Ant-associates of Palaearctic lycaenid butterfly larvae (Hymenoptera: Formicidae; Lepidoptera: Lycaenidae) – a review

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Abstract

Field data on ant associates of 98 species of Palaearctic Lycaenidae butterfly immatures were collated. Members of 21 ant genera from the three subfamilies Myrmicinae, Formicinae, and Dolichoderinae have been reported as ant attendants with certainty. All ants that visit lycaenid immatures also forage for other liquid carbohydrate food sources like extrafloral plant nectar or homopteran honeydew. Species of *Lasius* (recorded with 41 lycaenid species), *Formica* (24 spp.), *Camponotus* (24 spp; all Formicinae), *Myrmica* (25 spp.), and *Crematogaster* (26 spp.; both Myrmicinae) are the most important ant associates of Palaearctic lycaenids. Available data have almost doubled relative to the last synopsis 15 years ago, but general patterns remained robust. The recorded diversity of butterfly-ant associations has slightly increased due to the improved data-base, including the addition of six ant genera previously not reported as tending Palaearctic lycaenids. Ant associations in the Oriental, Australian, and Nearctic faunal regions are more diverse than in the Palaearctic, whereas those in Africa are less diverse. The number of lycaenid species associated with a particular ant genus correlates moderately, but significantly with species richness of that ant genus in the Palaearctic region. Exceptions to that rule can be explained by specific ecological and behavioural traits of the respective ants. Ecological dominance is the most important factor with regard to the involvement of ants in interactions with butterflies. Obligate myrmecophiles are rare among Palaearctic lycaenids and are highly host specific (but usually on the ant genus rather than species level), in contrast to opportunistic visitors in facultative associations. Obligate associations in the Palaearctic region are biased towards the genera *Myrmica* (hosts of the unique, socially parasitic *Phengaris-Maculinea* clade) and *Crematogaster* (hosts of Aphnaeini species).

Key words: Trophobiosis, mutualism, parasitism, Lycaenidae, Formicidae, diversity, myrmecophily.

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Introduction

In most terrestrial habitats ants are important ecosystem engineers which represent a major fraction of animal biomass (HÖLLDOBLER & WILSON 1990). The ecological success of ants can be attributed to their eusocial life-style. Their social organisation enables ants to surmount prey organisms far larger than an individual ant. Spin-offs of eusociality include sophisticated communication and defense strategies that are essential to exploit and monopolize resources efficiently. Even though ants are derived phylogenetically from predacious Hymenoptera (MOREAU & al. 2006), some of the most successful lineages of ants have gained access to lower trophic levels. Recent work on tropical rainforest ants (BLÜTHGEN & al. 2003, DAVIDSON & al. 2003) confirmed earlier considerations (TOBIN 1994) that only by combining carnivorous life-styles with resource retrieval at lower trophic levels ants could become as massively abundant as they are, for example in tropical canopy layers.

The key to this success is that such ants harvest nutrient rich liquids – a strategy that requires specialized anatomy (e.g., proventriculus and gaster: DAVIDSON & al. 2004) and behaviour (e.g., trophallactic exchange of liquid food within the colony). Nutritious liquids are obtained via a multitude of mutualistic interactions with various kinds of organisms. Ants are the prevalent consumers of extrafloral plant nectar (KOPTUR 1992, BRONSTEIN 1998). In addition they maintain trophobiotic associations with plant-feeding insects. Trophobiosis involves a more complex syndrome of morphological and behavioural traits than harvesting plant nectar (HÖLLDOBLER & WILSON 1990). The quantitatively most important trophobionts are sap-sucking homopterans whose excretions ("honeydew") are an essential energy source for many ants (DIXON 1998, STADLER & al. 2003). However, also the larvae of some Lepidoptera, notably in the butterfly families Lycaenidae and partially the Riodinidae, have evolved trophobiotic interactions with ants based on the delivery of nutrient rich liquids.

The Lycaenidae comprise more than 5,000 species worldwide. Larvae of the majority of species maintain some kind of association with ants (FIEDLER 1991a). Most of these associations are potentially mutualistic. Lycaenid larvae offer nutritious nectar secretions to ants (e.g., DANIELS & al. 2005). In return they are exempt from ant attacks and are even protected against other predators and parasitoids (PIERCE & al. 2002). However, relationships can be quite asymmetric. Caterpillars of certain lycaenids provide but marginal food rewards, yet escape ant attacks by exploiting their social communication systems (FIEDLER & al. 1996, DANIELS & al. 2005). Some associations are even parasitic with the butterfly larvae preying on ant brood or being fed by ants as nest inquilines (PIERCE 1995, FIEDLER 1998, THOMAS & al. 2005).

Since myrmecophily is so widespread among the Lycaenidae and is associated with manifold unusual specia-

lizations, the significance of ant-interactions for the evolutionary ecology of these butterflies has attracted much interest (reviews: FIEDLER 1991a, FIEDLER & al. 1996, PIERCE & al. 2002). In particular, obligate butterfly-ant associations have matured into model systems for mutualism (e.g., the Australian *Jalmenus evagoras*: PIERCE & NASH 1999) or host-parasite co-evolution (e.g., the *Phengaris-Maculinea* clade: ALS & al. 2004, SETTLE & al. 2005). The perspective of the ants, however, has been less intensively explored.

Five years ago I summarized the knowledge then available on the ants that associate with lycaenid immatures (FIEDLER 2001). At that time, representatives of 53 of the 296 extant ant genera worldwide (as recognized by BOLTON 1995) had been reported to attend lycaenid caterpillars or pupae (excluding the poorly known life-cycles of Neotropical lycaenids). All these ants are known to engage in trophobiotic mutualisms. Thus, by and large the same ants visit lycaenid caterpillars that also collect homopteran honeydew or (extrafloral) plant nectar (MALICKY 1969, DEVRIES 1991, OLIVEIRA & BRANDÃO 1991). Specialized predators (e.g., most Ponerinae), seed harvesters (a number of Myrmicinae), fungus-growers (Attini), litter-foraging ants, and socially parasitic ants do not associate with lycaenids.

