BULLETIN OF THE ALLYN MUSEUM

Published by
THE ALLYN MUSEUM OF ENTOMOLOGY
Sarasota, Florida

Number 55 27 September, 1979

MORPHOLOGY AND BIOLOGY OF THE IMMATURE STAGES OF LEPTOTES CASSIUS THEONUS (LUCAS) (LEPID.: LYCAENIDAE)

John C. Downey
Research Associate, Allyn Museum of Entomology, and Biology Department,
University of Northern Iowa, Cedar Falls, Iowa 50613
and
Arthur C. Allyn, Jr.
Director, Allyn Museum of Entomology

Breeding populations of the small blue butterfly, *Leptotes cassius* Cramer, occur commonly in Florida and Texas, and extend southward throughout Central and South America as far as Brazil. Five subspecies have been commonly accepted, with the trinomen *L. c. theonus* Lucas, originally described from Cuba, used for populations from the Greater Antilles and Florida. Brief aspects of the life history have been noted in Haskins (1933) for *L. c. theonus* in Florida, and by Turner (in Brown and Heineman, 1972) for the same entity in Jamaica, and by d'Almeida (1933) for *L. c. cassius* in Brazil. All three notes deal primarily with host plant records, length of time in each immature stage, and length and color of the larval instars. Except for possible inaccuracies or differences (they report five larval instars while we note only four in *theonus*) their work is not included in the notes and new data which follow.

Morphology of the Immature Stages

The Egg

Figure 24 is a micropylar view of the egg of *L. cassius* showing its typical lycaenid shape; round in upper view, echinoid in lateral view with the upper surface fairly level, though not as truncate as the lower surface. A series of light colored reticulations (ridges or ribs) covers the chorion, and knobbed, rounded prominences occur at the intersections of this network of ridges. The knobs are larger and higher toward the upper-lateral, and side areas, and give a very rough appearance to the egg surface in the manner of an echinoid test.

The micropylar area (Fig. 25) is only slightly depressed, perhaps exaggerated by the decreased height of the ribs forming the surrounding cells. The micropyle is (usually) an oblong pit or cavity, which may have several (3-4) tiny openings beneath the lip margins. The pit is defined by an encircling rosette or annulus of five cells, which, although petal-like in outline, are individually variable in size and shape. Most lycaenid species have three to five "petals" in the rosette, and intra-specific variability is not uncommon. The walls (=ribs, muri, or costules) of the cells are markedly variable in width and height along the margins of each petal, and appear to overlap one another at their junctures from the lateral areas toward the micropyle. That is, the ribs of lateral cells seem to overlie the ribs of cells positioned closer to the central axis of the egg as though they had originally been upright arches which fell inwardly against one another in a "domino-effect", leaving more lateral ribs shingled atop the inner ribs.

Cells in the annulus and in the immediately surrounding transition zone, have irregular shaped islands of "thicker" chorion, some of which take on the lighter, reflective properties (color) of the ribs. These islands are apparent in the scan photograph (Fig. **25**), but under a light microscope, they resemble discrete structures rather than an artifact of thickened chorion.

The transition zone averages two cells in diameter around the annulus. Nine cells of this zone border the petal cells forming the rosette. Because of the angulate nature of the cells, and the similar elevation and appearance of the inner walls of cells surrounding the transition zone, it is difficult to make an accurate measurement in this species. However, the average radius from the center of the micropyle to the outer margin of the transition zone is 0.025 mm. Thus the entire micropylar area, annulus and transition zone, averages .05 mm (see Fig. **25**).

In gross view, the ribs are positioned in a series of regular involute curves which can be traced diagonally from the transition zone of the micropylar region across the upper surface of the egg and down the sides. As they radiate from the central axis, the ribs gradually diverge as would the rays in a spiral nebula. Sixteen to eighteen such curves (depending on individual eggs) radiate in both clockwise and counterclockwise directions such that they intersect one another to form the cellular (honeycomb) meshwork of roughly diamond shaped cells. The egg in Figure **24** is slightly oblong as an aftermath of losing the symmetry of design of these radiating supportive ribs when they were originally laid down around the egg by the follicular tissue in the ovarioles of the female.

As noted above, there is a knobby prominence at each rib intersection, and these are largest and most obvious on the sides of the egg. The knobs become obsolescent at intersections near the transition zone, and they are also lacking on the ab-micropylar surface. The knobs lack aeropyles in *cassius*, though in many lycaenids there are openings at the apex of these projections.

Figure **26** indicates the chorionic sculpturing in typical cells outside of the micropylar area. The ribs are supported on trabeculae, short chorionic struts between which are larger aeropores. These openings lead to an inner chorionic meshwork forming an airspace as described in insect eggshells by Hinton (1970a, 1970b). This gas film within the chorion has a constant volume over an extensive surface area, and permits adequate respiration while retarding egg water loss. Apparently this gas film in *cassius* is also able to perform limited service as a plastron, since the eggs are capable of withstanding periodic wetting during rainstorms. In the laboratory survival of eggs was observed after complete coverage by rainwater for 72 hours. Since eclosion normally occurs in four days, this duration becomes more significant. Many butterfly eggs have a porous chorion, but lack plastronic respiration. At least part of the reason for this rests in the fact they have relatively few aeropyles and are unable to extract a sufficient amount of oxygen from this limited water-air interface. The number, size and position of the aeropyles thus contributes to the usefulness of this structure as a plastron when inundated.

In addition to the larger aeropores between the trabeculae, it may be noted in Figure **26** that the chorion of the interrib "cells" is also porous, but the openings are very tiny. Internally, the ribs themselves are not solid, but consist of a highly porous network of air spaces. Care must be taken in handling eggs and making slides, to preserve the external structure intact.

Measurements of 100 eggs indicated an average width of 0.46 mm and a range of 0.38 to 0.5 mm; egg height average was 0.24, range 0.22-0.26 mm. The micropyle area, including transitional cells outside the rosette, was 0.05 mm in diameter.

In the process of eclosion, the embryo is lying on its left side, and eats the shell in a clockwise direction. Rarely more than ⅓ of the upper surface is eaten, and often the micropylar region is left intact. The larva eats a hole sufficiently large to emerge, then dismounts from the egg immediately without additional feeding on the shell as characterized by some species. No correlation was noted between individuals in the shape and size of the emergence opening in the shell. Depending on external stimuli which sometimes affect or prolong inactive periods between alternate biting and chewing motions, the emergence can occur in as short a time as twenty minutes. With an average head width of 0.16 mm, and an egg external height averaging 0.26 mm, there is little extra room within the egg for lateral head movements for bringing the mandibles into contact with the upper egg surface. However, the cervical region is very flexible and both lateral and dorso-ventral head movements are accomplished with alacrity in spite of cramped quarters. The spinneret and projecting bristles of the lower head capsule are bent out of the way by the pressure necessary to bring the mandibles into contact with the internal surface of the chorion during the feeding necessary for eclosion.

Studies comparing the external egg sculpturing in long series of living eggs, including those of other lycaenid species such as *Strymon melinus* Hbn., indicate a great deal of individual variability. The eggs of *L. cassius* show consistent, albeit slight differences in linear dimensions, overall shape and geometric pattern, particularly the honeycomb pattern. Notation of this degree of variability is dependent not only on close observation under high magnification, but treating the characters individually, rather than collectively. Should this be done, it may very well be that no two eggs are externally alike in all particulars. On the other hand, there is an essential similarity that transcends these minor variations, and the immediate problem has been to attempt to identify the most stable features which may have value in taxonomy. In the past, descriptions of the micropyle of a species have implied, or it is often tacitly assumed, that this and other egg characters are unique and species specific. Even while studying and attempting to understand intra-population variability, perhaps more progress might be made at the interspecific level if students of egg variability would assume that all lycaenid eggs were similar, but with marked individual differences. Attempts to prove this might provide better data than the reverse.

The Larva

The terminology of the cranial sutures and sclerites has undergone considerable revision in the last several decades and we are here following the system of Hinton (1947) as modified in our earlier studies of lycaenids (Lawrence and Downey, 1966). The intention in the present study is to elucidate the morphology of *Leptotes*, and not to establish setal homologies or other evolutionary or taxonomic implications.

Width of the head capsule (Fig. **13**) provides a reliable index for determining the four larval instars in Florida populations of *Leptotes cassius theonus*. Other studies (d'Almeida, 1933 and Brown and Heineman, 1972) indicate five instars in *cassius* from Brazil and Jamaica. The marked difference in trunk size of early and late first instar larvae may have confused earlier observers, particularly if they confined several individuals to a container where cast skins could be detected. However, it is possible that in parts of its range, or with different foodplants (d'Almeida used both *Plumbago* and *Indigofera* for his larvae; Brown and Heineman report *Desmodium* was used) an additional instar is present. Sarasota populations use as a foodplant *Plumbago auriculata* Lam. (=*Plumbago capensis* Blumberg *auctt.*).

Head measurements averages (in mm) are: first instar, .161 (range .14 to .17); second instar, .258 (range .24 to .28); third instar, .402 (range .36 to .44) and fourth instar, .644 (range .60 to .70). Duration of instars (in sequence) is: 4.5 days (4 to 5); 2.2 (2 to 3); 3.4 (3 to 4); 3.5 (3 to 5); pre-pupal quiescent period 1.3 (1 to 2) days. These data were derived under laboratory conditions, 75° F temperature, 12 hour light-dark, and daily foodplant changes.

With data derived from larvae of 28 species of Lepidoptera, Dyar (1890) demonstrated the regular geometrical progression of head-capsule widths in successive instars. Although we know of many exceptions and that the ratio of growth is seldom exactly the same, the linear measurements of many cuticular structures are sufficiently regular that they serve Dyar's original purpose, to discover whether an instar has been overlooked. Richards (1949) pointed out the importance of taking into account the duration of time of instars in attempts to demonstrate uniformity of growth. Using Richards' findings in reverse, disparate growth between instars may indicate differences in elapsed time during these periods. Figure **14** indicates rather graphically that the smallest (percentage) growth rate of *Leptotes* occurs during the second instar, which likewise has the shortest duration (2+ days).

Figure **14** also indicates a minor amount of heterogonic growth, the significance of which has yet to be determined. Particularly marked in *Leptotes* larvae is the large increase in distance between the prothoracic puncture in the second instar larvae. These openings have been erroneously identified as lenticles (Lawrence and Downey, 1966) and appear with light microscopy to be small circles or punctures. Actually, they represent the circular opening out of which emerges a sensory seta (Fig. **21**, arrow) and although of relatively long length, the seta is difficult to observe. Other slight differences in growth rates during specific instars may be noted in Figure 14.

Antennae

The antennae (Fig. **1**, ant) are situated in a membranous area ventral and medial to the ocelli in a position between the anterior and posterior articulations of the mandibles. Ferris (1943) notes their lack of articulation with an antennal segment and that they arise from a basimandibular membrane, no longer within the boundaries of the sclerotized cranium. In *Leptotes*, as with most lycaenids, the antennae often remain "attached" to the mandibles, when the head capsule is teased into component parts preparatory to slide making.

