MORPHOLOGY OF *MYRMECOPHILA MANNI*, A MYRMECOPHILOUS CRICKET (ORTHOPTERA:GRYLLIDAE)[1]

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ABSTRACT

Scanning electron microscopy showed that the myrmecophilous cricket, *Myrmecophila manni* Schimmer, retains many structural features common to typical gryllids and has few of the morphological features often associated with myrmecophily. However, the mouth parts, particularly the labrum and epipharynx, are highly modified for strigilation and trophallaxis. The structure of the ovipositor is unique in that it can expand greatly to permit the passage of large eggs. This cricket also differs from typical gryllids in having stemmata instead of compound eyes, a feature probably related to its life inside dark ant nests where it does not need good vision. Behavioral, rather than morphological, attributes are probably more important in adapting the crickets for life with ants.

INTRODUCTION

Four species of *Myrmecophila* Latreille, small (2.3-4.0 mm), apterous crickets, are found in North America (Hebard 1920). *Myrmecophila* are the only myrmecophilous crickets known. Inquilines, especially myrmecophiles, often share a number of characteristics that enable them to live in the hostile but energy-rich environment of the ant nest. Often these adaptations include a myrmecoid body shape, a hard cuticle, reduction of certain appendages, and the use of glandular secretions appeasing to the ants. The degree of morphological change in myrmecophiles is probably directly related to the degree with which they have integrated into the colony (Wilson 1971). *Myrmecophila manni* Schimmer retains many of the structural features commonly found in the family Gryllidae and does not possess many of the adaptations often associated with myrmecophily.

The purpose of this study was to examine the morphological features of *M. manni* and to relate these finding to the crickets' relationship with their ant hosts.

MATERIAL AND METHODS

Eight *M. manni* were examined by scanning electron microscopy (SEM). Live specimens were fixed in 2% osmium tetroxide (OsO_4) for 1 h, and then 3% glutaraldehyde for 2 h at 4°C. Standard procedures for SEM preparation followed using an Omar SPC 1500 critical point dryer, Hummer V gold coater and EPTEC SEM, equipped with 55 P/N film. Field and laboratory observation of *M. manni* behavior were made to support interpretations of the functional morphology revealed by SEM.

RESULTS AND DISCUSSION

Sensory Apparatus

The SEM showed that *M. manni* has morphological features commonly found in the family Gryllidae. However, some pecularities of *M. manni* may be adaptations to myrmecophily. The antennae of *M. manni* are as long as the body and have a proportionately large scape. The row of hairs along the scape may help the cricket detect the source of a stimulus (Fig. 1). That is, when crickets are in a fixed position it can be demonstrated that they will follow a visual object with their antennae. The hairs on the scapes signal the angle the antennae are deflected, helping pinpoint the stimulus. The sensilla of the antennae occur in a repetitive fashion along the 44 + segments. Numerous filiform hairs cover the entire surface of the antennae and probably perceive sound or respond to air displacement vibrations (Haskell 1960) (Fig. 2). Coelomic pegs, considered to serve a chemosensory function, occur at the rate of about 1 per segment.

The cerci, like the antennae, are large in *M. manni* (Fig 2). They are usually held away from the body giving the cricket a larger surface area for perception. Their entire surface is covered with various-sized trichoid sensilla. The thinner hairs, which are also the longest, are bent by the slightest breeze. Cercal hairs of grasshoppers respond to sound frequencies of 30-1000 Hz and can be stimulated by air moving at 4 cm/sec (Haskell, 1961).

Reduction of appendages is common for myrmecophiles. However, *M. manni* retains its elaborate sensing structures, suggesting a beneficial function in the ant-cricket relationship. Behavioral studies show that *Myrmecophila* are often attacked by the host (Wheeler 1900, Henderson 1985). However, rarely is a cricket caught off guard and captured by an ant. The antennae and cerci probably warn the cricket of approaching ants. The cricket also uses its antennae to mimic the conspecific antennation used by ants preceeding mutual grooming

