Some Observations on the Endocrine Systems in the Embryos of the Gregarious And Solitary Phases of Schistocerca Gregaria (Forsk.) (Orthoptera: Acrididae) I - The Ventral Head Glands

by

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Some Observations on the Endocrine Systems in the Embryos of the Gregarious And Solitary Phases of Schistocerca Gregaria (Forsk.) (Orthoptera: Acrididae)
I - The Ventral Head Glands*

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(Received March 4, 1969)

The ventral head glands of the embryos of the gregarious and solitary phases of gregaria were examined histologically.

1. They originate as paired invaginations from the epidermis just anterior to and either side of the second maxillary segment in both phases just after revolution. They are located in a dorso-lateral position posterior to the dorsally situated primary head muscles and they curve downwards and backwards to a rejoin of the epidermis at a point opposite the sub-oesophageal ganglion.

2. The structure of the cytoplasm is syncytial and contains deeply staining nuclei of varying shape and size. It is supplied with tracheoles. At the active stage the nuclei become lobulated and increase their size, the cytoplasm shows vacuolation.

3. Two stages of periodic activity occur throughout the embryonic stages. The first maximum of activity in the ventral head glands coincide with retraction of the epidermis the cuticle. The second is at the formation of melanin.

4. The volume of the ventral head glands of the embryo of the solitary phase of S. gregaria seems smaller than those of the embryo of the gregarious phase. This suggests a relationship to their smaller body size more than to phase characters in the embryo.

5. Relationship of the ventral head glands to green pigmentation in the very early hatchlings is not clear.

* This researchwork was partly supported by a grant from the North Atlantic Treaty Organisation.
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INTRODUCTION

Since FUKUDA [10, 11] showed the importance of the prothoracic glands in the moulting and metamorphosis of Bombyx mori, the attention of many research workers was attracted to examining the endocrine centres of different insect groups.

In recent years, it has become increasingly evident that insect metamorphosis and some physiological processes (development, colour change etc.) and also behaviour, are under the control of a collection of factors generally suggested to be hormonal in character.

Something of the thoracic glands of insects has been known since 1762 at which date LYONET showed “granulated vessels” of a caterpillar’s thorax and described their innervation and tracheation. He did not mention anything about their function. This description was soon forgotten until TOYAMA [44], who described the “hypostigmatic gland” in a paper on the embryology of the silkworm in 1902, and suggested it to be a glandular organ from “the stucture of the nucleus”. The matter was again buried among literature on insect anatomy until the twentieth century.

Meanwhile the same organs were rediscovered and were being studied by various investigators. KE [23], used the term prothoracic glands for the first time. Variations in the name, such as prothoracic glands, thoracic glands, ventral head glands, tentorial glands have been used according to their location (in the thorax or head).

The evidence obtained from WILLIAMS’s studies (in Platsamia cecropia [46, 49] clearly showed that a brain factor released by the neurosecretory cells of the pars intercerebralis induces the thoracic glands to secrete their substances “moulting and metamorphosis hormone, ecdysone”. Since then various structures, the morphology of some of which has been known for a long time have been accepted to be homologous with the thoracic glands of Lepidoptera.

There are many papers about this subject, especially on the larval, nymphal and adult stages of insects but only a few on
the embryo [18, 19, 20]. Because of attention was directed towards the embryonic phase, JONES's experiments with the embryos of *Locusta pardalina* and *Lousha migratoria* are interesting and valuable.

According to ELLIS and CARLISLE [3, 4] the prothoracic gland of nymphs in isolated *S. gregaria* is larger than in crowded *S. gregaria* and is connected with colour change in the locust.

The main aim of this study is to see whether there is a difference in the ventral head glands of the embryos of the gregarious and solitary phases of *S. gregaria*.

**MATERIAL AND METHODS**

This paper is based on a study of the ventral head glands in the head of the embryos of gregarious and solitary phases of *S. gregaria* in order to compare the ventral head glands of both phases of embryos.

Some egg-pods of the gregarious phase of the insect laid on known dates were supplied by the Anti-Locust Research Centre, and sometimes adults, which were taken and permitted to oviposit in our laboratory. The egg-pods were collected daily. Thus, a series of eggs was obtained whose ages were known to within 24 hours.

