

## CHAPTER IV

## THE EXTERNAL STRUCTURE OF CICADAS\*

"Quam jucundo spectaculo, manus artifices caute et curiose acutissimum scalpellum et stylum pertenuem ducentes regentibus oculis, patebunt ista. Cicadarum rore victitantium fistula, atque striduli quem edunt soni per caniculae aestum viatorum aures importune obtundentis organa. . . ."

THEODORE DE MAYERNE, in Moufet, 1634,

*Epistola*, p. 5.

THE cicadas are among the largest insects included not only in the Homoptera, but in the whole order, Hemiptera. Their shape, with the body usually short and stout and the wings long or moderately so, is rendered characteristic by the short but wide head, with prominent compound eyes and conspicuous ocelli, frequently red in colour and arranged in a triangle upon the crown. The head may sometimes be produced, but never to such an extent as in the Fulgoridae—the only other Homoptera nearly rivalling the larger cicadas in size.

The first pair of legs shows great swollen spinose femora; while the wings, though strong, are usually transparent; but in some opaque and highly coloured. The venation is comparatively primitive and simple, with in addition, an ambient vein cutting off a fairly wide border.

The males of all save one genus possess a complicated sound-producing organ in the first abdominal segment, while both sexes are furnished with the most complex chordotonal or auditory organ known, housed in a swelling on each side of the second abdominal segment.

**The integument.**—The integument of cicadas is generally well-chitinised. The cuticle may be, rarely, entirely smooth, or covered with pubescence or pilosity. The pubescence is often fine, close, and continuous, and may completely obscure the colour beneath. Silvery or gold markings formed by patches of pubescence are frequent. Pruinosity is less frequent than in Fulgoroidea or in Sternorrhyncha. It is usually confined to the immediate neighbourhood—often a mere rim—of the more posterior abdominal spiracles, but may occur in larger patches elsewhere. Nevertheless waxy

\* A more detailed account of cicada morphology has recently been published in the *Proceedings* of the Zoological Society of London. Myers, 1928.

material may exist as an extremely thin and practically imperceptible covering over the whole of the body surface, as Fumouze (1888c) found in *Tibicen plebeia* and in *Huechys sanguinea* by the use of chemical methods.

Pilosity is associated chiefly with altitude. Among those New Zealand species of *Melampsalta* which enjoy a considerable range in altitudinal distribution, there is a clear correlation between elevation and hairiness. Alpine or subalpine species, however, are nearly always more hairy than closely related lowland forms. *Tettigarcta crinita* Dist., perhaps the most profusely hairy of known cicadas, occurs on Mount Kosciusko at an elevation of 5000 feet, according to Ashton.

The colour pattern of cicadas contains usually two elements—an arrangement of dark cuticular markings on a paler hypodermal

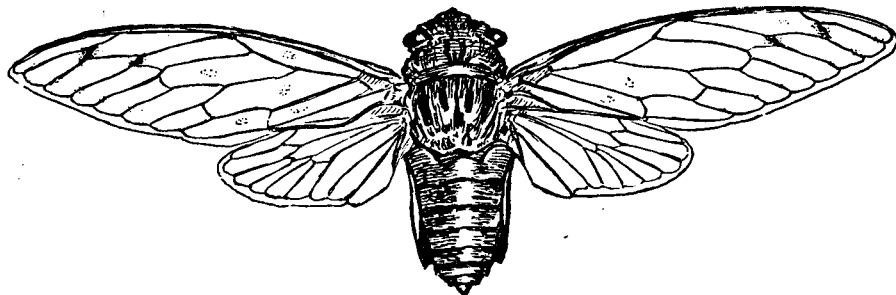


Fig. 4. *Cosmopsaltria moultoni* China. Male from Malaya.

M. T. Atkinson del.

ground colour. Sometimes one will predominate, sometimes the other.

Metallic colours would seem to be absent, but are occasionally simulated by pubescence.

An interesting study of the pigmentation in *Magicicada septendecim* has been made by Gortner (1911). He remarks that the rapid change from the pale-coloured, almost creamy nymph, to the deep black adult "presents one of the most remarkable changes in coloration" of which he is aware. From his earlier work on the pigmentation of the meal-worm (*Tenebrio molitor*) he had expected to find that this change in colour was an oxidation, induced by the action of an oxidizing enzyme, and his expectation was fully realized, although he found important differences. The colour "is due to the action of a tyrosinase acting on some aromatic amino phenol producing, as a result of the reaction, a black insoluble pigment. There was no difference in the intensity nor rapidity of colouration in insects kept, during and after moulting, in strong light, dim light, total darkness, or light filtered through blue glass. Inasmuch as the

colouration is a uniform black over the entire surface, Gortner makes the interesting suggestion that the entire new cuticula is formed by the reaction between the oxidase and the chromogen, in the same manner that the Japanese lacquer is formed by the action of laccase on the milky latex of the tree *Rhus vernicifera*."

The wings are usually colourless, but in some cases opaque and brilliantly coloured. Graf von Linden (1901) has studied the wing-markings especially in some of the species of *Platypleura*, which show spots and streaks. She finds the markings are always determined in position either by the position of the veins themselves or of the minute cross-folds which are visible in certain lights and which she believes to be relics of a close net-veining.

It is unfortunate that almost the only two cicada species on which the chemists have worked, were, from the pigmentation standpoint, highly anomalous. Fumouze studied the red medicinal cicada, *Huechys sanguinea*, of the Orient. This species is coloured a striking red and black, and possesses in addition an unpleasant smell, and thus belongs to the forms commonly regarded as protected and advertised by "warning colouration." Fumouze (1888b) isolated from it a red pigment—*rouge d'Huechys*—which gives the colour to the abdomen, and a yellow hygrometric substance.

**The head and its appendages.**—Aristotle believed that cicadas lacked a mouth, or rather that the mouth and tongue were united, so as to form a single part, through which, as through a root, the fluids on which they live are sucked up (*De Part. Animal.*, lib. IV, 5). The Egyptians also saw the rostrum or "aculeus" and interpreted it as the plectrum of the musical instrument (Horapollo, Valeriano Bolzani). Pliny (*lib. II*, cap. 37) quotes Nigidius to the effect that cicadas lack eyes—a statement which is repeated by Moufet (1634)—and is perhaps based on the lack of the wariness usual to cicadas and many other insects in the common European species, *Tibicen plebeia*.

In later days some of the most controverted questions in external insect anatomy have concerned the interpretation of Hemipterous head structure. Some member of the family Cicadidae has very often been the type studied, as in the case of Smith with his startling homologies in 1892, Marlatt (1895), Meek (1903), and Muir and Kershaw (1911a, 1911b, 1912). Writers on other families of Homoptera have often orientated themselves on the larger Cicadidae; thus Funkhouser (1917) and Doering (1922). The literature is therefore extensive, but in addition, the fact that Hemipterous head structure is remarkably uniform throughout both sub-orders, brings in as explanatory of cicadan conditions, interpretations based on other forms, and adds to the list such classical contributions as those of Geise (1883), Wedde (1885), and the more recent work of Bugnion and Popoff (1911) and Tower (1914). The latest treatment is by Snodgrass (1921, 1927) and by Muir (1926).

Viewed from the front the most striking feature is the large swollen transversely striated *frons* (fig. 5, fr.) of which the striations correspond with the insertions of the great dilator muscles of the sucking-pump. The upper edge of this sclerite passes into the crown

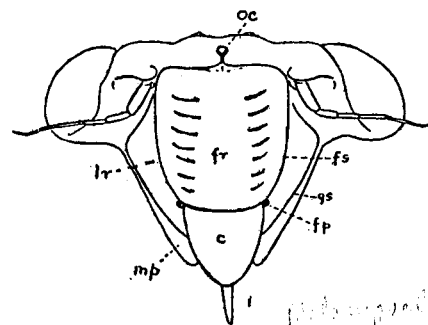


Fig. 5.

*Huechys sanguinea* Myers,  
New Zealand

or vertex from which it appears to be separated by a transverse fold rather than by a distinct suture. In the nymph at the final moult the split does not occur along this fold, but more caudally, along two sides of a wide triangle of which the fold in question is the base. This triangular piece, which bears the median ocellus in the adult, is apparently rather a part of the true frons than of the vertex. There seems no reason against considering the sides of the triangle as the arms of the *epicranial suture* (fig. 6, es).

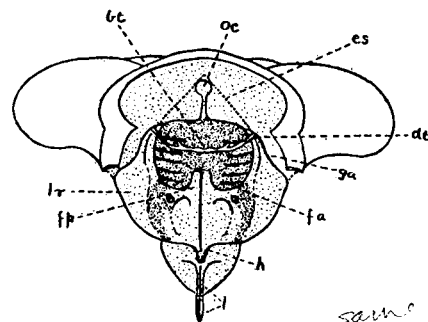


Fig. 6.

same

Posteriorly the crown passes into the occiput without further sutures. The paired ocelli are on the vertex just behind the arms of the epicranial Y. The compound eyes are large and protruding. The antennae comprise a shaft or peduncle and a whip or flagellum. The peduncle has two segments, the first hidden by the horizontal

antennal shelf, both simple, lacking sense-organs and considerably thicker than the first segment of the flagellum. The number of segments of the latter varies within close limits, but in *Melampsalta leptomera*, a fairly typical species, is six. These taper to the apex,

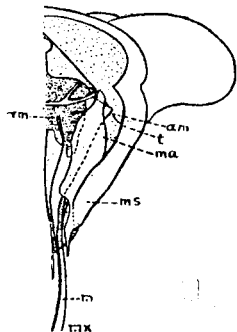


Fig. 7.

though in *Magicalada septendecim* especially, the apical one in a fresh condition may be somewhat swollen, while in the peculiar Argentine genus, *Semaiophora*, the last three segments are expanded and foliaceous. The sense-organs of the antennæ, to be described later, are confined to the flagellum.

