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NUTRITION, HOST-SEEKING BEHAVIOR, AND LIFE HISTORIES  
OF CERTAIN BEE-ASSOCIATED BLISTER BEETLES  
(COLEOPTERA: MELOIDAE)

by  
Eric H. Erickson Jr.

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A Dissertation Submitted to the Faculty of the  
DEPARTMENT OF ENTOMOLOGY  
In Partial Fulfillment of the Requirements  
For the Degree of  
DOCTOR OF PHILOSOPHY  
In the Graduate College  
THE UNIVERSITY OF ARIZONA

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THE UNIVERSITY OF ARIZONA

GRADUATE COLLEGE

I hereby recommend that this dissertation prepared under my direction by Eric H. Erickson, Jr. entitled NUTRITION, HOST-SEEKING BEHAVIOR, AND LIFE HISTORIES OF CERTAIN BEE-ASSOCIATED BLISTER BEETLES (COLEOPTERA: MELOIDAE) be accepted as fulfilling the dissertation requirement of the degree of DOCTOR OF PHILOSOPHY

Floyd S. Werner  
Dissertation Director

March 24, 1970  
Date

William L. Nutting  
Dissertation Co-Director

April 3, 1970  
Date

After inspection of the dissertation, the following members of the Final Examination Committee concur in its approval and recommend its acceptance:\*

L. G. Carruth

April 3, 1970

Kearse

4/3/70

David D. Rubin

4/3/70

M. A. Massingale

4/3/70

William L. Nutting

4/3/70

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SIGNED:

A handwritten signature in black ink, appearing to read "Eric H. Jackson", written over a horizontal line.

To my wife and parents, without  
whose encouragement this  
might never have been  
accomplished

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## ABSTRACT

The nutritional requirements and host-seeking behavior of the larvae of 12 species of bee-associated Nearctic Meloidae were investigated. A comparative analysis was made of the two subfamilies, Meloinae and Nemognathinae. Included are the life cycles for eight species reared successfully beyond the feeding stage and four species reared through to the adult. Several food materials were evaluated. A paste consisting of mixed pollen (from honey bees), honey, and a mold inhibitor was found to be the most acceptable. Eggs or larvae of bees were not necessary for normal development. The rearing temperature was maintained constant at  $31 \pm 1/2^{\circ}\text{C}$ . The effect of temperature on developmental rates is recorded for two species. The optimum temperatures for development coincide with field soil temperatures during the normal developmental period.

The most critical factor in rearing was the moisture content of the media, with larvae of the two subfamilies having significantly different requirements. Larvae of all species of Meloinae and some of the Nemognathinae readily accepted the pollen media, but several of the latter group did not feed on any of the materials provided. It is probable that some of the Nemognathinae are pollen-specific

and as a result host-specific, while the Meloinae are more general in their nutritional requirements. Head capsule width is summarized for the apparent instars and it substantiates the occurrence of the  $T_1 - FG_{2-5} - C_6 - SG_7 - P - A$  ontogenetic pattern in the normal development of both subfamilies. Diapause of the coarctate instar was broken in three species after 74 days at  $6 \pm 3^\circ C$ . Coarctate larvae of one species, Nemognatha nigripennis, did not enter diapause when held at  $31 \pm 1/2^\circ C$ , and completed three generations within six months at this temperature.

The effect of light and temperature on the host-seeking behavior of first instar larvae of both subfamilies was investigated in the laboratory. The results indicate that triungulins of both groups are photo- and thermo-tactic and that they may survive in the field for up to 30 days, depending upon the availability of suitable food and/or moisture. Silk spinning by the Nemognathinae was studied and an attempt made to determine the significance of silk production. The information obtained was inconclusive.

Additional bionomic data are included and evaluated as they relate to the life history of the species discussed.

## INTRODUCTION

All Nearctic Meloidae except the epicautines are presumed to be dependent in the larval stage on the provisions of wild bees. Existing host records are fragmentary and include only a few genera from among the Apoidea and the Meloidae. Nearly all known host associations have been identified through excavation of bee nests and subsequent rearing of the cell contents. The absence of many bee genera from the host list is undoubtedly due in part to the fact that the nests of these species have not yet been thoroughly studied. It is also likely that some meloid species do not over-winter within the bee cell, with the result that host identification is more difficult.

There has not been a systematic effort to analyze the bionomics of meloid larvae, probably because, until recently, very few of the host bees have been studied in detail. Little is known about host specificity or larval food preference among the blister beetles, but there is evidence that certain species have the capability of destroying entire bee populations within limited areas. Analysis of available information seems to indicate that a key to these parasite-host relationships may be found

in the diverse nutritional requirements and ecological adaptations of the Meloinae and Nemognathinae.

The investigations reported here were designed to yield a broad spectrum of life history data to be used in delimiting the potential host range of individual meloid species. The differences between the two subfamilies provide a suitable framework for discussion and it is for this reason that these taxa are treated separately.

#### Systematics

To avoid confusion and provide continuity between this and other recent papers on the Meloidae, Selander's (1964) classification of the family has been adopted. The Nearctic components of this classification are presented in Table 1.

#### Larval Bionomics

##### Host Associations of Nearctic Meloidae

Comparatively few wild bee-blister beetle associations are known and these involve only nine of the Nearctic meloid genera (Appendix A). Of the bee hosts, records implicate genera containing fewer than 25% of all Nearctic species from among the Andrenidae, Anthophoridae, Apidae, Colletidae, Halictidae, and Megachilidae.

Table 1. Classification of the Nearctic Meloidae\*

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Meloidinae	
Meloini	<u>Meloe</u>
Lyttni	Pyrotina
	<u>Pyrota</u>
	Euphomphina
	<u>Brachyspasta</u>
	<u>Cordylospasta</u>
	<u>Cysteodemus</u>
	<u>Eupompha</u>
	<u>Gynaecomeloe</u>
	<u>Megetra</u>
	<u>Negalius</u>
	<u>Phodaga</u>
	<u>Pleurospasta</u>
	<u>Tegrodera</u>
	Lyttina
	<u>Lytta</u>
	Epicautina
	<u>Epicauta</u>
	<u>Linsleya</u>
	<u>Pleuropompha</u>
Nemognathinae	
Tetraonycini	<u>Tetraonyx</u>
Nemognathini	Zonitina
	<u>Gnathium</u>
	<u>Pseudozonitis</u>
	<u>Zonitis</u>
	Nemognathina
	<u>Hornia</u>
	<u>Nemognatha</u>
	<u>Rhyphonemognatha</u>
	<u>Tricrania</u>

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\*Modified from Selander (1964).

The known host species appear to have little in common which might relate to their acceptance by meloids. Generally, these hosts belong to the large genera of bees. However, Andrena, the largest of the New World genera, has seldom been implicated. Most hosts are solitary species that tend to nest gregariously or in aggregations, but some nonhosts have similar nesting habits. Hosts and nonhosts alike include burrowing and nonburrowing species, which construct cells with or without moisture-proof linings. Most bee species deposit a pool of nectar before capping the cell. Foraging habits in both groups (host and non-host species) range from oligolecty to polylecty, and the pollen stores vary in consistency from that of gruel to dough (Stephen, Bohart, and Torchio, 1969).

Meloids known to be associated with wild bees represent both subfamilies known from the Nearctic region, Meloinae and Nemognathinae. It is significant that many of the species not yet associated with a bee host are those with apparently narrow adult host plant associations (Enns, 1956; MacSwain, 1956; Werner, Enns, and Parker, 1966). Few monolectic or narrowly oligolectic bee species are included in existing host records.

## Ontogeny

The metamorphosis of blister beetles is highly complex and variable. Depending on the species, eggs may be deposited on or near the flower of the host plant; on the plant without concern for flower proximity; on or in the ground but near the base of the plant; at random upon the ground; or near or in the host nest (Parker and Böving, 1924; MacSwain, 1956; Selander, 1960). Upon hatching the phoretic triungulins of most Nemognathinae and the meloine genus Meloe reach a flower and await an acceptable host; those of Hornia attach to the bee at the nest entrance. Nonphoretic meloine triungulins seek out a suitable host nest.

First instar larvae of the Nemognathinae possess a small pad on the tip of the abdomen, which they use as a pygopod (MacSwain, 1956). Most triungulins of this subfamily spin silk of unknown origin from the anal orifice; Beauregard (1890) suggested that it is produced by the Malpighian tubules. The significance of silk spinning behavior is unknown. It is assumed that the silk prevents the larvae from being dislodged from the flower, but it is also produced in Hornia, which attaches to a bee in the nest.

Hocking (1949) has observed that certain stimuli evoke a grasping stance in first instar larvae of Hornia

minutipennis. These stimuli include the touch of a camel's hair brush; "the approach of a small dark object from above; air currents, especially from above; a musical note of pitch E below middle C (frequency 160). Any of these stimuli applied alone resulted in a partial response . . .; the application of two or more stimuli simultaneously resulted in the full reaction . . . ." The in-flight wing beat frequency of the host species (Anthophora sodalis Cresson) was identical to that which was found to evoke the grappling reaction.

After entering the bee cell the meloid triungulin destroys the egg or the bee larva, eliminating competition for the limited food supply. Usually the chorion or soft larval integument of the host is pierced with the large mandibles and the fluid contents consumed. Should more than one triungulin reach a bee cell, each is destroyed soon after ecdysis to the grub stage, until only a single triungulin remains (Parker and Böving, 1924; Enns, 1956; Selander, 1960).

Ecdysis of the first instar larva produces the first grub phase through dehiscence along the frontal head and dorsal thoracic cleavage lines. Following this and successive molts, a period of several hours passes during which the exoskeleton hardens before the resumption of

feeding activity (Selander and Mathieu, 1964). It is presumed that the dorsal orientation of the spiracles prevents the immature larva from drowning in the soft to semi-fluid substrate. Later instars are capable of maneuvering within the cell without risk of drowning, according to Parker and Böving (1924). Pupation may occur after the fifth or sixth instar, but more commonly these later instars molt to form a resting or coarctate phase. Selander and Mathieu (1964) and Pinto and Selander (1969) suggest that in the Meloinae digging, followed by the formation of a resting or pupal chamber, is a stimulus necessary for molting to the coarctate phase. In all molts up to and including the fourth, the old larval skin is cast off and ingested. In the Meloinae the fifth larval skin splits but remains attached in a wrinkled mass at the apex of the abdomen, while in the Nemognathinae the coarctate is formed within the intact fifth larval skin (Enns, 1956; Selander, 1960).

Molting from the coarctate to the second grub stage effects complete removal of all previous skins in the Meloinae, and in some of the Nemognathinae. Following ecdysis from the second grub back to the coarctate or to the pupa, the exoskeleton splits and remains attached in the species of Lytta and Pyrota previously studied (Selander, 1960; Selander and Mathieu, 1964). The rate of development

is probably influenced by the environment and may be species-specific (Selander and Mathieu, 1964).

Adults feed on nectar (Nemognathinae) or the blossoms or leaves (Meloinae) of the host plant (Parker and Böving, 1924; MacSwain, 1956; Enns, 1956; Selander, 1960; Selander and Mathieu, 1964; Pinto and Selander, 1969).

#### Postembryonic Notation

Selander and Mathieu (1964) established a system of notation for use in referring to the various periods of postembryonic development and this system was subsequently employed by Pinto and Selander (1969). In order to maintain continuity this notation has been adopted here. The first larval instar is commonly referred to as the triungulin, T. Instars 2 through 5 and sometimes including 6 are referred to collectively as the first grub phase, FG<sub>2-5(6)</sub>. Pupation may terminate the first grub phase; usually the final FG larva molts to the coarctate phase (normally instar 6), C, which is a resting form characterized by diapause. Return, through metamorphosis, to an active but nonfeeding second grub phase (normally instar 7), SG, is obligatory for development to continue. This is followed either by the formation of a pupa, P, and emergence of the adult, A, or a return to a second coarctate phase.

### Laboratory Rearing

Laboratory rearing of grasshopper-associated blister beetles has been successful on a limited scale. Attempts to rear bee-associated blister beetles have been largely unsuccessful. Food materials used in these early attempts have included the pollen stores of several wild bees; pollen collected by the honey bee mixed with some liquid; sugars; egg yolk; egg albumen; and bee larvae. Various temperature regimes have been tried. However, none of the many techniques employed have produced consistent results. Techniques which would permit uninterrupted feeding are essential for delimitation of larval stadia and the length of an entire life cycle.

Ten species of meloids have been previously reared through all immature stages: *Lytta vesicatoria* (L.) reared by Lichtenstein (1879) and also by Beauregard (1890); *Cerocoma vahli* F. by Cros (1924); *Tricrania sanguinipennis* (Say) by Parker and Böving (1924); *Lytta cyanipennis* (LeConte) by Selander (1960); *L. corallifera* Haag-Rutenberg by Selander and Mathieu (1964); *Pyrota palpalis* Champion by Selander and Mathieu (1964); and *Meloe laevis* Leach and *M. dianella* Pinto and Selander by Pinto and Selander (1969). Also, Selander and Mathieu (1964) were successful in rearing two additional species of *Pyrota* beyond the feeding stage in the laboratory.

The investigations reported in this paper include the successful laboratory rearing of four species of the Meloinae and eight species of the Nemognathinae through the feeding stages. Diapause was successfully broken in four of the species. Included also are data on the suitability of various food materials, optimum developmental conditions, and larval behavior.

## METHODS AND MATERIALS

### Laboratory Rearing

The Nearctic Meloidae are divided into the sub-families, Meloinae and Nemognathinae, each being unique with regard to many aspects of its general biology and development. The most significant differences involve adult host plant associations, oviposition sites, host-seeking behavior, and larval nutrition and development. The investigations were designed to utilize these differences to elucidate the nutritional requirements and host-seeking behavior of meloids.

#### Meloinae

Eggs of Lytta magister Horn, L. mutilata (Horn), Pleurospasta mirabilis (Horn), Pyrota akhurstiana Horn, P. postica LeConte, and Tegrodera erosa aloga (Skinner) were obtained from laboratory colonies and field collections. Following eclosion rearing was carried through the feeding period to the coarctate and when possible to the adult stage. Rearing techniques were modified from those employed by Selander and Mathieu (1964).

Laboratory colonies consisted of paired adults maintained in 1/2 pint waxed paper cartons with perforated

clear plastic lids. Fresh plant material was provided at all times (see Appendix B, and Werner et al., 1966 for host plant data). Following oviposition the beetles and debris were removed, the carton sealed with an unperforated clear plastic lid, and the eggs held at ambient room temperatures (about 25°C). No attempt was made to provide the adults with either a moist and light environment or a soil substrate for oviposition.

Thirty to 40 additional paired adults of L. magister and P. akhurstiana were confined in each of two 12 X 12 X 18 in screen-wire cages with solid tops and bottoms, containing 1.5 in of nonsterile soil and plant debris. A similar number of T. erosa aloga were confined in each of three identical cages. Both cages of L. magister and P. akhurstiana and one of T. erosa aloga were positioned to receive maximum indoor daylight and held at room temperature, about 25°C. A second cage of T. erosa aloga was subjected to maximum indoor daylight plus artificial light throughout the night. The third cage was moved out-of-doors, where it was subjected to normal daily temperature, humidity, light, and shade. All cages were provided with fresh host plant material in a "bouquet" in an open container of water. All wax cartons and soil trays were checked daily and the location and egg mass concealment (protection), number of eggs per mass, and date of oviposition were

recorded. Each egg mass was then placed in a waxed container (as above) and held at room temperature. Adults of other species noted in this section were not available in sufficient numbers for caging.

Concurrent field observations were possible with L. magister and T. erosa aloga. The surface inch of soil, including rocks, plants, and debris, was excavated in several areas in an attempt to locate egg masses. These excavations were made on a random basis in areas of dense adult populations.

Notes on prefeeding behavior of the  $T_1$  larvae were made on laboratory colonies of the species listed.  $T_1$  larvae were confined within the waxed containers until they were introduced individually into pre-provisioned, sterilized rearing chambers (10 mm inside diameter glass tubing, 5 cm in length and plugged with cotton at both ends). One size of tube was used throughout the first four instars and changed as necessary when mold developed or when fresh food material was needed. The fifth instar was provided with a similar glass tube 13 mm in inside diameter. Following cessation of feeding and subsequent formation of the coarctate an identical clean tube was provided for the remainder of the life cycle. Temperature was held constant to within  $\pm 1/2^\circ\text{C}$  and relative humidity maintained in excess of 90%.

## Nemognathinae

Eggs and triungulins of Gnathium minimum (Say), G. obscurum MacSwain, Nemognatha nigripennis LeConte, N. nitidula Enns, N. lurida apicalis LeConte,<sup>1</sup> N. lurida lurida LeConte, N. lutea lutea LeConte,<sup>2</sup> Pseudozonitis brevis Enns, Tetraonyx fulvus LeConte, Zonitis atripennis flavida (Say), Z. dunniana Casey, and Z. punctipennis (LeConte) and an atypical egg mass (Nemognathinae sp.) were obtained from field collections and laboratory colonies. Following eclosion, those species which molted successfully to the FG<sub>2</sub> larval stage were reared through the feeding period to the coarctate and when possible to the adult stage. Rearing techniques were similar to those described for the Meloinae, with some exceptions.

Several paired adults were confined within clean 1/2 pint waxed paper cartons with perforated clear plastic lids. Each cup contained a cotton ball saturated with a solution consisting of equal amounts of honey and de-ionized water, and a flower bud taken from a primary host plant or a simulated bud made from a 1 in disc of 1/8 in balsa wood with a centrally inserted "stem". Again, no attempt was made to simulate other environmental conditions.

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<sup>1,2</sup>These species were not collected in Arizona. See Appendix B.

These containers were positioned in the laboratory to receive maximum indoor daylight. Following eclosion they were sealed with clear plastic lids and held at ambient room temperature, about 25°C.

Concurrent field observations were made when possible at most of the Arizona sites. Laboratory observations are available for some species.

T<sub>1</sub> larvae were confined within the containers until introduced into individual sterilized glass rearing chambers (1/4 dram, 7 mm inside diameter vials with cotton plug) containing a known amount of food material. A single chamber usually sufficed for the entire feeding period, as each contained an adequate amount of food and mold did not develop in vials containing living larvae. Following cessation of feeding and subsequent formation of the coarctate the vials were left undisturbed unless they were deemed excessively contaminated. Temperature was held constant at  $31 \pm 1/2^\circ\text{C}$  and relative humidity in excess of 90%.

