# THE NATURAL HISTORY OF SPEAR THISTLE-HEADS

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## I. INTRODUCTION

THE flower-heads of the spear thistle, *Cirsium vulgare* (Savi) Ten., provide a microhabitat for a distinctive group of insect species; the present paper is the result of a study of the relationships between these insects and the plant. Flower-heads of many Compositae form ideal material for the study of insect ecology because the microhabitat is a distinct unit whose limits can be defined. The spear thistle is common throughout the country and thistle-heads can be found at varying stages of development throughout most of the year.

The flower-heads of the spear thistle have not been studied before as complete units, although similar work has been done on other composites. The best-known is that of Varley (1947) on insects associated with the black knapweed, *Centaurea nemoralis* Jordan. The number of insect species involved is small so that identification is relatively simple. The plant is suitable either for a one-day project for a single student, or for a research project to cover a longer period of time. To work out long-term effects of parasitism and predation on the host populations, several years would be needed.

The field work was done during the years 1964 and 1965 while I was employed as Field Assistant at Preston Montford Field Centre in Shropshire. Collections were made from this and the following five Field Centres in England and Wales: Malham Tarn, Yorkshire; Orielton, Pembrokeshire; Flatford Mill, Essex; Juniper Hall, Surrey; and Slapton Ley, Devon. A seventh collecting site in the Lake District on Hampsfell near Grange-over-Sands, Lancashire, was chosen to provide a more northerly sample. In 1965, single collections were made in addition at Well House, near Lancaster, and at Coombs Dale, Derbyshire. In this way, different areas of England and Wales were covered to give some picture of several of the species studied.

Larvae of the trypetid fly, *Urophora stylata* (Fabricius), form a large woody gall in the receptacle of spear thistle-heads. This enlarges the receptacle and provides food and shelter for insects which otherwise would not live inside the flower-heads. Some species cannot exist without the gall, some prefer ungalled heads, and others can live in either microhabitat.

There are five mainly phytophagous species primarily associated with the flower-heads, dependent on the thistle-head for food as well as shelter. They are the larvae of two trypetid flies, *Urophora stylata* and *Terellia serratulae* L., the larvae of two moths, *Eucosma* sp. (probably *cana* (Haworth)) and *Metzneria* sp. (probably *neuropterella* (Zeller)), all of which live inside the thistle-head; the fifth primary species is the spear thistle lace-bug, *Tingis cardui* L., whose adults and nymphs live on the outside of the flower-heads.

Six species are secondarily associated with the thistle-heads, as being parasites or predators of the primary species, and so dependent on the plant for shelter but not for food. These include the three chalcid parasites of *U. stylata*: *Eurytoma tibialis* Boheman, *Habrocytus elevatus* (Walker), and *Torymus cyanimus* Boheman; two chalcid parasites of *T. serratulae*: both species of *Habrocytus*; and a predator of both trypetids and their parasites, the larva of the dipterous fly, *Lonchaea* sp.

A list of species associated with the flower-heads is included in the Appendix, together with a key and brief notes on the ecology of those which are not discussed in the paper.

*Materials and methods*

Spear thistle-heads were collected from seven sites in England and Wales at intervals of two to four weeks throughout the summer and autumn of 1964 and 1965. The habitats were waste ground or permanent pasture grazed by cattle or sheep and varied in altitude from almost sea level to 1,600 feet O.D. On each date, fifteen heads were collected at random from a plant, in the form of buds, flowering or dead heads, depending on the stage of development of the plant. The collections were sent for analysis to Preston Montford.

During the winter of 1964–1965, random collections of 100 dead heads were made from each of four sites: Preston Montford, Flatford Mill, Orielton and Slapton Ley. Galled heads were separated from ungalled; if the number of galled heads was below 50, more galls were collected to bring the number up to 50. Galled and ungalled heads from each site were kept in separate breeding cages (Fig. 1) until the insects had emerged. The cages occupied a disused greenhouse in the grounds of Preston Montford, which provided some shelter from the prevailing westerly winds, but rainfall and sunlight were almost unaltered from natural conditions because very little glass remained in the greenhouse.

Each cage consisted of a 14-inch garden riddle which formed the base. A nylon stocking was opened out and spread over the mesh of the riddle to keep the substrate of peat and sand in and any extraneous animals out. The cone of the breeding cage was made of cellulose acetate film (gauge 0·375 mm.), with loops at the bottom to secure it to the riddle. The peat and sand mixture was watered slightly to ensure a damp environment. The resulting condensation, which later would have trapped emerging insects, was reduced by making a muslin-covered window at the base of the cone. This provided a through draught with the muslin lid of the polythene trap at the top of the breeding cage. A strip of plastic foam was stuck to the top of the cone to ensure a tight fit with the trap and prevent insects crawling out between cone and trap. The inverted funnel in the base of the polythene trap prevented any insect from falling back into the cage. To induce the emerging insects to move upwards towards the light into the trap, the cone was covered with black polythene sheeting. This also protected the interior from excessive heat and helped to reduce condensation.

In March, April and May 1965, ten thistle-heads were removed from each cage and dissected to determine the duration of the larval and pupal stages of the trypetids and their parasites. Dissections were made of heads collected from the field at Preston Montford on the same dates, to compare the natural with the artificial environment. It was found that the emergence periods of the insects in the breeding cages was not noticeably different from those under natural conditions. By the autumn, all healthy insects had emerged and the remaining heads were dissected to find those which had failed to emerge and to determine the cause of death.

To complete the data on life histories, any insects still living after dissection of

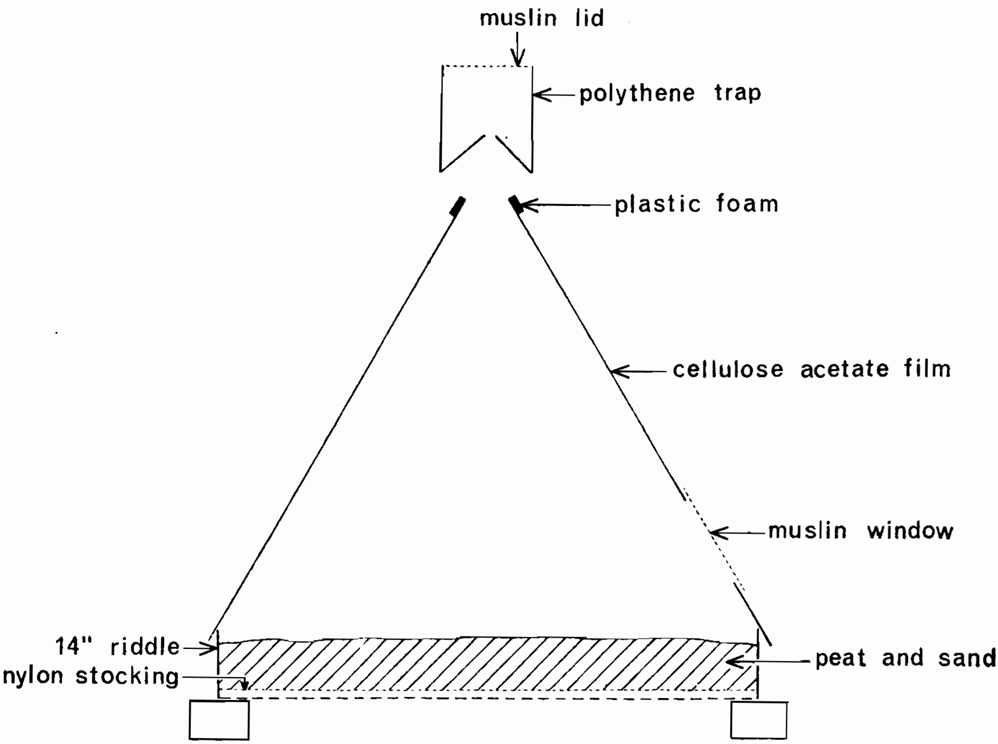



FIG. 1.
Breeding cage.

the heads were bred through to the adult stage in isolated conditions. Trypetid larvae and their parasites are tolerant of dry conditions and will complete their development in gelatine capsules (sizes 3, 0·3 c.c., and 4, 0·2 c.c.), as long as they are fully fed. These capsules are convenient because they can be pinned out individually in a cork-lined box with a reference number so that the development of any one specimen can be followed simply and quickly. The larvae of *Lonchaea* and the moths normally drop from the plant in autumn and pupate in the soil. These were kept above a layer of moist peat and sand in small polystyrene pots with plastic lids perforated to allow air to enter. These insects are more difficult than the trypetids to keep alive until emergence; very few moths and no *Lonchaea* reached the adult stage, which is why the specific names of these insects are in doubt.

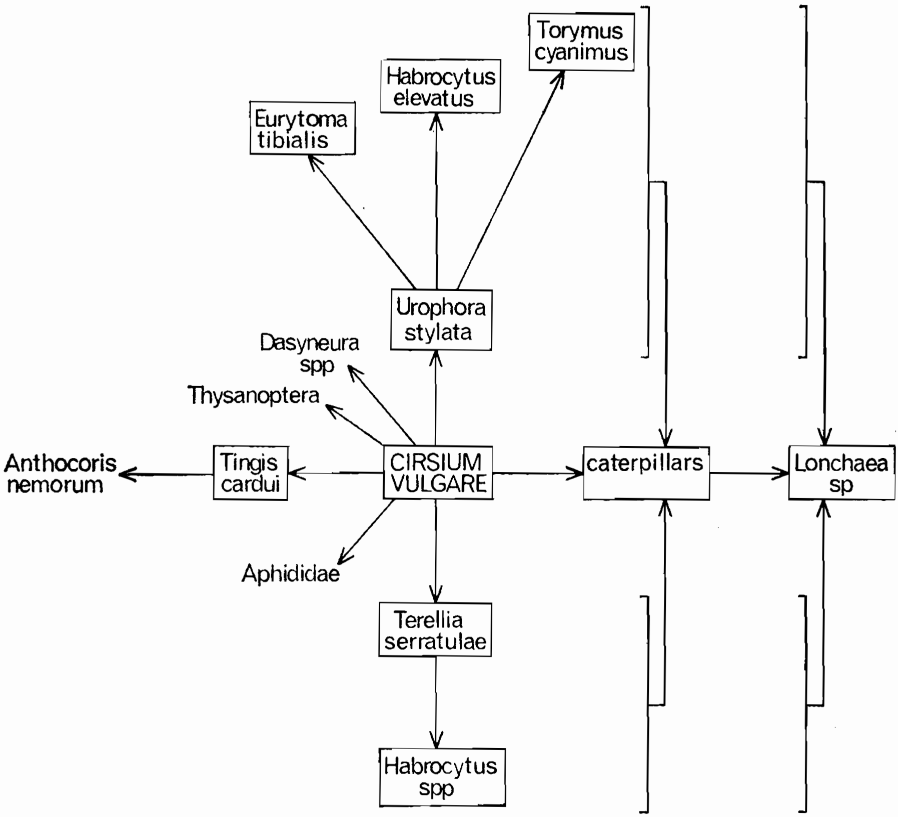



FIG. 2.
Food-chain summary of insects associated with the spear thistle, *Cirsium vulgare*. (Species studied in detail enclosed.)

## II. OBSERVATIONS AND RESULTS

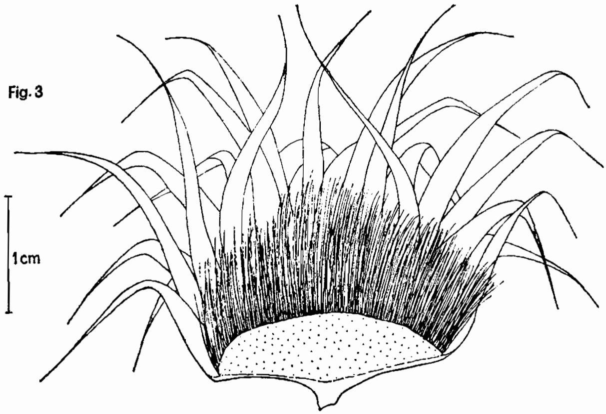
### (1) *Life-histories*

*The host plant, CIRSIUM VULGARE (Savi) Ten.*

*Cirsium vulgare* is a biennial herb belonging to the Compositae and common throughout the British Isles. The full-grown plant has a long tap-root and an upright stem 2–4 feet high, branched in the upper part. Both the stems and the undersurfaces of the leaves are covered with a thick down of hairs and carry long spines. For a detailed description of the plant, see Clapham *et al.* (1958).

The plant overwinters as a rosette growing close to the ground. Unchanged rosettes were found until the end of May. In 1965, the earliest rosettes continued their development in early May, when the growing point of the rosette began to extend. This stage lasted until the beginning of June when the plants had reached their full height and the first buds were formed.

The buds are borne singly or in small groups on the ends of the numerous branches. The florets are supported on a dome-shaped receptacle, which also



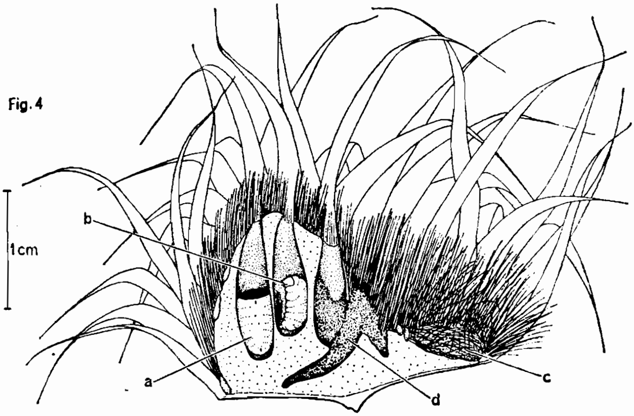




FIG. 3.
*Cirsium vulgare*: vertical section through undamaged head.
FIG. 4.
*Cirsium vulgare*: vertical section through galled head.
(*a*) *Urophora stylata*. (*b*) *Habrocytus elevatus*. (*c*) *Terellia serratulae* cocoon.
(*d*) Caterpillar frass.

bears layers of bracts, surrounding and protecting the florets. Flowering heads may be seen from mid-June to October although the period of flowering of an individual head is brief. They are visited and pollinated by hover-flies (Syrphidae), butterflies (e.g. *Pieris brassicae* (L.)) and several bees (e.g. *Bombus terrestris* L., *B. agrorum* (Fab.) and *Apis mellifera* L.). From late July onwards, dead heads increasingly predominate over buds and flowers on individual plants. The bracts and florets dry out and the bracts open out so releasing the thistle down, or groups of achenes each supported by a pappus of hairs, which is all that remains of the florets. These may be blown a considerable distance by the wind and, if they land in a suitable habitat, will germinate during September and October of the same year to form rosettes. These rosettes do not develop further until the early summer of the second year following their formation.

Fig. 2 summarizes the relationships of the spear thistle with the insects which are dependent on the heads. Figs. 3 and 4 show vertical sections through dead heads, one undamaged and the other showing the microhabitats of four of the species discussed.

## *UROPHORA STYLATA* (Fabricius) DIPTERA: TRYPETIDAE

*Urophora stylata* is found commonly associated with the spear thistle, its larva causing the formation of a gall in the flower-head. The gall is not obvious from the outside but can be felt as a hard lump inside the encircling bracts. It develops from the achenes and receptacle of the plant; the receptacle swells to many times its original size and becomes hard and woody. Usually the galls are multilocular, containing several larvae, each in a separate cell.

The male and female flies are similar in appearance except for the stout ovipositor of the female (Fig. 6). The body is black except for a pale yellow scutellum and the wings distinctively patterned with two interrupted bands. Adults, all males, were seen in the field early in June in 1964 and 1965 at Preston Montford. Females were not seen until July. In the breeding cages, both males and females started emerging early in June (Fig. 5). This suggests that the females which emerged earlier were overlooked in the field; they probably frequent other plants until the ova mature before coming to the thistles to mate and lay eggs when the buds are developed.

The adult stage lasts about two months, throughout June and July, and in 1965 the last adults were seen on 10 August. In June, they appear on the lower parts of the plant, where they seldom move except when disturbed. In early July when many buds are developed, males and females, often paired, are common on or near the buds. When mating, the male stands on top of the female, frequently rubbing her ovipositor with his third pair of legs. The flies copulated frequently and in captivity they would copulate as soon as the wings expanded; often they would pair in captivity with specimens of other species (e.g. *Urophora cardui* (L.)).

