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A REVIEW OF THE BIOLOGY OF SPECIES IN THE THE GENUS *MELITTOBIA* (HYMENOPTERA : EULOPHIDAE) WITH INTERPRETATIONS AND ADDITIONS USING OBSERVATIONS ON *MELITTOBIA AUSTRALICA*.

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ABSTRACT

This paper reviews published accounts of *Melittobia* biology and contains observations on the single Australian species *M. australica*. The species was found to be a highly polyphagous primary ectoparasite attacking the immature stages of nesting Hymenoptera, both solitary and social. It is also hyperparasitic on the immature primary parasites within the primary host's nests, and are reported parasitising the immature stages of hosts belonging to a variety of orders other than Hymenoptera. Females gain access to the host by entering the host cell before it is sealed (delaying oviposition until the host has reached a suitable developmental stage), excavation through the cell wall and enveloping membranes or by oviposition directly through enveloping membranes. Any one species can show this range of behaviour and the female's nutritional condition is important as a factor in deciding which occurs. Females puncture the host with their ovipositors to feed and to subdue an active host but not for oviposition. Males do not feed and are highly aggressive although male aggression seems to vary both within and between species. Courtship is extremely complex and the three basic patterns reported in the literature are summarised and some morphological features are correlated with them. Reproduction is also complex and the importance of parthenogenesis, sib-mating (including mother-son matings), multiple settling by females and sex ratios shifts is discussed. A nutritionally induced polymorphism occurs, as well as sexual dimorphism, and varies with species. The result is type-form and second-form individuals of both sexes which differ morphologically and physiologically. Second-form specimens of both sexes of an *acasta* group species are described and compared with second-form specimens of both sexes of *M. australica*. Dispersal is by flight and evidence suggests that it is wind assisted. The capability of *Melittobia* to use man's transport for dispersal is also discussed. A brief account of the life cycle of *M. australica* is included and compared with published accounts of other species.

INTRODUCTION

Species in the genus *Melittobia* are very efficient organisms. In all stages of their development they show remarkable plasticity of behaviour and adaptability to prevailing conditions. Theoretically, uninseminated females can survive and eventually produce progeny of both sexes even in the absence of preferred hosts. They make very good laboratory animals and their plasticity coupled with arrhenotokous parthenogenesis make them ideal subjects for laboratory investigations into the genetics of speciation and evolution.

Some of the reports on the biology of *Melittobia* species in the literature proved either confusing or inconsistent. Detailed study of the biology of *Melittobia australica* allowed many of the confusing and inconsistent aspects to be clarified. The following account is therefore a blend of previously published accounts on several species and my recent observations on the single Australian species. The outcome of this review has been of great assistance in understanding phylogeny in the genus and therefore of great assistance in making taxonomic decisions for my revision of the genus (Dahms 1983a)

MATERIALS AND METHODS

Cultures of *Melittobia australica* were maintained in excavated blocks with glass covers in the laboratory without controlled temperature or humidity. Behavioural observations were made with a Leitz TS stereomicroscope with fibre-optics, cold-light illumination. Hosts used for culture of *M. australica* were *Pison* spp., and *Sceliphron* spp. Larvae of the ant genus

Camponotus were tried as hosts but proved unsuitable. Although larvae of *Apis mellifera* proved suitable hosts for cultures they suffered high mortality due to mechanical damage during extraction and from not being in a controlled environment.

Investigations into the life history of *M. australica* were carried out using *Sceliphron formosum* prepupae, a supply of which was maintained in the refrigerator without deterioration. In this case the trials were carried out in plastic-stoppered glass vials. A constant temperature room was not available and the colonies were kept in a room with an air conditioner. Under these circumstances the temperatures recorded were 25°C (± 5°) and humidity 50% (± 5%).

All figures were drawn from cleared microscope slide-mounted specimens and each has the scale indicated. They were drawn with a camera lucida fitted to a Wild M20 compound microscope.

BIOLOGY

Hosts

To say that species of *Melittobia* are not host specific is a gross understatement. Waterston's 1917 view of *M. acasta* that it is remarkably polyphagous attacking everything within its limited range of action is more realistic.

In the main, *Melittobia* are primary parasites within the nests of wasps and bees, both solitary and social. Amongst the social species are: *Vespula acadica* (Salden) (H.C. Reed, USA, pers. comm. 1978); *Vespula germanica* (Fabricius) and *Bombus* sp. (R. Macfarlane, New Zealand, pers. comm. 1980); *Polistes exclamans* Viereck (H.C. Reed, USA, pers. comm. 1977); *Bombus pennsylvanicus* (DeGeer) (A.C. Haman, USA, pers. comm. 1977) and *Apis mellifera* Linnaeus (E.H. Erickson, USA, pers. comm. 1978). The last mentioned of course has serious economic implications although van den Assem (pers. comm. 1981) considers that sperm inside the spermathecae of female *Melittobia* do not survive at the relatively high temperatures found inside the hive of *A. mellifera*. *Melittobia* species have reached economic pest status wherever the Alfalfa Leaf-cutter Bee (*Megachile rotundata* (Fabricius) is cultured (Prof. Thorp, University of California Davis pers. comm. 1981). Four species, *M. acasta* (Walker 1839), *M. chalybii* Ashmead, 1892, *M. japonica* Masi 1966 (= *M. clavicornis* (Cameron 1908)) and *M. megachilis* (Packard 1864) have been recorded in the literature as being hyperparasitic within nests of Hymenoptera and in the present study *M. australica* Girault, 1912 was found to be hyperparasitic also.

There are published records of *Melittobia* naturally parasitising hosts belonging to orders other than Hymenoptera. Rau (1940) reports breeding *M. chalybii* from the ootheca of the cockroach *Periplaneta americana* (Linnaeus). Howard and Fiske (1911), and Graham-Smith (1916, 1919) have bred *M. acasta* from dipteran puparia. Swezey (1909) discovered *M. hawaiiensis* Perkins, 1907 breeding on the larvae of the bud-moth *Ereunetis flavistriata* Wilson. Howard (1892) reported a species from dipteran puparia within the cells of a mud-dauber's nest and *M. japonica* (= *M. clavicornis*) is noted as utilising similar dipteran hosts by Iwata and Tachikawa (1966). In the present study *M. australica* was bred from dipteran puparia within *Sceliphron* spp. nests.

Laboratory trials by various workers have shown a remarkable range of hosts that *Melittobia* will utilise under these conditions. Balfour-Browne (1922) and Thompson and Parker (1927) found *M. acasta* to be highly polyphagous in the laboratory, even attacking spiders and lepidopteran larvae taken from mud nests. However, the progeny failed to mature and Balfour-Browne felt this may have been due to desiccation of the hosts. These papers contain a very large number of species successfully parasitised from the insect orders Coleoptera, Hymenoptera, Lepidoptera and also from the arachnid order Araneae. Peck (1963) and Burks (1979) provide comprehensive host lists for North American species; Domenichini (1966) has host lists for *M. acasta* and *M. japonica;* (= *M. clavicornis*) and Thompson (1955) listed hosts of *M. acasta, M. hawaiiensis* and an unidentified species using Commonwealth Agricultural Bureau records. These lists are extremely long and it is not practical to duplicate them here.

Not all species of Hymenoptera, however, are successful hosts for *Melittobia*. Balfour-Browne (1922) found that *Osmia rufa* (Linnaeus) was rarely attacked in the wild. In the laboratory naked larvae and pupae of *O. rufa* were readily accepted by *M. acasta* females which fed and laid eggs. The eggs often failed to hatch and, if they did hatch, the resulting larvae failed to reach maturity. If he placed *M. acasta* females in a cell with larval *O. rufa* just before the cocoon was spun the *M. acasta* females often became entangled in the outer layers of the cocoon. This did not happen under similar circumstances with

other hosts. Where *M. acasta* females were presented with *O. rufa* pupae inside cocoons they were not attacked and Balfour-Browne suggested that this was due to the toughness of the cocoon. Malyshev (1911) had earlier suggested that some species may escape attack by *Melittobia* as the result of a mechanical barrier related to the type of nesting material used, e.g. those species which use resin for nest construction.

Jayasingh and Freeman (1980) also draw attention to the importance of nest material in host succeptibility to attack by *Melittobia*. They found the resinous nests of *Chalicodoma rufipennis* (Fabricius) to be a total barrier to *Melittobia*. They also found that another factor was direct attack by the mother on *Melittobia* e.g. females of *Pachodynerus nasidens* (Latreille) were observed to crush *Melittobia* females in their mandibles. I have observed parasitic mites which can normally be found on *Secliphron* spp. larvae acting in competition with *M. australica* larvae and in one case the mite larvae were feeding upon the *M. australica* larvae. From these observations it is clear that *Melittobia* do not have it all their own way.

There are a few indications in the literature that *Melittobia* spp. may be endoparasitic. Girault (1912), at the end of his descripton of *M. australica* quotes the collector, 'Mr. Tryon informs me that the parasites emerged from the host in its cocoon but not until after it had transformed into the adult, the latter died. A number of parasitic larvae make their way out of each *Pison* and pupate nakedly'. This record I regard as an error based upon an assumption. In all cases I have observed, *M. australica* is very definitely ectoparasitic. Perhaps Mr. Tryon on opening the host cocoon saw prepupal *M. australica* larvae with meconium and assumed that the larvae had emerged from within the host.

Malyshev (1911) states that under certain circumstances *M. acasta* is endoparasitic e.g. when the female oviposits through the cocoon of hymenopteran hosts or through the puparial wall of a dipteran host. Thompson and Parker (1927) found that *M. acasta* would not oviposit in fresh puparia of *Sarcophaga* sp. Oviposition occurs only after the body of the fly has separated from the wall of the puparium creating air spaces. Eggs are placed directly onto the surface of the pupa within. They found the same with some living but slightly desiccated pupae of the ant genus *Camponotus*. Air spaces had developed beneath the cuticle resembling the situation with dipteran puparia. Maeta and Yamane (1974) reported that one method of oviposition used by *M. japonica* (identification corrected to *M. acasta* by Maeta (1978)) was to oviposit through the wall of cocoons of species belonging to the hymenopteran genera *Osmia, Monodontomerus, Nematopoideus, Trypoxylon* and *Chalicodoma*. In all of these situations insertion of the ovipositor through enveloping membranes implies endoparisitism, but the eggs are placed on the surface of the body of the host which means they are in fact ectoparasitic.

