

BEHAVIORAL INTERACTIONS BETWEEN ANTS AND THEIR PARASITES

DANIEL P. WOJCIK
USDA, ARS,

Insects Affecting Man & Animals Research Laboratory,
P. O. Box 14565,
Gainesville, FL 32604

ABSTRACT

Ectoparasitic and endoparasitic arthropods of ants include species of Acarina (Antennophoridae, Uropodidae, Macrochelidae), Strepsiptera (Myrecolacidae), Hymenoptera (Formicidae, Diapriidae, Eucharitidae), and Diptera (Phoridae). Variation in the style of ectoparasitism is illustrated by the different lifestages involved and differing effects on the hosts by parasitic ants and eucharitids. Considerable variation in behavior occurs between related genera and species of phorids emphasizing the danger of over-generalization on the relationships of ants and their parasites.

RESUMEN

Artropódos ecto- y endoparásitos de homigas incluyen especies de Acarina (Antennophoridae, Uropodidae, Macrochelidae), Strepsiptera (Myrecolacidae), Hymenoptera (Formicidae, Diapriidae, Eucharitidae), y Diptera (Phoridae). Variación en el estilo de ectoparasitismo es ilustrado por las diferentes etapas de vida involucrados, así como por los diferentes efectos en los hospederos causados por hormigas parásitas y eucharitidos. Considerable variación en comportamiento ocurre entre géneros y especies relacionadas de phoridos, enfatizando el peligro de sobre generalización en las relaciones de hormigas y sus parásitos.

Arthropods that live with, or are associated with ants, are termed myrmecophiles. This relationship can be permanent or temporary, obligatory or facultative, integrated or nonintegrated.

The generally accepted classification of myrmecophiles is based on studies by Wasmann [translated into English by Wheeler (1910)]. The 5 behavioral categories Wasmann devised are: 1) synechthrans (persecuted guests), 2) synoeketes (indifferently tolerated guests), 3) symphiles (true guests), 4) ectoparasites and endoparasites, and 5) trophobionts (guests that provide secretions to the ants). While the categories are mutually exclusive, the myrmecophiles often can be placed in different Wasmannian categories at different stages of their life-cycles (Wilson 1971). Several other classification systems have been proposed (Kistner 1979), but none has become as generally accepted as the Wasmannian system. In most cases, the true relationships of the myrmecophiles are not known, indeed many are still being discovered and their relationships with their hosts defined.

Wilson (1971) divides myrmecophilous parasites into (1) ectoparasites that live on the body surfaces of their hosts, licking up their oil secretions, steal food from them, or bite through the exoskeleton and feed on their blood, and (2) endoparasites (parasitoids) that penetrate and develop in the host's body. He notes that the behavior of the internal parasites is not usually distinguishable from the behavior of similar species which parasitize nonsocial insects. This is not necessarily the case as I will show.

Some inquiline use chemical mimicry as a means of integrating themselves into the host colony. These organisms, several termitophilous staphylinids (Howard et al. 1980, 1982) and a myrmecophilous scarab (Vander Meer & Wojcik 1982), acquire the cuticular hydrocarbons of the host. Studies by Vander Meer, Wojcik, and Jouvenaz (unpublished) have shown chemical mimicry to be wide-spread in *Solenopsis* spp. myrmecophiles. I discuss some of these myrmecophiles in this paper. Other myrmecophiles use body shape, color, special morphological adaptations, and appeasement substances to become integrated into ant colonies (Wilson 1971, Kistner 1979).

ACARINA

Most mites found in ant nests are phoretic and are scavengers, parasites, or predators on organisms other than the host ants (Wilson 1971). Some [e.g., *Antennophorus uhlmanni* Haller (Antennophoridae)] are social parasites, and solicit food from the worker ants (*Lasius mixtus* Nylander) in the same manner as the ants and symphiles (Janet 1897). Other mites are ectoparasites. For instance, *Cillibano comato* (Berlese) (Uropodidae) attaches to the gaster of the *Lasius* spp. host ants, feeds on the hemolymph, and leaves feeding scars (Janet 1897). The mites associated with the New World army ants are the best known, but most species are not parasites of the ant host (Rettenmeyer 1961). Species of ectoparasitic mites usually are host-specific and may even be specific to a part of the ant. *Macrocheles rettenmeyeri* Krantz (Macrochelidae), for example, attaches to and feeds on the hind arolium of the host, *Eciton dulcius crassinode* Borgmeier; and the ants seem unaffected and use the mite bodies as part of their legs as they walk (Rettenmeyer 1962).