The pods, in cups that contained sterilized sand, were kept at 32°C. in an incubator from the first day until they hatched. At 24 hour intervals, the eggs were dissected from the egg-pods. The sand grains were brushed off gently, the eggs washed in water, dried with filter paper and fixed, the younger eggs with hot alcoholic Bouin's fluid and the older eggs with Carnoy lebrun [33, 21].

A variety of fixatives was tried for the eggs. Of these, alcoholic Bouin for the early stages, and Carnoy acetic alcohol (formula No. 2 Carnoy lebrun) for the late stages, gave the best results [33]. In order to secure proper fixation it was necessary to puncture the eggs in several places (on the side which does
not contain the embryo) with a fine needle after placing them in the fixative.

Locust eggs, even from the same pod, tend to develop at different rates. For this reason, the outer brown coloured chorion of the eggs was removed in a dilute solution of sodium hypochlorite to expose the transparent serosal cuticle. After this, it was possible to observe the growing embryo in RINGER's solution and to determine its position and state of development.

The eggs which were fixed in Carnoy lebrun were treated as follows: they were washed in iodized alcohol, cut in half and the halves that contained the embryos were stored in 70 % alcohol until needed. The eggs which were fixed in alcoholic Bouin's fluid were treated in the same way but without washing in iodized alcohol [37].

The difficulty of sectioning the yolky locust eggs was accentuated by the presence of a thick and almost impermeable vitelline membrane [33]. Because of these difficulties, SLIFER's and KING's methods [37] were applied. The eggs or embryos which had been kept in 70 % alcohol were exposed for 24 hours to 4 percent phenol in 80 % alcohol, dehydrated in 95 % alcohol and cleared in different agents, such as aurlane oil, amyl acetate [7], methyl benzoate + 1 % celloidin (PETERFI's celloidin-Paraffin method) and were washed in chloroform, toluene or benzene respectively. They were then infiltrated with paraffin wax (52°C., 56°C.) in the usual way and blocked out. The paraffin wax trimmed away from the face of the block until the yolk was just exposed and then the block was soaked in water for 24 to 48 hours.

The essential features of this process consisted of the treatment with phenol ad soaking in water [37]. These two combined steps gave a perfect ribbon. The clearing agents methyl benzoate and methyl benzoate + 1 % celloidin were used most often and gave the best results.

The serial sections were cut from 5 to 8 μ thick. Different stains were used. These were MAYER's haemalum, HEIDENHAIN's azan [28], GOMORI's chrome haematoxylin Phloxin [6, 14, 16]. Aldehyde-fuchsin (The GOMORI's technique [15]
was modified by HALMI [16] and DAWSON [6] and simplified by CAMERON and STEELE[2]). In this paper CHP stands for GOMORI's chrome haematoxylin and AF for Aldehyde-fuchsin and MH for MAYER's haemalum and HA for HEIDENHAIN's azan.

In the embryo the first three types of stain gave approximately the same results for the ventral head gland.

The results obtained with HA and CHP were better but the method for MH was easier.

The very early hatchlings (less than 24 hours old) of both phases of S. gregaria were also fixed in Bouin's fluid or Carney lebrun. PETERFI's celloidin-paraffin method was applied [28] and the above stains used. A micrometer eye piece was used for measurement of the nuclear diameter. Photomicrographs of selected slides were taken, using a Reichert microscope.

OBSERVATIONS

The dated egg-pods of both phases were kept in tiny deep slender cups containing damp sand, in an incubator at 32°C.

The embryonic development of gregarious phase of S. gregaria usually lasted about 12 days, on the 13 th day the first hatchlings appeared. Most of them were black in colour, no green one having been seen, but a few green hatchlings less than 24 hours old were supplied by the Anti-Locust Research Centre.

The embryonic phase of solitary locusts lasted about 14 days and on the 15 th day the locusts hatched. Many of them were green in colour and only a few became black in the 24 hours.

It is well known that the rate of development of locust eggs is variable; even eggs from the same pod tend to develop at different rates. For this reason the stage of development of the embryo was observed directly after removing the chorion.

After treatment as explained above, serial sections were cut from 1 st day eggs and from every age taken at 24 hours intervals afterwards until hatching age and from the very young hatchlings (less than 24 hours old).

Serial sections prepared from each different age of the embryos and from the first hatchlings, were stained with four dif-
ferent stains (MH, HA stain CHP, AF). The first three stains gave good results, but none of them were outstanding.