#### Breaking Diapause

Initial attempts to break diapause in the coarctate phase were generally unsuccessful. Approximately 20 C larvae of those species successfully reared, each within its respective rearing chamber, were exposed to each of the following environmental regimes: room temperature and

humidity (about 25°C and 40% R.H.); 30 days at room temperature followed by 60 days at  $6 \pm 3^\circ\text{C}$  and then an indeterminate period at  $31 \pm 1/2^\circ\text{C}$ ; 30 days at room temperature followed by 60 days at  $6 \pm 3^\circ\text{C}$  and an indeterminate period at  $31 \pm 1/2^\circ\text{C}$ ; and an indeterminate period at  $35 \pm 1^\circ\text{C}$  with a relative humidity of more than 90%. Diapause was finally broken in two species after 74 days at  $6 \pm 3^\circ\text{C}$  followed by incubation at  $31 \pm 1/2^\circ\text{C}$ .

Twenty C larvae of Lytta magister were placed in each of two unglazed clay flower pots containing 1 in of sterile sand and sealed with an unglazed clay lid and plastic foam weather stripping to exclude possible predators. These pots were buried beneath 1-1/2 in of soil at elevations of 2400 and 3100 feet. The pots were installed on October 1, 1968 and kept in place until emergence of the adults was complete.

#### Diet

After preliminary studies with the Meloinae, pollen mixed with commercially available honey and a mold inhibitor was selected as the standard diet for all species. Fresh pollen was obtained from foraging honey bees (Apis mellifera L.) by means of a standard pollen trap. Initial rearing was conducted using pollen from an unknown, but probably,

crop source<sup>3</sup> (hereafter referred to as pollen type C). This pollen was at least one year old prior to the initiation of these studies in 1968. Subsequent collections were made from an isolated honey bee colony and almost certainly consisted primarily of pollen from desert plants. These collections were made in the spring of 1968 (pollen type B) and the late summer of 1969 (pollen type A). All pollen was stored at below freezing temperatures and screened before use for removal of gross contaminants. Only intact pollen balls were utilized.

Selander and Mathieu (1964) and Pinto and Selander (1969) have noted that mold growing upon the media inhibited larval development. To alleviate this problem and reduce maintenance three similar pollen-base media were tested. The first was a simple combination of pollen and de-ionized water. The second consisted of pollen washed in 70 and 90% ethyl alcohol, air-dried, and mixed with de-ionized water. The third was a mixture of pollen, commercially available honey, and approximately 1.5 g per 1000 g of Moldex<sup>®</sup> mold inhibitor.

Rearing, to determine the acceptability of the various pollen preparations was attempted with Lytta.

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<sup>3</sup>This pollen sample was obtained from the Apiculture Research Laboratory, USDA, Tucson, Arizona.

magister. Mold developed within hours on the pollen and de-ionized water mixture, which then gradually dehydrated. The mixture of pollen washed in alcohol plus de-ionized water resisted fungal growth for up to seven days, but rapid dehydration was evident and the larvae soon rejected the medium. With increased mortality, this test group was changed over to the pollen and honey diet in the FG<sub>4</sub> instar. Generally the high relative humidity maintained within the climate control chamber retarded drying of the pollen and honey media throughout the feeding period. The mold inhibitor was effective through the early instars and as a result the larvae were fed only once (twice when quantity became a factor).

Although the pollen and honey medium was employed throughout subsequent rearing of L. magister and all other species, other materials were also tested for acceptability. A prepared pollen supplement, Karawaite<sup>®</sup>, which is available as a paste was fed to larvae of several species. A second pollen supplement, hereafter referred to as "Haydak's Mixture" (see Appendix C) was also tested as a complete diet. Because of a general lack of success these media were fed to only a few species.

Immature larvae of Apis mellifera were offered to FG<sub>4&5</sub> larvae of L. magister, T. erosa aloga, and all non-feeding T<sub>1</sub> larvae of the Nemognathinae. Mature larvae of

Chalicodoma occidentalis (Fox) and Diadasia rinconis Ckll. were included in the provisions of FG<sub>4&5</sub> larvae of T. erosa aloga. None of these were accepted and as a result the feeding of bee larvae was discontinued.

A homogeneous paste was prepared from each of the media tested (Appendix D). Although consistency varied slightly with individual preparations, it was noted that for the Meloinae the most acceptable provision appeared to be of a consistency where a film of surface moisture appeared within 30 seconds after formation of a "pellet", yet was not of sufficient quantity to permit pooling in the feeding chamber. Drowning of the T<sub>1</sub> larva usually occurred if a pool was present. These findings agree with those of Selander and Mathieu (1964).

The optimum medium consistency for the Nemognathinae was slightly fluid, conforming to the configuration of the vial and producing a pooling effect at the glass-medium interface when allowed to stand for 24 to 48 hours. However, unlike the Meloinae, the nemognathine T<sub>1</sub> larvae appear buoyant and able to resist drowning. In addition a minute pool of honey was provided initially for immediate larval ingestion. The word "pool" refers to the presence of a micro-drop of honey placed on the side of the glass vial to simulate a nectar pool placed near a pollen mass by the bee.

Fermentation altered the food material to a ropy consistency when glass bottomed vials were used for rearing (Nemognathinae). No solution to this problem was found except daily observation and removal of the excessive fluid. Other types of chambers were found to be unsatisfactory in maintaining a sufficiently high food moisture content for rearing of nemognathine larvae.

The number of  $T_1$  larvae fed varied according to the availability of specimens, but usually a minimum number of 25 per species was started on each of the substrates tested.

The quantity of food consumed was determined for each of the species by measuring the loss of weight of the quantity provided. These data are subject to error, the result of water gain and loss throughout the feeding period. They are accurate to  $\pm 5\%$  of the total weight, as shown by an analysis of hydration and dehydration of the pollen and honey medium maintained under the rearing conditions of these investigations in the absence of meloid larvae. The amount of food required for normal development was based on objective observations of larval size and postfeeding behavior. Tabulation of head capsule width for each species was made for exact determination of larval instar and growth analysis.

The length of larval stadia and cumulative days in rearing were calculated and the duration of all instars was completely summarized. Any individual cited in the analysis of a given instar was included only if it molted successfully to the subsequent instar.

In conjunction with these studies and for the purpose of comparison with meloid larval consumption rates, the contents of freshly provisioned cells of Chalicodoma occidentalis (Fox), Diadasia enevata (Cr.), D. rinconis Ckll., and Xylocopa brasilianorum varipuncta Patt. were examined and weighed. These data are summarized in Table 2.

Table 2. The weight of the pollen stored in individual cells of certain wild bees

	$\bar{x}$	$s_{\bar{x}}$	Range	N
<u>Chalicodoma</u> <u>occidentalis</u> (Fox)	0.24 g	0.007 g	0.12-0.37 g	74
<u>Diadasia</u> <u>enevata</u> (Cr.)	0.32	0.004	0.29-0.35	10
<u>Diadasia</u> <u>rinconis</u> Ckll.	0.30	0.096	0.24-0.48	10
<u>Xylocopa</u> <u>brasilianorum</u> <u>varipuncta</u> Patt.	1.65	0.098	1.28-2.31	10

### Prefeeding Larval Behavior

#### Tactic Response to Light and Temperature

Three arenas were erected and equipped as illustrated in Fig. 1. A 10 X 13 X 3 in clear plastic box was placed inside a 14 X 17 X 11 in pasteboard box. A bead of Tanglefoot<sup>®</sup> was distributed around the inside edge of the plastic arena to prevent escape of the  $T_1$  larvae (It has subsequently been noted that Tanglefoot<sup>®</sup> serves to repel rather than entrap the larvae.). The floor of the arena was covered with a lampblack-coated sheet of kymograph paper. Exterior light was excluded by a double layer of black fabric.

Diversiory structures were placed within the arena to test visual attractiveness and for behavioral stimulation. Towers of balsa wood, 1/4 X 2 X 7 in and covered with coated kymograph paper, were placed vertically in pairs in each of the arenas. Small angular pieces of balsa wood were included to provide surface irregularities for digging. Round #6 corks were used as corner weights and these also yielded data. One small pellet of pollen and honey paste was placed near one edge of each arena. All arenas were maintained in an air-conditioned room at ambient temperature and humidity ( $25 \pm 4^\circ\text{C}$  and  $40 \pm 10\%$  R.H.). The arena selected as a control was maintained in

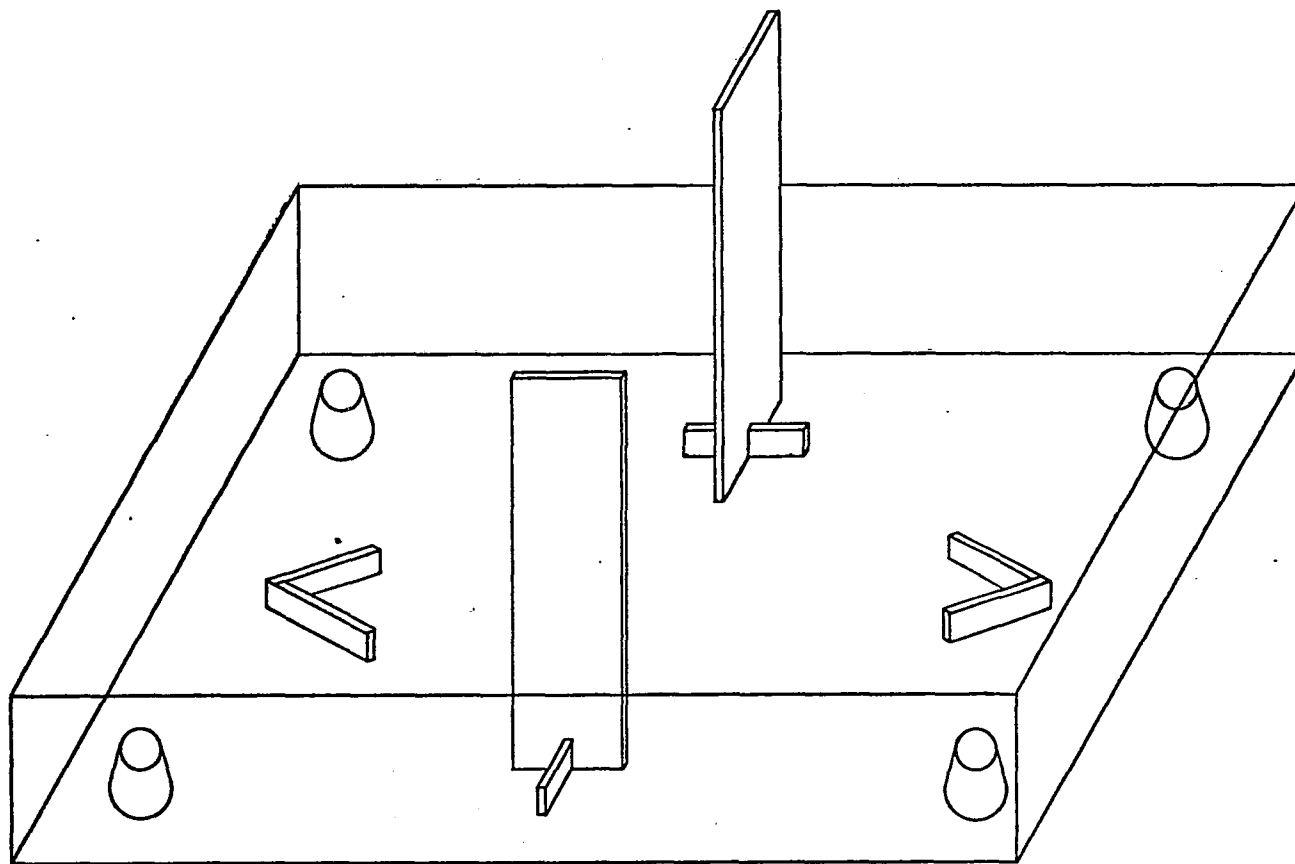


Fig. 1. Larval arena showing placement of diversionary structures

total darkness. Phototactic response was observed in an arena having a single low intensity light source. The source was a clear 25 watt incandescent bulb placed 15 in above the surface and insulated from the surface below by a pane of glass. Thermotactic response was observed in an arena having as a heat source an infra-red lamp situated 15 in above the surface and thermostatically controlled with a rheostat device.

#### Temperature and Larval Activity

These studies were conducted within a controlled climate chamber and in total darkness. Relative humidity was maintained constant at 50%.

Low Temperature Threshold.--Ten  $T_1$  larvae of each species studied were held at  $6^{\circ}\text{C}$  for 30 minutes, then transferred to coated kymograph paper in a climate chamber previously stabilized at  $10 \pm 1/2^{\circ}\text{C}$ . Two parameters were chosen as indicators of activity for each species. Indicators for the phoretic species were initiation of crawling and initiation of silk attachment. Those for the non-phoretic bee associates and epicautine species studied were the initiation of crawling and the initiation of a normal search pattern. The effect of low temperature on each of the parameters of activity was recorded after two hours. The temperature was advanced  $2^{\circ}\text{C}$  at the end of each

subsequent two hour period until activity became evident. Each test was repeated three times and the temperature data presented as a statistical mean.

Thermal Death Point.--Using similar techniques ten  $T_1$  larvae of each species were maintained at room temperature and humidity prior to being transferred to coated kymograph paper in a climate chamber previously stabilized at  $32 \pm 1/2^\circ\text{C}$ . Survival was noted after 12 and 24 hours, the temperature advanced  $2^\circ\text{C}$  after each subsequent period, and the temperature data reported as the statistical mean of three tests.

#### Silk Spinning in the Nemognathinae

The silk spinning behavior of the Nemognathinae and its importance in host selection by the  $T_1$  larva is a matter of primary concern in any study of the ecological associations of the groups involved. Within the limits of this study an attempt was made to elucidate the primary stimulus and subsequent advantage resulting from this behavior.

It was noted by accident that triungulins may be induced to spin silk by the application of an electrostatic charge. This observation led to extensive field and laboratory investigations using an ebonite rod rubbed with wool and motion picture photography. The charged ebonite

rod was held near the active  $T_1$  larvae and slowly withdrawn as the larvae began spinning. The behavioral information presented is based on a study of these films.

## RESULTS

### Nutrition

Rearing data for each species studied are summarized in Appendix D. Larval survival, together with the rate of development (length of stadia) and growth as evidenced by increase in head capsule width, provide the indicators used to determine the adequacy of food materials, in both quantity and composition. Each species was fed a standard pollen and honey diet and the data recorded under Group A in all tables (Appendices E & F). Group A data are considered to be representative of normal growth and development under laboratory conditions. Generally, developmental rates were high and mature larvae or adults comparable in size with field collected specimens. Other food materials were tested in some species and the data summarized under appropriate group designations.

#### Pollen Base Media

Lytta magister was used in the development of suitable pollen preparations for rearing bee-associated meloids. The mixture containing pollen and de-ionized water, and pollen washed in alcohol plus de-ionized water, were both

unsatisfactory, the former because of rapid fungal growth which restricted feeding and the latter as a result of moisture loss.

The effect of diet on the length of the individual instars and on the total length of the feeding period is evident (Appendix E-1). The mean duration of the first instar was not significantly different at the 5% level ( $t = 0.643$ ), in groups A, B, and C. Maturation rates in groups A and B were closely parallel until the  $FG_5$  instar, when the effect of insufficient food material produced a significant difference at the 5% level ( $t = 2.951$ ). Although the individuals in group B were considerably smaller than those of A, they entered the coarctate phase without difficulty.

The duration of the first four instars in group C was significantly greater than in group A at the 5% level ( $t = 8.395$ ). However, when group C was changed to the pollen and honey diet of group A in the  $FG_4$  instar, the  $FG_5$  instar was completed in less time than in group A ( $t = 1.804$ ,  $P < .05$ ). Thus, the feeding period of group C was completed in the same time as group B ( $t = 0.509$ ,  $P < .05$ ), which entered the coarctate phase with insufficient food for maximum growth.

Differences in behavior were noted in the  $FG_5$  instar of groups A and B. Fifth instar larvae of group A

ceased feeding and appeared to rest; those of group B became very active, burrowing through the cotton plugs of their tubes and crawling about. Some attempted to enter the tubes of others that were still feeding.

Triungulins of both subfamilies consumed pollen and liquid portions of the media; the contents of the intestine were visible through the integument and abdominal distension was evident. Mortality among  $T_1$  larvae on the standard diet (group A, Appendix D) was moderate or low in most of the species reared successfully, and was the result of improper moisture content of the food material. Triungulins of the Meloinae drowned in the meniscus of substrate surface moisture, while those of the Nemognathinae perished in the absence of adequate moisture.

Phoretic triungulins deprived of adequate moisture in the substrate burrow in the media. When subsequently provided with moisture in the form of a honey pool these larvae drink at length until replete. Generally, moisture requirements in the Meloinae are low in comparison to the Nemognathinae. Optimum moisture conditions are critical and difficult to maintain in the laboratory.

Triungulins of Pleurospasta mirabilis, Gnathium minimum, and G. obscurum did not feed on either the standard pollen and honey diet or on any of the substitutes provided. All  $T_1$  larvae of these species died within 24 hours

following introduction into a provisioned rearing chamber. Triungulins of Tetraonyx fulvus, Zonitis dunniana, and Z. punctipennis ingested both pollen and honey and showed abdominal distension. However, all except two specimens of Z. dunniana failed to molt to the FG<sub>2</sub> instar. In these three species feeding prolonged life in the T<sub>1</sub> instar (Appendix D). Honey bee larvae were rejected by T<sub>1</sub> larvae of all nonfeeding phoretic species.

Development throughout subsequent instars was most rapid on the pollen and honey medium. The quantity of food required to produce normal-sized mature larvae and adults is recorded in Table 3. Moisture requirements of FG<sub>2-5</sub> larvae are similar to those of the T<sub>1</sub> instar of each species. Larvae of the Meloinae are unable to survive under high moisture conditions as evidenced by the 100% mortality of Pyrota postica larvae which received high moisture content medium at the second feeding. Nemognathine larvae are unable to survive at the low moisture levels favored by those of the Meloinae.

