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OVIPOSITION BEHAVIOUR AND EGGSHELL STRUCTURE IN SOME LIBELLULID DRAGONFLIES, WITH PARTICULAR REFERENCE TO *BRACHYTHEMIS LACUSTRIS* (KIRBY) AND *ORTHETRUM COERULESCENS* (FABRICIUS) (ANISOPTERA)

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The eggshell of *Brachythemis lacustris* contains a trabeculate endochorion and an exochorion perforated by aeropyles; that of *Tholymis tillarga* is similar but it has a much higher density of aeropyles. In both spp. wetting the exochorion at oviposition causes it to become sticky and to attach firmly to the substrate. Later it hardens to form a more or less continuous, perforated covering over the eggs: no evidence for the addition of a spumaline in the vagina was obtained. It is suggested that the shells in these species act as plastrons with properties adjusted to the differing epiphytic modes of each. — The eggshells of *Orthetrum coerulescens* and *Sympetrum danae* are not trabeculate. On being wetted they produce, after a variable latency, a thick, sticky coat of jelly probably derived from material in the exochorion. It surrounds each egg, separating the eggs within a cluster, and it remains deformable throughout development.

INTRODUCTION

Many libellulid females scatter their eggs widely while in flight by making intermittent contact with the water surface, the eggs being released in small clusters. The members of a few libellulid genera, however, such as *Perithemis* (DUNKLE, 1976), *Micrathyria* (PAULSON, 1969), *Tetrathemis* (McCRAE & CORBET, 1982), *Zygonyx* (CORBET, 1962) and *Brachythemis* (CORBET, 1962; MILLER, 1982a; BEGUM et al., 1982) deposit an aggregated clutch of eggs on the surface of plants or rocks either while in flight or after settling. In addition, some corduliids and gomphids lay eggs in masses or long strings (INOUE & SHIMIZU, 1976; WINSTANLEY, 1981). *Brachythemis lacustris* attaches large egg clutches to the stems or leaves of emergent plants close to the water surface, usually doing so while on the wing (MILLER, 1982a) but sometimes after settling (CORBET, 1962), and this behaviour provides a convenient opportunity for measuring clutch size and oviposition rates. Previous information about oviposition rates in libellulids has been obtained mainly from hand-held females which were excited to dump their eggs into water-filled tubes. By this means McVEY (1984) showed that *Plathemis lydia* could reach the very high rate of 32 eggs s^{-1} at 32° C. An estimate of the natural egg-laying rate in *Tholymis tillarga* was made by observing the deposition of separate clusters of eggs, each containing about 9 eggs, and a value of about 7 eggs s^{-1} was obtained (MILLER & MILLER, 1985), similar to the rates measured in *Erythemis simplicicollis* (McVEY, 1984). Such high oviposition rates pose interesting problems about how the eggs can be shuttled through the female system and fertilised so rapidly.

Numerous studies of the structure of insect eggshells have shown that in many species the shell is remarkably complex (HINTON, 1981; MARGARITIS, 1985). There is, however, little information about the structure of the odonate eggshell and the investigations which have been carried out so far on a few species indicate that, although the normal layers are present, they are thin and relatively simple in structure (BEAMS & KESSEL, 1969; MATSUZAKI, 1971; FURNEAUX & MACKAY, 1972; KAWASAKI et al., 1974). HINTON (1981) concluded that although egg plastrons might be expected in dragonflies, no species examined had been found to contain one. However the endochorion of *B. lacustris*, like that of *T. tillarga* (MILLER & MILLER, 1985), is shown here to be trabeculate and if it held an air layer it might act as a plastron. A brief comparison is made with the eggshells of *Orthetrum coerulescens* and *Sympetrum danae* where I find no trabeculate structure and in which a jelly-like material is released after the eggs have been wetted.

MATERIAL AND METHODS

Brachythemis lacustris (Kirby) was studied at Hunter's Lodge in Kenya (37° 32'E, 2°15'S), (MILLER, 1982a, b), and comparisons were made with *Tholymis tillarga* (Fabr.) from the same site. Oviposition behaviour in *B. lacustris* was observed and timed, and the egg batches were then collected and stored in alcohol or 2% formaldehyde for subsequent study. *Orthetrum coerulescens* (Fabr.) and *Sympetrum danae* (Sulz.) were observed and collected at a site in Surrey, southern England.

