WING MECHANICS AND TAKE-OFF PREPARATION
OF *THRIPS* (THYSANOPTERA)

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SUMMARY

1. All of the wing fringe cilia of *Thrips physapus*, except those along the hindwing leading edge, pivot in elongated sockets which lock them into two positions.

2. The wings lie parallel over the abdomen when not in use, with the cilia locked in the *closed* position at an angle of 15–20° to the wing axis. The closing of the fringes prevents entanglement of the trailing edge cilia and lateral projection of the forewing leading edge cilia.

3. During flight the cilia are locked in the *open* position, doubling the wing area. The locking force is stronger than the combined aerodynamic and inertial forces on the cilia.

4. The fringes are opened by abdominal combing and closed by tibial combing.

5. The same morphological features are found in other members of the sub-order Terebrantia. Parallel wings at rest are characteristic of this sub-order, and the collapsible fringe system is viewed as an effective method for parking the wings.

6. The fringes of the sub-order Tubulifera are not collapsible. The wings overlap on the abdomen at rest and a similar parking problem does not arise.

INTRODUCTION

Flight of the dandelion thrips *Thrips physapus* L. has been studied by high-speed 16 mm cinematography of take-offs from a small support (Ellington, Runnalls & Machin, 1979). These thrips assume a posture with the wings *clapped* together dorsally (Weis-Fogh, 1973) just before take-off. Long hairs, which are conventionally known as cilia, form a fringe around the wings that can be seen during this period on some films. The fringe cilia appear to be at a much greater angle to the longitudinal wing axis in this posture than when the wings are in the rest position over the abdomen. A range of angles between the cilia and wing axes was also noted for mounted specimens: characteristic maximum and minimum values of this angle were found. The cilia were straight at all angles, indicating a pivot point at their insertion into the wing.

These observations suggest the existence of *open* and *closed* positions for the fringe cilia. The wings lie parallel along the dorsal abdominal surface when not in use, and a closed fringe may prevent entanglement of the long cilia. In the open

position the effective wing area would be increased for flight. The mechanisms and implications of a movable fringe are investigated in this paper.

<div align="center">MATERIALS AND METHODS</div>

Thrips were collected locally from dandelions, *Taraxacum*, and identified as *Thrips physapus* L. according to Mound *et al.* (1976). Females comprised 95% of the samples (*n* = 37), and all morphological details refer to them. The identification is somewhat uncertain; Pitkin (1976) demonstrated a considerable overlap of values of the first principle component distinguishing *T. physapus* from the very similar species *T. hukkineni* Priesner.

Upon return to the laboratory the insects were placed inside a small perspex flight chamber 3·3 cm in diameter and 4·5 cm high. A pin, or a fine glass tube, projected upwards about 1 cm from the centre of the chamber base. A lamp was used to heat the chamber until the thrips became active. They would climb up the pin towards a fibre optic light source and usually take off from the pin head.

Take-off preparation was observed and photographed through two small glass windows. A Nikon F camera with motorized film drive photographed the behaviour at four frames per second. Transmitted flash illumination was provided by a Dawe Strobotorch Type 1202C with a Point Source Lamp Unit fitted with a condenser system.

Most specimens were then mounted for light microscopy following the methods of Mound & Pitkin (1972). Scanning electron micrographs (SEMs) were taken of the remaining ones on a Cambridge S4 scanning electron microscope. Preparations for SEM involved dehydration in an ethanol series, critical point drying in CO_2 and sputter coating with gold/palladium.

The fringe cilia were manually manipulated under a stereomicroscope to investigate the range and properties of their movement. On separate occasions two hindwings and one forewing were cut from CO_2 anaesthetized specimens and glued at their base to a fine needle using a gum tragacanth solution. The needle was rigidly mounted, and individual cilia were moved with the tip of a glass microelectrode held in a micromanipulator.

<div align="center">RESULTS</div>

Morphology

The position of the wings and fringe cilia at rest is shown in Fig. 1 (*a*). The wings are nearly parallel over the abdomen normally; the right wings are somewhat extended in this specimen. The hindwings lie under the forewings and are not visible. The cilia along the trailing edges are mostly in the closed position and thus confined to their side of the body. With both pairs of wings in the normal position overlap and entanglement of these cilia would be minimal.