With regard to intimacy and specificity, lycaenid-ant interactions cover a continuum between two extremes. Most lycaenid species do not depend essentially on ant-attendance, even though mortality may be substantially reduced through ant visitors (PIERCE & al. 2002). Such cases are termed "facultative myrmecophiles" (Fig. 1). As a rule these larvae are not specific with regard to their ant associates (FIEDLER 2001). Rather, the dominance pattern within an ant community determines which ants will attend the caterpillars (MALICKY 1969, DEVRIES 1991, PETERSON 1995). Irrespective of this opportunism, preference hierarchies and species-specific effects of ants on lycaenid caterpillars are common (BALLMER & PRATT 1992, WAGNER 1993, WAGNER & MARTINEZ DEL RIO 1997, FRASER & al. 2001). Facultative myrmecophiles represent the majority of lycaenid species in most biogeographical regions except Australia (FIEDLER 1991a, EASTWOOD & FRASER 1999).

At the other end of the myrmecophily continuum are the obligate myrmecophiles which totally depend on their host ants. Most obligate myrmecophiles are ant mutualists (Fig. 2) which suffer so intensely from mortality that populations would go extinct when deprived of their ant attendants (e.g., *Jalmenus evagoras*: PIERCE & NASH 1999). A smaller group are social parasites of ants that depend on nutrient resources they derive from living in ant nests (FIEDLER 1998). In both groups of obligate myrmecophiles, ant associations occur almost invariably with only one ant species or genus (EASTWOOD & FRASER 1999, FIEDLER 2001). In obligate myrmecophiles, the presence and abundance of host ant colonies regulates the spatial and temporal distribution of the butterfly (SMILEY & al. 1988, JORDANO & al. 1992, SEUFERT & FIEDLER 1996, MOUQUET & al. 2005). Obligate myrmecophiles are generally more common with ecologically dominant ant species that form large, long-lived colonies and exhibit territorial behaviour (HÖLLDOBLER & WILSON 1990), but strikingly this does not fully apply to the Palaearctic lycaenid fauna (see below).

Here, I re-examine the diversity of ant associates involved in myrmecophilous relationships of the Palaearctic Lycaenidae. The last attempts to summarize all available information in this respect (FIEDLER 1991a for a global review, FIEDLER 1991b for a detailed analysis of the Western Palaearctic fauna) date back 15 years; since then many new records have been published. Specifically, I will address the following questions:

(1) Which ant genera participate in butterfly-ant interactions in the Palaearctic realm, and how do they rank in their importance?

(2) Did the increase in available data affect the patterns that had been extracted earlier?

The data base

Data sources: Extending from earlier published versions (FIEDLER 1991a, b), I collated as many new records of lycaenid-ant associations as possible. Recent comprehensive faunal treatments (e.g., FUKUDA & al. 1992, IGARASHI & FUKUDA 1997, 2000, TOLMAN & LEWINGTON 1998, BASCOMBE & al. 1999) were particularly rich data sources. In addition, a large number of journal papers, records published on websites, and personal communications from entomologists were incorporated. I attempted to search as exhaustively as possible, but certainly some records (e.g., published in local natural history journals) will have been overlooked. The data base and a full list of references (> 100 if including every bit of information used in the subsequent analyses) is available upon request. I took into account only field records of ant associations. Observations from experimentally staged encounters were excluded. Records were only accepted if attendant ants had been reliably identified to genus level, or if associations were figured in sufficient quality to allow identification of the ant genus. All associations collated in that manner are listed in the Appendix (digital supplementary material to this article, at the journal's web pages).

Butterfly taxonomy: Species level taxonomy follows recent faunal treatments (FUKUDA & al. 1992, HESSELBARTH & al. 1995, TOLMAN & LEWINGTON 1998, WANG & FAN 2000, GORBUNOV 2001). Generally, I favoured more inclusive species boundaries rather than extreme splitting. For example, I did not accept the Sardinian or Corsican island forms of *Polyommatus coridon*, *Plebejus argus* or *P. idas* as distinct species. Likewise I regarded all European local forms of the *Plebejus pylaon* complex as one species. I also followed recent molecular data that reveal very limited genetic segregation between *Maculinea alcon* and its "form" *rebeli* to treat them as but one species (ALS & al. 2004, STEINER & al. 2006). For a more thorough discussion of this "splitting vs. lumping" issue the reader is referred to DENNIS (1997). Among the Lycaenidae of the Palaearctic region, ant associations are not known from the very few representatives of the largely tropical subfamilies Miletinae and Curetinae. Palaeotropical Poritiinae are completely absent in temperate-zone Eurasia. The Riodinidae are a distinct clade in which trophobiosis with ants has evolved in parallel to the Lycaenidae (DEVRIES 1997, CAMPBELL & al. 2000); moreover Palaearctic riodinids are not myrmecophilous. Hence, all records to be analysed refer to the subfamily Lycaeninae sensu ACKERY & al. (1999).

Ant taxonomy: Even though ant taxonomy has progressed much in the past 10 years, BOLTON's (1995) cata-

Fig. 1: Final instar caterpillar of *Glaucopsyche alexis* (PODA, 1761) attended by worker ants of the species *Lasius alienus* (FÖRSTER, 1850). This butterfly species represents the most common type of ant-association among Palaearctic lycaenids, viz. facultative mutualism: the caterpillars are not always attended by ants, there is substantial spatial and temporal variation in the identity of ant attendants, and there is no specialization in the chemical communication between caterpillars and ants. The intimacy of facultative ant associations varies greatly across species, but facultatively myrmecophilous caterpillars are able to successfully appease a wide range of trophobiotic ant taxa.

