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John Hull Grundy Lecture
Eggs – The Neglected Insects

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I am grateful for this privilege of honouring the memory of John Hull Grundy, one of the outstanding teachers of medical entomology. I have chosen to discuss insect eggs for a number of reasons. Firstly, they are certainly neglected, even to the point that, while most textbooks of applied entomology contain pictures of the larva and adult of the species described, and of the pupa if there is one, eggs – if they are figured at all – are usually a characterless blob. An egg is just as much a living insect as is each of the other stages of its lifecycle. It is an understandable reaction of man that his first thought is to attack the things he sees actually doing damage or biting people and domestic animals, but killing eggs is a pre-emptive strike before any harm is done. And eggs are immobile – they cannot be disturbed by any treatment aimed at controlling them and fly away.

The insect egg-stage too has a particular significance in relation to the transmission of mammalian disease, because few if any of the micro-organisms of medical and veterinary importance, and certainly none above the level of viruses, are transmitted from the female insect to her eggs. If that were not so, the prevalence of insect-borne diseases would be far greater. Instead, each new generation of vector has to become infected from a vertebrate host, and with widespread diseases like malaria there must be two bites – one which achieves infection and another which transmits. The phenomenon is of wider implication. Amongst most recent developments in control methods is the use of viruses pathogenic to insect pests. These are not transmitted through the egg to the next generation, and therefore the virus does not persist. From one viewpoint this is an obvious disadvantage; it does however provide some degree of safety factor should an introduced virus prove to have unforeseen characteristics or mutate.

These features of insect pathology arise from the way in which each insect egg is protected during its formation, and which I shall describe later. In contrast, the process of egg production is quite different in the mites and the ticks, in both of which groups the transmission of pathogens into the egg from the mother has major significance in relation to important diseases. Thus the mite *Trombicula deliensis* which carries *Rickettsia orientalis* causing scrub typhus, which was such a problem in the Burma campaign in the last world war, only takes one meal in its entire life cycle, and could not therefore be a vector unless it was infected by its mother. Since a range of small mammals are reservoir hosts of the disease, a high proportion of the mites are infective. Similarly, this must account for the high incidence of disease organisms in tick populations, and to take a particular example of current concern, Lyme disease must be transmitted through the egg because it arises from the bite of the larval tick, and normally the larva takes only one blood meal before turning into the nymph.

As you all know, tick larvae are readily identifiable because they have only six legs, and the additional pair appear when they moult to nymphs. This curiosity is a favourite amongst examiners: except in Cambridge, after the occasion when the collection of specimens for identification put out for each first-year student included a corked tube containing ten live tick larvae, and two hundred students tipped the contents onto petri dishes, looked at them under their microscopes – and discarded the dishes on the benches. History does not relate how many of that class acquired ticks, but ultimately the laboratory had to be sealed and fumigated.

The change in the metabolic processes when an insect emerges from its egg is illustrated by an empirical scientific conundrum. Broadly speaking, chemicals which particularly kill eggs are not highly efficient insecticides for active stages, and *mutatis mutandis*, those which are good insecticides are not usually effective ovicides. This point was elegantly illustrated many years ago by my then colleague Professor Tony Lees, who had a sheep tick almost completely paralysed by DDT, which nevertheless managed to lay a large egg batch: the eggs all developed normally and hatched, whereupon the tiny tick larvae started to tremor, and died from the dose of poison which had already passed into them from their parent. It is differences in sensitivity of this kind which can enable one to be selective against eggs without necessarily doing widespread environmental damage to other insects.

Of course I also want to talk about eggs because I have worked on them on and off for a long time, most recently on those of mosquitoes; but it is over forty years ago that I carried out what was then the first detailed study of the structure of an insect eggshell, how it was formed, how it protects its contents and how poisons enter, and I hoped then that the research would become a type-study for subsequent investigations. I chose the egg of the blood-sucking bug *Rhodnius prolixus*, one of the vectors of Chagas' disease in South America, which was readily available in the London School of Hygiene and Tropical Medicine, and because, by insect standards, it was a nice big egg – about 1.5 mm long. Its surface (and we now know this is typical of so many shells) is complexly sculptured (Fig 1), such that it provides high mechanical strength for the amount of material used; this is one of countless examples where insects evolved good engineering systems millions of years before man discovered them.

