PARASITES OF APHIDS ON WHEAT AND SORGHUM IN OKLAHOMA: IDENTIFICATION BASED ON EMPTY MUMMIES

By

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PREFACE

The biological control of insects is an important alternative to chemical control, especially with the ever increasing awareness of the impact of toxicants on our environment. I am fortunate to be working in this area of entomology, and I hope that the material reported in this thesis will be useful in future biological control efforts. However, the professional training that is very much a part of a Master's program has been important to my personal development during this study. For introducing me to the role that entomological research fulfills, as well as encouragement in conducting, presenting, and critiqueing that research, I am grateful to Dr. Raymond D. Eikenbary, who served as graduate chairman for my committee. I am indebted to Dr. William A. Drew, not only for serving on my committee, but for valuable advice and exposure to new ideas and philosophies. I would like to thank Dr. Robert Burton, for serving as a committee member, for encouragement, and for providing greenhouse facilities for a portion of this study. Dr. John Sauer served as a committee member, and I thank him for his advice, as well as his thought-provoking questions that cause one to look beyond the scope of a particular issue.

I wish to express my gratitude to Dr. R. D. Morrison, for serving as a committee member, and assistance in the preliminary experimental design. My thanks go to Dr. Don Holbert, who assistance was instrumental to the statistical analysis of these data. To Don Arnold, Survey

Entomologist; Dr. Ken Pinkston; and numerous other members of the Oklahoma Cooperative Extension Service, I am indebted for their assistance in collecting specimens.

Financial support from the Oklahoma Agricultural Experiment Station, for portions of this study, is gratefully acknowledged.

I am deeply indebted to Ms. Lisa Seidman and Ms. Jacque McArt for their assistance in the Scanning Electron Microscopy that is so important to this study.

My thanks go to Russell Campbell, Bob Cartwright, Mary Leonard, and Keith Mirkes for their part in maintaining greenhouse facilities and cultures.

Without the friendship of all of my fellow graduate students, my education would not be complete. A heart-felt thanks is due to all of them.

A special debt of gratitude is expressed to Dr. William B. Peck, Central Missouri State University, for first introducing me to the realm of entomological science, and for his encouragement to pursue further experiences in this area.

Throughout this study, one of my guiding forces has been my wife, Helen. She has given much, and received little during this Master's program. It is to her and her understanding that I am forever grateful.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

The greenbug, Schizaphis graminum (Rondani), has been a serious pest of small grains since its introduction into the U.S. in 1882 (Webster 1909). It became a major pest on sorghum in 1968, when a form of the greenbug designated as C-biotype (Harvey and Hackerott 1969) caused severe damage throughout the central and southwestern United States (Wood et al. 1969). Other aphids, such as the corn leaf aphid, Rhopalosiphum maidis (Fitch), the oat-bird cherry aphid, R. padi (L.), and the English grain aphid, Macrosiphum avenae (Fabr.), occur frequently on sorghum and small grains, but they usually do not cause economic damage (Jackson et al. 1970).

Surveys of the parasites of the above-mentioned aphids were carried out in 1968, 1969 (Jackson et al. 1970), and 1972 (Archer et al. 1974) in Oklahoma. A similar survey was conducted in the high plains of Texas in 1970 by Walker et al. (1973).

In all three surveys, Lysiphlebus testaceipes (Cresson), a braconid parasite, was determined to be the most abundant primary parasite of the greenbug. Other primary parasites reported by Jackson et al. (1970) and Archer et al. (1974), included two aphelinids; Aphelinus nigritus (Howard), and an exotic parasite imported from France in 1969, A. varipes (Forester). Diaeretiella rapae (M'Intosh), a braconid, was recovered by Walker et al. (1973), in addition to L. testaceipes.

The most abundant secondary parasite reported by Walker et al. (1973) and Archer et al. (1974) was Pachyneuron siphonophorae (Ashmead); whereas Jackson et al. (1970) observed Aphidencyrtus aphidivorus (Mayr), an encyrtid parasite, as being the most abundant. Other species of secondary parasites recorded by Jackson et al. (1970) and Archer et al. (1974) were Asaphes lucens (Provancher) and Charips sp. In addition to these, Walker et al. (1973) reported Tetrastichus minutus (Howard).

Description of aphid mummies based on color has been used by many workers. Wood (1958), Jackson et al. (1970), Archer et al. (1974), and Walker et al. (1973), all described greenbug parasite mummies solely on the basis of color, either tan, gold, or black.

Rogers et al. (1972) identified mummies of three introduced and two native parasites of a sunflower aphid, Aphis helianthi Monell, on the basis of color.

Mackauer and Finlayson (1967) used color of the mummy in conjunction with other characteristics to identify a complex of eight hymenopterous parasites of the pea aphid, Acyrthosiphon pisum (Harris).

The exit or emergence hole of aphid parasites has been described by several workers, but few have used it as a means of identification. Stary (1974) compared the position of the exit hole in the world genera and subgenera of hymenopterous aphid parasites and found that the position of this hole is constant within particular generic groups.

Rogers et al. (1972) described the shape of the exit hole of five primary parasites of a sunflower aphid, A. helianthi, and indicated that all species preferred the posterior region of the mummy for exit.

One of the first workers to take into account the secondary aphid parasites and the form of their exit holes was Hafez (1964). He de-

scribed the exit holes, both by characteristic shape and location, of the primary and secondary parasites of the cabbage aphid, Brevicoryne brassicae (L.). The descriptions include the shape of the emergence hole, as well as the form of the hole margin. Hafez found that the primary parasite, Aphidius (=Diaeretiella) rapae (M'Intosh), almost always emerged between the cornicles on the dorsal side of the mummy with a more or less circular emergence hole with smooth edges. The secondary parasites in this study emerged from an irregularly shaped hole on various locations of the mummy.

The meconium is the waste contained in the gut of the parasite larva that is voided just before or after the pupal stage (Flanders 1942). In the case of aphid parasites, the meconium consists of groupings of pellets excreted by the pre-pupal stage of the insect.

Meconial pellets have been used by some workers in determining either presence or identity of hymenopterous parasites. Taylor (1935, p. 26) described the meconium of Aphelinus chrysomphali Mercet, a parasite of the coconut scale, Aspidotus destructor Sing., and determined that it is a "useful means of detecting fully grown larvae or pupae in situ." The meconia of several primary and secondary parasites of aphids were described by Spencer (1926), but no complete discussion of the differences in these meconia was attempted.

After a discussion of the larval meconia of various species of parasitic hymenoptera, Flanders (1942) summarized that the larval meconium may not be indicative of the species of a genus, but they may be useful in recognizing a species of a group of parasites from one host.

Hafez (1964) used the meconium along with other characters of the empty mummies of primary and secondary parasites as a basis for identi-

fication of the adult. The shapes of the meconia studied in his work were morphologically different enough that a reasonable identification of the parasite could be made, as well as determining if primary, secondary, or tertiary parasitization had occurred.

In determining the impact of these parasites on an aphid population, there are several factors that must be considered. The number of mummies on a plant cannot be a positive indication of percentage parasitism unless the aphid density is taken into account (Hagen and van den Bosch 1968). Hafez (1965) presented reasons for the overestimation of the percent parasitism by A. rapae. These include the immobility of a mummy due to being cemented to the substrate by the parasite's cocoon: after the remaining aphids migrated from the plant, the ratio of mummies to aphids would be excessively high. Also mentioned was the accumulation of aphid mummies through several generations, and the fact that although a mummy is formed, it does not indicate whether a primary or secondary parasite will emerge.

The effect of primary parasites on an aphid population in a field situation was observed by Hagen and van den Bosch (1968) as being difficult to determine, and when secondary parasitism was included, the problem became even more complex.

Shands et al. (1965, p. 74) concerning the parasites of potato aphids, reported that "hyperparasitism has had no appreciable, consistent effect upon the abundance of primary parasites, of aphids, or of the hyperparasites themselves" over a 12-year period.

During large-scale field releases of L. testaceipes in 1972 and 1973, Starks et al. (1976) found secondary parasitism ranging from 4.2% to 14.7% in samples taken throughout the field.

In data presented by Walker et al. (1973), it is reported that a large number of aphids were mummified by L. testaceipes, but adult primary parasites emerged from less than one-half of these mummies. The remaining adults that emerged were secondary parasites, mainly Charips sp. and P. siphonophorae.

These authors found this percentage of secondary parasitism substantial, and suggested further studies on the effect of secondary parasites before mass-releasing primary parasites.

In determining percent emergence of primary and secondary parasites, it is usually necessary to collect mummies and hold them until the adult emerges. Field identification would be facilitated if the empty mummy could be collected, and a method used to determine the identity of the adult parasite that had ultimately emerged.

With this in mind, a study was initiated to determine if, within the parasite fauna of aphids occurring in small grains and sorghum, there were characters of the empty mummies that would be of enough significance to use them in identifying both the host aphid and the parasite that emerged from the mummy.

