BIOLOGY OF SOME BRITISH PSOCOPTERA, WITH PARTICULAR REFERENCE TO SPECIES FREQUENTING FOLIAGE.

By

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ABSTRACT.

Aspects of the biology of foliage-freqenting Psocoptera were studied at Silwood Park, Ascot, Berkshire from Autumn 1965 to Spring 1968. These insects were considered especially in relation to the total arboreal psocid fauna and to their main habitat i.e. the foliage of different tree species.

Psocid samples from litter and from trees were taken concurrently and were counted and identified. Descriptions of the early stages and life histories of nine species are based on field and laboratory data. Several species were found only on some tree species and numbers of others showed large differences on different trees. Some of the factors that may influence the relative numbers of the same species of Psocoptera on different tree species were investigated. Counts of eggs on different tree species also revealed variations in psocid abundance.

Aerial dispersal of Psocoptera was assessed with the aid of suction traps. The potential food supply of psocids on foliage of a range of tree species was compared at different times of the year and also with that consumed by psocids. The fecundity of several psocid species fed on foods from different trees was compared. Laboratory experiments showed that selection of oviposition site was related to characteristics of different leaf surfaces. The biology of two groups of hymenopterous parasites of Psocoptera were examined, especially in relation to their fecundity and host specificity. A series of arthropods were identified as predators of psocids and their numbers on different species of trees were compared.

CONTENTS

INTRODUCTION.

Psocoptera are one of the more neglected orders of insects, and have attracted the attention of very few entomologists. Most species have no economic importance and all are small and inconspicuous. Nearly 90 species have been recorded from Britain (Broadhead, 1964), and these may be divided into three broad ecological groups:

I. Species associated with stored products, soil and ground litter, birds' nests and similar habitats.

2. Species found mainly on bark of many kinds of trees.

3. Species found mainly on arboreal foliage, rarely on bark.

Pearman (1928a,b,c) in a series of classic papers laid the foundations of biological knowledge of the British Psocoptera and since then Broadhead and Hobby (1944) have discussed the biology of a species of Liposcelis frequenting stored products and Broadhead and Thornton (1955), Broadhead (1958) and Broadhead and Wapshere (1966a,b) have given detailed accounts of the ecology of various species in the second of the above groups. No comprehensive accounts exist of the biology and ecology of species in the third category, i.e. the foliage-frequenting psocids. The present work is an attempt to provide such an account. Nine species are considered namely Trichopsocus dalii (Mclachlan), Ectopsocus briggsi Mclachlan, Stenopsocus immaculatus (Stephens), S.stigmaticus (Imhoff and Labram), Graphopsocus cruciatus (L.), Caecilius burmeisteri Brauer, C. flavidus (Stephens), C. fuscopterus (Latreille in Coquebert) and C. kolbei Tetens. The last seven belong to the Polypsocidae, and the other two to the Pseudocaeciliidae. The familiar classification of these insects is in doubt, but the above groupings, and all nomenclature in this thesis , follows that given in the most recent list of British species (Broadhead,I964) (see, however, Lee and Thornton, 1967 ; Thornton and Wong 1967 ;Smithers, (1967)). The biology of *Ectopsocus briggsi*, which is found in a variety of habitats, was discussed by Weber (I93I) and Sofner (I94I), but only fragmentary accounts exist of some aspects of the bionomics of the more characteristic foliage-frequenting psocids which belong to the Polypsocidae (Kolbe,I880; Ludwig, I908; Huie, I916; Stäger, I917; Pearman, I928a,b,c; Medem, I95I; Broadhead and Wapshere,I960)

It was hoped to describe the life histories of all arboreal foliage-freqenting psocids found in Britain, but one species (*Enderleinella obsoleta* (Stephens)) has not been found during the present study, and it has not been possible to obtain material from elsewhere. The other nine species were collected at Silwood Park, Berkshire, where most of the work described in the following pages was carried out. They all oviposit on foliage, and all stages live on and feed from leaf surfaces.

The aim of this work was to investigate the biology of this group of psocids, to relate it to the total psocid fauna on trees, and also to the foliage that they freqent. In a study limited to two to three seasons it seemed more valuable to investigate bionomics on the broadest possible basis, and to lay a foundation for future more detailed work, rather than to concentrate on one aspect in detail. Descriptions of the life histories and of early stages are followed by data on the numbers of psocids in leaf litterand on a number of tree species. Various factors influencing the numbers of foliage-freqenting psocids on different trees are considered in later sections of this thesis. Literature relevant to each section is quoted in context. Tables of detailed data are given in appendices, but figures are placed in context.

SECTION I. Rearing Methods for Psocoptera

Introduction.

Comparatively few authors have attempted to rear species of foliage-frequenting psocids, but there are several accounts of rearing stored-products psocids (see Broadhead and Hobby, 1944; Broadhead, 1961; Allen, 1960; Finlayson, 1949), and bark-frequenting psocids (Broadhead, 1947; Eertmoed, 1966; Jentsch, 1939; Mockford, 1957; Sofner, 1941; Sommerman, 1943 a, b, c, 1944). All methods used are essentially similar, and provide for the maintenance of a high humidity and easy renewal of food supply. Thornton and Broadhead (1954) found that laboratory attempts to rear Elipsocus resulted in a very high mortality. There are no complete accounts of rearing arboreal Polypsocidae, although Medem (1951) gives some fragmentary data. Pearman (in lit., 1967) did not succeed in rearing foliage-frequenting psocids, but he found that the other types were easier to breed. Several foliage species were maintained by Schneider (1955) in the laboratory, but he omits any account of rearing methods.

During the present work, 31 species of psocids were reared in the laboratory through at least one complete generation. Mortality and duration of development of some were compared under conditions of standard temperature and relative humidity. The species represented a wide range of ecological types, from those in stored products to the nine species of foliage frequenters here discussed.

Methods.

Several kinds of rearing containers were used with varying degrees of success. The most useful methods are of general application but others were designed for special purposes, which are mentioned in context. Sommerman's (1942) prime considerations in designing rearing cages for psocids, i.e. the maintenance of a high humidity and the ease of renewal of food supply, have been followed.

1. Small tube rearing cage (Fig. 1A). A 75 x 25 mm clear glass specimen tube containing food and psocids was closed by a cork with a large central hole covered with fine muslin on the end inside the tube. The tube was inverted and the protruding part of the cork was tapered to fit into the neck of a 50 x 25 mm tube containing water or a salt solution. Supersaturated solutions of different salts were used to provide the required relative humidities in the cages, and the two tubes were sealed together with 'Vaseline'. This cage was suitable for keeping and rearing psocids individually or in small groups. Large numbers of cage units could be made and stored cheaply, and could be easily transported in 'honey-comb' on trays. All parts of these cages are fully interchangeable, and their contents can be inspected easily and rapidly. Food, on a small length of twig or single leaf, was renewed when necessary, usually twice weekly. This unit is similar in size and use to the Sommerman No. 1 Cage. Similar units were used by Broadhead and Thornton (1955) for keeping adult psocids at constant humidities.

2. Polystyrene dishes. Circular clear polystyrene dishes, of 10 cm diameter, with close-fitting clip-on lids were used for clonal cultures. This substance is permeable to water vapour, and a high humidity can be maintained in the dishes by keeping a transpiring leaf in them (for foliage psocids), or by standing the dishes in shallow trays of water. Some nymphs are drowned in water condensing on the sides of the dishes unless the excess moisture is wiped off periodically. These dishes were very useful for stock rearing, since they are large

enough to hold an adequate food supply for many psocids, and require only infrequent inspection.

Various other polystyrene boxes were used. All are satisfactory, but that described is of a convenient size, cheap, and easy to clean and examine, as there are no vertical corners.

3. Potted trees. Small oak, hawthorn, and holly trees were used to maintain large stock cultures of various arboreal psocids for a whole season. They demanded little or no attention. Trees up to 80 cm high were selected in the field and transplanted into 40 cm diameter pots. Each was surrounded by a cylinder of clear cellulose acetate and covered by muslin.(Fig. 1B). Cellulose acetate has been reported to be toxic to foliage (Kiechefer and Medler, 1960) but only a small proportion of the foliage of any one tree was in contact with the cylinder, and no toxic effects were noticeable. These small trees were particularly suitable for keeping the foliage psocids. A thousand or more could be kept on a single small tree, and the psocids were easily removed with a pooter when required.

4. Leaf surface cages (Fig. 1C). At times it was necessary to confine psocids on leaves of different kinds, and to prevent them from straying onto any other surface such as the sides of a cage. Whole fresh leaves were clipped flat onto sheets of 2.5 cm thick expanded polystyrene by rings of cellulose acetate sheeting. The rings were coated with 'Fluon' on the inner surface, and standard areas of leaf were provided. In many experiments leaves remained fresh for several weeks when the polystyrene was stood in a tray of water: this also maintained a high humidity in the cages. Complete generations of psocids were reared in these cells without any further attention. Very few nymphs

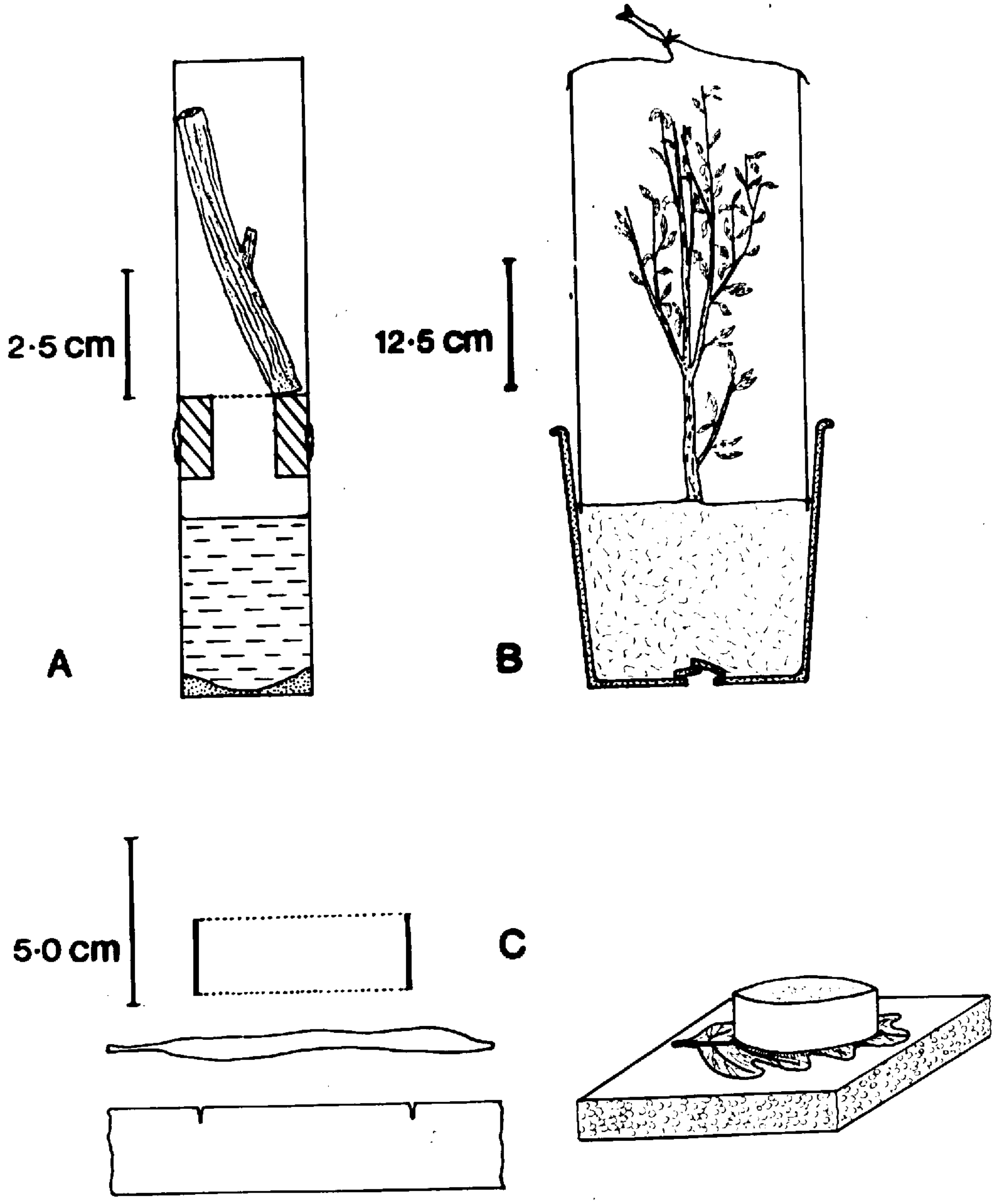


Fig. I.

Rearing containers for Psocoptera.

A. Small tube cage B. Potted tree C. Leaf Surface cage.

esoapod, and 'Fluon' was an effective barrier to adults if the wings were clipped.

5. Agar plates. Single psocids are easily maintained in clear polystyrene petri dishes containing a plate of malt agar. Fungi, from undigested spores in the psocids' faeces (Section 10), soon appear on the agar. Alternatively, leaves can be imprinted onto the surface of the plate. Particular species of fungi can be subcultured onto fresh plates and the different food constituents isolated and their effects compared. Small clonal cultures of E. briggsi were reared for three generations on a single plate.

The species of psocids which were successfully reared in each of the above cages are shown in Table 1. The first two rearing methods are of general application and can be used for rearing almost any British psocids. Potted trees are useful in rearing large numbers of the foliage species, and agar plates may prove to have wide application.

The effect of temperature and humidity on development.

Psocids were reared individually in the small tube cages at different constant temperatures and relative humidities. Humidity was controlled by using super-saturated salt solutions (Solomon, 1951) in the lower tubes. Several cages were calibrated with cobalt thiocyanate paper (Solomon, 1945) and in all cases the relative humidities in the cages stabilised close to the theoretical value of the salt solution provided, and remained almost constant throughout the experimental period.

Four constant-temperature rooms at a photoperiod of 16 light hours and at 15°C, 20°C, 25°C and 30°C were used in the rearing experiments.

1. Duration of the egg stage at different temperatures. Females of the summer generations of the nine species of foliage-

frequenting psocids were confined singly at the above temperatures, and the dates of oviposition and eclosion were recorded.

The rate of development of all the species increased markedly from 15°C to 25°C (Table 2), but most eggs failed to hatch at 30°C. Similar results were obtained for *Ectopsocus briggsi* and *E. meridionalis* Rib. by Sofner (1941) and *Cerobasis guestfalica* by Jentsch (1939).

b. Egg development at different relative humidities. Psocid eggs laid on bark and leaf surfaces are subject to a wide and varying humidity range. The eggs of most species of foliage-frequenting psocids are covered by a silken web which may confer some protection against desiccation.

Batches of freshly laid (0-1 day old) *C. flavidus* eggs were kept at eight relative humidities. The web was removed from ten batches at each humidity and the duration and mortality of the webbed and unwebbed batches were compared (Table 3). Eclosion was almost complete at all humidities over 50 per cent, but there was some mortality at lower humidities. Very few eggs hatched at very low humidities, but there was no striking difference between the two sets of batches. Duration of development did not change at different humidities. Smaller numbers of batches of other foliage-frequenting psocids gave similar results. (Table 4).

Eggs of several bark-frequenting psocids (*Elipsocus*, *Cerobasis*, *Amphigerontia*) were also kept at the eight relative humidities. Most of them hatched at humidities as low as about 20 per cent, but the pronymphs sometimes failed to emerge completely at these low humidities.

It is probable that the 'cement' covering of eggs of *Elipsocus* and *Amphigerontia* effectively reduces the rate of water loss from the eggs, and the sculptured chorion of *Cerobasis* may have a similar effect. The thin-shelled smooth eggs of foliage psocids are less resistant to desiccation but are usually laid in a comparatively wet habitat, namely on a leaf surface. They are also laid in batches, which may provide some protection from desiccation. In the Lepidoptera, Bartell (1967) showed that there was a strong relationship between oviposition sites and resistance to desiccation of eggs. Eggs of species which laid in wetter habitats often had thinner, less elaborated, chorions than those habitually laid in dry situations. A similar scheme was proposed by Southwood (1956 a) for the eggs of terrestrial Heteroptera. Fig. 2 shows the main oviposition sites of some British families of Psocoptera, and notes the appearance of the chorions (partly after Pearman, 1928). Eggs of families laying on bark have a sculptured chorion or are covered with faecal material, whereas most thin-shelled eggs are either laid on foliage or become covered with scattered particles. There is thus some correlation between the type of egg and oviposition site. Most eggs of arboreal psocids are laid in sites where the humidity is high and death due to desiccation is rare. In Britain few eggs die from unfavourable humidities and temperatures. Other mortality factors of the eggs are discussed in Section 8.

(c) Duration of nymphal stages at different temperatures. Single eggs of the nine species were kept in the tube cages at 100 per cent relative humidity at 15°C, 20°C or 25°C. The cages were inspected daily after the eggs had hatched and the presence of an exuvia was taken as evidence of a moult. Exuviae are only rarely eaten when adequate food is available, and food from different kinds of foliage was renewed twice a week. Developmental duration of nymphs of each species is summarised in Table 5. These figures are based on at least 20 complete rearings

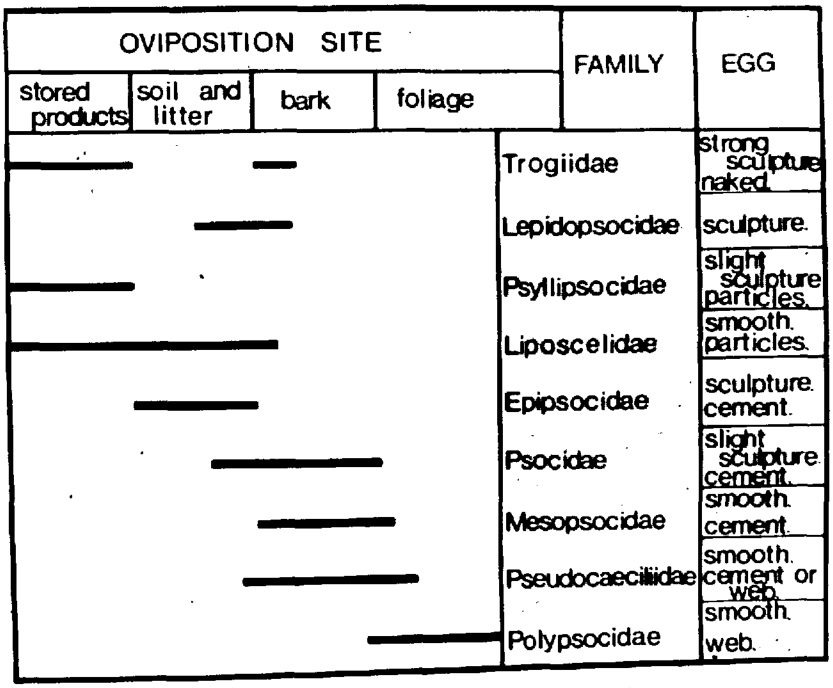


Fig. 2.

The relationship between oviposition site and egg form in some families of British Psocoptera.

of each species at each temperature, and show that development is accelerated at higher temperatures. The later nymphal stages of all species were of longer duration than the younger ones, but all stages developed faster at higher temperatures up to 25°C. Mortality was very high above 30°C, while below 10°C the nymphs were comatose and fed little.

In his study of the development of Cerobasis guestfalica, Jentsch (1939) found that the optimum temperature for nymphal development was 25°C, and that development was retarded at temperatures above or below this. Jentsch stated that the nymphs of S. stigmaticus showed a similar development, which was curtailed at 30°C. The optimum temperature for nymphal development of two species of Ectopsocus is also 25°C (Sofner, 1941).

(d) The development of nymphs at different relative humidities. The nymphs hatching from eggs at different relative humidities were maintained at those humidities at 20°C. Several species of bark-frequenting psocids were also used for comparison with the nine foliage-frequenting species. There were no large differences in duration of nymphal instars at different relative humidities, but there was a large difference in survival (Table 6), and this reflects the resistance to desiccation of these nymphs. Table 7 shows mortalities that occurred in three days after transference of last instar nymphs from 100 per cent to lower relative humidities. Mortality was high below 50 per cent humidity in all the species, and in many of them there was considerable mortality even at 70 per cent relative humidity. The nymphs of foliage psocids were very susceptible to desiccation, and those of some bark frequenters less so. This difference may be related to the primary habitat differences between these two categories.

SECTION 2. Early stages and life histories of British foliage-frequenting Psocoptera.

Introduction.

This section contains descriptions of the early stages and life histories of nine species of Psocoptera which frequent arboreal foliage in Britain. The early stages were obtained by breeding from parent stock caught in Berkshire. Their identification arose from the nee to interpret field samples of these Psocoptera, and it was eventually possible to identify living or freshly killed nymphs of these psocids to species and instar. No characters were found which enabled specific identification of all preserved material. The taxonomy of the early stages of Psocoptera has been largely neglected in the past, but there are short accounts of many of the British species (see Broadhead, 1947, 1961; Broadhead and Datta, 1960; Broadhead and Hobby, 1944; Broadhead and Wapshere, 1960; Jentsch, 1939; Kolbe, 1880; Medem, 1951; New, 1968; Pearman, 1928, 1932, 1955; Sofner, 1941; Thornton and Broadhead, 1954) and of other species (Eertmoed, 1966; Mockford, 1957; Sommerman, 1943 a, b, c, 1944). The species considered below are *E. briggsi*, *T. dalii*, *G. cruciatus*, *S. stigmaticus*, *S. immaculatus*, *C. flavidus*, *C. kolbei*, *C. fuscopterus*, and *C. burmeisteri*. Of these nine species, *C. kolbei* is found on bark and foliage, and at Silwood Park some overwintering eggs of *S. stigmaticus* were found on bark. The other species examined were confined to foliage in the arboreal phase.

Eggs.

The eggs of all species are ovoid and, except in *T. dalii*, are laid in small batches overlain with a web of labial silk. Those of *T. dalii* are often partially coated with black faecal material and suspended above the leaves on silken lines (Pearman, 1928). They are laid singly, but several eggs may be found on one leaf.

Twenty freshly laid eggs of each species, from at least three females, were measured using a micrometer eyepiece. The dimensions of these are summarised in Table 8 . The eggs of the two species of Stenopsocus are larger than those of the other genera, but those of S. stigmaticus, are consistently smaller than those of S. immaculatus, and taper more. The eggs of E. briggsi are the smallest examined, but those of G. cruciatus and the four species of Caecilius are all similar in size. The chorions of hatched eggs of all species were stripped of the fine overlying pellicle, and pieces mounted in water and examined under high power. The chorions of all the eggs are smooth, with faint traces of an irregular hexagonal sculpturing. This sculpturing is sometimes more pronounced in C. fuscopterus and the chorion of this species is more granular (Pearman, 1928), but no consistent differences were found in chorionic characters in different species.

The freshly laid eggs of all the species are pale, but some darken considerably within a few days, and the colour then aids further identification (Table 9). More advanced eggs with developing pronymphs show traces of the nymphal oviruptor (Pearman, 1928) and this is usually retained with the pronymphal cuticle protruding from hatched eggs. The form of the oviruptor differs considerably between different genera, but to a much smaller extent between species within a genus (Fig. 3).

The oviruptor of T. dalii resembles that of many bark-frequenting psocids. It is a simple knife-like blade, curving slightly towards the posterior end, and bears no teeth. The oviruptors of the other eight species with web overlying the eggs have numerous teeth. These are least developed in E. briggsi, which has a single row of 18 - 30 shallow teeth along a median keel. The arms (brachia) are smooth. *Stenopsocus* and *Graphopsocus* have better developed teeth on their oviruptors, but the brachia are smooth. *Graphopsocus* has a dark grey oviruptor with a single row of deep comblike teeth along the whole length. The number of teeth on 20 oviruptors of this species ranged from 30 to 37. In *Stenopsocus* a smaller number (12 -17) of similar teeth are concentrated at the anterior end of the oviruptor, in front of the brachia. The posterior part is produced into a long spine projecting along the ventral side of the pronymph.

In oviruptors of *Caecilius* the brachia also bear teeth, and all teeth are weaker and more irregular than in the other genera. There are often a few secondary teeth forming partial secondary rows along the blade of the oviruptor. All species of *Caecilius* examined have pale oviruptors which are not clearly visible through the chorion of unhatched eggs. No constant differences in tooth number or development were found in the four species, but Sommerman (1943 b) figured the oviruptor of *C. manteri* Som. without teeth. The oviruptor provides a ready generic identification of hatched and well developed eggs of this group of psocids, but is of very limited use in specific determination. The following artificial key enables partial identification of eggs of the nine species. Freshly-laid eggs of *Graphopsocus* and *Caecilius* species are at present indistinguishable, but subsequent development allows specific separation of all but a small proportion of *Caecilius* eggs.

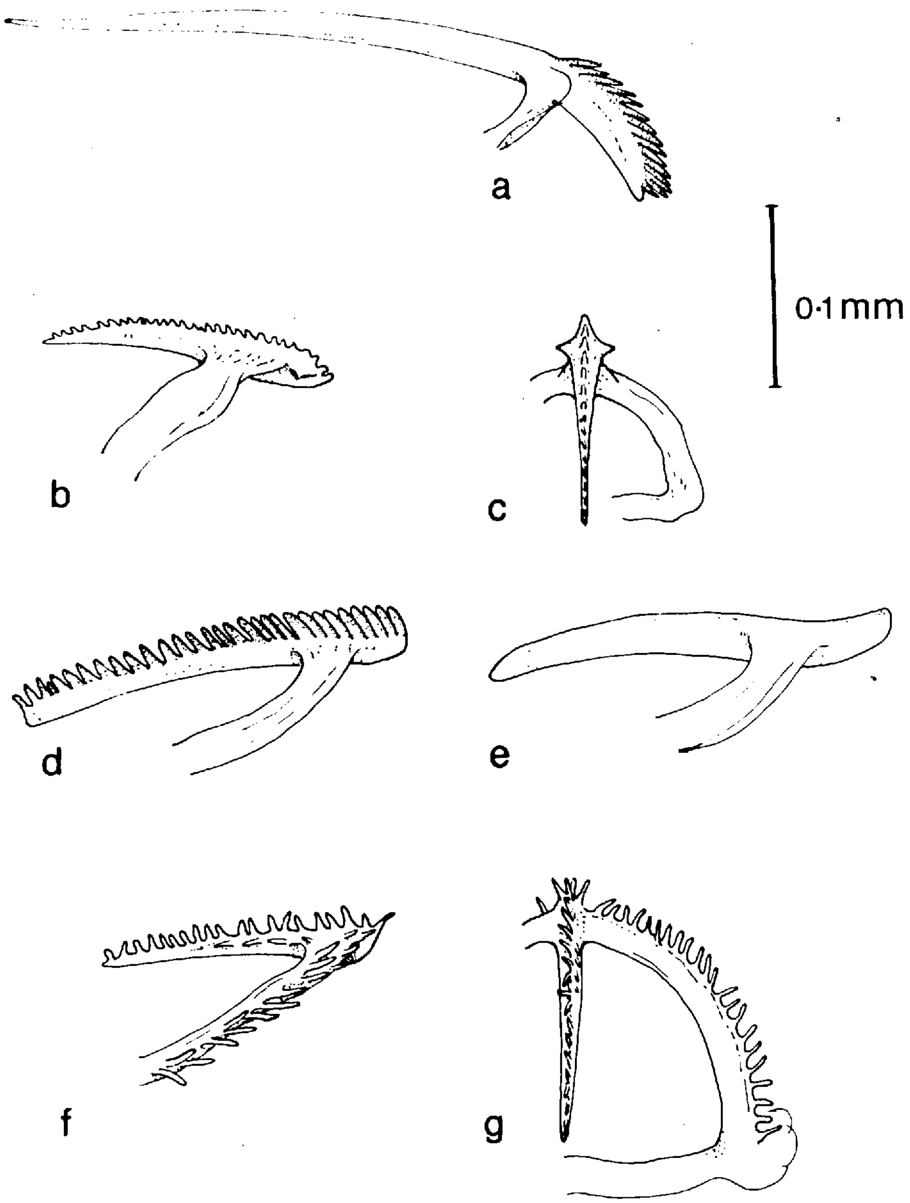


Fig. 3.
Oviruptors of British foliage-frequenting Psocoptera.
a. Stenopsocus, b.c. E. briggsi, d. G. cruciatus, e. T. dalii, f.g. C. flavidus.
a.b.d.e.f. lateral aspect (anterior towards right of Figure),
c.g. ventral aspect.

Key to eggs of some British foliage-frequenting psocids.

1. Eggs laid singly on threads suspended above leaf surfaces, or occasionally on leaves, partially enveloped in dark rectal material. Oviruptor a simple knife-like blade. - Trichopsocus dalii (Mclach

- Eggs laid in batches, occasionally singly, overlain with a silken web. Oviruptor toothed. - 2.

2. Eggs small (0.32 - 0.37 mm). Often small amounts of faecal material incorporated in web. Oviruptor with shallow teeth. - Ectopsocus briggsi Mclach.

- Eggs larger (0.42 - 0.65 mm). Web without traces of faecal material. Oviruptor with well-developed comb-like teeth. - 3.

3. Eggs longer than 0.55mm. Oviruptor with long free shaft extending along abdomen of pronymph, and with teeth only anterior to brachia. - (Stenopsocus) - 4.

- Eggs shorter than 0.55mm. Oviruptor without long free shaft. 5.

4. Eggs regularly oval, length 0.59 - 0.61 mm. Pale cream, white, greenish or bluish. - Stenopsocus immaculatus (Steph.)

- Eggs often tapering towards one end, length 0.55 - 0.61 mm. Pale cream or greenish. - S. stigmaticus (Imh. & Lab.

5. Oviruptor dark grey, with single row of deep teeth along median keel. Brachia toothless. Eggs pale yellow-white, darkening to deep yellow. - Graphopsocus cruciatus (L.

- Oviruptor translucent, with keel and brachia irregularly toothed. - (Caecilius) - 6.

6. Eggs laid on conifers. Size 0.42 - 0.45 mm. Darkening to iridescent brown/black. - Caecilius burmeisteri Brauer.

- Eggs laid mainly on broadleaved trees. - 7.

7a. Length 0.41 - 0.45 mm. Darkening to glossy grey-black. - *C. kolbei* Tetens

b. Length 0.42 - 0.46 mm. Darkening to glossy iridescent blue-black.
Chorion with slight sculpturing. - *C. fuscopterus* (Latr. in Coq.)

c. Length 0.43 - 0.46 mm. Darkening to grey-yellow, with matt dark brown at one end. - *C. flavidus* (Steph.)

Nymphs.

All the species considered here have six pre-imaginal instars. Medem (1951) gave brief notes on several species, and Broadhead and Wapshere (1960) briefly described the nymphs of *S. immaculatus* and *G. cruciatus*. Sommerman (1943 b) described the instars of *C. manteri* Som. and Weber (1936) and Sofner (1941), those of *E. briggsi*.

The first instars of all nine species have eight antennal segments, and all later stages have thirteen. There are no traces of wingpads in the first instar. Small meso- and meta-thoracic prominences are present in the second instar and small wingpads are clearly discernible in the third instar. The tarsi of all stages have two segments. All nine species have simple claws with an expanded pulvillus, and any psocid nymph possessing this character found in Britain can be assigned at once to the Polypsocidae, *Ectopsocus* or *Trichopsocus*. This character does not vary greatly between instars. An expanded pulvillus appears to have arisen several times in the order, and is closely correlated with the foliage-frequenting habit. It is found in several taxonomically anomalous psocids, such as *Matsumuraiella radiopicta* End. (Tsutsumi 1961, *in lit*. 1967). Most bark-frequenting psocids have claws with a subapial tooth, and slim rod-like pulvilli.

The nymphs of these species in Britain therefore form a well-defined taxonomic unit. Their identification is often difficult, especially if only preserved material is available. The colours given in the following notes are those of living or freshly killed nymphs; the nomenclature is after Ridgway (1912). Most nymphs turn pale after storage in alcohol, but the dark markings of Trichopsocus and Ectopsocus may be partially retained: those of the other species are retained to a lesser degree.

Different characters have been used in the past in attempts to separate nymphs of closely related psocid species (Pearman, 1932; Thornton and Broadhead, 1954), but there have been no attempts to evaluate a comprehensive range of structural characters for the identification of psocid nymphs in general. Identification beyond the generic level has proved difficult, and sometimes completely unsuccessful (see Broadhead and Datta, 1960, on Peripsocus). A few structural characters can be used in the generic classification of the nymphs of foliage psocids, notably the shape of the terminal segment of the antenna, and the number and shape of the bristles on the inner border of the paraprocts. All body hairs on the nine species are simple and unexpanded. Specific determination of all nine species are based on pigmentation, but some preserved material can be reliably identified only to genus. The nymphs of all Polypsocidae examined are structurally very similar. The value of characters of paraproct hairs are limited. Minor variations occur, and the nymphal bristles do not necessarily resemble those of the adult. The antennal tip is often lost in preserved material.

It is probable that a full multivariate analysis of measurements of nymphs may prove to be of value, but the small linear differences which have so far been found between small nymphs of closely related species are often obscured by the variation within any one species. Measurements of the head capsule and anterior wing-pad made on 20 unmounted nymphs of each instar of the nine species are given in Tables 10a-i, but there was sometimes considerable overlap between the same instars of different species. Other measurements, made on mounted specimens, proved of little value for identification: these included measurement of various antennal and leg segments.

Measurements of the head capsule and anterior wing pad together enable determination of the instars of each species, and the simple key to instars given below is based largely on characters of the developing wing pads. The key does not, therefore, include later stages of brachypterous individuals (some *G. cruciatus*, *E. briggsi* and *C. kolbei*), but these have simialr head measurements to macropters and can be separated from the Tables 10 . This key in some ways resembles that given for heteropterous nymphs by Southwood (1956b).

Brief descriptions of freshly-killed first and sixth instars of each of the nine species, and notes on the intervening stages are given below, and are followed by a key to species.

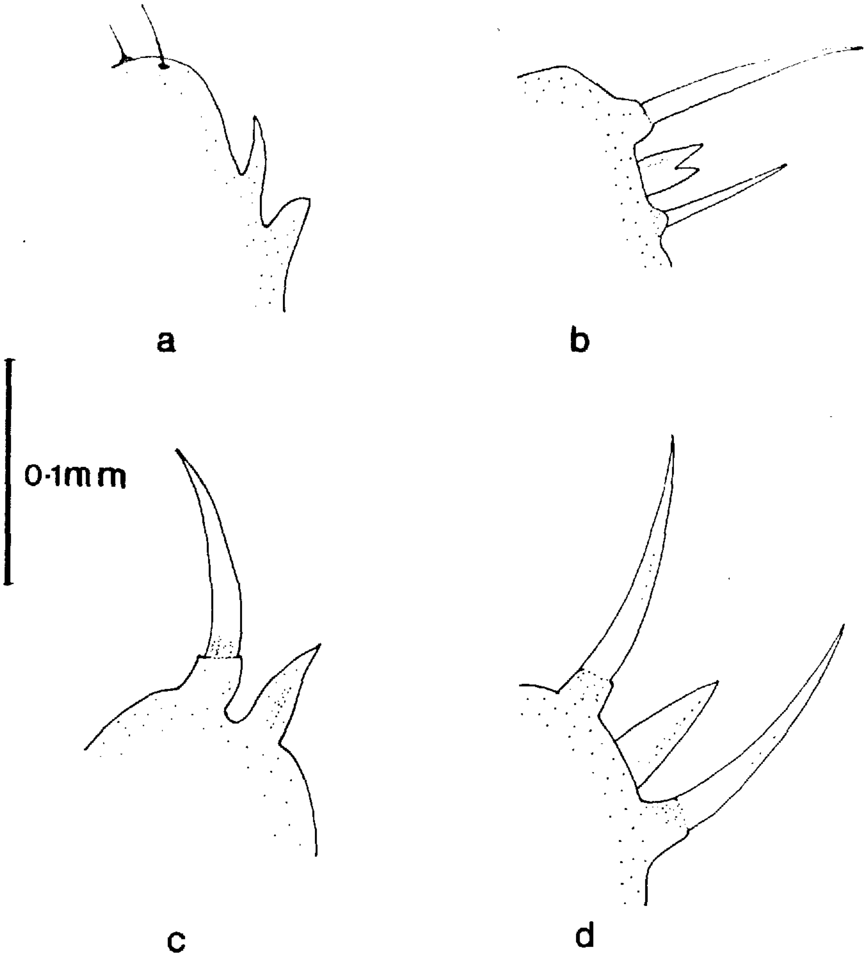


Fig.4.
Inner borders of left paraprocts of last instar nymphs of British foliage-frequenting Psocoptera. (ventral aspect, posterior towards top of page) a. *E.briggsi*, b. *T.dalii*, c. *Caecilius*, d. *Stenopsocus*, *Graphopsocus*.

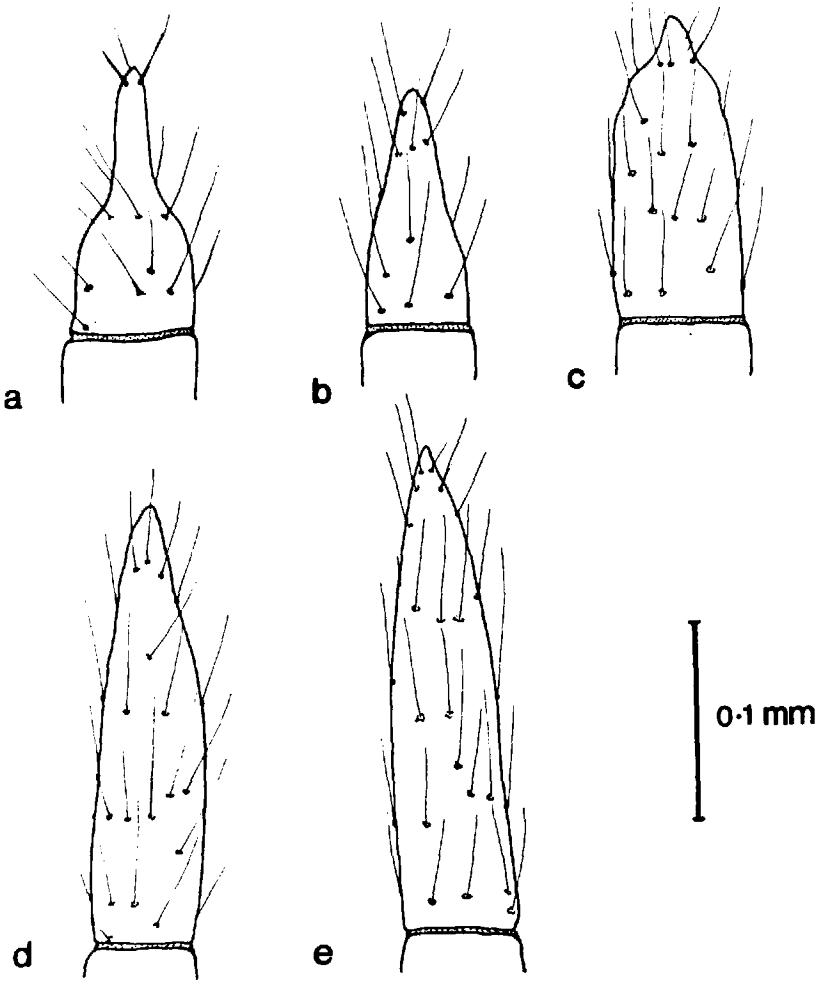


Fig. 5.
Terminal antennal segment of last instar nymphs of British foliage-frequenting Psocoptera. a. *T.dalii*, b. *E.briggsi*, c. *Caecilius*, d. *G.cruciatus*, e. *Stenopsocus*.

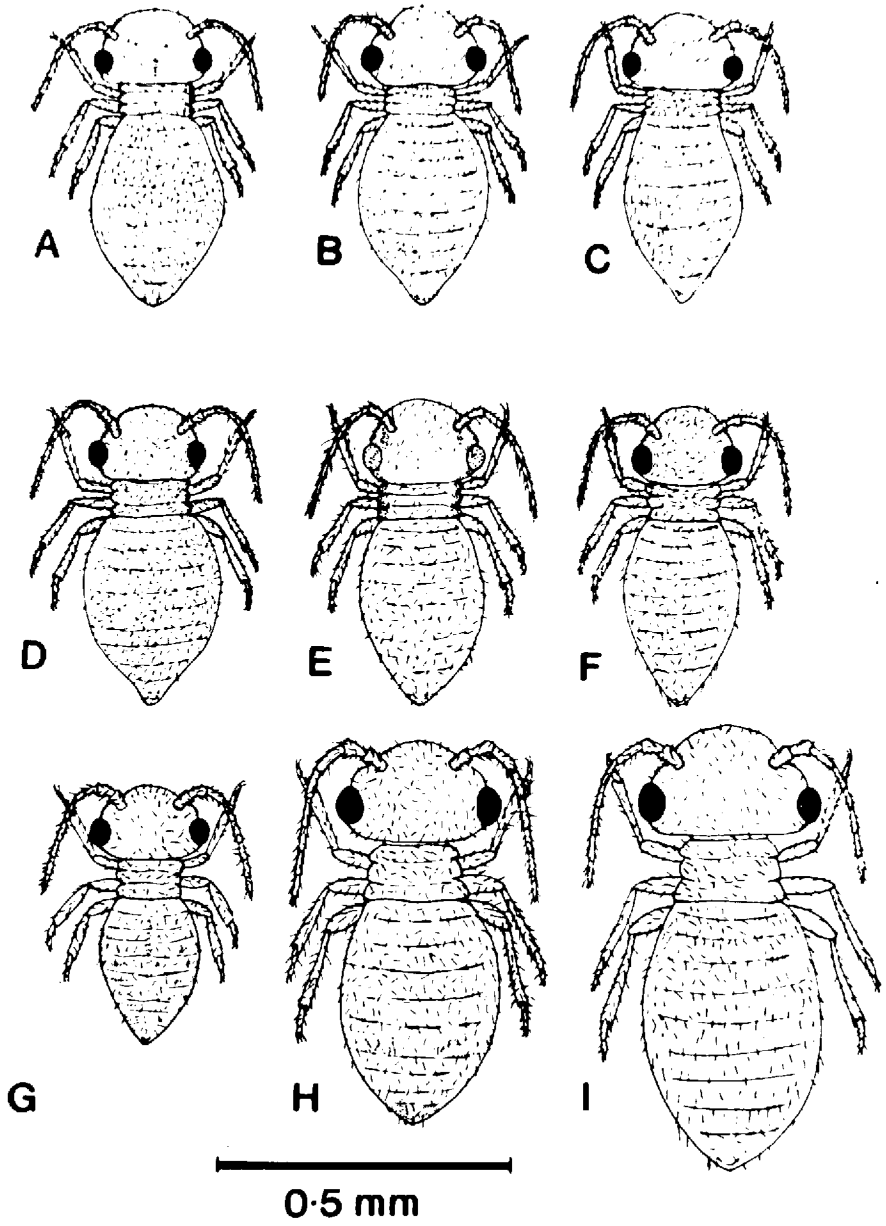


Fig. 6.

First instar nymphs of British foliage-frequenting Psocoptera.

A. *C. burmeisteri*, B. *C. fuscopterus*, C. *C. flavidus*, D. *C. kolbei*, E. *T. dalii*, F. *G. cruciatus*, G. *E. briggsi*, H. *S. stigmaticus*, I. *S. immaculatus*,

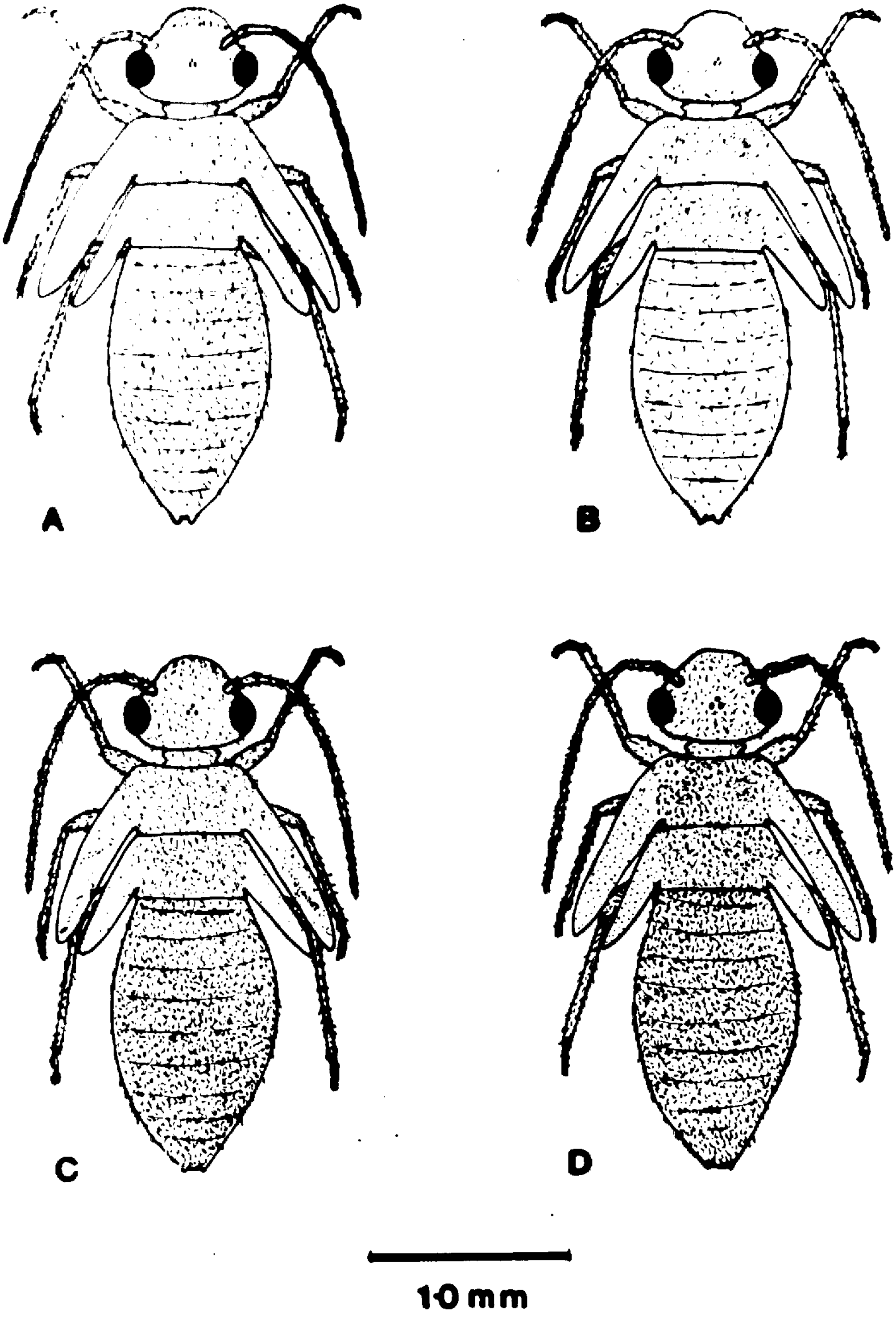


Fig. 7. Sixth instar nymphs of British foliage-frequenting Psocoptera.
A. C.burmeisteri, B. C.flavidus, C. C.fuscopterus, D. C.kolbei.

