) we see that the part here called the preepisternum continues on without interruption to the median line where it meets its companion piece from the opposite side of the body, the meeting forming a sharp furrow. Close to the posterior border of this preepisternum is a line, which—if we compare this species with *Agulla* and *Panorpa*—is evidently the pleural costa. Posterior to this costa is a narrow strip which continues on and impinges upon the coxa against which it forms a ventral condyle. This strip is what remains to represent the large anepisternum of *Agulla*.

It seems to us that, considering this species in the light of the previous studies presented on *Agulla* and *Panorpa*, the morphological situation in *Tipula*—and in the remainder of the Diptera—is crystal clear.

We can not at all accept the opinion expressed by Snodgrass (Principles of Insect Morphology, p. 172) that "In the pterothorax of the higher Diptera for example, the more primitive sutures of the sternal as well as the pleural areas have become almost wholly obliterated, and secondary grooves appear which divide the skeletal surface into parts that have little relation to those in more generalized orders. The large ventral plate in *Calliphora* is evidently composed of the sternum, the precoxal bridges and parts of the episterna;....."

We hold that, except for the sternum of the prothorax, there is absolutely no sternal element visible externally on the thorax of any Dipteran that we have seen. We hold that in the Diptera, as in the Mecoptera and the Neuroptera, the apparent sternal elements of the pterothorax are simply the ventral portions of the original subcoxal segment of the leg, which forms—especially on the mesothorax—a complete or practically complete ring about the base of the coxa. We hold, furthermore, that there is absolutely nothing in the thorax of a Tipulid Dipteran that can not be homologized directly with the thorax of a Neuropteran. Work now under way on a specialized species indicates that this generalization may be extended to the higher Diptera as well.

We have then, in the mesothorax of Diptera, the persistence and the enlargement—in some cases, as in the Nycteribiidae, to the point of hypertrophy—of the anapleural arc of the primitive subcoxal segment of the leg, this arc forming what has commonly been misinterpreted as the sternum. The continuity of this arc is interrupted from its juncture with the pleural fold to the ventral coxal condyle only by the pleural costa. The pleural costa, however, is not a suture in the sense of being the line of meeting of two areas of sclerotization; it is merely the external indication of an internal ridge and it can be regarded as dividing the anapleural arc into nothing more than two minor fields.

The two primitive subcoxal segments are so closely appressed to each other along the median ventral line that in the normal position merely a suture-like line separates them (Figure 80A) but there is no actual fusion of the two subcoxae along this line. They can be separated, and when this is done we have the appearance of a deep infolding of the body wall along the median line (Figures 77, 80B, C).

Where then is the sternum?

In the opinion here adopted there is no indisputably sternal element present other than the sternal apophyses, which are set close together at the apex of the median infolding formed by the closely appressed walls of the subcoxae (Figure 77, Figure 80C). It is possible that the median line of this ridge is also of sternal origin—theoretically it should perhaps be so—but there is certainly nothing more than this that can be assigned to the sternum.

The ventral condylar process supporting the coxa arises then from an extension of the anapleural arm of the subcoxa and is not sternal as has been supposed.

The trochantin is lacking, but the minute patch of setae, which has elsewhere been called the "trochantinal signum," is present.

The Metathorax

The modifications of the metathorax are associated primarily with the reduction of the wings to halteres. The notum is little more than a high, ridge-like, transverse band, overlying the infolded postnotum of the mesothorax and extending between the bases of the halteres (Figures 76, 81).

The pleural elements, although reduced in size, retain the same relations as are found in the mesothorax. The episternum is produced upward into a pleural wing process, here supporting the haltere, and is continued downward as a narrow band around the anterior margin of the coxa to the ventral side of the body where it terminates in a ventral coxal condyle. The epimeron fuses dorsally with a lateral extension of the notum and is continued downward as a very narrow postcoxal band which does not meet the precoxal band.

The Legs (Figure 85)

The legs call for no special comment, except to note developments in connection with the coxal meron. This piece seems to be lacking in the first and third legs, but is highly developed in the coxae of the mesothoracic legs. Here it is a large piece, which still retains a definite connection with the coxa but shows indications of the tendency to become closely associated with the pleural (= subcoxal) elements of the thorax (Figure 76).

The Wings (Figures 82, 83)

We are not here especially interested in the wings and have made no detailed study of them. The terminology of the veins has been indicated in accord with ideas developed by Alexander.

The wing bases have been examined carefully. They seem to accord so nicely with the general plan of the axillary sclerites as elucidated by Snodgrass (Principles of Insect Morphology, p. 218, Figure 122) that no detailed

discussion is necessary and reference may be had to the accompanying figure (Figure 82).

The Halteres (Figures 84, 91A)

The halteres themselves are merely long slender stalks with a swollen apex and present no obvious structural differentiations throughout their length. At the base of the stem there are slight indications of longitudinal thickenings which might possibly be regarded as vestiges of the bases of the original wing veins.

The articulation of the halteres is shown in Figure 84. In spite of the great reduction of the metathoracic wings (the halteres) the axillary sclerites adhere surprisingly closely to the arrangement seen in the fore wings. Pleural and notal wing processes seem to be present in their normal positions and distinct axillary sclerites occupying the same relative positions as those of the fore wings are present.

THE ABDOMEN

The abdomen in both sexes is broadly attached to the thorax (Figure 76) and in both sexes comprises ten clearly recognizable segments, the eleventh in both sexes apparently being entirely membranous and fused with the tenth. The unmodified segments consist of a tergite and a sternite, with a narrow membranous area between in which are borne the spiracles. In both sexes spiracles are present only on the first seven segments.

Terminalia of the Female (Figure 86)

Unfortunately the homologies of the parts of the terminalia of the female in this species are somewhat obscure and if we were restricted to this species alone for investigation we would be at somewhat of a loss to answer certain questions. There are at hand, however, specimens of *Limonia sciophila* (Osten Sacken), a species that is especially favorable for aiding in an understanding of these parts. Let us turn to it first.

In this species (Figure 87) the last spiracle is on the seventh segment and modification of the segments begins with the eighth. Here the tergite is present, but short. The sternite is definitely present and is separate from the tergite, although it is articulated to the latter. From the posterior dorsal angle of the sternite there arises an elongated, blade-like lobe, the base of which is partially set off by a deep furrow from the remainder of the sternite, although there is no actual separation of the parts. The view is here adopted that this lobe is actually a gonapophysis.

The genital opening lies immediately dorsad and at the base of these processes, thus being between the eighth and ninth segments.

The ninth tergite is somewhat similar to the eighth, but at its lower, posterior angle there is a plate which is distinctly set off by a furrow and an internal ridge. This plate extends on to the ventral side of the body, continuing on across the venter in a narrow band, which lies just above the vulva, and meeting its companion from the other side. From the posterior margin of this ventral band arises a short, pointed and mostly membranous median lobe and from its base an apodeme extends into the body. The appearance of all this suggests very strongly the presence of a gonopod and reduced and fused gonapophyses.

The tenth tergite is definitely separated from the ninth and is elongated. At its apex on each side is a small, sclerotized marginal plate and beyond each of these plates is an elongate, curved, tapering and heavily sclerotized process.

The view is here adopted that the terminal processes are definitely the cerci and we are immediately plunged into the problems associated with these

organs. Snodgrass (1931, p. 92) has considered these problems at some length, although his conclusions are by no means as satisfactory as may be desired.

It is pointed out by Snodgrass that the cerci seem definitely to belong to the eleventh segment, but that they come commonly to be closely associated with the tenth segment and that the only muscles associated with them arise always from the tenth tergite and seem merely to be the ordinary intersegmental muscles. He has also pointed out (1933, p. 67) that in several Orthopteroid insects there is a small sclerite present between the base of the one-segmented cercus and the tenth tergite. He has shown reason to believe that this sclerite is a fragment of the eleventh tergite. He seems, however, to have missed the very significant fact that the muscles which have their origin on the tenth tergite in the Orthopteroids insert not upon the cercus itself but upon this little basal sclerite and in overlooking this he has overlooked a neat bit of support for his view that this sclerite belongs to the eleventh tergite. It is easy to understand how the ordinary intersegmental muscles extending normally from the antecosta of the tenth tergite to the antecosta of the eleventh become the muscles which activate an appendage of the eleventh segment—they still insert in morphologically the same position as before.

Turning back to *Limonia* we find a comparable situation. The muscles which presumably move the terminal lobes originate on the antecosta of the tenth tergite. They insert not upon the terminal lobes but upon the little plates between these lobes and the tenth tergum. We have a situation which is exactly the same as that found in a grasshopper or a cricket.

We may quite confidently assume that the terminal lobes of *Limonia* are actually the cerci and that the little plates at their bases are fragmenta of the eleventh tergite, and they are so designated in the accompanying figures.

Lying immediately beneath the anus (Figure 87C) is a weakly sclerotized plate divided medially into two lobes. These may be accepted as the "paraprocts," in other words as the sternite of the eleventh segment. There is no indication of a tenth sternite.

If with these facts in mind we turn back to *Tipula*, the situation there presented becomes quite clear (Figure 86). The gonapophyses of the eighth segment are more closely united with the sternite, so much so that they show but the faintest suggestion of any separating lines. The ninth tergite is quite small and is very closely fused with the tenth. The sternite and gonapophyses of the ninth segment are much reduced and have lost all connection with the tergite. The sclerotized fragmenta of the eleventh tergite, lying between the tenth tergite and the bases of the cerci, are lacking, this area being membranous, but the tergal muscles of the tenth segment insert in exactly the same place as in *Limonia*. The eleventh sternite is present and somewhat more strongly developed than in *Limonia*.

We may call attention here to the peculiar spermathecae (Figure 86B).

Terminalia of the Male (Figures 88, 89, 90)

In the male, as in the female, the seventh segment is the last to bear a spiracle. The tergite of segment eight is short, but presents no peculiarities. The sternite of segment eight, however, is very highly modified (Figure 88) and presents a set of detached lobes or fragmenta. At each posterior lateral angle there is a large, pointed, apically free lobe which is fringed with stout setae and the base of this lobe is produced somewhat toward the meson, forming a small plate which bears a great cluster of long setae. Medially there is a tongue-shaped lobe, free except at its base, which projects posteriorly over the base of the ninth sternite. That these structures are merely fragmenta of the eighth sternite is indicated by the musculature, which seems to include only the ordinary intersegmental muscles.