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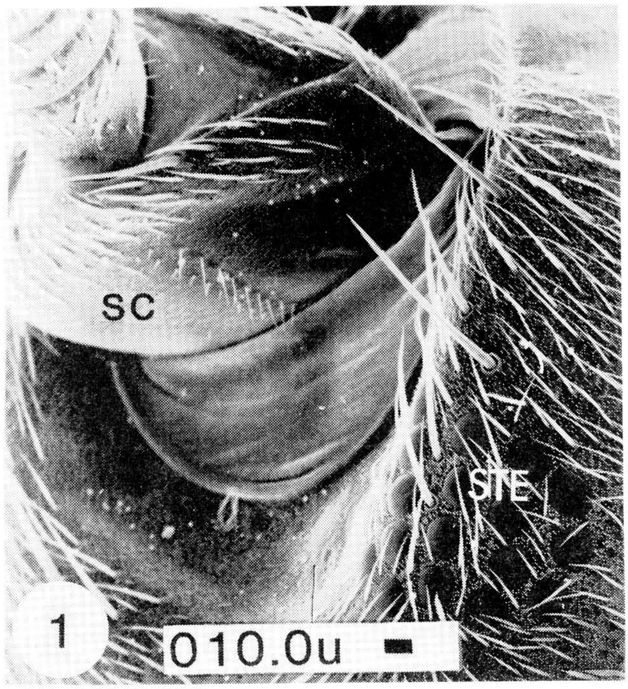


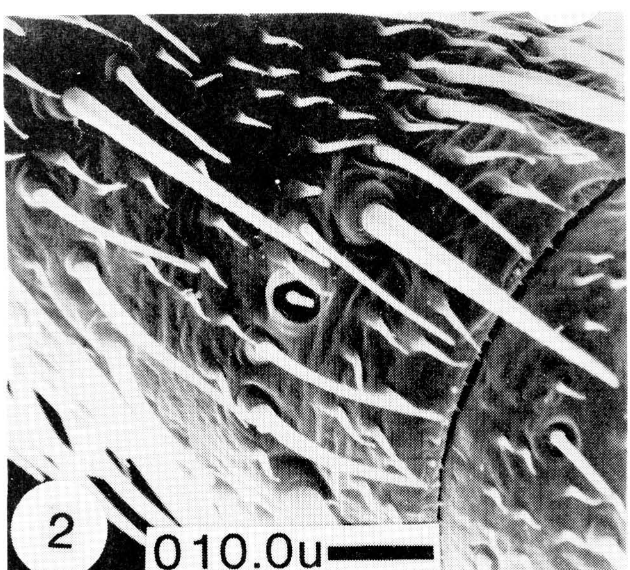
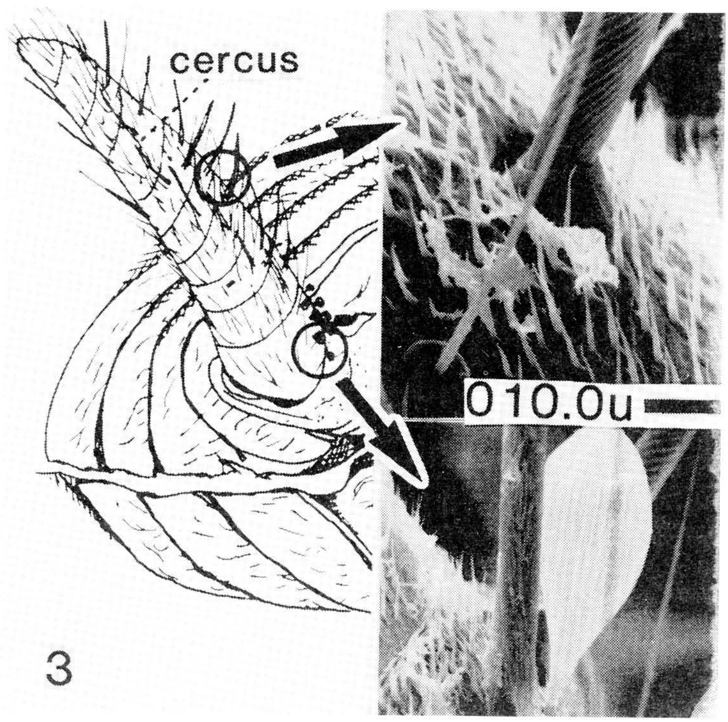


Fig. 1. Highly magnified SEM showing scape (sc) of the antenna and stemmata (ste). Note the row of hairs along the scape.

