BULLETIN OF THE ALLYN MUSEUM

3701 Bayshore Rd.
Sarasota, Florida 33580

Published By
The Florida State Museum
University of Florida
Gainesville, Florida 32611

Number...61 16 April 1981

Chorionic Sculpturing in Eggs of Lycaenidae. Part I.

John C. Downey

Biology Department, University of Northern Iowa, Cedar Falls, Iowa
and
Research Associate, Allyn Museum of Entomology

and

Arthur C. Allyn

Director, Allyn Museum of Entomology

It has long been thought that the egg stage of butterflies has both an actual and a potential value in determining or understanding the phylogeny and evolution of members of the order (Scudder, 1889; Chapman, 1896a, 1896b).★ Within the Lycaenidae, several works beginning with Doherty (1886) and as recent as Clark and Dickson's (1956, 1971) excellent research in South Africa, have indicated the taxonomic usefulness of the egg stage. Recently, more life history studies of particular lycaenid genera (Shields, 1973, 1974)+ or species (Nakamura, 1976; Downey and Allyn, 1979) have included scan electron photographs of the egg stage, and provided a new and detailed ultrastructural view. Most of these studies presented only the photographs or descriptions, but did not attempt to analyze similarities or differences of the included eggs with others. In our own ultrastructural studies, we have become increasingly aware of the lack of comparative details in order to assess the importance of observed differences. With this in mind, it was decided to reassess the chorionic sculpturing of available lycaenid eggs by means of scan electron microscopy. As incomplete as such a survey might be, it might still provide a comparative basis against which descriptions of single species in the future might be evaluated. We hope it will promote greater attention to this interesting stage of butterfly morphology.

The present study is a quest for an essential geometry in the chorionic sculpturing --an attempt to reduce the apparent complexities of egg structure, and to identify homologies between species. The immediate problem is one of elemental topology, that is, trying to determine what to describe and measure.

Scudder (1889, pl. 65, 68) figured the eggs and micropylar regions of 16 species of Nearctic Lycaenidae including *Feniseca*. All were done with the light microscope; some

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★Doring (1955) indicated that the eggs of Lepidoptera are relatively well known, but hardly yet truly classified.

+Shows micropylar region of *Philotiella speciosa* and *Euphilotes enoptes* (1974), and *Philotes sonorensis* (1973).

from hatched eggs, others from sections mounted in "jelly" (glycerin). As crude as some of these figures are (*loc. cit.,* see Figs. 16 and 18, pl. 65), some, like *Lycaena phlaeas* (*loc. cit.,* pl. 65, Fig. 21), are readily identifiable. Unfortunately, the details given in Scudder emphasize the differences in the artists' concept and rendering of the eggs, which reinforces the conclusion that each egg has species specific characters. In fact, six artists were involved in the renderings, and while there is an inherent trust by a reader in the accuracy of any illustrator, the complexity of the egg sculpturing coupled with the minute size of the chorionic ridges and changes produced by differences in light intensity and direction, suggest that caution be used in comparing Scudder's figures with others under consideration.

METHODS

Most eggs used in this study were field collected, obtained after observing the female oviposit. Some were obtained from confined females. A few were received from collections where the manner of collection was not given, but undoubtedly certain of these were extracted (dissected) from the dried reproductive tract of females. We dissected eggs from recently dispatched as well as long dead females in order to develop techniques and check egg development. Eggs were extracted from the common oviduct by gently teasing open the abdomen and appropriate tissues in 70% alcohol. With the soft tissue preparation, (Figs. 29, 30) organs were dissected and fixed in 3% gluteraldehyde and ringers solution, then processed with osmium-tetroxide for final fixation. The best success occurred when entire abdomens, with a longitudinal cut through the segments, were given the osmium tetroxide fixation. Subsequent fragmentation of the dried tissues (with inherent risks in the fragments being suitable views of specific structures) permitted mounting of select structures on an SEM button.

A JSM-U3 instrument was used for the SEM studies. Specimens were prepared for the latter by mounting on a JEOLCO specimen holder by means of doublesided tape edged with a conductive lacquer adhesive (Dotite paint, type D-550) prior to coating. They were coated with 40/60 gold-palladium in a Varian V-10 vacuum coater to a thickness of approximately 50 angstroms.

Names of subfamilies and tribes as used in this report follow Eliot (1973).

RESULTS

Shape and Size

Eggs of lycaenids are of the upright type, with the micropylar region on the uppermost side opposite the generally flattened side usually attached to the substrate. They are round when viewed from above (hexagonal only in the Oriental Poritiinae), and appear somewhat dorso-ventrally flattened in side or profile view. Eggs are wider in diameter than high (except in the Australian and Ethiopian *Liphyra*). As a generalized concept, the shape of a frustum (see Fig. **1A**), used to describe the base of a cone after the top is cut off, is very similar to the egg of most lycaenids, provided the upper and lower margins are rounded. The adjective tiarate, or crown or turban-shape, has often been used with egg descriptions in the family, as has the echinate or echinoid shape. The latter is particularly descriptive in reference not only to the basic shape, but to the many minute projections from the surface. Actually, as shown in Figure **1**, the upper, lateral and bottom surfaces of particular eggs might be convex, level or concave, and might or might not be parallel to the opposite side. Examples of different genera are shown in the figure. Not indicated is the fact that the micropylar region on top of the egg might be in various attitudes with respect to the uppersurface; depressed, convex, flush, elevated and concave. The size and elevation of the micropylar region should not influence the profile description of the egg.

Only one group, the Ethiopian genus *Thestor* (Lachnocnemini tribe of the Miletinae), is so far known to have an asymmetrical egg (Fig. **3C**) with a prominent, dorsal, unilateral bulge. Most of the North American lycaenids have dome-shaped eggs of the Lycaeninae type (Fig. **1D**) or of the Theclinae type (Fig. **2B**) which may be flattened on top to where the upper surface is almost parallel to the bottom.

The surface sculpturing of the lycaenids is highly variable, ranging from a clear cut and relatively simple reticular network of intersecting ridges (Polyommatinae type as shown in Figs. **18** and **20**) to the highly sculptured eggs of the Eumaeini, many of which resemble *Zinnia* flowers (see Figs. **4, 10**) when viewed from above. This complex appearance seems to be produced by the same elements, each existing in one or more of several character states, and it was felt expedient to present the descriptive results of our study character by character, rather than by taxonomic group. For convenience, these are arranged alphabetically; a brief definition of the structure is followed by annotations and SEM photographs describing the variability in the character states as we have noted them in the Lycaenidae.

Egg size varied with the species from the smallest *(Brephidium)* with an average width of 0.40 mm and height of 0.22 mm to the largest, with an average width of 1.2 mm and height of 0.50 mm. Clark and Dickson (1971) examined species which equaled or exceeded these, the smallest being *Zizula hylax* (F.) with an egg of 0.4 x 0.2 mm to *Capys alphaeus* Cram., 1.6 x 1.0 mm. A compilation of all species shows an average width of 0.724 mm and a height of 0.424 for the family. However, the eggs of most species are known to vary, and interspecific variation shows a high degree of overlap. Egg size is thus useful for separating only those species whose eggs are either very small or very large.

General Morphology: Egg Nomenclature with Annotations

AEROPYLES: tiny openings (arrows on Figs. **36, 37**; also Figs. **42, 60, 61**) extending by means of respiratory tubes or a porous meshwork through the outer chorion of the egg; may be present on ribs, nodules, or lower chorionic layers and connecting its gas layers to the ambient air. Synonymous with pores and aeropores, but usually used when openings are single and widely separated. See also plastron.

One of the most interspecifically variable features among lycaenid eggs, and very likely eggs of all Lepidoptera, is in the geometry of the aeropores on the surface. These openings may occur in clusters, where they form a porous network comprising a plastron (Figs. **38-41**). They may also occur singly on various chorionic structures, or on prominent stalks (Figs. **60, 61**) or volcano-like nodules (Fig. **32**) seemingly structured to elevate the aeropore above the general surface of the egg. The numerous plastronopores and the fewer and more scattered aeropores may occur on the same egg. When this occurs, the aeropyle pore is usually slightly larger (Fig. **36**), but the irregular size of some plastronic pores and their (rare) occurrence on both muri and cells (Fig. **41**) sometimes makes distinction difficult. According to Hinton (1969, p. 353), plastrons may be formed by an enlargement of the aeropyles or an increase in their number or both.

In the lycaenids, the most common location of single aeropyles is at the intersections of muri or ribs, where they may occur as a simple pore on an otherwise unadorned rib bulge. More often there is a swelling (Figs. **36, 42**) containing one (Fig. **56**) to several (Fig. **36**) pores; the swelling may even be elevated (Figs. **56, 57**). Some species have prominent spines at the rib intersections which adds to the echinoid appearance of the egg (Figs. **12, 13**). Aeropores may be present (Fig. **34**) in these "spines" as they are in *saepium,* or absent; the spines may have terminal lips (Fig. **60**) or bumps (Fig. **61**) or even be upturned as they are in *beon.* Rough treatment of the newly laid egg may bend or otherwise distort these delicate structures.

In addition to the number and position of the aeropyles, the diameter of the larger pores on prominent structures may ultimately prove to have some taxonomic (discriminatory) value (Fig. **42**). Unfortunately these measurements may not be possible with a light microscope.

ANNULUS: one to several rows of areolae or "cells" and associated ribs or depressions defining them, which surround the micropyle (Figs. **50, 62**). The inner ring of the annulus with its wedge-shaped cells is called a rosette (Fig. **43**). See also rosette.

The full nature of the annulus may not be appreciated unless it is magnified several hundred times. When this is done (Figs. **45, 55, 65**) the micropyle is usually disclosed by the primary row of cells (rosette). Only then can the nature of the outlining walls, and the structure of the floor of the cells be determined. Sometimes the wedge- or petal-shaped cells are depressed into the surrounding area so that the walls are simply vertical elements as deep as the depression (Fig. **62**). The typical condition is to have elevated ridges (Figs. **50, 54**) outlining the cells. In species with a heavy chorionic overlay (as in the Lycaeninae) these ridges are really muri, (Fig. **53**) which become so thick that they obscure the openings to the areola they envelope.

Secondary and tertiary rows of cells comprising an annulus may be characteristic of some eggs (Figs. **62, 63**) and the cell numbers in these rows may be no more variable than those of the rosette. In other species (Fig. **50**), the irregular and/or poorly defined nature of the cells may obscure any linear arrangement by row (beyond the rosette) and render cell counts more suspect. When the micropylar plate is porous (Fig. **64**) other rows of cells besides the rosette may be completely obscure. Figure **55** shows a primary and secondary pattern of cells, but subsequent rows (if present) may be hidden by the coalesced upper chorion.

Other elements in the annulus include the nature of the lower surface of the cell (smooth, porous, granular, etc.). In some species, irregular but always present "islands" of thickened chorion protrude from the floor of the rosette cells (Fig. **52**); they may also be highly regular in size and placement, as they are at the bottom of each wedge-shaped cell in Figure **63**.

Ridges or ribs in the annulus show so variability; they can be thicker or thinner in sibling eggs. One tenth of the 20+ eggs studied by SEM from a single *Strymon melinus* female had marked variations in the annulus area, usually in distortions of the cells in the rosette.

AREOLA, AREOLAE: an interstice, a small space within something as the spaces in a meshwork; sometimes used synonymously with the term "cell" (which we prefer on a historical basis) for inter-rib areas (Figs. **38-40**); it is more appropriate for repeated interstices in a network (Fig. **35**) where the openings are too large to be pores, and are visibly open on two sides (top & bottom). See also cells and fossa.

CARINA, CARINAE: longitudinal raised lines or ridges (Fig. **46**, arrow); small superficial elevations in the nature of wrinkles or folds parallel to the main axis of the structure on which they are found.

Not all ribs or ridges have carinae (see Fig. **35**), but where they occur (Figs. **34, 46**) they impart a distinct character to the ridges involved. In some cases they are incomplete, occurring only on parts of a rib such as at intersection sites.

CELLS: an inter-rib area; a depression or cavity in the chorion usually between delimiting walls (Figs. **12, 13**) or ridges (Fig. **38**); a smaller portion of the chorion bound by other surrounding elements.

