

Behaviour and morphology of an
aphytophagous lycaenid caterpillar :
Cigaritis (Apharitis) acamas Klug, 1834
(Lepidoptera : Lycaenidae)

Matthias SANETRA* & Konrad FIEDLER**

* Institut für Zoologie, Technische Hochschule Darmstadt, Schnittspahnstr. 3, D-64287 Darmstadt, Germany

** Theodor-Boveri-Biozentrum der Universität, LS Verhaltensphysiologie und Soziobiologie, Am Hubland, D-97074 Würzburg, Germany

Summary

Interactions between caterpillars of *Cigaritis (Apharitis) acamas* Klug, 1834 from Cyprus and their host ants, *Crematogaster* cf. *jehovae* Forel, 1907, were observed in captivity. At least final instar caterpillars permanently live inside ant nests where they mainly prey on ant brood. To a lesser extent, ant regurgitations also contribute to the caterpillars' nutrition. Caterpillars are permanently antennated and cleaned by their attendant ants. Details on the morphology of the myrmecophilous organs in *Cigaritis* larvae are provided for the first time. The relations of Cypriot *Cigaritis acamas* to other members of the genus from neighbouring arid zones and to related lycaenid species are discussed, especially with respect to myrmecophily and ecological requirements.

Zusammenfassung

Zwei Raupen von *Cigaritis (Apharitis) acamas* Klug, 1834 wurden auf Zypern einzeln in den Nestern der bodennistenden Ameisenart, *Crematogaster* cf. *jehovae* Forel, 1907 gefunden. In Labornestern wurden die Interaktionen zwischen Raupen und Ameisen beobachtet. Die Raupen wurden ständig von ihren Wirtsameisen betrollert. Die Ameisen leckten die gesamte Oberfläche der Raupen ab und zogen deren lange laterale Borsten durch ihre Mandibeln. Sekrete aus dem dorsalen Nektarorgan wurden sofort von den Ameisen aufgenommen, die auch den flüssigen Kot der Raupen abnahmen. Reaktionen der Ameisen auf Ausstülpungen der Tentakelorgane wurden nicht beobachtet. Hauptnahrung der Altraupe ist die Brut der Wirtsameisen, daneben werden auch durch taktile Stimulation mit den Vorderbeinen trophallaktische Regurgitationen erbettelt. Die Beobachtungen zeigen, daß zumindest die ausgewachsene Raupe von *C. acamas* (vorletztes und letztes Stadium) als permanenter, voll integrierter Myrmekophiler in den Nestern von *Crematogaster*-Arten lebt, wo sie den Wirten durch Brutfraß beträchtlichen Schaden zufügt. Die Epi-

dermalorgane der Raupe zeigen starke Anpassungen an ihre obligate Myrmekophilie. Neben einem dorsalen Nektarorgan und den für Raupen der Tribus Aphnaeini typischen großen Tentakelorgane besitzt die Larve sehr zahlreiche Porenkuppelorgane und dendritische Haare, außerdem laterale Gruppen langer Borsten und — caudal vom Nektarorgan gelegen — eine Gruppe pilzförmiger Haare mit stark poriger Oberfläche. Struktur und Verhaltensbeobachtungen legen nahe, daß alle Organe an der Kommunikation mit Ameisen teilhaben. Die Beobachtungen an zypriotischen *C. acamas* werden mit Angaben zur Larvalbiologie verwandter Bläulinge verglichen und im Kontext mit der Zoogeographie und Evolution der Aphnaeini diskutiert.

Résumé

Les auteurs ont trouvé sur l'île de Chypre deux chenilles de *Cigaritis (Apharitis) acamas* Klug, 1934, isolées, dans les nids de la fourmi terricole *Cremogaster cf. jehovae* Forel, 1907. Ils ont observé en laboratoire les relations entre ces chenilles et les fourmis dans des nids artificiels. Les chenilles étaient constamment titillées par les fourmis-hôtes, qui les léchaient sur tout le corps et tiraient à travers leurs mandibules les longs poils latéraux ; les sécrétions des organes nectarigènes dorsaux étaient immédiatement absorbées, de même que les excréments liquides. On n'a pas constaté de réaction des fourmis aux dégagements des organes-tentacules. La nourriture principale de la chenille adulte est constituée par les œufs et larves des fourmis-hôtes ; par stimulation tactile avec les pattes antérieures, celles-ci mendent aussi des régurgitations trophallactiques. Ces observations montrent que la chenille adulte de *C. acamas* (au moins aux dernier et avant-dernier stades) vit dans les nids des fourmis *Crematogaster* comme hôte myrmécophile permanent, complètement intégré. En se nourrissant des larves de ses hôtes, elle leur cause de sérieux dégâts. Les organes épidermiques de cette chenille montrent une adaptation très nette à leur vie en myrmécophilie obligatoire. Outre un organe nectarigène dorsal, et les grands organes-tentacules typiques des chenilles de la tribu des Aphnaeini, cette chenille présente de très nombreux organes pore-coupoles et des poils dendritiques, ainsi que des groupes latéraux de longues soies avec, du côté caudal de l'organe nectarigène, un groupe de poils en forme de champignon dont la surface est très poreuse. Cette structure et les comportements observés suggèrent que tous les organes participent à la symbiose avec les fourmis. Les auteurs comparent leurs observations sur *C. acamas* de Chypre avec ce qu'on sait de la biologie larvaire des Lycènes apparentées et, dans ce contexte, discutent de la zoogéographie et de l'évolution des Aphnaeini.

