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REVIEW ARTICLE

Insights on the association of American Cetoniinae beetles with ants

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Abstract

Cetoniinae beetles (Coleoptera: Scarabaeoidea: Scarabaeidae) can occupy the nests of social insects. In many cases the beetles located within the colonies of social insects encounter a place of shelter and food resources for both adults and immatures. Despite the numerous cohabitation records, the relationship of Cetoniinae beetles with their ant hosts remains mostly unexplored. In this review we provide hypotheses explaining this ant–beetle association. A conceptual model is presented on the processes underpinning the occupation of the nest and the consequences that unfold after occupation, including: (i) death of the ant colony; (ii) death of beetles; and (iii) coexistence. We also provide an exhaustive list of American Cetoniinae beetle species found associated with ants and discuss the symbiotic relationships occurring between the beetles and their host ants.

Key words: Cetoniini, Cremastocheilini, myrmecophilic beetles, myrmecophily, social behavior, social insects, symbiotic relationships.

INTRODUCTION

The presence of arthropods inhabiting nests of social insects is a common phenomenon also known in ants (Wilson 1971; Hölldobler & Wilson 1990), bees (Morse & Flottum 1997) and termites (Kistner 1969; Costa *et al.* 2009; Cristaldo *et al.* 2012). Individuals cohabiting the nests frequently find food, protection and climatic stability inside (Wilson 1971; Hölldobler & Wilson 1990). Ant colonies have a great diversity of other arthropods cohabiting their nests (Hölldobler & Wilson 1990; Mynhardt 2012; Lapeva-Gjonova 2013), which are known as "myrmecophiles" (Kronauer & Pierce 2011). Among the ant-guests, Cetoniinae beetles (Coleoptera: Scarabaeoidea: Scarabaeidae) form an important group of 52 species known to cohabit the nests of 73 species of ants in the Americas (see Appendix S1, Supporting Information).

The subfamily Cetoniinae contains about 4000 species worldwide (*sensu* Krikken 1984; Krajcik 1999), of which 300 are estimated to occur in the American continents (Orozco 2012a). The adults (commonly known as fruit or flower beetles) are relatively large (0.5–15.0 cm) beetles. They have a variable bright coloration, typically diurnal habit and are easily attracted to ripe fruits (Morón 1995) and flowers (Mawdsley *et al.* 2011; Puker *et al.* 2012) and are captured in baited-traps with fermented fruit (Mudge *et al.* 2012; Rodrigues *et al.* 2013; Touroult & Le Gall 2013; Puker *et al.* 2014). The larvae are predominantly saprophagous or sapro-xylophagous, and are found in the different locations such as soil organic matter, feces and rotten wood (Micó *et al.* 2000, 2008). Some American species are also found in termite (Luederwaldt 1911; Micó *et al.* 2001; Puker *et al.* 2012, 2013) and ant nests (Wheeler 1908; Cazier & Statham 1962; Cazier & Mortenson 1965; Alpert & Ritcher 1975; Ratcliffe 1976; Deloya 1988; Alpert 1994; Appendix S1).

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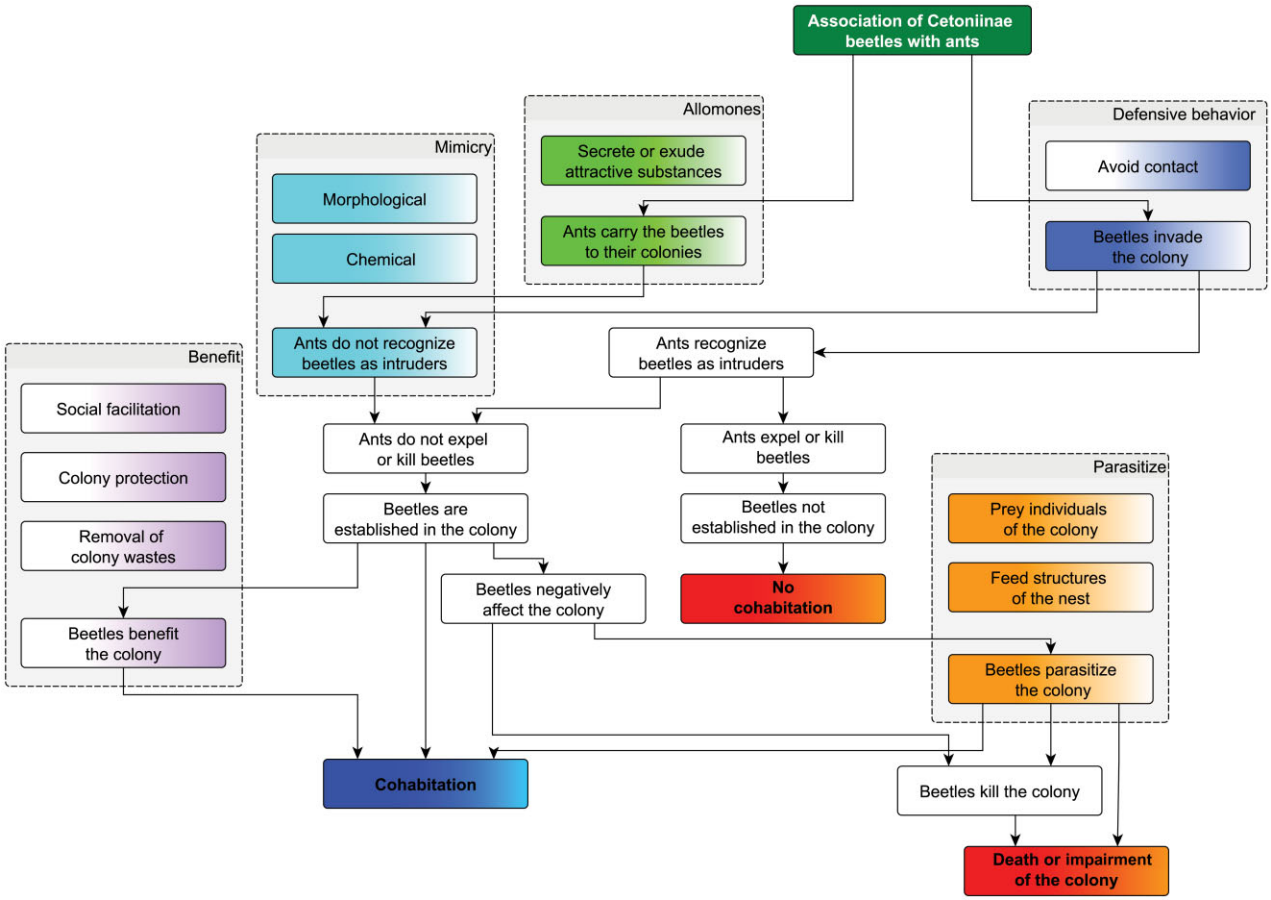

Figure 1 Flowchart summary of the hypotheses presented in the text with possible mechanisms to explain them.

