EUCARITIDAE (HYMENOPTERA: CHALCIDOIDAEA): BIOLOGY AND POTENTIAL FOR BIOLOGICAL CONTROL

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ABSTRACT

The biology of Eucharitidae is summarized, and the potential for biological control of ant pests using members of this family is reviewed. The morphology, habits, and life histories of these wasps are described. Their associations with thrips, and with plants during oviposition, are considered. The need for comparing infested and uninfested host colonies in a controlled setting is stressed. Aspects of eucharitid biology that may affect their use in biocontrol are examined, including dispersal, levels of parasitism, and possible synergistic effects with other natural enemies. Possible conflicts of interest in the use of these wasps for biocontrol are considered.

RESUMEN

Se sumariza la biología de Eucharitidae y se revisa el potencial del control biológico de plagas de hormigas usando miembros de esta familia. Se describe la morfología, hábitos, y la historia de la vida de estas avispas. Se consideran sus asociaciones con tisanópteros y con plantas durante la oviposición. Se acentúa la necesidad de comparar colonias infestadas y no infestadas en un ambiente controlado. Se examinan aspectos de la biología de eucharitidos que pueden afectar su uso en control biológico, incluyendo dispersión, niveles de parasitismo, y posibles efectos sinérgicos con otros enemigos naturales. Se consideran posibles conflictos de interés en el uso de estas avispas como control biológico.
The family Eucharitidae consists of small wasps (Hymenoptera) of the superfamily Chalcidoidea. The type genus is *Eucharis* Latreille (1802). Now 44 genera and over 300 species are recognized (Heraty 1985). Although the distribution of eucharitids is nearly world-wide, their diversity is greatest in tropical regions. The group is treated here as distinct from the related Perlampidae and Pteromalidae, in accordance with the findings of Heraty & Darling (1984) and Heraty (1985). In this communication, aspects of the biology of eucharitids are surveyed, and an evaluation is made of the potential for using them in biocontrol of their ant hosts.

**SUMMARY OF EUCHARITID BIOLOGY**

The life histories of these wasps are known from observation of a small number of species. It can be surmised that all are parasites of ants (Hymenoptera: Formicidae), although the full range of hosts utilized by eucharitids (as a group or even within a single species) is uncertain. Table 1 shows the known host associations for eucharitids. The taxonomically limited host preference of eucharitids as a group stands in contrast to the wider host ranges in related chalcidoid families such as Perlampidae (Iwata 1976).

**TABLE 1. HOST ASSOCIATIONS OF EUCHARITIDS*.**

<table>
<thead>
<tr>
<th>Eucharitid Genus</th>
<th>Ant Genus</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Chalcera</em></td>
<td><em>Formica</em> (12)</td>
</tr>
<tr>
<td></td>
<td><em>Odontomachus</em> (4,5)</td>
</tr>
<tr>
<td><em>Epimetaegea</em></td>
<td><em>Myrmica</em> (9,12)</td>
</tr>
<tr>
<td><em>Eucharis</em></td>
<td><em>Cataglyphis</em> (12)</td>
</tr>
<tr>
<td></td>
<td><em>Formica</em> (4,10)</td>
</tr>
<tr>
<td></td>
<td><em>Messor</em> (10,12)</td>
</tr>
<tr>
<td></td>
<td><em>Myrmecia</em> (12)</td>
</tr>
<tr>
<td><em>Eucharomorpha</em></td>
<td><em>Myrmecocystis</em> (10)</td>
</tr>
<tr>
<td><em>Isomeral</em></td>
<td><em>Pheidole</em> (12)</td>
</tr>
<tr>
<td><em>Kapala</em></td>
<td><em>Ectatomma</em> (12)</td>
</tr>
<tr>
<td><em>Orasema</em></td>
<td><em>Camponotus</em> (6,12)</td>
</tr>
<tr>
<td></td>
<td><em>Odontomachus</em> (3)</td>
</tr>
<tr>
<td></td>
<td><em>Pachycondyla</em> (12)</td>
</tr>
<tr>
<td><em>Pseudochalcura</em></td>
<td><em>Pheidole</em> (4,6,8,12,13)</td>
</tr>
<tr>
<td><em>Pseudometagea</em></td>
<td><em>Solenopsis</em> (6,13)</td>
</tr>
<tr>
<td><em>Psilopaster</em></td>
<td><em>Wasmannia</em> (4,9,12)</td>
</tr>
<tr>
<td><em>Rhipipallas</em></td>
<td><em>Camponotus</em> (7,12)</td>
</tr>
<tr>
<td><em>Schizaspidia</em></td>
<td><em>Lasius</em> (1,6)</td>
</tr>
<tr>
<td><em>Stilbula</em></td>
<td><em>Pheidole</em> (12)</td>
</tr>
<tr>
<td><em>Tricoryna</em></td>
<td><em>Myrmecia</em> (5,12)</td>
</tr>
<tr>
<td></td>
<td><em>Calomyrmex</em> (5,12)</td>
</tr>
<tr>
<td></td>
<td><em>Camponotus</em> (2,12)</td>
</tr>
<tr>
<td></td>
<td><em>Odontomachus</em> (8,4,5)</td>
</tr>
<tr>
<td></td>
<td><em>Camponotus</em> (3,4,5,10)</td>
</tr>
<tr>
<td></td>
<td><em>Polyrhachis</em> (5,11,12)</td>
</tr>
</tbody>
</table>