Introduction

Myrmecophily within the Lycaenidae is extremely widespread, and a variety of relationships, especially between caterpillars and ants, have been described. These interactions range from broadly unspecific

peaceful coexistence or facultative and unspecific mutualism to highly advanced mutualistic and sometimes parasitic associations with specific host ants (for review see Fiedler, 1991). Caterpillars of the predominantly African tribe Aphnaeini exhibit an extraordinarily high degree of myrmecophily. As far as their life-cycles are yet known, most Aphnaeini species are obligatorily associated with specific ants (Clark & Dickson, 1971 ; Fiedler, 1991). In particular, various reports on these fairly close and specific relationships between Aphnaeini caterpillars and ants (e.g. Larsen & Pittaway, 1982) hint towards commensalic or parasitic exploitation of host ant colonies (mostly in the myrmicine genus *Crematogaster*) rather than suggest mutualistic symbiotic associations. Thus, the peculiar ecology of Aphnaeini butterflies and the highly specialized morphology of their immature stages deserve further investigation.

The genus *Cigaritis* Donzel, 1847, consisting of two so-called subgenera (sometimes treated as separate genera), is the only clade of the Aphnaeini to reach the southern margin of the western Palearctic realm. *Cigaritis* s. str. contains three species endemic to northwestern Africa (*zohra*, *allardi*, *siphax*), which have adapted to a more temperate Mediterranean climate, while the six to nine species (depending on the taxonomic status attributed to some local forms or subspecies) of the subgenus *Apharitis* are centred in the arid zones of North Africa, Arabia and Asia (Larsen & Pittaway, 1982). *Cigaritis* (*Apharitis*) *acamas* Klug, 1834 is by far the most widely distributed member of the genus, recorded from the fringes of the Sahara across the Middle East to northwestern India. It is therefore not surprising that it has also managed to reach the island of Cyprus (Riley, 1925).

Cigaritis is closely related to the paleotropical genus *Spindasis*, which occurs with some 50 species throughout all of Africa south of the Sahara desert and extends across India eastwards to Sundaland, the Philippines, southern China and the Japanese island of Okinawa. While *Cigaritis* s. str. appears to be a monophyletic unit, the separation between *Apharitis* and *Spindasis* is all but clear-cut (e.g. Riley, 1925 ; Wynter-Blyth, 1982), and a thorough cladistic revision may well reveal that all taxa in question are best grouped into a more inclusive genus *Spindasis* to avoid paraphyletic rest groups.

Very little information is available on the biology of the genus *Cigaritis*, and the life-histories of all its species are far from being thoroughly investigated. Adults of *Cigaritis* are known to occur only very locally at low population densities, with the exception of the North African endemics *C. zohra* (Donzel, 1847) and *C. allardi* (Oberthür, 1909) which

can be very abundant in suitable habitats, but also very local (Thomas & Mallorie, 1985; Sanetra, personal observations). Caterpillars of *Cigaritis* are more or less closely associated with ants of the genus *Crematogaster*, and Dumont (1922) provided the earliest report on these myrmecophilous life habits. He observed that caterpillars of *C. myrmecophila* in Tunisia spent the day in subterranean tunnels in the outskirts of *Crematogaster* nests, but came out to feed at night on *Calligonum comosum* (Polygonaceae).

In Oman, Larsen & Pittaway (1982) discovered three-quarters grown caterpillars as well as a pupal exuvia of *C. acamas* inside the galleries of a *Crematogaster* ant inhabiting palm trunks, and these authors also observed adoption behaviour of newly hatched larvae, which were carried off into the nest by foraging ants. Larvae of herbivorous *C. zohra* from Morocco rest and diapause specifically in nests of *Crematogaster laestrygon* (Rojo de la Paz, 1992). Facultative myrmecophily occurs in *C. allardi* whose caterpillars feed on green plants and are attended by various *Crematogaster* species, but which never penetrate into ant nests (Rojo de la Paz, 1992). Similarly, caterpillars of the Asian *C. epargyros* (Eversmann 1854) have been reported to feed on plants in company with unspecified ants (Lukhtanov & Lukhtanov, 1994).

The findings of Larsen & Pittaway (1982) suggest that at least in Arabia *C. acamas* caterpillars spend their whole life cycle inside ant nests, and raises the important question as to whether the larvae of *C. acamas* are aphytophagous commensals or even parasites of their ant hosts. We here present observations on *C. acamas* caterpillars from Cyprus inside artificial ant nests, which shed new light upon the feeding strategy of this species. In particular, we demonstrate for the first time that final instar caterpillars essentially prey on the brood of *Crematogaster* ants. Furthermore, we present the first investigation of the epidermal organs of Aphnaeini caterpillars using SEM techniques.

Material and methods

Two caterpillars of *C. acamas* from Cyprus (for detailed information see next section) were reared together with their host ants, *Crematogaster* cf. *jehovae* Forel, 1907, in the laboratory for about five weeks. When collected, one of the caterpillars had already reached the final instar, while the other one was in the penultimate (probably fourth) instar. *Crematogaster* colony fragments containing caterpillars were maintained in artificial nests at a temperature cycle of 15 : 25°C (night : day). Both fragments did not comprise a fertile queen, hence egg production was

interrupted. The behaviour of caterpillars and their interactions with ants were observed every second day with variable duration using a stereomicroscope (magnification 12-25fold).

When the caterpillars died (see below), they were stored in a freezer, later fixed in ethanol and finally post-fixed in Bouin's fixative. One caterpillar was then critical-point dried, sputtered with gold and examined in a scanning electron microscope (Zeiss DSM 962). The other caterpillar was externally surveyed using a Wild Macroscope M 400 (magnification 10-64fold).

