

Review Article

The Host Genera of Ant-Parasitic Lycaenidae Butterflies: A Review

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Numerous butterfly species in the family Lycaenidae maintain myrmecophilous associations with trophobiotic ants, but only a minority of ant-associated butterflies are parasites of ants. *Camponotus*, *Crematogaster*, *Myrmica*, and *Oecophylla* are the most frequently parasitized ant genera. The distribution of ant-parasitic representatives of the Lycaenidae suggests that only *Camponotus* and *Crematogaster* have multiply been invaded as hosts by different independent butterfly lineages. A general linear model reveals that the number of associated nonparasitic lycaenid butterfly species is the single best predictor of the frequency of parasitic interactions to occur within an ant genus. Neither species richness of invaded ant genera nor their ecological prevalence or geographical distribution contributed significantly to that model. Some large and dominant ant genera, which comprise important visitors of ant-mutualistic lycaenids, have no (*Formica*, *Dolichoderus*) or very few ant-parasitic butterflies (*Lasius*, *Polyrhachis*) associated with them.

1. Introduction

Associations between ants and butterfly species in the families Lycaenidae and Riodinidae have attracted the interest of naturalists since more than 200 years. Building upon an ever-increasing number of field records and case studies (summarized in [1]) these interactions with their manifold variations and intricacies have developed into a paradigmatic example of the evolutionary ecology and dynamics of interspecific associations [2]. Interactions with ants are most well developed during the larval stages of myrmecophilous butterflies. To communicate with ants, myrmecophilous caterpillars possess a variety of glandular organs and often also use vibrational signals that may modulate ant behaviour [3, 4]. Essentially, interactions between myrmecophilous caterpillars and visiting ants comprise a trade of two commodities. The caterpillars produce secretions that contain carbohydrates and amino acids [5]. In turn, the ants harvest these secretions, do not attack myrmecophilous caterpillars and the presence of ant guards confers, at least in a statistical sense, protection against predators or parasitoids (reviewed in [2]). Thus, such interactions are basically mutualistic in

nature, even though the extent of benefits accruing to both partners may be asymmetric and manipulatory communication (by means of mimicking chemical or vibrational signals of ants) is not uncommon. In certain cases, especially if butterfly-ant associations are obligatory (from the butterfly's perspective) and involve specific host ants, interactions may extend into other life-cycle stages of the butterflies, such as pupae (if pupation occurs in ant nests or pavilions built by ants to protect their trophobiotic partners), adults (if egg-laying or nutrient acquisition occurs in company with ants), or eggs.

The vast majority of known butterfly-ant interactions are mutualistic or commensalic in nature. In the latter case the butterfly larvae benefit from their association with ants, while no costs accrue to the ants. Some few butterflies, however, have evolved into parasites of ants [6]. These unusual associations have served as models for host-parasite coevolution [7]. Ant parasitism requires very precise tailoring of the chemical and mechanical signals employed to achieve social integration into ant colonies. Accordingly, ant-parasitic lycaenid butterflies are highly specific with regard to their host ant use, which also renders them extraordinarily

susceptible to the risk of coextinction [8]. Indeed, many ant-parasitic lycaenids are highly endangered species [9], and the well-studied Palaearctic genus *Maculinea* is now regarded as a prime example of insect conservation biology [10].

In this essay, I will focus on the ant genera that serve as hosts of parasitic butterflies. First, I summarize which ant genera in the world are known to be parasitized by butterflies. I then discuss whether this host ant use reflects the macroecological patterns seen in mutualistic butterfly-ant associations. Finally, I will explore if the observed host use patterns allow for generalizations and testable predictions, for example, with regard to expected host ant affiliations in underexplored faunas. Specifically, I expected that the number of associated parasitic lycaenids per host ant genera increases with their ecological prevalence, geographical distribution, and species richness.

2. What Constitutes an Ant-Parasitic Butterfly Species?

I here use a rather restrictive definition of ant parasitism. I regard a butterfly species as a parasite of its host ants only if (a) the butterfly caterpillars (at least from some developmental stage onwards) feed on ant brood inside ant nests (“predators”) or (b) the caterpillars are being fed through trophallaxis by their host ants (“cuckoo-type” parasitism). Both these types of parasitism occur in *Maculinea* [11], but the extent of the nutrient flow from the ant colony to the caterpillars may vary across species. For example, in some lycaenid species feeding through trophallaxis apparently occurs only as a supplementary mode of nutrient acquisition. Yet include such cases here as parasites of ants, since the respective behavioural and communicative strategies are in place.

