

## An Integrative Study of Insect Adhesion: Mechanics and Wet Adhesion of Pretarsal Pads in Ants<sup>1</sup>

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**SYNOPSIS.** Many animals that locomote by legs possess adhesive pads. Such organs are rapidly releasable and adhesive forces can be controlled during walking and running. This capacity results from the interaction of adhesive with complex mechanical systems. Here we present an integrative study of the mechanics and adhesion of smooth attachment pads (arolia) in Asian Weaver ants (*Oecophylla smaragdina*). Arolia can be unfolded and folded back with each step. They are extended either actively by contraction of the claw flexor muscle or passively when legs are pulled toward the body. Regulation of arolium use and surface attachment includes purely mechanical control inherent in the arrangement of the claw flexor system.

Predictions derived from a ‘wet’ adhesion mechanism were tested by measuring attachment forces on a smooth surface using a centrifuge technique. Consistent with the behavior of a viscid secretion, frictional forces per unit contact area linearly increased with sliding velocity and the increment strongly decreased with temperature.

We studied the nature and dimensions of the adhesive liquid film using Interference Reflection Microscopy (IRM). Analysis of ‘footprint’ droplets showed that they are hydrophobic and form low contact angles. *In vivo* IRM of insect pads in contact with glass, however, revealed that the adhesive liquid film not only consists of a hydrophobic fluid, but also of a volatile, hydrophilic phase. IRM allows estimation of the height of the liquid film and its viscosity. Preliminary data indicate that the adhesive secretion alone is insufficient to explain the observed friction and that rubbery deformation of the pad cuticle is involved.

### INTRODUCTION

Adhesive pads on the legs of insects have fascinated biologists for centuries (*e.g.*, Hooke, 1665; Blackwall, 1830; West, 1862; Dewitz, 1884; Simmermacher, 1884). Insect adhesive organs feature surprising structural diversity (Beutel and Gorb, 2001) and striking performance. Some insects are capable of withstanding detachment forces equivalent to more than 100 times their own body weight on smooth substrates (Eisner and Aneshansley, 2000; Federle *et al.*, 2000) and yet able to run on these surfaces. However, the mechanism of how they master the conflicting tasks of running and of making stable adhesive contacts is still largely unknown. Adhesive leg pads are hybrid adhesive and mechanical systems. To analyze the mechanisms of controlled adhesion, it is necessary to study not only the adhesive system in isolation, but also the complex mechanical design of leg pads and their interaction with the adhesive function.

We have taken an integrative approach to investigate adhesive pads in Weaver ants (*O. smaragdina*) by 1) measuring adhesive performance, 2) analyzing the morphology and mechanics of the pretarsal attachment system, and 3) studying the properties of the adhesive liquid film.

### ECOLOGICAL SIGNIFICANCE OF ADHESIVE PADS IN ANTS

Life on plants would be impossible for insects if they had no adhesive pads providing attachment to

smooth cuticles of plant leaves and stems. This is especially true for ants as wingless insects. In terms of their abundance and biomass, plant-inhabiting ants dominate the canopies of tropical rainforests (Hölldobler and Wilson, 1990). For these insects, the capacity to run on smooth surfaces while staying safely attached is vitally important. Most of them would not survive falling off the trees where they live, because they would find themselves in territories of hostile ants where no odor trails guide them back to their nest. Consistently, we found exceptional detachment resistance in arboreal ants ranging from *ca.* 40 to 150 times their own body weight on a smooth surface (Federle *et al.*, 2000).

The species selected for this study, *O. smaragdina*, is well-known for its capacity to construct large leaf tent nests (Wheeler, 1915; Hölldobler and Wilson, 1983). In the first phase of the nest construction, individual ants (and often chains of workers) forcefully pull neighboring leaves together before they are connected with larval silk. The rearmost ants in these ‘living clamps’ are standing on a smooth leaf upper side for hours and sustain large forces parallel to the surface. How can this striking attachment capacity be explained in the context of wet adhesion?