Results

Habitat in Cyprus

As within its whole range, *C. acamas* has a very patchy distribution on Cyprus, from which island only five localities have as yet been recorded (Parker, 1983 ; Manil, 1990). It was early spring (2.iv.1994), when the first author was fortunate enough to discover a new site in the Greek part of Cyprus, Distr. Paphos. The locality was situated on a northeastern slope in the vicinity of the small village Kritou Marottou (elevation about 500 m) at the rise of the Troodos mountains. The vegetation of the habitat can be characterized as a typical Mediterranean garrigue, in the spring aspect dominated by flowers like *Asphodelus albus* (Liliaceae).

Within a small spot (estimated to be about 20 m in diameter), at which nests of the subterranean *Crematogaster* cf. *jehovae* were suddenly quite abundant, a single caterpillar of *C. acamas* was detected within the nest chambers. Thorough inspection of a further dozen of *Crematogaster* nests resulted in the discovery of a second caterpillar. The ant nests were built in the soil under stones and compared with arboreal *Crematogaster* species colonies appeared to be relatively small, containing a few hundred workers. In the bordering area of the spot, other ant species out of the myrmicine genera *Tetramorium*, *Pheidole*, *Messor* and *Aphaenogaster* were the dominant subterranean ants.

Interactions between caterpillars and ants

After the *Cigaritis* caterpillars had been transferred into artificial nests together with their host ants, they spent most of the time motionless inside the nest chambers. No signs of aggressiveness were observed between the *Crematogaster* ants and the caterpillars. On the contrary, caterpillars were highly attractive to their hosts (Fig. 1). While resting



Figs 1-2. Mature caterpillar of *Cigariitis acamas*. 1 — Attended by a group of *Crematogaster* worker ants in a laboratory nest. Note the conspicuous black sheaths of the tentacle organs on the eighth abdominal segment ; 2 — Feeding on *Crematogaster* brood. The predacious caterpillar is groomed and antennated while preying on the ants' young. (Photographs : M. Sanetra).

within the nest they were permanently surrounded by a large group of ant workers, estimated to number about 20-30 individuals. The attendants intensively groomed the caterpillars, thereby licking them all over their outer body parts as they usually did with their own nestmates and brood. In addition, they frequently pulled the long lateral setae of the caterpillars through their mandibles one by one very carefully. In order to take up the caterpillars' liquid excrements, the ants sometimes licked the anal region of caterpillars. We never observed a caterpillar to discharge solid faeces. After moulting of the prefinal instar caterpillar into the ultimate instar, the ants tore the remaining exuvia apart and converted it into food.

The two myrmecophilous organs commonly occurring within the family Lycaenidae, the dorsal nectar organ (DNO) and the tentacle organs (TOs), were well developed and functional in the caterpillars investigated from Cyprus. The vicinity of the DNO attracted the ants and was intensively antennated. When secretions were released from the DNO, these were eagerly imbibed by the attendant ants. Most of the time the TOs remained retracted. Eversions of tentacles could be observed either when the caterpillars wandered about or if they were disturbed. However, there was no visible reaction of the ants towards the periodically everted tentacles. About two weeks after collection (15.IV.1994) one of the caterpillars had freshly moulted into the final instar. Its colours were brighter than before and interestingly, though the caterpillar was not crawling around, its TOs were highly active. Again no specific reaction of the ants could be detected.

Caterpillars were fed via trophallaxis by their host ants in a similar way to ants feeding each other. With its forelegs the caterpillar stimulated an ant to regurgitate a droplet of liquid from its crop. This kind of feeding behaviour was observed occasionally (3-4 times during approx. 5 h of irregular observation periods), but not as frequently as would be expected if caterpillars totally depended on trophallactic feeding. Eventually, it became evident what the main food source is of caterpillars inside ant nests enabling larval growth until pupation. A hungry caterpillar approached the ants' brood chamber, grasped a piece of brood with its forelegs and pulled it down beneath the head (Fig. 2). Then immediately the caterpillar retracted its head under the sclerotized prothoracic shield, as if to protect itself against possible ant-attacks. Within a few minutes a caterpillar devoured several brood items (usually 3-5) in the described manner. The caterpillars seemingly preferred the larger brood pieces, such as prepupae and pupae, and later switched over to the younger larvae.

Since the predatory behaviour described above was observed in the final instar caterpillars during most observation periods, one can imagine that predation caused considerable harm to the ant nests. Unfortunately, neither of the *Crematogaster* colony fragments had a fertile queen, and due to the lack of new egg production the brood resources of both ant nests were depleted within a few days (by the 18th and 25th April, respectively) because of the caterpillars' great appetite. The total number of brood items which had been eaten by each caterpillar was estimated to be about 500 per nest, mainly small larvae. In the meantime, we tried to adapt the caterpillars to brood of the myrmicine genus *Leptothorax*, but without success. At the beginning of May both caterpillars, though almost fully grown, died of disease.

Morphology of the mature caterpillar

The mature caterpillars, 13 mm long and 3.5 mm in diameter, are almost round in cross-section (not flattened and woodlouse-shaped as many Lycaenidae larvae). Their ground colour is whitish, with complex red markings all over the dorsal surface (dark elements in Figs. 1-2). Inspection with the stereomicroscope and the SEM revealed the following characteristic epidermal organs :

- a) The prothoracic shield (Fig. 3) is sclerotized and appears blackish. Its central part is almost free of setae, but towards the margins there occur dendritic setae in numbers. The anal plate is flattened and less strongly sclerotized than the prothoracic shield.
- b) A large dorsal nectar organ (DNO) on the seventh abdominal segment (Fig. 7).
- c) Associated with the DNO is a group of large, mushroom-shaped setae (diameter of distal flattened end 30-40 μm). About 10-12 of these setae form a transverse row just posterior to the DNO (Figs. 7-8).

