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CHORIONIC SCULPTURING IN EGGS OF LYCAENIDAE. PART II

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The present study represents a continuation of our initial research (Downey and Allyn, 1981) on the chorionic sculpturing of lycaenid eggs. Basically it is a quest for a better understanding of the complex external patterns and forms observed in these highly ornamented eggs. In describing and comparing the geometric patterns of the different species, we are searching for meaningful architectural similarities or differences, which hopefully will have detectable adaptive and evolutionary significance.

METHODS

The methods and materials follow those presented earlier (*loc. cit.*) together with background and insights given in that work and in Downey and Allyn, 1980. Scan electron photographs are numbered consecutively with part one of the series and a species index (Table **2**) is compiled for ease in locating the lycaenid species treated in both parts of this study.

Results are presented in both descriptive and photographic form. It was not possible to show comparable SEM views of all egg samples examined, due mostly to artifacts encountered in sample preparation. Frequently eggs which were freshly collected and stored in alcohol, collapsed* during the coating process while under vacuum. We had no way of predicting when this would happen. Eggs stored in alcohol or other fixatives also had much surface detritus; not infrequently such material obscured desirable views of the micropyle or other minute structures. While most samples were satisfactory, occasionally a few eggs could not be coated properly so that electron charging prevented photos in particular areas of the egg. However, the high resolution of the SEM enabled us to determine improperly fixed or physically damaged eggs, as well as samples "not to be trusted" as species representatives. That is, we could often guess whether or not ribs and cells had been displaced (see Fig. **149**), malformed, or were other-

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*Of interest is that Sakaguchi *et al.* (1973) describe a lethal gene for "egg collapse" in *Bombyx mori.* While seemingly unrelated to the collapse of certain eggs in vacuum as described herein, a possible common cause (weakness of chorionic protein) is possible.

wise atypical specimens, which condition might never have been determined with light microscopy.

In part one of this work, we felt it expedient to present the descriptive results character by character rather than by taxonomic group. This, we had hoped, would focus attention on the character states, whose variation might result in rather drastic superficial differences. Having thus called attention to the character states, it is now our feeling that we can acquiesce to convention in part two, and consider the egg chorion by taxonomic rationale. In so doing, we hope to encourage comparative descriptions by future researchers who may enlarge the morphological platform, or extend the taxonomic usefulness of such data.

RESULTS

All lycaenid eggs studied were of the upright type. The micropyle was centered on the top surface opposite the somewhat flattened bottom surface usually attached to the substrate. All eggs observed were round when viewed from above and most tended to be dome- or bun-shaped when viewed laterally. The lateral profile, particularly when coupled with the size and elevation of the micropylar region may be diagnostic of some taxa. Lycaenid eggs tend to be twice as wide as they are high, particularly when they are somewhat flattened on the upper surface as they are in the Theclinae.

The chorionic sculpturing consisted of a number of differing and variable elements, among which elevated ribs and tubercles, often situated at rib intersections, provide prominent elements. The size and character of the inter-rib area also contributes to the overall reticular appearance of an egg and was another variable contributing to the chorionic architecture.

The micropyle was usually made distinct by an annulus, one to several rows of concentrically arranged areolae or "cells" lined by thin, low ribs. The inner ring of this group or rosette, forms a flower-like cluster of petal or wedge-shaped cells around the micropyle. The nature of the annulus, particularly the shape of component cells in the rosette, has been considered distinctive. Petal numbers may vary within a species as we have demonstrated several times (Downey and Allyn, 1979, p. 1, 3; 1980, p. 134, 140; 1981, p. 9). We have also found that the number of micropylar pores often matches the number of petals in the rosette, even when these vary. In some species the pores may be partially hidden, particularly when they are contained at the bottom of a single pit or central depression. These pores lead to minute ducts which lead through the chorion.

Descriptions and SEM photos of the eggs of individual species follow. Subfamilies and tribes used in this report follow Eliot (1973).

THECLINAE, APHNAINI

Tylopaedia sardonyx (Trim.)

Figs. **68, 69, 147**

d. (diameter), 1.10 mm; a. (annulus) 0.12 mm

Egg rounded in dorsal view; shaped like an upside-down turnip in profile view, with the tip cut off and somewhat depressed to form the central micropylar area; extremely rough chorion with enlarged muri and radiating ribs (Fig. **147**) forming an almost complete upper element to the chorion; irregularly placed openings of modest size in the valleys between ribs form the only communication to the lower chorionic envelope; most large muri have aeropyles near their medial mass; ribs high tending to reach a sharp apex except for numerous short pseudo-ordered villi which are twice as high as wide along the rib crests; villi have a tendency to pair, many of their bases nearly touching along the rib peaks (see Fig. **147**); rounded knobs, no higher than the villi, occur on the muri and infrequently along the ribs where they may be located on lateral slopes of the ribs or along the peaks between villi; the great number of these small projections (see Fig. **68**), gives a scabrous and unique appearance to the chorion of this species; micropylar region depressed and bowl shaped; rosette relatively indistinct (Fig. **69**), of five open-ended petals; ribs of petals and one or two indistinct annular cells, irregular and wedge-shaped (between cells); a narrow transition zone with indistinct limits occurs between the annulus and the upper and outermost walls of the fovea centralis; cells between ribs may be deep or shallow, tending to be deeper on the lateral surface where the muri and ribs are most distinct.

When we first examined the African *T. sardonyx* we were struck by the short, spiny processes, and spherical bumps and warts which added to the already irregular, rough appearance of the chorion. Having previously worked with the ultrastructure of scales, and the nature of their light reflecting and absorbing nature, we concluded that such a rough egg surface would serve very effectively as a light reflector, or as a heat radiator, or both. Where light reflection and heat radiation are important to egg viability, water retention would also be a prime requisite. *Sardonyx* eggs seem to be well structured for this latter problem since the upper ribs and muri are spread over the outer surface so as to nearly envelop the egg. Only a modest number of openings permit aerial access to lower elements of the chorion, which may also be porous and help to retard water loss. Further, this small number of aeropyles on fewer but larger muri suggest that water conservation might be an adaptive feature of this egg. We thus suggested (Downey & Allyn, 1981 p. 5) that the chorion might play a part in heat radiation and water retention in this species. Our opinion was somewhat fortified on finding that the species lives in a very hot, dry habitat. Additional data on radiation effects of the chorion will be brought out below.

THECLINAE, THECLINI*

Hypauriotis crysalus (W. H. Edw.)

Figs. **70, 71, 150**
d. 1.48 mm; a. 0.12 mm

Egg dome-shaped in profile, echinate appearance with numberous stout, gradually tapering, columnar spines (Fig. **70**); the latter three to four times as high as wide at the base with blunt apices; ribs indistinct at base of spines (Fig. **150**) and irregularly swollen (i.e. not of constant size) as they run the short distance between spines; chorion at base of cells with numerous small papillae giving it a grainy appearance; a few pores between papillae, but insufficient to form a plastron; aeropyles present on a few ribs in lateral areas; numerous thin chorionic streamers running between spines mostly on the basal half; micropylar region relatively small, three-petaled rosette outlined by thick muri and surrounded by several deep cells suggesting no more than two additional cellular rings in annulus (Fig. **71**).

THECLINAE, EUMAEINI

Evenus regalis (Cram.)

Figs. **131, 149**
d. 0.73 mm (h. 0.65 mm); a. 0.20 mm

Egg nearly as high as wide (ratio 6 to 7) with dorsal sculpturing similar to lateral sculpturing, but noticeably thinner and more elongate (Fig. **149**); ribs of low profile with sloping sides (Fig. **131**) and with carina, or noticeable keels on rib summits; aeropyles large, surrounded by six or more small nipples, which may or may not have carina between; six ribs radiating from aeropylar disc and running to other aeropyles such that three ribs tend to outline each interspace or areola; micropylar area ill-defined and appears slightly off-center; petals of rosette are mere depressions, not outlined by rib structures.

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*Two species of Theclini of the genus *Habrodais* were treated in Part I.

Pseudolycaena damo (Druce)
Figs. **72, 73, 138**
d. 0.68 mm; a. 0.14 mm

Turban shaped egg with modestly high, narrow ribs running between prominent aeropylar projections (Figs. **72, 138**); six parallel-sided ribs connect each stalk which is four to five times as high as each rib at their midpoint; the column of the aeropylar stalk appears to be externally composed of each rib so that they are highly angled on the sides; ribs without carina; aeropores large and prominent a third to half the diameter of the flattened upperstructure of the aeropylar stalk; aeropyle with crown of spurs around the tip, five to six lateral ray-like projections, giving them a starfish like appearance unique to this species; micropyle small, angulate, and outlined by five-petal rosette; ribs of rosette and second annular ring appear embedded in chorionic surface (Fig. **73**) so that only their mesial margins outline the cells.

Eumaeus atala (Poey)
Figs. **74, 75, 140**
d. 1.38 mm; a. 0.24 mm

Enlarged dome-shaped egg with recessed annulus; enlarged tubercles predominate laterally, while the ribs are reduced except for the transition zone, two or three cells around the annulus where they are thickened and plateau-like, with inter-rib areoles reduced to narrow slits (see Fig. **74**); aeropyles simple and unadorned pores, one to several, on the upper central surface of each tubercle; the arms extending from each aeropyle to the choronic surface below are enlarged and pillow-like and the spaces between them may take on the appearance of lateral pores (these do not communicate with interchorionic meshwork, however); micropyle a single small pit (Fig. **75**); rosette three petaled with ribs of rosette and annulus nearly identical width with parallel sides.

Egg surrounded by a palisade layer of elongate scales attached to the lateral surfaces by the female during oviposition (Fig. **140**). Other lycaenids are known to cover the dorsal surface of the eggs with scales, which are glued to the spumaline of freshly laid eggs by sidewise rubbing of the tip of the female abdomen. The parallel and near vertical attachment of *atala* scales, however, makes this species unique in this regard.

E. minijas Hbn.)
Figs. **76, 77, 126**
d. 1.26 mm; a. 0.20 mm

Tubercles enlarged to dominate egg sculpturing; one to four unadorned aeropyles at apex of each tubercle; the latter resemble five to six armed starfish with thickened arms whose central disc (containing the aeropyle) has been elevated from the substrate (see Fig. **126**) and whose arms slope back to broadly join the chorion beneath; ribs reduced to short tubular ribs or tendrils running between the enlarged tubercles; fovea centralis distinct as concave area marked by similar rib structure throughout (Fig. **76**); micropyle a single small pore marked by a rosette of four nearly circular closed cells (Fig. **77**); ribs of rosette and annulus of irregular width and height; floor of the cells with crenulations or with raised islands of chorion; chorionic streamers noted.

The unique appearance of the aeropylar tubercles is apparently a generic character.

Chlorostrymon simaethis sarita (Skin.)
Figs. **112, 136**
d. ?; a. 0.07 mm

Ribs rounded, appearing tubular; tubercles slightly enlarged at rib intersections about twice as high as ribs; tendency toward six ribs leaving each intersection so that areoles appear diamond shape (Fig. **136**); rather large aeropores on each tubercle, sometimes with other smaller pores; upper surface of aeropyles scabrose; micropylar area marked by two to four nearly circular rosettes with chorionic bars (Fig. **112**) tending to close the petals at their mesial margin adjacent to the micropyle; ribs of rosette flat-topped and parallel-sided, and twice as wide as other ribs in annulus.

Phaeostrymon alcestis oslari (Dyar)

Figs. **78, 79, 135**

d. 0.67 mm; a. 0.08 mm

Egg echinoid in appearance (Fig. **78**); spiny projections arch up from each rib intersection and may be slightly bent or recurved (Fig. **135**); aeropyles arranged on the sides of the walls beneath the spiny projections; aeropores only in a narrow band around the "shoulder" of the egg, lacking on lateral (side) margins and dorsal surface; ribs five times as high as wide and finely rugose; floor of areole flat and smooth, without pores; areole rather round in shape except in transition zone where they become more angulate; micropyle of a single pore with three-petaled rosette, the walls of which are irregular in width, and appear elevated from the rest of the annulus (Fig. **79**); areola of annulus filled almost to rib-height with chorionic folds.

Ministrymon clytie (W. H. Edw.)

Fig. **127**

d. 0.67 mm, a. ?

Egg echinoid, with projecting aeropyles terminating in a flattened crown (Fig. **127**); ribs seven to eight times as high as wide, parallel sided; ribs meeting at aeropyle number four, five or six, with the latter more common on the sides, the former near the transition zone; areola strongly angulate, with unporous lower chorion containing several irregular, upwardly projecting chorionic prominences in the manner of stalagmites; lateral aeropyles slightly exceed twice the height of the ribs; upper aeropore surrounded by five or six wrinkled and warty spur-like projections. The aeropylar area in our specimens was covered with extraneous material which precluded a description.

Oenomaus ortygnus (Cram.)

Figs. **80, 81, 137, 141**

d. 0.92 mm; a. 0.25 mm

Egg of *Strymon* shape (Fig. **1**); high "turret" aeropyles at rib intersections; these becoming taller on lateral surfaces (Fig. **80**); ribs are high, straightsided walls which unite and curve upward to form walls of aeropyles (Fig. **137**): tendency for four ribs to run between aeropyles so that interstices tend to be square-shaped, and for aeropyles to appear to be arranged in a straight line; ribs continue beneath egg almost to center of attached surface; aeropore large with four or five blunt, finger-like projections extending upward for about twice the diameter of an aeropore; projections extend from area between ribs forming the aeropyle; five-petaled rosette, the petals almost twice as long as wide; a smooth chorionic "island" in the middle of each petal (Fig. **81**).

Oenomaus apparently attach adult scales randomly to the upper egg surfae on oviposition (Fig. **141**). These may not completely cover the egg. In such cases we cannot ascribe a "hiding" function to the scale covering, nor would it break up the outline or silhouette. We suggest either an odor function, perhaps preventing other females from ovipositing near this site, or a dietary function. They apparently do not completely deter parasitoids, as the egg in Figure **141** shows either a wasp ovipuncture wound near the center, or the result of proboscis penetration by an hemipteran predator.

"*Thecla*" *metanira* Hew.

Figs. **121, 156**
(shell fragments only)

Only the partially consumed shell fragments of a hatched egg were available to us. These lack the micropylar area. The lateral chorion is unique among the Eumaeini if not other tribes, in having distinct upper and lowe chorionic elements which are easily separated from one another, and both of which have square geometric elements (Fig. **121**).

Upper chorion with ribs running at right angles to one another; intersections not expanded into tubercles, at same elevation as ribs, but with slightly rounded rib corners; areolae between ribs square, except for the rounded corners; lateral margins of ribs near intersections may have aeropyles, particularly on lateral margins; chorion surface at base of areolae highly undulate, with crenulations and irregularly placed pores; ribs with prominent elevated carinae at right angles to the rib axis, and midway between cross rib juncture; these elevated carina give a unique appearance to the ribs (Fig. **156**); the upper chorionic element is placed at an angle to the lower element such that the internal air spaces can mesh with the almost centrally located pore in the endochorion; Figure **121** is an internal view of the endochorion, showing the centrally located pore which permits passage of the ambient air from the upper chorionic meshwork; this view also shows the unique square pattern of the upper surface; most species lack any pattern and regularity of pores on the internal surface of the endochorion (see Fig. **122**).

Cyanophrys amyntor distractus (Clench)

Figs. **82, 83, 133**
d. 0.67 mm; a. 0.20 mm

Egg with prominent linear elements (Fig. **82**); ribs reduced to narrow tendril-like filaments (Fig. **133**) running between aeropyles; each rib has an adjacent plate of endochorion, the "floor" of adjacent areolae, which appears to be "rolled under" along its polygonal margins (Fig. **133**), forming what at first glance appears to be another rib paralleling the main rib and slightly larger; since each main rib has such rolled margin on each side, the rib structure appears somehwat exaggerated; the apex of each of these cell plats forms a duct-like structure which curls ventral to the lower surface at its juncture with each aeropyle; aeropyles enlarged apically and flattened and slightly flared back on the lateral margins; micropyle in depression surrounded by a rosette of seven petals almost three times as long as wide, which are very open (for almost half their length) on the mesial margins (Fig. **83**); annulus of three rings of cells with outlining ribs of equal width and height.