The eggs are laid in July in unopened buds. The female stands horizontally on the bract spines and the ovipositor is extended down between the bracts. The eggs are found in small batches in the gap above the developing florets and the overlying bracts; sometimes they are inserted individually into the tip of a floret. The florets in the immediate vicinity become retarded and die, perhaps

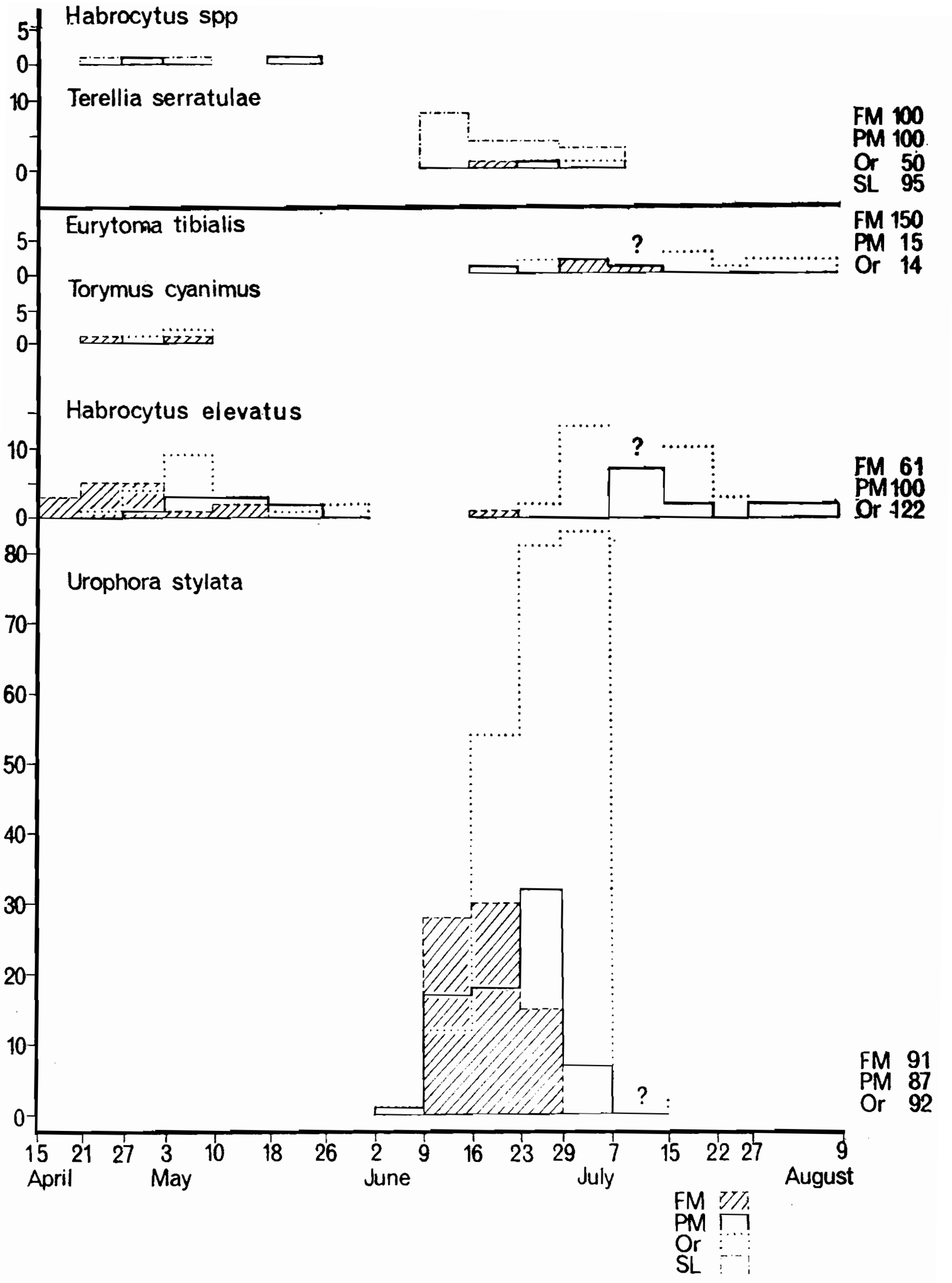



Fig. 5.
Emergence periods in 1965 from breeding cages.

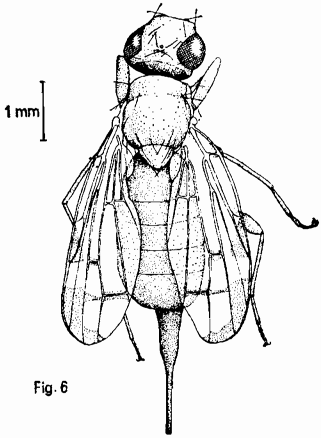



Fig. 6

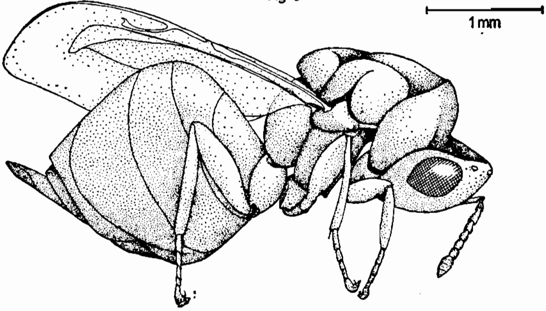



Fig. 9

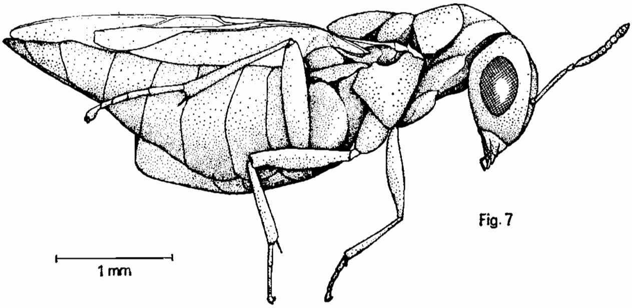



Fig. 7

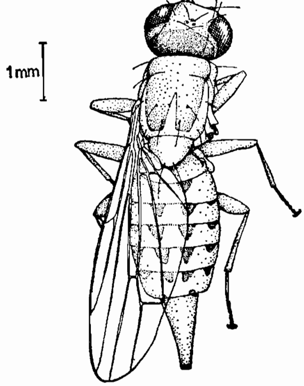



Fig. 10

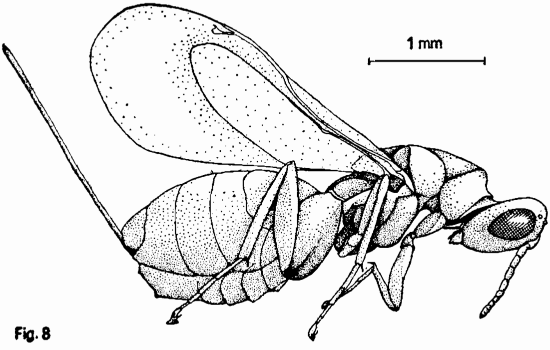



Fig. 8

FIG. 6.
*Urophora stylata*: adult ♀.
FIG. 7.
*Habrocytus elevatus*: adult ♀.
FIG. 8.
*Torymus cyanimus*: adult ♀.

FIG. 9.
*Eurytoma tibialis*: adult ♀.
FIG. 10.
*Terellia serratulae*: adult ♀.

due to mechanical injury by the ovipositor. The egg (Fig. 11) is white with a smooth surface, about 0·7 × 0·2 mm.

The first larval instar remains within the eggshell, so that the larva hatches in the second instar, which is about 0·4 mm. long (Fig. 12) and fairly active. These larvae were found between 16 July and 2 September in 1965. Florets were often seen with brown tips or with holes at the tip, and this damage may be caused by these young larvae in an initial wandering phase. Otherwise, moth caterpillars which are active at the same time may be responsible. Probably the larvae eat the eggshells as soon as they hatch, as none were found above the florets. Eventually, the young larva eats into a floret, leaving a more or less circular hole near the top of the corolla tube. It burrows down inside the

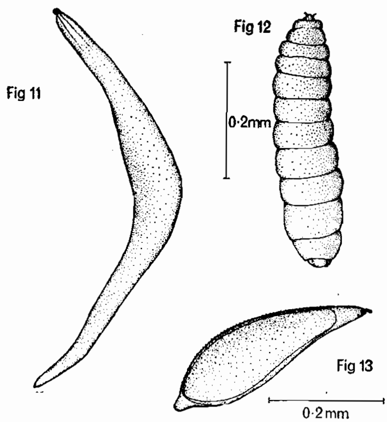



FIG. 11.
*Urophora stylata*: egg.
FIG. 12.
*Urophora stylata*: second instar larva.
FIG. 13.
*Habrocytus elevatus*: egg.

corolla tube, feeding on the floral tissues, leaving a brown streak on the inside of the tube and a trail of frass. Finally it reaches the achene and feeds on its tissues, by which time it is considerably larger, though still in the second instar.

The beginning of gall formation is apparent at an early stage. Before the larva has reached it, the achene becomes enlarged and distorted (Fig. 14b). When the larva has fed on the achene, the gall starts to form round it, and the adjacent region of the receptacle begins to swell. Usually there are several larvae in the same head and gall tissue forms round each one separately. In late July and early August the gall is apparent, although it may not be woody. At about this time, the larva moults to form the third and final instar, and the cell develops its full size and shape.

The third instar at first feeds actively on a layer of succulent tissue lining its cell, which therefore decreases giving the larva room to grow. Woody tissue, which develops as a thin layer outside the succulent tissue, increases in bulk until it meets and coalesces with similar tissue of adjacent cells, to form a hard multilocular gall. The fully fed larva (Fig. 15) is pale yellow in colour with a darkly sclerotized posterior spiracular plate. It fits tightly against the walls of its cell, with the head downwards so that the perispiracular plate blocks the opening to the cell. This may help to prevent parasitic attack.

The larva becomes fully fed during August and remains in its final instar throughout the winter. In late April or early May, it reverses its position and the skin becomes taut, gradually hardening and darkening to form the puparium. Adult flies started emerging in June 1964 and 1965 but pupae were found until

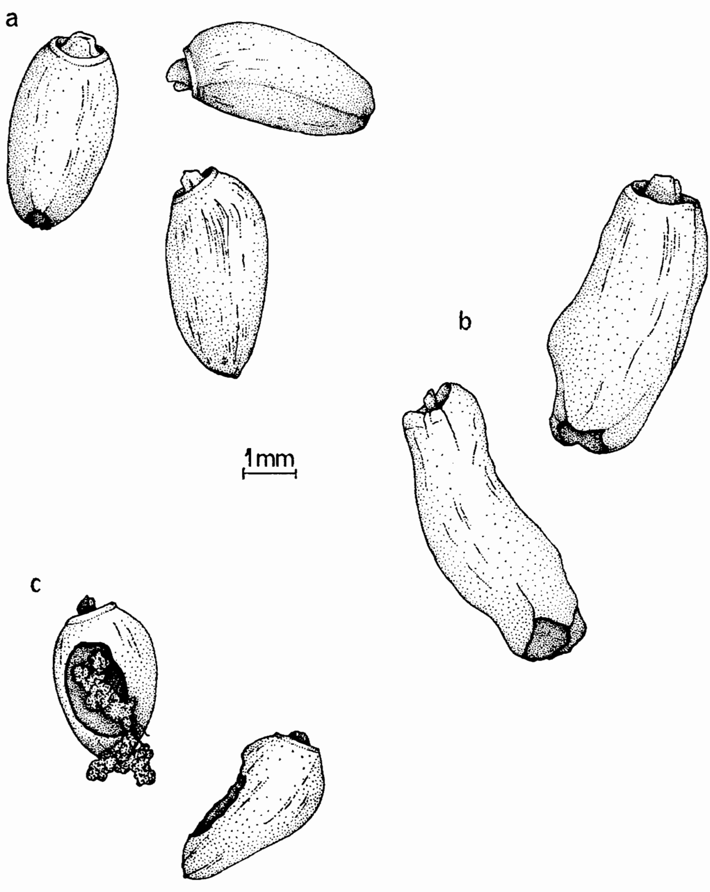



FIG. 14.
*Cirsium vulgare*: achenes.
(*a*) Undamaged. (*b*) Distorted due to gall formation. (*c*) Attacked by caterpillars.

Fig 15

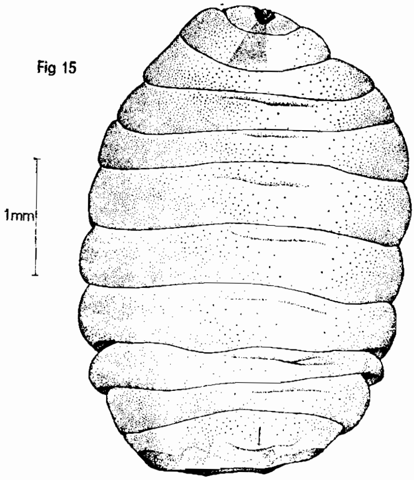
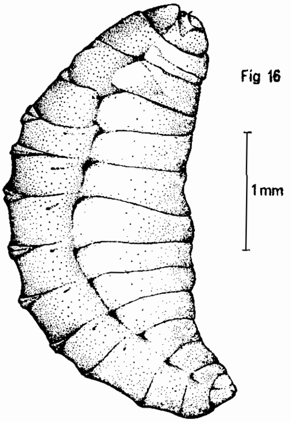



Fig 16



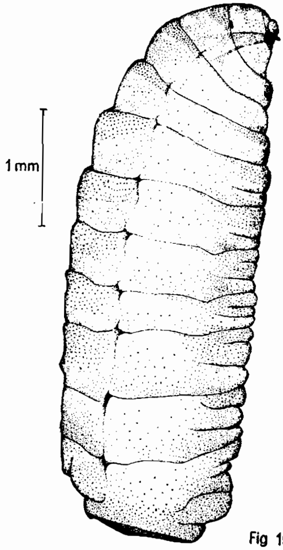




Fig 17

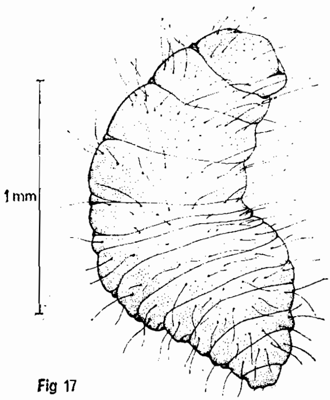



Fig 18

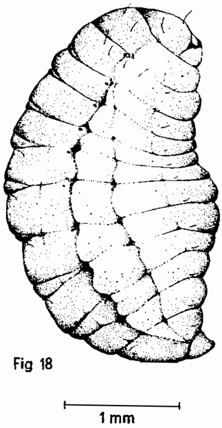



Fig 19

FIG. 15.
*Urophora stylata*: third instar larva (ventral surface).
FIG. 16.
*Habrocytus elevatus*: full-fed larva.
FIG. 17.
*Torymus cyanimus*: full-fed larva.
FIG. 18.
*Eurytoma tibialis*: full-fed larva.
FIG. 19.
*Terellia serratulae*: third instar larva.

mid July. The empty puparium (Fig. 21) is typical of a fly which uses a ptilinum with which to escape.

The life-history of *U. stylata* is summarized in Fig. 25; there is considerable overlapping of the stages. The third instar occupies 7 to 8 months while the other stages take place between May and September.

## *Parasites of* Urophora stylata

### *Habrocytus elevatus* (Walker) HYMENOPTERA: PTEROMALIDAE

This species was the commonest ectoparasite found attacking *U. stylata* larvae. The body of the adult (Fig. 7) is black with a green metallic sheen and the wings colourless with the reduced venation characteristic of the Chalcidoidea. During 1965, there were two periods during which adults emerged: 20 April to 2 June and 29 June to 27 August (Fig. 5).

The eggs (Fig. 13) are white with papillae covering part of the surface. They are laid on the third instar larvae of *U. stylata* or loose in the gall cell. If one is laid on the perispiracular plate or after formation of the puparium, the parasite larva probably will not survive because it cannot penetrate the sclerotized integument.

The full-grown larva (Fig. 16) is white with small darkly sclerotized mandibles (for description of the larval stages, see Varley (1937a)). It does not fill the cell and is always found with its own frass and shrivelled skin and perispiracular plate of its host. In 1965, larvae were found from 24 May to 8 June and from 6 September to early April 1966. The earlier larvae pupated between 8 and 23 June and emerged as adults during July and August of the same year. These mated and laid eggs which gave the second batch of larvae, which overwintered and pupated in April and May of the following year, giving flies in May and June.

The pupa (Fig. 22) is at first creamy-white with pale eyes; prior to emergence it becomes black with red eyes. Two individuals overwintered during 1964–1965 as pupae, but this is unusual. The life-history is summarized in Fig. 25.

### *Torymus cyanimus* Boheman HYMENOPTERA: TORYMIDAE

*Torymus cyanimus* is an ectoparasite of *Urophora stylata* larvae and was uncommon during the survey period. The eggs (see Fig. 4e in Varley (1937a)) are usually laid in small groups on full-fed *U. stylata* larvae in August, at the same time as eggs of *Habrocytus elevatus*. Only one of a batch will develop as the host can support only one larva to maturity. Larvae (Fig. 17) are full-grown by September or October and are found in the same microhabitat as larvae of *H. elevatus*. The larvae cannot be confused with those of *H. elevatus* because they are more strongly crescent-shaped and have whorls of long setae encircling each segment.

The full-grown larvae overwinter, normally pupating in the spring of the following year. In 1965, pupae were found between 28 March and 28 April and the adults emerged between 18 April and 10 May (Fig. 5). The ovipositor of the female is extremely long and in the pupal stage is curved forwards along the dorsal surface of the abdomen (Fig. 23). The body of the adult (Fig. 8) is black with a bright green metallic sheen with bluish reflections.

