COMPARISON OF THE DISTRIBUTION AND NERVOUS INNERVATION OF THE SENSILLA ON THE LABRUM OF GRYLLUS BIMACULATUS (DE GEER) AND ACHETA DOMESTICUS (L.) (ORTHOPTERA : GRYLLIDAE), AND AN ACCOUNT OF THEIR DEVELOPMENT IN A. DOMESTICUS

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Abstract — The labra of Gryllus bimaculatus (De Geer) and Acheta domesticus (L.) (Orthoptera : Gryllidae) were studied to reveal the distribution and nervous innervation of the sensilla, in order to provide morphological evidence of their function. Employing scanning electron microscopy and light microscopy, 9 types of sensilla are reported in G. bimaculatus and 10 types in A. domesticus. Of these sensilla, types 1 — 4 have setae ranging in size from 5 — 420 gm in G. bimaculatus and from 3 — 470 gm in A. domesticus. Secretory pores, coeloconic pegs, basiconic pegs and campaniform sensilla have been recorded in both species, while sensilla ampullacea are only present in A. domesticus. The different types of sensilla are found in discrete groups on the posterior surface of the labrum, but they are more randomly distributed on the anterior surface. The detailed innervation of the sensilla was revealed by means of nickel chloride infusion, followed by intensification using Timm’s sulphide — silver technique. The labra of both species are innervated by 2 major branches of the labral nerve. Each sensillum is usually innervated by a bipolar neurone, although some sensilla have been shown to be innervated by multiterminal neurones. The dimensions and shapes of the cell bodies and dendrites are provided and differences between the 2 species are identified. In general, the cell bodies and dendrites are larger in A. bimaculatus than they are in A. domesticus. The development of the sensilla through the nymphal instars to the adult is reported for A. domesticus. It is shown that for some types of sensilla, (types 8 and 13), the number remains constant throughout the developmental period, in some (type 1), the adult complement of sensilla is attained in the early instars, for others, (types 2, 6, 7, 9 and 10), there is a steady increase throughout development, while in others (types 3 and 4), sudden increases occur at specific moults.

Index descriptors (in addition to those shown in the title): Scanning electron microscopy, iontophoresis, sensilla basiconica, sensilla coeloconica, campaniform sensilla, sensilla ampullacea.

INTRODUCTION

Most work on the sensilla of the mouthparts of the Orthoptera has focused on the Acrididae, with the Gryllidae receiving relatively little attention. Liu and Leo (1960) and
Thomas (1966) briefly described the sense organs on the mouthparts, including the labrum, of *Locusta migratoria* and *Schistocerca gregaria* respectively. The fine structure of the contact chemoreceptors on the posterior surface and of the campaniform sensilla on the anterior surface of the labrum in *Locusta migratoria* was examined by Sinior *et al.* (1968), Louveau (1972) and Cook (1972, 1977, 1979). Marshall (1947) also described some of the sensilla on the labrum of *Melanoplus femur rubrum*, and the mouthparts of *Xenocheilia zarudnyi* were thoroughly investigated by Chapman (1966). A survey of the abundance and distribution of mouthpart sensilla of 106 species of Acridoidea was carried out by Chapman and Thomas (1978).

In comparison, there are few major works on the Gryllidae. Narula (1968) described the gross morphology of the head capsule and its appendages in *Gryllodes sigillatus*, while recently, Kubra (1978) has made a comprehensive study of the mouthparts and feeding behaviour of *A. domesticus*. Much of her work on the labrum sensilla is presented here. Fudalewicz-Niemczyk and his co-workers in Poland have also studied *A. domesticus*, in respect of the mouthparts of the last larval instar (Rościszewska and Fudalewicz-Niemczyk, 1974), the adult clypeo-labrum (Urvoy *et al.*, 1978) and a subsequent comparison with *Carausius morosus* (Urvoy *et al.*, 1981). However, although these works recognise certain groups of sensilla they give no quantitative data. In *G. bimaculatus* only the maxillary palp has received any detailed investigation (Klein and Muller, 1978; Klein, 1981, 1982).

Although the distribution of sense organs on the labrum has received some attention, details of their nervous innervation is not nearly so well known. In the Acrididae, Louveaux (1972) and Mordue (1975) have investigated this to some extent in *Locusta migratoria* and *Schistocerca gregaria* respectively, while in the Gryllidae reference is made to the nervous innervation of sensilla in the final larval instar of *A. domesticus* by Rościszewska and Fudalewicz-Niemczyk, (1974).

This paper presents a detailed examination of the types of sensilla, their distribution and nervous innervation on the labrum of adults of both sexes of the field cricket, *G. bimaculatus* and compares this with the labrum of adults of the house cricket, *A. domesticus*. In addition, the paper describes in *A. domesticus*, the development of the sensilla through the nymphal instars to the condition shown by the adult, a virtually unexplored subject.

The function of certain mouthpart receptors in relation to feeding has been considered, amongst others, by Haskell and Schoonhoven (1969) in *Schistocerca gregaria* and in *Locusta migratoria migratorioides* where electrophysiological techniques have been used to analyse the responses of chemoreceptors and mechanoreceptors on the labrum. The present paper forms a vital prerequisite for this type of work to be extended to the Gryllidae and such behavioural investigations will be reported in a subsequent paper.