### MECHANICS OF ADHESIVE PADS

The adhesive organ in ants and bees (Hymenoptera) is a flexible cuticle pad located between the pretarsal claws (Snodgrass, 1956). It can be unfolded and folded back with each step. Extension of the arolium brings it into contact with the surface and increases its adhesive contact area. We discovered that the arolium

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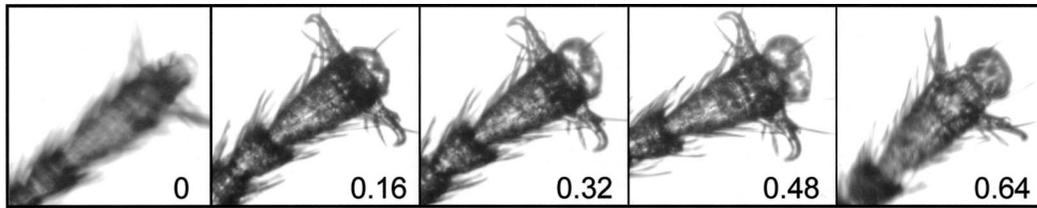


FIG. 1. Full step of a *Crematogaster* (*Decacrema*) msp.4 ant's foot while running upside down on glass (numbers are time in seconds).

can be moved by a combination of active and passive mechanisms (Federle *et al.*, 2001).

#### Active extension

High-speed video recordings of ants running upside down on smooth surfaces showed that the extension and inflation of the pad is coupled with the retraction of the claws (Fig. 1).

Experimental manipulation of the claw flexor apodeme in severed legs of *O. smaragdina* confirmed that the arolium is moved by the contraction (and release) of the claw flexor muscle. The elicited pad movements were similar to those observed in freely walking animals because they included a rotary motion (pad folded down to the surface) and a lateral expansion (inflation). Since the claw flexor muscle in insects has no antagonist (Snodgrass, 1935), claws and arolium are moved back by elastic recoil of stretched exocuticle (Federle *et al.*, 2001). The mechanical system leading to the conspicuous arolium movement can be technically described as the combination of a torsion spring and a hydraulic pump (for details see: Federle *et al.*, 2001).

#### Passive extension

Even in freshly killed ants and severed legs, a full extension of the pad and strong adhesive contact could be elicited by pulling the tarsus (with arolium partly in contact) across a smooth surface in the direction toward the body (Fig. 2, Federle *et al.*, 2001). This is not an active movement but a passive, "preflex"-like reaction of the mechanical system (Brown and Loeb, 2000; Dickinson *et al.*, 2000) that does not require neuronal feedback and has no delay. Such passive reactions might be biologically very important, because they can effectively prevent small insects running on smooth surfaces from being detached by sudden perturbations such as falling rain drops or wind gusts.

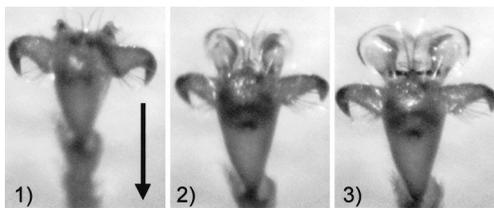


FIG. 2. Passive extension of arolium in *O. smaragdina* in dorsal view. Severed leg was pulled in the direction toward the body (arrow) across a glass surface (from Federle *et al.*, 2001).

Purely mechanical reflexes are probably widespread among legged adhesive systems. Maximal attachment is generally achieved when adhesive pads are pulled toward the body, but detachment occurs in the opposite direction. This general principle is found across a wide variety of animals with different adhesive morphologies and mechanisms (*e.g.*, flies [Niederregger *et al.*, 2002], bushcrickets [Gorb and Scherge, 2000], tree frogs [Hanna and Barnes, 1991] and geckos [Autumn *et al.*, 2000]).

#### Attachment and detachment

Despite the intricacy of the mechanical system of the pretarsus, its control is simple, because it involves only a single muscle and gross leg movements (see Frazier *et al.*, 1999, for cockroaches). Attachment is achieved by contraction of the claw flexor muscle or when the arolium is pulled toward the body. When the claw flexor relaxes and/or when the tarsus is pushed away from the body, the arolium is folded back and detaches from the surface by elastic recoil of the cuticle. As a rule, the arolium starts folding back and peeling off the surface before the foot is lifted (Fig. 3). Before detachment, the foot often moves a short distance away from the body, which helps retract the arolium. When a foot with an unfolded pad is rapidly detached, however, even a fully extended arolium can be peeled off the surface. As the foot is rolled off, peeling progresses from the proximal to the distal side of the contact area.