STREPSIPTERA

Strepsipterans of the family Myrmecolacidae are endoparasites of ants, and perhaps Orthoptera (Riek 1970, Teson & de Remes Lenicov 1979). Genera of ants parasitized include *Eciton*, *Pseudomyrmex*, *Pheidole*, *Solenopsis*, and *Camponotus*, which represent the majority of the major subfamilies of ants. Life cycles may be similar to those of the non-myrmecophilous species (Clausen 1940a). Stylopized ants behave unusually, lingering on the tips of grass stems even in bright sunlight (Riek 1970). Lingering on the tips of grass stems increases the chance of being found by the short-lived male parasites or puts them in a good position for male emergence. This type of behavioral modification has also been reported in ants parasitized with mermithid nematodes (Riek 1970), trematode worms (Paraschivescu 1982), or fungi (Loos-Frank & Zimmerman 1976).

HYMENOPTERA

Parasitic wasps (Ichneumonoidea, Chalcidoidea, Bethyloidea) have been observed ovipositing in the gasters of ants or have been found inside ant nests (Wheeler 1910, Weber 1972, Kistner 1982), but little is known about their relationships with their hosts. Some parasitic wasps are myrmecophiles even though they are not parasites of the host ants. *Paralypsis enervis* Nees is known from the nests of *Lasius niger* (L.) in France (Kistner 1982) and *P. eikoeae* (Yasumatsu) and *Aclitus sappaphis* Takada & Shiga are known from the nests of *L. niger* and *Pheidole fervida* F. Smith, respectively, in Japan (Takada & Hashimoto 1985). The wasps live unmolested in the nests and solicit food from the ants. The mouthparts of the wasps are modified to enable them to engage in trophallaxis with the ants (Kistner 1982). These aphidiid wasps are parasites of the aphids tended by the ants.

HYMENOPTERA: FORMICIDAE

Social parasitism of ants by other ants runs the gamut from temporary residence by a newly-mated queen, to slave-making, to obligatory parasitism (Buschinger 1986). For example, the temporarily parasitic *Lasius reginae* Faber queen attacks (throttles) the host *L. alienus* (Foerster) queen until she starves to death, while the *Bothriomyrmex decapitans* queen cuts off the head of the *Tapinoma* spp. host queen. These temporary parasites produce a worker caste and eventually usurp the host nest. The true parasitic ants do not produce a worker caste and are totally dependent on the host workers (Wilson 1971). An example of this group is *Solenopsis (Labauchena) daguerrei* Santschi, whose queens attach to the neck of the host *S. richteri* Forel queen, and steal the food the workers offer their mother queen (Silveira-Guido et al. 1968, 1973). If more than one parasite queen is present, they distribute themselves over the host queen's body. There is some evidence that the parasitic queen is fed preferentially to the host queen. Eventually the host queen is deprived of enough food so that her egg production declines, particularly when more than one parasite queen is present. The host queen eventually dies and the host colony's vigor and size decreases. *S. richteri* colonies have been found with over 3,300 parasite adults (males and females) and immatures (70% of the collected colony) (Silveira-Guido et al. 1965, 1973). The method of invasion and integration into the host colony is not understood, but good evidence exists that the parasite queen has a host cuticular-hydrocarbon pattern which masks her own cuticular-hydrocarbons (Vander Meer & Wojcik unpublished).

HYMENOPTERA: DIAPRIIDAE

Most of the small wasps of the family Diapriidae are parasites of Diptera or Coleoptera. Species in several genera have been found in ant nests or running with army ants on foraging trails (Huggert & Masner 1983, Masner 1959, 1976, 1977, Loiacono 1981). The best known myrmecophilous species, *Solenopsis imitatrix* Wasmann, which was first collected and observed in 1884 by Wasmann (reviewed by Wing 1951), has not definitely been shown to be an ant parasite. The male and female wasps live in the ant nests and solicit food from the ants. Although some species are thought to caste off their wings before entering the ant nest (Masner 1976), other species have their wings chewed off by the ants after they invade the ant nest (Masner 1959). Lachaud and Passera (1982) demonstrated that *Plagiopria passerai* Masner parasitizes queen cocoons of *Plagiolepis pygmaea* (Latreille).

