Proc. VII. Congr. Eur. Lepid., Lunz 3-8.IX.1990
Nota lepid. Supplement No. 4 : 11-13 ; 30.XI.1992 ISSN 0342-7536

Recent contributions to the behavioural ecology and evolution of lycaenid-ant associations (Lepidoptera, Lycaenidae)

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The larvae of numerous species of the butterfly family Lycaenidae associate with ants, these associations ranging from loose, facultative ones to close and obligate symbiotic or even parasitic relationships. Three types of glandular epidermal organs (pore cupola organs [PCOs], a dorsal nectary organ [DNO], and a pair of eversible tentacle organs [TOs]) mainly mediate these myrmecophilous associations, while further glandular structures (e.g. dendritic setae) or vibratory communication may play important roles, too. The secretions of the PCOs are attractive to ants and suppress their aggressiveness, the DNO produces nutritive liquids rich in carbohydrates or amino acids, and the TOs are supposed to release mimic substances of ant alarm pheromones.

Standardized laboratory experiments with 7 European lycaenids, 1 riodinid, and 2 ant species were conducted to further elucidate the function of the myrmecophilous organs. Measured were the attractiveness A of the larvae (mean number of attendant ants), and the permanence P of ant-attendance (relative proportion of experimental time during which a larva was visited by at least 1 ant). In experiments with the formicine ant *Lasius flavus* L., myrmecophilous caterpillars (*Polyommatus coridon* Poda, *P. icarus* Rott.) with a full set of ant-organs were significantly more attractive to, and more permanently visited by, ants than myrmecoxenous larvae lacking a (functional) DNO and TOs (*Lycaena phlaeas* L., *L. tityrus* Poda, *Callophrys rubi* L., *Hamearis lucina* L.) (Fig. 1). *P. coridon* had significantly higher myrmecophily parameters than its congener *P. icarus* and among the myrmecoxenous species, *C. rubi* and *H. lucina* were significantly less attractive and less permanently ant-attended than *L. phlaeas*. Larvae of *C. rubi* and *H. lucina* were even sometimes attacked and not antennated in the typical way. *C. rubi* caterpillars, although possessing a DNO, never produced any nectar-like secretions and were totally unattractive. Field observations revealed no ant-associations of this species, and according to SEM studies its DNO is a non-functional rudimentary organ. Thus, *C. rubi* is functionally myrmecoxenous. Experiments with the myrmicine ant *Tetramorium caespitum* L. yielded analogous results with the same lycaenid species.