Two other points should be noted here, both of which are based on objective observation rather than statistical analysis. Storage of pollen to be used in rearing, even at below freezing temperatures, seems to diminish its food value. Although not apparent in the Meloinae, it is obvious that in all species of the

Table 3. Quantity of food consumed by the immature stages of certain Meloidae

	$\bar{x}$	$s_{\bar{x}}$	Range	N
<u>Lytta magister</u> group A	2.25 g	0.21 g	1.75-2.50 g	25
group B	1.53	0.52	1.28-1.87	25
<u>Lytta mutilata</u>	1.40	0.42	0.91-2.03	6
<u>Tegrodera erosa aloga</u> group A	2.06	0.19	1.64-2.64	23
group B	1.38	0.63	0.98-1.77	21
<u>Nemognatha lurida apicalis</u> group A	0.37	0.27	0.29-0.45	10
<u>Nemognatha lurida lurida</u> group A	0.38	0.01	0.33-0.46	24
group B	0.36	0.01	0.28-0.44	25
<u>Nemognatha lutea lutea</u>	0.34	0.01	0.28-0.39	18
<u>Nemognatha nigripennis</u> group A	0.32	0.01	0.28-0.36	27
<u>Nemognatha nitidula</u> group A	0.37	0.03	0.29-0.43	18
<u>Pseudozonitis brevis</u>	0.35	0.12	0.26-0.42	6
<u>Zonitis atripennis flavida</u>	0.30	0.32	0.22-0.37	4

Nemognathinae permitting comparison, feeding of type C pollen resulted in the highest mortality index and type A the lowest. At the time of these investigations the type C pollen was more than two years old, type B pollen more than one year old and type A had been stored for less than three months.

Mold development within the rearing chamber is limited by the presence of a healthy larva of any instar, and to an extent beyond the disruptive influence of feeding. Mold inhibitor is essential for uninterrupted rearing, but it does not completely prevent fungal growth. A comparison of rearing chambers containing living or dead larvae demonstrates very dramatically that luxuriant fungal mats existing in chambers without living larvae are absent from those chambers containing healthy immatures. These observations are universal for all species studied and based on larvae, rearing chambers, and medial preparations of common origin.

#### Other Food Materials

Appendix D summarizes all materials (except bee larvae) fed instead of, or in addition to, the standard pollen and honey diet. When provided as a complete diet these materials were unsatisfactory and their use resulted in dwarfism and increased mortality. Substituting them

midway in the developmental period had an intermediate effect.

Neither of the pollen supplements, "Karawaite" or Haydak's Mixture, was adequate when compared to the standard diet.  $T_1$  larvae of Tegrodera erosa aloga molted successfully to the  $FG_2$  and subsequent FG instars when subjected to a complete diet of these supplements. However, interstadial periods were significantly extended and mortality reached 100% by the end of the  $FG_5$  instar (Appendix E-4). Dwarfism was evident in the  $T_1$  larvae of the Nemognathinae when fed to the  $FG_2$  instar on either of the supplements. When both supplements were substituted for the standard diet during the  $FG_3$  and  $FG_4$  instars of Nemognathus and T. erosa aloga, mortality was 100% by the end of the feeding period and dwarfism was evident.

Provisions of Chalicodoma occidentalis were fed to several species of the Nemognathinae (Appendix D). Mortality was complete in the first instar as a result of rapid fungal growth which prevented feeding of the triungulin.

Larvae of Apis mellifera, Anthophora occidentalis, and Chalicodoma occidentalis were fed to larvae of both subfamilies. The results were generally inconsistent and, with one exception, resist coherent summarization. Twenty

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five FG<sub>4&5</sub> larvae of L. mutilata, T. erosa aloga, N. lurida lurida, and N. nitidula all preferred the standard pollen and honey medium over larvae of each of the bee species noted above when allowed to choose between them in the rearing chamber. The bee larvae were unmolested through formation of the coarctate. Honey bee larvae offered to all nonfeeding T<sub>1</sub> larvae of the Nemognathinae failed to stimulate molting to the FG<sub>2</sub> instar. None of the tri-angulins attempted to feed on the bee larvae.

#### Host-Seeking Behavior

##### Phototactic Response

Strong positive phototaxis is exhibited by phoretic and nonphoretic bee-associated blister beetles as well as by the epicautine species tested, and with the tenor of response descending in that order. When placed within a bright circle of light, few individuals ventured outside of it; when placed opposite a light source, all individuals oriented toward and entered the area of greatest light intensity, crawling approximately 20 to 25 cm per hour. Phoretic species made silk attachments in the area of greater light intensity. When compared to the totally random patterns of search and silk attachment exhibited by control populations in total darkness, this phototactic response was both obvious and dramatic.

Diversions placed in the activity arena appeared to have little general influence. Phoretic triungulins sought out elevations of less than 1 mm above the flat surface of the arena floor for points of silk attachment, but ignored heights of several inches which were made available. These larvae appeared inclined to crawl only very short distances over a period of 2 to 3 days, and traveled farthest in total darkness. Nonphoretic larval activity was extensive but essentially at random. These larvae upon reaching a surface irregularity, crevice, corner, or base of an arenal diversionary structure, exhibited digging behavior, attempting to dig directly into the surface. This digging behavior, also exhibited by the epicautine forms, was almost entirely phototactically oriented and limited to the illuminated side of the obstacle or irregularity and in some cases to shadow outlines. In the control population, digging behavior was entirely at random. Patches of pollen-honey mixture placed within the arena had no influence on orientation behavior, at greater distances, of either of the bee associated groups. However, at distances of less than 3 cm, response by nonphoretic species was direct and digging behavior initiated at the immediate site. These triungulins did not attempt to feed.

### Thermotactic Response

Phoretic triungulins placed within a circle of radiated heat or opposite the heat source demonstrated movement toward the source and a definite concentration of silk attachment points within the circle of heat. Similarly, nonphoretic larvae exhibited random search patterns concentrated in but not entirely confined to the circle of heat. Oriented movement toward the heat source was obvious in both groups. However, random activity outside of direct-route pathways of orientation was significantly greater here than in phototaxis. The degree of random activity and proportion of silk attachments noted outside of, or away from, the heated area served as parameters of response.

General behavior patterns of the control groups were the same as described for the phototactic studies. In addition to the moderate degree of thermotaxis previously described, phoretic larvae selected areas of slight elevation for silk attachment. Masking tape used to splice together two sheets of paper to form a continuous substrate was particularly favored. Diversionary structures were ignored by all but a few individuals of the nonphoretic bee associates and epicautine species, which traversed these surfaces in the same random patterns exhibited on the substrate. As in phototaxis, the limited utilization

of the vertical dimension was demonstrated to the greatest extent by the epicautine species. Digging behavior was noted as before in the nonphoretic and epicautine species, and was obviously somewhat less thermotactically oriented than phototactically. As before, digging behavior in the control was entirely at random. The effect of the pollen-honey mixture present within the arena proved to be the same as that demonstrated within the control and illuminated arenas.

Reduced levels of activity were apparent at temperatures above  $33 \pm 1/2^\circ\text{C}$ . Exact definition of a high temperature activity threshold is impossible without consideration of the effects of relative humidity and available substrate moisture. These and other data reported in this section are supported by results obtained from the feeding behavior of *triungulins* reported in the section on life histories.

Negative thermotactic response to surface-radiated heat has been observed at higher temperatures. Using  $T_1$  larvae and a variable heat source, the upper limit of the preferred temperature range was determined. Temperatures below  $36 \pm 2^\circ\text{C}$  elicited a positive thermal response at a relative humidity of  $40 \pm 10\%$ . However, as the surface temperature rose above  $33 \pm 2^\circ\text{C}$ , the tenor of response declined markedly, becoming negligible at  $36 \pm 2^\circ\text{C}$ . Above

this threshold the response became negative, with the larvae demonstrating typical escape and avoidance reactions. When escape was made impossible, death became imminent.

Escape response at these temperatures was specifically measured when triungulins placed on a cotton ball located directly beneath the heat source immediately crawled off of the cotton and away from the circle of heat. Larvae placed on cotton in the control arena failed to leave the cotton and remained on it until death. Triungulins placed opposite the heat source failed to enter the circle of heat, as evidenced by their tracks. Others placed on the surface within the circle of heat, crawled out and failed to attach silk to the surface. These later tests were also confirmed by the control populations, which responded with random patterns of crawling and silk attachment, and by low (below 36°C) temperature trials demonstrating a concentration of activity and silk attachments within the circle of heat.

#### Effect of Temperature on the Prefeeding Activity of Triungulins

Data compiled from all species studied indicates that first instar,  $T_1$ , meloid larvae have a comparatively low temperature activity threshold. These lower limits (Table 4) are approximately the same for phoretic bee-associates as well as for epicautine forms. Two parameters

Table 4. Low temperature activity thresholds for  $T_1$  meloid larvae

	Initial Activity	Search Pattern	Silk Attachment
Meloinae			
<u>Tegrodera erosa aloga</u>	13±½°C	15±½°C	
<u>Lytta mutilata</u>	13	15	
<u>Epicauta maculata</u>	13	14.5	
<u>Epicauta segmenta</u>	12	13	
Nemognathinae			
<u>Gnathium obscurum</u>	13		14.5±½°C
<u>Nemognatha lurida lurida</u>	13		14.5
<u>Tetraonyx fulvus</u>	14		16
<u>Zonitis atripennis flavida</u>	13		14.5
<u>Zonitis dunniana</u>	13		14.5

of activity were chosen for each species: (1) Initiation of crawling from cold-induced immobility; and (2) silk attachment by the phoretic species or the demonstration of a search pattern in the nonphoretic species. Three tests using 10 larvae per test were conducted on each of the species discussed.

The phoretic species (Nemognathinae) began crawling at 13 to 14°C, but moved no more than 2 to 4 cm in 24 hours. At 14.5 to 16°C these larvae made silk attachments with the anal pad and crawled about this point of attachment in a circumferential manner at the end of 1 to 2 cm of silk. At these temperatures triungulins of the species were able to make several silk attachments within 24 hours, moving a total of 10 to 30 cm. The extent of activity was measurable from tracks left on the kymograph paper.

Triungulins of Lytta mutilata, the single nonphoretic bee associate studied, began crawling at 13°C, but traveled no more than 3 cm in 24 hours. At 15°C typical spiral and zigzag search patterns were established, and the distance traveled reached 30 to 50 cm in 24 hours.

Two members of the genus Epicauta were tested with results similar to L. mutilata, but with activity occurring at what appears to be a slightly lower temperature. Normal spiral and zigzag search patterns were demonstrated at 13 to 14.5°C, with the larvae capable of traveling 30 plus cm in 24 hours.

#### Silk Spinning and Attachment to Host

The importance of silk production by the Nemognathinae has been speculated upon by numerous authors. However, little is known beyond the fact that members of this

subfamily do spin silk and that this behavior must relate to the ecology of the triungulin. It is probably of significance that silk production by first instar larvae is unknown elsewhere in the order Coleoptera, even in the Rhipiphoridae, some of which are also phoretic on bees.

The preliminary investigations reported here were designed to provide some clue to the significance of this unusual activity and to establish a suitable framework for further study. It was assumed that the silk serves either to insure larval attachment to the flower until transfer to a suitable host has been completed, or that the silken strand facilitates transfer of the triungulin to the host. A third premise, that the attachment of the larva to a silken strand might function in host selection, was considered least likely.

Phoretic triungulins spin silk when disturbed physically or as the result of vibration of the substrate. Initially, the active  $T_1$  larva pauses and deflexes the abdomen, bringing the anal pad in contact with the substrate. With this action a small drop of fluid is exuded from the anal pore. This fluid material hardens immediately at excretion, forming a secure point of silk attachment. The silken thread, which varies in diameter and is formed from this same clear, viscous liquid, is trailed out from the point of attachment as the larva crawls or falls away

(Fig. 2). When the larva reaches a second substrate to which it can cling securely, it breaks the thread at the anal pore and crawls away. The triungulins use the anal pad as a pygopod when walking on extremely smooth surfaces or when negotiating precarious substrates.

Nemognathine triungulins may be induced to spin silk in response to a negative electrostatic field produced by rubbing an ebonite rod with wool. When the charged rod is held near the larva and then slowly withdrawn, the larva makes a silk attachment to the substrate and begins spinning, continuing until it reaches the rod. Using this method triungulins can be induced to spin up to 12 cm of silk in an unbroken strand. However, following this or repeated stimulation they appear unable to spin again for an undetermined period of time. In order to induce silk spinning within an electrostatic field it appears that the substrate must possess certain physical characteristics. Although these requirements have not yet been determined, wax-coated paper cartons and flower surfaces are adequate.

Triungulins dislodged from a substrate can easily climb back up the silk thread by curling the body around, grasping the silk with their tarsal claws, and by using the anal pad as a pygopod on the thread. This process is very similar to horizontal locomotion in these species. When crawling back up the silk, some larvae will often

Fig. 2. Electron micrographs of the silk produced by  
triungulins of Nemognatha lurida lurida LeConte

A - several strands of silk showing observed  
variation in diameter and the attachment of  
a single strand to several others (X3500);  
B - attachment of the silk to a transparent  
substrate (X3500)

A



B

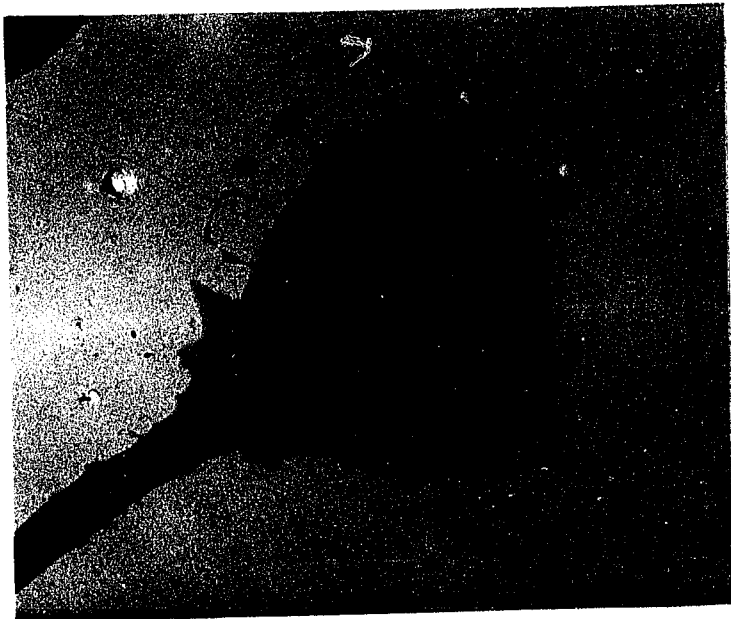


Fig. 2. Electron micrographs

grasp the silk between the lateral extension of the eighth abdominal segment and the abdominal wall.

#### Survival of Prefeeding Larvae

Longevity of the triungulins outside of a host cell (without pollen and nectar food material) is variable and directly related to climatic conditions in the case of the Meloinae, and to the physical condition of the flower in the Nemognathinae. Of the species studied, most survived for 6 to 10 days in the absence of food and moisture, but this period was extended up to 30 days with the provision of a 1:1 mixture of honey and de-ionized water in a cotton-stoppered vial. Since  $T_1$  larvae of both groups will drink when a suitable liquid is available, it is presumed that the availability of moisture in the soil or in a flower is a factor in survival. Generally, the phoretic species are affected by desiccation to a greater extent than the non-phoretic species. In view of the quantity of silk which a single triungulin is able to produce, a readily available source of moisture with some nutrient material may be necessary for silk spinning; especially if the presumptions of some authors (Beauregard, 1890; Parker and Böving, 1924; Hocking, 1949), that the silk is a product of the Malpighian tubules are correct.

Life History

## Meloinae

Egg.--Oviposition was not observed in the field. One egg mass of Lytta magister was found under a fallen saguaro cactus; no excavation was evident. Caged females of this species deposited single egg masses (Appendix G). Some attempted concealment of the eggs by ovipositing in crevices or under debris; others selected the surface of any available substrate. The eggs were lightly coated with a sticky secretion which appeared to bind them together. This secretion dried quickly and the eggs subsequently became scattered, probably the result of beetle activity in the crowded cage. After 24 hours they were fairly evenly distributed and mixed with soil and plant debris.

One female of Tegrodera erosa aloga was observed throughout oviposition. The subject remained motionless except for a wave of abdominal contractions which preceded each egg. Continued pressure displaced the entire egg mass rearward. Time required to deposit 252 eggs was 1.5 hours.

Time required for incubation in this subfamily is well in excess of that required for the Nemognathinae (Appendix G). Attempts to delay hatching by storage at

6 ± 3°C were only partially successful. Delay beyond five additional days resulted in almost total mortality.

Postembryonic Development.--Initially, all T<sub>1</sub> larvae ignored their provisions and exhibited a searching behavior within the rearing chamber. After a period of 12 to 18 hours the larvae descended to the food and subsequent growth was rapid. Early instars, T<sub>1</sub> to FG<sub>2-4</sub>, frequently burrow back and forth in the media while feeding, and it is probably this behavior which accounts for the high larval mortality on media high in moisture content.

Confinement of large numbers of T<sub>1</sub> larvae within a closed container appeared to increase mortality after 7 to 10 days. In order to further examine this phenomenon triungulins from five egg masses of Lytta magister were confined in an identical number of four-compartmented petri dishes, with a substantial quantity of pollen paste in each compartment. After 24 hours two larvae remained alive and after 36 hours only one survived in each dish--not in each compartment. All of the dead triungulins appeared unmarked, with no evidence of attack or cannibalism. The partitions in the dishes prevented the T<sub>1</sub> larvae from crossing over into another compartment, yet three compartments in each dish showed total mortality. The surviving FG larva in each dish actively sought out and consumed the

provisions of the other compartments. The five survivors developed normally and entered the coarctate phase.

Prior to ecdysis the triungulins crawled away from the provisions and attached to the side of the rearing chamber. During ecdysis the cuticle split first along the dorsal thoracic ecdysial line, and then along the epicranial line and a line of dehiscence involving several abdominal segments. After molting the larvae remained in the vicinity of the old exoskeleton for a period of 12 to 18 hours. Subsequent instars followed a similar molting behavior pattern. Mortality was usually low in the FG<sub>2-5</sub> instars (Appendix D).

