Malcolm J. Scoble

The Lepidoptera

Form, Function and Diversity

5

IMMATURE STAGES

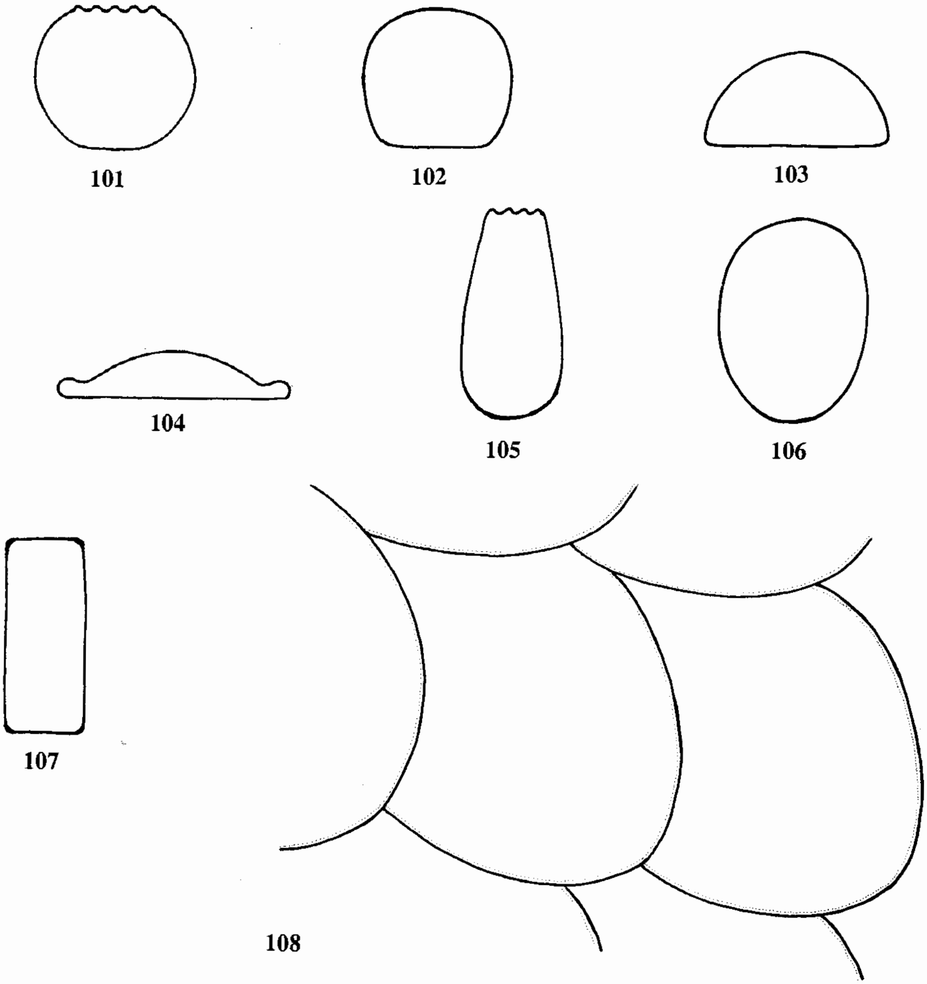
Egg

At the time at which it is laid, the insect egg is composed basically of a cytoplasmic and yolky core surrounded by a membrane and a shell. The cytoplasm is divided into a boundary layer, known as the periplasm, and a reticulum within the yolk. The nucleus of the zygote is found towards the posterior end of the egg. Around the periplasm is the vitelline membrane, which in turn is bounded by the 'shell' or chorion. A wax layer is found on the inside of the chorion. One or more funnel-shaped canals known as micropyles (e.g., see Fig. 112) run through the chorion permitting the passage of spermatozoa. In terrestrial insects, oxygen uptake through the chorion is enhanced by the presence of openings called aeropyles, which communicate with air-filled spaces in the lower part of the chorion.

