SIZE, SCULPTURING, WEIGHT AND MOISTURE CONTENT OF THE DEVELOPING EGGS OF THE DESERT LOCUST, *SCHISTOCERCA GREGARIA* (FORSKÅL) (ORTHOPTERA, ACRIDIDAE)

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With 4 Tables, 3 Text-figures and 2 Plates

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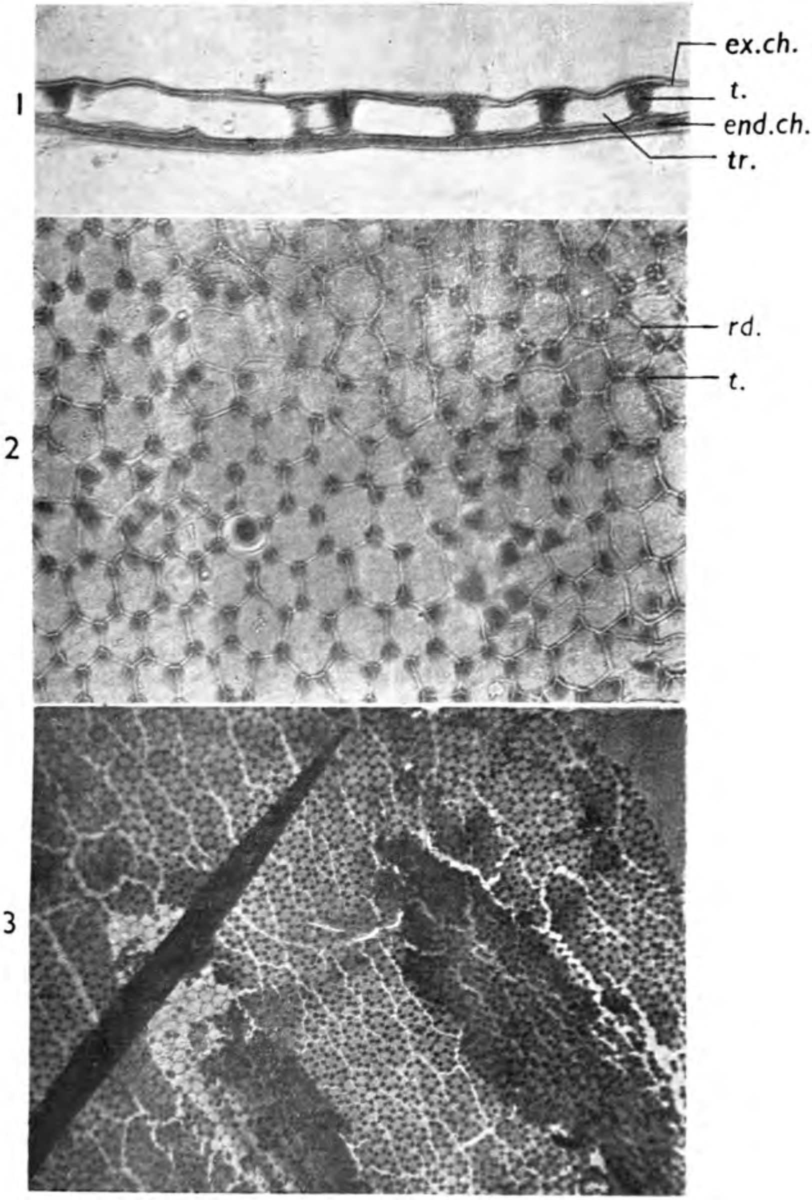
Contents

I. Introduction

Little is known of the egg-sculpturing and water-balance of the eggs of the Desert Locust, *Schistocerca gregaria* (Forskål). Husain and Roonwal (1933) described the structure of the micropylar canals. Mathur (1944) demonstrated that water is absorbed by the developing eggs from the surrounding moist soil (in which the eggs are laid) only through a specialized region at the posterior pole of egg. The specialized region exists even in the freshly laid eggs and corresponds to the area demonstrated earlier in *Melanoplus differentialis* (Th.) by Slifer (1938) and termed 'hydrople' by her. Shulov (1952) studied the intake of water by the eggs of *S. gregaria*, but he did not refer to the earlier work of Mathur (1944). Shulov stated that egg-development is interrupted if contact water is lacking and is resumed when the egg is moistened; this occurs during late anatrapsis (a stage in the process of blastokinesis or 'turning round' of the embryo), which is the stage in which the embryos of some other species of locusts and grasshoppers undergo diapause or temporary cessation of development.