Frequently one or more larval exuviae remained attached to the mid-ventral area of the abdomen of FG<sub>3-5</sub> larvae (Fig. 3). When dislodged, these often became mixed with the food or fecal material and were eaten. When disturbed, FG<sub>2-5</sub> larvae regurgitated dark brown fluids defensively, and worked their mandibles vigorously while swaying their heads from side to side. In an effort to induce molting to the coarctate, several FG<sub>5</sub> larvae of Lytta magister were released in terraria containing moist, sterile soil or sand. This effort actually delayed molting, probably because soil structure was unsuitable for cell formation. It was noted, however, that FG<sub>5</sub> larvae of

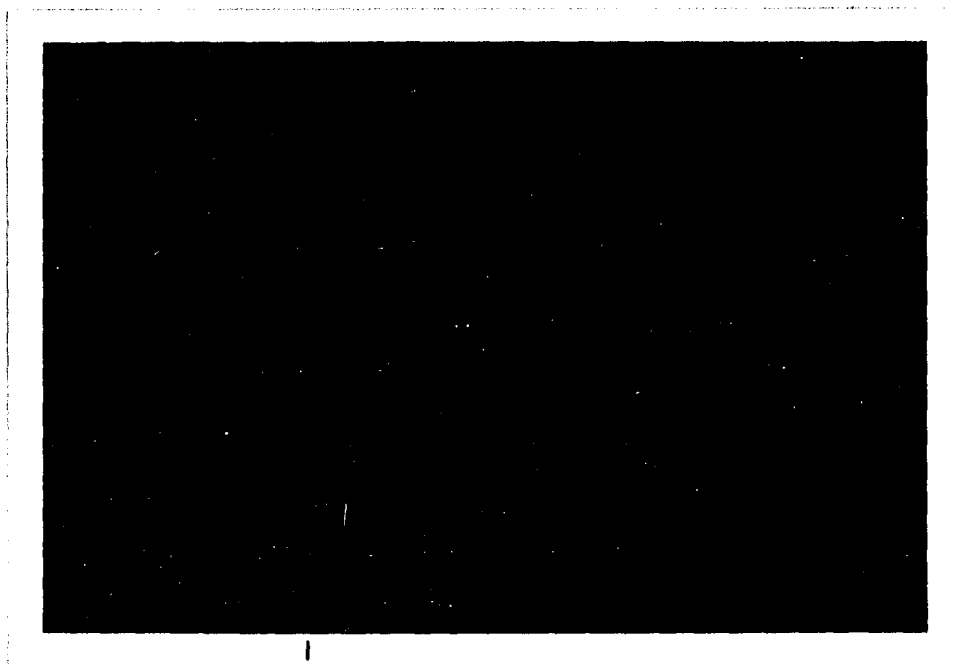


Fig. 3. FG<sub>3</sub> instar of Lytta magister Horn showing attached exuviae (X10)

L. magister are cannibalistic when in contact with other larvae of the species.

Cessation of feeding in the FG<sub>5</sub> instar (Fig. 4) usually did not occur until the total amount of food available was consumed (Table 3). The time interval between cessation of feeding and molting to the coarctate phase was variable and dependent in part upon the quantity of food provided. An excessive amount of food did not appear to prolong the FG<sub>5</sub> instar, but it did extend the feeding period until the time of molting to the coarctate.

Moisture loss in the FG<sub>5</sub> instar is apparently a prerequisite for molting to the coarctate; excessive moisture in the rearing chamber appeared to delay molting. Brown fluids were regurgitated, with an obvious decrease in body turgor and size. Larvae in cotton-stoppered tubes, using their mandibles and incorporating stomach fluids, worked the cotton fibers into a "cell". Some attempted to escape when the cotton plugs were separated by a distance greater than the approximate length of the fully formed coarctate.

The C larvae of the species studied possess a thick, heavily sclerotized, nontranslucent, brown to dark brown cuticle. In FG<sub>5</sub> exuviae are sloughed off and may or may not remain attached posteroventrally. The integumentary surface possessed rudimentary appendages and

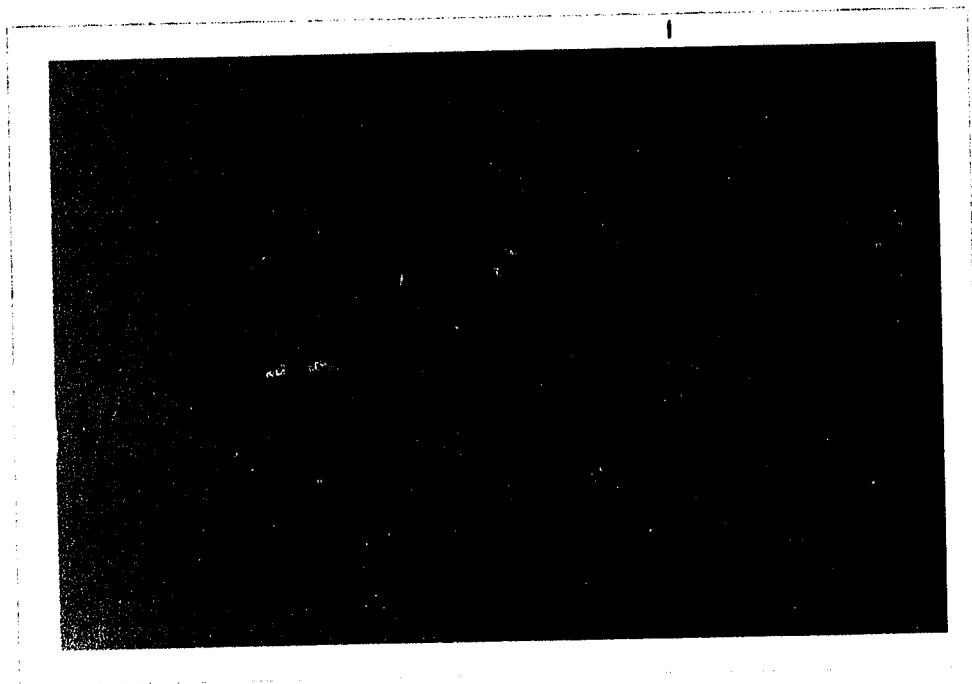


Fig. 4. FG<sub>5</sub> instar of Lytta magister Horn (X3)

spiracles, as well as a surface texture which appears to be characteristic of the species. All of the C larvae which failed to undergo maturation after one calendar year continue to survive at this writing.

Sixty days at  $6 \pm 3^\circ\text{C}$  were not sufficient to break larval diapause in the laboratory. Accelerated development, without diapause, did not occur at  $31 \pm 1/2^\circ\text{C}$ . Coarctate larvae of L. magister buried in the ground and subjected to the winter soil environment reached the adult stage between March 25 and April 23, in the second year. Diapause was followed by molting to the SG<sub>7</sub> larva, which appears morphologically similar to that of the FG instars with the exception of reduced sclerotization and rudimentary thoracic appendages. Pupation is preceded by an extension of the abdomen and the expansion and differentiation of the thorax. Eventually the spiny pupa becomes visible beneath the thin SG<sub>7</sub> cuticle, which ruptures dorsolaterally to expose the exarate pupa. A final molt produces the adult from within a final but very thin pupal cuticle.

The standard ontogenetic pattern, T<sub>1</sub> - FG<sub>2-5</sub> - C<sub>6</sub>, characterized immature development in all of the Meloinae studied. The mean length of the T<sub>1</sub> instar after feeding ranged from 2.3 to 3.3 days; the FG<sub>2</sub> instar from 1.1 to 2.7 days; the FG<sub>3</sub> instar from 1.3 to 1.9 days; the FG<sub>4</sub>

instar from 2.1 to 4.7; and the FG<sub>5</sub> instar from 12.3 to 34.7 days. The total number of days from initial feeding to formation of the coarctate varied from 21.2 to 43.0 days. Maturation in L. magister followed the pattern SG<sub>7</sub> - P<sub>8</sub> - A. None of the species of the Meloinae studied deviated from the standard pattern (Appendix E).

#### Nemognathinae

Egg.--Gravid females of all species studied oviposited readily in the laboratory. However, most egg masses used in this study were collected in the field. All species preferred to oviposit on the phyllaries of the host plant with the exception of Gnathium spp. which appear to prefer the face of the flower, and Zonitis dunniana which oviposits on the underside of the leaves. Oviposition by Tetraonyx fulvus was not observed in the field.

Females of several species, particularly Nemognatha nitidula frequently oviposited on buds or flowers of the wrong age. The young bud did not blossom before the triungulins had perished, or the flower was no longer attractive to bees and the triungulins never reached a nest. Apparently, triungulins stranded on an unattractive flower do not migrate to more suitable flowers nearby, even though they are accessible and within easy reach.

The eggs are coated with copious amounts of a sticky secretion which binds them together and serves to attach the mass to the flower or leaf. The number of eggs per mass is variable; accurate counts were not obtained for some species when counting would have destroyed the eggs. Most females were observed to deposit only a single mass. However, some went through two oviposition periods, during which they deposited an average number of eggs for the species (Appendix G). Nemognatha nitidula required 35 minutes to complete oviposition of approximately 200 eggs.

Incubation required from 6 to 11 days for all species studied (Appendix G). Attempts to delay hatching by storage at  $6 \pm 3^{\circ}\text{C}$  resulted in almost total mortality.

Postembryonic Development.--As in the Meloinae  $T_1$  larvae initially ignored the provisions in the rearing chamber and exhibited searching behavior, crawling continuously about the interior. After 18 to 36 hours they descended to the medium and began to feed. Triungulins usually fed with their head and most of their body immersed in the food material, with only the last two or three abdominal segments exposed.

In order to avoid injuring the  $T_1$  larvae the cotton stopper was used as a pickup device for transfer of the larvae to the vial. This practice usually resulted in the transfer of several individuals of the species to a single

vial. It was noted that these lived together for many days without observable antagonism or variation in behavior when compared with others introduced singly. Death of multiple larvae confined within a single vial was not immediate. Rather, it was progressive, without evidence of attack or cannibalism. On a single occasion the first of two triungulins of Zonitis dunniana molted to the FG<sub>2</sub> instar. On the day following the second T<sub>1</sub> attacked the FG<sub>2</sub> larva, feeding at the posterior end. After insuring the death of the larva the second triungulin molted two days later. No larvae of this species were reared successfully.

After a prolonged feeding period, triungulins crawl off the food material and attach to the side of the chamber before molting. The cuticle splits first along the dorsal thoracic ecdysial line and then along the epicrainial and abdominal sutures. First grub larvae, in all instars, remain near the exuviae for several hours before resumption of feeding activity. High first instar mortality is attributable to desiccation resulting from substrate moisture loss or from exposure to a dry atmosphere for prolonged periods. Drowning did not appear to be a factor in those species not molting successfully to the FG<sub>2</sub> instar, as the dead triungulins floated on the surface of substrate liquid and spiracular regions remained dry. Mortality in subsequent instars was minimal (Appendix D).

First grub larvae feed with their head and most of the abdomen immersed in the substrate and only the spiracles exposed. Subsequent instars appear buoyant (Fig. 5). Exuviae often remain attached to the tip of the abdomen and larvae have been observed to eat the exuviae on occasion. Attempts to induce the defensive or aggressive behavior patterns characteristic of the Meloinae failed. Unlike the Meloinae these first grub larvae exhibit diminished mobility in later instars; fully-developed FG<sub>5</sub> larvae lose the use of their legs as the result of obesity (Fig. 6). The length of the postfeeding period in the FG<sub>5</sub> instar is variable and dependent upon the quantity of food provided.

Moisture loss is a prerequisite to the formation of the coarctate, which is formed within the unbroken FG<sub>5</sub> larval skin. A reduction in turgidity and total volume follows the egestion of a dark brown, viscous material, which cements the FG<sub>5</sub> exuviae to the bottom or side of the chamber in the upright position. The coarctate is noticeably smaller than the FG<sub>5</sub> exuviae.

Molting to the second grub and subsequent pupal stage may occur within the unbroken FG<sub>5</sub> and C larval skins. However, the FG<sub>5</sub> exuviae usually split along a dorsal line and those of the coarctate along a ventral line of

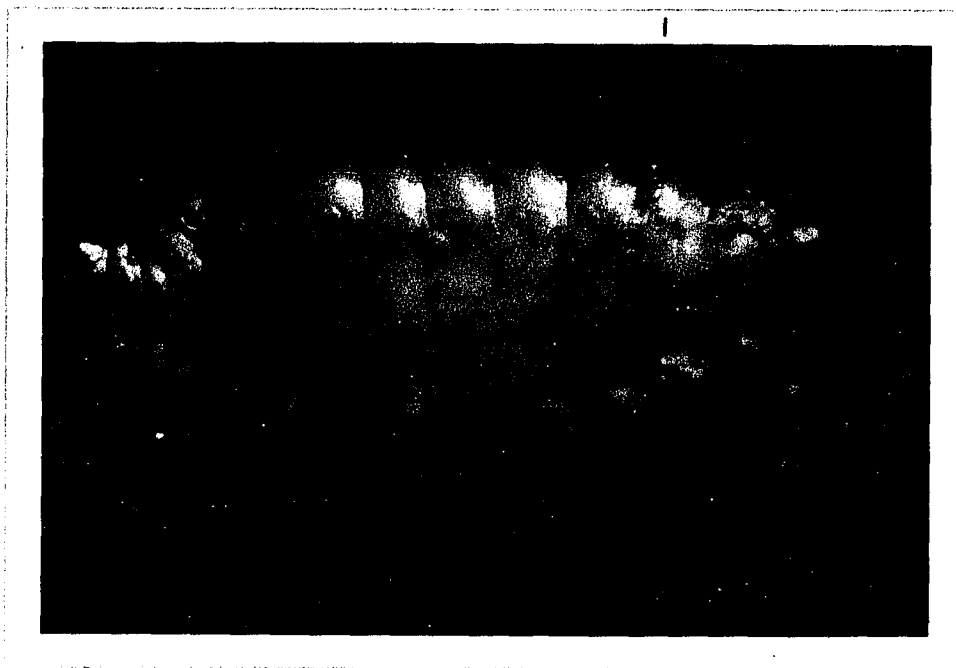


Fig. 5. FG<sub>3</sub> instar of *Nemognatha nitidula* Enns showing the typical feeding position of first grub nemognathine larvae (X40)

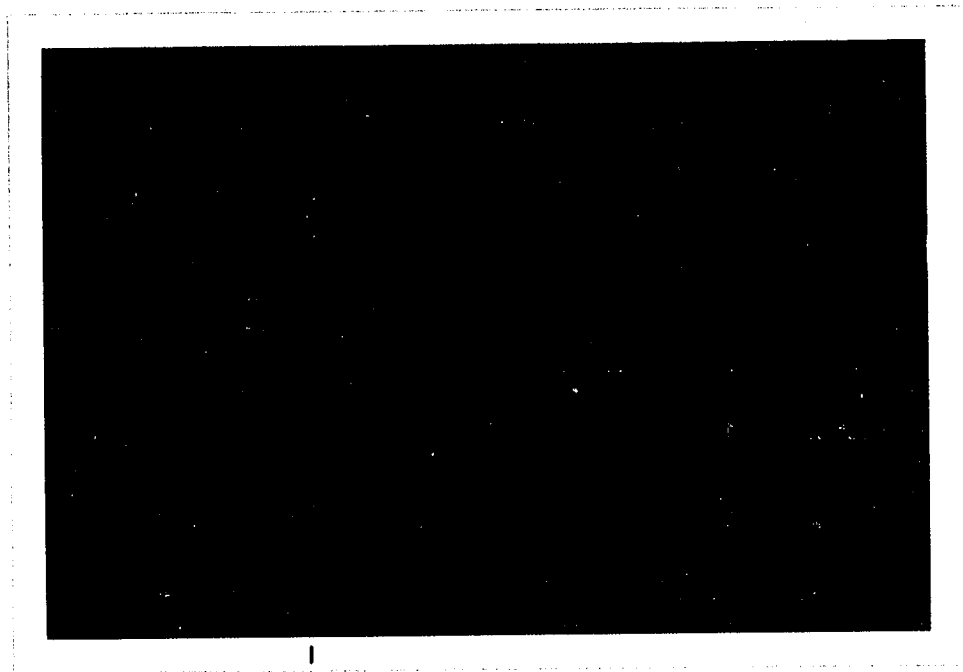


Fig. 6. FG<sub>5</sub> instar of Nemognatha nitidula Enns (X3)

dehiscence, partially exposing the SG<sub>7</sub> larva. Pupation occurs within the confines of the ruptured exuviae.

Two species of Nemognathinae were reared successfully to the adult stage (Appendix F). Approximately 10% of all Nemognatha nigripennis went into coarctate diapause. The remainder underwent accelerated development. Three generations occurred within six months. Diapause was not evident in this latter group even though all were maintained at  $31 \pm 1/2^\circ\text{C}$  throughout each life cycle including a brief coarctate phase. Accelerated development did not occur in any other species. A single generation of N. nitidula entered diapause, which was subsequently broken after 74 days at  $6 \pm 3^\circ\text{C}$ . Attempts to break diapause in this and all other species by subjecting them to 60 days at this same low temperature failed. Coarctate larvae of all species continue to survive, some after a full calendar year.

The effect of temperature on larval development was studied in two species of Nemognathinae, Nemognatha nigripennis and N. lurida lurida (Appendix H). Development in these species was most rapid at  $31 \pm 1/2^\circ\text{C}$ . Mortality was complete and feeding was not observed at constant temperatures above  $34 \pm 1/2^\circ\text{C}$  and below  $24 \pm 1/2^\circ\text{C}$ . However, development did occur in N. lurida lurida when the temperature was alternated for 12 hour periods between  $21 \pm 2^\circ$  and  $27 \pm 1/2^\circ\text{C}$ .

Development in all of the Nemognathinae studied followed the standard ontogenetic pattern, T<sub>1</sub> - FG<sub>2-5</sub> - C<sub>6</sub> - SG<sub>7</sub> - P<sub>8</sub> - A, without deviation. The mean length of the feeding T<sub>1</sub> instar ranged from 8.5 to 18.9 days; the FG<sub>2</sub> instar from 2.2 to 8.0 days; the FG<sub>3</sub> instar from 1.9 to 8.0 days; the FG<sub>4</sub> instar from 2.0 to 8.0; and the FG<sub>5</sub> instar from 7.7 to 15.3 days. The total number of days from initial feeding to formation of the coarctate varied from 21.9 to 44.5 days (Appendix F).

