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Morphology and ultrastructure of the female accessory sex glands in various crickets (Orthoptera, Saltatoria, Gryllidae)

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With 7 figures

Abstract

In the present study, the morphology and ultrastructure of the accessory sex glands in females of the three cricket species *Teleogryllus commodus*, *Gryllus bimaculatus*, and *Gryllus assimilis* were subject to a detailed comparison. Within the observed crickets, the pairy glands are uniformly located in the 6th and 7th abdominal segment, joining the genital chamber lateral to the terminal papilla. Each gland is composed of an apical region (R3), consisting of the end tubules which produce the main amount of secretion, a middle region (R2) storing and leading the secretion to the orifice, and a basal region (R1) defining the orifice and most basal part of the gland. Concerning the size, number of ramifications, and length/width ratio, the investigated organs are marked by great variations among the species, ranging from anisometric glands (length/width < or > 1) with low number of ramifications in *Teleogryllus commodus* and *Gryllus assimilis* to nearly isometric glands with very numerous (up to 30) ramifications in *Gryllus bimaculatus*. The morphology of the respective glands is uniformly expressed by an epithelium composed of a basal lamina, one layer of gland cells, and a luminal, duct-less cuticular intima forming specific spines and hair-like processes. The ultrastructure of single gland cells is marked by a basal region with a large elliptic nucleus and intracellular cisternae formed by deep invaginations of the basal cell membrane. The apical part contains numerous lipid- and protein-forming compartments, mitochondria of cristae type, vesicles, and lipid drops. The apical cell surface is enlarged by forming a dense layer of microvilli. The lipophilic secretion produced by the glands is thought to be used as a lubricant in the ovipositor during egg-laying.

Key words: *Teleogryllus commodus*, *Gryllus bimaculatus*, *Gryllus assimilis*, morphology, ultrastructure, cuticular intima, secretion, lipophilic.

Introduction

According to Gillott (1988) the female accessory sex glands are marked by the production of secretory material which is directly involved in the reproductive process. These glands are generally of ectodermal origin and can be found in many orthopteroid insects as well as the Thysanura, Odonata, Thysanoptera, and Homoptera (see reviews of Gillott 1988 and Kaulenas 1992). As outlined by Matsuda (1976), the glands are secondarily lost in the Ephemeroptera, Dermaptera, Psocoptera, Heteroptera, some Orthoptera, and most Coleoptera. Accessory sex glands are always paired and join the common genital tract behind or beside the orifice of the spermathecal duct. Their differentiation is widely controlled by juvenile hormone (JH) acting as an inhibitor and moulting hormone (MH) acting as a promotor (Bodenstein & Sprague 1959).

Gillott (1988) describes the histology of the accessory sex glands as quite uniform among female insects, including, from inside to outside, a chitinous intima, one or two layers of gland cells, and a basal lamina. A muscle coat outside the basal lamina can be formed occasionally. In the case of a gland epithelium that consists of only one cell layer, the gland cells secrete both the apical cuticular intima and the glandular product. In the other case, there are columnar secretory cells showing a central cavity with an end apparatus, while another group of cells produces the cuticular intima and the efferent ductule starting from the end apparatus and running to the lumen. The accessory sex glands of e.g. *Chironomus plumosus* (Wensler & Rempel, 1962) and *Heliothis zea* (Callahan & Cascio, 1963) belong to the first construction type, whereas the respective glands of e.g. *Hyalophora cecropia* (Berry, 1968), *Periplaneta americana* (Brunet, 1952), and *Rhodnius prolixus* (Lococo & Hueb-

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ner, 1980) are constructed in the second way described above. Morphological variations may also be observed within different regions of the same gland, as described by Brunet (1952) for *Periplaneta americana*.

As the few results of gland investigations show, the produced secretion is thought to have several functions, ranging from a basic ingredient of egg capsules in *Periplaneta americana* (Brunet, 1952) to a lubricant in insects with an ovipositor.

Detailed studies of the female accessory sex glands in various cricket species are so far limited to *Teleogryllus commodus* (Sturm 1998, 2000, Sturm & Pohlhammer 2000). The present study tries to improve our knowledge about these structures and therefore compares the prevailing results with new ones obtained from comprehensive investigations of the accessory glands in *Gryllus bimaculatus* and *Gryllus assimilis*. Beside discrepancies in shape and size, also possible contrasts in the morphology and ultrastructure of the specific glands are discussed.

Material and methods

For this investigation, 10 day-old adult females of *Teleogryllus commodus, Gryllus bimaculatus*, and *Gryllus assimilis* were used. All crickets were reared under standard conditions (Musiol et al. 1990) in a special laboratory at the Institute of Zoology, Salzburg. After the adult moult, male and female crickets were separated and kept in glass vessels filled with food, water, and paper for shelter. For the preparation of the accessory sex glands, females were anaesthetized in a stream of CO_2 and afterwards decapitated. The glands were removed in insect Ringer's solution (Musiol et al. 1990), coloured with specific dyes, and finally posited on a glass slide. The preparations produced in this way were investigated by differential interference contrast using a REICHERT POLYVAR microscope. For scanning electron microscopy, dissected glands were fixed in a paraformaldehyde-glutaraldehyde mixture (Karnovsky 1965) for three hours, washed in sodium-cacodylate buffer, dehydrated in a graded series of ethanol, and finally dried using the critical point method. The preparations were coated with carbon, sputtered with gold, and investigated with a CAMBRIDGE 250 scanning electron microscope (accelerating voltage: 10–30 kV). For transmission electron microcopy, the glands were prefixed after Karnovsky (pH: 7.3) for three hours, then postfixed in 1% OsO_4 for two hours, washed in cacodylate buffer, dehydrated in a graded series of ethanol, and embedded in EPON 812. The semithin sections which served as a control for the quality of the fixation were produced on a REICHERT OM-U2 microtom and stained with methylene blue. Ultrathin sections produced on the same instrument were stained with lead nitrate and 1% methanolic uranyl acetate and investigated with a PHILIPS EM 300 transmission electron microscope (accelerating voltage: 80 kV). All photographs of this study were either made on a KODAK TECHNICAL PAN film or an AGFA APX-100 black and white film. The quality of the gland's secretions was tested by using selected lipophilic and hydrophilic dyes (e.g. Carmine acetic acid, Oil Red O, methylene blue, etc.). Further, the secretions were tried to be mixed with Ringer's solution and acetone.