In contrast, I exclude two types of “indirect” parasitism. First, there are a few myrmecophilous lycaenid species that feed obligately on myrmecophytic ant plants. The best documented examples are certain SE Asian *Arhopala* species on ant-trees of the genus *Macaranga* [12, 13]. These caterpillars cause substantial feeding damage to the ant-trees and thereby likely inflict costs to the *Crematogaster* ants that inhibit these trees. *Arhopala* caterpillars on *Macaranga*, however, possess a nectar gland and secrete nectar at rates typical for ant-mutualistic lycaenids (K. Fiedler, unpublished observations). They are also not known to elicit trophallaxis or even to prey on ant brood. Accordingly, I did not score these associations as parasitic, but rather as competitors of ants for the same resource (namely, the ant-tree). Analogous cases are known, or suspected, to occur in other tropical lycaenid butterflies whose larvae feed on obligate myrmecophytes, such as various *Hypochrysops* species in Australia and New Guinea on *Myrmecodia* ant plants [14, 15].

Similarly, I do not include those lycaenid species (notably in the subfamily Miletinae) whose larvae prey upon ant-attended honeydew-producing homopterans and often also feed on homopteran honeydew [16–20]. In analogy to the case of myrmecophytes, these butterflies compete with ants for the same resources (here: trophobiotic homopterans), but

as a rule the caterpillars neither prey on ant brood nor elicit trophallaxis. Some species of the Miletinae, however, are known to supplement their diet through ant regurgitations, and these are included below since they show the behavioural traits considered here as essential for parasitism with ants.

Two further restrictions are (1) cases where trophallaxis or predation on ant brood have so far only been indirectly inferred, but not be confirmed through direct observational evidence, are largely excluded. This relates to a couple of tropical lycaenid species for which only old, or very incomplete or vague, information on their life cycles is available. In these cases, new data are needed, before any conclusions become feasible. (2) The butterfly family Riodinidae is also excluded. Ant-associations occur in at least two clades of Neotropical Riodinidae (tribes Eurybiini and Nymphidiini, see [21, 22] for many case studies and [23] for a tentative phylogeny). Circumstantial evidence exists that in at least one genus within the Nymphidiini (*Aricoris*) the larvae may feed on trophallaxis received from *Camponotus* host ants [21], but otherwise the existence of ant-parasitic life habits in the Riodinidae (though not unlikely to exist amongst Neotropical riodinids) must await confirmation.

3. Data Sources

Butterfly life-history data were compiled from a large variety of sources, ranging from faunal monographic treatments across hundreds of journal papers to databases in the Internet. The data tables in [1] formed the initial basis, and they have been continually extended and updated ever since [24, 25]. Here, I focus on that subset of sources where (a) the butterfly species qualifies as a parasite of ants according to the restrictions stated above and (b) the host ant has been reported at least at genus level. Three reasons justify the choice of the ant genus level for the subsequent comparisons. (1) For most ant genera, no modern revisions are available. Thus, proper species identifications are often impossible, especially in tropical realms. (2) Ant genus delimitations are quite stable and recognizable on a worldwide basis ([26], see also <http://www.antweb.org>). Accordingly, records (often reported by lepidopterists and not myrmecologists) should usually be reliable on this level. (3) Most ant-parasitic lycaenids are not bound to one single ant species, but are affiliated with a couple of congeneric ant species. For example novel *Myrmica* host ant species continue to be discovered in Eastern Europe for butterflies in the genus *Maculinea* [27, 28]. Therefore, I performed all analyses on the taxonomic level where the highest reliability can be achieved. Data on species richness of ant genera was extracted from the website antweb.org (as of 9 October 2011).

A complete bibliography of the evaluated literature would extend beyond the scope of this essay. For ant-parasitic Lycaenidae, many sources have been detailed in [6]. Full information on data sources is available upon request from the author.

4. Summary of Ant Genera That Are Confirmed as Hosts of Parasitic Lycaenid Butterflies

Of the 54 ant genera known to attend lycaenid larvae on a worldwide basis ([24], only *Liometopum* has been added to this list since) just 11 genera are for certain recorded as hosts of parasitic butterflies.

4.1. Subfamily Formicinae

4.1.1. *Camponotus*. This is one of the globally most prevalent ant genera in terms of species richness (>1050 described species) as well as ecological significance. It is also the numerically leading ant genus with regard to the number of associated parasitic lycaenid species. At least 9 species of the large Afrotropical genus *Lepidochrysops* have been recorded from nests of either *Camponotus niveosetosus* or *C. maculatus*. *Lepidochrysops* larvae have a life cycle similar to the *Maculinea-Phengaris* clade. They initially feed on flowers of plants (mostly in the families Lamiaceae, but also Verbenaceae and Scrophulariaceae). At the onset of their third instar they are adopted by *Camponotus* workers into the ant colonies where they turn into predators of ant brood. There are more than 125 described *Lepidochrysops* species [29]. Many of them are microendemics of high conservation concern [30]. Presumably all *Lepidochrysops* species are parasites of *Camponotus* ants. The small South African genus *Orachrysops* is the closest relative of *Lepidochrysops*. *Orachrysops* larvae are not parasites of ants, but live in close association with *Camponotus* ants as leaf, and later root, herbivores of various Fabaceae plants [31]. *Orachrysops* species may therefore be seen as models for the evolutionary transition between “normal” phytophagous ant-mutualistic lycaenids and species that are parasites of ants.

