

Review Article

Declassifying Myrmecophily in the Coleoptera to Promote the Study of Ant-Beetle Symbioses

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The symbiotic associations between beetles and ants have been observed in at least 35 beetle families. Among myrmecophiles, beetles exhibit the most diverse behavioral and morphological adaptations to a life with ants. These various associations have historically been grouped into discrete but overlapping behavioral categories, many of which are still used in the modern literature. While these behavioral classifications provide a rich foundation for the study of ant-beetle symbioses, the application of these systems in future studies may be less than effective. Since morphological characteristics often provide the only information of myrmecophilous beetles, they should be studied in a species-by-species fashion, as behavioral data are often limited or unavailable. Similarly, behavioral studies should focus on the target species at hand, avoiding discrete classification schemes. I formally propose the rejection of any classification scheme, in order to promote future studies of myrmecophily in both taxonomic and evolutionary studies.

1. Introduction

Myrmecophily is a charismatic biological phenomenon that defines the associations, whether casual or intimate, of various organisms with ants. Myrmecophilous life habits have been observed in at least 95 families of arthropods, including several genera of isopods, pseudoscorpions, many araneid spiders, mites, millipedes, and close to 100 families of insects [1]. Among insects, the beetles are often the most easily recognized and morphologically distinct myrmecophiles, leading to a significant body of work. Currently, at least 35 beetle families are known to be associated with ants in some form or another [1, 2], but for at least fifteen of these families behavioral data are entirely absent. In many cases, presumed ant associates, both within the Coleoptera and other myrmecophilous groups, are cited as myrmecophiles based on unobserved interactions with ants, especially if specimens were collected in or near an ant nest. Specifically, beetles are considered to be myrmecophilous if they bear unique morphological characteristics presumed to be linked to myrmecophily. These morphological modifications frequently include combinations of enlarged or reduced antennae, reddish or “ant-red” integument, and, less often,

modified mouthparts or appendages that are sometimes associated with a myrmecophilous habit [3]. Perhaps the most commonly documented and presumably convincing evidence for a life with ants is the presence of trichomes, or tufts of setae associated with exocrine glands, but similar clusters of putatively secretive hairs can be found in termitophilous beetles, as well [4–7], and are not necessarily unique to those beetles that share a life with ants.

Despite the great morphological diversity that exists among myrmecophilous Coleoptera, very little is known of the interactions that may be occurring between ant hosts and their respective associates. Detailed behavioral data are available for a few better-known species within the aleocharine and scydmaenine Staphylinidae [8, 9], the paussine Carabidae [10, 11], and various species within, for example, the Coccinellidae [12, 13], the Scarabaeidae [14–17], and the Ptinidae [18, 19]. The documented myrmecophilous habits of these few taxonomic groups capture the great diversity of ant-beetle interactions known for beetles, ranging from casual interactions, such as scavenging in and around middens and refuse deposits and preying on ants along migration trails, to more intimate associations involving being fed by ants or even being adopted as members of the colony.

The many interactions that have been observed in a few beetle groups have led to the creation of behavioral classification schemes, the first of which was proposed by Wasmann [4, 20]. Successive behavioral categories have since been suggested [3, 21–24], all of which have served as a shorthand in placing the many different kinds of myrmecophiles. While these systems have provided a basic framework from which to expand our current knowledge of myrmecophily, they have also posed some challenges. In order to bridge the gap between what is known and the many unanswered questions that remain, I pursue several objectives herein.

I provide a general overview of the existing classification systems of myrmecophily in the Coleoptera, discuss current applications and potential challenges of utilizing these systems, and propose the formal rejection of these classifications systems in order to reduce redundancy and better understand the complexities of myrmecophily, at least until more is known about the biology of ant-associated beetles and other myrmecophiles. Note that this review does not intend to discuss all the important biological facets involved in myrmecophilous associations, such as the innumerable types of morphological adaptations or the complexities of mimicry which are undoubtedly important in many ant-beetle associations.

2. Definitions and Classifications of Myrmecophily

In more than 140 papers the German myrmecologist, Erich Wasmann, laid the groundwork for studies of myrmecophily and termitophily, particularly within the Coleoptera. Before Wasmann's contributions, the first compilation of myrmecophilous arthropods estimated 284 species, including 274 beetle species that are associated with ants [25, 26]. Fifty years later, an approximation of 1246 species of arthropods was cited as ant associates, with 993 of those species belonging to the Coleoptera [20]. A few years later, at least 3000 beetles had been predicted to be myrmecophilous [3]. More than a century later, authors estimate that 80,000–100,000 species of insects [27] are presumed myrmecophiles and, undoubtedly, the majority of these belong within the Coleoptera.

Wasmann [20] provided descriptive comparisons between different myrmecophilous Coleoptera, and as a result of the various associations observed, he proposed several discrete behavioral categories, which successive authors, including Wheeler [3], Donisthorpe [22], Delamare-Deboutteville [28], Akre and Rettenmeyer [24], Paulian [29], Kistner [23], and Franc [30], have attempted to restructure or reconfigure. The categories proposed by Wasmann and his contemporaries are complex, although a great degree of overlap can be observed (see Table 1).