Eggs were prepared for scanning electron microscopy by sputter-coating them with gold after critical-point drying; they were then examined in a Philips PSEM 500. The numbers of eggs in clutches were counted from photographs and mean values are given with their standard deviations.

Egg-dumping was evoked by holding a female by the wings and dipping the terminal segments of her abdomen into a tube of water (cf. McVEY & SMITTLE, 1984).

Egg stickiness and jelly formation were examined in the eggs of *O. coerulescens* and *S. danae* in watch glasses under the microscope. Jelly was most readily seen using reflected light against a background divided into equal black and white halves. It could also be detected when small particles became attached to its surface or by manipulation with a needle.

The term "cluster" describes the eggs released during one oviposition movement (dipping stroke of the abdomen), and many clusters make up one clutch (or batch), the clutch being defined as the eggs released during one oviposition episode (visit to the water).

OVIPOSITION

B. lacustris males adopted and defended territories, often in the shade, from about 16:00 to 18:30 h E.A.S.T. (sunset, ca. 18:25 h) along the margins of a small lake and a stream at Hunter's Lodge. When a female entered a male's territory, a short courtship and aerial copulation sometimes followed, and the female then oviposited onto a stem or leaf (usually of *Cyperus involucratus* or *Typha domingensis*) at or close to the water surface (MILLER, 1982a). Females usually chose stems or leaves which were vertical or were leaning at not more than 45°, and they hovered close to the stem, repeatedly brushing the tip of the abdomen along the plant from the water surface upwards at about 0.5 to 1.0 s intervals, releasing eggs as they did so (MILLER & MILLER, 1985).

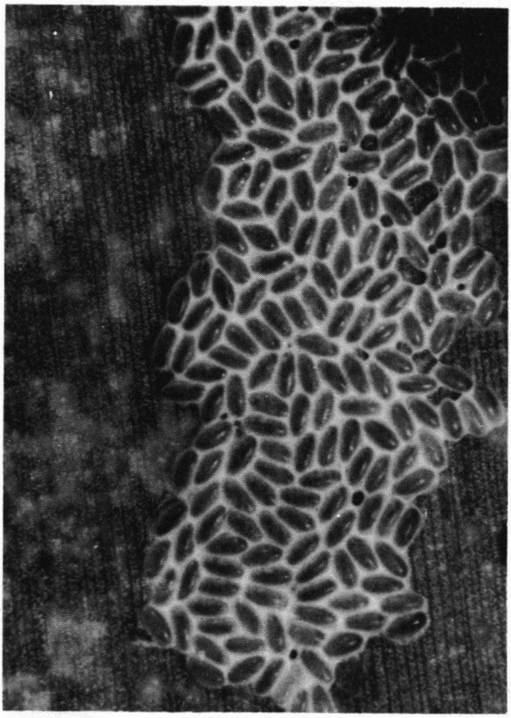

Fig. 1. A small egg clutch of *B. lacustris* on a bract of *Cyperus involucratus*. Each egg is about 560 μm long.

In counts of 26 egg clutches the mean number of eggs was 433 ± 89, which is similar to the figures of 325-450 eggs given by BEGUM et al. (1982) for *B. contaminata*. In nine, timed oviposition bouts (i.e. the time for laying one clutch) the mean duration was 98 ± 39 s giving an oviposition rate of 5 eggs s^{-1} (25-28° C). In four additional clutches which were individually timed and then counted, the rates were 6.0, 7.8, 8.0, and 9.2 eggs s^{-1}.

The eggs of a clutch were normally placed in a single layer, orientated in all directions, but with some regions in which the eggs were aligned in parallel rows (Fig. 1). Single clutches never contained superimposed eggs, but where successive oviposition bouts had occurred on the same leaf or stem, probably by different females, two or more layers were sometimes found on top of one another, and in one case five egg layers were superimposed in this way. Such egg piling would probably allow only the top layer to hatch (cf. KORMONDY, 1959).