Fig. 2 (*a*) is a composite diagram drawn from several mounted specimens with the wings extended. The fringe is closed on the right-hand side, and maximally open on the left-hand side. The mean length of the membranous forewings is 0·85 mm, and of the hindwings 0·79 mm. The forewings and hindwings are coupled by a hooked
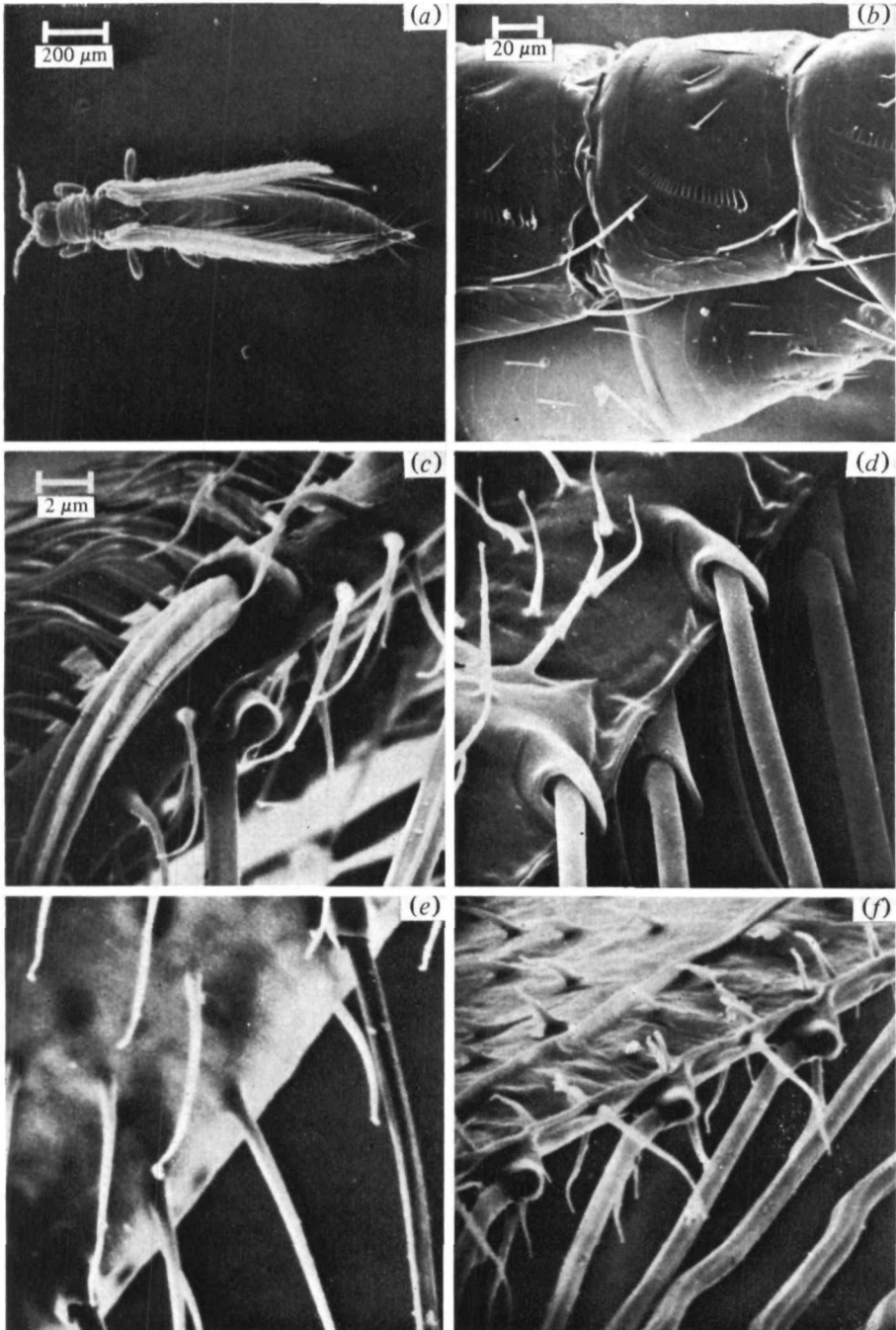
Fig. 1. SEMs of *T. physapus*. (*a*) Dorsal view. (*b*) Lateral view of VIIth abdominal segment showing combs and setae. (*c*) Edge-on view of forewing leading edge. A large costal seta is above the centre. The socket of a leading edge cilium is visible on the lower wing edge; cilium is in the closed position. (*d*)–(*f*) Scale is the same as (*c*). (*d*) Sockets along the forewing trailing edge viewed from the lower surface, showing the double row of cilia. (*e*) View of the lower surface of hindwing leading edge. Two cilia are visible near either border; they insert rigidly into sockets. (*f*) Hindwing trailing edge cilia and sockets viewed from slightly above the wing plane. Cilia are in the closed position.

