Zoomorphologie

Morphology of the Sense Organs in the Proximal Parts of the Tibiae of *Gryllus campestris* L. and *Gryllus bimaculatus* deGeer (Insecta, Ensifera)

Eckehard Eibl*

Max-Planck-Institut für Verhaltensphysiologie, Abteilung Huber,
D-8131 Seewiesen, Federal Republic of Germany

Summary. The tibial sense organs in the three pairs of legs from two cricket species have been compared, with special emphasis upon the CoS marking technique (Figs. 1 and 2). The main results are as follows:

1. The tibial surfaces directed outward when the leg is in the normal position have a considerably greater density of innervated hairs and bristles than the surfaces on the inner side of the leg. On the forelegs, hairs and bristles surround the tympana (Fig. 4). This arrangement of the sensilla is thought to be associated with the burrowing habit of the crickets.

2. The special cuticular differentiation (tympana, chitinous ridges) and the particular arrangement of the tracheal system in the vicinity of the auditory receptors (apposition of two tracheal tubes which are in direct communication with one another, Figs. 4, 6, and 7) seem to improve the ability of detection of airborne sound and seem to be important in the frequency analysis carried out by the ears. There are no such differentiated regions in the tibiae of the middle and hind legs.

3. On all three pairs of legs each tibia bears a group of 14–15 campaniform sensilla (Fig. 5); the groups have very similar spatial arrangements. Their nearness to the subgenual organ, and the fact that they are incorporated into the tibial cuticle immediately proximal to the crease, indicate that they measure the loading of the tibia.

4. The subgenual organs in all three pairs of legs consist of ca. 25 sense cells each; these, with their accessory structures, are spread out in a fanlike arrangement, and their dendritic processes bend to run in the hemolymph canal (Figs. 8–13).

5. Only in the anterior tibia is there a complete tympanal organ, with a main process consisting of a row of 30–35 sense cells parallel to the long axis of the leg (Fig. 9). Structures homologous to the caudal and frontal processes of the tympanal organ of the anterior tibia, with 25–30 sense cells, are also to be found

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*   *Present address:* Pädagogische Hochschule Rheinland, Abteilung Aachen, Ahornstr. 55, D-5100 Aachen, Federal Republic of Germany
Address for offprint requests: Prof. Dr. F. Huber, Max-Planck-Institut für Verhaltensphysiologie, D-8131 Seewiesen, Federal Republic of Germany

in the middle and hind tibia (Figs. 11—13). Therefore it is presumably the main process that is chiefly responsible for detection of airborne sound by the forelegs. The sensory apparatus in the middle and hind legs that corresponds to the caudal and frontal branches of the tympanal organ may well mediate the residual sensitivity to airborne sound which remains after ablation of the tympanal organs (cf. Nocke, 1972; E. Schuhmacher, 1975).

6. The paths followed by the sensory axons from the tibial organs described are almost identical in the three thoracic segments. The subgenual nerve (SGN, Fig. 9) and the tympanal nerve (TN, Fig. 9) each also contain axons of the campaniform sensilla; the tympanal nerve includes, in addition, axons of the sensory cells in the subgenual organ.

A. Introduction

The two sets of organs evolved in crickets for the detection of vibration are located in the proximal parts of the tibiae. They are the tympanal organs, which transduce airborne sound, and the subgenual organs, for which one effective stimulus is vibration of the substrate. The tympanal organs are externally identifiable only in the forelegs by the presence of two tympana.

Even after the tympanal organs in the anterior tibiae have been ablated and the antennae and cerci removed, crickets can respond to stridulatory sounds (Jones and Dambach, 1973); moreover, electrical responses of the homologous nerves in the middle legs have been recorded during stimulation with airborne sound (cf. Autrum, 1941; Wever and Vernon, 1959; Nocke, 1972; E. Schuhmacher, 1975). These findings suggest that components of the tibial sense-organ complex in the two posterior pairs of legs can also be employed in the detection of airborne sound.

As early as fifty years ago, Friedrich (1927—1930) described scolopale organs in the tibiae of the middle and hind legs of tettigoniids that closely resembled the foreleg tympanal organs in structure, arrangement, and position (cf. R. Schuhmacher, 1973a, b; Houtermans and R. Schuhmacher, 1974). Adult crickets were shown by Young and Ball (1974b) to have scolopidia in the middle legs that correspond in degree of differentiation to those observed in the anterior tibia of the fifth larval stage.

These physiological and morphological findings have prompted a more detailed study of the complement of sense organs in the proximal segments of all three leg pairs in crickets. In the present paper emphasis is laid on description of the cuticular differentiation, tracheal supply, and innervation of the sense organs in all leg pairs; the CoS technique (Pitman et al., 1972; Kater and Nicholson, 1973) was the chief method used to reveal the sensory structures. The paper also extends the light- and electron-microscope observations of other authors (cf. Herbig, 1902; Schwabe, 1906; Friedman, 1972a, b; Young, 1973; Ball and Young, 1974; Young and Ball, 1974a, b; Michel, 1974).

B. Materials and Methods

Both male and female imagines of *Gryllus campestris* L. and *Gryllus bimaculatus* deGeer were used. The animals, aged 2—4 weeks, were taken from laboratory colonies. The description that follows is based on examination of leg preparations from 60 crickets.
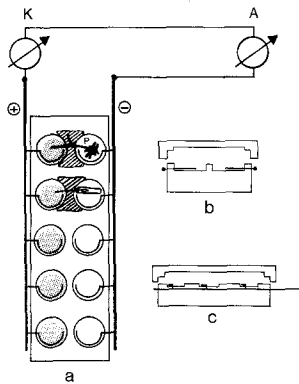
Fig. 1 a–c. The apparatus in which axons are filled with dye. a Overall diagram. $CoCl_2$ solution in the left dish (*stippled*); vaseline bridge between the dishes (*dashed*). The first pair of dishes (*top*) holds a prothoracic ganglion (*P*) with peripheral nerve; in the second pair is an anterior tibia (*right*) with nerve. *K* constant-current device; *A* ammeter. b Cross section through the apparatus, showing lid. c Longitudinal section through the apparatus, showing lid

CoS (Pitman et al., 1972; Kater and Nicholson, 1973) was used to mark the receptors in the tibia via the transected sensory nerves (Fig. 1). Since Co^{++} ions are taken up only by living tissue, successful marking requires the choice of a suitable Ringer solution. The most satisfactory results were achieved with a modification of the solution used by Colombo and Micciarelli (1967; composition, in g/l: NaCl, 7; KCl, 0.74; $CaCl_2 \cdot 2H_2O$, 0.22; $MgCl_2 \cdot 6H_2O$, 0.41; $NaHCO_3$, 2.0; $NaH_2PO_4 \cdot H_2O$, 1.2; glucose, 3.0) at a pH of 6.8–7.2; the filling time was 24–48 h and a 5% solution of $CoCl_2$ in Clark's Ringer was used in the chambers holding the transected nerves (left dishes in Fig. 1). After the precipitation of CoS the preparation was fixed in Carnoy, dehydrated, and transferred to monomeric styrol via acetone and acetone/styrol (1:1 mixture). All alcohol and acetone stages were saturated with CoS to prevent loss of the stain. In monomeric styrol the CoS-marked structures were clearly discernible after 1–2 min. The preparations were embedded in Canada balsam (cf. also Eibl, 1974).