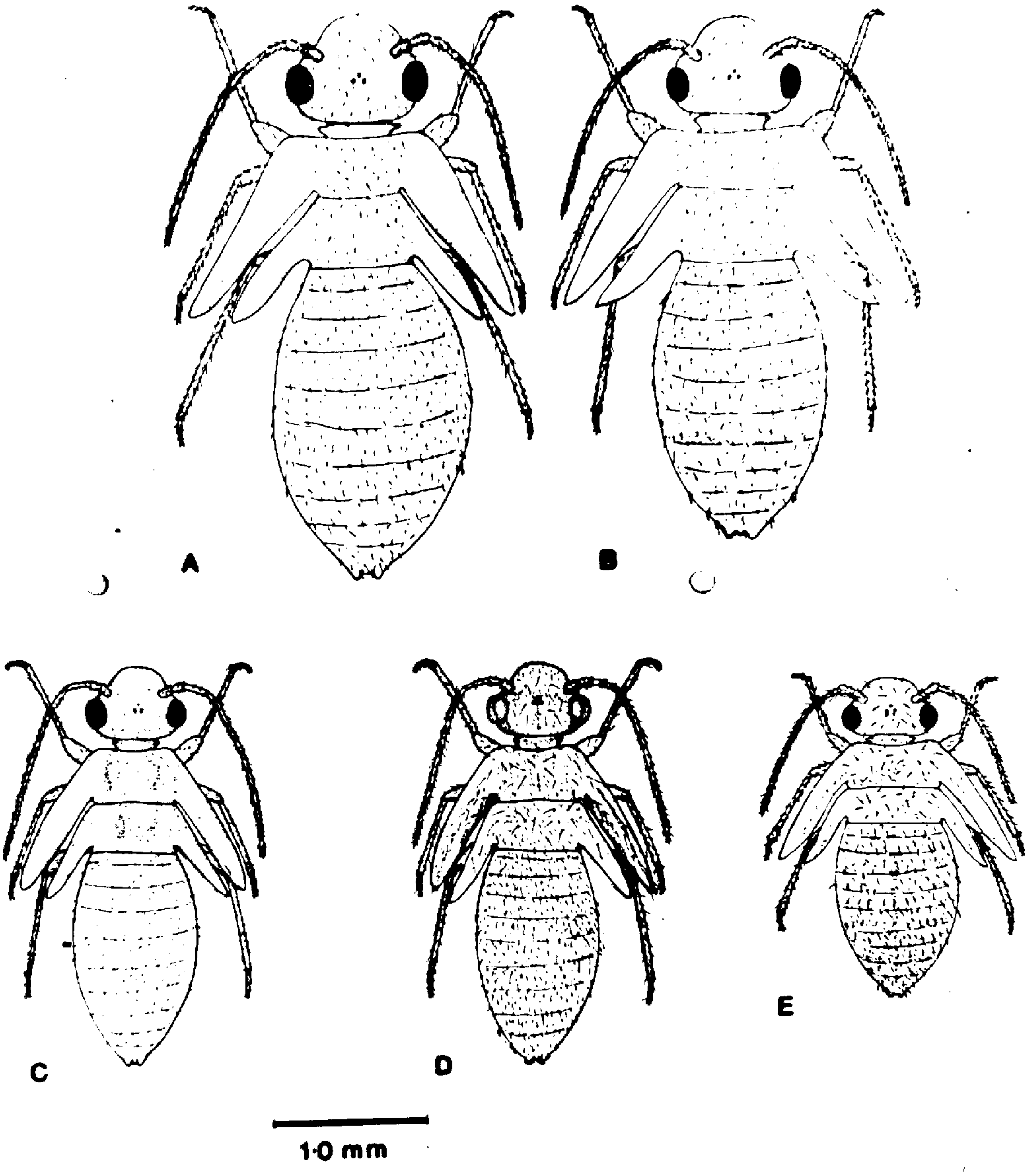


Fig.7 (II).

A. *S.immaculatus*, B. *S.stigmaticus*, C. *G.cruciatus*, D. *T.dalii*, E. *E.briggsi*.

Key to instars of some British foliage-frequenting psocids.

1. Antennae with eight segments. - Instar I

\- Antennae with thirteen segments (later stages) 2.

3. Wing pads indistinctly formed. Small lobes on lateral borders of meso- and meta-thorax. - Instar II

\- Wing pads clearly differentiated (later stages). - 3.

3. Anterior wing pad not extending beyond posterior border of meta-thorax - Instar III

\- Anterior wing pad extending beyond posterior border of meta-thorax. - 4.

4. Anterior wing pad extending beyond posterior border of meta-thorax by not more than the greatest length of meta-thorax. - Instar IV

\- Anterior wing pad longer. - 5.

5. Anterior wing pad slightly shorter than posterior wing pad. Usually not extending beyond third tergite of extended abdomen. Adult wing pattern and hairs not visible, venation very indistinct. - Instar V

\- Anterior wing pad as long as, or projecting slightly beyond, the posterior wing pad. Adult wing pattern, venation and hairs usually distinct. - Instar VI

Trichopsocus dalii (Mclachlan)

Previous accounts:- None. Measurements:- Table 10a.

First Instar (Fig. 6E) : Ground colour pale ivory yellow, with traces of castaneous stripe laterally along thorax and extending forwards to eye. Usually a castaneous patch between eye and base of antenna. No other markings. Antennal segments all with sparse long hairs. Terminal segment constricted (Fig. 5a). Eyes iridescent green/black. Head and thorax sparsely hairy, all hairs pale, simple. Legs translucent. Abdomen pale, hairs short.

Second - fifth Instars : Traces of lemon yellow on vertex, posterior borders of meso- and meta-thorax, and dorsal abdomen. Lateral castaneous streak darker, passing through eye to base of antenna. Body hairs dark, wing pads without markings, unicolorous ivory-yellow.

Sixth Instar (Fig.7D) : Ground colour ivory-yellow, lemon markings on vertex and thorax more pronounced. Lateral castaneous stripe as in earlier instars, extending dorsally in front of eye. Ocellar markings dark castaneous. Thoracic lobes tinged laterally with pale grey. Posterior border of anterior wing pad darkened with two lines of dark bristles. Similar dark bristles scattered on body. Antennae with numerous pale hairs, terminal segment constricted. Legs translucent. Hairs on inner borders of paraprocts (Fig. 4b).

Ectopsocus briggsi McLachlan

Previous accounts:- Weber (1931), Sofner (1941). Measurements:- Table 10b.

First Instar (Fig. 6G) : Ground colour pale olive-buff. Traces of lateral transverse striae on abdomen, only slightly darker than ground colour. No other markings. Antennae with numerous pale hairs, terminal segment unconstricted. Eyes dark grey. Head and thorax with short pale hairs. Legs translucent grey.

Second - fifth Instars : Ground colour darker. Head with dark castaneous and grey tinges along dorsal sides of eyes. Grey flushes across base of postclypeus, and indistinctly flanking epicranial suture at posterior of head. Scattered dark bristles in later stages, interspersed with more numerous short paler hairs. Thorax pale medially, with darker markings on lobes and laterally. Wing pads translucent, no markings. Abdomen with dark castaneous lateral markings along posterior borders of tergites, and smaller median patches.

Sixth Instar (Fig. 7E) : All markings more pronounced than earlier stages. Pale grey flushes extend forwards along epicranial suture to ocellar region, then diverge towards bases of antennae. Post clypeus with irregular castaneous markings. Eyes dark grey. Thorax darker, wing pads grey, no markings. Abdominal striae darker, median markings often coalesced. Ocellar markings dark castaneous, lateral ocelli elongate, arciform. Head and thorax with sparse long black bristles and large numbers of shorter pale hairs. Abdominal tergites each with 1 - 2 rows of dark bristles, directed posteriorly. Legs translucent grey. Hairs on inner borders of paraprocts as in Fig. 4a.

Stenopsocus immaculatus (Stephens)

Previous accounts:- Kolbe (1880), Broadhead and Wapshere (1960).

Measurements:- Table 10c

First Instar (Fig. 6I) : Ground colour white, or towards pale olive-buff. Sometimes yellowish-white. No markings. Antennal segments with sparse pale hairs, terminal segment elongate, unconstricted (Fig. 5e). Eyes black. Head, thorax and abdomen with numerous simple short pale hairs. Legs translucent.

Second-fifth Instars : Ground colour white, or faintly tinged with lemon yellow or light grey. Slight grey markings on thoracic lobes, more pronounced on basal half of wing pads.

Sixth Instar (Fig.7A) : Ground colour as in earlier stages. Eyes black. Postclypeus unmarked. Ocellar markings small, black. Head with many short dark hairs. Antennae grey-white, slightly darker than head, hairs dark. Thorax pale, but with grey markings on lobes, sometimes pronounced and dark brown. Wing pads grey or pale brown on basal half, pale apically. Abdomen pale, no markings. Hairs on inner borders of paraprocts as in Fig. 4d.

Stenopsocus stigmaticus (Imhoff and Labram)

Previous accounts:- Kolbe, 1880. Measurements:- Table 10d

First Instar (Fig. 6H) : Ground colour white or tinged with pale lemon yellow. Vertex and frontal region with definite yellow tinges. Abdomen with conspicuous white band (internal) across tergite VI, often interrupted medially. White material also concentrated at posterior end of abdomen. No other markings. Eyes red-brown-black. Antennae pale yellow, all segments with sparse pale hairs, terminal segment elongate, unconstricted. Head and thorax with short pale hairs. Legs translucent.

Second - fifth Instars : Ground colour pale lime green and lemon yellow on head and thorax, paler on abdomen. Abdominal band across tergite VI, white or bright lemon yellow. Antennae, femora and tibiae pale lime green. Wing pads translucent green-yellow, no markings.

Sixth Instar (Fig. 7B) : Ground colour as earlier stages. Eyes red-brown-black. Ocellar markings small, red-brown. Head with many short pale hairs. Antennae with numerous hairs, some dark. Thorax sometimes with darker green lateral markings. Wing pads usually unmarked, sometimes with slightly darker shading near base. Abdominal band pronounced, white or bright lemon yellow - similar internal concretions at posterior. Paraproct hairs as in S. immaculatus.

Graphopsocus cruciatus (L.)

Previous accounts:- Kolbe, 1880; Huie, 1916; Broadhead and Wapshere, 1960

Measurements:- Table 10e.

First Instar (Fig. 6F) : Ground colour lemon yellow. Faint castaneous markings on vertex. No other markings. Eyes very dark red, sometimes appearing black. Antennal segments with pale hairs, terminal segment elongate, unconstricted. Head, thorax and abdomen with numerous short, pale, simple hairs.

Second - fifth Instars : Ground colour pale lemon yellow - lemon yellow. Head with faint castaneous markings across posterior border, varying amount of castaneous markings on frontal and ocellar regions. Often also small castaneous markings dorsal and anterior to eyes. Post clypeus mainly castaneous in later (IV - V) stages. Thorax with castaneous patches on meso- and meta-thoracic lobes, underlain with pale grey in III and later stages. Wing pads with irregular traces of diagonal bar. Abdomen unicolorous, except for faint median castaneous stripe extending backwards to tergite IV in some specimens.

Sixth Instar (Fig. 7c) : Ground colour pale to dark lemon yellow. Head markings as in earlier stages. Eyes dark red-black. Ocellar markings small, black. Head hairs numerous, pale, short, - also antennal hairs. Discrete castaneous patches on meso- and meta-thoracic lobes, underlain with mid-grey. Base of anterior wing pad dark tinged, both pads with broad mid-grey transverse stripe extending from about 1/2 - 2/3 distance along costal edge across wing. Abdomen unicolorous, many short, pale hairs. Hairs on inner border of paraprocts as in Fig. 4d .

Caecilius flavidus (Stephens)

Previous accounts:- None. Measurements:- Table 10f.

First Instar (Fig. 6c) : Ground colour lemon yellow. No markings. Eyes dark-red to black. All antennal segments with pale hairs, terminal segment elongate, constricted at tip (Fig. 5c). Head with numerous short, pale or castaneous, simple hairs. Thorax and abdomen with short, pale hairs.

Second - fifth Instars : Ground colour lemon yellow. Variable amounts of castaneous across posterior border of head and along epicranial suture. Occasionally on post clypeus. Traces of castaneous on meso- and meta-thoracic lobes.

Sixth Instar (Fig. 7B) : Gouund colour lemon yellow - strontian yellow. Head markings as earlier stages. Eyes dark red - black. Ocellar markings small, dark castaneous. Head hairs numerous, pale. Meso- and meta-thoracic lobes with discrete castaneous patches. Slight castaneous markings at bases of wing pads, wing pads unicolorous, pale. Abdomen unicolorous, with many short, pale hairs. Hairs on inner borders of paraprocts as in Fig. 4c.

C. burmeisteri (Brauer)

Previous accounts:- None. Measurements:- Table 10g.

First Instar (Fig. 6A) : Ground colour aniline yellow to sulphine yellow. Prothoracic lobes slightly darker laterally. No other markings. Eyes dark red-black. Antennae translucent grey with numerous short hairs, terminal segment as C. flavidus. Head, thorax and abdomen with numerous short, pale, simple hairs.

Second-fifth Instars : Ground colour as above, sometimes towards pyrite yellow. Slight lighter patches dorsal to eyes. Post clypeus with 5 or 6 darker lines either side of mid-line, converging anteriorly. Numerous short, dark hairs.

Sixth Instar (Fig. 7A) : Ground colour as earlier stages. Markings as above, except for darker traces on thoracic lobes. Ocellar markings red-brown, Eyes dark red. Wing pads unicolorous. Hairs on inner borders of paraprocts as C. flavidus.

C. fuscopterus (Latreille in Coquebert)

Previous accounts:- None. Measurements:- Table 10h.

First Instar (Fig. 6B) : Ground colour pale fuscous. Slightly darker on lateral parts of all thoracic lobes. No other markings. Eyes dark red-black. Antennal segments with numerous pale hairs, terminal segment as in C. flavidus. Head, thorax and abdomen with numerous short, pale, simple hairs.

Second - fifth Instars : Ground colour fuscous-black fuscous. Slightly darker markings dorsal to eyes. Post clypeus with irregular darker markings. Meso- and meta-thoracic lobes darker. Abdomen paler.

Sixth Instar (Fig. 7C) : Ground colour as above, often glossy black-fuscous. Ocellar markings dark castaneous, small. Eyes black. Head hairs dark. Wing pads translucent fuscous, no markings, but characteristic adult wing patterning visible later. Abdomen medium fuscous, no markings. Many short pale or dark hairs. Hairs on inner border of paraprocts as in C. flavidus.

C. kolbei Tetens

Previous accounts:- None. Measurements:- Table 10i.

First Instar (Fig. 6D) : Ground colour pale fuscous. Grey-fuscous tinges along posterior of head and on thoracic lobes. No other markings. Eyes dark red-black. Antennae translucent grey with numerous short hairs, terminal segment as in C. flavidus. Head with short pale hairs. Thorax and abdomen with numerous short, pale, simple hairs.

Second - fifth Instars : Ground colour fuscous to dark fuscous. Darker markings anterior and dorsal to eyes. Thorax with blackish fuscous markings on meso- and meta- thoracic lobes.

Sixth Instar (Fig. 7D) : Ground colour fuscous to blackish fuscous. Markings as in earlier stages. Ocellar markings dark fuscous. Head hairs dark. Meso- and meta-thorax lobes darker, wing pads uniform grey-fuscous, no markings. Abdomen dark fuscous, no markings. Hairs on inner border of paraprocts as in *C. flavidus*.

Key to nymphs of some British foliage-frequenting psocids.

1. Nymphs with castaneous lateral stripe, extending at least along thorax. - 2.

\- Nymphs without such lateral stripe. - 3.

2. Eyes pale, iridescent green/black. Terminal segment of antenna constricted as in Fig. 5a . Ground colour pale ivory-yellow. - *Trichopsocus dalii* (McLach.)

\- Eyes dark grey. Terminal segment of antenna unconstricted. Ground colour pale olive-buff, with darker markings on thorax and abdomen. - *Ectopsocus briggsi* McLach.

3. Nymphs with elongated terminal segment of antenna, apex not constricted (Figs 5d-e). Ground colour white or yellow, sometimes lime green. Paraproct hairs as figure 4d. - 4.

\- Nymphs with apex of terminal segment of antenna constricted. Hairs on inner border of paraprocts as in Fig. 4c . - (*Caecilius*) 6.

4. Nymphs smaller, lemon yellow. Castaneous markings on thoracic lobes underlain with grey (later instars). Wing pads (VI) with transverse grey bar. - *Graphopsocus cruciatus* (L.)

\- Nymphs larger, white or lime green/yellow. Wing pads without transverse bar. - (*Stenopsocus*) 5.

5. Nymphs pale, white or yellow-white. Head hairs of larger nymphs dark. No distinct band across abdominal tergite VI. - *Stenopsocus immaculatus* (Steph.)

\- Nymphs darker, green or yellow. Head hairs of larger nymphs pale. Transverse band of white or lemon yellow across abdominal tergite VI, sometimes interrupted medially. - *Stenopsocus stigmaticus* (Imh. & Labr.)

6. Ground colour predominantly yellow. - 7.

\- Ground colour predominantly fuscous to blackish fuscous. - 8.

7. Aniline yellow to sulphine yellow, with no distinct darker markings. Found mainly on conifers. - *Caecilius burmeisteri* Brauer

\- Lemon yellow. Some castaneous markings on head and thorax. Found mainly on broadleaved trees. - *Caecilius flavidus* (Steph.)

8. Post clypeus with irregular darker markings. Wing pads fuscous. - *Caecilius fuscopterus* (Latr. in Coq.)

\- Post clypeus usually uniform. Wing pads grey-fuscous. - *Caecilius kolbei* Tetens

Life Histories.

The outline life histories given below are based on data from laboratory rearings and regular field sampling. The phenologies of the different species may differ slightly from year to year and in different localities: the following data were obtained in 1966 and 1967 in Berkshire.

All species overwinter mainly in the egg stage, but some adults of *G. cruciatus*, and adults and nymphs of *E. briggsi* also overwinter. The eggs of all species hatch from late March to early May, and all nine species have two or three generations in the spring and summer. The species laying on deciduous foliage pass the first (spring) generation in the ground litter, and the adults fly onto trees where there are one or two subsequent generations. The eggs re-enter the litter at autumnal leaf-fall. Those species laying on evergreens are largely confined to the trees, and all species are found on trees throughout the period of June to October. All stages may be present simultaneously towards the end of the summer, and distinct generations are detectable only by regular sampling throughout the season. Three species (E. briggsi, C. flavidus, and C. burmeisteri) are regularly trivoltine, and the others are all bivoltine. The few overwintering adults of G. cruciatus and E. briggsi lay eggs which hatch by the end of May, and overwintering nymphs of E. briggsi all matured by early April. This species is unusual in that several stages may be found together at any time of the year. Adults from the spring generation often remain in the litter and the adults of the next (second complete) generation fly onto trees in August, where a third generation occurs.

There is very little information on the life histories of these species in other parts of the world. Kolbe (1880) briefly described the life cycles of C. flavidus and S. stigmaticus. Vishniakova (1959) showed that C. flavidus was trivoltine in the Moscow area (U.S.S.R.), and the isolated observations of Badonnel (1943), Ludwig (1908), Stager (1919) and Medem (1951) suggest that the life histories of several of the other species on the mainland of Europe correspond closely to those given above. Martin (1892) recorded G. cruciatus in India, and found it from April to December.

The life histories of the nine species are compared and summarised in Fig. 8.

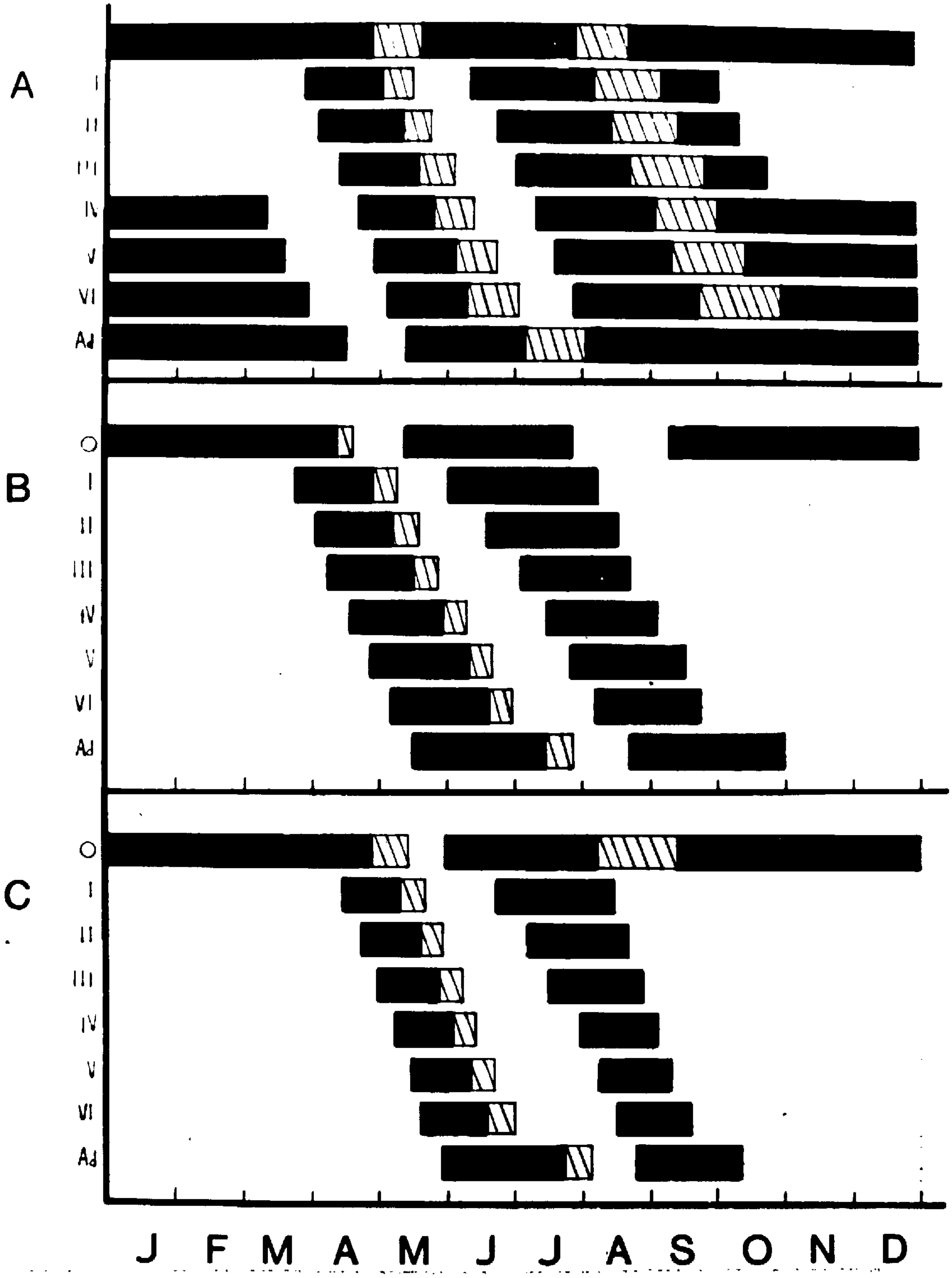


Fig.8. Schematic life histories of British foliage-frequenting Psocoptera (solid blocks indicate periods when each stage (O-Ad) was found in the field in 1966 or 1967. Cross hatched blocks show periods when individuals persisted in culture in unheated insectary).
A. *E.briggsi*, B. *T.dalii*, C. *C.kolbei*.

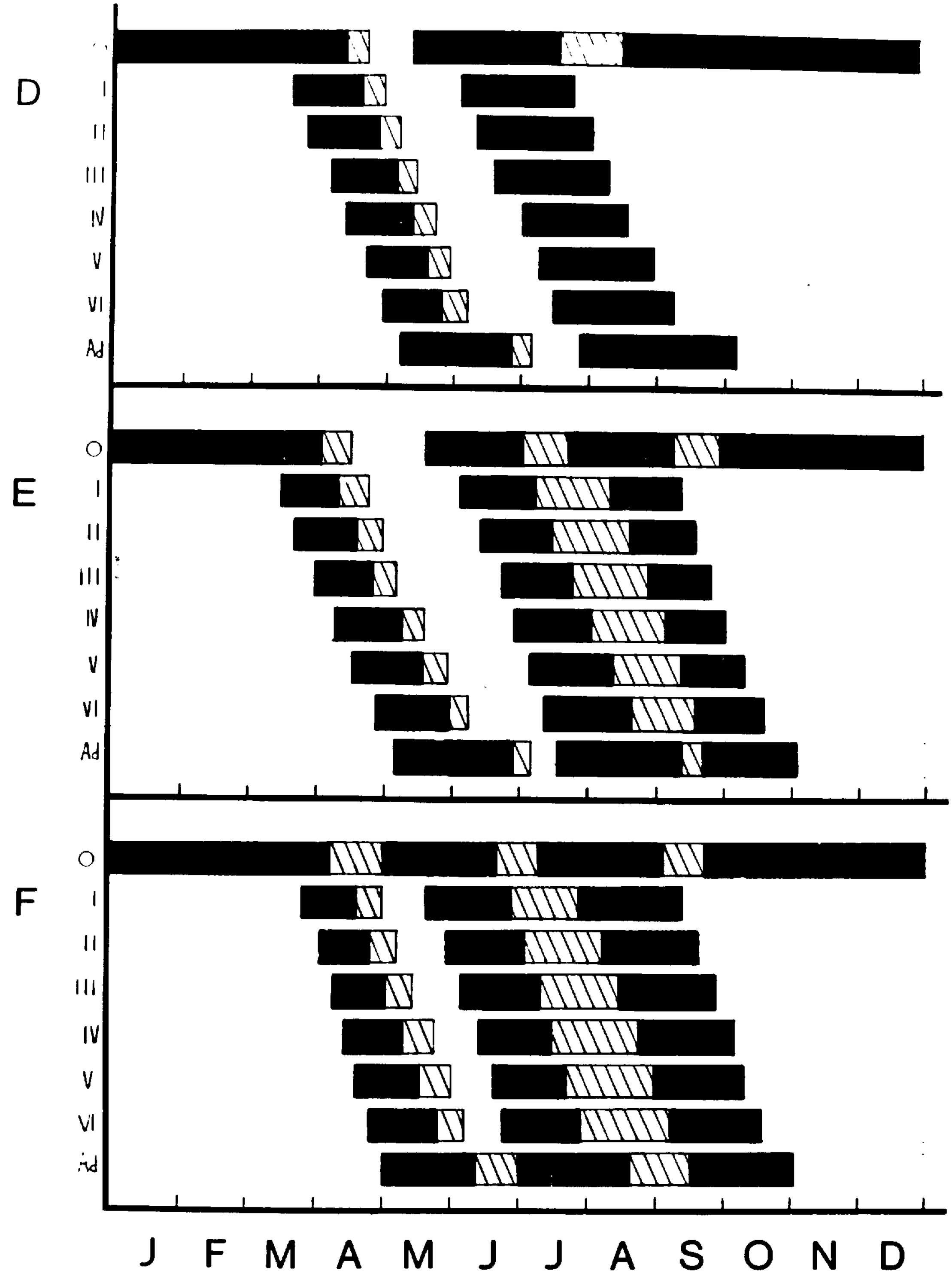


Fig.8.(cont.)

D. *C.fuscopterus* E. *C.flavidus* F. *C.burmeisteri*.

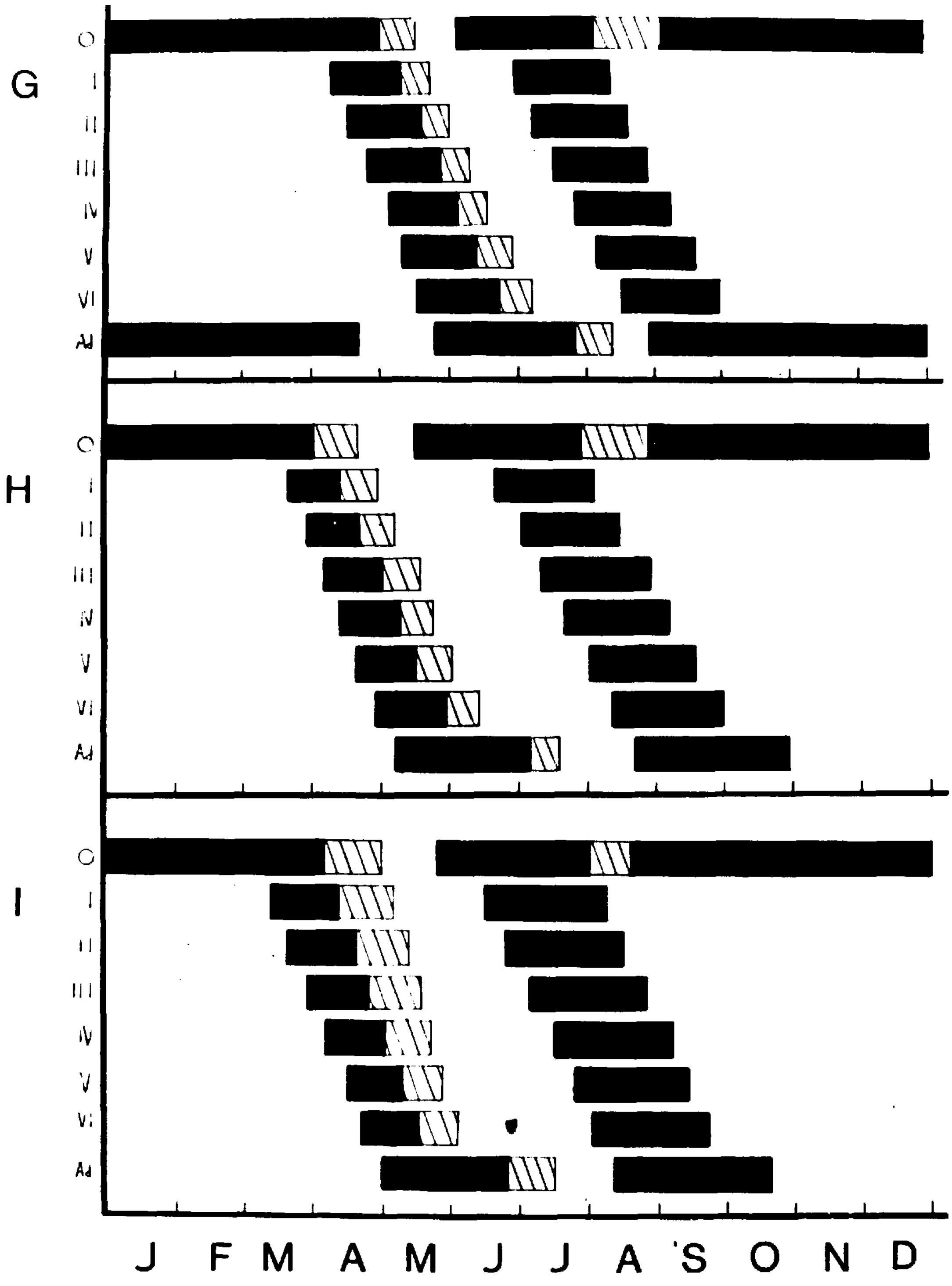


Fig.8.(cont.)

G. G.cruciatus H. S.stigmaticus I. S.immaculatus.

Overwintering in some Psocoptera.

Most species of British out-door Psocoptera pass the winter as diapausing pronymphs in the eggs, but a proportion of a few species overwinter as nymphs and/or adults. Elipsocus hyalinus (Stephens) may overwinter in the adult stage, as later instar nymphs, or as eggs (see Broadhead and Wapshere, 1966 a). E. briggsi has a similar life cycle to this, and large nymphs of Reuterella helvimacula are sometimes found in winter (Pearman, in lit). A few adults of Cerobasis guestfalica (Kolbe) overwinter on or under bark. All other bark-frequenting species examined at Silwood overwinter only in the egg stage. Very few specimens of Caecilius were found after mid-November, and none from December onwards.

Several possible overwintering sites were examined during the two winters of 1965-6 and 1966-7, but few psocids were found. G. cruciatus occurred in small numbers sheltering on the foliage of broadleaved evergreens, notably Ilex, on which this species is found at other times of the year (Section 4). Most specimens of E. briggsi were found on dead foliage remaining on oak trees, and very few on dead leaves on the ground under the trees (Table 11). None were found on or under bark of the oak trees examined. No specimens of T. dalii were found during the winter, but Pearman (1928) believed this species to overwinter in the nymphal stages.

Most of the psocids found in winter were active. Many of those dissected had food material in the gut, and those kept alive outside produced faeces and appeared to be feeding. It thus seemed that there was no true 'diapause', and experiments were carried out during 1966-7 to ascertain whether feeding continued throughout the winter, whether moulting occurred, and whether reproduction ceased at this time. Three species of psocids, namely E. briggsi, G. cruciatus and E. hyalinus, were used.

Groups of 15 adult females of each species were kept in muslin topped polystyrene boxes in the field, with dead twigs and oak leaves as a source of food. At the end of each month from November 1966 to March 1967, one box of each species was brought to the laboratory. The psocids were dissected, and their crop contents and state of reproductive organs was recorded. All other boxes in the field were examined on each occasion, and the numbers of eggs laid and deaths of psocids were recorded. Boxes of 20 E. briggsi nymphs were also examined each month, and any newly moulted adults recorded. The results of this survey are summarised in Tables 12a-c.

(a) Feeding. The dissections showed that food was present in the gut of all three species throughout the winter. There was usually food in both crop and rectum, and numerous faecal pellets were always present in the boxes. Faeces produced in the laboratory in February and March contained digested material, and feeding continued through the winter.

(b) Moulting and death. Several adults of all species died during the winter. Very few nymphs of E. briggsi moulted to the adult stage until March, but mortality was low. Development is evidently greatly retarded through the winter. Pearman (in lit.) considered that R. helvimacula nymphs pass the winter without growth, although they feed normally. A few nymphs of E. hyalinus were examined: all remained as nymphs until late March.

(c) Reproduction. The ovarioles of all three species contained mature oocytes in November, but very few large oocytes were found from then onwards. The ovarioles were small during January and February, and no eggs were laid during these months. A few eggs were laid in early December.

It is clear that these three species of psocids remain active throughout the winter: although development is greatly retarded. The eggs of other foliage-frequenting psocids can be induced to hatch during the winter by keeping them at 20°C in the laboratory, and eggs were laid by some females of *E. briggsi* transferred from the field to this temperature in January. A form of reproductive diapause occurs in the field during the winter.

SECTION 3 Psocoptera of Leaf Litter.

Introduction

Many groups of small arthropods are found in leaf litter; the most abundant and characteristic of these are some Mites, Spiders, Pseudoscorpions, Opilionids, Centipedes, Collembola, and smaller numbers of larvae and adults of many groups of higher insects. The fauna is in many ways intermediate in character between that of soil and that of low vegetation. Numerous studies of soil fauna have been made in recent years (see Kevan 1955, 1962), but there are fewer accounts of leaf litter arthropods. Psocoptera use part of the active mesofauna (*sens* Fenton 1947) of the litter, in which they comprise only a small proportion of the total arthropod fauna. There have been no ecological studies of Psocoptera in this habitat, but a number of edaphic psocids have been described from various parts of the world.

Some workers on other groups have enumerated small numbers of psocids extracted from soil or litter in Europe, but these have not in many instances been identified (see Salt *et al*, 1948). Stringer and Herrington (1963) recovered a few specimens of *Lachesilla pedicularia* (L.) and *Liposcelis* sp. from Black currant litter at Long Ashton, Bristol. Strickland (1947) recovered species of *Ectopsocus*, *Liposcelis* and *Psocatropos* from litter under Cacao in Trinidad, and Salt (1952) and Belfield (1956) both obtained small numbers of unidentified psocids from pasture soils in Africa by flotation methods. Two specimens of *Lachesiella* (*sic*) were found in soil from Giza by El Kifl (1959).

The aims of the present work were to discover the range and numbers of psocids in leaf litter throughout the year, and to examine the distribution of psocids in different types of litter.

Extraction Methods.

Extraction methods for soil and litter arthropods are similar, and have been reviewed by Kevan (1955, 1962), and MacFadyen (1962). Two methods of extraction were used in the present study; Tullgren funnels were used for the bulk of the extractions, and a Kempson Bowl Extractor (Kempson, Lloyd and Ghelardi, 1964) was also used. Both methods depend on downward movement of the animals in response to heat applied from above, but the latter provides for maintenance of a high humidity towards the bottom of the sample and in the air immediately under it. Comparative calibrations of the two methods should give a measure of the loss of animals caused by desiccation in the Tullgren funnels. Two sizes of funnel were available of 7.5 cm and 25 cm in diameter. Up to eleven of the larger funnels were used at any one time, and six of the smaller funnels were used at intervals as described below; because of their small size and the low density of psocids in litter they were useless for comparative extraction. The larger funnels were heated by 60 w bulbs suspended 15-20 cm above the samples.

Kempson et al (1964) discussed the efficiency of their extractor and methods of estimating this. El Kifl (1957) compared Tullgren funnels and 'Salt and Hollick flotation' as methods of extracting arthropods from soil. He obtained four psocids from Tullgren funnels and seventeen by flotation and, solely on this evidence, stated that funnels were more efficient than flotation for extracting Psocoptera. Lloyd (1967) extracted animals from Beech litter in Tullgren funnels after a preliminary sieving, but recorded that, in general, the funnels were a much less efficient extraction method than the Kempson bowls. The large funnels and the four-chambered Kempson extractor were calibrated by the following method (after Van der Drift,1951). All psocids were extracted from samples of Pinus and Quercus litter by treatment in the funnels for fourteen days, after which extraction was assumed to be complete. The 'clean' litter was left in the funnels for a few days to cool thoroughly, and then damped from the top. Known numbers of psocids of different species and stages were introduced near the top of the samples, which were then extracted for ten days. The collecting jars, which contained 70 per cent alcohol, were changed daily, and the rate of extraction was thus found. Comparison of the total number of psocids extracted with the number introduced was taken as a measure of the extraction efficiency of the funnels. Samples of psocid-free litter from the funnels were transfered to the Kempson bowls, and the above procedure repeated. The bowls of picric acid were changed daily, and all sample bowls were covered to prevent the escape of psocids. Ten samples of each kind of litter were examined in most cases for each psocid tested and for each extraction method. Results of these extraction tests are given in Table 13. The different types of psocids were all extracted more efficiently by the Kempson method, and some variations were seen in the Tullgren extractions. The young nymphs of foliage psocids (such as Caecilius flavidus) are more susceptible to desiccation than the other stages and were extracted less efficiently.

The amount of water in the ground litter varied considerably; during the winter, especially, drying samples to constant weight reduced the original weight by up to 85 per cent. The relative humidity on bare ground beneath the litter was rarely less than 60 per cent (measured by cobalt thiocyanate paper), and not infrequently the litter contained free water and appeared sodden. A comparison of the extraction efficiencies of Tullgren funnels for dry and sodden litter was made by the above method, and ten samples of each were extracted. The results are given in Table 14 , and indicate that a higher proportion of psocids is extracted from dryer than from sodden litter. It is likely that many small active animals become entrapped in water films in wet litter, and drown in the large amount of free water. Corpses of introduced psocids were found in the sodden litter on subsequent examination, but no conclusions could be drawn as to the cause of death.

Times of extraction.

The collecting tubes under the Tullgren funnels were changed daily and the numbers of psocids in them were counted. The figures given in Table 15 are the sums of psocids from numerous samples of various kinds of litter from April to August 1966. The majority of the psocids were extracted in the first three days, and only a very small number was found after seven days. The figure for E. briggsi may appear anomalous; this was due to a large incidence of first instar nymphs from eggs hatching in the litter, which may be dissociated confidently from the psocids present in the litter at the time of collection. The duration of the first instar of E. briggsi is 1-3 days and presence of this instar after the fourth day of extraction must result from hatching of eggs. This misleading trend may be found also in other species which have eggs in the litter.

The extraction time for all samples was standardised at seven days.

Types of litter sampled.

The kinds of leaf litter sampled, all from Silwood Park, Berks., are enumerated in Table 16 . The sample unit was standardised as the amount of litter covering a 30 x 30 cm square of ground. This sample is accurately replicable, although the actual amount of litter varies throughout the year. The main alternative, a known weight of litter, is incovenient to use as the samples cannot be sized until after extracting the psocids and drying to constant weight.

The amounts of litter per 900 cm^2 of ground at different times of the year are shown in Table 17. These figures are based on total leaf counts in fifteen samples of Oak litter per month from March to December 1966. Each petiole base found was counted as a leaf. The greatest amount of litter was found after autumn leaf-fall, and it progressively decreased to a minimum in July and August. This trend closely follows that found by Gabbutt (1956) in Oak litter in Devon.

Each sample extracted in the Kempson bowls consisted of one of the above units. The large funnels each contained four samples and were used for comparative bulk extractions from different types of litter. Three funnels were always used for Oak litter, and contained four bulked samples from under large oak trees, under small oak trees, and open ground between trees, respectively. Only Oak samples were used in the Kempson extractor, for comparison with the above, and both series of Oak extractions were continued throughout the year. Most of the other kinds of litter were sampled only from March to November, but samples were also taken at irregular intervals throughout the winter.

Psocoptera obtained.

All psocids extracted from leaf litter were identified to species and where possible, to instar. The total numbers obtained are shown in Table 18, which shows that the great majority of psocids were from Oak litter (41.3 per cent) and *Cupressus* litter (52.4 per cent), and that many types of litter were extremely poor in these insects.

Sixteen species of Psocoptera were recovered, most of them in very small numbers. Three species, C. flavidus, E. briggsi, and Epipsocus lucifugus (Ramb.), together formed 98.6 per cent of the total. The first two of these were largely confined to oak litter, but E. lucifugus was more widely distributed.

The numbers of each stage of C. flavidus found in oak litter in 1966 and 1967 are shown in Table 19. There was a simple succession of of instars throughout the period April to early June, and after this time occurence of C. flavidus in the litter was sporadic. The first generation of this species is passed in the litter, and the resulting adults fly onto trees. Individuals found later in the season are likely to have been washed or blown off the trees, or result from eggs on leaves which have entered the litter.

E. briggsi was found in the litter in small numbers for most of season, and there was a succession of instars in early summer. Adults fly onto trees in August, and from that time only a few are found on the ground.

E. lucifugus was found from June to September (Table 20). It is univoltine and apparently confined to litter. All the stages of this species are readily distinguishable from all other British psocids by the form of the lacinia (figured in Badonnel, 1943), and there are five instars. The adult female is wingless; the male is winged but very rare. A male fourth instar nymph taken from oak litter in July 1967 appears to be only the fifth recorded specimen of this sex.

The psocids found in leaf litter can be conveniently divided into three ecological groups:-

1. Primary litter dwellers, such as E. lucifugus, which spend their whole life history in the litter, and do not

frequent other types of habitat.

2. Secondary litter dwellers which have generations in two distinct habitats, at least one in litter and others elsewhere. All the British species which oviposit on the leaves of deciduous trees are in this category, which is exemplified by *C. flavidus*.

3. Casual litter dwellers, which do not normally breed in the litter. Individuals of many arboreal species are knocked off the trees in bad weather and enter the litter. Nymphs often complete their development in the litter and adults then re-enter the trees. This category includes most of the species found in very small numbers, and in late summer species included in category 2 above are also casual in the litter.

The two species of *Lepinotus* and the *Liposcelis* are believed to be primary litter frequenters. *Lepinotus* is normally a stored-products psocid but Guermonprez (in Donisthorpe, 1927) considered that the natural habitat of *L. inquilinus* Heyd. was in 'the nests of ants and other insects'. The primary habitat of *Pteroxanium kelloggi* (Rib.)has not been clearly defined. Pearman (1922) considered that this species feeds on a grey *Pleurococcus* on trees. The few specimens obtained at Silwood were from litter under Cupressus; none were found by beating the trees and it seemed that *P. kelloggi* was confined to the litter in this area. It has been beaten from Box (*Buxus*) in Bucks. (Pearman, 1953) and at Wokingham, Berks., and has been recorded also from other trees and bushes. Adults of this univoltine species were found in July and August. The first nymphs found, in mid-June were already large, and the number of instars is unknown.

Distribution in different types of litter.

Table 18 indicates that many species of psocids are limited to a few kinds of litter at Silwood, and are absent from others which appear to be equally suitable habitats. Psocids included as 'casual litter dwellers' are largely limited to the litter under or near the canopies of the trees they normally frequent, and this is partially true of the 'secondary litter dwellers'. These species normally overwinter as eggs in the litter, and much mixing and redistribution of the litter occurs both during and after leaf-fall. The changing compositions of the litter near a large oak tree and a large pine tree are shown in Table 21. These changes in amount and composition of the litter are largely dependent on climatic conditions, but the figures given are sufficient to show that psocid eggs attached to leaves may come to lie in a litter type different from that of the 'parent' tree. An attempt was made to assess the proportion of leaves on a large oak tree which remained under or near it throughout the winter, by marking large numbers of leaves at different heights with coloured paints. The results were sufficient only to indicate that in calm weather the majority of leaves from lower branches are deposited in the litter under the tree, and that the proportion of leaves from higher up the tree decreases. It is likely that even under calm conditions populations of eggs of psocids from different trees and tree species become mixed. Litter on flat ground tends to form a progressively even cover and to become a mixture of all the different kinds of leaves in the area. The distribution of eggs of foliage frequenting psocids will become increasingly random in the litter. The figures given in Tables 21 and 22 for C. flavidus support this. It will be shown in a later section that the numbers of this species on different tree species become clearly non-random during the arboreal phase, and the distribution of casual re-entrants to the litter is then correspondingly non-random. C. flavidus was virtually absent from pure grass litter and the Juncus litter, neither of which contained many tree leaves but otherwise appeared suitable.

In laboratory experiments newly-hatched nymphs of C. flavidus were placed on Juncus leaves and on constituents of oak litter and their survival on these media was compared. Table 23 shows that there was a high survival rate on dead oak leaves, rather less on dead grass, and heavy mortality on Juncus leaves, live grass, and bare soil. On soil, the nymphs fed at first but did not survive for more than one or two days. None were seen feeding on Juncus or live grass (Holcus), but the leaves appeared dirty and the food suitable. The nymphs seemed unable to reach the food on the surfaces of these leaves, because of the dense coating of short hairs. There appears to be a limitation in the litter distribution of this species linked with the availability of suitable food; it is only able to take food from comparatively 'smooth' surfaces. The same limitation probably applies to some other arboreal psocids.

Young nymphs of E. lucifugus, which has a wider distribution in the litter, are able to feed from hairy and rough surfaces. This species was abundant in loose coniferous litter in which complete leaves predominated to a depth of 15 cm. Vertical cores of this litter of depths 0-5, 5-10, 10-15 cms were extracted in the small funnels for seven days. The numbers of E. lucifugus extracted from ten samples of each stratum (Table 24) showed that it was almost completely confined to the top 5 cm of litter. Strickland (1947) sampled soils separated into 0-3.75 and 3.75-7.5 cm strata. Most of the few psocids he recovered were from the upper layer, and many of the psocids from his 'cacao' plot were in the shallow litter above the soil surface. Belfield (1956) found a similar tendency for psocids to be in the upper layer of soil.

The abundance of E. lucifugus varied greatly in different kinds of litter, but it was never completely absent (Table 25). The factors affecting the distribution of this species are not at present understood.

Temporal separation in litter.

The three dominant species of psocids were clearly separated in time in oak litter, and it is clear that there could not be any competition between them. The numbers of species taken in different months are shown in Table 27 , and show that the greatest diversity occurred at the time of least abundance, towards the end of the summer. The whole of the litter psocid populations are then of casual origin, and because of the extremely low density of these insects, competition is again unlikely to occur.

Habitat alternation and re-entry to the litter.

An attempt was made during 1966 to assess the numbers of psocids dropping into the litter from trees, both as insects and as eggs attached to leaves. Ten polythene covered frames, each 60 x 60 cm were covered with a film of banding gum ('Sticktite' - I.C.I. Plant Protection Ltd.) and placed on the ground beneath or between oak trees. These frames were examined at weekly intervals from June until October, and the numbers of psocids and of fresh leaves on them were recorded. The leaves of the current season were pliable and often partially green; they were easily distinguishable from the brittle brown leaves of previous seasons, which were often blown onto the frames. A few fresh leaves were found on the frames every week; there was a small amount of casual leaf-fall throughout the summer. The numbers of leaves rose drastically in mid-October, and leaf-fall from these trees was almost complete by the end of November. A few eggs of C. flavidus would therefore re-enter the litter during the summer.

The number of psocids recorded on the frames are shown in Table 26 . The majority of these were C. flavidus, but several bark frequenting species were also obtained. Large numbers of foliage frequenting psocids are 'knocked' off trees during bad weather, and will be regarded as 'mortality' when samples from the trees are considered alone, but most of them will complete development in the litter, and the adults re-enter the trees before laying. All the species found on the frames have been reared on damp dead leaves from litter.

The species regarded as secondary litter dwellers show a well-defined 'alternation of habitat', in which generations are passed in the litter and on the trees. A schematic life history of C. flavidus, which exemplifies this phenomenon, is shown in Fig. 9 . A certain amount of casual re-entry is found in both arboreal generations.

Psocids form only a minor constituent of the litter arthropod fauna, but the few species present may be divided into three distinct ecological categories, based on their degree of dependence on the litter as a habitat. The distribution of secondary and casual litter psocids is related to that of their other habitats - that is, of the trees they frequent at other times of the year. The distribution of the only abundant primary litter-dwelling psocid at Silwood, E. lucifugus, was broader but still tended to be non-random in different sorts of litter.