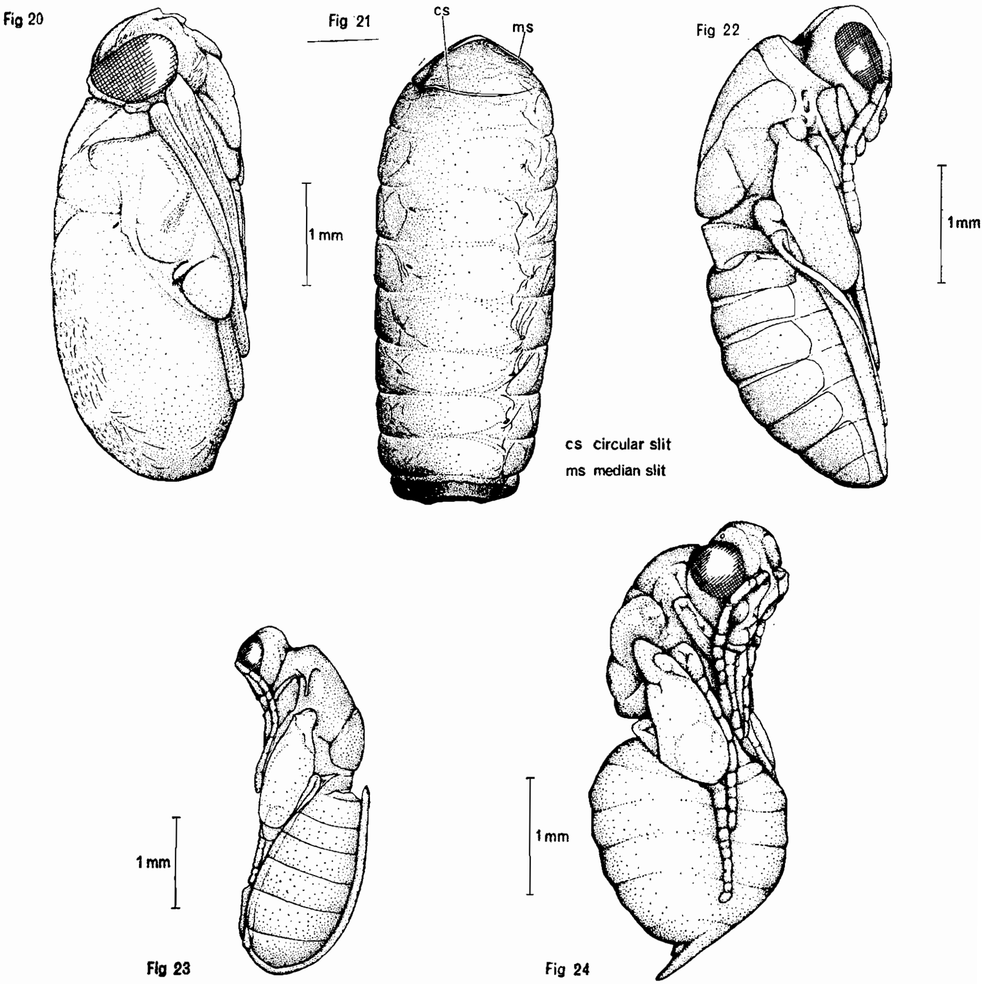



FIG. 20.
*Urophora stylata*: pupa (removed from puparium).

FIG. 21.
*Urophora stylata*: puparium after emergence of adult (dorsal surface).

FIG. 22.
*Habrocytus elevatus*: pupa.

FIG. 23.
*Torymus cyanimus*: pupa ♀.

FIG. 24.
*Eurytoma tibialis*: pupa ♀.

### *Eurytoma tibialis* Boheman HYMENOPTERA: EURYTOMIDAE

The endoparasite *Eurytoma tibialis*, the commonest parasite of *Urophora stylata*, was found at most of the sites at which galls were collected. The body of the adult (Fig. 9) is black without the sheen characteristic of the ectoparasites. The adults are on the wing during June and July (Fig. 25).

Although the larval parasite was common within the gall of *U. stylata*, adults were rarely seen in the field and none were seen mating or ovipositing. The host larvae are available for attack soon after hatching into the second instar. Varley (1957) records that no eggs have been found in the third instar. The host can support only one larva to maturity and superparasitism is rare. The egg is cylindrical with a long tail (see description and Fig. 1a in Varley (1937a)). The parasite at first grows slowly, having reached the third of its five instars by the time the host larva is full-grown. Healthy larvae of *U. stylata* will remain head downwards in their cells until the start of pupation the following spring. The parasitized larva, however, reverses its position when it is fully fed in August, and the larval skin hardens and darkens to form a typical puparium. Inside the puparium, the parasite larva grows rapidly and devours the host larva before the true pupal stage is reached.

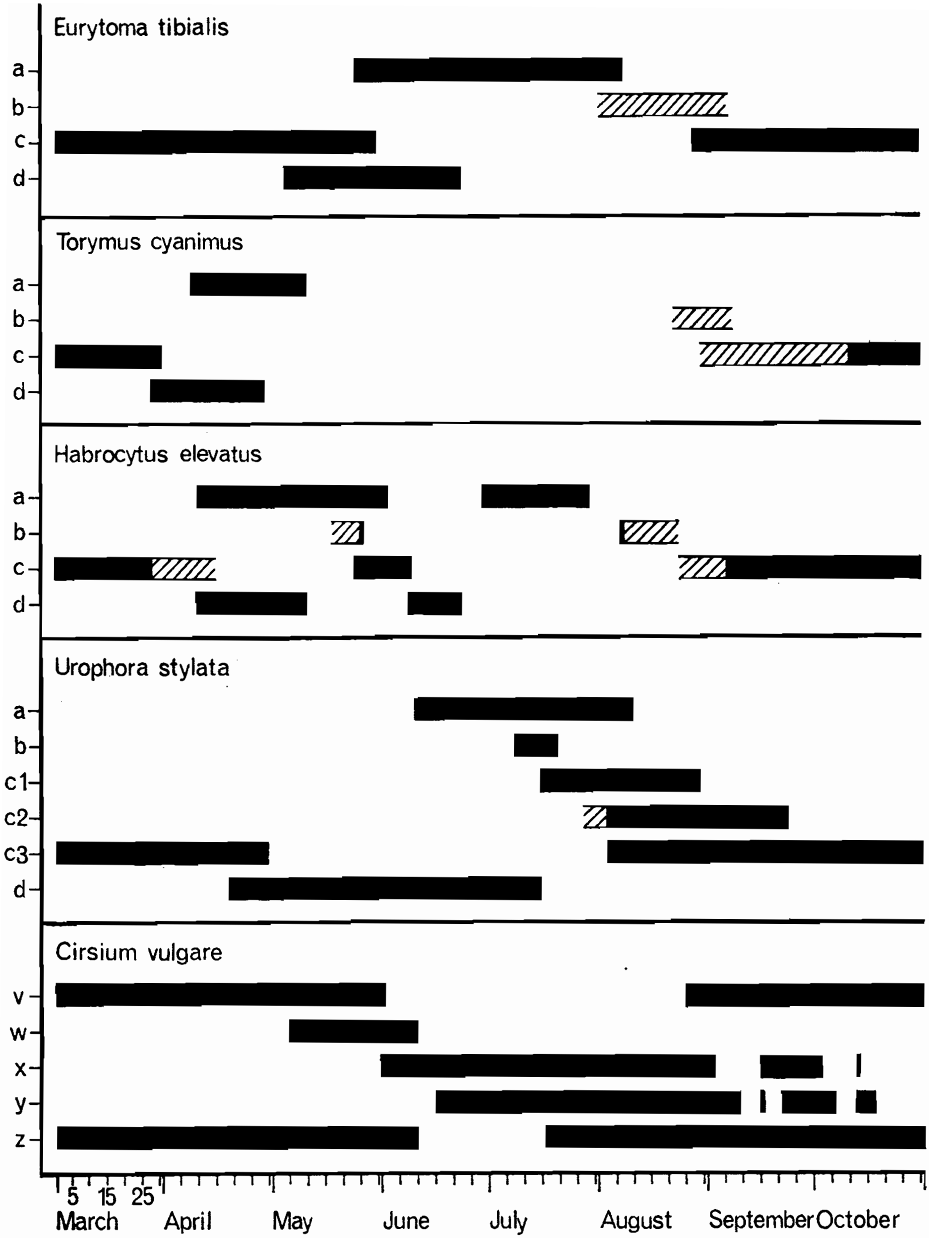
*E. tibialis* overwinters as a fully fed fifth instar larva (Fig. 18) inside the puparium of its host (for descriptions of larval stages, see Varley (1937a)). In 1965, pupae (Fig. 24) were found from 4 May to 23 July and the first adults emerged on 16 June (Fig. 5). The life-history is summarized in Fig. 25.

## *TERELLIA SERRATULAE* L. DIPTERA: TRYPETIDAE

This second trypetid fly is found associated with the flower-heads of *Cirsium vulgare* in much smaller numbers than *U. stylata*. The body of the adult (Fig. 10) is unlike that of *U. stylata* in being a pale greyish-yellow with black markings and the wings are colourless. They are found on the thistles during June and July. Presumably the eggs are laid during July and August. No details of mating or oviposition were collected because this fly is rare at Preston Montford; no adults were seen in the field and only three individuals were collected as larvae throughout the two-year observation period.

The third larval instar (Fig. 19) is dirty white in colour with a dark brown perispiracular plate, and is slimmer than larvae of *U. stylata*. Unlike *U. stylata*, it has creeping welts on the anterior half of each segment which enable it to move about. It does not cause the formation of a gall; it burrows down amongst the hairs of the florets and receptacle and may tunnel into the receptacle itself. It spins a cocoon of silk and floret hairs which may be lying above the receptacle (Fig. 4c) or be partly within a tunnel in the receptacle, previously excavated by the larva.

The larvae become fully fed in August and most overwinter, pupate in April or May of the following year, and emerge in June and July. During 1965, some larvae collected in August and September pupated between 15 September and 18 October, emerging later in the same October. Other larvae, collected from the same heads (possibly from the same oviposition) and kept under identical conditions overwintered and emerged in the summer of the following year.




actual
probable

a adults
b eggs
c larvae
c1 instar 2
c2 instar 3: not fully-fed
c3 instar 3: fully-fed
d pupae
v rosettes
w main stem growing upwards
x buds
y flowering heads
z dead heads

FIG. 25.
Summary of life-histories.

*Parasites of* Terellia serratulae

The only parasites found affecting *T. serratulae* were ectophagous, species of *Habrocytus*. These are probably *H. musaeus* (Nees), and *H. ariomedes* (Walker), but their identification has not been confirmed.

The larva is an ectoparasite of the full-grown larva of *T. serratulae*. The parasite becomes fully fed in August or September and overwinters in the cocoon of the host together with the remains of the host's skin. It usually pupates in April of the following year, emerging in late April or May. One specimen found in September 1965 pupated on 6 October and emerged later the same month.

## *EUCOSMA ?CANA* (Haworth), and *METZNERIA ?NEUROPTERELLA* (Zeller)

LEPIDOPTERA: EUCOSMIDAE and GELICHIIDAE

Caterpillars were amongst the commonest insects inhabiting the heads of *Cirsium vulgare*. The life-history of *E. ?cana* only has been studied in detail. The eggs are laid during June and July on the outer bracts of unopened buds and hatch in July or early in August. The egg (Fig. 26) is colourless or slightly pink with the surface pitted with small hollows. Usually they are laid singly, although occasionally they may be found in groups of two or three. Immediately prior to hatching, the developing larva can be seen curled up inside the egg, with its dark head and pronotum showing clearly through the shell.

Young larvae were seen during the second week of July in both 1964 and 1965. Empty eggshells were found in increasing numbers after this date. The young larva (Fig. 27) is pale in colour except for the dark brown head and pronotum. It bites its way out of the egg, leaving a lid, which often breaks off revealing an irregularly-shaped hole. The larva crawls up the outer bracts and between the tips of the inner bracts to the space above them and the developing florets. It wanders over the florets feeding on the tips of the corolla tubes, leaving brown marks or brown-edged holes. Eventually it burrows into a floret and down the corolla tube, or pushes down between the florets feeding as it goes and leaving a trial of frass. Only one larva out of the many studied followed a different course, boring into the head from a point midway down the outside bracts and leaving frass-filled holes in successive layers of bracts until it reached the florets inside.

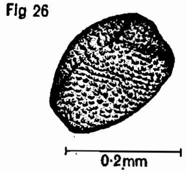
During its early life, the larva of both moth species feeds on the achenes and lower-parts of the florets of the thistle. On several occasions, young larvae were found inside achenes, which they left after feeding on the contents. By the time it is full-grown, the larva has tunnelled into the receptacle and into the gall of *Urophora stylata*. All the tunnels and hollows which have been excavated become filled with frass amongst which can occasionally be found the cast head capsule of a previous instar.

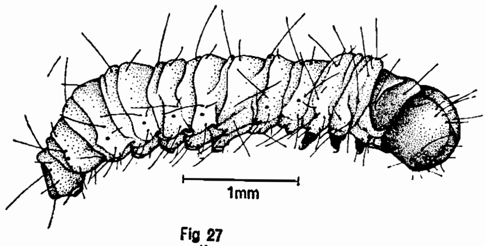
By September many of the larvae are fully fed, when they drop out of the thistle-head and bury themselves in the soil beneath. The larva constructs a cocoon of silk and soil particles in which it overwinters and pupates in the following spring. By the autumn, the thistle-heads are dead but still intact, and plenty of evidence of caterpillar attack is left in the head. If achenes are still present, these show characteristic damage (Fig. 14c). If a gall is present, it is extensively tunnelled, often the tunnels breaking into gall cells. These cells are usually packed with frass and may contain the remains of *U. stylata* larvae. The caterpillars are primarily plant feeders, but they will feed on any insect larvae that they happen to encounter.

### *LONCHAEA* sp. DIPTERA: LONCHAEIDAE

Larvae of this fly were found at all collecting sites except Lancaster. They were present in small numbers inside the thistle-heads from August to October in 1964 and 1965. The larva (Fig. 28) is active, dirty white in colour with prominent mouth-hooks and posterior spiracles.

The larva was found most often amongst caterpillar frass in the partly-eaten receptacle of the thistle-head. Occasionally it was found between the florets or



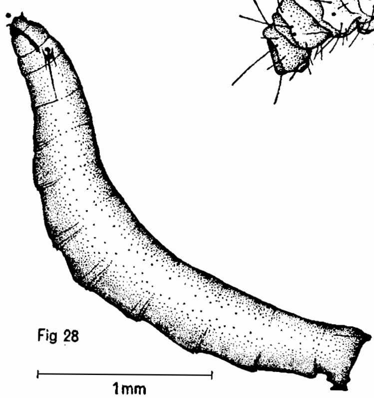




FIG. 26. *Eucosma ?cana*: egg.

FIG. 27. *Eucosma ?cana*: larva.

FIG. 28. *Lonchaea* sp.: larva.

bracts of the head, or in the gall cells of *U. stylata*, and sometimes several were coiled up inside the third larval skin of this species. It is probably exclusively a predator and *U. stylata* larvae may form the bulk of its diet in galled heads. *Lonchaea* larvae were found also in ungalled heads, where they were probably feeding on caterpillars and other inhabitants. When full-fed, the larvae probably drop out of the heads, as no puparia were found in the heads. An attempt was made to rear several to the adult stage, but none lived long enough to pupate.

*TINGIS CARDUI* L. HETEROPTERA: TINGIDAE

Most of the life-history of the spear thistle lace-bug, after the overwintering period, is spent on the involucre of the plant or on the region just below it. The adult (Fig. 29) is a dark olive-brown insect with the hemelytra attractively sculptured. From early May onwards, adults are seen in increasing numbers on the rosettes of leaves of the thistles. They are more common on the upper than

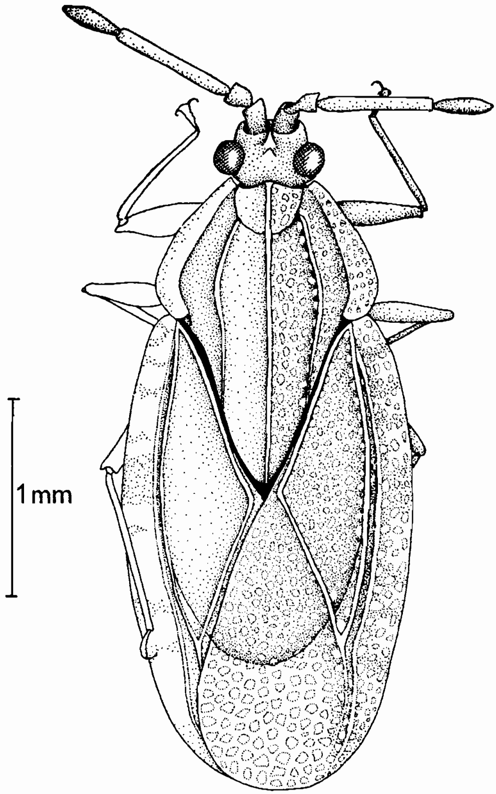



FIG. 29.
*Tingis cardui*: adult (pattern of left side not shown).

under surfaces of the leaves, perhaps because the felting hairs on the under surfaces make movement difficult.

After hibernation as adults, the lace-bugs become fairly active in June, running over the developing flower-heads and young leaves beneath the buds. The plant at this stage is growing upwards and may reach 2 feet in height. In early June, most of the females have a few mature ova in their ovaries and by early July, the majority have over half their eggs mature. The eggs are laid, usually singly, on each side of the midrib on either surface of young leaves close to the involucre (for a detailed description of eggs and nymphs, see Southwood and Scudder, 1956).

