

THE PHYSIOLOGY OF THE TETTIGONIID EAR

I. THE IMPLICATIONS OF THE ANATOMY OF THE EAR TO ITS FUNCTION IN SOUND RECEPTION

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INTRODUCTION

Ever since the anatomy of the Tettigoniid ear was described by Schwabe (1906) the previously inferred function of sound reception by the tympanal organ has undergone repeated anatomical (Sharp, 1922; Carpentier, 1924, 1927; Zeuner, 1936; Howse, 1968) and physiological (Pumphrey, 1940; Autrum, 1940, 1941; Haskell 1956; McKay, 1969, 1970; Zhantiev, 1970; and others) investigations, but the function of the tympanal organ has usually been interpreted on the basis of the tympanal region alone, even though suggestions as to the importance of the prothoracic acoustic trachea are found in the work of von Siebold (1844), Graber (1876), Carpentier (1924, 1927), Zeuner (1936) and others.

The Tettigoniids have cuticular folds protecting the external membranes and have developed a complex receptor, the crista acoustica, in addition to the subgenual organ and intermediate organ of the Gryllids (Schwabe, 1906; Howse, 1968; Freidman, 1972; Schumacher, 1973). The tracheal system which forms the tympanal air spaces behind the external tympanal membranes of Tettigoniids, takes origin from the large 'acoustic' portion of the double prothoracic spiracle which opens into a vesicle from which arises a horn-shaped trachea; this descends into the leg and splits in the region of the tympanal organ to form the anterior and posterior cavities. If the spiracular opening is large, if the trachea is horn-shaped, and if the trachea has no respiratory branches, then its importance in the functioning of the tympanal organ in sound reception may be greater than the resonance or damping function (Zeuner, 1936; Pumphrey, 1940) ascribed to it.

This paper considers the importance of the tracheal system for sound reception in Tettigoniids and the implications of the findings for the physiology of the ear. Subsequent papers will consider the role of the cuticular folds, the external and central membranes, and some aspects of the biophysics of the whole system. Finally, the implications of the findings to the existing theories of acoustic orientation behaviour, and acoustic feedback will be considered.

MATERIALS AND METHODS

Insects

Most of the present study was carried out on *Homorocoryphus nitidulis vicinus* (Walker), but comparative anatomical studies were made on species of the genus

Platypleis, on *Jamaicana subguttata* and *flava*, *Metrioptera brachyptera* and the Gryllid *Acheta domesticus*.

H. n. vicinus was subcultured from a culture at Nottingham University originating from Uganda, and was used in this study since most of the frequency range of its song is within the range of the recording and analysing equipment available in this Unit.

The specimens of the genus *Platypleis* were collected in the South of France, and *M. brachyptera* was caught near the New Forest. The two specimens of *Jamaicana* were obtained from Nottingham University, dead and preserved in Pampel's fluid. *A. domesticus* was cultured in this Unit.

Anatomy

Dissections of the 'acoustic' tracheal system of the prothorax were performed on all the available specimens, and the dimensions of the trachea and spiracle were obtained under $\times 30$ magnification. Internal views of the spiracle were obtained by making a longitudinal sagittal section of the prothorax and then carefully clearing away the tracheal and muscular tissue.

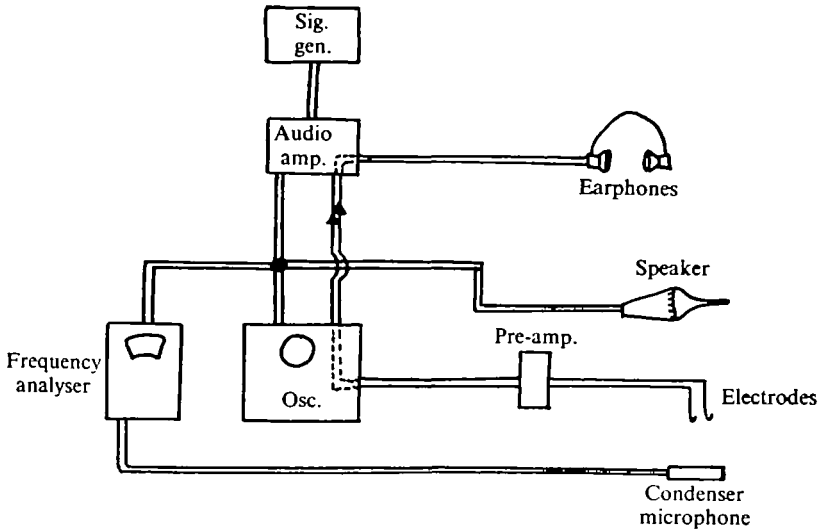
Sound stimulus production and calibration of intensity

Throughout the study, the sound stimuli used were generated by using a circuit modified from Jones (1966). This circuit produced pulse trains of sine waves at a constant predetermined rate, set by the output of a square-wave generator. The latter was also capable of varying pulse duration between 10 μ sec and 100 msec, but except for the preliminary experiments where pulses of 80 msec were used, all other stimuli were set for 8 msec. A diode was biased so that a signal was produced only when the square-wave generator produced a d.c. pulse. During this time a train of sine waves of a pre-selected frequency was delivered to the speaker.

The amplifier used was that of an Akai X-300 stereo tape-recorder modified to run at 15 i.p.s. and with circuitry modifications to produce a flat response up to 28 kHz. Signal intensity was controlled by means of the line input control knob.

Eight msec 'clipped' sine waves were used since the intention was to determine the effect of a sound stimulus comparable to that produced by the male of *H. n. vicinus*. Eight msec pulses are comparable to the syllable duration in the natural song, and the frequency components of the artificial signal were very similar to the frequency curve of the natural song. This artificial signal was more likely to give responses which were a closer approximation to the responses to the natural song than would be obtained from a long train of sine waves. However, there are certain disadvantages in using such a signal. First, the clipping of the sine waves will introduce harmonics and side bands into the signal such that any determination of thresholds will not be to a single frequency but to a frequency band centred on the relatively high intensity of the peak frequency. Secondly, the extremely short time-course of an 8 msec signal will give no indication as to the steady-state characteristics of the tympanal organ system. Investigations are now in hand to determine the side-band content of Tettigoniid songs and also the steady-state responses of the tympanal organ in the far field.

Natural insect song approximates to a point source. In order to reproduce this as nearly as possible and in order that the speaker could be moved near to the preparation when required, a small Akai X-IV microphone was used as a sound emitter.



