THE EGG-WALL OF THE AFRICAN MIGRATORY LOCUST, *LOCUSTA MIGRATORIA MIGRATORIOIDES* REICH. AND FRM. (ORTHOPTERA, ACRIDIDAE)

by M. L. Roonwal, *F.N.I., Forest Entomologist, Forest Research Institute, Dehra Dun*

(With 1 Table, 2 Text-figures and 2 Plates)

(*Received October 26, 1953; read May 7, 1954*)

Contents

I. Introduction

The composition of the egg-wall of the European Migratory Locust, *Locusta migratoria migratoria* Linn., was briefly described by Plotnikov (1926, pp. 271-272) and that of the African Migratory Locust, *L. migratoria migratorioides* Reich. and Frm., by me (Roonwal, 1936*a*). However, in the light of later findings, particularly those of Slifer (1937–1950) on the American grasshopper, *Melanoplus differentialis* Thomas [1], and of Matheé (1951) on the Brown Locust of South Africa, *Locustana pardalina* (Walker), a re-investigation of the egg-wall of the African Migratory Locust, *Locusta migratoria migratorioides* Reich. and Frm. (Orthoptera, family Acrididae), was carried out and the results are presented here. At 33° C. and in moist soil the total period of incubation from the moment of oviposition to that of hatching is about 12½-13 days, and blastokinesis or turning of the embryo occurs at the 5½ to 6-day stage. The developmental stages (*e.g.*, the 40-hour stage, 5-day stage, etc.) mentioned in the present paper refer to the above-mentioned temperature of incubation. For fixing, section-cutting and staining of eggs, the techniques mentioned in my earlier account (Roonwal, 1936*b*, pp. 392-393) were employed.

II. Composition of Egg-wall

(*a*) *Description of egg-wall*

The egg-wall of the fully formed egg, whether lying in the egg-calyx shortly prior to oviposition or freshly-laid, consists of the outer layer or chorion (composed of a thinner external layer or exochorion and a thicker internal layer or endochorion) and inside it a very fine vitelline membrane. As the embryo develops, the vitelline membrane disappears, and one of the two embryonic membranes, *viz.*, the serosa, successively secretes three membranes, one behind the other, in the following

[1] Slifer (1937, p. 494) stated that she examined certain stages of the eggs of *Locusta migratoria migratorioides* R. and F. also; she, however, did not give either a description or illustrations of that species.

chronological order: a thin 'yellow cuticle', a thick 'white cuticle' and a thin 'embryonic cuticle'. Of these, the last named persists until hatching when it is cast off by the freshly-hatched hopper as an 'intermediate moult'. The fate of the remaining two layers could be followed only up to 5 days before hatching, but it is presumably similar to that in *Melanoplus differentialis* (Slifer, 1937) in which the 'yellow cuticle' persists until hatching, while the 'white cuticle' is digested by a 'hatching enzyme' (secreted, according to Slifer, by the pleuropodia) sometime before hatching. The details of the composition of the egg-wall of *L. migratoria migratorioides* in various developmental stages may now be described.

The wall of the fully developed eggs (Pl. XI, Fig. 2; and Text-fig. 2*c*) which have descended from the ovarioles into the egg-calyx, ready for oviposition, has essentially the same composition as that of the freshly-laid egg described below, with this difference that in the former case the exochorion is more smooth and well-defined and the knob-like tubercles (*t.*) of the endochorion are more 'amorphous' and less compact. In the freshly-laid egg, on the other hand, the exochorion is more ragged, but the knob-like tubercles of the endochorion are more compact and better defined in sections of eggs.