#### THE ADHESIVE MECHANISM

Insect adhesive organs are either smooth and deformable cuticle pads or fields of adhesive setae (Beutel and Gorb, 2001). In both designs, surface contact is mediated by an adhesive liquid (*e.g.*, Walker *et al.*, 1985; Ishii, 1987; Lees and Hardie, 1988; Eisner and Aneshansley, 2000; Jiao *et al.*, 2000). This secretion appears to be released onto the surface of the pads through pore canals (Gorb, 1998), but its exact pathway still has to be explored in many systems.

A liquid film between two objects gives rise to adhesive forces due to surface tension and viscosity (Fig. 4).

Surface tension mainly creates static forces perpendicular to the surface, whereas forces parallel to the surface (due to contact angle hysteresis between the leading and the trailing edge of the meniscus) are probably negligible. Forces due to viscosity, on the other hand, can act both in the normal and in the par-

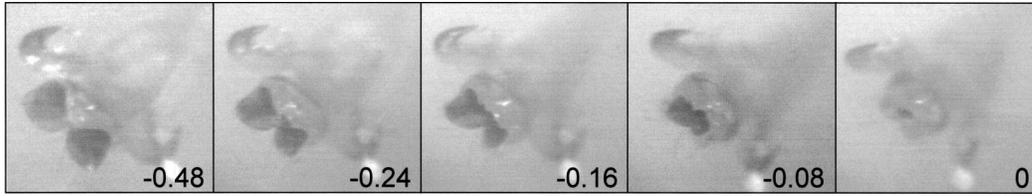


FIG. 3. Detachment of arolium in *O. smaragdina* recorded using epi-illumination (ventral view, numbers are time in seconds).

allel direction, but they are zero in the static case. Several predictions for insect attachment forces follow from these considerations (see Fig. 4):

1. Static friction should be small. A liquid film typically acts as a lubricant that enables smooth sliding. However, sufficient static friction appears to be required for the nest construction behavior in *O. smaragdina* (see above). Several studies on insect attachment reported frictional forces to be much larger than adhesive forces (Stork, 1980; Walker *et al.*, 1985). Unfortunately, velocity was not controlled in these experiments and it is unclear whether sliding was involved or not.
2. Friction should depend on velocity. Due to shearing of the liquid film, the friction force should be stronger at higher sliding velocities.
3. Because of the different temperature dependence of viscosity and surface tension (viscosity decreases much more strongly with temperature than surface tension), sliding friction should become smaller at higher temperatures, but static forces should be almost temperature-independent.

*Force measurements*

To test these predictions, we measured attachment forces of *O. smaragdina* using a centrifuge technique (modified from Federle *et al.*, 2000; Federle *et al.*, in preparation). Insects were placed onto smooth Plexiglass (PMMA) cylinders or turntables mounted in the rotor to measure vertical or parallel forces, respectively. By synchronizing a strobe light to the revolutions of the centrifuge, a standing image of the insects can be observed and recorded with a video camera. At-

tachment forces are calculated from the insect’s radius and rotation speed. Once the centrifugal acceleration surpasses a threshold, ants and many other insects stop running and show a “freezing” reaction. In the frozen position, all six legs are spread out and their arolia are fully extended (Federle *et al.*, 2000).

On the smooth turntable, the ants did not detach, but gradually slid outward (Fig. 5A), their adhesive pads being in continuous contact with the surface. We found positive, linear relationships between shear stress (*i.e.*, the acting centrifugal force divided by the ant’s adhesive contact area) and sliding velocity, consistent with the contribution of a viscous liquid film. All the obtained model II regression lines, however, had positive intercepts indicating the presence of a significant “static” friction force (Fig. 5B).

As predicted, sliding friction was smaller at higher temperatures (Fig. 6). There was a more than twofold difference between the slopes of the shear stress/velocity regression lines at 15 and 30°C. By contrast, the static components did not differ significantly between the two temperatures. A similar result was found in a separate experiment for low-rate perpendicular detachment forces. In the range of 15 to 30°C, no significant effect of temperature was detected (Federle *et al.*, in preparation).

As in other insects (Stork, 1980; Walker *et al.*, 1985), parallel forces were generally much larger than vertical forces. The parallel, static component alone corresponded to more than twice the perpendicular detachment force (184 vs. 85 times body weight at 20°C). As soon as sliding begins, frictional forces can be even several times greater. This increase of friction with velocity, in addition to the preflex-like attachment reaction of the pad (see above), helps reject rapid perturbations by providing attachment in cases when strong detachment forces are acting.

