THE PARASITE COMPLEX OF THE CITRUS PSYLLA, *TRIOZA ERYTREAE* (DEL GUERCIO) (HOMOPTERA).

PART I

by

J.R. MCDANIEL B. Sc. (Hons).

(nee J. R. Blowers)

THESIS PRESENTED TO RHODES UNIVERSITY
FOR THE DEGREE OF MASTER OF SCIENCE

Plant Protection Branch,
Department of Research and Specialist Services,
Ministry of Agriculture,
Rhodesia.

DECEMBER, 1970.

TABLE OF CONTENTS

Page no.

1. INTRODUCTION

The citrus psylla, Trioza erytreae (Del Guercio), which occurs on citrus throughout southern Africa, is of considerable economic importance, transmitting the disease of citrus known as 'greening' (McLean & Oberholzer, 1965a,b; Schwarz, 1964, 1965). This disease, possibly caused by mycoplasma- like bodies rather than a virus (Laflèche & Bové, 1970), causes fruit deformation, stunting of trees and many other symptoms and is a limiting factor in the growing of citrus in certain parts of South Africa.

Although insecticides are effective against the psylla on a short term basis, the habits of this insect make long term chemical control difficult. Reinfestation is rapid on the very young leaves which quickly grow out uncontaminated after spraying so that adequate chemical control necessitates frequent spraying. Furthermore indigenous plants of the family Rutaceae are also hosts of T. erytreae and may harbour a reservoir of the pest (Moran, 1967). With the trend of citrus pest control towards corrective rather than preventitive spray programming and towards integrated rather than chemical control alone, consideration of the natural enemies of the citrus psylla is essential.

Several authors acknowledge that parasites may be an important limiting factor of populations of citrus psylla (Van der Merwe, 1941; Catling & Annecke, 1968; Catling, 1969b) but very little is known of the biology of these parasites. Up until 1963 only two parasite species, Tetrastichus radiatus Waterston, a species previously recorded by Husain and Nath (1924) on the

Indian citrus psylla, and Psyllaephagus pulvinatus (Waterston), were known to attach T.erytreae in southern Africa (Annecke & Cilliers, 1963). More recently Catling and Annecke (1968) and Catling (1969b), in studies on the influence of parasites on the host psyllid in the field, have mentioned in addition to the two aforementioned primary parasites, the hyperparasite Aphidencyrtus sp. and some suspected hyperparasites. The citrus psyllid parasites Tetrastichus sicarius Silvestri and T.dryi Waterston from Kenya (Waterston, 1922) are not known to occur in southern Africa (Annecke & Cilliers, 1963) and the record of a parasite attacking the eggs of T.erytreae in the Congo (Ghesquière, 1958) has been invalidated (Ghesquière, 1968).

This study deals with the basic details of the biology and interrelationships of the parasites of T.erytreae, presenting an account of laboratory and field studies conducted in Salisbury, Rhodesia, from 1967 - 1970. A total of fifteen parasite species are involved, including two primary parasites and thirteen hyperparasites (Table 1). Seven of these proved to be new records and three are probably new species.

TABLE 1. Hymenopterous parasites of T.erytreae in Salisbury 1967-1970.

Superfamily	Family	Parasite	Status
Chalcidoidea	Eulophidae	Tetrastichus ?radiatus	Primary
		Tetrastichus sp.1	Hyperparasite
		Tetrastichus sp.2	Hyperparasite
	Encyrtidae	Psyllaephagus pulvinatus (Waterston)	Primary
		Aphidencytrus cassatus Annecke	Hyperparasite
		?Psyllaephagus sp.	Hyperparasite
		Cheiloneurus cyanonotus Waterston	Hyperparasite
	Aphelinidae	Marietta exitiosa Compere	Hyperparasite
		Euxanthellus sp.	Hyperparasite*
		Coccophagus pulvinariae Compere	Hyperparasite*
		Coccophagus ?eleaphilus Silvestri	Hyperparasite*
		Coccophagus sp.	Hyperparasite*
		Physcus sp.	Hyperparasite*
	Pteromalidae	? Pachyneuron sp.	Hyperparasite
Proctotrupoidea	Ceraphronidae	Ceraphron sp.	Hyperparasite

*Male only hyperparasitic, female probably primary on another host.

In Salisbury three of the above species were particularly abundant, namely P.pulvinatus, T.?radiatus and A.cassatus. P.pulvinatus is a primary, solitary, internal parasite while T.?radiatus is a primary, solitary, external parasite and both parasites attack the nymphal stages of T.erytreae. A.cassatus is a solitary hyperparasite which attacks both the above primary parasites.

These three important species are dealt with in detail in the laboratory and field studies which are reported here. The remainder of the species were very much less abundant and consequently were studied more briefly.

2. THE HOST PSYLLID

Trioza erytreae is a species of psyllid common locally and in southern Africa on all varieties of citrus and other members of the family Rutaceae. Its distribution extends through eastern Africa south of the Sahara and includes Mauritius, Madagascar, Réunion and St. Helena (Catling, 1970). There are several accounts of its life history (Van der Merwe, 1941; Annecke & Cilliers, 1963; Moran & Blowers, 1967; Catling & Annecke, 1968).

The adult psyllid is an active winged insect about 2 mm in length. Yellow, pear-shaped eggs are laid on very young growth, particularly on the margins of young leaves. The eggs hatch in 7 - 10 days, depending on the season, and the first instar nymphs crawl about for a short time in search of a favourable spot in which to settle, usually on the undersurface of new leaves. Thereafter the nymphal stage is sedentary, remaining in one place unless disturbed or crowded. Feeding activity of the nymphs affects the leaf which forms a pit-like gall beneath the nymphs. In this open gall the nymph is very closely applied to the leaf surface and only the flattened dorsal surface of the body is exposed. There are five nymphal instars all similar in general appearance being oval, yellow in colour and surrounded by a fringe of white waxy filaments. The fourth and fifth instars may be distinguished from the others by their size and the two brown spots present on the abdomen. The excreta of both adults and nymphs are in the form of white sugary pellets. One generation from egg to adult extends over approximately one month but the rate of development varies with temperature.

The citrus psylla thrives in cool, moist, high-lying areas and under these favourable conditions may have 6 - 7 distinct field generations per annum (Catling, 1969b). The annual fluctuation pattern of T.erytreae in South Africa consists of a rapid rise of numbers in early spring followed by a population crash in mid-summer. Three principal factors govern the fluctuations, namely extremes of climate, the flushing rhythm of citrus and the action of parasites (Catling, 1969a,b,c).

3. MATERIAL AND METHODS

Interrelationships between the parasites and details of their biology were determined from dissection of parasitised hosts and from rearing experiments in the laboratory. Samples of psyllid infested citrus leaves were collected and brought back to the laboratory where all parasitised speciments were isolated. Internally parasitised nymphs of T.erytreae may be recognised by their deep brown colour and bloated appearance, the host forming a hard 'mummy' around the parasite. Externally parasitized nymphs eventually become opaque when the parasite reaches larval maturity, the edges of the psyllid skin are strapped down to the leaf by silken threads and the parasite pupates beneath the psyllid remains. Parasitised psyllid specimens were closely examined and all healthy parasite specimens were isolated and reared through in small plastic pill boxes lined with filter paper. Each specimen was numbered and individual records were made from daily observations.

Details of fecundity, longevity, duration of each developmental stage and behaviour of the three most important parasite species were studied in further experiments. Newly emerged female parasites were caged, either individually or with males, in petri dishes lined with moistened filter paper. Twenty parasite-free psyllid nymphs, equal numbers of fourth and fifth instars feeding on fresh citrus leaves, were exposed each day to the primary parasites for a period of 24 hours or less. The psyllid nymphs were removed each day and a fresh number introduced into the cage. A colony of unparasitised psyllids was kept on hand to provide hosts for the parasites. Female parasites were fed on a honey solution and water, by placing a drop of each in the cage. The number of eggs laid each day by each female parasite was recorded (by dissection of the psyllid nymphs where an internal parasite was involved). Externally parasitised nymphs were removed each day, transferred to young citrus plants and the development of the parasites followed. Development of internal parasites was followed by dissection of psyllid nymphs at various intervals after exposure to a female parasite. Development of the hyperparasite was followed by a similar method, parasitised psyllid nymphs being exposed to the female hyperparasite for a 24 hour period.

All rearings and experiments were carried out in a controlled environment room with a fluctuating temperature and humidity. During the day the temperature reached a maximum of 27°C and the relative humidity dropped to a minimum of 50% while at night the temperature dropped to 13°C and the relative humidity rose to a maximum of 70%. Illumination from 6 a.m. to 6 p.m. in the rearing room was provided by a group of eight fluorescent tubes but light in the room (which was glassed on two sides) was also influenced by external conditions.

Information on host and parasite remains was obtained from dissections of parasitised psyllids from which known species of parasites had emerged. Data such as size and position of exit hole, colour and shape of meconium and pupal sclerites and other pertinent observations were noted. The terminology of Hill and Pinckney (1940) has been followed in describing the sclerites of the cast pupal exuviae. For illustration purposes the pupal exuviae were mounted on slides and microphotographs taken.

4. THE PRIMARY EXTERNAL PARASITE, TETRASTICHUS ?RADIATUS WATERSTON (EULOPHIDAE).

Tetrastichus radiatus was originally described by Waterston (1922) from specimens reared by Husain & Nath (1924) from the Indian citrus psylla, Diaphorina citri Kuw.(Euphalerus citri Kuw.) in the Punjab. Annecke and Cilliers (1963) were the first to publish a positive record of T.radiatus as a parasite of the citrus psylla, T.erytreae, in South Africa, as identified by Dr. B.D. Burks of the United States National Museum in Washington D.C. Morphologically similar specimens have since been recorded from T.erytreae in other parts of southern Africa (Swaziland (Catling, 1969b) and Rhodesia) and identified as T.radiatus and it is probable that this is the species referred to by van der Merwe (1941) in the first published account of the South African citrus psylla. Catling (1969b) has also reared it from another host psyllid, Trioza sp., on two other host plants. Moran (1967) noted that the specimens sent by Catling and Annecke to Burks differed slightly from the original description of T.radiatus and were morphologically slightly different from those specimens reared from T.erytreae in the Letaba and Salisbury areas. He suggests that there may be a whole complex of morphologically similar species of this parasite from T.erytreae which have been named T.radiatus. In the present study specimens of this parasite from Rhodesia and South Africa were compared with the original description of T.radiatus and were not found to fit entirely satisfactorily. The main differences are listed in Table 2.

TABLE 2. The main differences between T.radiatus Waterston as given in the original description (Waterston 1922) and T. ?radiatus from Salisbury.

CHARACTER	T.RADIATUS	T.?RADIATUS (Specimens from Salisbury).
♂♂ Antenna Scape	Almost equal in length to the club (excluding spur)	4/5 length of the club (i.e. 20% shorter)(excluding spur)
Sense organ	⅓ way up scape	½ way up scape
♀♀ Antenna Scape	1 1/5 length of club (excluding spur)(i.e. 20% longer).	Either 1 1/10 length of club (excluding spur) (i.e. 10% longer) or equal in length to club.
Club	Breadth = 53% length i.e. length almost twice breadth (at first joint).	Breadth = 29% length i.e. length 3 x breadth (at first joint).
Propodeon surface	Smooth with no lateral folds	Heavily sculptured, with marked reticulation and lateral folds. (similar to T.flavigaster Brothers & Moran, 1969)
median carina	broad	well developed, not markedly broad.
Both sexes legs	Almost entirely pale, at most hind femora with trace of infuscation dorsally.	Hind femora sometimes darkened dorsally, hind tibia often slightly infuscated.

From these findings it appears that the species of *Tetrastichus* from southern Africa is possibly not *T.radiatus* but a positive identification or perhaps description of a new species must await comparison of local specimens with those of *T.radiatus* from India. Meanwhile the species from *T.erytreae* will be referred to as *Tetrastichus ?radiatus*.

Illustrations (Catling & Annecke, 1968) and short accounts of the biology of *T.?radiatus* (Catling, 1967, 1969b) have been given in recent literature. The account of the biology of *T.radiatus* in India given by Husain & Nath (1924) is too brief and lacking in detail to be of much use in comparison with that of *T?radiatus*. The present study considerably extends our knowledge of the biology of this parasite. As pointed out by Moran, Brothers and Case (1969) in their study of *Tetrastichus flavigaster*, the primary external parasite of the South African chestnut psyllid, *Paurocephala calodendri* Moran, very little is known of the biology and behaviour of species of *Tetrastichus*. Their study of *T.flavigaster* is the only detailed account of a species of *Tetrastichus* closely related to *T.?radiatus* and, as such, it is compared with that of *T?radiatus* wherever relevant.

4.1. THE ADULT The adults of both sexes have a black head and thorax. They can be distinguished from the other parasites of *T.erytreae* by the large white spot on the dorsum of the abdomen and the largely pale legs. The coxae are darkish and the hind femora may be faintly brown dorsally (Fig 1a). The ventral surface of the abdomen of the female is whitish whereas that of the male is largely black. The mean length for females is 1.2 mm (range 0.7 - 1.3 mm, n=30) while the males are smaller, averaging 1.1 mm in length (range 0.7-1.2 mm, n = 20); (cf. Catling, 1969b, female averaging 1.19 mm, male 1.05 mm). In addition to size differences, antennal differences serve to distinguish the sexes. The male parasite has whorls of long hairs on the antennae (Fig 1b) which are not present on the slightly clavate antennae of the female.

The adult T.?radiatus feeds readily on the sugary excretions of its psyllid host but host feeding was not observed as common behaviour. A single incidence only of host feeding was observed during the present study. During a struggle to escape an ovipositing female parasite, a psyllid nymph overturned; after inspecting the overturned nymph for a few seconds with its antennae, the wasp pierced the exposed abdomen of the nymph with its ovipositor and fed from the exuding fluid for several minutes. Catling (1969b) observed no host feeding by T.?radiatus. It is interesting to compare this aspect of the behaviour of T.?radiatus with that of T.flavigaster Moran, which host feeds on several psyllid nymphs in the first day or two after emergence, piercing third, fourth or fifth instar nymphs and sucking them dry, (Moran, Brothers & Case, 1969). However this species has a preoviposition period of 2-3 days and the extra protein source is probably necessary for ovigenesis, (Doutt, 1964). T.?radiatus has a very short preoviposition period (Table 2) and may not need the extra food for egg maturation, or observation of host feeding behaviour may have been missed during this short period.

TABLE 3. Comparative record of the number of eggs laid daily by ten mated and three unmated females of <u>T.?radiatus</u> on nymphs of <u>T.erytreae</u>.

Days after emergence of female	Number of eggs deposited daily by female number												
	1	2	3	4	5	6	7	8	9	10	11*	12*	13*
1	0	0	2	0	0	0	0	0	0	1	1	0	1
2	3	1	6	7	1	0	2	6	2	4	9	0	8
3	4	2	11	3	5	5	9	8	2	7	7	2	13
4	1	0	11	7	7	7	9	7	8	5	11	4	11
5	0	0	18	13	8	8	12	6	8	3	5	4	8
6	12	1	15	5	7	4		6	12	4	10	8	12
7	8	5	21	13	6	9	4	4	13	5	5	9	16
8	9	3	15	10	6	6	5	7	6	3	10	7	11
9	9	7	15	12	3	11	9	3	4	8	11	7	15
10	9	3	10	17	7	3	10	++	+	2	8	9	6
11	7	3	14	18	10	+	4			**	13	5	***
12	3	3	9	9	3		8				7	9	
13	0	7	13	6	7		10				10	5	
14	6	3	8	3	2		5				9	3	
15	5	6	10	2	**		8				7	3	
16	5	2	12	++			2				7	+	
17	2	1	6				5				8		
18	1	2	10				10				6		
19	++	3	13				7				6		
20		4	14				**				6		
21		5	11								7		
22		+	11								8		
23			17								9		
24			11								6		
25			9								5		
26			9								7		
27			10								7		
28			6								1		
29			4								8		
30			7								7		
31			5								4		
32			9										
33			0								4		
34			2								2		

Days after emergence of female	Number of eggs deposited daily by female number												
	1	2	3	4	5	6	7	8	9	10	11*	12*	13*
35			2								4		
36			11								6		
37											5		
38			15								7		
39			9								7		
40			10								5		
41			15								4		
42			6								2		
43			7								+		
44			15										
45			9 +										
TOTAL	84	61	443	125	72	53	119	47	55	42	270	75	101
Average no/day	4.4	3	9.8	8.3	5.1	5.3	6.3	5.2	6.1	4.2	6.4	5.8	10.1
maximum no/day	12	7	21	18	10	11	10	8	13	8	13	9	16
Sex of progeny	Male and female										All male		

+	Female lost or escaped
++	Female injured and died
*	Unmated females
**	Females died from unknown causes
***	Experiment discontinued

4.2 OVIPOSITION AND THE EGG The female T.?radiatus oviposits on third, fourth and fifth instar nymphs of T.erytreae. The psyllid nymphs are examined very briefly by the female parasite with the antennae as she walks over the leaf in search of hosts. After tapping the dorsal surface of a potential host with the antennae for 3-4 seconds the wasp turns around and places its ovipositor beneath the lateral margin of the psyllid nymph, usually in the region of the posterior third of the body. The parasite probes the ventral surface of the psyllid with its ovipositor for about a minute, then withdraws the ovipositor, turns around and makes a further antennal inspection of the host before inserting the ovipositor finally to lay an egg. Duration of oviposition varies from one to several minutes and the wasp often exhibits wing vibrations during oviposition. The psyllid nymph usually reacts to the ovipositional probing by moving its abdomen from side to side or occasionally walking away. The general ovipositional behaviour of T.?radiatus is similar to that of T.flavigaster (Moran,Brothers & Case, 1969) except that the host psyllid is not paralyzed and the female wasp remains motionless during oviposition. After each act of oviposition the female parasite grooms itself, rests or feeds for a varying period of time. At each oviposition only one egg was deposited.

The egg of T.?radiatus (Fig 1c) is pale and hymenopteriform (Hagen, 1964) with a mean measurement of 0.2 mm x 0.08mm (negligible variation, n = 20). The egg is laid on the ventral surface of the psyllid host usually in the groove between the abdomen and thorax, just behind the hind coxae (Fig 2a). The position of the egg, however, was variable and, particularly where superparasitism occurred, eggs were sometimes laid on the underside of the head or abdomen or behind the pro- or mesothoracic coxae of the host psyllid. Of the 1547 eggs laid by T.?radiatus females in the laboratory, 20% were laid in positions other than behind the metathoracic coxae. A low proportion, up to 3.2%, of superparasitism was common where the level of parasitism was high, two being the most common number of eggs and four the maximum number found on a single host. Catling (1969b) recorded 6.8%, 3% and 3.5% nymphs having more than one egg and as many as six eggs on a single host psyllid.

The egg-laying potential and rate of oviposition of a number of T.?radiatus females was recorded and the results appear in Table 3. The results show that there was a short pre-oviposition period of one day in most cases. Following this the rate of egg-laying showed no regular pattern. The average number of eggs laid per day varied from 3 to 10 and the maximum number of eggs deposited by a female in one day was 21. There was no apparent difference in oviposition rate between mated and unmated females. Only male progeny resulted from eggs laid by all unmated females and progeny of both sexes from mated females. The egg laying period was not determined as most of the records were incomplete but one female continued egg-laying for 45 days before loss or escape, laying the maximum number of 433 eggs.

Ovipositing parasites were presented with equal numbers of fourth and fifth instar nymphs as hosts and their host size preference is recorded in Table 4.

TABLE 4 The number and percentage of fourth and fifth instar T. erytreae nymphs selected by ovipositing T.?radiatus females.

Female parasite no.	Total hosts parasitized	No. 4th	No. 5th	% 4th	% 5th
1	84	36	48	43	57
2	61	23	38	38	62
3	443	127	316	29	71
4	125	41	84	33	67
5	72	37	35	51	49
6	53	30	23	57	43
7	119	38	81	32	68
8	47	10	37	21	79
9	55	15	40	27	73

Female parasite no.	Total hosts parasitized	No. 4th	No. 5th	% 4th	% 5th
b/f	1059	488	702		
10	42	13	29	31	69
11*	270	104	166	39	61
12*	75	18	57	24	76
13*	101	37	64	37	63
TOTAL	1547	529	1018	34%	66%

* unmated females

Considerable differences were found in the number of each instar selected for oviposition. Despite this variation, results indicate that, under the laboratory conditions described, T.?radiatus females oviposited in approximately twice as many fifth as fourth instar psyllid nymphs. In only two cases (females 5 and 6) was the percentage of parasitized fourth instar nymphs higher than, or nearly equal to that of parasitized fifth instar nymphs. Catling (1967, 1969b) reports that from field collections the fourth instar nymphs appear the most attractive to T.?radiatus. Similarly, Moran, Brothers and Case (1969) found T.flavigaster attacked a higher proportion of fifth than fourth instar psyllids in the laboratory but their laboratory observations were supported by the field observations. It is, however, probable that the preference of the female varies according to the instars of the host available, which would depend on host-parasite synchronization in the field.

4.3 DEVELOPMENTAL STAGES. The eggs hatch within two days of being laid. The first instar larva of T.?radiatus is hymenopteriform and cylindrical whereas the later instars are dorso-ventrally flattened (Fig 2b). The parasite larva develops beneath the body of the psyllid, sucking the body contents of the nymph through a puncture on the ventral surface and the larval parasite and psyllid host lie with their ventral surfaces apposed (Fig 2b). During larval development of the parasite, which takes from 5-9 days (average 7 days, n=79), the psyllid host appears healthy and is almost indistinguishable from its unparasitised counterparts. Death of the host is brought about only when parasite larval maturity is attained and only the dry psyllid skin is left. The parasite utilizes the dry psyllid body as a covering and just prior to pupation fastens it to the leaf surface with a network of fine anchoring threads. The larva (Fig 1d) extends its posterior end from under the host to fix threads from all margins of the psyllid to the leaf surface, and to deposit its meconium on the dorsal surface of the psyllid shell.

After defaecation the parasite enters the prepupal stage which lasts only one day. The prepupa is pale and indistinctly segmented and is easily distinguishable from the prepupa of its hyperparasite A.cassatus by the lack of segmentation and rather tapering posterior end. The newly formed pupa of T.?radiatus is white, but eventually darkens to a dark grey or black with a distinct white dorsal spot on the abdomen. The ventral surface of the abdomen of the female pupa and the prosternum also remain pale. The colouration of the pupa is a useful distinguishing feature for the pupae of this species. The body of the pupa is dorso-ventrally flattened and slightly "hunchbacked" in side view (Figs 1e,f). The pupa always lies with its dorsal surface touching the leaf but may be orientated with its head pointing towards the anterior or posterior end of the host. The size difference between males and females of this species, as would be expected, is reflected in the pupal stage. Male pupae measure 0.7-1.13mm in length (average 1.09mm, n=90) whereas female pupae measure 0.9-1.35mm in length (average 1.17 mm, n=164), (cf. Catling, 1969b, pupal length of 10 unsexed pupae average 1.13 mm). The pupal stage lasts between 4 and 8 days (average 5.6 days, n=86).

The adult moults from its pupal skin then effects emergence through a circular hole chewed in the host's integument. The exit hole may be in the middle of the thoracic or abdominal region of the host remains, depending on the orientation of the parasite. The adult parasite may also emerge between the psyllid remains and the leaf, pushing its way under the margin of the psyllid shell. This latter type of emergence is more common where the host is a fourth instar psyllid, the anchoring threads around the margin of the psyllid remains being loosened through rapid growth of the leaf. The size of the exit hole varies from 0.3-0.5mm in diameter (cf. Catling, 1969b, 0.33-0.35mm) averaging 0.45mm in fifth instar hosts (0.32-0.50mm, n=24) and 0.38mm in fourth instar hosts (0.30-0.45mm, n=24).

The meconium of T.?radiatus consists of a fused mass of orange-brown pellets, usually in the form of a curl (Fig 2d). This is the only species of parasite associated with T.erytreae which deposits its meconium on the dorsal surface of the psyllid remains. The pupal remains of T.?radiatus, together with the meconium, are characteristic of the species and serve as a means whereby the parasite species can be identified after the adult has emerged from its host. The pupal remains of T.?radiatus comprise a mass of very pale, transparent, straw-coloured abdominal and thoracic sclerites (Fig 19) and a light brown oculoparietal plate (Fig 20). The former sclerites are usually found beneath the host remains at the end furthest from the exit hole (Fig 2c) and, because of their delicate nature and pale colour, are not very conspicuous. The abdominal sclerites form a crumpled mass at the base of the almost rectangular thoracic sclerites. The oculoparietal plate, or head capsule, is a curved, shiny 'cap' with the antennal bases attached to it. It is found at the extreme end of the host remains, close to the exit hole (Fig 2c).

The life cycle is completed in 13-16 days (average 14 days, $n = 98$) which compares favourably with the figure of 14-16 days at a mean temperature of 22°C given by Catling (1969b).

The results in Table 1 give some indication of the longevity of the adult female T.?radiatus. Although in nearly every case the female died from unnatural causes or escaped it seems that, under the conditions stated, adult female longevity may exceed that given by Husain & Nath (1924) (20-25 days with a maximum winter longevity of 31 days) as two females lived for at least 42 days.

4.4 SEX RATIO. Unmated *T.?radiatus* females produce only male offspring whereas mated females produce progeny of both sexes, so that the number of males in a particular generation greatly influences the sex ratio of the following generation. However, host size also seems to influence the sex ratio as a definite correlation was recorded between host instar and parasite sex. Preliminary sampling showed that only male parasites developed on third instar hosts while either sex developed on fourth and fifth instar hosts. Fourth instar hosts yielded a majority of male parasites while more females than males developed on fifth instar psyllid hosts. Further evidence of this was obtained by rearing through progeny of the females used in the egg-laying experiments. Of the surviving progeny from each female, the numbers of male and female parasites emerging from fourth and fifth instar psyllid nymphs are shown in Table 5.

TABLE 5. Numbers of male and female *Tetrastichus ?radiatus* progeny emerging from fourth and fifth instar *T.erytreae* nymphs.

Female parasite no.	No. of eggs laid	Surviving progeny	Progeny from 4ths		Progeny from 5ths		Total No. male	Total No. female
			male	fem	male	fem		
2	61	9	2	-	2	5	4	5
3	443	109	9	5	38	57	47	62
4	125	24	1	-	3	20	4	20
5	72	17	3	2	6	6	9	8
6	53	12	3	1	2	6	5	7
7	119	44	5	2	7	30	12	32
8	47	22	3	-	1	18	4	18
9	55	15	-	-	2	13	2	13
10	42	6	1	-	1	4	2	4
TOTAL			27	10	62	159	89	169
%			73%	27%	28%	72%	34%	66%

The above results are not necessarily a good reflection of the actual proportion of males and females produced as a large number of parasites, particularly from fourth instar hosts, failed to survive to the pupal stage at which time their sex could have been determined. As mentioned previously, a high proportion of males emerge from fourth instar psyllid hosts so this may have influenced the total percentage of males recorded, i.e. 34% which is slightly lower than the figure of 41% males recorded from field sampling by Catling (1969b). However the results do substantiate the evidence from field sampling as the ratio of males to females emerging from fourth instar psyllid hosts was nearly 3:1 and that from fifth instar hosts approximately 1:2. The influence of host size on sex determination has been noted in many parasitic Hymenoptera (Clausen, 1939; Wigglesworth, 1950), eggs laid in small hosts resulting in a predominance of males whereas the majority laid in larger hosts produce females. This appears to be common in parasites of psyllids attacking more than one nymphal instar, and has been recorded by Pletsch, (1947), Clarke (1962) and Moran, Brothers and Case (1969).