When a male's territory contained few oviposition sites, later females would be likely to superimpose eggs on those of earlier females. My observations showed that oviposition commonly took place close to where the pair had hovered during copulation, but females sometimes explored several stems or leaves before commencing to oviposit. If females choose to oviposit on top of the clutches of previous females, they may thereby benefit their own offspring at the expense of others, as may happen in some butterflies (PULLIN, 1986). Males, however, could reduce the risks to their own offspring from egg piling by switching territories on successive days when oviposition sites were scarce, but I have no evidence on this point.

EGGSHELL STRUCTURE

The eggs of libellulids commonly adhere loosely to each other as they are extruded from the genital opening: they collect under the 9th abdominal segment and are then flicked, brushed or washed off according to the species. After being laid, they may become more sticky and this tends to attach them to plants or other objects in the environment (CORBET, 1962).

The eggs in each cluster of *Tholymis tillarga* become glued firmly to each other and to the substrate shortly after being laid (MILLER & MILLER, 1985), and similarly the egg clutch of *B. lacustris* soon sticks firmly to the leaf or stem on which it has been deposited (Fig. 2A, B); in each species the outer sticky exochorion then hardens to form a porous covering (Fig. 2D, E). In some other species the eggs are surrounded by a soft jelly-like coat which has been thought to be derived from accessory glands in the female (spumaline) (HINTON, 1981). Accessory glands, however, have not been described in libellulids.

Examination of scanning electron micrographs of the fractured shells of recently laid eggs of *B. lacustris* showed the innermost layer to consist of a featureless and smooth vitelline membrane. It supports an endochorion which is wrinkled and folded, and which forms columns or pillars 11-16 μm in height, each usually with an expanded terminal piece, flat-topped or rounded and 3-5 μm wide (Fig. 3A-C; see also Fig. 2B). The pillars are formed at some of the foci of an endochorionic reticulum, but their occurrence is very irregular (Fig. 3A). The exochorion is a fibrous layer, 10-14 μm thick but in some regions up to 22 μm thick. It is pierced by holes, aeropyles, many of which correspond to the pillars of the endochorion; the pillars may protrude beyond the surface of the exochorion

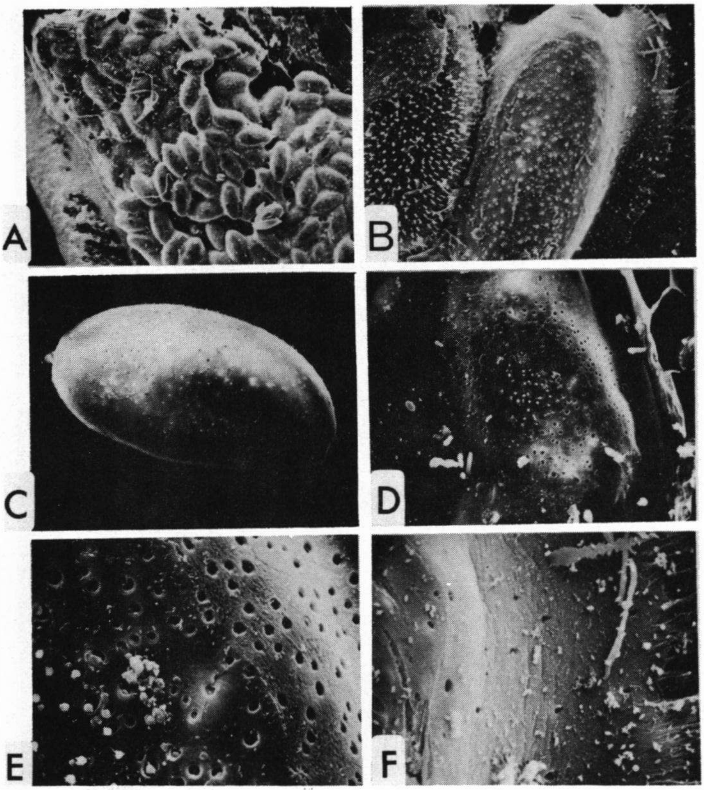

Fig. 2. Eggs of *B. lacustris:* (A) A small region of two clutches one partly overlying the other, probably laid by different females; — (B) On the left an egg is shown from which the exochorion has been removed to reveal the pillars of the endochorion; — (C) An egg removed from the oviduct; — (D) An egg, which has been laid, showing the aeropyles in the exochorion; — (E) The same at higher magnification; — (F) Part of the exochorion showing fibres where it has been pulled away from the substrate. — [Scales: (A) 1 mm; — (B, C, D) 200 μm; — (E, F) 50 μm].