In the present investigation *M. australica* was bred from the following hosts:-

1) *Pison aureosericeum* Rohwer
2) *Pison* spp.
3) *Sceliphron laetum* Smith
4) *Sceliphron formosum* Smith
5) *Megachile* sp.
6) *Stenarella victoriae* Cameron
7) Dipteran puparia in *Sceliphron* spp. nests
8) *Camponotus* sp.
9) *Apis mellifera* Linnaeus
10) *Anthrax angularis* Thomson

The host given by Girault for the type specimens of *M. australica* was *Pison spinolae* Schuckard. In the above list, 1–6 were naturally infested. *Stenarella victoriae* is an ichneumonid parasite on Sceliphron spp. The dipteran puparia in *Sceliphron* nests are thought to be parasites on the provisioned spiders since they are always found in cells fully stocked with dry spiders and without a *Sceliphron* larva. Hosts 8–10 were presented in the laboratory. Larvae of the ant genus *Camponotus* were tried as substitute hosts for laboratory work. Although the *M. australica* progeny developed through to maturity the resulting adults were small and lacked vigor. Honey bee (*Apis mellifera*) larvae were also tried as alternative hosts. They were readily accepted and produced vigorous parasite adults, but proved difficult to extract from the comb without a high percentage of deaths. *Anthrax angularis* was found as a parasite in *Sceliphron* nests. Two larvae were presented to fertilised *M. australica* females and were readily accepted. The resulting progeny were of normal size and vigour. Since *Anthrax angularis* is a natural parasite of *Sceliphron* spp. it is fairly safe to assume that it would be naturally attacked by *M. australica*.

Access to the Host

In the literature, workers have put forward several behavioural patterns associated with gaining access to the host as follows:-

1) excavation into the host cell and cocoon
2) entrance into a host cell before closure
3) oviposition through enveloping membranes

1) Excavation

Melittobia females have well developed, tridentate mandibles and there are several records in the literature which indicate that they have well developed excavatory powers.

Howard and Fiske (1911) stated that female *M. acasta* in search of a host (sarcophagid puparia in this case) entered damp soil for a distance of several inches. Graham-Smith (1916) however, suggested that the fly puparia buried in the soil were possibly connected to the surface by minute passages sufficiently large to admit *Melittobia*. There may in fact be minute passages left as the sarcophagid larvae dig into the soil and this may not be a case of true excavation by *Melittobia*. More direct evidence was provided earlier by Howard (1892) quoting observations by Giraud. The latter noted that a *M. acasta* female after walking around on the intact cell of the bee *Chalicodoma* sp., stopped and gnawed the membrane until a perforation was made through which she entered the cell. Malyshev (1966) observed that a *M. acasta* female in a host nest moved from one cell through the cell wall into the next cell and through the cocoon to gain access to another host. Graham-Smith (1916) stated that females of *M. acasta* emerged from intact fly puparia through a small hole which one of them excavated. He also noticed that females of *M. acasta* confined in glass tubes with cork stoppers immediately began to excavate a tunnel in the cork stopper. Similarly, Buckell (1928) found females of *M. chalybii* (= *digitata* Dahms 1983a) excavated their way out of glass vials through a 25 mm cork stopper. Torchio (1963) recorded excavation holes in the cell partitions of *Megachile rotundata* (Fabricius) made by *M. chalybii* (which I suspect was *M. acasta*). Cowley (1961) mentioned that *M. clavicornis* (= *M. hawaiiensis* Perkins) will excavate a hole in cocoon walls to gain access to *Pison spinolae* pupae within. Iwata and Tachikawa (1966) observed 1–5 excavation holes each of 0.5 mm made by *M. japonica* (= *M. clavicornis*) females in a series of mud cells of *Auplopus* sp. They also found several incomplete holes whose bottoms were obstructed by sand grains and from this postulated that the excavations were from the outside in. Observations by Maeta and Yamane (1974) on *M. japonica* (= *M. acasta* see Maeta (1978)) led them to conclude that female *Melittobia* have the capacity to excavate holes in plugs or partitions either of leaf fragments or mud, even if they were fairly thickly constructed.

In this investigation, inseminated female *M. australica* were presented with sealed nests of *Pison* sp. and *Sceliphron* spp. After presentation of the *Pison* nests, *M. australica* females were noted excavating the mud walls. Only one hole was constructed in each cell and several females were observed working at each site. Only one female worked at any one time at the one site with the others taking turns. Graham-Smith (1916) mentioned that *M. acasta* females produce one exit hole in each puparium, rarely two. Also when confined in glass vials he found that only one excavation tunnel was made in each cork stopper and that females worked singly at the excavation. For practical reasons one would expect that the economy in number of holes excavated per cell would be fairly general in the genus, although Iwata and Tachikawa (1966) observed 1–5 per host cell for *M. japonica* (= *M. clavicornis*) as mentioned above.

As soon as the hole in a *Pison* cell was large enough, the female *M. australica* passed through. The next day when the cells were broken open the host cocoon was seen to have a single excavated hole and the parasite females were inside on the body of the host. In the case of the *Sceliphron* spp. nests, excavation was not directly observed, but 24 hours after exposure to inseminated *M. australica* females there were no parasites to be seen. Examination of the host cell walls showed a single excavation in each and on breaking open the cells, I found that the parasite females had penetrated the cocoons to reach the host within by a further single excavation. Under these conditions more than one female had entered each cell. Similarly inseminated *M. australica* females gained access to *Megachile* sp. larvae within a sealed leaf nest lying uncovered on a bench about 2 metres from the release site.

In one instance where plastic stoppered tubes were used for cultures of *M. australica,* I found that adult females were capable of escaping by excavating their way through three sealing flanges on the inserted part of the cap and the rim of the cap where it fitted against the top of the glass tube. They did this in each of the 10 tubes being used.

If presented with *Sceliphron* cocoons outside their mud cells, inseminated *M. australica* females gnawed a hole in the cocoons and oviposition followed feeding. If naked *Sceliphron* prepupae and pupae were presented, oviposition followed feeding without delay. Therefore, as Thompson

and Parker (1927) found with *M. acasta,* the presence and penetration of enveloping membranes are not necessary prerequisites for oviposition in *M. australica.*

2) Entrance before the host cell is closed

Several workers have shown that *Melittobia* enter unsealed nests of their hosts and are able to delay oviposition until the host is at a suitable developmental stage.

Schmieder (1933), working with *M. chalybii* reported that female parasites gained access to the larvae of bees and wasps by entering host cells before they were completed. The only evidence to support this in his paper is the fact that examination of a *Trypoxylon* sp. cocoon did not reveal whether or not it contained *Melittobia.* He took this to indicate that the parasite gained access to the host before the cocoon was spun and became enclosed with the host. However, it does not necessarily mean that *M. chalybii* females entered before the nest was closed since they could just as easily have excavated their way into a sealed host cell before the cocoon was spun and then become enclosed with the host. Therefore, this is not conclusive evidence.

Balfour-Browne (1922) noticed *M. acasta* females becoming sealed up in cells being constructed by bees and wasps in elder stems and glass tubes he had provided in his garden. From observation of those in the glass tubes he discovered that their being sealed in the host nests was not accidental. He found that females can delay oviposition for up to 60 days when placed in a cell with an unhatched host egg. The parasite commenced oviposition only when the host reached full-grown larval condition. Feeding by the parasite on the developing host appeared not to affect the latter's development and he had many examples of eggs being pierced by the female's ovipositor for food without affecting development of the host. During his trials he placed up to 15 *M. acasta* females in a cell with a newly hatched *Osmia* sp. larva and allowed them to feed freely on the host for 14 days without apparently affecting the host which completed its development. When he placed *M. acasta* females with older larvae there were no ill effects on the host as long as the parasites were only feeding. He felt quite satisfied that feeding by *M. acasta* females was not necessarily injurious to the host. Malyshev (1966) also mentioned *M. acasta* females entering host cells before they were closed.

Maeta and Yamane (1974) found that, in most *Trypoxylon* sp. cells infested with *M. japonica* (= *M. acasta* see Maeta (1978)), the closing plugs did not show entrance holes. They concluded that the parasite had gained access to the host cell before it was sealed. When discussing oviposition, they mentioned the capacity of *M. japonica* (= *M. acasta* see Maeta (1978)) females to delay feeding until the host reached a suitable stage for parasitism; in fact they kept females of this species alive for more than 2 months without food.

In this investigation, *M. australica* females were not directly observed entering host cells before they were closed, but there is indirect evidence that this may occur. On numerous occasions *M. australica* females were kept for periods up to 3 weeks without food. At the end of this period, when a suitable host was provided, they fed and subsequently laid fertile eggs. Thus they can survive long periods without ovigenesis being adversely affected. Females accidentally released in the laboratory were later found residing in empty host cells of old *Sceliphron formosum* nests lying on the laboratory bench. When these cells were broken open the parasites showed the usual negative reaction to light which is displayed in the presence of a host. Feeding by *M. australica* females does not affect development of the host e.g. when inseminated females were allowed to feed on prepupal *Sceliphron formosum* larvae for a few days then removed the host successfully passed to pupal and adult stages. Several *Sceliphron formosum* early pupae were supplied each to 10 inseminated *M. australica* females and all hosts continued to develop to full adult colouration in spite of feeding by the parasites and their progeny. Death of the host pupae resulted ultimately due to feeding pressure of the parasites. Therefore, *M. australica* females will enter empty host cells, can delay feeding and oviposition for long periods, and are able to feed on the host larva or pupa without affecting its development.

This capability with its attendant behaviour patterns probably occurs in all species.

3) Oviposition directly through enveloping membranes

As mentioned before, Thompson and Parker (1927) found that *M. acasta* oviposits directly through the puparial wall of Diptera and that this takes place only after the fly pupa has separated from the puparial wall. Malyshev (1966) also mentions this. In all cases where I have reared *M. australica* from fly puparia there were no excavation holes in the puparial walls until emergence of the parasite, these being the exit

holes of the progeny. Maeta and Yamane (1974) stated that *M. japonica* (= *M. acasta* see Maeta (1978)) oviposited directly through the cocoon of species of the hymenopteran genera *Osmia, Monodontomerus, Trypoxylon* and *Chalicodoma*. However, there appears to be some versatility of behaviour here since they also found that in some cases the parasites entered the host cocoons of *Trypoxylon* and *Chalicodoma* before oviposition.

