

## The ant associated epidermal organs on the larva of the lycaenid butterfly *Curetis regula* Evans

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The surface ultrastructure of the setae and epidermal organs of the larva of *Curetis regula* is described. Their possible functions are discussed and comparisons made with similar structures found in other members of the Lycaenidae.

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### Introduction

The butterfly family Lycaenidae contains over one-third of all butterfly species (Vane-Wright, 1978; Robbins, 1982), and many of their larvae have associations with ants. These associations were among the earliest presumed mutualistic interactions between insects reported (Edwards, 1878a, b; Tutt, 1908; Newcomer, 1911, 1912; Lamborn, 1914), and within the last 50 years, a number of detailed works have appeared summarizing the ant/larval association data (Balduf, 1939; Hinton, 1951; Iwase, 1954; Downey, 1961). These studies, together with the earlier pioneering work on natural history, have provided the groundwork for framing ecological and evolutionary questions about lycaenids and ants (Malicky, 1969, 1970; Atsatt, 1981; Cottrell, 1984).

Concurrent with this work, research toward the understanding of lycaenid/ant associations has included morphological descriptions of the special myrmecophilous organs possessed by lycaenid larvae as adaptations to ants (Guenée, 1867; Edwards, 1878b; Newcomer, 1912; Lawrence and Downey, 1966; Malicky, 1969, 1970; Claassens and Dickson, 1977; Downey and Allyn, 1979; Kitching, 1983; Kitching and Luke, 1985; see also Cottrell (1984) for references). Following the terminology of Cottrell (1984), the most commonly cited ant associated organs are:

(1) the dorsal nectary organ (DNO) that provides a sugary, fluid reward (Newcomer, 1912; Malicky, 1970; Maschwitz *et al.*, 1975);

(2) the tentacular organs (TOs) that appear to modify ant behaviour by allomonal secretion (Claassens and Dickson, 1977; Henning, 1983);

(3) the setal homologues termed perforated cupola organs (PCOs) (Malicky, 1969, 1970; Lawrence and Downey, 1966; Downey and Allyn, 1979; Kitching, 1983; Kitching and Luke, 1985), which may, in some cases, secrete amino acid rewards (Pierce, 1984). Within the family Lycaenidae, DNOs and/or TOs are known only in the subfamilies Liphyrinae, Polyommatainae, Curetinae and Theclinae (Cottrell 1984), whereas PCOs have been found in virtually all Lycaeninae, Polyommatainae, Thec-

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linae, Miletinae and Riodininae examined, whether or not the larvae are attended by ants (Malicky, 1969, 1970; Kitching and Luke, 1985). However, even though PCOs have been found throughout the Lycaenidae, these organs vary considerably in morphology between taxa (Malicky, 1969; Kitching and Luke, 1985; Harvey, unpublished).

Although numerous taxa have been surveyed for the presence of any associated organs (see Malicky, 1969, 1970; Cottrell, 1984; Kitching and Luke, 1985 for lists), there are no published descriptions of these larval structures from the subfamilies Lipteninae, Poritiinae, Liphyrinae, Miletinae, Curetinae, Riodininae or Styginae (subfamilies follow Ackery, 1984) that have employed scanning electron microscopy (SEM). A better understanding of the evolution of these ant associated organs clearly requires their description from all major lycaenid groups.

Throughout most of the systematic history of the Lycaenidae, butterflies in the genus *Curetis* have always been somewhat enigmatic. Although their taxonomy and systematics has been treated by a variety of authors (De Nicéville, 1890; Bell, 1918; Chapman, 1915; Evans, 1954), their relationship (as the monobasic subfamily Curetinae) to other taxa within the Lycaenidae has never been clearly resolved (see Shirôzu and Yamamoto, 1957; Ehrlich, 1958; Eliot, 1973; Clench, 1955; Scott, 1985). Some unusual features of the larvae of *Curetis* (e.g. the sclerotized tentacle organs on the eighth abdominal segment) have been noted by various authors to emphasize the distinctness of *Curetis* (see Eliot, 1973; Cottrell, 1984; DeVries, 1984; Scott, 1985 for references), but the larval morphology has yet to shed light on the relationship of the Curetinae to other lycaenid taxa.

Until recently, ants have not been reported to associate with the larvae of *Curetis* (De Nicéville, 1890; Bell, 1918; Iwase, 1954; Eliot, 1973; Cottrell, 1984) but attendance of *C. regula* Evans by the formicine ant *Anoplolepis longipes* (Forel) has recently been observed in Borneo by DeVries (1984). In the same paper, the presence of apparent PCOs on the larvae was also noted. Because the larva of *Curetis* has never been critically surveyed for the presence of ant associated organs, it is important to describe the larval epidermal organs for eventual comparison to those of other lycaenid taxa. The purpose of this paper is to describe the surface ultrastructure of organs and setae found on a larva of *C. regula*, especially those thought to be involved in ant association, and to discuss these structures in relation to those found on other lycaenid taxa.

### Materials and methods

A late instar larva of *C. regula*, collected in Brunei (see DeVries, 1984), was preserved in the field by dropping it into a vial of alcohol. This specimen was later critical-point dried and sputter-coated with gold/palladium at the British Museum (Natural History). Initial SEM examinations were performed at the BM(NH), and subsequent photography and detailed examinations were done with a Super 1A SEM at the University of Texas. Wherever possible, the terminology of Cottrell (1984) has been employed to describe the various structures found on the larva.

