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On the Tympanic Organ in Chrysiridia ripheus Dru.

[*From the* Transactions of the Entomological Society of London, April 15, 1924.]

XXI. *On the Tympanic Organ in* Chrysiridia ripheus *Dru.*

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[Read October 17th, 1923.]

Plates XXIII–XXV.

In the Cambridge Natural History, Insecta, Pt. II, 1889, the late Dr. Sharp called attention, on p. 419, to a curious structure which he had observed in the abdomen of species of Uraniidae.* His remarks are as follows :—

"In all the species of the family we have examined, we have noticed the existence of a highly peculiar structure that seems hitherto to have escaped observation. On each side of the second abdominal segment there is an ear-like opening (usually much concealed by overlapping scales) giving entrance to a chamber in the body; this chamber extends to the middle line, being separated from its fellow by only a thin partition. At its anterior and lateral part is a second vesicle-like chamber, formed by a delicate membrane that extends as far forward as the base of the abdomen. There can be little doubt that this is some organ of sense, though it is much larger than is usual with Insect sense organs."

Ever since reading the above account I have hoped one day to have an opportunity of investigating the structure in *ripheus*. During a casual examination of specimens of Geometrid Moths I discovered a similar cavity in the abdomen, and, on dissection, observed the complicated tympanic organ, now well known to exist in this and other families of the Heterocera.

I had little hope that my discovery was original, and a search through records, in which I was then, and have since been, much assisted by my friend Dr. K. Jordan, soon proved that I had not underestimated the activities of my fellow-naturalists.

It is perhaps unnecessary here to describe all the known

* Comm. Walker has kindly called my attention to the fact that Dr. Sharp's first mention of the organ was at a meeting of the Cambridge Natural History Society on April 30, 1897, when he stated that he had observed it "some years ago."

references to tympanic organs. Swinton (Ent. Mo. Mag. 14, p. 121, 1877) appears to have described, not very clearly, some of the external features. The same author referred to the subject at subsequent dates (1880 and 1882), and it is mentioned by Minot (Am. Journ. of Otol. 4, p. 89, 1882). In 1909 (Zool. Jahrb. 27, Anat. p. 631) Deegener published a paper on a new sense organ in the abdomen of the Noctuidae, but seems not to have made a very complete examination of the structure, and has since been shown to be incorrect in his account of the histology. Dr. K. Jordan in 1905 (Novit. Zool. 12, p. 506) made certain observations on the external structure in relation to the sexes. In 1911 F. Eggers (Sitzb. Natf. Ges. Dorpat, 30, p. 138) published a preliminary account of the organ in Noctuidae, which was followed in 1912 by a similar short account of the corresponding feature in Geometridae by Prof. v. Kennel (Zool. Anz. 39, p. 163). Friedrich Eggers then proceeded to investigate more fully the morphology and histology of the tympanal organs in the Noctuidae and other families of the Heterocera. This work was completed in 1913, but owing to certain delays it was not submitted for publication till 1914, when the War intervened and it was not until 1919 that the very elaborate and fully illustrated paper appeared, entitled "Das thoracale bitympanale Organ einer Gruppe der Lepidoptera Heterocera" (Zool. Jahrb. Jena, Anat. xli, pp. 273–376). In it the author gives a list of some 155 species examined. The organ in varying degrees of complexity is thoracic in some groups and abdominal in others. It may be useful here to give a list from Eggers' work of those families in which the structure has been observed.

In the thorax :—

Notodontidae.	Hypaenidae.	Syntomidae (part).
Thaumatopaeidae.	Agaristidae.	Arctiidae.
Lymantridae.	Nolidae.	Hypsidae.
Noctuidae.	Cocytidae.	Lithosiidae.

In the abdomen :—

Drepanidae.	Geometridae.	Epiplemidae.
Cymatophoridae.	Uraniidae.	Pyralidae.
Brephidae.		

If some common Geometer such as *Xanthorrhoë mon-*

tanata be placed in weak spirit, and examined from the side, under the stereoscopic microscope, an opening will be observed at the anterior end of the abdomen, close to its junction with the thorax. This is the external orifice of the tympanal organ. If now the thorax be carefully removed, and the forward portion of the abdomen cut off at about the third or fourth segment, and this anterior part examined from the front, after removal of connective tissue, fat cells, etc., a paired structure will be seen, the most striking features of which are the two delicate tympana, which in certain angles reflect the light like small mirrors. Each has a rather elliptical shape with one side of the ellipse cut off straight. This straight side is the external edge, and forms the anterior margin of the external orifice. The rounded part of what may be called the framework of the drum is heavily bordered with chitin, whilst the straight distal edge appears to be more in the nature of a ligament. The rounded edges of the two drums nearly meet in the centre, and from these inner edges there arise a pair of chitinous bridges, one extending over each drum, from the central or inner curved side to the outer straight ligamentous margin. At its origin on the inner edge the bridge is continuous with the chitinous framework of the drum, but where it joins the outer edge, it appears to be connected thereto by short muscles, or perhaps fibrous bands. The bridge is broader at its centre and ends than elsewhere. From its centre there drops to the drum a delicate nerve, the chordotonal thread.