The appearance of these wasps is varied and often bizarre. In adult eucharitids, the head is small and the mandibles are falcate. In some, the head is triangular in frontal view and thin along the antero-posterior axis. The thorax of many forms is robust, and often sculptured distinctively. The scutellum in many species is modified, sometimes with a bifurcate process extending posteriorly beyond the tip of the abdomen (Clausen 1940a). The abdomen is petiolate, and in some forms the exposed portions of the terminal segments are small. This gives the appearance of compression or telescoping of the terminal abdominal segments (Ashmead 1897, Clausen 1940b).

The first-instar larva of the eucharitids is termed a planidium. The tergites of this legless larva are highly sclerotized and are mostly ring-shaped. Thus, they do not surround the body completely. The tergites allow some flexibility at the intersegmental membranes and telescoping of the segments (Clausen 1940b,c, Tripp 1961). Although Malychev (1966) considered Eucharitidae and Perlampidae to represent the so-called intermediate parasitic phase in the evolution of the Terebrantia (parasitic Hymenoptera in the wide sense, as opposed to the Aculeata), it has become evident through comparative morphological and systematic studies (Heraty & Darling 1984) that the planidium is a derived larval form within the Terebrantia.

Planidial larvae are known from two other hymenopteran families, namely the Ichneumonidae (subfamily Eucerininae; Tripp 1961) and Perlampidae (Smith 1912, Heraty & Darling 1984). Within the dipteran families Acroceridae, Tachinidae, and Sarcoptagidae (Wilson & Cooley 1972), and in the lepidopteran family Epiprydopidae (Kirkpatrick 1957) are species with legless first-instar larvae that search actively for a host. These larvae are sometimes called planidia, but possess a different morphology than the hymenopteran planidia.

The eucharitid planidium hatches from eggs deposited usually in or on plants (Clausen 1941). A caudal sucker and in some cases stout spines are used by the planidium to assume an upright position when waiting for a host (Clausen 1940c). The method of movement or transport of the planidium to the host brood has not been studied in detail, but it is thought generally that it may attach to an adult foraging ant, and be carried back into the nest. Here it develops as a parasite of an immature ant (Clausen 1941). In several cases studied, the planidium remains attached to the ant larva until the host begins to pupate, the parasite feeding comparatively little through one or more puncture(s) made in the integument. In some cases the planidium feeds with most of its body inside the host, with the caudal end emerging from the wound site. Tracheal breathing has not been demonstrated in the planidium, but the small size of these larvae would allow respiration by diffusion through the body surface. Indeed, the absence of spiracles in planidia is seen as a derived trait in this group by Heraty & Darling (1984).