Malyshev (1966) provided an explanation. When a *M. acasta* female's work was finished in one cell of a host's nest she made her way into the next cell with her jaws. If the host cocoon was in close contact with the cell partition the parasite gnawed through both the partition and the cocoon. However, if the cocoon was not in contact with the cell partition and the body of the host was some distance from the cocoon wall the parasite gnawed through the cocoon. Where the cocoon was close fitting he found that the parasite oviposited directly through the cocoon wall. Thus closeness of fit of the cocoon to the host appears to be important, i.e. it is necessary for the tip of the ovipositor to reach the host within and this is substantiated by my observations on *M. australica* outlined below.

For hosts with spacious cocoons this behaviour would not be possible, e.g., it is difficult to imagine *M. australica* ovipositing through the cocoon walls of *Sceliphron* spp. In all cases, whether the *M. australica* females had fed or not, when *Sceliphron* spp. cocoons were provided they were always entered before oviposition.

Although the hosts mentioned above by Maeta and Yamane (1974) are all small with close fitting cocoons, some were found to be entered also and I feel the nutritional condition of the female is important in these cases as well as the closeness of the cocoon to the cell partition. When I presented inseminated unfed females of *M. australica* with *Pison* sp. cocoons, which are close fitting, each was entered by the parasite. On one occasion on breaking open a *Pison* sp. cell collected from the wild I found two *M. australica* females with distended metasomas on the cocoon surface. They were observed to insert their ovipositors through the cocoon wall. The point of insertion was always on the side of the cocoon about 1/2 to 2/3 the way down the wall. The ovipositor was fully inserted followed by a pause of about 3–5 seconds, half withdrawn, reinserted followed by a pause of about 3–5 seconds then fully withdrawn. On one occasion, a female inserted her ovipositor at the upper, anterior end of the cocoon and was noticed to indulge in partial withdrawals and re-angling the direction of the ovipositor. No pausing occurred and the ovipositor was eventually withdrawn. This end of the cocoon housed the narrow, anterior end of the prepupal larva which from the upper surface of the cocoon was not accessible to the ovipositor of the female. No attempt was made by the females to enter the cocoon. On breaking open the cocoon about 15 eggs were visible on the lateral portions of the prepupal *Pison* larva — none on the anterior portion. It appears therefore that contact of the ovipositor with the host within is necessary before oviposition occurs and that oviposition through enveloping membranes occurs with close fitting cocoons where the parasite female has previously fed. No published records are available on penetration of fly puparia by the female parasite. I have tried *M. australica* on blow fly puparia but without success. Tachinid or sarcophagid puparia were not available. In the case of puparia, the parasite female may feed on the early pupa before it separates from the puparial wall or the pupa within may be close enough to the puparial wall in some areas to allow some body fluids to well out of a puncture site, e.g., Graham-Smith (1919) mentioned that fertilised or unfertilised females of *M. acasta* confined with fly puparia lived for long periods (up to 36 days) and seemed to derive nourishment from fluid exuding from the puparia at ovipositor puncture sites. Van den Assem (pers. comm. 1981) has confirmed this behaviour in all *Melittobia* species in his cultures. However, in some cases, the parasites gnawed their way into fly puparia. He found that in crossing experiments involving the *assemi* group, females gnawed holes in fly puparia and walked on the surface of the pupa within. Van den Assem (1976) found that virgin *M. acasta* females gnawed their way into fly puparia containing males of this species and mated with them.

Migration from one cell to another appears to be nutritionally governed as well. The relatively large eggs (0.3 mm long; females 1.1–1.5 mm long) mean that a female cannot produce her entire egg batch in 1 or 2 days. Oviposition and feeding were observed to be progressive throughout the life of female *M. australica*. It is reasonable to assume, therefore, that competition for food with her progeny may be an important factor in governing the number of eggs per host. On a relatively large host e.g. *Sceliphron* spp. there is probably enough food to support the larvae and the mother for the length of her life. On smaller hosts e.g. *Trypoxylon, Osmia, Pison*

etc. competition for food with her progeny would necessitate her migration from one cell to another. In this situation, if she has sufficient food for maturation of eggs she may oviposit directly through the enveloping membrane of the host in the next cell. What determines the number of progeny in this case is not known. Perhaps as she approaches the time for nutritional replenishment she might again migrate then penetrate the next cocoon. The whole process of oviposition and nutritional requirements is one deserving close study.

In summary, oviposition behaviour of inseminated *Melittobia* females is very flexible and is dependent upon a number of conditions. If the female parasite encounters a host cell before it is closed, she enters and feeds upon the developing host without affecting its development. She can delay oviposition until the host is at a suitable stage, i.e., the prepupal larva or pupa. If the host is large with a spacious cocoon she can become incorporated within during construction or gnaw in afterwards. She stays with this one host all her life and is assisted in its utilisation by specialised second-form progeny (discussed later). Where the host is small with a close fitting cocoon she can either become incorporated or oviposit through the cocoon wall. Because of the limited food supply on a small host she must seek another to attain her full egg laying potential and moves to another cell. If the cocoon is touching the cell partition and/or she requires additional food she gnaws through the cocoon wall. However, if the cocoon is not in contact with the cell partition and she does not require more food she can continue ovipositing through the enveloping membrane. Where the host cell is sealed she gnaws through the cell wall. If the host has not spun a cocoon she can follow the behaviour patterns above depending upon the size of the host and the closeness of fit of the cocoon. Should she enter a cell and encounter a cocoon, no matter how close fitting she gnaws through it to feed upon the host.

FUNCTIONS OF THE OVIPOSITOR

Female *Melittobia* use their ovipositors for feeding, to paralyse the host and for egg laying.

1) Feeding

When inseminated *M. australica* females were presented with quiescent larvae or pupae, I noticed the ovipositor was fully inserted and within a few seconds, withdrawn. The females moved back and fed on the drop of body fluid which issued from the host. Old wounds, visible as dark brown spots, were frequently revisited by the females who fed on the congealed body fluids of the host. There appeared to be no favoured spot for puncture of the host's body and on one occasion a female punctured the head capsule of a host larva. Torchio (1963) observed *M. chalybii* (which I feel was probably *M. acasta*) feeding on congealed host body fluids at old puncture sites.

Balfour-Browne (1922) observed this behaviour in *M. acasta* and even the eggs of the hosts were used as a food source. Malyshev (1966) also mentioned the habit of *M. acasta* females feeding on the body fluids of the host oozing from ovipositor penetration points. Schmieder (1933) mentioned this feeding behaviour in *M. chalybii.* Maeta and Yamane (1974) noted dark brown spots on the body of the host and assumed these to be the feeding spots of *M. japonica (= M. acasta* see Maeta 1978) females although they did not directly observe this feeding. It was recorded also for *M. japonica* (= *M. clavicornis*) by Iwata and Tachikawa (1966).

This behaviour is no doubt a general one for all species of *Melittobia* and feeding upon the host by the female is recorded amongst other parasitic Hymenoptera. In the case of *Melittobia* it can occur without death of the host and this, together with the female's ability to delay oviposition for long periods is a decided advantage when a host in an early stage of development is encountered.

Doutt (1959) in his review of the biology of parasitic Hymenoptera mentioned this feeding behaviour and that it is well established that feeding on the host body fluids is necessary to obtain protein for ovigenesis. In support he mentioned the work of Flanders (1942, 1953) on *Metaphycus helvolus* (Compere). Over a 3 week period at 80° F and away from its host, ovigenesis ceased in this species. When presented with a host at the end of this period the parasite fed without delay and oviposition began a few days later.

In this investigation, newly emerged, inseminated *M. australica* females when deprived of a host remained as they emerged, i.e., without distended metasomas. When presented with a host pupa after 7 days all females immediately inserted their ovipositors and fed at the puncture sites. Within 24 hours their metasomas were distended and well developed eggs were clearly visible through the intersegmental membranes of the metasoma. They began laying eggs 2–3 days after feeding. It would appear therefore that feeding upon the host is essential for egg maturation in *Melittobia.*

2) Preparation of the host

Buckell (1928) presented *M. chalybii* (= *M. digitata*) with active host larvae which became quiescent after 24 hours. He postulated that some paralysing fluid was injected. Balfour-Browne (1922) found that once an *M. acasta* female had oviposited on a host the latter was doomed even though the eggs were removed before hatching and the adult females removed as well. We have seen before that he found feeding by the adult females did not affect host development. He described a fluid oscillating in the ovipositor as it was being inserted. I have noticed movement in the ovipositor of *M. australica* but consider it more likely to be rotation of the valves of the ovipositor as the female works at insertion. A similar movement was seen during insertion of the ovipositor of *M. australica* for feeding. Balfour-Browne also noticed that the ovipositor was held fully inserted for a period before withdrawal and that the females did not feed at these sites.

When active last instar larvae of *Anthrax angularis* and *Sceliphron* spp. were presented to inseminated *M. australica* females they became very agitated and continually performed twisting and rolling movements. The parasites inserted their ovipositors in spite of the activity and within 24 hours the host larvae were quiescent. In these cases the ovipositor was inserted and held in position for some time before extraction. After withdrawal of the ovipositor the females moved away without attempting to feed at these sites. Once the host larvae were quiescent, the *M. australica* females were noted to insert their ovipositors and feed at the puncture sites after withdrawal.

The minute size of *Melittobia* relative to its hosts makes suppression of an active host seem an impossible task. Beard (1952) working with *Habrobracon hebetor* (Day) found that one part of the venom of this species to 200,000,000 parts of the host's blood was sufficient to cause permanent paralysis. If the levels of potency are similar in *Melittobia,* the task of subduing an active host would not be impossible.

Given the capacity of *Melittobia* to delay oviposition and its ability to feed on the host without affecting the latter's development one wonders whether paralysis of the host is necessary under natural conditions. In all cases where host cells have been broken open and *M. australica* found, the host has been able to produce a cocoon and in some cases development had reached the pupal stage and attained adult colouration before death. Malyshev (1966) suggested that the stinging by *M. acasta* was for preservation of the host and it may be that under certain circumstances the injection of venom prevents further development of the host. This is an aspect that requires further investigation.

4) Oviposition

Last but not least, the ovipositor is used for egg deposition. The ectoparasitic status of the genus has already been discussed. Oviposition therefore, does not involve insertion of the ovipositor into the host. In *M. australica* the tip of the ovipositor was braced against the surface of the host and the metasoma raised releasing the inner ovipositor valves which therefore became arranged at right angles to the metasoma. The relatively large egg appeared to flow down the ovipositor valves onto the host. No particular site on the host appeared to be favoured, but the eggs tended to be deposited in clusters. The surfaces of the eggs were moist, and this coating kept them attached to the host and to each other. This procedure for *M. australica* appears to be fairly standard for the genus.