The leg preparations were drawn (Wild M 20 with Variomag and drawing attachments) and photographed (Leitz, Orthoplan with Orthomat photo equipment). Three-dimensional viewing of the preparations was made possible by an apparatus (Fig. 2) developed in the laboratory to allow turning of the tibia about its long axis. The preparations were pushed into a glass capillary filled with Canada balsam, which could be clamped in a holder. The capillary was immersed in a glycerine bath (refractive index, 1.474) to minimize refraction of the light.

The arrangement of the sense cells, the internal organization and the compartmentation of the tibia were studied in serial sections; in preparing these, the method of contrasting with osmium tetroxide and intensifying with ethyl trihydroxybenzoate, as suggested by Wigglesworth (1957, 1959) and modified by Williams (1972, 1975), was used.

The cuticular structures on the external and internal surfaces of the tibial exoskeleton were examined by scanning electron microscope (Stereoscan 180) after
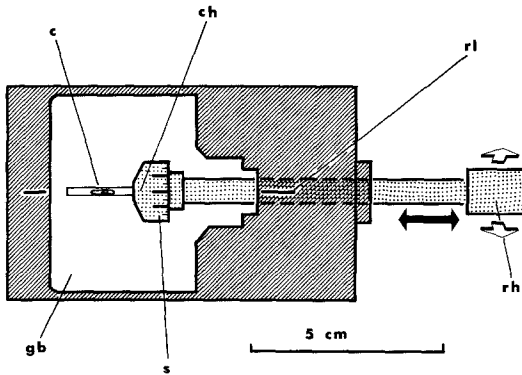
Fig. 2. Rotatable mount for three-dimensional viewing of leg preparations. *C* preparation in glass capillary; *ch* capillary holder; *gb* glycerine bath; *rh* rotating handle; *rl* reference line; *s* scale (thick subdivisions represent 30° intervals). The *arrows* show the directions of motion available
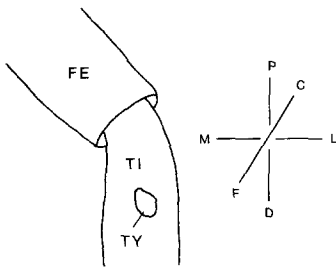

Fig. 3. *Left:* part of femur (*FE*) and the tibia (*TI*) of the left foreleg; frontal aspect, showing the small tympanum (*TY*). *Right:* positional relationships; *F* frontal; *C* caudal; *M* medial; *L* lateral; *D* distal; *P* proximal

fixation in glutaraldehyde, treatment with the detergent Triton X-100, dehydration, air-drying, and gold-coating[1].

The terminology used to specify spatial relationships is defined in Figure 3.

C. Results

1. Cuticular Structures

a) Anterior Tibia

In the proximal part of the anterior tibia the position of the tympanal organ can be externally identified, by the presence of two tympana of different sizes. The smaller (Fig. 4a) appears as an indentation in the frontal surface of the tibia, about 1 mm below the femur-tibia joint. The larger is recessed in the caudal surface (Fig. 4c). Although the areas of the two tympana can vary from one animal to another, their
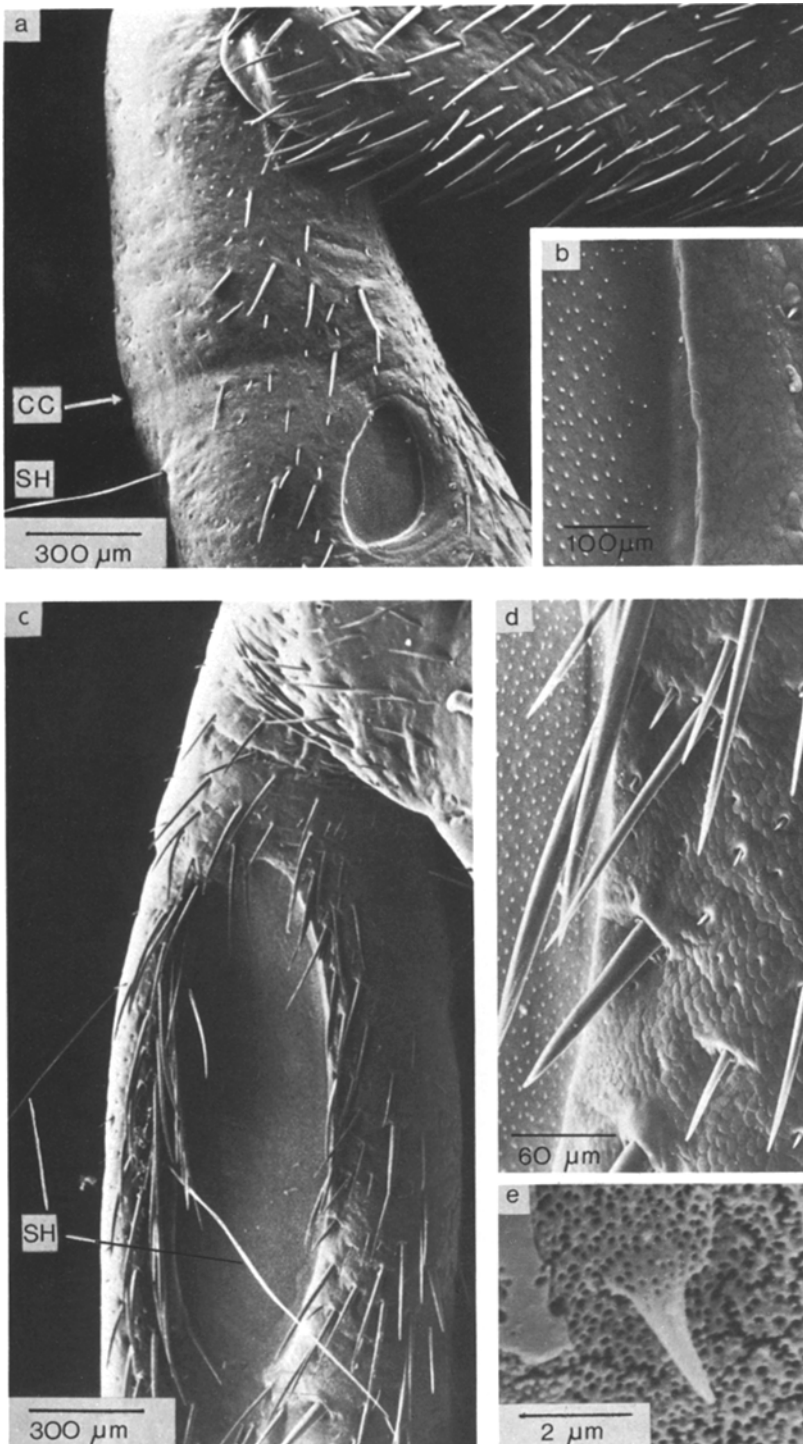