Text-fig. 1. Plan of the arrangement of the equipment for electrophysiological recording and monitoring of the sound intensity. (Further explanation in text.)

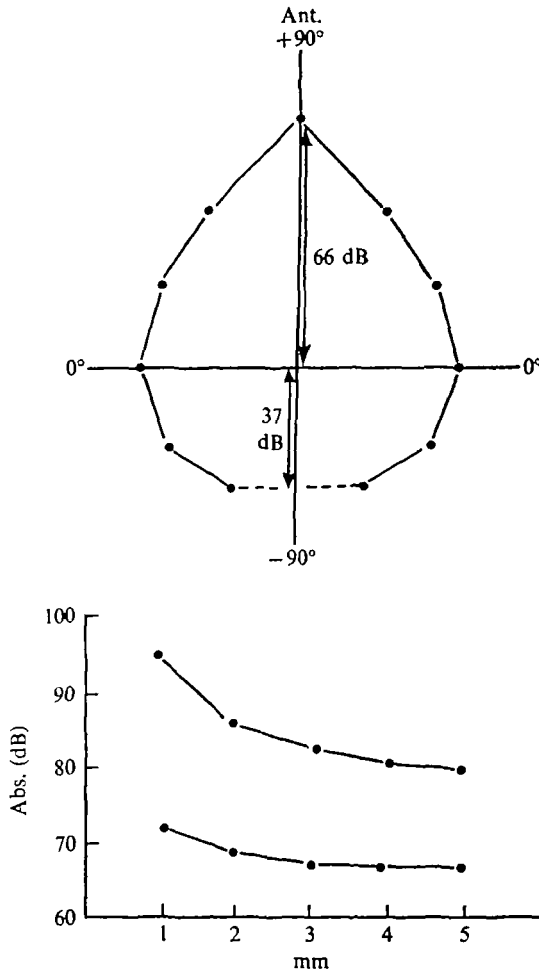
When a more specific and localized sound source was required an exponential perspex probe with a tip diameter of 1.0 mm was fitted over the head. By this means the sound stimulus could be directed at any small area of the preparation. Since the sound intensity at threshold was measured 1.0 mm from the emitter probe tip by means of a $\frac{1}{4}$ in. B & K microphone, the emitter probe and microphone specification was not measured in detail (but see below).

In those experiments where the probe was used, it was possible to measure the sound intensity emitted at the same time as recordings were made from the preparation. The amplifier output was therefore fed to the Tektronix 502A oscilloscope and to the amplifier input of a B & K Frequency Analyser Type 2107, as well as to the Akai microphone-emitter (Text-fig. 1). The input intensity delivered to these could be read directly in dB on the scale of the microphone amplifier section of the B & K Analyser. On completion of the experiments, the preparation was removed and the relative input intensities in dB were calibrated against the output intensities 1 mm from the probe tip using a B & K $\frac{1}{4}$ in. microphone with a 1 mm probe attachment. This diameter is comparable to that of the spiracle. Sound intensity levels (in dB relative to 0.002 dyn/cm²) at the structure under investigation were thus obtained. The directional characteristics of the emitter probe are given in Text-fig. 2.

Sound frequencies below 1 kHz and above 20 kHz were not utilized on account of the limitations of the available equipment. However, since the dominant frequency of the song of *H. n. vicinus* has been shown to be (Bailey, 1968) between 14 and 17 kHz, with a range of 6–36 kHz, a considerable portion of the frequency band will have been investigated.

Experimental procedure

Before commencing any series of physiological experiments, the specimen was first immobilized with carbon dioxide and held in position by Plasticine. In the preliminary experiments the recordings were made of the tympanal nerve activity at the



Text-fig. 2. Characteristics of the emitter probe. Top: directionality. Bottom: intensity drop with increasing distance from the probe tip.

point where this nerve entered the prothoracic ganglion. The connectives were cut, together with all the motor nerves leaving the ganglion, and the tympanal nerves were raised on hook electrodes. The common electrode was a pin pushed through the abdomen. This preparation remained active for about 6 h and allowed the comparison of the effect of blocking the spiracle on one side with the normal open spiracle of the opposite side. Before this was started, however, the specimen was allowed to recover from carbon dioxide narcosis. The stimulus was an 80 msec pulse of clipped sine-waves set at 8 kHz and 5 pulses sec^{-1} , an Akai X-IV microphone being used as a sound-emitter. The sound source was anterior, 12.5 cm away from the preparation, where the intensity was 45 dB absolute.

The blocking of the spiracle and later the tympanal slits was performed using a latex adhesive, Copydex, which could be peeled off after setting if necessary. The acoustic properties of the Copydex were investigated using a B & K $\frac{1}{4}$ in. microphone and probe attachment, the probe tip being 1 mm in diameter and equivalent to the

spiracular diameter. Sound pulses were produced such that the microphone gave a reading of 50 dB (relative to 0.0002 dyn/cm^2). The tip of the probe was then plugged with Copydex and the sound intensity as measured fell to a value too low to give a reading on the B & K Frequency Analyser Type 2107. After removal of the Copydex the reading returned to 50 dB.

The effects on sound reception of blocking and reopening both the spiracle and the tympanal slits were tested unilaterally, by recording from the femoral portion of the tympanal nerve just above the knee. The specimen could thus be held in a relatively normal position so that both the spiracle and the tympanal slits were constantly accessible. The high motor activity after recovery from carbon dioxide anaesthesia necessitated cutting the motor nerve to the leg near the ganglion, far enough away from the tracheal system to avoid damage. Because the haemocoelic pressure and muscle mass around the leg trachea may have been important, it was considered undesirable to cut a window in the cuticle of the femur. The horizontal insertion of a sharpened entomological pin as an electrode just below the surface of the cuticle gave large-amplitude recordings. Glass suction electrodes had no advantage over the hook electrodes. The sound stimulus was delivered through an Akai X-IV microphone with an exponential probe attachment placed 1 mm from the structure under investigation. The signal was an 8 msec pulse of clipped sine waves set at 12 kHz at a rate of 5 pulses sec^{-1} , and the intensity 1 mm from the probe tip was 47.5 dB referred to 0.0002 dyn/cm^2 .

Threshold determinations were made by placing the emitter microphone and probe at either the spiracle or the tympanal slits and then gradually decreasing the sound intensity until the responses of the tympanal organ as shown by the compound potentials in the tympanal nerve could no longer be distinguished aurally or visually from background activity. This intensity was taken as the threshold for that frequency.