5. THE PRIMARY INTERNAL PARASITE, *PSYLLAEPHAGUS PULVINATUS* (WATERSTON) (ENCYRTIDAE)

The original description of this species as *Encyrtus pulvinatus* was made by Waterston in 1922 from specimens parasitising *Trioza citri* Laing in Kenya. Robinson (1960) gave a synopsis of the synonomy of this species and more recently Annecke and Cilliers (1963) discussed its synonomy and finally placed it in the genus *Psyllaephagus*. Members of the genus *Psyllaephagus* are well known as either primary or secondary parasites of the Psyllidae (Jensen, 1957; Riek, 1962).

P.pulvinatus is a widespread parasite of the citrus psylla in southern Africa and records of an internal parasite of *T.erytreae* by Jack (1916)(called an *Encyrtus* sp. by Goldsmit and Wilson, 1962) definitely refer to *P.pulvinatus*. An *Encyrtus* sp. recorded by Smee (1944) probably refers to the same species. Catling and Annecke (1968) and Catling (1969b) have also recorded *P.pulvinatus* on another psyllid, *Trioza* sp., on two other host plants. There is no literature on the biology of *P.pulvinatus* and this is the first account but, because of the difficulties of following the development of an internal parasite, it is not as detailed as that of *T.?radiatus*.

5.1 THE ADULT

The adult parasite (Fig 4a) is a dark metallic green, almost black colour. The antennae are a very pale brown and the forelegs are predominantly pale except for the hind femora which are largely brown. Females vary in length from 1.0mm to 1.13mm (average 1.1mm, n=24) while the male is slightly smaller, 0.8 to 1.1mm (average 1.0 mm, n = 24). The sexes may be distinguished by the antennae which in the female differ both in shape and in the absence of long hairs (Fig 4b). Host feeding was not observed but the adults fed readily on the sugary faecal pellets of their host.

5.2 OVIPOSITION AND THE EGG

The female parasite runs rapidly over the leaf in search of hosts. After a very brief examination of a suitable host the female mounts the dorsum of the host and almost immediately inserts her ovipositor perpendicularly into its body in the region of the junction of the thorax and abdomen. The host usually reacts violently to the insertion of the ovipositor and often moves away, carrying the parasite on its back. Duration of oviposition varied from several seconds to half a minute and the female usually oviposited in several hosts in succession without a pause, unlike T.?radiatus which pauses to groom itself or feed between each act of oviposition. Details of the fecundity of P.pulvinatus are lacking but one female laid 16 eggs in one day as compared with T.?radiatus which laid a maximum of 21 eggs in a day with an average of 3 - 10 eggs per day. Third instar nymphs were the most favoured for oviposition by P.pulvinatus and 80% of the nymphs attacked were third instars although fourth and occasionally second instars were chosen for oviposition. The female showed no response to fifth instar nymphs.

The egg of P.pulvinatus is minute and oval with a small basal stalk (Fig 4c) and measures 0.1mm x 0.05mm (n=15). The egg is found floating freely in the haemocoel of the host. Dissection of nymphs exposed to a female P.pulvinatus showed that superparasitism does occur (at least under laboratory conditions) as over half of the parasitised nymphs that were dissected contained two eggs and on one occasion three eggs were found in a single host.

5.3 DEVELOPMENTAL STAGES

The larvae (Figs 4d, e) develop as endoparasites, living in the haemocoel of the host psyllid nymph. Often two and, on one occasion, three larvae were found in a single host although only one parasite eventually emerged from any single host psyllid. The host psyllid remained apparently healthy, moulting normally and showing no obvious signs of parasitism until the fifth, or occasionally fourth, instar. About a day prior to maturation of the parasite, parasitism became evident by which time the body contents of the psyllid nymph were almost completely devoured. The psyllid nymph became pale and immobile, scarcely more than a soft shell with the parasite filling almost its entire body cavity. The mature larva of P.pulvinatus (Fig 4e) is hymenopteriform, white with yellow-orange body contents and measures approximately 1.2mm in length. The assumption of a deep brown colour by the host psyllid and hardening of the 'mummy' marks maturation of the larval parasite and internally parasitised nymphs have a characteristic swollen appearance. The parasite eventually pupates within the host 'mummy'. Egg to prepupal stage takes 7 - 8 days (average 8 days, n = 20).

The prepupal stage lasts 1-2 days and both the prepupa and newly formed pupa are white in colour. The pupa (Figs 4f, g) eventually darkens to almost black and is recognizable by its shiny, unsculptured scutellum and smooth, shiny general appearance. Pupal length averages 1.1mm (range 1.0 - 1.1mm, n = 18) and the pupal phase lasts 7 - 8 days (average 8 days, n = 20). Darkening of the pupa is completed 3 - 4 days prior to emergence and the body of the parasite pupa is often apparent through the host's integument. The head of the former is always orientated towards the posterior of the host psyllid. The pupa lies on its ventral surface within the psyllid 'mummy'. After casting its pupal exuvium, the adult parasite cuts its way through the psyllid 'mummy', forming an exit hole in the dorsum of the host's integument. Average diameter of the exit hole of P.pulvinatus is 0.43mm (range 0.40 - 0.53mm, n = 50) (cf. Catling, 1969b, 0.43 - 0.45mm in diameter).

The meconium of P.pulvinatus (Fig 3b) is very characteristic of the species, consisting of several large, irregularly shaped, flattened pellets which are deep orange-red in colour. The meconium is deposited at the extreme anterior end of the host 'mummy' (Fig 3a) and can often be seen through the host's integument. The pupal exuvium (Fig 21), which is characteristic of the species, is shiny and dark brown to black in colour. The abdominal and thoracic sclerites are found in a single, flattened, conglomerate mass at the anterior end of the 'mummy' near the meconium (Fig 3a). The sutures between the segments of the abdomen are clearly defined and no leg sclerites are evident in the exuvium.

The life cycle of P. pulvinatus extends over a period of 19 - 22 days (average 20 days, n = 20).

5.4 SEX RATIO

P. pulvinatus reproduces both sexually and parthenogenically; in the latter case all progeny are male. In the present study records from sticky impact traps gave a total of 30% males which compares favourably with the figure of 31% males recorded by Catling (1969b) from emergence boxes and an insect sampling machine.

6. THE MAJOR HYPERPARASITE, APHIDENCYRTUS CASSATUS ANNECKE (ENCYRTIDAE).

First recorded by Catling (1967) from the Northern Transvaal, this parasite was found to be a new species of Aphidencyrtus. Subsequently it was found to occur in Rhodesia and citrus psyllid specimens mounted on slides in Rhodesia by Jack in 1914 were discovered during the present study to be parasitised by Aphidencyrtus sp. The species has since been described by Annecke (1969) as A.cassatus and been recorded as a parasite of T.erytreae in other parts of South Africa (Catling, 1968; Annecke, 1969) and as a parasite of two other species of psyllid (Catling & Annecke, 1968; Catling, 1969b; Annecke 1969). Its status as a secondary hyperparasite, attacking both the primary parasites of T.erytreae was discovered in the present study and no details of its biology have previously been recorded.

6.1 THE ADULT

The adult A.cassatus (Fig 5a) has a black body with metallic colouration. The legs are pale yellow marked with black on the femora and tibiae and the marking of the legs provides a distinctive feature by which this species can be distinguished from P. pulvinatus which has predominantly pale legs. A.cassatus females vary in size from 0.9mm to 1.1mm (average 1.0mm, n = 36). The males are smaller, ranging in size from 0.7mm to 1.1mm in length (average 0.9mm, n = 36) and may be distinguished from the females by their antennae (Fig 5b).

Host-feeding has been observed in this species. Females regularly fed from an ovipositional puncture (sometimes killing the primary parasite) or from one or several punctures made in the thoracic region of an apparently healthy psyllid nymph. Behaviour of the female prior to host-feeding is similar to that of the ovipositing female described below.

6.2 OVIPOSITION AND THE EGG

The female A.cassatus is extremely active, walking rapidly over the leaves in search of hosts. On encountering a psyllid nymph the female parasite examines it, walking back and forth over the psyllid four or five times, drumming it with its antennae. Ovipositional probing follows the antennal inspection. The wasp stands on the psyllid nymph, facing in the same direction as the nymph, bends the tip of the abdomen under its raised thorax and inserts the ovipositor in the region of the junction between the host's thorax and abdomen. The parasite probes its host several times in this manner before laying an egg. The psyllid host often reacted quite violently to the probing, sometimes walking off carrying the parasite on its back. Oviposition lasts about two minutes and is followed by a brief antennal re-examination of the host. Between each act of oviposition the female parasite paused to groom itself or host feed.

The egg of A.cassatus is typically encyrtiform (Hagen, 1964), comprising a body and stalk (Fig 5c). The newly laid egg is oval, transparent and 0.15mm in length. Length of the egg and stalk together is 0.3mm x 0.1mm (n = 15). The egg increases considerably in size from time of oviposition to hatching and just prior to hatching measures 0.5 x 0.25mm (n = 15), almost double that at oviposition. Superparasitism is normal and two to four eggs, usually three, were laid in a single host. Eggs of A.cassatus were deposited in the egg or larval stage of the host. Where T.radiatus is the primary host, A.cassatus may develop as an egg-larval parasite. Normally three eggs were deposited in a single egg of T.radiatus, hatched when the host had reached the first larval stage, and development of the hyperparasite was completed in the larval or prepupal stage of the host. Oviposition by A.cassatus in the egg stage of P.pulvinatus was never observed and this would seem to be impossible since the eggs of P.pulvinatus are approximately a third of the size of A.cassatus eggs. A.cassatus also attacks the larvae of T.radiatus and P.pulvinatus, laying its eggs within the host, but no details of its host preferenda are known. No evidence was found of attachment of the hyperparasite egg to the host egg or larva and the eggs are apparently laid in the host's haemolymph.

6.3 DEVELOPMENTAL STAGES

Irrespective of the developmental stage of the host at the time of attack, the newly hatched larvae of A.cassatus are found in the haemolymph of the host larva.

The young larva of A.cassatus (Fig 5d) is a transparent white colour with a clearly segmented, elongate, caudate body, characteristically curled in a C-shaped position. More than one A.cassatus larva was found in most of the host specimens dissected and although superparasitism by A.cassatus is common and most of the eggs hatch, only one larva reaches maturity. For the first few days after parasitisation, while the hyperparasite larva develops internally, the primary host parasite larva appears normal and may defaecate and enter the prepupal stage. Only when the hyperparasite reaches the final larval stages and can no longer remain contained within the body of the host does hyperparasitism become evident to the observer. Rupture of the host's body wall ensues and the hyperparasite's body protrudes from the remains (Fig 6a). The final instar larva of A.cassatus (Fig 5e) is entirely different in appearance from the earlier stage larvae, being hymenopteriform. It measures about 0.8mm (n = 10) in length and often has brown gut contents. Egg and larval development is usually completed in 7 - 8 days but may take up to 10 days.

The prepupa of A.cassatus is white in colour and this stage lasts 1 - 2 days (mostly one day, n = 12). The newly formed pupa is creamy white and blackens progressively, assuming its characteristic dull black colour two to three days prior to emergence. The pupa (Fig 5f, g) has a very distinctive ridge-like segmentation of the dorsal surface of the abdomen and the scutellum is sculptured, giving it a mat appearance. The average length of 16 females of A.cassatus was 1.0mm (range 0.9mm to 1.1mm) and the male pupae averaged 0.9mm in length (range 0.7 - 1.0mm, n = 16). The pupal stage lasted 8 - 9 days (average 8.5 days, n = 57). Results indicate that the pupal development of A.cassatus is slightly faster in fourth instar psyllid nymphs (average 8.0 days, n = 16) than in fifth instar psyllid nymphs (average 9.0 days, n = 33).

The meconium of A.cassatus (Fig 6c) is voided as a distinctive mass of small, sub-spherical pellets which are deposited either in a loose mass or partly joined end to end. The colour of the pellets varies from reddish-brown to pale pink-brown or cream. The meconium is voided at one end of the psyllid, usually the anterior end but occasionally at the opposite end, depending on the orientation of the parasite.

If P.pulvinatus is the primary host, the meconium of A.cassatus is deposited next to the meconium of its host, usually at the anterior end of the psyllid 'mummy' (Fig 6b). If the primary host is T.radiatus then the meconium of A.cassatus is voided quite apart from that of its host (which is found dorsal to the psyllid remains) beneath the psyllid remains. The pupal exuvium of A.cassatus is dark brown, almost black in colour and comprises very characteristic sclerites. The scutellum (Fig 22) which is circular in outline and clearly sculptured, is separated from the rest of the pupal sclerites, a distinctive character in itself. Most of the other sclerites remain attached together (Fig 23), the head sclerites rolled in a sleeve-like fashion, the thoracic sclerites densely papillose and the abdominal segmentation is very distinct. The antennal bases and sheaths may also be found with the rest of the pupal sclerites but are less conspicuous and not particularly characteristic. The pupal remains and meconium as they appear in a psyllid 'mummy' after parasite emergence are illustrated in Fig 6b.

The life cycle from egg to adult is completed in 14 to 18 days (average 16 days, n = 44).

6.4 SEX RATIO

There is a correlation between the size of the host psyllid and the sex of the hyperparasite A.cassatus, as seen in Table 6.

TABLE 6. Comparison of the numbers of male and female A.cassatus, developing on either of the primary hosts T.?radiatus or P.pulvinatus, emerging from 4th and 5th instar psyllid nymphs.

Primary Host	Psyllid instar	Sex of parasite Male	Female	Total
T.?radiatus	4th	20	-	20
	5th	1	7	8
P.pulvinatus	5th	6	24	30

Mostly male hyperparasites emerged from the smaller, fourth instar psyllid hosts and mostly females from the larger, fifth instar psyllid hosts. Since the primary parasite P.pulvinatus develops almost exclusively on fifth instar psyllid nymphs, mostly females and relatively few males of the hyperparasite A.cassatus develop on this host. The ectoparasite T.radiatus parasitises 3rd, 4th and 5th instar psyllid nymphs and where this is the primary host parasite, the ratio of A.cassatus males may be higher as only males of A.cassatus emerge from 3rd instar psyllids, mostly males from fourths and a majority of females only from fifth instar psyllid nymphs.

In the present study sticky impact trap records showed a low ratio of males, females always being the predominant sex. Catling (1969b) recorded 62% A.cassatus males at Malkerns, Swaziland, stating this to be consistent throughout the year. The correlation between psyllid nymph size and the sex of the hyperparasite A.cassatus discussed above may cause a variation in the sex ratio according to which primary parasite is dominant and the synchronization of the primary parasites with their host.

7. LESS IMPORTANT HYPERPARASITES

7.1 TETRASTICHUS SP. 1 (EULOPHIDAE)

As yet undescribed, this parasite has been placed in the genus Tetrastichus by Dr. B.D.Burks (Catling, 1967) It was first recorded as a parasite of Trioza erytreae in South Africa by Catling (1967) and its status as a hyperparasite was determined in the present study when Tetrastichus sp. 1 was recorded in Salisbury. Tetrastichus sp. 1 also forms part of the citrus psylla complex in Swaziland (Catling, 1969b) and has been recorded on another psyllid, Trioza sp., on two vines at Letaba (Catling & Annecke, 1968; Catling, 1969b). Apart from this the biology of this species was unknown.

Unlike Tetrastichus?radiatus, the adult of Tetrastichus sp. 1 (Fig 8a) has an all black body and dark markings on the legs. There is some variation in the femoral leg markings of Tetrastichus sp. 1 in Salisbury. Some specimens of this species are similar to those found in South Africa (Catling, 1967, 1969b) having the femora of all legs marked with black, while others have dark markings on the hind femora and only faint, if any, dark markings on the meso- and prothoracic femora. The adults range in size from 0.7mm to 1.2mm (n = 20) and antennal differences separate the males and females (Fig 8a, b).

A single observation was made of a female Tetrastichus sp. 1 host feeding from a T?radiatus pupa which it had been probing, but it was not ascertained whether this was common behaviour.

The major host of Tetrastichus sp. 1 is Aphidencyrtus cassatus and, because A.cassatus itself attacks both the internal and external primary parasites, Tetrastichus sp. 1 may be found in either externally or internally parasitised psyllid nymphs. Catling (1968) reports that the former case seemed to be the most common at Letaba. As a tertiary hyperparasite, Tetrastichus sp. 1 develops ectoparasitically on the larval, prepupal or pupal stages of its host, A.cassatus. Tetrastichus sp. 1 has proved to be a secondary hyperparasite in some cases, developing on either the larva, prepupa or pupa of T?radiatus or P.pulvinatus but examples of this were comparatively rare. Further, several cases of Tetrastichus sp. 1 developing on pupae of its own species were found in addition to evidence in the form of pupal remains. This occurrence was rare and was found only in externally parasitised psyllid hosts.

Oviposition by Tetrastichus sp. 1 was observed only where the host was external. The female wasp carries out a slow, "deliberate inspection" of its potential host, tapping the ventral surface of the psyllid with its antennae. Further exploration is made by means of ovipositional probing of the parasite beneath the psyllid remains. Several similar antennal tapping "inspections" followed by a probing with the ovipositor in a different position are performed, lasting 1½ - 2 minutes. Eventually the female wasp inserts her ovipositor under the psyllid remains in the region of the wing buds and lays an egg. No response was shown to unparasitised psyllid nymphs.

The egg (Fig 8c) is smooth, translucent white and hymenopteriform. The average egg size was 0.3mm x 0.1 mm (n = 10). Eggs were apparently not laid in any particular position but were attached either to the host's body or to the leaf surface near it beneath the psyllid remains. Superparasitism was common, two or sometimes three eggs being laid on a single host. More than one larva hatched and developed for a few days but only a single parasite completed development on one host. Incubation of the egg required about two days. The larvae live as ectoparasites, developing from small, spindle-shaped larvae to active hymenopteriform larvae (Fig 8d) almost as large as the host parasite. Later stage larvae display a characteristic undulating movement of the body and the gut contents are brown speckled with white. Larval development takes 6-7 days. The white, clearly segmented prepupal stage lasts one to two days. The newly formed pupa is white but darkens progressively to a very dark grey. The pupa (Figs 8e, f) is noticeably "hunchbacked" in side view and has distinct lateral extensions of the abdomen. As the pupa darkens a series of short dark bands or stripes develop on these lateral extensions and eventually the pupa turns a uniform dark colour 3-4 days prior to emergence. Pupal size varies from 0.7 to 1.1mm, averaging 0.9mm (n = 24) and pupal duration varies from 10 to 14 days.

The larval meconium is voided in the form of a smallish mass of very dark red to black pellets, partly or completely coalesced and deposited beneath the host remains (Fig 7b). The pupal exuvium of *Tetrastichus* sp. 1 is dark grey (Figs 24 - 28). The thoracic sclerites, wing pads and hind leg sheaths remain united in a mass with the abdominal sclerites (Fig 24). The oculoparietal plate (Fig 25) and frontoantennal plate (Fig 26) separate from the rest of the body segments. The frontoantennal plate is triangular in general outline with the anterior corners extended by the bases of the antennae; the mouthparts are sometimes attached to its anterior margin. The pro- and mesothoracic leg sheaths are also detached and the mesothoracic leg (Fig 27) has a well defined tibial spur. The prothoracic leg sheath (Fig 28) is characterised by the proximal area being attached like a hook. Most of the sclerites remain within the host remains after adult emergence (Fig 7a). Where the pupal stage of *A.cassatus* is the host, the dry pupal skin of *A.cassatus* (Fig 29) is also found within the psyllid remains.

Total duration of development was at least three weeks and the adult parasites emerged through a hole chewed in the dorsum of the psyllid. Size of the exit hole averaged 0.32mm in diameter (range 0.22 - 0.37mm, n = 32). In Salisbury, females were found to be the most abundant sex and Catling (1969b) reports that females were predominant at Malkerns where the ratio of males was found to be 29.8%.

7.2 MARIETTA EXITIOSA COMPERE (APHELINIDAE)

Marietta exitiosa is a parasite common throughout South Africa in citrus orchards and is found on a wide range of hosts including diaspine and soft scales in which it is always a secondary hyperparasite (Annecke, 1964). This species was reared from the citrus psylla in Salisbury and a few isolated specimens were reared in Malkerns district by Catling (1969b). These appear to be the only records of this parasite from psyllids, and until now nothing was known of its biology on psyllid hosts.

M. exitiosa was never found to be very numerous but both sexes appeared fairly regularly in small numbers in samples. It is a tertiary hyperparasite, attacking *A. cassatus* located both externally and internally on citrus psylla nymphs, but the actual stage of the host attacked by *M. exitiosa* has not been determined.

M. exitiosa *adults* (Fig 9a) may readily be distinguished from other parasites in the *T. erytreae* parasite complex by the distinctive pattern of dark and light setae on the forewings. It is a small species, ranging from 0.6-1.0mm in length (n = 5) and the adults of both sexes are predominantly yellowish with pale brown and white markings. The legs are mostly pale, patterned with a series of dark bands and spots. The sexes may be differentiated by their antennae (Figs 9a, b).

The *pupa* (Figs 9c, d) is small, 0.6 to 1.0mm in length (average 0.9mm, n = 10), a dull grey-black and is flattened dorso-ventrally. Segmentation of the abdomen is very evident on the dorsal surface, appearing as a series of small ridges. The antennae are short, not reaching to the distal end of the foreleg sheaths.

The meconium (Fig 9f) consists of a small number of dark grey-brown, irregularly-shaped pellets, deposited loosely beneath the host remains. The pupal exuvium of M. exitiosa (Figs 30-32) is dark brown and usually remains more or less intact within the host remains (Fig 9e). The abdominal sclerites collapse after eclosion forming a semi-circle of folds and the sternum is characterised by well developed apophyses (Fig 30). The frontoantennal plate (Fig 31) is detached and is triangular in general outline with the corners extended by the bases of the antennae which are sharply geniculated. The clypeus and mouthparts may be attached to the frontoantennal plate. The leg sheaths separate from the other sclerites and the proximal portion of each is folded over (Fig 32) in a manner characteristic to this species.

7.3 EUXANTHELLUS SP. (APHELINIDAE)

Members of the genus Euxanthellus often lack good morphological and colour characteristics for distinguishing the species and consequently many species have not yet been named. Some members of the genus attack soft brown scale and Annecke has separated these into several groups and comments that the above species from the citrus psylla resembles his Group IV (Annecke, 1964, 1967).

The colours of the adult male Euxanthellus sp. are yellow, brown and black. There is a large, conspicuous diamond-shaped black marking on the mesoscutum (Fig 10a). The pronotum, propodeum and abdomen are all brown or blackish while the remainder of the body is yellow. The legs are almost entirely pale yellow except for the basal part of the first tarsomere of the mesothoracic leg which is brown. The average length of the adult male is 0.95 mm (0.9 - 1.0mm, n = 10).

Only males of this species were found as hyperparasites in the T.erytreae parasite complex in Salisbury and Swaziland (Catling, 1969b). The biology of Euxanthellus sp. is probably similar to that of others of its genus (Flanders, 1959). The male is a hyperparasite while the female is likely to be a primary parasite on other hosts. Males were reared as tertiary hyperparasites from both internally and externally parasitised psyllid nymphs and in either case the host was the secondary hyperparasite A.cassatus. Euxanthellus sp. was also occasionally found to be secondary, attacking the prepupal or pupal stage of Tetrastichus ?radiatus.

The male egg (Fig 10b) of Euxanthellus sp. is white, oval and pedicellate, about 0.16 mm in length (n = 10), with a small papilla at one end. The position of the egg on the host was variable but it was usually laid either at the anterior or posterior end of the host, attached by the pedicel, which originates from the side of the egg, to a small wound in the host's integument

(Fig 11a). The incubation period was at least two days. Larval development is external on the larval, prepupal or pupal stages of A.cassatus or, occasionally T.?radiatus. The larva can be distinguished, particularly in the later instars, by the C-shaped bend of its body (Figs 10c, 11b) and is whitish with a definite head and thorax. The host parasite was completely devoured by the hyperparasitic Euxanthellus sp. and larval development was completed in about a week. The prepupa, which lasts from 1 to 2 days, is white with a clearly defined head and thoracic region and a distinctly segmented abdomen. The pupa (Figs 10d, e) is black, shiny and dorso-ventrally flattened, varying from 0.7mm to 1.15mm in length (average 0.9mm, n = 16). Duration of the pupal stage was between 11 and 14 days and the adult emerged from a hole in the dorsum of the psyllid. The entire life cycle was completed in 3-4 weeks.

The meconium (Fig 11d) comprises several grey-brown, irregularly-shaped pellets which may or may not be fused together and which are difficult to distinguish from those of M.exitiosa. The pupal exuvium (Fig 33) is dark brown. The abdominal sclerites collapse and, together with the thoracic sclerites, form a U- or V-shaped mass. The frontoantennal plate and antennal sheaths usually remain together (Fig 34) in the form of an open triangle. The appearance of the pupal exuvium in the psyllid remains after adult emergence is shown in Fig 11c.

7.4 ?PSYLLAEPHAGUS SP. (ENCYRTIDAE)

This undescribed encyrtid hyperparasite was reared from both internally and externally parasitised psyllid nymphs. Annecke (1967) comments that perhaps a new genus as well as a specific description may be needed for this parasite but suggests that it may be closely related to Psyllaephagus. ?Psyllaephagus sp. is a tertiary hyperparasite, attacking A.cassatus in the larval, prepupal or pupal stage. On rare occasions specimens were found attacking T?radiatus (pupal stage), Tetrastichus sp. 1 (prepupal stage, externally parasitised host psyllid) and possibly Psyllaephagus pulvinatus.

The adult female ?Psyllaephagus sp. (Fig 13b) is almost completely lemon yellow in colour, with very small markings of black on the pronotum and propodeum. The male parasite (Fig 13a) has a lemon yellow body with more extensive markings of black; the dorsal thoracic and abdominal sclerites are almost entirely black with two small patches of yellow on the lateral margins of the mesoscutum. The entire ventral surface of the body is yellow. The adults average 0.9mm in length (0.7 - 1.1mm, n = 10) and both sexes have been reared from parasites of the citrus psylla complex.

