Functional morphology and development of tibial organs in the legs I, II and III of the bushcricket *Ephippiger ephippiger* (Insecta, Ensifera)

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Summary. The anatomy of the complex tibial organs in the pro-, meso- and metathoracic legs of adults and larvae of the bushcricket *Ephippiger ephippiger* is described comparatively. The subgenual organ and the intermediate organ are differentiated in the same way in legs I, II and III; the anatomy of the crista acustica and the tracheal morphology are significantly different. The final number of scolopidia in the tibial organ of each leg is present at the time of hatching. In the subgenual organ, the number of scolopidia is the same in all legs; in the intermediate organ, and especially in the crista acustica, the number of scolopidia decreases from leg I to legs II and III. In the first larval instar, the morphology of the tibia, the course of the trachea and the anatomy of accessory structures are developed in the same way in each leg. The specific differentiations forming the auditory receptor organ in leg I, such as the acoustic trachea, the tympana and tympanal cavities, develop step by step in subsequent instars. The auditory threshold recorded from the tympanal nerve in the prothoracic leg of adults is remarkably lower than in the meso- and metathoracic legs. Morphometrical analyses of structures that are suggested to play a role in stimulus transduction on scolopidia of the crista acustica reveal significant differences in the three legs.

A. Introduction

The complex tibial organs in the prothoracic tibia of Tettigoniidae (Ensifera) have been known for a long time because of the external differentiations of the integument (review: Schumacher 1979). The serially repetitive atympanal tibial organs in the meso- and metathoracic legs were, for the first time, described by Friedrich (1927, 1928). In each leg, the tibial organs consist of three scolopale organs: the subgenual organ, the intermediate organ and the crista acustica (Schumacher 1973; Houtermans and Schumacher 1974). The tympana, the tympan-

al cavities and the slits are restricted to the prothoracic tibia.

During embryonic development, the tibial organs differentiate in all legs from an invagination of ectodermal cells of the tibia (Meier and Reichert 1990). The authors postulate that the auditory receptor organ in Ensifera evolved from a serially reiterated group of leg-associated mechanoreceptors, which in the prothoracic leg became specialised for the perception of airborne sound. During postembryonic development the tympana, tympanal cavities and the acoustic trachea are formed step by step in the prothoracic tibia (Rössler 1992).

Receptor cells of the complex tibial organs in the meso- and metathoracic legs also respond to low frequency airborne sound at high intensities (Autrum 1941). However, in contrast to the prothoracic tibia, the sensitivity in the meso- and metathoracic tibiae is not sufficient for the perception of the natural song. Thus, the function of the crista acustica in the meso- and metathoracic legs is still unknown.

To reveal the morphological basis for the differences in the auditory sensitivity, the adult structure and development of the tibial organs in all three leg pairs of the bushcricket *Ephippiger ephippiger* are investigated comparatively. The postembryonic development is studied with special attention to the differentiations forming the auditory receptor organ. The results of morphometric analyses of structures within the crista acustica of each leg are correlated with the hearing threshold. On the basis of these results, the function of the crista acustica in the meso- and metathoracic legs and its possible original function in the prothoracic leg are discussed.

B. Materials and methods

The anatomy of the complex tibial organs in the pro-, meso- and metathoracic legs of the bushcricket species *Ephippiger ephippiger* (Fiebig, 1784), was studied in sectioned material of about 35 animals of both sexes. All larval stages and adults were used. Eggs of *E. ephippiger* were obtained from Dr. J.C. Hartley, Nottingham, England and reared under constant conditions in the laboratory.

The number of larval instars in *E. ephippiger* is six. The larval stages were distinguished by measuring the length of the pronotum (Lakes 1988) and by determining the intermoult periods (Hartley and Dean 1974).

For sectioning, the tibiae of the pro-, meso- and metathoracic legs were severed towards the distal end of the tibia and at the femoro-tibial joint, and fixed for 24 h in 4% buffered glutaraldehyde. Preparations were dehydrated in graded ethanol and in 1,4-dioxane. Infiltration with Spurr's medium (Spurr 1969; modification after Mothes-Wagner et al. 1984) was achieved in three steps. After embedding, the preparations were polymerized for 16 h at 70° C.

For light microscopic analysis, serial sections were cut at a thickness of 5 µm and stained for 24 h with acid fuchsin, light green and orange g. For three-dimensional reconstructions and automatic measurements of dimensions, the structures of interest were digitized from camera lucida drawings of consecutive sections using a calibrated graphic tablet connected to a computer system (IBM compatible). The digitized data were processed with the programme AutoCAD (Autodesk AG) which was adapted to the specific tasks with the help of the integrated computer language AutoLISP. Three-dimensional reconstructions were achieved by a computer-guided drawing technique. Different structures within a section are digitized on separate layers. After a suitable perspective view is found, the different layers are plotted separately. The different structures are redrawn consecutively from these plots.

