Nota lepid. 11 (2) : 100-116 ; 31.VIII.1988 ISSN 0342-7536

The preimaginal epidermal organs of *Lycaena tityrus* (Poda, 1761) and *Polyommatus coridon* (Poda, 1761) (Lepidoptera : Lycaenidae) – a comparison

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Summary

The preimaginal epidermal organs of *Lycaena tityrus* (Poda, 1761) and *Polyommatus coridon* (Poda, 1761) are described. In addition to a number of specialized types of setae (pore cupola organs, mechanoreceptors, and others), both species possess epidermal pores and, in the case of *P. coridon*, myrmecophilous glandular organs. Both species are compared, and the significance of the preimaginal epidermal organs in regard to the higher classification of the Lycaenidae and the complex interactions between lycaenid preimaginals and ants are discussed.

Zusammenfassung

Die epidermalen Organe der Präimaginalstadien von *Lycaena tityrus* (Poda, 1761) und *Polyommatus coridon* (Poda, 1761) werden beschrieben. Neben zahlreichen spezialisierten Haartypen (Porenkuppelorgane, Mechanorezeptoren und weiteren) besitzen die Larven beider Arten epidermale Poren. Die Raupe von *P. coridon* hat zusätzlich myrmekophile Organe. Beide Arten werden verglichen, und die Bedeutung der Epidermalorgane für die Großsystematik der Lycaenidae und die komplexen Beziehungen von Bläulingsraupen und -puppen zu Ameisen werden diskutiert.

Introduction

Relatively few of the studies published on the epidermal organs of lycaenid larvae and pupae have employed the SEM-technique (Downey & Allyn 1973, 1979, Schremmer 1978, Wright 1983, Kitching 1983, 1987, Kitching & Luke 1985, De Vries 1986), despite the fact that this technique is highly adequate for identifying the ultrastructure of the cuticle and, especially, the numerous secondary setae. Indeed, in many cases the SEM investigations revealed structures intraceable with standard light microscopical techniques.

On the other hand, a more complete knowledge of the epidermal organs of the immature stages of the Lycaenidae may contribute significantly to the solution of important problems concerning the taxonomy and systematics of this most species-rich of butterfly families. For example, the higher classification of the Lycaenidae currently based primarily on imaginal characters (Eliot 1973, Scott 1985) should be improved significantly when supported by larval and pupal features, too. Another subject of particular interest are the manifold interactions between lycaenid preimaginals and ants, which are mediated by various types of epidermal organs.

In this publication the epidermal organs of the larva and pupa of *Lycaena tityrus* as well as of the pupa of *Polyommatus coridon* are illustrated for the first time using SEM photographs. Thus, this paper tries to fill a gap in our knowledge of lycaenid preimaginal morphology, especially concerning the pupae which have been neglected the most in the past. My objective is (1) to compare the mature larvae and pupae of two unrelated European lycaenids, (2) to discuss the results in the view of lycaenid systematics and evolution, and (3) to draw attention to the role of epidermal organs in lycaenid myrmecophily.

Materials and methods

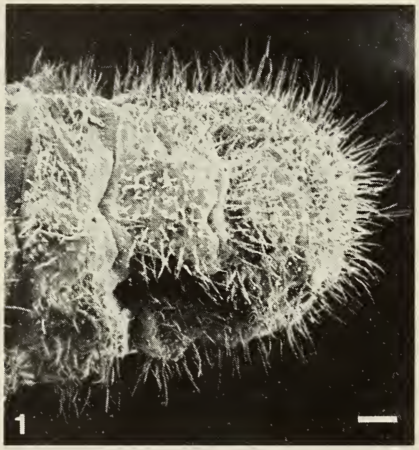
Larvae of *Polyommatus (Lysandra) coridon* (Poda, 1761) (Polyommatinae) were collected after hibernation in the vicinity of Würzburg, northern Bavaria, and reared in glass containers. Larvae and pupae of *Lycaena (Heodes) tityrus* (Poda, 1761) (Lycaeninae) were obtained from the ova of a female caught in the northern Spessart region, Hesse. Mature larvae and pupae of both species were fixed in 70% ethanol and dehydrated in 90, 96 and 100% ethanol. The completely dehydrated specimens were mounted on metal plates and examined in the SEM at a voltage of 20 kV after being sputtered with gold. Critical point dehydration turned out not to be necessary because the thick cuticle of both the larvae and pupae prevents shrinking or similar artifacts to a great extent.

