Selective breeding in parasite propagation


Variation and structure of the eyes in the desert locust, *Schistocerca gregaria* (Forskål)

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[Plates 13 to 15]

The compound eyes of the *solitaria* phase individuals of the desert locust, *Schistocerca gregaria* (Forskål), are vertically striped with mostly 6 and 7, rarely 5 and 8, dark brown stripes, and a number of cream-coloured interstripes. In phase *gregaria* the interstripes, which are more or less invaded by brown pigment, are partially or wholly masked, the eye in the latter case presenting an almost uniformly dark brown appearance.

The postembryonic development of the striped eyes, is described stage by stage. There is no stripe at the time of hatching. In the 6-striped eye one stripe is developed in the first-stage hopper and, subsequently a stripe is added at each of the five molts. In the 7-striped eye the one-moult-one-stripe relationship holds good in most stages, but the extra seventh stripe is produced in two ways: (i) By the addition of two stripes at the second moult (i.e. the third-stage hopper has four stripes instead of three); and (ii) by the interposition of an extra-moult, usually in the third stage and rarely in the fourth, during which a new stripe is added (stripe-positive extra-moult). But extra-moult does not necessarily lead to the addition of a stripe; stripe-neutral extra-molts are not infrequent.

The development of the dorsal spot and the subdorsal streak are described. The mechanism of growth and the homology and nomenclature of the stripes and interstripes are discussed.

The structure of the compound eyes and the pigments of stripe formation are described, and their effects on vision in *solitaria* and *gregaria* individuals discussed.

Vision is discussed on the basis of ommatidial structure and pigmentation. In *gregaria* eyes a perfect apposition image is formed, the image being sharply defined. An ‘anti-halation’ device, produced by the post-retinular layer of pigment, is present. The eye is suited for diurnal vision, and strong direct sunlight is not avoided. In *solitaria* eyes the image is of the apposition type in its mode of formation but of the superposition type in effect; it has been termed a ‘pseudo-superposition’ image, and is more diffuse but brighter than in *gregaria* eyes. The ‘anti-halation’ device is weak and ineffective. The eye is suited for vision in subdued light and perceives movements rather than sharp images. *Solitaria* individuals, especially hoppers, avoid strong, direct sunlight.

The effects of these differences in vision on the behaviour of *gregaria* and *solitaria*-phase individuals are as follows: the former, owing to mutual visual impact induced by the formation of sharp images, tend to be gregarious; and further, owing to the presence of light-absorbing mechanisms, they do not avoid strong sunlight; the latter, on the other hand, owing to the want or comparative ineffectiveness of the above-mentioned features, neither tend to congregate nor to go out boldly into the bright open.
In the desert locust, *Schistocerca gregaria* (Forskål), in both hoppers and adults, the compound eyes of *solitaria* phase individuals are vertically striped with brown to chocolate-coloured stripes and white or cream-coloured interstripes. In *gregaria* individuals, on the other hand, the interstripes are invaded to a greater or less extent by the dark brown pigment so that the stripes become either wholly or partially masked: the eye in the latter case presents an almost uniformly dark brown or chocolate-coloured appearance. Some years ago the writer (Roonwal 1936a) discovered two main types of *solitaria* adults in respect of eye-stripes—one 6- and another 7-striped.* Later (1937) he reported the rare occurrence of 8-striped adults; and Rao (1937) found some 5-striped ones. This variation has proved to be of great interest in many ways, both in the study of variations and in the study of fluctuations of locust populations (vide Roonwal 1936a–1946; Rao 1937–42; Rao & Gupta 1939; Volkonsky 1938a, b; and Mukerji & Batra 1938).

In the present paper are given, first, a complete description of the striped (*solitaria*) and unstriped (*gregaria*) eyes of *Schistocerca gregaria*, as an adequate description hitherto did not exist. Secondly, a detailed account of the postembryonic development of the stripes, first briefly reported by the author in 1937, is given. Thirdly, the microscopical structure of the eyes and the pigmentary basis of stripe-formation are described. Finally, the role of the differential distribution of the eye pigments in the vision of *gregaria*- and *solitaria*-phase individuals, and the resulting differences in behaviour in regard to gregarization and movements are discussed.

**Technique**

For the study of the postembryonic development of the eye-stripes, locusts obtained in nature in both *gregaria* (from swarms) and *solitaria* phases were bred in the laboratory under semi-natural conditions. Freshly hatched hoppers were reared singly in cylindrical wire gauze cages about 20 cm. long and 5 cm. in diameter, and the number of eye-stripes and dates of moulting noted by daily observations.

For the study of structure and pigmentation of eyes, hoppers reared in the laboratory at a temperature of approximately 30 ± 5° C were utilized. Individuals with *solitaria* (striped) and *gregaria* (unstriped or partially striped) eyes were obtained by isolated and crowded breeding respectively. Immediately previous to decapitation, the insect was kept in fairly strong, diffuse daylight for at least 2 or 3 hr., so that the eyes became fully daylight adapted. This procedure provided uniform material and precluded the possibility of confusion, should pigmentary migration take place in the eyes in dark or bright environments. After decapitation the head was fixed either in Carnoy’s fixative (formula no. 2) for 15 to 20 min.,

* Throughout this paper expressions like ‘6-striped eye’, ‘7-striped eye’, etc., have often been abbreviated to ‘6-striped’, etc.
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according to the stage of the hopper, or in hot alcoholic Bouin's fluid for 24 hr. Both fixatives, especially the former, gave good results. Immediately after dropping the head in the fixative, the air from the cephalic tracheae was removed by gently pressing the head with a pair of forceps until the greater part of the air was expelled and the head sank in the fixing fluid; care was taken not to distort the arrangement of the internal organs. Without this procedure good fixation is not ensured. The material was then dehydrated and sections 8 to 10\(\mu\) thick cut by the double-embedding (clove oil and celloidin) method. They were stained with either Delafield's or iron haematoxylin and counterstained with either eosin or orange G. For histological study of the various cell components of the eyes, sections were bleached in Grenacher's mixture before staining, as otherwise the structural details are obscured by the presence of the dark brown pigment granules in the cells. For the study of the pigment and its distribution, unbleached and unstained preparations were utilized. From the account of previous workers, specially Jörschke (1914) and Friza (1929), it would appear that both the reddish brown and greyish yellow eye pigments of Acridid eyes are not dissolved to any appreciable extent in the usual reagents employed for sectioning; no special methods were therefore employed beyond those already mentioned.

Description of striped (\textit{solitaria}) and unstriped (\textit{gregaria}) eyes

In addition to the two main types of eyes, viz. 6- and 7-striped, that Roonwal (1936a) found in \textit{solitaria}-phase individuals, Rao (1937) and Mukerji & Batra (1938) obtained in laboratory rearings some sixty full-winged and brachypterous 5-striped adults. The occasional appearance of 8-striped \textit{solitaria} individuals was also noted by Roonwal (1937, p. 151), and later by others, in the field as well as in laboratory rearings in India. Volkonsky (1938a, b) also recorded 5- and 8-striped individuals, in addition to the usual 6- and 7-striped ones, in field collections in North Africa.

An adequate description of the striped eyes of \textit{Schistocerca gregaria} does not exist. Such a description is, therefore, provided below; it is drawn from 6- and 7-striped individuals but applies equally well to 5- and 8-striped eyes.

The eye (figure 2) is oval and elongated dorso-ventrally. The anterior margin is almost straight, the posterior one markedly convex. The eye tapers slightly at the dorso-anterior angle which is rounded; no such tendency is seen at the lower or ventral edge of the eye.

The size of the eye is measured as follows: The length is measured as the longest vertical line from the upper to the lower margin of the eye, and the width as the longest horizontal line from the anterior to the posterior margin, the measurements being taken with an eyepiece micrometer under a binocular microscope. Measured thus, the average size of the eye in \textit{solitaria} individuals is about 3·6 \(\times\) 2·4 mm. in males and 4·4 \(\times\) 2·7 mm. in females.