The eggs hatch in early July into olive-brown nymphs of average length 0·68 mm. The early instars are found inside the bud above the developing florets and between the inner bracts, and also on the outside of the head on the oldest bracts, where the older instars are more common. The nymph feeds in the same way as the adult bug, piercing the plant tissue with its stylets.

Adults of this generation appear first in early August and usually remain on the plants until these die in September or October. They then disappear, presumably to their overwintering site. The life-history is summarized in Fig. 31 based on percentages drawn from Table A (Appendix). The life-history shown is for Preston Montford which is representative of the more southerly collecting sites. Further north, at Hampsfell, equivalent stages lag 2–3 weeks behind.

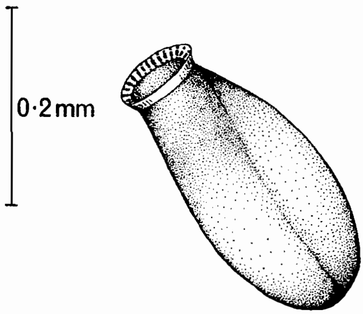



FIG. 30.
*Anthocoris nemorum*: egg.

## *ANTHOCORIS NEMORUM* (L.) HETEROPTERA: ANTHOCORIDAE

*A. nemorum* is a polyphagous predatory bug which feeds on adults and nymphs of *T. cardui*. It was the only predator of *T. cardui* seen and no parasites were recorded. The egg (Fig. 30) is similar to that of *T. cardui*, except that it is red due to the colour of the unhatched larva inside, and is often laid inserted into leaves so that only the operculum projects above the surface.

## (2) *Mortality factors affecting* Urophora stylata

Factors causing the death of the larvae and pupae of *U. stylata* are considered under the following six headings: parasite attack, predator attack, fungal and bacterial attack, death during adult emergence and death from unknown causes.

### *Parasite attack*

*Eurytoma tibialis* was the only endophagous parasite found. It is easily identified during the autumn and winter when the parasite larva is found within the host's puparium. Unaffected host larvae do not pupate before the

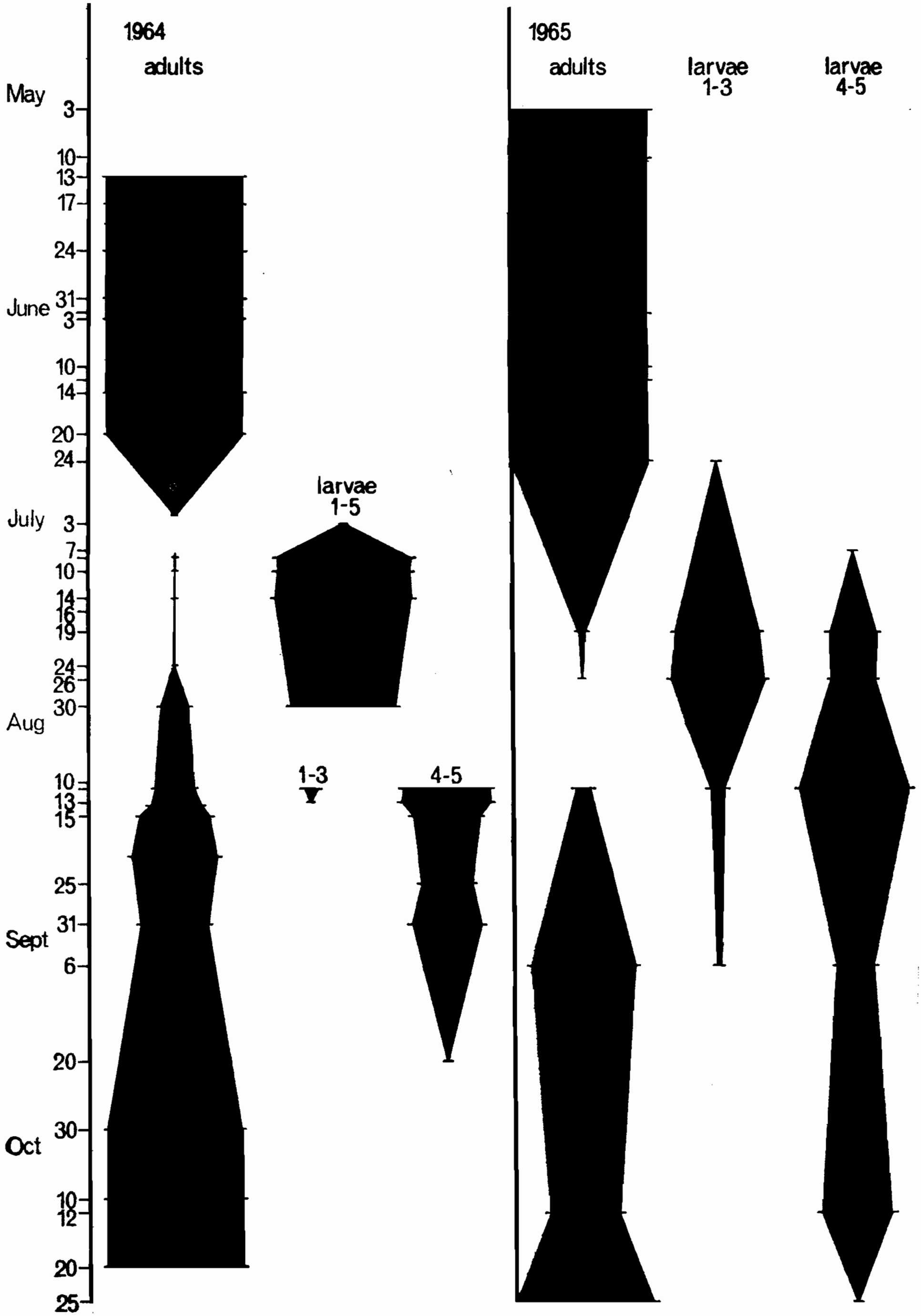



Fig. 31.
*Tingis cardui*: life-history at Preston Montford.

following spring. Before the host's puparium is formed, the presence of this parasite can be recognized only by dissection of the host. This period is brief, occupying only the month of July. If any apparently unaffected *U. stylata* larvae found during this stage are kept isolated in gelatine capsules, the formation of a puparium in early August will confirm that they have been parasitized.

During April and early May, healthy *U. stylata* are pupating, so that any puparia found at this time have to be opened to determine whether or not they are parasitized. The parasite larva is full-fed by April and does not completely fill the interior of the puparium. If removed from the puparium it will complete its development normally. After emergence of the adult, either host or parasite, it is easy to determine from the remains of puparia whether it was parasitized. The trypetid fly leaves a puparium with two flaps (Fig. 21) having used its

Table 1. Urophora stylata: *emergence and mortality factors*
a. 1964 b. 1965

| | | | Flatford Mill | | Preston Montford | | Orielton | | Slapton Ley | | Juniper Hall | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | No. | % | No. | % | No. | % | No. | % | No. | % |
| | galls | a | 64 | | 123 | | 77 | | 6 | | 1 | |
| | | b | 21 | | 11 | | 8 | | 8 | | 3 | |
| | cells | a | 277 | | 806 | | 747 | | 8 | | 1 | |
| | | b | 99 | | 61 | | 45 | | 35 | | 7 | |
| | *Urophora stylata* | a | 182 | 65.7 | 378 | 46.9 | 386 | 51.7 | 8 | 100.0 | 1 | 100.0 |
| | | b | 72 | 76.8 | 39 | 63.9 | 23 | 51.1 | 35 | 100.0 | 6 | 85.7 |
| factors causing death of *U. stylata* | ectoparasites | a | 37 | 13.3 | 40 | 5.0 | 49 | 6.6 | 0 | — | 0 | — |
| | | b | 1 | 1.0 | 2 | 3.3 | 1 | 2.2 | 0 | — | 0 | — |
| | *Eurytoma tibialis* | a | 8 | 2.9 | 82 | 10.2 | 59 | 7.9 | 0 | — | 0 | — |
| | | b | 2 | 2.0 | 9 | 14.7 | 0 | — | 0 | — | 0 | — |
| | caterpillars | a | 41 | 14.8 | 193 | 23.9 | 183 | 25.0 | 0 | — | 0 | — |
| | | b | 12 | 12.1 | 5 | 8.2 | 14 | 31.1 | 0 | — | 0 | — |
| | *Lonchaea* | a | ? | — | ? | — | ? | — | 0 | — | 0 | — |
| | | b | 2 | 2.0 | 1 | 1.7 | 7 | 15.5 | 0 | — | 0 | — |
| | fungus | a | 4 | 1.4 | 59 | 7.3 | 22 | 2.9 | 0 | — | 0 | — |
| | | b | 0 | — | 0 | — | 0 | — | 0 | — | 1 | 14.3 |
| | bacteria | a | 2 | 0.7 | 10 | 1.2 | 20 | 2.7 | 0 | — | 0 | — |
| | | b | 0 | — | 0 | — | 0 | — | 0 | — | 0 | — |
| | during adult emergence | a | 2 | 0.7 | 8 | 1.0 | 8 | 1.1 | 0 | — | 0 | — |
| | | b | 0 | — | 0 | — | 0 | — | 0 | — | 0 | — |
| | unknown | a | 6 | 2.2 | 38 | 4.7 | 21 | 2.8 | 0 | — | 0 | — |
| | | b | 6 | 6.1 | 5 | 8.2 | 0 | — | 0 | — | 0 | — |

ptilinum to break through the anterior end, whilst the adult *E. tibialis* cuts a circular hole with its mandibles leaving a lid which breaks off. The pupal skin of the parasite, left inside the puparium, is yellow whereas that of the host is white, and, in addition, there are always granules of frass in the parasitized puparium.

*E. tibialis* attacks *U. stylata* probably in all places in which galls are found (Table 1). The fact that none were recorded from Slapton Ley and Juniper Hall is not significant since the data from these sites are based on very small samples. The percentage parasitization was highest at Preston Montford, 10 per cent in 1964 and 15 per cent in 1965. At Orielton, 1964 yielded 8 per cent while none was recorded in 1965; this may be a reflection of the smaller sample in 1965. At Flatford Mill, smaller percentages were recorded in both years, nearly 3 per cent in 1964 and 2 per cent in 1965.

Species of *Habrocytus* were the commonest ectoparasites of *U. stylata*. *H. elevatus* was the only species recorded but as the species of *Habrocytus* are numerous and difficult to name there may have been others present. Included in the data for ectoparasites (Table 1) is attack by *Torymus cyanimus*, a less common parasite. The larvae of the two genera are easily distinguished as that of *Torymus* is hairy and of *Habrocytus* is not (Figs. 19, 20). The pupae are also distinctive (Figs. 22, 23). After emergence of the adult, the pupal remains cannot be separated unless the emerged adult was a female. For this reason, the data for ectoparasites (Table 1) have been lumped together, and show that ectoparasite attack varied considerably from site to site and from year to year.

*Predator attack*

The largest single mortality factor of *U. stylata* was predation by moth caterpillars. Most of the data (Table 1) comes from indirect evidence, the tunnelling and frass which remained after the larvae had left the head. There is no discrimination by the caterpillar; it will eat host and parasite larvae alike. Cells were frequently found packed with frass or almost completely destroyed.

Caterpillars were found at all the collecting sites. From the three sites where galls were most common (Table 1), the highest attack was found at Orielton (25 and 31 per cent) and the lowest at Flatford Mill (15 and 12 per cent). At Preston Montford, the percentage attack differed markedly in the two years, being similar to that of Orielton (24 per cent) in 1964 but lower than that of Flatford Mill in 1965 (8 per cent).

Larvae of *Lonchaea* sp. were found attacking *U. stylata* in small numbers. It is thought to be exclusively a predator (K. G. V. Smith, personal communication), and was found occasionally in the cell of *U. stylata* or within its skin. The figures (Table 1) are based on these records. It undoubtedly feeds on other insects as well, as it was found in ungalled heads as well as galled. Only at Orielton did attack by *Lonchaea* larvae become a serious mortality factor of *U. stylata*, reaching 15·5 per cent in 1965.

*Fungal and bacterial attack*

These two factors can be discussed together as it is possible that neither is a primary cause of mortality. Larvae and pupae attacked by fungus are shrivelled, hard and covered with hyphae. Those attacked by bacteria are dark in colour, the skins filled with the putrid liquid remains of the insect. There is no evidence that the fungi or bacteria caused death; the insect may have become affected after it had been killed by some other factor. The figures (Table 1) therefore may not mean a great deal. It may be significant that the data for both factors are higher in the west of the country than in the east.

*Death during adult emergence*

This factor accounts for the death of a very small percentage of flies. In many cases there was no obvious reason for this failure, but occasionally pupae were found the wrong way round with the posterior end upwards, giving the adult no room to escape.

Table 2. *Collecting sites: localities and altitudes*

| Site | Grid reference | Height in ft. O.D. | Year |
|---|---|---|---|
| Slapton Ley | SX 818441–3 | 50 | 1964 |
| | SX 819441 | 50 | 1964 |
| | SX 822446 | 50 | 1965 |
| | SX 824449 | 100 | 1965 |
| Juniper Hall | TQ 175529 | 200 | 1964 |
| | TQ 175528 | 200 | 1965 |
| Orielton | SR 955992 | 175 | 1964 and 1965 |
| Flatford Mill | TL 074332 | less than 25 | 1964 and 1965 |
| Preston Montford | SJ 432142 | 220 | 1964 and 1965 |
| (Stiperstones | SO 369992 | 1,600 | 1964) |
| Malham Tarn | SD 892674 | 1,375 | 1964 and 1965 |
| Hampsfell | SD 394786 | 600 | 1964 and 1965 |
| Coombs Dale | SK 228748 | 550 | 1965 |
| Lancaster | SD 494606 | 275 | 1965 |

Table 3. Urophora stylata: *number and percentage of thistle-heads with galls*

| Site | Thistle-heads | | Galls | | | |
|---|---|---|---|---|---|---|
| | 1964 | 1965 | 1964 No. | 1964 % | 1965 No. | 1965 % |
| Flatford Mill | 160 | 35 | 37 | 23.1 | 21 | 60.0 |
| Preston Montford | 157 | 50 | 53 | 33.7 | 11 | 22.0 |
| Orielton | 162 | 39 | 77 | 47.5 | 8 | 20.5 |
| Slapton Ley | 186 | 28 | 6 | 3.2 | 8 | 28.6 |
| Juniper Hall | 80 | 43 | 1 | 1.2 | 3 | 7.0 |
| Malham Tarn | 41 | 30 | 0 | — | 0 | — |
| Hampsfell | 65 | 36 | 0 | — | 0 | — |
| Lancaster | * | 100 | — | — | 0 | — |
| Coombs Dale | * | 50 | — | — | 0 | — |

* No sample taken.

*Death from unknown causes*

This section includes a variety of mortality factors. Intrinsic failure of the larva or pupa will make up part of the record as will attack by organisms which leave no trace of their presence. Adult females of *Habrocytus* species feed on their hosts without necessarily laying eggs; all that remains of the host larva is a shrivelled skin. Cells of *U. stylata* which were found empty are included here.

### (3) *Geographical variation*

At all sites the habitats were similar, being wasteground or pastureland grazed by cattle or sheep. The localities and altitudes varied and this information is summarized in Table 2.

*Urophora stylata*

Galls were found at the five southern collecting sites. Table 3 includes galls calculated as a percentage of the total thistle-heads for each year. Galls were common at Flatford Mill, Preston Montford and Orielton and rare at the two more southern sites, Slapton Ley and Juniper Hall, except in 1965 at Slapton. The numbers recorded from any one site differed widely, often the difference between years being greater than the difference between sites. In 1964, the highest percentage galling was recorded from Orielton (47·5 per cent) with a general decrease southwards to a minimum at Juniper Hall (1 per cent). The pattern in 1965 differed in that maximum records came from Flatford Mill (60 per cent) with Juniper Hall again having the lowest score (7 per cent). In 1965 the distribution was less regular than in 1964, with the Slapton Ley record (nearly 29 per cent) being higher than those of Orielton (20·5 per cent) and Preston Montford (22 per cent). The numbers of thistle-heads examined in 1965, however, was much smaller than in 1964.

The number of cells in a gall varied considerably. Several were single-celled while the maximum number was 34, found in a gall collected at Orielton. The range of cell number increased from east to west (Fig. 32). In 1964 at Flatford Mill, most galls had between one and six cells. At Preston Montford, the majority were less than 13-celled, while at Orielton the range of variation was wide, with several galls having over 20 cells. The higher cell numbers are probably the result of more than one oviposition in the thistle-head. As multiple ovipositions seem to be more common in the west, either *U. stylata* is more abundant there or there are fewer heads of spear thistle available.

