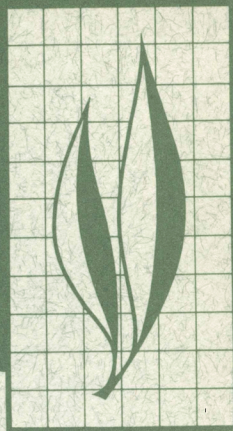


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**Courtship Behavior in the *Aphytis lingnanensis*  
Group, Its Potential Usefulness in Taxonomy,  
and a Review of Sexual Behavior  
in the Parasitic Hymenoptera  
(Chalcidoidea: Aphelinidae)**

**Gordon Gordh and Paul DeBach**





The aphelinid genus *Aphytis* contains the most important natural control agents of numerous armored scale insect pests. The genus consists of several species groups, including the *lingnanensis* group. This group has several sibling or near-sibling species which are exceptionally useful in biological control.

Accurate identification of these parasites is supremely important in biological control, but this is often difficult when sibling or cryptic species are involved, as morphological characters used to discriminate taxa are absent. Therefore, studies were conducted to determine the feasibility of using behavioral characters for the separation of such species in the *lingnanensis* group.

Qualitative analysis of courtship behavior revealed that it is possible to separate *A. lingnanensis* from *A. melinus* DeBach, *A. holoxanthus* DeBach, *A. fisheri* DeBach, and a semispecies of *A. melinus*, on the basis of overt male behavior and female response to male behavior.

Quantitative analysis of 16 cultures in the *lingnanensis* group showed that it is possible to identify different species by using precoital courtship duration, postcoital mount duration, precoital wing vibration pulse frequency, postcoital wing vibration pulse frequency, number of contacts between the sexes, and number of male courtship attempts, as characters. In some instances, the parameters tested are useful in grouping allopatric populations of a species.

Some antennal ablation experiments were done and antennae were chemically treated to determine their role in courtship. These studies indicated that antennae are essential for successful copulation.

Scanning electron microscope studies revealed a mesothoracic

(continued inside back cover)

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# Courtship Behavior in the *Aphytis lingnanensis* Group, Its Potential Usefulness in Taxonomy, and a Review of Sexual Behavior in the Parasitic Hymenoptera (Chalcidoidea: Aphelinidae)<sup>1</sup>

## INTRODUCTION

DOBZHANSKY (1951) noted that behavior may play an important role in the development of isolating mechanisms and the process of speciation. Behavioral isolating mechanisms operate prior to copulation. There may be differences in courtship pattern, seasonal or daily differences in sexual receptivity, encounter of the opposite sex, or a number of other factors. Behavioral isolating mechanisms seem important where sibling species exist sympatrically, and such species are common in *Aphytis*. We know that genetic reproductive isolation is involved to some extent (Rao and DeBach, 1969b, c). If Dobzhansky and others are correct, sexual behavior must also be involved in maintaining the genetic integrity of closely related species of *Aphytis*.

There are seven species groups in *Aphytis*, including the **lingnanensis group**. The **lingnanensis group** consists of at least nine morphologically similar species plus various infraspecific "forms" that are important in the biological control of diaspine scale insects. Those included in this study were: *A. lingnanensis* Compere, *A. melinus* DeBach, *A. coheni* DeBach, *A. fisheri* DeBach and *A. holoxanthus* DeBach.

If behavioral characters are valid for

identifying\* or classifying taxa, the questions then are what behavioral characters are most useful in separating taxa, and how much infraspecific variation occurs among allopatric populations of polytypic species. We selected sexual behavior for analysis because courtship and subsequent insemination are absolutely essential for reproduction in biparental species. Moreover, courtship is usually complex and therefore lends itself well to categorization into component phases, and to quantitative analysis. In our laboratory cultures, material is abundant for replication. Many parasitic Hymenoptera mate immediately after emergence (Askew, 1968), which makes observation relatively easy and permits standardization of environmental and physiological conditions.

The genetic relationship of some cultures has been discussed elsewhere (Rao and DeBach, 1969a), but the genetic status of others has not been determined (Table 1). The *A. lingnanensis* "Florida" culture was obtained from Alan Selhime from field recovery samples of scale insects attacking citrus in central Florida. Crossing tests indicated that the culture was conspecific with the standard culture of *A. lingnanensis*.

<sup>1</sup> Accepted for publication May 26, 1977.

Other cultures determined conspecific with the standard culture of *A. lingnanensis* include R-72-32, R-72-33, R-72-55, and R-74-5. (R- cultures refer to the year of importation—e.g., 1972, 1974 and the lot number. *Aphytis coheni* is a sibling of *lingnanensis*. Notes on each culture are on file at the Division of Biological Control, Riverside.)

Cultures R-73-93 and R-73-94 were imported from field collections of parasitized *Chrysomphalus bifasiculatus* Ferris (6/26/1973) on *Lithocarpus edulis*, and *Aonidiella taxus* Leonardi (6/26/1973) on *Podocarpus macrophylla*, respectively. Crossing tests indicated that the cultures were conspecific.

Crossing tests among cultures R-73-112 (imported 7/9/1973 from *Aonidiella taxus* on *Podocarpus macrophylla*) and R-73-113 (7/9/1973 from *Chrysomphalus bifasiculatus* on *Lithocarpus edulis*) indicated that they were conspecific. Crossing tests among R-73-93, R-73-94, R-73-112, R-73-113, and R-73-114 revealed a sex ratio comparable to homogamic crosses (55 to 65 percent females); thus all of these cultures were considered conspecific. All of these cul-

tures came from the same general area of Kyushu in southern Japan.

Morphologically, adults of all five of the latter cultures were similar to *Aphytis melinus*, *A. holoxanthus*, and *A. fisheri*. Consequently, crossing tests were conducted among those cultures. Tests revealed that the Japanese cultures were reproductively isolated from *A. fisheri* and *A. holoxanthus*. Results of crossing tests with *A. melinus* were unusual. When males from the Japanese cultures were crossed with females of *A. melinus*, the sex ratio of the  $F_1$  approximated 50 percent female, which indicated reproductive compatibility. Reciprocal crosses produced less than 3 percent females in the  $F_1$  generation. Rao and DeBach (1969a) have reported that one-way sterility occurs in the **lingnanensis group**. In the present study, these cultures were considered semispecies of *A. melinus* (*sensu* Mayr, 1963). However, there was a difference in pupal pigmentation, as compared to *A. melinus*. The pupal pigmentation of these cultures was more like that of *A. lingnanensis* or *A. holoxanthus*, than of *A. melinus*.

## MATERIALS AND METHODS

Table 1 lists the cultures involved in the study, their origin, scale-insect host, and taxonomic status of each, based on crossing tests (Rao and DeBach, 1969a; DeBach unpublished). Each parasite culture was maintained in a one or two-hole sleeve cage at  $26 \pm 2^\circ$  C and  $50 \pm 10$  percent RH. Lemons infested with scale insects were added weekly to each culture to maintain parasite populations. All studies were done with virgin adults which had been isolated in quarter-dram vials as green-eyed pupae. Courtship and copulation of newly emerged adults (less than 24 hours old) were observed with a stereomicroscope, and various aspects of courtship were quantified. Meristic data were tabulated with

the aid of a mechanical rotary counter, and durations of courtship phases were measured sequentially with several stopwatches.

Sexual behavior was observed and data recorded at all times of the day and night to ascertain whether diurnal differences were involved. An endogenous component mediating copulation apparently does not exist in the **lingnanensis group**, as males and females courted and copulated without regard to time of day. After copulation, each pair of wasps was discarded. All tests were conducted at a temperature of  $23 \pm 2^\circ$  C, and with variable room humidity.



TABLE 1  
DATE OF IMPORTATION, LOCALITY, SCALE HOST, AND TAXONOMIC STATUS  
OF ALL CULTURES OF THE *APHYTIS LINGNANENSIS* GROUP  
USED IN COURTSHIP ANALYSIS

Culture ( <i>Aphytis</i> spp.)	Importation date	Origin	Scale host (laboratory)	Taxonomic status
<i>coheni</i> DeBach	1960	Israel	<i>Aspidiotus nerii</i>	Sibling of <i>A. lingnanensis</i>
<i>fisheri</i> DeBach	1956	Burma	<i>A. nerii</i>	Sibling of <i>A. melinus</i>
<i>holoxanthus</i> DeBach	1959	Israel	<i>A. nerii</i>	Near-sibling of <i>A. melinus</i>
<i>lingnanensis</i> Compere Standard Culture	1948	South China	<i>A. nerii</i>	Sibling of <i>A. coheni</i>
<i>lingnanensis</i> * "California"	1973	San Diego, California	<i>Aonidiella aurantii</i>	Allopatric population of <i>A. lingnanensis</i>
<i>lingnanensis</i> * "Florida"	1973	Florida	<i>A. nerii</i>	Allopatric population of <i>A. lingnanensis</i>
<i>melinus</i> DeBach	1956	India and Pakistan	<i>A. nerii</i>	Sibling of <i>A. fisheri</i>
R-72-32*	1972	El Salvador	<i>A. nerii</i>	Allopatric population of <i>A. lingnanensis</i>
R-72-33*	1972	Brazil	<i>A. nerii</i>	Allopatric population of <i>A. lingnanensis</i>
R-72-55*	1972	Hong Kong	<i>A. nerii</i>	Allopatric population of <i>A. lingnanensis</i>
R-73-93†	1973	Japan	<i>A. aurantii</i>	Semispecies of <i>A. melinus</i>
R-73-94†	1973	Japan	<i>A. aurantii</i>	Semispecies of <i>A. melinus</i>
R-73-112†	1973	Japan	<i>A. aurantii</i>	Semispecies of <i>A. melinus</i>
R-73-113†	1973	Japan	<i>A. aurantii</i>	Semispecies of <i>A. melinus</i>
R-73-114†	1973	Japan	<i>A. aurantii</i>	Semispecies of <i>A. melinus</i>
R-74-5*	1974	Japan	<i>A. aurantii</i>	Allopatric population of <i>A. lingnanensis</i>

\* Conspecific with standard culture of *A. lingnanensis*.

† Conspecific with each other.

In the present study, mating is considered synonymous with copulation;

and insemination is the transfer of sperm from the male to the female.

## RESULTS

Based on observations, we arbitrarily subdivided sexual behavior into three phases: precoital courtship, coitus, and postcoital mount behavior. Behaviorists, especially ethologists, may regard this subdivision with misgivings, but it should be emphasized that our objective was taxonomic discrimination.

The sexual behavior of *A. lingnanensis* Compere (Standard Culture) will be described in qualitative detail, and all others will be described in relation to it.