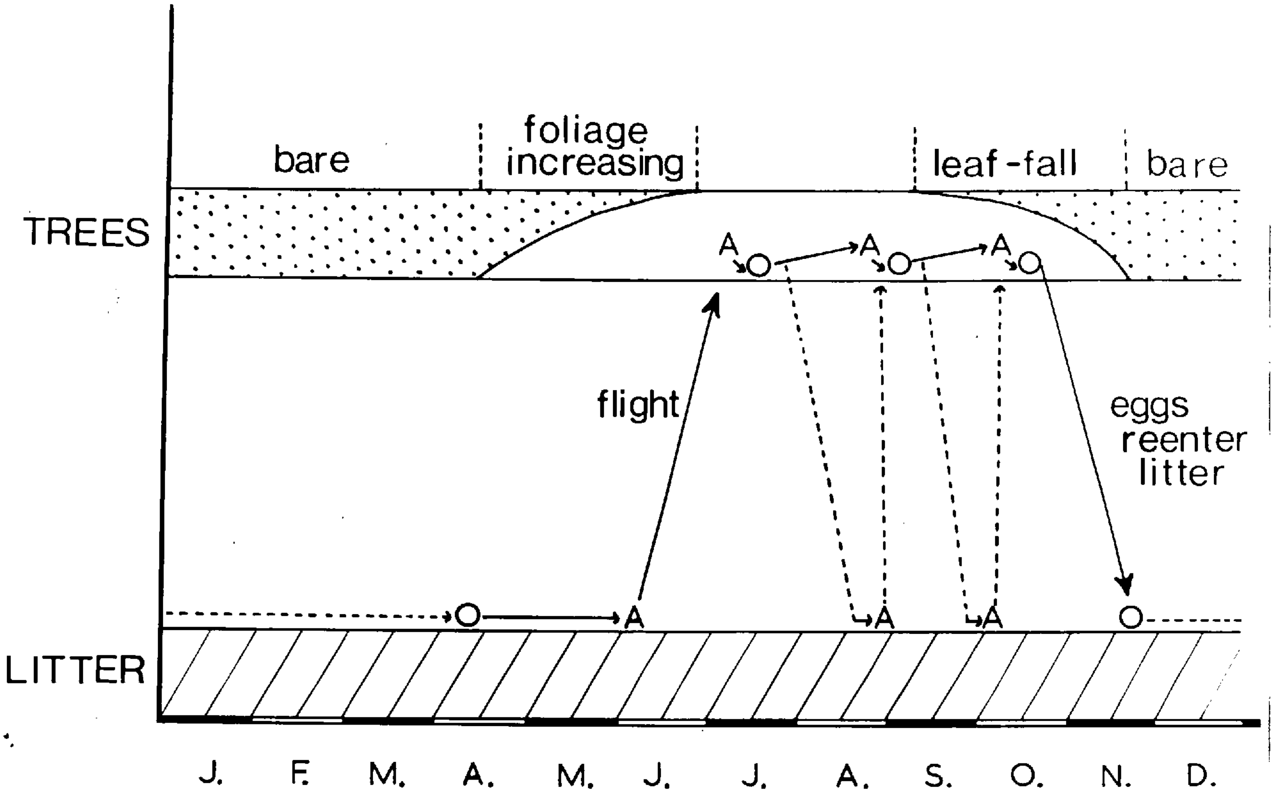


Fig.9.

Schematic life history of Caecilius flavidus to show alternation of habitats. (O, Ova A, Adults J-D, January-December)

SECTION 4. Psocoptera on arboreal foliage.

Introduction.

Many psocid species are totally arboreal and others are also largely confined to trees. Although Psocoptera often occur on trees in considerable numbers, they are frequently omitted from accounts of arboreal insects, or receive only a token mention. The papers considering these insects range from discussions of collections of all psocid species from the available tree species (Broadhead, 1958; Hartmann, 1951; Holzapfel, 1936; Vishniakova, 1959) or of psocid species from one particular tree (Broadhead, 1958; Broadhead and Thornton, 1955; Broadhead and Wapshere, 1966a), to intensive studies of one or two species on one tree species (Broadhead and Wapshere, 1966b). The numbers of particular psocid species on different trees are recorded in most of these accounts and may differ considerably between the trees. There is thus some casual evidence of 'host'-tree preference in at least some psocid species.

The present sampling programme was undertaken to see the extent to which psocids were randomly distributed on different tree species, and to attempt to find whether any apparently non-random distributions were real or accidental phenomena. About 15 species of trees were sampled weekly from April to November in 1966 and 1967 at Silwood Park, and trees in other parts of Berkshire were examined at infrequent intervals. All psocids found were identified later and these data are discussed below, together with those from the literature. As different tree species in different regions vary considerably in many characters, it is perhaps unlikely that the same trends in psocid distribution will be evident in different areas. The data below reflect the distributional trends of psocids at one place over two seasons. The causative factors of an apparent host-tree specificity are likely to be of general occurrence, but their relative effects may vary from region to region.

Sampling Methods.

Numerous authors have given brief notes on methods of sampling populations of arboreal insects and many of these are reviewed by Southwood (I966). Tree vegetation is a difficult habitat from which to take accurate and replicable samples of insects, and arboreal foliage is particularly difficult. Previous comparative accounts of arboreal psocids have been based on samples taken by beating or by direct examination of standard lengths of branch. Broadhead (I958), Broadhead and Thornton (I955), and Broadhead and Wapshere (I966a,b) all adopted a sample unit for beating based on a length of branch sufficient to cover a standard beating tray. Such a sample provided a replicable unit of habitat for bark-frequenting psocids. The main variations in total bark area are caused by relatively few factors, such as branch diameter and the numbers of side branches. On the same species of tree this type of sample can be standardised within narrow limits. The unit can also be used to compare the numbers of species on different tree species, but difficulties arise when accurate measurements of the density, that is the number per unit area of substrate, of a psocid species on different trees are required. This difficulty is much greater in foliage-frequenting psocids as the foliage density, i.e. the number of leaves per unit volume, varies greatly between different tree species and also from one tree to another of the same species. Aspect of tree, distance from other trees and height from ground are among the many factors which affect foliage density and the amount (total area) of foliage is affected by other, more variable factors such as infestation by foliage-eating animals. For example, tortricid larvae often cause severe defoliation on oak.

Any comparison between densities of foliage-frequenting psocids on different tree species must be based on an estimate of psocid numbers per known area of leaf surface. It is impracticable to enclose a large number of samples in which to count all the psocids and leaves, and some approximation is inevitable in a rapid sampling technique. Henson (1954), amongst others, suggested the use of immobile stages of foliage insects when sampling; this method has advantages over assessment of large numbers of small highly active isects if immobile stages are conspicuous. This method (i.e. counting the numbers of egg batches on known numbers of leaves) is very time-consuming, but was used periodically to check the trends that emerged from regular sampling by beating. Both the egg batch counts and beating gave absolute numbers.

Beating was adopted as the usual sampling method for foliage psocids, and a terminal branch of length Im together with all accompanying side branches and foliage was used as the basic sampling unit. A IxIm beating tray was held horizontally under the selected branch, which was then struck sharply with a stick ten times. Psocids on the tray were sucked into tubes. Trials were made with a black tray, but a white tray proved more suitable for most species of psocids. The young nymphs of some psocids are pale and translucent and these stages may have been slightly undersampled. Five minutes was spent searching for psocids on the tray after each sampling, and it is believed that the number of nymphs overlooked was small. This undersampling should be a fairly constant factor, and is assumed not to have affected estimations of the denser appearance to the foliage. Betula and Crataegus both have smaller leaves, but the foliage of Crataegus appears superficially to be much the denser.

It is impossible to standardise a unit area of foliage for beating samples, and it is evident that a number of units of the above trees will differ between tree species in August. The foliage density of other trees sampled, especially conifers, may be very different from those considered above. At Silwood Park the psocid fauna on foliage of conifers and on broadleaved trees are separate and distinctive and no attempt has therefore been made to assess the foliage area of conifers. It is believed that the differences in foliage area between samples from different trees are not large enough to obscure the major differences in psocid numbers or their distribution. The standard length of branch, on which this sample unit is based, provides a basis for replicable, if not identical samples. Until further accurate work on the estimation of foliage density of different plants is done, on the lines recently suggested by Philip (1965a, b, 1966) and Warren-Wilson (1965), it is considered to be the most suitable type of sample for work on foliage insects which are too mobile to enable one to search directly.

Each 'sample' in the following account refers to two of the above-defined sample units taken from one tree on the same occasion. Each sample on a particular date was from a different tree, and no tree was sampled on two consecutive sampling dates. It was hoped to take samples from the different trees at weekly intervals from April to November, but beating is a satisfactory sampling method only in calm weather and when the foliage is dry. Thus minor irregularities in sampling dates were unavoidable. All samples were taken between 10.00 and 16.00 B.S.T.. The numbers of samples from different tree species varied considerably and were approximately proportional to the relative abundance of these trees at Silwood. This difference in numbers of samples partially avoided oversampling the psocids on the less common trees. There is little advantage in having equal numbers of samples from each tree species, provided that sufficient samples were taken from each to be representative of the tree species rather than of an individual tree. All trees sampled were in a comparatively small area of about 400 x 250m .

The Numbers of Psocids on different Trees at different times of the year.

The total numbers of psocids collected from different tree species at Silwood Park from April to October in 1966 and 1967 are shown in Table 30 , and the average numbers per sample are given in Table 31 . The numbers of different species of psocids on different trees in the two seasons are given in Table 32 . It is clear that some species were much more abundant or widely distributed than others. Comparison of large numbers of separate samples from the same tree species at any time indicated that the differences in numbers of a psocid on trees of the same species were often small compared with those on different tree species. The distribution of the foliage species on a tree species with healthy foliage was fairly uniform from tree to tree.

Three species, E. briggsi, C. flavidus and E. hyalinus, were taken on all the tree species examined. Conversely several species of psocids, notably S. stigmaticus, C. burmeisteri and C. cyanops, were found in large numbers only on one or two species. Thus, over a whole season several psocid species showed a strongly non-random distribution between tree species. There is a clear distinction between species prevalent on conifers and species prevalent on broadleaved trees and bushes, and in the latter group *Quercus* and *Crataegus*, especially, had psocid species which appeared to be associated with them. The total numbers of psocids were far greater in 1967 than in 1966, but the same trends in distribution were evident in both years. These trends become more apparent when only the foliage-frequenting psocids are considered (Table 33), and it seems that the bark-frequenting psocids are more uniformly distributed between different broadleaved trees.

Only a few psocids were found in the early part of the year, and these were mainly overwintering adults and nymphs of *G. cruciatus*, *E. briggsi* and *E. hyalinus*. Table 34 shows that the total numbers of psocids increased gradually to a maximum in September and October. This was general on most of the tree species examined, but the magnitude of increase varied considerably between different trees. Figures 10 - 14 show the total numbers of psocids taken on selected tree species. Several trees, notably *Acer*, *Aesculus*, *Betula*, *Populus*, *Tilia* and *Ulmus* had very few psocids at any time of the year: whereas the numbers of psocids on all the deciduous tree species were small in April and May, they did not increase significantly on the above trees.

Fig. 13 shows the numbers of psocids taken from a group of *Crataegus*. In both years there was a large peak in numbers early in the summer, mainly of young nymphs of the univoltine *Mesopsocus* species. Several species contributed to a larger peak in late summer, but the most abundant constituent was *S. stigmaticus* which, at Silwood, is confined to *Crataegus*. The numbers of this species build up from July onwards and are at a maximum in mid September. Flushing of these trees occurred mainly during the hatching period of the bark-frequenting *Mesopsocus* and autumnal leaf-fall was complete by early November.

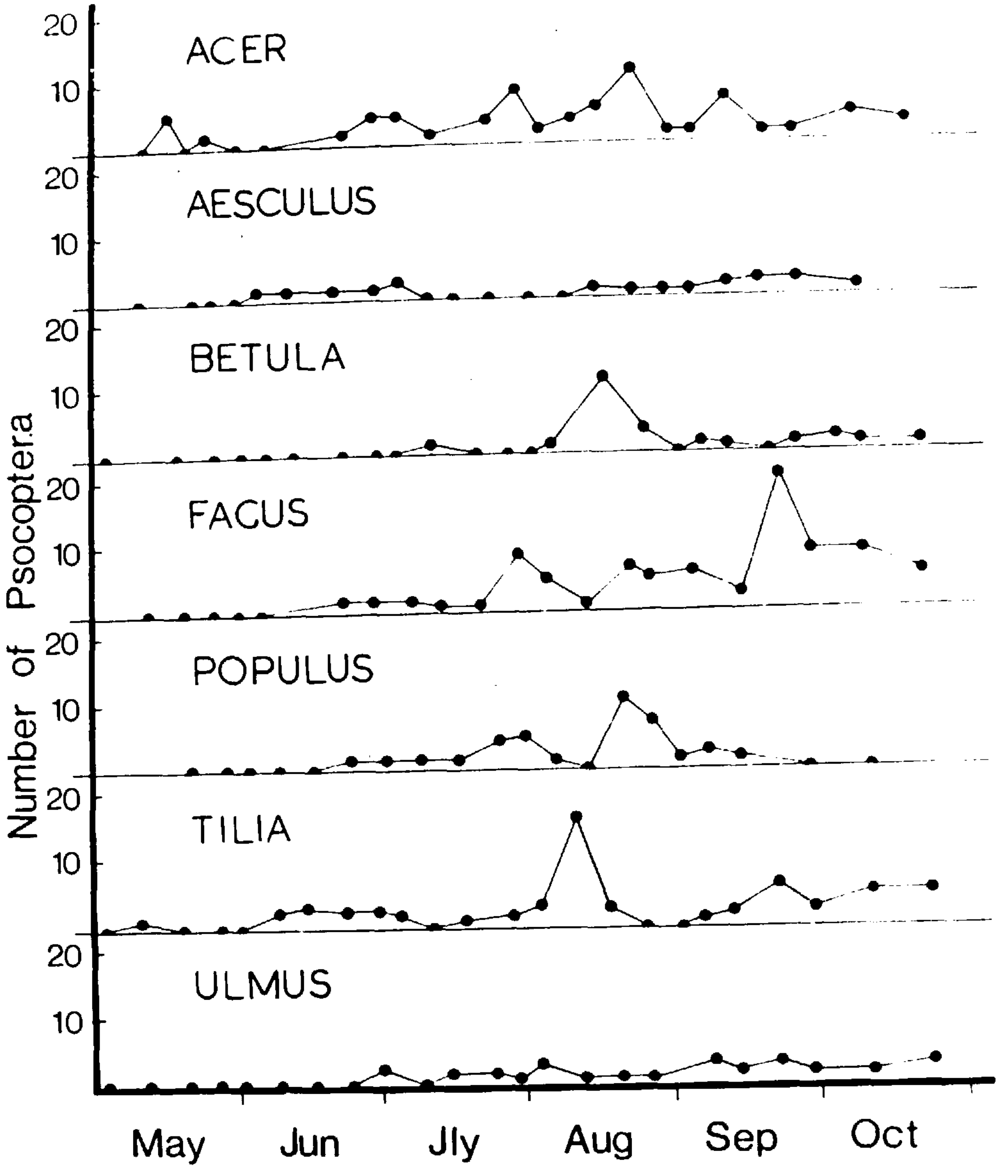


Fig.IO.

Total numbers of Psocoptera (nymphs and adults) in samples from different trees at Silwood Park in I966.

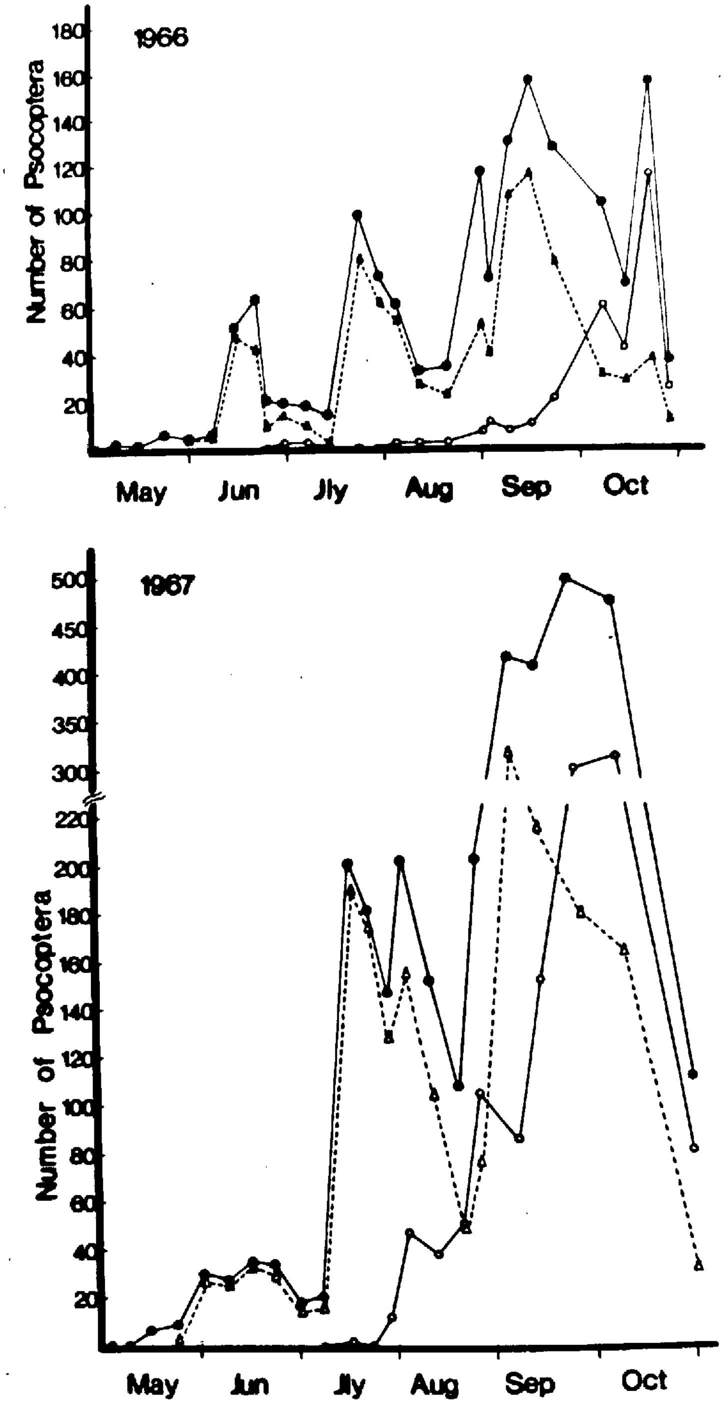


Fig.II.

Total numbers of Psocoptera (nymphs and adults) in samples from large oak trees at Silwood Park in 1966 and 1967.

●-● Total O-O E.briggsi Δ-Δ C.flavidus.

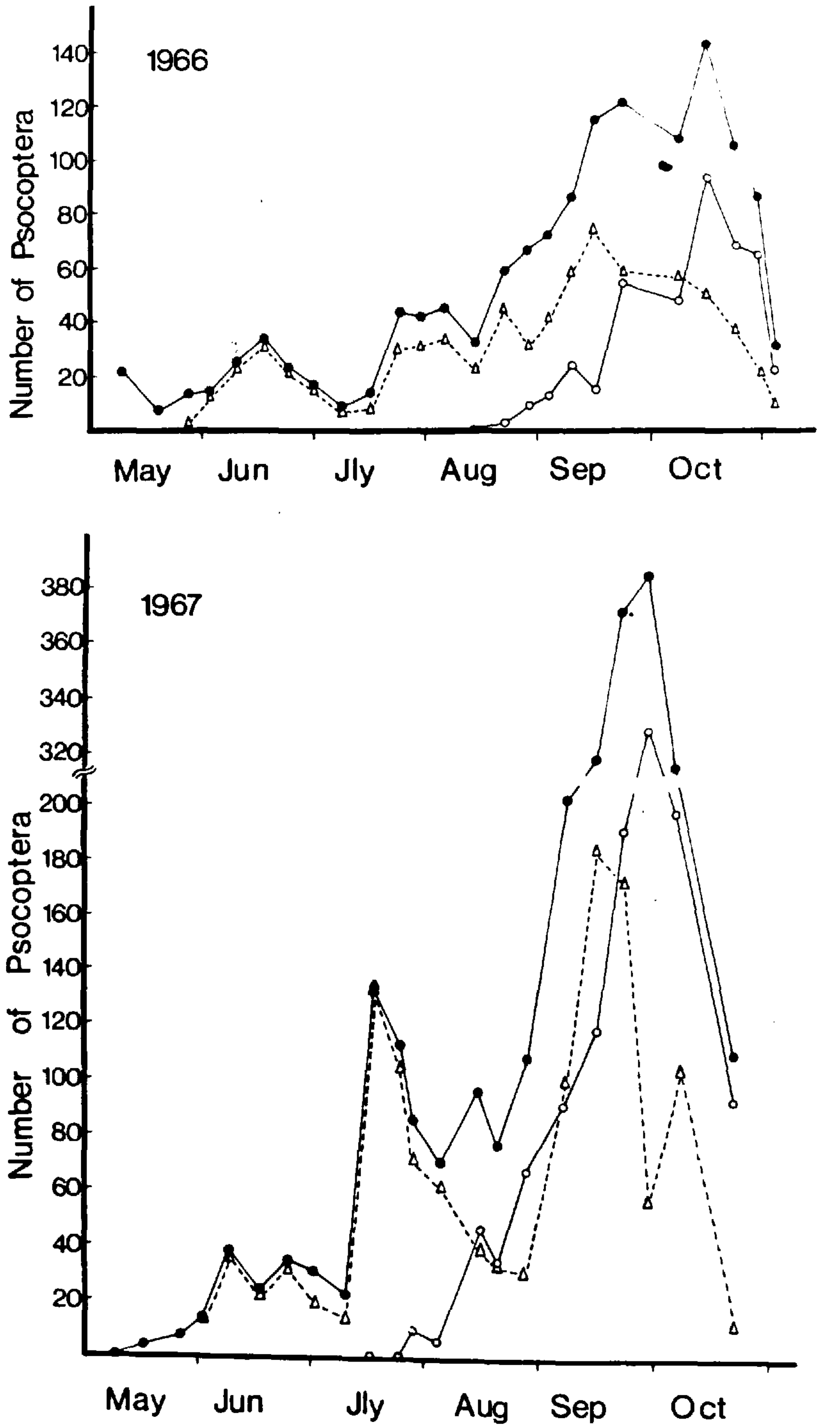


Fig.I2.

Total numbers of Psocoptera (nymphs and adults) in samples from small (to 4 m) oak trees at Silwood Park in 1966 and 1967.

●-● Total O-O *E.briggsi* Δ-▲ *C.flavidus.*

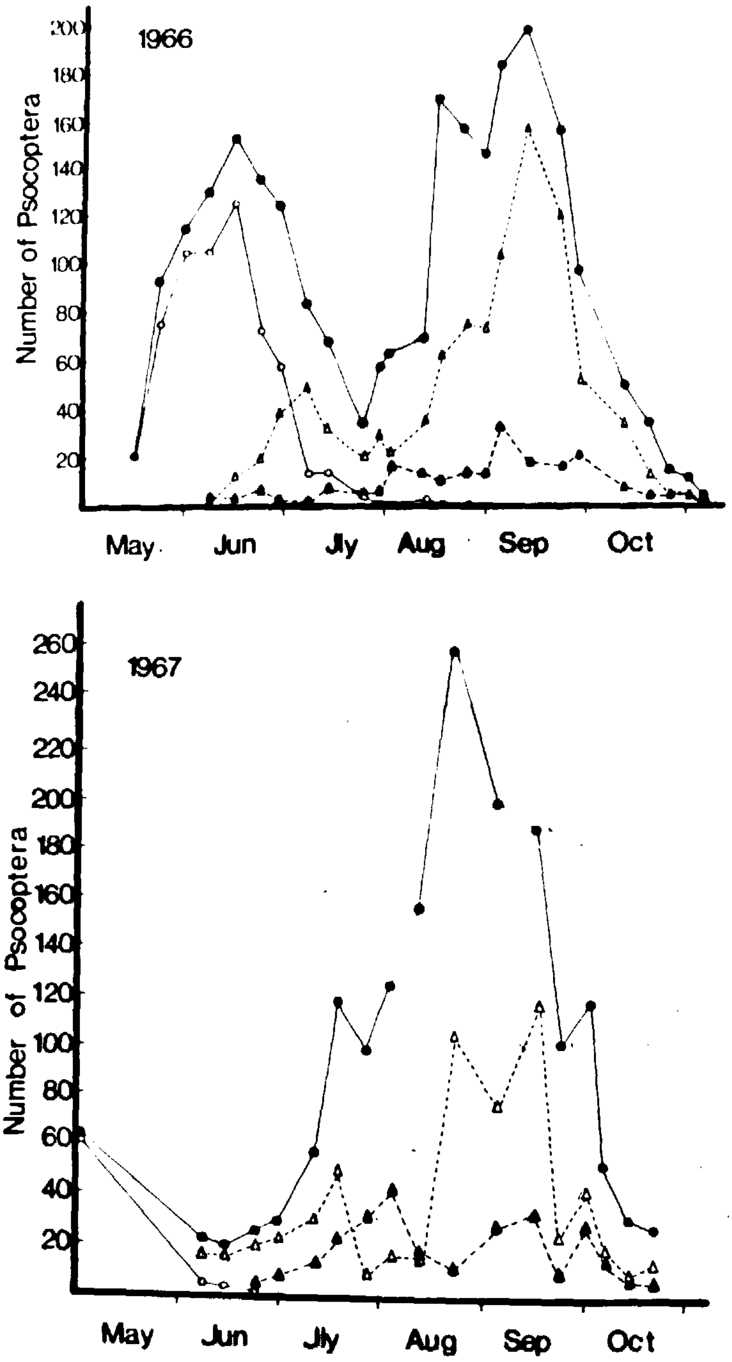


Fig.I3.
Total numbers of Psocoptera (nymphs and adults) in samples from Crataegus at Silwood Park in I966 and I967.

●-● Total O-O Mesopsocus ▲-▲ C.flavidus △-△ S.stigmaticus.

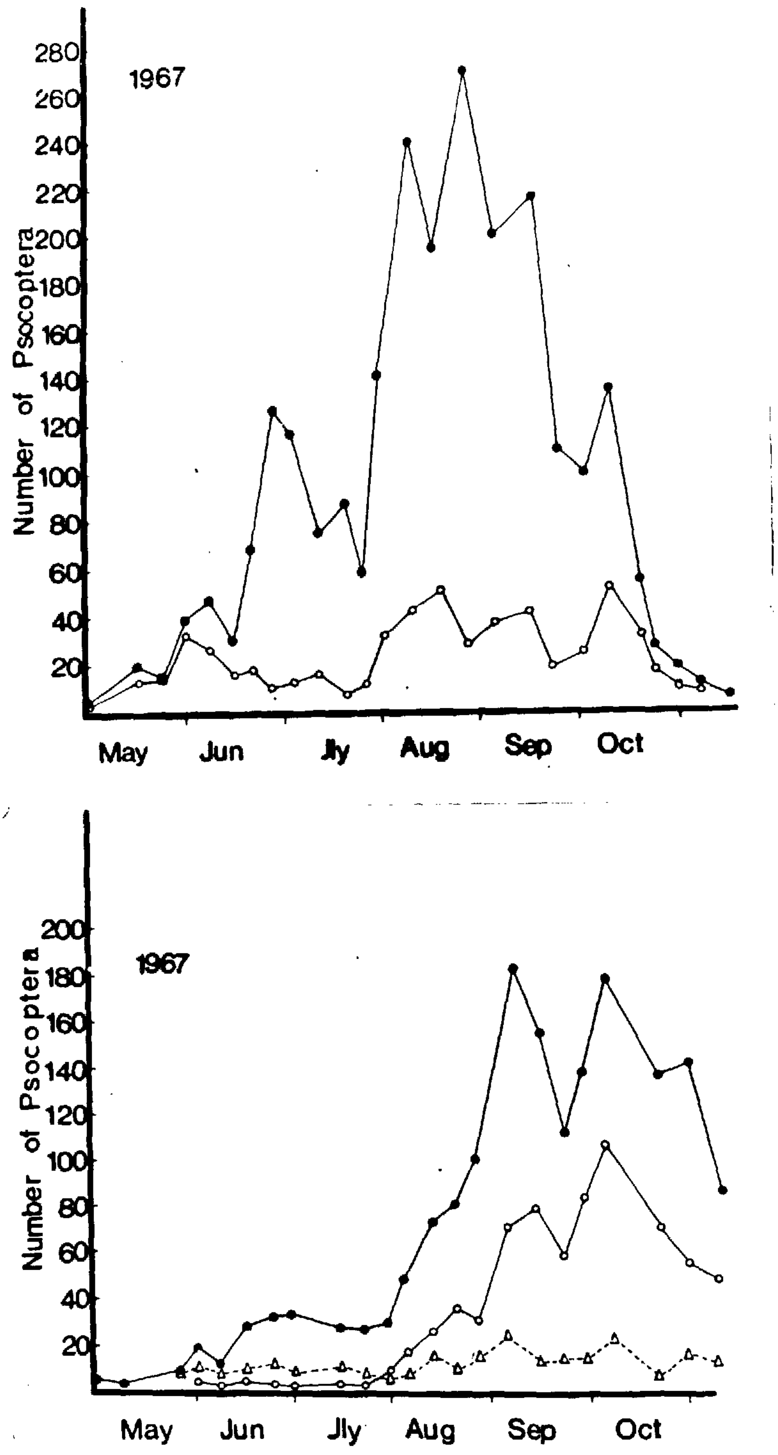


Fig.I4.

Total numbers of Psocoptera(nymphs and adults) in samples from *Cupressus* (I) and *Ilex* (2) at Silwood Park in I967:

●-● Total *Cupressus*: O-O *C.burmeisteri*

Ilex: O-O *C.flavidus* Δ-Δ *G.cruciatus*.

The numbers of psocids on small and large oak trees are shown in Figs. 11 and 12. These numbers were very low until the end of May, when adults of *C. flavidus* invaded from the litter. There was then a progressive increase in numbers throughout the two arboreal generations of this species, which formed the major part of psocid populations on *Quercus* until late August. Large numbers of *E. briggsi* flew up from the litter and further increased the numbers, and in September and October virtually the whole of the psocid fauna on oak consisted of these two species. *E. briggsi* persisted later into the autumn and gradually replaced *C. flavidus* as the numerically dominant species. On oak most of the buds open before *C. flavidus* reaches the trees from the litter, but most of the autumnal leaf-fall did not occur until mid November. The leaves remained on some trees throughout the winter.

In contrast to the two deciduous species, Fig.14.2 shows the numbers of psocids taken from a broadleaved evergreen, *Ilex* in 1967. Small numbers of psocids overwintered on the foliage of this tree, but the overall trends closely resembled those on *Crataegus* and *Quercus*. More psocids were present early in the season on *Ilex* than on *Quercus*, as the eggs of some foliage-frequenting psocids hatch on the trees. Recruitment from the litter occurred in May and June and the increase in total psocid numbers throughout the summer resulted almost entirely from the increase in numbers of the foliage-frequenting species.

The numbers of the most abundant foliage psocid on conifers at Silwood, *C. burmeisteri*, also increased throughout the season, but there is no well-defined phase in the litter in this species. All large increases of numbers on broadleaved trees were due to foliage-frequenting psocids. It is implied that the foliage of some species of trees provides more suitable habitats in which some species of psocids increase in numbers to a greater extent. All the trends outlined above were evident in two consecutive seasons at Silwood, and bulk sampling of psocids from Crataegus and Quercus in Windsor Great Park gave similar results (Table 35).

Most ofthe bark-frequenting psocid species are not found for the whole season, but E. hyalinus was present on most tree species for much of the year. Table 36 shows the distribution of E. hyalinus on tree species in May and October. There was no striking difference in distribution in these two periods. Similar calculations for C. flavidus are given in Table 37. This species was found in small numbers on most broadleaved trees early in the summer, at the time of its movement from the litter there is little or no selection of tree species by the adults of this species. However, in September C. flavidus showed a markedly non-random distribution. It was largely confined to oak, but small numbers were also found on most other trees.

E. briggsi bred in large numbers on oak and only a few adults were found on other trees such as Betula and Populus.

Thus, increase in numbers of some foliage-frequenting psocids coincided with an increase in apparent specificity of habitat. The number of psocid species on a particular tree was generally greatest in mid-summer, and only a few species were found at the time of the greatest total numbers.

The relative abundance of C. flavidus on different tree species was not related to the distribution of the trees. Large beech and oak trees grow closely together, sometimes with their foliage touching, in one area of Silwood. There were distinctly fewer C. flavidus on beech than on oak, despite the fact that they formed a continuous habitat.

Similarly, oak and birch grow close together in this area, but the psocid faunas on these trees were different. Hawthorn growing as an understorey to oak in Windsor Great Park had a distinctly different psocid complement to it. In this area S. stigmaticus was the dominant foliage species on hawthorn but was absent from oak, on which C. flavidus was abundant. A mixed series of trees that touched consecutively were sampled in July 1967 and the psocids found are shown in Table 38. C. cyanops was confined to Pinus and several other psocid species were found only on the other, broadleaved, tree species. There is a marked difference in the fauna of coniferous and broadleaved trees in the Psocoptera, as in many groups of strictly phytophagous insects. In this particular instance the different psocid species were at different stages of their life histories, and it may be unwise to say more after a single sampling occasion. These results were borne out by a complete season's sampling from other trees of these species. Broadhead and Thornton (1955) drew attention to the error of comparing numbers of different species of psocids on a particular tree when only a single sampling occasion was used, but the population densities of one psocid species on different trees can be compared on a single sampling date.

The effect of tree size on psocid numbers.

The numbers of psocids taken from small (to 4m) oak trees and large old trees did not differ greatly at any time of the summer (Figs. 11- 12). Holzapfel (1936) found more psocids on large trees than on small ones. The environments provided by both sizes of trees for foliage psocids are similar, and although the larger trees can support more psocids, their densities did not differ markedly on oaks of the two sizes. Regular samples were also taken from a number of seedling oaks (up to 1.5m high) which were abundant in the same areas as the larger trees. No foliage-frequenting psocids were found on these young trees, although conditions appeared to be suitable for them. The flight of the first generation of C. flavidus would take them away from these seedlings, but it is likely that there would be some casual colonisation later in the season. It appeared that these trees did not project sufficiently above the surrounding herbage.

Distribution on single trees.

Four isolated large Quercus trees were selected in 1966 on which to assess the distribution of C. flavidus at different times of the summer. Numbers of egg batches were selected as a suitable index of distribution, in preference to sampling small mobile insects high above the ground. Twenty samples of a hundred leaves were taken at three heights (0-3m, 5-7m, 12-15m) in June, August and October. These samples were taken from all aspects and were interspersed between the four trees. The numbers of egg batches on these leaves are shown in Table 39.

Table 40 shows the numbers of C. flavidus egg batches taken from a small evenly formed oak tree growing out of contact with nearby trees in October 1967. All leaves were removed from this tree and examined.

The distribution of egg batches is assumed to reflect the distribution of adults. The samples from the large trees were similar on the different trees at the same time, but showed clear differences on the three sampling occasions. In June, most of the egg batches were found in the lower parts of the trees, i.e. in the region which adults flying from the litter will reach first. Later samples show a progressively more even distribution of eggs throughout the trees and in October the distribution becomes uniform. This was also evident on the small tree. There were no consistent differences in the densities of egg batches on different aspects of the trees or at different distances from the bole. A number of egg batches of E. briggsi were also found in the October samples. The density of these did not differ greatly on different parts of the trees.

It appears that adults of C. flavidus entering trees from the litter remain in the region of their landing site, and that later trivial movement of nymphs and adults results in a more even distribution.

The sampling programme outlined above has shown that some tree species were frequented by more psocids than others and that increases in numbers of some foliage-frequenting psocids occurred only on some tree species throughout a season. It is evident that host-tree specificity becomes progressively clearer during a season, and it was also implied that there was little or no selection of tree species by psocids flying up from the litter. These differences in numbers towards the end of the season may be caused by any, or a combination, of many factors which affect both the physical and biotic environments.

Several authors have noted that the numbers of psocids on different broadleaved trees varied, but there have been no attempts to investigate the possible causes of these differences. None of these authors have taken account of the relative changes in numbers of psocids on different trees after their establishment, although different trees were sampled over an extended period. Holzapfel's (1936) results in some ways resemble those obtained at Silwood. He found C. flavidus on a wide variety of trees, but it was most abundant on Quercus. Badonnel (1943) considered this species to be especially common on oak, but Hartmann (1951) found greater numbers on larch. The numbers of samples taken are not given in the above accounts; there appears to be a markedly non-random distribution in some cases, but this cannot be confirmed without fuller data. Although such species as S. stigmaticus are often largely confined to one or two tree species, the trees are different in different accounts. It appears that host-tree specificity in a given area to a large extent depends on characters of the different trees in that area. For this reason the results obtained at Silwood will not be of general application unless the underlying mechanisms affecting the relative numbers of the same psocid species on different tree species can be clarified. Some of the factors which appear to be important in the development of this habitat specificity will be discussed in the remaining sections of this thesis.

SECTION 5. The Dispersal of Psocoptera.

Dispersal of psocid eggs.

Eggs of arboreal psocids are firmly cemented to the substrate, and any dispersal results from redistribution of the substrate and only rarely from detachment of the eggs from leaves or bark. As was shown in Section 3, some casual leaf fall occurs from Quercus throughout the summer. This process is probably widespread in deciduous trees, and small numbers of eggs of the foliage-frequenting psocids will be removed from the trees on which they were laid. More pronounced passive dispersal of eggs of these species occurs at autumnal leaf fall, involving whole populations of some psocid species on deciduous trees. Subsequent mixing and redistribution of the litter leads to further dispersal of the overwintering eggs. Passive dispersal of eggs laid on bark is negligible.

Dispersal of nymphs of foliage-frequenting psocids.

There are no large scale dispersive movements in nymphs of the foliage-frequenting psocids which have been examined. However, much trivial movement occurs and results in redistribution of the insects in and around the original habitat. Some of this trivial movement is of regular occurrence in response to particular stimuli, and primary or secondary aggregations of nymphs are found in some species.

The young nymphs of several species are positively phototactic, and tend to remain on the upper surfaces of leaves, where food is also most abundant. When these nymphs are disturbed by contact they immediately run to the underside of the leaf and remain stationary. An apparent chain reaction may ensue when one of a number of psocids on a leaf is touched, and all the insects move to the lower surface. This mechanism of 'evasive dispersal' may be similar to the 'spacing-out behaviour' exhibited by certain aphids, such as Drepanosiphum platanoides (Schrank) (Kennedy and Crawley ,1967); in both cases a disturbance at one point is propagated throughout the whole group of insects on the leaf, and results in their redistribution. Movement onto the lower leaf surface occurs also when the leaf is agitated, by raindrops for example. The psocids were only rarely seen to run off the leaves onto bark when touched, but much redistribution by this route occurs at other times.

Unlike Drepanosiphum the psocids are not, in this case, gregarious. They do not appear to show any intraspecific attraction between individuals, a factor which Badonnel (1951) stated was strongly evident in nymphs of Neopsocopsis pyrenaicus (Bad.) and Psococerastis gibbosus (Sulz.) and which Broadhead (1958) indicated in nymphs of Elipsocus mclachlani Kimmins.

After hatching the young nymphs of some species tend to remain in a primary aggregation near the original egg batch. Two of these species, S. stigmaticus and G. cruciatus, often form a nymphal feeding web, under which most of the early life is passed. Nymphs of several genera of psocids such as Reuterella, regularly remain under feeding webs spun by the adults. The nymphs of some species of Ectopsocus are sometimes found in small groups under loose webs (Mockford, 1957), but no nymphs of E. briggsi were found under webs at Silwood. Several small groups without webs were found. Nymphs of G. cruciatus and S. stigmaticus only rarely regroup when they are artificially dispersed from their primary aggregation.

Several small oak trees were ringed with banding gum during May and June in 1966 and 1967. No nymphs of C. flavidus were found on this gum and the first psocids beaten from these trees in June were adults. It is thus clear that nymphs do not ascend the trees. Two experiments were undertaken in an attempt to detect any large scale dispersal movements of *C. flavidus* in the litter in spring. These utilised a grid of gum-covered canes and a series of concentric roped circles around a central release point. The few specimens recovered indicated that some of the larger nymphs moved up to 4m in 24 hours. These experiments were conducted on ground at the edge of the canopy of a large oak tree. There was no preferential movement towards or away from the tree.

Dispersal of adults.

There are very few records of psocid flight in the literature. Imms (1957) commented that most winged forms are ' curiously reluctant to take flight', and other authors such as Badonnal (1934) have also implied that it is rare to find a psocid in flight. Winged psocids, as many other small insects, are likely to become incorporated in the ' aerial plankton' either during active flight or after being blown off vegetation. Lewis and Taylor (1965) commented that at times psocids ' fly in considerable numbers and drift through the air like winged aphids.' Freeman (1945) trapped at heights of 10-277 feet (3.3-84.43m) over Lincolnshire by using nets attached to wireless masts. He obtained 2355 psocids, and calculated that this group constituted 10.2 per cent of the aerial fauna. Glick (1939) trapped a few psocids when sampling the aerial fauna over Louisiana from a plane, and Thornton (1964) recorded various Psocoptera trapped on ships and planes in various parts of the Pacific. Hardy and Milne (1938) also recorded a psocid at a height of 850 feet (259.1m) over the North Sea.

In some instances the trapped Psocoptera have not been fully identified, but in several cases most of the psocids caught have been of a single species, *Lachesilla pedicularia* (L.). This species comprised 98.5 per cent of Freeman's catch and was recorded also by Glick and by Hardy and Milne. Pearman (1928) considered that post emergence migratory flight occurred in some psocid species, and swarms of L. pedicularia have been observed in Belgium (Lestage, 1935) and in Britain (McLachlan, 1900; Scott, 1916; Burton, 1950). These flights were all in late summer, as was the catch of 437 L. pedicularia in a suction trap at Rothamsted obtained by Lewis and Taylor (1965). McLachlan commented that this species was the only psocid voluntarily on the wing, and that it was seen on calm hot autumn days. Although L. pedicularia has been the subject of most of the notes on psocid flight, various other species have also been recorded. Britten (1916) recorded five species which he saw flying in the early mornings and Lewis and Taylor (1965) recorded numbers of E. briggsi, S. immaculatus and T. dalii. All of these were found in late summer and were captured mainly in the day time. Small numbers of Elipsocus species were taken on sticky traps situated near larch trees by Broadhead and Thornton (1955), and these authors considered the three species of this genus to be reluctant fliers. A few unidentified psocids were taken in a light trap by Williams (1939).

These records indicate that more psocids fly in late summer than at other times of the year, and imply that only a few species are active fliers. Johnson (1950) compared the efficiency of various trapping methods for Psocoptera, and obtained higher densities of L. pedicularia on sticky traps than in suction traps.

The present work is an attempt to assess the importance of aerial dispersal in psocid biology. Aerial Psocoptera were sampled by suction traps at Silwood Park over seven seasons, and analysis of the data so obtained forms the basis of this account. Other techniques were used for one or two seasons and will be described later.

Trapping Methods.

a. Suction Traps. Two 18 inch (45 cm) diameter Propellor type suction traps were operated from the beginning of May to the end of September for the seasons 1961-1967 inclusive. The traps remained in the same sites for the seven years, and were operated in a treeless area surrounded by grassland and arable land. One trap was operated at a height of 1.3m above the ground and the other at 9.2m above the ground. The catches were segregated daily, except at weekends, and preserved in alcohol.

b. Sticky Traps. Sticky traps were used during 1966 to capture psocids in the air under the canopies of trees and in the open spaces between close groups of trees. Wooden boards, size 30 x 10 cm were nailed to wooden stakes at heights of 30 cm or 120 cm from the ground. One side of each board was covered with polythene sheeting, which was coated with a layer of banding grease ('Stictite' - I.C.I. Plant Protection Ltd.). Eight boards were attached to each stake and 18 similar stakes were interposed between small oak trees, among hawthorn trees, and in the open spaces between large oak trees. On three large oak trees boards were also attached to ropes on pulleys, and psocids flying under the canopies of these trees were sampled at vertical intervals of 1.3 m to a height of 7.8 m. Both sets of sticky traps were inspected weekly from April to November, 1966. They were left in position throughout 1967, but were examined only infrequently.

c. Water Traps. Three sets of water traps were used in 1966. These consisted of trays (48.5 x 34.0 x 2.0 cm) supported 75cm above the ground. Four trays, painted black, white, green and yellow, were used in each set, and were emptied weekly from April to November. The three sets of trays were in an area of broom, in open grassland and near a large oak tree.

d. Light Traps. Three mercury vapour light traps were operating in or near Silwood Park in 1966. Two of these were near the oak trees around which sticky traps and water traps were sited. They were operated from dusk to dawn and emptied daily from April to November.

The numbers and species of Psocoptera trapped.

All psocids caught were identified to species, and when possible they were also sexed. By far the greatest numbers of psocids were obtained in the suction traps, and this material will be considered first. The small numbers of psocids caught in the other traps are discussed separately later.

Psocoptera in Suction Traps. A total of 1998 psocids was identified in the two traps over the seven seasons. Many of the specimens sorted from the total catches were incomplete. Odd wings and other fragments in each sample were summed and the minimum numbers of individuals which could be present are included in the totals which are given in Tables 41 and 42 . Twenty species of Psocoptera were found in the suction traps, but only five of these were numerous; most of the others were represented by a few individuals only. The numbers of different species obtained in each year are shown in Table 43. It is evident that some species were present every year in greater numbers while those of others fluctuated considerably. The most abundant species, L. pedicularia, comprised from 15 per cent to more than 90 per cent of the catches by different traps in different years. Elipsocus hyalinus was caught in both traps in each season. C. flavidus and Amphigerontia contaminata (Stephens) were also regularly present, but in smaller numbers. E. briggsi was extremely variable in its incidence in the traps; in some years only low numbers were found, but it was common in other seasons. No other species formed significant fractions of the catches, but several of them were present in small numbers in several seasons.

The temporal variations in the catch sizes are shown in Figs. 15 and 16, in which the occurrence of the five most abundant species is also indicated. Although the numbers of psocids caught varied in different seasons, several clear trends emerge from the figures. The numbers of psocids caught were much greater in August and September than in the early part of the year, and it is implied that more psocids fly during the late summer. Adult psocids are generally most abundant at this time of the year.

The greatest numbers of *C. flavidus* occurred in the early part of the year. The adults of the first generation move up from the litter onto the trees in late May and June, and most of the trap catches of this species coincided with this period of movement. *Elipsocus hyalinus* made up the greater part of the catches at the beginning of the season, and was found in varying numbers in August and September. At Silwoood Park, as at Harrogate, Yorkshire, (Broadhead and Wapshere, 1966a) a proportion of this species overwinters in the adult stage. The peak of numbers early in the season corresponds with the period of movement from overwintering sites, and those caught in the late summer may have been moving to overwintering sites. A distinct peak in numbers of *E. briggsi* is discernible in August. This species resembles *C. flavidus* in that the adults move from the ground litter onto trees: most of this movement occurs in August. Many adults of *E. briggsi* overwinter and the specimens caught later in September may be moving to overwintering sites (but see Section 2). Aerial samples of *L. pedicularia* also showed a peak in autumn, when many individuals have just become adult.