Fig. 2: Final instar caterpillar of *Plebejus argus* (LINNAEUS, 1758) attended by *Lasius niger* (LINNAEUS, 1758). This species is one of the few obligate myrmecophiles among the Palaearctic Lycaenidae with entirely phytophagous, non-inquiline caterpillars. Obligate myrmecophiles are highly specific with regard to their ant hosts (see Fig. 5). In temperate zones obligate associations are less common than in tropical or subtropical realms, and mostly occur in lycaenid species whose larvae are inquiline social parasites of ant colonies such as in the well known *Phengaris-Maculinea* clade.

logue is still the most complete and was deemed sufficient for the purpose of the present study. I retained "*Leptothorax*" in its more inclusive (and probably not monophyletic) delimitation (i.e., lumping *Temnothorax* into *Leptothorax*; cf. BOLTON 2003 for a more up-to-date classification), since in some of the (few) recorded ant-associations with "*Leptothorax*" the precise species identity was not given. Presumably, most of these associations involved species of *Temnothorax* rather than *Leptothorax* s.str. Records of attendant ants were analysed on the genus level for

the following five reasons. (a) For most ant genera, no modern revisions are available, thus proper species identifications are often impossible. (b) Generic delimitations are rather stable and recognizable on a worldwide basis (BOLTON 1995). (c) Due to the ongoing discovery of new sibling species complexes even in well studied ant faunas (e.g., SEIFERT 1992, SCHLICK-STEINER & al. 2006), species names reported in older accounts are suspect, unless they can be verified using voucher specimens. (d) Attendant ants at lycaenid larvae have only been identified to genus level in many sources. (e) Even obligate myrmecophiles are usually not bound to one single ant species, but mostly are affiliated with a couple of congeneric ant species. The prime example is the ant-parasitic genus *Maculinea* for which novel *Myrmica* host ants have been discovered recently (SETTELE & al. 2005). Therefore, I performed all analyses on the taxonomic level where the highest reliability can be achieved. Supraspecific taxa (such as genera or families) as "surrogates" of diversity have repeatedly proven to be useful when information on species level is too incomplete to allow for analysis of large-scale patterns (WILLIAMS & al. 1994, HUMPHRIES & al. 1995).

Geography: I defined the Palaearctic region as follows: Europe and temperate-zone Asia, especially all states on the territory of the former Soviet Union and China, southwards to the Himalaya, but excluding northern India and Pakistan. North Africa north of the Sahara, the Canary Islands, Asia Minor, the Near East, Japan and Taiwan were included, because their butterfly fauna is essentially Palaearctic in origin. The segregation of the Oriental and East Palaearctic realm is difficult in southern China and around the Himalayas. FELLOWES (2006) provided interesting new data on the ants in this regard, but for the butterfly fauna the situation is slightly different, with a more prominent northward extension of species with roots in the Oriental realm, probably due to the higher dispersal capacity of butterflies. The inclusion of records from Taiwan and southern China undoubtedly has slightly increased the list of recorded ant partners (e.g., *Anoplolepis, Polyrhachis*). However, there are overall so few records of attendant ants from these regions, that the inclusion of a few more "tropical" data did not affect the analyses presented below. In contrast, excluding Taiwan would have meant a significant loss of information (e.g., on host ant use in the parasitic *Phengaris-Maculinea* clade that is clearly Palaearctic in origin and confined to higher elevation habitats in Taiwan).

Analytical procedures

I used the number of recognized species from BOLTON's (1995) catalogue as a proxy of the species richness of ant genera that visit lycaenid immatures. To quantify the diversity of assemblages of recorded ant associations, I first considered every record pair [ant genus × lycaenid species] as one data point (termed "single records" below). If the same butterfly-ant association had been recorded by different authors, these records are just counted once. In many such cases, it remained unclear whether the sources really referred to independent records, or just repeated findings that had already been reported in earlier literature. If a lycaenid species has been recorded with several ant species belonging to the same genus, I counted these data se-
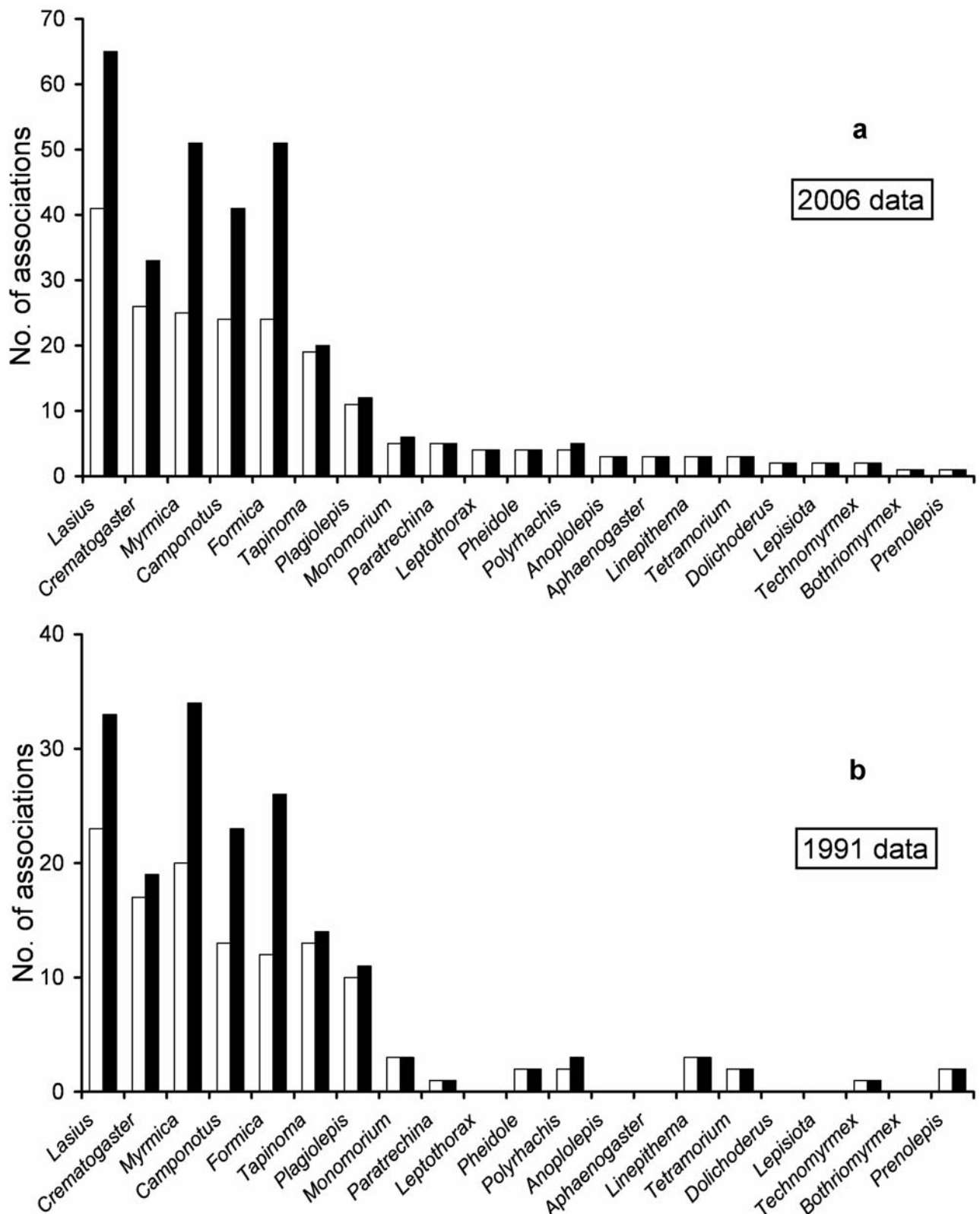
Fig. 3: Rank order of ant genera known to associate with Palaearctic myrmecophilous Lycaenidae (*Leptothorax* sensu lato including *Temnothorax*). Empty bars: number of associated lycaenid species; black bars: records of multiple species per ant genus counted separately ("multiple records" analysis, see text). (a) actual data; (b) data from FIEDLER (1991a).