The stripes (s.) consist of six or seven more or less thick streaks of deep reddish brown to chocolate-coloured pigment, running for the most part vertically from
the dorsal to the ventral margin of the eye. Stripe no. 1 (s.1)\(^*\) or the most posterior stripe is convex, with the upper and lower ends bending forwards, i.e. towards the anterior edge of the eye. In all others the middle portion runs straight and almost vertically, while the lower portion curves backwards, i.e. towards the posterior edge of the eye. As regards the upper portions, stripes no. 2 and 3 bend slightly forwards, no. 4 slightly backwards, while in the remaining stripes the upper portions bend distinctly backwards. Ventrally, the stripes reach up to the margin of the eye and do not converge appreciably towards one another. Dorsally, however, they converge towards the dorsal spot (vide infra) and do not reach the margin of

![Diagram of the compound eye of Schistocerca gregaria phase gregaria, showing the extent of dark brown pigmentation. The stripes are clear in some individuals, and either faintly distinguishable or not at all in others. Semi-diagrammatic. \(\times 15\).](http://rspb.royalsocietypublishing.org/)

Lettering for figures 1-4: Ant. anterior side; at. anterior margin of eye; d. dorsal spot; Dor. dorsal side; is.\(^{1-6}\), interstripes no. 1-8; os. ocular sclerite; Post. posterior side; ps. posterior pigment streak; pt. posterior margin of eye; s.\(^{1-7}\), stripes no. 1-7; sd. subdorsal streak; Vent. ventral side.

The stripes which have serrated margins, vary in thickness in different individuals, but, generally, stripes no. 1 and 2 are thicker than the rest. Each stripe is, as a rule, widest in the middle and becomes slightly narrower at the two ends. This feature is especially marked in stripe no. 1. Stripes never form the margin of the eye.

The interstripes (is.) are white or cream-coloured areas lying in between the adjacent stripes. The first and the last interstripes are exceptional in being bounded

* For nomenclature of stripes and interstripes, see p. 258.
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by a stripe on one side only. The interstripes always number one more than the stripes, so that there are seven or eight interstripes according as the number of stripes in an eye is either six or seven. As in the stripes, the width of the interstripes varies, and generally depends on the width of the former. Sometimes two adjacent stripes are so wide as to obliterate the intervening interstripe. Interstripe no. 2 (is.²) is generally the widest of all and forms a sort of landmark in the eye; no. 1 (is.¹), or the most posterior interstripe, comes next in order of thickness. The most posterior and the most anterior interstripes are widest in the middle and taper at the two ends; the latter is narrower in 7-striped than in 6-striped eyes.

![Diagram of eye structures](image)

**Figure 2a, b.** Side views of the right compound eyes of *Schistocerca gregaria* phase *solitaria*, showing the 6- and 7-striped conditions. Semi-diagrammatic. x about 18. (a) 6-striped eye of ♀; (b) 7-striped eye of ♂.

The interstripes of *gregaria*-phase individuals are invaded to a greater or less extent by the brown pigment of the stripes, so that the latter are often not clearly distinguishable except under strong illumination, and sometimes are even impossible to discern, the eye being more or less uniformly dark brown to chocolate- or claret-coloured (figure 1). In *solitaria* individuals taken from nature, on the other hand, the interstripes are, as a rule, not invaded by the brown pigment except in rare cases when some of the interstripes, especially the posterior ones, are invaded by irregular patches. Generally they are pure cream, the posterior ones sometimes being bluish; in some cases all the interstripes are grey-blue, bluish, pale or lemon-yellow, or a combination of these colours.
Along the posterior margin of the eye there is a thin streak of deep brown pigment extending from the dorsal spot to the ventral end of the eye. It is not a true stripe from which it differs in appearance as well as in the mode of development. It may be termed the posterior pigment streak (ps.).

At the dorsal end of the eye, nearer the posterior than the anterior side, there is a small, dark, chocolate-coloured area shaped somewhat like the head of a hammer, with the base pointing towards the anterior side and the narrower end towards the posterior. This is the dorsal spot (d.) (Roonwal 1936a).

All the stripes and interstripes converge towards the dorsal spot without actually touching it, a thin cream or yellow streak, the subdorsal streak (sd.), being left in between. Sometimes this streak is irregular or broken owing to some of the stripes reaching up to the lower edge of the dorsal spot.

When the interstripes are coloured other than cream, the wide interstripe no. 2 is always the palest. Under experimental conditions when the interstripes acquire the brown pigment owing to one cause or another, no. 2 is the last one to do so; no. 1 is, as a rule, the deepest coloured and is the first to acquire the brown pigment. Even in eyes in which other interstripes are pure cream without any trace of brown, no. 1 shows a few brown spots, especially towards the posterior margin; or, it may be grey-blue, while others show no trace of such pigment.

Postembryonic development of eye-stripes and associated structures

(1) Development of eye-stripes, dorsal spot, etc.

(a) Eye-stripes

Roonwal (1937, pp. 25–26 and 150–151) first elucidated the development of eye-stripes by rearing individual hoppers in isolation cages. He found that a freshly hatched first-stage hopper has no stripe, but develops one a few days later (figure 3a–c). Subsequently, one stripe is generally added at each of the five molts in 6-striped individuals (figure 3). In 7-striped individuals, however, in some cases two stripes instead of one are added at the second molt, i.e. in the third instar; in others the extra-stripe results from an extra-moult in the third and fourth instars. Thus, the 7-striped condition is produced in two ways. In several instances an extra-moult did not lead to the addition of a stripe.

Other workers who soon followed (Volkonsky 1938a, b; Mukerji & Batra 1938) confirmed in the main these observations, but maintained that the extra-stripe of the 7-striped eye resulted only from an extra-moult, and there is always a perfect correlation between the number of stripes and the number of molts. However, further work has shown, as discussed below, that this is by no means the case and that the extra-stripe is in fact produced in two ways. The development of stripes will now be described stage by stage, in 6- and 7-striped eyes, and then the limited extent of correlation between extra-stripes and extra-moults will be discussed.
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(a)–(g): posterior ← → anterior  (h)–(l): anterior ← → posterior

Figure 3. a–l. Postembryonic development of stripes and interstripes in 6-striped eye of *Schistocerca gregaria* in hoppers reared individually. Semi-diagrammatic. (a)–(g), × 15; (h)–(l), × 34. (a) Side-view of right eye of freshly hatched (3 hr. old) first-stage male hopper. The dorsal spot is clear, but there is no trace of a stripe. (b) Ditto, of same hopper a week later. Note the stripe which is in process of formation in the dorsal half of the eye. (c) Ditto, of same hopper about 2 weeks after hatching. The stripe is completely formed. (d) Side-view of right eye of a recently moulted second-stage male hopper, showing two stripes. (e) Ditto, of a third-stage male hopper, showing three stripes. (f) Ditto, of a fourth-stage male hopper, showing four stripes. Note the posterior pigment streak which first arises in this stage. (g) Ditto, of a fifth-stage female hopper, showing five stripes. (h) Dorso-lateral view of a portion of left eye of first-stage male hopper (same as in figure 3b) 1 week after hatching. Note specially the dorsal spot and the subdorsal streak. (i) Ditto, of a recently moulted second-stage female hopper. (j) Ditto, of a third-stage male hopper. (k) Ditto, of a fourth-stage male hopper. (l) Ditto, of a fifth-stage female hopper.
First stage (figure 3a, b, c and h). The eye of a freshly hatched green hopper (about 3 hr. after hatching) is completely devoid of brown pigment, except for the presence of the chocolate-coloured dorsal spot (d.); it is pale green and there is, as a rule, no stripe. In a few cases, however, a small, median, light brown stripe is found in the dorsal half of the eye below the dorsal spot (but always some distance from the latter, thus leaving in between the two a narrow line, the subdorsal streak (sd.)) and reaching only a short distance downward. In the majority of cases the first appearance of the stripe is delayed for a number of days after hatching. The stripe first makes its appearance in the dorsal part of the eye and gradually grows downward until it reaches the lower end, the whole process requiring some days. When this is complete (figure 3c), the stripe divides the eye into two interstripes, a posterior and an anterior or interstripes no. 1 and 2 respectively. The first stripe differs in its mode of development from all the rest; the latter, as shown below, make their first appearance at the anterior margin of the eye.

Some time before the hopper is due to moult into the second stage, there appears at the anterior margin of the eye a faint brown stripe (complete from the dorsal to the ventral end of the eye, but still below the surface, as it were) which gradually shifts backwards (posteriorward) and, at the same time, becomes better defined. It represents the stripe of the second-stage hopper and may thus, in so far as the first stage is concerned, be called a 'pseudo-stripe' which is to be distinguished from the 'true' stripe or stripes belonging to a particular stage. This mode of stripe formation applies to all the subsequent instars. A pseudo-stripe is liable to be mistaken for a true stripe; it becomes a true stripe only in the next stage.