HYMENOPTERA: EUCHARITIDAE

All eucharitid wasps are parasitic on ants (Heraty 1985, 1988). Some species are fastidious in their choice of hosts and oviposition sites, others are not. The females lay their eggs in plant tissue away from the hosts. The specific plant and plant part in which eggs are laid vary among species (Clausen 1940b, Parker 1937, 1942, Johnson et al. 1986). The genus *Orasema* and related genera (subfamily Oraseminae) have a highly sclerotized scimitar-shaped ovipositor (Heraty 1985) and insert their eggs singly into incisions in the leaf surfaces (Clausen 1940b); the remaining genera (subfamily Eucharitinae) generally lack the highly sclerotized ovipositor (Heraty 1985) and usually lay their eggs in cavities or spaces in floral or leaf buds or in cavities formed by leaf scars (Clausen 1940b). The eggs of *Schizaspidia tenuicornis* Ashmead over-winter in the buds (Clausen 1923).

After hatching, the planidia (first instar larvae) wait for an appropriate host. In several species, an association of planidia with thrips has been reported (Clausen 1940a,

Wilson & Cooley 1972, Johnson et al. 1986). The planidia attach to the thrips and appear to feed on them (Johnson et al. 1986). This association, and others like it, could enhance the longevity of the planidia. After locating an appropriate host ant, the planidium, which is legless (Heraty & Darling 1984), climbs on it, and rides phoretically back to the ant nest attached by means of an anal sucker. In the ant nest, the planidium leaves the adult ant and locates the ant brood (larvae and pupae). Upon locating an ant larva, the planidium burrows beneath its cuticle (Wheeler & Wheeler 1937, Heraty & Wojcik unpublished). The parasite does not seem to develop until the ant larva reaches the late prepupal stage (Wheeler 1907, Clausen 1941, Kirkpatrick 1957). Most of the time, the parasite feeds at least partially as an endoparasite (Wheeler & Wheeler 1937), resulting in a characteristically deformed pupa called a phthisergate (Wheeler 1907, Van Pelt 1950). Phthisergates are found only in the ant subfamilies which have naked pupae (Myrmicinae, Dolichoderinae, Pseudomyrmicinae, some Formicinae). In ants which pupate in a cocoon (Ponerinae, some Formicinae), the host is attacked after the pupal case is formed, and the deformed host is consumed so that only the exoskeleton remains (Wheeler & Wheeler 1924, Parker 1932, Ayre 1962).

My studies of *Orasema* spp., parasitic on *Solenopsis* sp. in Mato Grosso, Brazil, indicate that each individual parasite requires more than one host pupa. The size of the mature parasite larvae and the variable size of the phthisergates indicate that each *Orasema* larvae may feed on more than one victim. The parasites that feed on hosts which pupate in cocoons can feed only on one host (Wheeler & Wheeler 1924, Parker 1932, Kirkpatrick 1957, Ayre 1962). Phthisergates that survive being fed upon by the wasp larvae are not able to complete development and eventually die (Wheeler 1910, Van Pelt 1950).

