

MYRMECOMORPHY AND MYRMECOPHILY IN SPIDERS:  
A REVIEW

PAULA E. CUSHING  
The College of Wooster  
Biology Department  
931 College Street  
Wooster, Ohio 44691

ABSTRACT

Myrmecomorphs are arthropods that have evolved a morphological resemblance to ants. Myrmecophiles are arthropods that live in or near ant nests and are considered true symbionts. The literature and natural history information about spider myrmecomorphs and myrmecophiles are reviewed. Myrmecomorphy in spiders is generally considered a type of Batesian mimicry in which spiders are gaining protection from predators through their resemblance to aggressive or unpalatable ants. Selection pressure from spider predators and eggsac parasites may trigger greater integration into ant colonies among myrmecophilic spiders.

Key Words: Araneae, symbiont, ant-mimicry, ant-associates

RESUMEN

Los mirmecomorfos son artrópodos que han evolucionado desarrollando una semejanza morfológica a las hormigas. Los Myrmecófilos son artrópodos que viven dentro o cerca de nidos de hormigas y se consideran verdaderos simbios. Ha sido evaluado la literatura e información de historia natural acerca de las arañas mirmecomorfas y mirmecófilas. El myrmecomorfismo en las arañas es generalmente considerado un tipo de mimetismo Batesiano en el cual las arañas están protegiéndose de sus depredadores a través de su semejanza con hormigas agresivas o no apetecibles. La presión de selección de los depredadores de arañas y de parásitos de su saco ovopositor pueden inducir una mayor integración de las arañas mirmecófilas hacia las colonias de hormigas.

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Myrmecomorphs and myrmecophiles are arthropods that have evolved some level of association with ants. Myrmecomorphs were originally referred to as myrmecoids by Donisthorpe (1927) and are defined as arthropods that mimic ants morphologically and/or behaviorally. The literature on myrmecomorphs is enormous and has recently been reviewed by McIver & Stonedahl (1993).

Myrmecophiles were defined by Donisthorpe (1927) as arthropods that live in or near ant nests. Wasmann (1894) developed a classification system for myrmecophiles consisting of distinct categories, each suggesting increasing specialization and integration into the host colony. However, as pointed out by Hölldobler & Wilson (1990), such categorization of myrmecophiles can be misleading as some guests take on multiple roles within a colony.

McIver & Stonedahl (1993) stated that myrmecomorphy and myrmecophily both fall under the general category of ant mimicry, since even myrmecophiles which lack morphological resemblance to ants may mimic chemical or textural characters of their hosts. However, myrmecophiles may not mimic their hosts in any way and may simply be tol-

erated by their otherwise aggressive hosts because they are either neutral in odor or are below some critical size to be recognized by the hosts as intruders (Cushing 1995a). Because of this and because the selective pressures involved in the evolution of myrmecomorphy and myrmecophily are quite different (discussed below), it is more useful to view these as separate phenomena and not as subcategories under ant mimicry.

The literature on myrmecomorphs and myrmecophiles in general has been summarized by McIver & Stonedahl (1993) and by Hölldobler & Wilson (1990). The purpose of the present paper is to expand coverage of myrmecomorphs and myrmecophiles in the Order Araneae.

#### MYRMECOMORPHY IN SPIDERS

Table 1 presents information about known spider myrmecomorphs. The putative ant models are those to which the mimics bear a generic or specific resemblance and which are sympatric with the mimics. In fact, the majority of the models presented are found in the same microhabitat as the mimics and are often collected with them. Details about the natural history of the mimics or about the form of their mimicry are also presented. As far as possible, the taxonomy of the spider myrmecomorphs follows that presented by Brignoli (1983) or Platnick (1993). The taxonomy of the models follows that presented by Bolton (1995).

#### Morphological and Behavioral Adaptations

The morphological adaptations involved in achieving a resemblance to ants among spider myrmecomorphs were first discussed by Banks (1892). Reiskind (1972, 1977) lists and illustrates these morphological adaptations and they are described in McIver & Stonedahl (1993). They include a variety of color and body-form modifications that give the spider the appearance of having three body segments instead of two and of having long, narrow legs instead of shorter, more robust legs. Mandibles, compound eyes and even stings are sometimes mimicked by the spiders through modifications in the chelicerae, pigmentation in the cuticle, or special positioning of the spinnerets. In many cases, the extent to which the mimics resemble a particular model is extraordinary (see Fig. 1). Reiskind (1977) compares specific features of the mimic with similar features in the model which enhance the many cases of species-specific mimicry found among spider myrmecomorphs.

The overall body of spider myrmecomorphs is much narrower than non-mimics, and this appears to reduce their fecundity. Female myrmecomorphs lay fewer eggs per eggsac than non-mimetic spiders of similar size (Bristowe 1939, 1941, Collart 1941, Edmunds 1978, Wanless 1978, Bradoo 1980, Boevé 1992). However, myrmecomorphs may compensate for this limitation by laying more eggsacs so that their life-time fecundity may be about equal to that of non-mimetic spiders.

McIver & Stonedahl (1993) list myrmecomorphs which show morphological, behavioral, or pattern mimicry. All spider myrmecomorphs are morphological mimics, and the majority are also behavioral mimics. Spider myrmecomorphs move in a much more erratic, more ant-like fashion than non-mimics. This behavior is described throughout the literature for most of the species of myrmecomorphs (Pocock 1908, Donisthorpe 1927, Bristowe 1941, Marson 1946, 1947, Reiskind 1972, 1977, Wanless 1978, Wing 1983, Brignoli 1984, Fowler 1984, Oliveira 1988, Lighton & Gillespie 1989, Boevé 1992). Behavioral mimicry also involves raising either the first or second pair of legs and using them to mimic the movements of antennae (Reiskind 1977, Jackson 1986). This functionally reduces the number of legs in the mimic from four