### Results

The larva of *Curetis regula* examined was approximately 7 mm in length, as measured from the anterior margin of T1 to the posterior margin of A10. This specimen is presumed to be a penultimate instar larva (the length of a mature larva, estimated from photographs, is approximately 15 mm). The larva is slug-like in appearance, and its most conspicuous macroscopic features include the sclerotized

dorsal shield on T1 and the pair of permanently exerted, sclerotized tentacle organs on segment A8 (Fig. 1). Our description of the epidermal ultrastructure begins with structures found on all thoracic (T1–3) and abdominal (A1–10) segments, and proceeds to those structures of a more restricted distribution.

### Generally distributed structures

Two morphologically distinct structures are found scattered evenly over the dorsal surface of the thorax and abdomen: short, club-like setae ('short setae' hereafter) (Figs 2, 7, 8, 15), and domed structures ('dome setae' hereafter) (Figs 1, 3, 4, 6–8, 15–18). Both of these structures resemble the long tactile setae (Figs 1, 5) in that they are raised above the epidermal surface on fluted bases. The short setae are flattened and are widest near their apices. The dome setae have rounded, overhanging caps that rest on fluted bases (= chalazae). Unlike the PCOs (see below) the caps on the dome setae show no evidence of pores or of a sieve plate on their surfaces, even though many have a light covering of an unknown waxy material (see Figs 3, 4).

The dorsal portion of T1 bears a conspicuous, somewhat recessed shield that is roundly triangular in shape, has a rough appearing surface texture and occupies approximately one-third of the surface area of segment T1 (Fig. 1). In addition to bearing perforated chambers (see below), all areas except the posterior medial portion of the T1 shield are densely covered in small, round granulations interspersed with short and dome setae (Fig. 15). These granulations are also found on the tentacle organs. The short and dome setae occur on the T1 shield at densities slightly greater than on the surrounding areas.

In addition to these structures projecting from the epidermis, each segment has deep indentations of the cuticle on the lateral and dorsal surfaces, the bottoms of which were termed 'pores' by Kitching and Luke (1985) for other lycaenid taxa. Two pairs of dorsal pores are present on segments T2–A6 (Figs 1, 6–9). A unique feature of the dorsal pores on A7 is that the posterior pair are found within a single depression, whereas all others are found as distinct pairs. The posterior pair is located where a dorsal nectary organ occurs on many lycaenid larvae, and appears as a deep invagination along the segmental midline anterior to the bases of the TOs on A8 (Figs 1, 9). In addition, several pairs of lateral pores occur on all segments. The cuticle immediately surrounding all of these pores is not specially modified, except that short and dome setae are less numerous than on other cuticular areas.

### Perforated cupola organs (PCOs)

Adjacent to each spiracle is a cluster of perforated cupola organs (Figs 1, 10–14). Each of these globular PCOs has a depressed central region (the sieve plate of Malicky, 1970) that appears to be porous, secretory area, because accumulations of apparent exudate are scattered over its surface. The placement of the PCO clusters on T1 is anterior to the spiracle (Fig. 12), whereas all other PCO clusters are posterior to the spiracles (Figs 1, 13–14). The number of PCOs associated with each spiracle and their segmental location as observed on the left side of the larva is as follows (segment:number of PCOs): T1:8 (Fig. 12); A1:5 (Fig. 13); A2:4; A3:2; A4:3 (Fig. 14); A5:4; A6:3; A7:3; and A8:9.

### Perforated chambers

Located laterally on T1 and A7 are pairs of unusual structures that are here, for convenience, termed 'perforated' chambers. The pair of perforated chambers on T1 is

located at the lateral margin of the dorsal shield (Fig. 15), whereas that on A7 (Fig. 16) is located dorsal to the spiracle. Each perforated chamber consists of a small cluster of orifices on the cuticle. The opening of each orifice has a thickened rim (the thickest are on T1) that superficially resembles the chalaza of a seta, with the seta broken off (Figs 15, 16). The orifices appear to communicate with a common internal chamber, but confirmation of this morphology will require examination of fluid-preserved larvae (not available, but see *Discussion*).

### Tentacular organs

The most conspicuous feature of the *Curetis* larva is the pair of sclerotized cylinders directly above the spiracles on A8 that house the tentacle organs (Fig. 1). In the larva examined here, each cylinder is approximately 2 mm long and the proximal one-third of its surface bears minute granulations, similar to those found on the T1 shield (see above), and a scattering of short and dome setae (Figs 17, 18). The tentacle organ itself is retracted in the larva examined but the membranous proximal portion of the invaginated organ is clearly visible inside the cylinder opening (Fig. 18). The everted tentacle organ bears long, brush-like setae distally. The organ is rapidly everted and then retracted when a live larva is molested (Johnston and Johnston, 1980; DeVries, 1984).

### Discussion

The results presented here for *C. regula* show that certain myrmecophilous structures found in previously surveyed lycaenid taxa are also found on curetine larvae. Specifically, we have demonstrated that pore cupola organs are found on *C. regula*, and this information, together with other studies on lycaenid larvae (Malicky, 1969, 1970; Kitching, 1983; Kitching and Luke, 1985), establishes that PCOs are found in all subfamilies of Lycaenidae so far studied. This is further evidence that we should, with few exceptions, expect PCOs to be a general character shared by all members of the Lycaenidae. When compared with other lycaenid larvae, the only unusual characteristic of the PCOs found on *C. regula* is their tightly clustered distribution around the spiracles. Previously described PCOs from other taxa appear to be more generally distributed and less tightly clustered around the spiracles. However, Harvey (unpublished) has found that in some Riodininae (*Hades noctula* Westwood and *Euselasia* spp.) the PCOs are as tightly clustered around the spiracles as in *Curetis*, perhaps indicating that this type of distribution may prove to be more general as more lycaenid taxa are surveyed.

