

THE ROLE OF THE TYMBAL IN CICADA SOUND PRODUCTION

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Summary

1. The tymbal of *Cyclochila australasiae* consists of a biconvex membrane bearing alternating long and short ribs anteriorly and an irregularly shaped tymbal plate posteriorly. These sclerotised regions are coupled together by the surrounding highly flexible cuticle, which contains resilin. Dorsally, there is a thick pad of resilin, which functions as a spring, returning the tymbal to the out position and maintaining the stress on the long ribs.

2. Contraction of the tymbal muscle causes the tymbal plate to swing inwards, acting as a lever so that the surface of the tymbal moves through more than twice the distance of muscle shortening. This produces an inward movement and twisting of the dorsal ends of the long ribs, which then buckle in sequence, with each rib undergoing a sudden deformation from a convex to a V-shaped profile. Buckling takes place at the rib's weakest point, which is the narrow, highly sclerotised mid-region.

3. Inward buckling of the tymbal generates a loud click with a dominant frequency around 4 kHz. Resonances close to 4 kHz can be demonstrated in a buckled-in tymbal when driven by internal sound or by vibration at the tymbal plate. These resonances occur in sealed cicadas and those in which the abdominal air sac has been opened at both its anterior and posterior ends, which shows that the resonances are not due to the air sac; the tymbal itself is a resonant system. The maximum amplitude of tymbal vibration occurs at the V-shaped dimples in the centre of the long ribs.

4. When the tymbal plus abdominal air sac system is driven by vibration at the tymbal plate, the Q_{3dB} of the sound radiated through the tympana is about 12.5, which

is approximately the sum of those of the tymbal ($Q=9.3$) and of the air sac ($Q=3.4$) resonators. When the tymbal is not loaded by the air sac, i.e. in the sealed cicada and open cicada preparations, the Q_{3dB} of its resonance is higher, between 13 and 20.

5. The click produced as the tymbal pops out is over 20 dB quieter than the in-click and has a dominant frequency around 6 kHz. When driven in the resting position, resonances are found close to 6 kHz but there is only a weak general vibration of the ribs and tymbal plate. When the tymbal is pushed in gradually, the resonant frequency changes from about 5.5 kHz to about 4.3 kHz as the tymbal buckles inwards. The left and right tymbals of the same insect may differ slightly in their acoustic properties.

6. As the tymbal buckles inwards, it displaces a volume of approximately $6 \mu\text{l}$ into the abdominal air sac volume of about 2 ml. The resulting sound pressure inside the air sac attains peak values of 155–159 dB SPL; the root mean square values are 141–144 dB SPL. The mean peak value just outside the tympana is 148.5 dB SPL.

7. Overall, the present work supports and extends our earlier model of cicada sound production: the tymbal click provides a coherent resonant source that drives the abdominal resonator, from which sound is radiated *via* the tympana. At the same time, the system provides the pressure transformation between muscle power and sound power that is desirable for efficient sound radiation.

Key words: cicada, sound production, mechanical resonator, impedance matching, tymbal, *Cyclochila australasiae*.

Introduction

Cicadas are noted for the loudness of the songs produced by the males. These sounds are generated by a pair of tymbals, which are relatively small stiff membranes, located dorsolaterally on the anterior part of the abdomen (see Fig. 4A; Myers, 1929). Each tymbal buckles inwards when pulled by its large tymbal muscle, and this deformation of the

membrane generates a loud click or pulse of sound (e.g. Pringle, 1954).

It used to be thought that, as well as acting as sound-generating structures in this way, the tymbals were also the main surface from which sound is radiated into the environment (e.g. Michelsen and Nocke, 1974). However,

*Most of the experimental work reported here was carried out at the University of Melbourne.

when the sound levels around a singing cicada were actually measured, it was found that the sound at the outside of the tymbals is relatively quiet compared with that outside the tympana (Young, 1990). In male cicadas, the paired tympana are relatively large in area, but very thin, and are located ventrally on the anterior part of the abdomen (see Fig. 4A). The two tympana are lined internally by a large air sac, which fills most of the abdomen and extends to the inside of the tymbals (Young, 1990, see Fig. 1).

This led to the proposal that the abdominal air sac and tympana together act as the components of a Helmholtz resonator, which is excited internally by the tymbals and from which sound is radiated through the thin tympana (Bennet-Clark and Young, 1992). Experimental support for a model of this type was provided by the demonstration of an internal cavity resonance at a frequency close to the natural song frequency, when the body of a male cicada was excited by external sound. Further support for the Helmholtz resonator model was provided by studies using models of similar sizes to cicada bodies, which were driven by small internal sound sources. This allowed the models' sound output under different conditions to be compared with the real song of the insect. In particular, this comparison showed that a model with a cavity and openings having the same dimensions as the air sac and tympana of the cicada exhibited resonance at the natural song frequency of the cicada (Bennet-Clark and Young, 1992).

Studies using different types of artificial acoustic drive with the model led us to make two suggestions concerning the role of the tymbal. First, the acoustic excitation provided by the tymbal is a damped vibration at the same frequency as the resonant frequency of the abdominal resonator, which also corresponds to the natural song frequency. Second, the tymbal action produces a short train of coherent resonant impulses, which excite and then sustain the resonance within the abdomen, so as to produce the long, sustained sound pulse that is found in the insect's natural song (Bennet-Clark and Young, 1992).

The structure of the cicada tymbal in relation to its function was first considered by Pringle (1954); later it was examined in more detail by Simmons and Young (1978) and by Jiang (1989), both of whom reached similar conclusions. As described by Simmons and Young (1978), the tymbal membrane forms a convex dome, which is set in a ring of sclerotised cuticle. Posteriorly on the tymbal, there is an irregularly shaped region of sclerotised cuticle, the tymbal plate, onto which the tymbal muscle attaches dorsally. Anteriorly, there are a number of long sclerotised ribs, which alternate with short ribs arranged in a line. When the tymbal muscle contracts, the tymbal buckles inwards along the line of short ribs in a stepwise manner; each step results in a sound pulse and is due to the buckling of one or more long ribs, beginning with the most posterior (rib 1). These results were obtained by Simmons and Young (1978) using the bladder cicada, *Cystosoma saundersii*, from south-eastern Australia.

Our recent acoustic studies have been carried out mainly on another Australian species, *Cyclochila australasiae*. This is a

large cicada of typical appearance and it has a loud piercing song, in which the sound energy is confined to a comparatively narrow bandwidth around 4 kHz (Young, 1990). The tymbal of *Cyclochila* has been described briefly by Josephson and Young (1981) and conforms to the general pattern described above (see Fig. 4B). We now report an investigation of the anatomy and mechanics of the tymbal, and of its acoustics, in an attempt to show how excitation of the abdominal resonance occurs and to establish the tymbal's role in the chain of cicada sound production.

Materials and methods

Males of *Cyclochila australasiae* Donovan were collected around Melbourne during the early summer months. Most specimens were captured at night during eclosion, but some were caught as mature adults by day. Additional specimens were kindly air-freighted to us from Sydney, New South Wales, by Max Moulds.

Live cicadas were maintained on 1 m tall *Eucalyptus* trees in the laboratory at ambient temperature and usually survived for between 1 and 3 weeks after capture. Males collected during eclosion first began to sing after being maintained in captivity for 2 or 3 days. Insects that either sang spontaneously or produced a vigorous protest song were used for experiments on sound production, while other, less vigorous insects and recently dead insects were used for anatomical studies and for studies on the mechanics of the tymbal. Live insects survived for several days in a refrigerator at 4 °C and newly dead insects were kept for later use in a deep freeze at -18 °C.

Anatomical methods

Tymbals were prepared for examination by cutting them free from the surrounding cuticle and then dissecting the muscle and other tissues away from the inside surface under water. Prepared tymbals were tested for the presence of resilin (Weis-Fogh, 1960; Andersen and Weis-Fogh, 1964) by staining with a very dilute solution of Methylene Blue buffered to pH 7 for 18 h at 4 °C. The distribution of resilin was shown by the brilliant sapphire-blue staining of otherwise colourless regions of the tymbal and by the elastic nature of these regions when deformed with a seeker. The presence of resilin in these regions was confirmed by the fluorescence of the unstained cuticle when excited at 330 nm by an ultraviolet light source. The orientation of chitin fibrils in the tymbal ribs was examined by rotating them under a microscope between crossed polaroids.

Other tymbals were prepared for sectioning by cutting out a ring of cuticle containing both tymbals of one insect and placing it in fixative (glutaraldehyde, approximately 2% in locust saline; details in Josephson and Young, 1985) under vacuum. To facilitate penetration, a few drops of wetting agent (Photoflo) were added to the fixative and much of the tracheal air sac was picked away. After 30 min in the fixative, the individual tymbals were cut free of the surrounding cuticle and left in fixative under vacuum for a further 18 h. The tymbals were then rinsed in three changes of buffer wash, dehydrated

in alcohol and embedded in methyl methacrylate (JB4 Resin). Horizontal sections, 4 μm thick, were cut with a glass knife, mounted on slides and stained with Toluidine Blue for examination by light microscopy.

Drawings of the tymbals in various states (Figs 4, 7) were prepared using a dissecting microscope with a squared graticule in the eyepiece and drawing paper with corresponding squares on it. Drawings of the methacrylate sections through the tymbal (Fig. 6) were made by means of a Zeiss *camera lucida* attached to a compound microscope. The stages of tymbal buckling were obtained for study and drawing (Fig. 7) by pushing on the tymbal plate with a fine probe mounted in a micromanipulator, taking care to push on the point of insertion of the tymbal muscle (the apodeme pit, Fig. 4B) at approximately the same orientation as the muscle's apodeme. In these preparations, the distance through which the apodeme pit moved during buckling was measured from the vernier scale on the micromanipulator. Another fine probe mounted in a micromanipulator was used to measure the distance moved by the anterior edge of the tymbal plate at the same time.

The volume displaced by the inward movement of the tymbal was measured in two ways. First, measurements were made of the area of the tymbal plate and of the distance through which it moved when the tymbal buckled inwards. Second, a truncated glass cone was waxed at its wide end over the tymbal of an abdomenless cicada and a calibrated glass capillary tube was waxed into the narrow end of the cone. After filling the cone and capillary with water, the tymbal was buckled in and out by pulling on its apodeme with forceps. The displacement of the water column in the capillary tube was then measured.

General acoustic methods

Cicadas were prepared for acoustic experiments in four standard ways.

(1) To simulate the relative positions of the abdomen and the opercula, which cover the tympana, during production of the natural calling song, cicadas were waxed with the abdomen extended and raised upwards away from the opercula, leaving a gap of about 4 mm between the posterior edge of the opercula and the posterior rim of the tympana (Fig. 1A; cf. Young, 1990, Fig. 6). This is termed the intact cicada.

(2) To measure the properties of the tymbal when sound was not being radiated *via* the tympana, the opercula were carefully waxed down onto the tympanal rims, so as to occlude the whole area of the tympana (Fig. 1B). A hole made in the cuticle of the second abdominal segment allowed the attachment of a sound source or microphone. This is termed the sealed cicada.

(3) To replicate the experimental condition used by Young (1990), in which the abdominal air sac is cut open, the posterior part of the abdomen was cut off just posterior to the tympanal rim ventrally and around the segmental border behind the tymbals dorsally (Fig. 1C). This is termed the abdomenless cicada.

(4) To measure the sound produced by the tymbal when activated by its muscle but with as little influence from the

body or air sac as possible, the ventral part of the metathorax was cut away from an abdomenless cicada. In this condition, the abdominal air sac opened anteriorly through the cut thorax and posteriorly through the cut abdomen but the ring of cuticle that supports the tymbals, the tymbals themselves and their muscles were left intact and functioning (Fig. 1D). This is termed the open cicada.

In all cases, the experimental insect was waxed mid-dorsally (along the pronotum and mesonotum) to a 100 mm long brass rod that extended over the insect's head (Fig. 1A) and was held in a micromanipulator. Live insects mounted in this way normally survived for more than 4 h, and dead insects gave a consistent mechanical performance throughout a working day. The insect wax used in these experiments consisted of a mixture of 2 parts of beeswax to 1 part of violin resin (rosin) by weight (melting point 58 °C). In most experiments, the tymbal covers were cut away to allow free access to the tymbal surface (e.g. Fig. 1C).

The preparations, together with selected probes or microphones were held in Prior micromanipulators attached by magnetic clamps to a 12 mm thick steel base plate. Controlled mechanical movements were made using the rack-and-pinion or micrometer screw adjustments of the micromanipulators; the latter allowed calibrated movements to a precision of less than $\pm 10 \mu\text{m}$. Sheets of Sonex anechoic foam 85 mm thick were placed between the steel plate and the adjacent walls of the laboratory. The preparations were normally held at least 150 mm above the plate and separated from it by pieces of anechoic foam. Clamps and other devices used to hold microphones and models were less than 25 mm across and support rods were less than 12.5 mm in diameter.

