THE MECHANISM BY WHICH APHIDS ADHERE TO SMOOTH SURFACES

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Summary

1. The adhesive force acting between the adhesive organs and substratum for a number of aphid species has been studied. In the case of *Aphis fabae*, the force per foot is about $10\,\mu\mathrm{N}$. This is much the same on both glass (amphiphilic) and silanized glass (hydrophobic) surfaces. The adhesive force is about 20 times greater than the gravitational force tending to detach each foot of an inverted aphid.

2. The mechanism of adhesion was considered. Direct van der Waals forces and viscous force were shown to be trivial and electrostatic force and muscular force were shown to be improbable. An adhesive force resulting from surface tension at an air–fluid interface was shown to be adequate and likely.

3. Evidence was collected that the working fluid of the adhesive organ has the properties of a dilute aqueous solution of a surfactant. There is a considerable reserve of fluid, presumably in the cuticle of the adhesive organ.

Introduction

The mechanism by which certain insects can walk on smooth vertical and even inverted surfaces has long interested entomologists and recently there have been several studies on this subject (Stork, 1980; Wigglesworth, 1987; Lees and Hardie, 1988). The elegant study of Lees and Hardie (1988) on the feet of the vetch aphid *Megoura viciae* Buckt. and how it walks on smooth surfaces adds greatly to the pioneering work on this aspect of aphid biology by Mordvilko (1934). He showed that aphids of the sub-family Aphidinae could walk upside down on a clean glass surface even after their tarsal claws had been amputated and thought that they did this by means of a soft pad or eversible pulvillus (Solenblaschen of Weber, 1930) at the distal end of each tibia. The mechanism by which a pulvillus (articular membrane) is everted was described by Uichanco (1921). Some species of aphids (e.g. *Mastopoda pteridis* Oest. and *Atarsos grindeliae* Gill.) have only rudimentary tarsi and are dependent entirely on the tibial pulvilli for adhesion. Aphids of the sub-family Drepanosiphinae adhere to smooth surfaces by means of empodial pads (Kennedy, 1986). Interestingly, Mordvilko (1934) also found that species of aphids belonging to the subfamily Lachninae lack adhesive pads or pulvilli and are

Key words: adhesive organ, aphid, surface tension.

unable to walk upon a vertical glass surface. In addition to the adhesive structures on their feet, some aphids (*Neophyllaphis*) have eversible adhesive vesicles on their posterior abdominal sternites, which are everted and stuck to the underlying surface when the aphid is disturbed, as in high winds (White and Carver, 1971). The histological structure of these vesicles is very similar to that described for the eversible pulvilli of the vetch aphid (Lees and Hardie, 1988).

Both White and Carver (1971) and Lees and Hardie (1988) are of the view that liquid is secreted onto the surface of the adhesive structures and that it is the surface tension of this liquid film that accounts for the adhesion of aphids to smooth surfaces. The liquid secreted onto the surface of the abdominal vesicles of *Neophyllaphis* was suggested to be an aqueous solution, possibly haemolymph, and that on to the pulvilli of the vetch aphid, *M. viciae,* was suggested to be lipoidal.

As there is still some uncertainty about the mechanism of adhesion and whether a similar mechanism is used by other species of aphids, the following study was undertaken. We examined the anatomy and physical properties of the adhesive structures and measured the force required to dislodge several species of aphids from smooth surfaces.

Materials and methods

Aphids of the subfamily Aphidinae have tibial pulvilli whereas those of the subfamily Drepanosiphinae lack tibial pulvilli but have two empodial pads between the tarsal claws on each foot. The black bean aphid, *Aphis fabae* Scop., and the vetch aphid, *M. viciae*, belong to the Aphidinae and the sycamore aphid, *Drepanosiphum platanoidis* (Schr.), and the lime aphid, *Eucallipterus tiliae* (L), to the Drepanosiphinae.

Adult apterous *A. fabae* were collected within 24 h of final ecdysis from bean plants (*Vicia faba*) growing in long-day conditions. Adult apterous *M. viciae* were similarly collected from bean plants and transferred individually to young bean plants and allowed to give birth to offspring, which were subsequently used for experiments at different stages during their nymphal and adult development. Both the lime and sycamore aphids were collected as adults and nymphs from the field.