*Terellia serratulae*

The numbers of thistle-heads containing cocoons of *T. serratulae* larvae are expressed as percentages of the total heads collected (Table 4). *T. serratulae* was found at the same five sites recorded for *U. stylata*, none being recorded from the four northern ones. In 1964, the highest numbers came from Slapton Ley (10 per cent), with 7·5 per cent from Flatford Mill and 6 per cent from Juniper Hall. 2·5 per cent was recorded from Orielton and the lowest, 1 per cent, from Preston Montford. In 1965 the pattern was different, with Juniper Hall reaching a maximum of 28 per cent, Orielton 18 per cent and none from Flatford Mill

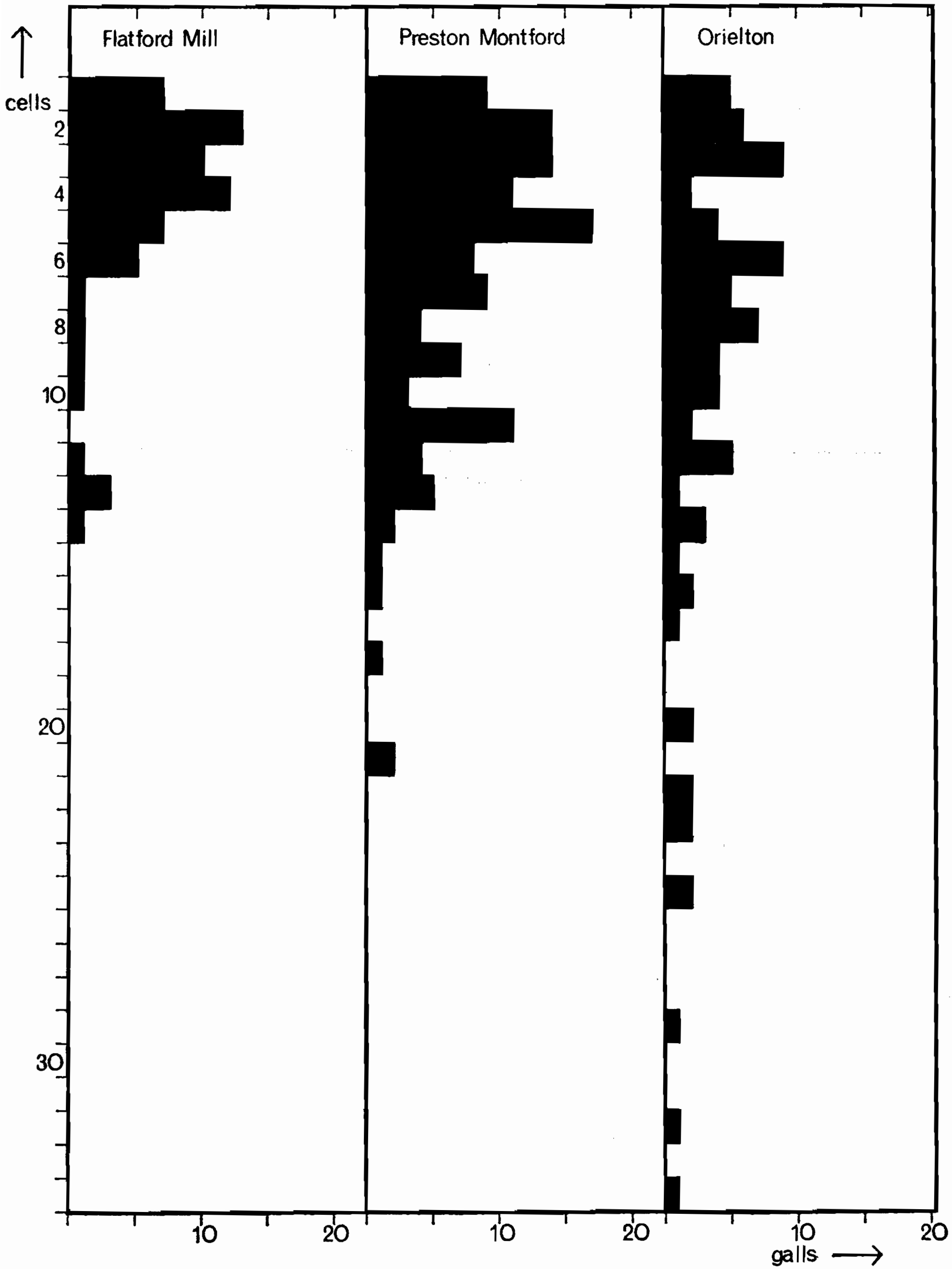



FIG. 32.
*Urophora stylata*: numbers of cells per gall in 1964.

Table 4. Terellia serratulae: *number and percentage of thistle-heads with cocoons*

| Site | Thistle-heads 1964 | Thistle-heads 1965 | Heads with cocoons 1964 No. | 1964 % | Heads with cocoons 1965 No. | 1965 % |
|---|---|---|---|---|---|---|
| Flatford Mill | 187 | 35 | 14 | 7·5 | 0 | — |
| Preston Montford | 277 | 50 | 3 | 1·1 | 0 | — |
| Orielton | 162 | 39 | 4 | 2·5 | 7 | 17·9 |
| Slapton Ley | 186 | 28 | 18 | 9·7 | 2 | 7·1 |
| Juniper Hall | 80 | 43 | 5 | 6·2 | 12 | 27·9 |
| Malham Tarn | 41 | 30 | 0 | — | 0 | — |
| Hampsfell | 65 | 36 | 0 | — | 0 | — |
| Lancaster | * | 100 | — | — | 0 | — |
| Coombs Dale | * | 50 | — | — | 0 | — |

* No sample taken.

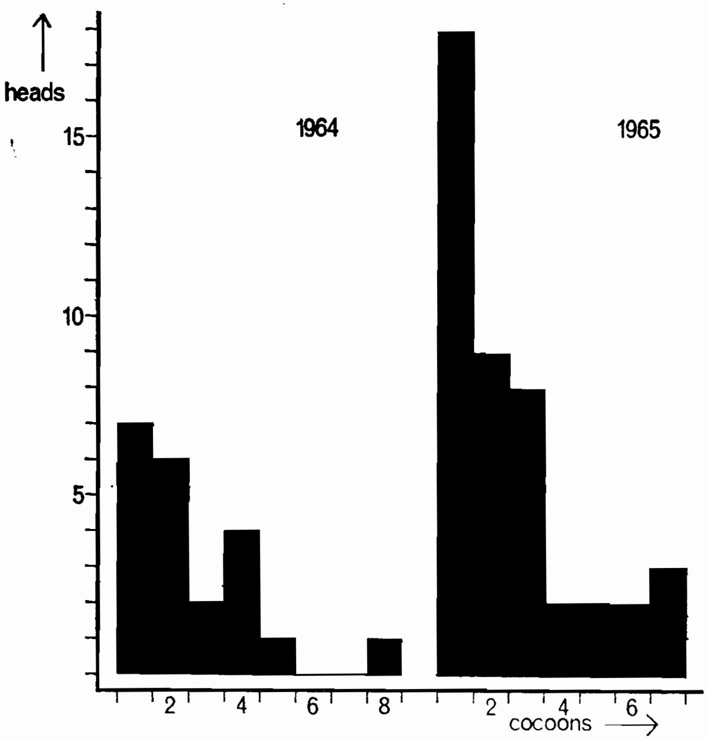



FIG. 33.
*Terellia serratulae*: numbers of cocoons per head (all sites).

or Preston Montford. The sample in 1965, however, was much smaller than in 1964, and less emphasis should be placed on these figures.

The maximum number of cocoons in a single head was eight, found on only one occasion (Fig. 33). The histograms represent numbers of larvae per head for all collecting sites in each year. The total numbers found were small and there was no obvious difference between sites. The majority of infected heads contained one, two or three cocoons.

*Caterpillars: Eucosma ?cana* and *Metzneria ?neuropterella*

Evidence of the presence of caterpillars was found at every collecting site (Table 5). In 1964, the highest number was recorded from Preston Montford,

Table 5. Eucosma ?cana *and* Metzneria ?neuropterella: *number and percentage of thistle-heads with larval frass*

| Site | Thistle-heads | | Heads with frass | | | |
|---|---|---|---|---|---|---|
| | 1964 | 1965 | 1964 No. | 1964 % | 1965 No. | 1965 % |
| Flatford Mill .. .. .. | 187 | 35 | 79 | 42.2 | 18 | 51.4 |
| Preston Montford .. .. .. | 277 | 50 | 157 | 56.7 | 19 | 38.0 |
| Orielton .. .. .. .. | 162 | 39 | 72 | 44.4 | 24 | 61.5 |
| Slapton Ley .. .. .. .. | 186 | 28 | 43 | 23.1 | 8 | 28.6 |
| Juniper Hall .. .. .. .. | 80 | 43 | 5 | 6.2 | 2 | 4.6 |
| Malham Tarn .. .. .. | 41 | 30 | 0 | — | 6 | 20.0 |
| Hampsfell .. .. .. .. | 65 | 36 | 11 | 16.9 | 16 | 44.4 |
| Lancaster .. .. .. .. | * | 100 | — | — | 75 | 75.0 |
| Coombs Dale .. .. .. .. | * | 50 | — | — | 18 | 36.0 |

* No sample taken.

Table 6. Eucosma ?cana *and* Metzneria ?neuropterella: *number and percentage of galled heads with larval frass*

| Site | Galled heads | | Galled heads with frass | | | |
|---|---|---|---|---|---|---|
| | 1964 | 1965 | 1964 No. | 1964 % | 1965 No. | 1965 % |
| Flatford Mill .. .. .. | 64 | 21 | 42 | 65.6 | 13 | 61.9 |
| Preston Montford .. .. .. | 123 | 11 | 83 | 67.5 | 7 | 63.6 |
| Orielton .. .. .. .. | 77 | 8 | 48 | 62.3 | 6 | 75.0 |
| Slapton Ley .. .. .. .. | 6 | 8 | 3 | 50.0 | 3 | 37.5 |
| Juniper Hall .. .. .. .. | 1 | 3 | 0 | — | 0 | — |
| Malham Tarn .. .. .. | 0 | 0 | 0 | — | 0 | — |
| Hampsfell .. .. .. .. | 0 | 0 | 0 | — | 0 | — |
| Lancaster .. .. .. .. | * | 0 | — | — | 0 | — |
| Coombs Dale .. .. .. .. | * | 0 | — | — | 0 | — |

* No sample taken.

Table 7. Eucosma ?cana *and* Metzneria ?neuropterella: *number and percentage of ungalled heads with larval frass*

| Site | Ungalled heads | | Ungalled heads with frass | | | |
|---|---|---|---|---|---|---|
| | 1964 | 1965 | 1964 No. | 1964 % | 1965 No. | 1965 % |
| Flatford Mill | 123 | 14 | 37 | 30.1 | 5 | 35.7 |
| Preston Montford | 155 | 39 | 75 | 48.4 | 12 | 30.8 |
| Orielton | 85 | 31 | 24 | 28.2 | 18 | 58.1 |
| Slapton Ley | 180 | 20 | 41 | 22.8 | 5 | 25.0 |
| Juniper Hall | 79 | 40 | 5 | 6.3 | 2 | 5.0 |
| Malham Tarn | 41 | 30 | 0 | — | 6 | 20.0 |
| Hampsfell | 65 | 36 | 11 | 16.9 | 16 | 44.4 |
| Lancaster | * | 100 | — | — | 75 | 75.0 |
| Coombs Dale | * | 50 | — | — | 18 | 36.0 |

* No sample taken.

Table 8. Lonchaea *sp.*: *number and percentage of larvae in galled and ungalled heads*

| Site | Year | Total thistle-heads No. | Total larvae No. | Total larvae % | Larvae in galled heads No. | Larvae in galled heads % | Larvae in ungalled heads No. | Larvae in ungalled heads % |
|---|---|---|---|---|---|---|---|---|
| Flatford Mill | 1964 | 61 | 2 | 3.3 | 2 | 3.3 | 0 | — |
| | 1965 | 35 | 14 | 40.0 | 14 | 40.0 | 0 | — |
| Preston Montford | 1964 | 57 | 24 | 42.1 | 22 | 38.6 | 2 | 3.5 |
| | 1965 | 50 | 34 | 68.0 | 23 | 46.0 | 11 | 22.0 |
| Orielton | 1964 | 62 | 1 | 1.6 | 1 | 1.6 | 0 | — |
| | 1965 | 39 | 24 | 61.5 | 13 | 33.3 | 11 | 28.2 |
| Slapton Ley | 1964 | 86 | 4 | 4.6 | 2 | 2.3 | 2 | 2.3 |
| | 1965 | 28 | 6 | 21.4 | 1 | 3.6 | 5 | 17.8 |
| Juniper Hall | 1964 | 80 | 0 | — | 0 | — | 0 | — |
| | 1965 | 43 | 2 | 4.6 | 1 | 2.3 | 1 | 2.3 |
| Malham Tarn | 1964 | 41 | 6 | 14.6 | 0 | — | 6 | 14.6 |
| | 1965 | 30 | 36 | 120.0 | 0 | — | 36 | 120.0 |
| Hampsfell | 1964 | 65 | 5 | 7.7 | 0 | — | 5 | 7.7 |
| | 1965 | 36 | 29 | 80.6 | 0 | — | 29 | 80.6 |
| Lancaster | 1964 | * | — | — | — | — | — | — |
| | 1965 | 100 | 0 | — | 0 | — | 0 | — |
| Coombs Dale | 1964 | * | — | — | — | — | — | — |
| | 1965 | 50 | 55 | 110.0 | 0 | — | 55 | 110.0 |

* No sample taken.

while Orielton and Flatford Mill scored 44 per cent and 42 per cent respectively. The percentage decreased both northwards to Hampsfell (17 per cent) and none at Malham Tarn, and southwards to Juniper Hall (6 per cent). In 1965, additional samples were taken from Lancaster and Coombs Dale. Lancaster provided the highest score in this year with 75 per cent of the heads attacked. 61·5 per cent was recorded from Orielton and 51 per cent from Flatford Mill, with again a decrease southwards to Juniper Hall (5 per cent).

In Table 6, the numbers of galled heads containing caterpillar frass are expressed as percentages of total galled heads, and similarly Table 7 shows numbers of ungalled heads with frass as percentages of total ungalled heads. These data are shown graphically in Fig. 34. No galls were recorded from Malham Tarn, Hampsfell, Coombs Dale or Lancaster. In both years, the percentage of galled heads with frass was higher than the percentage of ungalled with frass at all sites where galls were found, except at Juniper Hall where very few galls were recorded.

*Lonchaea* sp.

*Lonchaea* larvae were found at all sites except Lancaster, in both galled and ungalled heads and in heads with and without caterpillar frass. The numbers of *Lonchaea* larvae in galled and ungalled heads are recorded as percentages of total heads (Table 8) and plotted as histograms (Fig. 35). At all sites, fewer larvae were recorded in 1964 than in 1965. At the sites where galls were common (Preston Montford, Flatford Mill and Orielton) larvae were more numerous in galled than in ungalled heads. The highest numbers, however, were recorded in 1965 from Malham Tarn, Coombs Dale and Hampsfell, where galls were not found.

Table 9 shows numbers of larvae in heads with and without caterpillar frass, again expressed as percentages of the total heads collected. In Fig. 36 these data are presented graphically, larvae were found in both types of head, but were more common in frass-filled heads except at Malham and Slapton, where there were more in heads without frass.

*Tingis cardui*

The spear thistle lace-bug was found at six of the nine collecting sites (Table 10). In 1964, the highest number, 235, was found at Hampsfell and decreased southwards to 79 at Slapton Ley and none at Juniper Hall. In 1965, the pattern was different but in general, numbers in the west and north (Preston Montford 280, Hampsfell 113) were higher than those in the south and east (Flatford Mill 65, Juniper Hall 19).

## III. Discussion

The spear thistle is common throughout the British Isles and may become a serious pest of pasture land. It has been classified by the Ministry of Agriculture, Fisheries and Food as an injurious weed under section 1(2) of the Weeds Act

Table 9. Lonchaea *sp.*: *number and percentage of larvae in thistle-heads with and without caterpillar frass*

| Site | Year | Total heads No. | Total larvae No. | Total larvae % | Larvae in heads with frass No. | Larvae in heads with frass % | Larvae in heads without frass No. | Larvae in heads without frass % |
|---|---|---|---|---|---|---|---|---|
| Flatford Mill | 1964 | 61 | 2 | 3.3 | 2 | 3.3 | 0 | — |
| | 1965 | 35 | 14 | 40.0 | 14 | 40.0 | 0 | — |
| Preston Montford | 1964 | 57 | 24 | 42.1 | 24 | 42.1 | 0 | — |
| | 1965 | 50 | 34 | 68.0 | 24 | 48.0 | 10 | 20.0 |
| Orielton | 1964 | 62 | 1 | 1.6 | 1 | 1.6 | 0 | — |
| | 1965 | 39 | 24 | 61.5 | 23 | 59.0 | 1 | 2.5 |
| Slapton Ley | 1964 | 86 | 4 | 4.6 | 1 | 1.2 | 3 | 3.5 |
| | 1965 | 28 | 6 | 21.4 | 0 | — | 6 | 21.4 |
| Juniper Hall | 1964 | 80 | 0 | — | 0 | — | 0 | — |
| | 1965 | 43 | 2 | 4.6 | 1 | 2.3 | 1 | 2.3 |
| Malham Tarn | 1964 | 41 | 6 | 14.6 | 0 | — | 6 | 14.6 |
| | 1965 | 30 | 36 | 120.0 | 10 | 33.3 | 26 | 86.7 |
| Hampsfell | 1964 | 65 | 5 | 7.7 | 3 | 4.6 | 2 | 3.1 |
| | 1965 | 36 | 29 | 80.6 | 24 | 66.7 | 5 | 13.9 |
| Lancaster | 1964 | * | — | — | — | — | — | — |
| | 1965 | 100 | 0 | — | 0 | — | 0 | — |
| Coombs Dale | 1964 | * | — | — | — | — | — | — |
| | 1965 | 50 | 55 | 110.0 | 44 | 88.0 | 11 | 22.0 |

* No sample taken.

