The morphology and ontogeny of the exocrine glands of *Prorhinotermes simplex* (Isoptera: Rhinotermitidae)

Jan Šobotník\(^1\) & Jan Hubert\(^2\)

\(^1\) Institute of Organic Chemistry and Biochemistry, Flemingovo nám. 2, CZ–166 10 Praha 6, Czech Republic; e-mail: sobotnik@uochb.cas.cz

\(^2\) Research Institute of Crop Production, Drnovská 507, CZ–161 06 Praha 6, Czech Republic

Received March 15, 2002; accepted September 3, 2002
Published March 31, 2003

Abstract. Exocrine glands secrete their products outside the body. Several functions of the secretions of particular exocrine organs are documented (communication, defense, self-protection, digestion etc.), but that of other such glands is still poorly understood. The structure of the exocrine glands of *Prorhinotermes simplex* (Hagen, 1858) was investigated using histological techniques. The development of the frontal, mandibular, labial, sternal, posterior sternal and tergal glands is described in larvae of the first and second instar, pseudergates, presoldiers, soldiers, pharate imagos and imagos. The exocrine glands of *Prorhinotermes simplex* are not functional during the first instar, except the labial glands, which may function from the time of hatching. Mandibular, labial and sternal glands start to differentiate during the second instar and acquire their definite structure and full function in the following instars. The reversible reduction of the mandibular and sternal glands of presoldiers and pharate imagos is explained by a decrease in the size of the secretory cells. Faster changes occur in the presoldier and pharate imago stages: (i) the formation of the frontal gland; (ii) the loss of the characteristic arrangement of the sternal gland; (iii) the reduction in the size of the mandibular glands and the loss of their characteristic arrangement. The ontogenetical changes are discussed in detail.

Morphology, frontal gland, mandibular gland, labial (salivary) gland, tarsal gland, sternal gland, posterior sternal gland, tergal gland, ontogeny, Isoptera, Rhinotermitidae, *Prorhinotermes*

INTRODUCTION

Several types of secretions, with communicative, defensive, self-protective and digestive functions, are produced by exocrine glands. The following exocrine glands are found in the family Rhinotermitidae: frontal, mandibular, labial (salivary), sternal, posterior sternal, tergal glands (Noirot 1969, Ampion & Quennedey 1981, Grassé 1982). Tarsal glands are present in several species of Rhinotermitidae (Bachcus 1979) and in *Serritermes serrifer* (Hagen, 1858) (Costa-Leonardo 1994) but lacking in *Prorhinotermes simplex* (see Šobotník & Weyda 2001).

The structure of the frontal gland is known for a number of rhinotermitid soldiers (Deligne et al. 1982, Quennedey 1984). The general anatomy of the gland is similar, the secretory epithelium forms a simple sac-like structure that opens onto the frons via a frontal pore (fontanelle). The various species differ in the size of the gland. The secretory epithelium is formed by class 1 cells and only in *Coptotermes* (Wasmann, 1896) are class 3 cells also present (Quennedey 1984).

The structure of mandibular glands is similar in all species of termites (Lambinet 1969, Cassier et al. 1977, Greenberg & Plavcan 1986, Costa-Leonardo & Shields 1990). This gland is composed of a clump of class 3 cells that release their secretion close to the ventral mandibular condyle via a short common duct.
Labial glands are composed of the same elements in all species of termites (Noirot 1969, Billen J. et al. 1989, Kaib & Ziesmann 1992) – clumps of secretory cells (the acini), reservoirs (the water sacs) and ducts that connect the parts of labial gland and lead to the basis of the labium. The acini are usually composed of two principal kinds of secretory cells (central and parietal). The central cells are often of two types, at least in workers.

The sternal gland of rhinotermitids is situated on the anterior part of the fifth abdominal segment, always close to the fourth abdominal ganglion (Noirot 1969). This gland has a unique shape in this termite family. It is bilobed (Smythe & Coppel 1966, Mertins et al. 1971, Quennedey 1971, Ampion & Quennedey 1981), and composed of four different kinds of secretory cells. The anterior lobe consists of class 1, 2, and 3 (type 1) cells, and the posterior lobe of class 3 type 2 cells (Quennedey 1971, Ampion & Quennedey 1981).

Posterior sternal and tergal glands are present in Prorhinotermes Silvestri, 1909 (see Ampion & Quennedey 1981): The posterior sternal glands in males only, tergal glands are well developed in both sexes. These glands have the same structure and are composed of class 1 and 3 cells.