The ninth tergite is heavily sclerotized and forms the terminal plate of the dorsum (Figure 88). Its base is continuous on each side with a lateral plate that may be accepted as the sternum. On the ventral side this plate becomes extremely narrow (Figure 90B), consisting merely of the acrosternite, but

its lower posterior angle is produced posteriorly around the apex of the body (Figures 88, 89, 90). The apical region is broken up into fragmenta which are almost detached from the remainder of the sternite and the terminal fragmentum forms in this species a small, free lobe. In some other species this lobe becomes an enormous, sclerotized hook.

Along the dorsal posterior angle of the sternite there is attached a moderately large plate, which bears a branched structure that is commonly called the harpagone and is morphologically the style. It would appear that the plate which bears the style may be accepted as being at least a portion of the coxopodite. The arrangement of the muscles of the style suggests that perhaps a portion of the coxopodite is fused with the ninth sternite. The abductor muscle originates upon the apical plate, but the much larger adductor muscle originates upon what is here called the ninth sternite (Figure 90D). It is not possible, on the basis of material at hand, to be certain as to just how much of these structures may be the coxopodite.

The tenth and eleventh segments form a small, cone-shaped and entirely membranous proctiger, which lies just beneath the apex of the ninth tergite.

The genital structures are really quite simple (Figure 88). Just beneath the proctiger is the external opening of an invaginated sac. In the dorsal wall of this sac is formed the heavily sclerotic basal bulb of the penis. In its normal, inactive position, the penis itself arises from the anterior end of this bulb. The penis itself is sclerotic and suggests a delicate piece of wire. Through the basal half of its length it is perhaps imbedded in the wall of the sac; its apical half is certainly free. It apparently has some of the qualities of a wire spring and keeps the genital sac stretched by its pressure. Its apex passes through a groove on the dorsal side of a heavily sclerotized structure that is probably formed by the fusion of two lateral parts (Figures 88, 89). This structure seems to have originated as a sclerotization of the membrane between the ninth and tenth segments and may be regarded as a hypomere. A very small, somewhat Y-shaped piece lying in the membrane above the opening of the genital sac may be regarded as the epimere.

It is evident from this that the principal complications in the terminalia of this species are not in the genitalia themselves but in the surrounding structures.

The Spiracles (Figure 91B, 91C)

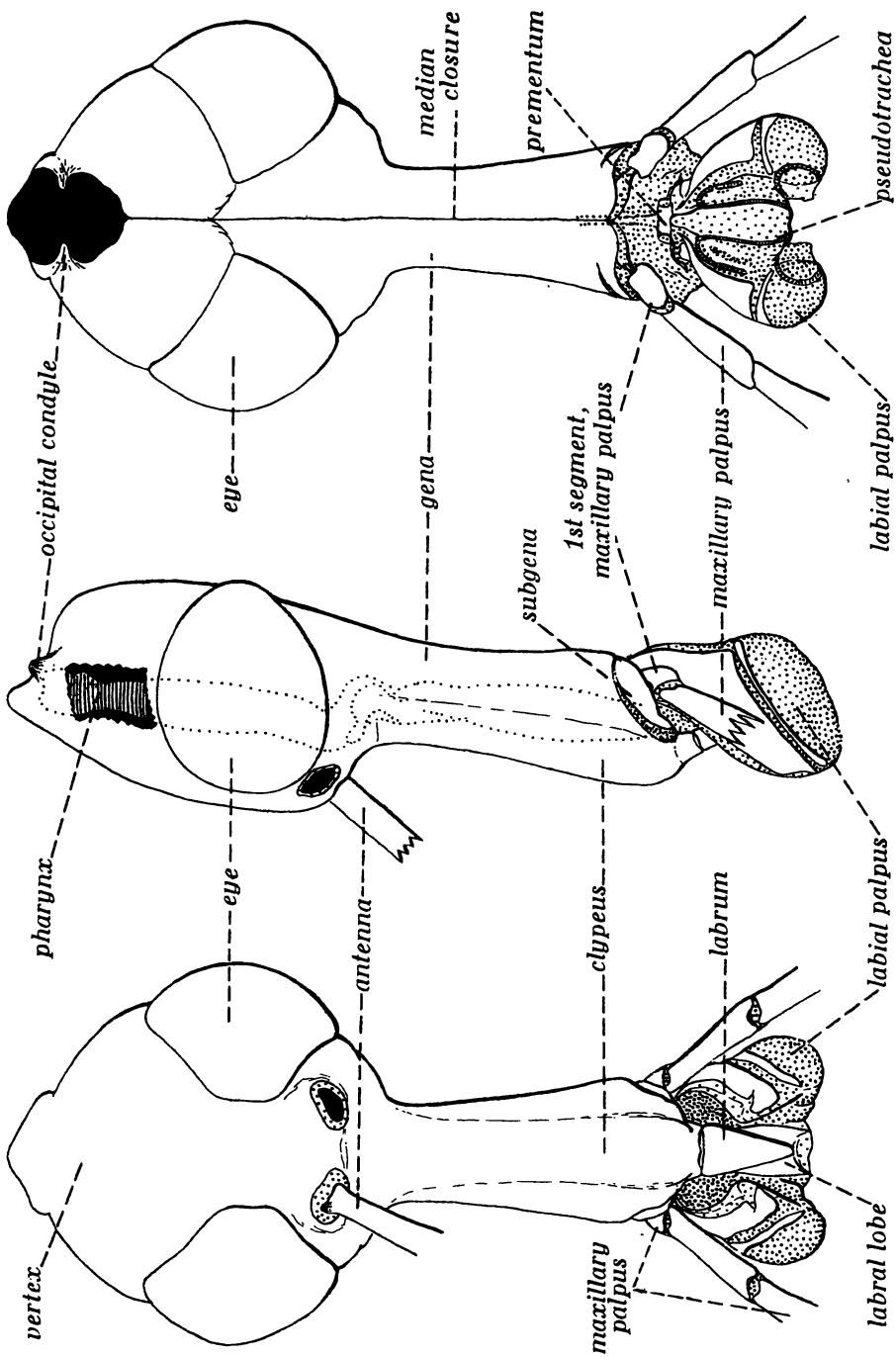
The thoracic spiracles (Figure 91B), while large, seem to be little more than simple slits leading into the tracheae and entirely lack the filter apparatus which reaches such an extraordinary development in the higher Diptera. On the abdomen spiracles are present on the first to seventh segments in both sexes and are situated in the membrane between tergites and sternites. The spiracles (Figure 91C) are very simple and present no features of special interest.

SOME GENERAL CONSIDERATIONS

By G. F. Ferris

Reflection upon the problems associated with the structure of the thorax in this species has led to the development of certain ideas which seem worthy of presentation.

It seems quite evident in considering the thorax that the prevailing concepts of its structure have arisen largely from a contemplation of Orthopteroid forms. This situation is due probably to two circumstances. One is the practical—but from any scientific point of view entirely extraneous—fact that the Orthopteroids include many large forms in which the structural elements