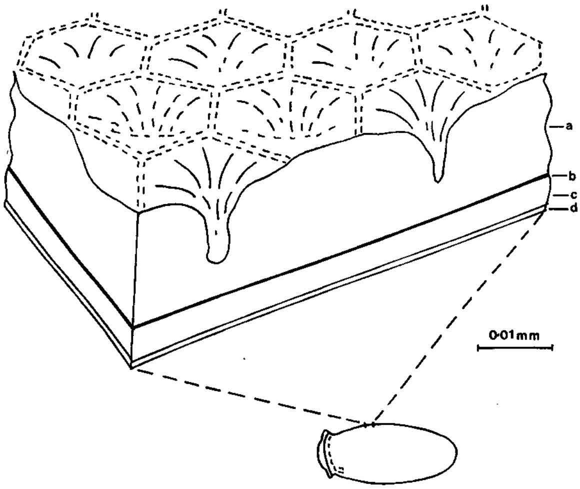

Fig 1. *Rhodnius* egg showing cap, and structure of the main shell.
***a.* Exochorion of lipoprotein; *b.* Polymerised lipid; *c.* Endochorion of tanned protein; *d.* Wax layer.**

The eggshell is chemically resistant[1]. The outer layers are of a hard structural lipoprotein, and this often has a property especially important to the ecology of an egg: it can be very difficult to wet with water. The main inner layer of shell is of tough tanned protein. Between these two layers in *Rhodnius* there is an extremely thin layer of polymerised oil; it is so chemically resistant that the only reagent I found which would dissolve it was strong nitric acid saturated with potassium chlorate – an experiment one carried out on a very small scale with considerable precautions (and preferably on a borrowed microscope!). The egg is therefore surrounded by formidable passive defences, but it is no good to live in a castle so strong you cannot leave it, and insect eggs have a fascinating variety of escape hatches. In *Rhodnius* there is a cap on one end of the shell, rather like a crown cork on a beer bottle (Fig 1). It is often overlooked that one reason why the shell must be rigid is that it must provide the creature with adequate purchase to push against and break open the pre-formed structure in the shell through which it emerges.

However, an egg is a tiny object, and the smaller the object the greater is the danger that it will dry up. Although the shell layers already described provide good mechanical and chemical protection, they are not impermeable to water. Waterproofing is provided by a minutely thin layer of wax[2], very similar to that which occurs on the outside of the cuticle of the active stages of insects[3]. Such wax layers are readily damaged; the active stages of insects can repair them. The waterproofing wax of eggs is on the very inside of the shell, where it is protected from mechanical damage (Fig 1).

One of the critical moments in the evolution of life was emergence onto dry land. Land was attractive because it had abundant oxygen, but hostile because the air was desiccating. Many kinds of small animal have invaded the land but are actually restricted to very damp places such as soil. The dominance of insects owes much to having overcome the problem, which is well illustrated by their eggs. Their wax layer resists water loss but anything which does so also resists oxygen gain. An egg is a rapidly-growing object with a high demand for oxygen. How does air get through all this armament? The vital clue about this came in the best tradition of science: by accident. There were many occasions during my research when I needed to observe specific eggs at regular intervals after particular treatments, but *Rhodnius* eggs are about as co-operative as a muddy rugger ball on a wet afternoon. So I fixed them in rows by sticking them to a layer of vaseline on glass slides. Some of them died – and they were the ones which were stuck down by the cap end. No harm was done by vaseline so long as the rim where the cap joins was clear.

A detailed examination revealed some two hundred tubes traversing the rim[4], though apparently not connected to the outside world or giving direct access to the inside of the shell (Fig 2). These were undoubtedly air-filled respiratory tubes. But this discovery provided only part of the answer. It is well established that a completely closed network of air-filled tubes in, for example, an aquatic insect can greatly enhance the movement of oxygen around the body by diffusion, yet a simple calculation showed that these tubes would not be adequate to provide the respiratory supply of the developing egg by delivering it just at one end. The yolk and developing embryo are compact structures and would need oxygen to be exchanged over a large surface of the wax lining of the shell in order to respire sufficiently. A clue that the tube system was part of a more extensive system was provided by applying a droplet of a light oil to the rim of the shell. It would run into the tubes, but there followed a change in the refractive index of the whole shell, strongly suggesting that air spaces were being filled.

The problem of looking for air in a structure is that you cannot see it; you have to replace it by something which can be readily identified, and where air spaces are minute, it it needs to be something with intense colour. The method used combined the discovery that oil would penetrate the system, with a bit of elementary chemistry[5]. A glass tube containing some eggs was evacuated and while under vacuum the eggs were immersed in a solution of lead novanate in oil in which it is very soluble. The re-admission of air at atmospheric pressure helped to drive the lead solution into the finest spaces in the shell. The eggs were removed, washed rapidly and exposed to hydrogen sulphide gas which precipitated black lead sulphide. Optical examination revealed a rosette of fine pores connecting the outer end of each tube to the surface of the rim, but also a grey layer all round the shell, just outside the wax layer. The electron microscope showed that a minute air-filled sponge enclosed the whole egg; it was connected to the tubes in the rim and was created between two laminae by regularly spaced pillars like pitprops in a coalmine (Fig 3). This provides a large surface for respiratory exchange, while simultaneously restricting the loss of any water vapour which passes out, because the tiny airspace will be saturated.