**MATERIALS AND METHODS**

Crickets were reared in an insectary at a temperature of 34°C, a 12L : 12D light regime and an RH of 70%. Breeding stocks were maintained in groups of about 50 insects in plastic aquaria. Food was supplied in the form of commercial rabbit pellets and water was continually available in gravel-filled petri dishes or water-soaked cotton wool pads.

The labra of both sexes of each species were examined, and those of all nymphal instars in *A. domesticus*. Each labrum was removed from the head, just dorsal to the clypeo-labral suture, boiled for 15 min in 10% caustic potash and rinsed thoroughly in distilled water. After dehydration, the labra were mounted in Euparal. The position of the sensilla was plotted with the aid of a camera lucida fitted to a Wild M5 stereoscopic microscope.
Comparison of the Distribution and Nervous Innervation of Sensilla

Labra from newly moulted adult crickets were used to investigate the nervous innervation of the sensilla; the low pigmentation of the integument and the thinner, softer cuticle facilitating microscopic examination. Study of the distribution of neurones was based on whole mounts stained intravitally with methylene blue and on heavy metal iontophoresis. A 0.4% stock solution of methylene blue was prepared in the physiological solution developed by Moulins (1971). The pH was adjusted to 5–7. Using a microsyringe, 0.2 ml of the solution was injected through the neck membrane and a further 0.2 ml injection given 15 min later. Specimens were left for 30 min, after which the head was severed from the rest of the body and fixed in 8% cold ammonium molybdate for 24–48 hr. After staining, the required parts were dissected under saline. For heavy metal iontophoresis, the labral nerve was dissected out under saline and backfilled using a 2.0% nickel chloride solution (Strausfield and Obermyer, 1976), for 12 hr at 6°C. The preparations were then washed in saline and transferred to a solution of rubeanic acid, (saturated to 75% in 75% alcohol) for 15 min (Quicke and Brace, 1979). Following this treatment, the intensification procedure of Bacon and Altman (1977) was followed, the silver deposit being carefully checked using a binocular microscope. This process usually took 30 min to 1 hr. Following intensification, the preparations were washed in distilled water, dehydrated slowly for 12 hr, cleaned in methyl salicylate and mounted in Canada Balsam. After intensification, neurone profiles appeared black on a straw coloured or light brown background.

For scanning electron microscopy (SEM), labra from freshly killed specimens were again used. Initially they were washed in distilled water containing a trace of detergent to remove the wax. They were then rinsed several times in distilled water to remove the detergent and then passed through the alcoholic grades (50%–100%) and finally into acetone or amyl acetate. The labra were then transferred to a critical point drying apparatus. After 2 hr, the labra were placed in anhydrous silica gel mixed with cobalt chloride and mounted on a stub using colloidal silver. Finally, they were each coated with gold palladium alloy (Nei and Fujikawa, 1977) in a splutter coater.

All figures and SEM micrographs are based on adult female insects, except where otherwise stated, and at least 10 replicates were used for data given in Tables 2 and 3.

RESULTS AND DISCUSSION

Gross morphology of the labrum

The general organisation of the labrum is similar in both species. It forms an upper lip to the preoral food cavity and is a broad almost symmetrical, freely moveable plate. The term anterior is used to describe the outer surface of the labrum, whilst the inner, epipharyngeal surface is termed posterior. The labrum is anteriorly convex and is attached to the distal margin of the clypeus by a flexible transverse membrane. The junction with the clypeus is included in this study. The posterior surface is concave and fits closely over the mandibles. The distal edge of the labrum is notched somewhat to the right of the midline. Two less heavily pigmented strips divide the anterior surface of the labrum incompletely into median and lateral areas and a transverse sulcus forms the ventral limit of a well-defined rectangular area.

Two curved sclerotized bars divide the epipharyngeal surface into a median and two lateral areas (Fig. 1). The position of these is seen on the anterior surface as the pigmented strips already mentioned. These bars are also found in the locust (Chapman, 1966; Thomas, 1966). Cook (1944) refers to them as fimbriate strips, while Reitschel (1953) in his study of the labrum of immature A. domesticus refers to them as “Verstärkungsleiste” (= strengthening rods). Their function appears to be to strengthen the anterior part of the head capsule. In the lateral angle of the epipharyngeal wall, between the labrum and the clypeus, there are 2 small sclerotized areas, the tormae (Fig. 1), to which the adductor muscles of the labrum are attached. A small ridge, known as the intertorma, is present on the epipharyngeal side between the tormae, and serves as the site of insertion of the compressor muscles of the mandible in A. domesticus (Kubra, 1978).

Types of sensilla

The description of sensilla is based on the earlier work of Kubra (1978) in which 13 types on the mouthparts of A. domesticus were identified based on their external form.
Types 5, 11 and 12 are omitted in this investigation since they do not occur on the labrum in either species. Type 13 is also absent in *G. bimaculatus*. In addition to the sensilla there are numerous microtrichia and some elaborate cuticular sculpturing. Table 1 gives the length of the setae in types 1—4, these being the only types with setae of any appreciable length.

*Type 1 (t₁).* Sensilla with the longest setae but of variable length. These sensilla are thin relative to their length and in *G. bimaculatus* they tend to be longer and to have a more pronounced socket than in *A. domesticus*. In both species they are scattered over the anterior surface of the labrum rather than forming a compact group.