parately in a second analysis (termed "multiple records" below) to give higher emphasis on ant genera that comprise many attendant species. This procedure results in two lists (one for single, one for multiple records) of how often lycaenids are associated with each particular ant genus. From their structure, such data are analogous to the num-
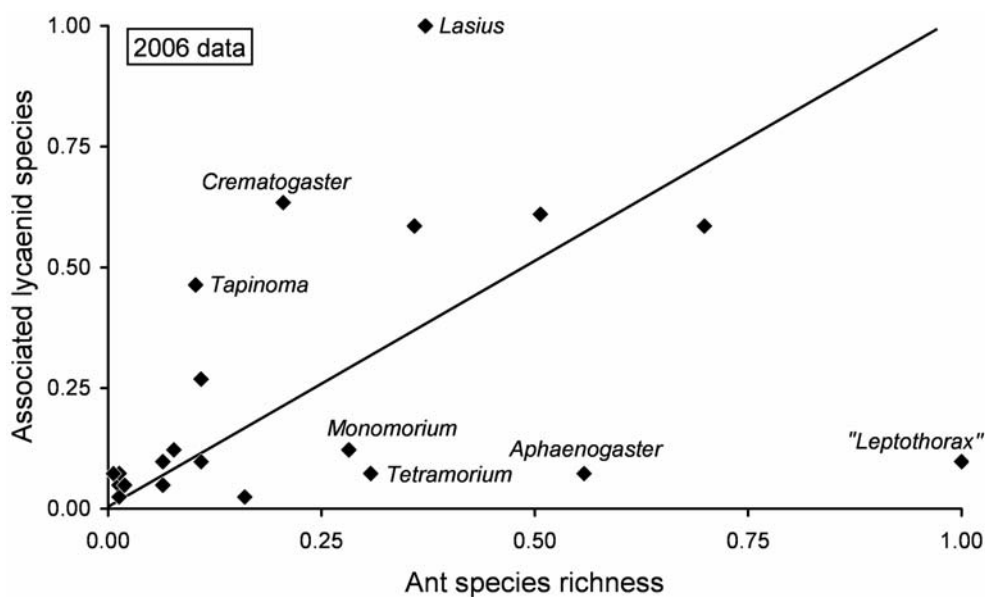
Fig. 4: Relationship between species richness of an ant genus (Palaearctic species numbers, according to BOLTON 1995) and number of associated lycaenid species (from Fig. 3a). Ant richness is scaled from 0 to 1 by dividing richness per genus through the maximum richness ("*Leptothorax*" sensu lato including *Temnothorax, N = 156* spp.). Number of associated lycaenid species is scaled in an analogous manner (maximum number of records: *Lasius, N = 41*). The bold line indicates if, for a given ant genus, its scaled species richness is equivalent to its scaled importance as associate of Palaearctic lycaenid butterflies. Ant genera that distinctly deviate from this relationship ($r_S = 0.563$, $p = 0.008$) are identified by their names.

ber of individuals that represent different species in a sample drawn from a community and, accordingly, can be subjected to standard diversity analysis. Here I used Shannon's information index as a measure of diversity. Different index values were statistically compared using the randomization test proposed by SOLOW (1993) as implemented by HENDERSON & SEABY (1998). In order to assess whether species richness of a genus is related to its significance as visitor of lycaenid immatures, I calculated Spearman rank correlation coefficients.