Fig. 2. Typical arrangement of sensory hairs that are found on each of the 44 + segments of the antennae. The hair in the centre is a coelomic peg, and its chemosensory function is well documented. The trichoid hairs surrounding the peg are mostly tactile sensing hairs.



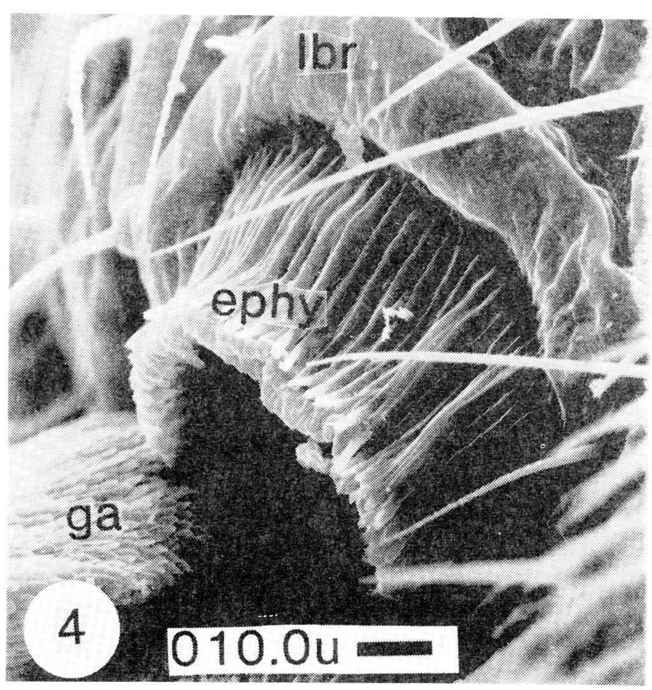
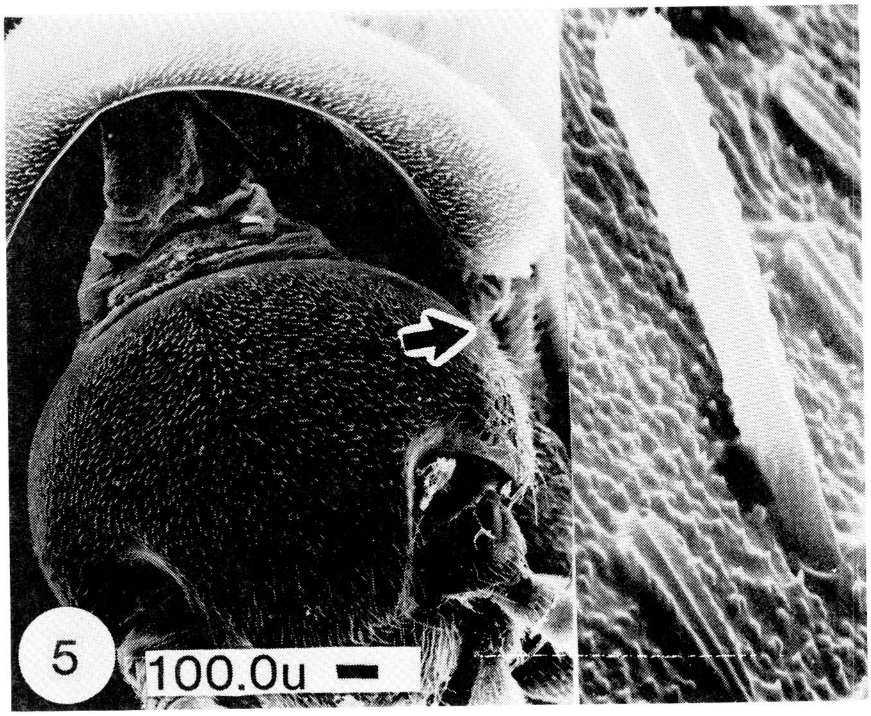


Fig. 3. Diagram showing the orientation of the cercus to the rest of the body. Two major types of hairs are located here. The top insert shows filamentous hairs that detect sound or vibration. These hairs are located over most of the cercal surface. The second type of hair, located only along the first two basal segments, are balloon hairs which help the insect orient to gravity (Bishof 1974).