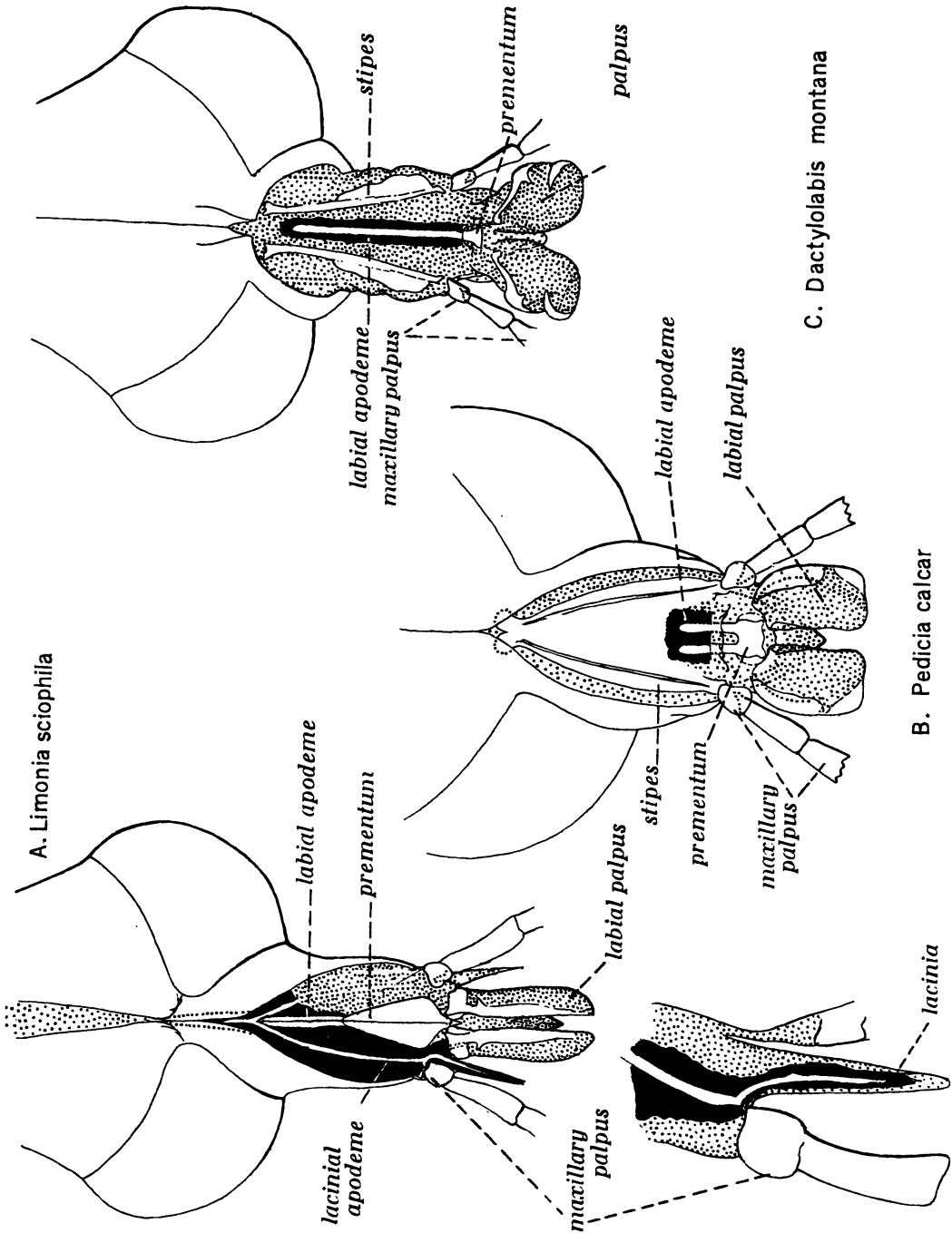


Tipula reesi, head

Figure 72

Tipula reesi, mouthparts

Figure 73

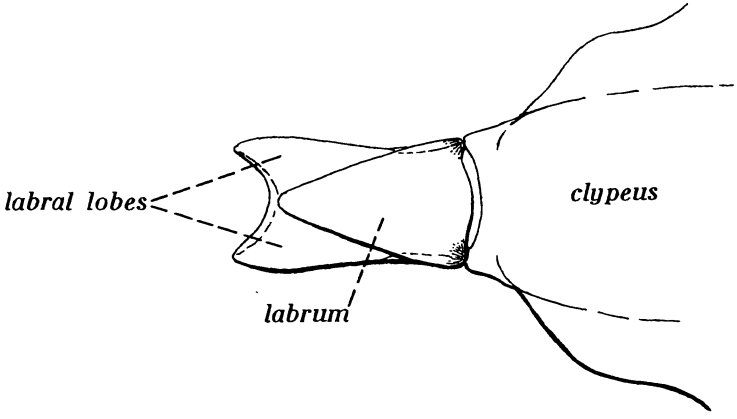


Tipuloidea, mouthparts

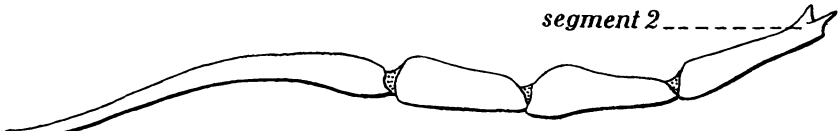
Figure 74

A. pharynx, lateral aspect

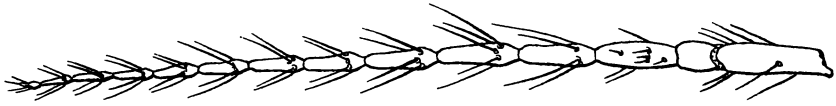
B. pharynx, dorsal aspect



C. labrum, aboral aspect