The approximate shearing force that *A. fabae* can withstand when resting on a clean glass surface was determined by allowing the aphids to climb the walls of glass centrifuge tubes and then finding the shear force required to dislodge them using a hand centrifuge. More precisely the vertical pulling force resisted when resting on a horizontal surface was determined for *A. fabae, M. viciae, D. platanoidis* and *E. tiliae* by placing them individually on a clean glass coverslip on the scale pan of a top-loading digital balance and then zeroing the balance. Once zeroed, a fine thread, the free end of which had been dipped in Araldite adhesive, was brought into contact with the dorsum of the aphid to which it adhered by virtue of its tackiness. A vertical pull was then applied to the thread *via* a micromanipulator. To prevent jerking, a short length of elastic was inserted in the

length of thread just behind the free end. The negative weight reading shown by the balance at the moment of dislodging the aphid was noted. The adhesive force can be expressed as the reading or, preferably, as the reading multiplied by the acceleration due to gravity and expressed as micronewtons (μN). This procedure was repeated for *A. fabae, M. viciae , D. plantanoidis* and *E. tiliae* using a silanized coverslip, which has an extremely smooth and water repellent surface. Silanized (hydrophobic) glass surfaces were prepared by first cleaning the surface in methanol and then, in some cases, exposing the surface to the vapour of *N,N*-dimethyl-trimethylsilyamin (Fluka) at 200°C for 2 h or, in most cases, dipping the surfaces in 2% dimethyldichlorosilane solution in 1,1,1-trichloroethane (BDH), rinsing with methanol and drying.

A fine scalpel was used to cut off the distal half of the tarsi and tarsal claws. This was done by placing a CO_2-anaesthetized aphid on a wax block and observing it under a binocular microscope. By tilting the wax block the tarsi could be exposed and easily severed.

Scanning electron microscopy was used to estimate circumference and area of contact with the substratum. Transmission electron microscopy was used to confirm the structure and to estimate the thickness of the pulvillar cuticle.

Results

Aphidinae

The vertical force required to dislodge *A. fabae* from a clean glass surface was equivalent to approximately 20 times the body weight and was about 10 μN/foot. The value was little affected by silanizing the surface (Table 1) or by anaesthetizing the aphids in a gentle stream of CO_2. In the case of *M. viciae,* the use of both young and apterous adults gave a wider range of weights and revealed that the pulling force resisted by an aphid increased with its size but not proportionately and silanizing the surface of the glass reduced slightly the pulling force an aphid could resist (Table 2). Small (1 mg) aphids had a safety factor of 15 on clean glass and 13 on silanized glass and large aphids (4 mg) had safety factors of 8 and 7, respectively.

The ability of *A. fabae* to adhere to a smooth surface is markedly affected by the

Table 1. *Average weight of* Aphis fabae *and the force, expressed as a weight, required to detach it from a clean and a silanized horizontal glass surface*

Surface	N	Mean weight of aphid (mg)		Force required to lift aphid expressed as weight (mg)		Safety factor	
Glass	12	0.383±0.021	***	6.4±0.59	NS	17.4±2.11	NS
Silanized glass	13	0.300±0.013		6.3±0.69		21.0±2.02	

Results given as mean±s.e.m., *** $P<0.001$; NS, not significant.

Table 2. *The logarithm$_{10}$ of the vertical force (mg) resisted (y) in relation to the logarithm$_{10}$ of the body weight (mg) (x) for vetch aphids* Megoura viciae *on a glass and a silanized glass surface (A) and the logarithm$_{10}$ area (µm^2) of the tibial pulvilli (a) in relation to the logarithm$_{10}$ body weight (µg) (x) (B)*

	Surface	N	Range in body weight (mg)	Regression equation	
A	Glass	35	0.1–4.7	$y=1.18+0.50x$	$F_{elevations}=6.68$ d.f.$=1/67$
	Silanized glass	35	0.2–4.3	$y=1.10+0.50x$	$P<0.05$
B		34	0.089–4.03	$a=1.74+0.27x$	$r=0.94,$ $P<0.001$