The chorion is produced by follicle cells while the egg is still in the ovary. In Lepidoptera, the microfibrils constituting the basis of the chorion are arranged in helicoids - a situation apparently unique to this order (Hinton, 1981). This arrangement, which is similar to the orientation of microfibrils found in arthropod cuticle, helps the eggshell to resist forces equally from any direction. Typically, the chorion consists of an endochorion and an exochorion. The endochorion bears air-filled spaces, and is supported by vertical columns or struts. This system is found in many groups of insects including the lower Ditrysia. In higher Ditrysia there are, in addition, many gas-filled layers between the outer layer of the chorion and the inner air-filled layer, although eggs of Papilionidae are of the primitive variety (Hinton, 1981).

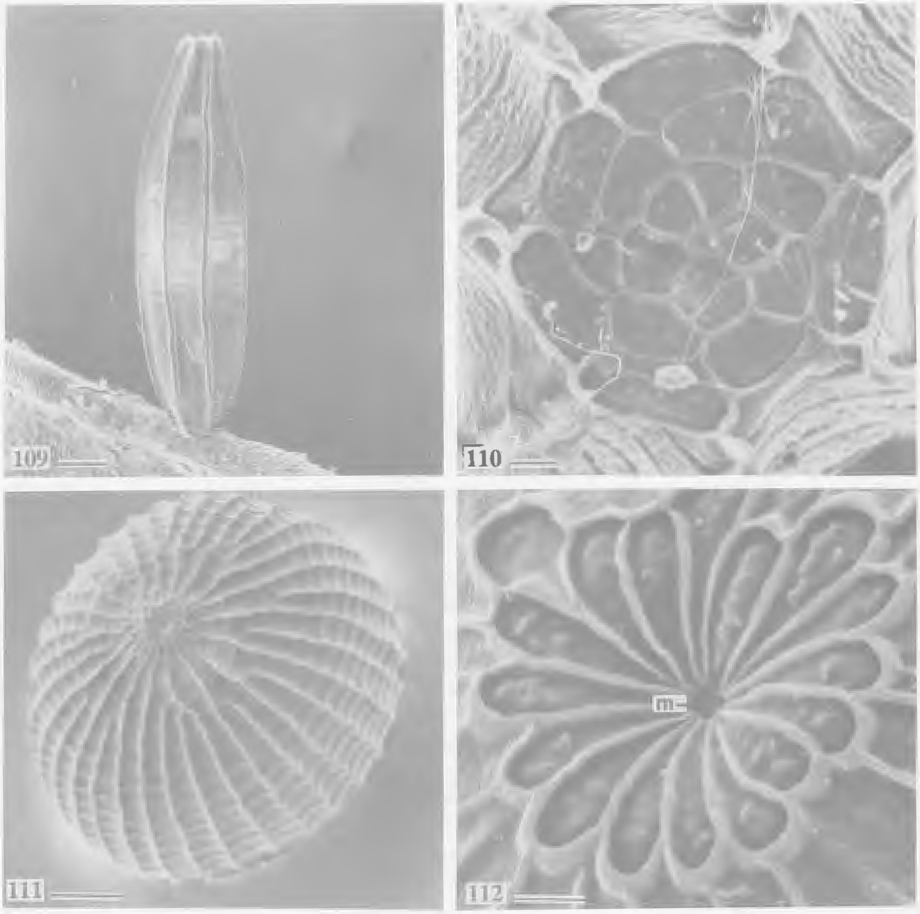
Lepidopteran eggs (Figs 101-112; Pl. 4) may be approximately spheroids or prolate spheroids (elongated in one direction), hemispherical, flat and scale-like, spindle-shaped, ellipsoidal, flattened-spherical, or rectangular cuboid. In the Yucca moth *Tegeticula* (Prodoxidae) the egg is elongated, the dimensions being up to 20 times as long as broad. Marked elongation tends to be seen amongst those eggs inserted into plant tissue. Döring (1955) illustrated a wide range of lepidopteran eggs indicating the variation in shape. There is also variation in colour. Other works in which lepidopteran eggs have been extensively figured include those of McFarland (1973a,b) and Salkeld (1983; 1984). Hinton (1981) provides an extensive list of references to the biology of lepidopteran eggs.