The ventral head glands in the embryo in eggs laid by the gregarious parents appeared for the first time on the 5,5 th day, just after revolution (Katatrepsis). At this stage, the embryo filled about half of the egg. The formation of the eye-pigments had not yet begun. The embryo was connected with the yolky material by the back of its head.

The ventral head glands arose in paired form from the epidermis just anterior to and on either side of the second maxillary segment (Fig. 1. A). It was located in a dorso-lateral position posterior to the dorsally situated system of primary head muscles and extended backwards and downwards to approach the body wall joining with the sub-oesophageal ganglion and the muscles and epidermis in the same region. At this early stage, the glands tapered towards each end and were therefore largest at the middle. Each was surrounded by a thin connective tissue, which did not appear to penetrate the substance of the gland. The cytoplasm seemed syncytial and contained deeply staining nuclei, all of approximately the same size. Sometimes, it was possible to see the boundary of the cells. The nuclei were stained blue, darker blue and red, according to the stain used (MH, CHP and HA respectively). However, according to the kind of fixative, these colours become a little lighter or darker. In some parts of the cytoplasm granules of various sizes were detected (Fig. I B).

These could be seen with various stains e. g. blue violet with MH, blue or deep blue with CHP and violet-yellowish and reddish with HA. Sometimes, it was possible to see some branches of nerves and tracheoles extending to the ventral head glands, but once inside it they could not be traced. Sometimes, in some nuclei it was possible to distinguish a nucleolus. At this stage the diameter of circular nuclei was measured in 10 different specimens and the figures from at least 100 nuclei were averaged. The mean, max. and min. diameters of the nuclei at 24 hour age intervals are shown in table I.
On the 6th day: The embryo filled 4/5 of the egg and showed the beginning of the formation of eye pigment. At this stage, the nuclei of the ventral head gland became a little larger. The cytoplasm showed a little vacuolation. Mitosis was seldom seen in the nuclei.

On the 7th day: The embryo filled the egg. The pigmentation of the eye was developed. But the formation of melanin in the body had not begun yet. At this stage, the gland contained deeply staining nuclei of various shapes and sizes. The nuclei became much larger and some of them lobulated and the cytoplasm looked like a network, with vacuoles and granules.

These granules stained dark and light violet-bluish with CHP (these colours changed a little according to the fixative used) and reddish, yellowish and light violet with HA. These organs now tapered much more noticeably at both ends and were more curved towards the inside than before. In fact, they reached the sub-oesophageal ganglion. They also began to show some branching.

On the 8th day: At this stage the pigmentation of the eye increased, but the formation of body melanin had not yet begun. The nuclei of the ventral head gland became much smaller and the size difference was much clearer. Some nuclei seemed to have broken down and chromatin droplets could seldom be seen in the cytoplasm. In some places, the cytoplasm appeared vacuolar and contained granules.

On the 9th day: The formation of melanin began in the head region. But it was a very pale brown in colour. The nuclei of the ventral head glands became much larger with regard to 8 day embryos. Chromatin droplets were also seen. Although mitosis was not often observed, it had been seen mostly at this stage. (Fig. I C).

On the 10th day: The teeth of the mandibles and the head region were a pale brown colour. At this stage the nuclei of the ventral head glands were much more lobulated than before, and they reached their maximum size. The cytoplasm was much vacuolated, in some places looking like a network, and it also
contained many granules. Small tracheoles were also distinguishable inside the cytoplasm. (Fig. 1 D).

On the 11th day: The mandibular teeth of the embryo were brown in colour and the head region was light brown. The nuclei of the ventral head glands became smaller and showed some break down. Mitosis was seldom seen.

On the 12th day: The embryo was ready to hatch. The mandibular teeth, leg spines and head capsule were brown in colour, but there was no pigmentation on the thorax or the abdomen. At this stage the nuclei became smaller and the glands, especially near the tentorium, had the appearance of a rope of one or two rows of cell.

After 12th day: On the 13th day at 32°C, many eggs of the egg-pod hatched. 24 hours after hatching (melanin pigmentation had appeared on the whole body), the structure of the ventral head glands was examined. They were at the back of the head. Anteriorly, the pair of ventral head glands (at both sides) were connected to the dorso-lateral epidermis and muscles, then curved inwards and crossed downwards to join the sub-oesophageal ganglion, epidermis and muscles (Fig. 1 E).