Despite the numerous records of cohabitation, the relationship of Cetoniinae beetles with their ant hosts still remains unclear. In the tribe Cremastocheilini, for example, the presence of exocrine glands, thanatosis behavior when in contact with ants, strongly sclerotized integument, retractable antennae and hidden mouthparts represent possible adaptations for life in the ant nests (Alpert & Ritcher 1975; Alpert 1994; Mynhardt & Wenzel 2010; Mynhardt 2012). The nature of these interactions is mostly unknown but some hypotheses are formulated here to explain these associations (Fig. 1). A flowchart is presented suggesting the processes involving the entrance to the nests and the possible mechanisms that occupation causes, including: (i) death of the ant colony; (ii) death of beetles; and (iii) coexistence of Cetoniinae beetles and ants (Fig. 1).

PRELIMINARY DEFINITIONS

1 In this review we provide a list of American Cetoniinae beetles associated with ants (Appendix S1). For this, we used only papers published in journals and/or books (References in Appendix S1, Supporting Information). Since many of these relationships are species-specific, only data from ants and beetles identified to species level were included.

2 Given the generic and specific alterations that taxa of Cetoniinae beetles and ants have experienced over approximately 190 years since the registering of this association in America (Haldeman 1848; Scudder 1869; Horn 1871), we verified the taxonomic validity of the names of all taxa cited (Appendix S1) and used current nomenclature corresponding to the taxon mentioned in the original.

3 We use the term "symbiosis" *sensu* Goff (1982): organisms are considered in symbiosis when they live in close relationship, without any implication of reciprocal positive or negative influences. This relationship leads to a range of results that can be linked and measured directly in the fitness of its participants (Douglas 2008). Among the possible outcomes of these relationships are: (i) mutual benefit; (ii) benefit of only one of the participants, but not causing harm

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to the other; and (iii) harm to one of the participants at the expense of the other (Bronstein 2001).

4 We use the term "colony" to refer to the biological structure of ant individuals living together, and includes the queen(s), workers, larvae, pupae and eggs. This is intended to be distinct from the "nest", which refers to the physical structure built by ants.

5 We use the term "mimicry" *sensu* Robinson (1981): mimicry is a system that involves an organism (the mimic) simulating signal properties of another organism (the model) so that the two are confused by a third organism (the operator) and the mimic gains protection, food or a mating advantage as a consequence of the confusion.

LOCATION OF CETONIINAE BEETLES IN ANT NESTS

The internal part of the nest of social insects is composed of several compartments that present specific variations among groups (Hölldobler & Wilson 1990). In ant nests, besides the compartments inside where the colony, there are several galleries in which the workers and soldiers (when present) move in the nest (Hölldobler & Wilson 1990).

The location in the colony where cohabitation is established can be considered to indicate what beetles seek and the degree of interaction with the host species (Thomas *et al*. 2005), as well as identify the defensive force of the ants (Witte *et al*. 2008). Thus, different species may occupy different locations within the nest. The location of Cetoniinae beetles in the nest may also aid in identifying the degree of specificity and relatedness of the species (Alpert 1994). This kind of knowledge (location of the beetles inside the nest and their interaction with ants) is known for a few species of Cremastocheilini (Wheeler 1908; Cazier & Statham 1962; Cazier & Mortenson 1965; Alpert 1994) but remains unknown for the majority of Cetoniini and Gymnetini.

It is therefore possible that the location of cohabitants of ant nests may be linked to: (i) the benefit they seek in the nest; (ii) the degree of cohabitant interaction with individuals of the host species; and (iii) the force of the defensive response used by the ants. Therefore, field and lab experiments are needed to elucidate what kind of interaction occurs between individuals of myrmecophilous Cetoniinae and their host ants.

MECHANISMS USED BY MYRMECOPHILOUS CETONIINAE IN THE COHABITATION OF ANT NESTS

Ant colonies have a variety of strategies and defensive adaptations that vary among species (von Beeren *et al*. 2011). One of the most important strategies is the ability of workers and soldiers (when present) to chemically recognize individuals not belonging to the colony (see Akino 2008, and references therein). In most instances, intruders are attacked by the ants but myrmecophilous Cetoniinae somehow bypass the defense mechanisms of the colony. Although the exact mechanisms used by the beetles to enter the nest are unknown, three possible strategies explaining this phenomenon can be hypothesized (Fig. 1): (i) allomones; (ii) mimicry; and (iii) defensive behaviors.

Allomones

Allomones are chemical substances that benefit the producer, but have a neutral effect on the receptor (Brown Jr *et al*. 1970; Nordlund & Lewis 1976). Cazier and Mortenson (1965) proposed that species of *Cremastocheilus* Knoch secrete an attractive substance that could increase their chances of being detected by the ants, and led or guided into their nests. Once in the nests, the beetles may receive preferential treatment because of odors produced (Cazier & Mortenson 1965). Kloft *et al*. (1979) suggested that trichomes of *Cremastocheilus castaneus* Knoch provide food that is ingested by workers of *Formica integra* Nylander. Alpert (1994) repeated the experiment of Kloft *et al*. (1979) in similar conditions and refuted its conclusions. He found that *Cremastocheilus* do not secrete food *per se*, but substances that trigger, for example, attraction and/or grooming of the beetles by the ants.

Because numerous individuals of *Cremastocheilus* species have been observed being carried by worker ants into their nests (Schwarz 1889; Lugger 1891; Wheeler 1908; Cazier & Statham 1962), and based on the findings of Alpert (1994), it is plausible to believe that beetles secrete or exude these attractive substances only at some stage of their life (Fig. 1). Furthermore, the presence of the gland, and quantity and composition of the glandular secretion may vary between sexes and species of myrmecophilous Cetoniinae.

Although many male–female pairs of *Cremastocheilus* have been observed near ant nests (Wheeler 1908; Alpert & Ritcher 1975; Usnick 2000), mating usually occurs outside the nests (Lugger 1891; Liebeck 1899; Cazier & Mortenson 1965; Alpert 1994; Usnick 2000). Since dissection has not yet been performed on individuals carried by ants into their nests, we suggest that females might have mated previously. A fact that supports our suspicion is that females of *Cremastocheilus armatus* (Walker) found near ant nests laid fertilized eggs when transferred later to the lab (Alpert & Ritcher 1975). We suspect after mating females release an odoriferous substance attractive to the ants that leads to

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them being carried inside the nest. Once in there, females of *Cremastocheilus* continue exuding the odor that enables them to live peacefully with the host ants and seek the waste chamber to lay their eggs. However, it appears that the defense system of ants is overcome only when they are deceived by the beetles. This seems very likely because *Cremastocheilus* beetles possessing exocrine glands are barred at the entrance of the nest when trying to freely invade it. A fact that supports our suspicion is the defensive behavior triggered by the *Dorymyrmex pyramicus* (Roger) ants, which attack individuals of *Cremastocheilus mentalis* Cazier trying to enter the nest (Cazier 1961). This author observed eleven *D. pyramicus* ants attacking the beetles at the nest entrance while four or five ants continued attacking the beetle as it moved away from the nest.