Considerable variation in the shape and sculpturing of eggs exists even among supraspecific taxa (Pl. 4), but the family to which an egg belongs can often be recognized by its shape, orientation, site of deposition, and whether it is laid singly or in small or large batches. Chapman (1896) recognized two main types within the order, one termed *upright* and the other *flat*. These names are still used regularly in descriptions. In the upright variety (e.g., Figs 109-112) the micropylar axis runs perpendicular to the surface on which the egg is laid. In the flat form, the axis runs parallel to the substrate. Chapman noted that among macrolepidopterans upright eggs are found, typically, in Noctuoidea and butterflies, whereas flat eggs are more widespread. Again within macrolepidopterans, he subdivided flat eggs into 'Geometrid' types, characterised by a greater roughness, and 'Bombycid' types, which are smoother and more polished.



Figs 101–108. *Egg profiles. 101,* Xanthia togata (*Noctuidae*)*; 102,* Mythimna ferrago (*Noctuidae*)*; 103,* Cerura vinula (*Notodontidae*)*; 104,* Craniophora ligustri (*Noctuidae*)*; 105,* Gonepteryx rhamni (*Pieridae*)*; 106,* Petrophora chlorosata (*Geometridae*)*; 107,* Hemistola chrysoprasaria (*Geometridae*)*; 108,* Acropolitis xuthobapta (*Tortricidae*). (*101-107, after Döring, 1955; 108, drawn from a photograph in Powell & Common, 1985.*)

Chapman considered that whereas upright eggs probably developed once in the more advanced members of the order, flat eggs developed independently twice. However, there are numerous exceptions to this generalization, and although 'upright' and 'flat' may be of use as descriptive terms they indicate no phylogenetic basis in the division of the order; both flat and upright eggs may occur within the same family (Hinton, 1981). For example, although most Geometridae have flat eggs, in some they are upright. The two kinds may occur even within the same genus, as in *Sterrha* and *Biston*. As a very broad generalization, upright eggs are characteristic of Cossoidea, Hedyloidea, Hesperioidea, Papilionoidea, and Noctuoidea. A flat egg occurs in most other Lepidoptera. Many Lepidoptera that glue their eggs together lay eggs of the flat variety, which appear upright in relation to the plant substrate. Examples are *Eriogaster lanestris* and *Malacosoma castrensis* (Lasiocampidae).



Figs 109–112. *Eggs. 109, 110, egg of* Macrosoma semiermis *(Hedylidae) showing chorion and micropyle area: 109, whole egg (scale, 130 µm); 110, micropyle area (scale, 9.0 µm). 111, 112, egg of* Adisura *sp. (Noctuidae): 111, whole egg (scale, 14.3 µm); 112, micropyle area showing micropyle (m) (scale, 1.4 µm). (109, 110, EM Unit, BMNH, specimens courtesy of Dr A. Aiello; 111, 112, courtesy of Dr M.J. Matthews/EM Unit, BMNH.)*

The chorion of lepidopteran eggs frequently bears longitudinal ribs, often connected by horizontal ridges (Figs 109, 111). Eggs may be pitted, wrinkled, or covered with a reticulate network. Sometimes they are smooth and polished. Prominent at the anterior pole of the egg is the micropylar area, which is usually surrounded by a rosette-like sculpture of the chorion (Figs 110, 112). Generally, there are four micropyles in lepidopteran eggs, but there may be more. For example, in 15 species of Notodontidae the number of micropyles were found to vary from four to twenty (Hinton, 1981).