Adult host plant and collection data for all species studied during these investigations are summarized in Appendix B.

## DISCUSSION AND CONCLUSIONS

These investigations show conclusively that pollen plus a liquid, probably nectar, is the primary food material of the meloid species studied and probably for all bee-associated Meloidae. Other food materials tested were either rejected by all species or proved to be nutritionally inadequate, resulting in dwarfism and increased mortality. Eggs or larvae of the host species may be consumed; however, these are not essential as feeding stimuli, for molting, or for development. When given a choice the larvae studied preferred a pollen and honey medium.

Analysis of the data obtained seems to indicate that some meloid larvae prefer or are dependent upon the pollen of specific plants, while others might well be classified as general feeders. The nonphoretic species appear to be rather nonspecific with regard to the pollen source. Lichtenstein (1879), Beauregard (1890), Cros (1924), Selander (1960), Selander and Mathieu (1964), and Pinto and Selander (1969) were all successful in rearing species of the Meloinae on unidentified pollen obtained from honey bees. The quantity of food necessary for maturation in the larger species, together with the observation that these may be cannibalistic and are able

to develop on a variety of materials including the eggs or larvae of bees, supports the hypothesis that the largest meloids are general feeders. Considering the host-seeking behavior of the nonphoretic species and the fact that the  $T_1$  larvae must find suitable provisions within walking distance, it is difficult to imagine the existence of a high level of host specificity in this group.

Some phoretic species are nonspecific pollen feeders, while others appear to be quite specific. Larvae of the genus Nemognatha developed readily on pollen obtained from honey bees, while those of Gnathium, Tetraonyx and some Zonitis did not. In view of this and the fact that the addition of honey bee larvae did not induce feeding or molting to  $FG_2$  larvae, it is assumed that the pollen provided came from unacceptable plant species. The failure of these species to feed or develop on the pollen provided may be the result of the presence of an unacceptable fraction in the provisions or the absence of an adequate quantity of pollen from a certain host plant species. Analysis of existing records indicates that adults of these species have a narrow host plant preference:

Tetraonyx fulvus is known only from Sphaeralcea spp.;  
G. minimum from Helianthus spp.; G. obscurum from Aplopappus gracilis, Aster parrulus, and Baileya multiradiata, all Compositae; Z. dunniana from blossoms of Chrysothamnus,

Baileya, Verbesina, and Sideranthus in the Compositae, and Eriogonum in the Polygonaceae, and Z. punctipennis from Helianthus spp.

The effects of diet in quantity and substance are evident in the length of the interstadial period as well as in the size of the mature larva or adult. The wide variation in size evident in field collected adults of the large, nonphoretic species of Meloinae appears to be a manifestation of the quantity of food consumed (Fig. 7.

Both the age and the source of the pollen must be considered when analyzing these and previous results obtained from laboratory rearing of meloids. Utilization of pollen stored for long periods, even at below freezing temperatures, results in high mortality, particularly in the  $T_1$  instar. Best results are obtained from pollen no more than three months old. This probably explains the difficulty encountered by some workers in rearing meloids and some of the inconsistencies reported.

Throughout all stages of development moisture is a primary factor in survival. Inadequate moisture in food material, substrate or atmosphere quickly induced mortality in all species studied. It was noted, however, that the nonphoretic species survived and developed in an optimum moisture range far below that of the Nemognathinae. Conditions favorable for one consistently proved fatal to the

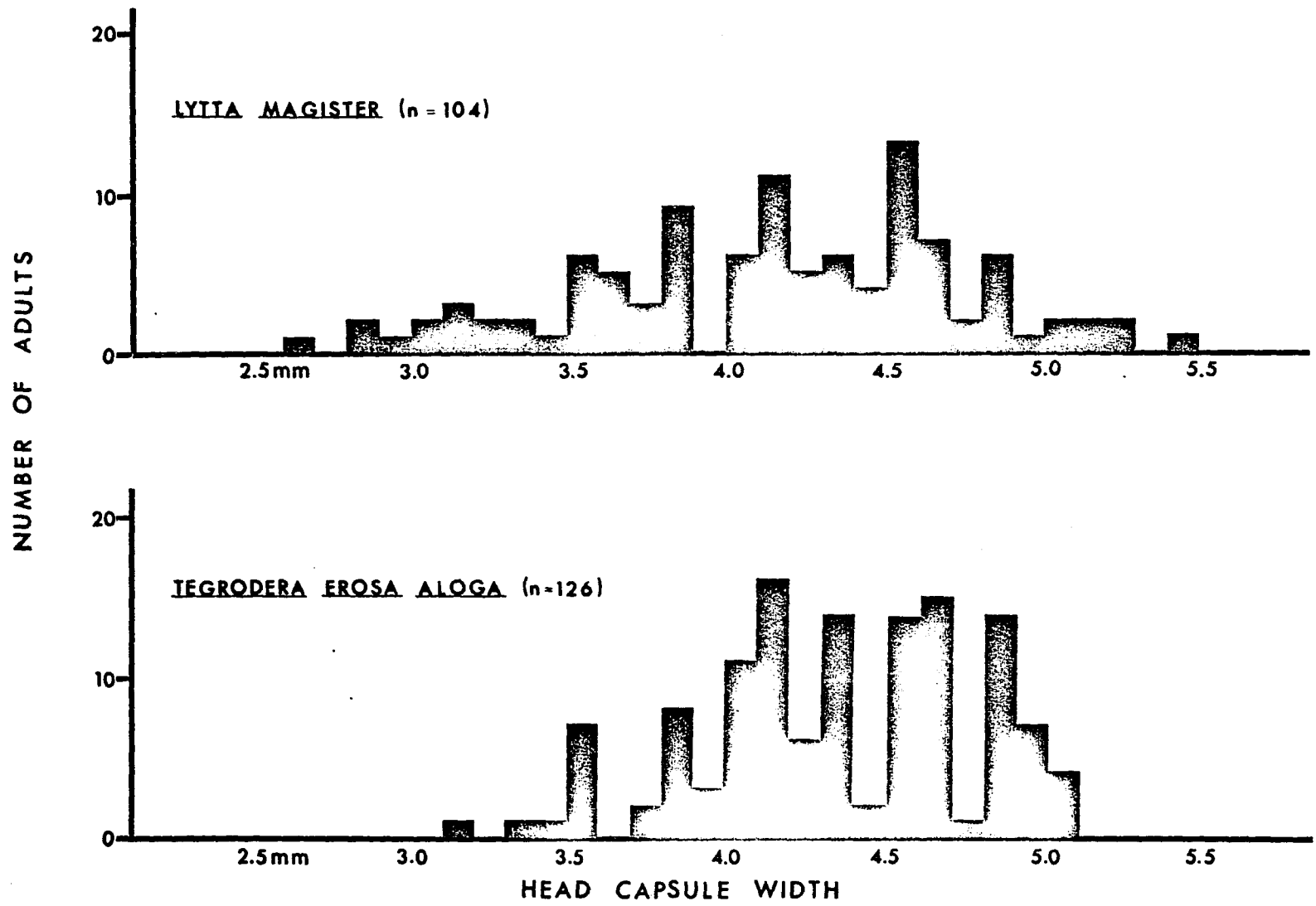


Fig. 7. Variation in adult head capsule width of two species of the Meloidae

other. Within either of these two groups, the physical conditions of moisture which proved to be optimum for one species appeared to be suitable for the remainder of the group tested.

Numerous gravid females of all species listed in Appendix B, as well as of other groups, both phoretic and nonphoretic, were collected and brought to the laboratory. Frequently many, and sometimes all, females failed to oviposit in the presence of fresh blossoms of the host plant which were renewed daily. It was noted that of those which failed to oviposit, abdomens previously distended with eggs became less distended, finally approximating normal or less than normal size prior to death. Near the end of the first season of study, gravid females of Lytta mutilata, Pyrota akhurstiana and P. palpalis were permitted to reach these limits of water loss and then provided with free water in a cotton-stoppered vial. These already stupefied individuals sought out the water source immediately, drank to repletion and distention, and proceeded to oviposit within 24 to 48 hours. It is of interest to note further that females of Tegrodera erosa aloga oviposited in the presence of available free water.

Entire egg masses frequently shriveled and failed to develop. Once detected, efforts to halt this trend with free water droplets, paper or cotton saturated with water,

were futile. It is assumed that these egg masses were deposited by females possessing a water deficit, although other factors may have influenced viability.

Moisture and free water availability seem most critical in the early larval stages, becoming progressively less significant in advanced stages. As previously noted, a high moisture level is most critical in the Nemognathinae. On the other hand, larvae of the nonphoretic groups will drown in the quantities of water required for nemognathine development. Prolonged exposure to a dry atmosphere will induce mortality in most stages of nemognathine larval development. However, this effect of atmosphere is negligible in the nonphoretic groups, particularly during later instars. The effect of moisture on the coarctate forms of both groups has not yet been determined and few observations have been made, however, it too appears to be negligible.

Larvae of all instars and of both subfamilies are capable of limiting the growth of fungi within the rearing chamber. Even with the addition of mold inhibitor to the food material, mold still develops in the absence of but not in the presence of the larva. This was also noted by Selander and Mathieu (1964). Undoubtedly, this ability is significant in the survival of the larvae in the host nest, especially in the Nemognathinae, which have an

extended feeding period in the  $T_1$  instar. Early instars are unable to penetrate fungal mats.  $FG_{4-5}$  larvae are not so inhibited.

Triungulins of the Meloinae are probably active throughout the day and night. The low temperature activity thresholds established for the species studied are well below the soil temperatures characteristic of the developmental period (Table 4). It is likely that the triungulins would have to escape the high daytime surface soil temperatures common in the spring and summer in southern Arizona. Thus, high rather than low temperatures are likely to be responsible for limiting host-seeking activity. Environmental moisture is a significant factor in the ability of the triungulin to remain active during high temperature periods.

The effects of temperature and environmental moisture on the activity of first instar larvae of the Nemognathinae are probably only indirect in that their influence is probably manifested in the flight activity of the bee host; the larva remains near the nectar source until a bee visits the flower. Based on the quantity of silk produced, these larvae probably consume some nectar for survival and perhaps for the production of silk.

Larvae of both subfamilies are positively phototactic. This phototaxis in the phoretic species enables

the larvae to move from the leaves or the phyllaries to the petals or anthers of the flower. It may also be phototaxis which prevents the triungulins from leaving an unattractive bud or dead flower, and crawling down the rachis or stem and back up to another flower.

Positive phototaxis in the nonphoretic species probably enables the triungulin to locate areas of sparse vegetation, typical of bee nesting sites (Stephen et al., 1969), and then to locate the burrow entrances through shadow contrast; an easily demonstrated ability of these species. In the laboratory, triungulins exhibit digging behavior in cracks and crevices as well as at the juncture of a shadow and a bright background.

Triungulins of both subfamilies are positively thermotactic at low temperatures and negatively thermotactic at high temperatures. Phoretic  $T_1$  larvae attach distally on petals and anthers during the cooler early morning and evening hours. However, during the day these larvae retreat deep inside the flower and emerge only when it is disturbed by a visiting insect.

Triungulins are stimulated by substrate vibrations. Nonphoretic species become excited and exhibit digging behavior. Phoretic species immediately make a silk attachment and assume a grasping pose, wielding their tarsal claws and balancing on the abdominal pad. It is possible

that nonphoretic species are capable of detecting the subterranean activity of bees with the caudal filaments. Nonphoretic species ignore available provisions and exhibit host-seeking behavior until within 3 cm of a food source. Since there frequently is a pile of pollen near the entrance of an active burrow, this behavior may prevent the investigation of inactive or improperly provisioned nests.

Stephen et al. (1969) report the occurrence of an odor of fermentation around the nest of certain wild bees. The role of this phenomenon in nest location by meloids is unknown. However, there is no indication that meloid triungulins react to odors.

Oviposition obviously relates to larval host selection in the species considered. Those species which oviposit on particular plants or in or near host nests probably have a narrow host range. Conversely, random oviposition, as it occurs in Lytta magister and Tegrodera erosa aloga, points toward either a broad host range or a host species which is somewhat gregarious to semisocial in nesting habit, or perhaps a combination of both.

This theory is further strengthened by consideration of beetle size and quantity of food consumed. Few species of bees, if any, would provide a sufficient amount of food material in a single preprovisioned cell for the large species of meloids; rather, multiple cells and

perhaps multiple host species would seem to be implicated. A further consideration is that of restricted migratory habits of adult populations, coupled with the greatly reduced flight range of gravid females and the low migratory potential of the triungulin. These facts indicate that the large populations of meloids frequently observed occur in close proximity to their respective host populations.

The prefeeding behavior of the triungulin in the cell appears to be a mechanism for finding and destroying competitors. However, the bee egg or larva is not essential for molting or development. Developmental rates, particularly in the Meloinae, appear maximal in all feeding instars, and it is difficult to imagine that these could be shortened with other food materials. Larvae of the Nemognathinae undergo an extended period in the T<sub>1</sub> instar before feeding and molting and it is conceivable that ecdysis might be hastened by the addition of an egg or larva of the host. However, in light of the moisture requirements and morphological adaptations (spiracles located on evaginations of the pleura on the eighth abdominal segment) of the Nemognathinae, it seems probable that the delay period represents a developmental adaptation to allow time for capping of the cell and stabilization of the food moisture content, and possibly fermentation of the provisions.

Once a suitable environment (food and moisture) has been established, the rate of development is controlled by temperature. As indicated by the soil temperature data in Appendix I, developmental rates during the spring and summer months should approximate those observed in the laboratory. The postfeeding period in the FG<sub>5</sub> instar is likely to be variable and dependent upon the amount of food available. Tests have shown that the larvae tend to consume all available food before molting to the coarctate. Cannibalism has been noted among members of both subfamilies, but particularly in the Meloinae. The effect of this carnivorous behavior on surviving bee or meloid larvae and on immatures of other parasites has not been determined.

Loss of water is a prerequisite for molting to the coarctate in both subfamilies. It is possible that, in the Meloinae, regurgitation of these fluids enables the FG<sub>5</sub> larvae to construct a resting cell in the soil, whereas in the Nemognathinae these fluids are defecated and serve to cement the FG<sub>5</sub> exuviae, containing the coarctate and subsequent instars, to the interior of the bee cell. During this period the larva is always oriented with the head pointed in the direction of emergence.

In the Meloinae the second grub stage closely resembles the FG larva except for the absence of heavy

sclerotization and reduced motor appendages. The pupa is exarate. The coarctate and subsequent instars in the Nemognathinae usually occur inside of the FG<sub>5</sub> exuviae. However, not infrequently SG larval activity ruptures the FG<sub>5</sub> exuviae ventrally and that of the coarctate dorsally. Normal development as it occurs in both subfamilies conforms to the standard ontogenetic pattern for the Meloidae; T<sub>1</sub> - FG<sub>2-5</sub> - C<sub>6</sub> - SG<sub>7</sub> - P - A. Variation in the number of molts reported by some authors may have been nutritionally or thermally induced. The size of the adult of any species is probably controlled by the quantity of food consumed. Wide variation in the size of field collected adults should serve as an indicator of multiple host species. Laboratory rearing consistently produced unusually large adults in both subfamilies.

Diapause was broken after 74 days at  $6 \pm 3^{\circ}\text{C}$  followed by a return to  $31 \pm 1/2^{\circ}\text{C}$ , but not after only 60 days at this temperature. Soil temperature data (Appendix I) indicate that the length of the cold period ranges from approximately 75 to 90 days in southern Arizona. At least one species, Nemognatha nigripennis, did not enter diapause at  $31 \pm 1/2^{\circ}\text{C}$ , and it is likely that it passes through two to three generations in a season.

