

Ant-mimicry in some Brazilian salticid and clubionid spiders (Araneae: Salticidae, Clubionidae)*

PAULO S. OLIVEIRA

*Departamento de Zoologia, Instituto de Biologia, C.P. 6109,
Universidade Estadual de Campinas, 13081 Campinas SP, Brasil*

Received 11 February 1987, accepted for publication 26 August 1987

This paper describes the morphological and behavioural adaptations responsible for ant-like appearance in eight species (genera *Zuniga*, *Synemosyna*, *Sphecotypus*, and *Myrmecium*) of salticid and clubionid spiders studied in Amazonian and SE Brazil. All ant-mimicking spiders have body and legs thin, and the shiny integument typical of their models. Light horizontal hair bands and constrictions of the cephalothorax and abdomen simulate, respectively, the head–thorax joint and segmented gaster of ants. The petiole and postpetiole of the ants are usually mimicked by a lengthened pedicel, together with a narrowing of the posterior cephalothorax and/or anterior abdomen. The prominent pedipalps of the spiders often simulate ant mandibles, but they may also be strikingly similar to an ant's head. All ant-mimicking spiders walked in a zig-zag ant-like pattern, and frequently raised and moved about the first pair of legs as 'antennae'. The mimics were found in the same microhabitats (foliage or ground) as their models, and displayed strong avoidance reactions toward the latter both in the field and in captivity. The inoffensive characteristics of the mimics and the noxious traits of their models (strong mandibles, potent sting, hard integument, venomous secretions) strongly suggest that the spiders are Batesian ant-mimics. The detailed structural and behavioural adaptations enhancing ant-mimicry provide strong circumstantial evidence that the selective agents involved must have good visual acuity, and are probably small insectivorous vertebrates (e.g. birds, lizards and toads) or arthropods (e.g. wasps and spiders) which avoid ants.

KEY WORDS:—Ant-mimicry – salticid spiders – clubionid spiders – Batesian ant-mimicry – ant Muellierian rings.

CONTENTS

Introduction	2
Materials and methods.	2
Results	3
<i>Zuniga</i> spp. and <i>Sphecotypus niger</i>	3
<i>Synemosyna aurantiaca</i>	7
<i>Myrmecium</i> spp.	8
Discussion	10
Acknowledgements	13
References.	13

* Part of this paper was presented at the Colloquium entitled "Aspects Actuels du Mimétisme" in Paris, December 1981, organized by G. Bernardi and M. Rothschild.

INTRODUCTION

Mimicry as a survival strategy has been known for over a century, and played a very important role in the general acceptance of the theory of natural selection among naturalists of the last century (Fisher, 1930). The books of Cott (1940), Wickler (1968) and Edmunds (1974) present ample reviews of what had been discovered about mimicry and other protective devices since the birth of mimicry theory with the work of Henry Bates (1862).

Ant-mimicry (myrmecomorphy) is a widespread phenomenon among arthropods. It has already been recorded in spiders (Peckham, 1889; Shelford, 1902; Pocock, 1909; Myers & Salt, 1926; Hingston, 1928; Reiskind, 1970, 1977; Oliveira & Sazima, 1984), hemipterans (Nicholson, 1927; Kumar, 1966; Schaefer, 1972; Edmunds, 1974; Oliveira, 1985), orthopterans (Poulton, 1898; Edmunds, 1972, 1976), beetles (Wasmann, 1925; Wheeler, 1931; Portmann, 1959; Holldobler, 1971), homopterans (Poulton, 1898; Robinson, 1969) and dipterans (Papavero, 1964).

The spider families Salticidae and Clubionidae contain a great number of species that bear a remarkable resemblance to ants (Peckham & Peckham, 1892; Simon, 1897). *Martella*, *Zuniga*, *Sarinda*, *Synemosyna* and *Myrmarachne* are among the most studied salticid ant-like genera (Galiano, 1964a, b, 1965, 1966, 1969). Among clubionids, genera like *Myrmecium*, *Apochinomma*, *Castianeira* and *Sphecotyplus* present a very refined resemblance to ants (Simon, 1897; Mello-Leitão, 1932, 1947; Reiskind, 1969, 1977). Other families, such as the Theridiidae, Araneidae, Eresidae, Thomisidae, Gnaphosidae, Zodariidae and Aphantochilidae, also have ant-like members (Reiskind & Levi, 1967; Bristowe, 1941).

This paper examines ant-mimicry in a few species of salticid and clubionid spiders. Its purpose is to describe the adaptations responsible for ant-like appearance in mimics, as well as to present circumstantial evidence from field and laboratory observations on the adaptive value of ant-mimicry in the group studied.

MATERIALS AND METHODS

Field work was done in tropical rain forest in Amazonian Brazil and in cerrado vegetation (subtropical savanna) of SE Brazil during 1979 and 1980. Two different localities were used in Amazonas: (1) The Estação Experimental de Silvicultura Tropical of the Instituto Nacional de Pesquisas da Amazonia, 45 km off the Manaus-Boa Vista highway (02°37'S, 60°02'W), in the State of Amazonas, and (2) The Reserva Biológica da Estação Experimental do Governo do Acre, Cruzeiro do Sul (07°55'S, 72°57'W), in the State of Acre. In SE Brazil, field work was carried out in the Cerrado Reserve of the Instituto de Botânica de São Paulo, in the municipality of Mogi-Guaçu (22°18'S, 47°13'W), State of São Paulo. Ant-mimicking spiders and their models were sought out on ground and plant substrates. The behaviour of mimics and models, as well as the interactions between them, were observed in the field and under laboratory conditions. Potential prey, including ants, were offered to the mimetic spiders under captivity. Laboratory experiments were carried out intermittently, with observation sessions lasting 15–30 min. To observe morphological changes with

development of the mimics, spiders were reared in 7×13 cm transparent plastic boxes containing a piece of moist cotton.

In the state of Acre, ants were sampled with baits prepared with small cloth rags (6×4 cm) wetted with honey-water solution. Baits were exposed in the morning (10.00 to 12.00 hours) along a 300 m trail in the forest. Fifty baits were placed on leaves 0.5–1.5 m above the ground, and 20 were distributed on the ground the next day. Each bait was 6.0 m apart from adjacent baits. The collection of the ants started 30 min after the placing of the last bait.

RESULTS

Zuniga spp. and *Sphecotypus niger*

The neotropical salticid genus *Zuniga* consists of two ant-mimicking species, *Zuniga magna* Peckham and *Z. laeta* (Peckham). A deep dorsal depression and a transversal white hair band separate the cephalic and thoracic regions in both species. The thoracic region has grooves and white hair bands radiating towards its lateral and posterior regions, it is also wider and less high than the cephalic region. The abdomen of both species is constricted in its anterior third, though this trait is less evident in *Z. laeta* and in young *Z. magna* (Fig. 1). Both species have bodies covered by golden hairs which, together with black and white hairs as well as light pigmentation, form conspicuous horizontal bands on the abdomen. Prominent and flattened pedipalps are also characteristic in these spiders.