Wasmann [20] introduced the terms “synecthrans” (persecuted guests), “synoeketes” (tolerated guests), “symphiles” (true or symbiotic guests), “ecto- and endoparasites” (parasites on and within ant bodies), and “trophobiotics” (those that feed ants with honeydew secretions and are provided protection in return). The only potential coleopterous ectoparasite belongs to the genus *Thorictus* in the family Dermestidae,

which is found to latch onto the antennal scape of ants [3]. While authors originally cited that it “sucked blood” of ants [31, 32], no studies thus far have indicated that this is the case. The trophobiotic category applies largely to the two well-studied myrmecophilous groups that include heteropterans and the majority of genera within the Lycaenidae, both of which are associated with ants by secretions of either honeydew or nectar, respectively, in exchange for ants' protection. Since the latter two categories are not found in beetles, they will be excluded from further discussion but are reviewed in detail in other works [33–35].

I outline the different categories proposed by different authors but present them under the more specific, inclusive scheme of Wasmann, largely because this system serves as the basis for much of what is known of myrmecophilous beetles and not because it is more useful than other systems.

2.1. “Synecthrans”. The synecthrans, as a whole, are classified as those associates that live in the vicinity of host nests, even within refuse deposits but only prey upon ants on raids and migrations [1, 4]. The synecthran classification is limited largely to staphylinids that often times bear defensive glands on the terminal abdominal segments and are able to either ward off ants in defense or may feed on ants during raids [24]. Taxa most often cited as being of the synecthran type include those staphylinids associated with army ants in the New World subfamily Ecitoninae. The singular species, *Eciton burchellii* (Westwood), hosts more than 300 species of ant associates, with 12 families and 59 species belonging to the beetles [36]. Most other authors have followed Wasmann's synecthran category, but the “extranidal” category of Donisthorpe [22] separated these associates from others, because they are found outside of the colony, unlike many other beetle species. Akre and Rettenmeyer [24] classified the typical synecthran types into what they named the “generalized species” (as opposed to specialized species), based on various behavioral characteristics as well as the absence of any morphological modifications found in these beetles. If following the categories of Delamare-Deboutteville [28], Wasmann's synecthrans would be considered as “accidental commensals;” similarly, if following Kistner's [23] groupings, the synecthrans would be considered as “nonintegrated” associates, as these beetles are not accepted as members of the colony.

2.2. “Synoeketes”. Wasmann's second group, the “synoeketes,” is a diverse group of myrmecophiles [3] and includes many species that are treated indifferently, being tolerated rather than attacked by ants. Synoeketes have been defined behaviorally as slow moving scavengers and occupy a range of morphological body types, including relatively small body size and being “neutral in odor,” as well as the absence of morphological adaptations to the colony. In addition, mimetic beetles were grouped into this category. Because of the range of both morphological and behavioral types of presumed synoeketes, Wheeler [3] further subdivided the group into the “neutral synoeketes,” which ignore hosts but live on nest materials and live in refuse piles; “mimetic synoeketes”

TABLE 1: Historical behavioral classification of myrmecophily by author. Categories marked with “—” indicate that the author did not consider the respective behavior in their classification scheme. Original terminology is used but translated if necessary.

Behavior	Wasmann [4, 20]	Silvestri [21]	Donisthorpe [22]	Paulian [29]	Delamare-Deboutteville [28]	Akre and Rettenmeyer [24]	Kistner [23]	Franc [30]
Scavengers or predators, ignored or tolerated by hosts	Synoebetes	Syncoxeni “Synoebetes”	Passive/intramidal guests “Inside nest guests”	Les clients “Clients”	Accidental/preferred or obligate commensals	Specialized species	Nonintegrated species	Synocious myrmecophiles
Scavengers or predators, treated with hostility; defensive	Synechthrans	Cleptoxeni “Cleptoketes”	Passive/intramidal guests “Inside nest guests”	Les clients or les associes “Clients” or “associates”	Accidental/preferred commensals	Defensive/generalized species	Non-integrated species	Prosynecthricans, synecthricans, or hypersynecthricans
Accepted into colony by being groomed, fed, or reared	Symphiles	Euxeni “True guests”	Passive/intramidal guests “Inside nest guests”	Les associes “Associates”	Obligate commensals	—	Integrated species	Symphillous myrmecophiles
Live on body surface of host, feed on secretions or food particles	Ectoparasites	Parasitoxeni “Parasites”	Passive/intramidal guests “Inside nest guests”	Les associes “Associates”	Obligate commensals	—	Integrated species	—
Penetrate body to feed on blood; parasite	Endoparasites	Parasitoxeni “Parasites”	Passive/intramidal guests “Inside nest guests”	Les associes “Associates”	Obligate commensals	—	Integrated species	—
Exchange of honeydew or nectar for protection	Trophobionts	Euxeni “True guests”	Active/extramidal guests “Outside nest guests”	Les associes “Associates”	Obligate commensals	—	Integrated species	—
Follow hosts on raids	Synechthrans	—	Active/extramidal guests	Les suivants “Followers”	—	Generalized/specialized species	Non-integrated species	Synecthricans