Researchers first describing eggs aided by light microscopes under transmitted light saw the thicker chorion of a rib as a dark linear element enveloping a lighter "cellular" region within. However, in using the name "cell" for this inter-rib area, they intended no direct comparison with protoplasmic cells, the basic unit of cytology. Rather, they were referring to the geometric, small, confined space in the same manner that the hexagonal, reticular appearance of some eggs (Fig. **12**) also strongly suggests the "cells" in the wax honeycomb of a beehive. We prefer to preserve this terminology, not only for historical reasons, but for its generic convenience. The almost universal presence of the micropylar rosette of wedge-shaped structures termed cells and their inclusion in basic descriptions, has resulted in excellent communication between egg morphologists, and argues for retention of the term. Greater interpretive difficulty stems from adapting the term for elsewhere on the chorion where the architecture is relatively not as simple. For example, in cases where wrinkles and folds in the chorionic skin form the delimiting linear elements (Fig. **41**), or where there is no abrupt juncture between the walls and the depressions between them (Fig. **36**) (much like the dimples on a golf ball), the situation is obviously much different than in the rosette. Nonetheless, if it is realized that there is no evoking of the principle of homology when referring to chorionic cells, and that it only means a confined space marked by fixed boundaries, it is a useful concept.

There is a tendency within the Polyommatinae particularly, but also in other subfamiles, for the ribs bordering the cells to be positioned in a series of regular involute curves which run diagonally from the annulus across the upper surface of the egg and down the sides. As they radiate out from the central axis the ribs gradually diverge as do the rays in a spiral nebula. Ribs radiate in both clockwise and counterclockwise directions such that they intersect one another to form a cellular meshwork of roughly diamond shape (Fig. **18**). The diamonds gradually enlarge on the sides and toward the bottom as the ribs get further apart, and individual eggs may have distorted cells if radiating ribs are missing (a fewer number in one direction than the other) or if the alignment is not symmetrical. Enlargements of the knobby prominences at rib intersections may further disrupt the angulate shape of the cells (Fig. **23**) and in other species (Fig. **37**) enlarged knobs and reduced ribs make the observer more conscious of cell depth than cell shape. That is, the character of the egg in gross view changes from a symmetrical, honeycombed architecture, to a knobby, porous surface.

Thus the overall shape of cells varies interspecifically; they may be polygonal (hexagons, pentagons, tetragons, etc.) or assume an irregular shape; they may be symmetrically arranged on the egg surface, or asymmetrical, without a regular pattern. They are more apparent in some species than others, and often they appear as deep pits. They are accentuated by the type of ribbing and structures at rib intersections.

In addition, the "floor" of the cells, actually the chorion adjacent to the egg membrane, may be highly sculptured (Figs. **35, 56**) or porous (Figs. **38-42**), and have raised "islands" (Fig. **52**) shaped like inverted funnels (Fig. **34**) or have other distinguishing features. These may vary between cells in the annulus, transition zone, and elsewhere on the same egg.

CHORION: the outer shell or covering of the egg which may be variously sculptured with ridges, depressions and reticulations, and which imparts a characteristic appearance to the various lycaenid species; it is of maternal rather than embryonic origin.

The chorion may be smooth or variously roughened in appearnace. In the Ethiopian *Tylopaedia s. sardonyx* (Trim.), an irregular, grainy surface is additionally covered with short spiny processes as well as spherical bumps and warts, which add to the already roughened appearance of the chorion. What function this might serve is a moot point, but among the possibilities in this species which lives in a very hot, dry habitat, might be to serve as a light reflector, a radiator, or both. In other words, the roughened chorion might play a part in elimination of heat through radiation. In the case of *sardonyx,* the muri and intersections are so enlarged that they cover the lower chorion, which further retards water loss through any pores in that surface and enhances the radiator effect of the upper surface. (See under reticulum for explanation of upper and lower chorionic surface.)

We were of the opinion (Downey and Allyn, 1979, p. 3) that no two eggs of *Leptotes cassius theonus* are exactly alike in all their external chorionic features. During this study we have not found evidence to the contrary (see under micropyle and rosette below), but must emphasize that the differences of which we speak are minor irregularities and inconsistencies in a highly irregular outer chorionic coat. Thus we have assumed these variations to be of no evolutionary significance.

COSTA (costule): an elevated ridge, or one of a series of raised ribs (Figs. **57, 58**) which are usually rounded on their crests. See ribs.

Costa and rib have been used interchangeably by some workers, but we suggest that in the lycaenids, a distinction be made on the basis of elevations above the surface. As can be noted in Figures **35** and **58**, the costa may be supported by delicate trabeculae; in other cases (Fig. **58**) a thin but solidly-appearing strut may hold the costule in an elevated position. Ribs on the other hand (Figs. **38, 40**) are lying against the underlying surface, or gradually slope downward (Figs. **34, 36**) where the term muri or wall might be more appropriate.

Like ribs, costules may form a reticular network over the egg surface, and at intersecting points (Fig. **57**) they may enlarge or form elevated knobs or protuberances termed tubercles. Like the ribs, many costa are porous (Fig. **33**), which is evidenced by the aeropyles on tubercles.

FOSSA, FOSSAE: a pit or marked depression between elevated ridges (Fig. **34**); may be used for a funnel or bowl-shaped cell whose depth is at least as great as its diameter. See also areola and cells.

In some species the micropylar region is depressed (Fig. **64**) and the shape and diameter of this fossa (better termed the central fovea) may be diagnostic. Most often in the lycaenids, the apparent depressed nature of the micropylar area (see Figs. **2, 8, 13, 17**) is an exaggeration produced by the marked elevation of the surrounding chorionic prominences. It is only at high magnification that one can determine the true contour of this region (see Figs. **53, 55**). In other regions of the egg, the fossa may be so deep (Fig. **12**) that their chorionic bottoms are not distinct in surface view.

FOVEA CENTRALIS: a deep depression or pit (Fig. **62**, arrow), with well-marked sides, in a medial or polar position on the egg and containing the micropylar openings.

In eggs with a globular, or even with a dome shape, there is a tendency for the micropylar region to be depressed (Figs. **2-6, 14-19**), and appear concave. The entire pit region would be the fovea, which may be visible to the unaided eye. Often it is exaggerated by the height of the surrounding chorionic structures. Less commonly, the floor of the fovea is level (Fig. **64**). With the enlargement made possible by the SEM, our attention is usually focused on the annulus, with its rosette, and other areolae and pores which may occur in the micropylar depression, and are not concerned that these occur in a depressed space (i.e., the fovea). However, the width of the fovea, ordinarily used in conjuntion with egg diameter, may be useful in separating some taxonomic groups. Scudder (1889) used this character to distinguish some tribes (his Theclidi from Lycaenidi) but additional material available to us indicates this is not a tribal character.

KNOBS or *KNOTS:* a swelling, thickening or protuberance; see tubercle.

MICROPYLE: one to several minute openings (Fig. **52**, **5** openings; arrow, Fig. **62**) through which the sperm will enter in passing through the chorion to reach the inner part of the egg in the process of fertilization. The micropylar openings lead to canaliculi, minute ducts which lead through the chorion.

Ordinarily the micropyle is marked by a single pit or depression, which may assume different shapes or tendencies in different species: circular (Eumaeini); oblong (*Leptotes*); triangular (*Lycaeides argyrognomon*), etc. The micropyles themselves open into this cavity; depending on the species, from three to six openings may be apparent, or may be partially hidden by the lips of the central depression. Most often there is the same number of micropyles as wedge-shaped "petals" in the surrounding rosette (note Figs. **52, 62**).

There is an indication that the size of the micropylar openings may be diagnostic of some species. That is, the openings in the riodinid *Emesis emesia* are fully twice as large as they are in other riodinid eggs of similar dimensions such as *Apodemia mormo.* This may be an aftermath of an increased respiratory function taken on by the micropyles of the former species, since chorionic aeropyles were not located in this species. The differing positions of the openings on the vertical to sloping plane of the micropylar depression increases the difficulty of obtaining diameter measurements. In most cases, the position of the openings with respect to one another, and to the ridgesand structures of the rosette, will probably be critical for taxonomic purposes, since the diameter of micropyle openings will overlap broadly between most species.

The position of the micropylar opening sometimes indicates the direction the canaliculi take as they issue from the central area. SEM photos of 2000 diameters or more are usually required to determine this tendency.

The entire micropylar area, including the rosette of the annulus, may be elevated as it is in the Ethiopian *Euchrysops malathana* (Bdv.). Most often, the micropyle is defined by the rosette, even when the rosette is depressed (Fig. **62**) or ill-defined (Fig. **65**). Sometimes there are bumps or islands of chorion at the apex of each cell of the rosette (Fig. **63**), and in some cases *(Hemiargus thomasi bahamensis* (Clench) the high elevation of these prominences emphasizes adjacent depressions, so that each petal in the rosette would appear to have two canals on each side of the prominence which flow to the central micropylar depression.

In the micropylar region the chorion is rather thin compared to elsewhere on the egg surface, and it is closely adherent to the underlying vitelline membrane. Not infrequently this is evidenced in SEM work by electronic "charging" in this area from the poorly grounded internal embryonic structures (note Fig. **65**). These often reflect more of the electronic charge back through the micropylar openings, which then appear lit from within, with corresponding difficulty in photograpy. The thinness of this region might facilitate both fertilization and respiration.

MOLE, MOLES: a small protuberance; term used by Clark and Dickson (1956) for tubercles at the intersection of ribs. See tubercle.

MURE, or *MURUS, MURI:* elevated chorinonic prominences appearing as walls or heavy ridges (Figs. **36**, **41**) forming the outer chorionic sculpturing on the surface of the egg; see also ribs.

In most cases muri appear as steep-walled folds (Figs. **45**, **53**) formed from the underlying chorion; in other cases (Fig. **46**) they are more or less elevated from the surface, which might be visible at the bottom of the pit or crater (fossa) formed by the sloping walls. Unlike ribs or costa, muri have ill-defined bases such that their lateral limits are obscure or even continuous with adjacent muri (Fig. **67**).

NODE, or *NODUS, NODI:* a knot or swelling protruding from a surface. See tubercles.

PLASTRON: a gas film of constant volume with an extensive water-air interface; the highly porous chorion in some areas of the egg surface serves as an air-store, plastronic network. This thin-film air mass serves as a physical gill when submerged in rain-water which is rich in dissolved oxygen. The external appearance of a plastron structure is shown in several species in Figures **38** to **42**.

PORES: perforations or openings in the outer chorion which communicate with an inner meshwork of spaces and ducts. When less numerous and associated with particular structures or positions on the outer surface (Figs. **36**, **37**, arrows) they may be termed aeropyles; when very numerous and aggregated so as to impart a sieve-like or lacy architecture (Figs. **38**, **41**) they form a plastron network. See also aeropyles and plastron.

The distinction between aeropyles (= aeropores) and plastronopores indicated above will serve to distinguish the two major kinds of openings by means of which molecules in the ambient air find their way into the chorion. It should be re-emphasized that the chorion is porous, as indicated in the fractured cross section in Figure **33**. Further, aeropyles and ribs are also a space-filled meshwork with thin pieces of chorion interspersed between the vacuoles.

Other openings occur on the egg surface which could be called pores but which may have other designations. The micropyles can be readily identified by location in the middle of the rosette on the upper surface. There can also be rather large openings in the annulus (Fig. **64**), too large for respiratory pores. They, like the under-rib spaces visible in Figures **35**, and narrow and deep cells as in Figures **45**, serve as larger communication ports to the lower chorion. Their high walls may serve as baffles to retard humidity loss near the egg surface.

RETICULUM: a net-like meshwork; usually refers to the linear, often honey-comb like network of elevations (ridges, or ribs) overlying a lower, usually smoother, chorion.