CHAPTER II

MATERIALS AND METHODS

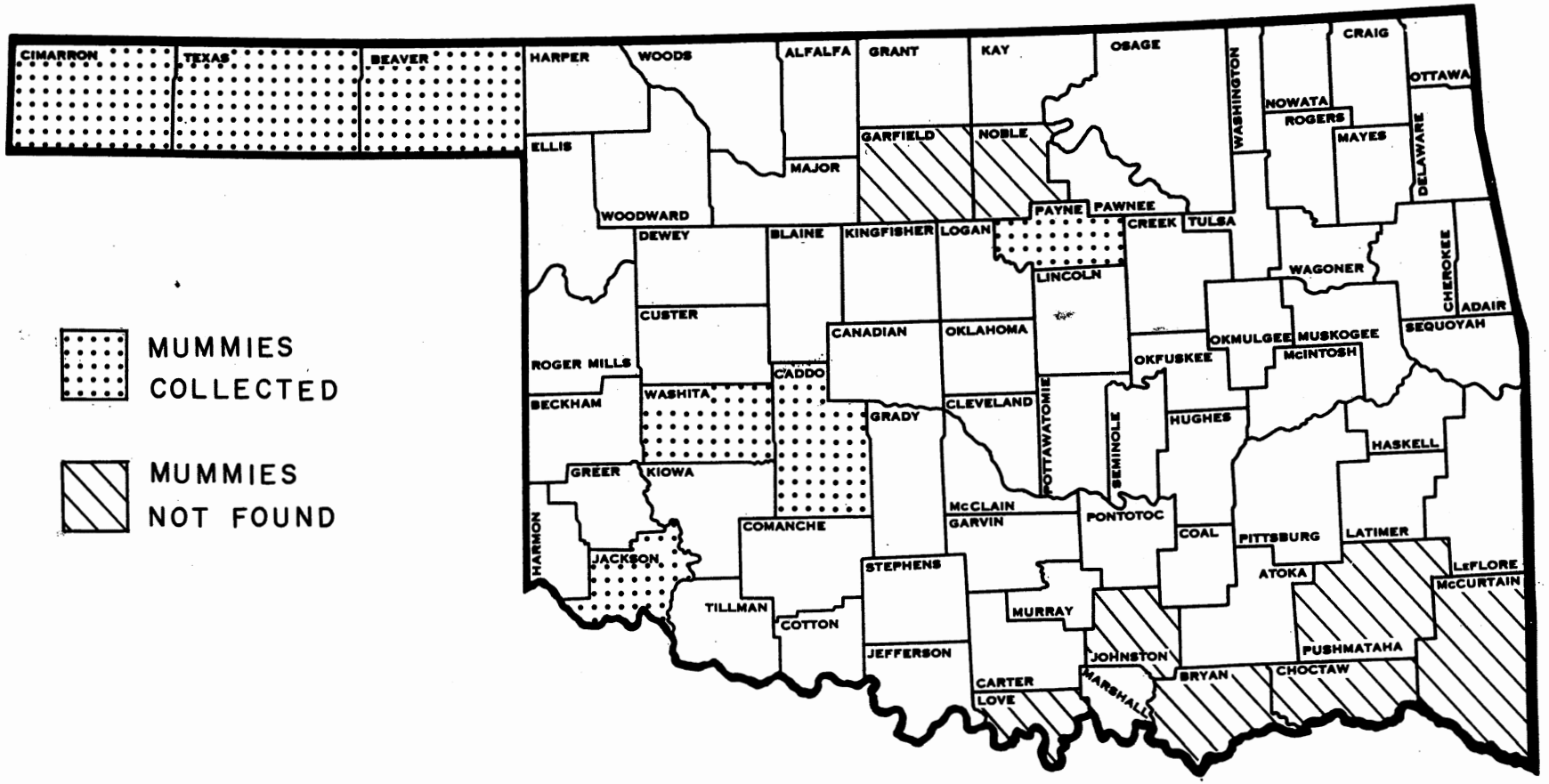
Survey

A survey was conducted in 1977 and early 1978 for parasite mummies of the greenbug, corn leaf aphid, oat-bird cherry aphid and the English grain aphid throughout the major grain-producing regions of Oklahoma (Figure 1). Sorghum and wheat fields were selected with the help of the Oklahoma State University survey entomologist and personnel of the Oklahoma Cooperative Extension service. Also, likely-looking fields along the roadside were sampled.

After a field was chosen, a sample was taken by walking approximately 100 feet into the field, and searching randomly selected plants for 15 minutes. Any leaves, or portion thereof, possessing mummies were removed. Samples were placed in a paper bag, labeled with the collection locality, and kept cool until returned to the laboratory. Mummies were removed from the leaves with a camel's hair brush and small metal probe, and placed in number three gelatin capsules. These mummies were stored at $70^{\circ} \pm 5$ F at ambient relative humidity in a temperature-controlled chamber until emergence.

Additional mummies were obtained from greenhouse cultures for those species which were not collected in the field or were poorly represented in the samples.

Figure 1. Outline map of Oklahoma showing the area surveyed in 1977, and the area where samples were collected


MUMMIES COLLECTED
MUMMIES NOT FOUND
CIMARRON
TEXAS
BEAVER
HARPER
WOODS
ALFALFA
GRANT
KAY
OSAGE
WASHINGTON
NOWATA
CRAIG
OTTAWA
ROGERS
MAYES
DELAWARE
ELLIS
GARFIELD
NOBLE
MAJOR
WOODWARD
PAYNE
PAWNEE
CREEK
TULSA
WAGONER
CHEROKEE
ADAIR
DEWEY
BLAINE
KINGFISHER
LOGAN
LINCOLN
CUSTER
CANADIAN
OKLAHOMA
OKMULGEE
MUSKOGEE
SEQUOYAH
McINTOSH
ROGER MILLS
CADDO
OKFUSKEE
BECKHAM
WASHITA
GRADY
CLEVELAND
POTTAWATOMIE
SEMINOLE
HUGHES
HASKELL
GREER
KIOWA
McCLAIN
GARVIN
PONTOTOC
COAL
PITTSBURG
LATIMER
HARMON
COMANCHE
JACKSON
STEPHENS
ATOKA
LEFLORE
McCURTAIN
TILLMAN
COTTON
MURRAY
JOHNSTON
PUSHMATAHA
JEFFERSON
CARTER
MARSHALL
BRYAN
CHOCTAW
LOVE

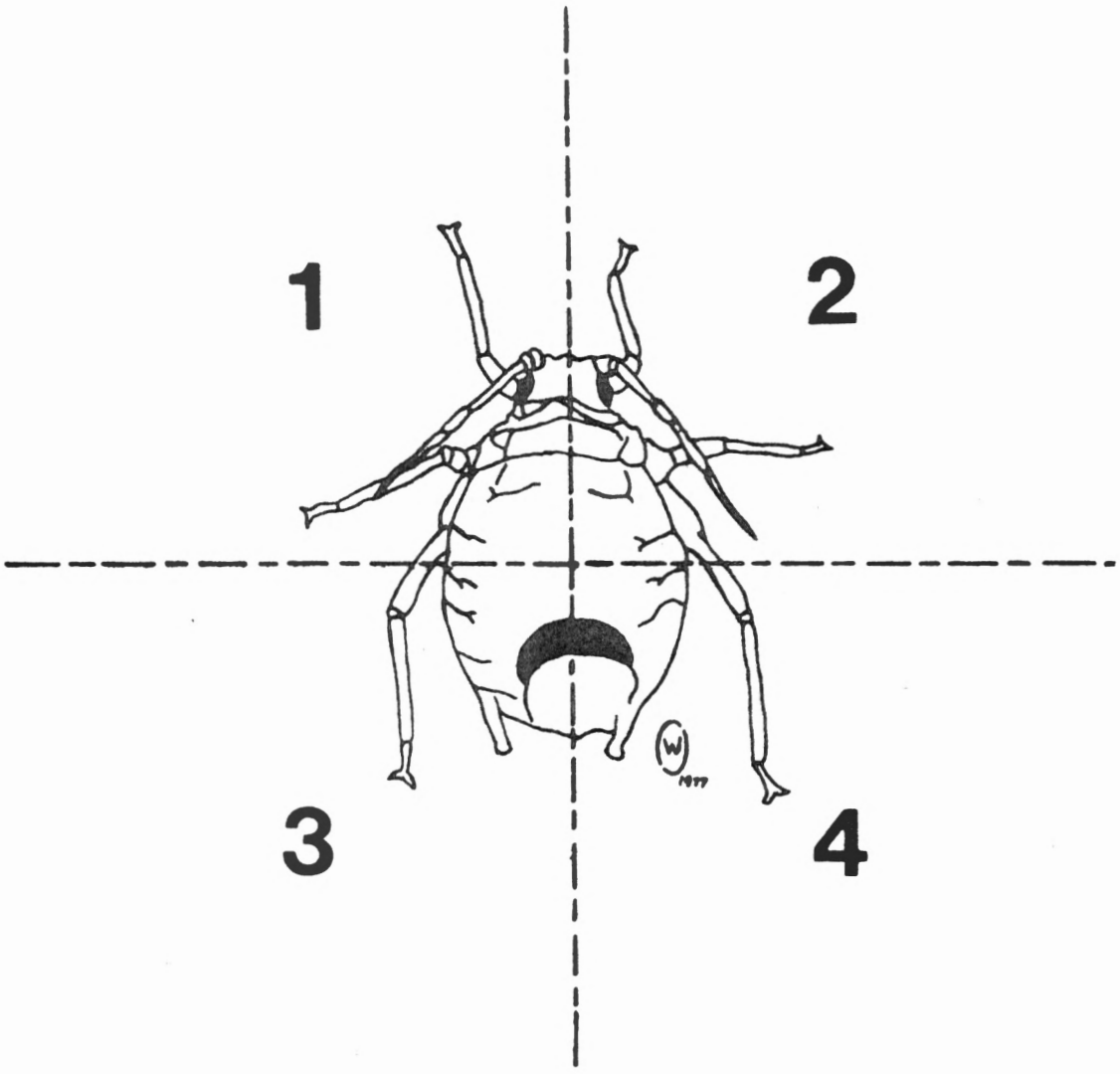
Compilation of Data

Preliminary identification of the emerged adults was made by comparison with a reference collection of primary and secondary greenbug parasites located at Oklahoma State University. The cynipid secondary parasites were identified by Dr. Fred Andrews, Division of Plant Industries, Albany California. The chalcid parasites were identified by Dr. E. E. Grissell, and the braconid parasites by Dr. Paul M. Marsh, both of the Systematic Entomology Laboratory, USDA-SEA, Washington, D.C.

After identification of the adults, mummies were sorted by species and the following evaluations made:

1. Color of the entire mummy and differences in color of any of the appendages of the mummy.
2. Measurement of the length and width of the mummy.
3. Location of the exit hole by quadrant (Figure 2) and position of the exit hole within that quadrant with respect to dorsal, ventral, or lateral orientation.
4. Measurement of the length and width of the exit hole.
5. Determination of the physical shape of the exit hole.
6. Determination of the shape of the margin of the exit hole.
7. Presence or absence of an operculum (emergence lid).
8. Observation of the shape of the meconial pellets.
9. Number of pellets in the meconial cluster.
10. Location of the meconial cluster by the same quadrant method used for the exit hole.
11. Measurement of the length and width of a representative pellet from the meconium.

Figure 2. Outline drawing of an aphid mummy showing the quadrant system used to designate location of exit holes and meconial clusters


1
2
3
4

Measurements were made with a calibrated ocular micrometer mounted in a steroscopic microscope.

Photographic Techniques

Both photomicrographs and scanning electron micrographs were taken in order to obtain the best resolution possible. The photomicrographs were taken with a Miranda® SLR camera mounted on either a Baush and Lomb® binocular microscope, or an AO® binocular compound microscope.

Scanning electron micrographs were taken with a JEOL JSM-35 scanning electron microscope. Standard techniques were followed, except that air-dried specimens were used, instead of the standard chemical drying procedure.