Electrophysiological experiments took place in a sound-proof room. The summed potential was recorded from the tympanal nerve near the junction with the prothoracic ganglion and from the corresponding nerves of the meso- and metathoracic legs using a hook electrode. The auditory threshold was determined audio-visually using headphones and an oscilloscope. The hearing threshold at a given frequency was defined as the intensity when a response can first be observed (for detailed description of the recording and stimulation conditions see Kalmring et al. 1978).

C. Results

I. Adult structure of the complex tibial organs in the pro-, meso- and metathoracic legs

The adult structure of the complex tibial organs was compared in the pro-, meso- and metathoracic legs of *E. ephippiger*. Figure 1 shows three-dimensional reconstructions from serial sections of the organs. At a first glance, the overall arrangement of scolopidia in the sub-genual organ, the intermediate organ and the crista acustica show similarities in the three legs, but also the differences in the tracheal morphology and size of the structures become evident immediately.

The number of scolopidia in the subgenual organ varies between 20 and 25 in each leg. In the intermediate organ, and especially in the crista acustica, the number of scolopidia decreases from the prothoracic to the meso- and metathoracic legs. In the intermediate organ, 14 ($\pm$1) scolopidia can be counted in the prothoracic leg, 12 ($\pm$1) in the mesothoracic leg and 11 ($\pm$1) in the metathoracic leg. A larger proximal group of scolopidia with longitudinally oriented dendrites and a smaller distal group with dendrites oriented as in scolopidia of the crista acustica can be distinguished in each leg. In the crista acustica, the number of scolopidia decreases from 28 ($\pm$1) in the prothoracic leg to 11 ($\pm$1) in the mesothoracic leg and 7 ($\pm$1) in the metathoracic leg. The overall length of the crista acustica (distance between the first and last scolopidium) is 560 ($\pm$50) µm in the prothoracic tibia, 270 ($\pm$15) µm in the mesothoracic tibia and 185 ($\pm$20) µm in the metathoracic leg.

Another striking difference is the morphology of the trachea. The two large branches of the acoustic trachea in the prothoracic leg are only separated by a thin wall (named the central membrane after Lewis 1974, the dividing wall after Nocke 1975 or the partition after Schumacher 1975). The smaller tracheal branches in the meso- and metathoracic legs run with greater separation and are connected to each other by tracheal epithelium. In the prothoracic leg, the volume of the anterior branch of the trachea is larger than that of the posterior branch; in the meso- and metathoracic legs, the conditions are reversed.

The tectorial membrane that covers the crista acustica and the intermediate organ is developed in each leg. Supporting bands on both sides of the cap cells are very marked in the prothoracic crista acustica, only poorly developed in the mesothoracic tibia and completely missing in the metathoracic crista acustica.

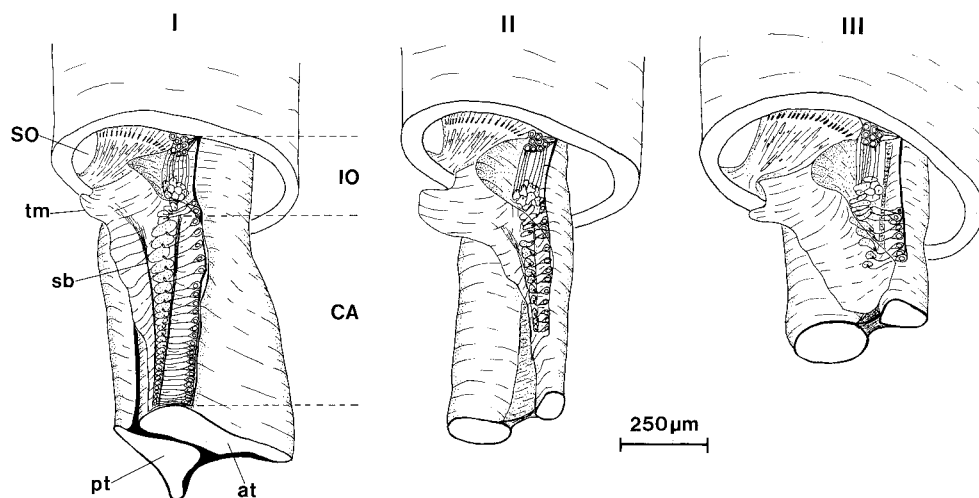Figure 2 shows transverse sections of the proximal tibia of the three legs at the plane of the subgenual or-