(a) *Thrips physapus*
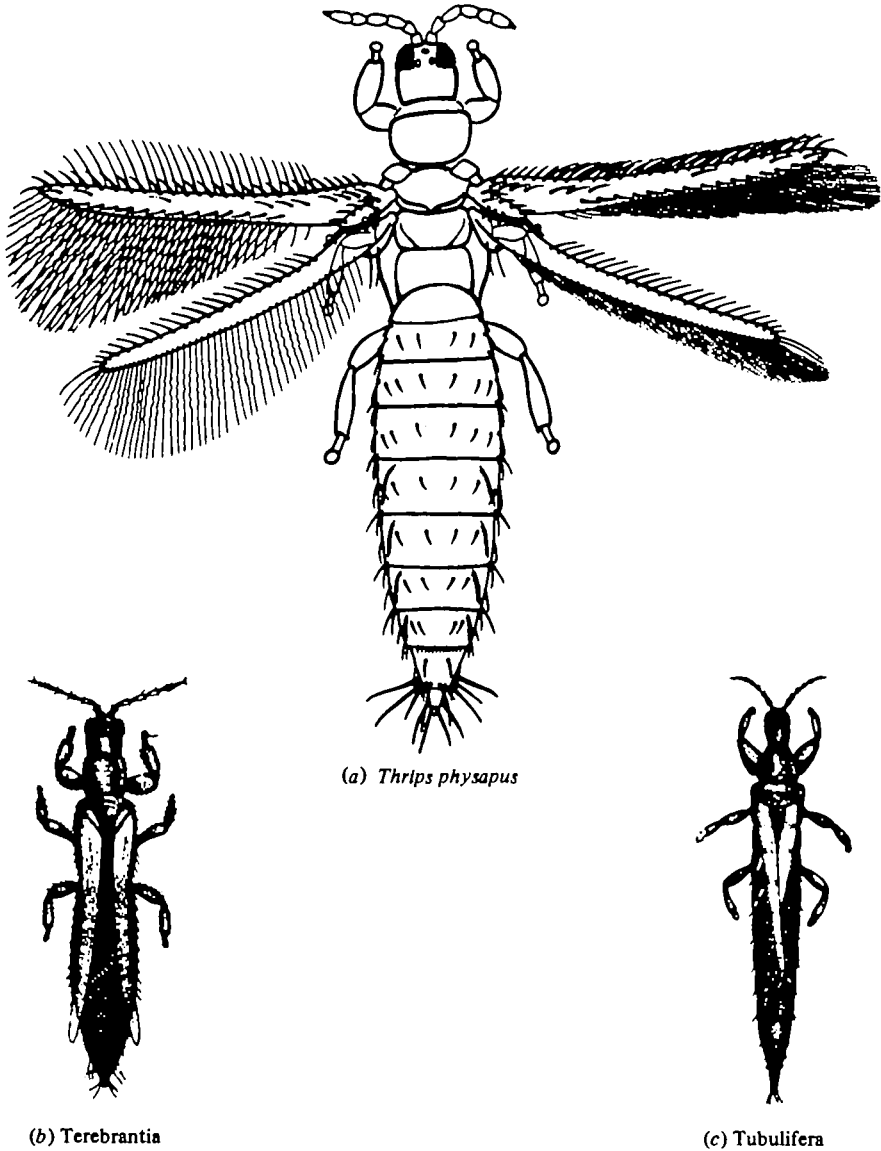
(b) Terebrantia

(c) Tubulifera

Fig. 2. Composite drawing of *T. physapus* from whole mounts. Fringes are shown in open and closed positions. (b) and (c) Typical wing positions at rest for the two Thysanopteran suborders (after Lewis, 1973). The wings lie parallel over the abdomen in the Terebrantia (b), but overlap in the Tubulifera (c).