Zuniga laeta was observed in amazonian forest walking on leaves close to nests of the abundant black ant *Camponotus femoratus* (Fabricius), which the spider closely mimics. Young *Z. magna* were seen on foliage in north and south-east Brazil, and resemble the common black ant *Camponotus crassus* Mayr (Fig. 2). Other black *Camponotus* species, such as the abundant and widespread *C. rufipes*

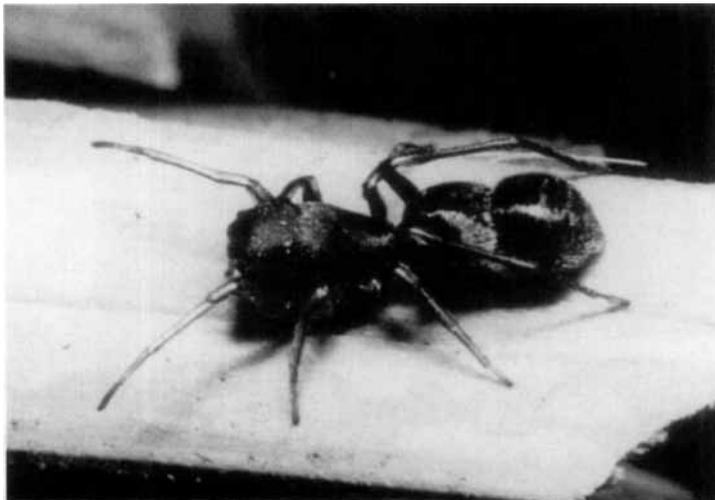


Figure 1. Young of *Zuniga magna*. Note the horizontal hair bands on the constricted abdomen and on the cephalothorax, and the first pair of legs raised as 'antennae'.

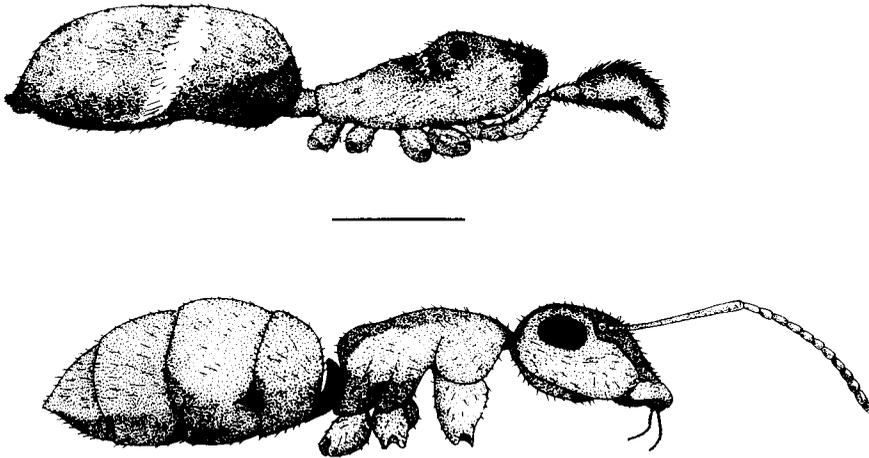


Figure 2. Young of *Zuniga magna* (upper) and its ant model *Camponotus crassus* (lower). Scale bar = 1 mm.

(Fabricius) and *C. blandus* (Fr. Smith) could also serve as models for *Z. laeta* and early stages of *Z. magna*.

Adult males of *Z. magna* bear a striking resemblance to *Pseudomyrmex gracilis* (Fabricius) (Fig. 3) and its relatives (Pseudomyrmecinae). The ant's postpetiole and the segmented gaster are accurately mimicked by the spider's elongate, hair-banded, and constricted abdomen. The well-developed and prominent pedipalps of mature males are highly differentiated and produce a convincing mimicry of the model's head. The tip of the palps are yellow and correspond with the yellow mandibles of the model, while an iridescent spot on the outer surface of the palp is remarkably similar to the large brilliant compound eye of *Pseudomyrmex* (Fig. 3).

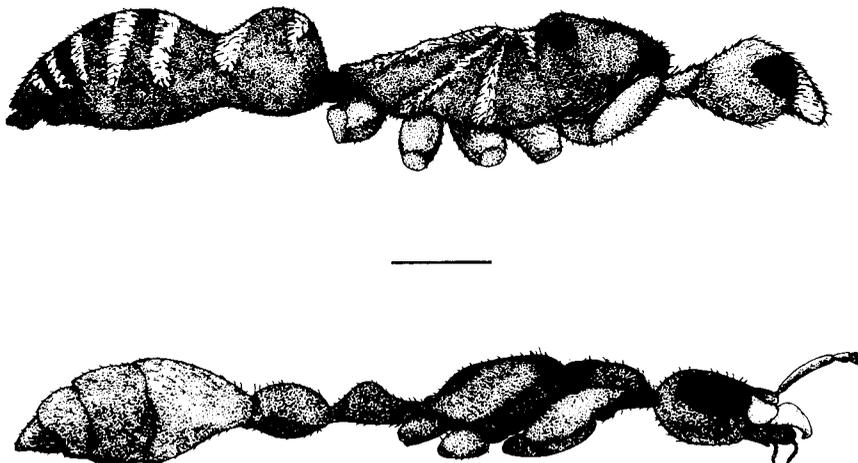


Figure 3. Adult male of *Zuniga magna* (upper) and its ant model *Pseudomyrmex gracilis* (lower). Note the hair bands on the mimic's abdomen simulating the segmented gaster of the model, and the close similarity between the spider's well developed pedipalps and the ant's head (antennae not entirely drawn). Scale bar = 1 mm.