Electrical and acoustic isolation of the preparation

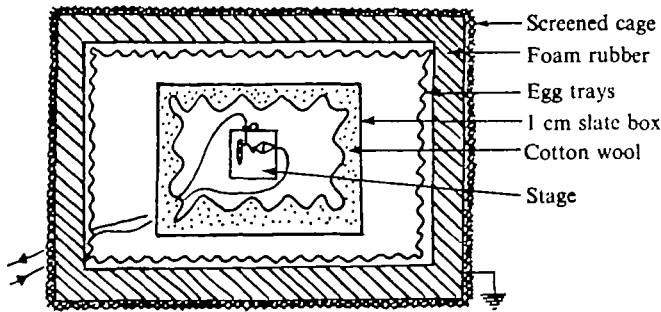
All investigations were carried out in a small-mesh copper-gauze Faraday cage resting on a steel plate 12.5 mm thick which was earthed (Text-fig. 3). The cage was lined with 5 cm of foam rubber overlaid with cardboard egg-trays to give some echo attenuation to low frequencies. A microscope lamp brought into position for dissection was swung away and disconnected when the preparation was set up, and the stereo dissecting microscope was also removed. The specimen rested on the stage of a Research Instruments micromanipulator which held the electrode, and the whole was enclosed in a box of slate 12.5 mm thick whose open end rested on the metal base-plate. The box was lined with 50–75 mm loops of cotton wool to attenuate high-frequency echoes. The front of the Faraday cage was then lowered and sealed off. By this means the high ($50 \pm 3 \text{ dB}$) background noise of the laboratory was reduced to $33 \pm 3 \text{ dB}$ inside the slate box.

RESULTS

Anatomical

Descriptive

The large prothoracic spiracle of *H. n. vicinus* is not fully visible externally, being almost covered, but not occluded, by the postero-lateral border of the pronotum.



Text-fig. 3. Plan of anechoic cage.

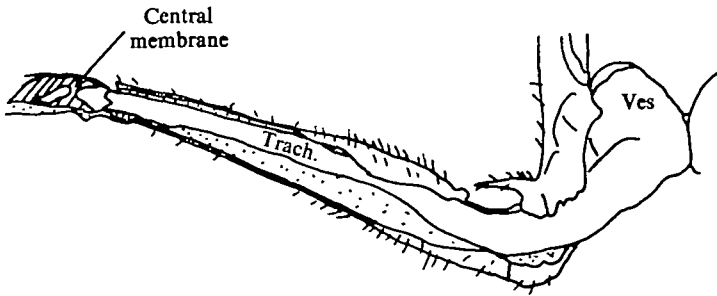
The angle between the pronotum and the plane of the spiracle is approximately 45° . Plate 1, fig. 1 shows the position of the large spiracle above the base of the first coxa after removal of the pronotal flap, and allows comparison with the small mesothoracic spiracle. The 'acoustic' opening of the prothoracic spiracle in Tettigoniids is devoid of lips but is protected by large hairs, and there is no obvious means of closing the spiracle. Plate 1, fig. 2 shows the double nature of the prothoracic spiracle, the acoustic opening being separate from the truncal opening which may be seen as two tracheal branches arising from its anterolateral border. These tracheae are possibly the posterior supraventral and posterior laterodorsal tracheae of Carpentier (1927).

The vesicula or large air sac behind the spiracle, together with the upper portion of the femoral trachea, forms a horn-shaped tube which descends into the leg to form the air spaces behind the external tympanal membranes. Text-fig. 4 shows the femoral vesicle and its trachea in *Homorocoryphys*. From its origin at the spiracle to its bifurcation at the tympanal region, no branches of this trachea were seen under $\times 30$ magnification. A communicating trachea between the vesicles is usually present (Zeuner, 1936), and was noted in all the Tettigoniids investigated except *J. flava*, where the vesiculae were widely separated. Thick sections of this communicating trachea in *H. n. vicinus* showed no patent cavity. The vesicular and tracheal walls are thick and rigid with the spiral thickenings of conventional tracheae appearing like a tightly coiled spring. These air spaces cannot therefore be compared to the flaccid air-sacs of the Acridids.

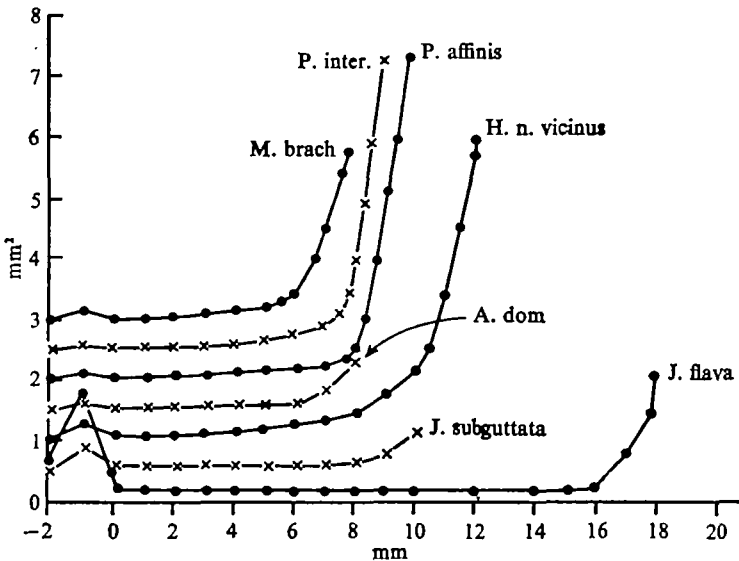
In the Gryllids, such as *A. domesticus*, the opening is covered, and can be closed by an opposable lip positioned over both divisions of the double spiracle. The vesiculae are extended medially and are still patent where they abut at the midline. The cavity is not continuous, however, the right and left vesiculae being separated by a membrane formed by the walls of the two vesicles. The 'acoustic' trachea descends into the leg as a branch of this transverse trachea and is therefore not in direct line with the acoustic spiracle as it is in Tettigoniids. The only flare associated with the tracheal system in *Acheta* occurs in the vesicle.

The diameters of the trachea of all the animals investigated was measured at 1 mm intervals along their lengths and their cross-sectional areas were calculated. The curves of the areas against the axial distances are given together for comparison in Text-fig. 5.

The narrowest portion of the femoral trachea in Tettigoniids occurs at the femoro-



Text-fig. 4. The large acoustic trachea of *H. n. vicinus* descending through the prothoracic leg and ending at the tympanal region. A portion of the central membrane is visible in the tympanal region.