Thus, distinct peaks in numbers in the trap catches of all the

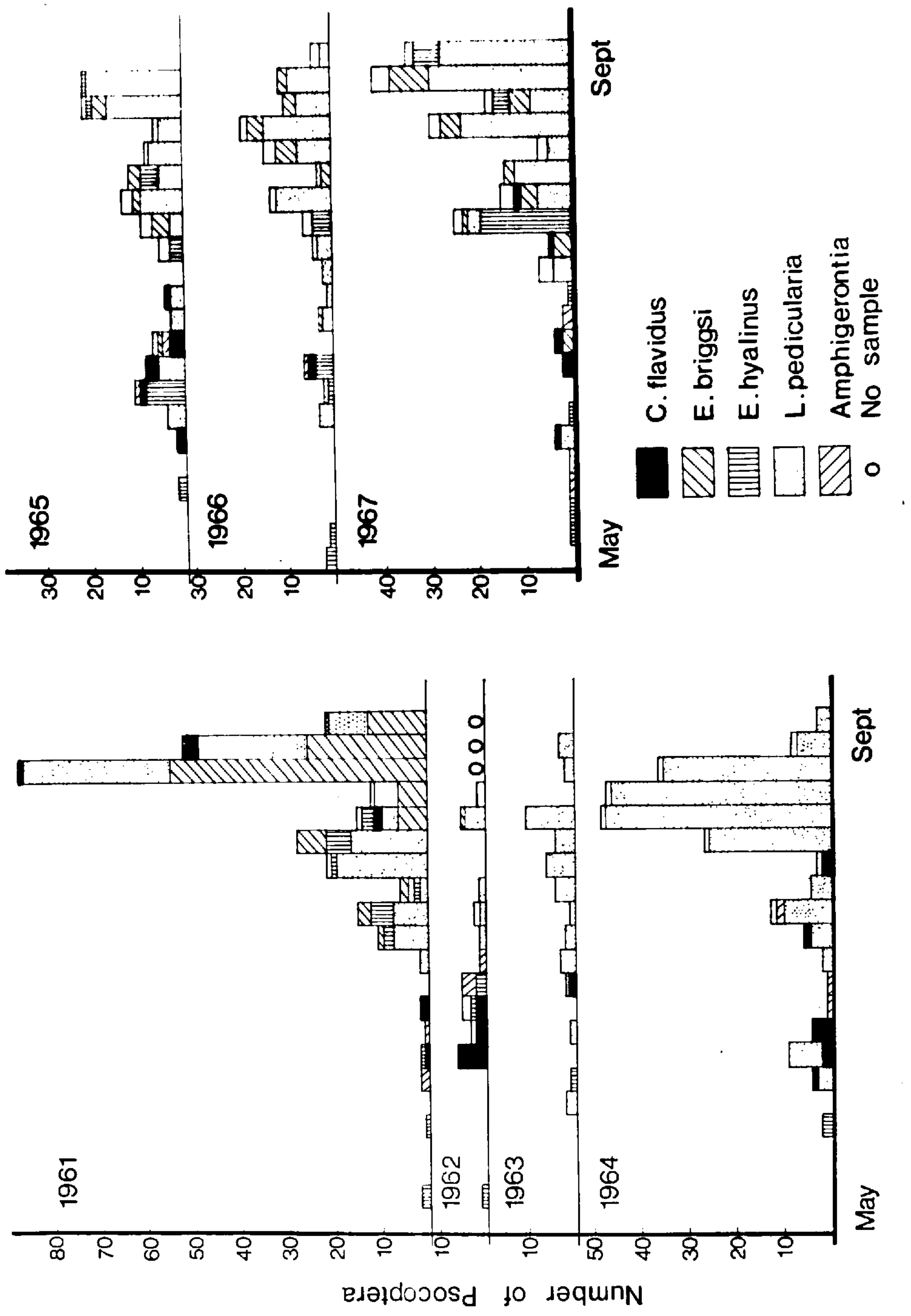


Fig.I5.

Numbers of Psocoptera taken in a 45 cm diameter suction trap operated at a height of I.3 m above the ground at Silwood Park in seven seasons. (Weekly groupings from May to September inclusive)

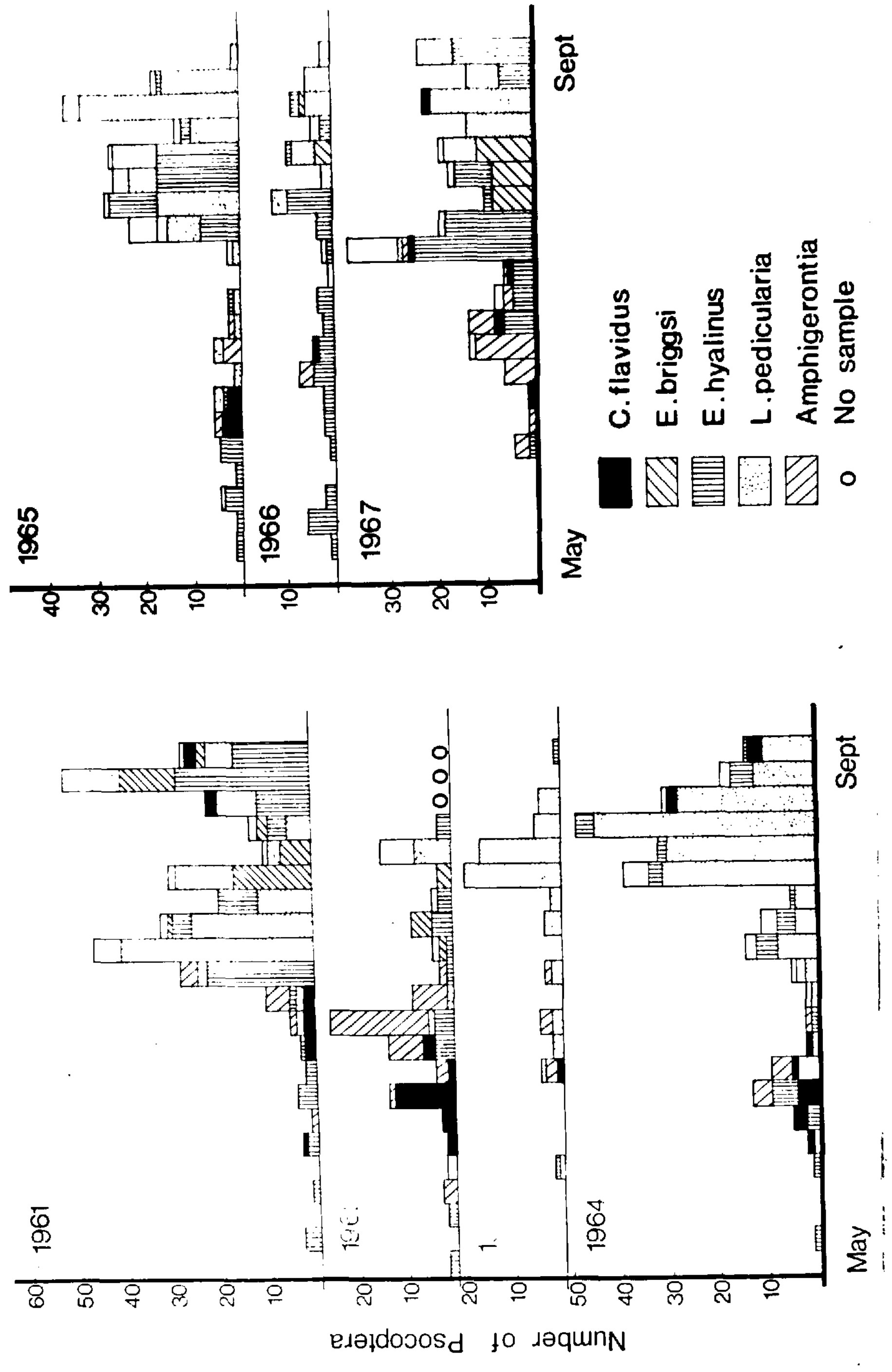


Fig.16.

Numbers of Psocoptera taken in a 45 cm diameter suction trap operated at a height of 9.2 m above the ground at Silwood Park in seven seasons. (Weekly groupings from May to September inclusive) more abundant species coincided with times when they were actively moving from one habitat to another. The trap catches of these species, therefore, reflect flight activity, and the periods of flight activity outlined above are an integral part of the life histories of these psocid species in southern England. The flight of E. hyalinus may be considered as a true migration, in the sense of movement between a breeding and a non-breeding habitat, but several of the other species breed in the habitats they leave and those they enter. Both the Amphigerontia species are bivoltine at Silwood Park and most of those trapped were adults of the first generation. Some extension of breeding range may occur after dispersal by flight of the first generation of members of this genus.

The times of first appearance of the different species of psocids in the suction traps are shown in Table 44. The data in this table also confirm that dispersal by flight is a regular feature of the life histories of the more abundant species. C.flavidus and E. hyalinus both regularly appeared early in the season, followed by the Amphigerontia species. In contrast, E. briggsi was never present in the aerial samples until July.

Variation in catch with height of trap. The total numbers of psocids caught in each trap in each season are shown in Tables 41 and 42. The total numbers did not differ greatly between the two traps, but the compositions of the catches from the two traps showed some clear differences. In general, it is likely that the specimens in the higher trap have been transported passively for greater distances than those in the lower one.

Many more E. hyalinus were taken in the higher trap throughout the season, and there were also more specimens of A. contaminata and

C. flavidus in the higher trap. More E.briggsi were taken in the lower trap and large numbers of L. pedicularia were obtained in both traps, but again rather more were caught in the lower than in the higher trap.

It is possible to correlate the relative abundance of these species in the two traps and their primary habitats. All the species are arboreal for at least a part of the year, but L. pedicularia is primarily a psocid of ground litter, hay stacks and other dead vegetation. E. briggsi occurs in litter for much of the early part of the year. The other three species are more characteristic of living trees, and less of low vegetation.

Sex Ratio. Males of two of the species found commonly in the suction traps, namely of E. hyalinus and C. flavidus are unknown in Britain. The male of Peripsocus subfasciatus (Rambur) is also unknown, and the females of Mesopsocus species are wingless. The remaining species are represented in Britain by both sexes; both males and females are winged and, therefore, may occur in suction traps. In most cases the sex ratio was close to unity, but in some years there was a preponderance of males. Only two bisexual species were sufficiently abundant to be able to compare their sex ratio in different years. These were L. pedicularia and E. briggsi, and their sex ratios are given in Table 45.

Psocoptera on Sticky traps. Few psocids were captured on the sticky traps, and they comprised representatives of only a few species. The total numbers of psocids taken on the 'stake' traps each month are shown in Table 46. The small numbers caught to some extent corroborate the data from the suction traps, as the largest numbers of E. hyalinus and C. flavidus were both taken early in the season. These traps were mostly situated amongst small trees, and a higher proportion of some arboreal species - notably L. fasciata and S. immaculatus - were taken than in the suction traps. These catches are likely to represent either trivial flight or insects blown off trees.

The numbers of psocids taken on the sticky traps on ropes in the trees was disappointingly low (Table 47). They were sufficient only to shov that C. flavidus was the most abundant aerial psocid under the oak canopies.

Psocoptera in water and light traps. Only a few psocids were taken and again these do not add to the information given above. The material in these traps was usually obtained in fresh, dissectable, condition.

The Range of Psocids that fly.

Altogether 2I species of psocids were caught in the various traps. It has been shown that the species occurring in the greatest numbers are active fliers, but it is not clear whether some of the species represented by only a few individuals fly actively, or are passive members of the plankton. On many occasions when psocids were beaten from trees at Silwood Park they were watched, and the numbers which took off from the beating tray were recorded. These observations are summarised in Table 48. It is evident that the majority of individuals of many species did not fly voluntarily,under these conditions, although some psocids of all species did take off. This voluntary flight was more pronounced on warm sunny days than at other times, but occurred outside the normal habitat. Lewis and Taylor (I967) suggest the use of Stenopsocus as an experimental animal that readily flies in the laboratory, and many of the other species listed above will also do this. It is thus possible that specimens of these species found in the traps were flying actively. Only a few of these, the foliage-frequenting psocids, are known to fly actively at particular times of the year, and these all occur at low densities at Silwood Park. Most individuals of these species, as well as some of the more abundant species are likely to be planktonic. All psocids are small insects, and during windy or rainy weather may be knocked off trees (Section 3). As their take-off is passive they come under the influence of air currents passively and may then be carried to considerable distances. In general, the higher the take-off point is above the ground, the greater will be the distance travelled. Alighting may be voluntary but psocids, like thrips (Lewis, 1965) can probably select their landing sites only in comparatively calm conditions. Most of them can become established on a variety of trees, although not all plant hosts are equally suitable to every psocid species.

The Reproductive State of flying psocids.

Johnson (1966) referred to Pearman's (1928) paper in which he stated his belief that many psocids fly as soon as they are 'flight-mature' Most of the species examined at Silwood Park attain this state within eight to ten hours after the final moult. Although at this time the wings are still slightly soft flight can occur - but it only rarely does so. At this stage ovarioles are small, and no well-developed eggs are present. Most species lay their first eggs within a few days of becoming adult and in C. flavidus, for example, each ovariole contains one or two fully developed eggs after about 36 hours of adult life. Many of the female psocids trapped at Silwood were dissected, and most of them had eggs which were almost ready to be laid. Although Johnson postulates that the majority of migratory flight in insects occurs in sexually immature females, which mature and lay eggs in new areas, it is unlikely that this is so in most psocids. Females of C. flavidus of the first generation taken from the litter- that is, before the flight onto the trees - usually contained mature eggs. The same condition was found in females of E. briggsi in August and those of E. hyalinus in late April and May. Mature eggs are almost continually present in these insects in spring and summer from the second or third day of adult life to a comparatively short time before death. It is thus unusual to find an immature female psocid at these times, and most of the flight that occurs will inevitably include a high proportion of females with eggs. Mating is not necessary for maturation of the ovarioles, and many species are obligatively or facultatively parthenogenetic. The rapid rate of egg maturation of psocids, combined with the long oviposition period, suggests that aerial dispersal will extend the breeding range of many of the individuals knocked off trees. In many insects (Johnson, 1966) flight and dispersal occurs early in adult life, but in psocids flight and extension of breeding range may occur at any time of adult life.

Flight Muscle Autolysis.

Autolysis of flight muscles following migratory flight has been described in aphids (B.Johnson, 1957,1959), in some beetles (see Chapman, 1956) and mosquitoes (Hocking, 1952). Lewis and Taylor (1965) suggested that this phenomenon might occur in psocids. Two sets of data which provide information on flight muscle autolysis clearly show that it does not occur in the species examined.

a. Adults of C. flavidus and E. briggsi were beaten from trees onto which they had recently flown and kept alive in the laboratory. No diminution in their ability to fly was evident after periods of six weeks or until the insects died. Many other psocid species were kept alive, often after flight had occurred, and all of those tested were able to fly.

b. Numbers of C. flavidus were fixed and the flight muscles were examined microscopically. Four categories of adult females were examined :-

i. Teneral unflown females

ii. Females which had flown, and were killed about one week afterwards.

iii. Females which had flown and were killed about three weeks afterwards.

iv. Females in which the wings were cut off while teneral and were killed about three weeks afterwards.

All the psocids were fixed in Dubosq-Brasil after removal of the tip of the abdomen, embedded in Ester Wax, cut at 8 u and stained with Mallory's Triple Stain. The sections were mounted in Euparal. The flight muscles were then examined in T.S. or L.S. , and those of ten females of each of the above categories were compared.

Badonnel (1934) described and discussed the flight muscles of Stenopsocus stigmaticus. The mesothorax and metathorax of this species have similar arrangements of muscles, but those of the mesothorax are more strongly developed. The most conspicuous and largest flight muscles are the tergo-sternals and the dorsal obliques (elevator muscles) and the dorsal longitudinals (depressor muscles). A number of other, smaller, muscles are also involved. The arrangement in C. flavidus is almost identical to that of Stenopsocus, and the different muscles are of the same relative sizes. No consistent differences in the size of flight muscles were detectable between the four sets of insects examined, and there was no evidence of histological autolysis as described in aphids by Johnson (1957). As no differences were detectable between the flight muscles of the freshly emerged C. flavidus and those that had flown several weeks before killing, it is clear that the flight muscles do not autolyse in this species. This species tends to remain in the same habitat after flight of the spring generation and is thus one in which autolysis might be supposed to occur. Psocids occupying more temporary habitats i.e. some other types of vegetation (Southwood, 1962) would be less likely to undergo degeneration of the flight muscles. If this supposition is correct, it is probable that this process does not occur in the Psocoptera.

Alary Polymorphism.

Many psocid species either have fully developed wings or show various grades of reduction in wing size culminating in aptery. This type of polymorphism has recently been reviewed by Mockford (1965a), who recognised three basic categories which he termed macroptery, brachyptery, and aptery. Mockford reviewed the occurrence of brachyptery in the order and also discussed the small amount of data on the possible control mechanisms. Badonnel (1959) used clonal material of *Psyllipsocus ramburii* Sélys to demonstrate that nymphs reared in isolation invariably produced adults, while those reared in groups of four or more always developed into the macropterous form. Similar observations on the effect of grouping have been made on *Archipsocus* (Mockford, 1957) and *Psoquilla* (Broadhead, 1961). Humidity has been suggested as a contolling factor in the wing size of *G. cruciatus*, and this factor probably operated in combination with low temperatures.

The most abundantly caught flying psocid, *L. pedicularia*, shows many degrees of wing reduction, and these variations have been illustrated by several workers (see Hartmann, 1951). These variations appear to be confined to the female sex, and this is also true of *G.cruciatus*. About 30 per cent of the females of *G. cruciatus* taken from vegetation at

Silwood Park showed a tendency towards wing reduction. In most of these insects the wings reached nearly to the end of the abdomen, and very short-winged individuals were rare. At Silwood this tendency towards brachyptery was apparent in females of both spring and summer generations, but in Switzerland Hartmann (I95I) found that it was limited to the later generation. About half of the females of C. kolbei at Silwood were brachypterous, and brachyptery was also found in two other foliage-frequenting species. All gradations between macroptery and extreme brachyptery were found in a single population of E. briggsi on broom, and a single short-winged female C. flavidus was beaten from oak in August I967.

I have repeated some of Badonnel's (I959) experiments on Psyllipsocus with G.cruciatus and E. briggsi. The psocids were reared at densities of I, 5 and 20 per small tube (50 x 25 mm), and fed on natural food from leaf surfaces.. Offspring of both macropterous and brachypterous parents were used. The results of these experiments are given in Table 49, and indicate that crowding has little effect in controlling wing length in these species. All the offspring of macropterous females were macropterous for two consecutive generations, as were all but a small proportion of those from the brachypterous parents. No brachypterous offspring were ever bred from macropterous parents. All individuals in which the forewing did not reach the tip of the abdomen are enumerated as brachypterous in Table 49, although there are no well defined size grades in these species.

The single brachypterous C. flavidus laid 76 eggs, from which 63 macropterous adults were reared.

It appears that the mechanisms controlling alary polymorphism in G. cruciatus and E. briggsi are different from that demonstrated by Badonnel in Psyllipsocus. The duration of development of the different forms of these two species do not differ significantly. In the Heteroptera, Teyrovsky (1920) suggested that short wings were sometimes a result of a shortened life cycle. Mockford (1965a) stated that the micropterous males of Archipsocus had only five nymphal instars, whereas macropterous females had six. Brachyptery has been considered as a juvenile character by many authors (see Southwood, 1961c), and future investigations should extend to the neuro-endocrine complex, as has been suggested by Mockford, and also to detailed work on the genetic control of alary polymorphism in Psocoptera.

Brachyptery may limit movements from a habitat, and there may be some value in the retention of a proportion of a population in one habitat, by the production of brachypterous females, since this may be a safeguard against futile or suicidal emigration. Conversely, production of winged females in species which are normally brachypterous (Broadhead, 1961) possibly enables extension of the breeding range. Badonnel (1951) remarked that the indirect flight muscles of brachypterous psocids are always less developed than in fully-winged forms.

No brachypterous or apterous psocids were caught in any of the flight traps at Silwood Park, although apterous and brachypterous psocids (Liposcelis and Lepinotus) were recorded in the upper air by Glick (1939, 1952) and Freeman (1945), and on ships by Thornton (1964). Thornton suggested that the presence of Liposcelidae in the upper air may be due to their small size. It appears from my results that there is much less aerial dispersal in apterous and brachypterous psocids than in the fully winged adults. Probably, in part, this is due to the greater buoyancy of the winged forms, but this is also a reflection of the much greater numbers of winged psocid species in the area of this study.

The main trends of psocid dispersal may be summarised as follows: In foliage-frequenting psocids there is regular small-scale passive dispersal of eggs throughout the year, with an increased dispersal at autumnal leaf fall. The nymphs of these species do not appear to show any large scale dispersal movements, although a certain amount of trivial short range movement is common. Adult winged psocids form a minor constituent of the aerial fauna. More are found in the late summer than at other times of the year, Much of the aerial dispersal of psocids is planktonic, but certain species undertake definite flights which result in a well-defined change of habitat. These flights are an integral part of the life histories of these species.

SECTION 6. The Insect Parasites of Psocoptera.

Introduction.

Psocoptera are parasitised by two groups of hymenopterous insects. Species of Alaptus, a genus of Mymaridae, are frequent parasites of psocid eggs, and several euphorine braconids attack psocid nymphs. Several species of both groups have been found at Silwood, and in other parts of Britain, and their biology is considered below.

There are several records of Protozoa and fungi being found in Psocoptera (Noland, 1924; Vishniakova, 1959), but there is no evidence that these are pathogenic.

Parasites of psocid eggs.

The Mymaridae, without exception, are parasites of the eggs of other insects. Many of them are strictly limited in their range of hosts, and different mymarid genera have been bred from eggs of Hemiptera, Coleoptera, Odonata, Lepidoptera, Diptera, Hymenoptera, and Psocoptera in this country (Hincks, 1950).

The genus Alaptus has been recorded from coccids (Mani, 1942), aleurodids (Nikolskaya, 1952) and Psocoptera. Annecke and Doutt (1961) gave the known distribution of the genus as 'Europe, Africa, U. S. A., Haiti, Peru, Hawaii, Australia, China, India': it may well prove to be cosmopolitan. Hincks (1959) recognised five British species of Alaptus and more recently (1961) described A. richardsi from eggs of C. flavidus at Silwood Park. A second new species (A. magnus Clark ms) was found in Yorkshire (Clark, 1962 - unpublished).

Vishniakova (1959) recorded rearing mymarids of the genera Parvulinus and Anaphes from eggs of several psocid species in the Soviet Union. She has kindly allowed me to examine her material, and only

Alaptus was found in the samples. Parvulinus Mercet 1912 is now considered to be a synonym of Alaptus Hal. in Westwood 1839, but was separated in Nikolskaya's (1952) key to Soviet Chalcidoidea. Alaptus is the only genus of Mymaridae of which material bred from psocid eggs is available, and seems to be the only genus which parasitises psocids. Species of several other mymarid genera (Ooctonus, Mymar, Anaphes, Enaesius)were given psocid eggs at Silwood, but they showed no interest in these possible hosts.

There are a number of references to specific psocid hosts of Alaptus, but early specific identifications of these mymarids cannot be accepted unless the actual material is available for examination. In the present work, Hincks's (1959) key was used as a basis for identification and additional information obtained from works by Soyka (1939), de Bauche (1948), and Kryger (1950). The taxonomy of some of the British species is to be reviewed in the near future (Broadhead and Clark, in prep.), and it is not proposed to discuss the adult taxonomy in this account.

About 1100 mymarid species are known, but the biology of only about twenty of these has been studied. Jackson (1958, 1961, 1966) discussed the biology of Caraphractus cinctus Walker in great detail and (1961) reviewed the kinds of mymarid larvae known up to that date. Caraphractus, which parasitised eggs of various waterbeetles, is a comparatively large mymarid. The average body length of an adult Alaptus (0.2 mm.-0.35mm.) is about one quarter that of Caraphractus. The larva of Alaptus minimus Hal. in Walk. was briefly described by Bakkendorf (1934), and the early stages of A. fusculus Hal. in Walk. mentioned by Broadhead and Wapshere (1966b). Spruyt (1927) gave notes on the biology of A. psocidivorus Gahan, but there are no fuller accounts of the life histories and biology of the genus.

Methods.

Egg batches of many foliage-frequenting psocids collected in the field at Silwood Park regularly showed about ten per cent parasitism (Section 8). Eggs of bark-frequenting psocids were also parasitised, often to levels of from 20 to 30 per cent. Host eggs brought into the laboratory usually yielded parasites within a week, and development of the parasites could be hastened or retarded by keeping the eggs in warmer or colder conditions. Adult Alaptus readily laid in newly-laid unparasitised psocid eggs, and a constant supply of host eggs was available from caged psocids. Host eggs of known ages could easily be supplied, and the duration of development of the parasites found to within a few hours. In order to measure the duration of early stages, the parasites were observed ovipositing and the host eggs dissected after a known time. Psocid eggs were dissected either in Insect Ringer Solution, or in Kahle's Fluid, in cavity slides. The chorion was cut with fine needles, and the eggs and young Alaptus larvae examined after mounting and staining in either Hoyer's Fluid with lignin pink or lactophenol with aniline blue. The larger larvae and pupae of mymarids are usually partially visible through the chorion of the host egg, and are easier to dissect out. Adult mymarids were dissected after hardening in Kahle's Fluid and mounted in lactophenol containing aniline blue.

Early stages and life history.

Egg.

The egg of Alaptus is pedunculate, of the general form found in many mymarids (Clausen, 1940). The freshly laid egg is slender with a relatively short pedicel, but this soon develops into a more ovoid egg, with a longer pedicel (Fig.I7A).

Larva.

Bakkendorf (1934) considered that Alaptus had two larval instars, but later authors (Jackson, 1961; Broadhead and Wapshere, 1966a) implied that three instars might be present. Three distinct stages were found in A. pallidicornis and A. richardsi, and these corresponded well to those noted in A. fusculus by Broadhead and Wapshere. (Figs.I7 B-D).

The first instar has distinct mandibles, but no other sclerites, or other cuticular projections. There is a small frontal process, and a tapering cauda. No segmentation is visible. Size 0.07-0.20 mm.

The second stage larva has lost the mandibles and much of the cauda, and is rather larger.(0.I6-0.24 mm).

The third stage larva almost wholly fills the host egg. It is cylindrical, but no external structure is visible; there are no mouthparts, and no setae or spines on the cuticle. Size 0.25-0.38 mm. The posterior part of this larva usually contains an irregular white or yellow patch, which is absent in earlier stages. These concretions probably represent waste products, and have been found in other mymarids. Bakkendorf (1934), however, failed to find mid-gut concretions in Alaptus, but the particles found resembled the white spots described by Jackson (1961) and Broadhead and Wapshere (1966b).

There is a short prepupal stage, which resembles the last instar larva, but has no gut movement. The pupa is at first pale, but darkens to resemble the adult insect. No specific differences were

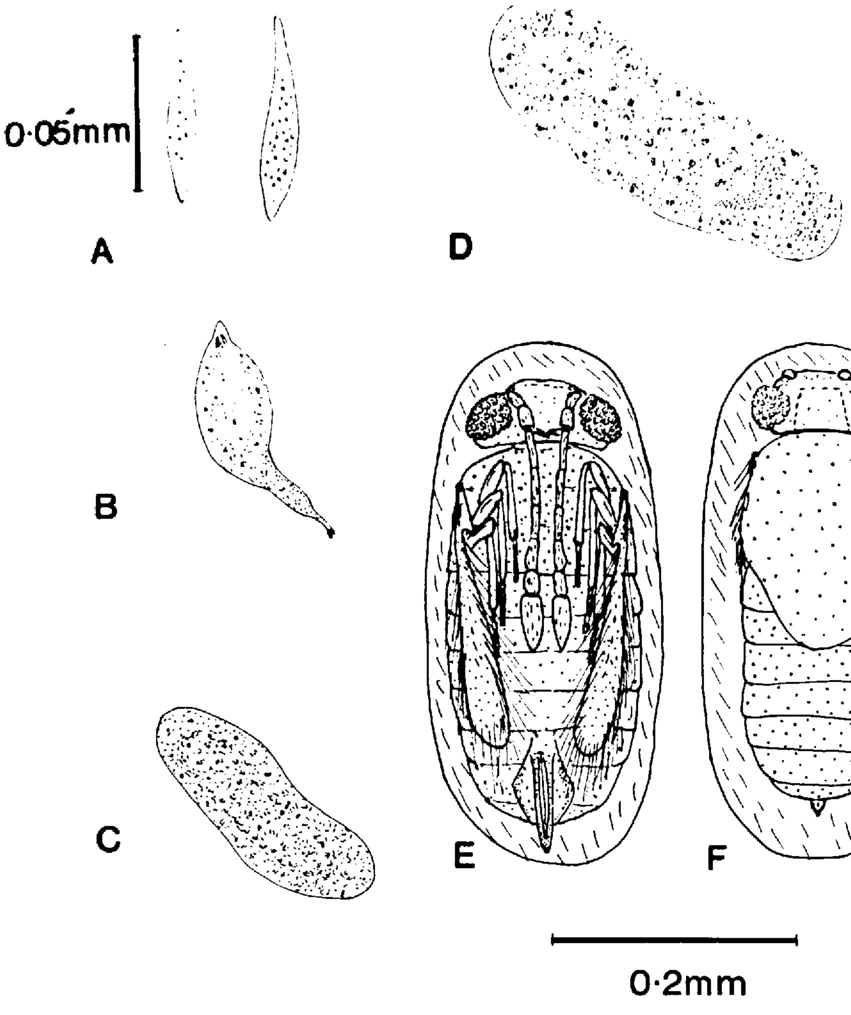


Fig.17.

Early stages of Alaptus richardsi Hincks.

A. Ovarian eggs B. First instar larva C. Second instar larva
D. Third instar larva E.F. Pupa in host egg (E ventral, F dorsal)

(larvae and pupa to same scale)

found in the early stages of *A. pallidicornis* and *A. richardsi* until just before hatching when the pupa shows the adult characters.

The life cycle of both *A. pallidicornis* and *A. richardsi* contrasts markedly with that of the univoltine *A. fusculus* (see Broadhead and Wapshere, 1966b): the life histories of the different parasites are closely correlated with those of their hosts. Eggs of foliage frequenting psocids are continually present on trees from June to October, and form possible hosts to parasites throughout this period. The duration of the life cycle of *A. pallidicornis* in an outdoor insectory was 18 - 25 days, and this, together with the unchanging levels of parasitism throughout the summer, suggests that there are six to eight overlapping generations through the summer. Overwintering does not occur solely in one stage, although most parasites found at this time were diapausing as pupae within the host eggs. Prepupae, larvae, and a few eggs were also found during the winter.

The effect of host on the parasite.

The size and duration of development of many polyphagous egg parasites differs in different hosts. The times of development of *A. pallidicornis* in eggs of three psocid species are shown in Table 50. All parent females were from clonal material bred in *C. flavidus* eggs, and then transferred to *E. briggsi* (smaller eggs) or *S. immaculatus* (larger eggs).

The size of parasites reared from these three hosts are compared in Table 51. Larger parasites were bred from larger host eggs, and also took longer to develop. Table 52 indicates that the larger females lived slightly longer, but their fecundity did not differ greatly from that of smaller parasites.

Parthenogenesis and sex ratio.

All species of Alaptus examined are regularly parthenogenetic. The males of A. richardsi are unknown, and this species appears to be thelytokous: the bisexual species are all amphitokous. Mating has not been observed, despite numerous attempts which involved confining virgin pairs in small capsules.

The sex ratio of A. pallidicornis reared from wild-collected eggs of C. flavidus in 1966 is shown in Table 53a. Collections of parasites at several times of the year all gave sex ratios close to unity. Similar results were obtained from the progeny of isolated virgin females, and on host eggs of several ages (Table 53b). These contrast markedly with Jackson's (1966) results from Caraphractus, which is arrhenotokous: female progeny were reared only from mated females.

Longevity, oviposition, and fecundity.

In the laboratory, Alaptus adults lived for periods ranging from five to nineteen days. They were kept in polystyrene petridishes and provided with small pieces of raisins and pads of sugar solution, but were only rarely seen to feed, although adults provided with food lived longer than those deprived of food (Table 54). An experiment in which single adults were kept in small boxes with food indicated that females live longer than males (Table 55).

Female Alaptus can oviposit immediately after emergence. Oviposition was repeatedly observed in four species of Alaptus and was closely similar on all occasions. There are no clear differences in oviposition behaviour in the different species. The female runs around until a batch of host eggs in found. She then moves onto the batch, continuously tapping the substrate with the clubs of her antennae.

When a 'suitable' egg has been found she straddles the egg or overlying web and may remain motionless for several minutes. The abdomen is then raised and the ovipositor inserted in the egg. The wings are held flat along the body throughout this period, and the antennae point forwards and diverge; when testing possible host eggs the antennae are held close together, and may touch. Slight rocking movements of the body usually occur during oviposition but the legs are not normally moved. The ovipositor remains inserted for several minutes (Table 56), and whilst ovipositing the female does not react to external stimuli such as bright light, heat, tapping the substrate, and even of being touched by other parasites. Up to three females have been seen simultaneously ovipositing in the same batch, without mutual interference. An egg batch with an ovipositing female can safely be moved and carried around without fear of losing the insect.

Withdrawal of the ovipositor takes about half a minute, and the female may then flex her wings and clean her antennae before moving to another egg. There does not appear to be any clear marking of parasitised eggs by the female, but _Alaptus_ very rarely oviposit in an already parasitised egg, although they may examine it for several minutes. Female _Alaptus_ will also examine very old (previous season) dead or hatched eggs, and occasionally probe them with their ovipositors. Lloyd (1956) considered that parasite egg laying was often accompanied by deposition of a characteristic secretion from the accessory gland. This 'marking' has been shown to occur in some egg parasites (see Wilson, 1961) but close observation of isolated female _Alaptus_ has failed to reveal any fluid deposited onto the egg. Jackson's (1966) observations showed that deposition of a mymarid egg into a host egg rendered the hosts unacceptable to future parasites. She suggested that a repellent substance was injected into the host at oviposition, and that the ovipositor bore sense organs which perceived this substance. The female Alaptus has a small reservoir at the base of the ovipositor, similar to that in Caraphractus, and it is likely that a similar method of host marking occurs in both genera.

More than one egg or larva of Alaptus has never been found in one host egg at Silwood; superparasitism is thus extremely rare. Broadhead and Wapshere (1966b) sometimes found two individuals of A. fusculus in Mesopsocus eggs, but again this was rare. Conversely, one or more eggs in a batch are often unparasitised. All the eggs in a batch of foliage psocid eggs are of about the same age, but females may move off the batch before laying in all the eggs. This is not due to inability to lay several eggs at short intervals, as several young females which had left partially 'clean' batches would lay in eggs in other batches immediately afterwards.

Wild egg batches of C. flavidus from which A. pallidicornis emerged are enumerated in Table 57. Batches of 2 - 11 eggs were found from which both parasites and psocids emerged: there was no evident correlation between batch size and amount of parasitism. Twenty batches each of 4 - 10 eggs were given separately to young female A. pallidicornis under one week old. Some batches of all sizes were incompletely parasitised (Table 58).

The age of the female parasite does not markedly affect the extent of parasitism up to about ten days (Table 59). Oviposition ceases soon after this time, and the maximum field longevity of females is probably little more than ten to twelve days.

Alaptus have mature eggs in the two fan-shaped ovaries at the time of emergence. Feeding is not necessary for initial oviposition and although the longevity of adults increases when food is available, the fecundity does not change greatly. It is inferred that food causes little further differentiation of oocytes. Dissections of adult females of known ages showed that they contained the greatest number of eggs soon after hatching, and that there was a progressive decline with age.

Single females of A. pallidicornis and A. richardsi were provided with freshly laid (1 - 2 days) egg batches of C. flavidus in petridishes maintained at 100 percent R.H. Fresh batches were provided on alternate days, and all batches previously present were removed and dissected. At least 40 eggs were always available to each parasite. Total counts of eggs and young larvae of Alaptus in the host eggs gave a measure of the fecundity of the adults. The results (Table 60) showed that from 50 to 80 eggs were usually laid by females of these two species. These figures are probably rather higher than would result in the field, as a regular supply of fresh suitable hosts was available in a small space. The adult parasites are active and will seek out many available egg batches. They were bred from wild egg collections on all species of trees examined and different areas of trees: they occurred in all the habitats where host eggs were found. Several unrelated females may also oviposit in different eggs in the same batch, and any subsequent mating between unrelated progeny from the same batch ensures some genetic interchange.

Host finding and specificity.

The adult parasites fly readily in the laboratory, but appear to search for hosts largely by running and short flits. It is likely that such small insects as Alaptus, and other mymarids, can control their flight very little in even gentle breezes, and much loss and redistribution of the adults must occur by this method. Host finding by walking, without taking to flight, may thus conserve a higher proportion of the parasite population in the original habitat, where there may be a constant supply of host eggs throughout the summer.

Single young females of A. pallidicornis were confined on small potted oak trees on which numbers of fresh C. flavidus egg batches were pinned at different points. These batches were replaced on alternate days, and the 'old' batches were dissected. Several of the parasites were lost in this experiment, but others oviposited in most of the available egg batches (Table 61). The greatest distances between parasitised egg batches in this experiment was 80 - 85 cm., with intervening foliage and branches.

Only young eggs are acceptable to A. pallidicornis and A. richardsi. Laboratory tests (Table 62) showed that oviposition was attempted, sometimes successfully, in older eggs, but parasites only rarely developed after host eggs had developed to the stage where the embryo eyespots were visible. Eggs of Alaptus were sometimes found in host eggs dissected at this time, but no later stages of parasites were ever found.

The few reliable specific host records in the literature of the Alaptus species parasitising psocids indicate some host specificity. A. pallidicornis and A. richardsi have been bred mainly from foliage-frequenting psocids, and not from bark-frequenters, whereas the reverse is true of A. fusculus and A. minimus. The species of Alaptus found at Silwood Park were tested in the laboratory with fresh eggs of all available psocid species. Attempted ovipositions and successful rearings were recordsd (Table 63), and each result given is based on at least five parasite females and twenty eggs of each host species. The results closely bear out the inferences in the literature. There was a very clear division of parasite species affecting foliage and bark psocids. It is notable that T. dalii, a foliage psocid with eggs resembling those of bark psocids, was successfully parasitised by A. fusculus in the laboratory and not by A. pallidicornis. Both categories of Alaptus sometimes attempted oviposition in alien host eggs, but were very rarely reared from these species. Clark (1962 - unpublished) found that there was a correlation between the lengths of Alaptus ovipositors and the thickness of chorion and protective covering of the host eggs. The short ovipositors of Alaptus species affecting foliage psocids prevent their penetrating the thick coating of rectal material which often surrounds the eggs of bark psocids. This does not, however, explain the reverse situation, in which Alaptus species with long ovipositors do not parasitise the eggs normally attacked by species with short ovipositors. All species of Alaptus are likely to encounter varied types of psocid eggs in the field and may attempt oviposition in them. The reactions of different host eggs to different parasites have not been studied, but may differ. None of the few mymarid eggs and young larvae found in alien hosts showed any signs of encapsulation.

Parasites of psocid nymphs and adults.

The only insect parasites recorded from psocid nymphs in

Britain are euphorine braconids of the genus *Leiophron* Nees. A closely related genus, *Euphoriella*, has been bred from many psocids in North America (Sommerman, 1956; Muesebeck, 1956) but this insect has not been found in the Old World. The genus *Leiophron* is known to parasitise Heteroptera and Psocoptera, and there are several accounts of the taxonomy and biology of species attacking Heteroptera (Brindley, 1939; Loan, 1964, 1966; Richards, 1967; Waloff, 1967). Notes on a species parasitising Psocoptera were given by Broadhead and Wapshere (1966b), and Vishniakova (1959) found braconid larvae in several species of psocids in the Soviet Union. There are no accounts of the biology and life histories of the *Leiophron* species attacking psocids, and their taxonomy is uncertain (Richards, 1967). '*Leiophron similis* Curtis' appears to consist of several very closely related species, all of which parasitise Psocoptera. Species of this group have been bred from psocids at Silwood. The adults and larvae are extremely similar, and I consider it unwise to erect new species at this stage: these specimens are therefore all referred to *L. similis* Curtis. A distinctive species, *L. claviventris* Ruthe, was recently added to the British list on the basis of a few adult specimens (Richards, 1967), and no host has hitherto been known for this parasite. It has been bred from *Mesopsocus immunis* (Steph) and *M. unipunctatus* (Müll) at Silwood Park. Broadhead and Wapshere (1966b) recorded rearing *L.* sp. n. *similis* Curtis from *Mesopsocus*.

Methods.

Regular collections of nymphs of many psocid species from many species of trees were examined for parasites. Nymphs were identified to species and instar (Section 2) and each collection was divided approximately into half. One half was dissected in alcohol, and the other half kept alive in an outdoor insectary. The levels of parasitism in the field were thus found at intervals throughout 1966 and 1967. Psocid nymphs containing large parasite larvae are readily detectable by the swelling and translucent appearance of the abdominal wall, but nymphs with small parasite larvae or eggs are not externally separable from healthy nymphs. Living parasitised nymphs were kept in polystyrene boxes with a layer of moss and sand on the floor: the parasite larvae pupated in this after leaving the nymphs, and emerged the following season. Early stages of the braconids were examined after mounting in Hoyer's Fluid, sometimes after staining in lignin pink. Head capsules of larvae were dissected from specimens softened in five per cent sodium hydroxide, and were then flattened and mounted unstained in Hoyer's Fluid and examined under oil immersion. Measurements of whole larvae were made from material stored in alcohol.

Amount of parasitism.

The numbers of braconids found in dissections of nymphs of various psocids in 1966 and 1967 are shown in Table 64. Nine species were found to be hosts of *Leiophron*. At least two species of *Leiophron* were reared, and the early stages and life histories of these are described below. *L. claviventris* is a univoltine parasite mainly infesting univoltine hosts (*Mesopsocus*), whereas the hosts of the univoltine *L. similis* are often bivoltine or trivoltine. Fig. 19 shows clearly that there was a high level of parasitism of *C. flavidus* by this species during the first arboreal generation (June - July), whereas the second arboreal generation was completely free of parasitism.

Collections of nymphs in early summer from many tree species showed similar levels of parasitism, and most psocid species were affected. The absence of these parasites from *Cuneopalpus* nymphs is surprising, especially as *Elipsocus* nymphs from the same trees showed about 15 per cent parasitism (New, 1968). The *Leiophron* species attacking Miridae are not strictly host specific (Waloff, 1967), and those attacking psocids have a similarly wide range of hosts. However, *L. claviventris* has been bred only from bark-frequenting psocids at Silwood, and *L. similis* only from foliage psocids. Broadhead and Wapshere's (1966) *Leiophron* from *Mesopsocus* is morphologically similar to '*L.* '*similis*', but adequate data on the early stages are not available. There seems to be a division of these parasites into those found predominantly on bark psocids and those mainly parasitising foliage psocids, a parallel division to the *Alaptus* species attacking psocid eggs.

It was rare to find more that one young larva in a single host (Table 65) and no more than one non-caudate larva was ever found. A similar suppression of supernumary larvae to that found in other *Leiophron* species (Waloff, 1967) probably occurs. Hyperparasitism was also extremely low; an occasional small ichneumonid larva was found, probably of *Mesochorus*, but no adults have been reared.

Early stages and life histories.

Eggs.

The eggs of both *L. claviventris* and *L. similis* are very small when laid, but enlarge to resemble those of related species (Waloff, 1967). Measurements of three stages of the larger eggs found in wild nymphs are given in Table 66; their outline shapes are shown in Fig. 18. The chorions are sometimes smooth, but more often appear slightly granular. Eggs were found invariably in the abdominal haemocoel of the host nymph, although larvae sometimes extended into the thorax. Towards hatching time, the young coiled larva is visible through the chorion. Hatching was not observed, but the cauda of the young larva may be used to 'flick' the larva out of the egg-shell (Jackson, 1928).

Larvae.

Larvae of Leiophron species were described by Ammah-Attoh (1959) and Waloff (1967). The young larvae are caudate, but the cauda is lost in later stages. General details of the larval form are given in Waloff's account.

The number of larval instars in this genus has not been satisfactorily clarified in the literature. Ammah-Attoh (1959) found four instars, and Loan (1964) considered there were five instars. Both these authors worked on the species parasitising Heteroptera. There appear to be four instars in the two species I examined, although the first two are distinguishable only with difficulty.

These may be separated as follows:

Instar I: Caudate, with small trapezoidal slightly sclerotised head bearing a conspicuous pair of heavily sclerotised falcate mandibles, and a pair of conical papillae on the antero-dorsal surface. A small pleural sclerite on each side of the head, probably representing the hypostoma and pleurostoma of later stages. No setae or projections on the body cuticle. The last abdominal segment contains a conspicous dorsally placed anal vesicle. The cauda is rounded at the tip and bears a few small distal spines.

Instar II: Caudate, and much resembling Instar I. Mandibles becoming progressively enclosed, and the bases of the conical papillae are less conspicuous, due to resorption. The cauda shows two distinct layers of cuticle, the first instar cuticle having separated.

Instar III: Usually slight remains of resorbed cauda. Mandibles mainly internal, small pointed triangular tips externally. Papillae almost completely resorbed. Head definitely hemispherical. No spines or setae on cuticle. Anal vesicle resorbed, but traces may persist.

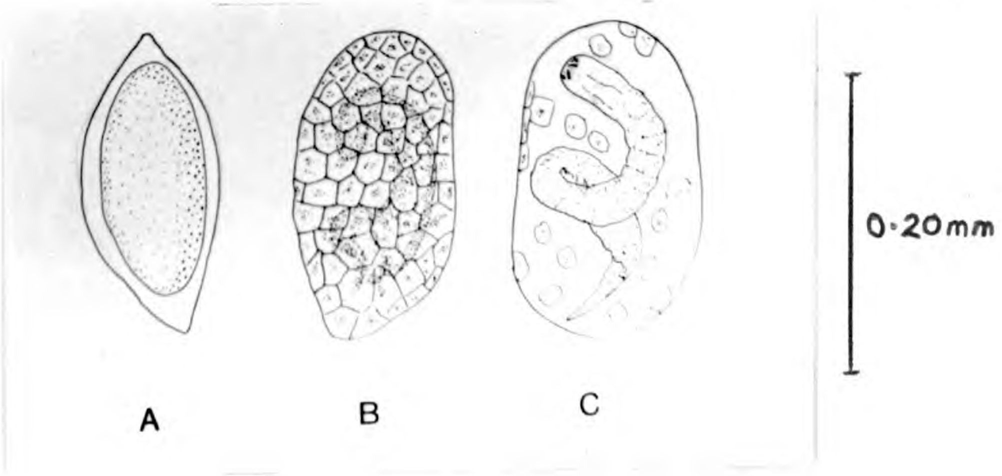
Instar IV: No cauda. Head capsule prognathous and non-retractile. Well defined head sclerites (Figs. 20) Antennae conical. Cuticle with microscopic setae and spines, the larger ones of taxonomic value.

Larvae showing the last combination of characters left the host and spun cocoons. There was no evidence of an additional ecdysis near the time of leaving the host, as Loan (1964) reported in L. pallipes. Curtis. The early instars of the two species are not separable, but the final instar larvae can be specifically identified on the form and chaetotaxy of the head capsules (Figs. 20). The taxonomy in these figures follows Short (1952), and the slight variations found in chaetotaxy are shown in Table 67. Overall measurements of larvae are given in Table 68 ; there is considerable size overlap between the stages, but the division into caudate and non-caudate larvae gives a primary separation into age groups.

The larvae leave the host laterally towards the anterior of the abdomen. The host may remain alive for up to a day, but invariably died. The larvae drop to the ground where they actively move into moss or into cracks in soil and spin cocoons within a day or two.

Cocoon and pupa:

The oval cocoons consist of three distinct layers of opaque white silk (Ammah-Attoh, 1959). Dimensions are given in Table 69.



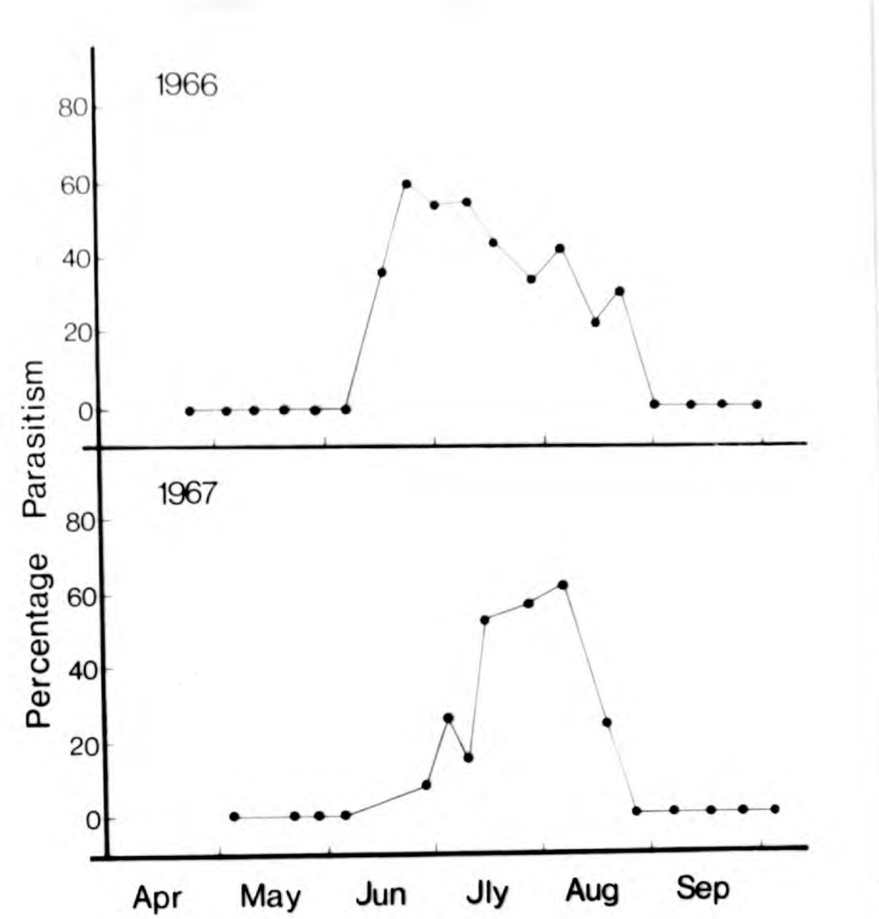


Fig.18.