Absorption of external water by eggs during development after they have been laid has been shown to occur in several species of locusts, grasshoppers, other insects and indeed many other Arthropods. (For a summary, see Roonwal, 1936*a*, 1942, 1944.) The sculpturing of the outer cuticle of the egg-wall has been studied by Roonwal (1936*a*, 1954) in the African Migratory Locust, *Locusta migratoria migratorioides* R. & F. The sculpturing presents interesting features which help in distinguishing eggs of different species of Acrididae, and a study of this feature is, therefore, of practical interest.

In the present account I have described first, the egg-sculpturing of *Schistocerca gregaria*. Secondly, I have presented the results of my observations on the swelling of eggs during development, on the increase of weight and of water-content of eggs as they develop, and finally, on the rate of loss of water in young eggs in a still dry atmosphere at a constant temperature, and on certain other related features.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II. Egg-sculpturing, etc.

(Pls. XV and XVI; and Text-figs. 1 and 2)

If the chorion of a freshly laid egg is cleaned, mounted on a slide and examined under the microscope, it presents a mosaic pattern of hexagonal (at places pentagonal) 'cell-walls', with a thick, circular dot or tubercle at each of the angles (Pl. XV, Figs. 2, 3 and Pl. XVI, Figs. 4, 5). In sections of the egg-wall (Pl. XV, Fig. 1 and Pl. XVI, Figs. 6–8) it is seen that the chorion is composed of two layers as follows: (i) A thin outer layer or exochorion which is about 6–8 μ thick near the poles and about 3–5 μ elsewhere. It is refractile, slightly granular and does not stain with haematoxylin. (ii) A thicker (*ca.* 9-10 μ at the poles and 6–8 μ elsewhere) inner layer or endochorion which stains deeply with haematoxylin and shows a semigranular, felt-like structure, similar to the one described by me (Roonwal, 1954) in *Locusta migratoria migratorioides* R. & F. Except in the micropylar region (Pl. XVI, Fig. 6) the exochorion and endochorion are not contiguous with each other but are widely separated by trabeculae or air spaces which are about 18–20 μ wide all over the egg except at the two poles where they are somewhat wider.

The trabeculae are divided into hexagonal or pentagonal cells, as the case may be, by means of endochorionic ridges which meet the exochorion and are the cause of the hexagonal (or pentagonal) chorionic pattern mentioned above. At the angles, the ridges are thickened so as to form a strut or pillar which is broad externally, *i.e.*, towards the exochorion, and narrows towards the endochorion (Pl. XV, Fig. 1 and Pl. XVI, Fig. 7); the struts appear in surface view as the 'dots' or tubercles mentioned above. The tubercles (*t.*) are wanting at the poles (Pl. XVI, Fig. 8) where only the ridges (*rd.*) are present. Inside the endochorion is the extremely thin (less than 1 μ thick), structureless vitelline membrane which, in sections of eggs, tends to adhere to the surface of the yolk-mass.