There are three segments in the antenna. The basal segment arises from a membranous area, the antacoria. This first segment is about two-thirds the size of the second segment, and is devoid of setae. The second segment is the largest of the three segments, and contains several appendages including sensory structures, a moderately long seta and a very long seta (exceeding the length of the entire antennae), two conical sensory papillae and one small seta-like projection. A puncture also occurs on the second segment, which can be oriented with the base of the primary seta. All the structures are located at the distal end of the second segment, as is the third segment, which causes some difficulty in discerning exact points of origin on cursory examination. The third segment is very small and contains on its apex one small conical sensorial papilla and two small seta-like structures.

Dethier (1941) points out the similarity of the antennae of lepidopterous larvae. He (*loc. cit.* pl. 5, fig. 74) figures *Celastrina argiolus pseudargiolus* (Bdv. & LeC.) which Lawrence and Downey (1966, p. 72) indicate is very similar to *Everes comyntas* Godt., and which is nearly identical with *Leptotes cassius theonus.* The only difference appears to be in relative lengths of some of the setae.

Labrum

The labrum (Figs. **1**, **LA**, **8**) is a rectangular, flat plate in a mesal position, just ventral (in the hypognathous head capsule) to the fronto-clypeal region. Its "lower", albeit anterior, margin is notched mesally, and sclerotized tormae are present at the posterolateral angles. These processes extend transversely from the labrum towards the epipharynx and provide a pivot point at their distal margins. The latter permits a modest amount of up and down motions of the labrum with a greater arc at its anterior margins. Figure **29** is an oral view of the membranous epipharyngeal lining of the inner surface of the labrum, and also shows the roughened anterior lip with numerous pegged and sensory setae. Its shape and position, together with the piliferous epipharynx, probably helps to hold and manipulate food, particularly during the extension movements of the mandibles. The right mandible is shown in Figure **29**, but the left has been removed; the incisor surfaces of the two mandibles would ordinarily mesh during adduction on a line at right angles to the labral notch.

There are eight pairs of setae on the facial surface of the labrum of the second and later instars. Four of these pairs are mesial in location, and four pair line the anterior and anterio-lateral margin, and whose origins may appear more on the oral surface. Our descriptions will involve only the left half of the labrum, and Figure 8 indicates the location on mature larvae. M1 is the innermost of the mesial group and corresponds to the "i seta" of Forbes (1910). A puncture, M1a, occurs between M1 and M2, which lies posterior to all of the labral setae. Seta M3 is the longest of the group, anterior to M2 and about equidistant from M2 as M1. This seta is presumed to be homologous to Forbes "seta ii", and there is a tendency for the position of the seta to move posteriorly in later instars. M4 is the most lateral of the mesial group, usually on a line transecting M1 and M3. The lateral group consists of L1, just posterior of an extension of the M1-M3 line; L2 is the largest of the lateral series and is anterior to L1, more nearly on the margin of the labrum. L3 and L4 are on the anterior margin and directed mesad. They are the shortest of the labral setae and the more mesal L4 is often observed to be blunted as may be noted on Figure **29**. It is just lateral of the labral notch, where its functional proximity to L3 and the flattened, more malleable, epipharyngeal setae may be noted in the photo.

Six setae and a puncture are on the first instar labrum. M2 and M4 are missing, so that puncture M1a lies between and behind the two mesal setae present M1 and M3. All the marginal setae are present.

Mandible

The mandible (Figs. **27**, **28**) has seven (1st instar) or eight (subsequent instars) teeth, all but one of which are in the same distal plane. The most posterior incisors are associated with a round, prominent condyle on the posterior mesial edge which articulates with the head capsule at the prominence below and mesad of the antennal socket. From this fulcrum, a prominent ridge, or retinaculum, runs across the aboral surface of the mandible to the anterior margin. It is from a posterior, distal position on this ridge, that thė eighth incisor develops in the second instar, and becomes increasingly larger and more evident in the 3rd and 4th instars. The seventh incisor (numbered from anterior to posterior) may appear to be recurved, or hooked in oral view (see Fig. **27**), but this tooth and the eighth are associated with the retinacular ridge, and are suggestive of the basal molar parts observed both in Coleoptera and other butterfly larvae (see Lawrence and Downey, 1966, p. 73). The fourth instar mandible can be readily compared to a hand-glove, with the incisors serving as fingers, and the base of the palm, the retinaculum. The analogy would be more complete if the glove were to be markedly inflated, so that the opening (around the wrist) would be circular, rather than collapsed, and about four to five times the width of the base of the incisors (see Fig. **28**). One would have to imagine the knob-like condyle projecting up from the palm-ridge, on the little finger margin.

From the retinaculum, relatively obscure sclerotized crests run to the incisors so that the "palm" below the teeth is thrown into a series of folds (pleats) running in the same direction as the incisors. The distal points of the incisors vary somewhat in shape from individual to individual, and, particularly the anterior two teeth, may appear "worn", and not as sharpily pointed as the others. Some of this variability is dependent on angle of veiew, but little morphological or taxonomic value is ascribed to this slight incisor variability. The mandibles of most lycaenids appear remarkably similar.

Two setae, one long, and one short, are present on the posterio-lateral margin of the oral surface. Their bases are just about opposite of the mandibular condyle (see Fig. **27**) which may therefore be used for orientation in locating these setae.

Maxilla

The large membranous underlip consists of a united maxilla and labium. The former have prominent lateral lobes consisting of several parts, all of which may be noted on Figure 1. The largest lobe or basistipes (BS) is characterized by a markedly sclerotized ridge (R) defining its medial and distal margins. Proximally, the basistipes contacts a small, triangular, bent sclerite, the cardo (CAR). The dististipes is visible as a membranous region distal to the transverse ridge of the basistipes and proximal to the palpifer (PFR) which comprises the inner of four sclerotized segments forming the terminal parts of the maxillary palpus (MP). The sclerotized portion of the palpifer is not complete near the mesial line. A prominent seta projects forward from the distal margin of the palpiger near its mesial sclerotized terminus; the seta is twice as long as the width of the palpifer. Three setae arranged in a line are on the distal margins of the basistipes near the ridge and each is twice as long as the seta on the palpiger. The number and location of these setae on the stipes may be most useful in distinguishing Lycaenidae, since they appear to be more variable between, rather than within, species.

A seta is also present on the distal part of the third segment, from which surface also arises the mesial galea, and the remaining two segments of the palpus. It is equal or subequal in size to the palpiger seta. The terminal three sclerotized rings form the free portion of the maxillary palp and sensory structures, including punctures, may be visible on the lateral side of the outer two segments. A placode sensillum is on the small terminal palp, opposite the galea, and its apex has seven small sensory pegs. The galea has an indistinct proximal ventral puncture, and its terminus is marked by two rather prominent cylindrical lobes, each topped with a small apical peg. Opposite these lobes, on the mesial part of the galea, are two rather long seta-like laciniae. Three other small sensory structures, one-third to one-quarter the size of the laciniae, project outward from the tip of the galea; two are setaceous and one is peg-like.

Labium

The membranous submentum lies between the medial ridges of the stipes and bears two elongate setae. The entire labium appears very similar in all Lepidoptera, and is probably one of the most conservative of the mouthparts in evolution. No ontogenic differences were noted and the following is based on mature larvae. The mentum is distal to the submentum and appears to lie between the maxillary palps. Its sclerotized premental arms surround a more membranous lobe containing paired labial palps, a U-shaped chitinized palpiger (Fig. 7, PGR), and a mesial spinneret, projecting ventrad between the open arms of the palpiger.

The lobe of the prementum with the spinneret can be swung in and out, and constitutes the silk spinning apparatus which is constantly probing the substrate as the larva feeds and moves.

Spinneret

The spinneret (Fig. 7) is composed of the fusulus (FS) whose sides are tapering in *Leptotes,* and a wedge-shaped basal component, the fusuliger (FG). The latter might be more properly termed the external lobe of the fusulus, since in many lycaenids such as *Strymon melinus,* the fusuliger envelopes the entire length of the remaining fusulus, which becomes an internal lobe. The apex of the fusulus in this species shows no evidence of its bilateral origin, and the opening through which the silk will flow is not at right angles to the internal canal, but tapers toward the anterior.

Length measurements of the spinneret show considerable individual variability, but a ratio of labial palp to spinneret length indicates no significant differences between instars. The fusulus of mature larvae averages 0.08 mm, measured on the posterior aspect. The fusuliger extends about one-third the length of the fusulus (.033 mm) along its anterior margin.

The fusuliger has a small puncture anterio-laterally. A small seta .02 mm in length is on the distal margin of the mentum adjacent to the sclerotized palpiger. The first segment of the labial palp averages .023 mm; the second segment is small, much less sclerotized, and difficult to detect. Two setaceous sensory structures, one two-thirds the size of the other, are on the apex of the seond segment of the labial palp.

Hypopharynx

The hypopharynx (Fig. **7**, HP) extends (curves) dorsad from the mentum, thence caudad, forming the floor of the mouth, mesially called the lingula. It is membranous and the lobes of the paraglossae are only apparent in living larvae as slight lateral swellings, covered with slightly longer spiny projections. The hypopharynx, as well as the epipharynx, which forms the upper surface of the buccal cavity, are densely covered with short hairs projecting posteriorly (see Fig. **29**). They probably serve to mop up any moisture liberated in the plant tissues by the adduction of the mandibles. No significant differences were found between instars. Eventually the pattern, type and size of the projections on the lingula and paraglossae in mature larvae may prove of taxonomic value. However, the difficulty of making appropriate dissections and other technical details (duplicatability of slide preparations, dessication of SEM preparations, etc.) renders the hypopharynx less useful for descrimination at this time.

Epipharynx

As indicated above, the membranous epipharynx is attached to the oral surface of the labrum. In addition to the dense covering of small pile, directed backward toward the pharyngeal opening, three broad, blade-like appendages (setae?) are found on the anterio-lateral margins (see Fig. **29**). These structures have their apices directed toward the notch of the labrum, and *in situ*, project between the labrum above, and the opposed mandibles below. They probably assist in manipulation of food during mastication. The broad base of each seta and its somewhat pliable nature cannot be depicted in the photograph. With reflected light, the origin of each blade appears circular, and attests to a nearly similar placement in all instars. The marginal location of the epipharyngeal blades in *Leptotes* may be diagnostic.

Chaetotaxy of the Cranium

Primary setae and punctures are those which appear in first instar larvae; they remain, with only minor shifts in relative position through subsequent instars. Secondary setae and punctures appear in second or later instars, and may be relatively stable in position and occurrence, or may be individually variable and even asymmetrical in terms of the usual bilateral condition. Only primary setae and punctures are usually designated following the system of Hinton (1946), except where noted.