seta of the hindwing which passes around two long setae from the posterior basal region of the forewing. A ridge along the posterior lower edge of this region is also hooked by three setae originating on the hindwing. The angle between the longitudinal axes of the forewing and hindwing is about 30° when they are coupled.

The large veinal setae of the forewings are characteristic of the genus; in *T. physapus* they are about 70 μm long and 2 μm in diameter at their bases. They are restricted to the upper wing surface forming rows with 20 μm spacing along the costa and

second vein, and an interrupted row along the first vein. The setae project some 40 μm above the wing surface on the first and second veins, and about half this distance on the costa. They are longitudinally ridged and insert into sockets which permit but little movement (Fig. 1c).

The upper and lower surfaces of all wings are covered with microtrichia arranged in longitudinal rows (Fig. 1c–f). About 5 μm above the surface the microtrichia bend sharply in a direction which is usually distal and marginal. Their total length is about 8 μm.

The fringe along the leading edge of the hindwings originates on the lower surface. It lies roughly in the plane of the wings but points slightly below it. The cilia are about 80 μm long and 1 μm in diameter at the base. They are spaced about 20 μm apart, and form an angle of some 45° to the leading edge tangent. The cilia insert into sockets which do not allow significant movement (Fig. 1e).

A row of cilia is found along the lower surface of the forewing leading edge. The position of these cilia vary between different mounted specimens; the two extreme positions commonly found are shown in Fig. 2 (a). In the open position the cilia extend about 100 μm in front of the leading edge at an angle of 70° to its tangent, pointing slightly below the plane of the wing. They pivot distally and downwards into the closed position, where they do not extend beyond the costal setae when viewed from above. The cilia are longitudinally ridged, about 1 μm in diameter at the base and spaced every 18 μm. They insert into sockets with elongated openings which are constricted in the middle, resembling a partially opened 'figure-of-eight' (Fig. 1c). The shape of these sockets plus cuticular elasticity should lock the cilia into the two extreme positions.

The trailing edge cilia of all wings can be found in various positions on the mounts. Although often found in the extreme positions, they are observed at intermediate angles more frequently than the forewing leading edge cilia. This may indicate either a weaker locking mechanism or the absence of such a mechanism. Length of the cilia varies along the wings, but the base diameter is about 1 μm for all of them. They are spaced about 12 μm apart. The trailing edge cilia of the hindwings are longitudinally ridged, but those of the forewings appear smooth. The cilia are wavy over most of their length, which is characteristic of most of the sub-order Terebrantia.

There are two rows of cilia along the forewing trailing edge. One row extends along the upper surface of the edge; these cilia open to a maximum angle of 55° to the edge tangent. Another row extends along the lower surface and opens to an angle of 80°. All cilia lie approximately in the plane of the wing when open. In the closed position the cilia lie some 15–20° to the tangent and point somewhat below the wing plane. Fig. 1 (d) shows the double row of cilia inserting into sockets with elongated openings, viewed from the lower surface. A mechanical lock similar to the leading edge sockets is not obvious, but in some SEMs the sockets appear slightly constricted in the middle.

A single row of cilia is found along the lower surface of the hindwing trailing edge. These cilia open to about 75°, lying in the plane of the wing. They close to 15–20°, pointing slightly below the wing plane. Their sockets are pinched into a 'figure-of-eight' and may lock the cilia into the extreme positions.

Mechanical properties of the sockets

Manipulation of the movable cilia provides further evidence about the freedom of movement permitted by the sockets. Cilia at either extreme position were pushed beyond that extreme: they bend without further pivoting at the base. When pushed towards the other position they bend slightly at first without any movement at the base. This bending ceases after a small displacement, and the cilia then pivot without noticeable bending. The range of movement is thus mechanically limited by the sockets, which also provide a locking mechanism for the extreme positions. These results are expected from the morphology of the forewing leading edge and hindwing trailing edge sockets. The locking system found for the forewing trailing edge cilia was not clearly indicated by the SEMs, however.