### Precoital phase

Males and females are sexually receptive upon emergence from the pupal exuvium. Males are protandrous and

capable of inseminating females immediately after both emerge. Thus, it seems that protandry is not correlated with sexual maturation. Encounter of the opposite sex occurs when: 1) The male is stationary and the female is moving, 2) The female is stationary and the male is moving, or 3) Both sexes are moving. If the male is stationary, the female may stop when encountering the male, or she may continue to move. If the female is stationary, the male may approach and mount the female from any angle. If the female and male are both moving, the male will chase the female for a variable distance (up to 8 cm), beating his wings rapidly, but not flying. In the last instance the female



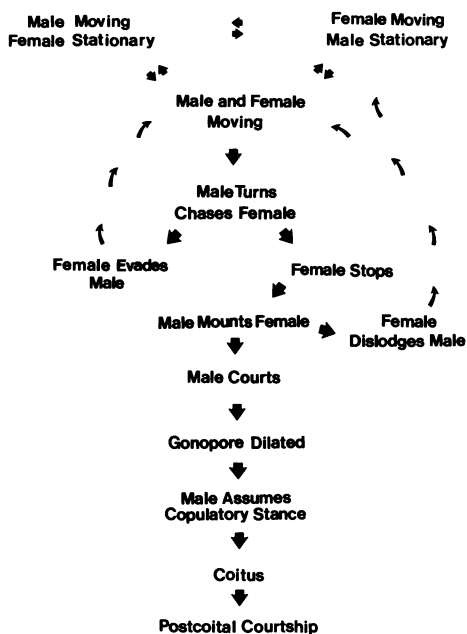


Fig. 1. Schematic diagram of hierarchical features of courtship behavior in the *lingnanensis* group.

may evade the male; if she stops, he mounts her dorsum from the rear. For a conspectus of the sequential steps see Fig. 1.

After mounting the motionless female, the male orients so that both sexes are facing the same direction. Courtship is apparently initiated by the male rapidly vibrating his antennae, with the proximoventral portion of the clubs pulsating at or near the apices of the female's clubs. The female antennae are initially mesally contiguous, with flagella bent downward (geniculate); but they are quickly raised with the flagella mesally juxtaposed and nearly parallel to the substrate (porrect).

Position of the male's legs is such that the foretarsi are placed on the female's compound eyes or foretibiae, middle legs are not in contact with the female's body, and the hind legs are on the anterior margins of the female's

wings, generally on the marginal vein near the stigma (Fig. 1A).

Precoital courtship is short ( $3.30 \pm 1.37$  seconds,  $n = 20$ ). The most likely factor involved in generating female receptiveness is probably chemoreception (Rao and DeBach, 1969a; Khasimuddin and DeBach, 1975). Sexually receptive females react to male courtship by manipulating gastral sterna so that the incident angle of the ovipositor shaft is increased with respect to the substrate and exerted slightly (Fig. 1B). This action by the female presumably serves to dilate the gonopore and enlarge the bursa copulatrix. We do not know how the male perceives the female's response to his stimulation, but he quickly moves rearward and simultaneously spreads and cants his wings (Fig. 1C).

### Coital phase

The copulatory stance of the male is precise (Fig. 1C). Because the gonopore is situated far from the apex of the gaster and near the base of the ovipositor shaft, the male is situated such that his hind tarsi are spread widely and touch the substrate providing support. His foretarsi are on the distal margin of the female's wings (held in repose over the female's gaster), and the middle tarsi are on the female's gastral tergites, near the vibrissae. The male's wings are flexed and partly rotated, with the distal margins touching the substrate and providing additional support. During insemination, the female remains motionless, and the antennal flagella are parallel to the substrate, with the inner margins contiguous (Fig. 1C). Male antennae are geniculate during copulation. The copulatory period is short ( $3.65 \pm 0.71$  seconds;  $n = 53$ ), and after insemination the male climbs upon the dorsum of the female and assumes a position similar to that in the precoital phase of courtship.



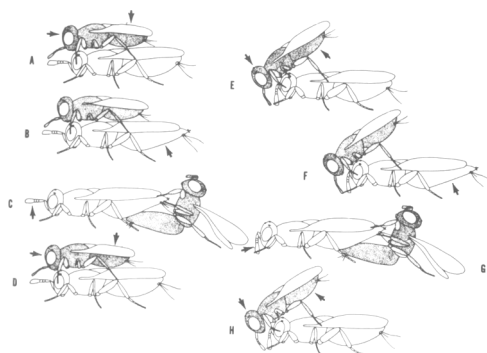


Fig. 2. Courtship features in the *lingnanensis* group. (A to D, *A. lingnanensis* type; E to H, *A. mccluskeyi* type.) Main differences are indicated by arrows.

### Postcoital phase

Male postcoital behavior has several features (Figs. 1 to 5). Initially, the male is motionless, with head above and slightly forward of the female's head. The female antennae are held in repose. Soon (5 to 25 seconds) the male antennae begin to vibrate in alternate pulses, and the male's mandibles touch, or are very near, the female's pedicels. The female slowly raises her flagella to a porrect position, and also lowers them oc-

asionally. The male continues to vibrate his antennae, touching or coming near the apices of the female's clubs in alternate pulses.

Male middle legs are moved semaphorally (Figs. 3-4). Three patterns have been observed. The right leg is slowly flexed antero-laterally and simultaneously raised, while the left leg is held in repose near the female's propodeum (Fig. 3, left). After the right leg is returned to a position similar to that of the left leg, the left leg is moved in an antero-lateral manner and elevated similarly to that previously done by the right leg. (Fig. 3, center). This pattern is repeated several times, with middle legs alternately extended and drawn rearward. Occasionally, both legs are simultaneously extended forward and brought rearward (Fig. 3, right). Legs in a position of repose often have tarsi and tibiae quivering.

During the postcopulatory mount, the male's wings are fanned rapidly and returned to a position over the gaster (Fig. 4). They also may be held partly open upon completion of a series of wing vibrations (pulse). During the

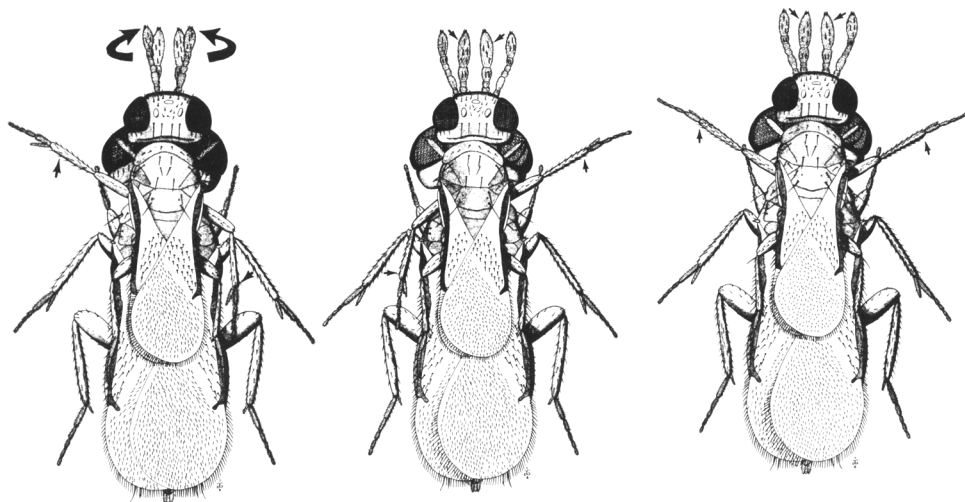


Fig. 3. Dorsal aspects of *A. lingnanensis* courtship stance with male middle legs moving semaphorally.



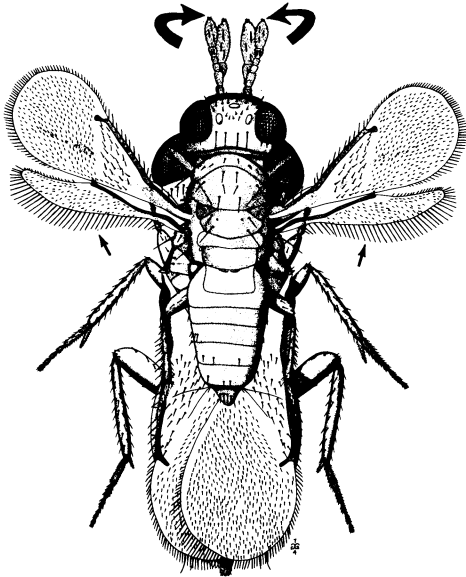


Fig. 4. Dorsal aspect of *A. lingnanensis* courtship stance with male wings vibrating.

postcopulatory mount the female's sterna move spasmodically.

The postcopulatory mount is comparatively long in *A. lingnanensis* ( $105.28 \pm 37.31$  seconds;  $n = 20$ ), and is terminated by either sex. The male may suddenly dismount the female for no apparent reason. Alternatively, the female may twist her head or lift either foretibia and groom the eye. Either action on the part of the female has a tendency to dislodge the male. Persistence in this activity, combined with running, usually results in dislodging the male.

Beside the *A. lingnanensis* standard culture, this qualitative courtship pattern is exhibited by *A. lingnanensis* "California" and "Florida," and *A. coheni* DeBach, R-72-32, R-72-33, R-72-55, and R-74-5.

"Abdominal dipping" is observed often in *Aphytis*, and does not appear associated with the discharge of excessive sperm. Newly emerged males perform this activity, and some males drag the apex of their gasters along the sub-

strate after coitus. Barrass (1969) quantitatively analyzed this behavior for the pteromalid *Nasonia vitripennis* (Walker), and suggested that dipping was a displacement activity. The irregularity of dipping in *Aphytis* makes interpretation of its behavioral significance difficult, but we believe it is associated with hindgut voiding.

### Interspecific differences in courtship patterns

*Aphytis melinus*, a closely related but distinct species, differs from *A. lingnanensis* as follows: 1) The incident angle of the male's body in the courtship stance, with respect to the dorsum of the female, is greater than that noted for *A. lingnanensis* (Fig. 1E). 2) The male's head is positioned in front of, and very near, the anterior aspect of the female's head, so that male and female compound eyes are equidistant to the substrate. 3) During courtship and coitus, the female maintains her antennae in a geniculate position (Fig. 1G). 4) Male antennal fanning is exaggerated, and pulses are synchronized. 5) The male raises his head and both antennae until his body and antennae are nearly parallel to the horizontal. His head and antennae are then brought down rapidly so that the latter come close or touch the female's face (Fig. 1H). This procedure is repeated several times in rapid succession, or in several episodes, during the postcoital mount. For a diagrammatic comparison of courtship differences see Figure 1. The pattern for *A. melinus* is indistinguishable from that observed for *A. holoxanthus*, *A. fisheri*, R-73-93, R-73-94, R-73-112, R-73-113, and R-73-114.