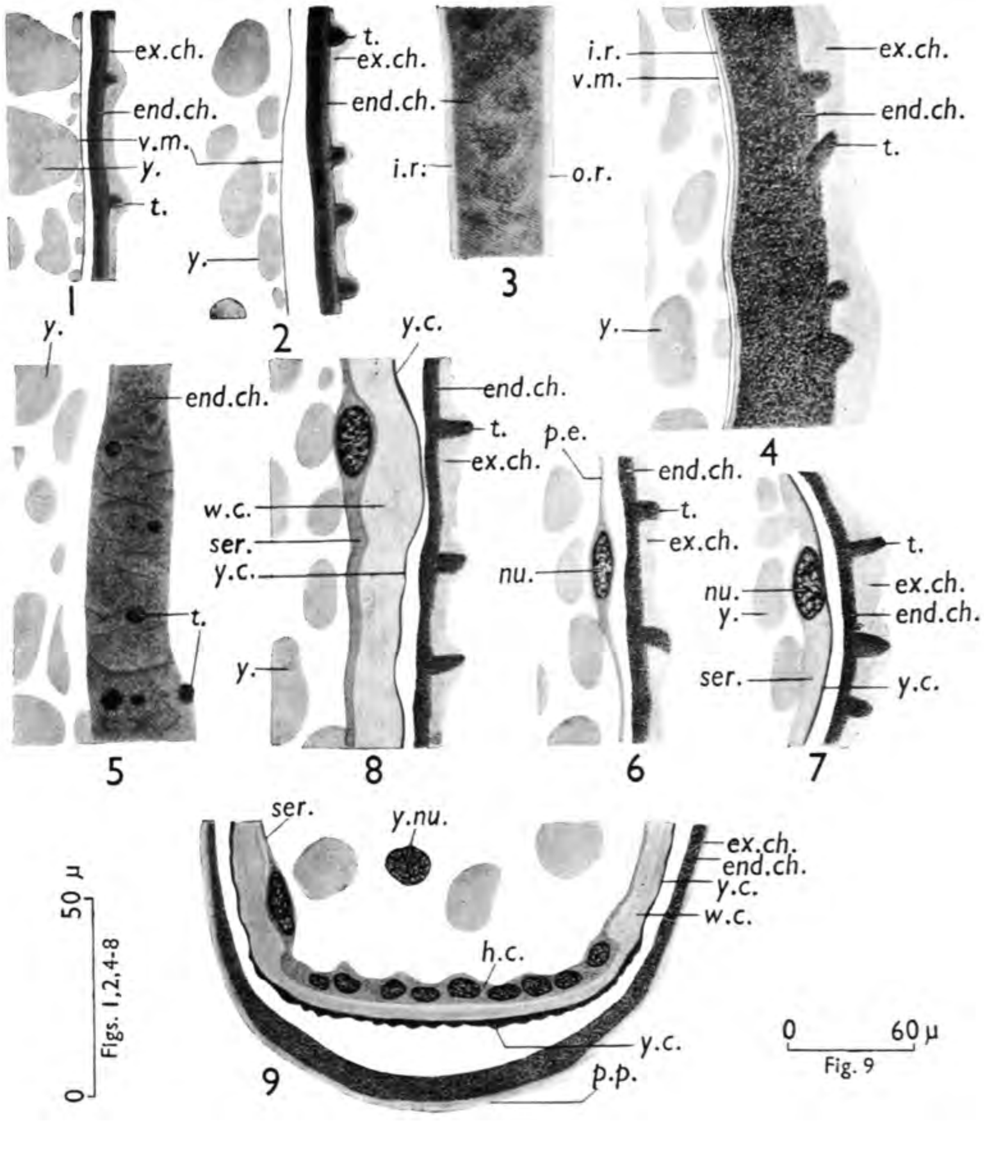
In the freshly-laid egg (Pl. XI, Fig. 2) the egg-wall consists of three layers in the following order from the outside: (i) the outer refractile layer or exochorion ('temporary coat' of Slifer, 1937); (ii) inside it, and contiguous [1] with it, the thick endochorion ('chorion' of Slifer); and, finally, (iii) the vitelline membrane (*vide* Table 1). Both the two outer layers, *viz.*, the exochorion and the endochorion, are much thicker at the poles (especially at the posterior pole of the egg, Pl. XI, Fig. 4) than elsewhere. The exochorion (*ex.ch.*) is comparatively thin (*ca.* 6 μ at the posterior pole and *ca.* 2–3 μ elsewhere), refractile and rather amorphous-looking, and does not stain with haematoxylin or with eosin. The endochorion (*end.ch.*) is *ca.* 28–30 μ thick at the posterior pole and *ca.* 5–6 μ elsewhere. It stains deeply dark-violet with haematoxylin and shows a semi-granular, felt-like structure of 'tangled hairs' except on the extreme outer and inner surfaces which are smooth and refractile (Pl. XI, Fig. 3). The felt-like structure is especially noticeable in a tangential section (Pl. XI, Fig. 5). On its outer face the endochorion is produced into a series of subcylindrical or rounded protuberances (*t.*) which, in surface view of the egg-wall, are visible (Pl. XI, Fig. 5; and Text-fig. 2*a*) as a pattern of closely lying, rather irregularly arranged tubercles (*t.*). Each tubercle is discrete and distinct and is not connected with its neighbours by means of hexagonal ridges (Text-fig. 2*b*) as obtains, for instance, in the Desert Locust, *Schistocerca gregaria* (Roonwal, 1954). In tangential sections (Pl. XI, Fig. 5) the tubercles often appear to lie in the 'body' of the chorion.

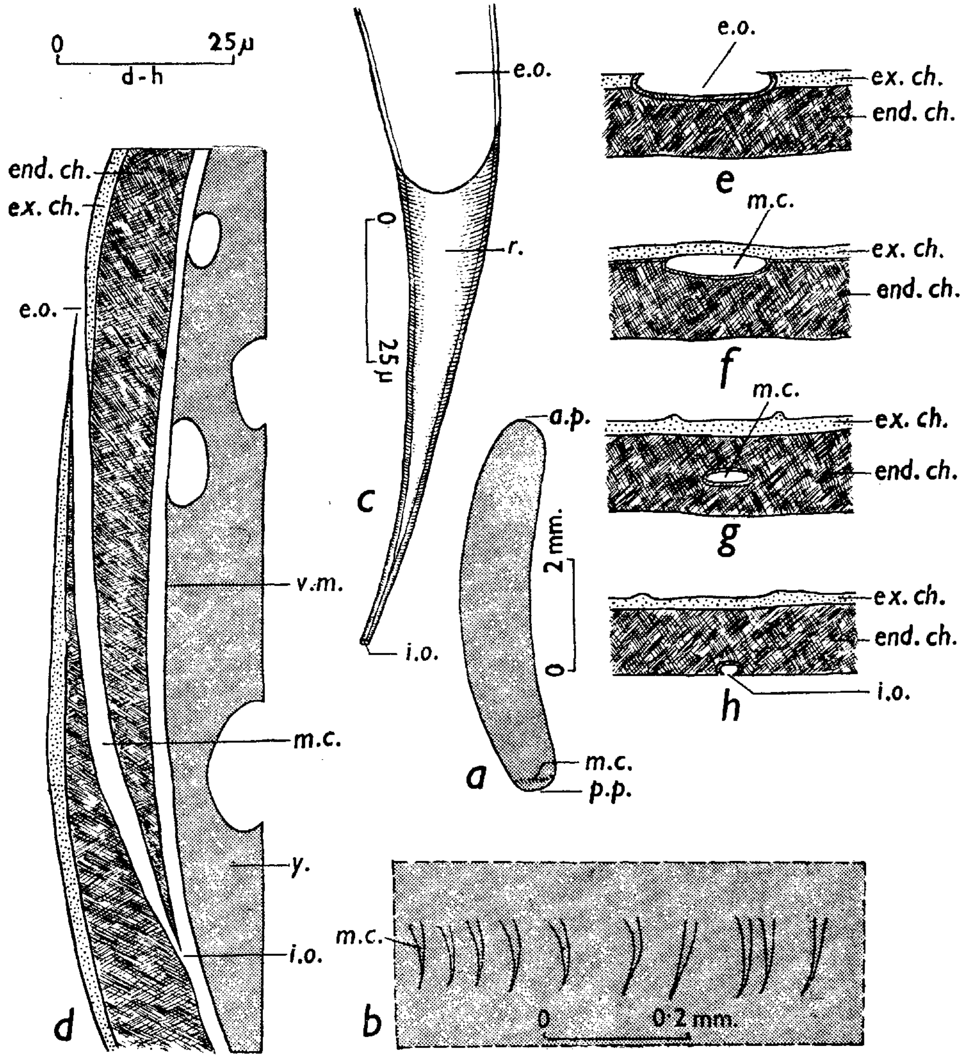
Next to the endochorion is the extremely thin (less than 1 μ) and structureless vitelline membrane (*v.m.*). In sections, at places where the yolk-mass (*y*) is separated from the egg-wall, the vitelline membrane adheres to the yolk-mass rather than to the chorion.