Fig. 4 a—e. Parts of the right anterior tibia of *Gryllus campestris*. **a** General and **b** higher-magnification view of the region of the small, frontally directed tympanum, showing lateral sensory hair (*SH*) and cuticular crease (*CC*). **c** General view of the caudal, large tympanum with the surrounding bristles and the two (laterally and caudally directed) sensory hairs (*SH*). **d** Higher-magnification view of the bristle border. **e** Tympanal membrane with spines and perforations, after treatment with a chloroform/methanol mixture to dissolve away the wax
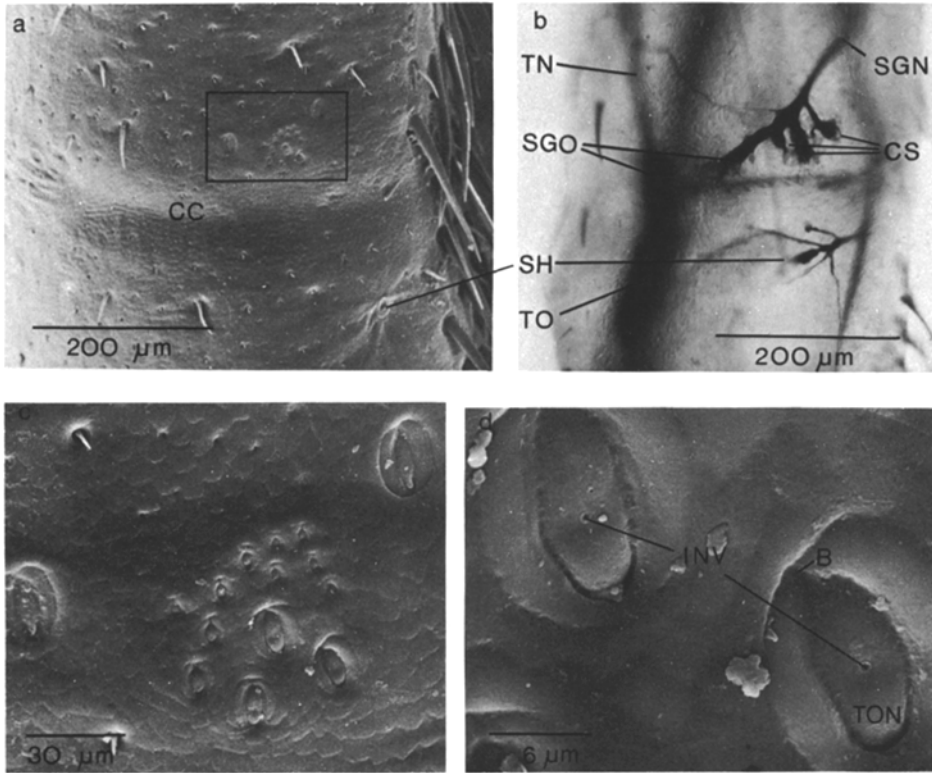
Fig. 5 a—d. The group of campaniform sensilla embedded in the lateral cuticle of the anterior tibia of *Gryllus campestris*. a General view with sensilla group outlined; *CC* cuticular crease in the proximal part of the tibia. b Sensilla group (*CS*) as revealed by CoS; *SGN* subgenual nerve; *SGO* part of the subgenual organ; *SH* filiform sensory hair; *TN* tympanal nerve; *TO* tympanal organ. c Higher-magnification view of the entire group and d of two large campaniform sensilla; *INV* invagination at tip of dendrite; *TON* tongue. For further explanation see text

relative dimensions (frontal: caudal = 1:5) are quite constant. Each tympanal membrane bears small spines (Fig. 4e) lacking innervation. These are 2—3 μm in length and separated from one another by about 6 μm; presumably they serve to improve the adhesion of the wax layer.

The larger of the two tympana (Fig. 4c), in particular, is surrounded by many innervated bristles (Fig. 4d), oriented along the axis of the leg with their tips pointing distally. The immediate surroundings of the smaller tympanum are free of bristles (Fig. 4b). Additional structures characteristic of the anterior tibia are two long sensory hairs (Pumphrey, 1940; SH, Fig. 4), which respond to the slightest mechanical displacement and presumably serve to protect the tympana from dangers associated with the burrowing habit of the crickets (Neumann, 1975). One of the sensory hairs arises from the lateral margin of the large tympanum about halfway along its length

and stands out from the tibia, perpendicular to the membrane (Fig. 4c). The other is situated somewhat distal to the cuticular crease on the lateral side; this, too, inserts into the tibia nearly at right angles to its surface (Fig. 4a, c).

   In all three pairs of legs, on the lateral side of the tibia a little above the cuticular crease there is a group of 14 campaniform sensilla (Fig. 5). Each sensillum is associated with one sense cell; in the middle of the sensillum is a tongue-shaped structure (TON, Fig. 5d), the center of the tongue being the point of attachment of the dendritic process beneath the cuticle. The spatial arrangement of the sensilla (Fig. 5c). varies hardly at all. There are always two large (ϕ 20 μm) sensilla in the outer proximal position; midway between these and further distal there are three medium-sized (ϕ 10 μm) sensilla forming a triangle that is surrounded proximally by nine small (ϕ ca. 5–6 μm) sensilla.
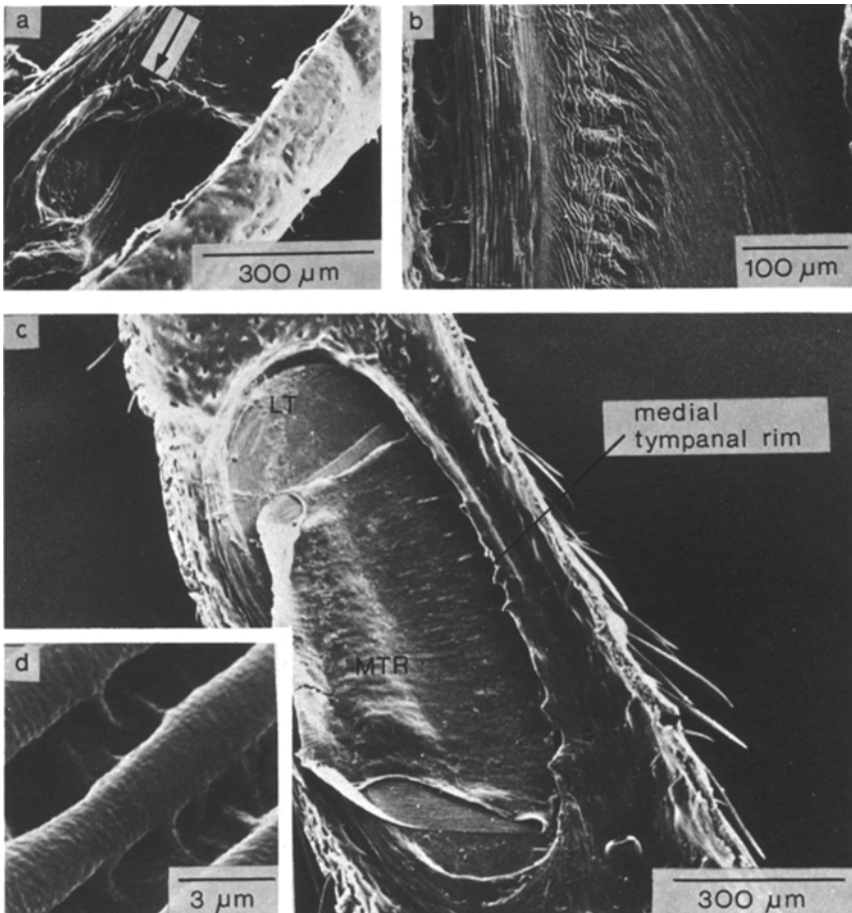