Allomones possibly play a key role in the interaction between myrmecophilous Cetoniinae and ants for its entrance or permanence inside the nest (Fig. 1). If both sexes of beetles produce these chemicals independently of their development stage or whether there is a species-specific relationship between beetles and ants still needs to be investigated.

Mimicry

Although ants have the ability to recognize and attack individuals not belonging to the colony, myrmecophilous Cetoniinae are found within the nests. Our hypothesis suggests that they possess different mimicry strategies that enable entry and permanence in these places without being recognized as intruders (Fig. 1).

Since the ant nest is completely dark inside, morphological mimicry can not be very efficient, except for individuals that interact with ants outside the nest, implying that chemical mimicry may be an explanation for cohabitation among myrmecophilous Cetoniinae and ants (Fig. 1). In social insects, one of the key functions of cuticular hydrocarbons (CHCs) is to protect the animal against water loss and different proportions of CHCs are used to recognize the species, colony or caste (Singer 1998; Howard & Blomquist 2005), being detected by antennal contact (Blomquist & Bagnères 2010). Chemical mimicry of CHCs can be acquired either by contact with other individuals or by contact with the internal environment of the nest (Lenoir *et al.* 2001, 2009). If this transfer is effective, it is possible that myrmecophilous Cetoniinae acquire CHCs from the host species through contact with the inner wall of the ant nest. The entrance to the nest through non-patrolled locations may be a possible mechanism for the acquisition of chemical mimicry and consequent cohabitation.

The specificity of CHCs is high up to the colony level of the same ant species (Akino 2008), and even with this ability to recognize members of the colony, the ants are constantly found interacting with other insects (e.g. Rettenmeyer *et al.* 2011; von Beeren *et al.* 2011). In the case of Cetoniinae cohabiting the nests of social insects, it is known, for example, that adults of *Oplostomus fuligineus* (Olivier) and *Oplostomus haroldi* (Witte) invade bee nests in Africa. They enter the colonies and prey on the bee brood, as well as feed on the stored nectar and pollen (Fombong *et al.* 2013). Such an invasion does not necessarily trigger defensive behavior in the honey bees (Fombong *et al.* 2012), but the true responses of the honey bees needs to be better elucidated. Thus, chemical mimicry seems to be a plausible hypothesis to explain the invasion and permanence of myrmecophilous Cetoniinae within ant nests (Fig. 1).

In social insects morphological mimicry seems to be particularly common, with several records of mimetic individuals of different species living inside colonies of ants (e.g. Hölldobler & Wilson 1990; McIver & Stonedahl 1993). Some species of Cremastocheilini have a reddish color, which is called by some authors "myrmecophily color" (Wheeler 1908) but this can be hardly considered a case of mimicry. However, several species of rove beetles (Staphylinidae) associated with ants are not only similar morphologically but also in the sculpturing of the integument of the host ant (Akre & Rettenmeyer 1966; Kistner 1966). Besides CHCs, ants use tactile cues to recognize nestmates or aliens (Witte *et al.* 2008; Maruyama *et al.* 2009) but several arthropods including some beetles (Vander Meer & Wojcik 1982; Geiselhardt *et al.* 2007) might use mimic strategies to stay inside the nest unnoticed (Akino 2008). Because ants frequently attack or even kill recognized intruders of their colonies (Witte *et al.* 2008), ant-associated beetles are far more exposed to selection favoring their body shape or surface sculpture to imitate the host ant (Hölldobler & Wilson 1990). In this way, although myrmecophilous Cetoniinae not exhibiting recognized morphological traits to promote cohabitation with host ants and/or to obtain ant-like body shape mimicry with ants, this idea can not be discarded. It is possible that myrmecophilous Cetoniinae exhibit an ant-like surface sculpturing that allows them to enter and stay inside the nest unnoticed (Fig. 1).

Defensive behaviors

To minimize conflicts with ants, some species can also use avoidance strategies when in contact with ants (Fig. 1). Cetoniinae beetles have been observed burrowing rapidly in the mound surface (<1 minute) when attacked by their host ants (Alpert & Ritcher 1975). Avoidance strategies are known in other groups of beetles. For example, rove beetles (Staphylinidae) found

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in nests of the ant *Lasius fuliginosus* Latreille avoid contact with the ants (Stoeffler *et al*. 2011). These beetles do not produce attractive substances for the host species or possess chemical mimicry, but use avoidance strategies to remain unnoticed in the nest (Stoeffler *et al*. 2011).

To analyze the defensive behavior of myrmecophilous Cetoniinae, Alpert and Ritcher (1975) removed larvae of *C. armatus* from ant nests and placed them in containers with ants. When attacked by the ants, a dark liquid was released from the mouthparts of the larva. As the larva squirmed in an attempt to escape it also expelled moist fecal pellets. Both the mandibular liquid and anal secretions were observed to have a strong, unpleasant odor and a somewhat deterrent effect on the ants. In the same experiment, when adults of *C. armatus* were attacked by the ants, they immediately exhibit thanatosis (Alpert & Ritcher 1975). If the beetle was violently disturbed or captured by the ants, a drop of viscous fluid is released from the anal opening. This liquid, just like the one from the larvae, was also observed to have an offensive odor and to be effective in repelling the ants (Alpert & Ritcher 1975).

Thus, the myrmecophilous Cetoniinae that possess no mimicry or attractiveness (as appears to occur in Gymnetini) may take advantage of some strategies and mechanisms that enable its invasion and establishment inside the ant nest.

OUTCOMES OF ASSOCIATION BETWEEN MYRMECOPHILOUS CETONIINAE AND ITS HOST ANTS

Once established in ant nest, the presence of the Cetoniinae beetles can have different consequences to the ant colony (Fig. 1). Some mechanisms beneficial to the colony may be proposed to explain this process: (i) social facilitation; (ii) colony protection; or (iii) removal of colony wastes. On the other hand, the ants may not be able to remove them, which may also lead to coexistence of Cetoniinae in anthills, potentially increasing costs to the colony (e.g. feeding on individuals of the colony).