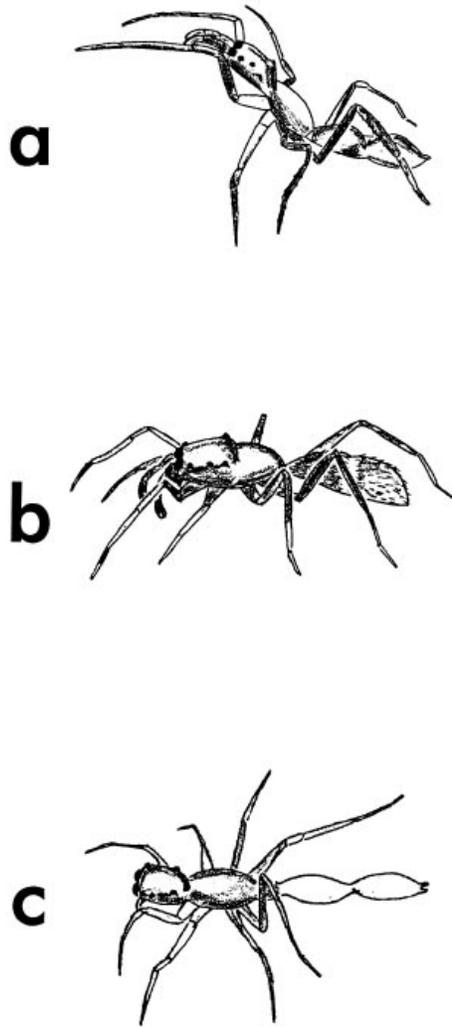


Fig. 1 (drawn from photographs in Reiskind 1977). a) A female *Zuniga magna* Peckham (Salticidae). Note how the front pair of legs is used as pseudo-antennae and how the abdominal constriction mimics the third body segment of the model. b) A female *Mymarachne parallela* (Fabricius) (Salticidae). Note the constriction of the cephalothorax and the lighter band of setae around the mid-section of the abdomen—both of which add to the illusion of additional body segments. The legs of this mimic have been effectively “shortened” through the lighter pigmentation of the terminal segments. The darkening of the metatarsal segments of the first pair of legs adds to the antennal mimicry as it gives the illusion that the pseudo-antennae are being held off the ground when, in fact, the legs are in contact with the substrate. c) A male *Synemosyna americana* (Peckham) (Salticidae). Note the constrictions of the cephalothorax and the abdomen. The color pattern of the spider also closely mimics the coloration of the model.

pairs to three. Sometimes the terminal segments of these mimetic antennae are darker giving the impression that the mimic has clubbed antennae (Reiskind 1977). Pocock (1908) suggests that behavioral mimicry may have evolved before morphological mimicry among spider myrmecomorphs. Bristowe (1941) agrees with this view.

#### Transformational and Polymorphic Mimicry

Spiders undergo gradual metamorphosis. During the earlier developmental stages (instars) only smaller ant species found in the vicinity would serve as appropriate potential models for young myrmecomorphic spiders. Because of this, it might be predicted that the suite of models would change as the spiders passed through each successive instar. A mimetic complex in which the identity of the model species changes as the mimic develops is called transformational mimicry (Mathew 1935) and has been documented for several species of myrmecomorphic spiders (see Table 1). In fact, McIver (1989) predicts that transformational mimicry "probably occurs in most systems where the ant-mimic develops through gradual metamorphosis." Wanless (1978) believes that transformational mimicry may occur in the majority of *Myrmarachne* myrmecomorphic species (Salticidae). In a study of transformational mimicry complexes among *Myrmarachne* spp., Edmunds (1978) demonstrated that the model species involved in each example of transformational mimicry were either positively associated with one another or tolerated each other's presence in the area. In other words, the set of models mimicked by each instar of the spider were always present in the same habitat.

In several species of myrmecomorphic spiders, the adults are polymorphic. It is thought that each morph mimics a different model. Such polymorphic mimicry appears to be fairly common among myrmecomorphic species (see Table 1). In some cases, there is sexual dimorphism among the adult spiders and the sexes each mimic a different model (Reiskind 1970, Cutler 1980, Wanless 1978, Oliveira 1988).

In all these cases of polymorphic mimicry each morph either corresponds to one model ant species that is also polymorphic or to two or more different model species. For example, light yellow or brown morphs of *Synemosyna aurantiaca* mimic *Pseudomyrmex flavidulus* (F. Smith) and *P. oculatus* (F. Smith) while black morphs mimic *P. gracilis* (Fabricius) and *P. sericeus* (Mayr) (Table 1 and Oliveira 1986). In these polymorphic mimicry systems, it is not known to what extent the different color forms of the mimic are sympatric nor to what extent the polymorphism is a result of differential predation. Predators could be eliminating the "wrong" color morph from an area where its model is absent creating an apparent geographic separation of the different morphs or the different color morphs could be genetically distinct.

#### Adaptive Significance of Myrmecomorphy

McIver & Stonedahl (1993) discuss the adaptive significance of myrmecomorphy in depth. Four different hypotheses have been proposed to explain myrmecomorphy: 1) Wasmannian mimicry, 2) Müllerian mimicry, 3) Aggressive, or Peckhamian mimicry, and 4) Batesian mimicry. In Müllerian mimicry, both the model and the mimic are unpalatable. As McIver and Stonedahl point out, the hypothesis that myrmecomorphs are Müllerian mimics is not well supported, especially for spider myrmecomorphs. Although the ant models may be unpalatable to most predators, there is no evidence that the spider mimics are unpalatable. Therefore, this hypothesis will not be discussed.

Wasmannian mimicry involves the evolution of resemblances between a model and its mimic that facilitates a mimic living with its host (Rettenmeyer 1970). Retten-

TABLE 1. MYRMECOMORPHIC ARANEAE TAXA. MODELS ARE THOSE ANTS WHICH EITHER SHARE A MORPHOLOGICAL RESEMBLANCE TO THE SPIDERS OR WHICH SHARE THE SAME HABITAT AS THE MIMIC.

Spider Mimic	Putative Ant Model	Notes on the Natural History of the Mimics	References
<b>APHANTOCHILIDAE</b>			
Aphantochilus sp.	Cephalotes sp. (probably atratus (L.))	preys on ants	Pocock 1908; Bristowe 1941
Aphantochilus rogersi O. Pickard-Cambridge	Cephalotes atratus (L.), Zacroptocerus pusillus (Klug)	preys on ants & carries dead ants (aggressive mimicry); polyphagous mimicry	Bristowe 1941; Oliveira & Sazima 1984; Oliveira 1986; Parker & Cloudsley-Thompson 1986
Bucranium sp.	Cephalotes sp. (probably atratus (L.))	preys on ants and carries dead ants (aggressive mimicry)	Bristowe 1941
Cryptoceroides cryptocerophagum Piza	Zacroptocerus pusillus (Klug)		Piza 1937; Reiskind 1972
<b>ARANEIDAE</b>			
Melycopharis cynips Simon			Pocock 1908
Micrathena sp.		only males and juveniles resemble ants; may be mimosis rather than mimicry	Reiskind 1977; Levi 1986
<b>CORINNIDAE</b>			
Castianeira cingulata (Koch)			Reiskind 1969
Castianeira cubana (Banks)	Camponotus planatus Roger		Myers & Salt 1926; Reiskind 1969
Castianeira dentata Chickering			Reiskind 1977
Castianeira dubia (O. Pickard-Cambridge)			Reiskind 1969; Reiskind 1977