Developmental stages of eggs of Leiophron similis from C.flavidus nymphs. (A, about two hours old. C, near hatching)

Fig.19.

Parasitism of C.flavidus nymphs by Leiophron in the field at Silwood Park in 1966 and 1967.

Fig.20.

Flattened head capsule of fully grown larva of Leiophron claviventris Ruthe.

Fig.20. (cont.)

Flattened head capsule of fully grown larva of **Leiophron similis** Curtis.

The pupae of both species, examined after slitting open the cocoons, were distinct within a week of cocoon formation. At this stage the pupa is grey-white, with the eyes and ocellar markings pale castaneous. The mature pupa is more heavily pigmented, and resembles the general form of the adult.

The instars of *L. claviventris* and *L. similis* found in hosts of different stages are shown in Table 70, Most parasite eggs and young (caudate) larvae were found in second to fourth instar nymphs of the host psocids. Larger larvae were found in later instars and in most cases left the host during the last (sixth) instar. A large parasite larva was occasionally found in an adult *C. flavidus*.

In 1967, a larger proportion of the older nymphs of *Mesopsocus* contained small parasite larvae. Field samples indicated that the nymphs appeared earlier in 1967 than in 1966. Parasitism commenced about the same time in both years, but the age range of available hosts differed. In the laboratory, the parasites would oviposit in all *Mesopsocus* instars except the small first stage, which could not easily be held by the parasite. Waloff (1967) recorded that the species of *Leiophron* she studied oviposited through the cervical membrane, but the psocid-infesting species do not have such a well-defined routine. Oviposition was seen to occur through the abdominal wall and rarely in the thorax, as well as through the cervical membrane.

Both these species of *Leiophron* are univoltine. They overwinter as pupae in cocoons on the ground, and the adults emerge in the late spring. Six specimens of '*L. similis*' taken by Varley and Gradwell at Wytham Woods, and now in the Hope Department, were found on dates varying from 25th May to 24th June in five separate years, and the few adults found at Silwood during this work were all around the beginning of June. Richards (1967) recorded this species between mid June and early July, and all species of the genus appear to have a closely similar univoltine life history. Young nymphs of C. flavidus are present on trees from about the middle of June onwards, but no braconids were found in nymphs from the earlier generation, which occurs in ground litter (Section 3). There is a close synchronisation between parasite emergence and host availability, and any minor discrepancies in this are offset by the parasite's ability to oviposit in several instars of the host.

The synchronisation of L. similis with C. flavidus is of particular interest in producing a heavy mortality due to parasites in one host generation, which is followed by a parasite-free generation. There is no evidence for a divided emergence of the parasite, and the second arboreal generation of C. flavidus was free from parasites. A fairly uniform level of parasitism on all tree species examined indicates that the searching capacity of the adult parasites, or their number, varied with the number of available hosts. The numbers of adult parasites on particular trees are likely to reflect the numbers developing on those trees the previous season, and overwintering in the litter under the trees. The area of discovery of the adult Leiophron appeared to increase when smaller numbers of hosts were present. Very small numbers of adult Leiophron were found in the field. Varley and Edwards (1957) showed that the area of discovery of Mormoniella decreased at high host densities, and Waloff (1967) indicated that L. heterocordyli Richards had a smaller area of discovery when the parasite density was high. The maintenance of a constant level of parasitism, by which a constant proportion of hosts are destroyed in all the different habitats frequented, will have a greater destructive effect when the hosts are initially present in low densities. The greater the initial density of hosts, the greater will be the number of survivors. It has been shown that the distribution of adult C. flavidus on different trees in June, although reflecting the numbers developing in the litter under the trees, is much more random than later in the season. Thus, more nymphs of this species were produced on Quercus than on the other trees examined, but parasitism was of the same level as on other trees. More nymphs survive and other factors, as well as freedom from parasitism in the second arboreal generation, enable a vast increase in numbers of C. flavidus on Quercus to occur by late summer. The initial host nymph density is less on some other tree species, and far fewer nymphs survive, even at a constant level of parasitism. Fewer adults result than on Quercus, and by the end of the first arboreal generation there is already a large discrepancy in the total numbers of C. flavidus on different tree species.

Effect of parasite on host.

Parasitism by Leiophron has several readily detectable effects on the host psocid, before death ensues. The ovaries, which are usually fully formed in the last instar nymph are very small, and the few parasitised adult psocids examined had reproductive systems resembling that of the normal sixth instar nymph.

The durations of healthy and parasitised nymphs in an outdoor insectary are shown in Table 71. It is clear that some nymphs of C. flavidus had longer developmental times when parasitised. This was especially noticeable in later instars, and the amount of retardation appeared to be related to the size of the parasite larva. If small larvae were present in final instar nymphs (indicated by slight abdominal swelling) the nymph still moults into an adult, but if a large larva is present the nymph remains as such until the parasite larva is fully developed. Nymphs spent up to three times the normal period in this instar, but the duration of previous instars was little affected

SECTION 7. The Arthropod Predators of Psocoptera.

Introduction.

There are surprisingly few records of arthropod predators of Psocoptera. Broadhead (1958) listed the animals he found with psocid prey in Yorkshire, and summaries of earlier predator records were given by Weber (1936) and Badonnel (1943).

Many predatory arthropods are arboreal, and may eat psocids. Whereas many phytophagous insects are strictly host-plant specific, only a few totally predacious insects are known to be similarly limited in habitat. Southwood (1961 a, b) demonstrated that different numbers of insect species were associated with different tree species, and although he primarily considered phytophagous insects the number of predator species are likely to vary similarly. More predator species may occur on trees where there are abundant and diverse prey than on trees where the prey are very limited. Southwood did not define the rather nebulous term 'insects associated with trees', but implied that he meant '...limited to or predominantly feeding or breeding on ...'. Most predators will accept a wide range of prey and are consequently likely to be found on a variety of trees. There are few accounts of prey selection by predacious insects, but recent work by Dempster (1963) indicated some preferences by Anthocorids, several species of which are strictly limited in host tree range (Anderson, 1962; Collyer, 1967). Some other groups of bugs, such as the Miridae, contain arboreal species which feed both on the host plant and animal matter. British Neuroptera show a partial separation into groups frequenting coniferous and broadleaved trees, but there is little evidence for prey-specificity. The possible predators of Psocoptera were collected from different tree species by beating, at approximately monthly intervals throughout the summers of 1966 and 1967. Psocids were always scarce on some of these trees (Section 4), and on others only became abundant in late summer. Records were kept of the few predators found with psocid prey.

It was hoped to study psocid predators by serological methods (see Dempster, 1960), but the rabbit available for injection proved exceptionally unresponsive to psocid antigen, and the great amount of labour involved in collecting several grams of dried psocids prohibited further attempts. Simple laboratory experiments were used to detect whether some of the possible predators would readily feed on psocids or select psocids from other prey.

The numbers and kinds of arthropod predators on different tree species.

The numbers of possible predators taken in ten samples from each tree species on each sampling date are shown in Table 72 . The main groups of predators and the numbers of species are given in Table 73 .

The numbers of predators and predator species differed greatly on different tree species. Few predators were found on some trees, and these trees often supported few psocids. Most predators were found on *Quercus*, which also supports the greatest range of prey (Southwood, 1961a). There were also numerous predators on *Crataegus*, but they were much less abundant on conifers. The figures obtained in some cases resemble the numerical trends of Southwood's data, but a large proportion of the predator species were found on more than one species of tree.

The numbers of predators were large during late summer, when psocids were most numerous. Psocids (*C. burmeisteri*, *C. guestfalica*) were virtually the only prey available on *Cupressus*, but there was a wider range of prey on most other tree species.

Predators taken with psocid prey.

The few records of predators with psocid prey found in the field by searching (egg predators) and beating are given in Table 74 . The latter figures are probably not a true representation of the number of predators taking psocid prey at any one time, as many predators release the prey when dislodged from the trees. Broadhead (1958b) considered that the tenacity of the mite *Anystis* in holding its prey after being dislodged from trees accounted for the larger numbers he found with psocids. A few simple experiments in which various predators with psocid prey were dislodged from small potted trees by shaking showed that most insect predators released their prey. *Anystis* released the prey less frequently than the other animals tested, and Opilionids were also tenacious.

The beating records are thus rather misleading if to be used quantitatively without supporting serological and laboratory evidence, but are still useful in indicating some of the possible predators of psocids. No assessment was made of the predators not living on the trees, such as the few aculeate hymenoptera known to take psocids.

The egg predators are discussed in Section 8 . Larvae of the three common species of Coniopterygidae were all found feeding on eggs, and larvae of *Conwentzia psociformis* Curtis also fed on large nymphs of *C. flavidus*. Several species of Hemerobiid and Chrysopid larvae also preyed on psocids (see also Broadhead, 1958b). Prey selection in these insects seems to be related to the activity of the prey rather than the kind; psocids move more than aphids, but many still appear to be eaten by larval Neuroptera. Several species of all three arboreal families are common on many broadleaved trees at Silwood. Only one Anthocorid was taken with psocid prey, but two mirids (adults of *Cyellocoris histrionicus* (L.) and *Dryophilocoris flavoquadrimaculatus* (de Geer) were found with nymphs of *C. flavidus* on *Quercus*. There are few prey records for these mirids, which are thought to be predominantly plant feeders. In contrast, *Ploiaralia*, found on *Cupressus*, is known to prey on psocids (Richards, 1943).

Selection of prey in the laboratory.

Laboratory experiments on prey selection by captive predators are of very limited value. Simple experiments can, however, be used to indicate whether particular predators 'preferentially' take dead or living prey, any particular size or age of prey, or whether there is any exclusion of possible prey species. A sharp distinction must be drawn between prey killed and prey eaten: in laboratory conditions the number killed and uneaten may be much larger than would occur under field conditions, and is misleading in attempts to assess mortality. Laboratory models are also of value in studies of the detailed behaviour of a predator (see Holling, 1966, 1968). The present work was undertaken to detect whether some of the possible predators of psocids found commonly in the field selected psocid prey of any particular stage, or whether all would readily take a wide range of prey. In the absence of serological data from field-collected predators, any further deductions are unwarranted.

Single predators were starved for 24 hours in petri dishes and then presented with prey. All prey provided for a given predator species was that found in the predator's natural habitat. No more than two kinds of prey were ever simultaneously available to one predator, and the numbers of prey killed and/or eaten were noted after 24 hours.

The predator was then starved for a further 24 hours, and a test repeated. Several different choice experiments were conducted with each kind of predator. The psocid prey comprised various stages of C. flavidus and S. immaculatus for predators from broadleaved trees and of C. burmeisteri for predators from conifers. The results of these tests are given in Table 75.

Small predators (Anystis and Coniopterygid larvae) took more inert and small prey than large animals, but did not select any particular type of prey. Baker (1962) reviewed earlier records of the prey of Anystis, and indicated that the only deterrent to Anystis was the size of prey. He stated that some prey, such as adult Collembola, were protected by a hardened exoskeleton, and suggested that different stages of Anystis would take different prey in the field. Only adult Anystis have been recorded with adult psocids at Silwood (see also Broadhead, 1958), and also with eggs. Both Anystis and Coniopterygid larvae are active predators, but it is likely that they take a high proportion of relatively small and inert prey.

The other Neuroptera tested did not select any particular kind of prey, but killed indiscriminately as the prey was encountered. Few eggs were eaten, especially by spiders. None of the predators refused stationary prey, and none showed any large degree of prey selection. Most of the species found probably take some psocids in the field.

SECTION 8. Distribution and Mortality of eggs of foliage-frequenting Psocoptera.

Introduction.

The numbers of some species of foliage-frequenting psocids are much smaller in the early summer than at the end of the summer. This discrepancy could be partially accounted for by a large mortality in overwintering eggs, and the differences in psocid numbers on different species of trees may be related to the survival of psocids on them, i.e. to differential mortality. The aim of the present investigation was to determine the main factors causing mortality of psocid eggs and to compare the incidence of these factors on different tree species at different times of the year.

Some species of bisexual psocids which fail to mate lay infertile eggs but otherwise sterility is rare. The eggs are attacked by various parasites and predators and "bad" weather removes eggs and leaves from the parent tree and thus affects their distribution. Temperature and humidity effects were briefly considered in Section 1 : their effects are not likely to differ significantly between different trees unless the degree of exposure of the oviposition sites of foliage-frequenting psocids on these trees is different. It is possible that the overwintering eggs are especially susceptible to low temperatures and desiccation just before hatching, as several authors have suggested for aphid eggs (see Way and Banks, I962). As the oviposition sites of foliage-frequenting psocids do not differ greatly between trees, comparative climatic factors are not considered further.

Methods.

Collections of egg batches of foliage-frequenting psocids were made from several sites in Berkshire in I966 and I967. All batches were retained in the laboratory and their fate recorded. Comparison was made between egg batches from different tree species at each of the three main laying periods (June, August, late September-October), between different regions on the same trees, between trees and litter, and between various overwintering sites. Each sample from broadleaved trees comprised I00 leaves taken and examined at random: Cupressus was sampled by examination of the foliage accompanying 60 cm terminal lengths of branch. The bark of a similar 60 cm sample was examined in conjunction with each foliage sample from all tree species, but only eggs of the foliage-frequenting psocids were recorded. Twenty foliage samples were taken from each tree species at each of the three sampling periods. Egg batch samples were taken from the litter by examining all leaves on ground areas 30 x 30 cm .

The eggs of these psocids were identified to species, but only six species of foliage psodids were common enough to provide meaningful results. The eggs collected were divided into seven categories, namely (I) hatched, (2) predated, (3) parasitised - parasites emerged, (4) parasitised - not emerged, (5) infertile, (6) 'dead' (fertile eggs killed by fungus, fungus-infected eggs) and (7) healthy eggs (see Figs.21a- f). Laboratory tests using various possible predators were used to indicate the different signs of predation by different animals. The above categories were distinguished by the following characters:-

(I) Hatched eggs - in most cases recognisable by the presence of the pronymphal cuticle with the oviruptor, left protruding from the egg and through the web.

(2) Predated eggs have the overlying web torn or holed to some extent, except rarely when the egg of a predacious mite was present on the oviposition site or laid through the web. In these few cases

a small oribatid mite was occasionally found in this situation. The degree of tearing of the web indicated the type of predator. Some eggs had collapsed or were completely missing. Laboratory tests indicated the following types of predator damage:-

(a) Mites - Web with many small irregular holes. Usually all eggs in a batch were attacked, but collapsed and remained in position.

(b) Spiders and opilionids - Web with pairs of punctures which vary in size and may coalesce. Eggs usually with a single tear, in any visible position. Collapsed.

(c) Neuropterous larvae - Web with pairs of punctures above the eggs. Often only one or two eggs attacked, and each egg shows small holes in the dorsal surgage of the chorion.

(d) Anthocorids - Web with a conspicuous tear rather than a small puncture. Generally all the eggs of a batch attacked, and may be dislodged.

(e) Earwigs,carabids - Web much torn, and eggs often removed completely.

(3) Parasitised - emerged. Eggs with round hole towards one end, and a corresponding hole in the web. Chorions uncollapsed, no trace of nymphal remains.

(4) Parasitised - unhatched. Eggs in which the mymarid is well developed show a median pale streak towards one end. Parasite pupae are visible through the chorion, but very young larvae are not detectable until they have developed further.

(5) Infertile eggs were taken as those which did not hatch after prolonged keeping, but which could not be placed in any of the other categories.

(6) 'Dead' eggs. A few eggs were found filled with fungal hyphae or black spores. It is often difficult to distinguish primary infection from fungal invasion following predator attack. Fungus-infected eggs under an apparently undamaged web were classed as 'dead' eggs.

(7) Healthy eggs are those from which nymphs subsequently hatched. The eyespots and oviruptor are visible in well developed eggs, and any darkening also indicates healthy eggs.

The numbers of egg batches on different trees.

Tables 76 - 80 show that the numbers of egg batches found on different tree species varied considerably at different times of the year. The numbers of C. flavidus egg batches closely followed the abundance of adults (see Section 4): the egg batches of the first generation females were far more evenly distributed than those of subsequent generations. The eggs of C. burmeisteri and S. stigmaticus were confined to Cupressus and Crataegus respectively.

The factors causing egg mortality on the various tree species at different times of the year are also shown in Tables 76- 80. There were no large differences in total egg mortality between different tree species at the same time, but different factors were predominant at different times of the year. Parasitism by Alaptus was rarely more than ten per cent, and remained nearly constant between generations. Only a small proportion of psocid eggs showed any signs of predation, but this proportion sometimes increased slightly throughout the summer as predators became more numerous. Other factors contributed only slightly to egg mortality. The overall differences in egg mortality on different trees were very small, and a more or less constant proportion of eggs survived

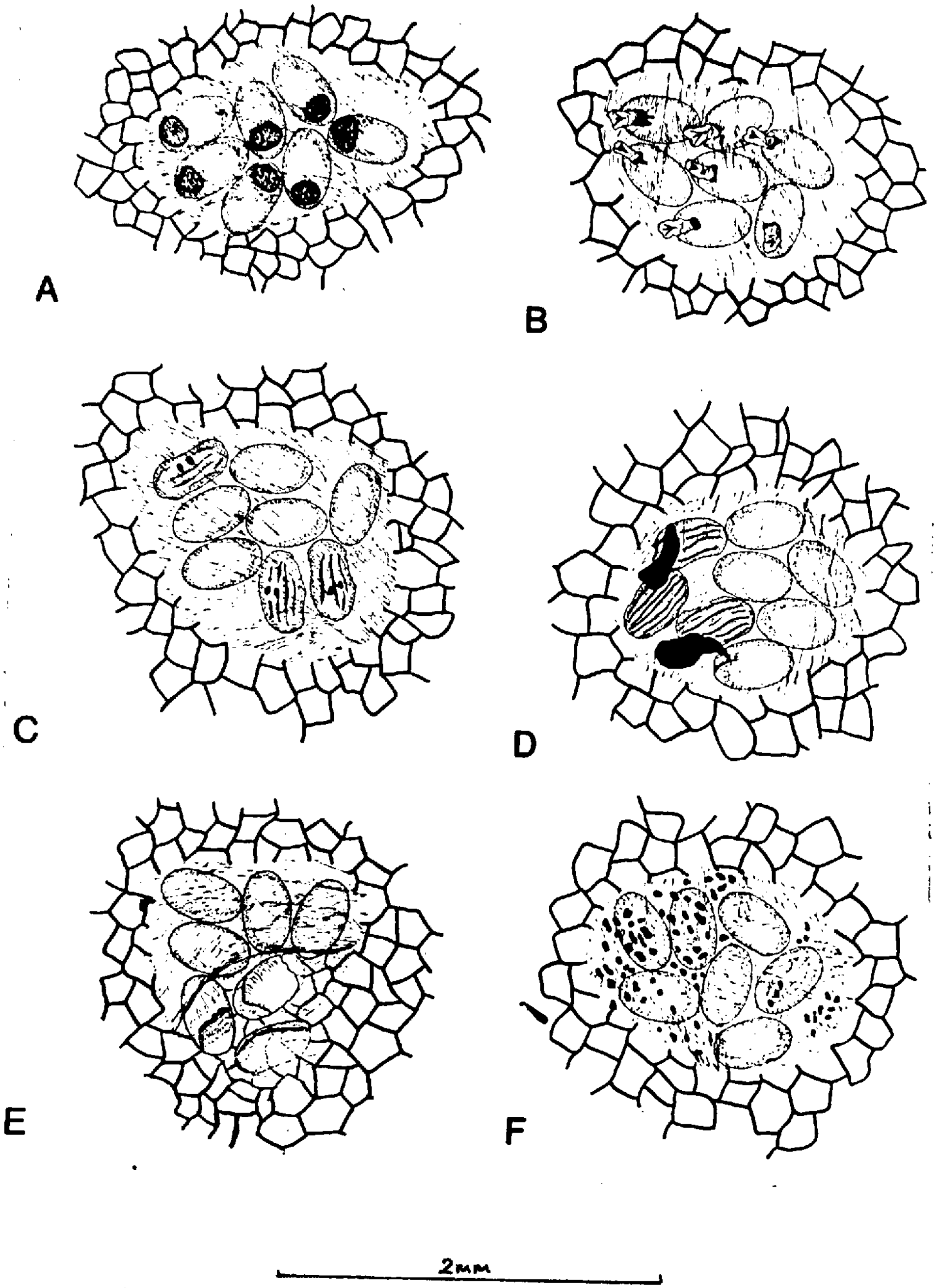


Fig.2I.

Egg Batches of *C.flavidus* in various conditions.

A. Parasitised - parasites emerged B. Hatched C. Marks of predation by neuropterous larva D. Marks of predation by anthocorid E. Marks of predation by larger arthropod such as carabid. F. Marks of invasion by mites.

on all the tree species examined. Psocid eggs from different regions of the same trees also suffered similar mortalities (Table 80).

Mortality of overwintering eggs from different sites.

The mortalities of overwintering eggs from different habitats in two seasons are given in Tables 81 and 82. Eggs were collected from the various sites in November and late March, as any significant differences between the survival of eggs collected during these two periods will indicate mortality occurring during the intervening months.

A proportion of the overwintering eggs of *S. stigmaticus* are laid on the stems of *Crataegus*, mainly below axillary buds. These are included in the tree samples in Table 81. Eggs of the other species overwinter either in the litter or on the foliage of evergreens.

The total foliage of four small *Ilex* bushes was examine in November 1966. All the psocid eggs were removed from two of them at this time and from the other two in March 1967. These data (Table 82) gave an exact measure of the loss of overwintering eggs on these trees.

There was no large difference in percentage survival in eggs collected in November and in March, and the same proportional mortalities were found on both occasions. The parasites overwinter in the host eggs, and no increase in parasitism thus occurs during the winter. A number of possible predators, notably opilionids, carabids and cantharid larvae, are active in the litter during the winter months, but there was no large increase in egg predation. A few batches disappeared completely from the *Ilex* trees during the winter, and some of these were probably removed incidentally by birds. The increasing number of 'hatched' eggs throughout the summer on all trees reflects both the extended oviposition period of the adults, and the persistence of hatched batches from previous generations.

Function of web covering egg batches.

The egg batches of foliage-frequenting psocids are usually covered by a web of silk produced from the labial glands of the female. Possible functions of this web have been discussed by several authors (Stager, 1917; Pearman, 1928; Sommerman, 1943 b; Medem, 1951), but no definite conclusions were drawn. The following simple experiments were undertaken to examine some of the possible functions of the web: in all cases 'unwebbed batches' refer to egg batches of C. flavidus from which the web has been carefully removed with fine needles without disturbing the underlying eggs.

(a) Protection against predators. Stager (1917) and Pearman (1928) indicated that the web was not a deterrent to or protection against predators. Although predation is low in the field, larvae of several Coniopterygidae, nymphal Anthocoridae, a mite (Anystis) and an opilionid (Nemostoma lugubre (Müller) have been observed feeding through the web. Laboratory choice experiments in which these animals were confined with webbed and unwebbed batches in petri dishes showed that there was little discrimination between the two types (Table 83); both were attacked readily by hungry predators.

(b) Protection against parasites. Clark (1962 - unpublished) showed that there was a correlation between the ovipositor length of Alaptus and the type of psocid eggs they attacked. The primary egg web of foliage psocids is usually in contact with the eggs and forms a very thin barrier. A secondary egg web may confer some protection against parasites when it is placed well above the primary web. The parasites do not select webbed or unwebbed eggs, but attack them indiscriminately (Table 84).

(c) The web as a food trap. Sommerman (1943) suggested that the egg-web acted as a trap for drifting fungal spores, and thus provided food for the first instar nymphs. Twenty wild webs of C. flavidus were examined after mounting in aniline blue in lactophenol and very little food was found on any of them; in all cases far more food was found on the leaf surrounding the egg-batch. The nymphs move off the web soon after hatching, and have not been observed to feed on the web. The presence or absence of a web does not affect successful completion of hatching.

(d) Retention of eggs on the leaf surface. The web may help to keep the eggs in place on the leaf (Pearman, 1928), and also afford protection against climatic extremes. Wind, rain and freezing may remove some of the firmly cemented eggs from the leaves, and all are likely to be more important during the winter when the eggs are on the leaves for up to eight months.

(i) Wind. Twigs and individual leaves bearing webbed or unwebbed batches were violently shaken on a laboratory shaker for periods of up to 36 hours. Thirty batches of each kind were tested, but no eggs were dislodged.

(ii) Rain. Leaves with webbed or unwebbed batches were supported in streams of running water, or bombarded with drops of water, for up to 24 hours. No eggs from 20 webbed batches were dislodged, and only three eggs from 15 unwebbed batches. A similar result resulted from keeping egg batches submerged in tubes of water: after 18 months a small proportion (7/138) of unwebbed eggs had become detached, but none of the webbed eggs.

(iii) Freezing. Alternate soaking and freezing, and warming and drying may affect overwintering eggs in the litter by breaking up the leaves and dislodging eggs. These conditions were repeated in the laboratory on 10 batches each of webbed and unwebbed batches. After six freezings eggs from three batches of unwebbed eggs were dislodged as well as well as one whole web of another batch. No further eggs were subsequently removed on further freezing.

Medem (1951) observed that denser webs were produced on batches collected after night frosts, and also suggested that the web gave protection against desiccation. It was shown in Section 1 that both webbed and unwebbed eggs can survive fairly low humidities and, although no comparison was made of relative humidity inside and outside the web, it is unlikely that any death from desiccation occurs when the web is absent.

The web does not afford protection against parasites and predators, and no clearly defined function was discovered during the present work. There is probably slight protection against climatic extremes. The egg-web is most fully developed in the Polypsocidae but the eggs of members of several other families of psocids may be covered with a few loose strands of labial silk. Several of these species also coat eggs with rectal matter, and apart from Clark's (1962) suggestion of protection from parasites,, the precise function of this is equally obscure. The Polypsocidae are among the highest Psocoptera, and the egg-silk may be a remnant of the greater amount of silk production which leads to a form of colonial existence in some of the more primitive families, such as the Archipsocidae (see Mockford, 1957). A few traces of nymphal webbing behaviour have persisted in the Polypsocidae (such as in <u>G. cruciatus</u> and <u>S. stigmaticus</u>), but the egg-web is found in most known members of the family. This suggests that it is functional, but in the absence of experimental proof of a protective function, the possibility of the egg-web being a relic of more pronounced silking behaviour cannot be ignored.

SECTION 9. Oviposition and fecundity of foliage-frequenting Psocoptera.

Introduction

It was shown in the previous section that the factors effecting egg mortality did not vary greatly between different tree species. The numbers of eggs, however, varied considerably and corresponded closely to the numbers of foliage-frequenting psocids, which were outlined in Section . These differing numbers can now result from two categories of factors. The survival of nymphs and adults may vary between tree species, and the fecundity of adults may also differ on different trees. Oviposition and fecundity of several species of foliage-frequenting psocids are discussed in this section.

The female reproductive system.

The reproductive system of female psocids consists of two ovaries, each with a small number of polytrophic ovarioles. The two oviducts join in a common oviduct, which leads to a highly modified and reduced ovipositor. A spermatheca is usually present, but other accessory glands are in most cases very small or absent.

The number of ovarioles is constant in a species, and it is often characteristic of the genus and of the family. Wong (unpublished) included most available data on ovariole number in different species, and many newly examined species in a Table which showed clearly that most Peripsocidae have five ovarioles in each ovary, as have Liposcelidae and Trogiidae. Most other species have four, and a few only three ovarioles in each ovary. I have compared Wong's figures for the Hong Kong psocids with those of the same or closely-related species in Britain, and for the most part they are the same. The small amount of data from North American psocids agree with these figures: Eertmoed (1966) showed that <u>Peripsocus quadrifasciatus</u>

Harris has five ovarioles. There was no variation in the number of ovarioles in large numbers of individuals of the same species dissected at Silwood, and it seems that the number is both constant and characteristic. Geographical variations in ovariole numbers have been noted in some insects, such as Orthoptera (Waloff, 1954), but it appears that this variation does not occur in the Psocoptera. The numbers of ovarioles in the British foliage-frequenting psocids are shown in Table 85.

Each oocyte is accompanied by three trophocytes. Goss (1954) showed that in Liposcelis there are four similar cells initially; one differentiates to form the oocyte and the other three become trophocytes. The number of trophocytes is remarkably constant in all the psocid species examined, and the arrangement shown in Liposcelis is probably general in the order. Different stages of ovarial maturation are found at different times in a psocid's life. There are small, fully-formed ovarioles in the last instar nymphs of many species. Sofner (1941) depicted different ovarial stages of Ectopsocus, and females of several species of known ages were dissected at Silwood. The ovarioles were removed and mounted either in polyvinyl-lactophenol containing aniline blue or in Sudan III (see Heron, 1966). Both methods facilitate counting of the oocytes, and the latter enables distinction between mature eggs and immature oocytes and trophocytes. Mature eggs remain unstained, as Sudan III does not penetrate the chorion.

Three categories of oocytes were recognised:-

1. Mature eggs. These had a regular shape, a shining chorion, and did not stain with Sudan III.
2. Large immature oocytes. These varied from nearly mature eggs to

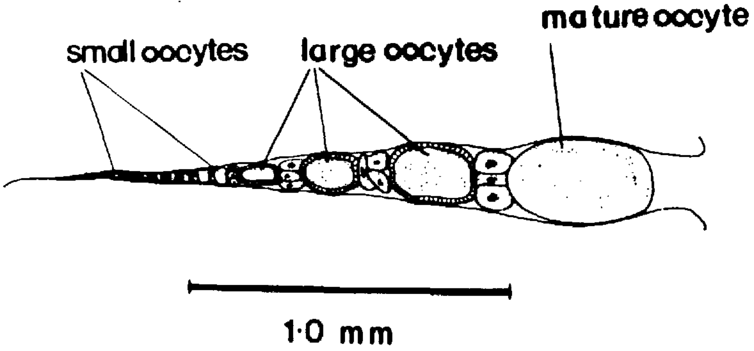
oocytes at least twice as long (measured along the ovariole) as their accompanying trophocytes.

3. Small immature oocytes. These include all oocytes smaller than the above which were sufficiently differentiated to have a distinct group of accompanying trophocytes. Numbers of smaller rudiments were frequently present in the long ovariole filament, but these were not counted.

These categories are shown in **Figs.**22-3, which also show the ovarioles of C. flavidus of known ages. The numbers of oocytes in several species reared in an outdoor insectary in 1966 are shown in Table 87 . In order to determine whether oocyte counts can provide an accurate basis for measuring reproductive capacity it is necessary to determine the extent of oocyte maturation during different periods of adult life.

Teneral females never contained mature eggs, and only rarely any large oocytes. Mature eggs are present after 48 hours, and the first egg batch may already have been laid. Seven days later, that is after two or three further batches have been laid, the total number of visible oocytes does not decrease significantly, and differentiation must still be occurring. After three weeks there was a decrease in oocyte number and a small progressive decline in numbers occurred from then onwards, only a few rudiments being present towards the end of the adult life. Under outdoor conditions therefore, differentiation continues for the first three weeks of adult life. No differences were found in any of the foliage psocids examined.

Normally, a maximum of two mature eggs occurred in any ovariole at any time. Dissections of females immediately after completion of laying a batch showed that all mature eggs were laid: none were found in



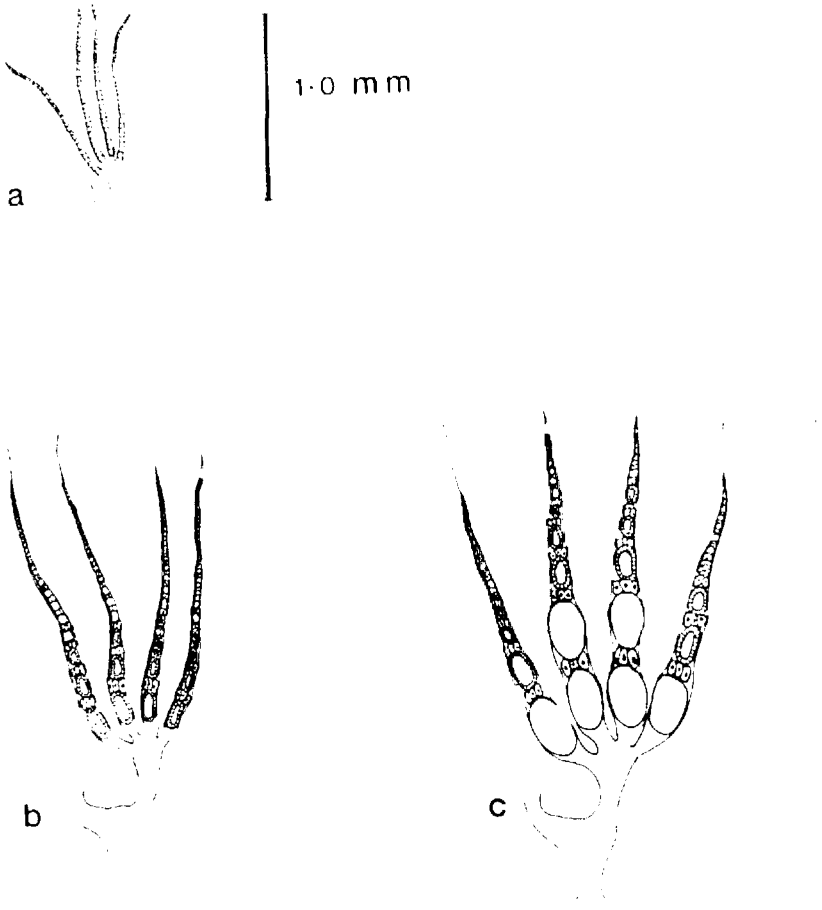


Fig.22.

Single ovariole of C.flavidus to show different stages of oocyte development.

Fig.23.

Ovary of C.flavidus at different stages. a. newly moulted sixth instar, b. teneral female, c. female more than two days old.

over a hundred C. flavidus, 76 Stenopsocus or 23 Graphopsocus dissected at this time. If no more than two eggs mature at any one time in an ovariole, and all these are laid in one batch, the normal batch should show a maximum size of 12 (Graphopsocus), 16 (Caecilius, Stenopsocus) or 20 (Ectopsocus) eggs. The numbers of eggs in many wild-collected batches are shown in Table 86 , and these figures largely bear out the above hypothesis. C. flavidus showed an average batch size of eight or nine eggs and large batches (over 12 eggs) were unusual. Similar results were found in the other species. Batches of more than 16 eggs have not been found at Silwood, although one batch was often found overlapping another giving the superficial appearance of an abnormally large batch. The few records in the literature of egg batch size of these species correspond well with the above, although Pearman (1928) recorded a batch of 31 eggs as 'the first laying of a reared female G. cruciatus'. This is certainly exceptional. Some bark-frequenting psocids regularly lay larger batches, and the presence of two mature eggs in an ovariole of Stenopsocus does not prevent maturation of further oocytes. Two specimens of S. immaculatus bred at Silwood were unable to lay; in one of them an egg had lodged across the common oviduct and prevented passage of further eggs. In both these insects oocytes continued to mature as long as feeding was possible. One eventually burst, and at the time of their deaths these two females contained 47 and 62 mature eggs. Pearman's unusual G. cruciatus might have laid only after a week or two of adult life.

The number of egg batches laid.

The intervals between deposition of successive batches reflect the time taken for the eggs to mature. 30 females of C. flavidus were reared separately on Quercus foliage at each of three temperatures, $15^{\circ}C$,

$20^{\circ}C$ and $25^{\circ}C$. They were kept at these temperatures and examined daily. Abundant fresh food was always available, and the cages were kept at 100 per cent R.H. Table 88 shows that the time of laying of the first batch decreased at the higher temperatures, but the total number of eggs laid and the number of batches were little affected. Smaller numbers of other psocid species (Table 88) gave similar results. A female sometimes laid two small batches on the same day, but the eggs laid in a single day never totalled more than 16. The intervals between successive batches tended to be smaller at higher temperatures, and rate of oocyte maturation increased.

The total numbers of eggs laid by isolated females of the nine species reared on a mixture of foods from Quercus, Crataegus and Cupressus foliage are shown in Table 89. These numbers do not vary greatly between species, except that T. dalii laid consistently fewer eggs than any of the other species.

The eggs laid total more than the number of oocytes present early in adult life. Towards the end of adult life, however, a few oocytes are present but laying becomes sporadic, or ceases altogether. The oviposition rate of reared parthenogenetic females of C. flavidus and S. stigmatucus on Quercus and Crataegus food respectively are shown in Table 90 . The greatest rates of egg production occurred when the females were one to three weeks old; subsequently there was a gradual decline to zero within a few days of death. This decline in egg production with age is widespread in psocids. It has been found at Silwood in Elipsocus, Cuneopalpus, Amphigerontia, Mesopsocus, Lepinotus and Cerobasis, as well as the above species. Psoquilla marginepunctata Hagen shows an increased oviposition rate soon after mating (Broadhead, 1961), and the gradual declines recorded in the above genera were all in isolated unmated females.

The effect of food on fecundity.

The amount and type of food available to psocids differs greatly between leaves of different tree species (see Section 10). Quality and quantity of food are known to affect the fecundity of many insects, including a psocid (Liposcelis granicola Broadhead and Hobby; see Broadhead and Hobby, 1944), and the available foods on different trees might affect the fecundity of psocids, and therefore the numbers of psocids found on those trees. Broadhead and Hobby showed that different foods significantly affected the numbers of eggs laid by Liposcelis females, and also their length of life and the duration of nymphal development. The food giving the shortest adult life-span was yeast, which also gave the largest total numbers of eggs. The oviposition rates of several species of bark-feeding psocids vary on different diets (Broadhead, 1958), but their fecundity was not compared.

Excess leaf debris and microflora on polystyrene chips (Section 10) was provided for isolated young nymphs of C. flavidus, C. burmeisteri, S. stigmaticus and E. briggsi which were then reared at 20°C and 16-hour day length at 100 per cent R.H. The 'debris' was obtained from leaves of Quercus, Crataegus and foliage of Cupressus; a green Pleurococcus from Quercus bark was also provided. 30 nymphs of each of the four species were reared on each food, and the fecundity of the adults recorded (Table 91). Teneral females reared on the food from their natural tree were transferred to other foods and their fecundity was compared.

Table 91 shows that there are consistent differences in both longevity and fecundity of the different species reared on foods from different trees. The differences were more pronounced between females, which had been reared on particular foods, than the tranferred teneral females. It is notable that, under these conditions of excess of food, these species had higher fecundity on resources from the tree species on which they are most common at Silwood Park. The fecundity of C. flavidus was greatest on oak food, and that of C. burmeisteri greater on Cupressus food than on the other diets. S. stigmaticus did slightly better on hawthorn food.

The quality of food affects both longevity and fecundity. Differences in kind and amounts of available food on the above trees are discussed in Section 10. Females of Mesopsocus lay more eggs when food was more abundant (Broadhead and Wapshere, 1966 b). When food is scarce or absent, the above species lay few or no eggs, and the number of eggs produced depends on both the quantity and quality of available food. The numbers of particular psocids species found on different trees to some extent depend on the food available. It seems that the availability of highly suitable food may be an important factor regulating the relative abundance of psocid species on different trees.

Selection of oviposition sites.

The oviposition sites of several bark-frequenting species of psocids coincide largely with the feeding sites of the adults (Broadhead and Thornton, 1955; Broadhead and Wapshere, 1966 b) and many domestic psocids scatter their eggs indiscriminately. The eggs of foliage-frequenting psocids were usually found on foliage, the only exceptions being E. briggsi and S. stigmaticus. The leaves of different tree species differ considerably in many physical and chemical characteristics, apart from the food present on their surfaces, and the following simple experiments were undertaken to detect selection of oviposition sites. The suitability of leaves of different tree species for oviposition were compared in several species of psocids. Preference for leaves showing certain characteristics may influence the occurrence of a psocid species on different species of trees.

1. *Smoothness of surface*. The leaves of the different trees from which psocids were sampled at Silwood Park differed greatly in their surface textures. They range from *Ilex* (hard, glossy, xerophytic leaves) to *Ulmus* (very rough, hard leaves) with many intermediate grades. It was shown in Section 3 that young nymphs of *C. flavidus* were unable to feed from very rough surfaces and if this is also true of the adults, few eggs may be laid on leaves of this type. *Ulmus* supports very few psocids at Silwood. Fifty reared females of each of three species, *C. flavidus*, *E. briggsi* and *S. stigmaticus* were divided into groups of ten individuals in petri dishes. They were provided with cleaned leaves of *Ulmus*, *Ilex* and *Quercus*, and a mixture of bark Pleurococci as food. The floors of the petri dishes were covered with damp filter paper, and the walls and roof coated with 'fluon'. 10 cm^2 of each of the three leaf types was used in each dish, and the egg batches laid on each kind of leaf were counted after seven days (Table 92). Very few eggs were laid on *Ulmus*, and all three species laid most eggs on *Ilex*. *E. briggsi* laid more randomly distributed batches than the other two species, but still laid most eggs on *Ilex* leaves.

If this difference in batch numbers is due to the texture of the leaf surfaces rather than their chemical properties, similar differences in oviposition responses should result from providing the psocids with a choice between chemically similar surfaces of different textures. Blank microscope slides were coated with 'seccotine', and well-washed sand scattered evenly on one side. These were allowed to dry thoroughly and then presented to psocids in petri dishes. The numbers of batches after seven days (Table 93) were far greater on the smooth unsanded surfaces than on the sanded sides. This experiment indicated that a smooth surface is attractive to ovipositing females of these three psocid species.

2. Chemical properties. Many phytophagous insects are attracted towards, or to remain on, their host plant by some olfactory or gustatory stimulus from the plant, and may leave the plant if such stimuli are absent. The chemical characters of leaves of different tree species are likely to differ greatly, and any substance on their surfaces having an attractant or repellant influence on psocids might influence the choice of oviposition site, as well as the number of psocids initially present. The above experiment indicated that the differences of suitability of Ulmus, Ilex and Quercus were due primarily to surface texture, but chemical factors have not been satisfactorily eliminated.

Four species of psocids, C. flavidus, C. burmeisteri, E. briggsi and S. stigmaticus were used to test the effect of leaf surface washings and of aqueous and alcoholic leaf extracts on the adults. The trees used were Ulmus, Ilex, Quercus and Cupressus, and the test substance was placed in the end chamber of a rectangular 'gradient apparatus' (Luff, 1964) (Fig. 24). Distilled water was used in the other end compartment as a control and to avoid large gradients in humidity, which themselves affect the movements of some psocids. Replicates of ten psocids were introduced between these extremes and their positions noted every five minutes for an hour. The apparatus was turned through 180° after every second reading, and constant top lighting was provided throughout, with a water filter between the psocids and the lamp.

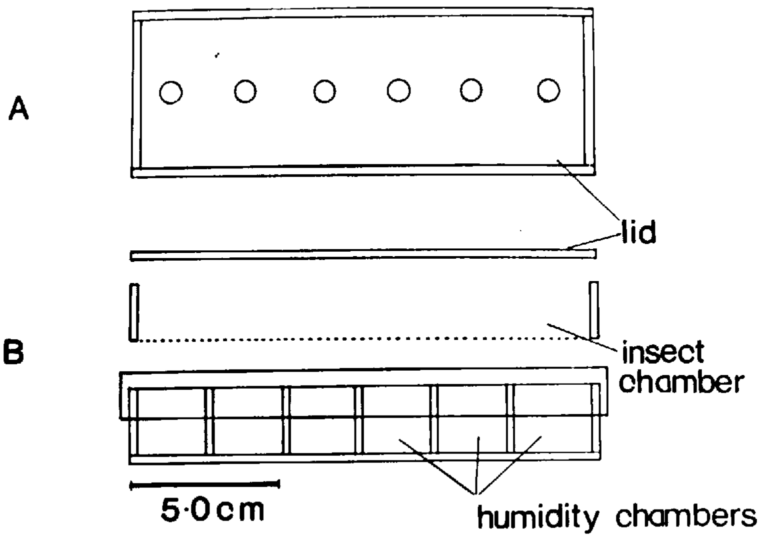


Fig.24.
Gradient apparatus used for choice experiments involving leaf washings or aqueous or alcoholic extracts of leaves. Contrasting solutions placed in two end 'humidity chambers' and psocids in 'insect chamber'.
A. Plan B. Profile.

The numbers of psocids in the different parts of the apparatus are shown in Table 94 . *C. burmeisteri* was slightly attracted to *Cupressus* leaf extracts, and these appeared to repel *C. flavidus*. The other psocids showed no strong or consistent responses to any test substance. These rather crude tests were of a very preliminary nature, and the concentrations and constitutions of the substances tested were unknown. It has been suggested (Section 4) that adult psocids flying from the litter do not actively select the species of tree on which they land, but the above results suggest that the marked coniferous/broadleaved division shown by some psocids may in part be due to an olfactory response. *C. flavidus* was very rarely found on conifers at Silwood, and *C. burmeisteri* not elsewhere. Nevertheless, when these two species are confined in the laboratory with leaves of the trees they do not normally frequent, given an adequate food supply, they will lay on those leaves; the scent of the leaves does not prevent oviposition.

3. *'Shape' of leaves*. Distinct depressions on leaves, such as those along the mid-rib and larger veins of some species are often selected as oviposition sites. In *Ilex*, for example, the points around the edges of the leaves are often turned downwards, and the angle so formed is often selected as an oviposition site by *G. cruciatus* and other species present. A secondary egg-web is often present in these situations, which may provide more sheltered conditions than on the blade of the lamina.

4. *Movement of leaves*. The amount of movement leaves undergo in wind may affect the number of psocids which settle and remain on them, and the number of eggs laid on different tree species may be thus affected. An experiment in which females of *C. flavidus* were confined in small cages on leaves of *Betula*, which were agitated on a laboratory shaker, showed

that this species will lay on rapidly shaking leaves.

Sprigs of different tree species were mounted in a small wind tunnel (Bartell, 1967) and subjected to low constant winds. Leaves with long slender petioles (Betula, Populus) were rapidly agitated by low wind speeds, whereas the larger more sessile leaves of other trees move very little in wind speeds up to 20 m.p.h.

Adults of C. flavidus were confined in a muslin cage containing twigs of Betula, which were then shaken rapidly for five days on a laboratory shaker. Only four egg batches were laid on the foliage by 50 females, whereas this number of females confined for the same period with stationary Betula foliage produced 83 batches on the leaves. In both cases, adequate artificial food was provided. It is probable that the small numbers of foliage-frequenting psocids on Betula and Populus is partially due to the amount of movement their leaves undergo.

It is clear that some characteristics of the leaves affect the numbers of eggs which may be laid on them by a particular species of psocid, either by affecting the numbers of insects originally present, or by their differential attractiveness as oviposition sites. Smooth leaves are particularly attractive to some species of foliage-frequenting psocids, and depressions on these are often selected for oviposition. Trees with rough leaves support very few foliage-frequenting psocids. Although little food is present on Ulmus at Silwood, the paucity of psocids is probably largely determined by the roughness of the leaves. These leaves were avoided as oviposition sites in the laboratory.

Trees with small mobile leaves also supported few foliage psocid Elton (1966) considered that Betula had few psocids because of its general lack of Pleurococcus. Adequate Pleurococcus is usually present in localised areas on the bark of this tree, but psocids are easily dislodged from the foliage. This may prevent initial colonisation and probably accounts for the small numbers of foliage-frequenting psocids found on this species. *Crataegus* has similar small leaves on long petioles, but the foliage appears to be much denser and the branches are much less flexible than those of *Betula* and *Populus*. The individual leaves do not move as much in wind, and fewer psocids are likely to be dislodged.

SECTION 10. The leaf surface and psocid food.

Introduction.

This section is concerned with the feeding requirements of foliage-frequenting psocids, and with the food available on leaves of different tree species. The psocids graze on leaves, and all stages of their life cycles are spent in the immediate environment of leaves. It was shown (Section 9) that some physical characters of leaves influence selection of oviposition sites: the amount of movement leaves undergo is also likely to affect the numbers of psocids dislodged from them. The fecundity of several psocid species differed when fed on food from different trees, and indicated that these psocid species would perform differently on different trees on which the available foods may differ in quality and amount. This hypothesis is further discussed in this section, in which the available foods are compared in several tree species, and in turn compared with the food ingested and digested.

The potential food of psocids on leaf surfaces.