time spent walking on an absorbent substratum (coarse silica gel, BDH). After 1 min, aphids are immediately able to walk up a clean vertical glass surface. However, after longer periods (up to 15 min), aphids were unable to adhere to a glass surface. The time that elapsed after such treatment before they were again able to walk up a vertical glass surface was equal to approximately $2.4t$ ($r=0.9$, d.f.$=11$, $P<0.001$), where t is the time spent on silica gel (Fig. 1). This suggests that the pulvilli act like sponges, each containing a reserve of the adhesive fluid. After spending 15 min walking on silica gel, an aphid needs approximately 30 min apparently to refill the reservoirs and so regain the ability to walk on smooth surfaces. Similarly, after 15 min of walking on a dried silica gel chromatography plate (Merck 60 F-254), *A. fabae* was unable to adhere to an inverted glass or silanized glass surface. If, however, after this period on the silica gel plate, they were permitted to walk for 2 min on filter paper moistened with water, they regained the ability to adhere to an inverted glass or silanized glass surface. In the
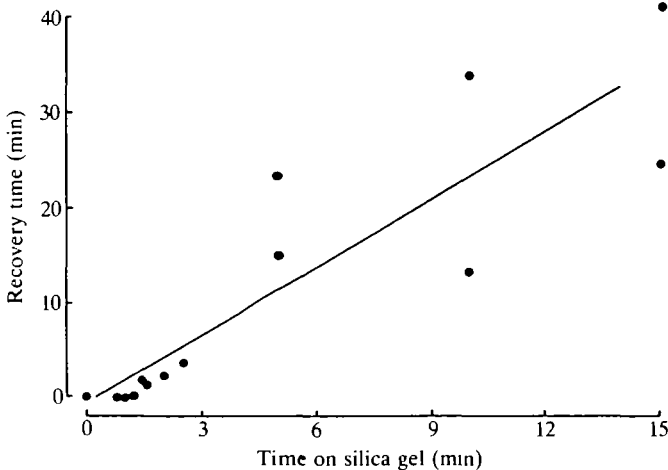

Fig. 1. Time required for *Aphis fabae* to recover its ability to adhere to a glass surface after various times on a silica gel surface.

latter case, the ability seemed less. In both cases, walking was difficult as the feet slid over the surface. Normal aphids had no difficulty in adhering to an inverted silica gel plate (rough surface). However, when their tarsal claws were removed ($N=10$), they were unable to adhere to an inverted plate.

An attempt was made to collect a quantity of this fluid. Some 200 aphids were placed in turn on a small marked area of a silica gel plate, anaesthetized with CO_2 and left for 2–3 min. Calibration quantities of lecithin solution were also placed on this plate, which was then developed by spraying with 10 % sulphuric acid and placing in an oven at 160 °C to char organic matter. As the organic material was scattered as irregular masses over the area on which the aphids were placed it was difficult to compare with the more uniform deposit of the standard. Thus, the result is only very qualitative but it seems that the total organic material, derived from about 1200 footprints, was about 0.5 μg.

Drepanosiphinae

The lime and sycamore aphids, which adhere by means of empodial pads rather than pulvilli, resist dislodgement relative to body weight in a similar way to *A. fabae* and *M. viciae* (Table 3). The gradients of the relationships for the lime and sycamore aphids are the same ($F_{slopes}=0.0003$, d.f. $=1/32$, NS) and not significantly different from that for *M. viciae* ($F=1.06$, NS). Thus, although the lime and sycamore aphids use a different structure for adhering to smooth surfaces, their ability to resist dislodgement shows the same functional relationship with weight as for the black bean and vetch aphids. Like the vetch aphid, the sycamore aphids' ability to adhere to a smooth surface is reduced if the surface is silanized (Table 4).

Table 3. *The logarithm$_{10}$ of the vertical force (mg) resisted (y) in relation to the logarithm$_{10}$ of the body weight (mg) (x) for lime and sycamore aphids on a glass surface*

Aphid	N	Range in body weight (mg)	Regression equation	Correlation coefficient
Lime	10	0.1–1.3	$y=0.95+0.39x$	$r=0.83$
Sycamore	26	0.1–2.0	$y=0.86+0.38x$	$r=0.73$

Table 4. *Average weight of adult sycamore aphids and the vertical force required to detach them from a glass and a silanized glass surface*

Surface	N	Mean weight of aphid (mg)	Force required to lift aphids (mg)
Glass	15	1.52	9.75
		$t=0.25$ d.f. $=24$ NS	$t=4.6$ d.f. $=24$ $P<0.001$
Silanized glass	11	1.48	2.56

The more marked effect in the case of the sycamore aphid is due to its much greater activity.

