NEW ASPECTS ON THE ASSOCIATION BETWEEN LYCAENID LARVAE (LYCAENIDAE) AND ANTS (FORMICIDAE, HYMENOPTERA)

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Introduction

The association between lycaenid larvae and ants is well known and has been discussed several times in the literature. The most recent survey is by Hinton (1951). Since the majority of published reports are purely descriptive it would seem both desirable and necessary to consider the evolutionary sources of the association using an experimental approach. It is the purpose of this paper to present a summary of the essential facts and new thoughts bearing on this association based on this approach; details of these investigations will be published elsewhere.

Current Hypotheses

The best known hypothesis advanced to explain the relationship between ants and the larvae originated with Thomann (1901). He suggested that ants are able to drive away the caterpillar's parasites, so that the lycaenids benefit from the presence of the ant. In order to attract the ants and keep them in attendance, the caterpillars exude a honey-like liquid from a particular glandular organ, which was first described by Newcomer (1912). According to this hypothesis the association is a symbiosis. This hypothesis, however, has several weak points. Firstly, it has not been confirmed that ants are able to drive away parasitic Ichneumonidae and Tachinidae or even notice their presence. Secondly, there is no evidence that the presence of the ant lowers significantly the rate of parasitism of the caterpillars. Field observations by this writer show that the degree of parasitism of lycaenid larvae fluctuates widely, as is usual in Lepidoptera, whether ants are present or absent. Thirdly, the behavior of ants in respect to lycaenid larvae shows no significant difference between species which lack Newcomer's gland and those which have it.

A second hypothesis has been advanced by Lenz (1917). According to him, the larval adaptations function to prevent aggression by the ant toward the lycaenid larvae, and the honey-like liquid is exuded as a "bribe" to the ants. Recent knowledge supports this hypothesis.

Present Investigations

Methods

According to Thomann's hypothesis the association of ant and lycaenid larvae should lower the rate of parasitism of the larvae in comparison with larvae of the same kinds which are not attended by ants. The examination of this supposition seems to be technically impossible. In field experiments it is not possible to exclude only the ants without changing other factors. Results of experiments under laboratory conditions, on the other hand, do not take into consideration other important field circumstances. It would seem necessary to divide complicated ecological phenomena as far as possible into factors, and to determine whether the presumed connections actually exist.

The behavior of more than 50 ant species in relation to about 35 species of lycaenid larvae has been investigated under both laboratory and field conditions. The anatomy of the larvae has been studied microscopically in the usual manner using serial sections, which were stained with *pafhalmi*. More than 60 species of lycaenid larvae and pupae, mainly European, have been dissected and/or investigated morphologically. Additional ecological investigations have been carried out in the field in order to find out the biotopes and strata inhabited by ants and caterpillars.

The particular behavior of ants and its releasing mechanism

When not excited, ants perform a slow antennal motion which may be called "groping" (Tasten). At excitement, under certain circumstances, their antennal motion becomes much faster and the antennae are bent into an acute angle. This motion may be called "palpation" (Trillern). The antennal positions of both motions are demonstrated in Fig. 1. Ants which are visiting a lycaenid larva perform intensive antennal palpation. This is symptomatic of the fact that the ants perceive the caterpillar as an object distinct from surrounding stones, litter, etc. Therefore palpating may be regarded as a sign for the particular association. The sucking of "honey" which originates from Newcomer's gland, cannot be such a sign because these glands are not present in many species which are attended in the same particular manner by ants. Releasers of groping are a number of common stimuli of less specific significance. Palpating may be released in different ways, but in lycaenid larvae presumably only in chemical ones because no particular mechanical structures could be detected on the integument of the caterpillars where palpation takes place. The ants do not palpate with the same intensity over the whole surface of the caterpillars. They prefer distinct spots whose situation differs according to the species but is constant within it.