Potential benefits to ants

There is the possibility that an ant colony is able to recognize the intruder and yet not remove it from the nest. The presence of Cetoniinae in ant colonies may occur when the myrmecophilous species directly provides some benefit to the colony. This may be due to any character that allows the ant to recognize the beetle as a partner. According to the theory of natural selection, any heritable behavioral change that entails adaptive benefit to the colony tends to increase the frequency of species populations. These benefits can increase the survival of the colony and probably its fitness. We envision at least three possible benefits that the Cetoniinae beetles can offer ant colonies that host them (Fig. 1):

1 Social facilitation, which may be defined as standard behavior of a determined animal that is initiated or increased in rate and frequency by the presence or action of other animals (Zajonc 1965; DeSouza *et al*. 2001). Among social insects, studies on social facilitation have been conducted on, for example, ants (Lamon & Topoff 1985), termites (DeSouza *et al*. 2001) and wasps (Ruxton *et al*. 2001). Social facilitation appears to play a key role on the survival of the colony, because survival of the individuals is strongly affected by rates of contact and interactions between them (Lenz & Williams 1980; Lamon & Topoff 1985). If the Cetoniinae beetles manipulate the behavior of ants inside or outside the nest (as it appears) in a way that maintain the colony as cohesive, they may contribute to increasing the rates of interactions between them. Therefore, we can assume that the presence of myrmecophilous Cetoniinae in anthills can contribute to social facilitation.
2 Cetoniinae beetles can provide colony protection. For example, *Genuchinus ineptus* (Horn), which cohabits the nests of five ant species (Appendix S1), not only feeds on ant brood but also on a variety of other adult and immature insects (Alpert 1994). Ants are continuously attacked by a variety of animals, including vertebrates (Redford 1987) and invertebrates (Wilson 1971; Hölldobler & Wilson 1990). Thus, we argue that some myrmecophilous Cetoniinae found inside the nests can have a positive effect on the ant colony by eliminating potential competitors or predators of ants even when some workers are preyed on.
3 Larvae of myrmecophilous Cetoniinae are often found in ant refuse (Cazier & Mortenson 1965; Ratcliffe 1976; Alpert 1994). The aggressive behavior of ants against larvae of myrmecophilous Cetoniinae has been observed only in lab conditions (Alpert & Ritcher 1975) or when the nests of host ants are excavated in the field (Alpert 1994). What usually happens is that the larvae of myrmecophilous Cetoniinae coexist in harmony with its host ants and inhabit the waste chambers (Alpert 1994). Therefore, it is plausible to believe that the larvae of myrmecophilous Cetoniinae also manipulate the behavior of ants or that the ants obtain some benefit from the beetle larvae feeding on the wastes. Besides the cycling of this material, larvae of myrmecophilous Cetoniinae can feed on potential sources of pathogen inoculum, such as discarded dead ants.

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Potential costs to ants

Establishment of myrmecophilous species that ants are not able to remove from the nests may also result in a cost to the colony (Witte *et al*. 2008; von Beeren *et al*. 2011). This cost can be defined as parasitism when the beetles feed on structures of the nest or prey on individuals of the colony (Hölldobler & Wilson 1990). Parasitism of the colony by myrmecophilous beetles can make the nest more susceptible to the ingress of other intruders by weakening its physical structure and shifting energy from the colony in an attempt to remove the intruder. Weakening caused by an invader occurs in ants that are preyed upon by the invader (Foitzik *et al*. 2009).

Some myrmecophilous Cetoniinae are predators of ant broods (Horn 1871; Cazier & Mortenson 1965; Alpert & Ritcher 1975; Alpert 1994), but it is not yet known if adults of both sexes are predators, or if predation occurs before, during or after oviposition. Alpert (1994) observed the behavior of beetles in artificial nests and found that during predation ants immediately performed grooming of the predatory beetles. At this critical moment when the beetle is preying on the ant brood it also manipulates the behavior of its host, probably with release of an odor that causes them to become distracted (Alpert 1994).

After predation and oviposition (not necessarily in this order), the beetles may reduce the release of the substance that maintains their coexistence with, and/or distraction of, the ants, and they are then again recognized as intruders (Fig. 1). We suspect that this is likely to occur because Cazier and Mortenson (1965), when observing the behavior of *Cremastocheilus stathamae* Cazier in artificial nests of *Myrmecocystus mimicus* Wheeler, recorded moments of both indifference and hostile expulsion of the beetles from their nests. Wheeler (1908) placed two individuals of *C. castaneus* in a nest of *Formica integra* Nylander and noted that initially the beetles ignored by the ants exhibited defensive behaviors, such as thanatosis and retracting appendages. After a certain time they were violently attacked by the ants. We suspect that the beetles expelled are not only those that were carried into the nests, but also those that emerged within the nests. Our suspicion is because a single ant nest may harbor many adults of Cetoniinae, as is the case in the nests of *Myrmecocystus mexicanus* Wesmael where 57 adults (29 males and 28 females) of *Cremastocheilus stathamae* Cazier were encountered (Cazier & Mortenson 1965). Therefore, it is plausible to believe that these individuals, after emergence can be initially tolerated by the ants only until they start feeding on the ant brood. After this, the beetles may reduce the release of the odor that permitted their living in harmony with the ants, and are therefore detected and expelled.

If the ant–beetle interaction is not governed only by release of the odor, it may be also that the ants reject the beetles due to their density since the rates of contact with the intruder would increase, or when perceiving the damage suffered by the colony due to predation on the ant brood (Fig. 1). From an evolutionary standpoint this strategy of expelling from the nests after feeding may be interesting because it alleviates costs to leave the nest of the host ant and avoids mating between siblings in the case that this occurs in the nest.

In summary, although our empirical base is old (>20 years) we envision several hypotheses for the potential benefits and costs that the myrmecophilous Cetoniinae provide the host ant colonies, although these are difficult to measure. This reflects the need to deepen research in these areas.

DIVERSITY OF CETONIINAE ASSOCIATED WITH ANTS

Appendix S1 provides a summary of 52 species distributed in three tribes and eight genera of Cetoniinae beetles known to be associated with ant nests in the Americas. Cremastocheilini, with two genera and 31 species, is the tribe with the highest number of species associated with ant nests, followed by Cetoniini (one genus and 13 species) and Gymnetini (five genera and eight species) (Appendix S1).

Cremastocheilus, with 30 species reported (57.69% of the total), is the genus with the largest number of species that cohabit ant nests, followed by *Euphoria* Burmeister with 13 (25.00%) and *Cotinis* Burmeister with three species (5.77%) (Appendix S1).