The East Asian *Niphanda fusca* is an obligate cuckoo-type parasite of various *Camponotus* ants [32]. Unusual for ant-parasitic lycaenids, larvae of this species retain a fully functional nectar gland whose secretions are tuned towards the gustatory preferences of their host ants [33]. Life histories of other *Niphanda* species, that all occur in East and South-East Asia, are unknown. Within the genus *Ogyris* (13 species in New Guinea and Australia) most species maintain obligate mutualistic associations with ants, but two are reported to occur inside nests of *Camponotus* species, namely, *O. idmo* and *O. subterrestris* [15, 34, 35]. Finally, for at least two representatives of the aphytophagous African genus *Lachnocnema* (*L. bibulus*, *L. magna*) there is evidence that caterpillars supplement their diet by eliciting trophallaxis from *Camponotus* ants (in *L. bibulus* reportedly also from *Crematogaster* ants). The major nutrient source of *Lachnocnema* larvae, however, is preying on homopterans and drinking their honeydew excretions.

4.1.2. *Oecophylla*. The two species of weaver ants in the genus *Oecophylla* are extremely dominant insects in their habitats in tropical Africa, southern and south-eastern Asia, Australia, and New Guinea. Two lycaenid genera are specialist parasites of weaver ants. *Liphyra* (*L. brassolis*, *L. grandis*)

are predators of the brood of *Oecophylla smaragdina* in the Oriental region [15, 25], while African *Euliphyra* (*Eu. mirifica*, *Eu. leucyana*) are cuckoo-type parasites of *Oe. longinoda* by means of trophallaxis and also steal prey items of their host ants [36]. Many more lycaenid species are associated with weaver ants, including striking examples of obligate and specific interactions, but these all appear to be mutualistic associations.

4.1.3. *Polyrhachis*. Even though this large ant genus (>600 described species) ranks rather high in the visitors list of lycaenid caterpillars, only one of its reported associated 27 myrmecophilous butterfly species is a parasite. The rare *Arhopala wildei* in Australia and New Guinea preys on brood in nests of *Polyrhachis queenslandica* [37, 38].

4.1.4. *Lasius*. Ant species of this moderately rich genus (>100 species) are frequent visitors of lycaenid caterpillars, especially in the Palaearctic realm [25]. *Shirozua jonasi* from East Asia is the only ant-parasitic butterfly known to be affiliated with *Lasius* ants (*L. spathepus*, *L. fuliginosus*, and *L. morisitai*). The caterpillars apparently receive occasional trophallactic regurgitations, but their principle mode of feeding is to prey on a variety of homopterans and to drink their honeydew excretions [39].

4.1.5. *Lepisiota*. Butterflies of the South African genus *Aloeides* all have an obligate relationship to ants. *Lepisiota capensis* is their major host ant [40]. As far as known, most *Aloeides* species are phytophagous ant mutualists (host plants in the Fabaceae and more rarely the Malvaceae, Zygophyllaceae and Thymelaeaceae), but older larvae of *A. pallida* have been observed to feed on ant eggs and appear to be completely aphytophagous [40].

4.1.6. *Anoplolepis*. Another endemic South African butterfly genus is *Thestor*, with about 27 recognized species [41]. The life histories of these butterflies are still very incompletely known, but for sure they are essentially aphytophagous, as is the rule in the Miletinae to which this genus belongs. Younger larvae prey on various homopterans, and in at least 3 species (*Th. yildizae*, *rileyi*, and *basutus*) older larvae live inside ant nests where they feed on brood of the ant *Anoplolepis custodiens*. It is suspected that all *Thestor* species share this habit [41].

4.2. Subfamily Dolichoderinae

4.2.1. *Papyrius*. The small endemic Australian butterfly genus *Acrodipsas* can be divided into two clades [42]. Larvae of one of these, comprising the species *A. brisbanensis* and *A. myrmecophila*, are obligate parasites of *Papyrius nitidus* [35] from their first instar onwards, that is, without a phytophagous phase as in *Lepidochrysops* or the *Maculinea/Phengaris* clade. *Papyrius* species are highly dominant components of Australian ant assemblages and serve as mutualistic partners for some additional Australian lycaenids [34].