Results

Position and shape of the accessory sex glands

The pairy accessory sex glands of the investigated crickets are uniformly posited within the sixth and seventh abdominal segment and embedded in layers of fatty tissue (Fig. 1). They join the genital chamber lateral to the orifice of the ductus receptaculi, which can be prooved by probing the respective area with a thin hair. As presented in Fig. 2, the shape of the investigated glands shows significant variations among the respective species. In general, each gland consists of three main regions: the basal region (R1) containing the orifice and very basal part of the gland, the middle region (R2) with the more or less complex system of ramifications, and the apical region with the terminal tubules. While the apical region represents the main production unit of the gland's secretion, the middle region mainly serves as unit storing and leading the secretion to the orifice.

The accessory sex gland of *Teleogryllus commodus* is marked by a rather flat shape and the number of ramifications ranging from less than seven to more than 12 (Fig. 2). The length/width ratio of the gland is always >1 with length varying between six to 15 mm and width ranging from five to 11 mm. The gland's shape is mainly characterized by a long and sporadically narrow middle region and a short basal region. The terminal parts are often distended or divided into two end tubules. The supply with oxygen is ensured by a dense web of tracheoles covering the whole gland.

In females of *Gryllus bimaculatus*, the accessory sex glands are chiefly marked by their impressive size and complexity (Fig. 2). Length and width of each gland are in the same order of magnitude, ranging from eight to 16 mm, respectively. The complexity of the gland is shown by numerous (up to 30) ramifications of various length which originate from the very dominant middle region. At its basal region, the gland is further characterized by a big orifice, whose diameter ranges from one to two mm. As in the case of *Teleogryllus commodus*, the terminal parts of the gland are either distended or branch out into two end tubules. The web of tracheas and tracheoles shows its highest density in the middle and apical region.

The accessory sex gland of *Gryllus assimilis* differs significantly from the both gland types de-