Cremastocheilus armatus is the species that cohabits the nests of more ant species ($n = 13$), followed by *C. castaneus* ($n = 12$) and *C. crinitus* (LeConte) ($n = 11$) (Appendix S1).

Knowledge on the association of species of *Cremastocheilus* with ant colonies has been available for more than a century (Haldeman 1848; Scudder 1869; Horn 1871). Of the estimated 45 species in the genus (Mynhardt & Wenzel 2010) we record 30 associated with ants (Appendix S1), but believe that species in the genus are myrmecophilous. *Cremastocheilus* beetles use unrelated subfamilies of ant species as main host (Appendix S1). This suggests that speciation between myrmecophilous Cetoniinae and its host ant is not parallel. Phylogenetic studies involving both beetles and ants may generate information for understanding the evolutionary history within *Cremastocheilus* and their association with ants.

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The pronotum is home to most of the glands that enable interaction between the members of the tribe Cremastocheilini and their host ants (Kloft *et al*. 1979; Alpert 1994). Nevertheless, interactions of the members of Cetoniini and Gymnetini with ants are unknown. Because both adult and immature beetles in these tribes are not known to prey on the ants and are at times found in abandoned nests it is suspected the main benefit they gain from the association is the stable environment the nest provides.

DIVERSITY OF HOST ANTS

Appendix S1 provides a summary of the 73 ant species distributed in three subfamilies, nine tribes and 15 genera, known to be associated with American Cetoniinae beetles. Formicini with two genera and 35 species is the tribe with the highest number of records of the association with Cetoniinae beetles, followed by Myrmicini (two genera and nine species), Lasiini (two genera and eight species), Pheidolini (three genera and seven species), Attini (two genera and five species), Camponotini (one genus and five species), Crematogastrini (one genus and two species) and Leptomyrmecini and Tapinomini with one species each (Appendix S1).

Formica L. (Formicini), with 33 species (45.21% of the total), is the genus with the greatest number of ant species in which Cetoniinae beetles associations are recorded, followed by *Pogonomyrmex* Mayr (Myrmicini) with eight (10.96%), *Camponotus* Mayr (Camponotini) and *Myrmecocystus* Wesmael (Lasiini) with five species each (6.85%) (Appendix S1).

Formica obscuripes Forel is the ant species that shows the highest diversity of Cetoniinae beetles ($n = 14$), followed by *Pogonomyrmex barbatus* Smith ($n = 10$) and *Atta mexicana* (Smith) ($n = 9$) (Appendix S1). *Formica obscuripes* seems the most common host of American Cetoniinae beetles. This is probably due to the abundance of their nests, primarily in western North America (Alpert & Ritcher 1975), or to the sampling effort in the region. This species builds large nests made of sand mounds and vegetation (Fig. 2), containing around 50 000 individuals (King & Walters 1950). Due to the large nests (Fig. 2), a single ant colony may host numerous adult individuals of more than one species of Cetoniinae. For example, in a nest of *Formica schaufussi* Mayr, 24 adults of *Cremastocheilus canaliculatus* (Kirby) and *C. castaneus* (Wheeler) were encountered; and in a single nest of *Formica* sp., Ratcliffe (1976) found 60 larvae and 85 adults of *Euphoria hirtipes* (Horn). Characteristics of the nest of an unidentified species of *Formica* that hosts numerous Cetoniini and Cremastocheilini species are provided by Ratcliffe (1976). Because ants in this genus are normally considered aggressive the idea that semiochemicals (mainly allomones) may be involved in the ant–beetle interaction is reinforced (Fig. 1).

Figure 2 Large (about 1.0 m across at the base and 0.5 m height) nest built by *Formica obscuripes* Forel, which host the greatest number of Cetoniinae beetle species. Image ©Alex Wild 2002, used with permission.

Nests of the leaf cutter ant *A. mexicana* may provide a place of shelter and food for Cetoniinae beetles. Among these beetles, adults of *Cotinis mutabilis* (Gory & Percheron) have been observed arriving and entering in trash deposits (Deloya 1988). Adults and/or larvae of *Euphoria biguttata* (Gory & Percheron) were found about 20 cm deep in trash deposits of this ant species (Deloya 1988). Of the nine species of Cetoniinae that are associated with nests of *A. mexicana*, six belong to *Euphoria* (see Appendix S1). Adults of *Euphoria* have been observed feeding on a variety of plant tissues (e.g. flowers, pollen, nectar, sap, fruit, shoots, roots) and feces (e.g. cow, horses, human) (Ritcher 1945, 1958; Orozco 2012b). Their larvae are commonly found in decaying organic matter, cattle dung, trash deposits and the nests of rodents (Ritcher 1945, 1958; Micó *et al*. 2000). Although the nests of *A. mexicana* may reach large proportions and thus provide large volumes of waste that could potentially be exploited by Cetoniinae species, no symbiotic relationships have yet been. This is because Cetoniinae species colonizing the nests of these ants are also found on other substrates.

In summary, this review presents several hypotheses to explain the association of Cetoniinae beetles with ants (Fig. 1). However, knowledge of the morphology, and especially the ethology of myrmecophilous Cetoniinae, is still lacking and does not allow for a clear view and understanding of this relationship. Notably, knowledge

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on "myrmecophilous" Cetoniini and Gymnetini is very limited. It is necessary to further investigate the role of glandular trichomes on the interaction between Cremastocheilini (and some Cetoniini) and their host ants. There are several difficulties in conducting behavioral studies between ants and their ant-guests (see the review of Mynhardt 2013), especially in their natural habitat. However, greater efforts should be made in this area in order to elucidate the mechanisms of these interactions.

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SUPPORTING INFORMATION

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Appendix S1 Biodiversity of American species (per tribe) of Cetoniinae beetles (Coleoptera: Scarabaeidae) which are associated with ants (Hymenoptera: Formicidae). **Beetles:** 1 – Cetoniini; 2 – Cremastocheilini; and 3 – Gymnetini. **Ants:** 4 – Attini; 5 – Camponotini; 6 – Crematogastrini; 7 – Formicini; 8 – Lasiini; 9 – Leptomyrmecini; 10 – Myrmicini; 11 – Pheidolini; and 12 – Tapinomini.

