BIOSYSTEMATIC STUDIES ON THE APHIDIIDAE OF ISRAEL (HYMENOPTERA: ICHNEUMONOIDEA) 1. INTRODUCTION AND KEY TO GENERA

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ABSTRACT

Background material regarding the aphid parasites of the family Aphidiidae, as known from world literature and studies of this group in Israel, are presented. General systematics, morphology, and bionomics of this family are discussed and a key for identification of the ten genera found in Israel is provided.

The damage caused by aphids (Homoptera: Aphidoidea) due to their feeding, honeydew production, disease transmission and plant contamination, combined with their exceptional fecundity, make them an important group of plant pests. Over 200 species of aphids have been recorded in Israel (Bodenheimer and Swirski, 1957; Swirski, 1963). Although many species are not known to be of economic importance, changes in the local flora, the upsetting of ecological balances and/or unusual climatic conditions could cause even "insignificant" species to attain pest status. Spraying with toxic chemicals, the most commonly practiced method of control, involves negative aspects such as the loss of effectiveness due to the development of resistance (Hussey and Bravenboer, 1971; Sawicki et al., 1978), the upsetting of ecological balances and environmental pollution.

During recent years, increasing attention has been directed toward biological control as a preferred alternative to the use of chemical pesticides. Natural enemies, searching out and destroying pests, may lower their population densities and maintain them below the economic threshold, thereby reducing or eliminating the need for other forms of control.

The family Aphididae (Hymenoptera: Ichneumonoidea), numbering about 400 known species world-wide, is generally considered one of the most effective and promising groups of natural enemies of aphids (Mackauer and Starý, 1967; Starý, 1988). These small wasps, generally ranging in size from 1.2 to 3.5 mm., are solitary internal parasitoids, developing exclusively in aphids. Development time from oviposition to emergence is usually 10-14 days in warm weather.

The present study was carried out in an attempt to survey, identify and revise the species of Aphidiidae occurring in Israel and to obtain pertinent biological information about them.

HISTORICAL BACKGROUND

The first published record of an aphid parasite appears in Linnaeus' Systema Naturae (1758) for the species *Ichneumon aphidum*. However, the description was inadequate by

modern standards and the type specimen was lost. Nees (1818) wrote the first monograph devoted to this group, and 16 years later updated it (Nees, 1834). Haliday studied these aphid parasites and in his 1833 monograph described them as a subfamily of the Braconidae. In 1834 he wrote a second monograph on this group and accorded it family status.

Some authors (e.g., Smith, 1944; Narayanan et al., 1960) considered these wasps as a subfamily of the Braconidae, while others (Mackauer and Starý, 1967; Marsh, 1971) have given them independent family status. Although the latter approach is now generally more accepted (Muesebeck and Walkley, 1951; Takada, 1968; Marsh, 1971), Tremblay (1967) analyzed their degree of specialization and expressed the opinion that they deserve subfamily rank among the Braconidae. The same opinion has been expressed by Van Achterberg (1984).

According to Short (1952), the genera of this family can be recognized by the spiracles of the first-instar larvae. However, using this trait is impractical. During this study we used only adult specimens, their diagnostic characters being more numerous, distinct and convenient for examination.

PREVIOUS RECORDS OF APHIDIDAE FROM ISRAEL

Knowledge of the Aphidiidae of Israel is rather sparse. The first listing of an aphidiid in Israel is that of Bodenheimer (1930), who mistakenly recorded Diaeretus (= Diaeretiella) rapae as a parasite of the imported cabbage worm, Pieris rapae (L.). This same parasite-host relationship is later mentioned, with an additional record of an Aphidius sp. as a parasite of an "Aphididae" sp. (Bodenheimer, 1937). This listing, while only to the generic level, is the first correct aphidiid-aphidid association recorded in Israel.

No new records of Aphidiidae were listed here until Plaut (1949) published his doctoral thesis of ecological and biological studies of aphids in Israel. The short-tailed almond aphid, *Brachycaudus amygdalinus* (Schouteden), provided him with two primary and four secondary parasites. Both of the primary parasites recorded were aphidiids. One, *Ephedrus persicae* (= pulchellus), was identified to the species level. The second was an *Aphidius* species.