After the eucharitid larva terminates its feeding, it leaves the host (in those cases where the host is not in a cocoon) and pupates, in the case of *Orasema* spp. with the assistance of the worker ants (just as ant larvae are assisted in molting by worker ants) (Silveira-Guido et al. 1964, Wojcik unpublished). After pupation, the parasites are mixed in with the host pupae, and are cared for in the same manner as ant pupae (Silveira-Guido et al. 1964, Williams 1980, Wojcik unpublished). Eclosion of the adult parasites is assisted by worker ants in the same manner as they assist their own pupae (Silveira-Guido et al. 1964, Wojcik unpublished). The adult parasites are integrated completely into the ant society, being fed and groomed by the worker ants (Wheeler 1907, Williams 1980, Wojcik unpublished). When a nest is disturbed, the pupal and adult parasites are rescued by the ants in preference to their own brood (Wheeler 1907, Mann 1914, Wojcik unpublished). Generally the ants either ignore the parasites when they are leaving the nest (Clausen 1923, 1941, Kirkpatrick 1957) or they actively remove them from the nest (Ayre 1962). The adult parasites are sexually mature when they leave the nest as the females all contain fully developed eggs (Wheeler 1907, Kirkpatrick 1957, Ayre 1962). Mating takes place immediately upon exiting the ant nest, as the males hover over the ant nest or rest on surrounding vegetation (Clausen 1923, 1941, Ayre 1962, Wojcik & Jouvenaz unpublished). Studies have shown that *Orasema* sp. larvae, pupae and adults possess only *Solenopsis* spp. host cuticular hydrocarbons while in ant nests; but that *Orasema* sp. adults acquire species-specific cuticular hydrocarbons upon leaving the nest (Jouvenaz et al. 1988, Vander Meer et al. in press).

DIPTERA: PHORIDAE

Phorid flies are among the most abundant myrmecophiles known (Rettenmeyer & Akre 1968). Some are scavengers, some predators, some symphiles, some parasites, but most are of unknown status (Kistner 1982). The references to attempted or suspected oviposition by phorid flies on ants are almost as numerous as the flies themselves.

In light of the work of Rettenmeyer and Akre (1968) which showed that many of the species of phorids associated with army ants are not army ant parasites, the numerous references to the behavior of these phorids must be reevaluated and will not be discussed here.

The site of oviposition by the parasites varies with the species of fly: ant head (Eidmann 1937, Greene 1938, Disney 1980, 1982, 1986, Williams & Banks 1987), thorax (Feener 1987), or gaster (Wasmann 1918, Donisthorpe 1927, Disney 1982, 1986). In only a few instances have eggs (Williams & Banks 1987), larvae (Pergande 1901, Foresti & Pereira da Silva 1970, Williams & Whitcomb 1974), or pupae (Wojcik et al. 1987) been observed on or in the host. Generally, when the flies attack the ants, they do so after hovering over foraging trails (Steyskal 1944, Eibl-Eibesfeldt & Eibl-Eibesfeldt 1967, Disney 1981, 1986, Williams & Banks 1987), over nests during mating flights (Smith 1928), or over disturbed nests (Brues 1902, LaBerge 1953, Williams et al. 1973). A fly darts down and quickly attempts to deposit an egg on the ant (Williams & Banks 1987) or insert its ovipositor in the appropriate place (Feener 1987). In some cases the females attempt to oviposit by landing on the ground, running up to the ants, and jumping on them (Disney 1986). The ants sometimes appear stunned after oviposition (Smith 1928, Williams et al. 1973). The ants defend themselves vigorously against the flies (Donisthorpe 1927, Smith 1928, Greene 1938, Weber 1972, Williams et al. 1973, Burges 1979, Feener 1981, 1987, Williams & Banks 1987, Wojcik unpublished), often chasing the flies away before they can oviposit (Williams et al. 1973, Burges 1979).

In attacking monomorphic ants, flies choose any worker present (Disney 1982, 1986), but when attacking dimorphic or polymorphic ants, they attack majors preferentially (Feener 1981, Disney 1982, Williams & Banks 1987). *Atta cephalotes* L. minima workers ride on pieces of cut leaves being transported by major workers (Eibl-Eibesfeldt 1967, Eibl-Eibesfeldt & Eibl-Eibesfeldt 1967); with their sole function being to prevent oviposition by *Apocephalus* sp. flies on the major workers. Phorids probably oviposit selectively on major workers because this caste represents a more reliable food source, because it is longer-lived (Feener 1981, 1987, Williams & Banks 1987). Alate ants are much less common in colonies and are rarely exposed to parasitism. Only one instance of phorid parasitism of alate ants is known (Wojcik et al. 1987).