Fig. 1. Adult structure of the complex tibial organs in the pro- (*I*), meso- (*II*) and metathoracic legs (*III*) of the bushcricket *Ephippiger ephippiger*. Three-dimensional reconstructions from a series of transverse sections showing the organs in an antero-dorsal view. In the reconstructions, the integument and the content of the nerve muscle channel is removed. *at* anterior tracheal branch; *CA* crista acustia; *IO* intermediate organ; *pt* posterior tracheal branch; *sb* supporting bands; *SO* subgenual organ; *tm* tectorial membrane. Anterior is to the *right*
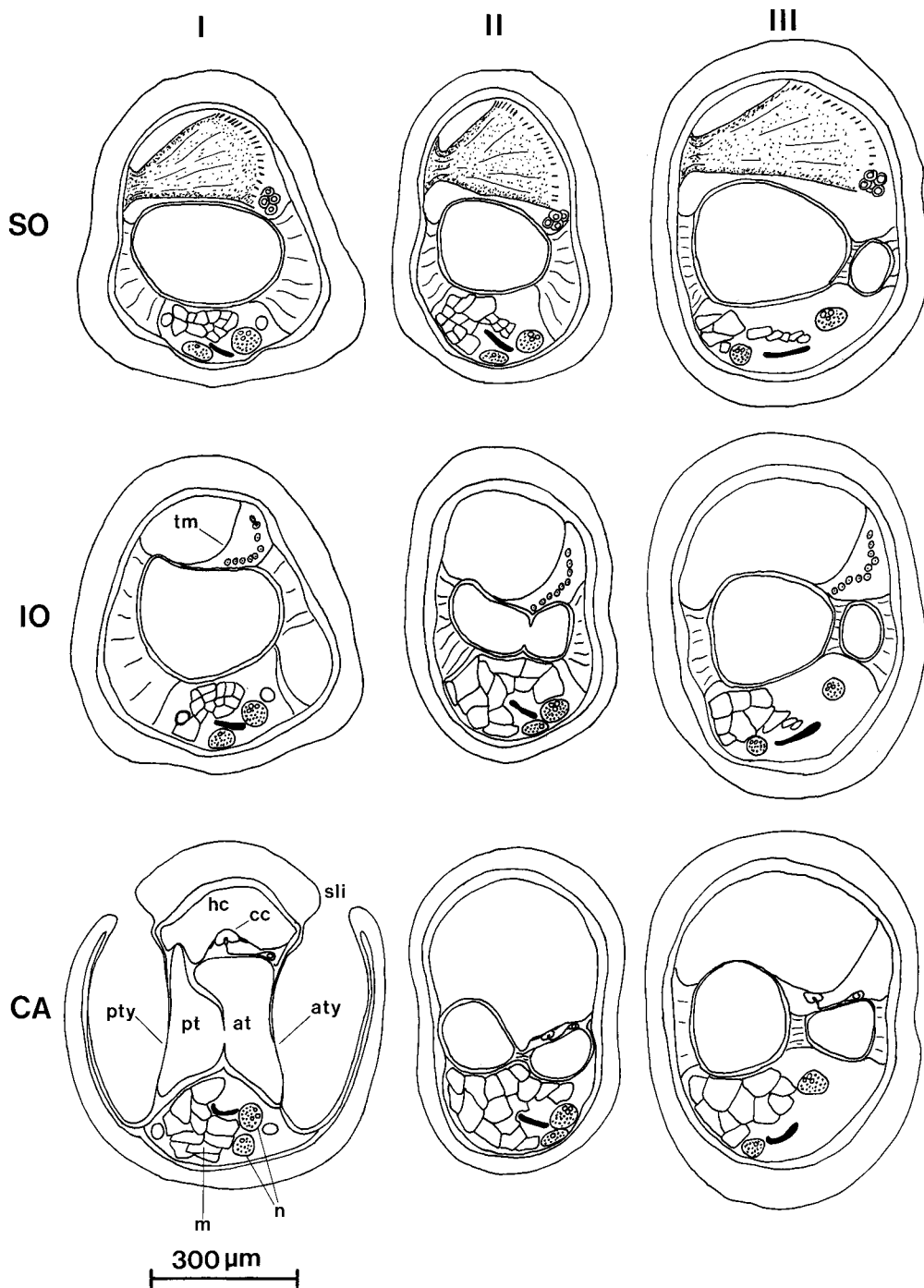
Fig. 2. Transverse sections of the proximal tibia in the pro- (*I*), meso- (*II*) and metathoracic legs (*III*) at the plane of the subgenual organ (*SO*), proximal part of the intermediate organ (*IO*) and crista acustica (*CA*). *at* anterior tracheal branch; *aty* anterior tympanum; *cc* cap cell of the scolopidium; *hc* haemolymph channel; *m* muscles; *n* tibial and tarsal nerve; *pt* posterior tracheal branch; *pty* posterior tympanum; *sli* slit; *tm* tectorial membrane. Anterior is to the *right*

gan, the intermediate organ and the crista acustica. The size and shape of the subgenual organ is nearly the same in the prothoracic and mesothoracic legs; the subgenual organ of the metathoracic leg is slightly larger especially in the anteroposterior direction. The arrangement of the dendrites of the proximal group of scolopidia in the intermediate organ is comparable in all legs. At the plane of the crista acustica, the absence of tympana, tympanal cavities and slits in the meso- and metathoracic tibiae is obvious. In addition, the arrangement and location of scolopidia within the crista acustica is different in the three legs because of the different size and course of the tracheal branches. In each case the scolopidia are located on the anterior branch of the trachea.