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Beetle	Ant	Reference
(3)*Cotinis laticornis* Bates, 1889	(4)*Atta mexicana* (Smith, 1858)	Rojas (1989)
(3)*Cotinis mutabilis* (Gory & Percheron, 1833)	(4)*Atta mexicana* (Smith, 1858)	Deloya (1988); Deloya and Ratcliffe (1988); Rojas (1989)
(3)*Cotinis nitida* (L., 1758)	(4)*Atta texana* (Buckley, 1860)	Walter *et al*. (1938)
(2)*Cremastocheilus angularis* Leconte, 1857	(10)*Pogonomyrmex montanus* MacKay, 1980	MacKay (1983)
(2)*Cremastocheilus armatus* (Walker, 1866)	(11)*Aphaenogaster fulva* Roger, 1863	Alpert (1994)
	(11)*Aphaenogaster rudis* (Emery, 1895)	Schwarz (1889); Alpert (1994)
	(7)*Formica argentea* Wheeler, 1912	Mann (1911b); Alpert (1994)
	(7)*Formica fusca* (L., 1758)	Mann (1911a); Alpert and Ritcher (1975); Alpert (1994)
	(7)*Formica haemorrhoidalis* Emery, 1893	Alpert and Ritcher (1975); Alpert (1994)
	(7)*Formica integra* Nylander, 1856	Ritcher (1966)
	(7)*Formica integroides* Wheeler, 1913	Ayre (1958); Cazier and Statham (1962)
	(7)*Formica neorufibarbis* Emery, 1893	Alpert (1994)
	(7)*Formica obscuripes* Forel, 1886	Mann (1911a); Cazier and Statham (1962); Alpert and Ritcher (1975); Alpert (1994)
	(7)*Formica subnitens* Creighton, 1940	Ayre (1958); Alpert (1994)
	(7)*Formica subpolita* Mayr, 1886	Cazier and Statham (1962); Alpert (1994)
	(11)*Messor andrei* (Mayr, 1886)	Cazier and Statham (1962)
	(10)*Pogonomyrmex montanus* Mackay, 1980	Alpert (1994)
(2)*Cremastocheilus beameri* Cazier, 1940	(10)*Pogonomyrmex barbatus* Smith, 1858	Cazier (1961); Cazier and Statham (1962); Alpert (1994)

Appendix S1 continued

Beetle	Ant	Reference
[2]*Cremastocheilus canaliculatus* (Kirby, 1827)	[5]*Camponotus pennsylvanicus* (DeGeer, 1773)	Cazier and Statham (1962); Alpert (1994)
	[7]*Formica exsectoides* Forel, 1886	Wheeler (1908); Cazier and Statham (1962)
	[7]*Formica fusca* (L., 1758)	Hamilton (1888); Cazier and Statham (1962); Alpert (1994)
	[7]*Formica rubicunda* Emery, 1893	Wheeler (1908); Cazier and Statham (1962); Alpert (1994)
	[7]*Formica schaufussi* Mayr, 1866	Wheeler (1908); Cazier and Statham (1962); Alpert (1994)
	[7]*Formica subsericea* Say, 1836	Wheeler (1908); Alpert (1994)
	[7]*Polyergus breviceps* Wasmann, 1901	Cazier and Statham (1962)
[2]*Cremastocheilus castaneus* Knoch, 1801	[11]*Aphaenogaster fulva* Roger, 1863	Schwarz (1889); Wheeler (1908); Cazier and Statham (1962); Alpert (1994)
	[11]*Aphaenogaster rudis* (Emery, 1895)	Alpert (1994)
	[7]*Formica argentea* Wheeler, 1912	Wheeler (1908)
	[7]*Formica exsectoides* Forel, 1886	Wheeler (1908); Cazier and Statham (1962); Alpert (1994)
	[7]*Formica fusca* (L., 1758)	Wheeler (1908); Cazier and Statham (1962); Alpert (1994)
	[7]*Formica glacialis* Wheeler, 1908	Wheeler (1908); Alpert (1994)
	[7]*Formica integra* Nylander, 1856	Wheeler (1908); Kloft *et al*. (1979); Alpert (1994)
	[7]*Formica nitidiventris* Emery, 1893	Wheeler (1908); Alpert (1994)
	[7]*Formica obscuripes* Forel, 1886	Wheeler (1908)
	[7]*Formica schaufussi* Mayr, 1866	Wheeler (1908); Cazier and Statham (1962); Alpert (1994)
	[7]*Formica subsericea* Say, 1836	Wheeler (1908); Alpert (1994)
	[7]*Polyergus lucidus* Mayr, 1870	Wheeler (1908); Cazier and Statham (1962)
[2]*Cremastocheilus constricticollis* Cazier, 1940	[11]*Aphaenogaster cockerell*, André, 1893	Cazier and Mortenson (1965); Alpert (1994)
	[8]*Myrmecocystus depilis* Forel, 1901	Cazier and Mortenson (1965); Alpert (1994)
	[8]*Myrmecocystus mendax* Wheeler, 1908	Alpert (1994)
	[8]*Myrmecocystus mexicanus* Wesmael, 1838	Alpert (1994)
	[8]*Myrmecocystus mimicus* Wheeler, 1908	Cazier (1961); Cazier and Statham (1962); Alpert (1994)
	[10]*Pogonomyrmex barbatus* Smith, 1858	Cazier (1961); Cazier and Statham (1962); Alpert (1994)
[2]*Cremastocheilus crinitus* (LeConte, 1874)	[7]*Formica argentea* Wheeler, 1912	Mann (1911a); Alpert (1994)
	[7]*Formica fusca* (L., 1758)	Wheeler (1908); Alpert (1994)
	[7]*Formica gnava* Buckley, 1866	Wheeler (1908)

Appendix S1 continued

Beetle	Ant	Reference
	[7]*Formica manni* Wheeler, 1913	Mann (1911b); Alpert (1994)
	[7]*Formica neoclara* Emery, 1893	Alpert (1994)
	[7]*Formica neogagates* Viereck, 1903	Mann (1911a); Alpert (1994)
	[7]*Formica obscuripes* Forel, 1886	Alpert (1994)
	[7]*Formica rufibarbis* F., 1793	Cazier and Statham (1962)
	[7]*Formica subintegra* Wheeler, 1908	Alpert (1994)
	[7]*Formica xerophila* Smith, 1939	Alpert (1994)
	[11]*Pheidole californica* Mayr, 1870	Alpert (1994)
[2]*Cremastocheilus excavates* Cazier, 1940	[10]*Pogonomyrmex barbatus* Smith, 1858	Alpert (1994)
[2]*Cremastocheilus harrisi* (Kirby, 1827)	[7]*Formica fusca* (L., 1758)	Alpert (1994)
	[7]*Formica nitidiventris* Emery, 1893	Wickham (1900); Alpert (1994)
	[7]*Formica pallidefulva* Latreille, 1802	Wheeler (1908)
	[7]*Formica rubicunda* Emery, 1893	Wheeler (1908)
	[7]*Formica schaufussi* Mayr, 1866	Wheeler (1908); Cazier and Statham (1962); Alpert (1994)
	[7]*Formica subintegra* Wheeler, 1908	Wheeler (1908); Cazier and Statham (1962)
[2]*Cremastocheilus hirsutus* Van Dyke, 1918	[11]*Aphaenogaster cockerell*, André, 1893	Cazier and Mortenson (1965); Alpert (1994)
	[10]*Pogonomyrmex barbatus* Smith, 1858	Cazier and Mortenson (1965); Alpert (1994)
	[10]*Pogonomyrmex californicus* (Buckley, 1867)	Alpert (1994)
	[10]*Pogonomyrmex maricopa* Wheeler, 1914	Cazier and Mortenson (1965); Alpert (1994)
	[10]*Pogonomyrmex rugosus* Emery, 1895	Alpert (1994)
[2]*Cremastocheilus incisus* Casey, 1915	[7]*Formica ciliata* Mayr, 1886	Wheeler (1908); Alpert (1994)
[2]*Cremastocheilus knochii* LeConte, 1853	[7]*Formica obscuripes* Forel, 1886	Alpert (1994)
	[8]*Lasius alienus* (Foerster, 1850)	Alpert (1994)
	[8]*Lasius coloradensis* (Wheeler, 1917)	Alpert (1994)
	[8]*Lasius neoniger* Emery, 1893	Alpert (1994)
	[10]*Myrmica americana* Weber, 1939	Alpert (1994)