The micropylar apparatus (Text-fig. 1*a–h*), as seen in a freshly-laid egg, consists of a ring of about 35–43 elongated (60–120 μ long), funicular canals—the micropylar canals (*m.c.*)—near the posterior pole of the egg. From its shallow and oblique external opening (*e.o.*), which is about 8·5–28 μ in width, each canal runs obliquely downward (posteriorward) and inward along the longitudinal axis of the egg-wall, traversing the entire chorion and opening, at the inner surface of the endochorion, into the interior of the egg by means of an extremely fine, rounded aperture or internal opening (*i.o.*). The canals do not appear to penetrate the vitelline membrane.

In the $40\frac{1}{2}$-hour old egg (Pl. XI, Fig. 6), the egg-wall is substantially as in the freshly-laid egg, except that the exochorion is less well-defined and has evidently

[1] See further (under Discussion) for two types of egg-walls in the Acrididae.


ex.ch.
end.ch.
v.m.
y.
t.
i.r.
o.r.
y.c.
w.c.
ser.
p.e.
nu.
y.nu.
h.c.
p.p.
1
2
3
4
5
6
7
8
9
50 μ
0
Figs. 1, 2, 4-8
0 60 μ
Fig. 9



TEXT-FIG. 1 (*a–h*). Micropylar apparatus of the freshly-laid egg of *Locusta migratoria migratorioides* R. and F.

(*a*) Egg in side view, showing the ring of micropylar canals near the posterior pole.

(*b*) Surface view of a portion of the egg-wall near the posterior pole of an egg, showing a few micropylar canals.

(*c*) A micropylar canal, from Fig. *b*, in surface view. Greatly enlarged.

(*d*) Longitudinal-vertical section of the egg-wall, showing the micropylar canal.

(*e*)–(*h*) Transverse sections of the egg-wall, showing a micropylar canal cut at various levels, from the outer surface (*e*) to the inner end (*h*). Only the exochorion and the endochorion are shown; the vitelline membrane and the yolk are not shown.

a.p., anterior pole of egg; *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; *v.m.*, vitelline membrane; *y.*, yolk.

begun to disintegrate, and the vitelline membrane is seen no longer. Between the yolk and the endochorion lies the thin primary epithelium [1] (*p.e.*) (membranous portion between the nuclei *ca.* 1 μ thick), a membrane whose extra-embryonic portion shortly afterwards, with the differentiation of the amnion, is termed the serosa and, as such, practically surrounds the entire yolk mass. According to Roonwal (1936*b*, p. 412), the serosa first makes its appearance as a fold at the cephalic end of the germ band in the 42-hour stage; by the 46-hour stage, the caudal and the lateral folds also make their appearance. The primary epithelium is thus converted into the serosa, and, by the 50-hour stage, completely envelops the yolk mass.