HABITS OF THE MALE

In all species for which the male is known he has reduced wings, modified antennae and reduced eyes. His sole function appears to be reproduction. Important aspects of his behaviour are feeding, aggression and courtship.

1) Feeding.

Waterston (1917) wrote ... 'The male is at first of a transparent yellowish brown colour, the head sometimes darker but after feeding, the abdomen may be opaque ...' Other workers (Balfour-Browne (1922) with *M. acasta,* Buckell (1928) with *M. chalybii* (= *M. digitata*), Schmieder (1933) with *M. chalybii* and Dahms (1973) with *M. australica*) have not observed males to feed. In most cases when males emerge the host is fully utilised leaving only brothers and sisters as potential food. Male aggression has been mentioned by different workers and Matthews (1975) suggested this aggression may be important for male nutrition as the opponent's body fluids could serve as an additional energy source. As more direct evidence in support he drew attention to the occasional killing by males of virgin female *M. chalybii* (= *M. australica*) presented to them in mating chambers. The male usually tore a hole in the female's metasoma and chewed vigorously on her for several minutes. Graham-Smith (1919) found that in some battles between male *M. acasta* the victor buried his mandibles in the

dorsal part of his adversary's head and continued to bite for several minutes.

I agree with van den Assem, Gijswijt and Nübel (1980) who felt that this suggestion is questionable. Although male aggression has been reported for several species there appears to be some variation in whether an opponent is mutilated or not, i.e., it is apparently not consistent in the genus. Balfour-Browne (1922) observed female mutilation by males in *M. acasta* but felt this was due to experimental conditions. He also noted that male to male aggression was less prominent where the cell was full of emerging females. In all the years I have been culturing *M. australica* (*M. chalybii* of Matthews (1975)) on only 2 occasions have I noted male aggression causing mutilation of other males and on only one occasion did I observe female mutilation. On these occasions I did not notice males pausing to gnaw on a victim.

The suspicion that males do not feed is substantiated by indirect evidence from my observations with *M. australica.* When males of this species emerge their metasomas are distended, but become increasingly deflated until finally they are very flat. Deflation of the metasoma would result from utilisation of food reserves for spermatogenesis and courtship. That this deflation would be dramatic can be seen from the extremely biased sex ratios recorded in the literature for several *Melittobia* species — 1–13% males. To quantify this — van den Assem, Gijswijt and Nübel (1980) found that the progeny from 29 host puparia each with a single *M. japonica,* (= *M. clavicornis*) female was 1843 individuals of which only 72 were males. The sex ratio of *M. australica* I found to be 3–4% males. If feeding were occurring without being observed then deflation of the metasoma would not have occurred or been so marked. Schmieder (1933) found the males of *M. chalybii* to be short lived. He attributed this to rapid depletion of food reserves resulting from abstinence from food during constant activity, which agrees with my assumption. Male aggression and feeding are topics deserving more detailed investigation.

2) Male aggression.

In the genus, males have not only undergone radical modification, e.g. head capsule and antennae, but also have undergone major reductions in non-required organs, e.g., eyes and wings. If males do not feed one would expect a reduction of the mouth parts. However, in all species, the mandibles of males are larger than those of females and each has a well differentiated, sickle-shaped, anterior tooth. That these mandibles function as weapons in male aggression is reported in many species. Graham-Smith (1919) found that *M. acasta* males were very aggressive and encounters between males resulted in the death of one of the opponents. Only rarely did he find more than one live male in each host puparium. Balfour-Browne (1922) also found *M. acasta* males very aggressive and bouts between males often resulted in death. However, he also noted that in a cell full of emerging females, the males were very busy and paid little attention to each other. Malyshev (1966) found *M. acasta* males to be very aggressive. Hobbs and Krunic (1971) found that some male *M. chalybii* (= *M. acasta*) fought and died before the first females emerged. Often all were dead before the last female emerged. This in addition to the biased sex ratio often meant that late-developing females had no males with which to mate. Buckell (1928) recorded aggression in *M. chalybii* (= *M. digitata*) and he found the males to be extremely pugnacious. They fight until only one is left and, as Graham-Smith (1919) found with *M. acasta,* dead pupae or parts of males were readily attacked. Schmieder (1933) did not observe such fierce fighting between males of *M. chalybii* when confined with or without females. The males, when they met, engaged in a brief excited tussle and then separated. Hermann (1971) did not observe duels between males of *M. chalybii* (= *M. australica*) confined together in gelatin capsules. However, she did find that the first male to emerge touched other male pupae frequently and that these failed to emerge. This same species in Kalamazoo (the *M. chalybii* of Evans and Matthews (1976)) is very aggressive. When I visited Dr. Evans in 1974 I observed battles between these *M. australica* males which frequently resulted in mutilation. The other species kept in culture by Dr. Evans, *M. evansi* (Dahms 1983a), according to him was not as aggressive. Matthews (1975) confirmed that adult male *M. chalybii* (= *M. australica*) in his cultures are highly aggressive and more so than *M. evansi.* In the latter case the first male to emerge systematically decapitates others just prior to emergence from the pupa or immediately after. However, when adult male *M. evansi* met, one adopted an inert or passive posture and the aggressor abandoned it without inflicting injury.

In my cultures of *M. australica* over several years, encounters between males resulted in a brief excited tussle with the males rolling about. After a few seconds the males disengage and go

their separate ways a little faster than usual. I have not observed males paying any attention to male pupae. Males which emerged first walked over the pupal mass palpating it with their antennae and paused only at close-to-emergence females. On two occasions I have noticed male aggression resulting in mutilation of other males and occasionally males confined without females indulged in fatal encounters.

It appears that male aggression is a standard behaviour pattern in the genus and that some species are more aggressive than others. It appears also that male aggression can vary in intensity within a species. Matthews (1975) remarks on *M. evansi* indicate that there may be some variation in the stage at which other males are attacked and his description of males adopting passive postures when encountered by another male is the first record of this type of behaviour in the genus. This aspect of male behaviour would make a very nice study. The implications of male aggression are discussed later under 'Reproduction'.

A peculiar aspect of male aggression is reported for *M. acasta* and *M. chalybii* (= *M. australica*). Balfour-Browne (1922) found that the killing of females by males was not uncommon, but he thought that this was related to experimental conditions. Hermann (1971) found that males of *M. chalybii* (= *M. australica*) eight days or older when placed with a receptive female would grasp her and feed on her. After feeding upon her for a few minutes the males began copulatory behaviour. Such females generally died during courtship or before oviposition. Matthews' (1975) observation on the same species where males chew on a females's metasoma for several minutes has been mentioned under 'Feeding' above. In my colonies of this species male aggression resulting in female mutilation was noticed on only one occasion and several females were affected. I did not observe males pausing to chew or feed upon females which they mutilated. Perhaps Balfour-Browne is correct in assuming male aggression towards females was due to experimental conditions. In the wild, fertilised females disperse fairly soon after mating, but in the laboratory they are kept crowded and confined for several days. With increasing numbers of mated females, presumably with remnants of male odour (see Dahms 1983b), there is an increase in aggression some of which may be directed towards females. Whatever the cause, it appears to be a rare occurrence and is certainly not what one would expect.

3) Courtship.

In *Melittobia,* courtship is a lengthy and involved process. Detailed accounts of a few species can be found in Parker and Thompson (1928), Hermann (1971), Hobbs and Krunic (1971), Dahms (1973), van den Assem (1975), Evans and Matthews (1976), van den Assem and Maeta (1978, 1980), and van den Assem, Gijswijt and Nübel (1980), van den Assem, et alia (1982). Van den Assem has been investigating this aspect of behaviour in several species of *Melittobia.* His published work and personal communications over the years have been of immense value in guiding taxonomic decisions in the genus.

Van den Assem's work proves that courtship patterns in the genus show specific characteristics. Within the genus there appear to be three basic patterns (plus another demonstrated only by *M. clavicornis* Cameron 1908). The three basic patterns, *acasta* group, *hawaiiensis* group and *assemi* group, together with that of *M. clavicornis* have been discussed by van den Assem and Maeta (1978, 1980) and van den Assem et alia (1982), but I will briefly outline the situation for the sake of completeness. The reader is referred to Dahms (1983a) for an explanation of the species groups.

In *M. australica* (*hawaiiensis* group) the male stands well forward on the female with his mouthparts depressing her facial triangle just below the ocelli. His scapes, placed over the flagella of the female, lie close to her face. Antennal contact is permanent during courtship and antennation has only one pattern i.e. alternating up and down movements of the flap-like pedicel. The female is held around the neck by the fore tarsi of the male, his mid legs are held forwards with their tarsi alongside the eyes of the female and his hind legs are braced against the wings or hind legs of the female. In *M. acasta* (*acasta* group), males stand with their heads a little further down the face of the female without the close contact of *M. australica.* The flagella of the female fit into cup-shaped depressions of the male scapes which are not pressed against the face of the female. Antennal contact is broken during the antennation sequence which has two consecutive phases: knocking, jerky movements involving the pedicel and at the end of this phase a strong pinch involving the pedicel plus the first funicle segment. Antennal contact is broken after the pinch when the male raises his antennae sideways. The female is held around the neck by the fore tarsi of the male, the mid legs are braced against the thorax of the female and the hind legs are held forwards alongside the thorax of the female.

In these two groups there is an alternation of antennation and leg movements. On the basis of these leg movements, the groups can be called mid leg courters (*hawaiiensis* and *assemi* groups) and hind leg courters (*acasta* group). During antennation, the mid legs of *M. australica* are held laterally and forward with their trembling tarsi alongside the female's eyes. Van den Assem and Maeta (1978) observed that at the start of the display in their 'species 2' (= *M. australica*) the male's middle legs are braced against the female's thorax, but after the first antennation sequence they are brought forward towards the female's head for the mid leg sequence. They do not fully return to the original position after this but are held out trembling and gradually move to the frontal position at the start of the mid leg sequence. From my observations the mid leg sequence involves an upward swing of the mid legs and a return to half way down the female's eyes slightly brushing them. They pause here for a few seconds then are suddenly swung down and backwards and this is accompanied by a strong jerk of the male's body. As with antennation there is no change in the pattern of movements in the mid leg phase until the finale when the male's body undergoes a series of convulsive movements accompanied by up and downward swings of the mid legs beside the female's eyes.