Appendix S1 continued

Beetle	Ant	Reference
	[10]*Pogonomyrmex occidentalis* (Cresson, 1865)	Wickham (1900); Alpert (1994)
[2]*Cremastocheilus lengi* Cazier, 1940	[11]*Aphaenogaster albisetosa* Mayr, 1886	Cazier and Mortenson (1965)
	[8]*Myrmecocystus depilis* Forel, 1901	Alpert (1994)
	[8]*Myrmecocystus mexicanus* Wesmael, 1838	Cazier and Mortenson (1965)
	[8]*Myrmecocystus mimicus* Wheeler, 1908	Cazier (1961); Cazier and Statham (1962)
	[11]*Pheidole desertorum* Wheeler, 1906	Alpert (1994)
[2]*Cremastocheilus mentalis* Cazier, 1940	[11]*Aphaenogaster albisetosa* Mayr, 1886	Cazier (1961); Cazier and Statham (1962); Cazier and Mortenson (1965); Alpert (1994)
	[9]*Dorymyrmex pyramicus* (Roger, 1863)	Cazier (1961); Cazier and Statham (1962); Cazier and Mortenson (1965); Alpert (1994)
	[10]*Pogonomyrmex barbatus* Smith, 1858	Cazier (1961); Cazier and Statham (1962); Cazier and Mortenson (1965); Alpert (1994)
	[10]*Pogonomyrmex maricopa* Wheeler, 1914	Cazier (1961); Cazier and Statham (1962); Cazier and Mortenson (1965); Alpert (1994)
[2]*Cremastocheilus mexicanus* Schaum, 1841	[7]*Formica gnava* Buckley, 1866	Wheeler (1908); Cazier and Statham (1962); Alpert (1994)
	[7]*Formica obscuripes* Forel, 1886	Wheeler (1908); Cazier and Statham (1962)
	[7]*Formica rufibarbis* F., 1793	Cazier and Statham (1962)
	[7]*Formica subcyanea* Wheeler, 1913	Mann (1914); Alpert (1994)
[2]*Cremastocheilus opaculus* Horn, 1894	[7]*Formica obscuripes* Forel, 1886	Cazier and Statham (1962)
	[7]*Formica rubiginosa* Latreille, 1802	Wheeler (1908)
[2]*Cremastocheilus planatus* LeConte, 1863	[5]*Camponotus maccooki* Forel, 1879	Cazier and Statham (1962)
	[5]*Camponotus semitestaceus* Snelling, 1970	Mann (1911a); Alpert (1994)
	[7]*Formica moki* Wheeler, 1906	Alpert (1994)
	[7]*Formica obscuripes* Forel, 1886	Cazier and Statham (1962); Alpert (1994)
	[7]*Formica rubiginosa* Latreille, 1802	Wheeler (1908)
	[7]*Formica rufibarbis* F., 1793	Cazier and Statham (1962)
	[10]*Pogonomyrmex barbatus* Smith, 1858	Smyth (1934); Alpert (1994)
[2]*Cremastocheilus planipes* Horn, 1885	[11]*Aphaenogaster albisetosa* Mayr, 1886	Alpert (1994)
	[11]*Aphaenogaster cockerell*, André, 1893	Cazier & Mortenson (1965); Alpert (1994)
	[7]*Formica obscuripes* Forel, 1886	Wheeler (1908); Cazier & Statham (1962); Alpert (1994)
	[7]*Formica rubiginosa* Latreille, 1802	Wheeler (1908)
	[8]*Myrmecocystus mimicus* Wheeler, 1908	Cazier and Mortenson (1965); Alpert (1994)