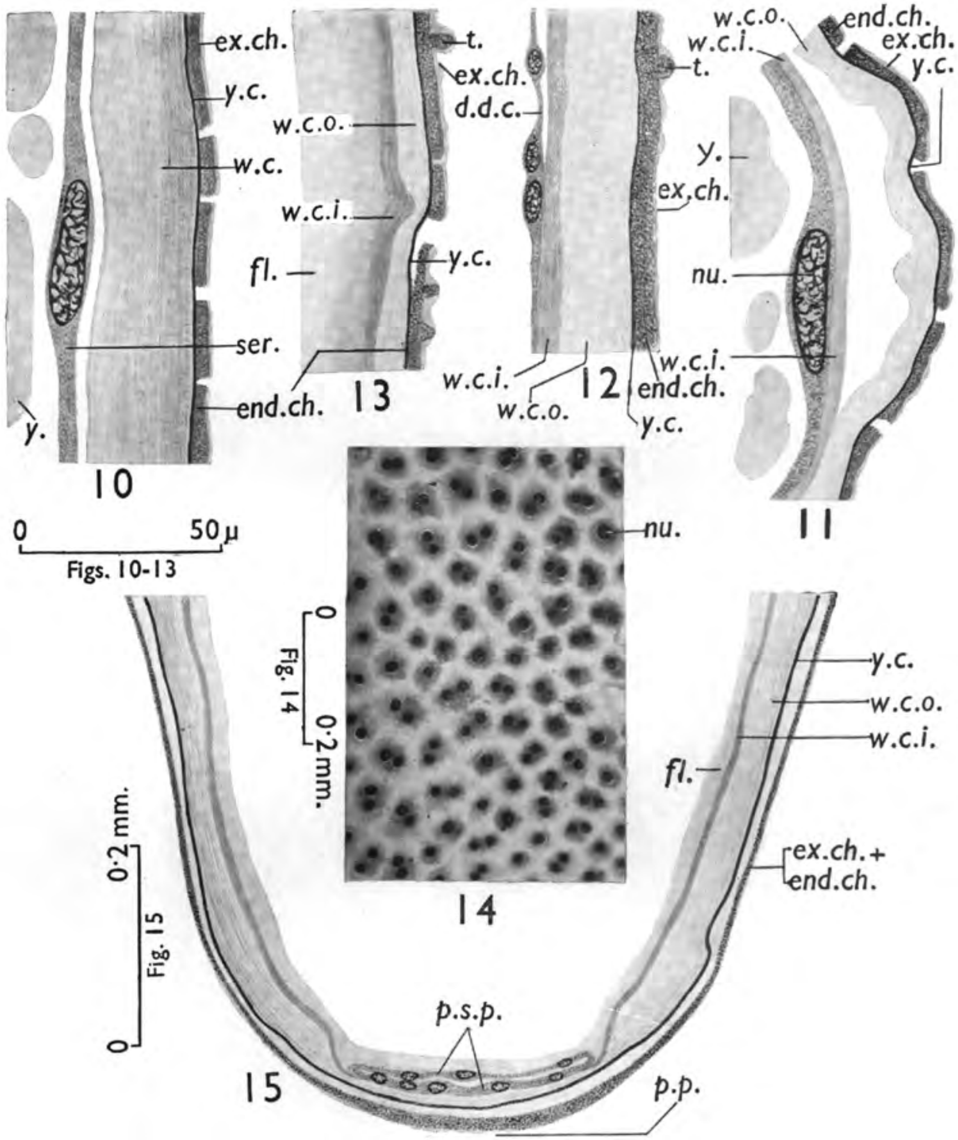
By the time the egg is 66 hours old (Pl. XI, Fig. 7), the serosa has become thickened, the membranous portion in between the neighbouring nuclei measuring about 3–4 μ thick. It has assumed secretory activity and has secreted on its outer surface (*i.e.*, between the serosa and the endochorion) a thin (*ca.* 1 μ thick) yellowish, refractile membrane which does not take either the haematoxylin or the eosin stain; this is the 'yellow cuticle' of Jahn (1935-1936) and of Slifer (1937). It is smooth throughout, and neither now nor later does it show in *Locusta* a spiny outer surface as was reported by Slifer (1937) in *Melanoplus differentialis* and by Matheé (1951) in *Locustana pardalina*.

About the 75-hour stage the serosa secretes, between its outer surface and the yellow cuticle, a second membrane which is thick (*ca.* 8–10 μ), whitish and granular in sections; this is the 'white cuticle' (Pl. XI, Fig. 8, *w.c.*) of Jahn and of Slifer. Like the yellow cuticle, it does not stain either with haematoxylin or with eosin. The serosa itself now appears to be somewhat thinner than in the 66-hour stage, evidently as a result of the secretory material largely having been released in the shape of the white cuticle.

The posterior pole in this stage presents interesting features (Pl. XI, Fig. 9). The yellow cuticle here is about double its normal thickness elsewhere and is crenulated on the outside. On the other hand, the white cuticle at the posterior pole is much thinner (*ca.* 2–3 μ) than elsewhere (*ca.* 5–6 μ). Beneath this small, circular polar patch of thickened yellow cuticle and thinned white cuticle the serosa cells are grouped together in a patch of large cells with numerous rounded nuclei lying close together; these are the 'hydropyle cells' of Slifer. This entire patch evidently corresponds to the 'water-absorbing' area or 'hydropyle' described by Slifer (1938, 1950) in *Melanoplus differentialis*. (Also see below, 7-day old stage.)

In an egg about 117 hours (*ca.* 4½ days) old (Pl. XII, Fig. 10), it is seen that the inner margin (*ca.* 2 μ wide) of the thick white cuticle (which in this stage is about 22–25 μ thick) is glassy, refractile and structureless and stains deeply with eosin, in contrast to the rest of the white cuticle which shows a pattern of fine, parallel laminations (in transverse sections of the egg) and stains lightly with eosin. This 'inner layer' almost presents the appearance of a new layer secreted by the serosa, but, as subsequent development shows, it is only a modified portion of the white cuticle. In this and subsequent stages, the chorion is seen to be longitudinally cracked in several place, a phenomenon recorded by me earlier (Roonwal, 1936*a*, pp. 10-11 and Fig. 3*b*). In the 125-hour or about 5¼-day stage (Pl. XII, Fig. 11), *i.e.*, shortly before blastokinesis or turning of embryo (which begins at the 5½ to 6-day stage), this inner layer (*w.c.i.*) of the white cuticle remains unchanged in appearance, but its width and discreteness from the outer layer (*w.c.o.*) of the white cuticle is even more marked than before, and it is seen, in sections of eggs, that at several places the inner layer is completely separated or torn away from the outer layer. The latter is now also appreciably thinner (*ca.* 8–15 μ). During blastokinesis (*ca.* 5½-day stage) (Pl. XII, Fig. 12), the inner layer is less glassy in appearance than before and becomes partly laminated like the outer layer; and the latter is now

