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THE HABITS OF THE EUCHARIDÆ

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From many points of view the Eucharidæ are the most interesting of the families of Hymenoptera of parasitic habit. Though world-wide in distribution their habits and host relationships are little known. Studies thus far made have shown a parallelism in habit and development with the Perilampidæ, though revealing an even higher degree of specialization and greater variations between species. Accounts are being presented elsewhere of the oviposition habits and on the morphology of the immature stages of the family, and the present article deals principally with the host preferences and the habits of the adults and larvæ.

Host Preferences

All species of Eucharidæ are, so far as known, parasitic upon the mature larvæ or pupæ of ants. The host preferences of the species observed by the writer, so far as they were determined, are as follows:

<i>Species</i>	<i>Host*</i>	<i>Country</i>
<i>Chalcura deprivata</i> (Walk.)	<i>Odontomachus hæmatodes</i> L.	Ceylon
<i>Kapala terminalis</i> Ashm.	<i>Odontomachus hæmatodes</i> <i>insularis pallens</i> Wheeler	Cuba
<i>Kapala</i> sp.	do.	Cuba
<i>Eucharis scutellaris</i> Gahan	<i>Formica fusca fusca</i> <i>japonica</i> Mots.	Chosen
<i>Schizaspidia convergens</i> (Walk.)	<i>Odontomachus hæmatodes</i> L.	Ceylon
<i>Stilbula tenuicornis</i> (Ashm.)	<i>Camponotus herculeanus</i> <i>japonicus</i> Mayr.	Japan
	<i>Camponotus herculeanus</i> <i>ligniperdus obscuripes</i> Mayr.	Chosen

*Determinations by W. M. Mann

Wheeler and Wheeler, in 1937, compiled the records of host preferences published up to that date, and their list comprises 31 species, of 15 genera. The questionable generic assignment of many species makes it difficult to summarize generic preferences, but 4 species of *Oreasema* are recorded only from *Pheidole*, 1 from *Solenopsis*, 1 from both these genera, and 1 from *Wasmannia*. *Eucharis* has been reared from *Messor*, *Cataglyphis*, *Myrmecia*, and *Formica*. Three species of *Stilbula* are known to parasitize *Camponotus*, while species of *Chalcura*, *Kapala*, and *Rhipipallus* have been reared from several subspecies of *Odontomachus hæmatodes*. Considering that the larval and pupal stages of most of the castes of the different species of ants known to be parasitized by Eucharidæ are usually of sufficient size to bring the parasites to maturity, we might assume that they will all be subject to attack. The available evidence, however, indicates that in some species certain castes are exempt, and these are not the same among different species. Wheeler (1907) states that only the soldiers, males, and females of *Pheidole instabilis* Emery are parasitized by *Oreasema*, as the workers are too small to provide sufficient food for the larvæ of the parasite. He also indicates that the single worker form of *Solenopsis validiuscula* Emery is immune to attack by *O. coloradenis* Wheeler for the same reason.

In his studies on *Stilbula cyniformis* Rossi, Parker (1932) noted that attack was limited to the large-headed wingless workers and to the winged forms of the same size, which are presumed to be the males.

An examination of the immature stages found in the nest of *Odontomachus hæmatodes* in the Botanical Garden at Peradeniya, Ceylon, indicated that only the slender, small-headed pupæ were parasitized by *Chalcura deprivata*, whereas *Schizaspidia convergens* developed also upon the pupæ of the larger workers having very large heads and long and heavy mandibles. These latter comprised a large portion of the host population.

Sufficient information is not yet available to explain the above limitations of eucharid attack to certain host castes. Even in *Solenopsis validiuscula*, mentioned above, where size is assumed to be the determining factor, some other cause may well be responsible. It is known that many para-

sitic insects possess a great adaptability in respect to the quantity of food required to bring them to maturity, and because of this some adults of certain species are as much as fifty times as large, by volume, as others.

Habits of the Adults

The adults emerge from the ant nest during the morning hours, the males usually slightly preceding the females, and mating takes place almost immediately. Swarms of males of *Stilbula tenuicornis*, numbering 100 or more, have been observed hovering in the air 1 or 2 feet above the entrance to a *Camponotus* nest (Clausen, 1923). As the females appeared at the entrance to the burrow they were pounced upon before they could take flight. A similar congregation of males over the host nest has been noted in *Eucharis scutellaris*. The stimulus which attracts these males to the host nest is not known; it may be the nest odor, or they may be able to detect the presence of the freshly-emerged females of their own species in the nest. Not all species show this extreme agitation and activity on the part of the males. Those of *Kapala terminalis* rest quietly upon foliage nearby and become active only when a female emerges from the host burrow.