Parasitism, or even the threat of parasitism, by phorids places the *Pheidole* spp. (which are dimorphic) at a competitive disadvantage with competing fire ants (Feener 1981). A similar disadvantage may exist for all ants having majors which defend a foraging arena. Attacks by phorid flies may cause *Iridomyrmex cordatus* (Smith) to use covered foraging tunnels and *Pheidologeton* sp. to shift its foraging area daily (Disney 1986).

A different behavioral scenario has been reported for *Apodicrania termilophila* (Borgmeier), a fly found in *Solenopsis* spp. nests in Brazil (Williams & Whitcomb 1974, Williams 1980). The adult flies walk around on the disturbed nest and are ignored by the ants. Immature fly larvae are endoparasitic in ant larvae while mature fly larvae and pupae are found in the nest being tended by the ants (Williams 1980). The only other report of a phorid attacking an ant immature is that of *Apocephalus aridus* Malloch attacking a *Pheidole dentata* Mayr pupa (LaBerge 1953). At least some species mate at the same sites where females oviposit (Disney 1986).

SUMMARY

The true relationship of most myrmecophiles with their ant hosts is unknown. Much of the older literature on myrmecophilous parasites needs reevaluation in light of recent knowledge. There appears to be a great deal more variation in biology and behavior between related genera and species than has been assumed in the past, and many

earlier generalizations are not valid. Detailed studies on the biology and behavior of myrmecophiles will result in a better understanding of the relationships between ants and their inquilines.

ACKNOWLEDGEMENTS

I would like to thank Drs. J. H. Frank and E. D. McCoy for providing the opportunity to prepare and present this paper and for their useful and concise editorial comments. Drs. C. S. Lofgren, R. S. Patterson, and A. H. Undeen provided valuable reviews.

REFERENCES CITED

- AYRE, G. L. 1962. *Pseudometagea schwarzii* (Asm.) (Eucharitidae: Hymenoptera), a parasite of *Lasius neoniger* Emery (Formicidae: Hymenoptera). Canadian J. Zool. 40: 157-64.
- BRUES, C. T. 1902. New and little-known guests of the texan legionary ants. American Nat. 36: 365-78.
- BURGES, R. J. 1979. A rare fly and its parasitic behavior toward an ant (Diptera: Phoridae, Hymenoptera: Formicidae). Florida Ent. 62: 413-4.
- BUSCHINGER, A. 1986. Evolution of social parasitism in ants. Trends Ecol. Evol. 1: 155-60.
- CLAUSEN, C. P. 1923. The biology of *Schizaspidia tenuicornis* Ashm., a eucharid parasite of *Camponotus*. Ann. Ent. Soc. America 16: 195-217, pl. 14-15.
- . 1940a. Entomophagous insects. McGraw-Hill, New York, 688 p.
- . 1940b. The oviposition habits of the Eucharidae (Hymenoptera). J. Washington Acad. Sci. 30: 504-16.
- . 1941. The habits of the Eucharidae. Psyche 48: 57-69.
- DISNEY, R. H. L. 1980. A new species of *Apocephalus* (Diptera: Phoridae) that parasitizes *Atta texana* (Hymenoptera: Formicidae) in Texas. Z. Angew. Zool. 67: 47-50.
- . 1981. *Apocephalus laceyi* n.sp. (Diptera: Phoridae) attacking *Camponotus femoratum* (F.) (Hymenoptera: Formicidae) in Brazil. Ent. Scandinavica 12: 31-4.
- . 1982. Three new species of scuttle-fly (Diptera: Phoridae) that parasitize ants (Hymenoptera: Formicidae) in North America. J. Zool., London 197: 473-81.
- . 1986. A new genus and three new species of Phoridae (Diptera) parasitizing ants (Hymenoptera) in Sulawesi. J. Nat. Hist. 20: 777-87.
- DONISTHORPE, H. 1927. The guests of British ants. Routledge, London, 244 p.
- EIBL-EIBESFELDT, J. 1967. On the guarding of leafcutter ants by minima-workers. Naturwissenschaften 54: 346.
- EIBL-EIBESFELDT, I., and E. EIBL-EIBESFELDT. 1967. Das Parasitenabwehren der minima-Arbeiterinnen der blattschneider-Ameise (*Atta cephalotes*). Z. Tierpsychol. 24: 278-81.
- EIDMANN, H. 1937. Die Gäste und Gastverhältnisse der Blattschneiderameise, *Atta sexdens* L. Z. Morphol. Oekol. Tiere 32: 391-462.
- FEENER, D. H., JR. 1981. Competition between ant species: outcome controlled by parasitic flies. Science 214: 815-7.
- . 1987. Size-selective oviposition in *Pseudacteon crawfordi* (Diptera: Phoridae), a parasite of fire ants. Ann. Ent. Soc. America 80: 148-51.
- FORESTI, L. AND V. PEREIRA DA SILVA. 1970. Nota sobre a ocorrência de um forideo parasito de formigas saúvas (Diptera: Phoridae). Proc. 22nd Meet. Soc. Bras. Progres. Cien., p. 287.