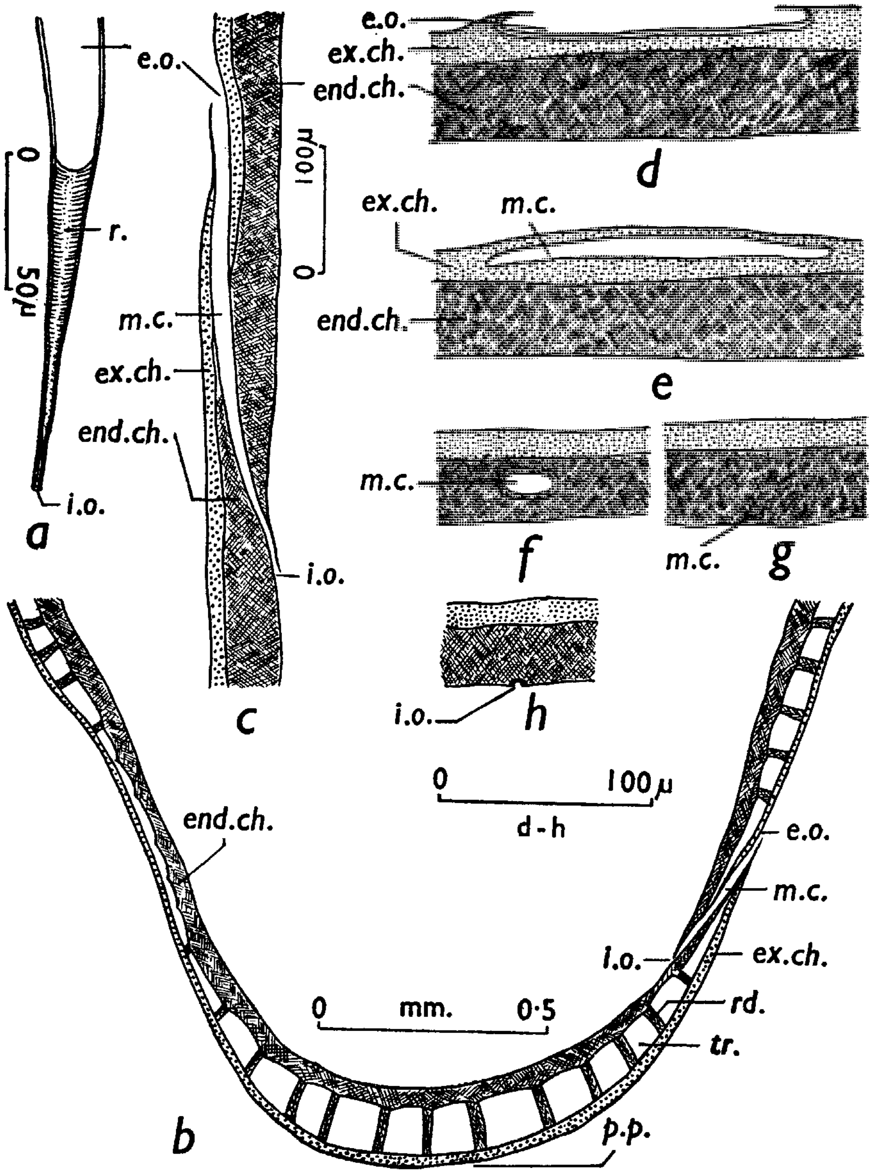
As shown by me recently (Roonwal, 1954), there appear to be two principal types of egg-walls in the Acrididae as regards the chorion, *viz.*, one in which the exochorion is throughout contiguous with the endochorion and is not separated from the latter by means of trabeculae of air spaces (example: *Locusta migratoria migratorioides*), and another which is characterized by the presence of the trabeculae or air spaces mentioned above (example: *Schistocerca gregaria*).

The micropylar apparatus (Pl. XVI, Fig. 4; and Text-figs. 1 and 2).—Around a slight constriction near the posterior pole of the egg of *Schistocerca gregaria* there runs, at a distance of about 0·4-0·5 mm. from the posterior pole, a ring of about 44–65 funicular canals (*m.c.*). Each canal runs obliquely throughout the width of the exochorion and the endochorion; its wide external opening (*ca.* 7–11 μ wide) lies anteriorly on the egg-surface, and the extremely fine inner opening lies posteriorly. These canals, which measure about 123–151 μ in length, are the micropylar canals (*vide* also Husain and Roonwal, 1933).

III. Size of Eggs

(Text-fig. 2)

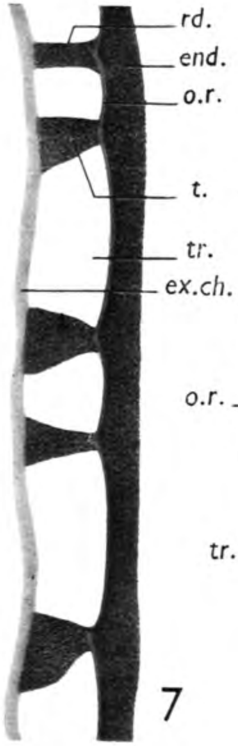
The egg of *Schistocerca gregaria* (Text-fig. 2) is slightly curved, more or less cylindrical and tapers towards both ends which are rounded. The size of eggs after oviposition (as measured by means of a vernier callipre reading up to 0·1 mm. and under a stereo-binocular-microscope) increases during development as follows:—The maximum length, measured as a straight line from pole to pole, increases from about 5·1–8·0 mm. (mean 6·93) in freshly laid eggs to about 8·1–9·6 mm. (mean 8·92) in eggs about to hatch, *i.e.*, there is a mean increase of about 29 per cent. Similarly, the maximum width or diameter (which occurs about the middle of the egg-length) increases from about 0·9–1·6 mm. (mean 1·25) in freshly laid eggs to about 1·5–2·9 mm.



TEXT-FIG. 1(*a–h*).—The micropylar apparatus of *Schistocerca gregaria* (Forsk.).