Ant genera associated with Palaearctic Lycaenidae butterflies

Thus far, representatives of 21 ant genera (30 % of the total generic diversity of the Palaearctic Formicidae) have been found in association with 98 lycaenid butterfly species (Fig. 3a). All tending ants belong to just three subfamilies, in the rank order Formicinae > Myrmicinae > Dolichoderinae. This differs slightly from the global pattern, with Formicinae (18) > Myrmicinae (14) = Dolichoderinae (14; FIEDLER 2001). However, relative to the numbers of genera known from the Palaearctic region this rank order changes considerably (Dolichoderinae: 5 of 5 genera, 100 %; Formicinae: 9 of 16 genera, 56.3 %; Myrmicinae: 7 of 31 genera, 22.6 %). Associations with ants from additional subfamilies, which do occur in other biogeographical realms (FIEDLER 2001), are not yet known from the Palaearctic. They are also quite unlikely to be found. Two candidates, *Tetraponera* (Pseudomyrmecinae) and *Gnamptogenys* (Ectatomminae), just marginally extend into the southeastern Palaearctic realm. Associations

of these ants with lycaenid immatures have very rarely been observed in the Oriental region (FIEDLER 2001), and they might finally also show up as attendant ants, for example in southern China where both genera occur (FELLOWES 2006). There are also two doubtful records that require confirmation and which have for the time being excluded from all quantitative analyses: *Cataglyphis "bicolor"* at *Apharitis myrmecophila*: DUMONT 1922 (probably a misidentification), and *Messor "rufitarsis"* at *Scolitantides orion* (NEL 1992; circumstances of observation not clear). All Palaearctic lycaenid-tending ants also feed on homopteran honeydew and / or plant nectar.

Overall, there are 212 (single records) or 317 record pairs (multiple records), respectively, available for analysis. The six top rank ant genera in the list (*Lasius* (with 41 lycaenid species), *Formica* (24), *Camponotus* (24), *Crematogaster* (26), *Myrmica* (25), *Tapinoma* (19)) together account for 159 (75 %, single records), or 211 (82.3 %, multiple records), of all lycaenid-ant associations, respectively. Hence, a small number of ant genera plays a disproportionally significant role in lycaenid-ant interactions, *Lasius* being by far the most prominent one. Globally, the top six attendant ant genera are *Crematogaster* (178) > *Camponotus* (90) > *Lasius* (46) > *Tapinoma* (41) > *Formica* (40) > *Pheidole* (39), which account for 53.1 % of all records. Two interesting differences emerge between the Palaearctic and the global pattern. First, in the northern temperate zones attendant ants are more concentrated in a few ant genera. This is expected since overall ant diversity is much higher in tropical and subtropical regions. Second, two ant genera that are highly prevalent under a

global perspective (viz. *Pheidole* and *Crematogaster*) are far less important in the Palaearctic region. Again, this pattern among attendant ants at lycaenids mirrors the overall much lower representation and ecological dominance of both these ant genera in non-tropical areas. In Europe, for example, *Pheidole* and *Crematogaster* are only represented by a few species which are largely confined to (sub-) Mediterranean regions. In contrast, *Lasius* and *Formica* are the dominant ant genera in many Palaearctic habitats, with *Camponotus* becoming increasingly important towards the south (e.g., in Mediterranean ant communities).

One case deserving further consideration is the ant genus *Myrmica*. Records of associations between *Myrmica* ants and lycaenids make up 11.8 % (single) or 16.1 % (multiple records) of all entries in the Palaearctic database. In the Nearctic region, where *Myrmica* ants are also quite common in forest biomes (FELLERS 1987, 1989), only 3 out of 97 records pairs (3.1 %) of tending ants refer to this genus. At a first glance one might be tempted to attribute this high Palaearctic score of *Myrmica* to the fact that such ants are the specific hosts of the socially parasitic *Phengaris-Maculinea* clade, and certainly the large number of recent *Maculinea* host records (SETTELE & al. 2005) has inflated the multiple records analysis. However, in the single records analysis *Myrmica* still scores more than three times as important in the Palaearctic versus the Nearctic region, and in this analysis each of the four *Maculinea* and two *Phengaris* species with documented *Myrmica* hosts counts just once. There are 19 facultatively myrmecophilous Palaearctic lycaenid species which have been found attended by *Myrmica* ants. Thus, *Myrmica* ants clearly have a high importance as tending partners of ant-mutualistic lycaenid immatures in the Palaearctic realm beyond the special case of the parasitic *Phengaris-Maculinea* clade. One might speculate that the relative commonness of *Myrmica* ants as visitors of lycaenid larvae has also been significant in the initial stage of the evolution of the parasitic life-style in the *Phengaris-Maculinea* clade (FIEDLER 1998).

The relative importance of ant genera as associates of Palaearctic lycaenids was significantly, but rather weakly related to the species richness of these same genera (single records: r_S = 0.563, p = 0.008; multiple records: r_S = 0.569, p = 0.007). Thus, species-rich genera tend to be more often seen in these associations, but there are many exceptions to this pattern (Fig. 4). Two ant genera that are conspicuously underrepresented (relative to their diversity) are the myrmicines "*Leptothorax*" sensu lato (or rather *Temnothorax* in the more restrictive sense: BOLTON 2003) and *Aphaenogaster*. Both genera are diverse and abundant in litter and soil, especially of temperate-zone forests. However, exactly this habitat preference renders these ants unlikely to encounter myrmecophilous lycaenid immatures, which mostly feed in the herb layer and usually thrive in warm, open microhabitats. Moreover, "*Leptothorax*" and *Aphaenogaster* ants rank low in the dominance hierarchies of their respective ant communities. Small colony sizes, small foraging territories and limited competitive strength in monopolizing food resources further contribute to the paucity of records of these ants as visitors of lycaenid immatures. It should be emphasized that the few records now available for non-parasitic lycaenid species have been collated only during the last 15 years. Two

Aphaenogaster records refer to cases where these ants serve as hosts of parasitic butterflies in the *Phengaris-Maculinea* clade. It remains to be tested whether *Aphaenogaster* ants are just minor or chance hosts, or whether species of the *Phengaris-Maculinea* clade parasitize *Aphaenogaster* ants in Eastern Asia on a regular basis. Two additional myrmicine genera, *Monomorium* and *Tetramorium*, are likewise underrepresented as lycaenid visitors relative to their species richness.