### Aberrations and male senescence

In other studies, it was discovered that male *Aphytis* will live up to 9 days; but, if mated to numerous females, generally will die 3 or 4 days after emergence. Males isolated for 5 days or



longer were placed with newly emerged virgin females, and courtship was observed. The following aberrations in the courtship pattern were noticed: 1) A male encountered a motionless female, climbed on and over the female, and continued to wander. (This pattern was observed for several aged males, but was not observed for males less than 24 hours old placed with homogamic females.) 2) A male backed up for the coital stance, but continued to back up for several millimeters behind the motionless female. (This pattern was observed only twice in old males). 3) A male courted the apex of the female's gaster. (This was the most common error in courtship behavior for aged males, and was observed on numerous occasions for newly emerged males also. After several seconds of the male courting the inappropriate end, the female generally ran, or, alternatively, the male dismounted. We noted that younger males tended to correct their posture and address the female's antennae, but older males rarely did). 4) Attempted insertion of the aedeagus into the female's bursa copulatrix a second, third or fourth time after initial coitus. (This was commonly observed, but it was not possible to associate the action with nervous system degeneration or sperm depletion. In such instances females invariably remained motionless and permitted reinsertion.) 5) Old males were apparently too slow in assuming the copulatory stance or inserting the aedeagus into the bursa copulatrix after initial stimulation, and the female ran. (This pattern was noted several times.)

### Polygyny and monandry

Numerous reports (Cousin, 1933; Hanna, 1934; Jackson, 1966; Jones, 1937; Schlinger and Hall, 1960, 1961; Sekhar, 1957; Abdelrahman, 1974) have indicated that male parasitic Hymenoptera are polygamous and females, mo-

nogamous. (In the present discussion—polygyny, one male mating with several females, and polyandry, one female mating with several males—are used.

To determine the extent of polyandry in *Aphytis lingnanensis*, virgin males and females were placed together in pairs in quarter-dram vials, and copulation was observed. Next, these same females, mated 6 hours earlier, were placed with virgin males in fresh quarter-dram vials. During a 5-minute observation period for each of 25 replicates (one lost), copulation with a second male was observed only twice. In most instances the female ran, jumped, or in some way eluded the male. In instances where the male succeeded in mounting the female ( $2.31 \pm 0.42$  times per 5-minute observation period), the female succeeded in dislodging the male by grooming, running, or jumping. In one instance, the male was observed in a coital stance without the female manipulating the gastral sterna to dilate the gonopore. In this case, the female made a grooming response with her right hind tibia, and then ran. Aedeagal intromission was not achieved. Immediately following the 5-minute observation period, the male from each test was placed with a virgin female, and the same observational procedure used. In 22 instances out of 24, the male copulated with the virgin female.

To establish the time of onset of female unreceptivity following insemination, males were allowed to copulate with females, but were driven off after coitus and before the postcoital mount. Immediately after elimination of the inseminating male, a virgin male was introduced into the vial and observed for 5 minutes. In 6 of 15 instances, the female accepted intromission by the second male. Statistical analysis using a t-test for independence of means, indicated that when once-rejected males were compared to virgin males offered sexually experienced females that had

not received the postcoital mount, the two male populations were different ( $p < 0.05$ ,  $t = 2.11$ ;  $t_{(38, 0.05)} = 2.03$ ). When virgin males that had been offered females mated 6 hours earlier, and had received postcoital mount behavior, were compared with virgin males offered sexually experienced females that had not received postcoital mount behavior, the populations were significantly different ( $p < 0.05$ ,  $t = 2.58$ ;  $t_{(38, 0.05)} = 2.03$ ).

These observations indicate that females are probably monandrous, and that unreceptivity occurs during or after the postcoital mount behavior. However, until the mechanism responsible for determining female receptivity subsequent to coitus is clarified, the results of these experiments can only be interpreted as correlative evidence. This experiment was repeated with *A. melinus*, and the results were similar. Only 3 of 15 females mated 6 hours earlier permitted a second insemination. Abdelrahman (1974) has also concluded that female *A. melinus* mate only once. He allowed mated females to oviposit throughout their lifetime until they produced only male progeny (based on egg position), and then offered the female two males for 3 consecutive days. These females, when provided suitable host material, did not produce female progenies; and Abdelrahman concluded the females had not mated. However, the possibility exists that the females were inseminated because no direct observations were made of the females and males together.

### Quantifying courtship behavior

Previously, we noted subtle, yet distinct, qualitative differences in courtship behavior patterns between the species *A. lingnanensis* and *A. melinus* within the *lingnanensis* group. However, if courtship behavior differences are used as a biosystematic tool, various *A. lingnanensis* cultures are qualita-

tively indistinguishable from one another. *Aphytis melinus*, *A. fisheri*, *A. holoxanthus*, and designated R cultures, are also indistinguishable from one another on this basis. Therefore, studies were conducted to determine whether quantitative differences exist in phase duration, and whether the frequency of wing vibration pulses can be used to separate different cultures which may be sibling species. Thus, studies were aimed at determining the extent of quantitative differences among species (*A. melinus*, *A. fisheri*, and *A. holoxanthus*), and the extent of variation among allopatric populations of the same species (*A. lingnanensis* (standard culture), "Florida," "California," R-72-32, R-72-33, R-72-55, and R-74-4, and the *A. melinus* semispecies cultures R-73-93, R-73-94, R-73-112, R-73-113, and R-73-114).

Courtship and copulation between virgin males and females (homogamic) were observed in the manner indicated previously. Sexual behavior was divided into precoital and postcoital phases. The former was measured from when the male mounted the female until he backed into the coital stance; the latter was measured from termination of coitus until the male left the dorsum of the female. The number of pre- and postcoital wing vibration pulses was counted (pulses defined as a series of beats separated from other clearly separated beats, not individual beats). The number of contacts (confrontations) before courtship and the number of courtship attempts per coitus, was also recorded. A variable number of matings per culture was tabulated, and an analysis of variance was performed for each of the six variables. Data were analyzed with a computer assist (IBM 360), using canned programs and specially prepared subroutines. Because the data were not normally distributed, a square root ( $x + 1$ ) transformation was performed. (Transformation was necessary

because of the test's sensitivity to non-normal distributions.) These studies revealed precoital courtship duration, postcoital mount duration, and pre- and postcoital wing vibration pulses were significantly different among cultures at  $p < 0.005$ . The number of contacts was significantly different at  $p < 0.01$ , but the number of courts did not differ significantly among cultures. Bartlett's Test indicated that the differences in pre- and postcoital mount duration, postcoital wing vibration pulses, and number of contacts was statistically significant at  $p < 0.005$ .

Results of the statistical analysis were

interesting enough to merit further scrutiny. Consequently, Duncan's Multiple Range Test was applied to the mean values of each variable for each culture. Means were ranked, and homogenous subgroupings were generated at  $p = 0.05$  and  $P = 0.01$  levels of probability. Data from these tests are presented in tables 2 to 7. There was a high degree of difference in the number of groups generated, depending upon the level of probability and the variable involved. Up to eight subgroups were generated for at least two variables (Table 3, postcoital courtship duration and Table 5, postcoital wing vibration

TABLE 2  
RESULTS OF DUNCAN'S MULTIPLE RANGE TEST FOR DIFFERENCES  
AMONG 16 **LINGNANENSIS GROUP** CULTURES FOR PRECOITAL  
COURTSHIP DURATION (VARIABLE 1)  
(MEANS TRANSFORMED)

Treatment	Mean	Homogenous subgroups					
		1	2	3	4	5	6
Significance at P = 0.05, means ranked :							
R-73-93	4.42	U					
R-73-94	4.10	U	V				
R-73-114	4.09	U	V				
R-73-113	3.60		V	W			
<i>A. holoxanthus</i>	3.34			W			
<i>A. melinus</i>	3.34			W			
<i>A. coheni</i>	3.18			W	X		
R-73-112	3.13			W	X	Y	
<i>A. fisheri</i>	3.10			W	X	Y	
R-72-33	2.67				X	Y	Z
R-72-32	2.59				X	Y	Z
R-72-55	2.58				X	Y	Z
Florida	2.50					Y	Z
R-74-5	2.18						Z
California	2.10						Z
Standard Culture	2.05						Z
Significance at P = 0.01, means ranked :							
R-73-93	4.42	V					
R-73-94	4.10	V	W				
R-73-114	4.09	V	W				
R-73-113	3.60		W	X			
<i>A. holoxanthus</i>	3.34		W	X	Y		
<i>A. melinus</i>	3.34		W	X	Y		
<i>A. coheni</i>	3.18			X	Y		
R-73-112	3.13			X	Y		
<i>A. fisheri</i>	3.10			X	Y		
R-72-33	2.67				Y	Z	
R-72-32	2.59				Y	Z	
R-72-55	2.58				Y	Z	
Florida	2.50				Y	Z	
R-74-5	2.18					Z	
California	2.10					Z	
Standard Culture	2.05					Z	



TABLE 3  
DUNCAN'S MULTIPLE RANGE TEST FOR DIFFERENCES AMONG 16  
LINGNANENSIS GROUP CULTURES FOR POSTCOITAL MOUNT DURATION  
(VARIABLE 2)

Treatment	Mean	Homogenous subgroups							
		1	2	3	4	5	6	7	8
Significance at P = 0.05, means ranked :									
R-73-112	13.83	S							
R-73-94	13.04	S	T						
<i>A. melinus</i>	12.58	S	T	U					
<i>A. coheni</i>	12.23	S	T	U					
Florida	12.09	S	T	U	V				
R-73-113	12.08	S	T	U	V	W			
R-73-114	11.89		T	U	V	W	X		
R-72-55	11.76		T	U	V	W	X		
R-73-93	11.46		T	U	V	W	X		
California	11.03			U	V	W	X	Y	
R-72-33	10.79			U	V	W	X	Y	
R-74-5	10.29				V	W	X	Y	
Standard Culture	10.14					W	X	Y	
<i>A. holoxanthus</i>	9.79						X	Y	
R-72-32	9.58							Y	Z
<i>A. fisheri</i>	8.11								Z
Significance at P = 0.01, means ranked :									
R-73-112	13.83	U							
R-73-94	13.04	U	V						
<i>A. melinus</i>	12.58	U	V	W					
<i>A. coheni</i>	12.23	U	V	W	X				
Florida	12.09	U	V	W	X				
R-73-113	12.08	U	V	W	X				
R-73-114	11.89	U	V	W	X	Y			
R-72-55	11.76	U	V	W	X	Y			
R-73-93	11.46	U	V	W	X	Y			
California	11.03		V	W	X	Y			
R-72-33	10.79		V	W	X	Y			
R-74-5	10.29			W	X	Y	Z		
Standard Culture	10.14				X	Y	Z		
<i>A. holoxanthus</i>	9.79				X	Y	Z		
R-72-32	9.58					Y	Z		
<i>A. fisheri</i>	8.11						Z		

pulses). We interpret a greater number of subgroups to reflect a greater discriminative ability of the variable for indicating culture differences. Thus, pre- and postcoital mount duration and postcoital wing vibration pulses are exceptionally useful in separating cultures, precoital wing vibration pulses are moderately useful in discriminating culture differences, and number of contacts and number of courts are not useful in discriminating culture differences. The latter two variables may be useful in determining compatibility in crossing tests, using different cultures, if females of different species reject

nondiscriminant males more frequently than conspecific males.

Overlap among homogenous subgroups among cultures is not uniform for each variable. In instances where more subgroups are generated, the extent of overlap among subgroups is greater.