- GREENE, C. T. 1938. A new genus and two new species of the dipterous family Phoridae. Proc. U.S. Natl. Mus. 85: 181-5.
- HERATY, J. M. 1985. A revision of the nearctic Eucharitinae (Hymenoptera: Chalcidoidea: Eucharitidae). Proc. Ent. Soc. Ontario 16: 61-103.
- . 1988. Of eucharitids and ants (Hymenoptera): biological conservatism and morphological explosion. Proc. 18th Int. Congr. Ent., Abstr.: 12.
- , AND D. C. DARLING. 1984. Comparative morphology of the planidial larvae of the Eucharitidae and Perilampidae (Hymenoptera: Chalcidoidea). Syst. Ent. 9: 309-28.
- HOWARD, R. W., C. A. MCDANIEL, AND G. J. BLOMQUIST. 1980. Chemical mimicry as an integrating mechanism: cuticular hydrocarbons of a termitophile and its host. Science 210: 431-3.
- , ———, AND ———. 1982. Chemical mimicry as an integrating mechanism for three termitophiles associated with *Reticulitermes virginicus* (Banks). Psyche 89: 157-67.
- HUGGERT, L., AND L. MASNER. 1983. A review of myrmecophilic-symphilic diapriid wasps in the Holarctic realm, with descriptions of new taxa and a key to genera (Hymenoptera: Proctotrupoidea: Diapriidae). Contrib. American Ent. Inst. 20: 63-89.
- JANET, C. 1897. Études sur les fourmis, les guêpes et les abeilles. Note 13: sur le *Lasius mixtus* l'*Antennophorus ulmanni* etc. H. Ducourtieux, Limoges, 62 p.
- JOHNSON, J. B., T. D. MILLER, J. M. HERATY, AND F. W. MERICKEL. 1986. Observations on the biology of two species of *Orasema* (Hymenoptera: Eucharitidae). Proc. Ent. Soc. Washington 88: 542-9.
- JOUVENAZ, D. P., R. K. VANDER MEER, AND D. P. WOJCIK. 1988. Chemical mimicry in a parasitoid, *Orasema* sp., (Hymenoptera: Eucharitidae) of fire ants. Proc. 18th Int. Congr. Ent., Abstr.: 243.
- KIRKPATRICK, T. W. 1957. Insect life in the tropics. Longmans, Green, London, 311 p.
- KISTNER, D. H. 1979. Social and evolutionary significance of social insect symbionts, Pp. 339-413 in H. R. Hermann [ed.], Social Insects. Academic Press, New York, Vol. 1, 437 p.
- . 1982. The social insects' bestiary, Pp. 1-244, in H. R. Hermann [ed.], Social Insects. Academic Press, New York, Vol. 3, 459 p.
- LABERGE, W. E. 1953. A note on a phorid parasite of *Pheidole dentata* Mayr. J. Kansas Ent. Soc. 26: 69.
- LACHAUD, J. P., AND L. PASSERA. 1982. Données sur la biologie de trois Diapriidae myrmécophiles: *Plagiopria passerai* Masner, *Solenopsia imitatrix* Wasmann et *Lepidopria pedestris* Kieffer. Insect. Soc. 29: 561-7.
- LOIACONO, M. S. 1981. Diapridos ectofilos sinfilos de la region Neotropical (Hymenoptera - Proctotrupoidea - Diapriidae). Rev. Soc. Ent. Argentina 40: 297-310.
- LOOS-FRANK, B., AND G. ZIMMERMAN. 1976. Über eine dem *Dicrocoelium*-befall analoge Verhaltensänderung bei Ameisen der Gattung *Formica* durch einen Pilz der Gattung *Entomophthora*. Z. parasitenkd. 49: 281-9.
- MANN, W. M. 1914. Some myrmecophilous insects from Mexico. Psyche 21: 171-84.
- MASNER, L. 1959. A revision of ecitophilous diapriid-genus *Mimopria* Holmgren (Hym., Proctotrupoidea). Insect. Soc. 6: 361-7.
- . 1976. Notes on the ecitophilous diapriid genus *Mimopria* Holmgren (Hymenoptera: Proctotrupoidea, Diapriidae). Canadian Ent. 108: 123-6.
- . 1977. A new genus of ecitophilous diapriid wasps from Arizona (Hymenoptera: Proctotrupoidea, Diapriidae). Canadian Ent. 109: 33-6.