Results

1. *Lycaena tityrus*

1.1. Fourth instar larva

The mature larva (length about 18-20 mm) is of typical lycaenid onisciform shape and is densely coated with straight, 0.5-1 mm long setae (fig. 1), which bear tooth-like projections in all directions every 10-20 µm (fig. 2). These typical secondary setae are distributed over the whole body surface. In addition, there are two further types of specialized setae. The first type are the mushroom-like setae (Wright 1983) (fig. 3, 4). In *L. tityrus* they have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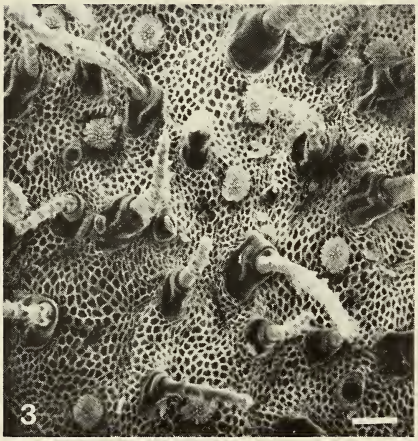
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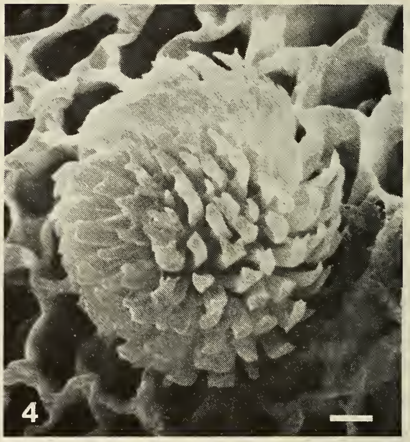
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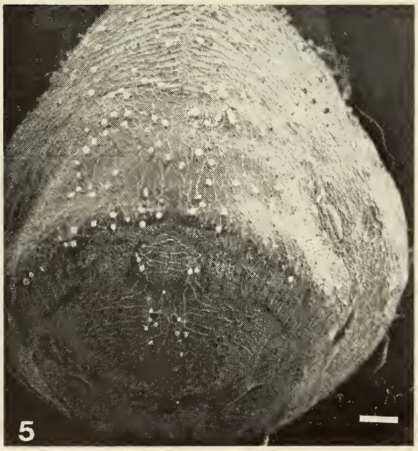
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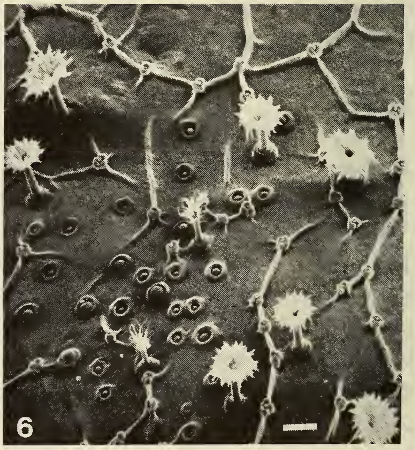
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a short shaft which does not protrude far from the cuticle. So the distal part of the mushroom-like setae, which is branched like an inflorescence of trefoil (*Trifolium* sp.), seems to sit directly on the cuticle. This is in remarkable contrast to the situation in species like, e.g., *Lycaena epixanthe* Boisduval & Leconte, [1833], in which Wright (1983) found the mushroom-like setae to have a conspicuous shaft.

The distal structure of the mushroom-like setae is nearly globular, with a diameter of 35-40 μm and a height of 30 μm. The mushroom-like setae are evenly distributed over the dorsal and lateral surface of the whole larva with a density of about 40 setae per mm^2 cuticle (fig. 3). Mushroom-like setae are found only on 4th instar larvae and are lacking in all preceeding instars.

The second type of specialized setae are the pore cupola organs (PCOs) and lenticles (Malicky 1969, Franzl et al. 1984, Kitching & Luke 1985), characterized by a reduced hemispherical hairshaft (sieve plate) of 20-25 μm in diameter and 10-15 μm in height. The density of the PCOs is highest around the spiracles (especially on the posterior abdominal segments) with 80 PCOs/mm^2. On the dorsal parts of the epidermis there are only 20-25 PCOs/mm^2. PCOs are present in all larval instars, but their number increases with every moult. No other specialized setae were found on the L_4 of *Lycaena tityrus.*

The cuticle itself has a characteristic wrinkled or honeycombed pattern : cuticle ledges form small chambers of about 5 μm diameter (fig. 3, 4).

Each segment has some dorsal and lateral depressions which are apparently locations of muscle insertions. Furthermore, there are epidermal pores in a typical arrangement on all segments (fig. 26).

1.2. Pupa

The pupa is 12-15 mm long and fairly stout. Its most intriguing epidermal organs are three types of specialized setae, of which the most conspicuous

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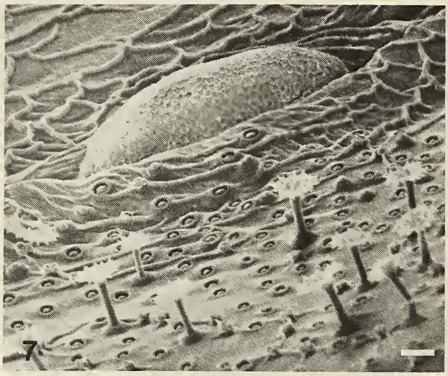
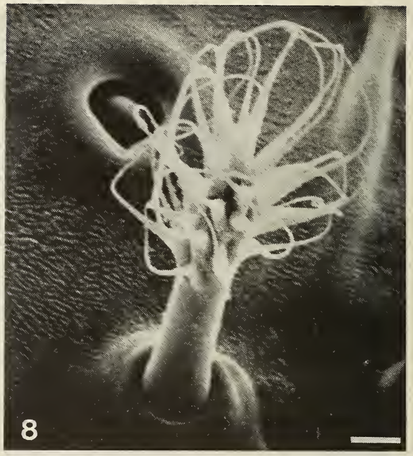
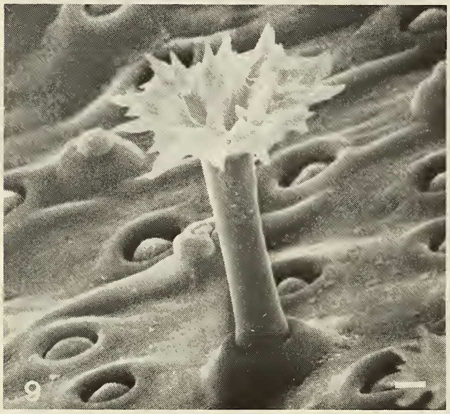
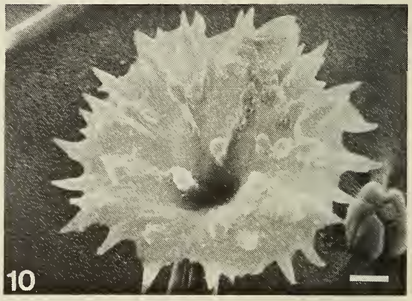
Fig. 1-14. *Lycaena tityrus* – mature larva.
Fig. 1. Posterior end of mature larva (scale 0.5 mm).
Fig. 2. Spiracle of 5th abdominal segment with spiny secondary setae, PCOs, and mushroom-like setae (scale 0.05 mm).
Fig. 3. Dorsal abdominal region of mature larva (scale 0.05 mm). Note the honeycomb structure of the cuticle.
Fig. 4. Mushroom-like seta (scale 0.005 mm).