that mimic ants; “loricate synoeketes” that are tear-drop shaped and therefore hard to capture or bite by an ant; and, “symphillid synoeketes,” which resemble true guests but have not yet achieved perfection; where “perfection” describes those myrmecophiles that are integrated into the ant nest. In addition to the various supposed synoeketes, Wheeler also included “myrmecocleptics” to denote those which snatched food from ants. Paulian’s [29] term “les clients” or ant clients includes all myrmecophiles that frequent debris piles and exploits ant bodies or excrement, as well as those that prey upon the insects that are attracted to these items, and is thus synonymous with synoeketes. Akre and Rettenmeyer [24] instead avoided the use of the term synoekete but proposed the term “specialized species,” based on various behavioral characteristics and the fact that many of these species appear to be close mimics of their respective ant host species, matching hosts in both color and body shape [37]. If following any of the other authors’ proposed categories, these species would be considered as “passive” or “intranidal” (within the nest) associates [22], “accidental” associates [28], or “nonintegrated associates” [23].

2.3. “*Symphiles*”. The “symphiles,” or true guests, is the most speciose group of myrmecophilous beetles, with likely more than 10,000 species being considered in this or synonymous categories [27]. The majority of authors including Wasmann and Wheeler cited “symphily” as the extreme form of myrmecophily or as the last step reached by myrmecophiles when compared to associates exhibiting more casual interactions with ants. This assumption of gradual, almost directional complexity has not been formally addressed, and no evidence supports the increasing complexity of any myrmecophilous group. This will be addressed in a separate paper.

One unique behavior, that is exhibited by the so-called symphiles, includes solicitation of liquid food from ant hosts, including larvae and adults, via trophallaxis [1, 35]. In nearly all known cases, beetles originally classified as symphiles also feed on brood, acting as obligate parasites.

The symphile category also typically includes beetles that are accepted into ant nests either by being carried in or entering without being detected and being successively integrated into the social life of the ant colony. The most likely cause for ants’ accepting these associates into their colonies involves chemical mimicry exhibited by beetles [1]. Some elegant studies have indicated that beetles are able to adopt specific ant chemical signatures [14, 38], largely by means of physical contact with the ants themselves. Thus far, no studies have confirmed that ant associates are able to biosynthesize hydrocarbons or produce these chemicals *de novo*; however, it has been confirmed for the termitophilous staphylinid beetle, *Trichopsenius frosti* [39]. Instead, studies have indicated that certain aleocharine Staphylinidae produce nonhydrocarbon alarm pheromones similar to that of their hosts [38, 40, 41]. It is important to note that, thus far, no presumed “symphilous” beetles, which are accepted as part of the colony, are known to be able to biosynthesize compounds.

Perhaps the most interesting difference between the “symphiles” and other myrmecophilous beetles is that this

group is almost always defined by the presence of trichomes, even without any behavioral information. These trichomes have been assumed to play a large role in the intimate associations between beetles that have them and their ant hosts. They are often discussed as being somehow attractive or “appeasing” to ants, with ants often licking, biting, or picking beetles up by these trichomes [3, 15]. It has also been demonstrated that exocrine glands associated with trichomes may play a role in ants’ acceptance of beetles into the colony, as seen in the scarab genus *Cremastocheilus* [15]. Trichomes are even present in the ectoparasitic *Thorictus*, which further complicates the matter of accepting either “ectoparasite” or “symphile” as a classifier for this genus.

After Wasmann, symphiles have been reclassified into the “active” or “intranidal” (inside the nest) category of Donisthorpe [22], the “obligate commensals” group of Delamare-Deboutteville [28], or the “integrated” species of Kistner [23]. In all cases, except for Wasmann’s and the subdivided system of Franc [30] are these highly integrated beetles grouped into broader categories that include many other ant associates. It is also evident that, while most of these beetles are highly “integrated,” if using Kistner’s terminology, the means by which these beetles become so is highly variable.

3. Problems with the Proposed Classifications of Myrmecophily

Several authors have mentioned the difficulty in accepting any one existing categorical scheme for myrmecophiles [1, 11, 23], and the most often cited problem associated with the use of any one scheme is the fact that many beetles fit into more than one category. Despite initial criticisms, Wasmann’s system has been claimed as the most useful [1] and has been adopted by authors in modern studies or in reviews [30, 42]. In attempting to utilize any one of these schemes, it becomes apparent that a single type of association with an ant host may be classified differently depending on the author and even depending on the taxon. But perhaps most problematic is the fact that so little is known about the majority of myrmecophiles, which renders many of the existing classification systems obsolete or inadequate to capture the behavioral diversity likely to be discovered for these taxa. Attempts to place myrmecophiles into one of these ethological schemes can be cumbersome and inadvertently leads to the unintended rejection of complex species-specific behaviors in favor of placing a species in one or more of the categories. Various specific challenges limit what may otherwise lead to much more informative studies of myrmecophiles, although it should be noted that many studies do not use these classifications schemes.