Adult females of *Z. magna* and of the clubionid *Sphecotypus niger* (Perty) are specific mimics of the large ponerine ant *Pachycondyla villosa* (Fabricius) (Figs 4, 5, see also Simon, 1897; Pocock, 1909; Reiskind, 1977). *Pachycondyla villosa* is a very aggressive arboreal species with large mandibles and potent sting. The ant is black, with a very dense and conspicuous golden pilosity covering its whole body (Fig. 4). Both mimics of *P. villosa* have the same colour pattern as the model. Constrictions in the cephalothorax of both spiders produce a head-thorax illusion. The ant's postpetiole and gaster are closely mimicked by the elongate and constricted ponerine-like abdomen of the mimics; pigmentation

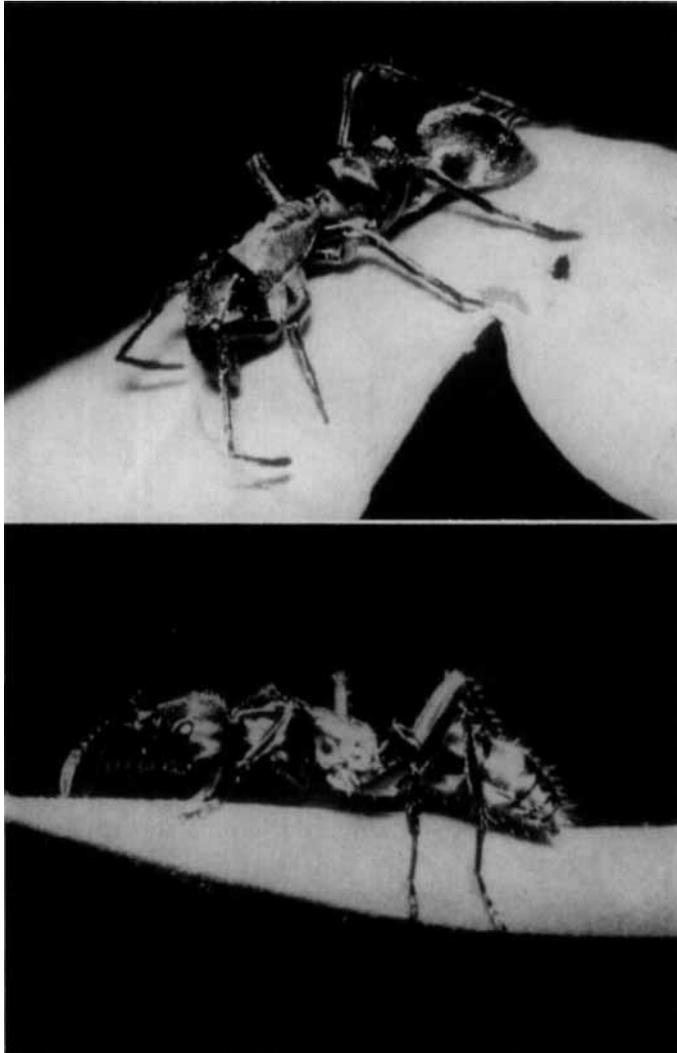


Figure 4. Adult female of *Zuniga magna* (upper) and its ant model *Pachycondyla villosa* (lower). Note the ponerine-like abdomen of the spider, and the dense golden pilosity covering the body of both arthropods.

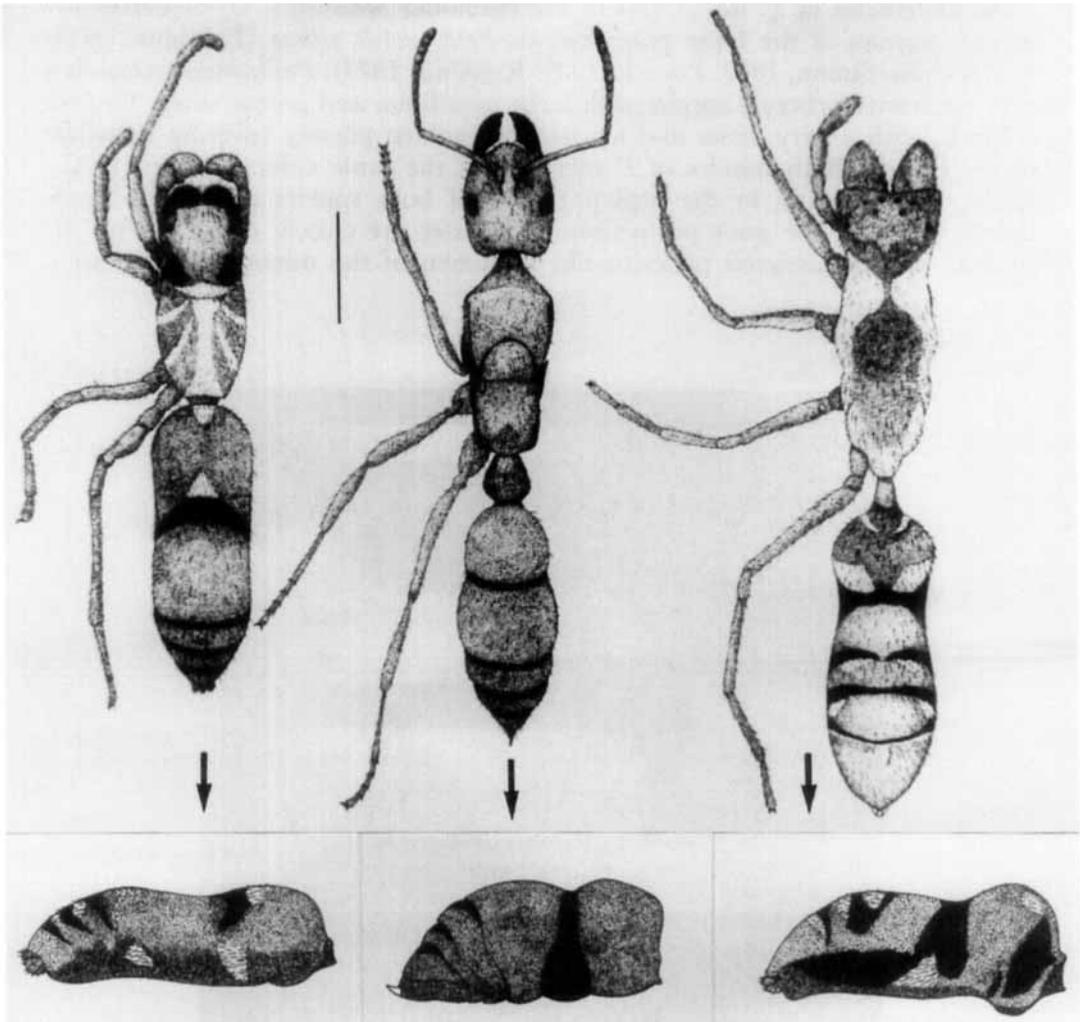


Figure 5. Adult females of *Zuniga magna* (left) and *Sphecotypus niger* (right), and the ant model *Pachycondyla villosa* (centre). Note the similarity between the spiders' abdomen and the segmented gaster of the ant, both in dorsal and lateral views. Scale bar = 2 mm.

and horizontal hair bands on the abdomen simulate the ant's segmented gaster both in dorsal and lateral views (Fig. 5).

Zuniga laeta, *Z. magna* and *Sphecotypus niger* walk in a zig-zag pattern, with the first pair of legs raised as 'antennae'. In cerrado vegetation, *Z. magna* was commonly observed next to extrafloral nectaries of plants (also visited by several ants, including *Camponotus* spp. and *Pachycondyla villosa*), where the spider presumably has an increased chance of capturing insects such as flies. In captivity *Z. magna* preyed on drosophilid and muscid flies and, as *Z. laeta*, displayed avoidance reactions towards their models. *Sphecotypus niger* also avoided encounters with *Pachycondyla villosa*, and in the field this spider was observed preying upon a non-mimetic araneid spider of the genus *Araneus*.