That insects can make surfaces which water does not wet readily, is vital to many of their adaptations: aquatic insects are entirely dependent on this property. Since water does not easily penetrate the tube system of the egg, it explains why most insect eggs will survive temporary immersion by rain[6]. This is of applied importance: for instance in the past, an important factor in the control of clothing lice has been the destruction of eggs by heat when clothes are washed. They can

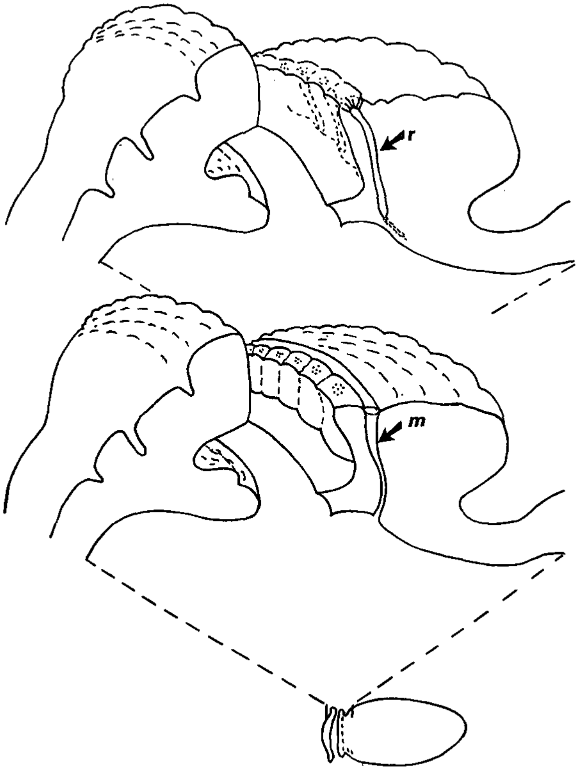

Fig. 2. *Rhodnius* egg with cap displaced. *m.* micropyle; *r.* respiratory tube.

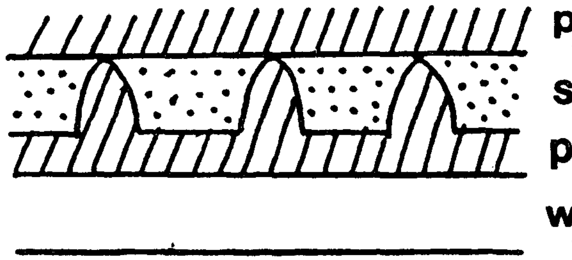

Fig. 3. An air-filled sponge *(s)* within the tanned protein layer *(p)* immediately outside the wax layer *(w)* surrounds an egg.

however survive the modern practice of low-temperature machine washing. We know that the egg's respiratory system allows an oil-soluble poison to enter the space in the shell. What we seem to have forgotten in this age of insecticides is that oil alone was used empirically for decades and does not involve the use of highly toxic material; what we now know is how it works – by asphyxiation. The old fashioned and very effective remedy for head lice was to soak hair for about ten minutes in ordinary lamp-burning kerosene – paraffin oil. The same principle was used on the farm where I was born, to deal with the horse bot-fly *Gasterophilus* which sticks its eggs on hair where the horse can lick; when they are swallowed, they hatch in the stomach and attack it. In summer, our carter wiped the appropriate areas of our horses with a rag soaked in paraffin, and I had long arguments with my father who held that the taste dissuaded the horse from licking, and the smell repelled the fly from laying. I failed to convince him that paraffin killed the eggs, but no matter.

However, there is an even bigger chink in the egg's armour, for virtually every insect egg so far examined has one or more holes in it which go right through the shell[4]. In *Rhodnius* there are a dozen or more around the rim, fertilisation tubes or micropyles (Fig 2), and it has always seemed to me a design fault that insects should complete the shell and fertilise the egg afterwards. The micropyle really is the Achilles heel because a poison dissolved in oil runs straight through this hole into the living material, and its critical importance was demonstrated in my research by immersing eggs in oil containing both a poison and a dye showing that every egg which was killed had at least one micropyle containing dye, while those which survived did not[6,7].