Homotypy of cranial setae in Lycaenidae is made difficult by their relatively small size, and by modifications induced by their ability to retract the head completely into the prothorax. This character is almost universal in the family, which therefore tends to have a hypognathous cranium with setae much reduced and clustered around the mouthparts. Setae and punctures on the vertex and lateral regions are much reduced, or absent, and even with the aid of scan electron microscopy, difficult to detect and to homologize. Those remaining no doubt function as proprioceptors but do not impede the withdrawal or extension of the smooth head capsule in its prothoracic fold.

For ease in the discussion of the setae below, the reader is asked to refer to Figures **1, 2, 3** and **9**. Setae and punctures of the left side only are discussed unless otherwise indicated.

Frontal and *Clypeal Setae* and *Punctures*: The fused frontoclypeal region forms an isosceles triangle defined by the adfrontal sutures laterally and anteriorly by the sclerotized margin of the clypeus adjacent to the membranous anteclypeus. Seta C1 is located at the lateral angle of the frontoclypeal triangle. Immediately mesad is a small structure resembling a puncture, Ca, not visible under SEM, but discernible with transmitted light in cleared specimens of all instars. Ca was first noted by Lawrence and Downey (1966) in *Everes comyntas*, but has not been reported by Hinton (1946) in other Lepidoptera. About half the length of C1 mesad, and also on the margin of the clypeus is another prominent seta, C2, which may be equal or subequal to C1 in length. An additional secondary seta is found between C2 and Ca in second and third instars, and fourth instars may have as many as three secondary setae in this same area. Dorsomesad of C2 is a puncture Fa, which is a prominent feature of the frons, but which, as with many punctures, is not as readily discernable with SEM photos as with light microscopy. No other punctures or setae are present on the frons in the first two larval instars, but third instars have a short seta, F1, dorsolateral of Fa, and fourth instars contain from one to five additional short setae above the frontal puncture and within the triangle. Individual variability may be noted in the number and position of these setae which may also be asymmetrically arranged on the frons.

Adfrontal Setae (AF): Lateral to and paralleling the adfrontal suture adnate to the frons, are three setae which are half the length of the clypeal setae. Closest to C1, and about the same level as Fa, is AF3; AF1 is halfway up the adfrontal suture about the level of F1; AF2 is closest to the junction of the lateral adfontal sutures. No aadfrontal puncture was noted.

Anterior Setae (A) *and Puncture* (Aa): Seta A1 is a long seta just above the antenna and close to the mandibular condyle (see Fig. 9). A1 is about ⅔ the length of O1, which is also above the antenna along with a cluster of secondary setae, particularly in later instars. A2 is caudolaterad of A1, and is about ½ the size of the latter. Puncture Aa is the same distance directly caudad of A2 that A2 is from A1. In mature larvae, small undesignated setae may obscure the relationship of these setae of the anterior group.

Ocellar Setae (O) *and Puncture* (Oa): O1 is the largest of the ocellar setae and is situated above the antenna on a line between A1 and ocellus III. See Figure 9 for visual reference to the ocellar and subocellar components. O2 is less than half the size of O1 and is just laterad and between ocellus III and IV. O3 is ⅔ the size of O1 and is as far posterior of ocellus I as seta O1 is anterior of ocellus III. Puncture Oa is just anterior and between ocellus III and IV, almost on line between O1 and O2. As with other setal groups, the ocellar area has several microsetae, ⅒ to ⅕ the size of O1, which may occur in mature larvae with some degree of consistency in size, position and primary direction (angle).

Subocellar Setae (SO) *and Puncture* (SOa): Seta SO2 is the longest of this group and is located just behind ocellus V. It is longer than O1 and approaches C1 in size. SO3 is closer to the margin of the dististipes, just posterior of a line transecting ocellus VI and SO2. SO1 is posterior to the antennal socket near the mandibular fulcral point, and is slightly larger than SO3. Between SO1 and SO3 in third and fourth instars are two or three undesignated setae. Puncture SOa is between and equidistant from SO1, SO3 and ocellus V, and is the only puncture present in the area.

Lateral (L) *and Genal* (G) *Setae and Punctures* (Ga): Seta L1 is about the size of the adfrontal sutures, dorsad of the ocellar region, and about on a line drawn between ocellus III and AF1 (see Figs. 2, 9). Puncture La is thought to be the small opening halfway between L1 and AF3, the most anterior of the adrontal setae. The genal seta and puncture is reduced and near the ventral notch of the head capsule, almost as far posterior as the lateral arm of the cervical sclerite. This can be noticed on Figure 3; the seta G1 is anterior to the adjacent puncture Ga. A second genal seta was not observed, though many lepidoptera have both G1 and G2.

Posterior Setae (P) *and Puncture* (Pa): Only one posterior seta was detected with the aid of the SEM. This much reduced P1 is directly posterior of L1 (see Fig. 2) and equidistant from AF2. Puncture Pa is located on a straight line between P1 and L1, and about half the distance between. P2 and a possible second puncture were not observed.

Vertex Setae (V) *and Puncture* (Va): The setae of the vertex, as were the gena and posterior groups, are extremely reduced and difficult to locate. Their size has been greatly exaggerated on Figures 2 and 3 in order to indicate their occurrence and location on the head capsule. Since they are frequently covered by the prothoracic head fold, they probably serve as proprioceptors. With the aid of the scanning microscope, they can be observed to project no more than their own width above the surface of the surrounding integument. V1 can be noted on Figure 2, as the first seta posterior of AF2. Puncture Va is posterior of V1 and slightly laterad, making it the most posterior puncture of the head capsule on the ventral slope of the vertex. V2 is lateral to Va, and about the same distance from the puncture as it is from V1. V3 is the most ventral and lateral of the vertex group and is located on a line extended through V1 and V2.

Chaetotaxy of the body

Except for a pair of cervical sclerites (Fig. **1**, CS), the neck is membranous and devoid of setae. It is capable of being extended at least 1.5 times the length of the head capsule (more in mature larvae), and can be retracted within a ventral pocket of the prothorax to such an extent the head is not visible externally.

Five types of setae were found on first instar larvae: 1.) major setae, which are rather long, finely serrate setae with pointed tips; these are borne on a chalaza, a pimple-like swelling or tubercle, which develops 5 to 7 lateral points in second and subsequent stages giving the base a strong stellate appearance (Fig. **16**); generally, the longer the seta the longer and larger the chalaza, and the more likely it is that a second papilla, or ring-like nipple can be detected at the base of the seta (see Figs. **15, 19**); 2.) major setae, same as in 1) above, except with varied apices; long and very slender (Fig. **17**) or capitate; 3.) microscopic setae, very small proprioceptors, distinguished from 1) and 2) above, mostly on the basis of size and position where they can be touched by opposing surfaces of the body in accomplishing their function; at present, a major obstacle to the taxonomic use of microscopic setae is the lack of studies based on SEM; light microscopy is usually insufficient to detect all these setae in first instar larvae; 4.) pegged setae, relatively short, club-shaped (clavate) structures (Fig. **15**) with serrate or grainy-textured surfaces and 5.) spiculate setae (Fig. **19**) with greatly enlarged setacious branches giving them hydroid, or tree-like, distal branching. Only the spiculate setae, occurring near the honey gland, usually do not develop stellate chalaza after the second instar, although some pegged setae (see Fig. **15**) also may retain a smooth, nipple-like tubercle, or have only one to several pointed prominences on the base.

One other structure of the integument should be mentioned in dealing with larval chaetotaxy. The term lenticles has been used (Lawrence and Downey, 1966) for tubercles which lack distal setae. In fact, most of these are either sensory or glandular structures (Fig. **18**) which are not derived from setal origins in the integument. The term may also apply to openings or punctations which, particularly with a light microscope, have the appearance of a small, light, circular (or lens shape) structure. Many of these are associated with, or adjacent to, particular setae, or are in nearly identical regions on different species of larvae, where they can be used for diagnostic purposes, particularly in first instar larvae. Older larval stages may have numerous lenticles in varying positions (sometimes even asymmetrically placed on the body) and their taxonomic utility remains more obscure or even becomes questionable. Glandular (?) lenticles, not unlike the setae, may develop stellate points (see Figs. **18, 20, 22**) in second and older stages, and the porous nature of their upper surfaces may not be visible except under scan microscopy (see Allyn's and Malicky's organs below).

In describing the specific setae and lenticles on each segment of the first instar larvae, reference should be made to Figure **4**, which also calls attention to the near equal width (except for prothorax and fused abdominal segments 9 and 10) and height of the body segments. Setal widths, particularly of the microscopic setae, are necessarily exaggerated in the schematic. Only structures on the left side of each segment, from mid-dorsal to mid-ventral, will be described following the terminology of Hinton (1946, as modified 1956). This procedure facilitates comparison of *Leptotes* with other described Lepidoptera, even though introducing the added complexity of chaetotactic homology.

Prothorax: The prothoracic shield (Figs. 4, 5) of first instar larvae is not markedly sclerotized as it is in other lycaenids, for example the hairstreaks, and is distinctive mostly through the clustering of setal sockets and lenticles on its surface. In dorsal outline it is shaped roughly like an inverted teacup, though its caudal margin is slightly convex. Its anterior-posterior axis is about two-thirds its lateral width. Width average is 0.13 mm (head capsule = 0.176 mm) but the lack of sclerotized margins makes precise measurements difficult. A major seta, SD1, is just laterad of the mesal region near the posterior margin of the shield. Two slightly smaller setae, SD2 and D2 are arranged with equidistant bases on a tolerably straight line projecting cephalo-mesad from SD1. D2 is thus the closest seta to the midline of the shield on its frontal margin. Posterior and lateral to D2 is a lenticle, which approaches the size of the prothoracic spiracle. Scan photography shows this lenticle to have a sieve-plate, not unlike those on the anal plate (see Fig. 22). The lenticle is equidistant from D2 and SD2 and is thus anterior-laterad of the latter.

Lateral and slightly anterior of the large seta SD1 is a very fine, capitate, sensory seta, XD2, which emerges from a circular opening (see Fig. 21). The latter has the appearance of a puncture using transmitted light. XD2 is responsive to air currents and other physical disturbances, particularly in mature larvae, and can be observed vibrating with almost a trembling motion in pre-pupal stages. The seta is thinner than other primary seta and is not as visible. It is distinct from other prothoracic setae in having a slight club at the tip.

On the anterior and lateral margins of the prothorax are four setae whose bases describe a diagonal line roughly parallel to the anterior-lateral margins of the shield. The most mesial of the four setae is the shortest, MD1, which is approximatley as long as D2. The base of MD1 is slightly mesad of an extended line dissecting the bases of SD2 and XD1. MSD1 is a slightly larger seta just posterio-laterad of this same line on the anterior margin of the prothorax. Setae MSD2 and L1 are the remaining two setae of this diagonal group of four, and their bases are situated at slightly increasing distances from one another. MSD1, MSD2 and L1 are approximately equal in size and together with the setae of the prothoracic shield project forward from the anterior and anterio-laterad margins of the prothorax, where they may serve a tactile function as they are the first structures to encounter objects as the larva moves forward.