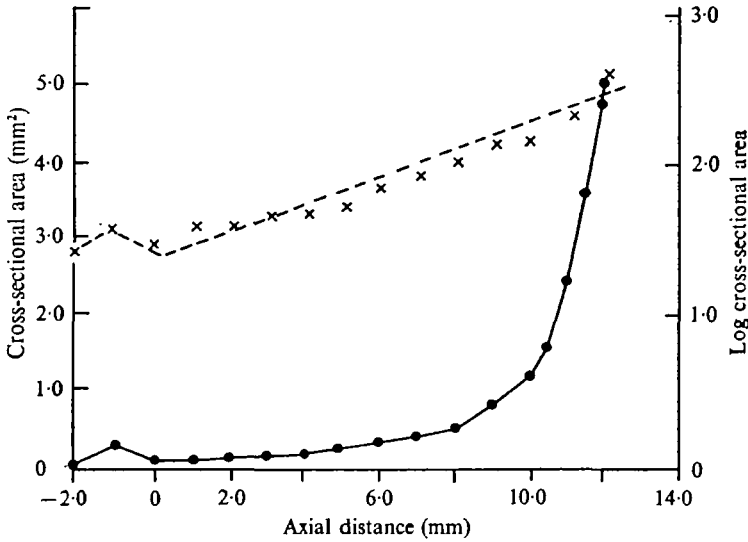
Text-fig. 5. The curves of length against cross-sectional area for a variety of acoustic tracheae. For clarity the base-line has been raised by 0.5 mm² for each successive curve.

tibial joint beyond which the tracheal cavity increases in total volume, dividing into two branches to form the tympanal air spaces, the apposed walls of these branches forming the central or secondary (Pumphrey, 1940) tympanic membrane. Measurements of the volumes of these cavities were made under $\times 32$ magnification and are given in Table 1. It is of interest that the posterior cavities have volumes approximately half the volumes of the anterior cavities in all the Tettigoniids.

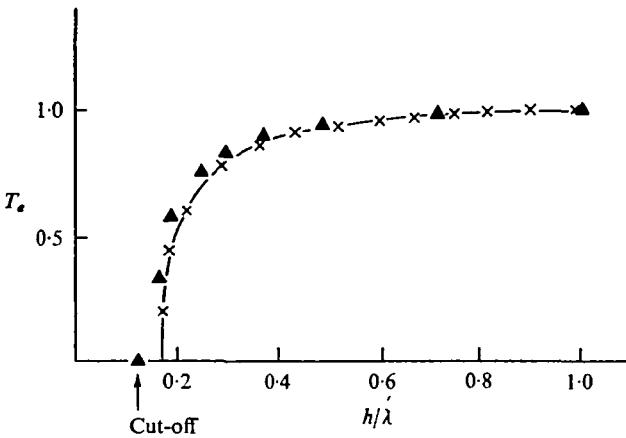
Derived data

The graph of cross-sectional area against axial distance for the femoral trachea of *Homorocoryphys* is given in Text-fig. 6 together with the logarithmic curve. Visual inspection suggests that these curves approximate very closely to those of an exponential horn.

The radiating or concentrating efficiency of a long exponential horn is the ratio of the power radiated out of a given horn to the power radiated by the same diaphragm



Text-fig. 6. The linear and logarithmic curve of area against axial distance for *H. n. vicinus*.



Text-fig. 7. The theoretical transmission coefficient curve (x—x) and the corresponding measured curve for *H. n. vicinus* (▲).

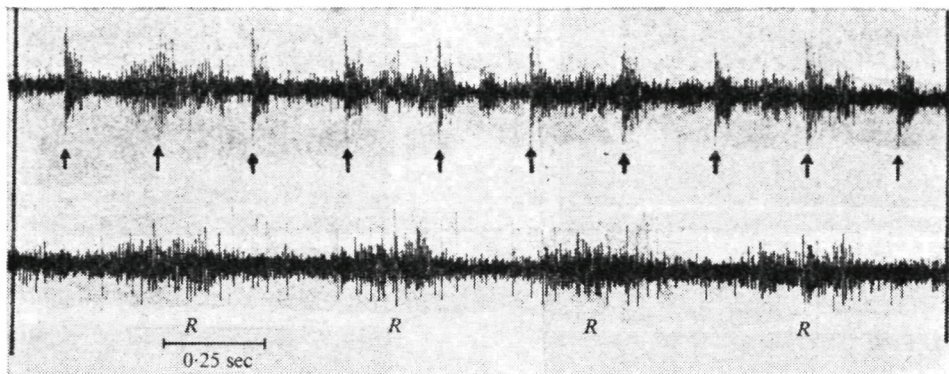
moving at the same velocity into a cylindrical tube of infinite length and having the same cross-sectional area as the small end of the horn (Morse, 1948). This ratio is called the transmission coefficient (T_e) and can be calculated from

$$T_e = \sqrt{1 - \left(\frac{\lambda}{2\pi h}\right)^2}, \tag{1}$$

where h is the scale factor (i.e. the distance in which the diameter of the horn increases by a factor $e = 2.718$), and λ is the wavelength.

The rate of increase of the diameter of the horn or the flaring constant (m) is given by

$$S = S_0 e^{mx}, \tag{2}$$



Text-fig. 8. Bilateral tympanal nerve recordings showing the responses to sound (↑) from an anterior source, in the tympanal organ with an open spiracle (upper) and in the tympanal organ with a closed spiracle (lower). (R shows respiratory activity due to spiracular closure.)

where S is the cross-sectional area in mm^2 at an axial distance of x mm from the point where the cross-sectional area is S_0 mm^2 . It is measured in inverse mm.