Figs 3-6. SEM photographs of epidermal structures observed in a mature *C. acamas* caterpillar. **3** — Smooth, strongly sclerotized prothoracic shield. The shield surface carries only small numbers of dendritic setae. Laterally and anteriorly the prothoracic shield is surrounded by long setae with a dentate surface. Scale : 500 μm ; **4** — Long seta with dentate surface and group of much shorter dendritic setae. The long setae are regularly pulled by the ants through their mandibles. Scale : 100 μm ; **5** — Dendritic hair on the sheath of a tentacle organ. Note the regular nests of microtrichia on the membraneous surface of the eversible part of the tentacle. Scale : 20 μm ; **6** — Spiracle of an abdominal segment surrounded by dendritic setae and pore cupola organs (arrow). Scale : 50 μm . (Photographs A. Gerber/K. Fiedler).



The surface of the mushroom-setae is highly perforated (pore diameter 0.1-0.15 μm ; Figs. 9-10) which, together with their large size and position, suggests that they are secretory and somehow involved in myrmecophily. Clark & Dickson (1971) figured apparently similar setae for a number of African Aphnaeini, but these are mostly situated at other locations (e.g. spiracles). Therefore, the homology of the mushroom-like setae in *C. acamas* awaits to be elucidated based on a broader survey of Aphnaeini immatures.

d) The tentacle organs (TOs), located on the eighth abdominal segment, are of the typical Aphnaeini type. They are inserted in black, strongly sclerotized, elevated sheaths which are easily seen without any optical equipment. The sheaths of the TOs are equipped with dendritic setae (Fig. 11; see below). At the top of each sheath there is a "crown" of long setae with a granulate surface. The eversible part of the TOs is membranous, covered with nests of microtrichia (Fig. 5), and carries long (0.5-1 mm), spiny setae on its distal end (Figs. 11-12), somehow resembling the spectacular TOs of Oriental *Curetis* larvae (Fiedler *et al.*, 1995).

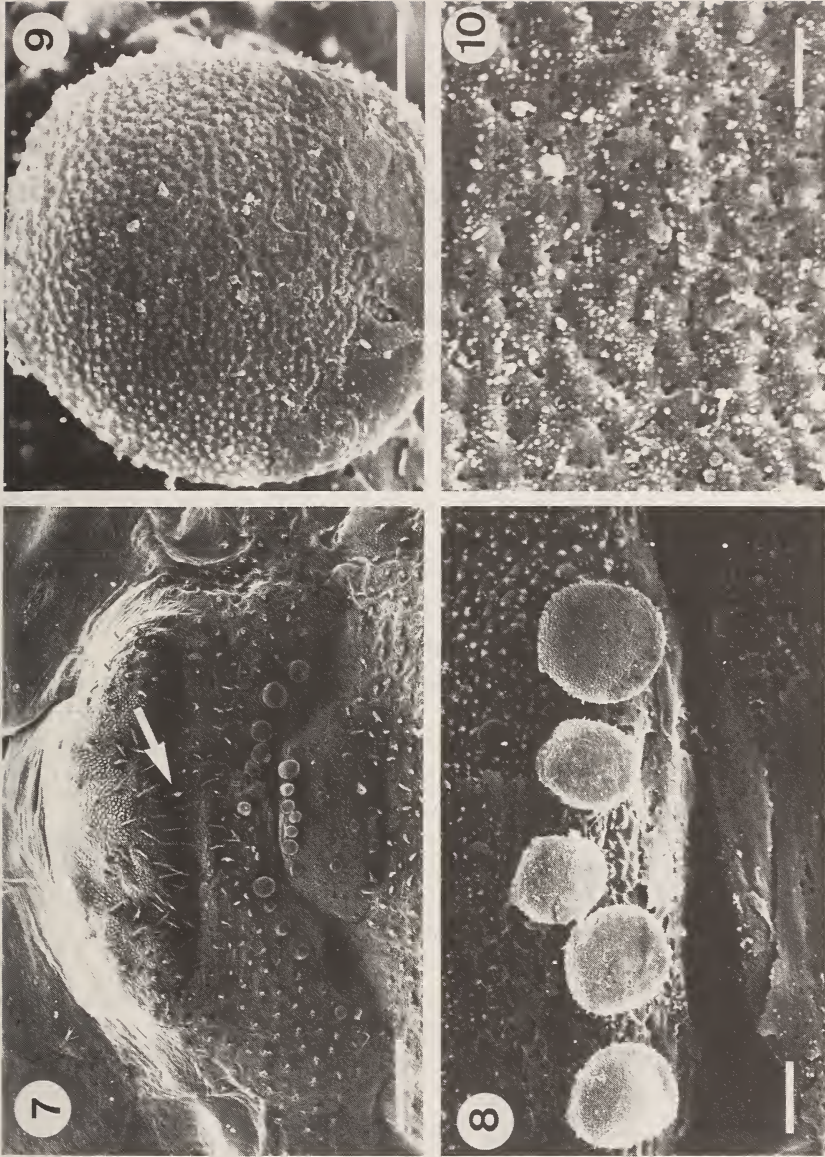
e) Pore cupola organs occur, scattered all over the skin. There are no conspicuous clusters of these glands around the DNO or the spiracles.

f) Tufts of long (0.6-1 mm) erect setae with a spiny surface (Fig. 4) occur in characteristic fashion. Above and below each abdominal spiracle there are two such tufts per segment, each comprising 4-8 hairs. Smaller groups (with ca. 4 hairs) occur at comparable locations on the thoracic segments.

g) Much shorter (50-80 μm) dendritic setae (Figs. 5-6) are present in very large numbers almost all over the larva, including the prothoracic shield and the sheaths of the TOs. Dendritic setae are likely to play a role in myrmecophily (Ballmer & Pratt, 1992). However, they usually occur in smaller numbers and concentrated at particular locations. As far as we are aware, a similarly dense cover of dendritic setae has as yet been observed only in the Oriental obligate myrmecophile *Rapala dienece* (Fiedler, unpublished data).