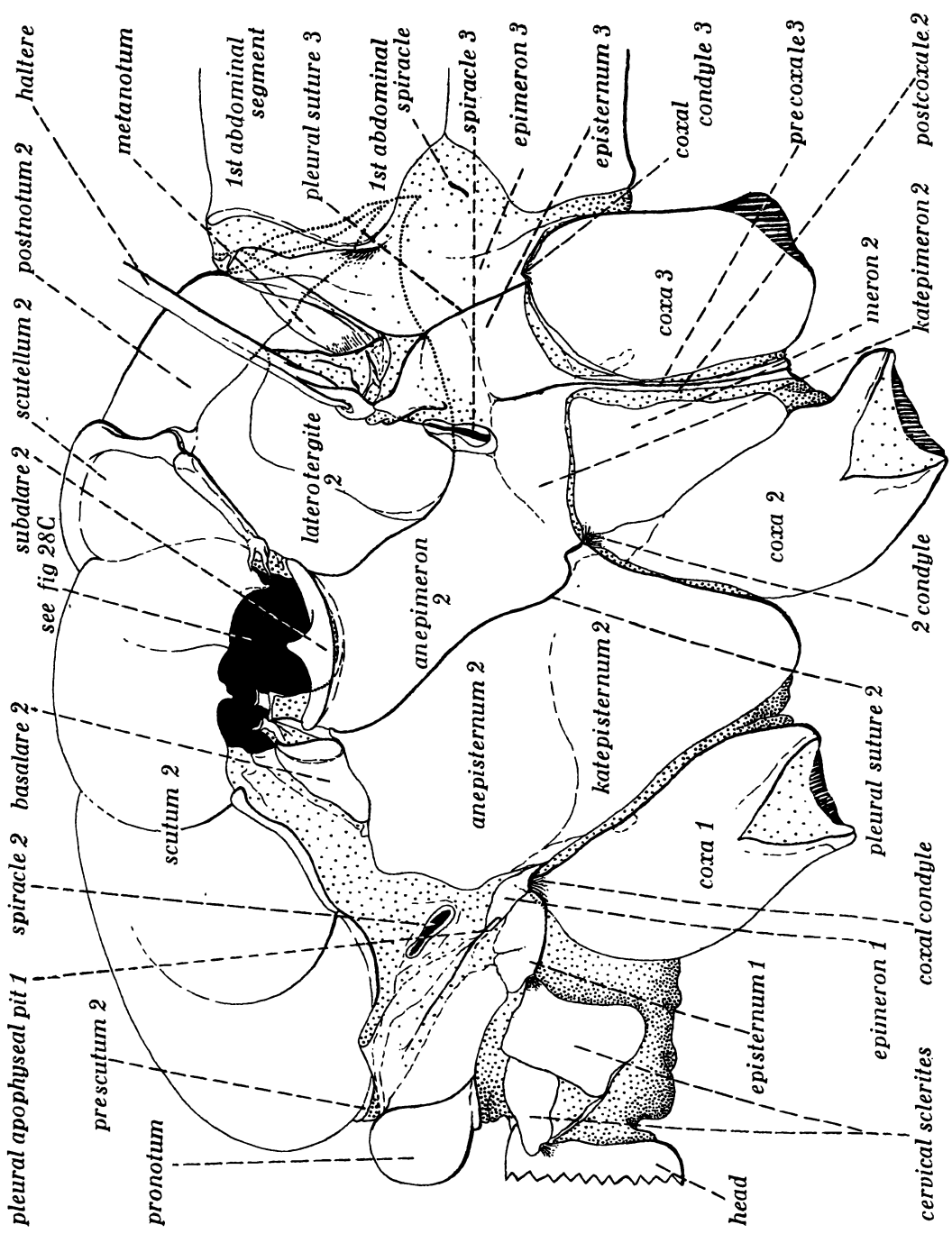
D. maxillary palpus



E. antenna

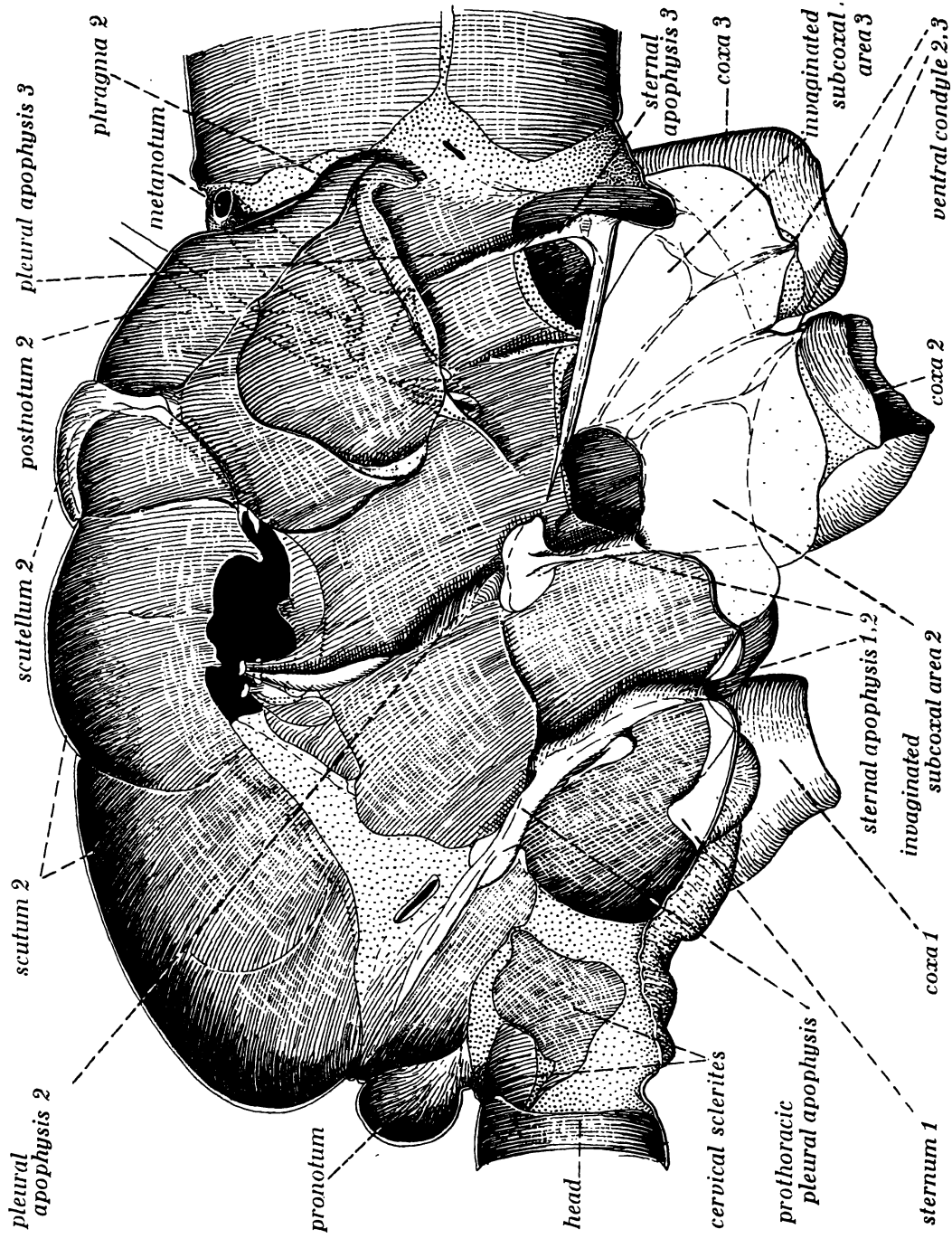
Tipula reesi, head structures, details

Figure 75



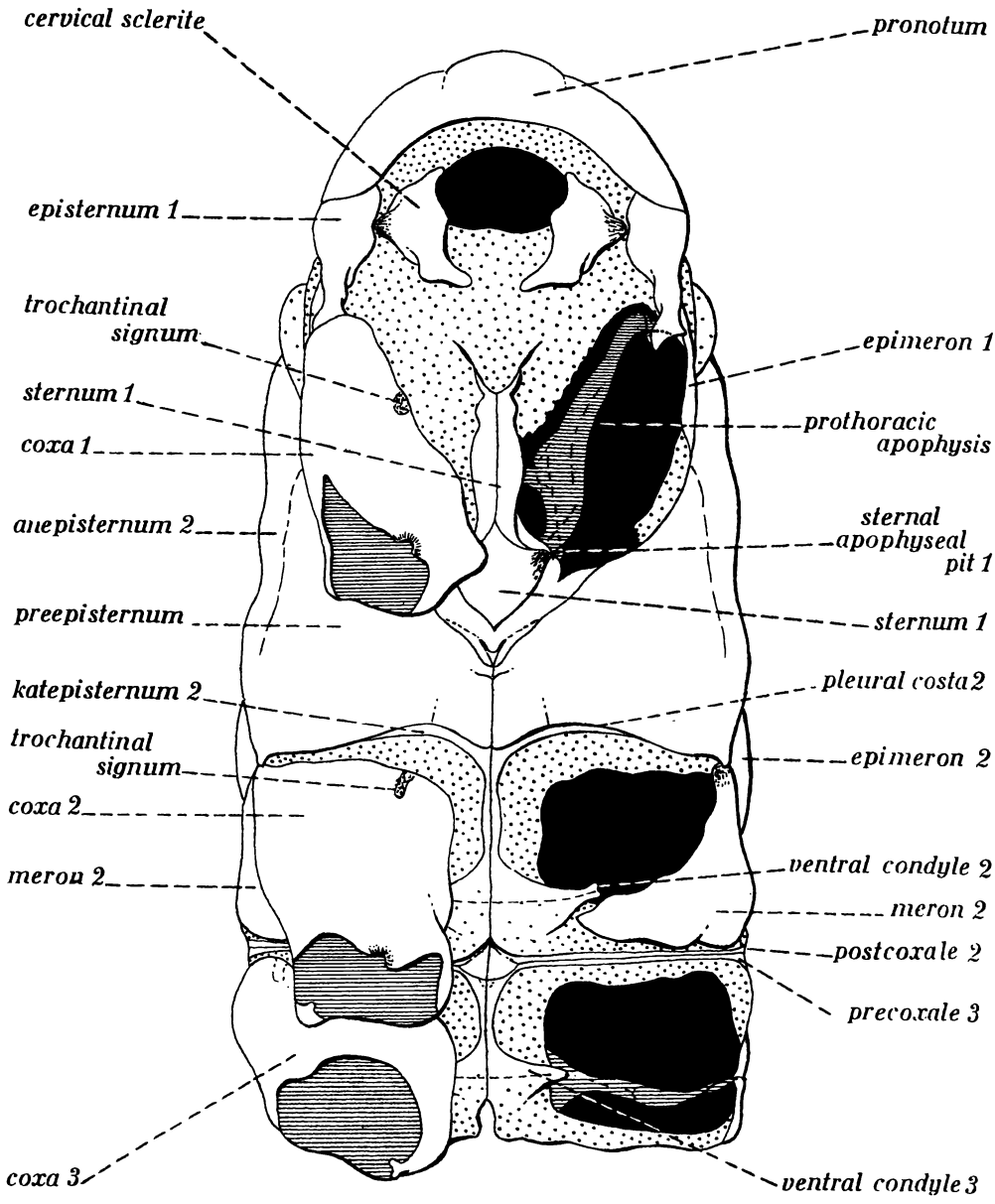
Tipula reesi, lateral aspect of thorax

Figure 76



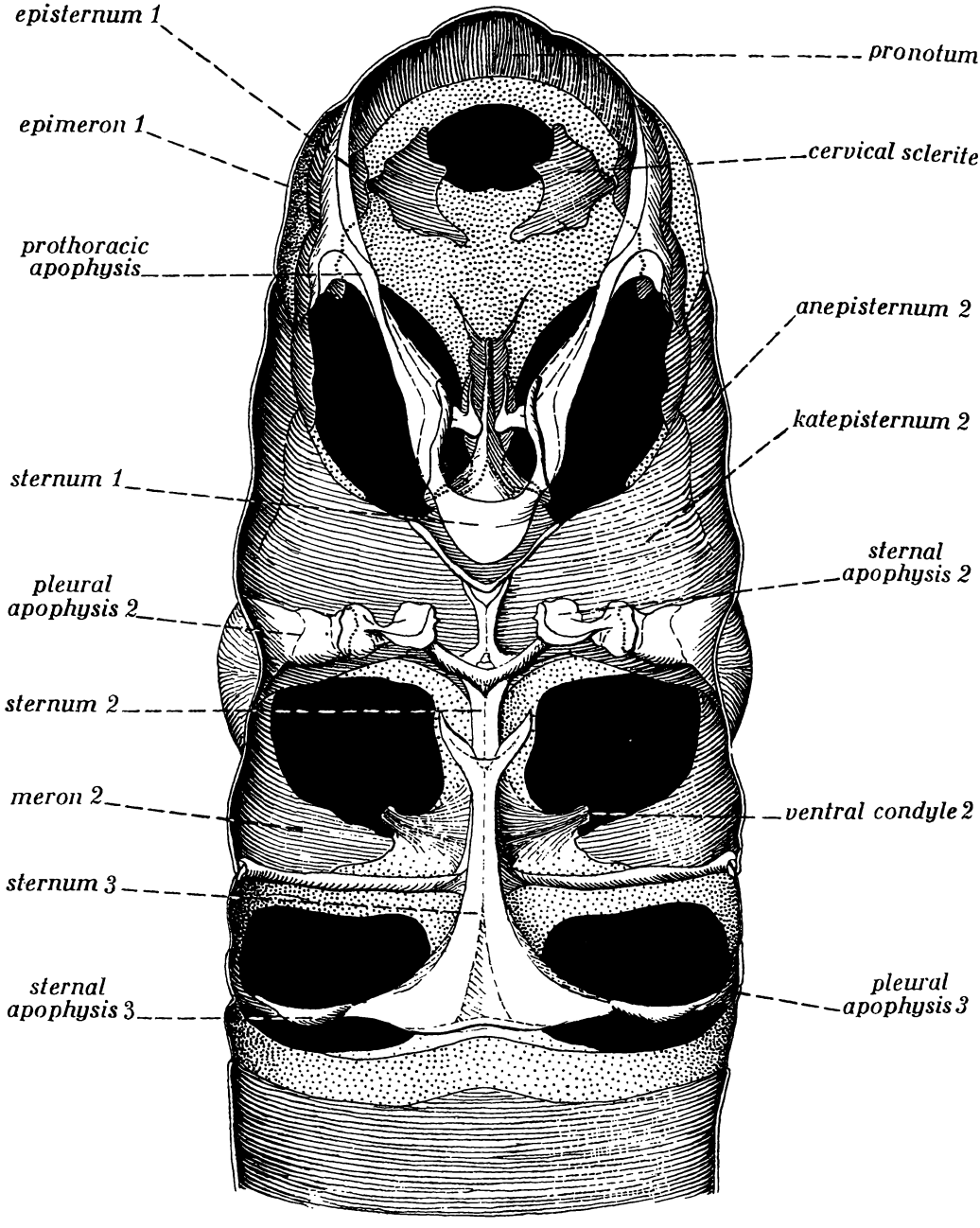
Tipula reesi, internal skeleton of thorax, longitudinal median section