From this description it will be gathered that the opposite or posterior surface of the tympanum to that on which the nerve is attached, forms the anterior wall of the cavity whose external orifice can be seen in a lateral view of the moth's body. The remaining interior surface of this cavity in the abdomen is formed by a bulbous invagination of the cuticle, sufficiently chitinised to preserve its shape, which is somewhat like that of the body of a kettle drum.

The side of the tympanum on which the nerve enters and over which the bridge lies is in the interior of the body, but apparently forms part of a tracheal vesicle, the chitin bridge serving to prevent pressure of internal organs on the drum.

The two drums are not quite in the same plane, their inner margins being rather posterior to their outward edges. So far as the nervous distribution is concerned there would appear to be a pair of nerve threads arising from the ventral cord and passing upwards and backwards to give off several branches, one of which passes to the chitin bridge, and running in the delicate connective tissue along its edge, ends in the chordotonal thread already referred to.

In those species which have the tympanal organ in the thorax, a more complicated structure exists. The organs are in the posterior part of the metathorax, and each consists essentially of a modified tracheal vesicle carrying *two* drums or tympana. One of these is the true tympanum with its chordotonal thread, and the other would seem to be a kind of resonator, which Eggers designates as the "*Gegentrommelfell*," a word which I think might conveniently be translated "*contratympanum*."

To those interested I would recommend a perusal of Eggers' work on the subject, since any attempt at a full description of this double-drummed organ would occupy more space than is at my disposal. Having given some account of known forms of these remarkable organs, we may now turn to the Uraniidae, as a type of which I propose to describe the structure and histology of the tympanal organ in *Chrysiridia ripheus*.

The Rt. Rev. the Bishop of Madagascar, who has in the past been a generous contributor to the Hope collections, kindly undertook, during a visit to this country, to obtain for me specimens of this moth, preserved in a manner suitable for histological investigation. For many reasons the consignment was delayed, and late last autumn I mentioned my requirements to Mr. W. F. H. Rosenberg, who promised to obtain, if possible, the desired material. I have to thank him for the great trouble he took in the matter, and for his ultimate success in obtaining the specimens, and I have also to thank the Bishop of Madagascar, since, through the medium of M. Herschell Chauvin of Tamative, his long-promised specimens arrived almost simultaneously with those from Mr. Rosenberg. What at first appeared to be an unnecessarily large amount of material ultimately proved to be a fortunate acquisition. Good histological preparations are difficult and uncertain of attainment with preserved specimens, and since, as will be described, the organs differ much in the two sexes, and the proportion of females secured was small, I could hardly have obtained satisfactory results from either of the consignments alone.

Methods and Technique.

My instructions to the collectors were to place the insects alive, or very fresh, in alcohol of about 90% mixed with half its bulk of a cold saturated aqueous solution of mercury bichloride. I am not sure whether this method was actually employed. The specimens arrived during my absence from Oxford, and since they might not have been fixed in the desired manner, they were given a bath of alcoholic mercury solution and afterwards placed in clean spirit.

In any case the histological results were on the whole good, though probably inferior to what might have been obtained by using a variety of fixatives applied to fresh material, followed by appropriate methods of staining. I should here make it clear that the preparation of such small and delicate objects as the tympanic nerves or chordotonal threads is a matter of some difficulty, and ample material is a necessity, for possible causes of failure are numerous and occur at all stages of the processes employed. The nerves themselves are ensheathed in a thin envelope of tracheal epithelium, unfortunately heavily nucleated, so that the staining is apt to obscure the nerve elements within. This envelope cannot be mechanically removed with much success, manipulation with the finest needles being somewhat like trying to handle with a crow bar the membrane beneath an egg shell. To see the nerve clearly longitudinal sections are necessary, and these must be extremely thin (2 to 3 μ) if they are to strike the nerve thread more than about twice. Correct orientation of so delicate an object in relation to the microtome knife is naturally difficult, and good results can hardly be expected from a few attempts. Added to this there is the difficulty that in order to see the object at all in the paraffin some of the surrounding tissue must be included, and this tissue is rather heavily chitinised, thus diminishing the chance of obtaining good sections. Nevertheless, with care and a sufficient number of preparations good results are not impossible of achievement. For the benefit of those who are interested in these matters I might mention a method of orientating a delicate object which I have found effective. Let us suppose it is required to cut a longitudinal section of a thin fibre or nerve. It should first be stained with some easily washed-out dye such as eosin, so as to make it visible under the stereoscopic microscope. Having brought it to the right condition for embedding, the watch-glass of melted paraffin containing the object is brought under the stereoscopic binocular, using a black tile for a stage. The paraffin will first begin to solidify at the bottom of the watch-glass, and the object should be lifted slightly with needles so as to allow a moderate thickness of solid wax to form beneath it. By this time the wax will have begun to solidify round the edges, and a very thin steel straight-edge, such as a six-inch steel rule, is laid across the watch-glass so that its edge is exactly in line with the long axis of the object. With a needle a slight mark is made on the solid edge of the wax at each side, just where the straight-edge crosses the glass. The wax is then rapidly cooled by floating the glass on water and finally plunging it beneath the surface. The wax being completely solidified, a fine line is drawn with a needle across its surface, using the straight-edge and the side marks already made. This line lies over, and gives the exact position of, the embedded object, and the block can then be mounted on the microtome so that the line is parallel with the knife blade, or, if transverse sections are required, at right angles to it.