APPENDIX A

HOST ASSOCIATIONS OF BEE-ASSOCIATED MELOIDAE  
INCLUDING SOME OLD WORLD SPECIES

A: Host associations of bee-associated Meloidae including some old world species

Meloid	Host	Family Code <sup>a</sup>	Source
Meloinae			
Meloini			
<u>Meloe autumnalis</u> <sup>b</sup>	<u>Andrena meloella</u> Perez	And.	Pinto and Selander, 1969
<u>M. barbarus</u>	<u>Anthophora pacifica</u> Cresson	Ant.	MacSwain, 1956
<u>M. cavensis</u> <sup>b</sup>	<u>Anthophora acervorum</u> (Linnaeus)	Ant.	Pinto and Selander, 1969
	<u>A. nigrocincta</u> Lepeletier	Ant.	Pinto and Selander, 1969
	<u>A. pennanta</u> Lepeletier	Ant.	Pinto and Selander, 1969
<u>M. cicatricosus</u> <sup>b</sup>	<u>Anthophora retusa</u> (Linnaeus)	Ant.	Pinto and Selander, 1969
	<u>A. acervorus</u> (Linnaeus)	Ant.	Pinto and Selander, 1969
	<u>A. parietina</u> (Fabricius)	Ant.	Pinto and Selander, 1969
<u>M. erythrocnemis</u> <sup>b</sup>	<u>Chalicodoma muraria</u> (Retzius)	Meg.	Pinto and Selander, 1969
<u>M. foveolatus</u> <sup>b</sup>	<u>Osmia saundersi</u> Vachal	Meg.	Pinto and Selander, 1969

Host associations continued

Meloid	Host	Family Code <sup>a</sup>	Source
<u>M. franciscanus</u>	<u>Anthophora edwardsii</u> Cresson	Ant.	Linsley and MacSwain, 1941
<u>M. niger</u>	<u>Colletes fulgidus</u> Swenk	Col.	Pinto and Selander, 1969
<u>M. opacus</u>	<u>Colletes fulgidus</u> Swenk	Col.	MacSwain, 1956
<u>M. tuccius</u> <sup>b</sup>	<u>Anthophora rhododactyla</u> Perez	Ant.	Pinto and Selander, 1969
<u>M. variegatus</u> <sup>b</sup>	<u>Anthophora femorata</u> (Olivier)	Ant.	Pinto and Selander, 1969
<u>M. violaceus</u> <sup>b</sup>	<u>Panurgus dentipes</u> Latreille	And.	Pinto and Selander, 1969

Lyttini

Eupomphina

Cysteodemus armatus      Osmia sp.      Meg.      MacSwain, 1956

Lyttina

Lytta chloris      Anthophora linsleyi  
Timberlake      Ant.      Linsley and MacSwain, 1942b

L. melaena      Diadasia bituberculata  
(Cresson)      Ant.      Linsley and MacSwain, 1952b

Host associations continued

Meloid	Host	Family Code <sup>a</sup>	Source
<u>L. moerens</u>	<u>Anthophora stanfordiana</u> Cresson	Ant.	Linsley and MacSwain, 1942b
	<u>Colletes fulgidus</u> Swenk	Col.	MacSwain, 1956
<u>L. occipitalis</u>	<u>Anthophora linsleyi</u> Timberlake	Ant.	Linsley and MacSwain, 1942b
<u>L. purpurascens</u>	<u>Anthophora linsleyi</u> Timberlake	Ant.	Linsley and MacSwain, 1942b
<u>L. stygica</u>	<u>Anthophora linsleyi</u> Timberlake	Ant.	Linsley and MacSwain, 1942b
<u>L. tenebrosa</u>	<u>Anthophora linsleyi</u> Timberlake	Ant.	Linsley and MacSwain, 1942b
<u>L. variabilis</u>	<u>Ptilothrix sumichrasti</u> (Cresson)	Api.	Linsley, MacSwain, and Smith, 1956
<u>L. vesicatoria</u> <sup>b</sup>	<u>Colletes</u> sp.	Col.	Selander, 1960
Nemognathinae			
Nemognathini			
Zonitina			
<u>Gnathium nitidum</u> Horn	<u>Perdita luteola</u> Cockerell <sup>c</sup>	And.	Bohart (new record), 1959

Host associations continued

Meloid	Host	Family Code <sup>a</sup>	Source
<u>Pseudozonitis maculicollis</u>	<u>Melissodes</u> sp.	Ant.	MacSwain, 1956
<u>Zonitis atripennis flavida</u>	<u>Nomia m. melanderi</u> Cockerell	Hal.	Selander and Bohart, 1954
<u>Z. immaculata</u> <sup>b</sup>	<u>Anthidium manicatum</u> (Linnaeus)	Meg.	Selander and Bohart, 1954
	<u>Anthocopa longispina</u> (Perez)	Ant.	Selander and Bohart, 1954
	<u>Hoplitis (?) cavigena</u> (Perez)	Meg.	Selander and Bohart, 1954
	<u>H. morawitzi</u> (Gerstaecker)	Meg.	Selander and Bohart, 1954
	<u>H. tridentata</u> (Dufour and Perris)	Meg.	Selander and Bohart, 1954
	<u>Icterantheidium (?) bellicosum</u> (Lepelletier)	Meg.	Selander and Bohart, 1954
	<u>I. discoidale</u> (Latreille)	Meg.	Selander and Bohart, 1954
	<u>Megachile muraria</u> (Retzius)	Meg.	Selander and Bohart, 1954
	<u>Osmia pseudoaurulenta</u> Dours	Meg.	Selander and Bohart, 1954
	<u>Osmia</u> sp.	Meg.	Selander and Bohart, 1954
<u>Z. praeusta</u> <sup>b</sup>	<u>Anthidium</u> sp.	Meg.	Selander and Bohart, 1954
	<u>Anthocopa longispina</u> (Perez)	Ant.	Selander and Bohart, 1954

Host associations continued

Meloid	Host	Family Code <sup>a</sup>	Source
	<u>A. saundersi</u> (Vachal)	Ant.	Selander and Bohart, 1954
	<u>Icteranthidium</u> (?) <u>bellicosum</u> (Lepeletier)	Meg.	Selander and Bohart, 1954
	<u>Megachile sericans</u> Fonscolombe	Meg.	Selander and Bohart, 1954
	<u>Megachile</u> sp.	Meg.	Selander and Bohart, 1954
	<u>Osmia pseudoaurulenta</u> Dours	Meg.	Selander and Bohart, 1954
	<u>Osmia</u> sp.	Meg.	Selander and Bohart, 1954
	<u>Paranthidiellum</u> <u>lituratum scapulare</u> (Latreille)	Meg.	Selander and Bohart, 1954
<u>Zonitis</u> sp. <sup>b</sup>	<u>Colletes daviesanus</u> var. <u>signatus</u> Verhoeff	Col.	Beauregard, 1890
<u>Z. sayi</u>	<u>Nomia</u> sp.	Hal.	Enns, 1956
<u>Z.</u> sp.	<u>Osmia</u> sp.	Meg.	Riley, 1877
Nemognathina			
<u>Hornia boharti</u>	<u>Anthophora linsleyi</u> Timberlake	Ant.	Linsley, 1942; Linsley and MacSwain, 1942a,b
	<u>A. stanfordiani</u> Cresson	Ant.	Linsley, 1942; Linsley and MacSwain, 1942a,b

Host associations continued

Meloid	Host	Family Code <sup>a</sup>	Source
<u>H. minutipennis</u>	<u>Anthophora abrupta</u> Say	Ant.	Riley, 1877; Rau, 1926, 1930
	<u>A. bomboides bomboides</u> Kirby	Ant.	Linsley, 1942
	<u>A. occidentalis</u> Cresson	Ant.	Mickel, 1928
	<u>A. stanfordian</u> Cresson	Ant.	Linsley, 1942
	<u>A. bomboides sodalis</u> Cresson	Ant.	Hocking, 1949
<u>H. mexicana blomi</u>	<u>Anthophora marginata</u> Smith	Ant.	MacSwain, 1958
<u>H. m. neomexicana</u>	<u>Anthophora bomboides</u> <u>neomexicana</u> Cockerell	Ant.	MacSwain, 1958; Hicks, 1926
	<u>A. occidentalis</u> Cresson	Ant.	Wellman, 1911; Williams and Hungerford, 1914; Mickel, 1928
	<u>A. vallorum</u> (Cockerell)	Ant.	MacSwain, 1958
<u>Cissites auricu-</u> <u>lata</u> <sup>b</sup>	<u>Xylocopa brazilianorum</u> (Linnaeus)	Ant.	Bianchi, 1962
	<u>X. fimbriata</u> Fabricius	Ant.	Bianchi, 1962
<u>Horia maculata</u> <sup>b</sup>	<u>X. aeneipennis</u> DeGeer	Ant.	Selander and Bouseman, 1960
<u>Nemognatha hurdi</u>	<u>Melissodes robustior</u> Cockerell	Ant.	Linsley and MacSwain, 1952a

Host associations continued

Meloid	Host	Family Code <sup>a</sup>	Source
<u>N. lurida</u> <u>apicalis</u>	<u>Anthophora linsleyi</u> Timberlake	Ant.	Linsley and MacSwain, 1942b
	<u>Melissodes</u> sp.	Ant.	Linsley and MacSwain, 1952a
<u>N. lurida lurida</u>	<u>Anthophora occidentalis</u> Cresson	Ant.	Mickel, 1928
	<u>Megachile occidentalis</u> Fox	Meg.	Linsley and MacSwain, 1952a
<u>N. lutea dichroa</u>	<u>Anthophora occidentalis</u> Cresson	Ant.	Enns, 1956
	<u>Melissodes mysops</u> Cockerell	Ant.	Linsley and MacSwain, 1952a
<u>N. lutea dubia</u>	<u>Anthidium emarginatum</u> (Say)	Meg.	Davidson, 1907
	<u>Megachile montivaga</u> Cresson	Meg.	Linsley and MacSwain, 1952a
<u>N. nigripennis</u>	<u>Anthidiellum erhorni</u> (Cockerell)	Meg.	MacSwain, 1956
	<u>Ashmeadiella</u> sp.	Meg.	Werner, Enns, and Parker, 1966
	<u>Calliopsis coloradensis</u> Cresson <sup>c</sup>	And.	Rust and Bohart (new record), 1965
	<u>Dianthidium</u> sp.	Meg.	MacSwain, 1956
	<u>Hoplitis biscutellae</u> (Cockerell)	Meg.	Enns, 1956

Host associations continued

Meloid	Host	Family Code <sup>a</sup>	Source
	<u>Megachile brevis</u> Say	Meg.	Linsley and MacSwain, 1952a
	<u>M. pratti</u> Cockerell	Meg.	Linsley and MacSwain, 1952a
<u>N. pallens</u>	<u>Anthocopa</u> sp.	Meg.	Linsley and MacSwain, 1952a
<u>N. piazzata bicolor</u>	<u>Anthophora occidentalis</u> Cresson	Ant.	Porter, 1951; Linsley and MacSwain, 1952a
<u>N. scutellaris</u>	<u>Alcidamea</u> sp.	Meg.	Linsley and MacSwain, 1952a
	<u>Anthophora linsleyi</u> Timberlake	Ant.	Linsley and MacSwain, 1942b
	<u>Ashmeadiella</u> sp.	Meg.	Linsley and MacSwain, 1952a
	<u>Callanthidium illustre</u> (Cresson)	Meg.	Linsley and MacSwain, 1952a
	<u>Hoplitis producta</u> (Cresson)	Meg.	Davidson, 1907
	<u>H. sambuci</u> Titus	Meg.	Linsley and MacSwain, 1952a
	<u>H. uvulalis</u> (Cockerell)	Meg.	Linsley and MacSwain, 1952a
	<u>Osmia laeta</u> Sandhouse	Meg.	Linsley and MacSwain, 1952a
	<u>O. lignaria</u> Say	Meg.	Linsley and MacSwain, 1952a
	<u>O. pikei</u> Cockerell	Meg.	Linsley and MacSwain, 1952a

Host associations continued

Meloid	Host	Family Code <sup>a</sup>	Source
	<u>Osmia</u> sp.	Meg.	Linsley and MacSwain, 1952a
	<u>Xylocopa</u> (? <u>orpifex</u> Smith)	Ant.	Davidson, 1907
<u>Tricrannia sanguinipennis</u>	<u>Colletes rufithorax</u> Swenk	Col.	Parker and Böving, 1924
	<u>C. inaequalis</u> Say	Col.	Parker and Böving, 1924
<u>T. stansburyi</u>	<u>Anthidium edwardsii</u>	Meg.	Linsley and MacSwain, 1951
	<u>Anthophora edwardsii</u> Cresson	Ant.	Linsley and MacSwain, 1951
	<u>Hoplitis cylindrica</u> (Cresson)	Meg.	Hicks, 1926
	<u>H. densa</u>	Meg.	Hicks, 1926
	<u>H. producta</u> (Cresson)	Meg.	Hicks, 1926
	<u>Osmia densa pogonigera</u> Cockerell	Meg.	Linsley and MacSwain, 1951

<sup>a</sup>And. - Andrenidae, Ant. - Anthophoridae, Api. - Apidae, Col. - Colletidae, Hal. - Halictidae, Meg. - Megachilidae. Taxonomy after Stephen, Bohart, and Torchio (1969).

<sup>b</sup>Old World, Central, and South American species.

<sup>c</sup>Specimens returned to Dr. G. E. Bohart, Wild Bee Investigations Laboratory, USDA, Logan, Utah.

APPENDIX B  
COLLECTION RECORDS

B: Collection records

	Date	Host Plant <sup>a</sup>	Location
<u>Meloe laevis</u> Leach	8/13/68	<u>Zexmenia podocephala</u> Gray	Parker Canyon Lake, Arizona
<u>Pyrota akhurstiana</u> Horn	7/28/69	<u>Caragana</u> sp.	Tucson, Arizona
	7/28/69	<u>Parkinsonia</u> sp.	Tucson, Arizona
<u>Pyrota postica</u> LeConte	7/26/68	<u>Larrea divaricata</u> Cav.	20 mi. S.E. Tucson, (Pantano) Arizona
	9/17/68	<u>Gutierrezia</u> sp.	Coyote Mtns., Arizona
<u>Cysteodemus armatus</u> LeConte	3/08/68	<u>Cryptantha angustifolia</u> (Torr.) Greene	Yuma, Arizona
<u>Eupompha elegans</u> (LeConte)	3/17/68	Compositae	S. of Yuma, Arizona
<u>Phodaga alticeps</u> LeConte	4/26/68	<u>Coldenia palmeri</u> Gray	Yuma, Arizona
<u>Pleurospasta mirabilis</u> Horn	4/28/68	<u>Amaranthus palmeri</u> Wats.	Yuma, Arizona
<u>Tegrodera erosa aloga</u> (Skinner)	5/02/69	<u>Ambrosia deltoidea</u> (torr.) Payne	Tucson, Arizona
	5/02/69	<u>Baileya pleniradiata</u> Haw & Gray	Tucson, Arizona
	5/12/68	<u>Beta vulgaris</u> (sugarbeet)	Marana, Arizona

## Collection records continued

	Date	Host Plant <sup>a</sup>	Location
	6/09/69	<u>Cryptantha barbiger</u> (Gray) Greene	Tucson, Arizona
	6/09/69	<u>Eriastrum diffusum</u> (Gray) Mason	Tucson, Arizona
	6/09/69	<u>Hymenoclea pentalepis</u> Rydb.	Tucson, Arizona
	6/09/69	<u>Solanum rostratum</u> Dunal.	Tucson, Arizona
<u>Lytta auriculata</u> Horn	3/16/68	<u>Calycoseris wrightii</u> Gray	S. of Kofa Mtns., Arizona
	4/11/68	<u>Calycoseris wrightii</u> Gray	Tucson, Arizona
	3/16/68	<u>Lesquerella gordonii</u> (Gray) Wats.	S. of Kofa Mtns., Arizona
	3/16/68	<u>Mirabilis bigelovii</u> Gray	S. of Kofa Mtns., Arizona
	3/16/68	<u>Phacelia crenulata</u> Torr.	S. of Kofa Mtns., Arizona
	3/16/68	<u>Sphaeralcia emoryi</u> var. <u>arida</u> (Rose)	S. of Kofa Mtns., Arizona
<u>Lytta biguttata</u> LeConte	9/04/69	<u>Helianthus</u> sp.	Bonita, Arizona
<u>Lytta magister</u> Horn	4/04/68	<u>Encelia farinosa</u> Gray	Tucson, Arizona
	3/24/68	<u>Eriophyllum lanosum</u> Gray	Olberg, Arizona
	3/21/68	<u>Phacelia distans</u> Benth.	Tucson, Arizona
	3/21/68	<u>P. coerulea</u> Greene	Tucson, Arizona

## Collection records continued

	Date	Host Plant <sup>a</sup>	Location
	3/21/68	<u>Plantago insularis</u> Eastw.	Tucson, Arizona
	4/05/68	<u>Pluchea sericea</u> (Nutt.) Coville	Tucson, Arizona
<u>Gnathium minimum</u> (Say)	8/24/68	<u>Helianthus</u> sp.	Sonoita, Arizona
	8/25/68	<u>Aster parvulus</u> Blake	Willcox Playa, Arizona
	8/09/69	<u>Helianthus</u> sp.	Lynndyl, Utah
<u>Gnathium obscurum</u> MacSwain	8/27/69	<u>Halpopappus gracilis</u> (Nutt.) Gray	Sonoita, Arizona
<u>Nemognatha lurida</u>	8/09/69	<u>Helianthus</u> sp.	Lynndyl, Utah
<u>apicalis</u> LeConte	7/08/69	<u>Helianthus</u> sp.	Marana, Arizona
<u>Nemognatha lurida</u>	7/15/69	<u>Helianthus</u> sp.	5 mi. N. Tucson, Arizona
<u>lurida</u> LeConte	8/27/69	<u>Helianthus</u> sp.	Sonoita, Arizona
	9/04/69	<u>Helianthus</u> sp.	Bonita, Arizona
<u>Nemognatha lutea</u> <u>lutea</u> LeConte	6/07/69	<u>Cirsium undulatum</u> (Nutt.) Spreng.	Morrison, Colorado
<u>Nemognatha meropa</u> Enns	3/16/68	<u>Lesquerella gordonii</u> (Gray/Wats.)	S. of Kofa Mtns., Arizona
	3/16/68	<u>Goraea canescens</u> TdG.	S. of Kofa Mtns., Arizona
<u>Nemognatha nigripennis</u> LeConte	5/11/69	<u>Haplopappus spinulosus</u> (Pursh) DC	Tucson, Arizona

Collection records continued

	Date	Host Plant <sup>a</sup>	Location
<u>Nemognatha nitidula</u> Enns	4/14/68	<u>Cirsium wheeleri</u> (Gray) P	Sabino Canyon, Arizona
<u>Pseudozonitis brevis</u> Enns	6/15- 20/68	U.V. light	Tucson, Arizona
<u>Tetraonyx fulvus</u> LeConte	8/08/68	<u>Sphaeralcea</u> sp.	Willcox Playa, Arizona
<u>Zonitis atripennis</u> <u>flavida</u> (Say)	7/27/68	<u>Wislizenia refracta</u> Engelm.	Willcox Playa, Arizona
	8/24/68	<u>Wislizenia refracta</u> Engelm.	Willcox Playa, Arizona
	8/08/69	<u>Helianthus</u> sp.	11 mi. S. of Sunizona, Arizona
<u>Zonitis dunniana</u> Casey	9/04/69	<u>Chrysothamnus</u> sp.	Bonita, Arizona
	8/25/68	<u>Hymenothrix wislizeni</u> Gray	Coyote Mtns., Arizona
<u>Zonitis punctipennis</u> (LeConte)	8/24/69	Compositae	Charleston, Arizona
Nemognathinae sp. (eggs)	8/27/69	<u>Helianthus</u> sp.	Sonoita, Arizona

<sup>a</sup>These records include only those where feeding or oviposition was observed.

## APPENDIX C

### COMPOSITION OF HAYDAK'S MIXTURE<sup>a</sup>

360 pounds	soy bean flour
120 pounds	dried brewers yeast
120 pounds	dried skim milk
120 pounds	dried meat scraps

Mix a small quantity of dry material with liquid consisting of:

30 percent	(by weight)	levulose
20 percent		dextrose
50 percent		de-ionized water

Mix to desired consistency.

