

CHEMICAL COMMUNICATION BETWEEN LYCAENID LARVAE (LEPIDOPTERA:
LYCAENIDAE) AND ANTS (HYMENOPTERA: FORMICIDAE)

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DECLARATION

I Stephen Frank Henning declare that this M.Sc. dissertation is all my own unaided work; that not part of this dissertation has been submitted or will be submitted for a degree in any university; that all the information used in this dissertation has been obtained by me while studying full time at the University of the Witwatersrand, Johannesburg.

Signed

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ABSTRACT

A causal explanation for myrmecophily in the Lycaenidae has long been sought. In this study experiments were carried out to establish whether the association between ants and lycaenid larvae is mediated by chemical signals.

The various lycaenid larval glands were examined histologically and the possible function of each was discussed. The various biological groups of the Lycaenidae, divided up on the basis of their feeding habits and associations with ants, were studied in an attempt to gain some insight into the possible pathways for evolution and development of the ant/lycaenid association.

Observations were made in formicaria and in the field of the behaviour of two species of ants with respect to the lycaenids with which they were associated. The two associations studied in detail were those between *Aloeides dentatis* (Swierstra) and *Acantholepis capensis* Mayr; and *Lepidochrysops ignota* (Trimen) and *Camponotus niveosetosus* Mayr. A third lycaenid species in the study area, *Euchrysops dolorosa* (Trimen), which was not observed to be ant associated, was also investigated to establish whether it could induce an ant association if provided with appropriate conditions. Three species of ants all known to associate with lycaenids were investigated with *E. dolorosa*. These three species were *Acantholepis capensis* Mayr, *Camponotus niveosetosus* Mayr and *Camponotus maculatus* (Fabricius). Besides the observations, experiments were undertaken to determine the ant's reactions to extracts from the lycaenid's glands impregnated on to inert material. The volatile secretions of the lycaenid glands and those of the ants were compared using gas chromatography.

It was found that in the two myrmecophilous species studied, the epidermal glands produced a gas chromatographic 'fingerprint pattern' which was very similar to and appeared to mimic the 'fingerprint pattern' given by the brood pheromones of the host ant. In *A. dentatis* it was also found that a second secretion from glands located on or near the tubercles appeared to mimic the gas chromatographic 'fingerprint pattern' of the alarm pheromones of the host ant.

With *E. dolorosa* which is not dependent on ants, it was found that its epidermal glands produced a volatile secretion which appeared to

mimic the brood pheromones of *C. maculatus* and to a lesser extent *C. niveosetosus*. The gas chromatographic 'fingerprint pattern' of *E. dolorosa* though did not resemble that of *A. capensis* at all and the ant completely ignored the lycaenid.

It was concluded from this study that at least some of the associations may be brought about by the lycaenid larvae mimicking volatile secretions produced by the host ant and its brood.

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1. INTRODUCTION

A remarkable number of animal species exploit the colonies of social insects in one way or another. Most do so only occasionally functioning as casual predators or temporary nest commensals. But a great many others are dependent on social insects during part or all of their life cycles. Depending on the identity of the host, such species are referred to as sphecophiles (symbionts of social wasps), myrmecophiles (symbionts of ants), melittophiles (symbionts of social bees), or termitophiles (symbionts of termites). The lycaenid larvae are solely myrmecophiles.

Erich Wasmann (1894) initiated the modern study of arthropod symbionts. He introduced a simple classification that divides the species into five behavioural categories. As more knowledge became available these categories have been redefined a number of times. The following definitions of the categories are based on Wilson (1971) and Hinton (1951).

1. Synechthrans or predators, species which prey on social insects or their brood and are treated in a hostile manner.
2. Synoeketes. Species that evoke no recognisable response from their hosts. They may be phytophagous, predaceous, coprophilous, or general scavengers.
3. Symphiles. Species that continually or occasionally evoke a response from their host that does not result in an attack upon themselves. They are usually accepted to some extent by their hosts as though they were members of the colony. They often produce some secretion that is eaten by their hosts, sometimes only after stimulation by the latter. Some symphiles solicit food from their hosts, but the majority are predaceous.
4. Trophobionts. These are the phytophagous homopterans, lycaenid and riodinid caterpillars that are not dependent on the social insects for food but actually supply their hosts with food in the form of honeydew. They apparently receive some protection from parasites and predators.

5. Parasitus are symbionts which live on or in the individual social insect and may therefore be classified as external or internal.