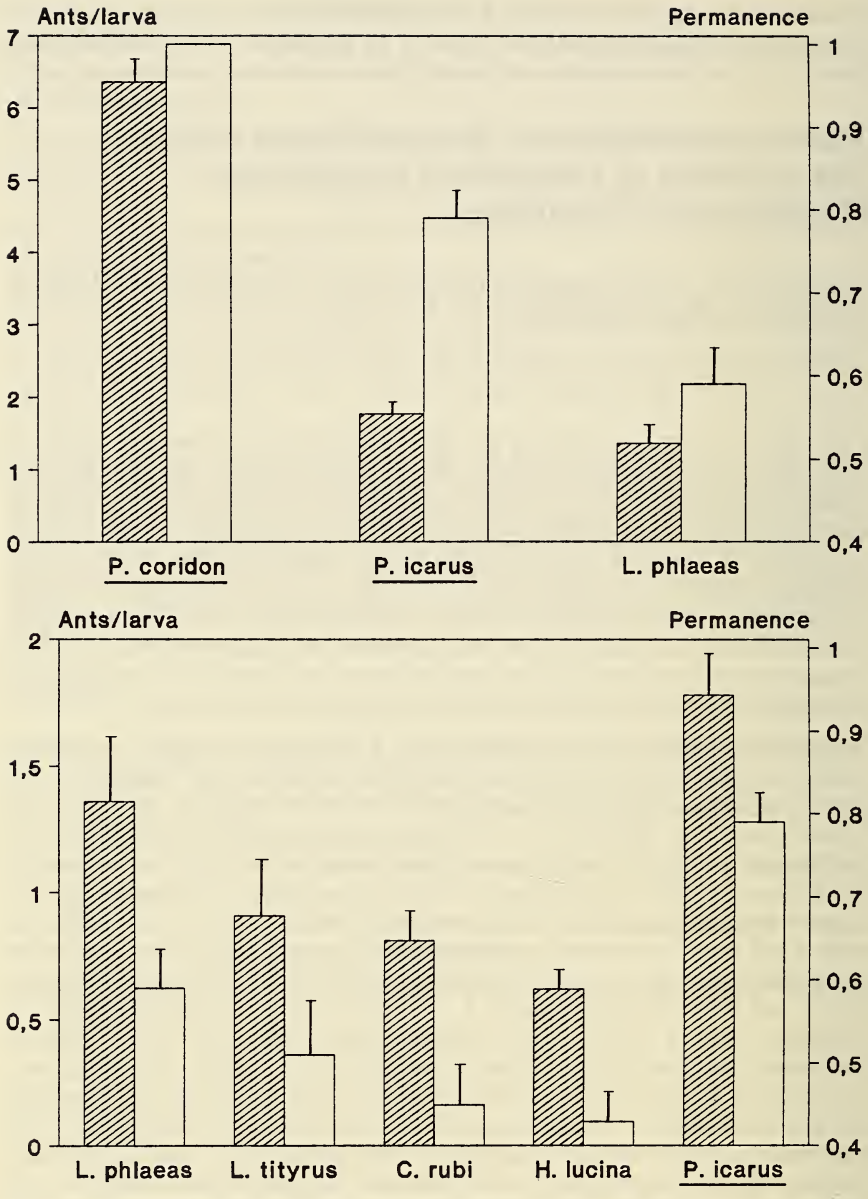

Fig. 1. Attractiveness (mean number of ants/larva ; hatched bars) and permanence of ant-attendance (relative proportion of experimental time during which a caterpillar received ant-attendance ; open bars) of 5 lycaenids and 1 riodinid from Europe in experiments (15 min) with the ant *Lasius flavus*. Given are the mean values and standard errors. Species with names underlined are myrmecophilous. Note the different scaling of A in the two graphs.

Exclusion of the DNO of *Polyommatus* caterpillars with a cap of glue decreased both parameters, A and P, significantly (experiments with *L. flavus*). *P. coridon* larvae retained a stable ant-association, but their mean attractiveness was reduced from 6.37 to 2.77, while *P. icarus* larvae became totally unattractive (A = 0.65, P = 0.41). Rearing larvae of *P. icarus* on foliage of the tree *Robinia pseudoacacia* L., as well, drastically reduced the myrmecophilous qualities of the larvae (experiments with *T. caespitum*), and these larvae had strongly restrained abilities to produce nutritive DNO secretions.

These results confirm the important role of the DNO in lycaenid myrmecophily : myrmecoxenous larvae without a functional DNO as well as myrmecophilous caterpillars, whose DNO had experimentally been rendered nonfunctional, were constantly less attractive to ants than intact myrmecophilous lycaenid caterpillars. The PCOs alone are in most cases not sufficient to maintain stable ant-associations. The TOs mainly act as accessory myrmecophilous organs. Formicine ants (e.g. *L. flavus*) are activated by the TOs of *Polyommatus* larvae, and in experiments with *P. icarus* and *L. flavus* the permanence of ant-associations was significantly correlated with the eversion rate of the TOs ($r_s = 0.56$, $p < 0.001$).

The DNO is confined to the tribes Aphnaeini, Theclini, Eumaeini, and Polyommatini within the subfamily Lycaeninae. Caterpillars of the tribe Lycaenini and of the 3 further lycaenid subfamilies (Poritiinae Miletinae, and Curetinae) never possess a DNO, and only *Curetis* and *Aslauga* larvae have TOs of a different structure than in the Lycaeninae. As a consequence, ant-associations of the trophobiotic type are confined to the tribes Aphnaeini, Theclini, Eumaeini, and Polyommatini, whereas larvae of the other tribes are usually not ant-associated at all. Only a few species live as parasites or commensales in ant-nests. It is suggested that the DNO (and possibly the TOs of the Lycaeninae types) are apomorphic characters of the more advanced Lycaeninae tribes Aphnaeini, Theclini, Eumaeini, and Polyommatini, while the remaining lycaenids primarily lack these organs.

Hence, the myrmecoxeny of the subfamilies Poritiinae, Miletinae, and Curetinae is regarded as a plesiomorphic character (primarily myrmecoxenous lycaenids), the myrmecophilous Miletinae species being secondarily derived. In the remaining 4 tribes, representing the vast majority (> 3500) of the extant species, the larvae are primarily myrmecophilous and mostly possess a DNO and TOs. In several genera of the Theclini (e.g. *Thecla* group and certain *Deudorix* spp.), Eumaeini (e.g. *Callophrys* spp., *Satyrium pruni* L.), and Polyommatini (*Vacciniina, Agriades*) ant-associations and the related ant-organs have been reduced to a varying degree (secondarily myrmecoxenous species). Factors such as endophytic life-habits of the larvae, nutrient-poor host plants, or low abundance of ants in arctic-alpine habitats appear to be major forces selecting against myrmecophily.