3.1. *Taxon-Specific Classifications*. Several existing schemes are based on specific taxa and are less useful in identifying myrmecophilous associations at higher taxonomic levels. For example, the classification proposed by Paulian [29] can be applied only to staphylinid beetles that are closely associated with army ants in the subfamily Dorylinae. Akre and Rettenmeyer [24] also based their system on

staphylinids associated with the ecitoninae army ants. A separate subdivision of the various synecthran staphylinids was created by Franc [30] to recognize the varied behaviors observed for Slovakian staphylinids. The fact that several behavioral classifications have been created solely for myrmecophilous Staphylinidae illustrates the great diversity of myrmecophilous associations that exist within the family and suggests that it may be more appropriate to limit some of the previously proposed behavioral classes to the family.

3.2. Same Class, Different Behaviors. In many cases, the broadly defined classification schemes unintentionally capture vastly different associations in a single category [1]. For example, the very commonly used term “synoekete,” which was used by nearly every author after Wasmann, is widely applied to many Coleoptera that vary greatly in their biology and in interactions with respective ant hosts. Wheeler’s subdivision of the synoeketes into four different classes places potentially every kind of ant-associated beetle within the group, including the many beetles that are ignored by ant hosts, the numerous genera that feed on debris in refuse piles, several Staphylinidae that are mimics of ants, and those that resemble but are not really “true guests.” In Wheeler’s attempt to capture this diversity of behavior and morphology, it appears as if each type is mutually exclusive but is not. For instance, ant mimics, which Wheeler placed in their own category, actually are ignored by ants and may feed on debris in refuse piles [24], but this behavior is classified separately from the mimic category. It may be useful in these cases to separate morphology from behavior.

When comparing different groups of myrmecophiles at higher taxonomic levels, the terminology used for one group may not be applicable to those of another group [43], which supports the notion that creating overarching behavioral classes may be less effective than intended. For example, the term “symphile” may be interpreted differently in different groups of beetles. If one considers the symphilous spider beetles, for which we have data for only a few species, these beetles may be scavenging in refuse piles, while also involved in trophallaxis with ants. In contrast, the “symphilous” scarab genus *Cremastocheilus* is known to be carried into or walk into ant colonies undetected and subsequently feeding on ant larvae or pupae. While these two beetle groups are “integrated” into the ant nest, the mechanisms used to integrate themselves are vastly different. The term “symphile” falls apart when considering these different taxonomic groups. In addition, even if behaviors appear to be superficially identical in unrelated taxonomic groups, there may be niche-specific differences [43] or even host-specific adaptations that are not immediately visible. Factors such as colony size, the type of habitat, movement patterns and frequency, and other within-nest variables may all play roles in how associates are interacting with ants [11].

Most recently, Ellis and Hepburn [42] unsuccessfully attempted to classify the small hive beetle, a bee parasite, according to the schemes proposed by Wasmann [20] and Kistner [23]. They noted that beetles’ associations with bee

hosts differed depending on geographic range, the level of predation exhibited by the beetles and also varied among naturally occurring or introduced populations. Similar complex factors are likely to affect many myrmecophiles, especially if they are generalists, or are associates of multiple ant hosts where interactions may differ from one ant host to another. Most recently, Geiselhardt et al. [11] proposed the use of the terms “obligate” or “facultative” to capture myrmecophilous associations to avoid the use of Wasmann’s system. Their scheme may be the most generalized, and probably the most practical, but still relies on authors knowing how closely species are associated with their ant hosts. For example, if one considers any of the staphylinid beetles that are associated with any of the various army ant genera, they could be considered obligate ant guests if associations are specific to the respective ant host; or, provided that many staphylinids are generalist predators and scavengers, they may all be considered facultative associates if the presence of ants or debris from ant nests are not required for survival. The usage of either of these terms is still problematic and may not be useful for many other myrmecophilous beetles, since few biological details are known for the majority of taxa.

3.3. Presumed Behaviors of Closely Related Taxa. In Hölldobler and Wilson’s [1] list of myrmecophiles and their respective interactions with ants, much of the information needed to describe these interactions is cursory or entirely absent. Specifically, in the list of Coleoptera associated with ants, nearly half of the mentioned families are completely unknown in a behavioral sense. In addition, many are presumed to interact with ants in a certain way depending on what is known about a close relative. For example, the scarab genus *Stephanuca* was recently documented to be associated with ants, although the observations only indicated that beetles land close to or near plants that were covered with ants, and no beetles were ever collected in an ant mound [44]. It was compared to a closely related, presumably myrmecophilous species, *Euphoria inda*, which has been found to be carried into ant nests for the purpose of laying eggs in debris inside the ant colony [3]. *Euphoria hirtipes* has also been collected in *Formica* thatches [45], but interactions with ants have not been observed. These three beetles, while all similar in morphology, may use similar strategies to gain entrance into the ant colony, but behavioral data are incomplete.