Though the device is of my own invention I do not claim any special originality for it, and other workers doubtless use it or some similar method; but I have often been asked by students for a means of correctly orientating an object in wax, and I can recommend this as simple, and much more accurate in its results than might be expected. For staining the nerve preparations here to be described I found the iron haematoxylin method the most satisfactory. Nerves were dissected out and lifted from the watch-glass by means of a fine pipette, transferred to slides rubbed over with glycerine and albumen, and placed on a 40° C. electric hot-plate to dry. At this stage it is well to draw with the writing diamond, under a low power, a small circle round the object, as an aid in finding it again quickly. Put the whole slide in absolute alcohol for ten minutes, gradually hydrate and transfer to 2% iron-alum solution for half an hour, wash, and stain in 5% haematoxylin for at least an hour, wash, and differentiate in 1% iron-alum. Eggers obtained good results with safranin-*O*, differentiating in alcohol, but this method was not, in my hands, so successful. Apathy's gold method and other formulae were tried, but with poor results. Some few preparations refused to take even the haematoxylin stain, but in the majority of cases it proved very effective.

The Position and Structure of the Organ in the Male.

Plate XXIII, fig. 1, is a sketch of a lateral view of part of the male abdomen, after partial removal of the scales. The first segment is indicated by the two small plates under 1. It will be noted that the second segment bears a thick pad of scales. These are large, densely packed and very numerous. The third segment shows a deep depression apparently leading forwards into a cavity beneath the scale pad. This is all that can be seen in such a view. If we now carefully remove the scales by scraping with a needle at their attachments, we shall obtain the preparation shown in fig. 2. The posterior margin of the second segment is seen to be thickened and its outline deeply indented in a forward direction. We also see a bladder-like structure, *V*, lying in the cavity formed by the depression of the third segment. It is for the most part a soft and rather delicate opaque membrane, but becomes transparent and still more delicate at *T*, which is the actual tympanum.

If we now cut out the whole side of the body over this area, clear away the fat, connective tissue, etc., with which its inner surface is lined, and turn it over so as to inspect the inner side, we see what I have endeavoured to represent in fig. 3. What was the right side in fig. 2 is now the left. The depression in the third segment is seen to form a more or less hemispherical chamber, *C*, through the wall of which can dimly be seen at *V*, the outline of the bladder-like structure, or tympanal vesicle, and the tympanum itself which looks paler owing to its transparency. On cutting away the invagination of the cuticle of the third segment as along the dotted line in fig. 3, the under or inner side of the tympanal vesicle is shown as in fig. 4, the tympanum again appearing owing to its greater transparency, though it is still on the other or outer side. The thin wall of the tympanal vesicle is much tougher than the tympanum itself, and in cutting it away great care must be exercised to avoid rupture. If the operation be successfully performed the preparation will now have the appearance of fig. 5, which was drawn under a much higher power. At *M* is a somewhat concave band of radiating muscle fibres. Their purpose is somewhat obscure, though, as they are attached to the membrane of the tympanal vesicle, they would seem to be capable of adjusting the tension of that structure. At *Vc* is the cut edge of the vesicle, *Ct* a mass of tracheal epithelium which at *G* forms a swelling containing a minute ganglion. From this ganglion there passes an extremely fine connection to *N*, which latter is the tympanal nerve or chordotonal thread and is pointed like a tiny arrow-head. Both the fine connection and the chordotonal thread are provided with a delicate sheath of tracheal epithelium. The chordotonal thread is joined to the tympanum *T* at its pointed end. The nerve fibres connecting the tympanic nerve to the ganglion are so delicate that so far I have been unable to remove them with the connection intact. The only practicable method is to mount them separately. Even the eyepiece micrometer becomes a clumsy instrument with which to measure this delicate connection, which, exclusive of the sheath and supporting cells, appears to have a diameter at its thinnest part of about ·0005 mm.