(*a*) One of the micropylar canals in surface view from the outside. (*b*) Longitudinal-vertical section of the egg-wall at the posterior end of egg, to show the micropylar canal (*m.c.*) and the trabeculae or air spaces (*tr.*) between the exochorion and the endochorion. Semidiagrammatic. (*c*) A longitudinal-vertical section of the micropylar canal. Greatly enlarged. (*d*)–(*h*) Portions of transverse sections of the egg-wall in the micropylar region, showing the course of a micropylar canal through the exochorion and the endochorion beginning from the outside (Fig. *d*) and ending (Fig. *h*) at the inner opening of the canal.

end.ch., endochorion; *e.o.*, external opening of micropylar canal; *ex-ch.*, exochorion; *i.o.*, internal opening of micropylar canal; *m.c.*, micropylar canal; *p.p.*, posterior pole of egg; *r.*, roof of micropylar canal; *rd.*, ridge of endochorion connecting the latter with the exochorion; *tr.*, trabeculae or air spaces between exochorion and endochorion.



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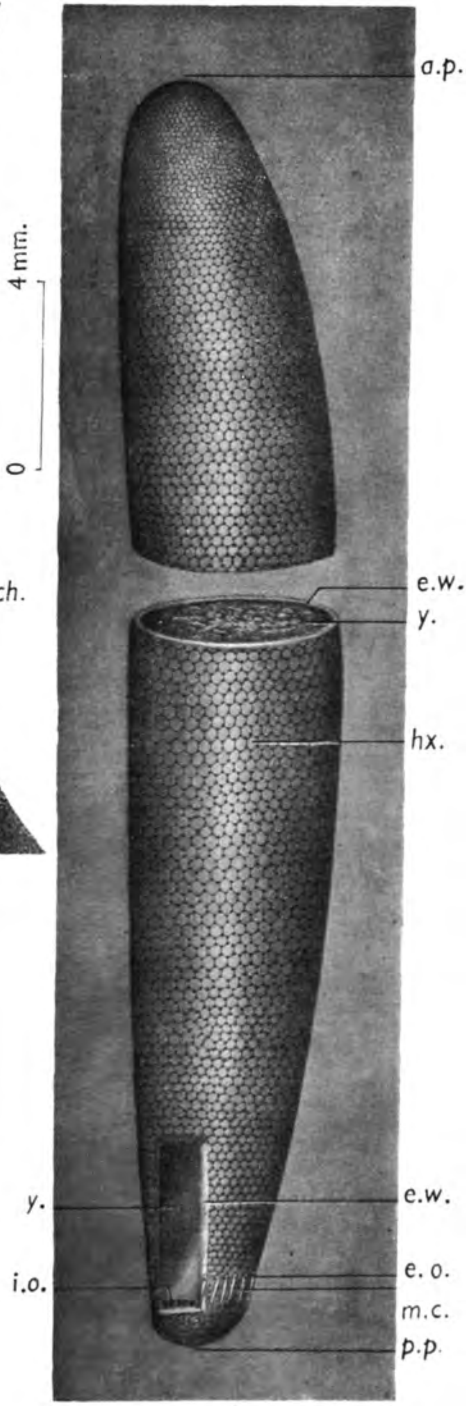

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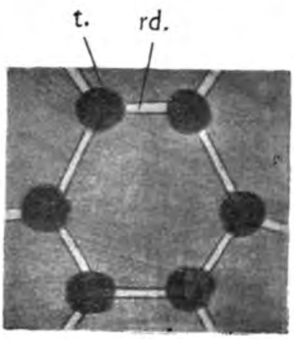
Figs. 6–8



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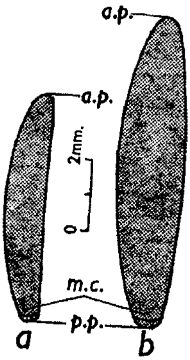
(mean 2·27) in eggs about to hatch, *i.e.*, there is a mean increase of about 70 per cent. Fully developed eggs obtained from the egg-calyx of females in the process of egg-laying are usually smaller than freshly laid eggs, and measure about 4·1–5·0 mm. in length and 0·4–0·5 mm. in width. This feature is probably explicable by two reasons: (i) That in the egg-calyx the eggs are crowded and are not able to swell up to their full dimensions; and (ii) that the egg-shell is still soft and pale yellow, whereas soon after egg-laying it becomes harder and darkens in colour by coming in contact with air. The post-oviposition eggs, therefore, which are now free from mutual pressure, swell up to their full dimensions and, because of the comparative hardening of the egg-shell, stay swollen.



TEXT-FIG. 2.—Eggs of *Schistocerca gregaria* (Forsk.), to show the increase in size during development after oviposition.

(*a*) Freshly laid egg, side view. (*b*) Same, about to hatch.

a.p., anterior pole of egg; *m.c.*, ring of micropylar canals; *p.p.*, posterior pole of egg.

As shown by Roonwal (1936*a*) for the African Migratory Locust, *Locusta migratoria migratorioides*, the swelling of eggs is due to the absorption of water from the outside. This phenomenon occurs in a large number of insects, other Arthropods of even other groups of animals. (For a review, see Roonwal, 1936*a*, 1942, 1944.)