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Spider Mimic	Putative Ant Model	Notes on the Natural History of the Mimics	References
Castianeira longipalpus (Hentz)	myrmicine or ponerine ant		Reiskind 1969
Castianeira memnonia (Koch)	Pachycondyla obscuricornis Emery		Reiskind 1977
Castianeira rica Reiskind	Atta sp., Odontomachus sp., etc.	transformational mimicry & poly-morphic mimicry	Reiskind 1969, 1970
Castianeira trilineata (Banks)	Camponotus castaneus (Latreille)		Reiskind 1969
Castianeira tenuiformis Simon	Pachycondyla obscuricornis Emery		Pocock 1908
Castianeira sp. (undesc.)	Camponotus parius Emery	preys on ants	Hingston 1928
Castianeira sp.	Camponotus sp., etc. (may mimic several different kinds of ants)	some prey on ants	Hingston 1928; Reiskind 1977
Corinna vertebrata Mello-Leitão	Acromyrmex fracticornis (Forel), Labidus praedator (F. Smith)	behavioral and morphological mimic; preys on ants (aggressive mimicry)	Fowler 1981, 1984
Mazax pax Reiskind	Ectatomma ruidum Roger		Reiskind 1977
Mazax spinosa (Simon)	Camponotus femoratus (Fabricius), Megalomymrux modestus Emery	polymorphic mimicry	Reiskind 1977
Myrmecium bifasciatum (Taczanowski)	Camponotus femoratus (Fabricius), Crematogaster limata F. Smith		Oliveira 1986
Myrmecium cf. gounellei Simon	Camponotus femoratus (Fabricius), Crematogaster limata F. Smith	transformational mimicry	Oliveira 1986
Myrmecium cf. velutinum Simon	Ectatomma lugens Emery		Oliveira 1986

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Myrmecium sp.	<i>Pachycondyla unidentata</i> Mayr		Oliveira 1986
Myrmecium spp.	<i>Anochetus</i> sp., <i>Atta</i> sp., <i>Dendromyrmex fabricii</i> (Roger) or <i>Megalomyrmex</i> sp.		Pocock 1908
<i>Myrmecotypus cubanus</i> Banks	<i>Camponotus planatus</i> Roger		Myers & Salt 1926
<i>Myrmecotypus fuliginosus</i> O. Pickard-Cambridge	<i>Camponotus planatus</i> Roger		Jackson & Drummond 1974
<i>Myrmecotypus pilosus</i> (O. Pickard-Cambridge)			Reiskind 1977
<i>Myrmecotypus rettenmeyeri</i> Unzicker	<i>Camponotus sericeiventris</i> (Guérin-Méneville)		Reiskind 1965, 1969; Lighton & Gillespie 1989
<i>Sphecotypus</i> (= <i>Myrmecium</i> ) <i>niger</i> (Perty)	<i>Pachycondyla villosa</i> (Fabricius)		Pocock 1908; Oliveira 1986
<b>DYSDERIDAE</b>			
<i>Harpactea hombergi</i> (Stopoli)	<i>Formica cunicularia</i> (= <i>fusca</i> var. <i>glebaria</i> ) Latreille, <i>F. fusca</i> L., <i>F. sanguinea</i> Latreille, <i>Lasius brunneus</i> (Latreille), <i>L. fuliginosus</i> (Latreille)	preys on ants; behavioral, not morphological, mimic	Domisthorpe 1927
<b>ERESIDAE</b>			
<i>Seothyra schreineri</i> Purcell	<i>Camponotus fulvopilosus</i> (De Geer)	male spiders mimic smaller castes	Pocock 1908

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<b>GNAPHOSIDAE</b>			
<i>Callilepis nocturna</i> (L.)	<i>Lasius niger</i> (L.)	preys on ants	Boevé 1992
<i>Micaria alpina</i> Koch		running near unident. models	Donisthorpe 1927; Bristowe 1941
<i>Micaria longipes</i> Emerton		mimic found running with various models	Banks 1892
<i>Micaria pulicaria</i> (Sundevall)	<i>Formica</i> spp., <i>Lasius niger</i> (L.), <i>Lasius</i> spp., and <i>Tetramorium caespitum</i> (L.)		Pocock 1908; Donisthorpe 1927; Bristowe 1941
<i>Micaria romana</i> Koch	<i>Formica fusca</i> L., <i>Formica rufibarbis</i> Fabricius		Pocock 1908; Donisthorpe 1927
<i>Micaria scintillans</i> O. Pickard-Cambridge	<i>Formica cunicularia</i> (=fusca var. <i>glebaria</i> ), <i>F. rufibarbis</i> Fabricius	mimic running with model	Donisthorpe 1927; Bristowe 1941
<i>Micaria</i> sp.	<i>Aphenogaster beccarii</i> Emery		Hingston 1928
<i>Micaria</i> sp.	<i>Pheidole indica</i> Mayr	only mimics smaller caste	Hingston 1928
<b>LINYPHIIDAE</b>			
<i>Linyphia furtiva</i> O. Pickard-Cambridge	<i>Formica sanguinea</i> Latreille	also mimics larvae of Hemipteran, <i>Alydus calcaratus</i> ; both found running w/ <i>F. sanguinea</i> workers	Donisthorpe 1927
<i>Meioneta beata</i> (=Micyrphantes beatus) (O. Pickard-Cambridge)	<i>Tapinoma erraticum</i> (Latreille)		Donisthorpe 1927
<b>LIOCERANIDAE</b>			
<i>Phrurolithus claripes</i> (Dönitz and Strand)	<i>Lasius niger</i> (L.)	may prey on ants	Komatsu 1961

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Phrurolithus festivus (Koch)	Formica fusca L., F. rufa L., F. sanguinea Latreille, Lasius flavus (Fabricius), L. fuliginosus (Latreille), L. niger (L.).	running with ants, preys on ants; may be myrmecophile*	Donisthorpe 1927, Bristowe 1941
Phrurolithus komurai Yaginuma	Formica fusca L., Myrmica scabrinodis Nylander, and Tapinoma erraticum (=nigerrima) (Latreille)	may also be a myrmecophile* running w/ants; preys on ants; may be myrmecophile*	Komatsu 1961 Donisthorpe 1927; Bristowe 1941
Phrurolithus minimus Koch			
Phruonellus sp.			Chamberlin 1925
<b>OONOPIIDAE</b>			
Opopaea (=Diblemma) donisthorpi (O. Pickard-Cambridge)	Wasmannia auropunctata (Roger)		Donisthorpe 1927
<b>SALTICIDAE</b>			
Belippo calcarata (Roewer)	Pheidole sp.		Roewer 1942; Wanless 1978
Belippo ibadan Wanless	Anochetus bequaerti Forel, Crematogaster depressa (Latreille), Pachycondyla (=Mesoponera) ambigua (Weber)		Wanless 1978
Bocus sp.	Polyrhachis sp.		Parker & Cloudsley-Thompson 1986
Consingis dakota Cutler	Leptothorax sp. & Myrmica americana Weber	transformational mimicry	Cutler 1970