Wheeler (1926) records the observations of W. M. Mann on a species of *Orasema*, five males of which were found mating with female pupæ in an ant nest.

The ants of the host colonies usually pay very little attention to the eucharid parasites following transformation of the latter to the adult stage, though Wheeler mentions that *Pheidole* workers carry the adults of *Orasema* about in the nest and even feed them. Field observations on *Eucharis scutellaris* revealed many freshly emerged adults being dragged about over the ground by *Formica* workers, evidently in an effort to carry them back into the nest.

Observations indicate that the adults of the majority of species do not feed. The entire quota of eggs in the ovaries is fully developed at the time of emergence of the adult female, and in many species these are all deposited that same day, so there is little need for food. Females of *Kapala furcata* (F.) of Panama were observed upon foliage heavily

infested with aphids and apparently they were feeding upon honeydew. This was noted only during the afternoons and was upon a plant species different from that utilized for oviposition earlier in the day.

The oviposition habits of the Eucharidæ are extremely varied but in no instance are the eggs laid in the nest of the host. They may be placed in masses in overwintering buds of trees, in expanding leaf and flower buds, or in seed receptacles or pods, singly or in small groups in incisions in leaf tissue, or at random upon the surface of leaves. One species, *Psilogaster antennatus* Gahan, oviposits on the leaf surface only in the immediate vicinity of a freshly deposited thrips egg.

The obligatory inclusion of one or more plant species, for oviposition purposes, in the economy of each species of Eucharidæ serves as a very definite check upon its local distribution. The presence or absence of the required oviposition plants directly governs distribution, and this, in many instances, is much more of a limiting factor than is host distribution or abundance. It is because of this that eucharid colonies are almost invariably of small size and widely separated. Each of the species which has been studied is known through definite colonies of very limited extent rather than of general occurrence in a locality. The several species found in the Botanical Gardens at Peradeniya, Ceylon, which are all parasitic on *Odontomachus*, were found to infest only the ant colonies situated immediately beneath the trees in which the eggs are laid. This is believed to be due to the members of these colonies monopolizing the areas in which their nests are situated. The exclusion of ants from other nests prevents their coming in contact with planidia on the surface of the ground beneath the trees, and consequently these latter are not transported to more distant nests.

The distribution of a eucharid parasite is thus controlled by a factor which may have no influence upon the host itself and, as a result, the latter may be entirely free from attack over the greater part of its range. The Eucharidæ are therefore relatively minor influences in the natural control of ants. Even within the colony limits the parasitization is relatively low. The colony of *Stilbula tenuicornis* under

observation at Koiwai, Japan, showed a maximum parasitization of 47 percent in a single nest in 1921. A total of approximately 10 million eggs, over 4 million of which were in a single tree, were deposited that season in an area about 100 yards square, yet in 1922 the resultant maximum parasitization declined to 16 percent.

The study of the biology and habits of the Eucharidæ was long handicapped by difficulties in associating the oviposition habits of the females with the immature stages in the ant nests. Sufficient is now known regarding the general habits of the family so that, in most cases, the infested nest can be found if a female can be found or captured or, if the infested nest from which adults are emerging is first found, the oviposition habit can be quickly determined. The females are intent upon oviposition immediately after emerging from the nest and, as they fly very slowly and can be readily kept in view, they can be followed and their method of oviposition observed. This normally takes place within 1 hour after emergence and often almost immediately.

If adult females have been captured or observed, the host nest can be located without difficulty. These females are usually limited to a radius of not exceeding 50 feet from the nest, and they fly no farther than is necessary to reach a tree or plant suitable for oviposition. In many species the actual nest entrance can be detected by the swarm of eucharid males hovering over it. In other cases the size of the parasites greatly restricts the number of possible hosts, so a relatively small number of nests need be examined definitely to establish the association. *Chalcura deprivata* and *Schizaspidia convergens* of Ceylon and *Kapala terminalis* and *Kapala* sp. of Cuba are all parasites of *Odontomachus*. A consideration of the size of the adults observed ovipositing in trees, and of the ant species present in the immediate vicinity, indicated that *Odontomachus* was the only one present of sufficient size to accommodate the parasites. In each case the first nest that was excavated confirmed the conjecture that this was the host.