Let us now turn to Plate XXV, fig. 4, which represents a very highly magnified view of the ganglion and the tympanic nerve. The figure is drawn from a longitudinal section of the ganglion combined with a whole preparation of the tympanic nerve. The ganglion is at the lower part of the figure. *Sh* is the sheath of tracheal epithelium, which in its proximal part shows numerous excrescences, each containing a nucleus *Sn*. As it passes to the distal end of the nerve it becomes thinner and the nuclei flatter. I have not shown this membrane as spread over the nerve, since its nuclei would confuse the figure. The structure of the ganglion is not easy to analyse. Cell-walls are hardly at all visible in my preparations, and apparently Eggers found the same difficulty in studying the tympanal nerves of other moths. Judging by the two granulated nuclei *Ln*, there are two large lateral cells. In the centre is a bipolar cell *Sc*, which, having become detached in the section, can be more easily distinguished, and its rather faint nucleus *Scn* can also be seen. For reasons which will presently appear I am inclined to think that there are at least two of these central cells, and that my section has touched only one of them. Proximally it is drawn out into a bundle of fibres doubtless continuous with the main nerve connection, while distally it diminishes to a delicate strand or axis fibre (already referred to) forming the core of the connection between the ganglion and the tympanic nerve. The remaining structure of the ganglion is peculiar and rather difficult to observe. In the drawing several broad curved dark lines are shown, *L.* These appear to be the indications of a kind of laminated structure. If a hyacinth bulb be cut in two similar lines are seen indicating the cut edges of the scaly leaves, and if one of these ganglia be mounted under compression the appearance is very like that of a crushed bulb. If, however, such a crushed preparation be stained with haematoxylin the effect is not that of scaly leaves, but still appears as black lines, from which I can only conclude that the ganglion contains concentrically arranged rods of a chromatophilous nature. Where the ganglion tapers off to the connecting thread two small nuclei are seen, and these I take to represent sheath or supporting cells.

We now reach the chordotonal thread in which the most conspicuous structures are the two little ribbed fusiform bodies *SS*, shown in the drawing. These or similar structures have been observed in all chordotonal organs, and have been named "scolopales" by Graber. They are hollow bodies, said to contain fluid, and in transverse section show an internally ribbed structure. Eight such ribs were found by Eggers in the forms he examined. Through the centre of the organ a delicate nerve filament passes. In the chordotonal threads of moths the number of these scolopales seems always to be two, and as Eggers has observed, one is always somewhat larger than the other. In the drawing (fig. 4) it will be noted that the proximal end of the scolopale is produced into a peg-like form. This terminal process is very transparent and not easy to see in all preparations. The opposite end seems solid and always stains deeply. It is produced into a filament of extreme delicacy, which also takes the stain, and can in most preparations be traced for some distance in the substance of the chordotonal thread. It should here be noted particularly that the dark solid end of the scolopale is distal, and it is so shown in all Eggers' drawings. We shall return to this point in describing the chordotonal thread of the female.

The remainder of the tympanic nerve shows a faintly fibrous structure, containing several pale nuclei, followed distally by elongated, proximally rounded, and darkly staining bodies, which end distally in two bundles of very delicate fibres also taking a deep stain. The sheath of tracheal epithelium is here extremely attenuated and permits a clearer view of the nerve structures.

Eggers points out that in other chordotonal organs as also in those of moths which he has investigated, the essential structures seem to be a bipolar sensory cell, proximally connected with the central nervous system and distally tapering into the scolopale, the latter being distally attached to a third body called a "cap cell." The other nuclei frequently observed must be regarded as belonging to sheath cells, supporting cells, and other accessory bodies. For this reason we must suppose that the bipolar cell whose nucleus is marked *Scn* in fig. 4 is, as I have already hinted, one of two which connect respectively with the two scolopales. The cap cells are not clearly evident, unless we so regard the elongated stained bodies shown in the distal portion of the figure.

The Position and Structure of the Organ in the Female.

It now remains to describe the corresponding organ in the female, and here we shall see marked differences from that of the male. Plate XXIV, fig. 1, is a sketch of a lateral view of part of the abdomen at its junction with the thorax, after partly removing the scales. The most conspicuous feature is a large flap-like evagination of the metathorax, projecting posteriorly over the first and part of the second abdominal segments.

The posterior edge bears a fringe of scales and hairs, though these are not so dense as in the scale pad which covers the tympanic organ of the male. If this structure be cut away we see beneath it a vesicular body, fig. 2, *Tv*, apparently for the most part buried in the second segment. Its surface is smooth, comparatively hard, and chitinous, while anteriorly it possesses a semicircular thickened margin which forms the framework of the tympanum *T*. In the male the tympanum is so placed as to be nearly parallel with the general lateral plane of the insect's body. In the female it faces more forward so as to be nearly in a transverse plane. Fig. 3 shows a more magnified view of the tympanal vesicle removed from the body, with part of the cuticle *C* of the second segment, and as viewed from the anterior position. The tympanum is now more distinctly seen and the tympanic nerve *N* can with favourable lighting be observed on its under surface.

If the preparation be now turned over, the rest of the tympanal vesicle can be seen projecting into the body cavity. Unlike the soft and membranous vesicle of the male it is hard and chitinous and of a globe-like formation. Cut away the greater part of it and we have the view illustrated in fig. 4, still more highly magnified, where *Tv* is the remains of the vesicle, *C* the cuticle, now seen from the inner side, *T* the tympanum, and *N* the tympanic nerve or chordotonal thread. In this case the tympanal nerve, while arising from a position similar to that in the male, is without any accessory ganglion. Moreover, whereas the tympanum of the male is a delicate membrane showing little structure, that in the female exhibits in the area immediately surrounding the attachment of the nerve, a dotted and opaque appearance, due to the presence of numerous heavily nucleated cells which project on the external side, *i.e.* the opposite side to that on which the nerve is attached.