Cyanophrys miserabilis (Clench)

Fig. **132**
d. 0.55 mm; a. 0.14 mm

Aeropyles rounded and button-like; aeropore unadorned with diameter approximately ⅙ of aeropyle width; ribs slender and parallel-sided, coursing upwards near junction with aeropyle; base of ribs flared outward on each side for a distance nearly twice as great as rib width, giving the ribs an enlarged appearance when viewed from above; six or seven ribs radiate from each aeropyle on lateral margins (Fig. **132**) so that areolae are mostly triangular; floor of cell level and unporous (though covered with alcohol extracted detritus in figure). Micropylar region obscured in specimens available.

Cyanophrys goodsoni (Clench)

Figs. **84, 85**
d. 0.60 mm; a. 0.18 mm

Aeropyles in lateral areas two to three times rib height, aeropyles parallel-sided (much less button-like than in *miserabilis*) and flat on top with a tendency to form lips, or swollen areas near margins (Fig. **84**); ribs almost triangulate in cross-section, forming a carina-like crest near junction with aeropyles; areolae rounded in transition zone, tending to be more angulate on shoulder and sides of egg; endochorion smooth, without pores or relief; micropyle a pit, with four very open ended petals (Fig. **85**); annulus of four rings of cells.

Mitoura nelsoni (Bdv.)
Fig. **113**
d. 0.52 mm; a ?

Egg available coated with detritus obscuring features except as follows: micropyle an angulate pit with four pores visible in lateral margins; rosette of four open-ended petals with rib widths variable (Fig. **113**); annulus of two or three rings of cells; endochorion highly porous and possibly forming plastronopores.

Mitoura siva (W. H. Edw.)
Figs. **86, 87**
d. 0.65 mm; a. 0.10 mm

Exochorion dominating external sculpturing, so that endochorion is only visible in annulus, and beneath sinuous and swollen ribs (Fig. **86**); aeropyles arching upward rather gradually from enlarged, rounded and sinuate ribs; surfaces scabriculous, although aeropores simple and unadorned near apex of most lateral rib junctures; lateral rib margins not conspicuous, and exochorion appears to cover indentations between ribs as well as the ribs themselves; micropylar pit angulate with pores in lateral margins; four- or five-petaled rosette (Fig. **87**), open ended; annulus of three tiers of cells; plastronopores visible beneath ribs in regions adjacent to annulus.

Mitoura hesseli Raw. & Zieg.
Figs. **88, 89, 125**
d. 0.74 mm; a. 0.09 mm

Dome-shaped egg bearing superficial resemblance to *gryneus* (Fig. **67**) in that the upper chorion covers the entire surface and no substructures are visible (Figs. **88, 125**); the egg appears wrinkled, with prominent knobs or elevations with gently rounded ridges running between them; prominent aeropyles mark the centers of these swellings, and the entire surface is pitted with rounded puctations which do not penetrate the chorion as the aeropyles do; they may be closed (coated) with spumaline as the egg is laid so that larger openings have deeper pits than the smaller punctations; micropyles open in single large central cavity (Fig. **89**); rosette of five unclosed petals, outlining ribs of irregular width and height; annulus of two cell rows, rather indistinct.

Xamia xami (Reak.)
Figs. **90, 91, 129**
d. 0.61 mm; a. 0.11 mm

Exochorion expanded to form a smooth covering over most of the egg (Fig. **90**), with regularly spaced round openings being the prominent structural feature; at 600 diameters (Fig. **129**) the chorion seems to surround these rounded areolae with gently rounded rib structures which are only slightly enlarged at their three to four rib junctures; irregularly shaped and spaced punctations cover these surfaces, as though they may have been pores filled with a covering fluid; micropyle a pit with pores visible on margins; rosette of four or five open-ended petals, two of which have islands of chorion in their floors (Fig. **91**); annulus of four indistinct cell rows.

Incisalia irus hadros Cook & Wats.
Fig. **128**

Only parts of a severely collapsed egg were available. Aeropyles of low profile with ribs running to distal surface and forming irregular lateral margins (Fig. **128**); upper surface of aeropyle irregular, crinkled and furrowed; ribs tubular above, narrowly attached along their lengths to the endochorion below; areolae angulate, with level, unscuptured floors.

Eggs of this genus appear to collapse readily on fixation, and should be allowed to dry thoroughly (and thus harden) before storing in alcohol.

Incisalia polios Cook & Wats.
Fig. **143**
d. 0.50 mm; a. 0.09 mm

Ribs of fairly uniform height and width on dorsal and lateral surfaces, enlarging only slightly at junctures (Fig. **143**); upper elements of ribs rather tubular in appearance with ventral supporting walls unparallel and slightly expanded at base; interstices between ribs tending toward a circular shape with level chorionic floors; the latter perforated with irregularly sized pores, perhaps too few to form a plastronopore network; micropyle of four or five openings near end of conjoined rosette ribs; rosette with four or five rather open-ended petals; annulus of three or four irregular rows the ribs of which are not of uniform width.

Incisalia henrici (Gr. & Rob.)
Fig. **134**
d. 0.52 mm; a. ?

Surface of ribs and aeropyles sinuous, rough and wrinkled (Fig. **134**); rib height and width irregular; many small riblets course away from the main ribs, forming an irregular reticulate network in the areolar spaces on top of the endochorion beneath; aeropores large and unadorned, though on highly wrinkled and rough aeropylar plateau. Other details were not available from the collapsed egg. It is possible that the highly roughened surfaces observed may be an artifact created by the collapse and shrinking of the samples available.

Arawacus jada (Hew.)
Figs. **92, 93**
d. 0.73 mm; a. 0.09 mm

Shape as in *Strymon* (Fig. **1, 2b**); tubercles at rib intersections not unlike *Strymon* form, gradually tapering toward the apex, but blunted, not sharp, nor terminally enlarged as in *S. acadica (Fig.* **61**); aeropyles are not present on all tubercles, but tend to be clustered around the lateral upper margin; aeropyles may also have two or three irregularly shaped and irregularly placed pores on lateral margins; ribs high, narrow, parallel-sided (Fig. **92**), forming deep cells, particularly toward lateral margins; cells tend to appear rounded, even though lined by ribs where three, four, five and occasionally six ribs join a single tubercle; micropyle a depression, with three pores clearly visible (Fig. **93**); rosette of three petals; annulus of four rows.

Euristrymon ontario (W. H. Edw.)
Figs. **94, 95, 145, 148**
d. 1.05 mm; a. 0.10 mm

Egg markedly echinoid with sharp pointed spines three to four times as high as basal width (Fig. **94**); some spines in lateral areas with aeropyles; each aeropyle is "coated" with material which appears to have exuded from the pore and dried around the apex of the spine giving it a roughened appearance (Fig. **148**); many such spines, coated at their tips, are gently recurved near the apex; ribs of constant diameter, thin and high, with a lower plateau of constant diameter (giving the rib an upside down "T" shape when sectioned); cells of square and polygonal shape (see Fig. **145**) with lower chorion imperforate, but corrugated with irregular folds and grooves; 4-petaled rosette with tapered muri; micropyles may be covered with a layer of material (Fig. **95**) perhaps laid down during the fertilization process; this material is structureless, and is found in many species where it may or may not obscure details of the micropyle; walls of annulus thick and rounded, almost as wide as the circular cells they surround; chorionic streamers were noted.

Euristrymon polingi (Barn. & Mc D.)

Figs. **96, 97, 144**
d. 0.68 mm; a. 0.15 mm

Ribs as in *E. ontario,* but texture slightly more irregular and roughened; tubercles elongate, particularly on sides, and covered apically with a roughened coating giving them a "dripping candle" effect (Fig. **144**); no two tubercles appear alike; no aeropyles were noted, although the coating and porous texture would make them difficult to detect; plastronopore surfaces were noted; the micropylar area and annulus appear to be of a different texture than the chorion (Figs. **96, 97**) and are somewhat elevated as though there were a surface coating; micropyle pit-like, with five-petaled rosette, the petals open and two and a half times as long as wide; annulus with four rows of cells, each cell containing a deep, circular basin sloping upward to the surrounding ribs.

Parrhasius m-album (Bdv. & LeC.

Figs. **98, 99, 118, 120**
d. 0.77 mm; a. 0.09 mm

Egg circular in dorsal views (Fig. **98**), bun shaped in side view with evenly rounded lateral surfaces; exochorion overlying lower elements so that ribs and junctures are covered; areolae four-sided and centrally depressed (Fig. **118**) giving the egg a superficial resemblance to a compound eye with individual facets; the surface of each areola resembles a composite flower with petals separated by slight depressions and each petal slightly tumenescent; tiny carinae ridge the top of each four-sided depression, and at their intersections are small aeropyles; the region of the aeropyles is marked by irregular chorionic ridges, bumps and protuberances as though small amounts of candlewax might have flowed from the pore before solidifying; tears in the exochorion reveal (Figs. **119, 120**) a highly vacuolated inner substructure into numerous airspaces, and tapering upward to form supporting struts fo the vaulting exochorion above. The micropyles are uniquely located at the joining ribs of the four-petaled rosette (Fig. **99**).

Strymon yojoa (Reak.)

Figs. **100, 101, 130**
d. 0.64 mm; a. 0.08 mm

Egg of typical *Strymon* shape (Fig. **100**); ribs rounded and tube-like above (Fig. **130**) and attached to the endochorion below by straight, parallel-sided, thin, upright walls which are one to two times as high as the height and width of the upper tubular element; not all rib intersections have tuberculate prominances, particularly on the upper side; tubercles of different sizes, all tending to be roundish and columnar, and of slightly rougher texture than the relatively smooth ribs; aeropyles on some tubercles, particularly on sides of egg; micropylar pit with prominent micropyles near bottom lateral margins (Fig. **101**); five-petaled rosette, with petals completely outlined by ribs except at pit margin; four-celled annulus with ribs flat or leaning mesially in contrast to more tubular ribs elsewhere; endochorion smooth.

Strymon alea (God. & Salv.)
Figs. **102, 103**
d. 0.58 mm; a. 0.12 mm

Shape and structures similar to *S. yojoa* (Fig. **102**); ribs rounded above, but tubes varying in thickness, and somewhat sinuous, particularly where they seem to be stretched and are correspondingly thinner; not all rib intersections bear tubercles; apex of tubercles, even those with aeropyles, are of somewhat grainy, roughened texture; aeropyles slightly smaller than in *yojoa;* endochorion somewhat undulate, with or without irregularly shaped and irregularly sized pores in cells on egg sides; micropyles apparent in circular pit (Fig. **103**); five-petaled rosette, with petals slightly open (lacking rib outlines) near pit area; ribs outlining cells of annulus of slightly different widths and heights.

Strymon columella istapa (Reak.)
Fig. **116**
d. 0.45 mm; a. 0.13 mm

Egg of *Strymon* type; ribs tubular and of equal widths; not all rib intersections have tubercles; tubercles shorter, more button like and less columnar than in congeners; not all tubercles with aeropyles; some cells have endochorion floors pierced by a pore-like opening with irregular sides; others have irregular small projections like islands in an otherwise level plane; micropyles in depression, not a pit (Fig. **116**); three-petaled rosette with petal length only slightly longer than width; cells of annulus modestly large compared to other *Strymon* species (additional samples may reveal that fewer cells are involved).

Strymon columella cybira (Hew.)
Fig. **117**
d. 0.47 mm; a. 0.13 mm

We were unable to detect what would be considered a significant difference between *S. columella cybira* and *columella istapa.* Our sample sizes were small, however, and it is possible that some of the modest variations in the structure of the annulus, ribs and tubercles may prove to be consistent differences between the subspecies. One such minor difference is shown in Figure **117**: there seems to be a greater number of endochorionic "islands" at the base of each cell in *cybira* than in *istapa;* the perforations in the endochorion may also be larger and more numerous in *istapa.*

Erora laeta (W. H. Edw.)
Figs. **104, 105, 139**
d. 0.87 mm; a. 0.12 mm

Elevated tubercles on sides and shoulder give egg an echinoid appearance (Fig. **104**); ribs of irregular widths with swellings, humps, and twists as they run between tubercles (Fig. **139**); some ribs with carinae; tubercles lacking or only modest elevations present in the transition zone, extending approx. 0.1 mm around the annulus; not all tubercles possess aeropyles, some of the latter appear closed (by spumaline ?); apices of tubercles appear slightly flattened, as though they were crushed from above, with the result that the lips of the aeropyles appear to be rolled inward; cells of highly irregular shape, their endochorionic bottom usually marked by a single island arranged in a strongly arched linear slash in the manner of a hieroglyph; micropyle a single pit (Fig. **105**) surrounded by ribs of the five, completely closed petals of the rosette; ribs of annulus rounded and tube-like dorsally, with a thinner non-porous connecting element running to the endochorion; annulus of five tiers.

Thirteen species of Emaeini of the following genera were treated in Part I: *Atlides, Harkenclenus, Satyrium* (7), *Mitoura, Calycopis* (2), *Strymon.*

POLYOMMATINAE

Celastrina ladon form "neglecta major" Tutt (*ladon* [Cram.] was recorded as *argiolus,* Fig. **19**)

Figs. **106, 107, 122, 123, 124**
d. 0.57 mm; a. 0.06 mm

Egg somewhat flat on top (see below); tubercles large and apparent on sides and lateral margins; ribs tubular on dorsal surface, of unequal width, and tending to dip down toward endochorion in the middle and course upward at each tubercle, where they expand laterally to contribute to the apex of the tubercle; ribs supported ventrally by narrow wall with highly irregular and porous appearing surface; most of the pores appear filled with a matrix; aeropyles on most tubercles in a broad band around the shoulder region of the egg; apex of tubercles of modestly smooth texture and composed of the swollen and fused terminal portions of the ribs (four to six) which meet at that tubercle; micropyles on margins of angulate pit; rosette of four petals, very open, outlined by flattened ribs which appear folded like ribbons (Fig. **107**) over one another (from outer to inner series); islands of endochorion in the floor of each cell of annulus, including rosette petals.

The porous nature of the exochorionic network is illustrated in Figures **123** and **124**. These figures show the cross-struts and trabecular braces which form the highly vacuolated interchorionic meshwork. Ambient air enters through aeropyles and plastronopores and communicates with the air spaces internally. Figure **122** is a view of the inner surface of the vitelline membrane. What appear to be pores are actually depressions associated with trabeculae in the endochorion on the other side, which support aeropyles. Most of the punctations lack membrane penetrating pores.

The flatness of the uppersurface of the egg in the Polyommatinae is exaggerated by a wide transition zone around the annulus, with low tubercles or tubercles absent at rib intersections (Fig. **106**). Thus the apparent height of the exochorion on sides and shoulders is due to the elongate tubercles which then diminish in size in the direction of the micropyle. This ostensible drop in chorion height compensates for any slight increase toward the midline which results from a slight dome shape. The result of these compensatory differences in level is that the upper surface appears flat.

Glaucopsyche lygdamus (Dbldy.)

Fig. **114**
d. 0.52 mm; a. 0.10 mm

Turban shaped egg almost flat on micropylar side; tubular ribs with enlarged tubercles at intersections; aeropyles lip-like, many closed (with spumaline ?); carinae when present on ribs limited to areas between knobs; tendency for four ribs between tubercles resulting in squarish or rectangular areoles; lower inter-rib chorion porous forming a plastronic network; pores of irregular size on multi-plateaued surface; micropylar pit with four to five micropores visible in lateral margins (Fig. **114**) giving pit an angular appearance; rosette of four to five irregularly sized petals with outlining ribs not of uniform height, appearing to overlap on distal margins; annulus of three to four cells ringed rather abruptly with enlarged ribs and tubercles so that it appears recessed; irregularly shaped chorionic islands in most cells of annulus.

The eggs of *lygdamus* were difficult to properly coat for SEM work so that they tended to show "charging" which precluded photos of the entire egg. Interestingly, the same difficulty was encountered with the pupal stages of this species. Both stages may possess an "oily" coating, in the case of the egg perhaps a spumaline coat, which prevented adequate deposition of the metallic coat necessary for SEM work.