Two other setae, L2 and L3, together with a lenticle, describe a second diagonal line on the lateral margins of the prothorax just anterior to the spiracle. The prothoracic spiracle is relatively small in *cassius*, its diameter is hardly twice as wide as the bases of the primary setae and only slightly larger than the lenticle which is just anterior and slightly dorsad from the spiracle.

Beneath the sublateral body fold are two setae, SV1 and SV2, which are not obvious, but whose position is indicated in Figure 4. Occasionally a third seta has been observed in this area, with the three arranged in a horizontal line, bases equidistant.

Mesothorax: Four dorsal and subdorsal setae plus a lenticle are present. MD1 is the most anterior and mesial of these setae; it projects forward just posterior to SD1 of the prothoracic shield. This same seta is reduced to a microseta on the remaining thoracic and abdominal segments. Directly posterior of MD1 is D1, the largest of the mesothorax setae. It also has the most prominant base or tubercle. D2 is ventral and slightly posterior of D1 and is about half to two-thirds as long. It projects almost straight caudally, while D1 arches upwards and recurves in a more gentle angle toward the rear. The subdorsal lenticle is prominent ventral and anterior to D2 and slightly closer to the latter than it is to D1. Just ventral to the lenticle on the mesothorax is a seta which projects anteriorly and is here designated SD1. It occurs on the metathorax in a more lateral position, and on abdominal segments it is dorsal and anterior of the spiracles. It may be slightly pegged or flattened distally.

The lateral cluster of four setae on this segment appear just behind and above the prothoracic spiracle. While their homologies are subject to question, we designate the most anterior-dorsal and smallest as MSD2, which along with L1, is rather more variable in position that the other setae. L1 is ventral and posterior to MSD2 and L2 and L3 are equidistant and aligned laterally. The latter three setae are of nearly equal size. Two subventral setae, SV1 and SV2, are based about one half the distance between the lateral setae and the mesothoracic leg.

Metathorax: MD1, D1 and D2 are present and the subdorsal lenticle is more lateral in position than on the mesothorax being almost twice its distance from D1. SD1 is also further lateral, about the same distance below the lenticle as the latter is from D1. MD1 is reduced to such an extent it is not easily observed, and would appear to serve as a proprioceptor on the anterior margin of the segment near its intersegmental fold.

MSD2, L1, L2 and L3 are present as a constellation of lateral setae in relatively the same position as on the mesothorax. They are smaller, however, and their bases appear to be only half as large as those on anterior segments. SV1 and SV2 are in a horizontal line, approximately half the distance between the lateral setae and the thoracic leg.

Abdomen: first segment: MD1, reduced to a microseta, D1, D2 and SD1 are present. The subdorsal lenticle is in its normal position and ventral and posterior to it is the supra-spiracular lenticle, which is less than ½ the size of the subdorsal one. Seta MSD2 is ventral and posterior to the supra-spiracular lenticle, and its short pegged nature is difficult to observe. Its base is posterior and slightly dorsad of SD1.

The first abdominal spiracle is further laterad, near the middle of the segment. A lateral lenticle is unique to this segment and is positioned anterio-ventrad of the spiracle, just dorsal to L2. The lateral setae are arranged with two in a horizontal line, L2 anterior to L3, and one seta, L1, placed dorsad and posterior to the first two. Their bases are equidistant, and L3 is the longest of the group, projecting at right angles to the body. L2 is ½ to ⅔ the length of L3, and L1 is subequal to L2 and projects away from the body at a slight posterior angle. Only one subventral seta, SV1, is present.

Second segment: All setae are present on this segment as on segment one, and in the same relative positions. The subdorsal and supra-spiracular lenticle as well as the spiracle are in the same relative position. There is no lateral lenticle.

Third to sixth segment: MD1, D1, D2, SD1, MSD2, L2, L3, L1, SV1 and SV2 are present in their normal positions. The subdorsal lenticle is in its normal position, except for segment 6 where it moves considerably posterior, to a position on a line drawn between D1 and D2. The supra-spiracular lenticle decreases in size toward segment six.

Laterally, on each proleg is a grouping of from 4 to 6 microsetae, the largest no more than half the length of SV2, and at most about the size of the crochets. These are arranged in slightly offset horizontal series around the fleshy proleg with their setae pointed downward. Very often the bases of the setae appear tilted ventrally, and it is the base of the seta rather than shaft, which establish setal direction and angle. Scan photographs at low magnifications indicate that most of these could serve as proprioceptors, since they contact opposing surfaces, and/or the substrate with suitable movements of the prolegs. Numbers of these microseta show individual variation; proleg 6 (segment 6) has three or four microsetae while prolegs 3, 4 and 5 may have four or five setae, some based on the anterio-mesial surface.

Seventh segment: The subdorsal lenticle is lateral to D1, almost touching its base. D2 and MSD2 are absent so that only SD1 and the supraspiracular lenticle are between the subdorsal lenticle and the spiracle. The microseta MD1 can be distinguished only with care. The lateral setae, L2, L3 and L1 are in their normal positions, with the longest of the group, L3, pointed slightly more toward the rear than it does on more anterior segments where it extends at right angles to the body. This same tendency is noted in all the tactile setae in 7 and 8 as the body segments gradually taper toward the rounded posterior segments. Setae on the latter segments point rearward so that when the larvae is viewed from above there is an equal and symmetrical arrangement of tactile setae pointing outward from the main axis of the body in all directions.

A prominent sublateral lenticle occurs ventral to L2. Its size approaches that of a spiracle. The lenticle and a single seta, SV2, which is posterior and ventral, are the only structures on the sublateral surface of segment 7.

Eighth segment: Only D1 of the dorsal and subdorsal setae persists. The subventral lenticle abuts the base of D1 and is smaller than on anterior segments so that it is easily overlooked. SD1 and the supra-spiracularlenticle are absent. The spiracle occurs dorsad, so it is nearly in line with the bases of the supra-spiracular setae (SD1, MSD2) of anterior segments. L2, L3 and L1 are prominent in their normal position adjacent to the lateral fold. Only one subventral seta can be noted which is tentatively designated SV2.

Ninth, tenth segment and anal shield: Intersegmental clefts or divisions are not apparent and the coalesence of segments is externally manifest mainly by the number of setae, particularly dorsally. A small mid-dorsal anal shield is present; it is devoid of setae, and its degree of sclerotization is similar to surrounding tissue so that care must be taken to distinguish it. Very likely it has some proprioceptors or other sense organs but these cannot be resolved externally. Later instars contain prominent lenticular organs as shown in Figure 22, which have a porous, sieve-like upper surface. Allyn first noticed these organs lining the posterior margins of the anal shield in third and fourth stage larvae, and Downey subsequently designated them Allyn's organs to distinguish them by position and general appearance from similar structures adjacent to the mouth of the honey gland. The latter were described and figured by Malicky (1970) who provided evidence of their pheromonal nature. Malicky's organs and Allyn's organs may be of similar integumental origin and function, but their occurrence on different body areas leads us to speculate a diverse function. With scan microscopy similar lenticle-like structures to Allyn's organs were observed on various parts of the body, usually singly, and not infrequently asymmetrically arranged in mature larvae. Perhaps the slight sclerotized thickenings and roughened surface of the anal shield in *cassius* represents the precursors of Allyn's organs, which may develop in latter instars.

Between the anal shield and the lateral setae, near the lateral fold, is a single sclerotized punctation. It is anterior and lateral of the anal shield in a position corresponding to a ninth abdominal spiracle, if such would have developed. L2, L3 and L1 of segment nine are nearly in anterior-posterior alignment on the margin of the lateral fold, and L3 may be recognized by its larger size. Medial to L1 and on the ventral side of the fold is L2 of segment 10. L3 of segment 10 is very large, projecting directly posteriorly, its base nearly in lateral alignment with D1 of segment 10 which also projects rearward. L1 of segment 10 can be distinguished in dorsal aspect as the smaller seta mesad of the large D1, but with its base on the ventral part of the body fold. L2 and L1 are thus just above the anal slit, and between them is a dense covering of micropile which also occurs on the mesial surface of the sub-anal fold mesad of SV2.

Dorsally, on the posterior aspect of the anal proleg, SV1 and SV2 of segment 10 project backward. At least two other microsetae which may function as proprioceptors may occur beneath and lateral to SV1 and SV2.

Protective Nature of the Stellate-based Seta: Figure 16 shows the seta which is characteristic of second and later instars. Particularly the fourth instar larva is covered by a layer of these short stout setae. Furthermore, the six to seven stellate points on the bases add to the apparent density as they become long and narrow and recurved distally away from the body in the manner of adjacent setae. Thus, each seta gives the appearance of a clump or cluster of seven or eight setae, rather than just one with an ornate five to seven fingered base. The tapering ends of the stellate bases permit them to be interdigitated to a remarkable degree. That is, when a segment is contracted, or a portion of the larvae is pulled inward, the bases of individual setae are brought closer to one another, and the stellate fingers of adjacent setae overlap. This interlocking maximizes the protective value of the setae, and while unconfirmed (in part because of the small size of the structures involved) they could conceivably trap, block or mechanically deter small predators from access to the integument beneath. Depending on the strength of the larval contractions which cause the setal bases to interlock, one could postulate that they could macerate small predators (mites) in the manner of overlapping incisors of canids. While the latter extreme is speculative and probably did not play a part in the evolutionary strategy of the stellate setae, it seems plausible that they did evolve with a protective function. Even the legs and mandibles of friendly attendant ants never gain complete access to the integumentary surface, but as the ants move astride the larva, or stand on the dorsum with the head at the honey-gland site, the tarsal segments contact only the elevated portions of the stellate setae. Further, the displacement of only one of these projecting elements, the central seta, results in tactile input to the larvae; the remaining stellate elements thus serve a damping effect reducing tarsal contact of the ant on adjacent setae.

A protective inference may also be made from the clustering of the stellate-based setae around the evertible tentacles and the honey-gland site, and to a more limited extent, around the spiracles. At these sites, there are twice as many setae per unit area of integument, arranged in a narrow band around the organ involved. The increased numbers in this position might be derived from an ontogenic displacement by the intrusion of the organ. Thus, one can imagine that there might have been a certain number of these setae per unit area of integument, and when a new organ developed, even though it may have stemmed from the development of a pre-existing structure, it may have displaced the setae, evolutionarily "pushing" them closer to other non-displaced setae such that setal density increased in a band encircling the organ. As may be noted in their present position, the setae afford a greater mechanical protection, and an increased tactile facility, to the marginal areas of the more delicate tissues.