by 5-6 μm (Fig. 3D-E). The outer ends of the aeropyles are 3-4 μm (exceptionally 2 or 5 μm) in diameter (i.e. 7 to 12.6 μm^2 in area); at an estimated 5000 holes mm^{-2}, this is equivalent to 3.5-6.3% of the egg surface. The micropyle, formed from the vitelline membrane, is about 36 μm long and protrudes through the exochorion at the anterior pole by about 25 μm.

In eggs dumped by a female into a tube of water and then immediately fixed, the exochorion is found to be swollen to a thickness of 28-39 μm, thereby concealing the ends of the pillars. At this stage the wetted exochorion is very soft and it can be pulled from the egg or it can be stretched into long, thin filamentous strands (Fig. 2F). The aeropyles can sometimes still be identified in stretched

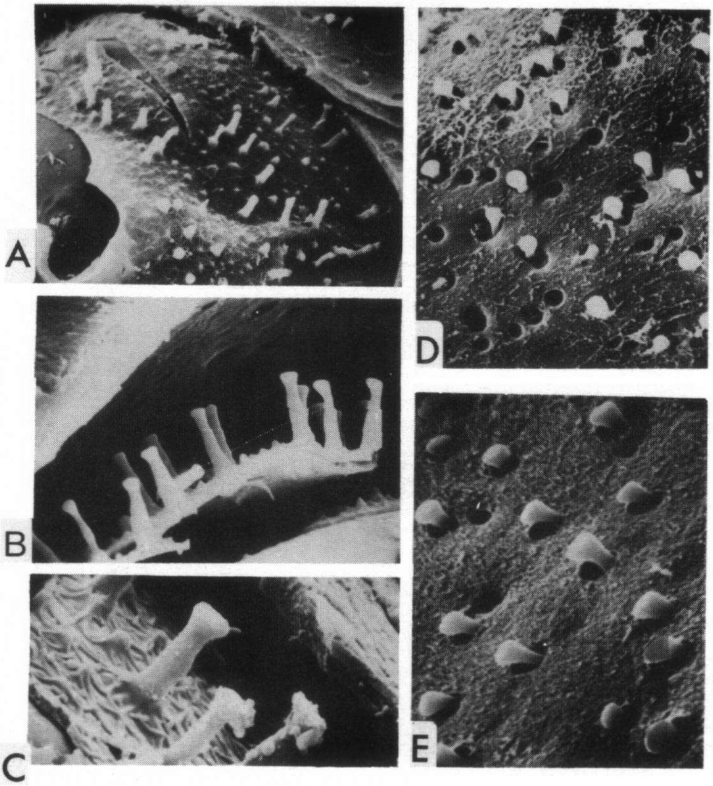

Fig. 3. Eggs of *B. lacustris:* (A) Part of a fractured eggshell showing exochorion (to the right) and endochorion with pillars (centre). An area of smooth vitelline membrane can be seen on the left; — (B) Part of a fractured shell with the exochorion (top) pulled away from the pillars of the endochorion (below); (C) The same showing also the reticular structure of the surface of the endochorion; (D, E) Views of the surface of the exochorion showing aeropyles through some of which endochorionic pillars protrude. — [Scales: (A) 50 μm; — (B, D, E) 25 μm; — (C) 10 μm].

regions. Some time after deposition the exochorion may shrink, pulling away from the endochorion in some places as it does so. It envelops the eggs of a clutch in a more or less continuous, hard, perforated sheet which is strongly attached to the plant surface.