Hemiargus ceraunus (Fabr.)
Figs. **108, 109, 146**
d. 0.59 mm; a. 0.08 mm

Reticulations less dense than in Eumaeini; tubercles usually less than twice as high as supporting ribs; tubercles nodular-like, surface covered wth "filled" pores, as are ribs (with spumaline ?); even some aeropyles (Fig. **146**) appear plugged, although internal braces and struts might appear to close the pore, air spaces might still be present; ribs rounded above, parallel-sided and continuous below; running straight from one intersection to the next where they may recurve upward to help form the gently rounded tubercle; aeropyles mostly in a wide band around the shoulder; tendency for each tubercle to have four ribs so that cells between are squarish except at rib junctions; endochorion floor of irregular, undulating and highly porous cells, with the majority of pores closed; a sufficient number of pores remain open in some cells on the side to indicate possible plastronic respiration; micropyles apparent in angulate depression (almost a pit in some specimens) (Fig. **108**); rosette of four petals closed everywhere except between micropyles; islands of chorion near base of each petal in rosette, and irregularly scattered in cells of annulus (Fig. **109**); annulus with three tiers of cells.

Hemiargus ammon (Lucas)
Figs. **110, 111, 142**
d. 0.48 mm; a. 0.06 mm

Egg similar to *ceraunus;* tubercles one and a half to two times as high as ribs; apices of tubercles have a a tendency to be narrowed in one direction (Fig. **110**); upper surface of tubercles grainy and roughened texture (Fig. **142**); ribs slightly narrower than *ceraunus;* interrib floors highly porous and of irregular levels, may function as plastronopore surface even though some pores apper to be plugged; micropylar pit rather large; four-petaled rosette with irregular small islands of chorion near base of petals; annulus with one to several irregular islands protruding up from floor of each cell; floor of cells of transition zone highly reticulate, with both open and plugged pores (Fig. **111**).

Icaricia acmon texana Goodpast.
Fig. **115**
d. 0.48 mm; a. 0.03 mm

Egg collapsed preventing most observations except as follows: ribs sinuate and scabrose with numerous punctations dimpling surface; micropylar depression very folded, micropyles enclosed within folds of endochorion; the irregular petals of the five bladed rosette contain mainly folds and chorionic outgrowths within, thus obscuring their own outline (Fig. **115**); annulus small, two or three tiers of cells; floors of cell contorted and undulating, helping to obscure any geometric regularity in the micropylar region.

Twelve species of Polyommatinae of the following genera were treated in Part I: *Leptotes, Zizeeria, Brephidium, Everes, Celastrina, Glaucopsyche, Euphilotes, Lycaeides* (2), *Icaricia, Plebejus, Hemiargus.*

In addition, six species of Lycaeninae (genera *Hyllolycaena, Epidemia* [3]) and one species of Miletinae (genus *Feniseca*) were treated in Part I of this series.

Additional Notes on General Morphology

The following annotations supplement those given in Part I of the study and are similarly arranged alphabetically by morphological feature. A telegraphic style is used to contrast character states.

AEROPYLES: vary in position and associated structures: fairly flush with surface (**126**) of tubercle; flush with surface but with surrounding nipples (**131**); on low rounded prominences (**139**); on sides of ribs (**135**); on high prominences with erect nipples (**137**), with horizontal nipples (**138**), with frothy, five and six part nipples (**127**); geometrically positioned, not on prominences (**118**); of more than one pore size (**136**); irregular pore shape (**139**); on tip of spines (**145**) with small candle-drip effect (**148**), or highly irregular "layered" deposits on spines (**144**).

Many aeropyles and plastronopores appear to be closed (**139, 146**) just inside their outer margins such that ambient air would not have direct access to the interchorionic meshwork (see **152**). In some cases (**125, 129**) the smaller pores are completely sealed, either by a thin outer chorionic layer, or by the spumaline coating each egg receives as it is oviposited.

CHORION: exochorion elevated and sculputred into ribs, tubercles, and spines as well as depressions and reticulations (**123, 157**); may completely cover underlying structures (**36, 67, 88, 118, 125, 147**) concealing its highly porous, vacuolated, and compartmentalized inner structure (**120, 123, 124**); endochorion mostly concealed externally, or visible between ribs (**133, 135, 143**) or at the base of deep reticulations of the exochorion (**117, 129**) or where it may fuse with the exochorion forming a porous plastronic unit (**142**); vitelline membrane smooth, regularly porous and showing symmetrical patterns (**121**) or irregularly porous (**122**).

MICROPYLES: micropylar pores elevated and on ribs (**99**), on surface, in shallow depressions (**52, 93**) where they are distinct, or on lateral margins of deeper pits (**89**) where individual openings are not distinct; central pits may be circular (**89**), oblong (**50, 51**), triangular (**93**), square (**101**) or irregular (**107, 109**); usually as many pores as there are petals in the rosette (**99, 107**); micropylar pores are located in the pits directly beneath the intersection of the pit and the conjoined ribs of adjacent rosette petals; presence of "guarding" ribs (**99**) rare.

PLASTRONOPORES: small pores giving a sieve-like or lacy architecture to the chorion (**38, 142**); may be widespread (**41**) or in irregular patches (**143**); some surfaces are highly honeycombed and appear porous (**111**) though the pores do not penetrate through to the lower surface; some filled in with spumaline (**146**) or other coatings which close the pores.

RIBS: may be smooth, unsculptured (**130**), porous (**129, 146**), warty (**147**); rounded at apex (**136**) or flat (**112**); straight (**132, 137**) or sinuous (**134**); of uniform size and shape (**136**) or irregular in size and shape (**134**); with high vertical, narrow and parallel sides (**127**) or non-parallel sides (**135**); expanded at their base (**132**) or with a narrow supportive beam below (**130**); with carinae (**131**); pillow-like, gently rounded on all surfaces (**130**); in insected "canyons", with rolled endochorion alongside giving the appearance of three ribs (**133**); with prominences at rib intersections (**130, 132**), or with transverse prominences between rib intersections (**156**); with aeropyles on lateral surfaces (**135**).

SCALES: It is known that some lycaenids, *i.e. Nordmannia* (Nakamura, 1976) conceal their eggs with scales during the ovi-position process. This is indicated (**141**) in *Oenomaus ortygnus* (Cram.) where the scales are irregular climps, and in *Eumaeus atala* (Poey) (**140**) where they form a pallisade layer around the lateral margins of the egg. Presumably the latter might provide a different type of protection than the former. Placing adult scales on eggs is a behavior derived independently in a number of families including, for example, the Lycaenidea and Hesperiidae in the butterflies, and Notodontidae and Saturniidae in the moths (Rothschild *et al.,* 1970).

SPINES: Parallel sided (**60**) or tapered (**148**) and needle-like (**145**); simple and unadorned (**145**) or highly ornamented along their length (**144**) or near their apex (**148**) where irregular coatings beneath aeropyles resemble candle-drippings*; apex may be blunt (**60**), pointed (**148**) rounded (**135**), hooked (**145**), recurved (**148**), bifid or trifid (Kitching, 1976) and with or without aeropyles (**148**).

The relationship between elongate, narrow chorionic protuberances or projec-

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*It is possible that some species may have modest amounts of exudations "pulsed" from openings after oviposition, which on hardening, appear to be chorionic in origin. Chauvin and Chauvin (1980) note such elaboration in moth eggs and state that they originate from the oocyte rather than the follicle cells.

tions (=spines) and lumps, knobs or swellings (=tubercles) can be noted in species with intermediate conditions on the same egg (Figs. **34, 70**). They occur in the same location at the intersections of ribs, both may have aeropyles at their apices, and seem to differ mostly by the elaboration and extent of their projection from the surface of the egg: squat rounded projections appear as spines, particularly to the unaided eye, and account for its echinoid appearance (**94**).

DISCUSSION

Chorionic Regions and Their Origin

We have identified four major chorionic surface regions in the Lycaenidae based largely on external elevations. These are not clearly distinct in every species. They include: an annulus surrounding the micropyle; a transition zone; a tubercle-aeropyle region; and a flat "structureless" surface.

The annulus consists of one to several rows of areolae or cells, including ribs or depressions defining them, and including its inner ring termed the rosette. The ribs are of generally low profile, though similar in height or increasing only slightly laterally, and lack punctations or pores. Rib intersections are not enlarged, nor appear to overlay one another from outer to inner rings.

The transition zone surrounds the narrower annulus and consists of areolae whose ribs are distinctly higher and broader than in the annulus, and are more or less uniform in width and height. They may contain carinae, and modest surface sculpturing including pores. The region is diagnostic of some groups like the polyommatines (arrow, Fig. **26**) and in other species which lack the high tubercles and aeropyles, the transition zone may appear to extend from the annulus all around the egg (Fig. **90**). This region tends to lack any enlargements at rib intersections, though laterally such prominences may begin to appear, gradually increasing in size to the following region.

The tubercle-aeropyle region covers the greater part of the outer surface of most eggs and often provides most of the distinguishing characteristics. These include the highest prominences of the chorion, including enlarged tubercles, aeropyles, spines, and enlarged ribs. The majority of aeropyles are in this region.

The flat region characterizes many of the ventral surfaces lying against the substrate on which eggs are laid. The chorion in this region is very thin, often transparent in the emerged egg, and while not completely devoid of structure, it may have only the slightest wrinkling or irregularities marking the rib area between adjacent polygonal cells. When the secretory cells of the follicles secrete a rather homogeneous outer chorion over the entire egg (Figs. **41, 125**), often covering ribs and tubercles alike in rather undulating low relief, or where spumaline coats the egg uniformly, eggs may appear to have "flat" surfaces broadly distributed on the upper parts. High magnification reveals that these coatings are superficial, and cover an intricate chorionic meshwork. Except on the lower surface, we have so far not observed these flat areas as extensively in this family as in others, such as the Riodinidae.

Most microscopists have generally agreed (Telfer and Smith, 1970) that the chorion of insects may be divided into two vertical layers, though the number of subdivisions and their terminology varies considerably: an inner endochorion overlaid by a substantially thicker exochorion. In addition the follicular cells have contributed protein to a vitelline membrane between the oocyte and themselves (Telfer and Smith, 1970) prior to the last step in their differentiation, the secretion of proteinaceious chorion around the vitelline membrane (Paul *et al.*, 1972a). Whether or not the vitelline membrane is formed solely by the follicular cells, or by the oocyte is a moot point (see discussion in Furneaux and MacKay, 1976, p. 170) but it seems likely that both sources may contribute to its formation.

The chorion, at maturity, can account for up to 30% of the dry weight of the egg (Paul *et al.*, 1972a). The range of architectural diversity in chorions is great compared to the general chemical similarity of the chorionins comprising them, even though the presence or absence of specific proteins may be a general difference between shells of different families of Lepidoptera (Kawasaki *et al.,* 1972). There is no chitin in the egg shell (see Kawasaki *et al.,* 1971). In some moth species (Chauvin and Chauvin, 1980) external "sculpturing" appears after the egg is oviposited. These external deposits represent exudations of the oocyte after the egg is laid and do not constitute a true chorion. Except for the possibility of minute quantities of material near the micropyle described below, this does not appear to happen in the Lycaenidae.

Interestingly, Paul *et al.* (1972b) has shown that egg shell proteins are deposited around the egg in succession, each with a characteristic time table. These may then become hydrated at specific time intervals causing a rather abrupt increase in egg size during morphogenesis. Paul *et al.* (*loc. cit.*) also demonstrated that chorionic proteins are not interconverted, but that each is synthesized and secreted as a distinct component.

The chorion in most lycaenids also consists of two layers (see Figs. **123, 124** and **152**), an outer elaborate exochorion*, and an inner, thinner and denser endochorion. Both layers may be highly ornamented (Fig. **157**) and may be variously modified and vacuolated with air spaces. Chorionic trabeculae may separate the layers, or may be found within one or both layers such that a rib or tubercle which appears solid may have an internal meshwork of air spaces and chorionic columns (Fig. **152**). As Hinton has noted (1981, Vol. 1, p. 100) there are specialized kinds of interchorionic meshworks, and the intricate sculpturing of the exochorion in lycaenids leads us to assume that the inner elaborations, as yet uninvestigated, are equally complex.

It is our opinion that the exochorion in this family forms the ribs as well as any outgrowths such as tubercles, spines and reticular networks. All of these may be noted in Figure **157**. Aeropyles may communicate with interchorionic air spaces, or by ducts directly to the endochorionic layer overlying the vitelline membrane. There may also be larger or smaller pores opening to these interchorionic gas layers.

The endochorion has its fibers arranged in lamellae parallel to the plane of the vitelline membrane; the lamellae in the exochorion may also be relatively horizontal, but are more compact and often run parallel to the orientation (main axis) of the ribs, trabeculae and aeropyles they help form. In some species the exochorion appears to be lacking between the ribs, and the endochorionic layer is exposed. In such cases the orientation of fibers, and even the external texture of ribs and floor of the areolae would argue for slightly different secretory origins or times or production (or both) in chorionic morphogenesis.

Most often the plastronopores occur in the endochorion layers, or on what would appear to be the "floor" of the reticular network or external architecture. It is assumed that there is a complex passageway for the ambient air to penetrate this layer and move through to the vitelline membrane coat beneath. While the micropores can be noted in the inner lining of some hatched eggs (see Fig. **122**), these pores may not completely penetrate the membrane. In other species (Fig. **121**) the pores may penetrate both the endochorion and vitelline membrane. Such pores may occur only in limited areas of the inner surface. Most species, however, appear to lack such internal openings.

Micropylar Region

The envelopes surrounding the egg are at their thinnest in the region of the micropyle. This is due mainly to the reduction of the depth of both exo- and endochorion, with a corresponding loss of the vacuolated air spaces which help contribute to the apparent thickness of the exochorion in other areas. Internally the vitelline membrane is in close proximity to the endochorion in the micropylar region, at least during

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*Various authors (Hinton, 1963; Koss and Edmunds, 1974) have suggested avoiding the terms endo- and exochorion until the various chorionic layers may be homologized. Indeed with the intricate sublayering, varying numbers of chorionic layers have been described, which adds to the complexity of determining homology. In the present work, we have used the terms mainly in a topographical sense for outer and inner layers, without implying homologies outside the family Lycaenidae.

the period of fertilization and (perhaps) for a few hours after oviposition. The micropyle proper consists of several minute openings arranged in a roughly circular manner near the center of the micropylar region. Depending on the species, the openings may be in different positions: on a horizontal plane on the upper surface of the chorion, on a sloping plane on the margins of a depression, or on the vertical walls of a pit. In the latter case, what may appear to be a single outer opening (of circular, triangular, or square shape) may in fact be a micropylar pit formed by the chorion, and the true micropyles will be located on the sides of this structure.

From these micropyles tiny canaliculi perforate the chorion and run to the vitelline membrane beneath. There are usually as many pores and canaliculi as there are petals in the rosette, and they are located directly below where the petal ribs would join the micropyle. The micropylar sperm channels do not take the shortest route through the chorion, but appear in most instances to be directed circumradially parallel to the outer surface for a short distance (Figs. **153**, **155**). They cross the chorio-vitelline space, which is thought to contain waterproofing material in most insect eggs, including *Pieris* (Beament & Lal, 1957). In attempts to view these canaliculi from inside the egg, it is necessary to separate top and bottom parts of the egg, remove the contents, and to pull away the vitelline membrane, together with any embryonic serosal layers, depending on the age of the ovum. When this is done, in most instances it has been our experience that all the canaliculi, which in all cases are extremely thin, appear to be of the same length (Fig. **153**), even though collapsed and folded. Had they been attached to the vitelline membrane, as thin as that structure is we would have expected some tearing, or fragmentation, with a corresponding loss of distal parts of some of the micropylar tubes, or with attached pieces of vitelline membrane. However, no such distal damage, shortening or attached detritus could be identified, leading us to conclude that the canaliculi had already lost whatever attachment to the vitelline membrane they may have possessed near the time of oviposition, or shortly after they have served their functions as channels for the sperm to penetrate these maternal secretions (chorion and vitelline membrane). Indeed, Beament & Lal (*loc. cit.*, p. 110) demonstrate in *Pieris* that the "yolk" retracts from the micropylar region within six hours after fertilization. Such retraction would serve to break the canaliculi, no doubt at their weakest point. In the case of the riodinids and lycaenids, this would appear to be at their distal extremities at the junction with the vitelline membrane.