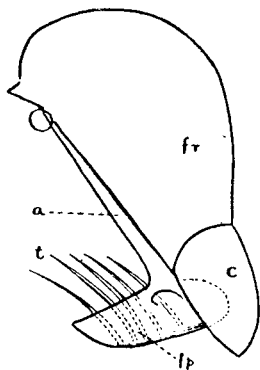


Fig. 8.

The lower margin of the frons passes into the clypeus (fig. 5, c), which is considerably flatter, with a more or less membranous structure arising from its inner surface and projecting as a narrow, grooved flap beyond its truncate apex. This structure—the labrum-epipharynx (fig. 5, l)—is throughout grooved on its inner surface for the reception of the mandibular and maxillary setae, which lie

basally between it and the closely appressed groove of the hypopharynx (fig. 6, h).

On each side of frons and clypeus is a crescentic *lorum*, occupying most of the true *genal* area or cheek (fig. 5, lr). Lateral to this in turn is a longer plate which it largely hides from facial view. This is the *maxillary plate* (fig. 5, mp) which apically meets the free extremity of its fellow to bound with it and the labrum a narrow pore through which the setae pass into the rostral furrow.

There are two pairs of mouth setae. The mandible is represented solely by a long stout seta (fig. 7, m) of the outer pair, and its fairly

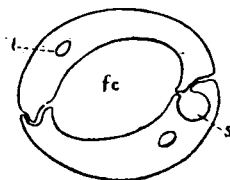
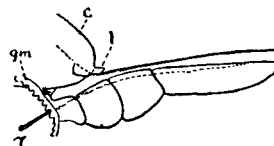
Fig. 9. *Melampsalta leptomera*

Fig. 10.

simple base. The mandibular setae are barbed at the tip and together loosely enclose the tightly conjoined maxillary setae within the rostrum. The maxillary setae are finer and intimately locked together, forming a watertight tube which is split with



Fig. 11.

difficulty and has often been described (e.g. by Buckton) as one piece. The lumen of the central tube is bounded on all sides by the inner walls of the maxillary setae (fig. 9), but the cross-section shows there are three holes enclosed also in the walls of the canal thus formed. Two are small, and are the lumina of these organs, allowing passage

of nerves and tracheae, which stand out as fine hairs when the setae are cut. The third passage is larger and is formed by a deep, nearly enclosed groove in one seta roofed over by the apposition of its fellow. The large central first-mentioned canal is for the passage of food, and the parietal canal for the ejection of saliva.

The labium forms the rostrum or sheath for the setae. In it three segments are recognisable, with signs of a fourth (fig. 10).

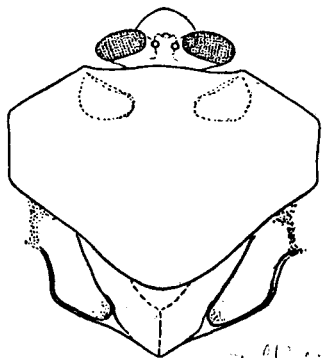


Fig. 12.

*Tettigarcta viridula* (Viel.)  
*phyllophaga*

**The thorax and its appendages.**—As in so many other characters, there is considerable homogeneity of thoracic structure throughout the family. A noticeable feature is the greatly enlarged mesothorax, and especially its notum (fig. 11), doubtless associated with the very

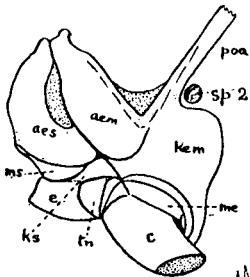


Fig. 13.

*Melampsalta sericea* (Waltz)  
*sericea*

stout and powerful fore-wings or tegmina. In the nymph on the other hand, the prothorax, carrying the musculature of the strong digging fore-legs, is much the largest of the thoracic segments; and such remains the condition in the adult of the queer, primitive *Tettigarcta*, where the hypertrophied pronotum (fig. 12) overshadows the much reduced mesonotum. In this archaic form the

tegmina are far weaker, without that massing of veins on the fore-border so characteristic of all other cicadas.

The only worker to deal especially with thoracic structure in the Cicadas is Taylor (L. H., 1918). We ourselves have studied *Melampsalta* (figs. 13, 14).

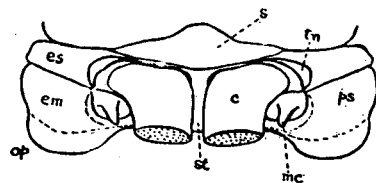


Fig. 14.

*Melampsalta rana*

In the prothorax the notum is curved down considerably laterally. Its *pleuron* is greatly reduced and practically fused with the notum. The *prosternum* is represented by a single plate.

The mesothorax, as we have seen, is the largest division of the normal cicada thorax. The anterior part of its notum projects beneath the pronotum, as an *anterior phragma* (*prophragma* of Berlese), almost to the occiput. The greater part of the notum is occupied by the *scutum*, but the *scutellum* is sharply and characteristically differentiated as the *cruciform elevation* of taxonomists.



Fig. 15.

*M. sericea*

On the pleuron the pleural suture is distinct and in addition there is a suture dividing the *episternum* into an upper *anepisternum* and a lower *katepisternum*. In the *mesosternum* both a *eusternum* and a *sternellum* are to be distinguished.

The metathorax is extremely short, especially dorsally. In the pleural region the *epimera* are produced backwards into sometimes very long sub-ventral plates forming the *opercula*, or lower covers of the sound-producing organs. The *metasternum* shows the same divisions as the mesosternum.

The subject of the internal or endo-skeleton of head and thorax is too technical to be treated adequately here.

The legs have been studied in detail by Hansen (1890). The prothoracic legs of the cicadas are highly characteristic both in the nymphal and adult stages. The femora of the former are much swollen and strangely modified for fossorial purposes; those of the later (fig. 15) are enlarged almost as much, and furnished ventrally usually with three stout spines. The coxae are very long, and the

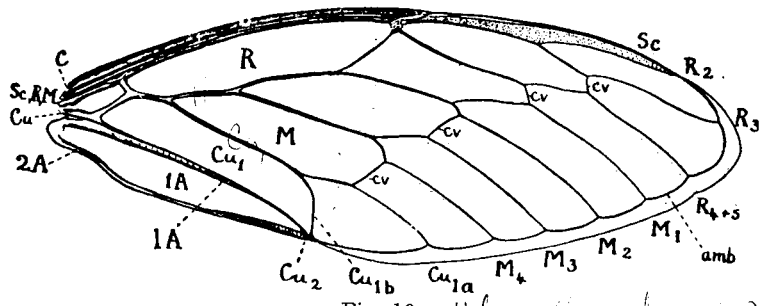


Fig. 16. *Melampsalta* (Fair)

trochanters thick, with a very oblique femoral articulation, producing a seesaw movement.

The second and third pairs of legs are unspecialised, with a probably primitive simplicity.

The tarsi are usually three-segmented as in all other Auchenorrhyncha, but cicadas differ in lacking any empodial formation. The claws are two—equal, stout, and simple.

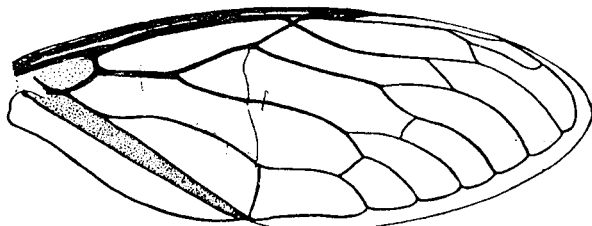


Fig. 17. *Chrysopa* (Fair)

In the universal habit of cicadas to rest habitually in a perpendicular position, whether the support be a tree, a herb, or a rock surface, we may see an explanation of the powerful fore-legs of the adult. The attitude is largely a suspensory one, in which the second and third pairs take little part, most of the weight falling on the first. A similar condition occurs in certain moths.

The wings of cicadas have been studied by Chabrier (1822), Amans (1885, 1915), Imhof (1901, 1905), Haupt (1913), Comstock

and Needham (1898), Woodworth (1906), Berlese (1909), and Horváth (1913). The first taxonomic division of the family was based, unsuccessfully as time has shown, on the venation of the wings.

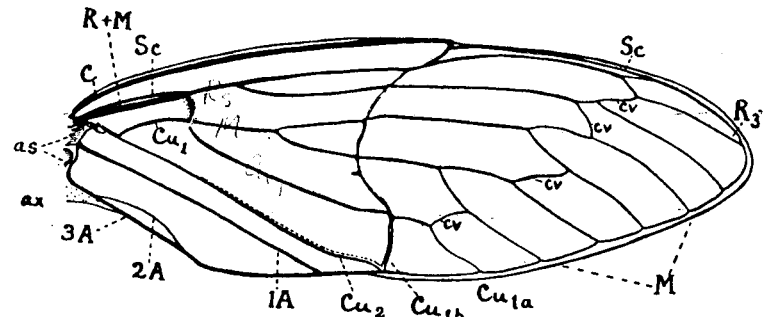


Fig. 18. *Attagorda crinita* Dist., Fresh

In our interpretation of the wing-venation we have followed, in company with Muir, Imms, Alexander, and many other workers, the Tillyard modification of the Comstock-Needham system of notation. The essentials of this will be more easily grasped from the illustrations (figs. 16-26) than from a lengthy description.

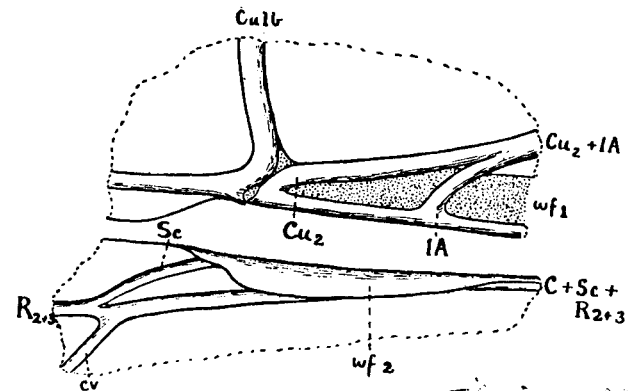


Fig. 19. *Tunica albissima*, N. Am.