But there is another side to this picture. In the ovary insect eggs are completely surrounded by a layer of follicle cells throughout their production, and these follicle cells then make the shell[4]. I believe that this envelope of cells has an important role in protecting the egg against invasion by any micro-organisms in the parent – whether pathogenic to insect or man, right up to the point where the egg is released for fertilisation, and that is why each generation of disease vector has to bite an infected host before it can transmit a disease to others. In some circumstances however, this protecting system can be a disadvantage to the insect itself; many species, especially those living on special diets, which include the blood-sucking ectoparasites, need gut or intra-cellular micro-organisms to manufacture essential substance lacking in their diet and which they cannot themselves synthesise[8]. Newly hatched insects have to infect themselves with these micro-organisms and can do so by licking the faeces passed by older insects. When I moved from the London School of Hygiene to Cambridge, some of the cultures of blood-sucking insects I took with me died out, and this was because my conscientious new laboratory assistant kept the cultures too clean.

In contrast, egg production in ticks and mites is quite different[9,10]; there is no corresponding protective layer of follicle cells round the developing eggs; the egg-cell is fertilised before the shell is put on, and this may account for the ease with which they can be invaded by disease organisms. But at least one important commensal insect diverges from the typical pattern and has a remarkable mating system: the bedbug[11]. The sperm are deposited in a separate pouch on the female abdomen. They burrow through the wall of the pouch and circulate in the blood where most of them are attacked and digested by the female's blood cells, while the few survivors burrow back into the ovary and into the egg. It is perhaps a singular blessing to mankind that the bedbug has not acquired a mammalian pathogen, because if it had, I think that its peculiar fertilisation system might give rise to a pathway by which pathogens could be transmitted through the egg.

Forty years ago I stuck my neck out and proposed that the *Rhodnius* eggshell provided the basic pattern of four layers on which all insect eggshells would prove to be variations. This idea of a unifying scheme was not readily accepted, particularly by the late Professor Howard Hinton who said as much[12] about the blowfly egg to one of our research students who was about start work on it. The student discovered that when the fly's egg hatches, the shell splits open along its length; the inner layers expand and the shell frequently turns inside out[13]; if one only examines hatched shells it is easy to fall into the trap of getting the structure the wrong way round. However there are a million species of insect, and I do appreciate now that one needs knowledge of a range of them before proposing a generalisation; perhaps one value to science of making a sweeping conclusion is that it acts as a stimulus to others – not excluding those who would like to prove you wrong!

As further research has unfolded the larger picture, some extreme variations have been found. Cockroaches (which are Dr Burgess' special area of expertise) enclose a group of eggs in a capsule or purse, which provides such protection that the shell itself is greatly reduced. The females carry these capsules almost up to hatching time, and in the knowledge that cockroaches will eat almost anything, I doubt eggs would have much chance of survival unless they were so protected. But the eggs need a respiratory supply, and the lead sulphide method revealed that tiny air channels are cast into the capsule, making an air-way to each of the enclosed eggs[5]. Here we have precision moulding of a plastic extrusion, invented millions of years before man. In the tsetse fly *Glossina,* vector of sleeping sickness, the eggshell is also reduced to a thin membrane, for the egg develops and hatches inside the mother who then retains the larva and provides it with nutrients analogous to milk. The problem of hatching is overcome by a device on the wall of the 'uterus' which grasps the shell, pulls it off the larva and neatly folds it up[14]. At the other extreme, the shells of some stick insects eggs are so heavily impregnated with minerals[5] that it is said they are viable even after passing through a bird's gizzard. It is a pretty piece of free-loading, for of course stick insects are flightless and they use the bird to distribute their species.

I conclude this rapid survey of insect eggshells, by summarising the recent work Dr Corbet and I[15] have done on the mosquito *Culex* which is an important nuisance in northern temperate climates and the vector of a filarial parasite of man in the tropics. It illustrates how the eggshell of an insect, very distantly related to *Rhodnius,* is constructed on the same basic plan, but adapted to remarkably different circumstances. This research was actually precipitated by my telling an undergraduate that a diagram in Hinton's account of the *Culex* egg[16] was 'bloody impossible', and then feeling a moral obligation to prove it was! *Culex* can pack up to five hundred eggs together in a beautiful hexagonal pattern, to create a raft which floats on water until the eggs hatch. Such a raft poses a number of questions: for example, how are the eggs joined together? That puzzled the first person to describe the raft, Reaumur in 1738, who also invented the mercury-in-glass thermometer, and would be as well known as Celsius if only he had chosen to divide the scale into 100 rather than 80 parts. He had watched mosquitoes laying on a water butt at his country cottage outside Paris, and it was amusing to come across this in his account[17], for I was working on rafts on an old water butt at a cottage in the middle of Thetford Forest. Raft construction (and why have a raft at all) puzzled the great medical entomologist Sir Rickard Christophers[18] too. As a rule the insects which produce large numbers of eggs scatter them, hoping that at least two will survive to replace the parents, while those producing very few eggs take great care of them. By putting all her eggs in a raft, *Culex* risks losing the lot to a large predator in one mouthful. Why there has to be a raft I discovered much later.