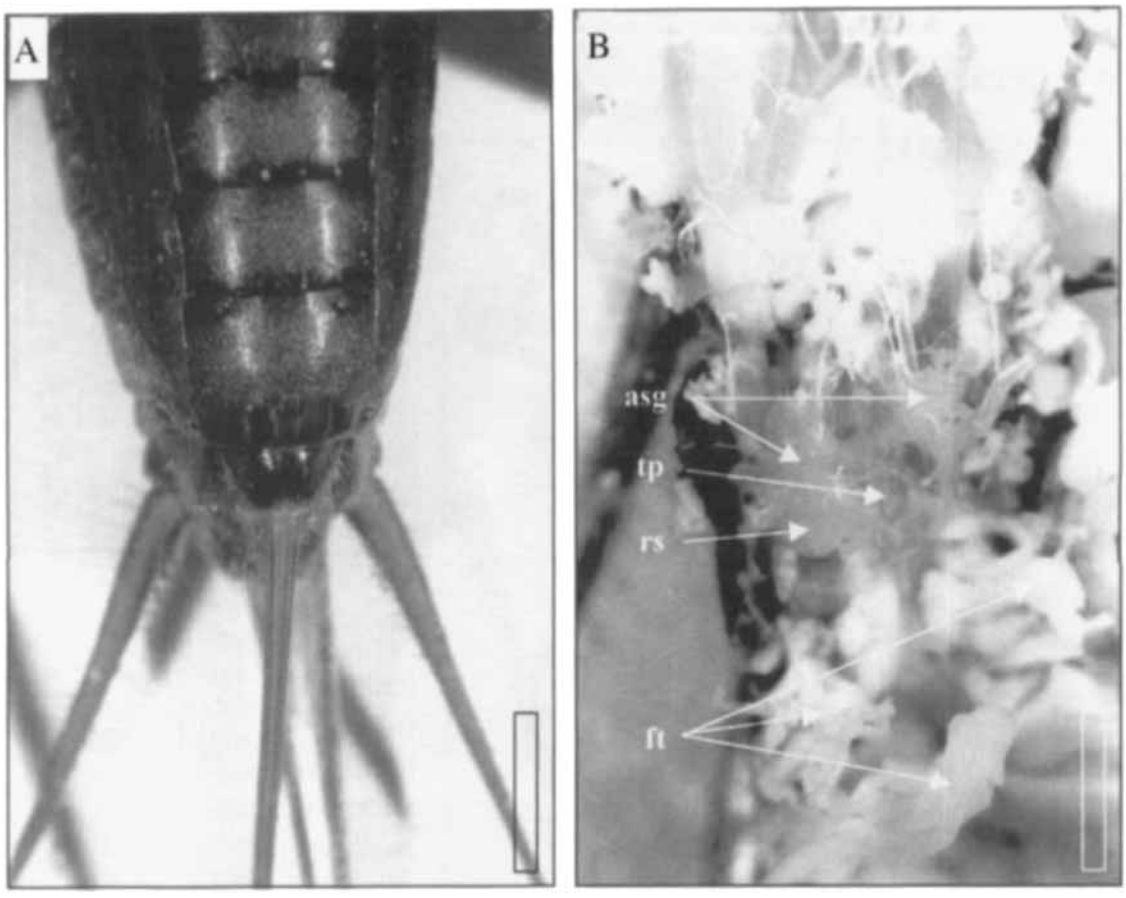


Fig. 1. Position of the accessory sex glands within the abdomen of the investigated female crickets. **A.** Ventral side of the abdomen (*Teleogryllus commodus*) with the segments 5–8, the ovipositor and the cerci. **B.** Opened abdomen exposing the female gonads with mature eggs on the top, the accessory sex glands (asg), receptaculum seminis (rs), and terminal papilla (tp) in the middle, as well as high amounts of fatty tissue (ft).

scribed above (Fig. 2). In contrast to the respective gland of *Teleogryllus commodus*, its length/width ratio is always <1. Beside this significant anisometric shape, the gland is characterized by a lower complexity due to a small number of ramifications (<10) originating from the middle region. This part shows, like in *Gryllus bimaculatus*, a clear predominance over the other regions of the gland. The ramifications are rather short and of the same shape as in the glands of the other investigated crickets. Tracheoles run over the whole organ and reach their highest density in the apical region.

Morphology of the accessory sex glands

In contrast to the shape and size, the morphology of the accessory sex glands is remarkably uniform among the investigated cricket species (Fig. 2). All glands consist of an epithelium and a lumen, into which the secretory products are released (Fig. 3). The size of the lumen depends on the observed region of the gland, but is largest in the distented end tubules and in the vicinity of the orifice. The epithelium of each gland is composed of only one cell type that secretes both the cuticular intima and the secretory substance. Under the light microscope, respective gland cells reveal a columnar shape as well as a large, basal-situated nucleus (Fig. 3D–F). On the outside of the epithelium, a thin basal lamina can be observed. The very basal region of each gland is characterized by a muscle coat around the epithelium consisting of circular and longitudinal muscle fibres, respectively (Fig. 4A). Another specific morphological feature are hair-like processes and spines of the cuticular intima that reach into the lumen and are mainly straightened to the direction of the orifice (Figs 3E–F, 4B).

In *Teleogryllus commodus* the epithelium of the accessory gland varies in height between 50 and 80 µm with up to one third of the cell volume occupied by the nucleus. The processes of the cuticular intima show their maximum length in the basal gland region (up to 20 µm) and continuously decrease in length in the distal parts of

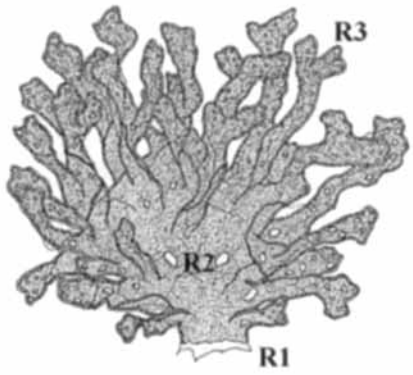
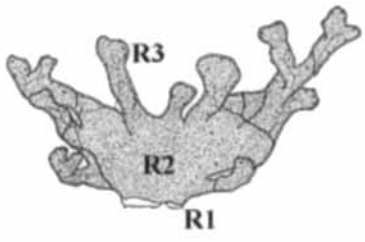
cricket species	accessory sex glands		
	shape	size	morphology
 *Gryllus bimaculatus* DE GEER		length: 8-13 mm, width: 7-12 mm	Very complex shape with numerous ramifications extending from R2, very wide orifice, epithelium consisting of basal lamina; one layer of gland cells, and cuticular intima.
 *Teleogryllus commodus* WALKER		length: 6-14 mm, width: 5-10 mm	Shape dominated by distended end tubules defining R3; small R1 and long R2; epithelium is composed of a basal lamina, one layer of gland cells and a cuticular intima.
 *Gryllus assimilis* LINNAEUS		length: 3-8 mm, width: 7-12 mm	Length/width ratio often <1; small number of ramifications extending from R2 which represents the main part of the gland; wide orifice; epithelium is one-cell-layer thick.

Fig. 2. Shape, size, and morphology of the accessory sex glands in the investigated cricket species.

the gland. In the apical region they are shortened to less than 10 µm. The basal lamina increases its thickness from about 0.5 µm in the apical region to about 2 µm in the basal region, where it is connected with an up to 15 µm thick coat of muscle fibres.

In *Gryllus bimaculatus* the height of the gland epithelium ranges from 60 µm to 100 µm with the nucleus also occupying a main part of the cell's volume. Cuticular processes and basal lamina behave in the same way as in the respective gland of *Teleogryllus commodus*. While the processes decrease their length from up to 25 µm in the basal gland region to about 10 µm in the distal parts, the thickness of the basal lamina decreases from c. 3 µm to c. 0.8 µm. The surrounding muscle coat in the very basal gland region is characterized by a thickness of up to 18 µm.