The wing mounts were made by breaking the wing from dry, pointed specimens; soaking in xylene; and mounting in a xylene-soluble permanent mounting material. Photographs were taken and line drawings were made from the original photographs. Reduction or enlargement of these images was effected with the use of a standard photo enlarger.

Construction of Keys

Diagnostic keys for adult parasites and mummified aphids (Appendix A) were constructed using structures or colors that, after comparison between individuals of the same species, were determined to be characteristic of that species. Specimens of mummified aphids were obtained from colonies of a known species before attempting to elucidate any differences.

The diagnostic key for parasite species based on mummies (Appendix A) was constructed after the statistical analysis of the data gathered

in this study.

Data Analysis

All data were recorded on computer cards for storage. Since the variables used in this study were predominately descriptive, a discriminant analysis using qualitative variables was performed on the data collected. Varying numbers of specimens were analyzed (from 24 to 92) depending on the abundance of the specimens and the time involved in evaluating these specimens.

The following formula from Tatsuoka (1971) was used to calculate the posterior probability of a given individual mummy, with the observed multivariate state "S_i", falling into a known species "V_j":

$$\frac{\Pr\{S_i|V_j\} \cdot P_j}{\sum_{k=1}^{m} \Pr\{S_i|V_k\} \cdot P_k} = \Pr\{V_j|S_i\}$$

where,

Pr = Probability

S_i = The various multivariate states, where i = 1,...n states

V_j = The species, where j = 1,...species

P_j = The prior probability, if any, of the individual belonging to any species V_j, j=1,...,m

Further data management was accomplished by using the Statistical Analysis System, both 1972 and 1976 procedures (Barr et al. 1976).

CHAPTER II

RESULTS AND DISCUSSION

Mummy Collections

During the survey portion of this study, 2820 mummified aphids were collected from 35 locations in seven counties in Oklahoma. Table 1 contains collection dates, plant host, number of mummies collected and percent emergence by species for the two colors of mummies collected. The objectives of this study did not include determining any temporal distribution throughout the season, or any spatial distribution for a given species within Oklahoma, and the data are not intended to imply such distributions.

Approximately 57% of the mummies collected had no emerging parasites. Possible explanations for this include mechanical damage during collection, disease, damaging host responses, diapausing conditions of the parasite, or desiccation of the larval form.

Aphid Fauna

Of the three species of aphids occurring in the fields, S. graminum, R. padi, and R. maidis; S. graminum was the most abundant. The parasitized forms of the greenbug, as well as non-parasitized nymphs, were found mainly on the underside of leaves on sorghum, and were widely distributed on wheat plants. When L. testaceipes parasitized this species, a light beige to medium tan colored mummy resulted. There were no differ-

Table 1. Aphid parasites emerging from mummies collected on wheat and sorghum - Oklahoma 1977*

Date of Collection	Plant Host	Number of Mummies Collected	Numbers of Parasites Emerging	% *L. testaceipes*	% *Aphelinus nigritus*	% *P. siphonophorae*	% *A. aphidivorus*	% *Charips sp.*
			Tan-colored mummies					
March 20-24	Wheat	78	78	92.3	------	------	-----	7.7
May 24	Barley	101	58	100	------	------	-----	-----
July 12-15	Sorghum	13	2	100	------	------	-----	-----
July 25-28	Sorghum	85	52	26.92	------	61.53	-----	11.53
Aug. 4	Sorghum	17	3	------	------	33.33	33.33	33.33
Aug. 18	Sorghum	623	37	3.85	------	32.34	8.90	54.30
Aug. 19	Sorghum	1,323	335	13.43	------	34.03	2.08	50.45
Aug. 25	Sorghum	0	---	------	------	------	-----	-----
			Black-colored mummies					
March 20-24	Wheat	0	---	------	------	------	-----	-----
May 24	Barley	0	---	------	------	------	-----	-----
July 12-15	Sorghum	3	3	------	------	100.00	-----	-----
July 25-28	Sorghum	248	159	------	26.51	20.75	44.65	8.17
Aug. 4	Sorghum	1	1	------	100.00	------	-----	-----
Aug. 18	Sorghum	242	124	------	42.74	12.09	41.13	4.83
Aug. 19	Sorghum	71	36	------	77.78	2.78	16.67	2.78
Aug. 25	Sorghum	15	1	------	------	100.00	-----	-----

*Total percent parasitism per time period may not equal 100 due to rounding.

ences in the coloration of the legs, cornicle, or body of the mummy. The cornicles were sub-cylindrical, and tapered slightly towards the apex. When a greenbug was parasitized by one of the species of Aphelinus, a black mummy formed. The legs were usually lighter than the rest of the body, and the cornicles were not completely black. Antennal length of mummified greenbugs was greater than 1/2 the length of the mummy.

The corn leaf aphid, R. maidis, was the next most frequently occurring aphid in this study. This species was typically found in the whorl on sorghum and was uncommon on wheat. The mummies of this aphid were distinguished by the solid black legs and cornicles, and the antennal length, which was usually less than or equal to 1/2 the length of the mummy.

The oat-bird cherry aphid, R. padi, was found in the cold months of the year at levels of less than 100 per row foot in small wheat. None were recovered from sorghum. When parasitized, this aphid shows a definite constriction of the cornicle just proximal to the flange, i.e., the end of the cornicle. This feature serves to identify the oat-cherry aphid from the other aphid species involved.

The English grain aphid, Macrosiphum avenae, was not found during the course of this study. Bottrell et al. (1973) report this species as infesting the heads of grain, but seldom causes losses in yield. Specimens were obtained from Dr. R. W. Kieckhefer, SEA, Brookings, SD, and cultured on sorghum-barley mixtures in the greenhouse.

Mummies of this species can be distinguished from the other species in this study on the basis of the antennae, which are usually as long as the body; the legs, which have alternating dark and light bands; and the

cornicles, which are entirely black, sub-cylindrical, and taper towards the apex.

Parasite Spectrum

Primary Parasites

Lysiphlebus testaceipes is the only braconid primary parasite collected from the field in this study. This species was reported by Webster (1909) as being associated with S. graminum in its native habitat and was responsible for "holding the pest in check in America". Muesbeck and Walkley (1951, p. 95) reported the nearctic distribution as "all U.S.; Mexico," on a variety of hosts.

Characters that distinguished adult L. testaceipes from other species collected in this study included its relatively large size and its wings with a moderately complete veination, including the presence of the interradial II vein (nomenclature after Stary 1976).

The main characteristic when describing a mummy formed by a L. testaceipes larva is the tan or beige color. Every L. testaceipes mummy in this study was tan in color. This consistent trait indicates that, regardless of the ultimately emerging parasite, the primary parasitization of the aphid was by L. testaceipes.

Other features that characterize L. testaceipes are the typically round exit hole and its smooth margin. These two characters were consistent in all but one of the 92 specimens evaluated, this specimen having an oblong exit hole with a jagged margin.

The presence of an operculum, or emergence lid, was an important indication of identity. Stary (1974) discussed the formation of this emergence lid and mentioned that it may be attached to the mummy, broken

off by the emerging parasite, or broken off later by mechanical means. The data gathered in this study show a 59% retention of this structure on mummies formed by L. testaceipes (Figure 4A).

Position of the exit hole was a character that was not entirely consistent in L. testaceipes; however, in general, it was located in quadrants 3 and 4 (Figure 2) usually between the cornicles in a dorsal position.

The meconial pellets of L. testaceipes have not been previously described in any detail, but the meconium of D. rapae, a braconid parasite that commonly attacks cabbage aphids, was described by Spencer (1926) and Hafez (1965). Although the two authors disagreed as to the number of pellets, the shape was described as a chain or group of "sausage links" (Spencer 1926) or spindle shaped (Hafez 1965). The pellets of L. testaceipes evaluated in this study were elongate, usually pointed at each end, and ellipsoid in cross-section (Figure 6A). I have designated this form as "cigar" shaped for convenience. The pellets ranged from 7 to 38 in number, with a mean of 18.8.

Aphelinus nigritus, a member of the family Eulophidae (=Aphelinidae), is a primary parasite commonly encountered on sorghum in Oklahoma. The species was originally described from six female specimens reared from S. graminum in South Carolina (Howard 1908). Wood (1958) first reported this species in Oklahoma from greenbugs in a greenhouse situation. Other distribution records list Kansas, Minnesota, New Mexico,(Webster and Phillips 1912) Arizona and California (Burks 1958).

The characters that best separated A. nigritus adults from the rest of the parasite fauna included: incomplete wing veination; dark or black non-metallic abdomen and thorax; and the yellow to hyaline coloration of

the legs and antennae.

A. nigitus, when forming the mummy, typically turns the exoskeleton of the dead aphid black. This coloration, as in the case of L. testaceipes, indicates primary parasitization by A. nigritus, regardless of what species of parasite emerges.

The exit hole resulting from an emerging A. nigritus was varied in shape but always has a jagged or dentate margin (Figure 5B). Of the 24 specimens studied, the shape of the hole was round in 54% and oblong in 46%. The elongation of the oblong hole was on a line perpendicular to the longitudinal axis of the body. Additional evaluation of the hole shape with regard to sex differences was conducted, but no differences were found between these two characters. As in L. testaceipes, the position of the exit hole was generally in quadrants 3 and 4, on the dorsum anterior to the cornicles.

The meconial pellets of this parasite ranged from 3 to 8 in number, with a mean of 5.6. The shape of the pellets was usually round in outline, flattened in cross-section, with an occasional small projection on the edge. The pellets, which were classified as "plate"-shaped, frequently had small ridges across one surface (Figure 6B). These pellets tended to be aligned in 2 rows on the bottom of the inside of the mummy, usually in the head and thoracic region.

Aphelinus asychis and Praon n. sp., two exotic primary parasites not recovered from the field, have been included in this study because of the possibility of their recovery in the future.

Aphelinus asychis is an old-world species that was introduced into the U.S. from Iran by the USDA in 1969. It was consequently reared and released in Oklahoma by Jackson et al. (1970). When surveying the para-

site fauna in 1972, however, Archer et al. (1974) failed to collect any A. asychis. This led to their questioning the status of this parasite with regard to establishment.

Adult A. asychis can be readily distinguished from the other parasites on the basis of the incomplete wing veination and the yellowish coloration of the abdomen. During mummy formation, the A. asychis larva turned the mummy black, as is the case with A. nigritus. With the constant position of the exit hole in quadrants 3 and 4 and the jagged margin of the exit hole, there was no basis for differentiating the two Aphelinus species on external mummy characteristics. The range in number of the meconial pellets was 3 to 8, with a mean of 5.3. The shape of the pellets is the same as described for A. nigritus. This closeness of characters indicates no reliable distinction between A. asychis and A. nigritus. A. asychis had meconial deposits aligned in the same manner as A. nigritus. This character is not consistent in all mummies, but serves as an indicator for these two species.