The anal area is much more developed in the hind-wing than in the fore, and folds under the corium when at rest. Both tegmen and hind-wing are surrounded by a strong border, between the ambient vein (fig. 16, amb.) and the edge of the wing.

The main features of the venation, as figured in *Melampsalta*, recur throughout the family. Netveining of the tegmen—a character on which Amyot and Serville based the first classification of the

family, has almost certainly arisen independently in several different branches of the family, and occurs to-day in several quite unrelated genera—*Polyneura*, *Angamiana*, *Talainga*, *Hemidictya*, and others. The condition, moreover, in such a form as *Polyneura*, brought about by excessive regular dichotomy of the longitudinal veins, differs greatly from the meshwork of irregular cells found in the Hemidictyine forms.

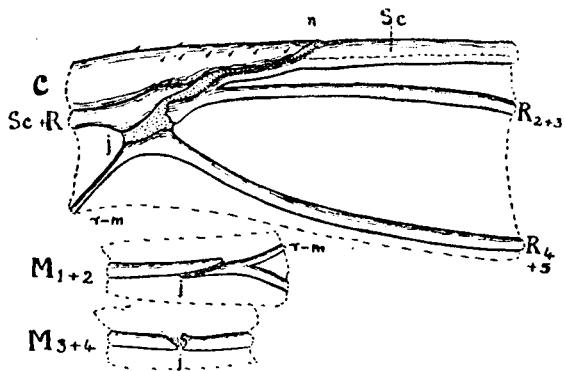


Fig. 20.

*Melampsalta muta*

*Lembeja* (fig. 24) and *Cystosoma* show a complete absence of the coriaceous border of the tegmen, the ambient vein corresponding with the wing-margin, which it slightly thickens.

More fundamental differences in venation occur in *Tettigarcta* and in the *Tettigadinae*, which show between them a gradation

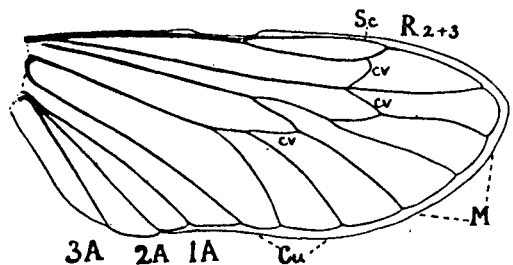


Fig. 21.

*Tettigarcta muta*

leading up to the specialised condition of the dominant and more typical cicadas. *Tettigarcta* is at the very base of the Cicadidae and is extremely primitive in far more respects than absence of sound-organs, and not least so in venation, as the figure (fig. 18) will show.

A striking and peculiar feature of the tegmen of the fossil *Mesogeron* and of all cicadas except *Tettigarcta*, is the presence of numerous cross-ridges, especially visible in certain lights and interpreted by Von Linden, and by Tillyard as a remnant of a close-meshed venation or *archedictyon*. W. T. M. Forbes (1922) saw these cross-ridges in an emerging cicada. For just a few minutes they were unusually distinct.

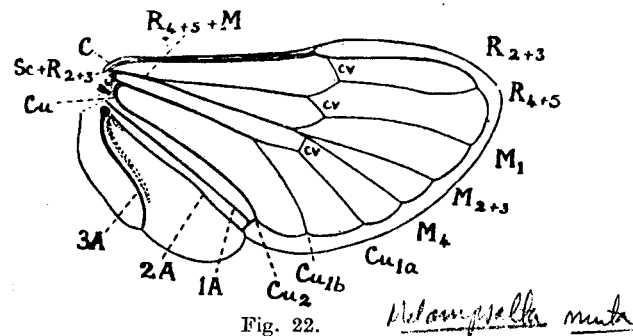


Fig. 22.

*Melampsalta muta*

The nodal line is a very remarkable structure present to some degree in the tegmen of all cicadas and especially marked in the very archaic *Tettigarcta*, in which, and in others, the basal portion of the tegmen is thus separated as a more coriaceous and opaque part, at least superficially resembling a typically Heteropterous, e.g. Pentatomoid condition. It is least developed in such forms as

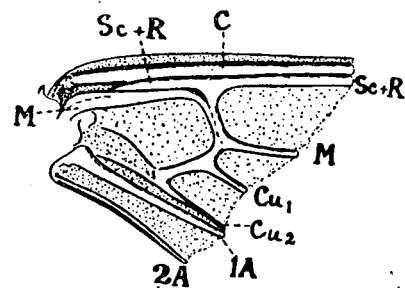


Fig. 23.

*Tettigarcta muta*

*Melampsalta* (figs. 16, 20, 26), but a point often overlooked is that the breaks in the wing-veins where the nodal line crosses them are always complete.

The arrangements for coupling the wings in flight are simple in the extreme. A recurved flange on the dorsal surface of the median part of the costal border, hind-wing, hooks in a similar flange on the ventral surface of the hind border of the tegmen.

The abdomen and its appendages.—Ten distinct segments are recognizable in the cicada abdomen in both sexes, and in addition, posterior to the tenth are two successive parts of the anal "segment"

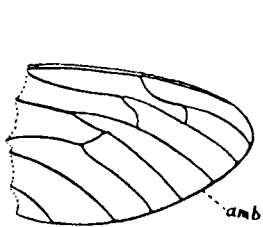


Fig. 24.

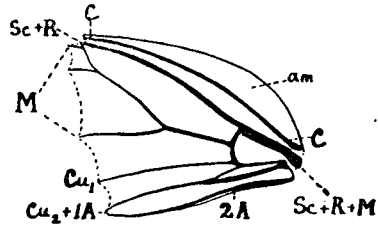


Fig. 25.

*Scaphocephalus* which may perhaps be interpreted as segment XI and a telson respectively.

Segments I and II are modified extremely in the service of hearing and sound-production in the male and of the former function alone in the female. They will be considered when we come to describe the organs concerned.

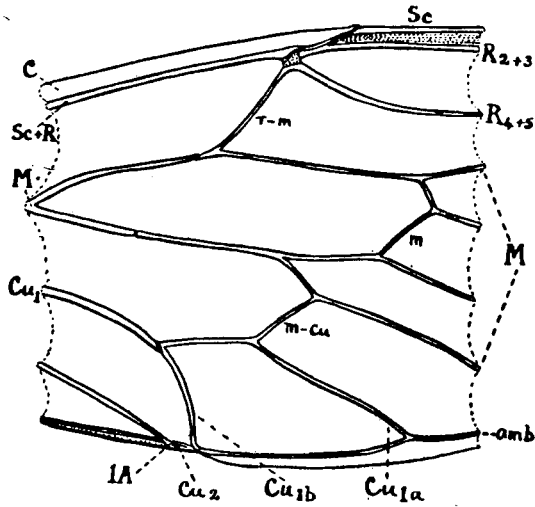


Fig. 26.

The tergites of the ordinary abdominal segments (fig. 27) are greatly developed and strongly arched round part of the ventral surface. The sternites, bearing the 5th to the 9th spiracles, are commensurately restricted.

The main appendages of the abdomen are, of course, the structures used in mating and egg-laying, and commonly known as the male

and female genitalia respectively. The male genitalia of cicadas, as emphasized by Kershaw and Muir (1922) are very distinct. The seventh sternite is large and produced backward (fig. 33); its shape affording a good taxonomic character.

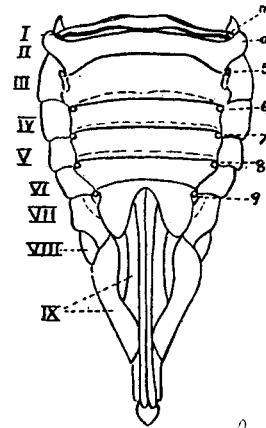


Fig. 27. *Neotoma palto mitta*

The eighth tergite is large and curved down latero-centrally so as almost to form a complete ring. The eighth sternite is large and boatshaped and constitutes the hypandrium, which protects the genitalia from below. This condition is peculiar to the cicadas.

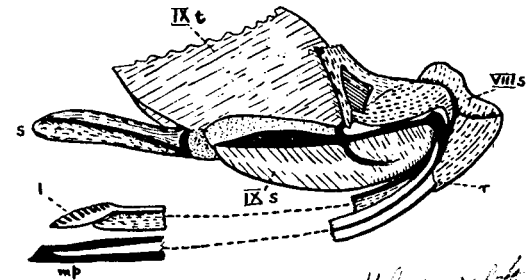


Fig. 28.

*Neotoma palto mitta*

The pygophor, lying in the trough of the hypandrium, is a strongly chitinised, more or less cylindrical case surrounding the termination of the gut and the genitalia. The whole of the dorsal and lateral portions are formed from the ninth tergite. Its ventral surface is membranous and of uncertain origin. The lateral margin bears on each side a process, entirely non-articulate, which Muir and Kershaw

homologise with the otherwise missing genital styles. True genital styles are present in *Tettigarcta*.

Distally the pygophor bears the anal "segment" made up chiefly of the tenth tergite, and produced ventrally into a more or less wide plate extending in *Melampsalta cingulata* (fig. 31) directly caudad, but in *M. muta* and its relatives directly ventrad. Proximally to



FIG. 29.

*Cornuta formosa*, S. D. 1911

FIG. 30.

*Tibicen chloromera*, N. H. 1912

this again the edge of the anal segment bears two downwardly directed, stout, curved non-articulate hooks which I call *copulatory claspers* (figs. 31, 34). They are possibly the *cerci*—organs usually supposed to be absent in Hemiptera—and when fused, as in the genus *Tibicen* (fig. 30), are known as the *uncus*. Between the bases of the copulatory hooks the *aedeagus* or penis-sheath passes to the exterior. It is a complicated structure varying greatly in different

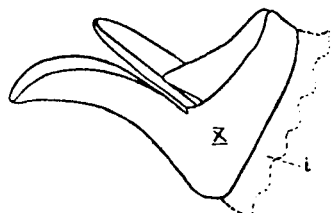


FIG. 31.