The key to understanding the raft lies in the delicate little frill on the end of every egg which is not even included in drawings in some text-books. The frill is like a flexible umbrella which can take up all configurations from being a cup hanging below the egg to being wrapped up round the egg. The frill also anchors the egg to the water because it is very readily wetted on the under-side, but the other side is quite unwettable. I saw at once from simple physics that surface tension would always pull the edge of the frill in the direction of the water surface and that was why Hinton's diagram[16] was impossible (Fig 4). The flexibility of the frill is important because the raft is not flat; the eggs taper slightly so that when they are packed side by side, the raft is dish-shaped. Thus the bottoms of the eggs in the middle of the raft are below surface level and their frills are pushed up round the eggs, while at the ends of the raft the frills hang down and lift the water up (Fig 5). Should a raft tilt, the end which rises lifts more water and so is pulled back level; the frills are stabilisers.

The curvature of the raft matches the curvature of the water meniscus at bits of grass or vegetation in a pond, which means that if rafts drift there, they tend to accumulate on the curved surface. One associates vegetation with shade and shade with the need to reduce water loss, but surely a tiny object floating on water will be in saturated air and have no such need? That supposition was shattered by an incidental observation that if the frills of eggs at either end of a raft got detached from the water, the eggs died – and they died because they were desiccated. So the humidity of the air over the water surface of the butt was measured by a simple field method[19]. If one makes tiny loops in a fine varnished wire, and puts a drop of potassium acetate solution in each loop, this can be suspended over a water surface for half an hour to equilibrate, after which the concentration of the droplets can be read by a pocket refractometer and the humidity profile obtained. Surprisingly, in sunlight the air less than 2 mm above the

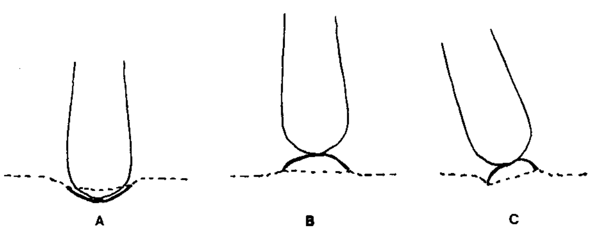

Fig. 4. The frill on the *Culex* egg must be reflexed *(A)* or extended *(B)* according to the position of the egg in the water surface and cannot be positioned as drawn by Hinton[16] *(C)*.

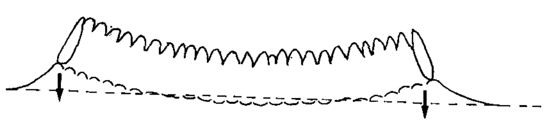

Fig. 5. *Culex* egg-raft: the frills at the ends lift water and stabilise the raft if it is tilted.

surface of the water is quite dry enough to desiccate the eggs.

Why does the attachment of the frill to the water prevent this? It became clear that the system was more complicated, for when rafts were floated on a solution of red dye, the shells went red in about ten minutes and no dye got into the egg itself. There is a hole in the middle of the under-surface of the frill (Fig 6); it feeds water into a sort of wick or water jacket which surrounds the egg within the thickness of the outer shell layer, and in this way the water which evaporates from the top of the egg is replenished while evaporation will also cool the egg. It follows that anything dissolved in the water will therefore be accumulated in the water-jacket through evaporation, and if rafts are floated on dilute salt solution, a sufficiently strong concentration accumulates in the water jacket to shrink the egg. It offers an explanation why *Culex* females test water with chemical sensors on their feet before selecting an egglaying site. One must assume that the several scientists who have worked on these eggs in the past missed the water jacket because they had lifted the rafts out of water to examine them, for the liquid in the jacket disappears very rapidly in air. It reinforces the message to all laboratory workers that there is virtue in observing things in their natural habitat too.

Similarly, the question of how the raft is put together had remained unsolved because it cannot be seen directly. The laying female holds her wings over her rear end and shields the process. I set up a small flat-bottomed dish of water with a reflecting prism which allowed observation from the side, together with a double-reflecting prism underneath (Fig 7). By persuading females to lay on the water (which was the most difficult part of the experiment) the whole raft-construction process could be watched from both angles through a microscope. The eggs are assembled simply by pushing them together. There are uniformly distributed pegs over the main surface of the shells which fit exactly into the spaces between the pegs on adjacent eggs (Fig 6B); you can actually break a raft into pieces and reassemble it again by very gentle pressure. It reminds one of an interlocking children's toy such as 'LEGO' and is yet another case where insects got the idea first.