There is only a small amount of literature on the microflora and other adventitious matter of arboreal leaf surfaces, other than accounts of pathogenic fungi. The region immediately surrounding the leaf, the phyllosphere, was studied by Ruinen (1961). She showed that micro-organisms formed a layer up to 22μ thick on leaves in Indonesia, and this thickness is probably greatly exceeded by some sooty moulds (see Fraser, 1935). The term 'phyllosphere' was used earlier by Last (1955) and Ruinen (1956), but Kerling (1958) preferred 'phylloplane' when considering actual leaf surfaces. Last and Deighton (1965) summarised most of the available data on non-pathogenic microflora of leaves, and there is evidence for at least a partial limitation of host range for several of these micro-organisms. Most groups of microflora are limited to the upper surfaces of leaves, but some are usually restricted to the lower sides. Various factors affect the amount, kind and distribution of microflora on leaves of different tree species; some of these will be considered below.

As well as microflora, many other plant and animal particles are found on leaf surfaces. Pollen grains of many kinds of plants, and bark flakes, usually occur in small numbers, and exuviae or remains of many small animals are often found. All plant and animal matter present on leaves constitutes possible food material for grazing insects. It has been shown (Section 9) that the fecundity of some psocid species differed when reared on this material taken from different tree species: the amounts and kinds of microflora on different leaves are considered here.

Techniques for examination of leaf microflora and debris.

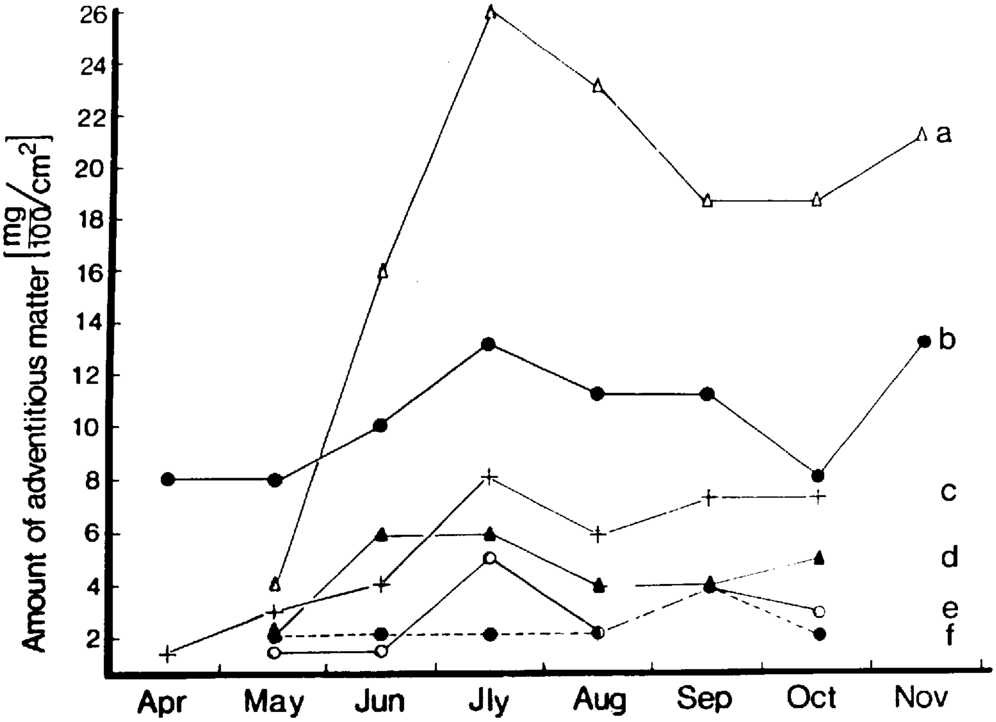
In order to compare the amounts of potential food for psocids on different leaves at any one time, the amount of food present on identical areas of different leaves was assessed. Attempts have been made to characterise leaf microflora by washing (see Voznyakovskaya and Khudyakov, 1960), but similar attempts at Silwood proved unsatisfactory because of the difficulty of recovering the washed-off material, the incompleteness of removal, and the difficulties of washing only a particular defined area of a leaf. Thus washing proved very time consuming, and provided results of uncertain value. Most conventional scraping materials may damage the leaf, and much of the adventitious matter is often lost. A satisfactory scraper of expanded polystyrene was developed in which the matter on known areas of leaves adhered to the scraper blade by electrostatic forces: very little was lost, and the area scraped could be standardised accurately. Expanded polystyrene is a cheap, easily obtainable dielectric which is soft enough not to damage the leaves and can easily be cut to any required size. Chips of this substance were cut with scraper blade length one cm, weighed on a torsion balance reading to 0.01 mg, and scraped several times over a known area of leaf, by moving the blade along a straight edge whilst held by clean forceps with the one cm axis at right angles to it. They were then reweighed and the difference in the two weights is the weight of debris removed from the area scraped. All figures in the following tables refer to areas of one cm^2. At least 200 such samples were taken from different leaves of each tree species at each sampling occasion, and no leaves with free water on the surface were used. Very little of the potential food material was lost or left on the leaves. The material can be stored on polystyrene chips for several months, and used for psocid food as required. For detailed examination of constituents it can be examined microscopically in aniline blue in lactophenol, after teasing from the polystyrene with fine needles.

This method was used to assess amounts and constituents of leaf surface adherents. The dispersion of particles on different leaves was examined on collodion peels of whole leaves. Various other substances can be used as peels, but collodion provides a useful permeable film, through which nutrient solutions can be diffused, and the microfloras grown in the absence of the leaf. This method has not been fully explored, but preliminary tests have shown that much of the leaf flora grows readily on collodion films.

The amounts, types and dispersion of adventitious matter on some leaf surfaces.

Approximately monthly samples of at least 200 x 1 cm^2 samples were scraped from different leaves taken from lower branches of each of several species of trees from April to November in 1966 and 1967. Twenty or thirty collodion peels of whole leaves were also taken on each sampling occasion. The total amounts of debris per cm^2 of adaxial surface recovered from these leaves are shown in Table 95. The ranges of amount of debris found are also given for each date. The amounts of debris on all the deciduous tree species were greater later in the season than in May and June, but during the late summer there were clear differences between species. Fig. 25 shows the monthly increments for selected tree species during 1967. An evergreen, Ilex, had more constant amounts of debris on leaves throughout the summer, and many of the deciduous tree species showed only a small increase in amounts of potential psocid food on the leaves. Quercus showed by far the greatest rate of increase, and in late summer the amounts of debris on the leaves greatly exceeded those on any other tree examined. The maximum amounts of debris were reached by August, after which no significant increase in weight was found. Large amounts of potential psocid food are therefore available on Quercus throughout late summers. Smaller amounts are found on Crataegus and Ilex but very little potential food is present on Fagus and Acer, and only negligible amounts on Betula, Populus and the other trees examined.

Comparison of the amounts of debris on upper and lower surfaces of leaves in late summer (Table 96) showed that most of the potentially available food was limited to the upper surface. This was not the case in samples taken from the litter in winter (Table 97) when there is a large amount of secondary colonisation by fungi hastening decomposition of the leaves (see Hering, 1967). Many of these are pectin-splitting fungi, which are universally amongst the first colonisers of dead leaves (see Smit and Wieringa, 1953). The amounts of debris recovered from oak



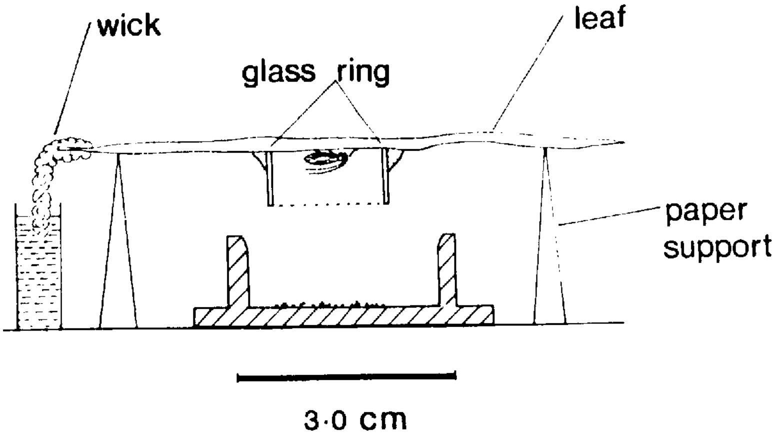


Fig.25.

Amounts of adventitious matter (microflora plus debris) on unit areas of adaxial leaf surfaces of various trees at Silwood Park in 1967.

a.Quercus b.Ilex c.Crataegus d.Fagus e.Betula f Ulmus.

Fig.26.

Small cage used to collect faeces from single psocids confined on small areas of leaf surface.

No attempt has been made to compile full floral lists for each kind of leaf; the particles present have been categorised simply into fungal spores, hyphae, algae, pollen grains, other plant particles and animal particles. No account has been taken of the bacteria and small yeasts. The first colonies of leaf surfaces are generally nitrifying bacteria which build up nitrogenous matter which enables progressive colonisation by other bacteria, yeasts, fungi and algae, but the flora of leaves towards the end of the season contained comparatively few bacterial elements. Some authors (Kerling, 1958; Etchells, Costilou, Bell and Rutherford, 1961) have shown that bacteria outnumbered fungi on several fruit and leaf surfaces throughout the year, but volumetrically and gravimetrically they are in a minority. The larger, non-bacterial particles which are present in far greater weights than bacteria are likely to be the more important food sources for insects requiring a large and rapid protein turnover for continuous egg production.

Potter (1910) developed a method of demonstrating microfloras of leaves by pressing the leaves onto gelatine plates, which were then incubated. Ten leaves each of Crataegus, Fagus, Ilex and Quercus were pressed onto plates of malt agar in September 1967, and the number of species of fungi developing on each plate after a week in the laboratory were recorded (Table 98). Only one or two fungal species were abundant on oak. More species were found on the other trees, but all were in very small numbers, and only grew from a few points on a leaf. The collodion peels indicated that there was a marked concentration of microflora along the large veins of all the species examined, and also in other depressions on the leaf; this tendency was again evident from the agar plates.

The main constituents of the oak leaf microflora were a black coccoid alga and black 'honeydew moulds'. The algal cells had parietal chloroplasts and appeared to be *Pleurococcus*. Most authors consider that this genus is monotypic, and the dark small cells found on leaves may represent a nutritional variety of this alga, resulting from honeydew. Samples have been sent to several experts, but the taxonomy of these algae is badly in need of revision, and no definite identification has been possible. This alga was present in large quantities towards the end of the season and represents the climax vegetation of deciduous oak leaves at Silwood. It was found only on *Quercus*, but a similar alga was common on the bark of *Crataegus*, but no alga was found on oak bark which resembled that on the leaves. The foliage of *Cupressus* is often covered with a green *Pleurococcus*, as found on the bark.

The 'honeydew moulds' were always present on oak, but the taxonomy of these is incompletely known. Their classification was discussed by Fraser (1933) and Fisher (1939). Spores were found which resembled Fraser's (1935 a) figures of *Capnodium* and (1935 b) *Atichia*. Fisher recognised six families of sooty honeydew moulds, but beyond noting that members of the Capnodiaceae and Atichiaceae (*sens* Fisher, 1939) were found commonly on oak at Silwood Park, identification is uncertain.

Leaves on different species of trees growing close together, in some cases with contiguous foliage, bore microfloras of very different kinds and amounts. Different constituents of the microflora appeared to be partially host-tree specific, but the flora on oak leaves was exceptional both for its amount and its uniformity. Many Quercus leaves were covered with a black layer of adventitious fungi and algae, but this was only rarely found on other tree species. There is some evidence that the amount of microflora increases with increasing age of the leaf (Kerling, 1958; Ruinen, 1956; Stout, 1960), but extraneous factors are also important in influencing the abundance of many micro-organisms. The trees examined at Silwood had very small weights of microflora on the very young leaves early in the summer, but the weight per unit area became finite on older leaves. There is considerable evidence (See Last and Deighton, 1965) that leaf materials entering water droplets on the leaf surfaces, and the differing chemical characters of leaf exudates, influence the development of fungi. Both inorganic and organic guttation products are important, and the relatively small amounts of data in the literature suggest that the fungal products are to some extent host-specific. Several typical leaf colonisers have been recovered from sugar solutions exuding from plant wounds and can probably also grow in insect honeydew (Last and Deighton, 1965). Honeydew has specific microflora associated with it: the sooty moulds characteristically grow in this habitat. The range of insects which produce honeydew, which are often extremely host-plant specific, have been reviewed by Zoebelein (1956). Honeydew is an important factor influencing the amount of microflora on leaves. It acts as a 'sticky trap' for spores, thus increasing the proportion of drifting spores trapped, and limiting dispersal of subsequent generations, and also greatly reduces the amount of microflora which is washed off by rain. On oak, which had abundant honeydew (produced by Tuberculoides annulatus Htg.), leavew on the inside and outside of the canopy did not differ in amounts of microflora, whereas other tree species without honeydew had most debris on the less exposed leaves. Honeydew also enables more rapid colonisation of leaf surfaces to the 'climax' stage. Ruinen (1961) implied that a succession of nutrient stages occurred on leaves, with a build up of nutrients from successive groups of colonising organisms. Some sugars in honeydew are unfavourable to some fungi, but a preponderance of honeydew early in the summer was probably the main cause of the large amounts of potential psocid food on oak at Silwood. Honeydew was also present on other trees at Silwood, notably Fagus (Phyllaphis sp.), Tilia (Eucallipterus tiliae L.) and Acer (Drepanoriphum platanoides Schr.); all these occurred much later in the year, and little food was ever found on the leaves of these trees. Bird-droppings may also provide a source of available nitrogen for fungi, but are usually washed off the leaves within a comparatively short time.

The approximate percentage compositions of the debris and microflora from 40 collodion peels of each of several tree species are shown in Table 99 . It is again clear that there are notable differences in the flora of different tree species. The total potential food available to psocids grazing on the leaves differs markedly in both amount and type. These differences are related mainly to characters of the leaf surface, but also depend on the exposure of the leaves to wind and rain, and to some extent on the age of the leaf.

The actual food of foliage-frequenting psocids.

It has been shown that the total potential food available to psocids differs on leaves of different tree species. The following account considers tha actual food of these psocids. Any selection of, or preferences for, individual constituents of the microflora would be important in considering the comparative diets of these animals, and necessitates examination of the food ingested and digested, as well as that available. Selection of food particles by psocids may occur at two levels, namely (1) at the time of ingestion and (2) during the passage of food through the gut. If no selection of food occurs, and the insects graze haphazardly, the differences in the leaf microfloras can be directly taken as the differences in the diets of psocids feeding on the leaves. The fecundity of the psocid species examined differed when they were fed on food from different leaf species (Section 9). This implies either that the microflora, that is the total foods available, differ in their suitability for these psocids, or that one or more particular constituents, which are actively selected as food, are present in different proportions on different leaves.

There is evidence that some bark-frequenting psocids prefer a particular kind of food when others are available (Broadhead, 1958), but this selection occurred mainly when the foods, lichen and Pleurococcus, were growing in discrete areas on dead and living larch twigs respectively. No data are available on whether psocids prefer - or select - particular particles growing in an intimate mixture or in small intermingled groups. Elipsocus mclachlani feeds only on fructifying cups of lichen, whereas Reuterella helvimacula grazes all the lichen (Broadhead, 1958), Broadhead and Wapshere (1966 b) produced slight evidence for particle selection related to the size of the psocid grazing; the larger nymphs of Mesopsocus that they examined had ingested more bark flakes than did the small nymphs.

The crop contents and faecal pellets of several species of foliage-frequenting psocids have been compared, and in turn related to the possible food present on the leaf surface. Three sets of 40 adults from each of the species E. briggsi, S. stigmaticus, C. burmeisteri and

C. flavidus were individually confined on leaves of Quercus (abundant food, mainly 'honeydew moulds'), Crataegus (smaller amounts of food, greater variety) and small fronds of Cupressus (almost wholly Pleuroccus). At the start of this experiment the left side of the upper surface of each leaf was covered with collodion to prevent grazing. When the psocid was removed, the rest of the leaf was painted with collodion. Comparison between the two peels from each upper surface indicated the amount and type of food grazed. In all cases at least 5 cm^2 of upper leaf surface were available to the psocid. These psocids were dissected after five days and their crop contents and faecal pellets were examined microscopically after teasing out in lactophenol containing aniline blue (Broadhead, 1958). Ten faecal pellets from each psocid were examined. The results of this experiment (Table 100) showed that these psocids grazed readily and apparently indiscriminately on all the foods offered. Under these conditions of excess food availability, the faeces contained large proportions of undigested material, and when the food constituents were mixed (Crataegus) the faecal contents did not differ greatly in relative composition from the crop contents, except that the proportion of unidentifiable material ('other' in Table 100) was higher. This included digested or partially digested matter. Some food was always present on the leaf surfaces after this experiment.

Similar results were obtained when nymphs were substituted for adults (Table 100). Small and large nymphs both fed indiscriminately, and there was little evidence of selection of particle size or type. Parts of large animal exuviae were found even in wild-collected second instar nymphs of C. flavidus, and the large number of crops of wild-collected psocids examined in 1967 indicated that there was little selection of particles from the leaves (Table 10e). It was, however, clear that most of these psocids fed from the leaves, and not from nearby bark. Many *Stenopsocus* from *Crataegus* had little *Pleurococcus* in their guts: little is present on the leaves, but much on the bark. Similarly, *C. flavidus* from *Quercus* only rarely contained the large *Pleurococcus* cells common on the bark.

The faeces usually contain a high proportion of utilisable food, and it appears that an inefficient digestion is compensated for by a rapid rate of food passage through the gut (about four hours in *C. flavidus*). Whereas some of the gut and faecal contents are unrecognisable, the faeces contained many apparently undamaged algal and fungal cells. Pollen grains and bark flakes are present in very small quantities on the leaves, and appeared to undergo little change in the gut. These particles may not be utilised as food by foliage-frequenting psocids, but otherwise there is little internal selection of particle type. Single faecal pellets from these psocids rapidly gave rise to colonies of fungi similar to those on the origanal leaf when left on plates of malt agar. Most of the psocids' faeces remain on the leaf near the original feeding site, and it is likely that recycling of some of the undigested food occurs. Coprophagy has been observed in the laboratory on many occasions, and the healthy spores in faeces can recolonise the leaf surface. Production of faeces containing large amounts of undigested material may therefore increase and prolong the available food supply in the psocids' habitat.

When only a little food is available, much less undigested food passes through the body. Table 101 shows the faecal composition on consecutive days of adults of *C. flavidus* which were confined to a small area of leaf (2.8 cm^2) by glass rings waxed onto the leaf (Fig. 26).

Almost all the faeces were removed from the leaf as they were produced, and single psocids lived for up to 15 days on these small areas of leaf. After this time collodion peels showed that almost no potential food remained on the leaf. It is clear that an increasing proportion of the food was digested as less became available. Holling (pers. com. 1967) considers this to be a functional response of the insect to a changing environment, and has found parallel cases in several other insects (unpublished). The rate of faecal production did not decrease greatly until food became very scarce. These psocids grazed the leaf surfaces throughout the day and night. Faeces were collected from C. flavidus with abundant food at two-hourly intervals over two separate 24-hour periods. No peak periods or cycles of feeding were detected.

It is evident that the foliage-frequenting psocids examined do not actively select any particular size or kind of particles from those present on the leaves, but graze indiscriminately. The actual food of these psocids does not, therefore, differ from the potential food present on the leaves. The microflora of different leaf species vary in their suitability as foods for different psocids, but the amount of suitable food is closely correlated with the abundance and fecundity (Section 9) of particular species. C. burmeisteri does better on Cupressus debris, which closely resembles bark flora. C. flavidus is well adapted to the abundant 'honeydew moulds' on Quercus leaves at Silwood, and S. stigmaticus does better on a mixture of constituents. The particular nutritive factors causing these differences have not been clarified. Many of the microflora can be grown easily in pure culture, and rearing psocids on these should indicate whether any particular flora have major influences on fecundity and longevity. Clarification of the metabolism and chemical analysis of such species may eventually isolate the particular factors involved.

Only a few groups of insects have exploited leaf microflora as food, and no experimental data on relative suitability of different foods is available. Many Collembola pass undigested material in their faeces, and can be cultured on agar plates as earlier described for Psocoptera (Healey, pers. com. 1968). Only a few species of Collembola, mainly Entomobryidae, are arboreal, and most of these are found on or under bark. Some are probably minor feeders on leaves. Ants, whilst tending honey-dew-producing aphids, clean much of the leaf surface of adventitious matter Many groups of phytophagous insects incidentally ingest microflora whilst devouring foliage, and may destroy much of the habitat available to foliage frequenting psocids.

SECTION 11. Discussion.

Several of the psocid species discussed in this thesis, notably C. burmeisteri and S. stigmaticus, were found only on one or two tree species, and others (such as C. flavidus) were found in strikingly different numbers on different tree species at some times of the year. Others were widely distributed on many tree species, but never in large numbers. Large numbers of particular species of foliage-frequenting psocids occurred only in late summer on particular tree species, although small numbers of the same species were often found concurrently on other trees. Some of these foliage-frequenting psocid species therefore showed 'host'-tree specificity and others, an 'acquired' 'host'-tree specificity which became more pronounced during late summer. This is largely determined by characters of the foliage of the different tree species which affect the suitability of the leaves as oviposition sites and influence the growth of adventitious microflora on which the psocids feed. The term thus differs in meaning from 'host specificity' as applied to truly phytophagous insects, which feed on the actual host plant rather than on adventitious matter, and more resembles 'antibiosis' (Painter, 1958). Host specificity in phytophagous insects is often largely determined by chemical factors influencing attraction to, and feeding on, the plants (see Schoonhoven, 1968). There is some evidence of olfactory selection of the host plant by foliage-frequenting psocids at the coniferous/broadleaved level, but otherwise chemical stimuli appear to be of little importance. The coniferous/broadleaved division of habitats is probably inherent and fundamental in these psocids, as in many groups of phytophagous insects. Thus Benson (1950) stated that no recent species of sawfly is known to feed on both conifers and angiosperms, although different species in the same genus (e.g. *Pristiphora*) may feed on plants in these two main groups. Recently Mockford (1965 b, 1966) produced evidence to show that separate natural species aggregates of some North American *Caecilius* species were found on grasses, sedges and Palmaceae, on coniferous foliage, and on foliage of broadleaved trees. Several authors (Holzapfel, 1936; Broadhead and Thornton, 1955; Broadhead and Wapshere, 1966 b) found very different numbers of various species of bark-frequenting psocids on different tree species, but there does not appear to be any large degree of host tree specificity in these species, except that a few species again show a division between coniferous and broadleaved trees (see New, 1968). The constitution of bark microflora does not differ greatly on different tree species, and is composed of comparatively few species. The foliage-frequenting habit is probably at an early stage of development in psocid species found predominantly on evergreen conifers, on which the foliage microflora closely resembles that on bark, more advanced in species mainly confined to such broadleaved trees as *Crataegus* and *Ilex* on which there is a mixture of food constituents, and reaches its most advanced form in species such as *C. flavidus* which are well suited to a highly specialised leaf microflora such as that found on *Quercus* at Silwood Park. Different species of Polypsocidae are therefore associated with different groups of tree species, and it seems that the most advanced species are those found solely or predominantly on foliage of broadleaved trees. The three species of Stenopsocinae appear to be comparatively unspecialised foliage psocids. Broadhead and Wapshere (1960) recorded small numbers of *S. immaculatus* and *G. cruciatus* on larch, and their eggs were then laid on bark, as were some eggs of *S. stigmaticus* on *Crataegus* at Silwood. Oviposition on bark and partial presence of a nymphal feeding web are both probably archaic characters.

It is again emphasised that psocids are not phytophagous in the accepted sense: the 'host' tree merely provides a substrate for their food. The present work has shown that 'acquired host-tree specificity', is a real phenomenon is several species of foliage-frequenting psocids, an has revealed several important biological characters in which this group differs from other psocids, which predominantly frequent bark or stored products. All seven Polypsocidae discussed have a well-defined web of labial silk covering the egg batches. Batched eggs of bark-frequenting psocids are typically covered with faecal material, and it is interesting to note the persistence of this habit in <u>E. briggsi</u> , which has varying amounts of such material incorporated in the egg web, and in <u>T. dalii</u> where the encrusted eggs are often suspended on silken lines above the leaf surface. The function of the egg web is not clear. No British foliage-frequenting psocid is univoltine, and those frequenting deciduous trees are characterised by a well-defined 'alternation of habitats' in which generations are passed in the litter and on trees each year. This division of habitat greatly complicates any population study of these insects, especially as small numbers of psocids are also removed from the trees during rough weather at other times of the year. These can survive in the ground litter and later return to the trees. In phytophagous insects with limited host plant range, those individuals similarly knocked off trees are removed from the population and classed as 'mortality': in a psyllid, <u>Cardiaspina</u>, Clark (1962) showed that many eggs were removed from trees on foliage and were lost. This complication, which necessitates concurrent examination of litter and tree samples, does not occur in bark-frequenting psocids (see Broadhead and Wapshere, 1966 b). Eggs of foliage psocids on leaves may be blown considerable distances from their 'parent' tree and hatch in a different kind of litter. Immature stages of many phytophagous insects on trees are dispersed passively by wind or 'silking' (Morris, 1963; Leonard, 1967), but again any which fail to find a new host tree of the same or similar species die. Aphids landing on an unsuitable host plant often take off again (Kennedy, 1965). Landing is an active process in aphids (Kennedy, 1965), and probably also in other small insects under comparatively calm conditions (see Lewis, 1965). Psocids do not appear to actively leave an unsuitable 'host' tree, as shown by the more random distribution of such species as *C. flavidus* early in the season after flying up from the litter, but the opportunities for dispersal of the adults of foliage species are largely governed by this alternation of habitats, and are more limited in those species frequenting evergreens. Those species which alternate between litter and trees (*E. briggsi*, *C. flavidus*) showed well-defined peaks of flight activity at the time of movement from litter to trees. This peak was not shown in suction trap catches of species on evergreen conifers (*C. burmeisteri*), species with most individuals on broadleaved evergreens (*G. cruciatus*) or in species on deciduous trees, whose growth habit makes wide distribution of litter unlikely (*S. stigmaticus* on *Crataegus*), but these species are all relatively scarce at Silwood. In common with many other small insects, many psocids are likely to become incorporated in the aerial plankton and may then drift a considerable way from their original habitats. The chance to reach, and settle on, a variety of tree species is greatest in species which undergo a period of voluntary flight. The life histories of foliage-frequenting psocids on different tree species therefore affect the dispersal potential of the adults. The Polypsocidae are among the most advanced psocids and the life histories of some species enable them to exploit temporary habitats such as the foliage of deciduous trees.

Different characters of foliage of different tree species affect the distribution of psocids in early summer. The amount of movement of foliage affects the ease with which psocids can settle and remain on the leaves. There are few species of small insects associated with the foliage of *Populus* and *Betula*, and examination of the effect of foliage movement on other groups of insects may clarify the reasons for this. Smooth leaves are more attractive than rough ones for oviposition of several psocid species, and may also be more accessible feeding sites for young nymphs. There is, however, no limitation to leaves of a particular age, as occurs in *Cardiaspina* (Clark, 1963), although the available food may differ on leaves of different ages.

Several factors are important in regulating the subsequent distribution and abundance of particular psocid species on different tree species. The most important of these appears to be the amount and quality of available food, and its effect on fecundity. Food must be regarded as a limiting resource, but the amount on unit areas of *Quercus* foliage at Silwood greatly exceeded that on other broadleaved trees during the summer. The fecundity of *C. flavidus* was greater on this specialised diet of honeydew moulds (see page 141) and black algae than on food from *Crataegus* or *Cupressus* leaves. Similarly, the fecundity of *C. burmeisteri* and *S. stigmaticus* was greatest on food from the foliage they usually frequent. Psocids again differ from foliage-eating insects, as they do not diminish the amount of substrate available for food growth: food is rapidly replaced by fast growth and by regeneration from psocid faeces, but may at times become scarce enough to produce some competition between individuals or species. As is the case with the bark-frequenting Mesopsocus species (Broadhead and Wapshere, 1966 b), the coexistence of small numbers of different foliage-frequenting species appears to be a fairly stable situation. The numbers of several species are large in late summer, but these species are mainly segregated on different tree species. E. briggsi and C. flavidus are both abundant on Quercus, but the numerical peak of E. briggsi occurs later than that of C. flavidus. Much food was present on the foliage at this time, and did not become scarce. Both species will take all of the food present, so that the general statement of Lack (1944) that spatially overlapping species often have different food preferences in not tenable in this instance. All the foliage-frequenting psocids examined will accept various kinds of food, but these foods differentially affect the psocids' longevity and fecundity. It can be argued, for example, that an individual of C. flavidus on Cupressus compares disadvantageously with one of C. burmeisteri, and with a C. flavidus female on Quercus, because of the relative effects of food on fecundity. The characteristic leaf floras of different deciduous trees do not develop until mid-summer, but the development of these characteristic floras is probably the greatest single factor influencing the gradual divergence of relative numbers of such species as C. flavidus on different tree species.

The food therefore influences the fecundity of these psocids, but the proportion of eggs which survive on different trees does not differ markedly. A constant proportion destroyed will leave different numbers of survivors on different trees if different numbers are initially present. Depending on the amount of redistribution of litter that occurs at the time of autumnal leaf-fall and during the winter, many of the adult psocids of the spring generation will fly onto the trees on which the eggs were originally laid, and only a minority of S. stigmaticus, for example, appear to be dispersed from the original habitat. In more open litter, such as that of Quercus, more adults of C. flavidus will become widely dispersed, but again more are likely to reach oak than other tree species. A small excess of adults on Quercus at this stage may result in many more nymphs. This difference in numbers is accentuated by parasitism of the nymphs by species of Leiophron. Only the first arboreal generation of foliage-frequenting psocids is affected by these braconids, and about half of these nymphs were parasitised on all the tree species examined. Again, a fairly constant proportion of nymphs was attacked, and by the end of the first arboreal generation of C. flavidus, there was a large discrepancy between the numbers on oak and other trees. Freedom from nymphal parasitism in the next generation, together with the presence of a well-developed leaf microflora at this time, enables further growth of the populations. The percentage parasitism is not clearly related to the host density, but the parasites are fairly specific. Several species of Alaptus and Leiophron parasitise only eggs or nymphs of the foliage-frequenting psocids. There are thus no alternative hosts, of which the abundance could affect the amount of parasitism of these psocids. The parasites also differ from those infesting Mesopsocus (Broadhead and Wapshere, 1966 b) where univoltine parasites attacked univoltine hosts. A univoltine parasite which is limited to breeding in one generation of a bivoltine or trivoltine host species is unusual, but subsequent absence of parasitism may produce marked differences in mortality in different host generations.

The amount of predation on psocid nymphs and adults by other arthropods is not clear. Many kinds of invertebrate predators found on various trees probably take some psocids, but these are likely to be of less importance when much alternative prey is present, as on Quercus. None are at present known to select psocids to the exclusion of other prey, or to be markedly prey specific. Some psocids are likely to be taken by birds (Betts, 1956; Broadhead and Wapshere, 1966 b) but there is at present no evidence that birds actively search out psocid prey, as Clark (1964) found some birds to do for Cardiaspina.

The data considered in this thesis were obtained in one area over two seasons. Psocid abundance and distribution were similar in the two years, but it is not known how general and widespread are the factors affecting relative abundance on different tree species. In all cases where a strongly non-random distribution of a foliage-frequenting psocid was found on different broadleaved trees, a study of the relationship between the psocid species and the facilities provided by the foliage of different trees provided valuable clues as to the mechanisms of this habitat limitation. Isolated samples of psocids from trees at any one time of the year are often misleading. The factors found to be important in regulating abundance are likely to be of general occurrence, but their magnitude and relative effects may vary from area to area. For example, the large amount of food on Quercus foliage at Silwood Park was caused in part by honeydew; the abundance of aphids may therefore affect the number of psocids on a tree. Psyllids and coccids may similarly affect psocid abundance, but this has not been noted at Silwood Park. Any future comparison between different leaf surfaces, especially in relation to chemical characters and specificity of microflora may lead to clearer understanding of their characteristic complement of psocids. This work has been concerned mainly with psocids frequenting foliage of broadleaved trees. Any confirmation of tree-specific microflora on different species of coniferous trees could lead to valuable future work. Some of the factors that appear to be important in affecting the relative abundance of the same psocid species on different trees have been considered, but much remains to be discovered by specialists in different disciplines.

Summary.

1. Rearing methods for Psocoptera in the laboratory are described. Several foliage-frequenting species were reared under conditions of controlled humidity and temperature. Development is accelerated at higher temperatures, up to about 30°C. Differences in tolerance of desiccation of eggs of foliage and bark-frequenting psocids were found to be related to oviposition site, and similar differences in nymphal tolerance were again related to their primary habitats.

2. The early stages and life histories of nine species of foliage-frequenting psocids are described. Figures and keys show the main structural characters that were used in generic identification, but specific characters were often less well-defined. All nine species are bivoltine or trivoltine. Seven of them overwintered only as eggs, but a proportion of E.briggsi and S.stigmaticus overwinter as nymphs and adults Overwintering in these two species is discussed and compared with that in a bark-frequenting psocid, E.hyalinus.

3. Psocoptera were extracted from several kinds of leaf litter by Tullgren Funnels and by a Kempson Bowl Extractor. The efficiencies of the two methods were compared. Litter psocids fall into three categories according to their degree of dependence on the litter as a habitat. The spring generation of species laying on deciduous foliage is passed in the litter, but these species are subsequently rare in the litter. They show a distinct 'alternation of habitats' in which complete generations are passed in litter and on trees each year.

4. Sampling methods for foliage insects on trees are discussed, and the difficulties of standardising samples between different tree species are noted. Psocoptera were sampled by beating from a range of tree species

during 1966 and 1967. Several psocid species were confined to one or two tree species (C.burmeisteri, S.stigmaticus) but others, especially bark-frequenters, were found on many trees. The numbers of some species of foliage psocids increased greatly throughout the summer and the distribution of C.flavidus became much less random between tree species as its numbers increased.

5. Dispersal of eggs and nymphs is largely passive. Catches of adult psocids in suction traps over seven seasons were examined. Several species were found mainly at times when they were actively flying, either from litter onto trees or to or from overwintering sites. Few species were common, and there was some correlation between the primary habitats of some species and their relative numbers in suction traps at 1.3m and 9.2m above ground level. Autolysis of flight muscles does not occur in the species examined but several species show alary polymorphism. This is briefly discussed.

6. The biology of two groups of hymenopterous parasites of psocids is discussed, especially in relation to their fecundity and hostspecificity. Several mymarids of the genus Alaptus parasitise psocid eggs but often only some eggs in a batch are parasitised. A.pallidicornis Foerst. and A.richardsi Hincks predominantly parasitise eggs of foliage-frequenting psocids, and other parasitic species are commonly found in eggs of bark-frequenting psocids. The species parasitising foliage psocids are polyvoltine. Braconids of the genus Leiophron (Euphorinae) parasitise psocid nymphs, and there is a similar separation into species parasitising bark and foliage psocids. Leiophron species are univoltine and attack various instars of the first arboreal generation of psocids. Many psocids are killed by Leiophron in this generation, but the next generation of

species such as C.flavidus is free from parasitism. The early stages and life histories of these parasites are described.

7. Most of the predatory arthropod species on trees probably take some Psocoptera, although those tested did not select psocids to the exclusion of other prey. Many probable predators were found on trees with a wide range of prey but on other trees, notably Cupressus, psocids were virtually the only possible prey of the few predators found.

8. Collections of egg batches were made from different habitats throughout the year and the various factors causing egg mortality assessed. Total mortality of eggs did not vary greatly between different sites or at different times of the year. The function of the silken web overlying eggs of the foliage psocids was investigated but remains unclarified.

9. The size of egg batches of foliage psocids is related to the structure of the female reproductive system. Several species prefer a smooth surface for oviposition. The fecundity of several species differs on food from different tree species. Selection of oviposition sites and fecundity are discussed in relation to the facilities provided by various tree species.

IO. Different characters of leaves influence the number of psocids on them. The amount of movement leaves undergo influences the ease with which psocids can settle on them and the ease with which they are removed in rough weather.

II. The amount and quality of potential psocid food on the leaves of different tree species were compared at different times of the year. The total amount of food varied considerably on different tree species, and the factors affecting this are discussed. Particular microfloras were found on leaves of different tree species. The total potential food available was compared with the actual food of psocids and it was found that little selection of particles occurred.

I2. The development of an 'acquired host-tree specificity' in some foliage-frequenting psocids results largely from characteristics of foliage on different tree species, which leads to differences in life histories, fecundity, and opportunity for dispersal. Some of the possible mechanisms of this are briefly discussed in relatiom to the evolution of the foliage-frequenting habit.

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Appendix I.

Specific identifications of trees and bushes from which Psocoptera were sampled at Silwood Park during 1966 and 1967.

Acer pseudoplatanus L.	Sycamore.
Aesculus hippocastanum L.	Horse chestnut.
Betula pendula Roth	Silver Birch.
Crataegus monogyna Jacq.	Hawthorn.
Cupressus (various introduced species).	
Fagus sylvatica L.	Beech.
Ilex aquifolium L.	Holly.
Pinus sylvestris L.	Scots Pine.
Populus nigra var. *italica* Duroi.	Lombardy poplar.
Quercus robur L.	Common Oak.
Q. petraea (Mattuschka) Liebl.	Sessile Oak.
Sarothamnus scoparius (L.) Wimmer ex Koch.	Broom.
Tilia x *europaea*	Common Lime.
Ulmus glabra Huds.	Wych Elm.

Table 1. The species of psocids reared by different methods described in the text.

(+ = reared for at least one generation, x = unsuccessful rearing attempt)

Species:	Method				
	1	2	3	4	5
T. sexpunctatum	+	+			
L. fasciata	+	x			
L. variegata	+	+			+
A. bifasciata	+	+			x
A. contaminata	+				+
S. immaculatis	+	+	+	+	x
S. stigmaticus	+	+	+	+	x
G. cruciatus	+	+	+	+	+
E. lucifugus	+	+			
T. dalii	+	+		+	
C. fuscopterus	+	+	+	+	x
C. flavidus	+	+	+	+	+
C. kolbei	+	+		+	+
C. burmeisteri	+	+		+	+
P. phaeopterus	+	+	x		
P. subfasciatus	+		x		
P. alboguttatus	+		x		
E. briggsi	+	+	+	+	+
M. unipunctatus	+	+			x
M. immunis	+	+			x
C. cyanops	+	+			
E. hyalinus	+	+			
E. westwoodi	+	x			
E. mclachlani	+	x			
P. picicornis	+	+			
L. paetus	+	+			+
L. bostrychophilous	+	+			+
P. ramburii	+				+
L. patruelis	+				
C. guestfalica	+	+		+	+

Table 2. Duration of egg stage of some British foliage-frequenting psocids at different constant temperatures. (All at 100 per cent R. H.)

Psocid	15			20			25			30		
	No. of batches	Duration (days)	Mean	No. of batches	Duration (days)	Mean	No. of batches	Duration (days)	Mean	No. of batches	Duration (days)	Mean
E. briggsi	25	12-16	14.4	34	6-9	7.4	50	4-8	6.8	26	-	
T. dalii	12	14-19	16.6	8	7-11	9.6	8	4-8	6.6	5	-	
S. immaculatus	36	13-17	14.1	52	6-9	8.0	29	4-7	6.4	15	-	
S. stigmaticus	28	13-16	14.8	23	6-9	7.8	17	5-8	6.8	12	-	
G. cruciatus	22	12-19	14.6	35	6-9	7.75	18	5-8	6.8	24	7.0(1 batch)	
C. flavidus	54	11-14	12.5	71	6-9	7.3	38	4-8	5.2	30	6.0(1 batch)	
C. burmeisteri	26	11-14	12.5	18	7-9	8.0	26	4-7	5.5	15	6.0(1 batch)	
C. fuscoptera	15	12-16	14.6	12	6-8	7.3	6	4-8	6.0	8	-	
C. kolbei	23	11-14	13.2	14	6-8	7.0	18	5-9	7.6	15	-	

Table 3. Development of webbed and unwebbed batches of C. flavidus at different relative humidities.

R.H.%	Webbed batches			Unwebbed batches		
	Total no. of eggs	No. developing	%age developing	Total no. of eggs	No. developing	%age developing
100	104	103	100	123	123	100
90	79	74	93	130	121	93
76	44	44	100	75	73	97
64	91	86	94.5	126	121	96
58	57	49	86	92	88	95.7
45	86	76	88.3	135	120	88.9
33	89	61	68.3	137	106	80.0
20	90	14	15.5	108	26	24.1

Table 4. Duration of egg stage of some British foliage-frequenting psocids at different relative humidities. (All at 20°C)

Development:	Relative humidity (per cent)											
	90			76			64			45		
Psocid	No. of batches	Duration (days)	Mean	No. of batches	Duration (days)	Mean	No. of batches	Duration (days)	Mean	No. of batches	Duration (days)	Mean
E. briggsi	16	6-9	7.8	23	6-10	8.5	18	5-9	7.7	20	6-9	8.0
S. immaculatus	12	6-9	7.5	12	6-9	7.5	9	6-9	8.0	12	6-8	7.0
S. stigmaticus	15	6-9	7.8	15	6-9	8.2	8	6-8	7.0	8	6-9	6.8
G. cruciatus	8	6-10	8.0	5	6-8	7.4	16	6-10	8.7	12	6-8	7.6
C. fuscopterus	12	7-9	8.3	15	6-9	7.8	18	7-9	8.0	15	7-9	7.8
C. burmeisteri	10	6-9	7.5	12	6-9	7.8	24	6-9	7.4	11	6-9	8.2

Table 5. Development times of nymphs of some British foliage-frequenting psocids at different temperatures. (All at 100 per cent R.H.)

	Temperature (°C)								
	15			20			25		
Species	No. of nymphs	Duration (days)	Mean	No. of nymphs	Duration (days)	Mean	No. of nymphs	Duration (days)	Mean
E. briggsi	30	32-44	37	30	18-27	22	30	14-18	16.2
T. dalii	22	41-49	45	25	34-42	38.4	20	26-32	29.6
S. immaculatus	26	36-45	38.4	30	25-32	28.6	30	18.23	21.5
S. stigmaticus	20	32-39	36	36	26-32	29.4	35	21-26	23.6
G. cruciatus	20	37-44	40.5	20	26-32	28.2	20	16-23	20.3
C. flavidus	28	38-47	42	43	20-29	24.6	35	16-23	20.6
C. burmeisteri	20	33-41	37.7	20	22-28	25.0	20	17-22	19.8
C. fuscopterus	20	36-45	40.6	20	19-24	22.5	20	18-22	20.6
C. kolbei	22	39-49	46.4	20	23-28	26.4	20	18-24	21.4

Table 6. Survival of nymphs of various arboreal psocids at different relative humidities. (Nymphs transferred from 100 per cent R.H. immediately after hatching.)

	Relative humidity (per cent)											
	100		90		76		58		45		33	
Species	No. hatching	No. completing development	No. hatching	No. completing development	No. hatching	No. completing development	No. hatching	No. completing development	No. hatching	No. completing development	No. hatching	No. completing development
E. briggsi	100	94	100	96	70	65	100	72	100	8	65	0
T. dalii	46	44	30	28	30	29	25	7	30	2	30	1
S. immaculatus	80	78	90	86	100	84	100	80	56	11	77	4
S. stigmaticus	80	76	80	76	80	76	75	43	80	15	60	0
G. cruciatus	40	40	40	38	40	39	40	32	40	9	40	0
C. flavidus	100	98	100	96	80	74	80	53	100	11	100	1
C. burmeisteri	45	43	26	24	50	38	50	38	40	8	44	3
C. fuscopterus	25	24	30	27	30	18	30	16	20	3	24	0
C. kolbei	25	25	30	28	30	28	30	21	30	9	30	4
M. immunis	20	18	20	17	20	20	20	18	18	15	20	14
E. hyalinus	40	40	40	37	52	50	30	24	46	42	35	22
C. cyanops	25	25	17	15	20	18	16	14	19	13	23	9
P. picicornis	18	16	24	22	20	20	20	17	20	14	20	8
C. guestfalica	30	27	30	27	25	22	24	22	18	14	20	14

Table 7. Survival of sixth instar nymphs of some foliage-frequenting psocids transferred from 100 per cent relative humidity to lower humidity regimes (Freshly- moulted nymphs transferred, nos. alive after three days counted)

Relative humidity (per cent)

	76		58		45		33	
	No. trans-ferred	No. of survivors	No. trans-ferred	No. of survivors	No. trans-ferred.	No. of survivors	No. trans-ferred.	No. of survivors
Species								
E. briggsi	40	40	40	38	40	33	40	26
S. immaculatus	40	40	40	40	40	36	40	28
G. cruciatus	30	30	25	23	30	29	30	27
C. flavidus	50	50	50	48	50	48	50	37
C. burmeisteri	24	23	20	19	30	26	30	23
C. fuscopterus	18	18	18	18	25	22	20	14
C. kolbei	12	12	12	12	17	15	14	10

Table 8. Dimensions of eggs of nine species of foliage-frequenting Psocoptera.

(mm ±0.003)

Species	No.	Range	Mean	Range	Mean
T. dalii	20	0.448 - 0.514	0.476	0.262 - 0.273	0.265
E. briggsi	20	0.318 - 0.366	0.340	0.240 - 0.252	0.246
S. immaculatus	20	0.590 - 0.652	0.630	0.309 - 0.321	0.316
S. stigmaticus	20	0.553 - 0.608	0.580	0.298 - 0.309	0.304
G. cruciatus	20	0.450 - 0.484	0.464	0.265 - 0.278	0.270
C. flavidus	20	0.426 - 0.460	0.438	0.250 - 0.262	0.256
C. burmeisteri	20	0.418 - 0.447	0.426	0.280 - 0.285	0.282
C. fuscopterus	20	0.416 - 0.458	0.430	0.258 - 0.266	0.264
C. kolbei	20	0.408 - 0.448	0.415	0.260 - 0.275	0.268

Table 9 . Darkening of eggs of nine species of foliage-frequenting Psocoptera.

Species	Colour	
	Freshly laid	At hatching time
T. dalii	White or grey-white	Pale yellow-white.
E. briggsi	Pale brown-white	Brown-white to olive-buff.
S. immaculatus	Cream white, or yellowish	Deeper, Greenish, yellowish or bluish green.
S. stigmaticus	Cream-white	Deeper cream or lime green.
G. cruciatus	Pale yellow-white	Deep lemon yellow.
C. flavidus	Pale yellow-white	Grey-yellow, darker brown at one end.
C. burmeisteri	Pale grey-white	Glossy, dark fuscous-black.
C. fuscopterus	Cream-white	Dark fuscous blue-black.
C. kolbei	Pale grey-white	Grey-black.

Table 10 . Dimensions of nymphs of nine species of foliage-frequenting Psocoptera. (mm ±0.003) (20 of each instar of each species.)