Development from egg to adult requires at least 18 days. Larval development is external and very rapid, being completed in about 5 days, while the pupal stage lasts 11-12 days. The pupa (Figs 13 c,d,e) is dark brown to black with a characteristic, triangular-shaped abdomen. Pupae measure 0.8 - 1.0mm (average 0.9mm, n = 30). The adult emerges from a hole with an average diameter of 0.3mm which is chewed in the thoracic or head region of the dorsum of the psyllid nymph.

The *meconium* of *?Psyllaephagus* sp. (Fig 12b) is dark grey-brown, similar in colour to that of *M.exitiosa* but the pellets have a very distinctive, regular, elongate shape and number about 5-7. The pellets are usually deposited on the ventral surface of the psyllid remains (Fig 14a). The *pupal exuvium* of this species (Fig 35) is dark brown to black. The abdominal, thoracic and head sclerites are found intact after eclosion and the laterally flattened abdominal sclerites, with clearly defined segments, are the most characteristic feature of the pupal remains of this species. Less conspicuous sclerites which may also be found in the host remains are the antennal sheaths but these are not distinctive to this species and are different in both sexes.

7.5 *PHYSCUS* SP. (APHELINIDAE)

Male specimens of this species of *Physcus* (undescribed, according to Annecke, 1970) were found in externally parasitised nymphs of *T.erytreae*, but were rare. From dissections of puparia and examination of remains after adult emergence it was established that males of *Physcus* sp. were associated with nymphs parasitised by *T?radiatus* but it was not ascertained whether they develop as secondary hyperparasites on *T?radiatus* or as tertiary hyperparasites on *A.cassatus*. Females of this genus usually develop as primary parasites (Flanders, 1959) and as no females of *Physcus* sp. were found associated with *T.erytreae* it is presumed that they develop on other hosts.

The adult males of Physcus sp. (Fig 14a) are small, 0.6 - 0.8 mm in length, with predominantly pale yellow bodies. The head is completely pale yellow and the eyes dark grey. The pronotum and anterior margin of the mesoscutum are dark and the dark axillae form two distinctive marks on the thorax. The abdomen is dark dorsally but the ventral surface of the body and the legs are entirely pale yellow.

Larval development is internal and the larva eventually ruptures the host's body wall and protrudes from the remains (Fig 15d). The pupal stage (Figs 15b, c) is easily differentiated from the pupae of the other parasites in the citrus psylla complex. It is black and shiny, about 0.7mm in length, very flattened dorso-ventrally and has a spine on the inner margin of each wing bud. This is the only species other than Ceraphron sp. which displays movement in the pupal stage. It makes small, but regular rocking movements in a dorso-ventral plane.

The meconium of Physcus sp. (Fig 14f) comprises a mass of dark brown pellets which are fused together. The pupal exuvium (Fig 36) is dark brown to black and the abdominal sclerites remain in a roughly triangular shaped mass with the attached thoracic and head sclerites partly rolled. The antennal sheaths are detached from the rest of the sclerites and are shaped like a figure seven (Fig 37). The triangular shape of the abdominal sclerites, the spines on the wing pads and the antennal sheath are diagnostic features of the pupal remains of this species. The pupal remains, as left within the host, are shown in Figure 14e.

7.6 CERAPHRON SP. (CERAPHRONIDAE)

This undescribed species of Ceraphron was identified by Dr. P.M.Marsh of the United States National Museum. Male and female specimens were reared from both internally and externally parasitised citrus psylla nymphs, more commonly from the latter. Its host relationships are not completely certain but it appears to be secondary in some cases (host T.?radiatus) while in others it is definitely tertiary, parasitising Aphidencyrtus cassatus.

The adult Ceraphron sp. (Fig 15a) is easily distinguishable in body form from the other parasites in the T.erytreae parasite complex which belong to the families Encyrtidae, Aphelinidae and Pteromalidae. It has an entirely dark brown, shiny body and long, 10-segmented antennae which are pale brown except for the last four segments which are dark brown. The adult is extremely active and males and females are difficult to distinguish. Ceraphron sp. adults measure between 0.6mm and 0.9mm in length (average 0.73mm, n = 17).

Eggs are deposited externally on the body of the host and hatch in approximately two days. The developmental stage of the host which is attacked has not been determined. Larval development is completed in 7-8 days, prepupal development in 1-2 days. The prepupa (Fig 15b) is white and distinctive in shape with a small papilla in the head region. Both prepupal and pupal stages are capable of movement and when disturbed display a violent wriggling, rotating motion of the abdomen. The newly formed pupa is completely white but by the second day the eyes have turned pale pink. The eyes darken to an orange-red by the third day and no further colour change occurs until a day or so prior to emergence when the eyes darken to red and the body finally turns a dark grey. The pupa (Fig 15c) is "hunchbacked" in side view and, unlike the pupae of the other parasites of T. erytreae, is laterally flattened and lies on its side beneath or within the host psyllid. Also peculiar to this species are the long antennal sheaths which lie apposed along the mid-ventral line of the body, extending almost to the distal tip of the hind leg sheaths. Pupae vary in length from 0.8mm to 1.05mm (average 0.9mm, n = 20). The pupal stage lasts 6-8 days (average 8 days, n = 8), and development from egg to adult takes 18-20 days. The adult emerges from a hole in the dorsum of the psyllid host which averages 0.34mm in diameter (0.25 - 0.35mm, n = 20).

The meconium of Ceraphron sp. (Fig 15e) is very characteristic and consists of a single shiny, dark red-brown sphere about 0.5mm in diameter. The pupal exuvium (Fig 38) is very thin and delicate and is a pale straw colour. Most of the sclerites are crumpled together in a small mass and due to its pale colour and delicate nature the exuvium is seldom evident within the host remains (Fig 15d) but the meconium is a clear distinguishing character for the species.

7.7 ?PACHYNEURON SP. (PTEROMALIDAE)

Male and female specimens of this unidentified Pteromalid, possibly a *Pachyneuron* sp. (Annecke, 1968), were found to occur rarely in parasitised nymphs of *T.erytreae* and in the majority of the areas sampled in this study it was absent. *?Pachyneuron* sp. only appeared in any numbers in one area east of Salisbury, as a hyperparasite of *A.cassatus* pupae in internally parasitised psyllid nymphs. Only a few adult specimens were reared and these have been sent to Dr. B.D. Burks of the United States National Museum for identification but as yet have not been positively identified to genus or species. Catling (1967, 1969b) records a *Pachyneuron* sp. as a minor parasite of *T.erytreae* probably attacking *T?radiatus* in the Letaba district which may possibly be the same species as recorded in Salisbury. Members of this genus have previously been recorded as psyllid parasites (Jensen, 1957).

The *adult* of *?Pachyneuron* sp. (Fig 16a) is a very dark brown parasite with a large head and thorax and comparatively small abdomen. The legs are pale with almost entirely dark brown coxae and femora and the hind tibiae usually have a slight infuscation of brown. A distinctive characteristic is that the first tarsomeres of all the legs are brown. The *larval* stage of *?Pachyneuron* sp. was never seen. The *pupa* (Figs 16b, c) is dark brown to black, averaging 0.8mm in length (n = 6), with a large head and large humped thorax.

The meconium of ?Pachyneuron sp. (Fig 16e) is a dark brown mass comprising partly fused pellets. The pupal exuvium of this species (Figs 39-41) is brown with a characteristically densely papillose surface. The abdominal sclerites collapse after eclosion into a semi-circle of folds and angles (Fig 41). The fronto-antennal plate (Fig 39) is detached and is triangular in general outline with the corners extended by the bases of the antennae, and the mouthparts and clypeus are often attached. The oculoparietal plate (Fig 40) also separates from the rest of the sclerites and is usually found within the host remains after parasite emergence. The appearance of the pupal remains of ?Pachyneuron sp. are shown in Fig 16d.

7.8 COCCOPHAGUS PULVINARIAE COMPERE (APHELINIDAE).

C.pulvinariae is a widely distributed parasite in South Africa, a common parasite of soft brown scale in several citrus-producing areas and has been collected from several coccid hosts (Annecke, 1964). Males of this species were reared from T.erytreae in Salisbury during the preliminary sampling in the present study and on several occasions in Letaba and Malkerns (Catling, 1968, 1969b). According to Flanders (1940) the life cycle of this species is similar to that of C.cowperi which is a direct secondary ectoparasite in the male sex and a solitary, primary parasite in the female sex. No details of its host relationships and life history on the citrus psylla are known but it is probable that the male only is hyperparasitic on the citrus psyllid, although the only evidence to support this assumption is the fact that only males were reared from this host.

The male C.pulvinariae (Fig 17a) is largely black, with yellow genae, face and antennae. The legs are lemon yellow, except for the middle and hind coxae which are black.

7.9 COCCOPHAGUS SP. (APHELINIDAE)

This species of Coccophagus is very similar to C.pulvinariae except that the middle coxae only and the hind tibiae are largely black (Fig 17b). Annecke (1967) places it somewhere near pulvinariae or isipingoensis but no females were available for identification. Only males have been reared from nymphs of T.erytreae. Notes given on C.pulvinariae probably apply to this species also and this is the first record of this species from parasites of the citrus psylla complex.

7.10 COCCOPHAGUS ? ELEAPHILUS SILVESTRI (APHELINIDAE)

Two male specimens of Coccophagus ? eleaphilus (which were tentatively identified by Dr.Annecke, 1968) were reared from internally parasitised nymphs of T.erytreae during the present study and dissection of the empty mummies showed that they had developed on A.cassatus and were therefore tertiary hyperparasites. The adult male is similar to the two abovementioned species of Coccophagus except that the coxae of all legs and the hind femora and tibiae are largely black. This is the first record of this species from the T.erytreae parasite complex.

7.11 CHEILONEURUS CYANONOTUS WATERSTON (ENCYRTIDAE)

Cheiloneurus cyanonotus is a species commonly hyperparasitic in chalcidoids which parasitise scales (Waterston, 1917). Various hosts have been recorded in Africa and Jensen (1957) lists two species of Cheiloneurus as probable secondary hyperparasites of psyllids but this is the first record of C.cyanonotus as a parasite of the T.erytreae complex. In the present study this species was found in internally parasitised psyllid nymphs and, like the other minor hyperparasites in the complex, its appearance was sporadic. Both males and females were collected and the specimens varied in size from 0.7-1.0mm (average 0.8mm, n = 7). C.cyanonotus develops as a tertiary hyperparasite, attacking A.cassatus. The larvae, pupae and pupal remains were not seen.

The adult female of Cheiloneurus cyanonotus (Fig 18a) has a black abdomen and the head and thorax are yellow except for the ocellar areas, most of the genae and face, the pronotum, mesoscutum and scutellum which are a bright metallic green. The legs are pale, marked with light brown. Noticeable features other than the metallic colouration are the antennae which are largely white with a black club, the single tuft of dark bristles on the scutellum and the brown infuscation of the forewings. Males are quite different from females, the colour of the body black with metallic markings; wings hyaline; the antennae (Fig 18b) dusky, not conspicuously coloured;

legs pale except for a slight infuscation on the hind femora and tibiae.

7.12 TETRASTICHUS SP. 2 (EULOPHIDAE)

Three male specimens of this species of Tetrastichus were collected during the study. In general body colouration the specimens resemble T.?radiatus, with a black body and a white dorsal abdominal spot, but the leg colouration is similar to that of Tetrastichus sp. 1 in that all the femora are marked with brown. Average size of this species was 0.8mm (range 0.7mm - 1.0mm, n=3). No details are known of its biology but it is a hyperparasite of the citrus psylla parasite complex.

8. KEYS TO THE PARASITES OF TRIOZA ERYTREAE.

The following key to the adult stage of the parasites in the T.erytreae parasite complex has been made as simple as possible for practical use and is based on the most conspicuous characters such as colour differences as well as salient structural differences. Consequently the parasites are not keyed out according to family differences. Specimens used in the construction of the key were either dry or preserved in alcohol.

8.1 Key to the adult primary parasites and hyperparasites in the T.erytreae parasite complex.

1. Forewings hyaline or infuscated with brown, not marked with a pattern of dark and light setae; antennae with more than 6 segments 2

   Forewings plainly marked with a pattern of dark and light setae (Fig 9a); antennae 6-segmented .... Marietta exitiosa Compere

2. No tuft of bristles on the scutellum; wings hyaline 3

   A single tuft of bristles on the scutellum; wings infuscated with brown..Cheiloneurus cyanonotus Waterston ♀♀

3. Body colours yellow and black 4
   Body colour dark brown or black with no yellow markings on the thorax or abdomen 7

4. Pronotum entirely black; body yellow marked extensively with black 5

Pronotum yellow with small black markings anteriorly; remainder of body almost entirely pale yellow (Fig 13a) .... *?Psyllaephagus* sp. ♀♀

5. Dorsal surface of abdomen dark, ventral surface yellow; legs entirely pale yellow 6

Dorsal and ventral surfaces of abdomen dark; first tarsomere of middle leg dark, rest of legs pale (Fig 10a) ...... *Euxanthellus* sp. ♂♂

6. Scutellum, metanotum and propodeum yellow, mesonotum largely yellow ... *Physcus* sp. ♂♂

Scutellum, metanotum and propodeum black, mesonotum largely black... *?Psyllaephagus* sp. ♂♂

7. Head and thorax black; abdomen with a conspicuous white spot on the dorsum 8

Body predominantly dark with no white markings9

8. Femora of all legs marked with brown .... *Tetrastichus* sp. 2

Fore-and mid femora completely pale, hind femora faintly marked with brown..*Tetrastichus ?radiatus* Waterston

9. Genae and face yellow .....Genus *Coccophagus* 10

Genae and face completely dark with no yellow colouration 11

10. Coxae of middle legs and hind tibae largely dark ....Coccophagus sp. ♂♂

Coxae of middle and hind legs dark, tibiae and femora of all legs yellow ....Coccophagus pulvinariae Compere ♂♂

Coxae and femora of all legs largely dark.. ....Coccophagus ?eleaphilus Silvestri

11. Spur of middle tibiae well developed 12
Spur of middle tibiae small and not well developed 14

12. Legs almost entirely pale except for a slight infuscation on the hind leg 13
Femora and tibiae of all legs marked with black (Fig 5a).............Aphidencyrtus cassatus Annecke

13. Hind femora largely brown, rest of legs pale.. ....Psyllaephagus pulvinatus (Waterston)
Hind femora with a slight infuscation at the distal end only, hind tibae slightly infuscated ....Cheiloneurus cyanonotus Waterston ♂♂

14. Antennae a uniform colour, last four segments not darker than the rest....................15
Antennae pale brown except for last four segments which are a dark brown (Fig 15a)....Ceraphron sp.

15. Tibiae of all legs pale........Tetrastichus sp. 1
Middle and hind tibiae with slight brown infuscations ....?Pachyneuron sp.

8.2 Key to the pupae of the primary parasites and hyperparasites in the *T. erytreae* parasite complex.

The following is the key to the pupal stage of ten of the parasites in the citrus psylla parasite complex. The three species of *Coccophagus*, *Cheilonurus cyanonotus* and *Tetrastichus* sp. 2 were not seen in the pupal stage and therefore do not appear in the pupal key.

1. Antennae not apposed along their length; pupa dorso-ventrally flattened 2
   Antennae apposed along their entire length, extending down the mid-ventral line; pupa laterally flattened (Fig 15c).............*Ceraphron* sp.

2. Large tibial spur on the mesothoracic legs (Fig 4f) 3
   No tibial spurs visible on the mesothoracic legs 5

3. Abdominal segmentation ill-defined and abdomen appearing smooth in dorsal and lateral view..... 4
   Abdominal segmentation clearly defined, forming distinct ridges in dorsal and lateral view (Fig 5g).............*Aphidencyrtus cassatus* Annecke

4. Abdomen triangular in outline (Fig 13c); sides of abdomen scarcely visible outside the legs in ventral view (Fig 13e)... *?Psyllaephagus* sp.
   Abdomen rounded in outline (Fig 4g); sides of abdomen clearly visible outside the legs in ventral view (Fig 4f).... *Psyllaephagus pulvinatus* (Waterston)

5. Pupa entirely dark with no pale markings..... 6
Pupa dark with a pale dorsal abdominal spot; prosternum and ventral surface of the abdomen pale................Tetrastichus ?radiatus Waterston

6. Distal ends of the antennae not touching each other and extending no further than the distal end of the prothoracic legs; no spine on the inner margin of the wing pad................ 7
Distal ends of the antennae touching in the mid-ventral line (Fig 14c) and extending almost as far as the distal ends of the mesothoracic legs; a spine present on the inner margin of the wing pad ....<u>Physcus</u> sp.

7. Viewed laterally the pupal outline ventrally is concave i.e. shaped like a shallow 'C'; the head is bent forward giving the pupa a 'hunchbacked' or stooped appearance....................... 8
Viewed laterally the pupal outline is either flat or convex, the head not bent forward......... 9

8. Lateral margins of the abdomen extended and visible outside the legs in ventral view (Figs 8e, f) ....<u>Tetrastichus</u> sp. 1
Lateral margins of the abdomen not extended and only just visible outside the legs in ventral view (Figs 16b,c)...?<u>Pachyneuron</u> sp.

9. Viewed laterally the pupal outline ventrally is flat (Fig 10e); head in a flat plane with the ventral surface of the body, antennae extending to the distal end of the prothoracic legs.................Euxanthellus sp.

Viewed laterally the pupal outline ventrally is convex (Fig 9d) the head set back in line with the dorsal surface of the body; antennae not extending as far as the distal end of the prothoracic legs (Fig 9c)..Marietta exitiosa Compere

8.3 Key to the pupal remains of the primary parasites and hyperparasites in the T.erytreae parasite complex.

The larval meconium and pupal remains of a parasite, although of little, if any, general value in identifying the species of a genus, may be of considerable value in the recognition of the species which compose the parasitic fauna of a host in the field (Flanders, 1942; Hill & Pinckney, 1940; Torgersen, 1969). Meconial pellets of the parasites of T.erytreae vary in size, shape and colour and there is significant variation in the colour and form of the cast pupal skin of each parasite species. Furthermore the form and position of the meconium and pupal exuvium of the various parasites remain unaltered long after the departure of the adult parasites. As a result ten of the species comprising the citrus psylla parasite complex may be identified, using the above characters, by means of the following key. The pupal remains of the three species of Coccophagus and of Cheiloneurus cyanonotus and Tetrastichus sp. 2 were not seen and these five parasites are not included in the key.

In using the key it is recommended that the pupal remains of the parasite be removed from the psyllid host and mounted on a slide in a medium such as alcohol so that the specimens may be examined under any magnification that may be necessary. Once familiarity with the specimens has been attained it should be possible to dispense with the mounting process and identify the parasite remains under a low power magnification as they appear dissected out from the psyllid host. This means of parasite species identification is extremely useful for the evaluation of parasite activity after emergence of the adult parasites and has been used extensively in the following field studies as a non-destructive sampling method.

1. Pupal remains external, lying beneath the ventral surface of the host psyllid.................. 2
   Pupal remains enclosed within the host psyllid 'mummy' 9

2. Pupal exuvium a delicate mass of translucent, pale straw-coloured sclerites............... 3
   Pupal exuvium black or translucent brown..... 4

3. Pupal exuvium with the abdominal sclerites crumpled and the thoracic sclerites almost circular in outline (Fig 38, 15d); meconium a single dark red-brown spherical pellet (Fig 15e) found beneath the psyllid remains. Meconium of <u>T.?radiatus</u> (Fig 2d) usually present

on the dorsal surface of the psyllid remains, occasionally meconium of A.cassatus (Fig 6c) also beneath psyllid remains......... Ceraphron sp.

Pupal exuvium comprising a mass of crumpled sclerites with the thoracic sclerites almost rectangular in outline (Fig 19, 2c) and a detached almost hemispherical pale brown fronto-antennal plate (Fig 20); meconium a curl of fused orange-brown pellets deposited on the dorsal surface of the psyllid remains (Fig 2d) ....Tetrastichus ?radiatus Waterston

4. Scutellum not separate from the other pupal sclerites 5

Scutellum separate from the rest of the pupal sclerites, circular in outline and characteristically sculptured (Fig 22); the remainder of the sclerites, except for the leg sclerites and antennal sheaths and bases, attached together (Fig 23, 6b), abdominal segmentation distinct, thoracic sclerites densely papillose, head sclerites rolled. Meconium comprising many small sub-spherical pellets (Fig 6c) varying in colour from dark brown to cream. Meconium of T.?radiatus (Fig 2d) present outside the psyllid remains...Aphidencyrtus cassatus Annecke

5. Meconium not black............................ 6

Meconium black, a mass of fused pellets (Fig 7b);

abdominal and thoracic sclerites joined together with the leg sheaths, wing pads and sternum clearly distinguishable (Fig 24, 7a). Oculoparietal plate and frontoantennal plate detached (Figs 25, 26), the latter roughly triangular in outline, extended by the antennal bases. Front and middle leg sheaths detached, distal portion of the mesothoracic leg (Fig 27) with the tibial spur sharply defined; prothoracic leg (Fig 28) with the proximal area attached like a hook. Pupal skin of A.cassatus (Fig 29) and its meconium (Fig 6c) also present within the host remains......... Tetrastichus sp. 1

6. Abdominal segments telescoped and flattened in a dorso-ventral plane; meconium of several irregularly shaped pellets, usually fused together..7

Abdominal segments flattened laterally with the segmentation distinct, sclerites finely papillose (Fig 35, 12a) with the thoracic and head sclerites attached. Meconium of regular, oval loose grey-brown pellets (Fig 12b). Also present may be the meconium and/or (rarely) pupal skin of T.?radiatus or the meconium and/or pupal skin of A.cassatus or, rarely, the pupal skin of Tetrastichus sp. 1 ....?Psyllaephagus sp.

7. Pupal exuvium united in a U- or V-shaped mass; sternum not distinct from the other sclerites.8

Pupal exuvium not united in a U- or V-shaped mass (Fig 30, 9e); sternum clearly discernible and with characteristic apophyses; frontoantennal plate (Fig 31) triangular with the antennal bases sharply elbowed; middle leg sheaths with proximal end folded over (Fig 32) and the median portion characterised by a distinct tibial spur. Meconium of A.cassatus and/or the meconium of T.?radiatus may also be present..............Marietta exitiosa Compere

8. Abdominal sclerites collapsed in a semicircular mass with the leg sheaths projecting from it (Fig 33, 11c); antennal sheaths attached to the frontoantennal plate (Fig 34). Meconium and/or pupal skin of A.cassatus or T.?radiatus may also be present......Euxanthellus sp.

Abdominal sclerites forming a triangular-shaped mass without projecting leg sheaths (Fig 36, 14e); a spine on the wing pads; antennal sheaths detached from the other sclerites and characteristically shaped like a figure seven (Fig 37). The meconium of T.?radiatus usually present outside the psyllid remains..............Physcus sp.

9. Pupal exuvium black or opaque dark brown......10

Pupal exuvium a translucent pale straw colour, a delicate crumpled mass of sclerites (Fig 38); meconium a single spherical red-brown pellet (Fig 15e). The meconium of P.pulvinatus (Fig 3b) and the meconium and/or pupal skin of A.cassatus (Figs 6c, 29) may also be present.....Ceraphron sp.

10. Scutellum not detached from the rest of the pupal sclerites.............................11

Scutellum detached from the rest of the pupal sclerites, almost circular and characteristically sculptured (Fig 22); head, thoracic and abdominal sclerites clearly discernible (Fig 23, 6b), head sclerites rolled, thoracic sclerites densely papillose, and the abdominal segmentation clear. Meconium of many, small sub-spherical pellets varying in colour from dark brown to cream (Fig 6c). Meconium of P.pulvinatus (Fig 3b) also present.....Aphidencyrtus cassatus Annecke

11. Meconium variously coloured but not black.....12

Meconium black, a mass of fused pellets (Fig 7b); pupal exuvium with the hind leg sheaths, wing pads, and sternum clearly distinguishable (Fig 24, 7a), Oculoparietal plate (Fig 25) and frontoantennal plate (Fig 26) detached from the other sclerites, the latter roughly triangular in outline, extended at the anterior by the antennal bases. Pro- and mesothoracic leg sheaths detached; distal portion of the mesothoracic leg (Fig 27) with tibial spur sharply defined, prothoracic leg sheath with the proximal portion attached like a hook, meconium of P.pulvinatus also present. Pupal skin of A.cassatus and its meconium often present......Tetrastichus sp. 1

12. Meconium not of regular, oval pellets.........13

Meconium of regular, oval grey-brown pellets (Fig 12b); pupal exuvium (Fig 35) with the abdominal sclerites laterally flattened and showing distinct segmentation, the sclerites finely papillose; head and thoracic sclerites attached to the abdominal sclerites. Pupal skin and/or meconium of A.cassatus and the meconium of P.pulvinatus usually present ....?Psyllaephagus sp.

13. Sternum indistinguishably crumpled with the other sclerites, no detached leg sclerites present within the psyllid mummy..........................14

Sternum clearly discernible in the pupal remains, attached with the rest of the thoracic sclerites to the abdominal sclerites and characterised by the distinct apophyses (Fig 30, 9e); frontoantennal plate extended at the anterior end by the antennal bases which are sharply elbowed (Fig 31); leg sclerites detached and the proximal portion of the middle leg sheath (Fig 32) folded over and the distal portion with a prominent tibial spur. Meconia of P.pulvinatus and A.cassatus may also be present .... Marietta exitiosa Compere

14. Frontoantennal plate present, detached from the rest of the pupal sclerites. Pupal exuvium with the abdominal sclerites collapsed into a series of folds.......................................15

Frontoantennal plate absent; pupal exuvium a single dark brown, flattened almost circular mass

(Figs 3a, 21); meconium comprising several large orange-brown flattened pellets (Fig 3b) lodged at the end of the mummy..*Psyllaephagus pulvinatus*(Waterston)

15. Frontoantennal plate coarsely punctate (Fig 39) extended by the antennal bases; oculoparietal plate (Fig 40) coarsely papillose and detached from the rest of the pupal sclerites. Pupal exuvium with the abdominal and thoracic sclerites collapsed into an almost circular, obtusely angled mass (Fig 41). Meconium and/or pupal shell of *A.cassatus* or *P.pulvinatus* (occasionally) also present.............?*Pachyneuron* sp.

Frontoantennal plate smooth, extended by the antennal bases and sheaths (Fig 34) forming an open triangle; oculoparietal plate not detached and the pupal exuvium forming a U-or V-shaped mass with the leg sheaths projecting from it. (Figs 33, 11c). Meconium and/or pupal shell of *A.cassatus* and the meconium of *P.pulvinatus* may also be present within the host mummy.*Euxanthellus* sp.