4.3. Subfamily Myrmicinae

4.3.1. *Crematogaster*. This diverse ant genus (>450 described species) ranks second in terms of associated ant-parasitic lycaenid butterflies. In the lycaenid tribe Aphnaeini (about 260 species, of which >90% occur in Africa) caterpillar-ant associations are nearly always obligatory, and the predominant host ant genus is *Crematogaster*. Few Aphnaeini species, however, are well established to be parasites of *Crematogaster* ants. Only one of these is a brood predator (*Cigaritis acamas* [43]), whereas in other cases trophallactic feeding has been reported (e.g., *Aphnaeus adamsi*, *Chrysoritis* (*Oxychaeta*) *dicksoni*, *Spindasis takanonis*, and also *S. syama*; [40, 44]). Beyond the tribe Aphnaeini, parasitic relationships occur in the Australian *Acrodipsas* of which three species (*A. cuprea*, *illidgei*, and *aurata*) are predators of *Crematogaster* ants [35, 42, 45]. According to one old account caterpillars of the aphytophagous African *Lachnocnema bibulus* (which essentially prey on homopterans and drink their honeydew exudates, see above) also supplement their diet by trophallaxis obtained from *Crematogaster* ants [46].

4.3.2. *Myrmica*. This genus is famous as being the host of the ant-parasitic *Maculinea* butterflies in temperate regions of Eurasia. *Maculinea* comprises about 10–15 species, depending on the status allocated to local forms and cryptic lineages detected through recent sequence analyses [47]. All *Maculinea* species are either brood predators or cuckoo-type parasites [11] of *Myrmica* ants. Host specificity was initially thought to be generally high [48], but research over the past two decades has revealed more complex, locally to regionally variable patterns of host specificity [27]. Especially in previously underexplored regions of central and east Europe many new local host associations have been elucidated through thorough field work [28]. Caterpillars of the closely related East Asian butterfly genus *Phengaris* also parasitize *Myrmica* species [44, 47].

4.3.3. *Aphaenogaster*. There are two *Maculinea* species from East Asia (*M. arionides*, *M. teleius*) for which the use of *Aphaenogaster* ant species as hosts has been recorded. Both these butterfly species are known to parasitize mainly *Myrmica* host ants. It remains to be shown to what degree *Aphaenogaster* ants really qualify as valid hosts. Alternatively, these records might be based on misidentifications or represent rare affiliations that only occur under exceptional circumstances (see the discussion about primary and secondary hosts in [27]).

4.3.4. *Rhoptromyrmex*. Representatives of this small Oriental ant genus have been observed to attend a range of lycaenid caterpillars in a mutualistic manner. Besides, trophallactic feeding does occur in one unusual case, the Miletinae species *Logania malayica*. *L. malayica* larvae prey essentially on homopterans and drink their honeydew exudates, but young larvae also elicit regurgitations from *Rh. wroughtonii* ants, with which the butterflies are closely and specifically associated over their entire life cycle [17, 49].

5. Macroecological Patterns of Host Ant Use among Ant-Parasitic Lycaenidae Butterflies

Myrmecophilous associations between lycaenid butterflies and ants are confined to that subset of ant genera which maintain trophobiotic interactions [24]. Trophobiotic ants form a highly significant fraction in terms of their ecological prevalence as well as species diversity. They essentially derive liquid nutrients from extrafloral plant nectar [50, 51] and from the excretions (“honeydew”) of sap-sucking homopterans [52, 53]. Lycaenid and riodinid butterfly species that offer nectar-like secretions in exchange for protection largely “hitch-hike” on the behavioural and ecological syndromes which are associated with ant trophobiosis. Harvesting nutrient-rich liquids requires specialized anatomy [54] and behaviour in ants (e.g., trophallactic exchange of liquid food within the colony), with trophobiosis demanding a more complex suite of morphological and behavioural traits than licking-up plant nectar [55].

Ant-parasitic lycaenids form a very small subset of myrmecophilous ant-attended species in that butterfly family. Not surprisingly, the host ants parasitized by them constitute a small subset of ant genera known to visit and attend caterpillars in mutualistic associations. In two earlier studies the ecological prevalence and geographical distribution of ant genera were shown to be the best predictors for their representation in mutualistic lycaenid-ant associations [24, 25]. For parasitic interactions, this pattern changes according to a similar analysis. In analogy to [24], I constructed a multiple linear regression model, with the number of recorded ant-parasitic lycaenids as response variable and the species richness (log-transformed), representation in lycaenid-ant interactions (log-transformed), ecological prevalence, and geographical distribution of ant genera as predictors. Geographical distribution was scored on a rank scale (from 1 to 10) as the number of faunal regions from which an ant genus is known, using the following 10 regions: West Palaearctic region (Europe eastwards up to the Ural mountains, including Africa north of the Sahara, Asia Minor, and the Near East); East Palaearctic region (Asia east of the Ural mountains, including Japan and Taiwan); India; South East Asia (comprising Thailand, the Malay Peninsula, and the large islands of the Sunda shelf like Sumatra, Borneo, and Java); New Guinea; Australia; Central Africa (south of the Sahara to approx. 15° southern latitude); Southern Africa (mainly comprising South Africa, Namibia, Botswana, and Zimbabwe); North America (north of Mexico); Central and South America. Ecological prevalence (sensu [56]) was scored on a rank scale from 1 to 5 (Table 1).