A description of the exocrine glands of the presoldier stage and features of the exocrine glands of younger stages and alate imagos has not been published. The aim of this study is to describe the exocrine glandular system of a model species Prorhinotermes simplex, to compare it within the castes and developmental stages, and to summarize the changes that occur during the ontogeny of the exocrine glands.

Prorhinotermes differs from other rhinotermitids, not only by plesiomorphic characters unique within the family, but also by several autapomorphies unique to termites (Štys & Šobotník 1999). The description of this species glandular system should provide significant data for testing its phylogenetic position, which is unclear.

MATERIAL AND METHODS

All individuals of Prorhinotermes simplex (Hagen, 1858) came from a colony collected by J. Křeček in Soroa (Pinar del Río, Cuba) on 14th December, 1964 and kept in a laboratory at 26 ± 1°C since then. Individuals were taken for investigation on 29th April 1998, when both nymphs and alate imagos were present in the colony. Sectioning revealed that the nymphs were in fact the pharate imagos. Because nymphs were not available, a study of this stage is lacking.

The development of the castes of the genus Prorhinotermes is as follows: (a) egg, (b) the first larva, (c) the second larva, (d) larva-pseudergate, (e) pseudergate (usually, but not necessarily undergoes several moults), (f) nymph, (g) alate imago. A soldier develops from any immature individual from the second instar onwards (c-f), always via a presoldier (Roisin 1988). We use the term pseudergate for all workers, at least in the 5th instar that lack wing buds, which differs from the common usage of this term (e.g. Noirot & Pasteels 1988, Thorne 1996).

The material consisted of 30 pseudergates, 30 soldiers, 15 presoldiers, 30 larvae of both the first and second instar, 9 pharate imagos, 6 alate males and 14 alate females. All specimens were fixed in modified Bouin-Dubosque-Brasil fluid (Smrč 1989) embedded in paraplast, sectioned (thickness 7–10 mm), and stained in Masson’s triple stain. Individuals categorized as pharate imagos had finished apolysis, but the formation of a new cuticle was in its initial stage. The measurement of the various characters of gland development was done on at least three individuals; so it is only a general indication.

The classification of the secretory cells follows Noirot & Quennedey (1974).

RESULTS

Mandibular, labial and sternal glands are present in all castes and developmental stages of Prorhinotermes simplex. The frontal gland is present in presoldiers, soldiers and imagos; tergal glands in imagos, and posterior sternal glands are developed only in alate males. The position of these glands is indicated in Fig. 1.
Tab. 1. The thickness of frontal gland cell layer in *Prorhinotermes simplex* (Hagen, 1858). The thickness was measured in the head (1) and abdomen (2) of soldiers and presoldiers, and as maximal (1) and minimal (2) thickness in imagoes and pharate imagoes (in μm).

<table>
<thead>
<tr>
<th>caste (or stage)</th>
<th>1</th>
<th>2</th>
<th>3&lt;sup&gt;rd&lt;/sup&gt; segment</th>
<th>6&lt;sup&gt;th&lt;/sup&gt; segment</th>
</tr>
</thead>
<tbody>
<tr>
<td>presoldier</td>
<td>7.1</td>
<td>11.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>soldier</td>
<td>14.0</td>
<td>5.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>pharate imago</td>
<td>48.0</td>
<td>20.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>imago</td>
<td>58.0</td>
<td>17.0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Frontal gland**

The gland cells form a single layered epithelium, their cytoplasm is slightly vacuolized and nuclei are granulated. The gland is always equipped with a thin cuticle. The inner space of the gland contains secretion, which always stains in the same way. For the thickness of the secretory epithelia in the particular castes see Tab. 1.

The gland is a sac-like tubular structure situated in the dorsal part of head, thorax and abdomen in presoldiers. It ends in the 3<sup>rd</sup> or 4<sup>th</sup> abdominal segment. The cells are cubic and the cuticle (intima) is relatively thick in presoldiers (Fig. 2).

The dorsally situated, sac-like frontal gland is also present in soldiers. The gland expands until it ends in the 6<sup>th</sup> or 7<sup>th</sup> abdominal segment. The cells forming the gland gradually flatten posteriorly: they are cubic in the head, but flat and rather tile-like in the abdomen (Fig. 3).