In some preparations, one tymbal muscle was stimulated through a pair of 80 μm insulated silver wire electrodes, which were implanted through a small hole made in the muscle's ventral attachment and secured with wax. Square pulses of 1 ms duration were delivered by a Grass S9D stimulator, either singly or in short trains at 10–100 Hz. The stimulus was recorded on one channel of a Nagra IVS tape recorder, and the sound produced by the tymbal was recorded on the other channel using a Bruel and Kjaer 4134 or 4138 microphone at a range of 1–10 cm.

Most measurements and recordings of the sound produced by singing cicadas were made with a Bruel and Kjaer type 4134 microphone feeding a Bruel and Kjaer sound level meter type 2209 *via* an input stage ZC0200 and flexible lead AO 0027. This sound level meter has peak hold and impulse hold ranges which allow transient sound levels to be measured. Tests with continuous 4 kHz sine-wave signals showed that the peak hold reading was 5–6 dB above the fast range, which measures the root mean square (RMS) amplitude of the signal. Further tests with tone bursts of known signal-to-space ratios showed that the impulse hold reading integrated the average power of signals with periods from 20 to 100 ms and signal-to-space ratios up to 1:9 but that the readings could be 2–3 dB over-estimates.

Internal sound pressures in singing cicadas were measured

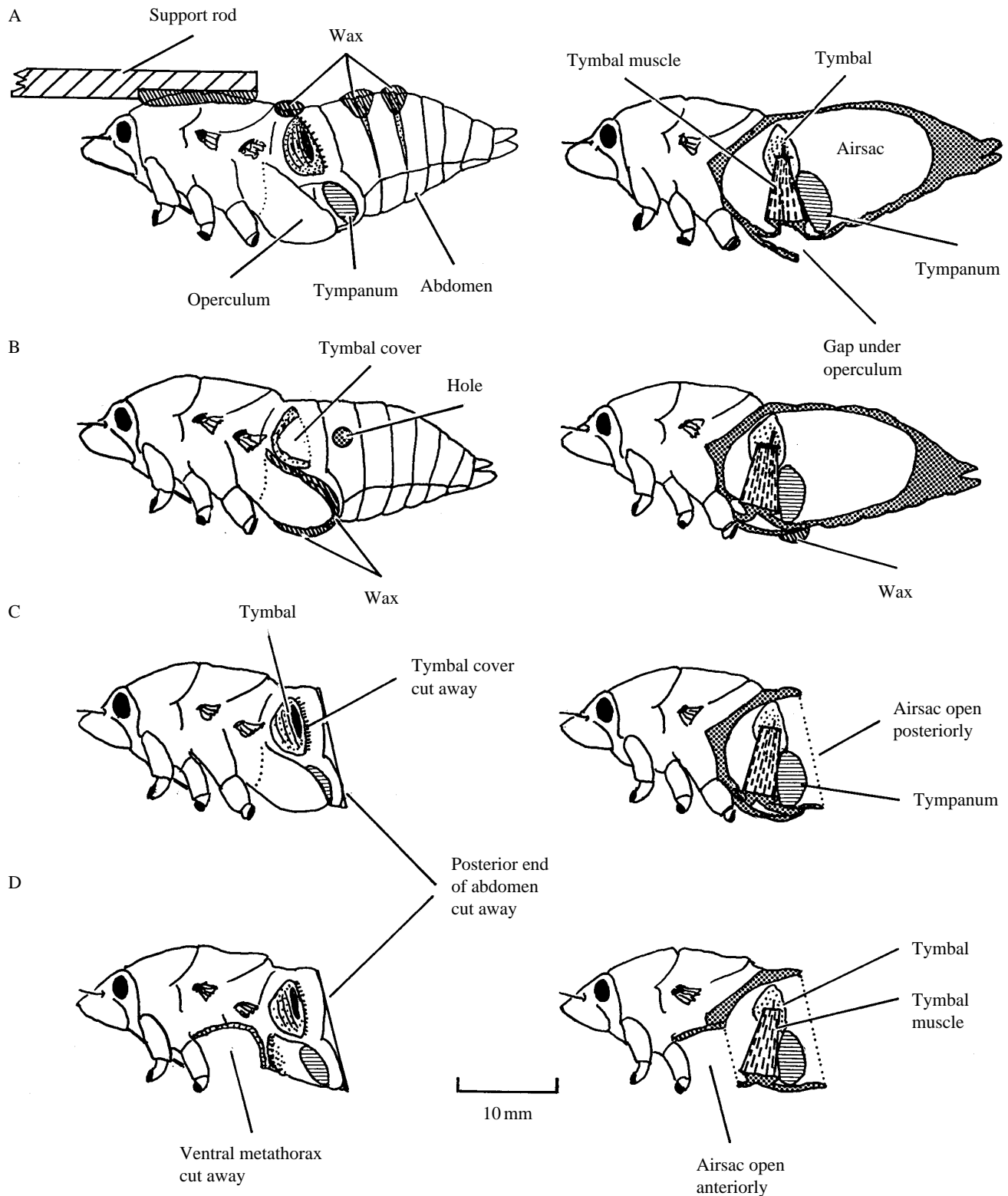


Fig. 1. The four standard preparations of male *Cyclochila australasiae* used in acoustic experiments. In each case, the external appearance is shown (left) together with a cut-away revealing internal features of the abdomen (right). (A) The intact cicada, in which insect wax was used to fix the abdomen in a position resembling that in natural calling song. (B) The sealed cicada, in which both opercula were waxed to the abdomen, so preventing the normal means of sound radiation through the tympana. (C) The abdomenless cicada, in which the posterior part of the abdomen is cut away, but leaving the tymbals and tympana intact. (D) The open cicada, in which an abdomenless cicada is opened up anteriorly to minimize acoustic influences on the performance of the tymbal.

by making a 3 mm diameter hole in the fourth abdominal tergite, to the outside of which was attached a coupling tube 10 mm long and 3.55 mm internal diameter. This tube had a 3.2 mm hole at its base that allowed a Bruel and Kjaer 1/8" microphone type 4138 to be inserted to within 1 mm of the inside of the cicada. The coupling cavity so created had a volume of less than 0.1 % of the air sac volume and its resonant frequency exceeded 40 kHz. The microphone was a close fit in the coupling tube but was also sealed in place with a ring of Blu-tack around the UA 0036 adaptor that connected it to the sound level meter.

The calibration of the sound level meter and microphones was tested and adjusted regularly using a Bruel and Kjaer type 4230 calibrator, *via* a specially made adaptor in the case of the type 4138 microphone.

Measurements of resonant frequency and quality factor (Q) followed the methods described earlier (Bennet-Clark and Young, 1992). As we reported there, the accuracy and repeatability of measurements of the resonant frequency was approximately $\pm 3\%$, and the repeatability of successive measurements or comparisons of Q was about $\pm 10\%$. In this paper, we have invariably used Q_{3dB} .

Oscillograms and frequency–energy spectra of cicada songs, and of the responses of driven tymbals, were obtained from tape recordings using a Kay DSP sonograph model 5500. The transform size was normally set to 600 Hz to provide a compromise between frequency and time resolution that allowed the frequency–energy spectra of individual song pulses to be measured.

Probe microphone

The probe microphone was made from a 6 mm diameter electret microphone element (from Henry's Radio, Edgware Road, London). The microphone element was glued into a 7 mm outside diameter aluminium alloy housing (Fig. 2A) into the end of which was sealed a probe tube made from a 5 mm long section of 1.25 mm outside diameter stainless-steel tubing from a hypodermic needle. The microphone and its housing were glued onto 100 mm long 6 mm diameter rod to fit onto a micromanipulator. The microphone drove a purpose-built preamplifier.

Calibration was made by inserting the microphone into a 6 mm long sealed cavity made from a 12 mm diameter polycarbonate tube, closed at one end by a Bruel and Kjaer microphone type 4134 (resonant frequency 25 kHz) and driven from the other end by an Aiwa miniature earphone, fed from a Tektronix function generator FG501 *via* a Toshiba power amplifier type SB-M30. The sound pressure in the cavity was adjusted to a constant level of 94 dB. The voltage output of the preamplifier was measured to the nearest 0.1 dB with a Fluke multimeter type 8060A, which measured the RMS value of voltages with a level frequency response ± 0.1 dB between 50 Hz and over 20 kHz.

Resonances in the probe microphone's frequency response were damped by pushing tufts of phosphor bronze wool into the probe tube, until, by trial and error, the response was non-

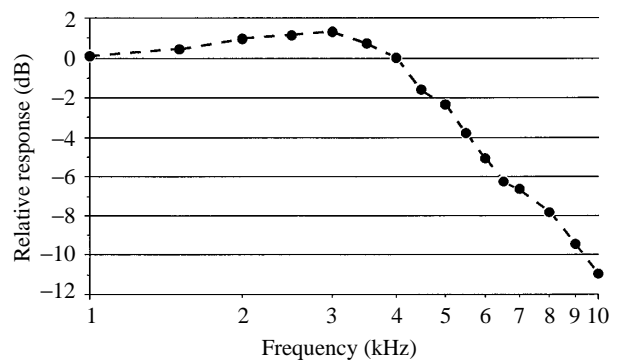
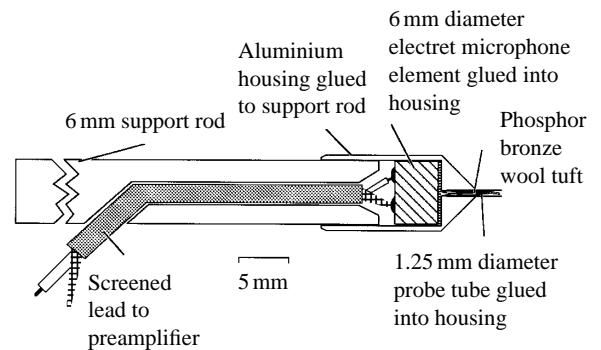


Fig. 2. (A) Diagram showing the construction of the probe microphone used to record sound close to the surfaces of the tymbals and the tympana. (B) Calibration curve for the probe microphone after inserting phosphor bronze wool into the probe tube.

resonant, with a smooth roll-off in the response at about 3.5 kHz (Fig. 2B). The gain control of the microphone preamplifier was adjusted so that the voltage output was 500 mV RMS for a sound pressure of 94 dB at 4 kHz. Because the response fell rapidly above 10 kHz, no attempt was made to extend the calibration above this frequency. The time delay due to the probe tube, microphone element and preamplifier was measured as $80 \pm 10 \mu\text{s}$, relative to that of the Bruel and Kjaer type 4134 microphone on a type 2209 sound level meter. Measurements with transient sound pulses showed that estimates of the rate of build-up or decay were within 5% of measurements made using the Bruel and Kjaer type 4134 microphone.

The probe tube internal radius was 0.8 mm. The effective acoustic radius of the orifice of such a tube is likely to be $16/3\pi$ times greater, or about 1.4 mm, so measurements using this probe microphone can be made to a spatial precision that is approximately equal to the external radius of the probe tube.

Vibration force transducer

The transducer element was a 6 mm diameter piezo-electric bender unit from a TDK RU40K ultrasonic acoustic transducer. After removal of the cover and the microphone cup, the unit was fixed to a Paxolin block glued to the end of a 6 mm diameter

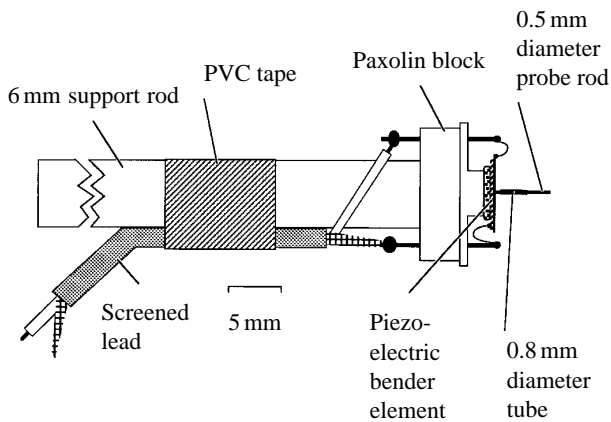


Fig. 3. Diagram showing the construction of the vibration force transducer, which was used both to record vibrations from the tymbal and to provide a vibration drive to the tymbal in the acoustic experiments.

support rod which could be mounted on a micromanipulator. This sensor was fitted with a collet made from a 5 mm length of 0.8 mm diameter steel tube, into which a 7 mm long steel probe pin was inserted (Fig. 3). This transducer was used both to measure vibration force and as a driver.

When used as a vibration force detector, the output of the transducer was measured by connecting it to a Bruel and Kjaer type 2209 sound level meter, which thus acted both as a preamplifier for tape recordings and as a voltmeter with a linear response from 5 Hz to 50 kHz.

In principle, such a detector behaves as a voltage source in series with the transducer capacitance and should give an output that is proportional to the force of imposed vibrations at frequencies far below its resonant frequency. Since, in this range, the transducer response is stiffness-limited, the output should also be proportional to the amplitude of the driving vibration. We did not have appropriate apparatus to make absolute calibrations of the transducer but, from the small size of the bender element and its high stiffness, we believe that its force *versus* voltage response was likely to be substantially linear between 1 and 10 kHz. Its performance was assessed as follows.