A few myrmecophiles often fit more than one category at different times of their life cycle, but in spite of such occurrences, Wasmann's nomenclature continues to be useful in designating the majority of cases. The lycaenid larvae fit into two categories, the trophobionts and the symphiles.

The association between lycaenid larvae and ants is well known and has been the subject of numerous publications over the years. The majority of papers are purely descriptive, but, in recent years especially, a number of papers have appeared in which attempts have been made to try and give a causal explanation for the association.

The first observation of myrmecophily in the Lepidoptera was made by an anonymous writer in 1785 (D ---- S, 1785), who described the habits of *Lycaeides argyrognomon* Bergstr. According to Hinton (1951) the association of *Plebejus argus* (L.) and *Callophrys rubi* (L.) with ants had been described by Pezold in 1793. Hinton records that later Freyer in 1836 and Piöitz in 1852 observed that ants attended the larva of *Lysandra coridon* Poda. The larval exudate organs do not appear to have been described until Guenée (1807) studied those of *Lempides boeticus* (L.).

Two of the earliest and most detailed accounts of the associations of African Lycaenidae with ants are those of Lamborn (1914) and Farquharson (1922). These two papers were based on observations made in southern Nigeria more than fifty years ago and provided the ground work for future studies on the African continent. Lamborn and Farquharson made detailed and painstaking observations in the field of many myrmecophilous lycaenid species which have proved invaluable to later workers. Over the next fifty years numerous life histories of African Lycaenidae were described mainly by Jackson (1937, 1947) and Clark and Dickson (Clark, 1940; Clark & Dickson, 1956, 1957a, 1957b, 1960, 1971). These authors also provided useful observations on the structure and function of the lycaenid larval organs.

One of the oldest and best known hypothesis used to explain the relationship between ants and lycaenid larvae is that of Thomann (1901). He suggested that the relationship is a symbiotic one, the lycaenid

larvae being protected from parasites and the ants obtaining a honeydew-like liquid from a medial gland on the seventh abdominal segment. Malicky (1970), however, points out that it has never been satisfactorily confirmed that ants are able to drive away parasitic Ichneumonidae or Tachinidae or even notice their presence. Claassens (1976), for example, found that 43.2% of his pupae of *Lepidochrysops* that pupated in his formicaria were parasitized by Ichneumonids. It must, however, be remembered that although the parasitism is high, it might be higher still without the presence of the ants. The level of parasitism in other Lepidopterous families that are not ant associated can often be quite high. For example, 80-90% of the *Charaxes vansonii* van Someren (Nymphalidae) larvae collected at Rashoop in the Transvaal are usually parasitized by a Tachinid fly (Henning, unpubl. data). Malicky (1970) also states that the behaviour of ants in respect of Lycaenid larvae shows no significant difference between species which lack the honey-gland and those that have it.

For Thomann's or any hypothesis to be valid it is probably better to think in terms of predators in general, or better still to think about the multiple effects of the association, rather than confining the hypothesis to protection from parasites alone. In this regard, Ross's (1966) interesting observation in Mexico where he found that 100% of the larvae not attended by friendly ants were killed by rapacious ant predators, lends some support to this idea.

A second hypothesis advanced by Lenz (1917) suggests that the honey-like liquid is produced to prevent aggression by the ants. Since some larvae lack the organ (and presumably therefore lack the presumed protective symbiosis) it would seem that they should suffer a greater loss due to predation whichever hypothesis is true, but this has never been shown.

Both these hypotheses seem to have oversimplified the problem. As it appears to me the problem is a general one of the Lycaenid insinuating itself into the communication system of the ants, it is not simply a matter of preventing aggression and parasitism.

Hinton (1951) observed that in *Lycaena dispar* Haw. both the honey-gland and the tubercles are lacking, but they were nevertheless

attended by ants. He believed that an ant attractant substance is secreted from widely scattered epidermal glands. He also found these glands in species that had both the honey-gland and tubercles. Jackson (1937) observed that ants attended the prothorax of *Anthene nigeriae* Auriv. and *Chloroseles pseudoseritis tytleri* Riley at least as much as they did the honey-gland and Hinton (1951) believed that this was probably due to a concentration of the small epidermal glands producing an ant attractant substance.

Malicky (1969, 1970) also suggested that the honey-gland is not of prime importance in ant/lycaenid associations as it is often lacking in myrmecophilous species. Malicky observed that ants tend to palpate with their antennae certain areas of the lycaenid larvae more intensively than others. When he investigated these areas he found that they all contained small epidermal glands (perforated cupolas) that were rare or absent elsewhere. With the single exception of the European *Nemeobius lucina* L. these organs were present in all the lycaenid larvae he investigated. *Nemeobius lucina* was also the only species he investigated that did not induce an ant association in the laboratory. From these studies he concluded that these epidermal glands produce a volatile substance which attracts the ants. He also suggested that the secretions of the perforated cupolas could be similar to, or identical with, ant pheromones.