Crochets on Prolegs

The family Lycaenidae is characterized by larval crochets being an interrupted mesoseries; that is, the hooklets occur on the mesial surface of each proleg with a hiatus or gap separating them into an anterior and a posterior cluster. A flesh lobe, or spatula, projects from the disto-mesial region of the proleg toward this gap, and is particularly noticeable as a "pad" in mature larvae. *L. cassius* larvae conform to this pattern and very likely parallel other family members in the following ontogenic differences, though insufficient comparative data are at hand for other species. First and second stage larva have crochets of one length (= uniordinal) and are uniserial, arising from a single line as they do in all larval stages. Third stage larvae are biordinal and mature larvae are triordinal, adjacent crochets never being of the same length. If the number of crochets is an odd number, there is a tendency for the longer hooklets to have the larger number; thus in 3rd stage larvae with a cluster of five crochets, typically there would be three long and two short hooklets. While some individual variability in the number of crochets on each proleg has been observed, the ventral prolegs on segments 3 to 6 have similar numbers, while the anal proleg may diverge from this constancy.

The following shows the number of crochets, on the prolegs of appropriately numbered abdominal segments expressed as a ratio of the anterior cluster to posterior cluster. Only the third abdominal and the tenth (anal) segment are given: 1st stage, 3 $^{2}/_{2}$, -10 $^{1}/_{2}$; 2nd stage, 3 $^{3}/_{3}$, -10 $^{4}/_{3}$; 3rd stage, 3 $^{5}/_{5}$, -10 $^{6}/_{6}$; 4th stage, 3 $^{13}/_{11}$, -10 $^{13}/_{11}$. Crochet numbers between instars are constant and thus distinguish these stages in *cassius* (4, 6, 10, 24).

Honey-gland and Eversible Tentacles

The external mouth of the "honey-gland" is a slit-like opening with a transverse axis on the dorsum of the seventh abdominal segment. It is found in second and subsequent instars, though the attention of attendant ants suggests that it is mostly functional in the final two instars. Clusters of small epidermal glandular organs with perforated lenticular surfaces (see Figs. **19**, **20**) occur on the inner margins of the honey-gland. The anatomy and histology of the honey-gland in the Lycaenidae was described by Newcomer (1912) and Ehrhardt (1914) and the histology of the perforated cupolas was described and their functional significance discussed by Malicky (1970).

Newcomer's gland is not present in all species of lycaenid larvae, but Malicky's cupolas may be a family character.

Paired eversible cylindrical organs occur on the eighth abdominal segment posterio-laterad of the spiracles. They are usually not everted, and in this case their position may be determined by the circular clustering of stellate setae which surround the area. The circular membranous area out of which they emerge is only slightly larger than the spiracle on the same segment. Twenty-seven to 30 spiculate setae are inserted distally on the everted tentacle, so that in the expanded state they radiate in all directions from the terminal axis of the tentacle. The relative size of the tentacular column is shown graphically in Figure **6**, and Figure **23** shows a partially everted tentacle with setae arranged in a sheave as they are in the contracted position. In operation, the tentacles are rapidly fluttered in and out, singly or together, and the sudden "bursting" of the radiating setae as they reach the fully extended position is visually pronounced. Attendant ants, even those inbibing liquid at Newcomer's gland, will quickly dart toward the tentacles, seemingly annoyed by either their movement, or by chemicals (irritants?) given off by the setae. While the function of the tentacles has been debated by many authors as having either an attracting or repelling function, in *cassius* at least, they appear to agitate ants within the radius of a centimeter.

Freeze-drying mature larvae, or dispatching them in hot fluid preservatives, will cause partial or complete eversion of the tentacles and the throat area of the honey-gland. When this occurs in *cassius,* Malicky's glands with their perforated cupolas can be noticed arranged in a hemicircle around the posterior and anterior-lateral inner margins of the lips of the honey-gland. In mature larvae from 25 to 30 glands line the inner posterior margin, in a rather narrow band, but randomly scattered so that they lack regularity or alignment (rows). Seven to nine of the glands are on each anterior-lateral margin, but the middle third of the anterior margin is devoid of these structures. Third stage larvae have five to seven glands on each posterio-lateral margin of the honey-gland site. The exudate gland in 2nd stage larva is small, and only four of Malicky's glands plus two stellate-based setae are on the posterior margin.

Spiracles

The outside diameters of spiracles were measured from anterior to posterior on individual larvae as well as in different instars. In spite of rather broad individual differences in diameter, no constant or significant differences were noted. The geometric progression of spiracular diameter is indicated in Figure **14**, and the actual measurements, with ranges indicated in parentheses, for each instar in order are: 10.5μ(8.0-118); 19.7μ(19.0-20.0); 35.6μ(30.7-40.0); and 82.0μ(78.0-85.0). Thus, the spiracles of the first instar larvae are proportionately much smaller than structures of the head capsule (labrum, frons) compared to their ultimate size in the fourth instar larvae.

Surface of Integument

The surface sculpturing of the larvae is highly suggestive of the general pattern found in both the pupal skin and the surface sculpturing of the egg. This may be noticed beneath the setae in Figure **15**. All of these structures have a series of elevated ridges connected to one another at elevated prominences. From these junctions a circular pimple erupts; in the egg it may be an elongated knob with an aeropyle; on the pupae it may be a chordatonal-like organ. In the larve the "eruption" consists of small round bumps protruding dorsally about one fourth as high as the circumference of the circle at the rib junction. They resemble piles of shot, or oranges (partially melted and coalesced) in a basket. Other areas of the integument, or the intermediate regions between ribs, may have irregular folds, creases or crenulations (fee Fig. **16**) which may contribute to the physical colors reflected from the surface of the larvae.

The Pupa

As noted by Haskins (1933, p. 155) there is a general resemblance of *theonus* pupa to *Everes comyntas.* Both are long and relatively slender and have sparse but prominent setae which are reduced on the wing areas. The sclerites and setal pattern are shown in Figures **10-12**.

Average length measurements (mm) for 25 males and 25 females are: body 7.3 (range 6.65 to 8.8); width 2.98 (2.66 to 3.52) and height at highest point (which is usually a hump on the mesothorax) 2.01 (2.26 to 2.88).

The vertex of the head is a small triangular sclerite just anterior to the prothorax and posterior and mesial of the bases of the antennae. It is devoid of setae and lenticles. In cast pupal skins it remains attached to the prothorax. The small size of the vertex, and its anterior position, preclude its being shown in the figures.

In some individual pupa a scar of Newcomer's gland is visible on the seventh abdominal segment. It is dorsal and posterior on the segment. It is most easily observed in cast pupal skins preserved in alcohol, where transmitted light through the pupal skin shows color differences. Evertible tentacle scars were not observed.

L. cassius pupae stridulate, as do most lycaenids, and the ultrastructure of the organs involved have been described elsewhere (Downey and Allyn, 1973) along with an analysis of the sounds produced (Downey and Allyn, 1978). The stridulatory devices of the file and scraper type are located in the dorsal intersegmental cleft between abdominal segments 5 and 6. A posterior series of tooth-like structures (file) are grated against an anterior roughened surface (stridulating plate) to produce the tiny creaking or chirping noises. An individual pupa must be placed in a vial or other resonating chamber in order to insure audibility to the human ear. Three types of sounds (primary, secondary and tertiary signals) are produced which are distinguished by differences in amplitude as well as other criteria. It is thought that these noises, while random in nature, coupled with the trembling or vibratory movements involved, serve a predator deterrent function, although the possibility of communication signals with ants cannot be ruled out completely.

Duration of the pupal stage averaged 7.5 days. Originally we noted a slight difference between the sexes as indicated in Table 1. This was confirmed in subsequent rearings and compilation of data from different years and months. We cannot explain why the females average four to five hours less than males in the pupa stage. June pupae of both sexes differ significantly from August specimens in that their pupal period is 1.5 days shorter. Since the specimens were reared under the same conditions of temperature, moisture and light, these differences were assumed to be induced by food plant differences, or conditions to which the earlier instars were subjected in the field, rather than environmental influences on the pupal stage itself.

YEAR	MONTH	SEX	DAYS DURATION		N		RANGE
1975	Aug.	♂	8.3	-	13	-	7-9
		♀	-	8.1	-	15	7-9
1976	June	♂	6.8	-	20	-	6-7
		♀	-	6.7	-	18	6-8
1977	July	♂	7.7	-	34	-	7-9
		♀	-	7.5	-	21	7-8
Total			7.6	7.4	67	54	6-9

Table 1. Duration of pupal period in Sarasota, Florida populations of *Leptotes cassius theonus.* All specimens were from field collected 3rd and 4th instar larvae, reared at 75 °F, 12 hr. light regime, and pupated during the month shown.

Notes on Biology

Adults trapped on host plant

Ovipositing females occasionally brush against the sticky knobbed hairs on the calyx of plumbago buds and become temporarily stuck to the plant. Vigorous wing beating usually enables the adult to escape, most often with missing scales or with distal pieces of the wing torn away. Escaped females with wings thus damaged are apparently not deterred from the oviposition responses. We have observed such a female laying an egg on a bud within one minute of a temporary entrapment (30 second duration). Occasionally, a dead and battered female is found stuck to the buds; a number of these have been assumed to be due solely to the adhesive properties of the plant, rather than to secondary entrapment after spiders and other predators have originally captured and killed the butterfly.

Friendly ants, as well as predators and parasites, are also trapped on the sticky knobbed hairs on the basal portions (calyx) of the flowers of Plumbago. Clark & Dickson (1971: 4, 65) note the same "protective" feature of the host plant in a closely related lycaenid genus in Africa, *Syntarucus* (both *S. telicanus* (Lang) and *S. brevidentatus* Tite).

Pre-imaginal parasites, predators

Braconid parasites are usually not apparent in host larvae until the last two weeks in July. At that time perhaps 1% of the third and fourth instar larva will appear to be "listless" and stretched out or distended in the longitudinal axis. A fourth instar larva may appear to be ready to undergo the pupal molt. If they are delayed in doing this for over two days (after their last meanderings), and if they appear light in color (almost off white) it may be assumed that they contain an ichneumonid parasite. Within a day or two, the anterior thoracic segments turn brownish, while the prothoracic sheld has a whitish cast which is distinctive against the brown surrounding. From such host larvae the parasites will emerge (through a dorso-posterior exit hole) in eight or nine days. The parasites would appear to have almost synchronous emergence in the few instances judged of adequate sample size.

The braconid *Pelecystoma sp.* appears to be single brooded - but has multiple hosts. While empirical data is lacking on differences in the voltinism and phenologic patterns between the hymenopteran and *Leptotes*, it is suggested that the other hosts which share this parasite (such as *Strymon melinus* on *Hibiscus* in the Sarasota region but not on *Plumbago*) may have an optimum overlap of vulnerable larval stages during the mid-July period. This might account for the apparent single generation of parasite during this relatively short time span.