After *M. acasta* males break antennal contact they stretch their fore legs increasing the distance between the heads of the courting couples. At this point the hind legs move forward making swaying movements beside the mesosoma of the female. This sequence is ended by a push against the female's mid legs. The alternation of antennation and leg movements continues for a period, but they begin to overlap at which time there is a change in behaviour pattern. Antennal contact becomes permanent and co-ordination of the hind leg movements change. The hind legs begin to rub up and down on the side of the female's mesosoma. In the finale, the male places his hind legs on the female's wing or metasoma and brings his mid legs forward to stroke the female's eyes with a downward movement. This is done with his antennae stretched downward over the female's face. He then breaks antennal contact, raises his wings at which point the female signals receptivity.

The *assemi* group comprises a new species complex from the Seychelles, India and Japan (van den Assem and Maeta (1980)). Here the courtship pattern resembles that of the *hawaiiensis* group. The male's scape is ventrally grooved and he is a mid leg courter. The male stands further forward over the female's head so that the distal part of his scapes touch her mouth parts. Antennation involves a quivering motion as in *M. australica* alternating with a pinch using the pedicel. Alternating with antennation van den Assem and Maeta describe the mid leg movements as a very rapid kick involving the synchronous movement of both legs as far forward as his own head. During this movement parts of the female's body are brushed by long bristles on the ventral surface of the femur of the male's mid legs and his tarsi brush the female's pilose eyes. The mid legs return to their initial position except that they are held out laterally from the female's mesosoma. As the sequence proceeds the alternation of antennation and mid leg movements accelerates up to the last quiver which ends in a prolonged pinch. Hereafter the mid leg movements become an asynchronous to and fro rubbing motion which lasts for a few seconds. In the finale, the mid legs are moved synchronously back and forth at which point the female may signal receptivity.

The species which stands alone is *M. japonica* Masi, 1936 (= *M. clavicornis*) and its courtship is reported by van den Assem and Maeta (1978) and van den Assem et alia (1982). Unlike that of the other species, the male scape lacks an obvious groove or cup-shaped depression but has a large clear area distally opposite the attachment of the pedicel. Male courtship position is the same as in *M. acasta* but his scape presses the female's flagellum against her face. Antennation involves a series of knocking movements as in *M. acasta* and alternates with leg movements, but in this species both mid and hind leg movements are prominent. The mid leg movements are rigidly stereotyped involving a rapid flick-like motion towards the female's eyes followed by a pause. At this point the male may raise his antennae sideways and break antennal contact, but this is not always done. The hind leg movements are less stereotyped and involve a walking motion alongside the female's metasoma or folded wings. Leg movements are carried out during antennal raising. There is no finale by the male and the female signals receptivity during the sequence, but always after a mid leg flick.

The courtship pattern in the genus is very complicated and in some species can last up to 30 minutes. I have timed *M. australica* up to 15 minutes.

It is possible to draw some tentative correlations between morphology and courtship patterns in the genus. The following discussion is restricted to those species for which courtship is known and where a species group is mentioned it

includes only *M. australica* and *M. hawaiiensis* (*hawaiiensis* group), *M. assemi* and *M. sosui* (*assemi* group) and *M. acasta, M. evansi* and *M. digitata* (*acasta* group). The reader is referred to Dahms (1963a) for figures illustrating morphology.

Broadly spaced facial grooves and densely setose eyes in females correlate with male position (mouth parts impinging on upper face of female) and mid leg courting in the *hawaiiensis* and *assemi* groups. The presence of a dense tuft of stiff setae on the ventral fore trochanters of males of the *hawaiiensis* group seems to indicate some difference in courtship position between males of this group and the *assemi* group where this tuft is absent. Dahms (1983b) discusses the application of this setal tuft by *M. australica* males. Narrowly spaced facial grooves and the sparcity of setae on the eyes of females of the *acasta* group and *M. clavicornis* correlate with the male head not closely applied to the head of the female and the predominance of hind leg action during courtship.

Narrow male fore wings correlates with the absence of male wing vibration during courtship in the *hawaiiensis* and *assemi* groups in contrast to broad male wings and male wing vibration during courtship in the *acasta* group. A grooved ventral scape and a geniculate scape gland in the male correlates with permanent antennal contact during courtship (*hawaiiensis* and *assemi* groups). A cup-shaped depression in the ventral scape and a non-geniculate scape gland in males correlates with antennal contact through only part of courtship (*acasta* group).

Amongst *acasta* group males there is some variation in the size of the scape gland relative to that in *M. acasta;* it is expanded in *M. evansi, M. femorata* and *M. chalybii;* similar in *M. digitata;* or reduced in *M. scapata.* Dahms (1983a, b) discusses the possible implications. Also in the *acasta* group there is variation in the size of the first funicle segment in males; large in *M. acasta, M. digitata, M. femorata* and *M. chalybii* (the last 2 also have an extra expanded ring segment) and relatively small in *M. evansi* and *M. scapata.* At first it was thought that a large first funicular segment in males might correlate with a pinch by the male at the end of each antennal vibration phase, but this does not appear to hold for *M. digitata* where, according to van den Assem et alia (1982), there is no pinch at the end of a series of antennal vibrations.

The mid femoral fringe in males varies between and within species groups. It would be interesting to see if these correlate with variations in male mid leg movements and/or parts of the female stroked during mid leg action in courtship.

There are a number of puzzling combinations of these correlatable features, e.g. in *M. chalybii* (*acasta* group) the male scape gland is geniculate, his ventral fore trochanters have a setal tuft resembling that of *M. australica* and the female has densely setose eyes (*hawaiiensis* group); the male scape has a ventral cup-shaped depression, his antennal flagellum has a large first funicle segment, his mid legs have an *acasta* group setal fringe, females have narrowly spaced facial grooves and a relatively thin scape in dorsal view (*acasta* group). It appears therefore that we are a long way from understanding species relationships within the genus and further study is required to confirm or rearrange correlations between morphology and courtship. Dahms (1983a) in his summary discusses the matter in greater detail.

REPRODUCTION

In the parasitic Hymenoptera, several aspects of reproduction are important in understanding evolution: parthenogenesis, sib-mating, biased sex ratios, and sex ratio shifts.

Parthenogenesis

It is widely accepted that all species of Hymenoptera reproduce parthenogenetically. Gordh (1979) lists three types of parthenogenesis: thelytoky, deuterotoky and arrhenotoky. A few species are thelytokous and the population consists of only females or females plus a few. non-functional males. Deuterotokous species are also relatively few in number and unfertilised eggs develop into both sexes. Most species are arrhenotokous, i.e. the population consists of diploid females and haploid males. The latter develop from unfertilised eggs and are therefore impaternate. In this case uninseminated females can and do produce eggs from which only males emerge.

The *Melittobia* species *acasta, chalybii* and *digitata* have been shown to be arrhenotokous — Howard and Fiske (1911), Malyshev (1911), Graham-Smith (1919), Balfour-Browne (1922), Buckell (1928) and Schmieder (1933). In the present study, eggs from uninseminated *M. australica* females produced males only, and those from inseminated females resulted in both sexes all of which indicates arrhenotokous parthenogenesis.

Sib-mating

In the parasitic Hymenoptera, particularly the Chalcidoidea to which *Melittobia* belongs, sib-

mating or close inbreeding appears to be the rule. Hamilton (1967), Askew (1968a) and Crozier (1977) list several biological features which indicate that a species practices close inbreeding:

a) males are apterous or brachypterous and therefore confined to the immediate area of their emergence. Male *Melittobia* are brachypterous and do not leave the host cell or puparium in which they emerge.

b) close inbreeders are gregarious with eggs laid in batches isolated from one another ensuring that males and females from the one mother emerge in spatial and temporal proximity to one another. *Melittobia* are gregarious ectoparasites and their host enveloping membranes (cell walls, cocoons or puparia) ensure isolation of the egg batches.

c) there is a tendency for mating to take place on emergence before dispersal. Female *M. australica* in my colonies would not disperse until after insemination. Dahms (1973) mentioned that uninseminated, freshly emerged females of *M. australica* were observed to solicit the attention of males and that it was not uncommon to observe groups of females standing around a male engaged in courtship, palpating him with their antennae. They made no attempt to disperse.

Therefore *Melittobia* fit the biofacies for close inbreeding.

Askew (1968), discussing speciation in the Chalcidoidea, pointed out that the effectiveness of sib-mating as an isolating mechanism is increased by monandry in females, i.e. unreceptivity after an insemination. Gordh and De Bach (1978) found that male polygony and female monandry are common in the Hymenoptera. Female monandry requires extreme economy of sperm utilisation and this has been demonstrated in the arrhenotokous eulophid *Dahlbominus fuscipennis* (Zetterstedt) by Wilkes (1965). He found that from a single mating involving 150 sperm, the female can produce as many off-spring, over 90% of which are females. Out of another batch of 254 eggs which he stained, only 4 contained more than one sperm. Such economy involved the synchronous release of ova and sperm from the storage organs.

In laboratory cultures of *M. australica* I noticed males frequently courting previously inseminated females. Dahms (1973) felt this was due to laboratory conditions where inseminated females could not disperse. In all cases where I have observed male *M. australica* courting previously inseminated females attempts at copulation by the male failed. The normal situation is that females disperse after insemination which precludes the attempted second mating by a male. This is general for the genus and therefore the species show male polygony and female monandry. However, I have found that *M. australica* females can and do mate a second time apparently when their sperm supply is depleted. Balfour-Browne (1922) considered that *M. acasta* females also are able to mate a second time when their sperm supply is depleted. In both cases the females mate with a son. Under laboratory conditions *Melittobia* exhibit another facet of sib-mating behaviour which appears to be widespread amongst arrhenotokous organisms i.e. virgin females lay only a few eggs which develop into males with which they mate (Hamilton 1967). Howard and Fiske (1911) found that virgin females of *M. acasta* laid 4–5 eggs only and these developed into males. The number of unfertilised eggs laid was equivalent to the number of unfertilised eggs laid if the female had mated. They found also that virgin females lived longer than fertilised females and survived to mate with their sons after which normal egg laying began. Balfour-Browne (1922) observed the same behaviour with virgin *M. acasta*. By removing unfertilised eggs from the hosts as they were laid by uninseminated females he was able to more than double the life of the female (up to 202 days) and increase the number of unfertilised eggs laid.

The habit of uninseminated females laying only a few eggs has been recorded for *M. chalybii* by Schmieder (1933) and *M. chalybii* (= *M. digitata*) by Buckell (1928). They do not, however, mention whether they mate with their sons. In the present investigation 5 uninseminated *M. australica* females were confined singly with a host and produced only one egg each after 5 days. When their sons emerged they mated and normal egg production began. The ability of uninseminated females to lay only a few eggs and mate with a son is probably general throughout the genus.