9. FIELD STUDY OF THE PARASITES OF TRIOZA ERYTREAE.

Five small sampling areas, where no chemical control was being used against citrus pests, were selected in the Salisbury area. Each area was a garden planting comprising only a few citrus trees and the location of the sites are shown in Figure 42. The total number of trees sampled was thirteen, two trees in each of the areas S_2, S_3 and S_4, three trees in area S_5 and four in area S_1. Weekly sampling was carried out in each area in order to obtain an estimate of the seasonal fluctuations of T. erytreae and its parasites and to substantiate laboratory observations. Two methods of sampling were used as follows:

(1) Sticky Impact Traps. These were used to sample the adult stage of both T. erytreae and its parasites. Each trap consisted of a yellow cylinder 60 cm in length and 12 cm in diameter which was hung in the centre of the tree. A sheet of plastic, coated with sticky 'Ostico', was placed around each cylinder and held in position with a clip. Five such traps were used in the study, one placed in each of the sampling areas S_1, S_2 and S_4 and two in area S_3. No traps were used in area S_5. This was the only destructive sampling method used.

(11) 'In situ' counts. Infested shoots on sample trees were labelled and weekly 'in situ' counts made on the psylla colonies on the shoots. Population trends of the

psyllid and its parasites were evaluated by recording the number of parasitised fourth and fifth instar psyllid nymphs in proportion to the total number of these two stages present on the labelled shoots. Separate records were kept for each tree and shoot. Details of whether parasitism was external or internal and the numbers of parasites emerging each week were recorded. Once a parasite had emerged the remains or 'mummy' of the parasitised host psyllid were removed and examined in the laboratory and the species of the parasites which had emerged was determined from pupal and meconial remains, i.e. the history of parasitism was determined from dead psyllid remains.

9.1 Results from Sticky Impact Traps

The combined results from the sticky impact traps in sampling areas S_1, S_2, S_3 and S_4 are given in Table 7 and illustrated in Figure 43. When field work was begun in January, 1968, the numbers of *T.erytreae* adults trapped were low. Thereafter the numbers began to rise, each population peak showing an increase compared with that preceeding it, reaching a maximum in early April. Adult psyllids were abundant until May when the numbers dropped rapidly and remained very low for the rest of the year with only one minor post winter peak in late September which did not lead to a second psylla build-up.

Only the more abundant parasites of *T.erytreae*, *T.?radiatus*, *P.pulvinatus* and *A.cassatus* were recorded on the sticky traps. The total number of primary parasites trapped early in the year was low and the numbers did not rise until nearly a month after the main psylla peak, then rose and fell sharply and remained negligible for the rest of the year. The figures in Table 7 show that the number of primary parasites trapped strongly reflected the population fluctuations of P.pulvinatus and the contribution of T.?radiatus to the total number of primary parasites trapped was insignificant in these sampling areas. The numbers of the hyperparasite A.cassatus trapped increased in April with a maximum peak coinciding with that of the primary parasites and a second similarly significant peak a fortnight later.

TABLE 7. Number of adult psyllids and parasites collected weekly from five sticky impact traps in sampling areas S_1 - S_4. T.?rad. - Tetrastichus ?radiatus, P.pulv. - Psyllaephagus pulvinatus, A.cass. - Aphidencyrtus cassatus.

Date		T.erytreae	T?rad	P.pulv	T.rad. P.pulv	A.cass
Jan.	5th	7	0	0	0	2
	12th	24	0	2	2	5
	19th	20	0	0	0	4
	26th	11	3	1	4	3
Feb.	2nd	5	1	0	1	3
	9th	19	0	0	0	1
	16th	70	0	1	1	2
	23rd	53	1	4	5	3
Mch.	1st	43	0	0	0	1
	8th	47	0	1	1	1
	15th	60	0	0	0	0
	22nd	53	0	0	0	1
	29th		No Record			
Apr.	5th	165	0	0	0	1
	11th	91	0	1	1	0
	19th	114	0	2	2	6
	26th	66	1	6	7	7

Date	T.erytreae	T?rad	P.pulv.	T.rad. P.pulv	A.cass
May 3rd	37	0	24	24	15
10th	13	1	7	8	8
17th	6	0	4	4	12
24th	12	0	0	0	14
31st	9	0	1	1	10
Jun. 7th	1	0	1	1	2
14th	3	0	0	0	4
21st	2	0	0	0	0
28th	0	0	0	0	0
Jul. 5th	0	0	0	0	1
12th	0	0	0	0	0
19th	0	0	0	0	0
26th	0	0	0	0	0
Aug. 2nd	0	0	1	1	0
8th	2	0	0	0	0
15th	1	0	0	0	0
23rd	0	0	0	0	0
30th	0	0	0	0	0
Sep. 6th	4	1	0	1	0
13th	7	0	0	0	0
20th	10	1	0	1	0
27th	17	0	0	0	0
Oct. 4th	7	0	0	0	0
11th	4	0	0	0	0
18th	2	0	0	0	0
25th	0	0	0	0	0
Nov. 1st	0	0	0	0	0
8th	1	0	0	0	1
15th	0	0	0	0	0
22nd	0	0	0	0	0
29th	1	0	0	0	0
Dec. 6th	1	0	0	0	0
13th	0	1	0	1	0
20th	0	0	0	0	0
27th	0	0	0	0	0
Jan. 3rd	2	1	0	1	0
10th	1	0	0	0	0
17th	2	0	0	0	0
24th	0	0	0	0	1
31st	0	0	0	0	0
Feb. 7th	0	0	0	0	0
14th	0	0	0	0	0
TOTAL	995	11	56	67	108
% of total parasites trapped		6.3%	32%	38.3%	61.7%

The primary parasites therefore were not very active or numerous during the period of greatest psyllid abundance in sampling areas S_1-S_4 in 1968. Their effective activity was limited to a very short period of little more than a month and was apparently curtailed by the action of the hyperparasite A.cassatus which became active at the same time. Neither T.erytreae nor its parasites recovered after winter to increase to significant numbers later in the year. The general pattern of psyllid and parasite fluctuations corresponds closely to that at Malkerns (Catling, 1969b), but the peaksof populations occur at a different time of year. The main psylla activity occurred between September and December at Malkerns and between February and May in Salisbury.

9.2 RESULTS FROM 'IN SITU' COUNTS

The numbers of visibly healthy and visibly parasitised (i.e. mummified or strapped down psyllids) fourth and fifth instar psyllid nymphs, based on weekly 'in situ' counts on labelled shoots from all sampling areas (S_1 - S_5) are compared in Table 8 and illustrated in Figure 44. As shown in the sticky traps results (Fig 43), the psylla population was highest during the March-April period, dropping off towards the end of April. The smaller peaks of fourth and fifth instar psyllids in May-June, July-August, September-October and October-November have little or no corresponding peaks of adults in Fig 43. This can be explained by the fact that the areas sampled by trapping (Areas S_1, S_2, S_3, S_4) showed little or no psyllid activity after the population crash in May whereas in Area S_5, in-

TABLE 8 Numbers of healthy and parasitised fourth and fifth instar psyllid nymphs and the percentage parasitism from weekly 'in situ' counts.

Date		No. unpar. psyllids	No. par. psyllids	Total No. psyllids	% par.
Mch.	1st	2147	125	2299	5
	8th	1790	113	1903	6
	15th	2232	156	2388	7
	22nd		NO RECORD		
	29th	2967	226	3193	7
Apr.	5th	2974	351	3325	11
	11th	3636	577	4213	14
	19th	1611	1019	2630	39
	26th	800	917	1717	53
May	3rd	715	619	1314	47
	10th	510	478	988	48
	17th	474	606	1080	56
	24th	1027	446	1473	30
	31st	1372	440	1812	24
Jun.	7th	1491	378	1869	20
	14th	1152	347	1509	23
	21st	136	291	427	68
	28th	32	216	248	87
Jul.	5th		NO RECORD		
	12th				
	19th				
	26th	420	107	527	20
Aug.	2nd	703	48	751	6
	9th	352	43	395	11
	16th	0	5	5	100
	23rd	240	0	240	0
	30th	1028	0	1028	0
Sep.	6th	768	100	868	12
	13th	563	260	823	32
	19th	450	96	546	18
	27th	309	120	429	28
Oct.	4th	397	267	664	40
	11th	54	346	400	87
	18th	30	104	134	78
	25th	260	37	297	13
Nov.	1st	423	19	442	4
	8th	509	60	569	11
	15th	178	66	244	27
	22nd		NO RECORD		
	29th				
Dec	6th	5	43	48	90
	13th	2	20	22	91
	20th	144	12	156	8
	27th	59	40	99	40

Jan. 3rd	16	38	54	70
10th	11	63	74	85
17th	36	48	84	57
24th	50	35	85	41
31st	58	4	62	7
Feb. 7th	23	17	40	43

cluded in the 'in situ' counts, the psyllid activity continued after this period. The population peaks in Figure 44 correspond fairly closely to the 6-7 distinct field generations described by Catling (1969b).

The *percentage visible parasitism* was never very high during the period of greatest psyllid abundance. The peak number of parasitised late instar psyllids (mid-April) gave 55% visible parasitism but by then the psyllid numbers were already declining. Only when the psyllid numbers had decreased towards winter did the percentage visible parasitism reach significant levels but then the number of hosts present was negligible. All the peaks in the percentage visible parasitism coincide with a drop in the number of fourth and fifth instar psyllids available for parasitism.

In order to compare the activity of the two primary parasites throughout the year, the number of internally and externally parasitised fourth and fifth instar psyllid nymphs are recorded in Table 9 and illustrated in Figure 45a. Both the external and internal species, *T.?radiatus* and *P.pulvinatus*, were active between March and July with peak numbers of both internally and externally parasitised nymphs falling in April.

TABLE 9 Detailed results of 'in situ' counts and numbers of each parasite species emerging weekly from tagged shoots in sampling areas S_1-S_5.

T?R - *Tetrastichus ?radiatus*
P.P. - *Psyllaephagus pulvinatus*
A.C. - *Aphidencyrtus cassatus*
T.sp 1- *Tetrastichus* sp. 1
M.E. - *Marietta exitiosa*

C.sp - *Ceraphron* sp.
?P.sp - ?*Psyllaephagus* sp.
Euxanth.sp.-*Euxanthellus* sp.
Cocc.pulv. - *Coccophagus pulvinariae*
Cheil.cyanon - *Cheiloneurus cyanonotus*

Date	No.par.nymphs		Emerged parasites			Total other	Details of other hyperparasite species				
	Ext. par.	Int. par.	T?R	PP	AC	hypers	Tsp1	ME	Csp	?Psp	Others
Mch. 1st	0	125	0	0	0	0	-	-	-	-	-
8th	3	110	0	0	20	0	-	-	-	-	-
15th	37	119	3	1	22	2	-	-	1	1	-
22nd		NO	RECORD								
29th	79	147	47	3	30	0	-	-	-	-	-
Apr. 5th	107	244	40	3	55	16	-	-	15	1	-
11th	231	346	9	2	18	11	6	1	2	2	-
19th	441	578	13	5	67	5	3	-	1	1	-
26th	448	479	14	35	36	18	3	1	-	14	-
May 3rd	248	371	8	97	281	27	1	23	1	-	*?Pachyneuron* sp. - 1
10th	238	240	2	30	156	2	1	-	-	-	*Euxanth* sp-1
17th	350	256	8	43	64	9	6	1	-	-	*Cocc.pulv.*-1
24th	260	186	41	4	63	9	5	1	3	-	*Cheil.cyanon* - 1
31st	275	165	22	0	62	8	-	5	3	-	-
Jun. 7th	267	111	12	1	29	7	-	-	6	-	*Physcus* sp-1
14th	267	90	3	0	62	0	-	-	-	-	-
21st	216	75	5	1	32	3	-	3	-	-	-
28th	162	54	0	0	14	2	2	-	-	-	-
Jul. 5th											
12th		NO	RECORD								
19th											
26th	88	19	4	0	41	19	12	2	5	-	-
Aug. 2nd	34	14	0	0	22	1	-	1	-	-	-
9th	39	4	1	0	21	1	1	-	-	-	-
16th	1	4	0	0	2	0	-	-	-	-	-
23rd	0	0	0	0	0	0	-	-	-	-	-
30th	0	0	0	0	0	0	-	-	-	-	-
Sep. 6th	100	0	0	0	0	1	-	-	1	-	-
13th	260	0	12	0	0	0	-	-	-	-	-
19th	96	0	148	0	0	0	-	-	-	-	-
27th	120	0	42	0	0	0	-	-	-	-	-

Date	No.par.nymphs		Emerged parasites			Total other	Details of other hyperparasite species				
	Ext. par.	Int. par.	T?R	PP	AC	hypers	Tsp1	ME	Csp	?Psp	Others
Oct. 4th	267	0	39	0	0	0	-	-	-	-	-
11th	346	0	97	0	0	1	-	-	1	-	-
18th	104	0	87	0	0	11	-	-	11	-	-
25th	37	0	5	0	3	4	-	-	4	-	-
Nov. 1st	19	0	0	0	20	3	-	-	2	-	Euxanth sp- 1
8th	49	11	2	0	0	0	-	-	-	-	-
15th	51	15	0	0	0	0	-	-	-	-	-
22nd	NO RECORD										
29th											
Dec. 6th	23	20	0	0	0	4	4	-	-	-	-
13th	5	15	0	2	0	4	4	-	-	-	-
20th	4	8	0	0	2	4	4	-	-	-	-
27th	2	38	0	0	0	0	-	-	-	-	-
Jan. 3rd	1	37	0	2	0	1	1	-	-	-	-
10th	1	62	0	6	2	0	-	-	-	-	-
17th	0	48	0	1	1	5	5	-	-	-	-
24th	0	35	0	0	5	2	2	-	-	-	-
31st	3	1	0	0	3	10	10	-	-	-	-
Feb. 7th	15	2	0	0	1	0	-	-	-	-	-
TOTAL	5294	4029	664	236	1134	190	70	38	56	19	7
PERCENTAGE			29%	11%	51%	9%					

This was the only peak in the numbers of internally parasitised nymphs and the numbers dwindled to zero in August and internally parasitised nymphs only started to appear again in November-December. The number of externally parasitised nymphs, however, after following a similar pattern in the first half of the year, showed a second rise after winter, with peaks in September and October.

These fluctuations in the number of externally and internally parasitised fourth and fifth instar psyllid nymphs can be compared with the numbers of parasites, (T.?radiatus, P.pulvinatus, A.cassatus and total other hyperparasites), actually emerging each week from nymphs on labelled shoots (Table 9) which are illustrated in Figure 45b-e. Although the numbers of both externally and internally parasitised nymphs were high between March and August (Fig 45a) only a comparatively small number of T.?radiatus and P.pulvinatus survived to the adult stage (Fig 45b, c). However the numbers of hyperparasite, A.cassatus emerging during the same period were high, suggesting that the mortality of the primary parasites had been considerably affected by hyperparasitism. In the latter half of the year when T.?radiatus was the only primary parasite active (September-October), hyperparasite activity was negligible and high numbers of T.?radiatus survived to emerge as adults. The total number of hyperparasites, including A.cassatus, recorded during the period of sampling comprised 60% of the total number of parasites recorded, of which 51% was A.cassatus.

10. DISCUSSION

The interrelationships between the species comprising the parasite complex of Trioza erytreae and their host psyllid in Salisbury, as determined from field and laboratory studies, are summarized in a composite diagram (Fig 46). Several minor species of hyperparasite, Coccophagus ? eleaphilus, Coccophagus sp., Cheiloneurus cyanonotus, Ceraphron sp., Physcus sp., ?Psyllaephagus sp. and Tetrastichus sp. 2 were recorded as parasites of T. erytreae for the first time. The interrelationships between the three main species of parasite and their host psyllid were straightforward but the interrelationships between the less important hyperparasites were more complex. Although most species were normally tertiary on Aphidencyrtus cassatus, several species were also occasionally secondary and other species tertiary on these. Most of the minor species of hyperparasite, however, may be regarded as of negligible importance on citrus in Salisbury. Not all species were present in all localities but T. ?radiatus, P. pulvinatus, A. cassatus and Tetrastichus sp. 1 were recorded in all sampling areas and the composition of the complex varied from area to area only in the species of less important hyperparasites.

Doutt (1964) suggests the use of the distinguishing term 'parasitoid' to describe entomophagous insects which have a parasitic habit as they differ from true parasites in several ways. He lists the six following points of difference:

(1) the development of an individual destroys its host;

(2) the host is usually of the same taxonomic class;

(3) in comparison with their hosts they are of relatively large size;

(4) they are parasitic as larvae only, the adults being free-living forms;

(5) they do not exhibit heteroecism; and

(6) as a parameter in population dynamics their action resembles that of predators more than that of true parasites.

Thus, although the term is not used in the text, there is justification for describing the species of Hymenoptera parasitising _T. erytreae_ as parasitoids instead of parasites.

The field data recorded present a fair picture of the dynamics of the host psyllid and its parasites and the control exerted by the parasites during the period of study at these representative locations in Salisbury. The seasonal fluctuations of _T. erytreae_ populations in Salisbury during 1968 differed quite considerably from those at Letaba, South Africa, and Malkerns, Swaziland. At Letaba the annual fluctuation pattern of the citrus psylla consisted of a rapid rise in numbers in early spring (September - October) followed by a population crash in midsummer (January-February) and at Malkerns the pattern was similar with the spring rise in population during the period July to December (Catling, 1967, 1969b). In Salisbury the main psyllid population rise occurred between February and May and the September-October peak was considerably smaller in some areas and negligible in others. A more favourable altitude and climate inducing prolonged flushing of trees probably accounts for this difference but a further explanation may lie in the following. According to Catling (1969a) flushing rhythm also varies considerably with tree age, variety and condition, and greening disease tends to induce heavier winter flushes and overlapping growth cycles in summer. As the sample trees in Salisbury were of differing age, variety and condition and all were probably greened, it is very likely that their flushing rhythm had been modified. This would have resulted in a different picture of flushing and hence psyllid fluctuations from that in a commercial planting of undiseased trees of similar age, variety and condition. The field results, however can be compared generally with those of Catling but much of their value lies in providing field information about the parasites of T.erytreae in relation to their host and to each other.

T.?radiatus and P.pulvinatus were the only species of primary parasite attacking T.erytreae in Salisbury and as such it is of relevance to compare their biology and importance. T.?radiatus attacks instars III - V of T.erytreae and although field studies (Catling, 1969b) indicate that it has a preference for fourth instar nymphs, in the present laboratory studies fifth instar nymphs were preferred by ovipositing females. P.pulvinatus on the other hand, was found to oviposit in nymphal instars II - IV, the third instar being the most favoured for oviposition according to laboratory studies. The fifth instar was not attacked although the parasite pupated almost exclusively in fifth instar nymphs. P.pulvinatus should therefore have the advantage at times when only second instars and younger are available while T.?radiatus has the monopoly of any fifth instar nymphs which have escaped parasitism. In spite of the fact that both primaries attack third and fourth instars there is probably little competition between them for oviposition sites as both are active at the time of greatest psyllid abundance when there should be ample hosts for both parasites. Only when the host psyllid is scarce is there probably some competition between ovipositing females of T.?radiatus and P.pulvinatus. Salt (1934, 1935, 1937) in experiments with Trichogramma evanescens Westw., concluded that Trichogramma is able to distinguish between healthy hosts and those already parasitized and tends to avoid attacking the latter although when hosts are few, or the parasite fails to find any unparasitized hosts, superparasitism does occur. Ovipositing females of T.?radiatus and P.pulvinatus, both of which examine the host with antennal tapping and ovipositional probing, may similarly be able to differentiate between healthy and parasitized hosts as, although superparasitism does occur, eggs or larvae of both species were never found on the same host. T.?radiatus has a shorter life cycle (average 14 days) than P.pulvinatus (average 20 days) but as the former parasite oviposits in later instar hosts, it should gain no significant advantage from this. However, the balance of the species will ultimately depend on host-parasite synchronization in the field.

'In situ' counts provided a non-destructive sampling method for the present study and gave good comparative results for the two primary parasites as parasitism by either species became apparent a few days prior to pupation of the parasite. Catling (1969b) admits that his method of leaf sampling probably underestimated the activity of P.pulvinatus as all immature stages of the external parasite, T.?radiatus, were counted while the internally parasitized nymphs were counted only when parasitism became apparent. Figure 45 shows that in Salisbury in 1968, P.pulvinatus was very active during the first half of the year (March - July), absent from August to November, and appeared thereafter in low numbers. T.?radiatus had two main periods of activity from March to July (as for P.pulvinatus) and September - October (when P.pulvinatus was absent). The seasonal activity of the two primary parasites in South Africa and Swaziland is similar but there, because populations of the host psylla are highest during September-October, T.?radiatus is the main primary parasite, usually challenged only by P.pulvinatus during the winter months and at low host densities. This point will be mentioned later in relation to population homeostasis.

When both primary parasites are active, during May-July, Aphidencyrtus cassatus is well synchronized with them. Figure 45 clearly illustrates the high numbers of internally and externally parasitised fourth and fifth instar psyllid nymphs, the relatively low resulting numbers of P.pulvinatus and T.?radiatus which survived to adulthood and the high numbers of A.cassatus emerging over the same period. A.cassatus has a short life cycle, averaging 16 days, and oviposits in the early stages of its hosts (either egg or young larva) so that it should emerge at approximately the same time as the primary parasites, particularly P.pulvinatus which has a slightly longer life cycle. This is substantiated by the field results (Figs 43, 45) as the peak of A.cassatus numbers coincides with the peak numbers of primary parasites, occurring approximately two weeks after the maximum number of fourth and fifth instar psyllid nymphs. After August A.cassatus was absent and the first post-winter peaks of T.?radiatus in September and October were unaffected by hyperparasitism. A.cassatus is a very efficient hyperparasite and is obviously of more importance in Salisbury area than in South Africa as the greatest psyllid abundance coincides with the time of the year when both primary parasites are active and when A.cassatus is most active. In Swaziland Catling (1969b) reports that although A.cassatus became numerically dominant in December, reducing the number of primaries, it did not prevent a small dominant peak of primary parasites in February. In Salisbury, however, the primary parasites did not recover following a peak of the hyperparasite until after winter. In both sticky trap records and 'in situ' counts A.cassatus comprised the largest percentage of the parasites recorded over the sampling period i.e. 67% of the total parasites trapped and 51% of the total parasites emerging from labelled shoots. In addition to its action in destroying the primary parasites by active parasitism, A.cassatus may also destroy primary parasites by host-feeding from parasitised psyllid nymphs but may have a beneficial action in feeding from unparasitised psyllid nymphs.

Because it was possible to determine accurately from meconial and pupal remains which species of parasite had emerged from a parasitised psyllid nymph, 'in situ' counts gave a good estimate of the relative abundance of each parasite species. This was important in the case of the less important hyperparasites as they did not appear in the sticky trap catches. The total number of hyperparasites, other than A.cassatus, emerging over the sampling period comprised 9% of the total number of parasites recorded. This is a fairly significant figure when compared with that of 11% for P.pulvinatus. The minor hyperparasites emerged in fairly constant, though low numbers almost throughout the period when A.cassatus was present (Fig 45). Two small peaks in October and

December (comprising Ceraphron sp. and Tetrastichus sp. 1 respectively) mark the periods when minor hyperparasites were secondary, taking over the role of A.cassatus in its absence. Of the less important hyperparasites Tetrastichus sp. 1 was the most abundant species and Marietta exitiosa, Ceraphron sp. and ?Psyllaephagus sp. comprised the bulk of the rest of the hyperparasites. Other species were rare.

According to Herbert Spencer's generally accepted concept of greater stability of heterogenous systems, the greater complex of checks and balances existing within a complex biotic community makes for greater stability within the species population and the ecosystem itself (Huffaker and Messenger, 1964). Thus a parasite complex, such as described for T.erytreae, should theoretically lead to host population stability or homeostasis. The existence of two primary parasites within the T.erytreae parasite complex permits alterations in the status efficiency or dominance of the two species according to seasonal changes. Furthermore, as seen in the differing seasonal activity of the two primary parasites in South Africa and Rhodesia, the dominant role of one parasite or the other can vary depending on climate. Although little is known of the influence of hyperparasites on the effectiveness of parasites, the conclusion of Muesbeck and Dohanian (1927) that hyperparasites play an important part in maintenance of the balance between insect species in nature supports the above theory.

The secondary hyperparasite, A. cassatus, acts as an efficient regulator of populations of both the primary parasites of T. erytreae in Salisbury, with its role as a secondary hyperparasite occasionally being taken over by the less efficient minor hyperparasites in its absence. It in turn, is regulated to some extent by the many less important hyperparasites in the complex.

Because of poor host-parasite synchronization early in the year, the primary parasites became active too late to affect the main psylla build-up in Salisbury in 1968 (March-April) but did apparently temporarily check the psyllid population towards the end of April when visible parasitism of the later instar psyllids reached levels of approximately 50% for several weeks before their action was curtailed by hyperparasitism. The October peak of T. ?radiatus, however, was not decimated by hyperparasitism and visible parasitism reached nearly 90%, further lowering the numbers of an already dwindling psyllid population. Thus in Salisbury, largely because of hyperparasitism, the primary parasites of T. erytreae exerted a relatively minor influence on psyllid numbers, acting only after psyllid numbers became high. Similarly in South Africa the parasite complex invariably failed to prevent large population increases of T. erytreae (Catling, 1969b) and there is thus probably little future for biological or even integrated control of T. erytreae in southern Africa.

11. SUMMARY.

1. Fifteen parasite species comprising the *T. erytreae* complex in Salisbury are listed.

2. Detailed, illustrated accounts are given of the biology of two primary parasites, *Tetrastichus ?radiatus* Waterston and *Psyllaephagus pulvinatus* (Waterston), and their main hyperparasite, *Aphidencyrtus cassatus* Annecke.

3. The biology of the remaining twelve less important hyperparasites is briefly described and illustrated.

4. Keys are given to the adults, pupae and pupal remains of the parasites.

5. The population fluctuations of *T. erytreae* and its parasites, as determined from field studies in the Salisbury area, are reported.

6. The interrelationships between *T. erytreae* and its parasites are summarised and discussed.

12. ACKNOWLEDGEMENTS

I wish to express my very sincere appreciation to my supervisor, Dr. V.C. Moran, for his invaluable guidance, encouragement and assistance throughout this study and for doing the microphotography.

This work was carried out while I was employed by the Department of Research and Specialist Services, Ministry of Agriculture, Rhodesia, without whose permission and support this study could not have been undertaken.

Many people allowed access to their land during the study and I am particularly grateful to Mr. and Mrs. W.M. Blair, Mr. and Mrs. H.B. Blowers, Mr. and Mrs. H. Varty, Mr. and Mrs. J.M. Kirkman and Mr. and Mrs. G.W. Smith for permission to work on their properties and for their hospitality.

Sincere thanks are also extended to the following persons:
Dr. D.P. Annecke of the Plant Protection Research Institute, Pretoria, for advice and for identification of parasites; Dr. B.D. Burks and Dr. P.M. Marsh of the United States National Museum, Washington, for identification of parasites; and my colleague, Mr. B.W. Blair, for helpful advice and for taking records on several occasions during my absence.

13. REFERENCES

ANNECKE, D.P. (1964) The encyrtid and aphelinid parasites (Hymenoptera; Chalcidoidea) of soft brown scale, Coccus hesperidum Linneus (Hemiptera: Coccidae) in South Africa. Entomology Mem. Dep. agric. tech. Serv. Repub. S.Afr. 7: 1-74

ANNECKE, D.P. (1967) Personal communication.