Interspecific relationships

Comparison of the average weight lifted (y) by adults of the four species of aphids indicates that relative to body weight (x) the lime and sycamore aphids with empodial pads are very comparable with the black bean and vetch aphids ($\log y = 1.03 + 0.62 \log x$, $r=0.95$, $N=4$). The exponent (0.62) in this interspecific relationship is not significantly different from 0.67, which implies that the ability to adhere to a smooth surface is a function of the area of the adhesive structures and that the safety factor of large species is less than that of small species.

Discussion

The mechanism by which insects adhere to smooth surfaces is of long-standing and continuing interest to entomologists (Hasenfuss, 1977, 1978; Stork, 1980; Walker *et al.* 1985; Ishii, 1987; Wigglesworth, 1987; Lees and Hardie, 1988). Aphids like the black bean aphid, *A. fabae*, are only dislodged from smooth surfaces by vertical pulling forces about 20 times greater than the gravitational force acting on their own body mass (weight). Each foot can withstand a pulling force of about $10 \mu N$. Various possible adhesive mechanisms will be considered and additional observations relating to the possible mechanisms will be considered.

Van der Waals forces are attractive forces that could act between two parallel plates, such as between a pulvillus and the surface of a leaf. The forces are strongly dependent on the distance separating the two surfaces (Hiemenz, 1986). If the separation is as little as $0.1 \mu m$ then for *A. fabae*, using a value of pulvillar area of $900 \mu m^2$, the force is about $5 \times 10^{-3} \mu N/\text{pulvillus}$, which is trivial. In order to obtain the observed adhesive force of $10 \mu N/\text{foot}$, the separation of the surfaces would need to be only about 8 nm or much less if there were a liquid with a large permittivity (water) between the surfaces. Such close approximation over the whole pulvillar area seems unlikely with such surfaces. This force could be considerably increased if there were a plastic matrix in contact with the two surfaces (adhesive). However, it is difficult to see how the feet could then be detached from the substratum. The calculation given here does not support the view of Stork (1980) that this mechanism could play a role in insect adhesion.

Electrostatic adhesion was considered and discounted by Stork (1980). This is the force that attracts the plates of a capacitor as the charge on the plates is increased (Kip, 1969). In order to obtain a force of $10 \mu N/\text{pulvillus}$, with an air gap of $0.1 \mu m$, the potential difference between the aphid and the substratum would have to be 5 V. The electrical field would be $50 \times 10^6 \text{ V m}^{-1}$, which is considerably greater than the dielectric strength of air. If the dielectric were a liquid with a large permittivity (water), the potential difference could be less. However, it is not clear how a potential difference between an aphid and its substratum could be

generated or maintained, particularly with a conducting dielectric (water). Experiments using a Zerostat anti-static pistol, that should abolish any potential difference, failed to dislodge any aphids from a vertical glass surface. Further, after *A. fabae* were allowed to walk on filter paper moistened with 1% NaCl solution, the aphids were still able to walk on inverted glass or silanized glass surfaces. As there must be traces of conducting solution present on their pulvilli, this is further evidence against an electrostatic adhesion mechanism.

If the central part of the pulvillus could be withdrawn by muscular action to create a pressure drop (vacuum cup) then aphids could hold on by this means (Fig. 2B). For a pressure drop of 101 kPa (1 atm), the force per pulvillus would be approximately 90 μN. However, there are no suitable muscles (Lees and Hardie, 1988). Furthermore, CO_2 anaesthesia, which might be expected to cause muscle relaxation, did not cause the aphids to detach. Also, exposure to a vacuum (4 Pa) did not cause the aphids to detach. In addition, gentle flooding of a clean slide with water detached CO_2-anaesthetized aphids.

An adhesion between two surfaces separated by a fluid film can arise as a result of the viscosity of the fluid (Bowden and Tabor, 1986). This effect is distinct from adhesion due to surface tension, which is described later. If the viscosity of the fluid is appreciable, the force required to separate the surfaces in a short time may be very large. Bowden and Tabor (1986) show that to separate 1 inch diameter disks in 10 s could theoretically require a load of nearly 10 tons. This mechanism has been considered important for adhesion in *Calliphora* (Wigglesworth, 1987). However, the force required to separate circular plates in a given time is proportional to the radius of the plates raised to the fourth power. In *A. fabae*, the radius of a pulvillus is about 17 μm. Thus, the force required to separate the pulvillus from its substratum in 1 s, if the fluid separating the surfaces is 1 μm thick and has the same viscosity as water, is only 0.2×10^{-3} μN. In an insect as small as *A. fabae*, the viscosity effect is totally trivial. This is confirmed by the ease with which a gentle stream of water will float CO_2-anaesthetized aphids off a glass surface. If this force were to be important in a large species, it would be as difficult for the insect to attach its feet to the surface as it would be to remove them.