The dome setae scattered over the cuticle (Figs 1, 3, 4, 6–9, 15–18) are unusual in general shape and, as far as we know, have not been reported from any other lycaenid taxa. They are probably homologous to setae (as are PCOs) as evidenced by the shape of their fluted bases; a character seen in both the short and tactile setae (Figs 2–5). The dusting of particulate matter over the surfaces of the domes suggests a possible secretory function. However, most areas on the cuticle of the *C. regula* larva examined were covered in this particulate matter, perhaps indicating a cuticular wax precipitated by the methods of killing and subsequent treatment of the larva.

From examination with the SEM, the various dorsal and lateral pores found on the *C. regula* larva appear to be very similar to those found in other lycaenid taxa. Of interest are the posterior dorsal pores on segment A7 (Figs 7, 9), which are in the same positions as the dorsal nectary organs found in a variety of other lycaenid genera (see Cottrell, 1984; Kitching, 1983; Kitching and Luke, 1985 for lists). However, we have

found no evidence that the pores on A7 or on any other segments of *C. regala* are secretory: no ants fed at or consistently antennated these areas on live larvae (see below). Corroborating the detailed anatomical studies of Lepidoptera by Matsuda (1970), Harvey (unpublished) has found that many of the pores found on larval lycaenids (including riodinines) are simply points of muscle attachment with no evidence of a secretory function. These data indicate that the equivocal statements about the presence of a DNO (= Newcomer's gland) in larval *Curetis acuta* by Scott (1985) require confirmation.

The perforated chambers found on segments T1 and A7 (Figs 1, 15, 16) are unusual and conspicuous features of *C. regala* larvae that can be seen with little magnification (visible in 35 mm transparencies taken in the field). However, they have never been reported previously in any other lycaenid taxon, although they may have been what Scott (1985) referred to as 'plate-like organ[s] (hollow beneath) above each spiracle on abdominal segment 7'. There is a general similarity between the perforated chambers described here and the secretory dish organs (Clark, 1951; Clark and Dickson, 1971) that are present in some species of the African genera *Spindasis* and *Crudaria* (Theclinae: Aphnaeini). The dish organs are found one per segment, located dorsally on a variable number of abdominal segments, and have a raised rim along their margin. Although they may be analogous to the perforated chambers in *C. regala*, the dish organs differ in position, and apparently, in structural details. The general configuration and morphology of the perforated chambers as seen with the SEM (Figs 15, 16) suggests a secretory function. However, the nature of the secretion (whether it be liquid or volatile) requires confirmation through dissection and field observations.

As has been noted by various authors (see Eliot, 1973; Cottrell, 1984; Scott, 1985), the sclerotized tentacle organs with their permanently exerted cylinders, are unique to the larvae of *Curetis* (Figs 1, 17, 18). The tentacle organs on *Curetis* are clearly homologous to the TOs found in the lycaenid subfamilies Liphyrinae, Polyommatainae and Theclinae (see Clark and Dickson, 1956; Cottrell, 1984; Kitching and Luke, 1985 for references). (It should be noted that although Scott (1985) correctly reports TOs on A8 in the Curetinae, his statement that TOs occur on A7 in his Lycaeninae is in error.) Although the TOs found in the genera *Aslauga* (Liphyrinae) and *Alooides* (Theclinae) are housed in short, sclerotized cylinders, the extreme length of these structures in the Curetinae appears to be an autapomorphy of the subfamily.

Although 'myrmecophilous' organs have been found on all lycaenid larvae so far examined (see Cottrell, 1984; Kitching and Luke, 1985), regardless of whether or not the taxa are known to be associated with ants, the function of the various organs and their use by ants is not well understood. Although PCOs, usually considered to be ant associated organs (Malicky, 1970; Cottrell, 1984; Pierce, 1984), and the perforated chambers described herein are both found on *Curetis* larvae and are likely sites for ant interaction, we have no evidence that ants pay particular attention to these, or any other structures, excepting the TOs in special circumstances (see below). The one documented case of a curetine-ant association (DeVries, 1984) concluded that the only attraction to the ants was plant exudate at the leaf tissue freshly damaged by *C. regala* larvae; a resource also utilized by adult *C. regala*. Although feeding by ants on larval-damaged leaf tissue has been reported in butterfly larvae that clearly do not have ant associated organs (Owen, 1971; Young, 1978), it is unknown whether such ant associated behaviour is common for the Curetinae.

In the case of *C. regala* then, how many of the structures that occur on the larvae have a function that is directly involved with ant association? From field observations

on *C. regula* larvae, it is clear that only the TOs have been demonstrated to produce a behavioural reaction in ants (DeVries, 1984). When molested by the observer with a splinter of wood, the larva quickly everts and then retracts the tentacle organs. This immediately produces a frantic activity response in the ants within 1 cm of the larva, and was likened to the reaction to a volatile ant alarm pheromone. The excited state of the ants diminishes soon after the TOs have been retracted, but will resume immediately if the larva is forced to evert the TOs again. Presumably an insect predator or parasitoid would also cause the eversion of the TOs, and the reaction of any nearby ants running frantically over the larva would deter attempts to kill or parasitize it (DeVries, 1984). This larval mediated ant behaviour in *C. regula* is quite similar to those ant behaviours observed in response to the volatile larval extracts and everted TOs in *Aloeides* (Claassens and Dickson, 1977; Henning, 1980). Although these observations on *Curetis* are anecdotal, they nonetheless strongly suggest that, as in other lycaenid groups, the volatile chemicals produced by the TOs of *Curetis*, and the TOs themselves, have evolved in response to ant association. Viewed in this light, it seems probable that ant association within the Curetinae will be found to be more widespread than previously thought (DeVries, 1984).

