

SHORT COMMUNICATION

HOW DOES A FLY CLING TO THE UNDER SURFACE OF A GLASS SHEET?

BY V. B. WIGGLESWORTH

Department of Zoology, The University, Downing Street, Cambridge CB2 3EJ, UK

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The climbing of flies on glass is a problem that still lacks an agreed solution. West (1862), who introduced the term 'tenent hairs' for the trumpet-like structures on the pulvilli, regarded these as suckers which ensured adhesion by atmospheric pressure. But it is generally agreed that they are too small for that. Dahl (1885), studying adhesive organs in insects in general, favoured adhesion by 'Capillarattraction' but he considered that other forms of cohesion and adhesion were operating as well. Rombouts (1884) opted for surface tension. In the most recent paper, Walker, Yule & Ratcliffe (1985) give a new description of the adhesive organs in the blowfly *Calliphora*, and conclude from calculations that surface tension of the lipid secretion under the tenent hairs provides an adequate adhesive force.

The pad of setae at the lower extremity of the tibia of the first two pairs of legs, which is present in the adult of the blood-sucking bug *Rhodnius* and is used in climbing on a smooth surface (Gillett, 1932), has a totally different structure from that of the adhesive organ of the fly. In making a combined investigation (Gillett & Wigglesworth, 1932) we believed at first that surface tension in the lipid secretion between the oblique endings of the hairs and the surface would prove to be the adhesive force. But after experiments on insects and models, helped by discussions with N. K. Adam, we decided that direct intermolecular attraction, generated when the lipid film breaks down during sliding (i.e. seizure or partial seizure), was probably the more important force.

The tibial organ is present only on the first two pairs of legs of the adult *Rhodnius*, but these large (2 cm) insects can climb a steeply sloping sheet of glass. When the glass is vertical they slip down very slowly. In the experiments of Edwards & Tarkanian (1970), some *Rhodnius* adults held on to glass at angles greater than vertical, up to a mean of 109°. Beyond that they fell off. These are characteristic properties of the frictional forces dependent on molecular attraction, which do not resist separation by forces acting in the axis normal to the surface unless the areas in contact are molecularly smooth (Bowden, 1957). Edwards & Tarkanian (1970), in repeating the experiments on *Rhodnius*, accepted our interpretation – with the proviso that meniscus (surface tension) forces will, of course, be operating at the same time.

Key words: adhesive organs, molecular attraction, *Calliphora*, *Rhodnius*.

We did not claim that this process was applicable directly to Diptera or other insects. The tibial organ of *Rhodnius* is very different in structure from that of the fly: it operates in the opposite direction (Fig. 1) but that does not preclude the same physical forces being generated. It can readily be imagined that the feet of a fly walking on the surface of glass could generate both adhesion and progression at the same time. But flies hanging under a glass sheet can apparently remain motionless, and that is the problem.

Many years ago I observed a large flesh fly, *Sarcophaga*, which rested in an inverted position under the glass of a glass-bottomed pill box. *Sarcophaga* is a rather stolid fly with very large feet, and on close inspection it could be seen that the feet were in constant slow motion: the feet of one tripod were moving slowly centripetally until the legs of the other tripod were extended and took over the centripetal movement. The stationary state was illusory and the systematic movement of the feet was evidently generating the required adhesion.

I have examined *Calliphora* in ventral view under the dissecting microscope while the fly was holding on to a glass sheet. These flies were far more restless than *Sarcophaga*, but if left undisturbed until they have recovered from their initial agitation, they will come to rest. They did not operate in the systematic way shown by *Sarcophaga*; the feet, with the pulvilli flattened against the glass, were all being drawn slowly towards the body. From time to time, when a leg neared the end of its run, it was extended in a flash, and resumed its centripetal movement. Sometimes two legs would extend at the same instant. It was generally quite easy to predict which leg was going to be extended next. There was no regular system such as that seen in *Sarcophaga*. Sometimes, it would seem almost in bravado, a fly would begin to rub its forelegs or its hindlegs together, and leave the remaining legs to continue the centripetal movements. During these operations the pulvilli were detached without any evidence of resistance; but that does not signify: they may perhaps have been peeled off through leverage by the claws, or lost their adhesion when movement was arrested.

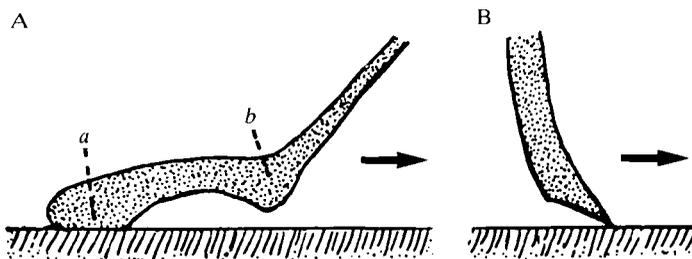


Fig. 1. (A). Diagrammatic longitudinal section of a single tenent hair of *Calliphora* (constructed from the scanning electron micrographs of Walker, Yule & Ratcliffe (1985)) showing that adhesion occurs chiefly at the distal rim (*a*) of the spatulate hair; the proximal rim (*b*) appears much less liable to adhesion. (B). A corresponding view of a tenent hair in *Rhodnius* (Gillett & Wigglesworth, 1932). In each case the arrow indicates the direction of movement of the hair that generates adhesion. Magnification approximately $\times 20\,000$.

The adult *Calliphora* weighs about 75 mg. When the weight was approximately doubled by attaching five small lead shot with wax to the upper surface of the thorax, the fly could still climb up a glass slope, and still hang from a horizontal sheet of glass. However, the legs were drawn away from the thorax; they were moved centripetally more rapidly and more irregularly; usually more than one leg would be unfolded at one time, and not surprisingly the fly was more liable to fall off.

These observations do not prove the sole use of molecular attraction, but they are highly suggestive. Movement of the adhesive organs might be expected to leave unchanged or even to depress the effect of surface tension (meniscus forces); yet the movements described are obviously necessary to support the fly, and movement can generate molecular attraction (frictional forces) (Bowden & Tabor, 1986). If a thin glass cover-slip is attached to a sheet of glass by a minimal amount of oil (surface tension) it can be moved over the surface by the finger. But resistance to this movement soon develops and as it increases Newton's coloured rings appear in the area where the oil film has become thinnest; finally a black spot appears at the centre of the rings – and seizure occurs.

This type of adhesion [as discussed at greater length in Gillett & Wigglesworth (1932) and in Stork (1980*a,b*)] should certainly be considered along with surface tension in studies of the adhesive organ of flies. It was not considered by Walker *et al.* (1985), on the ground that the findings of Gillett & Wigglesworth had been shown by Stork to be invalid. But in his own papers Stork (1980*a,b*) advances precisely these same mechanisms of adhesion as set out in this note. Indeed he approves of the conclusions of Edwards & Tarkanian (1970) who confirmed our observations on *Rhodnius* and who likewise accepted molecular cohesion as the major force involved. What Stork does not accept is the observation that the form and orientation of the tenent hairs on the tibial organs of *Rhodnius* are different, indeed almost the reverse of those familiar on the tarsal organs of other insects.

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