The economy of male production by uninseminated females is easy to understand as an adaptation for conservation of food supply that would be depleted by production of superfluous males (Schmieder and Whiting (1946)). In *Melittobia,* mother — son mating has at least two advantages. Where species have a high level of aggression between males, combat may result in total annihilation of males or the surviving males may die before all the females are fertilised. Hobbs and Krunick (1971) found that in *M.*

chalybii (= *M. acasta*) all males were often dead before the last of the females became adult, which meant that the last females to emerge had no males with which to mate.

Balfour-Browne (1922) felt that mother-son mating is part of the normal life cycle when a female exhausts her sperm supply. He placed 5 freshly emerged, inseminated *M. acasta* females in separate cells with a host. At the end of 6 to 7 weeks the females had ceased to lay eggs and he noted that the last eggs to be laid produced males only, indicating a depletion of sperm. After providing each female with a male, a second normal egg laying period began. Maeta (1978) has confirmed this with *M. acasta.* In this investigation I noticed egg laying had ceased in a stock colony containing 5 inseminated *M. australica* females on a *S. formosum* host. All of the progeny were in the larval stage. The host was not completely utilised, indicating that egg laying had ceased. The five females were separated and each supplied with a fresh *S. formosum* pre-pupa. Three of the females continued oviposition and produced progeny of both sexes indicating that the original host was probably unsuitable for further oviposition. The two remaining females produced 1 egg each which developed into males with which they mated and normal egg laying followed. It seems, then, that a second mating can occur after sperm depletion. If the host is nutritionally unsuitable for further oviposition, migration within the host nest may occur. Balfour-Browne (1922) with *M. acasta* felt that a female migrates from a cell only when her spermatheca is full. Once a female has completed her first egg laying, she waits for a second mating before migrating. As evidence he noted that in his glass cells the female was often to be seen on the cotton-wool plug after her second mating and that this occurred generally when the host was fully stocked with progeny or fully utilised.

Schmieder's work in 1933 on the polymorphic forms of *M. chalybii* presents a different procedure in host utilisation. The normal or type-form female produces from its first 12–20 eggs rapidly developing second-form females and males which are morphologically and physiologically different from the type-form. Second-form females begin laying eggs immediately after fertilisation and assist the mother in full host utilisation. The procedure adopted in host utilisation may be related to host size. In the case of larger hosts such as *Sceliphron* spp. Schmieder's system operates, and with relatively smaller hosts, e.g. *Pison* spp., migration of females occurs due to competition for food with her progeny. If sperm depletion occurs in the latter case a female may mate with a son. It is clear that such a close sib-mating situation would ensure maximum host utilisation and maximisation of a female's reproductive capacity. It also means that it is theoretically possible for a virgin female to colonise an area by mating with her son.

From the discussion above and from direct observations on *M. australica,* it is clear that sib-mating is an important part of the normal pattern of reproduction in *Melittobia.* Askew (1968), discussing evolution in the Chalcidoidea, concedes that a small amount of outcrossing occurs which mitigates against any tendency towards inbreeding depression. Crozier (1977) also considered that some outcrossing occurs. He argued that the continued production of males is puzzling if indeed there is no outcrossing. Hamilton (1967) regards male aggression as evidence that some outcrossing occurs in species which exhibit the biofacies of extreme inbreeding and arrhenotoky. He felt that outbreeding was brought about by male migration or multiple settling by females. In *Melittobia,* as males are brachypterous and non-dispersive, multiple settling of females must be the method by which outbreeding occurs. The host to parasite size ratio in *Melittobia,* in some cases, would certainly allow multiple settling and during the years I have been culturing *M. australica* there has been no reluctance by a female to oviposit on a previously parasitised host even in the presence of more than 20 other females. That multiple settling occurs in *Melittobia* can also be inferred from the occurrence of male aggression within the genus. That multiple settling of females is a fairly common event in *Melittobia* can be seen from the high degree of male aggression reported for some species and the enlargement of male mandibles — the weapons used in aggression.

Sex ratios

Amongst insects which exhibit extreme inbreeding and arrhenotoky, female biased sex ratios appear to be the norm, i.e., there is extreme economy in the production of males. In *Melittobia* spp. various workers have recorded depressed ratios of 1–13% males and these are made more biased by male aggression. In *M. australica* I have found ratios of 1–4% males. Multiple parasitism has been shown by Wilkes (1966) to result in a shift of sex ratio in the pteromalid wasp *Nasonia vitripennis* Walker, a parasite of house-fly pupae. Increasing the number of females per host resulted in a reduced percentage of female progeny. He postulated three causes for this shift:

1) Superparasitism resulted in a greater number of eggs per host and thus the number of eggs per host was in excess of the number of larvae the host could support. He assumed that supernumaries were eliminated by starvation and that reduced female progeny resulted from stronger male competition. This mechanism has been recorded for a number of hymenopterous species and Wilkes (1966) lists papers covering this subject.
2) Detection of previous parasitism.
3) Interference from other females on the host.

The last two mentioned result in a higher percentage of unfertilised eggs being laid. Wylie (1965) on reviewing the literature found that females of many hymenopterous species can distinguish between parasitised and unparasitised hosts. There are also cases in the literature where females mark a host that they have parasitised.

In *M. australica* where there is superparasitism, there appears to be a greater production of males but I have not quantified this. If there is a shift in sex ratio then differential larval mortality could be part of the shift since I have observed larval cannibalism on numerous occasions where the host was very crowded. Balfour-Browne (1922) observed similar larval cannibalism in *M. acasta*. Dr. van den Assem is currently working upon various aspects of sex ratio shifts in parasitic Hymenoptera e.g. Charnow, Hartogh, Los-den, Jones, van den Assem (1981). For this reason I have not pursued this aspect of *Melittobia* biology any further.

Therefore *Melittobia* exhibit the biofacies of extreme inbreeding and arrhenotokous reproduction. Outcrossing due to multiple settling by females appears to be part of the normal pattern of reproduction, and this is clearly indicated by male aggression perhaps coupled with sex ratio shifts in favour of males. The normal sex ratio is strongly female biased and this bias may be increased by male aggression. Males are polygonous and females monandrous, the latter dispersing after insemination. Mother-son mating occurs when the female is uninseminated or if she depletes her sperm supply.

POLYMORPHISM

Schmieder (1933) found two forms of each sex in *M. chalybii* which he called the type - (= typical) form and the second-form. The two forms showed marked morphological differences which he described and figured. To summarise

TABLE 1

		Type Form	*Second Form*
male			
	1)	pale	dark reddish-brown
	2)	3 ocelli	ocelli may be absent
	3)	eye spot pigmented	eye spot unpigmented
	4)	wing normal for male, uncrumpled	wing smaller, uncrumpled
female			
	1)	normal dark colour	paler than type form
	2)	wings normal, uncrumpled	wings small, crumpled as they emerged from pupa
	3)	cuticle normal, no fusion of sclerites	cuticle thinner, some fusion of sclerites e.g. on abdomen and antennae

He found that in addition to these morphological differences there were '... equally striking differences in their physiological characteristics and in their behaviour'. Courtship behaviour of the male second-form was less regular than in the type-form and he found that when he tried mating males of one form with females of another, the lack of synchrony proved troublesome. Van den Assem (pers. comm. 1981) does not agree with Schmieder's observations on second form male courtship. He has had no difficulty in mating one form male with the other form female. As there seems some doubt about this aspect and since Dr. van den Assem is working on the courtship behaviour of *Melittobia* I have not pursued the matter further.

The physiological differences between females of the two forms in *M. chalybii* are quite pronounced. Females of the second form have larger metasomas in the pupal stage and Schmieder (1933) suggested this was due to eggs developing within the pupa. Egg laying began on the day of emergence after mating in second-form females. He found the life span of second-form females to be shorter than that of the type-form and that they make no effort to disperse, whereas type-form females, after mating make their way out of the host cell and disperse.

Schmieder's investigations led him to conclude that the causal factor was nutritional. The first eggs laid develop rapidly to emerge as second forms and the '... interpolation of an additional

generation of adults in the life history is thus seen to constitute a remarkable biological adaptation which effects a more complete utilisation of the host and, as a corollary, secures the production of the maximum number of offspring from each host ...' The type-form he saw as being morphologically and physiologically the dispersive phase.

Van Lith (1955) found a polymorphism in *M. acasta* in which he mentioned only females which had distended metasomas full of eggs and short, often crumpled, wings. He did not feel there was any connection between the production of these females and nutrition.

Van den Assem and Maeta (1980) recorded male dimorphism in *M. sosui* Dahms 1983a but made no mention of dimorphic females. They did not find any overlap between the two forms of males and felt the causal factor was not nutritional since males of both types emerged from the same host at the same time. Van den Assem (pers. comm. 1981) has informed me that these dimorphic males are actually distinct morphs of the type-form. They are separate from type and second-form males which also occur in this species. This is a rather unusual phenomenon in the genus and is one under study by Dr. van den Assem. Detailed examination of the two morphs of the type-form male shows few differences except in size. In the larger morph the forewings are larger and slightly crumpled (cf. Figs 1 and 2) and the scape is about 1.2 times larger than that of the smaller morph.

I have received for identification some slide-mounted specimens from the U.S. National Museum which are obviously second-form males and females. There is little to use for identification since the dimorphism has affected most of the diagnostic morphological features. Those that appear to be unchanged cause uncertainty, e.g., the mid leg bristle pattern (Fig. 9) and the proportions and shape of the mid tibia of males resemble those of *M. acasta* males whereas the most common scape morphology is that of *M. evansi* (Fig. 11). For the present I have decided to label these specimens as *acasta* group and positive identification must await breeding of second-forms of all species in the *acasta* group. In the following discussion therefore, the features described are compared to those of the *acasta* group rather than to any particular species.