*Melampsalta cingulata* (Fabr.)  
New Zealand

cicada genera. In *Melampsalta* it consists usually of a stout, basal bilobate bulb, the *periandrium* and three long distal processes surrounding the penis itself, which opens usually at the distal extremity of the median one.

The chief workers on the male genitalia of the cicadas have been Malpighi (1687), Réaumur (1740), Dufour (1833), Newell, Heymons, Kershaw and Muir (1922), Muir (many papers), Lawson, Doering, and Singh-Pruthi.

The female genitalia consist essentially of three pairs of appendages frequently known as *valves*. These make up the *ovipositor*

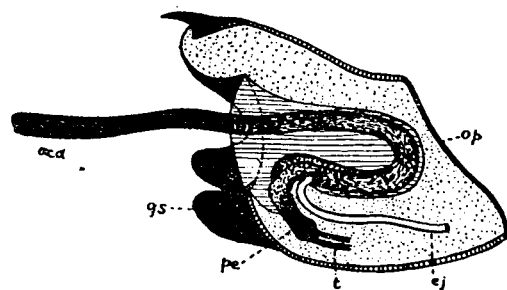


FIG. 32.

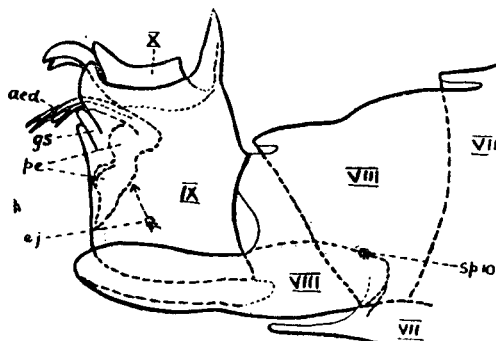
*Tibicen chloromera*, N. H. 1912

FIG. 33.

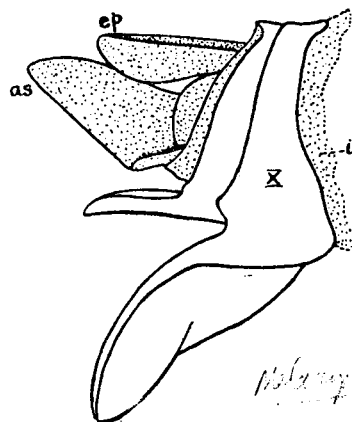
*Melampsalta cingulata*, New Zealand

FIG. 34.

*Melampsalta sericea*, N. H. 1912



and its sheaths. The central or inner pair is fused for the greater part of its length, forming distally a single solid piece (fig. 28) with sharp, strongly chitinised apex. The pygophor is not unlike that of the male in shape (fig. 28), with a longer and more tubular anal "segment" which lacks the armature of that of the other sex.

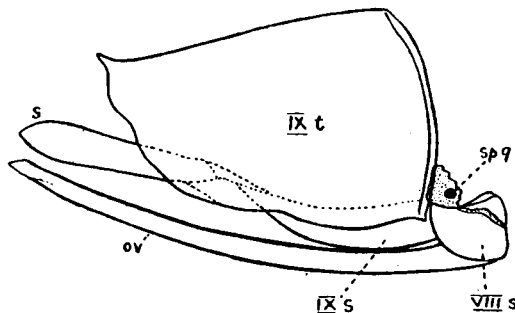
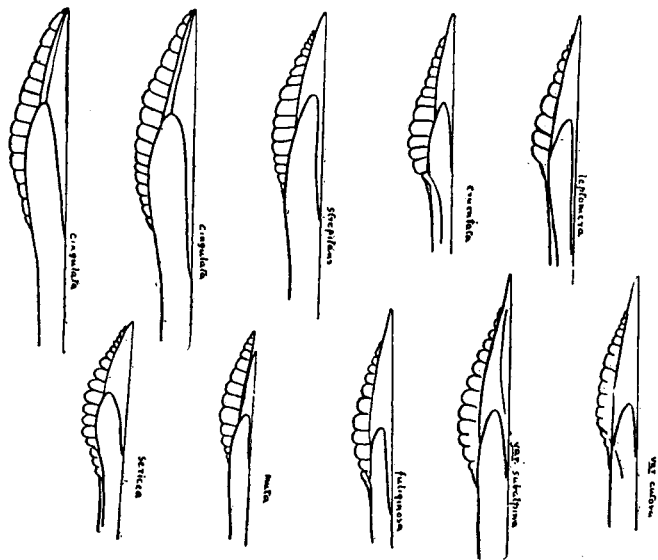


Fig. 35.

The central piece formed by fusion of the inner pair acts as guide-piece for the outer or proximal pair which partially encloses it (fig. 28). The three pieces are welded into a functionally single instrument by means of at least three pairs of interlocking grooves and ridges. Such interlocking, while effectually preventing lateral movement



Figs. 36-45.

of individual pieces, allows and indeed facilitates longitudinal sliding of the ventral or outer pair on the middle piece, the tip of which is sharp and hard. The apices of the ventral or lateral pieces (fig. 28) beyond the tip of their infolded portion clasping the middle piece, are likewise blackly, heavily chitinised and furnished with a number of oblique cutting edges. These are the effective instruments in perforating plant tissue in egg-laying.

The distal part of the ovipositor is ensheathed by the third pair of appendages, which are less strongly chitinised, are apically rounded and usually hairy (figs. 28, 35).

The various names applied in taxonomic and morphological literature to the three pairs of *gonapophyses* comprised in the ovipositor and its sheaths, are so confusing that we are impelled to submit a table of them :

- G. 1. =saw valves (fig. 28, l), ventral valves (Tillyard, Doering), anterior, outer or ventral processes (Muir and Kershaw).
- G. 2. =middle piece (fig. 28, mp), inner valves (Tillyard), median processes (Muir and Kershaw), dorsal valves (Doering).
- G. 3. =sheaths (fig. 28, s), dorsal valves (Tillyard), posterior processes (Muir and Kershaw), lateral valves (Doering).

The female genitalia have been described by Aristotle, Malpighi, Réaumur, Doyère (1837a), Hyatt (1896), Heymons, Verhoeff, Kershaw and Muir (1922).

## CHAPTER V

## THE INTERNAL STRUCTURE OF CICADAS

**The nervous system.**—Remarkably little is known about the nervous system of any Hemiptera, and there is but scanty material for comparison. It would appear, however, that the cicadas are considerably specialised in this direction, although less so in some respects than the leafhoppers (Jassoidea) in some of which Cogan (1916, Pl. 22, fig. 32) shows the whole central ganglionic system as practically one elongate mass, with a small aperture for the passage of the oesophagus.

The brain in *Melampsalta* is ensconced on the second swelling of the digestive canal, just behind the dorsal dilator muscles of this organ (figs. 53, 46). The optic nerves are huge and long; and the *corpora pedunculata* lacking. The ocellar nerves are joined until just beneath the ocelli which they serve. The oesophageal connectives are stout and rather long (fig. 46, c). The suboesophageal ganglion is rounded, joined by long, stout well-separated cords to the first thoracic ganglionic mass which lies largely in the prothorax. This has two short stout connectives to the second thoracic mass which is much longer than broad and shows signs of twofold origin. It lies wholly within the mesothorax and in fact does not reach the meso-phragma. Posteriorly it passes into a superficially single cord which splits into two as it enters the abdomen.

Binet (1894) discovered that the abdominal ganglia, though fused with the last thoracic mass, are nevertheless distinguished in section by the absence of crural lobes, correlated with the absence of legs in the abdominal segments. The first of these abdominal ganglia differs from the succeeding ones in possessing a swelling of the dorsal lobe, formed by two very distinct *additional* lobes. These *vocal lobes*, as Binet calls them, are intimately united with the dorsal lobe of the ganglion, which is essentially motor. They show no adherence to the ventral lobe, from which they remain distant for their whole extent. Thus they differ from the crural lobes which, situated laterally, in relation at once with the sensory (ventral) and motor (dorsal) lobes, are both sensory and motor. The vocal lobe "paraît être uniquement doué de fonctions motrices."

It will be interesting to study the relations of the auditory nerve, discovered since Binet's time, with the abdominal ganglion in

question. Vogel (1923) describes it as branching from the abdominal strand apparently in the II<sup>nd</sup> segment.

The cicadan nervous system has been studied by Meckel (1818), Dufour (1833) who laid the foundations for so many branches of Hemipterous anatomy, Brandt (1878), Rossi (1879-1880), Binet (1894), Berlese (1909), Swinton (1877b, 1879-1880), Will (1840), Grenacher (1879), and Vogel (1922, 1923).

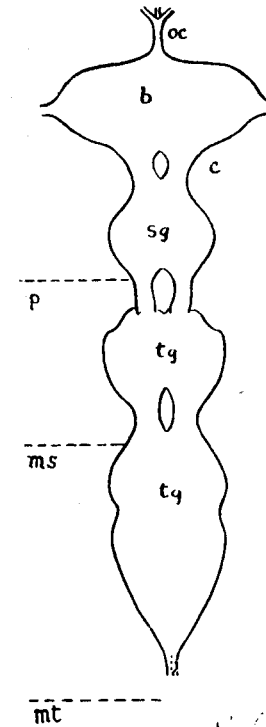


Fig. 46.

*Melampsalta semica*, Will, 1840

**Sense-organs.**—The compound eyes of cicadas have been described by Will (1840) and by Grenacher (1879). According to the former, each eye in *Cicada orni* has no fewer than 11,600 *ommatidia* or separate elements. The eyes are of the eucone type, i.e. each visual element contains a true crystalline cone, in front of which are the nuclei of the cone-cells.

The cicadan habit of dodging like a squirrel behind a branch, keeping it ever between themselves and the observer, is very amusing, and is shared also by certain Heteropterous bugs—notably

the Mirids. That the compound eyes are the chief sense-organs involved is suggested by the absence of ocelli in most Mirids.