Some ant genera, in contrast, rank higher in the list of attendant ants relative to their species richness in the Palaearctic region. Examples are *Lasius*, *Crematogaster*, and *Tapinoma*. The case of *Lasius* has been covered above and can be attributed to the high ecological dominance of this ant genus in many temperate-zone habitats. Moreover, *Lasius* ants often forage in the herb layer – where many of the myrmecophilous species feed as larvae. The high score of *Crematogaster* (recorded with 26 species) is partially due to a peculiarity of one lycaenid clade, the tribe Aphnaeini. This tribe is most strongly developed in Africa (HEATH 1997), but representatives of the genera *Spindasis* and *Cigaritis* (including *Apharitis*) occur at the southern and eastern margin of the Palaearctic region. As far as known, all these species live in close, obligate associations with *Crematogaster* ants (positively recorded for three *Spindasis* and five *Cigaritis* species in the Palaearctic region, e.g., ROJO DE LA PAZ 1993, SANETRA & FIEDLER 1996). The remaining 18 *Crematogaster* records are spread across a wide range of unrelated lycaenid genera and mostly stem from the Mediterranean area or the south-eastern margin of the Palaearctic realm. *Tapinoma* has been quite frequently recorded (at 19 species) as visitor of lycaenid immatures in the Mediterranean area and in xerothermic habitats of Central Europe. This genus is very strongly involved in trophobiotic associations and also ranks among the top visitors of lycaenids globally (FIEDLER 2001). Even though *Tapinoma* ants are usually not dominant in their habitats and may be replaced in trophobiotic interactions by competitively superior ants (for an example involving lycaenids, see PETERSON 1993), they obviously are able to gain access to caterpillars as nectar sources due to their opportunistic foraging strategy. Moreover, like many other dolichoderines *Tapinoma* ants are able to defend resources against much larger competing ants with the help of their defensive secretions (e.g., SEIFERT 1987). The formicine genus *Plagiolepis* is a similar case of a subordinated ant taxon that nevertheless makes up a sizeable fraction of records.

Diversity of Palaearctic butterfly-ant associations

As discussed above, the relative importance of ant genera as associates of myrmecophilous lycaenid butterflies is highly variable. Absolute numbers of record pairs available are still rather small and differ widely between regions. Thus, comparing just the length of lists recorded so far, without taking into account sampling effects, can yield misleading results. I here use Shannon's information index to quantitatively express the diversity of attendant ants. For the Palaearctic region this yields an H' = 2.515 (95 % bootstrap confidence interval CI: 2.345 - 2.586) for single records. This value can be compared to diversity estimates derived from data presented in FIEDLER (2001) for other biogeographical regions. Accordingly, diversity scores of atten-

dant ants are significantly higher than in the Palaearctic realm in southeastern Asia (H' = 2.780, CI: 2.575 - 2.830), Australia (H' = 2.721, CI: 2.443 - 2.762), and North America (H' = 2.637, CI: 2.342 - 2.695). All these estimates fall outside the 95 % confidence interval for the Palaearctic region. In contrast, diversity of recorded ant associations is significantly lower in tropical Africa (H' = 1.983, CI: 1.606 - 2.128). This observation can partially be explained by the higher generic diversity of ant faunas, especially if the Australian and Oriental faunal regions are contrasted with the Palaearctic realm. The more surprising results refer to North America and tropical Africa. In the latter region, (recorded) ant-associations of lycaenids are strongly biased towards the ant genera *Crematogaster* (27, with many Aphnaeini species, see above), *Pheidole* (21 records) and *Camponotus* (11 records, host ants of many socially parasitic *Lepidochrysops* butterflies, e.g., FIEDLER 1998). Such concentration of records inevitably reduces diversity estimates. In contrast, in North America only two ant genera have a sizeable fraction of records (*Formica*: 22, *Tapinoma*: 10), resulting in a more even spread of records despite a much smaller data base (97 record pairs: FIEDLER 2001). In all biogeographical realms further ant genera are expected to show up as associates of lycaenid butterflies. This will elevate diversity estimates, especially for under-explored tropical regions. However, in Australia the coverage of records is already very high due to intensive field work in the past 25 years (EASTWOOD & FRASER 1999).

Temporal trends and regional bias in data quality

These considerations lead to the question as to how "definitive" or robust conclusions can be given the present day knowledge of lycaenid butterflies and their interactions with ants. Differences between the actual data set and the one published 15 years ago yield some interesting insights. Overall, the number of available records has almost doubled (124 single and 177 multiple record pairs in 1991, as opposed to 212 and 317, respectively, in 2006). The six top rank ant genera were the same in 1991 and 2006, with only minor changes in the rank order (Fig. 3b). Six ant genera could be added to the list of attendant ants (*Anoplolepis, Lepisiota, Aphaenogaster, Leptothorax, Bothriomyrmex, Dolichoderus*), but none of these turned out to be commonly seen at lycaenid immatures. Records of *Anoplolepis* moreover refer to lycaenid species with essentially Oriental distribution ranges and which just marginally extend into the southeastern Palaearctic region, where they are facultatively attended by the invasive *A. gracilipes*. Therefore, further additions can be expected, but they will in all likelihood refer to ant genera that rather rarely visit lycaenid larvae.

The massive increase in records had only moderate effects on the diversity estimates. These increased slightly for single records (H'_{1991} = 2.305, H'_{2006} = 2.515, Solow test: p = 0.065), and even less so for multiple records (H'_{1991} = 2.208, H'_{2006} = 2.336, p = 0.19). Hence, earlier conclusions remain valid in view of the much improved data-base. Nevertheless, the available data on ants that attend Palaearctic lycaenid butterflies still show some important gaps, and filling these gaps could yield surprising results. The strong under-representation of Mediterranean species in the 1991 data has been partially levelled out due to records from Greece and Spain. Yet, for the European part of the Palaearctic the Mediterranean fauna still merits better coverage. Data are very scant from most of Russia (but see KORB 1998) and China (except Hong Kong: BASCOMBE & al. 1999), as opposed to the good coverage of the island faunas of Japan and Taiwan. Some of the most disturbing gaps in our knowledge concern species that are related to the ant-parasitic *Phengaris-Maculinea* clade, but whose life-histories remain terra incognita (e.g., *Caerulea* and most species of *Sinia*). For a better understanding of the evolutionary history of these social parasites (FIEDLER 1998, ALS & al. 2004, PECH & al. 2004) it would be most important to know at what point the specific associations with *Myrmica* and *Aphaenogaster* ants originated, and whether these outgroup species are parasites or mutualists of ants.