At fig. 5 I have shown the appearance of a small piece of the tympanum viewed from the inner side, and at fig. 6 a section of the same, showing the nucleated external prominences, which as will be noted have small setae arising from their surfaces. The finer structure of the female chordotonal thread is shown at Plate XXV, fig. 1. It has a sheath of tracheal epithelium which, from its proximal end to the first enlargement, is ringed with irregular ridges, which in this figure are only shown in section, but partly in a surface view at *Sh*, figs. 2 and 3. Except for its crinkled and irregular form one might compare it with an armoured hose-pipe. It contains many irregular darkly staining nuclei, which unfortunately much obscure a critical examination of the nervous structures within. As far as the first enlargement of the chordotonal thread the nerve appears to be of the ordinary fibrous structure. It then becomes swollen and shows distinctly the two scolopales *S*, and certain large nuclei *Ln*, of which three are visible in this preparation. The more distal of the scolopales is seen to taper off into a very delicate axis fibre which, expanding into the second enlargement, finally tapers off again to its point of attachment upon the tympanum. In this distal portion both large and small nuclei are seen, and a generally fibrous structure. In describing the male chordotonal thread it was pointed out that the most extensively dark-stained ends of the scolopales were distal. Now in the preparation shown in fig. 1 the reverse is the case, although both ends take the stain to some extent. And here it must be stated that the general shape of the tympanic nerve in the female is very irregular and variable. It can scarcely even be said that fig. 1 shows the commonest form, at least so far as my preparations indicate. Other examples show the first swelling of the organ, not symmetrically placed, but in the form of a lateral expansion of the thread, as in figs. 2 and 3, which are from two other preparations, each peculiar in form. In these two examples the second enlargement is broken away, but its relative position is towards the top of the figure. In fig. 3 the sheath obscures the underlying tissues so completely that only the scolopales can be seen. Nevertheless, all three preparations and also others not figured show the darker-staining portion of the scolopales proximal instead of distal as in the male, and moreover the smaller of the two scolopales is also proximal and not distal as in the other sex. In other words, the scolopales appear to be reversed in position in the female. What the significance of this may be I am unable to suggest. Before asserting that it is the normal condition I should prefer to have many more preparations than my present material affords. An idea which almost inevitably suggests itself is that the tympanal organ may be sound-receptive in one sex and sound-productive in the other, but we do not at present know that one sex of *ripheus* makes a noise of any kind, nor, so far as I am aware, are typical chordotonal nerve structures associated with sound-producing organs. So far as sound-production is concerned we should expect to find some muscular mechanism in connection with the tympanum, and this we certainly do find in the male (see Plate XXIII, fig. 5), but the male scolopales have the normal orientation, and the homologous organs in other moths are generally similar in both sexes, and it has not been suggested that these are other than sound-receptive. Much further observation of the living animal is necessary before we can profitably discuss the problem.

At Plate XXV, fig. 5, I have shown semidigrammatically the general nerve connections of the tympanal organs in the female. At *Tg* are the coalesced thoracic ganglia from which the central nerve cord *Cn* passes backwards to the abdominal region. Several branches are given off, not all of which are indicated, but at *Ba* is a delicate ramus which is the only connection I can find leading to the margin of the connective tissue bordering on the

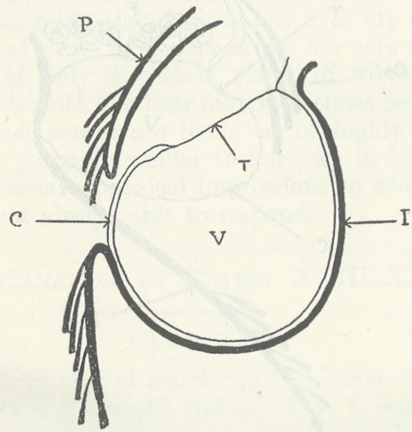


FIG. 1.

tympanum, and I take it to be the branch leading to the tympanic nerve. In spite of the apparent difference of structure in the two sexes, the vesicles are of essentially similar formation as I have illustrated in text-figures 1 and 2. Fig. 1 is a diagrammatic section of the female organ. *I* is the integument of the second abdominal segment which is seen to bend sharply backwards and so surround the vesicle *V*, the cuticle *C* of which lines the cavity so formed. This cuticle is itself lined with delicate tracheal epithelium, which, extending across at *T*, forms the tympanum. *P* is the evagination of the metathorax which forms a cover for the tympanum. At text-figure 2 a similar section of the male organ is shown. The invagination of the abdominal integument *I* is shallower, forming a mere depression. *V* is the vesicle with its cuticle *C*, thinner and less globular in form than in the female, but forming the small tympanum at *T*. *F* is a mass of fat and muscle cells adjacent to the anterior wall of the vesicle, and *Cs* is part of the pad of covering scales.