Once the host enters the pupal stage, feeding by the eucharitid is intensified. The parasite completes its development swiftly, and adults emerge within the ant nest (Heraty 1985). Some eucharitids consume the majority of the host pupae before beginning their own pupation (Ayre 1962), while others cause characteristic deformations of the host pupae (Wheeler 1907) which involves arrested development and eventual death. Moving out from the host colony, the adult parasites usually mate soon (within several hours) after emergence. In some cases females have been found to oviposit close to the host colony from which they emerged. Observations indicate that adults of some species do not feed (Clausen 1941).

Poor dispersal, as well as the specificity for particular host plants for oviposition, are among the factors thought to contribute to the seeming rarity of some eucharitids (Ayre 1962, Clausen 1941). However, some eucharitids are very good fliers (J. M. Heraty, Texas A&M University, College Station, TX, personal communication). Also, the known oviposition plants for some species are weeds throughout much of the ranges of the host ants, and the presumed specificity in oviposition plants may be an artifact of the limited data available.
The adult female eucharitid carries an abundance of eggs. These are minute, about 0.1 to 0.2 mm long, and stalked (Clausen 1940c). Dissections of females of *Pseudometagea schwarzi* (Ashmead) before and after oviposition (Ayre 1962) indicated that the full complement of approximately 450 eggs was deposited by a female during her life. The eggs are fully developed upon emergence of the adults from the nest. Individual females of some species of eucharitids may deposit as many as 10,000 to 15,000 eggs (Clausen 1940a) during their lives.

Eucharitid eggs are laid on or in the tissues of plants, but the exact site of oviposition on the plant, as well as the typical number of eggs laid per oviposition event, varies among different species. Eggs overwinter in some species (Clausen 1940a). They may be laid in overwintering leaf buds of mulberry, chestnut, oak, or birch; on expanding leaf and flower buds; or in leaf tissue incisions (Clausen 1940a,b). Some forms which oviposit into the surface tissues of leaves may deposit the eggs in characteristic designs or patterns. Some oviposit into seed receptacles, where the eggs may be dispersed on wind-borne seeds (Parker 1937).

The apparent specificity of oviposition sites chosen by eucharitids has been deduced from records based on field observations. These indicate that a given eucharitid oviposits on one or a few types of plant soon after emerging from the host colony (Clausen 1940a). Thus, the range of possible oviposition plants for a given species is uncertain. *P. schwarzi* is known to utilize several different plant species for oviposition, but it is not clear how this broad preference may affect dispersal of the parasite. It may limit distribution of the parasite (Ayre 1962) by allowing suitable oviposition sites to be found close to the nest from which the female just emerged. Or it may promote dispersal if, for example, a mated female is swept by winds away from the ant nest from which it emerged, and finds suitable oviposition sites near another host colony.

Some eucharitids oviposit at sites of prior oviposition by thrips. The eucharitid larva then attaches to the larval thrips, and may consume a portion of the hemolymph of the thrips. Probable feeding of *Oraesma* sp. on nymphal *Sericothrips* sp. was noted by Johnson et al. (1986), who suggested that thrips may serve as a facultative alternate host until the suitable host was found. Females of the eucharitid *Pseilogaster antennatus* Gahan will only deposit their eggs in close association with the eggs of *Selenothrips rubrocinctus* (Girard) (Clausen 1940a). In these types of interactions, it has been suggested that the planidium, in a phoretic relationship with the thrips, is transferred eventually to the ant host (Clausen 1940a). However, with at least one species of *Oraesma* in Florida (L. Davis, USDA, ARS, Gainesville, FL, personal communication), and with *P. antennatus* (Clausen 1940a), the thrips involved are not tended regularly by ants. In the case of the *Oraesma* in Florida (L. Davis, personal communication), as well as the eucharitid associated with the thrips *Frankliniella occidentalis* (Pergande) (Wilson & Cooley 1972), planidia were found imbedded partially in the body of a thrips in a manner similar to that in which they are found in ant larvae. However, no eucharitids are known to complete their development on thrips; therefore, the latter should not be considered alternate hosts. The thrips are at this time considered to be carriers or accidental hosts (J. M. Heraty, personal communication). The role of thrips in the life cycle of any eucharitid thus remains unclear.