The ocelli are three in number and are markedly red in colour. Berlese (1909) and Link (1909) have studied their structure in some detail. Their most striking feature is the presence of pigment-cells between the sense-cells—a characteristic of Auchenorrhyncha.

Link repeats the well-known hypotheses that the function of the ocelli may be connected with the need for sudden movements—since they are well-developed in most jumping-insects—or with orientation, as suggested by their position. In an insect like a cicada, with the head and prothorax almost immovably fixed to the rest of the body, the ocelli would certainly seem to complete the visual equipment so far as direction is concerned. The field of the great compound eyes is largely lateral; the paired ocelli look directly upward, while the median one is often on an eminence which directs it forward.

Whatever be the respective functions of this rather complicated visual apparatus, no one who has collected cicadas will question the ability of the insects to use it very effectively.

The supposed absence of auditory organs in cicadas was for long one of the chief arguments against any sexual significance in the song. To Swinton (1877b, 1879, 1880) must be given the credit of discovering an organ to fill this lack. Unfortunately Swinton wrote in such an involved style, euphuistic, highly allusive and abounding in long irrelevant discussions, that he effectually disguised the solid scientific contribution often contained in his writings. The masterly and detailed description of cicadan auditory organs by Vogel in 1923 involved their discovery anew, and it was not until Vogel's work was well on the way to completion that he found Swinton's long-forgotten account.

The first detailed descriptions of cicada sound-producing organs had made known the mirror—an extremely thin and delicate, beautifully iridescent membrane closing the cavity of the sound-apparatus posteriorly. In spite of at least some experiments to indicate the contrary, almost every observer since and including Réaumur has assumed that the mirrors act merely as resonators. Swinton's contribution consisted in his recognition of the mirror as the tympanum of an auditory organ. Swinton was largely an untrained observer and could not have elucidated the microscopic structure of the chordotonal organ itself even had he seen it. He described, however, the auditory nerve, the thickened line on the tympanum, the spatulate process at its lateral extremity and the external appearance of the auditory capsule.

To Vogel alone we owe a complete account of this truly remarkable organ and its accessory structures, and to his paper we must refer the reader for detailed information, contenting ourselves here with a brief general description. The mirror is seen at M (fig. 76).

It is an exceedingly fine membrane only  $5\mu$  thick in the middle according to Vogel. The lateral part of each tympanum is crossed by a dark, thickened line (fig. 76, p) which extends towards the centre. From the broadened lateral end of this thickening arises a spatulate process running obliquely into the auditory capsule where it serves as an attachment surface for the sense-organ itself.

The auditory capsule is a more or less hemispherical swelling (a) on the ventro-lateral portion of the second abdominal tergite. In its cavity is stretched the sense-organ between two spring-like chitinous pieces. One of these is the spatulate process from the tympanum while the other is an invagination of the outer wall of the capsule. The sense-organ shows all the structure of a *chordotonal organ* in so far as its sense-cells terminate in the usual rod-like bodies or *scolopales*, and are stretched by means of fibrillar differentiated hypoderm cells between two points of the cuticle. It is, however, distinguished from all hitherto-described chordotonal organs by the enormous number of sense-cells or *scolopophores*. Schwabe found upwards of 100 in the tympanal sense-organs of grasshoppers and crickets; the cicada studied by Vogel had about 1500. Vogel speculates as to whether the scolopophores, in their tremendous numbers, are capable of sound analysis in a manner analogous to that of the fibres of Corti in man. In Vogel's cicada—a *Melanopsalta*—they vary in length from 0.2 to 0.31 mm., as compared with 0.04 to 0.5 in man (Helmholtz). He decides there would probably be only a small range. If this were demonstrated it would go far to explain the great effect of certain sounds on cicadas and their indifference to others, as in Fabre's classical experiment with the festal cannon, which the cicadas ignored entirely.

Female cicadas possess well-developed auditory apparatus, with the mirror somewhat reduced in size; but the primitive and soundless *Tettigarcta* lacks them apparently in both sexes.

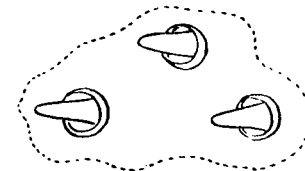


Fig. 47. *Melanopsalta* (Vogel)

The antennæ bear a number of minor sense-organs or sensillae usually considered as olfactory (Berlese, 1909), although I know of no experimental evidence in direct support of this view (fig. 47).

The tip of the rostrum in both nymphs and adults is furnished with numerous hairs which conceivably subserve a sensory function. At least such an hypothesis is more probable than that held by

Nathaniel Potter (1839) who believed that moisture, or rather "exhalations of vegetable barks," were absorbed through them.

**The muscular system.**—A very detailed account of the numerous muscles of the cicada body is supplied by Berlese (1909), to whom the reader must be referred.

The tymbal muscles form the largest and strongest pair of muscles in the whole body.

**The respiratory system.**—The general tracheal system in cicadas has received no comprehensive treatment since the work of Dufour (1833). The *spiracles* or *stigmata*, by which the tracheae open to the exterior on the sides of the body, have been studied by Dufour,

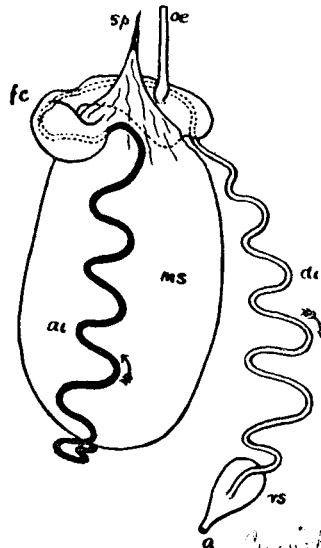


Fig. 48.

Landois (1867, 1874), Handlirsch (1899), Heymons (1899), Hansen (1902), Mammen (1912), and Vogel (1923). We have examined them in *Melampsalta muta* (figs. 13, 27, 62, 67, 68, etc.). Of the ten spiracles, two must be considered thoracic in origin and eight abdominal. They are connected by transverse tracheae, and on each side by longitudinal ones. There is also, in connection, a conical air-sac on each side of the mesothoracic cavity. The large abdominal sac is really a part of the alimentary system.

**The alimentary system.**—The widespread classical belief that cicadas lived only on dew was based probably on the absence of any striking signs of injury to the plants frequented by these insects, and partly no doubt on the lack of any structure which the unskilled observer could recognize as an effective mouth.

The first name associated with an actual dissection of the cicada digestive system is that of Meckel, who, in 1808, gave a surprisingly sound and detailed account of conditions in *Tibicen plebeia*. Follow-

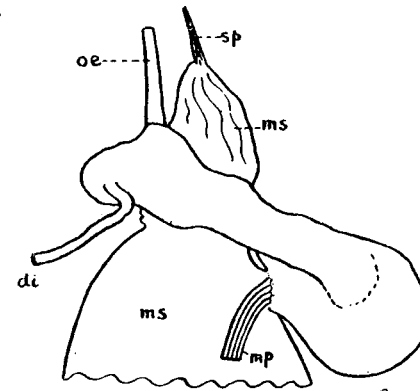


Fig. 49.

*C. formosa*

ing workers were Ramdohr (1809, 1811), Marcel de Serres (1813), Dufour (1825, 1833), and Doyère (1839). Later students of cicada splanchnology have been Schindler (1878), Nassonow (1899), Quaintance (1902), Gadd (1902, 1910), Hargitt (1903, 1923), Licent

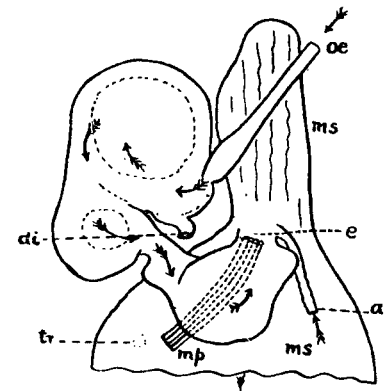


Fig. 50.

*C. formosa*

(1911a, 1911b, 1912), Berlese (1909), Kershaw (1913, 1914), Hickernell (1920, 1923), Snodgrass (1921b).

Finally there are those who, like Carus and Graber, interested primarily in the sound-producing apparatus, took the mesenteric sac for an air-bladder of the tracheal system. Apparently the only

one who has held to this belief after dissecting the whole alimentary tract is Snodgrass (1921b).

Functionally the first part of the alimentary canal (figs. 48-50) consists in cicadas, as in all other Hemiptera, of an extremely fine passage between the closely apposed mouth setae which are themselves enclosed in the trough-like rostrum. Soon after entering the head the food-passage widens into a capacious and powerful sucking-pump, a dilated portion of the pharynx, which is succeeded by a smaller but muscular swelling just below the entrance to the thorax. At the posterior extremity of the thorax the oesophagus enters the peculiar complex known first by Lubbock (in scale-insects) as the *internal gland*, but now more generally termed the *filter-chamber*. The essence of this arrangement consists in the zig-zagging of the ascending part of the mid-intestine in close association with the

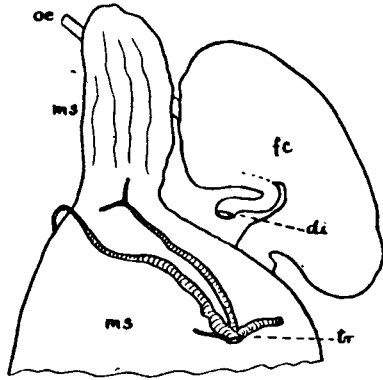


Fig. 51.

attached portions of the Malpighian tubules, in the actual walls of the anterior part of the stomach. By this construction it is believed that the watery constituents of the plant sap (Licent), or these and the surplus sugars (Berlese), pass directly by dialysis through the lining of the stomach and the walls of the intestine, and thus are carried direct by the rectum to the exterior; while the more nutritious elements are selected to pass by the more circuitous digestive route. The forepart of the intestine thus forms a long and very intricately coiled loop which appears finally to end in the stomach, as indeed Dufour originally believed it to do. The position already complicated by the serpentine twistings of the intestines and Malpighian tubules, is further obscured in cicadas by the extraordinary development of a huge, thin-walled *mesenteric sac*, occupying most of the abdominal cavity in the male and considered by Graber, Snodgrass, and many others as an air-sac of the tracheal system. It is, however, a part of the stomach, in direct communica-

tion with the cavity of the interior part of the latter (not merely of the filter-chamber) and gives rise at its own posterior extremity to the ascending mid-intestine which, after many convolutions, enters the main stomach wall near the junction of this with the mesenteric

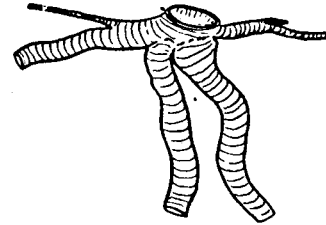


Fig. 52.