The linear model revealed that only the number of associated lycaenid species had a significant and positive relationship with the number of recorded cases of lycaenid-ant parasitism in an ant genus (see Table 2 for full documentation). All three other potential predictors were far from having any significant effect. Inspection of residuals confirmed that the model assumptions were met with reasonable accuracy. Moreover, application of a Ridge correction (with $\lambda = 0.1$) to account for collinearity among predictors did not change the overall model outcome (data

TABLE 1: Classification of ant genera known to associate with Lycaenidae caterpillars into prevalence groups. Ant genera are classified into that group which corresponds to the dominance status of its most dominant component species involved in butterfly-ant associations. For example, *Formica* is scored as “top dominant” since many (but not all) *Formica* species are territorial key-stone ant species in their respective habitats and communities, adapted from [24].

Class	Score	Criteria	Genera
Top dominant	5	Dominant ants in habitat; defend territories and resources intra- as well as interspecifically; monopolize resources against all heterospecific competitors	Myrmicinae: <i>Pheidole</i> ; Formicinae: <i>Formica</i> , <i>Oecophylla</i> ; Dolichoderinae: <i>Anonychomyrma</i> , <i>Azteca</i> , <i>Forelius</i> , <i>Froggattella</i> , <i>Iridomyrmex</i> , <i>Papyrius</i>
Second-order dominant	4	Subordinate relative to top dominants, but may become dominant in the absence of these; monopolize resources [†]	Myrmicinae: <i>Crematogaster</i> , <i>Meranoplus</i> , <i>Monomorium</i> , <i>Myrmicaria</i> , <i>Solenopsis</i> , <i>Tetramorium</i> ; Formicinae: <i>Anoplolepis</i> , <i>Camponotus</i> , <i>Polyrhachis</i> , <i>Lasius</i> , <i>Lepisiota</i> , <i>Myrmecocystus</i> ; Dolichoderinae: <i>Dolichoderus</i> , <i>Linepithema</i> , <i>Liometopum</i> , <i>Ochetellus</i> , <i>Philidris</i> ;
Submissive	3	Subordinate to both classes of dominants; usually opportunistic species with generalized feeding habits; rarely defend and monopolize resources against heterospecific ants	Myrmicinae: <i>Acanthomyrmex</i> , <i>Aphaenogaster</i> , <i>Myrmica</i> , <i>Rhoptromyrmex</i> ; Formicinae: <i>Echinopla</i> , <i>Notoncus</i> , <i>Paratrechina</i> , <i>Prolasius</i> ; Dolichoderinae: <i>Dorymyrmex</i> , <i>Tapinoma</i> , <i>Technomyrmex</i> ; Ponerinae: <i>Ectatomma</i>
Solitary	2	Foraging individually; rarely monopolize resources	Myrmeciinae: <i>Myrmecia</i> ; Myrmicinae: <i>Cataulacus</i> ; Ponerinae: <i>Gnamptogenys</i> , <i>Odontomachus</i> , <i>Rhytidoponera</i> Pseudomyrmecinae: <i>Tetraponera</i> , <i>Pseudomyrmex</i>
Cryptic	1	Minute species foraging on the ground or in leaf litter; inferior to all other ants in direct confrontation	Myrmicinae: <i>Leptothorax</i> ; Formicinae: <i>Brachymyrmex</i> , <i>Plagiolepis</i> ; Dolichoderinae: <i>Bothriomyrmex</i>

[†] Includes many species that become dominant in disturbed habitats or when introduced as alien species into non-adapted ant communities.

not shown). In a stepwise forward model selection, again only the frequency of nonparasitic associations remained as significant predictor. Likewise, using Poisson-type (instead of Gaussian) error distributions did not affect the outcome of this analysis (data not shown).

Hence, it is not the ecological or geographical prevalence that is decisive for the establishment of parasitic relationships between lycaenid butterflies and ants. Rather, the more butterfly species do interact with a given ant clade, the more likely it is that some of these interactions may turn, in evolutionary time, into parasitic relationships.

This also becomes evident when the incidence of ant-parasitism is plotted against the rank the ant genera have in interactions with lycaenid caterpillar species (Figure 1). Instances of social parasitism are more likely amongst those ant genera that are numerically more important in lycaenid-ant associations in general, whereas again species richness of the respective ant genera had no significant influence (Table 3).