We have at least one other indication of the natural rupture of the canaliculi. In the riodinid *Emesis tenedia* C. & R. Feld. the severed and collapsed microtubules were variously embedded in a secreted matrix which would have precluded their sperm carrying function. This event, we feel, must have occurred after fertilization, and very likely was a natural event not produced, for example, by fixation of the egg in alcohol. Similarly, canaliculi of *Hypaurotis crysalus* and *Parrhasius m-album* were also found to be embedded in a matrix, probably of a fluid nature, prior to fixation. It is presumed that the invasion of the fluid increased the volume of the space between the endochorion and the vitelline membrane thereby rupturing any previous connection these microtubules had between the layers.

Eggs of *Harkenclenus titus* demonstrate the complexityof the situation and indicate that a connection between the canaliculi and the vitelline membrane may not be absolutely necessary. In this species the microtubes are sack-like (Fig. **155**) and closed at their distal extremities and appear as tiny nipples indented into the chorio-vitelline interspace from the endochorion. Their lateral Orientation radiating away from the micropyles, while noticeable, is not pronounced (Figs. **154**, **155**). They may never have penetrated the vitelline membrane*, but only have fitted against it.

Why the micropylar tubes do not run at right angles to the chorion, in other words, take the shortest distance from the outside to the inner egg membrane, is as yet unknown. The occurrence of this condition in both moths (Regier *et al.*, 1980; Hsia, 1980)

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*Barbier and Chauvin (1977) have homologized the vitelline membrane with a fertilization membrane in other organisms and as such, believe this function to be controlled by a factor produced by the oocyte. Various changes in this membrane occur near the time of oviposition (Miya, 1978) and during sperm entry into the egg.

and butterflies would suggest a vital physiological function. These could be related to the primary function of sperm penetration, but might also be involved in respiration and/or water conservation. In an attempt to obtain some data on this point we compared the canaliculi in *Emesis emisia* (Hew.) a riodinid whose eggs had been reported by us (Downey & Allyn, 1980) to lack aeropyles and plastronopyles, and whose mycropylar openings would therefore seem to serve also as respiratory pores. We were unable to detect any internal differences between the micropylar tubes in this species with congeners or other riodinids or lycaenids which had both pastronopores and/or aeropyles. The canals did not appear to be connected in any way with chorionic airspaces or other possible respiratory structures. We are left with the opinion that respiration is not a function of the micropylar tubule system in these butterfly species.

We have some evidence that the micropyles of several species become "plugged" externally. Some eggs (see Figs. **83, 85, 151**) have the micropylar region, including the base of the petals of the rosette, covered with a thin layer of material. This material covers the holes and other surface sculpturing, and thus far has been observed only in this region. The material does not resolve well for SEM scrutiny, and appears flat and structureless. We have assumed this to be a residue after the fertilization process, perhaps left over after the delivery of the sperm. However, its origin could just as likely be from a regurgitation of matter from the micropyles occurring after fertilization and perhaps concurrently with any yolk pulse or waterproofing process in the vitelline membrane. Indeed, we are at a loss to explain the absence of this extraneous material near the micropyles in the majority of species, whose eggs at the time of examination we assumed to be fertilized. We acknowledge that there could be an interspecific difference in the amount of sperm carrier fluids involved. The external "plugging" of the micropyles however, is not inconsistent with the internal rupturing of the microtubules; either way, a respiratory function is precluded at the time of either event.

Taxonomic Implications and Phylogenetic Utility

As is well known, it is difficult to omit bias from taxonomic judgments. For example, we commenced our studies with the knowledge (=presumption) that the eggs sampled were from different species as determined by other (mostly adult) characteristics. If the eggs were from congeners, we tended to look for similarities, while if the eggs were from species of different genera, we expected them to be more divergent, and tended to look for differences. In an attempt to dampen this taxonomic bias, we preferred to work with unidentified scan photos and base judgments solely on the chorionic characters. On the other hand, in so doing it was also easy to develop quick generalizations based on superficial resemblance. For example, as was pointed out in Part I, when tubercles predominate on the chorionic surface, 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 are variable, eggs of congeners with a modest number of differences may still appear dissimilar. Conversely, eggs of nonrelatives may take on a superficial resemblance due to a predominance of one or two similar chorionic characters. Not all knobby eggs belong to related groups, nor do they argue for common phylogeny. Further, there may exist a relatively simple relationship in the development of certain egg characters between species such as might occur, for example, in size relationships. Thus there could be a trend in tubercle or spine development from low, narrow-based elements through medium sized to large tubercles or spines. The latter might also have progressed further to elaborated tips, or bases, or both. While we can conceive of a sequential scheme from small to large, on reflection, we would also argue that all large-spined eggs are not related because of this feature alone. Indeed each genus might contain species with large-spined eggs which may thus superficially resemble one another more closely than they resemble their short-spined, heavily ribbed congeners.

Cognizance of this dificulty helped modify the subjectivity of the judgments, particularly when further attempts were made to relate architectural similarity to adaptive significance. For example, are all tall sharply-spined eggs better protected from hymenopterous egg parasitoids than their shorter-spined or spineless congeners? The adaptive and evolutionary significance of most of the egg characters remains to be determined.

In spite of rather marked differences between eggs of congeners, we are beginning to recognize some features which might be used with caution at taxonomic levels above the species. The following are possible examples of generic characters:

1. *Strymon* species (see **58**, **117**) invariably have rounded-ribs held elevated from the lower surface by a thin, solid parallel-sided ridge, attached to the bottom of the rib in the six o'clock position;
2. *Cyanophrys* species (*amyntor*, Fig. **52**; *goodsoni*, Fig. **84**) show similar features in both ribs and tubercles;
3. Short spines and deep fossae unmistakably relate *Calycopis* species (see *isobeon*, Fig. **12**; and *cecrops*, Fig. **13**);
4. The broad muri of *Mitoura* eggs (see *gryneus*, Fig. **67**, and *hesseli*, Fig. **125**) place them in related groups.

the following examples illustrate the difficulty of using single characters:

1. *Satyrium liparops* (Fig. **4**) looks more like *Harkenclenus titus* (Fig. **10**) than the former does to all it congeners (Figs. **2**, **3**, **5**, **6**, **7**) because of the similarity of the expanded tubercles.
2. *Eumaeus atala* (Fig. **74**) and *E. minijas* (Fig. **76**) have similar tubercles, but dissimilar micropyles (compare Figs. **75**, **77**).
3. On the basis of tubercles alone, one would relate *Euristrymon polingi* (Fig. **96**) to other Eumaeini before placing it with *E. ontario* (Fig. **94**).

At the higher taxonomic levels, certain characters show taxonomic promise:

1. *Leptotes* and *Celastrina*, though placed in different sections of the Polyomatini than are *Lycaeides* and *Icaricia*, still share a marked transition zone with the latter groups.
2. *Habrodais* would appear to be related to *Favonius* and other Theclini figured by Hara (1979), particularly in micropylar structures, although the relationship of *Hypaurotis* to the latter group is less easily seen in the egg stage. Hara (*loc. cit.*) using egg characters was able to corroborate the phylogenetic scheme for *Zephyrus*, which was based on other taxonomic features by Shirozu.

Single representatives of many distinct genera were examined, *i.e. Tylopaedia*, *Hypaurotis*, and *Feniseca*. Also, many distinct groups within one tribe were sampled; *i.e. Azulides*, *Arawacus*, *Atlides*, and *Erora*. As might be expected, their eggs were distinctive, though their degree of divergence could not be labeled by taxonomic hierarchy above the species level. Other features, such as the micropyle and associated structures, and the type, number, and position of the aeropyles would also appear to have some taxonomic utility at the higher levels, particularly as ultrastructural studies become available for more taxa. However, as indicated in Part I, we continue to suggest that a degree of caution be used in assigning diagnostic value to certain character states until more comparative data are at hand. This is especially necessary for generalizations made using light microscopy. Striking differences in appearance can result from rather modest changes in predominance of chorionic structures, most of which may require scan electron photomicrographs for detailed comparison. The reader is referred to Part I (page 15) where explanations of chorionic dissimilarity of congeners are discussed in more detail.

For these reasons we suggest that overall differences in egg shape may have greater taxonomic utility at this time than many of the nuances of sculpturing. The lateral profile of an egg, together with the elevation (depressed, level, or raised) of the micropylar area may still be one of the most useful egg characters at the generic level or above.

Compared to other butterflies, and to most families of moths as well, the eggs of Lycaenidae are highly sculptured. It is our opinion that this type of chorionic ornamentation is derived from a simpler ancestral type. Table 1 summarizes our assessment of the ancestral *vs.* derived condition for no fewer than 40 character states of 13 morphological features. Judgments were based on morphological associations and frequency of occurrence throughout a wide range of taxa as based on other (mostly adult) features. As subjective as such decisions were, we hope that this first attempt at chronology of egg character states within the family (if not the order) will lead others to deduce sequential pathways of possible evolutionary importance, and to challenge these viewpoints.

It is thus somewhat of a paradox that we can speak of the phylogenetic chronology of the egg character states, but are really much less certain of the taxonomic usefulness of these characters. This is the reverse of the usual situation where taxonomic features, already proven to be diagnostic, are additionally meant to reflect "natural" groupings and hence plausible phylogenetic relationships. However, it should be remembered that the chorionic sculpturing is secreted on the egg by the follicular epithelium of the genital tract of the female. As such it is a manifestation of an adult character state, and is not uniquely produced by the egg itself. It consists of molds and casts of soft epithelial cells and includes folds and gaps in the secreting structures producing these chorionic proteins. We might thus understand, since the producing cells are soft and malleable, that the chorion is also very soft and plastic, particularly if in contact with water. Exposure to low humidities, or drying (heat) or normal air exposure at oviposition procues irreversible hardening. We are here suggesting that non-rigid casts of soft somewhat irregular structures will contain various degrees of variability, not all of which will be genetically fixed, and not all of which will have the same selective advantage. Since the follicular epitheium is unique and used only once before being resorbed (having covered a single egg from the beginning of its existence) it is understandable that no two chorions might be exactly alike in all details. The situation might be compared to the frosting on a layer cake. All layer cakes produced by one cook using essentially the same equipment and ingredients will be much alike (size, shape, layering) but the frosting laid on and spread with slightly different motions (and differing drying times) may vary considerably. Similarly, in some species, minor differences in chorionic details, just like the frosting, might be expected, and may not be ecologically adaptive or taxonomically significant. We are anxious to study additional eggs of disparate affinities to assist with taxonomic and ecological implications.

SUMMARY

1. Eggs of 34 taxa (23 genera) were described and figured using SEM photographs. A total of 67 species belonging to four subfamilies and eight tribes were treated in both parts of this study. A species index to the photographs is given, as well as an index of SEM photos of lycaenids in other works prior to 1982.

2. Morphological features described and illustrated include the micropyle, canaliculi, rosette and remaining annulus, plastronopores, aeropores, ribs, tubercles, spines and other chorionic structures. Variation in these elements was described within species, and chronologies for over 40 character states were hypothesized. While only a modest number of eggs from this large family have been examined by SEM, this first attempt at egg character analysis will hopefully lead others to deduce sequential pathways and to challenge viewpoints.

3. Four major surface regions were noted, though these are not distinct in each species: the annulus (with its inner ring or rosette), a transition zone, a tubercle-aeropyle region, and a flat structureless surface.

4. While there is much individual variation in particular egg character states, with proper knowledge and caution these can be used taxonomically. For example, knowing that petal numbers in the rosette may vary from three to six, a good taxonomist would not make discrimination judgments on two otherwise similar eggs, one of which had four petals and the other five. Caution would suggest these may not belong to different taxa, and more input should be sought. We have come to the conclusion that each of these character states shows some degrees of variability, and that eventually most of

them may prove to have some taxonomic value somewhere in the famliy.

5. Disparate patterns in congeneric groups whose taxonomic positions are not debated on other grounds indicate that phylogeny alone does not determine egg morphology. We have tried to relate some features to ecological conditions (arid climate, inundation with rain, parasitoids) but evidence is scanty and subjective. There is some evidence that certain superficial differences in surface sculpturing (sinuous patterns, cell size, tubercle widths, etc.) have little meaningful adaptive (or taxonomic) significance.

ACKNOWLEDGMENTS

We are grateful to the many generous Lepidopterists listed in Part I who continue to contribute specimens to the project. Our sincere thanks are also given to Jacqueline Y. Miller, Lee D. Miller and Ruth Ratliff for reading and critical review of the manuscript.