Fig. 4. The feeding mechanism of *M. manni* is modified to increase the efficiency of its feeding habits. Labrum (lbr), Ephipharynx (ephy), Galea (ga).



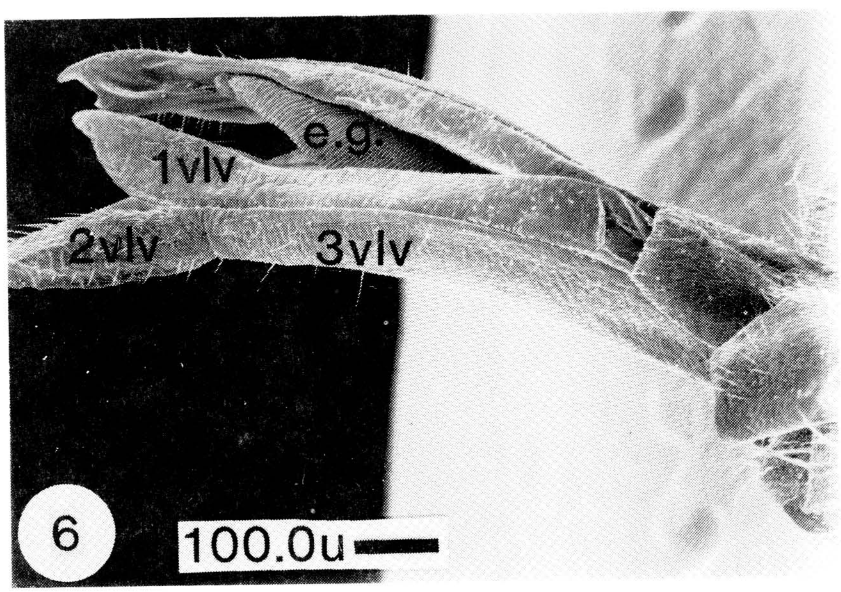


Fig. 5. SEM shows the top of the head, cervix, and pronotum of *M. manni*. The arrow points to a single hair scale, its serrated nature is shown, greatly enlarged, to the right.

Fig. 6. SEM reveals the expanding nature of the ovipositor of *M. manni*. This allows for oviposition of large eggs. The first valvulae (1 vlv) can spread apart and the spiraled egg guide (e.g.) can unspiral, increasing the total surface area. The third valvulae (3 vlv) are fused and wrap around the sclerotized tips of the second valvulae (2 vlv).

and trophallaxis. The length of the antennae aids the cricket in mimicking these signals which allows the cricket, in a sense, to parasitize its host. In addition, observations show that *M. manni* uses its antennae and cerci in elaborate displays during mating and intraspecific aggression (Henderson 1985). Cercal shaking has also been observed in field crickets and may aid in directing the female into proper position for copulation (Alexander 1961).

The eyes of *M. manni* are not compound, as in most crickets, but are composed of 18 to 20 stemmata located above each antenna. Visual perception for this type of eye is believed to be of a coarse mosaic that can only differentiate shapes and sharply contrasting images (Dethier 1943, Meyer Rochow 1974). Morphological regression of the eyes is associated with myrmecophily (Wilson 1971), and although stemmata are not a regressed form of compound eye, the end result is much the same. Fine visual acuity is probably not necessary since the crickets spend most of their lives inside a dark nest.

Locomotory Apparatus

M. manni are both saltatorial and cursorial, thus they retain the jumping and running abilities typical of Gryllidae. With *M. manni* retaining sensilla to allow for perception of approaching ants, it follows that they should retain their speed and jumping ability to allow for escape. Wheeler (1900) believed that the complicated zig-zag path of *Myrmecophila* was the major factor in allowing them to live with ants. Observations in the laboratory revealed that *M. manni* also retains the ability to lose a hind leg if seized by an ant. Steiner (1968) was the first to recognize this adaptation in field crickets as well as some grasshoppers as a possible means of escape. *M. manni* appeared to function normally with a leg missing and lived as long as intact *Myrmecophila* (Henderson 1985).

Feeding Apparatus

The mouth parts of *M. manni* are of the general orthopteran type with a large number of chemosensory sensilla on the tips of the labial and maxillary palpi. However, SEM revealed that the epipharynx and labrum are modified in *M. manni*. The labrum is reduced and the epipharynx protrudes from beneath it in finger-like projections, fused proximally and slightly separate distally (Fig. 4). Epipharyngeal projections of this type are sometimes found in aquatic insects (Haliplidae, Coleoptera, pers. observ.) and are probably used for scraping food loose from various substrates.