Second stage (figure 3d, i). There are two stripes and three interstripes. The third interstripe as, indeed, all those that follow, is formed not by a subdivision of a pre-existing unpigmented area, but as a new formation which appears at the anterior margin of the eye and shifts backwards. The stripes are brown, and the interstripes transparent cream with a greenish tinge. In some hoppers caught in nature the two stripes are so faint as to be hardly discernible; the interstripes are cream with a greenish tinge; the dorsal spot, however, is deep chocolate as in normal hoppers.

In the later part of the second stage one or two faint, narrow pseudo-stripes appear at the anterior margin of the eye. They shift backwards in the same way as in the first stage.

Third stage (figure 3e, j and figure 4a, d). There are three or four stripes and four or five interstripes. In 6-striped individuals only one stripe is added (figure 3e). In 7-striped individuals, on the other hand, either two stripes are added simultaneously (figure 4a); or, there is an extra-moult (giving an extra-third stage), one stripe being added at each moult. The third stage is, therefore, exceptional. Interstripe no. 2 is now the widest of all, and remains so in subsequent stages. The posterior interstripe (no. 1) is narrower than interstripe no. 2 but is broader than all others. The stripes are deep brown, and the interstripes cream; this condition is maintained in subsequent stages.
Fourth stage (figure 3f, k and figure 4b, c). One more stripe is added in this stage, the number now being four or five depending on whether their number in the previous stage was three or four. The interstripes number five or six. Stripe no. 1 is now the widest. The posterior pigment streak first develops in this stage as a thin streak of brown pigment extending all along the posterior margin of the eye from the upper to the lower tips of stripe no. 1. It is not a distinctive stripe, being distinguishable from the latter in its mode of development—at the posterior instead of at the anterior margin of the eye.
Fifth stage (figure 3g, l and figure 4c, f). One more stripe is now added, bringing the total to five or six; the interstripes number six or seven. Stripe no. 1 is no longer broader than the others. The posterior pigment streak is more prominent than in the last stage and extends to the lower margin of the eye nearly up to the second stripe from the anterior side.

Adult (figure 2a, b). One more stripe is now added, bringing the total to six or seven; the interstripes number seven or eight. As a rule, no further increase occurs. Frequently, the stripe added in this stage is visible only faintly at the time of eclosion and becomes clear and well-defined some days after.

Discussion. Volkonsky (1938a, b) and Mukerji & Batra (1938), while confirming in the main my earlier (1937) account of the development of stripes, maintained that there is always a perfect correlation between the number of stripes and the number of moults; the 7-striped condition is produced only as a result of an extra-moult, and, similarly, 5- and 8-striped eyes are believed to result only from a 4- and 7-moult development. While the one-moult-one-stripe rule, in the majority of cases, was already evident in my earlier observations, further work has confirmed the exceptions mentioned by me. Out of 215 isolated hoppers reared by me, 43 or 20% underwent one or more extra-moults (table 1). The exact nature of the relationship between eye-stripes and extra-mouling is as follows:

Table 1. Analysis of extra-mouling and eye-stripes in Schistocerca gregaria

<table>
<thead>
<tr>
<th>stages in which extra-moults occurred</th>
<th>number of extra-moults</th>
<th>total number of examples, and sex</th>
<th>number of examples with 6, 7 and 8 eye-stripes</th>
<th>remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>III</td>
<td>1</td>
<td>37</td>
<td>1♀</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(6♂♂, 31♀♀)</td>
<td>(6♂♂, 29♀♀)</td>
<td></td>
</tr>
<tr>
<td>IV</td>
<td>1</td>
<td>2♀♀</td>
<td>1♀</td>
<td>1♀</td>
</tr>
<tr>
<td>III, IV</td>
<td>2</td>
<td>3♀♀</td>
<td>—</td>
<td>1♀</td>
</tr>
<tr>
<td>(1 in III, 1 in IV)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>II, IV</td>
<td>2</td>
<td>1♀</td>
<td>—</td>
<td>1♀</td>
</tr>
<tr>
<td>(1 in II, 1 in IV)</td>
<td></td>
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</tbody>
</table>

(i) Extra-mouling does not necessarily lead to the addition of a stripe. In case of addition, only one stripe is added as a result of such moult. An extra-moult in which a stripe is added may be termed 'stripe-positive'; that in which no stripe is added, 'stripe-neutral'. Both stripe-positive and stripe-neutral extra-moults sometimes occur in the same hopper. Thus, the contention of some authors that an individual with $n$ moults must always present $n + 1$ stripes is not true.
(ii) Extra-moult ing generally does not occur in 6-striped individuals, and all the five moult s are stripe-positive. In two exceptions (table 1) the extra-moult s were stripe-neutral.

(iii) Extra-moult ing generally occurs only in 7-striped (and 8-striped) individuals, but the reverse is not true. In other words, all 7-striped individuals do not extra-moult. Stripe-neutral extra-moult s also occasionally occur.

(iv) The 7-striped eye is produced in two ways: (a) In some by the addition of two stripes instead of one at the second moult,* there being no extra-moult. (b) In others by the occurrence of a stripe-positive extra-moult usually in the third stage, rarely in the fourth. Out of 215 isolated rearings, fifty-one were 7-striped, the remainder mostly 6-striped. The extra-stripe in the former was produced by an extra-moult in thirty-eight (75 %) individuals, and without an extra-moult in the remaining thirteen (25 %).

(v) Indirect evidence from two independent sources provides striking confirmation of this dual mode of origin of the extra-stripe. The evidence is: (a) From the relative proportion of 6- and 7-striped individuals, it is known that 7-striped individuals constitute about 30 to 70 % (average about 49 %) of a mixed solitaria population in the field, the remainder being 6-striped (Roonwal 1936 a, 1945 a; Volkonsky 1938 a, b; Rao 1942). Thus, if all 7-striped individuals resulted from an extra-moult, at least 30 %, probably more, of a mixed 6- and 7-striped population must undergo a stripe-positive extra-moult. Actual isolated rearings of 215 mixed cases, however, gave only forty-three (20 %) extra-moultings; of these, thirty-eight (18 %) were 7-striped, and the remainder 6- and 8-striped. This small percentage (18 %) accounts for only about one-half or less of the total expected proportion (30 % or more) of 7-striped individuals; those not thus accounted for evidently belong to the alternative category. (b) From sex-ratios in 7-striped individuals: In 7-striped individuals the sex-ratio varies with the mode of development (whether with or without an extra-moult) of the additional stripe, as is evident from rearings (tables 1, 2). In extra-moult ing individuals, females are more common than males; in thirty-eight examples the sexes were: 6 ♂♂ and 32 ♀♀ or 16 % ♂♂ and 84 % ♀♀. In individuals without an extra-moult, males are more common than females;† in thirteen examples the sexes were: 7 ♂♂ and 6 ♀♀ or 54 % ♂♂ and 46 % ♀♀. Neither of these methods alone accounts for the sex-ratios obtaining among large populations of 7-striped individuals in nature, viz. about 35 % ♂♂ and 65 % ♀♀ on average (Roonwal 1936 a, 1945 a); extra-moult ing accounts for only about one-half (16 % as against 35 %) the number of males.

* It is instructive to compare this ‘exceptional’ condition with the development of antennal segments. In this respect, too, the second moult and the resulting third stage are exceptional. Two kinds of individuals are produced in that stage, one with twenty and another with twenty-one segments (Rao 1938; Mukerji & Batra 1938). This condition, unlike eye-stripes, however, applies to both 6- and 7-striped individuals. As pointed out some time ago (Roonwal 1938 b, 1940), the third stage is exceptional in many other respects as well.

† This is the case also in 6-striped solitaria individuals which, as a rule, do not undergo an extra-moult.
However, an average of the two methods (table 2) gives a sex-ratio which is remarkably similar to that obtained in nature.

Thus, both by direct and indirect evidence it is seen that only in about one-half to three-quarters of the number of individuals in a 7-striped population is the extra-stripe produced by extra-moulting.

