The Shell of Acridid Eggs

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SUMMARY

The shell of the newly-laid egg of *Locusta migratoria* is composed of a chorion and an outer layer, here termed the extrachorion. The development of the chorion and extrachorion has been followed. The structures of the egg-shells of *Schistocerca gregaria*, *Romalea microptera*, and 6 species of British grasshoppers are also described and are found to conform to the same pattern. The chorion has a meshwork structure which may be filled with air or water. Wound repair in the eggs is also noted.

INTRODUCTION

SLIFER (1937) mentions a temporary coating on the eggs of *Melanoplus differentialis*, a layer which Roonwal (1954*a*) terms exochorion. Jahn (1935) considers the chemical nature of the egg-membranes and shows a difference between the inner and outer layers of the chorion. An investigation of the egg-shells of some Acrididae revealed that the egg-wall in the freshly-laid eggs was not wholly of follicular origin and that it therefore should not be termed chorion. In this paper the chorion and extrachorionic layers are described in various Acrididae. Descriptions are given of the egg-shells of *M. differentialis* (Slifer, 1937, 1949), *Locusta migratoria* (Roonwal, 1954*a*), and *Schistocerca gregaria* (Roonwal, 1954*b*). Kulagin (1932) has also described the structure of the egg-shell of *L. migratoria* and *S. peregrina* (*gregaria*), but in *Locusta* he calls the chorionic layers 'ectochorion', the outer zone of the white cuticle 'endochorion', and the inner zone 'oolemma'.

THE STRUCTURE OF THE EGG-WALL OF *LOCUSTA MIGRATORIA MIGRATORIOIDES*

The egg of *Locusta* is about 6·5 mm long and 1·3 mm wide. The surface is covered by a series of granules except at the posterior end beyond the ring of micropyles, where there is slight hexagonal sculpturing. The wall of the freshly-laid egg consists of 4 layers in the following order, beginning with the innermost: (1) the viteline membrane, with the primary wax layer; (2) the endochorion; (3) the exochorion; (4) a layer which is here called the extrachorion.

The endochorion (fig. 1, *end*) is a meshwork layer, 4 to 8 μ thick, except at the posterior end where it is up to 30 μ thick. This layer consists of an interlocking, tangled system of fine struts. Air in the spaces can be rapidly displaced by water or alcohol, which can enter through the inner surface or through the exochorion. Entry of water is even more rapid through cut or torn edges.

The exochorion (fig. 1, *exo*) is an outer layer, less than 1 μ thick, overlying the endochorion. Both the endo- and exochorion stain weakly with haematoxylin, strongly with eosin, and red with the Azan stain.

The extrachorion (fig. 1, *ext*) is a thin layer containing granules. The granules are 6 to 8 μ high and about 4 μ wide, but the remainder of the layer is very thin and is usually rather fragmentary. The nature and appearance of

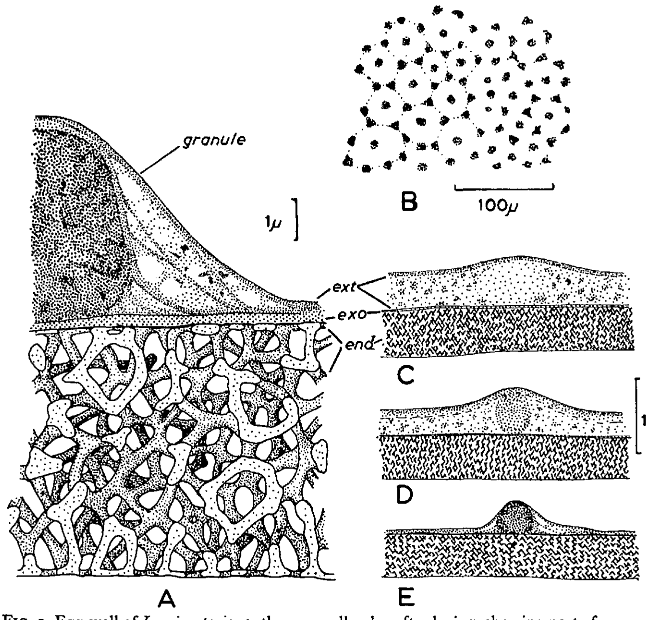

FIG. 1. Egg-wall of *L. migratoria*. A. the egg-wall 1 day after laying, showing part of a granule; B, surface view of chorion 1 hour after laying; the dots between granules on the left have been added to emphasize the hexagonal pattern; C to E, stages in the shrinkage of the extrachorion while the egg is in the common oviduct, showing development of a granule. *ext*, extrachorion; *exo*, exochorion, *end*, endochorion.

this layer changes with age as will be described in the following section. In the dried-out condition this layer stains strongly with haematoxylin and blue with Azan. The extrachorion has been called the temporary coating by Slifer (1937, 1949), but Roonwal (1954*a*) has termed it the exochorion. As this layer appears after the egg has separated from the follicular cells it can hardly be termed chorion. It is also rather more persistent in *Locusta* than it appears to be in *Melanoplus* (Slifer, 1937).