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Consingis spp.			
Corcovella aemulatrix Galiano	Camponotus sp.	general mimic	Cutler 1970
Martella furva (Chickering)	Camponotus spp.		Galiano 1975
Martella spp.	Camponotus spp.		Reiskind 1977
Myrmarachne chapmani Banks			Galiano 1965
Myrmarachne collarti Roewer	Odontomachus troglodytes Santschi		Banks 1930
			Wanless 1978
Myrmarachne dundoensis Wanless	Camponotus sp.		Wanless 1978
Myrmarachne elongata Szombathy	Pheidole megacephala (Fabricius), Tetraponera anthracina (Santschi)	transformational mimicry	Edmunds 1978; Wanless 1978
Myrmarachne foenisex Simon	Crematogaster castanea F. Smith, Oecophylla longinoda (Latreille)	transformational & polymorphic mimic; tends coccids and imbibes their exudate (also feeds on coccids); may be myrmecophile*	Collart 1929a, 1929b, 1941; Edmunds 1978; Wanless 1978,
Myrmarachne foreli Lessert	Tetraponera natalensis (F. Smith)		Wanless 1978
Myrmarachne formicaria (De Geer)	Formica cunicularia (=fusca var. rubescens) Latreille, m F. rufa L., F. rufibarbis Fabricius, Myrmica rubra (=laevinodis) (L.), M. scabrinodis Nylander	transformational mimic	Pocock 1908; Donisthorpe 1927; Bristowe 1941; Galiano 1969a
Myrmarachne inermichelis Bösenberg & Strand			Komatsu 1961

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Myrmarachne inflatipalpis Wanless	Crematogaster sp.		Wanless 1978
Myrmarachne insulana Roewer	Tetramorium sp.		Wanless 1978
Myrmarachne kiboschensis Lessert	may mimic Camponotus vestitus (F. Smith), Odontomachus troglodytes Santschi		Wanless 1978
Myrmarachne legon Wanless	Acantholepis sp., Camponotus acvapimensis Mayr & Crematogaster sp.	transformational mimicry	Edmunds 1978; Wanless 1978
Myrmarachne marshalli Peckham & Peckham	Camponotus spp.		Wanless 1978
Myrmarachne nigeriensis Wanless	Camponotus sp.		Wanless 1978
Myrmarachne parallela (Fabricius)	Pachycondyla spp.		Reiskind 1977
Myrmarachne plataleoides (O. Pickard-Cambridge)	Anoplolepis gracilipes (=Plagiopis longipes) (F. Smith), Oecophylla longinoda (Latreille), O. smaragdina (Fabricius), Plagiopis sp., Prenolepis sp., Solenopsis geminata (Fabricius), Solenopsis sp.	transformational mimicry	Bhattacharya 1939; Marson 1946, 1947; Mathew 1934, 1954; Edmunds 1978; Wanless 1978
Myrmarachne platypalpus Bradoo	Camponotus sp.		Bradoo 1980
Myrmarachne providens (Peckham)	Tetraponera (=Sima) rufonigra (Jerdon)		Pocock 1908

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Myrmarachne richardsi Wanless			Wanless 1978
Myrmarachne transversa (Mukerjee)	Diacamma vagans (Smith), Camponotus sericeus (Fabricius)		Mukerjee 1930
Myrmarachne uvira Wanless	Camponotus flavomarginatus Mayr; C. sericeus (Fabricius)		Edmunds 1978; Wanless 1978
Myrmarachne spp.	Camponotus compressus (Fabricius); Oecophylla sp., Paratrechina (=Prenolepis) longicornis (Latreille), Pheidole indica Mayr; Polyrachis lacteipennis (=simplex) Smith	some may prey on ants	Hingston 1928
Paradamoetas cara (Peckham & Peckham)	Zacryptocerus sp.	found on Acacia trees w/ Pseudomyrmex ferrugineus (F. Smith)	Cutler 1981
Peckhamia picata (Hentz)	Camponotus sp.		Pocock 1908
Sarinda camba Galiano	Camponotus sp.		Galiano 1969b
Sarinda imitans Galiano	Camponotus sp.		Galiano 1967
Sarinda linda Reiskind	Camponotus planatus Roger		Jackson & Drummond 1974
Sarinda marcosi Toledo-Piza	Camponotus sp.		Galiano 1965
Synageles occidentalis Cutler			Cutler 1991
Synageles venator (Lucas)	Lasius niger (L.), Myrmica scabrinodis Nylander		Donisthorpe 1927; Bristowe 1941; Engelhardt 1970

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<i>Synemosyna americana</i> (Peckham & Peckham)	<i>Pseudomyrmex boopis</i> (Roger), <i>Pseudomyrmex</i> spp.	polymorphic mimicry	Reiskind 1977; Cutler 1985
<i>Synemosyna aurantiaca</i> (Mello-Leitão)	<i>Pseudomyrmex flavivicius</i> (F. Smith), <i>P. gracilis</i> (Fabricius), <i>P. ocellatus</i> (Fr. Smith), <i>P. phyllophilus</i> (F. Smith), & <i>P. sericeus</i> (Mayr)	polymorphic mimicry	Galiano 1965; Oliveira 1986
<i>Synemosyna decipiens</i> (O. Pickard-Cambridge)	<i>Pseudomyrmex</i> sp.	polymorphic mimicry	Cutler 1985
<i>Synemosyna edwardsi</i> Cutler	<i>Crematogaster</i> sp.		Cutler 1985
<i>Synemosyna formica</i> Hentz	<i>Camponotus</i> sp., <i>Formica</i> sp., & <i>Myrmica</i> sp.		Cutler 1985
<i>Synemosyna smithi</i> Peckham	<i>Pseudomyrmex cubaensis</i> (Forel), <i>P. pazosi</i> (Santschi)	polymorphic mimicry	Myers & Salt 1926; Galiano 1965
<i>Synemosyna</i> sp. (undesc.)	<i>Pseudomyrmex gracilis</i> (=mexicanus) (Fabricius)		Reiskind 1977
<i>Synemosyna</i> spp.	<i>Pseudomyrmex</i> spp.		Pocock 1908; Cutler 1985; Oliveira 1986
<i>Tuttilina</i> cf. <i>similis</i> (Banks)	<i>Camponotus</i> sp.	preys on ants; one mimic found w/ two dead workers of <i>Pogonomyrmex occidentalis</i> (Cresson)	Wing 1983
<i>Uluella formosa</i> Chickering <i>Zuniga laeta</i> (Peckham)	<i>Camponotus femoratus</i> (Fabricius)		Reiskind 1977 Oliveira 1986

TABLE 1. (CONTINUED) MYRMECOMORPHIC ARANEAE TAXA. MODELS ARE THOSE ANTS WHICH EITHER SHARE A MORPHOLOGICAL RESEMBLANCE TO THE SPIDERS OR WHICH SHARE THE SAME HABITAT AS THE MIMIC.