Although rarely laid under water, lepidopteran eggs are sometimes prone to flooding. Whereas plastron respiration accounts for respiration in eggs of most other aquatic insects, in Lepidoptera the air-water interface is too small to make it effective, and, according to Hinton (1981), eggs probably survive as a result of a reduced metabolic rate. However, it was suggested (Downey & Allyn, 1981) that in eggs of Lycaenidae perforation of the chorion enables plastron respiration to occur when eggs are submerged in rain water. Eggs of Micropterigidae are typically laid in moist places.

They may be covered with brittle, rod-like structures that are able to hold water, or (as in *Neomicropterix nipponensis*, see Chapter 9) covered with gelatinous material that swells on contact with water or moisture. In their apparent need for surrounding moisture, micropterigid eggs differ from those of other members of the order (Kobayashi & Ando, 1981).

Depending on the taxon, eggs may be laid singly or in batches. While they are generally placed on or near the hostplant (or animal host in the case of carnivorous Lepidoptera), in some groups, such as Hepialidae and certain Nymphalidae, they are scattered by the female in flight.

Enormous numbers of eggs may be laid by some Hepialidae. A single female of *Abantiades magnificus* may lay more than 18000, and a similar figure has been estimated for *Xyleutes encalypti* (Cossidae) (Nielsen & Common, 1991).

Eggs are potentially a source of food for predators and a variety of means of protection have evolved (summary and references in Hinton, 1981). Many Lepidoptera lay their eggs in places concealed from many predators (e.g, in crevices in bark, or within plant tissue). Eggs of many Pyralidae and Olethreutinae (Tortricidae) are scale-like and transparent so making them difficult to distinguish from the substrate on which they are laid. Examples of eggs that mimic plant tendrils (as in *Hemiostola immaculata*: Geometridae), leaf galls (as in *Cerura vinula*: Notodontidae), and seeds (as in *Langsdorfia franckii*: Cossidae) also exist. Some eggs are disruptively coloured (as in *Gastropacha quercifolia*: Lasiocampidae). Several examples occur in which the eggs of Lepidoptera are poisonous. Those of *Danaus plexippus* (Nymphalidae) contain cardiac glycosides, and in some species of Zygaenidae hydrocyanic acid is present in the eggs. Females often cover their eggs with setae from the anal tuft. Setae from the adult may simply provide a mechanical defence (as in many Lymantriidae). But often urticating setae from the larva picked up by the anal tuft of the emerging adult from the inner lining of the cocoon are used either exclusively to cover the eggs, or mixed with the adult (non-urticating) setae. Examples of Lepidoptera making use of urticating setae in this way occur in Lymantriidae, Notodontidae (including Thaumetopoeinae), and Saturniidae (Hemileucinae).

Larva

Essentially, the larva is the feeding stage in Lepidoptera. In many adult Lepidoptera the mouthparts are functionless, and even in those adults that do feed the larva provides most of the adult resources. The larva faces two major problems - obtaining enough to eat and avoiding being eaten. Elaborate defence mechanisms, both structural and behavioural, have evolved. In this section, the basic structure of lepidopteran larvae is considered together with the relationship of structure to function. There is considerable convergence in larval structure since similar modes of life have been adopted in many groups that are not closely related. Therefore, those features of larval structure, particularly the primary setae, that are less obviously related to function are also emphasized for the value they provide in systematic studies. Comments on the natural history of the relationship between lepidopteran larvae and their foodplants are made in Chapter 7.

Head

The head capsule (Figs 113) is strongly sclerotized. Hinton (1947) interpreted the dorsal sutures and ecdysial cleavage lines of the head as indicated in the Figure. The length of the epicranial suture is related to the angle at which the head is positioned