In imagoes and pharate imagoes the gland is situated in the posterior part of the head, behind the brain. Its shape varies as the epithelium is usually folded (Fig. 4). The gland cells are relatively large, narrow and tall (Fig. 5, Tab. 1). The thickness of the secretory epithelium varies, but in general is thinnest anteriorly (close to the brain) and thickest posteriorly. In imagoes, nuclei are

![Diagram](image_url)

**Fig. 1.** Schematic illustration of the arrangement of the exocrine glands in *Prorhinotermes simplex* (Hagen, 1858).
Tab. 2. Size of mandibular glands and mandibular gland secretory cells in the various castes of *Prorhinoterme simplex* (Hagen, 1858) (in μm)

<table>
<thead>
<tr>
<th>caste (or stage)</th>
<th>length</th>
<th>width</th>
<th>cell dimension</th>
</tr>
</thead>
<tbody>
<tr>
<td>larva instar I</td>
<td>58</td>
<td>55</td>
<td>?</td>
</tr>
<tr>
<td>larva instar II</td>
<td>67</td>
<td>60</td>
<td>18</td>
</tr>
<tr>
<td>pseudergate</td>
<td>177</td>
<td>55</td>
<td>24</td>
</tr>
<tr>
<td>presoldier</td>
<td>52</td>
<td>47</td>
<td>21</td>
</tr>
<tr>
<td>soldier</td>
<td>146</td>
<td>59</td>
<td>21</td>
</tr>
<tr>
<td>pharate imago</td>
<td>102</td>
<td>51</td>
<td>21</td>
</tr>
<tr>
<td>imago</td>
<td>112</td>
<td>78</td>
<td>21</td>
</tr>
</tbody>
</table>

arranged in the outer parts of the cells, while in pharate imagoes they occur anywhere in the cells. In pharate imagoes, the gland cells are slightly smaller but in other aspects similar to those of imagoes.

**Mandibular glands**

Each gland is situated near the ventral base of a mandible, close to the ventral condyle (Figs 6 and 7). The following description of mandibular gland development is based on the situation in pseudergates, imagoes and soldiers (Figs 7 and 8) where the glands look similar, and the difference between these castes is in the size of the gland (Tab. 2). The gland is composed of class 3 cells arranged in a compact clump (with the gland cells on the outside and the canal cells on the inside). The cells are widely columnar. Each of them is apically differentiated into a relatively large extracellular reservoir (Fig. 8). The extracellular reservoir is usually round, but reservoirs of an irregular round shape were also observed. The nuclei of the secretory cells are oval, granulated and arranged marginally. The nuclei of the canal cells are flat and granulated. The common duct arising from the central part of the gland is short and curvy (Fig. 7). The cells forming the common duct are flat and are unmodified epithelial cells of the preoral cavity. The dimensions of the mandibular glands in the castes of *Prorhinoterme simplex* are summarized in Tab. 2.

In larvae, the glands are organized differently. In first instar larvae they consist of undifferentiated clumps of cells, with no general structure. Neither cytoplasm vacuolization nor extracellular reservoirs are apparent; all nuclei are equivalent. In second instar larvae, there is the general structure, but with some differences. The glands and secretory cells are relatively small. Extracellular reservoirs are present in most of the secretory cells, but are of an irregular rounded shape. There are fewer small secretory vacuoles than in the castes where the gland is fully developed (i.e. pseudergates or soldiers). The common duct connects the gland directly to the preoral cavity in larvae of the first and second instar (Fig. 6) but is curvy in subsequent instars.

The glands development in pharate imagoes and presoldiers differs slightly from the general scheme. Glands are reduced in size due to the smaller volume of the secretory cells. The extracellular reservoirs are apparent in only some of the secretory cells.

⇒

Figs 2–5. Frontal gland of *Prorhinoterme simplex* (Hagen, 1858): 2 – Sagital section through the dorsal part of the abdomen of a presoldier; r = reservoir of frontal gland, dt = digestive tract; arrows mark a secretion of frontal gland. 3 – Sagital section through the dorsal part of the abdomen of a soldier; r = reservoir of frontal gland, c = outer cuticle; arrows mark the frontal gland epithelium. 4 – Sagital section through the dorsal part of the head of a pharate imago; r = the reservoir of frontal gland, b = brain; arrow marks the secretion of frontal gland. 5 – Sagital section through secretory epithelium of an alate male; r = reservoir of frontal gland (scale bar = 0.1 mm in all Figs).
Tab. 3. Extent of the acini (1), the water sac (2) and mean size of the acinus (3) in μm in the various castes and developmental stages of Prorhinotermes simplex (Hagen, 1858). Infrequent observations are in parentheses. D – distal part of segment, P – proximal part of segment, th. – thoracic segment, abd. – abdominal segment