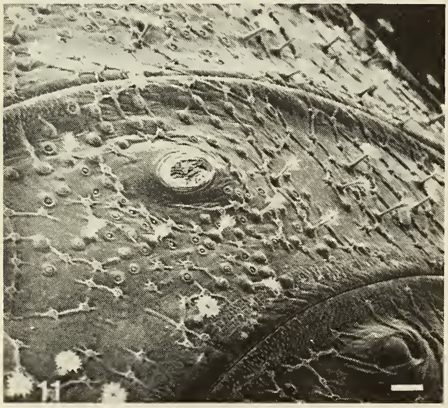
Fig. 5-12. *Lycaena tityrus* – pupa. For figs 7-12, see overleaf.
Fig. 5. Frontal view of the pupa with trumpet setae (scale 0.5 mm).
Fig. 6. Cuticle area in the frontal region of the pupa with trumpet setae, multibranched hydroid setae, and pore cupola organs (scale 0.05 mm).











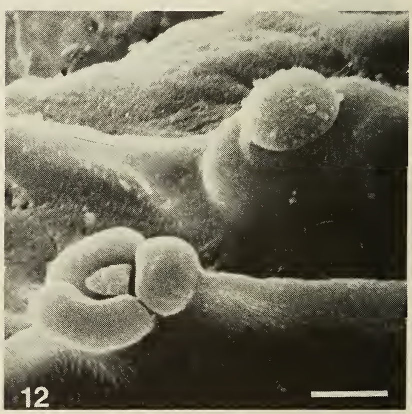


Fig. 7. *Lycaena tityrus* — Remnant of pupal prothoracic spiracle with trumpet setae and a dense clustering of PCOs (scale 0.05 mm).

Fig. 8. Multibranched hydroid seta (scale 0.01 mm).

Fig. 9. Trumpet seta, surrounded by PCOs (scale 0.01 mm).

Fig. 10. Distal structure of trumpet seta and a doughnut-like papilla (scale 0.01 mm).

Fig. 11. Spiracles of 6th and 7th abdominal segment ; around the spiracle of A6 hydroid setae, trumpet setae, and a cluster of PCOs ; around the reduced spiracle of A7 nearly no specialized organs (scale 0.1 mm).

Fig. 12. Doughnut-like papilla (left) and pore cupola organ (right) (scale 0.01 mm).

are the trumpet setae (Chapman 1905) (fig. 9, 10). The trumpet setae are 75 µm long with a funnel-shaped distal structure of 75 µm diameter. Trumpet setae are distributed evenly all over the pupa. They are sparse only on the wing covers and the latero-frontal parts of the head (fig. 5, 28).

The second type of secondary setae are PCOs again. They differ from the larval PCOs in having a ring-like collar around the sieve plate (fig. 12). The sieve plate has a diameter of 12-25 µm and either projects above its collar (PCO type A) or does not (PCO type B). Transitions between both types exist. Accumulations of PCOs occur around the spiracles with, e.g., a density of 80-100 PCOs of both types per mm^2 (fig. 7, 11). On the remainder of the body PCOs are distributed more sparsely (fig. 6, 28).

The last type of setae are the multibranched hydroid setae (Downey & Allyn 1973) (fig. 8) which occur only on two parts of the pupa : in the frontal region of the head (fig. 6) and around the spiracle of the 6th abdominal segment (fig. 11). They are 50 µm long with numerous fine branches of about 30 µm length in the distal half of the hair shaft. These hydroid setae are present on the pupa only in small numbers : less than 10 in the frontal part and about 10 on each side around the spiracle of A6. They are always associated with accumulations of PCOs.

The pupal cuticle shows a network of ribs (height 5-10 µm) (fig. 6, 7) which bear conspicuous papillose organs, the "doughnut-like papillae" (Wright 1983) (fig. 12). The rib network is interrupted irregularly forming polygonal cuticle areas of various size.

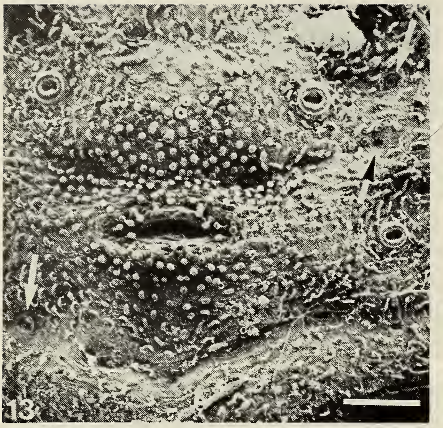
The last epidermal organ of the *Lycaena tityrus* pupa to be mentioned here is a stridulatory organ between the 5th and 6th abdominal segment. It is nearly identical to the one described by Wright (1983) and others (fig. 28).

2. *Polyommatus coridon*

2.1. Fourth instar larva

The mature larva of this species has been described in detail by Kitching & Luke (1985). It is about 20 mm long and onisciform. Its cuticle is verrucose and thick (fig. 19). Most of the body surface is covered with two different types of secondary setae : straight hairs of 0.5-1 mm length and curved setae of 70 µm length. Both types bear tooth-like projections and thus appear serrate. The straight hairs occur mainly laterally, whereas the shorter curved hairs are found on the dorsal parts of the caterpillar.