In the case of *P. schwarzi*, development proceeds through three instars prior to pupation (Ayre 1962). During the first instar, the planidium, developing inside the ant larva, increases greatly in size. Development proceeds quickly, pupation occurring only four to five days after the first molt. The parasite is shed, prior to its own pupation, at the host's prepupal molt. At this point the wasp becomes an ectoparasite and consumes more or less the entire host (leaving only the integument). Precor digestive, perhaps by regurgitation of enzymatic alimentary secretions, may facilitate such a complete consumption of the host. This possibility is supported by the observation in thin sections of destruction of host epithelial tissue at the locus of feeding of the first instar parasite.
A switchover from endoparasitism to ectoparasitism is not limited to a single eucharitid species. Development of an *Oraexam* sp. on fire ant (*Solenopsis* sp.) brood in Brazil is also known to involve such a change in the ontogeny of the parasite (D. P. Wojcik, USDA, ARS, Gainesville, FL, personal communication).

After consuming the host, *P. schwartzii* pupates, and the worker ants sometimes assist in the emergence of the adult from the pupal skin. In some cases the workers carry the adults away from the nest, in a behavior that appears similar to that used for refuse disposal. Hostile behavior was not observed to be directed toward the parasites (Ayre 1962). In disturbed fire ant nests in Brazil, the worker ants rescue *Oraexam* pupae and adults before they rescue ant brood (D. P. Wojcik, personal communication).

Thus, the eucharitids are a group with varied habits. Species exhibit differences in fecundity, oviposition behavior, developmental times, stage morphology, and host preference.

**Potential for Using Eucharitids in Biological Control of Ant Pests**

Many ant species have been considered pests (Table 2). Some of these, such as species of *Solenopsis* and *Pheidole*, are known to be hosts of eucharitids. The assessment of the potential of these wasps in biological control of pest ants is made difficult by the paucity of information on the factors affecting levels of parasitism and colony vigor. It is also hindered by a scarcity of biological and systematic information for the eucharitids. Since ant colonies may be maintained in the laboratory, studies should be instigated in controlled conditions in which uninfested (control) ant colonies are compared to colonies infected with eucharitids.

Laboratory studies conducted with different ant-eucharitid combinations would allow an assessment of the impact of variations in abiotic factors such as temperature and humidity on levels of parasitism. These studies would suggest which eucharitids might best be used to induce mortality in a given environment. Biotic factors affecting mortality induced by eucharitids could also be investigated if colony size and composition were varied in the laboratory, and the level of parasitism could be varied in different

**TABLE 2. Some ant genera with species considered to be pests.**

<table>
<thead>
<tr>
<th>Ant Genus</th>
<th>Reference(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atta</td>
<td>1,5,6</td>
</tr>
<tr>
<td>Camponotus</td>
<td>1,2,3,4,5,6</td>
</tr>
<tr>
<td>Crematogaster</td>
<td>6</td>
</tr>
<tr>
<td>Formica</td>
<td>1,3</td>
</tr>
<tr>
<td>Iridomyrmex</td>
<td>1,2,5,6</td>
</tr>
<tr>
<td>Lasius</td>
<td>2,5,6</td>
</tr>
<tr>
<td>Monomorium</td>
<td>2</td>
</tr>
<tr>
<td>Myrmecia</td>
<td>2,6</td>
</tr>
<tr>
<td>Pheidole</td>
<td>2,6</td>
</tr>
<tr>
<td>Pogonomyrmex</td>
<td>2</td>
</tr>
<tr>
<td>Polyrhachis</td>
<td>7</td>
</tr>
<tr>
<td>Solenopsis</td>
<td>6</td>
</tr>
<tr>
<td>Tapinoma</td>
<td>2,5,6</td>
</tr>
<tr>
<td>Technomyrmex</td>
<td>2</td>
</tr>
<tr>
<td>Tetramorium</td>
<td>5,6</td>
</tr>
</tbody>
</table>

experiments by altering the ratios of wasps to ants. Analyzing the mortality induced by eucharitids in a quantitative and rigorous fashion may allow a reliable assessment to be made of the potential for using the wasps in applied biocontrol.