Examining more closely those variables which reflect the greatest amount of subgrouping (variables 1, 2, and 4), we note that genetically dissimilar cultures may be grouped together, i.e., variable 1, *A. coheni* and *A. melinus*; variable 2, R-72-32 and *A. fisheri*; variable 4, *A. holoxanthus* and *A. ling-*

TABLE 4 .  
DUNCAN'S MULTIPLE RANGE TEST FOR DIFFERENCES AMONG 16  
LINGNANENSIS GROUP CULTURES FOR PRECOITAL MALE  
WING BEAT PULSES (VARIABLE 3)  
(MEANS TRANSFORMED)

Treatment	Mean	Homogenous subgroups		
		1	2	3
Significance at P = 0.05, means ranked :				
<i>A. holoxanthus</i>	2.08	X		
R-73-114	2.04	X		
R-73-94	1.86	X		
R-73-113	1.44		Y	
R-73-93	1.44		Y	
<i>A. fisheri</i>	1.30		Y	Z
<i>A. melinus</i>	1.26		Y	Z
R-72-32	1.19		Y	Z
R-72-33	1.17		Y	Z
R-73-112	1.14		Y	Z
R-74-5	1.05			Z
Standard Culture	1.05			Z
California	1.04			Z
R-72-55	1.02			Z
<i>A. coheni</i>	1.00			Z
Florida	1.00			Z
Significance at P = 0.01, means ranked :				
<i>A. holoxanthus</i>	2.08	X		
R-73-114	2.04	X		
R-73-94	1.86	X	Y	
R-73-113	1.44		Y	Z
R-73-93	1.44		Y	Z
<i>A. fisheri</i>	1.30			Z
<i>A. melinus</i>	1.26			Z
R-72-32	1.19			Z
R-72-33	1.17			Z
R-73-112	1.14			Z
R-74-5	1.05			Z
Standard Culture	1.05			Z
California	1.04			Z
R-72-55	1.02			Z
<i>A. coheni</i>	1.00			Z
Florida	1.00			Z

*nanensis* "California." In general, however, dissimilar cultures do not associate among variables.

How does the phenomenon of allopatry relate to the differences in response among member cultures of a single species? Cultures R-73-93, R-73-94, R-73-112, R-73-113, and R-73-114 were conspecific, and all were obtained from field collections of parasitized armored scale insects from the same area in Japan. Comparing this with the results in tables 2 to 7, we find that different variables reflect different culture groupings. Thus variable 1 (precoital court-

ship duration, Table 2) reveals that means of all of the above-mentioned cultures, except R-73-112, were cohesive in the sense that no mean value of a nonconspecific culture was interposed. The cultures formed two homogenous subgroups with considerable overlap at  $p < 0.05$  (subgroups U and V). Variable 2 (postcoital mount duration, Table 3) results were not as conclusive: R-73-112 and R-73-94 were adjacent, whereas R-73-113 and R-73-114 were juxtaposed. Variable 3 (precoital male wing pulses, Table 4) results were similar to those obtained from variable 1

TABLE 5  
DUNCAN'S MULTIPLE RANGE TEST FOR DIFFERENCES AMONG 16  
LINGNANENSIS GROUP CULTURES FOR POSTCOITAL MALE  
WING BEAT PULSES (VARIABLE 4)  
(MEANS TRANSFORMED)

Treatment	Mean	Homogenous subgroups							
		1	2	3	4	5	6	7	8
Significance at P = 0.05, means ranked :									
R-73-113	4.64	S							
R-73-114	4.59	S	T						
R-73-94	4.09	S	T	U					
R-73-112	3.82		T	U	V				
R-72-93	3.60			U	V	W			
<i>A. melinus</i>	3.36			U	V	W	X		
R-72-32	3.17				V	W	X		
<i>A. holoxanthus</i>	2.96					W	X	Y	
California	2.76					W	X	Y	
R-74-5	2.74						X	Y	
Standard Culture	2.60						X	Y	
R-72-55	2.59						X	Y	
R-72-33	2.51						X	Y	
<i>A. coheni</i>	2.25							Y	Z
Florida	1.70								Z
<i>A. fisheri</i>	1.61								Z
Significance at P = 0.01, means ranked :									
R-73-113	4.64	T							
R-73-114	4.59	T	U						
R-73-94	4.09	T	U						
R-73-112	3.82	T	U	V					
R-72-93	3.60	T	U	V	W				
<i>A. melinus</i>	3.36		U	V	W	X			
R-72-32	3.17			V	W	X			
<i>A. holoxanthus</i>	2.96			V	W	X			
California	2.76			V	W	X	Y		
R-74-5	2.74			V	W	X	Y		
Standard Culture	2.60				W	X	Y	Z	
R-72-55	2.59				W	X	Y	Z	
R-72-33	2.51				W	X	Y	Z	
<i>A. coheni</i>	2.25					X	Y	Z	
Florida	1.70						Y	Z	
<i>A. fisheri</i>	1.61							Z	

i.e., all cultures except R-73-112 were included in two adjacent subgroups at  $p < 0.01$  (subgroups X and Y). Variable 4 (postcoital male wing pulses, Table 5) indicated that all Japanese culture means were homogenous at  $P < 0.01$ , and means were nearest those of *A. melinus* (subgroup T). The patterns for variable 5 (contacts) and variable 6 (courtship attempts) were random, in the sense that no grouping was evident. Results with the grouping of the allopatric populations of *A. lingnanensis* were comparable to those with the Japanese cultures of the *A. melinus* semi-

species. For variable 1, means of all seven cultures were adjacent, forming one homogenous subgroup at  $P < 0.01$  (subgroup Z). Variable 2 indicated five of the seven cultures formed a homogenous subgroup at  $P < 0.05$ , with *A. holoxanthus*, an outlier, included (subgroup Y). Variable 3 rendered seven cultures of *A. lingnanensis* in a single homogenous subgroup at  $P < 0.05$ , with *A. melinus*, *A. fisheri*, R-73-112, and *A. coheni* included (subgroup Z). Variable 4 (postcoital male wing pulses) revealed that six of seven culture means were homogenous at  $P < 0.01$  with the



TABLE 6  
DUNCAN'S MULTIPLE RANGE TEST FOR DIFFERENCES AMONG 16  
LINGNANENSIS GROUP CULTURES FOR NUMBER OF  
CONTACTS (VARIABLE 5)  
(MEANS TRANSFORMED)

Treatment	Mean	Homogenous subgroups	
		1	2
Significance at P = 0.05, means ranked:			
<i>A. holoxanthus</i>	1.87	Y	
<i>A. melinus</i>	1.67		Z
R-73-112	1.64		Z
R-74-5	1.64		Z
R-73-94	1.64		Z
Standard Culture	1.63		Z
<i>A. fisheri</i>	1.56		Z
R-72-33	1.55		Z
Florida	1.55		Z
R-72-55	1.55		Z
R-73-93	1.54		Z
R-72-32	1.52		Z
R-73-113	1.51		Z
<i>A. coheni</i>	1.51		Z
R-73-114	1.50		Z
California	1.46		Z
Significance at P = 0.01, means ranked:			
<i>A. holoxanthus</i>	1.87	Y	
<i>A. melinus</i>	1.67	Y	Z
R-73-112	1.64	Y	Z
R-74-5	1.64	Y	Z
R-73-94	1.64	Y	Z
Standard Culture	1.63	Y	Z
<i>A. fisheri</i>	1.56		Z
R-72-33	1.55		Z
Florida	1.55		Z
R-72-55	1.55		Z
R-73-93	1.54		Z
R-72-32	1.52		Z
R-73-113	1.51		Z
<i>A. coheni</i>	1.51		Z
R-73-114	1.50		Z
California	1.46		Z

sibling species included (subgroup Y). The patterns for variable 5 (contacts) and variable 6 (courtship attempts) were random, in the sense that no grouping was evident.

These data indicate that some features of sexual behavior are apparently reliable for identifying closely related cultures, whereas, in other instances, such features are not reliable. The isolation of the Japanese cultures was newly imposed. These cultures were obtained from field collections made in the same area, and isolation was instituted in the laboratory. In the case of *A. lingnanensis* cultures, it is not possible to say for certain how long the isolation in nature had persisted. Indeed, the history of some cultures (R-72-32, R-72-33) is unknown. If *A. lingnanensis* originated in South China, then the standard culture has been isolated from all others for at least 25 years and isolated from the California culture for about 15 years. The fact that the results of the two conditions of isolation are comparable for each variable tested indicates some usefulness of behavioral characters. Variables such as number of courts and number of contacts appear of little im-

TABLE 7  
DUNCAN'S MULTIPLE RANGE TEST FOR DIFFERENCES AMONG 16  
**LINGNANENSIS GROUP** CULTURES FOR NUMBER OF MALE  
COURTSHIP ATTEMPTS (VARIABLE 6)  
(MEANS TRANSFORMED)

Treatment	Mean	Homogenous subgroups
		1
Significance at P = 0.05, means ranked :		
R-72-33	1.52	Z
<i>A. coheni</i>	1.50	Z
Standard Culture	1.50	Z
R-73-114	1.49	Z
R-72-55	1.47	Z
Florida	1.46	Z
R-74-5	1.46	Z
R-73-113	1.45	Z
R-73-112	1.45	Z
California	1.45	Z
R-73-94	1.44	Z
R-72-32	1.44	Z
<i>A. holoxanthus</i>	1.43	Z
<i>A. fisheri</i>	1.43	Z
<i>A. melinus</i>	1.41	Z
R-73-93	1.41	Z
Significance at P = 0.01, means ranked :		
R-72-33	1.52	Z
<i>A. coheni</i>	1.50	Z
Standard Culture	1.50	Z
R-73-114	1.49	Z
R-72-55	1.47	Z
Florida	1.46	Z
R-74-5	1.46	Z
R-73-113	1.45	Z
R-73-112	1.45	Z
California	1.45	Z
R-73-94	1.44	Z
R-72-32	1.44	Z
<i>A. holoxanthus</i>	1.43	Z
<i>A. fisheri</i>	1.43	Z
<i>A. melinus</i>	1.41	Z
R-73-93	1.41	Z

portance in culture discrimination and have little use as taxonomic characters. In contrast, others, such as wing-beat frequency, appear highly sensitive to changes among cultures, and at the same time capable of identifying closely related sibling species.

Although the variables were arbitrarily selected, they were chosen on the basis of numerous observations before the study was formally conducted. One of the most interesting questions is to what extent, if any, one variable is correlated to any other variable. To answer this question a correlation analysis was con-

ducted (Table 8). Four combinations of two variables were positively correlated at  $p < 0.005$ , and two variables were positively correlated at  $p < 0.05$ .

Variables 1 and 3 (precoital courtship duration and precoital wing vibration pulse frequency) were strongly correlated. Interpretation of the significance of the correlation can only be speculative, but it seems that this can be the result of two phenomena, or possibly an interaction of the two. If a male spends more time in courtship, then he can utilize the extended period of time to vibrate his wings more often.