- PARASCHIVESCU, D. 1982. Freiland- und Laboruntersuchungen zum Entwicklungskreislauf von *Dicrocoelium dendriticum* (kleiner Leberegel) in einem Wald/Feld-Biotop bei Würzburg (Unterfranken) unter besonderer Berücksichtigung des 2. Zwischenwirtes *Formica pratensis*. Waldhygiene 14: 141-57.
- PARKER, H. L. 1932. Notes on a collecting spot in France and a chalcid larva (*Stibula cynipiformis* Rossi) (Hymenop.: Eucharidae). Ent. News 43: 1-6.
- . 1937. On the oviposition habits of *Stibula cynipiformis* Rossi (Hymen., Eucharidae). Proc. Ent. Soc. Washington 39: 1-3.
- . 1942. Oviposition habits and early stages of *Oraema* sp. Proc. Ent. Soc. Washington 44: 142-5.
- PERGANDE, T. 1901. The ant-decapitating fly. Proc. Ent. Soc. Washington 4: 497-502.
- RETTENMEYER, C. W. 1961. Behavior, abundance and host specificity of mites found on Neotropical army ants. (Acarina; Formicidae; Dorylinae). Proc. XI Int. Congr. Ent. 1: 610-3.
- . 1962. Notes on the host specificity and behavior of myrmecophilous macrochelid mites. J. Kansas Ent. Soc. 35: 358-60.
- , and R. D. AKRE. 1968. Ectosymbiosis between phorid flies and army ants. Ann. Ent. Soc. America 61: 1317-26.
- RIEK, E. F. 1970. Strepsiptera, Pp. 622-35, in *The Insects of Australia*. Melbourne Univ. Press, 1,029 p.
- SILVEIRA-GUIDO, A., J. CARBONELL, AND C. CRISCI. 1973. Animals associated with the *Solenopsis* (fire ants) complex, with special reference to *Labbauchena daguerrei*. Proc. Tall Timbers Conf. Ecol. Anim. Control Habitat Manage. 4: 41-52.
- , J. CARBONELL-BRUHN, C. CRISCI, AND P. SAN-MARTIN. 1968. *Labbauchena daguerrei* Santschi como parásito social de la hormiga *Solenopsis saevissima richteri* Forel. Agron. Trop. (Maracay, Venezuela) 18: 207-9.
- , C. CRISCI-PISANO, P. SAN-MARTIN, AND J. CARBONELL-BRUHN. 1965. Investigations on the biology and biological control of the fire ant, *Solenopsis saevissima richteri* Forel in Uruguay. Final report. Depto. Sanid. Veg., Fac. Agron., Univ. Repub., Montevideo, Uruguay, 70 p., 36 pl.
- , P. SAN-MARTIN, C. CRISCI-PISANO, AND J. CARBONELL-BRUHN. 1964. Investigations on the biology and biological control of the fire ant, *Solenopsis saevissima richteri* Forel in Uruguay. Third report. Depto. Sanid. Veg., Fac. Agron., Univ. Repub., Montevideo, Uruguay, 67 p.
- SMITH, M. R. 1928. *Plastophora crawfordi* Coq. and *Plastophora spatulata* Malloch (Diptera: Phoridae), parasitic on *Solenopsis geminata* Fabr. Proc. Ent. Soc. Washington 30: 105-8.
- STEYSKAL, G. 1944. A new ant-attacking fly of the genus *Pseudacteon*, with a key to the females of the North American species (Diptera, Phoridae). Occas. Pap. Mus. Zool., Univ. Michigan 489: 1-4.
- TAKADA, H., AND Y. HASHIMOTO. 1985. Association of the root aphid parasitoids *Aclitus sappaphis* and *Paralipsis eikoeae* (Hymenoptera, Aphidiidae) with the aphid-attending ants *Pheidole fervida* and *Lasius niger* (Hymenoptera, Formicidae). Kontyû 53: 150-60.
- TESON, A., AND A. M. M. DE REMES LENICOV. 1979. Estrepsipteros parasitoides de himenopteros (Insecta - Strepsiptera). Rev. Soc. Ent. Argentina 38: 115-22.
- VANDER MEER, R. K., D. P. JOUVENAZ, AND D. P. WOJCIK. Chemical mimicry in a parasitoid (Hymenoptera: Eucharitidae) of fire ants (Hymenoptera: Formicidae). J. Chem. Ecol. (in press.)