The highly myrmecophilous larva has a dorsal nectar organ (DNO, formerly often called "Newcomer's organ") on the 7th abdominal segment (fig. 13) which is surrounded by an area with club-like setae and many PCOs (fig. 14).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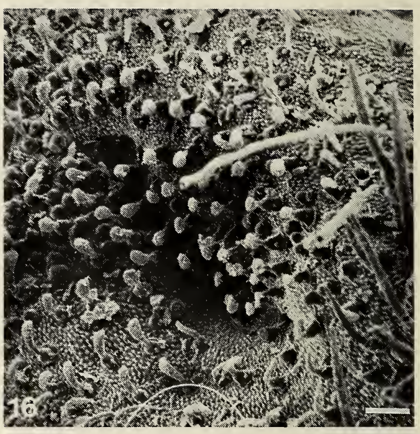
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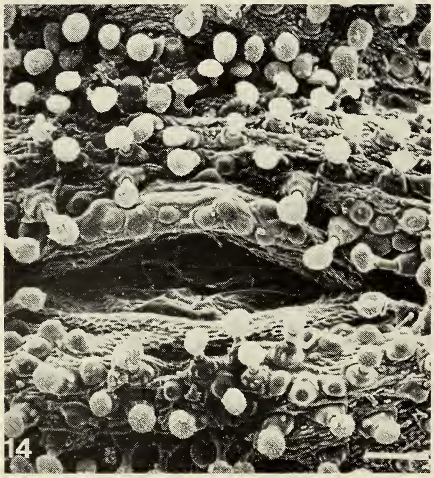
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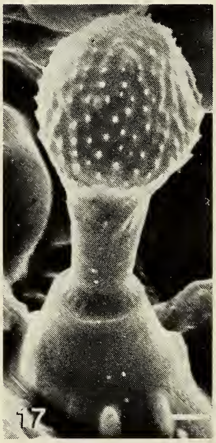
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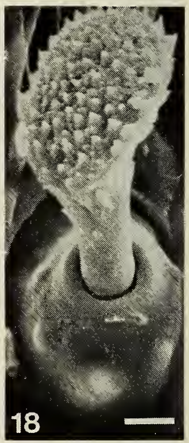
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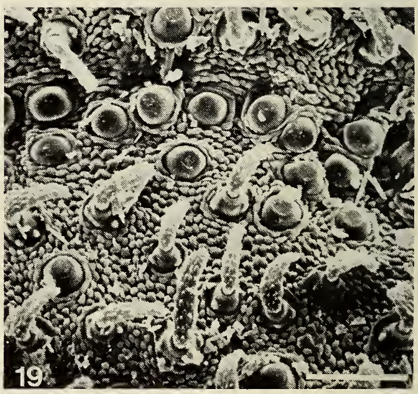
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The sieve plates of the PCOs are 40 μm in diameter, and these setae are scattered all over the larva with characteristic accumulations around the DNO and the spiracles. The club-like setae are 70 μm long with a globular spiny distal end of 45 μm diameter (fig. 17). They occur in considerable numbers around the DNO and in a lateral pit on the first abdominal segment around one of the epidermal pores (fig. 16, 18). Such epidermal pores are present laterally or dorsally on most segments in characteristic positions (fig. 13, 27).

Additionally, the larva possesses another myrmecophilous organ : the tentacle organs (TOs) on the 8th abdominal segment, a pair of eversible cuticular tubes with numerous branched hairs of 50 μm length (fig. 15). Other epidermal organs could not be found on the caterpillar.

2.2. Pupa

The pupa is 12-15 mm long, but not as stout as the one of *L. tityrus.* Its cuticle again shows a network of ribs (fig. 20), which is less regular and pronounced than in *L. tityrus* and lacks characteristic papillae on the ribs. The pupa has only a few straight secondary setae, concentrated in the frontal region. PCOs also occur scattered all over the body, but are heavily clustered around the spiracles of the prothorax (fig. 23) and the abdomen (fig. 21). Their sieve plates are 15-25 μm in diameter and their habitus is similar to the pupal PCOs of *L. tityrus.* There are two types of PCOs as well : with a sieve plate elevating hemispherical over the basal cuticle ring (type A) or with a flattened sieve plate reaching only the height of the collar and not protruding above it (type B) (fig. 17). A remnant of the DNO is visible on the 7th abdominal segment (fig. 20) and a stridulatory organ is present between the abdominal segments A5 and A6. No traces of the larval TOs are present (fig. 29).

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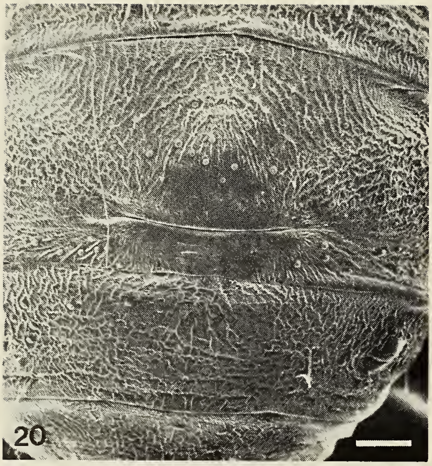
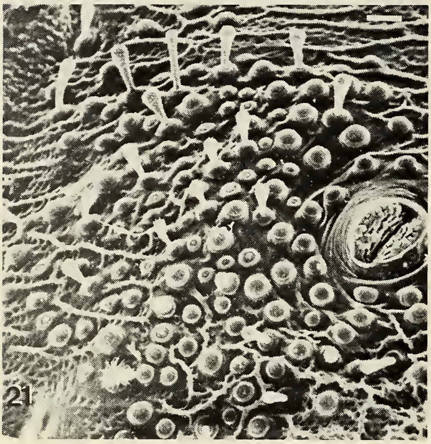
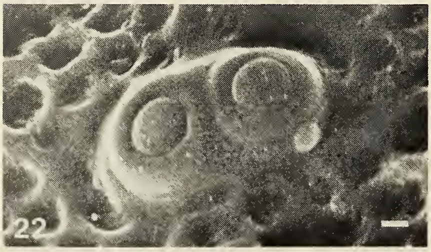
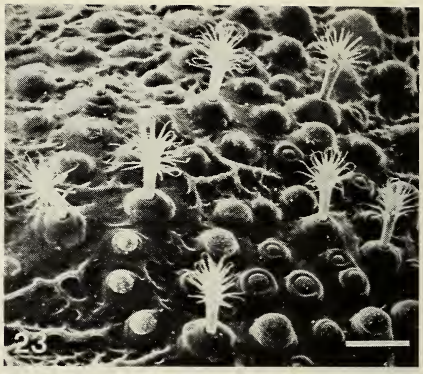
Fig. 13-19. *Polyommatus coridon* — mature larva.
Fig. 13. Dorsal view of 7th and 8th abdominal segment with the dorsal nectar organ (DNO). Arrows : epidermal pores (scale 0.5 mm).
Fig. 14. DNO with the field of club-like setae and numerous PCOs (scale 0.1 mm).
Fig. 15. Tentacular organ (retracted) of the 8th abdominal segment with numerous branched hairs (scale 0.01 mm).
Fig. 16. Lateral pit of the first abdominal segment with club-like setae (scale 0.1 mm).
Fig. 17. Club-like seta from the DNO region (scale 0.01 mm).
Fig. 18. Club-like seta from the lateral pit of fig. 16 (scale 0.01 mm).
Fig. 19. Part of the cuticle (dorsal view of 8th abdominal segment) with curved secondary setae and PCOs (scale 0.1 mm). Note the verrucose structure of the cuticle.