<table>
<thead>
<tr>
<th>Table 2. Percentage of sex-ratios in 7-striped individuals of Schistocerca gregaria in nature and in experimental rearings</th>
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<tr>
<td>source</td>
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<tr>
<td></td>
</tr>
<tr>
<td>I. From nature</td>
</tr>
<tr>
<td>II. From laboratory rearings:</td>
</tr>
<tr>
<td>(a) with extra-moult</td>
</tr>
<tr>
<td>(b) without extra-moult</td>
</tr>
<tr>
<td>(c) average of (a) and (b)</td>
</tr>
</tbody>
</table>

(vi) In one evidently exceptional female (table 3) the 8-striped eye was produced by the addition of the eighth stripe some days after eclosion, although at first a 7-striped eye resulted by the addition of two striped at the second moult; in addition, there was a stripe-neutral extra-moult (Roonwal 1937, p. 151). An 8-striped eye may also be produced as a result of two stripe-positive extra-moults.

| Table 3. Exceptional development of 8-striped eye in Schistocerca gregaria |
|-----------------------------|-----------------------------|-----------------------------|
| III | stage | B (extra-moult) | adult | 4 days after eclosion |
|     | number of eye-stripes | I | II | A | IV | V | just eclosed |
|     |                      | ? | 2 | 4 | 4 | 5 | 6 | 7 |

(b) Dorsal spot and subdorsal streak

Dorsal spot (d.). The dorsal spot is present in all stages and is always dark chocolate. With each stage it grows in size, elongates antero-posteriorly and also changes in shape. In the first stage (figure 3a, b, c and h), even in the freshly hatched hopper (3 hr. after hatching) it is present as a dark chocolate area, more or less triangular in shape with rounded angles, the base of the triangle pointing posteriorly. In the second stage (figure 3i) it is narrower and more elongate; in the third (figures 3j, 4d) it becomes markedly curved, with the base pointing postero-ventrally. In the fourth stage (figures 3k, 4e) there is a reversal of the base which now points antero-dorsally. This new orientation is maintained in the fifth stage (figures 3l, 4f) and the adult.

Subdorsal streak (sd.). This makes its appearance in the first stage when the single stripe of that stage begins to develop at the dorsal end of the eye; it is found in all subsequent stages. In the first and second stages it is pale green; in the third,
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cream; in the fourth and fifth, generally cream but sometimes yellow; and in the adult, generally cream but not infrequently yellow.

(c) Discussion

Besides Schistocerca gregaria, the development of eye-stripes has been studied in only five other Acridids, namely, Anacridium aegyptium, A. moestum melanorhodon, Calliptamus italicus, Thysiocercus littoralis and Schistocerca paranensis (Volkonsky 1938a, b). The development here is fundamentally similar to that in Schistocerca gregaria, with minor variations. Thus, in Anacridium moestum melanorhodon the first stripe is complete only in the second stage when the second stripe is already fully developed. In Schistocerca paranensis the transition between the mode of development (as seen in S. gregaria) of the first stripe on the one hand, and subsequent stripes on the other, is clearly observed. The first stripe develops, as in S. gregaria, at the mid-dorsal edge of the eye; the second arises from the dorsal pole of the eye and subsequently develops along the inner edge of a hyaline band at the anterior margin of the eye. (In S. gregaria, it will be recalled, the second and subsequent stripes arise, from the very start, along the entire anterior edge of the eye and move backwards.) The third and subsequent stripes in S. paranensis develop along the anterior edge of the eye. In all these cases Volkonsky claims an absolute moult-stripe correlation. Rao (1938, p. 19) and Rao & Gupta (1939) claim the same feature for Calopiganopsis sp., Catantops sp. and Acrida sp., but evidently without sufficient breeding evidence. In view, however, of the conditions discussed above for Schistocerca gregaria, it seems probable that detailed study of breeding would show important exceptions to this allegedly absolute correlation. A careful comparative study of eye-stripe development in Acrididae is likely to be productive of valuable results.

(2) Mechanism of growth of stripes and interstripes

With the exception of stripe no. 1, which first appears in the mid-dorsal region of the eye and extends downwards, all other stripes in S. gregaria appear along the anterior margin of the eye and shift backwards (posteriorwards). This indicates that the anterior margin of the eye is the region of active growth. The entire margin from the dorsal to the ventral tip is involved, and the growth of the eye may be regarded as a kind of gradual unfolding at this margin. The posterior margin, on the other hand, does not appear to be a region of active growth, at any rate in the same sense and degree as the anterior margin.

The pigment present in the secondary pigment cells alone is visible externally in the form of stripes (for details vide infra). The development of a stripe thus depends on the gradual extension of pigment, in a row of ommatidia, from the lower ends of the secondary pigment cells to their outer ends. For each developing stripe this process is usually complete when the hopper is about to moult. Exceptionally, the process may be accelerated or retarded. With acceleration, the stripe which would appear in a certain stage is already distinct in the previous stage;
with retardation, the stripe becomes distinct in the stage following the one to which it normally belongs. These points should be borne in mind in determining the number of stripes in the eyes of a random collection of hoppers whose developmental history is unknown, particularly when the hoppers are about to moult. As a rule, unless the life history is followed through at least one moult, it is not safe to assert the exact number of stripes at any stage.

(3) Homology and nomenclature of stripes and interstripes

In the original account the writer (Roonwal 1936a) had numbered the stripes and interstripes from the posterior to the anterior side of the eye. The correctness of this nomenclature has been borne out by the study of development. Since, after the first stage, new stripes and interstripes appear first at the anterior margin of the eye and then travel backwards, it is necessary, from the point of view of development, to number them from behind (posterior end) forwards in order of their appearance. This provides a uniform nomenclature for all types of eye and, at the same time, indicates the correct homologies, thus:

6-striped eye. The single eye-stripe in the first stage is stripe no. 1 (s.\(^1\)), while the posterior and anterior 'interstripes' are interstripe no. 1 (is.\(^1\)) and 2 (is.\(^2\)) respectively. In the second stage the posterior stripe is the same as stripe no. 1 of the first stage. The anterior stripe, which is a new formation, is stripe no. 2 (s.\(^2\)). The most posterior stripe is homologous to interstripe no. 1 of the first stage, the middle interstripe to the anterior interstripe (no. 2) of that stage, while the most anterior interstripe (no. 3, is.\(^3\)), which is the last one to appear, is a new acquisition in the second stage. Following this procedure, we have in the adult eye stripe no. 1 to 6 and interstripe no. 1 to 7, each number being strictly homologous to a similar number in the younger stages.

7-striped eye. The condition in the first and second stages is the same as in the 6-striped eye. In the third stage two stripes (no. 3, 4) and two interstripes (no. 4, 5) are added one behind the other, resulting either from or without an extra-moult. Stripe no. 4 and interstripe no. 5 have no counterpart in the third stage in the 6-striped eye; they are homologous to similarly numbered structures in the fourth stage. Following this procedure, we have in the adult eye stripe no. 1 to 7 and interstripe no. 1 to 8. These are homologous to similarly numbered structures in the 6-striped eye, only stripe no. 7 and interstripe no. 8 being new formations. A similar nomenclature would apply to 5- and 8-striped eyes.

_Structure, pigmentation and vision in compound eyes, and their role in the behaviour of individuals in the gregaria and solitaria phases

(1) General and historical

The following aspects of gregaria or unstriped and solitaria or striped eyes may now be considered: (i) microscopic structure, (ii) pigmentation, (iii) nature of vision, and (iv) the role of differential vision in the behaviour of the two phases.
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For a proper appreciation of some of these aspects a brief history of our knowledge of Acridid eyes is necessary.