This constant can be used to determine the frequency at which the throat resistance of the horn falls to zero; that is, the lowest frequency that can be radiated or received. This low cut-off frequency (f) is given by

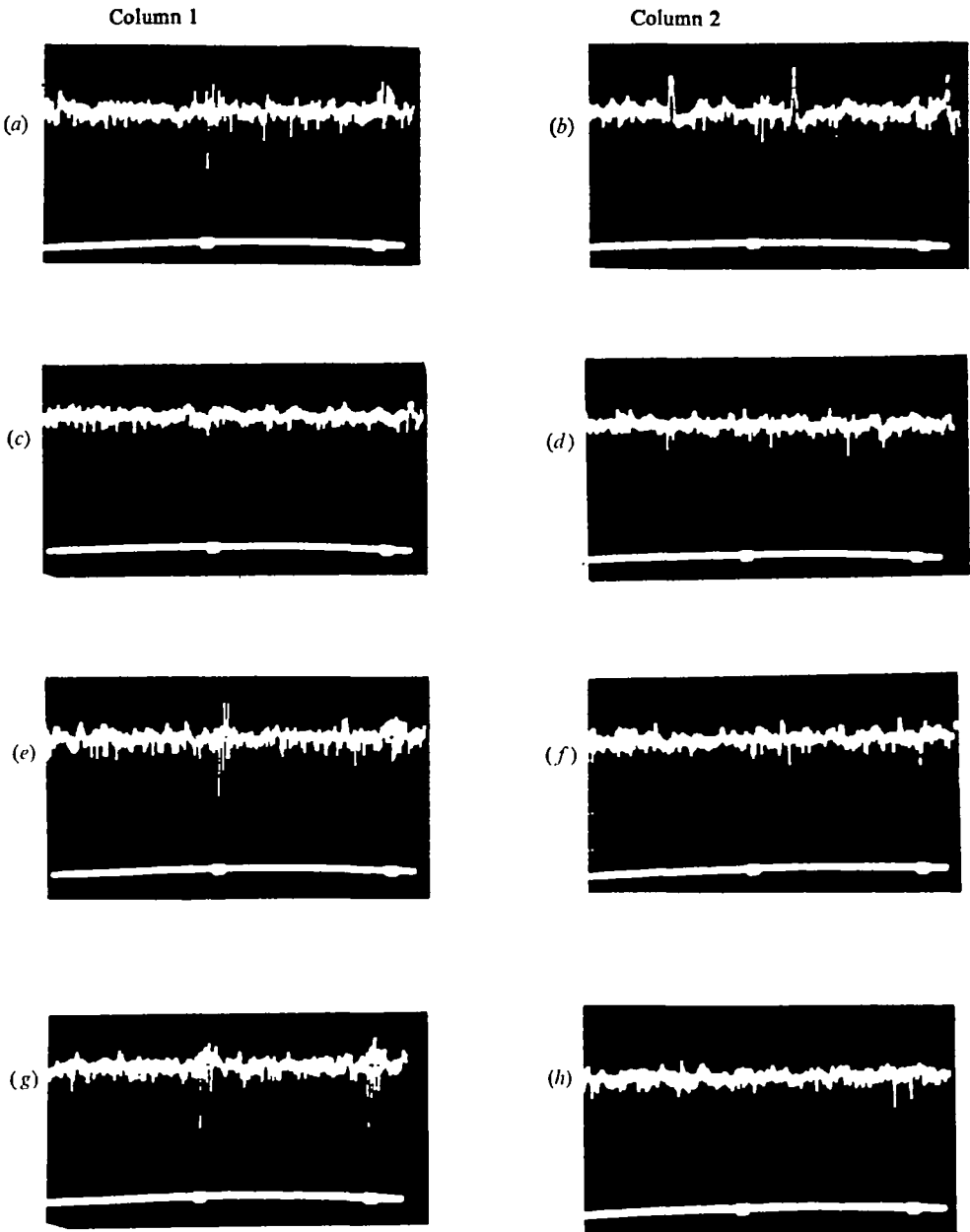
$$f = mc/4\pi, \quad (3)$$

where m is the flaring constant and c is the velocity of sound in air.

Calculation of the transmission coefficient (T_e) for the femoral trachea of *H. n. vicinus* gives the results of Table 2 and the curve of Text-fig. 7. The flaring constant for the trachea is 0.2489, which gives a calculated cut-off frequency of 5.6 kHz. This cut-off frequency is low when compared to the peak frequency of the species song (14–17 kHz) and with its frequency band (6–36 kHz).

Bilateral recordings of tympanal nerve activity

The large surface area of the prothoracic spiracle and the dimensions of the acoustic trachea in *H. n. vicinus* and other Tettigoniids, together with the fact that the trachea is totally isolated from the respiratory tracheal system, suggested to us, as to Carpentier (1924), that the spiracle and tracheal system had a much greater role in sound reception than had been previously suspected. Experiments were therefore undertaken in order to determine the effects of blocking the prothoracic spiracle on sound reception as indicated by the neural activity of the right and left tympanal nerves. The results are shown in Text-fig. 8. Right and left tympanal nerve responses are shown on the upper and lower beams respectively. The neural responses to 80 msec sound pulses set at 8 kHz and with an intensity of 45 dB are arrowed and can be seen to occur only in that tympanal nerve associated with the open spiracle; the closed spiracular system showed no response. Respiratory activity is difficult to eliminate in closed spiracle preparations since the application of Copydex to the acoustic spiracle also tends to occlude the respiratory opening. The sound source was anterior to the preparation and in the sagittal plane; there was therefore no measurable differential in the sound input. Such an experimental procedure does not, however, preclude



Text-fig. 9. Unilateral recordings of the tympanal nerve activity (upper) to incident sound (lower). In column 1 are the responses to sound directed at the spiracle, and in column 2 to sound directed at the tympanal slits. (Further explanation in text.)

differential sensitivity of the two tympanal organs either as the result of some inherent incapability or as a result of damage during dissection, although the results do suggest that the spiracular opening has an unforeseen role. To overcome the question of differential sensitivity a series of investigations were performed unilaterally.

Table 1. *Volumes (mm³) of the anterior and posterior tympanal air spaces of a variety of Tettigoniids, and of the Gryllid A. domesticus*

	<i>H. n. vicinus</i>	<i>J. flava</i>	<i>P. inter.</i>	<i>P. affinis</i>	<i>M. brach.</i>	<i>A. dom.</i>
Anterior	0.055	0.88	0.014	0.022	0.014	0.055
Posterior	0.03	0.58	0.009	0.011	0.0076	0.0025

Table 2. *Values of the transmission coefficient (T_e) for the prothoracic trachea at varying frequencies (F) ($m = 0.2489$; $h = 2/m = 8.04$)*

F (Hz)	5611	7000	8000	10000	12000	14000	16000	40000
λ (mm)	66.26	47.33	41.41	13.13	27.61	23.67	20.70	8.28
T_e	0.0	0.3493	0.5736	0.7550	0.8373	0.8839	0.9122	0.9865
h/λ	0.1213	0.1698	0.1941	0.2426	0.2911	0.3396	0.3884	0.9710