A number of ant genera (e.g., *Pheidole*, *Dolichoderus*, *Formica*, and *Iridomyrmex*) that are ecologically dominant in

TABLE 2: Results of general linear model relating the number of parasitic lycaenid species associated with an ant genus to its species richness (log-transformed), ecological prevalence, geographical distribution, and importance in nonparasitic lycaenid-ant associations (log-transformed). Given are standardized regression coefficients β , and the F and p scores for each variable. SS: sum of squares; MS: mean of squares. Overall model fit: $R = 0.5394$, $R^2_{\text{korr}} = 0.2332$, $F_{4;49} = 5.0288$; $P = 0.0018$.

	SS	df	MS	β	F	p
constant	12.78	1	12.78		2.607	0.113
dominance	0.35	1	0.35	-0.0370	0.072	0.789
associated lycaenid spp.	47.54	1	47.54	0.5051	9.698	0.003
species richness	3.44	1	3.44	0.1201	0.702	0.406
geographic regions	0.018	1	0.018	-0.0097	0.004	0.952
error	240.21	49	4.90217			

their habitats and serve as hosts for many well-integrated myrmecophilous ant parasites from other insect groups (e.g., [55]) are thus far completely missing in the host list of

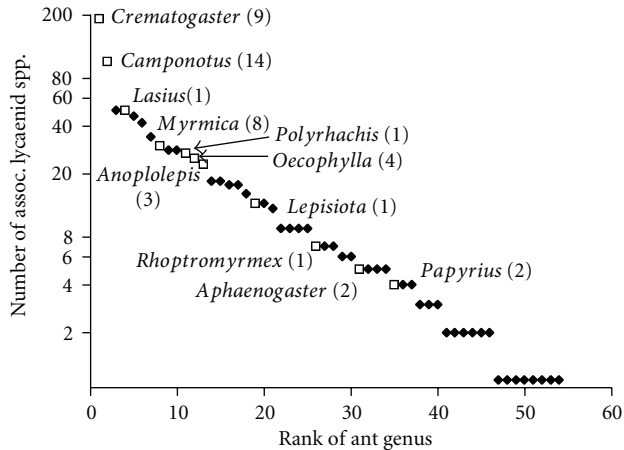


FIGURE 1: Rank-frequency plot of ant genera of the world involved in myrmecophilous associations of Lycaenidae butterflies, based on 927 record pairs of 497 butterfly species with 54 ant genera. Rank 1: ant genus with largest number of associated lycaenid species reported. Ranks 47 to 54: ant genera with only one associated lycaenid species known thus far. Filled diamonds: ant genera only known to be involved in mutualistic interactions with butterflies; open squares: ant genera that also serve as hosts for ant-parasitic Lycaenidae larvae (with genus name included; figure in parentheses: number of confirmed ant-parasitic lycaenid species). Note log-scale of y-axis.

TABLE 3: Results of a bivariate logistic regression, modelling the incidence of ant-parasitic associations within an ant genus ($N = 54$ ant genera), in relation to species richness and number of nonparasitic associations with lycaenid immatures (both log-transformed) per ant genus. Given are the regression coefficients b_i , their standard errors and corresponding t and p values. Overall model score: $\chi^2_{2df} = 6.577$; $P = 0.0373$.

	$b_i \pm 1 \text{ SE}$	t	p
Constant	-3.0864 ± 1.1160	2.766	0.008
Number of associated lycaenid species	0.9105 ± 0.3936	2.313	0.025
Species richness of genus	-0.1799 ± 0.2327	0.773	0.443

ant-parasitic lycaenids. Even considering that trophobiosis is an important evolutionary prerequisite for the establishment of lycaenid-ant interactions (thereby excluding nontrophobiotic ants such as army ants, leaf-cutter ants or harvester ants as potential hosts), the discrepancy in host use between ant-parasitic lycaenids, and other well-integrated myrmecophilous parasites remains striking.

Only two ant genera, *Camponotus* and *Crematogaster*, have been the target of multiple evolutionary trajectories towards parasitic life habits amongst the Lycaenidae. Even though complete phylogenetic analyses are still lacking for the family Lycaenidae, there can be no doubt that parasitism of *Camponotus* through the butterfly genera *Lepidochrysops*, *Niphanda*, *Ogyris*, and *Lachnocnema* has evolved independently—these four butterfly genera are far apart from each other in all systematic accounts of the family Lycaenidae, and they represent all three potential pathways

to ant-parasitism suggested earlier [6]. Likewise, parasitism of *Crematogaster* ants by *Acrodipsas* is certainly unrelated in phylogenetic terms to the multiple (and probably again: independent) occurrences amongst single species of Aphnaeini that all belong to larger genera where the majority of species is nonparasitic (*Cigaritis*, *Spindasis*, and *Aphnaeus*).