*Type 2 (t₂).* These sensilla have setae which are shorter than type 1 and have a spiral sculpturing in *G. bimaculatus* but not in *A. domesticus*. In both species they are found on the anterior surface of the labrum in 2 lateral areas associated with type 3 sensilla.
Comparison of the Distribution and Nervous Innervation of Sensilla

<table>
<thead>
<tr>
<th>Table 1. Length of setae from type 1–4 sensilla</th>
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<tbody>
<tr>
<td>Species</td>
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<tr>
<td>---------</td>
</tr>
<tr>
<td>G. bimaculatus</td>
</tr>
<tr>
<td></td>
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<tr>
<td>A. domesticus</td>
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</table>

Type 3 (t₁ : Fig. 2). Sensilla with setae which are always less than 96 µm in G. bimaculatus and 48 µm in A. domesticus but include sensilla with very short, slender setae that may be level with the surface of the cuticle, extend just above it, or remain below it. In both species, these sensilla are scattered all over the anterior surface of the labrum, but they are confined to discrete areas on the posterior surface.

Type 4 (t₄ : Fig. 6). Sensilla with a thick rigid wall. These are extremely variable in size in both species and have sockets with protective projections. A group of type 4 sensilla is present on the posterior surface of the labrum.

Type 6 (t₆). Campaniform sensilla, which are mostly spindle shaped. They vary in length (range 8 – 10.5 µm in G. bimaculatus, 4 – 14 µm in A. domesticus) and breadth (range 4.8 – 6.5 µm in G. bimaculatus, 2.1 – 7.5 µm in A. domesticus). They are situated on the posterior surface of the labrum in discrete groups.

Type 7 (t₇ : Fig. 7). These are referred to as secretory pores by Arnold (1974) and plate organs by Slifer (1970). When seen with the light microscope, they consist of a shallow depression with a small notch on the proximal border. In G. bimaculatus they range in length from 8.2 – 9.8 µm, whilst in A. domesticus they are always less than 8 µm. They occur on the anterior surface of the labrum.

Type 8 (t₈ : Fig. 3). These sensilla are coeloconic pegs with sunken sockets and stout peg-shaped setae. The thickness of the seta is relatively constant throughout its length, but is slightly more depressed in its socket in G. bimaculatus. They are found on the posterior surface of the labrum and vary in socket diameter (5 – 8 µm in G. bimaculatus, 4.2 – 7.5 µm in A. domesticus). In A. domesticus, they are larger in size than the other coeloconic sensilla found on the posterior surface of the labrum (type 10), but in G. bimaculatus they are smaller.

Type 9 (t₉ : Fig. 4). Sensilla, which are basiconic pegs. In G. bimaculatus all these sensilla possess a rather raised socket and the setae are slightly dented at the tip. In A. domesticus, however, there is slight variation in the form of the setae. One form has wavy setae, which arise from a sunken socket, while the other has stout setae, which are broadest at their distal end. In both species they are found on the posterior surface of the labrum.
Type 10 (t10; Fig. 5). These are round, coeloconic pegs with a depression in the centre, which is even visible under the light microscope. The diameter of the socket varies from 7.5 – 10.5 µm in G. bimaculatus to 3.0 – 6.2 µm in A. domesticus. Projections of variable form arise from the depressed sockets. These sensilla are present on the posterior surface of the labrum in both species.

Type 13 (t13). These are absent in G. bimaculatus. In A. domesticus they are flask-shaped sensilla that are often called sensilla ampullacea owing to their shape. The depth of the cavity varies from 22 – 25 µm, while the diameter is 7.6 – 7.8 µm. They are found on the distal part of the anterior surface of the labrum.

Distribution and abundance of sensilla types

In the 2 species investigated, both surfaces of the labrum are well supplied with sensilla. Those on the anterior surface are scattered more or less randomly (Fig. 8), while on the posterior surface they are arranged in discrete groups of different types (Fig. 1: referred to as groups A1 – A10). Table 2 gives the abundance of each type of sensilla on the 2 labral surfaces, while Table 3 gives the precise numbers of sensilla associated with the discrete groups. Thus, in the text only approximate numbers occurring in the groups are cited.

In both species the anterior surface of the labrum is well supplied with sensilla of types 3 and 7 with a much smaller number of types 1 and 2 (Fig. 8). Type 3 sensilla are more numerous on the anterior surface of A. domesticus, but in both species this type is widely distributed. Type 7 are also generally distributed in G. bimaculatus, but occur mainly on the lateral areas of the labrum in A. domesticus. In this respect, type 2 are rather similar in distribution although only relatively few are present. In G. bimaculatus type 7 sensilla are also found in 2 distinct areas, each of 8 – 10 sensilla, one on each side of the notch.

The type 1 sensilla tend to be arranged in pairs although unpaired sensilla of this type may occasionally be present. In G. bimaculatus one unpaired and 2 pairs of type 1 sensilla are situated in the central part of the labrum, whilst in A. domesticus 3 pairs are situated in the central part, with another 3 pairs occurring on the weakly sclerotized distal zone. The distal end of the labrum is notched and is furnished with a double fringe of hairs in both species. However, in addition, in G. bimaculatus 4 pairs of the type 1 sensilla are located around the notch area, whereas in A. domesticus 2 pairs of the type 13 sensilla are located one on each side of the notch.