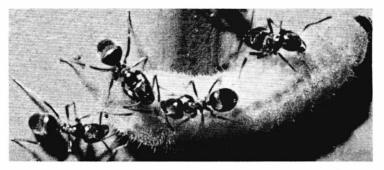


Fig. 1. Ants (*Lasius alienus* Foerster) attending a lycaenid larva (*Plebejus argyrognomon* Bgstr.). Notice the antennal positions: groping (extreme left, right above) and palpating (central left).

In the majority of species examined, one of these spots for increased rate of palpation is the dorsal part of the prothorax. Another is situated laterally near the spiracles, principally those near the posterior part of the body (esp. in Lycaeninae and Theclini). A third spot is on the dorsal part of the 7th and 8th abdominal segments surrounding the mouth of Newcomer's gland (esp. in many species of "blues" and Strymonini). These spots contain accumulations of small epidermal glandular organs which may be called "perforated cupolas" (Fig. 2). These organs are, like Newcomer's organ, homologous to hairs. They consist of two cells, one of which is homologous to the trichogen cell of the hair and is sometimes interlaced by longitudinal cavities which enclose the enormous nucleus. It must be supposed that they produce the volatile substance which releases the ant's palpation. The second cell, homologous to the tormogen cell, forms a plasmatic tube which serves as pipe-line for the secretion. The distal part of the organ consists of a cuticular sclerotized perforated plate of about 20 μ m in diameter.

The "perforated cupolas" and their secretion, which acts as pheromone, are of major importance for the association between lycaenid larvae and ants. With the single exception of the European Nemeobius lucina L., these organs are present in all lycaenid larvae investigated. In some of them (e.g. Feniseca tarquinius, Apodemia mormo, Phasis thero, and Poecilmitis thysbe) the perforation of the distal plate can not be recognized distinctly with the equipment used, so that investigation with an electron microscope is necessary. For comparison, caterpillars of several other families have been investigated, but nowhere could perforated cupolas be detected. They are likewise present in the pupae of lycaenids which are attended by ants in the same manner as the larvae.

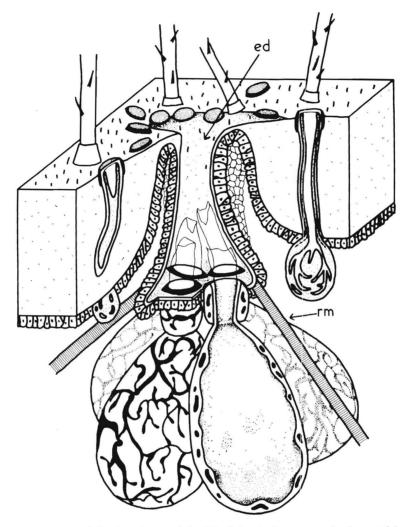


Fig 2. Section of the dorsal part of the 7th abdominal segment of a lycaenid larva, with glandular organs. Center: Newcomer's gland with four glandular bladders, exudation duct (ed) and retractor muscles (rm). Right: "perforated cupolas" section. Above: external parts of several cupolas.

Lack of "beat reflex" in lycaenid larvae

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Experiments indicate that when the majority of non-lycaenid lepidopterous larvae are physically disturbed, they perform a reflex lateral beating motion. The biological function of this motion is presumably to shake away rapacious arthropods. Nevertheless, this has little efficiency against attacks of ants since fast motions usually release aggression in ants. In the lycaenid larvae examined (with the exception of *Nemeobius lucina* and *Phasis thero*) this reflective motion is not performed. This behavior is an additional adaptation to the association with ants.

Interrelations between the construction of integument of the caterpillars and the mandibles of ants

The lycaenid larvae examined have, without exception, soft but tough cuticles of unusually thick dimensions. Caterpillars other than lycaenids of the same size have cuticles about 5–10 μ m, but in full grown lycaenid larvae, 200–300 μ m thicknesses are usual (Fig. 3). Except for a thin epicuticular layer of less than 1 μ m, the integument consists of endocuticle only. The exocuticle is restricted to local sclerotizations, e.g. those in the dorsal part of the prothorax, the head capsule, the thoracic legs, the hooks of abdominal legs and the like.