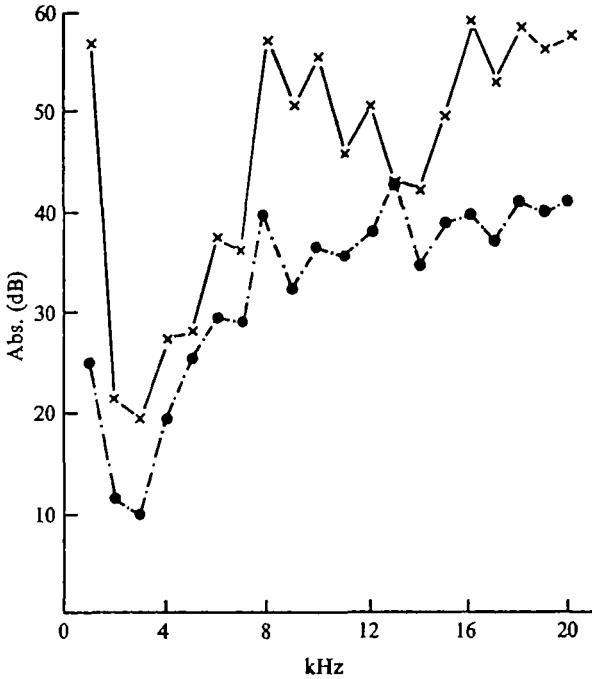
Unilateral recordings and the effects of blocking and reopening the spiracle and tympanal slits

The results of this procedure are given in Text-fig. 9. The sound stimulus used was a signal of 8 msec duration set at 12 kHz with an intensity of 47.5 dB. The sound was directed at either the spiracle or the tympanal slits at a distance of 1 mm from each structure. In Text-fig. 9, column 1 shows the responses to sound directed at the spiracle, and column 2 shows the responses to sound directed at the tympanal slits. (a) and (b) are the responses obtained when both the spiracle and the tympanal slits were open; (c) and (d) show the responses obtained when the spiracle was blocked and (e) and (f) when the spiracle was reopened. (g) and (h) are the responses obtained from the tympanal nerve when the tympanal slits were blocked. The large deflexions of the upper beam in 2(b) were not time-correlated with the sound, and may have been due to residual motor activity resulting from cutting the motor nerves.

The response to sound incident upon the open tympanal slits (2b) was largely indistinguishable from background activity at the intensity used, but the response to sound at the open spiracle (1a) was obvious. When the spiracle was blocked, the correlated response to sound at this position disappeared (1c) and no change occurred in activity to sound at the open slits (2d). The neural response to sound at the spiracle returned on reopening the spiracle (1e); no correlated activity was recorded at the open tympanal slits (2f). (1g) and (2h) show the responses obtained on blocking the tympanal slits. This procedure had no apparent effect on the spiracular responses and clearly no change could be expected to sound directed at the tympanal slits. The lower beam in all cases shows the sound stimulus.

Threshold curves for the tympanal organ during sound entry via the spiracle and via the tympanal slit

A critical examination of the methods used for the determination of threshold values has been undertaken by Michelsen (1971) and he emphasizes that thresholds determined by whatever means are quite arbitrary; but this does not exempt the experimenter from the need for precision. Clearly, the most accurate method at present available is the determination of the sound level necessary to produce a single action



Text-fig. 10. Threshold curves for the spiracle (●—●) and the tympanal slits (x—x) to a sound stimulus of 8 msec duration repeated at 5 pulses sec.⁻¹.

potential above background level. This requires analysis of long series of visibly recorded responses and the equipment necessary was not available. Recourse was therefore made to that level of sound stimulus which produced a just audible or just visible response. Because of the possibility of variation in the subjective judgement of the investigator from day to day, a three-way statistical analysis of variance was carried out on the data with the aid of a computer, and tests of significance between means were performed using the *Q*-test (Snedecor & Cochran, 1967). The overall tests show an *F*-ratio significant in each case to well below the 0.01% level with a very low within-group variance, so that there is justification in accepting the differences between curves as being significant if the *Q*-test supports this contention.

The frequency-intensity curves at threshold for the spiracle and for the tympanal slits are given in Text-fig. 10. Between 1 and 7 kHz the curves differ by values between 2 and 17 dB, while between 8 and 20 kHz, a 25 dB difference is reduced to zero at 13 kHz as a result of a low tympanal slit threshold at this frequency.

DISCUSSION

The prothoracic spiracle is partly covered by the lateral hind border of the pronotum, just above the articulation of the first coxa, and is truly double with an acoustic opening entirely separate from the truncal or respiratory opening (Carpentier, 1924, 1927; Dufour, 1841; v. Siebold, 1844). An argument for the isolation of the acoustic trachea from the respiratory system has been outlined by Carpentier (1924), who maintained that this trachea is simply intended to equilibrate the external pressures

exerted at the tympana and therefore does not need to be closable. A respiratory opening on the other hand must be closable otherwise sufficient pressure cannot be exerted by muscular contraction to force the inspired air into the head. Carpentier's contention on equilibration, which this investigation suggests is unlikely, does not invalidate his argument for the separation of the two openings.

The vesicula, or air-sac behind the spiracle, forms together with the trachea a horn-shaped tube which descends to form the air-space behind the tympanal organ. Text-figs. 5 and 6, show how closely the dimensions of the prothoracic femoral trachea correspond to those of an exponential horn, and such a close correspondence with those required by theory would seem unlikely unless this form was of some importance. The traditional theory of sound reception implies, on very little evidence, that the sound enters via the tympanal slits. The fact that the spiracular sound entry shows a lower threshold level clearly contradicts this and the implication must be that the importance of the large prothoracic spiracle has never been fully appreciated. If, as Pumphrey (1940) suggested, the function of the tympanal air space is to reduce the damping and effective inertia in this region, then the elaboration of a near-perfect exponential horn would seem an over-indulgence. A cylinder, or at most a conical horn, would seem adequate for this purpose (Morse, 1948). This would also be the case if the trachea functioned as a resonator (Zeuner, 1936) since a horn shape tends to reduce resonance, at least at certain frequencies, and an exponential horn does so at all frequencies.