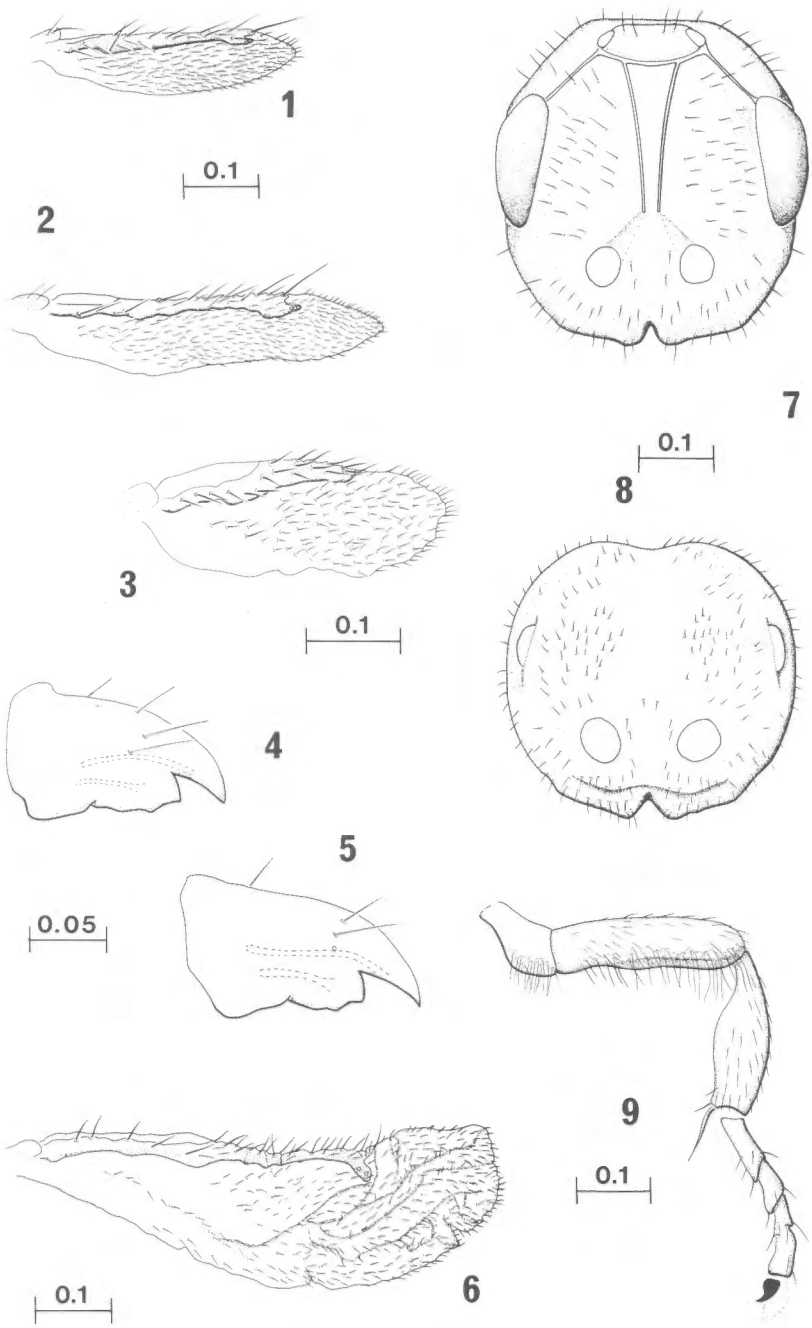
Female: Larger than type-forms, 1.7–2.1 mm long. Colour brown except flagellum which is infuscated. Head in frontal aspect quite broad and more rounded than in type-forms. Eyes relatively smaller. Ocelli variously reduced as follows: 2 normal posterior ocelli with either a very small or absent median ocellus; normal right, posterior ocellus and with median ocellus; or small right ocellus only. Scrobes shorter than type-forms. Mandibles (Fig. 4) more like those of the male. Antennae variable (Figs 13–15) even between right and left on the same specimen; scapes of variable shape with some showing expansion similar in form but not size to those of some males; flagellum showing fusion of segments in some specimens e.g. fusion of funicle 2 and funicle 3 is the commonest, but fusion of funicle 3 and club 1 also occurred and in some, the delimitation of club segments is imperfect; plate organs in some specimens are modified to peg-like structures (Fig. 16). In lateral aspect the head appears to be more inflated than in type-forms.

Mesosoma in dorsal aspect (Fig. 10) appears broader and shorter than in type-forms; setal fringe on posterior margin of prothorax shorter; sutures on mesonotum less distinct than type-form particularly those delimiting the axillae; position of setae on scutellum variable even from right to left on the one specimen e.g. normal position as in type forms or with anterior setae moved close to posterior setae; propodeum much broader and shorter than type-form, more angular in shape resembling the propodeum of the male. Legs similar to those of type-forms. Wings reduced (Fig. 6), crumpled, remaining as they emerge from the pupa; postmarginal and stigmal veins poorly developed, the stigmal in some specimens closely resembling that in type-form male wings. Lateral aspect not visible.

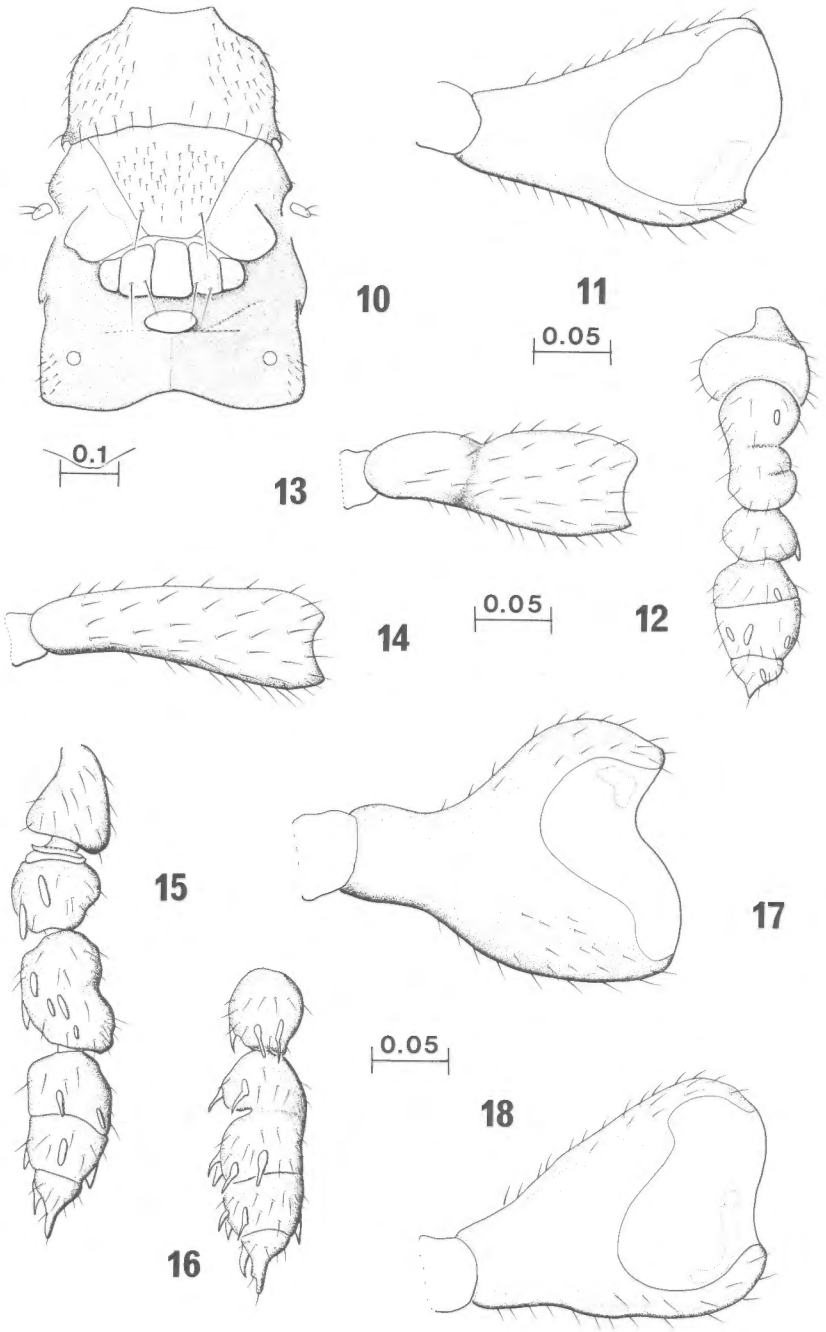
Metasoma in dorsal aspect much larger than that of pre-feeding type-form females.

Male: 1.6–1.8 mm long. Colour light brown.

Head in frontal aspect (Fig. 8) rounded, not contracted ventrally as in some type-forms. Mandibles (Fig. 5) not unlike those of the female second-form. Eyes are much larger than those of the type-forms. Ocelli variously developed as follows: median ocellus reduced or absent, posterior ocelli normal; only the right, posterior ocellus developed, the others absent; or all ocelli absent. Antennae (Figs 11, 12, 17, 18) variable, the predominant scape morphology is as in Fig. 11, but there is variation even between left and right on the same specimen (Figs 17,18), scape glands vary



FIGURES 1, 2 — *Melittobia assemi* (sp. nov.) male fore wings.
FIGURES 3-9, *Melittobia acasta* group second-form male and female; 3 — Male fore wing; 4 — Female mandible; 5 — Male mandible; 6 — Female fore wing; 7 — Frontal aspect, female head; 8 — Frontal aspect, male head; 9 — Male mid leg.



FIGURES 10–18, *Melittobia acasta* group second-form male and female. 10 — Dorsal female thorax; 11 — Male scape; 12 — Male flagellum; 13,14 — Female scapes; 15,16 — Female flagella; 17,18 — Male scapes from the same specimen.

in shape and development even between right and left on the same specimen funicular segments all fairly uniform in size unlike those of type-form *M. acasta* group where segment 1 is enlarged; flagellum showing different degrees of segmental fusion even between right and left on the same specimen as follows: funicle segments 1 and 2; 1, 2 and 3; 2 and 3; 4 plus club segment 1; and in some the delimitation of club segments is imperfect; plate organs appear to be reduced. Lateral aspect not visible.

Mesosoma in dorsal aspect similar to the type-forms. Legs not greatly modified; mid leg (Fig. 9) similar to that of *M. acasta,* some specimens showing fusion of tarsal segments 3 and 4; in some specimens tarsal segments 3 and 4 of hind legs are also fused. Wings (Fig. 3) not much reduced in size, stigmal vein absent in most specimens, poorly developed in others.

Metasoma of normal proportions.

Material Examined:

14 ♀♀, 2 ♂♂, on microscope slides labelled 20 mi. South Washington D.C. December 1974 *Trypoxylon* sp. nest Col Gordh; 8 ♀♀, 8 ♂♂ on microscope slides, data as before but collected 10 January, 1975; 10 ♀♀, 6 ♂♂ on microscope slides labelled, Augusta West Virginia February 1975 ex *Trypoxylon* nest Col. A. Menke. These are in the collections of the U.S. National Museum, Washington, D.C.