In evaluating the potential for using eucharitids in biocontrol of ant pests, it is useful to consider aspects of (1) dispersal, (2) levels of parasitism, (3) habits of the host that may affect parasitism, and (4) the effect of these and other factors on the survival and vitality of the host colony. In order to evaluate the potential for biocontrol of a given eucharitid, we must have information on these factors, as well as an understanding of the dynamics of the choice of the host species and oviposition site. The host range as well as the range of suitable oviposition sites should be known before a eucharitid is used in a biocontrol project, in order that beneficial ant fauna and flora are not affected adversely.

In a given area there may be found infested and uninfested colonies of a given host ant species. Dispersal of these parasites may be affected by the flight ability of the adults, and by the area controlled by the host colony. These parameters vary widely among different species within the respective groups. Although it has been thought (Clausen 1941, Ayre 1962) that the area monopolized by the hosts tends to limit dispersal of the parasites, this has not been proven. The short life spans of some adult eucharitids, requirements for certain oviposition plants, and abiotic factors such as wind may also affect dispersal.

Poor dispersal may hinder the establishment of an introduced biocontrol agent, but establishment may not be required in some control programs. The provision of plants to promote oviposition by the adult parasites may be accomplished in the field by setting out potted plants close to an infested colony. If the plants are monitored for the presence of eucharitid eggs, they could be moved at appropriate times to facilitate distribution of the parasites to other (uninfested) colonies.

The factors influencing the level of parasitism in a colony are not well understood. Parasitism of larvae of the ant Lasius neoniger Emery by P. schwartzii was found by Ayre (1962) to exceed 30% in some colonies. The levels of parasitism dropped with increasing distance from centers of infestation. In one instance collection data indicated a drop to 30% parasitism at a distance of 120 feet from the center of infestation. Parasitism of Camponotus sp. by Stilbula tenuicornis (Ashmead) was reported to be 47% by Clausen (1841), but the next year the level declined to 16%.

It is not clear how levels of parasitism within a colony affect colony vitality and longevity. Temporal determinants of parasite development may interact with seasonal patterns of development of host brood. As noted by Ayre (1962), an important factor may be the impact of parasitism on the worker:brood ratio.

Ants are not known to exhibit any behavior intended to harm or to prevent parasitism by a eucharitid. The behaviors which appear to aid the parasite, such as helping an emerging adult eucharitid out of the host cocoon and the transporting of adults away from the center of the colony, may be normal behavior patterns of the workers. However, it should be noted that interactions between the parasites and their hosts within the nest have been observed for a very limited range of species. There has been no rigorous study of these interactions for any eucharitid-plus-host system.

One approach to measuring the success of a biocontrol project involving eucharitids would be to determine the effects of parasitism on colony longevity or vitality. Colony vitality may be measured as the number of reproductive forms (or the ratio of these to workers in the colony) produced during the regular season of production of such forms. Vigorous biotypes of the parasites could be screened and selected in the laboratory using artificial colonies. Such studies might yield data that suggest other control practices that act to enhance the level of parasitism within an infested colony. The problem of providing the correct conditions in the laboratory to approximate those occurring in
the field is not trivial, but such an approach would surely yield insights into the interrelations between abiotic factors, parasitism, and other biotic factors influencing total mortality of the host brood.

Experimentation may reveal a synergistic action of eucharitids with other natural enemies of ants. As with any endeavor to achieve biological control, preliminary investigation must be directed toward the discovery and characterization of natural enemies of the pest.