The posterior surface of the labrum may be subdivided into different regions or fields containing groups of sensilla. Adults of both sexes show a similar distribution of sensilla, though minor differences in numbers do occur.

Field 1. This represents the area at the distal end of the clypeus and bears 3 groups of sensilla, A1, A2, and A4 (Fig. 1).

In G. bimaculatus group A4 occurs in a central position as 2 sub-groups, one on each side of a central longitudinal furrow, whereas in A. domesticus the 2 small sub-groups occur one above each torna. Each sub-group normally consists of 6 – 7 type 8 sensilla in G. bimaculatus and of around 17 type 10 sensilla in A. domesticus, although in the latter the number differs slightly between the sexes.

In both species group A1 is also sub-divided into 2 groups, one on each side of the midline. There are 41 sensilla in each sub-group in G. bimaculatus and approximately 48 in A. domesticus. These sensilla are type 10 sensilla and are probably comparable to the
Comparison of the Distribution and Nervous Innervation of Sensilla

Figs 2–7. Scanning electron micrographs of sensilla types.

Fig. 2. t₁ (G. bimaculatus). × 6,000.

Fig. 3. t₂ (G. bimaculatus). × 9,000.

Fig. 4. t₃ (G. bimaculatus). × 9,000.

Fig. 5. t₄ (G. bimaculatus). × 4,000.

Fig. 6. t₅ (A. domesticus). × 1,000.

Fig. 7. t₆ (A. domesticus). × 9,000.
A\textsubscript{1} group of Thomas (1966). Group A\textsubscript{2} is located in a medial position below the two A\textsubscript{1} sub-groups. This group consists of type 10 sensilla, 25–30 in \textit{G. bimaculatus}, with the surrounding cuticular plates or tiles encroaching on to the socket (this encroachment may be due to the considerable folding, which occurs here at the clypeo-labral junction), and 12–14 in \textit{A. domesticus}, with sockets slightly larger in diameter than those in the A\textsubscript{1} group.

Lateral to the A\textsubscript{1} and A\textsubscript{2} groups of sensilla, and just medial to the tips of the tormae, are 2 large areas of fine hairs or microtrichia. These hairs, which extend from here into the lateral areas of field II between the type 4 sensilla and the sclerotized bar, are cuticular processes without sockets and probably have a purely mechanical function, directing food particles to the sensilla of groups A\textsubscript{1} and A\textsubscript{2} prior to swallowing. In \textit{G. bimaculatus}
### Table 2. Abundance of Sensilla Types on the Anterior and Posterior Surfaces of the Labrum of *G. bimaculatus* and *A. domesticus*.

<table>
<thead>
<tr>
<th>Type</th>
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<td>Anterior</td>
<td>Posterior</td>
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<td></td>
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<td>13</td>
<td>26</td>
<td>346</td>
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<td>104</td>
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<td>Female</td>
<td>13</td>
<td>25</td>
<td>334</td>
<td>—</td>
<td>—</td>
<td>111</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>A. domesticus</em></td>
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<td>12</td>
<td>24</td>
<td>581</td>
<td>—</td>
<td>—</td>
<td>91</td>
<td>—</td>
<td>—</td>
<td>4</td>
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<td></td>
<td></td>
<td>—</td>
<td>—</td>
<td>252</td>
<td>196</td>
<td>22</td>
<td>11</td>
<td>27</td>
<td>150</td>
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<td>98</td>
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<td>194</td>
<td>21</td>
<td>13</td>
<td>24</td>
<td>150</td>
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Values are means expressed to the nearest whole number.
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<tr>
<th>Group</th>
<th>A₁</th>
<th>A₂</th>
<th>A₃</th>
<th>A₄</th>
<th>A₅</th>
<th>A₆</th>
<th>A₇</th>
<th>A₈</th>
<th>A₉</th>
<th>A₁₀</th>
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<tr>
<td>G. bimaculatus</td>
<td>41.3±1.41</td>
<td>27.1±1.61*</td>
<td>12.4±1.31</td>
<td>—</td>
<td>8.6±0.21</td>
<td>21.4±4.81</td>
<td>6.4±3.06</td>
<td>88.3±4.91</td>
<td>6.1±1.12</td>
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<td>31.7±2.10</td>
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<tr>
<td>Male</td>
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<td>13.4±1.84</td>
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<td>A. domesticus</td>
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<td>14.4±0.89</td>
<td>—</td>
<td>9.2±0.83</td>
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<td>99.9±9.31</td>
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<td>88.0±4.33</td>
<td>16.8±0.58</td>
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<td>36.4±0.81</td>
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<tr>
<td>Female</td>
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<td>6.4±0.24</td>
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<td>10.4±0.32</td>
<td>25.6±0.81</td>
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<td>92.2±4.26</td>
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<td>Male</td>
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<td>Female</td>
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<td>6.7±0.17</td>
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<td>10.3±0.76</td>
<td>77.7±0.97</td>
<td>17.1±0.63</td>
<td>61.1±1.11</td>
<td>36.2±0.84</td>
</tr>
</tbody>
</table>

Upper value = right side; lower value = left side; *whole surface; given as mean ± standard error.
these hairs are single or double pointed but in *A. domesticus* trifid hairs have also been identified. Chapman (1966) has found similar hairs on the posterior surface of the clypeo-labrum in *X. zarudnyi* although Thomas (1966) does not record their presence in *S. gregaria*.