From the data presently available, we conclude that ant association with *C. regula* is entirely facultative and that the association depends upon where a larva is found within a habitat, much like the facultative ant associations suggested for a wide variety of other lycaenid taxa (see Lenz, 1917; Malicky, 1970; Harvey and Webb, 1980; Cottrell, 1984). Of the epidermal organs described here for *C. regula*, we propose that when a larva is associated with ants, only the TOs may be actively used as an anti-predator defence that is aimed at small arthropods through direct manipulation of ant behaviour, whereas the PCOs, dome setae and perforated chambers may function passively to nullify ant aggression. However, the details of a facultative ant association with *Curetis*, the specifics of how ants respond to all of the epidermal organs found on larvae and how they vary with the interactions among various ant and curetine taxa must await further field observations and experimentation.

It has been suggested that a detailed study of larvae may be useful in resolving the relationships of taxa within the Lycaenidae (Henning, 1983; Cottrell, 1984). Although we have not examined chaetotaxy or head and proleg morphology for any instar, we had hoped that the present study would shed some light on the systematic position of the Curetinae within the Lycaenidae. However, it is clear that the relationships of *Curetis* to the rest of the family cannot be established solely from the information presented here and that such conclusions require detailed comparative studies between the larvae of curetines and all other lycaenid subfamilies. The most that can be said at present is that the larvae of *Curetis* bear ant associated structures homologous to those of other lycaenid groups (i.e. TOs, PCOs) and that some of the structures may be unique to the curetines (i.e. dome setae, perforated chambers and sclerotized TOs).

This study provides further support for the hypothesis that ant association occurred early in the evolution of the Lycaenidae (Hinton, 1951; Vane-Wright, 1978). We are confident that the robustness of this hypothesis will be borne out when the larvae of all lycaenid groups have been surveyed for myrmecophilous organs.

A next logical step in the study of ant/lycaenid evolution should be to develop methods of assessing the hypothesis that ants were important factors in speciation events (Pierce, 1984). Perhaps phylogenetic analysis in conjunction with studies on population biology and ant associations of *Curetis* would be a good place to begin.

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### References

- ACKERY, P. R., 1984. Systematic and faunistic studies on butterflies. *Symposia of the Royal Entomological Society of London* **11**, 9–21.
- ATSATT, P. R., 1981. Lycaenid butterflies and ants: selection for enemy-free space. *American Naturalist* **118**, 638–654.
- BALDUF, W. V., 1939. *The Bionomics of Entomophagous Insects*. St Louis: John S. Swift and Co.
- BELL, T. R., 1918. The common butterflies of the plains of India (including those met within the hill stations of the Bombay Presidency). Part XII. *Journal of the Bombay Natural History Society* **26**, 98–140.
- CHAPMAN, T. A., 1915. An analysis of the species of the genus *Curetis*, chiefly based on an examination of the specimens in the Zoological Museum, Tring. *Novitates Zoologicae* **22**, 80–118.
- CLARK, G. C., 1951. The life history of *Crudaria leroma*. *Journal of the Entomological Society of Southern Africa* **14**, 127–132.
- CLARK, G. C. and DICKSON, C. G. C., 1956. Proposed classification of South African Lycaenidae from early stages. *Journal of the Entomological Society of Southern Africa* **19**, 195–215.
- CLARK, G. C. and DICKSON, C. G. C., 1971. *Life Histories of Southern African Lycaenid Butterflies*. Cape Town: Purnell.
- CLAASSENS, A. J. M. and DICKSON, C. G. C., 1977. A study of the myrmecophilous behaviour of the immature stages of *Aloeides thyra* (L.) (Lep.: Lycaenidae) with special reference to the function of the retractile tubercles and with additional notes on the general biology of the species. *Entomologist's Record and Journal of Variation* **89**, 225–231.
- CLENCH, H. K., 1955. Revised classification of the butterfly family Lycaenidae and its allies. *Annals of the Carnegie Museum, Pittsburgh* **33**, 261–274.
- COTTRELL, C. B., 1984. Aphytophagy in butterflies: its relationship to myrmecophily. *Zoological Journal of the Linnean Society of London* **79**, 1–57.
- DE NICÉVILLE, L., 1890. *The Butterflies of India, Burmah and Ceylon*, 3. Calcutta.
- DEVRIES, P. J., 1984. Of crazy-ants and Curetinae: are *Curetis* butterflies tended by ants? *Zoological Journal of the Linnean Society of London* **79**, 59–66.
- DOWNNEY, J. C., 1961. Myrmecophily in the Lycaenidae (Lepidoptera). *Proceedings of the North Central Branches, Entomological Society of America* **16**, 14–15.
- DOWNNEY, J. C. and ALLYN, A. C., 1979. Morphology and biology of the immature stages of *Leptotes cassius theonus* (Lucas) (Lepid.: Lycaenidae). *Bulletin of the Allyn Museum* **55**, 1–27.
- EDWARDS, W. H., 1878a. Notes on *Lycaena pseudoargiolaus* and its larval history. *Canadian Entomologist* **10**, 1–14.
- EDWARDS, W. H., 1878b. On the larva of *Lycaena pseudoargiolaus* and its attendant ants. *Canadian Entomologist* **10**, 131–136.
- EHRlich, P. R., 1958. The comparative morphology, phylogeny and higher classification of the butterflies. *Kansas University Science Bulletin* **39**, 305–370.
- ELIOT, J. N., 1973. The higher classification of the Lycaenidae (Lepidoptera): a tentative arrangement. *Bulletin of the British Museum (Natural History) (Entomology)* **28**, 371–505.
- EVANS, W. H., 1954. A revision of the genus *Curetis*. *Entomologist* **87**, 190–194, 212–216, 241–247.
- GUENÉE, A., 1867. D'un organe particulier que présente une chenille de *Lycaena*. *Annales de la Société entomologique de France* **7**, 665–668.
- HARVEY, D. J. and WEBB, T. A., 1980. Ants associated with *Harkenclenus titus*, *Glaucopsyche lygdamus* and *Celastrina argiolus* (Lycaenidae). *Journal of the Lepidopterists' Society* **34**, 371–372.