Synemosyna aurantiaca

Of all the Salticidae, the genus *Synemosyna* is one of the most ant-like, and it seems that differentiation toward myrmecomorphy may have reached one of its highest points within this group (Peckham & Peckham, 1892). *Synemosyna* species are genus-specific mimics of *Pseudomyrmex*, a neotropical ant genus with more than a hundred species described (see Kempf, 1972). Most *Pseudomyrmex* ants possess potent stings and many are very aggressive; some species maintain obligate mutualisms with plants and fiercely attack intruders on their nest plants (Wheeler, 1942; Janzen, 1966).

Synemosyna aurantiaca (Mello-Leitão), as other species in this genus, is polymorphic but lacks sexual dimorphism in its mimicry (Galiano, 1966). Yellow morphs closely resemble yellow *Pseudomyrmex*, such as *P. flavidulus* (Fr. Smith) and *P. oculatus* (Fr. Smith) (Fig. 6). Black morphs mimic black *Pseudomyrmex*, such as *P. gracilis* (and other species in the *gracilis* group). The vast majority of *Pseudomyrmex* species have arboreal nests (Kempf, 1960) and normally forage on foliage, as do *Synemosyna* spiders. Both mimetic morphs of *S. aurantiaca* were observed foraging on plants, together with their potential models, in north and southeast Brazil.

Synemosyna aurantiaca has an elongate body, with thin and short legs which

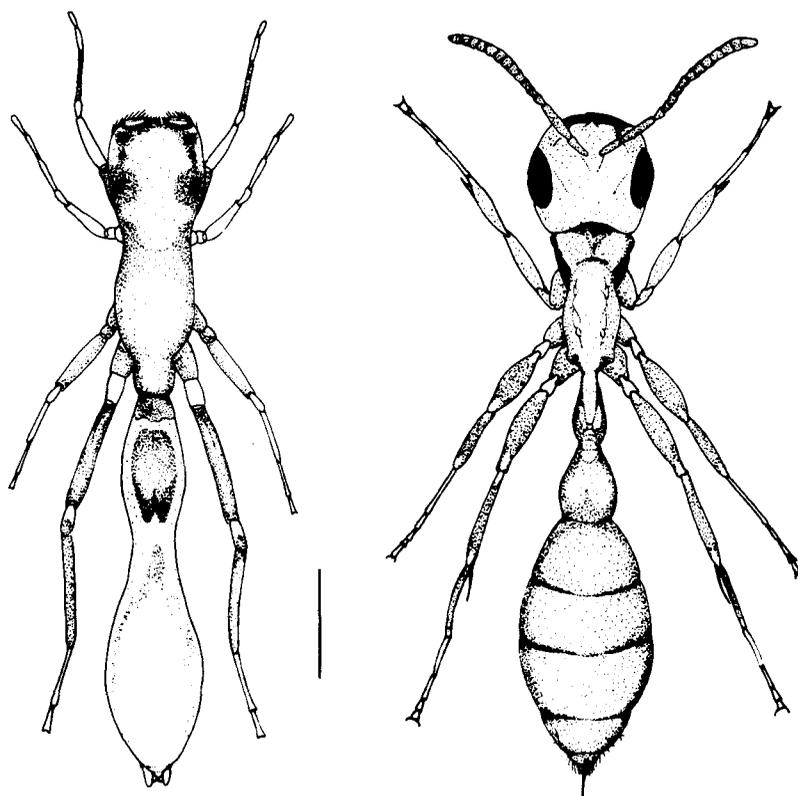


Figure 6. Yellow morph of *Synemosyna aurantiaca* (left) and its ant model *Pseudomyrmex oculatus* (right). Note the overall structural resemblance between the arthropods, and particularly the dark pigmentation around the posterior lateral eyes of the spider simulating the large compound eyes of the ant. Scale bar = 1 mm.

closely resemble the *Pseudomyrmex* morphological pattern (Fig. 6). Cephalic and thoracic regions are separated by a constriction of the cephalothorax which is evident both dorsally and laterally, and simulate the model's head and thorax. Dark pigmentation (in yellow morphs) and white hairs (in black morphs) between cephalic and thoracic regions also enhance the illusion of separate head and thorax. Dark spots around the posterior lateral eyes of yellow morphs closely mimic the large compound eyes of yellow *Pseudomyrmex* (Fig. 6). A second constriction of the posterior portion of the cephalothorax mimics the ant petiole. The spider's abdomen is elongate and constricted, its anterior and posterior regions accurately mimic model's postpetiole and gaster, respectively. In the field the mimics displayed the same jerky movements of the ants, as well as their zig-zag gaiting pattern. When stopping, the mimics frequently raise and move about the first pair of legs as 'antennae'. Jumping behaviour, characteristic of salticids, is reduced in *Synemosyna* and only takes place when the spider is strongly disturbed. *Synemosyna aurantiaca* does not build a web for food capture, though it constructs two-exit silken tent-like retreats where it rests, hides from enemies, and protects the eggs. Both in the field and under captivity, this spider avoided encounters with its ant models, as well as with other ants such as *Camponotus* and *Crematogaster*. Avoidance reactions were also observed in the ants, though these were less pronounced than those of the spiders. The commonest behaviour of the mimics, when encountering an ant on a leaf, consisted of running quickly to the opposite leaf surface and/or hiding in its silken retreat when this was close by.

Except for a brief citation by Peckham (1889) that *Synemosyna formica* Hentz consumes gnats in captivity, nothing is known about the feeding habits of these spiders. *Synemosyna aurantiaca* rejected *Drosophila* flies and membracid nymphs (Homoptera) under laboratory conditions.

Myrmecium spp.

The genus *Myrmecium* is perhaps the most ant-like of all clubionids (Simon, 1897). All *Myrmecium* species have cephalothorax double-constricted, which simulates the head, promesonotum and propodeum of the ant models, and the lengthened pedicel mimics the ant petiole (Figs 7, 8). Horizontal hair bands on the abdomen resemble the segmented gaster of ants, while the prominent palps mimic large mandibles. Table 1 lists all *Myrmecium* spiders found in Amazonian forest, and their respective ant models.