- , AND D. P. WOJCIK. 1982. Chemical mimicry in the myrmecophilous beetle *Myrmecaphodius excavaticollis*. *Science* 218: 806-808.
- VAN PELT, A. F. 1950. *Orasema* in nests of *Pheidole dentata* Mayr (Hymenoptera: Formicidae). *Ent. News* 41: 161-3.
- WASMANN, E. 1918. Zur Lebensweise und Fortpflanzung von *Pseudacteon formicarium* Verr. *Biol. Zentbl.* 38: 317-28.
- WEBER, N. A. 1972. Gardening ants, the attines. *Mem. American Philos. Soc.* 92: 1-146.
- WHEELER, G. C., AND E. H. WHEELER. 1924. A new species of *Schizaspidia* (Eucharidae), with notes on a eulophid ant parasite. *Psyche* 31: 49-56.
- , AND ———. 1937. New hymenopterous parasites of ants (Chalcidoidea: Eucharidae). *Ann. Ent. Soc. America* 30: 163-73, pl. 1-2.
- WHEELER, W. M. 1907. The polymorphism of ants, with an account of some singular abnormalities due to parasitism. *Bull. American Mus. Nat. Hist.* 23: 1-93, pl. 1-6.
- . 1910. *Ants: Their Structure Development and Behavior*. Columbia Univ. Press, New York, 663 p.
- WILLIAMS, D. F., AND W. A. BANKS. 1987. *Pseudacteon obtusus* (Diptera: Phoridae) attacking *Solenopsis invicta* (Hymenoptera: Formicidae) in Brazil. *Psyche* 94: 9-13.
- WILLIAMS, R. N. 1980. Insect natural enemies of fire ants in South America with several new records. *Proc. Tall Timbers Conf. Ecol. Anim. Control Habitat Manage.* 7: 123-34.
- , J. R. PANAI, D. GALLO, AND W. H. WHITCOMB. 1973. Fire ants attacked by phorid flies. *Florida Ent.* 56: 259-62.
- , AND W. H. WHITCOMB. 1974. Parasites of fire ants in South America. *Proc. Tall Timbers Conf. Ecol. Anim. Control Habitat Manage.* 5: 49-59.
- WILSON, E. O. 1971. *The Insect Societies*. Belknap, Cambridge, MA, 548 p.
- WILSON, T. H., AND T. A. COOLEY. 1972. A chalcidoid planidium and an entomophilic nematode associated with the western flower thrips. *Ann. Ent. Soc. America* 65: 414-8.
- WING, M. W. 1951. A new genus and species of myrmecophilous Diapriidae with taxonomic and biological notes on related forms. *Trans. Roy. Ent. Soc. London* 102: 195-210.
- WOJCIK, D. P., D. P. JOUVENAZ, AND C. S. LOFGREN. 1987. First report of a parasitic fly (Diptera: Phoridae) from a red imported fire ant (*Solenopsis invicta*) alate female (Hymenoptera: Formicidae). *Florida Ent.* 70: 181-2.