Leydig (1855, 1864) appears to have been the first to describe the structure and pigmentation of the eyes of an Acridid, viz. Oedipoda [Acridium] coerulescens. Several structures were, however, not correctly understood by him. Thus, according to his description of the crystalline cone, the eyes would belong to the acone type (under Grenacher's classification), whereas they are actually, as in all other Acridids, of the eucone type. Again, he interpreted the thread-like secondary pigment cells as muscles. These errors were pointed out by Grenacher (1879) who was himself, however, unable to determine the number of elements composing the retinula of Oedipoda [Acridium] because, as he remarked: 'The longitudinal sections gave no information...and I was not lucky with transverse sections.' Exner (1891) observed that the eyes of Psophus stridulus could be divided into two different halves according to colour. His conjecture, arrived at without studying historical details, that this was a case of 'double eyes' was shown to be incorrect by Jörschke (1914) and Friza (1929). Stefanowska (1892) studied pigment distribution in Stenobothrus pratorum; and Tümpe (1914) mentioned casually the striped pattern of eye in Anacridium aegyptium. Jörschke (1914) was the first investigator to give a comprehensive comparative account of the structure and pigmentation of Acridid eyes. He studied members of the following genera: Gomphocerus, Psophus, Calliptamus [Caloptenus], Pezotettix and Acrydium [Tettix]. A detailed account of Calliptamus alone was given, however, as the others did not exhibit any great departure from that type. Friza (1929) gave a comprehensive account of Anacridium aegyptium, with special reference to the pigmentary basis of the striped eye pattern and the nature of vision. He also studied the genera Calliptamus, Acrydium [Tettix], Sphingonotus, Oedipoda and Psophus, and elucidated the pigmented basis of the various colour patterns found in them. Roonwal (1936a) briefly mentioned the pigmented basis of the striped (solitaria) and unstriped (gregaria) patterns in the eyes of Schistocerca gregaria.* Bernard (1937) studied the relative growth of the various components of the eye of S. gregaria in the hopper stages; he did not study ommatidial structure and pigment distribution. Volkonsky (1938a, b) made a brief reference to pigmentation in the eyes of the same insect.

(2) Eye structure

It may be stated at once that between the striped and unstriped eyes of S. gregaria there is no structural difference except in the distribution of pigment. Each eye is composed of an aggregation of a large number of ommatidia which are of the eucone type of Grenacher, and are so constructed as to form an apposition image. In striped eyes each stripe involves a vertical row of about 4 to 7 ommatidial

* In that note the primary pigment cells were termed distal, and the secondary ones proximal. According to current nomenclature, however, and the one adopted in the present account, the proximal ones should be regarded as the primary pigment cells and the distal ones secondary.
facets; the corresponding number in the region of the interstripes is slightly larger and is rather more variable. The elements comprising each normal or fully developed ommatidium may now be described; the condition that obtains in the region of the dorsal spot of the eye will be described at the end of the section on eye-pigmentation.

(a) The cornea or facet

The outermost portion of an ommatidium consists, in surface view, of a cuticular, colourless, transparent and hexagonal cornea or facet. In longitudinal sections it shows two layers: an outer, thinner, un laminated layer (cr.c.) not staining with eosin, and an inner, thicker layer (cr.i.) which stains with eosin and is irregularly laminated with transverse laminae. Volkonsky's statement (1938b) that the facets are absent on the dorsal spot is incorrect. They are present there in all stages, but are smaller than in the remaining portion of the eye.

Jörschke (1914) found that in Calliptamus [Caloptenus] and Acrydium [Tettix] small hairs are sometimes present on the corneal surface. In Anacridium aegyptium Friza (1929) found that each hair is associated with a canal which traverses the entire breadth of the cornea and contains a nerve fibril. In Schistocerca these structures are wanting.

(b) The crystalline cone (c.c.)

This is a long, slender, transparent and truncated cone, lying beneath the cornea and running down to the region of the primary pigment cells (p.) described below. It is composed of four closely-fitting similar parts (figure 8, plate 14), and proximally passes (figure 5, plate 13), without any clear demarcation, into the rhabdom (rh.). The distal end or base of the cone is capped by a group of four deeply staining areas which are evidently the degenerate nuclei of the crystalline cone (Semper's nuclei, nu.c.c.). Unlike typical nuclei, which in haematoxylin-eosin preparations stain blue and show large and distinct chromatin granules, Semper's nuclei invariably take a dirty purple stain and their chromatin is diffuse and indistinct. This peculiarity is present even in the first-stage hoppers in which, it may be added, no trace of cone cells could be seen; it would thus appear that the cells are already converted into cones before hatching. Because Semper's nuclei show a marked affinity for eosin and an antipathy for haematoxylin, they are probably in a state of cuticularization.

In Oedipoda [Acridium] Leydig (1864) claimed to have observed distinct nuclei of the cone cells and regarded each cone element as a separate cell; the eye accordingly would belong to the acone type. Grenacher (1879) corrected Leydig and showed that the Acridid eyes are of the eucone type, a fact confirmed by later workers. Schistocerca agrees with that condition.

(c) The corneagen cells (cr.c.)

It is seen in longitudinal sections of ommatidia that the inter-ommatidial space between the rounded distal ends of Semper's nuclei and the inner face of the
cornea is filled with triangular areas (figure 5, plate 13). They stain like Semper’s nuclei but are, nevertheless, distinguishable from the latter by means of a clear line of demarcation. These areas probably represent the corneagen cells; the number of these cells could not be accurately determined.

Neither Jörschke (1914) nor Friza (1929) refer to these cells in other Acrididae, although the former represents them in Calliptamus [Caloptenus] italicus.

(d) The pigment or iris cells

Two kinds of pigment cells, the primary and the secondary, are present in Schistocerca gregaria; they are described below.

The primary pigment cells (figures 5 to 10, plates 13, 14). These consist of two small, stout cells which completely surround the apex of the crystalline cone. Proximally they abut on the distal ends of the retinular cells, while distally their outer borders slope inwards to meet the crystalline cone. Each cell has a large, oval nucleus which, like the cell itself, is kidney-shaped in transverse section.

Stefanowska (1892), Jörschke (1914) and Friza (1929) have recorded a similar condition in other Acrididae.

The secondary pigment cells (figures 5 to 12, s., plates 13, 14). These are long, slender, thread-like cells, varying in number from eleven to fourteen, though twelve is the more usual number. They encircle the crystalline cone and the retinula, and are distinctly assignable to each ommatidium. Distally, near the base of the crystalline cone, this arrangement is somewhat disturbed owing to overcrowding. The cells extend from the cornea to less than half-way down the retinula. Proximally they gradually taper to a point. Their nuclei (nu.s.) are long and oval and lie in the distal one-third of the cells.

Hesse (1901) contended that in Pterygotan insects the secondary pigment cells are ‘indifferent’ cells and cannot be assigned to each individual ommatidium; they lie between the ommatidia, but not in such a way as to let each ommatidium have its own circle of cells. Schistocerca and other Acrididae do not, however, conform to this condition. In Stenobothrus pratorum (Stefanowska 1892) they are very long and completely surround the retinula. In the Acrididae studied by Jörschke (1914) they are stated to reach below to the basement membrane, although in his figure of Calliptamus [Caloptenus] italicus they are shown as reaching only down to about two-thirds of the retinular length; no mention of their number is made. In Anacridium, Friza (1929) found sixteen cells, but did not mention how far down the retinula they ran; in Oedipoda [Acrídim] coerulescens he clearly stated that they are definitely assignable to individual ommatidia.

(e) The retinula and its various components (figures 5 to 7, plate 13; and figures 11 to 13, plate 14)

The retinula (r.), which forms the posterior portion of an ommatidium and lies proximal to the crystalline cone, is composed of a central cuticular rod or rhabdom
(r.h.) and, surrounding it, a number of visual or retinular cells (r.c.). It comprises the percipient portion of the eye; the dioptric or recipient portion is formed by the cornea and the crystalline cone, with the primary and secondary pigment cells as accessories.

The rhabdom (r.h.). The rhabdom is a long, cylindrical, cuticular, structureless, transparent, and highly refractile rod which is continuous with the apex of the crystalline cone and runs inwards to stop short some distance from the basement membrane (b.). It is not divided into rhabdomeres, not does it show the neuro-fibrils (‘Stiftchensäume’) of Hesse (1901). The cone and the rhabdom together form an entity of exactly similar optical appearance. There is no visible line of demarcation between them; it can be determined, in transverse sections, only by the presence of four divisions in the cone, a feature which is absent in the rhabdom. It seems that the apparent fusion of the cone apex with the rhabdom occurs in the embryo before hatching.