Three species of *Pelecystoma* have been reported from Florida: *P discoideum* (Cresson) which ranges northward into Michigan, obviously on hosts other than *Leptotes; P. eupoeyeae* Ashmead, endemic to florida on the host *Alarodia slossoniae** (Pack.); and *P. harrisinae* (Ashmead) a wide-ranging wasp known from as far north as Pennsylvania and Virginia south to Mexico and Cuba and associated with the host *Harrisina americana* (Guer.). These braconid wasps belong to the subfamily Rogadinae, which are mostly parasites of Lepidoptera.

Predacious Hymenoptera of several species are often observed patroling the stems of plumbago. Casual observations indicate they are not as successful as the investigators in locating lycaenid larvae on the same bushes, since we continuously find all instars of the butterfly and have rarely witnessed a kill by the wasps, in spite of hours of watching for predation. The latter includes exposing laboratory larvae on the blossoms to greatly increase their density in order to attract more predators. *Polistes metricus* Say has been observed locating and dispatching a mature larvae of *Leptotes*, and in this instance, had to fly four times carrying the prey during the mastication and

---

*Notodontidae *ex Populus* (3 species) and *Rhizophora* feeding in order to protect the food from other hymenopterous competitors.

The tachinid fly, *Eusisyropa boarmiae* (Coq.), emerged from *cassius* pupae of July populations. The resulting adult flies were very undersized specimens which typically result from relatively small hosts. The tachinid parasitizes several lepidopteran hosts. Only 1.8% of field collected larvae had these parasites, but the rate of parasitism is apparently higher in July populations.

Seventeen percent of the eggs collected in early June (66 of 393) were parasitized by *Trichogramma minutum* Riley (Trichogrammatidae), a very common egg parasite of almost any insect. Presumably because of the small size of the host egg, hyperparasitism was not detected: one wasp emerged from each parasitized egg. Parasites emerged up to 11 days after egg collections. Rate of egg parasitism decreased in July and August populations.

Crab spiders (Thomisidae) are often observed concealed on blossoms of plumbago, and we have collected *Misumenops celer* (Hentz) feeding on adult *Leptotes.* Other species of *Misumenops* (*M. bellulus* (Banks)) have also been collected on the same host plants and presumably also prey on the butterflies. Fales and Jennings (1977) record adults of 12 butterfly species (mostly skippers but including also some lycaenids) as prey of *Misumenops,* from this it is inferred that members of the spider genus habitually prey on many species of butterflies over a wide geographic range. If butterflies of particular species are attracted to one type of host plant, as *Leptotes cassius* is to plumbago, a higher percentage of these will fall victim of ambush by crab spiders oncealed in these particular flowers. Ovipositing females of *cassius* are also statistically more likely to be taken in this manner, as males usually do not alight on the plant surface.

Webs of *Achaeranea* sp., particularly the immature stages, are very common on the plumbago, and while we have not observed feeding directly, are among the hazards encountered by ovipositing females as they habitually fly between blossoms under the outermost canopy of blossoms and leaves in search of oviposition sites. Other spider species are also to be noted on plumbago, but their densities are much less than the above kinds, and presumably therefore, may not be individually as significant in lowering the population density of the adult butterfly.

Cannibalism

As is common in the Lycaenidae, laboratory reared larvae of *L. cassius* will eat other larvae or pupae under crowded conditions or when insufficient or dried foodplant is all that is available. Immotile premolt larvae or pupae are the victims of this cannibalism. Motile larvae are apparently able to avoid being cannibalized, although dark spots apparently due to salivary juices, occur on the dorsal surface of many larvae. As with cannibalism, these "salivary tracings" are found with increased frequency when many larvae are confined to one vial, or when insufficient foodplant induces the stress of hunger.

Carnivorous propensities of larvae on pupae are also noted by Clark and Dickson (1971, pg. 65) in the African *Syntarucus telicanus* (Lang) whose larval foodplant is also plumbago. It seems likely that the same chemical cues present in the host plant which induce larvae to eat the tissues, also stimulates their feeding response and induces cannibalism when present in animal tissues. More work on this relationship is needed.

Pathogens

Laboratory reared larvae occasionally succumb to one-or more pathogens. These are first evident through watery frass, which may adhere to the anal area of the larvae, or "cement" smaller larvae to the substrate. It kills larvae in all instars, but is most evident in third and fourth instars which are larger and most subject to being noticed with the disease. Infected larvae become weakened, darken and move very slowly. Eventually, they stop feeding and die on the plant, usually in a darkened condition. Within a day or so the dead larvae become brown to blackish in appearance.

Older foodplant, such as might be left in an unventilated food container for several days, is most likely to harbor the pathogen, or at least the same conditions which promote mold on a plant, and on larval droppings, has also been associated with a higher disease rate in confined *Leptotes.*

The disease is highly infectious. For example, six of nine larvae taken from lab to field in order to place them on the host plant buds for biological association succumbed to the disease within 24 hours. No doubt the disease was transferred artificially in the lab, perhaps by camel hair brush and fingers used to move the larvae from bud to bud, and to containers, etc.

The disease is not uncommon in nature. Dead larvae in the darkened conditioned with fecal smears covering the posterior end have been found on plumbago buds in June and July.

Pupae are also subject to pathogens which tend to kill the host within 30 hours of the time it pupates. Infected pupae are usually dark in appearance (rather than the normal light brown or "freckled" (mottled) pupa). However, one pupa out of over 500 rearings died approximately 50 hours after pupation while retaining its normal light color. The specimen appeared to start "leaking" body fluids in the ventral abdominal region. It partically collapsed as the fluid gradually flowed about 10 mm from the now deceased pupa.

Myrmecophily

Several species of ants are associated in a facultative way with third and fourth instar larvae. The relationship has been assumed to be symbiotic in that attendant ants distract or drive away potential parasites and predators, and in turn, receive an exudation from Newcomer's gland on the dorsum of the seventh abdominal segment. This gland has more recently been claimed (Malicky, 1970) to function as an ant "bribe" or appeasement organ, to prevent ant aggression toward the larva. While it was not our purpose to determine the exact role of the honey-gland in this species, on at least one occasion it failed in both appeasement and protection. *Pseudomyrmex gracilis mexicanus* (Roger) was observed carrying a dead third instar larva beneath a plumbago plant. The larva had been severely mauled with what appeared to be manidbular "marks" of the ant. Other predacious ants are known to feed on lycaenid larvae, so ant relational organs are not universally effective.

Observations over a four-year period involving *cassius* and their attendant ants lead us to agree with Malicky concerning the appeasement nature of Newcomer's gland. Based on ethological and morphological observations, we also support the contention that Malicky's glands have an odoriferous function, attracting ants to the honey-gland site. It may also be that Allyn's glands, singly or in clusters of two to several, also have an attractant function, used by the ants both in recognition and to deter aggression. Additional data are much needed.

The following ants were found in direct association with the mature larvae. At one time or another, all were observed on the dorsal surface soliciting "honey gland" secretions and moving their antennae in typical positions described as palpating and groping: *Pheidole anastasii* Emery; *Nylanderia bourbonica amia* Forel; *Brachymyrmex heeri obscurior* Forel and *Crematogaster ashmeadi* Mayr. All of these ants continued to tend the larvae when both were returned to the laboratory on plumbago blossoms.

Several other species of ants occur on or beneath the plumbago blossoms, but have not as yet been recorded with the larvae. One of these, *Tapinoma melanocephalum* (Fabr.) is known to associate with the larvae of at least three lycaenid species in the Oriental and Ethiopian regions. Most all of the species mentioned are opportunistic as to food source and will readily attend aphids, or come to plant nectaries if available. Their presence on the plant was always associated with one of these food sources, and numbers of ants on a blossom was a good sign that the cryptic, green lycaenid was also there.

UV Reflectance

Adults of both sexes show a high intensity of UV reflectance. This reflective property stems from laminar structures inside wing scales, although a minor amount may be produced by mirror reflection from the wing membranes. In other butterflies, such as *Phoebis philea*, as well as other pierids, UV reflectance is produced in the longitudinal ridges of the scales, and the yellow pigment bodies within such scales are UV absorbing. Behavioral studies of the adult *cassius*, which are still in progress and will be reported elsewhere, indicate they perceive in the UV range and use these wavelengths along with others, during courtship recognition procedures. An unexpected finding during this study is that the larvae also show UV reflectance. The pattern reflected when photographed with UV light corresponds to the visible markings of the larvae; dark green or reddish-brown areas show greater wavelength absorption and less reflection than lighter regions of the larvae. The dark, dorso-mesial stripe, in which the pulsating dorsal vessel and flowing blood can be observed in living larvae, is a highly absorbant region. Larvae which are nearing a molt stage, show a loss of pattern, and a rather uniform mirror-like reflectance when photographed in UV light. This is assumed to be produced just beneath the integument to be shed, and not in any appendages or processes on the outer skin.

Neither the flower nor other foliage of the plumbago plants show UV reflectance, and while speculative, it is doubtful that the UV reflectance of the larvae has any important evolutionary strategy. It may be simply an additional property of the structural components of the integument. On the other hand, since some Hymenoptera have been shown to be able to perceive in the UV range, it is possible that some wasp predators are better able to locate host larvae in the plant flowers by their UV wavelengths, in which case the character would be detrimental, and selected against. Additional work is warranted, since we have also found other lycaenid larvae to be UV reflectant.

Acknowledgment

We are grateful to many taxonomists for invaluable determinations of their specialties: C. W. Sabrosky, Tachinidae; Paul W. Marsh, Braconidae; W. F. Buren, Formicidae; D. T. Jennings, Thomisidae; E. O. Bush, data on Plumbago host plant.

Thanks are also given to A. C. Haman and Jacqueline Y. Miller for critical review of the manuscript.

Literature Cited

d'Almedia, R. Ferreira. 1933. Les Chenilles des genres *Hemiargus* et *Leptotes*. Lambillionea, 33:230-236.

Brown, F. Martin and Bernard Heineman. 1972. Jamaica and its butterflies. xv + 478 pp. E. W. Classey, Ltd., London.

Clark, Gowan C. and C. G. C. Dickson 1971. Life histories of the South African Lycaenid butterflies. xvi + 272 pp. Purnell and Sons, Ltd., Cape Town.

Dethier, V. G. 1941. Antennae of lepidopterous larvae. Bull. Mus. Comp. Zool. Harvard, 87:45.

Downey, John C. and Arthur C. Allyn. 1973. Butterfly ultrastructure. 1. Sound production and associated abdominal structures in pupae of Lycaenidae and Riodinidae. Bull. Allyn Mus., (14): 47 pp.

------------. 1978. Sounds produced in pupae of Lycaenidae. Bull. Allyn Mus., (48): 14 pp.

Dyar, H. G. 1890. The number of moults of lepidopterous larvae. Psyche, 5:420-422.