<table>
<thead>
<tr>
<th>Caste (or stage)</th>
<th>1</th>
<th>2</th>
<th>3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Larva instar I</td>
<td>D 1. th. – P 2. th.</td>
<td>D. 1. th. – 2. th.</td>
<td>21.4</td>
</tr>
<tr>
<td>Larva instar II</td>
<td>D 1. th. – 2. th.</td>
<td>2. th. – 3. th.</td>
<td>47.3</td>
</tr>
<tr>
<td>Pseudergate</td>
<td>2. th. (D 1. th.) – 1. abd.</td>
<td>3. th (D 2. th.) – 1. abd.</td>
<td>86.0</td>
</tr>
<tr>
<td>Presoldier</td>
<td>2. th. (D 1. th.) – 1. abd.</td>
<td>3. th. – 1. abd.</td>
<td>70.4</td>
</tr>
<tr>
<td>Soldier</td>
<td>3. th. – 1. abd. (2. abd.)</td>
<td>1. abd. – P 2. abd.</td>
<td>60.5</td>
</tr>
<tr>
<td>Pharate imago</td>
<td>2. th. (D 1. th.) – 3. th. (2. abd.)</td>
<td>3. th. (D 2. th.) – 1. abd. (2. abd.)</td>
<td>85.0</td>
</tr>
<tr>
<td>Imago</td>
<td>2. th. – 1. abd.</td>
<td>D 3. th. – 1. abd.</td>
<td>82.3</td>
</tr>
</tbody>
</table>

Labial glands
The acini of the labial glands are situated along the side of the foregut, surrounding it usually from mesothorax to the 1st abdominal segment (Fig. 11, Tab. 3). Some acini may occur in adjacent segments. The acini are always in a compact group in larvae, pharate imagos, presoldiers and soldiers, but spaced in other stages. The general shape of an acinus is globular but becomes irregular as the crowding of acini increasing. The water sacs are situated dorsally and posteriorly to the acini (Fig. 11). The cells forming the water sac are large and extremely flat, their nuclei are granulated and cytoplasm lacks vacuolization. The water sac has a very thin cuticle as well as its duct. The cytoplasm of the cells forming the ducts contains no vacuoles. Their nuclei are granulated and oval in shape. The extent of the acini and the water sacs, and some other characteristics of labial glands are summarized for each caste in Tab. 3.

The acini are formed by central and parietal cells. The nuclei of the secretory cells are usually situated in the periphery of an acinus. The central cells are large, up to 40 μm. There are two kinds of central cells (type I and II). The type I cells are lighter in colour and their cytoplasm contains predominantly differently sized vacuoles (usually from 1 to 15 μm). The type II cells are relatively dark in colour and contain fewer vacuoles of one size (about 1 μm). The parietal cells are considerably smaller (about 15 μm), dark in colour and contain no vacuoles.

The acini of the first instar larvae are of globular shape, small in size and the cell nuclei are relatively large (Fig. 10). They are formed by parietal, central and undifferentiated cells. The parietal cells are considerably smaller (about 7 μm) than is usual in the older stages. The central cells contain a small number of relatively large vacuoles (up to 4 μm). The undifferentiated cells are grouped in the center of each acinus; they are apparent only as an accumulation of several ovoid nuclei without cytoplasm.

A smaller proportion of the undifferentiated cells persist into the second instar, but are present only in some acini. The type I cells are very common and contain smaller vacuoles (from 1 to 5 μm). The type II cells are rare and they have few vacuoles.

The acini of pseudergates are large (see Tab. 3) and are formed by typical type I central cells, type II cells and parietal cells. The proportion of each cell type in the acini is similar.

Figs 6–9. Mandibular glands of Prorhinotermes simplex (Hagen, 1858): 6 – Transverse section of the head of a second instar larva; dt = digestive tract, s = suboesophageal ganglion; arrows mark mandibular glands. 7 – Sagittal section of the head of a pseudergate; gl = mandibular gland, m = cuticle of the mandible; arrows mark the common duct. 8 – The same as Fig. 7, but under higher magnification; cc = canal cells; arrows mark the extracellular reservoirs. 9 – Sagittal section of mandibular gland of a presoldier; i = moulted intima of the canal cells; arrow marks the extracellular reservoir (scale bar = 0.1 mm in all Figs).
The acini of pharate imagoes are packed together and sometimes it is difficult to recognize the border of a single acinus. They are composed of similar numbers of central cells, type I and II, and parietal cells.