[1] For a definition, see Roonwal (1936*b*, p. 411; and 1939, p. 25).


ex.ch.
y.c.
w.c.
ser.
end.ch.
y.
10
0
50μ
Figs. 10-13
t.
ex.ch.
w.c.o.
w.c.i.
fl.
y.c.
end.ch.
13
d.d.c.
t.
ex.ch.
w.c.i.
w.c.o.
12
end.ch.
y.c.
w.c.o.
w.c.i.
end.ch.
ex.ch.
y.c.
y.
nu.
w.c.i.
11
nu.
0
0·2 mm.
Fig. 14
14
y.c.
w.c.o.
w.c.i.
fl.
ex.ch.+
end.ch.
0·2 mm.
Fig. 15
0
p.s.p.
p.p.
15

evidently thicker (*ca.* 16 μ). The serosa has ruptured and has turned over (Roonwal, 1937).

Soon after blastokinesis (*ca.* 6½-day stage) (Pl. XII, Fig. 13), the inner layer of the white cuticle has lost its glassy and structureless appearance and is fully laminated like the outer layer, but it is still clearly discernible from the latter by taking a deeper eosin or orange *G* stain. The outer layer of the white cuticle is again considerably thinner, being only about 8–10 μ thick. (Also *vide infra*, under Discussion.) In a 7-day old egg (*i.e.*, 1 day after blastokinesis) the position remains substantially unaltered except in the following respects:—(i) The posterior remnants of the serosa form a circular area, termed the 'posterior serosal patch' by Roonwal (1937, p. 195). The patch corresponds to the 'hydropyle cells' described above in the 75-hour stage. (ii) The embryonic body-wall secretes a thin 'embryonic cuticle'. In an egg 8 days old (2 days after blastokinesis), no substantial change is noticeable, but the 'hydropyle area' is now well-defined and is characterised by the presence of the thinned white cuticle (Pl. XII, Fig. 15). The inner layer of the white cuticle is still distinguishable from the outer layer but less clearly than before.

The further fate of the layers of the egg-wall was not followed owing to want of material of the older stages. But, if the fate is similar to the one shown by Slifer (1937, 1938) for *Melanoplus differentialis*, it may be presumed that the white cuticle is digested by the 'hatching enzyme' secreted, according to Slifer, by the pleuropodia, while the yellow cuticle and the chorion persist. As for the embryonic cuticle it has already been shown by me (Roonwal, 1937, pp. 234-235) that it acquires a pattern of spine-like papillae which aid in the hatching operation; the cuticle is cast off during the intermediate moult immediately after hatching.

(*b*) *Discussion*

The chemical and physical properties of some of the egg-coverings of the grasshopper, *Melanoplus differentialis*, have been investigated by Campbell (1929) and Jahn (1935*a*, *b*; 1936), while Slifer (1937–1950) has studied in detail the morphological structure of the egg-coverings in the same species. The chorion (especially the endochorion) is semi-opaque and non-chitinous and, according to Slifer (1945), can be rapidly (within about 2 minutes) and completely dissolved in a 2 per cent solution of sodium hypochlorite with no apparent effect on the development of the embryo. Slifer (1948) has further shown that the chorion is covered, on both the outer and inner surfaces, by a thin layer of hard, white, waxy material at least a portion of which seems to be deposited on the inner surface of the chorion before the egg is laid; a secondary wax layer is probably deposited at the hydropyle near the posterior pole of the egg when diapause begins.

Regarding the physico-chemical nature of the membranes of *Melanoplus* eggs, Jahn (1935*a*, p. 38) concluded as follows: '. . . it seems as if the exochorion and either one or both layers of the cuticle (the "yellow cuticle"[1] and the "white cuticle") are impermeable to $K_4Fe(CN)_6$ or $FeCl_3$. Similar results were obtained with methylene blue and acid fuchsin. Since these layers are apparently freely permeable to water, CO_2 and O_2, we must classify them as semi-permeable membranes.' The endochorion of *Melanoplus* freely took the Prussian blue [$K_4Fe(CN)_6$ and $FeCl_3$] stain. In *Locusta*, as stated above, the endochorion stains deeply with iron-haematoxylin, but the other layers, *viz.*, the exochorion, the yellow cuticle and the white cuticle, do not take that stain.

The yellow cuticle in *Melanoplus*, according to Jahn (1935-1936), is non-chitinous, possesses a high degree of ionic impermeability and may be related to the 'cuticulin' of the insect exoskeleton. The thick and fibrous 'white cuticle' consists, according to the same author, of chitin or a compound closely related to

---

[1] The yellow cuticle is highly impermeable (see further).

chitin. Slifer (1937, p. 498) has pointed out that 'the yellow layer confers a high degree of impermeability [1]; while the white layer is responsible for a greatly increased toughness and resistance to mechanical injury.'