The raft is assembled in such a rigid pattern that one can say on inspection exactly the order in which every one of four or five hundred eggs comprising any raft was laid. It seemed rather an academic discovery at the time, particularly because the value to an applied biologist of having such a large batch of eggs laid all at once would typically be to use one portion of a raft for experimental treatment and the remainder as a control, because they are 'all the same age'. In fact such an assumption proved far from the case. The first indication that the time of laying is significant came from observing the droplet of oil which is exuded and grows till its stands up like a golf-ball on a tee on the top of each egg. It starts to appear

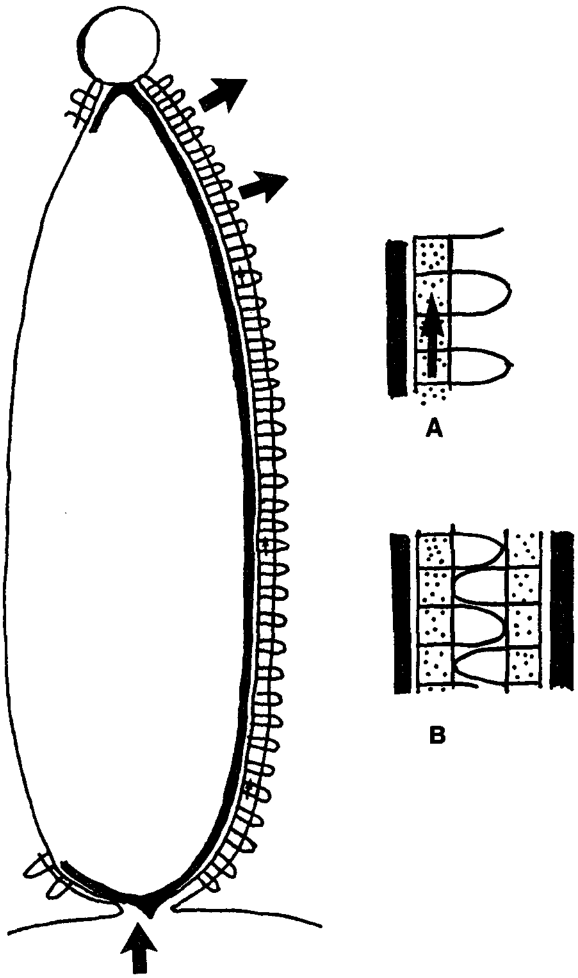

Fig. 6. *Culex* egg: water enters at the centre of the frill and forms a jacket between the lower parts of the papillae on the shell. It flows upwards *(A)* as it evaporates from the top of the egg. The raft is assembled by interdigitating papillae of adjacent eggs *(B)*.

around nine minutes after each egg is laid, so that on a large raft, the eggs first laid have produced quite large drops before they have even begun to appear on the youngest ones. There have been many theories about the function of this oil, even the imaginative (but ridiculous) one that if the raft got turned upside-down, the oil would help it to right itself[20]! Hinton's suggestion that it was repellent to ants[16] could be true, though it is hard to believe the situation would ever occur in nature where it actually happened. Bruno and Laurence[21] have shown that the oil contains a pheromone attractive to egg-laying females, which makes more biological sense. What I now describe for the first time to any audience, is where the oil comes from and how it is extruded.

My starting point was that the oil could not be secreted by the living material of the egg itself after it is laid, because it could not pass through the inner layers of the shell. It must therefore be in the shell when the egg is laid. The timing of the oil's appearance suggests that the mechanism depends on making contact with air and/or water. The shell is white and very soft when it is laid. Over the next few hours it slowly darkens, which is commonly associated with the tanning and hardening of proteins, but studies of the corresponding process in cuticle when an insect moults have shown that significant mechanical strength is produced by the tanning process well before any colour change is apparent[22]. It was thus possible that similar mechanical changes were taking place in the shell in the first few minutes after it emerged from the female: the period during which the oil was exuded.

I realised that because I knew the exact order in which every egg in a raft is laid and that one egg is laid every 2.3 seconds, if I collected a raft the moment the female stopped laying, it would contain a complete sequence of eggs of precisely known age from a few seconds old to fifteen or more minutes old. It was possible therefore to apply a single treatment to a raft and discover in detail how that affected the shell when in a succession of changing states. In particular, the tanning process in insects requires oxygen which activates enzymes. That type of enzyme is blocked by cyanide, so that the hardening process could be stopped at any stage of its development. I collected rafts immediately laying was completed, floated them in a dish of dilute hydrochloric acid to which potassium cyanide was added, and closed the container for ten minutes. Then the rafts were rapidly mopped of excess fluid with filter paper, transferred to clean water, mopped again and floated on dishes of clean water overnight, to be examined twelve hours after the treatment.