Spider Mimic	Putative Ant Model	Notes on the Natural History of the Mimics	References
Zuniga magna Peckham	Camponotus crassus Mayr; Camponotus spp.; Pachycondyla villosa (Fabricius), Pseudomyrmex gracilis (Fabricius), Pseudomyrmex spp.	transformational mimicry	Reiskind 1977; Oliveira 1986
<b>THERIDIIDAE</b>			
Anatea formicaria Berland	Lordomyrma sp., Monomorium (=Chelaner) croceiventre Emery, Monomorium sp., Pheidole sp., or Tetramorium (=Xiphomyrmex) tenuicrine (Emery)	males only; females are not known	Berland 1927; Reiskind & Levi 1967; Reiskind 1972; Levi 1986
Ceroecida strigosa Simon			Reiskind & Levi 1967
Coleosoma floridanum Banks		males only; females stay on web and are not ant-like	Reiskind & Levi 1967; Levi 1986
Helvibis brasiliana (Keyserling)			Reiskind & Levi 1967
Helvibis chilensis (Keyserling)			Reiskind & Levi 1967
Heleosoma floridanum Banks		males only	Reiskind & Levi 1967
<b>THOMISIDAE</b>			
Amyciaea forticeps O. Pickard-Cambridge	Oecophylla smaragdina (Fabricius)	preys on ants; uses behavioral mimicry to attract and kill ants (aggressive mimicry)	Shelford 1902; Hingston 1928
Amyciaea lineatipes O. Pickard-Cambridge	Oecophylla smaragdina (Fabricius)		Pocock 1908

TABLE 1. (CONTINUED) MYRMECOMORPHIC ARANEAE TAXA. MODELS ARE THOSE ANTS WHICH EITHER SHARE A MORPHOLOGICAL RESEMBLANCE TO THE SPIDERS OR WHICH SHARE THE SAME HABITAT AS THE MIMIC.

Spider Mimic	Putative Ant Model	Notes on the Natural History of the Mimics	References
Amyciaea spp.	Oecophylla spp.	only found in company w/ models	Brignoli 1984
Strophius nigricans	Camponotus crassus	preys on ants & carries dead ants (aggressive mimicry)	Oliveira & Sazima 1985
<b>ZODARIIDAE</b>			
Storena spp.	Iridomyrmex purpureus (F. Smith)	three different spp. mimic three morphs of model I. purpureus sensu strict., I. purpureus var viridioneus Viehmeyer, and undesc. var.)	Greenblade & Halliday 1983
Zodarion gallicum (Canestrini)	Messor barbarus (L.)	preys on ants	Boevé 1992
Zodarion sp.		preys on ants	Hingston 1928

\* see Table 2

meyer considers the relationship between the model and mimic to be either exploitative on the part of the mimic or beneficial to both the model and the mimic. As Wasmannian mimics are, by definition, myrmecophiles, they will be discussed in the section on spider myrmecophiles.

At least some spider myrmecomorphs are clearly aggressive, or Peckhamian mimics (Table 1 and McIver & Stonedahl 1993). Aggressive mimicry complexes involve a predator mimicking its prey (Wickler 1968). In such a system, the prey species acts as both model and operator (in the terminology of Vane-Wright 1980), or as both model and selective agent. The aggressive mimics often use both morphological resemblance as well as behavioral tactics to attract and prey on the models. For example, the thomisid, *Amyciaea forticeps* O.P.-Cambridge, assumes the alarm attitude of its model (abdomen and "antennae" raised). This apparently attracts workers of the model, *Oecophylla* sp. (which have good eyesight). When an ant approaches, the spider attacks it (Table 1, Hingston 1927, Bristowe 1941). The aphantochilid, *Bucranium* sp. carries dead ants of the genus *Cephalotes* aloft, perhaps as a mimetic device (chemical mimicry?) to attract other ants (Table 1, Bristowe 1941). This same strategy is used by *Aphantochilus rogersi* O.P.-Cambridge (Table 1, Oliveira & Sazima 1984). Oliveira & Sazima (1984) suggest that "close similarity of integument texture (granular) and pilosity of body and legs (sparse hairs) apparently facilitates the obligatory intimate contact *A. rogersi* must make with cephalotines in order to capture an ant among other ants." The models may, therefore, exert selective pressure for more perfect mimicry in their own predators.

However, not all myrmecomorphs that prey on their models are aggressive mimics. In order for the spider to be considered an aggressive mimic, the model must be the operator, or selective agent. This is unlikely for models which have poor eyesight (the majority of ants) or which do not approach or investigate the spider. Table 1 lists as aggressive mimics only those spiders that lure their prey to them using a behavioral strategy and/or a behavioral strategy combined with morphological similarity.

Most myrmecomorphic spiders are probably Batesian mimics (Pocock 1908, Bristowe 1941, Marson 1947, Reiskind 1977, Edmunds 1978, Wanless 1978, Parker 1984, Oliveira & Sazima 1984, Oliveira 1986, Parker & Cloudsley-Thompson 1986, Cutler 1991, McIver & Stonedahl 1993). Ants are generally considered to be distasteful, noxious, or unpalatable to vertebrate and invertebrate predators. Many species are particularly aggressive and will mob predators that attack individual ants (Hölldobler & Wilson 1990). Others have particularly potent bites or stings or a hard cuticle with spines making them less appealing prey for most vertebrate and invertebrate predators. Myrmecomorphic spiders would, therefore, gain protection against generalist arthropod predators.

However, it has been suggested that myrmecomorphy in spiders is not an example of Batesian mimicry since there are so many predators that do specialize on ants (Brignoli 1984). The myrmecomorph would be trading one set of predators for another. Instead, Brignoli (1986) proposed that myrmecomorphy allows the spider "to live in many different habitats from which most other species, which ants perceive as different from themselves, are excluded." Certainly, specialized ant predators exist. Certain species of Crabronid wasps stock their nests with ants (Pocock 1908, Bristowe 1941). Species of wasps in the genus *Tracheliodes* are also ant specialists (Krombein 1967). Some spiders are specialist ant predators (Hölldobler 1971, MacKay 1982, Porter & Eastmond 1982). McIver & Stonedahl (1993) cite additional examples of vertebrate and invertebrate ant predators.