The epithelium of the accessory sex gland in *Gryllus assimilis* reaches a height of about 60 µm. Contrary to the glands of the other cricket species, the cuticular processes are not as well

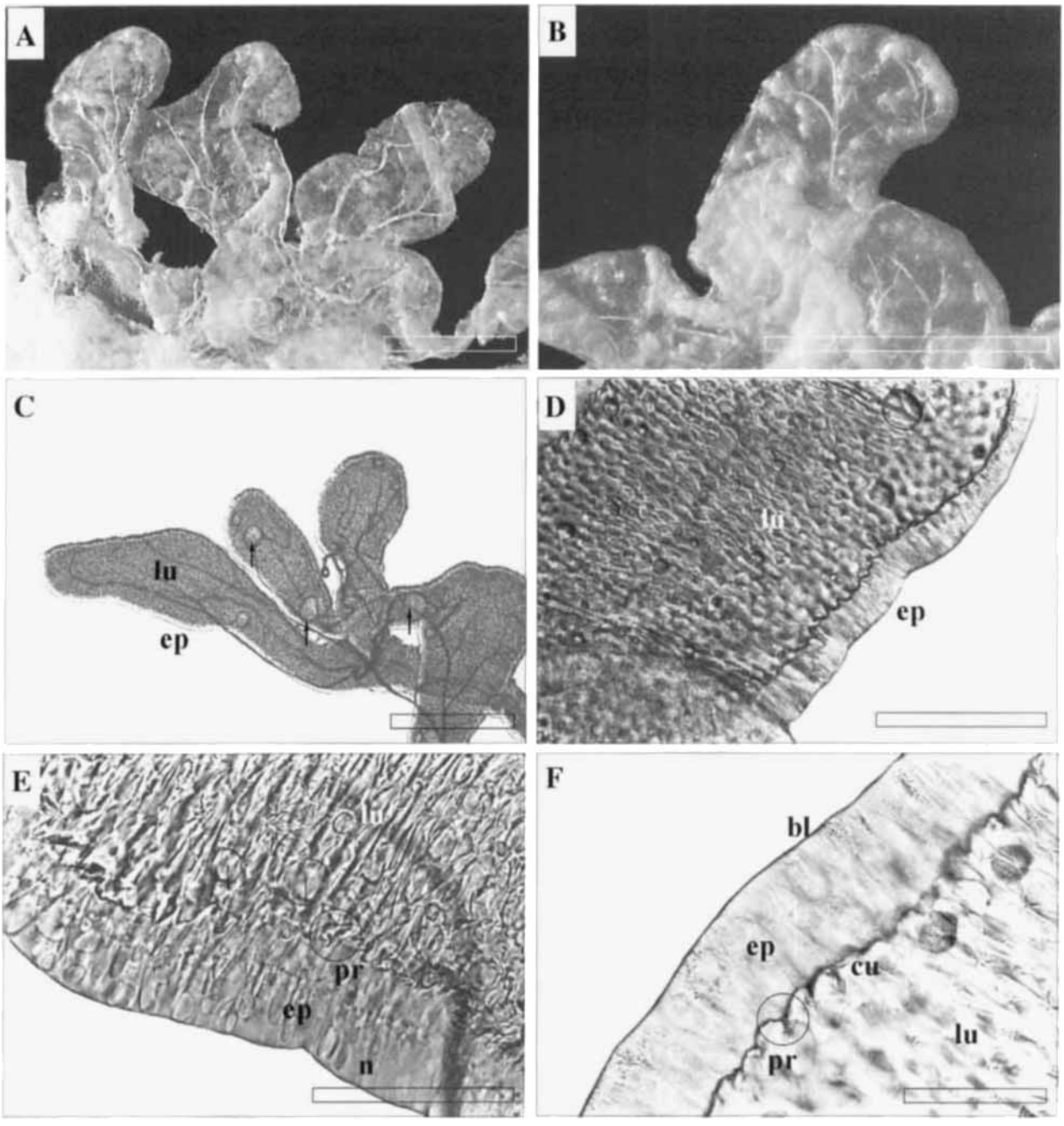


Fig. 3. Micrographs of the accessory sex glands. **A.** & **B.** Light microscopic images of the gland (*Gryllus bimaculatus*) with distended end tubules and dense web of tracheoles running over the whole organ. **C.–F.** Interference contrast images of the gland (*Teleogryllus commodus*) showing the epithelium (ep) with its cuticular intima (cu) and basal lamina (bl) as well as the wide lumen (lu). Under the light microscope, the cuticular processes (pr) and nudeiln) are clearly visible. Black arrows indicate single drops of the gland's secretion. Bars: **A–C**: 1 mm; **D**: 500 µm; **E–F**: 100 µm.

developed, ranging from 5 µm length in the apical region to 12 µm length in the basal region. The thickness of the basal lamina varies from 0.4 to 2 µm, whereas the muscle coat near the gland's orifice is up to 10 µm thick.

Ultrastructure of the gland cells

As in the case of basic morphology, the ultrastructure of single gland cells does not deviate significantly between the investigated cricket species. Each cell of the epithelium can be roughly divided into a basal part including the nucleus and intracellular cisternae of irregular shape as well as an apical part mainly containing the protein- and lipid-producing compartments (Figs 5–7). The basal cell membrane is connected with a basal lamina of various thickness (see above), representing the outermost layer in the middle and apical region of each gland. The apical cell membrane is rearranged to a dense layer of microvilli with a maximum length of