In agrotines (see Salkeld, 1975) and other moths whose chorionic pattern is limited to the upper one-third or less of the egg, very often only the rosette, and one or two other rows of cells in the annulus have ridges or ribs around the cells. Otherwise the egg surface is fairly smooth, and lacks overlying materials. In lycaenids, most of the egg surface except the bottom, has both an upper and a lower element, both of which may have structural features. In such cases, the overlying structures have been referred to as chorionic reticulations, and the latter word used as a noun, rather than an adjective. Even in the lycaenids, the ribs or muri are usually distinct as an overlying material, and since they intersect with one another, the use of the term "reticulum", or "chorionic reticulations" would be proper. Our only difficulty would be with certain eggs such as *Lycaena phlaeas* (Fig. **14**) where there is no distinction between the ridges or muri and the chorion in the basin of the cell. In this case, one is uncertain whether or not the entire outer chorionic envelope (reticulation?) has covered a lower one, masking it from view. Note Figure **67** (*C. gryneus*) where the highly modified muri would also make the use of the term reticulum inappropriate. However, even in the latter case, one can detect in the deepest depressions, evidences of a lower chorionic element. It is in the latter surface only that plastrons occur.

RIBS: chorionic prominences or ridges (Figs. **38**, **43**) whose shape or texture impart a distinction from the material across or through which they may traverse; may be elevated (termed costae, Fig. **35**) or wall-like (termed muri, Fig. **36**), or in low relief (Fig. **41**). See also costa and murus.

Unlike most muri, ribs usually have better definition, particularly their ventral and lateral limits, and the term is most likely to be used when repeated geometric design implies a structural supportive function (witness "cross-rib"). When they surround circular cells (Fig. **40**) or are part of a very porous plate (Fig. **64**) they are more likely to be referred to as reticulations. Ribs may have carina (arrow, Fig. **46**) on their surfaces.

It is usual for lycaenid eggs to have more than one type of rib. The rosette around the micropyle may have ribs (Fig. **43**) differing from those in the transition zone (arrow, Fig. **26**) or on the lateral margins of the egg. Most ribs are internally porous and vacuolated (Fig. **33**), but the small size and rigid structure of others (Fig. **43**), particularly in the micropylar region, suggest that some are rather solid.

Ribs differ in shape: height versus breadth; uniform or varying in dimension; compressed or elevated; straight or sinuous; delicate, coarse or heavy in appearance. The sculpturing or texture of the ribs also varies: smooth or unsculptured versus textured; delicate (linear or transverse elements) versus coarse (bold, raised, netted, pitted, spinous) elements. The ribs usually intersect one another and these junctures may be unadorned (Fig. **39**) or there may be slight swellings (Fig. **35**) to raised tubercles (Fig. **32**) or spines (Fig. **60**) but the enlargement in some species becomes so prominent (Fig. **37**) as to obscure the ribs. Ribs may be with or without aeropyles.

The position and nature of the ribbing together with the tubercles at their points of juncture provide the distinguishing chorionic architecture for lycaenid eggs. While similar elements are involved, the gross appearance of eggs may impart striking dissimilarities depending on which structures are more prominent. This is best demonstrated by examples: tubercles predominate, Figs. **10** (see enlargement in Fig. **37**), **15**; tubercles enlarged spaced by ribs, Figs. 6, 10; ribs hexagonal, spinous aeropyles, Figs. **12**, **13**; ribs reticulate, tubercles enlarged laterally, Figs. **23-26**; ribs involute curves, Fig. **18**. Parallel and circular ribs (horizontal radii, vertical radii) are known for some African lycaenids not available to us, in which the longitudinal and lateral rib elements are distinct.

ROSETTE: a cluster of wedge- or petal-shaped areolae (Figs. **50-55**) or cells and associated structures forming the first or primary row surrounding the micropyle; the inner ring of the annulus (Figs. **62**, **63**).

The rosette seems to show a great deal of interspecific variability which may belie its taxonomic usefulness, partly for reasons given below. Its surface may be level with the annulus, or it may be depressed into the chorion, or elevated on a pimple-like hillock.

The shape of component cells imparts a distinct character. While basically wedge-shaped, they may be regular (Fig. **62**) or irregular (Fig. **51**), with pointed apex (Fig. **43**), rounded (Fig. **53**) or irregular (Fig. **50**) outer margins. Confluent sides shared by adjacent cells may be less than half the length of the cell (Fig. **62**), about half of cell length (Fig. **43**) or greater (not shown), but the ridge between may be enlarged or wedge-shaped

(Fig. **65**) so that the cells may appear far apart.

Ribs which outline the petals of the rosette may be elevated or depressed, of similar height or variable, and may even appear to overlap one another (Fig. **50**) at junctures. See discussion under ribs above. In enveloping the cells, the ribs usually do not touch at the micropyle with the result that the cell appears open ended (Fig. **43**). In this opening may appear chorionic islands (Fig. **52**) or pimples (Fig. **63**) which may also occur elsewhere in the cell. The ribs may touch the micropylar depression (Fig. **50**) or end some distance from it (Fig. **54**), or from the micropyles (Figs. **43, 45**) when the depression is lacking. The chorionic surface of the cells may be porous, but are more likely to be unpitted.

We attempted some study of variability in eggs available in quantity. Rosettes of 20 eggs from one female of *Strymon melinus* were examined: eight had five petals (cells) in their rosettes; 12 of the 20 had four petals. The same number of field-taken eggs of *Leptotes cassius* were examined by means of SEM and a count made of the cells in the rosette with the following result: 1 egg had 6 petals; 5 eggs had 5; 11 eggs had 4 petals; 3 eggs contained 3 petals. We might have expected less variability in the eggs from one female (attesting to lesser genetic variability) than field-taken eggs where more females were involved. We had not anticipated such a wide range of differences however, and this data, together with variations in the rosettes of the two to five specimens of other species examined, lead us to conclude that the infraspecific variability is too large in this character for it to have priority as a species diagnostic character. Tendencies may be projected, but if one or two eggs of a population are found to have 4 petals, and one or two eggs of another population of the same species are discovered to have 5 petals in the rosette, one should be very leary of using this as "evidence" of subspecific distinction until additional data are at hand.

TRANSITION ZONE: a belt of areoles (Fig. **26**, brackets) on the outer margin of the annulus, and between the latter and the lateral region which is usually marked by distinct muri, tubercles, fossae, etc. The presence and/or limits of this zone may not be as distinct in some species as in others.

Most of the transition zones we have identified in the lycaenid eggs so far examined have been in the Polyommatini tribe of the Polyommatinae (Figs. **20-27**). In some species of this group however (Figs. **18, 19**) it is not well marked. Much more data will need to be gathered to assess whether or not the character has potential taxonomic value.

TUBERCLE, TUBERCULI: a small protuberance (Fig. **35**), projection (Fig. **34**), lump or swelling (Figs. **36, 37**), often located at the intersections of ribs or muri. See also discussion under aeropyle and ribs.

Tubercles have been variously termed knobs, nodules, bulges, moles, projections, protuberances, mushroom-like elevations, and papillae, all of which terms indicate their common feature: they project up from a lower or surrounding surface. In the lycaenids the majority of the tubercles are located at rib intersections. Sometimes they appear only as slight thickenings or swellings in the ribs (Fig. **35**), but it is usual for them to be quite large (Fig. **32**) and crater-like (Fig. **42**). They may be so enlarged (Fig. **37**) as to obscure the ribs running between them, and they may join adjacent tubercles (Fig. **36**) to form confluent prominences. In some species, they are elongate and spine-like (Figs. **34, 60**). They may or may not have aeropyles, which are usually apical when present. Tubercles on adjacent rib-junctures are usually of the same height or gradually increasing in elevation from the transition zone to the shoulder and lateral margins of the egg where they are the largest. In a few species however, adjacent tubercles are of different sizes (Fig. **66**). Not infrequently tubercles appear as the roughened peaks of mountains which flow downward, ending in the ridges of muri (Fig. **67**) with depressed valleys between. As indicated earlier, the prominence of the tubercles markedly affects the appearance of the egg and usually accounts for the "echinoid" description given to most lycaenid eggs.

WALL: elevated, linear prominences appearing as ridges; more properly termed muri. See costa, ribs, mure.

Differences - Eggs Laid Normally Versus Those Extracted From Females.

Egg variability was studied in detail in both *Strymon melinus* and *Leptotes cassius theonus* (see under rosette above), and to a lesser extent in other species. Attention was given to eggs laid by single females with the assumption that they might be closer genetically than random samples of field eggs. We also compared eggs laid by females with samples extracted from the vagina and common oviduct of the same female shortly after death. Some unexpected differences were noted.

Extracted eggs from recently deceased females *(melinus, cassius)* invariably collapsed (Fig. **27**), while most eggs which were laid (85%) did not show any gross external evidence of change irrespective of the dispatching process; by freezing, cyanide fumes, or alcohol submergence. It is surmised that once the chorionic sculpturing on the egg surface has been dried, its rigidity is usually sufficient to prevent collapse of the egg on death and cytoplasmic dessication. Further, both *melinus* and *cassius* eggs removed from females invariably had incomplete chorionic sculpturing when viewed under SEM (see Fig. **59**), mostly manifest in the thinner portions, such as the vertical elements which support the ribbing.* The thinness and porosity of even the ribbing of *melinus* is evident in Figure **59**, which can be compared to the same structures in relatively the same view of a field taken egg in Figure **58**. Whereas the ribbing is generally sponge-like and porous internally (note Fig. **33**), the supporting braces are solid, unporous structures from 0.0025 mm to 0.003 mm thick in hatched eggs. In unlaid eggs, these elements are a mesh-like network, with almost as much air-space as matrix. The ribs and other areas likewise appear to be thinner, with a few showing a type of porosity (Fig. **59**) not observed in even the freshly laid egg. It thus appears that the outer chorionic structuring is not completed in its final form until the egg is laid. It may be that the viscous fluid from the accessory glands dries down and accumulates in these pores. This may add strength to the chorionic members and would also help to trap air for plastronic purposes in the inner meshwork of the shell, and prevent undue dessication. A close look at the aeropyle projections on Figures **32** and **42**, as well as the rib on Figure **33**, shows what appears to have been a porous surface, but there are no openings. Rather, each pore appears to be a small crater, or indentation, exactly as it might if overrun and filled by a rather glutinous substance.

The differences between the chorionic structures of extracted versus laid eggs has given us pause in using eggs from dried adults stored in collections. Knowledge of this has also helped explain the appearance of some structures on eggs obtained in collections from unidentified sources. We are confident, for example, that given the appearance of the aeropyle in Figure **61**, the egg of *Satyrium acadica* was extracted from the adult, and not oviposited. However, it should be noted that the general and micropylar pattern are formed fairly early in egg development as they move posteriorly in the lateral oviducts (Fig. **30**), and such data may be used with the above cautions.

Egg Coatings

Like other Lepidoptera, eggs of Lycaenidae are usually coated with a secretion from the accessory glands as they are laid. These secretory organs are called colleterial glands since they commonly produce this adhesive cement. Eggs touching two surfaces in a flower spike may adhere with equal tenacity to both surfaces, indicating that the material is not limited to the lower egg surface during oviposition. Ordinarily the amount of material this requires is minimal, since it dries quickly and is not visibly evident on the egg surface, nor even as a superfluous squeezing from beneath the lower surface at the plant-egg interface. However, in some species excessive amounts of secretions may embed the eggs in a matrix of material which may be confused with, or cover the chorionic sculpturing. For example, a transparent, bubble-like material, presumably solidified froth of maternal origin, surrounds the eggs of the Samoan *Jamides argentina* (Prittw.) (Hopkins, 1927, p. 52). Figure **47** shows the same situation in *Feniseca targuinius* where fluids, presumably from the accessory glands, forms a

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*Apparently not all species may show this; Salkeld (1975) noted in the noctuid genus *Euxoa* that the chorionic sculpturing was the same on both laid and dissected eggs (fully developed ones in the oviduct).

highly vacuolated sheath. This coating is fairly brittle on drying, and is more generously applied to some eggs than others. On eggs such as the hatched one shown in Figure **47**, the material covers the egg and flows to the surrounding plant tissue where it may accidentally incorporate plant and aphid detritus. Figure **22** illustrates the "accidental" inclusion of adult scales on an egg surface (sibling eggs lacked them) and Figure **49** shows pollen grains partially embedded in the relatively smooth surface of a field-taken egg of *Papilio.* Whether or not the female can control the amount of fluid as an egg is issued, or whether the amount is a function of the length of individual oviposition time, has not been determined.