Field II. This field starts below the intertorma and is enclosed by the sclerotized bars (Fig. 1). In *G. bimaculatus* there are 2 groups of sensilla, A₁ and A₁₀ and a number of microtrichia, whilst in *A. domesticus* there is an additional group, A₅. The A₁ group in *G. bimaculatus* is arranged in 2 rows of 12–14 sensilla, with each row being composed of a more or less single line of type 8 and approximately twice as many type 9 sensilla randomly distributed in each row. In *A. domesticus* the A₁ group consists of type 8 sensilla only and these are arranged in 2 rows of 6–7 sensilla on each side of the midline. The A₅ group, which is distal to the A₁, consists of a cluster of 10–12 type 3 sensilla. In both species, the A₁₀ group consists of 2 large patches of type 4 sensilla (Fig. 1), which lie lateral to the other groups in this field, but inside the area demarcated by the sclerotized bars. The stout setae of the sensilla vary considerably in length and are directed mainly towards the midline. They are slightly less numerous in *G. bimaculatus* than in *A. domesticus*. Chapman (1966) found similar hairs in *X. zarudnyi* extending from the tormae (X group of Thomas, 1966) but these were less dense and had smaller setae. They appear to have a mechanical function and probably help to direct food particles towards the hypopharynx. Between these type 4 sensilla and the sclerotized bar are finely sculptured microtrichia (Fig. 6) which extend from field I and interspersed with these are a few very fine cone-shaped hairs.

Field III. This field includes the area lateral and distal to the sclerotized bar and, in both species, has several distinct and similar groups of sensilla. Group A₅ consists of a small cluster of type 10 sensilla (Fig. 1), distal to the end of the sclerotized bar (Fig. 5). Each cluster has an approximately equal number of sensilla and this is similar in both species and in both sexes. The SEM micrographs show that in *G. bimaculatus* the sensilla are surrounded by plates of cuticle and so closely resemble those found in group A₂. In *A. domesticus* the sensilla can be seen to have sockets with a very small central protuberance that hardly projects above the surface of the cuticle, the socket being round and varying in diameter from 5–6 μm. Below group A₅ in both species is a bunch of very fine hairs.

Distal and slightly median to the A₁ group in both species, is another group, A₆. This group is situated on the lateral side of the inverted Y depression. There are more sensilla in this group than in group A₁ and the number in the right and left group can vary considerably. The female generally has more sensilla in this group than the male. They are probably type 3 sensilla since each socket is round with a very small slender seta. In *G. bimaculatus*, most of the setae of this type are 8–10 μm long, with a basal diameter of 4–6 μm and a socket diameter of 8–10 μm, whilst in *A. domesticus* the setae are 3–8 μm long, with a basal diameter of 1.5–2.2 μm and a socket diameter of 4–6 μm. At the distal end of the labrum a group of A₅ sensilla is situated on each side of the notch. They are type 6 campaniform sensilla and may represent the group A₅ of Thomas (1966). In *G. bimaculatus* there are usually 6–9 sensilla in each group, while in *A. domesticus* there are commonly 11 in each group, although a range of 7–17 has been recorded. Running along the outer edge of the sclerotized bar in a lateral position on each side, from just below the tormae to almost the distal tip, is an irregular line of type 3 sensilla,
comprising group A₄. In both species the number in the group varies in the two sexes, the female consistently having fewer sensilla. In \textit{G. bimaculatus}, however, the sensilla differ from those found on the anterior surface of the labrum, they have the same shape and length but the socket is more pronounced and sometimes bears cuticular projections to protect the seta. Outside the A₄ group in both species very finely divided microtrichia are present. Spreading around the distal margin of the labrum from the notch is the dense marginal A₈ group of type 4 sensilla. In \textit{G. bimaculatus} most of the setae are directed towards the mid-line, while in \textit{A. domesticus} the outermost setae are directed outwards and the slightly smaller inner setae inwards, towards the mid-line. It is likely that they serve a purely mechanical function.

Finally, while in both species the notch itself is bordered by a double fringe of hairs with blunt tips, in \textit{G. bimaculatus} there are also some smaller hairs situated just behind this double fringe. The fringe of hairs presumably serves to prevent food particles falling from the pre-oral cavity.

\textit{Nervous innervation of the labrum}

The labral nerve "Lmn", which is motor and sensory, originates from the tritocerebrum of the brain. It bifurcates into two major branches "A" and "B", the bifurcation being more proximal in \textit{G. bimaculatus} than in \textit{A. domesticus} (Figs. 9a and b).

The distribution of the axons to the different types of sensilla and the shape and dimensions of the neurones are presented in Appendix I.

On the anterior surface towards the centre of the labrum, sensilla of types 1, 3, 7 and 13 (the latter only being present in \textit{A. domesticus}) are innervated by branch "A", while branch "B" innervates the type 1, 2 and 3 sensilla present on the more lateral areas of the labrum. Each sensillum is usually innervated by a single bipolar neurone, although some type 1 sensilla have been shown to be innervated by multiterminal neurones (Mn). In \textit{G. bimaculatus} at least 3 multiterminal neurones have been observed, each with triangular-shaped cell bodies (5—8 \textmu m in diameter) and 3 dendrites (9—17 \textmu m in length). In \textit{A. domesticus}, 2 multiterminal neurones have been identified, again with triangular-shaped cell bodies (3—6 \textmu m in diameter) and 3 dendrites, (8—16 \textmu m in length). As can be seen from Appendix I the shape and dimensions of the rest of the neurones supplying the sensilla on the anterior surface are remarkably similar in both species.