The acoustic trachea in the prothoracic leg divides into two branches at the plane of the proximal part of the crista acustica. The two branches are separated by the thin dividing wall. In the mesothoracic leg, the trachea is divided at the beginning of the proximal part of the intermediate organ. In the metathoracic tibia, the trachea is divided into a small anterior and a larger posterior branch before the subgenual organ. At the plane of the intermediate organ and the crista acustica, the size of the haemolymph channel differs in the three legs.

The volume of the haemolymph channel is significantly smaller in the prothoracic tibia than in the meso- and metathoracic tibiae because of the large volume of the acoustic trachea.

II. Postembryonic development

The final number of scolopidia in the three parts of the complex tibial organs of all legs is present at the time of hatching. Figure 3 shows details of the crista acustica and the intermediate organ in the pro-, meso- and metathoracic legs in the first larval instar. Even at this stage of development, the scolopidia of the intermediate organ can be distinguished from those of the crista acustica. In contrast to the adult structure, the cap cells of scolopidia within the crista acustica are compressed in the longitudinal axis and the scolopales are lying horizontally. In the second instar, the dendrites are bent towards the haemolymph channel. The scolopale caps and rods are already differentiated but they are of a smaller size than in the adults. In Fig. 4a–c transverse sections at the plane of the crista acustica in the pro-, meso- and metathoracic tibiae are shown in the first larval instar. The integument and trachea are differentiated similarly in all three legs. In the adult, the three legs can be clearly distinguished in a transverse section at the plane of the crista acustica (cf. Fig. 2).

Figure 5 shows reconstructions from transverse sections at the plane of the fifth scolopidium within the crista acustica in the pro-, meso- and metathoracic tibiae in instars 1, 3 and 5. In the first larval instar, the anatomy looks similar in the three legs. The leg morphology, the tracheal morphology, the size of the haemolymph channel and the arrangement of the scolopidia is nearly
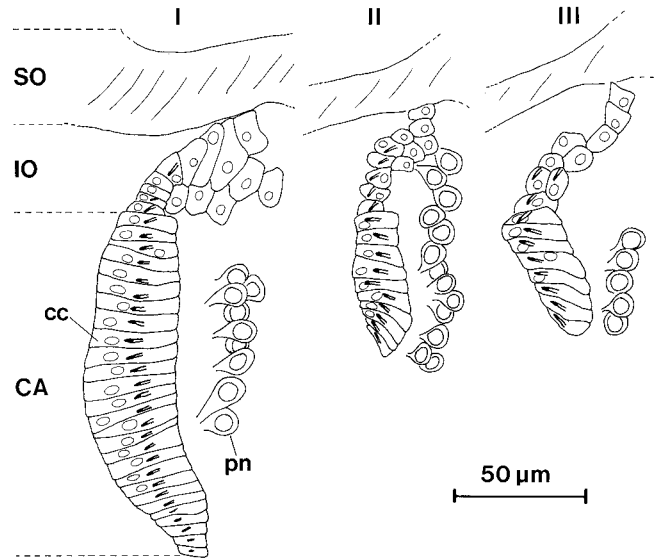

Fig. 3. Development of the tibial organ in the pro- (*I*), meso- (*II*) and metathoracic legs (*III*). Reconstructions from longitudinal sections of the proximal tibiae in the first larval instar. The border of the subgenual organ is drawn schematically; all the cap cells of the scolopidia of the intermediate organ and crista acustica (including the scolopales) and some of the perikarya of the sensory neurons are shown. *CA* crista acustica; *cc* cap cell with scolopale; *IO* intermediate organ; *pn* perikaryon of a sensory neuron; *SO* subgenual organ. Anterior is to the *right*