It is interesting to note that in *Locusta* the 'thinning' of the white cuticle begins even before blastokinesis. In *Melanoplus*, Slifer (1937) reported that the digestion of the white cuticle, resulting in its ultimate complete dissolution, begins about 7 to 8 days before hatching (at 25° C., when development is much slower), *i.e.*, long after blastokinesis, from a 'hatching enzyme' secreted by the embryonic pleuropodia. It may be mentioned that in the 75-hour stage (*i.e.*, a considerable time before blastokinesis which begins about the 5½-day stage) in *Locusta*, either the embryo or the serosa or both start secreting a clear fluid which first accumulates in the posterior part of egg. During blastokinesis this fluid fills almost the entire posterior half of the egg and also extends between the serosa and the white cuticle. I (Roonwal, 1936*a*, p. 11) called attention to the presence of this fluid and had assumed that the absorption of this fluid by the 'vitelline membrane' ('white cuticle' of the present account) 'not only causes it to swell but is also responsible for the change into a laminated structure.' This fluid has probably little to do with the 'hatching enzyme' of Slifer (1937) which is secreted by the pleuropodia in *Melanoplus* and is responsible for the digestion of the white cuticle. In *Locusta* also, as mentioned above, a certain degree of thinning of the white cuticle is observable before and soon after blastokinesis, but its cause is problematic.

For facility of comparison, the various interpretations and the nomenclature of the layers of the egg-wall of the Acrididae are given in Table 1.

TABLE 1

Interpretation and nomenclature of the layers of the egg-wall of the Acrididae by various authors.

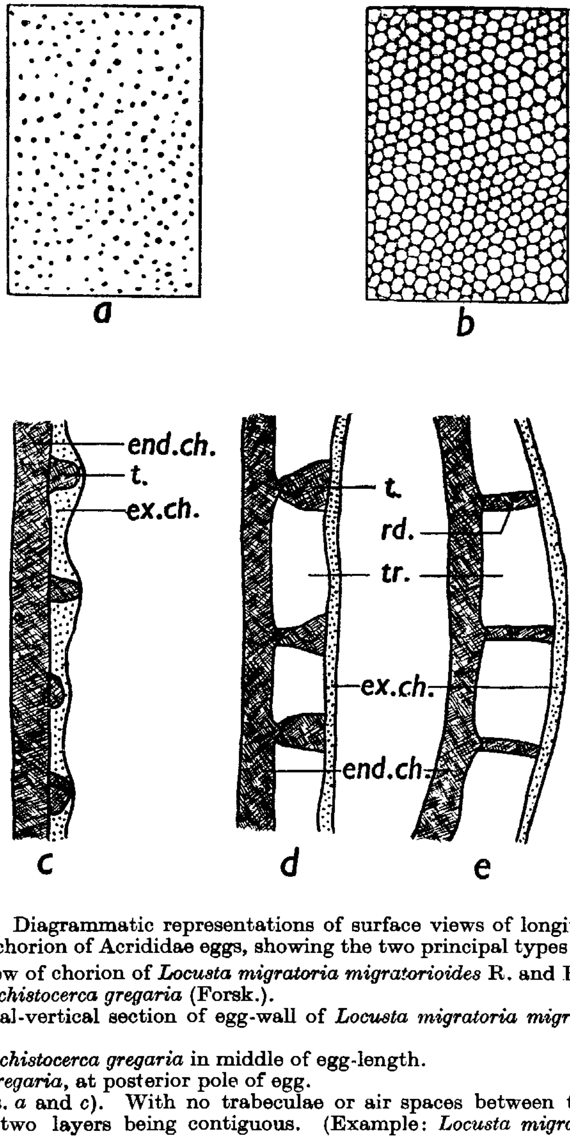
Schistocerca gregaria (Forsk.) (Husain and Roonwal, 1933); *Locusta migratoria migratorioides* R. and F. (Roonwal, 1936*a*, 1937)	*Melanoplus differentialis* (Th.) (Slifer, 1937, 1938)	*Locusta migratoria migratorioides*, R. and F. (Roonwal, present paper)
1. Exochorion	1. Temporary coating ..	1. Exochorion
2. Endochorion.. .. 3. Vitelline membrane ..	} 2. Chorion ..	} 2. Endochorion
	3. Vitelline membrane .. 4. Yellow cuticle ..	3. Vitelline membrane 4. Yellow cuticle
	5. White cuticle ..	5. White cuticle (*a*) Outer layer (*b*) Inner layer
4. Embryonic cuticle ..	6. Embryonic cuticle ..	6. Embryonic cuticle

Two types of egg-wall in the Acrididae.—As regards the chorion, the eggs of the Acrididae appear to fall into two principal types (Text-fig. 2) thus:

Type I, in which the exochorion throughout lies contiguously with the endochorion and is not separated from the latter by means of large, discrete trabeculae or air spaces. (Example: *Locusta migratoria migratorioides* R. and F., Text-fig. 2, *a*, *c*)

[1] Except in the hydropyle area at the posterior pole where it is freely permeable to water.

Type II, in which the exochorion does not lie contiguously with the endochorion (except in certain narrow areas, *e.g.*, the micropylar area), but is largely separated from the latter by means of large, well-defined trabeculae or air spaces. (Example: *Schistocerca gregaria*, Text-fig. 2, *b*, *d*, *e*; see Roonwal, 1954, for fuller details.) The physiological function of the air spaces is problematic.



TEXT-FIG. 2 (*a*–*e*). Diagrammatic representations of surface views of longitudinal-vertical sections of the egg-chorion of Acrididae eggs, showing the two principal types of arrangements.

(*a*) Surface view of chorion of *Locusta migratoria migratorioides* R. and F.

(*b*) Same, of *Schistocerca gregaria* (Forsk.).

(*c*) Longitudinal-vertical section of egg-wall of *Locusta migratoria migratorioides* in middle of egg-length.