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<sup>a</sup>Haydak (1968)

APPENDIX D

FEEDING SCHEDULE AND RESULTANT MORTALITY OCCURRING  
IN THE SPECIES OF MELOIDAE STUDIED

## D-1. Feeding schedule for the species of Meloidae studied

	Group	Diet	
		Pollen Type	Preparation of source <sup>a</sup>
<u>Lytta magister</u>	A	C	P, H, & MI
	B	C	P, H, & MI <sup>b</sup>
	C	OH	washed pollen & H <sub>2</sub> O
<u>Lytta mutilata</u>	A	C	P, H, & MI
	B	C	P, H, MI, & Pl Karawaite <sup>®</sup>
<u>Pleurospasta mirabilis</u>		C	P, H, & MI
<u>Pyrota akhurstiana</u>		B	P, H, MI, & Pl
<u>Pyrota postica</u>		B	P, H, MI, & Pl
<u>Tegrodera erosa aloga</u>	A	B	P, H, & MI
	B	C	P, H, & MI <sup>b</sup>
			Karawaite <sup>®</sup> Haydak's Mix.
<u>Gnathium minimum</u>	A	A	P, H, MI, & Pl
	B	B	P, H, MI, & Pl
	C	C	P, H, MI, & Pl
	D		provisions of <u>Chalicodoma occidentalis</u>
<u>Gnathium obscurum</u>	A	A	P, H, MI, & Pl
	B	B	P, H, MI, & Pl

D-1 continued

	Group	Diet	
		Pollen Type	Preparation of source <sup>a</sup>
	C	C	P, H, MI, & P1
	D	provisions of <u>Chalicodoma occidentalis</u>	
<u>Nemognatha lurida apicalis</u>	A	A	P, H, MI, & P1
	B	B	P, H, MI, & P1
	C	C	P, H, MI, & P1
<u>Nemognatha lurida lurida</u>	A	A	P, H, MI, & P1
	B	B	P, H, MI, & P1
	C	C	P, H, MI, & P1
	D	provisions of <u>Chalicodoma occidentalis</u>	
	E		Karawaite <sup>®</sup>
	F		Haydak's Mix
<u>Nemognatha lutea lutea</u>	A	A	P, H, MI, & P1
	B	B	P, H, MI, & P1
	C	C	P, H, MI, & P1
	D	provisions of <u>Chalicodoma occidentalis</u>	
	E		Karawaite <sup>®</sup>
	F		Haydak's Mix
<u>Nemognatha nitidula</u>	A	A	P, H, MI, & P1
	B		Karawaite <sup>®</sup>
	C		Haydak's Mix

## D-1 continued

	Group	Diet	
		Pollen Type	Preparation of source <sup>a</sup>
<u>Pseudozonitis brevis</u>	A	C	P, H, MI, & Pl
<u>Tetraonyx fluvis</u>	A	C	P, H, MI, & Pl
<u>Zonitis atripennis</u> <u>flavida</u>	A	C	P, H, MI, & Pl
	B		Karawaite <sup>®</sup>
	C		Haydak's Mix
<u>Zonitis dunniana</u>	A	A	P, H, MI, & Pl
	B	B	P, H, MI, & Pl
	C	C	P, H, MI, & Pl
	D		provisions of <u>Chalicodoma</u> <u>occidentalis</u>
<u>Zonitis punctipennis</u>	A	A	P, H, MI, & Pl
	B		provisions of <u>Chalicodoma</u> <u>occidentalis</u>
<u>Nemognathinae sp.</u>	A	A	P, H, MI, & Pl

<sup>a</sup>P - pollen, H - honey, MI - mold inhibitor,  
Pl - micro-drop of honey (pool)

<sup>b</sup>Inadequate quantity of food provided for development of normal-sized mature larvæ.

D-2: Resultant mortality occurring in species of Meloidae studied:

	Number T <sub>1</sub> larvae fed	Percent mortality post-fed T <sub>1</sub> instar	Maximum length of T <sub>1</sub> instar on media (days)	Percent total mortality to C instar
<u>Lytta magister</u>	128	3.1	8	6.3
	82	35.4	7	36.6
	82	46.6	8	80.5
<u>Lytta mutilata</u>	16	43.8	7	62.5
	25	100	-	-
	25	100	2	-
<u>Pleurospasta mirabilis</u>	35	100	-	-
<u>Pyrota akhurstiana</u>	25	100	3	-
<u>Pyrota postica</u>	5	40.0	3	100
<u>Tegrodera erosa aloga</u>	50	46.0	8	78.0
	35	0.0	8	40.0
	25	48.0	19	100
	25	52.0	15	100

## D-2 continued

	Number T <sub>1</sub> larvae fed	Percent mortality post-fed T <sub>1</sub> instar	Maximum length of T <sub>1</sub> instar on media (days)	Percent total mortality to C instar
<u>Gnathium minimum</u>	25	100	2	-
	25	100	2	-
	25	100	2	-
	25	100	2	-
<u>Gnathium obscurum</u>	25	100	2	-
	25	100	2	-
	25	100	2	-
	25	100	2	-
<u>Nemognatha lurida</u>	25	52	17	52
<u>apicalis</u>	25	44	20	48
	25	84	9	88
<u>Nemognatha lurida</u>	50	48	22	54
<u>lurida</u>	75	46.7	28	57.3
	35	60.0	35	71.4

## D-2 continued

	Number $T_1$ larvae fed	Percent mortality post-fed $T_1$ instar	Maximum length of $T_1$ instar on media (days	Percent total mortality to C instar
	25	100	10	-
	25	100	2	-
	25	100	4	-
<u>Nemognatha lutea</u> <u>lutea</u>	25	68	21	72
<u>Nemognatha nigripennis</u>	25	20	25	68
	85	71.8	13	94.1
	25	76	29	96.1
	25	100	21	-
	25	100	11	-
	25	100	9	-
<u>Nemognatha nitidula</u>	125	28.8	18	67.2
	25	100	6	-
	25	100	13	-
<u>Pseudozonitis brevis</u>	60	41.7	13	10

## D-2 continued

	Number T <sub>1</sub> larvae fed	Percent mortality post-fed T <sub>1</sub> instar	Maximum length of T <sub>1</sub> instar on media (days)	Percent total mortality to C instar
<u>Tetraonyx fluvus</u>	75	100	18	-
<u>Zonitis atripennis</u>	66	94.1	30	97.5
<u>flavida</u>	25	100	3	-
	25	100	7	-
<u>Zonitis dunniana</u>	100	99	13	100
	25	100	10	-
	25	100	31	-
	25	96	11	100
<u>Zonitis punctipennis</u>	75	100	6	-
	25	100	8	-
Nemognathinae sp.	10	60	20	90

APPENDIX E

LENGTH OF INSTARS AND HEAD CAPSULE WIDTH  
(LARVAL INSTARS 2-5) OF THE SPECIES  
OF MELOINAE STUDIED

E-1: Length of instars and head capsule width (larval instars 2-5) of Lytta magister reared at  $31 \pm 1/2^\circ\text{C}$

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
Group A								
eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)	3.3	0.08	2-6	124	-	-	-	-
FG <sub>2</sub>	1.7	0.07	1-4	121	0.69	0.02	0.6-0.8	10
FG <sub>3</sub>	1.9	0.05	1-4	120	1.12	0.02	0.9-1.4	10
FG <sub>4</sub>	2.1	0.06	1-4	120	2.14	0.03	1.9-2.3	10
FG <sub>5</sub>	16.5	0.11	10-22	58	3.15	0.07	2.8-3.3	10
Total to C	25.9	0.45	17-31	58	-	-	-	-
C	261.7	2.55	251-287	15	-	-	-	-
SG <sub>7</sub>	27.3	1.20	23-38	13	-	-	-	-
P	22.6	1.82	7-35	13	-	-	-	-
Group B								
eclosion to feeding	3	-	-	-				

## E-1 continued

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
T <sub>1</sub> (on food)	2.7	0.125	2-7	50				
FG <sub>2</sub>	2.5	0.06	1-3	50				
FG <sub>3</sub>	1.8	0.09	1-3	51				
FG <sub>4</sub>	3.0	0.10	2-5	54				
FG <sub>5</sub>	21.9	0.39	16-26	30				
Total to C	32.1	0.33	27-36	30				
C	270.5	2.95	244-287	8				
SG <sub>7</sub>	34.3	6.77	21-43	3				
P	22	-	-	1				
Group C								
eclosion to feeding	3	-	-	-				
T <sub>1</sub> (on food)	3.6	0.19	2-8	43				
FG <sub>2</sub>	2.6	0.15	1-5	36				
FG <sub>3</sub>	5.0	0.53	1-11	21				
FG <sub>4</sub>	7.2	0.58	1-12	17				

## E-1 continued

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
FG <sub>5</sub>	14.0	0.43	10-17	16				
Total to C	31.8	0.53	27-36	16				
C	-	-	-	-				
SG <sub>7</sub>	-	-	-	-				
P	-	-	-	-				

E-2: Length of instars and head capsule width (larval instars 2-5) of Lytta mutilata reared at  $31 \pm 1/2^\circ\text{C}$

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
eclosion to feeding	8	-	-	-	-	-	-	-
T <sub>1</sub> (on food)	3.3	0.22	2-4	9	-	-	-	-
FG <sub>2</sub>	1.1	0.33	1-2	9	0.53	0.02	0.5-0.6	9
FG <sub>3</sub>	1.7	0.22	1-3	9	0.92	0.11	0.8-1.1	9
FG <sub>4</sub>	3.0	0.38	1-5	9	1.76	0.04	1.6-2.0	8
FG <sub>5</sub>	12.3	0.71	10-15	6	3.01	0.15	2.6-3.8	8
Total to C	21.2	0.79	19-25	6	-	-	-	-

E-3: Length of instars and head capsule width (larval instars 2-5) of Pyrota postica reared at  $31 \pm 1/2^\circ\text{C}$

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)	2.3	0.27	2-3	3	-	-	-	-
FG <sub>2</sub>	2.7	0.54	2-4	3	-	-	-	-
FG <sub>3</sub>	1.3	0.27	1-2	3	0.83	-	-	1
FG <sub>4</sub>	4.7	0.27	4-5	3	1.43	0.07	1.4-1.6	3
FG <sub>5</sub>	-	-	-	-	2.50	0.05	2.4-2.6	3
Total to C	-	-	-	-	-	-	-	-

E-4: Length of instars and head capsule width (larval instars 2-5) of Tegrodera  
erosa aloga reared at  $31 \pm 1/2^\circ\text{C}$

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
Group A								
eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)	2.8	0.16	1-4	27	-	-	-	-
FG <sub>2</sub>	1.5	0.11	1-3	26	0.66	0.14	0.5-0.8	27
FG <sub>3</sub>	1.6	0.10	1-2	26	1.33	0.21	1.2-1.5	22
FG <sub>4</sub>	2.3	0.12	1-3	26	2.29	0.30	2.1-2.5	11
FG <sub>5</sub>	34.7	1.99	21-44	11	3.38	0.52	3.2-3.5	11
Total to C	43.0	2.07	29-52	11	-	-	-	-
Group B								
eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)	3.7	0.24	2-8	35	-	-	-	-
FG <sub>2</sub>	2.0	0.17	1-6	35	0.70	0.03	0.6-0.9	28
FG <sub>3</sub>	2.3	0.13	1-4	35	1.18	0.01	1.1-1.4	35
FG <sub>4</sub>	3.0	0.14	1-5	35	1.91	0.03	1.7-2.3	35

## E-4 continued

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
FG <sub>5</sub>	35.7	1.46	27-53	21	2.43	0.04	2.2-2.9	35
Total to C	46.5	1.32	39-66	21	-	-	-	-
Group C eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)	6.9	1.32	3-19	13	-	-	-	-
FG <sub>2</sub>	2.6	0.22	2-4	10	0.65	0.01	0.6-0.8	12
FG <sub>3</sub>	5.9	0.32	4-7	10	1.02	0.02	1.0-1.2	10
FG <sub>4</sub>	6.9	0.95	3-10	8	1.54	-	-	1
FG <sub>5</sub>	-	-	-	-	2.19	0.07	2.1-2.3	4
Total to C	-	-	-	-	-	-	-	-
Group D eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)	7.6	1.02	3-16	12	-	-	-	-
FG <sub>2</sub>	3.2	0.29	2-5	10	0.64	0.01	0.5-0.8	13
FG <sub>3</sub>	4.1	0.13	4-5	8	1.01	0.02	1.0-1.1	10

E-4 continued

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
FG <sub>4</sub>	4.3	0.48	3-5	4	1.55	0.02	1.5-1.6	10
FG <sub>5</sub>	30.0+	-	-	1	2.17	0.05	1.9-2.3	8
Total to C	-	-	-	-	-	-	-	-

APPENDIX F

LENGTH OF INSTARS AND HEAD CAPSULE WIDTH  
(LARVAL INSTARS 2-5) OF THE SPECIES  
OF NEMOGNATHINAE STUDIED

F-1. Length of instars and head capsule width (larval instars 2-5) of Nemognatha lurida apicalis reared at  $31 \pm 1/2^\circ\text{C}$

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
Group A								
eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)	11.4	0.82	9-17	12	-	-	-	-
FG <sub>2</sub>	2.3	0.13	2-3	12	0.23	0.01	0.2-0.3	12
FG <sub>3</sub>	2.3	0.18	1-3	12	0.40	0.01	0.4-0.5	12
FG <sub>4</sub>	2.2	0.17	1-3	10	0.74	0.01	0.7-0.8	12
FG <sub>5</sub>	15.3	0.83	10-19	10	1.15	0.02	1.1-1.2	12
Total to C	33.6	1.47	26-43	10	-	-	-	-
Group B								
eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)	13.7	0.87	8-20	14	-	-	-	-
FG <sub>2</sub>	2.5	0.22	1-4	13	0.23	-	-	14
FG <sub>3</sub>	2.2	0.22	1-3	13	0.42	0.01	0.4-0.5	13
FG <sub>4</sub>	2.9	0.24	2-4	13	0.76	0.01	0.7-0.8	13

## F-1 continued

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
FG <sub>5</sub>	12.8	0.71	9-19	13	1.13	0.02	1.1-1.2	13
Total to C	33.8	1.31	28-45	13	-	-	-	-
Group C eclosion to feeding	3	-		-	-	-	-	-
T <sub>1</sub> (on food)	8.0	0.41	7-9	4	-	-	-	-
FG <sub>2</sub>	3.8	0.85	2-6	4	0.23	-	-	4
FG <sub>3</sub>	2.3	0.34	2-3	3	0.39	-	-	4
FG <sub>4</sub>	2.7	0.34	2-3	3	0.77	-	-	3
FG <sub>5</sub>	17	0.58	16-18	3	1.13	0.02	1.1-1.2	3
Total to C	33	0.58	32-34	3	-	-	-	-

F-2: Length of instars and head capsule width (larval instars 2-5) of Nemognatha lurida lurida reared at  $31 \pm 1/2^\circ\text{C}$

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
Group A								
eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)	12.5	0.59	8-19	26	-	-	-	-
FG <sub>2</sub>	2.3	0.15	2-5	23	0.29	0.01	0.2-0.3	26
FG <sub>3</sub>	2.2	0.13	1-4	22	0.49	0.01	0.4-0.6	23
FG <sub>4</sub>	3.1	0.23	1-5	21	0.83	0.02	0.7-1.0	23
FG <sub>5</sub>	11.2	0.37	7-14	21	1.49	0.02	1.4-1.5	21
Total to C	31.7	0.73	26-38	23	-	-	-	-
Group B								
eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)	10.7	0.50	5-18	40	-	-	-	-
FG <sub>2</sub>	2.2	0.14	1-5	33	0.29	0.01	0.2-0.3	40
FG <sub>3</sub>	2.4	0.14	2-5	33	0.52	0.01	0.4-0.6	33
FG <sub>4</sub>	2.8	0.16	2-5	32	0.83	0.01	0.7-0.9	33

F-2 continued

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
FG <sub>5</sub>	10.2	0.33	6-13	31	1.49	0.01	1.4-1.5	32
Total to C	28.3	0.48	22-32	32	-	-	-	-
Group C eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)	11.9	0.56	8-16	14	-	-	-	-
FG <sub>2</sub>	2.3	0.16	2-4	14	0.25	0.01	0.2-0.3	14
FG <sub>3</sub>	2.0	0.11	1-3	14	0.52	0.2	0.4-0.6	14
FG <sub>4</sub>	2.0	0.11	1-3	14	0.85	0.23	0.8-1.0	14
FG <sub>5</sub>	11.6	0.64	9-16	10	1.45	1.1	1.5	14
Total to C	29.6	0.37	25-38	10	-	-	-	-

F-3: Length of instars and head capsule width (larval instars 2-5) of Nemognatha lutea lutea reared at  $31 \pm 1/2^\circ\text{C}$

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)	15	1.36	10-21	8	-	-	-	-
FG <sub>2</sub>	2.6	0.43	2-5	7	0.19	0.01	0.2-0.2	7
FG <sub>3</sub>	2.2	0.26	1-3	7	0.40	0.01	0.4-0.5	7
FG <sub>4</sub>	2.0	-	-	7	0.87	0.07	0.8-1.2	6
FG <sub>5</sub>	8.7	0.36	7-10	7	1.52	0.01	1.5-1.6	7
Total to C	30.6	1.38	22-37	7	-	-	-	-

F-4: Length of instars and head capsule width (larval instars 2-5) of Nemognatha nigripennis reared at  $31 \pm 1/2^\circ\text{C}$

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
Group A								
eclosion to feeding	-	-	-	-	-	-	-	-
T <sub>1</sub> (on food)	12.1	0.55	9-19	20	-	-	-	-
FG <sub>2</sub>	2.7	0.20	2-4	18	0.15	-	-	20
FG <sub>3</sub>	1.9	0.13	1-3	18	0.32	0.01	0.3-0.5	18
FG <sub>4</sub>	2.5	0.23	1-5	18	0.67	0.02	0.5-0.8	17
FG <sub>5</sub>	14.9	1.07	8-21	13	1.26	0.02	1.1-1.4	17
Total to C	34.1	0.98	29-39	13	-	-	-	-
C	9.6	2.92	3-24	7	-	-	-	-
SG <sub>7</sub>	4.3	0.28	3-5	7	-	-	-	-
P	6.0	0.44	4-7	7	-	-	-	-
Adult	8.8	1.76	3-15	8	-	-	-	-