Nevertheless, Edmunds (1978) points out that myrmecomorphy in spiders probably provides protection, despite the existence of specialized ant predators, since spiders respond much differently to disturbance (including attack by an ant predator)

than the models. Ants, when disturbed, tend to respond aggressively to the threat, whereas spiders tend to dodge the threat, hiding beneath a leaf or in a crevice, or dropping on a drag line. It has been noted that spider myrmecomorphs, which are also behavioral mimics, abandon their ant-like gait when disturbed (Emerton 1911, Marson 1947, Fowler 1984, Brignoli 1984). This sudden, unexpected change in the behavior of the spider would most likely facilitate its escape from an ant predator. Marson (1947) points out that living in close proximity to their models (often in the midst of foraging ants), as do many spider myrmecomorphs, also reduces the risk of predation, even by ant predators, simply because the likelihood of an ant predator preying on a less common mimic than one of the more common models is slim.

Important agents selecting for myrmecomorphy in spiders are probably spider predators such as sphecid or pompilid wasps (Pocock 1908, Bristowe 1941, Edmunds 1978, Wanless 1978, Parker & Cloudsley-Thompson 1986). These predators might not recognize myrmecomorphic spiders as potential prey. However, it has been reported that some wasps, such as *Trypoxylon placidum* Cameron, *Pison* sp., and an unidentified sphecid wasp, had myrmecomorphic spiders of the genus *Myrmarachne* in their nest cells (Richards 1947, Edmunds 1978). However, these may be isolated instances of individual wasps that have learned to differentiate *Myrmarachne* mimics from their models. It is generally uncommon to find myrmecomorphic spiders in the nest cells of spider hunting wasps (Bristowe 1941).

Indirect support for the hypothesis that myrmecomorphs are Batesian mimics lies in the fact that, in general, myrmecomorphic spiders mimic either the dominant ants in a habitat or aggressive, well protected ants (Edmunds 1978). Edmunds (1978) further points out that transformational and polymorphic mimicry provide indirect support for the hypothesis that myrmecomorphy in spiders evolved as an anti-predator strategy. "Evidence for the strength of predator selection in perfecting the resemblance between mimic and model is the infrequency of finding a *Myrmarachne* with the 'wrong' species of ant, and the occurrence of different color morphs of mimic wherever the model has a different colour" (Edmunds 1978).

Direct experimental studies in which arthropod predators have been presented with choices between myrmecomorphic and non-mimetic prey also support the hypothesis that myrmecomorphs are Batesian mimics (Oliveira 1985, McIver 1987, McIver 1989, and Cutler 1991). The results of these experimental studies are summarized in McIver & Stonedahl (1993). In general, the predators avoid the myrmecomorphs and the models while preying readily on the non-mimetic species, and they treat the mimic as if it were an ant.

#### MYRMECOPHILY IN SPIDERS

Table 2 presents information about known spider myrmecophiles. Included in this table are those spiders that have either occasionally or exclusively been found in or just outside ant nests. Hölldobler & Wilson (1990), in their review of myrmecophiles, included as myrmecophiles spiders that were specialized ant predators such as *Steatoda fulva* (Keyserling) (Theridiidae) (Hölldobler 1971), *Euryopsis coki* Levi (Theridiidae) (Porter & Eastmond 1982), and *Latrodectus hesperus* Chamberlin & Ivie (MacKay 1982). Although these spiders have evolved specialized hunting strategies for capturing ants, they probably do not feed exclusively on ants and are only occasionally or never found inside ant nests. Therefore, they are omitted from Table 2. A few other spider genera listed as myrmecophiles in Hölldobler & Wilson (1990) are more accurately described as myrmecomorphs and are included, instead, in Table 1.

The ants with which the myrmecophilic spiders are associated are also listed in Table 2, as is information about the natural history of the spiders. Very little informa-

tion is known about spider myrmecophiles. Only a very few studies have investigated aspects of the spider-ant associations in any depth (Shepard & Gibson 1972, Noonan 1982, Porter 1985, Cushing 1995a, 1995b). Much more work must be done to determine how the spiders become integrated into the host colonies, how the ants react to these guests, what adaptations enable the spiders to live inside the nests, and to what extent the spider affects the life of the host colony.

#### General Information about Myrmecophily

Many arthropods have evolved symbiotic relationships with ants. Some are found at the periphery of the nest, either near the entrances or on refuse piles; others are found within the chambers of the nest, either in the peripheral chambers or deeper in the nest in the brood and storage chambers (Hölldobler 1977, Hölldobler & Wilson 1990). They range from tiny collembolans to beetles and caterpillars many times the size of their hosts. These myrmecophiles have evolved various adaptations enabling them to exist in this hostile environment. Many of the myrmecophiles acquire cuticular hydrocarbons similar or identical to those of their hosts (Vander Meer & Wojcik 1982, Vander Meer et al. 1989). This allows them to become integrated with hosts that are otherwise hostile to intruders with foreign, non-colony odors. Others, such as some staphylinid beetles and lycaenid caterpillars, have evolved specialized glands that produce appeasement substances (reviewed in Hölldobler & Wilson 1990).

In many myrmecophiles, the evolution of a symbiotic association can be intimated through an examination of extant species that show varying degrees of behavioral integration (Hölldobler & Wilson 1990). For example, Akre & Rettenmeyer (1966) described species of staphylinid beetles that show varying degrees of association with army ants. Some species live only around the edges of the bivouacs or in the refuse piles but are not otherwise integrated into the colonies, others are found running along the edges and sometimes within the emigration columns of ants, and yet others are found directly in the midst of ants in the center of the emigration colonies. Some species even hitch rides on the booty or the brood carried by ants. Certain staphylinid species can only live within a narrow range of conditions found within colonies and die shortly after removal from the colonies.

If each stage in this process of gradual integration into colonies is correlated with the evolutionary history of the lineages, then the various adaptations of the myrmecophiles leading to greater integration could be viewed as characters on the phylogenetic tree (Brooks & McLennan 1991). Kistner (1979) takes this idea a step further by superimposing the phylogenies of termites in the family Rhinotermitidae with their associated termitophiles in the family Staphylinidae to illustrate the evolution of host specificity.

#### Adaptations of Myrmecophilic Spiders

Myrmecophilic spiders are unique because their close relatives apparently have no preadaptations to a symbiotic lifestyle. Most spiders are solitary predators and symbiosis with other arthropod groups should be rare; yet myrmecophilic spiders are found in at least 12 different families (Table 2). Some of these species may be only occasional visitors into ant colonies, using the entrance and upper chambers as temporary refuges (see Table 2). However, some appear to be commensals that have become more dependent on the conditions present within the nest and spend their entire lives within this complex ecosystem.

*Masoncus pogonophilus* Cushing (Linyphiidae) is the best known example of the latter group of spider myrmecophiles (Porter 1985, Cushing 1995a, 1995b). This spi-

TABLE 2. MYRMECOPHILIC ARANEAE TAXA. THESE ANT GUESTS HAVE BEEN COLLECTED EITHER OCCASIONALLY OR EXCLUSIVELY INSIDE THE COLONIES OF THE HOSTS.