The continuity or otherwise between the crystalline cone and the rhabdom in insects is a somewhat disputed point. Some writers (e.g. Leydig 1864; Eltringham 1919) maintain the continuity of the two structures, while others (e.g. Grenacher 1879; Hesse 1901; Deegener 1913) regard them as distinct. For the Acrididae, Jörschke (1914) wrote that ‘as in all apposition eyes, the rhabdom lies closely adpressed to the crystalline cone, and it can be seen only with difficulty that it does not go over directly into the crystalline cone’; while Friza (1929) made no definite statement on this point. Jörschke found that the Acridid rhabdom is not divided into rhabdomeres, except in Acrydium [Tettix] bipunctatum where, however, he could not determine their exact number. Friza mentioned the existence of ‘never more than seven rhabdomeres’ in Anacridium aegyptium.

The visual or retinular cells (r.c.). The visual or retinular cells vary irregularly in number from five to six (though five is more usual) in the different ommatidia of the same individual. The number, however, is constant throughout the length of each retinula. These cells surround, in a rosette-like manner, the entire length of the rhabdom, and are believed to secrete the latter. Distally they smoothly curve inwards to form a dome, while proximally they reach down almost to the basement membrane (b.) and continue across the latter as nerve fibres (pr.n.f.). Their nuclei are long and cylindrical and lie in two planes; three of them (nu.r.d.) lie in the distal one-third of the cells, and the remaining two or three (nu.r.p.), depending on the number of cells in the ommatidium, in the proximal one-third.

Grenacher (1879) stated that the number of retinular cells in the eucone eyes of insects varies from four to eight, and that seven must always be regarded as the typical number to start with. The phenomenon, recorded in insects from time to time, of a varying number of retinular cells in the same eye has two aspects: first, the number is the same throughout the length of each retinula in an ommatidium, but varies in the different ommatidia of that eye. Secondly, the number varies in the proximal and distal portions of the same ommatidium. Both phenomena are found in the Acrididae. Jörschke (1914) wrote thus for the Acrididae.
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studied by him: 'Regarding the number of retinular cells I cannot give here any
definite conclusions since, in the Acrididae, only in the distal section of the retinula
is it possible to discover cell-boundaries which can no more be clearly seen in the
proximal portion.' And further: 'Around the distal end of the rhabdom of Caloptenus [Calliptamus] there group themselves six cells of which, however, one soon
disappears since, in section across the more deeply lying region, I could mostly
count only five cells. Probably towards the basal region, as is at any rate evident
from the position of the retinular nuclei in longitudinal sections, two more visual
cells are present, so that in the Acrididae also, as in other Orthoptera, eight cells
might compose a retinula. There must be at least seven of them since in some grass-
hoppers, e.g. Tettix [Acrydium] bipunctatus L. I have found seven-rayed rosettes
right on the basement membrane.' In Anacridium aegyptium Friza (1929) found
five to six cells in the distal region, and two more, i.e. seven to eight, in the proximal;
the eighth one, however, is rudimentary and is not regarded as taking part
in the formation of the rhabdom. As described above, the condition in Schistocerca
is simpler both as regards the number of cells (five to six throughout an ommati-
dium) and the arrangement of the nuclei (in two rows instead of three found in the
Acridids studied by Jörschke).

(f) The basement or fenestrated membrane, the tracheae and the nervous elements
(figures 5 to 7 and 13, plates 13, 14; and figures 15 to 19, plate 15)

The basement membrane (b.) is a very thin, transparent, irregularly striated and
non-cellular septum between the ommatidia and the optic lobe. It is perforated
for the passage of retinular nerve fibres and the associated tracheae, one hole or
fenestra (fn.) corresponding to each retinula. There are no separate fenestrae for
the tracheae.

Immediately beneath the basement membrane there is a row of small distal
tracheae (figures 15 and 17, t.d., plate 15) which give rise to extremely fine branches
or tracheoles. Farther inwards, between the distal tracheae and the periopticon
(vide infra), there is a row of large proximal tracheae (t.p.); it is seen in transverse
sections that there is usually one trachea between each two adjoining retinular
nerve bundles.

Friza (1929), in Anacridium, makes no mention of this more or less regular
arrangement of the distal and proximal tracheae and the distinction between them.
In some insects the distal tracheae have been stated to pass through minute perforations in the basement membrane and run for some distance up the retinulae; in Anacridium, according to Friza, they occasionally wind themselves spirally
up the retinulae. In Schistocerca I could not detect such a condition.

The nervous elements. The nervous elements of the eye are composed of several
parts. Proximally, each retinular cell of an ommatidium goes over into a bundle of retinular nerve fibres (r.n.f.) which join up with the bundles from other retinular
cells in that retinula before reaching the basement membrane. The fibres from each
retinula pass as a single unit through the membrane beneath which the fibres from
a number of retinulae unite to form the post-retinular nerve fibres (pr. n. f.). Embedded in these fibres and lying proximal to the large tracheae are large groups of nerve cells (figure 15, n. c., plate 15), one group to each large trachea; each group is enclosed in a sheath. Smaller groups and isolated cells are scattered throughout the post-retinular mass of nerve fibres. The whole complex of nervous tissue lying between the basement membrane and the periopticum constitutes the so-called ‘terminal anastomosis’ of Hickson (1885); it leads to the optic lobe.

In the optic lobe (figures 16 and 17, plate 15) three regions or ‘opticons’ are distinguishable. They are composed of the ‘neurospongium’—a tissue formed mainly of a fine, granular matrix traversed throughout by a fine meshwork of minute fibrillae—and are enclosed in a sheath (n. c. s.) of nerve cells. The outermost region or periopticum (p. op.) is thin and plate-like and does not exhibit any bundle-like structures. The middle region or epiopticum (e. op.) is large and is kidney-shaped in sagittal sections of the head. The innermost region or opticon (op.) is small and rounded and is connected with the cerebral ganglion (e. g.) through the stout optic nerve (op. n.). The periopticum is connected with the epiopticum, and the latter with the opticon, by means of parallel bundles of nerve fibres, the spaces between the bundles being filled with nerve cells (figure 17, n. c., plate 15). These fibres do not cross or decussate, at least in the hoppers, and, therefore, do not form the ‘chiasma’ which is found in certain other insects. The whole optic lobe is enclosed in a sheath (n. c. s.) of densely packed nerve cells which is specially thick in the region between the peri- and epiopticons.

(3) Pigmentation in striped (solitaria) and unstriped (gregaria) eyes

The pigment-bearing regions of the eye are the primary and secondary pigment cells, the retinular cells and the nerve fibres above and beneath the basement membrane. All other elements of the eye are devoid of pigment. As seen under the microscope, the principal pigment consists of minute, highly refractile granules (figures 6 and 7, rp., plate 13) of a dark red-brown to chocolate colour with a faint violet hue. It is widely distributed both in gregaria and in solitaria eyes. In addition, a small amount of dirty or greyish yellow pigment (yp.) occurs in a portion of the secondary pigment cells, especially in gregaria eyes; in solitaria eyes it is comparatively scanty. As shown earlier in Locusta (Roonval 1936b), pigment in Schistocerca eyes also first appears in embryos shortly before blastokinesis as deep orange-red granules, giving the eyes that colour; gradually the red changes to brownish before hatching. The time of appearance of the greyish yellow pigment could not be determined.

The distribution of pigment in striped and unstriped eyes varies, and is described below. In the following account, except when otherwise stated, ‘pigment’ refers to the red-brown pigment granules.

Unstriped eyes. In unstriped eyes (figure 6, plate 13) all the pigment-bearing elements, viz. the primary and secondary pigment cells, the retinular cells, and the post-retinular tissue, are densely pigmented with red-brown granules (rp.).
The primary pigment cells and the areas immediately surrounding them, especially proximally, are the most densely pigmented portions of an ommatidium; the pigment is particularly dense around the nuclei. There is thus formed around the apex of the crystalline cone a dense collar of dark pigment which is almost impenetrable to light rays. The secondary pigment cells also show dense pigmentation throughout their length except at the extreme proximal ends which bear little or no pigment. The pigment present is the usual brown one except in the middle portion (immediately distal to the level of the primary pigment cells) which bears the greyish yellow pigment only (figure 6, yp., plate 13); this pigment functions as the *iris-tapetum* of Exner (1891). The secondary pigment cells thus serve to isolate the distal portion (i.e. the crystalline cone and a small portion of the distal end of the retinula) of an ommatidium from its neighbouring fellows. The distal and proximal one-thirds of the retinular cells are densely pigmented, while the middle one-third contains little pigment. At and around the proximal tips of the retinular cells there is a small aggregation of pigment which extends into the retinular and post-retinular nerve fibres up to the peri-opticon, thus forming a thin, densely pigmented post-retinular pigment layer (*pr.p.l.*).