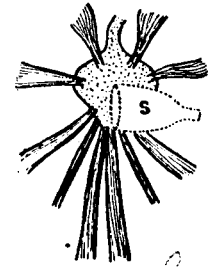


Fig. 53.

sac. After a tortuous course *within* the walls this tube receives the Malpighian tubules which have accompanied it within the investment of the stomach and then joins the posterior intestine at the anterior end of the stomach, which it leaves near the entrance of the oesophagus, and proceeds, after much winding, to the muscular

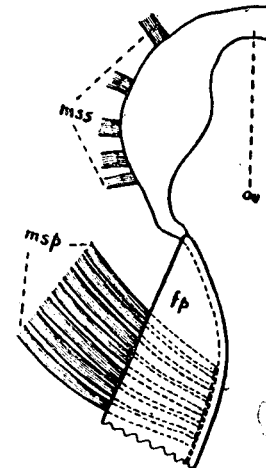


Fig. 54.

rectal sac opening to the exterior on the anal segment X. This complicated arrangement of the parts will be understood by reference to the figures (figs. 48-54).

The salivary glands appear as bunches of lobules filling the greater part of the head cavity. Their deferent canals unite to form

a single duct carrying the salivary secretion to the salivary pump (fig. 55) or *syringe*, which forces it down the smaller of the two maxillary channels into the pierced plant-tissue. The juice from the latter is sucked up the larger or food-canal formed by the close apposition of the maxillary setae themselves.

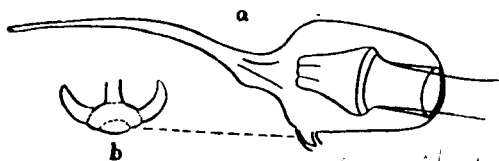


Fig. 55. *Mizopoda leptomera*.

The function of the huge and enigmatical mesenteric sac is not definitely known. We may note that it lies posterior to the filter-chamber, and is thus concerned, if our theory of the latter be true, only with the more concentrated nutritious portion of the sap. Histologically both Licent and Hickernell found it to be lined with digestive epithelium, characterized by secretory and absorbant

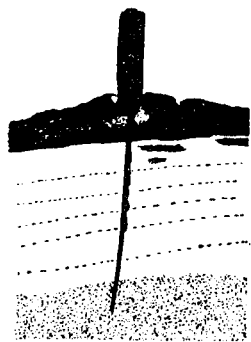


Fig. 56.

activity apparently not less in froghoppers (Cercopidae) where it is of moderate size, than in cicadas where it is very large and in Typhlocyidae where it is tremendous. Were it largest in cicadas one would perhaps explain such development as due to a function accessory to the auditory tympanum (mirror) as claimed by Vogel. This would then be a case slightly analogous with that of the Teleost swim-bladder, though in the cicadas the sac has probably not lost so completely its alimentary capacity. But its still greater evolution in the apparently silent Typhlocybid leafhoppers, in which, moreover, no auditory organ has yet been described, renders a predominantly gastronomic explanation more logical. That the mesenteric sac may still receive air and thus act secondarily to

maintain normal air-pressure on the inner surface of the auditory tympanum is rendered probable by the fact that in froghopper nymphs, according to Kershaw (1914, p. 5):

"The air, which all sucking-insects doubtless imbibe in quantity along with the liquid food, appears to pass through the alimentary canal and be utilised in forming the air bubbles coated with mucinoid

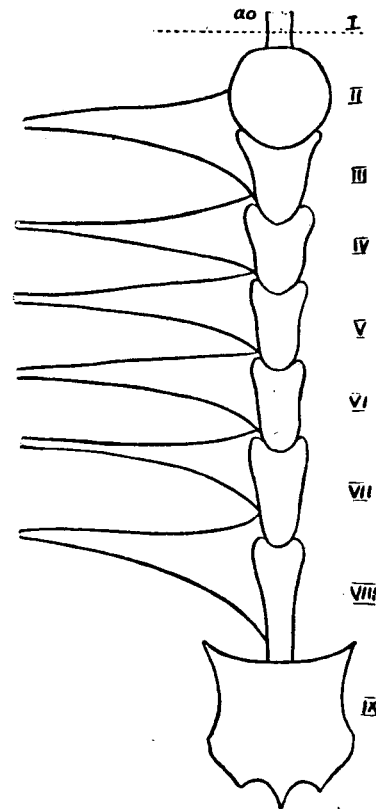


Fig. 57. *Aspidicta sylvana*, S. Kershaw.

which are emitted from the anus and form the froth in which the nymph lives. After examining this Cercopid I am the more inclined to believe that . . . the 'food-reservoir' in the head of *Flata* functions in part as an air-separator to rid the liquid food of superabundant air before it passes through the alimentary canal."

**The circulatory system.**—The dorsal vessel or heart stretches practically the entire length of the abdomen, with a compartment in nearly every segment, and lateral muscular wings (fig. 57). The

first or most anterior of these compartments is largest and almost circular. It is situated in the second abdominal segment, and sends forward the *aorta*, which reaches thus from the second segment to the head, passing between the great lateral thoracic muscle masses. Thence it threads the foramen between the oesophageal connectives and leads above the oesophagus to the posterior swelling of the pharynx, where it ends in an open mouth in close relation with the bases of the posterior dorsal dilator muscles of this organ.

The aorta is colourless or white, while the heart itself, at least in alcohol material, is dark-coloured.

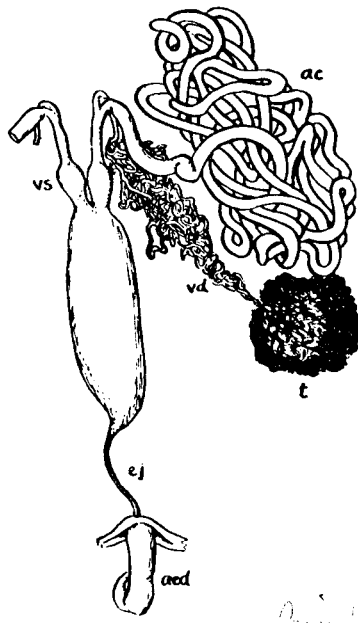


Fig. 58.

**The fat-body.**—The fat-body, representing a tissue rather than an organ, was first considered in cicadas by Dufour (1825) who described it as glaucous green in colour, and most plentiful near the end of the abdominal cavity.

It is diffuse and plentiful in nymphs and in adults of both sexes, especially in the abdomen. It is permeated by tracheae and tracheoles, and binds in sheets the intestines and Malpighian tubes.

The function of the fat-body is problematical. Comstock considers it is devoted primarily to the storage of nutriment and secondarily to excretion. It plays an interesting rôle in the cicadas and other Homoptera in supplying housing to the supposedly

symbiotic yeast, *Saccharomyces*. According to American observers, infection by the parasitic fungus, *Massospora cicadina*, which causes such a heavy mortality among males of the famous seventeen-year cicada, increases with the reduction in the fat-body during adult life. Is it possible that there is an antagonism between the *Saccharomyces* and the *Massospora* spores? Sulc has already suggested a bactericidal function for the symbiotic yeasts.

**The reproductive system.**—The so-called genitalia or appendages of the reproductive system have been treated with the rest of the chitinous skeleton in general in the previous chapter. The gonads themselves have received little attention from students. The first account of the male organs is that of Meckel (1808) and the best general description extant remains that of Dufour (1833). We have studied these organs in *Carineta formosa* (fig. 58). The two testes are roughly spherical, but at the same time diffuse. The *vas deferens* from each is extremely long and complexly coiled (fig. 58, vd). An apparently equally long and very much thicker *accessory gland* of

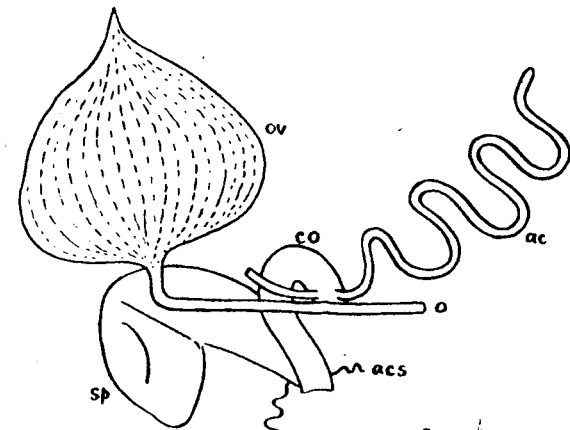


Fig. 59.

unknown function opens with it into the base of the common *ejaculatory duct*; but just before this fusion the *vas deferens* and *accessory gland* together form a small swelling which may be considered a *vesicula seminalis*. The proximal portion of the *ejaculatory duct* is inordinately swollen and thick-walled; but the distal part, joining the base of the *aedeagus*, is of much smaller calibre.

In the female there are two large ovoid ovaries (fig. 59). These contain, according to Berlese, in a European species, no fewer than 70 to 80 meristic ovarioles. The oviduct (fig. 59, o) bends shortly and runs to join its fellow and form a stout, short common oviduct or vagina (fig. 59, co). This bends over very sharply near its begin-

ning and just after the union of the oviducts receives a long, winding accessory gland from each side. These appear homologous with the very similar structures in the male, but are shorter. They can, of course, be considered neither spermathecal nor colleterial glands, and their function remains for the present unknown.