Fig. 6 a–d. Parts of the inner aspect of the anterior tibia of *Gryllus campestris*. a Small tympanum (*arrow*) with cuticular ridge. b Part of the large tympanum and c large tympanum (*LT*) showing the apposed main tracheal branch (*MTR*). d Tracheal ribs. For further explanation see text

On the inner surface of the cuticle the tympana are rimmed by sturdy ridges of cuticle (Fig. 6a, c), the "tympanal ridges" (*Tympanalleisten*) of Schwabe (1906). These are more massive frontally and caudally; they serve to support the tracheae apposed to the tympanum. At the proximal ends of the tympana the rim extends as a ridge underlying the externally visible cuticular crease. The tympana themselves are smooth on their internal surfaces, except for some texture in the lateral part of the large tympanum (Fig. 6b), resembling that described in tettigoniids (R. Schuhmacher, 1975). Such inhomogeneities in the membrane may significantly affect the analysis of sound frequencies (cf. Michelsen, 1971).

b) Middle and Hind Tibiae

In the tibiae of the middle and hind legs, there are no structures comparable to the tympana of the anterior tibiae, nor are there circlets of bristles like those surrounding the large tympana. The frontal surfaces of middle and hind tibiae are more densely covered with innervated bristles. The filiform sensory hairs are represented on the middle tibia by the laterally inserting hair only; the posterior tibia lacks both hairs.

On the other hand, the groups of campaniform sensilla (cf. Fig. 4c) are found on both middle and hind tibiae, identical in number, form, and position to those on the forelegs.

2. Tracheal Arrangement

a) Anterior Tibia

A massive "main trachea" (Fig. 10, MTR) passes from the femur into the tibia. Just below the femur-tibia joint a side branch diverges toward the frontal surface (Fig. 10, STR); Schwabe (1906) described this as the "ascending branches." At the level
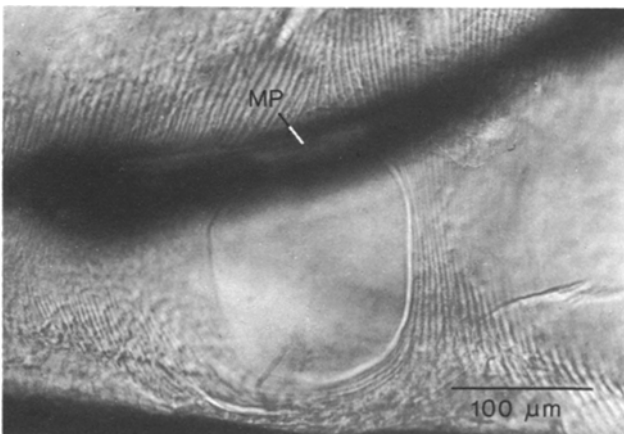

Fig. 7. Anterior tibia: whole mount showing the opening connecting the two tracheae (*MP* main tympanal process). For further explanation see text

of the tympanal organ, the side branch exhibits a sacklike expansion (cf. Michel, 1974) with an opening, ca. 100 μm away from the mouth of the sack, through which side branch and main trachea communicate (Fig. 7; P, Fig. 10). Distal to this junction the two tracheae continue to run close together for about 200 μm, where the side branch again joins the main trachea.

The main trachea (MTR, Fig. 6c) is directly apposed to the membrane of the large tympanum. In the region of the tympanal organ, the tracheal ribs are 2−3 μm in diameter and 2−3 μm apart along the trachea (Fig. 6d). The small tympanum is separated from the wall of the side branch by a layer of tissue about 100 μm thick (cf. the "suspensorium" described by Schwabe, 1906).

The cuticular differentiation on the inside of the tympanum, together with the arrangement of the two tracheae, provides a particular compartmentation of the tibial interior at the level of the sense-organ complex. The hemolymph canal contains the sense organs; opposite this, and separated from it by the two tracheae, is another compartment which encloses the tibial muscles and the tibial and tarsal nerves.
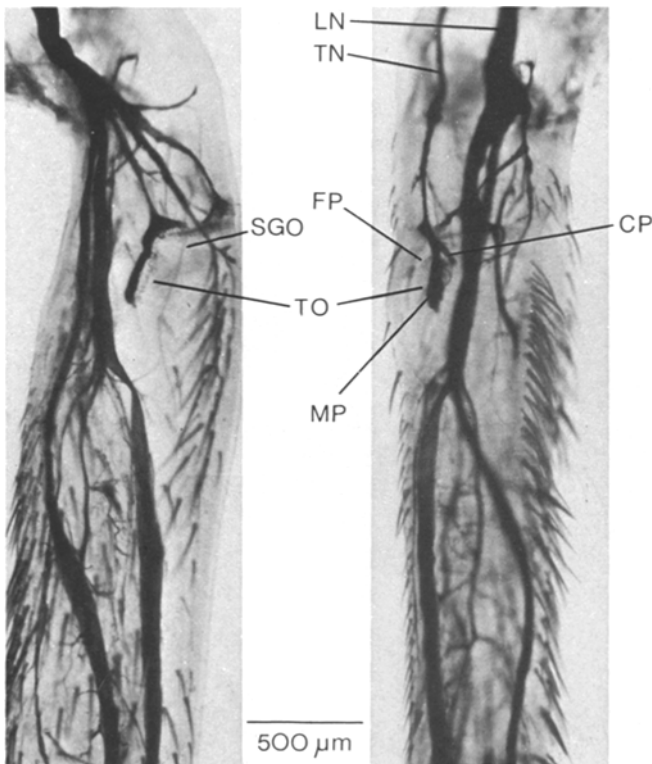

Fig. 8. "Capillary" preparation (see Fig. 2) of the proximal part of the anterior tibia of *Gryllus bimaculatus*, cleared to show pattern of innervation marked with CoS. *Left*: view from caudal (120°). *Right*: view from mediofrontal (210°). *CP* caudal process of the tympanal organ; *FP* frontal process of the tympanal organ; *LN* leg nerve; *MP* main process; *SGO* subgenual organ; *TN* tympanal nerve; *TO* tympanal organ (crista acustica)

Because of the ridge underlying the cuticular crease at its proximal end, and a bulge at its distal end, the inner surface of the large tympanum is effectively apposed by tracheal air so that sound-pressure-driven deflections of the tympanum and underlying tracheal membranes are not damped by contact with hemolymph or muscle.

b) Middle and Hind Tibiae

The main tracheae in the middle and hind tibiae also send out side branches after entering the segment; here, however, the side branch has neither an expanded region nor a special port of communication with the main trachea; after ca. 1.5 mm the two branches rejoin (Figs. 12 and 13, MTR, STR).