*Striped eyes.* The pigmentation of striped eyes (figure 7, plate 13) differs from that of unstriped eyes in two important respects: (i) In general, the pigment, wherever present, is less dense than in unstriped eyes. (ii) In the region of the interstripes the secondary pigment cells are entirely devoid of pigment, except for the presence of a small amount of greyish yellow pigment; in the region of the stripes the pigmentation is similar to that in unstriped eyes, though less dense. Thus, the alternate groups of pigmented and unpigmented secondary pigment cells correspond to the stripe- and interstripe-regions respectively as seen externally, and are the cause of the striped pattern. The cream colour of the interstripes is due to the yellow pigment which shows through as a result of the incident rays reflected from it; in unstriped eyes, even though the yellow pigment is present in larger quantities, its external visibility is masked by the covering layer of brown pigment. There are no structural differences between the striped and unstriped regions of the eye. The other pigment-bearing areas, viz. the primary pigment cells, the retinular cells and the post-retinular pigment layer, contain the red-brown pigment exactly as in unstriped eyes, except that it is less dense.

From these differences it is evident that the externally visible colour of the eye is due to the pigment present in the secondary pigment cells; pigment present elsewhere is, as a rule, not visible externally. The cornea is entirely unpigmented.

*Discussion.* Leydig (1864) had observed both dark (violet) and light (yellow) pigments in *Oedipoda* [Acridium] *coeruleascens.* He, however, did not properly understand their distribution in the eye and their role in vision; the secondary pigment cells were regarded by him as muscles. Stefanowska (1892) described the pigmentation of *Stenobothrus pratorum,* and her account has been substantially confirmed in other Acrididae by later workers, e.g. Jörschke (1914) and Friza (1929). Friza first elucidated the pigmentary basis of the striped and other patterns.
in Acridid eyes. My observations on *Schistocercus* largely confirm the findings of these workers; and, in addition, I have elucidated the cause of the pigmented differences between *solitaria* and *gregaria* eyes. Some differences that were noticed between my observations and those of other workers may now be discussed.

Friza stated that the primary pigment cells of *Anacridium* contain the brown pigment in the lower or proximal part only; the distal, more slender portion is devoid of pigment. In *Schistocerca*, on the other hand, the pigment is distributed throughout these cells, but is denser around the nuclei. Again, Stefanowska and Jörschke maintained that the yellow pigment is present throughout the entire length of the secondary pigment cells; in *Schistocerca* as far as I could observe, it is confined to the middle portion. Friza did not clearly define the distribution of yellow pigment in the secondary pigment cells.

*The dorsal spot.* In the region of the dorsal spot of *Schistocerca* the facets and other portions of the ommatidia are smaller, more compactly packed and generally less fully developed than in the remainder of the eye. Towards the eye-margins the partially differentiated ommatidia go over into the undifferentiated hypodermal (ectodermal) cells of the head-wall. All the pigment-bearing elements are heavily pigmented, and this is the cause of the uniformly dark colour of the dorsal spot. The spot forms the so-called ‘growth zone’ of Friza (1929) and is found, according to that author, in all Orthoptera.

(4) **Physiological considerations:** *Vision in striped* (solitaria) *and unstriped* (gregaria) *eyes*

(a) **Vision**

As already mentioned, there is no structural difference in the striped and unstriped eyes of *Schistocerca*, except in the density and distribution of pigment. Structurally, the eyes of *Schistocerca* are of the eucone type which is adapted for diurnal vision and forms the apposition image of Exner (1891). The cornea and the crystalline cone constitute the dioptic or recipient portion of the eye, and the retinula the percipient portion. Exner showed that in apposition eyes the corneal facets and the crystalline cone underlying it act together as a lens cylinder of a length equal to its focal length, and, as a result, an inverted image is formed at the cone-apex. The apposition image formed by the eye is, therefore, an aggregation of light spots or images, each image corresponding to that portion of the light rays which is vertically or nearly vertically incident on a single facet—the mosaic image of Müller (1826). The sharpness and purity (i.e. absence of contamination from the light rays entering the neighbouring ommatidia) of each image depends on the completeness of the optical isolation of an ommatidium from its neighbours. On these considerations, the nature of the image formed in the two kinds of *Schistocerca* eyes may now be discussed.

*Unstriped* (gregaria) *eyes.* In *gregaria* eyes the optical isolation of an ommatidium is fairly complete owing to the abundant amount of the dark-brown, light-
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absorbing pigment throughout all the pigment-bearing elements. In the portion of the secondary pigment cells immediately distal to the level of the primary pigment cells, the brown pigment is absent and there is present, instead, the dense dirty yellow pigment forming the iris-tapetum. The tapetum is not a light-absorbing but a light-reflecting structure, so that obliquely incident rays falling on the tapetum are partly or wholly reflected and again pass out of the eye. A few rays, however, might remain inside and stimulate the tips of the retinular cells and thus serve slightly to contaminate the apposition image. In the butterflies studied by Eltringham (1919) the dioptic apparatus is similar to that of *Schistocerca* except for the presence, in the former, of a layer of transparent material called the 'processus corneae' between the cornea and the crystalline cone. The 'processus', however, does not affect the optical working of the eye-apparatus in any way. According to Eltringham, the light rays emerging from the apex of the crystalline cone are practically parallel so that they pass down the rhabdom and stimulate the retinular cells not only at the distal ends but also all along the inner edge of each cell. If, by comparison, the same were to occur in *Schistocerca*, it is clear that a number of light rays would penetrate deep into the eye, especially in dazzling illumination. Under these circumstances, the function of the dense post-retinular pigment layer in *Schistocerca* is evidently to absorb the deeply penetrating rays, and thus serve to prevent halation in much the same way as the red coating at the back of the so-called 'anti-halation' photographic plates of some manufacturers. On all these considerations, the apposition image formed in *gregaria* eyes may be regarded as true and perfect.

**Striped (solitaria) eyes.** In striped eyes there are four factors which contribute towards making the apposition image less perfect than in unstriped eyes. These are: (i) The comparative poverty of pigmentation all over the eye; (ii) the absence of the light-absorbing brown pigment in the secondary pigment cells in the ommatidia lying in the region of the interstripes; (iii) the comparative scarcity of the yellow pigment, thus rendering the iris-tapetum practically functionless as a light-reflecting structure; and (iv) the comparative thinness of the post-retinular pigment layer, thus rendering the 'anti-halation' device very weak or even ineffective. The combined result of these differences is that the ommatidia, particularly those lying in the interstripe region, no longer stand in efficient optical isolation from their neighbouring fellows. Thus, they are stimulated not only by the vertically or nearly vertically incident rays but also by several of the oblique rays which pass from one ommatidium into another. As a result, a condition is produced, especially in the interstripe region, in which the image, although still of the apposition type in its initial mode of formation, is of the superposition type in effect. In other words, the image is diffuse owing to contamination, and brighter owing to more light rays entering an ommatidium; each image also corresponds to a larger field of vision. In the region of the stripes, where the secondary pigment cells are pigmented, though less heavily than in *gregaria* eyes, an apposition image must still obtain although it would be less sharp and brighter than in *gregaria* eyes.
The reasons why I do not regard a true superposition image to obtain in the inter-stripe regions are as follows: In the typical superposition eye of Exner each crystalline cone is optically isolated from its fellows, and the intermingling of light rays entering a number of ommatidia takes place in the region between the crystalline cone and the rhabdom. The overlapping of the images thus occurs on the percipient (proximal) portion of the eye, i.e. after the light rays have traversed the dioptic (distal) portion. In *Schistocerca*, on the other hand, whereas the proximal portion of the crystalline cone and the whole of the retinula are optically isolated fairly completely from their fellows, the distal two-thirds of the crystalline cone is not so isolated. As a result, the interference of light rays would occur not in the percipient portion as in superposition eyes, but in the crystalline cone (dioptic portion); the image so produced may conveniently be termed a 'pseudo-superposition' image.