When the cilia are in intermediate positions variable results are obtained. In some cases, especially for the forewing leading edge cilia, the position of the cilia is meta-stable. When placed at the mid-position the cilia stay there, but click to either extreme if slightly encouraged by the manipulator. For other cases the cilia remain in inter-mediate positions and only click into an extreme if very close to it. These results indicate that surface friction between cilia and sockets may be comparable to the force exerted on cilia by deformed sockets: if the surface friction were negligible all sockets with a 'figure-of-eight' locking mechanism would be metastable. The forewing leading edge sockets are deeply constricted which provides an elastic restoring force significantly greater than surface friction. Thus these cilia are rarely found in intermediate positions on slide preparations. The trailing edge sockets are much less constricted and provide a small restoring force comparable to surface friction. These cilia are frequently found in intermediate positions on slides.

In flight the aerodynamic and inertial forces on the cilia will tend to close the fringes during some portions of the wingbeat. This would have a profound and possibly deleterious effect on the aerodynamic characteristics. Isolated hindwings mounted on a pin were attached to the diaphragm of a loudspeaker and vibrated with the longitudinal wing axis perpendicular to the motion. The amplitude and frequency of vibration were the same as during flight (Ellington *et al.* 1979), and experiments included motion of the wings parallel and perpendicular to the wing plane. The wing was viewed under a stereomicroscope with stroboscopic illumination. The position of the movable trailing edge fringe does not alter under these conditions; the locking force of the sockets must be greater than the aerodynamic and inertial forces during flight. The cilia do not bend significantly either, and may be considered as rigid under flight conditions.

Combing

Observations and cine film records show that the fringe cilia are always in the open position before take-off. Dorsal flexion of the abdomen during flight preparation provides a combing action responsible for opening the fringes. I have always observed this abdominal combing behaviour prior to take-off in *T. physapus*: the number of combings is variable, from a single one to a dozen or more.

Fig. 3 shows abdominal combing in a series of 35 mm photographs of different

insects arranged in a sequence agreeing with cine film records; the duration of the sequence is about 0·3–0·4 s. Initially the wings are parallel over the abdomen at rest (*a*), and the abdomen then begins to flex dorsally. Setae along the abdomen catch the trailing edge fringes, clicking the cilia into the open position and pulling the wings dorsally (*b–f*). The sharp bending of the cilia (*d–f*) shows that the abdominal combing pulls them beyond the maximum angle permitted by the sockets. The hindwings slip antero-ventrally from underneath the forewings in (*d*), which opens the forewing leading edge fringe. The antero-dorsal view in (*g*) shows the abdomen fully flexed and the fringes combed into the open position. The abdomen then returns to the horizontal (*h–k*), and the open fringes are clearly seen in (*j*). The forewings are raised dorsally into the clapped position (*k–m*), and then the hindwings (*l, m*). The forewings are sometimes raised before the abdomen has completely returned to the horizontal, as in (*k*). Wing coupling must occur around (*m*), and the clapped wings ready for flight are shown in anterior view in (*n*). Finally the head, thorax and forelegs are raised above the substrate in the take-off posture (*o*).

Abdominal segments V–VIII seem responsible for combing the fringes, but the setae involved are not identified with certainty. Combs are laterally located on the tergites of these segments (Figs. 1*b*, 2*a*). Each hair is about 7 μm long and they are spaced every 3 μm along the combs. Three long setae are also found below the combs on tergites VI–VIII, and four are found on tergite V. These combs and setae are well-placed for engaging the fringes during abdominal flexion, although the comb size is small enough to question its effectiveness. The four setae located more dorsally on each segment may also function in combing.

The dorsal comb on tergite VIII and the long setae at the abdominal tip are normally too posterior to the fringes to assist in opening them (Fig. 1*a*). I have observed specimens damp with condensation attempt abdominal combing unsuccessfully: perhaps the surface tension forces are too great for the wings to separate. Under these conditions the abdomen sometimes bows ventro-laterally near its middle to bring the tip of the abdomen near the wing tips. The abdomen is then flexed dorsally and straightened laterally, and normal combing ensues. Thus the dorsal comb and tip hairs may function to lift and separate the wings from the body when condensation causes the wings to adhere to the abdomen.