TABLE 8  
CORRELATION ANALYSIS OF COURTSHIP BEHAVIOR COMPONENTS  
OF THE LINGNANENSIS GROUP

Number	Variable	Mean	Standard deviation
1	Precoital Courtship	2.995	1.085
2	Postcoital Courtship	11.163	2.718
3	Precoital Wing Pulses	1.289	0.575
4	Postcoital Wing Pulses	2.974	1.398
5	Contacts	1.585	0.282
6	Courtship Attempts	1.458	0.136

Variables	Correlation coefficient
1 2	0.01352
1 3	0.49946 ***
1 4	0.12217 *
1 5	- 0.01120
1 6	0.01244
2 3	- 0.08634
2 4	0.41107 ***
2 5	- 0.09423
2 6	0.04402
3 4	0.21499 ***
3 5	0.13556 *
3 6	- 0.00380
4 5	- 0.00968
4 6	- 0.01189
5 6	0.26138 ***

\* p = 0.05  
\*\*\* p = 0.005

If the function of wing vibrations is to stimulate a female into receptivity, then the duration of courtship may be a direct function of female receptiveness. The length of time a male spends on a female increases with unreceptivity and the greater the number of wing vibrations that may be necessary to render the female sexually receptive. There is some experimental data in support of this hypothesis. *Aphytis holoxanthus* females are generally unreceptive to initial male courtship. This is reflected in the number of male-female contacts, which is greatest of all cultures involved in the study. Also, *A. holoxanthus* spends the fifth longest amount of time in precoital courtship and generates the most precoital wing vibration pulses. Similar trends were noted for R-73-93 and R-73-114.

The high level of statistical significance in correlation for variables 2 and 4 (postcoital mount duration and number of postcoital wing vibration pulses)

may also be attributed to the hypothesis just given.

The strong correlation between variables 3 and 4 (precoital and postcoital wing vibration pulse frequency) is interesting and difficult to explain. The data may be interpreted as indicating that the state of male sexual arousal is involved with wing vibration frequency. The correlation is positive, so this would mean that males that are "predisposed" to vibrate their wings do so consistently. Wing vibrations may be genetically or environmentally induced. A functional explanation may be that initially unreceptive females require more precoital stimulation, also more stimulation after coitus. This touches upon the concept of male parental investment and sexual selection and will be discussed later.

The strong positive correlation between the number of contacts and courtship attempts (variables 5 and 6) also can be explained in terms of sexual receptivity. Although the animals used



TABLE 9  
MEAN AND STANDARD DEVIATION OF BEHAVIORAL RESPONSES OF *A. LINGNANENSIS* DURING 5-MIN. COURTSHIP  
MODIFIED BY TREATMENT OF THE ANTENNAE

Treatment	Number of responses					
	Chase or approach	Touch	Mount	Court	Attempted copulation	Copulation
Amputation of Flagellum*						
Female normal	4.77 ± 1.19	4.36 ± 2.17	0	0	0	0
Male normal	7.65 ± 5.89	5.18 ± 2.68	1.08 ± 1.55	0.36 ± 0.90	0	0
Control	2.16 ± 1.84	1.89 ± 0.61	1.08 ± 0.49	0.92 ± 0.49	0.89 ± 0.44	0.80 ± 0.44
HC1 Application†						
Female normal	5.46 ± 4.86	4.93 ± 4.18	0.20 ± 0.56	0.13 ± 0.51	0.06 ± 0.25	0.06 ± 0.25
Male normal	8.53 ± 4.54	6.20 ± 3.42	1.43 ± 1.06	0.66 ± 1.06	0.33 ± 0.89	0
Control	2.86 ± 1.88	1.46 ± 0.74	1.13 ± 0.51	1.06 ± 0.45	1.00 ± 0.45	0.86 ± 0.35

\* 25 replicates  
† 15 replicates

in all tests were less than 24 hr old and presumably similar physiologically, an endogenous component, i.e., circadian rhythm, of female or male sexual responsiveness or arousal could occur. We observed that males and females copulate at all times of the day and night. However, the manifestation of the sexual act is not the same as the relative state of arousal, which may fluctuate with the time of day or physiological conditions. Unfortunately, the times of matings were not recorded, so the hypothesis of circadian rhythm cannot be subjected to analysis.

The correlation of precoital courtship duration (variable 1) and postcoital wing vibrations (variable 4) is probably spurious and a statistical artifact of the strong correlation of variables 1 and 3 or variables 3 and 4.

The correlation of variables 3 and 5 (precoital wing vibration frequency and contacts) is puzzling. If the correlation is genuine, then perhaps male arousal is stimulated by a negative response (such as repeated contact, rather than courtship, from the female. Such a hypothesis has not been tested, however.

### Components of courtship behavior

Because of the distinctive and stereotyped features of courtship behavior in *Aphytis*, experiments were conducted to determine the factors involved in mediating sexual behavior. In some instances, amputation or ablation experiments were not possible because the appendages or organs involved were essential for normal functioning of the organism. For instance, amputation of the middle legs rendered the animal sufficiently debilitated so that no confidence could be placed in the observed behavioral response. Amputation of the wings of the male made insemination difficult, and in some instances impossible. Therefore results of those experiments are not presented.

**Elaborate antennal fanning** of the male, and contact or near contact of the apices of the female's antennal clubs, indicated that they play an important role in courtship behavior. Experiments were conducted to determine the level in the courtship behavior hierarchy at which these appendages become important in mediating sexual behavior. Virgin male and female *A. lingnanensis*, reared in the manner indicated previously, were lightly anesthetized with carbon dioxide, and the antennal flagella removed. Results of the experiment are presented in Table 9. When normal males are placed with flagellumectomized females, the male is capable of mounting the female and courting her, but copulation does not occur. The number of contacts between males and females increases, but this can be attributed to incessant male attempts at courtship. Flagellumectomized females are strongly unreceptive, and unresponsiveness is characterized by the female jumping, or evading the male, when the latter approaches. When a male succeeded in mounting the female, it was usually because the female was attempting to groom the missing antennae, and was unaware of the male's proximity. In the reciprocal experiment (Table 9) we noted that flagellumectomized males do not mount, court, or attempt copulation with females. These data imply that when the antennae are removed, the antenna-less sex does not react to the other as a sexual object. These findings are similar to those of Rao and DeBach (1969a), who reported that antenna-less *A. lingnanensis* females were not inseminated after one-half hour with normal males. The antennae possibly may be used as visual releasers of courtship behavior (receptor correlate *sensu* Thorpe, 1948); thus their absence precludes courtship. To investigate this possibility, virgin males and females were anesthetized, and the apices of the clubs were treated with a

microcapillary filled with concentrated hydrochloric acid. The experimental animals were allowed 1 hr to recover and then were placed with untreated members of the opposite sex. Results (Table 9) were comparable to those obtained in the amputation experiment and indicate that the courtship behavior mediated tactually or chemically—and not appreciably visually—is stimulated. In the single instance where the treated male successfully copulated with a normal female, it is presumed that insufficient HCl was applied.

Scanning electron micrographs of the antennal clubs revealed a group of specialized sensilla at the apex of the club in both sexes. These receptors are found nowhere else on the body of either sex. Female sensilla are long, tapered, and beveled at the apex (Fig. 5, left). Close examination of the sensilla apices reveals they are hollow. Male sensilla are also hollow (Fig. 5, right), but the apices are more truncate. (The corkscrew appearance of the trichoid sensilla is a scanning electron microscope (SEM) artifact). These sensilla are presumed to be chemoreceptors in both sexes and probably are responsible for mediating some aspect(s) of courtship behavior. In pilot studies, HCl-treated females did not parasitize scale insects, which indicates that the receptors may be important in host finding. However, it is uncertain whether one receptor has two functions, or different receptors function in mediating different behavior patterns.

The intricate fanning pattern demonstrated by male *Aphytis* and most other chalcidoids that have been examined closely, is noteworthy. Male fanning possibly may be attributed to males perceiving their own pheromone concentration and adjusting the level in order to keep the female receptively quiescent.

A pheromone in female *Aphytis* species has been clearly demonstrated by

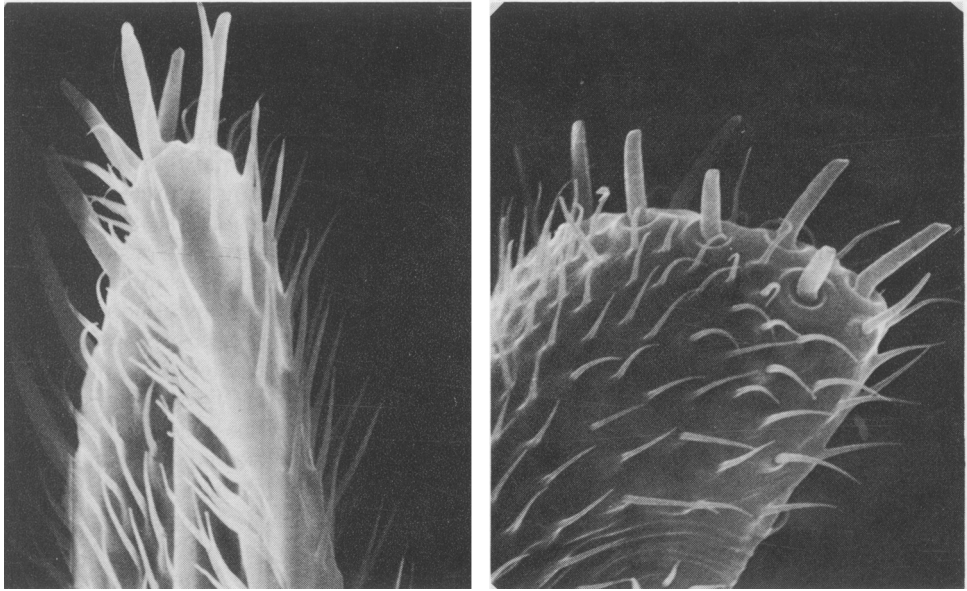


Fig. 5. Scanning electron micrographs of *A. lingnanensis* club apex illustrating chemoreceptors (orig. X3000). Female is on the left, male is on the right.

Rao and DeBach (1969a). Moreover, it is thought to be released from somewhere on the thorax. Scanning electron microscopic study of the female thorax of *A. lingnanensis* (Fig. 6, left) revealed a small pore; this may be the site of pheromone release. Studies by Khasimuddin and DeBach (1975) indicate a male pheromone in *A. maculicornis* (Masi). Figure 6, right, shows a small pore on the male thorax of *A. lingnanensis*. In both sexes, the pore is situated in the median furrow just posterior to the discrimen. The pore has also been observed on the mesosterna of *A. fisheri* and *A. melinus*, but attempts have not been made to confirm its presence on the mesosterna of other species.