Overall, the scattered occurrence of ant-parasitism amongst the Lycaenidae gives evidence that such interactions have evolved multiple times, rather independently from another, and under quite different circumstances [6]. Only few such cases have given rise to moderate or even substantial radiations, most notably in the African genus *Lepidochrysops* (over 120 species) and in the Eurasiatic *Phengaris-Maculinea* clade (some 10–20 species). The host ant use of the latter remains a mystery in terms of its evolutionary and ecological roots. *Myrmica* ants are visitors of only a moderate number of ant-mutualistic lycaenids in the Holarctic region (recorded with 22 species thus far). Moreover, *Myrmica* ants usually neither form very large colonies nor are they territorial and ecologically dominant in most habitats where they occur today. Hence, they lack typical characters of other host ants of parasitic myrmecophiles. On the other hand recent phylogenetic evidence [47] strengthens the notion that evolution of parasitic associations with *Myrmica* ants occurred just once, at the base of the *Phengaris-Maculinea* clade. Similarly, the affiliation with *Camponotus* ants in parasitic *Lepidochrysops* as well as mutualistic *Orachrysops* suggests that specialization on *Camponotus* hosts predated the evolution of parasitism in that butterfly lineage.

Host shifts among ant-parasitic butterflies from one ant host genus to another have apparently rarely occurred in the Lycaenidae. One well-documented case is the Australian genus *Acrodipsas*, where some species parasitize *Papyrius* ants, but one clade subsequently shifted to *Crematogaster* hosts [42]. This rare case even implies a switching of hosts across ant subfamily boundaries. In contrast, the significance of *Aphaenogaster* recorded as host ants of some East Asiatic *Maculinea* needs to be rigorously addressed. In all likelihood, these are stray (or even erroneous) records rather than an indication of host shifts beyond ant genus boundaries.

6. Which Cases of Ant-Parasitism Might Await Detection amongst the Lycaenidae?

Starting from the patterns of host-ant use among ant-parasitic Lycaenidae, and in combination with other information on life-history traits of lycaenid butterflies, I here finally outline a few expectations in which butterfly clades and biomes further instances of parasitic interactions might most likely be uncovered. These expectations are amenable to testing by systematic assembly of further life history data or by evaluating earlier inconclusive reports.

One major group of lycaenid butterflies where a larger number of instances of trophallactic feeding by ants can be expected is the subfamily Miletinae. Miletinae larvae are essentially predators of homopterans. Since many homopterans are attended by ants and since quite a number of Miletinae larvae also drink honeydew, it would not come as

a surprise to see more cases of trophallaxis with ants being documented in the future. Particularly likely candidates are those Miletinae species that are specifically adapted to spend their entire life cycle (including adult feeding on homopteran honeydew) with individual ant species. This is the case for *Logania malayica* with *Rhoptromyrmex wroughtonii*, and analogous candidate species occur in tropical SE Asia (*Miletus* spp. with *Dolichoderus* spp.; *Allotinus unicolor* with *Anoplolepis longipes*; [18, 20]). In two cases (*Allotinus apries* with *Myrmecaria lutea* [17]; *Logania hampsoni* with *Iridomyrmex* [15]) parasitic interactions have explicitly been suspected to exist, but until now these cases remain unsupported by direct observations of parasitic behaviours of the lycaenid caterpillars (A. Weissflog, personal communication for *A. apries*). As stated above, it is also quite likely that most, if not all *Thestor* species in South Africa will turn out to maintain parasitic relationships to *Anoplolepis custodiens* and allied ants [41]. Such cases of ant-parasitic relationships may also occasionally shift from the lower trophic level of cuckoo-feeding to the higher trophic level of brood predation (as in the genera *Liphyra* and *Euliphyra*). However, certain Miletinae do not interact intensively with ants that attend their homopteran prey [17, 57–59]. It is unlikely that traits required to entering into host-specific parasitic butterfly-ant interactions have evolved here. All further examples of ant-parasitism derived from predation on homopterans would obviously fall into the “Miletinae type” [6].

Another lycaenid clade where further cases of ant-parasitism can surely be expected to occur is the tribe Aphnaeini. Even though the few confirmed cases of ant-parasitism are rather isolated incidences nested within larger clades of ant-mutualists (e.g., *Chrysoritis dicksoni* in the genus *Chrysoritis* [60]), further species may show up to depend on nutrients derived from their close association with ants, as has been speculated many times in the literature (for critical reviews see [40, 61, 62]). Most additional instances of ant-parasitism in the Aphnaeini are expected to involve *Crematogaster* ants (the prevalent ant partner in mutualistic Aphnaeini species), but in *Aloeides* also further incidences of *Lepisiota*-parasitism may be found.