## F-4 continued

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
Group B								
eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)	15.8	0.86	10-25	24	-	-	-	-
FG <sub>2</sub>	3.7	0.27	2-5	11	0.15	-	-	18
FG <sub>3</sub>	2.5	0.18	2-3	10	0.39	0.01	0.3-0.5	10
FG <sub>4</sub>	3.4	0.41	2-6	9	0.65	0.02	0.5-0.8	5
FG <sub>5</sub>	20	3.38	7-34	10	1.21	0.04	1.1-1.5	11
Total to C	41.6	3.20	26-63	12	-	-	-	-
C	17	12.25	1-53	4	-	-	-	-
SG <sub>7</sub>	4	0.37	3-5	6	-	-	-	-
P	6.2	0.59	4-7	5	-	-	-	-
Adult	19.6	2.39	12-27	5	-	-	-	-
Group C								
eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)	12.7	1.28	7-16	6	-	-	-	-
FG <sub>2</sub>	2.3	0.24	2-3	4	0.14	0.01	0.1-0.2	6

F-4 continued

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
FG <sub>3</sub>	2	-	-	2	0.35	0.01	0.3-0.4	4
FG <sub>4</sub>	2	1.00	1-3	2	0.62	-	-	2
FG <sub>5</sub>	9.5	2.50	7-12	2	1.12	0.04	1.1-1.2	2
Total to C	28.5	1.50	27-30	2	-	-	-	-
C	2	-	-	1	-	-	-	-
SG <sub>7</sub>	2	-	-	1	-	-	-	-
P	7	-	-	1	-	-	-	-
Adult	13	-	-	1	-	-	-	-

F-5: Length of instars and head capsule width (larval instars 2-5) of Nemognatha nitidula reared at  $31 \pm 1/2^\circ\text{C}$

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
Group A								
eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)	9.7	0.26	5-18	96	-	-	-	-
FG <sub>2</sub>	2.2	0.08	1-4	73	0.16	0.01	0.1-0.2	21
FG <sub>3</sub>	2.1	0.08	1-4	76	0.38	0.01	0.3-0.5	74
FG <sub>4</sub>	2.2	0.10	1-4	75	1.09	0.01	0.8-1.4	82
FG <sub>5</sub>	7.7	0.70	4-12	80	1.85	1.01	1.7-2.3	83
Total to C	21.9	0.27	17-27	84	-	-	-	-
Interim period	60	-	-	-	-	-	-	-
Cold temperature period	74	-	-	20	-	-	-	-
Post diapause to adult	59	0.43	43-69	20	-	-	-	-

## F-5 continued

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
Group B								
eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)			pollen diet		-	-	-	-
FG <sub>2</sub>			pollen diet		-	-	-	-
FG <sub>3</sub>	3.3	0.16	3-4	8	-	-	-	-
FG <sub>4</sub>	8.0	0.48	7-9	4	0.90	0.03	0.8-1.0	9
FG <sub>5</sub>	-	-	-	-	1.47	0.04	1.3-1.5	7
Total to C	-	-	-	-	-	-	-	-
Group C								
eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)			pollen diet		-	-	-	-
FG <sub>2</sub>			pollen diet		-	-	-	-
FG <sub>3</sub>			pollen diet		-	-	-	-
FG <sub>4</sub>	4.3	1.31	2-8	4	-	-	-	-
FG <sub>5</sub>	14.5	2.50	12-17	2	1.52	0.03	1.5-1.6	5
Total to C	-	-	-	-	-	-	-	-

F-5 continued

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
Group D eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)			pollen diet		-	-	-	-
FG <sub>2</sub>			pollen diet		-	-	-	-
FG <sub>3</sub>	1.9	0.23	1-3	10	-	-	-	-
FG <sub>4</sub>	2.7	0.34	2-3	3	0.98	0.03	0.5-1.1	9
FG <sub>5</sub>	-	-	-	-	1.48	0.02	1.4-1.5	3
Total to C	-	-	-	-	-	-	-	-
Group D eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)			pollen diet		-	-	-	-
FG <sub>2</sub>			pollen diet		-	-	-	-
FG <sub>3</sub>			pollen diet		-	-	-	-
FG <sub>4</sub>	2.2	0.27	1-4	13	-	-	-	-
FG <sub>5</sub>	20.7	1.77	13-27	9	1.79	0.01	1.7-1.9	13
Total to C	34.8	1.82	27-41	9	-	-	-	-

F-6. Length of instars and head capsule width (larval instars 2-5) of Pseudozonitis brevis reared at  $31 \pm 1/2^\circ\text{C}$

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)	8.5	0.33	6-13	29	-	-	-	-
FG <sub>2</sub>	4.2	0.64	1-11	15	0.28	0.01	0.2-0.3	24
FG <sub>3</sub>	3.1	0.33	2-5	8	0.42	0.01	0.4-0.5	8
FG <sub>4</sub>	6.3	1.06	4-12	7	0.78	0.04	0.6-0.9	5
FG <sub>5</sub>	11.3	1.82	6-20	6	1.40	0.07	1.10-1.5	6
Total to C	32.7	2.17	25-38	6	-	-	-	-

F-7: Length of instars and head capsule width (larval instars 2-5) of Zonitis atripennis flavida reared at  $31 \pm 1/2^\circ\text{C}$

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
eclosion to feeding	3	-	-	-	-	-	-	-
T <sub>1</sub> (on food)	18.9	1.63	11-30	9	-	-	-	-
FG <sub>2</sub>	8	0.63	1-4	5	0.11	0.01	0.1-0.1	8
FG <sub>3</sub>	7	-	-	4	0.46	0.05	0.3-0.6	5
FG <sub>4</sub>	5.3	0.5	5-6	4	0.96	-	-	3
FG <sub>5</sub>	8	1.68	3-10	4	1.08	0.04	1.0-1.2	3
Total to C	44.5	2.33	40-49	4	-	-	-	-
Adult	143	-	-	1	-	-	-	-

F-8. Length of instars and head capsule width (larval instars 2-5) of *Nemognathinae* sp. reared at  $31 \pm 1/2^\circ\text{C}$

	Length of Instar (days)				Head Capsule Width (mm)			
	$\bar{x}$	$s_{\bar{x}}$	Range	N	$\bar{x}$	$s_{\bar{x}}$	Range	N
eclosion to feeding	5	-	-	-	-	-	-	-
T <sub>1</sub> (on food)	17.3	-	13-20	4	-	-	-	-
FG <sub>2</sub>	4	-	-	1	0.23	-	-	3
FG <sub>3</sub>	8	-	-	1	0.38	-	-	-
FG <sub>4</sub>	8	-	-	1	0.83	-	-	-
FG <sub>5</sub>	8	-	-	1	1.20	-	-	-
Total to C	42	-	-	1	-	-	-	-

APPENDIX G

PHYSICAL CHARACTERISTICS OF EGGS AND LENGTH OF  
INCUBATION PERIOD FOR THE SPECIES  
OF MELOIDAE STUDIED

G-1. Physical characteristics of eggs for the species of Meloidae studied:

	Egg color	Egg length (mm)	Length to diameter ratio	Adhesive coating
<u>Lytta magister</u>	yellow to orange	1.65	5-1	minimal
<u>Lytta mutilata</u>	pale yellow	1.50	5-1	minimal
<u>Pleurospasta mirabilis</u>	yellow to orange	1.50	4-1	minimal
<u>Pyrota akhurstiana</u>	pale yellow	1.20	4-1	minimal
<u>Pyrota postica</u>	pale yellow	1.20	4-1	minimal
<u>Tegrodera erosa aloga</u>	yellow to orange	1.65	5-1	minimal
<u>Gnathium minimum</u>	yellow to orange	0.7	3-1	copious
<u>Gnathium obscurum</u>	yellow to orange	0.7	3-1	copious
<u>Nemognatha lurida lurida</u>	yellow to orange	0.75	3-1	copious

## G-1 continued

	Egg color	Egg length (mm)	Length to diameter ratio	Adhesive coating
<u>Nemognatha lutea lutea</u>	yellow	0.75	3-1	copious
<u>Nemognatha nigripennis</u>	pale yellow	0.7	3-1	copious
<u>Nemognatha nitidula</u>	white and yellow	1.0	3-1	copious
<u>Pseudozonitis brevis</u>	opaque, yolk visible	0.8	3-1	copious
<u>Tetraonyx fluvus</u>	pale yellow	0.7	3-1	moderate
<u>Zonitis atripennis flavida</u>	pale yellow	0.94	3-1	copious
<u>Zonitis dunniana</u>	yellow	1.0	3-1	moderate
<u>Zonitis punctipennis</u>	yellow	0.9	3-1	moderate
Nemognathinae sp.	pale yellow	0.8	3-1	copious

G-2. Number of eggs per mass and length of incubation period for the species of Meloidae studied:

	Number of Eggs Per Mass			Time to Eclosion		
	$\bar{x}$	Range	N	$\bar{x}$	Range	N
<u>Lytta magister</u>	416	298-517	3	13.0	12-15	3
<u>Lytta mutilata</u>	636	619-653	2	14.5	14-15	2
<u>Pleurospasta mirabilis</u>	142	107-177	2	18.0	18	2
<u>Pyrota akhurstiana</u>	532	-	1	14.0	-	1
<u>Pyrota postica</u>	496	489-504	2	18.0	11-12	2
<u>Tegrodera erosa aloga</u>	181	100-252	4	17.0	11-20	6
<u>Gnathium minimum</u>	57.5	38-87	8	8	-	1
<u>Gnathium obscurum</u>	10.5	6-16	8	8.8	8-10	8
<u>Nemognatha lurida</u> <u>apicalis</u>	150+	-	1	-	-	-
<u>Nemognatha lurida lurida</u>	200+	-	3	7.3	7-8	3
<u>Nemognatha lutea lutea</u>	200+	-	1	-	-	-
<u>Nemognatha nigripennis</u>	150+	-	6	7.5	7-8	4

## G-2 continued

	Number of Eggs Per Mass			Time to Eclosion		
	$\bar{x}$	Range	N	$\bar{x}$	Range	N
<u>Nemognatha nitidula</u>	150+	-	5	9.8	9-11	5
<u>Pseudozonitis brevis</u>	269	196-328	4	6.7	6-7	4
<u>Tetraonyx fluvus</u>	150+	-	3	9	7-10	3
<u>Zonitis atripennis</u> <u>flavida</u>	150+	-	7	10.3	10-11	7
<u>Zonitis dunniana</u>	248	184-311	2	9	-	1
<u>Zonitis punctipennis</u>	150+	-	3	11	11	3
Nemognathinae sp.	100+	-	-	-	-	-

APPENDIX H

EFFECT OF TEMPERATURE ON LARVAL DEVELOPMENT

H-1. Effect of temperature on larval development in  
Nemognatha lurida lurida

Temperature	Instar	Length of Instar (days)			
		$\bar{x}$	$s_{\bar{x}}$	Range	N
21 ± 2° to 27 ± 1/2°C	eclosion to feeding	3	-	-	-
	T <sub>1</sub> (on food)	32.3	1.91	25-38	7
	FG <sub>2</sub>	3.8	0.47	3-5	4
	FG <sub>3</sub>	4.0	0.71	2-5	4
	FG <sub>4</sub>	4.8	1.03	2-7	4
	FG <sub>5</sub>	21	0.71	19-22	4
	Total to C	60	2.68	54-67	4
24 ± 1/2°C	mortality complete in T <sub>1</sub> instar				
27 ± 1/2°C	eclosion to feeding	3	-	-	-
	T <sub>1</sub> (on food)	17.3	2.11	8-33	15
	FG <sub>2</sub>	4.3	0.35	2-7	15
	FG <sub>3</sub>	4.7	0.40	2-7	14
	FG <sub>4</sub>	4.2	0.40	2-8	13
	FG <sub>5</sub>	20.0	1.17	13-26	13
	Total to C	49.9	2.35	36-66	13
29.5 ± 1/2°C	eclosion to feeding	3	-	-	-
	T <sub>1</sub>	16.1	0.68	11-22	19
	FG <sub>2</sub>	2.9	0.23	2-5	15
	FG <sub>3</sub>	2.9	0.40	1-7	14

## H-1 continued

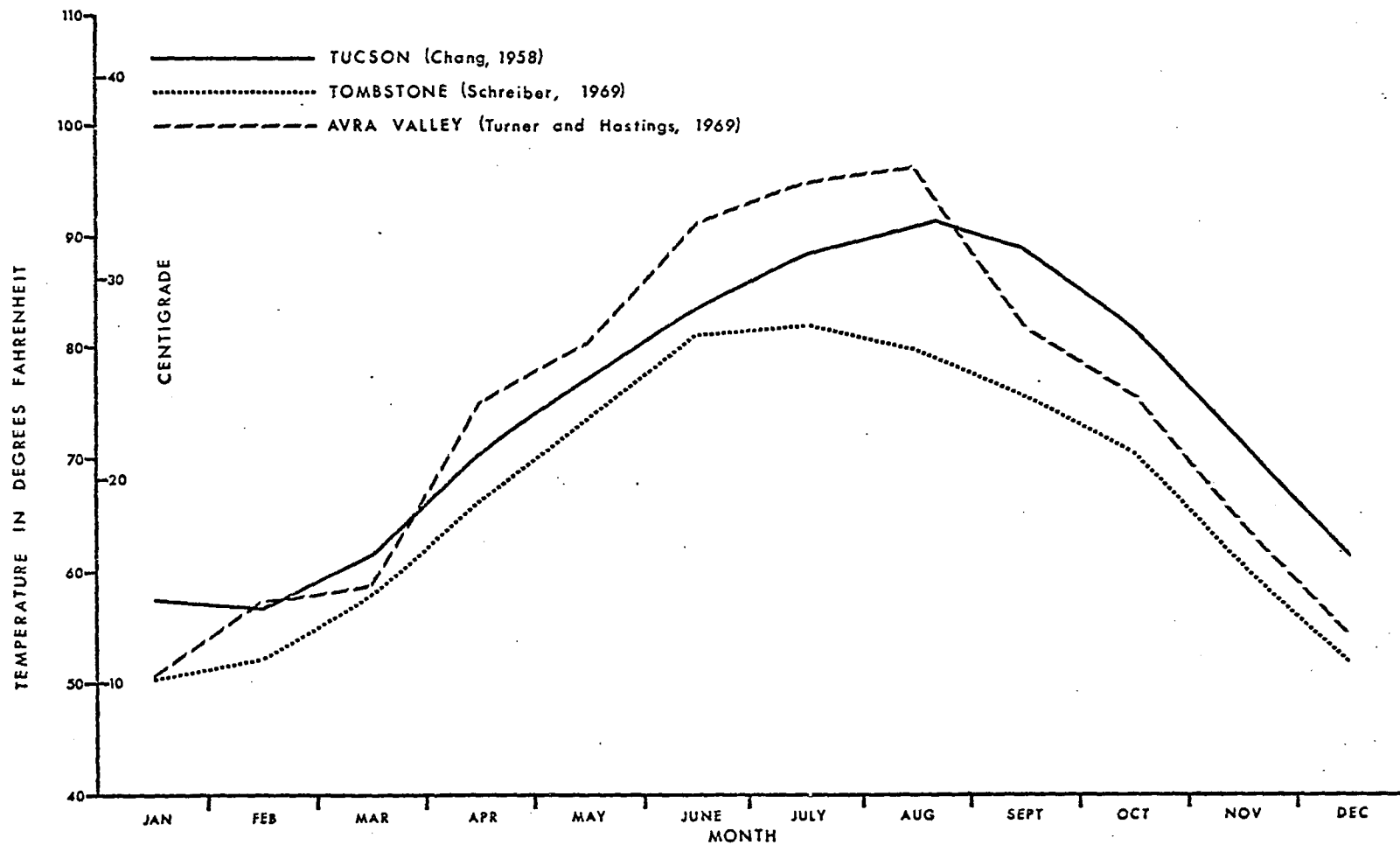
Temperature	Instar	Length of Instar (days)			
		$\bar{x}$	$s_{\bar{x}}$	Range	N
	FG <sub>4</sub>	5.6	1.12	2-14	13
	FG <sub>5</sub>	18.7	1.28	10-25	12
	Total to C	44.7	1.42	36-52	12
31 ± 1/2°C	eclosion to feeding	3	-	-	-
	T <sub>1</sub> (on food)	12.5	0.59	8-19	26
	FG <sub>2</sub>	2.3	0.15	2-5	23
	FG <sub>3</sub>	2.2	0.13	2-5	23
	FG <sub>4</sub>	3.1	0.25	1-5	21
	FG <sub>5</sub>	11.2	0.37	7-14	23
	Total to C	31.7	0.73	26-38	23
34 ± 1/2°C	mortality complete in T <sub>1</sub> instar				

H-2. Effect of temperature of larval development in  
Nemognatha nigripennis

Temperature	Instar	Length of Instar (days)			
		$\bar{x}$	$s_{\bar{x}}$	Range	N
21 ± 2° to 27 ± 1/2°C		No development			
24 ± 1/2°C		No development			
29.5 ± 1/2°C	T <sub>1</sub> (on food)	22	3.30	17-28	3
	FG <sub>2</sub>	5	-	2-8	2
	FG <sub>3</sub>	2	-	-	1
	FG <sub>4</sub>	3	-	-	1
	FG <sub>5</sub>	13	-	-	1
	Total to C	50	-	-	1
31 ± 1/2°C	T <sub>1</sub> (on food)	12.1	0.55	9-19	20
	FG <sub>2</sub>	2.7	0.20	2-4	18
	FG <sub>3</sub>	1.9	0.13	1-3	18
	FG <sub>4</sub>	2.5	0.23	1-5	18
	FG <sub>5</sub>	14.9	1.07	8-21	13
	Total to C	34.1	0.98	29-39	13
34 ± 1/2°C		No development			

APPENDIX I

AVERAGE MONTHLY BARE SOIL TEMPERATURE AT A  
DEPTH OF 12 INCHES IN SOUTHERN ARIZONA



APPENDIX I. AVERAGE MONTHLY BARE SOIL TEMPERATURES AT A DEPTH OF 12 INCHES IN SOUTHERN ARIZONA

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