Spider Guest	Ant Host	Notes on the Natural History of the Guests	References
<b>CORINNIDAE</b>			
<i>Corinna bacalcarata</i> (Simon)	<i>Pogonomyrmex</i> sp.	collected from inside the nests and from the surface of mounds in California & New Mexico	Fowler 1984
* <i>Corinna vertebrata</i> Mello-Leitão	<i>Acromyrmex fracticornis</i> (Förel)	associated with nest turrets; seen in foraging columns; preys on ants	Fowler 1984
<b>CTENIZIDAE</b>			
<i>Bothriocyrtum</i> sp.	<i>Atta texana</i> (Buckley)	collected inside fungus garden	Walter et al. 1938; Waller and Moser 1990
<b>DICTYNIDAE</b>			
<i>Circurina robusta</i> Simon	<i>Atta texana</i> (Buckley)	collected inside detritus chambers	Walter et al. 1938; Waller and Moser 1990
<i>Mastigusa</i> (= <i>Tetrilus</i> ) <i>arietina</i> (Thorell)	<i>Formica rufa</i> L., <i>L. asiaticus brunneus</i> (Latreille), <i>L. fuliginosus</i> (Latreille), <i>L. umbratus</i> (Nylander)	females fasten egg-sacs to walls of nest cells and galleries; collected both outside and inside nests	Donisthorpe 1908, 1927
<b>DYSDERIDAE</b>			
<i>Harpactea hombergi</i> (Scopoli)	<i>Formica cunicularia</i> (= <i>fusca</i> var. <i>glebaria</i> ) Latreille, <i>F. fusca</i> L., <i>L. asiaticus brunneus</i> (Latreille), <i>L. fuliginosus</i> (Latreille)	collected near and in nests; feeds on ants; behavioral mimic; only occasional guest	Donisthorpe 1927

TABLE 2. (CONTINUED) MYRMECOPHILIC ARANEAE TAXA. THESE ANT GUESTS HAVE BEEN COLLECTED EITHER OCCASIONALLY OR EXCLUSIVELY INSIDE THE COLONIES OF THE HOSTS.

Spider Guest	Ant Host	Notes on the Natural History of the Guests	References
<b>GNAPHOSIDAE</b>			
<i>Cesonia bilineata</i> (Hentz)	<i>Atta texana</i> (Buckley)	collected from fungus garden inside nests	Walter et al. 1938; Waller and Moser 1990
<i>Eilica puno</i> Platnick & Shadab	<i>Camponotus inca</i> Emery	adults found only inside nests; when rocks covering nests were removed, hosts transported spider eggsacs inside nests; spiderlings seen to enter nests	Noonan 1982
<i>Micaria pullicaria</i> Sundevall		found inside nests	Bristowe 1941
<b>LINYPHIIDAE</b>			
<i>Acartauchenius scurrilis</i> (O. Pickard-Cambridge)	<i>Formica rufa</i> L., <i>Lasius flavus</i> (Fabricius), <i>Tetramorium caespitum</i> (L.)	found in nest galleries moving around with ants	Donisthorpe 1908, 1927
<i>Cochlembolus formicarius</i> Dondale & Redner	<i>Formica obscuripes</i> Forel	collected inside nests	Dondale & Redner 1972
<i>Evansia merens</i> O. Pickard-Cambridge	<i>Formica cunicularia</i> (=fusca var. glebaria) Latreille, <i>F. fusca</i> L., <i>F. sanguinea</i> Latreille, <i>Lasius niger</i> (L.)	most spiders collected inside nests of <i>F. fusca</i> ; lives in galleries of nests where hosts ignore spiders; adults found throughout year but males found mainly in Sept. & Oct.	Donisthorpe 1908, 1927
<i>Grammonota pictilis</i> (O. Pickard-Cambridge)	<i>Atta texana</i> (Buckley)	collected inside detritus chambers	Walter et al. 1938; Waller and Moser 1990

TABLE 2. (CONTINUED) MYRMECOPHILIC ARANEA TAXA. THESE ANT GUESTS HAVE BEEN COLLECTED EITHER OCCASIONALLY OR EXCLUSIVELY INSIDE THE COLONIES OF THE HOSTS.

Spider Guest	Ant Host	Notes on the Natural History of the Guests	References
Masoncus pogonophilus Cushing	Pogonomyrmex badius (Latreille)	obligate guest; all instars found throughout the year inside chambers of nest; spiders emigrate with ants; females attach eggsacs to chamber ceilings; spiders feed on collembolans inside the nest	Porter 1985; Cushing 1995a, b
Masoncus sp.	Atta texana (Buckley)	collected inside galleries and empty chambers	Waller and Moser 1990
Thyreosthenius biovatus O. Pickard-Cambridge	Formica fusca L., F. pratensis Retzius, F. rufa L., F. rufa var. rufopratensisoides Forel	found inside nest galleries; females lay eggs inside the nests	Donisthorpe 1908, 1927
<b>LIOCRANNIDAE</b>			
Attacobius leuderwaldti (Mello-Leitão) (= Myrmeques attarum Roewer)	Atta sexdens L.	found inside fungus gardens where it is transported on the backs of the ants; appears to be phoretic, although the adaptive significance of the phoresy is unknown; carried to new nests on back of female alates	Roewer 1935; Eidmann 1937
*Phrurolithus festivus (Koch)	Formica rufa L., F. sanguinea Latreille, Lasius brunneus (Latreille), L. fuliginosus (Latreille), L. niger (L.)	common inside nests as well as outside; sometimes preys on ants; only occasional guest	Donisthorpe 1927; Bristowe 1941; Boevé 1992
*Phrurolithus komurai Yaginuma		always found beneath stone covering ant nest of undescribed species	Komatsu 1961

TABLE 2. (CONTINUED) MYRMECOPHILIC ARANEAE TAXA. THESE ANT GUESTS HAVE BEEN COLLECTED EITHER OCCASIONALLY OR EXCLUSIVELY INSIDE THE COLONIES OF THE HOSTS.