The resonant frequency of the unmodified transducer was quoted as being 40 kHz and the total mass of the bender unit was 0.25 g. After attachment of the 30 mg additional mass of the pin and collet, the resonant frequency of the transducer fell to a measured 31.4 kHz. In general, the mass of the insect parts that were being measured was far less than the mass of the transducer, so it is unlikely that the added mass of the insect reduced the resonant frequency of the transducer to a value within the 1–10 kHz band in which we were interested. When loaded by the mass of parts of the cicada, such as the tymbal, transducer resonances at between 20 and 25 kHz were sometimes observed. These resonances had a Q of about 5 and were over twice the highest frequency that was to be measured. Also, there was a correspondence to within 1 dB between the waveform measured from this transducer resting against the

tymbal plate and a probe microphone placed 1 mm away from the surface of the tymbal when the tymbal resonance was excited by sound (see Fig. 12).

The measured capacitance of the piezo-electric transducer was 2.6 nF, which was shunted by a negligible 100 pF of the coaxial connecting cable. This source capacitance, in turn, was shunted by the 146 k Ω input impedance (which is largely resistive) of the Bruel and Kjaer type 2209 meter. This resistive shunt on the transducer acts as a high-pass filter which theoretically will cause a 3 dB decrease in the output at 400 Hz and a 6 dB per octave decay in the output below this frequency. Thus, in this measuring set-up, the theoretical low-frequency response extends to below 1 kHz.

The sensitivity of the isolated transducer to airborne sounds was extremely low. Hand claps, which produced sound pressures of about 130 dB, were only just detectable and over 40 dB below the amplitude of tymbal vibrations under examination.

The same transducer was also used as a vibration source. It was driven directly by the output of a Toshiba SB-M30 power amplifier, which overloaded at an output of 80 V peak-to-peak. At 70 V_{p-p}, the mechanical vibration along the probe rod was great enough to excite tymbal vibrations that generated sound 20–40 dB louder than the background amplifier and room noise. This allowed useful measurements to be made of driven vibrations using the probe microphone. When driven in this way, the sound produced by the free vibration of the transducer at 4–8 kHz was over 40 dB less than the sounds that were produced when it was in contact with cicada tymbals.

Electrical test signals

Tone bursts and steady-state test signals were generated by triggering a Tektronix function generator type FG 501 with pulses from a Tektronix pulse generator type PG505. In this way, bursts of one or more complete cycles of sinusoidal or other types of waveforms were produced. Carrier frequencies were set to the nearest 10 Hz between 500 Hz and 20 kHz using a Testlab TL 3400 multimeter. Waveforms were measured on a B.W.D. 845 storage oscilloscope.

Tone bursts were fed through a 0–59 dB 600 Ω attenuator and amplified by a Toshiba SB-M30 power amplifier. The combined output of the function generator and amplifier were measured as being flat to ± 0.5 dB from 15 Hz to over 10 kHz with the power levels and load impedances used here.

Miniature sound source

A Sony miniature earphone was waxed to a short cone made from the end of a 5 ml polycarbonate hypodermic syringe opened out to a 4 mm diameter hole at the apex, to which was attached one end of a 15 mm long, 4 mm square section brass tube, with flanges at both ends. The other end of the tube could be waxed to the abdomen of a cicada. This delivery tube was packed with phosphor bronze wool to damp tube and cavity resonances. No absolute measurements of the frequency response were made but the aperiodic (non-resonant) nature of the response was established by placing a Bruel and Kjaer 1/8'

microphone at the open end of the delivery tube and driving the earphone with both steady-state signals and tone bursts at between 1 and 10 kHz; the response built up to a plateau and decayed within 1.5 cycles, suggesting that any irregularities in the response were of low Q and that their effects could be disregarded.

Results

Anatomy of the tymbal

The tymbal is surrounded by a frame of rigid sclerotised cuticle. The posterior border of this frame is formed by the vertical bar, which is a steep infolding of the abdominal cuticle (Figs 4B, 6B). From the ventral end of the vertical bar a strong fold of cuticle, approximately semi-circular in section, runs forward to form the ventral border of the tymbal. We term this the horizontal bar (Fig. 4B; in preference to 'tymbal bar' of Simmons and Young, 1978). The anterior tymbal frame consists of a complex fold of cuticle, which curves round from the anterior end of the horizontal bar to the dorsal end of the vertical bar. Whereas the vertical bar and horizontal bar are both quite rigid, the anterior tymbal frame shows some degree of flexibility and is less highly sclerotised in places.

The tymbal plate is a thin, lightly sclerotised sheet of cuticle, on which the tymbal muscle inserts dorsally. The point of insertion is visible on the outside of the tymbal plate as a slight concavity, the apodeme pit (Fig. 4B); the muscle apodeme extends inwards from the dorsal extremity of this concavity as a thin flexible rod about 3 mm long, which then expands into the large oval muscle attachment. The posterior edge of the tymbal plate is slightly curved and runs approximately parallel to the edge of the vertical bar.

There are four long ribs on the tymbal of *Cyclochila* (Josephson and Young, 1981), with traces of an incomplete fifth rib anteriorly. The long ribs are curved along their length, forming a gentle arc when seen in anterior or posterior view (see Fig. 7). At their dorsal ends, the long ribs are convex in section and moderately sclerotised. At their ventral ends, they become considerably wider and flatter in section but are only lightly sclerotised (Figs 4B, 6C). In the middle part of their length, the long ribs are narrower and relatively flat in section, but they are highly sclerotised (Figs 4B, 6B). The orientation of the chitin fibrils in the long ribs is along their length. The pear-shaped short ribs are thin but highly sclerotised regions that lie on the inner surface of the tymbal membrane between the narrowest parts of the long ribs (Figs 4B, 6B).

The sclerites forming the ribs and tymbal plate are all interconnected by the dome-shaped tymbal membrane, which is colourless and flexible. Our tests on the intact tymbal show that resilin is present throughout this membrane (Fig. 4B; cf colour photograph, Fig. 5). In sectioned material, the resilin is also evident through staining much more strongly with Toluidine Blue than the sclerotised parts of the tymbal. The presence of resilin in cicada tymbals has already been reported by Scott (1970), but without details of its distribution or possible function.

Dorsally, there is a thick resilin pad, roughly triangular in shape, which joins the dorsal ends of the tymbal plate and long ribs together and attaches them to the dorsal arc of the tymbal frame (Figs 4B, 5). Immediately above and anterior to the dorsal tip of the tymbal plate, this resilin pad may be as much as 0.4 mm thick (Fig. 6A). Along the posterior edge of the tymbal plate, a strip of resilin acts as a hinge between it and the vertical bar; here the resilin is generally between 0.05 and 0.1 mm thick, though somewhat thicker at the dorsal and ventral ends. Strips of thin resilin, mostly between 0.01 and 0.03 mm thick, connect adjacent long and short ribs and connect rib 1 to the tymbal plate. Near the middle of rib 1, the strip of resilin connecting it to the tymbal plate angles sharply inwards (Fig. 6B) so that the anterior edge of the tymbal plate is hidden by rib 1 in lateral view (Fig. 4B).

Mechanics of tymbal buckling

The action of the tymbal muscle in buckling the tymbal can be mimicked by pushing on the apodeme pit with a fine probe (see *Anatomical methods*). As the probe is advanced, the tymbal plate hinges along the resilin strip at its posterior edge and swings inward. The distance travelled by the tymbal plate is greater at its dorsal end, where the muscle attaches, than at its ventral end, and the tymbal plate is to some extent distorted. In turn, this movement of the tymbal plate produces a progressive distortion of the thick resilin pad and of the dorsal ends of the long ribs. The resilin pad shows strain birefringence during this movement. The dorsal ends of the long ribs are both carried inwards and rotated, but their ventral ends hardly move at all.

Eventually a point is reached where the long ribs buckle inwards, undergoing a sudden deformation, which is accompanied by a distinctly audible click. Rib 1, which is nearest to the tymbal plate, buckles first and is followed successively by the more anterior ribs. As it buckles, a long rib changes in shape from a smooth crescent shape, in lateral view, to develop a V-shaped dimple, with the apex of the V pointing anteriorly along the line of short ribs (Fig. 7). Thus, the apex of the dimple occurs in the narrow, highly sclerotised mid-region of the ribs. In posterior view, it can be seen that the buckled ribs have not only moved inward but also rotated so that they present their outer face rather than their edge to the viewer (Fig. 7). This effect is greater at the dorsal end than at the ventral end of the long ribs, showing that the ventral end of tymbal plate does swing inwards as the ribs buckle but not as much as the dorsal end. Videos of the tymbal movement, recorded during protest song, show that up to three of the long ribs normally buckle inwards.

When rib 1 buckles in, forming the V-shaped dimple, its sclerotised mid-region clearly moves in further than the adjacent edge of the tymbal plate. Rib 2, at this initial stage, remains in the out position. The large inward movement of the mid-region of rib 1 is accommodated posteriorly by the folding of the strip of resilin between it and the tymbal plate and anteriorly by the inward hinging of the first short rib. As the sclerotised mid-region of rib 2 buckles in, its deformation is

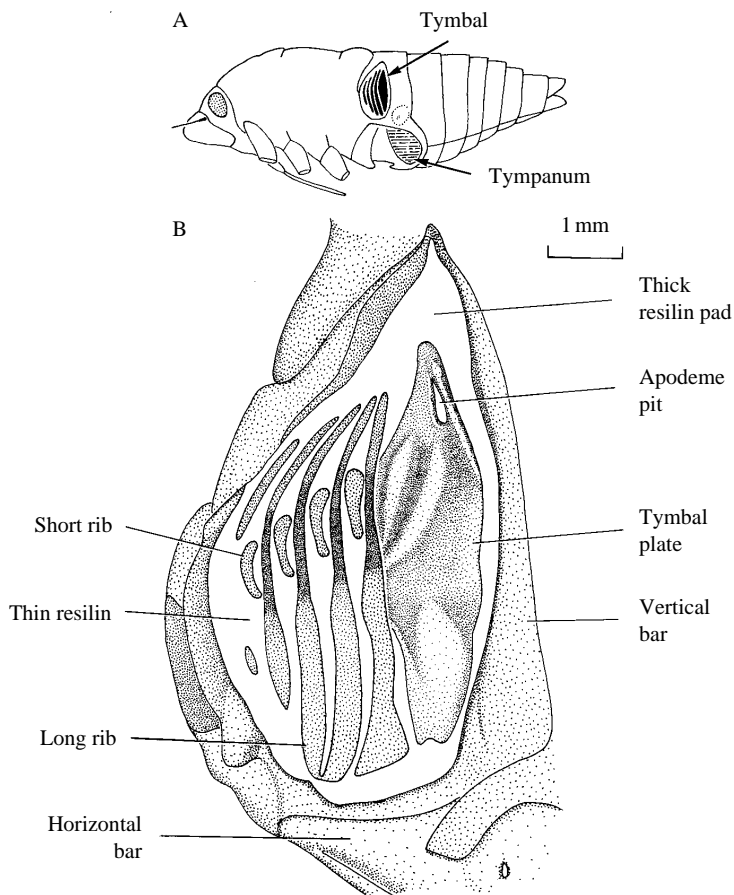


Fig. 4. (A) Outline of a male *Cyclochila australasiae* in lateral view, showing the locations of the tymbal and tympanum. (B) The tymbal in lateral view, drawn to show the distribution of the sclerotised elements (stippled) and of the unsclerotised membrane containing resilin (no stippling). The long ribs are numbered (1–4) in the order in which they buckle during sound production.

accommodated posteriorly by the first short rib and anteriorly by the second short rib. A reconstruction of this movement, as it would appear in horizontal section, is given in Fig. 8, which also serves to illustrate further the change in aspect of ribs 1 and 2 shown in Fig. 7.

Once the tymbal plate reaches the critical point on the inward movement, two or sometimes three long ribs buckle in sequence with little or no further movement at the dorsal end of the tymbal plate. However slowly the probe is advanced, it is almost impossible to obtain a stable condition with only rib 1 buckled. But rib 4 does not buckle unless the tymbal plate is pushed further in. As the probe is withdrawn, the tymbal returns to its resting position in a sequence that is the reverse of the inward movement: the most anterior ribs pop out first and the tymbal plate completes its out-swing last. During the outward movement, it is an easy matter to obtain a stable position with only rib 1 buckled.