Habits and Development of the Immature Stages

During the course of incubation the eggs change in color from the original translucent white to deep amber, this

being due to the pigmentation of the skin of the developing embryo. In some species, notably *Stilbula cyniformis*, there is a distinct bluish reflection in the older eggs. The egg stalk, of course, retains its original color.

The very incomplete information on the habits of the planidia during their free-living period indicates that they attach themselves to worker ants and are thus carried into the nest, where they transfer to the larvæ. Those of *Stilbula tenuicornis* were found upon the twigs and foliage of aphid-infested plants frequented by worker ants in their search for honeydew. In the alert position they stand erect upon the caudal sucker and the body is braced by the long spines of the posterior abdominal segment and by the spinelike projections of the pleural plates. They quickly attach themselves to any moving object that comes within reach.

In the study of *Kapala terminalis* and *Kapala* sp. in Cuba it was found that the planidia have a highly developed capacity for jumping. They stand erect upon the caudal sucker and, without any distinguishable preliminary movements, hurl themselves into space. The horizontal distance covered is about 10 millimeters, which is approximately one hundred times their own body length. This habit, if general in the family, would explain how *Parapsilogaster læviceps* Gahan and *Kapala terminalis*, which oviposit in incisions in leaves, reach their hosts. In their foraging the *Odontomachus* workers do not ascend trees and consequently, if the parasite planidia remained upon the foliage, they would have no opportunity to attach themselves to an ant carrier and be transported into the nest. By jumping they reach the ground, where they may encounter worker ants of the host species.

The intervention of a carrier other than the adult of the host species is apparently obligatory in *Psilogaster antennatus* Gahan. The eggs of the parasite are deposited on the leaf surface only in the immediate vicinity of an egg of *Selenothrips rubrocinctus* (Giard), and the eggs of the two species hatch simultaneously. As the thrips larva scrambles about among the erect eggs of *Psilogaster* the planidia of the latter attach themselves to it and are carried away. They remain attached by their mandibles to the thrips larva,

but without noticeable feeding, until its first molt, when they disappear. One young larva collected in the field carried 53 planidia upon its body, yet did not seem to be inconvenienced thereby. These thrips are not attended by ants nor is the host of the parasite known, so the significance of this relationship cannot yet be determined.

Stage of the Host Which Is Attacked

Because of the habits of the planidia, which are carried into the nests by the adult ants, it is assumed that that transfer is effected mainly, if not entirely, to the ant larvæ rather than to the pupæ. This would seem to be obligatory in attack upon hosts which pupate in cocoons. In all species which have been studied the parasite planidia have been found upon the larvæ, even though development may not take place upon this stage. The majority of species permit the host to attain the perfect pupal form before death. Wheeler found that feeding by the larvæ of *Orasema* was upon the prepupæ and that the host never attained the typical pupal form. He designates the deformed host pupæ, with reduced heads and appendages, as phthisergates, while depleted semipupæ of females and males, such as result from attack of *Orasema* upon *Pheidole instabilis*, are designated as phthisogynes and phthisaners, respectively. The abstraction of a portion of the body fluids has halted the development of these individuals and they eventually die. *Schizaspidia convergens* also kills its host in the prepupal stage and the antennal sheaths never extend beyond the middle of the thorax.

There are a number of variations in habit of the immature stages of the species which develop ectoparasitically. These relate to the position of the larva on the host body, the stage of its development at the time of transfer to the host prepupa, and the time at which death of the host takes place. After the planidia reach the host larvæ in the nest they attach themselves within a relatively limited area on the body. Those of *Kapala terminalis* are invariably found laterally on the throat, while *Stilbula tenuicornis* and *Schizaspidia* are found there or in one of the sutures between the thoracic segments. Occasional individuals attach themselves to the abdomen.

In the earlier account of the biology of *Stilbula tenuicornis* it was pointed out that the planidium feeds and attains its full growth while still upon the *Camponotus* larva, and that the first molt takes place just as the host is transforming to the pupal stage. The newly-formed second-instar larva makes its way from the larval skin of the host as soon as the latter is freed from the prepupa at the point of attachment of the parasites and it then takes up a feeding position, constant for the species, on the pleural region of the metathorax, beneath a wing pad, or beneath one of the hind legs, of the pupa. The exuviae of the planidium remains attached to that of the host larva and is found with it at the base of the cocoon. This is the only species known to undergo the first molt prior to transfer to the host pupa. *Orasema wheeleri* Wheeler, *S. cyniformis*, *Chalcura deprivata*, *Eucharis scutellaris*, and *Kapala* sp. are still first-instar larvae at the time of the host molt. The planidia of *Kapala* sp. are fully fed and consequently fully distended at this time, whereas those of *C. deprivata* and *E. scutellaris* show no increase in size or separation of the segmental bands, and they presumably do not feed extensively until the host pupa is reached.