the same. Beginning with the third instar, the tympanal covers start to grow out from the lateral integument in the prothoracic tibia. The tracheal branches are slightly larger than in the meso- and metathoracic tibiae, and the anterior branch becomes larger than the posterior branch. The situation is completely different in instar
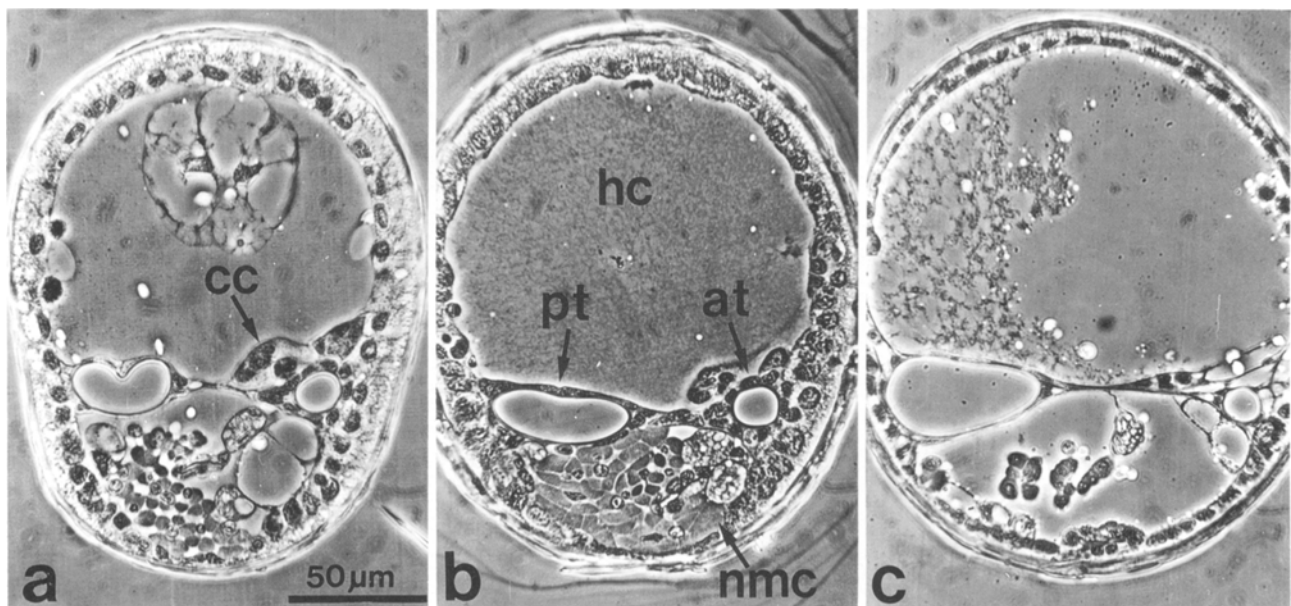

Fig. 4a–c. Development of the crista acustica in the first larval instar shown in transverse sections of the pro- (**a**), meso- (**b**) and metathoracic tibiae (**c**) at the plane of the crista acustica. *at* anterior tracheal branch; *cc* cap cell with scolopale *hc* haemolymph channel; *nmc* nerve muscle channel; *pt* posterior tracheal branch
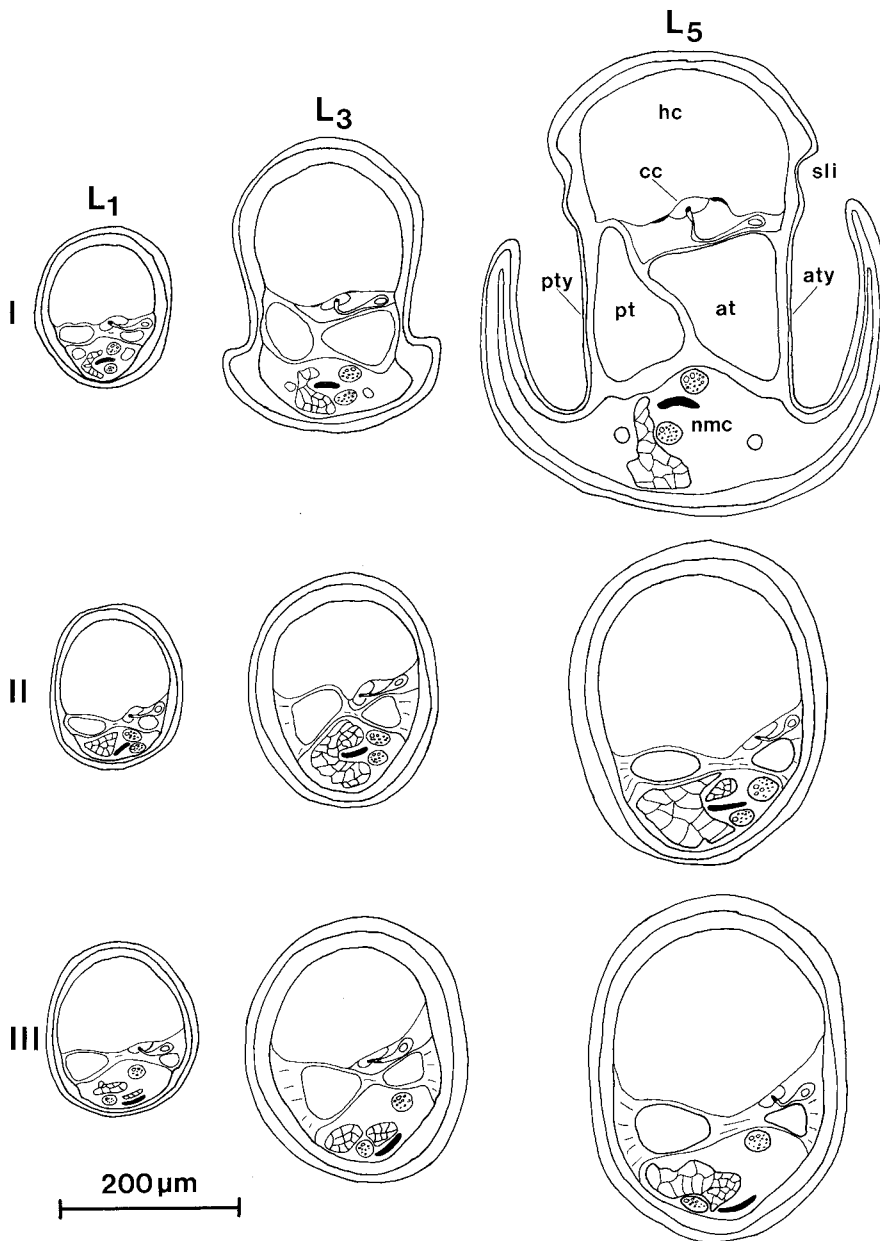
Fig. 5. Changes in the anatomy of the crista acustica in the pro- (*I*), meso (*II*) and metathoracic tibiae (*III*) during postembryonic development. Drawings from transverse sections at the plane of the fifth scolopidium (counted from proximal) of the crista acustica of each leg in the first (L_1), third (L_3) and fifth (L_5) larval instars. *at* anterior tracheal branch; *aty*, anterior tympanum; *cc* cap cell of scolopidium; *hc* haemolymph channel; *nmc* nerve muscle channel; *pt* posterior tracheal branch; *pty* posterior tympanum; *sli* slit. Anterior is to the *right*