3. Nerve Pathways

On the flexor side of the femur-tibia joint two nerves enter the *anterior tibia,* a leg nerve (LN, Figs. 8 and 10) and a thinner tympanal nerve (TN, Figs. 8—10) which passes along the frontal aspect of the tibia. The leg nerve divides into the tibial and
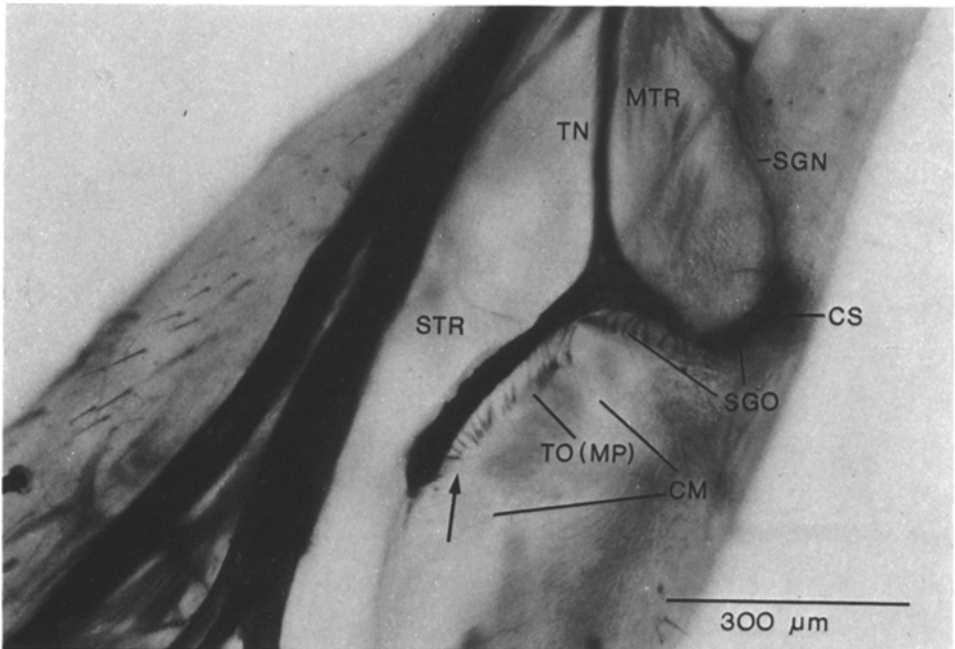

Fig. 9. Tibial sense-organ complex in the foreleg of *Gryllus campestris,* with tympanal organ (*TO*), subgenual organ (*SGO*), the groups of campaniform sensilla (*CS*), the subgenual (*SGN*) and tympanal (*TN*) nerves. *CM* covering membrane; *MP* main process; *MTR* main branch of the trachea. In the region of the *TO* and *SGO* the individual scolopidia can be seen. *STR* small trachea. Stained with CoS

FRONTAL   LATERAL

PROXIMAL

MTR

LN

TN

SGO

CS

CS

SGO

SH

H

SH

TO

TO

CM

ST

TIN

STR

LT

MOT.
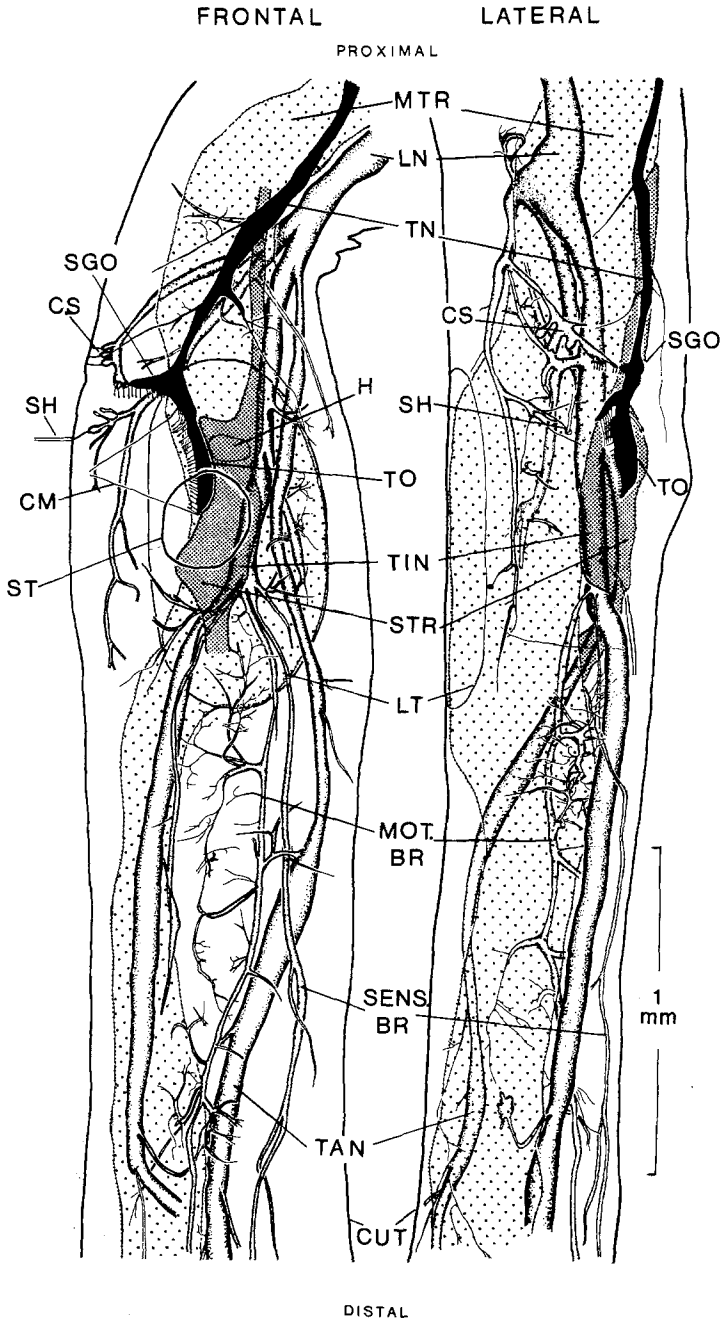BR

1
mm

SENS
BR

TAN

CUT

DISTAL

Fig. 10. Semidiagrammatic view of the arrangement of tracheae and nerves in the anterior tibia of *Gryllus campestris* and *Gryllus bimaculatus*. *Left:* frontal view; *right:* lateral view; *Black,* tympanal nerve; *white with stippled outline,* leg nerve; *dense dotting,* frontal trachea; *open dotting,* main trachea. *BR* motor (*MOT*) and sensory (*SEN*) branches of the nerve; *LT* large tympanum; *CM* covering membrane; *CS* campaniform sensilla; *CUT* cuticle; *H* port connecting tracheae; *LN* leg nerve; *MTR* main trachea; *SGO* subgenual organ; *SH* sensory hair; *ST* small tympanum; *STR* small trachea; *TAN* tarsal nerve; *TIN* tibial nerve; *TN* tympanal nerve; *TO* tympanal organ