In other cases where behavior is known, interactions of beetles with respective ant hosts can vary quite significantly among closely related taxa. The North American scarab genus *Cremastocheilus* is presumed to be exclusively myrmecophilous, and all known species bear conspicuous trichomes that would indicate a “symphilous” habit, if using the terminology of Wasmann. Most *Cremastocheilus* species have abundant ant-host records [15], but little is known about behavior, except for a few species. Two closely related species within the same subgenus *Trinodia* [15, 46], including *C. hirsutus* and *C. saucius*, use entirely different strategies to gain entrance into an ant mound. *Cremastocheilus hirsutus* enters *Pogonomyrmex* ant nests on its own, while *C. saucius*

feigns death and relies on the ants to carry it into the nest [15], suggesting that colony entrance behaviors are highly variable among closely related species within the genus. Similar studies of the rove beetle genus *Pella* [47] or the ladybird genus *Coccinella* [48] have also indicated vastly different behaviors among three congeners, which makes it nearly impossible to classify either genus as a specific type of myrmecophile and suggests that ant-beetle interactions are often species-specific, where each species may be classified differently according to Wasmann's or several other classification systems. The utility of behavioral categories becomes less reliable as one examines more taxa and may be little effective in truly understanding how complex phenomena like myrmecophily evolve.

3.4. Confounding Behavior and Morphology. The majority of categorical schemes include aspects of both behavior and morphology, no doubt because these two factors are inextricably connected. Therefore, the behavioral categories proposed by various researchers often hinge on morphological justifications to support purported behavioral interactions. Morphology often provides information, that is used to predict a certain behavior, but in many other cases such claims should be approached with caution, especially since various behavioral interactions with ant hosts may be occurring in taxa that bear similar morphological adaptations, such as the *Cremastocheilus* example cited earlier. The presence of trichomes is often immediately associated with a "symphilous" habit; while this appears to be true in many cases, behavioral information is absent for the majority of taxa that bear these trichomes. Even among taxa that bear trichomes, their interactions with ants still appear to be highly variable.

Wasmann's "symphile" category is almost always discussed in terms of trichomes [3], and the mere presence of trichomes has been cited as being immediately predictive of an intimate association with ants [3, 6, 49], even though trichomes are also found in many termite-associated beetles [4, 5, 7]. In other categories, particularly Wasmann's "synoeketes," the morphology among these beetles is highly varied, including various mimics "tear-drop shaped" beetles [3]. In addition, beetles often bear different combinations of morphological adaptations to a life with ants. These morphological modifications frequently include enlarged or reduced antennae, reddish or "ant-red" integument, and less frequently, modified mouthparts [18, 46] or "digging" appendages that are sometimes associated with myrmecophily [3, 15].

While it should not be assumed that each morphological modification is adaptive, that is, it serves a definite function in terms of behavior, it may be useful for future studies to investigate whether certain morphological characteristics are actually predictors of a certain behavior, instead of making *a priori* assumptions. In addition, both morphological and behavioral aspects of a presumed myrmecophile should be examined on a species-specific basis rather than on one that attempts to lump the target species into one of the existing categories for sake of simplicity.

4. Rejection of Previous Classification Systems

The descriptions used by authors often circumscribe significantly different behaviors and morphological character suites that may or may not be adaptations to myrmecophily. Many of these intended groupings of myrmecophilous interactions envelop the range of myrmecophilous interactions that have been observed, but none of the existing categories provide us with an effective method for describing these interactions. In part, creating categories for different ant associates may not be useful at any scale, particularly if applied to various unrelated taxa. Instead, examining each presumed myrmecophile as its own entity on its own evolutionary trajectory may be favorable.

Various factors that are discussed in the different categorical schemes should be considered when describing myrmecophiles. For example, the classification schemes of both Donisthorpe [22] and Kistner [23] focused on associates' relative occurrence inside or outside the ant colony. Those species that infrequently encounter ants are less likely to bear the behavioral or morphological adaptations than those which closely interact with ants on raids or inside the colony [24]. Therefore, behavioral descriptions should focus on the potential level of interaction between host and associate.

It is evident that myrmecophilous associations do not occur as discrete and easily identifiable interactions but rather on a behavioral gradient. The varying combinations of morphology found in different myrmecophiles may also be viewed as operating on a gradient, so that some body parts evolve in response to myrmecophilous interactions and others do not. While it is often easy to look at a myrmecophilous beetle and claim that it is an ant associate, based on the "typical myrmecophile" characteristics, these morphological traits may be relatively labile in an evolutionary context [35, 43] and are able to evolve rapidly in response to myrmecophilous interactions. Morphological convergence in response to myrmecophily may in itself be worth examining more closely.