In the hatchlings of the gregarious phase of *S. gregaria*, green pigmentation has not been met in our material, but a few very early green hatchlings were given by the Anti-Locust Research Centre.

In the black and green locusts, the mean, max. and min. diameters of the nuclei were measured and the figures were also given at the table I.

The same experiments were made on the embryo of the solitary parents phase of *S. gregaria*. The speed of embryological development was slower than that of the gregarious phase. They hatched on the 14th or 15th day. Most of them had green, but some of them had black pigmentation.

On the 5,5th day: None of the embryos had completed revolution although some were just beginning of it.
On the 6th day: Some of the embryos had just completed revolution and some of them were just before revolution. The embryos that had completed revolution were chosen and treated for this stage.

The ventral head glands were first met at this stage of the embryos. The structure and location of the ventral head glands in the solitary phase of S. gregaria were like those of the gregarious phase embryos. At 24 hour age intervals the diameters of the nuclei were measured and the mean diameter was calculated. After 7 days the shape and size of the nuclei were altering. For this reason circular nuclei were chosen for measurement. All measurements were taken from 7–10 specimens from every stage and from at least 100 nuclei, the averages being as follows (at the table 1).

**TABLE 1.**

Diameter of the nuclei in the embryos of the both phases of S. gregaria (FORSK.)

<table>
<thead>
<tr>
<th>Age of embryos (days)</th>
<th>Mean diameter</th>
<th>Max.</th>
<th>Min.</th>
<th>Age of embryos (days)</th>
<th>Mean diameter</th>
<th>Max.</th>
<th>Min.</th>
</tr>
</thead>
<tbody>
<tr>
<td>5 5</td>
<td>6.88</td>
<td>8.75</td>
<td>3.75</td>
<td>6</td>
<td>5.39</td>
<td>7.50</td>
<td>3.75</td>
</tr>
<tr>
<td>6</td>
<td>7.38</td>
<td>10</td>
<td>6.25</td>
<td>7</td>
<td>7.98</td>
<td>12.50</td>
<td>3.75</td>
</tr>
<tr>
<td>7</td>
<td>10.29</td>
<td>15</td>
<td>6.20</td>
<td>8</td>
<td>7.14</td>
<td>11.25</td>
<td>5</td>
</tr>
<tr>
<td>8</td>
<td>8.97</td>
<td>15</td>
<td>5</td>
<td>9</td>
<td>7.08</td>
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<td>3.75</td>
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<td>9</td>
<td>9.10</td>
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<td>5</td>
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<td>10</td>
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<td>5</td>
<td>13</td>
<td>8.01</td>
<td>15</td>
<td>5</td>
</tr>
<tr>
<td>24 hours after hatching</td>
<td>8.32</td>
<td>12.50</td>
<td>5</td>
<td>24 hours after hatching</td>
<td>8.41</td>
<td>13.75</td>
<td>3.75</td>
</tr>
<tr>
<td>Green</td>
<td>10.91</td>
<td>17.50</td>
<td>5</td>
<td>Black</td>
<td>8.50</td>
<td>12.50</td>
<td>5</td>
</tr>
</tbody>
</table>

Variations in the size of the nuclei of both phases were shown in the graphs as follows:

If graph I is examined, two cyclic activations of the ventral head glands can be seen easily for both phases. The activation of the ventral head glands can be judged by the increase
in size of the nuclei, their lobulated shape and much more deeply staining cytoplasm [45, 19, 20, 39].

In the embryos of gregarious and solitary phases of S. gregaria, the first peak in size of the ventral head glands, coincided with the 7th day embryos. On this day, the epidermis was retracted from the cuticle. Jones has suggested that in locust embryos these glands are exclusively concerned with the retraction of the epidermis from the cuticle [19].

The second peak in the embryos of the gregarious phase of S. gregaria was coincident with the 10th day. The formation of melanin first began as a very pale brown in colour in the head region of the gregarious phase embryos on the 9th day. On the 10th day this colour became much darker in the head region.
I have never seen the spreading of melanin pigmentation over the abdomen of the embryo as in Locusta migratoria and Parda\-lia. In the gregarious phase this pale pigmentation over the head appeared to be connected with the activation of the ventral head glands. This also agreed with Jones's paper [20], (The amount of melanin deposited appears to be correlated

Graph 2: Max and min diameter of nuclei of v.h.g. of embryos and first hatchlings of S. gregaria gregarius
with the amount of development hormone released from the ventral head glands).