In behavior experiments, it often happened that ants attacked the lycaenid caterpillars despite the presence of perforated cupolas and Newcomer's glands but, as a rule, the caterpillars were not damaged because of the particular construction of the ant's mandibles. This mandible construction is unique within predacious arthropods. The molar part, a ledge with a row of small teeth, prevents the penetration of the sharp, elongate incisive part through the thick cuticle. Thin cuticles of caterpillars other than Lycaenidae may be easily penetrated. On the other hand, the construction of the mandibles of predacious Carabidae, Staphylinidae, and Silphidae, and the chelicera of spiders, penetrate even this voluminous lycaenid cuticle without difficulty.

The thickness and plasticity of the cuticle is, therefore, a goal adaptation specifically for ants since it does not protect from attacks of other predators. Ant mandibles without this molar ledge also exist (e.g. in Dorylinae and in the social parasites *Polyergus* and *Strongylognathus* etc.), but their owners are not associates of lycaenid larvae.

In addition to its thickness, the lycaenid cuticle is folded in a particular manner, to which fact the larvae owe their woodlice-like appearance. Very vulnerable organs, such as the dorsal blood vessel and ventral nerve cord, are protected under concavities (see Fig. 3). The prominent protrusions contain less important structures such as fat bodies etc. A biting ant is forced to crush one of the prominent cuticular ledges or protrusions between its mandibles, thus giving additional protection to the caterpillar, because its important organs become folded inward and not damaged. It is noteworthy that the size of these ledges corresponds well with the size of the mandibles of medium-sized ants but not with those of other caterpillar predators, which are much larger (Fig. 3).

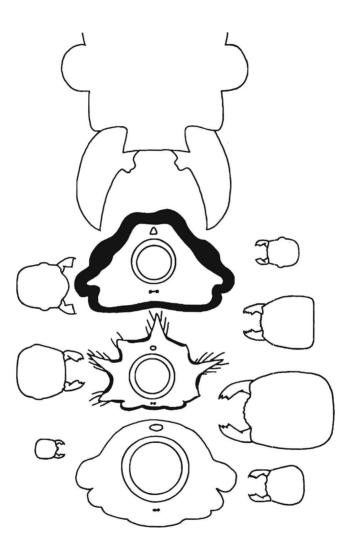


Fig. 3. Cross-section of a lycaenid (above), a nymphalid (center) and a noctuid (below) larva, each with comparative cuticular thickness. Lateral figures are outlines of ant heads. Left from top to bottom: Myrmica scabrinodis, Cremastogaster scutellaris, Solenopsis fugax. Right: Leptothorax lichtensteini, Camponotus ligniperda (small worker), ditto. (big worker), Prenolepis nitens. Above: Outline of the head of a caterpillar-hunting beetle (Calosoma inquisitor, Carabidae). Drawn to the same scale.