- HENNING, S. F., 1980. *Chemical communication between lycaenid larvae (Lepidoptera: Lycaenidae) and ants (Hymenoptera: Formicidae)*. M.Sc. thesis, University of Witwatersrand, Johannesburg, South Africa.
- HENNING, S. F., 1983. Biological groups within the Lycaenidae (Lepidoptera). *Journal of the Entomological Society of Southern Africa* **46**, 65–85.
- HINTON, H. E., 1951. Myrmecophilous Lycaenidae and other Lepidoptera—a summary. *Proceedings and Transactions of the South London Entomological and Natural History Society* **1949–1950**, 111–175.
- IWASE, T., 1954. Synopsis of the known life-histories of Japanese butterflies. *The Lepidopterists' News* **8**, 95–100.
- JOHNSTON, G. and JOHNSTON, B., 1980. *This is Hong Kong: Butterflies*. Hong Kong Government.
- KITCHING, R. L., 1983. Myrmecophilous organs of the larvae and pupae of the lycaenid butterfly *Jalmenus evagoras* (Donovan). *Journal of Natural History* **17**, 417–481.
- KITCHING, R. L. and LUKE, B., 1985. Myrmecophilous organs of the larvae of some British Lycaenidae (Lepidoptera): a comparative study. *Journal of Natural History* **19**, 259–276.
- LAMBORN, W. A., 1914. On the relationship between certain West African insects, especially ants, Lycaenidae and Homoptera. *Transactions of the Entomological Society of London* **1913**, 436–498.
- LAWRENCE, D. A. and DOWNEY, J. C., 1966. Morphology of the immature stages of *Everes comyntas* Godart (Lycaenidae). *Journal of Research on the Lepidoptera* **5**, 61–96.
- LENZ, F., 1917. Der Erhaltungsgrund der Myrmekophilie. *Zeitschrift für Induktive Abstammungs und Vererbungslehre* **18**, 44–46, 71–72.
- MALICKY, H., 1969. Versuch einer analyse der ökologischen Beziehungen zwischen Lycaenidae (Lepidoptera) und Formiciden (Hymenoptera). *Tijdschrift voor Entomologie* **112**, 213–298.
- MALICKY, H., 1970. New aspects of the association between lycaenid larvae (Lycaenidae) and ants (Formicidae, Hymenoptera). *Journal of the Lepidopterists' Society* **24**, 190–202.
- MASCHWITZ, U., WUST, M. and SCHURIAN, K., 1975. Blaulingsraupen als Zuckerlieferanten für Ameisen. *Oecologia* **18**, 17–21.
- MATSUDA, R., 1970. Morphology and evolution of the insect thorax. *Memoirs of the Entomological Society of Canada, Ottawa* **71**, 1–431.
- NEWCOMER, E. J., 1911. The life histories of two lycaenid butterflies. *Canadian Entomologist* **43**, 83–88.
- NEWCOMER, E. J., 1912. Some observations on the relations of ants and lycaenid caterpillars, and a description of the relational organs of the latter. *Journal of the New York Entomological Society* **20**, 31–36.
- OWEN, D., 1971. *Tropical Butterflies*. Oxford: Clarendon Press.
- PIERCE, N. E., 1984. Amplified species diversity: a case study of an Australian lycaenid butterfly and its attendant ants. *Symposia of the Royal Entomological Society of London* **11**, 196–200.
- ROBBINS, R. K., 1982. How many butterfly species? *News of the Lepidopterists' Society* **1982**, 40–41.
- SCOTT, J. A., 1985. The phylogeny of the butterflies (Papilionoidea and Hesperoidea). *Journal of Research on the Lepidoptera* **23**, 241–281.
- SHIRÔZU, T. and YAMAMOTO, H., 1957. The systematic position of the genus *Curetis* (Lepidoptera: Rhopalocera). *Sieboldia* **2**, 44–51.
- TUTT, J. W., 1907–1908. *A Natural History of the British Lepidoptera, their World-wide Variation and Geographical Distribution*, Volume IX. London: Swan Sonnenschein & Co.
- VANE-WRIGHT, R. I., 1978. Ecological and behavioural origins of diversity in butterflies. *Symposia of the Royal Entomological Society of London* **9**, 56–70.
- YOUNG, A. M., 1978. Possible evolution of mutualism between *Mechanitis* caterpillars and an ant in northeastern Costa Rica. *Biotropica* **10**, 77–78.