Myrmecium cf. *gounelley* Simon mimics two different ant species according to the developmental stage of the spider. Spiderlings have triangular abdomens and closely mimic the small *Crematogaster limata* Fr. Smith. Adult *M.* cf. *gounelley* are strikingly similar in shape and colour to *Camponotus femoratus* (Fig. 8A, B). These two ant species live in parabiosis (i.e. utilize the same nest and odour trails; see Wilson, 1971), and were the most frequent species on honey baits placed in the rain forest of Cruzeiro do Sul (Acre). *Camponotus femoratus* and *Crematogaster limata* were present on 28 and 24% of the baits placed on foliage, respectively (six other species were each present on 4% or less of these baits). The two parabiocytic species also appeared on 81% and 43% of the ground baits, while eight other species were each present on 10 or less of these. *Myrmecium* cf. *gounelley* rejected *Drosophila* flies in captivity. In the field, however, the spiders

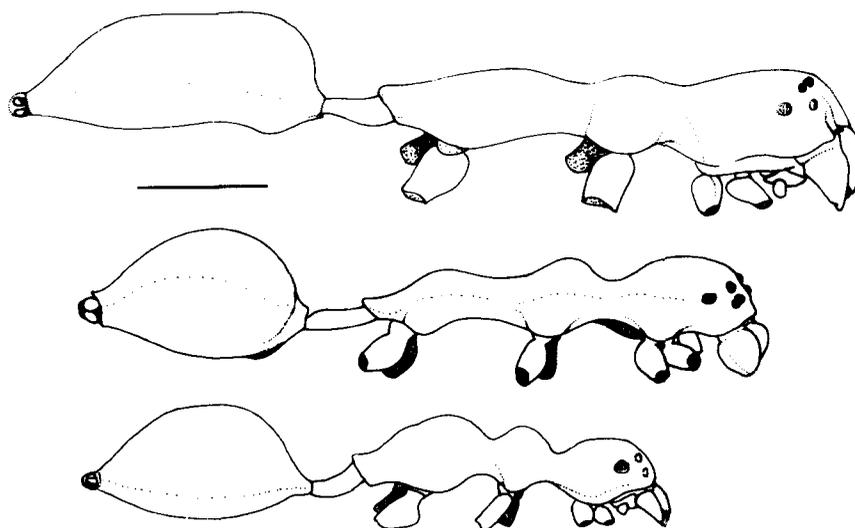


Figure 7. Lateral view of *Myrmecium* cf. *velutinum* (upper), *Myrmecium bifasciatum* (middle) and *Myrmecium* cf. *gounelley* (lower). Note the lengthened pedicel (similar to an ant petiole) and the double-constricted cephalothorax of the spiders. Scale bar = 1 mm.

were observed capturing minute arthropods such as mites, homopterans and beetles on foliage.

Myrmecium bifasciatum (Tacz.) is polymorphic; yellow morphs mimic yellow *Megalomyrmex* ants, and black morphs resemble black *Camponotus* species (Fig. 8C–E, Table 1). *Myrmecium* cf. *velutinum* Simon (Fig. 7) and *Myrmecium* sp. (Fig. 8F) are ponerine-like spiders that mimic *Ectatomma lugens* Emery and *Pachycondyla unidentata* (Mayr), respectively. The mimics have elongate ponerine-like abdomens and are found in the same microhabitats as their models (Figs 7, 8F, Table 1).

All *Myrmecium* species reported here walk in an ant-like manner and raise the first pair of legs as ‘antennae’. They also displayed conspicuous avoidance

TABLE 1. *Myrmecium* spp. and their ant models studied in Amazonian forest, Brazil

Mimic	Potential model(s)	Microhabitat		Mimetic specificity
		Spider	Ant	
<i>Myrmecium</i> cf. <i>gounelley</i> Spiderling (black) Adult (black)	<i>Crematogaster limata</i>	Leaves	Leaves and ground	Specific
	<i>Camponotus femoratus</i>	Leaves	Leaves and ground	Specific
<i>Myrmecium bifasciatum</i> Yellow morph Black morph	<i>Megalomyrmex modestus</i>	Leaves	Leaves and ground	Generic
	<i>Megalomyrmex balzani</i>		Leaves and ground	
	<i>Camponotus femoratus</i>	Leaves	Leaves and ground	Specific (?)
<i>Myrmecium</i> cf. <i>velutinum</i> Adult (reddish brown)	<i>Ectatomma lugens</i>	Ground	Ground	Specific
<i>Myrmecium</i> sp. Adult (body black, legs yellow)	<i>Pachycondyla unidentata</i>	Leaves	Leaves	Specific