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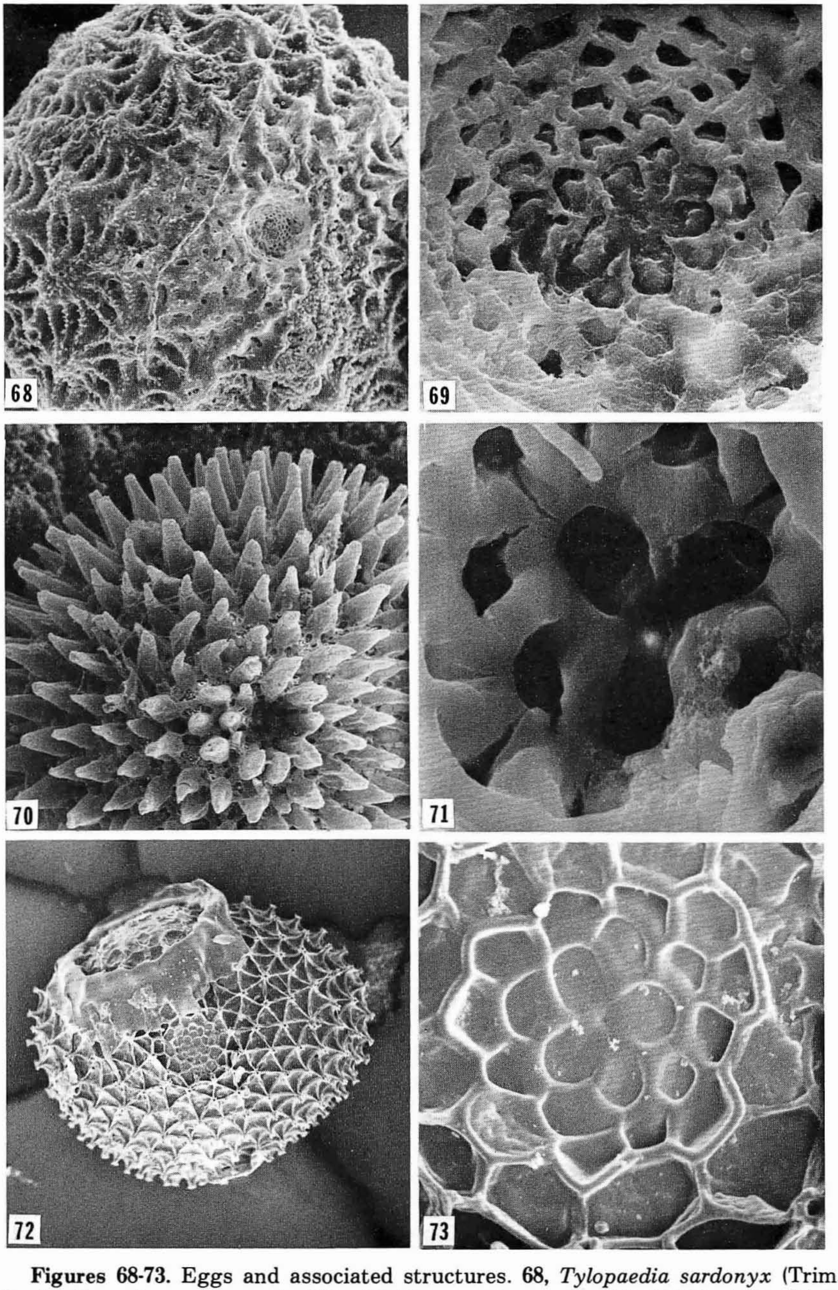
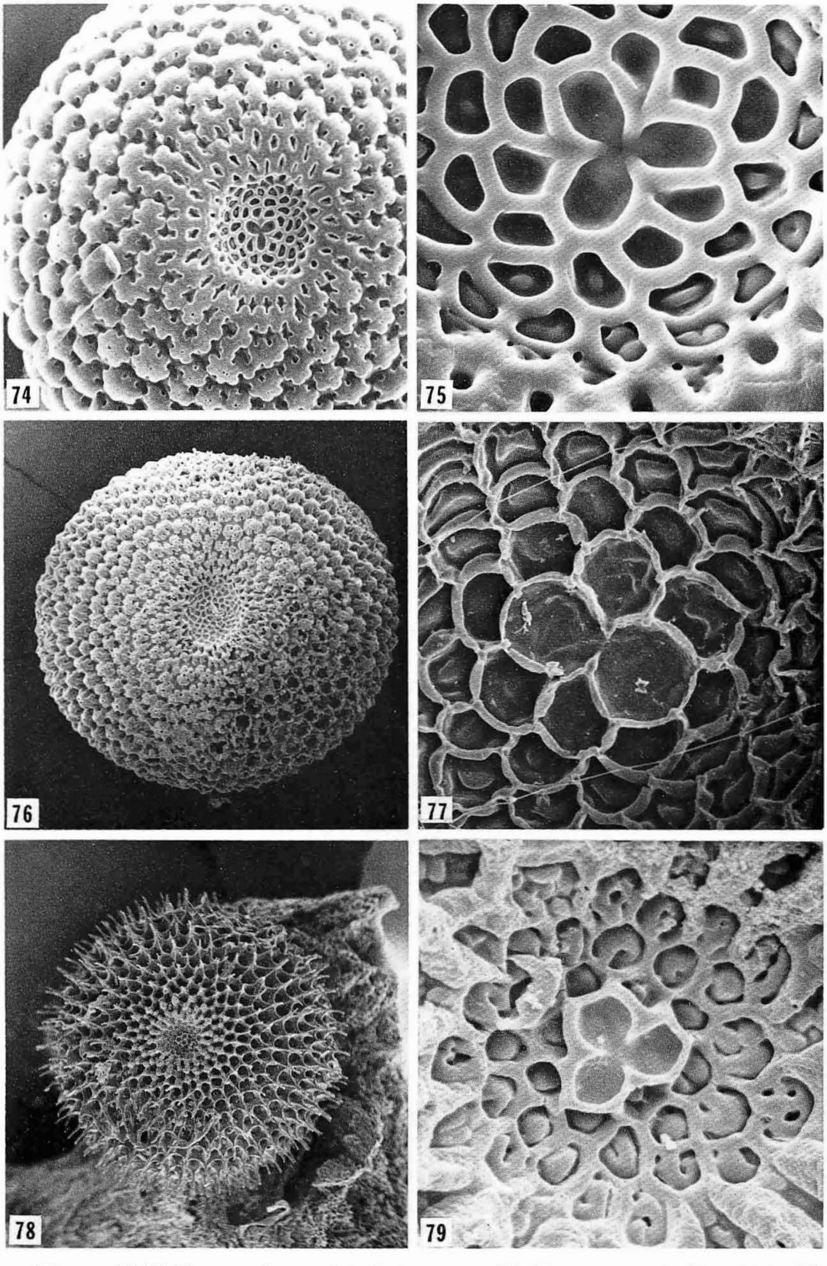
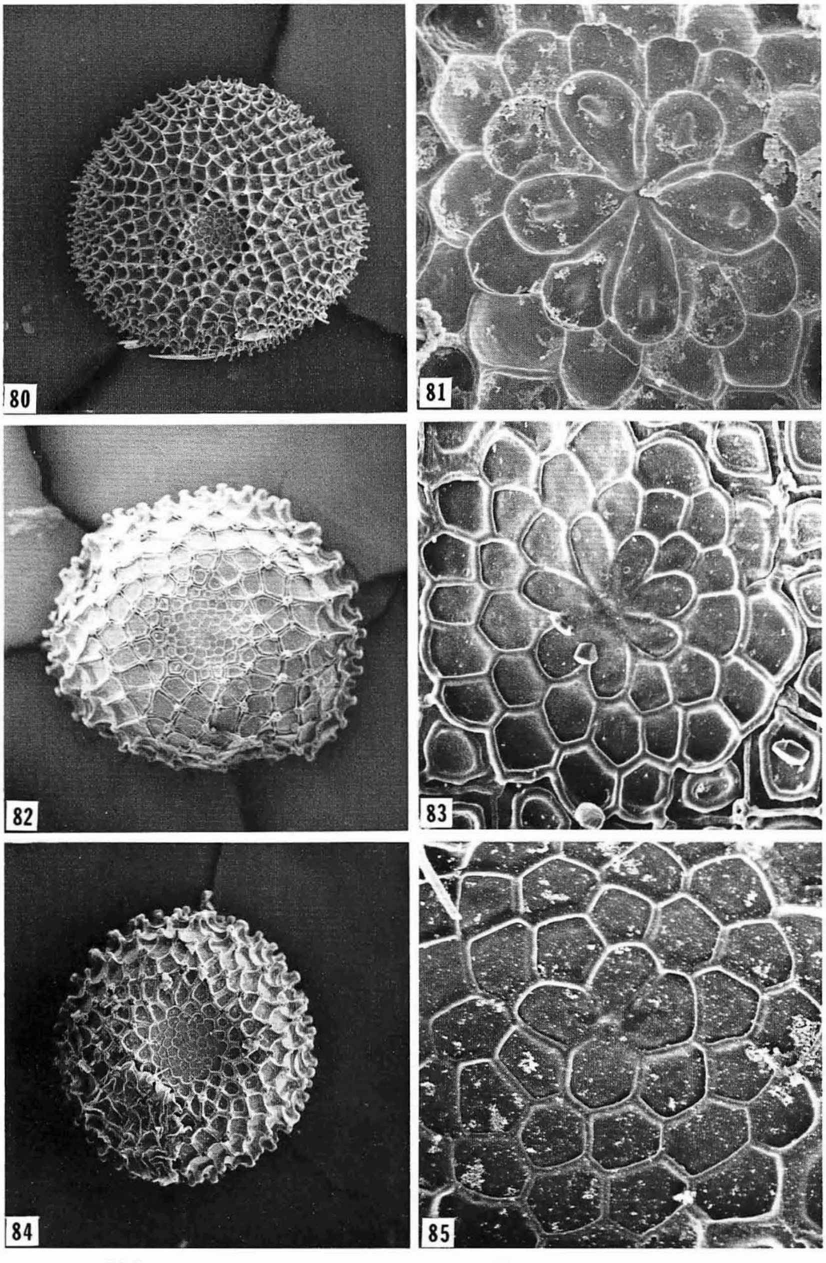


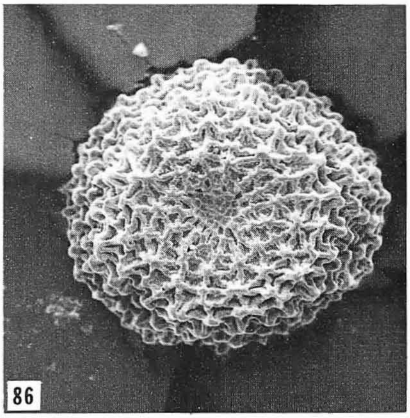
Figures 68-73. Eggs and associated structures. **68,** *Tylopaedia sardonyx* (Trim.) 60x. **69,** *T. sardonyx* micropyle 600x. **70,** *Hypaurotis crysalus* (W. H. Edw.) 60x. **71,** *H. crysalus* micropyle 1200x. **72,** *Pseudolycaena damo* Druce) 55x. **73,** *P. damo* micropyle 360x.



Figures 74-79. Eggs and associated structures. **74,** *Eumaeus atala* (Poey) 60x. **75,** *E. atala* micropyle 300x. **76,** *E. minijas* (Hbn.) 40x. **77,** *E. minijas* micropyle 300x. **78,** *Phaeostrymon alcestis oslari* (Dyar) 60x. **79,** *P. a. oslari* micropyle 600x.



Figures 80-85. Eggs and associated structures. **80,** *Oenomaus ortygnus (Cram.) 55x.* **81,** *O. ortygnus* micropyle 420x. **82,** *Cyanophrys amyntor distractus* Cl. 60x. **83,** *C. a. distractus* micropyle 300x. **84,** *C. goodsoni* (Cl.) 60x. **85,** *C. goodsoni* micropyle 350x.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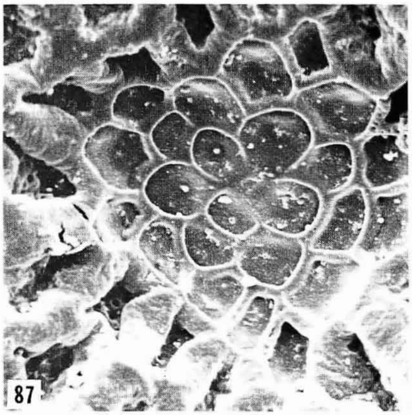
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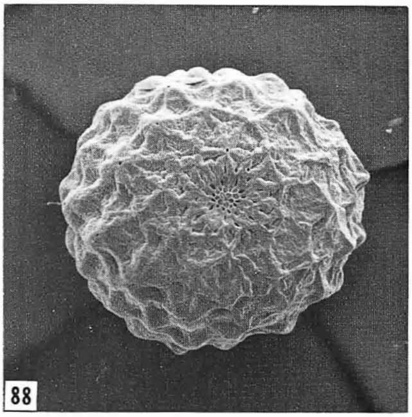
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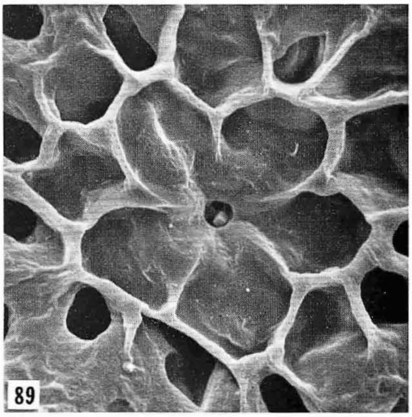
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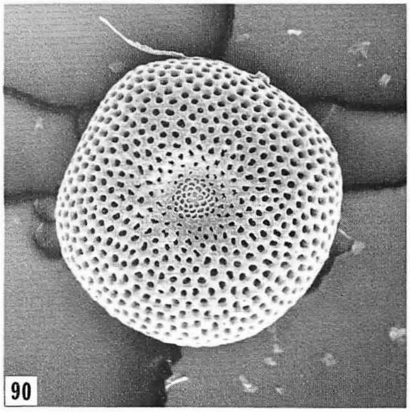
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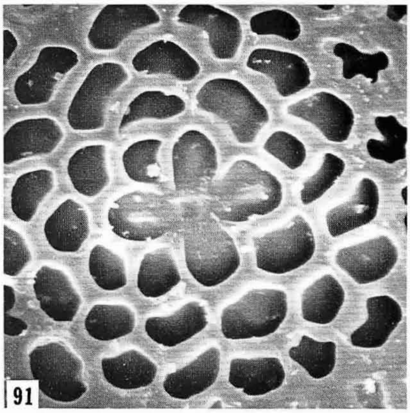
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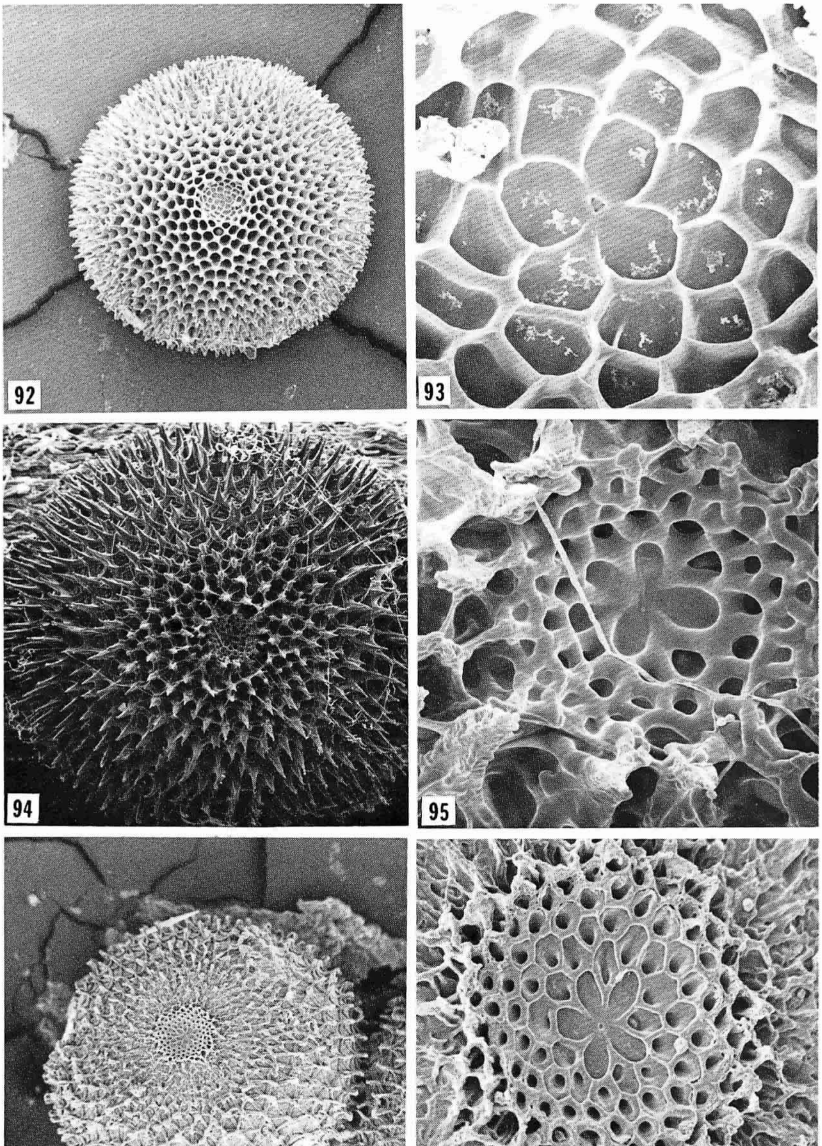
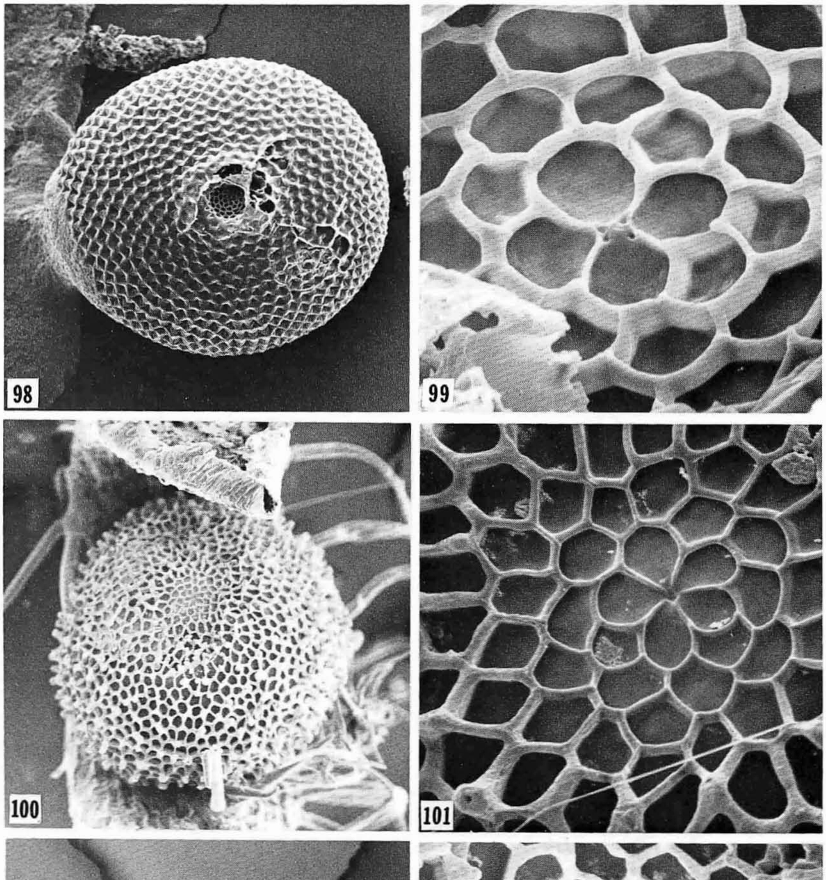
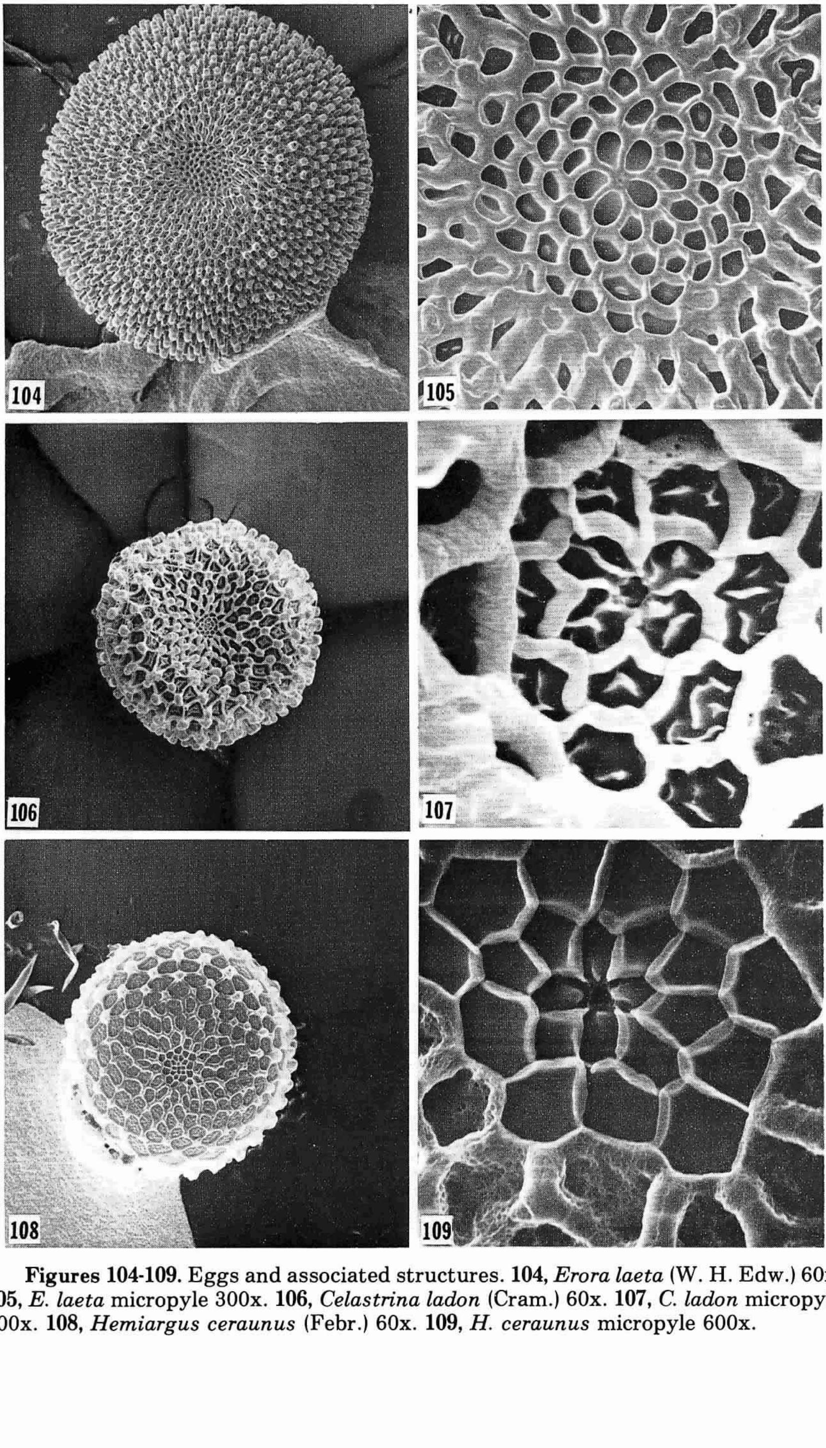
Figures 86-91. Eggs and associated structures. **86,** *Mitoura siva* (W. H. Edw.) 60x. **87,** *M. siva* micropyle 500x. **88,** *M. hesseli* Raw. & Zieg. 60x. **89,** *M. hesseli* micropyle 900x. **90,** *Xamia xami* (Reak.) 60x. **91,** *X. xami* micropyle 600x.