If the viscosity effect is trivial, it might be expected that an aphid would slide quite rapidly down a vertical surface. However, it has been shown that the shear force required to dislodge *A. fabae* is at least as great as the vertical force. The
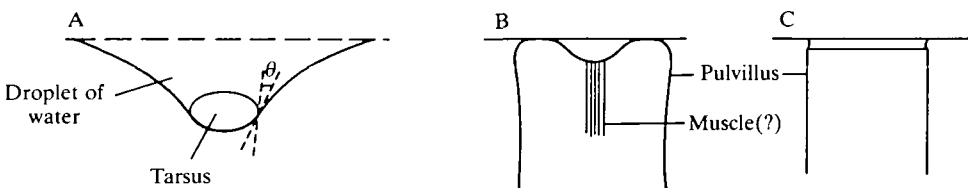

Fig. 2. Some of the adhesive mechanisms considered. (A) Droplet adhesion to a liquid surface; (B) vacuum-cup adhesion; (C) surface-tension adhesion. For further explanation see text.

explanation is that, if a sliding aphid pulls its adhesive fluid with it, the velocity gradient in the fluid must be confined to the immediate vicinity of the stationary surface. This would greatly increase the frictional effect.

A. fabae can walk on an inverted aqueous surface (1.5 % agar in water) or glass surface smeared with light paraffin oil. In both cases the whole tarsal surface was wetted and the animal was suspended from droplets of liquid (Fig. 2A). This indicates that the tarsal surfaces, including the pulvillus, are amphiphilic, i.e. wetted by both water and oil. In this, the surfaces resemble a clean glass surface. The gravitational force (F) acting on an aphid is:

$$F = mg, \qquad (1)$$

where m is the mass of the aphid and g the acceleration due to gravity. This is balanced by the surface forces:

$$F = c\gamma\cos\theta, \qquad (2)$$

where c is the circumference of the wetted surface, γ the surface tension of the liquid and θ the contact angle. Using a value of the circumference of the wetted tarsal surface of $344\,\mu m$, the force per foot, when the medium is water and assuming the contact angle is zero, is about $25\,\mu N$. The observations indicate that on a wet surface such droplet adhesion is effective.

A mechanism that has been considered previously (Stork, 1980; Lees and Hardie, 1988) is that a drop of liquid between two surfaces can hold the surfaces together by surface tension (Fig. 2C). The hydrostatic pressure drop across the air–liquid interface (P) between two flat surfaces is independent of the contact area and is given by:

$$P = \frac{\gamma}{\delta}(\cos\theta_1 + \cos\theta_2), \qquad (3)$$

where δ is the distance between the pulvillus and substratum and θ_1 and θ_2 are the contact angles at the pulvillus and substratum, respectively. Then the force (F) is given by:

$$F = PA, \qquad (4)$$

where A is the area of contact. This force would draw the surfaces together until the meniscus reaches the edge of the adhesive organ, where the curvature becomes important in limiting the force.

The adhesion of many macroscopic bodies is strongly dependent on atmospheric humidity. Capillary condensation occurs and results in adhesion (Israelachvili, 1985). Because of the presence of an unstirred layer, the surface of a transpiring leaf is likely to be of higher humidity than ambient air (Ramsay *et al.* 1938). Thus, this method of adhesion must be almost inevitable for an aphid.

If the separation of the surfaces is $1\,\mu m$, the surface tension of the liquid is $73 \times 10^{-3}\,N\,m^{-1}$ (pure water) and the contact angle is zero, then the hydrostatic pressure drop is $146\,kPa$, which is well within the tensile strength of pure water (Scholander *et al.* 1965). Using a value of pulvillar area of $900\,\mu m^2$, the force per

pulvillus is 130 μN. This value is much greater than the gravitational force acting on *A. fabae* ($\approx$0.6 μN/pulvillus) and could account for the large safety factor.