**Middle-leg posture** is noteworthy because the legs do not contact the female's body during courtship, or do so only briefly if the female is attempting to dislodge the male. Although experimental analysis of the functional significance of middle leg position was not possible, several explanations for their

position and movement are possible. Semaphoral movement may be necessary for balance, but this is unlikely because four legs are in contact with the female's body at all times, and this appears adequate for maintaining the male on the female. Alternatively, this lack of contact could serve to maximize stimulation at centers of contact by eliminating extraneous "noise." This view is sensualist, however, and does not seem consistent with our knowledge of insect behavior. Another explanation is that the middle legs are alternately dispersing a pheromone which inhibits movement of the female. Alternate forward thrust of the male indicates a bilateral dispersal. The reader is reminded that the pore just described is situated just anterior to the middle coxae.

**Male wing vibrations** in *Aphytis* spp. during courtship were first noted by Rao and DeBach (1969a). They demonstrated that wings are not necessary for successful insemination, and the present study indicates these vibrations seem



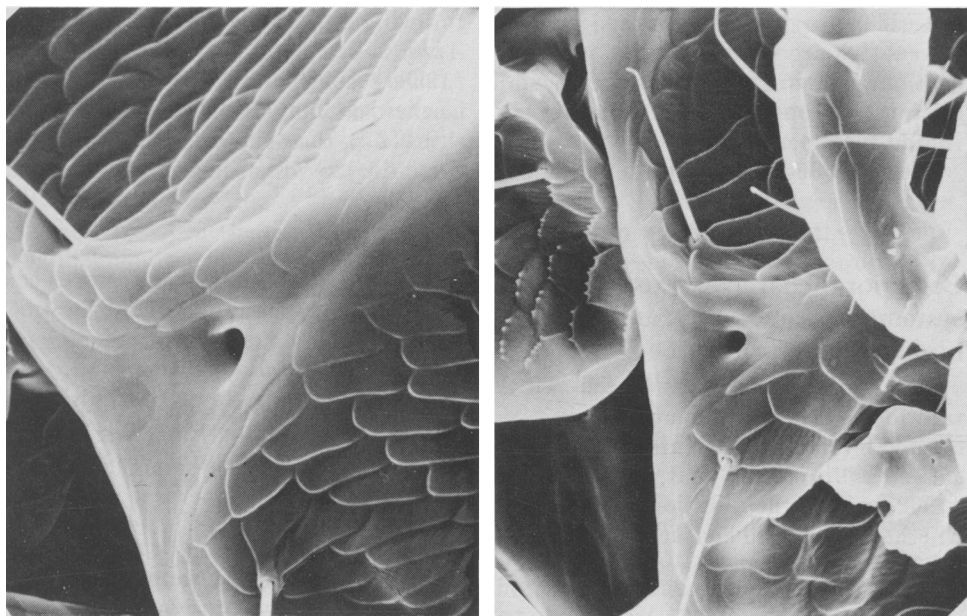


Fig. 6. Scanning electron micrograph of *A. lingnanensis* mesothoracic pores. Female is on the left (orig. X1350) ; male is on the right (orig. X1200).

restricted (to a greater extent) to the postcoital mount behavior. The vibrations vary in frequency and intensity but also seem correlated with female movement. At least when a female moves or attempts to move, the male vibrates his wings. The wings are also vibrated when the female is quiescent, so other explanations for the significance of such movements are possible. First, wing vibrations, generated by male flight muscles and transmitted via the tarsi and/or the thorax, are tactually stimulating to the female. This explanation cannot be eliminated on theoretical grounds; but Rao and DeBach (1969a) suggested that females would not be able to discriminate between conspecific and alien males on the basis of wing-beat frequency alone, and that perhaps a more subtle mechanism may be involved. Secondly, females may be inhibited by the sight of vibrating wings. As indicated in a preceding paragraph, the antennae have no such function, and it seems improbable that the

wings have. The wings of *A. lingnanensis* group members are hyaline. In those taxa for which visual displays have been suggested or implicated, the wings have conspicuous mottling or color patterns (viz. diurnal species of Lepidoptera). A third possibility is that male wing beats are dispersing a pheromone, or preventing habituation to a prevailing one. Rapid wing vibrations may disperse a freshly emitted pheromone for which the middle legs' semaphoral movement was not operating effectively. This hypothesis is difficult to test in *Aphytis* because all species are exceedingly small, and surgical removal of the wings hampers coitus. This, in turn, precludes postcopulatory mount behavior. On the other hand, wing vibrations may prevent habituation to a prevailing pheromone because habituation may result in female movement. Rapid wing movement may expunge a pheromone and thus restore female sensitivity to a subsequently emitted pheromone. The

critical factors to be considered in each alternative are the velocity of wing vibrations, amount of air displaced, and pheromone concentration necessary to inhibit female movement.

The conspicuously large setae in the

forewing delta of both male and female *Aphytis* are notable. Rao and DeBach (1969a) suggested that a stridulating mechanism may be involved in courtship. If so, the delta setae may be implicated during wing vibrations.

## DISCUSSION

### Behavioral characters: use in systematics, taxonomy, and biological control

Some investigators have been reluctant to use behavioral characters in taxonomic, systematics, or applied biological control programs; but, as Alexander (1962) noted, the question is no longer whether behavioral characters should be used, but rather when and how they should be used.

Behavioral characters are useful in classification (Ducke, 1914; Plath, 1934; Given, 1954; Emerson, 1938; Petrunkevitch, 1926; Pinto, 1972a, b), to separate sibling species, or morphologically indistinguishable forms (Thorpe, 1940; Adriaanse, 1948; Evans, 1953; Assem and Povel, 1973), and to provide valuable insight into evolutionary trends (Evans, 1953, 1966; Speith, 1952; Heinrich, 1911; Linsley *et al.*, 1952; Nielsen, 1932). Behavioral characters can be important in biological control for separating similar species or forms in the field. Also, they may be useful in separating sibling species upon importation.

Convergent evolution may present a problem when trying to apply behavioral information to classification and phylogeny. Sexual selection and character displacement may obscure evolutionary trends when attempting to utilize sexual behavior in classification. Isolating, identifying, and describing the stimuli involved in courtship behavior and in tracing neural pathways does not provide conclusive evidence, because there is no *a priori* reason why these features should have a common origin or should have evolved harmoniously.

Complexities of behavioral patterns can be used to help establish homology between related taxa. If the principle of parsimony is valid, the possibility of two behavioral patterns being similar through convergent evolution is roughly inversely proportional to the complexity of the pattern itself.

Assem and Povel (1973) have shown how courtship behavior provides an insight into evolving species complexes. Working with the pteromalid fly parasites *Muscidifurax* spp., they noted differences in male antennal movement among three sibling species during courtship, but female behavior was not overtly different. They concluded that courtship acts as an isolating mechanism among sympatric species of *Muscidifurax*. Similar findings have been reported by Goodpasture (1975) for *Monodontomerus*.

The *Aphytis* species studied have two basic antennal fanning systems: 1) that of *A. lingnanensis*, where clubs are vibrated more or less alternately at the apex of the female's clubs, and 2) that of *A. melinus*, where clubs are vibrated together. *Aphytis melinus* types raise their heads, but *A. lingnanensis* types do not. Body position during courtship is also different in the two types.

In contrast to the *Muscidifurax* complex, *Aphytis* females show different responses toward male courtship. Sexually receptive females of the *A. lingnanensis* type maintain their antennae parallel to the substrate, whereas females of *A. melinus* and related types keep their antennae geniculate during courtship and copulation.

The *Aphytis* courtship pattern is useful qualitatively in identifying taxa, and in separating live field material. This is pertinent to biological control studies, because all forms of the **lingnanensis group** are similar morphologically, and only certain of them can be separated by specialists using cleared and slide-mounted specimens.

### Postcopulatory mounting: is it sexual selection?

Darwin (1871) regarded all characters that influence reproduction as being the product of sexual selection. Huxley (1938) noted that there are two components of sexual selection: epigamic (male-female behavior or morphological adaptations) and intrasexual (male-male or female-female interaction, overt or otherwise). While Selander (1972) (in Campbell, 1972) feels that these often merge imperceptibly, we regard postcoital mounted behavior by male *Aphytis* as an indication of intrasexual sexual selection.

We doubt that female unreceptivity is instantaneous in any hymenopterous species, and that subsequent copulation is possible. Female guarding by the male is well documented in insects (Foster, 1967; Michelsen, 1963; Johnson, 1962), and may be pre- or postcoital, active or passive (Parker, 1970a, b; 1974). We feel that mounted behavior by male *Aphytis* is the equivalent of guarding.

The purpose of guarding has been attributed to sperm precedence, or sperm competition, in Orthoptera (Hunter-Jones, 1960), Lepidoptera (Clarke and Sheppard, 1962), and Coleoptera (Schlager, 1960). Sperm precedence has been taken by Parker (1970a, b; 1974) to mean that the last male to inseminate fertilizes most eggs subsequent to terminal insemination.

Parental investment is any activity on the part of a parent that increases offspring survival rate (Trivers, 1972),

and may be 1) extended courtship or coitus, 2) female guarding, or 3) cooperative parental care (Parker, 1974). Aspects of parental investment as they relate to sexual selection have been treated by Thornhill (1976). *Aphytis* spp. do not cooperate between the sexes in rearing progeny, nor do they extend courtship or coitus. Male parental investment in *Aphytis* is rather short, consisting of the time spent in courtship, coitus, and postcopulatory mount. When the relative amount of time spent in each activity is considered (precoital courtship 3 to 5 seconds, postcopulatory mount 2 to 5 minutes), male investment strongly favors postcopulatory guarding. A male that remains on a female for an extended period of time reduces the rate at which he encounters virgin females. This is a disadvantage to the male, but is counterbalanced through the preservation of his genes by ensuring that his inseminative effort will not be supplanted during the female's relative refractory period of courtship receptivity immediately following insemination.

Our observations of more than one male confined with only a single female *A. lingnanensis* show that some males active in postcopulatory mounting behavior back up on a female when a second male approaches, or attempts to mount. Although postcopulatory mounted males occasionally leave the dorsum of a female when challenged, in general the backing and forward movement persists, precluding courtship and copulation by a second male. After a period of time (in our design 6 hours, but probably considerably shorter) the inseminated *A. lingnanensis* female is not receptive to male courtship, and the unreceptiveness is almost complete. We did not determine precisely when, after insemination, a female became unreceptive, only that it occurred sometime during the 6 hours following insemination, and that the unreceptiveness was

statistically different from that of the controls.

If she's been adequately supplied with viable sperm, a second copulation may be disadvantageous to the female. She can better invest her time in searching for hosts or ovipositing. Each female competes with others for ovipositional sites, and the female that produces the greatest number of progeny is the superior competitor.

The spermatheca of parasitic Hymenoptera are small. It has been suggested that a superabundance of sperm cannot be utilized by the female (Flanders, 1945). If the amount of sperm delivered per ejaculation is adequate for fertilization of a female's eggs throughout her lifetime, a second insemination may be superfluous. This is not to imply that ejaculate size is the limiting factor; but rather, when a male fails to adequately inseminate, the female may copulate a second time.