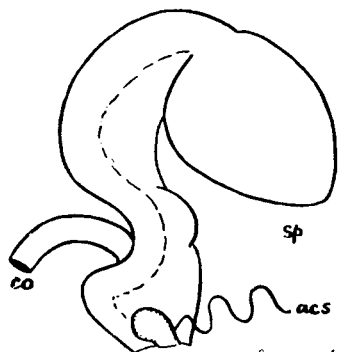


Fig. 60. *Carineta formosa*

Near the external opening the vagina receives a large sac-like *spermatheca*, which shows a marked differentiation into a relatively soft-walled apical pouch (fig. 61) and a very stout and muscular proximal portion. At each side of the entrance of the *spermatheca* is a tiny rather thin-walled sac receiving a long, much-coiled, thin and thread-like white gland discovered in other species by Gadd in

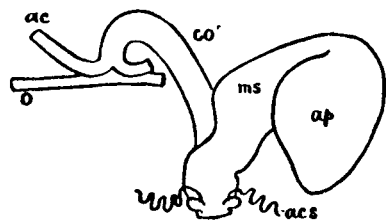


Fig. 61.

1910 (figs. 60, 61). These glands, which are cut short in our figures, are to be considered as spermathecal.

Both Dufour and Gadd found a large, very long unpaired gland opening into the vagina near its apex. We have not found this present in *Carineta formosa* nor *Melampsalta scutellaris*.

The female gonads of cicadas were studied by Meckel (1808), Dufour, Doyère (1837b), Holmgren (1899), Henneguy (1904), Berlese (1909), and Gadd (1910).

## CHAPTER VI

### THE SOUND-ORGANS

“ Ne sommes-nous point un peu humiliés, quand, après nous être crus en tous points l'ouvrage par excellence du Créateur, nous voyons que les parties, qui été employées pour mettre le mâle d'un cigale en état de se faire entendre par sa femelle, le disputent par leur nombre, par la singularité de leur matière et de leur structure, et par l'art avec lequel elles sont disposées aux organes de notre voix ? ”

(RÉAUMUR, 1740, p. xi.)

WE come now to those parts of the cicada anatomy which, above all others, have enabled these insects, in more senses than one, to make a noise in the world. We have here to deal with perhaps the most complicated sound-producing organ in the animal kingdom, and one which usurps such a large part of the cicada economy as to remind us forcibly of Plato's story that these insects were once men who gave up their whole lives to song, neither eating nor drinking, and, singing, died.

The first recorded observation on the method of sound-production in cicadas—that of Hesiod, about the eighth century before Christ—we have seen to be accurate so far as it goes. The tettix “ pours forth from under his wings, his shrill song.”

Aristotle's much later and more detailed account, an extension as far as the scientific equipment of the time would allow, of Hesiod's observation, was the first attempt at a formal explanation. The relevant passages (*Hist. anim.*, lib. IV, cap. 9; *De part. anim.*, lib. III, cap. 16) though short have given considerable trouble to the commentators. The following interpretation is based on the various editions and commentaries cited in the bibliography and on the exegetical notes of Landois (1867). The explanation involves Aristotle's conception of respiration, which he regarded as essentially a process of cooling. Vertebrates he believed to accomplish this result by taking air into the body and expelling it again. Insects did not breathe in this sense, but achieved the same end by the agitation of the air enclosed within their bodies. By this movement the body fluids were brought into contact at the “ *hyposoma* ” with the thin membrane which there separates them from the cooler outer air. Ogle and Landois think that the *hyposoma* is the waist-line between thorax and abdomen, in its ventral part. In flies, bees, and similar buzzing insects, thought Aristotle, the sound was produced by the vibration of the membrane brought about “ *attritu*



spiritus." In the cicadas the hyposomatic insinking was much more greatly developed, but the song was produced in the same way. Landois compares the agitation of the "innate spirit" (Ogle) with the movement we might impart to the air in our chest by moving our diaphragm up and down while keeping nostrils and lips closed. We do not think Ogle's above translation for *πνευμα* is well-advised, for Aristotle apparently meant the term to connote merely enclosed air, without any metaphysical implication.

Such was the explanation which held sway until after the Renaissance. It possessed the merit of distinguishing clearly between the song of cicadas and the stridulation of crickets and grasshoppers. The absence of even the rudiments of knowledge concerning muscular action on the one hand and respiration on the other, in invertebrates, made it impossible to distinguish in principle the song of cicadas from the buzzing of bees and flies.

There were several more superficial notions which competed but little with the Aristotelian hypothesis. The latter was repeated by mediæval and later writers down to Aldrovandi (1618) and Mofet (1634); and constituted from the scholastic viewpoint a perfect explanation requiring only abstention from renewed investigation to ensure its indefinite perpetuation.

The first to dispute, in the opening of the seventeenth century, the authority "che per tant' anni avea celato il vero," were Casserius and Galileo. Galileo's statement made a clean sweep of tradition and was a clear expression of the modern spirit.\* A contemporary of Galileo had already discovered the effective organs of cicada sound, even before the statement of Galileo was published. Giulio Casserio (Casserius), erstwhile domestic in the household of Fabricius ab Aquapendente and later his successor in the chair of Anatomy and Physics at Padua, published in 1600 a detailed, illustrated account of several species, figuring not only the tymbals but also the muscles which work them.

\* Quando il mentovato uomo si credeva non poter esser quasi possibile, che vi fossero altre maniere di formar voci, dopo avere, oltre ai modi narrati, osservato tanti organi, trombe, pifferi, strumenti da corda di tante e tante sorte, e sino a quella linguetta di ferro, che sospese fra' denti, ai serve con modo strano della cavità della bocca per corpo della risonanza e del fiato per veicolo del suono; quando dico ai credeva d'aver veduto tutto, trovossi piccchumai rivolto nell' ignoranza e nello stupore, nel capitargli in mano una Cicala, e che non per serrarle la bocca, nè pur fermarle l' ali poteva nè pur diminuire il suo altissimo stridore, nè le vedeva muovere squamme, nè altra parte; e che finalmente alzandole il casso del petto, e vedendovi sotto alcune cartilagini dure ma sottili, e credendo che lo strepito derivasse dallo squoter di quelle, ai ridusse a romperle per farla chetare; e tutto fu in vano; sinchè spingendo l' ago piu addentro, non le tolse trafigendola colla voce la vita. Sicchè nè anche poté accertarsi, se il canto derivava da quello; onde si ridusse a tal diffidenza del suo sapere; che domandato come si generavano i suoni, generosamente rispondeva di sapere alcuni modi, ma che teneva per fermo potervene essere cent' altri incogniti e inopinabili. *Il Saggiatore*, Rome, 1625.

Pontedera (1718), Felici (1724), and Laurenti (in Zanotti, 1731) all described the same organs with more or less accuracy, so that by the latter date four times at least had the true sound-organs been independently discovered and their mechanism explained. It is



Fig. 62.

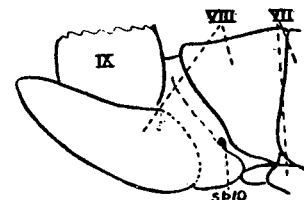


Fig. 63.

significant that the poorest of these accounts was that of the investigator who placed the most emphasis upon the teaching of the classics. To the extent that these isolated experimenters broke away from traditionalism, to that extent also did they tend to ignore the work of their contemporaries and immediate predecessors. In no one were both tendencies more clearly displayed than in the fifth

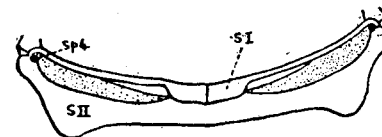


Fig. 64.

independent discoverer of these organs. But it was due to the unflinching accuracy and patience of his observations, to the clarity and detail of his illustrations and to the lucidity and charm of his literary style that Réaumur (1740) not only escaped the oblivion which has largely swallowed the work of his forerunners, but supplied the account which is the basis of nearly all subsequent accurate accounts.

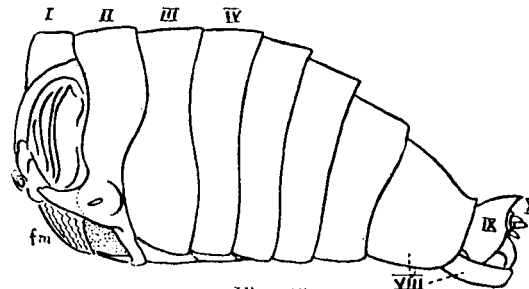


Fig. 65.

Later workers who, while adhering to and confirming the essence of the Réaumurian interpretation, have in many cases added greatly to our detailed knowledge of cicada-sound-organs are Carlet (1876, 1877, 1879), Fabre, Haswell (1887), Lucas (1887), Mayer (1877),

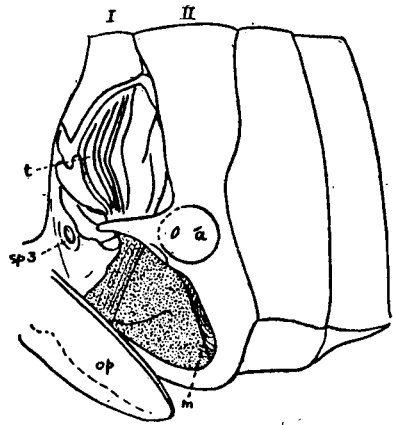


Fig. 66.

Lepori (1869), Goureau (1837, 1838), Targioni (1867), Medici (1847), Latrille (1822), Middlemiss (1886), Hingston (1922), Dugès (1838), Graber (1872, 1876, 1877), N. Potter (1839), Lloyd Morgan (1880, 1886).

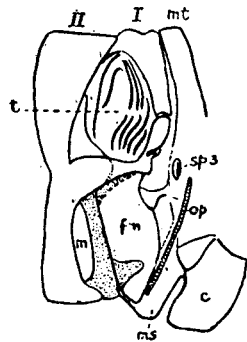


Fig. 67.