This second peak size in the embryo of the solitary phase of *S. gregaria* occurred in the 11th day embryos. (because of their much slower development process). After the second peak the nuclei of the ventral head glands became smaller before hatching.

Graph 3. Max and min. diameter of nuclei of v.h.g. of embryos and first hatchlings of *S. gregaria* solitary
The activation of the ventral head glands seemed to be cyclic in both phases, but according to the measurements of the nuclei of the ventral head glands in the embryos of the gregarious phase of *S. gregaria* were larger than those of the embryos of the solitary phase. It is clear that a gland which contains nuclei of great diameter has a large volume because of the number of nuclei and in both phases of the same species this should be constant. [WELLS [45]] showed that the number of nuclei in each thoracic gland is surprisingly constant, being about 300 in almost all the species examined in the same family, (*Hemiptera-Heteroptera*) the volume of the gland being greater in the larger insects by increase in the size of the individual nuclei.

In the 24 hour black hatchlings, the mean diameter of the nuclei was larger than that of the green hatchlings of the same age. But in the solitary phase this difference was not very marked according to colour. The mean diameter of the nuclei of the black appeared to be a little larger than that of the green, but from some of the green hatchlings measured, the nuclei were much larger than those of black specimens. This suggested that there was no direct relation between the ventral head glands and the green colour. STAAL [38] also suggested the same conclusion about locusts.

**DISCUSSION**

Recent studies have demonstrated that the glands which are known as ventral glands or tentorial glands, pericardial glands, and prothoracic glands have an important role in the growth and moulting processes of metamorphosis in insects.

The possibility of a homology between these organs which have been described by different authors, has only been shown in a small number of insects such as *Thysanurans* [12], *Carausius morosus*, the larva of *F. auricularia* [29, 30, 31], *Forficula* [25], *Locusta migratoria*, [39, 40], *L. migratoria* [17], *L. migratoria* embryo [19, 20].

The thoracic glands (*Hemiptera - Heteroptera*) originate embryonically from the walls of the second maxillary segment as invaginations [45]. In many insects, the prothoracic glands
develop into two parts, one forming the ventral head glands with a final position in the head [Thysanurans [12], Forficula auricularia [25], Carausius morosus [28], L. migratoria [38]. L. pardalina and L. migratoria embryos [19, 20]) and the other the prothoracic glands proper with a final position in the prothorax (Leucophae-cockroach [35, 36], Lepidoptera [24], Platy- samia cecropia [46, 47, 48, 49], Silkworm [9, 10, 11], Hemiptera-heteroptera [45, 8], coleoptera [42, 43], Gryllides [34], Periplanata americana [1], Cockroach [5], Iphita limbata-hemiptera [27], L. migratoria [17], Rhodnius [50, 51].

It can be seen that the glands in the primitive groups tend to be in the head region, while in the more advanced groups, there is a tendency for them to be located more posteriorly.

The presence of a pair of ventral head glands in the locust embryos homologous with the thoracic glands was first determined in L. pardalina and L. migratoria by JONES [18, 19, 20]. He was the first to trace these organs after revolution and these embryos which had completed katatrepsis.

In also my experiments the ventral head glands were first detected just after revolution, and the embryo had attained only half the size of the egg. This pair of glandular organs originated as invaginations from the epidermis just in front of the second maxillary segment. But it is difficult to be certain of this fact i.e. in front of the second maxillary segment since at this stage in Schistocerca the mandibles and maxillae have already become pushed into the head. PFUGFELDER [29, 31] describes in carausis morasus their development from epidermal proliferations in the ventro-caudal part of the head, but that they soon separate from the epidermis and become bladder-like. JONES [19] suggests their origin as invaginations in the head region only of embryos of L. migratoria and L. pardalina.

The ventral head glands in S. gregaria are located in the posterior region of the head and are connected with the suboesophageal ganglion, epidermis and muscles at the ventro-caudal end and also joined to the muscles and epidermis at the dorso-anterior end. Their location in the embryos of L. pardalina and L. migratoria is the same. In the embryos of S.gregaria, these
organs appear to taper at each end before joining the epidermis and muscles. This fact is also the same in the embryos of *L. migratoria*, but in *L. pardalina* there does not seem to be any tapering at each end [19, 20]. The structure of the ventral head glands in *S. gregaria* was similar in the embryos of *L. migratoria* and *L. pardalina*. The cytoplasm was syncytial, and contained deeply staining nuclei of various shapes and sizes, according to the embryological stage. The activation of the ventral head glands can be understood by reference to the cyclic changes in the nuclei of the glands [45]. At the active stage, the nuclei of the ventral head glands became much larger and more lobulated on the 7th day and 10th day in the embryos of the gregarious phase of *S. gregaria* at 32°C.