Ehrhardt, R. 1914. Uber die Biologie und Histologie der myrmekophilen Organe Von *Lycaena orion*. Ber. Naturf. Ges. Freiburg, i. Br., 20:XC-XCVIII.

Fales, John H. and Daniel T. Jennings. 1977. Butterflies as prey for crab spiders (Thomisidae). Jour. Lepid. Soc., 31(4):280-282.

Ferris, G. F. 1943. The basic materials of the insect cranium. Microentomology, 8(1):8-24.

Forbes, William T. M. 1910. A structural study of some caterpillars. Ann. Ent. Soc. Amer., 3:94-143.

Haskins, J. R. 1933. The life histories of *Eurema demoditas, Lycaena theonus* and *L. hamo* (Lepid.: Pieridae, Lycaenidae). Ent. News, 44(6):153-156.

Hinton, H. E. 1946. On the homology and nomenclature of setae of lepidopterous larvae, with some notes on the phylogeny of the Lepidoptera. Trans. Roy. Ent. Soc. Lond., 97:1-37.

------------. 1947. The dorsal cranial area of caterpillars. Ann. Mag. Nat. Hist., 14:843-852.

------------. 9586. The larvae of the species of Tineidae of economic importance. Bull. Entom. Es., 47(2): 251-346.

------------. 1970a. Some structures of insects as seen with the scanning electron microscope. Micron., 1:84-108.

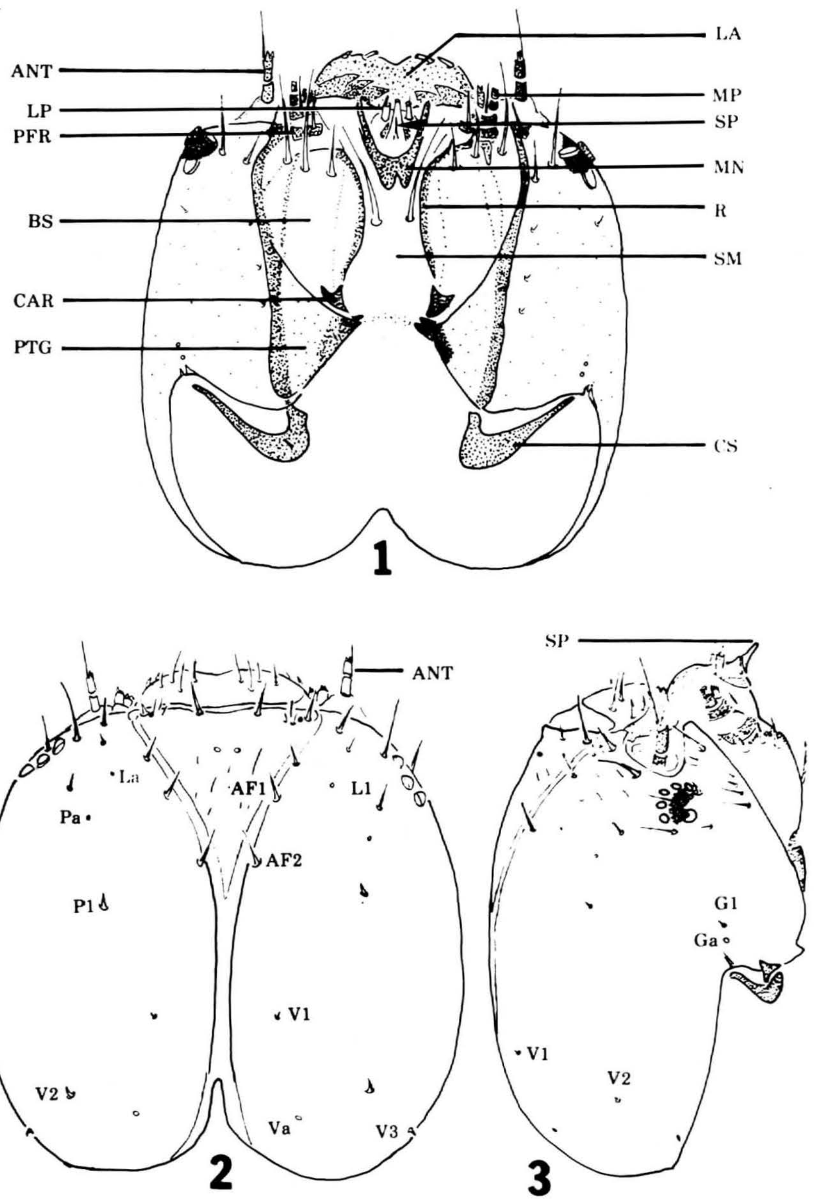
------------. 1970b. Insect eggshells. Scientific American 223(2):84-91.

Lawrence, Donald A. and John C. Downey. 1966. Morphology of the immature stages of *Everes comyntas* Godart (Lycaenidae). Jour. Res. Lepid., 5(2):61-96.

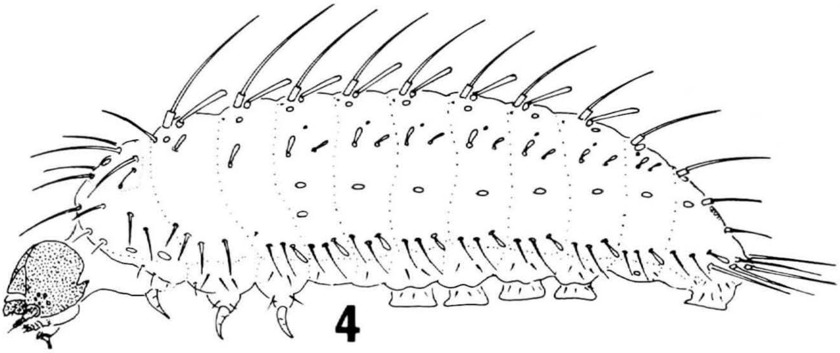
Malicky, Hans. 1970. New aspects on the association between lycaenid larvae (Lycaenidae) and ants (Formicidae, Hymenoptera). Jour. Lepid. Soc., 24(3):190-202.

Newcomer, E. J. 1912. Some observations on the relations of ants and lycaenid caterpillars, and a description of the relational organs of the latter. Jour. New York Ent. soc., 20:31-36.

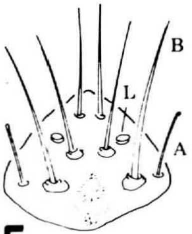
Richards, O. W. 1949. The relation between measurements of the successive instars of insects. Proc. Roy. Ent. soc. Lond., (A), 24:8-10.



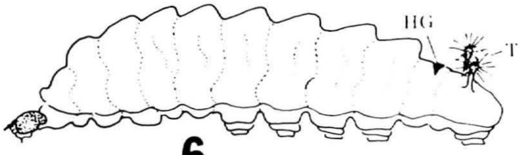
Figures 1-3. Head capsule of fourth instar larvae of *Leptotes cassius theonus* showing structure and chaetotaxy. Setae somewhat darkened and emphasized compared to living form. 1. Ventral view. 2. Frontal view. 3. Lateral view. Key to abbreviations: **ANT**-antenna; **BS**-basistipes; **CAR**-cardo; **CS**-cervical sclerite; **LA**-labrum; **LP**-labial palp; **MN**-mentum; **MP**-maxillary palp; **PFR**-palpifer; **PTG**-postgena; **R**-ridge of stipes; **SM**-submentum; **SP**-spinneret. Other lettering refers to specific setae or punctures.