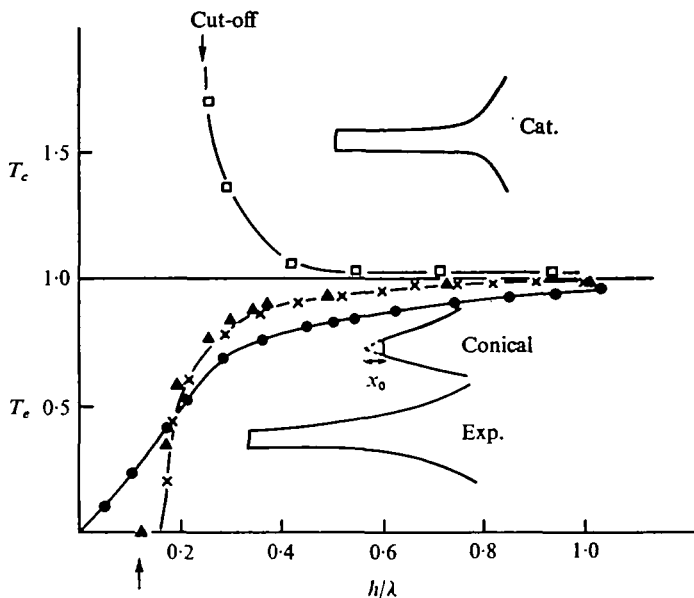
Text-fig. 9 shows that, at the frequency and intensity used, a response is obtained in the tympanal nerve only when the sound source is directed at the open spiracle; when the spiracle is blocked, no such response is obtained. Further, sound incident on the tympanal slits alone is ineffective whether the spiracle is open or not, though a response is obtained at the spiracle when the slits are blocked. It might be suspected from these results that when the spiracle is blocked, the sound is prevented from activating the receptor and that the tympanal slits are effectively closed. Consideration of the threshold curves shown in Text-fig. 10 shows that 47.5 dB is above the threshold for the spiracle and marginally below the threshold for the tympanal slits at 12 kHz. The above conclusion is thus probably correct for this intensity. The same is not true, however, for all frequencies and all intensities, and it should be stressed that the intensity values above the threshold of the tympanal slits are still within the physiological range. Normally, therefore, sound may be incident upon both the internal and the external aspects of the external tympanal membranes, though the preferential effect must be due to sound passing via the spiracular opening. This after all seems reasonable, since the larger the opening the more likely sound is to enter, and the spiracle is much larger in sectional area than the tympanal slits. In addition, the horn system will have a vast concentrating effect, effectively amplifying the sound energy. The ratio of the cross-sectional area of the throat and mouth of the acoustic trachea provides a step-up of sound intensity of about 56 times. The power entering the flare of the tracheal horn is transmitted to the throat with only about 0.9% loss at 16 kHz, since the T_c (transmission coefficient) at this frequency is 0.9122. Deducting this loss in transmission from the intensity increase of 56 times, results in an increase in effective intensity of over 25 dB. Variation in this intensity level may produce a degree of peakiness in the threshold curve which may be due to the vibration modes

of the tympanal membranes, as demonstrated by Michelsen (1971) for the locust ear. However, the spiracular threshold curve is so much lower than that obtained for the tympanal slits that an 'amplification' function is strongly suggested. The acoustic performance of a long exponential horn has been considered by Rayleigh (1895), Morse (1948) and Olson (1960). An exponential horn emitter is an acoustic transformer which provides a high resistive load to a small diaphragm such that a larger proportion of the mechanical work performed by the driving system is converted to sound. By the Law of Reciprocity (Rayleigh, 1895) the statements made for an exponential speaking horn apply equally to the hearing horn. In the latter case, a larger proportion of the sound would be converted to mechanical work. Although the exponential horn transduces practically nothing below the lower cut-off frequency, T_e rises much more rapidly to unity above the cut-off than in a conical horn (Text-fig. 11). A long horn is necessary to reproduce low frequencies effectively, and if h , the scale factor, is made large enough (i.e. the flaring constant, m , in equation 2 is low), the cut-off frequency, f (in equation 3), is lower and T_e will be constant over almost the entire range of frequencies. At frequencies above the cut-off, but close to it, the throat resistance is low and therefore the efficiency of the horn as a transformer is reduced.

The determination of any frequency-dependent characteristics is further complicated, however, by the presence of the pronotal flap partially covering the spiracular mouth of the horn. Since it is not possible to know to what extent the horn mouth is physiologically closed by the pronotal flap, the theoretical calculations of the frequency characteristics of the organ system are likely to be only approximations. The flap may well confer some resonant characteristics on the exponential horn, since the open end may not be large enough to radiate or accept all the sound coming to it, and so transmit a 'flat' response to the throat. Even horns designed to avoid resonance at most frequencies cannot avoid some resonance at the lowest frequencies (Morse, 1948). A certain amount of flare (h large but not infinite) does not alter resonant frequencies very much, and a larger mouth radiates or accepts more efficiently.

Consideration of the threshold curve of the spiracle in relation to the exponential trachea alone raises a number of points. The cut-off frequency for the acoustic trachea is calculated to be 5 kHz, and on the basis of theoretical physics any sound incident upon the spiracle of a frequency lower than 5 kHz should be ineffective. From Text-fig. 11 it is clearly not so; indeed the threshold at 2-3 kHz is lower than the threshold for all frequencies above 5 kHz. For some reason, perhaps due to its small size or the presence of the pronotal flap, or to other features of the organ, the acoustic trachea does not entirely conform to a theoretical horn in its transmission capabilities. Its cut-off, if it exists, is likely to be in the region of 2 kHz rather than 5 kHz since the threshold sound intensities below 2 kHz were very high.

The sensitivity of the Tettigoniid ear with its horn is no greater than that of the ears of other Orthoptera, but its sensitivity in its absence could well be very much less. The crista acoustica of the Tettigoniids extends down the tibia and is attached to the thicker branch of the trachea (Schumacher, 1973). In the Gryllids, which have more primitive vesiculae, the crista is missing and is replaced by a simpler sense organ (Friedman, 1972). In this latter group the sound produced has a much lower dominant frequency and is much more of a pure tone than in Tettigoniids. Zeuner (1936) con-



Text-fig. 11. The transmission coefficient curves for conical (●—●), exponential (×—×), and catenoidal (□—□), horns, together with the curve for *H. n. vicinus* (▲).

cluded that the crista was especially developed in the Tettigoniids for the reception of sound through the walls of the femoral trachea. Autrum (1941) found electrophysiologically that the subgenual organ responded to vibration and the crista exclusively to air-borne sound, and this has been confirmed by Zhantiev (1970).

Thus, it may be that the enlargement of the prothoracic femoral trachea and its isolation from the tracheal respiratory system is in some way associated with the advanced development of the crista acoustica in Tettigoniids. The argument may not be that the horn does not make the Tettigoniid ear more sensitive than other Orthoptera, but that the high-frequency sensitivity of the crista would be very much less in the absence of the horn. The development of a horn rather than a tube may be some attempt to provide a broad-band response necessary for non-steady-state reception rather than resonance to a pure tone signal at a particular frequency.