Imagoes possess acini containing all similar numbers of cell types (type I and II, and parietal cells). The number of vacuoles in the central cells is relatively low, especially in the type II cells. No sexual differences were observed.

The acini of presoldiers rarely contain type I cells. The majority of the central cells are of type II but they contain fewer vacuoles (about 1 μm in diameter) and the cytoplasm is considerably lighter than in non-soldier individuals. Parietal cells do not differ from those in the other castes.

The acini are relatively small in soldiers. They are also compressed but their borders are always apparent. They are composed of typical parietal cells and two kinds of central cells. Both contain one size of vacuoles (about 1 μm in diameter). The common ones are light in colour. The other type is very rare and is similar to type II cells.

The relative size of the water sac is similar in all castes except soldiers where it is smaller. The size of the water sac varies greatly in pseudergates, where it is sometimes reduced in volume by wall folding.

Sternal gland
The typical bilobed structure of this gland (as described for rhinotermitids, e.g. Quennedey 1971, Ampion & Quennedey 1981) is seen only in pseudergates and soldiers (Fig 17). A lumen is present in the anterior lobe of the gland and is connected with an external reservoir by cuticular ducts. The external reservoir is formed by a posterior extension of the fourth abdominal sternum, an anterior part of the fifth sternum and an intersegmental membrane. The external reservoir has a posteriorly situated opening. The anterior part of the anterior lobe of sternal gland is formed by oval-shaped cells and the central part by elongated cells. The oval-shaped cells are probably class 1 and 2 cells (Quennedey 1971) but these cells do not appear to differ when viewed under a light microscope. Their nuclei are situated randomly in the cells. The elongated cells are either secretory or sensory (campaniform sensilla; Smythe & Coppel 1966, Mertins et al., 1971, Quennedey 1971). The two types can be distinguished by the cytoplasmic vacuolization of the secretory cells. Nuclei of all these cells are situated basally (from the body wall). The central part of sternal gland (with the constriction between anterior and posterior lobe) is made up of class 3 cells (type 1), which that are smaller in size. Larger class 3 cells (type 2) form the posterior part of the gland. The class 3 type 2 cells dominate in the lateral parts of the gland. Nuclei of class 3 cells are situated randomly within the cells. Measurements of some characteristics of the sternal gland are summarized in Tab. 4.

Sternal gland is present but not differentiated in the first instar. It is present in the form of a cluster of cells containing basally arranged nuclei. Particular cell types are not recognizable. It lacks the lumen and the external reservoir is present as relatively large broadly open cavity (Fig. 15).

Figs 10–14. Labial glands of Proxhinoterms simplex (Hagen, 1858): 10 – Sagital section of group of acini of a first instar larva; dt = digestive tract, g = mesothoracic ganglion; arrows mark borders of the acini (scale bar = 0.05 mm). 11 – Sagital section of the posterior part of the thorax and anterior part of abdomen of a presoldier; dt = digestive tract, ws = the water sac; the white arrows mark groups of acini, the black arrow marks frontal gland (scale bar = 0.5 mm). 12 – Sagital section of the acini of a pseudergate. T1 = the type I central cell, T2 = the type II central cell, arrows mark the parietal cells (scale bar = 0.05 mm). 13 – Sagital section of group of acini of a pharate imago; T1 = the type I central cell, T2 = the type II central cell, arrows mark the parietal cells (scale bar = 0.05 mm). Fig. 14 – Sagital section of groups of acini of a soldier; cc = central cell of soldier, arrow marks the parietal cell (scale bar = 0.05 mm).
Tab. 4. Measurement of length and width of whole gland, size of lumen, length of elongated and posterior cells (class 3 type 2) of sternal glands in the various castes of *Prorhinotermes simplex* (Hagen, 1858) (in µm)