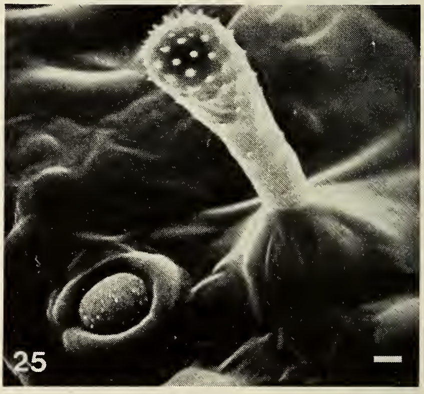


Fig. 20-25. *Polyommatus coridon* – pupa.

Fig. 20. Dorsal view of 7th to 9th abdominal segment with the remnant of the DNO and few PCOs (scale 0.25 mm).

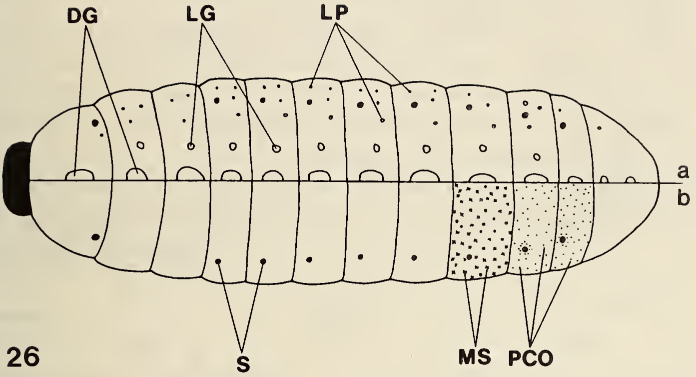
Fig. 21. Spiracle of 6th abdominal segment with club-like setae, one multibranched hydroid seta, and a cluster of PCOs (scale 0.05 mm).

Fig. 22. Double pore cupola organ (scale 0.005 mm).

Fig. 23. Area with multibranched hydroid setae and numerous PCOs from the remnant of the prothoracic spiracle (scale 0.05 mm).

Fig. 24. Multibranched hydroid seta from fig. 23 (scale 0.005 mm).

Fig. 25. Club-like seta (right) and PCO (left) from the prothoracic spiracle (scale 0.005 mm).



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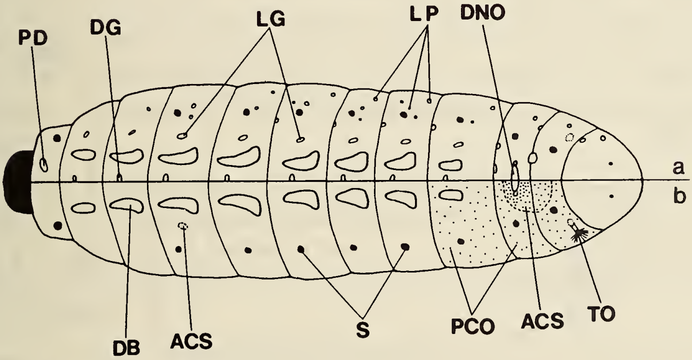

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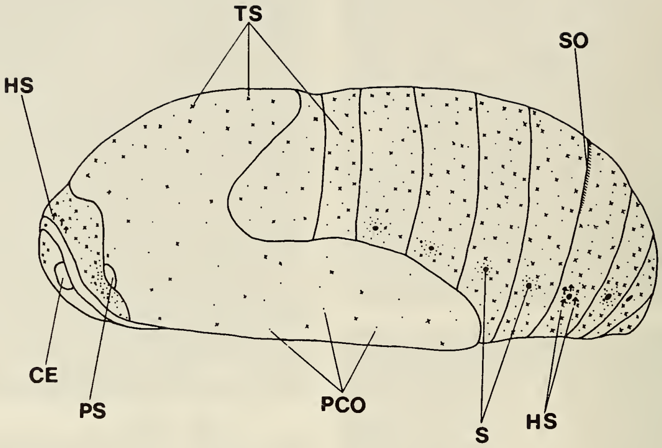
Fig. 26/27. Mature larvae of *Lycaena tityrus* (fig. 26) and *Polyommatus coridon* (fig. 27), schematic. *L. tityrus* is myrmecoxenous (without DNO and TOs), *P. coridon* myrmecophilous. The upper half of each drawing (a) shows the distribution of the epidermal pores and grooves, the lower half (b) the distribution of specialized setae. Normal secondary setae are omitted. ACS : accumulation of club-like setae ; DB : dorsal bulge ; DG : dorsal groove ; DNO : dorsal nectar organ ; LG : lateral groove ; LP : lateral pore ; MS : mushroom-like setae ; PCO : pore cupola organs ; PD : prothoracic depression ; S : spiracle ; TO : tentacular organ.