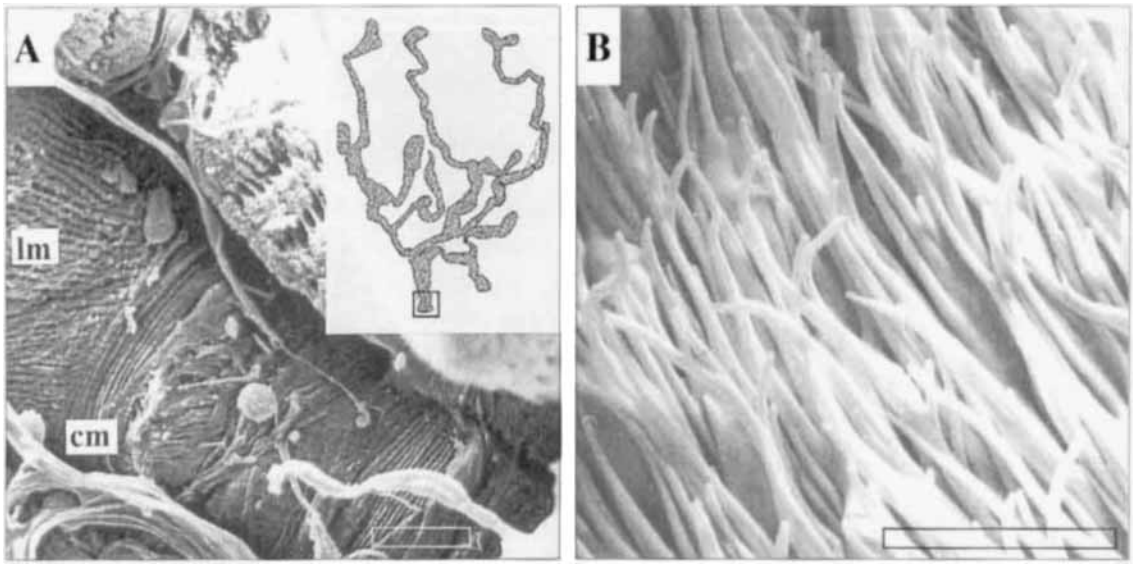


Fig. 4. Special features of the gland epithelium. **A**. Muscle coat surrounding the epithelium at the very basal part of the gland and consisting of longitudinal (lm) and circular muscle fibres (cm; bar: 100 µm). **B**. Hair-like and spiny processes of the cuticular intima (bar: 10 µm).

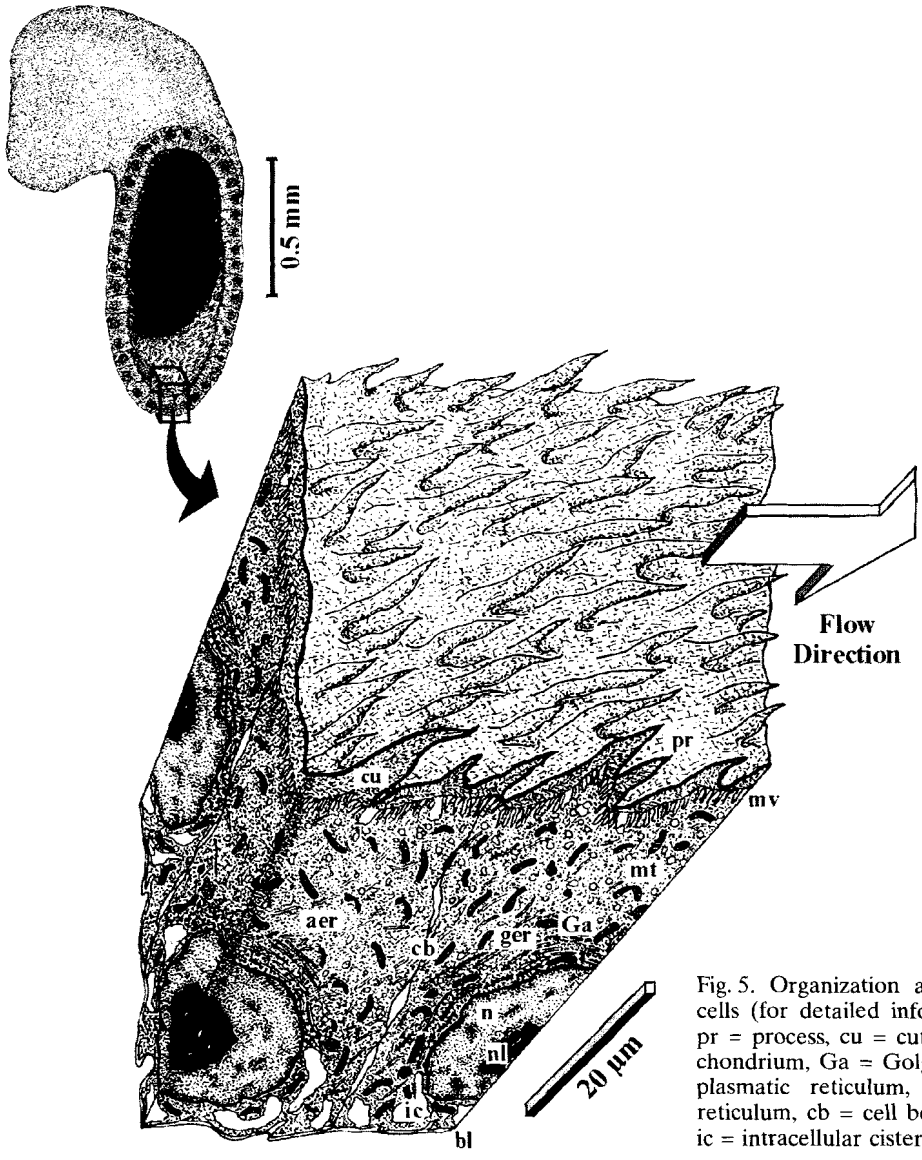


Fig. 5. Organization and ultrastructure of single gland cells (for detailed information see text). Abbreviations: pr = process, cu = cuticula, mv = microvilli, mt = mitochondrium, Ga = Golgi apparatus, ger = granular endoplasmatic reticulum, aer = agranular endoplasmatic reticulum, cb = cell border, n = nucleus, nl = nucleolus, ic = intracellular cisterna, bl = basal lamina.