As the probe is advanced from the resting position to the point where ribs 1 and 2 are buckled, the apodeme pit travels a distance of 0.36 ± 0.049 mm (s.d.; $N=6$). Since the tymbal

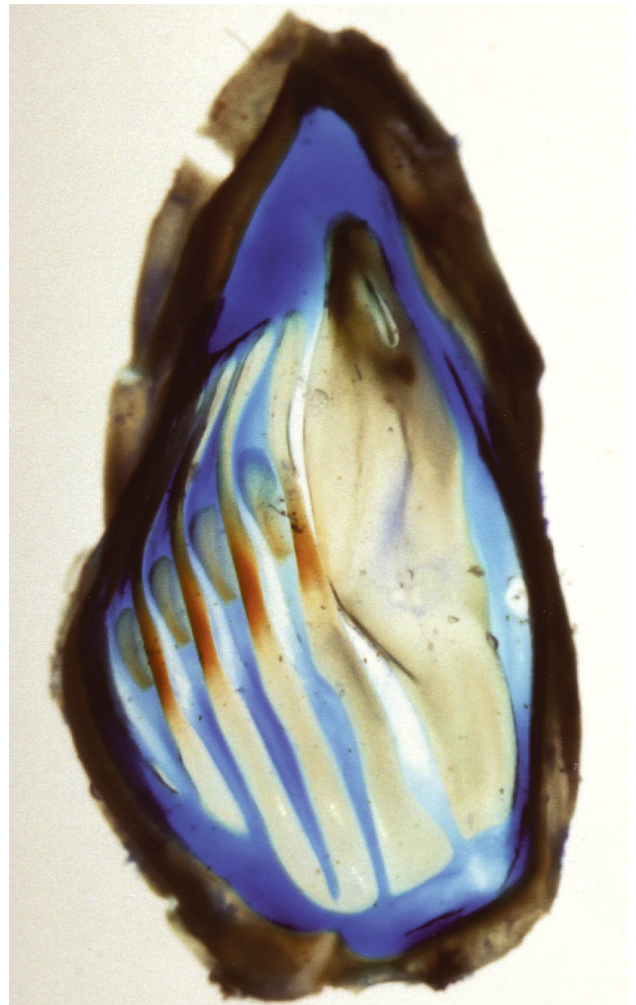


Fig. 5. An isolated tymbal of *Cyclochila australasiae* seen in lateral view after removal of the muscle and other tissues from the inside surface. The distribution of resilin is shown by the brilliant sapphire-blue staining, following immersion overnight in a very dilute solution of Methylene Blue. For identification of the various structures, see the labels in Fig. 4. Photographed by Mandy Naylor and David Paul.

muscle is about 8 mm in length, this is equivalent to a muscle shortening of just under 5%, which seems broadly compatible with the contraction kinetics of the muscle (Josephson and Young, 1981). At the same time, the anterior edge of the tymbal plate, measured at a point close to the row of short ribs, travels a distance of 0.82 ± 0.001 mm (s.d.; $N=5$). Hence, the tymbal plate acts as a lever, with the surface of the tymbal moving through more than twice the distance of muscle shortening.

The volume change displaced by the inward buckling of the tymbal can be calculated from these measurements. Taking round figures of a calculated tymbal plate area of 9 mm^2 , and an inward excursion of the anterior edge of the tymbal plate of 1 mm when two ribs are buckled, yields a volume change of $4.5 \mu\text{l}$. Under natural muscle contraction, the edge of the tymbal plate may swing in a little further before returning; a

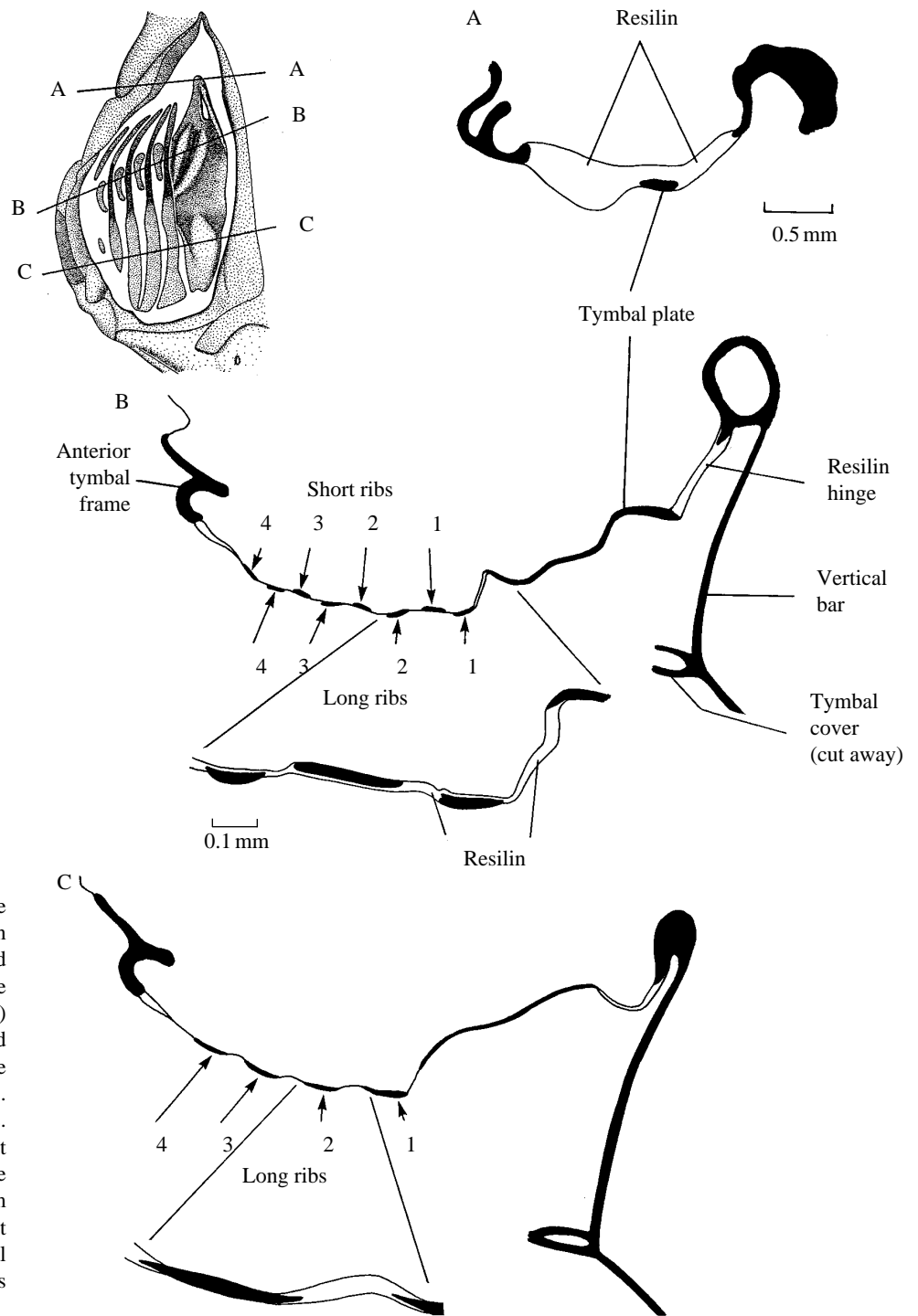


Fig. 6. Sections through the tymbal at the levels indicated by the labelled lines on the inset drawing (top left). Sclerotised cuticle is drawn in solid black and the resilin is drawn in outline only. (A) Section through the thick resilin pad and the dorsal tip of the tymbal plate. The 0.5 mm scale bar also applies to B and C. (B) Section along the line of short ribs. The enlargement shows the arrangement of resilin and sclerotised ribs between the tymbal plate and long rib 2. The 0.1 mm scale bar also applies to the enlargement in C. (C) Section through the ventral region of the tymbal where the long ribs are at their widest.

further 0.5 mm at its anterior edge would contribute an additional $2.3 \mu\text{l}$, giving a calculated total volume change of $6.8 \mu\text{l}$. Using the displacement of the water column in a capillary, the total volume displaced by inward buckling of the tymbal was measured as $6 \mu\text{l}$ (range $4.5\text{--}7.5 \mu\text{l}$). While these measurements with the water column were being made, it was not possible to see how many tymbal ribs were buckled but these values are similar to those calculated above.

The vibrations of the tymbal during buckling were

visualised by covering it with *Lycopodium* powder; the powder is agitated maximally in regions where vibration is greatest (Faraday, 1831). When a tymbal covered in *Lycopodium* powder is buckled in, the vibration is so great that the powder is thrown clear. Video pictures of the tymbal show that the maximum movement of the particles occurs at the sclerotised mid-regions of the long ribs. During the outward movement of the tymbal, there is a more general, but weaker, vibration of the whole surface of the tymbal.

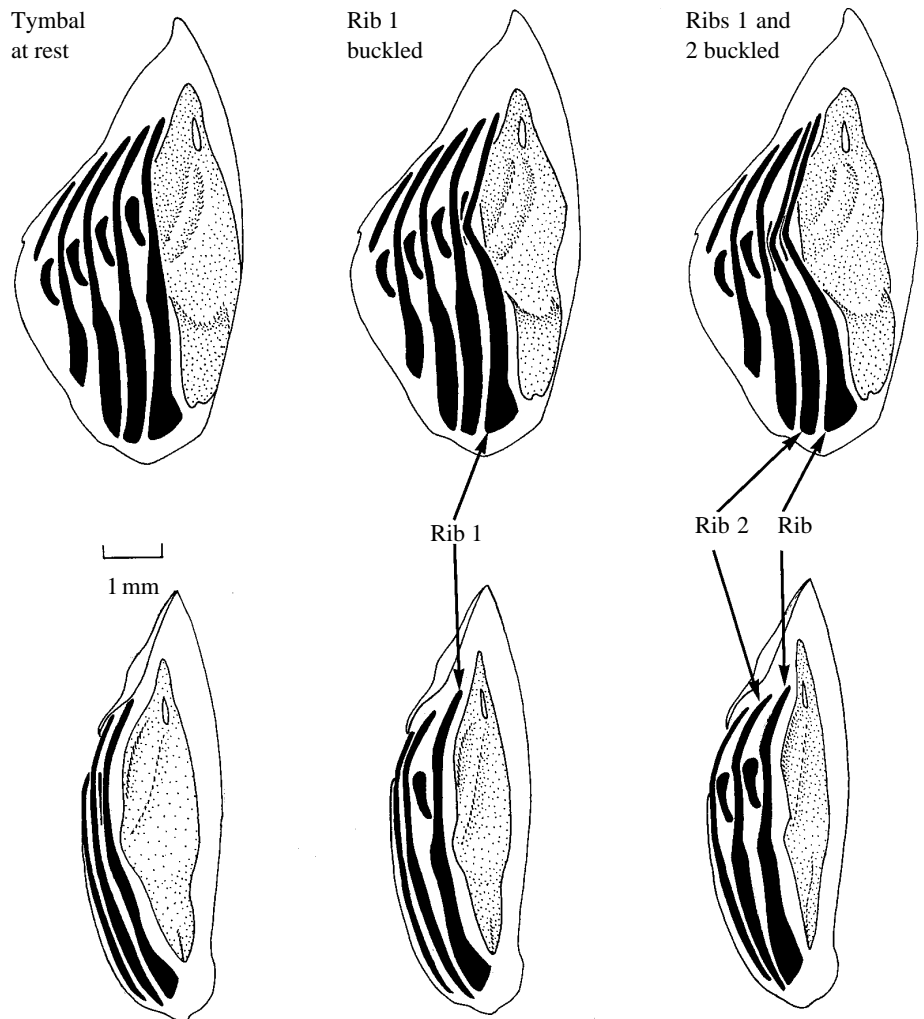


Fig. 7. Stages in buckling of the tymbal, drawn in lateral view (top row) and posterior view (bottom row); lateral and posterior views with respect to the tymbal are indicated by the arrows in Fig. 8. The stages of buckling were held for drawing by applying a small probe to the apodeme pit (see *Anatomical methods*). Since a stable position with rib 1 buckled could only be obtained during the outward movement, the position of the tymbal plate in the centre drawings is not quite correct for the inward buckling (see text).

Observations were also made with *Lycopodium*-covered tymbals on sealed cicadas, when excited with an internal sound source. When the tymbal is held in the buckled position by the probe, the maximal amplitude of vibration occurs along the row of dimples formed in the sclerotised mid-regions of the long ribs with a driving frequency of 4.3 kHz. The more weakly sclerotised dorsal and ventral parts of the long ribs and the tymbal plate show a weaker vibration, suggestive of a coupling between the long ribs and the tymbal plate. When the tymbal is returned to the resting position, only a weak general vibration of the ribs and tymbal plate is detected, in response to an internal sound drive at frequencies around 6 kHz. Thus, both sets of observations indicate that high-amplitude vibration occurs only in the sclerotised mid-region of the long ribs and only during the inward movement of the tymbal.

The function of various parts of the tymbal was clarified by excising different parts in turn and noting the effect this has on buckling, as the probe is advanced and withdrawn. When an approximately horizontal cut is made across the long ribs, just below the line of short ribs, the long ribs no longer buckle to produce any sound, but their upper and lower portions both bend in with the inward swing of the tymbal plate. When an approximately vertical cut is made along the resilin strip

between ribs 1 and 2, passing posteriorly to short rib 1 and extending along the whole length of rib 1, then rib 1 continues to buckle as the tymbal is pushed in, but rib 2 no longer buckles inwards. Hence, the structural integrity of the sclerotised mid-regions of each rib and the resilin linkage between one rib and the next are both essential for normal buckling.