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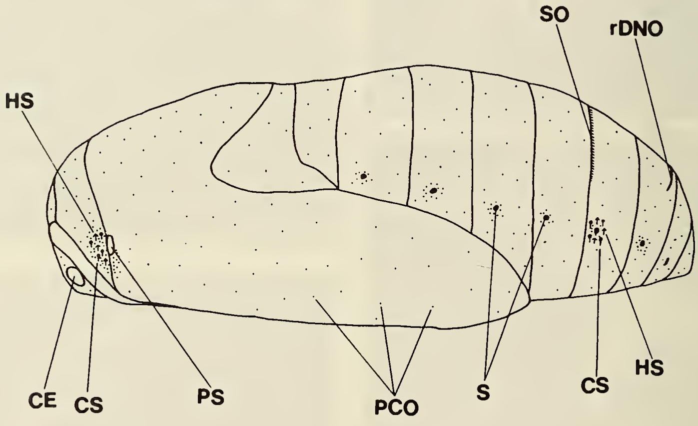

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Fig. 28/29. Pupae of *Lycaena tityrus* (fig. 28) and *Polyommatus coridon* (fig. 29), schematic. CE : compound eye ; CS : club-like setae ; HS : multibranched hydroid setae ; PCO : pore cupola organs ; PS : prothoracic spiracle ; rDNO : remnant of the DNO ; S : spiracle ; SO : stridulation organ ; TS : trumpet setae.

The most striking epidermal organs are two types of specialized secondary setae. Around the nonfunctional remnant of the prothoracic spiracle and the spiracle of A6 there occur club-like setae (fig. 25) and multibranched hydroid setae (fig. 24) within dense clusters of PCOs. The club-like setae are 70 µm long. Their thickened distal part is spiny as in the larval club-like setae, but less sharply pronounced and globular. Around the prothoracic spiracle there are only 5-10 club-like setae and around the spiracle of A6 there are 20-25. The multibranched hydroid setae are 50 µm long and bear numerous branches of 20-30 µm length in the distal half, thus being very similar to those of *L. tityrus* pupae. The prothoracic segment has less than 10 (fig. 23), the 6th abdominal segment less than five multibranched hydroid setae on each side (fig. 21).

Discussion

1. Comparison of both species

1.1. *Lycaena tityrus*

Mature larvae and pupae of this species show only minor differences to other *Lycaena* species. The mushroom-like setae of *L. tityrus* are figured here in detail for the first time. They are similar in construction to those of e.g. *L. epixanthe* (Wright 1983) with the exception of lacking a pronounced hairshaft. The pupal epidermal organs closely resemble those of other *Lycaena* species. The trumpet hairs are nearly indistinguishable from those of related species.

Lycaena tityrus, in addition, has multibranched hydroid setae, which have been reported also from other *Lycaena* species (*L. dispar* Haworth, 1803), but seem to lack in e.g. *L. phlaeas* Linnaeus, 1758, *L. helloides* Boisduval, 1852, and *L. epixanthe* (Downey & Allyn 1973, Wright 1983, and other references therein).

All *Lycaena* species, including *tityrus*, are myrmecoxenous in the terminology of Kitching & Luke (1985), because they have neither a DNO nor TOs. Their only myrmecophilous organs are the PCOs, and this is of particular importance with respect to their relationships towards ants (Fiedler & Maschwitz 1988a).

The mushroom-like and trumpet setae seem to be synapomorphic characters of the genus *Lycaena* or, perhaps, the whole subfamily Lycaeninae. They have never been reported from other lycaenids. Whether the occurrence or structure of the multibranched hydroid setae are useful to divide taxonomic subgroups within *Lycaena* remains open. Further studies concerning a broader spectrum of species are urgently needed to clarify this.

1.2. *Polyommatus coridon*

Compared with the results of Kitching & Luke (1985), two differences were found concerning the larvae of this lycaenid : the specialized setae are larger than stated by these authors, and the club-like setae additionally occur strictly localized in one lateral pit on A1. In all other aspects my results agree completely with those of the article cited above.

Pupae of the Polyommatinae have only rarely been investigated with the SEM. Downey & Allyn (1979) and Kitching (1983) did not mention the multibranched hydroid setae or club-like setae. Various types of specialized setae of Polyommatinae and many other lycaenid groups were depicted by Clark & Dickson (1971), but the current knowledge is too fragmentary to allow further speculations on the systematic value of these structures. The only type of setae present in all lycaenid pupae (and larvae) seem to be the PCOs which may be a synapomorphic character of the family Lycaenidae. Functional DNOs have never been observed in lycaenid pupae, but cuticular remnants of this myrmecophilous organ have been reported from various lycaenid species including *P. coridon* (fig. 20). The larval TOs are entirely absent in Polyommatinae pupae. Stridulation organs are apparently common in many lycaenids of several subfamilies (Downey & Allyn 1978).

It is of interest that larvae of *Polyommatus coridon* (as well as those of *P. bellargus* Rottemburg, 1775) have no branched hairs around their DNO, while many other polyommatine lycaenids possess such setae (Downey & Allyn 1979, Kitching 1983, Kitching & Luke 1985), including the related *Polyommatus icarus* Rottemburg, 1775. Perhaps the reduction of these branched hairs around the DNO is a synapomorphy of the *Lysandra* group within the genus *Polyommatus.*

2. Higher classification

The epidermal organs of lycaenid preimaginals may serve as valuable characters for the systematics of the family Lycaenidae. As far as is known today, most lycaenid subfamilies have unique types of setae or other organs which are apparently synapomorphies of them : trumpet and mushroom-like setae in the Lycaeninae, papillose and cauliflower organs in the Miletinae (Kitching 1987), dome setae in the Curetinae (De Vries 1986), and actiniform setae in some Riodininae (Schremmer 1978). The same is true for the glandular epidermal organs : DNO in the Polyommatinae and Theclinae, perforated chambers in the Curetinae, and a "pseudo-Newcomer organ" in the Miletinae. These glandular organs are supposed to be derivatives of the various epidermal pores that are found on lycaenid larvae in considerable numbers (Kitching & Luke 1985, De Vries 1986, Kitching 1987).