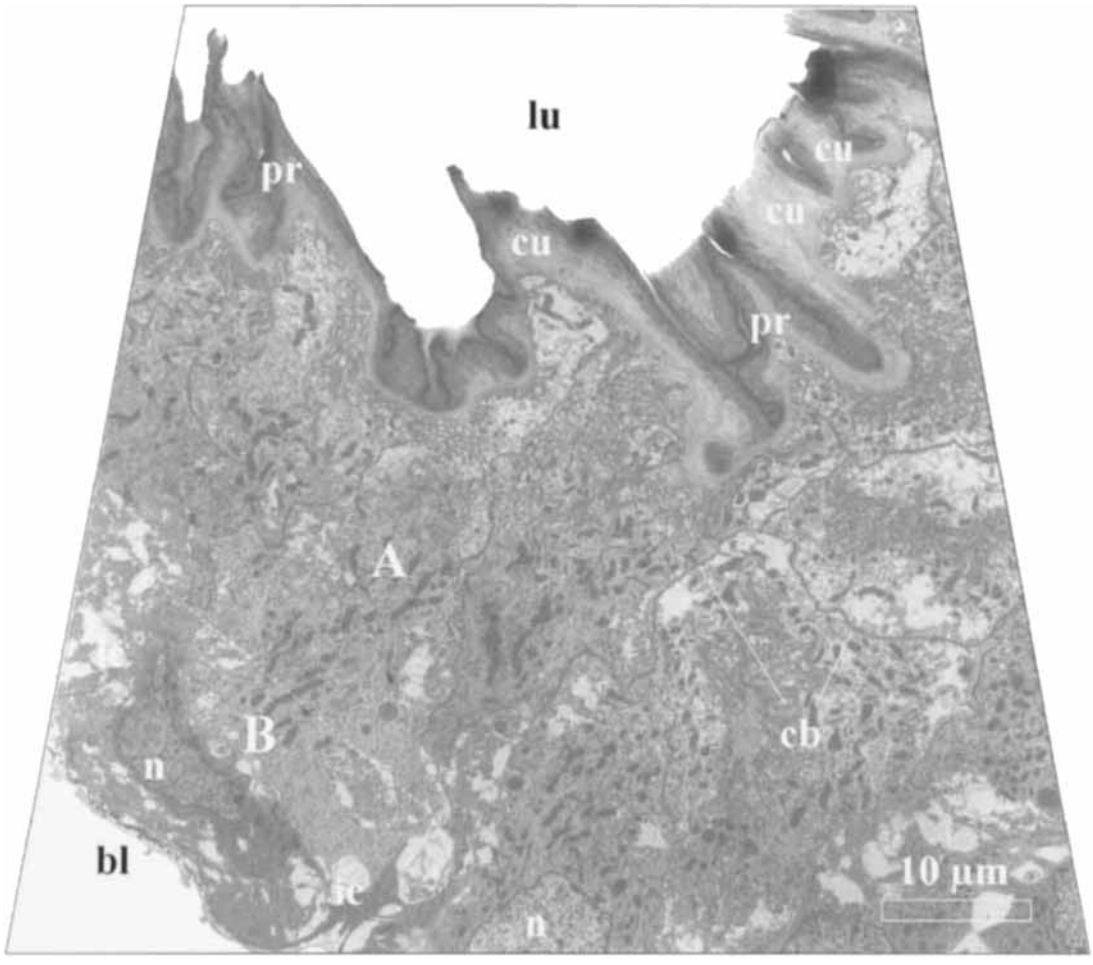


Fig. 6. Electron micrograph of the gland epithelium (*Gryllus bimaculatus*). Each cell can be divided into two typical parts: the basal part (B) containing the nucleus and lots of intracellular cisternae and the apical part (A) with lipid- and protein-producing compartments and mitochondria (abbreviations: see Fig. 5).

2 µm (Fig. 7A–C). The demarcation of the epithelium from the gland lumen is realized by a cuticular intima which varies in thickness from 0.2 µm to 3 µm and forms up to 25 µm long hair-like and spiny processes (Figs 5, 6). The intima itself is composed of 3 subunits which, in agreement with other cuticular structures in insects, are termed endocuticula, mesocuticula, and epicuticula. Except the epicuticular, these chitinous layers are marked by great variabilities concerning their thickness (Fig. 7A, C). At basal parts of large cuticular processes, they may be also completely reduced. As confirmed by transmission electron microscopy, the cuticular intima misses any channel-like structures or breaks that might facilitate the permeation of the glandular secretion to the lumen.

Two adjacent gland cells are usually connected by tight junctions and septate desmosomes which are typical features of secretory-active tissues (Fig. 7B, F). The intercellular spaces between these cell-cell connections are mainly very small in volume. The nucleus in the basal part of a gland cell shows an irregular, but approximately elliptic shape in the electron micrograph (Fig. 7E). Its main features are a large and irregularly shaped nucleolus in the centre as well as fluctuating amounts of electron-dense, genetically inactive heterochromatine. The volume ratio between nucleus and the entire cell depends on the developmental stage of the gland and therefore ranges from about 0.2 to 0.35. In a fully differentiated secretory-active cell, the nucleus is usually surrounded by intracellular cisternae (Figs 5, 6, 7F) which have been formed due to intensive invagination of the basal cell membrane and remarkable enlargement of the basal cell surface. In some of these cavities fragments of former cell membrane are enclosed (Fig. 7F).