The remarkable, and quite unexpected, discovery was that eggs which had been laid for more than twelve

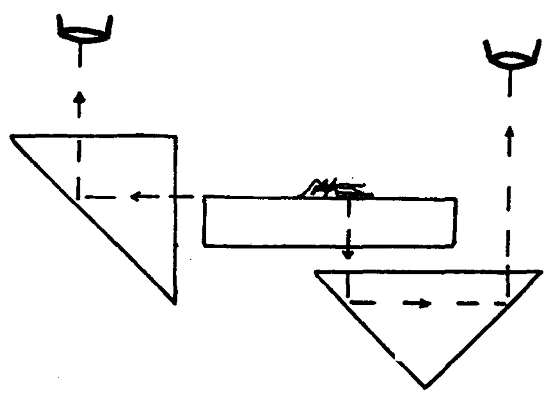

Fig. 7. Method of observing an egg-laying mosquito from side and below, using two prisms.

minutes before exposure to cyanide were apparently normal; indeed they subsequently hatched. Younger than that and the cyanide had entered and killed them. Between 11.5 and 12 minutes after laying, an impermeable layer which can only be of wax, is formed inside the shell, and if it keeps out hydrogen cyanide it will be a very effective barrier to most other water-soluble poisons. It had obviously occurred to me much earlier when I saw how evaporation could concentrate salts of dyes in the water jacket, that a poison at a very low concentration in a pond could be similarly concentrated, perhaps to a lethal level. It now became clear that any such poison would have to be present at a high enough level to provide a toxic dose in the first eleven minutes of the egg's life, and its presence would be likely to deter females from laying in that water at all. But if eggs could be as well protected as that, why were they not equipped with such an advantage from the moment of laying?

When I examined the various states of the sequence of eggs in the raft twelve hours after exposure to cyanide, the answer was there. As soon as it is laid, the egg starts to absorb water and the shell starts to harden, but if the enzymes causing hardening are blocked during the first six minutes, the shell is so weak that it subsequently blows up and bursts. The next oldest group of eggs had shells strong enough to prevent bursting, but they were very swollen, and they had not produced any oil droplets. Those that were eight minutes old on exposure to cyanide were more normal in size; some had produced minute droplets, and others which were slightly older bore still larger ones. The live eggs had normal droplets on them. Translating this into mechanism, one of the peculiarities of the *Culex* eggshell is that it consists of two concentric envelopes which are attached to each other only at the two ends of the egg. Over the whole of the rest of the shell they are separated – by a layer of oil. The egg absorbs water and swells, and at the same time the outer layer begins to harden. The internal pressure pushes the inner shell against the outer and squeezes the oil from between them, and out through a hole at the top of the shell. When sufficient pressure has been generated, and the shell is hard enough, the tap is turned off by laying down the impermeable barrier: wax, on the inside of the shell. Subsequently, the inner shell layer hardens too (Fig 8). It is an entirely mechanical process because if new-laid eggs are prevented from swelling by putting them on a strong salt solution, the shells harden and darken but no oil droplets appear. These eggs die, but if they are subsequently transferred to pure water they will swell and exude oil. I later demonstrated by more direct means that the oil was in between the two main shell layers.

But it is the peculiar nature of a scientist that while it was satisfying to have discovered so much (and so much more than I have had time today to describe) about this extraordinary machinery in a tiny eggshell, my real

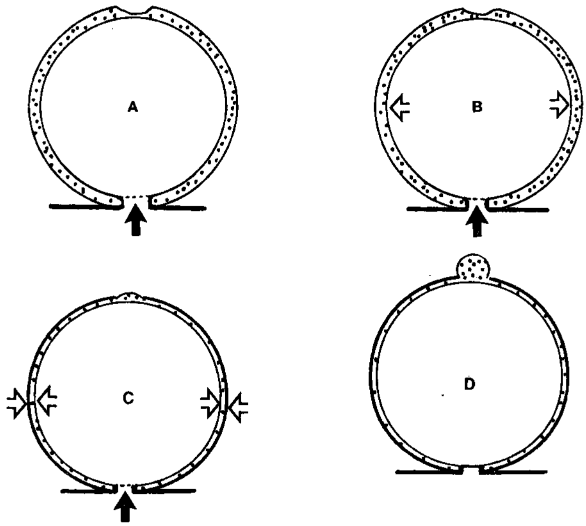

Fig. 8. Extrusion of the apical droplet on the *Culex* egg. *A.* Oil lies between the exo- and endo-chorions; at laying the shell is permeable. *B.* By 6 min pressure increases inside. *C.* by 9 min the exochorion is hardening and oil is squeezed out. *D.* After 12 min the whole shell hardens and becomes impermeable to water.