When the thick resilin pad is excised from its position dorsal to the long ribs and tymbal plate, inward buckling of the long ribs still occurs, but is weaker, and the associated click is barely audible; there is also a noticeable delay between the buckling of ribs 1 and 2. In addition, the outward movement is much slower than before; ribs 1 and 2 no longer snap back into place, but return to the out position in a leisurely fashion as the tymbal plate swings out under the influence of the resilin hinge along its posterior edge. When a similar area of cuticle is cut out ventrally, including the ventral ends of ribs 1 and 2, this makes no noticeable difference to either the inward or outward movements of the tymbal. Hence, the thick resilin pad appears to act as a return spring that is largely responsible for causing the outward movement of the tymbal. The long ribs are evidently stable in the out position because of their long bow-shaped structure combined with the restoring force of the resilin pad. During the inward movement, the tymbal muscle

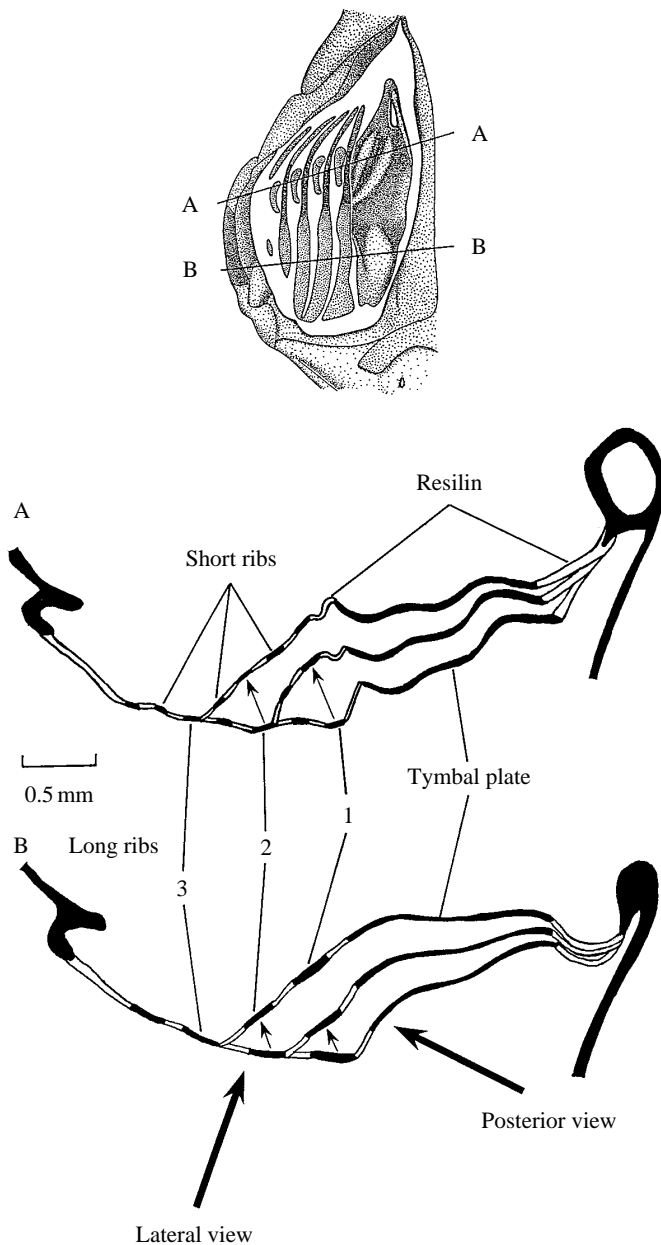


Fig. 8. Reconstruction of the stages of tymbal buckling, based on the horizontal sections in Fig. 6B,C. Using these two sections of the tymbal at rest, we have reconstructed the buckling of ribs 1 and 2 as it would appear in equivalent sections, on the basis of measured dimensions and extents of movement. The plane of these sections is indicated by the labelled lines on the inset drawing (top). The small arrows at long ribs 1 and 2 show the movement of each rib as it buckles. The large arrows indicate the lateral and posterior views of the tymbal shown in Fig. 7. Sclerotised cuticle is drawn in solid black and the resilin is drawn in outline only (the thickness of the latter is exaggerated slightly for clarity in this figure).

or probe must overcome both these factors to produce the sudden buckling of the long ribs.

Taken together, the observations on tymbal buckling reported here suggest that buckling of the long ribs occurs as follows. As the tymbal plate swings inwards, it produces an

inward movement and twisting of the dorsal ends of the long ribs. This causes the arc formed by a long rib to flatten, but the rib is constrained at its two ends so that its chord cannot lengthen. Consequently, the flattening leads to the buckling of the arc when the force producing the flattening is greater than the restoring force of the resilin pad and the intrinsic stresses of the rib's curvature. The long rib buckles at its weakest point, which is the thinner sclerotised mid-region. Buckling is localised to this region because the dorsal and ventral ends bend less easily, being wider and more convex in cross section (Fig. 6).

Furthermore, the long ribs are tightly coupled to each other, and rib 1 is coupled to the tymbal plate, by narrow strips of resilin at their dorsal and ventral ends, but they are only loosely coupled in the mid-region by much wider strips of resilin and the intervening short ribs (Fig. 4B). This arrangement communicates the flattening effect from one rib to the next at their dorsal ends but leaves their mid-regions free to buckle independently and to vibrate. Though strongest in the mid-region, the vibration is communicated to the ends of the ribs and thence to the tymbal plate *via* the narrow strips of resilin.

Acoustics of the tymbal when driven by its muscle

In the first series of experiments, sound pulses were elicited by stimulating the tymbal muscle. The resulting pulses have a waveform similar to that of natural protest song, but are quieter; the in and out movements of the tymbal are also more widely separated, making it possible to analyse their sounds independently (Fig. 9).

With the intact cicada, the in-click consists of a pulse that closely resembles one from a natural protest song, though the envelope is somewhat more ragged (Fig. 9A). The calculated Q of the pulse decay is between 4 and 5. The dominant peak in the frequency spectrum is also typical of that of normal song at around 4 kHz (Fig. 9B). The out-click is over 20 dB quieter than the in-click; this in part is because it is far briefer. The frequency spectrum of the out-click shows that it has an important component at a higher frequency of 5.7 kHz (Fig. 9C).

The same insect was then sealed and the sound was recorded at a range of 3 mm from the outside of the tymbal (Fig. 10A). The dominant peak in the frequency spectrum of the in-click is at 3.84 kHz (Fig. 10C), which is similar to the value from the intact cicada. Subsidiary peaks are seen at approximately +4 and +8 kHz; these two peaks can be ascribed to modulation in the pulse envelope (see Bennet-Clark and Young, 1992, pp. 144–147). This modulation occurs at every second cycle early in the pulse (arrows on Fig. 10A mark cycles 1, 3, 5). This sound pulse decays far more slowly than that from the intact cicada, with a Q of 12.9, implying that the tymbal resonance is less damped in this preparation.

One striking feature of this sound pulse is that the 10 or more cycles at the decaying end of the pulse have a wavelength that is about 1.3 times that of the first six cycles of the pulse (Fig. 10A). This free decay occurs at about 3.2 kHz, whereas the first half of the pulse has a dominant frequency of 3.84 kHz.

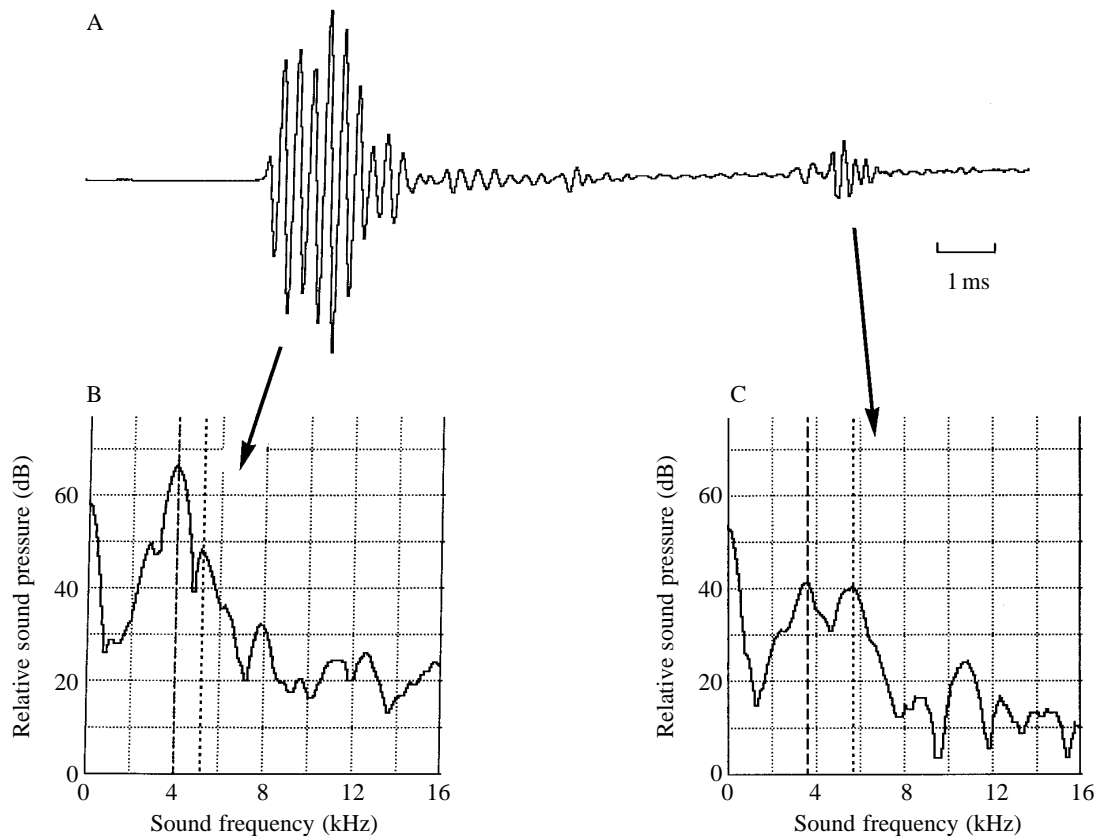


Fig. 9. Sound produced by the tymbal following stimulation of the tymbal muscle in the intact cicada (Fig. 1A). (A) Oscillogram of sound produced by a single in-out movement of the tymbal. (B) Power *versus* frequency spectrum of the in-click shown (left) in A. (C) Power *versus* frequency spectrum of the out-click shown (right) in A.

In the decay of the sound pulse of the intact cicada and in normal song, the dominant frequency appears to be the same as that of the first few cycles of the sound.

The sound pressure was also recorded inside the same sealed cicada (Fig. 10B). The phase of the internal sound pressure change seen in the oscillogram is inverted relative to that in Fig. 10A (with the Bruel and Kjaer equipment used, a compression causes a negative-going voltage). During the in-click, the internal sound pressure rises sharply in the first half-cycle (cycle 0.5) of compression and rises again at cycle 2.5 and cycle 4.5 (arrows on Fig. 10B). Although the pulse envelope is more irregular, it resembles that recorded from outside the tymbal. In the frequency spectrum, the dominant frequency peak is at 3.84 kHz (Fig. 10D), which is the same as that outside the tymbal (Fig. 10C). The out-click shows an initial rarefaction with two cycles of oscillation (R1 on Fig. 10B) followed by a re-compression then rarefaction (R2 on Fig. 10B), on which are superimposed two or three cycles of vibration at a higher frequency.

Since sound is no longer being radiated through the tympana in the sealed cicada, the abdominal Helmholtz resonator is effectively put out of action. The similarity between the sound pulses produced by the intact and sealed cicada is therefore consistent with the view that the tymbal itself is a resonant system excited by the inward buckling of the long ribs.

Furthermore, the pattern of the modulation in the sealed cicada (arrows in Fig. 10A,B) suggests that long rib 1 clicks in at the start of the pulse and that this is followed by rib 2 two cycles later and by rib 3 after another two cycles.

These experiments do not, however, preclude the possibility that the apparent resonance is due to the air sac of the insect or to its body wall cuticle. Accordingly, the same insect was operated upon to open the abdominal air sac both anterior and posterior to the tymbals (Fig. 1D). The in-click of the tymbal, recorded at a range of 3 mm from the outside of the tymbal, shows a pulse envelope (Fig. 11A) and frequency spectrum (Fig. 11B) similar to that of the sealed cicada (Fig. 10), including a similar pattern of modulation (arrows mark cycles 1, 3, 5 on Fig. 11A) and final decay at a lower frequency. There is an even higher Q of 19.9 calculated for the decay of the pulse. The first two cycles of the out-click are at a lower frequency than the last half dozen cycles of the pulse, as is the case with the out-click recorded from inside the sealed cicada (Fig. 10B).