(*d*) Same, of *Schistocerca gregaria* in middle of egg-length.

(*e*) Same, *S. gregaria*, at posterior pole of egg.

Type I. (Figs. *a* and *c*). With no trabeculae or air spaces between the exochorion and endochorion, the two layers being contiguous. (Example: *Locusta migratoria migratorioides* R. and F.)

Type II (Figs. *b*, *d*, and *e*). With trabeculae or air spaces present between the exochorion and endochorion. (Example: *Schistocerca gregaria* Forsk.)

end. ch., endochorion; *ex.ch.*, exochorion; *rd.*, ridge of endochorion; *t.*, tubercle of endochorion; *tr.*, trabeculae or air spaces between exochorion and endochorion.

III. Summary

1. In the fully developed egg which lies in the egg-calyx and in the freshly-laid egg, the egg-wall is composed of three layers, which, starting from the outside, are as follows:—A thin exochorion; a thicker endochorion with outer tubercles; and an extremely thin vitelline mambrane.

2. The micropylar apparatus, as seen in the freshly-laid egg, consists of a ring of about 35–43 small, funicular canals—the micropylar canals—near the posterior pole of the egg. Each canal obliquely traverses the entire width of the exochorion and the endochorion and opens into the egg at the inner end by means of an extremely fine aperture.

3. By the 40-hour stage (incubation in all cases at 33° C. and in moist sand), the vitelline membrane is no longer seen.

4. By the 66-hour stage, one of the embryonic membranes, *viz.*, the serosa (which was formed earlier), has secreted on its outer side (*i.e.*, between itself and the inner face of the endochorion) a thin 'yellow cuticle'.

5. About the 75-hour stage, the serosa secretes a second layer, *viz.*, the thick, laminated 'white cuticle'. Later on (117-hour stage), the white cuticle is seen to be divisible into two sharply defined layers, *viz.*, and outer laminated layer which is much thicker and an inner and much thinner, glassy, non-laminated layer. The distinction between the two layers gradually disappears after blastokinesis.

6. Copious amounts of fluid accumulate in the posterior half of the egg from the 75-hour stage onward. This fluid may be responsible for the initial swelling and lamination of the white cuticle.

7. From the 75-hour stage onward is discernible, at the posterior pole of the egg, a small, circular area which is composed of a thickened and crenulated yellow cuticle, a greatly thinned white cuticle and a close accumulation of heavily nucleated serosal cells. This area constitutes the water-absorbing area or hydropyle.

8. Shortly before and after blastokinesis, the white cuticle is comparatively shrunk in thickness apparently through chemical digestion by means of some secretions of the embryo. The precise cause of this shrinkage is not known.

9. In the 7-day stage (about one day after blastokinesis), the embryonic body-wall secretes a thin 'embryonic cuticle' which covers the embryo until hatching and is then cast off as the 'intermediate moult'.

10. The final fate of the egg-membranes, during the last 4 days of development, was not followed.

11. As regards the chorion, there are two types of egg-wall in the Acrididae, thus; Type I, in which the exochorion and the endochorion are throughout contiguous with each other (as in *Locusta migratoria migratorioides*); and Type II, in which the exochorion and the endochorion do not usually run contiguously but are separated by means of large trabeculae or air spaces (as in *Schistocerca gregaria*).

IV. References

Campbell, F. L. (1929). The detection and estimation of insect chitin; and the irrelation of 'chitinization' to hardness and pigmentation of the cuticula of the American Cockroach, *Periplaneta americana* L. *Ann. Ent. Soc. Amer.*, Columbus (Ohio), **22**, 401–426.

Husain, M. A. and Roonwal, M. L. (1933). Studies on *Schistocerca gregaria* Forsk. I. The micropyle in *Schistocerca gregaria* Forsk. and some other Acrididae. *Indian J. Agric. Sci.*, Delhi, 3(4), 639–645, 1 pl.

Jahn, T. L. (1935*a*). The nature and permeability of the grasshopper egg membranes. I. The E.M.F. across membranes during early diapause. *J. Cell. Comp. Physiol.*, Philadelphia, 7(1), 23–46.

Jahn, T. L. (1935*b*). The nature and permeability of the grasshopper egg membranes. II. Chemical composition of membranes. *Proc. Soc. Exp. Biol. Med.*, New York, **33**, 159–163.

Jahn, T. L. (1936). The nature and permeability of the grasshopper egg membranes. III. Changes in electric properties of the membranes during development. *J. Cell. Comp. Physiol.*, Philadelphia, 8(2), 289–300.

Mattheé, J. J. (1951). The structure and physiology of the egg of *Locustana pardalina* (Walk). *Sci. Bull. Dept. Agric. S. Afr.*, Pretoria, No. 316. (Locust Res. Ser., No. 13, 1–83.)

Plotnikov, V. J. (1926). *Insects Injurious to Cultivated Plants in Central Asia.* (In Russian.) 1–292.—Tashkent (Uzbekistan Exper. Sta. Plant Prot.).

Roonwal, M. L. (1936*a*). The growth-changes and structure of the egg of the African Migratory Locust, *Locusta migratoria migratorioides* R. and F. (Orthoptera, Acrididae.) *Bull. Ent. Res.*, London, **27**(1), 1–14.

Roonwal, M. L. (1936*b*). Studies on the embryology of the African Migratory Locust, *Locusta migratoria migratorioides* R. and F. I. The early development, with a new theory of multiphased gastrulation among insects. *Philos. Trans. R. Soc. Lond.* (B), London, **226**, 391–421, 3 pls.