Swirski (1952) studied 13 species of aphids on fruit trees grown in Israel. For one year he recorded the monthly levels of parasitism on the mealy plum aphid, *Hyalopterus pruni* (Geoffroy), but the parasites were not identified. Swirski concluded that "though percentages of parasitism were moderate during some months, the parasites were not responsible for the collapse of populations which occurred towards the summer" (authors' translation from the Hebrew text). Swirski's published records show, however, that of all the natural enemies he recovered (his list includes parasitic Hymenoptera, syrphid flies, lady-bird beetles, gall-midges and predaceous mites), only the parasitic wasps were found throughout the year.

Harpaz (1953) studied the aphids on graminaceous plants. He reared aphidid parasites from six additional aphid species, but most of the parasites he collected were identified only to the generic level.

Bodenheimer and Swirski (1957) summarized the known information about Aphidiidae and their host records for Israel. From the two hundred and seven species of aphids recorded, nine aphidiid parasites were listed. Four were identified to the generic level only,

and of the 5 identified species, two have subsequently proved to be incorrect determinations.

Several additional species were recorded in the late 1950's and in the 1960's. Mackauer (1959a, 1959b, 1960a, 1962, 1963) published new records of Aphidiidae and their hosts in Israel based on material collected by I. Harpaz. van den Bosch (1957) collected one species in the spotted alfalfa aphid and Rosen (1964) recorded seven species from aphids infesting citrus.

TABLE 1. LIST OF APHIDIDAE RECORDED IN ISRAEL BEFORE THE START OF THIS STUDY

PARASITE SPECIES

HOST APHIDS 1. Aphidius ervi Haliday Acyrthosiphon pisum (Harris) [2] = (Diaeretus ervi Haliday) [4] 2. Aphidius matricariae Haliday Myzus persicae (Sulzer) [12] Aphidius colemani Viereck Toxoptera aurantii (Boyer de Fonscolombe) [12] 3. = (Lysaphidus platensis Bréthes) 4. Aphidius? transcaspicus Telenga Hyalopterus pruni (Geoffroy) [2] = (Aphidius sonchi Matshall) 5. Diaeretiella rapae (M'Intosh) Schizaphis graminum (Rondani) [2] = (Diaeretus rapae Curtis) Myzus persicae [13] 6. Diaeretus leucopterus (Haliday) no host listed [13] 7. Ephedrus persicae Froggatt Aphis craccivora Koch [11] = (Ephedrus pulchellus Stelfox, A. ruborum (Börner) [7] = (Ephedrus nitidus Gahan) A. umbrella (Börner) [11] Brachycaudus amygdalinus (Schouteden) [1] Rhopalosiphum maidis (Fitch) [7] R. padi (L.) [7] Toxoptera aurantii [12] 8. Lysiphlebus confusus Tremblay & Eady Aphis ruborum [9] Toxoptera aurantii [12] = (L. ambiguus (Haliday)) 9. Lysiphlebus fabarum (Marshall) Aphis gossypii Glover [13] Toxoptera aurantii [12] Pauesia silana Tremblay Cinara palaestinensis Hille Ris Lambers [3] = (Aphidius varius Wesmael) = (Pauesia pini (Haliday)) 11. Praon exsoletum palitans (Nees) Therioaphis trifolii maculata (Buckton) [6] 12. Praon volucre (Haliday) Macrosiphum (Sitobion) fragariae (Walker) [6] Myzus persicae [12] Rhopalosiphum padi (L.) [6] 13. Binodoxys angelicae (Haliday) Aphis craccivora [13] = (Trioxys angelicae Haliday) A. gossypii [8] Toxoptera aurantii [12] Hyadaphis foeniculi (Passerini) [7] 14. Trioxys brevicornis (Haliday) 15. Trioxys complanatus (Quilis) Therioaphis trifolii maculata [5,7] = (Trioxys utilis Muesebeck) = (T. pallidus (Haliday))

First references: [1] Plaut, 1949; [2] Harpaz, 1953; [3] Bodenheimer and Neumark, 1955; [4] Bodenheimer and Swirski, 1957; [5] van den Bosch, 1957; [6] Mackauer 1959a; [7] Mackauer 1959b [8] Mackauer, 1960a; [9] Mackauer 1960b; [10] Mackauer, 1962; [11] Schlinger and Mackauer, 1963; [12] Rosen, 1964; [13] Avidov and Harpaz, 1969.

Currently accepted names are listed first, followed by incorrect names (synonyms, misidentifications) as reported in these references.

Rivnay (1968) attempted to summarize records of the known Aphidiidae in Israel, but failed to include in his review records from articles published outside the country.