In the apical part of the gland cell, scattered cisternae of the granular and agranular endoplasmatic reticulum are exposed. Together with the Golgi apparatus also appearing in this region, they form the compartments essential for the production of the gland's secretions. The amounts of these compartments depend on the

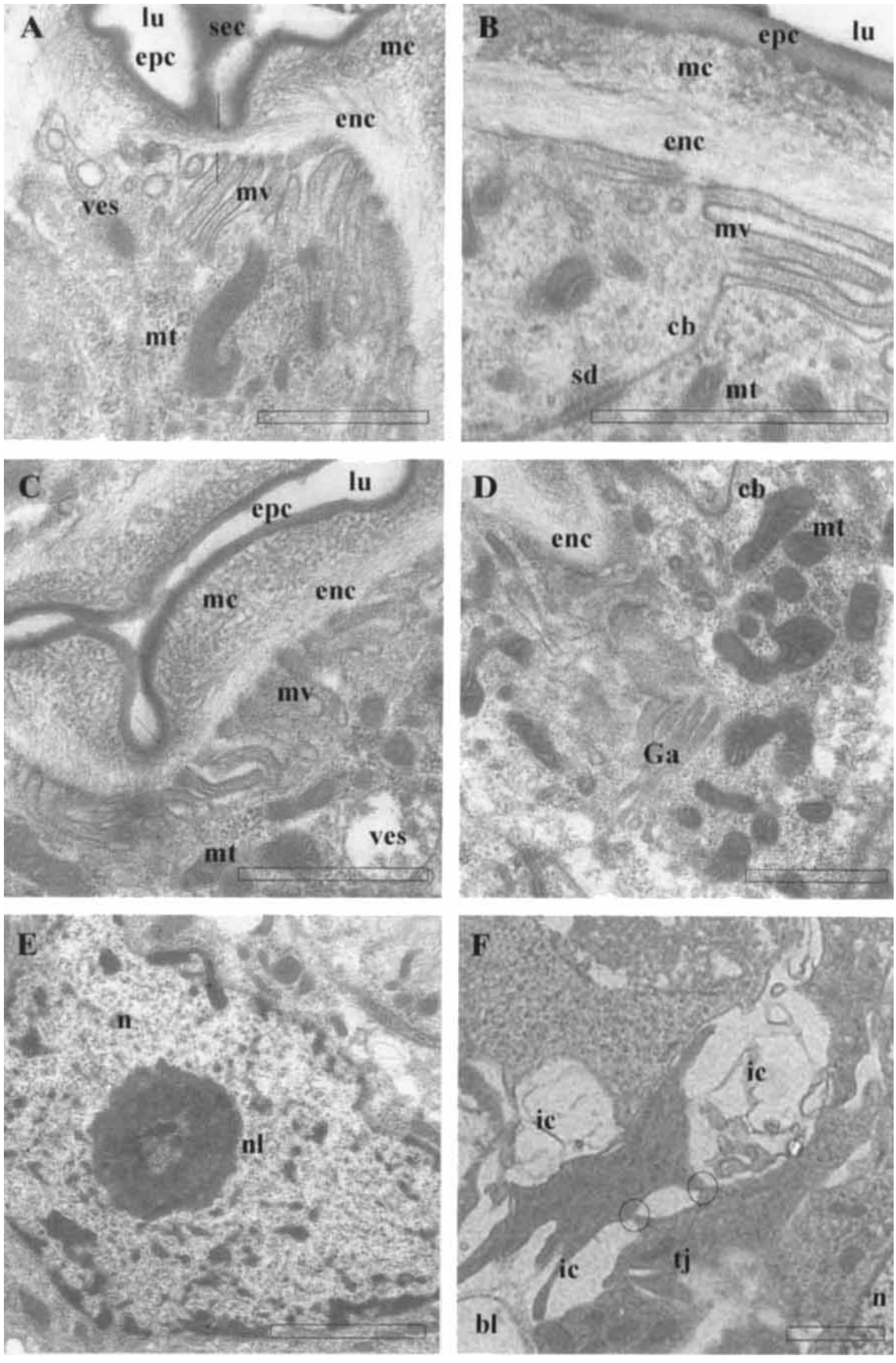


Fig. 7. Electron micrographs showing details of the apical cell part (A–D) and the basal part (E–F). Detailed descriptions of single features are available in the text. Very eye-catching is the significant decrease of the cuticula thickness at the basis of long processes (arrows). These places are thought to be the main diffusion paths for the lipophilic secretion. Abbreviations correspond with those in Fig. 5. Additional abbreviations: epc = epicuticula, mc = mesocuticula, enc = endocuticula, sec = secretion, ves = vesicle, sd = septate desmosome, tj = tight junction. Bars in A–F: 2 µm.

stage of cell differentiation, respectively, but reach their maximum during the egg-laying period of the female cricket. The energy supply of each cell is quaranted by numerous mitochondria of cristae type which vary in size from 0.5 to 2 µm (Fig. 7A, D). Depending on the orientation of the histologic section, their shape ranges from spherical to bent and elliptically elongated. Between the production units and the apical layer of microvilli, numerous vesicles and lipid drops can be detected. At those places, where the contents of the vesicles and oil drops are released from the cell, the microvilli layer becomes continuously desintegrated (Fig. 7A).

Onset of secretory activity and characteristics of the secretion

After the accessory sex glands in female crickets are fully differentiated, they start their secretory activity. While for *Teleogryllus commodus* this starting point is five to six days after the adult moult, in *Gryllus bimaculatus* and *Gryllus assimilis* the onset of secretory activity could be determined four to five days after the adult moult. In all investigated cricket species development of the gland is accompanied by a significant color change from white and translucent to yellow-brown. This is mainly due to an increase of cellular compartments and vesicle production.