Praon n. sp. is a braconid parasite that was introduced from Pakistan by the USDA in 1976. It has been cultured by researchers at Oklahoma State University and preliminary field tests have indicated it can overwinter in Oklahoma. This parasite has been included in this study because of the possibility of its establishment in Oklahoma.

Adult Praon resemble L. testaceipes more closely than the other species in this study. It can be distinguished from L. testaceipes by the well-developed distal portion of the median vein and the lack of the interradial II vein (Figure 3B).

The coloration of the mummy formed by Praon is very similar to that of L. testaceipes. All specimens evaluated had mummies that were beige

to tan in color, with the appendage coloration dependent upon the species of aphid.

The most useful diagnostic character of a Praon mummy is the external pupal cocoon (Figure 4C). This feature is found only in the genera Praon, Dyscritulus, and Aeropraon, all of which are Aphidiidae (Stary 1974). The Praon larva forms this cocoon by splitting the venter of the dead aphid, raising the mummy somewhat by arching the body, and spinning the cocoon underneath (Ainslie 1917).

The exit hole of Praon was round and had a smooth margin in all 25 specimens evaluated. The adult emerged mainly from quadrants 3 and 4, but 20% emerged from the anterior end of the mummy, in quadrants 1 and 2. Two specimens (8%) emerged from quadrants 1 and 3, but the cocoon was not in the typical orientation for this parasite. In these mummies, the longitudinal axis of the cocoon was perpendicular to the longitudinal axis of the mummy rather than being aligned with this axis. Stary (1974) mentioned this character in reference to Aeropraon and the fact that it is difficult to determine the position of the exit hole since the cocoon is not always oriented with the aphid.

Secondary Parasites

Charips sp. (megourae complex) is a cynipid parasite that is a solitary, larval endoparasite of Aphidiidae and some species of Aphelinus (Hagen and van den Bosch 1968). The distribution of this complex is not well known, but seems to occur throughout Oklahoma.

The adult Charips was distinguished from the remaining parasites by two main characters, the wings and the abdomen. The wing veination was very reduced except for the radial cell (cf. Gutierrez and van den Bosch

1970) in the forewing (Figure 3D). The presence of this cell set Charips apart from all the parasites under study, with the exception of L. testaceipes and Praon, which have a more complete veination. The abdomen of Charips is sub-triangular in profile. This character is distinctly different from the flattened or convex abdomen of the other parasites.

Since Charips is a secondary parasite, the color of the mummy depends upon the primary parasite of the aphid host. Of all parasites emerging from tan and black mummies, the percent Charips was 42% and 6%, respectively (Table 1).

The exit hole made by emerging Charips was round in 96% of the specimens evaluated with all of these exit holes having jagged margins. The location of the exit hole was not found to be constant in Charips. While many exit holes corresponded with the previously discussed hole location for the respective primary parasites, 38% of the exit holes made by Charips were in atypical positions or locations on the mummy.

Meconial pellets deposited by immature Charips were oblong in outline and ellipsoid in cross-section in 78% of the specimens evaluated. Round pellets, also ellipsoidal in cross-section, constituted the remaining 22% of the Charips meconia.

Aphidencyrtus aphidivorus was reported by Griswold (1929) as being definitely secondarily parasitic on Aphelinus. Before that time, several workers reported this species as a primary parasite (Hagen and van den Bosch 1968; Peck 1963). The distribution of this parasite is generally widespread and was given by Peck (1963) as New York to Connecticut, Virginia, Indiana, Florida, Louisiana, and Idaho on various aphidiid and aphelinid hosts.

This larval endoparasite of primary aphid parasites is classified by Griswold (1929) as being arrhenotokous, i.e., when parthenogenic reproduction occurs, only males are produced.

The adult A. aphidivorus is generally metallic black or blue-black in color with the abdomen relatively short and broadly joined to the thorax. The wing veination is very reduced and the legs are banded with alternating light and dark horizontal stripes.

Since A. aphidivorus is a secondary parasite, as is Charips, the mummy color depends upon the primary parasite of the aphid host. Of the samples collected in the survey, 4% and 39% of the emerging A. aphidivorus came from tan and black mummies, respectively.

The exit hole formed by the emerging parasite was round in 68% of the specimens, the remaining 17% oblong. The exit hole margin was jagged in all cases (Figure 5A).

The location of the exit hole was in the third and fourth quadrants 76% of the time, but was variable in the remaining specimens evaluated. On mummies of the geranium aphid that had been removed from leaves, Griswold (1929) noted that the exit holes of Aphidencyrtus that were on the venter probably would have been somewhere on the dorsum, if the mummy had remained on a leaf or other surface.

The meconial deposits of A. aphidivorus were found to be round or oblong with a frequency of about 70%. A peculiarity noticed when taking data was that when the meconial cluster was in the head region of the mummy (quadrants 1 and 2), the pellets were of a pale to dark red or reddish brown. The pellets in the other portions of the mummy were black in color. This agrees with statements made by Griswold (1929, p. 446) in which she described the head capsule of the dead aphid as being

filled with "tiny orange ovoid pellets of excrement voided by the Aphidencyrtus."

Pachyneuron siphonophorae was first reported from S. graminum by Howard (1891) from Tennessee, Indiana, and Washington, D.C. Essig (1926) found it parasitizing L. testaceipes, and listed the distribution as the entire U.S. This secondary parasite is described by Spencer (1926) as being solitary and ectoparasitic on pupae or "late larvae" of L. testaceipes and other primary parasites.

Adult P. siphonophorae are generally metallic green in color with the petiolate abdomen flattened or depressed discally. The wings have a distinctive thickening of the marginal vein of the forewing (Graham 1969) (Figure 3E). The femur, and usually the entire leg, is banded with alternating dark and light horizontal stripes. All of these characters serve to distinguish this parasite from the other parasites in this study.

As with the other secondary parasites, the color of the mummy that P. siphonophorae emerges from is dependent on the primary parasite of the aphid host. Of the parasites collected in the survey, 29.5% of the tan mummies and 16% of the black mummies had P. siphonophorae emerge from them (Table 1).

The exit hole shape was about evenly divided between round and oblong shapes. Since differences in hole shape based on sex were not found in Aphelinus, the lengthy process of sexing P. siphonophorae was not attempted. The exit hole margin was jagged in all specimens.

The location for 40% of P. siphonophorae exit holes was in quadrants 3 and 4 on the dorsum; above or some times below the cornicles. The other 60% were in various locations on the mummy surface with 24%

in quadrants in 1 and 2, 16% in quadrant 4, and 20% in quadrant 3.

Before discussing the meconia of P. siphonophorae, the effect of the trophic relationship between the secondary parasite and the primary host must be understood. Hafez (1965) discussed this relationship between A. rapae and its complement of secondary parasites. When a larval endoparasitic parasite such as Charips attacks the primary parasite, the primary will not reach the prepupal stage, so the meconium cannot be deposited. Upon emergence of the adult parasite, only the meconium of the secondary parasite will be found. When P. siphonophorae or Asaphes attack the pupa rather than the larva of the primary parasite, two types of meconia could remain in the mummy; that of the primary parasite, as well as that of the secondary parasite. If, however, the secondary parasite oviposited into a late larval or early pre-pupal stage, the meconium of the primary parasite would not be deposited. In this case, only the meconial deposits of the secondary parasite would remain in the mummy.

Hafez (1965) mentions a case where tertiary parasitism could possibly leave three different types of meconia: that of a primary; a larval secondary parasite; and finally, a pupal tertiary parasite. Griswold (1929) documents this type of trophic relationship, using Aphelinus, Aphidencyrtus, and Asaphes, as the primary, secondary, and tertiary parasite, respectively.

In this study, P. siphonophorae emerged from mummies that had both one and two meconial clusters in them. The mummies with one meconial cluster (that of P. siphonophorae), had pellets that were round or oblong and ellipsoid in cross-section. This would indicate that P. siphonophorae parasitized the primary parasite in the late larval or early pre-pupal stage. When two meconial clusters were found in a mummy, one

of the clusters was as described above and the other was of the same type as the primary host, either L. testaceipes or Aphelinus spp.

The round pellets of P. siphonophorae had a range of 4 to 11 with a mean number of 7.5 when Aphelinus was the primary parasite. In mummies primarily parasitized by L. testaceipes, the round to oblong pellets ranged from 6 to 35, with a mean of 13.4.

In evaluating these figures, a possible fault inherent to the data collection procedure must be considered. When the meconial clusters were first observed, they were arbitrarily assigned as either cluster '1' or '2', since there was little prior knowledge of the pellet shape. However, this lack of prior knowledge of the shape of the pellets was necessary in order to take an unbiased sample. Although this introduced variation may have some effect on the range and mean number of the pellets, the shape of the meconial pellets of P. siphonophorae should be distinguishable from those of the primary parasite.

One other character of P. siphonophorae mummies, the pupal exuviae, was indicative of the species, even though it was not consistent in all specimens examined. This exuviae retains the shape of the antennae and head, which help serve to identify the emergent parasite.

Asaphes lucens was shown by Griswold (1929) to be both a secondary, as well as a tertiary, parasite. The host stage attacked, according to Spencer (1926) and Griswold (1929), is the late larval or pupal stage. Normally, A. lucens is a solitary external parasite, but instances of more than one egg per host have been reported (Griswold 1929). Distribution of this parasite includes most of the U.S. and portions of Canada (Burks 1958; Peck 1963).

The adult A. lucens can be distinguished from the other parasites

in this study by the metallic green body color; the typically convex venter of the abdomen, the lack of an enlarged marginal vein in the forewing, and the lemon-yellow coloration of the legs.

Only two specimens of A. lucens were collected during the parasite survey, and attempts to procure additional specimens from researchers from other states or countries were not successful.

The two specimens collected emerged from black mummies, indicating A. nigritus as a primary host, but this species has been reported from L. testaceipes (Spencer 1926). One specimen was destroyed by handling, but the features of the remaining one are as follows: the exit hole is round, located on the dorsum between the cornicles, and has a jagged margin; and the meconial pellets, 24 in number, are round to slightly oblong, and somewhat flattened in cross-section.