Other obvious candidates to furnish more ant-parasitic lycaenids are the genera *Lepidochrysops* (with *Camponotus*), *Maculinea*, and *Phengaris* (hitherto undescribed host associations in East Asia expected to refer to *Myrmica*), and *Niphanda* (probably with *Camponotus*). Beyond that, no valid extrapolations seem feasible at present. For example, the parasitic association between *Arhopala wildei* and *Polyrhachis queenslandica* does not seem “predictable” in a phylogenetic framework [13]. The most likely candidates for the discovery of novel ant-parasitic lycaenids of the “Aphnaeini type” are clades where a number of butterfly species show intimate host-specific mutualistic relationships towards specific host ants.

From the ant perspective, two genera which account for a very substantial fraction of records with lycaenids (namely, *Lasius* and *Formica*) score strikingly low as hosts of ant-parasitic butterflies. The only confirmed case with *Lasius* involves a species (*Shirozua jonasi*) whose larvae obtain most of their nutrient income from preying on homopterans and

drinking their honeydew. This hairstreak species is ecologically similar to Miletinae butterflies and does not enter into *Lasius* nests to prey on ant brood. Possibly, the lack of brood being present in *Lasius* nests over winter poses a constraint in the evolution of ant-parasitism in temperate-zone climates. This would also explain why so far no case of ant-parasitism has been confirmed from the genus *Formica*. In East Asia, larvae of *Orthomiella rantaizana* have been found in *Formica* nests (Shen-Horn Yen, personal communication), but whether these are parasites, commensals, or mutualists of ants remains to be uncovered. Clearly, *Lasius* as well as *Formica* species serve as hosts for a large range of well-integrated myrmecophiles [55], but the majority of these parasites have evolved from detritivorous or predacious ancestors, and not from herbivores.

Two other sociobiological traits of ant colonies that have been suggested to be related to the evolution of parasitic myrmecophily are the level of polygyny or polyandry, and the brood cycle. With regard to the latter, as already noted above the absence of winter brood may have prevented the intrusion of Holarctic lycaenids as parasites into *Lasius* and *Formica* colonies. With regard to ants from the humid tropics, however, seasonal fluctuations in brood availability are less likely to constrain the evolution of lycaenid butterflies into parasites of ants, so that this factor (if valid at all) would have to be restricted to seasonal climates. Genetic intracolony heterogeneity, which can result from the presence of multiple queens and/or the occurrence of multiple matings during their nuptial flight, may facilitate the intrusion of social parasites as well as of parasitic myrmecophiles [63]. It is presently impossible to rigorously test these two hypotheses, since data on the colony structure and population demography of many tropical and subtropical ants that are parasitized by lycaenids are too scant. Polygyny seems to be common among ants that serve as hosts [64], but in at least one instance (*Camponotus japonicus*, the host ant of *Niphanda fusca*) monogyny and claustral colony foundation have been confirmed [65].

7. Perspective

Ant-parasitic lycaenid butterflies are a bewildering evolutionary outcome: carnivores or cuckoo-type feeders in an otherwise phytophagous clade of insects. The communication modes required for integration into their host colonies, the phylogenetic roots, and population genetic consequences of their unusual interactions with ants, and their repercussions into conservation biology [66, 67] will continue to attract the interest of scientists. However, these parasitic interactions encompass only a small minority of myrmecophilous Lycaenidae butterfly species. Also the ant genera involved comprise but a small minority as compared to the range of trophobiotic ants that could potentially be parasitized. For sure, some further extensions can be expected, especially in hitherto underexplored tropical regions or in butterfly clades whose life histories are thus far very poorly documented. Most known ant-parasitic lycaenids occur in seasonally cold and/or dry regions [6], where

both the butterfly and the ant faunas are comparatively well covered. It has even been suggested, though not yet rigorously tested, that avoidance of unfavourable seasons might have promoted the entering of ant nests as safe places for lycaenid caterpillars. The detection of additional cases of butterfly-ant parasitism in these regions in all likelihood will not radically turn the robust patterns described here upside down. For tropical faunas, some more unexpected incidences of ant-parasitism may await discovery, yet it does not seem likely that many instances of butterfly caterpillars living in brood chambers of ant nests would have gone undetected thus far. Rather, future progress will be made in uncovering the microevolutionary steps that drive host-parasite co-evolution [7]. It will also be rewarding to rigorously assess the macroevolutionary pathways leading to ant-parasitism in a phylogenetically controlled manner. To achieve this goal, besides elucidating the phylogenetic relationships of lycaenids and their ant hosts, more bionomic data on both of these players, but especially a better documentation of the sociobiology and ecology of the host ants (beyond the well-studied *Myrmica* case) will be essential.

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