IV. Weight and Moisture Content of Eggs

(Tables 1–4 and Text-figs. 2 and 3)

(*a*) *Increase of weight and moisture content during development* (Table 1).

For the determination of moisture content, normally developing eggs (laid in moist soil) of various stages were washed quickly in distilled water and cleaned with a fine sable brush to remove sand particles and other foreign matter adhering to them. The eggs were then quickly dried by rolling them on a filter paper, transferred to a previously dried glass tube and weighed in an analytical balance. Weighments were usually made in lots of 10–35 eggs, each lot being taken from a single egg-pod. Subsequent drying was done over concentrated sulphuric acid in a dessicator until the weight was constant. The developmental stages of eggs studied were as follows: (i) just-laid; (ii) about 6–12 hours after oviposition (at 33·3° C.); (iii) about two-thirds developed; and (iv) about to hatch (these being taken from eggs-pods from which hatching had already started). Eggs were incubated at 33·3° C. (in one case at 32° C.) in moist sandy-loam but without 'apparently free' water. The results are discussed below.

TABLE 1

Schistocerca gregaria. Weight and moisture content (determined by drying over concentrated sulphuric acid) of eggs after oviposition. (Except where otherwise stated, eggs were weighed in lots of 10–35 in an analytical balance.)

G., from parents cage-bred under crowded conditions; Sw., from parents captured from swarms.

Serial No.	Developmental stage of eggs after oviposition	Source of eggs	Number of eggs weighed in sample	Weight (mg.) of eggs in sample			Calculated average weight (mg.) of one egg			Percentage of water in terms of wet wt. of eggs	Remarks
				Wet wt.	Dry wt.	Loss in wt.	Wet wt.	Dry wt.	Loss in wt.		
1	2	3	4	5	6	7	8	9	10	11	12
1	Just laid	G.	20	171	93	78	8·6	4·65	3·95	45·6	....
2	,,	G.	35	330	175	155	9·4	5·0	4·4	47·0	....
3	,,	Sw.	10	90	48	42	9·0	4·8	4·2	46·7	....
	AVERAGE (just laid)					..	9·0	4·8	4·18	46·4%	....
4	*Ca.* 6–12 hours old at 33·3° C.	G.	1	9·3	4·5	4·8	9·3	4·5	4·8	51·6%	Weighed in torsion balance.
5	24 hours old at 33·3° C.	G.	10	64	27	37	6·4	2·7	3·7	57·5	....
6	,,	G.	10	87	37	50	8·7	3·7	5·0	57·5	....
	AVERAGE (24 hours old)					..	7·6	3·2	4·4	57·5%	....

7	*Ca.* 2/3rds developed *	G.	10	118	52	66	11·8	5·2	6·6	55·9%	* *Ca.* 8 days old at 32° C. (when total incubation period is about 12 days).
8	Just before hatching	G.	1	17·6	3·6	14·0	17·6	3·6	14·0	79·6	Weighed in torsion balance.
9	,,	G.	1	15·2	4·6	10·6	15·2	4·6	10·6	69·7	,, ,,
10	,,	Sw.	10	192	51	141	19·2	5·1	14·1	73·4	....
11	,,	Sw.	(9-10)	177 (10 eggs. Calculated for 9 eggs as 159·3)	44 (9 eggs)	115·3 (9 eggs)	17·7 (Average of 10 eggs)	4·9 (Average of 9 eggs)	12·1 (Average of 9 eggs)	72·4	Out of 10 eggs, one hatched the day after the start of expt., and 9 eggs were, therefore, weighed. For comparison, the average calculated wet wt. of eggs was taken as 159·3 mg.
	Average (just before hatching) ..						17·4	4·6	12·7	73·8%	....

Wet weight.—The wet weight of a single egg increases from about 8·6–9·4 mg. (average 9·0 mg.) when freshly laid to about 11·8 mg. (31·1 per cent increase) when two-thirds developed and, finally, to about 15·2–19·2 mg. (average 17·4 mg.) (93·3 per cent increase over freshly laid eggs) when about to hatch[1]. The weight of the egg is thus nearly doubled during development.