5 when the tympanal covers, tympana and tympanal trachea are nearly completed in the prothoracic leg. In the meso- and metathoracic legs, tympanal covers and tympana are absent, the tracheal branches are much smaller, the scolopidia are located laterally on the small anterior branch of the trachea and the volume of the haemolymph channel becomes larger than in the prothoracic tibia.

*III. The auditory threshold
in the pro-, meso- and metathoracic legs*

The auditory threshold of adult males and females of *E. ephippiger* was determined by recording the summed activity from the tympanal nerve in the prothoracic leg and from the corresponding nerves in the meso- and metathoracic legs. Frequencies from 2 to 40 kHz were tested.

The minimum auditory threshold in the prothoracic leg lies between 10 and 20 kHz and is around 30 dB SPL (sound pressure level) (Fig. 6). In the meso- and metathoracic legs, the minimum threshold for airborne sound lies at 2 kHz and is around 75 dB SPL in the mesothoracic leg and 85 dB SPL in the metathoracic leg. The threshold values rapidly increase at higher frequencies. Above 6 kHz the threshold values are higher than 95 dB SPL.

The fine structure and arrangement of the scolopidia and accessory structures in the crista acustica of the three legs was compared. The auditory threshold curves show that receptor cells of the crista acustica in the meso- and metathoracic legs are obviously not specialized for the perception of airborne sound. In addition
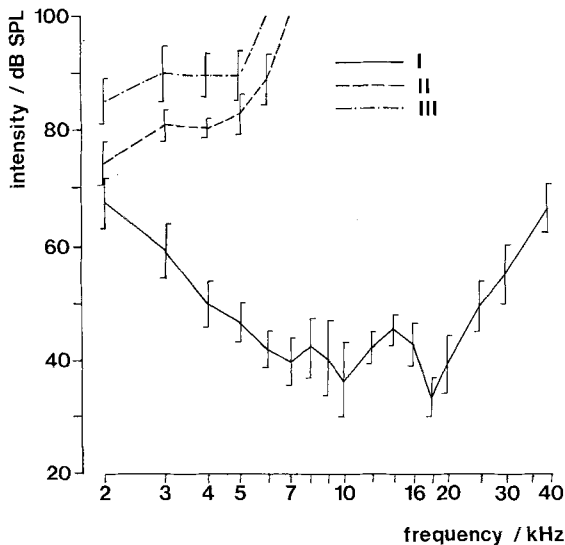
Fig. 6. Auditory threshold curves determined by recording the summed potential from the tympanal nerve in the prothoracic leg (*I*; *n* = 10) and the corresponding nerves in the meso- (*II*; *n* = 6) and metathoracic legs (*III*; *n* = 6) of adults of *E. ephippiger*. Ipsilateral stimulation with pure tone bursts of 20 ms duration, rise and fall time 1 ms, repetition rate 2/s

to the differences in the leg morphology and tracheal morphology, the anatomy of the scolopidia and accessory structures in the crista acustica of the three legs is different. In Fig. 7a details of the scolopidia in the crista acustica of the pro-, meso- and metathoracic tibiae are shown in a transverse section. The fifth scolopidium (counted from proximal) is drawn in each case. The shape and size of the cap cells and the arrangement of the scolopidia and accessory structures is remarkably different in the crista acustica of the three legs. The scolopale caps and rods are largest in the prothoracic crista acustica. The cap cells in the prothoracic crista acustica are pressed between supporting bands and the tectorial membrane is very tightly attached to the cap cells. In the mesothoracic crista acustica, the cap cells are more loosely attached to the tectorial membrane and supporting bands are only poorly developed. Supporting bands are completely missing in the tectorial membrane of the metathoracic crista acustica. In this case, the tectorial membrane is stretched broadly within the haemolymph channel, even at the distal part of the crista acustica (cf. Fig. 1).