As in so many anatomical investigations, so in this, we may arrive at more or less satisfactory conclusions as to the structure and histology of an organ, but the manner and extent of its functions remain in a great measure in doubt. Eggers devotes some space to the function of

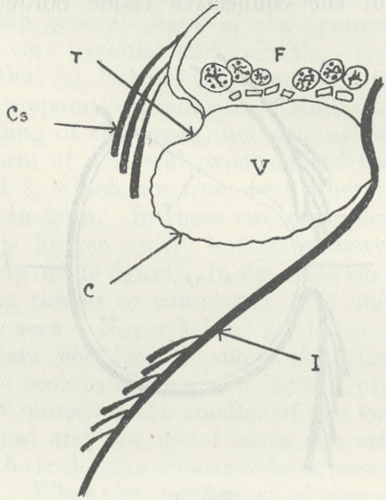


FIG. 2.

these organs, but comes to no very certain conclusions in regard to them. That some insects can hear has been shown by Regen's experiments on *Liogryllus campestris* (Zool. Anz. 40, p. 304, 1912) in which the females were only uninfluenced by the chirping of the males, when their auditory organs had been removed. Several experiments on the hearing powers of moths have been described, but apparently none have been carried out so as to eliminate all sources of error. We know that some moths and butterflies do make noises (*Ageronia*, *Aegocera*, *Halias prasinana*, etc.), but the power so far as at present known is rare, whilst the presence of tympanal organs is of common occurrence. Chordotonal organs have been detected in the wings, antennae, legs, and bodies of various insects, notably by Vogel in the wings of Lepidoptera (Zeit. Wiss. Zool. 100, p. 210, 1912), and Eggers recalls the presence of swollen nervures in the wings of many species, such dilations being possibly connected with the chordotonal organs found in the wings. Probably in the present imperfect state of our knowledge of insect senses, we can do little more than record the fact that these peculiar nerve structures, or scolopales, are prominent features of organs which in Orthoptera we know to be auditory, and that their presence in moths in conjunction with tympana and tracheal vesicles strongly supports the view that such moths can hear. As to the sounds which they are adapted to detect, we must remember that just as our eyes are sensitive to only a limited range of the spectrum, our ears can respond to sounds of only a certain range of vibrations. The sounds that a moth can hear may sometimes be beyond our range. Insect senses are liable to be highly specialised, and though probably similar to our own in kind, may be adapted to receive physical impressions to which our own senses are not always able to respond.

Explanation of Plates XXIII–XXV.

PLATE XXIII.

Fig. 1. Lateral view of anterior part of abdomen and part of metathorax of ♂ *Chrysiridia ripheus.* 1, 2, 3, segments of the abdomen.

Fig. 2. The second and third abdominal segments after removal of the scale pad. *V*, the tympanal vesicle; *T*, the tympanum.

Fig. 3. View of the inner side of the depression in segment 3. *C*, the abdominal integument; *V*, the tympanal vesicle seen through the chitinous integument.

Fig. 4. Same as fig. 3, but with the abdominal integument cut away to show the vesicle *V*.

Fig. 5. Same as fig. 4, but more highly magnified, and part of the tympanal vesicle cut away. *Vc*, the cut edge of the vesicle; *M*, band of muscle fibres; *Ch*, chitinous ridge; *T*, tympanum; *N*, chordotonal thread; *G*, the ganglion; *Ct*, mass of connective tissue and tracheal epithelium.

Note.—The magnifications vary, but some idea of the actual sizes may be gathered from the length of the chordotonal thread *N*, fig. 5, which is ·1 mm.

PLATE XXIV.

Fig. 1. Lateral view of anterior part of abdomen and part of metathorax of ♀ *Chrysiridia ripheus.* 1, 2, 3, abdominal segments; *Thp*, the evagination of the metathorax covering the tympanum.

Fig. 2. The same with the metathoracic evagination removed. 1, 2, abdominal segments; *Tv*, the tympanic vesicle; *T*, the tympanum.

Fig. 3. The vesicle with surrounding tissue removed from the body and seen from a more anterior point of view. More highly magnified. *C*, the abdominal integument; *T*, the tympanum; *N*, the chordotonal thread seen through the tympanum.

Fig. 4. Same as 3, but turned over and viewed from inner side, the inner half of the vesicle cut away, and more highly magnified. *C*, the abdominal integument; *Tv*, the remains of the tympanal vesicle; *T*, the tympanum; *N*, the chordotonal thread.

Fig. 5. A small piece of the tympanum, stained with haematoxylin and showing the nuclei.

Fig. 6. A section of the tympanum showing the nucleated projections and their processes.

Note.—The magnifications vary, but some idea of the actual sizes may be gathered from the thickness of the tympanum, fig. 6, which is ·008 mm. including the projections.

PLATE XXV.

Fig. 1. The chordotonal thread of the ♀ *Chrysiridia ripheus. Sh*, sheath of tracheal epithelium; *N*, nuclei of nerve; *Ln*, nuclei in first enlargement; *S, S*, scolopales; *Sn*, sheath nuclei.