5. Conclusion

I suggest that each target taxon, whether a single species or entire genera, should be studied in terms of its respective behavioral and morphological suite of characteristics. In the few cases where behavioral data are available, noting species-specific interactions with respective ant hosts is more likely to be informative than attempting to place taxa within a categorical scheme, at least until more is known of biology. A recent review of the Dermestidae suggests that examining taxa at lower levels, that is, below the family level [50], may provide insights into patterns of evolution that would not be possible if one attempted to group a diverse array of ecologically diverse taxa into a single behavioral category. Therefore, studies of myrmecophily, especially those attempting to elucidate patterns or processes underlying the evolution of myrmecophilous associations, may be pursued by viewing beetle-ant interactions from a declassified or deconstructed perspective.

Historically, the vast diversity of myrmecophilous interactions that occur within or around ant nests have both baffled and amazed biologists, and continued studies of ant associated beetles will undoubtedly fill in the gaps and answer some of the many questions that we have about this syndrome. It is this fascinating behavior and the bizarre morphological adaptations that evolve in response to it and that lure so many of us to the study of myrmecophily; however, relying on the need to classify or name myrmecophiles adds unnecessary confusion and redundancy to the field. Furthermore, the term “myrmecophily” should be approached with caution. I also suggest that studies should be pursued on a species-specific basis, both in terms of the associates and their respective ant hosts. Ants are rarely discussed in studies of myrmecophily, unless a specific ant host is mentioned. Instead, the focus is typically placed on those animals that are associated with ants, and it is likely that ant-specific behaviors may be just as interesting and complex as those of their respective associates. Finally, I urge amateurs, experts, and willing graduate students that are interested in rich, complex behavioral and morphological systems to begin to delve into the still largely unknown system of myrmecophily, especially in the Coleoptera. This phenomenon provides a rich area of research, both in terms of taxonomic and basic behavioral studies, as well as one that can be pursued to examine the evolution of complex morphology, behavior, and underlying molecular processes that may give greater insights into what we know as “myrmecophily.”