The ventral head glands were surrounded by a thin connective tissue membrane, but this was untraceable inside the ventral head glands as in gryllides and *L. migratoria* [39]. On the contrary, in *Leucophaeae* [35], and *Bacillus rosii-Phasmidae* this membrane penetrates inside the ventral head glands.

In *Leucophaeae* its longitudinal axis is occupied by a trachea, several parallel fibres of striated muscle and a nerve derived from the prothoracic ganglion [35].

The ventral head glands in the embryo of *S. gregaria* may be situated very close to trachea. However some small tracheoles can be recognized in some sections of the older embryos. In *Rhodnius* [50, 51] in *Hemiptera-Heteroptera* [45], and in *Gryllides*, [34], the glands are well supplied by tracheoles. Connection of small nerves to the ventral head glands can be seen in the embryos of *S. gregaria*, but no nervous tissue can be detected inside it as in, *L. migratoria* [39], the embryos of *L. pardalina* and *L. migratoria* [19, 20], *Hemiptera* [45], *Gryllidae* [34], *Coleoptera* [42], and *Rodnius* [50, 51]. On the contrary, in *thysanurans* [11], *Lepidopterous*, [24, 47], cockroaches [35], and *Stenobothrus rufipes* [31], the glands are innervated.

Although the ventral head glands are distinctly paired in origin in most insects an exception is in the *gryllidae*, when they are completely fused to form one organ, as described by SEL-
LIER [34]. Though mitosis seemed seldom to occur, it was mostly seen in the 9th day embryos of *S. gregaria*. SELLIER [34] also described mitosis as occurring very infrequently in the last larval stages of Gryllides. But STRICH [39] described it at every nymphal stage of *L. migratoria* and determined the function of the ventral head gland according to the number of cells undergoing mitosis.

The ventral head glands of *S. gregaria* are ductless as in other insects.

The results of studying the ventral head glands in the embryos of *S. gregaria* (both gregarious and solitary phases) showed that there were two cyclic activation periods (graph 1). The first maximal activity was concerned with the retraction of the epidermis from the cuticle. The experiments of JONES [19], on the embryos of *L. pardalina* and in *L. migratoria* gave the same results. He also showed some relationships between the beginning of deposition of melanin and the ventral head glands by his ligaturing experiments [20]. The deposition of melanin in *Locusta* embryos began at the end of the abdomen and spread towards the anterior of the embryo. In the gregarious phase of *S. gregaria* embryos, deposition of melanin first took place, eye-disc excepted, in the head region (anterior) of the embryo. At this time on the 10th day, the nuclei of the ventral head glands reached their largest and most lobulated shape. This maximal point coincided with the deposition of melanin on the 10th day. JONES also claimed that in Locust embryos the deposition of melanin is initiated after the moult has taken place, and its gradual spread continues up till time the embryo is ready to emerge.

The ventral head glands, nuclei decreased in size after their second maximal active period and began to increase in size again after hatching.

CARLISLE and ELLIS [3, 4] suggested that the prothoracic glands may also have an influence on the phase characters in locusts. In nymphs newly emerged adults the prothoracic glands of isolated reared insects are larger than those of
crowded insects. The extirpation of the greater part of one of the pair of prothoracic glands in the fourth instar solitary nymphs leads to the assumption of a gregarious habit and the gregarious pattern of pigmentation. Finally, they stated that there were positive quantitative relations between the green colour of *Schistocerca* and the prothoracic glands. (I preferred to use the name of ventral head gland because of its location). But at the same symposium (1961) CARLISLE accepted that the pigmentation, the biometric ratios and behaviour were presumably affected by two or more hormones released from two or more endocrine organs. STRICH HALBWACHS [39, 40] did not find any direct effect on the differentiation of the adult structure and pigmentation with the implantation and extirpation experiments in *L. migratoria*. I also did not find any really direct relation between green colour and the ventral head glands in the solitary phase. But in the gregarious phase embryos and hatchlings there appeared to be some relation between melanin pigments and the ventral head glands. The function of the ventral head glands has apparently not been found to influence the determination of phase dimorphism. The ventral head glands exert no appreciable influence upon the pigmentation of Locusta larvae [38]. ALBRECHT found the decreasing number of nymphal instars to be connected with the gregarious status of the hatchlings [38]. And STAAL [38] states that in his experiments the development within fewer instars was a result of increased the ventral head gland activity. He compares this result with the greater volume of the ventral head gland in solitary nymphs of *Locusta* and *Schistocerca* observed by ELLIS and CARLISLE and presents an unexplained contradiction when it is indeed true that a greater volume of the ventral head gland means more secretion.