I have observed the fringes collapsing into the closed position when the hind tibiae comb the wings after landing. Tibial wing combing is commonly observed for thrips (Lewis, 1973), and I have seen the forewings and hindwings combed separately. A thorough combing often occurs after landing in *T. physapus*, ending with the wings parallel over the abdomen and the fringes collapsed. Apart from a role in general wing grooming behaviour, tibial combing thus appears to be an antagonistic process to abdominal combing.

<div align="center">DISCUSSION</div>

An elaborate morphological and mechanical system has been described for the wing fringes of *T. physapus*. It will prove useful to summarise this system briefly before attempting to draw any general conclusions for the Thysanoptera. The forewing veinal setae and the hindwing leading edge cilia are not movable, but all
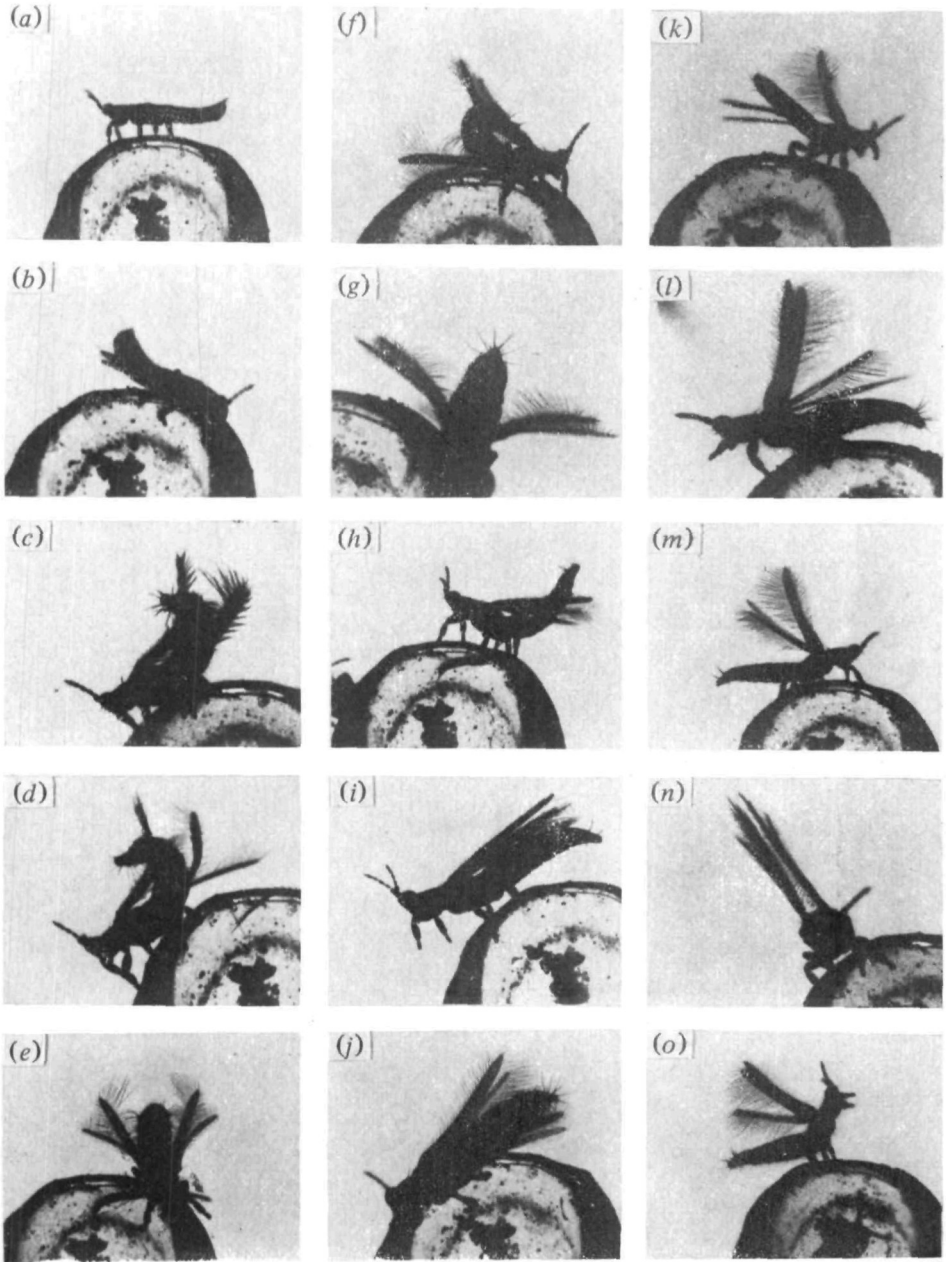
Fig. 3. A series of photographs showing abdominal combing during flight preparation, which opens the wing fringes. See text.