### Use of quantitative data

Except for the study of Barrass (1961) and the present one, little quantitative data on sexual behavior are available on parasitic Hymenoptera, but it is possible to use such data to separate closely related sibling species. This is important to biological control, because morphological criteria are of-

ten not adequate to assign organisms to preexisting taxa. Differences in courtship patterns can be used by field workers to quickly separate sibling species that are sympatric. Also, detecting differences in courtship behavior can lead to the discovery of new taxa.

Predictability of behavioral characteristics necessitates replication and the use of appropriate statistical tools. Multiple range tests are appropriate when several taxa are studied, but cluster analysis and discriminant function are also useful. If little variation is noted between taxa of equal rank, a character may be useful at higher taxonomic levels. An invariable character at the generic level may be variable at the family level. However, plastic behavioral characters may generate so much noise as to be worthless for the purposes outlined above. Character plasticity may be due to genetic variation or to a lack of standardization. Temperature is important to poikilothermous organisms, and observations made over a wide range of temperatures rather than at comparable temperatures may hide the potential usefulness of a character. Quantifying results obtained from data on organisms of different ages or physiological states may also obscure potentially useful characters.

## SEXUAL BEHAVIOR IN THE PARASITIC HYMENOPTERA (LITERATURE REVIEW)

Although sexual behavior has been studied in some groups, e.g., Orthoptera, Lepidoptera, Diptera (cf. Richard, 1974), it has been only poorly studied in the parasitic Hymenoptera. Table 10 lists taxa for which some features of sexual behavior have been noted. (Most aculeate parasites have not been treated because we are unfamiliar with them). The question marks in table 10 reflect our inference that the category was

represented even though the author did not specifically so state.

Mate attraction has been attributed to sight, sound and/or smell. Heatwole *et al.* (1964) suggested that sound is responsible for male aggregations of *Megarhyssa* spp. on logs from which females are about to emerge, but they were unable to identify the frequency which attracted the males. Evidence for visual orientation stems from

TABLE 10  
TAXONOMIC ASSOCIATIONS OF VARIOUS ASPECTS OF COURTSHIP BEHAVIOR IN PARASITIC HYMENOPTERA \*

Taxon	Initial perception	Wing vibrations	Antennation	Mounted courtship	Postcoital mount behavior	Polygyny	Polyandry	Authority
ICHNEUMONOIDEA								
Aphidiidae								
<i>Aphidius</i> spp.	Visual ?	Yes	Yes	Yes		Yes	No	Mackauer (1969)
<i>Lyssiphtebus testaceipes</i> Cresson	Olfaction ?	Yes		Yes		Yes	No	Spencer (1926) Sekhar (1957)
<i>Praon pallians</i> Mues.	Olfaction		Yes			Yes	No	Schlenger & Hall (1960)
<i>Trioxys utilis</i> Mues.	Olfaction		Yes			Yes	No	Schlenger & Hall (1961)
Braconidae								
<i>Alysia manducator</i> Pz.		Yes	Yes			Yes	?	Altson (1920)
<i>Apanteles medicaginis</i> Muesebeck		Yes	Yes	Yes				Allen (1958)
<i>Apanteles ruficornis</i> Haliday						Yes	Yes	Hafez (1947)
<i>Chelonus eleaphilus</i> Silvestri		Yes	Yes	No	No			Arambourg (1968)
<i>Cosmophorus henschelti</i> Ruschka			Yes	No				Seitner & Nötzl (1925)
<i>Dinocampus rutilus</i> Nees		Yes	Yes	No	No	Yes	?	Jackson (1928)
<i>Homotropus decoratus</i> Cresson			Yes	Yes				Kamal (1939)
<i>Leiothron</i> spp.		Yes	Yes	Yes				Waloff (1967)
<i>Microbracon chelonius</i> Viereck			Yes					Cherian & Narayanaswami (1942)
<i>Microbracon mellitor</i> (Say)		Yes	Yes	Yes				Willard (1927)
<i>Macrocentrus ancylivorus</i> Rohwer						Yes	Usually no	Finney et al. (1947)
<i>Opius oophilus</i> Fullaway		Yes				Yes	Yes	Haramoto (1957)
<i>Phanerotoma bennetti</i> Muesebeck		Yes				Yes	Yes	Bennett (1960)



TABLE 10—Continued

Taxon	Initial perception	Wing vibrations	Antennation	Mounted courtship	Postcoital mount behavior	Polygyny	Polyandry	Authority
<b>ICHNEUMONOIDEA (continued)</b>								
Ichneumonidae								
<i>Agrotheresutes tunetanus</i> Haber			Yes	Yes	No			Kugler & Wollberg (1967)
<i>Angitia armillata</i> Gravenhorst		Yes	Yes	No	No	Yes		Beling (1933)
<i>Devorilla canescens</i> (Gravenhorst)		Yes	Yes	No		Yes		Hase (1937)
<i>Diadegma chrysostictum</i> (Gmelin)		Yes						Fisher (1959)
<i>Ephialtes ruficollis</i> (Gravenhorst)				Yes				Juillet (1959)
<i>Eulimneria rufifemur</i> (Thomson)		Yes	Yes	Yes		Yes	No	Juillet (1959) Heatwole et al. (1963); Abbott (1934); Heatwole et al. (1964)
<i>Megarhyssa</i> spp.	Sound ?							Whiting (1932); Grosch (1947, 1948)
<i>Microbracon hebetor</i> Say	Olfaction ?	Yes	Yes					
<b>PROCTOTRUPOIDEA</b>								
Scelionidae								
<i>Asolcus basalis</i> (Woll.)			Yes	Yes				Wilson (1961)
<i>Asolcus</i> spp.			Yes	Yes	No	Yes	No	Safari (1963)
<i>Hadronotus ajaz</i> (Girault)			Yes	Yes		Yes		Schell (1943)
<i>Telenomus ulijetti</i> Nixon				Yes		Yes usually	No	Jones (1937)
<b>CYNIPOIDEA</b>								
Cynipidae								
<i>Pseudeucoila bochei</i> (Weid)	Olfaction	Yes	Yes	Yes			No	Jenni (1951); Assem (1969)
<i>Pseudeucoila mellipes</i> (Say)			Yes	Yes				Assem (1970)
<i>Trigonaspis megaptera</i> (Pantzer)			Yes	Yes			Yes	Assem (1970)

	Yes	Yes	Yes	Chrysal (1930)
<b>Ibaliidae</b>				
<i>Ibalia leucospoides</i> Hochenw.	Yes	Yes		
<b>CHALCIDOIDEA</b>				
<b>Aphelinidae</b>				
<i>Aphytis lingnanensis</i> group	Visual?	Yes	Yes	Present study
<i>Coccophagoides utilis</i> Doutt	Olfaction?	Yes	Yes	No
<i>Encarsia pergandiella</i> Howard	Olfaction?	Yes		Broodryk & Douth (1966)
<i>Phycus</i> spp.			Yes	Gerling (1966)
<i>Pteroptrix smithi</i> (Compere)	Yes	Yes	Yes	No
<b>Chalcididae</b>				Williams (1972)
<i>Euchalcidia caryobori</i> Hanna		Yes	Yes	Bar & Gerling (1971)
<b>Encyrtidae</b>				Hanna (1934)
<i>Aphidencyrthus inquisitor</i> (Howard)	Yes	No	No?	Griswold (1929)
<i>Anagyrus pseudococci</i> (Girault)	Yes	Yes	Yes	Avidov et al. (1967)
<i>Comperia merceti</i> (Compere)	Visual?	No	No	No
<i>Comperiella bifasciata</i> Howard	Visual?	Yes	No	Gordh (1972)
<i>Copidosoma boucheanum</i> Ratzeburg		Yes	Yes	Gordh (unpublished)
<i>Metaphycus taxi</i> Alan	Yes	Yes		Parker & Thompson (1928)
<i>Microterys ferrugineus</i> Nees	Yes	Yes	No	Alam (1957)
<i>Ooencyrtus submetallicus</i> (Howard)	Visual?	No	No	Parker & Thompson (1928)
<i>Plagiomerus diaspidis</i> Crawford	Visual	Yes	No	Wilson & Woolcock (1960)
				Gordh & Lacey (1976)

TABLE 10—Continued

Taxon	Initial perception	Wing vibrations	Antennation	Mounted courtship	Postcoital mount behavior	Polygyny	Polyandry	Authority
<i>Tetraneura pretiosus</i> Timberlake						Yes	No	Clancy (1934)
Eucharitidae								
<i>Schizaspidia tenuicornis</i> (Ashmead)	Olfaction			Yes		?	No	Clausen (1923)
Eulophidae								
<i>Chrysocharis larinellae</i> (Ratzeburg)	Olfaction ?	Yes	Yes	No	No			Quednau (1967)
<i>Dahlbominus fuscipennis</i> (Zetterstedt)	Visual ?	Yes	Yes	Yes		Yes	No	Morris & Cameron (1935) ; Wilkes (1965)
<i>Entedon pharnus</i> Walker		Yes		No				Fisher (1970)
<i>Entedon</i> sp. nr. <i>longulus</i> Erdős		Yes	Yes	No				Fisher (1970)
<i>Eulophus viridulus</i> Thomson		Yes	Yes	Yes				Parker & Smith (1933)
<i>Euplectris agaristae</i> Crawford				Yes		Yes		Noble (1938a)
<i>Melittobia acasta</i> (Walker)		Yes	Yes	Yes	No	Yes	No	Balfour-Browne (1922) ; Parker & Thompson (1928)
<i>Melittobia australica</i> Girault	Olfaction ?	Yes	Yes	Yes		Yes	No	Dahms (1973)
<i>M. chalybii</i> Ashmead			Yes	Yes		Yes	No	Hobbs & Krunic (1971) ; Buckell (1928) ; Torchio (1963)
<i>Mesochorus bimaculatus</i> (Dalman)		Yes		Yes				Jackson (1964)
<i>Oxyomorpha intermedia</i> Thomson		Yes	Yes	Yes	No			Parker & Thompson (1928)
<i>Pnygalio mediterraneus</i> Ferr. & Deluc.		Yes	Yes	Yes	Yes			Delanoue & Arambourg (1967)