ANNECKE, D.P. (1968) Personal communication.

ANNECKE, D.P. (1969) Records and descriptions of African Encyrtidae - 5 (Hymenoptera: Encyrtidae) J.ent. Soc.sth.Afr. 32 (2): 443-459.

ANNECKE, D.P. (1970) Personal communication.

ANNECKE, D.P. & CILLIERS, C.J. (1963) The citrus psylla, Trioza erytreae (Del Guercio) and its parasites in South Africa. S.Afr.J.agric. Sci. 6: 187-192.

BROTHERS, D.J. & MORAN, V.C. (1969) A new species of Tetrastichus Haliday, 1944 (Hymenoptera:Eulophidae) parasitic on the nymphs of Paurocephala calodendri Moran (Homoptera:Psyllidae) Proc.R. ent. Soc. Lond.(B).38 (3-4): 40-46.

BURKS, B.D. (1968) Personal communication.

CATLING, H.D. (1967) Studies on the ecology of the South African citrus psylla, Trioza erytreae (Del Guercio) (Homoptera:Psyllidae) Unpublished M.Sc thesis, Potchefstroom University.

CATLING, H.D. (1969a) The bionomics of the South African citrus psylla, Trioza erytreae (Del Guercio). (Homoptera:Psyllidae)
1. The influence of the flushing rhythm of citrus and factors which regulate flushing. J.ent.Soc. sth Afr. 32:191-208.

CATLING, H.D. (1969b) The bionomics of the South African citrus psylla, Trioza erytreae (Del Guercio) (Homoptera:Psyllidae)
2. The influence of parasites and notes on the main species involved. J.ent. Soc.sth. Afr. 32: 209-223.

CATLING, H.D. (1969c) The bionomics of the South African citrus psylla, Trioza erytreae (Del Guercio) (Homoptera:Psyllidae).
3. The influence of extremes of weather on survival. J. ent. Soc. sth. Afr. 32: 273-290.

CATLING, H.D. (1970) Distribution of the psyllid vectors of citrus greening disease, with notes on the biology and bionomics of Diaphorina citri. FAO Plant Prot. Bull., 18(1): 8-15.

CATLING, H.D. & ANNECKE, D.P. (1968) Ecology of the citrus psylla in the Letaba district of Northern Transvaal. S.African Citrus J. 410: 8-17.

CLAUSEN, C.P. (1939) The effect of host size upon the sex ratio of hymenopterous parasites and its relation to methods of rearing and colonization. J. N.Y. ent. Soc.47: 1-9.

CLARKE, L.R. (1962) The general biology of Cardiaspina albidextura (Psyllidae) and its abundance in relation to weather and parasitism. Aust. J. Zool. 10:537-586.

DOUTT, R.L. (1964) Biological characteristics of entomophagous adults pp 145-67. In - Biological Control of Insect Pests and Weeds. Ed. P. De Bach. London: Chapman and Hall.

FLANDERS, S.E. in COMPERE, H. (1940) Parasites of the black scale, Saissetia olea, in Africa. Hilgardia 13(7): 387-425.

FLANDERS, S.E. (1942) The larval meconium of parasitic Hymenoptera as a sign of the species. J.econ. Ent. 35: 456-457.

FLANDERS, S.E. (1959) Differential host relations of the sexes in parasitic Hymenoptera. Ent. exp. & appl., 2: 125-142.

GHESQUIÈRE, J. (1958) Le premier oviparasite de psylle et son hôte Trioza erythreae (Del Guercio) au Congo Belge. Proc. Xth. Int. Congr. Ent. 1, 1956: 275-280.

GHESQUIÈRE, J. (1968) Ethologie, biogéographie et brachypterisme de Psyllechthrus oophagus Ghesquière. Revue Zool.Bot. afr. LXXVIII, 1-2: 46-52.

HAGEN, K.S. (1964) Developmental stages of parasites, pp. 168-246. In - Biological Control of Insect Pests and Weeds. Ed.P. De Bach, London: Chapman and Hall.

HILL,C.C. & PINCKNEY, J.S. (1940) Keys to the parasites of the hessian fly based on remains left in the host puparium. U.S.D.A. Tech.Bull.No. 715: 1-24.

HUFFAKER,C.B. and MESSENGER,P.S. (1964) The Concept and Significance of Natural Control. pp.74-117. In - Biological Control of Insect Pests and Weeds. Ed. P.De Bach. London: Chapman and Hall.

HUSAIN, M.A. & NATH, L.D. (1924) The life history of Tetrastichus radiatus, parasitic on Euphalerus citri Kuw., and its hyperparasite. Rep.Proc. 5th ent. Meet. Pusa: 122-128.

JACK, R.W. (1916) Rhodesian citrus pests. Rhodesia agric. J. 13: 215 - 233.

JENSEN, D.D. (1957) Parasites of the Psyllidae. Hilgardia 27(2): 71-99.

LAFLÈCHE, D. & BOVÉ, J.M. (1970) Structures de type Mycoplasme dans les feuilles attients de la maladie du "Greening". C.R. Acad. Sc. Paris. 270: 1915-1917.

MCLEAN, A.P.D. & OBERHOLZER, P.C.J. (1956a) Greening disease of sweet orange. S.afr. J. agric. Sci. 8: 253-275.

MCLEAN, A.P.D. & OBERHOLZER, P.C.J. (1956b) Citrus psylla, a vector of the greening disease of sweet orange. S.Afr. J. agric. Sci. 8: 297-298.

MORAN, V.C. (1967) Studies on the biology of the Cape chestnut psylla Paurocephala calodendri Moran and the South African citrus psylla Trioza erytreae (Del Guercio) (Homoptera:Psyllidae). Unpublished Ph.D. thesis. Rhodes University.

MORAN, V.C. & BLOWERS, J.R. (1967) On the biology of the South African citrus psylla, Trioza erytreae (Del Guercio)(Homoptera:Psyllidae). J.ent.Soc. sth. Afr. 30 (1): 96-106.

MORAN, V.C., BROTHERS, D.J.B. and CASE, J.J. (1969) Observations on the biology of Tetrastichus flavigaster Brothers & Moran (Hymenoptera: Eulophidae), parasitic on psyllid nymphs (Homoptera). Trans. R. ent. Soc. Lond. 121(2):41-58.

MUESBECK, C.F. and DOHANIAN, S.M. (1927) A study of hyperparasitism with particular reference to the parasites of Apantales malanoscelus (Ratzeburg), U.S. Dept. Agric. Bull. 1487

PLETSCH, D.J. (1947) The potato psyllid, Paratrioza cockerelli (Sulc), its biology and control. Tech. Bull. Mont. agric. Exp. Stn. 446: 1-95.

RIEK, E.F. (1962) The Australian species of Psyllaephagus (Hymenoptera:Encyrtidae), parasites of psyllids (Homoptera). Aust. J. Zool. 10: 684-757.

ROBINSON, D.M. (1960) Synonymic notes of Aphidencyrtus pulvinatus Waterston (Hymenoptera: Encyrtidae) Ann. Mag. nat. Hist. (13) 3: 491-492.

SALT, G. (1934) Experimental studies in parasitism. II Superparasitism. Proc. Roy. Soc. Ser. B., 114: 455-476

SALT, G. (1935) Experimental studies in parasitism III. Host selection. Proc. Roy. Soc. Ser. B., 117: 413-35.

SALT, G. (1937) The sense used by Trichogramma to distinguish between parasitized and unparasitized hosts. Proc. Roy. Soc. Ser. B., 122: 57-75.

SCHWARZ, R.E. (1964) An insect-transmissible virus, trapped on sweet orange seedlings in orchards where greening disease is common. S.Afr. J. agric. Sci. 7: 885-890.

SCHWARZ, R.E. (1965) A fluorescent substance present in tissues of greening affected sweet orange. S.Afr. J. agric. Sci. 8; 1177-1179.

SMEE, C. (1944) Report of the entomologist, 1944. (Zomba, Dep. Agric.) Nyasaland (1945).

TORGERSEN, T.R. (1969) Hymenopterous parasites of the hemlock sawfly, Neodiprion tsugae Middleton, in Southeast Alaska, with a key to larval remains. J.Entomol.Soc. Brit.Colombia, 66: 53-62

VAN DER MERWE, C.P. (1941) The citrus psylla. (Spanioza erytreae del G.) Sci. Bull. Dep. Agric. For. Un. S.Afr. 233: 1-12.

WATERSTON, J. (1917) Notes on coccid-infesting Chalcidoidea II. Bull. ent. Res. 7: 247-249.

WATERSTON, J. (1922) On the Chalcid parasites of Psyllidae. Bull. ent. Res. 13: 41-58.

WIGGLESWORTH, V.B. (1950) The principles of Insect Physiology, Methuen: London.

WILSON, K. & GOLDSMID, J.M. (1962) Rhodesian citrus pests and their control. Rhodesia agric. J. 59: 41-61. Bull. No. 2127.

THE PARASITE COMPLEX OF THE CITRUS PSYLLA, TRIOZA ERYTREAE (DEL GUERCIO) (HOMOPTERA).

Part II

by

J.R. McDaniel B.Sc. Hons.

THESIS PRESENTED TO RHODES UNIVERSITY FOR THE
DEGREE OF MASTER OF SCIENCE.

Plant Protection Branch,
Department of Research and Specialist Services,
Ministry of Agriculture,
Salisbury,
Rhodesia.

LIST OF ILLUSTRATIONS

Fig. 1

TETRASTICHUS ?RADIATUS

a. Adult female
b. Male antenna
c. Egg
d. Larva
e. Female pupa (lateral view)
f. Female pupa (ventral view)

1

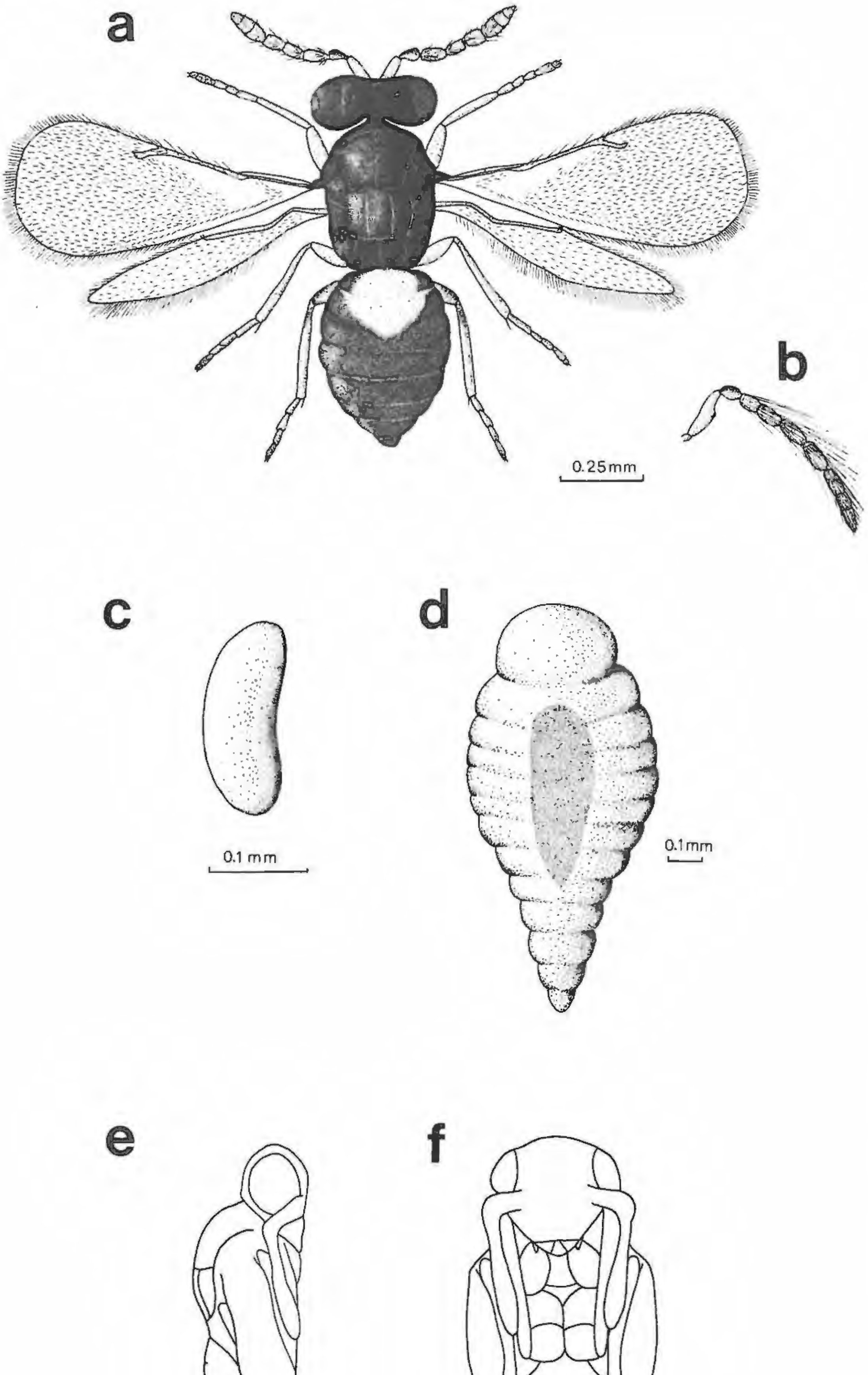


Fig. 2

TETRASTICHUS ?RADIATUS

a. Egg of T. ?radiatus on the ventral surface of a psyllid nymph.
b. T. ?radiatus larva on ventral surface of a psyllid nymph.
c. Ventral view of psyllid showing arrangement of T. ?radiatus pupal remains.
d. Meconium of T. ?radiatus.

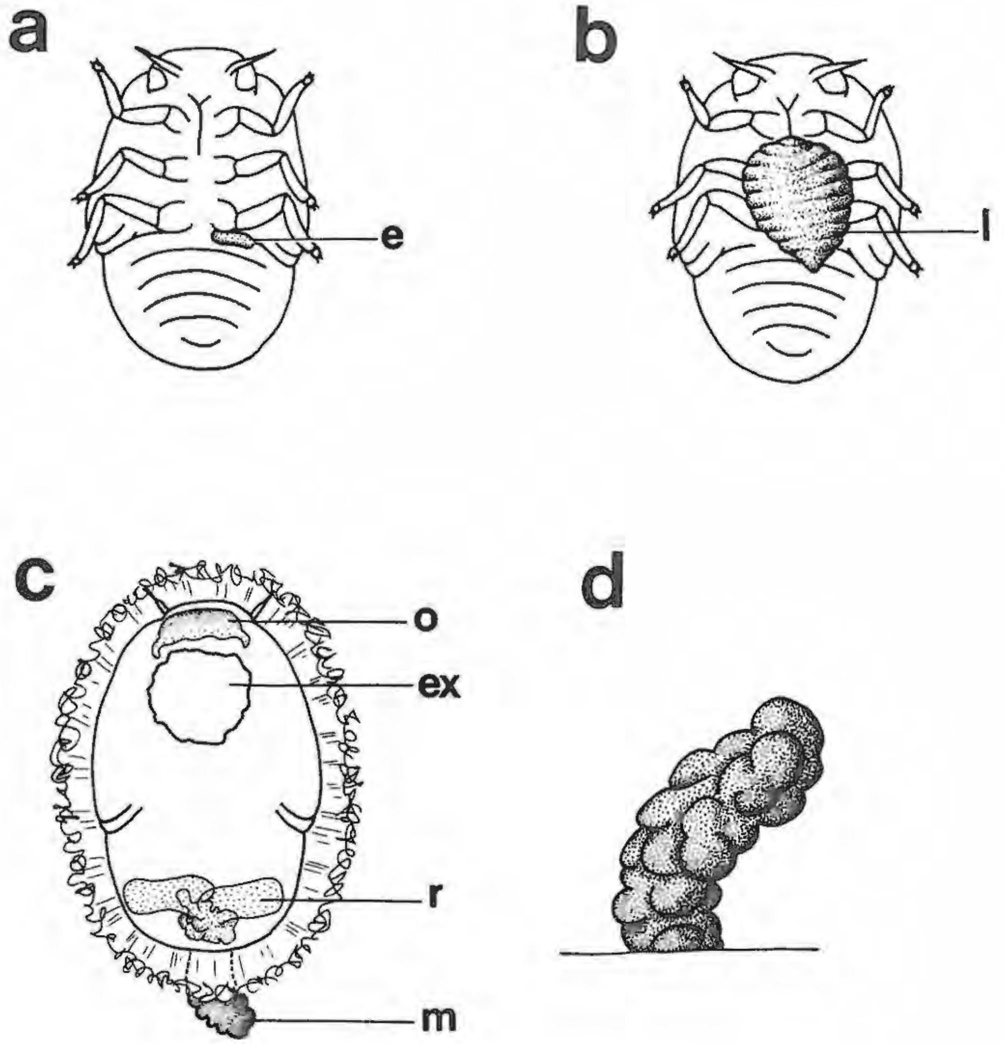
Fig. 3

PSYLLAEPHAGUS PULVINATUS

a. Dorsal view of mummified psyllid showing arrangement of P. pulvinatus pupal remains.
b. Meconium of P. pulvinatus.

e - egg, l - larva, o - oculoparietal plate, ex - exit hole,
m - meconium, r - abdominal and thoracic sclerites.

2



3

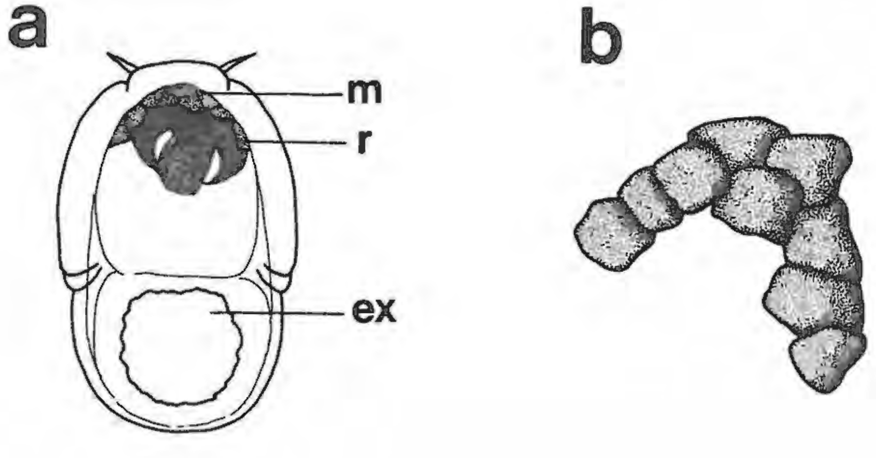


Fig. 4

PSYLLAEPHAGUS PULVINATUS

a. Adult female
b. Male antenna
c. Egg
d. Young larva
e. Mature larva
f. Male pupa, ventral view
g. Male pupa, lateral view

t - tibial spur.

4

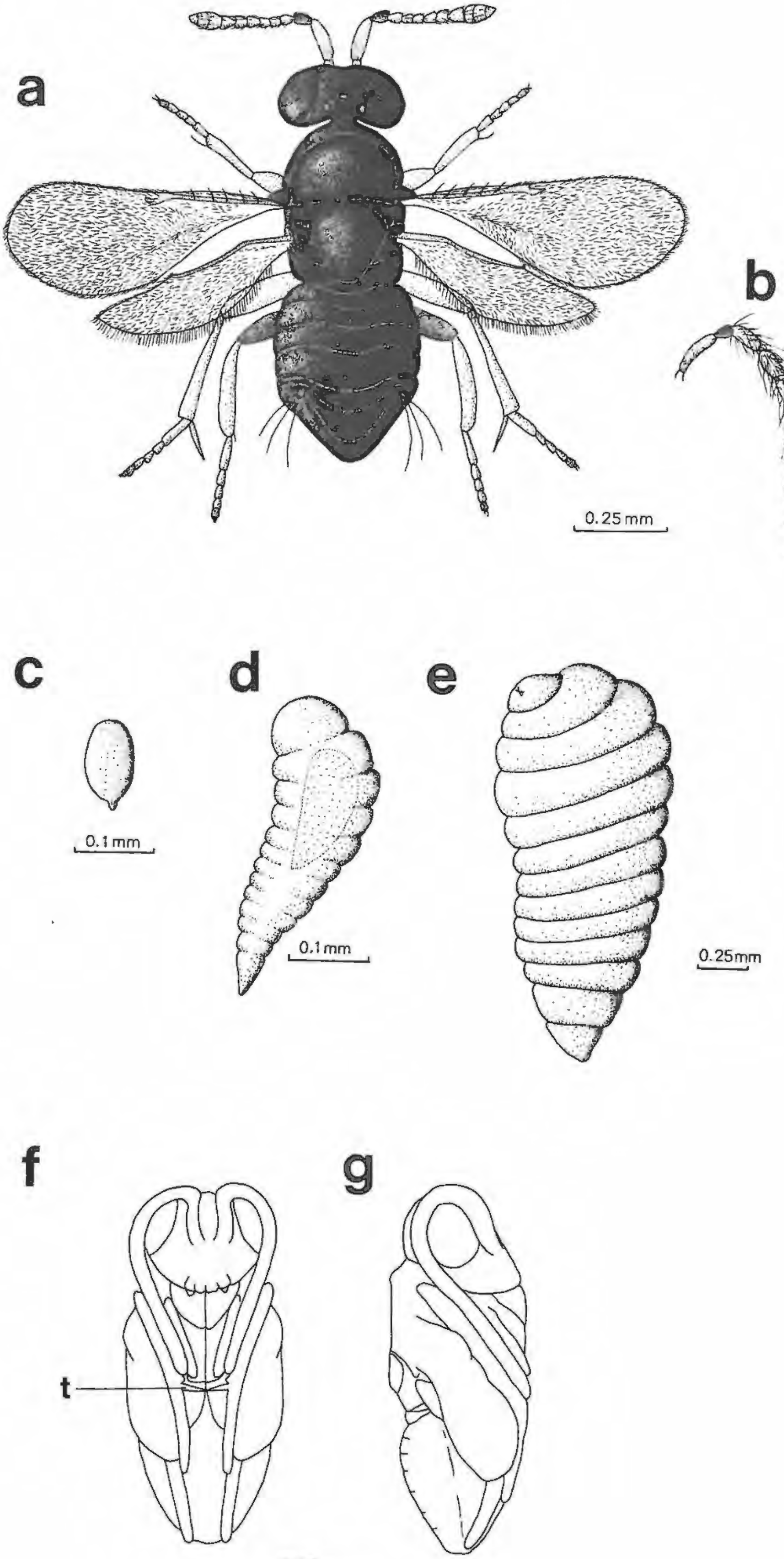


Fig. 5

APHIDENCYRTUS CASSATUS

a. Adult female
b. Male antenna
c. Egg
d. Young larva
e. Mature larva
f. Male pupa, ventral view
g. Female pupa, lateral view.

5

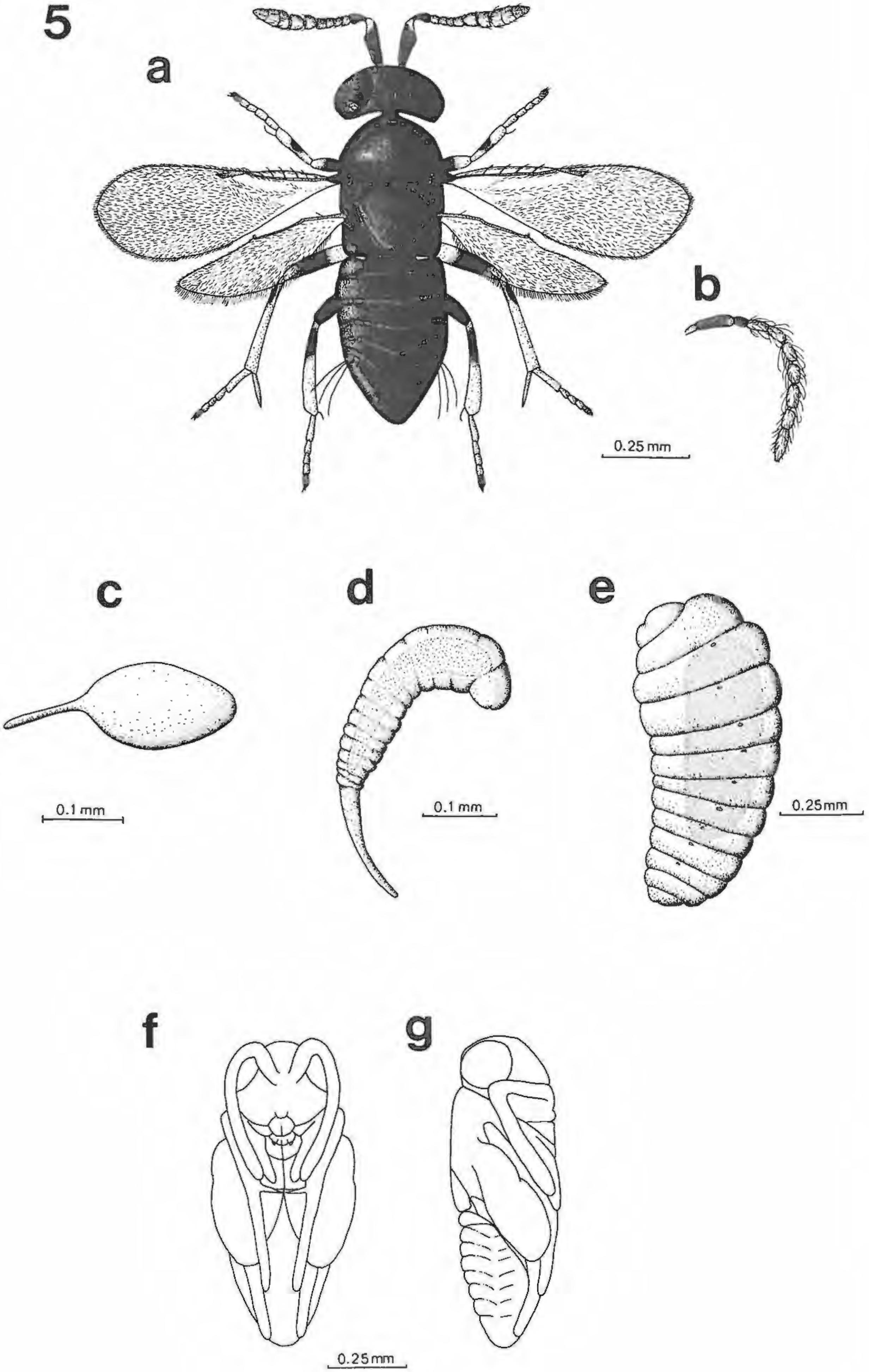


Fig. 6

APHIDENCYRTUS CASSATUS

a. Ventral view externally parasitised psyllid nymph showing A. cassatus larva with remains of its host, T. ?radiatus.

b. Dorsal view internally parasitised psyllid 'mummy' showing arrangement of pupal remains of A. cassatus.

c. Meconium of A. cassatus.

l - larva of A. cassatus, pr - remains of primary host, T.?radiatus, m - meconium of T. ?radiatus, m_1 - meconium of P. pulvinatus, m_2 - meconium of A. cassatus, r - abdominal and thoracic sclerites, s - scutellum, op - ovipositional punctures, ex - exit hole.