No further studies were reported until the beginning of this project. Table 1 lists the Aphidiidae and their hosts as known in Israel prior to the start of the present study. By eliminating misidentifications and combining redundant records, we are left with a list of 15 species of Aphidiidae, 17 aphids known to serve as their hosts, and a few biological notes regarding members of the family.

OVERVIEW OF THE PRESENT STUDY

Beginning in 1974 and continuing for a period of over ten years, Aphidiidae were surveyed and studied throughout Israel. Field collections of parasitized and unparasitized aphids and laboratory colonies provided information on the biology and systematics of the Aphidiidae. The present series of papers provides a compilation of the biological information gathered, presents new descriptions of the genera and species found and keys for their identification. Special attention has been given to intraspecific variation, which proved to be much greater than previously assumed. Several new diagnostic characters are presented.

As a result of this extended study, 31 aphidiid species (5 of them new to science), representing 10 genera and 60 identified aphid host species have now been recorded in Israel.

APHIDIIDAE

The Aphidiidae belong to the order Hymenoptera, suborder Apocrita, superfamily Ichneumonoidea. They resemble Braconidae, are small (about 2 mm. in length), elongate, antenna filiform (about half body length), head width about equal to thorax, prothorax hidden by gibbous mesoscutum, propodeum connected by narrow petiole to lanceolate gaster. Wings at rest folded flat over dorsum, extending to tip of abdomen.

TAXONOMIC DETERMINATION OF APHIDIDS

This section deals with only the most important of the diagnostic characters necessary for the generic and specific identification of aphidiids. During the course of this study, a limited number of diagnostic characters, several in common use and some new, were found to be adequate for accurate identification at the species level. For a complete general description of the Aphidiidae, one is referred to Starý (1970).

For generic identification, foremost in importance is wing venation. Though there are two systems of nomenclature in common use for wing venation of aphidiids, (Smith, 1944; Starý, 1958) we have chosen that of Starý because of its more thorough application to all aphidiid genera, leaving no veins or cells unnamed. Narayanan et al. (1962) compare these two systems in detail. All genera found in Israel can be identified easily by wing venation either alone or supplemented by one or more of the following: number of antennal segments, general shape and carination of propodeum, contour of petiole and ovipositor sheaths, coloration of mummy and method of pupation.

Species identification is a more involved procedure and generally requires that specimens be slide-mounted after having been dissected and the various body parts placed in a position for optimal viewing. The head is best viewed anteriorly, the mesoscutum,

propodeum and petiole dorsally, and the ovipositor sheaths laterally. With species of *Aphidius* it is also often necessary to view the head dorsally and the petiole laterally. However, experience and large series of specimens can often make the need for slide preparation unnecessary.

The following diagnostic traits have been found most valuable for accurate species identification.

Head: Number and shape of antennal segments. These traits are not absolute, and generally one can find a variation of 2-3 segments in different samples of the same species (especially those with long antennae) and slight variations of relative sizes of the segments. The ocellar triangle may be either acute, obtuse or right-angled. The shape and pilosity of the clypeus are important in separating species of certain genera. Lateral to the clypeus are two tentorial pits. The tentorial index, i.e., the ratio of the tentorio-ocular distance divided by the intertentorial distance, is important for the identification of several species of Aphidius. However, one must allow for intraspecific variation which is often greater than 10%, especially when considering that pressure by the cover-slip can cause some distortion. Of specific value are the number of segments of the maxillary (2-5) and labial (1-3) palps and the contour of the occipital carina (round, oval, invertedly U-shaped).

Thorax: The pronotum, because of its hidden position, is generally not used for identification; however, the gibbous mesoscutum is quite useful. Although generally smooth, the notaulices which arise anterolaterally have characteristic outlines, and the extent and manner in which they proceed posteriorly, coupled with patterns of setae which may or may not be present, are quite valuable diagnostic characters. Wing venation is an excellent trait for the separation of some species. Patterns of origin of the upper intermedian and lower cubital vein from the second cubital cell (together, near but separate, or widely separated) and the shape of the radial vein, are distinct and reliable traits.