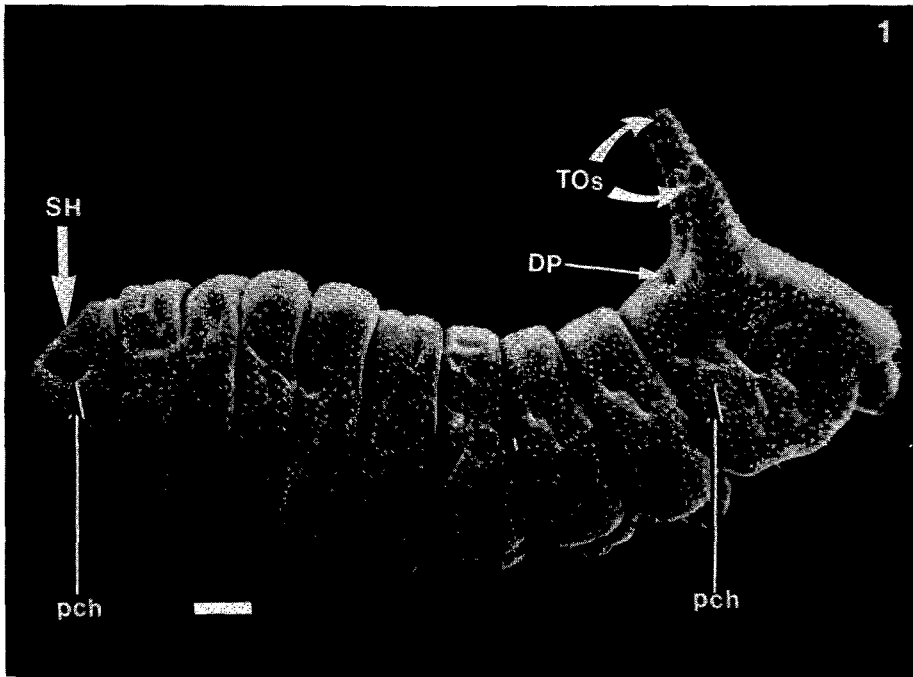
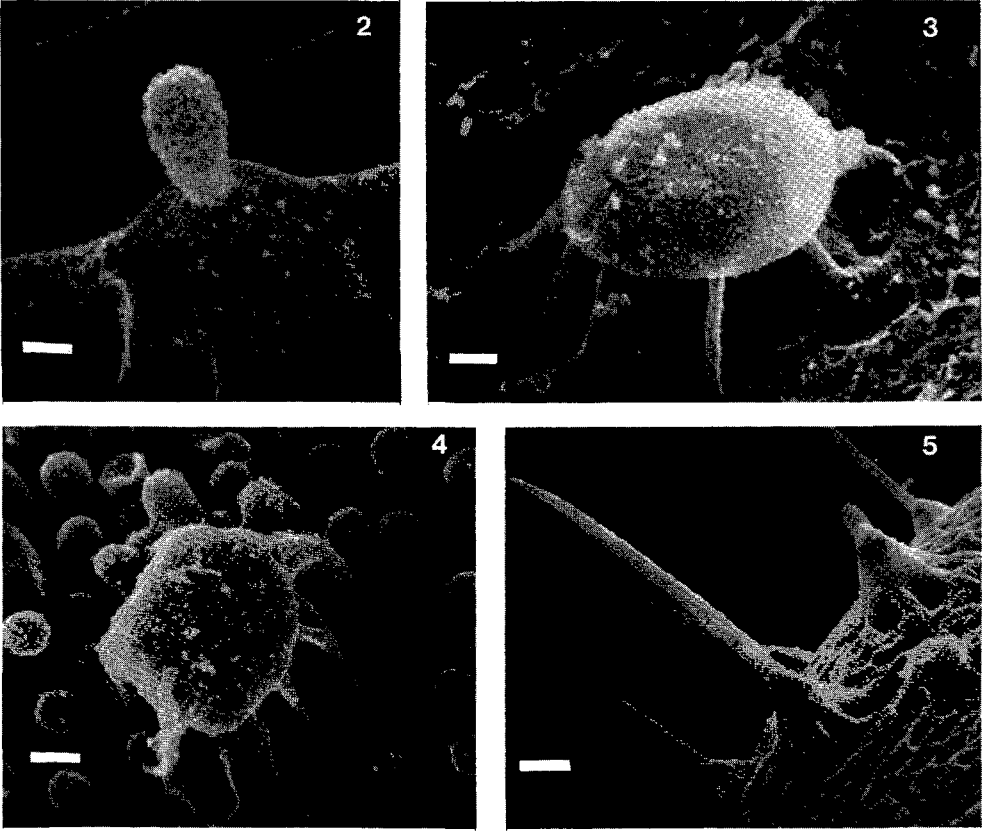
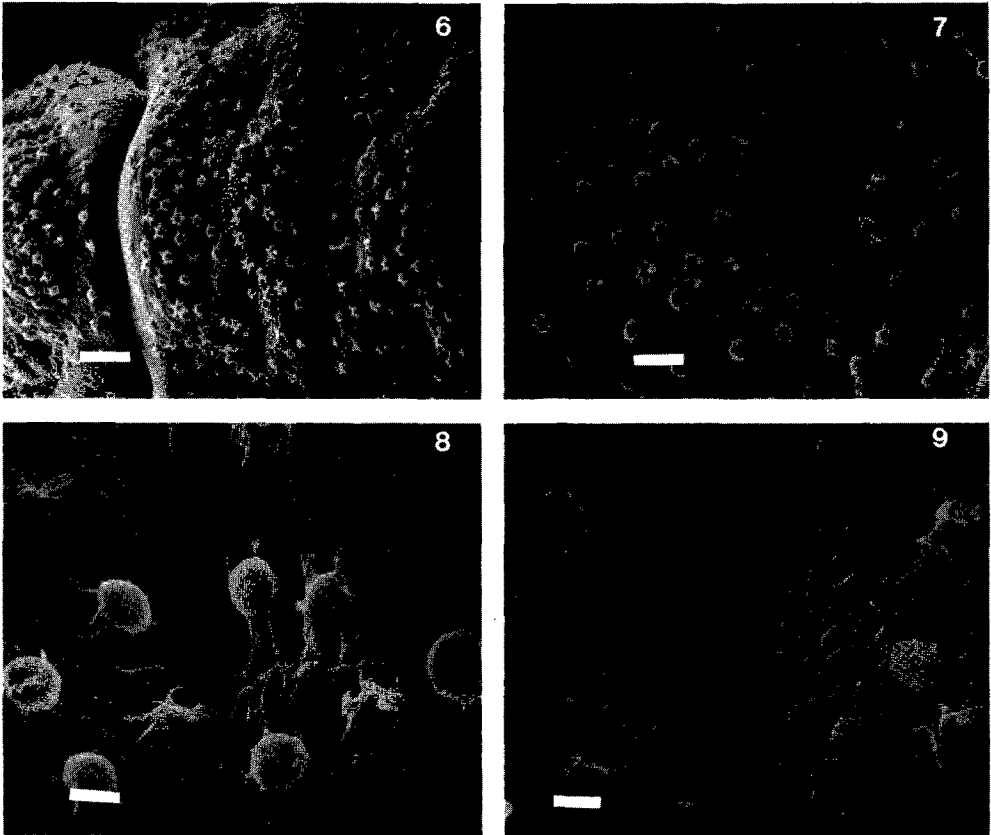