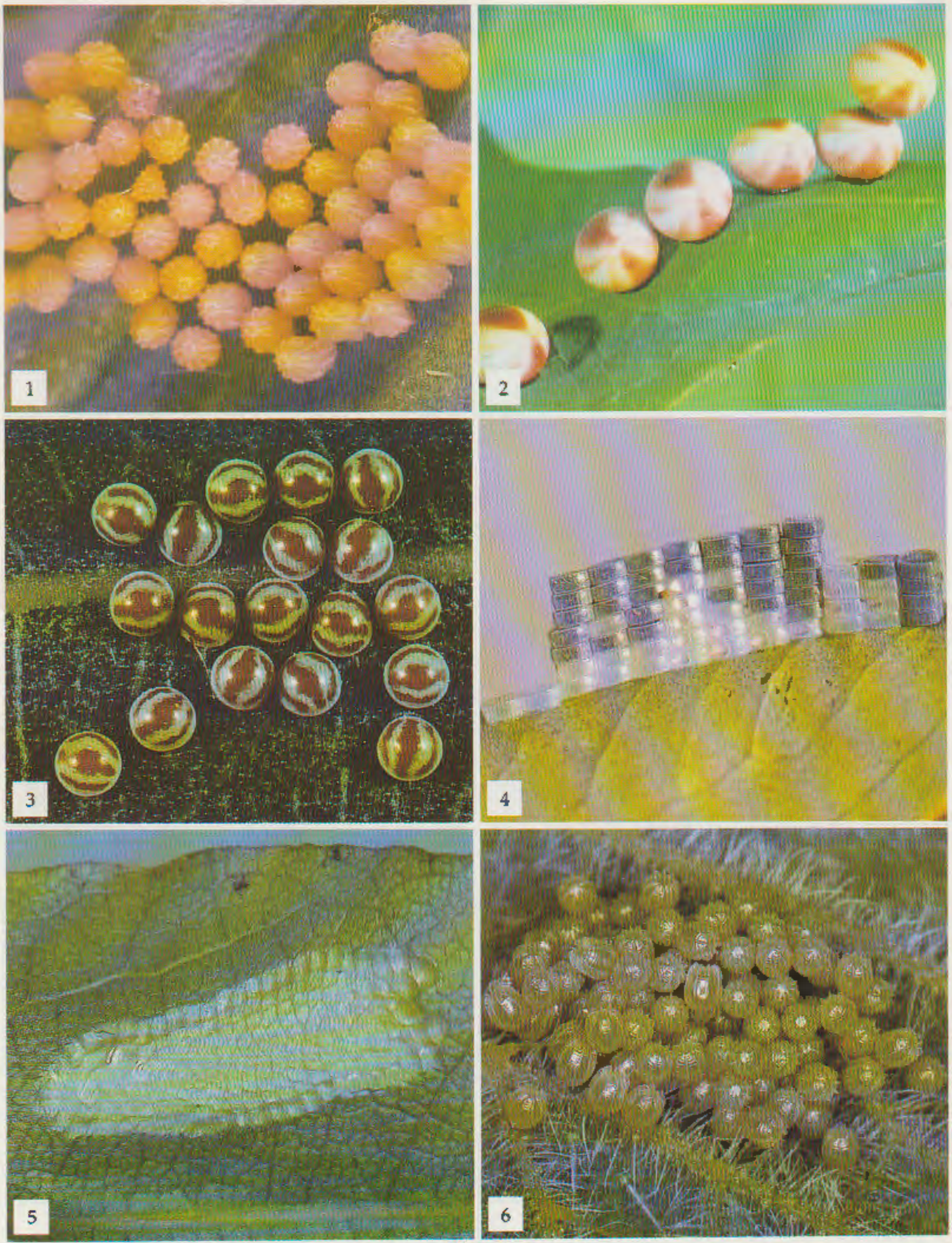


Plate 4

Eggs. 1, *Pieris brassicae* (Pieridae); 2, *Attacus atlas* (Saturniidae); 3, *Clostera anastomosis* (Notodontidae); 4, *Trilocha ficicola* (Bombycidae); 5, *Cacoecimorpha pronubana* (Tortricidae); 6, *Aglais urticae* (Nymphalidae). (Photographs: 1, Becker/Shell U.K., Ltd; 2, 3, Mike Bascombe; 4, H. O'Hefferman; 5, 6, Martin Honey/BMNH.)