Obligate ant-associations among Palaearctic Lycaenidae

As with lycaenid butterflies in general, obligate ant associations occur only in a minority of the Palaearctic fauna. These involve representatives of six ant genera: *Crematogaster* (8 spp.), *Myrmica* (7), *Aphaenogaster* (2), *Formica* (2), *Lasius* (2) and *Camponotus* (1). This pattern is at odds with the general prediction that dominant ant species with large, long-lived colonies should harbour the largest fraction of associated guests and parasites (HÖLLDOBLER & WILSON 1990) – an observation that also is true for lycaenids on a global scale (FIEDLER 2001). Under that premise one would expect more obligate myrmecophiles to occur with *Formica*, *Lasius* and *Camponotus* species. Apparently, the high unpredictability of ant partners in temperate-zone habitats has thus far prevented a higher incidence of specialist myrmecophiles among the Lycaenidae. One reason for this is the cost that lycaenid larvae incur when becoming obligate myrmecophiles: obligate associations tend to be far more host-specific. Host ranges of Palaearctic obligate myrmecophiles are far more narrow than the visitor ranges of facultative myrmecophiles (Kolmogorov-Smirnov test, D = 0.515, p < 0.001; Fig. 5). Host specificity usually means that chemical communication systems are tuned towards the "true" host ant, at the cost of failing in encounters with other ants (e.g., FIEDLER & al. 1996, SEUFERT & FIEDLER 1996). In this regard, obligate myrmecophily in lycaenids differs markedly from obligate trophobiosis in homopterans (STADLER & al. 2003). As a consequence, selection has rarely favoured the evolution of host ant specificity in phytophagous Palaearctic lycaenids. Even in low diversity ant communities there is a substantial likelihood for any given caterpillar individual on its host plant to encounter workers of various ant species or even genera during its life cycle which usually takes weeks to months. Trophobiotic associations are for example usually disrupted during cool nights, during spells of inclement weather, or during hibernation. It is then not uncommon that tending ants differ before and after such an interruption. Under these conditions, specializing on one host ant would carry severe costs if increased efficiency of chemical communication with one ant is accompanied by higher risks of attack through all other ants that forage on the host plants. It is therefore not surprising that among the Palaearctic lycaenids host-ant specialization is mostly confined to species that pass at least some fraction of their life cycle inside ant nests (e.g., *Phengaris-Maculinea* clade,
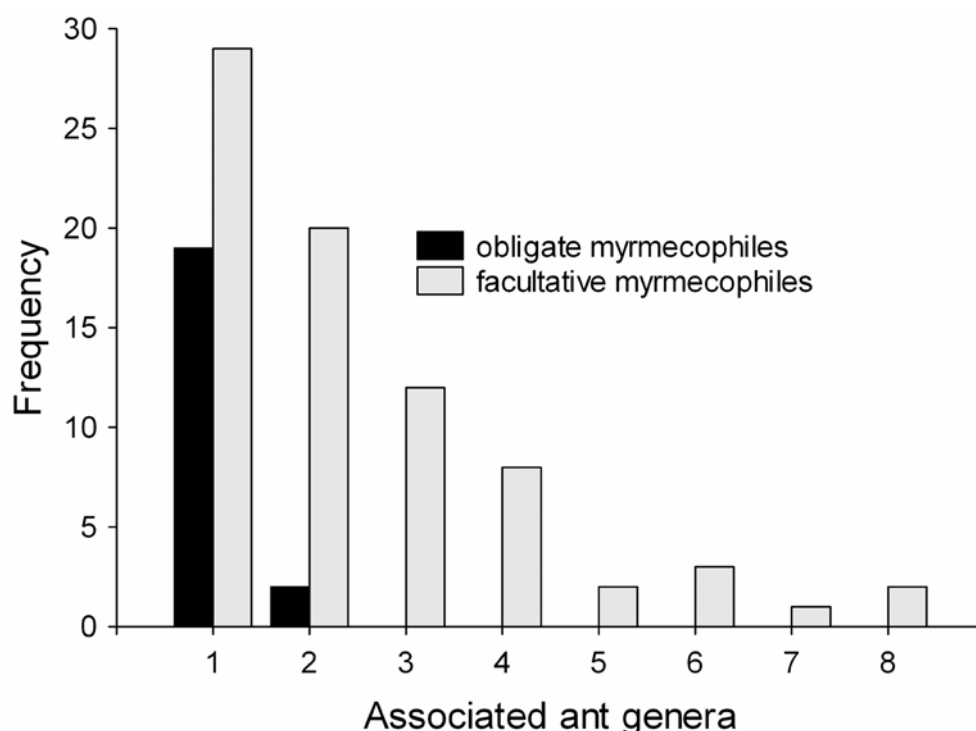
Fig. 5: Frequency distribution of the number of associated ant genera known per lycaenid species in the Palaearctic region. Facultative myrmecophiles (shaded bars) have significantly broader visitor ranges than the host ranges of obligate myrmecophiles (black). See text for statistics.

Cigaritis spp.), or where the host ants are super-dominant at the local habitat scale (*Plebejus argus, P. idas*). In tropical regions, in contrast, host-specific and obligate ant associations are more common even among non-inquiline phytophagous lycaenids (FIEDLER 2001).

Twenty of the 98 Palaearctic lycaenid species for which I could trace information on the generic identity of associated ants are obligate myrmecophiles. This figure should, however, not be mistaken as evidence that close to 20 % of the Palaearctic lycaenid fauna were obligately associated with ants. First, all non-myrmecophilous species of course are missing in this compilation. These are sizeable fractions, especially most copper butterflies (Lycaenini) and many hairstreak species (Theclini and Eumaeini). Second, for many facultative ant mutualists the identity of associated ants has never been reported, or available data just indicate that functional ant organs (especially a dorsal nectar gland) are present. Again, such species do not show up in the data-base. Overall, hardly 10 % of the Palaearctic lycaenid species will finally qualify as obligate mutualists.