tarsal nerves (TIN, TAN, Fig. 10). Another branch of the leg nerve, the subgenual nerve (SGN, Fig. 9), is purely sensory, carrying axons of the subgenual organ (SGO, Figs. 8–10) as well as fibers from the campaniform sensilla (CS, Figs. 9 and 10) and axons of the long tibial sensory hairs (SH, Fig. 4).

The tympanal nerve (TN, Figs. 8–10) runs frontolaterally near the main trachea; with it merge several small nerve branches containing axons from sense cells of the cuticle. This nerve, too, comprises fibers from the group of campaniform sensilla, plus some from the subgenual organ and, of course, all the neurites of the tympanal scolopidia. Thus the tympanal nerve cannot be regarded strictly as an "auditory nerve."

The pattern of innervation in the *middle and hind tibiae* is very similar (Figs. 12 and 13).

4. Sense-Organ Complex

a) Anterior Tibia

For present purposes, the tibial sense-organ complex will be considered to include the two closely adjacent scolopidia arrays of the tympanal and subgenual organs, plus the group of campaniform sensilla. The latter sends axons into both the subgenual and tympanal nerves.

The ca. 25 scolopidia of the subgenual organ are spread out like a fan, lying under the cuticular crease on the frontal side of the tibia (Figs. 8–10). Their dendrites, 50–60 μm long, bend and enter the hemolymph space. The 10–15 scolopidia situated more laterally send their axons into the subgenual nerve, whereas the fibers of the remaining, more medial scolopidia enter the tympanal nerve.

Table 1. Number and distribution of the scolopidia in the tympanal organs of various cricket species, with the terminology used by different authors

Author	Species	Terminology			Total number of sense cells
Eibl (1976)	G.bimaculatus G.campestris	Frontal process 8–10	Caudal process 10–12	Main process ca. 35	55–60[a]
Schwabe (1906)	A.domesticus	no data	Trachealorgan no data	no data	ca. 60[a]
Friedman (1972)	G.assimilis	anterior ganglion no data	intermediate organ no data	no data	ca. 70
Michel (1974)	G.bimaculatus	proximaler Abschnitt 10–12	hinterer Tympanalnerv 10–12	35–40	55–60[a]
Young and Ball (1974a)	T.commodus	proximal anterior group 7–9	proximal main group ca. 20	distal group	up to 70[a]

[a] Suspensorium present

The 55–60 scolopidia of the tympanal organ lie at an angle of about 120° to those of the subgenual organ (Fig. 9); these, too, are arranged in a row that extends along the tibia on its frontal side. Three sections are distinguishable: one in which the scolopidia are oriented caudally (caudal process), another with frontal orientation (frontal process), and a main process paralleling the long axis of the tibia. A survey of the terminology used by different authors and the numbers of scolopidia in the various sections of the tympanal organ of different cricket species are given in Table 1.

Caudal Process. About 100 μm distal to the subgenual organ lies a group of 10–12 scolopidia (the proximal main group of Young and Ball, 1974a; the posterior tympanal nerve of Michel, 1974) with dendritic processes running in the long direction of the tibia before they turn laterally and terminate, via sheath cells, at the common cuticular attachment site of all scolopidia of the tympanal organ.

Frontal Process. About 50 μm distal to the point of departure of the caudal process there is a group of 8–10 scolopidia which send dendrites forwards (Fig. 8, FP). These dendrites run distally along the tibia without deviating from this course (proximal neurons of Young and Ball, 1974a; proximal section of Michel, 1974).

Main Process (crista acustica). With its 30–35 scolopidia, arrayed like a string of beads in the long direction of the tibia, the main process is the predominant part of the organ. The dendrites emerge caudally from the somata (diameter ca. 15 μm), then turn laterally and

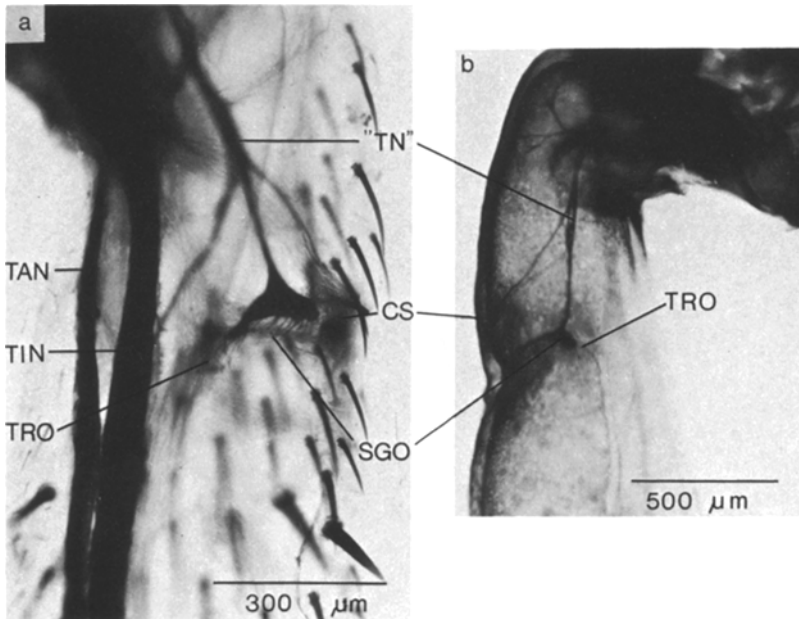**Fig. 11 a and b.** Tibial sense-organ complex of **a** middle tibia and **b** hind tibia of *Gryllus campestris*, marked with CoS. *TRO* tracheal organ (the part of the sense-organ complex homologous to the tympanal organ in the foreleg). Other labels as in Figure 10

Fig. 12. Semidiagrammatic view of the positions of tracheae and nerves in the middle tibia of *Gryllus campestris* and *Gryllus bimaculatus*. *Left:* frontal view; *right:* lateral view. Shading and labels as in Figure 10; *STR* small trachea, elongated in this leg