Shulov (1952), from eggs of *Schistocerca gregaria* obtained in the Jordan Valley, Jerusalem, recorded the average increase as from 10·5 when freshly laid to about 24·6 mg. at the beginning of hatching (incubation at 27° C.), an increase of about 134 per cent. These values, especially the last two, are much higher than those obtained by me. At first sight it seems difficult to reconcile the differences, but a consideration of the remarks made by Shulov may perhaps help in doing so. Shulov wrote (p. 474): 'The maximum weight of an egg that develops normally is about 27 mg., but some eggs weighing only 16 mg. may also hatch under conditions of contact moisture. These weights represent increase of 170 per cent and 60 per cent respectively of the original weight. Experimentally, it is possible to obtain fully developed embryos, and even for some of them to hatch, from eggs weighing as little as 11 mg.' The great diversity recorded by Shulov may be due to the greatly differing conditions of moisture availability in the soil or other media in which Shulov incubated his eggs—he did not mention precisely the nature of the medium which he used and the state of its wetness. In my experiments, it may be stated, the eggs were uniformly incubated in moist sandy-loam but without any apparently free water.

Dry weight.—The dry weight of an egg apparently decreases during development—from about 4·8 mg. in the freshly laid egg to 4·6 mg. when about to hatch, a decrease of nearly 4 per cent. It would be desirable to obtain more extensive data in this respect for *Schistocerca gregaria.* It has been demonstrated (Roonwal, 1936*a*) from extensive data that in the African Migratory Locust, *Locusta migratoria migratorioides,* there is a decrease of about 20 per cent in dry weight, the greater part of the decrease occurring in the second half of the developmental period. Roonwal explained it as 'due to the energy expended upon the normal activities of the developing embryo' (p. 7).

Moisture content.—The amount of water in eggs, in terms of the wet weight of eggs, increases during development by about 27·4 per cent, as follows (*vide* also Table 1):—

Stage		*Water content*
Just laid	..	46·4% of wet weight of egg
6–12 hrs. old	..	51·6% ,, ,,
24 hrs. old	..	57·5% ,, ,,
⅔rds developed	..	55·9% ,, ,,
About to hatch	..	73·8% ,, ,,

The *absolute* amount of water present in an egg increases from about 4·18 mg. in freshly laid eggs to about 12·7 mg. in eggs about to hatch, an increase of nearly 3 times. A similar order of increase (3·3 times) was found in *Locusta migratoria migratorioides* by Roonwal (1936*a*, p. 5).

(*b*) *Resorption of water from atmosphere by dehydrated eggs* (Table 2)

When freshly laid eggs are dehydrated and then exposed to moist atmosphere at a fairly high temperature, they re-absorb a small quantity of water from the

[1] The decline of average weight in 24 hours old eggs to 7·6 mg. (*vide* Table 1) is difficult to explain. It may be fortuitous, due possibly to the special smallness of the size of eggs in the different eggs-pods taken for these experiments. In another experiment, where 10 freshly laid eggs from a pod were weighed together, allowed to develop normally, and then re-weighed after 24 hours the weight *increased* during the first 24 hours from 6·7 mg. per egg (calculated) to 8·7 mg., an increase of 2 mg. or nearly 30 per cent.

atmosphere. This was demonstrated in two experiments in which freshly laid eggs, which were experimentally dehydrated for determining their moisture content, were exposed to an atmosphere of 80 per cent relative humidity at 33° C. This moderately high temperature was employed in order to preclude the possibility of condensation of atmospheric water on the eggs which would have occurred at low temperatures. The number of eggs employed was 35 in one experiment and 17 in another; the former lot re-absorbed 0·43 mg. of water per egg, the latter lot 0·47 mg. It took about 24 hours for the maximum resorption, after which there was no further increase of weight.

TABLE 2

Schistocerca gregaria. Resorption of water from the atmosphere (80% R.H.; 30° C.) by freshly laid dehydrated eggs

Expt. No.	Total No. of eggs in expt.	Final weight of dehydrated eggs (mg.)	Weight of eggs after full resorption of water (mg.)	Amount of water resorbed (mg.)	Calculated amount of water resorbed by one egg (mg.)
1	35	175	190	15	0·43
2	17	165	173	8	0·47

(c) ***Rate of loss of water in young eggs in still, dry air at constant temperature*** (33·3° C.) (Tables 3-4; and Text-fig. 3)

The rate of loss of water was studied for just-laid and for 24-hour-old eggs. After the usual cleaning, eggs were weighed and kept in dry glass tube in dry air in a desiccator over sulphuric acid. The desiccator was kept in an electric incubator at a constant temperature of 33·3° C., and weighments were made periodically in a chemical balance.

Just-laid eggs (Table 3; and Text-fig. 3).—In the first 1¼ hours, the total loss of water is 4·68 per cent of the initial wet weight of egg or at the average rate of 3·74

TABLE 3

Schistocerca gregaria. Rate of loss of water from 20 fresh-laid eggs in still, dry air at a constant temperature of 33·3° C.