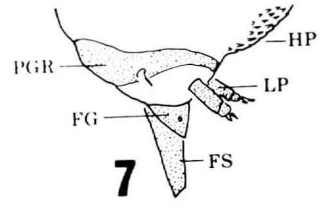
4



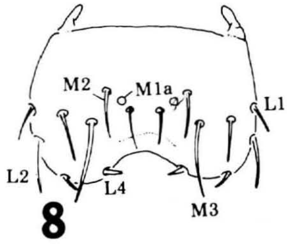
5



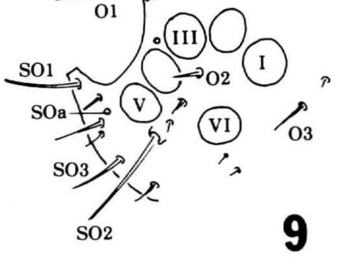
6



7

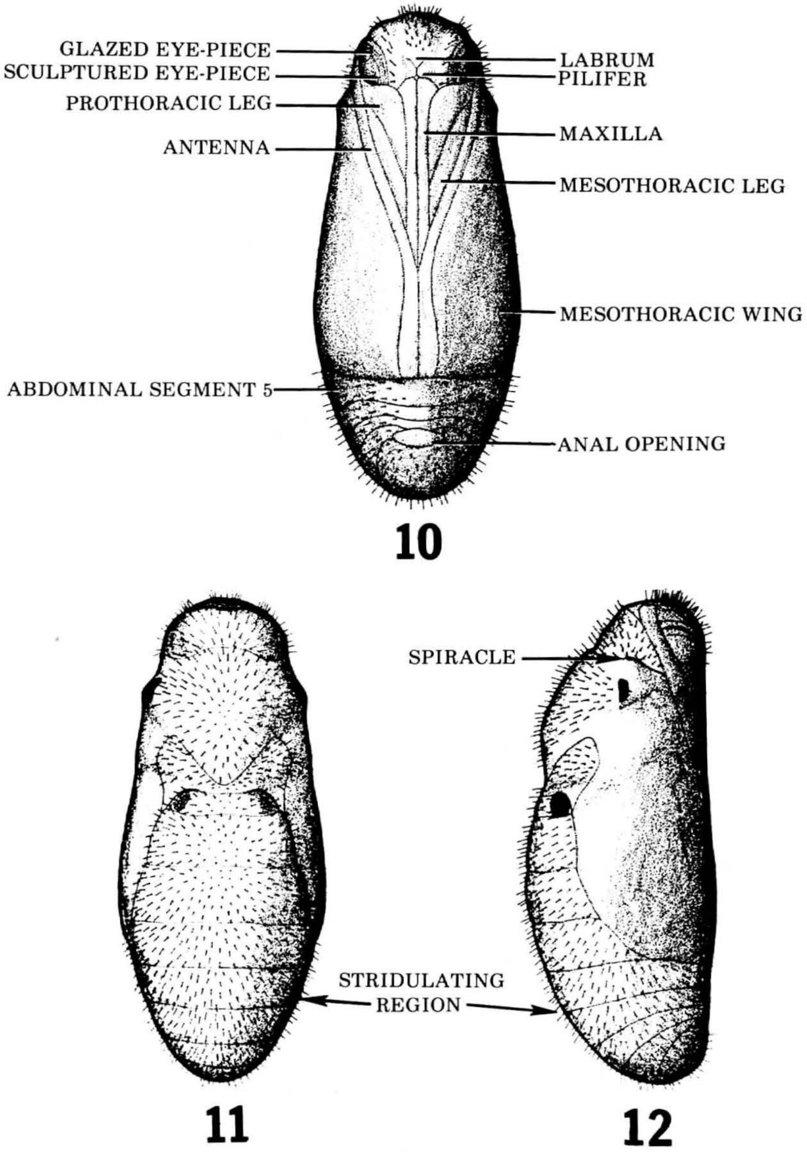


8

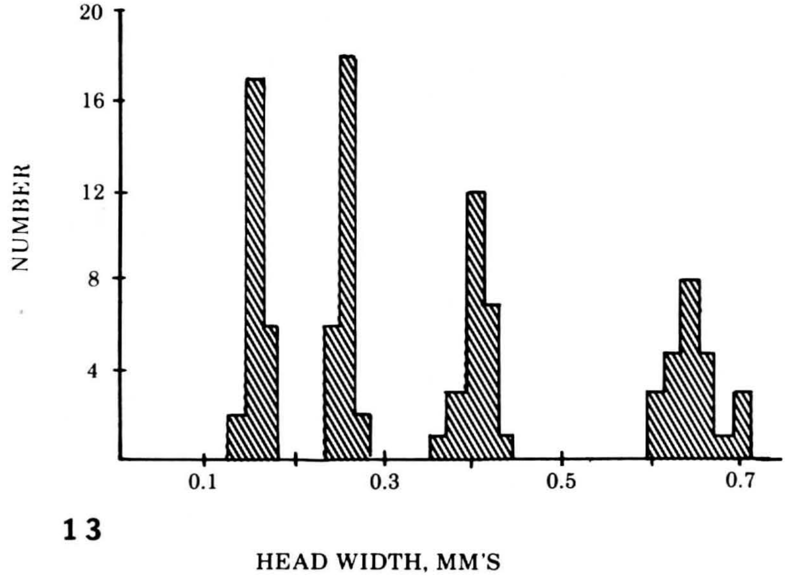


9

Figures 4-9. Larval structures of *Leptotes:* 4. Lateral view, first instar larvae, to show setal arrangement. 5. Dorsal view, prothoracic shield, first instar. 6. Outline of mature larvae, with everted tentacles, and honey gland indicated. 7. Spinneret and associated structures. 8. Labrum, mature larvae. 9. Ocular area of head capsule to show chaetotaxy. Key to abbreviations: **FG**-fusuliger; **FS**-fusulus of spinneret; **HG**-honey-gland; **HP**-hypopharynx; **LP**-labial palp; **PGR**-palpiger; **T**-evertible tentacle. Other lettering refers to specific setae, lenticles or ocelli.

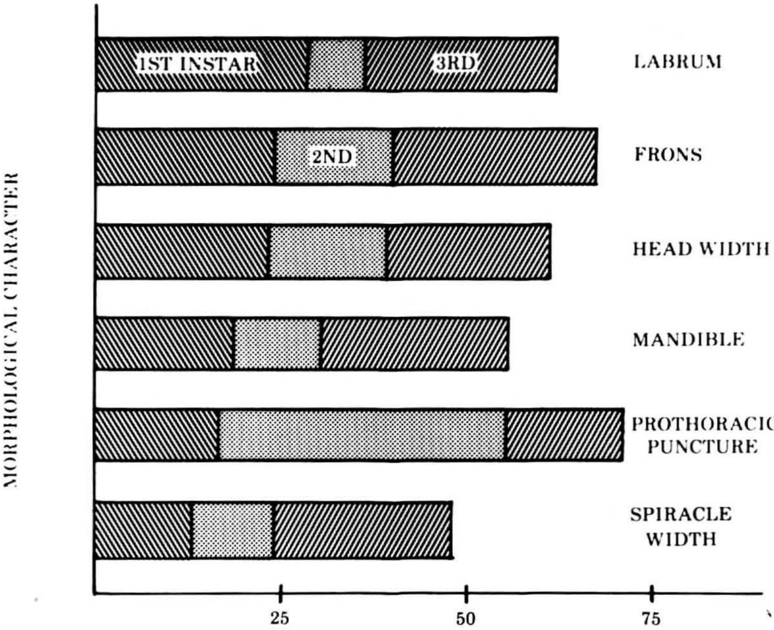


Figures 10-12. Pupa of *Leptotes cassius theonus* showing sclerites and setal pattern. 10. Ventral view. 11. Dorsal view. 12. Lateral view.



13

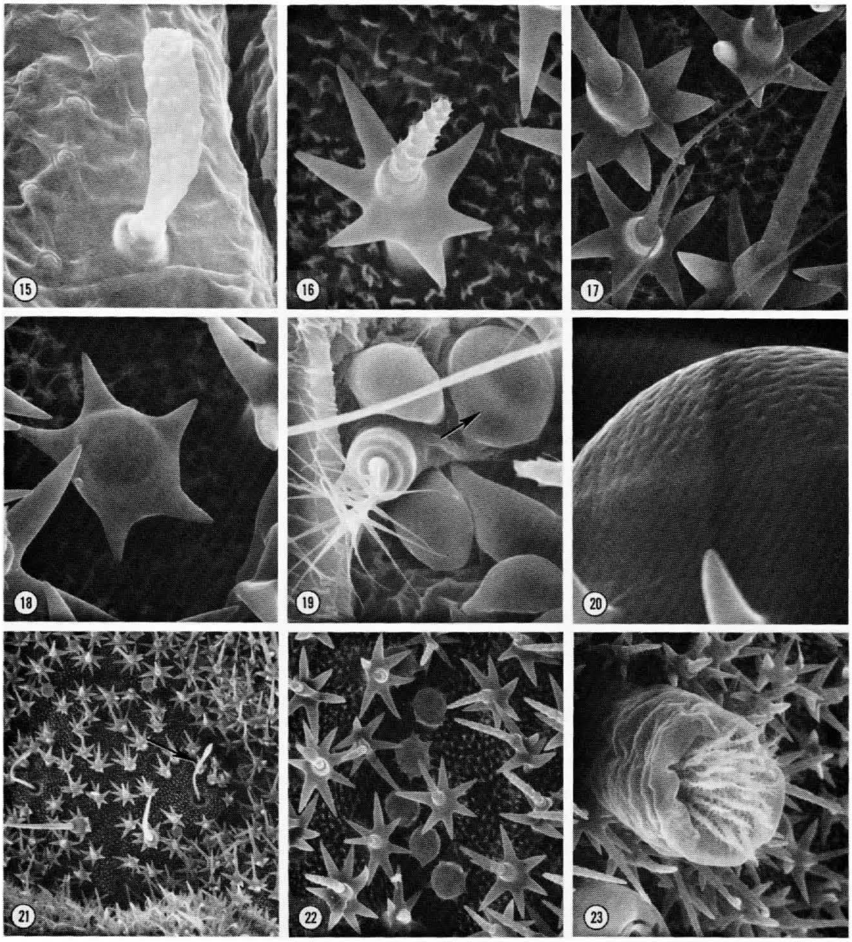
Figure 13. Graph Showing differences in the width of the larval head capsules of *Leptotes cassius theonus* from a population in Sarasota, Florida. Note the lack of overlaps, *i.e.*, the significant morphological gaps between the four different instars. Five instars had been previously reported for this species. N=100.



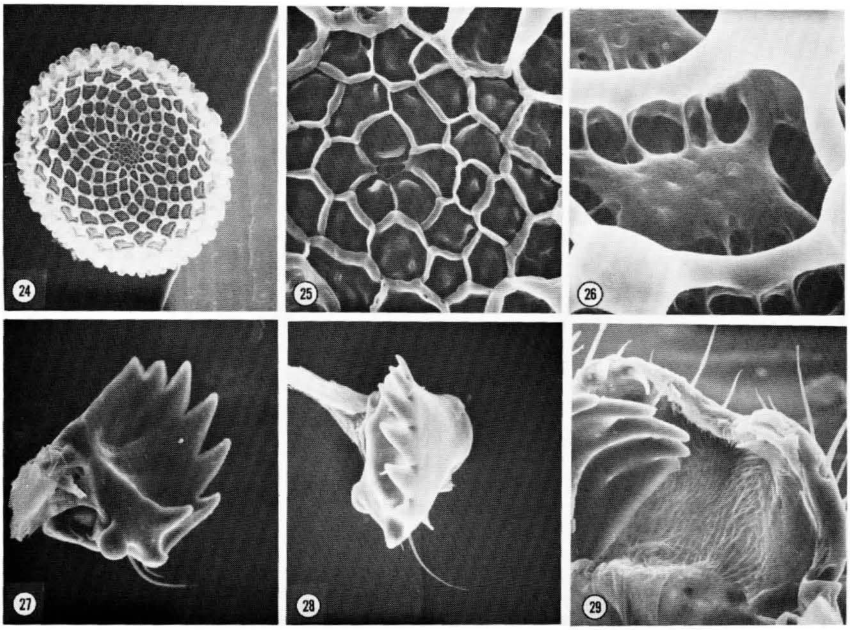
14

PERCENTAGE OF SIZE
OF STRUCTURE IN MATURE LARVAE

Figure 14. Relative size of larval structures in percentage values, with the size of the structure in the fourth instar being 100%. Growth curve is not allometric, even though the tendency may be noted. The second instar, in all cases except one, shows the smallest gain presumably correlated with the shortness of time in this stage compared with others.



Figures 15-23. Details of larval structures of *Leptotes cassius theonus*. Figures 15-19. Setal types. 15. "Clubbed" setae from segment 6, lateral surface, second instar larva, note surface sculpturing, 750X. 16. Stellate based setae characteristic of second and later instars, from prothoracic shield, second instar, 850X. 17. Elongate narrow seta from prothoracic shield, third instar, 500X. 18. Anal shield, third instar, stellate organs from eighth abdominal segment, 750X. 19. Multibranched "hydroid" seta of fourth instar and Malicky's sieve plates (arrow) from lip of honey-gland, seventh abdominal segment, 750X. 20. Close-up of surface of sieve plate at honey-gland site to show porous nature, 5000X. 21. Prothoracic shield, third instar; noting sensory setae (arrow) emerging from circular opening which appears as a "puncture" under light microscopy and has been so designated in other works, 80X. 22. Anal plate of third instar, five Allyn's sieve plates line the posterior margin of the anal shield, 215X. 23. Partly everted fleshy "tentacle" with apical setae arranged in a sheave, 225X.



Figures 24-26. Eggs of *Leptotes cassius theonus*. 24. Entire egg, dorsal view, 75X. 25. Micropylar area showing 5-petal rosette and transition zone, 750X. 26. Chorionic sculpturing of lateral cells showing trabeculae supporting the ribs; note aeropyles in porous chorion, 1000X. Figures 27-29. Larval structures. 27. Oral aspect of left mandible, 150X. 28. Edge on distal view of cutting surface of left mandible, 150X. 29. Facial aspect of epipharynx. Note blade-like structures on anterior margin and position of setae on lip of labrum, 250X.