Since sufficient numbers of this parasite could not be obtained, an analysis of the meconial pellets was not attempted. However, Griswold (1929, p. 449) mentions that the larva voids the gut contents in the form of "tiny black ovoid pellets". Also mentioned was the fact that A. lucens emerged from various locations on the mummy, mainly in the posterior region.

Assessment of Data Analysis

Several characters were measured or observed on each mummy in this study. In order to determine which of these would be reliable indicators of a species, two-way frequency tables (Barr et al. 1976) of the type "Parasite x Character" were done for all characters. The quantitative measurements of the following were found to be too variable to be of any use: length and width of the mummy; length and width of the exit hole;

and the length and width of a representative pellet from the meconium. The location of the meconial cluster by quadrant also showed too much variation to be a reliable character.

A total of 57 multivariate states were generated by the data (Table 2). A multivariate state consists of the combination of eight characteristics, namely; mummy color, number of meconial clusters, exit hole shape, hole margin shape, shape of pellets in the first cluster, range indicator of the pellet count in the first cluster, shape of pellets in the second cluster (if present) and range indicator of the pellet count in the second cluster (if present). The range indicators for pellet counts were assigned as follows:

	Value of Range Indicator				
	0	1	2	3	4
Number of Pellets in Cluster '1'	1-5	6-10	11-15	16-25	>25
Number of Pellets in Cluster '2'	1-3	4-6	7-9	10-12	>12

For example, a particular mummy might be in the multivariate state S_6 = (Black, 1, Round, Jagged, Plate, 0). Due to the number of specimens evaluated, many of these states included only one specimen. The analysis might have been more reliable if additional specimens had been evaluated, but the time factor was prohibitive.

The characters used to build the multivariate states were well-defined and consistent within a group of mummies from one species of parasite. There are other characters, however, that are indicative of the identity of the parasite. If, for example, the investigator has information that three times as many of one species of parasite is present in the field than any other, he may develop an intuitive feeling, or a "prior probability", about the specimens that are being investigated.

Using multivariate state six as an example, the probability that a

Table 2. Generated multivariate states, and the conditional probability of species membership for each given state

State Number	Mummy Color	Cluster Number	Exit Hole Shape	Margin Shape	Pellet '1' Shape	Pellet '1' Range	Pellet '2' Shape	Pellet '2' Range	AAA	ANG	ASY	LTE	PRA	CHS	PAS
1	Black	1	Oblong	Jagged	Oblong	1			0	0	0	0	0	0	1 (1)*
2	Black	1	Oblong	Jagged	Plate	0			0.164(2)*	0.343 (4)*	0.493 (6)*	0	0	0	0
3	Black	1	Oblong	Jagged	Plate	1			0	0.75 (9)	0.25 (3)	0	0	0	0
4	Black	1	Round	Jagged	Oblong	0			0	0	0	0	0	0	1 (1)
5	Black	1	Round	Jagged	Ovoid	0			1 (1)	0	0	0	0	0	0
6	Black	1	Round	Jagged	Plate	0			0.227(3)	0.3939(5)	0.3787 (5)	0	0	0	0
7	Black	1	Round	Jagged	Plate	1			0	0.3623(6)	0.6434(11)	0	0	0	0
8	Black	1	Round	Jagged	Plate	2			1 (1)	0	0	0	0	0	0
9	Black	1	Round	Jagged	Round	0			0.667(2)	0	0	0	0	0	0.333(1)
10	Black	1	Round	Jagged	Round	1			0	0	0	0	0	1 (2)	0
11	Tan	1	Oblong	Jagged	Cigar	4			0	0	0	1(1)	0	0	0
12	Tan	1	Oblong	Jagged	Oblong	0			0	0	0	0	0	1 (2)	0
13	Tan	1	Oblong	Jagged	Oblong	1			0	0	0	0	0	0	1 (1)
14	Tan	1	Oblong	Jagged	Oblong	2			0	0	0	0	0	0	1 (3)
15	Tan	1	Oblong	Jagged	Oblong	3			0	0	0	0	0	0	1 (1)
16	Tan	1	Oblong	Jagged	Oblong	4			1 (3)	0	0	0	0	0	0
17	Tan	1	Oblong	Jagged	Round	0			0	0	0	0	0	1 (1)	0
18	Tan	1	Round	Jagged	Chunk	0			0	0	0	0	0	0	1 (1)
19	Tan	1	Round	Jagged	Cigar	2			0	0	0	1(3)	0	0	0
20	Tan	1	Round	Jagged	Cigar	3			0	0	0	1(3)	0	0	0
21	Tan	1	Round	Jagged	Oblong	0			0	0	0	0	0	1 (36)	0
22	Tan	1	Round	Jagged	Oblong	1			0	0	0	0	0	0.50(1)	0.50 (1)
23	Tan	1	Round	Jagged	Oblong	2			0	0	0	0	0	0	1 (4)
24	Tan	1	Round	Jagged	Round	0			0	0	0	0	0	1 (6)	0
25	Tan	1	Round	Jagged	Round	1			0	0	0	0	0	1 (2)	0
26	Tan	1	Round	Jagged	Round	4			1 (1)	0	0	0	0	0	0
27	Tan	1	Round	Smooth	Chunk	0			0	0	0	0	1(1)	0	0
28	Tan	1	Round	Smooth	Cigar	1			0	0	0	1(3)	0	0	0
29	Tan	1	Round	Smooth	Cigar	2			0	0	0	1(20)	0	0	0
30	Tan	1	Round	Smooth	Cigar	3			0	0	0	1(51)	0	0	0
31	Tan	1	Round	Smooth	Cigar	4			0	0	0	1(5)	0	0	0
32	Tan	1	Round	Smooth	Oblong	1			0	0	0	1(1)	0	0	0
33	Tan	1	Round	Smooth	Oblong	3			0	0	0	1(4)	0	0	0
34	Tan	1	Round	Smooth	Plate	3			0	0	0	1(1)	0	0	0
35	Tan	1	Round	Smooth	Ovoid	2			0	0	0	0	1(2)	0	0
36	Tan	1	Round	Smooth	Ovoid	3			0	0	0	0	1(21)	0	0
37	Tan	1	Round	Smooth	Ovoid	4			0	0	0	0	1(1)	0	0
38	Black	2	Oblong	Jagged	Round	2	Plate	1	1 (1)	0	0	0	0	0	0
39	Black	2	Oblong	Jagged	Oblong	0	Round	3	0	0	0	0	0	0	1 (1)
40	Black	2	Round	Jagged	Round	0	Oblong	1	1 (1)	0	0	0	0	0	0
41	Black	2	Round	Jagged	Oblong	1	Plate	1	1 (1)	0	0	0	0	0	0
42	Black	2	Round	Jagged	Round	1	Plate	1	1 (2)	0	0	0	0	0	0
43	Black	2	Round	Jagged	Oblong	2	Oblong	0	1 (2)	0	0	0	0	0	0
44	Black	2	Round	Jagged	Round	3	Oblong	1	1 (2)	0	0	0	0	0	0
45	Black	2	Round	Jagged	Round	1	Plate	1	1 (1)	0	0	0	0	0	0
46	Black	2	Round	Jagged	Round	1	Round	1	0	0	0	0	0	0	0 (1)
47	Tan	2	Oblong	Jagged	Oblong	4	Round	1	1 (1)	0	0	0	0	0	0
48	Tan	2	Oblong	Jagged	Round	4	Oblong	1	1 (1)	0	0	0	0	0	0
49	Tan	2	Oblong	Jagged	Oblong	1	Oblong	4	0	0	0	0	0	0	1 (1)
50	Tan	2	Oblong	Jagged	Round	1	Cigar	4	0	0	0	0	0	0	1 (1)
51	Tan	2	Oblong	Jagged	Cigar	2	Oblong	2	0	0	0	0	0	0	1 (1)
52	Tan	2	Oblong	Jagged	Cigar	3	Oblong	3	0	0	0	0	0	0	1 (1)
53	Tan	2	Oblong	Jagged	Cigar	3	Round	3	0	0	0	0	0	0	1 (1)
54	Tan	2	Round	Jagged	Cigar	2	Oblong	2	0	0	0	0	0	0	1 (1)
55	Tan	2	Round	Jagged	Cigar	3	Oblong	2	0	0	0	0	0	0	1 (1)
56	Tan	2	Round	Jagged	Cigar	4	Round	1	0	0	0	0	0	0	1 (1)
57	Tan	2	Round	Jagged	Cigar	4	Oblong	4	0	0	0	0	0	0	1 (1)
								Column Totals	(25)	(24)	(25)	(92)	(25)	(50)	(25)

AAA = Aphidencyrtus aphidivorus; ANG = Aphelinus nigritus; ASY = Aphelinus asychis; LTE = Lysiphlebus testaceipes; PRA = Praon n.sp.; CHS = Charips sp. (megourae complex); PAS = Pachyneuron siphonophorae.

*Numbers in parentheses indicate number of specimens evaluated from each species.

mummy would be assigned to a particular species is computed as follows. First, obtain the conditional probability Pr $\{S_6|V_j\}$ of that state for each species:

$$\Pr\{S_6|\text{AAA}\} = \frac{3}{25};\ \Pr\{S_6|\text{ANG}\} = \frac{4}{24};\ \Pr\{S_6|\text{ASY}\} = \frac{5}{25};$$

$$\Pr\{S_6|\text{LTE}\} = \Pr\{S_6|\text{PRA}\} = \Pr\{S_6|\text{CHS}\} = \Pr\{S_6|\text{PAS}\} = 0.$$

Next compute the species membership probabilities, using equal prior probabilities in the formula on page 13. The resulting probabilities are:

$$\Pr\{\text{AAA}|S_6\} = .120/.528 = .227;\ \Pr\{\text{ANG}|S_6\} = .208/.528 = .394;$$

$$\Pr\{\text{ASY}|S_6\} = .200/.528 = .379;$$

$$\Pr\{\text{ATE}|S_6\} = \Pr\{\text{PRA}|S_6\} = \Pr\{\text{CHS}|S_6\} = \Pr\{\text{PAS}|S_6\} = 0$$

A mummy that generated this multivariate state would be placed in either group ANG or ASY, due to the closeness of their probabilities.