<table>
<thead>
<tr>
<th>caste (or stage)</th>
<th>size of gland</th>
<th>length</th>
<th>tallness</th>
<th>lumen</th>
<th>length of cells elongated</th>
<th>posterior</th>
</tr>
</thead>
<tbody>
<tr>
<td>larva instar I</td>
<td>89</td>
<td>25</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>larva instar II</td>
<td>137</td>
<td>22</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>19</td>
</tr>
<tr>
<td>pseudergate</td>
<td>279</td>
<td>41</td>
<td>34</td>
<td>18</td>
<td>21</td>
<td>21</td>
</tr>
<tr>
<td>presoldier</td>
<td>289</td>
<td>34</td>
<td>–</td>
<td>21</td>
<td>16</td>
<td>–</td>
</tr>
<tr>
<td>soldier</td>
<td>253</td>
<td>75</td>
<td>43</td>
<td>21</td>
<td>15</td>
<td>40</td>
</tr>
<tr>
<td>pharate imago</td>
<td>225</td>
<td>37</td>
<td>28</td>
<td>20</td>
<td>15</td>
<td>–</td>
</tr>
<tr>
<td>imago</td>
<td>238</td>
<td>37</td>
<td>37</td>
<td>21</td>
<td>19</td>
<td>–</td>
</tr>
</tbody>
</table>

It is still not fully developed in the second instar larvae. It lacks the lumen but the external reservoir is well developed. Undifferentiated cells without cytoplasm vacuolization mainly form the central part of the gland. Some other cells are differentiated, i.e. an anterior group of oval shaped cells and a few class 3 cells. There are one to five class 3 type 1 cells and two to seven class 3 type 2 cells in the posterior part of the gland. The corresponding canal cells are well developed.

It is large and typically developed in pseudergates. The external reservoir is reduced in volume in some pseudergates. The reservoir becomes smaller due to the stretching of the intersegmental membrane caused by the increased abdominal volume (increasing degree of gut filling).

The lumen is not differentiated in presoldiers. The whole gland is flatter than in both pseudergates and soldiers, and the bilobed shape of the gland is not developed (Fig. 16). Both types of class 3 cells are considerably smaller compared to those in pseudergates and soldiers. Nuclei can be situated anywhere in the cells except close to the body wall. The distal part of the gland is shortened, and the border between the anterior and the posterior part is not apparent. The external reservoir is fully developed.

The sternal gland is largest in soldiers (Fig. 17, Tab. 4), especially the anterior lobe.

It is reduced in size in pharate imagos in comparison to pseudergates (mainly the class 3 type 2 cells). Both lobes are only slightly separated. The lumen exists but it is relatively small.

In imagos, the central cells are shorter. The class 3 type 2 cells are also relatively small, and they are present in lower numbers in comparison not only to pseudergates and soldiers but also to pharate imagos (Fig. 18). The bilobate structure is not apparent.

**Posterior sternal and tergal glands**

Posterior sternal glands are present only in alate males and are situated on the posterior part of the eighth and ninth sternum. Their structure is similar to the tergal glands of males (Figs 21 and 22). Tergal glands are present in imagos of both sexes on the anterior part of the eighth, ninth and tenth abdominal tergites. Each gland consists of one layer of columnar cells. The tallest cells are situated in the center of a gland and decrease in size towards the margins (Fig. 19). The cytoplasm

---

Figs 15–18. Sternal glands of *Prorhinotermes simplex* (Hagen, 1858): 15 — Sagital section of sternal gland of a first instar larva. g = ganglion of the fourth segment, arrow marks sternal gland. 16 — Sagital section of sternal gland of a presoldier; g = ganglion of the fourth segment, arrow marks sternal gland. 17 — Sagital section of sternal gland of a soldier; oc = anterior oval shaped cells, ec = elongated cells, s3 = smaller class 3 (type 1) cells, l3 = larger class 3 (type 2) cells, l = lumen. 18 — Sagital section of sternal gland of an alate female; l = lumen. IV. = fourth sternite, V. = fifth sternite in all Figs (scale bar = 0.05 mm in all Figs).
Tab. 5. Size of tergal and posterior sternal glands (maximal width) in males and females of *Prorhinoterme simplex* (Hagen, 1858) (in μm)

<table>
<thead>
<tr>
<th></th>
<th>male</th>
<th>female</th>
</tr>
</thead>
<tbody>
<tr>
<td>tergal glands</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8th</td>
<td>218 (14)</td>
<td>153 (27)</td>
</tr>
<tr>
<td>9th</td>
<td>177 (14)</td>
<td>177 (34)</td>
</tr>
<tr>
<td>10th</td>
<td>163 (20)</td>
<td>221 (47)</td>
</tr>
<tr>
<td>posterior sternal glands</td>
<td>159 (16)</td>
<td>–</td>
</tr>
<tr>
<td>9th</td>
<td>203 (15)</td>
<td>–</td>
</tr>
</tbody>
</table>

of the secretory cells is vacuolated and their nuclei are granulated. The glands are composed of class 1 and 3 cells. The class 1 cells predominate.