| Spalginae | | | Tentacles |
|---|---|------|-----------|
| Feniseca tarquinius F. | + | _ | _ |
| | 1 | | |
| Aphnaeinae Phasis thero L. | 1 | | - 1 |
| Poecilmitis thusbe L. | ++ | +(?) | + |
| | -1- | 1(.) | 1 |
| Theclinae | | | |
| Thecla betulae L., Quercusia quercus L., | | | |
| Calycopis beon Cram. | + | - | - |
| Strymonidia acaciae F., Fixsenia pruni L., Strymon melinus Hb. | + | R? | |
| Strymon meanus Hb. Strymonidia spini Den. et Schiff., S. w-album Knoch, S. ilicis Esp., Callophrys rubi L., C. | ÷ | R: | - |
| avis Chapm., C. henrici Grote et Rob., C. | | | |
| gryneus Hb., C. nelsoni Bdv., "Thecla" | | | |
| palegon Stoll | + | + | |
| Tomares ballus F., T. callimachus Ev., T. mauretanicus Lucas | + | - 1 | + |
| | Ŧ | Ŧ | T |
| Lycaeninae | | | |
| Lycaena phlaeas L., L. thoe Guer., | | | |
| + 7 additional European spp. | + | - | _ |
| Zizeeriinae | | | |
| Zizina labradus Godt. | + | + | + |
| Lycaenopsinae | | | |
| Lycaenopsis argiolus L. | + | + | + |
| | , | | • |
| Everinae | , | ĩ | ĩ |
| Everes comyntas Godt., E. argiades Pall. | +++++++++++++++++++++++++++++++++++++++ | + | + |
| Cupido minimus Fuessly | Ŧ | Ŧ | _ |
| Lampidinae | | | |
| Cosmolyce boeticus L. | + | + | + |
| Glaucopsychinae Scolitantides orion Pall., Philotes vicrama Moore, Glaucopsyche alexis Poda | + | + | + |
| Iolana iolas O., Maculinea, 4 European spp. | + | + | - |
| Plebejinae Plebejus icarioides Bdv. + 3 addit. European spp., Aricia 4 spp., Cyaniris semiargus Rott., Polymmatus 9 spp. | + | + | + |
| | 1 | 1 | 1 |
| Hamearinae Nemeobius lucina L. | - | - | - |
| Ancylurinae | | | |
| Apodemia mormo Felder | + | _ | _ |

TABLE 1. Presence of particular organs in lycaenid larvae (only new results, literature records are not included).

+ means present, - means absent, R means reduction stages.

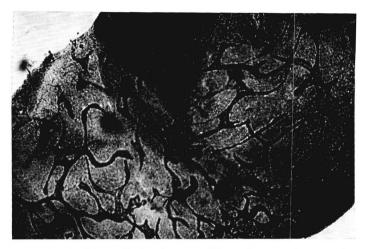


Fig. 4. Part of a glandular cell ("trichogen cell") of Newcomer's organ of a lycaenid larva (*Cupido minimus*) with extremely divided nucleus. Stained with KES (aceto-carmine).

The role of Newcomer's gland

The larger glands whose external mouth is situated dorsally on the 7th abdominal segment were mentioned by Guenée (1867) and described anatomically and histologically by Newcomer (1912), Ehrhardt (1914), and Fiori (1958). Although the descriptions of these authors do not agree in detail, I found that the construction of the organ is the same in all species which I have investigated (Fig. 2). Ehrhardt noticed that the vast glandular bladders consisted of only two big cells each with one branched nucleus (Fig. 4) and not, as Newcomer and Fiori presume, of an epithelium of many small cells or a syncytium. Additional details, including the ontogeny of these organs, are given by Malicky (1969).

Newcomer's organ is not present in all species of lycaenid larvae. Members of the same subfamily, tribe or even genus may have or lack this organ (Table 1). Some species, e.g. *Strymon melinus* Hb., *Strymonidia acaciae* F. and *Fixsenia pruni* L. appear to be actually in a stage of reduction of the organ. It may be presumed that this organ was present in all ancestral lycaenids (except for some "riodinids") and has been subsequently reduced or lost in all lycaenid caterpillars where it does not occur now.

It is well known that attending ants imbibe the honey-like liquid which is exuded by the glands. The organ and its secretion plays an important role within the association. Nevertheless, the lack of Newcomer's organ in many species suggests that the secretion of the perforated cupolas is more effective in the relationship between the two kinds of insects.

The function of the tentacles

The paired eversible cylindric organs on the 8th abdominal segment of some lycaenid larvae have been known for a long time. They may be termed "tenacles." D...S (1785) noted as early as the eighteenth century the "rote Wärzgen" in the larva of *Plebejus argus*. Several authors suggested that these tentacles have an odoriferous function which might signal the presence of a honey-producing caterpillar to ants. I can not confirm this suggestion. I have never noticed any significant reaction of ants to the tentacles, and I could not find any glandular structures in, on or near them. They contain only distally inserted setae of usual construction but minor size. Therefore, the function of the tentacles still must be regarded as unknown. They may be rudimental structures, developing from organs such as Ross (1964), Bourquin (1953) and Bruch (1926) found in several Ancylurinae and Hamearinae.