The posterior surface of the labrum is also innervated by branches "A" and "B" in both species (Figs. 10, 11). Branch "A" passes to the central area where it supplies groups A₁ to A₄ in both species, as well as the brush border of the notch at the tip of the labrum. Branch "B" ramifies the periphery of the labrum to supply groups A₇, A₈, A₁₀ and A₁₁. Only in the supply to group A₉ is there any difference in the innervation between the species; in \textit{G. bimaculatus} the type 8 sensilla of group A₉ are supplied by branch "A" while in \textit{A. domesticus}, the sensilla are type 10 and are supplied by branch "B". However, this difference is probably due to the different position that the A₉ group occupies on the labrum in the 2 species. With 1 or 2 exceptions, the shape and dimensions of the neurones are again quite similar in both species (Appendix I), but they are usually somewhat larger in \textit{G. bimaculatus} than they are in \textit{A. domesticus}. Finally, in both species, a number of stretch receptors are present towards the edge of the posterior surface of the labrum. These appear to penetrate the soft transparent cuticle and may provide an independent source of information on distortion of the labrum.
Development of the adult complement of sensilla in *A. domesticus*

The number of nympha1 instars in *A. domesticus* is known to vary from 11 to 13 (Rummel, 1963; Ragge, 1965). The number of immature instars in the culture used in the present study was found to be 11. Table 4 gives the numerical abundance of each sensilla type for both labral surfaces of each instar, while Table 5 summarises the number of sensilla present in each of the groups (A₁ - A₁₁) on the posterior surface of the labrum. Figure 12 illustrates the stages of development of the sensilla in the 1st, 5th and 8th instars.

On the anterior surface of the labrum of the 1st instar, sensilla of types 1, 2 and 13 occur. Of the 10 type 1 sensilla, 6 are arranged in 2 rows in the middle of the labrum, thereby closely resembling the condition found in the adult. By the 3rd instar this type has attained the number found in the adult. The rudiments of the 4 type 13 sensilla present in the adult are apparent in the 1st instar, but are only fully developed in the 5th instar. Eight type 2 sensilla are present in the 1st and 2nd instars and are widely scattered in the area.
lateral to the type 1 sensilla. These increase in number in the 3rd instar and continue to do so until the adult complement of 24 is reached in the 8th instar. As the number increases, this type of sensillum spreads to the lateral margins of the labrum. The most widespread type in the adult, type 3, is absent from the anterior surface of the 1st instar. After the 2nd instar the type 3 sensilla generally increase at each ecdysis by 10 or more, although a far more striking increase occurs at the moult into the 5th instar, where the number increases from 16 to 70, and also at the moult into the 7th instar when the number reaches 182. A similar picture is seen in the type 7 sensilla but the increase in number is more gradual.

It is on the posterior surface of the labrum that the discrete groups of sensilla are seen in the adult (Fig. 12). Even in the 1st instar the vestiges of all 11 groups (A₁, A₂,...) occur. In most groups, there is a gradual increase in the number of sensilla throughout development (Table 5). Group A₃ is centrally positioned and distal to the intertorma, and is the only group where the number of sensilla remains constant. Groups A₄, A₅, and A₆ have only a relatively small number of sensilla in the adult and this is reached by a steady increase in

Fig. 10. Semischematic representation of nervous innervation of posterior surface of labrum of G. bimaculatus, showing sensilla innervated by sub-branches "A" and "B". Arrow marks direction of infusion of labral nerve with nickel chloride.
Comparison of the Distribution and Nervous Innervation of Sensilla

### TABLE 4. ABUNDANCE OF SENSILLA TYPES ON THE TWO SURFACES OF THE LABRUM OF ALL INSTARS IN *A. domesticus*

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Values are means expressed to the nearest whole number. Number of specimens given in Table 5.

### TABLE 5. NUMBER OF SENSILLA IN GROUPS ON THE POSTERIOR SURFACE OF THE LABRUM OF ALL INSTARS OF *A. domesticus*

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Values are means for right side expressed to nearest whole number.

Each instar, although a more marked increase in the number of sensilla in group A₁ occurs at the moults into the 2nd and 8th instars. A more dramatic increase occurs in group A₄, and to a lesser extent in group A₁₁, at the moult to the 8th instar. Group A₄ is composed of
a fairly consistent number of sensilla up to the 9th instar when an increase occurs. Group A₁ is represented by a single sensillum in the 1st instar and it is not until the 4th instar that any marked increase occurs. The number of sensilla in group A₁₀ increases rapidly in the early instars, while in group A₁₁, the greatest increases occur at the moults to the 6th and 8th instars.