Fig. 7

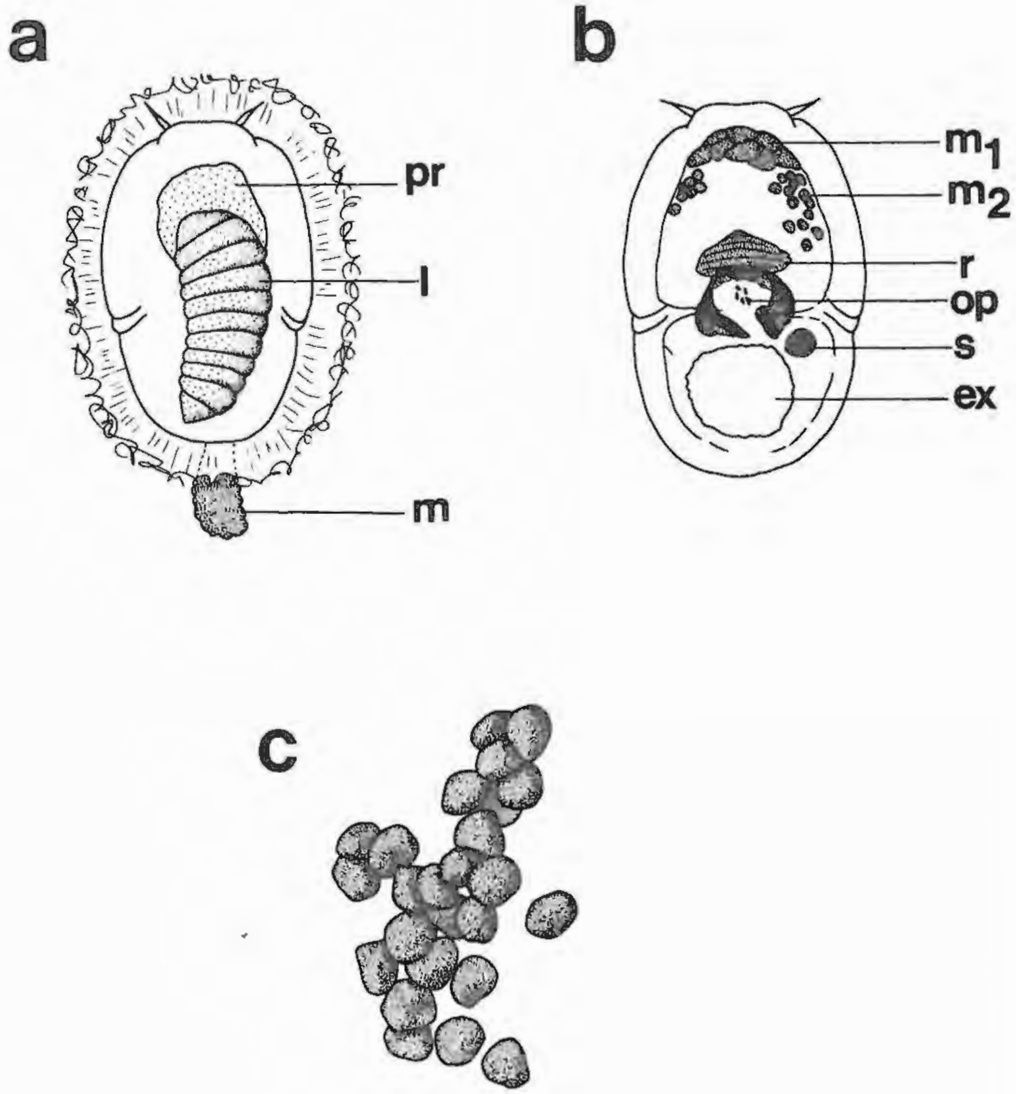
TETRASTICHUS SP. 1

a. Arrangement of pupal remains of Tetrastichus sp. 1 on ventral surface of externally parasitised psyllid nymph.

b. Meconium of Tetrastichus sp. 1.

m_1 - meconium of T. ?radiatus, m_2 - meconium of Tetrastichus sp. 1, r - abdominal and thoracic sclerites, o - oculoparietal plate, ls - leg sclerite, f - frontoantennal plate, ex - exit hole.

6



7

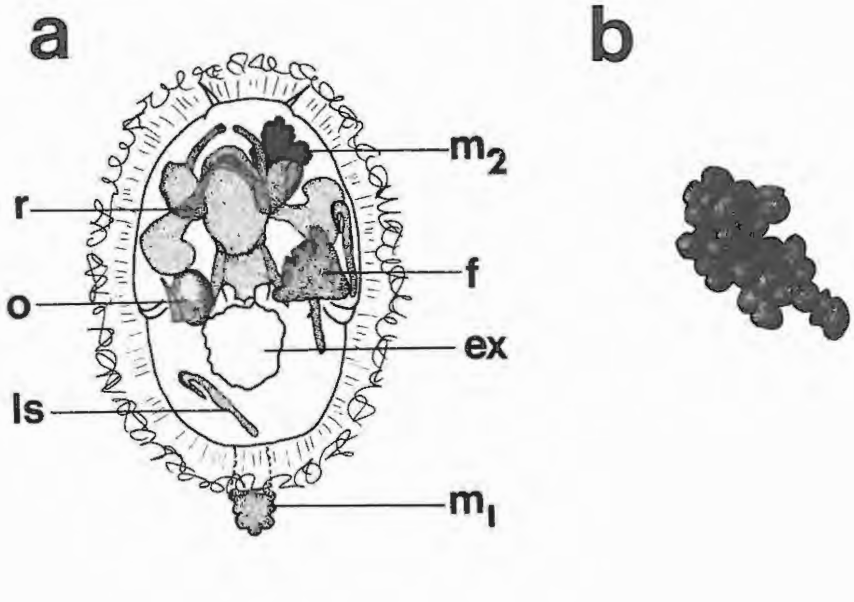


Fig. 8

TETRASTICHUS SP. 1

a. Adult female
b. Male antenna
c. Egg
d. Mature larva
e. Female pupa, ventral view
f. Female pupa, lateral view

le - lateral extensions of the abdomen.

8

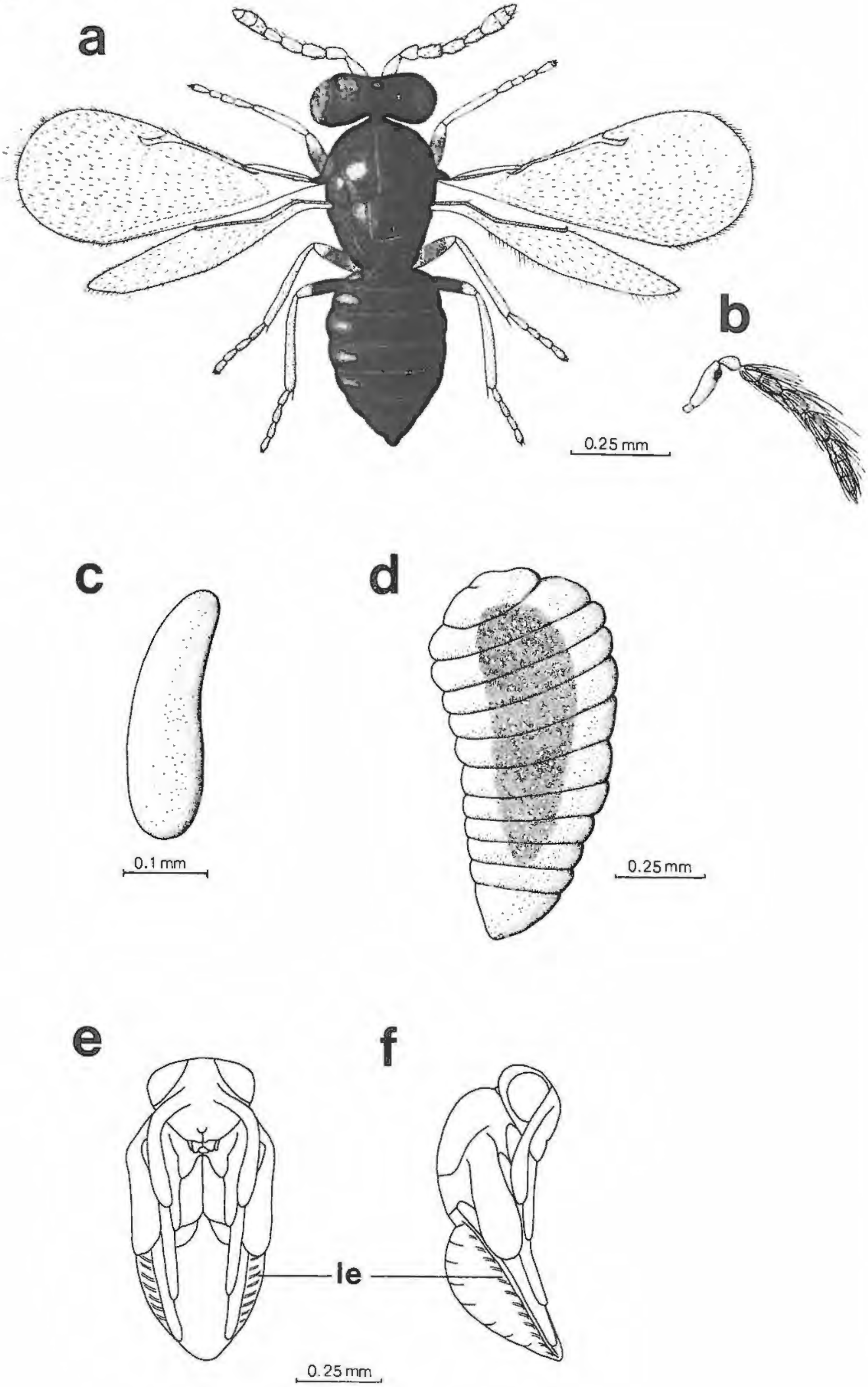


Fig. 9

MARIETTA EXITIOSA

a. Adult female

b. Male antenna

c. Male pupa, ventral view

d. Male pupa, lateral view

e. Ventral view of internally parasitised psyllid showing pupal remains of *M. exitiosa*.

f. Meconium of *M. exitiosa*.

m_1 - meconium of *P. pulvinatus*, m_2 - meconium of *M. exitiosa*, r - abdominal and thoracic sclerites, op - ovipositional punctures, ex - exit hole, f - frontoantennal plate.

9

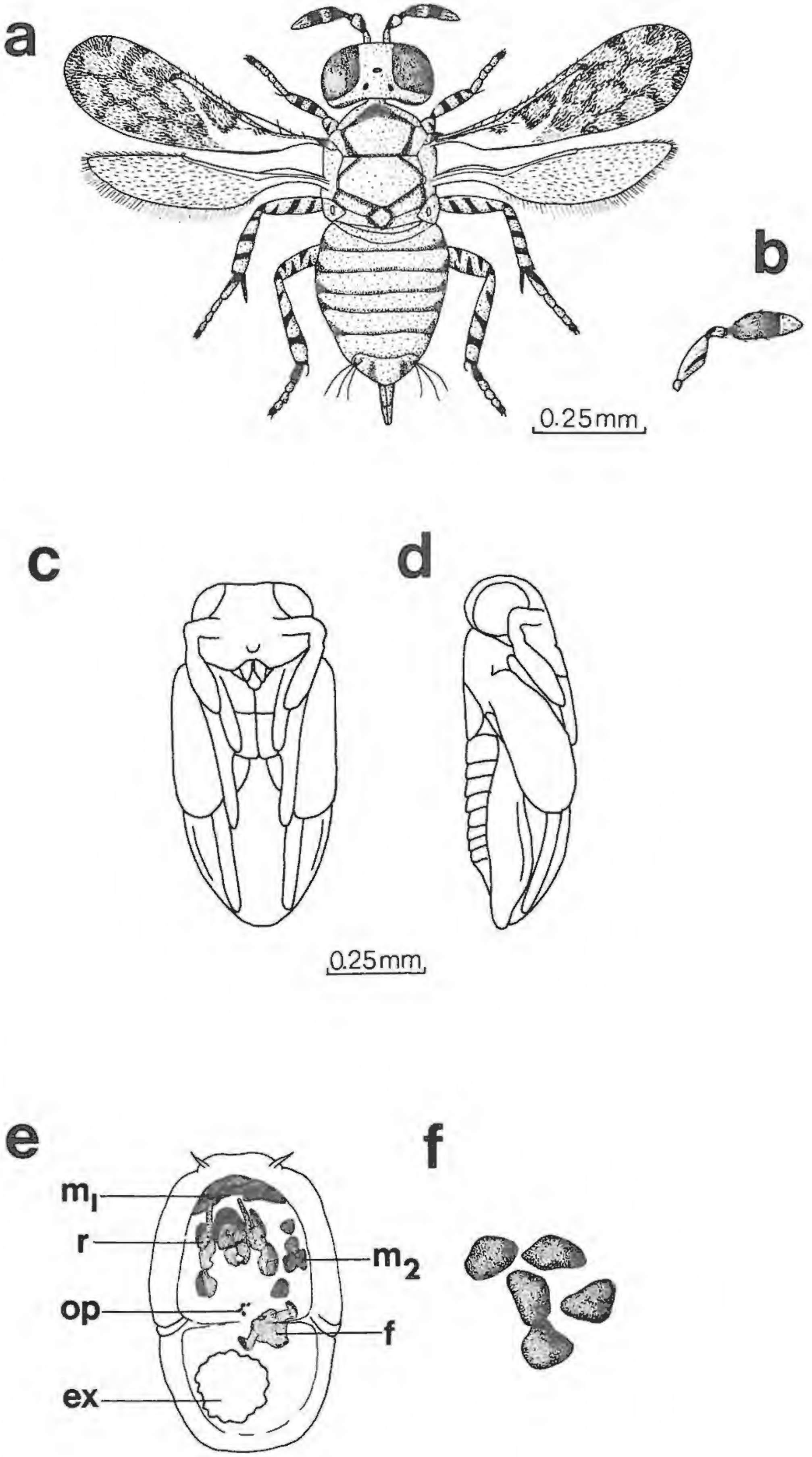


Fig. 10

EUXANTHELLUS SP.

a. Adult male
b. Egg
c. Larva
d. Male pupa, lateral view
e. Male pupa, ventral view

pe - pedicel

10

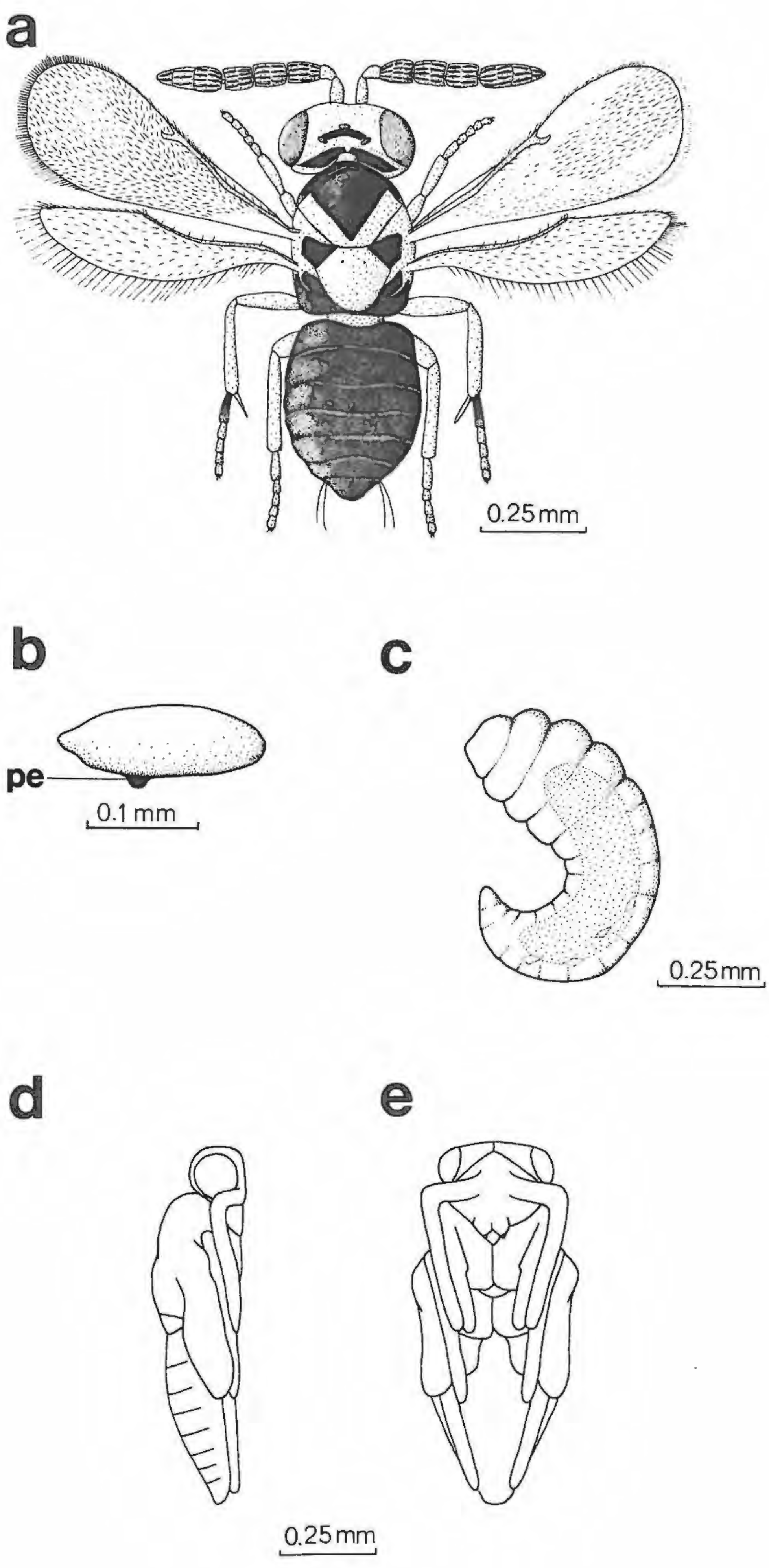


Fig. 11

EUXANTHELLUS SP.

a. Ventral view of externally parasitised psyllid nymph showing egg of Euxanthellus sp. on the prepupa of T. ?radiatus.

b. Developing larva of Euxanthellus sp. on prepupa of T. ?radiatus, ventral view of psyllid.

c. Ventral view of externally parasitised psyllid nymph showing the arrangement of the pupal remains of Euxanthellus sp.

d. Meconium of Euxanthellus sp.

pp - prepupa of T. ?radiatus, l - larva Euxanthellus sp., f - fronto-antennal plate, r - abdominal and thoracic sclerites, m_1 - meconium of T. ?radiatus, m_2 - meconium of Euxanthellus sp., ex - exit hole.

Fig. 12

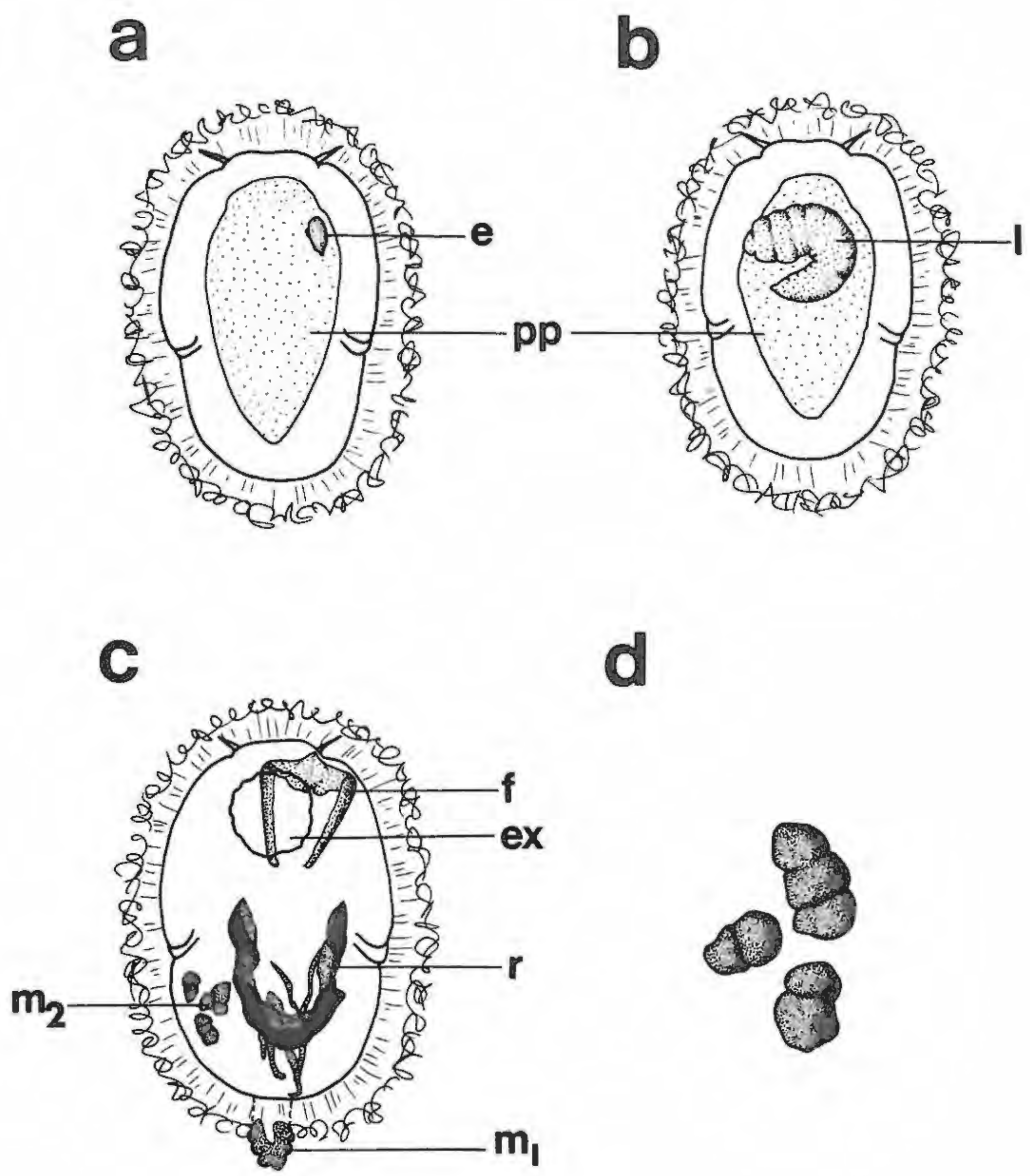
?PSYLLAEPHAGUS SP.

a. Ventral view of externally parasitised psyllid nymph showing pupal remains of ?Psyllaephagus sp.

b. Meconium of ?Psyllaephagus sp.

ex - exit hole, r - abdominal, thoracic and head sclerites,
m_1 - meconium of T. ?radiatus, m_2 - meconium of A. cassatus,
m_3 - meconium of ?Psyllaephagus sp.

11



12

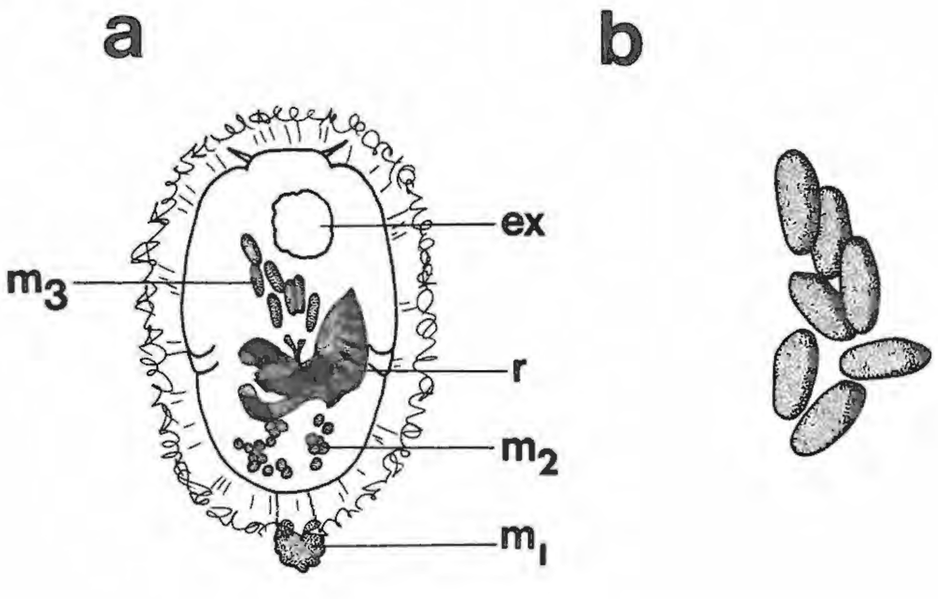


Fig. 13

?PSYLLAEPHAGUS SP.

a. Adult male
b. Adult female
c. Female pupa; dorsal view
d. Female pupa, lateral view
e. Female pupa, ventral view

13

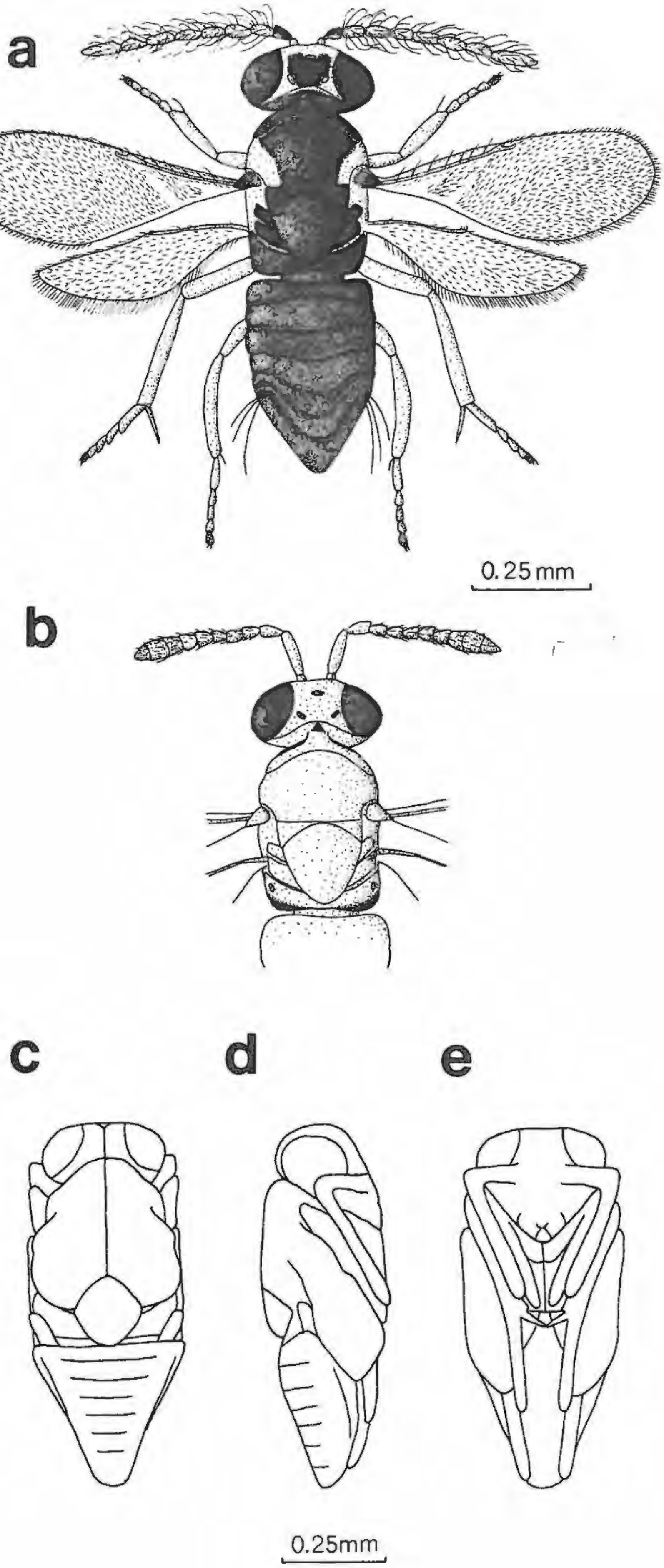


Fig. 14

PHYSCUS SP.

a. Adult male
b. Male pupa, lateral view
c. Male pupa, ventral view
d. Ventral view externally parasitised psyllid nymph showing *Physcus* larva with the remains of its host parasite.
e. Ventral view externally parasitised psyllid nymph showing arrangement of pupal remains of *Physcus* sp.
f. Meconium of *Physcus* sp.

sp - spine, pr - remains of host parasite, l - larva of *Physcus* sp., m_1 - meconium of *T.* ?*radiatus*, m_2 - meconium of *Physcus* sp., ex - exit hole, a - antennal sheath, r - abdominal and thoracic sclerites.