Sl. No. of weighing	Age of eggs from moment of ovi-position (hours)	Interval from previous weighing (hours)	Actual wet weight of 20 eggs (mg.)	Loss in weight of 20 eggs (mg.) by drying	Calculated weight of one egg (mg.)	Loss in weight of one egg by drying	Percentage loss of water	
							Total loss	Loss per hour
1	0	0	171	0	8·55	0	..	..
2	1¼	1¼	163	8	8·15	0·4	4·68	3·74
3	3¼	2	155	8	7·75	0·4	4·68	2·34
4	22¼	19	103	52	5·15	2·6	30·41	1·6
5	45½	23¼	93	10	4·65	0·5	5·84	0·25
6	69½	24	93	0	4·65	0	0	..
		Total loss in weight:		78	..	3·9	45·61%	..

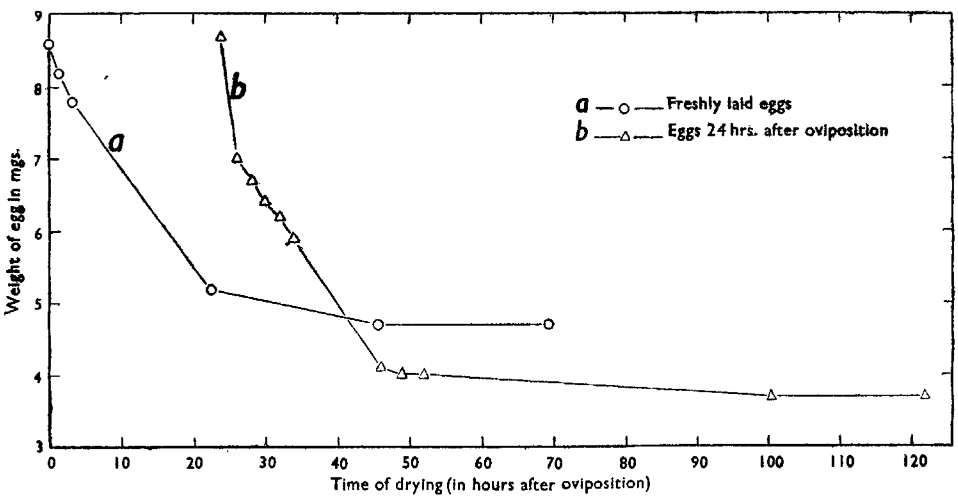
per cent per hour. In the next 2 hours the average rate of loss declines to 2·34 per cent per hour, in the next 19 hours to 1·6 per cent, and in the next 23¼ hours to 0·25 per cent. It will thus be seen that the rate of loss of water is the fastest in the

TABLE 4

Schistocerca gregaria. Rate of loss of water from 10 young eggs (24 hours after oviposition) in still, dry air at a constant temperature of 33·3° C.

Sl. No. of weighing	Age of eggs from moment of ovi-position (hours)	Interval from previous weighing (hours)	Actual wet weight of 10 eggs (mg.)	Loss in weight of 10 eggs (mg.) by drying	Calculated wet weight of one egg (mg.)	Loss in weight of one egg (mg.) by drying	Percentage loss of water	
							Total loss	Loss per hour
1	0	0	(67)	(—)	(6·7)	(—)	..	..
2	24	24	87	*(Increase 20 mg.)	8·7	*(Increase 2 mg.)	..	..
3	26	2	70	17	7·0	1·7	19·54	9·77
4	28	2	67	3	6·7	0·3	3·45	1·73
5	30	2	64	3	6·4	0·3	3·45	1·73
6	32	2	62	2	6·2	0·2	2·30	1·15
7	34	2	59	3	5·9	0·3	3·45	1·73
8	46	12	41	18	4·1	1·8	20·69	1·72
9	49	3	40	1	4·0	0·1	1·14	0·38
10	52	3	40	0	4·0	0	0	0
11	100	48	37	3	3·7	0·3	3·45	0·006
12	121½	21½	37	0	3·7	0	0	0
			Total loss in weight:	50	..	5·0	57·47%	..

* Eggs not dried but kept in moist sand.



TEXT-FIG. 3.—*Schistocerca gregaria* (Forsk.). Graph to show the rate of loss of water from young eggs in still, dry air at a constant temperature of 33·3° C. (*a*) Freshly laid egg. (*b*) Egg 24 hours old.

first few hours, and then gradually slows down until about 22 hours by which time the bulk of the water loss has occurred. The loss continues very slowly until about 45 hours, after which there is no further loss. The total loss is about 45·5 per cent of the wet weight of egg.