The posterior surface of the labrum is devoid of sensilla of types 1, 2 and 13 (5, 11 and 12 are totally absent from the labrum (Kubra, 1978)). The number of type 8 sensilla may remain constant throughout development, but sometimes an additional sensillum is added in the 9th instar. Type 3 sensilla increase in number gradually from the 1st to the last instar, while type 4 sensilla increase in number more erratically, the greatest increases occurring in 4th, 6th and 8th instars. Type 6 sensilla are present in group A₁ only and their development has already been described. Type 10 sensilla display a steady increase in number throughout postembryonic development. The number of type 9 sensilla slowly increases from the 1st to the 9th instar after which no further increase occurs.
It is interesting to note that the different types of sensilla display a range of developmental patterns, some not increasing in number at all (e.g. type 13) others increase steadily (types 2, 6, 7, 8 and 10) and others with more abrupt changes in the number of sensilla (types 3 and 4).

*Comparison with other insects*

*The sensilla.* According to Slifer (1970) the classification of sensilla may be based on the thickness of the sensillum cuticle. In this study however, a scheme based on the shape of the sensillum has been used. A similar scheme was adopted by Thomas (1966) and Kubra (1978).

Articulated sensory hairs, known as trichoid sensilla, are excited by the mechanical deformation of some part of the receptor (Dethier, 1963; McIver, 1975). Types 1, 2 and 4 sensilla in *G. bimaculatus* and *A. domesticus* are mechanoreceptors and are innervated by a single neurone. Type 3 sensilla probably play a role in mechanoreception and the
number of neurones innervating these sensilla varies from 1 – 3 depending upon their position. Trichoid sensilla of type 2 are sometimes grouped together to form hair plates. Similar hairs are found at certain joints in cockroaches and these have a slow rate of adaptation, according to Pringle (1938). In *S. gregaria* Thomas (1966) describes the type 2 and 3 sensilla as sensory pegs and Slifer (1956) found them on almost all parts of the body that came into contact with the external environment.

Sensilla of type 1 appear to have one neurone and seem to be the same as the ‘Type III’ of Blaney and Chapman (1969b) and of Cook (1977). It is possible that in *G. bimaculatus* and *A. domesticus* some of the long setae of type 1 present on the labrum may respond to vibrations of the substrate. In these species, as in other insects studied, it is evident that setae are innervated by a single neurone. These hairs may bear cuticular sculpturings such as grooves or spicules, while the sockets sometimes bear inwardly projecting ribs or diaphragms. Bernays et al. (1976) also report the presence of longitudinally grooved trichoid sensilla on the outer dorsal surfaces of the 1st instar nymph of *S. gregaria*.

The campaniform sensilla are referred to as type 6 in *G. bimaculatus* and *A. domesticus* and are innervated by a single neurone. The shape of such sensilla has been described by a number of authors as semi-spherical (Ismail, 1962; Schneider and Kaissling, 1957), and these authors suggest their function to be proprioception. McIver (1975) describes similar sensilla in other arthropods and again suggests a proprioceptive function for them. Their position in the 2 gryllid species studied here would also support this view.

Of the chemoreceptors, type 7 are probably olfactory in function. They appear as thin, oval or elliptical plates of cuticle and are present mostly on the anterior surface of the labrum. There are a variety of contact chemoreceptors, e.g. sensilla trichoidea, basiconica and coeloconica. Typically, insect contact receptors possess 4 or 5 neurones, although 6 have been reported by Blaney and Chapman (1969a) in *S. gregaria*. Trichoid sensilla of type 3, present in *G. bimaculatus* and *A. domesticus*, are likely to serve, at least in part, as gustatory sensilla. However, it has been reported in many insects that sensilla of type 3 may have an olfactory function (Jefferson et al., 1970). Le Berre et al. (1967) recognized two types in this situation, one with a blunt end and an opening and the other with a pointed end and no pore. The latter type may serve as mechanoreceptors.

In *G. bimaculatus* and *A. domesticus* the sensilla basiconica are represented by type 9, present on the posterior surface of the labrum. These are comparable to the sensilla basiconica of Dethier (1955), which respond to various chemical stimuli. Dethier has shown that the intensity of the response varies according to the nature of the chemical stimuli. The importance of these sensilla in feeding has been demonstrated in lepidopteran larvae by Schoonhoven (1969).

Type 13 sensilla of *A. domesticus* are comparable to the sensilla ampullacea or sensory flasks reported by a number of authors (Barbier, 1961; Rościsiewska and Fudalewicz-Niemczyk, 1974; Urvoy et al., 1978). They are innervated by a single neurone and it may be suggested that they act as mechanoreceptors. Boo and McIver (1975) found sensilla ampullacea on the antennae of *Aedes stephensi* and *Aedes aegypti* (L.), these have an elliptical-shaped chamber. However, these are innervated by 3 neurones and are thought to have a role in thermoreception.

*Nervous innervation.* This is a seriously underworked area and there are therefore few comparisons to be made with other insects. It is encouraging that the general organisation
Comparison of the Distribution and Nervous Innervation of Sensilla

of the nervous supply to the labrum of final instar *A. domesticus* illustrated by Urvoy et al. (1978) bears a close relationship to the more detailed description of the adult given here.