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other fringe cilia pivot at their bases. These cilia insert into sockets with elongated opening slits which lock the cilia into two extreme positions. The elastic locking mechanism is strong enough to prevent movement of the cilia during flight. When the wings are not in use they lie parallel over the abdomen with the fringes collapsed; in this closed position the trailing edge cilia do not entangle and the forewing leading edge cilia do not project laterally to a significant degree. During flight the fringes are open; the cilia are nearly perpendicular to the wing axis, which increases the total wing area by a factor of 2·1 (based on Fig. 2 *a*).

The fringes are opened by abdominal combing and closed by tibial combing. The waviness of the trailing edge cilia may increase the effectiveness of these operations by making the cilia more liable to catch in the combing setae. It is suggested that an open fringe is a prerequisite for flight, and that abdominal combing repeats until the fringe is in flight condition. Towards this end it would be very advantageous if the locking sockets were innervated to distinguish the two extreme positions.

Because the cilia do not alter position during flight, this collapsible fringe system seems to be an extravagant solution to a parking problem: the large wing area necessary for flight may prove cumbersome for an insect with noted preferences for tiny crevices (Lewis, 1973). *T. physapus* belongs to the sub-order Terebrantia, and Lewis (1973) notes that wavy cilia and parallel wings at rest characterize this sub-order (Fig. 2 *b*). Perhaps a collapsible fringe is also associated with these characteristics to provide an efficient parking mechanism.

The Tubulifera form the other sub-order of Thysanoptera, and Lewis (1973) points out that the cilia are straight and the wings overlap on the dorsal abdominal surface at rest (Fig. 2 *c*). With overlapping wings the cilia would not significantly entangle, so the fringes need not collapse. Kuethe (1975) presents SEMs of the fringe cilia of a mullein thrips *Haplothrips verbasci* Osborne, a member of the Tubulifera. Except for the few duplicated cilia on the distal posterior wing margin, the cilia insert directly and deeply between the two cuticular layers of the wings. There are no sockets for the cilia, and the fringes cannot be collapsible.

I have attempted to check whether a collapsible fringe is always found in the Terebrantia and absent in the Tubulifera. The elongated fringe sockets of *T. physapus* are visible under high magnification on a light microscope. I examined 42 specimens representing the three British families from the small Thysanoptera collection in the Insect Room, Museum of Zoology, Cambridge. The Phlaeothripidae are the only Tubuliferan family: all specimens had straight cilia deeply inserted like *H. verbasci*, and the fringes were not collapsible. For the Terebrantian families Aeolothripidae and Thripidae the main features of the fringe cilia and sockets were the same as *T. physapus*, except for the lack of forewing leading edge cilia in the Aeolothripidae. A variable angle for the trailing edge cilia was in general also found.

The results from this small sample support the hypothesis that collapsible fringes and elongated sockets are associated with the parallel wings at rest and wavy cilia of the Terebrantia. The overlapped wings of the Tubulifera would not require these morphological features to prevent entanglement and lateral projection of the cilia, and none are found. The insertions of the cilia into the wings are so different between the two sub-orders that it is indeed difficult to think of them as homologous: Mound

& O'Neill (1974) have already suggested that the distal wing membrane in the Phlaeothripidae is a secondary development from a micropterous condition, and not strictly homologous with the wings of the rest of the Thysanoptera.

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