1.1 Exocrine glands and other adaptations of the Lycaenidae to a myrmecophilous life style.

Most lycaenid larvae have a median dorsal organ (honey-gland) on the seventh abdominal segment and a pair of dorsolateral eversible organs (tubercles) on either side of the eighth segment. Either or both these organs may be lacking. Ants tend to palpate with their antennae certain areas of the lycaenid larvae more intensively than others. Malicky (1969, 1970) found that these areas contain small epidermal glands that are rare or absent elsewhere. He believes that they produce a volatile substance which releases the ant's palpation;

although the nature of the chemical is unknown. These glands are also present in the pupae of lycaenids which are attended by ants in the same manner as the larvae.

The dorsal, honey or Newcomer's glands were first mentioned by Guenée (1867) and described anatomically and histologically by Newcomer (1912), Ehrhardt (1914), Fiori (1958) and Malicky (1969, 1970). These glands produce a substance that has been compared to the honeydew excreted by aphids and is imbibed by the attending ants.

The function of the dorsolateral eversible organs (tubercles or tentacles) is still in doubt. Several authors (Thomann, 1901; Ehrhardt, 1914; Claassens & Dickson, 1977) suggested that they have an odoriferous function which might signal the presence of a honeydew-producing caterpillar to ants. In support of this Ehrhardt (1914) found a large pyriform secreting cell at the base of each long spiculate seta of the tubercles in *Scolitantides orton* Pall. Malicky (1969, 1970), however, could find no glandular structures in, on or near the tubercles of the lycaenids he studied and suggested that they may be rudimental structures of organs which have no or little function in attracting ants or deterring them. It has been observed though that if ants are too persistent in their efforts to obtain secretions from the honey-gland they will be deterred by the action of the tubercles when these come into play (Clark, 1940; Clark & Dickson, 1956; Claassens and Dickson, 1974). Clark and Dickson (1956) suggested that the tubercles could perhaps be used in the same way to prevent small insects other than ants from interfering with the honey-gland. Claassens and Dickson (1977) have made the most recent observations of importance, with respect to the tubercles of *Aloeides thyra* (L.). Although the larvae of this species are phytophagous they do, at least in the fourth to the sixth instars, remain in ants' nests under stones during the day, but come out at night to feed on their foodplants. They possess the highly evolved type of tubercle with long setae, but are now known not to possess any honey-gland of the usual form. When studying these larvae in artificial ants' nests they noticed an excited reaction by the ants

whenever the tubercles of a larva were extended, and their temporarily greatly increased activity around the larva. The attraction is mutual since these larvae will follow the trail of the ants leading from a nest to the foodplants when they emerge from the nests at night to feed. The larvae ensure the company of the ants as they travel by rapidly and repeatedly extending and retracting their tubercles. Claassens and Dickson suggest that the tubercles produce a volatile chemical of brief effectiveness which causes the ants to act in this manner.

So it appears that most lycaenid larvae have small epidermal glands concentrated in certain areas that possibly produce a volatile chemical substance that attracts ants. Some larvae also have a large dorsal honey-gland on the seventh segment which produces a substance that has been compared to the honeydew excreted by aphids. This substance is imbibed by the ants. On the eighth abdominal segment there is often a pair of dorsolateral eversible organs (tubercles) whose possible function has caused some controversy. It appears that they may be used in some species to keep the honey-gland from being over exploited, while in other species there appears to be a communicatory function.

The cuticle of lycaenid larvae is many times thicker than that of other lepidopterous larvae which confers valuable protection against attack by ants (Malicky, 1970). Furthermore, most lycaenid larvae, unlike the majority of other lepidopterous larvae do not perform jerky lateral movements when physically disturbed. Since fast motions of this sort are very effective in releasing aggressive behaviour in ants, their absence in lycaenid larvae may be a further adaptation to their association with ants (Common and Waterhouse, 1972). Wilson (1971) observed that ants have excellent form vision and are especially keen at detecting moving objects. He found that workers do not respond to prey insects standing still, but ran toward them as soon as they began to move. Sturdza (1942) showed with laboratory experiments that the sight of a running *Formica nigricans* worker alone was enough to set another worker running.