14

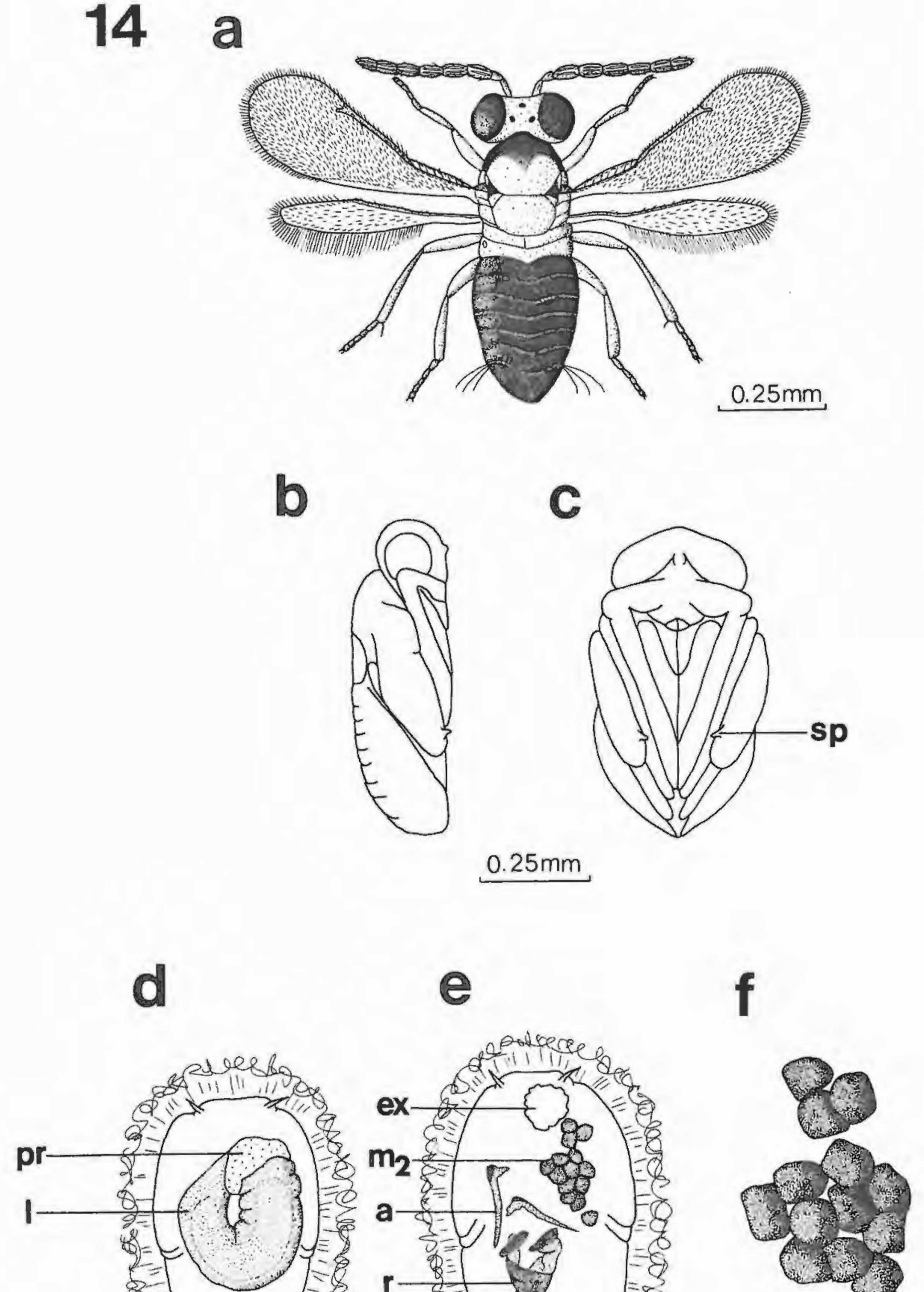


Fig. 15

CERAPHRON SP.

a. Adult

b. Prepupa

c. Pupa, lateral view

d. Ventral view externally parasitised psyllid nymph showing pupal remains of *Ceraphron* sp.

e. Meconium of *Ceraphron* sp.

p - papilla, ex - exit hole, m_1 - meconium of *T.* ?*radiatus*, m_2 - meconium of *Ceraphron* sp., r - thoracic, abdominal and head sclerites.

15

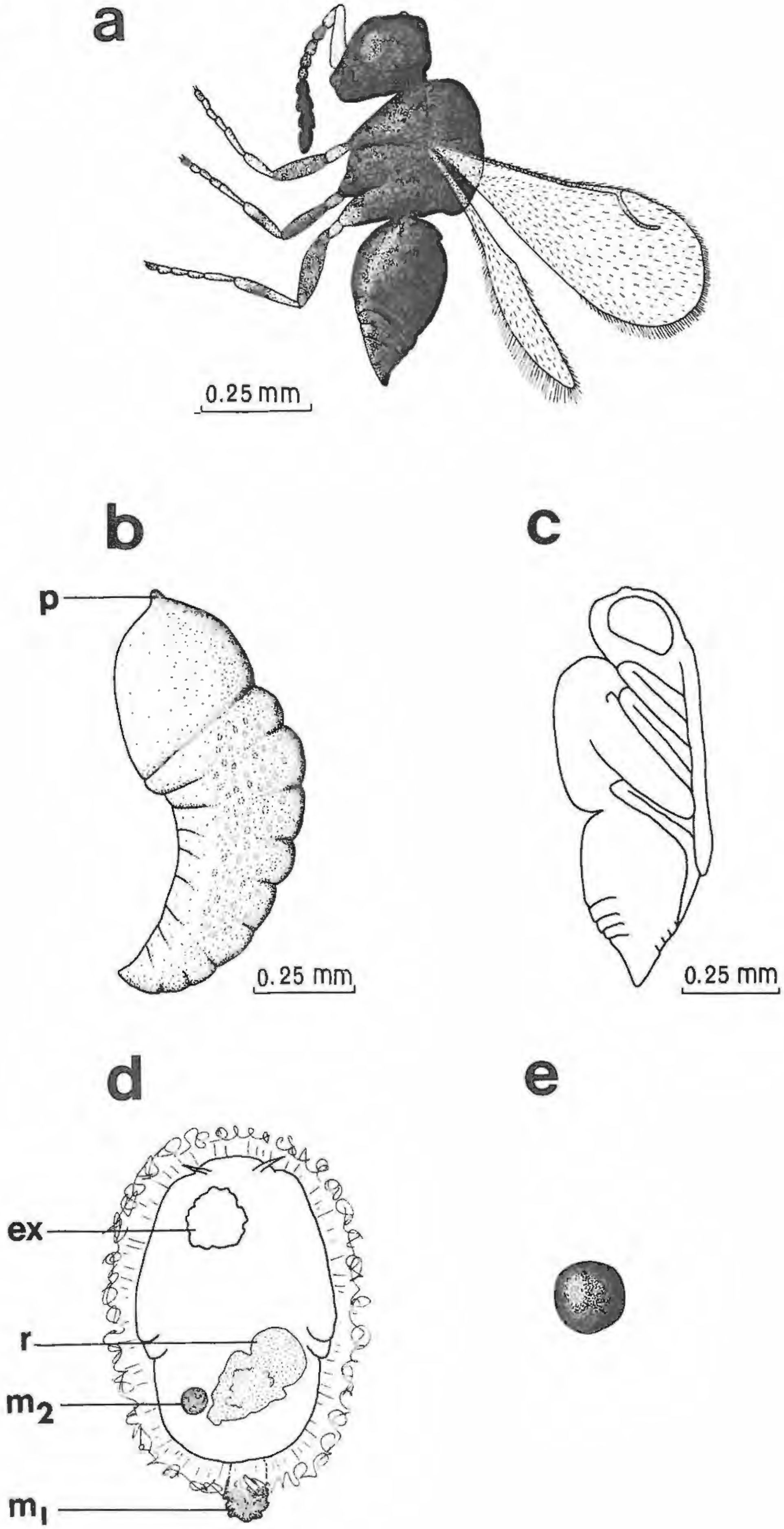


Fig. 16

?PACHYNEURON SP.

a. Adult female

b. Female pupa, ventral view

c. Female pupa, lateral view

d. Dorsal view psyllid 'mummy' showing pupal remains of ? *Pachyneuron* sp.

e. Meconium of ?*Pachyneuron* sp.

m_1 - meconium of *P. pulvinatus*, m_2 - meconium of *A. cassatus*, m_3 - meconium of ?*Pachyneuron* sp., r - abdominal and thoracic sclerites, op - ovipositional punctures, f - frontoantennal plate, o - oculoparietal plate, ex - exit hole.

16

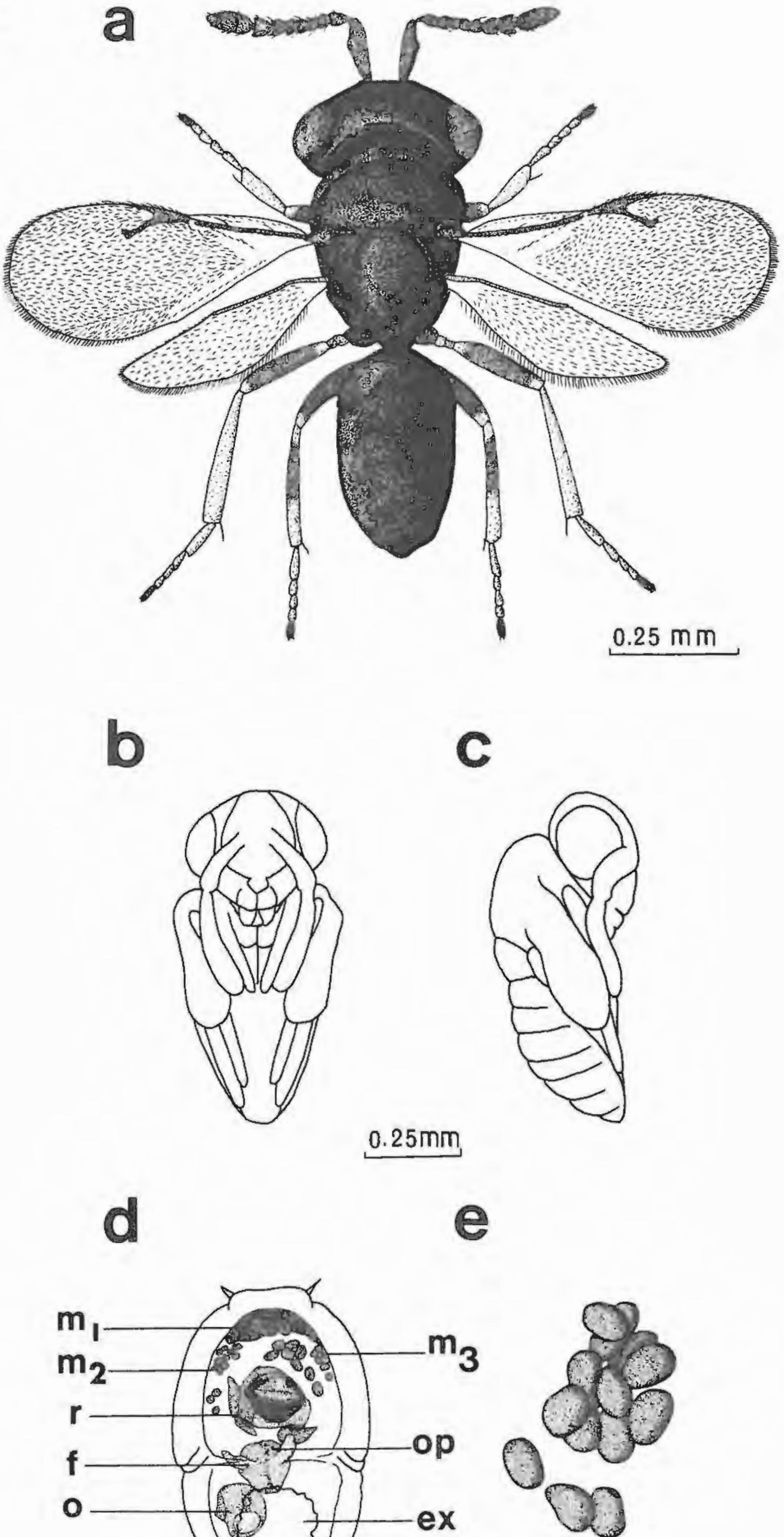


Fig. 17

a. Adult male *Coccophagus pulvinariae*

b. Hind leg of *Coccophagus* sp.

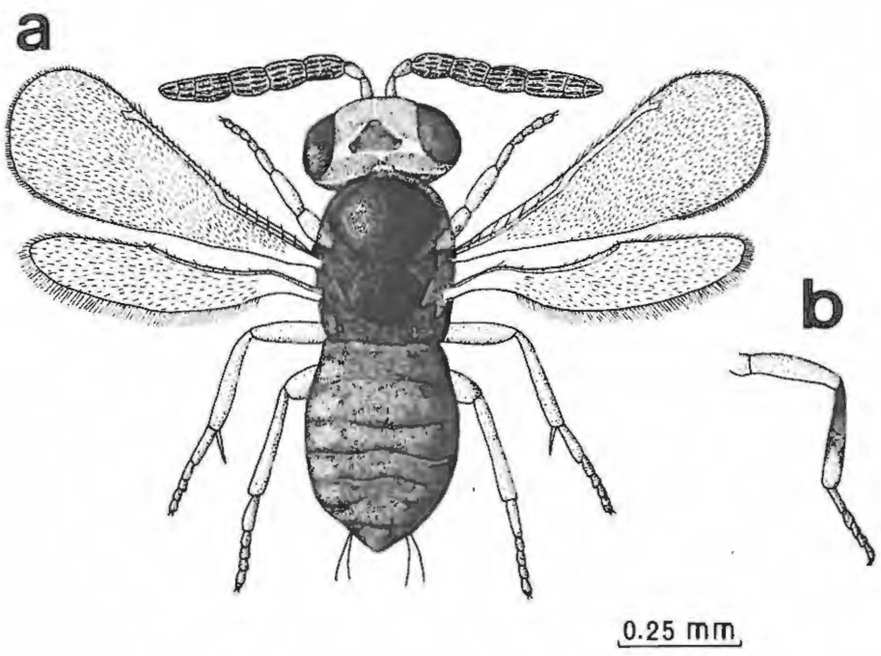
Fig. 18

CHEILONEURUS CYANONOTUS

a. Adult female

b. Male antenna

17



18

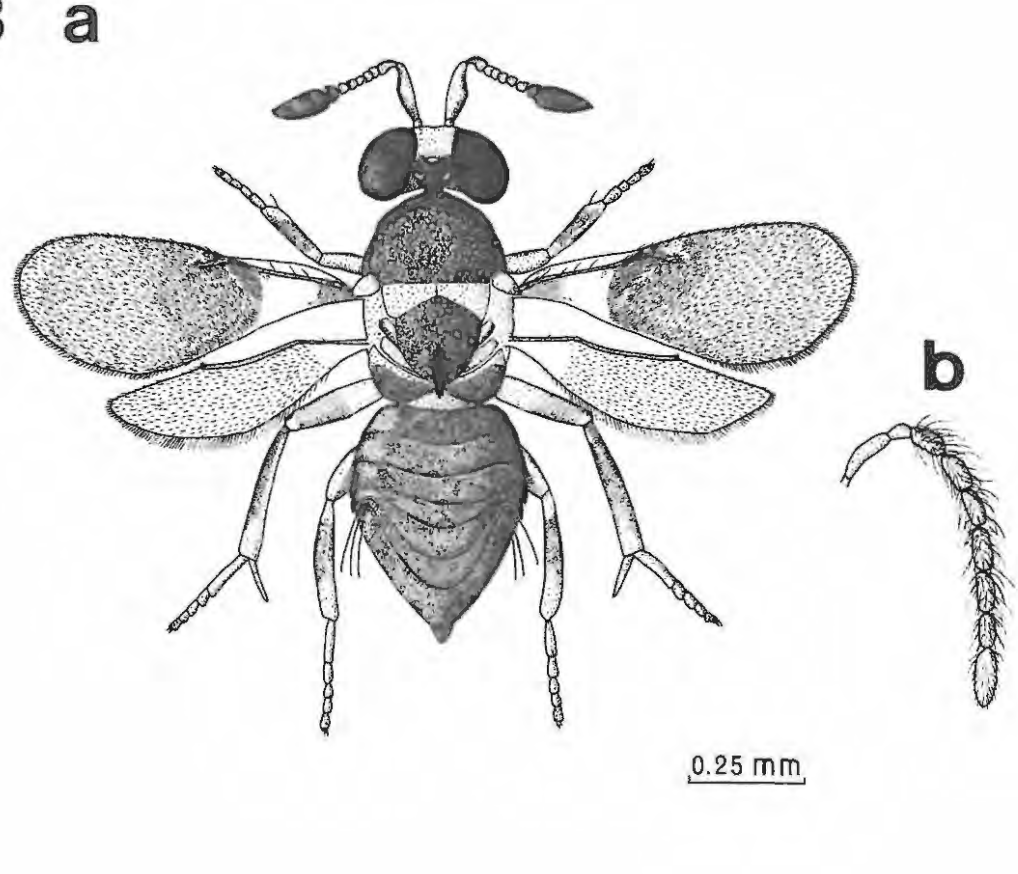


Fig. 19

T. ?*radiatus*, abdominal and thoracic sclerites

Fig. 20

T. ?*radiatus*, oculoparietal plate

Fig. 21

P. pulvinatus, abdominal and thoracic sclerites

Fig. 22

A. cassatus, scutellum

Fig. 23

A. cassatus, abdominal, thoracic and head sclerites

Fig. 24

Tetrastichus sp.1, abdominal and thoracic sclerites

Fig. 25

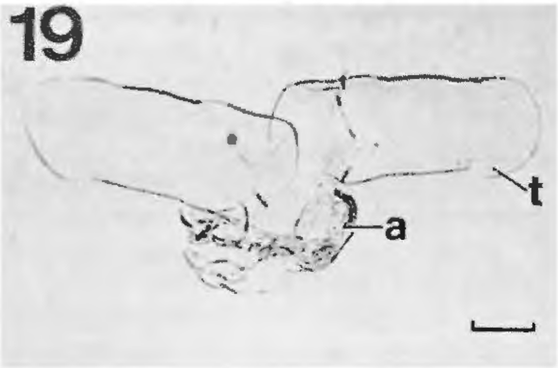
Tetrastichus sp.1, oculoparietal plate

Fig. 26

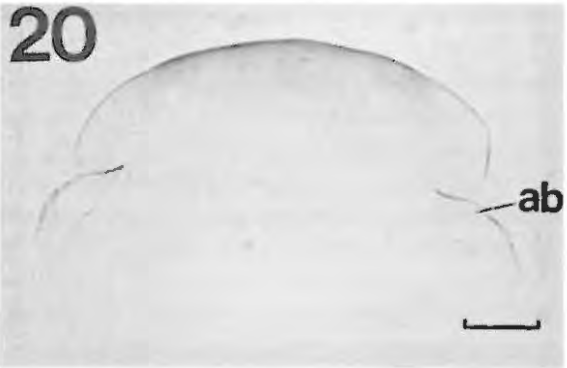
Tetrastichus sp.1, frontoantennal plate

a - abdominal sclerites, t - thoracic sclerites, h - head sclerites, ab - antennal base, l - leg sclerite.

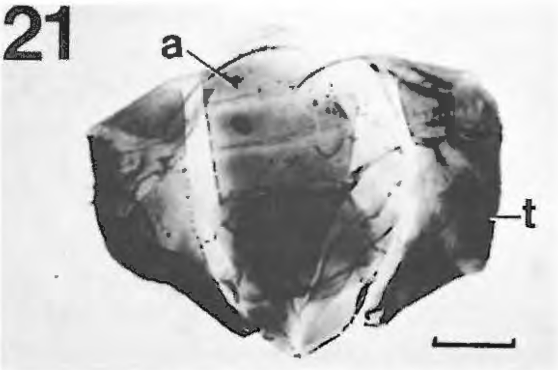
19



20



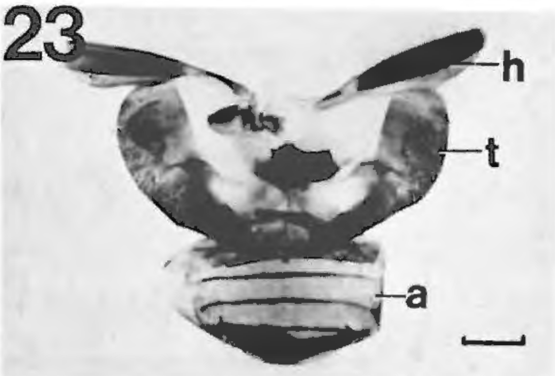
21



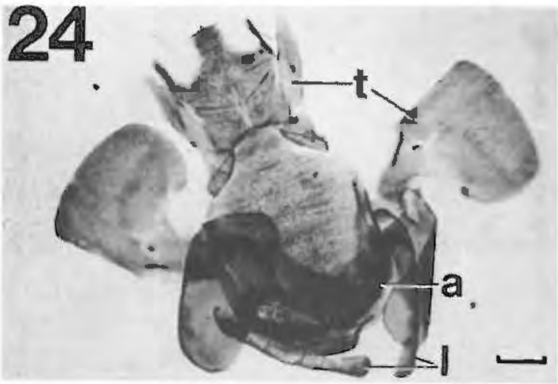
22

ALL SCALES: 0·1 mm

23



24



25

26

Fig. 27

Tetrastichus sp.1, mesothoracic leg sheath

Fig. 28

Tetrastichus sp.1, prothoracic leg sheath

Fig. 29

Aphidencyrtus cassatus, dry pupal skin

Fig. 30

Marietta exitiosa, abdominal, thoracic and head sclerites

Fig. 31

Marietta exitiosa, frontoantennal plate

Fig. 32

Marietta exitiosa, leg sheath

Fig. 33

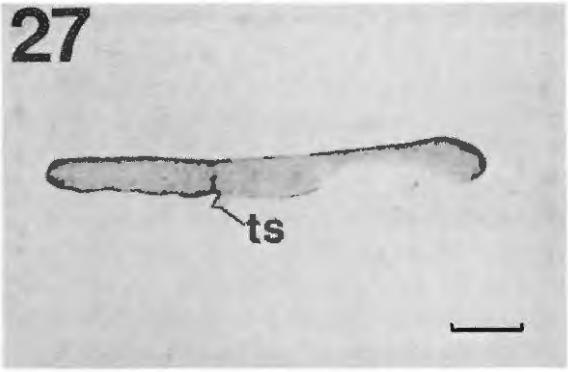
Euxanthellus sp., abdominal, thoracic and head sclerites

Fig. 34

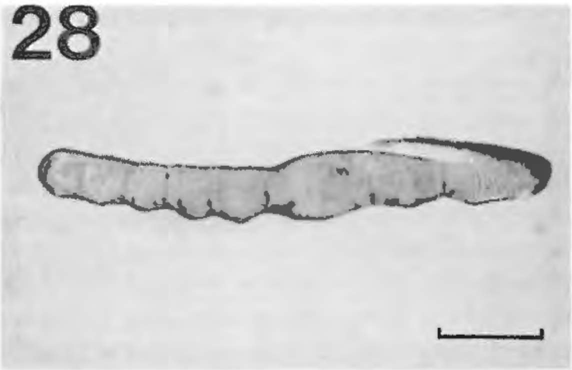
Euxanthellus sp., frontoantennal plate and antennal sheaths

a - abdominal sclerites, ab - antennal base, ap - apohysis,
h - head sclerites, s - scutellum, ts - tibial spur,
l - leg sheath, as - antennal sheath.