The aim of the following remarks is to draw attention to some striking differences between the widely adopted lycaenid classification by ELIOT (1973) and the results of investigations on preimaginal morphology. The hypotheses proposed are intended to stimulate further intensive discussions on lycaenid phylogeny.

a) The current higher classification of the Lycaenidae postulates that the Polyommatinae, Theclinae, and Lycaeninae together form a monophyletic group. In contrast, the lycaenine preimaginals differ completely from the Polyommatinae + Theclinae in their secondary setae equipment as well as in lacking both a DNO and TOs. The Lycaeninae seem to be extremely homogeneous in preimaginal morphology (WRIGHT 1983). I propose the hypothesis that the Lycaeninae are a very old and distinct group which can not be included in a monophyletic taxon with the Theclinae + Polyommatinae. This hypothesis agrees well with the striking zoogeography of the Lycaeninae (mainly holarctic distribution, but represented also weakly and as a relict in the southern hemisphere : South Africa, New Guinea, New Zealand), which suggests a very early separation (at least 80-100 millions of years ago) from the other lycaenid groups (MILLER & BROWN 1979). The myrmecoxenous habits of lycaenine caterpillars would thus be a plesiomorphic character in contradiction to, e.g., the hypothesis of MALICKY (1969), who assumed that the PCOs evolved at a stage where the DNO (and possibly the TOs) were already present.

Further investigations on lycaenine preimaginals, especially on other genera than *Lycaena*, are needed to prove the hypothesis suggested above. Also the significance of the similarity between the mushroom-like setae of the Lycaeninae and the papillose organs of the Miletinae has to be investigated.

b) The Curetinae might form a monophyletic group together with the Polyommatinae + Theclinae. They have TOs of basically similar structure at the same locations and a dorsal depression which might be homologous to the DNO (DE VRIES 1986), but such homology needs confirmation by histological examination. The dome setae and perforated chambers could be interpreted as synapomorphies of the Curetinae. Possibly the genus *Curetis* is derived from Theclinae-like ancestors.

c) The Miletinae and Riodininae seem to have split from the other Lycaenidae even earlier than the Lycaeninae. They both have unique characters in preimaginal morphology. The only epidermal organ they have in common with other lycaenid subfamilies are the lenticles and PCOs. Whether the "pseudo-Newcomer organ" of the Miletinae (KITCHING 1987) has anything to do with the DNO of the Polyommatinae + Theclinae is still unknown.

The above considerations show that much work has still to be done to clarify the higher classification of the Lycaenidae. Further extensive studies on preimaginal morphology would contribute well to this. The SEM technique is an adequate tool which should be further supplemented by histological and ultrastructural investigations.

3. Lycaenid-ant interactions

The myrmecophily of lycaenid preimaginals has been intensively studied (Warnecke 1932/33, Hinton 1951, Malicky 1969, Cottrell 1984). Epidermal organs are of special significance for these myrmecophilous relationships. The PCOs are supposed to be appeasement organs to overcome ant aggressiveness, and, in addition, they might produce amino acids as additional food for ants (Malicky 1969, Pierce 1983, 1984). The DNO secretes sugar solutions (Maschwitz et al. 1975) that enable the larvae to maintain symbiotic (i.e. trophobiotic) relationships with ants (Fiedler & Maschwitz 1988a, b). Thus, such larvae are protected against parasitoids and predators (Pierce & Mead 1981, Pierce & Eastseal 1986, Pierce et al. 1987). The TOs alert attendant ants (Downey & Allyn 1979, Henning 1983, De Vries 1986, Fiedler & Maschwitz 1988c), thereby probably increasing the effectiveness of the attendant ants in driving away parasitoids and predators. Epidermal organs (PCOs, DNO and possibly others) are also involved in the parasitic relationships of some lycaenids towards ants (Cottrell 1984).

In contrast, the function of all other epidermal organs of lycaenid preimaginals is completely obscure. The club-like setae are probably mechanoreceptors, as *P. coridon* larvae release DNO secretions only after mechanical stimulation of these structures, but experimental evidence for this view is needed. The other setae may also be receptors or they may be glandular hairs. The lenticles have been shown to be both innervated and secretory (Malicky 1969, Franzl et al. 1984). Another point for further investigations is the chemical composition of the secretions of the PCOs, TOs, and possibly other organs. Also the histological structure and function of the epidermal pores remains unknown.

Since the ant-lycaenid interactions are of fascinating complexity and have certainly heavily influenced the evolution and speciation within the Lycaenidae (Pierce 1984, Pierce & Young 1986, Maschwitz & Fiedler 1988), more information on morphology, histology, and life history of lyceanid preimaginals is needed to understand these phenomena.

Acknowledgement

I am indebted to the following persons: Dr. D. KOVAC for taking the SEM photographs, Dipl.-Biol. J. KLEIN for her help with the illustrations, Dipl.-Biol. W. A. NÄSSIG and R. W. KLEIN for their critical comments on the manuscript. I am grateful to Prof. Dr. U. MASCHWITZ for providing a laboratory place in his research group where the present study has been conducted.

References

CHAPMAN, T. A., 1905. Pupal skin of *Chrysophanus phlaeas. Entomol. Rec. J. Var.* 17 : 172-173.

CLARK, G. C. & DICKSON, C. G. C., 1971. Life histories of the South African lycaenid butterflies. Cape Town, Purnell.

COTTRELL, C. B., 1984. Aphytophagy in butterflies: its relationship to myrmecophily. *Zool. J. Linn. Soc.* 80 : 1-57.

DOWNEY, J. C. & ALLYN, A. C., 1973. Butterfly ultrastructure. I. Sound production and associated abdominal structures in pupae of Lycaenidae and Riodinidae. *Bull. Allyn Mus.* 14 : 1-47.

DOWNEY, J. C. & ALLYN, A. C., 1978. Sounds produced in pupae of Lycaenidae. *Bull. Allyn Mus.* 48 : 1-14.

DOWNEY, J. C. & ALLYN, A. C., 1979. Morphology and biology of the immature stages of *Leptotes cassius theonus* (LUCAS) (Lepid. : Lycaenidae). *Bull. Allyn Mus.* 55 : 1-27.