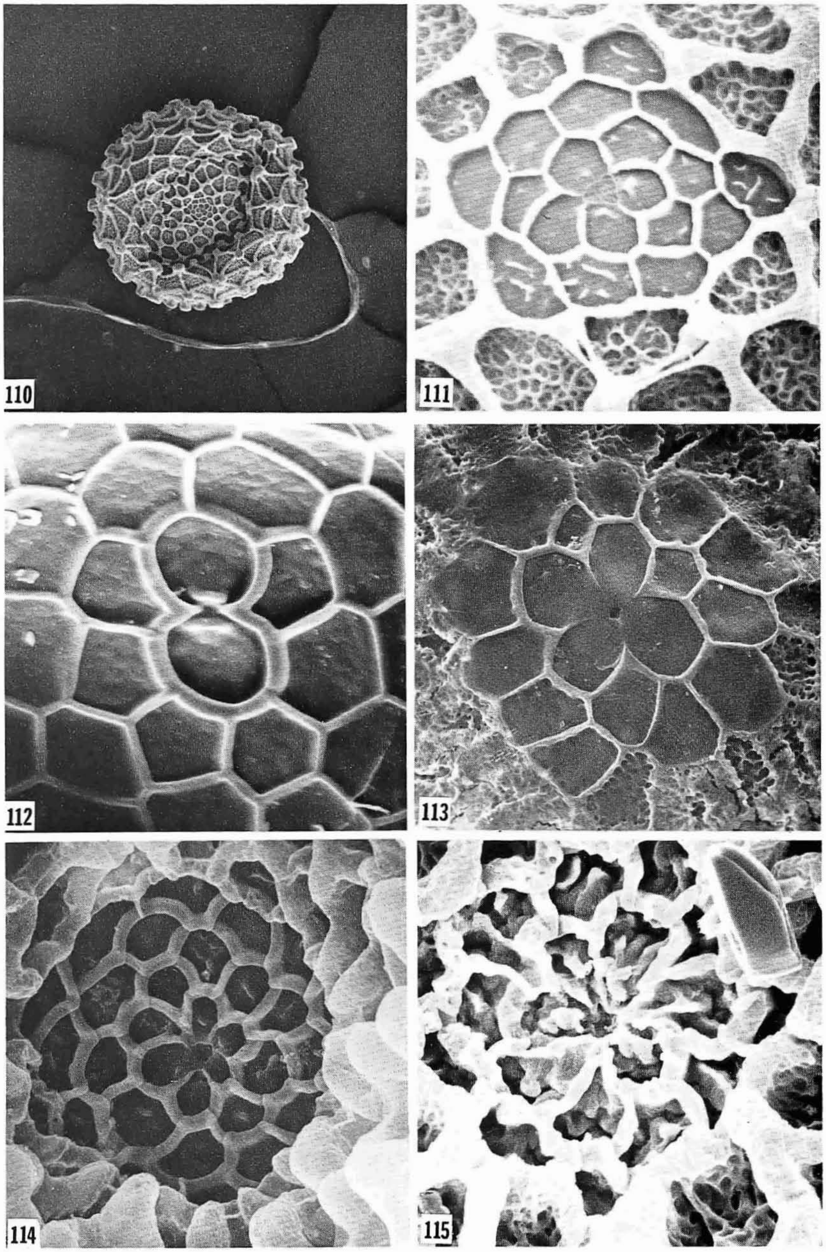
Figures 92-97. Eggs and associated structures. **92,** *Arawacus jada* (Hew.) 55x. **93,** *A. jada* micropyle 600x. **94,** *Euristrymon ontario* (W. H. Edw.) 60x. **95,** *E. ontario* micropyle 360x. **96,** *E. polingi* (B. & McD.) 45x. **97,** *E. polingi* micropyle 210x.



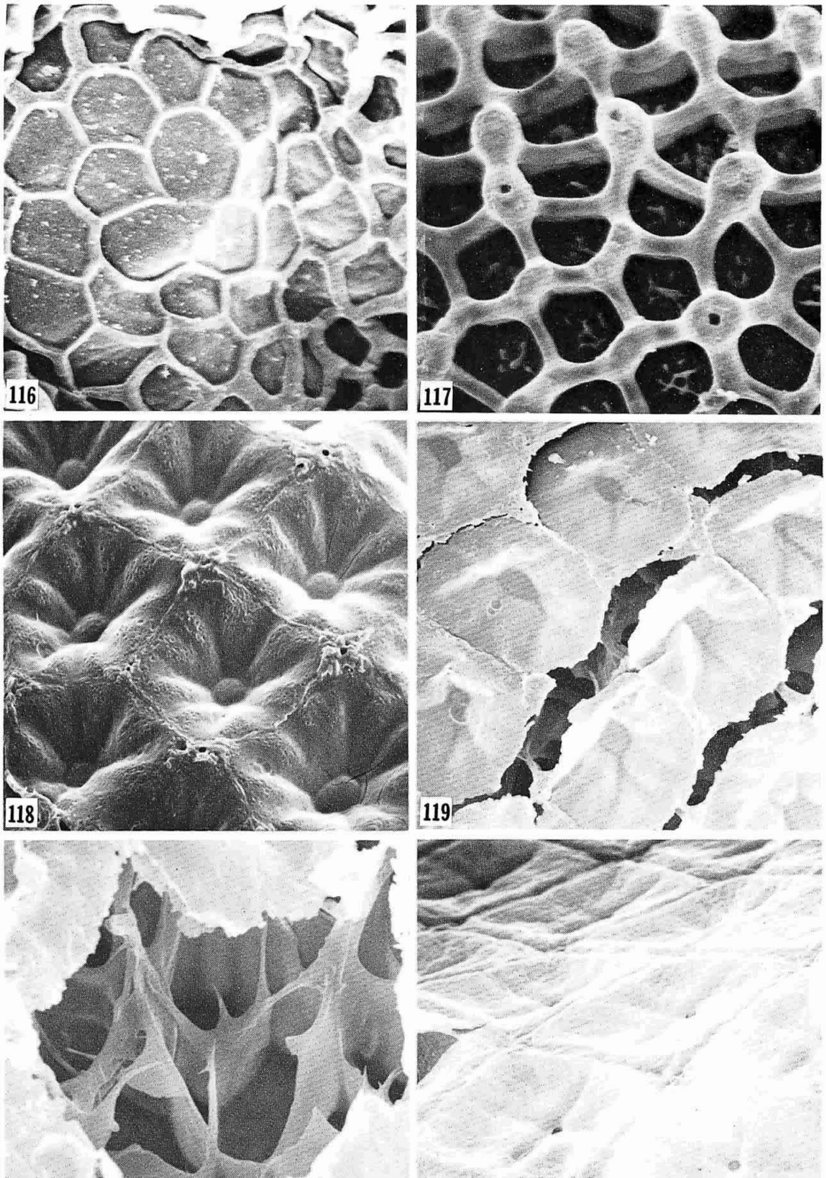
Figures 98-103. Eggs and associated structures. **98,** *Parrhasium m-album* (Bdv. & LeC.) 60x. **99,** *P. m-album* micropyle 900x. **100,** *Strymon yojoa* (Reak.) 60x. **101,** *S. yojoa* micropyle 360x. **102,** *S. alea* (God. & Salv.) 60x. **103,** *S. alea* micropyle 360x.



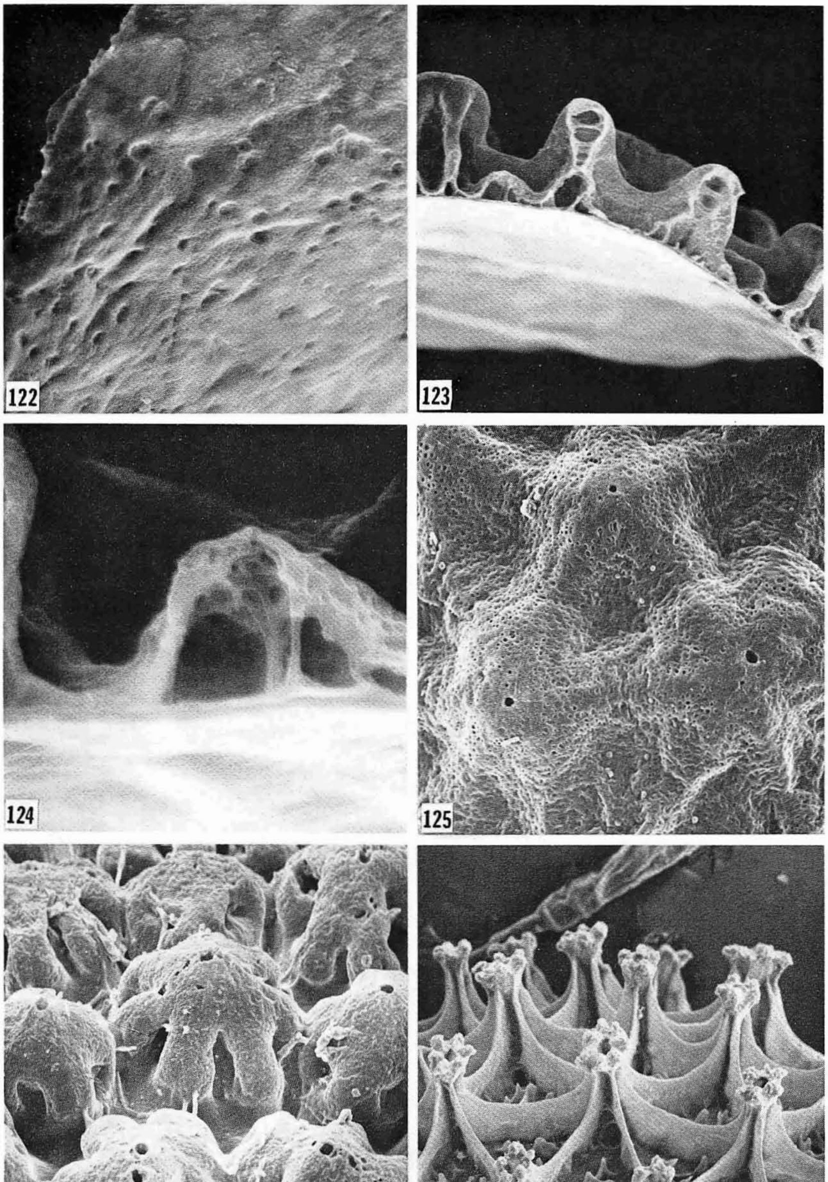
Figures 104-109. Eggs and associated structures. **104,** *Erora laeta* (W. H. Edw.) 60x. **105,** *E. laeta* micropyle 300x. **106,** *Celastrina ladon* (Cram.) 60x. **107,** *C. ladon* micropyle 900x. **108,** *Hemiargus ceraunus* (Febr.) 60x. **109,** *H. ceraunus* micropyle 600x.