The shells of mature but unlaid eggs obtained from the oviduct appear similar in structure to those which have been laid, and there is no evidence for the addition of material (spumaline) just before laying (Fig. 2C). Immature eggs from follicles, however, showed a pattern of hexagonal islands of material on their outer surfaces (Fig. 4), which probably represents the secretions of individual follicle cells. Similar patterns are well known in the immature eggs of other

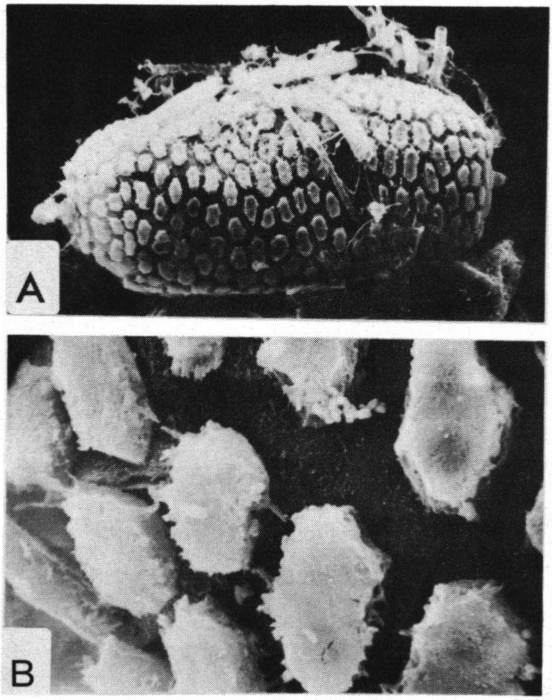

Fig. 4. A developing egg of *B. lacustris* removed from the follicle and showing patches of secreted material on its surface. — [Scales: (A) 200 μm; — (B) 25 μm].

species (MARGARITIS, 1985).

The structure of the eggshell of *T. tillarga* is in general similar to that of *B. lacustris* (MILLER & MILLER, 1985) (Fig. 5). The endochorion bears numerous short, squat pillars each 6-7 μm thick at the base and 8-11 μm tall. They occur regularly and close together, and they correspond to the numerous perforations, or aeropyles, in the exochorion which are wider and much more abundant than in *B. lacustris*, being 7-10 μm in diameter and occupying approximately half of the surface. The exochorion is 18-23 μm thick and, in eggs removed from the oviduct, it is soft and deformable and sometimes shows folds . On wetting, it becomes sticky and the exochorions of neighbouring eggs in a cluster adhere strongly to each other and to the substrate, later hardening to form a protective mesh uniting the eggs of a single cluster.

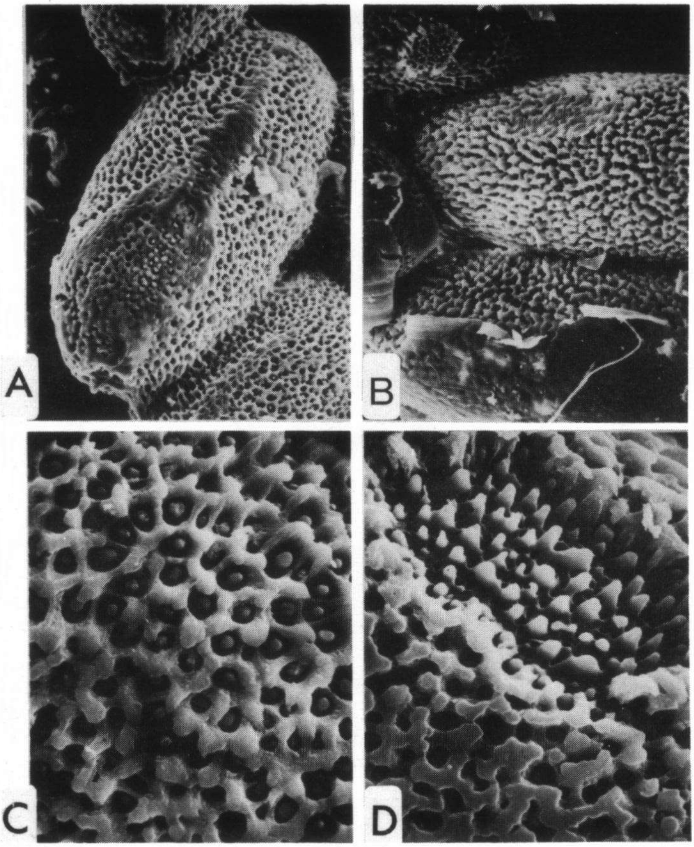

Fig. 5. Eggs of *T. tillarga:* (A) Eggs which have been laid, showing the fusion of their exochorions; — (B, C, D) Eggs removed from the oviduct. In B the similarity of the exochorion to that in A can be seen; — (C) View of the surface of the exochorion showing aeropyles through which endochorionic pillars protrude; — (D) Part of the exochorion has been removed to reveal the numerous pillars of the endochorion. — [Scales: (A-B) 200 μm; — (C-D) 50 μm].