h) Two groups of short (80-120 μm), erect, smooth bristles (probably mechanoreceptors) occur near the opening of the DNO (Fig. 7) and amidst the two TOs.

i) We found no evidence whatsoever of "dish organs" on the abdominal segments 5-7. Such organs have been described and figured from a couple of African Aphnaeini species (*Spindasis*, *Crudaria*; Clark & Dickson, 1971), but until more material becomes available for a study



Figs 7-10. SEM photographs of epidermal structures observed in a mature *C. acamas* caterpillar. 7 — Dorsal nectar organ on the seventh abdominal segment. The glandular opening (arrow) is accompanied by a group of short, erect setae. Posterior to the glandular opening there is a group of large mushroom-like setae. Scale : 250 μm ; 8 — Group of mushroom-like setae behind the DNO, enlarged. Scale : 25 μm ; 9 — Mushroom-like seta. Scale : 10 μm ; 10 — Top surface of mushroom-like seta with numerous large pores. Scale : 2 μm . (Photographs A. Gerber/K. Fiedler).

of their fine structure, the nature and significance of these organs remains mysterious.

Discussion

The few available records of *Cigaritis acamas* caterpillars (Larsen & Pittaway 1982; this study) suggest that the species is obligatorily myrmecophilous over its whole range. *Crematogaster* cf. *jehovae* serves as host ant for *C. acamas* on Cyprus and Benyamini (1990) mentioned the same ant species with respect to Israeli populations. *Crematogaster jehovae* is morphologically very similar to *C. auberti* Emery, 1869 which has been reported to maintain close myrmecophilous relationships with caterpillars of *Cigaritis myrmecophila* in Tunisia (Dumont, 1922). On the other hand, the specific identity of the host ants from Oman remains to be elucidated. By comparison with other species of the genus (Table 1), ant-dependence can be regarded as a common feature in *Cigaritis*, since caterpillars of this genus have always been found more or less closely associated with ants. Neither in the genus *Cigaritis* nor in other Aphnaeini genera is there any evidence of a single species being myrmecoxenous (Fiedler, 1991).

In all *Cigaritis* species where the attendant ants have as yet been identified, these belong to the myrmicine ant genus *Crematogaster*. This ant genus also serves as host for most Aphnaeini species (33 out of 41 species, 80.5 %), for which the identity of associated ants has been reported (e.g. in the genera *Aphnaeus*, *Spindasis*, *Axiocerses*, *Chloroselas*, *Phasis*, *Poecilmitis*, *Oxychaeta*: Clark & Dickson, 1971; Fiedler, 1991; Schlosz & Brinkman, 1991; Callaghan, 1993). Exceptions only occur in two closely allied African genera (*Aloeides* and *Erikssonia*; with the formicine genus *Lepisiota* = *Acantholepis*), in *Axiocerses amanga* and *Poecilmitis pyroeis* (with the formicine genus *Camponotus*), and in a few *Spindasis* species and *Axiocerses harpax* (with the myrmicine genus *Pheidole*). This pattern of host use suggests that a tight connection with *Crematogaster* ants was the ancestral condition among Aphnaeini lycaenids. Shifts to novel ant hosts occurred only in a small number of lineages.

The only host ant record for *Cigaritis* involving an ant genus other than *Crematogaster* is that of *Cataglyphis "bicolor"* (see Agosti, 1990; Keegans *et al.*, 1992 for recent contributions to the still unresolved taxonomy in that ant genus) reported by Dumont (1922) for *Cigaritis myrmecophila*. Our current knowledge of the biology of *Cataglyphis* ants (Wehner, 1987) suggests that this record is based on a misinterpretation of Dumont's observations in the Tunisian desert. Dumont

Table 1
Review of ant-associations known within the genus *Cigaritis*.

Species	Degree of myrmecophily	Locality	Associated ants	Reference(s)
<i>C. (Cigaritis) allardi</i>	facultative	Morocco	<i>Crematogaster auberti</i> <i>C. antaris</i> <i>C. scutellaris</i>	Rojo de la Paz (1992)
<i>C. (C.) zohra</i>	obligatory	Morocco	<i>Crematogaster laestrygon</i>	Rojo de la Paz (1992)
<i>C. (Apharitis) acamas</i>	obligatory	Oman Israel	<i>Crematogaster</i> sp. (arboreal) <i>Crematogaster jehovae</i>	Larsen & Pittaway (1982) Benyamini (1990)
<i>C. (A.) myrmecophila</i>	obligatory	Cyprus	<i>Crematogaster</i> cf. <i>jehovae</i>	this study
<i>C. (A.) epargyros</i>	facultative ?	Tunisia Tajikistan	<i>Crematogaster auberti</i> unspecified	Dumont (1922) Lukhtanov & Lukhtanov (1994)

supposed the small *Crematogaster* ants to be slaves of the much bigger *Cataglyphis* ants. However, the solitary *Cataglyphis* workers, which Dumont had observed near the nests of *Crematogaster*, were almost certainly individual foragers and had no sociobiological relationship to the *Crematogaster* ants. Workers of *Cataglyphis* are well known to forage dozens of metres away from their home nests (Wehner, 1987). Socially parasitic associations between *Cataglyphis* and *Crematogaster* ants have never been discovered as yet (Hölldobler & Wilson, 1990), and such a relationship would be extremely unlikely to occur among members of two different ant subfamilies (Buschinger, 1990). Finally, no associations between *Cataglyphis* ants and larvae or pupae of other lycaenids have ever been observed (Fiedler, 1991 and unpublished data). Hence, *Cataglyphis* should be eliminated from the host ant list of *Cigaritis* butterflies, unless new field data become available. Unfortunately, Larsen & Pittaway (1982), when citing Dumont (1922), have uncritically reinforced this erroneous assumption.