The major difference observed between the sound produced by tymbal buckling in the intact cicada and in the sealed or the open cicada is that, in the two latter cases, the pulse decays more slowly (or has a higher Q) than the sound pulses from the intact cicada. Though the sound levels have not been measured, it was noticed that the pulses produced by the intact

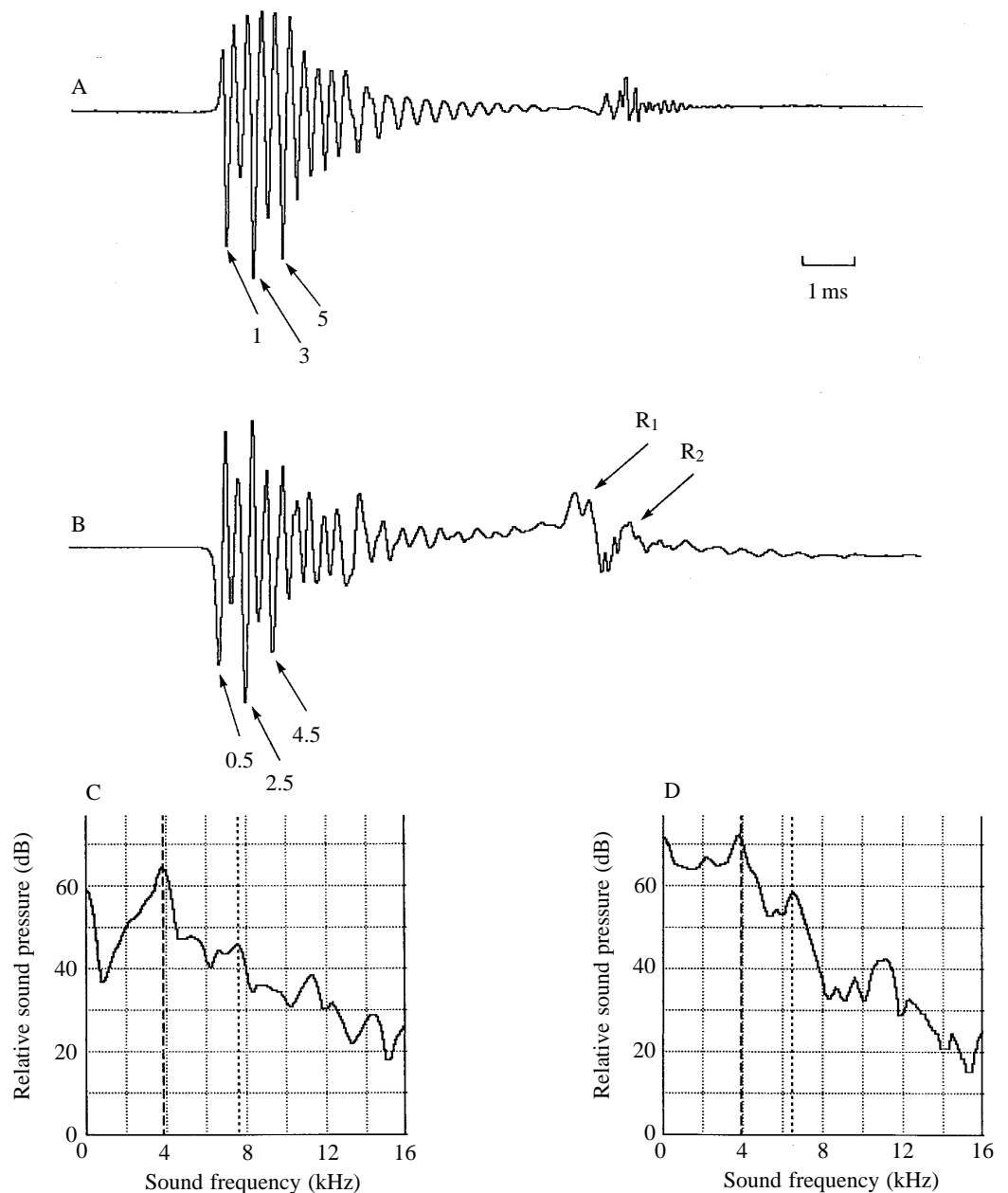


Fig. 10. Sound produced by the tymbal following stimulation of the tymbal muscle in the sealed cicada (Fig. 1B). (A) Oscillogram of sound recorded outside the tymbal during a single in-out movement of the tymbal. (B) Oscillogram of sound recorded inside the air sac during a single in-out movement of the tymbal. The numbered arrows in A and B mark significant modulation of the pulse envelope that occurs at the indicated cycle number. (C) Power *versus* frequency spectrum of the in-click shown in A. (D) Power *versus* frequency spectrum of the in-click shown in B. R1, R2, rarefactions 1 and 2 (see text).

cicada are far louder than those from either the closed or open cicada, which implies that the tymbal and its resonance are more heavily damped in the intact cicada, when sound is radiated *via* the abdominal resonator and eardrums (Young, 1990; Bennet-Clark and Young, 1992).

Driven resonances of the tymbal

Here measurements were made on sealed cicadas with the tip of the probe microphone placed 1–2 mm outside the tymbal ribs and with the vibration force transducer pushing on the tymbal plate, while sound pulses were delivered inside the insect's body.

Preliminary experiments with the transducer showed that the sound produced by the tymbal depended on the position of the transducer on the tymbal plate, the angle at which it was

pushed against the tymbal and the distance through which the tymbal plate was pushed. The most consistent results were obtained when the tip of the transducer was placed on the apodeme pit, with the rod aligned along the axis of the muscle apodeme. These preliminary experiments showed that the envelope of the tymbal vibration recorded *via* the force transducer (Fig. 12A) closely resembles the envelope of the sound recorded *via* the probe microphone (Fig. 12B), which suggests that there is indeed a causal relationship between the tymbal vibration and the sound that it produces.

In further experiments with fresh cicada bodies, the apodeme pit was pushed inwards in 50 μm steps by the vibration force transducer. The resonant frequency of the tymbal vibration and of the sound radiated to the outside of the tymbal were measured from the oscilloscope screen during

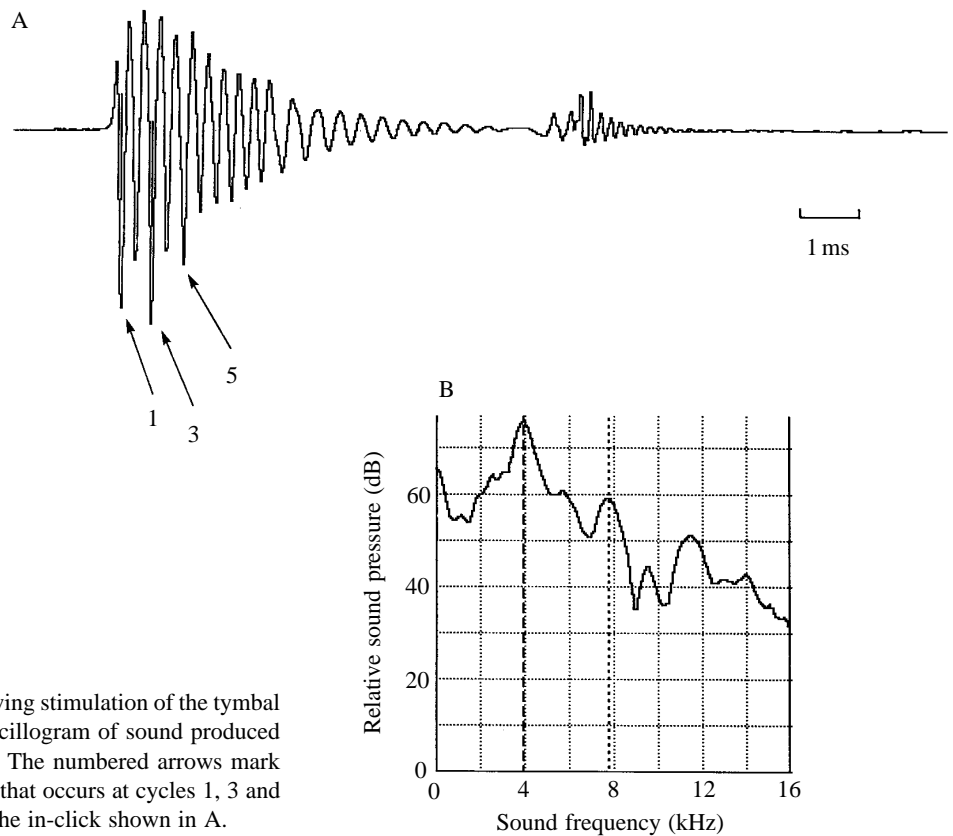


Fig. 11. Sound produced by the tymbal following stimulation of the tymbal muscle in the open cicada (Fig. 1D). (A) Oscillogram of sound produced by a single in-out movement of the tymbal. The numbered arrows mark significant modulation of the pulse envelope that occurs at cycles 1, 3 and 5. (B) Power *versus* frequency spectrum of the in-click shown in A.

both the inward and the outward movement. These values were then plotted against tymbal position (Fig. 13).

The resonant frequencies of the vibration and of the sound were closely similar. During the inward movement, the resonant frequency fell gradually from about 5.7 to 5.2 kHz through the first 0.35 mm of the movement. The tymbal buckled inwards after between 0.35 and 0.4 mm of the movement, which agrees well with the mean value of 0.36 mm obtained above (see *Mechanics of tymbal buckling*). The resonant frequency then fell to about 4 kHz and further inward movement caused this to fluctuate between 4 and 3.5 kHz. As the tymbal plate was allowed to move outwards, the resonant frequency rose, with some fluctuations, to a value of 4.3–4.5 kHz just before the tymbal popped out and its resonant frequency returned to the original value of about 5.7 kHz. This shows that the resonant frequency of the tymbal at rest (the out position) is far higher than the natural song frequency but, when the tymbal is buckled in, its resonant frequency is similar to that of the natural song.

This experimental situation does not closely mimic the natural pull on the apodeme pit by the flexible apodeme of the tymbal muscle because the tymbal plate is likely to be only lightly loaded by the apodeme after the tymbal has buckled in. However, the tymbal resonant frequency most closely approaches the natural song frequency just before the tymbal pops out (Fig. 12), which is the stage when the external loading by the transducer rod on the tymbal plate is likely to be least and hence the tymbal vibration is most likely to resemble that in the singing cicada.

Similar observations were made with another cicada body in the open cicada configuration, which was driven by a tone burst of vibration at the apodeme pit. The resonant frequency of the sound produced by the tymbal was 4.29 kHz, when buckled in, with a Q of 16.8. The same tymbal, at the out position, resonated at 5.9 kHz with a Q of 10. This confirms that the resonance of the lightly loaded, and hence lightly damped, tymbal is of high Q , as we found with the muscle-powered tymbal in the open cicada (see above, Fig. 11). It also confirms that the resonant frequency of the tymbal is independent of any abdominal air sac resonator.

Sound pressure measurements were also made outside the tymbal, at both the in and out positions, in sealed cicadas driven by an internal sound source. The resonant frequency of the buckled-in tymbal was first found, which varied between 3.8 and 4.3 kHz in three individuals, and the sound pressure level was measured by the probe microphone 2 mm outside the tymbal. The tymbal was then allowed to return to the out position, and the sound pressure level at the same driving frequency dropped by between 12 and 20 dB. Similarly, the resonant frequencies were measured with the tymbal at the out position, and these varied between 5.6 and 6.5 kHz; when the tymbal was then buckled in, the sound pressure level at the same frequency fell by between 18 and 24 dB. This experiment shows that the change in the resonant frequency of the tymbal is also accompanied by a change in its effective sound transparency; at its resonant frequency, the tymbal radiates sound, but moved to the alternative in or out position it becomes more opaque to sound. An important consequence of

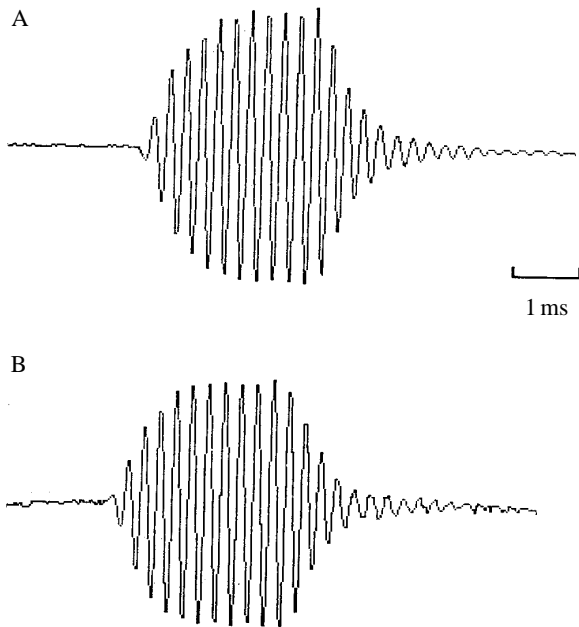


Fig. 12. Response of the tymbal to a single sound pulse from a source inside the abdominal air sac, recorded simultaneously with the vibration force transducer and the probe microphone. (A) Vibration recorded by the force transducer with its probe rod touching the tymbal plate. (B) Sound recorded by the probe microphone just outside the tymbal ribs.

this property of the tymbal is that, as one tymbal buckles in and resonates to produce pressure changes within the abdomen, these will not readily be transmitted or dissipated by the contralateral tymbal at the out position.