Appendix S1 continued

Beetle	Ant	Reference
	[10]*Pogonomyrmex barbatus* Smith, 1858	Cazier and Mortenson (1965); Alpert (1994)
	[10]*Pogonomyrmex maricopa* Wheeler, 1914	Cazier and Mortenson (1965); Alpert (1994)
[2]*Cremastocheilus pulverulentus* Cazier, 1940	[7]*Formica gnava* Buckley, 1866	Alpert (1994)
[2]*Cremastocheilus puncticollis* Cazier, 1940	[8]*Myrmecocystus mexicanus* Wesmael, 1838	Snelling (1970); Alpert (1994)
[2]*Cremastocheilus retractus* LeConte, 1874	[7]*Formica ciliata* Mayr, 1886	Cazier and Statham (1962)
	[7]*Formica gnava* Buckley, 1866	Wheeler (1908); Alpert (1994)
	[7]*Formica obscuripes* Forel, 1886	Paulsen (2002)
	[7]*Formica rufibarbis* F., 1793	Cazier and Statham (1962)
[2]*Cremastocheilus quadricollis* Casey, 1915	[10]*Pogonomyrmex barbatus* Smith, 1858	Alpert (1994)
[2]*Cremastocheilus saucius* LeConte, 1858	[10]*Pogonomyrmex occidentalis* (Cresson, 1865)	Wickham (1900); Cazier and Mortenson (1965); Alpert (1994); Usnick (2000)
[2]*Cremastocheilus schaumi* LeConte, 1853	[11]*Messor andrei* (Mayr, 1886)	Mann (1911a); Cazier and Statham (1962); Alpert (1994)
	[10]*Pogonomyrmex subnitidus* Emery, 1895	Horn (1871); Alpert (1994)
[2]*Cremastocheilus setosifrons* (Casey, 1915)	[10]*Pogonomyrmex barbatus* Smith, 1858	Alpert (1994)
[2]*Cremastocheilus spinifer* Horn, 1885	[11]*Pheidole desertorum* Wheeler, 1906	Wheeler (1908); Cazier and Statham (1962); Alpert (1994)
[2]*Cremastocheilus squamulosus* LeConte, 1858	[5]*Camponotus atriceps* (Smith, 1858)	Wheeler (1908); Cazier and Statham (1962); Alpert (1994)
	[5]*Camponotus floridanus* (Buckley, 1866)	Schwarz (1889); Wheeler (1908)
[2]*Cremastocheilus stathamae* Cazier, 1961	[11]*Aphaenogaster cockerell*, André, 1893	Cazier and Statham (1962); Alpert (1994)
	[8]*Myrmecocystus depilis* Forel, 1901	Alpert (1994)
	[8]*Myrmecocystus mexicanus* Wesmael, 1838	Cazier and Mortenson (1965); Alpert (1994)
	[8]*Myrmecocystus mimicus* Wheeler, 1908	Cazier and Statham (1962); Cazier and Mortenson (1965); Alpert (1994)
	[8]*Myrmecocystus navajo* Wheeler, 1908	Alpert (1994)
[2]*Cremastocheilus westwoodi* Horn, 1879	[10]*Pogonomyrmex subnitidus* Emery, 1895	MacKay (1983)
[2]*Cremastocheilus wheeleri* LeConte, 1876	[7]*Formica ciliata* Mayr, 1886	Wheeler (1908); Cazier and Statham (1962); Alpert (1994)
	[7]*Formica criniventris* Wheeler, 1912	Cazier and Statham (1962); Alpert (1994)
	[7]*Formica densiventris* Viereck, 1903	Alpert (1994)
	[7]*Formica exsectoides* Forel, 1886	Cazier and Statham (1962)
	[7]*Formica microgyna* Wheeler, 1903	Wheeler (1908); Cazier and Statham (1962); Alpert (1994)
	[7]*Formica obscuripes* Forel, 1886	Wheeler (1908); Cazier and Statham (1962); Alpert (1994); Paulsen (2002)
	[7]*Formica oreas* Wheeler, 1903	Wheeler (1908); Cazier and Statham (1962); Alpert (1994)
	[7]*Formica rufa* L., 1758	Wheeler (1908)

Appendix S1 continued

Beetle	Ant	Reference
[1]*Euphoria areata* (F., 1775)	[7]*Pogonomyrmex badius* (Latreille, 1802)	Orozco (2012)
[1]*Euphoria biguttata* (Gory & Percheron, 1833)	[4]*Atta mexicana* (Smith, 1858)	Hinton and Ancona (1935); Deloya (1988); Rojas (1989)
[1]*Euphoria canescens* (Gory & Percheron, 1833)	[4]*Atta mexicana* (Smith, 1858)	Deloya (1988); Orozco (2012)
[1]*Euphoria dimidiata* (Gory & Percheron, 1833)	[4]*Atta mexicana* (Smith, 1858)	Hinton and Ancona (1935); Deloya (1988); Orozco (2012)
[1]*Euphoria discicollis* Thomson, 1878	[4]*Atta texana* (Buckley, 1860)	Walter *et al*. (1938)
[1]*Euphoria hirtipes* (Horn, 1880)	[7]*Formica dakotensis* Emery, 1893	Ratcliffe (1976)
	[7]*Formica haemorrhoidalis* Emery, 1893	Ratcliffe (1976)
	[7]*Formica obscuripes* Forel, 1886	Wheeler (1908); Windsor (1964); Ratcliffe (1976)
[1]*Euphoria inda* (L., 1758)	[7]*Formica integra* Nylander, 1856	Wheeler (1908)
	[7]*Formica obscuripes* Forel, 1886	Lago *et al*. (1979); Paulsen (2002)
[1]*Euphoria leucographa* (Gory & Percheron, 1833)	[4]*Atta mexicana* (Smith, 1858)	Hinton and Ancona (1935); Deloya (1988); Rojas (1989)
[1]*Euphoria lurida* (F., 1775)	[4]*Acromyrmex subterraneus* Forel, 1893	Eidmann (1938)
[1]*Euphoria levinotata* Orozco, 2012	[10]*Pogonomyrmex barbatus* Smith, 1858	Orozco (2012)
[1]*Euphoria pilipennis* (Kraatz, 1883)	[7]*Formica obscuripes* Forel, 1886	Paulsen (2002)
[1]*Euphoria pulchella* (Gory & Percheron, 1833)	[4]*Atta mexicana* (Smith, 1858)	Hinton and Ancona (1935); Deloya (1988)
[1]*Euphoria subtomentosa* (Gory & Percheron, 1833)	[4]*Atta mexicana* (Smith, 1858)	Deloya (1988)
[2]*Genuchinus ineptus* (Horn, 1885)	[6]*Crematogaster californica* Wheeler, 1919	Cazier (1961); Cazier and Statham (1962)
	[6]*Crematogaster coarctata* Mayr, 1870	Cazier and Statham (1962); Cazier and Mortenson (1965); Krikken (1981)
	[7]*Formica obscuripes* Forel, 1886	Cazier and Statham (1962); Krikken (1981)
	[7]*Formica rubiginosa* Latreille, 1802	Wheeler (1908)
	[12]*Liometopum occidentale* (Emery, 1895)	Cazier and Statham (1962); Cazier and Mortenson (1965); Krikken (1981)
[3]*Gymnetis chalcipes* (Gory & Percheron, 1833)	[4]*Acromyrmex lobicornis* Emery, 1888	Bruch (1929)
	[4]*Acromyrmex lundii* (Guérin-Méneville, 1838)	Bruch (1929)
[3]*Gymnetis semiopaca* Moser, 1907	[4]*Acromyrmex lundii* (Guérin-Méneville, 1838)	Bruch (1929)
[3]*Hologymnetis cinerea* (Gory & Percheron, 1833)	[4]*Atta mexicana* (Smith, 1858)	Deloya (1988); Ratcliffe and Deloya (1992)
[3]*Marmarina tigrina* (Gory & Percheron, 1833)	[4]*Acromyrmex lobicornis* Emery, 1888	Bruch (1929)
	[4]*Acromyrmex lundii* (Guérin-Méneville, 1838)	Bruch (1929)
[3]*Neocorvicoana reticulata* Kirby, 1818	[4]*Acromyrmex lobicornis* Emery, 1888	Bruch (1929)
	[4]*Acromyrmex lundii* (Guérin-Méneville, 1838)	Bruch (1929)