CHALCIDOIDEA (continued)						
<i>Tetrastichus flavigaster</i>						
Brothers and Moran						
	Yes	Yes	Yes	Yes	No	Moran et al. (1969)
Eulophidae						
<i>T. incertus</i> (Ratz.)	Visual?	Yes	Yes	Yes		Miller (1966)
<i>T. turionum</i> (Hartig)		Yes	Yes	Yes		Juillet (1959)
Eupelmidae						
<i>Eupelmus</i> nr. <i>microzonus</i>	Visual?	No	Yes	Yes	Yes	Gordh (unpubl.)
Forster						
<i>Eupelmus urozonus</i>	Visual?	No?	Yes	Yes	Yes	Delanoue & Arambourg (1965)
Dalman						
Eurytomidae						
<i>Eurytoma curcutionum</i> Mayr		Yes	Yes	Yes	Yes	Fisher (1970)
<i>Eurytoma fellis</i>						
Girault		Yes	Yes	Yes	Yes	Noble (1936)
<i>Eurytoma martelli</i>						
Domenichini	Visual?	Yes	Yes	Yes	Yes	Delanoue & Arambourg (1969)
<i>Macrorhinea oecanthi</i>						
(Ashmead)			Yes	Yes		Smith (1930)
Mymaridae						
<i>Anaphoidea conotracheli</i>						
Girault		Yes	Yes	Yes		Bakkendorf (1934)
<i>Caraphractus cinctus</i>		Yes	Yes	Yes	No	Jackson (1966)
Walker						
<i>Cleruchus pluteus</i>						
Enock	Olfaction	Yes		Yes	Yes	Bakkendorf (1934)
<i>Erythmelus goochi</i>						
Enock				Yes		Bakkendorf (1934)
<i>Ooconus heterotomus</i>						
Förster		Yes			Yes	Bakkendorf (1934)
<i>Polynema ovulorum</i>						
Haliday	Yes			Yes		Bakkendorf (1934)
Pteromalidae						
<i>Chlorocytus laogore</i>						
(Walker)	Yes		Yes	Yes	Yes	Fisher (1970)

TABLE 10—Continued

Taxon	Initial perception	Wing vibrations	Antennation	Mounted courtship	Postcoital mount behavior	Polygyny	Polyandry	Authority
<i>Cyrtogaster</i> sp.	Visual?	Yes	Yes	Yes		Yes	No	Gordh (unpubl.)
<i>Habrocytus cerealellae</i> (Ashmead)		Yes	Yes	Yes		Yes	No	Noble (1932)
<i>Lariophagus distinguendus</i> (Förster)		Yes	Yes	Yes	Yes	Yes	?	Hase (1919) Kashef (1955) Burkhardt (1916) Assem (1970)
<i>Nasonia vitripennis</i> (Walker)	Visual?	Yes	Yes	Yes	Yes	Yes	Yes No	Altson (1920) Myers (1929) Girault & Saunders (1910); Barrass (1960a,b; 1961) Assem & Visser (1976)
<i>Pachyneuron allograptae</i> Ashmead	Olfaction?		Yes	Yes				Kamal (1939)
<i>Pachycerropideus vindemiae</i> (Rondani)		Yes	Yes	Yes		Yes	No	Crandall (1939)
<i>Pteromalus venustus</i> (Walker)		Yes	Yes	Yes		Yes	No	Hobbs & Krunic (1971)
<i>Spalangia drosophilae</i> Ashmead		Yes	Yes	Yes	No	Yes	Yes?	Simmonds (1953)
<i>Spalangia muscarum</i> Girault			Yes	Yes				Pinkus (1913)
<i>Spalangia nigra</i> Latreille			Yes	Yes		Yes	No	Parker & Thompson (1928) Assem (1970)
<i>Stenomatalina liparae</i> (Girault)	Visual?	Yes	Yes	Yes	No			
Signiphoridae								
<i>Signiphora borinquensis</i> Quezada, DeBach & Rosen		Yes	Yes	Yes				Quezada et al. (1973)
Torymidae								
<i>Idarnes</i> spp.	No	No		No	No	Yes	?	Gordh (unpubl.)
<i>Megastigmus acaciae</i> Noble			Yes	Yes	Yes			Noble (1939)



## CHALCIDOIDEA (continued)

Torymidae									
<i>Megastigmus brevitarsis</i> (Girault)		Yes		Yes					Noble (1938b)
<i>Megastigmus spermotrophus</i> Wachtl	Visual ?	Yes		Yes					Hussey (1955)
<i>Monodontomerus aureus</i> Walker		Yes		Yes			Yes	No ?	Muesebeck (1931)
<i>Monodontomerus obscurus</i> Westwood	Visual ?	Yes	Yes	Yes			Yes	No	Hobbs & Kronic (1971)
Trichogrammatidae									
<i>Chaetostricha pulchra</i> Kryger		Yes		No					Bakkendorf (1934)
<i>Ophioneurus signatus</i> Ratzeburg				Yes	No				Bakkendorf (1934)
<i>Trichogramma pretiosum</i> Riley	Visual ?	No	No	No	No		Yes	?	Gordh (unpubl.)
<i>Trichogramma minutum</i> Riley	Visual ?			No			Yes		Martin (1927)
<i>Trichogramma retortidum</i> (Girault)	Visual ?	No	No	No	No		Yes	?	Gordh (unpubl.)
BETHYLOIDEA									
Bethyloidae									
<i>Goniozus claripennis</i> Förster		No	Yes	Yes	No		Yes	?	Voukassovitch (1924)
<i>Goniozus gallicola</i> Fouts	Visual + Olfaction ?	No	Yes	Yes	No		Yes	?	Gordh (1976)
<i>Goniozus aethiops</i> Evans	Visual + Olfaction	No	Yes	Yes	No		Yes	?	Gordh & Evans (1976)
<i>Parasterola emigrata</i> (Rohwer)		No	Yes	Yes	No				Gordh (unpubl.)
<i>P. nigrifemur</i> (Ashmead)	Visual + Olfaction ?	No	Yes	Yes	No		Yes	?	Gordh (unpubl.)

\* In some instances we have doubts as to the generic placement of species listed in this table. This is due primarily to conflicting statements in the literature and an absence of authoritative taxonomic pronouncement. Some names given are almost certainly junior synonyms.  
Blanks indicate lack of published information for a particular category; question marks reflect our inference that the category was represented, even though the author did not specifically so state.

observations of *Nasonia vitripennis* (Walker) by Barrass (1960a, b), *Eurytoma martellii* Domenichini by Delanoue and Arambourg (1969), *Monodontomerus obscurus* Westwood by Hobbs and Kronic (1971), and *Trichogramma pretiosum* Riley by Gordh (unpublished), in which the males swayed from side to side when approaching the females. Wigglesworth (1950) believes this prevents image loss due to retinal fatigue. Alternatively, males may have chemoreceptors on the body that are used in mate location. Such males would be orienting chemoklinotactically or chemotropotactically. Hussey (1955) reported that female *Megastigmus spermotrophus* Wachtl are attracted to swaying males that are non-locomotive. Male-swaying apparently has evolved several times, because all of these species are distantly related chalcidoids.

Some studies indicate that olfaction is used in mate attraction in certain parasitic Hymenoptera (Fink, 1926; Mürr, 1930; Parker, 1931; Cox, 1932; Grosch, 1948; Schlinger and Hall, 1960, 1961). We found that once male *Aphytis* discovered female pupal exuvia, they immediately antennated the cast pupal skins and attempted copulation with them. The action of the chemical communicant may be different in different groups. Quednau (1967) reported that *Chrysocharis larcinellae* (Ratz.) will not mate by single pairs immediately after emergence, but readily mate when several pairs are placed together. An aggregation pheromone could operate in a manner similar to that of scolytid beetles (Vité and Pitman, 1968, 1969a, b).

Male antennation is common in courtship behavior in parasitic Hymenoptera and reinforces the hypothesis of chemotactile-mediated courtship behavior. In Table 10, no distinction is made between fanning while the male is on or

near the female, or whether contact is made between the antennae of the male and the female's body. Antennation reaches high expression in *Melittobia*, in which males of some species have notches on the mesal surfaces of each scape apex. Female antennae are pressed into each notch by the male flagellum (Dahms, 1973; Buckell, 1928).

Wing vibration is another feature of male courtship which appears frequently in the parasitic Hymenoptera. Wing vibrations have not been observed in many species of encyrtids (Table 10). The family is enormous, with nearly 500 genera described, and the lack of knowledge about courtship in the family may conceal the fact that male wing vibrations are common. The Aphelinidae and Signiphoridae are closely related families, and wing vibrations are common in these groups. Quezada *et al.* (1973) produced males with high temperatures in the thelytokous signiphorid *Signiphora borinquensis* Quezada, DeBach and Rosen, and these males vibrated their wings during courtship. Wing vibrations are common in the more primitive Clistogastra (Ichneumonoidea), but some primitive Bethylinae do not vibrate their wings. Lack of male wing vibrations may be a derived character in this last instance, because male Bethylinae are protandrous and mate with females in the latter's cocoon before female emergence. When males encounter females after emergence, wings are not vibrated (Gordh, 1976).

Male-mounting of the female is another feature of male courtship that commonly appears in the parasitic Hymenoptera. It has been observed in aphidiids, scelionids, braconids, cynipids, bethylids, and many chalcidoids. It does not appear common in the encyrtids, however. Some male eulophids (*Chrysocharis larcinellae*; *Entedon* spp.) do not mount the female, but

place a foretarsus on the female and copulate from the side. Both behavior patterns (side courtship and mating) appear aberrant.

The male-above attitude is common throughout the Insecta, and Alexander (1963) believes it represents male dominance. In chalcidoids, however, male-mounting may not necessarily reflect male dominance, but rather ensures that the female does not evade the male during the period between initiation of male courtship and the onset of female receptivity.

Semaphoral movement of middle legs has been reported in several species of chalcidoids. Parker and Smith (1933) noted it in *Eulophus viridus* Thomson, and Askew (1961) reported that the middle legs of *Eupelmus urozonus* Dalman do not contact the female's body. We have shown this for all species of the **lingnanensis group**. Scanning electron microscopic analysis of *Aphytis* spp. revealed a medially situated pore which is possibly ectocrine in function. The significance of the semaphoral movement of middle legs was not reported for the eulophid or the eupelmid.

Mandibular involvement (not tabulated in Table 10) in courtship also seems an adaptation of some species. The male mandibles of *A. melinus* types come near, or touch, the female's pedicels during courtship and postcopulatory mounted behavior. Mandibulation has been suggested or noted in many

divergent taxonomic groups (*Aphidius* spp., Mackauer, 1969; *Comperia merceti* (Compere), Gordh, 1972; and *Eupelmus* sp. nr. *microzonus* Foerster, Gordh, unpubl.), and can be on any part of the female's body. For instance, male *C. merceti* nip the apex of the female gaster several times prior to coitus. *Eupelmus* sp. nr. *microzonus* female antennae are erect and mesally contiguous while the male spreads his mandibles and moves the inner margins up and down along the outer margin of each female flagellum (segments 2 to 5), and simultaneously fans his clubs near the female's clubs. The mandibles of most chalcidoids possess two, three, or four gland-like ducts which may be ectocrine in function (Gordh, 1975).

Some chalcidoid males exhibit postcopulatory mounting behavior (*Nasonia vitripennis* (Walker), *Melittobia chalybii* Ashmead, *Pteropterix smithi* (Compere), *Entedon* sp. nr. *longulus* Erdős, and others), and this reaches elaborate expression in *Aphytis* spp., with male leg movements, wing vibrations, and antennal fanning.

Male polygyny and female monandry are common throughout the Hymenoptera, with the exception of the honey bee and some other bees (Michener, 1974). Monandry is usually characterized by female unreceptivity following insemination, but other factors may also be involved, such as mating plugs, prolonged copulation, or morphological adaptations.

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