COMPARISON WITH THE EGGSHELLS OF *ORTHETRUM COERULESCENS* AND *SYMPETRUM DANAE*

The eggshells of *O. coerulescens* and *S. danae,* like those of many other libellulids, do not contain trabeculate structures and the eggs, after being laid, are contained within an expanded jelly which remains soft throughout development.

Hand-held females of *O. coerulescens* and *S. danae* were excited to dump their eggs into water contained in watch glasses, while being observed under a binocular microscope. In *O. coerulescens* the eggs passed out of the genital opening in a single file at about 5 eggs s^{-1} with each egg pressed into the one ahead, but to one side of the midline. This allowed the micropyle of each to project slightly to one side, which might have brought it rapidly into contact with sperm at the fertilisation pore as it was shuttled through (cf. SIVA-JOTHY, 1987). On entering the water, the eggs could easily be separated from one another and they were only slightly sticky at this stage. The watch glasses were covered and then observed at intervals. In *O. coerulescens* hatching started after 9 days at 25° C.

The production of jelly and changes in size and colour were observed in the eggs of *O. coerulescens* in the peaty water of the stream where natural oviposition had been witnessed. During the first two hours there was a reduction in length from a mean of 646 ± 24 μm (± standard deviation; n=10) to 537 ± 23 μm (n=10), together with an increase in diameter from a mean of 300 ± 12 μm (n=10) to 339 ± 18 μm (n=10); after 3 days, the eggs were 525 ± 19 μm (n=13) long and 393 ± 17 μm (n=13) wide. These changes probably reflect the uptake of water, well known in the eggs of some other insects (WIGGLESWORTH, 1972). Assuming the egg to be a prolate spheroid, its volume increased by 6% in 2 h and by 39% after 3 days. At the same time the egg gradually darkened from almost white to orange or light brown. After a variable interval a sticky envelope of jelly with a thickness of up to 500 μm, through more usually of 200-300 μm,

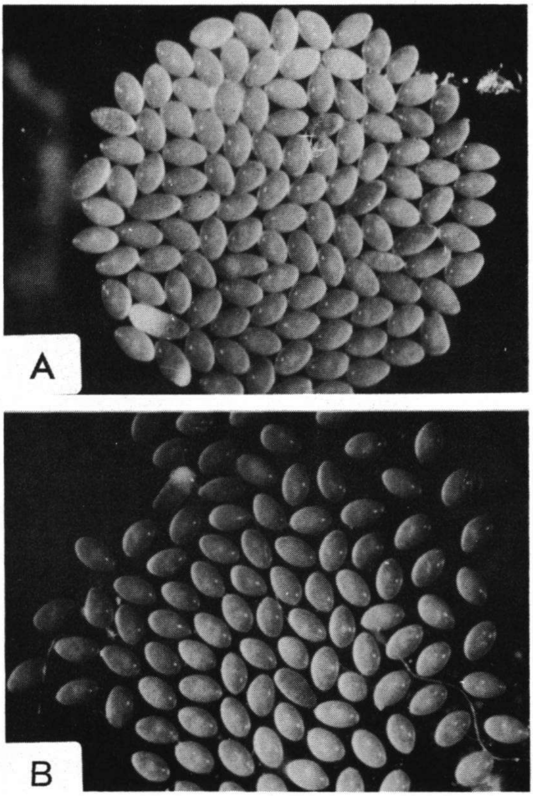

Fig. 6. Eggs of *O. coerulescens:* (A) Eggs in contact with one another immediately after being laid into a watchglass filled with water; — (B) 2 hours after being laid, the eggs are well separated by surrounding layers of jelly, particularly those eggs at the margins.

was produced. In batches in which the eggs were initially in contact, the jelly formed a unified mass within which the eggs were separated from each other by 200-500 μm (Fig. 6).