Our findings are largely consistent with the predictions for a wet adhesion mechanism (Fig. 4). Pads slid smoothly and their friction increased linearly with sliding velocity. As predicted by the differential effects of surface tension and viscosity, only the dynamic forces were temperature-dependent, whereas static forces were not or only weakly so.

However, the static friction forces were much greater than expected for a lubricated contact (friction coefficient, related to body weight:  $\mu_{\text{static}} > 80$ ). A possible source of this static friction is the surface contact of body parts other than the arolium (claws, tarsi). Assuming that these parts are pressed down with the

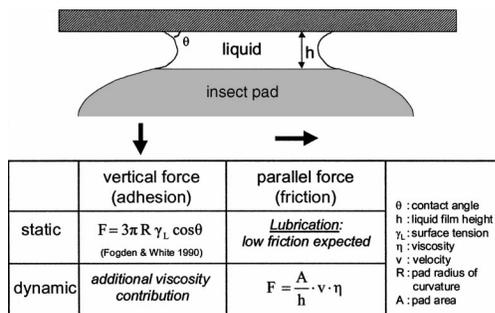


FIG. 4. Predictions from a ‘wet’ adhesion mechanism. Static vertical force predictions modeled the arolium as a soft sphere. Dynamic parallel force predictions assumed a simple parallel plate model with a Newtonian liquid.

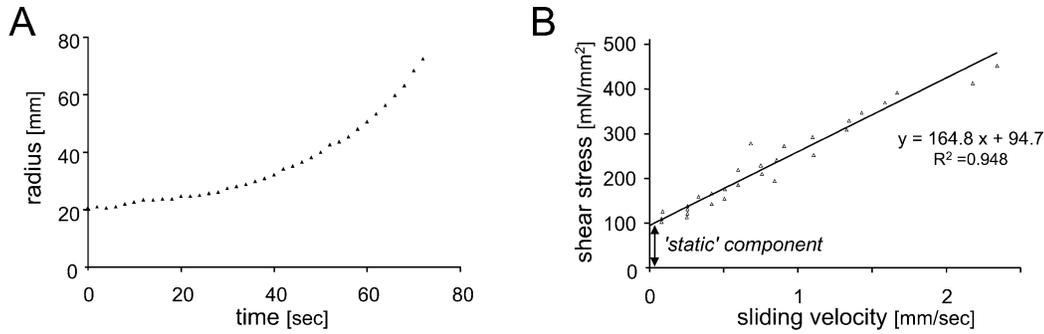


FIG. 5. A. Typical run of an *O. smaragdina* ant sliding radially on a smooth turntable at 15°C. B. Relationship between velocity and shear stress for the data shown in A.

maximal adhesive force of the arolium, smaller friction coefficients would be found, but they are still greater than 2. This range exceeds typical values for the friction between rigid solids, but is possible for the friction of viscoelastic materials such as rubber (Grosch, 1963). Thus, our findings indicate that part of the observed forces are caused by the direct interaction of the viscoelastic arolium cuticle with the surface (Gorb *et al.*, 2000) and not only by the liquid film alone. To test this conclusion, we studied the properties and dimensions of the adhesive liquid film.

*Study of the adhesive contact using interference reflection microscopy (IRM)*

IRM measures the reflection of a specimen under monochromatic illumination. By analyzing interference images it is possible to measure the distance of reflecting interfaces with nanometer resolution and to achieve a three-dimensional reconstruction of the surface microtopography (see Gingell and Todd, 1979; Rädler and Sackmann, 1993; Wiegand *et al.*, 1998). We used IRM to study the adhesive contact of insects by analyzing 1) “footprint” droplets and 2) adhesive pads in surface contact. Here we present preliminary results of this work.

*Contact angle of “footprint” droplets.* Figure 7A shows an IRM image of a footprint droplet of *O. smaragdina* on glass. If the liquid’s refractive index is

known, the height profile of a droplet can be reconstructed from visible interference fringes (Rädler and Sackmann, 1993). We determined the refractive index of the footprint fluid to range from 1.46 to 1.48 by quantifying the fringe contrast and comparing it with calibration liquids (Federle *et al.*, in preparation).