References

- [1] B. Hölldobler and E. O. Wilson, *The Ants*, Belknap Press, Cambridge, Mass, USA, 1990.
- [2] E. O. Wilson, *The Insect Societies*, Belknap Press, Cambridge, Mass, USA, 1971.
- [3] W. M. Wheeler, *Ants, Their Structure, Development and Behavior*, Columbia University Press, New York, NY, USA, 1910.
- [4] E. Wasmann, “Vergleichende studien über ameisengäste und termitengäste,” *Tijdschrift voor Entomologie*, vol. 33, pp. 27–96, 1890.
- [5] J. Krikken and J. Huijbregts, “Southeast Asian *Termitodius*: a taxonomic review, with descriptions of four new species (Coleoptera: Aphodiidae),” *Zoologische Mededelingen Leiden*, vol. 61, no. 7, pp. 97–111, 1987.
- [6] M. S. Caterino, “Descriptions of the first Chlamydopsinae (Coleoptera: Histeridae) from Wallacea,” *Tijdschrift voor Entomologie*, vol. 143, no. 3, pp. 267–278, 2000.
- [7] M. Maruyama, “A new genus and species of flightless, microphthalmic Corythoderini (Coleoptera: Scarabaeidae: Aphodiinae) from Cambodia, associated with *Macrotermes* termites,” *Zootaxa*, vol. 3555, pp. 83–88, 2012.
- [8] B. Hölldobler, “Communication between ants and their guests,” *Scientific American*, vol. 224, pp. 86–93, 1971.
- [9] S. T. O’Keefe, “Ant-like stone beetles, ants, and their associations (Coleoptera: Scydmaenidae; Hymenoptera: Formicidae; Isoptera),” *Journal of the New York Entomological Society*, vol. 108, no. 3–4, pp. 273–303, 2000.
- [10] W. Moore, X. B. Song, and A. di Giulio, “The larva of *Eustra* (Coleoptera, Paussinae, Ozaenini): a facultative associate of ants,” *ZooKeys*, vol. 90, pp. 63–82, 2011.
- [11] S. F. Geiselhardt, K. Peschke, and P. Nagel, “A review of myrmecophily in ant nest beetles (Coleoptera: Carabidae: Paussinae): linking early observations with recent findings,” *Naturwissenschaften*, vol. 94, no. 11, pp. 871–894, 2007.
- [12] J. Orivel, P. Servigne, P. Cerdan, A. Dejean, and B. Corbara, “The ladybird *Thalassa saginata*, an obligatory myrmecophile of *Dolichodeurs bidens* ant colonies,” *Naturwissenschaften*, vol. 91, no. 2, pp. 97–100, 2004.
- [13] A. Vantaux, O. Roux, A. Magro, and J. Orivel, “Evolutionary perspectives on myrmecophily in ladybirds,” *Psyche*, vol. 2012, Article ID 591570, 7 pages, 2012.
- [14] R. K. Vander Meer and D. P. Wojcik, “Chemical mimicry in the myrmecophilous beetle *Myrmecaphodius excavaticollis*,” *Science*, vol. 218, no. 4574, pp. 806–808, 1982.
- [15] G. D. Alpert, “A comparative study of the symbiotic relationships between beetles of the genus *Cremastocheilus* (Coleoptera, Scarabaeidae) and their host ants (Hymenoptera, Formicidae),” *Sociobiology*, vol. 25, no. 1, pp. 1–266, 1994.
- [16] F. Z. Vaz-De-Mello, J. N. C. Louzada, and J. H. Schorereder, “New data and comments on scarabaeidae (Coleoptera: Scarabaeoidea) associated with attini (Hymenoptera: Formicidae),” *Coleopterists Bulletin*, vol. 52, no. 3, pp. 209–216, 1998.
- [17] F. T. Krell, “Dung beetles unharmed by army ants in tropical Africa (Coleoptera: Scarabaeidae; Hymenoptera: Formicidae, Dorylinae),” *Coleopterists Bulletin*, vol. 53, no. 4, pp. 325–328, 1999.
- [18] J. F. Lawrence and H. Reichardt, “Revision of the genera *Gnostus* and *Fabrasia* (Coleoptera: Ptinidae),” *Psyche*, vol. 73, no. 1, pp. 30–45, 1966.
- [19] T. K. Philips, “Phylogenetic analysis of the new world Ptininae (Coleoptera: Bostrichoidea),” *Systematic Entomology*, vol. 25, no. 2, pp. 235–262, 2000.
- [20] E. Wasmann, *Kritisches Verzeichniss der Myrmecophilen und Termitophilen Arthropoden*, Berlin, Germany, 1894.
- [21] F. Silvestri, “Contribuzioni alla conoscenza dei Mirmecofili, I: osservazioni su alcuni mirmecofili dei dintorni di Portici,” *Annuario del Museo Zoologie della R. Universita di Napoli*, vol. 1, no. 13, pp. 1–5, 1903.
- [22] H. Donisthorpe, “The ants (Formicidae), and some myrmecophiles, of Sicily,” *The Entomologist’s Record*, vol. 38, no. 12, pp. 6–9, 1927.
- [23] D. H. Kistner, “Social and evolutionary significance of social insect symbionts,” in *Social Insects*, H. R. Hermann, Ed., vol. 1, pp. 339–413, Academia Press, New York, NY, USA, 1979.
- [24] R. D. Akre and C. W. Rettenmeyer, “Behavior of Staphylinidae associated with army ants (Formicidae: Ecitonini),” *Journal of the Kansas Entomological Society*, vol. 39, no. 4, pp. 745–782, 1966.
- [25] F. Maerker, “Beiträge zur Kenntniss der unter Ameisen lebenden, Insekten, Erstes Stück,” *German’s Zeitschrift für die Entomologie*, vol. 3, pp. 203–225, 1841.
- [26] F. Maerker, “Beiträge zur Kenntniss der unter Ameisen lebenden, Insekten, Zweites Stück,” *German’s Zeitschrift für die Entomologie*, vol. 5, pp. 193–271, 1844.
- [27] K. Schönrogge, J. C. Wardlaw, J. A. Thomas, and G. W. Elmes, “Polymorphic growth rates in myrmecophilous insects,” *Proceedings of the Royal Society B*, vol. 267, no. 1445, pp. 771–777, 2000.
- [28] C. Delamare-Deboutteville, “Recherches sur les Collemboles termitophiles et myrmecophiles (écologie, éthologie, systématique),” *Archives de Zoologie Experimentale et Generale*, vol. 85, no. 5, pp. 261–425, 1948.