The possibilities for achieving increased host mortality using more than one natural enemy of ants should be investigated. For example, fire ants may be parasitized by phorid flies (Williams & Whitcomb 1973, Williams 1980, Borgmeier 1963), and colonies may be weakened by social parasites (Bruch 1930, Silveira-Guido et al. 1973). There is evidence that a virus infects fire ants (Avery et al. 1977), and eucharitids may be able to spread these pathogens through a colony. Natural enemies of ants, including fungi, nematodes, and strepsipterans (Britton et al. 1970), may act synergistically in the control of their hosts.

An issue important in applied biocontrol projects is the potential for conflict of interest between the goals of the project and the interests of others. There are two possibilities in the ant-eucharitid system as regards conflict of interest. First, the wasps are known to cause damage to the tissues of plants during oviposition. This may result in economic damage to crops, as noted, for example, in tea (Das 1964, 1965, Kerrich 1963) and bananas (Kerrich 1963). This type of damage must be considered in biocontrol projects involving eucharitids. It could be prevented or minimized by proper choice of locations chosen for dispersal of the eucharitids, as well as the choice of a eucharitid species which is known not to oviposit on the types of crop plants being grown in the vicinity.

The other form of possible conflict of interest may occur where ants are considered beneficial in some circumstances but pests in other contexts. The fire ants provide an example of this type of conflict, as they have been considered to be beneficial as predators of crop pests in certain agroecosystems (see, for example, Table 8.2 in Lofgren 1986). In many situations, however, fire ants are considered a direct threat to human welfare (they sting, and some people are allergic to their venom; Baer et al. 1979). In addition, they are also known to reduce the yield or quality of certain crops (Adams et al. 1976, Adams et al. 1983, Smitile et al. 1983, Glancey et al. 1979). In view of the possible types of conflict of interest in controlling ants, a limited dispersal of eucharitids may be a valuable trait. It would provide localized control while allowing the beneficial presence of the host ant in nearby areas to continue.

There are no known natural enemies of eucharitids, but the unknown degree of host specificity of these parasites is a hindrance to their effective use as control agents. There is much potential in their use in the control of ant pests, but much work needs to be done in assessing their effect on ant brood mortality. This may be done initially in the laboratory, and subsequently in field tests. The influence of other biocontrol organisms that may act synergistically with eucharitids to debilitate the hosts should be investigated. In addition, the oviposition habits of eucharitids used as biocontrol agents must be defined in order to allow optimization of the control of host numbers, and to avoid conflicts of interest.

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CURRENT STATUS OF THE USE OF PREDATORS, PATHOGENS AND PARASITES FOR THE CONTROL OF MOSQUITOES

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ABSTRACT

The control of mosquito populations with predators, pathogens and parasites is discussed. Fish and canibalistic mosquitoes offer the greatest potential as mosquito predators. Bacterial pathogens such as Bacillus thuringiensis var. israelensis and B. sphaericus along with the fungal pathogens Coelomomyces spp., Culicinomyces clavosporus, and Lagendidium giganteum are also discussed. The parasites of mosquitoes are limited, but the parasitic nematode Romanormis culicivorax is discussed.

RESUMEN

Se discute el control de la población de mosquitos con predadores, patógenos y parásitos. Peces y mosquitos caníbales ofrecen el mayor potencial como predadores de mosquitos. También se discuten los patógenos bacterianos como Bacillus thuringiensis var. israelensis y B. sphaericus, junto con los patógenos fungosos Coelomomyces spp., Culicinomyces clavosporus, y Lagendidium giganteum. Los parásitos de los mosquitos son limitados, pero se discute el parásito nematodo Romanormis culicivorax.

Mosquitoes (Diptera: Culicidae) provide a major threat to human health and well-being. Diseases vectorized by mosquitoes include malaria, yellow fever, dengue, encephalitis and filariasis. Harwood & James (1979) report that approximately 300 million people world-wide suffer from mosquito borne diseases, primarily malaria and filariasis. The livestock industry also suffers economic losses from mosquitoes. Steelman (1976) estimates a loss of 10 million dollars annually in the dairy industry alone can be attributed to mosquitoes. Mosquitoes also are an important nuisance in many parts of the