The height profiles obtained (Fig. 7B) show that the droplets are flat and have mean contact angles of  $17.6 \pm 7.0^\circ$  ( $n = 70$ ) on glass. Contact angles on hydrophobic surfaces were much lower (*e.g.*, Polyimide,  $1.3 \pm 0.4^\circ$ ,  $n = 20$ ). The hydrophobic nature of the footprint droplets is easily demonstrated by their insolubility in water. Droplets were still present after immersing the glass surface in water for five minutes. IRM images showed that their volume remained virtually unchanged.

*Two-phase adhesive secretion in the pad contact zone.* Because of the small difference of refractive indices, the adhesive contact zone is less reflective than the interface glass–air. For this reason, the pad contact area is visible with strong contrast as a homogenous,

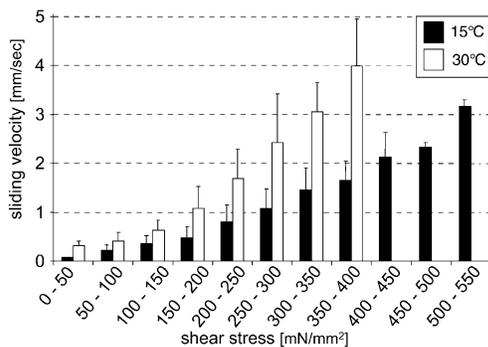


FIG. 6. Temperature dependence of friction in *O. smaragdina*. Graph summarizes data of 25 (32) “ant slides” at 15 (30)°C, respectively, by giving the mean sliding velocities for each shear stress class.

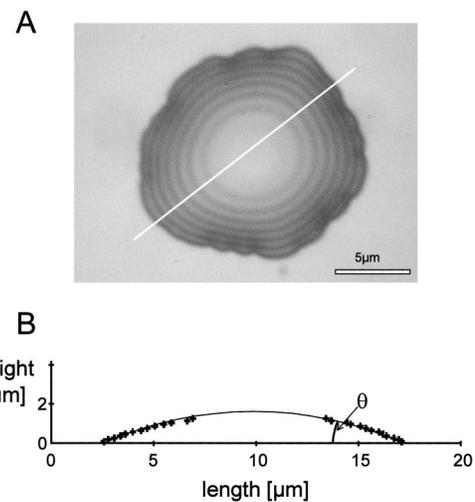


FIG. 7. IRM analysis of footprint droplets. A: IRM image of a footprint droplet of *Oecophylla smaragdina* at  $\lambda = 546$  nm. B: reconstruction of the height profile ( $\theta$ : contact angle). Data points represent the positions of intensity maxima and minima along the line in Figure A; the liquid height at each point was calculated according to Rädler and Sackmann (1993).

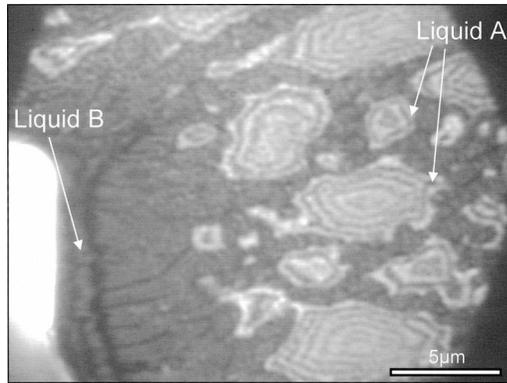


FIG. 8. Two-phase adhesive secretion (Liquids A and B) in the pad contact zone. IRM image of an arolium of *O. smaragdina* upside down in contact with glass.

dark zone on a bright background. Using high magnification and large illuminating numerical aperture, however, IRM revealed details within the pad contact zone and showed that the adhesive secretion consists of two separate liquid phases ('Liquid A' and 'Liquid B,' see Fig. 8).

Liquid A does not form a homogenous film, but occurs in droplets between the pad and the surface. These droplets are surrounded by liquid B, which can be recognized by low-contrast interference fringes along the edge of the pad contact zone (Fig. 8). We found that liquid A is highly volatile (droplets exposed to air evaporate within fractions of a second). The remaining hydrophobic footprint material mainly consists of liquid B, which is highly persistent. Thus, liquid A is apparently hydrophilic.

Surprisingly, the presence of liquid A depended on the nature of the surface. It was abundant on glass, but absent on hydrophobic polyimide and PMMA surfaces. Several lines of evidence indicate that liquid A is indeed a secretion and not water that had been present on the glass surface before.