- [29] R. Paulian, "Observations sur les Coléoptères commensaux d'*Anomma nigricans* en Côte d'Ivoire," *Annales des Sciences Naturelles*, vol. 10, no. 1, pp. 79–102, 1948.
- [30] V. Franc, "Myrmecophilous beetles of Slovakia with special reference to their endangerment and perspectives for protection," *Acta Universitatis Carolinae Biologica*, vol. 36, pp. 299–324, 1992.
- [31] A. Forel, "Les formicides de la Province D'Oran (Algérie)," *Bulletin de la Société Vaudoise des Sciences Naturelles*, vol. 30, no. 114, pp. 1–47, 1894.
- [32] E. Wasmann, "Zur Kenntnis einiger schwieriger *Thorictus*-Arten," *Deutsche Entomologische Zeitschrift*, vol. 39, no. 1, pp. 41–44, 1895.
- [33] K. Fiedler, "Systematic, evolutionary, and ecological implications of myrmecophily within the Lycaenidae (Insecta: Lepidoptera: Papilionoidea)," *Bonner Zoologische Monographien*, vol. 31, pp. 1–210, 1991.
- [34] N. E. Pierce, M. F. Braby, A. Heath et al., "The ecology and evolution of ant association in the Lycaenidae (Lepidoptera)," *Annual Review of Entomology*, vol. 47, pp. 733–771, 2002.
- [35] A. W. Shingleton and D. L. Stern, "Molecular phylogenetic evidence for multiple gains or losses of ant mutualism within the aphid genus *Chaitophorus*," *Molecular Phylogenetics and Evolution*, vol. 26, no. 1, pp. 26–35, 2003.
- [36] C. W. Rettenmeyer, M. E. Rettenmeyer, J. Joseph, and S. M. Berghoff, "The largest animal association centered on one species: the army ant eciton *burchellii* and its more than 300 associates," *Insectes Sociaux*, vol. 58, no. 3, pp. 281–292, 2011.
- [37] D. H. Kistner and H. R. Jacobson, "Cladistic analysis and taxonomic revision of the ecitophilous tribe Ecitocharini with studies of their behavior and evolution (Coleoptera, Staphylinidae, Aleocharinae)," *Sociobiology*, vol. 17, pp. 333–480, 1990.
- [38] T. Akino, "Chemical camouflage by myrmecophilous beetles *Zyras comes* (Coleoptera: Staphylinidae) and *Diaritiger fossulatus* (Coleoptera: Pselaphidae) to be integrated into the nest of *Lasius fuliginosus* (Hymenoptera: Formicidae)," *Chemoecology*, vol. 12, no. 2, pp. 83–89, 2002.
- [39] R. W. Howard, C. A. McDaniel, and G. J. Blomquist, "Chemical mimicry as an integrating mechanism: cuticular hydrocarbons of a termitophile and its host," *Science*, vol. 210, no. 4468, pp. 431–433, 1980.
- [40] R. W. Howard and G. J. Blomquist, "Ecological, behavioral, and biochemical aspects of insect hydrocarbons," *Annual Review of Entomology*, vol. 50, pp. 371–393, 2005.
- [41] M. Stoeffler, T. S. Maier, T. Tolasch, and J. L. M. Steidle, "Foreign-language skills in rove-beetles? Evidence for chemical mimicry of ant alarm pheromones in myrmecophilous Pella beetles (Coleoptera: Staphylinidae)," *Journal of Chemical Ecology*, vol. 33, no. 7, pp. 1382–1392, 2007.
- [42] J. D. Ellis and H. R. Hepburn, "An ecological digest of the small hive beetle (*Aethina tumida*), a symbiont in honey bee colonies (*Apis mellifera*)," *Insectes Sociaux*, vol. 53, no. 1, pp. 8–19, 2006.
- [43] B. Stadler, P. Kindlmann, P. Šmilauer, and K. Fiedler, "A comparative analysis of morphological and ecological characters of European aphids and lycaenids in relation to ant attendance," *Oecologia*, vol. 135, no. 3, pp. 422–430, 2003.
- [44] M. J. Paulsen, "Observations on possible myrmecophily in *Stephanucha pilipennis* Kraatz (Coleoptera: Scarabaeidae: Cetoniinae) in Western Nebraska," *The Coleopterists Bulletin*, vol. 56, no. 3, pp. 451–452, 2002.
- [45] B. C. Ratcliffe, "Notes on the biology of *Euphoriaspis hirtipes* (Horn) and descriptions of the larva and pupa (Coleoptera: Scarabaeidae)," *The Coleopterists Bulletin*, vol. 30, no. 3, pp. 217–225, 1976.
- [46] G. Mynhardt and J. W. Wenzel, "Phylogenetic analysis of the myrmecophilous *Cremastocheilus* Knoch (Coleoptera, Scarabaeidae, Cetoniinae), based on external adult morphology," *ZooKeys*, vol. 34, no. 2, pp. 129–140, 2010.
- [47] M. Stoeffler, T. Tolasch, and J. L. M. Steidle, "Three beetles—three concepts. Different defensive strategies of congeneric myrmecophilous beetles," *Behavioral Ecology and Sociobiology*, vol. 65, no. 8, pp. 1605–1613, 2011.
- [48] J. F. Godeau, J. L. Hemptinne, A. F. G. Dixon, and J. C. Verhaeghe, "Reaction of ants to, and feeding biology of, a congeneric myrmecophilous and non-myrmecophilous ladybird," *Journal of Insect Behavior*, vol. 22, no. 3, pp. 173–185, 2009.
- [49] F. T. Krell and T. Keith Philips, "*Formicdubius* Philips & Scholtz from South Africa, a junior synonym of *Haroldius* Boucomont, and a survey of the trichomes in the African species (Coleoptera, Scarabaeidae, Onthophagini)," *ZooKeys*, vol. 34, no. 2, pp. 41–48, 2010.
- [50] R. D. Zhantiev, "Ecology and classification of dermestid beetles (Coleoptera, Dermestidae) of the Palaearctic fauna," *Entomological Review*, vol. 89, no. 2, pp. 157–174, 2009.



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