Which kinds of ants may be associated with lycaenid larvae in the field

In my experiments, only European representatives of Formicinae, Dolichoderinae, Myrmicinae, and Ponerinae were studied. Only five of them proved to be incapable of reacting specifically to lycaenid larvae. They were: one extremely specialized social parasite (Polyergus rufescens Latr.), three specialized grain collectors (Messor mutica Nyl., M. rufitarsis F., Aphaenogaster subterranea Latr.) and two soil-inhabiting species (Murmecina graminicola Latr., Ponera coarctata Latr.). The majority of species investigated, such as members of the genus Formica, Camponotus, Lasius, Myrmica, Solenopsis, Leptothorax, etc. showed the same reaction in qualitative respects. Field data furnished by Downey (1962) from the Nearctic Plebejus icarioides (Bdv.) help confirm this, since no less than 11 different ant species of diverse taxonomic affinities were found attending one species of butterfly. In general, the ant species which attend lycaenid larvae seem to be the same ones which also attend Homoptera and which have a high-developed trophallaxis between adults and larvae. This hypothesis may contribute to an explanation of the evolution of the association between ants and lycaenids.

Which kinds of lycaenid larvae are attended by ants in the field

With the single exception of *Nemeobius lucina*, all species investigated in the laboratory induced an ant association. Several species were frequented less intensively by the ants but the behavior of the ants toward the larvae was the same in a qualitative sense. This result does not agree with field notes, because while several kinds of lycaenid larvae (e.g. *Plebejus argus* L., *Scolitantides orion* Pall.) are never found without ants, other species have never been recorded as being ant-attended. Therefore, additional field research was undertaken which led to the idea that for the association of certain partners, a common biotope preference is most important. There is an additional preference of activity of certain kinds of ants and caterpillars for the soil surface (e.g. in *Tetramorium caespitum* L., *Lasius flavus* F., and *Plebejus argus* L.), for the herbaceous vegetation (e.g. in *Myrmica scabrinodis* Nyl. and several *Polyommatus* and *Lycaena* spp.) or for the shrub and tree stratum (e.g. in *Colobopsis truncata* Spin., *Dolichoderus quadripunctatus* L., and several Theclinae).

Exceptions

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As already mentioned, the majority of lycaenid larvae and ants may be associated only in a facultative way. The caterpillars do not need the ant's presence. Nevertheless, in a few cases, close relations exist between specific lycaenids and ants. In Europe, the four species of the genus Maculinea are associated with ant species of the genus Myrmica. These caterpillars are phytophagous up to the last molt and are then carried into the ant nests by worker ants. There they live as social parasites, feed on the ant's brood, and are fed orally by the adults. This association is based upon additional adaptations. The molts take place at very short intervals so that the last molt occurs only a few days after the larval emergence from the egg. I presume that this is necessary for the accumulation of the highest number of perforated cupolas at the time when the caterpillar is ready to be carried into a Myrmica nest. It therefore resembles the ant larva in size, consistence and presumably odor. In addition, the critical stage to be carried into the nest is well synchronized with the activity of the host: in July and August, in the biotopes of these lycaenids, only members of the genus Murmica are in full activity, because the majority of other Central-European ants have very low activity during summer. Another adaptation is that the Maculinea larvae perform a distinct begging behavior similar to that of the ant's larvae, which releases the feeding response in the worker ants.

In the literature several lycaenids are also recorded to have carnivorous associations, e.g. *Lachnocnema bibulus* F. (Cripps and Jackson, 1940), *Niphanda fusca* Brem.-Grey and *Spindasis takanonis* Mats. (Iwase, 1953, 1955), *Euliphyra mirifica* Holl. (Lamborn, 1914) and *Liphyra brassolis* Westw. (Chapman, 1902). However, such association depending in an obligate way on the ant's care is exceptional. Bionomical data are availa-

ble for about 800 lycaenid species, but only 10 are known to belong to these exceptions.