Once the symphilic lycaenid larvae have been carried, or have

made their way into the host nest, they become fully integrated into the colony. The lycaenid larvae are groomed and generally treated as the ants do their own brood. This appears to me to be the key to the whole relationship since the above can only be achieved by means of communication.

Claassens (1976) observed an extraordinary behaviour pattern in which symphilic *Lepidochrysops* larvae appeared to "lick" the host ants' legs, head and abdomen. The ants responded to this tactile stimulus by remaining motionless, or in some cases lying on their sides. Claassens examined these ants but could find nothing unusual about them which could have induced this behaviour in the larvae. This is probably a type of grooming behaviour which has also been observed in other myrmecophiles, for example, the symphilic Staphylinidae and Historidae (Coleoptera) (see page 17). Claassens also noted that when brood was scarce in the nest *Lepidochrysops* larvae would attempt to solicit regurgitated food from the ants. The larva would lift its head from the floor of the nest so that its mouth was exposed and would approach an ant attempting to touch its mandibles with its own. Claassens says that the larvae of the host ants, *Camponotus maculatus* F., showed similar behaviour which sometimes seemed to result in trophallaxis. Feeding of lycaenid larvae by ants has been observed in several non-South African species, including *Maculinea alcon* F. from Europe (Elfferich, 1963; Hinton, 1951; Malicky, 1969).

Ants also show considerable 'interest' in lycaenid pupae. This may also be due to the production of pheromones as the small epidermal glandular organs which possibly produce the chemical in the larvae are also present in the pupae. The pupae of the symphilic *Lepidochrysops* have extraordinarily shaped setae (Cottrell, 1965; Claassens, 1976) the ends of which usually appear to be covered with a shiny dried substance. The setae are hollow and Claassens (pers. comm.) has shown that the ants obtain a fluid from them which they appear to find extremely attractive. The ants also continue to visit empty pupal cases after the emergence of the imagos. Claassens (1976) observed that some pupal cases of the *Lepidochrysops* were discarded

and carried to the debris corner a few hours after emergence, while some were visited for days and others for weeks. What the difference was between these empty pupal cases was not apparent, possibly different amounts of chemical present due to different rates of evaporation. These empty pupal cases were carried around, like the brood, when the ants were disturbed. Before emergence of the imagos the host ants show an increased 'interest' in the pupae. Claassens observed that they turn suddenly towards such pupae as if they had received some cue. Once an imago has succeeded in breaking the pupal case during emergence, the ants were seen to seize a free edge and pull on it, apparently attempting to tear it apart so as to free the imago. This behaviour by the ants is very similar to that shown by them to emerging ant cocoon as described by Skaife (1961). Claassens (1976) suggests that the attractive pupal remains act as a 'decoy' allowing the emerging adult lycaenids to escape from the ants nest without being attacked or eaten, but this has not been adequately demonstrated.

The body and appendages of the newly emerged adult symphylid lycaenid are covered by a temporary coating of easily detachable scales. These scales function to prevent the ants from developing an effective attack on the delicate adult as it makes its way out of the nest (Hinton, 1951). The scales are detached and adhere to any part of the ant that comes into contact with them. Scales stick to the antennae, mouth-parts and legs of the ants, which then retreat and become so fully occupied cleaning themselves that the newly emerged adult is able to escape. When the adult has made its way out of the nest, it expands its wings, and a stroke or two suffices to detach any of the temporary scales that may still remain. (Hinton, 1951).

When one reviews the literature on myrmecophilous Lycaenidae the extent to which they are adapted to living within the ants nest indicates that they must be able to participate to some extent in the chemical communication within the colony. Malicky's (1970) suggestion that the lycaenid larvae produce a volatile chemical that mimics the ant's pheromones is therefore a reasonable hypothesis.

1.2 Communication in ants.

The main ant species to have symbiotic relationships with Lycaenidae in southern Africa belong to the following genera: *Crematogaster* Lund, *Pheidole* Westwood (Myrmicinae); *Anoplolepis* Santachi, *Acantholepis* Mayr and *Camponotus* Mayr (Formicinae).

It has been found in recent years that in the social biology of ants much of their behaviour is released and controlled by pheromones. This field has been reviewed by Wilson (1963), Blum (1969), Birch (1974) and Parry & Morgan (1979). It is now well known that workers of many species possess alarm and trail pheromones. It has also been established that pheromones are associated with recognition and brood tending (Glancey *et al.*, 1970; Wilson, 1971).