Table 10. Tingis cardui: *number and percentage of adults and larvae* (*no.*/100 *thistle-heads*)

| Site | Thistle-heads 1964 | Thistle-heads 1965 | *T. cardui* on thistle-heads 1964 No. | 1964 % | 1965 No. | 1965 % |
|---|---|---|---|---|---|---|
| Flatford Mill | 65 | 55 | 14 | 21.5 | 36 | 65.4 |
| Preston Montford | 62 | 78 | 138 | 222.6 | 218 | 279.5 |
| Orielton | 62 | 57 | 118 | 193.4 | 29 | 50.9 |
| Slapton Ley | 91 | 48 | 72 | 79.1 | 33 | 68.8 |
| Juniper Hall | 85 | 73 | 0 | — | 14 | 19.2 |
| Malham Tarn | 52 | 49 | 0 | — | 0 | — |
| Hampsfell | 78 | 57 | 183 | 234.6 | 70 | 122.8 |
| Lancaster | * | 100 | — | — | 0 | — |
| Coombs Dale | * | 50 | — | — | 0 | — |

* No sample taken.

1959 (Min. of Ag., Fish. and Food, 1962). The thistle spreads by achenes alone; there is no asexual reproduction. As the formation of a gall affects the viability of the achenes produced by the thistle, it might appear that the spread of the weed could be controlled by the artificial introduction of *U. stylata*, if the majority of flower-heads in an area could become galled. The number of achenes produced by ungalled heads varies enormously. Thus from a sample of 68 heads collected after flowering in September 1965, the mean number of achenes produced was 248, with extremes of 52 and 427. If a gall is present, the achenes adjacent to it become distorted (Fig. 14b) and are not viable. The number of achenes eaten by *U. stylata* larvae or distorted by the gall increases with the size of the gall, but even so, all heads found contained at least some healthy achenes, and these would be sufficient to propagate the weed. The biological control of the spear thistle by increasing the population of *U. stylata* can therefore be disregarded as a practical method of limiting the spread of the weed. In any case, biological control of the thistle is unnecessary as it is succeptible to cutting back and the application of herbicides (Min. of Ag., Fish. and Food, 1962). The plants should be prevented from reaching the fruiting stage by either spudding out below ground when in the rosette stage or by cutting with a mower when in the bud stage. The plant is susceptible to several sprays; spraying should take place before flowering, when the plant is growing strongly.

*Urophora stylata* (Fabricius)

The life-history of the fly does not appear to have been studied before in detail. Varley (1937b) described briefly the morphology of the larva and Collin (1947) included the adult in his key to the British genera. Niblett (1953, 1956) recorded it as commonly forming galls in both *Cirsium vulgare* and the musk thistle, *Carduus nutans* L., and rarely in the flower-heads of the creeping thistle, *Cirsium arvense* (L.) Scop. Amsden (personal communication) has once bred *U. stylata* from *C. arvense*.

Adult flies of *U. stylata* were never seen to feed on the spear thistle in the field, although they probably do feed as their mouthparts are well developed. The most obvious foods available at the right time are nectar and aphid honey-dew. Varley (1947) dissected adults of *U. jaceana*, which were on the wing at about the same time as *U. stylata*, and found the crops distended with a fluid which was found to contain reducing sugars. He concluded that, on that occasion at least, honey-dew was the likely food source. He also commented that as the population density of the aphids and the flowering time of plants suitable to provide nectar are so variable, the food source is inconstant. Perhaps male flies do not need to feed but fecundity of the females is increased if they do feed. It seems, however, that the flies can reproduce if no food is available. Newly-emerged females from the breeding cages dissected in July had some mature ova in their ovaries; perhaps all the eggs will not mature unless the fly can feed.

The details of larval and pupal life of *U. stylata* are similar to those of *U. jaceana* (Varley, 1947). Both have heavily sclerotized perispiracular plates, which plug the neck of the gall cell during the life of the third instar. It has been suggested that the plate may help to prevent parasitism. This could happen when attacked by ectoparasites whose eggs are laid on the third instar. The eggs of *Eurytoma tibialis*, however, are laid within the second instar, before the plate is sclerotized.

*Habrocytus elevatus* (Walker) (=*H. musaeus* Nees, =*H. trypetae* Thoms.)

*H. elevatus* has been recorded as attacking a wide variety of hosts including the trypetids *Urophora jaceana* (Hering), *U. cardui* (L.), *Terellia serratulae* L., *Noeëta pupillata* (Fallén) and the moth *Sparganothis pilleriana* (Schiffermueller) (Varley, 1947). It has been reared from the flower-heads of composite genera *Centaurea*, *Carduus*, *Arctium* and *Hieracium*. Some of the records may be erroneous as *Habrocytus* species are difficult to name. Varley claimed that *H. elevatus* does not attack non-gall-forming hosts and Amsden has failed to breed it from *T. serratulae* (personal communication). There is evidence that it prefers the gall-forming typetids and not their parasites as hosts, although it has been recorded as attacking a host already parasitized by *Eurytoma* sp.

According to Varley (1947) there may be two or three generations a year. In 1935, he recorded adults emerging from parasitized *U. jaceana* in May, July and September. In the colder year of 1936, they emerged in June and September. From galls of *U. stylata* in the field in 1965, *H. elevatus* emerged in April-May and late June; there was no evidence of a third generation. The breeding cage data (Fig. 5) also show two emergence periods, in April-May and June-July. All the thistle-heads in the cages had been collected during the previous winter so that all the host larvae belonged to the same generation. There are three possible explanations for the two periods:

(i) The two emergence periods may represent a staggered life-history, some larvae pupating and emerging earlier than others. They may represent different periods of egg-laying during the previous year, the April-May adults having developed from eggs laid the previous June, and the June-July adults from eggs laid the previous July or August.

(ii) The two emergence periods may represent two generations, the second being offspring of the first. The newly-emerged females are not mature at any stage of the year, and so presumably must feed before laying eggs. Therefore, if the June-July adults are a second generation, there must have been food available in the breeding cages for the April-May batch. Apparently, the female parasite feeds on *U. stylata* larvae before laying any eggs (Varley, 1947). It pushes the ovipositor down the neck of a gall cell, stabbing and paralyzing the host. The parasite remains motionless while a secretion hardens round the ovipositor forming a tube. When the ovipositor is withdrawn, the blood of the host exudes up the tube and is drunk by the parasite. Many larvae may be killed in this way without the parasite having laid any eggs. Therefore there was food available for the April-May adults. Many of the host larvae would have pupated by May, but there was probably a large enough number still in the larval stage to feed the small number of adult parasites which emerged in April and May. The females may also be able to feed on puparia, although this is unlikely as no shrivelled puparia were found on dissection of the galls after all insects had emerged.

Although food was available, it is unlikely that the adult parasites mated and laid eggs in the breeding cages. They would have had to find food and mates in the dark and to have remained in the cages for a considerable period before reaching the trap at the top. The fact that all species emerged during distinct periods suggests that they were attracted upwards as soon as they had emerged, so that *H. elevatus* adults would not have had a chance to feed, mate and lay eggs.

(iii) Owing to the difficulty of identifying *Habrocytus* species, it is possible that there was more than one species in the breeding cages, which may explain the two emergence periods.

On the few occasions that eggs of *H. elevatus* were found, there were always more than one. Superparasitism is apparently common and may be related to the ectoparasitic habit of this species. As the ovipositor does not pierce the host larva, it is probable that the presence of eggs laid during a previous parasitic attack could not be detected. Only one of a batch will develop as the host can support only one larva to maturity.

*Torymus cyanimus* Boheman

This species has been recorded (Varley, 1947) as attacking the larvae of trypetids *Urophora jaceana* (Hering), *U. cardui* (L.) and *Tephritis truncata* (Loew).

In 1965, evidence was found of only one generation which emerged in May (Figs. 5, 25). Varley (1947) recorded the same month for the parasite emerging from *U. jaceana* larvae. Although there are hosts available in May, June and July, no eggs were found until August, when the next generation of host larvae are well grown. *T. cyanimus* may find an alternative host during May, such as a trypetid in the flower-head of another plant, so that the eggs laid in August would belong to a second generation, or the adult may wait from May until August, and then mature its eggs and attack the hosts (Varley, 1947).

Most larvae developing from eggs laid in August will overwinter. According to Varley (1947), some may pupate and emerge later in the same year, during September. These adults presumably lay eggs on full-grown host larvae, which are abundant during September. Although during the present survey, *T. cyanimus* was found only to attack *U. stylata* larvae, it shows no preference between healthy *U. jaceana* larvae and those already attacked by *Eurytoma tibialis* (Varley, 1947).

*Eurytoma tibialis* Boheman (=*E. curta* auctt.nec. Walker)

This endoparasite attacks a wide variety of trypetid larvae, especially those causing the formation of galls. It has been bred from *Urophora jaceana* in *Centaurea nemoralis*; *U. solstitialis* L. in *Carduus nutans*; *U. cuspidata* Meigen in the greater knapweed, *Centaurea scabiosa* L. (Claridge, 1961). Varley (1947) stated that it has been recorded as a parasite of the gall-flies *U. eriolepidis* (Loew), *U. stylata*, *U. cardui* (L.), *Tephritis vespertina* (Loew), and the gall-wasp *Aulcidia hieracii* (Bouché). Many records have been published from non-gall-forming hosts, but these are unconfirmed.

Before oviposition, the female parasite walks over the flower head, tapping it with the antennae (Varley, 1947). Whether it can detect the presence of a host is uncertain, as it may insert the ovipositor into a head devoid of hosts. Apparently it shows a high degree of discrimination to prevent superparasitism

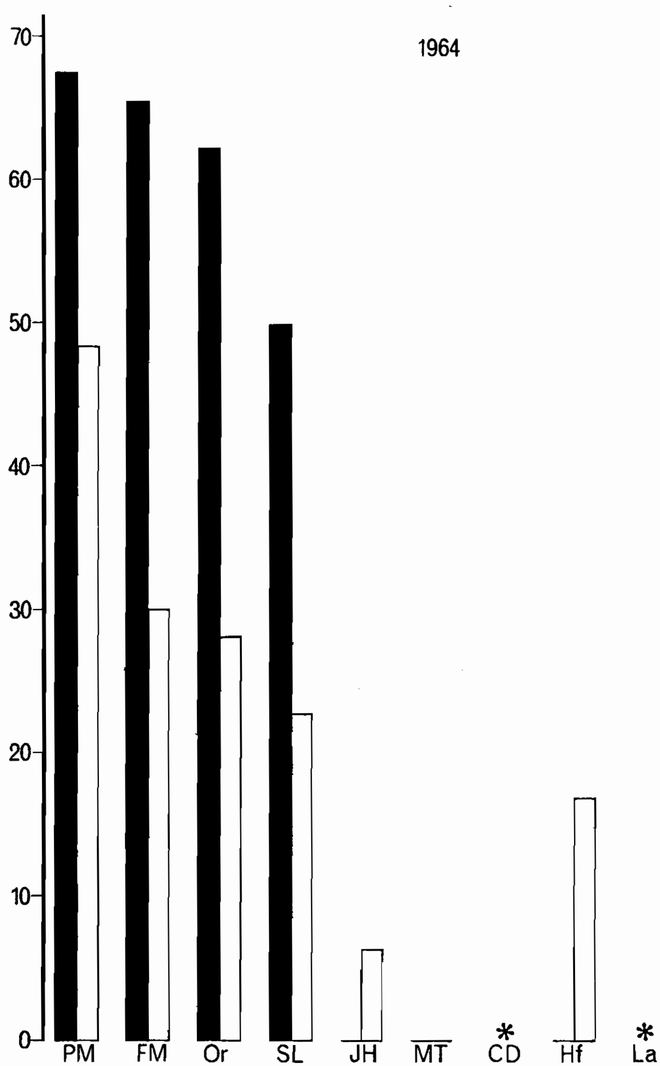



FIG. 34.
Caterpillar frass in galled (■) and ungalled (⊓) heads (per cent).
* No sample collected.

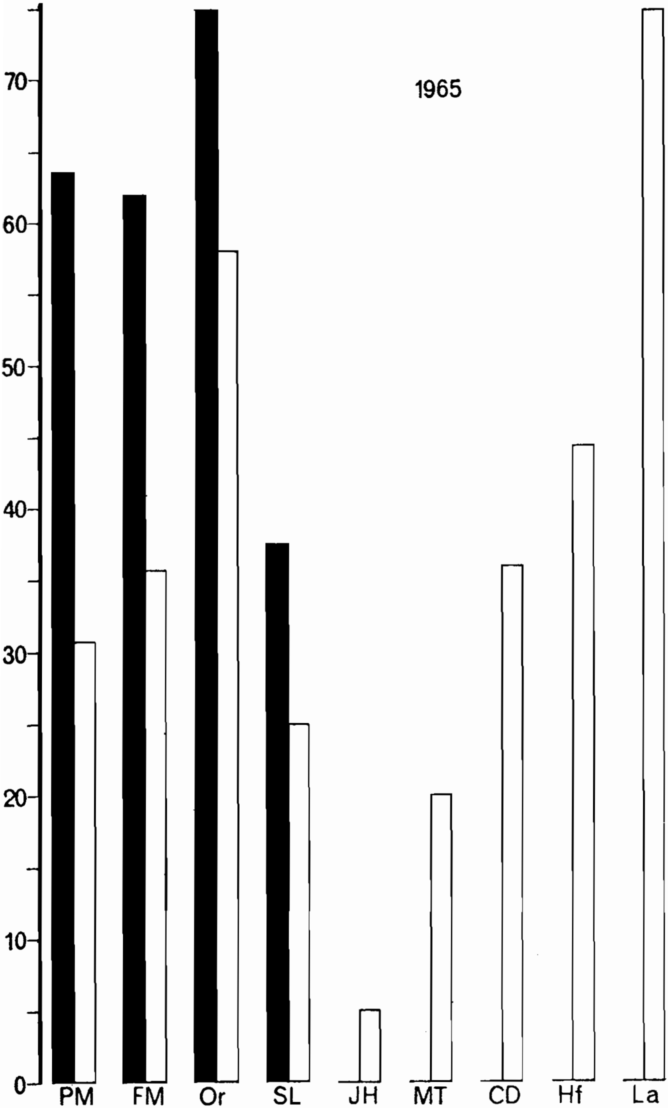



Fig. 34 continued.

(Varley, 1941). It probably detects parasitized hosts by sense organs located in the tip of the ovipositor.

*E. tibialis* causes the so-called premature pupation of the host larva in the autumn instead of the following spring. In fact, a puparium but no true pupa is formed since the parasite destroys it before the pupal stage is reached. This phenomenon is widespread amongst internal parasites of dipterous larvae (Claridge, 1961).

The emergence period of adult *E. tibialis* is well synchronized with that of the host (Figs. 5, 25). The earliest parasite emerged about 2 weeks after the first *U. stylata* and emergence continued for about 3 weeks after the last gall-fly. Adults of *U. stylata* would therefore be mating and laying eggs while *E. tibialis* adults were emerging, so that by the time the parasite was ready to oviposit, the host larva would have reached the second instar. The period of the second instar is short, so that the time of emergence of the parasite is critical.

*Terellia serratulae* L.

*T. serratulae* is the only other trypetid, besides *U. stylata*, found in the flower-heads of *Cirsium vulgare* (Amsden, personal communication). According to Niblett (1956), it is found also in the flower-heads of *Carduus nutans* L. and a hybrid *Carduus acanthoides* × *nutans*, but never in large numbers.

It normally emerges in June and July, having overwintered as a larva, but small numbers will emerge in the previous September if the larvae are kept in above normal temperatures or if the late summer is unusually mild (Amsden, personal communication). It is not known what happened to the newly-emerged adults in September. All the thistle-heads are dead by October so that there would be no food for larval progeny of these adults. Perhaps they overwinter as adults or lay eggs which overwinter, or perhaps they or their offspring die because they are out of step with the spear thistle.

The parasites of *T. serratulae* have presented problems in identification. According to Amsden (personal communication), there are at least five parasites, of which three are species of *Habrocytus*. One which is endophagous was not found during the present survey. None of the ectoparasites were common, but probably the majority of individuals were *H. musaeus* (Nees) (=*trypetae* Thoms.). At least one specimen may have been *H. ariomedes* (Walker).

*Eucosma ?cana* (Haworth) and *Metzneria ?neuropterella* (Zeller)
(=*Catoptria cana* Haworth and *Parasia neuropterella* Zeller)

*E. cana* has been recorded before from *Cirsium vulgare* and other thistles and also from *Centaurea nemoralis*, feeding on the achenes (Barrett, 1880). Swatschek (1958) records it as living in the flower-heads of composites, including *Cirsium oleraceum* (L.) Scop. and *C. vulgare*. *M. neuropterella* has been bred from the flower-heads of the stemless thistle, *Cirsium acaule* (L.) Scop., and the knapweeds, *Centaurea scabiosa* and *C. nemoralis* (Bankes, 1909).