Spider Guest	Ant Host	Notes on the Natural History of the Guests	References
*Phrurolithus minimus Koch	Formica fusca L., Myrmica scabrinodis Nylander, Tapinoma erraticum (=nigerrima) (Latreille)	found inside nests and outside; sometimes preys on ants; only occasional guest	Donisthorpe 1927; Bristowe 1941
Phruronellus formica (Banks) (described as Phrurolithus formica Banks)	Crematogaster lineolata (Say)	probably obligate guest; when ants emerge from nests in Spring, spiders found amongst them; disappear into nest when disturbed	Banks 1895; Emerton 1911
<b>LYCOSIDAE</b>			
Aulonia albimana (Walckenaer)	Tapinoma erraticum (Latreille)	may be occasional associate	Boevé 1992
Pirata spiniger (Simon)	Atta texana (Buckley)	collected inside galleries and empty chambers	Waller and Moser 1990
<b>MYSMENIDAE</b>			
Brucharachne ecitophila Mello-Leitão	Neivamyrmex raptor (=Eciton raptans) (Forel)	found in nests; appears to have trichome-like structures on femurs of second legs	Mello Leitão 1925; Fage 1938
<b>OONOPIDAE</b>			
Gamasomorpha sp.	Myrmecia dispar (Clank)	found in general utility & main brood chambers	Gray 1971
Myrmecosaphiella borgmeyeri Mello Leitão	Eciton sp.	found in nests; appears to have trichome-like structure on its palps	Mello-Leitão 1926; Fage 1938

TABLE 2. (CONTINUED) MYRMECOPHILIC ARANEAE TAXA. THESE ANT GUESTS HAVE BEEN COLLECTED EITHER OCCASIONALLY OR EXCLUSIVELY INSIDE THE COLONIES OF THE HOSTS.

Spider Guest	Ant Host	Notes on the Natural History of the Guests	References
<b>SALTICIDAE</b>			
<i>Continusa</i> sp.	<i>Tapinoma melanocephalum</i> (Fabricius)	spider built silken retreats at periphery of nest; seem to emigrate with host	Shepard & Gibson 1972
* <i>Myrmarachne foenisex</i> Simon	<i>Oecophylla longinoda</i> (Latreille)	sometimes found inside nests where it may feed on ant larvae (only occasional guest)	Wanless 1978
<b>THERIDIIDAE</b>			
<i>Dipoena</i> sp.	<i>Pheidole indica</i> Mayr	found on pile of debris outside nest &, when alarmed, curls up to mimic the decapitated heads of its hosts scattered in the debris	Hingston 1928
<i>Theridion riparium</i> Blackwall	<i>Formica sanguinea</i> Latreille, <i>Lasius niger</i> (L.), <i>Myrmica rubra</i> (= <i>laevinodis</i> ) (L.)	collected in nest of <i>F. sanguinea</i> ; sometimes preys on ants; only occasional guest	Donisthorpe 1927
<b>ZODARIIDAE</b>			
<i>Zodarium frenatum</i> (Simon)	<i>Cataglyphis bicolor</i> (Fabricius)	preys on ants; digs open nests in order to force the hosts outside; spends most of its hunting time near nests of host	Harkness 1977

\* These taxa are also myrmecomorphs (see Table 1)

der lives within the colony chambers of the Florida harvester ant, *Pogonomyrmex badius* (Latreille). All life stages of *M. pogonophilus* are found inside the nests throughout the year. The spiders feed on collembolans (springtails) found in the nest chambers. When the host ants emigrate to a new nest site, the spiders (and collembolans) move with the ants along the emigration trails (Cushing 1995a, 1995b). There is also evidence that spiders disperse between ant nests (Cushing 1995a, and in prep.). The mechanism by which spiders locate new host colonies or become integrated into new colonies is not yet known.

#### Adaptive Significance of Myrmecophily

Some myrmecophilic spiders may be considered Wasmannian mimics since they are also myrmecomorphs (see Table 2). However, in Wasmannian mimicry, the model itself (in this case, the host ant) is the selective agent (Rettenmeyer 1970). In other words, the resemblance of the spider to the host ant must have been selected for by the host itself and must facilitate the integration of the spider into the host colony. However, very little is known about any of the myrmecomorphic myrmecophiles. Most of them apparently spend at least some of their time outside the ant nests (see Table 2) where they would be subject to predation by visually hunting predators in which case their morphological resemblance to the host ants may simply be another example of Batesian mimicry. The host ants may have little, if anything to do with their myrmecomorphy.

As Hölldobler & Wilson (1990) propose, an ant colony can be considered an isolated ecosystem. Arthropods that have evolved mechanisms for integrating themselves into this specialized community are greeted with a stable microclimate, abundant food, and protection from predators and parasites. Predation pressures, in particular, may trigger greater integration into the ant societies in these myrmecophilic spiders since association with the aggressive hosts may afford a high degree of protection to the guests. Several of the myrmecophiles, such as *Mastigusa arietina* (Thorell) (Dictynidae), *Eilica puno* Platnick and Shadab (Gnaphosidae), *Masoncus pogonophilus* (Linyphiidae), and *Thyreosthenius biovatus* O.P.-Cambridge (Linyphiidae) lay their eggsacs inside the chambers of the host's nest (Donisthorpe 1908, 1927, Noonan 1982, Porter 1985, Cushing 1995a, 1995b). Spiders are particularly vulnerable to eggsac parasitism (Bristowe 1941). Eggsac parasitism or predation may also be a particularly important factor selecting for greater integration into ant colonies.

#### CONCLUSIONS

Detailed studies of myrmecomorphic spiders and their associated models can provide insight into the ecological and evolutionary implications of mimicry. The hypothesis that myrmecomorphic spiders are Batesian mimics must be further tested experimentally (Cutler 1991). It is important to use not only generalist predators in such experiments, but also, if possible, spider predators as these may also be important selective agents for the evolution of more exact mimicry.

The distribution of mimics and models, especially in transformational or polymorphic mimetic complexes must be documented as Edmunds (1978) has done for *Myrmarachne* spp. in order to determine what effect community structure among the model species has on the distribution and survival of color morphs in the mimic. It is not known to what extent the geographic distribution of intraspecific polymorphic mimics is dictated by genetic patterns or by differential predation of morphs in areas with and without the appropriate model.

A great deal more research must be done to uncover (literally) the basic natural history of myrmecophilic spiders. For most spider myrmecophiles, it is unknown to what extent they are obligate versus occasional guests in ant nests. For the obligate guests, it must be determined how the spiders become integrated into the nests, how they maintain the association, what part they play in the life of the colony, and what part the colony plays in the survival of the guest. Noonan (1982) indicates that, for the myrmecophile *Eilica puno* Platnick and Shadab (Gnaphosidae), the host ants protect and tend the spider's eggsacs (see Table 2).

Certain families of spiders, such as the Linyphiidae and Liocrannidae, seem to have more myrmecophilic representatives than others. It would be interesting to determine the phylogenetic relationship between myrmecophilic taxa and their free-living relatives. Are there certain preadaptations that make myrmecophily more likely for certain lineages and less likely for others? It is important to document those myrmecophilic spiders that may be encountered in the field. Studies of myrmecophilic spiders can provide insight into the evolution of interspecific associations between social hymenopterans and their guests.

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