There are considerable differences between the tergal glands of males and females. In females, they are much larger, and the cells are very narrow and tall (Fig. 20). The largest gland is situated on the tenth segment, the smallest on the eighth segment (Tab. 5). The nuclei of the gland cells are situated distal to the body wall.

In males, the gland cells are cubic (Fig. 21) and, in contrast to females, the largest gland is situated on the eighth and the smallest on the tenth segment (Tab. 5). The nuclei of the gland cells occur in any position in the cell except close to the body wall.

**DISCUSSION**

The frontal gland differs in the soldier and imago lines. It is always large and has a simple sac-like structure in presoldiers and soldiers and is much smaller in pharate imagoes and imagoes. The frontal gland epithelium is often folded in imagoes, probably reflecting the degree of filling of its reservoir. This gland is composed of similar cells in all individuals in spite of the differences in shape and size of the whole gland and the secretory cells. Our observations on *Prorhinoterme simplex* correspond with the published ultrastructural data on *Prorhinoterme* soldiers (Quennedey 1984). That of imagoes of *Prorhinoterme simplex* seems to be considerably larger than that of *Reticulitermes lucifugus* (Rossi, 1792), as depicted by Grassé (1982, p. 82, Fig. 80A). The frontal gland appears in pharate imagoes, when there is no sign of tergal glands, although Noiro (1969) mentioned that the differentiation of frontal and tergal glands occurs simultaneously during the imaginal moult. The earlier start to the differentiation of the frontal gland in *Prorhinoterme simplex* is probably because of its larger size.

The main function of the frontal gland secretion is colony defense (Noiro 1969, Quennedey 1975, Costa-Leonardo 1992), but some ingredients could also act as alarm pheromones (Quennedey 1975, Costa-Leonardo 1992). The main component of the soldier's frontal gland secretion in *Prorhinoterme simplex* is E-1-nitropentadecene (Vrkoč & Ubik 1974). This compound is toxic to other insects, but non-toxic to nest-mates (Kuldová et al. 1999) because they have autodetoxification mechanisms (Spanton & Prestwich 1981). The nature of the frontal gland secretion of imagoes is
unknown. Its basic composition probably does not differ from that of soldiers because the gland secretion stained similarly in our specimens.

The general development of the mandibular glands in *Prorhinoter mes simplex* is similar to that observed in other termite species (*Kaloter mes flavicollis* (Fabricius), see Lambinet 1959, Cassier et al. 1977; *Constrictoter mes cyphergaster* (Silvestri, 1901), see Costa-Leonardo & Shields 1990).

The function of the mandibular gland secretion is unknown, although Greenberg & Plavcan (1986) demonstrated the presence of hydrocarbons in the mandibular glands of *Zootermopsis angusticollis* (Hagen, 1858). Instead of a communicative function, we hypothesize the secretion has a role in protecting the mandibular condyle from wear. The development of mandibular glands in particular castes and developmental stages of *Prorhinoter mes simplex* supports this hypothesis: the size of these glands decreases in the following sequence: pseudergate, imago, soldier, pharate imago, presoldier, second larval instar, first larval instar. The mandibular glands are fully developed and functional from the time of hatching in *Kaloter mes flavicollis* (Lambinet 1959). The situation in *Prorhinoter mes simplex* is different. Mandibular glands start to differentiate during the second instar and acquire their definite structure and full function in the following instars.

Mandibular glands are temporarily reduced in size in the presoldier stage. The presence of extracellular reservoirs in some of the secretory cells indicates that the glands are at least partially functional. The reduction in size of the gland is probably due to the smaller quantity of secretion produced by the gland in this stage compared with other castes. The reduction in gland size in pharate imagoes is probably connected with moulting.

The labial glands of *Prorhinoter mes simplex* have the same principal structure as in other termites (Noirot 1969, Grassé 1982, Billen et al. 1989, Kaib & Ziesmann 1992). The development of the acini in larvae and following instars indicates that labial glands become functional during the second instar. The acini and the water sacs were originally situated at the boundary of the first and second thoracic segment. They increase in volume (both absolutely and relatively) during the differentiation of the glands and expand posteriorly. The most anteriorly localized acini stay in their original positions in the distal part of the prothorax; the posterior acini reach the first abdominal segment during ontogenesis.