The following stages in the production of jelly could be distinguished (Fig. 7): (1) The outer layer of the shell softened and formed folds (Fig. 7B) (sometimes folds or rims were seen in the exochorion immediately after oviposition). It then began to expand, usually at first in localised regions, and it became bubbly in appearance (Fig. 7 C, D). It was very sticky at this stage and eggs were difficult to detach from a needle or from each other. Long, very thin strands of jelly could be pulled out to several mm in length. — (2) The bubbly regions then extended over the whole egg except for the region close to the micropyle (Fig. 7E). — (3) The bubbly regions disappeared as the jelly expanded maximally (Fig. 7F). About 24 h after the jelly had been formed it became less sticky, and it was more visible as small particles accumulated on its outer surface.

The delay before the surrounding jelly appeared varied between 30 min and 12 h depending on several factors, including the water temperature, the ionic content of the water and other factors which will be described elsewhere (Miller, in prep.). In contrast, the volume increase and the darkening occurred within 2 h regardless of whether jelly was formed or not. Jelly was also occasionally formed by eggs which remained pale and did not increase in volume, indicating that these changes are separately controlled.

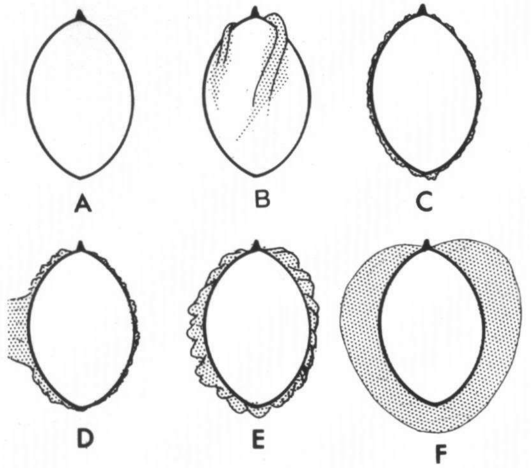

Fig. 7. Stages in the formation of jelly in the eggs of *O. coerulescens:* (A) Immediately after being laid; — (B) The appearance of folds on the exochorion (stage 1); — (C) First appearance of jelly; — (D) Maximal expansion of jelly in one small region; — (E) Jelly expanding evenly all over the egg (stage 2); — (F) Maximal expansion of the jelly all round except close to the micropyle (top) (stage 3).

Very similar changes were observed in *S. danae,* with the eggs turning brown and the jelly envelope being up to 700-800 μm thick in many eggs, corresponding to the thicker appearance of the exochorion before wetting.

In order to determine if passage through the vagina and fertilisation were necessary for jelly formation (cf. REGIER et al., 1982; MARGARITIS, 1985), three abdomens were isolated in each species and the last four segments including the vagina and sperm storage organs were then excised. Eggs were obtained from the more anterior segments and they were placed in stream water. In *O. coerulescens* 66 of 100 eggs tested produced jelly coats similar in appearance to those of eggs which had been dumped by females. In *S. danae,* all 73 eggs tested in this way produced a sticky jelly coat. This indicates that the production of jelly is not dependent on passage through the vagina.

Most of the eggs collected from the oviduct not only produced jelly but also turned orange-brown and increased in volume, as did eggs which had been laid normally. They did not, however, develop further because they were infertile. Thus none of these changes can be taken as an indicator of fertilisation.

The natural oviposition of *O. coerulescens* was observed in the field and eggs were then found and collected. This species oviposits in acid streams and bogs by flicking drops of water with the abdomen towards the bank or emergent vegetation (cf. ROBERT, 1958), a method of oviposition known in some other libellulids (CORBET, 1962). Most of the eggs which were found were lying on the bottom in a few cm of water where their white colour made them relatively easy to spot, or they were lodged among the leaves of sphagnum moss. Jelly formation was seen to occur only after a delay and the eggs then became attached to moss leaves or to flocculent organic material in the water. The changes observed in eggs laid in the wild were the same as those in eggs dumped by females in the laboratory.