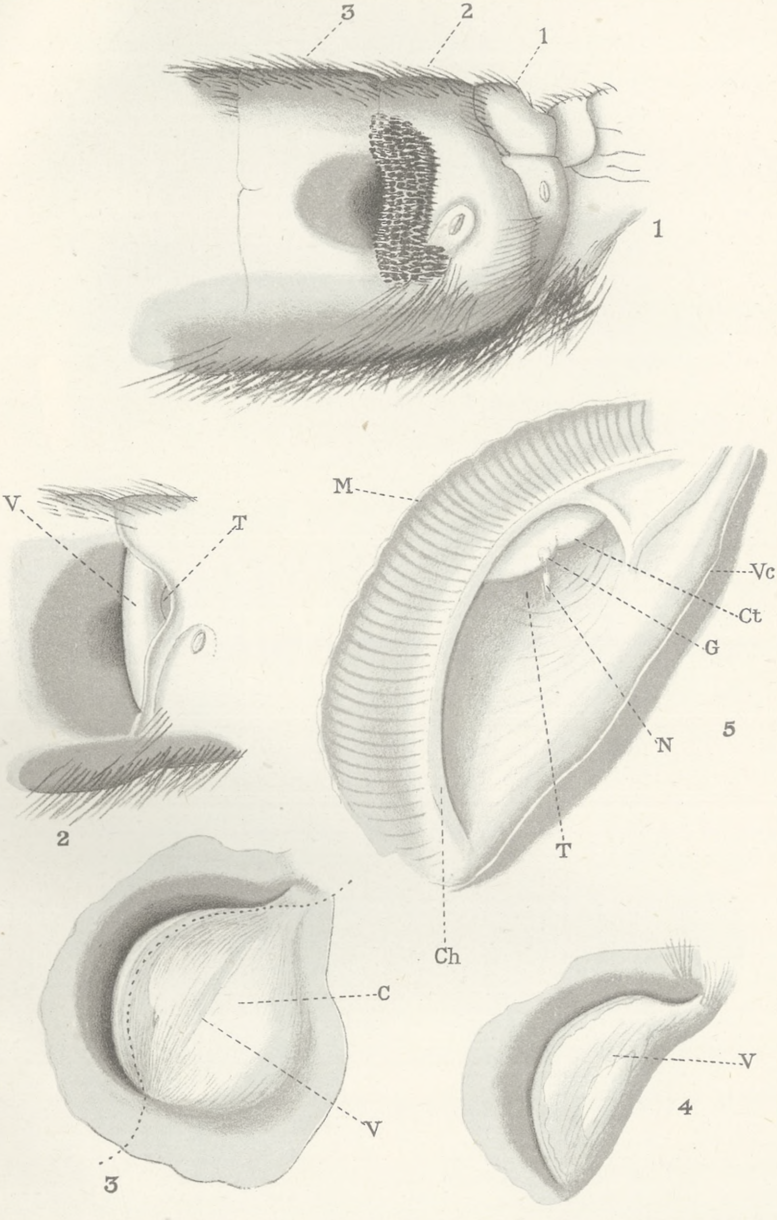
Fig. 2. First enlargement of ♀ chordotonal thread of another example. Lettering as before.

Fig. 3. Ditto from another example.

Fig. 4. The chordotonal thread of the ♂ *Chrysiridia ripheus. L*, Dark staining lines of the ganglion; *Ln*, large nuclei in ganglion; *Sh*, the sheath of tracheal epithelium; *Sn*, sheath nuclei; *Sc*, bipolar cell; *Scn*, nucleus of same; *S, S*, scolopales.

Fig. 5. Diagram of nerve connections. *Tg*, the thoracic ganglia; *Cn*, central nerve cord; *Va*, the tympanal organs; *Ba*, the auditory nerve branch (?).

Note.—Length of ♀ chordotonal thread ·222 mm. Length of a scolopale ·01 mm. Length of ♂ nerve without ganglion ·1 mm. Diam. of axis cylinder joining ♂ ganglion to chordotonal thread ·0005 mm. Length of ganglion in ♂ ·133 mm.