Cigaritis caterpillars apparently use a broad range of feeding strategies. Our observations revealed that prefinal and final instars of Cypriot *C. acamas* mainly prey on ant-brood, but additionally receive trophalactic regurgitations. Such a feeding behaviour, though not definitively observed before, had been postulated for *C. acamas* from Oman where caterpillars spend their whole life inside ant nests (Larsen & Pittaway, 1982). We assume that, once adopted into *Crematogaster* nests, larval behaviour and utilization of food sources are very similar between *C. acamas* populations from Cyprus and Oman. Besides this aphytophagous feeding strategy of *C. acamas*, caterpillars of other *Cigaritis* have been found to feed on green plants of the families Fabaceae, Polygonaceae, or Cistaceae, like *C. allardi*, *C. zohra* (Rojo de la Paz, 1992), *C. myrmecophila* (Dumont, 1922) and *C. epargyros* (Lukhtanov & Lukhtanov, 1994). However, at least in the latter two species, where available information is very scant, we can at present not rule out the possibility that caterpillars obtain at least part of their food as predators or commensals in ant nests.

On the other hand, we can as yet not ascertain if Cypriot *C. acamas* caterpillars are entirely aphytophagous during all instars. Wynter-Blyth (1982) assumed *Cassia* trees to be food-plants in India, but it remains unclear whether or not he really had found *C. acamas* larvae feeding on plant tissue or deduced this from having observed females laying eggs on these trees. The observations of Larsen & Pittaway (1982) on Omani populations indicate that *C. acamas* females deposit their eggs on certain plants nearby *Crematogaster* ant nests (e.g. date trunks in Oman, *Cassia* trees in India probably for the same reason). Ant-



Figs 11-12. SEM photographs of epidermal structures observed in a mature *C. acamas* caterpillar. **11** — Partially everted tentacle organ. The eversible part is covered with nests of microtrichia. Long hairs with dentate surface structure are protruding from the (invaginated) top of the eversible part. The sheath carries a large number of dendritic hairs. Scale : 100 μm ; **12** — Dorsal view of partly everted TO with central long hairs and cuticular fine structure (microtrichia). The long, stiff erect setae with dentate surface, which surround the distal end of the TO sheath, have been lost prior to fixation (arrow points to insertion of one such hair). Scale : 50 μm . (Photographs A. Gerber/K. Fiedler).

dependent oviposition is common among obligatorily myrmecophilous lycaenid butterflies (Pierce & Elgar, 1985 ; Fiedler, 1991) and ensures the establishment of the "right" caterpillar-ant association from the egg stage onwards. Later, caterpillars are adopted by the ants either directly after hatching or during one of the following instars. A similar strategy occurs among Australian *Acrodipsas* species, whose entirely aphytophagous larvae are adopted immediately after hatching from the eggs laid nearby the host ants' nest (Samson, 1989).

We could trace more or less reliable information on oviposition substrates, larval food resources and/or myrmecophily for 86 Aphnaeini species (Fiedler, 1991 & unpublished data ; Schlosz & Brinkman, 1991 ; Callaghan, 1993). Although most authors agree on the extraordinarily close relationships between Aphnaeini immatures and ants, our observations on *C. acamas* are the first proof that preying on ant brood does really occur in this tribe. Although preying on ant brood has been postulated for species like *Oxychata dicksoni*, *Spindasis takanonis* and others, conclusive evidence is still lacking. Otherwise among the Lycaenidae, there are very few taxonomic groups where this feeding strategy has independently evolved (review : Cottrell, 1984). Besides the well-known genera *Maculinea* (Thomas *et al.*, 1993 ; Elmes *et al.*, 1994) and *Lepidochrysops* (Henning, 1983), where young caterpillars are herbivorous and later turn into carnivores, examples are known from a couple of tropical Miletinae species (Fiedler, 1991) or Australian *Acrodipsas* (Samson, 1989), and strongly suspected from Indian *Zesius chrysomallus* (Yates, 1932).

Trophallactic feeding is more widespread among myrmecophilous insects in general (Hölldobler & Wilson, 1990), and among lycaenids in particular. Besides *C. acamas*, this type of interaction has been confirmed in *Aphnaeus adamsi* and *Spindasis takanonis*, and is likely to occur in various other Aphnaeini species (*Spindasis nyassae*, *Chloroselas umbrosa*). Trophallaxis also occurs, at least occasionally, in some Miletinae species, in *Shirozua jonasi*, *Anthene levis* and *Niphanda fusca* (Fiedler, 1991).

Morphologically, the caterpillars of *C. acamas* are largely similar to other Aphnaeini whose immatures have been figured (Clark & Dickson, 1971). The lack of any other SEM studies on Aphnaeini species, however, presently hampers exact comparisons. The significance of the long lateral hairs for the interactions with ants is suggested by the characteristic behaviour of attendant ants, which pulled these hairs through their mandibles. This behaviour could assist in collecting some putative secretions. Likewise, the intensive licking behaviour all over

the surface could well be caused by the numerous dendritic setae. From other lycaenids it is known that antennation behaviour of tending ants concentrates at locations with dendritic setae (Ballmer & Pratt, 1992 ; Fiedler, unpublished data). The mushroom-like setae with their large pores (much larger than in most pore cupola organs of lycaenid immatures) and the morphological associations of these setae with the nectar organ also suggest a strong connection of these organs with myrmecophily. On the other hand, we failed to find any equivalents of so-called “dish organs” which have been reported from a couple of Aphnaeini species with extremely close associations with ants. Given their tight relationships towards ants, the structure and function of epidermal organs of Aphnaeini immatures is one of the most rewarding fields for further studies on myrmecophilous lycaenids.