DISCUSSION

Oviposition rates in endophytic odonates are slow. For example in *Calopteryx maculata,* they vary from 5 to 10 eggs min^{-1} according to the plant species utilised (WAAGE, 1978). In contrast many libellulids which oviposit exophytically scatter their eggs at rates of 5-10 s^{-1}, or even faster (McVEY, 1984), a practice which may cause many eggs to fall into unsuitable regions. Epiphytic species achieve high rates of egg deposition (7-8 s^{-1} in *T. tillarga* and 5-10 s^{-1} in *B. lacustris*) while still being able to select suitable oviposition sites. Epiphytic oviposition may therefore be a good compromise, allowing the high rates of exophytic oviposition to be combined with selection of the oviposition site as in the endophytic method. Its cost to females, however, may possibly be in an increased risk of predation, for example from frogs or the water-spider *Dolomedes,* since the female remains at one spot longer (cf. PAULSON, 1969). It may also attract egg predators, as was thought to occur in *T. tillarga* (MILLER & MILLER, 1985).

In *B. lacustris* and *T. tillarga* extruded eggs adhere together loosely on the ventral surface of the 9th abdominal segment. After being deposited and wetted, the exochorion becomes softened and very sticky, and it then adheres strongly to the substrate forming a porous covering which later hardens. It is sometimes pulled out into long strands as the female brushes her abdomen along the plant surface. Scanning electron micrographs have shown the exochorion to be similar in appearance before and after deposition, and there is no evidence for the addition of extra material shortly before the eggs are laid. A similar conclusion was reached from experiments on *O. coerulescens* and *S. danae*, in which wetting causes, after some delay, the formation of a thick and sticky jelly coat which later loses its stickiness but remains soft throughout embryonic development. Eggs removed from the anterior region of the oviduct reacted to water similarly. Spumaline is not therefore added from the posterior region of the oviduct or the vagina just before deposition (cf. HARTLEY, 1961; KIMBER, 1980). Extra-chorionic material could, however, be added higher in the oviduct, as occurs for example in fleas (ROTHSCHILD et al., 1986). Water is probably necessary to initiate changes in exochorionic substances and most libellulid eggs are either laid in water or wetted before being laid. In some Tetratheminae, however, such as *Tetrathemis polleni*, wetting is not essential for egg adhesion, the eggs being laid well above water level (McCRAE & CORBET, 1982).

The eggshells of some libellulids and gomphids preserve the pattern of follicle cells on the exochorion, although this is not the case in *B. lacustris* or *T. tillarga*, indicating perhaps a more fluid state of the exochorion in these species. The appearance of hexagonal secretions in developing eggs, noted here, which may represent the activities of individual follicle cells, has also been seen in some Lepidoptera (REGIER et al., 1982; MARGARITIS, 1985). In the latter, microvilli form aeropyles at points where three follicle cells meet and the microvilli secrete a flocculent material which acts as a scaffolding for the aeropyle. In the species studied here, aeropyles were normally associated with endochorionic pillars which protruded part-way or wholly through them, but their formation may be similar.

In some other odonates which have been examined, the chorion has been found to be simple in structure and lacking trabeculae. In *Sympetrum infuscatum*, for example, a vitelline membrane 9 μm thick supports a thin inner chorion (0.3 μm) and a thicker but featureless outer chorion (3 μm) (KAWASAKI et al., 1974). In Aeshnidae, the vitelline membrane is 2 μm thick and the chorion forms a homogeneous inner layer and a myelin-like outer layer (BEAMS & KESSEL, 1969; MARGARITIS, 1985). The structure of the chorion of *T. tillarga* and *B. lacustris* resembles that of some Diptera, Lepidoptera and Acrididae in having an inner trabeculate layer and an outer layer pierced by aeropyles. The exochorion of *T. tillarga* contains numerous aeropyles which, if air-filled, could provide an air-water interface occupying about half of the surface. In *B. lacustris* the corresponding interface occupies only 3.5 to 6.3 % of the surface. In each species the eggshell may be able to act as a respiratory plastron, if it is air-filled, although that of *B. lacustris* may be rather inefficient.

The eggs of *T. tillarga* are usually laid just below the water surface, but they may occasionally become exposed. In *B. lacustris*, the eggs are laid on the stems or leaves of *Cyperus* and *Typha* just above the water surface, but they are often subsequently submerged as the plants collapse into the water. The eggs of both species are therefore probably capable of respiration in air and underwater, but those of *B. lacustris*, with a low density of aeropyles, may be better able to withstand desiccation when in air.

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