If the investigator assigned a prior probability of 0.6 to AAA, 0.2 to each of ANG and ASY, and 0 to the remaining species, because of information that he had about the abundance of this species in the field, the probabilities would be:

$$\Pr\{\text{AAA}|S_6\} = \frac{(.120)(.6)}{(.120)(.6) + (.208)(.2) + (.200)(.2)} = \frac{.072}{.1536} = .468 = 46.8\%$$

$$\Pr\{\text{ANG}|S_6\} = \frac{(.208)(.2)}{(.120)(.6) + (.208)(.2) + (.200)(.2)} = \frac{.0416}{.1536} = .270 = 27.0\%$$

$$\Pr\{ASY|S_6\} = \frac{(.200)(.2)}{(.120)(.6) + (.208)(.2) + (.200)(.2)} = \frac{.040}{.1536} = .260 = 26.0\%$$

$$\Pr\{LTE|S_6\} = \Pr\{PRA|S_6\} = \Pr\{CHS|S_6\} = \Pr\{PAS|S_6\} = 0$$

With this degree of prejudice on the sample, the specimen would be placed in group AAA. If the prior probability was assigned without sound reasoning, the placement of the sample could be an error.

In the group of parasites evaluated during this study, there were several features that were not constant, yet they occurred frequently enough to be at least indicative of the identity of the parasite or a group of parasites.

The location of the exit hole was one character that was extremely variable in nature. A typical location for the primary parasite exit hole was in the posterior region of the mummy, and located on the dorsum. In all three species of secondary parasites, the exit holes frequently were located in several different quadrants, and in lateral or ventral positions on the mummies. Hafez (1965) mentioned this in regard to the secondary parasites of D. rapae. Having this prior knowledge, an investigator could assign a prior probability of zero to one that is appropriately weighted.

Other characters that would allow assignment of a prior probability are the pupal exuviae of P. siphonophorae and the location of meconial deposits of Aphelinus that were described earlier. These characters were not completely consistent within a species, but occurred often enough to be indicative of a species when they were present.

When speaking of prior probabilities, it must be understood that these are entirely subjective criteria, and useful only in quantifying

the investigator's prejudice on the sample. Ideally, these prior probabilities should be assigned only after examination of a number of specimens.

CHAPTER IV

SUMMARY

This study was undertaken to determine if an empty parasite mummy possessed characteristics that could be used in the identification of the emergent adult parasite.

A total of four species of primary parasites and four species of secondary parasites were reared from mummies from either field collections or laboratory cultures. Characters of four aphid species were evaluated in order to identify the host of the parasite. Only two specimens of Asaphes lucens (Prov.), a secondary parasite, were collected. Due to insufficient numbers, this parasite was not evaluated statistically. The data gathered were compared among species, then analyzed by means of a discriminant analysis using qualitative variables.

The main findings were:

1. The species of aphid host could be determined by color and structural differences of the mummy.
2. Features of the empty mummies; including color, exit hole shape, hole margin shape, as well as number and shape of meconial pellets, were found to be consistent for a given species.

The characters that were found to be consistent within a species were incorporated into diagnostic keys. These keys were designed to distinguish adult parasites, aphid species based on empty mummy features, and parasite identity based on empty mummy characteristics.

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APPENDIX A

DIAGNOSTIC KEYS TO PARASITES AND APHIDS

KEY TO THE SPECIES OF GREENBUG PARASITES

BASED ON ADULT FORMS

1. Wing veination complete (Figures 3A,B).....2.

   Wing veination at least somewhat reduced (Figures 3C,D,E).....3.

2. Radial vein well developed apically, interradial II vein absent (Figure 3B).....Praon n.sp.....

   Radial vein absent apically, interradial II vein present (Figure 3A).....Lysiphlebus testaceipes....

3. Radial cell enclosed distally (Figure 3D), abdomen sub-triangular in profile.....Charips sp. (megourae complex)..

   Radial cell not enclosed, abdomen not as in 3.....4.

4. Body color metallic, usually black or green.....5.

   Body color not noticeably metallic.....7.

5. Body color metallic black; abdomen joined broadly to thorax; wings much longer than abdomen.....Aphidencyrtus aphidivorus..

   Body color metallic green; abdomen definitely petiolate; wings not much longer than abdomen..... .....6.

6. Abdomen strongly convex ventrally; marginal vein of forewing not noticeably thickened (Figure 3C); legs entirely yellow.....

   .....Asaphens lucens..

   Abdomen flattened or depressed ventrally; marginal vein of forewing noticeably thickened along its entire length (Figure 3E); entire leg, or at least femora, with alternating dark bands.....

   .....Pachyneuron siphonophorae...

7. Abdomen entirely or partially black.....8.
   Abdomen predominately yellow; legs, and flagella of antennae yellow to testaceous.....*Aphelinus asychis*...
8. Legs with alternating dark bands; antennae completely dark.....
   .....*Aphidencyrtus aphidivorus*...
   Legs and antenna yellow to hyaline in color.....*Aphelinus nigritus*.

KEY TO APHID SPECIES BASED ON EMPTY MUMMIES

1. Body color black.....2.
   Body color light beige to dark tan.....5.
2. Antennal length less than or equal to ½ the mummy length; tips of cornicles dark.....*Rhopalosiphum maidis*...
   Antennal length greater than ½ the mummy length; other characters variable.....3.
3. Cornicles black along entire length.....*Macrosiphum avenae*...
   Cornicles same color as body of mummy; may be darkened at apex....4.
4. Cornicles constricted just proximad to flange..*Rhopalosiphum padi*...
   Cornicles sub-cylindrical or tapering, not constricted proximad to flange.....*Schizaphis graminum*...
5. Antennal length less than or equal to ½ the mummy length; tips of cornicles and all legs entirely black.....*Rhopalosiphum maidis*...
   Antennal length greater than ½ the mummy length; other characters variable.....6.
6. Cornicles, with darkened tips, constricted just proximad to flange; body color generally medium to dark tan.....*Rhopalosiphum padi*...
   Cornicles sub-cylindrical or tapering; not constricted proximad to flange; body color generally light beige to medium tan.....7.
7. Cornicles and legs same color as rest of mummy, never darkened or black.....*Schizaphis graminum*...
   Cornicles dark or black; legs with alternating dark and light bands. .....*Macrosiphum avenae*...

KEY TO THE SPECIES OF GREENBUG PARASITES

BASED ON EMPTY MUMMIES

1. Mummy generally tan or beige in color.....2.

   Mummy generally black in color.....8.

2. Pupal cocoon inside mummy; silken strands support shell of mummy..3.

   Pupal cocoon outside of and below mummy; shell of mummy thin, often easily broken (Figure 4C).....*Praon* n. sp...

3. Exit hole smooth, hole shape usually round, meconium consisting of 16-25, sometimes 11-15 cigar-shaped black pellets (Figure 4A, 6A)...

   .....*Lysiphlebus testaceipes*...

   Exit hole margin jagged or dentate, other characters variable.....4.

4. One meconial cluster present.....5.

   Two separate meconial clusters present.....7.

5. Exit hole shape usually round; meconial cluster contains 1-5 pellets, usually oblong in outline, sometimes round (Figures 4B, 7A).....

   .....*Charips* sp. (*megourae* complex)...

   Hole shape oblong, meconium not as above.....6.

6. Meconial cluster contains 11-15 oblong, black pellets.....

   .....*Pachyneuron siphonophorae*...

   Meconial cluster contains more than 25 round to oblong black pellets

   .....*Aphidencyrtus aphidivorus*...

7. Meconial cluster '1' with more than 12 oblong pellets; cluster '2' with 3 or fewer round to oblong pellets.....

   .....*Aphidencyrtus aphidivorus*...

Meconial cluster '1' with more than 9 cigar-shaped pellets; cluster '2' with more than 3 round or oblong pellets (Figures 6A, 7B).....
.....*Pachyneuron siphonophorae*...

8. One meconial cluster present.....9.
Two separate meconial clusters present.....11.

9. Meconial cluster composed of 4-10 plate shaped pellets, obviously flattened in cross-section, usually with several wave-like ridges on one surface (Figure 6B,C).....*Aphelinus* spp...
Meconial pellets not as above, definitely without wavelike ridges on one surface.....10.

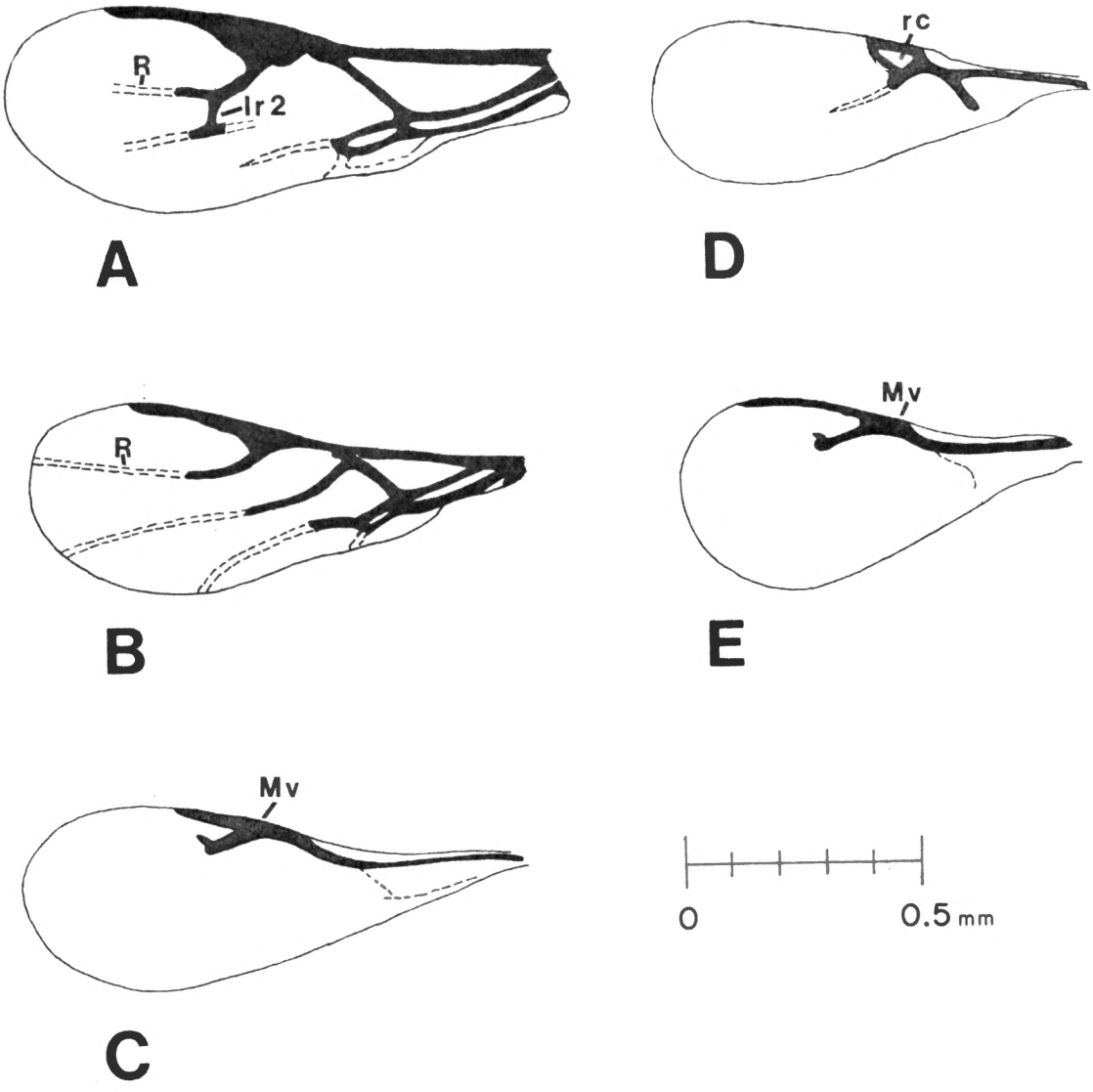
10. Meconial cluster composed of 5 or fewer plate-shaped or round pellets, hole shape variable (Figure 7C).....
.....*Aphidencyrtus aphidivorus*...
Meconial cluster composed of 6-10 pellets, exit hole shape variable (Figure 7A).....*Charips* sp. (*megourae* complex)...