According to Clark and Dickson (1971) eggs of *Alaena amazoula* Bdv. are originally pink in color, but fluid from an "ink-sac" (presumably the accessory glands) gives them a dark color on being laid. *Durbania amakosa* (Trim.) eggs are also pink if dissected from the female, but pass through a brown "ink sac" on being laid *(loc. cit.). Euchrysops malathana* (Bdv.) eggs have a "slimy" coating, and the glutinous substance on the eggs of *Epamera sidus* (Trim.) not only gives the white egg a yellow appearance, but is reputedly a partial protection against parasitoids, even though such eggs have been found to be parasitized.

As noted above, semi-deciduous adult scales from the abdomen may accidentally be included in the fast-drying egg coat, but females of some species have evolved a specialized hair tuft on the tip of the abdomen which, among other possible functions, furnish batches of long scales to the egg surface. Presumably this has an egg-camouflaging function (Nakamura, 1976). Further, in addition to the long-scale abdominal patches, species such as *Nordmannia myrtale* (Klug) has evolved a particular behavior pattern of side-to-side brushing of the abdominal tip over newly laid eggs. These factors suggest a genetically fixed pattern of some selective advantage. In the genus *Phasis,* black spinous scales in the tuft open up like a brush, presumably to aid in the adhering process. A few hesperiids cover their eggs with scales to such an extent the shell may not be visible, though most lycaenids having this trait appear to hatch far fewer scales than would be necessary to camouflage the egg, or even break up its silhouette, which factors might be of presumed utility in search behaviors of predators or parasitoids. In *Cruderia leroma* (Wallengr.), Clark and Dickson (1971) note a decrease in the number of scales attached to eggs laid later in the life of the female, which therefore might lessen any selective advantage.

Two other possible functions of adult scales on eggs should be noted both which might be easily tested under proper circumstances. The scales could have a repellent chemical which serves as a deterrent against parasitoids. Hair tufts on females should quickly demonstrate such function when exposed to such cosmopolitan egg parasites as *Trichogramma.* Additionally, the deterrent nature could ward off females searching for oviposition sites in order to disseminate the eggs. It is also possible that the scales directly or indirectly serve a dietary function. That is, in most of the lycaenids having this behavior (such as *Trimenia wallengrenii* (Trim.), a remarkably high percentage have larvae which consume the entire egg shell (and included scales!). On the other hand, species with scaleless eggs, in the vast majority of cases, have larvae which eat only a small exit hole in the chorion (see Fig. **47**) and dismount the egg surface almost immediately on emergence. It is distinctly possible that adult scales adhering to the egg shell contain some chemical of advantage to the young larvae. These could even serve as "attractomones", for example, to keep the larvae on the egg for a longer period, or cause it to consume the entire shell, presumably for some dietary advantage. At least this possibility should be explored, perhaps first by studies involving a measure of the comparative success of larvae permitted to consume the scales and shells, with siblings removed from the egg on first emergence. It would also be interesting to determine the degree of egg consumption when adhering scales have been removed.

We have derived sufficient evidence to support the contention that the colleterial glands function not only to provide material to "glue" the egg to the substrate, and provide ancillary features (such as protective covering, color, scale glue, chemical deterrents, etc.), but that their main function may be as final hardening agents of the chorion. They may also play a part in modifying the respiratory function of the chorion between the intra-oviductal and post-oviposition phases. That is, the vitelline membrane and the chorion are mechanical barriers in the process of egg respiration, but this role may be modified somewhat within and outside maternal tissues. On the inside, the egg may be bathed in fluids, but undoubtedly respires (ultimately) from gaseous exchange made possible by trachea around and in the ovarioles. After oviposition the egg is surrounded by air but may also have to withstand periodic inundation with rainwater and dew, depending on the oviposition site and longevity. Perhaps the aeropores, with their relatively larger openings, together with their position on elevated stalks, ridges and knobs, are a requirement of the pre-laid egg. It may even be that these openings function directly with the trachioles around the vitellarium since they protrude into that tissue further than other parts of the chorionic network. They very porous plastronic network may also function as a respiratory vehicle in the pre-laid egg: it is possible that the aerospaces of the chorion become air-filled while within the maternal tissues and the flow of air-displaced liquid might also be via the aeropyle system. The important point here is to understand that the mechanical function of the chorion in respiration may operate differently when the egg is inside and outside maternal tissues, and that this is in spite of the fact that the pores of the plastron could function early (particularly if there was routine diffusion from the follicular surface as well as direct tracheal connection). The only modifying factor affecting the porosity of the chorion between the two locations is the secretion of the accessory glands. We have shown above that this material coats the entire surface of the egg, even though the absolute amount of the substance may vary with the species and with any "added" function, *i.e.* adherence of scales. This material settles onto (and into) the chorionic surfaces, undoubtedly closing many of smaller pores, and modifying quite substantially the total amount of interface between the ambient air and the gaseous layer within the walls of the chorion. This difference may be visually confirmed with SEM photos taken before and after oviposition (Figures **59**, **58**). Two additional functions of this coating may be noted: it retards dessication by decreasing the amount of exposed surface, and it imparts increased rigidity (strength) to the outer chorion.

It should also be noted that pores of the plastron and chorion as described herein are morphological descriptions and that the physiological functions have not been tested. It is possible that parts or all of the pores do not actively function in the respiratory process either *in situ* in maternal tissues, or on being laid. We have observed butterfly eggs *(Emesis emesia* (Hew.), Riodinidae) where the only chorionic openings appeared to be the micropyles, and respiration could be accomplished through these structures only. Further, the egg membrane beneath the chorion may not be equally permeable throughout its surface, perhaps beneath some of the pores which might otherwise be perfectly functional. However, the widespread presence of plastronic size pores as well as the larger aeropyles, not only in the Lepidoptera but in most insects, attests to a common need and function.

Additional and compelling evidence for the anti-desiccant function of the outer egg coating comes from *Feniseca tarquinius* (Fig. **47**) in which, as indicated above, the frothy material completely covers the egg. The chorion of this species (Fig. **41**) is extremely porous over much of its surface and presumably such an extensive field of plastronopores would greatly enhance respiration, but would by the same factor, increase the rate of water loss. While the structure of the egg is no doubt a compromise between these seemingly contradictory requirements, water loss in *Feniseca* is retarded by this water insoluble outer coat. We are of the opinion these eggs would succumb from drying out should the outer vacuolated sheath be removed. Too few eggs were available to satisfactorily test this hypothesis; it is difficult to remove the coat without injury to the egg. An important consideration here is that the eggs of *Feniseca* lack any reticular network over the plastronic chorion, which network is almost universal in the family. The majority of the family also has eggs characterized by significantly less frothy-covering stemming from the accessory glands. In other words, the evolutionary gain of the frothy outer coating in *Feniseca* might have permitted a concurrent or subsequent loss of any ancestral reticular coating. It is our contention that the overlying reticular structure in the lycaenids serves to retard waterloss through surface evaporation under dry conditions. Additionally, the highly ridged and fluted frameworks may serve to strengthen the egg, particularly from the increased hydrostatic pressures placed on the plastron on impact of a falling raindrop.

Indirect evidence for the strengthening (or hardening) function of the accessory fluid is the fact mentioned above that some eggs are incomplete in appearance just prior to oviposition, but are complete as soon as laid. Eggs collapse on drying if they are extracted from the common or lateral oviducts, but usually do not collapse after oviposition. Also, muri (walls or ribs) and tubercles are formed early in the ovarioles, and must achieve final size by maintaining plasticity. It appears that they gradually "stretch" into final size to cover the fully mature egg while the egg is growing by addition to its yolk stores in the vitellarium. The secreting follicular tissue gradually becomes thinner and thinner, reducing its chorionic secretory function lower in the zone of egg growth, prior to its resorption at the pedicel of the ovariole. This plasticity is maintained in the newly laid egg and is attested to by the fact that when the egg is detached from a leaf on which it is laid the base shows a replica of the leaf-surface in which the stomata of the leaf may be clearly represented (see Tutt, 1905-06, p. 440). It is our contention that the final hardening agent of the chorion is the accessory fluid. Interestingly, it also serves as a quick-drying oval cement, and the chorionic thickness on the lower or bottom surface which is embedded in this material is very thin. This is demonstrated in hatched eggs by observing the transparency of this area compared with the balance of the egg shell.

Secretion of the Chorionic Coat

The inner epithelial cells of the ovarian follicles of *Leptotes cassius theonus* (Lucas) are shown in Figure **29** enlarged 600 times. This is the epithelium which secretes the chorion of the egg shell and the contour of the tissue and the distribution and nature of the secreting cells determines the pattern of the egg surface. Depressions (channels, grooves, pits, indentations) in this surface form a mold which will cast the chorionic elevations (ridges, muri, ribs, walls); elevations or prominences in the ovarian surface will produce depressions (cells, fossae). Compare Figure **29** with the egg of the same species (Figure **18**), particularly as viewed *in situ* as shown in Figure **30.** As mentioned above, surface reticulations are laid down fairly high in the egg chamber, and their pliability (really "stretch-ability") permits the egg to enlarge to its final size.

In some genera such as *Lycaena,* the follicular secretory cells apparently do not readily terminate their connections with their chorionic secretions with the result that some bridging chorionic streamers are formed between the egg and the epithelium. As parturition occurs between the egg and follicular membrane, presumably low in the pedicel or stalk of the ovariole, these streamers break and come to rest on the egg surface. Figure **31** shows a tangled mass of such streamers forming a dense webbing on the surface. In other cases (Fig. **36**) single streamers may occur on the egg surface where they are easily mistaken for the single silken strands left from the spinneret of a larva as it walked over the egg. Only when these strands are traced back to their juncture with the chorionic surface is one certain of their origins. Figure **45** indicates by arrow a chorionic streamer in the micropylar region of *Epidemia dorcas* (W. Kirby) in which the fusion of the streamer with the chorion of the egg is quite apparent. We have observed these streamers in published SEM photos of lepidopteron eggs, but until now have been uncertain of their origin and significance.

DISCUSSION

What is the meaning of the observed differences in egg sculpturing? Can we attach any adaptive significance or evolutionary strategy to the different types? Does chorionic sculpturing and other differences have taxonomic utility? All of these questions can only be hinted at with the data at hand.

A word about evolutionary philosophy might be in order. The larval stage of development, as well as the egg, pupa, and the adult stage, have gradually developed simultaneous and concurrent specializations in diverging directions. That is, the larvae may evolve at a faster or slower "rate" than the adult, but the optimum factors of the larval environment, and their adaptive responses, are expected to permit them to exploit a *lebensraum* quite different from that of the adult. In fact, the success (no matter how measured) of a particular butterfly species may be a direct result of the singular adaptive "success" of its larval stage, even though the adult may have less, or even fairly neutral selective advantage.

It may be argued that the characters of egg and pupa are passed on by a preceding stage, and that they are more passive in evolutionary response, than the larva or adult stage. Indeed, immature stages have no gene flow of their own, but only that of the adults. Theoretically, immature and adult characters are thus equivalent for taxonomy. For example, most of the characters used in classifying butterfly eggs are involved in the shell or chorion or associated details (glue secretions from accessory glands, etc.). The structures of the chorion reflect the shape of the follicular cells in the ovariole and are thus the manifestation of a character of the adult (van Emden, 1957). Whatever is their significance for taxonomy, it must therefore be identical with that of other adult characters.

That this situation is complex is illustrated by such a simple character as color in the egg. There is usually a characteristic color described for the eggs of most species, even though some color change may occur during development, particularly the darkening that occurs a day or so preceding eclosion. As indicated above, egg contents are derived partly from tissue of the developing ovum, and partly from tissue derived from the female parent. The latter is under the direct control of the female's genotype, and thus color in the egg may be solely maternally determined (see Robinson, 1971, pg. 56). Color produced by embryonic tissue may have paternal contributions into its genetic system, and while its genotype cannot be completely divorced from this and the maternal contribution as well, the embryonic color is contained within the new immature stage. The most important aspect here is that the color in this system will be subject to its own selective pressures as distinct from those acting on the egg color component attributed to the female follicular tissue.