The caterpillars of these moths invariably will enter a gall if one is present. They are mainly phytophagous, but will eat any larvae if they encounter them. Caterpillars probably search for galled heads (Fig. 34) where these are common, and it is likely to be the succulent gall tissue which attracts them.

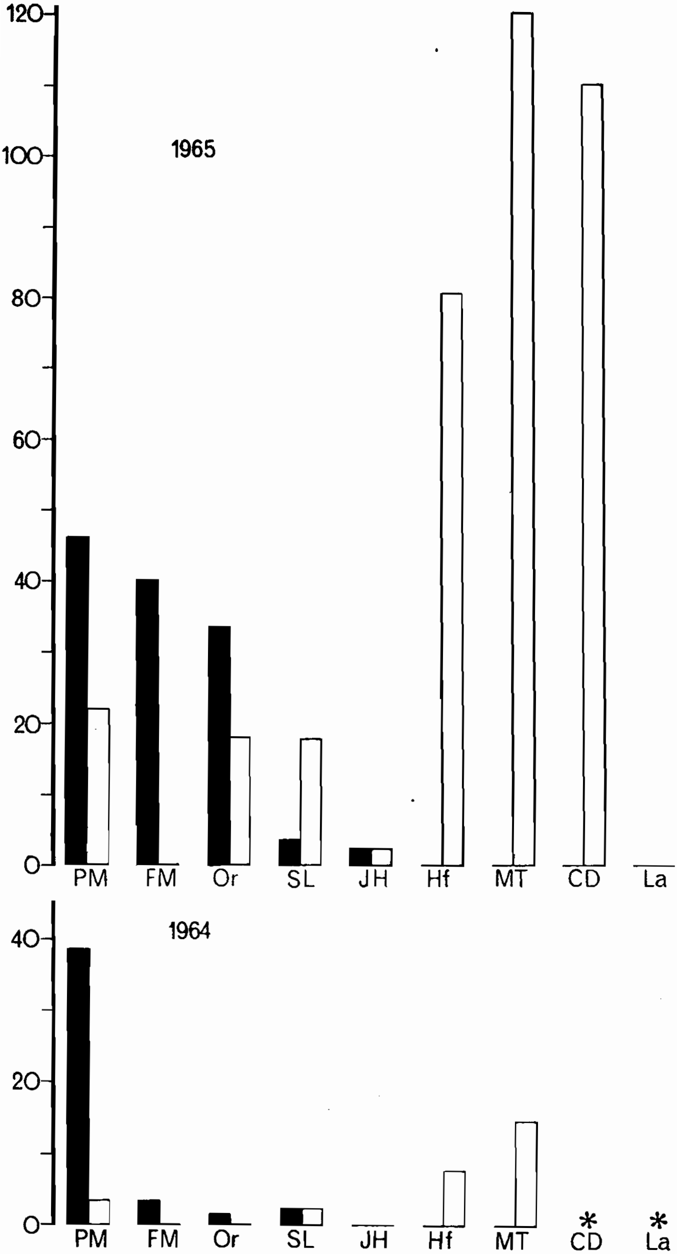



FIG. 35.
*Lonchaea* larvae in galled (■) and ungalled (⊓) heads (per cent).
* No sample collected.

The majority of caterpillar damage in the heads was probably caused by *E. ?cana*. *M. ?neuropterella* was identified from the larva only and was rare; it pupates in the thistle-head (Varley, personal communication), unlike *E. ?cana* which pupates in soil, and no lepidopterous pupae were found in the heads during the survey period.

*Lonchaea* sp.

This genus has not been recorded before as inhabiting the flower-heads of spear-thistles (K. G. V. Smith, personal communication), but has been found under tree bark. A species of a related genus, *Priscoearomyia nigra* Meigen, has been reared from stems of *Cirsium vulgare*.

*Lonchaea* is predaceous on other larvae in the thistle-heads. At sites where galls were common (Fig. 35), *U. stylata* may have formed the bulk of its food supply. However, the highest numbers of larvae came from sites at which galls were not found (Coombs Dale, Malham Tarn and Hampsfell). Here they may have been feeding on moth caterpillars; Fig. 36 shows a positive correlation between *Lonchaea* and caterpillar frass for most of the sites. There must also be other food sources because at several sites larvae were found in heads containing neither galls nor caterpillars.

*Tingis cardui* L.

According to Southwood and Scudder (1956), in Britain *T. cardui* occurs almost entirely on *Cirsium vulgare*, although it has been found occasionally on the marsh thistle, *Cirsium palustre* (L.) Scop., the musk thistle, *Carduus nutans* L., and *Carduus acanthoides* L. It is not found on *Cirsium arvense* although this plant grows in abundance in the same areas as *C. vulgare*. Even where leaves and buds of the two species are touching, there appears to be no migration of *T. cardui* from one to the other.

Southwood and Scudder (1956) suggested that the life-history of *T. cardui* may be bivoltine, and they found last instar nymphs in late July and late August. During the present study, evidence of only one generation was found at all collecting sites (Fig. 31). The irregularities in the graph reflect the small number and size of samples rather than any real variation in numbers.

Where the adults spend the winter is not known. They may overwinter in leaf litter or soil beneath the pasture or waste ground in which the thistles normally grow. Southwood and Scudder (1956) record leaf litter and moss as the overwintering site of *Tingis ampliata* Herrich-Schaeffer, which feeds on *Cirsium arvense*. Unlike *C. arvense* which is perennial, *C. vulgare* is a biennial plant, so that overwintered adults must find new plants on which to feed. They seem more inclined to fly during May and late September which would coincide, firstly, with dispersal to thistle rosettes after hibernation, and secondly, with death of the thistle plants and subsequent dispersal to the site of hibernation.

## *Geographical variation*

For all species, numbers collected in each year varied and in many cases the difference between years was greater than the difference between sites. The samples collected during 1965 were much smaller than in 1964 so that less

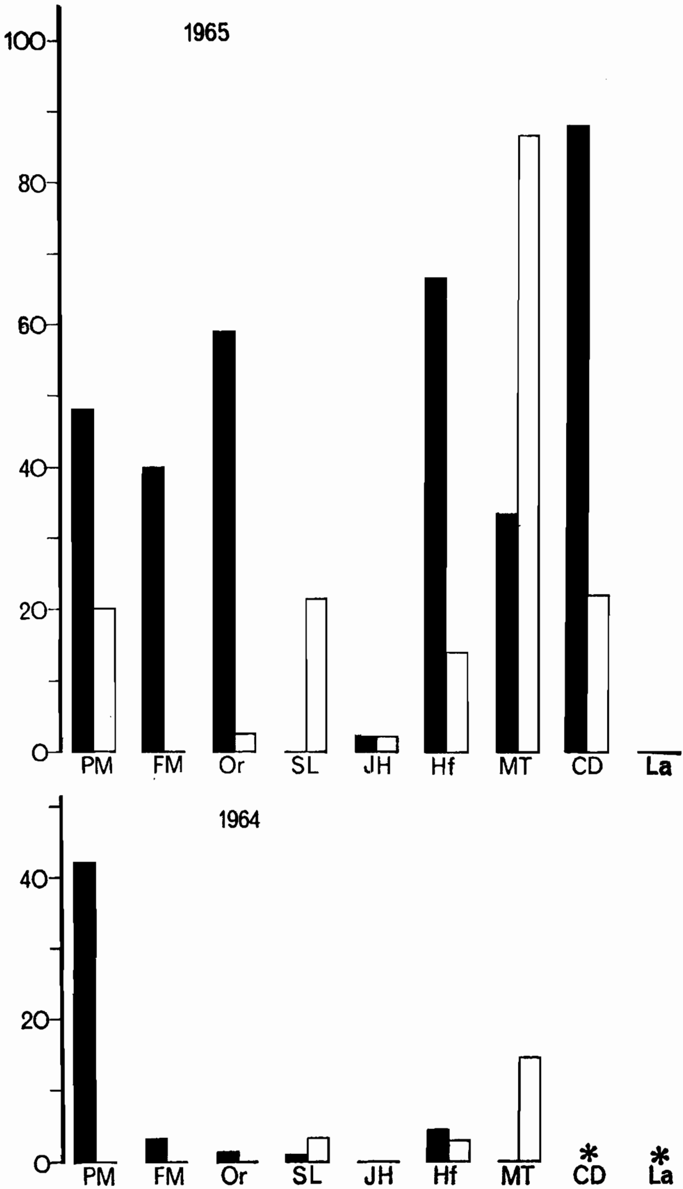



Fig. 36.
*Lonchaea* larvae in heads with (■) and without (□) caterpillar frass (per cent).
* No sample collected.

emphasis should be placed on the records of this year, which sometimes appear to contradict the pattern produced by the 1964 samples. Analyses of variance were calculated for each species for 1964 to check whether the apparent geographical variation was a real one. The results of these tests for *Urophora stylata*, *Terellia serratulae* and the moth caterpillars are significant at the 1 per cent or 0·1 per cent level, which means that geographical variation is different from the variation due to local patchiness and sampling error.

Altitude probably limits the distribution of *U. stylata*. No galls were found at Coombs Dale, 550 feet, or on the Stiperstones, 1,600 feet, near Preston Montford, although both these areas are within the zone in which galls occur. Further north, no galls were found at Lancaster, 200 feet, which is a height at which galls did occur further south. Altitude cannot therefore be the only limiting factor.

The percentage of adult flies which emerged successfully and the causes of death of those which did not are shown comparatively in Fig. 37 for the three sites at which galls were common. The numbers of healthy flies reduced from east to west in 1964 (P=<1 per cent). The mortality factors were the same at all sites but their relative importance varied. Parasite and predator attack were the chief causes of death. Parasite attack was similar at the three sites in 1964 (Flatford Mill 16 per cent, Preston Montford 15 per cent, and Orielton 14·5 per cent), although endoparasites were less common in the east. At all sites, predation by moth caterpillars is the largest single mortality factor and increases from east to west. The other mortality factors are small and do not apparently vary geographically.

*Terellia serratulae* is distributed over the southern half of the country but is nowhere very common. Preston Montford is apparently near the northern limit of its range. *U. stylata* and *T. serratulae* may compete for the same thistle-head and *T. serratulae* may increase in numbers where there are fewer galls. Two examples were found of both trypetids living in the same head. In both instances, only one *T. serratulae* larvae was found and the galls were small, so leaving enough undamaged receptacle tissue for *T. serratulae* to feed on. Climate is probably a more important limiting factor than competition with *U. stylata*, since none were found in the north, in the absence of galls.

The density of moth caterpillars in general increased northwards, although in Lancashire and Yorkshire and further north the density decreased, as with the distribution of *U. stylata*. This pattern supports the idea that there is a positive correlation between these caterpillars and galling. Because the distribution of caterpillars is based on records of their frass, damage caused by the two species could not be separated.

The distribution data for *Tingis cardui* (Table 10) show a distinct pattern in 1964 but this cannot be supported statistically (P=> 5 per cent). The numbers fluctuated widely at each site partly because the local distribution of this species is extremely patchy. The bugs tend to cluster together so that on a single plant, the heads on one side may be heavily infested, while those in the other are unaffected. On a single flower-head, the bugs are usually found on one side only. As the spear thistle is a large plant both horizontally and vertically, there must be a difference in microclimate between north- and south-facing sides of a plant and of a single flower-head. Unfortunately, no microclimatic data were

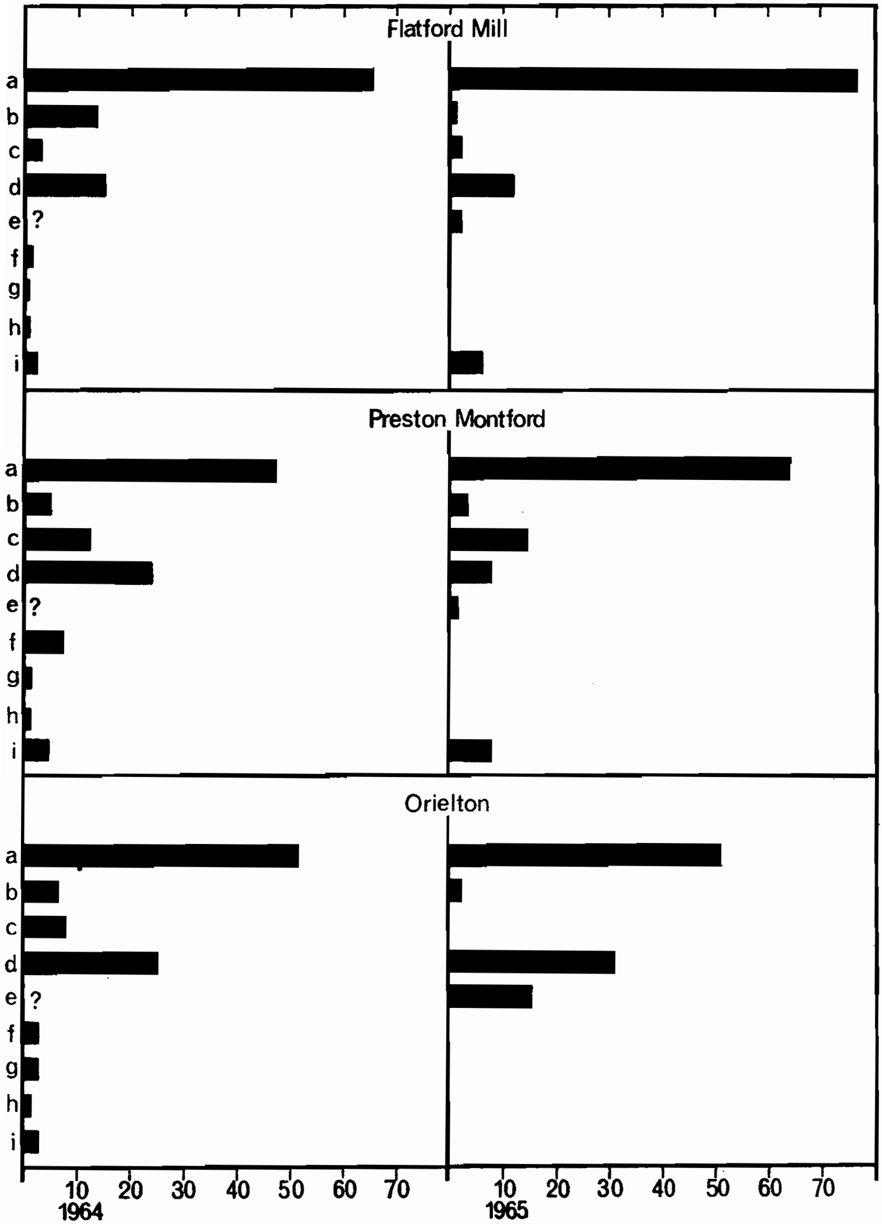



FIG. 37.

*Urophora stylata*: emergence and mortality factors.
(a) *U. stylata* (b) ectoparasites (c) *Eurytoma tibialis* (d) caterpillars (e) *Lonchaea* (f) fungus (g) bacteria (h) during adult emergence (i) unknown.

collected, but from casual observation there was no apparent correlation between aspect and density of lace-bugs. The bugs are limited to the flower-heads after hatching and they move very little when they have found a suitable feeding site. The extreme patchiness is probably partly due to this fact; the progeny of a single female will tend to remain together.

Although the apparent differences in distribution of *T. cardui* cannot be supported statistically, they may indicate a real trend. The highest densities were recorded from the west and the lowest from the east and south. None were found at Lancaster and Coombs Dale, but these samples were collected in November after the lace-bugs had left the plants. Why none were found at Malham Tarn is more difficult to explain, but the altitude (1,375 feet) and comparative ecological isolation may account for this.

## IV. SUMMARY

1. Collections of flower-heads of the spear thistle, *Cirsium vulgare* (L.) Scop., were made from nine sites in England and Wales during 1964 and 1965.

2. Larvae of the trypetid *Urophora stylata* (Fabricus) caused the formation of a woody gall in the thistle-head, which provided microhabitats for several other insect species. Its life-history was investigated.

3. Three chalcid wasps parasitized *U. stylata* larvae: *Habrocytus elevatus* (Walker), *Torymus cyanimus* Boheman, and *Eurytoma tibialis* Boheman. Their life-histories were studied.

4. Caterpillars of the moths *Eucosma ?cana* (Haworth) and *Metzneria ?neuropterella* (Zeller) fed on the florets and receptacle of the thistle-heads and were probably abundant in galled heads, feeding on the succulent gall tissue.

5. The carnivorous larvae of *Lonchaea* sp. probably fed mainly on larvae of *U. stylata* and moths where these were common.

6. The percentage of flies of *U. stylata* which emerged and the causes of death of those failing to do so was investigated at three sites.

7. The life-history of a second trypetid, *Terellia serratulae* L. was studied; the larvae constructed cocoons of silk and floret hairs and fed on receptacle tissue, usually in ungalled heads.

8. *T. serratulae* was parasitized by species of *Habrocytus* and eaten by *Lonchaea* sp.

9. The life-history of *Tingis cardui* L., living on the outside of the thistle-head, was studied.

## V. ACKNOWLEDGEMENTS

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## B. *Notes on other animals associated with the spear thistle*

Inside heads:

*Collembola*

Several species (not identified) often numerous especially in dead heads. Probably detrital feeders.