M. manni strigilate ants and engage them in trophallaxis. The brush-like epipharynx appears to be a adaptation for taking this food.

The protruding epipharynx increases the surface area that comes in contact with the ball of liquid regurgitated by the ant. The surface tension of the liquid is easily broken and adheres to the mouth parts of the cricket. Also, the mandibles are recessed behind the labrum, and when the cricket scrapes the integument of the ant the epipharynx may act as a scoop. The galeae, used to pull food into the mandibular area, have a reticulated surface and are positioned to sweep any particles scraped by the mandibles into the epipharynx. Highly modified mouth parts also occur among those inquilines which are well integrated into ant colonies (e.g., Pselaphidae, Akre and Hill 1973).

Odor Camouflage

M. manni are attacked by ants, but they are also found at the very heart of the ant nest, the brood chamber (Henderson 1985). One means by which the cricket attains entrance into the chamber is through behavioral mimicry. Odor camouflage may be another means. *M. manni* are covered with serrated scales on the dorsum of the head, thorax, and abdomen that may be used to acquire odors (Figs. 5). Acquisition of the nest odor by myrmecophiles through mechanical means is common. Host odors are transferred by histerid beetles associated with army ants by rubbing their tibial brushes on the ants (Rettenmeyer 1961, Akre 1968). The myrmecophilous beetle *Myrmecaphodius excavaticollis* (Blanchard) (Scarabaeidae) has recently been found to acquire species-specific hydrocarbons from its host by contact, by grooming behavior, and by ingestion of regurgitated ant postpharyngeal gland contents (Vander Meer and Wojick 1982). The serrated scales on *M. manni* might scrape particles off the walls and galleries of the ant nest during the cricket's travels. Wheeler (1900) reported that the walls and galleries of ant nests are covered with cuticular lipids deposited by the constant travel of the ants. Although attacks by ants on their cricket guests suggest that host hydrocarbon acquisition is not fully effective, acquisition of even a small amount of host hydrocarbons may help in the cricket's commensal existence.

Reproductive Morphology

Schimmer (1909) found that the ovipositor of *Myrmecophila* has unique articulation as a result of elongation and fusion of the eighth and ninth terga plurally. Gorokhov (1980) suggested that the column gave the ovipositor the ability to extend and retract; a necessary ability since the insect oviposits eggs nearly one-third as long as its body. SEM showed that the membranous egg guide is spiraled (Fig 6). The spiraling permits expansion of the egg guide, and we suggest that this also is an adaptation for laying proportionately large eggs. As the egg travels down the egg guide the spiral opens up giving the egg the area it needs while still providing a smooth pathway.

Summary

M. manni is morphologically well equipped for myrmecophily. The antennae and cerci are densely clothed with sensory hairs that quickly detect approaching ants. This early warning system, coupled with the propensity of the crickets to run in zig-zag patterns and to jump when escape by running is impossible, ensures that few crickets are caught by ants. In addition, the large hind legs readily detach when they are seized by attacking ants, and crickets lacking one hind leg are apparently able to continue to function normally. These slight morphological modifica-

tions, coupled with appropriate behavior, permit these crickets to integrate into the colonies of their host ants without much difficulty. Also important is their small size (2.3 to 4.0 mm) which makes them difficult to catch even with a determined attack by an ant.

Well integrated myrmecophiles frequently have greatly modified mouth parts to take advantage of food within the ant colony, and these crickets are no exception. Their brush-type epipharynx probably helps sweep food into the buccal cavity when the cricket is strigilating an ant. During trophallaxis the large and irregular surface of the epipharynx may aid in the transfer of the regurgitated liquid. Much more importantly, it appears that the mimicking of recognition signals of the ants enables the cricket to tap a nearly unlimited resource, the contents of the crops of foraging workers.

These small crickets have used a minimum of morphological adaptations and a maximum of behavioral modifications to integrate themselves into colonies of their host ants. The number of crickets in these colonies (one nest harbored over 300 crickets) suggests that they are at least as successful as myrmecoid inquilines.

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