The secretions of the majority of the exocrine glands of ants are associated with defensive or aggressive behaviour (Blum & Brand, 1972). Bradshaw *et al.* (1979a) notes that the term 'alarm pheromones' used to describe the secretions of these glands has now been found to be increasingly less informative, particularly where comparisons are made between species. They point out that in the most detailed study to date, the social defensive behaviour of *Myrmica rubra* is shown to be controlled in a complex manner by the secretions of the mandibular glands, Dufour's gland and the poison gland, which regulate the behaviour of nest-mates by a number of kinetic and tactic agents, aggression intensifiers and inhibitors. They also point out however that the functions of the individual glands are somewhat more general since they may be used in other contexts. For example the poison gland is used to lay odour trails to food sources in the absence of aggressive behaviour. Bradshaw *et al.* (1979a, b) found in their studies on the formicine ant *Oecophylla longinoda* (Latreille) that social aggression and food retrieval appear to be regulated by separate sets of exocrine organs. They decided to retain the term 'alarm' for the former, although they note that the diversity of reactions observed in response to the various components of the secretions indicates that a refinement of terminology would be valuable.

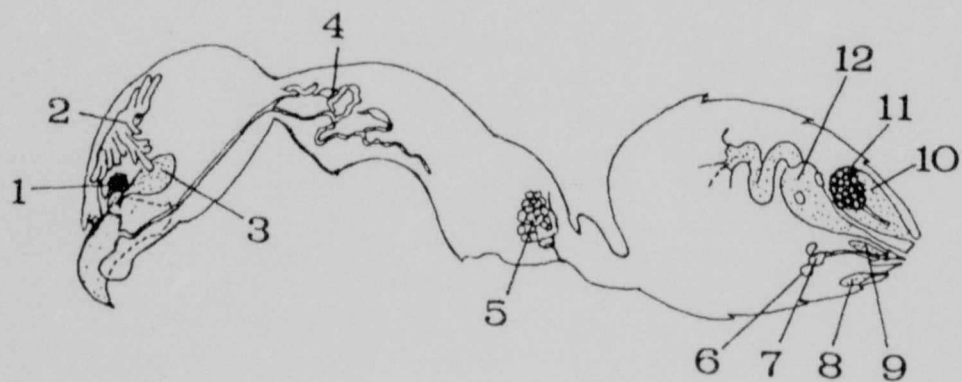


Fig. 1. Exocrine gland systems of a worker ant (Pavan's gland and the anal gland are found only in the ant subfamily Dolichoderinae). 1. Hypopharyngeal. 2. Postpharyngeal gland. 3. Mandibular gland. 4. Thorax labial gland. 5. Metapleural gland. 6. Poison gland. 7. Vesicle of poison gland. 8. Pavan's gland. 9. Dufour's gland. 10. Reservoir of anal gland. 11. Anal gland. 12. Hindgut with rectal gland (After Wilson, 1971).

Blum (1974) also noted that alarm pheromones possess several functions clearly separate from that of merely causing alarm in workers. The other most important function for the purpose of this study is that it serves as an attractant. Wilson (1958) noted that high concentrations of the alarm pheromone of the myrmicine *Pogonomyrmex badius* released strong alarm behaviour, whereas low concentrations acted as excellent attractants. Hölldobler (1971) demonstrated that workers of the formicine *Camponotus socius* Roger fortify their recruitment trails with an alarm pheromone formic acid, which is highly effective in attracting excited recruits. Similarly, Ayre (1968) demonstrated that alarm pheromones were utilized by three species of ants as recruitment stimuli when used in conjunction with trail pheromones. Blum (1974) believes that because of their capacity to function as low level attractants, alarm pheromones have probably been frequently utilized to increase the stimulating efficiency of a recruitment signal.

Another aspect to chemical communication is the manner in which the chemical signals themselves alter in space and time. Bradshaw *et al.* (1979a) point out that fundamental to this is the concept of the 'active space', as the zone around the point of emission within which the concentration of the chemical stimulus is at or above that required for behavioural response. They point out that in a social context, the relationship between the active spaces of a number of chemical releasers will largely determine the behaviour patterns of responding ants.

In species of the subfamily Formicinae it has been established that the mandibular glands in the head and the poison and Dufour's glands in the abdominal tip play an important role in attraction and alarm (Ayre & Blum, 1971).

Bradshaw *et al.* (1979a) found that the mandibular gland secretions of the major workers of the formicine ant *Oecophylla longinoda* released in other major workers a complex pattern of behaviour including components of alerting, attraction and biting. In a behavioural study they found that all ants within a range of 5-10cm were alerted within 30 seconds of the presentation of the

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