Conclusions and perspective

This quantitative account of the diversity and identity of ant-associates of Palaearctic Lycaenidae butterflies corroborates generalizations that had been derived in previous analyses from much less extensive data (FIEDLER 1991a, b). Ecological opportunism governs partner assembly in facultative associations (the majority), whereas ant hosts of obligate myrmecophiles are far more specific. Dominant trophobiotic ant taxa of the northern hemisphere, like *Lasius*, *Formica*, and *Camponotus*, make up the most prevalent

visitors of lycaenid immatures with but limited leverage for specializations. Obligate ant-associations show a striking bias towards two host ant genera (*Crematogaster*, *Myrmica*) which can be explained by phylogenetic effects (radiations of Aphnaeini and the *Phengaris-Maculinea* clade, respectively). Even though the data-base has improved significantly over the past 15 years, important gaps remain, especially with regard to the southern and eastern part of the Palaearctic region (notably Russia and China). Overcoming this bias might add important new facets to the growing picture and even reveal some surprises. Nevertheless, the large-scale patterns are robust as apparent from this analysis in comparison with the status of data 15 years ago. This suggests that changes will likely be marginal, rather than radical.

Having established robust large-scale patterns concerning ant-associates of lycaenid butterflies, two promising directions for future research emerge which have hardly been explored in the Palaearctic region. First, there is very little knowledge about preferences and specializations on local scales – and the emerging knowledge is by and large confined to the ant-parasitic *Phengaris-Maculinea* clade (SETTELE & al 2005; for an obligate Australian ant-mutualist see EASTWOOD & al. 2006). Co-evolution theory predicts that local specializations should occur, but may be highly dynamic in space and time (THOMPSON 1999). Studies on genetic divergence patterns in Palaearctic obligate ant mutualists are very scant so far and do not generally take into account the ant-host dimension (e.g., PÉTÉNIAN & NÈVE 2003 for the obligate ant-mutualist *Plebejus argus*). Uncovering the genetic and ecological architec-

ture of local preference hierarchies and specializations in butterfly-ant interactions will provide important insights into the evolutionary dynamics of these systems, and may also be of conservation relevance.

A second line to be explored relates to invasive ants. At least in the southern parts of the Palaearctic region invasive ants such as *Linepithema humile*, *Tapinoma melanocephalum*, *Anoplolepis gracilipes* or *Pheidole megacephala* have established as important new components of local ant communities. Larvae of quite a number of lycaenids have been observed being tended by such ants (especially in the tropics). Some lycaenids even appear to quickly specialize on invasive ants if these become available (e.g., in southeastern Asia: FIEDLER & MASCHWITZ 1989). However, it remains to be seen if and how invasive ants change the balance and outcome of lycaenid-ant interactions. Current scant evidence suggests that protective mutualisms are less affected than, for example, dispersal mutualisms involving ants (NESS & BRONSTEIN 2004), but pertinent studies in Palaearctic communities are thus far lacking and could open up a rewarding new field. Again, such studies could also have an important conservation dimension.

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Zusammenfassung

Freilanddaten zu Ameisenassoziationen der Präimaginalstadien von 98 paläarktischen Arten der Tagfalterfamilie Lycaenidae weisen Vertreter von 21 Ameisengattungen aus den drei Unterfamilien Myrmicinae, Formicinae und Dolichoderinae als Begleiter bzw. Wirte aus. Alle Ameisen, die Bläulingsraupen besuchen, ernähren sich auch von anderen flüssigen Kohlenhydratquellen (extrafloraler Nektar von Pflanzen, Honigtau von Homopteren). Arten der Gattungen *Lasius* (beobachtet an 41 Lycaeniden-Arten), *Formica* (24 spp.), *Camponotus* (24 spp.; Formicinae), *Myrmica* (25 spp.) und *Crematogaster* (26 spp., Myrmicinae) sind die wichtigsten Partner paläarktischer Bläulinge. Obwohl sich der Datenbestand seit der letzten Synopsis vor 15 Jahren nahezu verdoppelt hat, erwiesen sich zuvor erkannte Muster und Regeln in den Bläulings-Ameisen-Beziehungen als sehr robust. Die Diversität der Ameisenassoziationen stellt sich heute etwas höher dar als vor 15 Jahren, im wesentlichen verursacht durch Neunachweise von sechs Ameisengattungen als Partner paläarktischer Bläulinge. Ameisenassoziationen von Bläulingen in der Orientalischen, Australischen und Nearktischen Faunenregion sind vielfältiger als in der Paläarktis, während solche in Afrika besonders wenig divers sind. Die Zahl der Bläulingsarten, die von Vertretern einer bestimmten Ameisengattung besucht werden, korreliert nur mäßig, aber signifikant mit dem Artenreichtum dieser Ameisengattungen in der Paläarktis. Abweichungen von dieser Regel lassen sich durch ökologische und verhaltensbiologische Eigenschaften der jeweiligen Ameisen erklären. Ökologische Dominanz ist der wichtigste Prädiktor für die Beteiligung von Ameisen an Interaktionen mit Bläulingsraupen. Obligate Myrmekophile sind in der Paläarktischen Lycaenidenfauna nur spärlich vertreten. Solche Bläulingsarten sind sehr spezifisch bezüglich ihrer Wirtsameisen, aber eher auf dem Gattungs- als auf dem Artniveau. Im Gegensatz dazu sind die Besucherspektren fakultativ myrmekophiler Bläulingsraupen stark opportunistisch geprägt. Obligate Ameisenassoziationen kommen in der Paläarktis besonders häufig mit Ameisen der Gattungen *Myrmica* (Wirte der sozialparasitischen Arten der *Phengaris-Maculinea*-Gruppe) und *Crematogaster* (Wirte einiger Arten der Tribus Aphnaeini) vor.

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