THE MICROTOPOGRAPHY OF AVIAN LICE EGGS

by R. S. BALTER

1 Chantry Road, West Bridgford, ... Nottingham

Adult lice in many cases lack significant intergeneric morphological features and are thus often difficult to classify. Presumably this situation is due to parallel and convergent evolution. However, their eggs, especially those laid on avian hosts, show a number of fascinating adaptive differences appropriate to the particular habitat of the bird concerned.

Some lice confine their activities to the head. These are much stouter when compared with those occurring mainly on the body. The most slender of all lice are those found only on the host's wings. This shape allows them to flatten between the grooves of the wing flight feathers.

Unlike other parasites, the louse never leaves its host voluntarily, except as the consequence of accident or disaster when it has been known to hitch-hike on the back of flat-flies, dragonflies, and even flies.

In order to identify further characters to aid the classification of avian lice (Mallophaga), a detailed morphological study has been made of various distinctive microstructures visible on the chorionic shell of the louse egg. In its simple form, the louse egg is an oval capsule, and the extent of its elongation is variable, being related to the gross shape of the adult female's abdomen. The anterior end is always provided with a cap or operculum which breaks open to permit exit of the nymph. With rare exceptions, the egg is laid with this end oriented away from the base of the hair or feather to which it is attached by means of a cement produced by maternal accessory glands.

The site and method of attachment vary within and between genera. For example, some species attach their eggs solely to feather barbules, others to a barb or barbs and others between the main shaft and after-shaft of a feather. Some eggs are laid even within the quills of the wing flight feathers. Cementation is variable and can be very elaborate; eggs may be cemented basally, laterally or bilaterally. In some cases, a cup is formed, in others a cement stalk is constructed or the cement may be moulded into various forms of ornate brackets and strands. Cementation is employed sparingly by some species whereas in others it may almost enclose the egg.

Experiments to introduce various alkaline, oil and water stains into the stigma tubules (Fig. 1C) were attempted without success. Inconclusive results were obtained using silver nitrate. Finally, a modification of Wiggleworth's (1950) tracheal staining technique succeeded. An 8 per cent aqueous solution of cobalt chloride was introduced through the egg stigma tubules and then precipitated with hydrogen sulphide gas to give cobalt sulphide. As seen in Fig. 3H and Fig. 4G, a black precipitate within the egg and within the stigma resulted. Similar results were again achieved using eggs stained in situ on the feathers; the cobalt chloride passed through the cement into the stigma tubules.

From these results one may perhaps conclude that the stigma is able to function as a water-absorbing organ or hydropyle. If this is the function of the apparatus then an interesting point arises. The skin of a bird lacks sweat glands. The feathers and skin are not easily wetted. No data about humidity among feathers on the living bird are available and indeed this would be very difficult to obtain under natural conditions. If the stigma organ does function as a hydropyle (the cement is hygroscopic), it seems possible that the egg has a mechanism that enables it to make use of atmospheric water.

From the order Phthiraptera, six genera of the sub-order Mallophaga were selected for examination. These consisted of two examples from the super-family Ichneumonea, represented by the family Philopteridae. Four examples from the super-family Amblycerae represent the families Laemobothridae and Menoponidae.

For each genus, identification of the eggs has been carefully checked by comparison with a mature egg isolated by dissection from an identified female.

The illustrative evidence, covering six species, is presented in atlas form on the following twelve pages.

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References


1 Light microscopy: The best results were obtained with unstained material mounted on glass slides in Dapco or Paraplast's medium as the refractive index and colour of Canada balsam obscure the structures under study. A 1000/150 oil immersion objective was used in a quarter inch camera on Euborn F. 2.5 objective in varying conditions from 0.5 to 1 minute according to the magnification and nature of the material. Scanning electron microscopy (SEM): Specimens were mounted dry on a thin film of pterocnand and coated with about 500 A of evaporated gold-palladium. Specimens were examined with an accelerating voltage of 20 kV, except in the case of Fig. 1 C, D and E when 9 kV was used.
Fig. 1 (text continued)

...earliest informative description is that of Leuckart (1874). Gross (1906) gave the first detailed description and figured its structure.

(c) SEM. In the past no satisfactory interpretation has been advanced for the function of the egg stigma. It consists of a group of canals completely traversing the chorionic shell. It has been thought that the function of this structure is to 'key' or hold the egg into the cement. From this picture it may well be thought to serve this purpose. Graber (1972) interpreted it as a means of aeration, but in most cases it is covered over; this would be essential during hatching since, according to Sikes and Wigleyworth (1931), the embryo escapes from the egg by pumping air through its alimentary canal to increase pressure and force open the operculum.

(d) SEM. Demonstrates difficulty of removing cement from base of egg when preparing specimens for the Stereoscan. Nine plugs of cement within the stigma indudes in both this and previous figure. The excretion in this figure and in (a) can be seen to be very lightly sculptured.

Fig. 2

2A

2B

Columbiosila columbae (Linn) 1758. The Pigeon Wing Louse (Ischnocera: Philopteridae) Type host: Columba livia domestica; the Domestic Pigeon. The biology of this louse has been studied by several authors. The egg was figured by Martin (1934), Eschler (1932) and Coni (1956). These authors failed to observe the mushroom form and structure at the base of this egg or appreciate its significance.