## VI. APPENDIX

### A. Tingis cardui: *Number and percentage of adults and nymphs per thistle-head*

(a) *Preston Montford 1964*

| 1964 | | Adults No. | Adults % | Larvae I-III No. | Larvae I-III % | Larvae IV-V No. | Larvae IV-V % |
|---|---|---|---|---|---|---|---|
| May | 13 | + | 100.0 | 0 | | 0 | |
| | 17 | + | 100.0 | 0 | | 0 | |
| | 24 | + | 100.0 | 0 | | 0 | |
| | 31 | + | 100.0 | 0 | | 0 | |
| June | 3 | + | 100.0 | 0 | | 0 | |
| | 14 | + | 100.0 | 0 | | 0 | |
| | 20 | + | 100.0 | 0 | | 0 | |
| July | 3 | 0 | | 0 | | 0 | |
| | | | | | Larvae I-V No. | Larvae I-V % | |
| | 8 | 1 | 1.8 | | 53 | 98.1 | |
| | 10 | 1 | 3.8 | | 25 | 96.1 | |
| | 14 | 0 | | | + | 100.0 | |
| | 24 | + | ? | | ++ | ? | |
| | 30 | 25 | 20.8 | | 95 | 76.2 | |
| | | | | | % | No. | |
| August | 11 | 46 | 27.9 | 13 | 7.9 | 106 | 64.2 |
| | 13 | 27 | 35.1 | 0 | | 50 | 64.9 |
| | 15 | 40 | 51.3 | 0 | | 38 | 48.7 |
| | 25 | 10 | 62.5 | 0 | | 6 | 37.5 |
| | 28 | 4 | 100.0 | 0 | | 0 | |
| | 31 | 19 | 48.7 | 0 | | 20 | 51.3 |
| September | 20 | 0 | | 0 | | 0 | |
| | 30 | 2 | 100.0 | 0 | | 0 | |
| October | 10 | 0 | | 0 | | 0 | |
| | 20 | 1 | 100.0 | 0 | | 0 | |

(b) *Preston Montford 1965*

| 1965 | | Adults No. | Adults % | Larvae I-III No. | Larvae I-III % | Larvae IV-V No. | Larvae IV-V % |
|---|---|---|---|---|---|---|---|
| May | 3 | + | 100.0 | 0 | | 0 | |
| | 10 | 36 | 100.0 | 0 | | 0 | |
| June | 2 | 39 | 100.0 | 0 | | 0 | |
| | 10 | + | 100.0 | 0 | | 0 | |
| | 12 | 51 | 100.0 | 0 | | 0 | |
| | 23 | 2 | 100.0 | 0 | | 0 | |
| | 24 | 6 | 100.0 | 0 | | 0 | |
| July | 7 | ++ | ? | + | ? | 0 | |
| | 16 | + | ? | + | ? | + | ? |
| | 19 | 3 | 4.0 | 46 | 62.2 | 25 | 33.8 |
| | 26 | 0 | | 53 | 67.9 | 25 | 32.1 |
| August | 10 | + | ? | + | ? | ++ | ? |
| | 11 | 1 | 10.0 | 1 | 10.0 | 8 | 80.0 |
| September | 6 | 24 | 70.6 | 1 | 2.9 | 9 | 26.5 |
| October | 12 | 9 | 50.0 | 0 | | 9 | 50.0 |
| | 25 | 2 | 100.0 | 0 | | 0 | |

+, ++=few, many, present but not counted.

*Lachesilla pedicularia* (L.) Psocoptera: Caeciliidae
(det. D. E. Kimmins) Common in dead heads covered in moulds; feeds on *Pleurococcus*, fungi and organic detritus. Nymphs and adults most numerous during July and August.

*Thysanoptera*
(det. T. Lewis) Species identified: *Limothrips denticornis* Haliday, *L. cerealium* Haliday, *Taeniothrips* sp., *Thrips* sp. Adult and immature stages present. *Limothrips* spp. feed on grasses, other genera may feed on floral parts of thistle.

*Corticarina gibbosa* Herbst Coleoptera: Lathridiidae
(det. M. E. Bacchus) Adult beetle found on or between corollas of florets when in full bloom. Said to feed on minute moulds being common in plant debris.

*Dasyneura* spp. Diptera: Cecidomyidae
(det. T. Lewis) Larvae very common in thistle-heads between bracts, in floret hairs or inside corolla tubes; probably feed on soft floral tissues. Some species pupate in flimsy cocoons attached to floret hairs; most leave head before pupating.

*Bracon* sp. Hymenoptera: Braconidae
(det. A. F. Amsden) Larva probably a parasite of moth larvae in thistle-heads. Pupates in papery cocoon in confined space, e.g. gall cell, space between bracts.

*Misocyclops* sp. Hymenoptera: Proctotrupoidea: Platygerterinae
(det. T. Lewis) Possible parasite of *Dasyneura* larvae. Adults found April to August.

*Acari*
Not identified. Very common especially in dead heads.

Outside heads:

*Aphididae* Homoptera
(det. V. F. Eastop) Species identified: *Aphis* spp. of *fabae* group, *Brachycaudus cardui* L., *B. helichrysi* Kaltenbach. Youngest instars often inside head between bracts; older stages form colonies on outer bracts and stem just beneath head.

*Anthocoridae* Heteroptera
(det. G. M. Black) Nymphs and adults of several species seen; plant feeders or predators.

*Depressaria arenella* Schiffermueller Lepidoptera: Oecophoridae
(det. J. Bradley) Larva common feeding on undersurface of leaves; darts rapidly into silken tent when disturbed. During summer and autumn unusual to find a leaf undamaged. Pupates in cocoon of silk and debris on ground in August and September. Emerges in September and adult hibernates in thatch, etc. (Varley, personal communication.)

*Spilographa zoë* Meigen Diptera: Trypetidae
(det. K. G. V. Smith) Larva uncommon, forms small linear mines on leaves.

*Syrphidae* Diptera
Abundant in summer visiting flowers.

*Bombidae* Hymenoptera
Several species in summer visiting flowers.

*Apis mellifera* L. Hymenoptera: Apidae
Abundant in summer visiting flowers.

*Myrmica rubra* L. Hymenoptera: Formicidae
(det. I. H. H. Yarrow) Workers often found attending aphid colonies. Species common on thistles and umbelliferous plants.

*Angitia rufipes* Gravenhorst Hymenoptera: Ichneumonidae
(det. J. F. Perkins) Probably parasite of moth larvae. Adult seen during summer running rapidly over flowers, occasionally jabbing into head with ovipositor.

## C. *Key to animals associated with spear thistles*

(a) *Adults*

| | | | |
|---|---|---|---|
| 1. | With 4 pairs jointed legs | ARACHNIDA | 2 |
| | With 3 pairs jointed legs | INSECTA | 3 |

| | | | | |
|---|---|---|---|---|
| 2. | $<2$ mm. in body length, head not separated from body | | ACARI (mites) | |
| | $>2$ mm. in body length, head separated from body by waist | | ARANEAE (spiders) | |
| 3. | Without wings | | | 4 |
| | With wings | | | 5 |
| 4. | Thorax not separated from abdomen by waist, with springing organ (Fig. 38a), jumps actively | | COLLEMBOLA | |
| | With waist, no springing organ | | ants e.g. **Myrmica rubra** | |
| 5. | 1 pair wings | DIPTERA | | 6 |
| | 2 pairs wings, first pair may be hardened | | | 8 |
| 6. | Body mimicking bee or wasp, wings colourless, hovers in flight | | SYRPHIDAE | |
| | Body not bee- or wasp-like, wings colourless or banded, ♀ with stout ovipositor | TRYPETIDAE | | 7 |
| 7. | Body mainly black, wings banded (Fig. 6) | | **Urophora stylata** | |
| | Body yellow-grey with black markings, wings colourless (Fig. 10) | | **Terellia serratulae** | |
| 8. | Forewings not hardened to protect hindwings | | | 9 |
| | Forewings hardened and covering hindwings | | | 18 |
| 9. | Fore- and hindwings of similar size, narrow with long fringing hairs (Fig. 38b) | | THYSANOPTERA | |
| | Hindwings smaller than forewings | | | 10 |
| 10. | No waist between thorax and abdomen, no linking mechanism between fore- and hindwings | | | 11 |
| | Waist between thorax and abdomen, fore- and hindwings linked by hooklets (Fig. 38c) | HYMENOPTERA | | 12 |
| 11. | Antennae shorter than body, cornicles on abdomen (Fig. 38d) | | APHIDIDAE | |
| | Antennae as long as body, no cornicles, wings held as roof over abdomen | | PSOCOPTERA e.g. **Lachesilla pedicularia** | |
| 12. | Wing venation characteristically reduced (Fig. 38c) | CHALCIDOIDEA | | 13 |
| | Wing venation not as in Fig. 38c | | | 15 |
| 13. | Body black, no metallic sheen (Fig. 9) | | **Eurytoma tibialis** | |
| | Body black with green metallic sheen | | | 14 |
| 14. | Usually body length $<4$ mm., with ovipositor in addition $>1.5$ mm. held posterior to abdomen (Fig. 8) | | **Torymus cyanimus** | |
| | Usually body length $>4$ mm., ovipositor held along ventral surface of abdomen when at rest (Fig. 7) | | **Habrocytus** spp. | |

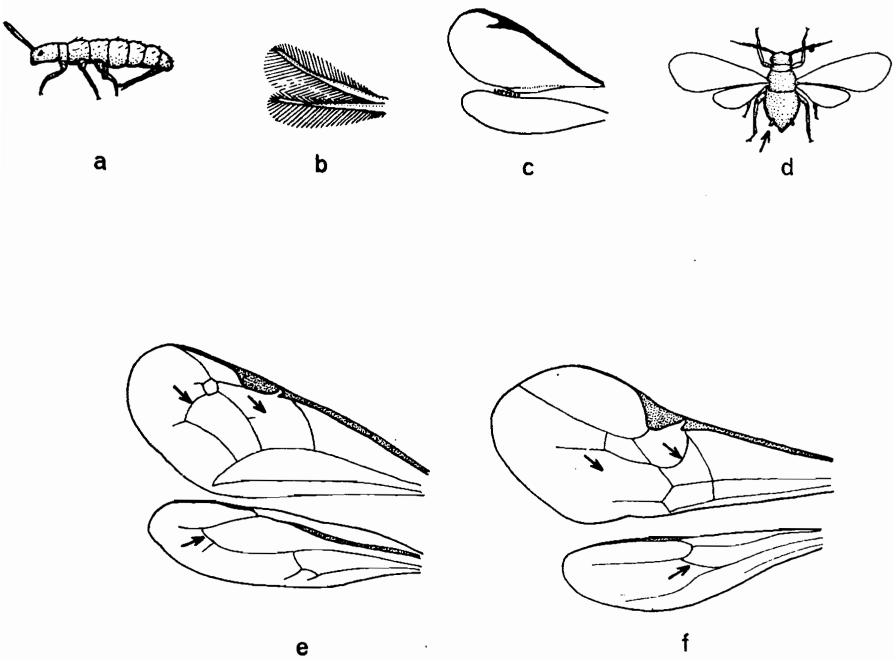


FIG. 38.
For explanation, see Key to Adults.
(*a*) and (*d*) after Lewis and Taylor (1967); (*b*), (*e*) and (*f*) after Imms (1960).

| | | | |
|---|---|---|---|
| 15. Body slender, not hairy, ovipositor distinct, not modified into sting | ICHNEUMONOIDEA | | 16 |
| Body robust, ± hairy, ovipositor modified into sting, pollen-baskets on hind legs | APIDAE | | 17 |
| 16. Forewing with 2m–cu vein, usually lacking first sector of M+Rs, r–m of hindwing distal (Fig. 38e) | | ICHNEUMONIDAE e.g. **Angitia rufipes** | |
| Forewing without 2m–cu vein, usually with first sector of M+Rs, r–m of hindwing proximal (Fig. 38f) | | BRACONIDAE e.g. **Bracon** sp. | |
| 17. Body thickly hairy | | **Bombus** spp. | |
| Body sparsely hairy | | **Apis mellifera** | |
| 18. Forewings completely sclerotized to form elytra, no proboscis, <3 mm. long, black | COLEOPTERA: | **Corticarina gibbosa** | |
| Distal part of forewings membraneous, mouthparts form a proboscis (Fig. 39b) | HETEROPTERA | | 19 |

| | | | | |
|---|---|---|---|---|
| 19. | Body and hemelytra with reticulate pattern (Fig. 29) | | **Tingis cardui** | |
| | No reticulate pattern | | other HETEROPTERA e.g. ANTHOCORIDAE | |

(b) *Immature stages*

| | | | | |
|---|---|---|---|---|
| 1. | Without jointed thoracic legs, no distinct head | | | 2 |
| | With jointed legs and distinct head; if a pupa also with wing pads | | | 8 |
| 2. | Larva barrel-shaped, with dark-brown posterior spiracular plate | TRYPETIDAE | | 3 |
| | Larva not barrel-shaped, posterior spiracles if conspicuous not on a sclerotized plate | | | 4 |
| 3. | In gall cell; no creeping welts (Fig. 15) | | **Urophora stylata** | |
| | In cocoon of silk and floret hairs; with creeping welts (Fig. 19) | | **Terrellia serratulae** | |
| 4. | Crescent-shaped (tapering towards both ends), parasitic with remains of host larva | CHALCIDOIDEA | | 5 |
| | ± cylindrical, predators or scavengers | | | 7 |
| 5. | Inside puparium of host in gall-cell (Fig. 18) | | **Eurytoma tibialis** | |
| | Not inside puparium | | | 6 |
| 6. | Strongly hairy, in gall cell (Fig. 17) | | **Torymus cyanimus** | |
| | Not hairy, in gall cell or *Terellia* cocoon (Fig. 16) | | **Habrocytus** spp. | |
| 7. | Dirty-white, tapering towards anterior end, with creeping welts (Fig. 28) | | **Lonchaea** sp. | |
| | Pink or yellow, ± parallel-sided, no creeping welts, usually with sternal spatula (Fig. 39a) | | CECIDOMYIDAE e.g. **Dasyneura** spp. | |
| 8. | Larva a caterpillar, body soft with sclerotized head and pronotum (Fig. 27), no wing pads | LEPIDOPTERA | | 9 |
| | Nymphs and pupae not caterpillar-like, with wing pads or if without body not softer than head | | | 10 |
| 9. | Inside thistle-head, not violently active | | **Eucosma cana** | |
| | In a silk tent on undersurface of leaves, violently active | | **Depressaria arenella** | |
| 10. | Pupae, inactive, usually protected in case or gall cell | | | 11 |
| | Nymphs, active, not in a case | | | 16 |
| 11. | In puparium or cocoon, may also be in gall cell | | | 12 |
| | Not in puparium or cocoon, in gall cell | | | 15 |
| 12. | In papery cocoon, usually 2 or 3 attached | | BRACONIDAE | |
| | In puparium, always single | | | 13 |
| 13. | Pupa not completely filling puparium, also with frass in puparium (Fig. 24) | | **Eurytoma tibialis** | |
| | Pupa completely filling puparium, faeces as blob on outside of puparium at anal aperture (Figs. 20, 21) | TRYPETIDAE | | 14 |

| | | |
|---|---|---|
| 14. | In gall cell | **Urophora stylata** |
| | In cocoon of silk and floret hairs | **Terellia serratulae** |
| 15. | Tip of hindwing protruding beneath forewing, ovipositor curved along dorsal surface of abdomen (Fig. 23) | **Torymus cyanimus** |
| | Hindwing not visible, ♀ not distinguishable from ♂ (Fig. 22) | **Habrocytus** spp. |
| 16. | Mouthparts biting, not modified into proboscis | 17 |
| | Mouthparts piercing, modified into proboscis (Fig. 39b) | 18 |
| 17. | Antennae almost as long as body | PSOCOPTERA e.g. **Lachesilla pedicularia** |
| | Antennae no longer than head and thorax | THYSANOPTERA |
| 18. | With cornicles on abdomen (Fig. 39c) | APHIDIDAE |
| | No cornicles on abdomen | 19 |

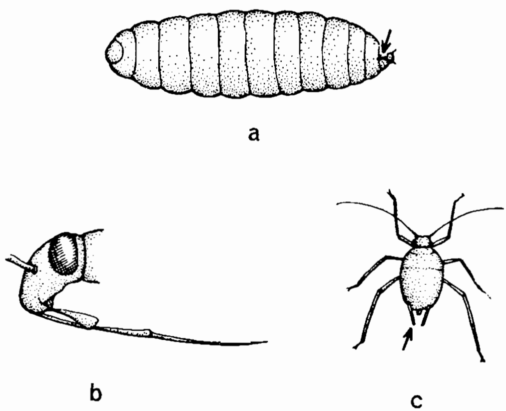


FIG. 39.
For explanation, see Key to Immature stages.
(*b*) and (*c*) after Lewis and Taylor (1967).

| | | |
|---|---|---|
| 19. | Olive-brown, in colonies on outer bracts of thistle-head | **Tingis cardui** |
| | Variously coloured, usually solitary | other HETEROPTERA |

3– 9 larvae
12–15 pupae
17–19 nymphs