—The total volume of liquid A droplets present per unit contact area corresponds to the volume of a homogenous film of *ca.* 30 to 200 nm height. This is more than glass surfaces are known to adsorb even at high air humidity (Bowden and Tabor, 1986). Moreover, heating of the glass surfaces to 200°C immediately before observation had no visible effect on the abundance of liquid A droplets.

—IRM analysis of the brightness and fringe contrast of liquid A droplets yielded a refractive index estimate of 1.43, which is inconsistent with the assumption that it is water ( $n_{\text{water}} = 1.333$ ).

—In one out of 15 *O. smaragdina* ants investigated liquid A was absent even on glass under the same experimental conditions. This observation suggests that the presence of liquid A is subject to some unexplained biological variation.

The two-phasic nature of the adhesive secretion found in ants appears to be widespread among insects. We observed the same pattern in members of other

insect orders (*Carausius morosus* [Phasmida] and *Periplaneta americana* [Blattodea]). Existing chemical analyses of insect footprints using thin layer and gas chromatography found mixtures of  $C_{22}$  to  $C_{29}$  *n*-alkanes and *n*-alkenes (Attygalle *et al.*, 2000), alcohols, fatty acids (Ishii, 1987) and waxes (Kosaki and Yamaoka, 1996), but no hydrophilic components have been detected. By using AFM and TEM of carbon-platinum replicas, Gorb (2001) discovered nanostructures on fly footprint droplets. These structures possibly represent residues of an evaporated hydrophilic component similar to the liquid A we observed.

The functional significance of the two-phasic nature of the adhesive liquid is still unclear and requires further exploration. IRM has proved to be a particularly suitable method to study this phenomenon *in vivo*.

*Estimation of the thickness of the adhesive liquid film.* IRM enables an estimation of the thickness of the liquid film between the pad and the surface. Similar to the analysis of the droplet height profiles (see above), interference fringes visible at the edges of the pad contact zone contain height information. In this case, however, the fringe pattern is ambiguous, since the interference order number is unknown. To solve this problem, we took images of the pad contact zone at two different wavelengths (436 and 546 nm) and compared the interference pattern with predictions from IRM theory. Using this method, the thickness of the adhesive liquid film can be estimated (Fig. 9). Preliminary results for *Carausius morosus* and *O. smaragdina* suggest it to be of the order of 90 to 160 nm near the edge of the contact zone.

*Estimation of the liquid viscosity.* IRM observation of the dynamic behavior of the adhesive secretion makes it possible to estimate its viscosity. When an adhesive pad slides on glass, an apparently homogenous film of secretion is deposited at the trailing edge of the pad. However, the film is unstable and disintegrates into small droplets. This process is known as 'dewetting' and starts with the formation of round dry patches that grow at a constant radial velocity. Dewetting velocity has been shown to depend on the surface tension and viscosity of the fluid as well as on its contact angle with the surface, but to be independent of film thickness (De Gennes, 1985; Redon *et al.*, 1991; Jacobs *et al.*, 1998). Preliminary measurements for *O. smaragdina* gave a mean dewetting velocity of  $60 \pm 10 \mu\text{m}/\text{sec}$  ( $n = 5$ ). Assuming a surface tension of about 30 mN/m, this leads to a viscosity estimate of 40 to 150 mPas (Redon *et al.*, 1991).

#### *Can the adhesive liquid film explain the measured forces?*

The estimates for the thickness and viscosity of the liquid film can be used to test whether the adhesive liquid film alone is sufficient to explain the frictional forces observed in the centrifuge experiments (see above). We find that the velocity-specific shear stress produced by a thin liquid film of 90 nm height and 150 mPas viscosity is one order of magnitude smaller