The forces holding an aphid on a surface are, in the case of *A. fabae,* as great or even greater on a hydrophobic silanized surface than on a clean glass surface. Qualitative observations were made of the adhesive force between two flat surfaces separated by a thin layer of liquid and indicate that surface tension forces can operate between amphiphilic (glass) and hydrophobic (silanized) surfaces (Table 5). The pressure drop in such a situation can be calculated from the two contact angles (θ_1, θ_2). If the contact angle at the insect surface is zero (fully wettable), there would still be adhesion to a hydrophobic surface provided that the contact angle there is less than 180°. This is well above the values for water drops on plant cuticles given by Fogg (1947). In the case of *M. viciae,* adhesion was marginally better on clean glass. These observations suggest that the fluid secreted onto the surface of the pulvilli has interesting properties. An aqueous solution containing a surfactant would have the required properties and make adhesion less sensitive to the nature of the substratum. These properties could be similar to that of 1 % aqueous solution of Triton X-100 (Table 5). An oil-based working medium seems less likely, as aphids can be detached by gently irrigating the surface with water but not with light paraffin oil.

If aphids adhere to smooth surfaces by surface tension, the force required to detach an aphid should be proportional to the surface area of the pulvilli (A). In *M. viciae,* the decline in the safety factor with increase in body mass is associated with large aphids having proportionately smaller adhesive pads than small aphids, i.e. a fourfold increase in weight is accompanied by only a 1.5-fold increase in the area of the pulvilli not the 2.5-fold increase that would be expected if the large animal is a magnified small animal. An analysis of the relationship between the adhesive force and weight and between pulvillar area and weight (Table 2) indicates that the adhesive force is proportional to A^2. In terms of the preferred

Table 5. *Adhesion between flat clean and silanized glass surfaces when separated by a thin layer of water (W), 1 % aqueous solution of Triton X-100 (T) or light paraffin oil (O)*

	Surfaces	
	Glass	Silanized glass
Glass	W+	W+
	T+	T+
	O+	O+
Silanized glass	W+	W−
	T+	T+
	O+	O+

Adhesion is indicated as + and little adhesion is −.

surface-tension model, this suggests that the volume of working fluid per pulvillus is constant and, as a consequence, the separation of the surfaces would be less for large individuals of a species and for large species. This gives the relationship between force and area. However, even with such an effect, the safety factor of large species like *M. viciae* is significantly less than that of a smaller species like *A. fabae*.

Lees and Hardie (1988) argue that the material they obtained by puncturing a pulvillus was a lipoprotein precursor of the actual adhesive fluid, which they identified with the oily droplets that they sometimes found as footprints. As aphids that spend 15 min walking on silica gel need approximately 30 min before they regain the ability to adhere to smooth surfaces, it is likely that the cuticle of the pulvillus acts like a sponge, containing a reserve of adhesive liquid. Although an estimate of the quantity of organic matter absorbed into the silica gel plate is only very approximate, a value of 0.4×10^{-12} kg/footprint corresponds to a thickness of 0.5μm. If this material is in a dilute aqueous solution, the volume of fluid available in the reservoir is considerable. In sections, the thickness of the cuticle is about 10μm. However, this is after fixation and preparation for electron microscopy. If this structure is an easily deformable sponge, it may have shrunk during preparation. The material obtained by puncturing this reservoir is likely to be the adhesive liquid rather than its precursor. The very fine pores in the epicuticle of the pulvilli of Aphidinae observed by Lees and Hardie (1988) and in this study and in the ventral surface of empodial pads of Drepanosiphinae would allow the easy passage of the fluid onto the surface. Small drops of a 1 % aqueous solution of Triton X-100 placed on a glass surface dry out very rapidly and fragment to give a pattern of droplets strikingly similar to the footprint depicted in Lees and Hardie (1988). Because an actual surfactant would orientate at the air–surfactant interface as the solvent evaporated, these droplets might appear to be insoluble in water and to dissolve readily in lipid solvents, which misleadingly would indicate that the actual adhesive medium is lipoidal. From measurements of volume of footprint material, Lees and Hardie (1988) estimate the thickness of the layer between pulvillus and substratum to be 17.7 nm, well below the value suggested in this paper. If this footprint material represents a dried-down surfactant solution, it suggests that the actual working medium contains 1–2 % surfactant or less if the occasionally observed footprints represent cases when the working fluid had, for some reason, been added to from the reservoir.