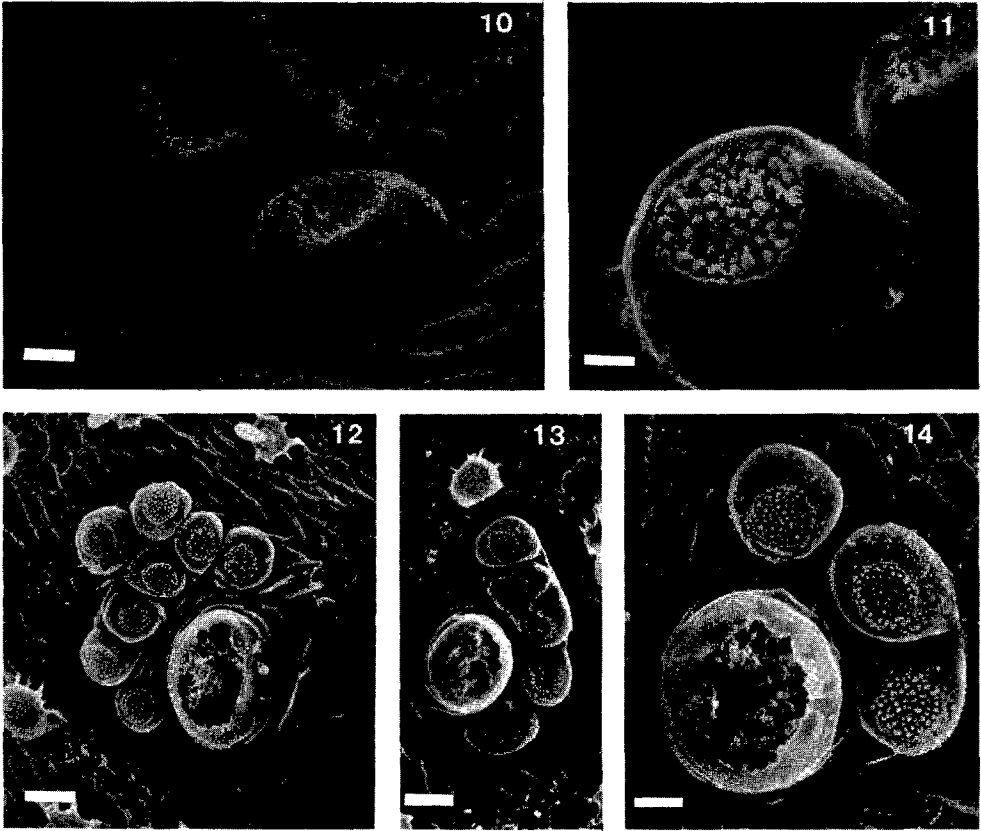
FIG. 1. Immature larva of *Curetis regula* showing major morphological features and body areas. Note the conspicuous scattering of dome setae over the entire surface of the cuticle. Also readily visible are the conspicuous T1 shield (SH), the tentacle organs (TOs), the perforated chambers (pch) on segments T1 and A7, the clusters of PCOs around the spiracles and the various dorsal and lateral pores. The posterior dorsal pore (DP) on segment A7 is located where many other lycaenid taxa bear the dorsal nectary organ. Scale bar = 0.27 mm.