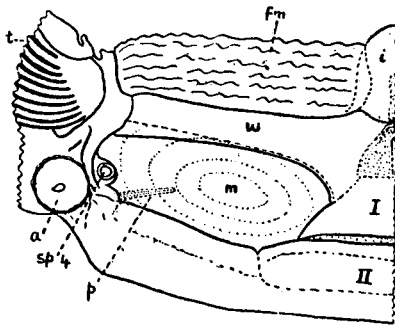
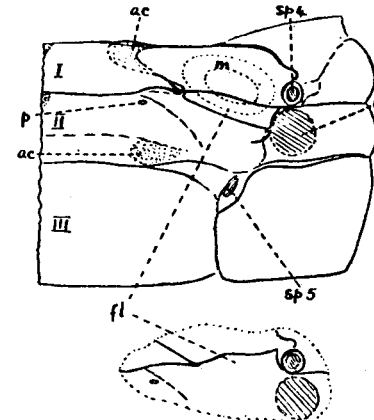


Fig. 68.

Our description of this now famous mechanism is based on *Melampsalta sericea* and *M. muta*—species in which conditions are relatively simple.

The opercula are two large plates on the under-side of the body, extending posteriorly from the metathorax and covering a large

cavity. They are extensions of the metathoracic epimera (fig. 66, op). The operculum is immovably attached to the thorax, and the space between it and the abdomen, which in some species is varied during singing, is altered by lifting the abdomen from the opercula. The



Figs. 69, 70.

effect, of course, is the same. The cavity beneath the opercula is bounded anteriorly on each side by a yellowish *folded membrane* which is apparently the intersegmental membrane between thorax and abdomen; and posteriorly by a *mirror*, which has already been

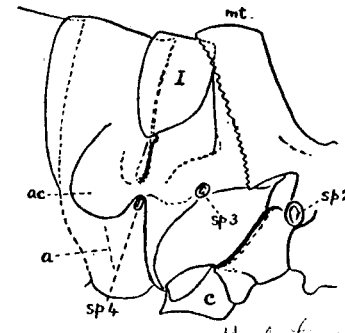


Fig. 71.

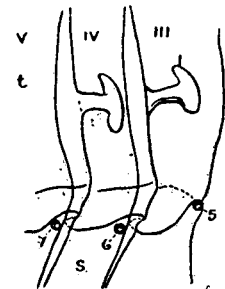


Fig. 72.

described as the *tympanum* of the hearing (chordotonal) organ. All these structures are at most protective and accessory. We now come to the effective instrument of sound. The sides of the first abdominal segment show as tergal modifications, two convex, oval, strongly chitinised, pale-coloured plates in a strong frame. These are the *tymbals*, the surface of each of which is ornamented with

strong, more or less parallel ribs. Dissection is now necessary to lay bare the musculature which puts these organs in motion (figs. 76, 77). It is convenient to cut off the abdomen at about the third

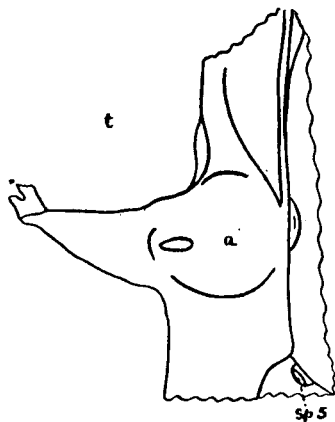


Fig. 73. *Hymenoptera*

segment. In rear view the mirrors are then very conspicuous, and the other organs may be seen through them. Prominent among the latter is a large chitinous V, standing on the sternal surface and reaching its arms up almost to the dorsum. These arms are not endo-

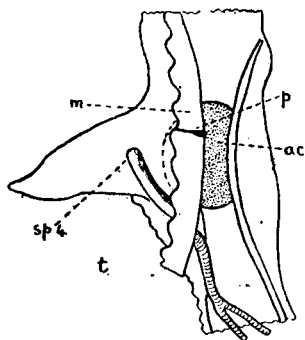


Fig. 74. *Diptera*

skeletal, but are differentiated anterior parts of the first sternite.\* Parallel but dorsal to the arms of the V and inserted in a ridge in the basal portion of each, are two large *muscles*—the largest single muscles in the body. These are the *tymbal-muscles*. Each bundle

\* For a discussion of the homology see Myers, 1928.

ends distally in a chitinous plate from which a slender tendon stretches to its attachment on the inner face of the tymbal (fig. 77).

Such is the complete sound-producing apparatus as it appears in its simplest form. In the most specialised subfamily the tymbals are

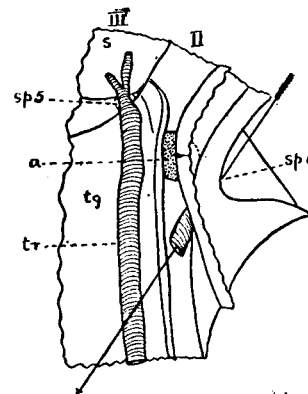


Fig. 75. *Palaemon scutellatus*

completely hidden from view by a forward, lateral expansion of the second abdominal tergite, which forms on each side an accessory cavity of which the *inner wall* is formed in part by the tymbal.

The essential elements of the apparatus are the tymbals and the tymbal-muscles. The experiments of Laurenti (Zanotti, 1731),

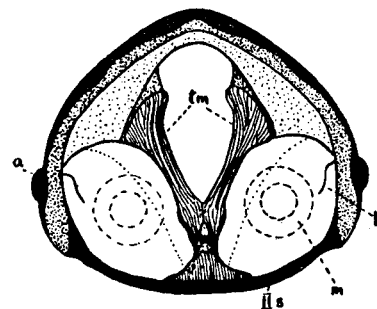


Fig. 76. *Hymenoptera*

Lépori (1869), Mayer (1877), Solier (1837), Goureau (1838), Medici (1847), and Lucas (1887), to mention only a few, all attest the fact that the destruction of actual or supposed accessory parts—opercula, folded membranes, mirrors, so-called tracheal (really mesenteric) sac—and the stoppage of the adjacent spiracles, exert but the slightest, if any quantitative effect on the production of sound in the living

cicada. Landois's theory that the third spiracles (1st abdominal) were the instruments of sound never had the slightest experimental foundation, but on the other hand went clear athwart all previous evidence. The more reasonable belief of Carus and others that the spiracles acted as accessories by supplying air to the "tracheal" sac was based on observations made on *Tibicen plebeia* while singing. This species, like several of the *Melampsaltes*, modulates the sound by alternately widening and narrowing the entrance to the main cavity by raising or lowering the abdomen. This rhythmical movement was mistaken by Carus for a respiratory one.

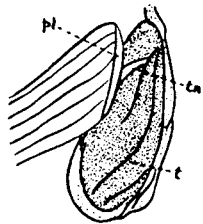


Fig. 77.

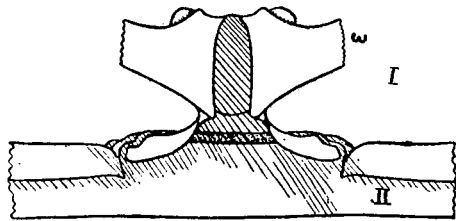


Fig. 78.

We are reduced then to the tymbals and their muscles. The former are convex, and if they be pulled inward and released by manipulation of the muscles in a moist specimen, they will regain their former convexity by the elasticity residing especially in the strongly bowed ribs. This is accompanied by a sharp click like that emitted by a tin can similarly indented—and these clicks, rapidly repeated, constitute the song of the cicada.

Carlet attempted (1877) to measure the vibrations of the tymbal by fixing a fine glass thread with wax to this organ and placing the other end of the fibre in contact with a revolving cylinder furnished with a smoked surface. The experiment was not very successful, largely because a captive cicada never sings "properly" but emits an "alarm-cry" like that of a bird under similar circumstances.

In all cicadas the sound-organs are confined entirely to the males. In the archaic Australian *Tettigarcta* they lack in this sex also.

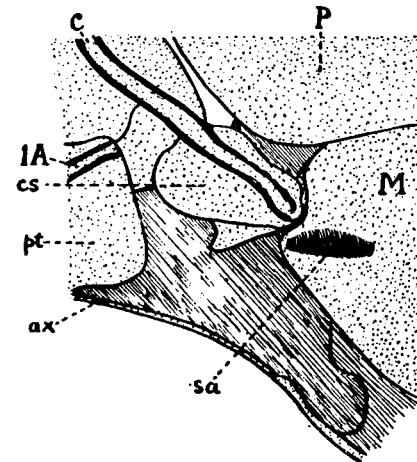
**The accessory stridulating apparatus of the Tettigadinae.**—Jacobi (1907c) was the first to signalize in the cicadas the existence of a second sound-producing apparatus of a far less anomalous and complicated character than the one we have just studied.

The subfamily Tettigadinae, poor in genera and species, is a neotropical group of fairly large cicadas, with extremely well-developed tymbals, heavily ribbed. On the lateral angle of the mesonotum is an inconspicuous oval, hairless area bearing a series of transverse striae (fig. 79). While in other cicadas the hind-base of the tegmen or fore-wing forms approximately a right angle, in

these forms it is more or less drawn out, and even lobed. This lobe is said to be the plectral portion of the stridulatory apparatus. But no one has yet recorded observations in the field, and the mechanism is largely conjectural.

The apparatus is equally developed in both sexes.

In this connection it is interesting that in *Melampsalta cingulata* and in *M. strepitans* there is a loud wing-clicking produced by both

Fig. 79. *Chonocis crassipennis*

sexes and additional to the males' song. It results from a rapid lateral movement of the wings from the roof-like resting-position to one at an acute angle with the body; but the movement is so quick that one cannot be sure whether the noise is produced by friction between tegmina and hind-wings on each side or between one or both pairs and the body. If the latter, then the development of the stridulating areas on the mesonotum of the Tettigadinae is only a further step in the same direction.