Figure 77



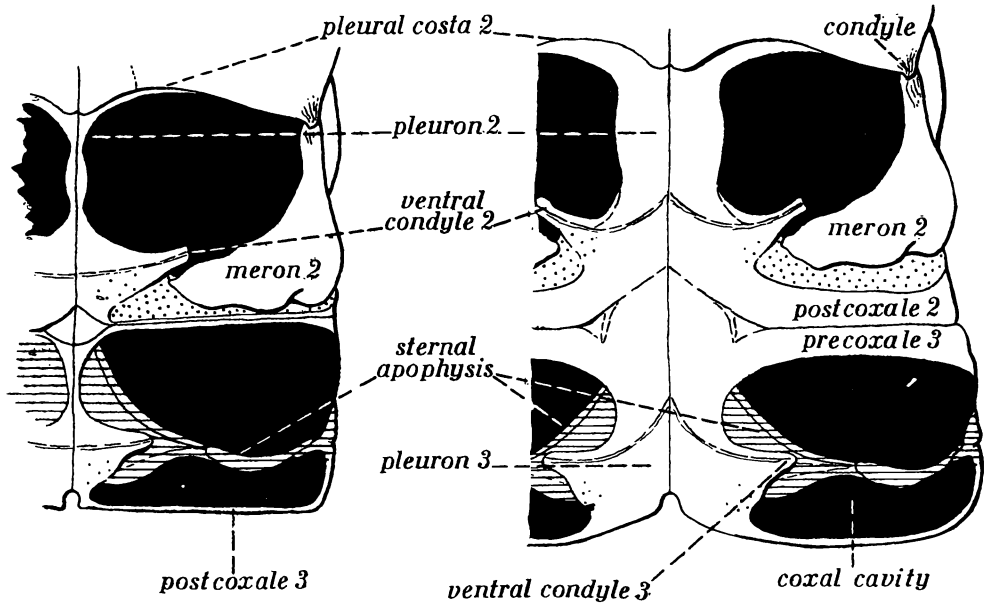
Tipula reesi, ventral aspect of thorax

Figure 78



Tipula reesi, internal skeleton of thorax, dorsum removed

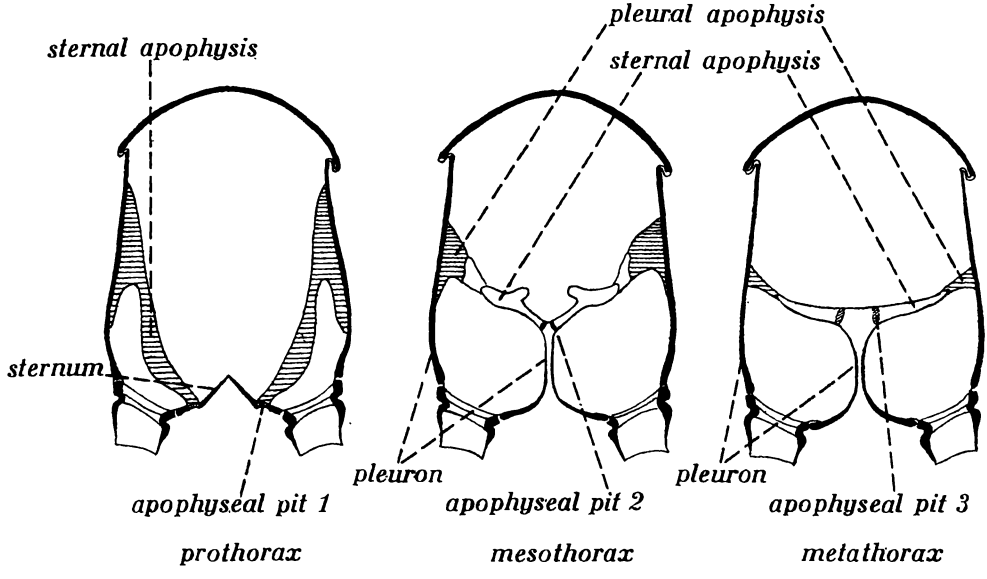
Figure 79



A. normal position

B. expanded position

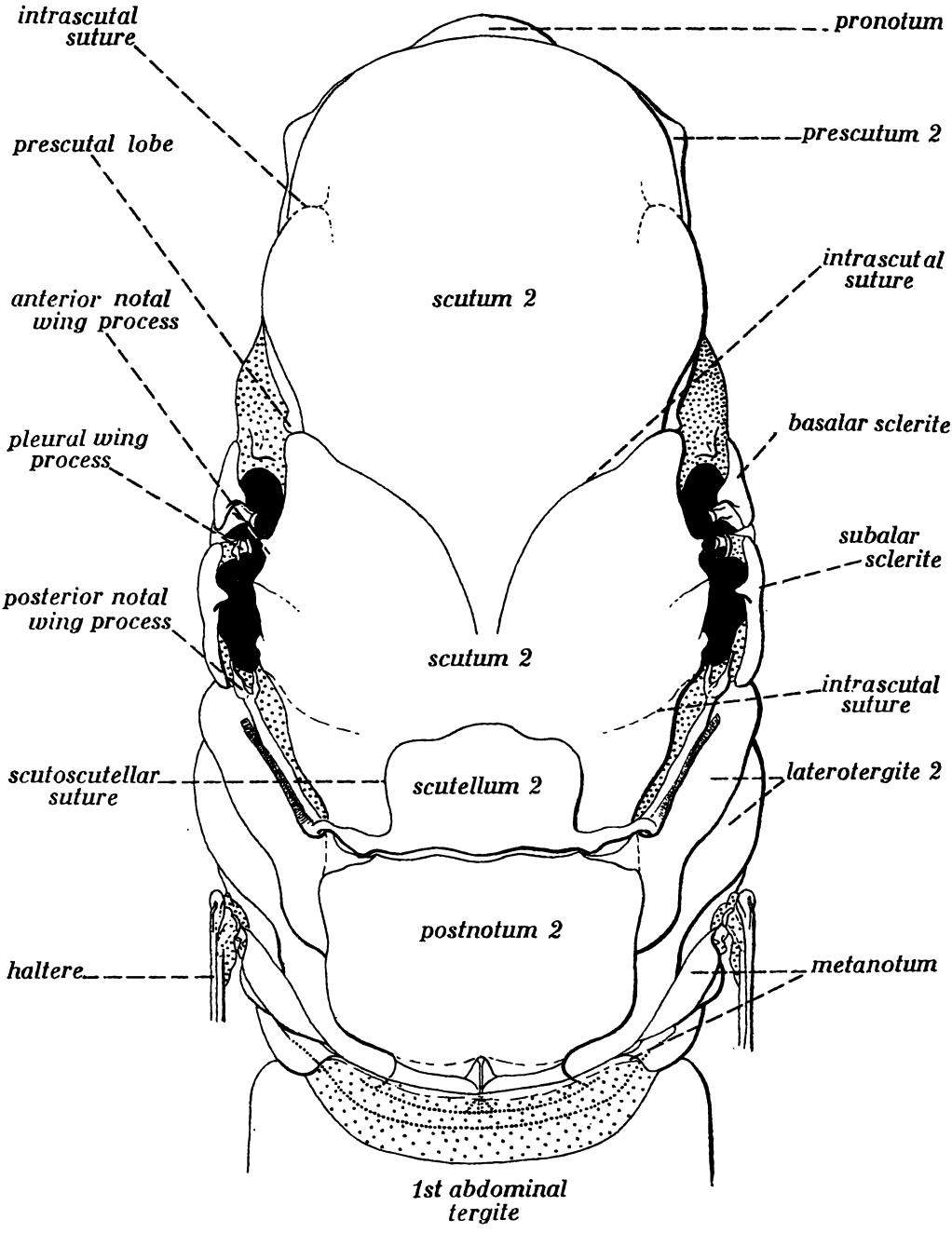
ventral aspect of pterothorax



C. diagrammatic cross sections illustrating sternal involution

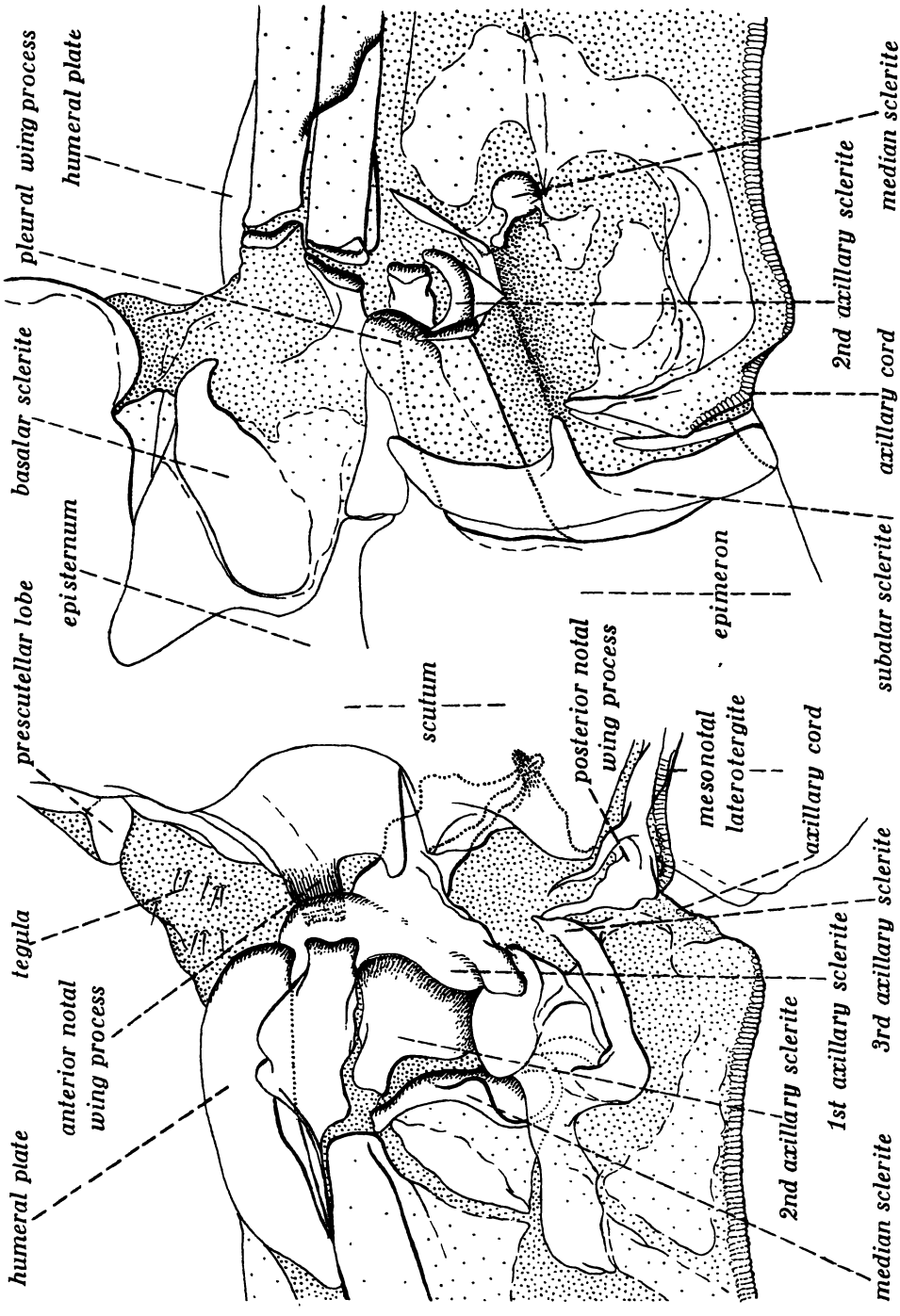
Tipula reesi, infolding of thoracic venter