FRONTAL   LATERAL

PROXIMAL

LN

MTR

TN

CS

SGO

TRO

STR

TIN

1
mm

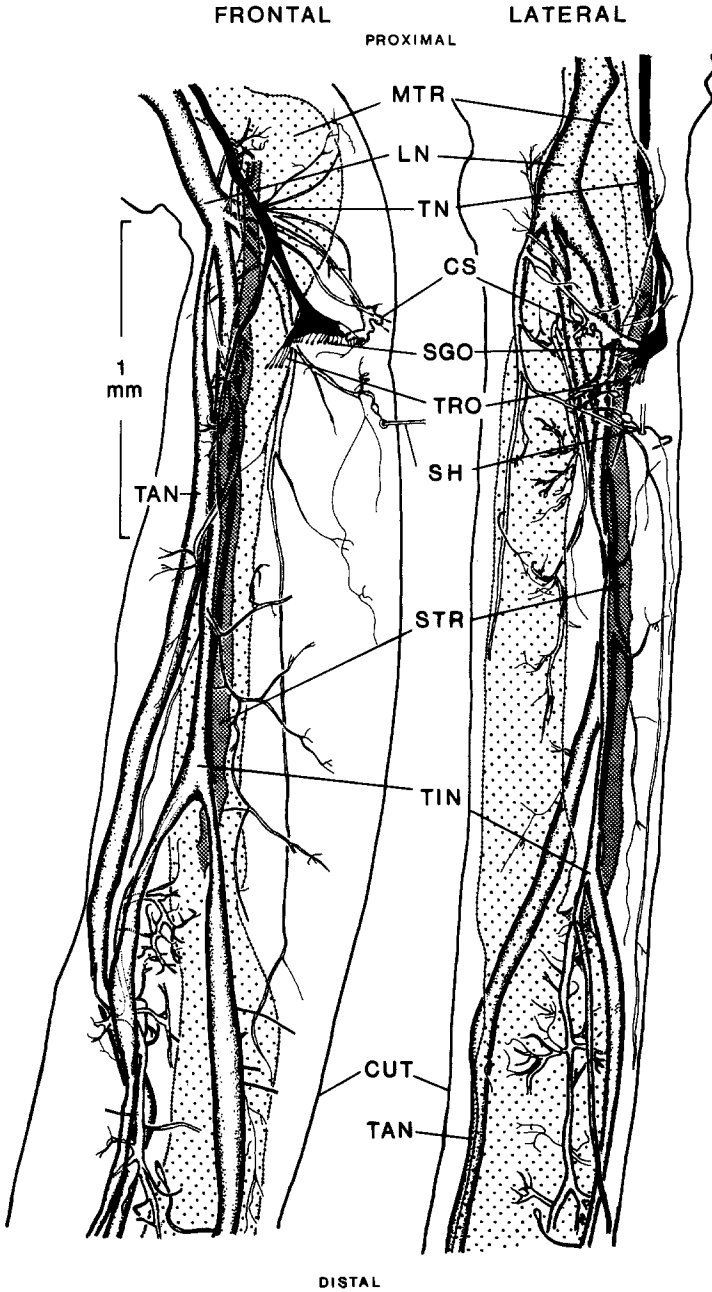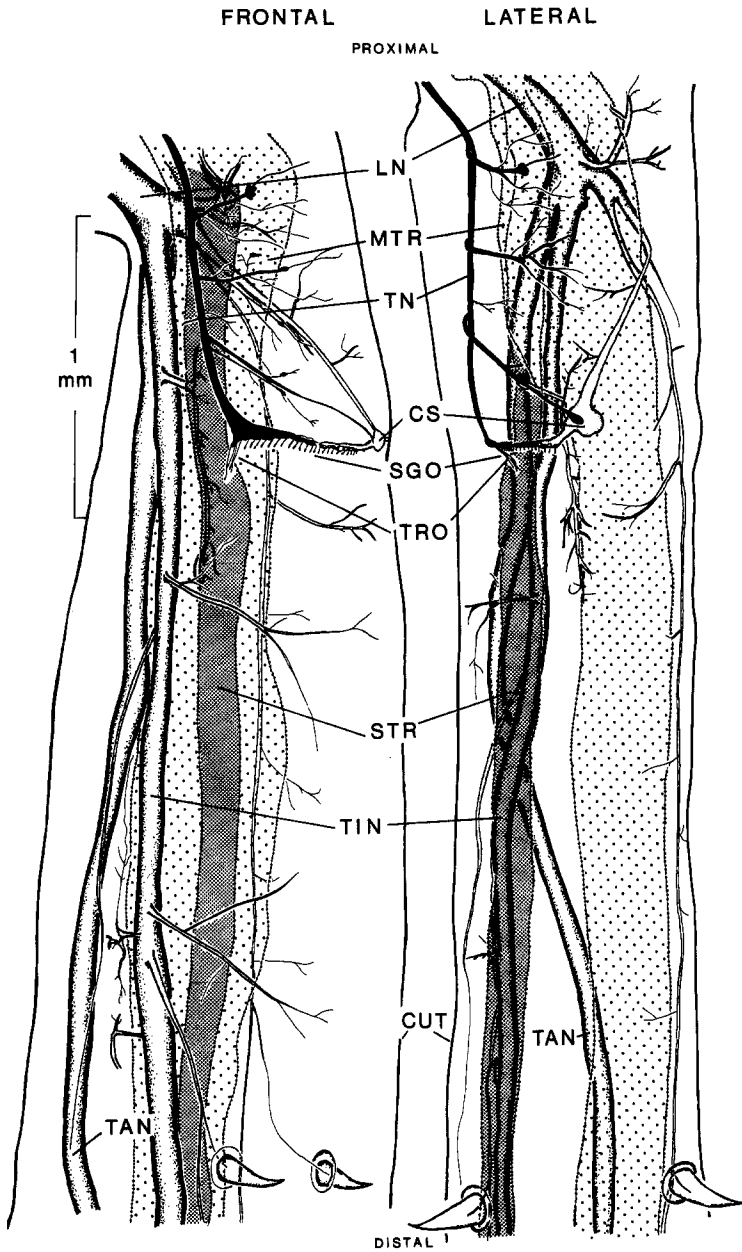CUT   TAN

TAN

TAN

DISTAL

Fig. 13. Semidiagrammatic view of the positions of tracheae and nerves in the hind tibia of *Gryllus campestris* and *Gryllus bimaculatus*. *Left:* frontal view; *right:* lateral view. Shading and labels as in Figure 10

pass to the common attachment region on the cuticle (Fig. 9). This attachment region is shorter than the main process; accordingly, the distally located dendrites bend more sharply (Fig. 9, arrow).