Principles, function and evolution of the association

The association between lycaenid larvae and ants is based upon several ethological, morphological and chemical goal adaptations of the caterpillars to the behavior and the social biology of the ants. There is no reference to any adaptation of ants to the lycaenid's habits. Some of the caterpillar's adaptations are based upon copies of signals (Signalkopien) which are important in the ant's social life. The secretion of the perforated cupolas is presumed to be similar to, or identical with, ant pheromones. The Maculinea larvae copy a Myrmica larva in size and habits. The lack of the beating-reflex and the presence of a thick cuticle are adaptations to the aggressive behavior and to the mandible construction of ants. Therefore, the biological function of the association is to protect the caterpillars from the ant's aggression. Protection from ant aggression is, however, not restricted to lycaenids. Among insects and other arthropods many ways are realized which serve the same purpose. Armoured cuticles (e.g. in many Coleoptera), dense pilosity (larvae of Arctiidae, Lymantriidae etc.), chemical repellents (Coccinellidae, Zygaenidae), construction of protecting cases (Psychid and Tortricid larvae) and other devices prevent ant aggression or render it ineffectual. In this respect, the particular association of the lycaenids is only one of several realized chances.

The evolution of this association can only be sketched in broad outlines, since the details of anatomy and histology are available only in few kinds of caterpillars. Presumably the present day larvae originate from a kind which differed from other lepidopterous larvae by its voluminous cuticle. Larvae such as *Nemeobius lucina* may derive directly from this stage. Another evolutionary pathway lead to the development of big and eversible glandular equipment similar to Newcomer's organ, which are presumed to have been serial in their earliest ancestral stage. On this evolutionary line the perforated cupolas developed which proved to be more effective than the big glands, which were subsequently modified and reduced. The result of this evolution is a caterpillar which is provided only with perforated cupolas, as it is demonstrated by species of *Lycaena* and several Theclini.

The well known carnivorous habits of many lycaenid larvae (Dethier 1927, Clausen 1962) have no connection with the above mentioned evolution. It is certain that the obligate rapacious lycaenids evolved independently from each other, originating their carnivorous habits from different levels of ant adaptation. I agree with Brues' (1936) ideas, but I can not accept the Lamarckian suggestions of Balduf (1938).

VOLUME 24, NUMBER 3

Suggestions for future work

It is highly desirable that we investigate the anatomy and histology of many additional kinds of lycaenid caterpillars, particularly additional subfamilies which are well represented in the Ethiopian, Indoaustralian and Neotropic regions. It would be very revealing to research the details of the specialized organs by means of ultra-optical methods. The chemistry of the secretions and their interrelations with ant's pheromones are still unknown and need to be investigated. The behavior of additional ant species, particularly those of other than European origin, may shed new light on these relationships.

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Summary

Comparative anatomical, histological and ethological studies in about 60 kinds of lycaenid larvae and pupae and ethological studies in about 50 kinds of ants were undertaken. The particular adaptations of the lycaenid larvae correspond with details of behavior, eidonomy and social biology of ants and are regarded as protection from the ants' aggression. Individual species of lycaenids are dependent social parasites of ants, but the majority are associated with ants only in a facultative way. True symbiosis is unknown. The evolutional pathway is suggested.

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OCCURRENCE OF COENONYMPHA INORNATA (SATYRIDAE) IN MAINE

It has been noted in recent years that *Coenonympha inornata* (Edwards) has been expanding its range in the northeastern portion of the United States and Canada.

On July 5, 1968 I collected a female of this species in a roadside bog between Enfield and Passadumkeag, Penobscot Co., Maine. The specimen, which was taken in the early afternoon, appeared to be about one to two days old. Poor weather conditions and a subsequent collecting trip to Canada prevented further collecting in this area.

The specimen has been determined by F. Martin Brown as being closest to C. *inornata inornata* (Edwards). As far as can be determined, this is the first record for this species in the State of Maine.

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