To recapitulate, the differences between the vision in unstriped and striped eyes of *Schistocerca* may be summed up as follows: *Unstriped eyes*: a true and perfect apposition image is formed; the eye is suitable for vision in bright daylight; the images of objects within range of vision are sharply defined. *Striped eyes*: a 'pseudo-superposition' image is formed; it is brighter and more diffuse than in unstriped eyes; the eye is suitable for vision in subdued light and is able to perceive movements rather than discrete, sharply defined images.

*Discussion*. In the absence of experimental evidence it is difficult to say whether the image produced in the apposition eyes of *Schistocerca* is erect or inverted. In the pseudocone apposition eyes of flies, Exner (1891) found an inverted image, while in the eucone apposition eyes of butterflies which are, as mentioned above, structurally almost similar to that of *Schistocerca*, the image is erect (Eltringham 1919). A comparison would, therefore, suggest an erect image in *Schistocerca*. Friza (1929), who discussed in detail the nature of vision in striped eyes of *Anacridium*, concluded that the eye produces a typical apposition image as in the 'diurnal' eyes of insects. I have, however, concluded that the striped eyes of *Schistocerca* produces a pseudo-superposition image; a true apposition image is formed only in unstriped eyes.

(b) *Accessory optical phenomena*

If one looks at the eye of *Schistocerca* from above, one sees, deep down, a small but distinct dark spot, the so-called pseudo-pupil. This spot is always opposite the observer's eye and moves as the insect is moved. It is nearly round but when moved towards the eye margins, where the curvature of the eye surface is less than in the central part, it appears more elongate. The pseudo-pupil is not a discrete morphological structure but an optical phenomenon, first observed by Exner (1891) in flies. In the unstriped eyes of *Schistocerca* six more spots, larger and more diffuse than the pseudo-pupil, are seen in a ring around the latter; these are the pseudo-pupils of the second order, and are not visible in striped eyes. The causes of this optical phenomenon are not understood.
(5) **Role of vision in the behaviour of individuals in the gregaria and solitaria phases**

The probable effect of the difference in vision on the behaviour of individuals in the *gregaria* and *solitaria* phases is briefly as follows:

**Gregaria individuals.** First, as a result of the apposition vision, the mutual visual impact of individuals produced by bright, sharply defined images tends to keep the individuals together, i.e. assists in gregarious behaviour. Secondly, since the eyes are well adapted for diurnal vision, the individuals do not avoid strong sunlight; even dazzling light is not avoided because of the heavy pigmentation all over the eyes and the presence of the anti-halation device. *Gregaria* individuals, therefore, boldly march or fly together out in the bright open.

**Solitaria individuals.** First, owing to the pseudo-superposition mode of image formation, the eyes are suited for vision in weak light. The images are diffuse and, owing to the resulting lack of mutual visual impact, the individuals do not tend to keep together. Secondly, as the eyes are not adapted for bright light, their possessors, especially hoppers, avoid strong light; they tend to retire to bushes during the day rather than march out into the bright open. *Solitaria* adults show a weaker degree of light-avoidance than hoppers; even so, their glare-tolerance is lower than in *gregaria* adults, as far as one can judge from field observations.

The phenomenon, first noticed by Fraenkel (1929, 1930) in *Schistocerca gregaria*, of the orientation of adults and older hopper stages to sun’s rays, has evidently no relation to the mode of vision. It occurs in both *gregaria* and *solitaria* individuals, and is a heat-absorbing, not a light-sensitive, mechanism.

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**References**

(Those not seen in original are marked with an asterisk: *)

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EXPLANATION OF PLATES 13 TO 15

Lettering

b. basement membrane

c.c. crystalline cone

c.g. cerebral ganglia
cr. cornea
cr.c. corneagen cells
cr.i. inner layer of cornea
cr.o. outer layer of cornea
e.op. epiopticon

fn. fenestra or hole in basement membrane

n.c. nerve cells

n.c.s. sheath of nerve cells

n.f. nerve fibres

nu.c.c. nuclei of crystalline cone (Semper's nuclei)

nu.p. nuclei of primary pigment cells

nu.r.d. distal nuclei of retinular or visual cells

nu.r.p. proximal nuclei of retinular or visual cells

n.u.s. nuclei of secondary pigment cells

om. ommatidia
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Plate 13

Compound eyes of Schistocerca gregaria. All figures are semi-diagrammatic camera-lucida drawings of sections of eyes.

Figure 5. Median-longitudinal section of an ommatidium of the unstriped eye of a black (phase gregaria) fifth-stage hopper, showing the component parts. Section bleached in Grenacher's mixture and stained with Delafield's haematoxylin and eosin. × about 375.

Figure 6. Median-longitudinal section of an ommatidium of the unstriped eye of a black (phase gregaria) fifth-stage hopper, showing the distribution of pigment. Section unbleached and unstained. × about 375.

Figure 7. Ditto, in the interstripe region of the striped eye of a green (phase solitaria, fifth-stage hopper. Note the absence of pigment in the secondary pigment cells. × about 375)

Plate 14

Figure 8. Transverse section of an ommatidium of the striped eye of a green (phase solitaria) fifth-stage hopper passing across the distal region of the crystalline cone (line A–A in figure 5), to show the structure of the various parts. Section bleached in Grenacher's mixture and stained with Delafield's haematoxylin and eosin. × about 1330.

Figure 9. Ditto, across the middle region of the primary pigment cells (line B–B in figure 5). × about 1330.

Figure 10. Ditto, across the proximal region of the primary pigment cells (line C–C in figure 5). × about 1330.

Figure 11. Ditto, across the distal nuclei of the retinular cells (line D–D in figure 5). × about 1330.

Figure 12. Ditto, across the proximal nuclei of the retinular cells (line E–E in figure 5). × about 1330.

Figure 13. Ditto, across the basement membrane. × about 1330.

Plate 15

Compound eyes of Schistocerca gregaria. All figures, except figure 19, are photomicrographs.

Figure 14. Portion of a section of head of fifth-stage black (phase gregaria) hopper passing through the unstriped eye and showing the transversely cut ommatidia. Section bleached in Grenacher's mixture and stained with Delafield's haematoxylin and eosin. × about 286. For clarity, the outer edge of the cornea and some of the ommatidia cut in the following regions are outlined in black ink: sections passing through: A, Semper's nuclei; B, further inward, i.e. through the distal portion of the crystalline cone and the secondary pigment cells; C, the middle region of the primary pigment cells; and D, the retinula in the region of its distal nuclei.

Figure 15. Portion of a vertical-transverse section of the head of a fifth-stage black (phase gregaria) hopper passing through the unstriped eye and showing the longitudinally cut ommatidia, the post-retinular tracheae, etc. Section bleached in Grenacher's mixture and stained with Delafield's haematoxylin and eosin. This is a portion of figure 16 more highly magnified. × about 80.
The effect of heat-denaturation on the base-binding capacity of beef-muscle press-juice

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The hydrogen ions absorbed (AB) on heat-denaturation of dialysed and centrifuged beef press-juice is shown to vary with the pH of denaturation along a smooth curve. The values of AB are remarkably constant from sample to sample. The main features of the curve are a positive peak at pH 4.1 with troughs on either side, a plateau extending from pH 6.5 to 8.0, and the assumption of negative values of AB from pH 8.5 to 10.5. The curve differs from those of undialysed samples and globulin X preparations. The peaks and troughs bear no direct relation to the isoelectric point or the degree of aggregation.

Heat-denaturation results in reduction of buffering capacity in the range pH 3.5 to 5.0, and to a new peak in the buffer curve at pH 6.0 to 7.0. Acid-denaturation at pH 3.60 has a similar but smaller effect. The evidence suggests that imidazole groups are released and terminal carboxyl groups absorbed during denaturation. There is no evidence that other amino groups are released or absorbed. These changes in buffering capacity are unlikely to be due merely to changes in physical configuration, not involving chemical bonds, since they occur whether a true coagulum is formed or not.

It is suggested that heat- or acid-denaturation result in a fission of the protein chain at labile linkages involving imidazole, sulphydryl and hydroxyl groups, followed by hydrogen-bond formation between carboxyl and amino groups, to give a new configuration. It is shown that these hypothetical changes would give rise to large shifts in pH, and the apparent release or absorption of hydrogen ions (AB) in a way similar to the actual results.

The marked difference in behaviour of the undialysed samples and globulin X preparations, on the one hand, and the crude myogen fraction on the other, suggests a fundamental difference in structure.
Roonwal


(Facing p. 272)