(continued)
(2.4) x 63.9. Light microscopy. A further example of an egg laid by a wing looper. The usual laying site is on the upper surface of the underlying leaves. When heavy infestation takes place, eggs may also be found on the lower neck and upper breast feathers. In this figure it is just possible to discern several funnel-shaped microtubules arranged around the perimeter of the operculum. These microtubles are canals traversing the horn of the operculum and are the means by which the ovipositing egg is fertilized.

(2.0) x 252. Light microscopy. The mushroom-shaped basal organ shown in this and other figures becomes somewhat everted when the cement is removed. Note the stigma tubules in the neck of this structure and the protoplast connecting stigma to the endocytoblast.

(2C) x 281.5. SEM. Shows sculpturing of the operculum. Microtubules are just discernible.

(2D) x 1,003. SEM. Neck of mushroom-shaped organ. This region is normally embedded in a thick hygroscopic cement. When dry, the cement holds the egg rigidly in position. When moistened, the cement becomes rubbery and elastic.

(2E) x 900. SEM. Base of mushroom-shaped organ showing large number of open-ended stigma tubules.

Fig. 3 Laemobothrinus tinnunilis (Linn) 1758. AMBYLYCERA: LAMEROTRIDEAE. Type host: Falco tinnunulidae, Keestrel hawk. An egg from this genus has previously been described by Bliagowicz (1925). Laemobothrinus tinnunilis (Feuerer) 1875 in Falco gyrfalcus (Linn). Blagowiczky states "The operculum is slightly impressed with one fairly large funnel-shaped microtubule excavation." Examination of eggs from several different species within this genus has shown that this excavation is not a true microtubule. Stains cannot be introduced into the egg through this structure.

(2F) x 113.5. SEM. View showing upper portion of the egg. Perimeter of the operculum is defined by a single line of aerogles. A single microtubule is in focus above the line of aerogles in the centre of the picture. At the apex of the egg a single large tubular excavation is clearly visible. This genus is also to be found infesting the wader rued, Fulica atra and Gallinula chloropus, when the tubular structure is raised to an even greater extent. On the keestrel, the eggs are laid on the upper breast, back of the neck, thighs and lower back. The egg is almost completely enclosed up to the operculum in a tough gelatinous pocket of cement. (concluded)
Fig. 3 (text continued)

(S38) x 558. Light microscopy. In this flattened slide preparation cement can be seen almost completely covering the egg. Note that in this preparation a light scattering of the chorion is discernible, which is not apparent when the egg is viewed with the electron microscope.

(S39) x 90. SEM. View of apex of egg as seen in a transverse section of a section of tubule exocytosis.

(S40) x 235. Light microscopy. Shows detail of chorion at base of raised tubules exocytosis. Function of this structure is at present unknown. It has not been seen on the eggs of any other genera of line eggs examined.

(S41) x 337. SEM. Surface view of operculum edge showing a single micropyle placed centrally above a line of aeropyles.

(S42) x 3375. SEM. The same micropyle as seen in (S1). The micropyle is slightly raised but shows little structure, an unusual feature of micropylles on the mollusk eggs.

(S43) x 292. SEM. Resolution of tubules (the stigma-like structure) protruding at different angles from the base of the egg.

(S44) x 900. SEM. Enlargement of stigma tubules showing small particles of cement still adhering to the organ.

Fig. 4

(Amblycera: Menoponidae). Host: Physium cuticulans (Linn.). The Pseudostiga. An egg from this species has previously been briefly described and illustrated by Begg (1955). Amblycera laevis (G. F.) 1880 on Tetraogallus Linn. Capricornis. Eggs are laid mainly on the neck and are fixed basally in cement briefly, in pairs or in clusters, according to the weight of infestation. A globule or cement circle the shaft at the base of the small neck feathers attaching the eggs close to or touching, the host's skin. At a general rule it has been found that Amblycera fastens their eggs low on the feathers close to the host's skin, whereas Locustinae tend to occupy the centre third portion of the feather.

(4A) x 90. SEM. This figure illustrates the complete egg. Attached to the apex of the operculum are numerous fine threads which are clearly visible as a scalloped structure on the exterior egg. When the egg is laid, these fine threads become symmetrical and form a single opercular strand. The opercular strand has been observed on numerous eggs of different genera. Many of these strands contain pieces of cement and are formed as the eggs are laid. Since these strands appear most (continued)
Fig. 4 (text continued)

4E. Light microscopy. Illustrates the opercular region of the egg. A ring of tooth-like processes circles the egg at the operculum flange. These are most clearly seen at the top left and bottom right of the picture. It is thought that these processes, often more exaggerated in other genera, and which I have named pre-opercular hooks or pre-opercular processes, are to prevent surplus cement from interfering with ejection of the operculum.

4F. (A4H) x225. SEM. Detail of opercular strand showing fine threads and cement holding them together to form the strand. (continued)

4G. (A4H) x245. SEM. View of egg showing retracted operculum with strand, double row of pre-opercular processes and single row of concave micropyles situated around perimeter of operculum.