Generic parameters may be rather subjective, depending on whether one tends to split or lump related kinds, but there seems to be no question that certain "genera" exhibit greater egg variability between congenors than others. Many examples from different realms could be given: the African *Euchrysops barkeri* (Trim.) does not have much chorionic sculpturing and has the micropyle on a central elevation or "pimple"; *E. osiris* (Hopff.), on the other hand, has prominent sculpturing and a flat or level upper surface. *Zintha hintza* (Trim.) has a cupola-shaped egg with a concave upper surface, while most of the other members of the genus are flat on top. The Nearctic *Lycaena phleas americana* Harris has dome or bun-shaped eggs superficially resembling the African genera *Poecilmitis* and *Baliochila* more than other North American *Lycaena* to which it is obviously more closely related. It is here suggested that a degree of caution must be used in using egg characters for taxonomic discrimination, at least until we are more certain of the usefulness, reliability and parameters of the characters involved. It is for this reason we do not advance specific taxonomic decisions at this time.

Both *Hyllolycaena hyllus* (Cram.) and *Lycaena phlaeas* (Linn.) feed on curly dock *(Rumex crispus)* and we have found the egg (though not commonly) of both species on the same individual plants in southern Illinois. Both coppers are at least double-brooded, but *phlaeas* overwinters in the pupal stage, while *hyllus* hibernates in the egg stages, perhaps as a first instar larva within the egg shell. Nonetheless, with this apparent difference, one might suspect there to be some externally apparent adaptive difference in the eggs of the two species. Indeed, the egg differences are marked (see Figs. **14, 15**), and we are left to assess whether such differences reflect taxonomic differences of the adults, adaptive features of the eggs, (or both) or be produced by other factors. Miller and Brown (1979) figure the egg of *phlaeas,* but fail to use the egg differences in arguing for the separation of their genus *Hyllolycaena* from *Lycaena*.

Dormancy (i.e., diapause) is a commonly used (and readily accepted explanation) advanced as a strategy for survival of eggs, or larvae in egg shells, during adverse or unsuitable periods. One might anticipate the egg chorionic sculpturing could reflect both some morphological and physiological responses (adaptations) to some of these adverse ecological conditions. For example, more apparent plastronic respiratory systems in eggs undergoing wet or rainy seasons, and suitable antidessication structures under dry or desert-like conditions. If differences in the eggs of butterflies which diapause during wet periods *versus* dry periods can be detected, what might be expected in eggs of tropical or semi-tropical species who reproduce during the entire year? Might eggs laid in January be different from July eggs? Or might the egg of such species represent an evolutionary amalgamation of morphological and physiological features suited for the extremes of physical conditions in their niche throughout the year?

Eggs of lycaenids can be placed in two groups according to "hatching" times: 1.) those in which there is never any detectable "diapause" of embryonic contents such that the larvae emerge (= hatch) within a short period of time, usually less than two weeks; and 2.) those in which there is an extended period (aestivation or hibernation) of the life span spent in the egg stage, amounting from approximately 25 to 75% of the entire life of the individual. To the latter group belong those few multivoltine species where late fall generations produce eggs which overwinter in that stage. More commonly in multivoltine forms, the "resistant" stage is as a larva or pupa, and other stages of the life cycle, including oval stages, ordinarily succumb to the cold.

The second grouping of lycaenid egg types can thus be subdivided into those with obligate egg diapause, and those which have a facilitative diapause. A brief discussion of corresponding physiological problems could help in understanding egg sculpturing.

Obviously the chorion of the egg must be sufficiently porous as to permit oxygen molecules to enter. However, water molecules are smaller than oxygen molecules, and as indicated in the results, water loss might be fatal in terrestrial eggs with highly porous chorions. Further, the smaller the egg, the greater is the surface area in relationship to its volume with the correspondingly increased risk of water loss by evaporation. The evolution of insect eggs shells has no doubt included a balance of the requirements for respiration, and the prevention of water loss. As Hinton (1970a, 1970b) and others (i.e. Ward and Ready, 1975) have pointed out, this problem has been solved by the evolution of a plastronic meshwork in the chorion. This plastron is a gas film of constant volume and an extensive surface area, held in position by a system of water-repellent structures. We have earlier (Downey and Allyn, 1979) described the external appearance of the plastron in eggs of the multivoltine lycaenid *Leptotes cassius*.

Hinton (1970b, p. 84) conjectures that the struts and braces of the inner chorionic meshwork are coated with a water-repellent, fatty material which reduces the adhesion between the meshwork and the original fluid contained in the developing egg. This permits, or aids, in the removal of the liquid, either by the meshwork becoming filled with gas as the egg dries out after being laid, or (as in stick insects and in flies) as the fluids are removed and the meshwork spaces filled with gas while the egg is still immersed in the fluid of the oviduct.

In considering the rather marked chorionic dissimilarity of eggs of congenors, several explanations are possible:

1.) the present adult taxonomy does not reflect natural groupings; in other words, the chorionic characters may educe relationships more (or less) accurately than our interpretation of the summary of other adult character states;

2.) the chorionic structures of the eggs do not mirror taxonomic groupings based on other characters;

3.) the proper Rosetta stone for interpretation of the observed differences has not as yet been found;

4.) observed differences are manifest by rather modest genetic involvement with the follicular tissue secreting the chorion; in other words, minor changes in the follicular epithelium could produce rather marked changes in the chorionic pattern, which therefore (perhaps after a basic threshold is reached) have less consequence in both an evolutionary and a taxonomic sense.

5.) chorionic sculpturing serves much the same purpose regardless of superficial differences in design, so there need be no meaningful adaptive (or taxonomic) significance to the majority of chorionic differences.

6.) the differences reflect (*i.e.* are barometers of) rather sensitive, but as yet unknown differences in the niches of the species involved.

7.) there is no plausible explanation for the differences noted.

In our opinion, several, if not all of the above explanations are involved in the differences which can be noted in lycaenid eggs, particularly those noted in what appear to be well accepted and "natural" genera erected on the basis of other characters. No doubt factors two and three above loom largest in our present thinking, and while we accept the premise that the present adult taxonomy need not be correct, and may even be enhanced by the incorporation of data from chorionic sculpturing, it would seem prudent to await more information concerning the eggs before deriving taxonomic decisions.

SUMMARY

1. The chorionic architecture, particularly ribs and tubercles, provide the main elements distinguishing lycaenid eggs. Striking differences in appearance may be produced depending on which structures predominate. When tubercles predominate, eggs take on a knobby or a spinous appearance; when ribs predominate, often a symmetrical honeycombed character is produced. Since all of these chorionic structures exist in variables, the total effect is that eggs of congenors may appear dissimilar. Conversely, eggs of non-relatives may take on superficial resemblance due to similar predominance of chorionic characters.

2. While eggs of species appear to be distinct, some less than others, no generic egg characters were as yet recognized.

3. There is as much variability in the micropyle and surrounding structures, including the rosette, as there is elsewhere in the egg, suggesting a degree of caution in using these features as species specific characters until ample knowledge of the variability exists.

4. Some differences were noted between eggs extracted from the abdomen and those laid by the same female, which dictate caution in the use of eggs removed from the body of the female after death.

5. As they are laid, eggs are coated by fluids from the accessory glands. In addition to the function of this material as a glue to attach eggs to the substrate, evidence is presented that the material also serves as a final hardening agent of the chorion. This also strengthens the chorion. In addition, the accessory gland fluids affect the surface porosity of the chorion, retarding desiccation and modifying egg respiration from its pre-oviposition condition.

a.) Egg coatings may affect egg color, offer partial protection from parasitoids, and permit semi-deciduous adult scales to be attached to the egg surface. In addition to their previously suggested protective function, these scales might also have chemical repellent properties (against additional egg deposition on the same leaf, or against parasitoids) or serve a direct or indirect dietary function.

6. The heavy reticular network in the outer sphere of chorionic covering serves to retard water-loss and strengthen the egg. It also lessens the tremendous increase in hydrostatic pressure placed on the plastron on impact of a raindrop.

ACKNOWLEDGMENT

We are grateful to many Lepidopterists for their invaluable help and generous nature in providing determined eggs on which much of this report is based. These include Roy and Connie Kendall, who have the Midas-touch in obtaining hitherto unknown eggs from species in the field, and the following: N. W. Elfferich, Dr. N. G. Escott, Dr. Clifford D. Ferris, Donald J. Harvey, Dr. Donald A. Lawrence, Dr. William W. McGuire, Gregory Nielsen, Stephen J. Roman, Dr. Oakley Shields, and Dr. Orley R. Taylor, Jr. Appreciation is also expressed to Dr. Joseph Boatman of the Mote Marine Laboratory for assistance in the fixation of the soft tissues of the adult females.

Our thanks are also given to Jacqueline Y. Miller and Lee D. Miller for reading and critical review of the manuscript.