(a) T. dalii

Instar	Greatest width of head-capsule		Length of anterior wing pad	
	Range	Mean	Range	Mean
I	0.206 - 0.239	0.218	-	-
II	0.252 - 0.298	0.286	-	-
III	0.306 - 0.371	0.328	0.079 - 0.103	0.086
IV	0.396 - 0.437	0.416	0.228 - 0.296	0.248
V	0.514 - 0.562	0.539	0.427 - 0.514	0.473
VI	0.579 - 0.614	0.588	0.872 - 0.980	0.913

(b) E. briggsi

Instar	Greatest width of head capsule		Length of anterior wing pad	
	Range	Mean	Range	Mean
I	0.186 - 0.198	0.194	-	-
II	0.219 - 0.252	0.239	-	-
III	0.306 - 0.329	0.318	0.032 - 0.106	0.084
IV	0.427 - 0.450	0.446	0.220 - 0.246	0.234
V	0.488 - 0.506	0.494	0.396 - 0.472	0.448
VI	0.556 - 0.593	0.578	0.765 - 0.794	0.742

(c) S. immaculatus

Instar	Greatest width of head capsule		Length of anterior wing pad	
	Range	Mean	Range	Mean
I	0.259 - 0.290	0.276	-	-
II	0.317 - 0.362	0.346	-	-
III	0.448 - 0.494	0.460	0.100 - 0.108	0.102
IV	0.538 - 0.593	0.572	0.283 - 0.324	0.312
V	0.642 - 0.729	0.703	0.580 - 0.674	0.628
VI	0.809 - 0.873	0.846	0.886 - 1.306	1.235

(d) S. stigmaticus

Instar	Greatest width of head capsule		Length of anterior wing pad	
	Range	Mean	Range	Mean
I	0.236 - 0.270	0.258	-	-
II	0.289 - 0.337	0.314	-	-
III	0.382 - 0.426	0.405	0.078 - 0.095	0.084
IV	0.514 - 0.549	0.529	0.206 - 0.264	0.239
V	0.595 - 0.662	0.635	0.538 - 0.614	0.572
VI	0.730 - 0.804	0.783	0.958 - 1.146	1.106

(e) G. cruciatus

Instar	Greatest width of head capsule		Length of anterior wing pad	
I	Range	Mean	Range	Mean
I	0.208 - 0.273	0.246	-	-
II	0.286 - 0.319	0.307	-	-
III	0.362 - 0.408	0.383	0.090 - 0.104	0.095
IV	0.458 - 0.496	0.473	0.228 - 0.271	0.246
V	0.532 - 0.580	0.560	0.519 - 0.536	0.529
VI	0.625 - 0.670	0.656	0.938 - 1.041	0.982

(f) *C. flavidus*

Instar	Greatest width of head capsule		Lenght of anterior wing pad	
	Range	Mean	Range	Mean
I	0.204 - 0.246	0.218	-	-
II	0.286 - 0.342	0.313	-	-
III	0.368 - 0.417	0.390	0.092 - 0.115	0.108
IV	0.464 - 0.532	0.501	0.254 - 0.292	0.273
V	0.543 - 0.586	0.568	0.470 - 0.534	0.492
VI	0.604 - 0.654	0.630	0.932 - 0.993	0.976

(g) *C. burmeisteri*

Instar	Greatest width of head capsule		Length of anterior wing pad	
	Range	Mean	Range	Mean
I	0.227 - 0.258	0.243	-	-
II	0.286 - 0.314	0.306	-	-
III	0.355 - 0.382	0.367	0.088 - 0.098	0.092
IV	0.416 - 0.478	0.442	0.236 - 0.289	0.255
V	0.517 - 0.550	0.536	0.492 - 0.529	0.513
VI	0.592 - 0.643	0.609	0.866 - 0.928	0.887

(h) *C. fuscopterus*

Instar	Greatest width of head capsule		Length of anterior wing pad	
	Range	Mean	Range	Mean
I	0.214 - 0.250	0.226	-	-
II	0.317 - 0.346	0.324	-	-
III	0.358 - 0.382	0.371	0.097 - 0.110	0.103
IV	0.407 - 0.436	0.419	0.238 - 0.256	0.242
V	0.518 - 0.559	0.524	0.470 - 0.496	0.483
VI	0.593 - 0.684	0.617	0.900 - 0.983	0.928

(i) C. kolbei

Instar	Greatest width of head capsule		Lenth of anterior wing pad	
	Range	Mean	Range	Mean
I	0.235 - 0.270	0.255	-	-
II	0.302 - 0.339	0.316	-	-
III	0.364 - 0.392	0.380	0.080 - 0.094	0.085
IV	0.419 - 0.474	0.439	0.228 - 0.269	0.259
V	0.516 - 0.549	0.523	0.514 - 0.549	0.527
VI	0.580 - 0.636	0.596	0.920 - 0.992	0.949

Table 11. Numbers of Ectopsocus briggsi nymphs and adults found overwintering in various sites at Silwood Park, Berks., in 1966 - 1967.

Site	No. of Leaves	E. briggsi			Date
		Adults	Nymphs	Total	
Dead oak leaves on trees	897	18	55	73	Dec. 1966
Oak leaves from litter	2551	2	1	3	Dec. 1966
Grass tussocks - 25 Dactylis				0	Dec. 1966
Tullgren funnel extracts of oak litter				0	Dec. 1966 - March 1967

Table 12. Overwintering of three species of psocids at Silwood Park, 1966 - 1967.

(a) Ectopsocus briggsi - Adult females.

Box	Date	No. alive (of 15)	No. of egg batches per box					No. with full crop	No. with large oocytes
			1	2	3	4	5		
1	Nov. 1966	15	8	11	7	7	9	14	11
2	Dec. 1966	12		4	4	9	4	12	4
3	Jan. 1967	14			0	0	0	14	1
4	Feb. 1967	11				0	0	9	0
5	Mar. 1967	14					0	12	0

(b) Elipsocus hyalinus - Adult females.

Box	Date	No. alive (of 15)	No. of egg batches per box					No. with full crop	No. with large oocytes
			1	2	3	4	5		
1	Nov. 1966	14	37	12	14	9	24	14	8
2	Dec. 1966	15		8	4	4	11	11	4
3	Jan. 1967	15			0	0	0	11	0
4	Feb. 1967	12				0	0	12	0
5	Mar. 1967	14					0	9	1

(c) Graphopsocus cruciatus - Adult females.

Box	Date	No. alive (of 15)	No. of egg batches per box					No. with full crop	No. with large oocytes
			1	2	3	4	5		
1	Nov. 1966	13	5	2	2	2	7	13	4
2	Dec. 1966	13		0	1	0	0	9	1
3	Jan. 1967	15			0	0	0	12	0
4	Feb. 1967	12				0	0	11	0
5	Mar. 1967	15					0	12	0

Table 13. Extraction efficiencies of Tullgren Funnels and Kempson Bowl Extractor for various Psocoptera from Leaf Litter.

	Psocids introduced				Psocids extracted	
Litter	Species	No.	Stages	Replicates	No.	Percent.
A.						
Oak	*Liposcelis* sp.	50	Ad+N	I0	380	76.0
"	*E.briggsi*	I00	Ad	I0	726	72.6
"	"	50	N	I0	347	69.4
"	*C.flavidus*	I00	Ad	I0	886	88.6
"	"	50	V-VI	I0	424	84.8
"	"	50	II-IV	I0	309	6I.8
"	*E.lucifugus*	50	Ad+N	5	227	90.8
Pine	*C.guestfalica*	40	Ad	I0	278	69.5
"	*E.briggsi*	50	Ad	I0	396	79.2
"	"	50	N	I0	4I7	83.4
"	*C.flavidus*	50	Ad	6	260	86.7
"	"	50	V-VI	I0	403	80.6
B.						
Oak	*E.briggsi*	50	Ad	I0	468	93.6
"	*C.flavidus*	50	Ad	I0	483	96.6
"	"	50	V-VI	I0	398	79.6
"	"	50	II-IV	8	3I6	79.0

(A, Tullgren Funnels. B, Kempson Bowls - covered.)

Table 14. Comparison of extraction efficiency of Tullgren Funnels with wet and dry oak litter.

	Psocids introduced				Psocids extracted	
Litter	Species	No.	Stages	Replicates	No.	Percent.
Dry	*C.flavidus*	50	Ad	I0	390	78.0
"	"	50	V-VI	I0	406	8I.2
"	"	40	II-IV	I0	293	70.3
Wet	"	50	Ad	I0	306	6I.2
"	"	50	V-VI	I0	397	79.4
"	"	40	II-IV	I0	260	60.5

Table 15. Times of extraction of psocids from leaf litter by Tullgren Funnels.

			Numbers extracted on day:									
Litter	Psocid	Stages	I	2	3	4	5	6	7	8	9	IO
A. Calibration tests,												
Oak	C.flavidus	Ad.	86	230	216	I33	I89	2	8	-	-	-
"	"	N	I09	204	I38	I59	48	5I	20	-	4	-
"	E.lucifugus	All	3I	I06	I9	26	35	5	4	-	-	I
"	E.briggsi	Ad	57	200	308	89	50	3	-	I7	2	-
"	"	N	72	II5	29	2I	I03	7	-	-	-	-
Pine	"	Ad	84	I86	44	26	34	2	9	II	-	-
"	C.flavidus	Ad	59	I07	I6	70	6	-	2	-	-	-
B. Natural samples.												
Oak.I966	C.flavidus.	All	2	7	7	I8	I2	2	3	-	-	-
" "	E.lucifugus	All	86	37	I5	II	9	I5	7	-	-	-
" "	E.briggsi	All	4	2	2	3	3	38	I7	-	-	-

Table 16. Types of leaf litter sampled and numbers of sample units extracted at Silwood Park in two years.

	No.sample units			Months sampled											
Litter	I966	I967	Total	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.
Oak leaves,under large trees	372	360	732	*	*	*	*	*	*	*	*	*	*	*	*
" " , under small trees	280	256	536	*	*	*	*	*	*	*	*	*	*	*	*
" " ,between trees	280	256	536	*	*	*	*	*	*	*	*	*	*	*	*
Pine needles	48	I80	228			*	*	*	*	*	*	*	*		
Cupressus needles	-	220	220					*	*	*	*	*	*		
Hawthorn leaves	36	76	II2			*	*	*	*	*		*			
Beech leaves	-	84	84					*	*	*	*	*	*	*	
Broom litter	-	63	63				*	*	*		*	*			
Bracken litter	-	40	40					*	*	*	*		*		
Juncus litter	-	48	48					*	*	*	*	*	*		
Dactylis litter	-	30	30			*	*	*	*	*	*	*	*		
Holcus litter	-	32	32			*	*	*				*	*		

(* samples taken)

Table 17. Variation in amount of oak litter per unit area of ground at different times of the year.

Area sampled	Month	No. of oak leaves Extremes	Mean	3 Month running average
I5x (30x30cm)				
	March I966	90-I8I	I46	
	April I966	57-280	203	I89
	May I966	I05-24I	2I9	I73
	June I966	8I-I49	98	I40
	July I966	64-II3	I04	II0
	Aug. I966	87-I56	I28	I33
	Sept. I966	55-206	I69	I63
	Oct. I966	II5-360	I93	2I4
	Nov. I966	I38-3I9	280	243
	Dec. I966	I07-284	256	

Table 18. Psocids obtained from various kinds of litter at Silwood Park, 1966-67.

Litter Psocid	Oak	Pine	Cupressus	Hawthorn	Beech	Broom	Bracken	Juncus	Dactylis	Holcus	Total
C.flavidus	2I8	0	3	I7	5	0	0	0	0	0	243
C.kolbei	2	0	0	2	0	0	0	0	0	0	4
G.cruciatus	I	0	0	I	0	0	0	0	0	0	2
E.briggsi	96	0	II	I	I	3	0	I	0	0	II3
T.dalii	I	0	0	0	0	0	0	0	0	0	I
Epipsocus lucifugus	3I7	I4	782	5	28	I	I	4	I	I	II54
Lepinotus patruelis	0	I	0	0	0	0	0	0	0	0	I
L.inquilinus	I	0	0	0	0	0	0	0	0	0	I
Trogium pulsatorium	0	0	0	0	0	0	I	0	0	0	I
Liposcelis sp.	2	0	0	0	0	0	0	0	0	0	2
Cerobasis guestfalica	0	5	7	0	I	0	0	0	0	0	I3
Pteroxanium kelloggi	0	0	I8	0	0	0	0	0	0	0	I8
E.hyalinus	3	I	0	0	0	0	0	0	0	0	4
Philotarsus picicornis	3	0	0	0	3	0	0	0	0	0	6
Lachesilla pedicularia	I	0	0	0	0	0	0	0	0	0	I
Loensia sp.	I	0	0	0	0	0	0	0	0	0	I
Total:	646	2I	82I	26	38	4	2	5	I	I	I565

Table 19. <u>Numbers of Caecilius flavidus in oak litter at Silwood Park, I966-67.</u>

Date		Stage							
I966	I967	I	II	III	IV	V	VI	Ad	Totals
6/4	28/3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
I8/4	I7/4	I2.I5	I.2	0.0	0.0	0.0	0.0	0.0	I3.I7
25/4	24/4	0.22	0.8	0.3	0.0	0.0	0.0	0.0	0.33
-	I/5	-.0	-.0	-.0	-.2	-.I	-.I	-.0	-.4
-	8/5	-.0	-.0	-.2	-.5	-.3	-.0	-.0	-.I0
-	I6/5	-.0	-.0	-.I	-.4	-.3	-.4	-.3	-.I5
24/5	23/5	I.0	I.0	I.0	0.I	0.3	0.I6	0.3	3.23
30/5	30/5	0.0	I.0	0.0	5.0	6.0	I4.0	4.I2	30.I2
6 /6	5/6	0.0	0.0	0.0	0.0	0.0	4.0	4.6	8.6
II/6	I2/6	0.0	0.0	0.0	0.0	5.0	3.0	3.0	II.0
I8/6	I9/6	0.0	0.0	0.0	0.2	0.2	0.0	0.I	0.5
25/6	26/6	0.0	I.0	0.0	0.0	0.0	0.0	0.0	I.0
3/7	3/7	0.0	0.0	0.0	0.I	0.0	3.0	0.8	3.9
I0/7	I0/7	0.0	2.0	0.0	I.0	0.0	0.0	0.0	3.0
I7/7	I7/7	0.0	0.0	0.0	0.0	3.0	0.0	I.0	4.0
24/7	23/7	0.0	0.0	I.0	0.0	0.0	I.0	I.I	3.I
3I/7	30/7	0.0	0.0	0.0	0.0	0.0	0.0	I.0	I.0
7/8	6/8	0.0	0.0	0.0	0.0	0.0	0.0	2.0	2.0
I4/8	I3/8	0.0	0.0	0.0	0.I	0.0	0.I	0.0	0.2
2I/8	20/8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
28/8	27/8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sept.		0.0	0.0	0.0	0.0	I.0	0.0	I.0	2.0
Oct.		0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.3

Table 20 Numbers of Epipsocus lucifugus (Rambur) in oak and conifer litter at Silwood Park, I966-67.

		Nymphs				Adults					
Date		Oak		Conifer		Oak		Conifer		Totals	
I966	I967	I966	I967	I966	I967	I966	I967	I966	I967	I966	I967
24/5	23/5	0	0	0	0	0	0	0	0	0	0
30/5	30/5	7	2	0	0	0	0	0	0	7	2
6/6	5/6	39	I2	I	0	0	0	0	0	40	I2
II/6	I2/6	2I	I6	4	0	0	0	0	0	25	I6
I8/6	I9/6	22	I9	4	II	0	0	0	0	26	30
25/6	26/6	I0	3	0	68	I	0	0	0	II	7I
3/7	3/7	4I	9	II	52	I5	0	I	I8	68	79
I0/7	I0/7	I2	I6	5	I03	0	7	5	7	22	I33
I7/7	I7/7	I2	0	0	I22	4	7	5	28	2I	I57
24/7	23/7	0	0	0	94	7	8	35	46	42	I48
3I/7	30/7	0	0	3	2I	5	8	36	30	44	59
7/8	6/8	0	0	0	5	3	5	I2	28	I5	38
I4/8	I3/8	0	0	I	0	I	3	6	23	8	26
2I/8	20/8	0	0	0	0	I	0	0	3	I	3
28/8	27/8	0	0	0	0	0	I	0	2	0	3
4/9	3/9	0	0	0	0	0	0	0	6	0	6
I2/9	II/9	0	0	0	0	0	0	0	0	0	0
I8/9	I8/9	0	0	0	0	0	0	0	0	0	0
24/9	24/9	0	0	0	0	0	0	0	0	0	0
I/I0	I/I0	0	0	0	0	0	0	0	0	0	0

Table 21. Composition of litter from under oak and pine trees at different times of the year. (Silwood Park, I966. Oak samples of Table 17)

Oak litter	Percentage composition (± 2)									
Constituents	Mar.	Apr.	May	Jun.	Jly.	Aug.	Sep.	Oct.	Nov.	Dec.
Oak leaves	90	94	80	75	68	65	80	90	94	94
Beech leaves	8	4	20	23	30	30	I5	IO	3	5
Birch leaves	2	0	0	0	2	2	5	0	3	I
Sycamore leaves	0	2	0	2	0	3	0	0	0	0
Pine litter (5 sample units per month)										
Pine needles	98	96	96	96	I00	99	94	95	90	98
Other leaves	2	4	4	4	0	I	6	5	IO	2

Table 22. Numbers of three psocid species in oak litter from three sites at Silwood Park in I966.

	Site of Litter			
Psocid	Open ground between trees	Under small oaks	Under large oaks	Total
C. flavidus	II (2I.6%)	I3 (25.5%)	27 (52.9%)	5I
E. lucifugus	60 (33.3%)	64 (35.3%)	57 (3I.4%)	I8I
E. briggsi	I7 (24.6%)	29 (42.I%)	23 (33.3%)	69

Table 23. Survival of *C. flavidus* nymphs on different constituents of leaf litter.

Constituent	No. unfed first instar nymphs	No. alive after seven days	No. reaching adult stage
Dead oak leaves	I30	II6	93
Dead grass leaves	76	70	50
Living grass leaves	I80	8	0
Juncus leaves	55	3	0
Bare soil	I50	0	0

Table 24. Vertical distribution of E.lucifugus in Cupressus litter.

Depth of litter	No.7.5 cm diameter cores	No. E.lucifugus extracted	Percent total E.lucifugus
0-5 cm	I0	64	92.7
5-I0 cm	I0	5	7.3
I0-I5 cm	I0	0	0.0

Table 25. Numbers of E.lucifugus extracted from different kinds of litter from June to August I966-67 at Silwood Park.

Litter:	Oak	Pine	Cupressus	Hawthorn	Beech	All others	Total
No. sample units	I44	80	I06	28	52	76	486
No.E.lucifugus obtained	308	I4	782	5	28	8	II45
No.expected	339	I88	250	66	I22	I80	II45
Non-random distribution		-	* +	-	-	-	

(* X^2 significant at five per cent level)

Table 26. Numbers of psocids captured on gum covered frames under or near oak trees at Silwood Park, I966.

Month: Psocid		Jun.	Jly.	Aug.	Sep.	Oct.
C.flavidus	Ad	4	0	I5	5	I
"	N	0	I	7	I	0
L.fasciata	Ad	0	0	0	I	0
E.hyalinus	Ad	I	I	0	0	I
P.picicornis	Ad	0	0	I	0	0
E.briggsi	Ad	0	0	3	2	2
"	N	0	I	0	2	0

Table 27. Numbers of psocid species in litter at different times of the year.

	No. of Species											
Month: Litter	Jan.	Feb.	Mar.	Apr.	May.	Jun.	Jly.	Aug.	Sep.	Oct.	Nov.	Dec.
Oak leaves	0	0	I	I	2	4	4	I2	6	2	0	0
Beech leaves	0	0	0	I	I	3	3	4	I	0	0	0
Conifer litter	0	0	0	0	I	3	3	6	0	I	0	0

Table 28 . Leaf dimensions of four species of trees at Silwood Park, August 1966.

	Betula	Crataegus	Fagus	Quercus
Number of leaves	200	200	200	200
Mean length (mm)	36.48	26.25	67.85	73.64
Mean breadth (mm)	33.23	22.22	45.85	41.55
Mean area (mm)	741.76	281.63	2316.76	1794.00
Limits of area (mm^2)	480-1158	136-518	746-3990	384-4126
Regression of length on area	$y=12.01 + 0.033x$	$y=25.16 + 0.0388x$	$y=67.42 + 0.0018x$	$y=70.97 + 0.0015x$
Significance ('t' Test)	$P < 0.01$	$P < 0.05$	$P < 0.01$	$P < 0.001$
Regression of breadth on area	$y=11.49 + 0.029x$	$y=20.88 + 0.0477x$	$y=42.56 + 0.0014x$	$y=25.59 + 0.0087x$
Significance ('t' Test)	$P < 0.001$	$P < 0.01$	$P < 0.01$	$P < 0.01$

Table 29 . Leaf areas and numbers in samples of each of four species of trees at Silwood Park, August 1966.

		Betula	Craeaegus	Fagus	Quercus
Number of samples		15	15	15	15
Mean number of leaves		412	482	305	273
Limits of leaf numbers		318-630	239-756	280-370	156-312
Mean calculated area of samples (cm^2)		3056.0	1357.5	7066.1	4897.6
Limits of calculated areas of samples	Min.	2358.8	673.1	6486.9	2798.6
	Max.	4673.1	2129.1	8572.0	5597.3

Table 30. Total numbers of psocids from different trees at Silwood Park in 1966 and 1967.

(a) 1966.

	Acer	Aesculus	Betula	Crataegus	Fagus	Ilex	Pinus	Populus	Quercus	Tilia	Sarothamnus	Ulmus
C. guestfalica	-	-	-	107	-	2	319	-	72	2	70	-
A. bifasciata	-	-	-	1	-	-	-	-	-	-	44	-
A. contaminata	-	-	-	4	-	-	-	-	-	-	57	-
L. variegata	-	-	-	-	1	-	-	-	1	1	-	-
T. sexpunctatum	-	-	-	-	-	-	-	-	2	-	-	-
M. immunis	-	-	1	52	-	-	16	-	8	2	-	2
M. unipunctatus	-	-	-	8	-	-	-	-	-	-	-	-
T. dalii	-	-	-	3	-	-	-	-	-	-	-	-
E. briggsi	13	13	13	28	26	-	11	1	315	21	122	12
P. subfasciatus	-	-	-	1	-	-	-	-	-	-	-	-
P. alboguttatus	-	-	-	-	-	-	-	-	-	-	2	-
P. phaeopterus	-	-	-	1	-	-	-	-	-	-	3	-
P. didymus	-	-	-	1	-	-	-	-	-	-	-	-
C. cyanops	-	-	-	-	-	-	718	-	-	-	-	-
Ph. picicornis	-	-	-	153	-	-	41	-	6	-	52	-
E. hyalinus	22	1	9	212	8	1	111	19	51	4	281	2
E. westwoodi	2	-	-	62	-	-	2	4	16	-	22	-
E. mclachlani	-	-	-	5	-	1	1	-	1	-	5	-
L. pedicularia	-	-	-	2	-	-	-	-	2	-	1	-
R. helvimacula	-	-	-	-	-	-	-	-	-	-	1	-
C. flavidus	34	17	5	217	45	13	1	11	868	37	59	17
C. fuscopterus	-	-	-	15	-	-	-	-	-	-	-	-
C. kolbei	-	-	-	53	-	-	1	-	-	-	96	-
C. burmeisteri	-	-	-	-	-	-	62	-	-	-	1	-
S. immaculatus	5	-	-	385	5	9	-	-	14	1	-	-
S. stigmaticus	-	-	-	386	-	-	-	-	-	-	-	-
G. cruciatus	-	-	-	89	-	-	-	-	3	-	1	-

Table 30 (cont.)

(b) 1967

	Acer	Aesculus	Betula	Crataegus	Cupressus	Fagus	Ilex	Pinus	Populus	Quercus	Tilia	Sarothamnus	Ulmus
C. guestfalica	-	-	-	-	1852	-	-	68	-	7	-	-	-
A. bifasciata	-	-	-	-	3	-	-	-	-	-	-	31	-
A. contaminata	-	-	-	-	23	-	-	-	-	-	-	19	-
L. variegata	-	-	-	-	-	-	-	-	-	3	-	-	-
T. sexpunctatum	-	-	-	-	-	-	7	-	-	4	-	-	1
M. immunis	2	-	-	4	21	4	-	4	-	3	-	-	-
M. unipunctatus	-	-	-	3	2	-	-	1	-	-	-	-	-
T. dalii	-	-	-	-	-	-	30	-	-	4	-	-	-
E. briggsi	23	-	17	57	20	46	477	4	22	1594	8	31	7
P. subfasciatus	-	-	-	-	28	-	-	-	-	-	1	-	-
P. phaeopterus	-	1	2	133	8	-	-	-	-	-	-	-	-
Ph. picicornis	-	-	1	193	19	-	-	-	2	14	2	-	-
C. cyanops	-	-	-	-	-	-	-	130	-	-	-	-	-
E. hyalinus	19	6	5	29	45	17	11	19	25	58	10	31	7
E. westwoodi	-	-	-	4	7	-	2	4	2	7	-	-	-
E. mclachlani	-	-	-	1	-	-	-	-	1	-	-	3	-
L. pedicularia	-	-	-	-	1	-	-	-	-	-	-	-	-
C. flavidus	40	1	14	409	2	133	389	2	28	2786	27	18	9
C. fuscopterus	-	-	-	7	-	-	-	-	-	-	-	-	-
C. kolbei	-	-	-	2	-	-	-	-	-	-	-	-	-
C. burmeisteri	-	-	-	1	426	-	-	-	-	-	-	-	-
S. immaculatus	-	-	2	244	-	11	209	-	-	28	4	-	-
S. stigmaticus	-	-	-	637	-	-	-	-	-	-	-	-	-
G. cruciatus	-	-	2	40	-	-	105	-	-	17	1	-	-

Table 31 . Numbers of psocids per sample from different trees at Silwood Park in 1966 and 1967.

(a) 1966

Samples:	125	125	120	245	110	20	275	85	282	145	270	135
	Acer	Aesculus	Betula	Crataegus	Fagus	Ilex	Pinus	Populus	Quercus	Tilia	Sarothamnus	Ulmus
C. guestfalica	-	-	-	0.44	-	0.10	1.16	-	0.26	0.01	0.26	-
A. bifasciata	-	-	-	0.004	-	-	-	-	-	-	0.16	-
C. contaminata	-	-	-	0.016	-	-	-	-	-	-	0.21	-
L. variegata	-	-	-	-	0.09	-	-	-	0.003	0.007	-	-
T. sexpunctatum	-	-	-	-	-	-	-	-	0.007	-	-	-
M. immunis	-	-	0.01	0.21	-	-	0.06	-	0.03	0.01	-	-
M. unipunctatus	-	-	-	0.03	-	-	-	-	-	-	-	-
T. dalii	-	-	-	0.01	-	-	-	-	-	-	-	-
E. briggsi	0.10	0.10	0.11	0.11	0.24	-	0.04	0.01	1.12	0.15	0.45	0.09
P. subfasciatus	-	-	-	0.004	-	-	-	-	-	-	-	-
P. alboguttatus	-	-	-	-	-	-	-	-	-	-	0.01	-
P. phaeopterus	-	-	-	0.004	-	-	-	-	-	-	0.01	-
P. didymus	-	-	-	0.004	-	-	-	-	-	-	-	-
C. cyanops	-	-	-	-	-	-	2.61	-	-	-	-	-
Ph. picicornis	-	-	-	0.62	-	-	0.15	-	0.02	-	0.19	-
E. hyalinus	0.78	0.01	0.08	0.87	0.07	0.05	0.40	0.22	0.18	0.03	1.04	0.015
E . westwoodi	0.02	-	-	0.25	-	-	0.01	0.05	0.06	-	0.08	-
E. mclachlani	-	-	-	0.02	-	0.05	0.004	-	0.003	-	0.02	-
L. pedicularia	-	-	-	0.01	-	-	-	-	0.01	-	0.004	-
R. helvimacula	-	-	-	-	-	-	-	-	-	-	0.004	-
C. flavidus	0.27	0.14	0.04	0.89	0.41	0.65	0.004	0.13	3.08	0.26	0.22	0.13
C. fuscopterus	-	-	-	0.06	-	-	-	-	-	-	-	-
C. kolbei	-	-	-	0.22	-	-	0.004	-	-	-	0.36	-
C. burmeisteri	-	-	-	-	-	-	0.23	-	-	-	0.004	-
S. immaculatus	0.04	-	-	1.57	0.05	0.45	-	-	0.05	0.01	-	-
S. stigmaticus	-	-	-	1.57	-	-	-	-	-	-	-	-
G. cruciatus	-	-	-	0.36	-	-	-	-	0.01	-	0.004	-

Table 31. (cont.)

(b) 1967

Samples: Species	Acer 55	Aesculus 25	Betula 80	Crataegus 125	Cupressus 145	Fagus 85	Ilex 100	Pinus 35	Populus 100	Quercus 370	Tilia 55	Sarothamnus 100	Ulmus 60
C. guestfalica	-	-	-	-	12.77	-	-	1.94	-	0.019	-	-	-
A. bifasciata	-	-	-	-	0.021	-	-	-	-	-	-	0.31	-
A. contaminata	-	-	-	-	0.158	-	-	-	-	-	-	0.19	-
L. variegata	-	-	-	-	-	-	-	-	-	0.0081	-	-	-
T. sexpunctatum	-	-	-	-	-	-	0.07	-	-	0.011	-	-	0.01
M. immunis	0.036	-	-	0.032	0.145	0.047	-	0.114	-	0.0081	-	-	-
M. unipunctatus	-	-	-	0.024	0.0138	-	-	0.028	-	-	-	-	-
T. dalii	-	-	-	-	-	-	0.30	-	-	0.011	-	-	-
E. briggsi	0.42	-	0.21	0.46	0.14	0.54	4.77	0.114	0.22	4.31	0.114	0.31	0.12
P. subfasciatus	-	-	-	0.19	-	-	-	-	-	-	0.018	-	-
P. phaeopterus	-	0.04	0.025	1.06	0.055	-	-	-	-	-	-	-	-
Ph. picicornis	-	-	0.0125	1.54	0.13	-	-	-	0.02	0.038	0.036	-	-
C. cyanops	-	-	-	-	-	-	-	3.7	-	-	-	-	-
E. hyalinus	0.34	0.24	0.06	0.23	0.31	0.20	0.11	0.54	0.25	0.16	0.18	0.31	0.12
E. westwoodi	-	-	-	0.032	0.048	-	0.02	0.114	0.02	0.019	-	-	-
E. mclachlani	-	-	-	0.008	-	-	-	-	0.01	-	-	0.03	-
L. pedicularia	-	-	-	-	0.0068	-	-	-	-	-	-	-	-
C. flavidus	0.73	0.04	0.175	3.27	0.014	1.56	3.89	0.057	0.28	7.53	0.49	0.18	0.15
C. fuscopterus	-	-	-	0.056	-	-	-	-	-	-	-	-	-
C. kolbei	-	-	-	0.016	-	-	-	-	-	-	-	-	-
C. burmeisteri	-	-	-	0.008	2.93	-	-	-	-	-	-	-	-
S. immaculatus	-	-	0.025	1.95	-	0.13	2.09	-	-	0.076	0.073	-	-
S. stigmaticus	-	-	-	5.96	-	-	-	-	-	-	-	-	-
G. cruciatus	-	-	0.025	0.32	-	-	1.05	-	-	0.045	0.018	-	-

Table 32.(a) Numbers of psocid species from different tree species at Silwood Park in 1966 and 1967.

Tree:												
Total species	5	3	4	21	5	5	11	4	13	7	16	4
Foliage species	3	2	2	8	3	2	4	2	4	3	5	2

(b) The numbers of psocid species from different selected tree species at different times of the year in 1966 and 1967.

Tree:	Crataegus	Pinus	Quercus
April	-	1	-
May	4	3	3
June	13	4	7
July	13	4	7
August	13	8	8
September	11	7	8
October	10	4	3
November	6	3	3

Table 33. Numbers of foliage-frequenting psocids per sample from different trees at different times of the year in 1966 and 1967.

	May		June		July		August		September		October	
Tree species	1966	1967	1966	1967	1966	1967	1966	1967	1966	1967	1966	1967
Acer	0	0	0.15	0.14	0.60	0.10	0.76	2.05	0.55	4.20	0.67	x
Aesculus	0	0	0.28	0	0.15	0.10	0.12	0	0.45	x	0.80	x
Betula	0	0	0	0.03	0	0.20	0.55	0.20	0.10	1.55	0.33	1.40
Crataegus	0.46	0.20	3.00	4.00	3.72	12.20	10.45	21.95	14.03	28.70	3.30	7.20
Cupressus	x	2.27	x	3.88	x	2.96	x	8.80	x	4.80	x	3.96
Fagus	0	0	0.20	0.20	0.55	2.47	0.70	2.35	1.60	6.20	1.33	3.60
Ilex	0	1.80	0.30	4.60	x	5.20	x	14.10	4.40	28.00	x	33.80
Pinus	0	0	0	0	0.05	0	0.30	1.40	0.25	0	0.75	0
Populus	0	0	0	0.25	0.15	0.50	0.32	0.95	0	0.75	0	0.47
Quercus	0.13	0.20	2.48	2.63	4.07	9.24	4.33	13.50	9.95	38.44	8.90	40.20
Tilia	0	0	0.32	0.10	0.25	0.33	0.76	1.65	0.55	x	1.13	0
Sarothamnus	0	0.10	0.42	0.13	0.85	0.70	1.38	0.80	2.42	x	1.10	x
Ulmus	0	0	0.13	0.08	0.10	0.27	0.24	0.85	0.45	0	0.53	0

(x = no sample)

Table 34. Total numbers of psocids taken from all trees at Silwood Park throughout the period March - April to October, 1967.

Months	Total samples	Total psocids	Psocids/sample
March/April	125	205	1.64
May	65	154	2.37
June	330	1007	3.05
July	280	2036	7.27
August	270	3358	12.44
September	170	4219	24.82
October	95	1372	14.40

Table 35. Numbers of C. flavidus and S. stigmaticus on Crataegus and Quercus in Windsor Great Park in 1967.

(50 samples from each tree species on each date)

Date	Crataegus		Quercus	
	C. flavidus	S. stigmaticus	C. flavidus	S. stigmaticus
9/5/1967	0	0	0	0
31/5/1967	5	0	18	0
18/6/1967	37	18	51	0
7/7/1967	102	116	215	0
11/8/1967	126	782	863	0
23/8/1967	84	716	1792	1
8/9/1967	182	1032	2007	0

Table 36 . Distribution of E. hyalinus in samples from different trees Silwood Park in May-June and September-October, 1966.

	May-June				September-October			
		E. hyalinus				E. hyalinus		
	No. Samples	Obs.	Exp.	± Signif. at 5% (X2)	No. Samples	Obs.	Exp.	± Signif at 5% (X2)
Acer	50	9	13.1		35	2	11.2	-
Aesculus	50	1	13.1	-	30	0	9.6	-
Betula	40	0	10.5	-	35	2	11.2	-
Crataegus	80	49	21.0	+	70	23	22.5	
Fagus	35	0	9.2	-	35	2	11.2	-
Pinus	80	40	21.0	+	80	31	25.7	
Quercus	112	7	50.3	-	80	8	25.7	-
Tilia	65	3	17.1	-	35	2	11.2	-
Sarothamnus	80	75	21.0	+	90	101	28.9	+
Ulmus	50	0	13.1	-	35	1	11.2	-

Table 37. Distribution of C. flavidus in samples from different trees at Silwood Park in May-June and September-October, 1967.

	May & June				Sept. & Oct.			
		C.flavidus		+ or - significance		C.flavidus		+ or - significance
	No. of samples	Obs.	Exp.	at 5%(X^2)	No. of samples	Obs.	Exp.	at 5%(X^2)
Acer	20	4	4.7		25	17	171.1	-
Aesculus	20	1	4.7		25	0	171.1	-
Betula	25	3	5.8		30	1	205.3	-
Crataegus	25	14	5.8	+	40	216	273.8	
Cupressus	40	1	9.4	-	45	0	308.0	-
Fagus	25	4	5.8		25	51	171.1	-
Ilex	30	18	7.0		25	308	171.1	
Quercus	90	56	21.1	+	65	1724	650.0	+
Tilia	20	2	4.7		30	0	205.0	-
Ulmus	25	2	5.8		30	0	205.3	-

Table 38. Numbers of adult psocids from consecutive trees bordering the North Gravel, Silwood Park on 24th July, 1967.

Tree species: Psocid	Crataegus	Quercus	Acer	Aesculus	Pinus	Quercus	Acer	Aesculus	Tilia
(Elipsocus nymphs	-	1	-	-	1	-	2	-	-)
E. hyalinus	-	1	-	-	2	1	1	-	-
C. cyanops	-	-	-	-	53	-	-	-	-
M. immunis	-	-	-	-	1	-	-	-	-
C. guestfalica	-	-	-	-	3	-	-	-	-
S. immaculatus	1	1	1	-	-	2	-	1	-
G. cruciatus	-	1	-	-	-	-	-	-	-
C. burmeisteri	-	-	-	-	14	-	-	-	-
C. flavidus	4	7	1	-	-	2	1	1	3

Table 39. Numbers of C. flavidus egg batches in leaf samples from large oak trees at three times in 1966.

Month	Total No. of Batches found at three heights 0-3m	5-7m	12-15m	Total	Average
June	304	249	89	642	214.0
August	348	279	309	936	312.0
October	352	303	345	1000	333.2

Table 40. Numbers of C. flavidus egg batches at different heights on a small oak tree at Silwood Park in October 1967.

	Height (m)	Total Leaves	Total Batches	Leaves/ Batch
	0-1	956	104	9.2
	1-2	17204	1468	11.7
	2-3	16522	1390	11.9
	3-4	9715	961	10.1
	4+	3800	407	9.3
Total		48197	4330	11.1

Table 41. Annual sizes of aerial samples of psocid species in a suction trap at Silwood Park. (45cm diameter, 1.3m above the ground)

Species	1961	1962	1963	1964	1965	1966	1967	Total
A. contaminata	4	6	0	4	2	0	2	18
A. bifasciata	0	0	0	0	0	1	1	2
T. sexpunctatum	0	0	0	0	0	2	0	2
E. hyalinus	20	2	2	3	16	8	15	66
E. westwoodi	2	1	0	0	0	0	1	4
P. picicornis	0	0	0	0	0	0	2	2
M. unipuctatus	1	0	0	0	0	0	0	1
R. helvimacula	0	0	0	1	0	0	0	1
L. pedicularia	120	12	39	196	76	71	54	568
E. briggsi	102	1	0	1	9	13	64	190
P. alboguttatus	0	1	0	1	0	0	0	2
S. immaculatus	0	0	0	1	0	0	0	1
G. cruciatus	0	0	0	0	1	0	0	1
C. kolbei	0	0	0	0	0	0	1	1
C. fuscopterus	0	0	0	1	1	0	0	2
C. burmeisteri	1	1	0	0	1	0	2	5
C. flavidus	7	7	2	18	12	1	11	58
Total:	257	31	43	226	119	96	153	925

Table 42. Annual sizes of aerial samples of psocid species in a suction trap at Silwood Park. (45cm diameter, 9.2m above the ground)

Species	1961	1962	1963	1964	1965	1966	1967	Total
A. contaminata	14	48	5	9	10	0	20	106
A. bifasciata	0	0	0	3	0	3	2	8
L. fasciata	0	0	0	0	0	1	0	1
E. hyalinus	141	14	1	21	71	49	85	382
E. westwoodi	0	1	0	0	0	1	1	3
P. picicornis	0	0	0	0	0	0	2	2
M. unipunctatus	3	1	0	0	0	0	0	4
M. immunis	0	0	0	0	0	0	1	1
R. helvimacula	0	0	0	0	1	0	0	1
L. pedicularia	86	15	56	63	103	16	34	373
E. briggsi	42	0	0	0	1	6	40	89
P. subfasciatus	0	0	0	0	0	0	2	2
S. immaculatus	0	1	0	5	0	0	0	6
G. cruciatus	0	0	0	0	3	0	1	4
C. fuscopterus	0	2	0	0	0	0	0	2
C. burmeisteri	2	0	0	2	1	0	2	7
C. flavidus	16	22	2	24	6	2	10	82
Total:	304	104	64	127	196	78	200	1073

Table 43. Numbers of species of poocids in suction traps at Silwood Park.

Year	Trap (1.3m)	Trap (9.2m)	Total species
1961	8	7	8
1962	8	8	11
1963	3	4	4
1964	9	7	10
1965	9	8	10
1966	6	7	7
1967	10	12	13

Table 44. Dates of first appearance of different psocid species in suction traps.

Species	1961	1962	1963	1964	1965	1966	1967
A. contaminata	9/v	15/v	16/vi	18/vi	22/vi	-	11/vi
A. bifasciata	-	-	-	18/vi	-	17/vii	26/vi
T. sexpunctatum	-	-	-	-	-	8/vii	-
L. fasciata	-	-	-	-	-	18/vii	-
E. hyalinus	9/v	5/vii	2/vii	13/v	8/v	17/v	5/vi
E. westwoodi	4/viii	26/vi	-	-	18/ix	11/viii	21/vii
P. picicornis	-	-	-	-	-	5/viii	16/vi
R. helvimacula	-	-	-	19/ix	24/v	-	-
M. unipunctatus	21/viii	28/vi	-	-	-	-	-
M. immunis	-	-	-	-	-	-	18/vii
L. pedicularia	2/vi	5/v	6/vi	29/v	24/v	17/v	22/vi
E. briggsi	24/vii	3/ix	-	3/ix	6/vii	8/viii	27/vii
P. alboguttatus	-	4/viii	-	10/ix	-	-	-
P. subfasciatus	-	-	-	-	-	-	5/vii
S. immaculatus	-	30/vii	-	24/vi	-	-	-
G. cruciatus	-	-	-	-	21/viii	-	17/viii
C. kolbei	-	-	-	-	-	-	8/ix
C. fuscopterus	-	17/vii	-	23/ix	27/vi	-	-
C. burmeisteri	2/viii	12/vii	-	22/vii	12/viii	-	6/viii
C. flavidus	10/vi	13/v	30/v	9/vi	5/vi	26/v	1/vi

Table 45. Sex ratios of L. pedicularia and E. briggsi in different years.

Male:female

	L. pedicularia		E. briggsi	
	Trap (1.3m)	Trap (9.2m)	Trap (1.3m)	Trap (9.2m)
1961	1:1.07	1:0.69	1:0.79	1:0.62
1962	1:0.71	1:0.67	-	-
1963	1:0.70	1:1.07	-	-
1964	1:1.04	1:0.65	-	-
1965	1:0.65	1:0.91	1:0.76	-
1966	1:0.80	1:1.02	1:0.87	-
1967	1:0.76	1:0.70	1:0.68	1:1.25

Table 46. Psocoptera caught on Stake Sticky Traps at Silwood Park, 1966.

Species	Apr.	May	June	Jly.	Aug.	Sept.	Oct.	Nov.	Total
L. variegata	-	-	7	5	-	2	-	-	14
E. hyalinus	4	13	2	-	-	3	-	-	22
P. picicornis	-	-	-	-	1	-	-	-	1
E. briggsi	-	-	-	1	-	2	17	-	20
S. immaculatus	-	-	-	4	-	3	-	-	7
G. cruciatus	-	-	1	1	-	-	-	-	2
C. flavidus	-	-	7	1	-	1	2	-	11
Total:	4	13	17	12	1	11	19	-	77

Table 47. Psocoptera caught on Rope Sticky Traps at Silwood Park, 1966.

Species	Apr.	May	June	Jly.	Aug.	Sept.	Oct.	Nov.	Total
E. hyalinus	-	4	1	5	3	-	1	-	14
E. briggsi	-	-	-	-	4	2	-	1	7
S. immaculatus	-	-	-	-	1	-	-	-	1
G. cruciatus	-	-	-	-	1	-	-	-	1
C. flavidus	-	-	7	12	18	9	2	-	48
Total:	0	4	8	17	27	11	3	1	71

Table 48. Psocids observed to fly from the beating tray at Silwood Park, 1966-67.

	Observed flight.		
Species	Never	Rarely	Often
A. contaminata		+	
A. bifasciata		+	
T. sexpunctatum		+	
L. fasciata		+	
L. variegata	+		
E. hyalinus			+
E. westwoodi		+	
E. mclachlani		+	
C. cyanops	+		
P. picicornis			+
M. unipunctatus		+	
M. immunis			+
L. pedicularia			+
E. briggsi		+	
P. alboguttatus		+	
P. subfasciatus		+	
P. phaeopterus			+
S. immaculatus			+
S. stigmaticus			+
G. cruciatus			+
C. kolbei		+	
C. fuscopterus		+	
C. burmeisteri			+
C. flavidus			+
T. dalii	+		
Total:	3	12	10

Table 49. Inheritance of Brachyptery in G. cruciatus (L.)

Female parent	Density of offspring (No./tube)			Offspring reared
	1	5	20	
Macropter (5 expts. at each density)	0	0	0	Brachypters
	3	24	87	Macropters
Micropter (5 expts. at each density)	1	2	1	Brachypters
	4	20	92	Macropters

Female grandparent	Female parent				
Macropter	Macropter	0	0	0	Brachypters
(5 expts.)		5	22	97	Macropters
Micropter	Micropter	1	0	9	Brachypters
(3 expts.)		2	12	42	Macropters
Micropter	Macropter	0	0	0	Brachypters
(5 expts.)		4	20	79	Macropters

Table 50. Times of development of *Alaptus pallidicornis* Foerst. in the eggs of three psocid species.

Host species:	Number	Temp. (°C)	Total development times (days) Minimum	Mean	Maximum
C. flavidus	35	15	24	27.0	32
	30	20	18	23.4	29
	28	25	17	19.5	22
E. briggsi	30	15	21	24.0	28
	32	20	18	22.6	26
	30	25	16	18.3	22
S. immaculatus	30	15	26	30.6	36
	27	20	22	25.0	29
	28	25	18	22.4	26

Table 51. Sizes of *Alaptus pallidicornis* bred from eggs of three species of psocids.

(Mean measurement in mm, ±0.003)

Host:	*C. flavidus*	*E. briggsi*	*S. immaculatus*
No. ♀ parasites:	20	20	20
Antenna length	0.384	0.340	0.425
Forewing length	0.464	0.446	0.528
Hindwing length	0.458	0.444	0.521
Thorax length	0.260	0.250	0.264
Ovipositor length	0.146	0.142	0.158

Table 52. Longevity and fecundity of *Alaptus pallidicornis* females bred from eggs of three species of psocids at 20°C. (Food provided.)

		Longevity (days)			Total progeny reared	
Host:	Number	Minimum	Mean	Maximum	Mean	Extremes
C. flavidus	20	11	15	20	62	43 - 87
E. briggsi	20	8	13.5	17	56	31 - 80
S. immaculatus	20	10	15.8	19	61	49 - 76

Table 53. Sex ratio of *Alaptus pallidicornis* bred from field-collected eggs and in laboratory stocks.

(a) Field collections.

Date of collection	Total parasites bred	Males : Females
Nov. 1965	184	82 : 102
Mar. 1966	230	106 : 124
June 1966	78	34 : 44
Aug. 1966	218	130 : 88
Oct. 1966	283	136 : 147
Mar. 1967	320	143 : 177
June 1967	260	125 : 135
Aug. 1967	242	108 : 134
Oct. 1967	294	166 : 128

(b) Isolated virgin females in the laboratory.

Age of host eggs (days)	Total parasites bred	Males : Females
0 - 1	168	72 : 96
2 - 3	314	186 : 128
5	86	31 : 55
7	152	89 : 63
10	57	24 : 33

Table 54. The effect of food on the longevity of *Alaptus pallidicornis* bred from *Caecilius flavidus*.

Food	No.	Longevity (Days)	Mean
+	73	8 - 15	11.8
-	58	10 - 19	15.0

Table 55. The longevity of male and female *Alaptus pallidicornis*. (Food provided)

Sex	No.	Longevity (Days)	Mean
Male	46	11 - 17	14.3
Female	38	13 - 19	15.8

Table 56. Times of oviposition of *Alaptus pallidicornis*.

Age of female (days)	No. of females	No. of observations of oviposition	Duration of oviposition (minutes)	
			Extremes	Mean
1	25	37	6 - 27	12.6
2 - 3	25	46	4 - 18	9.8
5	25	28	3 - 14	7.0
7 - 8	17	29	8 - 22	14.4
10 - 12	20	37	3 - 16	9.5
16 - 18	4	8	5 - 11	8.5

Table 57. The size of parasitised egg batches of *C. flavidus* collected from oak trees at Silwood Park, 1966 - 67. (Total batches - 66)

Eggs per batch	No. of batches	No. fully parasitised	No. with developing psocids	No. with 'dead' eggs
2	1	0	1	0
3	4	3	1	0
4	6	5	1	0
5	11	7	4	0
6	5	4	1	3
7	12	5	7	0
8	21	15	6	5
9	2	2	0	1
10	2	2	0	0
11	2	0	2	0

Table 58. Laboratory experiments on the amount of parasitism of *C. flavidus* egg batches of different sizes by *A. pallidicornis*. (20 batches of each size)

Batch size - No. of eggs:	4	5	6	7	8	9	10
No. of batches fully parasitised:	18	16	12	19	18	14	12
No. of batches with developing psocids:	2	4	8	1	2	6	8

Table 59 . The amount of parasitism of C. flavidus eggs by female Alaptus of different ages.

Age of female (days)	No. of females	Total No. of eggs offered. (1 batch per ♀ per day)	Total no. of eggs parasitised	Per cent parasitism
1	23	162	143	88.3
2	23	160	152	95.0
3	23	149	130	87.2
4	23	158	137	86.7
5	23	164	142	86.5
6	23	153	120	78.4
7	23	159	134	84.3
8	21	139	114	82.0
9	20	142	105	73.9
10	17	138	113	81.9
11	16	124	89	71.8
12	12	88	34	38.6
13	12	94	11	11.7
14	9	68	0	0.0
15	8	52	0	0.0

Table 60 . The fecundity of Alaptus pallidicornis and A. richardsi on eggs of C. flavidus in the laboratory.