The Cypriot populations of *C. acamas* differ in some aspects from those investigated by Larsen & Pittaway (1982) in Oman. The habitat on Cyprus has a typical Mediterranean climate which contrasts with the extreme desert conditions in Oman. Furthermore, host ant species of both populations are quite different according to their nesting niche preferences (a subterranean *Crematogaster* species on Cyprus, an arboreal species in Oman). Thus, caterpillars of either population might have evolved local host preferences, which are probably correlated with the prevailing ecological conditions. Geographical “host races” with respect to the ant species used for larval development have recently been described from another obligate myrmecophile, *Maculinea alcon* (Elmes *et al.*, 1994).

The apparent differences in habitat and host ants may corroborate the idea that Cypriot and Arabian populations of *C. acamas* deserve the status of valid subspecies. Originally, all subspecies around *C. acamas* have been exclusively defined on the grounds of adult morphology, while ecological or life-history characters still remain largely unknown.

Larsen (1983, 1990) and Larsen & Pittaway (1982) arranged the described taxa in a more reasonable zoogeographical manner. However, the subspecific taxonomy of *C. acamas* remains unsatisfactory. Ssp. *cypriaca* Riley, 1925 is probably best regarded as a synonym of nominotypical *acamas* Klug, 1834 (Type locality : “Syria”) which occurs in Asia minor and the eastern Mediterranean (from southern Turkey eastwards to Iran, southwards across Syria, Lebanon, Israel, East Jordan and the Sinai to Egypt and probably into northern Arabia : Larsen 1974, 1990 : Larsen & Nakamura, 1983 ; Benyamini, 1990). In south-western Arabia there occurs *C. acamas bellatrix* Butler, 1886,

while *C. acamas hypargyros* Butler, 1886 ranges from Oman eastwards across Iran and Pakistan to Afghanistan and India.

Nevertheless, given the extremely localized and fragmented distribution in relation to the arid environments and strong dependence on its host ants, the applicability of the traditional subspecies concept in a case like *C. acamas* appears doubtful.

According to Larsen & Pittaway (1982), *C. acamas* and its congeners (like *C. myrmecophila*) are eremic species confined to arid environments, although nominotypical *C. acamas* also extends into the Mediterranean biome. At least these two species and probably many more members of the tribe Aphnaeini (e.g. the numerous local endemics of the genera *Poecilmitis* or *Aloeides* in southern Africa) are ant-dependent low density species which only occur at very restricted locations. Ant-dependence in obligate myrmecophiles like *Cigaritis* might have particularly affected speciation processes, possibly leading to a great number of environmentally differentiated entities to which traditional taxonomic concepts can hardly be applied. Especially in xeric environments, where suitable habitats ("oases") are patchily distributed, small in size, and often highly isolated, local specializations with regard to myrmecophily could be a driving force of evolution (Pierce, 1984 ; Smiley *et al.*, 1988). Hence, some of the taxonomic difficulties within *Cigaritis* could be influenced by this highly specialized way of life. Furthermore, much of the variation in size and colour observed between usually small samples from widely distant localities may be due to the extremely harsh and variable environmental conditions (unpredictable rainfall, resource competition inside ant nests).

To approach a more complete understanding of the taxonomy and evolution of *Cigaritis* butterflies, but also to fill the still significant gaps in the mere documentation of the life-cycles of these interesting butterfly species with their spectacular biology, we hope that this report encourages a larger number of lepidopterists as well as myrmecologists to pay attention to these highly advanced offshoots from the Ethiopian fauna, when studying natural history at the southern fringe of the Palearctic realm.

Acknowledgements

We thank A. Gerber (Würzburg) for her assistance with the SEM and Dr. R. D. Schumann (Darmstadt) for his help attempting to rear caterpillars with *Lepto thorax* ant brood. A. Schulz (Leverkusen) kindly provided the determination of the *Crematogaster* species.