4I. (A4J) ×925. SEM. Compare this figure with (E) and note differences in detail in sculpturing and micropyles due to differing depth of focus shown by conventional methods.

4J. (A4K) ×540. Light microscopy. Mushroom structure situated concentrically at base of egg. Specimen stained with cobalt sulphide. The sigma tubules project from the mushroom structure. A break in the column of stain demonstrates that the tubules have joined to form a single tube passing through the structure.

(4F) ×245. Light microscopy. Details of sigma structure and tube passing through basal mushroom organ. As one extremity the tube is connected to the developing embryo and at the other it becomes bulbous and contains numerous very fine tubules.

(4G) ×252. (A4H) ×835. SEM. Detail of basal mushroom organ. Note magnified depth of focus shown in figure photographs.

(4I) x300. (A4J) x990. SEM. Resin of sigma tubules at base of mushroom organ. Particles of cement still adhere to the structure.
Fig. 5. Menacanthus sternunus (Nitzsch) 1818. (Type B) (AMBLICERAE; MENOPONIDAE) Host: Gallus domesticus. The Domestic Fowl. This egg has previously been described by Fisher (1939) and Blagoweskovsky (1955), but details and functions of structures have not been discussed. One of two distinct types of egg A or B is laid by this species; B is the most common. Egg laying starts at the base of the feather and successive eggs are laid in layers one upon the other until, in cases of heavy infestation, a large mass of eggs and cement is formed, frequently occupying about two-thirds of the feather. It appears that where infestation is heavy, competition for suitable laying sites acts as a control since the eggs beneath these mass masses are unable to hatch. Eggs are laid on the feathers of the thighs, lower back and around the vent.

(SE) x 99. SEM. View of complete egg. At the apex of the opercular strand, around the upper portion of the egg are two rows of hooks and anchors. The first and second rows have identical bifurcate hooks and the third row filaments terminate in an anchor-shaped structure. At the base of the egg is the stigma organ. There is no stigmata of the chorion.

(SE) x 2315. SEM. Apex of egg showing opercular strand, circle of microtyle and pre-opercular bifurcate hooks.

(SE) x 1080. SEM. Detail of opercular strand made up of fine threads; a single button-shaped microtyle is also visible.

(SE) x 1125. Light Microscopy. Operculum with opercular strand showing microtyle. The opercular strand, which is formed in the ovary, is drawn to a fine point by means of copious secretion around the strand as the egg is laid. A function of this strand, apart from aiding attachment, may be to make the insect more well away before laying the next egg.

(SE) x 2315. SEM. The third row of hooks showing single filaments terminating in an anchor-shaped structure. These are encircled around the fine feather barbs and may be lightly cemented.

(SE) x 2315. SEM. Show origin of single filaments and mass of chitin which is initially formed.

(SE) x 2385 SEM. Detail of anchor-shaped hook. Note small particles of cement still adhering to structure. In some species within this group the hooks are uniformly asymmetrical in shape.

(SE) x 301. SEM. Base of egg showing central rows of tubules and the stigma structure plugged with cement. In this case there is little doubt that the stigma, as part of its function, aids in keying cement to the base of the egg.
Fig. 4 Boerophagus alectonius (Bridge) 1979. (AMB.
LYCERA: Xenoponidae) Type host: Boerana
(KP), the African Hornbill. Eggs are laid on the
neck and upper breast and are attached to the
calumna at the bottom of the feather
by a girdle of cement panning around the feather
shaft and base of the egg. The most interesting
feature of this egg is that the endochorion is
protected by a heavily sculptured exochorion. It is
possible that the reason for the complex
sculpturing of the exochorion is related to the unique
life history of the host. When nesting, these large birds
occupy hollow trees or stumps for as long as 13 weeks, with

the male occasionally relieving his mate during
incubation. Prior to egg laying, both birds collect
large numbers of insects which live in the nest, eat
the birds' excreta and keep the nest clean. In one
such hole, 438 insects were found, mostly cater-
pillars. The excreta induce in the caterpillars a
type of parasitism which prevents their escape. The
function of this tough outer case might be to keep
the developing embryo cool as a high temperature
and high humidity could come from the bottom of the
nest. Alternatively, it could offer protection to the
egg constancy from the symbiotic scavenging insect.
(6F)×49. SEM. View of egg showing heavily
sculptured exochorion. The spculum is well
raised and located to a point. The perimeter of the
spculum cup is sunk into the exochorion. At the
base of the egg is a slightly raised mushroom
structure.
(6F)×306. (6C)×990. SEM. Detail of the
exochorionic sculpturing.
(6D)×32. SEM. A detailed view of one of the
many very regular pores passing through the
exochorion.
(6E)×33. Light microscopy. Egg in situ
attached to calumna of a neck feather. Note
outline of the endochorion within the exochorion.
(6H)×24. Light microscopy. The double sper-
culum. The endochorion is protected by a raised
cap of exochorion. Note the line of microwires
around the perimeter of the endochorion cap.