Roonwal, M. L. (1937). Studies on the embryology of the African Migratory Locust, *Locusta migratoria migratorioides* Reich. and Frm. II. Organogeny. *Philos. Trans. R. Soc. Lond.* (B), London, **227**, 175–244, 7 pls.

Roonwal, M. L. (1939). Some recent advances in insect embryology, with a complete bibliography of the subject. *J. R. Asiat. Soc. Bengal* (*Sci.*) (N.S.), Calcutta, **4**(2) [1938], 17-105.

Roonwal, M. L. (1954). Size, sculpturing, weight and moisture content of the developing eggs of the Desert Locust, *Schistocerca gregaria* (Forskål) (Orthoptera, Acrididae). *Proc. Nation. Inst. Sci. India*, Calcutta, **20**.

Slifer, E. H. (1937). The origin and fate of the membranes surrounding the grasshopper egg; together with some experiments on the source of the hatching enzyme. *Quart. J. Micr. Sci.*, London, **79**(3), 493–506, 3 pls.

Slifer, E. H. (1938). The formation and structure of a special water-absorbing area in the membranes covering the grasshopper egg. *Quart. J. Micr. Sci.*, London, **80**(3), 437–457, 1 pl.

Slifer, E. H. (1945). Removing the shell from living grasshopper eggs. *Science*, New York, **102**, 282.

Slifer, E. H. (1948). Isolation of wax-like substance from the shell of the grasshopper egg. *Discussion of Faraday Society*. (Interaction of water and porous materials), 182–187.

Slifer, E. H. (1950). A microscopical study of the hydropyle cells in the developing egg of the grasshopper, *Melanoplus differentialis*. *J. Morph.*, Philadelphia, **87**(2), 239–274 (10 pls.).

V. Explanation of Plates

Lettering

a.p., anterior pole of egg.
d.d.c., 'definitive dorsal closure' of embryo.
end.ch., endochorion.
e.o., external opening of micropylar canal.
ex.ch., exochorion.
fl., fluid.
h.c., 'hydropyle cells' of serosa.
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.
nu., nucleus.
o.r., outer refractile portion of endochorion.
p.e., primary epithelium ('blastoderm' of some authors).
p.p., posterior pole of egg.
p.s.p., posterior serosal patch (hydropyle cells).
r., roof of micropylar canal.
rd., ridges of endochorion.
ser., serosa.
t., tubercle or protuberance of endochorion.
tr., trabeculae or air spaces between exochorion and endochorion.
v.m., vitelline membrane.
w.c., white cuticle.
w.c.i., inner layer of white cuticle.
w.c.o., outer layer of white cuticle.
y., yolk.
y.c., yellow cuticle.
y.nu., nucleus of secondary yolk cells.

Plate XI

Sections of eggs of *Locusta migratoria migratorioides* R. and F., to show the structure of the egg-wall. (Eggs incubated at 33° C. and in moist soil).

Fig. 1. Portion of longitudinal-vertical section in middle of egg-length of fully developed egg in egg-calyx shortly before oviposition.

Fig. 2. Ditto of freshly-oviposited egg.

Fig. 3. Ditto. Portion of endochorion greatly enlarged, to show the refractile margins and the granular, felted core.

Fig. 4. Ditto. Portion of egg-wall at the posterior pole of freshly-laid egg. Note the thick endochorion.

Fig. 5. Portion of tangential section of freshly-laid egg in middle of egg-length, to show the felted structure of the endochorion.

Fig. 6. Portion of longitudinal-vertical section in middle of egg-length of 40½-hour old egg. Note the absence of the vitelline membrane and the presence of the extra-embryonic portion of the primary epithelium (the future serosa).

Fig. 7. Portion of transverse section of 66-hour old egg near posterior one-third of egg-length. Note the yellow cuticle.

Fig. 8. Portion of longitudinal-vertical section near middle of egg-length of 75½-hour old egg.

Fig. 9. Ditto of posterior pole of 75½-hour old egg. Note the 'hydropyle cells' and the related structures.

PLATE XII

Sections, etc. of eggs of *Locusta migratoria migratorioides* R. and F., to show the structure of the egg-wall. (Eggs incubated at 33° C. and in moist soil).

FIG. 10. Portion of transverse section near middle of egg-length of 117½-hour old egg. Note the thick, laminated white cuticle and the chorion (*ex.ch.*; *end.ch.*) which is cracked in several places.

FIG. 11. Portion of transverse section near middle of egg-length of egg about 125 hours (*ca.* 5¼ days) old, *i.e.*, shortly before blastokinesis. Note the inner (*w.c.i.*) and outer (*w.c.o.*) layers of white cuticle.

FIG. 12. Portion of longitudinal-vertical section near middle of egg-length of egg during blastokinesis (*ca.* 5½-day stage).

FIG. 13. Portion of transverse section near middle of egg-length of egg soon after blastokinesis (*ca.* 6½- to 7-day stage). Note the fluid (*fl.*) next to the white cuticle.

FIG. 14. Photomicrograph of a flat mount of serosa from middle portion of egg soon after blastokinesis (*ca.* 6½- to 7-day stage). Serosa stained with borax carmine. Note that several serosal cells have two nuclei.

FIG. 15. Longitudinal-vertical section of posterior end of 8-day old egg (2 days after blastokinesis), to show the egg-wall and the serosal remnants. Note the 'posterior serosal patch' in the hydropyle area. The yolk-mass inside the egg is not shown.

Issued August 13, 1954.