The acini are composed of the same cell types in the same proportions in all older non-soldier stages of *Prorhinoter mes simplex*. This contrasts with the situation in *Schedorhinoter mes lamanianus* Sjöstedt 1911 where the type II cells are lacking in the acini of alate imagoes (Kaib & Ziesmann 1992). In *Macroter mes bellicosus* (Smeathman, 1781), the central cells in nymphs and alate imagoes contain vacuoles of between 1.5 and 2 mm in size (Billen et al. 1989). In soldiers of *Prorhinoter mes simplex*, labial glands are reduced in size and are pushed ventrally and posteriorly, probably due to the development of the frontal gland. The common type of central cells may be a specific modification of type I cells, from which they differ only in the smaller and uniform size of vacuoles. Our observations on acini of the soldier differ from those reported for other species; the acini of soldiers of *Schedorhinoter mes lamanianus* consist only of typical type I and parietal cells (Kaib & Ziesmann 1992), while those of the soldiers of *Macroter mes bellicosus* only one specific type (Billen et al. 1989). The acini of presoldiers of *Prorhinoter mes simplex* are intermediate between those of pseudergates and soldiers.

Labial glands have several confirmed functions. They are associated either with the acini, e.g. production of a non-volatile pheromone used for marking the food (Kaib & Ziesmann 1992, Reinhard & Kaib 1995, Reinhard et al. 1997), production of digestive enzymes (Noirot 1969, Veivers et al. 1991), or with the water sacs, e.g. retention of water for regulation of microclimatic conditions inside the nest (Grube & Rudolph 1999a), moistening of material during nest building (Grube & Rudolph 1999b). The food marking pheromone was recently identified as hydroquinone (Reinhard et al. 2002). The acini of the soldiers of Macrotermiteinae (Termitidae) produce a defensive sub-
stance (for review see Deligne et al. 1981, Prestwich 1984). Other functions of the secretion have been proposed but not confirmed, e.g. provision of food for dependent castes or a glue for building purposes (Noiriot 1969).

The sternal gland is not functional in the first instar larvae and acquires its definite structure and function during the second and following instars. Analogous to the changes in mandibular glands, the sternal gland of presoldiers (less so in pharate imagos) loses its characteristic features (bilobate structure, presence of a lumen). The vacuolization of the gland cells indicates that the gland is functional, but it may produce smaller amounts of secretion or secretion different from that of the other castes. The posterior part of sternal gland is reduced in imagos, even in comparison to pharate imagos. Its function seems to be supplied by tergal glands (and posterior sternal glands in males). The general structure of sternal gland is similar to that observed in other species of Rhinotermitidae (Smythe & Coppel 1966, Noiriot 1969, Mertins et al. 1971, Quennedey 1971, 1975). In general, the secretion of the sternal gland may serve as a trail or sexual pheromone (Pasteels 1972, Quennedey & Leuthold 1978). The presence of well-developed tergal glands in both sexes and posterior sternal glands in males of Prorhinotermes simplex, suggests that the secretion of sternal gland is used probably only in trail following.

The structure of the tergal (and posterior sternal) glands in Prorhinotermes simplex is similar to that in other termite species (Noiriot 1969, Varma 1980). The secretion of tergal glands is used for mate attraction during the post flight pairing of reproductives (Noiriot 1969, Varma 1980). The secretion of the male posterior sternal glands has probably the same function. If they are developed equally in both sexes, females may follow males but this behavior was not observed in species where tergal glands are lacking in males (Noiriot 1969). Tergal glands are larger in females of Prorhinotermes simplex, which may indicate a high probability of the females being followed by males. Tergal glands were not observed in pharate imagos, in contrast to the frontal gland. The organization of posterior sternal and tergal glands is simpler in comparison to the frontal gland and there is therefore no need for an early differentiation of these glands.

Acknowledgement

We are grateful to Ivan Hrdý (Institute of Organic Chemistry and Biochemistry, CAS, Prague) for his extensive help during the preparation of this paper. We thank Pavel Štys (Faculty of Sciences at Charles University, Praha) for critical reading of the manuscript, to František Weyda (Institute of Entomology, CAS, České Budějovice) for his help, and to Martina Janoušková (Institute of Botany, CAS, Praha) and Ester Fleischcróvá (Praha) for English review. This research was supported by the grant agency of the Czech Republic, project No. 522/97/0126.

REFERENCES