Abdomen: The first abdominal segment, the propodeum, is fused with the thorax. This relatively flat segment is often marked with carinae, dividing it into several characteristic areolae, and it often bears various numbers of long or short setae, situated in characteristic positions or patterns. The second abdominal segment, the petiole, is generally elongate and narrow, and of characteristic shape for each genus. However, fine variations in shape and characteristic markings of dorsal and/or lateral carinae are often important for specific determination. The apex of the female abdomen, with its ovipositor and accompanying sheaths, are characteristic for the various genera. Their shapes and relative sizes, as well as the number and distribution of their setae, provide many important taxonomic traits. Some of these of these differences do not render themselves well to verbal descriptions, but pictures make them quite obvious. The unique ventral prongs of Trioxys and Binodoxys species, which extend posteriorly and enable the wasp to grasp its host during oviposition, are fitted dorsally and apically with setae and bristles of characteristic numbers, sizes and shapes and are important for species identification in these genera. In the male, the apex of the gaster is spatulate and conceals the genitalia. Although there are differences in males genitalia, and these have been used to place different genera into systematic groupings and for species identification (Tremblay, 1979, 1981, 1983), identification by use of female genitalia is much simpler and is standard practice for the family.

Coloration: The value of coloration as a diagnostic character for the Aphidiidae has been a subject of debate. Smith (1944) considered coloration to be consistent within the

species, and his keys often rely heavily on color for identification. Tremblay (1975) regards coloration to be widely variable within the species, and even gives separate descriptions for light and dark forms of the same species. Starý (1974) points out that coloration is variable, darker forms of the same species developing when temperatures are low and lighter specimens appearing when the wasp develops in warm weather. Starý states that, "on the one hand, colorations may be a useful character for a preliminary orientation, on the other hand, it may be misleading." Observations during the course of this study concur with the "color range" approach to the Aphidiidae. Specimens of the same species, reared in the laboratory under different conditions, can show striking differences in overall coloration, so much so as to give the impression of belonging to separate species. It is important to note, however, that for many species, the pattern of coloration (relative lightness or darkness of segments and appendages) is highly consistent, and provides an easy and reliable means for separating similar species. Johnson (1987) notes this consistency in his study of North American Praon.

In conclusion, although the Aphidiidae are a fairly homogeneous group with regard to size, color, general morphology and behavior, separation of this family into genera is relatively simple. Easily observed traits such as forewing venation, numbers of antennal segments, shape and carination of segments (especially propodeum and petiole) and appendages (especially ovipositor sheaths) serve well to distinguish the genera. However, recognition of species is often very problematic. Examination of catalogues (Narayanan et al., 1960, 1962; Mackauer and Starý, 1967; Mackauer, 1968) articles and monographs (Starý 1975, 1976, 1979) shows many species to have been described, even by the same author, under several synonyms. Two reasons for this are: (1) an insufficient number of diagnostic characters have been used on the species level; (2) investigators have not always been aware of the range of intraspecific variation for the characters used. During the past 20 years or so, by uniting several former species under one name, taxonomists have shown that they now accept the intraspecific variation to be much greater than was originally thought. Many aphidiids are known to be biologically distinct species, but, due to the recognized wide range of variability of their morphological characters, they are very difficult to separate. This problem of sibling species plagues systematists of many insect groups, and it seems as if it will be some while yet before the true value of many diagnostic characters in common use will be fully understood (Gauld, 1980).

Many previously ignored morphological traits have been examined in this study and several, already mentioned, have been found to be of practical application. Investigators should be well aware of the fact that conspecific specimens, when aligned differently for examination, can misleadingly give the impression of belonging to more than one species. To avoid such pitfalls, many conspecific specimens should be examined, so as to develop a clear picture of the range of variation within the species.

BIONOMICS OF THE APHIDIDAE

All species of Aphidiidae are solitary internal parasites of the Aphidoidea. Records of Aphidiidae as parasites of other insect groups have all proved to be erroneous.

Adult female wasps oviposit by inserting their ovipositor through the aphid host's integument. The egg, inside the body cavity, develops in two ways. The serosa (outer membrane) divides into a large number of cells, while the insect embryo develops within.

After hatching, the serosa cells lose their contact, become free in the host's hemolymph and develop into teratocytes or giant cells. Circumstantial evidence suggests that these cells may act as trophic coadjutors of the parasite larva (Tremblay and Caltagirone, 1973). The first and fourth (last) larval instars are mandibulate, whereas the second and third instars are amandibulate. The well developed mandibles of the 4th instar larva are used to tear apart the host's internal organs, which supply the food necessary to complete development. At this stage the aphid host is killed (Tremblay, 1966; Starý, 1970).