The increase in size of the planidium before the first molt is relatively enormous, and Parker (1932) mentions an increase of 1,000 times in *Stilbula cyniformis*. In *Schizaspidia convergens* the body length is approximately 1 millimeter as compared with one-tenth that length for the newly hatched individuals, and the increase in volume approximates the figure given by Parker. There was some doubt that this larva was actually the first instar, rather than the early second with the exuviae still enveloping the body. Upon close examination, however, the mandibles of the heavily sclerotized first-instar head were seen to move, and when the larva was removed from the host and then replaced the mandibles were again imbedded in the skin.

As soon as the larva, in either its first or early second stage, becomes attached to the host prepupa or pupa its feeding and consequent growth are exceedingly rapid. Only a single feeding puncture is made, and in *Stilbula tenuicornis*, *Schizaspidia convergens*, *Kapala terminalis* and *Chalcura deprivata* the contents of the host pupa are completely

sucked out, leaving only the white collapsed skin. According to Parker this occurs also in *Stilbula cyniformis*. Wheeler has pointed out that the *Orasema* larva consumes only a portion of the body contents of the *Pheidole* prepupa, and that the latter may still be alive after the completion of feeding by the parasite. *Eucharis scutellaris* likewise only partially exhausts the available food supply in the host body, though death of the host occurs before the parasite larva is mature.

The complete consumption of the pupal contents by several species indicates an appreciable amount of preoral digestion. It is improbable that suctorial action alone, through a single minute feeding puncture, could accomplish such a complete withdrawal of the body contents without a more thorough liquefaction than normally takes place during the period covered by the feeding of the third-instar parasite.

Parker has called attention to the apparently complete lack of tegumentary muscles in the mature larva of *Stilbula cyniformis*, and states that no indication of muscular action could be detected at any time. The same is true of *S. tenuicornis*, but in several of the other species mentioned above feeble contractions were observed in the younger larvæ of this stage. In no instance was there any movement of the body as a whole.

When the mature larvæ are examined it is found that the cast skins are present and adhere closely in a characteristic way. In all species examined, with the exception of *Stilbula tenuicornis*, the two adhere ventrally to the thoracic and anterior abdominal segments. They are readily recognizable because of the darkened segmental bands of the first exuviae. The line formed by these widely separated bands is transverse in *Chalcura deprivata* and diagonal in *Schizaspidia convergens* and *Eucharis scutellaris*. The head of the first exuviae is detached and remains fixed in the feeding puncture in the skin of the host pupa. In *Schizaspidia tenuicornis* only the second exuviae are present in this position, as the first are cast before pupation of the host and remain attached to the larval skin of the latter.

In the majority of species which develop upon hosts that

form cocoons prior to pupation, the remains of the host prepupa or pupa are found as a deflated envelope upon which the parasite pupa lies. There is no crumpling of the remains into a mass, and the parasite pupa occupies the same position as that previously held by the feeding larva. However, the remains of *Odontomachus* pupæ which have died as a result of attack by *Chalcura deprivata* or *Schizaspidia convergens* are found in a crumpled mass at the posterior end of the cocoon. In these species the mature larva is capable of only feeble muscular contractions, although these may be sufficient to push the host remains into the position mentioned.

Incomplete information indicates that all Eucharidæ normally develop as solitary parasites, though the quantity of food material available may be sufficient to bring several to maturity. In a number of species it has been noted that an occasional host cocoon contains two parasite individuals, one on each side of the parasitized pupa. Thus the solitary habit is not obligatory, though the number of exceptions to this habit is small when compared with the number of host larvæ which bear several planidia.