Apart from adhering to surfaces, insects have the problem of rapidly detaching themselves. The surface tension mechanism has the advantage that by tilting the attached surface, the force required to remove (peel) the surface from the substratum could be reduced.

The high humidity associated with the surface of plants will lead to capillary condensation wherever two surfaces come into close proximity with one another. Therefore, it is unlikely that aphids would be able to avoid using water to help them adhere to smooth plant surfaces. The widespread presence of surfactant substances on the surfaces of insects would serve to make the mechanism more

effective on a hydrophobic substratum. The development of sponge-like pulvilli and empodial pads, which act as reservoirs for the adhesive fluid and which, because of their flexibility, achieve a close contact with even quite irregular surfaces, further improves the ability of aphids to adhere to smooth surfaces.

Aphids of the sub-family Lachninae lack empodial pads and pulvilli. Interestingly, none of these aphids live on the flat leaf laminae of angiosperms. They feed on the needles of gymnosperms where, because of the curvature of the surface, they are able to hold on using their claws. It is tempting to speculate that the near absence of this group of aphids from the leaves of angiosperms is because they lack the means of adhering to smooth surfaces.

References

BOWDEN, F. P. AND TABOR, D. (1986). *The Friction and Lubrication of Solids.* Oxford: Clarendon Press.

FOGG, G. E. (1947). Quantitative studies on the wetting of leaves by water. *Proc. R. Soc.* B **134**, 503–522.

HASENFUSS, I. (1977). Die Herkunft der Adhäsionsflüssigkeit bei Insekten. *Zoomorph.* **87**, 51–64.

HASENFUSS, I. (1978). Uber das Haften von Insekten on glatten Flachen – Herkunft der Adhäsionsflüssigkeit. *Zool. Jb. (Anat.)* **99**, 115–116.

HIEMENZ, P. C. (1986). *Principles of Colloid and Surface Chemistry.* 2nd edn. New York: Dekker.

ISHII, S. (1987). Adhesion of a leaf feeding ladybird *Epilachna vigintioctomaculata* (Coleoptera: Coccinellidae) on a vertically smooth surface. *Appl. Ent. Zool.* **22**, 222–228.

ISRAELACHVILI, J. N. (1985). *Intermolecular and Surface Forces.* London: Academic Press.

KENNEDY, C. E. J. (1986). Attachment may be a basis for specialization in oak aphids. *Ecol. Ent.* **11**, 291–300.

KIP, A. F. (1969). *Fundamentals of Electricity and Magnetism.* 2nd edn. Tokyo: McGraw-Hill Kogakusha.

LEES, A. D. AND HARDIE, J. (1988). The organs of adhesion in the aphid *Megoura viciae. J. exp. Biol.* **136**, 209–228.

MORDVILKO, A. (1934). On the evolution of aphids. *Arch. Naturgesch. N.S.* **3**, 1–60.

RAMSAY, J. A., BUTLER, C. G. AND SANG, J. H. (1938). The humidity gradient at the surface of a transpiring leaf. *J. exp. Biol.* **15**, 255–265.

SCHOLANDER, P. F., HAMMEL, H. T., BRADSTREET, E. D. AND HEMMINGSEN, E. A. (1965). Sap pressure in vascular plants. Negative hydrostatic pressure can be measured in plants. *Science* **148**, 339–346.

STORK, N. E. (1980). Experimental analysis of adhesion of *Chrysolina polita* (Chrysomelidae: Coleoptera) on a variety of surfaces. *J. exp. Biol.* **88**, 91–107.

UICHANCO, L. B. (1921). Musculature and mechanism of movement of the tarsi in aphids. *Psyche* **28**, 63–68.

WALKER, G., YULE, A. B. AND RATCLIFFE, J. (1985). The adhesive organ of the blowfly, *Calliphora vomitoria*: a functional approach (Diptera: Calliphoridae). *J. Zool., Lond.* A **205**, 297–307.

WEBER, H. (1930). *Biologie der Hemipteren.* Berlin: Julius Springer.

WHITE, D. AND CARVER, M. (1971). Adhesive vesicles in some species of *Neophyllaphis* Takahashi, 1920 (Homoptera: Aphididae). *J. Aust. Ent. Soc.* **10**, 281–284.

WIGGLESWORTH, V. B. (1987). How does a fly cling to the under surface of a glass sheet? *J. exp. Biol.* **129**, 373–376.