With the death of the host aphid, its integument, containing the fully developed larva, undergoes several modifications and becomes mummified. Observations of laboratory colonies maintained during the course of this study have indicated that larval movements, pushing and twisting within the host's integument during the final stages of feeding, may cause the characteristic bloated appearance assumed by the aphid mummy. While this takes place, the integument hardens and develops its characteristic color. Having completed feeding, the larva cuts a slit in the venter of the aphid and attaches it to the substrate. Subsequently, the larva spins a loose cocoon around itself within the mummy. An exception to this pattern is found in the genera *Praon*, *Lipolexis* and *Dyscritulus* (the latter two not found in Israel): Larvae of these genera emerge from the ventral slit in the mummified aphid and spin their cocoon beneath the remains of the host. As a result, the mummy assumes the characteristic appearance of a statue mounted on a wide-rimmed pedestal.

Most frequently, development to the adult stage goes on without interruption. However, some species during some seasons undergo a diapause, wherein the mature larva spins a thicker cocoon around itself and remains in an arrested state of development. This has been observed to last 1-3 months in Israel. The 4th-instar larva then pupates and metamorphosis proceeds as usual.

Aphidiid pupae are exarate. During this study, numerous final-instar larvae and pupae were carefully dissected out of their mummies without apparent injury, yet even when maintained in a humid environment, their development stopped. Pupae on the verge of emerging when dissected out were capable of molting and functioning as normal imagoes, but when extracted even 1-2 days before their scheduled emergence, all development ceased.

After completing development, the adult wasp gnaws a circular hole, most often in the posterior dorsum of the aphid, and emerges. For a short while after emergence it cleans itself. Both sexes are capable of mating almost immediately after emergence, and the preoviposition period of the female is 1-2 hours (Vevai, 1942; Sekhar, 1957).

In biparental species, mated females may lay fertilized (diploid) eggs which develop into females or unfertilized (haploid) eggs which develop into males (arrhenotoky). No differences in ovipositional behavior have been noticed between mated and unmated females. In Israel, all species of the genus *Lysiphlebus* are uniparental, unmated females producing only female offspring (thelytoky).

When observed in the laboratory, virgin females of biparental species, caged with conspecific males, did not display the heightened activity shown by males (much wing-flapping, antennal tapping and constant roaming). In most observed instances, virgin females were passive when approached by males. Not infrequently they attempted to avoid contact with males, and actively to prevent mating. Males caged with just-mated females usually did not show the same heightened activity as they did with virgin females. Mated females, if mounted by a male, actively avoided coition and were never observed to mate a second time.

Development time from oviposition to adult emergence varies according to the species and seasonal temperatures. Starý (1962) reported most rapid development of Aphidius ervi Haliday in Czechoslovakia (9-10 days) to occur at temperatures of 27°C. Below and above this temperature development is retarded, ceasing at about 2° and 32°C. Simpson et al. (1975) found Diaeretiella rapae to complete development 3 days sooner than Praon sp. at ca. 19°C. Campbell and Mackauer (1975) studied rates of aphid, aphidiid and hyperparasite development at different temperature regimens and were able to quantify the effect of temperature on development. Flint (1980) found variations in optimal temperatures for the development of different ecotypes of the same species.

Adult longevity in various species has been found to range from 1-2 days to over 50 days. Temperature, relative humidity and diet are the factors which most strongly affect longevity. The most extended longevity has been observed with temperatures about 20°C and 50% RH. Fresh or dry honeydew of aphids supply carbohydrates and amino acids to parasites in the field. Honey diluted with water is the best food for extending the longevity of these wasps in laboratory colonies (Starý, 1962, 1970).

HABITAT

Literature on the Aphidiidae frequently refers to various species as being generally confined to specific geographic regions or habitats. In Israel, for most of the species reared, the presence or absence of the aphid host has been found to be the critical factor. The presence of aphids is dependent on the availability of acceptable plant hosts, and only from such habitats were parasites reared. Monophagous Aphidiidae were found only in the habitats occupied by their single host, whereas polyphagous species could be reared from a wide range of climatic regions. A few species, however, despite the widespread availability of acceptable hosts, have been restricted to certain regions: Some species of Aphidius have been reared only in the very northernmost sections of the country; Adialytus thelaxis has been found only at altitudes of 600 m above sea level.

KEY TO THE GENERA OF APHIDIIDAE RECORDED IN ISRAEL (females)

This key is based primarily on morphological characters easily discernable upon microscopic examination. Characters such as color, type of mummy and host associations have been included whenever these have been found unique for the genus. Generic determination can be carried out using live or dead material, without requiring any special preparation.

Various authors have organized the family into tribes and subtribes, however, since only 10 genera are represented in Israel, these groupings have not been included.