The dimensions of structures that are in direct contact with the scolopidia of the crista acustica were analysed
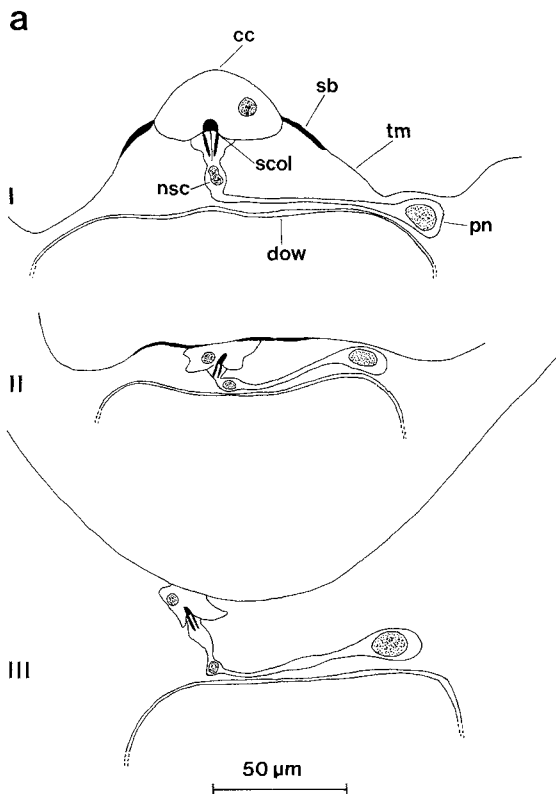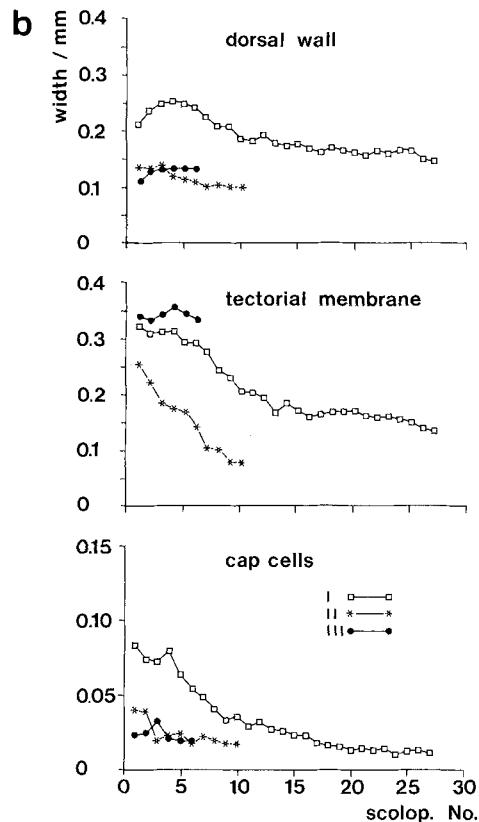

Fig. 7a, b. Dimensions of the scolopidia and accessory structures in the crista acustica of the pro- (*I*), meso- (*II*) and metathoracic tibiae (*III*). a Transverse sections of typical examples of the fifth scolopidia in the crista acustica of each leg. *cc* cap cell; *dow* dorsal wall of the anterior trachea; *nsc* nucleus of the scolopale cell; *pn* perikaryon of sensory neuron; *sb* supporting band; *scol* scolopale cap and rods; *tm* tectorial membrane. Anterior is to the *right*.

b Dimensions of the dorsal wall of the anterior trachea, the tectorial membrane and the cap cells within the crista acustica of the pro- (*I*), meso- (*II*) and metathoracic tibiae (*III*) of *E. ephippiger*. The width of the dorsal wall and the tectorial membrane and the largest diameter of the cap cells was measured from transverse sections at the positions of each scolopidium in each leg, respectively. Mean values of four animals in each case

morphometrically. The micromechanical properties of these structures may be involved in stimulus transduction. Figure 7b shows the variation of the width of the dorsal wall of the anterior trachea, the width of the tectorial membrane and the diameter of the cap cells along the crista acustica of the three legs. The structures were measured in transverse sections at the positions of all scolopidia in each leg, respectively. In the prothoracic leg, the width of the three structures shows a continuous decrease from the proximal to the distal end of the crista acustica. The same is true for the tectorial membrane and the dorsal tracheal wall in the mesothoracic tibia. However, the diameter of the cap cells does not decrease significantly. In the metathoracic leg none of those structures decreases significantly in width along the crista acustica.