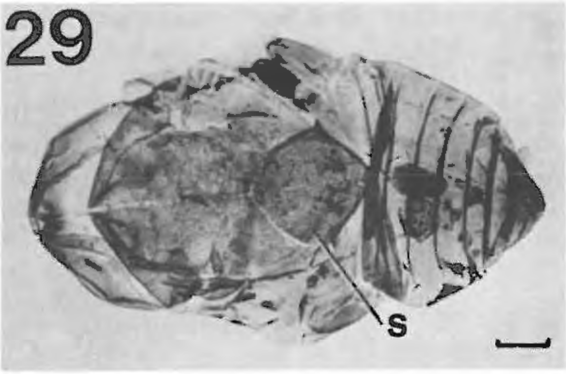
27



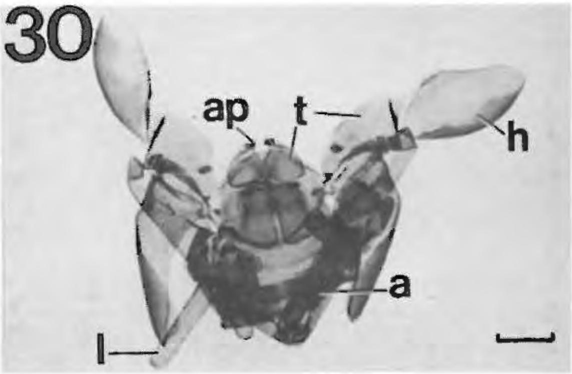
28



29

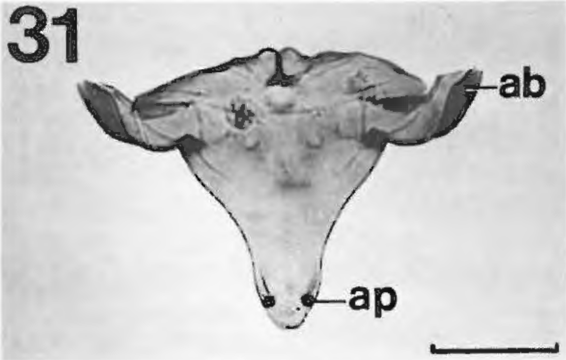


30

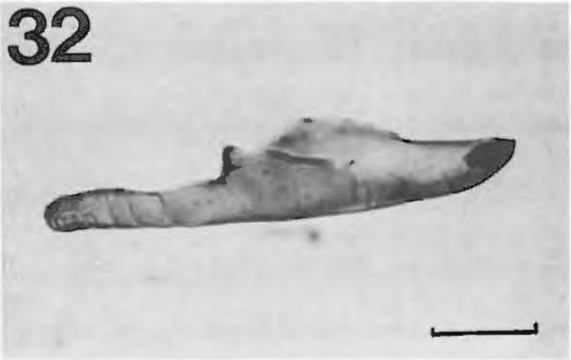


ALL SCALES: 0·1 mm

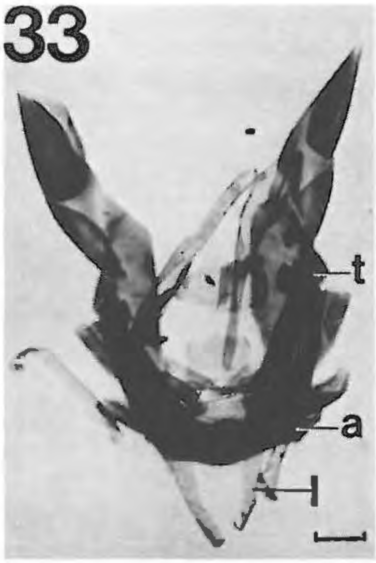
31



32



33



34

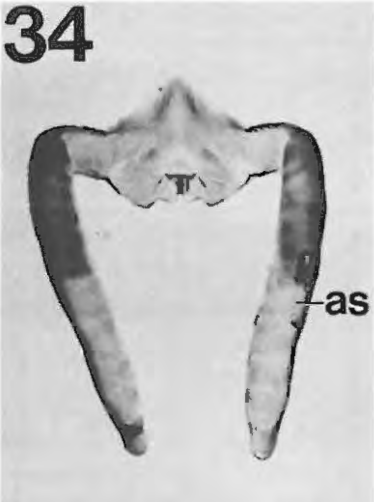


Fig. 35

?*Psyllaephagus* sp., abdominal, thoracic and head sclerites

Fig. 36

Physcus sp., abdominal, thoracic and head sclerites

Fig. 37

Physcus sp., antennal sheath

Fig. 38

Ceraphron sp., abdominal, thoracic and head sclerites

Fig. 39

?*Pachyneuron* sp., frontoantennal plate

Fig. 40

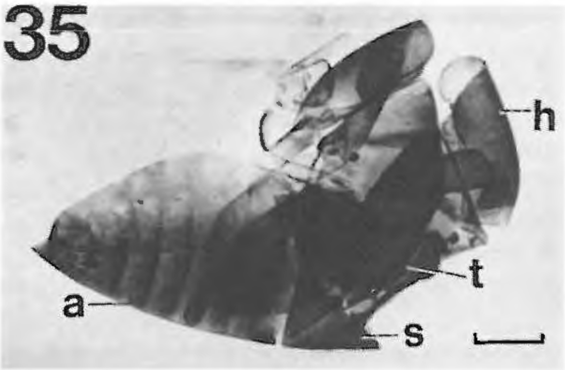
?*Pachyneuron* sp., oculoparietal plate

Fig. 41

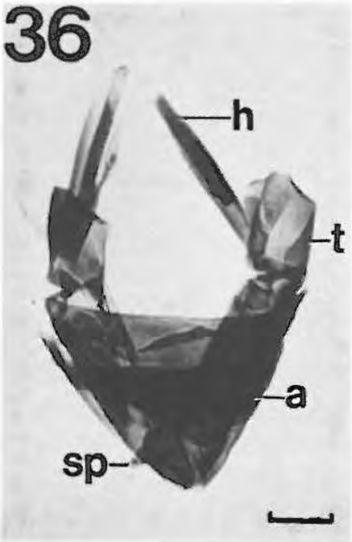
?*Pachyneuron* sp., abdominal and thoracic sclerites

s - scutellum, h - head sclerites, a - abdominal sclerites,
t - thoracic sclerites, sp - spine, ab - antennal bases.

35



36

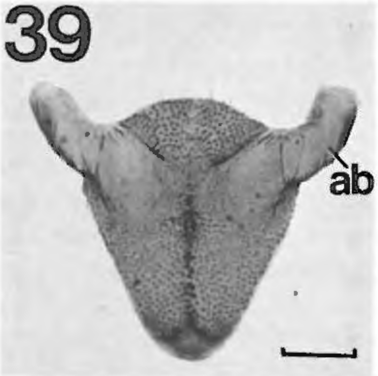


37

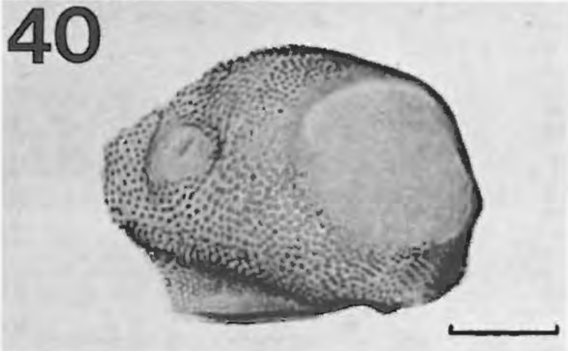
38

ALL SCALES: 0·1 mm

39



40



41

<u>Fig. 42</u>

a. Map of Southern Africa showing location of Salisbury.

b. Map of Salisbury area showing the position of sampling sites $S_1 - S_5$.

42

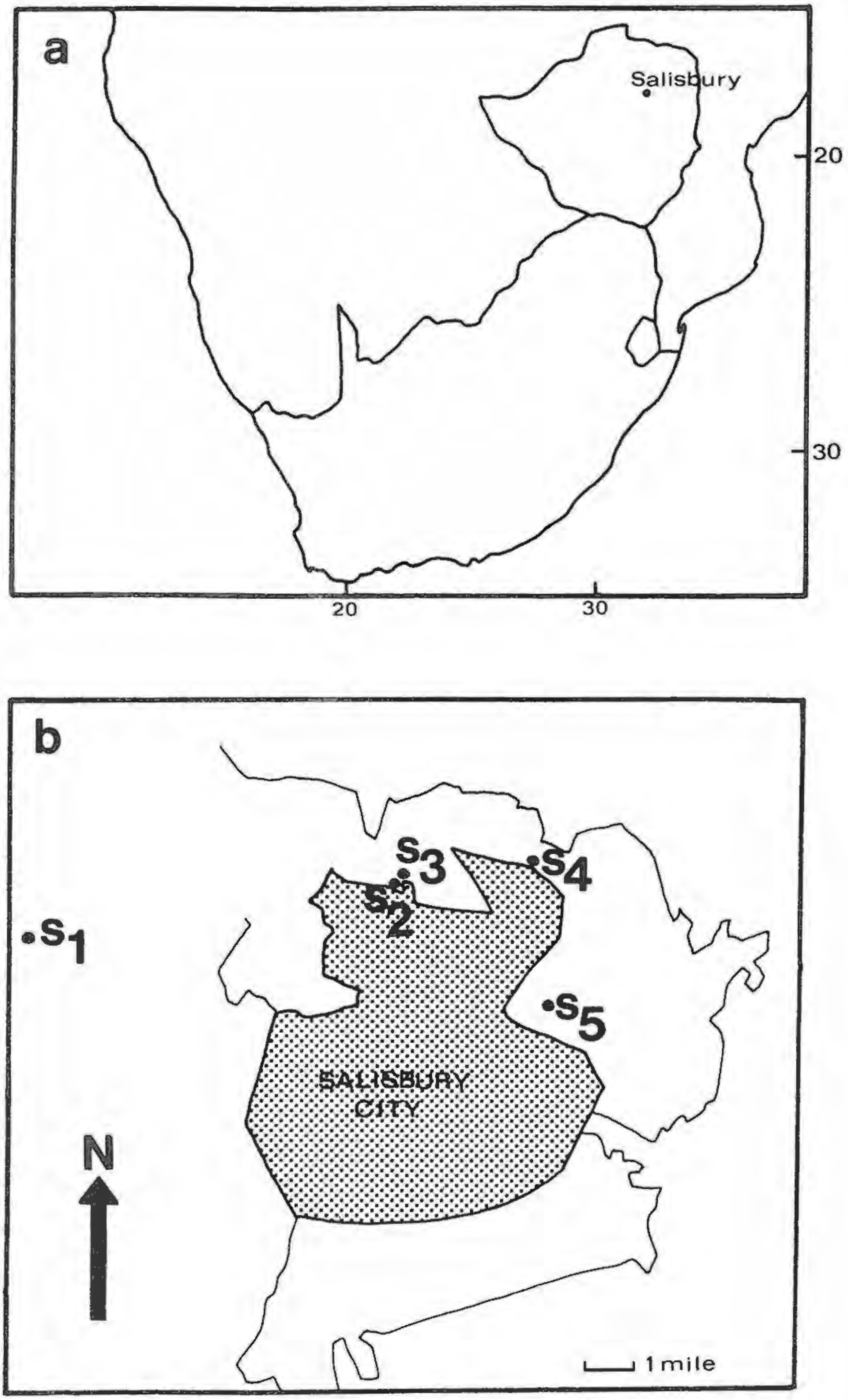


Fig. 43

Total weekly catches of adult *Trioza erytreae*, primary parasites (*T.* ?*radiatus* and *P. pulvinatus*) and the main hyperparasite, *A. cassatus*, recorded from sticky impact traps during the period 5th January 1968 to 7th February 1969.

43

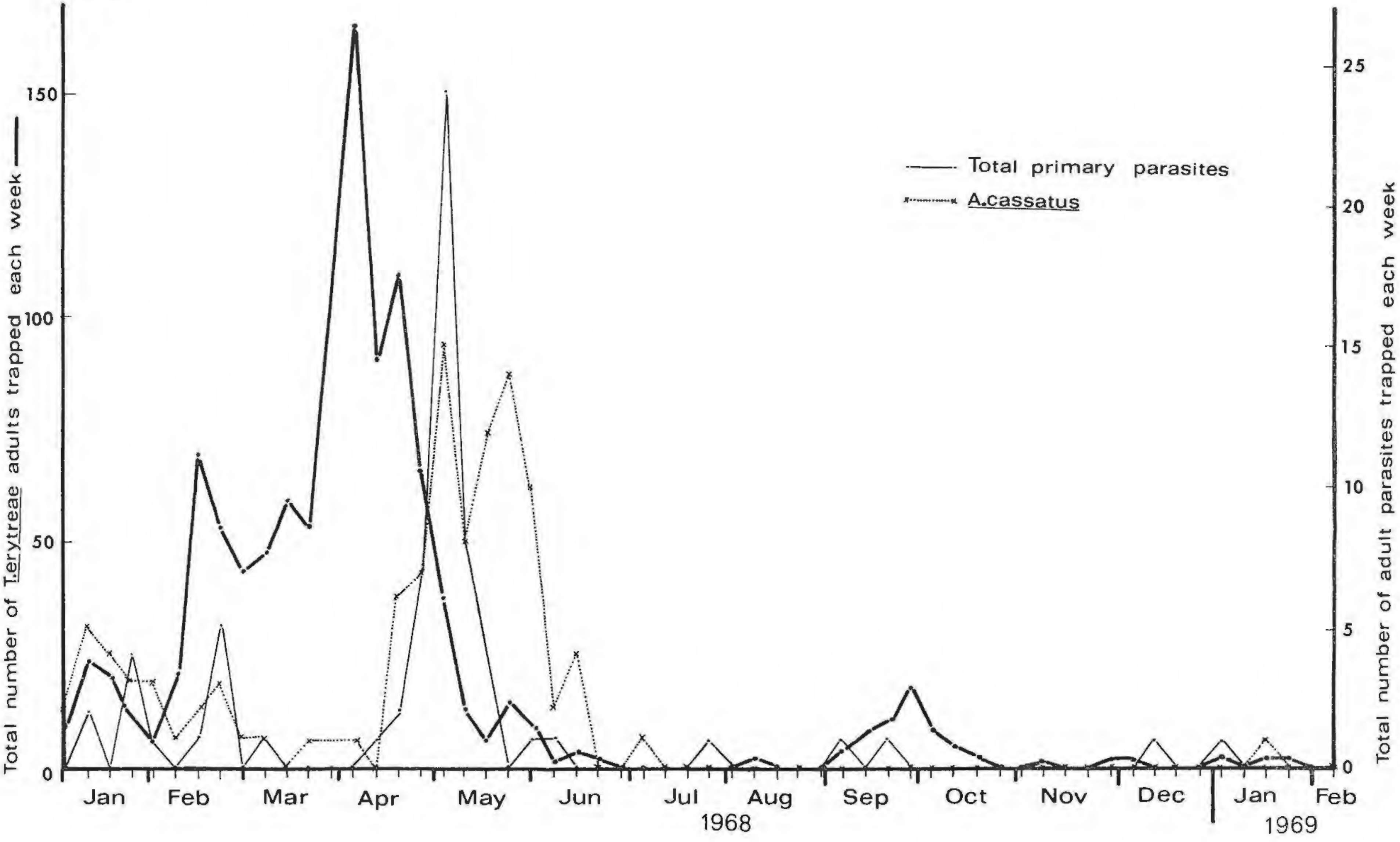
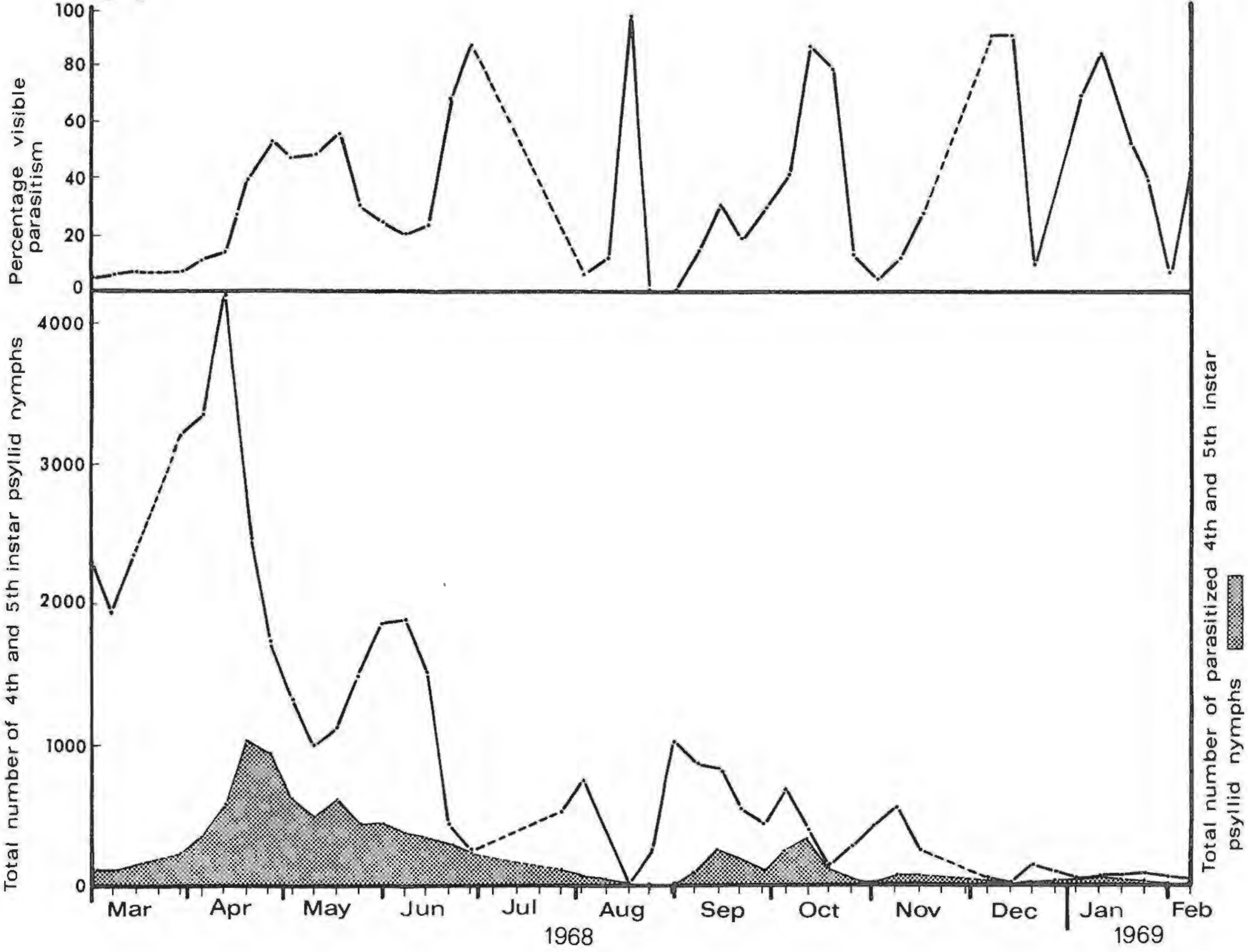

Total number of T.erytreae adults trapped each week
0
50
100
150
Total primary parasites
A.cassatus
Total number of adult parasites trapped each week
0
5
10
15
20
25
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
1968
1969

Fig. 44

Weekly totals of 4th and 5th instar nymphs of T. *erytreae* recorded from "in situ" counts made on tagged shoots between 1st March, 1968, and 7th February, 1969. The number of parasitised 4th and 5th instar psyllid nymphs and percentage parasitism of these stages during the same period are also plotted. Broken lines indicate missing records.

44


Percentage visible parasitism
100
80
60
40
20
0
Total number of 4th and 5th instar psyllid nymphs
4000
3000
2000
1000
0
Total number of parasitized 4th and 5th instar psyllid nymphs
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
1968
1969

45

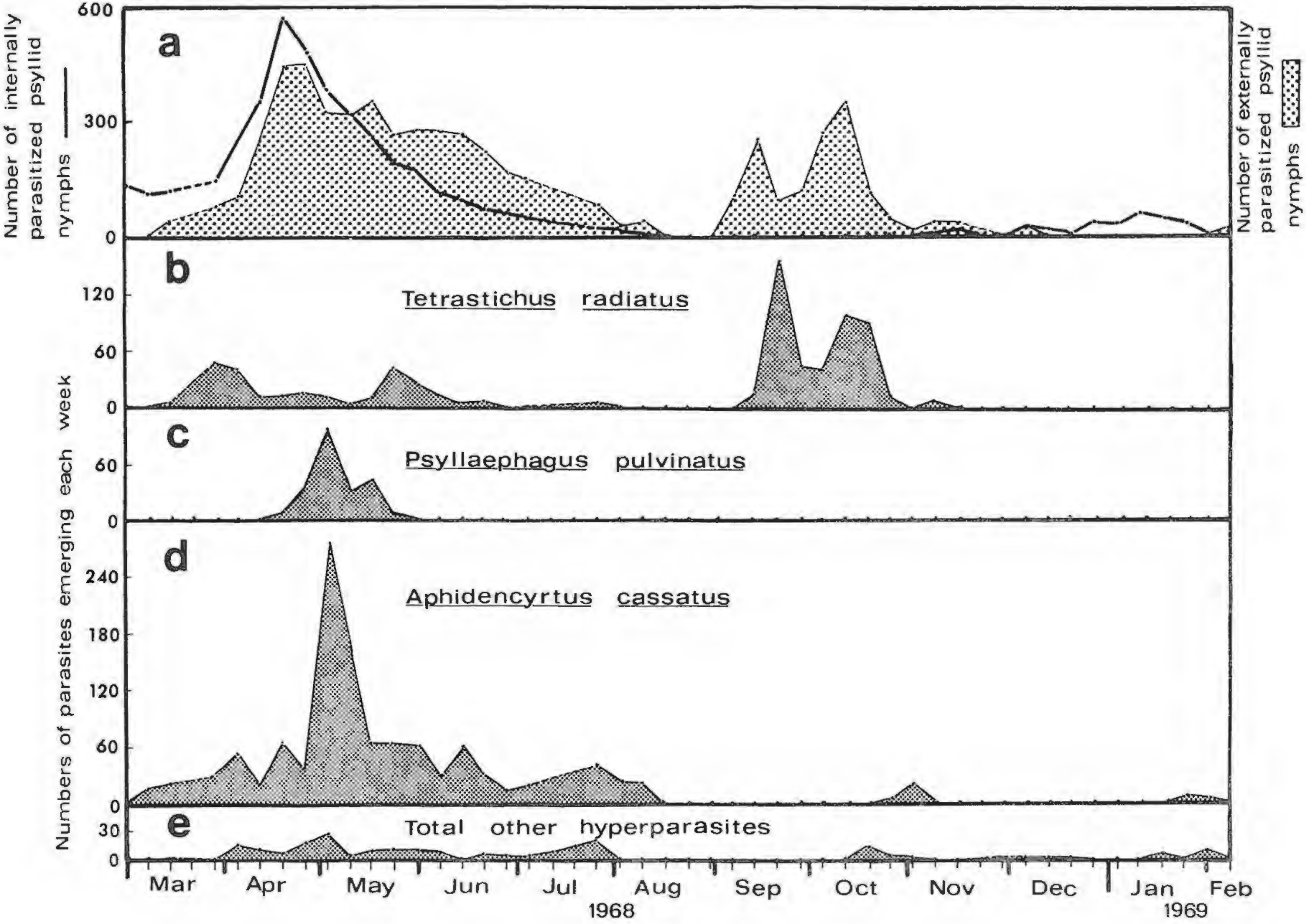
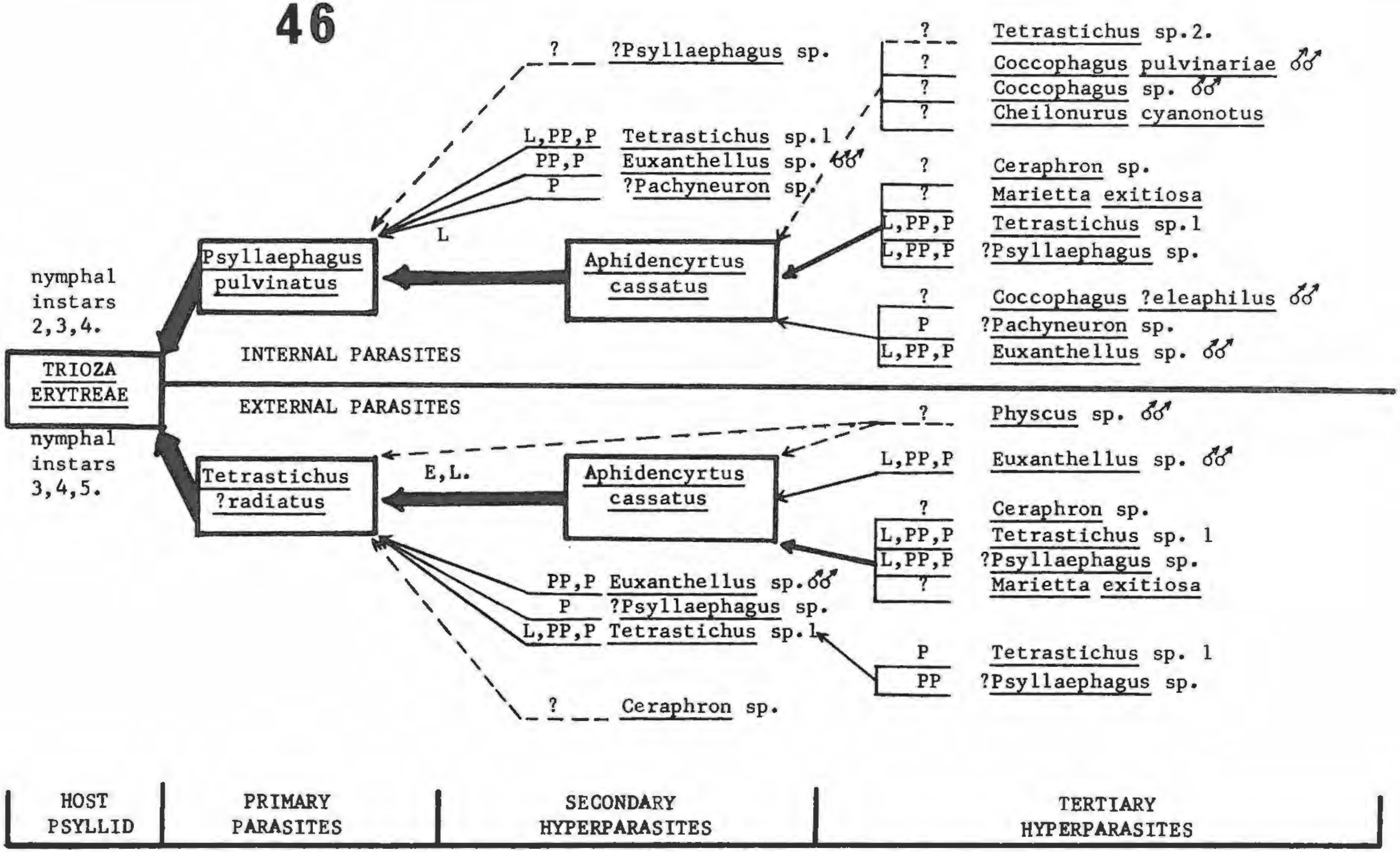

a
b
c
d
e
Number of internally parasitized psyllid nymphs
Number of externally parasitized psyllid nymphs
Numbers of parasites emerging each week
600
300
0
120
60
0
60
0
240
180
120
60
0
30
0
Tetrastichus radiatus
Psyllaephagus pulvinatus
Aphidencyrtus cassatus
Total other hyperparasites
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
1968
1969

Fig. 46

Diagram to illustrate the interrelationships between the primary parasites and hyperparasites in the *T. erytreae* parasite complex. Both males and females of each species form part of the complex except where otherwise indicated. The thickness of the arrows indicates the importance of the species in the complex.

E - egg, L - larva, PP - prepupa, P - pupa, ? - stage of host attacked not known.

46



E = Egg: L = Larva; PP = Prepupa: P = Pupa.