24-hour old eggs (Table 4; and Text fig. 3).—The general trend here is similar to that in the just-laid eggs, *viz.*, that the rate of loss of water is the fastest in the first few hours and gradually declines; the bulk of the water is lost by about 22 hours (Table 4, Serial No. 8), after which the loss is negligible. Some differences in detail are, however, noticeable. Thus, the average rate of loss in the first 2 hours is about 9·77 per cent per hour as compared to about 3·7 per cent or less in the just-laid eggs. Subsequently, that is, between about 2–22 hours (Table 4, Serial Nos. 4–8), the average rate of loss is nearly constant, being about 1·15–1·73 per cent; this is similar to the rate in the just-laid eggs (1·6 per cent) during a nearly similar period.

V. Summary

1. The egg-wall of the freshly laid egg consists of 3 layers, *viz.*, a thin outer layer, the exochorion, next to it a thicker endochorion and, finally, an extremely fine and structureless vitelline membrane.

2. The endochorion presents a mosaic pattern of hexagonal (occasionally pentagonal) ridges and tubercles and is separated from the exochorion by means of large trabeculae or air spaces.

3. The micropylar apparatus consists of a ring of small, funicular canals which obliquely traverse the exochorion and the endochorion and open on the inside by means of an extremely fine aperture on the inner surface of the endochorion.

4. The eggs increase in size during development from mean dimensions of about 6·93 × 1·25 mm. when freshly laid to about 8·92 × 2·27 mm. when about to hatch.

5. The mean wet weight of an egg increases from 9·0 mg. when freshly laid to 11·8 mg. (31·1% increase) when two-thirds developed and 17·4 mg. (93·3% increase over freshly laid egg) when about to hatch.

6. The dry weight of an egg decreases from about 4·8 mg. when freshly laid to about 4·6 mg. (a decrease of about 4%) when about to hatch.

7. The moisture content of an egg increases from about 46·4% (of the wet weight of egg) when freshly laid to about 73·8% when about to hatch. The absolute amount of water increases from about 4·18 mg. in the freshly laid egg to about 12·7 mg. when about to hatch.

8. Dehydrated eggs, when exposed to moist air, re-absorb a very small quantity of moisture.

9. The rate of loss of water from young eggs in still, dry air at a constant temperature (33·3° C.) was studied. The rate of loss, which progressively declines, is very rapid in the first few hours. The bulk of the water is lost by 22 hours; the loss continues slowly until about 45 hours after which there is no further loss.

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VII. Explanation of Plates

Lettering

a.p., anterior pole of egg.
end. ch., endochorion.
e.o., external opening of micropylar canal.
e.w., egg-wall.
ex.ch., exochorion.
hx., pattern of hexagonal ridges on endochorion.
i.o., internal opening of micropylar canal.
i.r., inner refractile portion of endochorion.
m.c., micropylar canal.
p.p., posterior pole of egg.
rd., ridges of endochorion.
t., tubercle or protuberance of endochorion.
tr., trabeculae or air spaces between exochorion and endochorion.
y., yolk.

Plate XV

Egg-wall of *Schistocerca gregaria* (Forsk.)

Fig. 1.—Longitudinal section of the egg-wall of a freshly laid egg, showing the exochorion, endochorion, tubercles and trabeculae or air spaces. Greatly enlarged.

Fig. 2.—Surface view of the chorion of an egg 6 hours after oviposition, showing the hexagonal (occasionally pentagonal) pattern formed by ridges, with the 'round' tubercles at the angles. Greatly enlarged.

Fig. 3.—Surface view of the chorion of an egg about to hatch. Note the hexagonal (occasionally pentagonal) pattern and tubercles as in Fig. 2; also note the cracks in the chorion. Low magnification.

Plate XVI

Egg and egg-wall of *Schistocerca gregaria* (Forsk.)

Fig. 4.—Egg, to show the sculpturing and the micropylar canals. The egg is cut transversely in the centre; also, a portion of the egg-wall near the posterior pole is removed to show the disposition of the micropylar canals.

Fig. 5.—Surface view of the egg-wall, to show one of the hexagons formed by the ridges of the endochorion of egg-wall, enlarged to show the position of the tubercles. (*Cf.* Pl. 1, Figs. 2 and 3.)

Fig. 6.—Portion of longitudinal-vertical section of egg-wall in the posterior region of the egg near the micropyle, but not passing through a micropylar canal. Note the absence of tubercles. The vitelline membrane is not shown.

Fig. 7.—Ditto, near middle of egg. Note the endochorionic tubercles and the trabeculae or air-spaces.

Fig. 8.—Ditto, at the posterior pole of egg. Note that the endochorionic tubercles are long and thin rather than stout and broadened externally (*cf.* Fig. 7).

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