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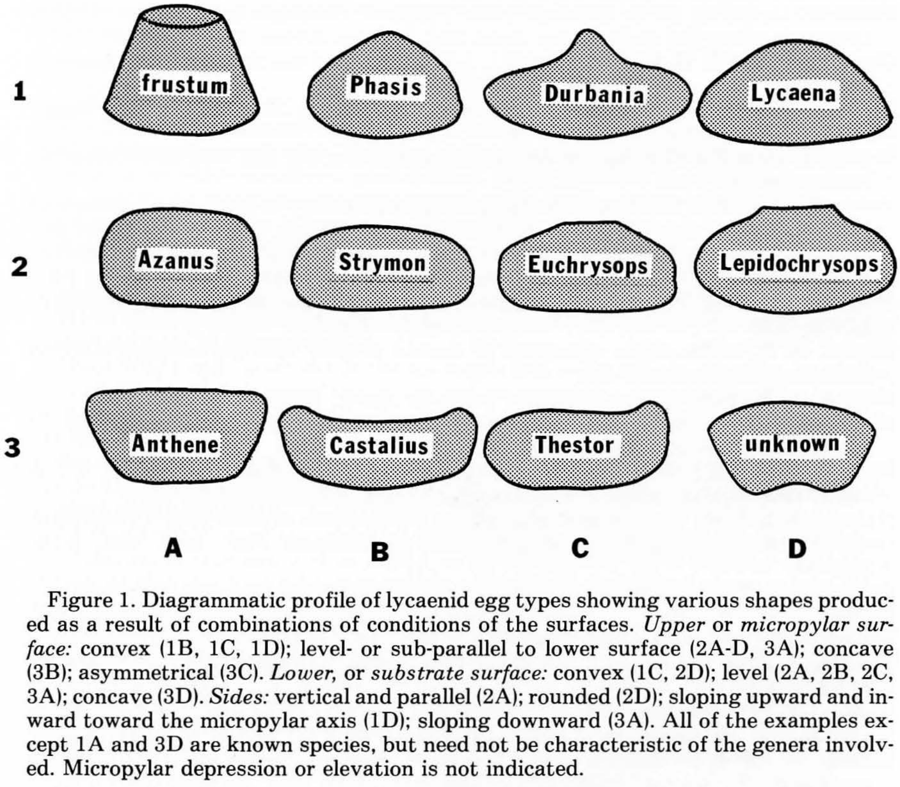
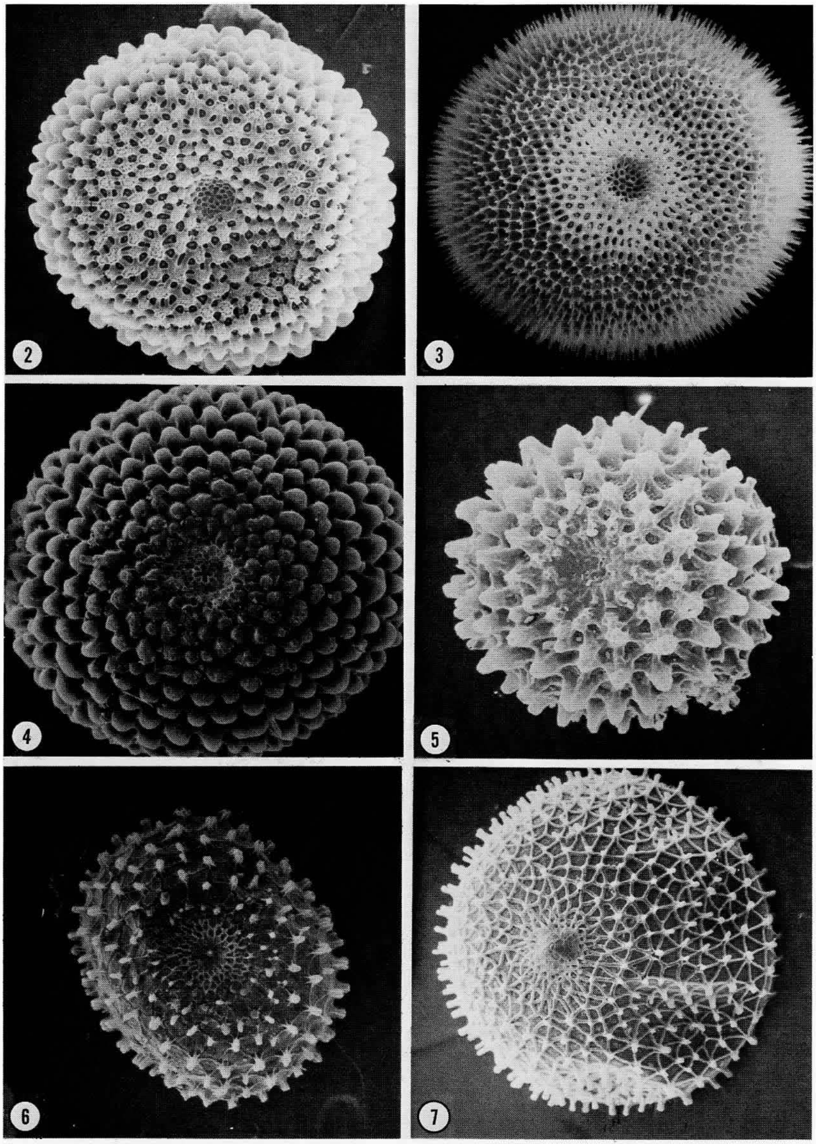
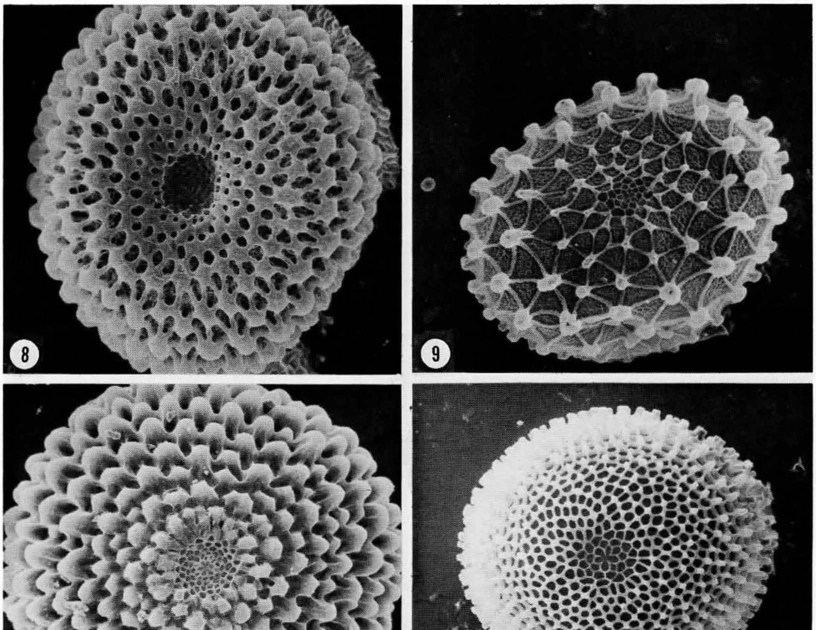


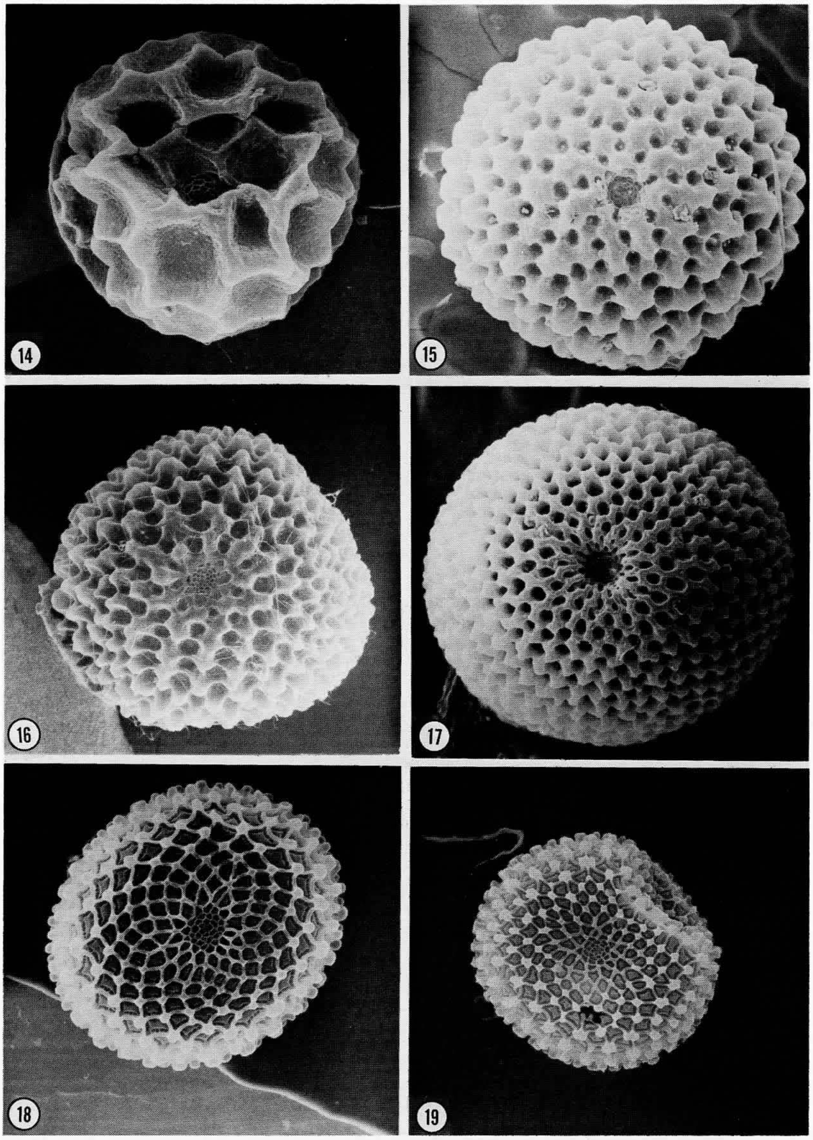
Figure 1. Diagrammatic profile of lycaenid egg types showing various shapes produced as a result of combinations of conditions of the surfaces. *Upper* or *micropylar surface:* convex (1B, 1C, 1D); level- or sub-parallel to lower surface (2A-D, 3A); concave (3B); asymmetrical (3C). *Lower,* or *substrate surface:* convex (1C, 2D); level (2A, 2B, 2C, 3A); concave (3D). *Sides:* vertical and parallel (2A); rounded (2D); sloping upward and inward toward the micropylar axis (1D); sloping downward (3A). All of the examples except 1A and 3D are known species, but need not be characteristic of the genera involved. Micropylar depression or elevation is not indicated.



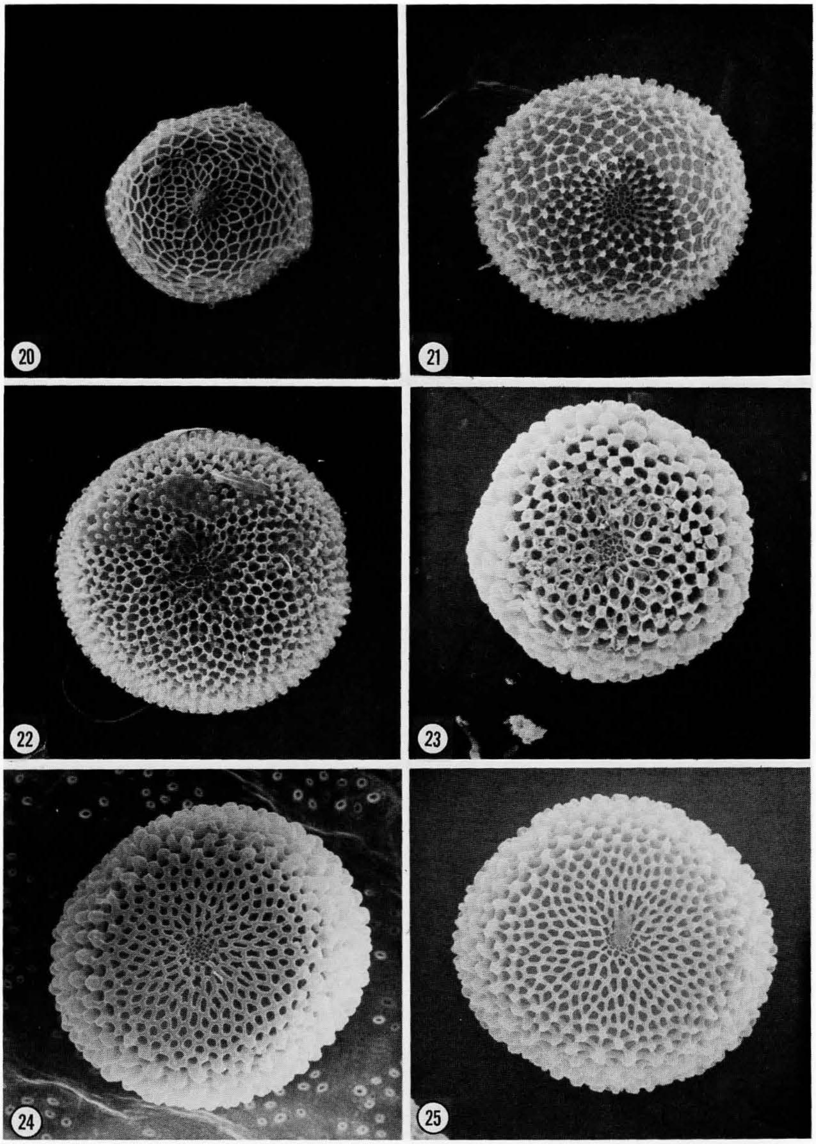
Figures 2-7. Eggs of *Satyrium,* 60x. 2, *S. behrii* (Edw.). 3, .*S. saepium* (Bdv.). 4, *S. liparops* (Bdv. & Lec.). 5, *S. calanus falacer* (Godt.). 6, *S. caryaevorus* (McD.). 7, *S. edwardsii* (Gr. & Rob.).