11. Meconial cluster '1' consisting of 4-12 round or oblong black pellets; cluster '2' consisting of 1-6 oblong or plate shaped red or reddish brown pellets.....*Aphidencyrtus aphidivorus*...
Meconial cluster '1' consisting of 1-6 round or oblong pellets; cluster '2' consisting of 4-12 round black pellets; neither cluster having any red or reddish brown pellets.....
.....*Pachyneuron siphonophorae*...

APPENDIX B

FIGURES OF SOME DIAGNOSTIC CHARACTERS

Figure 3. Forewings of primary and secondary parasites: A. Lysiphlebus testaceipes, veination after Stary (1976); B. Praon n.sp., veination after Stary (1976); C. Asaphes lucens, veination after Graham (1969); D. Charips sp. (megourae complex), veination of. Gutierrez and van den Bosch (1970); E. Pachyneuron siphonophorae, veination after Graham (1969). Ir 2-interradial II vein; R-radial vein; Mv- marginal vein; rc-radial cell


R
Ir 2
A
rc
D
R
B
Mv
E
Mv
C
0
0.5 mm

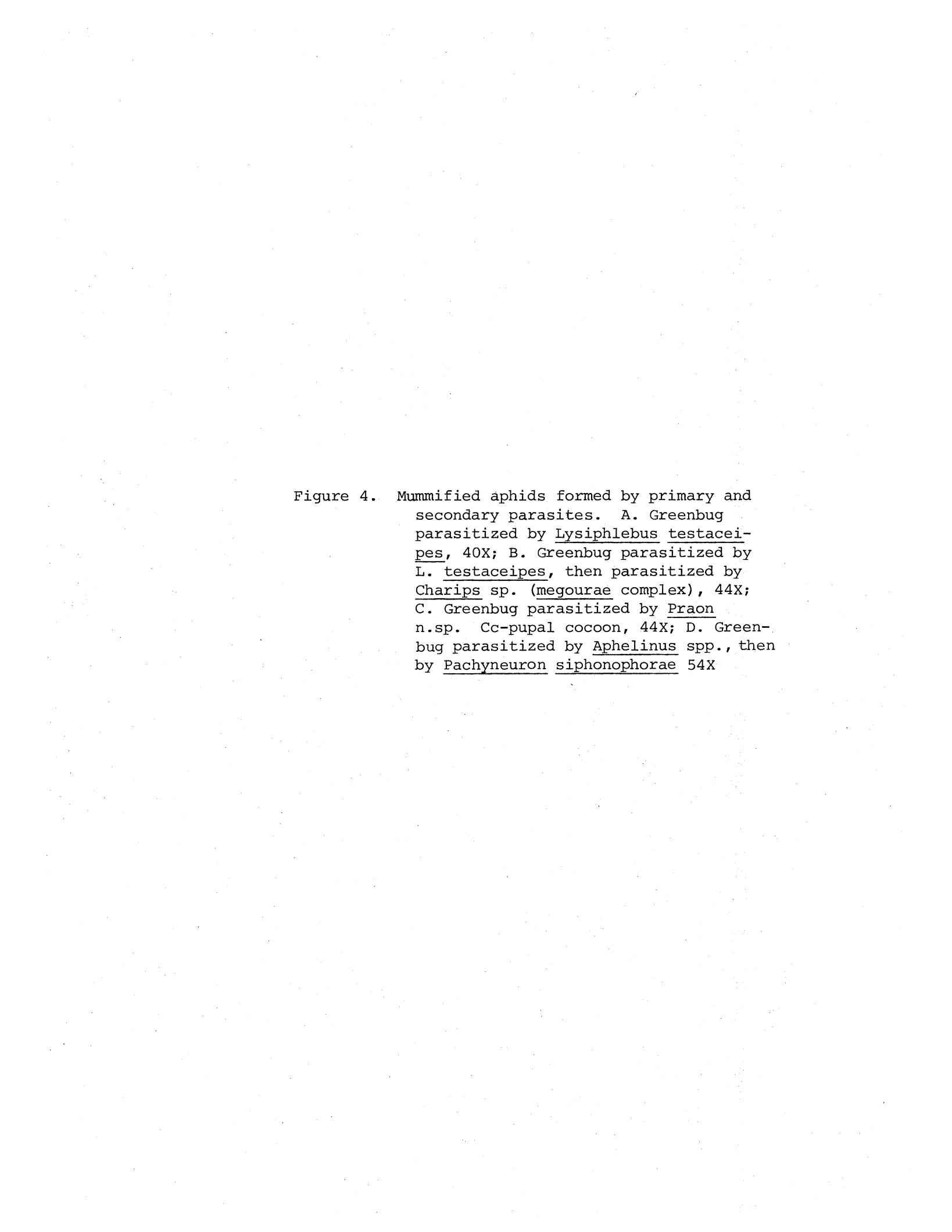


Figure 4. Mummified aphids formed by primary and secondary parasites. A. Greenbug parasitized by Lysiphlebus testaceipes, 40X; B. Greenbug parasitized by L. testaceipes, then parasitized by Charips sp. (megourae complex), 44X; C. Greenbug parasitized by Praon n.sp. Cc-pupal cocoon, 44X; D. Greenbug parasitized by Aphelinus spp., then by Pachyneuron siphonophorae 54X

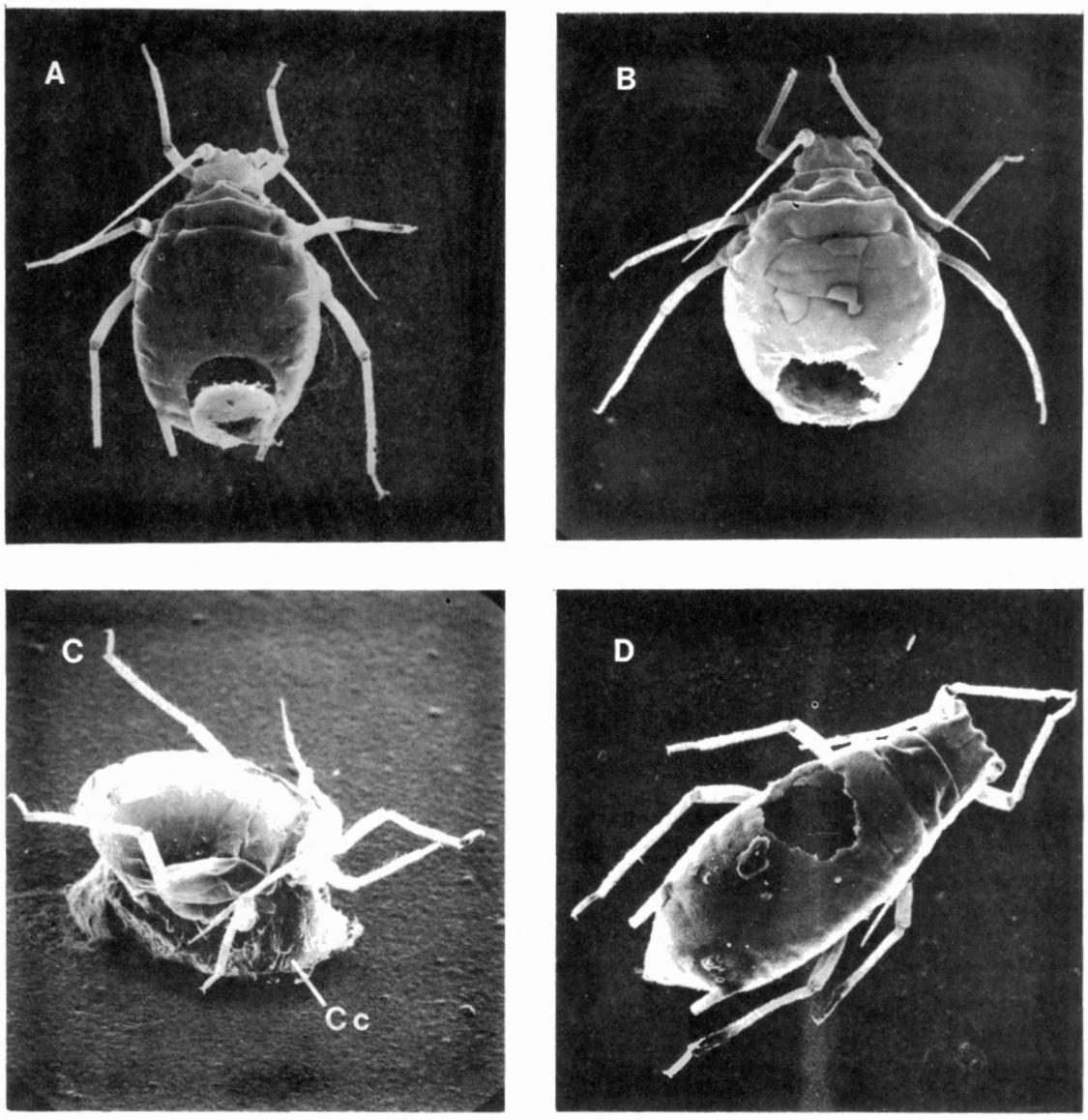
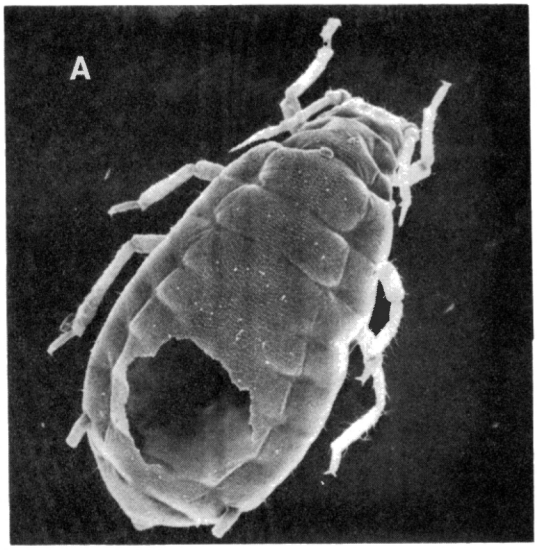