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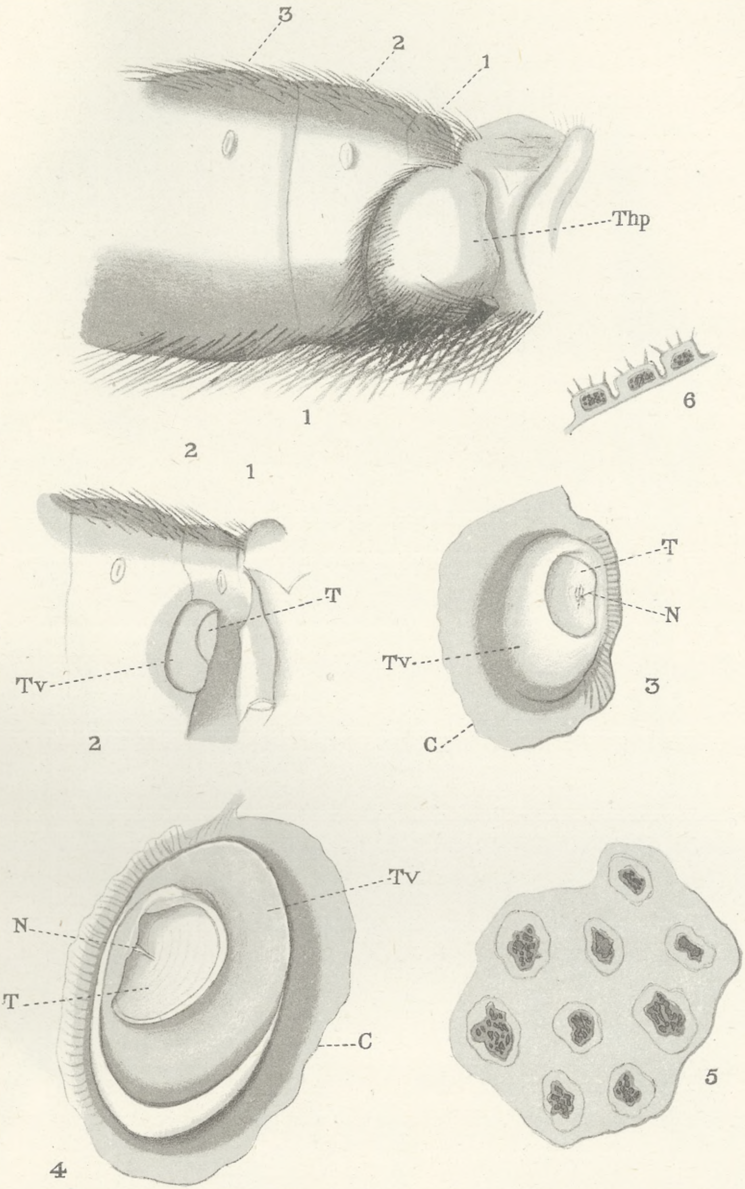
TYMPANIC ORGAN IN C. RIPHEUS. MALE.



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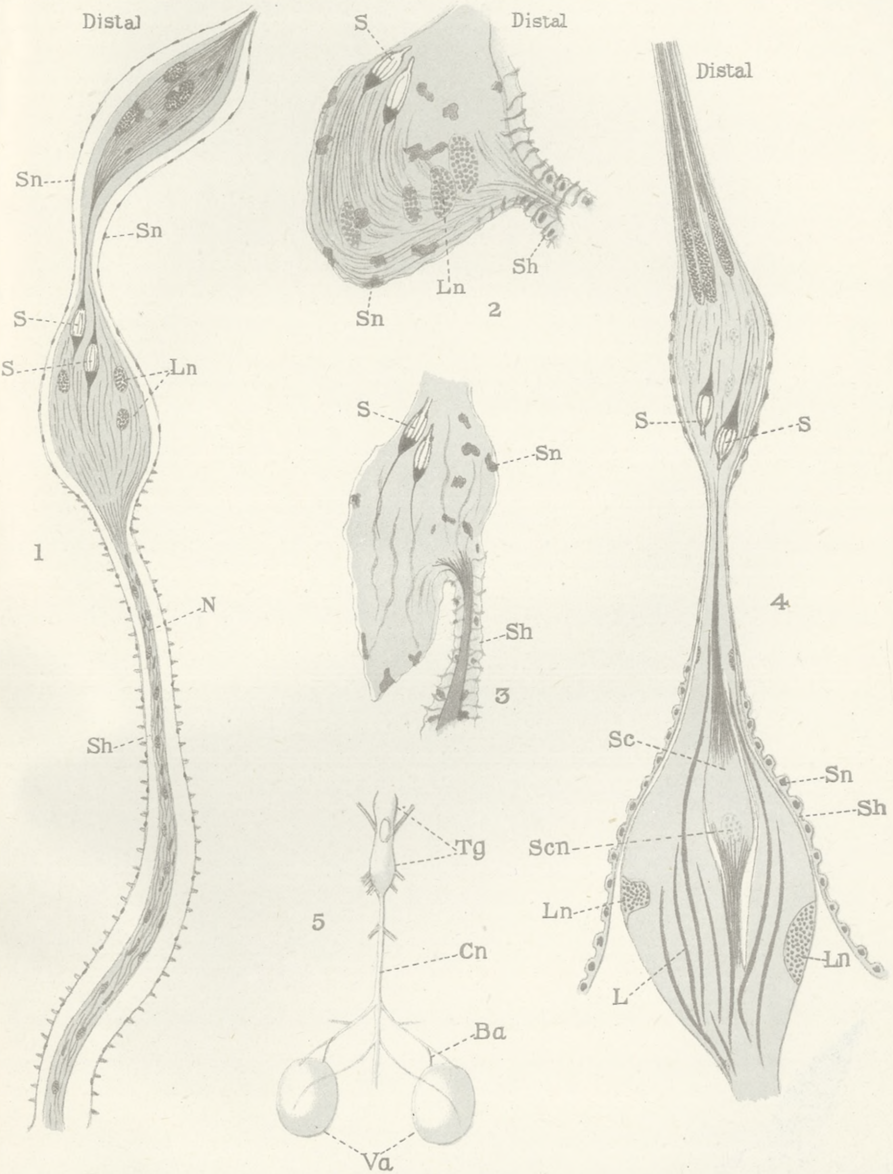
TYMPANIC ORGAN IN C. RIPHEUS. FEMALE.



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TYMPANIC NERVES IN C. RIPHEUS.