ADDENDUM

The difference between means that is required for 5% significance can be calculated from the $Q_{0.05} (\sqrt{(S^2/n)})$, where S^2 is the residual variance (in this case 3.4) and n is the number of replicates (in this case 5). Q may be found from a table = 5.19. D (difference between means) = 4.285 at 5% level.

SUMMARY

1. The acoustic opening of the large, double prothoracic spiracle gives rise to a vesicula and a trachea which descends into the leg and divides to form the anterior and posterior tympanal air spaces, their apposed walls forming the secondary tympanal membrane. This trachea is independent of the respiratory system.

2. The trachea is exponential or catenoidal in form in the Tettigoniids investigated, and the physics of horns is discussed in relation to the tracheal system.
3. Bilateral recordings from the tympanal nerves have shown that blocking the spiracular opening eliminates the response to a sound signal at an intensity of 45 dB.
4. Unilateral recordings during the blocking and reopening of both the spiracle and the tympanal slits has shown that at a sound intensity of 47.5 dB a response is obtained from the tympanal organ only when the sound is directed at an open spiracle; blocking the spiracle eliminates the response.
5. Threshold curves for the 'spiracle' and for the 'tympanal slits' show a sensitivity difference of between 2 dB and 25 dB, the difference varying with frequency. The implications of this finding are discussed.

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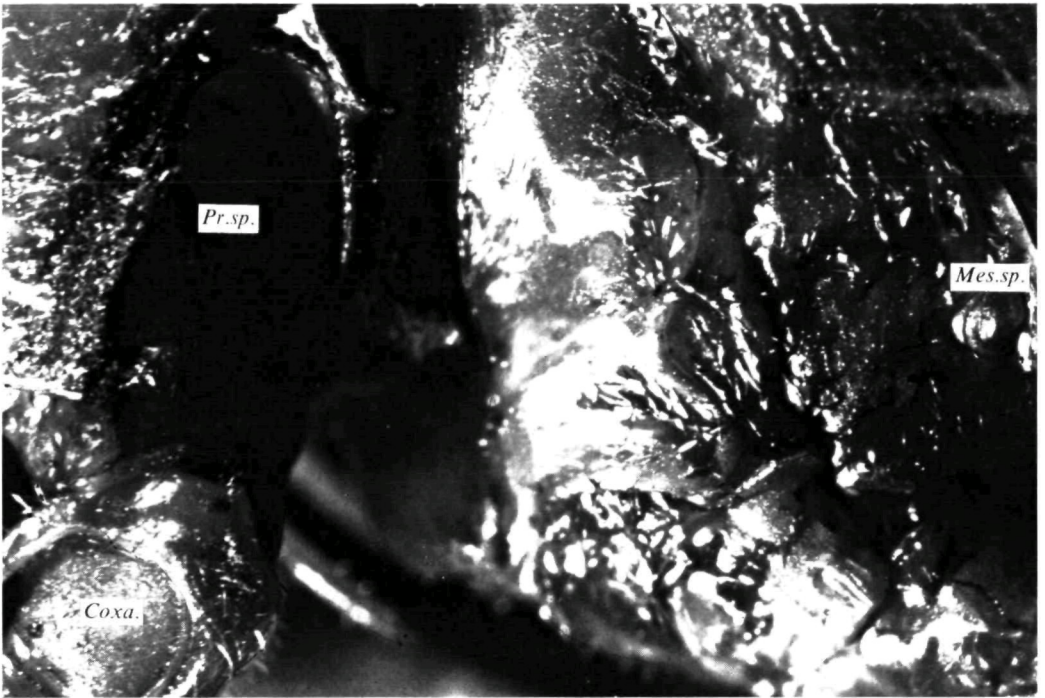


Fig. 1

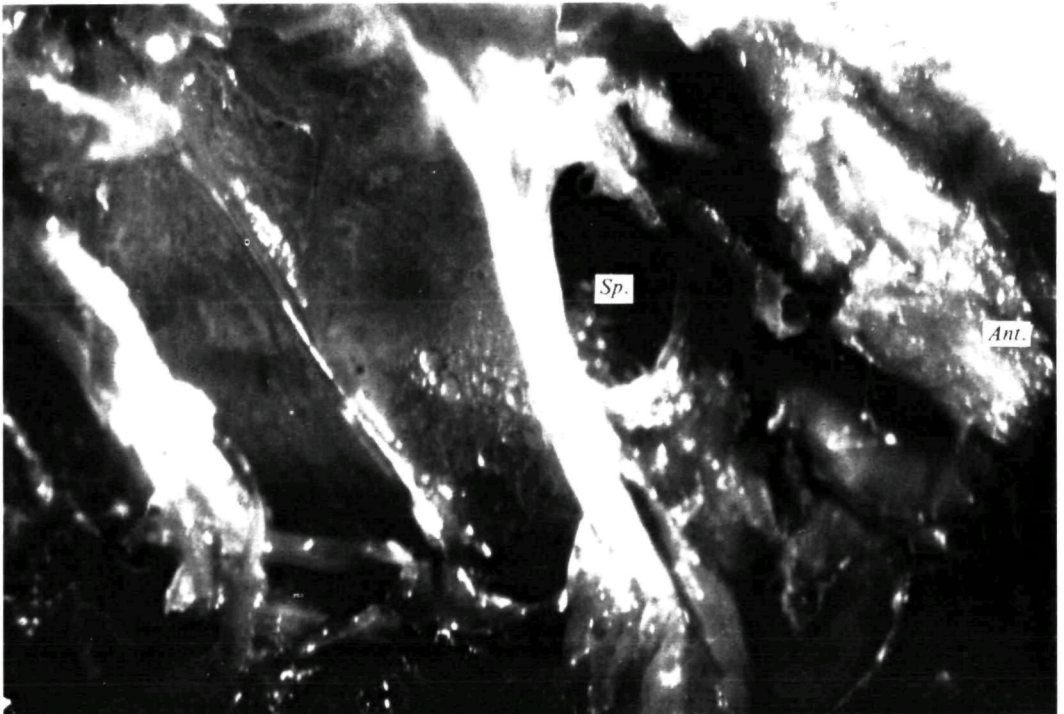


Fig. 2

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EXPLANATION OF PLATE

Fig. 1. External view of the pro- and meso-thoracic spiracles of *H. n. vicinus* with pronotal flap cut away.

Fig. 2. Internal view of the prothoracic spiracle of *H. n. vicinus* to show the large acoustic spiracle and the separate twin respiratory tracheae.