Since the two tymbals buckle alternately in normal sound production, some asymmetry in their performance might be expected to show up in the cicada's song. This is not usually obvious in natural song but can be seen clearly in recordings of the internal sound in sealed cicadas, which show the sound pressure generated by the tymbal buckling without any modifying influence of the abdominal resonator (Fig. 14). The oscillogram of protest song in a sealed cicada (Fig. 14A) clearly shows an alternating sequence of pulses, evidently corresponding to the sound from the left and right tymbals. The left and right pulses differ noticeably in their envelope (Fig. 14B) and in their frequency spectra (Fig. 14C,D). One has a relatively cleanly decaying envelope, for which a Q of 13 was calculated, while the other has a more ragged envelope associated with a distinct subsidiary peak at 5.4 kHz (Fig. 14D).

Acoustics of the tymbal-to-abdomen coupling

Intact cicadas (Fig. 1A) were fitted with an internal sound source and arranged so that one tymbal could also be vibrated at the apodeme pit using the vibration force transducer as a source (see Materials and methods). The sound produced was measured with the probe microphone either 2 mm away from the outer surface of the tymbal or inserted under the raised opercula. These experiments allowed comparison between the

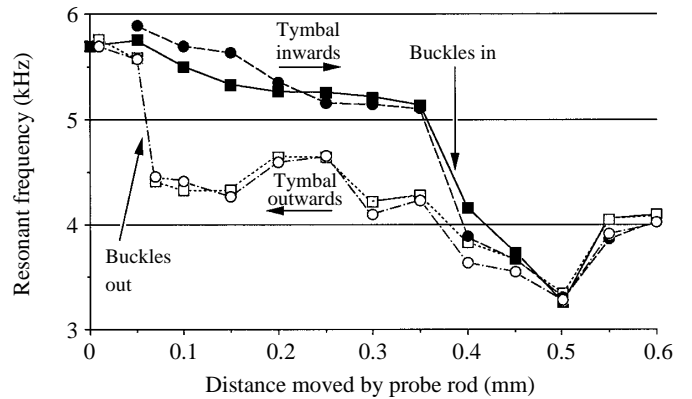


Fig. 13. Resonant frequency of the tymbal, when driven by a sound source inside the air sac, at different stages of buckling. The resonant frequency was measured with the probe microphone (squares) and the force transducer (circles) as the probe rod was advanced inwards (filled symbols) and then withdrawn again (open symbols). Labelled arrows mark the points at which the tymbal ribs buckled inwards and popped back out to the resting position.

sound radiated by the tymbal, and hence its vibration, with the sound radiated through the tympana when the abdominal air sac was excited either by sound or by tymbal vibration.

The results for one insect are summarised in Table 1. The Q of the sound produced by the tymbal vibration is closely similar with the two types of excitation. The Q of the air sac resonance, excited by internal sound, is similar though rather lower than that found earlier (Bennet-Clark and Young, 1992). The combined Q of the system, in which the tymbal is driven by vibration and excites the abdominal resonator, is higher than that of the tymbal alone and approximately equals the sum of the Q of the tymbal and the Q of the abdominal resonator, as was predicted by Bennet-Clark and Young (1992).

Fig. 15 shows a comparison of sound pulses produced by vibration of the tymbal in another preparation, recorded 2 mm from the tymbal surface (Fig. 15A) and recorded in the cavity between the operculum and the tympanum (Fig. 15B). It can be seen that the build-up and decay of the pulse radiated from the tymbal is more rapid, with a lower Q , than the build-up and decay of the pulse radiated from the tympana. In this preparation, the tymbal was excited at 3.9 kHz, which had previously been found to be its resonant frequency; 3.9 kHz also seems to be close to the resonant frequency of the abdominal Helmholtz resonator in this preparation. Similar

Table 1. Response of an intact *Cyclochila* body to tone bursts at 4.2 kHz

Type of excitation	Position of measurement	Q of response
Vibration at tymbal	Outside of tymbal	9.4
Vibration at tymbal	Tympanal opercula	12.5
Sound inside abdominal airsac	Outside of tymbal	9.3
Sound inside abdominal airsac	Tympanal opercula	3.4

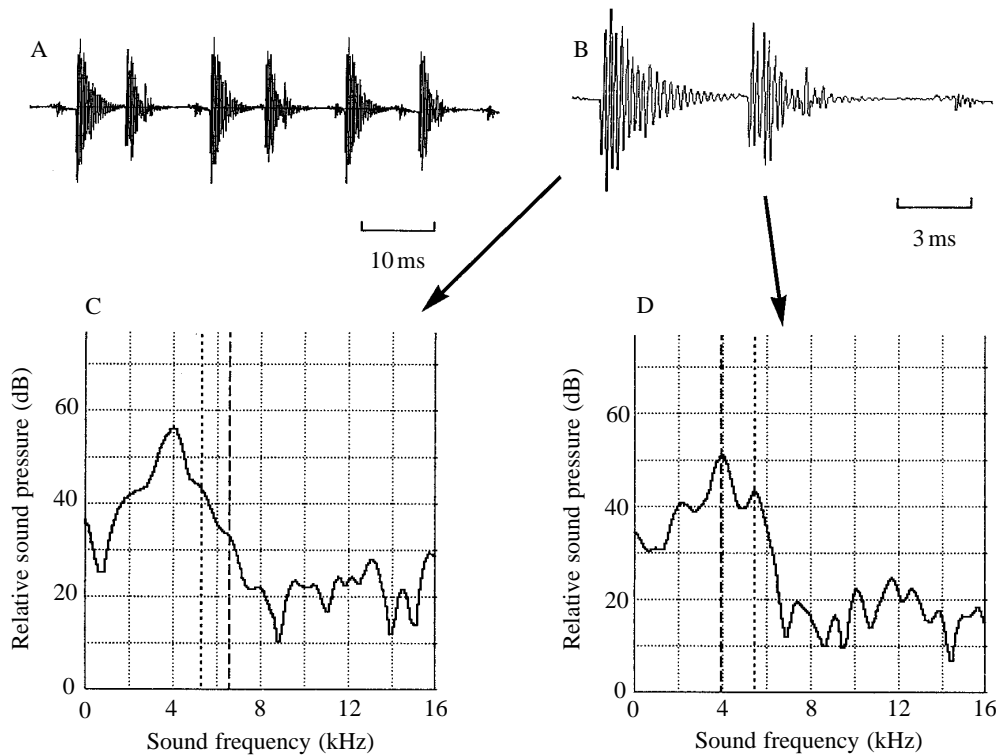


Fig. 14. Protest song recorded inside the air sac of a sealed cicada (Fig. 1B). (A) Oscillogram of the sound produced by both tymbals showing paired left/right pulses. (B) Expanded oscillogram of one left and one right pulse (it is not possible to tell which is which). (C) Power *versus* frequency spectrum of the 'left' pulse shown in B. (D) Power *versus* frequency spectrum of the 'right' pulse shown in B.

results were obtained with other preparations at frequencies between 3.9 and 4.4 kHz.

Sound pressures inside the air sac

Measurements were made of the sound pressure changes that occurred in the abdominal air sac in both intact and sealed cicadas during protest song. Using the peak hold range of the sound level meter, the mean value of successive readings in a single intact cicada was 157.75 dB SPL ($N=8$) and, in the same cicada when sealed, 156 dB ($N=8$). With other intact insects, peak internal values of 155–159 dB SPL were recorded. The peak hold reading captures the sound pressure peak of signals of 50 μ s or longer duration, so this measurement gives an approximation to the highest pressure that occurs inside the abdominal air sac.

Using the impulse hold range of the sound level meter, the same preparations gave internal values of 141–144 dB SPL; the impulse hold range measures the maximum averaged sound pressure integrated over a 150 ms period. This measurement indicates that the average internal sound pressure during protest song is about 15 dB quieter than the peak pressure, or that the average pressure is about one-sixth of the peak pressure. From oscillograms of the protest song that have been recorded inside the abdominal air sac (Fig. 14A), this pressure ratio seems feasible.

The sound pressure was also measured in the cavity between the opercula and the tympana in the intact cicadas. The peak hold reading was 148.5 dB SPL ($N=8$).

The static volume displaced by the inward buckling of two or three tymbal ribs is about 6 μ l (see above) into an abdominal air sac volume of about 2 ml (Bennet-Clark and Young, 1992).

Since the change in volume is about 1/330 of the total, the tymbal buckling should raise the internal pressure suddenly by a mean value of 3.3×10^{-3} bar. If the tymbal buckles inwards elastically, its peak inward displacement may be greater than the mean displacement that we have measured, so the pressure pulse as the tymbal buckles may be greater than that. An RMS

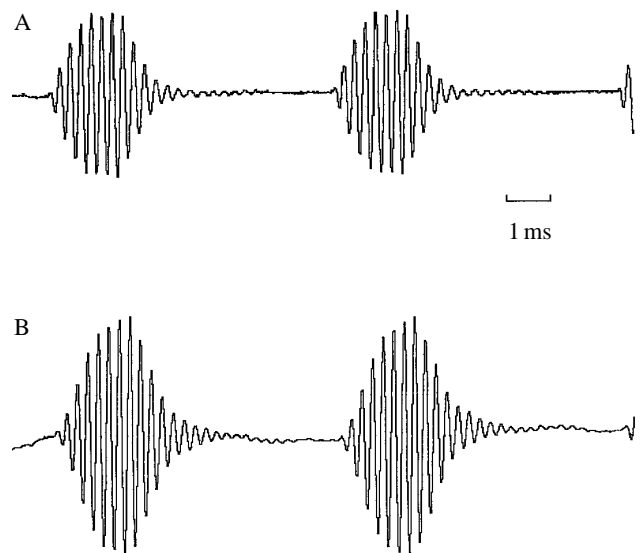


Fig. 15. Sound pulses recorded with the probe microphone when the tymbal is driven by the vibration force transducer acting on the tymbal plate. (A) Sound recorded with the microphone placed just outside the tymbal ribs. (B) Sound produced by the same driving signal as A, when recorded with the microphone placed in the gap between the operculum and tympanum.

sound pressure of 1 N m^{-2} (approximately 10^{-5} bar) is 94 dB; the *peak* pressure in such a sound will be 100 dB. Consequently, the inward tymbal displacement observed here should produce *peak* sound pressure levels of at least $330\text{--}660 \text{ N m}^{-2}$ or between 150 and 156 dB. Hence, the observed peak pressures inside the abdominal cavity of 156–158 dB SPL are consistent with the observed displacement of the tymbal.

Discussion

Properties of the tymbal

It is clear from the results presented here that the tymbal is a resonant structure. This conclusion is supported by the fact that the sound pulses produced by muscle action in the sealed and open cicadas are so similar to those of the intact cicada (Figs 9A, 10A, 11A). The sealed cicada preparation prevents normal sound radiation through the tympana and so puts the abdominal Helmholtz resonator out of action. The open cicada preparation effectively eliminates any resonances in the air sac or body wall, and so the relatively pure 4 kHz pulses produced in this preparation must be due to resonance in the tymbal itself. Similarly, a resonance around 4 kHz was demonstrated in the buckled-in tymbal of sealed cicadas, when driven by a sound source inside the abdomen (Fig. 13). And this resonance was still present in the open cicada preparation when the tymbal was driven by vibration at the apodeme pit.

These findings are consistent with the model put forward by Bennet-Clark and Young (1992), in which it was suggested that the sound-producing system of cicadas usually consists of two coupled resonators. One of these is a Helmholtz resonator, consisting of the abdominal air sac and tympana, and the other is the sound-generating tymbal. If the tymbal vibration is resonant at the same frequency as the abdominal resonator, then the tymbal will be maximally efficient at exciting and sustaining resonance in the abdominal cavity. Our present results suggest that this is indeed the case and hence that the tymbal is a major determinant of the insect's song frequency.

An alternative model, in which the tymbal is treated as a membrane (or shell) backed by a cavity, has been outlined briefly by Fletcher (1992, p. 242). Here the tymbal and air sac constitute a resonator with a single mode, the frequency of which is determined by the volume of the cavity and the elasticity of the membrane. If this model were correct, the frequency of sound produced by the tymbal ought to be quite different in the intact and open cicada configurations, but no such difference is observed in our results. In any case, this model does not take account of the fact that most of the sound is radiated from the large tympana, *via* the air sac, rather than from the tymbals (Young, 1990).

One unexpected finding from our present work is that the resonant frequency of the tymbal depends on its position in the cycle of in–out movement. When the tymbal buckles in, it exhibits a resonance close to 4 kHz, but when it returns to the out position, its resonant frequency rises to about 6 kHz (Fig. 13). Accordingly, the loud in-click has a dominant

frequency of about 4 kHz while the quieter out-click is dominated by frequencies around 6 kHz (Fig. 9). This result is not so surprising when it is realised that the primary resonators within the tymbal appear to be the long ribs, judging from our observations of the movement of particles on the tymbal surface. The mass and compliance terms of these resonators remain to be described, but it is easy to see that these terms are likely to be different at the buckled-in position, when the ribs have a V-shaped dimple, and at the out position, when the ribs are evenly curved.