The only other reports on the innervation of the labrum in Orthoptera are those on *Locusta migratoria* (Mordue, 1975) and *Schistocerca gregaria* (Louveaux, 1972), although detail is lacking in the former. In both of these insects each labral nerve bifurcates above the tormae, one branch passing laterally and the other medially. Each branch supplies nerves to both the anterior and the posterior faces of the labrum. In this study it was shown that in *Gryllus bimaculatus* the median branch of the labral nerve, "A", supplies nerves to the median, long and short hairs (t₁, t₂ and t₃) and the pores (t₄) on the anterior surface. This branch supplies nerves to the same sensilla in *A. domesticus* but also to the ampullae (t₂₁). A similar distribution is seen in *Locusta migratoria* (Louveaux, 1972). The lateral branch also supplies nerves to types 1 and 2 and to the pores (t₁) in *A. domesticus* and *L. migratoria*, but only to the type 2 and type 7 sensilla in *G. bimaculatus*. Mordue (1975), makes no reference to the distribution of nerves to the anterior surface of the labrum in *L. migratoria*.

On the posterior surface in *A. domesticus* groups A₁ – A₆ are supplied by nerves from the median branch "A", of the labral nerve and groups A₇ – A₁₁ by the lateral branch "B". A similar distribution is seen in *G. bimaculatus* except that group A₆ is supplied by branch "A" and not branch "B". In *Locusta migratoria* (Louveaux, 1972), areas corresponding to A₁, A₂, A₃ and A₆ are supplied by the median branch "A" of the labral nerve and A₄ and A₅ by the lateral branch "B". A₈ appears to be supplied by both branches while A₄ and A₆ have no corresponding groups in *L. migratoria*. In *S. gregaria* (Mordue, 1975) only the innervation to areas A₁ and A₂ is stated with certainty and this is by the median branch "A".

Other authors have looked at the innervation of the labrum in other insect orders: Albert (1980) in a lepidopteran, *Choristoneura fumiferana*; Barbier (1961) in a trichopteran, *Limnephilus rhombicus*; Petryszak (1975) in a dictyopteran, *Periplaneta americana*; Quennedey (1975) in an isopteran, *Schedorhinotermes minorpotorius* and Rościszewska (1981) in a coleopteran, *Cassida viridis*. All examined the innervation of the labrum to some extent or other while investigating the distribution of the various types of sensilla. It is interesting to note that only in the minor soldier castes of the termite *S. minorpotorius* is the innervation markedly different from the other insects studied. Here the main purpose of the labrum is to act as a weapon of chemical defence, while in all other cases it seems that the labrum and its sensilla are mainly concerned with the reception of different chemical stimuli.

*Development of the adult complement of sensilla.* Apart from studies of single immature instars (e.g. Urvoy et al., 1978), to the authors knowledge there are no comparable studies in which the quantitative development of sensilla types is followed throughout development. Obviously this is an area for further investigation. Particularly rewarding may be the confirmation of the "allometric" trends in the numbers of certain sensilla types. One might speculate that sudden, abrupt changes may be associated with dietary or behavioural events during nymphal development.

**REFERENCES**


Comparison of the Distribution and Nervous Innervation of Sensilla


APPENDIX I

Nervous innervation of the sensilla of the labrum in G. bimaculatus and A. domesticus

<table>
<thead>
<tr>
<th>Group</th>
<th>Sensilla</th>
<th>Species</th>
<th>Innervation</th>
<th>Cell body shape</th>
<th>Cell body diam. (μm)</th>
<th>Dendrite shape</th>
<th>Dendrite length (μm)</th>
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<tr>
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<td>Type 1</td>
<td><em>G. bimaculatus</em></td>
<td>A, B</td>
<td>Round</td>
<td>7 – 10</td>
<td>Straight</td>
<td>8 – 11</td>
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<tr>
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<td></td>
<td><em>A. domesticus</em></td>
<td>A, B</td>
<td>Round</td>
<td>6 – 8</td>
<td>Straight</td>
<td>7 – 10</td>
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<td>B</td>
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<td>6 – 8</td>
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<td>6 – 9</td>
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<tr>
<td></td>
<td></td>
<td><em>A. domesticus</em></td>
<td>A, B</td>
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</tr>
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<td>6 – 9</td>
<td>Straight</td>
<td>9 – 11</td>
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<tr>
<td></td>
<td></td>
<td><em>A. domesticus</em></td>
<td>A</td>
<td>Oblong</td>
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<td>Straight</td>
<td>5 – 11</td>
</tr>
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<td></td>
<td>Type 13</td>
<td>—</td>
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T. CARLINE, K. KURA, V. K. BROWN and R. BECK
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<th>Species</th>
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<th>Cell body shape</th>
<th>Cell body diam. (µm)</th>
<th>Dendrite shape</th>
<th>Dendrite length (µm)</th>
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<td>Type 10</td>
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<td>Round</td>
<td>7 - 10</td>
<td>Straight</td>
<td>4 - 7</td>
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<tr>
<td></td>
<td></td>
<td><em>A. domesticus</em></td>
<td>A</td>
<td>Round</td>
<td>4 - 6</td>
<td>Curved</td>
<td>3 - 5</td>
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<tr>
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<td>Round</td>
<td>8 - 10</td>
<td>Straight</td>
<td>4 - 8</td>
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<td><em>A. domesticus</em></td>
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<td>4 - 6</td>
<td>Curved</td>
<td>3 - 6</td>
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<tr>
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<td>3 - 7</td>
<td>Straight</td>
<td>3 - 5</td>
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<td>3 - 5</td>
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<td>Straight</td>
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