A polymorphism without the marked morphological differences of *M. chalybii* and the *M. acasta* group discussed above occurs in *M. australica.* In my trials where up to 20 *M. australica* larvae per host were bred on *Sceliphron formosum* prepupae, second-form progeny resulted. Trials were not carried out to determine the upper limit of parasite to host larvae for second-form production. Males of *M. australica* second-form were larger than the type-form but otherwise appeared morphologically similar to the latter. Second-form females were larger than the type-form with reduced eyes, shortened wings and enlarged metasomas. In neither sex was there any evidence of fusion of tarsal or antennal segments and the scapes of both forms were normal. The shortened wings of the second-form females were not crumpled, but fully expanded without any alteration of venation.

Second-form *M. australica* females differ behaviourally and physiologically from type-form females. They are ready to lay eggs immediately after insemination, i.e. on the day of emergence. Type-form, inseminated females begin laying 4–5 days after being placed on a host. Second-form females make no attempt to disperse from the breeding chamber, but remain on or under the host and show a negative reaction to light typical of laying, type-form females with a host. Type-form females, after insemination, make their way to the top of breeding jars and show a positive reaction to light, e.g. if released they move in a direct line towards windows.

Some of the features of second-form *M. acasta* group females are similar to those in type-form males. In comparison to type-form females, the head is shorter, broader and more inflated and the eyes are relatively smaller. The mandibles more closely resemble those of a male; the scapes are expanded and some resemble the sorts of expansions found in male scapes (Fig. 13); the mesosoma, particularly the propodeum, is shorter and broader as in males; and in some cases the stigmal vein in the crumpled wings resembles that in males.

It is interesting that the *M. acasta* group females on hand show modifications resembling those from which the present male morphology appears to have arisen and that these modifications are nutritionally induced, at least in part. Males tend to emerge first e.g. Buckell (1928) found that *M. chalybii* (= *M. digitata*) males emerge after 21 days and females after 37 days. Schmieder (1933) found that the first progeny to emerge in *M. chalybii* were second-form individuals. Differential development of the sexes is no doubt related to their dispersive and non-dispersive roles, and in the male subsequent modifications plus embellishments would be related to the restriction of their role to combat, courtship and copulation.

In addition, the second-form males of the *acasta* group on hand show quite an amount of variation in both head and scape morphology, e.g. Figs 17, 18 are right and left scapes of the same specimen. This is in contrast to males of the *hawaiiensis* group. I have not seen polymorphic forms of the *assemi* group. From our knowledge of species at the moment the *acasta* group contains the greatest number of species (7), the *hawaiiensis* group contains 2 and the *assemi* group contains 4. Perhaps this apparently greater diversity of species in the *acasta* group is related in part to the variability found amongst second-form *acasta* group males. However, this is speculative since the world fauna is not properly known and the full implications of polymorphic forms in *Melittobia* require much more study.

LIFE HISTORY OF *M. AUSTRALICA*.

No particular part of the host was favoured for oviposition and eggs were laid in clusters generally in the intersegmental grooves of prepupae. Eggs are large relative to the female's metasoma; 0.38 mm long by 0.1 mm wide. The length of the metasoma of inseminated, unfed females is 0.6 mm. Eggs are elongate, slightly curved with broadly rounded ends, one end being slightly wider than the other. They fit the hymenopteriform type of Clausen (1962). They are white and translucent with a thin, smooth chorion. The surface appears moist and coated with a substance that makes them loosely adhere to each other and to the host.

Larvae hatched in 3–4 days and the newly hatched larvae fitted the hymenopteriform type of Clausen (1962), i.e., white, translucent, visibly segmented grub unadorned by obvious spines, setae etc. The head and mouth parts are relatively small. The eggs, larvae and larval head of *M. australica* resembles the figures of *M. acasta* (Balfour-Browne 1922). As feeding proceeds waste material can be seen accumulating within the larva. No attempt was made to determine the number of larval moults, but Balfour-Browne (1922) recorded 2 larval moults plus the larva to pupal moult in *M. acasta*. After 7–9 days, larvae were fully grown and measured 1.6 mm long by 0.5 mm wide. They were distended and smooth without obvious segmentation. When feeding finished, the larvae rolled from the host remains and voided waste material as faecal pellets resembling strings of beads. One day later they pupated. At this stage it was easy to distinguish the sexes because of the enlarged scape and absence of eyes in the male. The pupal stage lasted 3–4 days and the total life cycle was therefore 14–18 days. In the case of second-form progeny, the life cycle duration was 12–13 days. The above figures were obtained from rearings at 25–30°C.

The average total production from 10 type-form females, each on a separate *S. formosum* prepupa was 370 females and 7 males. The percentage males varied between 1 and 4% in newly emerged adults.

The literature reports a wide range for life cycle duration. Balfour-Browne (1922) obtained a time of 17–23 days for *M. acasta* at an unspecified temperature which compares with 25–29 days (second-form) and 37–47 days (type-form) recorded by van Lith (1955) for the same species at 18–19°C. Buckell (1928) found that male *M. chalybii* (= *M. digitata*) took a total of 21 days compared to 37 days for females but did not specify any rearing temperatures. Schmieder (1933) bred *M. chalybii* at 19–25°C and recorded a life cycle length of 90 days for type-form individuals and 14 days for second-form individuals. It appears therefore that some standardisation of rearing temperatures is required before results can be compared. Even so, the result of 90 days for *M. chalybii* type-form individuals obtained by Schmieder (1933) seems excessively long in comparison with other figures. My results with *M. australica* show very little difference in life cycle time between type and second-form individuals.

DISPERSAL

There are two aspects to dispersal, natural and man assisted. The latter is important since the plastic behaviour exhibited by *Melittobia* has allowed it to avail itself of man's travelling facilities.

Males do not disperse, but die in the host cell or puparium in which they emerge. Inseminated type-form females escape from the host cell or puparium either by excavation or through entrance holes made by the mother. From this point on workers provide a variable story.

Graham-Smith (1916, 1919) observed that female *M. acasta* can fly for a considerable distance. Malyshev (1911) in contrast, found that *M. acasta* females could fly only a few millimetres. Balfour-Browne (1922) observed that female *M. acasta* fly only 25 mm or so at a time and for the most part do not use their wings. He suggested they might disperse by phoresy, but there is no evidence to support this. Buckell (1928) did not observe *M. chalybii* (= *M. digitata*) flying, but noted they hop like fleas when disturbed and concluded that although they were winged they were flightless, relying on their legs for dispersal. Krombein (1967) found that *M. chalybii* females do not fly frequently but rely on walking. Van den Assem (pers. comm. 1981) considers that flying in *Melittobia* spp. is partially a matter of temperature. At higher temperatures or in direct sunlight *Melittobia* females will fly away, but at temperatures less than 20°C they will not.

Evidence in the literature seems to suggest that the dispersal power of female *Melittobia* is limited, but my observations and some recent work by Freeman (1977) and Freeman and Parnell (1973) indicate that this is not so. When I released inseminated *M. australica* females in the laboratory they dispersed initially by hopping and

running. Later they flew. They were noted to be capable of flying 3 metres towards a closed window where they accumulated. Within 5 minutes there were no females left in a 1 metre radius of the release area. This area had been cleared prior to release to avoid females hiding or being unobserved. When the window was opened the females flew outside. I suggest that all emerging fertilised female *Melittobia* have functional wings used for dispersal. This dispersal is no doubt assisted by air currents.

Freeman and Parnell (1973), investigating the mortality of *Sceliphron assimile* Dahlbom caused by *M. chalybii* (= *australica*) in Jamaica, found that the parasite accounts for 76% of developmental mortality in the host. Moreover, where *Sceliphron* forms large breeding populations the parasite kills a higher proportion of them. Freeman (1977) found some variations in the percentage mortality expected on the basis of a linear density-dependent relationship and that these were often partly due to the effects of the prevailing easterly or south-easterly winds carrying *Melittobia* across Jamaica. Each host cell can yield up to 300 alate *Melittobia* which means that large numbers of females can be released into the air from host nests. Freeman (1977) argued that the further inland or westward a host cell might be the greater its chances of being found by a flying *Melittobia* since there would be an increasing number up-wind of host nests producing *Melittobia*. Conversely, nests near the sea shore or towards the east would have less chance of being found. He concluded there is circumstantial evidence that the higher percentages of *Melittobia* parasitism observed away from the shore and to the west were caused by dispersal of the parasite by the wind.

Further circumstantial evidence exists to support long range dispersal. Using figures provided by Freeman (1977) it is seen that each host cell can produce up to 300 alate females. At 10 high-density sites the host had 3499 cells with 3458 eggs laid of which 1430 were killed by *Melittobia*. The maximum yield from these cells is nearly 500,000 alate female *Melittobia*. Dispersal would be necessary just to find enough hosts and if it did not occur one could probably expect a higher percentage developmental mortality by *Melittobia* than the 41.4% recorded by Freeman and Parnell (1973) in areas of host density. Since *Melittobia* are delicate insects one would expect passive wind dispersal to result in high mortality. The production of large numbers of alate females could offset the risk factors in wind dispersal.

Man's ability to travel on a global scale has provided *Melittobia* with an added means of dispersal. Several features of its biology allow it to take advantage of man's travelling facilities.

1) *Melittobia* are highly polyphagous. One could reasonably expect to find mud nesting Hymenoptera and cockroach oothecae associated with ships and packing crates. In the past, hygiene on sailing ships was probably not of a high standard and some fly puparia were no doubt present. On long journeys more hosts could be taken on board at port stops. All of the above hosts are recorded for *Melittobia*.

2) Females are able to delay feeding and oviposition for several weeks until a host is at a suitable stage for oviposition or until a suitable host is located. Modern, rapid transport reduces the risk for *Melittobia* and packing crates provide the necessary hosts rather than air craft e.g. the North American *Sceliphron caementarium* (Drury) is spreading rapidly through the Pacific region and in July 1979 was intercepted at Alice Springs, Australia in packing crates from North America (Naumann 1980 unpublished report). In December 1980 this species was collected from Eight Mile Plains near Brisbane from nests in a dwelling.

3) *Melittobia* females have the capacity to be very efficient founder organisms. It is theoretically possible for an uninseminated female to begin a new population by laying a few unfertilised eggs. These develop into males with whom she then mates. This aspect has been discussed more fully under 'Reproduction'.

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