delight lay in something quite different and entirely academic. I was right forty years ago when I said that eggshells would prove to be variations on a pattern revealed by the *Rhodnius* shell (Fig 9). Both have wax on the inside. The outer structure of both eggs is lipoprotein, with specialised surface properties and sculpturing. The inner layer of both is of tanned protein. And between the two there is oil; in *Rhodnius* it is polymerised into a layer with extreme chemical resistance, but in *Culex* it is squeezed out to form the droplet on the tip of the egg. This is a simple illustration too of the change in our scientific attitude over the past forty years, for I was a heretic to suggest an underlying pattern then; it would be very awkward for our ideas of evolution today if there was none.

And eventually I saw why the eggs were assembled in a raft. There is a line of weakness around the shell, just above the frill, so that the emerging larva pushes the end of the shell down into the water, escapes through the hole and swims away. If eggs are separated, they will float; they will develop normally, and push open the hatch. But the frill hangs onto the water, the main part of the shell falls over, and the larva comes out into the air, usually resulting in death (Fig 10). In other words, a funny egg has to be in a funny raft, simply in order to hatch successfully.

I crave your indulgence for a brief coda. A monumental work on insect physiology, biochemistry and pharmacology has recently been published in 13 huge volumes[23]. There is a long chapter on insect egg-shell, but it is very largely about the genetics and

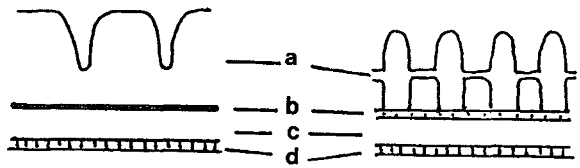

Fig. 9. Although the *Rhodnius* shell (left) is ten times as thick as the *Culex* shell (right) they consist, like most eggshells, of the same four layers of lipoprotein *(a)* oil *(b)* polymerised in *Rhodnius,* tanned protein *(c)*, and wax *(d)*.

molecular biology of the cells producing the eggshell of the fruitfly *Drosophila*. The chapter includes two paragraphs each of about five lines. One says that nothing is known about the waxes waterproofing insect eggs but it is presumed they are like those on the cuticle, while the other paragraph says that very little is known of the nature of exochorion, except for my publications in the 1940s. What I have shown throughout my research on eggs is that they depend totally for their protection against desiccation and against water-soluble poisons on their wax layers, while each egg's interface with its environment is the multiplicity of surface properties and structures of the exochorion. Those are the two critical things upon which the survival of that stage of every insect is dependent. Those are the things which govern methods of control, including any new methods which may add to our weapons against what undoubtedly is the group of animals – the insects – which are the most serious competitors to man and his domestic animals for the face of this planet. And while I too have enjoyed the pleasure of academic discovery, I have always tried to preserve a balance with useful and applicable research, for without that balance it is impossible to justify the luxury of pure research for its own sake. There is a desperate need today to restore that balance in the whole of biology, so that at least a sensible amount of research money and effort are put into the real problems which are facing the real world. Indeed unless we do, it will not be long before those who can teach medical and veterinary entomology to a next generation will have disappeared.

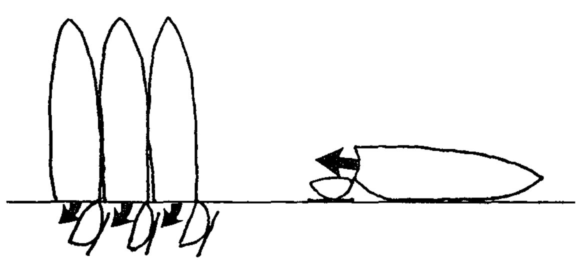

Fig. 10. Larvae from a raft can hatch successfully because the eggshells remain upright; an isolated egg falls over and the larva emerges into the air.

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Surgeon Commander Roger J Leicester, OBE, Consultant General Surgeon and Head of Surgical Department at Royal Naval Hospital in Haslar, Hants, has been awarded the 1989 Smith & Nephew Foundation Service Doctor Scholarship.

The scholarship will enable him to carry out an investigation into the incidence and aetiology of colorectal cancer in Indonesia. Surgeon Commander Leicester hopes to set up collaborative studies between the UK and Indonesia as well as a teaching programme for local doctors in the techniques for early detection of cancer by means of colonoscopy.

The Smith & Nephew Foundation was established in 1974 by Smith & Nephew plc, headquartered in London. The Foundation supports international training and research fellowships for doctors and surgeons from the UK and overseas as well as study scholarships for nurses.