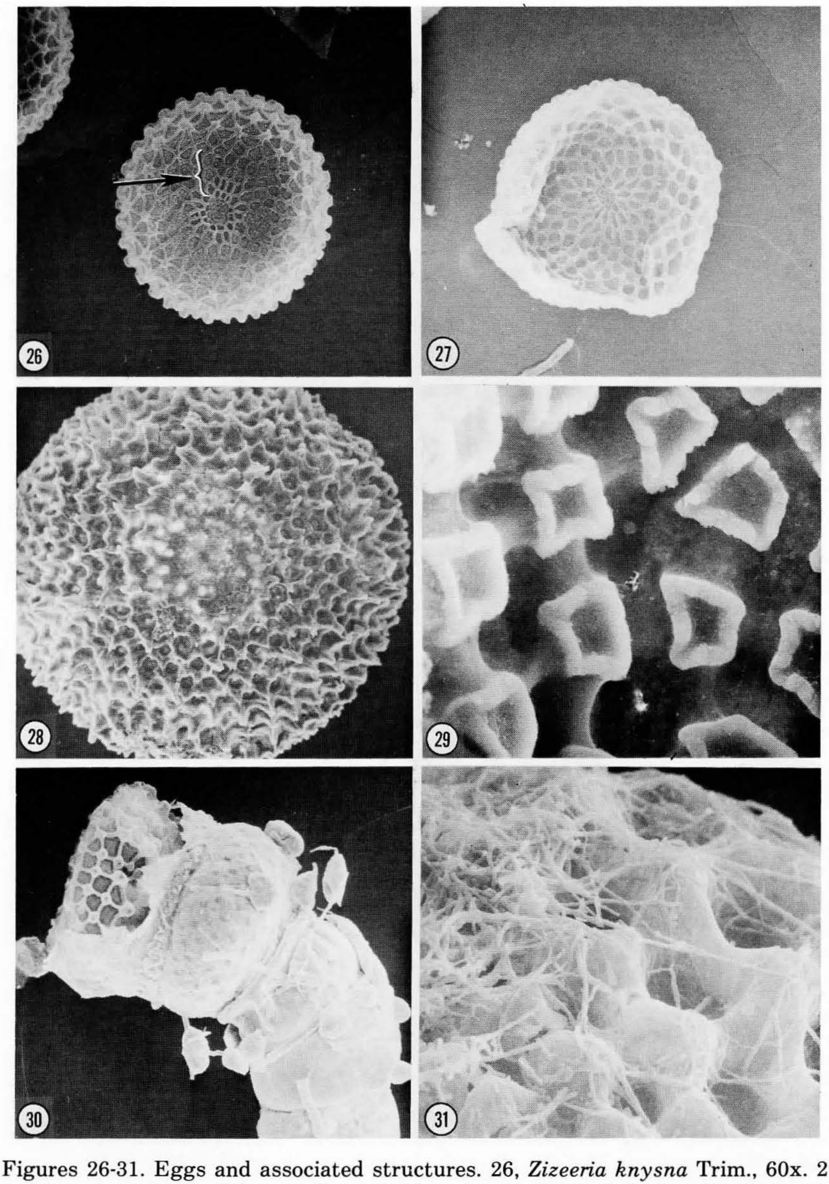
Figures 8-13. Eggs of Lycaenidae. 8, *Atlides halesus* Cram, 60x. 9, *Hemiargus thomasi* Clench, 90x. 10, *Harkenclenus titus* (Fabr.), 60x. 11, *Strymon melinus* Hbn, 60x. 12, *Calycopis isobeon* Butl. & Dru, 60x. 13, *C. cecrops* (Fabr.), 60x.



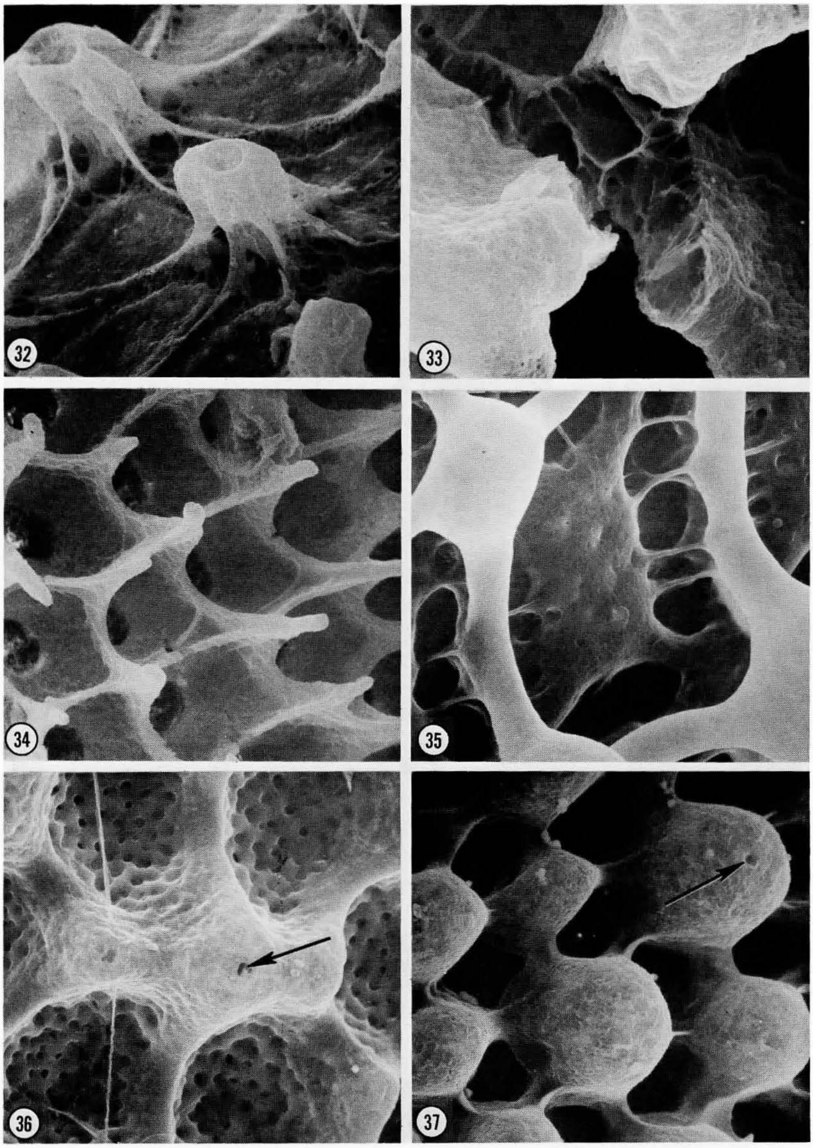
Figures 14-19. Eggs of Lycaenidae. 14, *Lycaena phlaeas* (Linn.), 78x. 15, *Hyllolycaena hyllus* (Cram.), 60x. 16, *Epidemia dorcas* (Kirby), 60x. 17, *E. nivalis browni* (dos Passos), 60x. 18, *Leptotes cassius theonus* (Lucas), 90x. 19, *Celastrina argiolus* (Linn.), 60x.



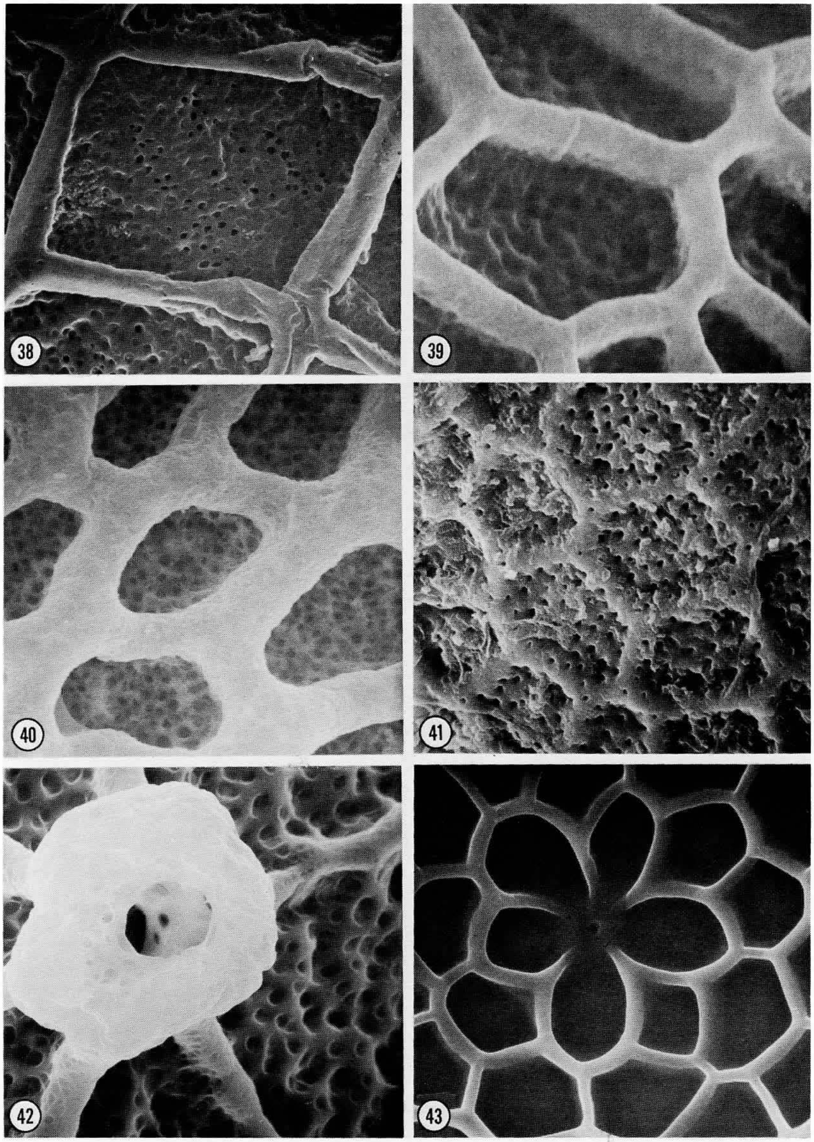
Figures 20-25. Eggs of Lycaenidae. 20, *Euphilotes battoides bernardino* Bar. & McD., 60x. 21, *Phaedrotes piasus* (Bdv.), 60x. 22, *Plebejus icarioides* (Bdv.), 60x. 23, *Everes comyntas* (Godt.), 84x. 24, *Plebejus argyrognomon* (Bergstr.), 60x. 25, *P. melissa* (Edw.), 60x.



Figures 26-31. Eggs and associated structures. 26, *Zizeeria knysna* Trim., 60x. 27, *Brephidium pseudofea* (Morr.) collapsed after storage in alcohol, 90x. 28, *Habrodais grunus* (Bdv.), 60x. 29-30, *Leptotes cassius theonus* (Lucas). 29, surface cells of the follicular epithelium which secrete the egg chorion, 600x. 30, partially exposed egg in follicle of ovariole, 90x. 31, chorionic streamers form a dense webbing on egg surface in *Lycaena cupreus snowi* (W. H. Edw.), 300x.



Figures 32-37. Details of egg chorion. 32, aeropyles of *Satyrium caryaevorus* (McD.), 600x. 33, fractured rib & lower chorion of *Epidemia nivalis browni* (dos Passos), 900x. 34, aeropyles and fossae, *Satyrium saepium* (Bdv.), 600x. 35, ribs and supporting trabeculae, *Leptotes cassius theonus* (Lucas), 1200x. 36, aeropyles on conjoined nodules, *Epidemia dorcas* (W. Kirby), 600x. 37, nodules at rib intersections with or without aeropyles, *Harkenclenus titus* (Fabr.), 360x.