		No. of progeny reared		
Species	No.	Minimum	Mean	Maximum
A. pallidicornis	20	38	57.5	82
A. richardsi	20	47	69.0	76

Table 61. Parasitism of egg batches of C. flavidus on small potted oak trees by A. pallidicornis.

Female	Total no. of batches offered	Total no. of batches parasitised
1	26	21
2	18	14
3	30	27
4	15	2
5	14	8
6	23	11
7	23	3
8	22	18
9	14	9
10	34	8
11	21	16
12	9	7
13	26	24
14	18	5
15	18	14
16	29	22
17	17	13

Table 62. The effect of host age on parasitism by Alaptus females up to five days old.

Age of host eggs (days)	No. of Parasites	No. of ovipositions observed	No. of progeny reared from these eggs
0 - 1	20	37	34
2 - 3	20	52	51
5	20	32	32
7	20	26	9
10	20	4	0
15	20	1	0

Table 63. Host specificity of *Alaptus* species parasitising psocid eggs at Silwood Park

Parasite:	*A. pallidicornis*		*A. richardsi*		*A. fusculus*		*A. minimus*	
Psocid genus:	Wild eggs	Lab. exp.	Wild eggs	Lab. exp.	Wild eggs	Lab. exp.	Wild eggs	Lab. exp.
Caecilius	+	+	+	+	-	y	-	-
Stenopsocus	+	+	+	+	-	y	-	-
Graphopsocus	+	+	+	+	-	y	-	-
Ectopsocus	+	+	-	+	-	-	-	-
Trichopsocus	-	y	-	-	-	+	-	-
Elipsocus *Cuneopalpus* *Philotarsus*	-	y	-	-	+	+	+	+
Mesopsocus	-	-	-	-	+	+	+	0
Amphigerontia	-	-	-	-	+	0	-	0
Peripsocus	-	-	-	y	-	0	-	0
Cerobasis	-	-	-	-	+	0	-	0
Liposcelis	0	-	0	-	0	-	0	0

(+ denotes rearing; - denotes not found, or no interest shown; y denotes oviposition observed, but no progeny reared; 0 denotes no data)

Table 64. The numbers of braconid larvae found in different psocid species at Silwood Park and Windsor Great Park, 1966 - 1967.

Psocids dissected	No.	Year	Numbers parasitised	Psocid generation
C. flavidus	83	1966	0	I (litter)
	389	1966	203	II (June-July)
	452	1966	0	III (Sept.)
	29	1967	0	I (Sept.)
	283	1967	164	II (Sept.)
	252	1967	1	III (Sept.)
C. burmeisteri	18	1966	0	I (May)
	73	1966	27	II (June-July)
	59	1966	0	III (Sept.)
	0	1967	0	I (Sept.)
	106	1967	17	II (Sept.)
	84	1967	0	III (Sept.)
S. immaculatus	18	1966	5	I (May-June)
	52	1966	0	II (Aug.-Sept.)
	23	1967	4	I (Aug.-Sept.)
	41	1967	0	II (Aug.-Sept.)
S. stigmaticus	118	1966	0	II (Aug.-Sept.)
	17	1967	2	I (May-June)
	236	1967	0	II (May-June)
E. briggsi	216	1966	0	III (Aug.)
	305	1967	0	III (Aug.)
Elipsocus	135	1966-67	26	All (May-Sept.)
Cuneopalpus cyanops	286	1966-67	0	I & II (May-Sept.)
Philotarsus picicornis	153	1966-67	37	I (July-Aug.)
Cerobasis guestfalica	258	1966-67	4	I & II (June-Sept.)
Mesopsocus	193	1966	58	I (Apr.-July)
	305	1967	136	I (Apr.-July)
Amphigerontia	38	1966	14	I (May-June)
	26	1966	0	II (Sept.)
	57	1967	34	I (Sept.)
	109	1967	0	II (Sept.)

Table 65. The numbers of braconid larvae per psocid host at Silwood Park, 1966-67.

Psocid	No. *Leiophron* larvae per host		
	One	Two	More than Two
C. flavidus	244	6	0
C. burmeisteri	43	1	0
S. immaculatus	9	0	0
S. stigmaticus	2	0	0
Elipsocus	26	0	0
Philotarsus picicornis	35	2	0
Cerobasis guestfalica	4	0	0
Mesopsocus	181	3	0
Amphigerontia	48	0	0

Table 66. Dimensions of eggs of two species of Leiophron.

(mm, all ∓ 0.02 mm)

Species:	*L. claviventris*			*L. similis*		
Stage of egg (see Figs.)	No.	Length	Greatest breadth	No.	Length	Greatest breadth
I	7	0.06 - 0.14	0.04 - 0.09	15	0.04 - 0.22	0.03 - 0.15
II	6	0.08 - 0.20	0.04 - 0.12	11	0.06 - 0.18	0.04 - 0.12
III	12	0.16 - 0.30	0.06 - 0.16	8	0.13 - 0.28	0.08 - 0.15

(Stages of eggs - I - Swollen egg, no contents visible.
II - Distinct lining of trophamnion cells.
III - With coiled larva, near hatching.)

Table 67. Variations in chaetotaxy on head capsules of fully grown larvae of two species of Leiophron.

(IO larvae of each species examined)

L. similis Curtis.

Sclerites and regions	Setae
Stipital	IO-(0 + 0)
Frontal	IO-(0 + 0)
Genal	9-(I + I), I-(0 + 0)
Clypeal	9-(2 + 2), I-(I + 2)
Labral	IO-(2 + 2)
Maxillary	8-(2 + 2), 2-(I + I)
Prelabial	7-(4 + 4), 3-(2 + 2)
Postlabial	7-(3 + 3), 2-(2 + 2), I-(2 + I)

L. claviventris Ruthe

Sclerites and regions	Setae
Stipital	IO-(0 + 0)
Frontal	9-(I + I), I-(0 + 0)
Genal	IO-(0 + 0)
Clypeal	IO-(0 + 0)
Labral	8-(0 + 0), 2-(I + I)
Maxillary	IO-(I + I)
Prelabial	9-(2 + 2), I-(I + I)
Postlabial	8-(0 + 0), I-(I + I), I(2 + 2)

[Table arrangement follows that in Waloff (I967) i.e. 'No. of larvae (Setae on left side + Setae on right side)]

Table 68. Measurements of larvae of two species of Leiophron.

(mm, all ∓ 0.01 mm)

Species	Instar	No.	Total length	Cauda length	Greatest breadth
L. claviventris	I	8	0.18 - 0.38	0.06 - 0.17	0.04 - 0.12
	II	14	0.26 - 1.50	0.10 - 0.36	0.10 - 0.52
	III	12	1.44 - 2.45	-	0.60 - 1.18
	IV	20	1.83 - 2.64	-	0.86 - 1.32
L. similis	I	20	0.24 - 0.47	0.10 - 0.24	0.08 - 0.16
	II	15	0.35 - 1.48	0.15 - 0.40	0.12 - 0.40
	III	20	1.32 - 1.86	-	0.56 - 1.24
	IV	20	1.70 - 2.20	-	0.70 - 1.28

Table 69. Measurements of cocoons of two species of Leiophron.

(mm, all ∓ 0.01 mm)

Species	No.	Length	Greatest breadth
L. claviventris	7	1.64 - 1.80	0.88 - 0.95
L. similis	12	1.52 - 1.57	0.84 - 0.88

Table 70. Stages of Leiophron claviventris Ruthe and L. similis Curtis found in different host instars at Silwood Park, 1966 - 1967.

Psocid	Parasite		Parasite stages Egg	 I - II (Caudate larvae)	 III - IV
Mesopsocus	L. claviventris	No.:	10	67	114
		Host instars:	II - III	III - V	IV - Ad.
C. flavidus	L. similis	No.:	34	134	100
		Host instars:	II - III	III - VI	III - Ad.

Table 71. Development times of healthy and parasitised psocid nymphs of C. flavidus in outdoor insectary at Silwood Park, 1967.

	Nymphs.			
	Healthy.		Parasitised.	
Instar	No.	Duration (days)	No.	Duration (days)
II	30	2 - 4	8	3 - 4
III	30	3 - 6	23	3 - 5
IV	30	3 - 5	12	3 - 6
V	30	5 - 8	40	5 - 11
VI	30	4 - 7	36	6 - 20

Table 72. Total numbers of arthropods which are possible predators on psocids beaten from different tree species at Silwood Park, Berks., at monthly intervals from April to October in 1966 and 1967.

(Ten samples for each tree per month; each sample 1m length of branch with foliage.)

(a) 1966

Month/Tree:	Apr.	May	June	July	Aug.	Sept.	Oct.
Acer	6	8	6	14	34	11	4
Aesculus	3	3	4	18	26	9	7
Betula	2	0	3	9	11	8	4
Crataegus	12	23	28	52	73	39	16
Fagus	3	7	6	12	58	32	15
Ilex	18	12	8	29	43	19	26
Pinus	7	14	17	11	8	23	14
Populus	2	6	3	4	9	1	0
Quercus	5	10	76	143	192	228	68
Tilia	3	4	5	18	26	54	11
Ulmus	3	3	11	16	9	17	4

(b) 1967

Month/Tree:	Apr.	May	June	July	Aug.	Sept.	Oct.
Acer	4	2	4	9	21	25	8
Aesculus	2	7	5	8	52	12	8
Betula	0	4	3	17	8	4	0
Crataegus	7	12	37	104	113	68	21
Cupressus	11	8	14	23	57	30	14
Fagus	4	4	3	8	21	35	11
Ilex	3	17	5	47	104	68	28
Pinus	8	4	8	17	29	12	8
Populus	4	3	3	4	3	0	0
Quercus	7	21	39	74	246	289	52
Tilia	2	6	6	15	7	11	4
Ulmus	0	2	5	12	8	2	3

Table 73 . The groups and numbers of species of predatory arthropods beaten from different trees at Silwood Park in 1966-67.

			Total numbers and species					
Tree:	Total individuals	Total species	Acarina	Opilionida	Araneae	Hemiptera	Neuroptera	Others
Acer	156	20	11 (1)	9 (4)	74 (3)	36 (4)	23 (6)	3 (2)
Aesculus	115	28	16 (1)	17 (2)	52 (11)	16 (7)	9 (4)	5 (3)
Betula	73	12	8 (1)	8 (1)	36 (6)	18 (3)	(0)	3 (1)
Crateagus	395	58	107 (1)	54 (7)	113 (18)	79 (12)	18 (7)	24 (13)
Cupressus (1967)	121	14	38 (1)	9 (3)	49 (6)	22 (3)	3 (1)	(0)
Fagus	217	29	69 (1)	7 (2)	59 (9)	38 (9)	38 (4)	6 (4)
Ilex	419	43	34 (1)	28 (6)	204 (18)	48 (4)	94 (8)	11 (6)
Pinus	180	14	37 (1)	19 (2)	79 (6)	26 (2)	19 (3)	(0)
Populus	32	9	3 (1)	(0)	16 (3)	8 (2)	5 (3)	(0)
Quercus	1452	70	314 (1)	46 (5)	688 (23)	155 (26)	230 (10)	19 (5)
Tilia	122	38	15 (1)	11 (4)	38 (17)	28 (6)	23 (6)	7 (4)
Ulmus	62	17	8 (1)	5 (3)	22 (6)	19 (3)	6 (3)	2 (1)

(Numbers of species identified given in parentheses.)

Table 74. Arthropods found with psocid prey at Silwood Park, 1966-67.

Group:	Predator:	Prey:		Tree:	Month:
ACARINA	*Anystis* sp.	*C. flavidus*	III	*Quercus*	June 1966
	Anystis sp.	*C. flavidus*	III	*Quercus*	June 1966
	Anystis sp.	*C. flavidus*	III	*Quercus*	June 1967
	Anystis sp.	*C. flavidus*	V	*Quercus*	June 1967
	Anystis sp.	*C. flavidus*	VI	*Quercus*	July 1966
	Anystis sp.	*C. flavidus*	Ad.	*Quercus*	Aug. 1966
	Anystis sp.	*C. flavidus*	Ad.	*Quercus*	July 1967
	Anystis sp.	*C. flavidus*	Ad.	*Tilia*	Aug. 1966
	Anystis sp.	*C. flavidus*	Eggs	*Quercus*	Aug. 1966
	Anystis sp.	*S. stigmaticus*	Eggs	*Crataegus*	Aug. 1966
	Anystis sp.	*Elipsocus* sp.	VI	*Pinus*	July 1966
	Anystis sp.	*E. hyalinus*	Ad.	*Craetagus*	July 1967
	Anystis sp.	*C. cyanops*	Ad.	*Pinus*	Aug. 1966
	Anystis sp.	*Amphigerontia* sp.	III	*Sarothamnus*	June 1966
	Anystis sp.	*Amphigerontia* sp.	V	*Sarothamnus*	June 1966
OPILIONIDA	*Nemostoma lugubre*	*C. flavidus*	Eggs	*Quercus*	June 1967
	Nemostoma lugubre	*Elipsocus* sp.	IV	*Crataegus*	Aug. 1967
	Oligolophus sp. (imm.)	*C. flavidus*	V	*Quercus*	Sept. 1966
	Opilio sp.	*C. flavidus*	Ad.	*Quercus*	July 1966
ARANEAE	*Xysticus lanis* (Koch)	*C. flavidus*	V	*Quercus*	July 1967
	Theridion sp. (imm.)	*Elipsocus*	III	*Crataegus*	May 1966
	T. pallens Blackwall	*E. briggsi*	IV	*Quercus*	Sept. 1967
	Erigone sp. (imm.)	*C. flavidus*	II	*Quercus*	Aug. 1967
	Erigone sp. (imm.)	*S. stigmaticus*	III	*Crataegus*	Aug. 1967
	Linyphia sp. (imm.)	*C. flavidus*	II	*Quercus*	July 1967
NEUROPTERA	*Conwentzia psociformis* III	*C. flavidus*	Eggs	*Quercus*	Sept. 1966
	Conwentzia psociformis III	*C. flavidus*	II	*Quercus*	Sept. 1967

Table 74 (cont.)

Group:	Predator:	Prey:		Tree:	Month:	
NEUROPTERA	*Semidalis aleyrodiformis* III	*C. flavidus*	Eggs	*Crataegus*	July	1966
	Coniopteryx tineiformis III	*C. flavidus*	Eggs	*Quercus*	July	1966
	Hemerobius lutescens III	*C. flavidus*	Eggs	*Quercus*	July	1967
	Hemerobius lutescens III	*C. flavidus*	IV	*Quercus*	Aug.	1967
	Hemerobius stigma III	*Elipsocus* sp.	V	*Pinus*	June	1966
	Chrysopa ciliata Wesm. III	*C. flavidus*	Eggs	*Quercus*	June	1966
	Chrysopa flava III	*C. flavidus*	Ad.	*Acer*	July	1967
HEMIPTERA	*Anthocoris nemoralis* Ad.	*M. immunis*	IV	*Crataegus*	May	1966
	Cyellocoris histrionicus Ad.	*C. flavidus*	III	*Quercus*	July	1966
	Dryophilocoris flavoquadrimaculatus Ad.	*C. flavidus*	VI	*Quercus*	Aug.	1967

Table 75. Experiments on selection of psocid prey by arthropod predators in in the laboratory.

Predator:	Prey offered:		Replicates	Total Prey killed:	
	A	B		A	B
Anystis sp.	5 Psocid Eggs	5 Psocid Nymphs	10	12	7
	5 Aphid Nymphs	5 Psocid Nymphs	8	9	17
	5 Psyllid Nymphs	5 Psocid Nymphs	10	4	8
	5 Psocid Adults	5 Psocid Nymphs	10	7	4
Opilio sp.	5 Psocid Eggs	5 Psocid Nymphs	10	14	8
	5 Aphid Nymphs	5 Psocid Nymphs	8	3	7
	5 Psocid Adults	5 Psocid Nymphs	5	9	0
Linyphia sp.	5 Psocid Eggs	5 Psocid Nymphs	12	5	14
	5 Aphid Nymphs	5 Psocid Nymphs	10	13	9
	5 Psyllid Nymphs	5 Psocid Nymphs	8	8	12
	5 Psocid Adults	5 Psocid Nymphs	8	5	2
Ciniflo sp.	5 Psocid Eggs	5 Psocid Nymphs	6	3	5
	5 Aphid Nymphs	5 Psocid Nymphs	6	6	11
Conwentzia psociformis III	5 Psocid Eggs	5 Psocid Nymphs	10	4	6
	5 Aphid Nymphs	5 Psocid Nymphs	10	8	12
	5 Psyllid Nymphs	5 Psocid Nymphs	10	3	6
	5 Psocid Adults	5 Psocid Nymphs	10	11	4
Hemerobius lutescens III	5 Aphid Nymphs	5 Psocid Nymphs	8	17	12
Chrysopa ciliata III	5 Psocid Eggs	5 Psocid Nymphs	5	6	9
	5 Aphid Nymphs	5 Psocid Nymphs	10	8	3
	5 Psyllid Nymphs	5 Psocid Nymphs	10	10	7
	5 Psocid Adults	5 Psocid Nymphs	10	18	11

Table 76. <u>Numbers and survival of eggs of C. flavidus and G. cruciatus on foliage of some broadleaved trees at Silwood Park, Berks. in 1966 and 1967</u>.

(Samples of 2000 leaves)

(a) <u>1966</u>

Tree	Sampling date	Batches	Eggs	Predated	Parasitised	Dead	Healthy + hatched	% survival
Acer	June	14	92	5	17	2	68 + 0	73.9
"	Aug.	8	52	7	9	2	34 + 0	65.4
"	Oct.	19	138	11	14	0	95 + 18	81.9
Aesculus	June	5	41	0	0	4	37 + 0	90.2
"	Aug.	11	108	6	6	0	88 + 8	88.9
"	Oct.	7	68	3	7	5	15 + 38	77.9
Betula	June	5	31	2	5	0	24 + 0	77.4
"	Aug.	7	38	0	4	0	22 + 12	89.5
"	Oct.	Leaf-fall complete by mid-September						
Crataegus	June	17	142	0	7	2	115 + 18	93.7
"	Aug.	38	330	18	26	4	242 + 40	85.5
"	Oct.	126	1235	50	84	14	927 + 260	96.1
Fagus	June	7	32	3	1	3	25 + 0	78.1
"	Aug.	23	184	12	24	11	137 + 0	74.5
"	Oct.	34	307	17	26	9	240 + 15	83.1
Ilex	June	37	326	15	17	7	270 + 17	88.0
"	Aug.	52	413	8	29	12	341 + 23	88.1
"	Oct.	104	874	26	67	12	741 + 28	88.0
Populus	June	3	12	0	0	2	10 + 0	83.3
"	Aug.	0	0					
"	Oct.	Leaf-fall complete by mid-September						
Quercus	June	106	854	6	82	2	746 + 18	89.5
"	Aug.	304	2954	43	238	6	2548 + 119	90.3
"	Oct.	362	3386	105	296	8	2415 + 562	87.9
Tilia	June	18	79	5	4	2	68 + 0	86.1
"	Aug.	7	37	5	7	0	18 + 7	67.6
"	Oct.	12	92	7	11	0	35 + 29	69.6
Ulmus	June	3	14	0	0	0	14 + 0	100.0
"	Aug.	3	11	2	3	0	6 + 0	54.5
"	Oct.	7	62	8	8	3	17 + 26	69.4

Table 76 (cont.)

(b) 1967

Tree	Sampling date	Batches	Eggs	Predated	Parasitised	Dead	Healthy + hatched	% survival
Acer	June	5	37	8	3	0	26 + 0	70.3
"	Aug.	14	126	12	8	4	87 + 15	81.0
"	Oct.	11	83	5	8	0	52 + 19	85.5
Aesculus	June	3	32	0	5	0	27 + 0	84.4
"	Aug.	3	19	4	0	0	15 + 0	78.9
"	Oct.	3	17	0	0	2	7 + 8	88.2
Betula	June	11	116	11	0	8	72 + 24	82.8
"	Aug.	4	30	5	0	0	25 + 0	83.3
"	Oct.	4	34	5	8	4	11 + 6	50.0
Crataegus	June	8	72	3	9	6	53 + 11	88.9
"	Aug.	83	719	8	85	0	609 + 17	87.1
"	Oct.	152	1362	18	187	17	1011 + 129	83.7
Fagus	June	15	97	0	0	5	92 + 0	94.8
"	Aug.	33	300	21	26	5	151 + 96	82.3
"	Oct.	62	594	16	72	8	460 + 38	83.8
Ilex	June	62	567	28	49	11	377 + 102	84.5
"	Aug.	90	803	37	58	0	562 + 146	88.2
"	Oct.	184	1464	74	107	16	730 + 437	79.7
Populus	June	0	0					
"	Aug.	6	46	0	5	0	41 + 0	89.1
"	Oct.	Leaf-fall complete by mid-September						
Quercus	June	153	1386	5	280	5	1084 + 12	79.1
"	Aug.	336	3025	110	256	29	1558 + 1069	86.8
"	Oct.	429	4205	129	315	12	3085 + 864	93.9
Tilia	June	12	79	4	7	0	63 + 5	86.1
"	Aug.	43	376	38	19	7	278 + 34	83.0
"	Oct.	27	238	11	12	32	117 + 66	76.9
Ulmus	June	4	14	0	0	0	14 + 0	100.0
"	Aug.	10	65	3	5	0	51 + 6	87.7
"	Oct.	7	39	3	8	3	20 + 5	64.1

Table 77. Numbers and survival of eggs of C. burmeisteri on Cupressus foliage at Silwood Park, Berks., fromm 1965 to 1967. (20 samples on each date.)

	Date		Batches	Eggs	Predated	Parasitised	Dead	Healthy + hatched	% survival
O.W.	Nov.	1965	107	986	35	104	6	803 + 38	85.3
	Mar.	1966	59	502	26	49	18	393 + 16	81.5
	June	1966	187	137	5	18	9	93 + 12	76.6
	Aug.	1966	139	796	16	9	12	650 + 109	95.4
O.W.	Oct.	1966	86	738	30	53	0	450 + 205	88.8
	Mar.	1967	96	923	12	23	8	762 + 118	95.2
	June	1967	74	531	23	26	8	371 + 103	89.2
	Aug.	1967	130	433	38	17	2	168 + 208	86.8
	Oct.	1967	153	1025	52	59	21	482 + 411	87.1

Table 78. Numbers and survival of eggs of E. briggsi on foliage of Quercus at Silwood Park, Berks., in 1966 and 1967. (2000 leaves on each sampling date.)

Date	Batches	Eggs	Predated	Parasitised	Dead	Healthy + hatched	% survival
June 1966	11	82	0	11	0	59 + 12	86.6
Aug. 1966	56	568	23	46	8	483 + 8	86.4
Oct. 1966	203	1734	57	134	18	1502 + 23	87.9
June 1967	8	40	4	0	2	34 + 0	85.0
Aug. 1967	25	186	11	16	0	139 + 20	85.5
Oct. 1967	168	1260	23	73	5	1050 + 109	92.0

Table 79. Numbers and survival of eggs of Stenopsocus on several species of broadleaved trees at Silwood Park, Berks., in 1966 and 1967.

(a) S. immaculatus

Tree	Date	Batches	Eggs	Predated	Parasitised	Dead	Healthy + hatched	% survival
Quercus	Aug. 1966	5	22	0	4	0	18 + 0	81.8
"	Oct. 1966	8	37	3	8	0	23 + 3	70.2
"	June 1967	7	53	3	4	2	44 + 0	83.0
"	Aug. 1967	13	122	7	12	0	77 + 26	84.4
"	Oct. 1967	21	169	5	28	11	85 + 40	74.0
Ilex	June 1966	28	178	12	7	4	140 + 15	87.0
"	Aug. 1966	53	482	24	26	17	387 + 28	86.1
"	Oct. 1966	60	503	11	36	10	337 + 109	88.7
"	Mar. 1967	43	422	0	59	22	161 + 170	78.4
"	June 1967	32	183	7	11	4	131 + 30	88.0
"	Aug. 1967	16	147	7	8	4	92 + 36	87.1
"	Oct. 1967	28	267	11	37	0	170 + 49	82.0
Crataegus	June 1966	15	137	4	12	5	116 + 0	84.7
"	Aug. 1966	22	199	0	6	5	170 + 18	94.5
"	Oct. 1966	38	309	21	32	21	121 + 114	76.1
"	Mar. 1967	0	0					
"	June 1967	12	124	5	8	4	101 + 8	87.9
"	Aug. 1967	14	117	4	8	0	92 + 13	89.7
"	Oct. 1967	56	485	17	36	7	324 + 101	87.6

(b) S. stigmaticus

Tree	Date	Batches	Eggs	Predated	Parasitised	Dead	Healthy + hatched	% survival
Crataegus	June 1966	58	506	12	46	3	445 + 0	87.9
"	Aug. 1966	42	382	5	18	18	325 + 16	89.3
"	Oct. 1966	109	964	17	105	5	631 + 206	86.8
"	Mar. 1967	47	417	6	28	0	360 + 23	91.8
"	June 1967	32	306	4	26	0	268 + 8	90.2
"	Aug. 1967	51	493	12	65	12	352 + 52	81.9
"	Oct. 1967	87	826	23	54	8	624 + 137	92.1

Table 80. Egg survival of C. flavidus at different heights of large oak trees at Silwood Park, Berks., in 1966.

Height	Month	Batches	Eggs	Predated	Parasitised	Dead	Healthy + hatched	% survival
0 -3m	June	304	2902	77	226	103	2496	86.0
	Aug.	348	3297	188	177	188	2714	82.4
	Oct.	352	3371	231	359	187	2594	76.9
5-7m	June	249	2358	72	182	85	2019	85.6
	Aug.	279	2702	127	157	150	2268	84.3
	Oct.	303	2921	219	185	183	2344	80.2
12-15m	June	89	850	34	120	36	658	77.4
	Aug.	309	2049	80	159	123	1677	81.8
	Oct.	345	3400	183	290	206	2721	80.0

Table 81. Survival of eggs of some foliage-frequenting psocids overwintering in litter at Silwood Park, Berks., 1965-6 and 1966-7.

(50 samples each occasion of Quercus; 20 samples each occasion of Crataegus)

(a) Quercus litter

Date	Psocid	Batches	Eggs	Predated	Parasitised	Dead	Healthy + hatched	% survival
Nov. 1965	C. flavidus	246	2238	238	206	18	1719 + 57	79.3
Mar. 1966	"	219	1983	160	241	31	1511 + 40	78.2
Nov. 1966	"	183	1680	82	137	12	1431 + 18	86.2
Mar. 1967	"	292	2762	102	343	26	2354 + 37	86.6
Nov. 1965	E. briggsi	193	2014	112	172	12	1688 + 30	85.3
Mar. 1966	"	137	1244	86	105	8	1045 + 0	84.0
Nov. 1966	"	170	1538	97	94	8	1324 + 15	87.1
Mar. 1967	"	267	2506	142	170	119	1971 + 104	82.8

(b) Crataegus litter

Date	Psocid	Batches	Eggs	Predated	Parasitised	Dead	Healthy + hatched	% survival
Nov. 1965	S.stigmaticus	138	1130	42	86	48	954 + 0	84.4
Mar. 1966	"	162	1483	79	169	103	1109 + 23	76.3
Nov. 1966	"	79	683	23	92	18	550 + 0	80.5
Mar. 1967	"	152	1419	30	113	11	1265 + 0	89.1

Table 82. Overwintering psocid eggs on Ilex trees at Silwood Park, Berks., 1966-67.

(a) November 1966

Tree	Leaves	Batches	Eggs	Predated	Parasitised	Dead	Healthy + hatched	% survival
1	1927	71	571	18	26	13	462 + 52	90.0
2	3704	139	936	31	79	26	750 + 40	84.4
3	1431	68	532	15				
4	2676	92	741	11				

(b) March 1967

Tree	Leaves	Batches	Eggs	Predated	Parasitised	Dead	Healthy + hatched	% survival
3	1350	57	409	12	42	18	310 + 27	82.3
4	2539	79	683	8	59	37	522 + 57	84.7

Table 83. Predation on webbed and unwebbed egg batches of C. flavidus in the laboratory.

Predator	Batches provided		Replicates	Total no. of batches attacked after 48 hrs.	
	Webbed	Unwebbed		Webbed	Unwebbed
Larva of *C.psociformis*	5	5	10	31	24
Larva of *C.tineiformis*	5	5	8	17	28
Nymph of *A. nemorum*	5	5	10	21	26
Mite (*Anystis* sp.)	5	5	10	36	23
Opilionid (*Nemastoma*)	5	5	10	18	12

Table 84. Parasitism of webbed and unwebbed egg batches of C. flavidus in the laboratory.

Parasite	Batches provided		Replicates	Total no. of batches from which parasites developed	
	Webbed	Unwebbed		Webbed	Unwebbed
A. pallidicornis	5	5	10	32	40
A. richardsi	5	5	6	18	21

Table 85. The numbers of ovarioles in British foliage-frequenting psocids.

Species	No. of ovarioles	Previous authors
T. dalii	4 + 4	Ribaga (1906)
E. briggsi	5 + 5	Sofner (1941)
S. stigmaticus	4 + 4	Noland (1924)
S. immaculatus	4 + 4	-
G. cruciatus	3 + 3	-
C. flavidus	4 + 4	-
C. burmeisteri	4 + 4	-
C. kolbei	4 + 4	-
C. fuscopterus	4 + 4	-

Table 86. Egg batch size from wild collections at Silwood Park, 1966-67.

			No. of eggs per batch															
Species	Tree	Batches	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
C. flavidus	Quercus	416	-	8	5	29	13	27	36	106	115	46	20	8	-	3	-	-
C. flavidus	Crataegus	185	2	15	3	12	38	37	51	26	-	-	1	-	-	-	-	-
C. burmeisteri	Cupressus	138	5	-	11	16	34	50	8	11	3	-	-	-	-	-	-	-
E. briggsi	Quercus	205	1	-	5	7	17	14	18	58	43	31	3	7	1	-	-	-
S. stimaticus	Crataegus	123	-	1	3	3	9	6	13	49	31	5	-	2	-	-	1	-
S. immaculatus	Various	86	-	-	-	8	5	5	24	38	3	1	-	-	-	2	-	-
G. cruciatus	Ilex	52	-	-	1	-	3	6	15	21	5	-	-	-	-	-	-	-

Table 87. Oocyte counts in female psocids of known ages, kept in outdoor insectary at Silwood Park, 1966, with constant excess food supply.

			No. of oocytes (averaged totals in all ovarioles)			
Species	No.	Age (Days)	Mature Eggs	Large Oocytes	Small Oocytes	Total
C. flavidus	20	0-1	0	7	90	97
	20	1-3	5	12	84	101
	20	6-7	7	19	80	106
	20	12-14	7.5	26	93	126.5
	20	20-22	6	16	87	112
	20	27-28	6	16	60	82
	20	34-35	7	14	55	76
	10	42	8	11	43	62
	12	48-49	3	5	12	20
S. stigmaticus	20	0-1	0	5	67	72
	20	1-3	3	14	64	81
	15	6-7	6	23	74	103
	15	13-14	8	20	62	90
	15	21	5.5	22	60	87.5
	15	27-28	6	16.5	54	76.5
	15	34-35	8	8	31	47
	10	40	5	8	17	30
E. briggsi	20	0-1	0	6	93	99
	20	1-3	3	24	105	132
	20	6-7	8	30	89	127
	20	12-14	11	23	113	147
	20	20-21	7	19	91	117
	20	27-28	7	26	83	114
	20	35	5	20	50	75
	20	41-42	8	14	36	58
	10	49	4	8	19	31

Table 88 . The effect of temperature on time of laying of first egg batch.

Species	No.	Temp.(°C)	Day (adult life) of laying 1st. egg batch				
			1	2	3	4	5
C. flavidus	25	15	-	3	7	15	-
	25	20	-	5	17	2	1
	25	25	-	11	10	4	-
C. burmeisteri	15	15	-	1	8	6	-
	20	20	-	3	12	5	-
	20	25	1	6	10	3	-
S. immaculatus	18	15	-	-	3	9	6
	24	20	-	1	16	7	-
	22	25	-	5	12	5	-
S. stigmaticus	20	15	-	1	4	12	3
	20	20	-	2	8	10	-
	20	25	-	7	13	-	-
G. cruciatus	20	15	-	3	3	12	2
	18	20	-	3	8	7	-
	20	25	-	8	8	4	-
E. briggsi	25	15	-	-	11	11	3
	25	20	-	8	6	9	2
	20	25	2	10	6	2	-

Table 89. Total numbers of eggs laid by females of nine psocid species kept in cold insectary. (Only females living more than 30 days are enumerated)

Species	No.	Mean no. of eggs	Maximum	Minimum
T. dalii	15	57	81	40
E. briggsi	30	84	106	57
S. immaculatus	30	78	103	50
S. stigmaticus	30	94	118	78
G. cruciatus	30	102	117	71
C. flavidus	30	113	128	87
C. burmeisteri	30	79	92	60
C. fuscopterus	14	86	102	63
C. kolbei	25	86	97	78

Table 90 . Oviposition rates of C. flavidus and S. stigmaticus on natural food when kept in cold insectary.

(a)

Species	No.	Total no. of eggs laid on days													
		1-3	4-6	7-9	10-12	13-15	16-18	19-21	22-24	25-27	28-30	31-33	34-36	37-38	40-42
C. flavidus	30	133	217	186	234	265	197	239	190	-	-	-	-	-	-
"	28	-	-	-	-	-	-	-	-	157	130	118	96	-	-
"	24	-	-	-	-	-	-	-	-	-	-	-	-	64	38
S. stigmaticus	20	84	163	190	150	170	130	156	138	117	109	-	-	-	-
"	17	-	-	-	-	-	-	-	-	-	-	87	74	56	29

(b) Five longest-lived females of each species.

Species		No. eggs laid on days									
C. flavidus	Longevity	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50
a.	47	12	19	15	18	16	11	7	3	0	0
b.	44	15	23	18	18	14	12	6	5	0	x
c.	44	16	20	22	27	15	8	3	0	0	x
d.	42	9	23	18	16	16	12	8	1	0	x
e.	42	16	21	20	23	19	12	6	2	0	x
S. stigmaticus											
a.	46	9	16	20	15	17	21	11	7	1	0
b.	46	12	12	17	14	20	16	14	13	0	0
c.	42	12	18	20	14	14	10	12	8	3	x
d.	42	11	15	12	13	16	18	9	8	1	x
e.	41	12	18	15	17	16	18	12	7	0	x

Table 91 . The effect of different foods on longevity and fecundity of some foliage-frequenting psocids.

(a) Reared at 20°C and 16-hour daylength on different foods, and adults kept on the same foods under the same conditions. (Isolated females)

Species	No.	Food	Longevity (days) Max.	Mean	Min.	Fecundity (Eggs laid) Max.	Mean	Min.
C. flavidus	30	Crataegus	38	31	24	100	94	80
"	30	Cupressus	37	34	25	97	83	63
"	30	Quercus	44	40	33	126	119	102
"	30	Pleurococcus	36	28	23	92	85	69
C. burmeisteri	30	Crataegus	30	27	18	83	72	65
"	30	Cupressus	43	39	34	102	90	83
"	30	Quercus	37	33	30	90	81	64
"	30	Pleurococcus	38	33	27	90	86	78
S. stigmaticus	30	Crataegus	47	41	34	115	97	89
"	30	Cupressus	40	34	30	85	64	59
"	30	Quercus	37	32	26	94	89	80
"	30	Pleurococcus	41	35	22	87	82	71
E. briggsi	30	Crataegus	48	39	32	93	80	71
"	30	Cupressus	44	36	29	102	83	74
"	30	Quercus	48	40	32	92	76	68
"	30	Pleurococcus	39	33	27	105	88	81

(b) Females reared on 'natural food' and transferred to other foods while teneral. Kept at 20 C and 16-hour daylength.

Species	No.	Reared	Transferred to	Longevity Max.	Mean	Min.	Fecundity Max.	Mean	Min.
C. flavidus	20	Quercus	Crataegus	39	34	30	112	96	84
"	20	"	Cupressus	34	29	22	109	102	92
"	20	"	Pleurococcus	37	34	30	98	93	86
C. burmeisteri	20	Cupressus	Crataegus	34	26	23	89	82	78
"	20	"	Quercus	38	32	24	91	74	65
"	20	"	Pleurococcus	41	32	24	87	79	66
S. stigmaticus	20	Crataegus	Cupressus	40	34	28	102	83	72
"	20	"	Quercus	43	29	24	96	90	83
"	20	"	Pleurococcus	33	24	16	94	79	68
E. briggsi	20	Quercus	Crataegus	36	31	18	112	94	79
"	20	"	Cupressus	44	38	32	95	83	68
"	20	"	Pleurococcus	38	36	33	103	80	74

Table 92. The numbers of egg batches laid on different leaves in the laboratory. Leaf choice provided: *Ulmus*, *Quercus*, *Ilex*.

				Leaf		
Species	No.	Expt.	Ilex	Quercus	Ulmus	Total
C. flavidus	10	A	20	11	0	31
"	10	B	15	8	3	26
"	10	C	12	14	2	28
"	10	D	21	10	0	31
"	10	E	25	14	0	39
		Total	93	57	5	
E. briggsi	10	A	14	19	3	36
"	10	B	25	13	7	45
"	10	C	18	9	6	33
"	10	D	17	11	3	31
"	10	E	11	14	3	28
		Total	85	66	22	
S. stigmaticus	10	A	22	10	0	32
"	10	B	18	8	1	27
"	10	C	15	11	3	29
"	10	D	22	17	3	42
"	10	E	19	14	0	33
		Total	96	60	7	

Table 93. The numbers of egg batches laid on smooth and rough surfaces of sanded microscope slides in the laboratory.

Species	No.	Expt.	Rough	Smooth	Total
C. flavidus	10	A	5	22	27
"	10	B	3	17	20
"	10	C	9	23	32
"	10	D	3	14	17
"	10	E	8	13	21
		Total	28	89	
E. briggsi	10	A	7	19	26
"	10	B	4	22	26
"	10	C	11	16	27
"	10	D	9	24	33
"	10	E	7	15	22
		Total	38	96	
S. stigmaticus	10	A	11	18	29
"	10	B	8	25	33
"	10	C	3	16	19
"	10	D	7	22	29
"	10	E	3	9	12
		Total	32	90	

Table 94. The reactions of several psocid species to aqueous or alcoholic extracts of leaves of different trees.

Species	Leaf	Leaf Washings		Aqueous Extract		Alcoholic Extract	
		Leaf	Water	Leaf	Water	Leaf	Water
C. flavidus	Cupressus	180	221	93	356	78	169
"	Ilex	220	186	153	206	138	160
"	Quercus	193	126	115	163	182	130
"	Ulmus	120	93	138	231	78	121
C. burmeisteri	Cupressus	123	86	297	183	157	116
"	Ilex	118	130	156	138	216	119
"	Quercus	57	140	126	93	138	124
"	Ulmus	86	112	134	106	100	158
E. briggsi	Cupressus	118	83	57	86	139	104
"	Ilex	146	140	126	109	54	128
"	Quercus	182	126	119	162	76	104
"	Ulmus	103	138	84	142	153	127
S. stigmaticus	Cupressus	56	119	87	113	129	156
"	Ilex	129	186	128	139	79	128
"	Quercus	152	117	116	80	173	119
"	Ulmus	140	128	231	179	129	96

(Figures represent sums of five experiments, each containing 10 psocids. 11 readings were taken for each experiment. Psocids in the end quarter-length of the apparatus only were recorded.)

Table 95 . The amounts of debris on 1cm^2 areas of adaxial leaf surfaces from April to November in 1966 and 1967. (mg) (200 samples from each tree species on each occasion)

Year		April	May	June	July	August	September	October	November
Quercus									
1966	Mean	-	-	0.12	0.21	0.20	0.24	0.14	0.16
	Range	-	-	0.04-0.17	0.04-0.29	0.07-0.38	0.07-0.48	0.05-0.26	0.04-0.27
1967	Mean	-	0.04	0.16	0.26	0.23	0.19	0.19	0.22
	Range	-	0.01-0.07	0.03-0.23	0.05-0.51	0.09-0.42	0.09-0.36	0.08-0.34	0.07-0.29
Ilex									
1966	Mean	-	-	0.07	0.11	0.11	0.06	0.13	0.09
	Range	-	-	0.04-0.12	0.05-0.16	0.03-0.15	0.03-0.13	0.05-0.16	0.03-0.13
1967	Mean	0.08	0.08	0.10	0.13	0.11	0.11	0.08	0.13
	Range	0.02-0.17	0.03-0.13	0.04-0.16	0.07-0.18	0.05-0.17	0.04-0.18	0.04-0.17	0.03-0.21
Crataegus									
1966	Mean	-	-	0.03	0.03	0.05	0.05	0.04	-
	Range	-	-	0.00-0.05	0.01-0.06	0.03-0.11	0.02-0.11	0.03-0.07	-
1967	Mean	0.01	0.03	0.04	0.08	0.06	0.07	0.07	-
	Range	0.00-0.03	0.00-0.05	0.00-0.09	0.04-0.15	0.03-0.11	0.03-0.14	0.03-0.09	-
Fagus									
1966	Mean	-	-	0.03	0.03	0.03	0.05	0.03	-
	Range	-	-	0.00-0.05	0.00-0.06	0.02-0.07	0.02-0.11	0.02-0.06	-
1967	Mean	-	0.02	0.06	0.06	0.04	0.04	0.05	-
	Range	-	0.00-0.04	0.00-0.09	0.03-0.11	0.01-0.07	0.02-0.07	0.03-0.10	-
Betula									
1966	Mean	-	-	0.01	0.01	0.04	0.02	0.03	-
	Range	-	-	0.00-0.03	0.00-0.02	0.01-0.07	0.01-0.04	0.01-0.05	-
1967	Mean	-	0.01	0.01	0.05	0.02	0.04	0.03	-
	Range	-	0.00-0.03	0.00-0.04	0.03-0.07	0.00-0.05	0.02-0.07	0.01-0.06	-
Ulmus									
1966	Mean	-	-	0.02	0.01	0.03	0.03	0.03	-
	Range	-	-	0.00-0.04	0.00-0.04	0.01-0.06	0.00-0.05	0.00-0.08	-
1967	Mean	-	0.02	0.02	0.02	0.02	0.04	0.02	-
	Range	-	0.00-0.03	0.00-0.05	0.00-0.04	0.01-0.06	0.01-0.08	0.00-0.05	-

Table 96 . Comparison of amounts of debris on 1 cm^2 areas of upper and lower leaf surfaces in September, 1967. (mg) (200 samples from each surface of each tree species.)

Tree	Surface	Mean	Range
Quercus	Upper	0.19	0.09 - 0.36
Quercus	Lower	0.02	0.00 - 0.05
Ilex	Upper	0.11	0.04 - 0.18
Ilex	Lower	0.04	0.00 - 0.06
Crataegus	Upper	0.07	0.03 - 0.14
Crataegus	Lower	0.02	0.00 - 0.04
Fagus	Upper	0.04	0.02 - 0.07
Fagus	Lower	0.01	0.00 - 0.02
Betula	Upper	0.04	0.02 - 0.07
Betula	Lower	0.01	0.00 - 0.03
Ulmus	Upper	0.04	0.01 - 0.08
Ulmus	Lower	0.01	0.00 - 0.02

Table 97 . Comparison of amounts of debris on 1 cm^2 areas of upper and lower surfaces of Quercus leaves taken from ground litter, December 1966.(mg

	Surface	Mean	Range
Quercus	Upper	0.13	0.04 - 0.22
Quercus	Lower	0.08	0.02 - 0.15

Table 98. Numbers of fungal species on agar plates from upper surfaces of leaves of different tree species, September 1967. (Seven days growth)

Tree	No. of plates	Total no. of fungal spores	No. of abundant species.
Crataegus	10	11	1
Fagus	10	8	0
Ilex	10	11	0
Quercus	10	3	2

Table 99 . The approximate percentage compositions of adventitious matter from leaf surfaces, shown on 40 collodion peels of each species, September 1967. (Visual division of each peel into 10 abundance-groups, summed.)

Tree	Fungal spores	Fungal hyphae	Algae	Pollen	Animal remains	Other
Crataegus	50	30	10	5	5	-
Ilex	30	33	30	-	2	5
Quercus	30	5	55	3	2	5
Fagus	30	15	30	5	5	15

Table 100. Comparison of available food with that ingested and digested by several psocid species fed on leaves of different tree species. (Visual estimates of percentages for each specimen summed and avaeraged to the nearest 5%. 40 of each psocid species on each tree species) - Adult psocids and nymphs.

			Leaf		Crop		Faeces	
Psocid	Tree		Adults	Nymphs	Adults	Nymphs	Adults	Nymphs
E. briggsi	Quercus	Algae	55	55	40	45	25	20
		Fungus	30	30	40	40	20	20
		Others	15	15	20	15	55	60
	Cupressus	Algae	90	90	100	90	65	30
		Fungus	10	5	0	0	0	0
		Others	0	5	0	10	35	70
	Crataegus	Algae	30	35	30	35	25	30
		Fungus	50	40	50	35	20	20
		Others	20	25	20	30	55	50
S. stigmaticus	Quercus	Algae	55	60	50	55	25	30
		Fungus	30	30	30	30	20	15
		Others	15	10	20	15	55	55
	Cupressus	Algae	90	90	95	100	55	45
		Fungus	5	5	0	0	0	0
		Others	5	5	5	0	45	55
	Crataegus	Algae	30	40	30	35	25	30
		Fungus	35	40	35	35	20	15
		Others	35	20	35	30	55	55

Table 100 (cont.)

Psocid	Tree		Leaf		Crop		Faeces	
			Adults	Nymphs	Adults	Nymphs	Adults	Nymphs
C. burmeisteri	*Quercus*	Algae	55	65	50	65	25	35
		Fungus	30	20	25	20	25	15
		Others	15	15	25	15	50	50
	Cupressus	Algae	90	85	95	90	60	55
		Fungus	5	10	5	5	0	0
		Others	5	5	0	5	40	45
	Crataegus	Algae	30	30	35	25	25	20
		Fungus	40	55	40	50	20	25
		Others	30	15	25	25	55	55
C. flavidus	*Quercus*	Algae	50	50	40	50	30	25
		Fungus	35	40	30	35	35	30
		Others	15	10	30	15	35	45
	Cupressus	Algae	90	100	80	95	60	50
		Fungus	5	0	5	0	0	0
		Others	5	0	15	5	40	50
	Crataegus	Algae	40	40	35	35	20	25
		Fungus	40	40	40	40	20	25
		Others	20	20	25	25	60	50

Table 101. Faecal composition of C. flavidus on consecutive days: the effect of decreasing food supply. (10 faecal pellets for each psocid on each day, percentage compositions summed and averaged to nearest 5%). All samples on Quercus leaves.

Day	No. of females	Faecal Composition. Algae	Fungi	Others (Digested)
1	30	30	15	55
2	30	25	20	55
3	30	30	20	50
4	30	30	15	45
5	28	30	10	60
6	27	25	15	60
7	25	30	15	55
8	20	20	20	60
9	20	20	10	70
10	15	15	5	80
11	12	20	10	70
12	7	10	5	85
13	4	10	5	85
14	3	10	5	85
15	3	15	5	80

Table 102. Crop contents of foliage-frequenting psocids collected at Silwood Park during 1967. (Visual estimation of percentage compositions for each individual, summed, and averaged to the nearest 5%)

Psocid	No.	Stage	Crop contents Algae	Fungi	Others	Host tree
G. cruciatus	14	Adults	20	55	25	Ilex
G. cruciatus	17	Nymphs	25	70	5	Ilex
S. stigmaticus	43	Adults	30	50	20	Crataegus
S. stigmaticus	30	Nymphs	25	65	10	Crataegus
S. immaculatus	18	Adults	30	60	10	Crataegus
S. immaculatus	30	Nymphs	35	50	15	Crataegus
S. immaculatus	12	Nymphs	20	55	25	Ilex
C. flavidus	45	Adults	50	40	10	Quercus
C. flavidus	40	Nymphs	55	30	15	Quercus
C. flavidus	20	Nymphs	25	55	20	Crataegus
C. burmeisteri	40	Adults	85	5	10	Cupressus
C. burmeisteri	30	Nymphs	95	0	5	Cupressus
C. fuscopterus	5	Adults	40	45	15	Crataegus
C. kolbei	15	Adults	30	40	30	Sarothamnus
E. briggsi	30	Adults	45	40	15	Quercus
E. briggsi	30	Nymphs	50	40	10	Quercus