STAGES IN THE FORMATION OF THE EGG-WALL OF *LOCUSTA*

1. When the oocyte is fully formed the endochorion is secreted by the follicle cells.

2. The exochorion is secreted as a thin layer over the endochorion. It is without surface structure but when stained with haematoxylin it shows, in surface view, an indistinct hexagonal pattern. Each hexagon has an indistinct central spot. The hexagonal pattern corresponds with the boundaries of the follicle cells. It is not apparent in sections.

3. As the egg enters the common oviduct the extrachorion is secreted. It rapidly attains its maximum thickness and is fully present on any part of the egg by the time that part has passed 0·7 to 0·8 mm into the oviduct.

4. The extrachorion starts to shrink or condense while in the common oviduct. As the layer shrinks small islands remain. At first these islands are less granular than the rest of the layer (fig. 1, C). They correspond in position to the angles of the hexagonal pattern and to the central spots (see 2, above). As the extrachorion further contracts, the islands become denser while the rest of the layer shrinks down on to the chorion (fig. 1, D).

5. When the egg is laid the extrachorion is still not fully shrunk (fig. 1, E). The chorion is still filled with liquid. If exposed to the air it may dry out in a few hours. Under moist conditions, such as might be found in the egg-pod in damp soil, this may never happen. If the chorion dries out, the extrachorion also rapidly dries out into a thin layer, but under moist conditions the extrachorion will still continue to shrink, although more slowly. The denser islands of the extrachorion persist as the surface granules, and the rest of the layer remains as thin rather fragmentary sheets.

6. As the egg develops it absorbs water and expands. At first the chorion stretches, but later it may break. By this time, however, the serosal cuticle is fully formed and is the principal wall of the egg.

THE EGG-WALL OF OTHER ACRIDIDAE

Schistocerca gregaria. The egg is about 7 mm long and 1·3 mm wide. Its appearance has been described by Roonwal (1954*b*). The chorion has raised ridges forming an approximately hexagonal pattern corresponding to the edges of the follicular cells. The chorion does not show any differentiation into exo- and endochorion, although the outer zones are slightly more dense. The structure of the chorion, including the ridges, is similar to the endochorion of *Locusta*. There is no separation between the ridges and the endochorion as shown by Roonwal (1954*b*). A layer of extrachorion covers the egg, bridging over the ridges and leaving spaces beneath them. When the extrachorion is first produced it fills the spaces between the ridges. It later shrinks, while still in the oviduct, to form the layer over the ridges, and it also forms thickenings on the tops of the ridges, especially at the angles of the ridges.

Romalea microptera. The egg is 9 to 10 mm long and 2 mm wide. The structure of the shell is similar to that of *Schistocerca*. The raised ridges of the chorion form a deep honeycomb pattern which is bridged over by a layer of extrachorion. The chorion is about 30 μ thick and the ridges extend a further 100 μ outwards. The chorion shows two zones: the endochorion, which has a similar structure to that of *Locusta* and extends a little way up the ridges; and the exochorion, which forms a layer up to 8 μ thick over this. The structure of the exochorion is similar to the endochorion but the meshwork is much finer and denser. The extrachorion is present as a thin layer over the ridges and it also forms the thickenings on the tops of the ridges.

Chorthippus parallelus. The egg (fig. 2, A) is about 3·7 mm long and 1 mm wide. The external appearance of this and other eggs of the British Acrididae

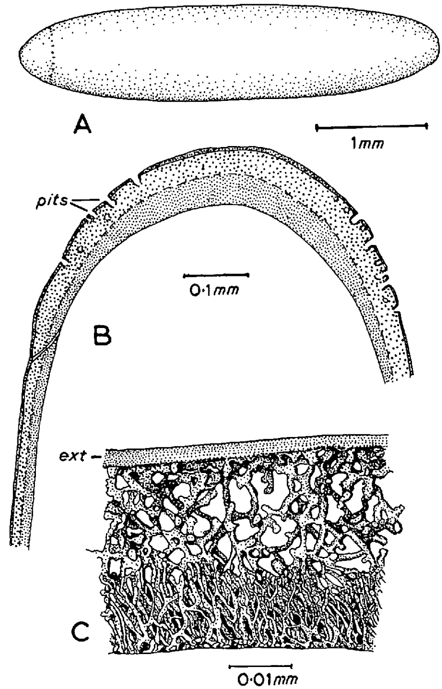

FIG. 2. Egg of *C. parallelus*. A, the whole egg. B, semi-diagrammatic section of the posterior end of the egg, showing pits, micropyle, extrachorion, and two zones of endochorion. C, the egg-wall of the side of the egg near the posterior end; note thick extrachorion (*ext*).

is described by Waloff (1950). It has a prominent sculpturing of low hexagonal ridges on the surface. The total thickness of the shell varies from about 35 μ at the sides to about 100 μ at the posterior end. The endochorion, which accounts for most of the thickness, has two distinct zones (fig. 2, B, C). The inner zone has a much finer and denser tangled meshwork than the outer zone. There is a thin, continuous exochorion about 0·5 μ wide and a thicker extrachorion about 2 μ. There is a series of small pits forming a ring around the posterior tip of the egg. These pits pass through the outer layers and enter the outer zone of the endochorion. Water readily enters the chorion through these pits, but elsewhere the surface is hydrofuge.