ELIOT, J. N., 1973. The higher classification of the Lycaenidae (Lepidoptera): a tentative arrangement. *Bull. Br. Mus. nat. Hist., Entomol. Ser.* 28 : 373-505, 6 plates.

FIEDLER, K. & MASCHWITZ, U., 1988a. Functional analysis of the myrmecophilous relationships between ants (Hymenoptera : Formicidae) and lycaenids (Lepidoptera : Lycaenidae). I. Release of food recruitment in ants by lycaenid larvae and pupae. *Ethology* (in press).

FIEDLER, K. & MASCHWITZ, U., 1988b. Functional analysis... II. Lycaenid larvae as trophobiotic partners of ants — a quantitative approach. *Oecologia (Berlin)* 75 : 204-206.

FIEDLER, K. & MASCHWITZ, U., 1988c. Functional analysis... III. New aspects of the function of the retractile tentacular organs of lycaenid larvae. *Zool. Beitr. N.F.* 31 (3) : 409-416.

FRANZL, S., LOCKE, M. & HUIE, P., 1984. Lenticles : innervated secretory structures that are expressed at every other moult. *Tissue & Cell* 16 : 251-268.

HENNING, S. F., 1983. Chemical communication between lycaenid larvae (Lepidoptera : Lycaenidae) and ants (Hymenoptera : Formicidae). *J. Ent. Soc. Sth. Afr.* 46 : 341-366.

HINTON, H. E., 1951. Myrmecophilous Lycaenidae and other Lepidoptera — a summary. *Proc. Trans. S. London Ent. Nat. Hist. Soc.* 1949-50 : 111-175.

KITCHING, R. L., 1983. Myrmecophilous organs of the larvae and pupae of the lycaenid butterfly *Jalmenus evagoras* (DONOVAN). *J. Nat. Hist.* 17 : 471-481.

Kitching, R. L., 1987. Aspects of the natural history of the lycaenid butterfly *Allotinus major* in Sulawesi. *J. Nat. Hist.* 21 : 535-544.

Kitching, R. L. & Luke, B., 1985. The myrmecophilous organs of the larvae of some british Lycaenidae (Lepidoptera) : a comparative study. *J. Nat. Hist.* 19 : 259-276.

Malicky, H., 1969. Versuch einer Analyse der ökologischen Beziehungen zwischen Lycaeniden (Lepidoptera) und Formiciden (Hymenoptera). *Tijdschr. Ent.* 112 : 213-298.

Maschwitz, U. & Fiedler, K., 1988. Koexistenz, Symbiose, Parasitismus : Erfolgsstrategien der Bläulinge. *Spektr. Wiss.* 1988 (5) : 56-66.

Maschwitz, U., Wüst, M. & Schurian, K., 1975. Bläulingsraupen als Zuckerlieferanten für Ameisen. *Oecologia* 18 : 17-21.

Miller, L. D. & Brown, F. M., 1979. Studies on the Lycaeninae (Lycaenidae). 4. The higher classification of the American coppers. *Bull. Allyn Mus.* 51 : 1-30.

Pierce, N. E., 1983. The ecology and evolution of symbioses between lycaenid butterflies and ants. Doctoral dissertation, Harvard University.

Pierce, N. E., 1984. Amplified species diversity : a case study of an Australian lycaenid butterfly and its attendant ants. *In* Vane-Wright, R. I. & P. R. Ackery (eds), The Biology of Butterflies. *Symp. Royal Ent. Soc. London* 11 : 197-200.

Pierce, N. E. & Eastseal, S., 1986. The selective advantage of attendant ants for the larvae of a lycaenid butterfly, *Glaucopsyche lygdamus. J. Anim. Ecol.* 55 : 451-462.

Pierce, N. E., Kitching, R. L., Buckley, R. C., Taylor, M. F. J. & Benbow, K. F., 1987. The costs and benefits of cooperation between the Australian lycaenid butterfly, *Jalmenus evagoras*, and its attendant ants. *Behav. Ecol. Sociobiol.* 21 : 237-248.

Pierce, N. E. & Mead, P. S., 1981. Parasitoids as selective agents in the symbiosis between lycaenid butterfly larvae and ants. *Science* 112 : 1185-1187.

Pierce, N. E. & Young, W. R., 1986. Lycaenid butterflies and ants : two-species stable equilibria in mutualistic, commensal, and parasitic interactions. *Am. Nat.* 128 : 216-227.

Schremmer, F., 1978. Zur Bionomie und Morphologie der myrmekophilen Raupe und Puppe der neotropischen Tagfalter-Art *Hamearis erostratus* (Lepidoptera : Riodinidae). *Ent. Germ.* 4 : 113-121.

Scott, J. A., 1985. The phylogeny of butterflies (Papilionoidea and Hesperioidea). *J. Res. Lepid.* 23 : 241-281.

Warnecke, G., 1932/33. Übersicht über die bisher als myrmekophil bekannt gewordenen paläarktischen Schmetterlingsraupen der Familie Lycaenidae. *Int. Ent. Z. Guben* 26 : 165-171, 215-219, 238-242, 285-291, 375-378, 431-433, 460-462, 479-480, 514-516 ; 27 : 44-46, 121-127, 145-150, 178-180, 305-309, 3 plates.

Wright, D. M., 1983. Life history and morphology of the immature stages of the bog copper butterfly *Lycaena epixanthe* (Bsd. & Le C.) (Lepidoptera : Lycaenidae). *J. Res. Lepid.* 22 : 47-100.

Zeitschrift/Journal: Nota lepidopterologica

Jahr/Year: 1988

Band/Volume: 11

Autor(en)/Author(s): Fiedler Konrad

Artikel/Article: The preimaginal epidermal organs of Lycaena tityrus (Poda, 1761) and Polyommatus coridon (Poda, 1761) (Lepidoptera : Lycaenidae) — a comparison 100-117