A
B
C
Cc
D

Figure 5. Mummified aphids formed by primary and secondary parasites. A. Greenbug parasitized by Aphelinus spp., then by Aphidencyrtus aphidivorus; 54X; B. Greenbug parasitized by Aphelinus spp., 54X


A

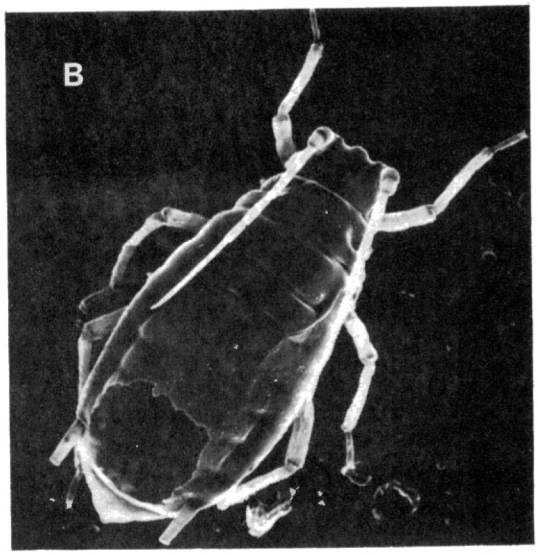

B

Figure 6. Meconial deposits of primary parasites. A. Lysiphlebus testaceipes, 86X; B. Aphelinus asychis, 100X; C. A. nigritus, 130X; D. Praon n.sp., 240X

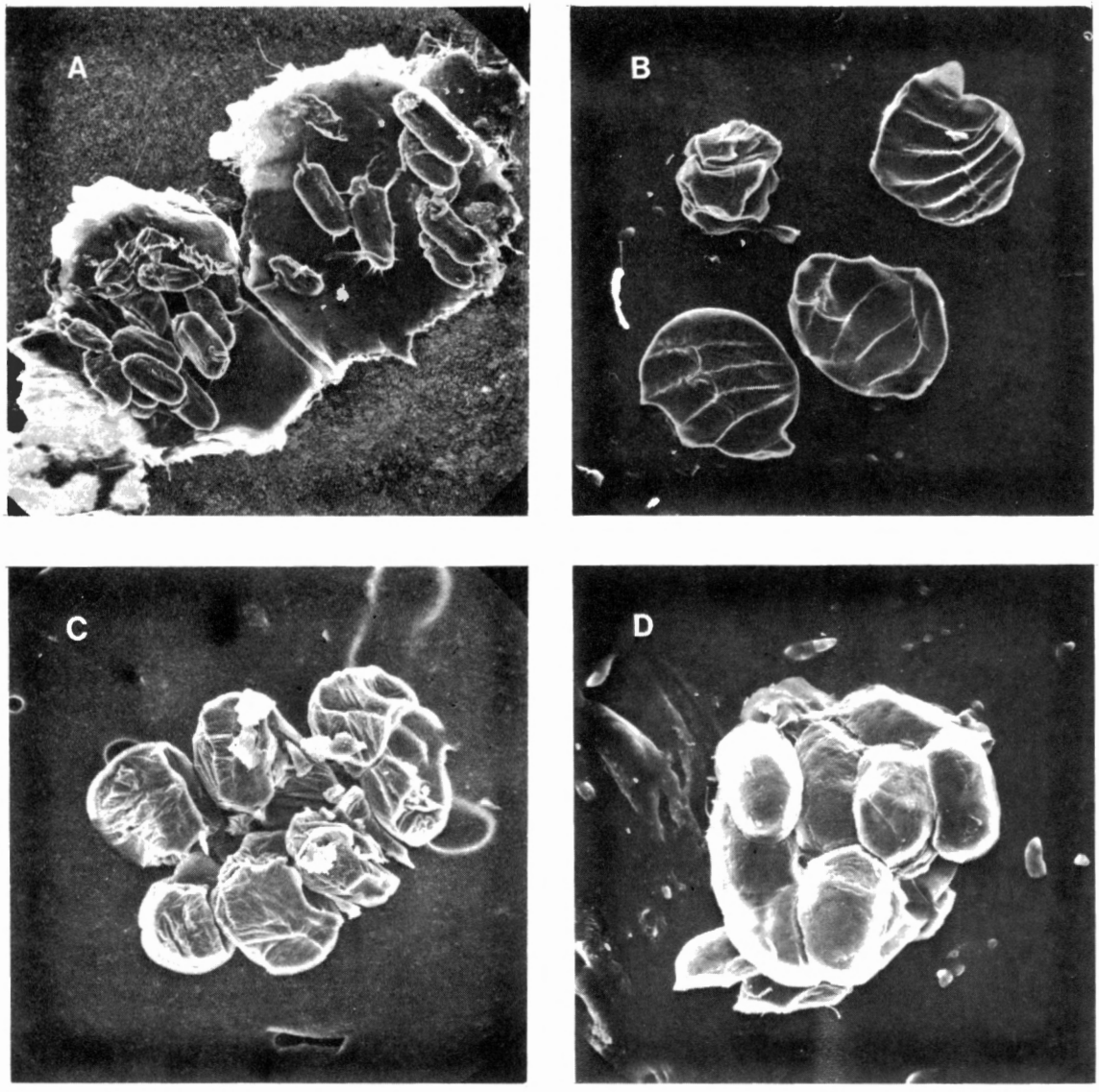
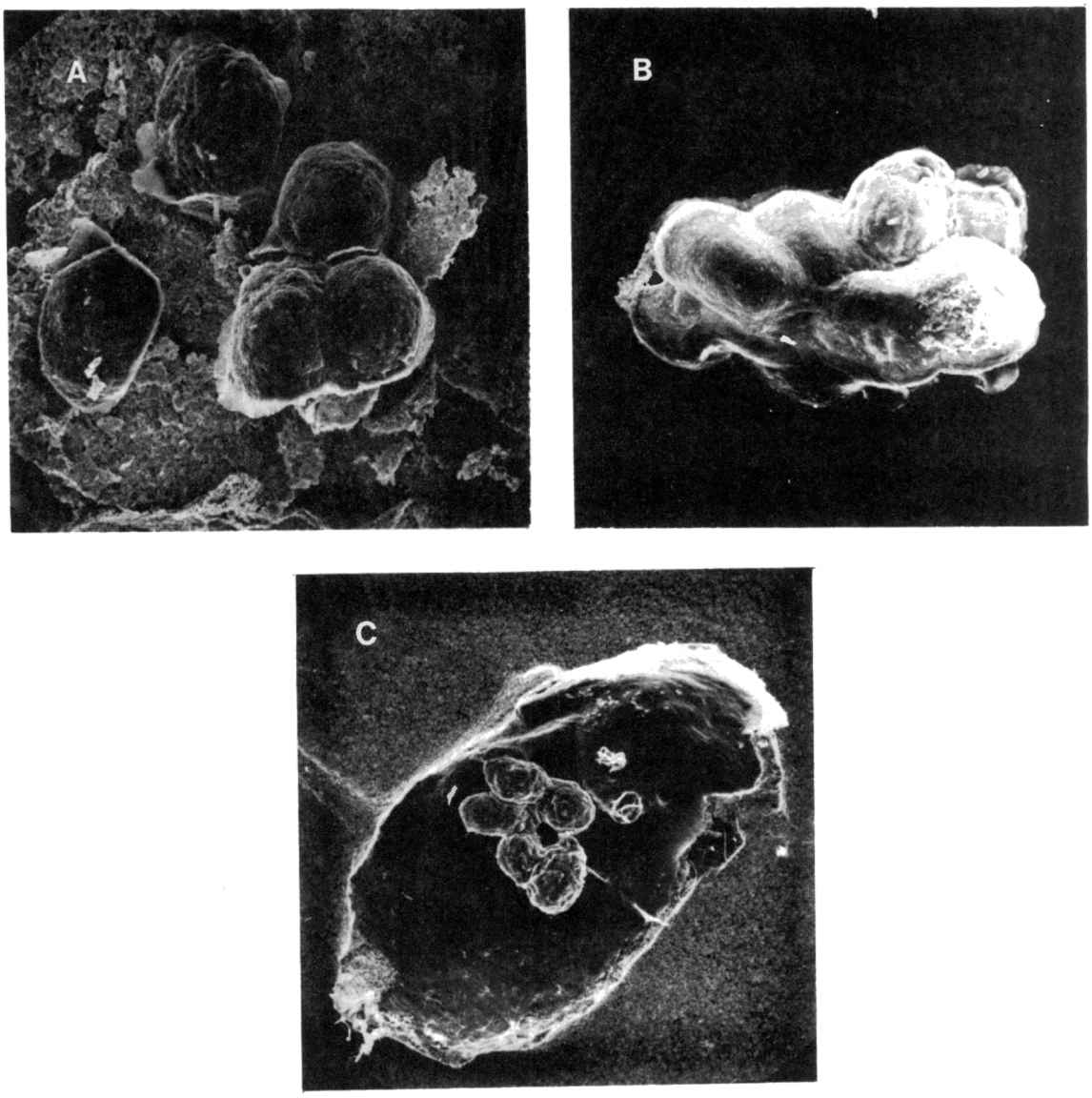

A
B
C
D

Figure 7. Meconial deposits of secondary parasites. A. Charips sp. (megourae complex), 200X; B. Pachyneuron siphonophorae, 160X; C. Aphidencyrtus aphidivorus, 86X


A
B
C

VITA[2]

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