Chorthippus brunneus. The egg is slightly larger than that of *C. parallelus* and is without sculpturing. The endochorion is about 8 μ thick and consists of a dense meshwork throughout. The appearance is very like that of *Locusta*, which is slightly less dense than the denser part of the chorion of *C. parallelus*. There is a slight tendency for the inner part to be denser. The endochorion is thicker at the posterior end. The exochorion and extrachorion are very like those of *C. parallelus*. The posterior end of the shell also has pits in it running into the endochorion, but these do not have any special permeability to water. The whole of the egg-wall takes up water fairly readily.

C. albomarginatus (*elegans*), *Omocestus viridulus*, *Stenobothrus lineatus*, and *Myrmeleotettix maculatus* all have an egg-wall structure very like that of *C. brunneus*. Their behaviour to water is also the same. The illustration of the egg-wall of *Melanoplus differentialis* (Slifer, 1949, fig. 7) indicates a structure similar in general form but with a thicker exochorion.

Discussion

In the newly-laid egg the layers of the shell are of maternal origin. During subsequent development a thick serosal cuticle, which is almost completely reabsorbed before hatching, is produced beneath the shell (Slifer, 1937). Jahn (1935) distinguished two layers in the chorion of *Melanoplus* eggs by their chemical reactions. Slifer (1949) refers to a 'mucus-like temporary coating' which covers the newly-laid egg. It is now found that the egg-wall is formed in two stages: (1) the chorion, which may itself be separated into two zones, and (2) an outer layer produced as the egg enters the oviduct. This outer layer is here called the extrachorion.

Kulagin (1932) claims that in *Locusta* possibly his ectochorion and also his endochorion are formed after the egg has left the ovary, and that the only layer present in the ovary is the oolemma. However, his fig. 4 clearly shows that both his endochorion and oolemma are parts of the serosal cuticle.

Slifer (1937) states that the temporary coating of *Melanoplus* eggs shrinks and disappears during the first few days after laying. This has not been found in the eggs examined. The extrachorion shrinks and may, as a result, crack; but it persists as a thin rather fragmentary layer. Further evidence of this persistence is shown in *Locusta*, where the surface granules are part of this layer. The granules are still evident in hatched eggs. During the process of expansion by the egg, all the egg-wall layers appear to become thinner as they stretch before breaking. This process has made some authors suggest that dissolution of the white cuticle starts at a much earlier stage than it does. The extrachorion in *C. parallelus* eggs renders the egg impermeable to water except at the posterior end. It is probable that this layer also has the same properties in *Locusta*, as the egg is not uniformly wettable. The layer in the latter is very thin and has many cracks. In other species of *Chorthippus*, which have an extrachorion nearly as thick as that of *C. parallelus*, no barrier to water absorption is produced, and in these eggs water enters anywhere through the surface. Water will enter a damp egg more rapidly than a dry one. The reason is that the chorion itself, rather than the air spaces, absorbs water and expands as a result. This in turn facilitates the entry of water into the spaces of the chorion.

The endochorion is composed of a close network of fine struts which produce a felt-like structure. This structure has many advantages for eggs of this nature. It conducts water, thereby enabling the egg to collect water efficiently through only a small area from a water supply anywhere on the surface of the shell. Under dry conditions water loss from the egg in the gaseous phase is restricted. The endochorion can also be compressed and stretched before it breaks, particularly when it is wet. This allows the egg to expand without destroying the means of water conduction or affecting the structural support. The chorion of a fully expanded egg cracks if it is allowed to dry, but at this stage the serosal cuticle has taken over the structural support of the egg. The frothy nature of the egg-pod also allows the eggs to expand while still allowing water and air to reach them.

The expansion of the egg involves a certain risk from abrasion, particularly if the eggs are laid in a pod in the ground. Jones (1958) shows that the liquid filling the space between the serosa and serosal cuticle can rapidly form a tanned protein-lipid membrane. This occurs when the liquid is released through punctures in the egg-wall. Slight damage by abrasion, and even by the effects of differential drying in strong light, cause small drops of this liquid to appear in swollen eggs. These drops immediately form a skin and then dry up. Examination of the swollen eggs of *Locusta* has shown that damage has occurred and been repaired in this way many times. The fluid in other acridid eggs also has this wound-repairing property.

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