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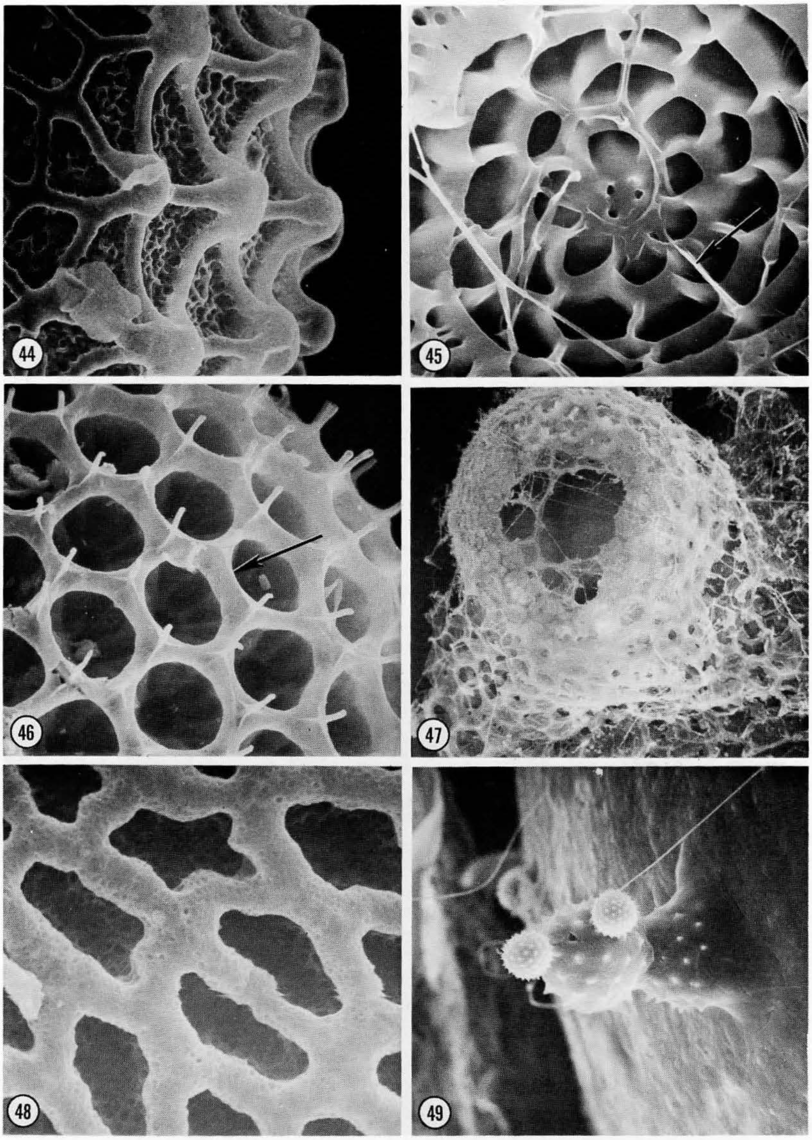
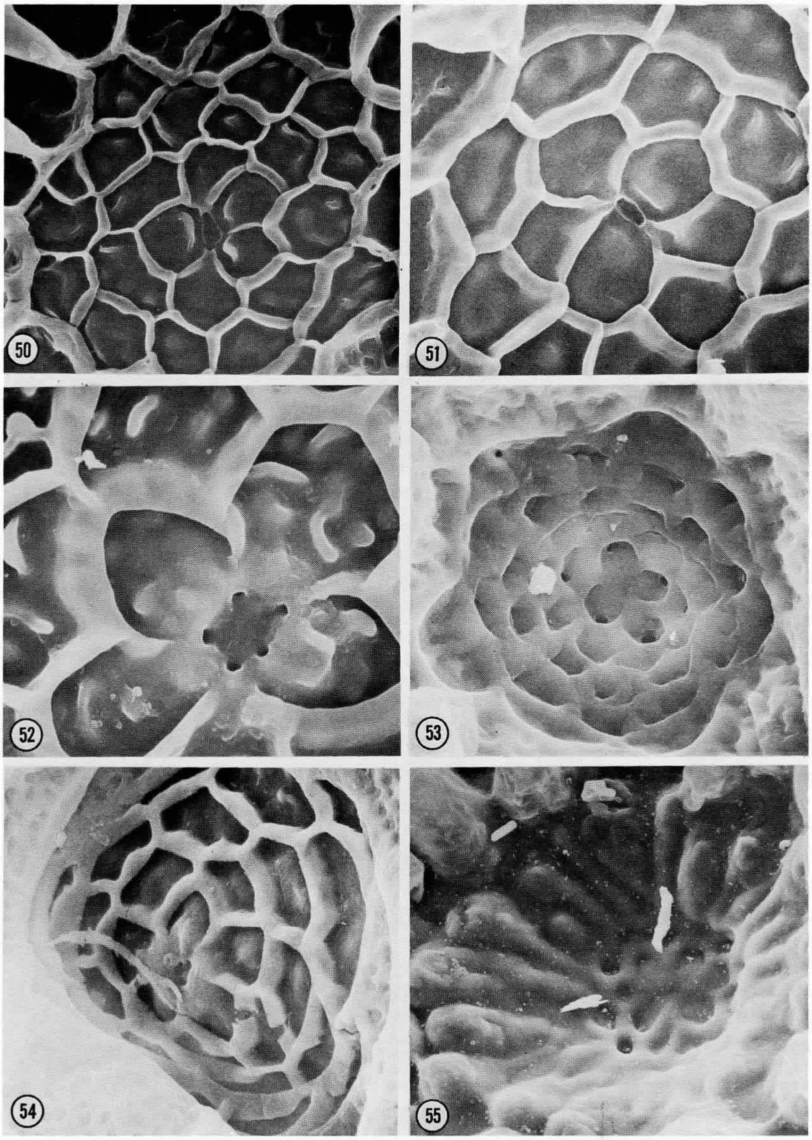
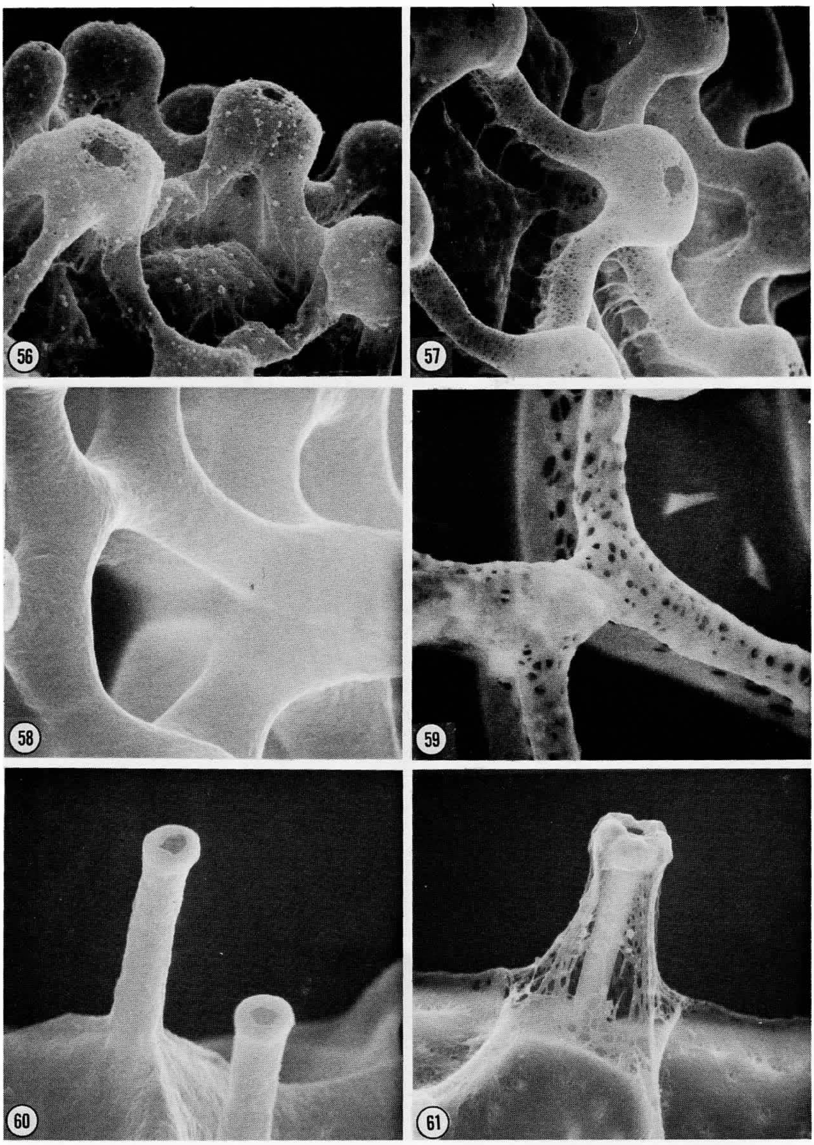


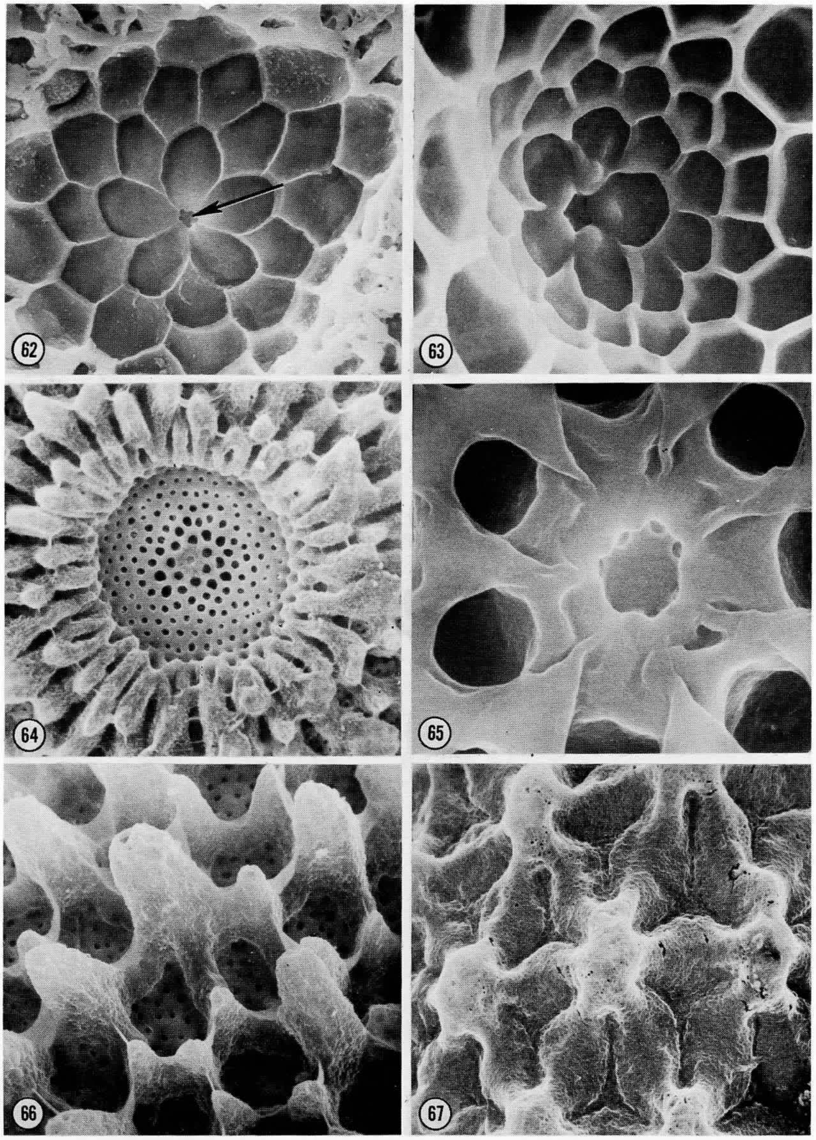
Figures 44-49. Details of egg chorion. 44, lateral margin of transition zone, *Zizeeria knysna* Trim., 420x. 45, micropylar region of *Epidemia dorcas* (W. Kirby), 900x, arrow marks chorionic streamer from incomplete detachment of follicular secretory cells. 46, aeropyles and fossae, *Calycopis isobeon* Butl. & Dru., 300x. 47, hatched egg embedded in matrix, *Feniseca tarquinius* Fabr., 60x. 48, sinuous ribs, *Plebejus argyrognomon* (Bergstr.), 600x. 49, pollen grains embedded and attached to chorion, *Papilio polyxenes asterius* Stoll, 360x.



Figures 50-55. Micropylar regions. 50-51, variability in *Leptotes cassius theonus* (Lucas). 50, 900x. 51, 1200x. 52, *Epidemia helloides* (Bdv.), 1200x. 53, *Hyllolycaena hyllus* (Cram.), 600x. 54, *Lycaena phlaeus* (Linn.), 780x. 55, *Satyrium calanus falacer* (Godt.), 300x.



Figures 56-61. Details of egg chorion. 56-57, *Leptotes cassius theonus* (Lucas) extracted from female abdomen, 900x. 56, dissected in alcohol, note detritus. 57, dissected in water. 58-59, *Strymon melinus* Hbn., 1800x. 58, normal ribs and supporting structures. 59, incomplete ribs and supports in extracted eggs. 60, aeropyles of *Calycopis isobeon* Butl. & Dru., 1800x. 61, aeropyle of *Satyrium acadica* (W. H. Edw.) presumably from extracted egg, 1020x.



Figures 62-67. Details of egg chorion. 62-65, micropylar regions. 62, *Satyrium acadica* (W. H. Edw.), 600x. 63, *Calycopis cecrops* (Fabr.), 600x. 64-66, *Habrodais* sp. 64, 600x. 65, 1800x, note seven pores in micropyle. 66, 350x, wrinkled tubercles of unequal sizes, lateral area. 67, *Callophrys gryneus* (Hbn.), 600x, muri and tubercles, lateral area.

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