Figure 80



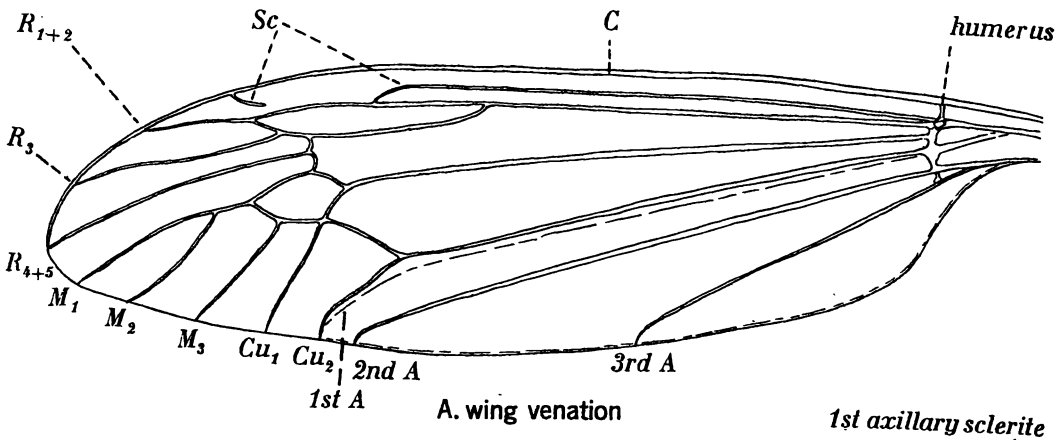
Tipula reesi ,dorsal aspect of thorax

Figure 81

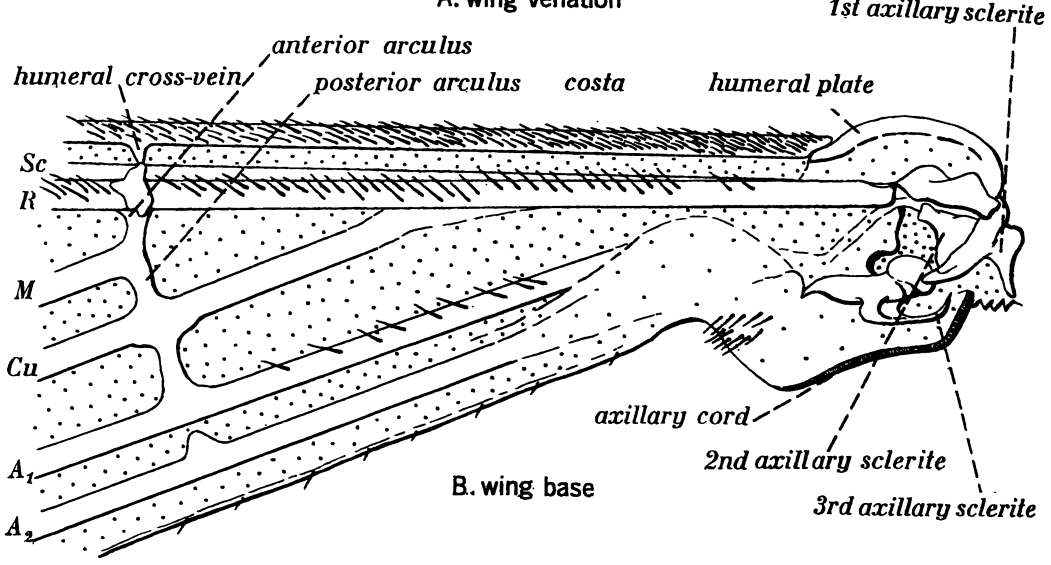


Tipula reesi, articulation of wing

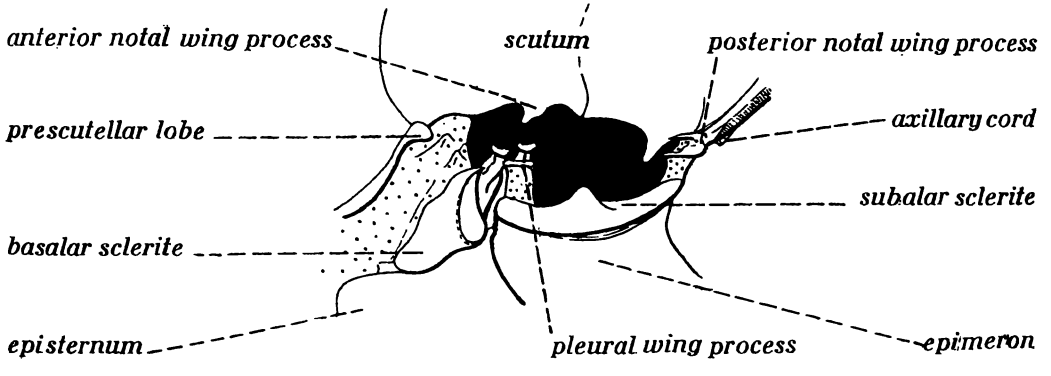
Figure 82



A. wing venation



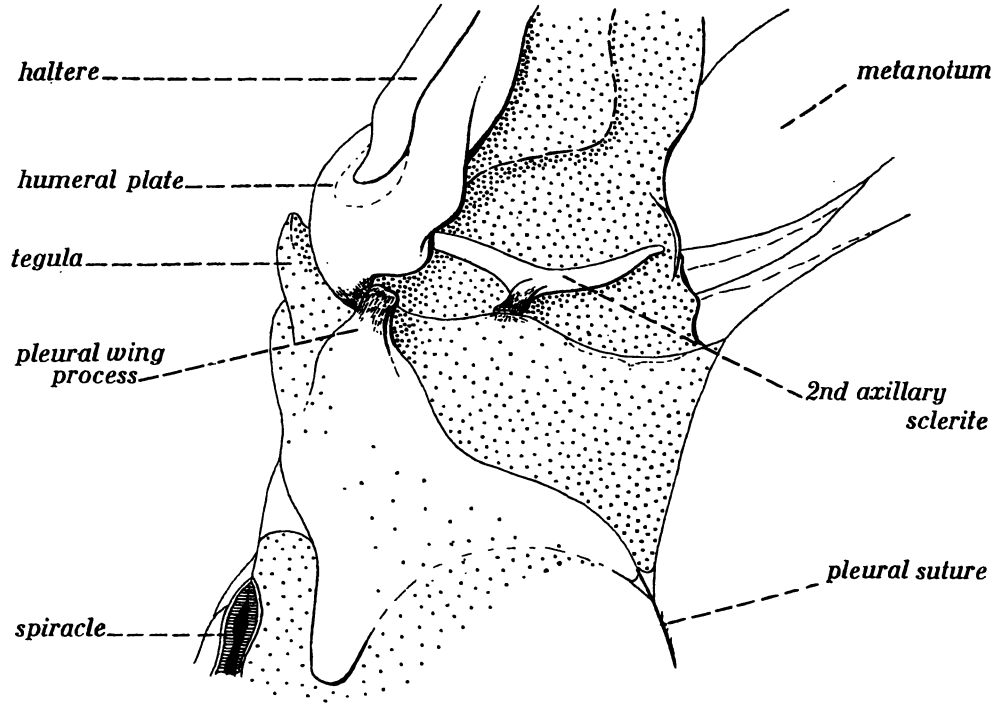
B. wing base



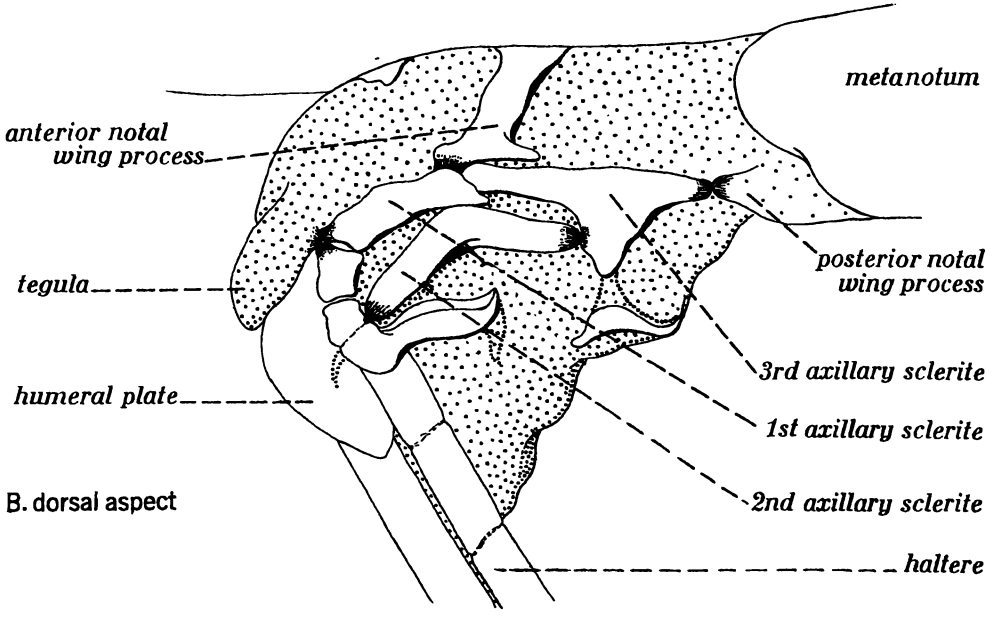
C. wing foramen

Tipula reesi, wing venation, wing base, wing foramen