D. Discussion

I. Functional morphology of the tibial organs

The comparative investigations on the anatomy of the complex tibial organs in the pro-, meso- and metathoracic legs of *E. ephippiger* show that the subgenual organ and intermediate organ are developed in the same way in all three legs; the structure and function of the crista acustica is significantly different. The comparison of the auditory threshold curves recorded from the three legs indicates that only the crista acustica in the prothoracic leg can function in species specific acoustic communication. The same conclusion was drawn by Autrum (1941) for the bushcricket species (*Decticus verrucivorus* (Linné, 1758) and *Tettigonia cantans* (Füssly, 1775). *E. ephippiger* produces maximum intensities of about 100 dB SPL at a distance of 10–20 cm in its stridulatory song (Keuper et al. 1988). The main energy of the spectrum is distributed at frequencies between 10 and 40 kHz. At this frequency range the auditory threshold of the receptor cells in the meso- and metathoracic legs is above 100 dB SPL. In contrast to the auditory receptor cells, the physiology of vibration receptors was shown to be similar in all legs (Kühne 1982).

In the prothoracic crista acustica, the specializations that enhance the sensitivity for airborne sound up to high frequencies are certainly the acoustic trachea with its large spiracle opening in the prothorax, the tympana, tympanal cavities and slits. The spiracles are the main input for airborne sound of higher frequencies (Lewis 1974; Nocke 1975; Michelsen and Larsen 1978). In addition to the absence or differences of these sound-conducting structures and the lower number of receptor cells, the fine structure and attachment of scolopidia in the crista acustica of the meso- and metathoracic tibiae shows significant differences. These differences may also influence the micromechanical properties of these scolopidia resulting in a low sensitivity for airborne sound. The cap cells of the prothoracic crista acustica are very tightly fixed in the tectorial membrane between two strong supporting bands. The volume of the cap cells decreases in a very characteristic way from the proximal

to the distal end of the crista acustica. The tectorial membrane and the dorsal wall of the anterior trachea also decrease in width along the crista acustica. This was shown to be realized even in larvae, and it is therefore suggested that the above-mentioned structures play a role in frequency tuning of individual auditory receptor cells (Rössler 1992; Kalmring et al. 1992). The scolopidia and accessory structures within the crista acustica of the meso- and metathoracic legs do not show the same characteristic variations in their dimensions. The cap cells of the scolopidia are of a completely different shape and are only loosely attached to the tectorial membrane. Supporting bands are only poorly developed in the mesothoracic crista acustica and absent in the metathoracic crista acustica. The scolopales in the meso- and metathoracic cristae acusticae are as small as those in the intermediate organs and are therefore sometimes hard to distinguish from those. This may give a hint that the function of the scolopidia in the crista acustica of the meso- and metathoracic legs is comparable with the function of those in the intermediate organs. Receptor cells of the intermediate organ respond to both low frequency airborne sound and vibration (Zhantiev and Korsunovskaya 1978).

II. Postembryonic development

The comparison of the postembryonic development of the complex tibial organs in the three legs reveals that the specific differentiations forming the auditory receptor organ in the prothoracic leg appear relatively late. The number of receptor cells of the crista acustica of each leg is fixed after embryonic development. Apart from the different number of receptor cells in the crista acustica, the anatomy of the pro-, meso- and metathoracic tibiae is nearly the same up to the third larval instar. In contrast to the conditions in the prothoracic tibia, the anatomy of the crista acustica in the meso- and metathoracic tibiae is not changed significantly during succeeding instars (apart from the changes in the overall size). The development of the tibial organs may give a hint that the evolutionary original situation in the prothoracic tibia might have been comparable to that in the meso- and metathoracic tibiae. Ball and Young (1974) also demonstrated that the mesothoracic tibial scolopale organs of the cricket species *Teleogryllus commodus* (Walker, 1869) are similar to those of the prothoracic leg in fifth instar larvae. The embryonic development of the complex tibial organs in bushcrickets also points to an originally similar situation in all three legs (Meier and Reichert 1990).

III. Function of the crista acustica in legs II and III

The sensitivity for low frequency airborne sound in the meso- and metathoracic cristae acusticae and also in the prothoracic crista acustica seems to be mainly caused by induced vibration of the legs. This may also be the case for the receptor cells of the intermediate organ.

This is supported by the fact that occlusion of the spiracles and slits does not significantly alter the sensitivity for airborne sound of frequencies below 6 kHz in the prothoracic leg (Nocke 1975; own unpublished results). Investigations of Mason (1991) on the auditory system of a primitive ensiferan species (*Cyphoderris monstrosa* Uhler, 1864; Orthoptera, Haglidae) revealed nearly the same auditory thresholds in the pro- and mesothoracic legs with a maximum sensitivity at frequencies between 1 and 2 kHz. The hearing threshold of this species is not matched to the song spectrum (main energy between 10 and 15 kHz). These results indicate that the possible original function of the ensiferan hearing system, which is closely associated with the vibratory system, could have been the detection of low frequency noises caused by predators (for example crushing of vegetation). The specific differentiations making the auditory receptor organ in the prothoracic leg highly sensitive to airborne sound of higher frequencies might then have evolved in common with the ability of sound production and the necessity of species-specific acoustic communication over long distances.

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