Keys to species will be found in subsequent papers of this series, with the discussions of each genus. All keys and specific descriptions are based on Israeli material examined by the authors.

Terminology used generally follows that of Starý (1970) and is illustrated in figures 1-5.

1. Wing venation complete, dividing forewing into 5 major closed cells: basal, median, two radial cells and pterostigmal cell. Parts of the veins may be lightly colored or clear,

	but they are distinct. Antenna of both sexes always 11-segmented. Adult wasps and
	the aphid mummies shiny black Ephedrus Haliday
_	Wing venation incomplete, with less than 5 closed major cells. Mummies not black . 2
2(1).	Radial cells of forewing confluent, median vein having no interradial veins attached to
	it anteriorly. Notaulices complete. Clypeus and at least part of mesoscutum densely
	covered with long setae. Pupation in cocoon, attached to substrate, the empty
•	integument of the mummified aphid mounted above it. Both mummy and cocoon pale
	brown to white
_	Venation of forewing different. Notaulices incomplete. Clypeus and mesoscutum with
	sparse long setae. Pupation inside mummified aphid, which is attached directly to
	substrate
3(2).	Median cell and two radial cells confluent, creating a very large cell in central area of
` ,	forewing, its center located beneath proximal aspect of pterostigma. Second interradial
	vein closes the cell distally and is sometimes partially or completely transparent but
	distinct
_	Venation of forewing further reduced; median, radial and pterostigmal cells confluent
4(3).	Pterostigma broadly triangular, its length along the anterior edge of forewing less than
	twice its width. Propodeum with weak transverse carina separating a posterior
	depressed region from anterior aspect of segment
-	Pterostigma elongate, usually 3 or more times longer than wide. Propodeum generally
	divided into 5 distinct areolae, one narrow and centrally located, the remaining 4
	distributed peripherally
5(3).	Second interradial vein connects radial vein and short remnant of median vein.
	Propodeum convexly rounded, smooth, no prominent carinae. Petiole triangular,
	widening posteriorly Lysiphlebus Foerster
_	Wing venation further reduced, only radial vein present beneath pterostigma 6
6(5).	Apex of abdomen without auxiliary prongs
	Apex of abdomen with auxiliary prongs 9
7(6).	Propodeum smooth or with 2 short, divergent carinae at posterior aspect. Petiole
	elongate, slightly widening posteriorly. Exclusive parasites of Chaitophorinae and
	Thelaxinae Adialytus Foerster
_	Propodeum with fully-developed carinae creating a distinct central areola 8
8(7).	Transverse carina near center of propodeum divides the segment into a wide posterior
1	and an anterior region, sometimes further divided. Specific parasites of aphids of the
	genus Eulachnus
	Carinae divide propodeum into 4 peripheral and one elongate very narrow central
	areola
9(6).	Petiole with a single pair of spiracular tubercles Trioxys Haliday
_	Petiole with two pairs of tubercles, the anterior pair bearing the spiracles
	Binodoxys Mackauer

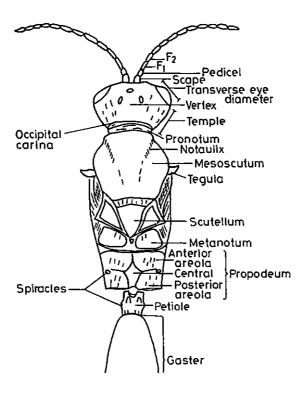


Fig. 1. General structure of an aphidiid: dorsal view.

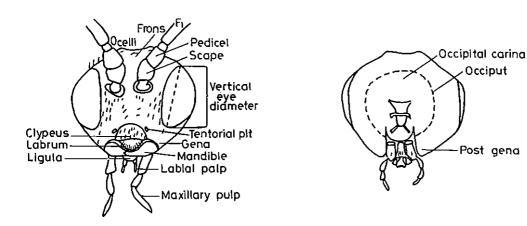


Fig. 2, Head, anterior view.

Fig. 3. Head, posterior view.

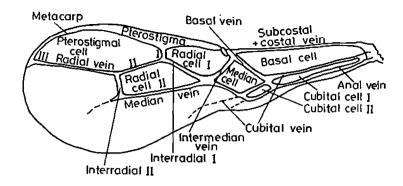


Fig. 4. Fore wing.

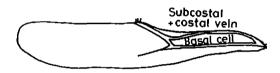


Fig. 5. Hind wing.

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