Figure 83



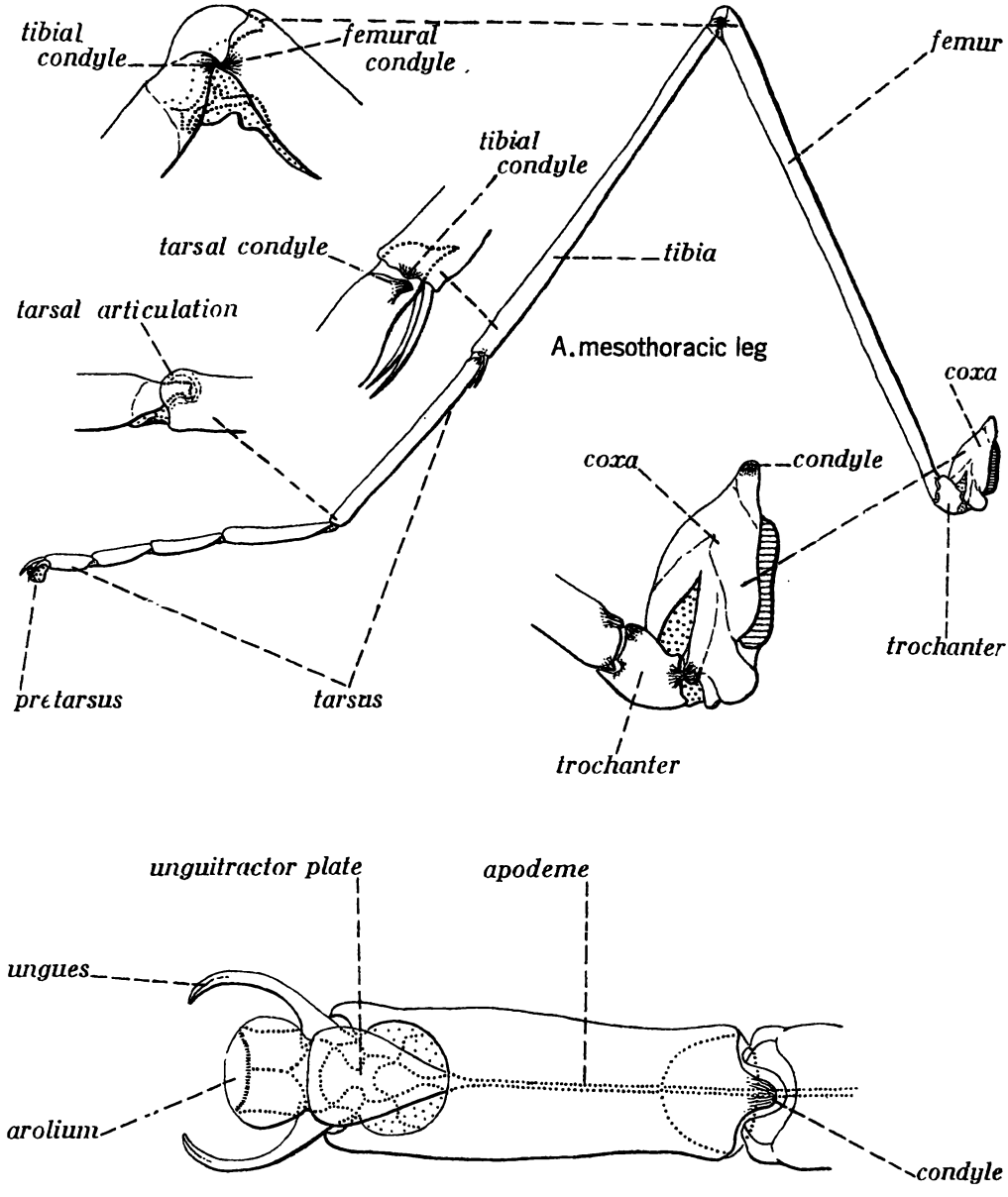
A. lateral aspect



B. dorsal aspect

Tipula reesi, articulation of haltere

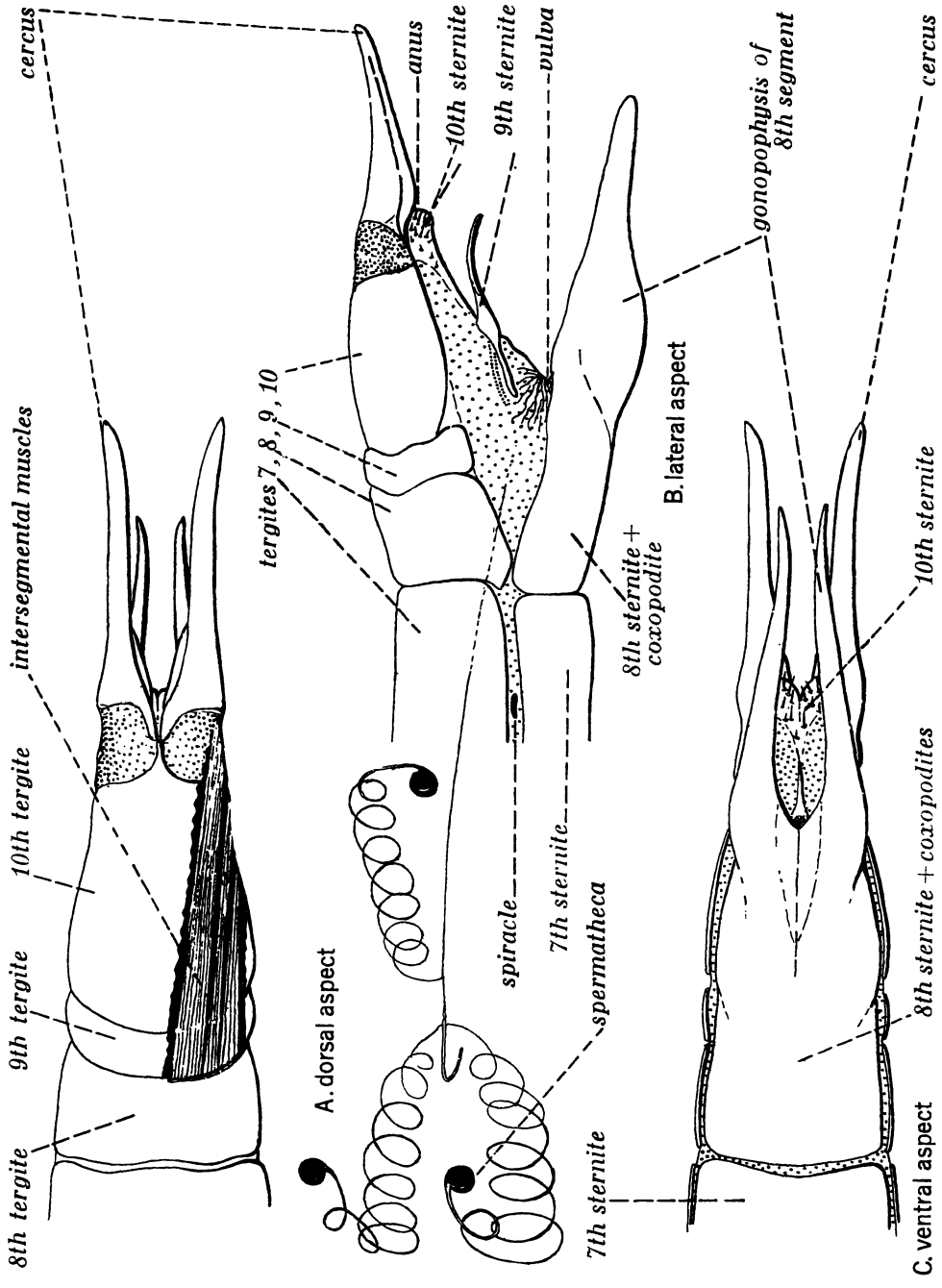
Figure 84



B. ventral aspect of 5th tarsal segment and pretarsus

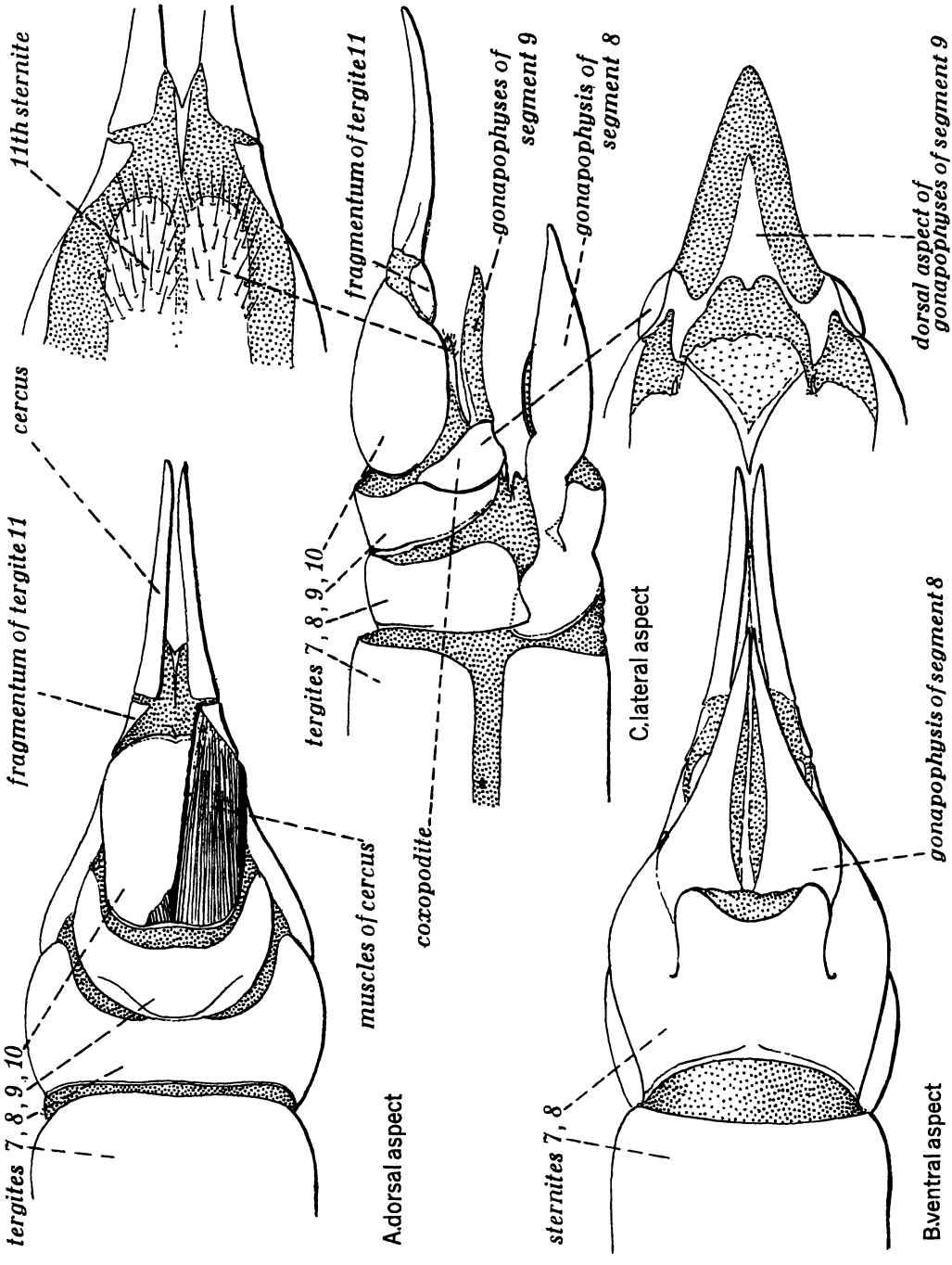
Tipula reesi, details of mesothoracic leg

Figure 85



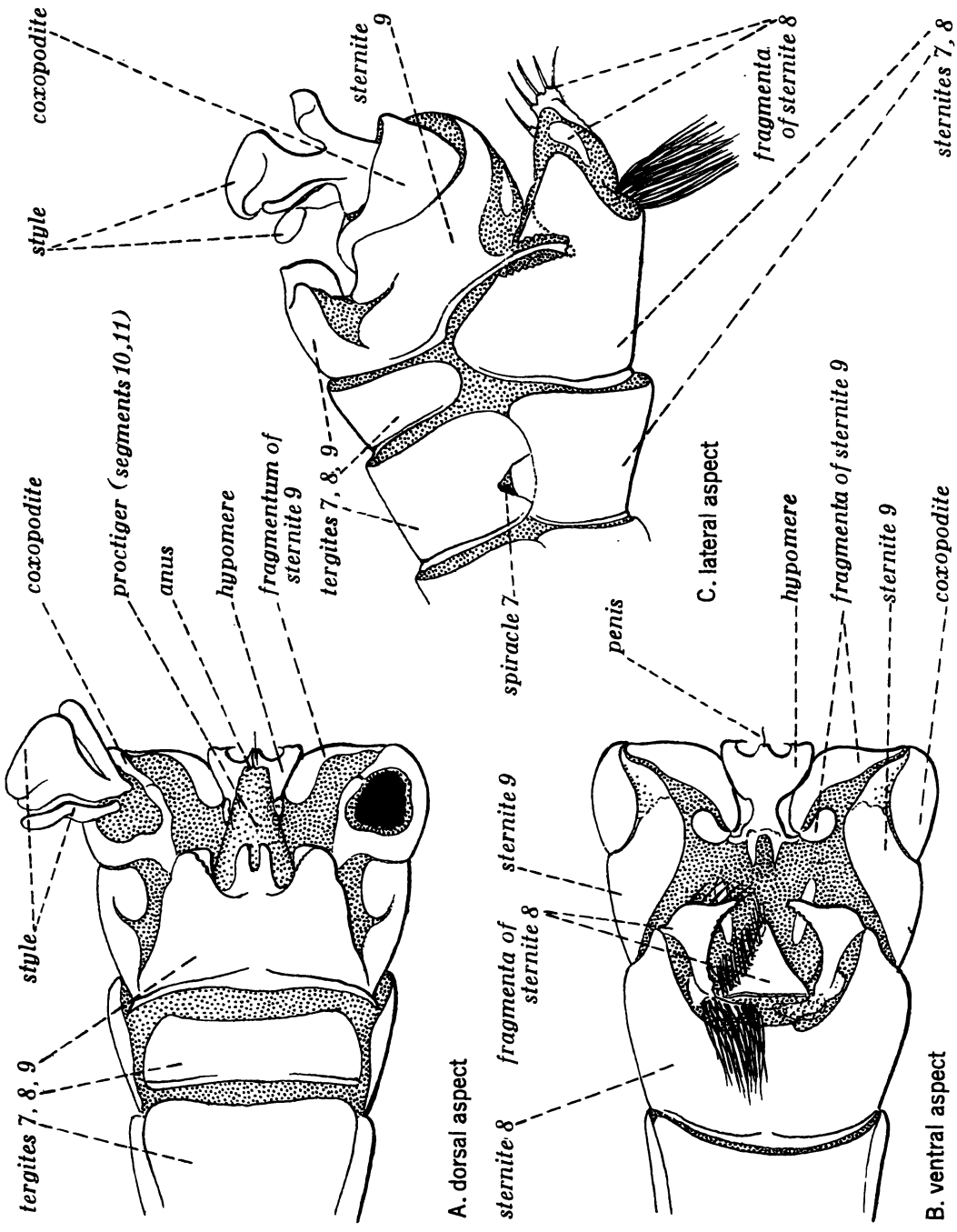
Tipula reesi, terminalia and genitalia of female