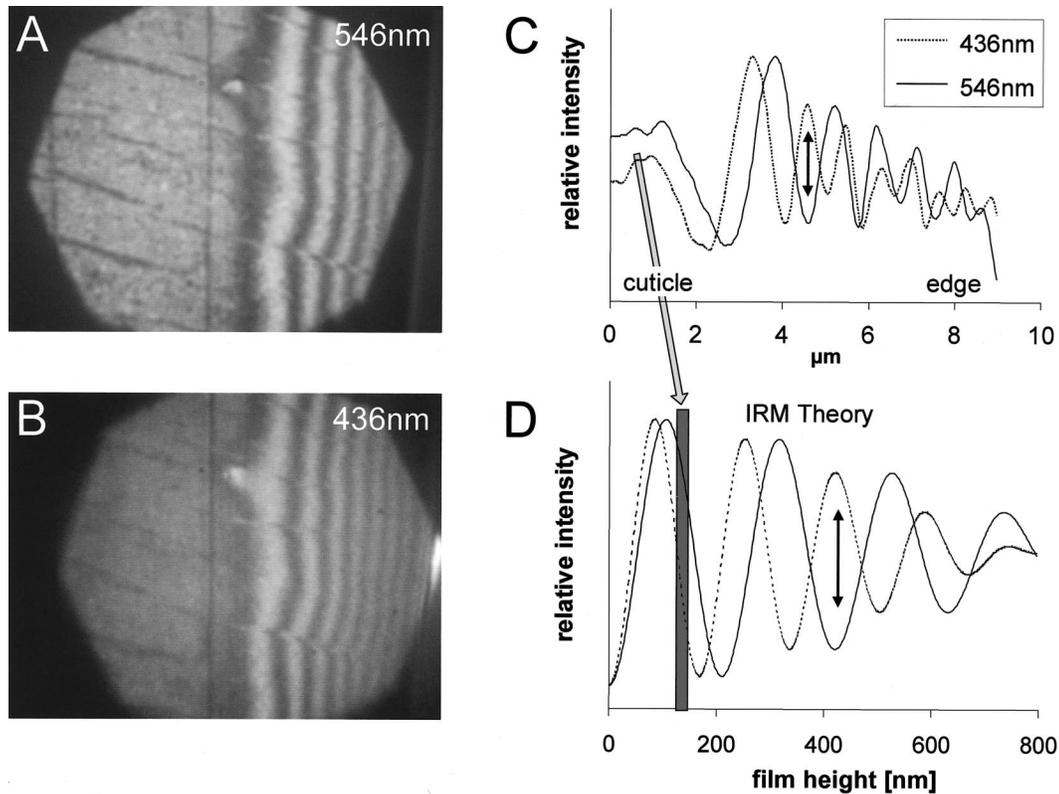


FIG. 9. Method to estimate the thickness of the adhesive liquid film (shown here for an arolium of the phasmid *Carausius morosus*). One section of the edge of the pad contact zone is imaged at two different wavelengths (A and B) and the fringe pattern (C) compared with theoretical predictions for the relationship between reflectivity and film height (D, Rädler and Sackmann, 1993). Arrows in C and D denote corresponding segments of the curves. The liquid film thickness in the left part of Figure 9A and B was estimated to be ca. 130 to 150 nm.

than the shear stress measured (1.7 vs. 89 [mN/mm<sup>2</sup>/mm/sec] at 30°C).

This result indicates that the adhesive secretion alone cannot explain the large frictional forces observed. The adhesive liquid film thickness was measured under static conditions for ants standing upside down on glass. In the course of sliding, however, the thickness of the adhesive liquid film will probably decrease so that it eventually becomes thinner than the amplitude of surface roughness (<50 nm for the PMMA substrate we used). Under such conditions, the soft cuticle of a sliding pad has to deform to follow the surface topography. Since insect adhesive pad cuticle is a viscoelastic material (Gorb *et al.*, 2000), this process causes energy dissipation and may thus contribute to the friction (Grosch, 1963; Persson, 1998).

#### CONCLUSIONS

The adhesive pads on the legs of ants are highly dynamic organs. Increase of contact area and strong attachment are achieved either actively by a contraction of the claw flexor muscle or passively when the leg is pulled toward the body. Arolia are peeled off the surface by elastic retraction of the pad and by rolling off the foot.

Our findings show that adhesion in *Oecophylla smaragdina* ants is mediated by a two-phase liquid

secretion. As predicted for a wet adhesion mechanism, frictional forces increased with sliding velocity, the increment being strongly temperature-dependent. However, the non-negligible static friction, the dimensions and the estimated viscosity of the adhesive liquid film indicate that the adhesive secretion alone is insufficient to explain the observed forces. A large part of the friction is probably caused by the rubbery deformation of the viscoelastic pad cuticle when it slides on the surface. Further integrative studies are needed to determine the relative roles of the pad cuticle and adhesive secretion, explore their properties and analyze the interaction of adhesion and locomotion.

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