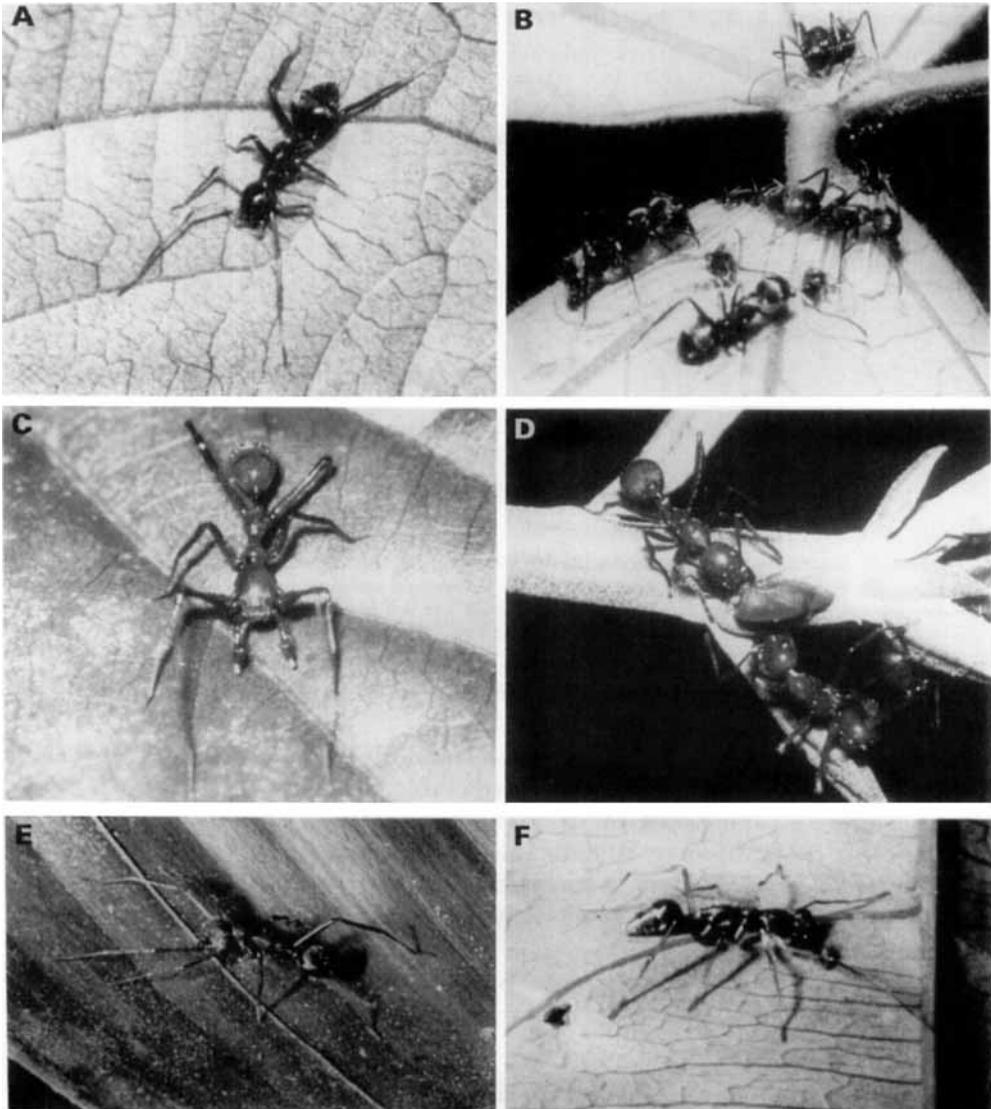


Figure 8. Ant-mimicking *Myrmecium* and their potential models studied in Amazonian Brazil. A, *Myrmecium* cf. *gounelley*. B, *Camponotus femoratus* (tending lepidopteran larvae). C, Yellow morph of *Myrmecium bifasciatum*. D, *Megalomyrmex balzani* (with a honeydew-producing homopteran). E, Black morph of *M. bifasciatum*. F, *Myrmecium* sp. Note the remarkably ant-like shape of the spiders.

reactions toward their models in the field and in captivity. The ant models also did not attack their mimics in either situation. These spiders probably all prey on minute arthropods, as was directly observed for *Myrmecium* cf. *gounelley*.

DISCUSSION

The following characteristics of ants are assumed to be responsible for their unpalatability to generalized predators: (1) potent sting; (2) strong mandibles; (3) distasteful flesh; (4) hard integument, sometimes with spines; (5) secretion of

irritating acid substances. These traits, added to eusociality (each colony has many individuals) and to the facts that ants occur in almost all kinds of habitats (Wheeler, 1910), and that formicid morphology is quite repetitive, make ants very suitable organisms to be mimicked by innocuous animals. Recent field studies with bees and wasps have shown that these stinging insects can form assemblages of similar-looking species and act as Muellierian mimics in relation to potential predators, which avoid all species within the assemblage through the reinforcement of a unique aposematic pattern (Waldbauer, Sternburg & Maier, 1977; Plowright & Owen, 1980). Analogously, similar-appearing ant species such as the abundant and widespread species in the genus *Camponotus*, or the stinging ponerines and pseudomyrmecines, could share warning cues to predators and be mutual Muellierian mimics. The inoffensive characteristics of the ant-mimicking spiders reported here, and the noxious traits of their models, strongly suggest that these spiders are Batesian ant-mimics. There is much indirect evidence strengthening this suggestion (Jackson, 1982, 1986; Parker & Cloudsley-Thompson, 1986; and citations therein; but see Brignoli, 1986). All mimics conspicuously avoided encounters with their ant models and preyed on arthropods other than ants, a fact that makes the aggressive ant-mimicry hypothesis (i.e. when the mimic deceives and feeds on its model) highly improbable. Indeed, ant-hunting spiders (mimetic or not) are very specialized predators and usually reject alternative non-ant prey (Oliveira & Sazima, 1984, 1985). Moreover, as a general rule, the spatial association observed between the spider mimics and ant models was restricted to the microhabitat level only (foliage or ground), as contrasted with the regular and more pronounced association (i.e. close proximity to ant nests) that aggressive ant-mimicking spiders typically maintain with their ant prey (see Hingston, 1928; Mathew, 1954; Oliveira & Sazima, 1984).

The detailed morphological and behavioural adaptations responsible for ant-resemblance in salticid and clubionid spiders provide strong circumstantial evidence that the selective agents involved in their evolution must have good visual acuity. Bristowe (1941) and Edmunds (1974) argue that ants have poor eyesight and that aggressive ant-mimics, in contrast with Batesian ones, are likely to bear only a superficial resemblance to their models in order to attack them safely. According to Bristowe (1941) 'an ability to speak the ant-language' would be a more important trait for deceiving and capturing ants with safety. In fact, Holldobler (1971) showed that morphological resemblance is not an essential trait for the adoption of myrmecophilous beetles by their chemically-orientated ant hosts. Therefore the refined structural resemblance of the spiders with ants must be the product of selective action exerted by animals other than ants.

Hymenopterans are generally well-protected against predators (Eisner, 1970; Blum, 1981). Furthermore, toads (Brower & Brower, 1962, 1965), birds (Mostler, 1935) and lizards (Vogel & Brockhuzen-Holzer, 1984) can learn visually to avoid bees, wasps and ants, respectively, after a few unpleasant experiences. Since ants, bees and wasps share many noxious traits, and few vertebrates regularly feed on formicids (Wheeler, 1910; Edmunds, 1974), it is assumed that visually-hunting insectivorous vertebrates were the main selective agents involved in the evolution of Batesian ant-mimicry (Cott, 1940; Bristowe, 1941; Wickler, 1968; Edmunds, 1974, among others).

Among invertebrates, spider-hunting wasps are known to show alarm at the approach of an ant (Peckham & Peckham, 1905). Edmunds (1974) presented good evidence that *Pison* wasps (Sphecidae) hunt using a searching image, and hence could be important selective agents for ant-mimicry in certain spiders. Bristowe (1941) states that spiders are the worst enemies of spiders. Since most hunting spiders have excellent eyesight (Turnbull, 1973) and several avoid attacking ant-mimicking spiders (Bristowe, 1941), they could also have exerted selection for ant-mimicry in several spider taxa. Thus it seems plausible to suppose that combined selective pressures from both vertebrates and invertebrates that avoid ants, have provoked the evolution of Batesian ant-mimicry in salticid and and clubionid spiders.

The term 'transformational mimicry' was originally proposed by Mathew (1935) for cases in which an animal mimics different models in different phases of its developmental stages. This phenomenon has already been reported for ant-mimicking hemipterans (Mathew, 1935; Oliveira, 1985), spiders (Reiskind, 1970; Edmunds, 1978) and orthopterans (Jackson & Drummond, 1974). In this study transformational mimicry was detected in *Zuniga magna* and *Myrmecium* cf. *gounelley*, but it might as well occur in other species whose early stages were not obtained. Ant-mimicry in *Myrmecium* cf. *gounelley* is particularly interesting since the spider associates mimetically with two dominant parabiocotic ant models (*Crematogaster limata* and *Camponotus femoratus*); young spiders change their ant models without having to move through territories of other ants to be near to alternative models. Edmunds (1978) described a similar case for the Ghanaian ant-mimicking salticid *Myrmarachne foenisex* Simon, whose model for the young spiders is also positively associated with the model for the adults.