The amount of produced secretion varies considerably between the species and can be roughly correlated with the gland size, respectively. While in *Teleogryllus commodus* and *Gryllus assimilis* the total amount of secretion is in the order of 0.01 to 0.03 ml, in *Gryllus bimaculatus* the respective amount is up to ten times higher.

The quality of the secretions was tested with simple mixing and staining experiments. The secretions of all three accessory glands did not mix with insect Ringer's solution at all, but were otherwise affected by a perfect miscibility with acetone. Staining of the secretory substances was only possible with lipophilic dyes (e.g. oil red O). All these results confirm the oily, lipophilic nature of the glandular secretions.

Discussion

The results of the present study show that the female accessory sex glands of *Teleogryllus commodus*, *Gryllus bimaculatus*, and *Gryllus assimilis* differ in size and shape, but are otherwise marked by a significant correspondence concerning their basic morphology and the ultrastructure of single gland cells. As could be found by microscopic investigations, the epithelium of all selected glands is composed of only one type of gland cell. This cell produces both the glandular secretion and the cuticular intima demarcating the epithelium from the lumen of the gland. Therefore, the investigated glands clearly correspond with the first morphological type defined by Gillott (1988) (see introduction). Sturm & Pohlhammer (2000) could distinguish three main regions (R1, R2, and R3) for the accessory sex gland of *Teleogryllus commodus* which differ among each other due to morphological specificities. This concept of partitioning can be also applied successfully to the respective glands of *Gryllus bimaculatus* and *Gryllus assimilis*. In the glands of all three cricket species, the apical region was determined as main production unit of the secretory substances, while the middle and basal region could be recognized as storing and conducting units. A similar organization as described above was considered in the case of the ductus receptaculi of *Teleogryllus commodus*, as outlined by Essler et al. (1992). Here, the three defined regions can be mainly distinguished by the exclusive appearance of gland cells in the middle region and the variable width of the lumen.

Although the investigated glands show a rather simple architecture, some properties of their morphology are very specific. One of these features are the spiny and hair-like processes of the cuticular intima, whose function is not known exactly by now. On the one hand, it is assumed that the processes could support the flow of the secretion to the orifice. On the other hand, a role of these spines could be the conservation of a minimum volume of the lumen as well as a stabilization of the gland's shape. However, similar structures are observed in the receptaculum seminis of *Teleogryllus commodus* (Essler et al. 1992), where they probably cause the spermatozoa which actively move along the receptacular wall to be directed into the ductus receptaculi. The muscle coat surrounding the most basal parts of the glands serves as a closing mechanism that allows the outflow of secretion only during the period of egg-laying. A frequent peristaltic contraction of the muscle fibres might also cause a force pumping the secretion actively out of the gland, when needed in high amounts.

The ultrastructure of single gland cells is mainly identical in the three cricket species and can be subdivided into two parts: a basal part with the nucleus and numerous intracellular cisternae

and an apical part with protein- and lipid-producing compartments as well as specific cristae-type mitochondria. The system of cisternae is formed by deep invaginations of the basal cell membrane, enlarging the basal surface of the gland cell dramatically. The cisternae develop during the main differentiation of the gland and reach a steady state, when the gland starts its secretory activity. It is thought that the larger basal surface area might allow an increased endocytosis of nutriments from the hemolymph during the period of highest fertility of the crickets. Similar invaginations of the basal cell membrane are e.g. documented in the femal accessory gland of *Hyalophora cecropia* (Berry, 1968). Before being delivered into the lumen, the glandular secretion produced in the apical compartments has to pass the cuticlar intima. As high-magnified electron micrographs show, the intima misses any channel-like structures, ducts or even breaks that might facilitate the efflux of the secretion. Such structures are mainly documented for gland cells producing hydrophil substances (Treherne 1957). The gland cells of the ductus receptaculi in *Teleogryllus commodus* are demarcated from the lumen by a uniform, nearly 20 µm thick cuticular layer that would make it impossible for the proteinacous secretion to pass without running through a specific channel system (Essler et al. 1992). Similar structures can further be observed in the wax glands of e.g. *Anomoneura mori* (Waku, 1978). In the case of the accessory sex glands, the produced lipophilic substances are supposed to pass the cuticula by simple diffusion mainly at those places, where only the epicuticula is fully developed (see 'Results' and Fig. 7A). Such diffusive transport through a chitinous layer was reported for the cornual gland in male *Apis mellifera* (Koeniger et al., 1996) and pheromone glands in female *Bombyx mori* (Schneider, 1994). The diffusion theory is also supported by the experiments of Eidmann (1922) who tested the permeability of chitinous structures.

The lipophilic quality of the gland's secretions which could be pointed out by e.g. their perfect miscibilities with acetone rises the question of their main function(s). However, different functions of the oily substances may be assumed. Above all, the secretions probably facilitate the movement of the eggs through the ovipositor, acting as a kind of lubricant. Another extern function might be the formation of a protective layer around the eggs to withstand organic and inorganic influences. The relationship between the gland secretion and egg-laying is confirmed by the fact that the onset of secretory activity mostly happens at the same time as the onset of egg fertilization (4 to 8 days after adult moult).

As the present study showed, female accessory sex glands are uniformly structured among various crickets and seem to play an important, but not fully understood role during reproduction. To solve any open questions, further detailed studies on the accessory glands of orthopteroid insects and especially of crickets are necessary.

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