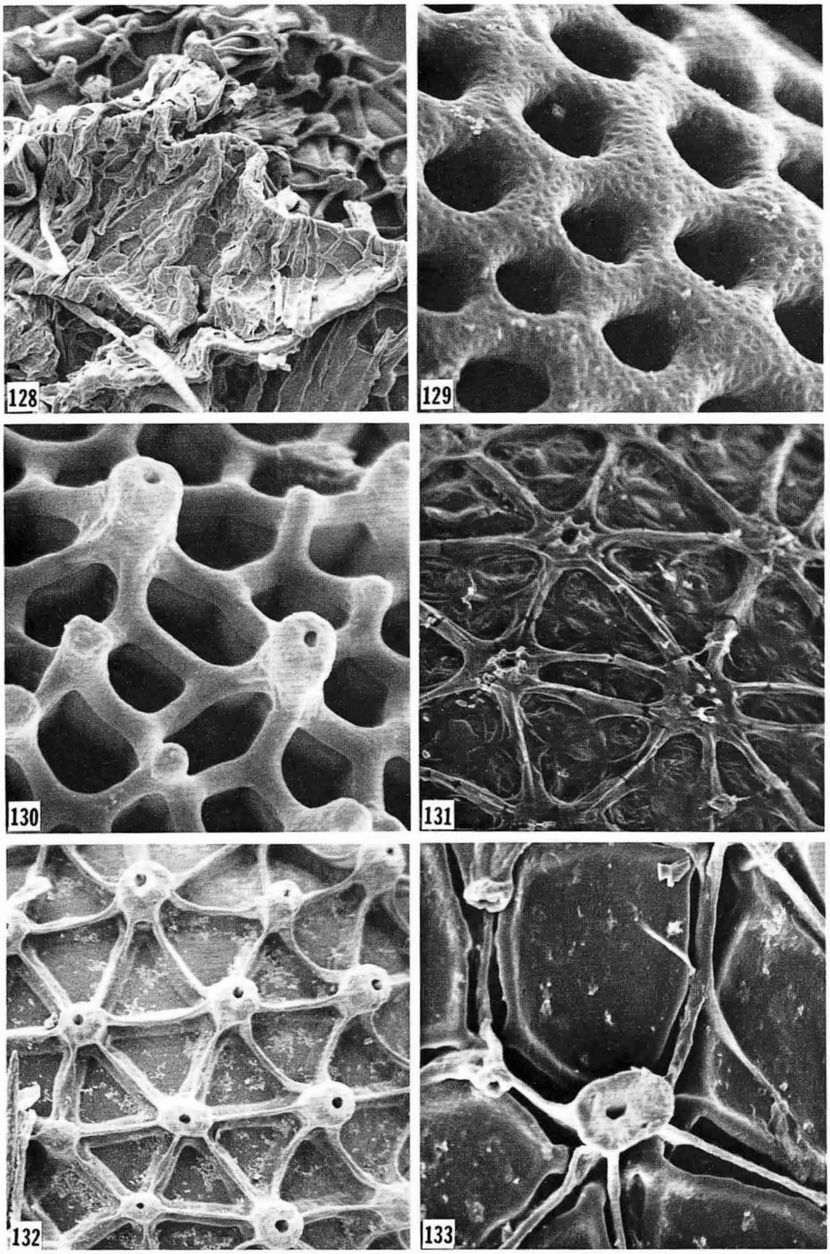
Figures 110-115. Eggs and associated structures. **110,** *Hemiargus ammon* (Lucas) 60x. **111,** *H. ammon* micropyle 600x. **112,** *Chlorostrymon simaethis sarita* (Skin.) micropyle 600x. **113,** *Mitoura nelsoni* (Bdv.) 360x. **114,** *Glaucopsyche lygdamus* (Dbldy.) micropyle 600x. **115,** *Icaricia acmon texana* Goodpast. micropyle 1100x.



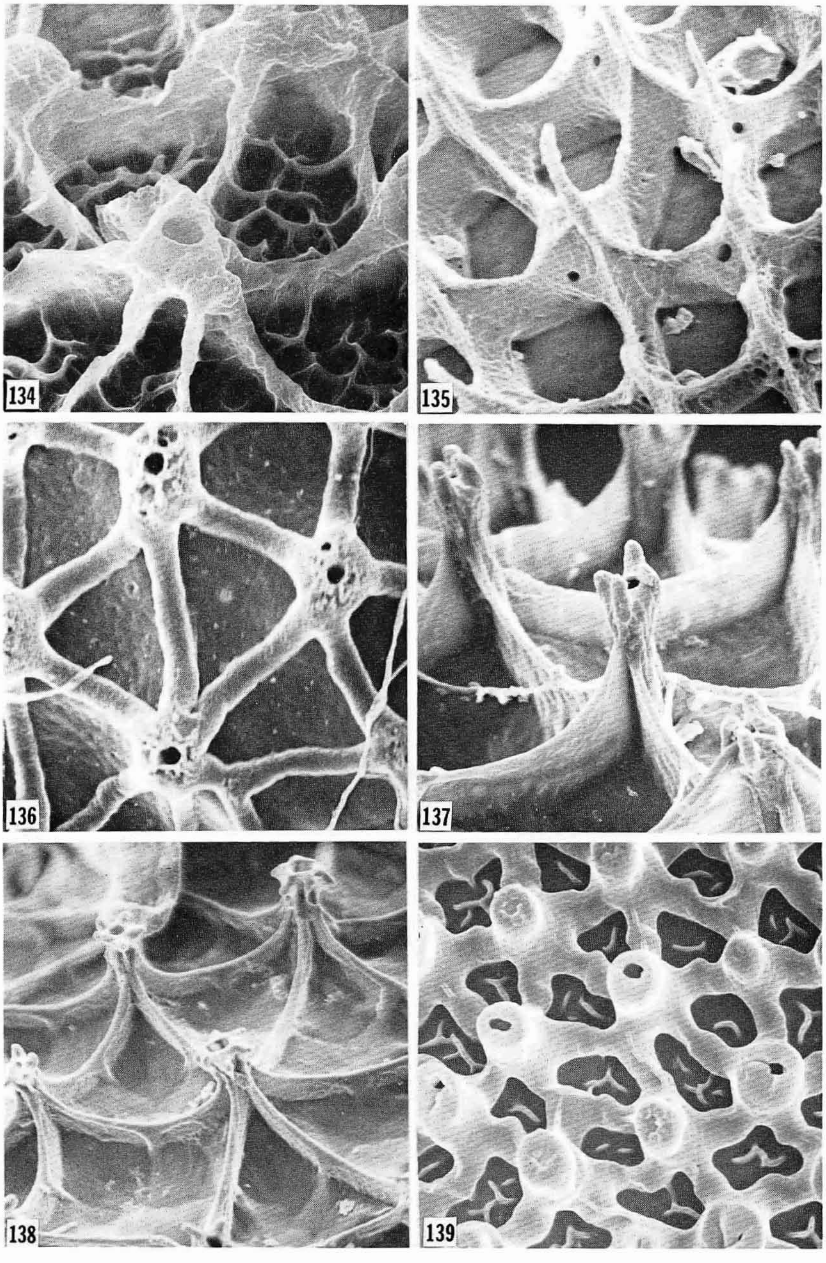
Figures 116-121. Details of egg chorion. **116,** *Strymon columella istapa* (Reak.) micropyle 480x. **117,** *S. c. cybira* (Hew.) aeropyles, chorion 600x. **118,** *Parrhasius m-album* (Bdv. & LeC.) outer chorion 600x. **119,** *P. m-album* chorionic tears 600x. **120,** *m-album* chorionic tear revealing trabecular network 1140x. **121,** *"Thecla" metanira* Hew. vitelline membrane viewed from inside 600x.



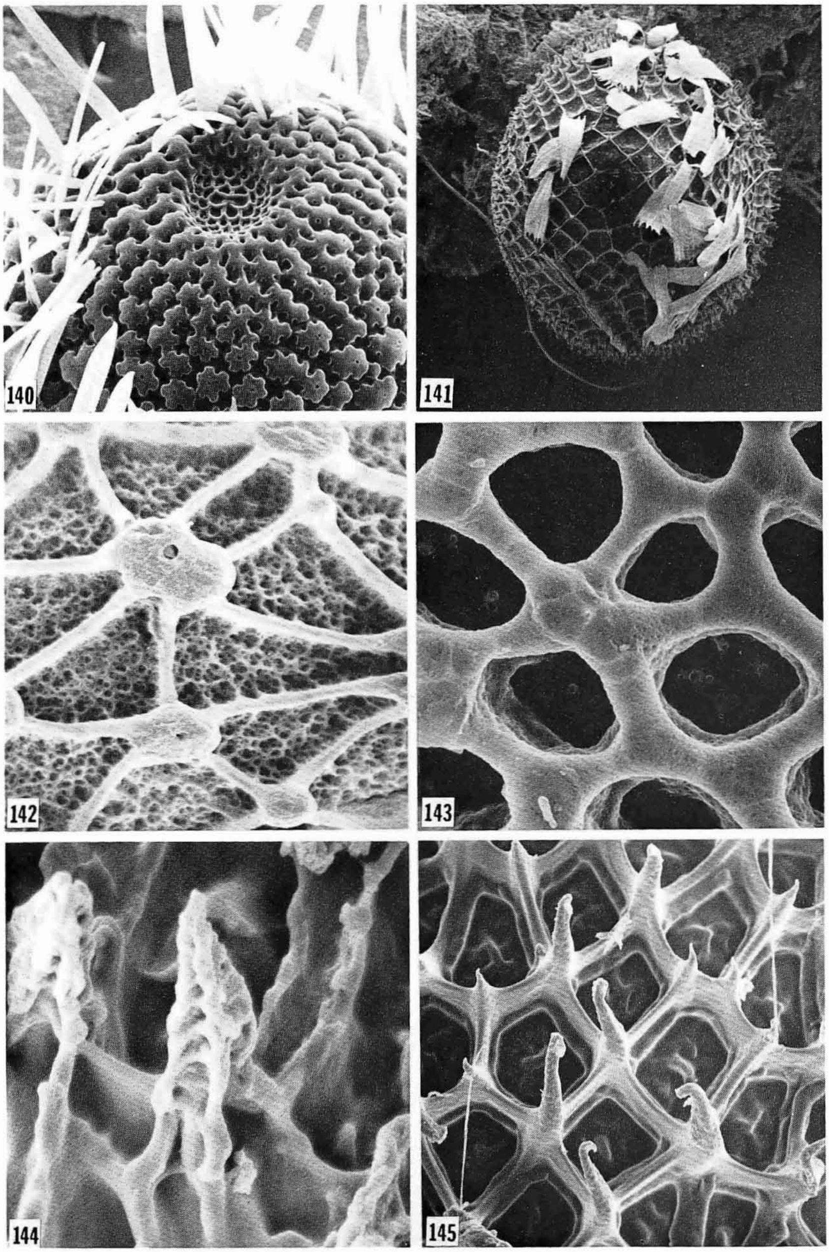
Figures 122-127. Details of egg chorion. **122,** *Celastrina ladon* (Cram.) vitelline membrane viewed from inside 720x. **123,** *C. ladon* chorion cross-section 480x. **124,** *C. ladon* chorion cross-section 2400x. **125,** *Mitoura hesseli* Raw. & Zieg. chorion outer covering 270x. **126,** *Eumaeus minijas* (Hbn.) chorionic sculpturing 420x. **127,** *Ministrymon clytie* (W. H. Edw.) vertical ribs and aeropyles with sculpturing on lower chorion 350x.



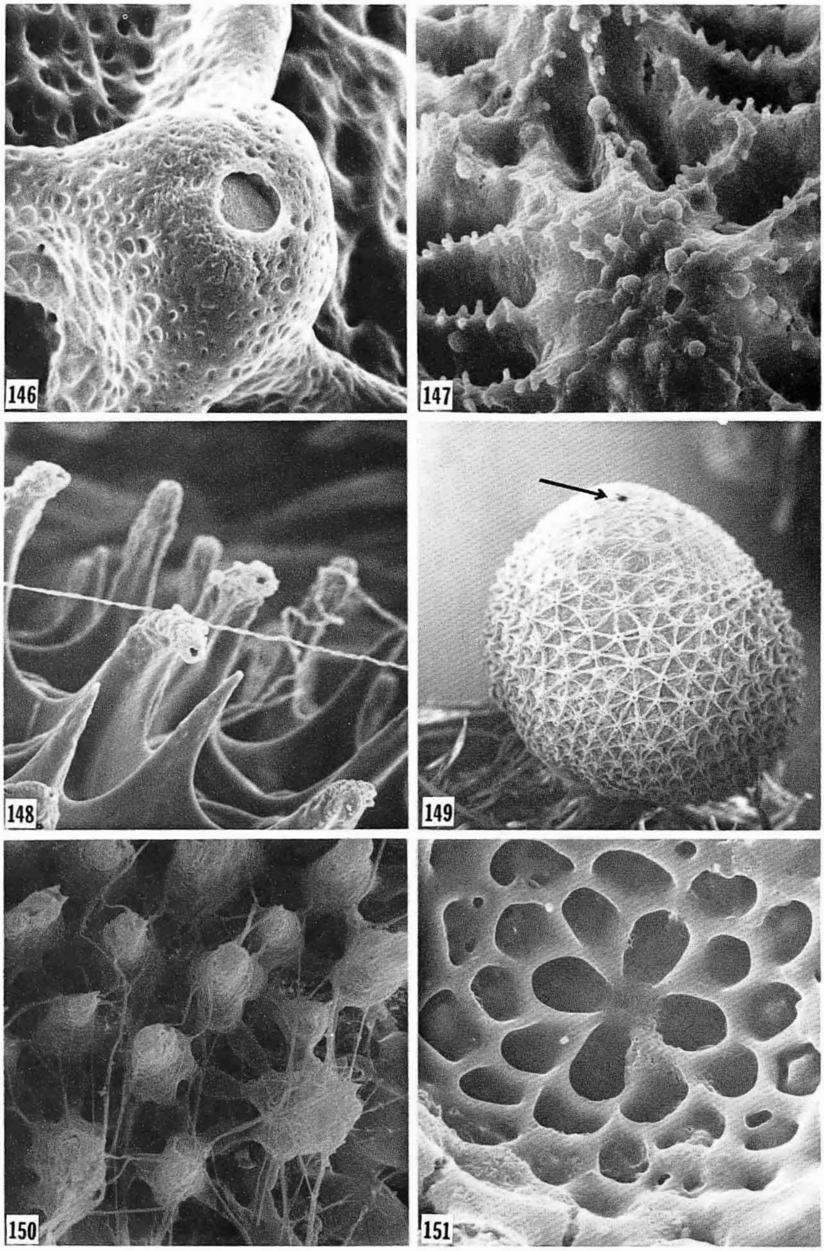
Figures 128-133. Details of egg chorion. **128,** *Incisalia irus hadros* Cook & Wats. ovariole extrusion on egg 120x. **129,** *Xamia xami* (Reak.) chorion 600x. **130,** *Strymon yojoa* (Reak.) aeropyles and chorion 600x. **131,** *Evenus regalis* (Cram.) aeropyles and chorion 240x. **132,** *Cyanophrys miserabilis* (Cl.) aeropyles and chorion 240x. **133,** *C. amyntor distractus* Cl. aeropyles and chorion 600x.



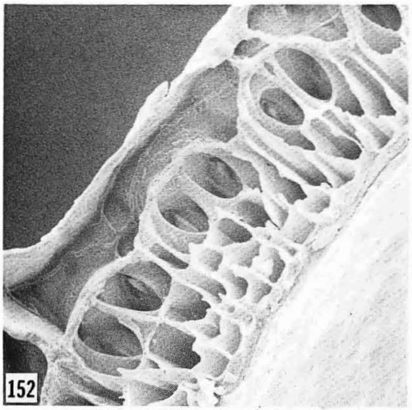
Figures 134-139. Details of egg chorion. **134,** *Incisalia henrici* (Gr. & Rob.) aeropyles and chorion 600x. **135,** *Phaeostrymon alcestis oslari* (Dyar) aeropyles and chorion 540x. **136,** *Chlorostrymon simaethis sarita* (Skin.) aeropyles and chorion 540x. **137,** *Oenomaus ortygnus* (Cram.) aeropyles and chorion 720x. **138,** *Pseudolycaena damo* (Druce) aeropyles and chorion 360x. **139,** *Erora laeta* (W. H. Edw.) aeropyles and chorion 600x.