The simultaneous association with various noxious models by a palatable species can also be achieved through sexual dimorphism (only one sex being mimetic, or each sex mimicking a different model) and mimetic polymorphism (two or more morphs mimicking different models). These strategies are more common and best studied in mimetic butterflies (see examples in Edmunds, 1974), but they are also known to occur in mimics of Hymenoptera (Wickler, 1968; Reiskind, 1970; Opler, 1981). Sexual dimorphism was observed in *Zuniga magna*, where adult spiders of each sex mimic quite different ant models. Polymorphic mimicry was recorded in *Synemosyna aurantiaca* and *Myrmecium bifasciatum*, with both species having black and yellow morphs respectively resembling available ant models with these colour patterns.

Transformational, sex-limited and polymorphic mimicries are means whereby mimetic species can maintain a high population without exceeding a small proportion of the population of available models, and thus optimize the protective advantage of Batesian mimicry (Huheey, 1964; Rettenmeyer, 1970). The social mode of life of ants makes them very peculiar models for Batesian mimicry systems. In a relatively small area of any tropical environment one can find thousands of similar-looking individuals foraging on every substrate and belonging to various different species, which presumably act as mutual Muellerian mimics. Thus various mimetic spiders can coexist in the same area and, even if they share ant model species in the same size/colour category, the mimic population as a whole would remain less abundant relative to those of their social models. However, despite the high abundance of ant models, frequency-dependent selection on Batesian mimics (Ayala & Campbell, 1974),

together with the spatial heterogeneity of models (differently coloured ant Muellierian rings), would still favour polymorphisms in populations of ant-mimics.

ACKNOWLEDGEMENTS

I am grateful to W. W. Benson and I. Sazima for reading a previous version of the manuscript. I also thank Mirian Rothschild for encouraging the publication of this paper. B. A. M. Soares, M. J. B. Vianna and U. Caramaschi helped with the identification of the spiders. C. R.F. Brandão helped with the identification of the ants. The Fundação Projeto Rondon supported field work in Acre; the Instituto Nacional de Pesquisas da Amazonia gave permission to work in its reserves in Amazonas, during field courses (Ecologia de Campo I/III) sponsored by UNICAMP. The study received financial support from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

REFERENCES

- AYALA, F. J. & CAMPBELL, C. A., 1974. Frequency-dependent selection. *Annual Review of Ecology and Systematics*, 5: 115–138.
- BATES, H. W., 1862. Contributions to an insect fauna of the Amazon valley. Lepidoptera: Heliconidae. *Transactions of the Linnean Society of London*, 23: 495–556.
- BLUM, M. S., 1981. *Chemical Defenses of Arthropods*. New York: Academic Press.
- BRIGNOLI, P. M., 1986. Myrmecomorphism again. *Newsletter of the British Arachnological Society*, 47: 4–5.
- BRISTOWE, W. S. 1941. *The Comity of Spiders*, 2. London: Ray Society.
- BROWER, J. V. Z. & BROWER, L. P., 1962. Experimental studies of mimicry. 6. The reaction of toads (*Bufo terrestris*) to honeybees (*Apis mellifera*) and their dronefly mimics (*Eristalis vinetorum*). *American Naturalist*, 96: 297–307.
- BROWER, J. V. Z. & BROWER, L. P., 1965. Experimental studies of mimicry. 8. Further investigations of honeybees (*Apis mellifera*) and their dronefly mimics (*Eristalis* spp.). *American Naturalist*, 99: 173–187.
- COTT, H. B., 1940. *Adaptive Coloration in Animals*. London: Methuen.
- EDMUNDS, M., 1972. Defensive behaviour of Ghanaian praying mantids. *Zoological Journal of the Linnean Society*, 51: 1–32.
- EDMUNDS, M., 1974. *Defence in Animals*. Harlow: Longman.
- EDMUNDS, M., 1976. The defensive behaviour of Ghanaian praying mantids with a discussion of territoriality. *Zoological Journal of the Linnean Society*, 58: 1–37.
- EDMUNDS, M., 1978. On the association between *Myrmarachne* spp. (Salticidae) and ants. *Bulletin of the British Arachnological Society*, 4: 149–160.
- EISNER, T., 1970. Chemical defense against predation in arthropods. In E. Sondheimer & J. B. Simeone (Eds), *Chemical Ecology*: 157–217. New York: Academic Press.
- FISHER, R. A., 1930. *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.
- GALIANO, M. E., 1964a. Salticidae (Araneae) formiciformes. I. Revision del genero *Martella* Peckham, 1892. *Physis*, 24: 353–363.
- GALIANO, M. E., 1964b. Salticidae (Araneae) formiciformes. II. Revision del genero *Zuniga* Peckham, 1892. *Acta Zoologica Lilloana*, 20: 67–79.
- GALIANO, M. E., 1965. Salticidae (Araneae) formiciformes. IV. Revision del genero *Sarinda* Peckham, 1892. *Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia*, 1: 267–312.
- GALIANO, M. E., 1966. Salticidae (Araneae) formiciformes. V. Revision del genero *Synemosyna* Hentz, 1846. *Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia*, 1: 339–380.
- GALIANO, M. E., 1969. Salticidae (Araneae) formiciformes. VII. El genero *Myrmarachne* MacLeay, 1839, en America. *Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia*, 3: 107–148.
- HINGSTON, R. W. G., 1928. Field observations on spider mimics. *Proceedings of the Zoological Society of London*, 1927, 4: 841–858.
- HOLLOBLER, B., 1971. Communication between ants and their guests. *Scientific American*, 224: 86–93.
- HUHEEY, J. E., 1964. Studies of warning coloration and mimicry. IV. A mathematical model of model-mimic frequencies. *Ecology*, 45: 185–188.