The dendrites of the sense cells in the tympanal organ (Fig. 9) are about 100 μm in length; when marked with CoS they exhibit a swelling at the distal end which is presumably an actual expansion of the dendrite (cf. Michel, 1974).

b) Middle and Hind Tibiae

With respect to spatial arrangement, number of sense cells, diameter of the somata and length of the dendrites, the group of campaniform sensilla and the scolopidia of the subgenual organ are similar to the homologous structures in the anterior tibia (cf. SGO, CS, Fig. 11).

The fundamental difference between the sense-organ complexes in the proximal parts of the anterior, middle, and hind tibiae consists in the "reduced" development of the "tympanal organ" in the middle and hind legs; that is, the main tympanal process is absent (cf. Figs. 11–13).

The 15 scolopidia in the middle tibia, and the 8–10 scolopidia in the hind tibia, can be regarded as homologous — on the basis of position and arrangement — to the caudal and frontal processes of the anterior tibia (TRO, Fig. 11); in the posterior legs presumably only the elements of the caudal process are present. The dendrites of the sense cells — about 100 μm long, as in the anterior tibia — parallel the long axis of the tibia. They do not bend laterally, corresponding in this respect to the dendrites of the caudal process in the foreleg. Otherwise the scolopidia resemble structurally those of the frontal process in the foreleg, though in the middle leg they fan out more broadly and are more separated than in the posterior tibia (Figs. 11–13).

D. Discussion

The proximal parts of the anterior tibiae of *Gryllus campestris* and *Gryllus bimaculatus* are characterized by the presence of two tympana, unequal in size, that are not found at the corresponding sites on the middle and hind legs. Whereas the membrane of the smaller, frontally directed tympanum is relatively uniform in structure and lies over a layer of tissue about 100 μm thick, that of the large, caudally located tympanum is directly adjacent to the main trachea and is inhomogeneous, with textured regions (Fig. 6).

According to Johnstone et al. (1970), the capacity for frequency discrimination demonstrated by the cricket ear (Nocke, 1970, 1972; Zhantiev and Tschukanov, 1972; Markovich, 1976) could — as is the case in locusts (Michelsen, 1971) — be determined by the oscillatory properties of the tympana, and/or underlying tracheae (cf. Paton et al., 1977). Larsen and Michelsen (1977) have recently shown that the large tympanum of *Gryllus campestris* oscillates as a uniform membrane in the range from 1–30 kHz. This has been confirmed by Paton et al. (1977) for other species of crickets where the large membrane vibrates in the same simple mode in response to tones from 4–20 kHz with a peak in the mechanical response near 5 kHz. Nocke (1972), after ablating the

small tympanum (again in *Gryllus campestris),* found that there was no electrical response of the auditory nerve to tones above 12 kHz; he interpreted this result in terms of a selective filtering of high frequencies by the small tympanum. On the basis of their measurements of the oscillatory properties of the small tympanum and comparison with those of the neighboring leg cuticle, Larsen and Michelsen (1977) and Paton et al. (1977) regarded the contribution of this tympanum to excitation of the auditory cells as negligible. This conclusion would be consistent with the finding that only the small tympanum is underlain by a thick layer of tissue, which presumably provides considerable damping.

The investigations of·tettigoniids by Lewis (1974) and Nocke (1975) and the studies of crickets by Zhantiev et al. (1975), Hill and Boyan (1976), and Larsen and Michelsen (1977) have underlined the significance of the specially developed prothoraric tracheal system present in many species in the two groups; this system is involved in sound conduction within the body and affects directional hearing and localization of sound. It is not yet completely clear whether the particular arrangement of compartments in the proximal part of the anterior tibia described in this paper, and the unique communication between the two tracheae that is found here (Fig. 7), is critical to the transmission of sound to the laterally situated complex of sensory cells. But the tuning of the large tympanic membrane and of the organ to around 5 kHz, the main component of the calling song, might be due to tracheal resonance (Paton et al., 1977).

Oscillations of the tracheal membranes can be detected by the tympanal organ (Autrum, 1941; Paton et al., 1977) and presumably also by the subgenual organ. The results of CoS marking of the sense cells have laid new emphasis on the close spatial relationship of the two tibial sense organs; this is so close that the proximal section of the tympanal organ is hardly distinguishable from the median region of the subgenual organ. The fact that sensory axons from both organs enter the "auditory-nerve" makes it understandable that recordings from the nerve also reveal responses to substrate vibration and low frequencies (under 1000 Hz; cf. Autrum, 1941; Autrum and Schneider, 1948; Dambach, 1972; Nocke, 1972).

The two organs can be separated functionally, at the level of the receptors, only in that the subgenual receptors are found to be tuned to frequencies below 2000 Hz (Dambach, 1972; Dambach and Huber, 1974). Moreover, the lack of a response to airborne sound above 2000 Hz is evidence that a receptor belongs to the subgenual organ.

The arrangement of the scolopidia in longitudinal rows, in conjunction with the results of ablation experiments, has given rise to the view that the tuning of the receptors to different frequencies derives from their spatial relationships (Zhantiev, 1971; Zhantiev and Tshukanov, 1972; Rheinlaender, 1975; Markovich, 1976). However, no one has yet succeeded in selectively marking functionally identified sensory axons so that their more distal structures could be determined. Thus it is not yet possible to assign low-frequency and high-frequency function to particular scolopidia in the crista acustica. Moreover, analysis of the varying extent to which the dendrites bend toward the proximal attachment sites (cf. also Young and Ball, 1974a), even in conjunction with electron microscopy (Friedman, 1972; Young, 1973; Michel, 1974) has not yet revealed any relationship between receptor structure or arrangement and tuning to different frequencies (cf. also Huber, 1975).

Nocke (1972) and E. Schuhmacher (1975) have approached the problem electro-physiologically, by recording from mesothoracic and metathoracic nerves homologous to the auditory nerve of the first thoracic segment; they found responses to tones at frequencies represented in the cricket sounds which extended far beyond the response range of the subgenual organ. Jones and Dambach (1973) provided related evidence with freely moving crickets, by ablating the tibial sense organs in both forelegs as well as the antennae and the cerci; they noted the persistence of the response of two males to each other's calls, and of one male to an artificial call. Thus airborne sound can also be detected — though less efficiently — by way of the middle and hind tibiae. The morphological correlate of this ability is surely the presence of scolopidia which are apparently homologous to the frontal and caudal processes of the tympanal organ. The raised thresholds to airborne sound under these conditions presumably result from the absence of tympana in the middle and hind legs, and from the different arrangement of the tracheae (Figs. 12 and 13).

The uniform morphology of the fields of campaniform sensilla described in this paper is, to my knowledge, a novel finding. That is, we have here a group of campaniform sensilla in the proximal part of the cricket tibia which is arranged identically, or nearly so, in all three pairs of legs. In structure these sensilla are like those described by Spinola and Chapman (1975) in the cockroach leg, which respond to deformation of the cuticle (cf. also Pringle, 1938; Blaney and Chapman, 1968). Their proximity to the subgenual organ and their incorporation into the leg cuticle directly above the cuticular crease make it likely that these sensilla measure the load on the tibia.

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