References

- AGOSTI, D., 1990. Review and reclassification of *Cataglyphis* (Hymenoptera, Formicidae). *J. nat. Hist.* 24 : 1457-1505.
- BALLMER, G. R. & PRATT, G. F., 1992. Quantification of ant attendance (myrmecophily) of lycaenid larvae. *J. Res. Lepid.* 30 : 95-112.
- BENYAMINI, D., 1990. A field guide to the butterflies of Israel including Mt. Hermon and Sinai. 234 pp. Keter Publishing House [in Hebrew].
- BUSCHINGER, A., 1990. Sympatric speciation and radiative evolution of socially parasitic ants — heretic hypotheses and their factual background. *Z. zool. Syst. Evolut.-Forsch.* 28 : 241-260.
- CALLAGHAN, C. J., 1993. Notes on the biology of a myrmecophilous African lycaenid, *Aphnaeus adamsi* Stempffer (Lepidoptera, Lycaenidae). *Bull. Soc. ent. Fr.* 97 : 339-342.
- CLARK, G. C. & DICKSON, C. G. C., 1971. Life histories of the South African lycaenid butterflies. xvi + 272 pp., 108 pls. Purnell, Cape Town.
- COTTRELL, C. B., 1984. Aphytophagy in butterflies: its relationship to myrmecophily. *Zool. J. Linn. Soc.* 79 : 1-57.
- DUMONT, C., 1922. Diagnoses de Lépidoptères nouveaux du Nord del'Afrique. *Bull. Soc. ent. Fr.* 1922 : 215-220.
- ELMES, G. W., THOMAS, J. A., HAMMARSTED, O., MUNGUIRA, M. L., MARTIN, J., & VAN DER MADE, J. G., 1994. Differences in host-ant specificity between Spanish, Dutch and Swedish populations of the endangered butterfly, *Maculinea alcon* (Denis et Schiff.) (Lepidoptera). *Memorabilia Zool.* 48 : 55-68.
- FIEDLER, K., 1991. Systematic, evolutionary, and ecological implications of myrmecophily within the Lycaenidae (Insecta : Lepidoptera : Papilionoidea). *Bonn. zool. Monogr.* 31 : 1-210.
- FIEDLER, K., SEUFERT, P., MASCHWITZ, U. & AZARAE, I., 1995. Notes on larval biology and pupal morphology of Malaysian *Curetis* butterflies (Lepidoptera : Lycaenidae). *Tyô to Ga* 45 : 287-299.
- HENNING, S. F., 1983. Biological groups within the Lycaenidae (Lepidoptera). *J. ent. Soc. sth. Afr.* 46 : 65-85.
- HÖLLDOBLER, B. & WILSON, E. O., 1990. The Ants. 732 pp. Belknap Press of Harvard Univ. Press, Cambridge, Massachusetts.
- KEEGANS, S. J., MORGAN, E. D., AGOSTI, D. & WEHNER, R., 1992. What do glands tell us about species? A chemical case study of *Cataglyphis* ants. *Biochem. Syst. Ecol.* 20 : 559-572.
- LARSEN, T. B., 1974. Butterflies of Lebanon. xv + 256 pp. Nation. Council Sci. Res., Beirut.
- LARSEN, T. B., 1983. Insects of Saudi Arabia. Lepidoptera, Rhopalocera (A monograph of the butterflies of the Arabian Peninsula). *Fauna Saudi Arabia* 5 : 333-478.
- LARSEN, T. B., 1990. Butterflies of Egypt. 112 pp. Apollo Books, Svendborg.
- LARSEN, T. B. & NAKAMURA, I., 1983. The butterflies of East Jordan. *Entomologist's Gaz.* 34 : 135-208.

- LARSEN, T. B. & PITTAWAY, A. R., 1982. Notes on the ecology, biology and taxonomy of *Apharitis acamas* (Klug) (Lepidoptera : Lycaenidae). *Entomologist's Gaz.* 33 : 163-168.
- LUKHTANOV, V. & LUKHTANOV, A., 1994. Die Tagfalter Nordwestasiens. *Herbipoliana* 3 : 1-440.
- MANIL, L., 1990. Les Rhopalocères de Chypre (Lepidoptera : Papilionoidea et Hesperioidea). *Linn. belg.* 12 (8) : 313-391.
- PARKER, R., 1983. The butterflies of Cyprus. *Entomologist's Gaz.* 34 : 17-53.
- PIERCE, N. E., 1984. Amplified species diversity : a case study of an Australian lycaenid butterfly and its attendant ants. In Vane-Wright, R. I. & Ackery, P. R. (Eds) : *The Biology of Butterflies*. Symposium of the Royal Entomological Society of London, No. 11, pp. 197-200. Academic Press, London.
- PIERCE, N. E. & ELGAR, M. A., 1985. The influence of ants on host plant selection by *Jalmenus evagoras*, a myrmecophilous lycaenid butterfly. *Behav. Ecol. Sociobiol.* 16 : 209-222.
- RILEY, N. D., 1925. Species usually referred to the Genus *Cigaritis* (Lep. Lycaenidae). *Novit. zool.* 32 : 70-95.
- ROJO DE LA PAZ, A., 1992. Two new cases of myrmecophily in the Lycaenidae (Lepidoptera) : biology of *Cigaritis zohra* (Donzel, 1847) and *Cigaritis allardi* (Oberthür, 1909) in Morocco. *Nota lepid. Suppl.* 4 : 14-17.
- SAMSON, P. R., 1989. Morphology and biology of *Acrodipsas illidgei* (Waterhouse and Lyell), a myrmecophilous lycaenid (Lepidoptera : Lycaenidae : Theclinae). *J. Aust. ent. Soc.* 28 : 161-168.
- SCHLOSZ, M. & BRINKMAN, T., 1991. The life history of *Tylopaedia sardonix peringueyi* (Aurivillius). *J. ent. Soc. sth. Afr.* 54 : 81-84.
- SMILEY, J. T., ATSATT, P. R. & PIERCE, N. E., 1988. Local distribution of the lycaenid butterfly, *Jalmenus evagoras*, in response to host ants and plants. *Oecologia* 76 : 416-422.
- THOMAS, C. D. & MALLORIE, H. C., 1985. Rarity, species richness and conservation : butterflies of the Atlas mountains in Morocco. *Biol. Conserv.* 33 : 95-117.
- THOMAS, J. A., ELMES, G. W. & WARDLAW, J. C., 1993. Contest competition among *Maculinea rebeli* butterfly larvae in ant nests. *Ecol. Ent.* 18 : 73-76.
- WEHNER, R., 1987. Spatial organization of foraging behaviour in individually searching ants, *Cataglyphis* (Sahara desert) and *Ocymyrmex* (Namib desert). *Experientia Suppl.* 54 : 15-42.
- WYNTER-BLYTH, M. A., 1982. Butterflies of the Indian Region. xx + 523 pp. Reprint ed., Today & Tomorrow's Printers & Publ., New Delhi.
- YATES, J. A., 1932. Note on *Zesius chrysomallus* Hub. *J. Bombay nat. Hist. Soc.* 35 : 911-913.

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Nota lepidopterologica](#)

Jahr/Year: 1995

Band/Volume: [18](#)

Autor(en)/Author(s): Sanetra Matthias, Fiedler Konrad

Artikel/Article: [Behaviour and morphology of an aphytophagous lycaenid caterpillar : Cigaritis \(Apharitis\) acamas Klug, 1834 \(Lepidoptera : Lycaenidae\) 57-76](#)