Figure 86



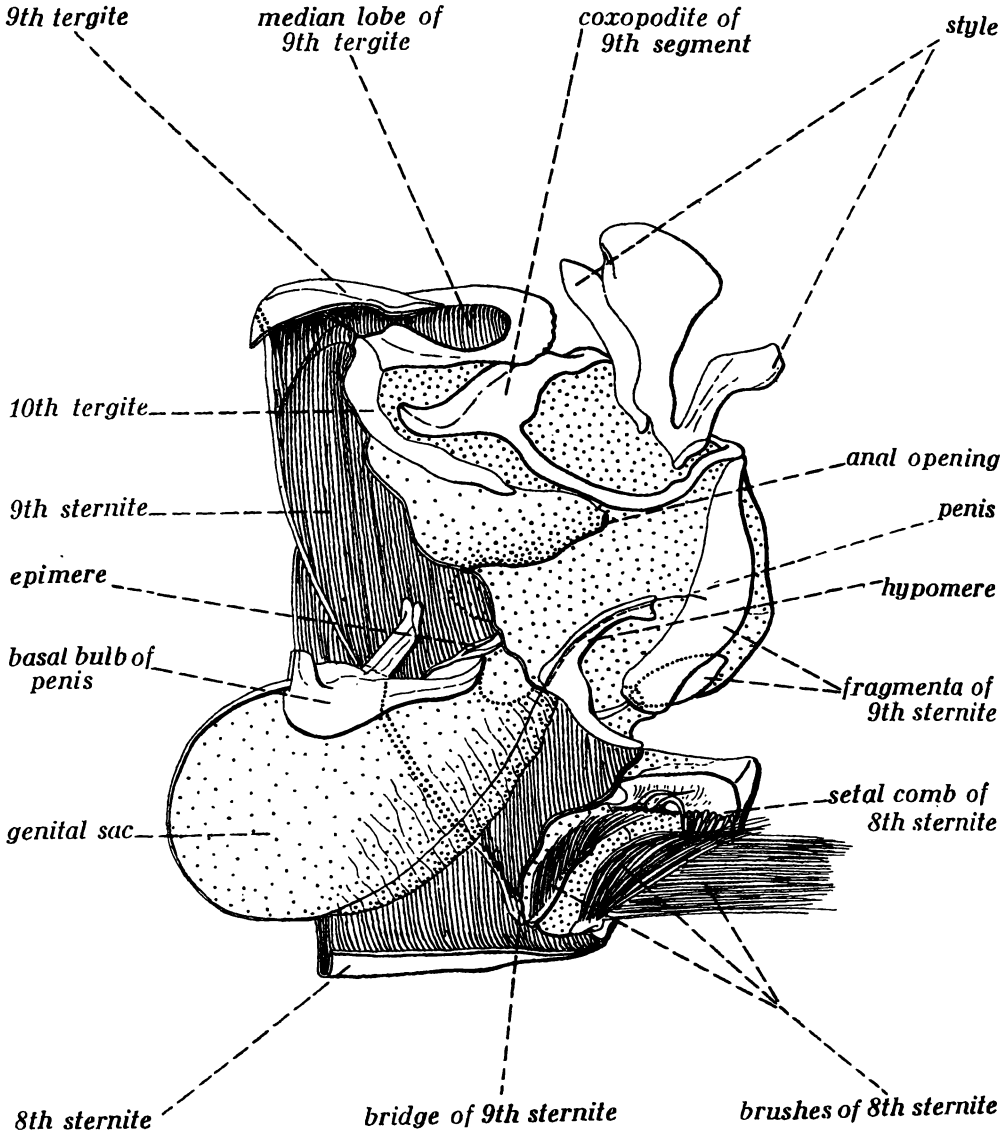
Limonia sciophila, terminalia of female

Figure 87



Tipula reesi, terminalia of male

Figure 88



Tipula reesi, terminalia of male, median longitudinal section

Figure 89

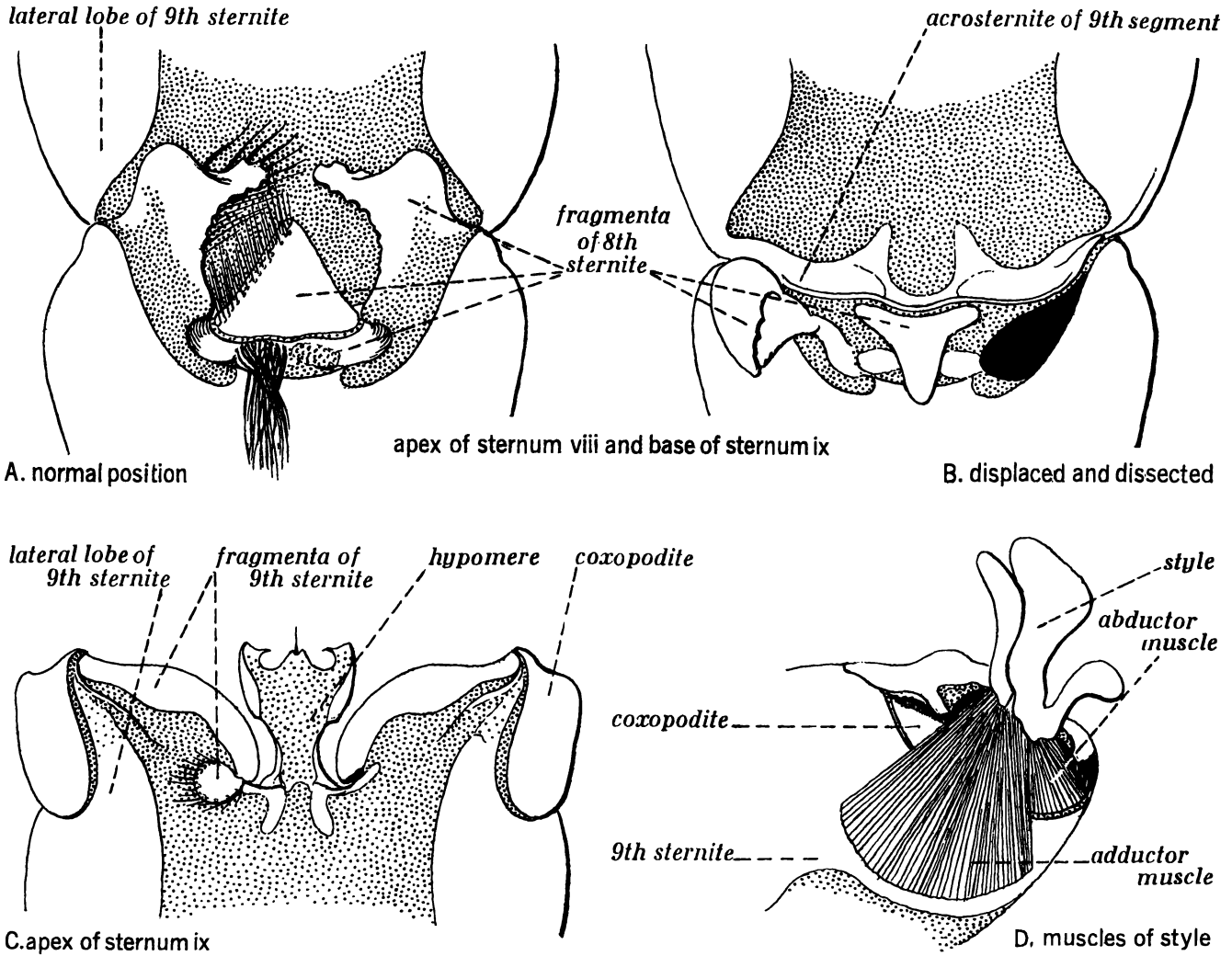
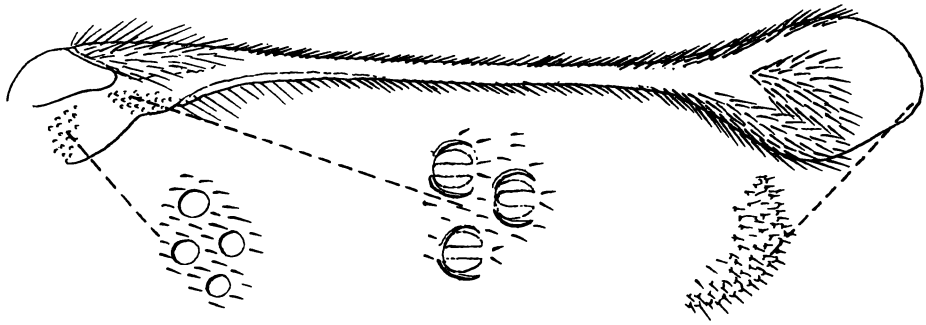
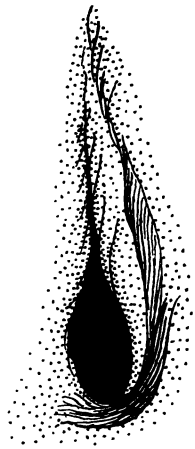


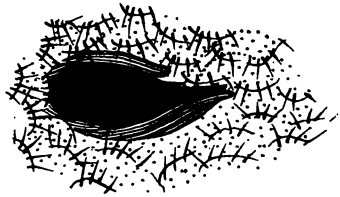
Figure 90 Tipula reesi, details of terminalia of male



A. metathoracic wing (haltere)



B metathoracic spiracle



C abdominal spiracle

Tipula reesi, haltere and spiracles

Figure 91