- JACKSON, R. R., 1982. The biology of ant-like jumping spiders: intraspecific interactions of *Myrmarachne lupata* (Araneae, Salticidae). *Zoological Journal of the Linnean Society*, 76: 293-319.
- JACKSON, R. R., 1986. The biology of ant-like jumping spiders (Araneae, Salticidae): prey and predatory behaviour of *Myrmarachne* with particular attention to *M. lupata* from Queensland. *Zoological Journal of the Linnean Society*, 88: 179-190.
- JACKSON, J. F. & DRUMMOND, B. A., 1974. A Batesian ant-mimicry complex from the mountain pine ridge of British Honduras, with an example of transformational mimicry. *American Midland Naturalist*, 91: 248-251.
- JANZEN, D. H., 1966. Coevolution between ants and acacias in Central America. *Evolution*, 20: 249-275.
- KEMPF, W. W., 1960. Estudos sobre *Pseudomyrmex*. I. *Revista Brasileira de Entomologia*, 9: 5-32.
- KEMPF, W. W., 1972. Catálogo abreviado das formigas da região neotropical. *Studia Entomologica*, 15: 3-334.
- KUMAR, R., 1966. Studies on the biology, immature stages, and relative growth of some Australian bugs of the superfamily Coreoidea (Heteroptera). *Australian Journal of Zoology*, 14: 895-991.
- MATHEW, A. P., 1935. Transformational deceptive resemblance as seen in the life-history of a plant bug (*Riptortus pedestris*), and of a mantis (*Evantissa pulchra*). *Journal of the Bombay Natural History Society*, 37: 803-813.
- MATHEW, A. P., 1954. Observations on the habits of the two spider mimics of the red ant *Oecophylla smaragdina* (Fabr.). *Journal of the Bombay Natural History Society*, 52: 249-263.
- MELLO-LEITÃO, C. F., 1932. Notas sobre o gênero *Myrmecium* Latr. *Anais da Academia Brasileira de Ciências*, 4: 149-169.
- MELLO-LEITÃO, C. F., 1947. Aranhas do Paraná e Santa Catarina das coleções do Museu Paranaense. *Arquivos do Museu Paranaense*, 6: 231-304.
- MOSTLER, G., 1935. Beobachtungen zur Frage der Wespenmimikry. *Zeitschrift für Morphologie und Oekologie der Tiere*, 29: 381-454.
- MYERS, J. C. & SALT, G., 1926. The phenomenon of myrmecoidy, with new examples from Cuba. *Transactions of the Royal Entomological Society of London*, 74: 427-436.
- NICHOLSON, A. J., 1927. A new theory of mimicry in insects. *Australian Zoologist*, 5: 10-104.
- OLIVEIRA, P. S. 1985. On the mimetic association between nymphs of *Hyalymenus* spp. (Hemiptera: Alydidae) and ants. *Zoological Journal of the Linnean Society*, 83: 371-384.
- OLIVEIRA, P. S. & SAZIMA, I., 1984. The adaptive bases of ant-mimicry in a neotropical aphantochilid spider (Araneae: Aphantochilidae). *Biological Journal of the Linnean Society*, 22: 145-155.
- OLIVEIRA, P. S. & SAZIMA, I., 1985. Ant-hunting behaviour in spiders with emphasis on *Strophius nigricans* (Thomisidae). *Bulletin of the British Arachnological Society*, 6: 309-312.
- OPLER, P. A., 1981. Polymorphic mimicry of polistine wasps by a neotropical neuropteran. *Biotropica*, 13: 165-176.
- PAPAVERO, N., 1964. Notes on the myrmecomimicry of *Syringogaster rufa* Cresson, 1912 (Diptera, Acalyptratea, Megamerinidae). *Papéis Avulsos do Departamento de Zoologia, São Paulo*, 16: 89-95.
- PARKER, J. R. & CLOUDSLEY-THOMPSON, J. L., 1986. Myrmecophilous spiders. *Newsletter of the British Arachnological Society*, 45: 2-4.
- PECKHAM, E. G., 1889. Protective resemblances in spiders. *Occasional Papers of the Wisconsin Natural History Society*, 1: 61-113.
- PECKHAM, G. W., & PECKHAM, E. G., 1892. Ant-like spiders of the family Attidae. *Occasional Papers of the Wisconsin Natural History Society*, 2: 1-84.
- PECKHAM, G. W., & PECKHAM, E. G., 1905. *Wasps: Social and Solitary*. London: Archibald Constable.
- PLOWRIGHT, R. C. & OWEN, R. E., 1980. The evolutionary significance of bumble bee color patterns: a mimetic interpretation. *Evolution*, 34: 622-637.
- POCOCK, R. L., 1909. Mimicry in spiders. *Journal of the Linnean Society, Zoology*, 30: 256-270.
- PORTMANN, A., 1959. *Animal Camouflage*. Ann Arbor: The University of Michigan Press.
- POULTON, E. B., 1898. Natural selection the cause of mimetic resemblance and common warning colours. *Journal of the Linnean Society, Zoology*, 26: 558-612.
- REISKIND, J., 1969. The spider subfamily Castianeirinae of North and Central America (Araneae: Clubionidae). *Bulletin of the Museum of Comparative Zoology, Harvard*, 138: 163-325.
- REISKIND, J., 1970. Multiple mimetic forms in an ant-mimicking clubionid spider. *Science*, 169: 587-588.
- REISKIND, J., 1977. Ant-mimicry in Panamanian clubionid and salticid (Araneae: Clubionidae, Salticidae). *Biotropica*, 9: 1-8.
- REISKIND, J. & LEVI, H. W., 1967. *Anatea*, an ant-mimicking theridiid spider from New Caledonia (Araneae: Theridiidae). *Psyche*, 74: 20-23.
- RETTENMEYER, C. W., 1970. Insect mimicry. *Annual Review of Entomology*, 15: 43-74.
- ROBINSON, M. H., 1969. Defenses against visually hunting predators. *Evolutionary Biology*, 3: 225-259.
- SCHAEFER, C. W., 1972. Clades and grades in the Alydidae. *Journal of the Kansas Entomological Society*, 45: 135-141.
- SHELFORD, R., 1902. Observations on some mimetic insects and spiders from Borneo and Singapore. *Proceedings of the Zoological Society of London*, 2: 230-284.
- SIMON, E., 1897. *Histoire Naturelle des Araignées*, 2. Paris: Encyclopédie Roret, L. Mulo.

- TURNBULL, A. L., 1973. The ecology of the true spiders (Araneomorphae). *Annual Review of Entomology*, 18: 305-348.
- VOGEL, P. & BROCKHUSEN-HOLZER, F. von, 1984. Ants as prey of juvenile *Anolis lineatopus* (Rept., Iguanidae) in prey choice experiments. *Zeitschrift für Tierpsychologie*, 65: 66-76.
- WALDBAUER, G. P., STERNBURG, J. G. & MAIER, C. T., 1977. Phenological relationships of wasps, bumblebees, their dipteran mimics and insectivorous birds in an Illinois sand area. *Ecology*, 58: 583-591.
- WASMANN, E., 1925. Die Ameisenmimikry. *Abhandlungen sur Theoretischen Biologie*, 19: 1-164.
- WHEELER, W. M., 1910. *Ants: Their Structure, Development and Behavior*. New York: Columbia University Press.
- WHEELER, W. M., 1931. The ant *Camponotus (Myrmepomis) sericeiventris* Guérin and its mimic. *Psyche*, 38: 86-98.
- WHEELER, W. M., 1942. Studies of neotropical ant-plants and their ants. *Bulletin of the Museum of Comparative Zoology, Harvard*, 90: 1-262.
- WICKLER, W., 1968. *Mimicry in Plants and Animals*. New York: McGraw-Hill.
- WILSON, E. O., 1971. *The Insect Societies*. Cambridge, MA: Belknap Press.