Endoparasitic Development in Orasema

One of the most surprising of the recent discoveries in the biology of the Eucharidæ is the endoparasitic mode of development of two species of *Orasema* (Wheeler & Wheeler, 1937). The first-instar larvæ, both unfed and fully distended, of *O. sixaolæ* W. & W. and *O. costaricensis* W. & W. were found within the bodies of different sized larvæ of *Solenopsis tenuis* Mayr and *Pheidole flavens* Roger var. in Costa Rica. They had evidently entered the host bodies by direct penetration of the skin and remained there with the posterior segments of the abdomen protruding from the entry hole. The fully distended planidia were found to lie with the dorsum immediately beneath the host skin, rather than free in the body cavity. The posterior portion of the body of these individuals is enveloped by a "collar" which projects inward from the periphery of the wound. This formation is apparently identical in origin with the respiratory funnel of the Tachinidæ, but its function is not so

clearly indicated. These larvæ do not possess the posterior spiracles; in fact the presence of spiracles is not mentioned in the descriptions, and the occurrence of an open tracheal system in the planidia of this family is still debatable. The small size of the planidia would permit of cutaneous respiration, and sufficient air may possibly enter the opening of the funnel and surround the body to provide for their needs.

Eighteen planidia of *Orasema sixaolæ* and seven of *O. costaricensis* were found in the bodies of *Solenopsis* and *Pheidole* larvæ and none was found externally upon either larvæ or pupæ. The intermediate instars were not found but the mature larvæ of *O. costaricensis* occurred free in the nest. It is therefore not known whether the larvæ are endo- or ectoparasitic after the first molt.

The ectoparasitic manner of development of *Orasema* had been conclusively demonstrated by W. M. Wheeler in his early work (1907) upon *O. wheeleri* Wheeler¹ and others in Texas and Colorado, and later authors found the same habit in other genera. It was consequently believed that the habit was general in the family. It was doubly unexpected that the endophagous habit should appear in species which belong to this same genus and are parasitic upon the same genera of hosts.

Another feature in the biology of the two species of *Orasema* above mentioned is that they appear to be strictly larval parasites, whereas other species of the family are known to complete their development only on the prepupa or pupa. The endophagous habit may be associated with the change in the host stage which is attacked. Somewhat similar differences in developmental habits are known in the related Perilampidæ.

The Life Cycle

The complete life cycle, with the duration of the different developmental stages, has been determined only for *Stilbula tenuicornis*. This species passes the winter and a large portion of the following season, representing an elapsed time

¹According to A. B. Gahan (U. S. Natl. Mus. Proc. 88: 425-458, 1940) the biological data presented by Wheeler under *Orasema viridis* Ashm. relate to *O. wheeleri* instead.

of approximately 11 months, in the egg stage in the buds of trees. The larvæ are fully formed in the eggs within 20 days after deposition and they then remain in diapause for the remainder of the period. The duration of the first larval stage is variable, depending upon the length of time from hatching to entry of the planidium into the host nest, after which it must await pupation of the host individual before proceeding with its own development. The second and third larval stages and the pupal stage are passed very quickly and require 3, 4 and 6 days, respectively.

The incomplete data presented by Parker (1937) on *Stilbula cyniformis* indicate that its cycle may be similar to that of *S. tenuicornis*. Adults are present only during August and the females oviposit in the seed receptacles of *Picris*. The egg masses are blown away with the seeds a short time later and they may not hatch until the following spring.

Practically all the species found in distinctly temperate regions have only a single generation each year. *Eucharis scutellaris* of Chosen, which appears in the adult stage only during June, oviposits in flower buds, and the incubation period is only 15 days. In 1928 an examination of the colony site on June 4 revealed no adults, but these were present in numbers on June 7. A large quantity of *Formica* cocoons, comprising those of both the large females and the smaller workers, was collected on the latter date. In the large cocoons all parasites except two were in the pupal stage, and these two were prepupæ. In the worker cocoons, however, the hosts had not yet transformed to pupæ and their parasites were consequently in the first larval stage. There being only one generation per year, it appears that the winter must have passed by all individuals in the first larval stage upon the ant larvæ.

A similar annual cycle is followed by *Orasema coloradensis* in Virginia. Oviposition occurs only during July, and the eggs hatch in less than 2 weeks. In the tropics the cycles of the species of the various genera observed are much shorter, probably not exceeding 1 month, and adults are present throughout the year if climatic conditions are favorable. The incubation period of *Schizaspidia convergens* of

Ceylon and *Kapala* sp. of Cuba is 10 to 14 days, while Ishii (1932) states that it is only 1 week for *Kapala foveatella* Gir., *Parapsilogaster montanus* Gir., and *Losbanos uichancoi* Ishii in the Philippine Islands.

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