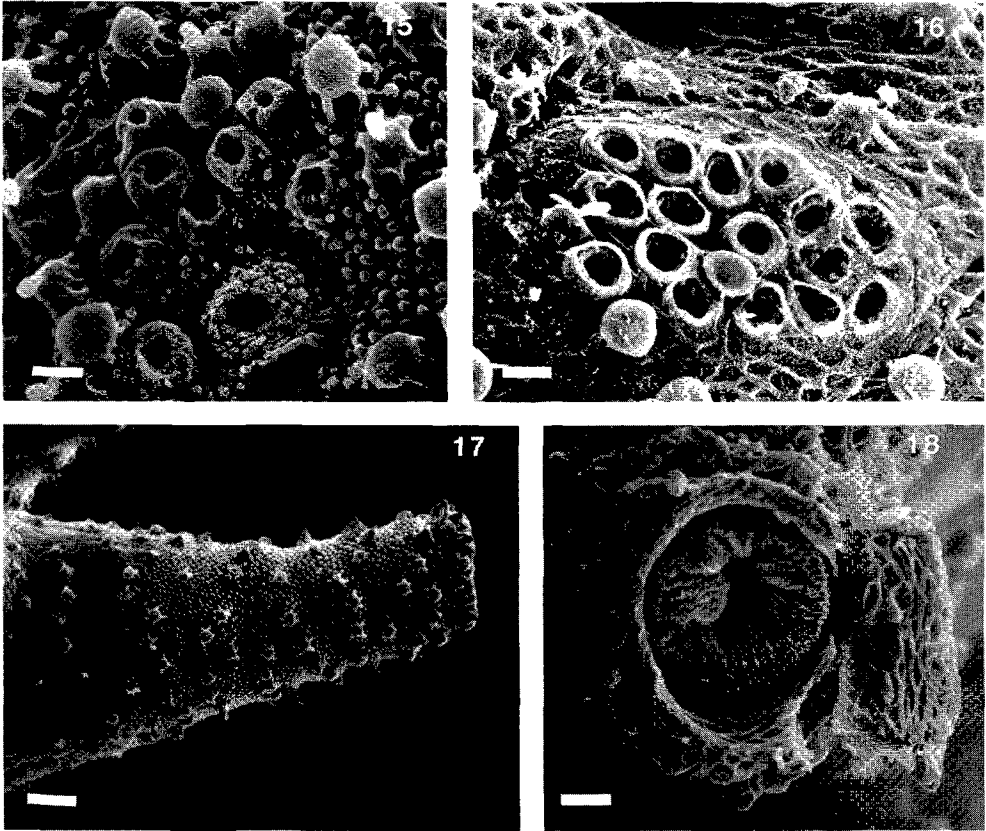
FIGS 2–5. FIG. 2. Short seta from A5. These short setae are found scattered over the cuticular surface of the larva. Note the fluted bases that are similar to other setal types. The nature of the waxy material covering the seta is unknown. Scale bar = 4  $\mu\text{m}$ . FIG. 3. Dome seta on A3. The nature of the waxy material scattered on the dome surfaces is unknown. Scale bar = 4  $\mu\text{m}$ . FIG. 4. Dome seta on tentacle organ surrounded by the round granulations that are also found on the T1 shield. These dome setae are scattered over the cuticle and have fluted bases that elevate the dome above the cuticle. Scale bar = 6.7  $\mu\text{m}$ . FIG. 5. Tactile setae found as a lateral fringe. Note that the bases are fluted as in the short and dome setae. Scale bar = 20  $\mu\text{m}$ .



FIGS 6–9. Dorsal and lateral pores. FIG. 6. Dorsal view of a portion of T1–3 and a portion of A1 showing paired dorsal and lateral pores and the scattering of short and dome setae. Scale bar = 125  $\mu\text{m}$ . FIG. 7. View of segment A7 showing the pairs of dorsal pores. The extreme right of the photograph shows the bases of the tentacle organs. Scale bar = 67  $\mu\text{m}$ . FIG. 8. Anterior dorsal pore on A7. Scale bar = 20  $\mu\text{m}$ . FIG. 9. Posterior dorsal pore on A7. This is the location where many lycaenid larvae bear the dorsal nectary organ. Note the similarity of this pore to the orifice of the DNOs found on other lycaenid taxa (eg Kitching and Luke, 1985). Scale bar = 20  $\mu\text{m}$ .



FIGS 10–14. The perforated cupola organs surrounding the spiracles. FIG. 10. A general close-up of PCOs, spiracle and dome seta found on segment A7. Scale bar =  $6.7\ \mu\text{m}$ . FIG. 11. Detail of PCO showing the globular shape, the sieve plate and the apparent secretion arising from the depressed central region. Scale bar =  $4\ \mu\text{m}$ . FIG. 12. The cluster of eight PCOs anterior to the T1 spiracle. Scale bar =  $20\ \mu\text{m}$ . FIG. 13. The cluster of five PCOs posterior to the A1 spiracle. Scale bar =  $20\ \mu\text{m}$ . FIG. 14. The cluster of three PCOs posterior to the A4 spiracle. Scale bar =  $10\ \mu\text{m}$ .



FIGS 15–18. The perforated chambers and tentacle organs. FIG. 15. The perforated chamber found on the lateral edge of the T1 shield. Note the dense scattering of short setae, dome setae and granulations. Scale bar = 20  $\mu\text{m}$ . FIG. 16. The perforated chamber found on A7. The orifices here have fewer attendant setae and lack the granulations seen on T1. Note that each of the orifices appears to communicate with a larger chamber beneath the cuticular surface. Scale bar = 20  $\mu\text{m}$ . FIG. 17. General view of right tentacle organ showing disparate distribution of surface granulations. Scale bar = 100  $\mu\text{m}$ . FIG. 18. Close-up view distal end of right tentacle organ. Note the short and dome setae, as well as the high density of granulations. These granulations are also found on the T1 shield. A portion of the distal end of the cylinder has been broken away exposing the inner surface. Scale bar = 67  $\mu\text{m}$ .