Figures 140-145. Eggs and details of chorion. **140,** *Eumaeus atala* (Poey) scales on egg 60x. **141,** *Oenomaus ortygnus* (Cram.) scales on egg 55x. **142,** *Hemiargus ammon* (Lucas) aeropyles and plastron sculpturing 480x. **143,** *Incisalia polios* Cook & Wats. plastronopores and chorion 600x. **144,** *Euristrymon polingi* (B. & McD.) chorionic spines 900x. **145,** *E. ontario* (W. H. Edw.) chorionic spines 300x.



Figures 146-151. Details of chorion and egg. **146,** *Hemiargus ceraunus* (Fabr.) closed aeropyle 1800x. **147,** *Tylopedia sardonyx* (Trim.) chorion and aeropyle 300x. **148,** *Euristrymon ontario* (W. H. Edw.) aeropyles 600x. **149,** *Evenus regalis* (Cram.) egg; semilateral view showing a typical swelling and possible parasite hole 55x. **150,** *Hypaurotis crysalus* (W. H. Edw.) spines with chorionic streamers 180x. **151,** *Satyrium behrii* (W. H. Edw.) micropyle 600x.



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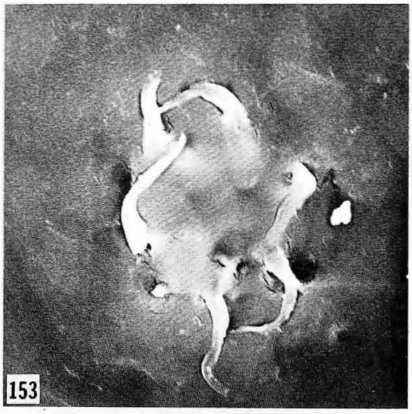

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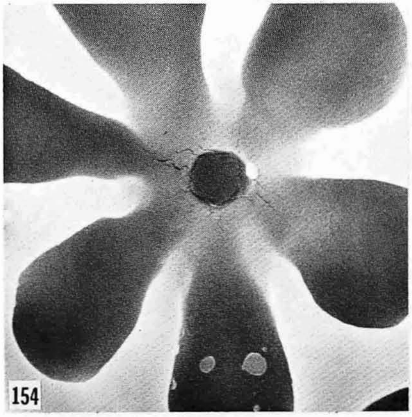

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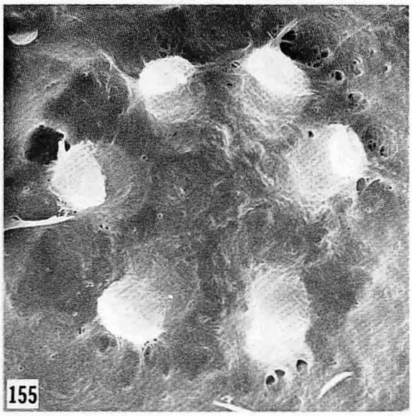

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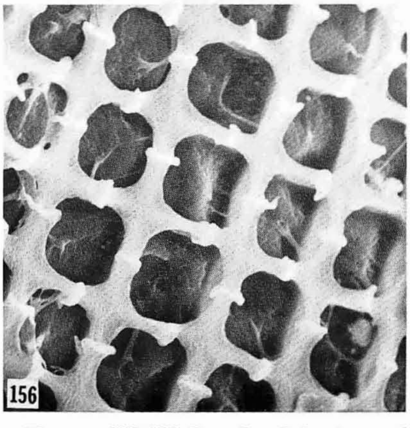

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Figures 152-156. Details of chorion and egg. **152,** *Parrhasius m-album* (Bdv. & LeC.) cross section through chorion showing highly vacuolated exochorion 360x. **153,** *Emesis emesia* (Hew.) internal view of canaliculi some embedded in matrix 1200x. **154,** *Harkenclenus titus* (Febr.) micropyle 1800x. **155,** *H. titus* internal view of micropylar area showing "closed" canaliculi 1800x. **156,** *"Thecla" metanira* (Hew.) chorion 360x.

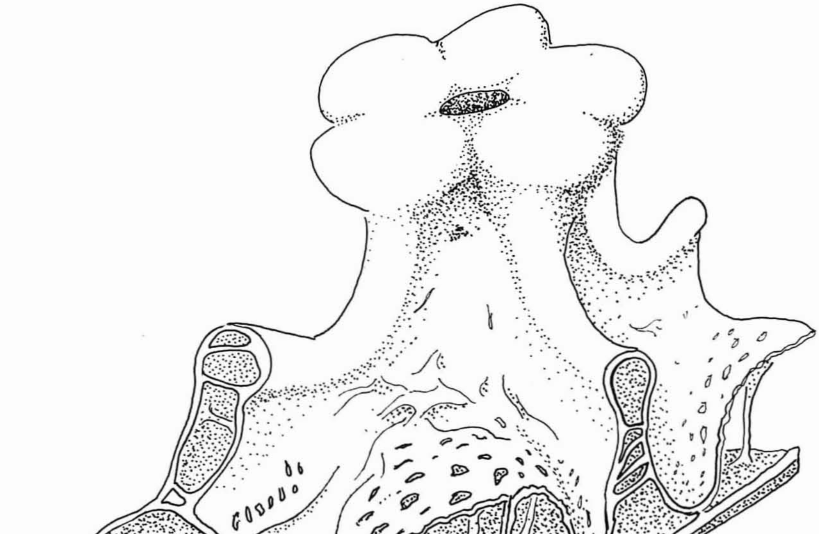

Figure 157. Diagrammatic section of the egg shell of *Celastrina ladon* (Cram.) showing a tubercle with a prominent aeropyle and the porous nature of the ribs and the intrachorionic meshwork. A thin vitelline membrane, also of maternal origin, underlies the endochorion. Compare with figures **123, 124,** and **152.**

Table 1. Suggested chronology of Egg Character States in the Family Lycaenidae.

FEATURE	CHARACTER STATE	
	ANCESTRAL	DERIVED
aeropyles	widely and/or uniformly distributed	limited to specific regions, i.e. shoulder of egg
	irregularly sized pore at rib intersections	uniformly sized pore on elevated prominences or on side walls of ribs
annulus	irregularly shaped cells, poorly defined	regularly shaped cells, well defined by ribs
	primary, secondary and tertiary rows similar in rib structure	rosette well defined, secondary and tertiary rows with markedly different shape and rib structure
rosette	petal-shaped, side ribs not parallel	round or square-shaped petals
	ribs of irregular width and height	ribs uniform in width and height
areolae (=cells)	of shallow depth	deeply insected
	polygonal shape	square or irregular in shape
chorion	ventral surface smooth, unsculptured	ventral surface sculptured
fovea centralis	obscure	well-marked
	level with surface	elevated or depressed
micropyle	several openings	single opening
	pores flush with surface	depressed in pit
canaliculi	almost vertical to plane of chorion	45° or less to plane of chorion
	parallel-sided	irregularly spaced sides or swollen distally
plastron	non-porous chorion	highly porous chorion
ribs	carinae absent	carinae present
	smooth, unsculptured	porous
	small size, solid	large, vacuolated
	uniform elevation	arched, buttressed, of varying heights
	side walls as wide as or wider than top	ribs supported by trabeculae or walls narrower than ribs

Table 1. *Continued.*

FEATURE	**CHARACTER STATE**	
	ANCESTRAL	DERIVED
spumaline (adhesive layer)	thin, not obvious	forming a vacuolated coating over egg
tubercles, spines	tubercles or prominent elevations absent (rib junctures unadorned)	tubercles, knobs or spines present
	short tubercles or spines with unsculptured tops	elongate tubercles or spines with apical sculpturing
transition zone	present	absent

Table 2. Index of Lycaenidae Treated. Numbers are Figure Numbers

SPECIES	FIGURE NUMBER				
	ENTIRE EGG	MICROPYLE	AEROPYLE	PLASTRON	OTHER
acadica (W.H.Edw.), *Satyrium*		62	61		
acmon texanan Goodpast, *Icaricia*		115			
alcestis oslari (Dyar), *Phaeostrymon*	78	79	135		
alea (God. & Salv.) *Strymon*	102	103			
ammon (Lucas), *Hemiargus*	110	111		142	
amyntor distractus Cl., *Cyanophrys*	82	83	133		
argyrognomon (Bergstr.), *Lycaeides*	24			48	
atala (Poey), *Eumaeus*	74, 140	75			
battoides bernardino (B. & McD.), *Euphilotes*	20			39	
behrii (Edw.), *Satyrium*	2	151			
calanus falacer (Godt.), *Satyrium*	5	55			
caryaevorum (McD.), *Satyrium*	6		32		
cassium theonus (Lucas), *Leptotes*	18	50,51	56,57	35	29,30
cecrops (Fabr.), *Calycopis*	13	63			
ceraunus (Fabr.), *Hemiargus*	108	109	146		
clytie (W.H.Edw.), *Ministrymon*			127		
columella cybira (Hew.), *Strymon*			117		
columella istapa (Reak.), *Strymon*		116			
comyntas (Godt.), *Everes*	23				
crysalus (W.H.Edw.), *Hypaurotis*	70	71			150
cupreus snowi (W.H.Edw.) *Lycaena*					31
damo (Druce), *Pseudolycaena*	72	73	138		
dorcas (W. Kirby), *Epidemia*	16	45	36		
edwardsii (Gr. & Rob.), *Satyrium*	7				
goodsoni (Cl.), *Cyanophrys*	84	85			
grunus (Bdv.), *Habrodais*	28				
gryneus (Hbn.), *Mitoura*				67	
halesus (Cram.), *Atlides*	8				
helloides (Bvd.), *Epidemia*		52			
henrici (Gr. & Rob.), *Incisalia*			134		
hesseli Ra. & Zieg., *Mitoura*	88	89	125		
hyllus (Cram.), *Hyllolycaena*	15	53			
icarioides (Bdv.), *Icaricia*	22				
irus hadros Cook & Wats., *Incisalia*					128
isobeon Butl. & Dr., *Calycopis*	12		46,60		

Table 2. *Continued.*

SPECIES	**FIGURE NUMBER**				
	ENTIRE EGG	MICROPYLE	AEROPYLE	PLASTRON	OTHER
jada (Hew.), *Arawacus*	92	93			
knysna Trim., *Zizeeria*	26		44		
ladon (Cram.), *Celastrina*	106	107			122, 123,124
laeta (W.H.Edw.), *Erora*	104	105	139		
liparpos (Bdv. & LeC.), *Satyrium*	4				
lygdamus (Dbldy.), *Glaucopsyche*		114			
m-album (Bdv. & LeC.), *Parrhasius*	98	99	118		119, 120, 152
melinus (Hbd., *Strymon*	11	43			58,59
melissa (Edw.), *Lycaeides*	25			40	
metanira Hew., *Azulides*					121,156
minijas (Hbn.), *Eumaeus*	76	77	126		
miserabilis (Cl.), *Cyanophrys*			132		
nelsoni (Bdv.), *Mitoura*		113			
nivalis browni (dos Passos), *Epidemia*	17				33
ontario (W.H.Edw.) *Euristrymon*	94	95	148		145
ortygnus (Cram.), *Oenomaus*	80,141	81	137		
phlaeus (Linn.), *Lycaena*	14	54			
piasus (Bdv.), *Glaucopsyche*	21				
polingi (Bar. & McD.), *Euristrymon*	96	97			144
polios Cook & Wats., *Incisalia*					143
poodiae Br. & Faulk., *Habrodais*		64,65		66	
pseudofea (Morr.), *Brephidium*	27				
regalis (Cram.), *Evenus*	149		131		
saepiolus (Bdv.), *Plebejus*				38	
saepium (Bdv.), *Satyrium*	3		34		
sardonyx (Trim.), *Tylopaedia*	68	69			147
simaethis sarita (Skin.), *Chlorostrymon*		112,136			
siva (W.H.Edw.), *Mitoura*	86	87			
tarquinius (Fabr.), *Feniseca*	47			41	
thomasi Cl., *Hemiargus*	9		42		
titus (Fabr.), *Harkenclenus*	10,154		37		155
xami (Reak.), *Xamia*	90	91			129
yojoa (Reak.), *Strymon*	100	101	130		

Table 3. Index of SEM Photos of Lycaenidae Species in Other Works Prior to 1983 (not exhaustive).

SPECIES	**AUTHOR, DATE**	**FIGURE PUBLISHED**				
		ENTIRE EGG	MICRO-PYLE	AERO-PYLE	PLAS-TRON	OTHER
alboserícea (Miskin), *Nesolycaena*	Sands, 1971	X				
argiolus ladonides de l'Orza, *Celastrina*	Hara, 1981 in Takayanagi, K., 1981		X			
ataxus Dbldy. & Hew., *Chrysozephyrus*	Hara, 1979	X	X			
attila Brem., Antigius	Hara, 1979	X	X			
aurorinus Oberth., *Chrysozephyrus*	Hara, 1979	X	X			
bellargus (Rott.), *Lysandra*	Hinton, 1981	X	X	X	X	
butleri Fent., *Antigius*	Hara, 1979	X	X			
cassius theonus Lucas, *Leptotes*	Downey & Allyn, 1979	X	X			X
cognatus Staud., *Favonius*	Hara, 1979	X	X			
dorcas (Kirby), *Epidemia*	Ferris, 1977		X		X	X
dorcas (Kirby), *Epidemia*	Miller & Brown, 1979		X			
enoptes (Bdv.), *Euphilotes*	Shields, 1974					X
enthea Janson, *Araragi*	Hara, 1979	X	X			
evagoras (Don.), *Jalmenus*	Kitching, 1976	X	X	X		X
fujisana Mats., *Quercusia*	Hara, 1979	X	X			
helloides (Bdv.), *Epidemia*	Ferris, 1977				X	
helloides (Bdv.), *Epidemia*	Miller & Brown, 1979		X			

Table 3. *Continued.*

SPECIES	AUTHOR, DATE	FIGURE PUBLISHED				
		ENTIRE EGG	MICRO-PYLE	AERO-PYLE	PLAS-TRON	OTHER
hisamatsusanus Nag. & Ish., *Chrysozephyrus*	Hara, 1979	X	X			
icarus (Rott.), *Polyommatus*	Hinton, 1981		X			X
jebelia Nak., *Strymonida*	Nakamura, 1976a	X	X	X		
jezoensis Mats., *Favonius*	Hara, 1979	X	X			
jonasi Janson, *Shirozua*	Hara, 1979	X	X			
latifasciatus Shir. & Hay, *Favonius*	Hara, 1979	X	X			
lutea Hew., *Japonica*	Hara, 1979	X	X			
myrtale (Klug), *Nordmannia*	Nakamura, 1976b	X	X	X		X
orientalis Murr., *Favonius*	Hara, 1979	X	X			
orsedice Butl., *Iratsume*	Hara, 1979	X	X			
phlaeas (L.), *Lycaena*	Hinton, 1981	X	X		X	
phlaeas americana (Har.), *Lycaena*	Miller & Brown, 1979	X				
piasus (Bdv.), *Glaucopsyche*	Ferris & Brown, 1981	X				
pryeri Murray, *Artopoetes*	Hara, 1979	X	X			
raphaelis Oberth., *Coreana*	Hara, 1979	X	X			
saepestriata Hew., *Japonica*	Hara, 1979	X	X			
saphirinus Staud., *Favonius*	Hara, 1979	X	X			
signata Butl., *Wagimo*	Hara, 1979	X	X			
sinaicus Nak., *Pseudophilotes*	Nakamura,	X	X			X

Table 3. *Continued.*

SPECIES	AUTHOR, DATE	FIGURE PUBLISHED				
		ENTIRE EGG	MICROPYLE	AEROPYLE	PLASTRON	OTHER
smaragdinus Brem., *Chrysozephyrus*	Hara, 1979	X	X			
sonorensis (F. & F.), *Philotes*	Shields, 1973		X			X
speciosa (H. Edw.), *Philotiella*	Shields, 1974		X			
stygiana Butl., *Ussuriana*	Hara, 1979	X	X			
taxila Brem., *Neozephyrus*	Hara, 1979	X	X			
theon medocus (Fruhst.), *Hypochrysops*	Daniels, 1976	X				
ultramarinus Fixs., *Favonius*	Hara, 1979	X	X			
yuasai Shir., *Favonius*	Hara, 1979	X	X			