When a tymbal is coupled to the abdominal air sac, the sound of the in-click is enhanced and sustained by the air sac resonance, but the higher-frequency sound of the out-click is suppressed. This effect is reinforced by the way that the left and right tymbals buckle alternately in natural song: the timing of tymbal muscle contractions is such that the out-click of one tymbal normally coincides with the in-click of the other. Since its resonant frequency rises during the out-click, a tymbal becomes effectively opaque to the insect's song frequency and so does not dissipate the pressure changes within the abdomen caused by the contralateral tymbal. As a consequence of these effects, the sound radiated into the environment during the calling song of *Cyclochila* shows a dominant frequency component at about 4 kHz, and the components around 6 kHz are at least 30 dB below the 4 kHz peak (Young, 1990, Fig. 2).

Where this kind of overlap between left and right tymbals is not present and the abdominal resonator is less sharply tuned, the out-click of each tymbal may make a significant contribution to the calling song in some other species. On the basis of the present results, one would expect the out-pulses of the radiated song to differ slightly in frequency from the in-pulses in such cases. For example, Hennig *et al.* (1994) describe such a song in the species *Tibicen linnei* and mention that the out-pulses have a somewhat higher frequency band than the in-pulses, but they give no details. The tymbal in-click is always likely to make a greater contribution than the out-click to cicada songs because it is powered by the tymbal muscle, whereas the out-click is powered only by the thick resilin pad and resilin hinge described above.

In the sealed cicada and open cicada preparations of *Cyclochila*, where the influence of the abdominal resonator is prevented, muscle-powered in-clicks show three significant modulations of the pulse envelope at cycles 1, 3 and 5 (Figs 10, 11). It is likely that these three successive increases in sound amplitude are due to the buckling of three successive long ribs during the inward movement of the tymbal. Either two or three ribs buckle in a single movement when the tymbal plate is moved in with the probe, and three ribs are normally seen to buckle in videos of the tymbal during protest song. Hence, the arrangement of long ribs would seem well designed to provide a large initial impulse to the resonant air sac of the insect's abdomen and then sustain the resonance by a series of coherent impulses at more-or-less the same frequency. In natural calling song, this has the effect of building up the pulse amplitude rapidly and then sustaining the sound to produce a long, loud pulse. However, it is not known whether, as successive tymbal

ribs buckle inwards, they all produce sounds of similar resonant frequencies.

Close coupling between adjacent tymbal ribs, and between the first tymbal rib and the tymbal plate is evident from the similarity between the sound that the tymbal produces and the vibration that may be detected *via* a transducer on the tymbal plate (Fig. 12). The tymbal plate by itself does not appear to resonate at the song frequency, but it does appear to be driven by the resonant clicks of the tymbal ribs, which will increase the effective volume change that accompanies the vibration of the ribs and thus increase the internal pressure changes caused by the tymbal clicks.

Tymbal function in Tympanistalna gastrica

The suggestion that the tymbal forms the first of two coupled resonators in the sound-producing system of cicadas (Bennet-Clark and Young, 1992) appears to be strongly supported in *Cyclochila*, but this model does not necessarily apply to all other species. An analysis of a species where this model may not apply has been published by Fonseca and Popov (1994) after the present work was submitted for publication. They studied sound radiation in *Tympanistalna gastrica*, which is much smaller than *Cyclochila* and has a very different song pattern consisting of a pair of loud clicks followed by a train of soft pulses. Their measurements show that sound is radiated from both the tymbals and the tympana, and even from the body wall of the abdomen; they conclude that the tymbals are the major sound source, rather than the tympana, and that the abdominal cavity does not seem to act as a resonator.

Despite this point of difference, there is much in common between their results and ours regarding the function of the tymbal. Like us, they find that the tymbal vibration is a major determinant of the peak frequencies in the insect's song and that the tuning of the tymbal to these frequencies is unaffected by experimental alterations to the abdominal cavity. *T. gastrica* differs from *Cyclochila* in having a tymbal that generates a broad band of frequencies rather than a narrow band; this could be explained if individual ribs were tuned to different frequencies, which would then contribute to the loud clicks as the tymbal buckled in. Another similarity is that during the first cycle of movement, which produces the loud clicks, the tymbal has very different properties on the inward and outward stages of movement. Although Fonseca and Popov (1994) do not explicitly discuss this point, it is clearly evident from their Fig. 1B. The in-click is some 10–12 dB louder and has a peak frequency about 1.5 kHz lower than the out-click; in *Cyclochila*, the differences between the in-click and out-click are similar but even more pronounced (Fig. 9).

In considering whether the abdominal cavity might be acting as a resonator coupled to the tymbal, Fonseca and Popov (1994) estimate the resonant frequency of the cavity using the equation for a Helmholtz resonator given in Bennet-Clark and Young (1992). They obtain a figure of 9.8 kHz and state that this is not in good agreement with the spectral peaks found in the song, but this statement is not entirely borne out by their

own data. This estimate is about 1 kHz below the largest peak in the loud clicks (their Fig. 1C), but their Fig. 4E shows a significant peak at 10 kHz in the sound emerging from the tympana, just as one would expect from a Helmholtz resonator, and this overlaps with the main peak produced by the tymbal (10–12 kHz). Significant peaks close to 10 kHz can also be seen in the song recordings shown in their Figs 6A and 7A. Furthermore, these peaks are reduced in size when the tympana are covered (their Fig. 6A) or the abdominal volume is reduced (their Fig. 7A), which is consistent with the Helmholtz resonator model.

It would seem possible, therefore, that the abdominal cavity and tympana are acting as a resonator and that, in this role, they make a modest contribution to the sound output of the loud clicks. This role is not a major one because of the wide range of frequencies generated by the tymbal and because of the complicating factor of the thin-walled abdomen. By contrast, in *Cyclochila* both the tymbals and the abdominal cavity are specially tuned to a narrow frequency band, and so the Helmholtz resonator makes an important contribution to producing a loud pure-tone song.

It is obvious that the tymbal of *T. gastrica* is operating in a different mode when the soft pulses are being produced. Fig. 1B of Fonseca and Popov (1994) shows that there is an increase of approximately 50% in the delay between the in and out sounds in the soft pulses, compared with that found in the loud clicks. From this and the quietness of the sounds, it would appear that the tymbal is under much less stress during the soft pulses. This change could be due to the action of the tensor muscle, which is certainly capable of altering the stress on the tymbal (Simmons and Young, 1978; Hennig *et al.* 1994) as is noted by Fonseca and Popov (1994).

Fig. 1B of Fonseca and Popov (1994) also shows that the in and out sounds are very similar in the soft pulses and that these sounds closely resemble the quiet out-click that follows the loud in-click during the first cycle of tymbal movement. Since our finding is that the inward buckling of a stressed rib produces a loud click (see also Simmons and Young, 1978), this result suggests that the ribs may not actually buckle during the production of the soft pulses in *T. gastrica*. Possibly the tymbal is slackened off so much that the ribs merely bend rather than suddenly deforming under the action of the tymbal muscle. If this were so, it would explain why the spectral peaks of the loud clicks and soft pulses are distinctly different (Fonseca and Popov, 1994, Figs 1C, 4A, 5A) and why the spectrum of induced tymbal vibrations, presumably measured with the tymbal in the resting (out) position (their Fig. 9), resembles that of the soft pulses but not that of the loud clicks. Whatever is the case, the properties of the tymbal during the soft pulses are quite different from those found in *Cyclochila*, which produces no such delicate murmurings; on the contrary, the tymbal and associated structures of *Cyclochila* appear well designed to produce a song that is as loud and penetrating as possible.

The overall performance of the sound-producing system

The chain of sound production in a cicada such as

Cyclochila can be summarised thus: muscle power → tymbal clicks → excitation of abdominal resonator → radiation of sound *via* tympana. The cicada sound production system is an attractive area for research because the links in the chain are capable of separate analysis. This allows the properties of each link to be evaluated, both as an entity and as a component in the system.

One notable problem in producing airborne sound from muscle contraction is that the pressure-to-area relationships produced by muscle are very different from those appropriate for a sound wave. Thus, muscle typically produces stresses or pressures of about 1 bar (10^5 N m^{-2}), which is several orders of magnitude greater than that of any biologically significant sound in air. In other words, muscle produces high pressures over small areas, but sound waves exert small pressures over larger areas. An ideal transduction process should, therefore, provide the acoustic transformation that changes the pressure-to-area relationships from those of the muscle to those appropriate for a sound wave.

Such a system may be seen here, in two stages. In the first, muscle power, at high pressure, is used to produce a tymbal click which generates as high acoustic pressures as have been recorded in any animal. But the peak pressures recorded inside the cicada are still some 30 dB less than the pressure that might be produced by the tymbal muscle directly. These high acoustic pressures are used to excite the resonator of the abdominal cavity, in which there is further reduction of the sound pressure accompanied by an increase in the area from which the sound is radiated, from the smaller area of the tymbal to the larger area of the paired tympana.

By using the tymbal as a high-pressure source providing an internal drive to the abdominal cavity, the system provides, in two stages, a mechanism that transduces high-pressure muscle power into lower-pressure sound power. The large area of the tympana is important because the effective sound source must be large relative to the sound wavelength to obtain a good impedance match between the sound source and the fluid medium (see, for example, Olson, 1957). This fact limits even the largest insects to operating at relatively high sound frequencies, such as the 4 kHz employed by *Cyclochila*. Since even the fastest tymbal muscles cannot contract repetitively at anywhere near 4 kHz (Josephson and Young, 1985), transduction also involves a process of frequency multiplication (Michelsen and Nocke, 1974). In cicadas, frequency multiplication is evidently carried out by the tymbal ribs, which vibrate at about 4 kHz in *Cyclochila* when buckled by the tymbal muscle, oscillating at a rate of about 120 Hz. The way in which sound-producing insects overcome the problems posed by the serious pressure and area mismatch between muscle and airborne sound is discussed further elsewhere (Bennet-Clark, 1995).

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References

- ANDERSEN, S. O. AND WEIS-FOGH, T. (1964). Resilin. A rubber-like protein in arthropod cuticle. *Adv. Insect Physiol.* **2**, 1–65.
- BENNET-CLARK, H. C. (1995). Insect sound production: transduction mechanisms and impedance matching. *Symp. Soc. exp. Biol.* **49** (in press).
- BENNET-CLARK, H. C. AND YOUNG, D. (1992). A model of the mechanism of sound production in cicadas. *J. exp. Biol.* **173**, 123–153.
- FARADAY, M. (1831). On a peculiar class of acoustical figures: and of certain forms assumed by groups of particles on vibrating elastic surfaces. *Phil. Trans. R. Soc. Lond.* **121**, 299–318.
- FLETCHER, N. H. (1992). *Acoustic Systems in Biology*. New York: Oxford University Press.
- FONSECA, P. J. AND POPOV, A. V. (1994). Sound radiation in a cicada: the role of different structures. *J. comp. Physiol. A* **175**, 349–361.
- HENNIG, R. M., WEBER, T., MOORE, T. E., KLEINDIENST, H.-U. AND POPOV, A. V. (1994). Function of the tensor muscle in the cicada *Tibicen linnei*. *J. exp. Biol.* **187**, 33–44.
- JIANG, J.-C. (1989). Mechanical characteristics and sounding mechanism of sounding membrane in black cicada (*C. atrata* Fabricius). *Sci. China (Ser. B)* **32**, 64–77.
- JOSEPHSON, R. K. AND YOUNG, D. (1981). Synchronous and asynchronous muscles in cicadas. *J. exp. Biol.* **91**, 219–237.
- JOSEPHSON, R. K. AND YOUNG, D. (1985). A synchronous insect muscle with an operating frequency greater than 500 Hz. *J. exp. Biol.* **118**, 185–208.
- MICHELSEN, A. AND NOCKE, H. (1974). Biophysical aspects of sound production in insects. *Adv. Insect Physiol.* **10**, 247–296.
- MYERS, J. G. (1929). *Insect Singers*. London: Routledge.
- OLSON, H. F. (1957). *Acoustical Engineering*. Princeton, NJ: Van Nostrand.
- PRINGLE, J. W. S. (1954). A physiological analysis of cicada song. *J. exp. Biol.* **32**, 525–560.
- SCOTT, J. A. (1970). Resilin in the sound-organs of Pyralidae and Cicadidae (Lepidoptera; Homoptera). *Pan-Pacific Ent.* **46**, 225–231.
- SIMMONS, P. AND YOUNG, D. (1978). The tymbal mechanism and song patterns of the bladder cicada *Cystosoma saundersii*. *J. exp. Biol.* **76**, 27–45.
- WEIS-FOGH, T. (1960). A rubber-like protein in insect cuticle. *J. exp. Biol.* **37**, 889–906.
- YOUNG, D. (1990). Do cicadas radiate sound through their ear-drums? *J. exp. Biol.* **151**, 41–56.
- YOUNG, D. AND JOSEPHSON, R. K. (1983). Pure tone songs in cicadas with special reference to the genus *Magicicada*. *J. comp. Physiol.* **152A**, 197–207.