In my study of the solitary phase embryos of *S. gregaria*, the ventral head glands are much smaller than those of the gregarious phase. The embryos of the solitary phase and also the hatchlings were smaller than those of the gregarious phase. KENNEDY [22] also found with *Nomadacris* and *Schistocerca* that isolated parents produced offspring that were smaller at hatching than the offspring of crowded parents, grew more slowly, and more often underwent an additional moult as nymphs. My
result agrees with STAAL's [38], and WELLS's paper [45]. According to WELLS's description of the thoracic glands of *Hemiptera-Heteroptera*, the volume of the gland is made greater in the larger insects by an increase in the size of individual nuclei. The mean diameter of the nuclei of the ventral head glands of all the very youngest black hatchlings of both phases, is larger than that of the green hatchlings. But the difference is not very evident, especially in the solitary phase. Sometimes the max. diameter of the nuclei was found to be larger in the ventral head glands of individual solitary green specimens.

It is clear that there is no direct relation between the ventral head glands and green pigmentation. It is necessary to continue experiments and much more time is needed to get exact results. It might be true that the pigmentation, biometric ratios and behaviour are all affected by two or more hormones secreted by two or more endocrine organs.

ACKNOWLEDGMENTS

This research work was carried out at the Department of Zoology of the University of London (Queen Mary College).

I am much indebted to Prof. Dr. J. E. Smith for his generous hospitality, to Dr. J. Carthy for providing facilities and for reading the manuscript, and to Dr. D. B. Carlisle and Dr. P. E. Ellis from Anti-Locust Research Centre for proposing this subject and supplying materials and for helpful advice, and to all technicians of Queen Mary College for their kind help.

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ÖZET

Schistocerca gregaria (Forsk.) un greger ve soliter faz embriyolarında ventral baş bezlerinin yapısı tetkik edildi. Bu bezler embriyonyun yumurtanın posterior kutbu etrafında çökelşinden lemen sonra epidermisten, ikincisi maksiller segmentin her iki tarafından meydana gelir, ilkel baş kaslarının dorzalinden başlayarak içeriye ve geriye doğru uzanarak sub-oesophagus gangiliyonu ile birleşirler.

Bez sinisyal bir yapıdadır, koyu boyanan loplu nükleüsleri vardır. Sitoplazmada vakuoller görülür.

Her iki fazın embriyonik devreleri boyunca besin yapısında peryodik iki aktif devre görülür. Birincisi maksimum aktif devre embriyonik kutikulanın epidermisten ayrılmış, ikincisi de me'lanın pigmentinin teşekkülü ile aynı zamana rastlar.

Soliter faz embriyolarına ventral baş bezleri gregerlerden daha küçüktür. Bu küçük'lik faz karakterinden ziyade esasen daha küçük olan embriyo boyları ile ilgili görülür.
Fig. 1: Photomicrographs of sections of ventral head gland of embryos in *S. gregaria* (gregarious phase).

A-On the 5, 5th day. Fixed with alcoholic Bouin, stained MH. 8 x 10 x 3 = x 240.

B-On the 5, 5th day. The same treatment. 12, 5 x 63 x 3 = , x 2362.5

C-On the 8 th day. Mitose (telophase). Fixed carnoy lebrun, stained with MH. 12, 5 x 40 x 3 = x 1500

D-On the 10 th day. Fixed carnoy lebrun, stained with CHP 12, 5 x 40 x 3 = x 1500.

E-Connection of ventral head gland with sub-oesophageal ganglion fixed carnoy lebrun, stained with MH. 8 x 10 x 3 = 240

vhg-Ventral head gland, gr. granule, m-mitosis n-nucleus. sog-suboesophageal ganglion v-vacuole.
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